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New record of *Epistylis hentscheli* (Ciliophora, Peritrichia) as an epibiont of *Procambarus* (*Austrocambarus*) sp. (Crustacea, Decapoda) in Chiapas, Mexico

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Abstract

Epibiosis is very common between crustaceans and ciliates where the calcified surface of the crustacean body provides a suitable substrate for ciliate colonization. The aim of this contribution is to provide data about a new record between the epistylid ciliate *Epistylis hentscheli* Kahl, 1935, and the crayfish *Procambarus* (*Austrocambarus*) sp. The distribution of the epistylid on the basibiont body and its cellular/colonial characteristics were analyzed. *Procambarus* (*Austrocambarus*) sp. harbored colonies of *E. hentscheli* only on the pereiopods. This is the first record of this peritrich ciliate as an epibiont on Crustacea, having been previously found on algae and fish.

Keywords

ciliate, colonies, epibiosis, epistylid, Montebello

Introduction

Epibiosis is a facultative and interspecific association between two organisms, the epibiont and the basibiont, the latter providing a substrate for the attachment of the former (Wahl 2008). The basibionts are usually significantly larger than epibionts, have body surfaces that are physiologically inactive, and are sessile or slow-moving (Threlkeld et al. 1993; Wahl and Mark 1999). Epibiosis is a continuous and dynamic process in which the benefits and costs for basibionts and epibionts can change depending on environmental conditions (Fernandez-Leborans 2010).

Epibiotic associations between crustaceans and ciliates are very common, since the calcified surface of the crustacean functions as a semi-permanent substrate, providing an optimal habitat for epibionts ciliates, especially in those areas where other substrates are not suitable for long-term colonization (Fernandez-Leborans 2010). Among the ciliate epibionts of crustaceans, the Peritrichia (Fernandez-Leborans and Tato-Porto 2000a), Suctoria (Batisse 1994; Fernandez-Leborans and Tato-Porto 2000b) and Chonotricha (Fernandez-Leborans 2010) are the most commonly reported. Regarding the 13 species of the sessilid peritrich genus *Epistylis* (Table 1), so far there have been no reports of *E. hentscheli* as epibiont of crustaceans.

Ciliates of the genus *Epistylis* include colonial organisms with a non-contractile and branched stalk; each zooid has a well-defined peristomial lip and epistomial disc in the oral region, being the zooids elongated and generally in the shape of a vase (Lynn 2008). *Procambarus* (*Austrocambarus*) sp., a member of the family Cambaridae, is a freshwater decapod inhabiting dams, streams, and rivers. Species of this genus are considered important macro- invertebrates in temperate and tropical areas, participating in maintaining the balance in the food chain through the processes of degradation of the organic matter of the systems (Álvarez et al. 2012; Yazicioglu et al. 2016). The crayfish can represent up to 85% of the zoobenthic biomass, are considered strong engineers of the ecosystems, and can be considered as ecological regulators (Veselý et al. 2015).

The goal of this contribution is to provide data of *E. hentscheli* and its distribution on the body of the crayfish *Procambarus* (*Austrocambarus*) sp., including some cellular/colonial characteristics of the epistylid.

Materials and methods

Sampling. Specimen of *Procambarus* (*Austrocambarus*) sp. were collected in an artificial pond of Montebello Chiapas, Mexico [16°04.40N, 91°37.40W (DDM)], 1,507 m above sea level, during the rainy and dry seasons in years 2014–2015, being the mud and clay the principal substrate. Collections during the rainy season and the dry season were performed every three months, and in each sampling the following physical and chemical parameters were measured: water temperature, conductivity, and pH by a YSI model 85 multiparameter sonde and dissolved oxygen concentration was measured with an oximeter YSI model 55/12.

Technique procedures. Crustaceans were transported alive to the Protozoology laboratory (Faculty of Sciences, Universidad Nacional Autónoma de México, Mexico City),

Table 1. Species of the genus *Epistylis* reported previously as epibionts of freshwater decapods.

Decapod host	Ciliate species	Infected body regions	Sources
***Pontastacus leptodactylus* Eschscholtz, 1823**	*Epistylis* sp.	Antennae Carapace Pleopods Telson Uropods Gills	Zaikov et al. (2000), Harlioglu (1999), Hüseyin and Selcuk (2005), Nekuie et al. (2015)
	E. niagarae Kellicott, 1883		
	E. chrysemidis Bishop & Jahn, 1941		
	E. astaci Nenninger, 1948		
	E. cambari Kellicott, 1885		
	E. crassicollis Stein, 1867		
***Astacus astacus* Linnaeus, 1758**	*E. astaci*	Rostrum Antennules Antennae	Fernandez-Leborans and Tato-Porto (2000a)
	E. bimarginata Nenninger, 1948		
	E. crassicollis		
***Cherax tenuimanus* Smith, 1912**	*Epistylis* sp.	Pereiopods	Villarreal and Hutchings (1986)
***Cambarellus patzcuarensis* Villalobos, 1943**	*E. bimarginata*	Uropod Antennules Rostrum Gill Pereiopods Pereiopod Uropod Telson	Mayén-Estrada and Aladro-Lubel (2001)
	E. branchiophila Perty-Stein, 1859		
	E. carinogammari Stiller, 1949		
	E. gammari Precht,1935		
	E. lacustris Imhoff, 1884		
	E. niagarae		
	E. stammeri Nenninger, 1948		
	E. variabilis Stiller, 1953		

and maintained alive in aquaria. Specimens were later dissected to separate the telson, pleopods, pereiopods, carapace, chelipeds, antennae, eyes, gills, and mouthparts. Peritrichs were observed with a Nikon stereoscopic microscope (SMZ 800). Photomicrographs and morphometric records were obtained using a Nikon digital camera (Digital Sight DS2Mv) adapted to a Nikon microscope (Labophot2/AX70).

Ciliates were fixed in 70% alcohol, to reveal their cellular structure with the pyridine silver carbonate technique (Fernandez-Leborans and Castro 1986), and the protargol impregnation technique (Foissner 2014). Peritrichs measurements were obtained from live and stained individuals and included: length and width of the zooid, macronucleus, stalk and also width of the peristomial collar. *Epistylis hentscheli* was identified based on morphological characteristics described by Foissner et al. (1992), including the measurements of length and width of the zooids, and the width of the peristomial collar. Main morphological features of this species include the shape of the zooids and tall of the entire colony.

Results

The physical and chemical parameters data recorded during the dry (DS) and rainy season (RS) of the pond, which were measured each three months were: temperature (DS: 18.7 °C ± 2.1, RS: 21.2 °C ± 1.8), pH (DS: 7 ± 0.5, RS 6 ± 0.4) conductivity (DS: 321 µS ± 56, RS: 243 µS ± 64), and dissolved oxygen (DS: 7.46 mg/L ± 0.9, RS:8.85 mg/L ± 0.87).

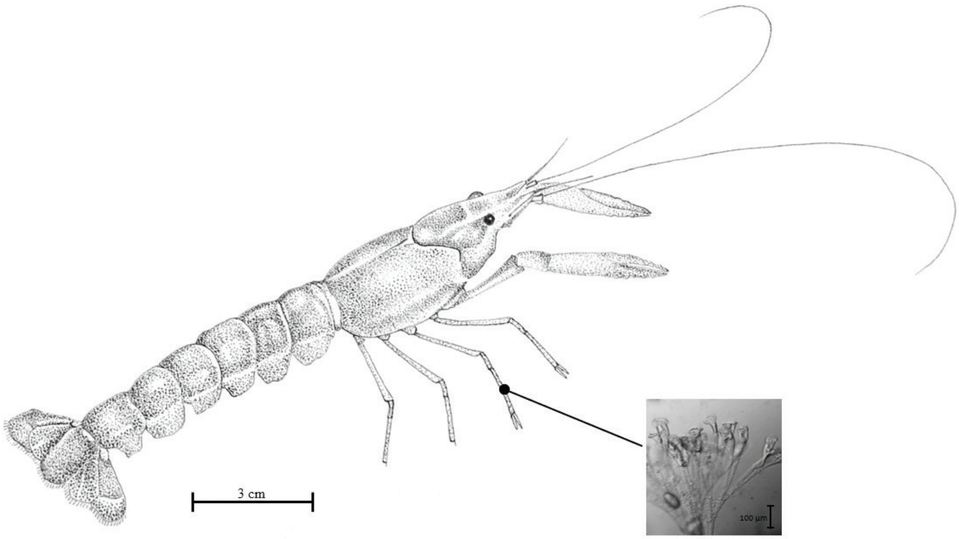

Figure 1. *Procambarus* (*Austrocambarus*) sp. from Montebello, Chiapas, Mexico. Dorsal view. Colonies of *Epistylis hentscheli* are shown.

Ninety-six crayfish specimens were collected, 46 in the dry season and 50 in the rainy season. *Epistylis hentscheli* was recorded only during the dry season of year 2015 on 36 individuals of the crayfish (prevalence of 78%), and only on pereiopods, between the merus and the carpus (Figure 1); the number of colonies on individual crayfish varied between one and three.

Forty colonies of *E. hentscheli* with 20–30 zooids were observed with a dichotomously branched pattern, with a long and rigid main stalk that contained peripheral fibers arranged longitudinally (Figure 2E). The observation of 38 zooids in vivo showed uncontracted and trumpet-shaped zooids (Figure 2A, B), with a peristomial disc slightly raised above the peristome; and with the infundibulum reached more than half the length of the zooid (Figure 2B). The single contractile vacuole was located above the C-shaped macronucleus (Figure 2B, D).

From stained zooids we observed one spherical micronucleus located close to the central macronucleus (Figure 2G). The oral infraciliature comprised the haplokinety and polykineties running parallely, which made approximately one and a quarter turns around the peristomial disc. At the opening of the infundibulum the haplokinety separated from the polykinety (Figure 2H–I). Biometric data of *E. hentscheli* are shown in Table 2.

Discussion

The current study represents the first ever record of *Epistylis hentscheli* as an epibiont of Crustacea. Some ciliate species have been recorded on decapods in Mexico (López-

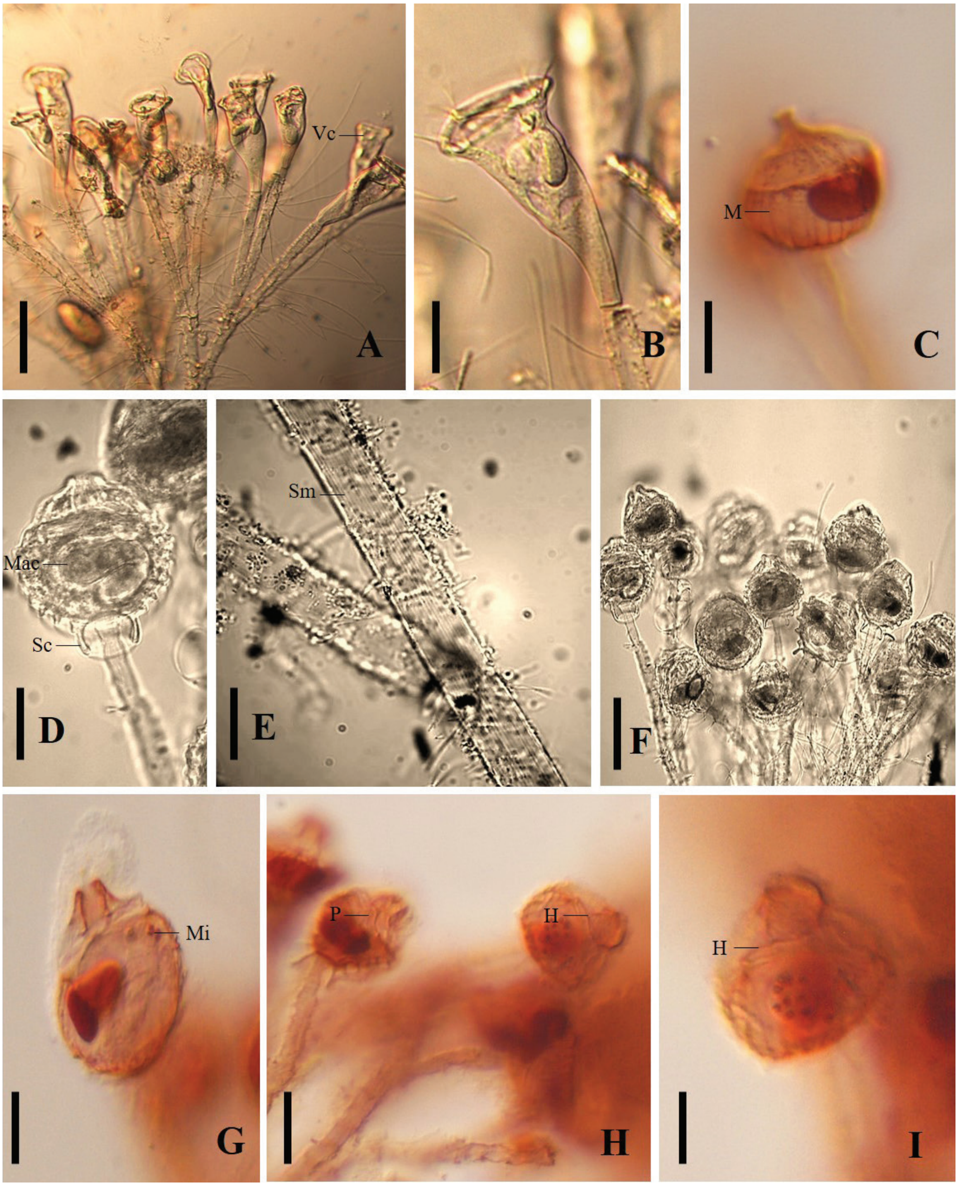

Figure 2. A–B *Epistylis hentscheli* in vivo, **A** colony **B** detail of zooid **C–F** zooid after silver carbonate staining **C** details of myonemes and macronucleus **D** details of stalk **E** detailed longitudinal fibers in the stalk **F** colony showing contracted zooids **G–I** protargol-stained zooids. Abbreviations: Cv. contractile vacuole; H. haplokinety; M. myonemes; Mac. macronucleus; Mi. micronucleus; Po. polykinety; Sc. scopula; Sm. stretch marks. Scale bars: 100 µm (**A**), 25 µm (**B–D, F–H**), and 10 µm (**E, I**).

Ochoterena and Ochoa-Gasca 1971; Mayén-Estrada and Aladro-Lubel 1998, 2000, 2001, 2002, Vidal-Martínez et al. 2002), but there are no records from Chiapas state. *Epistylis hentscheli* has been previously recorded as an ectoparasite of *Cyprinus carpio*

Table 2. Biometric features of *Epistylis hentscheli* in vivo and after protargol staining, colonizing *Procambarus* (*Austrocambarus*) sp. (measurements in µm, n=38; Min. minimum; Max. maximum; S.D. standard deviation; C.V. coefficient of variation).

Attribute	Measurements in vivo					Measurements after protargol staining				
	Min.	Max.	Mean	S.D.	C.V	Min.	Max.	Mean	S.D.	C.V
Zooid length	111	140	120	21.4	0.17	32	76	54	14.6	0.27
Zooid width	58	87	73	9.85	0.13	65	91	78	7.43	0.09
Width of peristomial collar	62	90	76	9.71	0.12	20	34	28	4.06	0.14
Macronucleus width	4	6	5	0.88	0.17	3	5	4	0.81	0.20
Macronucleus length	37	44	40	2.46	0.06	25	34	30	3.05	0.10
Primary stalk length of colony	511	700	606	62.7	0.10	511	700	606	62.7	0.10
Primary stalk width of colony	7.3	7.5	7.4	0.08	0.01	7.3	7.5	7.4	0.08	0.01

(Chordata, Cyprinidae) in Mexico (Herróz-Zamorano 1998), and Zaleski and Claps (2001) found this species on *Enteromorpha* sp. (Plantae, Chlorophyta) in Argentina.

Epistylis hentscheli colonies were formed by 20–30 zooids each and were attached to the pereiopods of *Procambarus* (*Austrocambarus*) sp. It is likely that the constant movement of these pereiopods provide a constant water flow carrying suspended food particles and oxygen to the ciliates. In contrast, the dorsal surface of the basibiont is subject to comparatively little water flow and also is exposed to more abrasion forces, possibly preventing the ciliate attachment. The ciliate colonies of *E. hentscheli* on the pereiopods were very long, with a stalk of 600 µm. This result agrees with that of Camacho and Chinchilla (1990) who reported that the location of epibiont ciliates is determined by the structural characteristics of the ciliates, and genera such as *Zoothamnium*, *Vorticella*, and *Epistylis*, with long stalks, adhere to body regions exposed to water currents, such as uropods and pereiopods. Fernandez-Leborans and Gabilondo (2006) and Key et al. (1997) also indicated that the adhesion site of the ciliates not only depends on the epibionts, but also depends on a series of other characteristics such as the locomotion, shape, molting period, sex, and the behavior of the crustacean.

Epibiosis is a facultative association, in which both participants gain advantages but also have disadvantages from this interaction (Fernandez-Leborans 2010). In this case, the advantage for the epibiont *E. hentscheli* is some protection against predators and a constant water flow providing food and oxygen. However, there are also some associated disadvantages, for example: the exoskeleton is molted as the crayfish grows, necessitating recolonization of the new exoskeleton by the ciliate epibiont (Mayén-Estrada and Aladro-Lubel 2000; Fernandez-Leborans and Gabilondo 2006). The advantages for the basibiont *Procambarus* (*Austrocambarus*) sp. include protection against desiccation and harmful ultraviolet radiation (Wahl 2008), while disadvantages include the alteration of the body surface and reduced efficiency of locomotion and defense (Fernandez-Leborans 2010).

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RESEARCH ARTICLE

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Doubling the known endemic species diversity of New Caledonian armored scale insects (Hemiptera, Diaspididae)

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Abstract

Fourteen species of armored scale insects are known only from New Caledonia. Here, the adult female of fourteen more are described: *Agrophaspis ansevatae* **sp. n.**, *Aonidia montikoghis* ***sp. n.***, *Aonidia pauca* **sp. n.**, *Fernaldanna whita* **sp. n.**, *Furcaspis costulariae* **sp. n.**, *Greeniella casuarinae* **sp. n.**, *Greeniella dacrydiae* **sp. n.**, *Lepidosaphes monticola* **sp. n.**, *Leptaspis pege* **gen. et sp. n.**, *Leucaspis montikoghis* **sp. n.**, *Melanaspis nothofagi* **sp. n.**, *Neomorgania nothofagi* **sp. n.**, *Pseudaonidia dugdali* **sp. n.**, and *Pseudaonidia yateensis* **sp. n.** We note that the diversity of New Caledonian armored scale insects appears to have resulted more from trans-oceanic dispersal than in situ speciation.

Keywords

biodiversity hotspot, taxonomy, southern hemisphere

Introduction

New Caledonia is a biodiversity hotspot. Before 80 Ma, it was part of the southern super-continent Gondwana, and much of its current biota is phylogenetically related to lineages inhabiting other Southern Hemisphere landmasses. But in the Oligocene,

~37 Ma ago, New Caledonia was completely submerged in the South Pacific (Grandcolas et al. 2008). Therefore, the terrestrial species that live there today are presumably descended from ancestors that managed to make it across an ocean and establish a new New Caledonian population. Since its reemergence, how many times has New Caledonia been colonized? How much of its biota is the product of in situ diversification? How did it come to be so diverse so rapidly? Here we add to our store of the basic information that we will need to answer these questions – information about what species actually occur in New Caledonia. Specifically, we describe fourteen new species of armored scale insects endemic to New Caledonia.

Prior to this work, 56 species of armored scale insects had been recorded from New Caledonia (García Morales et al. 2016, Mille et al. 2016, Hamilton et al. 2017). Only 14 of these, including five species of *Andaspis* described recently (Hamilton et al. 2017) are known only from New Caledonia. With the exception of a handful of species that are also found in a few other locations in the South Pacific, the other armored scale insects in New Caledonia are polyphagous, cosmopolitan pest species. Thus, the fourteen species we describe here increases the total species richness by 25%, and the endemic species richness by 100%.

Materials and methods

This work is mostly based on specimens that were collected from New Caledonia 40–50 years ago, and were slide-mounted and deposited in the Natural History Museum, London, UK (**NHMUK**) or the US National Scale Insect Collection in Beltsville, Maryland (**USNM**). The number of specimens examined for each species is provided at the beginning of each description. When a sufficient number of specimens were in hand, we deposited paratypes in the NHMUK, USNM, and the Muséum national d'Histoire naturelle in Paris, France (**MNHN**). For each species, we mostly describe just one side of the body, including the mid line. This avoids the ambiguity that can arise when reporting the numbers of structures that occur on each side of a bilaterally symmetrical animal. It also spares us the repetition of chasing each count with the qualifier that it applies to each side of the body. Nevertheless, in some cases, a description of both sides of the body is easier to comprehend, and we eschew the efficiency of one-sided description in favor of enhanced comprehension. Specimens were viewed under 100–400× magnification, and phase contrast, with a Nikon Ni-E light microscope equipped with a Z-axis-motorized stage. Digital images and measurements were performed with the aid of NIS elements software. Digital images were focus-stacked with Zerene Stacker (Zerene Systems LLC). All measurements are maximum dimensions. The morphological terminology follows Williams and Watson (1988). Digital images were used as the starting point for line drawings. Following the convention for scale insects, each illustration shows the dorsal body surface on the left side, and the ventral body surface on the right side. We refer to pygidial lobes with a shorthand notation, combining the letter L with an index that increments from posteromedial to anterolateral. For example, on each side of the body, the medial-most lobe is referred to as L1, and the lobe immediately anterolaterad of it is referred to as L2.

Taxonomy

Agrophaspis ansevatae sp. n.

http://zoobank.org/53E449E7-B273-4070-B311-1059062CDFC1
Figure 1

Material examined. *Holotype*: New Caledonia: 1 adult female (0.49 mm long, 0.46 mm wide): *ex* undetermined tree, shore south of Anse Vata, Noumea, 17.viii.1963, leg. SW Brown, SWB accession 252 (USNM). *Paratypes*: New Caledonia: 1 adult female, same data as holotype; exuviae of 1 second-instar: on same slide as holotype, SWB accession 252 (USNM).

Description. Adult female, n = 2. Pupillarial. Body 0.38–0.49 mm long, broadest at anterior abdominal segments (0.36–0.46 mm); outline roughly triangular, posterior margin truncate, thorax and head tapering anteriorly.

Pygidium truncate, with four long tapering caudal projections, lacking typical lobes and plates. Dorsum with sclerotic patches around and behind anus. Anus circular, near center of pygidium. Venter of pygidium with vulva near center, about as far from posterior margin as anus. No perivulvar pores. Microducts scattered along margin, at least one near base of each caudal projection.

Prepygidial segments. Venter with microducts along margin of abdominal segments; small setae in submedial and marginal areas of abdomen. No pores present near spiracles. Antennae each with three fleshy setae.

Puparium (cuticle of second-instar female) (not illustrated). *Pygidium* with three pairs of lobes, medial lobes each with lateral and medial notch, second and third lobes each with lateral notch; fringed plates between lobes. Macroducts one-barred. Anus near posterior margin, diameter less than width of medial lobe. Margin with many gland tubercles.

Comments. Borchsenius and Williams (1963) erected the genus *Agrophaspis* by monotypy for the New Caledonian pupillarial species *Aonidia buxtoni* Laing. The adult female of that species shares several traits with the adult of *A. ansevatae;* for example, both lack perivulvar and spiracular pores. Most strikingly, they both lack typical lobes and plates on the pygidium, and have in their place long, tapering caudal projections. In *A. buxtoni* there are seven, and each is bifid or trifid. In *A. ansevatae* there are four. On the holotype, at least one of these also appears to have a slightly bifid apex. The puparia are also similar, but in *A. ansevatae* the diameter of the anus is less than the width of L1, whereas in *A. buxtoni* it is greater than the width of L1.

Etymology. The species epithet is taken from the specimens' provenance, near Ansa Vata.

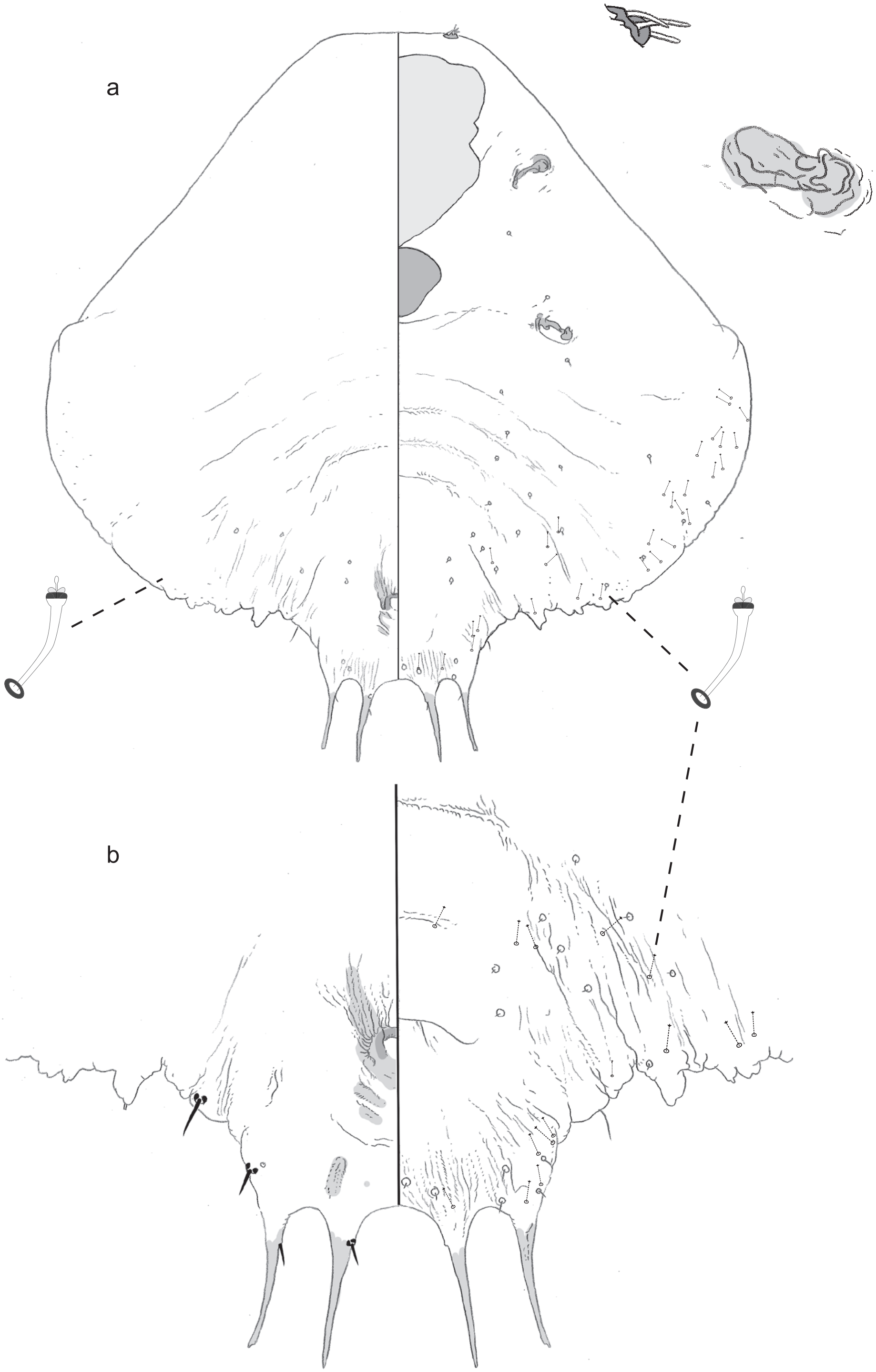

Figure 1. a Adult female of *Agrophaspis ansevatae* sp. n. with **b** enlargement of pygidium.

***Aonidia montikoghis* sp. n.**

http://zoobank.org/821958F8-75E4-4DA3-9E25-E76087B4DC8D
Figure 2a, b

Material examined. *Holotype*: New Caledonia: 1 adult female (0.49 mm long, 0.28 mm wide): *ex* ?*Metrosideros* sp., Mt. Koghia [sic], 5.x.1978, leg JS Dugdale, BM 19 13 (NHMUK). *Paratypes*: New Caledonia: 3 adult females and exuviae of 3 second-instars (i.e., puparia) on five slides: same data as holotype, BM 19 13 (NHMUK, USNM, MNHN).

Description. Adult female, n = 4. Pupillarial. Body 0.48–0.51 mm long, broadest at anterior abdominal segments (0.28–0.31 mm); outline roughly fusiform, posterior margin truncate.

Pygidium without differentiated lobes. Dorsum of pygidium becoming more sclerotic from anterior to posterior end, membranous patches of cuticle in anterior half, narrow linear furrows of membranous cuticle near and perpendicular to posterior margin. Anus circular (~ 11 µm in diameter), near anterior edge of the pygidium. No ducts detected. Venter of pygidium with vulva in anterior half. No perivulvar pores. A few setae scatted along dorsal and ventral submargin and medial areas.

Prepygidial segments. Dorsum with fine, hair-like setae, scattered along margin, few also present on medial areas of abdomen. Ducts absent. On venter, small setae in loose longitudinal submedial and submarginal lines across abdominal segments. No ducts or pores present. Antennae each with two fleshy setae. No pores present near spiracles.

Puparium (cuticle of second-instar female) (Figure 2c). *Pygidium* with only medial lobes, each with lateral notch on apex. Anus circular in anterior half of pygidium. Two-barred macroducts on margin, four on each side, posterior three ducts stemming from distinct pore prominence. A basal sclerosis extending from inner edge of each L1 on each side of body, converging medially to form a triangular carina. One simple gland spine just mesal of second pore prominence, and another just mesal of the third. Few microducts present in submarginal area.

Comments. The adult female of *A. montikoghis* shows little that can be used to make a generic assignment. The second-instar female / puparium is of more use. The pygidium of the second-instar female is most similar to that of the Australian species *Alioides tuberculatus* (Laing). That also has (1) a triangular carina diverging from the inner edges of the medial lobes, (2) only the medial pygidial lobes present, (3) two-barred marginal macroducts, each stemming from a distinct pore process, and (4) no other dorsal macroducts on the pygidium (Brimblecombe 1958). The adult female of *A. tuberculatus* is not pupillarial, but unpublished DNA-sequenced based phlogeny estimates recover *Alioides* nested within the pupillarial genus *Aonidia* (B. Normark pers. comm.). Thus, *Aonidia* seems to be the best fit for this species.

Etymology. The species epithet is taken from the specimens' provenance, Mount Koghis. It is also meant to reflect that this species, like the type species, is known from a mountain on an island. The name is a noun in apposition.

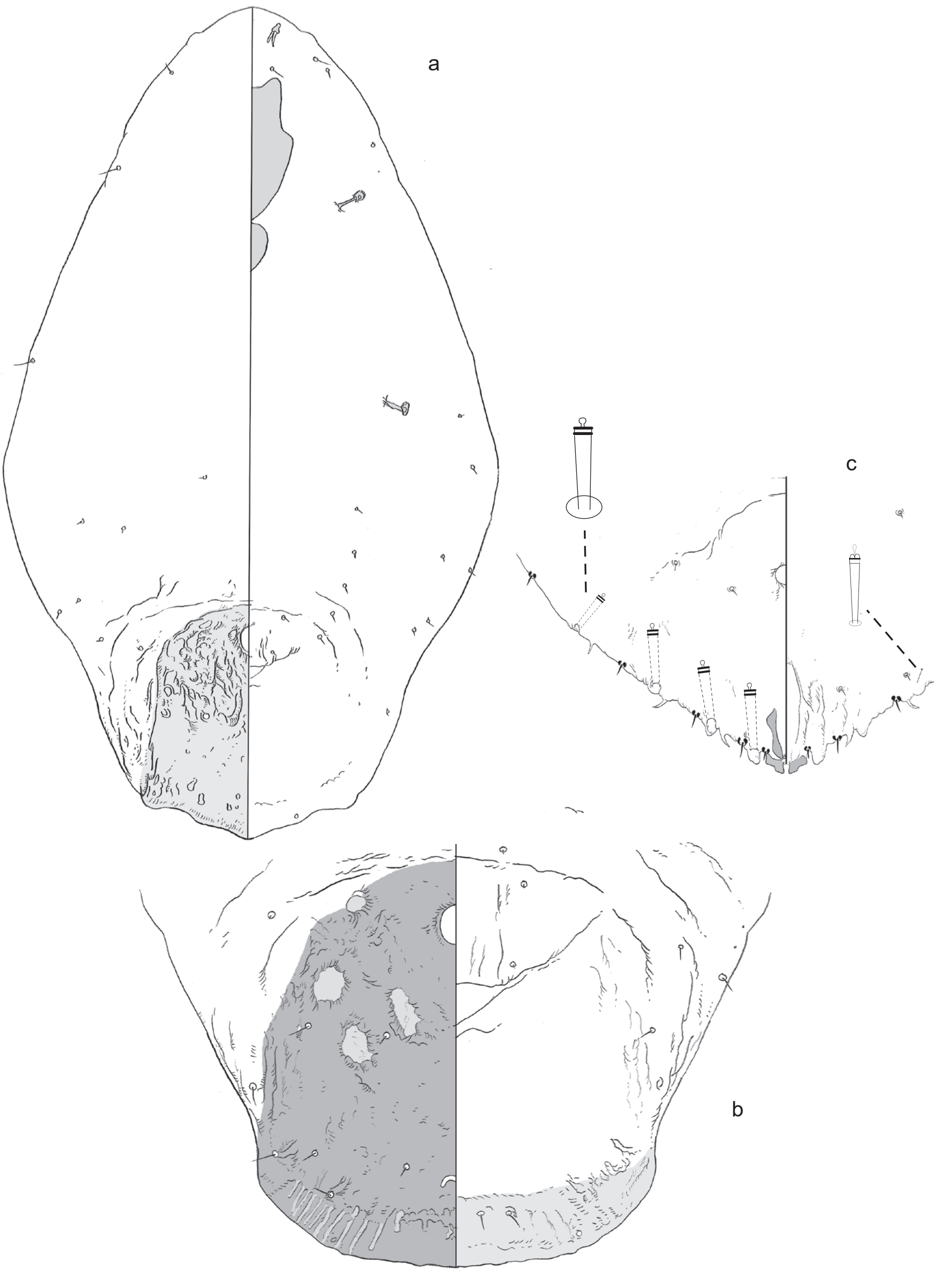

Figure 2. a Adult female of *Aonidia montikoghis* sp. n. with enlargements of pygidium of **b** adult and **c** 2nd-instar.

