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HIGHLIGHTING THE ELUSIVE: NEW FINDINGS AND A REDESCRIPTION OF THE RARE ANT *LEPTANILLA PLUTONIA* LÓPEZ, MARTÍNEZ ET BARANDICA, 1994, PRESENTING MORPHOLOGICAL NOVELTIES FOR THE GENUS

SERGIO PÉREZ-GONZÁLEZ[1,*], JOSÉ M. GÓMEZ-DURÁN[2] and M. DOLORES MARTÍNEZ-IBÁÑEZ[1]

[1]*Departamento de Biodiversidad, Ecología y Evolución, Unidad Docente de Zoología y Antropología Física, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, 28040, Madrid, Spain*
[2]*Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Ctra. de La Coruña, km. 7.5, 28040 Madrid, Spain*
[*]*Corresponding author: e-mail: seper01@ucm.es*

Abstract.— *Leptanilla* Emery, 1870 includes 47 species of strictly endogean ants, distributed through Africa, Europe, Asia and Australia, characterized by many peculiarities, such as their tiny size (between 1.0–2.5 mm long), lack of pigmentation, lack of eyes and very narrow elongate bodies. Queens are apterous and dichthadiigynes. Males have wings and eyes. Their lifestyles remain virtually unknown. The Western Mediterranean region hosts a high diversity, with 9 species in north Africa and 5 in the Iberian Peninsula. Recent sampling in Central Spain (Tortuero, Guadalajara province) led to the discovery of a colony of a large-sized *Leptanilla* species. This population can be assigned to *L. plutonia*, a species known from a single worker (the holotype) until now, easily distinguished from other Iberian species by its large size. These specimens allowed for a redescription of the species, also giving the first insights into its intraspecific variability and morphological structures not mentioned in the original description, such as the presence of a secondary labrum, large apodemes in the postpetiole or a promesosternal keel, among others. The distribution range of the species is also increased, being cited for the first time outside of the type locality. An identification key to the large-sized *Leptanilla* species from Western Mediterranean region is provided.

Key words.— endemism, endogean, Formicidae, Hymenoptera, Iberian Peninsula, taxonomy

INTRODUCTION

Leptanilla Emery, 1870 (Formicidae, Leptanillinae) is a genus of ants represented by 47 described species distributed through Africa, Europe, Asia and Australia (AntCat 2019). The subfamily Leptanillinae Emery, 1910 includes 8 genera and 68 species, being one of the older groups of Formicidae (Brady *et al.* 2006, Ward and Sumnicht 2012). A sister group relationship of Leptanillinae + Martialinae to virtually all other extant ant groups is currently supported by several authors (Moreau *et al.* 2006, Rabeling *et al.* 2008,

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Kück *et al*. 2011, Branstetter *et al*. 2017, Borowiec *et al*. 2019), although was initially questioned by others (Brady *et al*. 2006, Ward 2007).

The genus *Leptanilla* shows certain peculiarities among ants. They are fully adapted to endogean lifestyle. Workers lack eyes and are unpigmented, with elongated narrow bodies of very small size, ranging between 1.0–2.5 mm long. *Leptanilla* is recognized by a distinct postpetiole, subtriangular mandible, with 2–5 teeth, an exposed antennal insertion close to the anterior margin of clypeus, pronotum and mesonotum completely separated by mobile promesonotal suture (usually deeply constricted) and slender body shape (Bolton 1990, Yamane and Ito 2001).

Queens lack eyes and wings or wing sclerites and have an enlarged petiole and gaster, a character termed 'dichthadiigyne'. Males have developed eyes and wings, the latter with venation absent or highly reduced, even to a single vein (Bolton 1990).

Their way of life remains largely unknown, however, they have been reported to be specialized predators of geophilomorph centipedes (documented for *L. japonica* Baroni Urbani, 1977 by Masuko 1989, 1990). The queens are known to feed on hemolymph produced by specialized organs of larvae (Masuko 1989), a behavior also documented in workers.

Obtaining specimens of these ants is extremely difficult, given their tiny size, relatively small colonies and endogean lifestyles (Bolton 1990). Males, capable of flight and found outside the colony, are easier to collect by a diverse range of traps, while collecting of queens and workers usually requires special techniques. Nowadays, the soil sampling procedures facilitate the captures, but often relies on indirect methods such as processing soil samples with Berlese apparatus (Baroni Urbani 1977, Bolton 1990, López *et al*. 1994, Wong and Guénard 2016, 2017, Man *et al*. 2017), whereas direct sampling is fortuitous and very rare (Zaballos and Pérez-González, pers. obs.). It has been stated that the probability of finding colonies is higher within a 50 m radius from the surroundings of water bodies (ponds, fountains, etc.) where males have been collected (Gómez-Durán 2017).

All of this makes *Leptanilla* very scarce in collections. Together with their fragility and small size, this results in a great challenge in their study. The strong bias in the findings due to differences between sexes led to a "parallel taxonomy" (Bolton 1990), where many species have been described from a single sex/caste (or even a single specimen) given the limited available material (e.g., Baroni Urbani 1977, López *et al*. 1994). This implies that the probability of synonymies between male-based species and female-based species could be expected to a certain extent, due to unawareness and potential overlap.

There are 13 species known from males only and 24 species known from workers only (AntCat 2019). Proper association between males and females (queens and workers) is highly problematic and such task is virtually impossible without DNA extraction procedures (yet it is possible, but extremely rare, to find males and females together in the field, Gómez-Durán, pers. comm.). Thus, it is strongly needed that new findings include specimens stored in ethanol (95% or higher concentration), so further molecular data could be gathered in order to elucidate the complex taxonomy of this interesting genus. So far, unequivocal association of males and females is registered only in *L. japonica* (Ogata *et al*. 1995), one species out of the 47 known for *Leptanilla*. Association of queens and workers is known in more cases, for eight species. Larvae are known in six species, in all cases associated to workers and in four of them also to queens (AntCat 2019).

The Western Mediterranean region hosts a high diversity of *Leptanilla* species (Leo and Fancello 1990, Mei 1995, Scupola and Ballerin 2009, Ward and Sumnicht 2012, Verdinelli *et al*. 2016), with five species in the Iberian Peninsula (Spain and Portugal) and nine species in the north of Africa (Morocco, Algeria and Tunisia) currently recorded. Recent sampling for endogean fauna carried out in the center of the Iberian Peninsula led to the finding of a colony of a large-sized *Leptanilla* species.

The history of the study of *Leptanilla* in the Iberian Peninsula dates back to the discovery of an unnamed species ("*L.* sp. *B*") based on a single male cited from Jaén by Baroni Urbani (1977: 479). Some years later, Tinaut (1987) cited the capture of a worker of *L. revelierii* in Granada. This species has been also recorded in Catalonia (Espadaler 1997a, Herraiz and Espadaler 2011), Málaga (Trigos Peral and Reyes López 2013) and Portugal (Espadaler *et al*. 2008, Boieiro *et al*. 2009).

