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Inflated taxonomy in the West Mediterranean *Temnothorax algiricus* complex (Hymenoptera, Formicidae) revealed by quantitative morphology

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Abstract

Temnothorax is one of the largest ant genera, with most taxa described from the Mediterranean. The western Mediterranean *Temnothorax algiricus* complex (Hymenoptera, Formicidae) is a well-defined lineage of dark-reddish arboreal species, whose taxonomy has never been comprehensively addressed. We conducted a comprehensive taxonomic revision using quantitative morphological analysis complemented by qualitative observations to clarify the systematic relationships within this group. Our analysis of 13 previously described taxa reveals only three valid species: *T. algiricus* (Forel, 1894), *T. atlantis* (Santschi, 1911), and *T. trabutii* (Forel, 1894). We establish several new synonymies: *Leptothorax angustulus brunea* Santschi, 1918, *Leptothorax gazella* Santschi, 1932, *Leptothorax gazella monticola* Santschi, 1932, *Temnothorax mediterraneus* Ward, Brady, Fisher, & Schultz, 2014, and *Temnothorax atlantis veneris* Galkowski & Cagniant, 2017 are considered junior subjective synonyms of *T. algiricus*. *Leptothorax kiudiria* Espadaler, 1997, *Leptothorax angustulus silvanus* (Forel, 1907), *Temnothorax atlantis suturalis* Galkowski & Cagniant, 2017, and *Temnothorax continentalis* Galkowski & Cagniant, 2017 are synonymized under *T. atlantis*. *Leptothorax lindbergi* Santschi, 1931 is considered a synonym of *T. trabutii*. *Leptothorax convexus timida* Santschi, 1912 is a junior synonym of *Temnothorax convexus* (Forel, 1894), and excluded from the complex. This revision resolves the oversplit nomenclature characteristic of North African myrmecology and establishes taxonomic consistency with European classifications. Our quantitative morphology-based framework provides the foundation for future integrative taxonomic studies investigating intraspecific variation and potential cryptic diversity within this ecologically important ant lineage.

Key words: ant taxonomy, Myrmicinae, Crematogastrini, morphometrics

Introduction

Temnothorax (Hymenoptera, Formicidae, Myrmicinae), with over 500 taxa, is one of the largest ant genera (Bolton 2025). Belonging to the tribe Crematogastrini (Ward *et al.* 2015), *Temnothorax* ants are mostly Holarctic, with a few lineages venturing into the Afrotropics and Neotropics (Prebus 2015; 2017; Guénard *et al.* 2017). The Mediterranean region is recognized as a global hotspot for rare ant species and is home to a considerable proportion of the global diversity of the genus (Guénard *et al.* 2017; Kass *et al.* 2022). It hosts over 200 *Temnothorax* taxa, most of which have never been revised (Borowiec 2014). Complicating the matter is the historical difficulty in defining monophyletic species groups, with phylogenomic efforts now playing a crucial role in disentangling the relationships within the genus (Ward *et al.* 2015; Prebus 2017; Schifani *et al.* 2022). At the current stage, the taxonomy of the group still sees many new taxa being described each year, but also several others being synonymized because of modern revisions (see Bolton 2025; Csősz *et al.* 2025a; 2025b).

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The *T. algiricus* complex represents a distinctive western Mediterranean lineage characterized by wood-nesting habits, arboreal-foraging behavior and dark reddish pigmentation. This complex spans southern Europe from the Iberian Peninsula eastward to Croatia, extending into North Africa from Morocco to Tunisia. The complex currently encompasses ten valid taxa, all of which were described based on morphological distinctions: *T. algiricus* (Forel, 1894), *T. atlantis atlantis* (Santschi, 1911), *T. atlantis brunea* (Santschi, 1918), *T. atlantis silvanus* (Forel, 1907), *T. atlantis suturalis* Galkowski & Cagniant, 2017, *T. atlantis veneris* Galkowski & Cagniant, 2017, *T. continentalis* Galkowski & Cagniant, 2017, *T. kiudiria* (Espadaler, 1997), *T. mediterraneus* Ward, Brady, Fisher, & Schultz, 2014, and *T. trabutii* (Forel, 1894) (Galkowski & Cagniant 2017; Bolton 2025). Two more, *Leptothorax gazella* Santschi, 1923, and *L. gazella monticola* Santschi, 1923, are currently considered synonyms of *T. algiricus*, while *Leptothorax lindbergi* Santschi, 1931 is considered a synonym of *T. trabutii*, bringing the total number of described taxa within this complex to 13 (Bolton 2025). Historically, these taxa have been frequently associated with *T. angustulus* in taxonomic treatments (Nylander, 1856) (e.g., Emery 1916; Bondroit 1918; Santschi 1918; 1923; Bernard 1968; Galkowski & Cagniant 2017). However, *T. angustulus* is morphologically distinct from the core complex, notably in lacking a median clypeal carina (Espadaler & Collingwood 1982; Galkowski & Cagniant 2017).

Two additional species have been proposed as potentially related to the complex, though both show significant morphological difference. *Temnothorax convexus* (Forel, 1894) differs markedly through its characteristically convex mesosomal dorsal profile, absence of a clear median clypeal carina, and distinctive surface sculpturing pattern (Galkowski & Cagniant 2017; Arcos *et al.* 2022). In the eastern Mediterranean, *Temnothorax dessyi*, described from the Dodecanese islands, is geographically isolated from the rest of the complex and morphologically distinct in the shape of spines and mesosoma (Salata & Borowiec 2018). An undescribed Greek species potentially related to the group was mentioned by Borowiec *et al.* (2022).

This revision, we focused on the 13 West Mediterranean taxa, primarily those described from North Africa, that constitute a morphologically cohesive complex. Despite the comprehensive treatment of South European species by Galkowski & Cagniant (2017), phylogenetic relationships within this group remain incompletely resolved. We address taxonomic uncertainties through qualitative morphological assessment to test current species hypotheses.

Materials and Methods

Examined material

We examined and measured a total of 121 worker specimens belonging to the complex, either directly under the microscope (n = 108) or through images available from AntWeb.org (n = 13). These originated from Algeria, Croatia, France, Italy, Morocco, Spain, and Tunisia. Part of the examined specimens are stored in the following public institutions: Natural History Museum of Basel, Switzerland (NHMB), Natural History Museum of Geneva, Switzerland (NHMG), Natural History Museum of London, UK (NHMUK), National Museum of Natural History of Paris (France), and the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine (Kyiv, Ukraine). The rest are stored in the authors' personal collections, and two further specimens belong to the personal collections of Emmett Collins-Sussman and Matthew M. Prebus.

We produced morphometric data from 34 type specimens of *T. algiricus*, *T. atlantis atlantis*, *T. atlantis brunea*, *T. atlantis silvanus*, *T. atlantis suturalis*, *T. atlantis veneris*, *T. kiudiria*, and *T. trabutii*. The taxonomic position of *Leptothorax linbergi, T. continentalis* and *T. mediterraneus* was assessed based on their descriptions and available images (see Galkowski & Cagniant 2017 and AntWeb CASENT0904755 respectively) as well as biogeography. The remaining 87 measured non-type specimens belonged to 49 colony samples.

A complete list of the examined material as well as the morphometric data produced in this study is available in the Supplementary material file.

Numerical character recording

Physically examined specimens were measured under three stereoscope settings (either Zeiss Stemi 2000-C 0.65-5× stereomicroscope equipped with a CMEX PRO- 5 DC.5000p digital camera and ImageFocus 4 software, Olympus SZX16 0.7–11.5× equipped with WHSZ10x-H/22 micrometric oculars, or Zeiss SteREO Discovery.V12 stereomicroscope equipped with an AxioCam Erc5S digital camera and AxioVision software), while those examined through images available from AntWeb.org were measured with the software ImageJ (Schneider *et al.* 2012).

A total of 18 continuous numerical characters were recorded in μm on each specimen, including 17 linear morphometric characters and the measure of an angle: cephalic length (CL), cephalic width (CWb), eye length (EL), eye width (EW), mesosoma length (ML), mesosoma width (MW), petiolar width (PW), petiolar height (PeH), postpetiolar width (PPW), postocular distance (PoOC), maximal propodeal height (PropH1), minimal propodeal height (PropH2), scape length (SL), spine base width (SPBA), spine-stigma distance (SPST), spine tips width (SPTI), spines width (SPWI), and spines angle (SpANG) (Table 1). Their definitions are given in Table 1 and mostly follow Csősz *et al.* (2015; 2025).

TABLE 1. List of the numerical morphological characters recorded in this study and their definitions.

