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REDESCRIPTION OF *TETRAMORIUM ATLANTE* CAGNIANT, 1970, NEW STATUS (HYMENOPTERA: FORMICIDAE: MYRMICINAE)

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Abstract.— *Tetramorium atlante* Cagniant, 1970, **new status**, a member of *Tetramorium semilaeve* complex is redescribed based on new material from northern Morocco. Detailed descriptions of gyne and male are given for the first time. Diagnosis differentiating this species from *T. semilaeve* is given, along with colour photographs of all castes and male genitalia.

Key words.— Mediterranean Subregion, Crematogastrini, taxonomy, *Tetramorium semilaeve* complex

INTRODUCTION

Borowiec *et al*. (2015) redescribed *Tetramorium semilaeve* André, 1883 a species considered to be widely distributed in the Mediterranean Basin. Their studies showed that the true *Tetramorium semilaeve* is distributed only in the western European part of the Mediterranean and most records from North Africa and the eastern part of the Mediterranean basin apply to other taxa, some of which are currently recognized as an infra-specific taxa of various rank. The status of these taxa is difficult to assess because most of them have been described only from worker caste. A recent study showed that only examination of sexual forms allows correct identification of species belonging to the *T. semilaeve* complex (Borowiec *et al*. 2015 and unpublished data). Due to political reasons, field work in Northern Africa is deeply hampered, making efforts at revising the status of taxa described from this region more difficult.

One of such infra-specific taxa is *Tetramorium caespitum* st. *punicum* var. *atlantis* Santschi, 1918 described from Tunisia, Kairouan, Le Kef. Despite the fact that this name was unavailable for nomenclature, Cagniant (1970) recorded this taxon from Algeria under trinomial *Tetramorium semilaeve* subsp. *atlante*, making it available for the nomenclature with "Cagniant, 1970" as the author name. Later, Cagniant (1997) also recorded this taxon from Morocco, with a note that it is widely distributed in north-western Africa, from northern Morocco to Tunisia and still treated it as a subspecies of *T. semilaeve*.

After a study of nest samples from Morocco corresponding with both syntypes of "*atlante*" preserved in Basel Museum and material described by Cagniant (1997) as ssp. *atlante*, we concluded that it represents a good species of the *Tetramorium semilaeve* complex and decided to redescribe this taxon.

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Material and methods

Specimens were compared using standard methods of comparative morphology. Photos were taken using a Nikon SMZ 1500 stereomicroscope, Nikon D5200 photo camera and Helicon Focus software.

All given label data are in their original spelling; a vertical bar (|) separates data on different rows and double vertical bar (||) separates labels.

Abbreviation to collections:

DBET – Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland;

NHMB – Naturhistorisches Museum Basel, Basel, Switzerland.

Measurements and indices:

CL – length of head in full-face view, measured in a straight line from the anteriormost point of median clypeal margin to the mid-point of the posterior margin of the head. Concavity of posterior margin reduces CL;

CW – maximum width of head in full-face view, including compound eyes;

CS – cephalic size; calculated from the arithmetic mean of CL and CW. It is used as a less variable indicator of body size;

EH – the minimum diameter of the compound eye;

EL – the maximum diameter of the compound eye;

EYE – eye size index, calculated from the arithmetic mean of EL and EH, divided by CS;

OMD – oculo-malar space. The minimal distance between anterior (lower) margin of the compound eye and the mandibular junction in profile;

FL – the maximum distance between external borders of the frontal lobes;

FR – the minimum width of the frons between the frontal carinae;

ML – the diagonal length of mesosoma measured in lateral view from the anteriormost point of the pronotal slope to the posterior (or postero-ventral) margin of the propodeal lobes;

MW – the maximum width of the pronotum from above;

NOH – the maximum height of the petiolar node;

NOL – the length of the petiolar node;

PEH – the maximum height of the petiole;

PEL – the distance between the posteriormost point of the petiole and the petiolar spiracle;

PEW – the maximum width of the petiole in dorsal view;

POC – postocular distance. Measured from the reference line fitted on the posterior margin of compound eyes to median posterior margin of the head;

PPH – the maximum height of the postpetiole in lateral view;

PPL – the maximum length of the postpetiole in lateral view;

PPW – the maximum width of the postpetiole in dorsal view;

SL – the maximum length of the scape, measured from the proximal point of scape lobe to the distal end of scape;

SPL – the minimal distance between the center of propodeal spiracle and the propodeal declivity;

SPSP – the maximum length of propodeal teeth, measured in lateral view from the tip of spine to the propodeal spiracle; WAIST – (gyne only), waist index, calculated as (PEW+PPW)/CS.

Scheme of description corresponding with revisions of *Tetramorium chefketi* and *T. ferox* groups (Csösz *et al*. 2007, Csösz and Schulz 2010: see Figs 1–4 on p. 4).

Taxonomy

Tetramorium atlante Cagniant, 1970 new status (Figs 1–13)

Tetramorium caespitum st. *punicum* var. *atlantis* Santschi, 1918: 155 (terra typica: Tunisia), unavailable name.
Tetramorium semilaeve subsp. *atlante* Cagniant, 1970: 430, 1997: 98.

Material examined. Type material: syntype worker on photo (AntWeb resources: Photo by Alexandra Westrich | URL: https://www.antweb.org/specimen/CASENT0915045; accessed 1 April 2015): T. caespitum L. | st. punicum Sm | var. atlantis Sants | Type || Kairouan | (Santschi) || Tunisie | Kairouan | Dr. F. Santschi || 135 || Sammlung | Dr. F. Santschi | Kairouan || Type || NATURHIST. | MUSEUM | BASEL || ANTWEB | CASENT | 0915045 (NHMB).