***Aonidia pauca* sp. n.**

http://zoobank.org/49478016-4BCD-465A-A094-6D4BCFE06295
Figures 3, 4

Material examined. *Holotype*: 1 adult female (0.34 mm long, 0.23 mm wide), ex myrtaceous shrub, Mont D'Or, roadside fountain, 24.viii.1963, leg. SW Brown, SWB accession 260 (USNM). *Paratypes*: New Caledonia: 3 adult females (1 in mounting medium just outside of cover slip, on right side of slide), 1 second-instar, exuviae of 2 second-instars (i.e., puparia), and exuviae of two first-instars: *ex* unknown host, Yaté, 10.iv.2014, leg. S Cazères, 137-14, COCHE/34/14 (NHMUK).

Description. Adult female, n = 3. Pupillarial. Body 0.34–0.50 mm long, broadest at metathorax (0.18–0.27 mm); outline roughly fusiform, posterior margin truncate.

Pygidium with 3–4 differentiated lobes on each side, but no plates or gland spines. Dorsum of pygidium more sclerotic on posterior than anterior end, membranous patches of cuticle in anterior half. Anus circular (~11 µm in diameter), near anterior edge of the pygidium. Microducts scattered along submargin. No macroducts detected. Venter of pygidium with vulva in anterior half. No perivulvar pores. Distinct transverse ridge present anterior of lobes.

Prepygidial segments. Dorsum with fine, hair-like setae, scattered along margin. Ducts absent. Conspicuous tubercle on each side of head. On venter, small setae in loose longitudinal submedial and submarginal lines across abdominal segments. A few microducts in marginal areas of abdominal segments. Each anterior spiracle with a cluster of three trilocular pores. Antennae each with two fleshy setae.

Second-instar female. *Pygidium* with only medial lobes, each with lateral notch. Anus circular in anterior half of pygidium. Large two-barred macroducts on margin, four on each side, posterior three ducts opening into distinct pore prominence. A basal sclerosis extending from inner edge of each L1 on each side of body, converging medially to form a triangular carina. One simple gland spine just mesal of each pore prominence. A few microducts present in submargrinal area.

Comments. Like the adult female of *A. montikoghis*, that of *A. pauca* is bereft of many diagnostic characters. It can be easily distinguished from the former by having well-developed pygidial lobes and tilocular pores near the anterior spiracles.

Etymology. The specific name *pauca* is the Latin feminine adjective *paucus*, meaning few and referring to the simplicity of the morphology of the adult female.

***Fernaldanna whita* sp. n.**

http://zoobank.org/7947E043-AB40-498D-A6B5-134FF317825B
Figure 5

Material examined. *Holotype*: New Caledonia: 1 adult female (0.84 mm long, 0.28 mm wide): *ex* undetermined host, Whita River area, 5.ix.1963, SW Brown, SWB accession 270 (USNM).

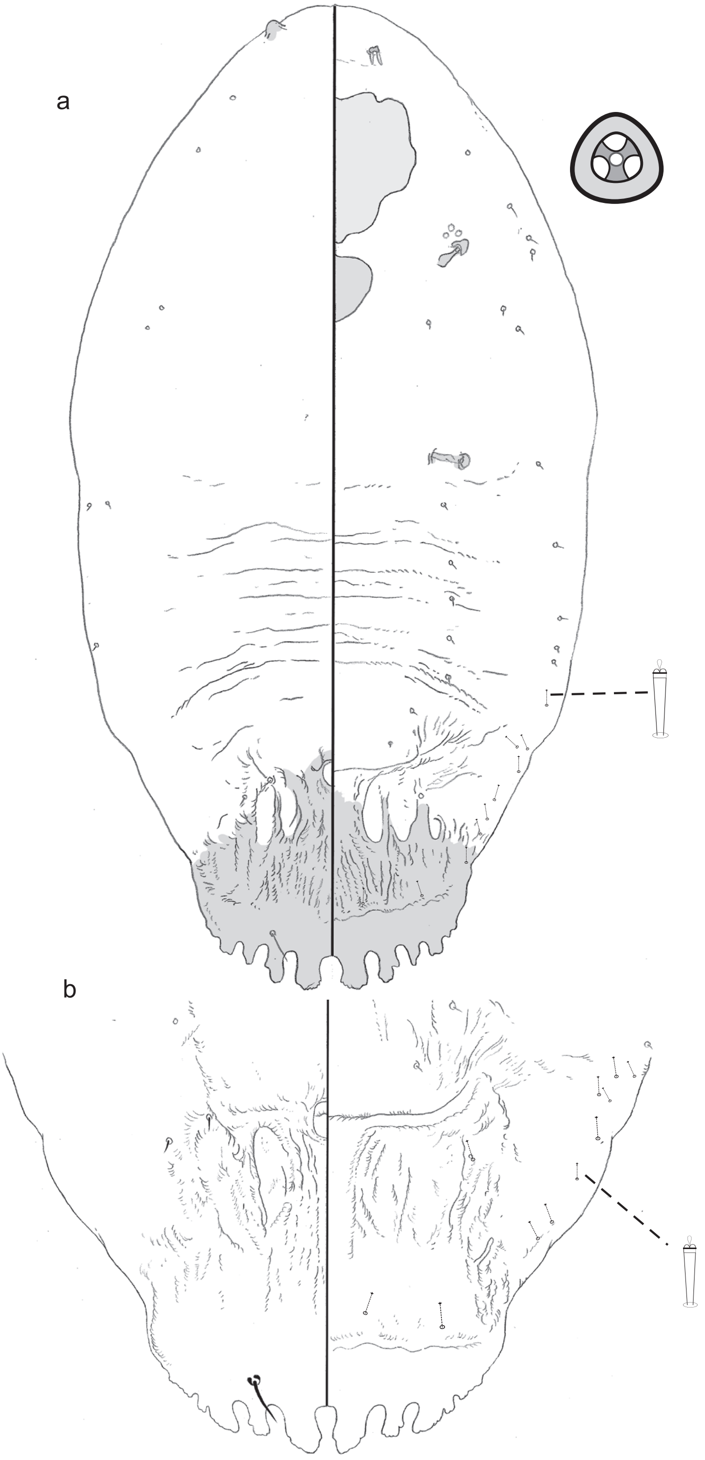

Figure 3. a Adult female of *Aonidia pauca* sp. n. with **b** enlargement of pygidium.

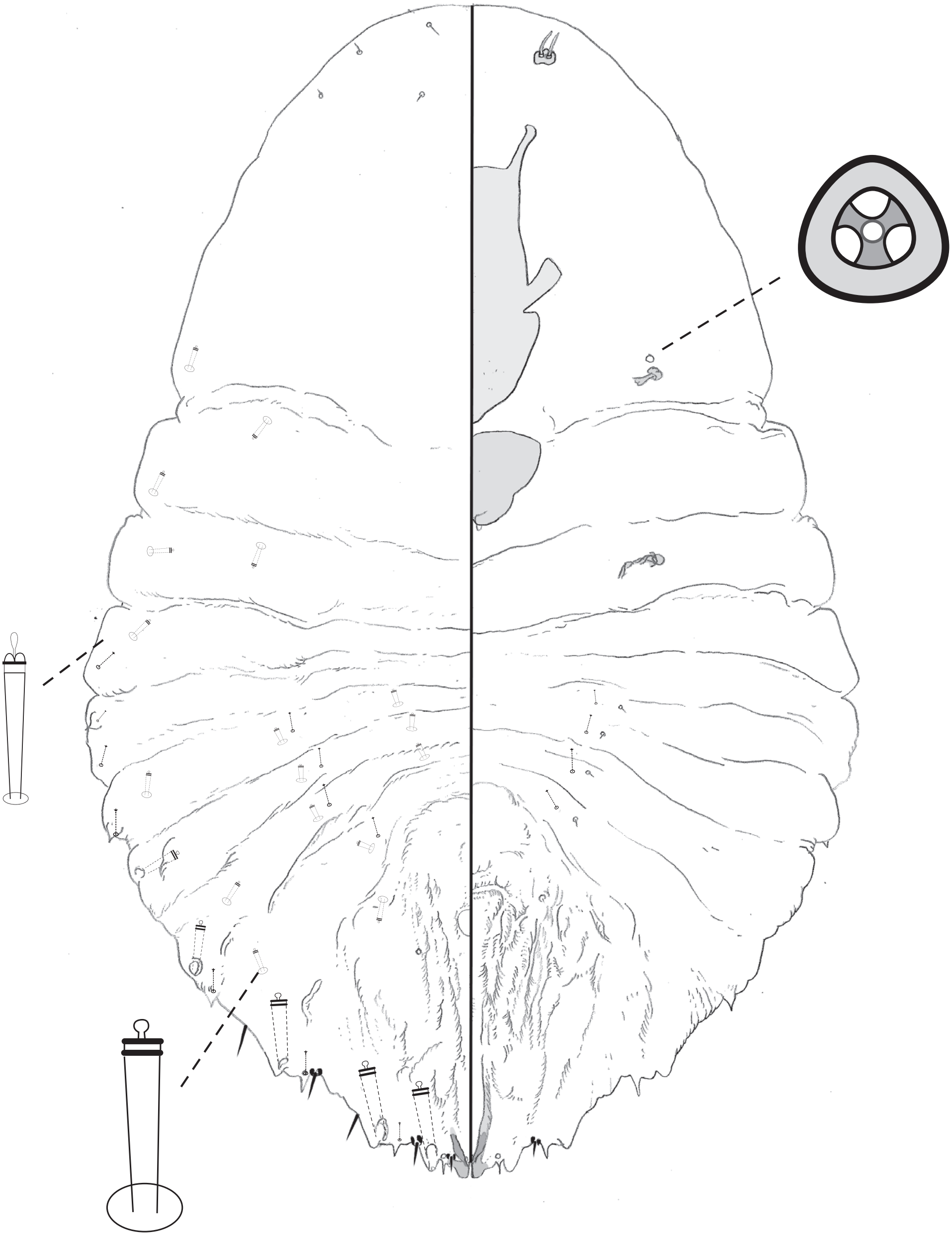

Figure 4. Second instar of *Aonidia pauca*.

Description. Adult female, n = 1. Body of holotype 0.84 mm long, broadest at metathorax (0.28 mm); body outline elongate.

Pygidium longer than wide; with two distinct lobes on each side. Median lobes wider than long, each with slightly rounded apex. L2 much wider (~2×) than L1. Py-

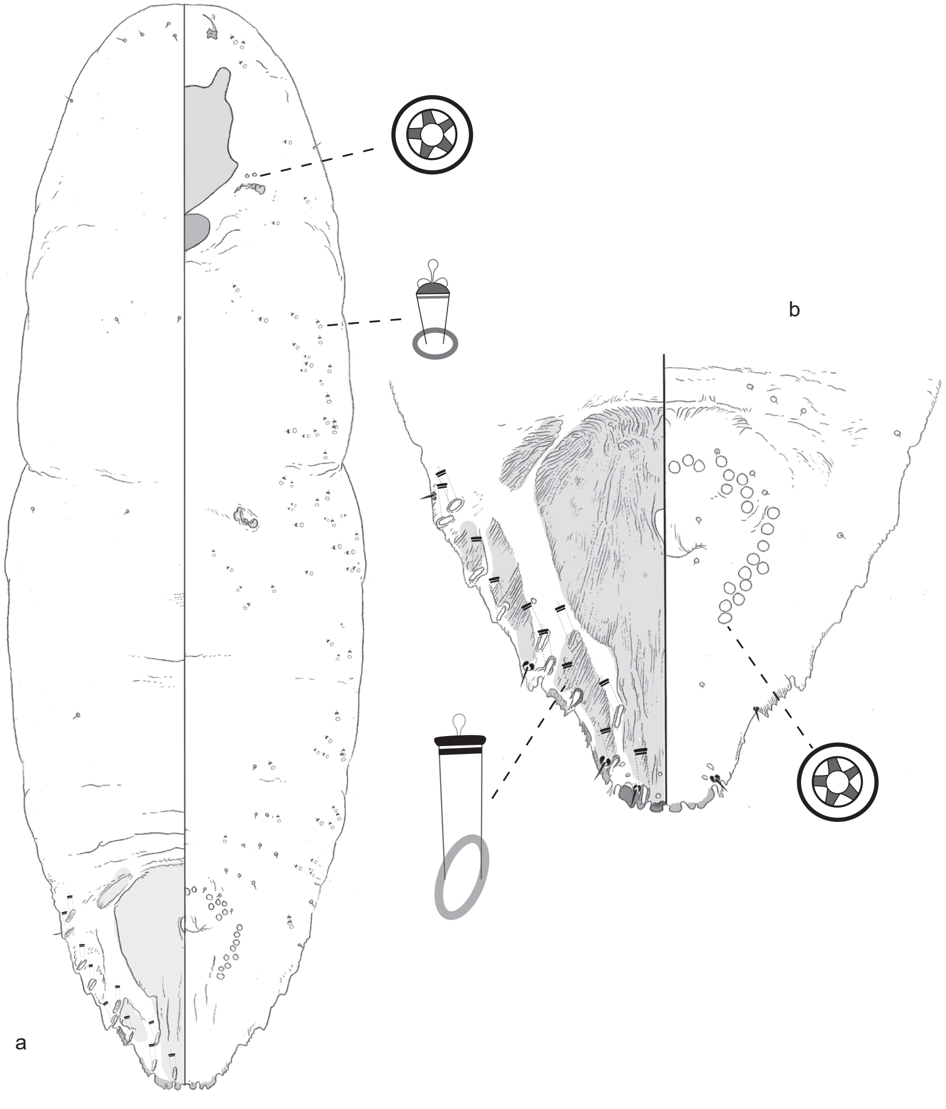

Figure 5. a Adult female of *Fernaldanna whita* sp. n. with **b** enlargement of pygidium.

gidial margin anterior to L2 serrate, with narrow sclerotic straps. Distinct paraphyses not discerned. No plates between median lobes or between L1 and L2; one fringed plate lateral of L2. Anus in anterior third of pygidium. Dorsal macroducts two-barred, restricted to margin and submargin; one arising from pore prominence adjacent to medial base of L2, one in pore furrow above lateral subunit of L2, seven anterior of L2. Dorsum with distinct patches of sclerotic cuticle, one large medial patch broadest just anterior of anus, tapering caudally; 2–3 marginal patches and one near anterolateral corner of medial patch. Venter of pygidium with vulva close to level of anus. Perivulvar pores ~5 µm in diameter, in two distinct groups (anteromedial and anterolateral groups confluent on holotype); ~10 in posterolateral group, ~10 anterolateral and anteromedial of vulva.

Pre-pygidial segments. Dorsum with few, fine, hair-like setae along anterior margin of head and a few on submargin and medial areas of thorax and anterior abdominal segments. On venter, small macroducts scattered along margin and submargin, few in medial areas of meso-, meta-thorax, and anterior abdominal segments. Abdomen with fine, minute setae on submedian and margin of segments just anterior of pygidium. Antenna with one long fleshy seta. Anterior spiracle with 2–3 quinquelocular pores. Posterior spiracle without pores.

Comments. The genus *Fernaldanna* MacGillivrary (1921), previously contained only the type species *F. indentata* (Green), described from Australia on an unidentified host. The pygidium of the adult female of the type species shares several features with that of *F. whita*: (1) few or no plates; (2) two pairs of lobes, L1 with rounded apex, L2 broader than long and much broader than L1; (3) one marginal macroduct between L1 and L2, one at lateral base of L2, and a few more anterior. In *F. indentata* pygidial plates are completely absent; in *F. whita* there is just one plate laterad of L2. Both species have pores near the anterior spiracle, but only *F. whita* has pervivular pores. The adult female of *F. indentata* is pupillarial. We are not sure if the same is true of *F. whita*.

Etymology. The species epithet is taken from its provenance, the Whita River area. It is a noun in apposition.

Furcaspis costulariae sp. n.

http://zoobank.org/192624C6-9DD1-483D-9BF1-88B2F6388D9E

Figure 6

Material examined. *Holotype*: New Caledonia: 1 adult female (1.46 mm long, 1.23 mm wide): *ex Lophoschoenus* sp. [current valid name is *Costularia chamaedendron*], Mont d'Or, roadside fountain, 24.viii.1963, SW Brown, SWB accession 258 (USNM). *Paratype*: New Caledonia: 1 second-instar nymph, same data as holotype, SWB accession 258 (USNM).

Description. Adult female, n = 1. Presumed to secrete scale cover. Body of holotype 1.46 mm long, broadest at mesothorax (1.23 mm); body outline turbinate (margin of head and thorax almost circular, abdomen tapering to truncate pygidium), margin of pre-pygidial abdominal segments slightly convex. Cuticle sclerotized (or at least heavily stained).

Pygidium wider than long, with three lobes on each side. Median lobes longer than wide, each with rounded apex, separated by ~2.5× their width. L2 and L3 as long as median lobe but broader, with more truncate apex. Pygidial margin anterior to L3 with a few long setae (up to 65 μm) and several tooth-like projections, pointed or truncate, smaller than lobes; posterior terminus of pygidium heavily sclerotized, distinct paraphyses not discerned. Plates each bifid, longer than lobes; two between median lobes, two between L1 and L2, 3 between L2 and L3, two anterior of L3. Anus in anterior third of pygidium, obstructed by detritus under cover-slip of slide mount.

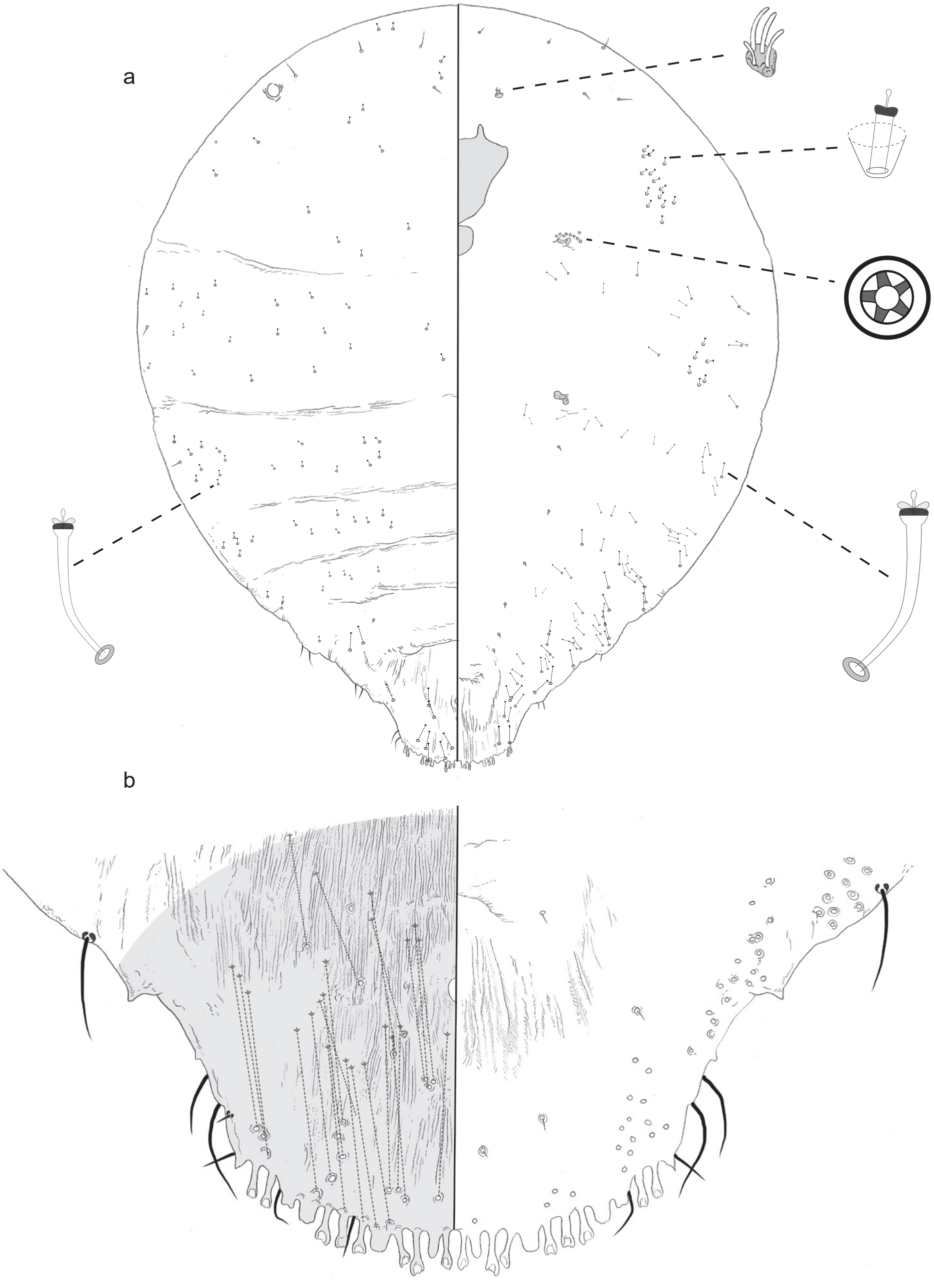

Figure 6. a Adult female of *Furcaspis costulariae* sp. n. with **b** enlargement of pygidium.

Thin one-barred macroducts abundant along posterior margin, ~18 on each side away from margin, some anterior of anus. Venter of pygidium with vulva in anterior half. Perivulvar pores absent.

Pre-pygidial segments. Dorsum with fine, hair-like setae along margin and submargin. Eye a subcircular disk on dorsal submargin lateral of antenna. Microducts scattered across head and thorax, along submarginal and submedial parts of abdominal segments grading into one-barred macroducts along margin of posterior pre-pygidial segments. On venter, microducts in loose transverse bands from submedian to margin of mesothorax and metathorax, posterior to each spiracle, also scattered along abdominal margin and submargin. Patches of gland tubercles on prothorax and mesothorax, 23–26 on each side of body, most on prothorax. Abdominal segments each with a small submedial seta with proportionately large, sclerotized collar, forming longitudinal rows from near lateral edge of vulva to posterior spiracles. Antennae each with four long setae. Anterior spiracle with cluster of nine quinquelocular pores. Posterior spiracle without pores.

Comments. For a synthetic treatment of the genus *Furcaspis*, see the revision of Williams et al. (2006). Paraphrasing their diagnosis, adult females of *Furcaspis* have (1) simple bifurcate (rarely trifurcate) pygidial plates; (2) 3 pairs of notchless plates; (3) the antenna with multiple setae; (4) thin macroducts; (5) paraphyses; and (6) pores absent from the posterior spiracles. Currently, 29 species are recognized, two of which are endemic to New Caledonia: *F. cyphokantiae* Williams & Miller and *F. matileae* Williams & Miller. The adult female of *F. cyphokantiae* differs from that of *F. matileae* by having (1) gland tubercles on the venter of the mesothorax; (2) sclerotized lateral areas on the thorax; and (3) medial lobes that are closer together, and more similar in size and shape to the other lobes on the pygidium. The adult female of *F. costulariae* can be distinguished by having (1) only four long setae on the antenna (5–8, but usually six in *F. cyphokantiae* and *F. matileae*); (2) 23–26 gland tubercles, with only 2–3 on the mesothorax (tubercles absent from meso thorax, of *M. matileae*, and total 36–40 in *M. constulariae*); (3) uniformly sclerotic cuticle, and (4) lacking discernible paraphyses, although they may simply be impossible to detect against the background of sclerotic cuticle on the pygidial margin. All three New Caledonian species feed on monocotyledons; *F. cyphokantiae* and *F. costulariae* feed on sedges (Cyperaceae). It is possible that these three species are, in fact, just host-induced phenotypic variants of one New Caledonian metapopulation. Our decision to name the female from *Costularia* formalizes the alternative hypothesis that each host-associated form is a good species.

Etymology. The species epithet is taken from the genus name of the host, a sedge that is endemic to New Caledonia.

Greeniella casuarinae sp. n.

http://zoobank.org/E2FCD996-4725-45DB-8996-F7DE71F58504
Figure 7

Material examined. *Holotype*: New Caledonia: 1 adult female (0.43 mm long, 0.36 mm wide): *ex Casuarina* sp., near Yaté Dam, 3.ix.1963, SW Brown, SWB accession 267 (USNM).

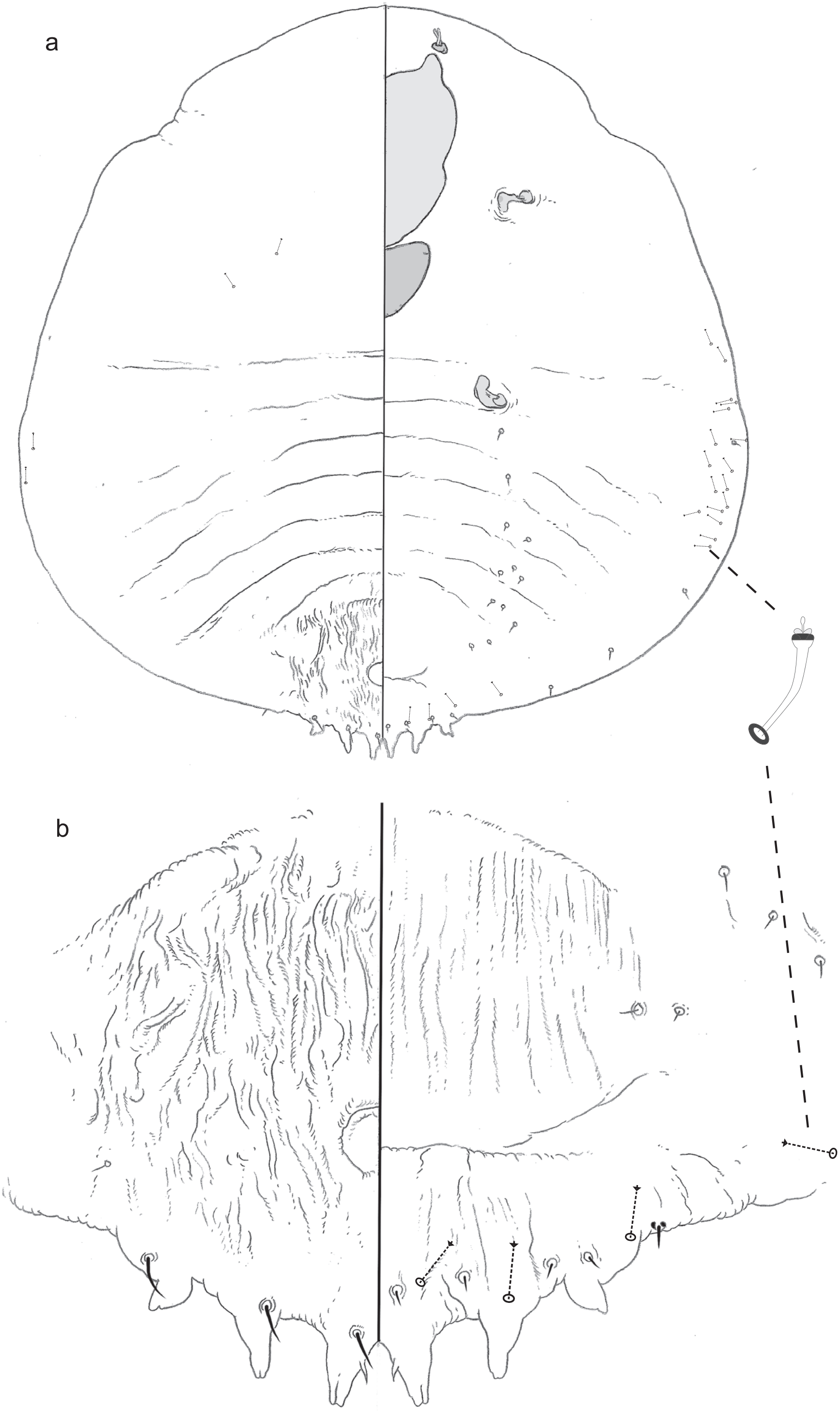

Figure 7. a Adult female of *Greeniella casuarinae* sp. n. with **b** enlargement of pygidium.

Description. Adult female, n = 1. Presumed pupillarial. Body of holotype 0.43 mm long, broadest at anterior abdominal segments (0.36 mm); body outline circular, with slight constriction at head.

Pygidium truncate, without dorsal macroducts, typical lobes, or plates; with six projections, each subtriangular, slightly bifid at apex. Anus circular, in posterior half of pygidium. Venter with vulva in posterior half, at level of anus. Perivulvar pores absent. Microducts scattered along posterior margin.

Pre-pygidial segments. Microducts scattered along margin of anterior abdominal segments, meta- and mesothorax. Fine setae in distinct submedial and marginal series; setae not detected on head and thorax. Antennae each with two long setae. Spiracles without pores.

Comments. Before this work, the genus *Greeniella* Cockerell (1897) contained 14 valid species, all but two occurring in southern Asia. The exceptions are two Australian species, *G. capitata* Brimblecombe and *G. ornata* Brimblecombe. The defining feature for the group is that the pupillarial adult females have unusual pygidia, with caudal projections in addition to or instead of the normal lobes and plates. Nevertheless, the taxonomy of pupillarial armored scale insect species undoubtedly needs sorting, and the boundaries between the genera *Greeniella*, *Eugreeniella*, and *Aonidia* are blurry (B. B. Normark pers. comm.). The adult female of *G. casuarinae* is unique in having six short, sub-triangular, bifid caudal projections.

Etymology. The species epithet is taken from the genus name of the host.

Greeniella dacrydiae sp. n.

http://zoobank.org/50D7573E-59B7-4901-8F77-EE3EB25290AD
Figures 8, 9

Material examined. *Holotype*: New Caledonia: 1 adult female (0.49 mm long, 0.38 mm wide): *ex Dacrydium auricarioides* [sic; the correct spelling of the epithet is *araucarioides*], 5 miles north of Yaté Dam Lake, 5.ix.1963, SW Brown, SWB accession 275 (USNM). *Paratype*: New Caledonia: 1 second-instar exuviae: on same slide as holotype, SWB accession 275 (USNM).

Description. Adult female, n = 1. Pupillarial. Body of holotype 0.49 mm long, broadest at meta-thorax and anterior abdominal segments (0.38 mm); body outline ovoid, with slight constriction at head.

Pygidium truncate, without dorsal macroducts, or typical lobes and plates; with ~20 short papilliform projections. Anus circular, in anterior half of pygidium. Venter with vulva in posterior half, well behind anus. Perivulvar pores absent. Microducts scattered along posterior margin and submedial areas.

Pre-pygidial segments. Dorsum with few setae along margin. Venter with microducts scattered across abdominal segments, in clusters around each spiracle. Fine setae in distinct submedial and marginal series. Antennae each with one long setae. Spiracles without pores.