Character	Definition
CL	Cephalic length. Maximum cephalic length in the median line.
CWb	Cephalic width. Maximum width of the head capsule, measured posterior to the eyes.
EL	Eye length. Maximum diameter of the compound eye (including unpigmented marginal ommatidia).
EW	Eye width. Minimum diameter of the compound eye (including unpigmented marginal ommatidia).
ML	Mesosoma length. In lateral view, the maximum diagonal between the point where the pronotum meets the cervical shield and the posterior basal angle of the propodeal lobe (Weber's line).
MW	Mesosoma width. Maximum width of the mesosoma in dorsal view (correspondent to the pronotum).
PeH	Petiolar height. Maximum height of the petiolar node in profile view, measured in a perpendicular line from the basis.
PoOC	Postocular distance. Distance between the median occipital margin and the median head at the level of the posterior eye margin, representing a segment of the cephalic length.
PPW	Postpetiolar width. Maximum width of the postpetiolar node in dorsal view.
PW	Petiolar width. Maximum width of the petiolar node in dorsal view.
PropH1	Maximal propodeal height. In lateral view, maximum distance measured between the anteroventral point of the metapleuron and the highest point of the propodeum before the metanotum.
PropH2	Minimal propodeal height. In lateral view, maximum distance measured between the caudoventral point of the metapleuron and the highest point of the propodeum coinciding with the basis of the propodeal spines.
SL	Scape length. Maximum straight line scape length excluding the articular condyle.
SpANG	Spines angle. In lateral view, the angle formed between the spines and the dorsal profile of the propodeum. The measurement is taken using the tip of the propodeal spine as the end of one arm, the basis of the spine as the vertex, and the highest point of the propodeum before the metanotum as the end of the other arm. In this study exclusively measured through images and the software ImageJ.
SPBA	Spine base width. In dorsal view, the distance between the lateral margins of the spines at their base.
SPST	Spine-stigma distance. In lateral view, distance between the center of the propodeal stigma and the spine tip. The stigma center refers to the midpoint defined by the outer cuticular ring but not to the center of the real stigma opening that may be positioned eccentrically.
SPTI	Spine tips width. In dorsal view, the distance between the spine tips. If spine tips are rounded or truncated, the centers of spine tips are taken as reference points
SPWI	Spines width. In dorsal view, the maximum distance between the outer margins of the spines.

Data analysis

Morphometric indices were calculated to evaluate shape variation among specimens. Following established protocols for ant morphometry (e.g., Csősz *et al.* 2015; 2025a), cephalic size (CS) was calculated as the arithmetic mean between cephalic length (CL) and width (CW) and used as a size proxy. All linear morphometric characters were then standardized by dividing by CS to generate size-independent shape indices.

In addition, we calculated the following additional indexes to capture specific aspects of propodeal and spine morphology: PropH2/PropH1, describing the proportional difference in height of the mesosoma next to the metanotum and at the level of the dorsal base of propodeal spines, in lateral view (indirectly quantifying the steepness of the slope of dorsal propodeum); SPWI/SPTI, describing the difference between the maximum dorsal divergence of the spines and the distance between their tips (the spines of some specimens having an arcuated shape in dorsal view); SPWI/SPST, describing the difference between the maximum dorsal divergence of the spines and their length (some specimens having shorter but more divergent spines than others).

All analyses were conducted using the software R and RStudio (R Core Team 2025; RStudio Team 2025). Principal Component Analysis (PCA) was used as an exploratory data analysis to investigate the structure of the morphological dataset and visualize the overlap between clusters representing hypothetical species, using the prcomp() function from the stats package. Two separate PCAs were run, one using raw values of all 18 characters, and a second one using all indices and the spines angle (SpANG). The first three components of the second PCA were used as input variables in a Linear Discriminant Analysis (LDA) was used as a confirmatory discriminant analysis to confirm species hypotheses based on clusters delimited on the PCAs scores using the lda() function from the package MASS (Venables & Ripley 2002). Kruskal-Wallis tests followed by Dunn's post hoc tests (p-values adjusted with the Benjamini-Hochberg method) were conducted for pairwise comparisons for all morphometric indices and the angle size (SpANG) to assess differences between clusters character by character. Kruskal-Wallis tests were run using the kruskal.wallis() function from the package stats, while Dunn's tests were run with the dunnTest() function of the package FSA (Ogle *et al.* 2025). Based on Dunn's tests, we computed mean and maximum size effect differences between the clusters for each character analyzed.

Species delimitation

Species hypotheses were formulated by combining morphometric evidence and the assessment of qualitative morphological characters in non-cryptic taxa (Schifani *et al.* 2022). We also took into consideration biogeographic patterns, taxonomic histories and relevant literature on the ecology and biology each taxon whenever available. We defined valid taxa with non-overlapping PCA clusters distinct by multiple significantly different quantitative characters—using morphospecies as an operational proxy to assess species diversity within the group. The final hypotheses were compared to the separation threshold proposed in the GAGE species concept operative criteria, suggesting to define separate species with a <4% classification error of exploratory data analyses relative to the confirmatory discriminant analyses (Seifert 2020).

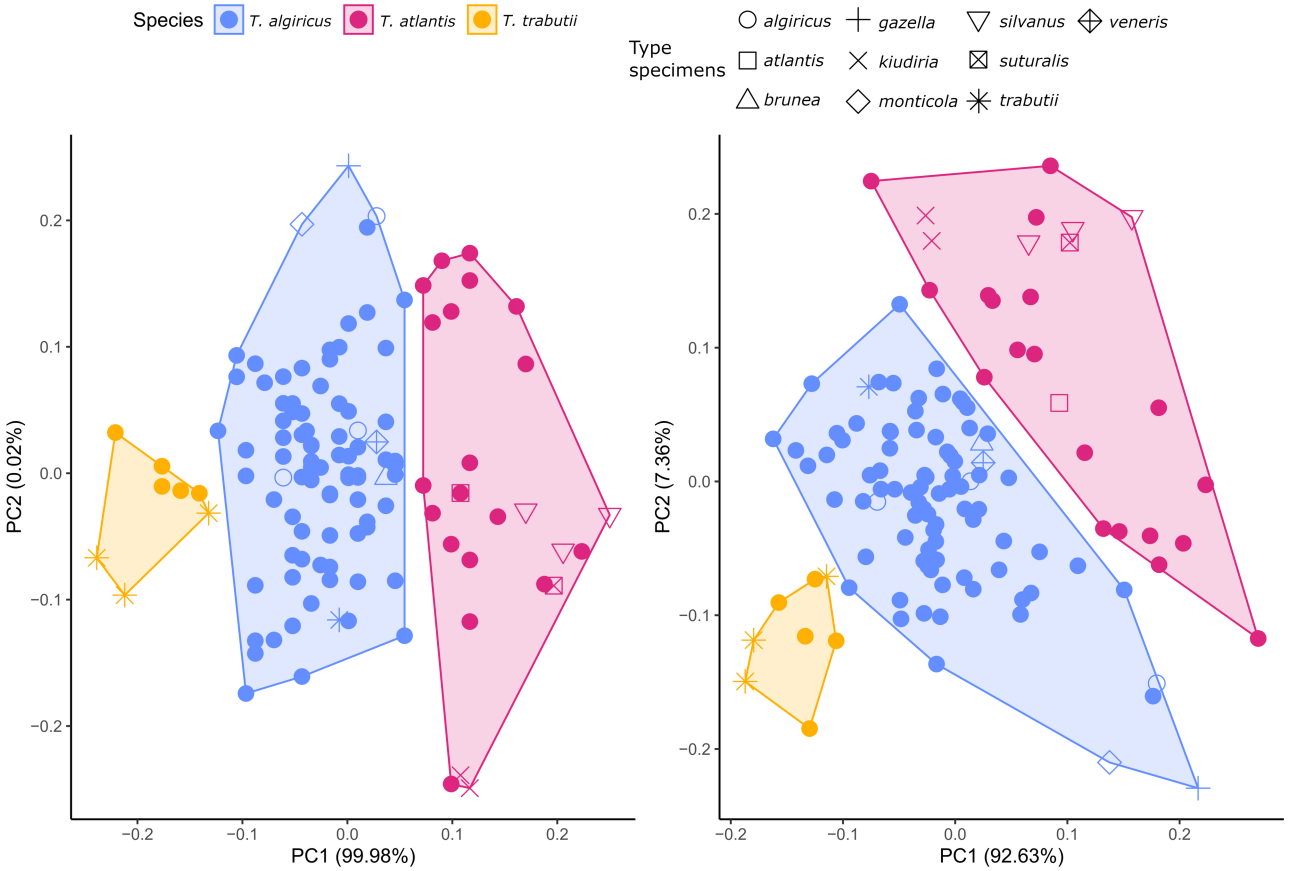

FIGURE 1. Principal Component Analysis (PCA) results describing the structure of the quantitative morphological dataset in a two-dimensional space. On the left, an analysis run on raw morphometric characters and the angle of the spines (SpANG); on the right, an analysis run on indices and SpANG. Symbols indicate specimens with type status.

Results

We identified three valid taxa: *T. algiricus*, *T. atlantis*, and *T. trabutii*. The three, which can be identified by subjective assessment by a trained myrmecologist, correspond to non-overlapping morphological PCA clusters (Fig. 1). The first two components of the PCA explained about 100% of the variation between the species, with the first component alone ranking between 93–99%, depending on whether absolute morphometric characters or indices were used on top of SpANG (Fig. 1). The interpretation of these as separate species was confirmed by the subsequent LDA (Fig. 2). The distinction between *atlantis* and *algiricus* was supported with a <4% classification error, with two non-type *algiricus* specimens misclassified as *atlantis* (2.29%) and one non-type *atlantis* specimen misclassified as *algiricus* (3.8%). Posterior probabilities were 0.925 and 0.764 for the two misclassified *algiricus* specimens, and 0.973 for the misclassified *atlantis* specimen. In the case of *trabutii*, one type specimen was misclassified as *algiricus*, implying a high misclassification rate (12.5%) due to the small sample size available to us for this taxon (eight workers measured). However, the posterior probability for the classification of this specimen was inconclusive (0.559).