Other material examined. 4 gynes, 5 males, 10 workers: Morocco | Meknès-Tafilale | Aïn Vittel n. Ifrane, 1600 m | 35.5409° / -5.113°, 10 VII 2010 | C. Galkowski || Collection L. Borowiec | Formicidae | LBC-MOR00010 (DBET).

Redescription. **Worker** (Figs 1–3). Measurements and indices (n=10): CL: 0.77 ± 0.03 (0.737–0.844); POC: 0.3 ± 0.02 (0.268–0.324); CW: 0.755 ± 0.04 (0.704–0.866); FR: 0.27 ± 0.017 (0.257–0.313); FL: 0.271 ± 0.016 (0.257–0.313); SL: 0.535 ± 0.02 (0.506–0.575); OMD: 0.192 ± 0.015 (0.17–0.212); EL: 0.146 ± 0.08 (0.128–0.291); EH: 0.098 ± 0.01 (0.078–0.101); ML: 0.827 ± 0.039 (0.782–0.927); SPSP: 0.148 ± 0.013 (0.112–0.17); SPL: 0.106 ± 0.011 (0.089–0.126); PEL: 0.191 ± 0.014 (0.179–0.229); NOL: 0.153 ± 0.011 (0.134–0.179); PPL: 0.176 ± 0.007 (0.162–0.19); PEH: 0.25 ± 0.013 (0.235–0.282); NOH: 0.177 ± 0.016 (0.165–0.223); PPH: 0.243 ± 0.011 (0.229–0.268); MW: 0.471 ± 0.024 (0.441–0.531); PEW: 0.235 ± 0.013 (0.215–0.267); PPW: 0.261 ± 0.01 (0.246–0.285); CS: 0.763 ± 0.035 (0.721–0.855); EYE: 0.16 ± 0.01 (0.138–

0.167); CL/CW: 1.021 ± 0.02 (0.975–1.047); FR/CS: 0.353 ± 0.009 (0.341–0.367); FL/FR: 1.009 ± 0.01 (1.0–1.043); SL/CS: 0.703 ± 0.016 (0.672–0.741); MW/CS: 0.618 ± 0.008 (0.6–0.632); PEW/PPW: 0.902 ± 0.03 (0.857–0.937); NOH/NOL: 1.163 ± 0.08 (1.057–1.336); NOH/PEL: 0.928 ± 0.05 (0.852–1.0); NOL/PEL: 0.801 ± 0.04 (0.729–0.872); PEH/NOL: 1.637 ± 0.08 (1.538–1.722); PEW/PEH: 0.943 ± 0.03 (0.914–0.979); CS/PEW: 3.245 ± 0.07 (3.14–3.351); CS/PPW: 2.927 ± 0.08 (2.816–3.065); CW/MW: 1.619 ± 0.02 (1.582–1.666).

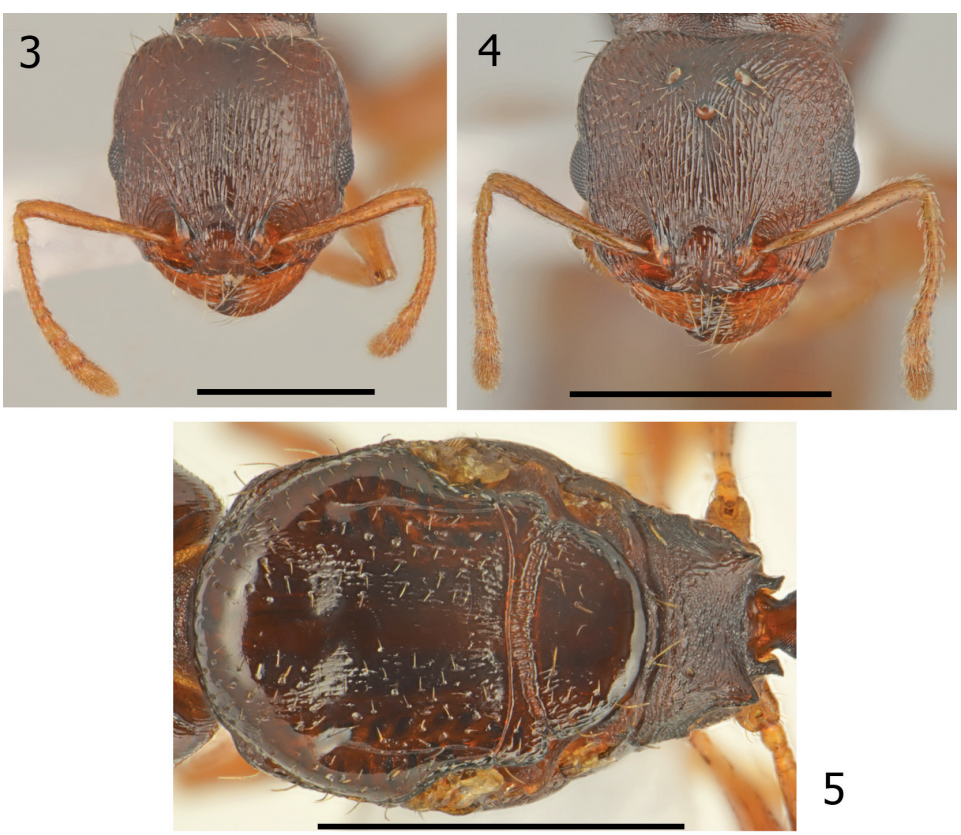
Small to medium size, CS 0.763 [0.721–0.855]. Whole body brown to dark brown and appendages yellow, the palest specimens never yellow. Head nearly square CL/CW 1.021 [0.975–1.047], with almost parallel to slightly rounded sides, straight or slightly concave occipital margin and regularly rounded occipital corners. Eyes small, EYE 0.16 [0.138–0.167]. Frons moderately wide, FR/CS 0.353 [0.341–0.367], frontal lobes as wide as frons, FL/FR 1.009 [1.0–1.043]. Scape short, SL/CS 0.703 [0.672–0.741], without dorsal carina basally, surface smooth and shiny. Promesonotal dorsum slightly convex, metanotal groove shallow, but distinct. Propodeal teeth short, spiniform, apex of spine located approximately at 2/3 height of mesosoma (Fig. 2). Dorsal surface of petiole flat, NOH/NOL 1.163 [1.057– 1.336], petiole relatively high, PEH/NOL 1.637 [1.538–1.722], postpetiole distinctly transverse. General appearance moderately rugose, ground surface finely sculptured. Head dorsum mostly longitudinally rugose and shiny between rugae, rugae extend occipital margin of head, occiput mostly smooth and shiny, sides in anterior half longitudinally rugose and shiny between rugae. In most specimens short band without rugosities runs between frontal rugose area and rugosities along ocular area on each side (Fig. 3) but smooth area never exceeds $^{1}/_{7}$ length of anterior surface of head; in extremely sculptured specimens almost entire frontal surface of head with long rugae with very