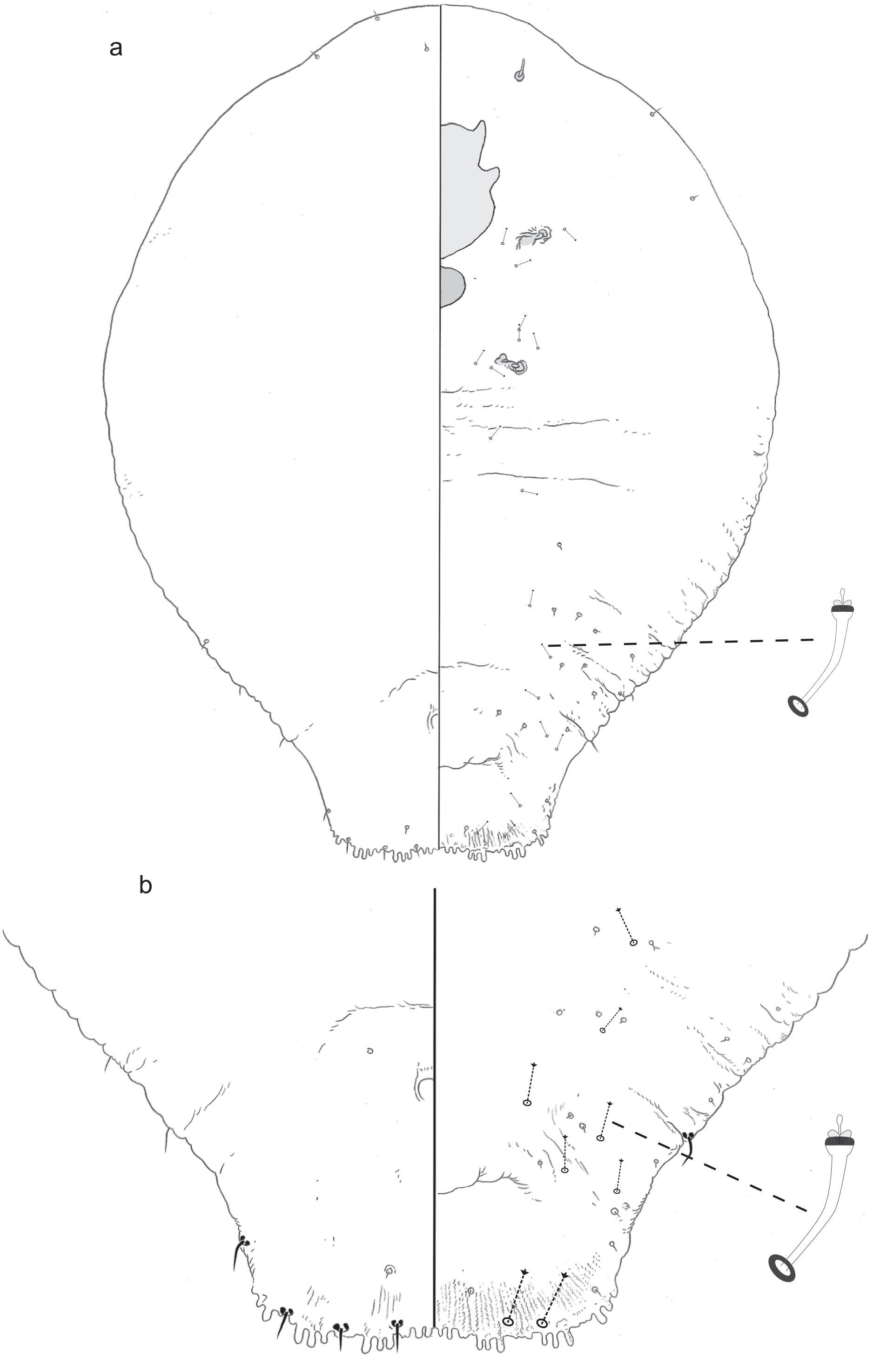

Figure 8. a Adult female of *Greeniella dacrydiae* sp. n. with **b** enlargement of pygidium.

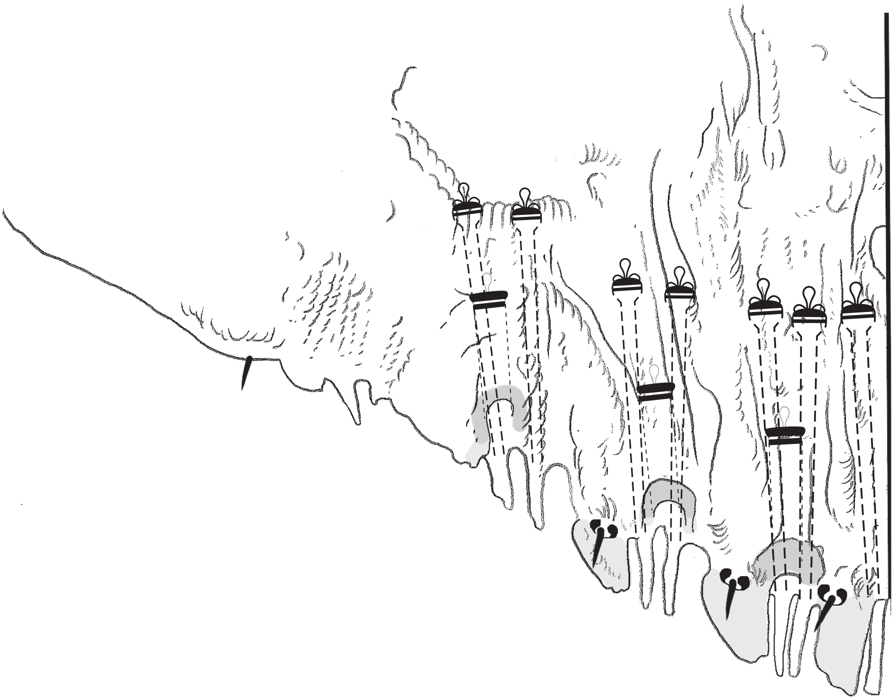

Figure 9. Pygidium of 2nd instar of *Greeniella dacrydiae* sp. n.

Second-instar female. *Pygidium* with three lobes on each side; L1 longer than wide, parallel-sided, apex oblique; L2 and L3 sub-triangular, with oblique caudal edge, medial margin much longer than lateral margin. Two simple gland spines in each interlobal space, and lateral of L3. Marginal two-barred macroducts with thick sclerotization around orifice; one between L1 and L2, L2 and L3, and laterad of L3; longer slenderer macroduct arising from base of each marginal gland spine. Anus circular, near middle of pygidium.

Comments. The adult female of *G. dacrydiae* can be easily distinguished from those of other described species by the ~20 papilliform projects along the truncate posterior margin of the pygidium. See comments under *G. casuarinae* for further discussion of genus assignment.

Lepidosaphes monticola sp. n.

http://zoobank.org/1D189785-917C-4E7D-850E-908367B85A3E

Figure 10

Material examined. *Holotype*: New Caledonia: 1 adult female (1.75 mm long, 0.75 mm wide): *ex Podocarpus ?logifolatus*, Mt. Koghis, 900 m, 12.x.1978, PN Johnson, BM 19 2 (NHMUK). *Paratypes*: New Caledonia: 1 adult female: same data as holotype; 2 adult females: *ex* undetermined host, Mt. Mou (near Sanitarium), 19.viii.1963, SW Brown, SWB accession 254 (NHMUK, USNM); 1 adult female: *ex Podocarpus longifolatus*, Mt. D'Or, 900 m, 31.x.1978, J. S. Dugdale, 78-3266 (NHMUK). *Other material*: New Caledonia: 1 teneral adult female: same data as holotype but with accession BM 19 17.

Description. Adult female, n = 4. Presumed to secrete scale cover. Body 1.25–1.88 mm long, broadest near anterior spiracle (0.5–0.83 mm); outline roughly fusiform, head and prothorax fused into circular prosoma, margin incised between pro- and mesothorax, margins of posterior pre-pygidial abdominal segments strongly convex.

Pygidium with three lobes on each side, L2 and L3 bilobed, each with lateral marginal slightly divergent near base, L1 and sublobes of L2 each with pair of convergent paraphyses. A pair of bifid gland spines between L1s, a pair of simple gland spines between L1 and L2, another pair between L2 and L3. Dorsum of pygidium weakly sclerotic, with longitudinal striations. Anus small, 10 µm in diameter, in middle of pygidium. Margin of pygidium with five large two-barred macroducts (~25 µm long, 10–13 µm wide at distal end) with elongate, oblique orifices: one on pore prominence between L1 and L2, one between L2 and L3, one just anterior to first sublobe of L3, two anterolateral of L3. Other dorsal macroducts (away from margin) as long as marginal ducts but less wide at distal end, ~7 µm, scattered along submargin and arranged in longitudinal line from L3 to anterior of anus. Venter of pygidium with vulva in anterior half of pygidium. Perivulvar pores quinquelocular, 5–9 µm in diameter, in five groups: 8–11 pores in posterior group, 11–12 in anterolateral group, 3–5 in medial group.

Prepygidial segments. Dorsum with fine, hair-like setae, sparse along margin, few on medial areas of head and thorax. Each abdominal segment with submedial and submarginal group of macroducts. In holotype, submedial group in transverse line, submarginal group divided into anterior cluster and posterior transverse line. Some other specimens with fewer ducts and without differentiated subdivisions of submarginal group. Each posterior abdominal segment with cluster of macroducts associated with 1–3 gland spines. Antennae each with two long setae. Anterior spiracle with cluster of 3–10 trilocular pores. Posterior spiracles without pores. Some specimens with distinct clusters of microducts on head or prothorax.

Comments. Shimmer (1868) erected the genus *Lepidosaphes* by monotypy for the species *Mytilococcus communis* Amerling (now *Lepidosaphes ulmi*). There are 167 species currently recognized in the genus (García Morales et al. 2016). Takagi (1970) gives a thorough diagnosis: adult females tend to have (1) an elongate or fusiform body shape, the margins of anterior abdominal segments convex; (2) two pairs of well-developed pygidial lobes, and in some species an additional 1–2 pairs of rudimentary lobes; (3) median pygidial lobes separate and symmetrical; (4) L2 bilobate; (5) if basal scleroses present on pygidium, they are slender and extend from the basal edges of lobes; (6) gland spines present between medial lobes as well as in the space between L1 and L2; (7) large marginal macroducts with oblong orifice and sclerotic rim, usually six on each side of pygidium, stereotypically with one near junction of abdominal segments VIII and VII, two near junction of segments VII and VI, and three anterior to segment VI; (8)

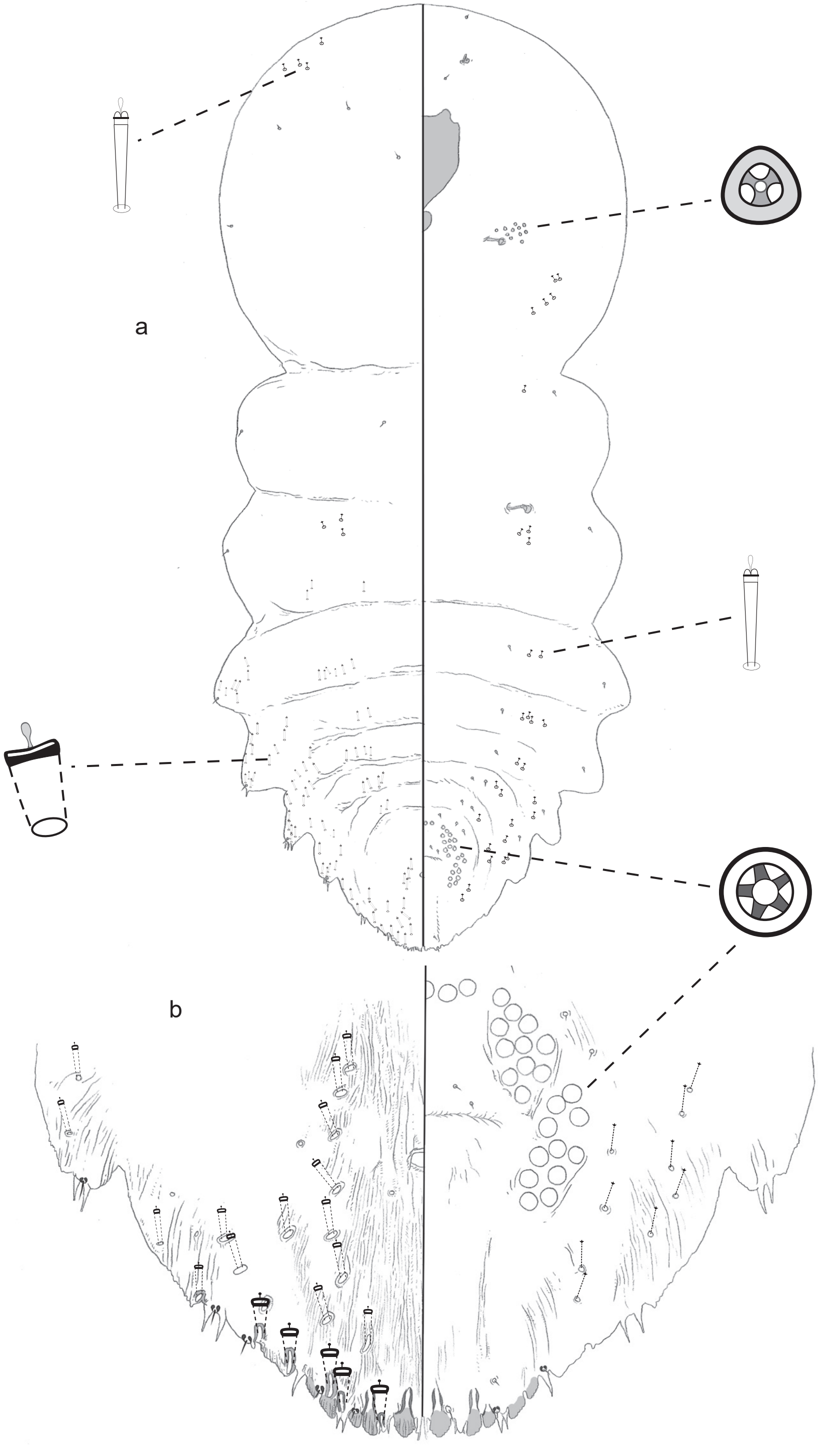

Figure 10. a Adult female of *Lepidosaphes monticola* sp. n. with **b** enlargement of pygidium.

antenna usually with two or more long setae; (9) anus near anterior edge of pygidium; (10) perivulvar pores in five groups; and (11) pores near anterior spiracles. For the most part, this diagnosis works for the adult female of *L. monticola*, although it does have some less common character states, for example L3 is relatively well developed, and the anus is farther posterior of the anterior pygidial edge (opposite the posterior group of perivular pores) than it is in most species (at the base of the pygidium or almost opposite the center of the frame formed by the perivulvar pores). The most striking difference is the circular prosoma, which, to the naked eye, makes the body of the *L. monticola* female appear unlike other species of *Lepidosaphes*. This body shape is typical of many species of *Aulacaspis* Cockerell, but the pygidium of *Aulacaspis* species is quite different (Takagi 1999). Two Neotropical species of *Pseudoparlatoria* Cockerell have a body shape and pygidium similar to that of *L. monticola* (Ferris 1941; Wolff 2001; Wolff and Claps 2008). Nevertheless, species of *Pseudoparlatoria* invariably lack pores near the anterior spiracles of the adult female. In a forthcoming paper, B. B. Normark will show that in comparison to body shape, the presence or absence of pores near anterior spiracles is more phylogenetically conservative. Hence, we describe *L. monticola* as an odd-bodied species of *Lepidosaphes*, rather than an odd-pored species of *Pseudoparlatoria*.

Lepidosaphes monticola belongs to a group of Pacific species that share a row of microducts on segment VII, forwards from the second lobes. In the other Pacific species this group only extends anteriorly to each side of the anus, but in *L. monticola* this group extends well anterior to the anus. *Lepidosaphes monticola* is similar to *L. carolinensis* Beardsley, described from The Federated States of Micronesia, *L. esakii* Takahashi, known from The Federated States of Micronesia and The Republic of Kiribati, and to *L. karkarica* Williams & Watson, described from Papua New Guinea. *Lepidosaphes carolinensis* has sclerotized spines on the lateral margins of the anterior abdominal segments, and *L. karkara* possesses well-developed lateral tubercles in these positions but *L. monticola* lacks these structures.

Note that we have excluded from the type series a teneral adult female specimen from the type locality, Mt. Koghis. This specimen differed from the others in having a distinct patch of short microducts along the submargin of the prosoma, lateral of the clypeolabral shield. The adult females from Mt. Mou also have clusters of microducts on the margin of the head, although not as many as the teneral Mt. Koghis female, and in a different location (the anterior margin). The teneral Mt. Koghis female also has smaller perivulvar pores than those found in the other specimens examined (5 versus 9 µm in diameter).

Etymology. The species name refers to its mountainous habitat and is a noun in apposition.

Leptaspis gen. n.

http://zoobank.org/2D39CBD6-EA5C-4742-A3EB-E08F8E45DCD2

Type species. *Leptaspis pege* sp. n. by monotypy and original designation.

Diagnosis. A pupillarial genus. Adult female with body outline elongate, nearly four times as long as wide. Pygidium without lobes, plates or macroducts. Perivulvar and perispiracular pores absent. Gland tubercles in marginal series. Eye a subcircular disk on dorsal submargin lateral of antenna. Antenna with one long fleshy seta. Second-instar female with three pairs of pygidial lobes, fimbriate plates, and slender one-barred macroducts. Anus at anterior end of medial furrow delimited by sclerotic carinae.

Comments. As has been done many times before, we erect a new monotypic genus for a pupillarial species with no obvious taxonomic affinity. In this case, the adult female has the unusual combination of gland tubercles and anterior spiracles without pores. Pupillarial life histories have evolved repeatedly in armored scale insects (Andersen et al. 2010) and have spurred extensively parallel evolution of a variety of morphological reductions. Some features of the new genus are similar to those of *Neoleucaspis* Green described from India, but the latter genus possesses a series of lobe-like structures around the pygidial margin and lacks gland tubercles. Moreover, the lobes of the second-instar of *Neoleucaspis* are pointed whereas the lobes of the new genus are rounded. Because the genus is monotypic, the description of the type species also describes the genus.

Leptaspis pege **sp. n.**

http://zoobank.org/645176E4-341C-4422-8D21-EB689F1380F0

Figure 11a, b, c

Material examined. *Holotype*: New Caledonia: 1 adult female (1.46 mm long, 0.38 mm wide): *ex* sedge, Mont D'Or, roadside fountain, 24.viii.1963, SW Brown, SWB accession 257 (USNM). *Paratype*: New Caledonia: exuviae of 1 second-instar: on same slide as holotype, SWB accession 257 (USNM).

Description. Adult female, n =1. Pupillarial. Body of holotype 1.46 mm long, broadest at meta-thorax (0.38 mm); body outline elongate.

Pygidium without lobes or plates, on each side with ~10 microducts along margin. Anus circular, in posterior third of pygidium. Venter with vulva in posterior half, slightly anterior of anus. Perivulvar pores absent.

Pre-pygidial segments. Eye well developed. Dorsum with few setae along margin and medial areas. Venter with gland tubercles, in linear submarginal series along abdominal segments, a few on margin of metathorax, and extending from anterior spiracle to antenna. Fine setae in distinct submedial and marginal series. Antennae each with one long setae. Spiracles without pores.

Second-instar female. *Pygidium* with three lobes on each side; each lobe with rounded apex; L1 much smaller than L2 and L3. Medial side of base of L2 and L3 confluent with sclerotized rim around orifice of marginal microduct. Microducts also scattered along submargin. Two fimbriate plates between medial lobes, two between L1 and L2, 3 between L2 and L3, 2 laterad of L3. Anus elongate, at anterior end of medial furrow extending from base of medial lobes.

Figure 11. a Adult female of *Leptaspis pege* gen. et sp. n. with enlargements of pygidium of **b** adult female and (c) 2nd-instar.

Etymology. The genus name is based on the Greek word *leptos* meaning thin, referring to the shape of the body, combined with *aspis*, the Greek world for shield. The species name is taken from the Greek *pege*, for fountain, in reference to the one located near the type locality. It is a feminine noun, used here in apposition.

Leucaspis montikoghis sp. n.

http://zoobank.org/4B28BBB5-529C-4A9D-8C89-1BDBD7A5A0DB
Figure 12

Material examined. *Holotype*: New Caledonia: 1 adult female (2.06 mm long, 0.54 mm wide): *ex Podocarpus* sp., Mt. Kohgis, 12.x.1978, PN Johnson, BM 19 17 (NHMUK). *Paratypes*: New Caledonia: 2 adult females, 6 puparia (2 of which contain embryos), and 1 first-instar nymph on 9 slides: same data as holotype, BM 19 17 (NHMUK, USNM). Note that one slide further specifies that the elevation was 900 m, and that a possible species assignment for the host was *P. longifollatus.*

Description. Adult female, n = 3. Pupillarial. Body 0.94–2.06 mm long, 0.51–0.54 mm wide; outline elongate, margins of head and pygidium rounded.

Pygidium with two lobes on each side, each longer than wide, lanceolate (i.e., distal half tapering to pointed apex), base slightly overlaying venter of pygidium. Plates spiniform, slightly longer than lobes, two between L1s, two between L1 and L2, ~8 anterolateral of L2. Dorsum with sclerotic area containing anus, plus two smaller patches posterior to anus, medial patch confluent with that around anus in some specimens; anus ~20 µm long and ~15 µm wide. Few small ducts scattered along posterior margin, each ~5 µm long. Venter of pygidium with perivulvar pores in five distinct groups, each side of the body with a lateral group of ~20 pores, and an anterolateral group of ~25 pores, anteromedial group with 10–20 pores.

Prepygidial segments. Dorsum with few fine, hair-like setae. On venter, four groups of pre-pygidial pores, one group of 12–20 pores on the submargin of each of abdominal segments IV-VI, plus one group of 2–6 pores on submedian area of segment VI. Longitudinal band of 65–85 gland tubercles running from anterior to spiracle to posterior of labium. Antennae each with five long setae, two short ones evidenced by sockets. Anterior spiracles each with cluster of 24–28 quinquelocular pores. Posterior spiracle without pores.

Comments. The genus *Leucaspis* Signoret was erected for the type species *Aspidiotus pini* Hartig. There are 34 nominal species of *Leucaspis* (García Morales et al. 2016). Nineteen of these occur in New Zealand (~2000 km south of New Caledonia), 16 of which are endemic, and one of which is only known from New Zealand and Australia (which is home to only this one species of *Leucaspis*). The true species diversity of New Zealand's *Leucaspis* is apt to be much greater (Henderson 2011; personal observations of material in the USNM). The species *L. bugnicourti* Cohic is endemic to New Caledonia, but would appear to be more closely related to species outside of *Leucaspis*, for example *Fijifiorinia* spp. (Williams and Watson 1988). Takagi (1969) gives us a meticulous diagnosis of the genus. We paraphrase it here. The adult female can be recognized by (1) being pupillarial, and by having (2) an elongate body outline; (3) small sclerotic patches on dorsum of pygidium; (4) each side of the pygidium with 1–4 lobes, with medial lobes well separated; (5) plates absent, spiniform or fimbriate; (6) gland tubercles on venter of thorax; (7) dorsal ducts absent or present only along the pygidial margin, when present short, with sclerotized oral rim; (8) antenna with 2–6

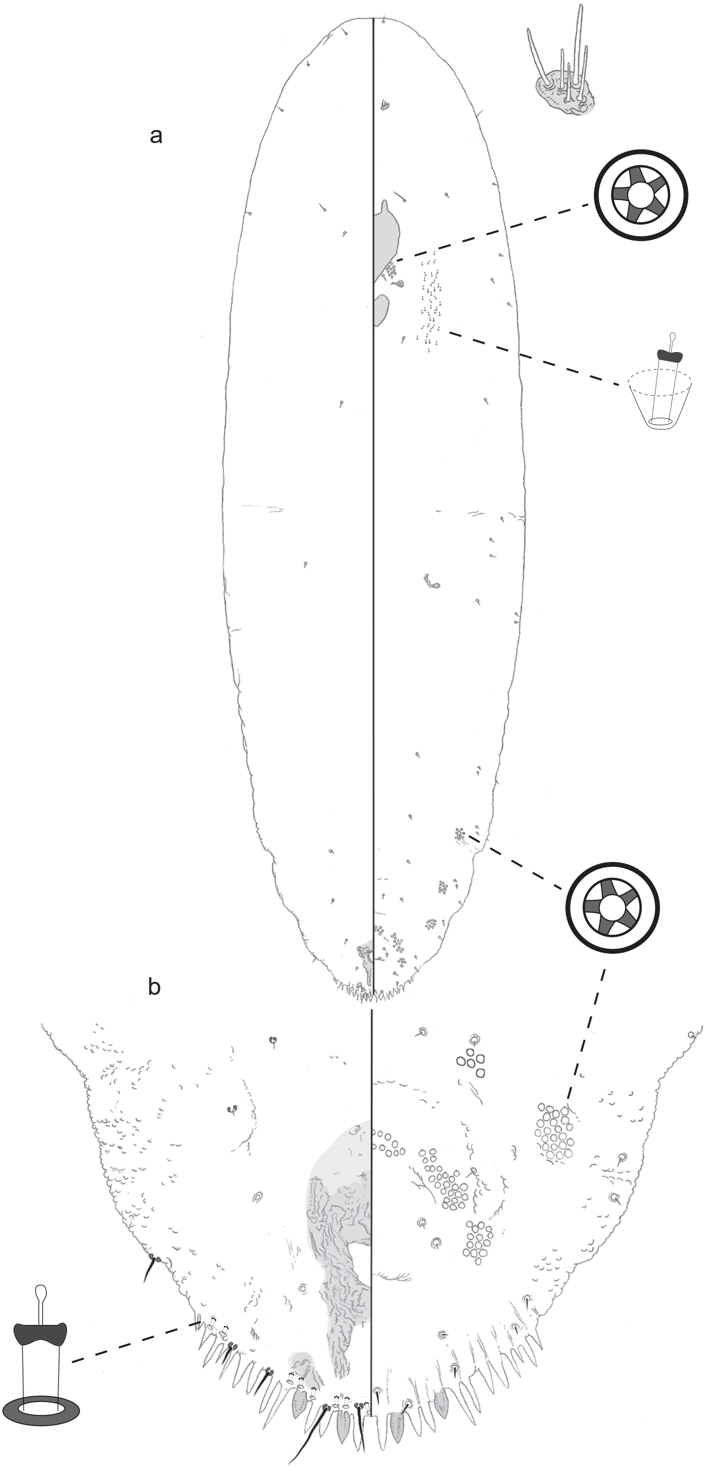

Figure 12. a Adult female of *Leucaspis montikoghis* sp. n. with enlargement of **b** pygidium.

fleshy setae; (9) anterior spiracle with cluster of disc pores adjacent; (10) anus in anterior third of the pygidium; (11) perivulvar disc pores in five groups; (12) many species with pre-pygidial pores. The new species, *L. montikoghis*, can be recognized by having two pairs of broad lanceolate pygidial lobes, spiniform plates, and many pores (~20) in the posterior pre-pygidial group. The latter trait is especially distinctive; there are about twice as many pores in this group as in any described species.

Brittin (1937) provides a synthetic treatment of the *Leucaspis* species occurring in New Zealand that he was aware of at that time (13 in all). We recommend this, along with Takagi's diagnosis, as good resources to start gaining familiarity with this group. de Boer and Valentine (1977) provide an excellent re-description of *L. gigas*, along with four similar species, one of which was new at that time. Henderson et al. (2010) described an additional two New Zealand species.

Etymology. The species epithet is taken from the type locality and is a noun in apposition.

Melanaspis nothofagi sp. n.

http://zoobank.org/7AA6F01A-37FD-484B-9523-928275B99768
Figure 13

Material examined. *Holotype*: New Caledonia: 1 adult female (0.79 mm long, 0.74 mm wide): *ex Nothofagus aequilateralis*, Pic du Pin, 6.x.1978, JS Dugdale, BM 19 7 (NHMUK).

Description. Adult female, n = 1. Presumed to secrete scale cover. Body 0.79 mm long, 0.74 mm wide; outline circular, margin of posterior abdominal segments sinusoidal, i.e., appearing lobed, posterior part of each lobe bearing sclerotic tooth, tip pointed or rounded.

Pygidium with four lobes on each side of body, each roughly rectangular in shape, with apex notched or emarginate. L1 longer than wide; L2, L3, and L4 wider than long. One linear paraphysis between L1s, two paraphyses in every other interlobal space, lateral one in each pair near medial base of lobe delimiting lateral edge of interlobal space, this lateral paraphysis much shorter than medial one in same interlobal space. One simple plate with blunt apex between L1 and L2, and another between L2 and L3 (these are difficult to make out on holotype). Dorsum of pygidium with subtriangular area of smooth sclerotic cuticle, lateral edges converging to space between L2 and L3, two smaller elongate, oblique sclerites lateral of this sclerotic area, separated by furrows of membranous cuticle, the medial one near L3 and the lateral one anterior of L4. One-barred macroducts near L2, in and near furrows between sclerites, and along margin, decreasing in length anterolaterally. Anus small and compressed lateromedially (~5 μm wide and 15 μm long) in the posterior half of pygidium. Venter of pygidium with vulva in anterior half. One cluster of 8–10 quinquelocular perivulvar pores anterolaterally of each side of vulva.

Pre-pygidial segments. Dorsum with fine, hair-like setae, especially dense along margin, decreasing in length mesally. one-barred macroducts much shorter than those on

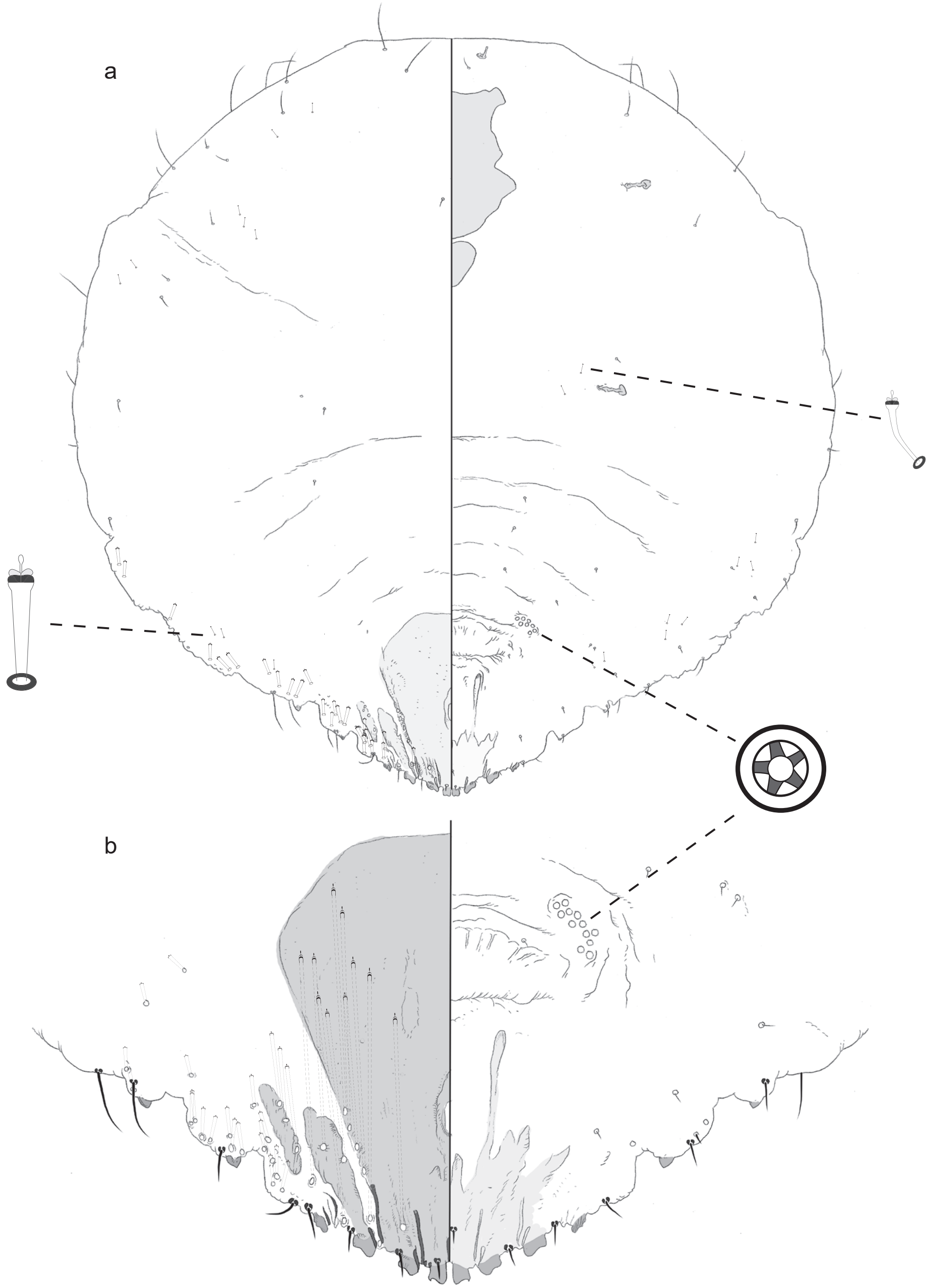

Figure 13. a Adult female of *Melanaspis nothofagi* sp. n. with enlargement of **b** pygidium.

posterior pygidial segments (~13 µm long scattered along margin of abdomen. Microducts scattered along submargin. On venter, microducts scattered along submargin of anterior abdominal segments, plus a few near posterior spiracle. Small setae in distinct longitudinal submedial and submarginal lines across abdominal segments, a few additional setae between these lines. Antenna with one long seta, one short seta evident from socket. No pores near spiracles.