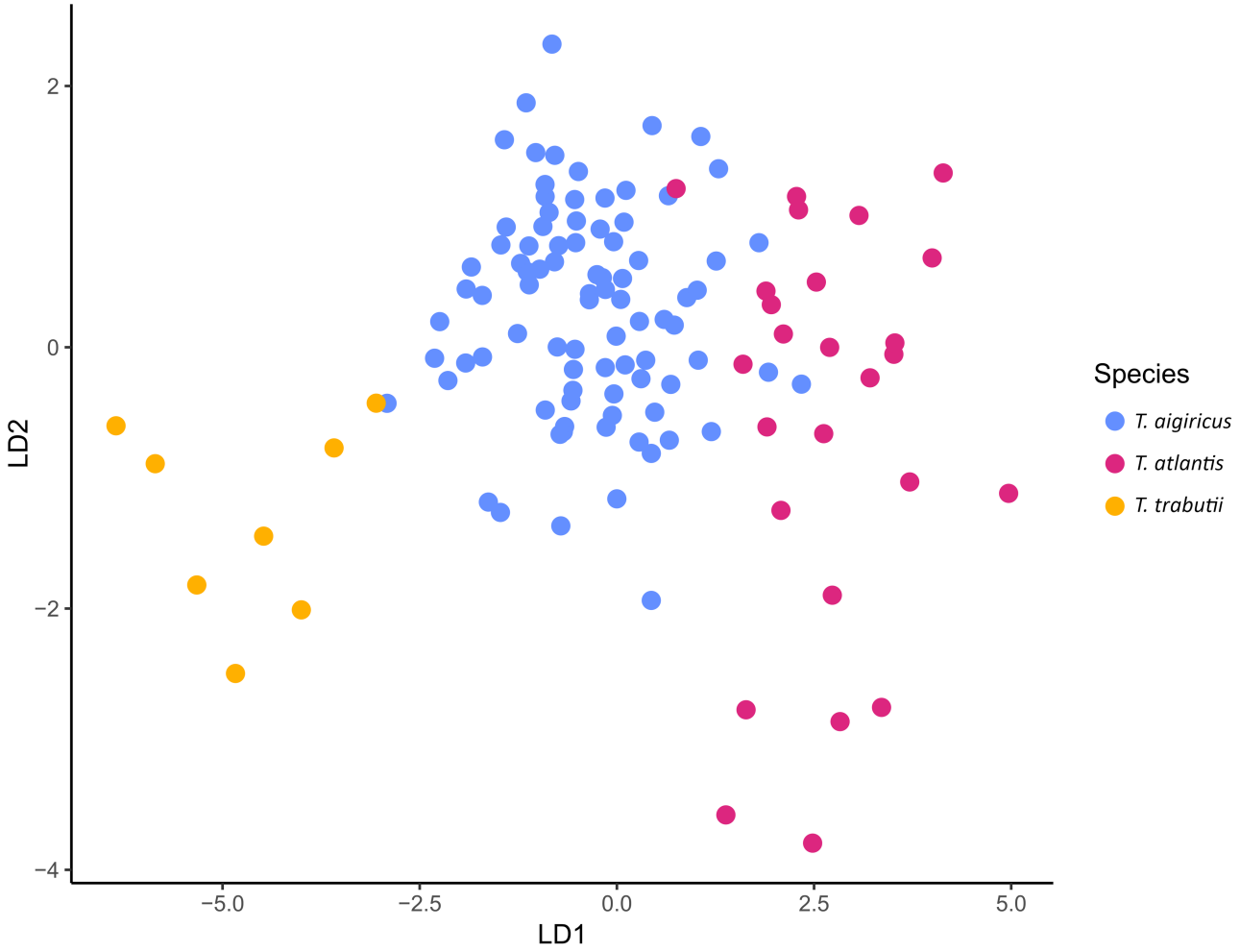

FIGURE 2. Linear Discriminant Analysis (LDA) run on the first three components of a PCA of the 17 indices and SpANG, confirming the species hypotheses based on the PCA scores. Two *algiricus* samples were misclassified as *atlantis* (2.29%, posterior probability = 0.925 and pp = 0.764 respectively), one *atlantis* sample was misclassified as *algiricus* (3.8%, pp = 0.973), and one *trabutii* sample was misclassified as *algiricus* but with an inconclusive posterior probability (pp = 0.559).

According to Kruskal-Wallis and Dunn's tests, multiple characters were significantly different between the three species, of which the following four were associated with the highest differences in post hoc tests: SpANG (max diff. 7.03, mean diff. 6.07), SPWI/SPST (max diff. 5.70, mean diff. 4.80), SPST/CS (max diff. 4.98, mean diff. 4.67), and PropH2/PropH1 (max diff. 4.14, mean diff. 3.07) (Fig. 3). In particular, SpANG was different among the three species ($\chi^2_{(2)} = 7.43$, $p < 0.001$, and $p < 0.001$ in all pairwise comparisons), and the same was true for SPWI/

SPST ($\chi^2_{(2)} = 49.83$, $p < 0.001$, and $p < 0.001$ in all pairwise comparisons) and SPST/CS ($\chi^2_{(2)} = 44.05$, $p < 0.001$, and $p < 0.001$ in all pairwise comparisons), while PropH2/PropH1 was significantly different between *T. trabutii* and the other species, but not between *T. algiricus* and *T. atlantis* ($\chi^2_{(2)} = 17.42$, $p < 0.001$, and $p = 0.183$ between *algiricus* and *atlantis*, $p < 0.001$ in the remaining pairwise tests) (Fig. 2).

All the three species were sympatric in some areas of the western Maghreb, and *T. algiricus* and *T. atlantis* also in southern Iberia (Fig. 4), convincingly maintaining their distinctiveness in the area of sympatry based on the PCA and LDA results, with no geographical clustering separating North Africa from South Europe (Fig. 1).

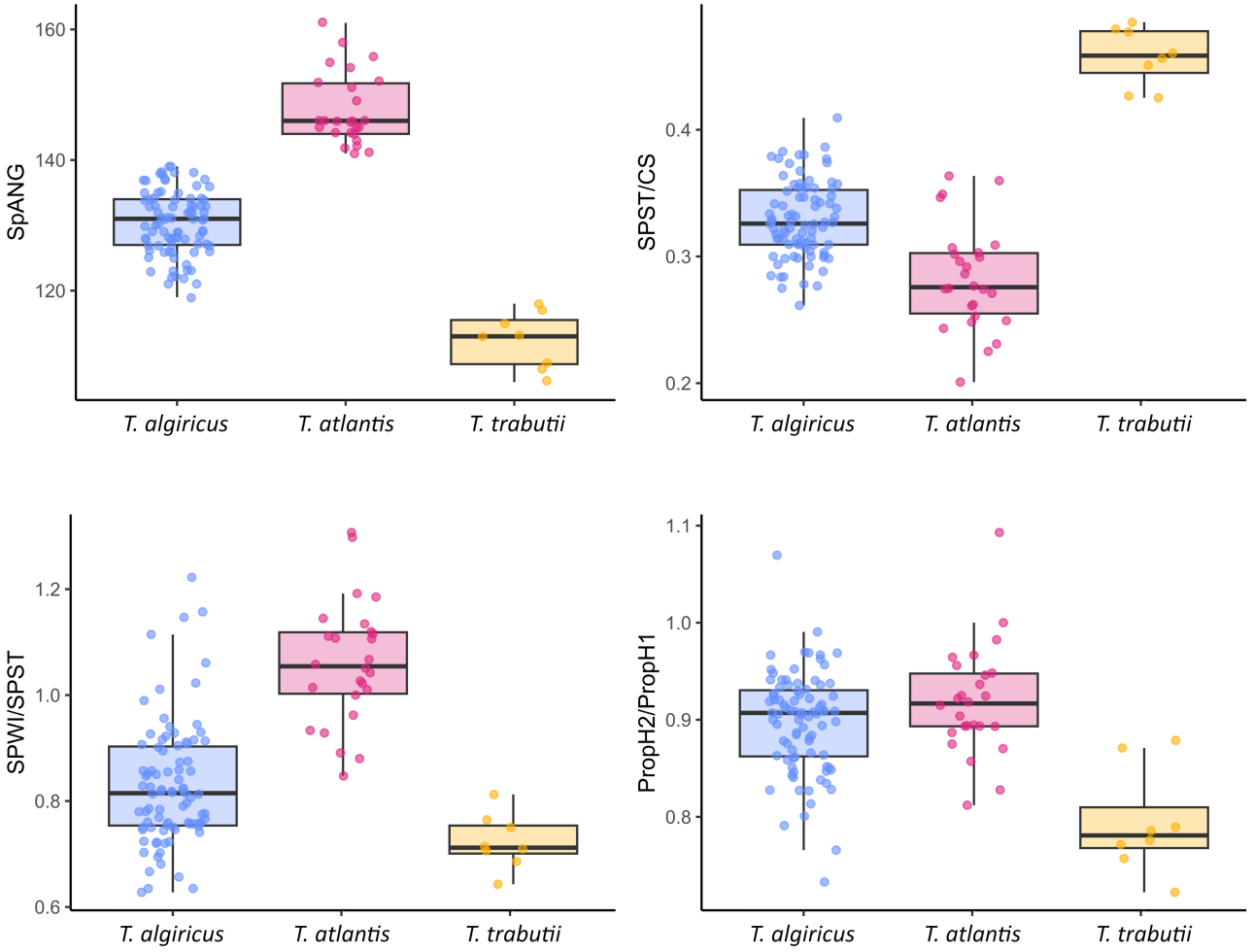

FIGURE 3. Differences between *T. algiricus*, *T. atlantis*, and *T. trabutii* in the four most diverging characters among indices and the spines angle: PropH2/PropH1, SPST/CS, SPWI/SPST, and SpANG. According to Kruskal-Wallis tests followed by Dunn's post hoc tests for pairwise comparisons, the three species were all significantly different from each other for all of the abovementioned characters except for PropH2/PropH1, for which only *T. trabutii* was significantly different from the others.