Figures 1–2. *Tetramorium atlante* Cagniant, worker: (1) dorsal view; (2) lateral view. Scale bar = 1 mm.

small smooth patch between interrupted rugae and occiput with fine rugosities. Mesosoma dorsum longitudinally rugose and microreticulate but never reticulate, only occasionally rugae on pronotum partly interrupted with indistinct microreticulation but pronotum never with distinct smooth and shiny areas (Fig. 1). Sides of pronotum and meso- and metapleuron usually coarsely microreticulate, sometimes reticulation tends to form transverse lines but surface never appears striate or rugose (Figs 2). Dorsum of petiolar node smooth and shiny with sides carinate, lateral surface microreticulate. Dorsum of postpetiole smooth and shiny, sides microreticulate. First gastral tergite smooth and shiny. Whole dorsum, including head, covered with sparse setae, the longest on pronotum and the shortest on frons. Ventral surface of head with sparse short and 2–3 moderately long setae not forming a psammophore.

Gyne (Figs 4–7). Measurements and indicates (n=3): CL: 1.05 ± 0.013 (1.039–1.065); POC: 0.388 ± 0.013 (0.374–.4); CW: 1.17 ± 0.02 (1.148–1.187); FR: 0.409 ± 0.007 (0.4–0.413); FL: 0.389 ± 0.01 (0.379–0.398); SL: 0.727 ± 0.022 (0.704–0.749); OMD: 0.21 ± 0.016 (0.201–0.229); EL: 0.287 ± 0.007 (0.279–0.291); EH: 0.227 ± 0.02 (0.212–0.246); ML: 1.849 ± 0.001 (1.848–1.85); SPSP: 0.294 ± 0.02 (0.268–0.313); SPL: 0.216 ± 0.006 (0.212–0.223); PEL: 0.29 ± 0.02 (0.279–0.313); NOL: 0.214 ± 0.008 (0.207–0.223); PPL: 0.315 ± 0.011 (0.302–0.324); PEH: 0.458 ± 0.011 (0.446–0.469); NOH: 0.287 ± 0.025 (0.257–0.302); PPH: 0.436 ± 0.007 (0.425–0.446); MW: 1.125 ± 0.01 (1.11–1.135); PEW: 0.39 ± 0.01 (0.38–0.4); PPW: 0.488 ± 0.02 (0.475–0.508); CS: 1.11 ± 0.014 (1.094–1.12); EYE: 0.232 ± 0.012 (0.224–0.246); CL/CW: 0.898 ± 0.015 (0.88–0.907); FR/CS: 0.368 ± 0.01 (0.357–0.378); FL/FR: 0.953 ± 0.04 (0.918–0.995); SL/CS: 0.655 ± 0.014 (0.644–0.671); MW/CS: 1.014 ± 0.09 (0.995–1.032); PEW/PPW: 0.801 ± 0.014 (0.787–0.815); NOH/NOL: 1.345 ± 0.168 (1.152–1.459); NOH/PEL: 0.989 ± 0.08 (0.921–1.082); NOL/PEL: 0.74 ± 0.07 (0.661–0.799); PEH/NOL: 2.139 ± 0.03 (2.103–2.16); PEW/PEH: 0.853 ± 0.04 (0.83–0.897); CS/PEW: 2.845 ± 0.106 (2.734–2.946); CS/PPW: 2.278 ± 0.12 (2.152–2.357); CW/MW: 0.987 ± 0.02 (0.967–1.005); WAIST: 0.792 ± 0.035 (0.764–0.83).

Moderate size, CS 1.11 [1.094–1.12]. Head and mesosoma dark brown, abdomen brown, appendages yellowish. Head wider than long, CL/CW 0.898 [0.88–0.907], with straight subparallel sides, shallowly emarginate occipital margin and regularly rounded occipital corners. Frons moderately wide, FR/CS 0.368 [0.357–0.378], frontal lobes as wide as frons, FL/FR 0.953 [0.918–0.995]. Scape short, SL/CS 0.655 [0.644–0.671],



Figures 3–5. *Tetramorium atlante* Cagniant: (3) worker head, scale bar = 0.5 mm; (4) gyne head; (5) gyne mesosoma. Scale bar 4, 5 = 1 mm.