Comments. With 63 described species, *Melanaspis* Cockerell is one of the more diverse genera of armored scale insects (García Morales et al. 2016). The type species is *Aspidiotus obscurus* Comstock. They occur world-wide, but more than half of the species (35) can be found in the Nearctic Region. Only *Melanaspis bromiliae* has been recorded from the South Pacific (in Guam). If we liberally define the Australasian biogeographic zone in a way that extends as far north as the Bonin Islands, we can also find *Melanaspis marlatti* (Parrott). Both of those species feed on monocots. If we cast our net even further afield, to include the Indian Ocean, we find five species recorded from Madagascar: *M. artemisiae* Mamet, *M. casuarinae* Mamet, *M. madagascariensis* Mamet, *M. philippiae* Mamet, and *M. sansevii* Mamet.

Following the generic diagnosis of Dietz and Davidson (1986), the adult female of *Melanaspis* species have (1) a circular body outline; (2) four lobes on each side of pygidium; (3) paraphyses arising from interlobal spaces, and in some species the bases of lobes or the margin up to a short distance anterior to L4; (4) dorsum of pygidium with a large medial sclerotic area, and a smaller sclerotic strap extending anterolaterally from L3 and L4; (5) interlobal areas with small plates, each with simple or slightly fringed apex. With the addition of this new species, *M. nothofagi*, no change to this diagnosis is necessary. The adult female of *M. nothofagi*, can be recognized by having (1) one group perivulvar pores on each side; (2) sclerotic teeth on marginal protrusions of posterior pre-pygidial abdominal segments; (4) a pair of linear apophyses in each interlobal area; (5) no other apophyses; (6) a sclerotic tooth on posterior of marginal lobes of posterior pre-pygidial segments.

Etymology. The epithet is taken from the genus name of the host plant genus *Nothofagus*.

Neomorgania nothofagi sp. n.

http://zoobank.org/60F7F46C-7473-49D1-9D35-B63B8510CFEE
Figure 14

Material examined. *Holotype*: New Caledonia: 1 adult female (1.08 mm long, 0.76 mm wide): *ex Nothofagus codonandra*, Riviera Bleue, 10.x.1978, JS Dugdale, BM 19 11 (NHMUK). *Paratypes*: New Caledonia: 5 adult females on 5 slides: same data as holotype, BM 19 11 (NHMUK, USNM); 6 adult females and 1 second-instar nymph on 7 slides: *ex Nothofagus baumanii*, Mt. Mou, 2.xi.1978, PN Johnson, BM 19 5, BM 19 20 (NHMUK, USNM, MNHN).

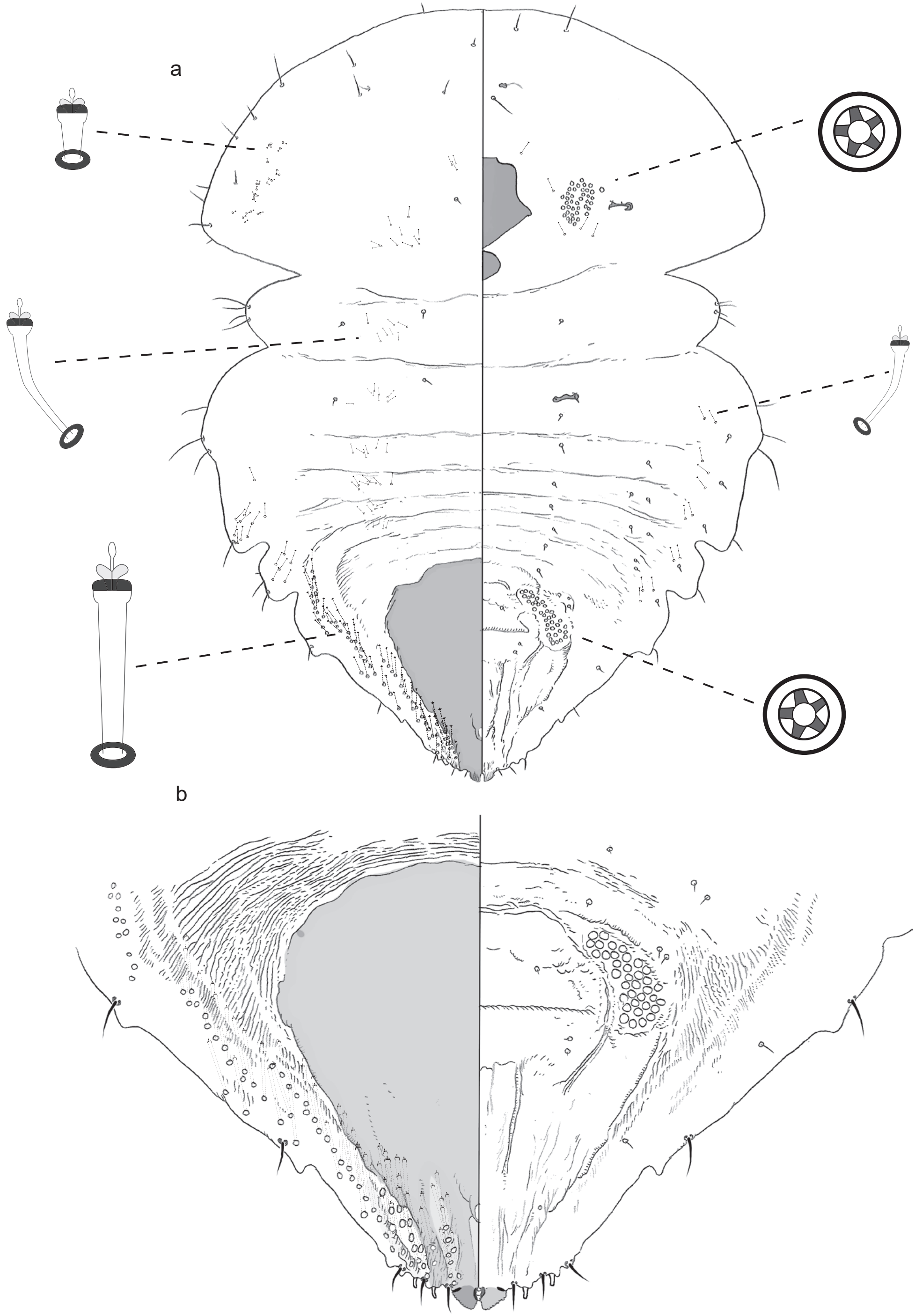

Figure 14. a Adult female of *Neomorgania nothofagi* sp. n. with enlargement of **b** pygidium.

Description. Adult female, n = 12. Presumed to secrete scale cover. Body 1.07–1.56 mm long, broadest near posterior end of fused head and prothorax (0.76–1.17 um); outline roughly turbinate (head and thorax broad, abdomen tapering caudally), deeply incised between thoracic segments and between posterior pre-pygidial abdominal segments.

Pygidium only with one lobe, L1, on each side of body, triangular in shape, with medial edge in close proximity to midline and parallel to it, apex oblique, extending to body margin. Dorsum of pygidium with subtriangular sclerotic area of smooth cuticle, lateral edges converging to posterior margin lateral of L1, with narrow, bifurcate groove in sclerotic area lateral of L1, one smaller oblique sclerite lateral of main sclerite, separated from it by membranous furrow. Anus mediolaterally compressed, ~12 μm long, 4 μm wide, in posterior third of pygidium, at anterior end of triangular, medial groove in sclerite. Two simple plates, each with blunt apex, laterad of L1 on each side of body, at base of membranous furrows. One-barred macroducts in base of bifurcate groove lateral of L1, in furrow between central sclerite and lateral sclerite, in line along submargin, decreasing in size anterolaterally. Venter of pygidium with vulva in anterior half. One cluster of perivulvar pores (30–41) on each side of body, anterolaterally of vulva.

Prepygidial segments. Dorsum with fine, hair-like setae, scattered along margin, decreasing in length mesally, one in each side of submargin and one in the submedial area of meso- and meta-thorax, only submedial seta present on prothorax. Cluster of short macroducts (~5 μm) on submargins of fused head + prothorax. Microducts in submedial clusters on each thoracic segment and anterior abdominal segments. On venter, microducts scattered along submargin of anterior abdominal segments, a few near anterior spiracle, surrounding and mixed in with cluster of disc pores. Small setae in distinct longitudinal submedial and submarginal lines across abdominal segments, a few additional setae between these lines. Antennae each with one long seta, one small seta evidenced by second socket. Large cluster of 40–55 quinquelocular pores medial of anterior spiracles. Posterior spiracles without pores.

Comments. The genus *Neomorgania* was erected by MacGillivray (1921) for the three species *Aspidiotus junctiloba* Marlatt, *A. acaciae* Morgan, and *A. eucalypti* Maskell. Brimblecombe (1954) considered these to be one and the same, and synonomized the names under *Neomargania eucalypti*, which Ferris (1941) had designated as the type species of the genus. Following Brimblecombe (1954), the following characters are diagnostic of *Neomorgania*: (1) margin of thorax with pronounced incision; (2) pygidium with only one pair of lobes, L1s, which are adpressed but not fused beyond base; (3) basal scleroses absent; (4) paraphyses present: in *N. eucalypti* these are distinct only at the lateral edge of the medial lobes, and are slightly longer than the lobes themselves; (5) no more than a single small plate lateral of the medial lobe; (6) one-barred macroducts smaller than the average across armored scale species; (7) anus small, at anterior end of triangular groove that terminates between the medial lobes; (8) margin of pygidium crenulate near medial lobes; (9) perivulvar pores absent. With a few of exceptions, the adult female of the new species, *N. nothofagi*, fits each of these definitions. The exceptions are that it has one group of perivulvar pores on each side of the body, it has two simple plates on each side of the pygidium, and the paraphyses are shorter than the medial lobes. *N. nothofagi* can also be distinguished by having the body outline incised between the meso- and metathorax, in addition to between the pro- and mesothorax. Furthermore, it has a large cluster of quinquelocular pores mesal of each anterior spiracle; pores are absent from this location in Brimblecombe's illustration of *N. eucalypti*, and he does not mention them in his diagnosis.

Etymology. We follow the practice of previous taxonomists, and take the species epithet of a *Neomorgania* species from its host plant, in this case *Nothofagus.*

Pseudaonidia dugdali sp. n.

http://zoobank.org/F94537B5-1798-430D-97BD-6E2ED6725BF5
Figure 15

Material examined. *Holotype*: New Caledonia: 1 adult female (1.64 mm long, 1.32 mm wide): *ex Nothofagus aequilateralis*, Pic du Pin, 6.x.1978, JS Dugdale, BM 19 7 (NHMUK). *Paratypes*: New Caledonia: 7 adult females (5 damaged by fungus) and 1 second-instar male on 8 slides: same data as holotype, BM 19 7, 16 (NHMUK, USNM, MNHN). *Other material:* New Caledonia: 1 adult female: same data as holotype, BM 19 16; 1 second-instar female: *ex N. aequilateralia*, Ridge of Pic du Amua, 26.x.1978, JS Dugdale, BM 19 24 (NHMUK).

Description. Adult female, n = 8. Presumed to secrete scale cover. Body 1.22–1.53 mm long, broadest near posterior end of prosoma, that is, fused head and prothorax (0.82–1.01 mm); body outline roughly turbinate (head and thorax broad, abdomen tapering caudally), incised between pro- and mesothorax, each pre-pygidial abdominal segment with membranous tooth on margin, each tooth with seta at base.

Pygidium with three well-developed lobes on each side, each roughly rectangular in shape, with distinct longitudinal striations, notch on lateral corner of apex, small paraphysis extending longitudinally from near medial edge. Each lobe extending out from body margin approximately parallel to longitudinal body axis. A small sclerotic tooth anterolateral of L3 may represent L4. Two fimbriate plates between medial lobes (L1), two between L1 and L2, 2–3 between L2 and L3, 3 anterior of L3. Pygidial margin serrate anterior to L3. Dorsum of pygidium with large medial sclerite, subtriangular, with lateral edges converging to base of L2 on each side, texture reticulate, becoming striate posteriorly, short furrow of membranous cuticle between L1 and L2, not reaching anus. Two additional dorsal sclerites, each with striated texture, first extending anterolateral from base of L3, separated from medial sclerite by membranous furrow, second lateral of the first, with another membranous furrow between them. Anus small, lateromedially compressed (15 µm long, 10 µm wide) in posterior third of pygidium. One-barred macroducts mostly in membranous furrows between sclerites, orifice of posterior-most duct in each furrow with heavy sclerosis on one or both sides. Venter of pygidium with vulva in anterior half. One cluster of 12–18 perivulvar pores, anterolateral of vulva.

Figure 15. a Adult female of *Pseudaonidia dugdali* sp. n. with enlargement of **b** pygidium.

Prepygidial segments. Dorsum with fine, hair-like setae decreasing in size posteriorly, scattered along submargin and mid line of head and prothorax, one in the submargin and one in the submedial area of meso- and meta-thorax, along with anterior abdominal segments. Microducts scattered along submargin of head and prothorax. One-barred macroducts present along margin of abdomen. On venter, microducts scattered along medial and submarginal areas of abdominal segments, a few near anterior spiracle. Antenna with one long seta, socket of second, short seta evident. Anterior spiracle with cluster of 4–6 quiquelocular pores. Posterior spiracle without pores.

Comments. Cockerell (1897) erected *Pseudaonidia* for the species *Aspidiotus duplex* Cockerell. Prior to this work, 20 species were recognized, five of which are presumed to be endemic to Australia (García Morales et al. 2016). Feng and Wei (2011) provide a diagnosis. Adult females of *Pseudaonida* have (1) a deep constriction of the body outline between the prothorax and mesothorax; (2) reticulations on the pygidial dorsum; (3) four pairs of pygidial lobes, each similar in shape and parallel to the longitudinal axis of the body; (4) well-developed plates; (5) paraphyses present or absent; if present, short; (6) slender, one-barred dorsal macroducts, each with a sclerotic rim around orifice; (7) submarginal macroducts in pore furrows; (8) the antenna with one long seta; (9) quinquelocular pores near each anterior spiracle; (10) anus small, in posterior third of pygidium; (11) the vulva anterior to anus; and (12) perivulvar pores present or absent. The adult female of *P. dugdaleii* fits each of these specifications. It can be distinguished from its congeners by (1) having a membranous tooth-like projection on the posterolateral corner of each prepygidial abdominal segment, (2) lacking perivulvar pores posterior to the vulva, and (3) having macroducts near the posterior margin of pygidium with heavy sclerotization along one or both sides of the orifice.

We have excluded one adult female specimen from the type series, although it was part of the same collection event (and presumably from the same host plant). We also excluded this specimen from the description above. This specimen differs from the others in several ways. Specifically, it (1) is longer, 2.14 mm, 40% longer than the next longest specimen; (2) has more quinquelocular pores near the anterior spiracles (11, whereas the others have between 4 and 6); (3) lacks distinct marginal teeth on prepygidial abdominal segments; and (4) has a well-developed L4. In all other respects, it looks like the other females in the same lot.

Etymology. The species epithet is a patronym in honor of John S. Dugdale, who collected much of the material on which this study is based.

Pseudaonidia yateensis sp. n.

http://zoobank.org/B9760573-24DC-4A51-AA01-D12996E7C264
Figure 16

Material examined. *Holotype*: New Caledonia: 1 adult female (0.66 mm long, 0.51 mm wide): ex *Citrus* sp., Yaté, 18.xii.2013, S Cazères, 722 7, COCHE/40/17 (NHMUK).

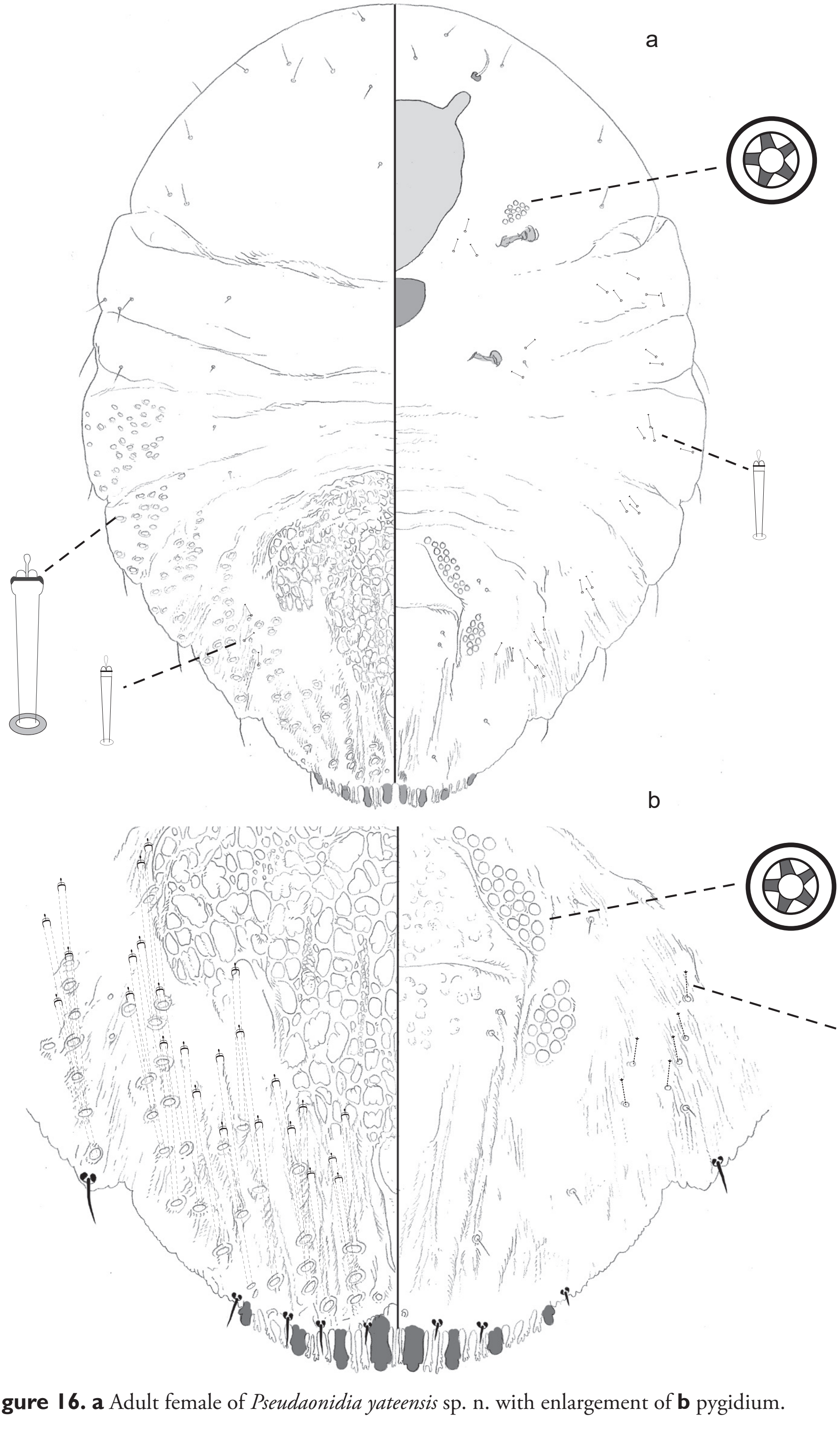

Figure 16. a Adult female of *Pseudaonidia yateensis* sp. n. with enlargement of **b** pygidium.

Paratypes: New Caledonia: 1 damaged adult female and 1 exuviae of second-instar on same slide as holotype (NHMUK).

Description. Adult female, n = 2. Presumed to secrete scale cover. Body 0.62–0.66 mm long, broadest near anterior end of abdomen (0.51–0.54 mm); body outline roughly ovate.

Pygidium with four lobes on each side, each roughly rectangular in shape, longer than wide, each extending out from body margin approximately parallel to longitudinal body axis, with notch on lateral corner of apex, medial lobes each with additional notch on medial corner. Two fimbriate plates between medial lobes (L1), three between L1 and L2, three between L2 and L3, three anterior of L3. Pygidial margin serrate anterior to L3. Dorsum of pygidium with large medial sclerotic area, subtriangular, with lateral edges converging to base of L2 on each side, texture reticulate, becoming striate posterior of anus, area of membranous cuticle between L1 and L2 expanding cephalad and extending to anus. Two additional sclerotic areas on each side of the dorsum, each with striated texture, first area may be subdivided into two sclerotic patches, extending anterolateral from base of L3, separated from medial sclerite by membranous furrow, second area lateral of the first, with another membranous furrow between them. Anus lateromedially compressed (15 µm long, 7 µm wide) in posterior third of pygidium. One-barred macroducts mostly in sclerotic areas. Venter of pygidium with vulva in anterior half. One cluster of 22–24 perivulvar pores, anterolateral of vulva, a second cluster of 13–20 pores posterolateral of vulva; on one side of body of holotype, antero- and posterolateral clusters contiguous; on paratype, one pore present anteromedial of vulva. Microducts scattered along submargin.

Prepygidial segments. Dorsum with hair-like setae scattered along submargin of head and thorax, one smaller seta in submedial area of mesothorax, metathorax and anterior abdominal segments, one long seta on posterolateral corner of each thoracic and prepygidial abdominal segment. One-barred macroducts dense along margin of abdomen. A few microducts intermixed. On venter, microducts scattered along submarginal areas of thorax and abdomen, a few near each spiracle. Antenna with one long seta. Anterior spiracle with cluster of 12–15 quinquelocular pores. Posterior spiracle without pores.

Comments. The adult female of *P. yatensis* can be easily distinguished from that of *P. nothofagi,* by (1) having four groups of perivular pores (only two in *P. nothofagi*); (2) having more pores near the anterior spiracle; (3) having most of the dorsal macroducts arise from sclerotic areas of cuticle; (4) lacking membranous teeth on margins on abdominal segments; and (5) lacking pygidial paraphyses.

Etymology. The species epithet refers to its provenance, Yaté, in the South Province of New Caledonia.

Conclusions

We have added fourteen species to the tally of armored scale insects that are endemic to New Caledonia. Given how little the New Caledonian armored scale insect fauna has been surveyed, we have every reason to suspect that a considerable amount of the species diversity is yet to be discovered. Looking at the current catalog, we can see that it has been independently colonized by armored scale insect lineages at least 17 times. This number is the most conservative estimate; it excludes non-endemic species that may have been brought to New Caledonia by people. For example, this is likely for cosmopolitan species such as *Aspidiotus nerii* (Bouche). On the other hand, this also excludes some lineages that are apt to have crossed an ocean without our help, for example *Lindingaspis buxtoni* (Laing), which has been recorded only from New Caledonia and western Samoa. If we take the current catalog at face value, it also suggests that trans-oceanic founder events may have been an especially important generator of new species diversity. Of 28 endemic species, 16 appear to share a most recent common ancestor with another New Caledonian endemic: the five species of *Andaspis* described by Hamilton et al. (2017), three species of *Furcaspis*, and two species each of *Agrophaspis*, *Aonidia, Greeniella*, and *Pseudaonidia*. This could simply be an indication that the current catalog only scratches the surface of the endemic species diversity. If not, and *in situ* speciation of armored scale insects is relatively rare in a place where it has been explosive in other lineages, this would pose an interesting biogeographical question.

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The quest for the identity of *Orthoceratium lacustre* (Scopoli, 1763) reveals centuries of misidentifications (Diptera, Dolichopodidae)

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Abstract

Recently, a species of *Orthoceratium* was collected in Greece that differs morphologically from the European species commonly presumed to be *Orthoceratium lacustre* (Scopoli, 1763). Verification of the identity of the Greek species through comparison with 460 specimens of *Orthoceratium* from 17 West Palaearctic and one Afrotropical country, and examination of existing type material, revealed that the species recognized as *O. lacustre* in northwestern Europe for over 250 years is actually *O. sabulosum* (Becker, 1907), the other known species in the genus, which was originally described from Tunisia. Although the types of *O. lacustre* have been lost, a comparison of the distribution ranges of both species in Europe provided evidence that the species collected in Greece is conspecific with *O. lacustre*. Both species have distinct distributions in the West Palaearctic, with *O. lacustre* largely restricted to the northern border of the Mediterranean basin, and *O. sabulosum* more widespread, occurring in northwestern Europe, the western, southern, and eastern Mediterranean, the Middle East, and the Afrotropical Region (Tanzania). Both species are redescribed and fully illustrated, a neotype is designated for *O. lacustre* and a lectotype for *O. sabulosum*, and a key to males and females is provided. The misidentifications that lasted for over two centuries are explained by the omission by previous authors to study the type specimens, and inaccuracies in species descriptions and keys.

Keywords

distribution, Dolichopodidae, ecology, Europe, North Africa, Mediterranean basin, *Orthoceratium lacustre*, *Orthoceratium sabulosum*, taxonomy, types

Introduction

Orthoceratium Schrank, 1803 is a nearly exclusively West Palaearctic dolichopodid genus in the subfamily Hydrophorinae (Parent 1938), with only two known species (Yang et al. 2006). *Orthoceratium lacustre* (Scopoli, 1763) has also been reported from Tanzania (Grichanov 1997, Grichanov and Brooks 2017), though the presence of this genus in subsaharan Africa has been considered doubtful (see Pollet et al. 2017). It seems most closely related to *Liancalus* Loew, 1857 and both differ from the other Palaearctic Hydrophorinae by uniseriate acrostichal bristles and a fore femur lacking ventral spines. The main features that separate *Orthoceratium* from *Liancalus* (based on the examination of two species in each genus) are given in the following key:

1 Seven dorsocentral bristles. Two large inner and two smaller outer scutellar bristles. Two basal postpronotal bristles. One proepisternal bristle. Proepimeron simple. Male: fore femur with posteroventral pollinose spot. Fore tarsus simple. Abdomen with 5th tergite with lateroventral process. Fore tarsus with one claw. Hypopygium with robust, large cercus .... ***Orthoceratium* Schrank, 1803**

\- Six dorsocentral bristles. Six equally strong scutellar bristles. One basal postpronotal bristle. Proepisternal bristles absent. Proepimeron with distinct ventral acute process. Male: fore femur simple. Fore tarsus with 2nd tarsomere flattened. Abdomen with 5th tergite simple. Fore tarsus with two claws. Hypopygium with small cercus with apical filiformous process.. ***Liancalus* Loew, 1857**

Pollet et al. (2017) reported on the recent and rather unexpected rediscovery of *O. lacustre* in Flanders (northern Belgium) after an absence of nearly 40 years. The authors also provided a full account of the distribution records of this conspicuous species in the western Palaearctic realm (Europe, North Africa, Middle East), and remarked that another *Orthoceratium* species had been collected in a mountainous region in Greece (further referred to as ‘species B’). At present, this hydrophorine genus only includes one other species, *O. sabulosum* (Becker, 1907), thus far only recorded from Tunisia.

In the process of verifying the identity of ‘species B’, the depository and availability of the type specimens of both described species was checked. This revealed that the Scopoli types of *O. lacustre* had been lost (Lorenzo Munari, pers. comm.), and that the status of *O. sabulosum* type specimens in Becker’s collection could be questioned. Moreover, series of *Orthoceratium* specimens from different European museums contained both *O. sabulosum* and ‘species B’. It thus appeared crucial to establish whether 'species B' actually corresponded with *O. lacustre* or represented a new, third species.

In the present paper, we present the results of this study, and give (re)descriptions of the species and information on their distribution and ecology. We finally discuss the plausible reasons for the continuous series of misidentifications, and the significance of type specimen examination.

Materials and methods

Two specimens of *Orthoceratium sabulosum* from the Becker collection (Museum für Naturkunde, ZMHB, Berlin, Germany) with a lectotype and paralectotype label resp., were examined. Although the validity of their designations might be questioned (see Redescription of *O. sabulosum*), there is no doubt that these specimens are part of Becker's original type series. Types (presumably syntypes) of both *O. sabulosum* (initially deposited in the Hungarian Natural History Museum, HMHN, Budapest, Hungary) and *O. lacustre* (Scopoli collection) appear to be lost. All insects collected by Scopoli in Carniola were destroyed during fires in Scopoli's house in Idria (Italy) in 1787 (Smith 1793, Roller and Haris 2008). None of these specimens could be located in the Museo Civico di Storia Naturale (MSNV, Verona, Italy) (Leonardo Latella, pers. comm.) or the Museo di Storia Naturale, Università degli Studi (MSNP, Pavia, Italy) (Carlo Giovanni Violani, pers. comm.). In addition, specimens determined as '*Orthoceratium lacustre*' from nine major European museums, one Turkish museum, one Bulgarian institute, the private collections of both authors (see further) and that of Miroslav Barták (Prague, Czech Republic) were also investigated.

(Re)descriptions are based on a large number of representative specimens of each species, both in alcohol and pin-mounted. A total of 173 character states was scored, with 35, 61, and 77 related to the head, thorax/abdomen/wing, and legs respectively. This allowed us to determine the most reliable and consistent decisive diagnostic features that were subsequently applied in the key.

Relevant non-genitalic diagnostic characters in collected specimens were photographed by the junior author. The hypopygium and tergite V of each species were drawn using a camera lucida. The left lateral view of the hypopygium is illustrated here. In describing the hypopygium, 'dorsal' and 'ventral' refers to the morphological position prior to genitalic rotation and flexion. Thus, in the drawings showing a lateral view of the hypopygium, the top is morphologically ventral, while the bottom is dorsal.

Biometrics were generally based on five specimens (wet = preserved in alcohol solution) of each gender in each of the two species unless otherwise mentioned, and include: (i) face width, (ii) body length, (iii) wing length (= distance between basis of basicosta and wing apex), (iv) relative wing width, (v) proximal versus apical section of vein M_1, (vi) proximal versus apical section of vein CuA_1, (vii) CuA_x ratio (= crossvein dm-cu versus apical section of vein M_1) and (viii) relative lengths ratio of femur, tibia and tarsomeres of each leg. The latter relative lengths were recalculated so that the shortest leg part represents a value of "1". Wing length was measured in both dry and wet specimens. All values given in this paper are average values, unless otherwise mentioned. Palp and proboscis size is compared to the eye size, measured as the vertical diameter (from about ocellar tubercle to the lower eye margin). Wing length was measured in 76 and 142 specimens of *O. lacustre* and *O. sabulosum* resp., to find out if differences occurred between both species and separate populations (see Table 1).

Capture locations of *Orthoceratium* specimens are given in Figure 1, if sufficient information on the site was available either from the label of the specimen or – if this was lacking – as provided by the collection curator. Only specimens were considered which had been effectively examined, in most cases by the senior author. Each location has been positioned on the map as accurately as possible, based on the information available. If only the locality (e.g., a city) was known, then the symbol in Figure 1 is shown in the centre of this locality which might not necessarily correspond exactly with the actual collecting site.

The general morphological terminology follows Cumming and Wood (2009), while Brooks (2005) was used for male genitalia. The following abbreviations were used:

ac	acrostichal bristles;
ad	anterodorsal;
ant pprn	anterior postpronotal (= humeral *sensu* Parent 1938);
ap	apical;
apv	apicoventral;
av	anteroventral;
bas pprn	basal postpronotal (= posthumeral *sensu* Parent 1938);
bv	basoventral;
dc	dorsocentral bristle pairs;
ds	dorsal;
MSSC(s)	male secondary sexual character(s);
npl	notopleural;
pal	postalar;
pd	posterodorsal;
psut ial	presutural intra-alar (= presutural *sensu* Parent 1938);
pv	posteroventral;
S	abdominal sternite;
spal	supra-alar;
sut ial	sutural intra-alar (= sutural *sensu* Parent 1938);
ta	tarsomere, $_{1\text{-}5}$ in the descriptions of tarsi refers to basal ($_{1}$) to apical ($_{5}$) tarsomeres;
T	abdominal tergite;
vt	ventral;
I, II, III	refers to fore, mid and hind leg;
I–VI	in the descriptions of abdominal segments (tergites/sternites) refers to basal ($_{I}$) to caudal ($_{VI}$) segments.