In 1994, four more species were described from Spain (López *et al*. 1994): *L. zaballosi*, *L. charonea*, *L. plutonia* and *L. ortunoi*. The last however, is known from Ceuta, in north Africa and has not been recorded in the Iberian Peninsula. Of them, larval stages are known for *L. zaballosi* and *L. charonea* (Barandica *et al*. 1994). *L. charonea*, moreover, was described from workers and a queen, captured in the same sample directly digging, thus belonging to the same colony.

In 2012 another species, *L. theryi* Forel, 1903 was cited from Murcia (Catarineu and Tinaut 2012). This makes a total number of five formally described species of *Leptanilla* currently documented for the Iberian Peninsula.

However, this number is likely far from reflecting the real diversity of the group. Sporadic mentions have been recorded of several "*Leptanilla* sp." mainly

based on male specimens from Zaragoza (Espadaler 1997b), Barcelona (Espadaler and López Soria 1991, García *et al*. 2009), Almería and Murcia (Catarineu *et al*. 2017, 2018), Madrid (Nieves-Aldrey *et al*. 2003) and Jaén (Baroni Urbani 1977, Notario *et al*. 1995). Moreover, one of the authors (JMGD) has collected more than 1500 males on the Iberian Peninsula between 2013 and 2016 (Gómez-Durán 2017), and around 1000 males between 2017 and 2019 (JMGD, pers. obs.) representing a total of 11 different morphotypes. All these data suggest that a higher number of species is present in this territory, making a future revision of the genus necessary to confirm the presence in the Iberian Peninsula of *L. revelierii* and *L. theryi*, whose type localities are, respectively, Corsica and Algeria.

The newly found specimens reported here are remarkable by their large body size and have been compared to the species of similar size present in the Western Mediterranean Region: *L. ortunoi*, *L. plutonia*, *L. poggii*, *L. theryi* and *L. vaucheri*. The morphology of the new population closely matches *L. plutonia*, a species currently known from a single worker (the holotype) but unlike any other *Leptanilla* from Iberian Peninsula. These findings increase the available material of the species, allowing its redescription. A more thorough morphological analysis provides the first insights to the intraspecific variability of the species, and an increase in its range of distribution, found for the first time outside the type locality (Navas de Estena, Ciudad Real, Spain), in the region of Guadalajara (Spain).

Materials and methods

Collecting

The new population was found in the surroundings of the locality of Tortuero, Guadalajara province (Spain) during field campaigns in years 2013 and 2014 (Fig. 1). The sample included superficial and deep soil layers (horizons A and B) up to 30–50 cm deep and was processed in the field using an optimized version of the soil washing technique (Normand 1911), consisting in putting soil sample in a plastic bucket, cover with water, stirring vigorously, then letting the sample rest (so organic matter floats and the mineral part sinks), then sieving the "foam" generated in this process with a colander and storing it in a fine cloth of single-thread nylon mesh, tied into a small bag. This mesh (mesh size about 0.5 mm) allows to carefully rinse the sample, getting rid of any clay residue without losing the organic sample, resulting in a highly efficient reduction of the final sample size and weight. The fauna was extracted from the samples with Berlese apparatus (Berlese 1905). A total of 63 specimens were collected and stored in absolute ethanol.

Material from collections

To assess the identity of the new population and for comparative purposes, the holotypes of *L. plutonia* and *L. ortunoi* were consulted, deposited at Coll. Universidad Complutense de Madrid (UCME). Additional non-type specimens of *L. ortunoi* from Coll. Universidad de Córdoba (UCO) were also included. Data from other species was gathered from literature.

Morphological study

Observation and manipulation of the specimens were made using light microscopy with an Olympus SZH stereomicroscope (Germany), an Olympus BH2 (Germany) with polarized filters and an Olympus CKX31 inverted microscope (Germany).

A random sample of 20 workers was photographed in dorsal and lateral view using a Canon Eos 700D with microscope adapter. Each worker was submerged in a drop of glycerine on a microscope slide, then carefully stretched in a dorsal position and finally covered with a coverslide. To avoid damage of the specimen, the drop of glycerine was placed inside the hole of a thin plastic ring (1 mm thick, inner diameter of 13 mm) adhered to the slide. The procedure was repeated placing each specimen in a lateral position. This method allowed accurate measurements of these tiny ants, usually difficult to handle.

For a better interpretation of mouthparts, presclerites of abdominal segments III (helcium) and IV and the internal muscle insertion and apodemes, one worker was fully cleared by immersion in a solution of KOH at 10% for 24 h, later rinsed in distilled water for 30 min. Mouthparts were studied under inverted microscopy, with the cleared specimen submerged in a drop of glycerin, allowing easy changes of position for an optimal three-dimensional observation and manipulation of the structures without damage. For muscles and apodemes, the specimen was observed under light microscopy with polarized filters. For the abdominal presclerites, the petiole and postpetiole were cut transversally in the middle and the first gastral segment in the anterior part. These pieces were mounted vertically in a drop of glycerine over a microscopic slide.

The remaining specimens were kept intact, fluid-preserved in ethanol for future molecular studies after ensuring their identification.

Measurements (Fig. 2) were done after the criteria of Leong *et al*. (2018) for the following features (with exception of MPL and MPW, not used in Leong *et al*. 2018):