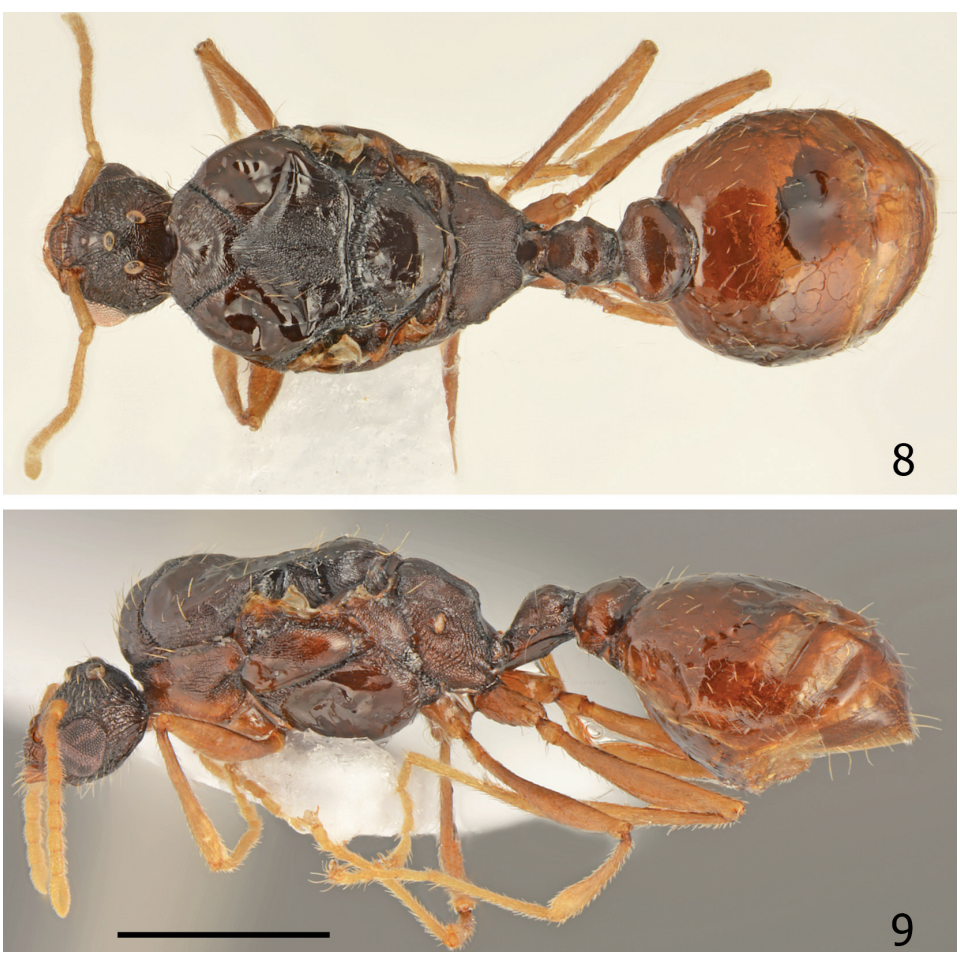
without dorsal carina basally, smooth and shiny. Head as wide as scutum, MW/CS 1.014 [0.995–1.032]. Propodeal teeth short, triangular. Dorsal crest of petiolar node in frontal view slightly convex. Petiolar node dorsum steeply rounded backward. Petiole and postpetiole relatively narrow, WAIST 0.792 [0.764–0.83]. General appearance partly sculptured. Head dorsum, occiput and sides distinctly rugulose, ground surface shiny or indistinctly microreticulate. Frons longitudinally rugulose (Fig. 4). Mesosoma flat, pronotal sides visible from above. Anterior margin, sides, and median part of scutum smooth and shiny, lateral to shiny median band punctate and longitudinally striate, striae extending from base to $^{2}/_{3}$ length of scutum, in the strongest sculptured specimens median smooth band very narrow and whole base of scutum striate. Scutellum mostly smooth and shiny, only corners or corners and sides with oblique striation and punctate (Fig. 5). Sides of pronotum ruguloso-reticulate and feebly microreticulate, anepisternum in upper part with fine longitudinal rugae and rest smooth and shiny, katepisternum mostly smooth and shiny but posterior corners and sometimes whole posterior third with fine longitudinal rugae and microreticulation (Fig. 7). Whole surface of petiolar node distinctly reticulate, posterior surface granulate without or with indistinct transverse rugae. Postpetiole distinctly transverse, sides rounded (Fig. 7), dorsum of postpetiole smooth, sides granulate

Figures 6–7. *Tetramorium atlante* Cagniant, gyne: (6) dorsal view; (7) lateral view. Scale bar = 1 mm.

and reticulate. First gastral tergite smooth and shiny. Whole dorsum, including head, covered with short, sparse setae. Ventral surface of head with several short setae, as long as to 1.5 times longer than frontal setae, arising posteriorly to buccal cavity.