Institutional, collection and other abbreviations:

ANSC	Andreas Stark private collection, Halle/S., Germany;
NHMUK	The Natural History Museum, London, UK;
HMNH	Hungarian Museum of Natural History, Budapest, Hungary;
IBER	Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria;
MAPC	Marc Pollet private collection, Welle, Belgium;

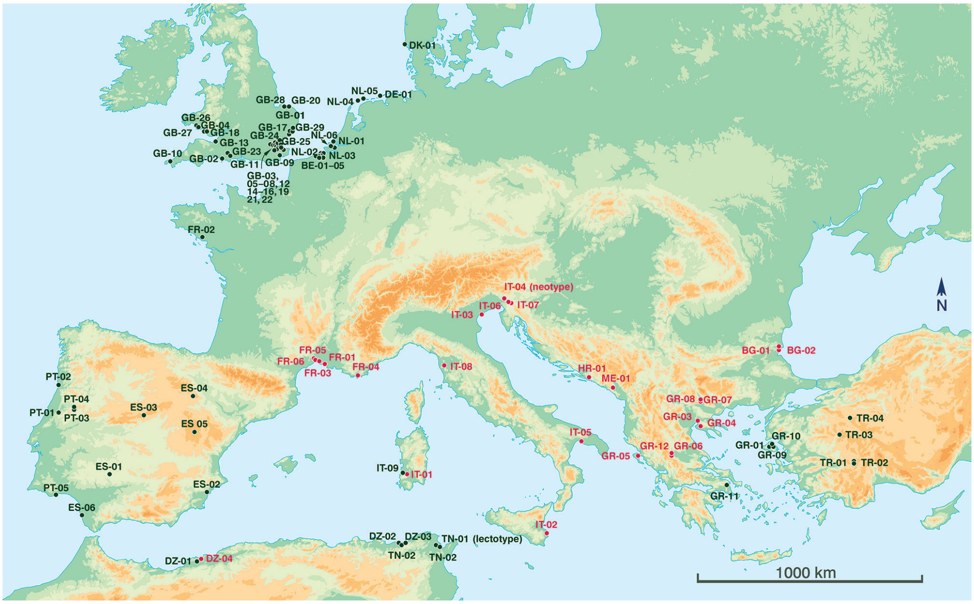

Figure 1. Distribution ranges of *Orthoceratium lacustre* (red symbols, incl. type locality of neotype) and *O. sabulosum* (black symbols, incl. type locality of lectotype) in the West Palaearctic (Iranian records not included). Information related to the site codes is given in Suppl. material 1. List of (non-type) records of *Orthoceratium*.

MIBC	Miroslav Barták private collection, Prague, Czech Republic;
MNHN	Muséum national de l'Histoire naturelle, Paris, France;
MLUH	Zentralmagazin naturwissenschaftlichen Sammlungen, Martin-Luther-Universität, Halle/S., Germany;
NHMW	Naturhistorisches Museum, Vienna, Austria;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMNH	Naturalis Biodiversity Centre, Leiden, Netherlands;
ZFMK	Zoologisches Forschunginstitut und Museum A. Koenig, Bonn, Germany;
ZLKU	Zoology Laboratory, Department of Biology, Faculty of Science, Muğla Sıtkı Koçman University, Muğla, Turkey;
ZMHB	Museum für Naturkunde, Berlin, Germany;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

Other abbreviations: **MT**: Malaise trap, **SW**: collected by sweepnet.

Label information of mounted specimens is provided in full and with the original spelling. If not indicated otherwise, the label was white and rectangular, and information is from the top side. Label information is given from the top downward, with data from each label between quotation marks, and data from different lines on the same label separated by a slash (/). Information from different labels is separated by a semicolon (;). The species record is followed by the repository of each specimen between square brackets [ ]. In addition to the label information, for non-type specimens, the most relevant label information is enriched, uniformly structured and given in the following format: "(site code) – COUNTRY: ♂, ♀, province (or equivalent administrative division), locality, location/area, latitude, longitude, altitude, sampling date (start) – sampling date (end), sampling method, collector [collection]" (see Suppl. material 1. List of (non-type) records of *Orthoceratium*). The site code is also used in Figure 1. All specimens examined were pinned, unless otherwise mentioned (W: wet alcohol sample).

Results

A total of 428 specimens of *Orthoceratium* from eight European museums and three other collections has been examined, mainly by the senior author; the identity of two, two, five and 23 additional specimens from HMNH, ZMUC, ZLKU and MIBC was kindly checked by Zoltán Soltész, Thomas Pape, Alper Tonguç, and Miroslav Barták, resp. Laurence Clemons (Kent, UK) also confirmed the identity of the specimens listed in Clemons (2003). The following museums did not hold any identified *Orthoceratium* material: NMPC: National Museum (Natural History), Prague, Czech Republic; MSNVE: Museo di Storia Naturale, Venice, Italy. The specimens originated from 17 different countries in the West Palaearctic, including 13 European, two North African and two Middle East ones, and one Afrotropical country.

Literature study

To our surprise, the examination of the type material of *Orthoceratium sabulosum* revealed that the species widely known (and collected) as '*O. lacustre*' in northwestern Europe was conspecific with this species. This held true for nearly all specimens of '*O. lacustre*' examined from North Africa and the Middle East (Turkey, Iran) as well. The question evidently raised if 'species B' then represented the true *O. lacustre* or not. As mentioned before, establishing the species concept of the latter species proved difficult due to the loss of the type material. Hence, the original description and other literature sources were studied carefully in search for information on significant diagnostic features that matched those of 'species B'.

Scopoli (1763) described *Musca lacustris* (later transferred to *Orthoceratium*, most presumably by Schrank (1803)) as follows:

"Diagn. Thorax aeneus. Abdomen viridi-aeneum. Ambulat super aquas stagnantes tanquam *Cimex Lacustris* [now in *Gerris*]. Habitat in lacubus. Frons subargentea. Oculi virides. Pili duo divaricati in occipite. Antennae nigrae, clavatae, obtusae. Rostrum palpis subvillosis, parvis. Thorax aeneus, glaber. Alae hyalinae, immaculatae; costa antice ferruginea. Scutellum edentatum, rotundatum, pilosum. Abdomen lineam longum, viridi-aeneum, albido villo adspersum, subtus subfuscum: segmentis lateraliter punctatis. Pedes longi: lamellis unguium pallidis."

Unfortunately, all listed characters fit both *O. sabulosum* and 'species B'. Scopoli's species, however, seemed to occur in stagnant water bodies (see original description) like e.g., inland lakes, and did not seem to be confined to saltmarshes or brackish marshes like *O. sabulosum* in northwestern Europe.

As the Scopoli type specimens of *O. lacustre* were destroyed as early as 1787, it is unlikely that Haliday (1851), Loew (1857), Schiner (1862) or Mik (1878) had the opportunity to examine these specimen(s). Haliday's (1851: 182–183) description of this species only contains the following relevant information:

"Wings hyaline, usually tinged with ferruginous towards the fore edge, … Abdomen of the male … lamella oblong, compressed, broad at tip and truncated. … On waters, both fresh and brackish. (E[ngland]. I[reland])."

However, it can be assumed that Haliday based this description on '*O. lacustre*' from England or Ireland, which now appears to be *O. sabulosum*.

Schiner (1862) gives the following description (of *Liancalus lacustris*):

"Beine schwarz mit gelben Knieen und Gelenken. — Metallisch-grün. Untergesicht silberweiss schimmernd. Fühler schwarz. Rückenschild undeutlich gestriemt. Analanhänge länglich, zusammengedrückt, am Ende breit und abgestutzt. Schenkel oben grün, auch der hinterste Metatarsus. Flügel glashell, gegen den Vorderrand gewöhnlich bräunlich, gelblich tingirt, die vierte Längsader gebrochen. 2 2/3 '". Nach Scopoli in [Herzogtum] Krain; ich erhielt die Art durch Hrn. Micklitz aus dem Küstenlande."

Neither Loew (1857) nor Mik (1878) provided useful information for the recognition of *O. lacustre*. The former author did mention that *O. lacustre* (then in *Liancalus*) was considered much rarer than *Liancalus virens* (Scopoli, 1763) and that its distribution ranged from England to Sicily. It seems like he actually saw specimens as he reports on the colour of teneral specimens.

Becker (1907) described *Alloeoneurus sabulosus* on the basis of specimens from Tunis (HMHN); two years later this genus was listed as synonym of *Orthoceratium* by Kertész (1909). Becker (1907) initially remarked that this species is different from the known and described species, larger than *A. lacustris* and featuring brownish wings. In his key to the species, he summarizes the most diagnostic features that separate both species as follows:

> "Face white, hardly wider than postpedicel (length) (male). Mesonotum dusted whitish grey on dorsum; sternite IV with ventral process (male). Wing entirely hyaline. Size 5 mm .... *O. lacustre* (Scopoli, 1763)
> Face grey, about 2 × as wide as postpedicel (length) (male). Mesonotum dusted yellowish grey on dorsum; sternite IV normal (without process) (male). Wing brownish. Size 6 mm.. *O. sabulosum*" [trans.]

The only feature of *O. lacustre* in this key that matches 'species B' is the narrower face, compared to *O. sabulosum*. But specimens of both species show an equally large variation in the colour of the wings and the dusting of their pronotum. This is quite remarkable as we believe that Becker actually had specimens of both species at hand when he described *O. sabulosum*, as he repeatedly refers to *O. lacustre*. Why he used doubtful differences in his key or even mixed up features (see further) is unclear, but possibly he only had one single or a small number of *O. lacustre* specimens to compare with.

Ten years later, Becker (1917) published a similar key and added a drawing of the hypopygium and wing of *O. lacustre*. The shape of the ventral process of the 5th tergite (not 4th sternite, as mentioned by Becker 1907!) and the dense pubescence on the cercus apex clearly match those of 'species B'.

Parent (1938) mentioned that *Orthoceratium* includes littoral species that occur at the borders of small streams and lakes in saltmarshes ('*Slikke des Belges*'), and reported *O. lacustre* from France, and *O. sabulosum* from Tunisia. His description of *O. lacustre*, however, clearly points to *O. sabulosum*: face wide, about 2/5 of eye width, and a black bristle present amid coxa I. Some of his figures (fig. 466: postpedicel, fig. 467: abdomen, especially the posteroventral process of T_V) confirm this conclusion.

The key to both species by Negrobov (1979) is largely a copy of the Becker (1907) key. He omitted the body length as a diagnostic feature and corrected the sternite IV into tergites IV–V. He also gives a full description of both species. Only drawings of the genitalia of *O. lacustre* are included (Negrobov 1978) though the author mentions to have examined the *O. sabulosum* types (ZMHB), however, without giving details on the specimens. On the basis of the description and especially the drawings of the hypopygium (figs 1331–1334, 1335, 1337), we can conclude that Negrobov's *O. lacustre* matches 'species B' exactly. Next to the fact that it was unclear where the specimens – that he used for the description of *O. lacustre* – originated from (Oleg Negrobov, pers. comm.), the question remained if his species (and 'species B') was the true *O. lacustre*. Indeed, Negrobov was not able to examine the type specimens of *O. lacustre* nor did the extant literature provided decisive information (as shown above).

Distribution patterns

In a second stage of the verification process the type locality was considered to comprise a possible clue about the identity of *O. lacustre*. Scopoli collected the species in Carniola ('Krain' in German), a historical region that corresponds mainly with inland parts of present-day Slovenia, including mountains. Since Scopoli stated that the species skated on backwaters ["*ambulat super aquas stagnantes*"] and occurred in or along lakes ["*in lacubus*"], it could further be assumed that he collected the species in inland wetland habitats (and not along the coast).

To find out exactly where this type locality was situated within the distribution ranges of *O. sabulosum* and 'species B', capture locations of both species were plotted on a map of the West Palaearctic (see Figure 1). This clearly revealed that the ranges of both species only just overlap at three sites (Algeria, Greece, Sardinia) but otherwise show a distinctly different distribution: *O. sabulosum* seems to occupy the coastal region of northwestern Europe, western (Spain, Portugal), southwestern (Algeria and Tunisia in North Africa) and eastern borders of the Mediterranean basin (Greece, Turkey), but also Iran (not indicated on the map, see Kazerani et al. 2014) and Tanzania (not indicated on the map, Grichanov and Brooks 2017; see also further). In contrast, 'species B' seems to be largely restricted to the northern Mediterranean region. As the type locality of *O. lacustre* is situated within the distribution range of 'species B', and no other species has been detected in the extensive examined material, it could finally be concluded that 'species B' must be conspecific to *O. lacustre*. Subsequently, a male specimen collected in Görz [= Gorizia] (Italy), the locality closest to the type locality of this species, was selected as neotype (see below, Figure 2).

Systematic accounts (see Pape et al. 2011)

Order Diptera Linnaeus, 1758
Suborder Brachycera Macquart, 1834
Clade Eremoneura Lameere, 1906
Superfamily Empidoidea Latreille, 1804
Family Dolichopodidae Latreille, 1804
Subfamily Hydrophorinae Becker, 1917
Genus *Orthoceratium* Schrank, 1803 (monotypic)

Orthoceratium lacustre **(Scopoli, 1763)**

Figs 1, 2, 3A–B, 4A, B, D, F, 5A–B, 6A–B, 7, 10B

Musca lacustris Scopoli, 1763: 343. Type locality: Carniola (= present-day Slovenia) – presumably transferred to *Orthoceratium* by Schrank (1803)

Notes on synonyms. *Musca formosa* Haliday, 1832 and *Medeterus viridipes* Macquart, 1834, previously listed as synonyms of *O. lacustre*, clearly refer to *O. sabulosum* (see further).

Diagnosis. Large, short-bodied, slender, entirely green species with abdomen 1.6 × as long as thorax (Figs 2, 3A, B). All legs mainly dark and metallic with narrowly yellow knees. Wing smokey reddish yellow, with reddish yellow veins (Fig. 5A, B). Apical section of vein M_1 with strong sinous bend at ½. Posterior border of wing indented at vein CuA_1. Coxa I with strong white pubescence, and with three black bristles only at apex. Coxa II with only pale bristles at apex anteriorly. Pedicel with short apical bristles (Figure 4F). Ac uniseriate, rather small, at most 1/3 as long as dc. Male: face not as wide as postpedicel is long (Figure 4A). Postpedicel elongate triangular, at least 1.2 × as long as deep (Figure 4D). T_V with blunt ventral process at each side bearing short dark separate bristles (Figure 10B). Femur I with small ovoid brownish yellow pv tuft just beyond basal 1/4, about 1/8 of femur length (Figure 6A). Femora I–II with multiple rows of very short white erect setae on basal ½. Tibia II with three ad bristles, with basal bristle shorter, and with one av bristle. Tibia III with four strong and one small pd bristles. Tarsus I with only one claw, and tarsomere taI_1 mostly unmetallic (Figure 6B).

Figure 2. *Orthoceratium lacustre*, habitus (male neotype), and the original labels.

Redescription. Male. Body length: 5.0–5.7 mm (n = 25); wing length: 5.2–6.2 mm (n = 44), 0.3 × as wide as long. **Head** (Fig. 4A, B, D, F). Face silvery white, slightly narrowing towards middle of face, then widening towards clypeus, latter with triangular lower margin, weakly projecting; face 0.9 × as wide as postpedicel (length), with short white pubescence. Frons with metallic green ground colour, strongly dusted yellowish white. Occiput with metallic green ground colour, dusted whitish, convex in middle. Palp 1/5–1/4 of eye, triangular, dark brown, strongly dusted whitish, with white pubescence, and apical bristle absent. Proboscis dark brown. Eyes red, with short white pubescence. Uppermost seven to nine postocular bristles erect, black, and lower bristles curved, white, forming whiskers. One pair of black postocel-

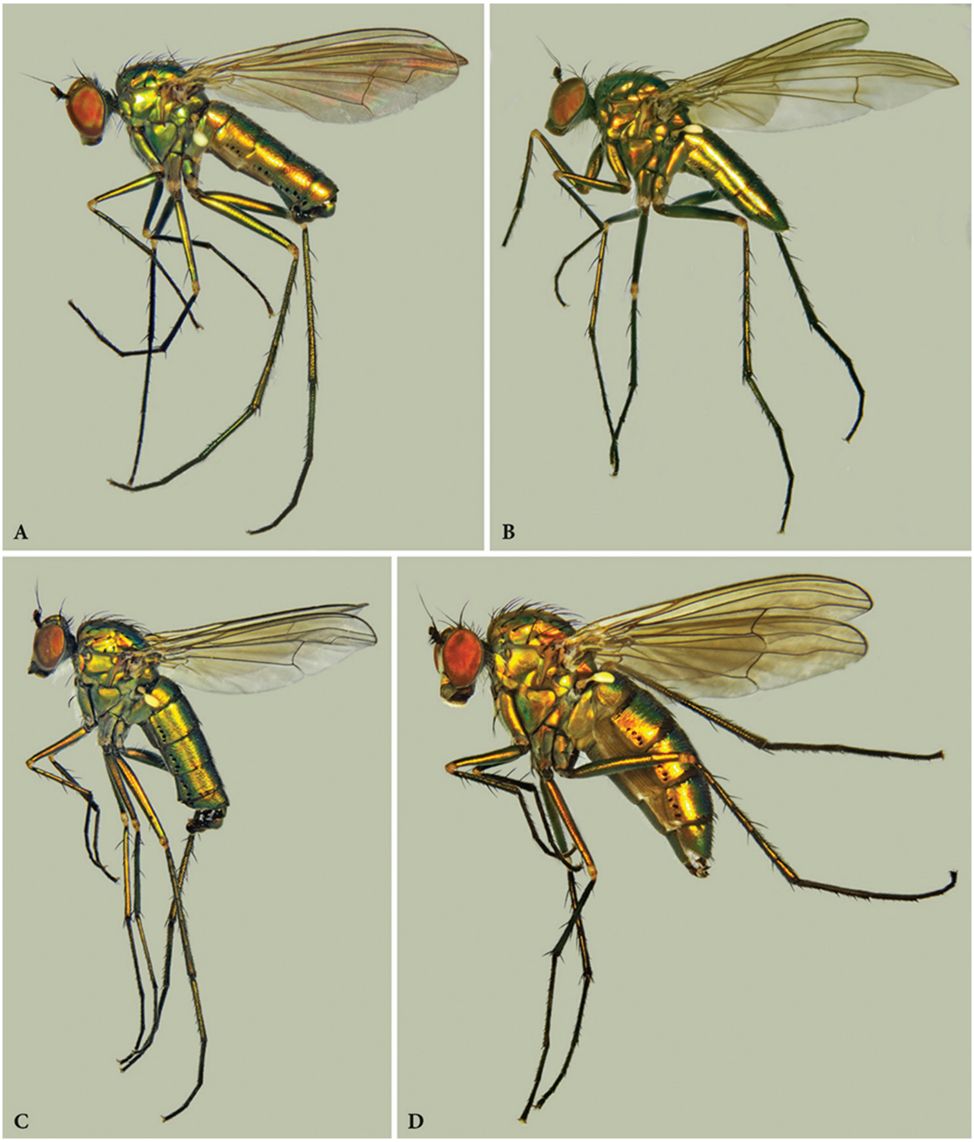

Figure 3. *Orthoceratium lacustre*, habitus (W): **A** male **B** female. *Orthoceratium sabulosum*, habitus: **C** male **D** female. Same scale in all pictures.

lar bristles. Antenna entirely dark brown, with scape bare and pedicel with apical crown of short bristles; postpedicel dark brown, elongate triangular, with blunt apex, 1.2–1.4 × as long as deep, 0.9–1.3 × as long as scape and pedicel combined, with short pubescence; arista-like stylus dorsal, inserted at middle of upper rim of postpedicel, 2.0–2.4 × as long as first three antennal segments combined, bare. **Thorax** (Figs 2, 3A). Mesonotum entirely brilliant metallic green with sometimes bluish violet tinge, strongly dusted greyish white on pleura and certain zones on dorsum, only

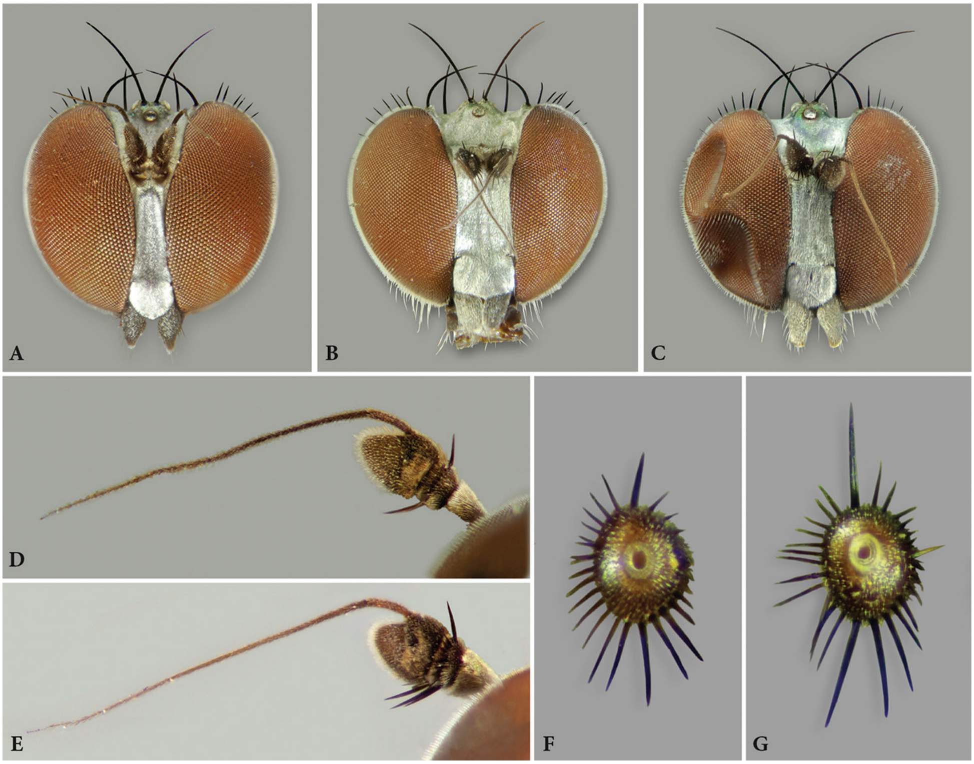

Figure 4. *Orthoceratium lacustre*, head: **A** face (male) **B** face (female) **D** antenna (male) **F** pedicel, posterior view (male). *Orthoceratium sabulosum*, head: **C** face (male) **E** antenna (male) **G** pedicel, posterior view (male).

without dusting between dc and ac, and between dc and npl areas; scutellum bluish violet, bare on dorsum, with four marginal bristles, lateral pair much smaller than median pair. Anterior spiracle with group of multiple curved, yellowish white, long setae. Thoracic bristles black. Seven dc, with 1st dc laterally off-set, and 6–7th dc stronger; three to five ac, uniseriate, reaching level between 5th and 6th dc, rather small, at most 1/3 × as long as dc; with two strong black and one minute white ant pprn, one internal and one external bas pprn, one psut ial, one sut ial, two npl, two spal, and one pal bristles. Upper proepisternum with a large group of long yellowish white curved setae; lower proepisternum with one strong black curved bristle and a small group of yellowish white curved setae. **Wing** (Figure 5A). Smokey reddish yellow, with reddish yellow veins. Vein R_{4+5} sinuous near wing apex, there parallel with vein M_1; apical section of vein M_1 with strong sinous bend at ½ (MSSC); crossvein dm-cu rather straight; posterior border of wing indented at vein CuA_1. Proximal section of vein M_1 1.9 × as long as apical section. Proximal section of vein CuA_1 8.5 × as long as apical section. CuA_x ratio: 1.7. Halter pale, calypteral fringe yellowish white. **Legs** (Figs 2, 3A, 6A–B). Overall dark, metallic green to violet, with pale yellow knees in all legs, and with black bristles. Coxae dark, with metallic green ground

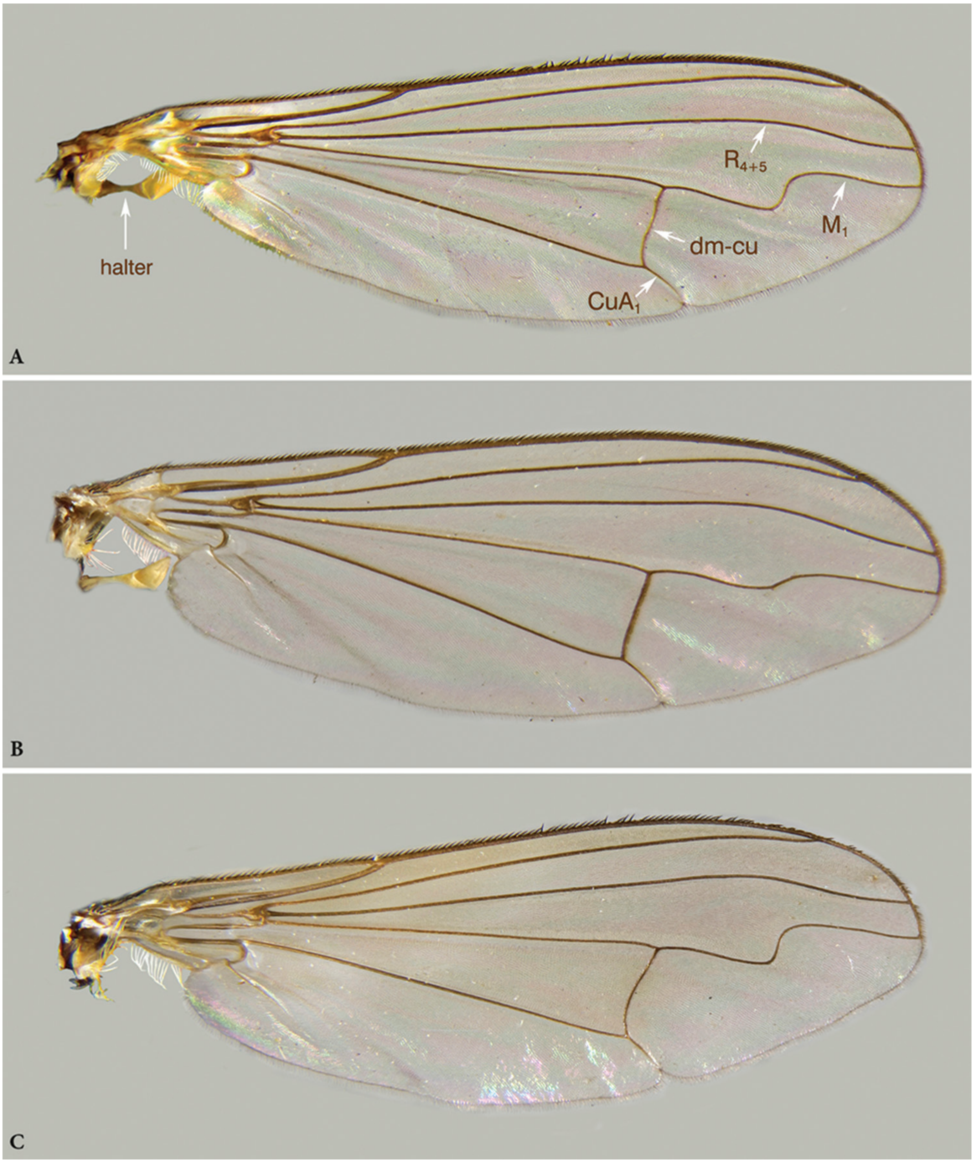

Figure 5. *Orthoceratium lacustre*, wing and halter: **A** male **B** female. *Orthoceratium sabulosum*: **C** wing (male). Veins R_{4+5}, M_1, CuA_1, and dm-cu indicated.

colour and strongly dusted whitish, coxae I–II with about apical 1/4 yellow, coxa III with about apical 1/3 yellow. Coxa I with dense, white pubescence and three rather small, black ap bristles. Coxa II with dense white pubescence on anterior face, and one black inclined bristle at 1/2 on margin; lateral face bare. Coxa III with one black, erect external bristle, inserted at 1/2, with vertical row of white setae. Trochanters dark brown. Femora I–III brilliant metallic green, sometimes with violet tinge, fem-

Figure 6. *Orthoceratium lacustre*, male: **A** femur I (posteroventral view) **B** tarsomere I_5, with left tarsus on the left and right tarsus on the right hand side (dorsal view). *Orthoceratium sabulosum*, male: **C** femur I (posteroventral view).

ora I–II with pale yellow knee on apical 1/8, and on apical 1/10 in femur III. Femur I with multiple rows of very short white erect setae on basal ½ (MSSC); with small ovoid brownish yellow pv tuft just beyond basal 1/4, about 1/8 of femur length (MSSC); with one rather small pv preapical bristle. Femur II with one strong ad preapical bristle, at less than apical 1/5, and with one small pv preapical bristle; with one row of very short white erect vt setae on basal 1/3 (MSSC), and with one row of short inclined pv setae along entire length, white on basal 2/3 and black on apical 1/3, longest at basis and apex. Femur III with one strong ad preapical bristle, at about apical 1/3, and one small pv preapical bristle; sometimes with some thin inclined (thus not erect!) ds bristles in basal 1/5. Tibiae I–III brilliant metallic green to violet, tibia I with basal 1/8, tibia II with basal 1/9, and tibia III with less than basal 1/10 pale yellow. Tibia I with two ds bristles, 2–3 × as long as tibia is deep; with two small ad bristles, 1–1.5 × as long as tibia is deep, and with two to three pv bristles, 2–3 × as long as tibia is deep; with white pilosity on av face along entire length, and with two small ap bristles. Tibia II with three ad bristles, about 3 × as long as tibia is deep,

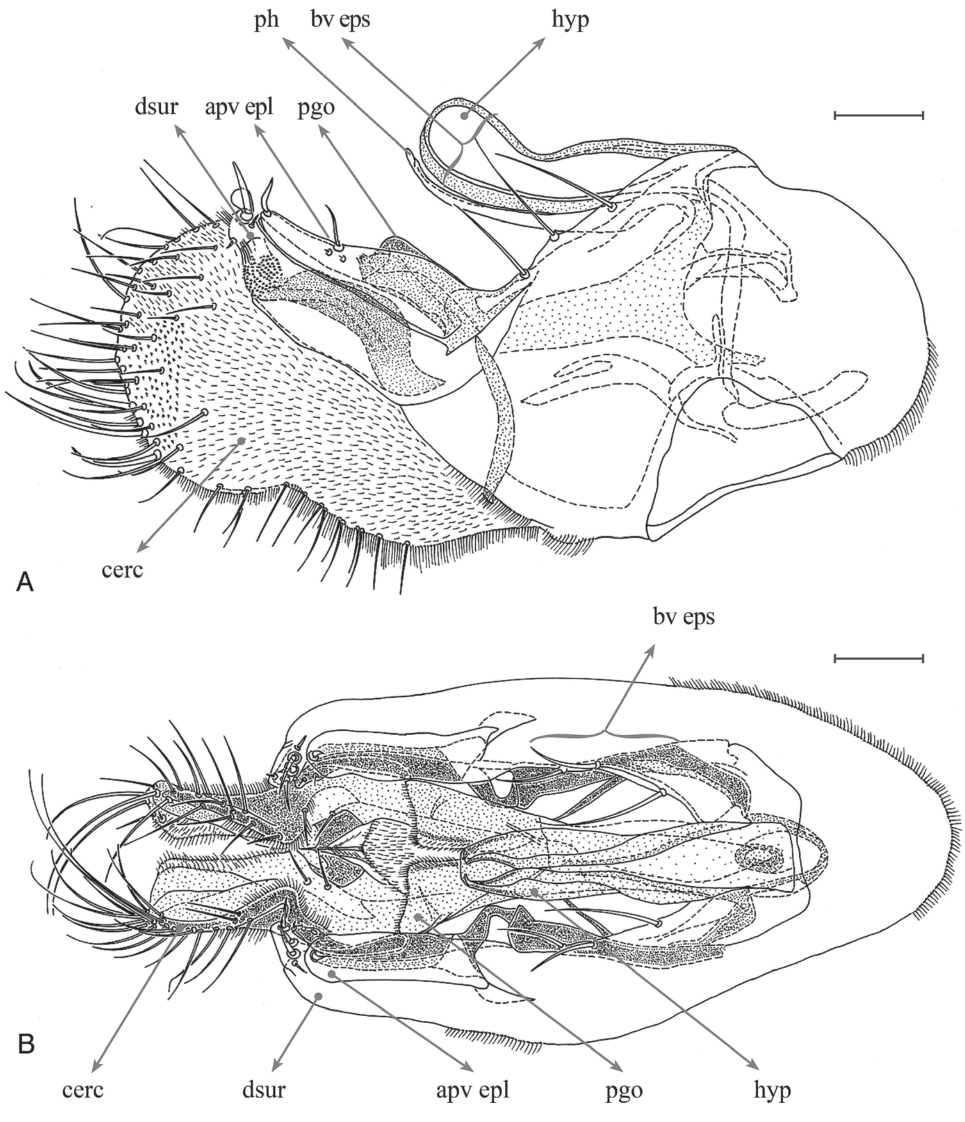

Figure 7. *Orthoceratium lacustre*, hypopygium: **A** left lateral view **B** ventral view. Abbreviations: hyp: hypandrium, ph: phallus, bv eps: basoventral epandrial setae, apv epl: apicoventral epandrial lobe, dsur: dorsal surstylar lobe, pgo: postgonites, cerc: cercus. Scale bars: 0.1 mm.

with basal bristle shorter; with two pd bristles, 2 × as long as tibia is deep, with basal bristle shorter, and with four ap bristles; with one av bristle at basal 2/3 and one pv bristle at basal 1/5, both 2 × as long as tibia is deep; and two small pv bristles in apical 1/2, not as long as tibia is deep. Tibia III with five ad bristles, about 2.5 × as long as tibia is deep, four strong and one small pd bristles, former about 2.5 x, latter not as long as tibia is deep, and four strong ap bristles; with distinct pd row on apical 1/2;

with three-four av bristles, 1–1.5 × as long as tibia is deep, and with multiple shorter pv setae along entire length. Tarsi I–III dark brown, with taI_1 mostly unmetallic and $taII_1$ and $taIII_1$ with metallic green to violet reflection. Tarsus I with taI_1 with pale ventral pubescence (MSSC) with some darker short bristles; taI_5 with long curved dorsal setae at apex, 0.7 × as long as taI_5 length; only inner claw present (MSSC). Tarsus II with $taII_1$ with multiple short vt bristles, nearly as long as $taII_1$ is deep. Tarsus III with $taIII_1$ with multiple inclined vt bristles, longest about as long as $taIII_1$ is deep. Ratio of femur/tibia/tarsomeres 1–5 in leg I: 10.3/11.4/6.3/2.2/1.5/1/1.1, in leg II: 9.5/12.2/8.4/3.7/2.4/1.3/1, and in leg III: 10.6/15.3/6.7/4.6/2.8/1.4/1. **Abdomen** (Figure 2, 3A). Basal five segments pubescent, 6th bare, minute, only visible dorsally. T brilliant metallic green, with bluish or with bronze tinge in some specimens, strongly dusted whitish on lower margins, with short dense black pubescence on dorsum, long yellowish white setae laterally, strongest on sides of T_I, and $T_{I–IV}$ with black bristles on posterior margin, strongest on T_I; T_V brilliant metallic green without prominent dark bristles on posterior margin, with blunt ventral process at each side, with short dark separate bristles (MSSC) (Figure 10B). ST with green ground colour, strongly dusted whitish, with yellowish white, erect bristles. Hypopygium (Figure 7) with epandrium concolorous with tergites; hypandrium rather stout with subcircular apex, with ventrally curled up sides forming a gutter; phallus slender and strongly curved; three basoventral epandrial setae of subequal size, and apicoventral epandrial lobe pale reddish yellow, stout, narrowing towards apex and adjacent to outer surstylar lobe; surstylus with robust pale reddish yellow outer (or dorsal) lobe with area of minute spines near apex and with subcircular bristle at apex, inner (or ventral) surstylar lobe dark, robust with tapering apex baring a few bristles; postgonites robust, dark, with apical pubescence and a vt process; cercus dark brown, medium-sized, rather rectangular, apex large subcircular, with dense yellow pubescence, dark brown. **Female** (Figure 3B). Body length: 5.4–6.2 mm (n = 23); wing length: 5.2–6.7 mm (n = 51), 0.3 × as wide as long. As male, except for: abdomen 1.4 × as long as thorax, slender. Face 1.7–2.3 × as wide as postpedicel (length). Frons ground colour metallic green, strongly dusted yellowish white. Palp ovoid. Uppermost eight to ten postocular bristles black. Antenna dark brown, with scape sometimes paler (yellowish brown); postpedicel triangular, with blunt apex, 0.9–1.1 × as long as deep, 0.8–0.9 × as long as scape and pedicel combined; arista-like stylus 2.4–2.7 × as long as first three antennal segments combined. Thorax with four to five ac, reaching between 4th or 5th dc. Wing (Figure 5B) with vein R_{4+5} bended but straight near wing apex, there parallel with vein M_1; apical section of vein M_1 with weak bend (sinuous) at 1/2; crossvein dm-cu straight. Proximal section of M 1.7 × as long as apical section. Proximal section of CuA_1 6.9 × as long as apical section. CuA_x ratio: 1.6. Coxa I with two to three rather small, black ap bristles. Femur I bare ventrally. Femur III often with some thin inclined ds bristles in basal 1/5. Tibiae I–II with basal 1/10 pale yellow; tibia I with three pv bristles. Tibia II with two av bristles at basal 2/5 and 2/3, 2–2.5 × as long as tibia is deep, and four small pv bristles on entirely length, not as long as tibia is deep. Tibia III with ad bristles about 3 × as long as tibia is deep, and with four strong pd bristles, 2.5–4 × as long as tibia is deep. Tibia III with av bristles 1.5–2.0 × as long as tibia is deep. Tarsus I with taI_1 with multiple short black ventral bristles, nearly as long as taI_1 is deep; taI_5 with both claws. Ratio of femur/tibia/tarsomeres 1–5 in leg I: 8.6/9.5/5.7/2.3/1.5/1/1.1, in leg II: 9.1/11.6/8.1/3.4/2/1.2/1, and in leg III: 10.6/15/6.4/4.3/2.6/1.4/1. Abdomen with five pubescent segments, 6th invisible; also ST_{IV} with strong whitish dusting.