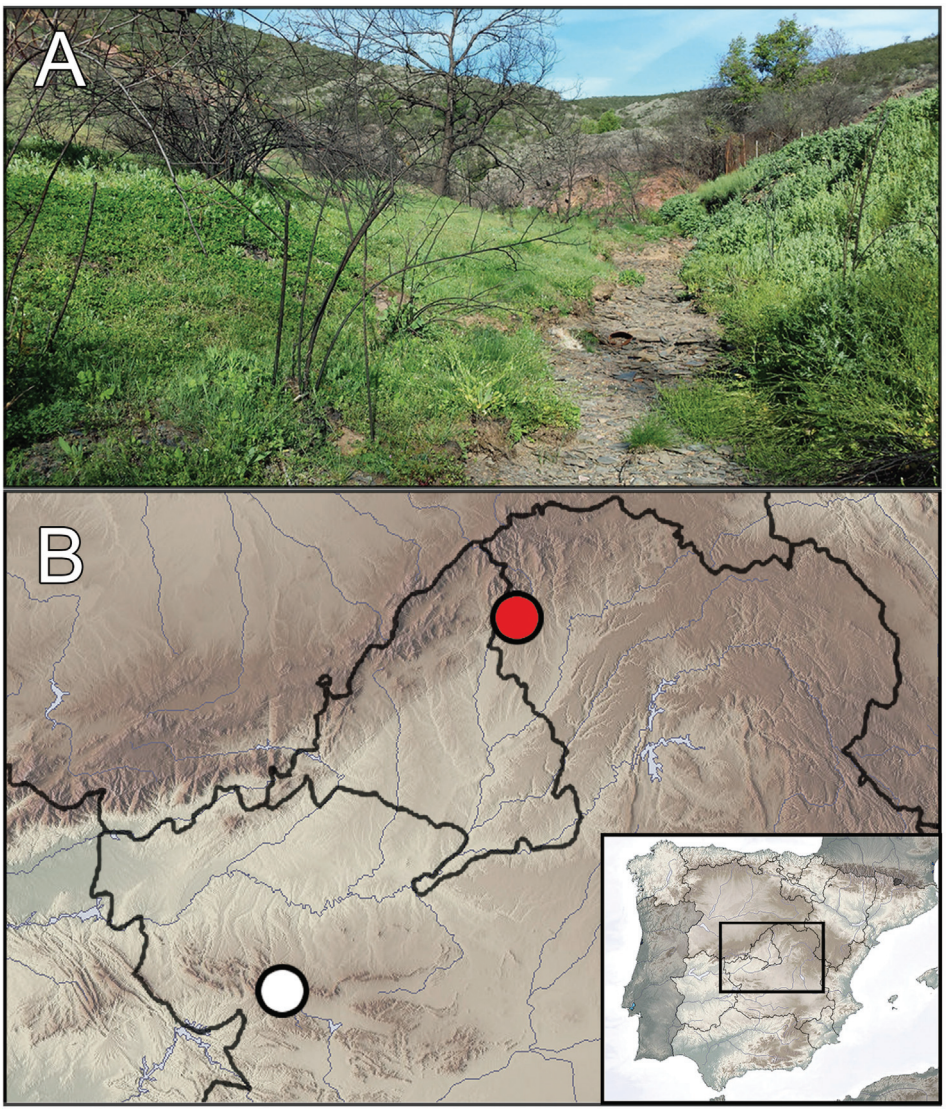

Figure 1. (A) Sample site in the locality of Tortuero where the new specimens were found. (B) Distribution map of *Leptanilla plutonia:* white dot – type locality, Navas de Estena, Ciudad Real (Spain); red dot – new locality, Tortuero, Guadalajara (Spain).

Head:

SL – scape length (straight length of first antennal segment excluding basal condyle);

HL – Head length (from the midpoint of the anterior margin of clypeus to the midpoint of the posterior margin of head, in dorsal view);

HW – head width (measured at widest region, in dorsal view).

Mesosoma:

ML – mesosomal length (from the anteriormost point of pronotum to the posteriormost point of propodeum, in dorsal view);

MPL – mesothoracico-propodeal length (from the promesonotal suture to the posteriormost point of propodeum, in dorsal view);

MPW – mesothoracico-propodeal width (maximum width perpendicular to the mesothoracico-propodeal axis);

PnW – pronotal width (measured at widest region, in dorsal view).

Metasoma:

PtL – petiole length (maximum length of petiole, in dorsal view);

PtW – petiole width (maximum width of petiole, in dorsal view);

PtH – petiole height (maximum height of petiole, from dorsalmost point of the node to the ventralmost point of the sternite, in lateral view);

PpL – postpetiole length (maximum length of postpetiole, in dorsal view);

PpW – postpetiole width (maximum width of postpetiole, in dorsal view);

PpH – postpetiole height (maximum height of postpetiole, from dorsalmost point of the node to the ventralmost point of the sternite, in lateral view);

GL – gastral length (excluding sting);

TL – total length (measured as the maximum length between the midpoint of the anterior margin of the clypeus and the tip of gaster excluding the sting, this is equivalent to HL + ML + PtL + PpL + GL, but adding also the length of the joints between segments). The reasons to keep TL measured as a whole are i) because the original descriptions of the species we are comparing with these new specimens (*L. ortunoi*, *L. doderoi*, *L. poggii*, *L. theryi* and *L. vaucheri*) use that concept of TL and ii) because the methodology used in allows a high precision in the observations and measurements, thus the obtained data can be tested from the photographs of the aforementioned 20 workers.

Indexes:

CI – cephalic index: (HW/HL) × 100;

SI – scape index: (SL/HW) × 100;

PI – petiolar index: (PtW/PtL) × 100;

PHI – petiolar height index: (PtW/PtH) × 100;

PPI – postpetiolar index: (PpW/PpL) ×100;

PHI – postpetiolar height index: (PpW/PpH) × 100.

The 20 workers were measured using the public domain software ImageJ (Rasband 1997). Non treated specimens were measured with a Wild Heerbrugg M8 stereomicroscope (Switzerland). The terminology used follows Baroni Urbani (1977) and Bolton (1990).

Specimens from collections were treated as detailed before, except the holotypes of *L. plutonia* and *L. ortunoi*, which were mounted in permanent microscopic slides, without option of further manipulation.

After observations, the specimens were stored in tubes with ethanol, were assigned voucher code and are deposited in Coll. UCME.

The description given in this work is limited to specify those features that are new or different from those stated in the original description by López *et al*. (1994), features that do not differ are not mentioned.

Results

Leptanilla plutonia López, Martínez et Barandica, 1994

Type material. Holotype, worker, Navas de Estena, UTM 30SUJ77, Ciudad Real, SPAIN, 10-5-1988, 690 m, V. Ortuño leg. (Coll. UCME).

Additional, new material examined. 60 workers, Tortuero (0,4 km, SW) (40°56'N, 03°21'W), Guadalajara, SPAIN, 29-04-2014, 912 m, J.P. Zaballos and S. Pérez leg. (Coll. UCME); 3 workers, Tortuero (2 km, SW) (40°55'N, 03°21'W), Guadalajara, SPAIN, 4-06-2013, 894 m, J.P. Zaballos and S. Pérez leg. (Coll. UCME).