Male (Figs 8–13). Measurements and indicates (n=5): CL: 0.694 ± 0.013 (0.673–0.715); POC: 0.284 ± 0.01 (0.268–.302); CW: 0.836 ± 0.014 (0.81–0.854); FR: 0.258 ± 0.009 (0.246–0.274); FL: 0.292 ± 0.006 (0.285–0.302); SL: 0.311 ± 0.008 (0.302–0.324); OMD: 0.076 ± 0.007 (0.061–0.084); EL: 0.315 ± 0.008 (0.302–0.324); EH: 0.258 ± 0.005 (0.249–0.263); ML: 1.81 ± 0.113 (1.617–1.935); SPSP: 0.243 ± 0.01 (0.235–0.263); SPL: 0.216 ± 0.011 (0.201–0.232); PEL: 0.32 ± 0.011 (0.302–0.335); NOL: 0.244 ± 0.019 (0.212–0.268); PPL: 0.304 ± 0.018 (0.279–0.324); PEH: 0.333 ± 0.01 (0.313–0.346); NOH: 0.206 ± 0.015 (0.19–0.235); PPH: 0.464 ± 0.029 (0.425–0.503); MW: 1.108 ± 0.049 (1.067–1.2); PEW: 0.36 ± 0.005 (0.351–0.366); PPW: 0.518 ± 0.02 (0.492–0.547); CS: 0.765 ± 0.014 (0.742–0.785); EYE: 0.374 ± 0.002 (0.372–0.379); CL/CW: 0.831 ± 0.004 (0.824–0.837); FR/CS: 0.337 ± 0.01 (0.32–0.349); FL/FR: 1.134 ± 0.06 (1.044–1.228); SL/CS: 0.407 ± 0.009 (0.395–0.421); MW/CS: 1.449 ± 0.06 (1.389–1.565); PEW/PPW: 0.696 ± 0.03 (0.655–0.744); NOH/NOL: 0.85 ± 0.093 (0.739–0.955); NOH/PEL: 0.644 ± 0.05 (0.6–0.725); NOL/PEL: 0.762 ± 0.044 (0.702–0.821); PEH/NOL: 1.372 ± 0.08 (1.25–1.476); PEW/PEH: 1.084 ± 0.05 (1.014–1.169); CS/PEW: 2.185 ± 0.06 (2.042–2.191); CS/PPW: 1.478 ± 0.06 (1.402–1.561); CW/MW: 0.691 ± 0.027 (0.639–0.719).

Whole body dark brown, appendages yellowish. Head behind eyes almost trapezoidal, occipital margin slightly convex, occipital corners subangulate. Scutum distinctly wider than head. Propodeum in profile with distinct angulation in position of propodeal teeth. Dorsal crest of petiolar node with obtuse transversal edge, slightly emarginated in frontal view. Head distinctly granulate, dull. Sides of pronotum microreticulate with fine transverse striation. Scutum between sutures in anterior part with oblique striation and microreticulate only along middle runs shiny band, laterally smooth and shiny, rest microreticulate with longitudinal and oblique striation. Scutellum at base and laterally



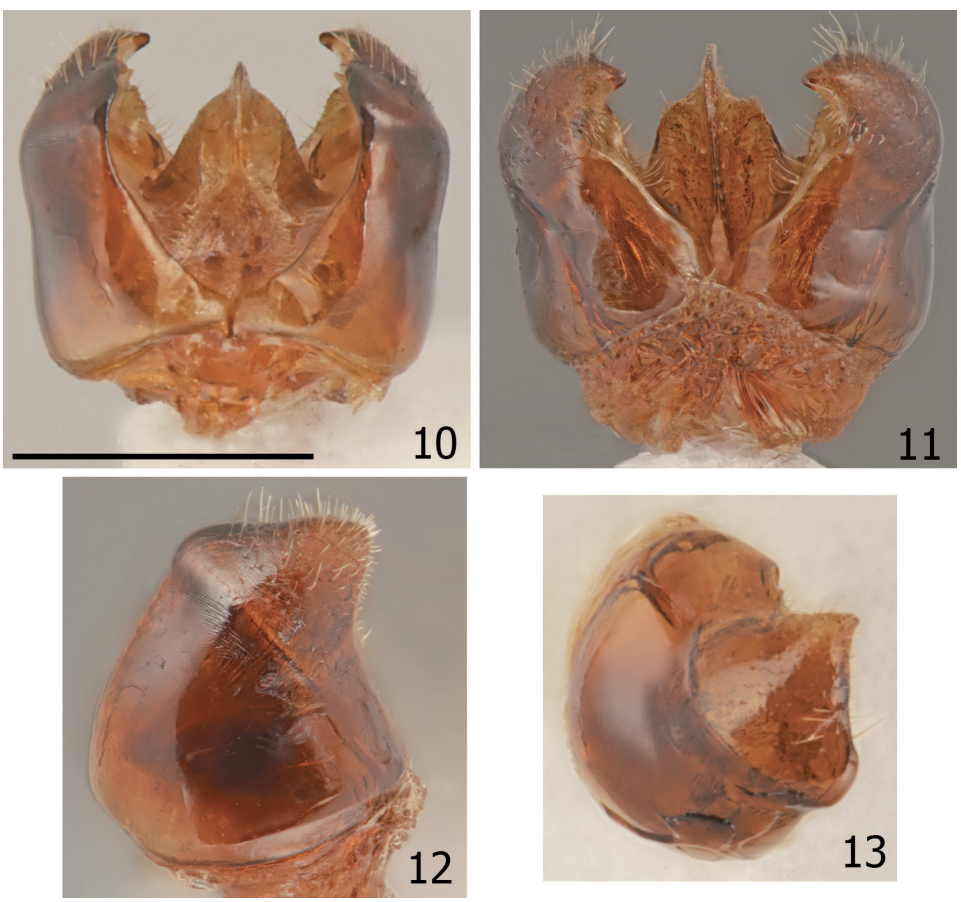
Figures 8–9. *Tetramorium atlante* Cagniant, male: (8) dorsal view; (9) lateral view. Scale bar = 1 mm.

with longitudinal striation, rest smooth and shiny. Anepisternum in anterior half smooth and shiny in posterior half with oblique striation, katepisternum in both dorsal angles distincty striate and microreticulate. Whole surface of petiolar node microgranulate and microreticulate, dull, postpetiole mostly microreticulate only top partly smooth and shiny. Whole surface of propodeum microreticulate, dull. First gastral tergite smooth and shiny. Male genitalia stout (Figs 10–13), in lateral distinctly slightly constricted before apex with obtuse inner angle, top shortly and sparsely pubescent, ventral and dorsal margins of parameres shallowly incised, top of inner margin of paramere before apical denticle straight, without dentiform plate extending beyond the sharp edge of paramere (Fig. 13).