Type specimens. ITALY: **NEOTYPE** (here designated to fix the identity of the species) ♂, [brownish rectangular] "*Liancalus*/ *lacustris* Scp"/ "Görz." [= Gorizia, in Friuli-Venezia Giulia region]; "Zool. Mus."/ "Berlin"; "*Orthoceratium lacustre*"/ "(Scopoli, 1763)"/ "det. Marc Pollet, 2017"; [red rectangular] "NEOTYPE" / "des. Marc Pollet, 2018" (2017 on initial label in Figure 1) [ZMHB] (IT-04).

Other material examined. See Suppl. material 1. List of (non-type) records of *Orthoceratium*.

Remarks. In order to fix the identity of the species, a neotype of *O. lacustre* was selected on the basis of the locality (closest to the original type locality or region), and the preservation status of the specimen (see Figure 2).

Of all examined specimens (n = 131) one Trieste specimen featured a strong curved black bristle on the right fore coxa.

Distribution. As a result of the taxonomic mix-up between both species in the past, previous distribution records of *O. lacustre* in the literature – many of which refer to *O. sabulosum* in reality – must be considered unreliable. Our present study revealed that *O. lacustre* has been collected nearly exclusively along the northern border of the Mediterranean basin (incl. adjacent islands), both in coastal habitats and inland (montane) habitats (see Figure 1). Its current distribution range includes: France (depts Hérault, Var, Bouches-du-Rhône, Gard), Italy (Sardinia, Gorizia, Livorno, Syracuse, Taranto, Veneto), Slovenia (see Scopoli 1763), Montenegro (Central Region), Croatia (Dubrovnik-Neretva Co.), Greece (Ionian and North Aegean Islands, Serres, Thessaloniki, Trikala), Bulgaria (Burgas), and Algeria (Oran). Its range overlaps with that of *O. sabulosum* only in Oran (Algeria), and on the islands of Sardinia (Italy) and Lesvos (Greece). In the latter site, both species have been collected (in different years by different collectors) in the same area.

Previous records from Austria, Ireland, Madeira or Crimea (Ukraine) could not be verified due to a lack of specimens, but it is very likely that the Irish and Madeiran records refer to *O. sabulosum* (see Figure 1).

Ecology. With only two clear exceptions, *O. lacustre* has been recorded from mostly lowland locations in a 25 km zone along the Mediterranean coast, where it seems to occur along inland lakes which also corresponds with the description of the habitat of the type specimens (Scopoli 1763). Only on Sardinia (at 480m) and in Greece (prov. Serres) has the species been collected in habitats less or not affected by the sea. At the two Greek sites, both above 1,100m, and presumably also in Sardinia, the species occurred along small streams in mixed forest (beech and spruce forest in Greece).

Orthoceratium sabulosum (Becker, 1907)

Figs 1, 3C–D, 4C, E, G, 5C, 6C, 8, 9, 10A

Alloeoneurus sabulosus Becker, 1907: 112. Type locality: Tunis (Tunisia) [ZMHB] – *Alloeoneurus* presumably synonymized with *Orthoceratium* by Kertész (1909)

Musca formosa Haliday, 1832: 356. Type locality: Cheshire (Great Britain) [unknown] **syn. n.**

Medeterus viridipes Macquart, 1834: 452. Type locality: Bordeaux (France) [unknown] **syn. n.**

Notes on synonyms. *Musca formosa* Haliday, 1832 and *Medeterus viridipes* Macquart, 1834 were previously listed as synonyms of *O. lacustre* by Becker (1917). Our attempts to retrieve and examine the specimens proved unsuccessful (the latter specimen could not be located, Christoph Daugeron, pers. comm.). However, taking the position of their capture localities into account (see Figure 1), there is little doubt that they are conspecific to *O. sabulosum*.

Diagnosis. Rather large, short-bodied, rather slender (but stouter than *O. lacustre*), brilliant green species with abdomen 1.3 × as long as thorax (Fig. 3C–D). All legs mainly dark and metallic with narrowly yellow knees. Wing smokey reddish yellow, with reddish yellow veins (Figure 5C). Apical section of vein M_1 with strong sinuous bend at ½. Posterior border of wing indented at vein CuA_1. Coxa I with strong white pubescence, and with one strong curved black bristle at basal 1/3 and three black bristles at apex (Figs 3C–D). Coxa II with one to three small black apical bristles on anterior face. Pedicel with strong apical bristles, with some ventral ones 1.5 × as long as pedicel is deep (Figure 5G). Ac uniseriate, rather strong, some about ½ × as long as dc. Male: face at least 1.4 × as wide as postpedicel is long (Figure 4C). Postpedicel with variable shape, at most as long as deep (Figure 4E). T_V with tapering ventral process at each side baring coalescent bristles (Figure 10A). Femur I with large avoid brownish spot in basal 2/5, about 1/4 of femur length, covered with a conspicuous yellow pubescence (Figure 6C). Femora I–II bare ventrally. Tibia II with two ad bristles, rarely with 3rd much shorter basal bristle, and with two av bristles. Tibia III with two strong and two small pd bristles. Tarsus I with only one claw, and tarsomere taI_1 with metallic reflection.

Redescription. Male. Body length: 5.5–6.2 mm (n = 54); wing length: 5.2–6.1 mm (n = 77), 0.3 × as wide as long (n = 15) mm. **Head** (Fig. 4C, E, G). Face silvery white, rather parallel-sided, clypeus with triangular lower margin, strongly projecting; face 1.4–1.8 × as wide as postpedicel (length), with short white pubescence. Frons with metallic green ground colour, dusted yellowish white, less on posterior 1/2 in some specimens. Occiput brilliant metallic green, with weak dusting in some specimens, convex in middle. Palp about 1/4–1/3 of eye, trapezoid – elongate triangular, dark brown, dusted whitish, with white pubescence, and apical bristle absent. Proboscis dark brown. Eyes red, with short white pubescence. Uppermost eight-eleven postocular bristles bristles erect, black, and lower bristles curved, white, forming whiskers. One pair of black postocellar bristles. Antenna entirely dark brown, with scape bare, and pedicel with

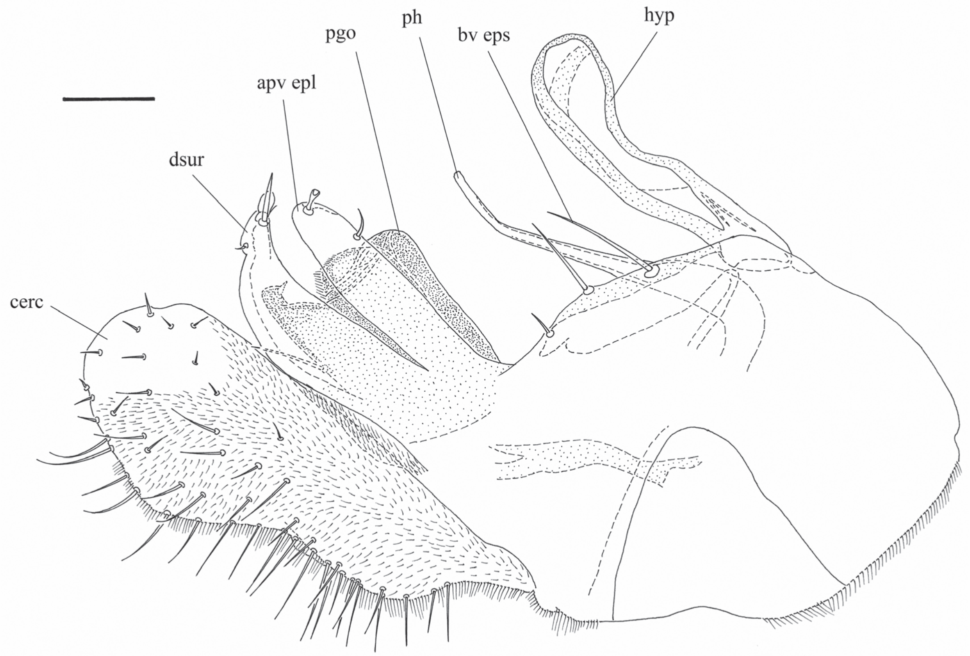

Figure 8. *Orthoceratium sabulosum*, hypopygium (left lateral view). Abbreviations: hyp: hypandrium, ph: phallus, bv eps: basoventral epandrial setae, apv epl: apicoventral epandrial lobe, dsur: dorsal surstylar lobe, pgo: postgonites, cerc: cercus. Scale bar: 0.1 mm.

apical crown of strong bristles, with some ventral bristles about 1.5 × as long as pedicel is deep; postpedicel of rather variable shape, mostly rounded triangular, rarely rather subcircular, sometimes *Hydrophorus*-shaped, as long as deep, 0.7–0.8 × as long as scape and pedicel combined, with distinct pubescence; arista-like stylus dorsal, inserted at middle of upper rim of postpedicel, 2.3–2.7 × as long as first three antennal segments combined, bare. **Thorax** (Figure 3C). Mesonotum entirely brilliant metallic green with sometimes bluish violet tinge, strongly dusted greyish white on pleura and certain zones on dorsum, only without dusting between dc and ac, and between dc and npl areas; scutellum dark green to bluish green with violet tinge, bare on dorsum, with four marginal bristles, lateral pair much smaller than median pair. Anterior spiracle with group of multiple curved, yellowish white, long setae. Thoracic bristles black. Seven dc, with 1st dc laterally off-set, and 6–7th dc stronger; six to nine ac, uniseriate, reaching till 5th dc, rather strong, some about 1/2 × as long as dc; with two strong black, and one minute white ant pprn, one internal and one external bas pprn, one psut ial, one sut ial, two npl, two spal, and one pal bristles. Upper proepisternum with a large group of long yellowish white curved setae; lower proepisternum with one strong black curved bristle and a small group of yellowish white curved setae. **Wing** (Figure 5C). Slightly smokey reddish yellow, with reddish yellow veins. Vein R_{4+5} sinuous near wing apex, there parallel with vein M_1; apical section of vein M_1 with strong sinuous bend at ½ (MSSC);

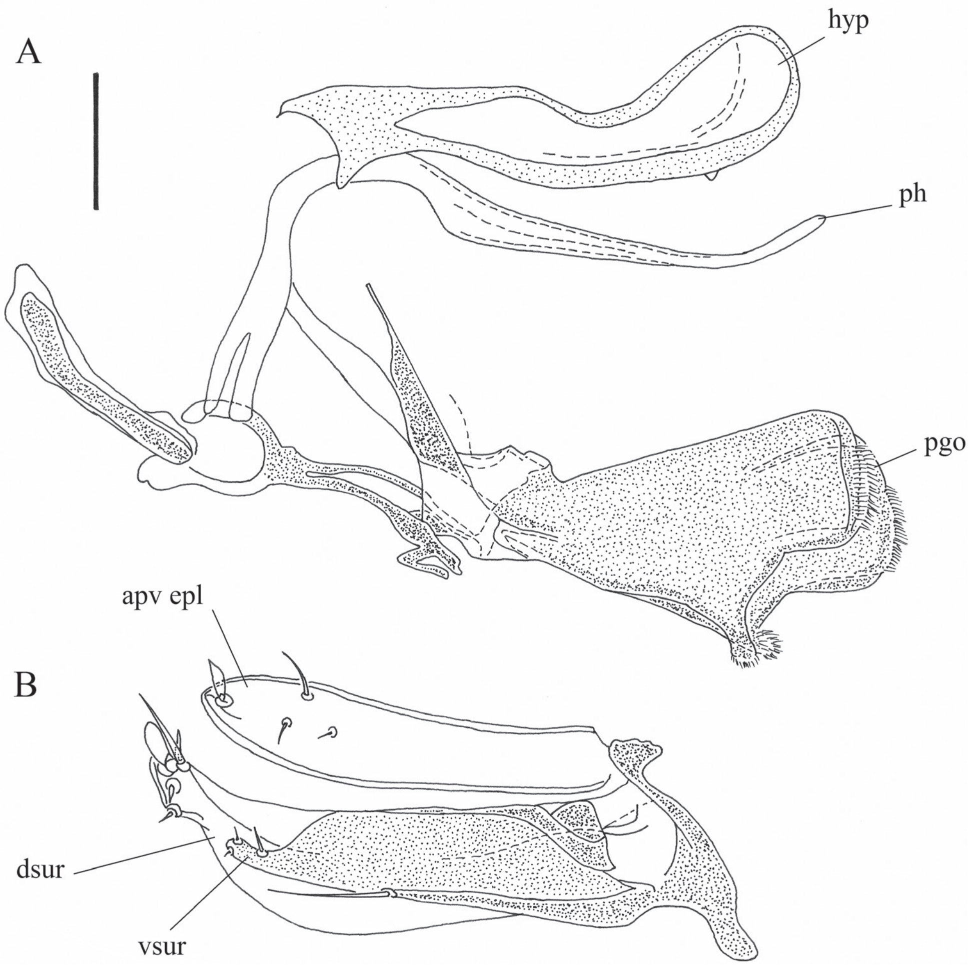

Figure 9. *Orthoceratium sabulosum*, hypopygial appendages: **A** hypandrium (hyp), phallus (ph) and postgonites (pgo) (right lateral view) **B** apicoventral epandrial lobe (apv epl), dorsal (dsur) and ventral surstylar lobes (vsur) (inner view of left surstylus). Scale bar 0.1 mm (applicable for **A, B**).

crossvein dm-cu slightly concave; posterior border of wing indented at vein CuA_1. Proximal section of vein M_1 2.0 × as long as apical section. Proximal section of vein CuA_1 7.1 × as long as apical section. CuA_x ratio: 1.6. Halter pale, calypteral fringe yellowish white. **Legs** (Figs 3C, 6C). Overall dark, metallic green, with pale yellow knees in all legs, and with black bristles. Coxae I–III dark, with metallic green ground colour, strongly dusted whitish, coxae I and III with extreme apex, and coxa II with less than apical 1/4 yellow. Coxa I with dense, white pubescence and one strong black curved bristle at basal 1/3, about 0.5 × as long as coxa I is long, and three strong, black ap bristles. Coxa II with dense white pubescence on anterior face, one inclined black bristle at 1/2, and one to three smaller black bristles at apex; lateral face bare. Coxa III with black, erect external bristle, inserted at 1/2, with vertical row of white setae. Trochanters dark

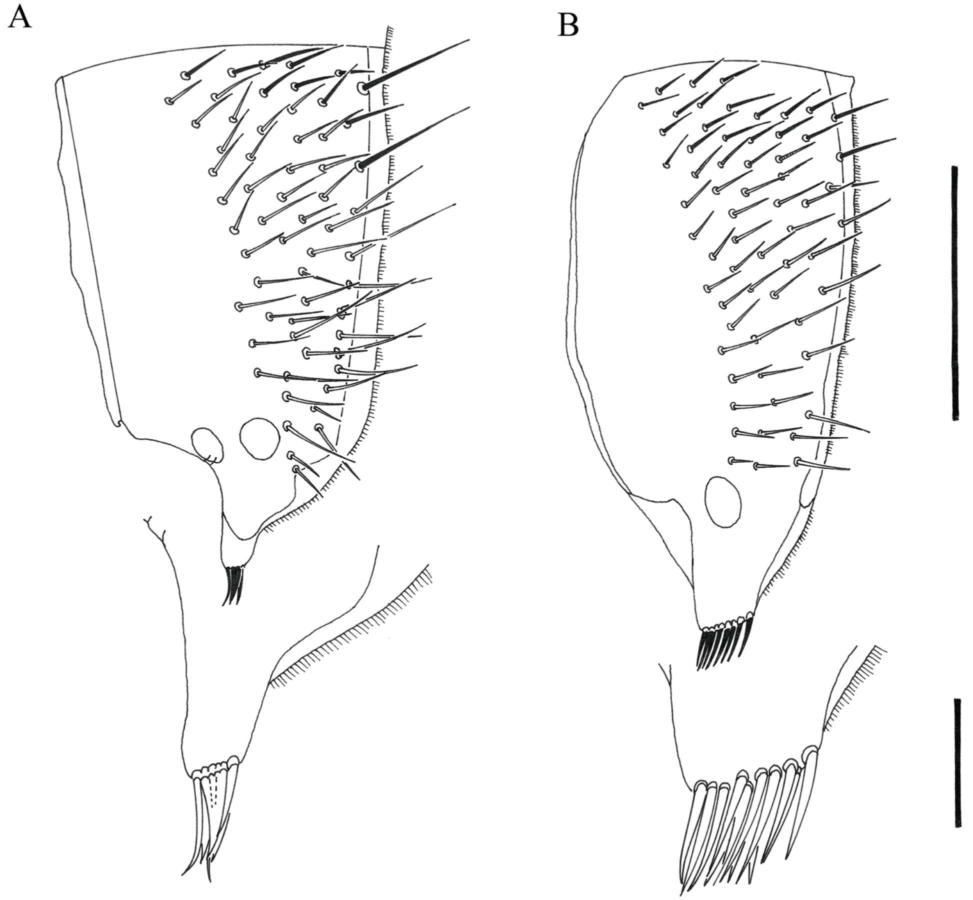

Figure 10. Posteroventral process on 5th tergite, male: **A** *O. sabulosum* **B** *Orthoceratium lacustre*. Scale bars: 0.5 mm (tergites) and 0.1 mm (processes).

brown. Femora I–III brilliant metallic green, femora I–II with pale yellow knee on apical 1/8, and on apical 1/10 in femur III. Femur I with large avoid brownish pv spot in basal 2/5, about 1/4 of femur length, covered with a conspicuous yellow pubescence (MSSC); with one rather small pv preapical bristle. Femur II with one strong ad bristle, at less than apical 1/5, and one small pv preapical bristle; with one row of short inclined pv setae along entire length, white on basal 2/3 and black on apical 1/3, longest at basis and apex. Femur III with one strong ad bristle, at about apical 1/3, and with one small pv preapical bristle; with one thin erect black ds bristle at about basal 1/5, nearly 0.5 × as long as femur is deep. Tibia I brilliant metallic green, and tibia I with basal 1/8, tibia II with basal 1/9, and tibia III with basal 1/10 pale yellow. Tibia I with two ds bristles, 2–3 × as long as tibia is deep; with two small ad bristles, 1–1.5 × as long as tibia is deep, and with three pv bristles, 2 × as long as tibia is deep; with white pilosity on av face along entire length, and with two small ap bristles. Tibia II with two ad bristles, 4 × as

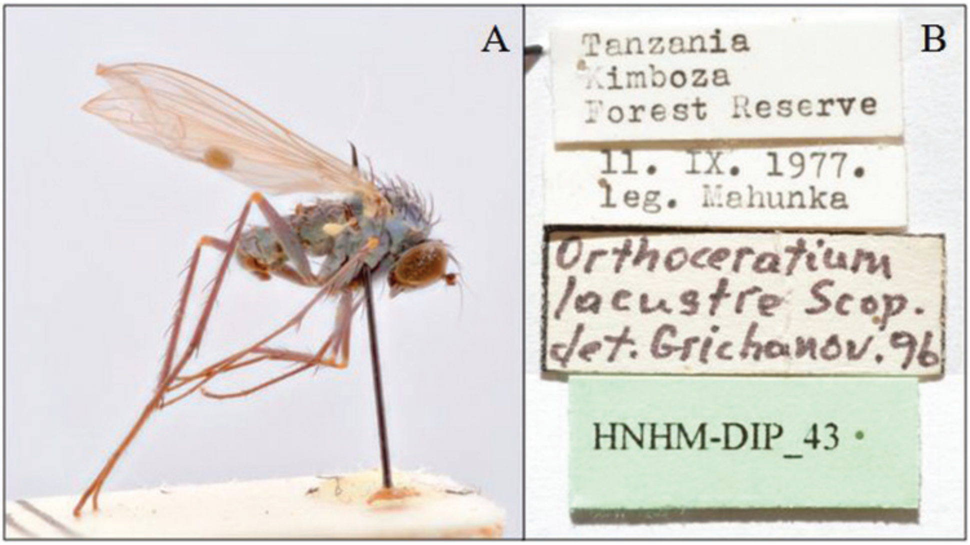

Figure 11. *Orthoceratium sabulosum* from Kimboza Forest Reserve, Tanzania: **A** male specimen **B** labels (photos by Zoltán Soltész).

long as tibia is deep, rarely with 3rd much shorter basal bristle; with two pd bristles, about 2.5 × as long as tibia is deep, with basal bristle shorter, and with four ap bristles; with two av bristles, at basal 1/3 and 2/3, 2 × and 1.5 × as long as tibia is deep resp.; with one pv bristle, at basal 1/6, 2 × as long as tibia is deep, and two small pv bristles in apical 1/2, not as long as tibia is deep. Tibia III with five ad bristles, about 3 × as long as tibia is deep, two strong and two small pd bristles, former about 3.5 ×, latter 2 × as long as tibia is deep, and four strong ap bristles; with distinct pd row on apical 1/2; with four to five av bristles, 1.5 × as long as tibia is deep, and multiple shorter pv setae along entire length. Tarsi I–III black, with taI–III$_1$ with metallic green to bluish reflection and with multiple short black vt bristles, nearly as long as taI–III$_1$ is deep; taI$_5$ with long curved dorsal setae at apex, 0.8 × as long as taI$_5$ is long; only inner claw present (MSSC). Ratio of femur/tibia/tarsomeres 1–5 in leg I: 9/10/5.4/2.1/1.5/1/1.1, in leg II: 9/11/8/3.5/2.3/1.2/1, and in leg III: 9.8/13.8/6/4.2/2.6/1.3/1. **Abdomen** (Figure 3C). Basal five segments pubescent, 6th bare, minute, only visible dorsally; T brilliant metallic green, with bluish or with bronze tinge in some specimens, strongly dusted whitish on lower margins, with short dense black pubescence on dorsum, with long yellowish white setae laterally, strongest on sides of T$_I$, and T$_{I–V}$ with black bristles on posterior margin, strongest on T$_I$; T$_V$ brilliant metallic green with prominent dark bristles at posterior margin, with tapering ventral process at each side baring coalescent bristles (MSSC) (Figure 10A). ST with green ground colour and strong whitish dusting, with yellowish white, erect bristles. Hypopygium (Figures 8–9) with epandrium concolorous with tergites; hypandrium rather stout with subcircular apex, with ventrally curled up sides forming a gutter; phallus slender and strongly curved; two larger and one smaller basoventral epandrial setae, apicoventral epandrial lobe pale to reddish brown, stout, elongate ovoid and close to outer surstylar lobe; surstylus with robust pale to reddish brown outer (or dorsal) lobe with subcircular bristle at apex, inner (or ventral) surstylar lobe dark, robust with tapering apex baring a few bristles; postgonites robust, dark, with apical pubescence and a ds process; cercus dark brown, medium-sized, rather rectangular, with apex nearly bare. **Female**. Body length: 6.4–6.6 mm (n = 47); wing length: 5.2–6.5 mm (n = 65), 0.3 × as wide as long (n = 15). As male, except for: abdomen 1.4 × as long as thorax. Face 2.0–2.3 × (n = 5) as wide as postpedicel (length). Palp about 1/5–1/4 of eye, ovoid. Uppermost six to nine postocular bristles erect, black. One pair of postocellar bristles, rarely with two pairs. Pedicel with some ventral bristles longer than pedicel is deep; postpedicel 0.8–1.0 × as long as deep; arista-like stylus 2.4–2.7 × as long as first three antennal segments combined. Thorax with five to eight ac, reaching between 4th and 5th dc. Vein R_{4+5} bended but straight near wing apex, there parallel with vein M_1; apical section of vein M_1 with weak bend (sinuous) at 1/2; crossvein dm-cu rather straight. Proximal section of M 1.7 × as long as apical section. Proximal section of CuA_1 6.5 × as long as apical section. CuA_x ratio: 1.5. Femur I bare ventrally. Femur III with two to four thin erect black bristles in basal 1/5, about 1/3 × as long as femur is deep. Tibia II with two large ad bristles, and often 3rd shorter basal bristle. Tarsus III black, unmetallic, taI_1 with multiple short black ventral bristles ventrally, nearly as long as taI_1 is deep; taI_5 with both claws. Ratio of femur/tibia/tarsomeres 1–5 in leg I: 8.5/9/5.3/2/1.5/1/1, in leg II: 9/10.5/7.8/3.2/1.9/1/1, and in leg III: 10.1/14.5/6.2/4.2/2.4/1.2/1. Abdomen with five pubescent segments, 6th invisible; also ST_{IV} with strong whitish dusting.

Type specimens examined. LECTOTYPE (here designated to fix the identity of the species) ♂, **TUNISIA**: [Tunis governate] "Tunis904" / "Ujhelyi", [bottom side] "X 26"; "*Alloeoneurus*" / "*sabulosus* Beck." / "det. Becker"; [red rectangular] "Lectotypus"; "Zool. Mus." / "Berlin" [ZMHB] (TN-01). **PARALECTOTYPE** ♀, **TUNISIA**: "Tunis904" / "Ujhelyi", [bottom side] "XI 2"; [red rectangular] "Typus"; "Zool. Mus." / "Berlin" [ZMHB] (TN-01).

Notes on type material. The original description of this species by Becker (1907) is based on multiple specimens (males and females) from Tunis, present in the HMNH at the time of the description. A holotype was not formally designated in Becker (1907) and it remains uncertain if the two specimens from the ZMHB were part of the type series. Fact is that both specimens in the ZMHB were collected by Ujhelyi in 1904 in Tunis, where Biró (HMNH) also collected Diptera in 1903 (Horn et al. 1990). And as indicated by Becker (1906) all Tunis specimens were examined at the same time which led to the description of the species in 1907. It is thus very likely that the ZMHB specimens, indeed, belonged to the type series. As it remains uncertain who attached the existing lectotype and paralectotype lables to the ZMHB specimens and when, a formal designation is provided here. We have no explanation, though, how they ended up in Becker's collection (ZMHB). The Becker catalogues at the ZMHB list a few specimens that he received as a gift from Biró, but these specimens always carry according labels (Jenny Pohl, pers. comm.). However, no such labels were found on the current lectotype and paralectotype.

Other material examined. See Suppl. material 1. List of (non-type) records of *Orthoceratium*.

Distribution. Compared to *O. lacustre*, *O. sabulosum* is much more widespread in the West Palaearctic and currently known with certainty from 14 countries, although it has not (yet) been collected in the northern part of the Mediterranean basin (see Figure 1): Denmark (South Jutland), Germany (Niedersachsen), Netherlands (Friesland, Zeeland, Zuid-Holland), Belgium (West-Vlaanderen), Great Britain (Cornwall, Dorset, Essex, Glamorganshire, Kent, Norfolk, North Somerset, Suffolk, Cheshire?), Ireland?, France (Morbihan, Gironde?), Portugal (Algarve, Beira Alta, Beira Litoral, Douro Litoral), Madeira?, Spain (Alicante, Cádiz, Córdoba, Segovia, Teruel, Zaragoza-Soria), Italy (Sardinia), Greece (Attica, North Aegean Islands), Algeria (Algiers, El Tarf, Oran), Tunisia (Ben Arous, Jendouba, Tunis), Turkey (inner Western Anatolia) and Iran (East Azerbaijan). Previous doubts about the occurrence of *Orthoceratium* in subsaharan Africa proved incorrect. However, specimens of *O. lacustre* identified and recorded by Grichanov (1997) from Tanzania, in fact, proved to belong to *O. sabulosum* (Figure 11). These records (see Appendix) from inland forest areas far beyond its West Palaearctic distribution range remain unexplained.

Ecology. Based on the current records, the distribution range of *O. sabulosum* differs significantly from that of *O. lacustre*. Despite that, however, both species seem to display a surprisingly similar ecological amplitude. In northwestern Europe (from Great Britain over Belgium and the Netherlands to Germany and Denmark), it is confined to humid coastal habitats, with a strong preference for salt marshes and brackish marshes. In Belgium, the species has only been collected in sea-aster (*Aster tripolium*) vegetations, bordering shallow brackish to saltwater ponds (Pollet et al. 2017) and in wet to slightly flooded *Salicornia* vegetations in brackish marshes and salt marshes (Pollet, unpubl. data). Also in Greece (Lesvos), Portugal (Algarve, Douro Litoral), Spain (Alicante) and north Africa (Algeria, Tunisia), records originate from locations close to the sea. In sharp contrast, the species is also known from locations between 700 m and 1,907 m in Portugal, Spain, Turkey and Iran, mostly in (coniferous) forest habitat and often with or close to small streams or open water (lakes).