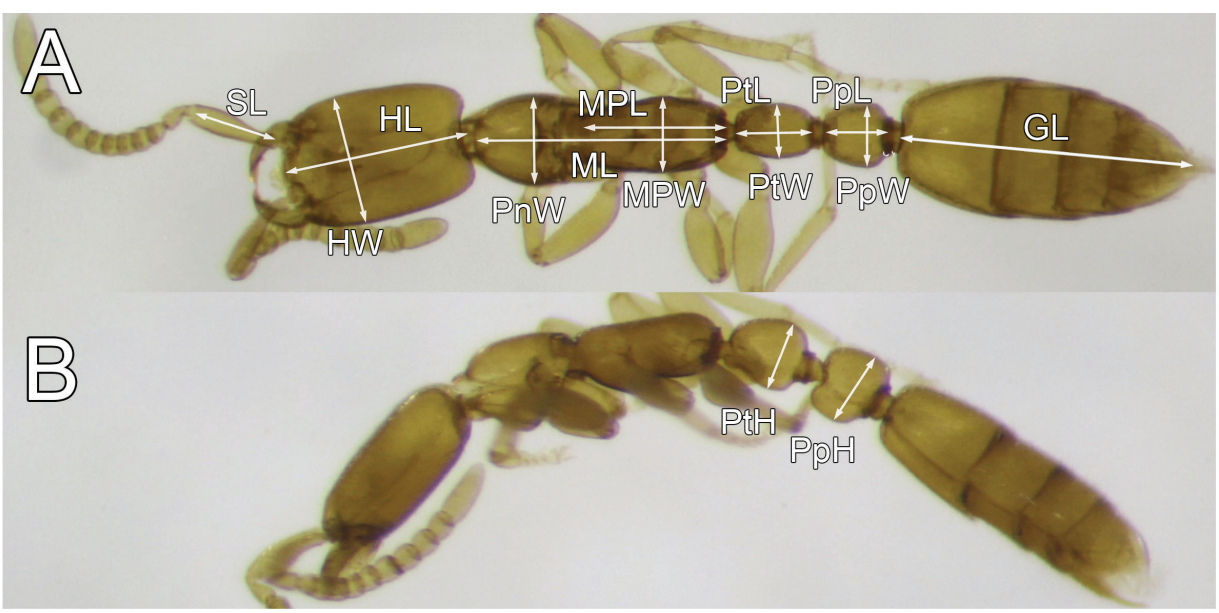

Figure 2. Measurements taken in this work (after Leong *et al*. 2018). (A) Dorsal view. Head: SL – scape length; HL – Head length; HW – head width. Mesosoma: ML – mesosomal length; MPL – mesothoracico-propodeal length; PnW – pronotal width; MPW – mesothoracico-propodeal width. Metasoma: PtL – petiole length; PtW – petiole width; PpL – postpetiole length; PpW – postpetiole width; GL – gastral length. TL – total length measured as HL + ML + PtL + PpL + GL, adding the length of the joints between segments. (B) Lateral view. PtH – petiole height; PpH – postpetiole height.

Measurements (mm) and indexes. Workers (n=20): HL: 0.32–0.36; HW: 0.23–0.27; SL: 0.16–0.18; PnW: 0.16–0.18; MPL: 0.25–0.29; MPW: 0.14–0.15; ML: 0.43–0.52; PtL: 0.13–0.16; PtW: 0.10–0.11; PtH: 0.12–0.14; PpL: 0.12–0.14; PpW: 0.12–0.14; PpH: 0.14–0.16; GL: 0.52–0.66; TL: 1.68–1.91; CI: 68–72; SI: 64–72; PI: 66–77; PHI: 73–86; PPI: 92–111; PPHI: 80–97.

Diagnosis of worker. Large sized *Leptanilla*, up to 1.91 mm long, yellowish–caramel color (Fig. 3), recognizable by the following combination of features: head with smoothly convex lateral sides and occiput almost straight on average; covered in a single type of long pilosity; labrum bilobate with secondary labrum associated. Profile of propodeum convex, petiole clearly longer than wide, postpetiole as long as wide. Petiole and promesosternal region each with a well-developed ventral keel or process. Sting visible in dorsal view.

Description. **Head.** Lateral margins of cephalic capsule smoothly convex, occiput ranges from straight to moderately concave. Labrum markedly bilobate. The lobes, separated by a deep medial notch, diverge about 60°, the outer margins are straight or slightly concave and the inner margins are convex in their posterior half, with the distal ends pointing apicolaterally. Each lobe has, at least, 2 large setae (Fig. 4A). At the suture between labrum and clypeus there is another thin lamina, also bilobate and resembling a "secondary labrum", with lobes diverging 120° and laterally standing out from the lobes of labrum (Fig. 4A). Mandibles show more than three long setae at the inner margin: four long setae along the margin and a central seta (Fig. 4B–C). Labial and maxillary palpi formed by a single segment, each with 3 long apical setae (Fig. 4D). In both labial palpi, there is a digitiform sensillum (*sensu* Hashimoto 1991, 1992) under the setae, in the lateral surface of the palpi. Internal antennal sensilla: apical antennomere with a pattern of 2 *sensilla ampullacea* and 1 *sensillum coeloconicum*, in the posterior half

Figure 3. Habitus of *Leptanilla plutonia*, worker. (A) Lateral view. Arrows indicate the promesosternal and subpetiolar keels. (B) Dorsal view.