Differental diagnosis. *Tetramorium atlante* and *T. semilaeve* at first glance look similar, and workers are especially difficult to identify. Males and gynes, however, have constant differences in the morphological characters and biometric data (see Table 1).

Workers of *T. atlante* differ from workers of *T. semilaeve* (in parentheses characters for *T. semilaeve*) in brown to dark brown body (usually pale yellow to yellowish brown, occasionally brown), head sculpture with longitudinal rugosities, more distinct spread over the frontal surface with very small lateral areas without striation (rugosities less distinct on sides of frontal surface, usually with longitudinal areas without striation). Nevertheless, dark and strongly sculptured workers of *T. semilaeve* are extremely similar to *T. atlante* and a proper identification requires a nest sample with sexual forms. Workers of *T. depressum* Forel and *T. punctatum* Santschi, two other well-defined species of *T. semilaeve* complex, differ in reduced sculpture of head with at least half frontal surface smooth and shiny.

Gynes of *T. atlante* distinctly differ from gynes of *T. semilaeve* (characters for *T. semilaeve* in parentheses) in larger size with ML 1.848–1.850, MW 1.11–1.35, CW 1.148–1.187 and SPL 0.212–0.223 (1.053–1.813, 1.0–1.14, 0.978–1.161 and 0.173–0.201**)**, scutum at base and laterally with striation extending from base to at least half length of scutum (scutum completely smooth and shiny or with short striation at base never extending to half length of scutum), scutellum with distinct striation in angles (completely smooth and shiny or with rudiments of striation), anepisternum in



Figures 10–11. *Tetramorium atlante* Cagniant, male genitalia: (10) dorsal view; (11) ventral view; (12) lateral view; (13) apical view. Scale bar = 0.5 mm.

posterior half with distinct striation and microreticulation (mostly smooth and shiny), katepisternum along posterior margin with broad area of distinct sculpture (narrow area or reduced to posterior corners), postpetiole less transverse and more sculptured with smooth and shiny area reduced to the middle of top (postpetiole more transverse, less sculpture with whole dorsal surface smooth and shiny).

Males of *T. atlante* distinctly differ from males of *T. semilaeve* in higher petiole with NOH 0.19–0.235 and PEH 0.313–0.346 (0.156–0.179 and 0.257–0.313), lower SL/CS ratio 0.395–0.421 (0.436–0.478), head behind eyes trapezoidal (rounded), scutum between sutures mostly striate and microreticulate (mostly smooth and shiny), scutellum at whole base microreticulate and striate (completely smooth and shiny or in basal corners with fine sculpture), propodeum slightly angulate (round), anepisternum in posterior half with oblique striation (smooth and shiny, at most with few striae close to upper margin), katepisternum in both upper corners with broad microreticulate and striate area (narrow sculptured areas), male genitalia in lateral view distinctly constricted before apex (shallowly constricted) and top of inner margin of paramere without dentiform plate extending beyond the sharp edge of paramere (with dentiform plate).

Biological notes. Although locus typicus Kairouan in Tunisia is placed only 70 m a.s.l. Cagniant (1970, 1997) noted than *T. atlante* prefers mountainous habitats. Its known localities are mostly between 1600 m (our material) to 2300 m (Haut Atlas). Ants were collected in agricultural habitat such as farmlands, pastures, and in scrubs, luminous forests, roadsides. Preference for mountain habitats additionally differentiates *T. atlante* from *T. semilaeve*, which, according to Borowiec *et al.* (2015), prefers littoral habitats located usually below 700 m a.s.l. and only occasionally reach to the elevation of just over 1000 m a.s.l.

Table 1. Measurements and indices for *Tetramorium atlante* and *T. semilaeve* (the most important differences marked with bold).