Key to species of *Orthoceratium* Schrank (both sexes)

1 Coxa I with one strong curved black bristle at basal 1/3 (Figure 3C). Coxa II with one to three small black apical bristles on anterior face. Pedicel with strong apical bristles, with some ventral ones 1.5 × as long as pedicel is deep (Figure 4G). Ac rather strong, some about ½ × as long as dc. Male: face at least 1.4 × as wide as postpedicel is long (Figure 4C). Postpedicel mostly rounded triangular, at most as long as deep (Figure 4E). T_V with prominent dark bristles at posterior margin, and tapering ventral process at each side baring coalescent bristles (Figure 10A). Femur I with large avoid brownish pv spot in basal 2/5, about 1/4 of femur length, covered with a conspicuous yellow pilosity (Figure

6C). Femora I–II bare ventrally. Tibia II with two ad bristles, rarely with 3rd much shorter basal bristle, and with two av bristles. Tibia III with two strong and two small pd bristles. Tarsomere taI_1 with metallic reflection .... ***O. sabulosum* (Becker, 1907)**

– Coxa I without a black bristle at basal 1/3 (Figures 2, 3A). Coxa II with only pale bristles at apex anteriorly. Pedicel with short apical bristles (Figure 4F). Ac rather small, at most 1/3 × as long as dc. Male: face not as wide as postpedicel is long (Figure 4A). Postpedicel elongate triangular, at least 1.2 × as long as deep (Figure 4D). T_V without prominent dark bristles on posterior margin, with blunt ventral process at each side with short dark pubescence (Figure 10B). Femur I with small ovoid brownish yellow pv tuft just beyond basal 1/4, about 1/8 of femur length (Figure 6A). Femora I–II with multiple rows of very short white erect setae on basal ½. Tibia II with three ad bristles, with basal bristle shorter, and with one av bristle. Tibia III with four strong and one small pd bristles. Tarsomere taI_1 mostly unmetallic.......................... .... ***O. lacustre* (Scopoli, 1763)**

Biometrics

Table 1 gives a summary of the wing lengths measured in 76 and 142 specimens of *O. lacustre* and *O. sabulosum*, resp. On average, wings in males (+ 0.1 mm) and females (+ 0.2 mm) of *O. lacustre* are only very slightly longer than in *O. sabulosum*. Indifferently, both overall and in separate populations or datasets per country, wings in males of both species were approximately 0.5 mm shorter than in females. Size variations within the same sex in separate populations mostly proved higher in the females, with a maximum of 0.9 mm in males of Greece and even of 1.5 mm in females of France, both in *O. lacustre*. Size differences between both species in the keys by Becker (1907) and Negrobov (1979) hereby prove unreliable.

Discussion

Considering the fair size of *Orthoceratium* – compared to other dolichopodid lineages, it remains surprising that key features of this genus have been overlooked by previous authors. The ventral process of the 5th tergite was only mentioned by Becker (1907) and Negrobov (1979) – incorrectly as 4th sternite! – and the posteroventral spot on the fore femur only by Parent (1938). In describing *O. sabulosum* Becker (1907) even omitted the most decisive character to separate this species from *O. lacustre*, i.e. the strong black bristle on the fore coxa. All authors ignored the presence of one single claw of the fore tarsus in the male and Negrobov (1979) even emphasized that claws are well developed.

Even more worrisome is the fact that Becker (1907) seems to have mixed up both species in the original description of *O. sabulosum*. The description of the ventral process

Table 1. Wing lengths (in mm) in males and females of *O. lacustre* and *O. sabulosum*. Measurements per country are given for those countries where at least five specimens of each sex were examined.

Biometrics	Mean (min–max)	No. specimens	Mean (min–max)	No. specimens
Sex	**Male**		**Female**	
Orthoceratium lacustre				
BULGARIA	5.8 (5.5–6.2)	9	6.3 (5.8–6.7)	11
FRANCE	5.7 (5.4–6.0)	13	6.1 (5.2–6.7)	13
ITALY	5.8 (5.4–6.2)	5	6.2 (5.7–6.5)	5
GREECE	5.8 (5.2–6.1)	7	6.4 (5.9–6.6)	8
All specimens	5.7 (5.2–6.2)	35	6.2 (5.2–6.7)	41
Orthoceratium sabulosum				
BELGIUM	5.6 (5.3–5.9)	20	6.1 (5.8–6.4)	20
Dudzele	5.6 (5.3–5.9)	5	6.1 (6–6.3)	5
Lissewege	5.8 (5.6–5.9)	5	6.2 (5.9–6.4)	5
Knokke (Het Zwin)	5.7 (5.5–5.9)	5	6.1 (5.8–6.3)	5
GREAT BRITAIN	5.5 (5.2–5.8)	19	5.9 (5.2–6.4)	17
NETHERLANDS	5.8 (5.5–6.0)	6	6.1 (5.7–6.5)	5
SPAIN	5.4 (4.5–5.8)	14	5.8 (5.5–6.1)	5
All specimens	5.6 (4.5–6.1)	77	6 (5.2–6.5)	65

of the 5th sternite "… aber der vierte Bauchring ist anders und hier [in *O. sabulosum*] ganz einfach gebildet, während er bei *All. lacustris* spitz dreieckig endigt und vorsteht …" clearly points towards *O. lacustre*. This erroneous interpretation was copied by Negrobov (1979). The latter assumption seems to be confirmed by the description of the hypopygium and the cercus by Becker (1907): "… an den Seiten des Hinterleibes, am Bauche und auf dem grau bestäubten Hypopygium stehen zarte weisse Haare." Indeed, the cercus is only clearly pubescent in *O. lacustre*.

Unlike Negrobov (1978, 1979), Parent (1938) clearly used specimens of *O. sabulosum* in his description of *O. lacustre*, which must have been simple misfortune. In fact, Parent listed records of his '*O. lacustre*' from localities in the north of France (Pas-de-Calais, Morbihan) and the south (Hyères, Hérault), two regions where either *O. sabulosum* or *O. lacustre* have been recorded, resp. (see Figure 1). Apparently, he had no idea that he was dealing with two different species.

But most of all, it is remarkable that *O. sabulosum* has been ignored as a species since its description. Indeed, apart from its Tunis type locality and its inclusion in the Becker (1917) and Negrobov (1979) keys, this species has further never been mentioned in the literature. As a result, all Diptera workers dealing with Palaearctic dolichopodids automatically considered any *Orthoceratium* they encountered being *O. lacustre*. That group of dolichopodid workers even includes esteemed contemporary colleagues or peers from this and the previous century: CE Dyte, H Ulrich, O Parent, and H Meuffels. Also the senior author misidentified *O. sabulosum* as *O. lacustre* when he termed the species "Extinct in Flanders" (Pollet 2000) and when he recently reported on its rediscovery (Pollet et al. 2017).

One wonders how this series of mistakes could happen and last for over 250 years? A first reason seems to be that no previous researcher made the effort to compare with the type specimens, not even in the post-World War II era. Next to the fact that the type of *O. lacustre* was lost, most dolichopodid workers seemed to believe that *O. sabulosum* was a strictly southern Mediterranean species. With the present study we clearly proved that this species has a considerably larger distribution range. A second equally important reason are the insignificant, even misleading, characters used in species descriptions and identification keys, and the mere copying of those keys by subsequent authors. Scopoli (1763) described the eyes as green, while they are clearly red (see Figs 2, 4A, B, C) and stressed – for unknown reasons – the colour of the tarsal pulvilli. Of the five characters used in the keys by Becker (1917) and Negrobov (1979), only the face width proves to be diagnostically significant. In contrast, as can be concluded from the key given in the present paper, in males as well as in females a number of reliable features can be found to separate both species. But, of course, this requires a detailed examination and characterization of the species.

Some authors tend to build elaborate and detailed species descriptions (see e.g., Brooks and Ulrich 2012, Pollet et al. 2015, Kazerani et al. 2017) using a large number of characters (173 in the two latter papers) in order to avoid misidentifications (or to correct misinterpreted species identities from the past). This type of tedious time-consuming work is sometimes considered unnecessary or unwanted by peers for the simple reason that it might prevent researchers tackling the current and ever growing taxonomic impediment (Wheeler et al. 2004; Borkent et al. 2017), and this statement certainly contains some truth. However, it should not be forgotten how much (precious) time is invested not only to correct taxonomic mistakes from the past (e.g., current paper, Kazerani et al. 2017), but also to verify the identity of species on the basis of insufficiently detailed descriptions without type material at hand. In our opinion, a description should stand on itself and must allow its user to decide unequivocally whether he is dealing with the described species or not. In case the species description is not satisfactory, and at present, this is very often the case, the only solution is the examination of the type material.

Here lies the importance of type material that cannot be underestimated. Only after the examination of the types of *O. sabulosum* did we realize that researchers had been misidentifying *O. lacustre* for more than 2.5 centuries (and every correct identification might merely be considered as a fortunate coincidence). Indeed, only when the type locality of *O. lacustre* proved to be situated within the distribution range of 'species B', it became apparent that both species were conspecific. If this would not have been the case, and assuming that the face width would have been unreliable like the other four features used in the extant identification keys, *O. lacustre* might as well have rendered *nomen dubium*, and 'species B' might have been described as new. In this respect, the use of alternatives to physical type specimens deposited in a museum (and photos thereof) like e.g., field images of uncollected specimens as promoted by Minteer et al. (2014) and applied by Marshall and Evenhuis (2015) would most likely not have solved this issue. Therefore, we strongly support the strict interpretation of Article 16.4.2 of the ICZN Code (ICZN 1999).

Conclusion

For more than 2.5 centuries the *Orthoceratium* species that occurs in northwestern Europe has indifferently been considered as *O. lacustre*, while it was, in reality, *O. sabulosum*. This is all the more surprising since *Orthoceratium* species are among the larger and more conspicuous dolichopodid species in Europe. The main reasons for this continuous series of misinterpretations seemed to be the mere copying of keys by successive authors that contained misleading information, the omission of examining type specimens of *O. sabulosum*, and the loss of the type specimens of *O. lacustre*. The importance of type specimens and the examination thereof is stressed, as well as that of unequivocal, detailed, and well-illustrated descriptions to avoid this kind of taxonomic confusion.

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Supplementary material 1

List of (non-type) records of *Orthoceratium*

Author: Marc Pollet

Data type: species data

Link: https://doi.org/10.3897/zookeys.782.26329.suppl1

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RESEARCH ARTICLE

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Description of a Cretaceous amber fossil putatively of the tribe Coprophilini (Coleoptera, Staphylinidae, Oxytelinae)

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Abstract

An unusual and well-preserved fossil staphylinid is described and figured from a single specimen in Upper Cretaceous Burmese amber. *Gollandia planata* **gen. et sp. n.** is tentatively placed in the extant oxyteline tribe Coprophilini, although it lacks a few characteristic features of present-day members of the group, likely indicating it to be either a stem group of the tribe or prove to be distinct pending future discoveries. The discovery of this genus suggests that early oxytelines were more morphologically diverse during the Cretaceous and their evolutionary history was more complicated than previously documented. Tribal placement as regards fossil oxyteline taxa is discussed.

Keywords

Burmese amber, Cenomanian, Mesozoic, Myanmar, new genus, new species

Introduction

The staphylinid subfamily Oxytelinae Fleming, 1821 is a relatively large group with over 2049 valid extant species placed in 40 genera (Thayer 2016). Oxytelines are distributed worldwide and have proven to be remarkably diverse. This diversity is so far not fully known as in several geographical areas the species are incompletely known, in many cases a vast portion (up to 80%) still await formal description. The generic revision of Herman (1970), which was also a first attempt at a phylogenetic analysis, set the foundation for a better understanding of relationships within the subfamily and for all subsequent revisionary and evolutionary research on oxytelines.

Despite Herman's (1970) monumental study, the classification of tribes within Oxytelinae remains unsettled. The most primitive oxytelines (formerly as tribe Deleasterini, sensu Makranczy 2006, based on abdominal segments with only one pair of laterosclerites) are now often split into three separate tribes: Deleasterini Reitter, 1909, Euphaniini Reitter, 1909, and Syntomiini Böving & Craighead, 1931. The higher oxytelines, comprising 98% of the described valid species in the subfamily, are variously classified in the more primitive Coprophilini Heer, 1839, as well as the now widely accepted Blediini Ádám, 2001 and Planeustomini Jacquelin du Val, 1857. The more derived clades seem to belong into a once again unified Oxytelini (sensu Makranczy 2006), although this remains debated and awaits support from molecular studies.

The tribe Coprophilini is currently without identified synapomorphies, and is instead defined by a lack of features of the more derived lineages (i.e., it is presently circumscribed by putative plesiomorphies, may be paraphyletic, and is in need of considerable revisionary and phylogenetic exploration). The extant coprophilines are characterised by the following combination of traits: mesocoxae narrowly separated by mesosternal process or contiguous, tarsal formula 5-5-5, abdominal segments with two pairs of laterosclerites, and with only six sternites visible. According to Herman (2001), the tribe contains three extant genera, *Coprophilus* Latreille, 1829, *Coprostygnus* Sharp, 1886, and *Homalotrichus* Solier, 1849, although a poorly described genus, *Coprotrichus* Hayashi, 2005 (based on a single species from Japan) was later added and is presently considered as valid but requires detailed study. The number of species in these genera is not great; *Coprophilus* stands in the last catalogue with 30 valid species (Herman 2001), *Homalotrichus* and *Coprostygnus* are being revised by the first author, standing with at least 13 and five species, respectively (Makranczy, unpubl. data). *Coprophilus* is widespread in the Northern Temperate zone, *Homalotrichus* is known from Australia (including Tasmania) and South America, while *Coprostygnus* is confined to New Zealand. It is remarkable that all of these species prefer cold climates, often occurring at the highest elevation where one can find oxytelines, up to 4000–4200 m.

The various records of fossil Oxytelinae and its related subfamilies were summarized by Cai et al. (2017). Hitherto, the only definitive fossil Coprophilini described is a rather poorly preserved compression fossil (without counterpart), *Mesocoprophilus clavatus* Cai & Huang, 2013. A further fossil genus, *Sinoxytelus* Yue, Zhao, & Ren, 2010 was subsequently transferred to Coprophilini, but this placement is tentative as the abdomen has basolateral ridges, a trait of Oxytelini. The genus originally contained three extinct species (*Sinoxytelus euglypheus* Yue, Zhao, & Ren, 2010, *S. breviventer* Yue, Zhao, & Ren, 2010, and *S. longisetosus* Yue, Zhao, & Ren, 2010) from the Yixian Formation (Lower Cretaceous, ca. 126 Mya, 41°36’44”N, 120°49’48”E), Liaoning, China (Yue et al. 2010), and a fourth taxon, *S. transbaicalicus* Cai, Yan, & Vasilenko, 2013 was later described from the Urey beds (Lower Cretaceous, 50°38.730’N, 112°50.338’E), Transbaikalia, Russia (Cai et al. 2013). Here we describe a new genus and species from the Upper Cretaceous amber of northern Myanmar.

This new taxon represents the second fossil occurrence of Oxytelinae documented from Mesozoic amber, and is also the oldest amber inclusion presently recorded for the subfamily along with *Prajna tianmiaoae* Lü et al., 2017, a species of Thinobiini (a more derived tribe) described from the same deposit.

Materials and methods

Specimen photography was done with the amber piece mounted on a small plastic plate surface with a drop of viscous glycerine covered with a glass cover slip to eliminate distortions from the otherwise rounded amber surface. The habitus photographs were made with a Canon 5D Mark III camera and C Canon MP-E 65mm f/2.8 1–5× macro lens with two Canon Macro Twin Lite MT-24EX flash units and a Canon Speedlite 430EX III-RT flash unit standing on the shoe foot directly in front of the specimen (shooting directly into the head of the specimen). The light was diffused by a single ring of mylar. Raw photograph files were imported to Adobe Lightroom 5.7.1, and layers stacked with ZereneStacker (Richland, Washington, USA). Details of the specimen were photographed with a Canon EOS 6D camera attached to a Leica M205 C stereomicroscope with the help of a Canon EOS Utility 3.4.30.0 software, before being stacked using the same software as previously mentioned. Abbreviations for measurements are defined as follows:

HW	head width with compound eyes;
TW	head width at temples;
PW	maximum width of pronotum;
SW	approximate width of shoulders;
MW	maximum width of elytra;
AW	maximum width of abdomen;
HL	head length at the middle-line from front margin of clypeus to the beginning of neck;
EL	compound eye length;
TL	length of temple;
PL	length of pronotum at the middle-line;
SL	length of elytra from shoulder;
SC	length of elytra from hind apex of mesoscutellum;
FB	fore-body length (combined length of head, pronotum, and elytra);
BL	approximate body length.

The specimen is exceptionally well preserved but in a rather unfortunate position within the amber piece. Under UV-light examination it can be seen that the specimen is sitting within a dip in the internal flow of the amber (the amber flowed in layers when it was originally exuded from the tree and the beetle is in a dip within these flows). The result of its placement within the dip in the flow means ideal, clear images cannot be produced at high magnification unless some of the flows can be polished away. Whoever made the original preparation (probably local workers in Myanmar) polished the specimen too close to the amber surface and cut the piece poorly. The result is that it is now impossible to cut and polish the piece closer to minimize the optical impact of the flow lines.

The recent commercial amber mines are located in the Hukawng Valley (26°16.5'N, 96°34.0'E), Kachin, northern Myanmar. The minimum age of the amber is estimated to be 98.79 ± 0.62 Mya (by radioisotope dating of zircon crystals obtained from the volcanoclastic matrix, Shi et al. 2012), and so just slightly into the base of the Cenomanian. Cruickshank and Ko (2003), Ross et al. (2010), and Grimaldi and Ross (2017) provide a geological account of the deposits, and these authors also note that many of the amber pieces appear to have at some point eroded from sediments and been redeposited, at least suggesting the possibility that the inclusions could be slightly older, perhaps from the latest Albian. Recent studies speculate that the West Burma Plate/Block (west of the Sagaing fault line in Myanmar) was of Gondwanan origin (Poinar 2018), and the resin-producing tree was hypothesized to be of *Agathis* Salisb. (Araucariaceae) (Poinar et al. 2007). The paleoclimate of Burmese amber producing forests were suggested to be tropical with an average temperature range of 32–55 °C (Grimaldi et al. 2002; Ross et al. 2010).

Systematic Palaeontology

Family Staphylinidae Latreille, 1802
Subfamily Oxytelinae Fleming, 1821
Tribe Coprophilini Heer, 1839

Gollandia gen. n.

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Type species. *Gollandia planata* sp. n., (described below).

Diagnosis. *Head*. Head somewhat retracted under large pronotum; head capsule rather short. Epistomal sulcus not well visible, but presence suggested by a tranvserse 'run' of air between amber and cuticle. Supraantennal prominences weak. Antennomeres with long tactile setae near apices (prominent on articles 3–11). Labial palp trimerous, basal two palpomeres rather stout, last palpomere thin. Labrum with two thick, forward-directed setae. Mandibles not prominent, apices acute. Maxillary palp tetramerous, basal three palpomeres moderately elongate, last palpomere much wider and long, not reduced, apex pointed. Gular sulci seemingly widely separated at base but confluent anteriorly (this area is not well visible as preserved). Neck separated by gentle constriction and (at least laterally) a groove. *Thorax*. Pronotum strongly explanate, margin slightly reflexed, marginal bead present, lateral edge finely serrate/sinuous. Laterally with a strong seta at each of 'anteroangularis' and 'lateralis' positions, plus strong seta on both sides well inside lateral margin at about 1/3 length, posterior edge appearing slightly concave (might be artefact of preservation). Pronotal disc with shallow impressions, with fine and dense punctation and setation. Procoxae contiguous, projecting; procoxal fissure present and open (Figure 7). Mesoscutellum (Figure 8) with apex exposed and somewhat impressed without distinct pattern. Elytra finely and randomly punctate. Mesocoxae narrowly separated by mesosternal process (Figure 9). Legs slender (metatibia especially elongate), with regular rows of tibial spines (more slender than strong), and a conspicuous mesotibial spur (and a second spur half size at half-length towards femoral joint). Tarsal formula 4-4-4, no tarsal lobes (Figure 10), but empodial setae strong (Figure 11). Elytra with epipleural ridge, seemingly with a fine and shallow dorsal groove following it from inside, epipleura strongly deflexed and rather wide but epipleural fold thin to inconspicuous. Post-scutellar area with a pair of elongate impressions along suture. Shoulders prominently developed, narrowly rounded, even slightly projecting forward in relation to anterior edge at mesoscutellar area, posterior margin slightly oblique but straight from suture to outer 3/4, slightly incurved (concave) in outer 1/4 thereby producing a somewhat sharp outer corner in dorsal view. *Abdomen*. Abdomen with only six visible segments (not counting segments IX–X, often retracted under VIII), second abdominal segment not developed. With two pairs of laterosclerites. Apex of tergite VII seemingly without well-developed palisade fringe (difficult to judge; an air bubble under this structure obscures almost its entire width), apex of segment conspicuously widening (not narrowing to base of next segment), surface somewhat concave. Tergite VIII with apical edge truncate medially or slightly concave. Apex of sternite VIII without modification.

Differential diagnosis. All extant Coprophilini have a 5-5-5 tarsal formula, and even the fossil genus *Mesocoprophilus* has five tarsomeres, so the 4-4-4 condition in *Gollandia* is significant. The new genus differs greatly from *Mesocoprophilus* in the antennal structure, stout and short in *Mesocoprophilus*, slender and elongate with well-developed tactile setae on all antennomeres in the present fossil. The neck (lateral constriction, postoccipital groove) also differentiates this genus from *Mesocoprophilus* where these features are absent. The lack of striae or puncture rows on the elytra makes this genus distinct from all extant Coprophilini, while a distinction from *Mesocoprophilus* cannot be made as that fossil lacks its dorsal portion (Cai and Huang 2013). The present fossil is also peculiar in the slender and elongate appendages. The present-day representatives of Coprophilini lack such strongly formed, almost forward-projecting shoulders and the new genus has more slender antennae and palp, more slender tibiae, a procoxal cavity far removed from the pronotal margin, a prominently explanate pronotum, and the mesosternal process extending much more posteriorly. Two unusual traits for this subfamily are the posteriorly slightly incised elytral corners and the cylindrical, wide apex of segment VII (not narrowing to the base of segment VIII), both features otherwise characteristic of the subfamily Aleocharinae.

Systematic placement. The only feature that clearly unites the fossil with extant Coprophilini is the lack of the well-developed second sternite. Beyond that, the head shape is reminiscent of *Homalotrichus*, while the pronotum bears some similarity to that of some *Coprophilus* (e.g., *Coprophilus striatulus* (Fabricius, 1793) plus its close relatives) and to a lesser extent some *Homalotrichus* (e.g., *Homalotrichus impressicollis* Solier, 1849), but none of these are as explanate as in the fossil.

Etymology. The new genus is named after Susan Golland, exhibition developer at the Field Museum of Natural History, Chicago, whom the first author met at 10:32am on 14 March 2018 in front of Crystal Maier's office. The fossil specimen described here was shown to him by the second author later on the same day. The gender of the name is considered feminine.

Gollandia planata sp. n.

http://zoobank.org/CC08CCA8-D767-4E16-BB55-5D343BE06492

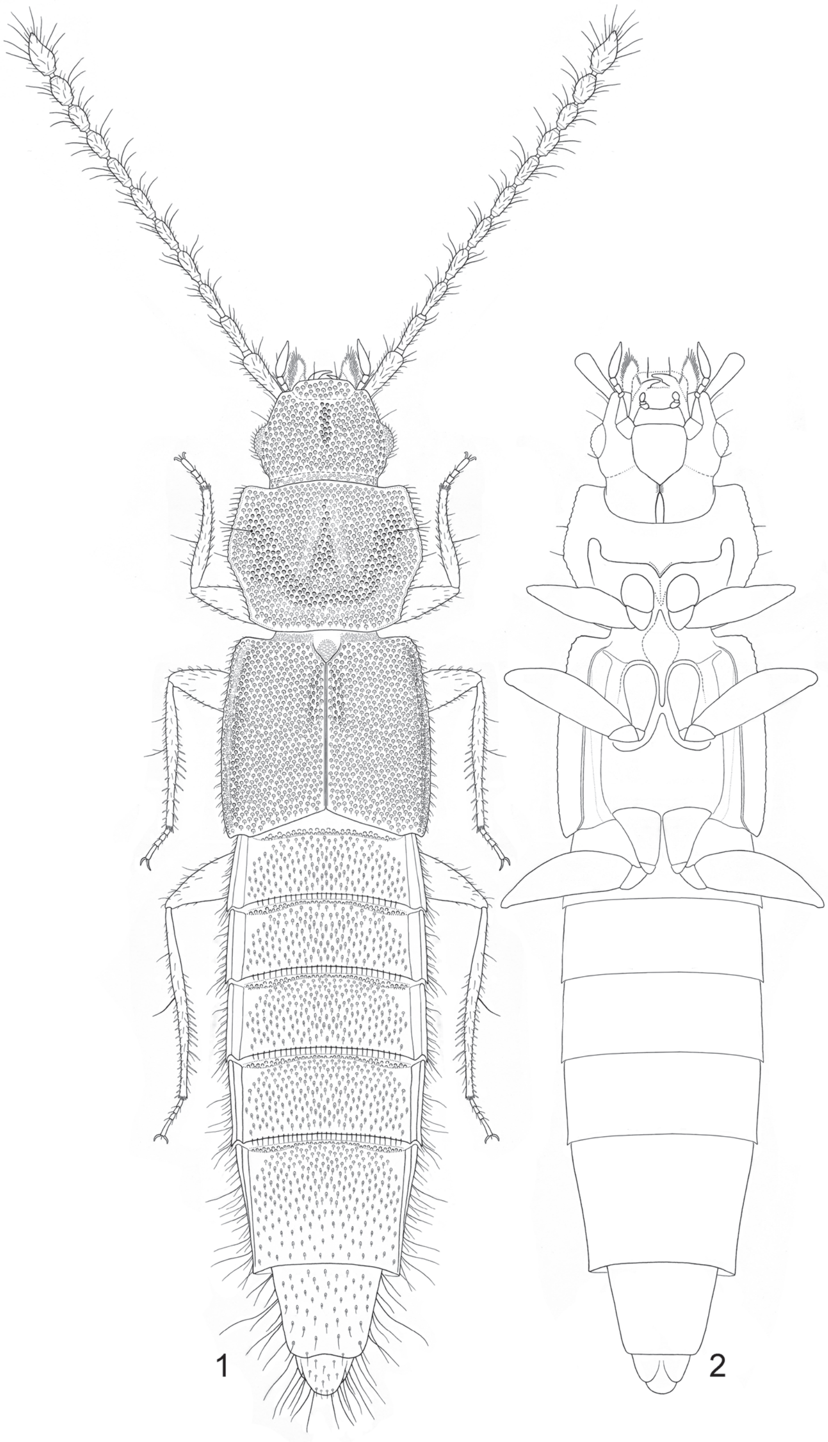
Figures 1–11

Holotype. Sex unknown, probably male, in a flattened drop shaped, light yellow amber piece (20.0 × 9.9 × 4.5 mm, 0.98g): "FMNHINS 3729858 ex S. Yamamoto collection (SYAC0482)" deposited in Field Museum of Natural History (Chicago, USA).

Locality and horizon. Noije Bum hill near Tanai Village, SW part of Hukawng Valley (SW of Maingkhwan), Kachin State, northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Diagnosis. As for the genus (vide supra).

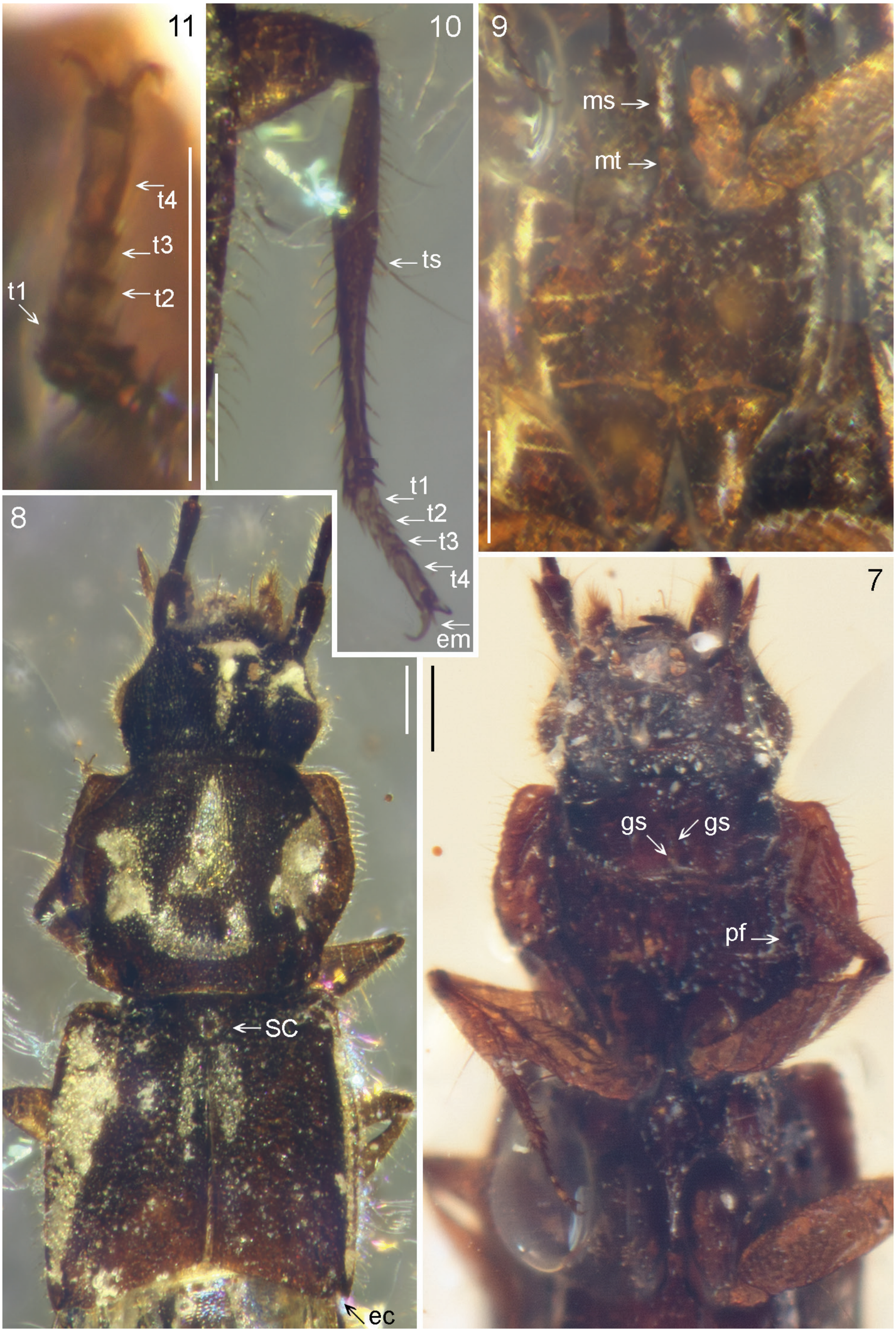
Description. *Measurements*: HW = 0.45; TW = 0.41; PW = 0.64; SW = 0.59; MW = 0.68; AW = 0.70; HL = 0.29; EL = 0.10; TL = 0.04; PL = 0.50; SL = 0.66; SC = 0.55; FB = 1.47; BL = 3.29 mm (all measured from dorsal view). *Habitus:* General habitus as in figures 1–6. Colour reddish dark brown. Body moderately lustrous, covered with fine microsculpture and forebody finely, not very densely setose. Abdomen with longer and stronger lateral setae posteriorly. *Head.* Head rather short. Antennae rather elongate, scape almost twice as wide as pedicel and not much longer, second antennomere (pedicel) more than 3.5× as long as wide, third antennomere (first flagellomere) slender at base and almost as long as previous. Further antennomeres spindle-shaped and each with rudimentary basal dish, gently constricted above them. Antennomeres 4–7 at least 2.5× as long as wide, from antennomere 8 becoming wider, gently clubbed, last three antennomeres only about 1.5× as long as wide. Compound eyes more than 2× as long as weakly formed temples. Neck not constricting strongly. *Thorax*. Pronotum rather large, widest point slightly before middle with both anterior and posterior corners rather narrowly rounded, lateral margin slightly concave before quite acute posterior angles. Surface finely microsculptured, thereby punctation partly obscured. Disc transversally impressed before base (in a curved fashion), also with a



Figures 1–2. *Gollandia planata* gen. et sp. n. **1** habitus, dorsal view **2** sketch of main body parts, ventral view.

Figures 3–4. *Gollandia planata* gen. et sp. n. photographed with macro lens and three flash units. **3** dorsal view **4** ventral view.

Figures 5–6. *Gollandia planata* gen. et sp. n. photographed through microscope, strong backlighting. **5** dorsal view **6** ventral view.