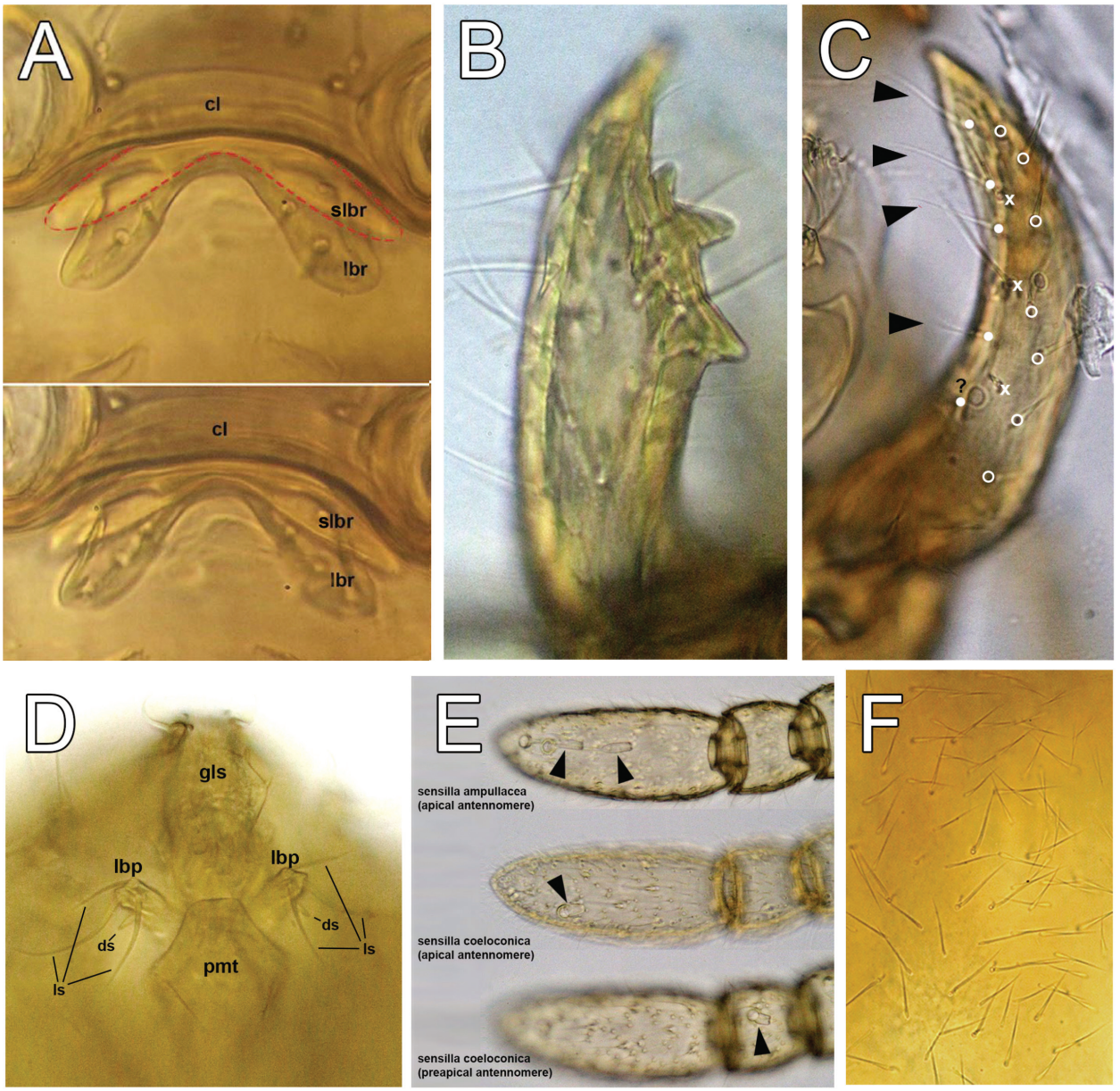

Figure 4. Cephalic structures of *Leptanilla plutonia*. (A) Labrum and secondary labrum, cl – clypeus, lbr – labrum, slbr – secondary labrum; (B) Left mandible, showing the four teeth; (C) Right mandible, showing the setae: black arrowheads – intact setae of the inner margin; full circles– base of the setae in the inner margin (inner row); x – base of the setae of the second row; hollow circles – base of external setae; (D) Mouthparts, ventral view, gls – glossa, pmt – prementum, lbp – labial palpi, ds – digitiform sensilla, ls – long setae; (E) Antennal sensilla: different views of the last antennomere showing the patterns of sensilla ampullacea and sensilla coeloconica; (F) Pilosity of cephalic capsule.

of the antennomere; preapical antennomere with 1 *sensillum coeloconicum* (Fig. 4E). Cephalic capsule covered by a single type of scarce, long pilosity (Fig. 4F). Rest of features as described by López *et al*. (1994).

Mesosoma. There is a large promesosternal "keel", visible in lateral view (Fig. 5A), covered by coarse microsculpture giving the structure a serrate appearance. Mesopleura with a noticeable irregular reticulate microsculpture (Fig. 5B). Rest of features as described by López *et al*. (1994).

Legs. Basitarsus of the first pair of legs projected (Fig. 5C). Arolium present (Fig. 5D) in the tarsi of the three pairs of legs. Rest of features as described by López *et al*. (1994).

Metasoma. General shape in dorsal and lateral view of petiole and postpetiole as described by López *et al*. (1994) (Fig. 6A, F–I), but in dorsal view the anterior

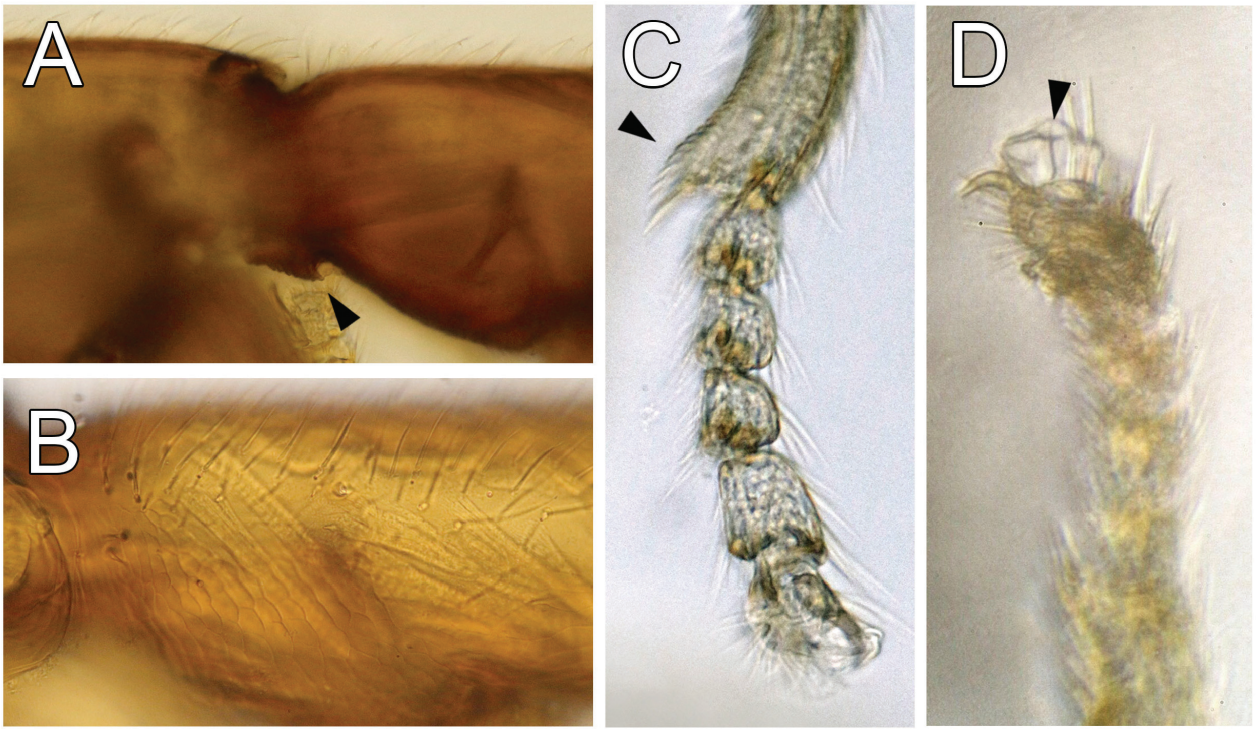

Figure 5. Thoracic structures of *Leptanilla plutonia*. (A) Detail of promesosternal keel (lateral view); (B) Detail of mesopleural microsculpture; (C) Tarsus of the first pair of legs, black arrowhead indicates the projected basitarsus; (D) Detail of the arolium.

margin of petiole is straight, not emarginate in any of the new specimens. Sagittal view of petiole with an "inverted tear" shape, postpetiole more rounded, larger and "pumpkin-shaped", showing tergosternal constriction (Fig. 6B, D). Petiole with a clearly visible, strong keel (= subpetiolar process, *sensu* Leong *et al*. 2018), also covered by coarse microsculpture giving the structure a serrate appearance (Fig. 6F–G). Postpetiole with strong apodemes, visible by transparency (Fig. 6H–I). These structures are convex and long, about 2/3 of the total length of postpetiole. Apodemes start at the anterolateral corners of the presclerite of IV abdominal segment and end by the suture of the tergosternal joint of postpetiole. Each apodeme supports the insertion of a muscle connected to presclerite IV. The other muscles of the postpetiole are inserted in the inner walls or come from helcium, also going to presclerite IV. The helcium is pseudo-annular (Fig. 6C), with tergosternal fusion. Presclerite IV (slightly bigger) is ring-shaped (Fig. 6E), with pretergite and presternite articulated, not fused; internally it presents diverse ridges where several muscles are attached. Gaster and sting as described by López *et al*. (1994).

Habitat. The locality where the new specimens were found is in the slopes of a low hill system, close to the road that goes out the village of Tortuero (Fig. 1). The main vegetation was composed by patches of oak forest (*Quercus faginea* Lam.), with scattered hawthorns (*Crataegus monogyna* Jacq.), wild roses (*Rosa canina*, L.), rockroses (*Cistus* sp. L.) and lower herbaceous vegetation. The lower part of the slope included the dry bed of an intermittent stream, where long grasses and rushes (*Juncus* sp. L) were also abundant.