	Gyne		Male		Worker	
	T. atlante	*T. semilaeve*	*T. atlante*	*T. semilaeve*	*T. atlante*	*T. semilaeve*
CL	**1.05 ± 0.013 (1.039–1.065)**	**0.999 ± 0.015 (0.983–1.027)**	**0.694 ± 0.013 (0.673–0.715)**	**0.667 ± 0.018 (0.637–0.693)**	**0.77 ± 0.03 (0.737–0.844)**	**0.723 ± 0.034 (0.637–0.771)**
POC	0.388 ± 0.013 (0.374–.4)	0.378 ± 0.019 (0.34–.413)	0.284 ± 0.01 (0.268–.302)	0.279 ± 0.019 (0.263–.313)	0.3 ± 0.02 (0.268–.324)	0.293 ± 0.021 (0.246–.324)
CW	1.17 ± 0.02 (1.148–1.187)	1.09 ± 0.05 (0.978–1.161)	**0.836 ± 0.014 (0.81–0.854)**	**0.807 ± 0.024 (0.771–0.827)**	**0.755 ± 0.04 (0.704–0.866)**	**0.693 ± 0.037 (0.606–0.749)**
FR	0.409 ± 0.007 (0.4–0.413)	0.397 ± 0.009 (0.38–0.412)	0.258 ± 0.009 (0.246–0.274)	0.238 ± 0.012 (0.221–0.257)	0.27 ± 0.017 (0.257–0.313)	0.253 ± 0.015 (0.234–0.279)
FL	0.389 ± 0.01 (0.379–0.398)	0.385 ± 0.018 (0.357–0.413)	0.292 ± 0.006 (0.285–0.302)	0.292 ± 0.013 (0.277–0.307)	0.271 ± 0.016 (0.257–0.313)	0.262 ± 0.017 (0.235–0.291)
SL	0.727 ± 0.022 (0.704–0.749)	0.715 ± 0.015 (0.693–0.737)	0.311 ± 0.008 (0.302–0.324)	0.333 ± 0.016 (0.307–0.358)	0.535 ± 0.02 (0.506–0.575)	0.534 ± 0.03 (0.503–0.626)
OMD	0.21 ± 0.016 (0.201–0.229)	0.223 ± 0.016 (0.212–0.257)	0.076 ± 0.007 (0.061–0.084)	0.068 ± 0.016 (0.056–0.089)	0.192 ± 0.015 (0.17–0.212)	0.18 ± 0.021 (0.145–0.223)
EL	0.287 ± 0.007 (0.279–0.291)	0.274 ± 0.01 (0.257–0.291)	0.315 ± 0.008 (0.302–0.324)	0.312 ± 0.01 (0.302–0.324)	0.146 ± 0.08 (0.128–0.291)	0.13 ± 0.01 (0.106–0.145)
EH	0.227 ± 0.02 (0.212–0.246)	0.218 ± 0.012 (0.193–0.235)	0.258 ± 0.005 (0.249–0.263)	0.251 ± 0.011 (0.235–0.263)	0.098 ± 0.01 (0.078–0.101)	0.091 ± 0.006 (0.078–0.101)
ML	**1.849 ± 0.001 (1.848–1.85)**	**1.699 ± 0.217 (1.053–1.813)**	1.81 ± 0.113 (1.617–1.935)	1.716 ± 0.069 (1.626–1.785)	0.827 ± 0.039 (0.782–0.927)	0.781 ± 0.043 (0.737–0.894)
SPSP	0.294 ± 0.02 (0.268–0.313)	0.267 ± 0.015 (0.24–0.291)	0.243 ± 0.01 (0.235–0.263)	0.226 ± 0.014 (0.212–0.246)	0.148 ± 0.013 (0.112–0.17)	0.133 ± 0.015 (0.112–0.179)
SPL	**0.216 ± 0.006 (0.212–0.223)**	**0.193 ± 0.01 (0.173–0.201)**	0.216 ± 0.011 (0.201–0.232)	0.205 ± 0.013 (0.184–0.223)	0.106 ± 0.011 (0.089–0.126)	0.099 ± 0.007 (0.089–0.112)
PEL	0.29 ± 0.02 (0.279–0.313)	0.298 ± 0.014 (0.279–0.324)	**0.32 ± 0.011 (0.302–0.335)**	**0.275 ± 0.017 (0.257–0.302)**	0.191 ± 0.014 (0.179–0.229)	0.184 ± 0.01 (0.167–0.201)
NOL	0.214 ± 0.008 (0.207–0.223)	0.225 ± 0.022 (0.179–0.256)	**0.244 ± 0.019 (0.212–0.268)**	**0.176 ± 0.018 (0.156–0.201)**	0.153 ± 0.011 (0.134–0.179)	0.144 ± 0.013 (0.128–0.168)