***Temnothorax algiricus* (Forel, 1894)**

Figure 5

= *Leptothorax angustulus* var. *brunea* Santschi, 1918 **syn. n.**
= *Leptothorax gazella* Santschi, 1932
= *Leptothorax gazella* var. *monticola* Santschi, 1932
= *Temnothorax mediterraneus* Ward, Brady, Fisher, & Schultz, 2014 **syn. n.**
= *Temnothorax atlantis veneris* Galkowski & Cagniant, 2017 **syn. n.**

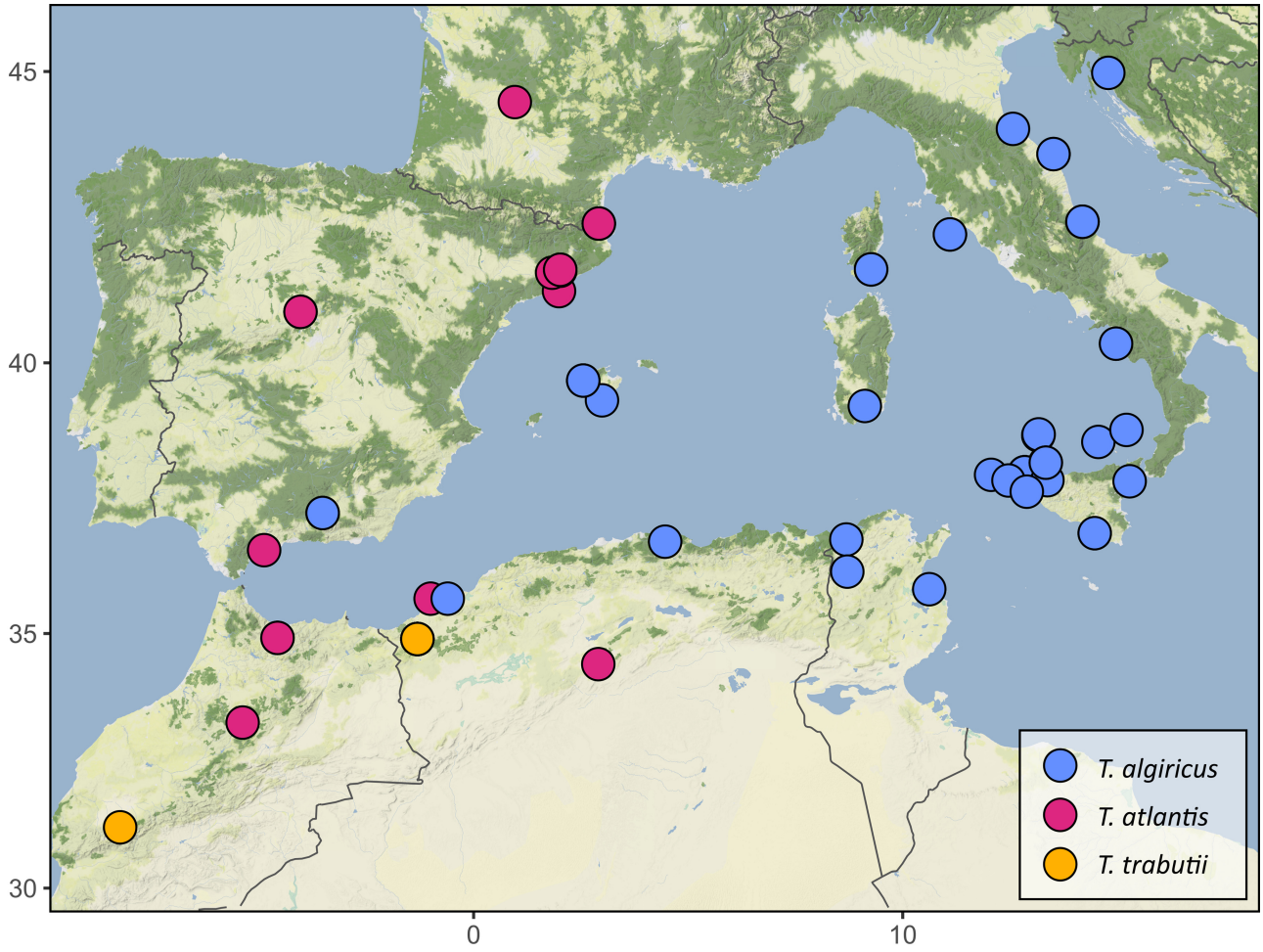

FIGURE 4. Distribution of the species belonging to the *Temnothorax algiricus* complex in the West Mediterranean based on the examined material of this study. Map from Stadia Maps - stadiamaps.com and Stamen Design (stamen.com), plotted using the R package "ggmap" (Kahle and Wickham 2013).

Investigated type material: 2 syntype workers of *algiricus* (Msila Forest, Oran, Algeria) from the MHNG (Geneva, Switzerland), being the mid and bottom specimens of a pin in which the top worker had its head missing with the labels "TYPUS // *L. angustulus* / Nyl / / [worker symbol] / v. *algiricus* Forel / Foret de Msila / (Algerie) // Coll. A. Forel // *algiricus* Forel". 1 syntype worker of *T. algiricus* investigated through AntWeb (CASENT0909011—MHNG, Geneva, Switzerland). 1 syntype worker of *brunea* investigated through AntWeb (CASENT0912895—NHMB, Basel, Switzerland). 1 syntype worker of *gazella* investigated through AntWeb (CASENT0912940—NHMB, Basel, Switzerland). 1 syntype worker of *monticola* investigated through AntWeb (CASENT0912941—NHMB, Basel, Switzerland). 1 syntype worker of *veneris* investigated through AntWeb (CASENT0917823—SIZK, Kiev, Ukraine). 1 syntype worker of *mediterraneus* (= *Leptothorax angustulus kraussei* Emery, 1916) (Cagliari, Sardinia, Italy) investigated through AntWeb (CASENT0904755—MSNG, Genoa, Italy).

Investigated non-type material: 79 workers from 39 colonies from Algeria, Italy, Croatia, France, and Spain.

Worker redescription. Body either concolor dark brown to blackish, or bicolored, with parts or the entirety of the mesosoma and nodes being reddish or ferruginous and contrasting with the head and gaster. Antennae, legs, and mandibles often lighter than the body.

Head subrectangular with rounded margin, clypeus and mandibles rounded. Antennae of 12 segments, antennal clubs of 3 segments. Compound eyes are ovoidal. The mesosoma may or not present a slight metanotal impression visible in lateral view on the dorsal profile. Propodeal spines relatively long and erect, sometimes arched in dorsal view, and slightly curved in lateral view. The petiole has a triangular shape, with a small tooth-like subpetiolar process. The postpetiole has an ordinary ovoidal lateral profile and may appear subhexagonal in dorsal view.

FIGURE 5. Worker specimens belonging to the type series of *T. algiricus* and its synonyms (excluding the glued type of *mediterraneus*, CASENT0904755), in head (left), profile (center), and dorsal (right) view, available from AntWeb.org. From above: *algiricus* Forel (Algeria, CASENT0909011, photo by Z. Lieberman), *brunea* Santschi (Algeria, CASENT0912895, W. Ericson), *gazella* Santschi (Tunisia, CASENT0912940, Z. Lieberman), *monticola* Santschi (Tunisia, CASENT0912941, Z. Lieberman), *veneris* Santschi (Tunisia, CASENT0917823, K. Martynova).

Surface sculpture is generally fine, with larger parts of the head becoming dull in smaller specimens; a fine irregular sculpture in the rest of the body, with some striae on the dorsum of the mesosoma, often on the head, and always a central carina in the clypeus.

Very sparse, usually erect setae all over the body; dense, fine, and mostly adpressed pilosity on the antennae.

Diagnosis. Compared to *T. trabutii*, the propodeal dorsum has a gentler transition with the rest of the mesosoma and is less steep [PropH2/PropH1: 0.897 (0.732, 1.069)]. Several morphometric characters have an intermediate position between *T. atlantis* and *T. trabutii*. Spines form a narrower angle with the mesosoma than in *T. atlantis* but not as much as in *T. trabutii* [no range overlaps in SpANG: 130 (119, 139)]. On average, the propodeal spines are shorter than in *T. trabutii* but longer than in *T. atlantis* [SPST/CS: 0.329 (261, 409)]. In dorsal view these are divergent at first but may curve inwards in their distal part, the ratio between their maximum width and the width between their tips being averagely larger than in *T. atlantis* but smaller than in *T. trabutii* [SPWI/SPBA: 1.382

(1.108, 1.750)]. The ratio between the spines divergence and their length is also intermediate [SPWI/SPST: 0.829 (0.628, 1.222)]. Pigmentation can be concolor dark, or bicolored with dark head and gaster contrasting with the reddish mesosoma and nodes (as in the types of *mediterraneus* and *veneris*).