The soil sample (a 30 kg sac) was taken near the slope of the streambed, near hawthorn and rockrose bushes. The soil was reddish, rich in clay, fresh and moist, with plenty of flat slate fragments of different sizes.

DISCUSSION

These ants are well known by their fragility and scarce numbers of specimens usually available for studies. Their way of life makes them very elusive and captures are very rare and fortuitous. The chance of having more than 50 specimens to study is very unusual and allowed to apply different techniques, novel for Leptanillinae, leading to the observation of new or obscure morphological features that could not be studied otherwise, because they need an adequate treatment of specimens, usually not applied due to the associated risks of manipulating unique specimens.

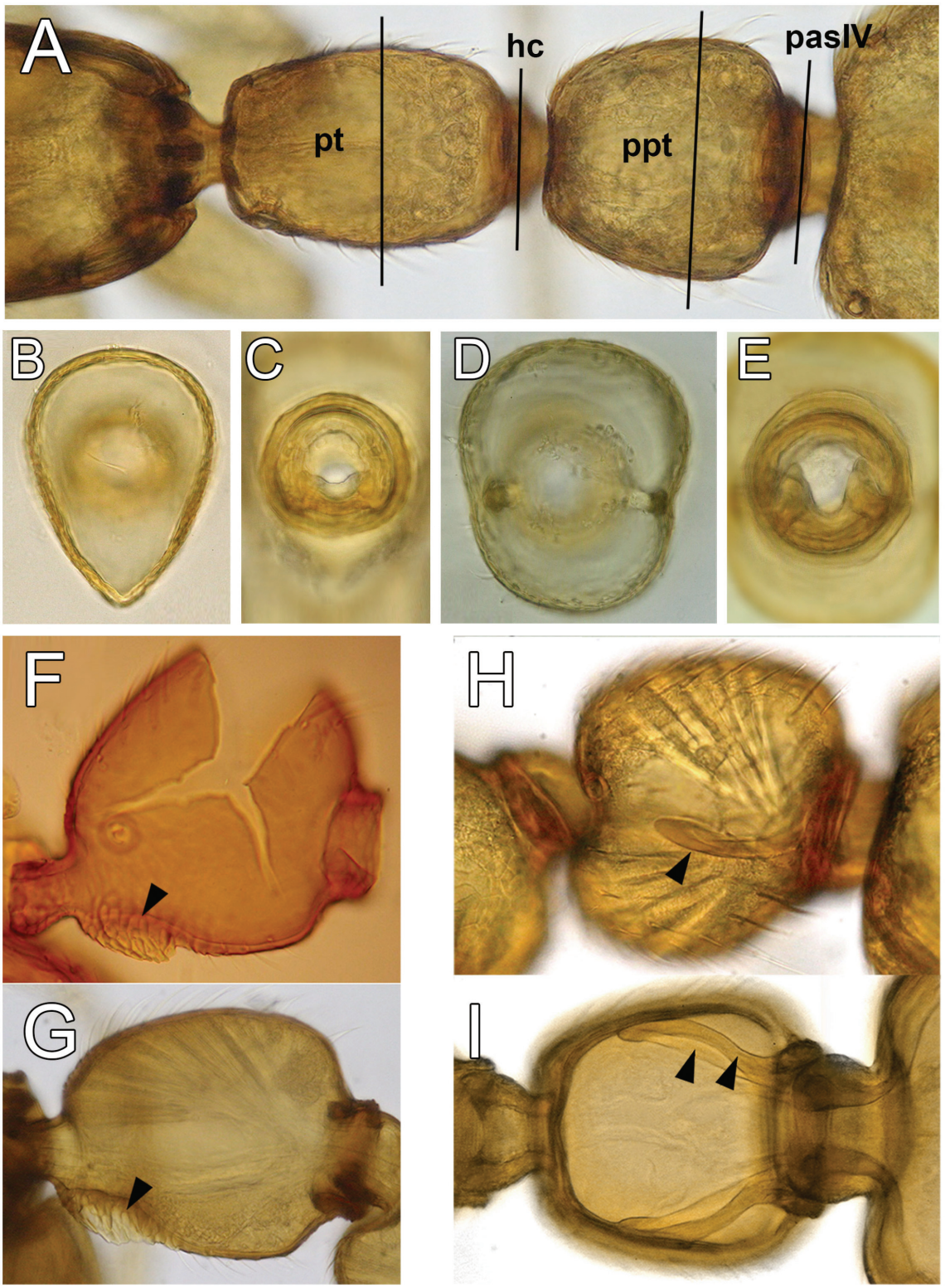

Figure 6. Abdominal structures of *Leptanilla plutonia*. (A) Dorsal view of petiole and postpetiole, pt – petiole, hc – helcium, ppt – postpetiole, pasIV – presclerite of abdominal segment IV; lines indicate the cross sections in B–E; (B) Cross section of petiole; (C) Cross section of helcium; (D) Cross section of postpetiole; (E) Cross section of presclerite of abdominal segment IV; (F–G) Petiole in lateral view: (F) holotype, (G) specimen from Tortuero. Black arrowhead indicates subpetiolar keel; (H–I) Pospetiole: (H) detail of lateral view, (I) inner parts, in dorsal view. Black arrowheads indicate the apodeme (darker part) and the attached muscle (clearer part).

Figure 7. Photograph of the holotype of *Leptanilla plutonia* as currently preserved (photo taken in 2019). Note that body parts are not articulated and many show signs of damage.

Differences with the original description

Leptanilla plutonia has been known from a single worker for more than 20 years. However, after the original study by López *et al*. (1994) the holotype was mounted in Hoyer liquid as a permanent slide and suffered some damage in the process (Fig. 7).

Fortunately, the original description is well detailed and allowed to identify the new population as *L. plutonia*, and their study revealed the appearance of several traits that were not mentioned by López *et al*. (1994) and could not be reevaluated in the holotype because they are damaged or not visible. Larvae and other castes (queen and males) are still unknown.

Most of these traits that increase the morphological knowledge of *L. plutonia* were very small structures of mouthparts, legs and integument, observed by detailed microscopic observation. Another important novelty from the original description is the record of the intrapopulation variability for this species. Some features were confirmed to be diagnostic for *L. plutonia*, while others like the shape of cephalic capsule, the occiput or the number of certain setae, were observed to slightly vary within a colony.

This led to the redefinition of the diagnostic features for *L. plutonia* and is a good reminder of the importance, in taxonomy, of periodically revisiting the knowledge in already described species. Re-examination of the type specimens in collections under new observational techniques and the eventual access to new specimens give new information that often provides valuable additions for the taxonomy of a group.

New morphological structures

Among the newly observed features, the most significant are: the sensilla of antennae and labial palpi, the labrum, the apodemes, the promesosternal keel, the cross sections of petiole and postpetiole and the presence of a developed arolium in all legs.