Table 1. Continued

	Gyne		Male		Worker	
	T. atlante	*T. semilaeve*	*T. atlante*	*T. semilaeve*	*T. atlante*	*T. semilaeve*
PPL	0.315 ± 0.011 (0.302–0.324)	0.301 ± 0.01 (0.285–0.313)	0.304 ± 0.018 (0.279–0.324)	0.287 ± 0.017 (0.263–0.302)	0.176 ± 0.007 (0.162–0.19)	0.176 ± 0.009 (0.156–0.19)
PEH	**0.458 ± 0.011 (0.446–0.469)**	**0.424 ± 0.011 (0.408–0.447)**	**0.333 ± 0.01 (0.313–0.346)**	**0.286 ± 0.022 (0.257–0.313)**	0.25 ± 0.013 (0.235–0.282)	0.239 ± 0.018 (0.212–0.291)
NOH	0.287 ± 0.025 (0.257–0.302)	0.283 ± 0.019 (0.257–0.313)	**0.206 ± 0.015 (0.19–0.235)**	**0.163 ± 0.01 (0.156–0.179)**	0.177 ± 0.016 (0.165–0.223)	0.158 ± 0.017 (0.14–0.218)
PPH	0.436 ± 0.007 (0.425–0.446)	0.423 ± 0.017 (0.391–0.447)	**0.464 ± 0.029 (0.425–0.503)**	**0.418 ± 0.015 (0.391–0.425)**	0.243 ± 0.011 (0.229–0.268)	0.228 ± 0.02 (0.201–0.291)
MW	**1.125 ± 0.01 (1.11–1.135)**	**1.069 ± 0.04 (1.0–1.141)**	1.108 ± 0.049 (1.067–1.2)	1.125 ± 0.056 (1.056–1.223)	0.471 ± 0.024 (0.441–0.531)	0.45 ± 0.027 (0.413–0.508)
PEW	0.39 ± 0.01 (0.38–0.4)	0.393 ± 0.022 (0.348–0.419)	0.36 ± 0.005 (0.351–0.366)	0.337 ± 0.023 (0.307–0.368)	0.235 ± 0.013 (0.215–0.267)	0.22 ± 0.014 (0.201–0.246)
PPW	0.488 ± 0.02 (0.475–0.508)	0.509 ± 0.019 (0.48–0.547)	0.518 ± 0.02 (0.492–0.547)	0.478 ± 0.022 (0.453–0.503)	0.261 ± 0.01 (0.246–0.285)	0.256 ± 0.018 (0.223–0.307)
CS	**1.11 ± 0.014 (1.094–1.12)**	**1.046 ± 0.032 (0.986–1.094)**	**0.765 ± 0.014 (0.742–0.785)**	**0.737 ± 0.019 (0.704–0.755)**	**0.763 ± 0.035 (0.721–0.855)**	**0.707 ± 0.036 (0.622–0.76)**
EYE	0.232 ± 0.012 (0.224–0.246)	0.235 ± 0.012 (0.219–0.251)	0.374 ± 0.002 (0.372–0.379)	0.382 ± 0.009 (0.37–0.395)	0.16 ± 0.01 (0.138–0.167)	0.155 ± 0.007 (0.143–0.166)
CL/CW	0.898 ± 0.015 (0.88–0.907)	0.917 ± 0.038 (0.882–0.985)	0.831 ± 0.004 (0.824–0.837)	0.826 ± 0.023 (0.797–0.857)	1.021 ± 0.02 (0.975–1.047)	1.042 ± 0.013 (1.015–1.075)
FR/CS	0.368 ± 0.01 (0.357–0.378)	0.377 ± 0.011 (0.36–0.393)	0.337 ± 0.01 (0.32–0.349)	0.323 ± 0.012 (0.314–0.345)	0.353 ± 0.009 (0.341–0.367)	0.358 ± 0.01 (0.345–0.378)
FL/FR	0.953 ± 0.04 (0.918–0.995)	0.978 ± 0.035 (0.913–1.027)	1.134 ± 0.06 (1.044–1.228)	1.228 ± 0.06 (1.132–1.306)	1.009 ± 0.01 (1.0–1.043)	1.025 ± 0.02 (0.996–1.066)
SL/CS	0.655 ± 0.014 (0.644–0.671)	0.686 ± 0.019 (0.654–0.717)	**0.407 ± 0.009 (0.395–0.421)**	**0.452 ± 0.015 (0.436–0.478)**	**0.703 ± 0.016 (0.672–0.741)**	**0.756 ± 0.03 (0.732–0.841)**
MW/CS	1.014 ± 0.09 (0.995–1.032)	1.024 ± 0.043 (0.94–1.088)	1.449 ± 0.06 (1.389–1.565)	1.528 ± 0.093 (1.411–1.684)	0.618 ± 0.008 (0.6–0.632)	0.636 ± 0.018 (0.612–0.682)
PEW/PPW	0.801 ± 0.014 (0.787–0.815)	0.773 ± 0.035 (0.692–0.821)	0.696 ± 0.03 (0.655–0.744)	0.705 ± 0.04 (0.668–0.767)	**0.902 ± 0.03 (0.857–0.937)**	**0.861 ± 0.033 (0.801–0.918)**
NOH/NOL	1.345 ± 0.168 (1.152–1.459)	1.266 ± 0.136 (1.094–1.587)	0.85 ± 0.093 (0.739–0.955)	0.928 ± 0.076 (0.812–1.0)	1.163 ± 0.08 (1.057–1.336)	1.1 ± 0.113 (0.929–1.298)
NOH/PEL	0.989 ± 0.08 (0.921–1.082)	0.949 ± 0.053 (0.883–1.036)	0.644 ± 0.05 (0.6–0.725)	0.595 ± 0.059 (0.517–0.668)	0.928 ± 0.05 (0.852–1.0)	0.86 ± 0.085 (0.819–1.085)
NOL/PEL	0.74 ± 0.07 (0.661–0.799)	0.755 ± 0.059 (0.63–0.847)	0.762 ± 0.044 (0.702–0.821)	0.643 ± 0.069 (0.559–0.75)	0.801 ± 0.04 (0.729–0.872)	0.784 ± 0.045 (0.705–0.871)
PEH/NOL	2.139 ± 0.03 (2.103–2.16)	1.9 ± 0.175 (1.746–2.374)	**1.372 ± 0.08 (1.25–1.476)**	**1.625 ± 0.114 (1.502–1.788)**	1.637 ± 0.08 (1.538–1.722)	1.66 ± 0.152 (1.399–1.922)
PEW/PEH	0.853 ± 0.04 (0.83–0.897)	0.931 ± 0.048 (0.818–0.971)	1.084 ± 0.05 (1.014–1.169)	1.182 ± 0.061 (1.1–1.284)	0.943 ± 0.03 (0.914–0.979)	0.926 ± 0.049 (0.805–1.0)
CS/PEW	**2.845 ± 0.106 (2.734–2.946)**	**2.62 ± 0.123 (2.475–2.879)**	2.185 ± 0.06 (2.042–2.191)	2.216 ± 0.165 (2.019–2.438)	3.245 ± 0.07 (3.14–3.351)	3.215 ± 0.089 (3.026–3.336)
CS/PPW	**2.278 ± 0.12 (2.152–2.357)**	**2.052 ± 0.085 (1.947–2.185)**	1.478 ± 0.06 (1.402–1.561)	1.558 ± 0.085 (1.443–1.652)	2.927 ± 0.08 (2.816–3.065)	2.769 ± 0.154 (2.425–3.024)
CW/MW	0.987 ± 0.02 (0.967–1.005)	1.02 ± 0.057 (0.911–1.129)	0.691 ± 0.027 (0.639–0.719)	0.719 ± 0.045 (0.639–0.783)	1.619 ± 0.02 (1.582–1.666)	1.541 ± 0.046 (1.435–1.602)
WAIST	**0.792 ± 0.035 (0.764–0.83)**	**0.871 ± 0.035 (0.817–0.918)**				

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