Distribution. Southern Spain, Balearic Islands, Morocco, Algeria, Tunisia, Sicily (including circum-Sicilian islands), Sardinia, Corsica, Italian peninsula (including the Tuscan archipelago), and Croatia. Records from the Maltese Islands should be attributed to this species.

Taxonomic history. *Temnothorax algiricus* was described by Forel (1894) from Algeria (Oran province) as a North African variety of the European *T. angustulus* with a different color. Some following authors kept considering it a variety of *angustulus* (Santschi 1911; 1918; Emery 1924; Bolton 1995). However, it was mostly treated as a species since Cagniant (1968) elevated it to species rank, although he did not provide a justification for his decision (e.g., Cagniant & Espadaler 1997; Bračko 2006; Cagniant 2006; Guillem 2009; Borowiec 2014; Galkowski & Lebas 2016; Lebas *et al.* 2016; Galkowski & Cagniant 2017). Later, Cagniant & Espadaler (1997) synonymized under *T. algiricus* four other taxa. Nonetheless, Galkowski & Cagniant (2017) could not provide a morphological distinction from *T. mediterraneus* Ward *et al.*, 2014. The name *T. algiricus* was almost exclusively used in North Africa, with two exceptions: Bračko (2006) listed it among the species of Croatia, and Guillem (2009) recorded it in the Balearic Islands.

Leptothorax angustulus algiricus bruneus Santschi, 1911 is an unavailable infrasubspecific name (Santschi 1911), while Santschi (1918) made the first available use of the name as *Leptothorax angustulus* var. *brunea* Santschi, 1911. It was described from Algeria (Yakouren) and defined as more strongly sculptured than *T. algiricus*, darker than *T. trabutii*, and "transitional" to *silvanus* (Forel, 1907). Cagniant & Espadaler (1997) synonymized this taxon under *T. atlantis*, considering it a dark-colored variety and speculating that the darker pigmentation could be caused by an association with more humid environments. Galkowski & Cagniant (2017) raised it to the subspecies level as *T. atlantis brunea*, again suggesting the same mechanism behind the dark pigmentation and stronger sculpture. In general, selective pressure for darker pigmentation in ants has been demonstrated to be associated with either high UV exposure on one hand or low temperatures on the other (Law *et al.* 2019; Bishop *et al.* 2021).

Leptothorax gazella Santschi, 1932 was described from Tunisia (Sousse, see Santschi 1932) and said to be similar to "*L. angulatus*" (almost certainly a mistype of *T. angustulus*, as no "*L. angulatus*" has ever been described). Santschi (1932) differentiated *L. gazella* from "*L. angulatus*" due to the first having a less pronounced metanotal impression. In the same paper, Santschi (1932) described *L. gazella* var. *monticola*, also from Tunisia (Aïn Draham), based on a darker gaster and minor sculpture differences from *L. gazella* s. str. Both taxa were considered synonyms of *T. algiricus* by Cagniant & Espadaler (1997) without providing an explanation.

Temnothorax mediterraneus Ward, Brady, Fisher, & Schultz, 2014 is a replacement name for *Temnothorax kraussei* Emery, 1916 (= *Leptothorax angustulus kraussei* Emery, 1916), a junior secondary homonym of *Temnothorax kraussei* Emery, 1915. The latter is a socially parasitic species originally described as *Epymyrma kraussei*, but the genus *Epymyrma* was found to be a synonym of *Temnothorax* by Ward *et al.* (2014). Under either of the two different names, this species has long been considered part of the faunas of Italy (Baroni Urbani 1971; Schifani 2022), France (Casevitz-Weulersse & Galkowski 2009), Malta (Schembri & Collingwood 1995), and Spain (Arcos & Garcia 2023). The original description by Emery (1916) as a variety of *T. angustulus* (*Leptothorax angustulus* var. *kraussei*) considered it to occur in Corsica, Sardinia, and Sicily, and the type is from Sardinia. Emery (1916) distinguished the var. *kraussei* by having a stronger head sculpture and sometimes a ferruginous mesosoma (in other specimens very dark). While Baroni Urbani (1971) treats *T. mediterraneus* as a distinct species based on its sympatry with *T. angustulus* in Sicily, Rigato & Toni (2011), in a faunistic paper on Sardinian ants, suggested potential synonymy between *T. mediterraneus* and *T. angustulus*. Eventually, Espadaler & Collingwood (1989), working on Iberian ants, defined the presence of a middle clypeal carina and the reddish mesosoma as distinctive features separating *T. mediterraneus* from *T. angustulus*. Ultimately, the taxon was redescribed by Galkowski & Cagniant (2017), who further demonstrated its distinctiveness from *T. angustulus*. In addition, they separated the populations of mainland Iberia and mainland France that were until that point considered to belong to *T. mediterraneus* by describing them as *T. continentalis*, while considering *T. mediterraneus* a valid species exclusive to Corsica, Sardinia, and Sicily. Coherently with the original description, *T. mediterraneus* was defined as a taxon of variable pigmentation (with a reddish to dark mesosoma), different from *T. continentalis* because of the longer and differently shaped spines, and together with *T. continentalis* separate from *T. angustulus* by the middle clypeal carina (Galkowski & Cagniant 2017). However, Galkowski & Cagniant (2017) could not identify any character separating *T. mediterraneus* from *T. algiricus*.

Leptothorax angustulus trabutii veneris Santschi, 1918 is an unavailable (infrasubspecific) name (Bolton 1995). Santschi (1918) described it from Tunisia (Le Kef) as similar in color to *T. trabutii* but characterized by a stronger sculpture and different spines. Galkowski & Cagniant (2017) described the subspecies *T. atlantis veneris* based on one of the syntypes of the taxon described by Santschi, providing a valid name for it. However, they could not find characters to separate the subspecies *veneris* from the nominal subspecies of *T. atlantis* (Galkowski & Cagniant 2017). At the same time, Galkowski & Cagniant (2017) also considered other syntypes (all from the same locality), including "CASENT0912897", as "typical *T. mediterraneus*" and one as *T. santschii* (Forel, 1905) due to its longer spines [*T. santschii* is a species with a long petiolar peduncle considered close to *T. flavispinus* (André, 1883)]. Furthermore, they stated that they had never found *T. mediterraneus* but only *T. algiricus* in Tunisia and kept considering *T. mediterraneus* a European taxon. There is no "CASENT0912897" on AntWeb, and we have no data of *T. atlantis* east of central Algeria; while we have not examined the same specimens that Galkowski & Cagniant (2017) used to make their assessments, we based our evaluation on the only specimen present on AntWeb (CASENT0917823), which due to its availability we suggest to consider the lectotype of the taxon in future revisions.

Leptothorax convexus var. *timida* Santschi, 1912, described from Morocco (Cap Spartel, near Tangier, see Santschi 1912) was considered a junior synonym of *T. algiricus* by Cagniant & Espadaler (1997), who did not provide any argument for this decision as for the other synonymizations of taxa under *T. algiricus*. It is notable that, in the same paper, Cagniant & Espadaler (1997) also treated *T. convexus* (Forel, 1894) as a separate taxon but member of the same *angustulus* group. Pictures of the type of *L. convexus* var. *timida* are available on AntWeb (CASENT0912920) and clearly show that it does not belong to the *T. algiricus* complex but instead bears all the typical features of *T. convexus* including the shape of the mesosoma, propodeal spines, nodes, and the surface sculpturing (also see Arcos *et al.* 2022). Therefore, we remove *L. convexus* var. *timida* from synonymy with *T. algiricus* and consider it as a junior synonym of *T. convexus*.

Comments. The works of Espadaler & Collingwood (1989) and, more importantly, Galkowski & Cagniant (2017) were fundamental contributions for the understanding of this species in Europe (under *T. mediterraneus*), by separating it first from *T. angustulus*, and then from *T. atlantis* (under *T. continentalis*). However, the relationship between the populations in South Europe (under *kraussei* Emery, 1916 and then *T. mediterraneus*) and those in North Africa (under *T. algiricus*) remained unresolved, with no character found to tell them apart for more than a century, during which a parallel taxonomy existed. Furthermore, we found significant oversplitting in North Africa, where *brunea*, *gazella*, *monticola*, and *veneris* were all found to be indistinguishable from, and thus synonymized to, *T. algiricus*. Biogeographically, the distribution of *T. algiricus* mirrors the distribution of many North African ant species that also occur in southern Europe: in Italy (Schifani *et al.* 2022; Schifani & Alicata 2023), with some species extending to Croatia at their easternmost limit (Baroni Urbani 1971) and in the very south of Iberia and the Balearic Islands (Arcos & Alarcón 2024). Worth noting, a worker from Italy (Taormina, Sicily; CASENT0906170) currently listed as *T. angustulus* on AntWeb belongs to *T. algiricus* based on our morphological analysis.

***Temnothorax atlantis* (Santschi, 1911)**

Figure 6

= *Leptothorax angustulus silvanus* (Forel, 1907) **syn. n.**
= *Leptothorax kiudiria* Espadaler, 1997 **syn. n.**
= *Temnothorax atlantis suturalis* Galkowski & Cagniant, 2017 **syn. n.**
= *Temnothorax continentalis* Galkowski & Cagniant, 2017 **syn. n.**

Investigated type material: 1 syntype worker of *atlantis* investigated through AntWeb (CASENT0912894—NHMB, Basel, Switzerland). 2 syntype workers of *kiudiria* investigated through AntWeb (CASENT0915388, CASENT0912953—NHMB, Basel, Switzerland). 3 syntype workers of *silvanus* from the MHNG (Geneva, Switzerland) with the label "TYPUS // *L. angustulus silvanus* / [worker symbol] [....] Foret de Msila / Oran (Forel) // *L. silvanus* Forel // ANTWEB CASENT0909012 // MHNG ENTO-0100926 // Silvanus Forel". 1 syntype worker of *suturalis* investigated through AntWeb (CASENT0912896—NHMB, Basel, Switzerland).