In Leptanillinae, antennal sensilla have been recorded mainly in larvae, where several authors refer to the presence of 2 sensilla, but their type is not specified (Wheeler and Wheeler 1965, 1988, Barandica *et al*. 1994, Brady and Ward 2005). For adults, Hashimoto (1990, 1991) recognized 5 types of sensilla in the antennae of *Leptanilla japonica* Baroni Urbani, 1977: *sensilla trichodea curvata*, *s. basiconica*, *s. trichodea* (referred as *s. chaetica* by author), *s. coeloconica* and *s. ampullacea*. The two latter, *s. coeloconica* and *s. ampullacea* are located in chambers inside the antennal cuticle and are of special interest in *Leptanilla* given their large size with respect to other sensilla (Fig. 4D), their scarce number and distinctive patterns in the two apical segments of the worker's antennae. *Sensilla ampullacea* have been assigned as CO_2 and heat receptors (Kleineidam *et al*. 2000, Kleineidam and Tautz 1996); *s. coeloconica* have been referred as thermoreceptors (Rutchy *et al*. 2009). The pattern found in the new specimens of *L. plutonia*, (2 *s. ampullacea* and 1 *s. coeloconicum* in the last antennomere and 1 *s. coeloconicum* in the preapical antennomere) has been corroborated also in workers of other three species of *Leptanilla* from Spain (*L. charonea*, *L. zaballosi* and an undescribed species, pers. obs.), suggesting this pattern could be relatively constant within the workers of *Leptanilla*.

So far, sensilla of labial and maxillary palpi in *Leptanilla* have been described in larvae of several species (Wheeler and Wheeler 1965, Barandica *et al*. 1994) and in the workers of *Leptanilla japonica* (Hashimoto 1991, 1992). Here, we record this feature for the first time in workers of *L. plutonia*.

The bilobate labrum is common within Formicidae (Gotwald 1969, 1970, 1973), ranging in a wide spectrum of shapes, from rounded to peglike, or sharp and spikey and is often overlooked in descriptions. The presence of a "secondary labrum" as seen in *L. plutonia* (Fig. 4A) has never been registered in ants and implies a morphological novelty that would need further study in other species. The function of such structure remains unknown.

Plate-like ventral keels are not uncommon within the genus, and they have been often described in the ventral surface of petiole (e.g., López *et al*. 1994). This structure resembles a "hook" in lateral view, and the coarse microsculpture of the cuticle gives it a serrated/dentated look (Fig. 6F–G). Its function remains unknown, and, while it is known to vary within species (e.g., AntWeb 2019), this data is not registered systematically and sometimes is mentioned in the descriptions, sometimes not, but usually no mention of its shape or size is given. It seems, however, that it might be in correlation with body size (pers. obs.), and in *L. plutonia* is strongly developed.

The new specimens also show another plate-like keel, very similar to that of the petiole, but located in the ventral surface of promesosternal region. This feature, hence called promesosternal keel/process, was not registered in the original description and it is not mentioned in any other species of *Leptanilla*, but can be seen in *Leptanilla macauensis* (Leong *et al*. 2018: Fig. 8). However, its presence suggests that ventral keels might be prone to develop in the ventral surface of thorax and petiole, probably associated to a specific, yet unknown function, like stridulation, protection or mechanic attachment.

The cross sections of petiole and postpetiole have not been used in descriptions of *Leptanilla* species and they have not been properly illustrated or compared. The techniques used in this work with the

workers of *L. plutonia* allow generating good quality photographs of this frontal view (Fig. 6B–E), very difficult to observe. These techniques could be applied in other species to evaluate how the shape of petiole and postpetiole, in particular the tergosternal joint, vary within the genus.

The conspicuous apodemes observed in the postpetiole of *L. plutonia* (Fig. 6H–I) are probably associated with the ability to move the abdomen and might show different development/shape in species of different size. It could be noteworthy to register this structure in other species of *Leptanilla*, to see whether, as in the case of the tentorium (López *et al*. 1994), it shows any potential taxonomic variation.

Freeland *et al*. (1982) reported the absence of arolium in the workers of *Leptanilla escheri* (Kutter, 1948), and generalized that this structure might be absent in Leptanillinae as a result of their full adaptation to endogean lifestyles. Later, Keller (2011) mentioned the presence of this structure in the workers of *Leptanilla swani* Wheeler, 1932. In the workers of *L. plutonia*, the arolium is present in all legs (Fig. 5D), supporting the idea that arolium has not disappeared within Leptanillinae, yet it is possible that in certain species the structure might be reduced or even absent.

All these features can be useful either for the diagnosis of *L. plutonia* and for differentiating species of *Leptanilla*. Hence, it becomes necessary to take in account these features in future descriptions and revise throughout the genus. The results shown in this work suggest that the morphology of *Leptanilla* species is way more varied than previously known, increasing the number of available taxonomic traits for these elusive ants.

Affinities with other species of *Leptanilla*

Leptanilla size range is quite large, with species ranging from 1.0 mm to 2.5 mm long. The workers found in Tortuero can be considered large within the genus, with an average length of 1.8 mm. The large sized species from Western Mediterranean region (over 1.5 mm long, *sensu* López *et al*. 1994) are: *L. doderoi*, *L. theryi*, *L. plutonia*, *L. ortunoi*, *L. poggii* and *L. vaucheri*. All of them share a deep and well-marked promesonotal furrow.

All the morphological evidences indicate that the specimens from Tortuero are conspecific with the type of *L. plutonia* and can be clearly differentiated from the other large sized species.

L. vaucheri Emery, 1899, from Morocco, is immediately recognized from any other species by a narrow and pear-shaped petiole in dorsal view (Baroni Urbani 1977).

L. poggii Mei, 1995, from the islands of Pantelaria and Sicily (Italy) (Mei 1995, Schiffani 2018), is also well differentiated as the only species with two different types of pilosity on the cephalic capsule, with long and short setae interspersed instead of a single type of setae as in the other species.

L. doderoi Emery, 1915, from Sardinia has a strongly punctured propodeum, much more pronounced and crowded relative to other parts of the body (Baroni Urbani 1977). *L. doderoi* has been synonimized with *L. revelierii* by Baroni Urbani (1977) but Leo and Fancello (1990) recognized it as a valid species. The punctured propodeum does not appear in any of the other species and is also a clear difference from the otherwise similar *L. theryi* Forel (1903), cited from Algeria (workers), Tunisia (queen and workers), and Spain, in Murcia (Catarineu and Tinaut 2012).

L. theryi resembles and it is probably closely related to the other two large-sized species from the same distribution range: *L. ortunoi* (Ceuta, north of Africa) and *L. plutonia* (center of the Iberian Peninsula) (Fig. 8). According to López *et al*. (1994) it can be distinguished from both by a protuberance in tentorium; the shape of the occiput, referred as concave for *L. theryi* (Baroni Urbani 1977) and straight for *L. ortunoi* and *L. plutonia* (López *et al*. 1994); a long apical seta in the inner part of each mandible; a deeper promesonotal sulcus; basitarsus of the first pair of limbs with a projection in the ventral anterior margin; less protruding katepisternum; rounder petiolar and postpetiolar nodes, with anterior margin not emarginate; anterior dorsal margin of petiolar node more rounded in lateral view; lack of ventral keel in petiole; anterior dorsal margin and posterior ventral margin of prothorax and ventral area of petiole stem with microsculpture forming a serrated ridge. The pilosity is much more scarce than in *L. plutonia* and *L. ortunoi*.