Investigated non-type material: 19 workers from 9 colonies.

FIGURE 6. Worker specimens belonging to the type series of *T. atlantis*, and some of its synonyms, as well as a non-type worker. Head (left), profile (center), and dorsal (right) view, images available from AntWeb.org. From above: *atlantis* Forel (Algeria, CASENT0912894, photo by Z. Lieberman), *kiudiria* Espadaler (Morocco, CASENT0915388, W. Ericson), *suturalis* Galkowski & Cagniant (Morocco, CASENT0912896, W. Ericson), *silvanus* Forel (Tunisia, CASENT0909012, Z. Lieberman), and a non-type worker from Spain (CASENT0914411, Z. Lieberman).

Worker redescription. Body normally bicolored, with parts or the entirety of the mesosoma and nodes being reddish or ferruginous and contrasting with the dark head and gaster, but sometimes also concolor dark brown. Antennae, legs, and mandibles yellow reddish to dark.

Head subrectangular with rounded margin, clypeus and mandibles rounded. Antennae of 12 segments, antennal

clubs of 3 segments. Compound eyes are ovoidal. The mesosoma may or not present a slight metanotal impression visible in lateral view on the dorsal profile. Propodeal spines relatively short and more horizontal, normally divergent in dorsal view, and often slightly curved in lateral view. The petiole has a triangular shape, with a small tooth-like subpetiolar process. The postpetiole has an ordinary ovoidal lateral profile and may appear subhexagonal in dorsal view.

Surface sculpture is generally fine, with larger parts of the head becoming dull in smaller specimens; a fine irregular sculpture in the rest of the body, with some striae on the dorsum of the mesosoma, often on the head, and largest specimens with a more developed sculpture on all surfaces. Clypeus always with a central carina.

Very sparse, usually erect setae all over the body; dense, fine, and mostly adpressed pilosity on the antennae.

Diagnosis. Compared to *T. trabutii*, the propodeal dorsum has a gentler transition with the rest of the mesosoma and is less steep [PropH2/PropH1: 0.919 (0.812, 1.092)]. Spines form a wider angle with the mesosoma than in *T. algiricus* and *T. trabutii*, with no range overlaps [SpANG: 147 (141, 161)]. On most other individual characters, it has average different but some overlaps with *T. algiricus*, and no overlaps with *T. trabutii*. The propodeal spines are shorter than in the other species [SPST/CS: 0.283 (0.201, 0.364)]. In dorsal view these are divergent and do not tend to curve inwards, the ratio between their maximum width and the width between their tips being averagely smaller than in the other species [SPWI/SPTI: 1.287 (1.026, 1.055)]. The ratio between the spines divergence and their length is higher than in the other species [SPWI/SPST: 1.060 (0.847, 1.307)].

Distribution. Algeria, France, Morocco, Spain—not known from any island. A record from Portugal by Henin *et al.* (2001) was suspected to represent misidentified *T. convexus* according to Arcos & Garcia (2023); while we believe it could truly represent *T. atlantis*, the publication does not provide enough information to reach a conclusion.

Taxonomic history. *Temnothorax atlantis* was described from the Atlas Mountains of Algeria (Takersan) by Santschi (1911) and said to be similar to *T. angustulus* ("almost an extreme race of it") and to be distinguished from *T. algiricus* by pilosity length (without further details). However, Santschi (1921) reconsidered it as a subspecies of another species, *T. normandi* (Santschi, 1912), that he had earlier described. *Temnothorax normandi* is a very different species, morphologically resemblant of the *T. nylanderi* group (Csősz *et al.* 2015), and Santschi (1921) did not elaborate on this relationship, while he described the 'variety' *suturalis* of *atlantis*. While most articles treated *T. atlantis* as a good species (e.g., Emery 1924; Bernard 1945; Cagniant 1964; 2006; Cagniant & Espadaler 1997; Galkowski & Cagniant 2017), Cagniant (1970) treated it as a subspecies of *T. angustulus*, similar to *algiricus* and replacing it in the Saharan Atlas. Finally, Cagniant & Galkowski (2017) considered *T. atlantis* to be a "superspecies", including the subspecies *atlantis*, *brunea, silvanus*, *suturalis*, and *veneris*. The only European record of this species from Portugal was published by Henin *et al.* (2001).

Leptothorax angustulus silvanus was described from Algeria (Msila Forest, Oran) initially considered by Forel (1907) as an "intermediate" form between *T. convexus* and *T. trabutii* (the latter considered a subspecies of *T. angustulus*). However, Cagniant & Espadaler (1997) moved it into synonymy with *T. algiricus*, not providing an explanation. Galkowski & Cagniant (2017) treated it as a subspecies of the "superspecies" *atlantis*.

Leptothorax kiudiria was described from Morocco (Bab Besene, Rif) and exclusively compared to *T. trabutii* in its description (Cagniant & Espadaler 1997), while Galkowski & Cagniant (2017) state that it is separated from *T. continentalis* and the "superspecies" *atlantis* because of longer scapi and declivous propodeum.

Leptothorax normandi atlantis suturalis Santschi, 1918 is an unavailable infrasubspecific name (Santschi 1918). Santschi (1918) described this variety from Morocco (Aïn Leuch, Fès-Meknès) stating that it differed from *atlantis* by having brighter colors. Galkowski & Cagniant (2017) use the first available name of *T. atlantis suturalis*, which they consider as part of the "superspecies" *atlantis*.

Temnothorax continentalis was described from France by Galkowski & Cagniant (2017), who separated it from the "superspecies" *atlantis* by considering it more strongly bicolored and by the presence of a clypeal carina.

Comments. The description of *T. continentalis* by Galkowski & Cagniant (2017) fundamentally improved the understanding of this species in Europe by separating it from *T. angustulus* and *T. algiricus* (under *T. mediterraneus*). However, their separation of the European populations as *T. continentalis* and those of North Africa as the "superspecies" *atlantis* was dismissed by our morphometric analyses; furthermore, contrary to what was suggested by the dichotomic key in Galkowski & Cagniant (2017), *T. atlantis* populations of North Africa appear usually bicolored (with only the *silvanus* types being uniformly dark) and do not differ from the European counterparts concerning the clypeal carina. The "superspecies" concept adopted by Galkowski & Cagniant (2017) is

not endorsed in modern ant taxonomy (Oberski *et al.* 2025). The subspecies *silvanus* and *suturalis* that Galkowski & Cagniant (2017) established appear to be synonyms of *atlantis* in our analyses. Finally, the same applies to *kiudiria*, apparently described from large-sized *T. atlantis* workers; our data dismiss the idea that *T. kiudiria* has exceptionally longer scapi or that a propodeal declivity is a distinctive characteristic. Biogeographically, the distribution of *T. atlantis* mirrors that of many West Mediterranean ants that occur continuously through North Africa (at least in the Western Maghreb), Iberia, and southern France across the Gibraltar strait, like *Aphaenogaster dulcineae* Emery, 1924, *Camponotus sylvaticus* (Olivier, 1792) or *Messor barbarus* (Linnaeus, 1767) (Guénard *et al.* 2017). A worker from Spain (Málaga, Adalusia; CASENT0914411) currently listed as *T. mediterraneus* on AntWeb belongs to *T. atlantis*.

***Temnothorax trabutii* (Forel, 1894)**

Figure 7

= *Leptothorax lindbergi* Santschi, 1931

Investigated type material: 2 syntype worker of *trabutii* from the MHNG (Geneva, Switzerland) with the label "*L. angustulus*//[worker caste symbol] Nyl//*Trabutii*//Forel//Tlemcen// *L. trabutii* Forel //Coll. A. Forel // ANTWEB CASENT0909013 // MGHNG ENTO 0100927 // *trabutii*". 1 syntype worker investigated through AntWeb (CASENT0912958—NHMB, Basel, Switzerland).

Investigated non-type material: 5 workers with the same collecting data of the type series.

Worker redescription. Body bicolored, with the entirety of the mesosoma and nodes reddish or ferruginous, contrasting with the dark head and gaster. Antennae, legs, and mandibles yellow reddish to dark.

Head subrectangular with rounded margin, clypeus and mandibles rounded. Antennae of 12 segments, antennal clubs of 3 segments. Compound eyes are ovoidal. The mesosoma dorsal profile in lateral view has a stark discontinuity between the metanotum and the propodeum, with the propodeum profile presenting a steep declivity. Propodeal spines very long and erect, often arcuated in dorsal view, and rather straight in lateral view. The petiole has a triangular shape, with a small tooth-like subpetiolar process. The postpetiole has an ordinary ovoidal lateral profile and may appear subhexagonal in dorsal view.

A fine irregular sculpture over the body, with some striae on the dorsum of the mesosoma, often on the head, and largest specimens with a more developed sculpture on all surfaces. Clypeus always with a central carina.

Very sparse, usually erect setae all over the body; dense, fine, and mostly adpressed pilosity on the antennae.

Diagnosis. Compared to the other species, the propodeal dorsum forms a sudden, angulate transition with the rest of the mesosoma and is steeper [PropH2/PropH1: 0.794 (0.722, 0.878)]. Spines form a smaller angle with the mesosoma than in *T. algiricus* and *T. atlantis*, with no range overlaps [SpANG: 112 (106, 118)]. On most other individual characters, it has average differences but some overlaps with *T. algiricus*, and no overlaps with *T. atlantis*. The propodeal spines are longer than in the other species [SPST/CS: 0.458 (0.425, 0.485)]. In dorsal view these are divergent at first and then tend to curve inwards, the ratio between their maximum width and the width between their tips being averagely smaller than in the other species [SPWI/SPBA: 1.416 (1.227, 1.625)]. The ratio between the spines divergence and their length is smaller than in the other species [SPWI/SPST: 0.723 (0.643, 0.812)].

Distribution. Algeria, Morocco.

Taxonomic history. It was described from Algeria (Tlemcen, Oran) by Forel (1894) as a "race" of *T. angustulus* with longer spines and different mesosoma Later, Cagniant (1968; 1970) elevated it to species rank but without explaining this decision. Cagniant & Espadaler (1997) considered it a subspecies of *T. algiricus*, stating that it has a lighter pigmentation and it is the form typical of *Quercus ilex* forests and semi-arid environments in the Atlas Mountains of Algeria, Morocco, and Tunisia, while *T. algiricus algiricus* would be typical of coastal environments. Galkowski & Cagniant (2017) reverted its status back to species rank stressing the steep declivity of the propodeal dorsum in profile view and the long spines.

Leptothorax lindbergi Santschi, 1931 was described from Morocco (Amizmiz, Marrakech Safi; 1931) as similar to *angustulus* and especially to "its race *trabutii*" (Santschi 1931). Cagniant & Espadaler (1997) synonymized it under *trabutii* without providing any explanation.

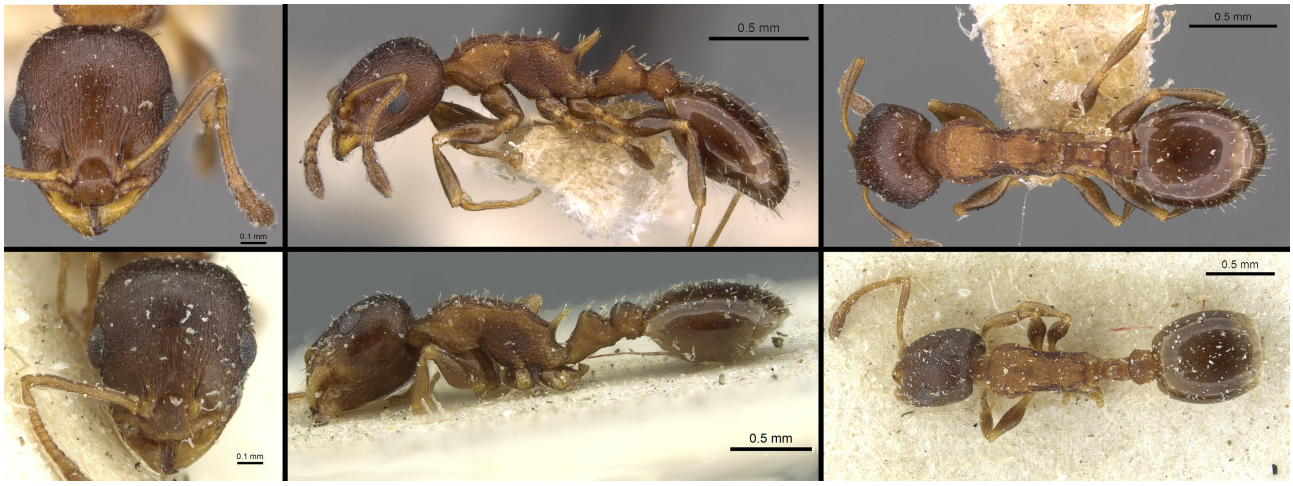

FIGURE 7. Worker specimens belonging to the type series of *T. trabutii*, in head (left), profile (center), and dorsal (right) view, available from AntWeb.org: CASENT0909013 (above) and CASENT0912958 (below), both photographed by Z. Lieberman.

Comments. This is the most distinctive of the three species we recognize in the complex in terms of qualitative morphology, with our qualitative observations mirroring those of Galkowski & Cagniant (2017). The steep declivity of the propodeal dorsum in profile view is unique in the complex and, alongside the long propodeal spines, is well represented in the drawing of *lindbergi* by Santschi (1931); although he mentions that spines could be 'shorter' than *trabutii*, we maintain it as a synonym of *trabutii* as established by Cagniant & Espadaler (1997).

We found a large dark-colored *T. algiricus* worker as the top specimen of a *T. trabutii* syntypes pin from the NHMG; however, despite being in the same pin with type *T. trabutii* specimens, it was the only worker glued on the side of the mesosoma instead of on the coxae, as all the *T. trabutii* specimens of that and the other pins were (and as myrmecologists normally prefer). This anomaly suggests that this very different specimen may have been added to the pin by mistake and not by Forel as a part of the original type series.

Dichotomic key to the worker caste of the *Temnothorax algiricus* complex

- Spines more erect [SpANG: 112.4 (106, 118)] and longer [SPST/CS: 0.458 (0.425, 0.485)], a stark angulate discontinuity between the dorsum and the steep posterior declivity and PropH2/Proph1: 0.794 (0.722, 0.878). Only Algeria and Morocco . . . . . *T. trabutii*
- Spines forming a larger angle with the mesosoma (SpANG 119 to 161) and shorter (SPST/CS 0.201 to 0.409), propodeal declivity absent or less steep, without a more gentle transition of the dorsal profile. 2

2. Spines forming a smaller angle with the mesosoma [SpANG: 130.24 (119, 139)], are on average longer (SPST/CS: 0.329 [0.261, 0.409]) and less divergent dorsally [SPWI/SPST: 0.829 (0.628, 1.2222)]. In many regions, entirely dark colored colonies are prevalent, but others have the same reddish component of the other two species. North Africa, southern Iberia, Balearic Islands, Italy (including Sardinia, Sicily and minor islands), Corsica, Croatia. . . . . *T. algiricus*
- Spines forming a larger angle with the mesosoma [SpANG: 147.5 (141, 161)], are on average shorter (SPST/CS: 0.283 [0.201, 0.364]) and more divergent dorsally [SPWI/SPST: 1.060 (0.847, 1.307)]. Algeria, Morocco, Iberia and mainland France, unknown on islands . . . . . *T. atlantis*

Discussion

This revision presents the first comprehensive data-driven analysis of the *Temnothorax algiricus* complex, including South European and North African taxa in a unified framework. Our quantitative approach resulted in the recognition of only three valid morphospecies out of ten taxonomic names (*T. algiricus*, *T. atlantis*, and *T. trabutii*) placed in the complex. Most of the taxa we reviewed had never been fully reassessed after their initial descriptions, and many names were never recorded outside the very localities from which they had been described, as no identification key allowed to discern the species they were supposed to indicate (e.g., *brunea*, *silvanus, suturalis*, *veneris*, see Guénard *et al.* 2017). The taxonomic status of many others has changed over time from subspecies to species or

from subspecies of one species to subspecies of another, but in most cases without empirical evidence or explicit justifications for these changes (e.g., Cagniant & Espadaler 1997).

While Galkowski & Cagniant (2017) made crucial contributions to clarifying the species boundaries of the European species within this group, their work did not address the relationships with the many taxa described from North Africa. Recent studies have revealed similar patterns of taxonomic oversplitting in North African ants belonging to other groups (e.g., Schifani & Alicata 2023; Csősz *et al.* 2025b). This oversplitting stems primarily from historical practices including the proliferation of vaguely defined "races" and "varieties" later elevated to subspecific rank, and the extensive application of now-abandoned "subspecies" and "superspecies" concepts in ant taxonomy (Schifani & Alicata 2023; Oberski *et al.* 2025). The Maghreb is undoubtedly one of the richest areas for ant biodiversity in the Palearctic (Kass *et al.* 2022), and even in the context of the present revision it hosts all the three *algiricus*-complex species. However, inflated nomenclature where valid names exceed clearly defined species creates noise in biodiversity datasets and estimations, as well as much confusion in the process of species identification for ecological or faunistic studies (Schifani & Alicata 2023).

TABLE 2. Mean ± SD (min, max) values of the numerical morphological characters recorded in this study.