However, most of these features turned out to be problematic for identification purposes: the appearance of the occiput and some other structures, including the tentorium, is very susceptible to be altered by subtle differences in the transparency and position of a specimen. The new specimens of Tortuero have shown certain variability in the shape of the occiput, ranging from straight to slightly concave occiputs within the same population. These observations and the fact that of the two photographs available of the types of *L. theryi* (AntWeb 2019), the concave occiput is only visible in one, suggest caution when using this feature as a diagnostic trait to identify species. The long mandibular seta and the projection in the basitarsus of the first limbs are also difficult to observe at a first glance, but appear to be present in *L. plutonia* as well, when observed under well-prepared microscopy techniques (Figs 4C, 5C). The anterior margin of petiole in the specimens of Tortuero is also akin to the shape

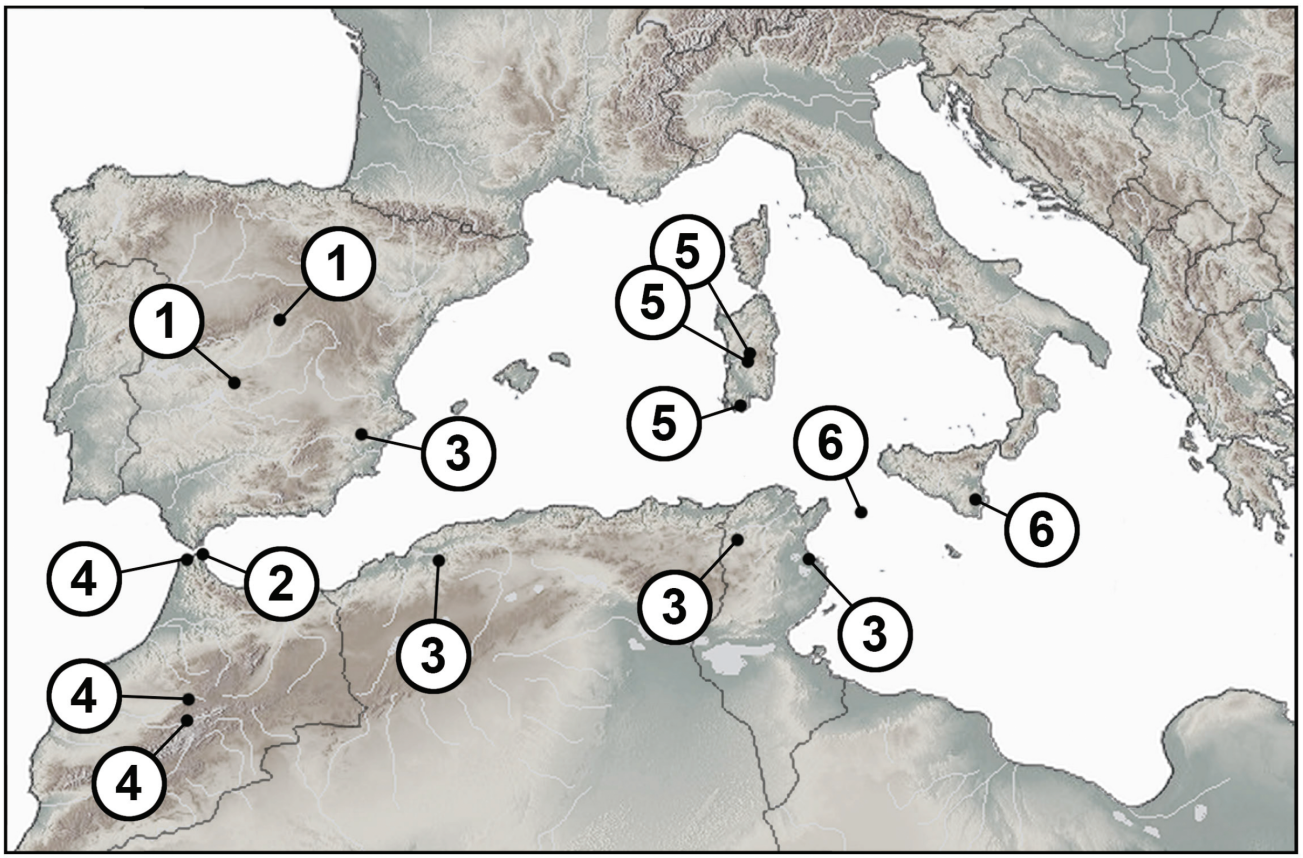

Figure 8. Distribution map of the large-sized *Leptanilla* species found in the Western Mediterranean region (after AntMaps 2019). (1) *L. plutonia*; (2) *L. ortunoi*; (3) – *L. theryi*; (4) – *L. vaucheri*; (5) – *L. doderoi*; (6) – *L. poggii*.

described for *L. theryi*, with no emargination, and, about the ventral keel, one of the photographs of a type of *L. theryi* available in AntWeb (2019) suggests this structure is indeed present in the species. The "serrated effect" of the microsculpture seems to be frequent within *Leptanilla* (JMGD, pers. obs.).

In summary, the main differences between *L. theryi* and *L. plutonia* can be seen in the petiole, subquadrangular in dorsal view, almost as long as wide in *L. theryi*, while in *L. plutonia* it is clearly longer than wide in all the observed specimens. Also, *L. theryi* is slightly smaller (average length of 1.5 mm) than *L. plutonia* (average length of 1.8 mm).

Finally, *L. ortunoi* is easy to differentiate from both, *L. theryi* and *L. plutonia* by the shape of propodeum in lateral view, clearly angulate and smoothly inclined downwards, much flatter than in the other two species. *L. ortunoi* is also smaller (length of 1.6 mm) than *L. plutonia*, within the same size range as *L. theryi*. In the original description, *L. ortunoi* and *L. plutonia* are differentiated as well by the number of setae in the mandible (3 in *L. plutonia*, 4 in *L. ortunoi*), however, the new specimens do not support this difference.

Identification key for workers of large-sized (body length over 1.5 mm on average) species from Western Mediterranean region

1. Narrow petiole, pear-shaped in dorsal view ..... ***L. vaucheri***
–. Petiole not narrow or pear-shaped **2**
2. Propodeum angulate with distinct dorsal and posterior face ..... ***L. ortunoi***
–. Propodeum roundly convex in lateral view **3**
3. Propodeum strongly punctate, more pronounced and tightly spaced than on other body parts ..... ***L. doderoi***
–. Propodeum without this punctation pattern **4**
4. Two types of pilosity in cephalic capsule (long and short) ..... ***L. poggii***
–. One type of pilosity in cephalic capsule (long) **5**
5. Petiole "stout", roughly quadrangular in dorsal view, slightly longer than wide, PI: 84.6–100; average length 1.5 mm ..... ***L. theryi***
–. Petiole "slender", clearly longer than wide, PI: 66–77; average length 1.8 mm ..... ***L. plutonia***

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