	***T. algiricus* (n = 87)**	***T. atlantis* (n = 26)**	***T. trabutii* (n = 8)**
CL	690.890 ± 50.497	687.384 ± 73.408	689.674 ± 33.512
	(528.000, 790.000)	(554.000, 840.000)	(621.739, 721.739)
CWb	569.787 ± 47.912	581.340 ± 62.474	589.625 ± 25.178
	(435.000, 674.000)	(459.000, 707.000)	(539.130, 617.391)
EL	168.659 ± 20.138	168.001 ± 20.010	171.370 ± 9.532
	(122.000, 213.000)	(129.000, 215.000)	(160.870, 186.957)
EW	123.831 ± 18.134	119.776 ± 14.521	121.147 ± 6.784
	(97.000, 216.000)	(89.000, 147.000)	(113.043, 130.435)
ML	803.826 ± 73.246	817.547 ± 115.597	790.212 ± 63.112
	(613.000, 981.000)	(644.000, 1061.000)	(704.348, 913.000)
MW	380.774 ± 42.372	393.276 ± 51.602	403.092 ± 15.540
	(204.000, 469.000)	(323.000, 502.000)	(382.609, 430.435)
PPW	222.506 ± 24.615	228.153 ± 35.226	240.538 ± 11.011
	(153.000, 278.261)	(183.000, 302.000)	(226.087, 253.000)
PW	152.719 ± 18.348	156.755 ± 23.630	165.902 ± 8.750
	(99.000, 189.000)	(126.000, 215.000)	(156.522, 182.609)
PeH	217.332 ± 22.607	227.909 ± 34.905	238.272 ± 8.441
	(161.000, 294.000)	(180.000, 306.000)	(226.087, 254.000)
PoOC	255.338 ± 22.012	260.869 ± 27.777	235.223 ± 17.685
	(191.304, 300.000)	(212.000, 318.000)	(208.696, 252.174)
PropH1	283.137 ± 31.509	287.617 ± 52.071	317.489 ± 34.626
	(205.000, 367.000)	(180.000, 377.000)	(269.565, 366.000)
PropH2	253.409 ± 25.738	263.142 ± 43.537	251.261 ± 24.053
	(185.000, 315.000)	(180.000, 337.000)	(226.087, 286.957)
SL	501.698 ± 38.601	498.061 ± 57.719	523.842 ± 33.326
	(390.000, 586.000)	(390.000, 629.000)	(469.000, 573.913)
SPBA	124.892 ± 22.486	147.377 ± 24.579	150.277 ± 18.348
	(67.000, 188.000)	(110.000, 191.000)	(137.000, 191.304)
SPST	206.980 ± 22.740	180.284 ± 37.194	292.609 ± 15.154
	(150.000, 269.565)	(114.000, 261.000)	(269.565, 313.043)
SPTI	154.483 ± 29.027	181.798 ± 39.174	164.810 ± 18.299
	(76.000, 247.000)	(134.000, 276.000)	(134.783, 191.304)
SPWI	171.214 ± 27.604	189.611 ± 38.234	211.413 ± 15.922
	(106.000, 265.000)	(138.000, 287.000)	(191.304, 234.783)
SpANG	130.328 ± 4.869	147.692 ± 5.483	112.375 ± 4.340
	(119.000, 139.000)	(141.000, 161.000)	(106.000, 118.000)

TABLE 3. Mean ± SD (min, max) values of indexes based on morphological characters recorded in this study.

	***T. algiricus* (n = 87)**	***T. atlantis* (n = 26)**	***T. trabutii* (n = 8)**
CL/CS	1.214 ± 0.048	1.184 ± 0.049	1.171 ± 0.071
	(1.060, 1.338)	(1.034, 1.244)	(1.007, 1.218)
CS	0.630 ± 0.048	0.634 ± 0.067	0.640 ± 0.022
	(0.482, 0.732)	(0.507, 0.773)	(0.598, 0.661)
CWb/CS	0.904 ± 0.019	0.917 ± 0.023	0.922 ± 0.032
	(0.855, 0.951)	(0.891, 1.000)	(0.902, 0.996)
EL/CS	0.259 ± 0.031	0.259 ± 0.026	0.268 ± 0.017
	(0.173, 0.314)	(0.188, 0.293)	(0.248, 0.291)
EW/CS	0.196 ± 0.025	0.189 ± 0.019	0.190 ± 0.013
	(0.159, 0.354)	(0.161, 0.234)	(0.173, 0.204)
EYE	0.144 ± 0.020	0.142 ± 0.017	0.146 ± 0.007
	(0.104, 0.190)	(0.109, 0.181)	(0.137, 0.159)
EYE/CS	0.228 ± 0.023	0.224 ± 0.018	0.229 ± 0.013
	(0.173, 0.308)	(0.188, 0.261)	(0.211, 0.247)
ML/CS	1.275 ± 0.051	1.287 ± 0.086	1.236 ± 0.092
	(1.152, 1.435)	(1.141, 1.482)	(1.066, 1.386)
MW/CS	0.603 ± 0.040	0.620 ± 0.043	0.630 ± 0.022
	(0.319, 0.669)	(0.501, 0.691)	(0.600, 0.655)
PPW/CS	0.351 ± 0.022	0.360 ± 0.039	0.376 ± 0.010
	(0.265, 0.399)	(0.285, 0.458)	(0.356, 0.389)
PW/CS	0.243 ± 0.019	0.252 ± 0.029	0.259 ± 0.013
	(0.157, 0.277)	(0.198, 0.314)	(0.246, 0.276)
PeH/CS	0.345 ± 0.021	0.359 ± 0.038	0.373 ± 0.012
	(0.301, 0.422)	(0.256, 0.432)	(0.360, 0.393)
PoOC/CS	0.406 ± 0.028	0.412 ± 0.019	0.368 ± 0.031
	(0.321, 0.469)	(0.374, 0.461)	(0.329, 0.422)
PropH1/CS	0.402 ± 0.028	0.414 ± 0.043	0.393 ± 0.036
	(0.312, 0.467)	(0.331, 0.497)	(0.356, 0.444)
PropH2/CS	0.449 ± 0.033	0.452 ± 0.054	0.496 ± 0.048
	(0.363, 0.547)	(0.331, 0.552)	(0.413, 0.566)
SL/CS	0.797 ± 0.032	0.786 ± 0.049	0.819 ± 0.050
	(0.701, 0.917)	(0.671, 0.892)	(0.712, 0.868)
SPBA/CS	0.197 ± 0.025	0.232 ± 0.025	0.235 ± 0.027
	(0.130, 0.271)	(0.188, 0.276)	(0.208, 0.296)
SPST/CS	0.329 ± 0.030	0.283 ± 0.041	0.458 ± 0.023
	(0.261, 0.409)	(0.201, 0.364)	(0.425, 0.485)
SPTI/CS	0.244 ± 0.033	0.285 ± 0.041	0.258 ± 0.032
	(0.157, 0.349)	(0.232, 0.378)	(0.212, 0.309)
SPWI/CS	0.270 ± 0.029	0.292 ± 0.040	0.330 ± 0.022
	(0.208, 0.372)	(0.243, 0.393)	(0.304, 0.364)
PropH2/PropH1	0.897 ± 0.052	0.919 ± 0.056	0.794 ± 0.054
	(0.732, 1.069)	(0.812, 1.092)	(0.722, 0.878)
SPWI/SPTI	1.382 ± 0.132	1.287 ± 0.132	1.416 ± 0.120
	(1.108, 1.750)	(1.026, 1.055)	(1.227, 1625)
SPWI/SPST	0.829 ± 0.116	1.060 ± 0.116	0.723 ± 0.052
	(0.628, 1.222)	(0.847, 1.307)	(0.643, 0.812)

Our recognition of three species within the *algiricus* complex for the West Mediterranean region provides a foundation for further studies and should not represent the final chapter in the exploration of this group. While we established a clear methodological framework for our study, several refinements could allow future investigations to better explore intraspecific patterns or detect potential cryptic diversity. For example, a larger series of workers per colony would allow for a more refined understanding of interspecific differences by better evaluating intracolonial variation. Also, the direct measurement of specimens here investigated through AntWeb images can significantly improve accuracy (Csősz *et al.* 2023). But even more promising would be an integrative taxonomic approach making use of phylogenomic data from across the vast distribution of the complex, with the potential of clarifying the evolutionary relationships within it (Csősz *et al.* 2025a; Oberski *et al.* 2025).

Over a century after *T. algiricus*, *T. atlantis*, and *T. trabutii* were described, our knowledge on the biology and ecology of these species remains overall scarce. They belong to a minority of *Temnothorax* species that have developed arboreal nesting and foraging habits (Prebus 2017). According to our data, *T. algiricus* and *T. atlantis* range from evergreen Mediterranean vegetation to deciduous forests, and from coasts to low montane regions, while less is known about the much rarer and geographically restricted *T. trabutii*, which is presently only known from two localities. In deciduous forests of Sicily, *T. algiricus* was one of the most frequent ant species acting as secondary colonizers of oak galls induced by *Andricus quercustozae* (Bosc. 1792) together with *Crematogaster scutellaris* (Olivier, 1792) and *Colobopsis imitans* Schifani, Giannetti, Csősz, Castellucci, Luchetti, Castracani, Spotti, Mori & Grasso, 2021 (Giannetti *et al.* 2022). They are likely all generalist species, with *T. algiricus* observed preying upon aphids (authors' personal observations), drinking from the extrafloral nectaries of the invasive tree of heaven *Ailanthus altissima* Swingle (Schifani *et al.* 2025), and being an efficient predator penetrating the galleries of the ambrosia beetle *Xylosandrus compactus* (Eichhoff, 1875) in laboratory experiments (Giannetti *et al.* 2022). Like most *Temnothorax*, these ants seem to form relatively small colonies, and foraging workers are usually observed in very low numbers. Nonetheless, they appear to be very frequent and widespread in the West Mediterranean, likely having a significant ecological impact that awaits to be investigated.

Despite a long history of taxonomic studies, research must still be undertaken to disentangle the taxonomy of Mediterranean ants, especially in species-rich genera like *Temnothorax*, creating better conditions for biological, ecological, and conservation studies.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

Geographic, morphological, and repository data of the specimens examined in this revision.