Figures 7–11. *Gollandia planata* gen. et sp. n. **7** head, pro- and mesothorax, ventral view **8** fore-body, dorsal view **9** meso- and metacoxae, ventral view **10** mid leg, dorsal view **11** protarsus, ventral view. t 1–4 = tarsomeres, em = empodial seta, ts = mesotibial spur, sc = mesoscutellar impression, ec = elytral posterior corner, gs = gular sulcus, pf = procoxal fissure, ms = mesosternal, and mt = metasternal process. Scale bars: 0.15 mm.

semi-triangular mid-longitudinal impression anteriad; rather large but shallow paralateral depressions on sides. *Elytra*. Elytra together just slightly broader than pronotum, trapezoidal, shoulders well developed, narrowly rounded, even slightly projecting forward in relation to anterior edge at mesoscutellar area. Dorsal surface finely punctate and setose, no major lateral setae, epipleural ridge with moderately long setae at regular intervals. *Abdomen*. Sides of abdomen gently curved, almost parallel. Surface of tergites with moderately fine, longitudinally elongate punctures, apical edges of tergites (up to tergite VI) with row of equal-sized setae at regular intervals. Specimen is without any feature suggesting strong sexual dimorphism. No genital traits observable.

Etymology. The specific epithet is a Greek adjective derived from *platys* (= wide) and refers to the pronotum of the species being unusually explanate.

Preservation. The specimen is exceedingly well preserved, with the hind wings unfolded over part of the abdomen, minor air bubbles under segmental edges, a thin air layer over some sculptured dorsal parts, and the ventral side exceptionally clearly visible. As explained before, the specimen is sitting within a layer of resin covered by another layer, and this creates an effect similar to the specimen being glued to a glass, evident in the photos of the ventral side. The legs are somewhat distorted (but each pair is almost perfect on one side). Primitive oxytelines often have distinctive coxites and styli in females (if not exposed, then setation gives them away), and in their absence the specimen is presumed to be a male.

Discussion

There can be a great debate on how to place fossil species in higher taxa when the classification is otherwise based entirely on present-day species. Naturally, fossil species placed cladistically within the crown group are not difficult, but when potential stem groups are discovered some difficulties and strong differences of opinion arise. Does one include them within the formal group, necessitating a new circumscription of the taxon boundaries in order to accommodate the fossil, or, at another extreme, more radically establish a new group for the fossil as a potential sister to its extant relatives? The latter will inevitably lead to a proliferation of meaningless and often monobasic groups based on limited characters (e.g., often lacking critical data on genital traits) and collectively forming a pectinate stem to any lineage circumscribed solely on the basis of its extant constituents, the end result becoming a classification of little explanatory power. Ideally, there one desires a balance between maintenance of a good diagnostic power and keeping the classification simple while simultaneously reflecting the hierarchical relationships supported among the various taxa being classified and granting the system maximal explanatory and predictive significance. These goals are sometimes simultaneously achieved, but more often than not the former objective becomes muddied while attempting to adequately reflect the latter. This challenge is particularly great for ancient groups, such as the Oxytelinae whose history goes back at least 150 Mya, where there has been inevitably considerable extinction over the intervening epochs between the first divergence of a given clade and its modern fauna. Cretaceous deposits will undoubtedly supply for generations to come a continuous stream of unusual fossil species that will force us to rethink our estimates of relationship and concomitantly the classifications from which they are built. Descriptive science (Grimaldi and Engel 2007) has undergone an unprecedented boom in the past few years with new techniques (tomography, confocal microscopy) providing details that bring the examination of fossil morphology more comparable to that of extant species. The result of this increase in available character data and extinct taxa will be finer phylogenetic placement of peculiar fossil species and, hopefully, greater clarity on how best to tackle each classificatory alteration as they arise.

In the case of the presently known fossil oxytelines or putative oxytelines this challenge is acute as there are limited character data available. The four fossil species presently placed in *Sinoxytelus* possess a mixture of ancient and relatively modern traits. The basolateral ridges on the abdominal tergites are a trait of the tribe Oxytelini, while the somewhat reduced second abdominal sternite suggests placement in more primitive tribes. A solid age estimate is available for part (Lujiatun Bed) of the Yixian Formation and at approximately 126 Mya, or Aptian (Chang et al. 2017). If *Sinoxytelus* is truly either a stem group to Oxytelini or Oxytelini + other higher oxytelines, then the subfamily Oxytelinae as whole was apparently already diverse by the latter part of the Early Cretaceous. It seems apparent that there has been considerable extinction within the subfamily, resulting in only a few lineages surviving and diversifying to their present state. These fossils may be rather distantly related to the ancestors of the present Coprophilini or Oxytelini, with potentially numerous additional extinct stem groups (yet to be discovered) present before the divergence of the crown groups of these latter tribes. Characters that Cai et al. (2013) cite for placing *Sinoxytelus* within Coprophilini (e.g., metasternal process slightly protruding but not meeting mesosternal process) are more indicative of particular genera rather than the tribe, as there is considerable variation within the present day genera for these traits and are not strictly diagnostic for coprophilines (Herman 1970).

The current Burmese amber fossil species has a similarly conflicting combination of traits, on the one hand it can be placed in Coprophilini because of the plesiomorphic condition of the basal abdominal segments (although the tribe is presently defined on putative plesiomorphies and so this feature alone indicates nothing more than the potential for the fossil to belong therein or to belong to stem-group coprophilines, assuming the tribe is truly monophyletic). On the other hand, the apomorphically reduced number of tarsomeres, is a derived feature, but currently cannot be considered anything more than autapomorphic for the genus. Thus, given the lack of abundant evidence definitively demonstrating its phylogenetic placement relative to modern oxyteline genera, we prefer to tentatively consider the genus as a member (a stem group member) of Coprophilini. Hopefully, in time further material and other fossil species will be discovered that will ultimately permit a clarification of its relationships along with its broader implications toward affinities among lineages of Oxytelinae, and at which time a redefinition of oxyteline tribes may be attempted.

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The genus *Mercuria* Boeters, 1971 in Morocco: first molecular phylogeny of the genus and description of two new species (Caenogastropoda, Truncatelloidea, Hydrobiidae)

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Abstract

The western Palearctic freshwater snail genus *Mercuria* (Caenogastropoda: Hydrobiidae) comprises 26 species primarily distributed in lowland localities of Western Europe and North Africa. Although this genus in North Africa has received considerable attention in terms of species discoveries through morphological descriptions, its distribution and phylogenetic patterns remain unknown. Based on morphological and mitochondrial DNA (mtCOI) evidence, this study examines the three *Mercuria* species (*M. bakeri*, *M. tingitana,* and *M. targouasensis*) from Morocco identified so far. Besides expanding on information regarding the anatomy of these species, two new species (*M. midarensis* **sp. n.** and *M. tensiftensis* **sp. n.**) are described for this region and phylogenetic relationships inferred between these species and the European *M. emiliana* and *M. similis*. All Moroccan and European species were recovered as independent entities according to these phylogenetic inferences (uncorrected p-distances 2.8–8.5%) and DNA barcode data. Moroccan *Mercuria* species clustered with *M. emiliana* from Spain, although basal relationships within this clade were not well supported. Given that factors such as the season when specimens are collected, habitat type, and parasites could be responsible for the remarkable intraspecific variation observed in shell and penis morphology, it is proposed that the most efficient approach to delimit and identify *Mercuria* species is to combine morphological descriptions with genetic data.

Keywords
Anatomy, endemism, freshwater, molluscs, mtCOI, parasitism, systematics

Introduction

The gastropod genus *Mercuria* Boeters, 1971 (Truncatelloidea, Hydrobiidae) is widely distributed in continental aquatic systems of western Mediterranean territories and islands (Giusti 1979, Boeters 1988, Glöer et al. 2010, Patzner and Glöer 2013, Boeters and Falkner 2017) and more rarely in those of the Atlantic coasts of North Africa (Glöer et al. 2015) and Western Europe (Boeters 1988, Kadolsky 2011, Glöer et al. 2015, Boeters and Falkner 2017) and Madeira (Glöer et al. 2015). This genus currently comprises 26 species occurring mainly in lowland regions of North Africa (nine species; Glöer et al. 2015), continental France (six species; Boeters and Falkner 2017), and the Iberian Peninsula and Balearic Islands (four species, Boeters 1988, Glöer et al. 2015). *Mercuria* species occupy a wide variety of aquatic habitats, typically living in high abundance in springs and their outflows, coastal streams, and tide areas of rivers. Less frequently they appear in brackish meadows and ponds. Despite their high representation in lowland aquatic biotopes, phylogenetic relationships among *Mercuria* congeners have been scarcely explored. Species assignments of these snails have been based on conchological and anatomical studies. However, given their small size (shell height 1–5 mm) and featureless shells, molecular tools could help confirm the taxonomy and the phylogenetic position of *Mercuria* within the family. Based on molecular data obtained for the species *Mercuria similis* (Draparnaud, 1805), Wilke et al. (2013) recovered this genus as an independent lineage within the Hydrobiidae, which was further designated as the subfamily Mercuriinae (Boeters and Falkner 2017).

Northwestern Morocco harbors a relatively large proportion (four species) of the *Mercuria* species richness of North Africa. The earliest record of this genus in southern Morocco was *M. confusa* (Frauenfeld, 1863) (BackHuys and Boeters 1974), which has been recently placed in synonymy with *M. similis* (Boeters and Falkner 2017). Over the years, *M. similis* (=*M. confusa*) has been reported from several springs and streams in central and western Morocco (Ghamizi et al. 1997, Berrahou et al. 2001, Touabay et al. 2002, Boulal et al. 2017, Taybi et al. 2017). However, these records require confirmation through additional anatomical descriptions and molecular data. Based on penis and shell features, Glöer et al. (2015) recently described three new species, each found only in a single pond or spring in the coastal regions of Morocco: *M. tingitana*, *M. bakeri*, and *M. targouasensis*. Moreover, these authors identified two potential new *Mercuria* species but these have not been formally described. One was previously referred to as *M.* '*mirlheftensis*' (nomen nudum) by García et al. (2010), who included this species as 'Endangered' in the IUCN Red List of Threatened Species. However, this taxon has not been properly described and this name cannot therefore be considered valid.

Here we examined morphologically, anatomically, and molecularly a few paratypes of the species *M. tingitana* and *M. bakeri* as well as individuals from the population of *M.* '*mirlheftensis*' and other Moroccan localities. Our objectives were: (1) to delimit the formerly known and potential new Moroccan species of *Mercuria* under the phylogenetic species concept (i.e., a monophyletic assemblage of populations that possesses a unique combination of morphological traits) previously applied to hydrobiids (e.g., Delicado et al. 2012, Hershler et al. 2013); (2) to examine intra- and interspecific genetic variation and resolve phylogenetic relationships based on mtCOI sequences; and (3), to provide habitat and ecological data for future conservation plans.

Materials and methods

Individuals of *Mercuria* were collected from 16 localities, ranging from north-eastern to south-western Morocco (Figure 1), either by sieving mud or by hand with fine forceps. For anatomical studies, a share of the specimens of every locality was relaxed with menthol crystals following the protocols described in Ramos et al. (2000) and Arconada and Ramos (2001) and then preserved in 80% ethanol. The remaining specimens were preserved directly in 80% ethanol for genetic analyses. Type material was deposited into the Museo Nacional de Ciencias Naturales (**MNCN**) collection, Madrid, Spain. Voucher material and DNA samples were deposited in the University of Giessen Systematics and Biodiversity (**UGSB**) collection (Diehl et al. 2018) in Germany and in the Hydrobiid collection at Muséum d'Histoire Naturelle de Marrakech in Morocco.

We sequenced two *Mercuria* specimens per locality in most cases and analyzed together with other *Mercuria* sequences available in GenBank (Table 1). The final dataset comprised 30 sequences and two outgroup taxa, *Pseudamnicola lucensis* (Issel, 1866) and *Pyrgulopsis bedfordensis* (Hershler & Gustafson, 2001) [GenBank accession numbers AF367651 (Wilke et al. 2001) and EU700483 (Hershler et al. 2008), respectively]. Genomic DNA was extracted following the CTAB protocol of Wilke et al. (2006). LCO1490 (Folmer et al. 1994) and COR722b (Wilke and Davis 2000) primers were used to amplify a fragment of the cytochrome *c* oxidase subunit I (COI) gene. A shorter fragment of COI was obtained for *M. bakeri* and *M. tingitana* by using the sequence PCOIF4 (5'-TAGCTATTTTTCTYTACATYTRGC-3') as forward and COR722b as reverse primers. The PCR cycling conditions were as described in Schreiber et al. (2012) and Delicado et al. (2012). Products were sequenced in an ABI 3730 XL sequencer (Life Technologies, Carlsbad, CA, USA) using a Big Dye Terminator Kit (Life Technologies). New DNA sequences were edited in SEQUENCHER 4.6 (Gene Codes, Ann Arbor, MI), assembled together with sequences from GenBank and unambiguously aligned using MEGA 7.0. (Kumar et al. 2016). Sequence divergences (uncorrected p-distances) were also calculated in MEGA. Prior to the phylogenetic analyses, we employed jModelTest 2.1.4 (Darriba et al. 2012) under corrected Akaike's information criterion (AICc; Akaike 1974, Sugiura 1978, Hurvich and Tsai 1989) to obtain the best-fit substitution model for our data set.

Phylogenetic relationships among European and Moroccan *Mercuria* species were inferred based on Maximum Likelihood (ML) and Bayesian Inference (BI) using the

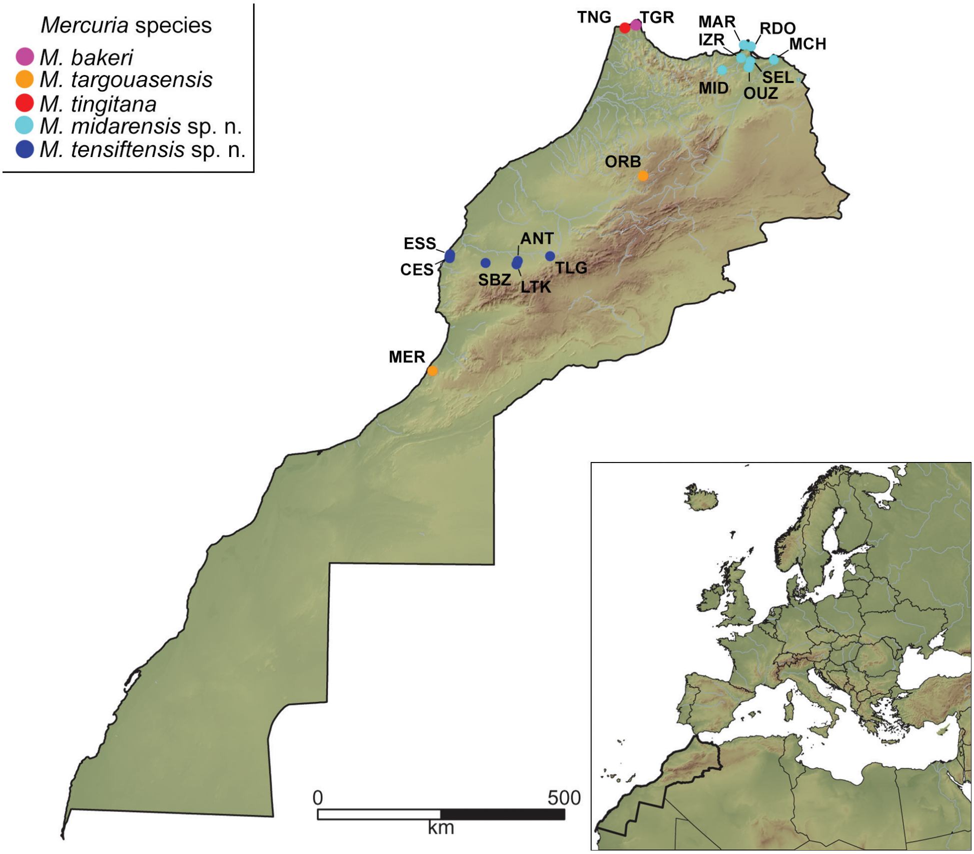

Figure 1. Map of Morocco showing sample locations and codes of the studied *Mercuria* populations. Locality codes are from Table 1.

substitution model HKY (Hasegawa et al. 1985) +G (including variation among sites) suggested by jModelTest. ML analysis was conducted in PhyML v. 3.1 (Guindon et al. 2010) with the above-mentioned evolutionary model and 100 random starting trees. Bayesian inference was performed with MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) through two independent runs of four parallel Markov Chain Monte Carlo (MCMC) simulations with 1.5 million generations each and a sample interval of 1000 generations. Convergence of the MCMC chains was examined by ensuring an average standard deviation of split frequencies lower than 0.01 in MrBayes and by checking with Tracer 1.6 (Rambaut et al. 2014) that all effective sample sizes (ESS) were higher than 200. After discarding the first 10% of the trees (burn-in), the remaining trees were used to construct a 50% majority-rule-consensus tree. Branch support was assessed by nonparametric bootstrapping (Felsenstein 1985) using 1000 pseudoreplicates for ML and by posterior probabilities (BPPs) for the BI. Trees and support values of branches were finally visualized in FigTree 1.3.1 (Rambaut 2010).

Table 1. Species name, locality information, locality code used in the phylogenetic analyses, and GenBank accession numbers for the *Mercuria* mtCOI sequences.

Species name	Locality	Locality code	GenBank number
Mercuria similis	Canale Panigai near Panigai, Friuli-Venetia-Julia, Udine, Aquileia, Italy (45°44.49'N, 13°20.448'E)		AF367646 (Wilke et al. 2001)
M. emiliana	Ullal Baltasar, Amposta, Tarragona, Spain (40°40.252'N, 00°35.212'E)		JX081888 (Delicado et al. 2013)
	Mallorca, La Puebla, Spain (39°47.467'N, 3°6.283'E)		AF213346 (Wilke et al. 2000)
M. tingitana	Swampy area between Tangier and Ksar es Seghir, Morocco (35°49.008'N, 5°43.644'W)	TNG	MH315899 (Present study)
M. bakeri	Spring at 3.5 km N of Taghramt, Morocco (35°48.912'N, 5°27.618'W)	TGR	MH315900 (Present study)
M. targouasensis	Ditch in Mirleft, Morocco (29°35.0167'N, 10°1.845'W)	MER	MH315885 (Present study)
	Oum Rbii Springs, Khenifra, Morocco (33°3.2059'N, 5°24.8797'W)	ORB	MH315886, MH315887 (Present study)
M. tensiftensis sp. n.	Ditch in Talkount, N-E of Marrakesh, Morocco (31°40.5775'N, 7°16.0298'W)	TLG	MH315888, MH315889 (Present study)
	Ditch in Sidi Bouzid, near Chichaoua, Morocco (type locality) (31°29.6133'N, 8°47.1116'W)	SBZ	MH315890, MH315891 (Present study)
	Agadir N'tachraft, S of Marrakesh, Morocco (31°23.0917'N, 8°7.5033'W)	ANT	MH315892 (Present study)
	Spring near Lalla Takerkoust Dam, Morocco (31°22.5491'N, 8°7.6385'W)	LTK	MH315893, MH315894 (Present study)
	Ditch in Haddada Bouzerktoun, Essaouira, Morocco (31°37.95'N, 9°35.0983'W)	CES	MH315895, MH315896 (Present study)
	Pond near Lahjar Spring, Essaouira, Morocco (31°38.7583'N, 9°35.0983'W)	ESS	MH315897, MH315898 (Present study)
M. midarensis sp. n.	Mariouari River, near Melilla, Morocco (35°18.36'N, 2°58.6483'W)	MAR	MH315874, MH315875 (Present study)
	Rio de Oro, Melilla, Spain (35°17.2483'N, 2°56.6283'W).	RDO	MH315876 (Present study)
	Izerouan River, W of Nador, Morocco (35°9.8333'N, 3°6.6'W)	IZR	MH315877 (Present study)
	Selouan River, S of Nador, Morocco (35°4.6117'N, 2°55.485'W)	SEL	MH315878, MH315879 (Present study)
	Ouzej River, Al Aaroui, Morocco (35°0.3634'N, 2°59.5133'W)	OUZ	MH315880, MH315881 (Present study)
	Ditch near Midar, Morocco (type locality) (34°54.5795'N, 3°34.0292'W)	MID	MH315882, MH315883 (Present study)
	Cherarba Ponds, W of Saidia, Morocco (35°6.3116'N, 2°20.75'W)	MCH	MH315884 (Present study)

Additionally, we tested the assignment of the Moroccan sequences to the species identified as new by the ML and BI approaches using the Automatic Barcode Gap Discovery (ABGD: Puillandre et al. 2012). The ABGD analysis was conducted at the web interface http://wwwabi.snv.jussieu.fr/public/abgd/ using the aligned matrix of COI sequences as input file, and the default settings, which consisted in the uncorrected genetic distances, a relative gap width of X = 1.5, and intraspecific divergence (P) values between 0.001 and 0.100.

A series of adults (number specified in the corresponding sections of the text and tables) from each locality and a few paratypes of the species *M. tingitana* and *M. bakeri* were morphologically examined. Morphological and anatomical characteristics were studied under a binocular Olympus SZX12 and photographed using a Keyence VHX 2000 3D Digital Microscope in combination with the program VHX-2000 Communication software version 2.3.5.0 (Keyence Corporation 2009–2012). Spire whorls were counted following Ramos et al. (2000). Before dissection, shells were dissolved in HCl or Ethylenediaminetetraacetic acid (EDTA). Radulae were extracted by applying the first step of the Proteinase K protocol for DNA isolation (Wilke et al. 2006). After mounting on stubs and drying, radulae were covered with gold (Balter Sputter Coater SCD004) for 50 sec. and then photographed with a field emission scanning electron microscope (FESEM) DSM982 Gemini (Carl Zeiss GmbH, Germany). Anatomical illustrations were obtained from camera lucida drawings carried out under a WILD HEERBRUGG stereomicroscope. Morphological and anatomical character states are based on the terminology of Hershler and Ponder (1998).

Abbreviations used in the text and tables

Shell and operculum characters: AH: aperture height; AL: aperture length; AW: aperture width; LBW: length of body whorl; NSW: number of spire whorls; SL: shell length; SW: shell width; WAW: width of the antepenultimate whorl; WBW: width of the body whorl; WPW: width of the penultimate whorl.

Anatomical characters: Ag: albumen gland; Bc: bursa copulatrix; CC: cerebral commissure; Cg: capsule gland; Ct: ctenidium; dBc: duct of the bursa copulatrix; LCG: left cerebral ganglion; LPG: left pleural ganglion; Os: osphradium; P: penis; PA: penial appendix; Po: pallial oviduct; Pr: prostate gland; RCG: right cerebral ganglion; Ro: renal oviduct; RPG: right pleural ganglion; SR: seminal receptacle; Ss: style sac; St: stomach; SubC: suboesophageal connective; SubG: suboesophageal ganglion; SupC: supraoesophageal connective; SupG: supraoesophageal ganglion; L: length; W: width. Concentration of the nervous system was measured as the "RPG" ratio (Davis et al. 1976) and described by applying the categories of Davis et al. (1984, 1986, 1992) as follows: dorsal nerve ring concentrated (RPG ratio ≤ 0.29); moderately concentrated (RPG ratio 0.30–0.49); elongated (RPG ratio 0.50–0.67); extremely elongated (RPG ratio ≥ 0.68).

Collections: MHNM: Muséum d'Histoire Naturelle de Marrakech, Morocco; MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain; UGSB: University of Giessen Systematics and Biodiversity Collection, Giessen, Germany.

Collectors: K.B., K. Boulaassafer, D.D., D. Delicado, M.G., M. Ghamizi, T.H., T. Hauffe.

Results

Phylogenetic relationships and genetic distances

The resulting COI data set yielded 658 bp. All new sequences obtained in this work were deposited in GenBank under accession numbers MH315874–MH315900. In both the ML and BI analyses, the Moroccan specimens clustered with the three previously described species and the two new species described below. ABGD analysis confirmed these assignments. Based on ca. 400 bp obtained from their paratypes, *M. bakeri* and *M. tingitana* were recognized as potentially different sister species. The additional sampling effort made for this study also extends the distribution range of *M. targouasensis* from southern to central Morocco.

ML and BI topologies were congruent and thus only the ML topology is depicted in Figure 2. This topology showed seven morphologically distinct clades/lineages within *Mercuria*. Moroccan *Mercuria* species clustered together with *M. emiliana* from Spain. This clade was well supported by both ML and BI (75% and 0.95, respectively). All Moroccan specimens formed monophyletic groups, which corresponded to the previously described species and to those described here, except those of *M. targouasensis*. Basal relationships within the *Mercuria* clade were better supported in BI (BPP = 0.93) than in ML (bootstrap value 63%). Within this clade, the species from the Rif Mountains, *Mercuria midarensis* sp. n., and the Atlas Mountains, *M. targouasensis*, clustered together as sister species (85% in ML and 1.00 in BI), as did the species from the northern Moroccan Atlantic coast: *M. tensiftensis* sp. n., *M. tingitana*, and *M. bakeri* (90% in ML and 1.00 in BI). The latter two species were poorly supported as sisters (67% in ML and 0.81 in BI).

Mercuria midarensis sp. n. and *M. targouasensis* differed from each other by 2.8% (mean sequence divergence, see Table 2). Mean sequence divergence within this first species was 1.8% (0%–3.4%) and 1.3% (1.3%–1.3%) within the second species. Mean sequence divergence between *M. tingitana* and *M. bakeri* was 3.4%. These two species differed from *M. tensiftensis* sp. n., which shows the lowest intraspecific variation (0%), by 4.7%.

Table 2. Distance matrix of mean COI sequence divergence (uncorrected p-distances in percentage) within species (on diagonal) and among *Mercuria* species and the selected outgroups (bellow diagonal).

	1	2	3	4	5	6	7	8	9
1. *Pyrgulopsis bedfordensis*	0.0								
2. *Pseudamnicola lucensis*	13.3	0.0							
3. *Mercuria emiliana*	14.2	15.0	0.0						
4. *M. similis*	14.2	13.3	7.7	0.0					
5. *M. targouasensis*	14.4	14.6	7.4	4.2	1.3				
6. *M. midarensis* sp. n.	13.5	15.2	7.6	6.0	2.8	1.8			
7. *M. tensiftensis* sp. n.	14.6	15.5	7.7	6.4	6.0	6.9	0.0		
8. *M. bakeri*	15.9	16.3	7.3	6.4	4.8	6.8	4.7	0.0	
9. *M. tingitana*	16.7	15.9	8.2	7.3	6.5	8.5	4.7	3.4	0.0

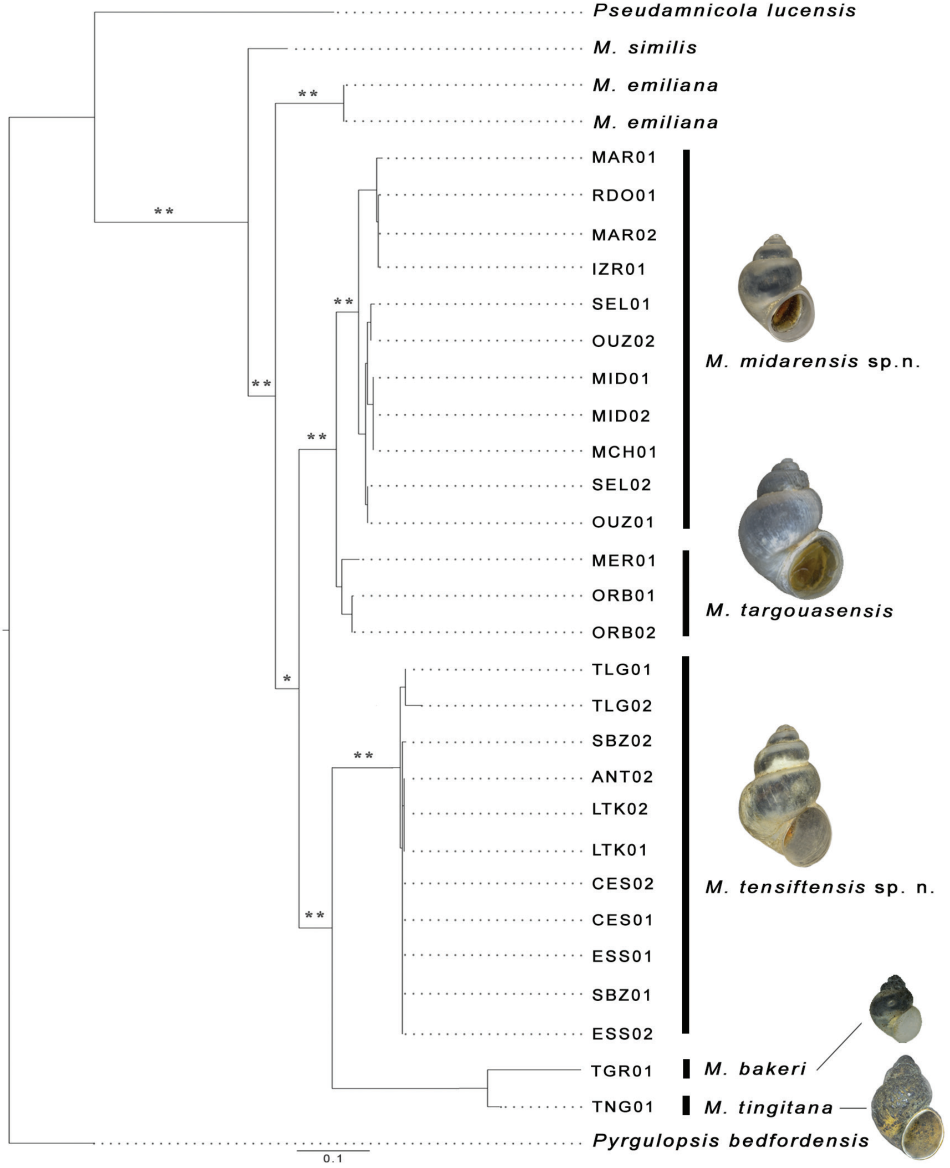

Figure 2. Maximum Likelihood tree based on mtCOI sequences of seven *Mercuria* species. One asterisk represents ML bootstrap values below 75% and BPPs above 0.9; two asterisks represent ML bootstrap values above 75% and BPPs above 0.9. Black bars on the right denote species assignments. Scale bar: expected change per site.

Systematic descriptions

Family Hydrobiidae Stimpson, 1865
Genus *Mercuria* Boeters, 1971

Mercuria bakeri Glöer, Boeters & Walther, 2015

Examined material. MOROCCO. Paratype (one male): UGSB 18986, Taghramt, 3.5 km towards N, Tangier-Titouan, 23/03/2014 (35°48.912'N, 5°27.618'W).

Revised diagnosis. Shell ovate-conic; periostracum greyish; body whorl large, convex, occupying approximately 3/4 of total shell length; aperture ovate and complete; umbilicus narrow, not covered by the inner lip; central radular tooth formula (3)4–C–4(3)/1–1; bursa copulatrix elongate; bursal duct shorter than bursa length; one seminal receptacle fingerlike, with a short duct; penis strap-like, pigmented from brown to dark grey; penial appendix unpigmented, shorter than penis, base wide, medially positioned on inner edge of penis; nervous system moderately concentrated (mean RPG ratio = 0.40).

Description. Shell ovate-conic (Figure 2), height 3.0–3.5 mm (Glöer et al. 2015). Periostracum greyish. Teleoconch whorls convex, separated by deep sutures. Body whorl occupying approximately 3/4 of total shell length. Umbilicus narrow, partially covered by the inner lip. Aperture ovate, complete, in contact with the body whorl; inner lip thicker than outer lip.

Radula with approximately 65 rows of teeth (Figure 3A), medium sized (23% total shell length), 7.5 times longer than wide. Central tooth formula (3)4–C–4(3)/1–1; central cusp long, V-shaped. Lateral tooth formula 3–C–3; central cusp long, V-shaped (Figure 3B, C). Inner and outer marginal teeth having approx. 16 and 20 pointed cusps, respectively (Figure 3D).

Head brown pigmented except for white patches surrounding tentacles and eyes (Figure 4A). Ctenidium well-developed, with ca. 21 gill filaments, occupying most of pallial cavity; osphradium elongate, positioned middle of ctenidium (Figure 4C). Bursa copulatrix elongate. Bursal duct shorter than bursa length. Seminal receptacle fingerlike, with a short duct, joining renal oviduct above the insertion point with bursal duct (based on Glöer et al. 2015). Penis strap-like, attached to central area of head. Penis brown to dark grey pigmented. Penial appendix and base of penis unpigmented. Penial appendix shorter than penis, base wide, medially positioned on inner edge of penis (Figure 4B). Terminal gland large, occupying the whole distal end of the appendix.

Distribution. Only known from the type locality.

Remarks. Based on a short fragment of the mitochondrial COI gene, our phylogenetic analysis depicts *M. bakeri* as sister to *M. tingitana* with a mean uncorrected sequence divergence of 3.4%. A greater genetic distance is not unexpected when including longer sequences. Despite this relatively low genetic distance, morphological differences between these two species are striking, especially in terms of penis shape (penis slender, 3.5 times longer than appendix in *M. bakeri* and penis and appendix

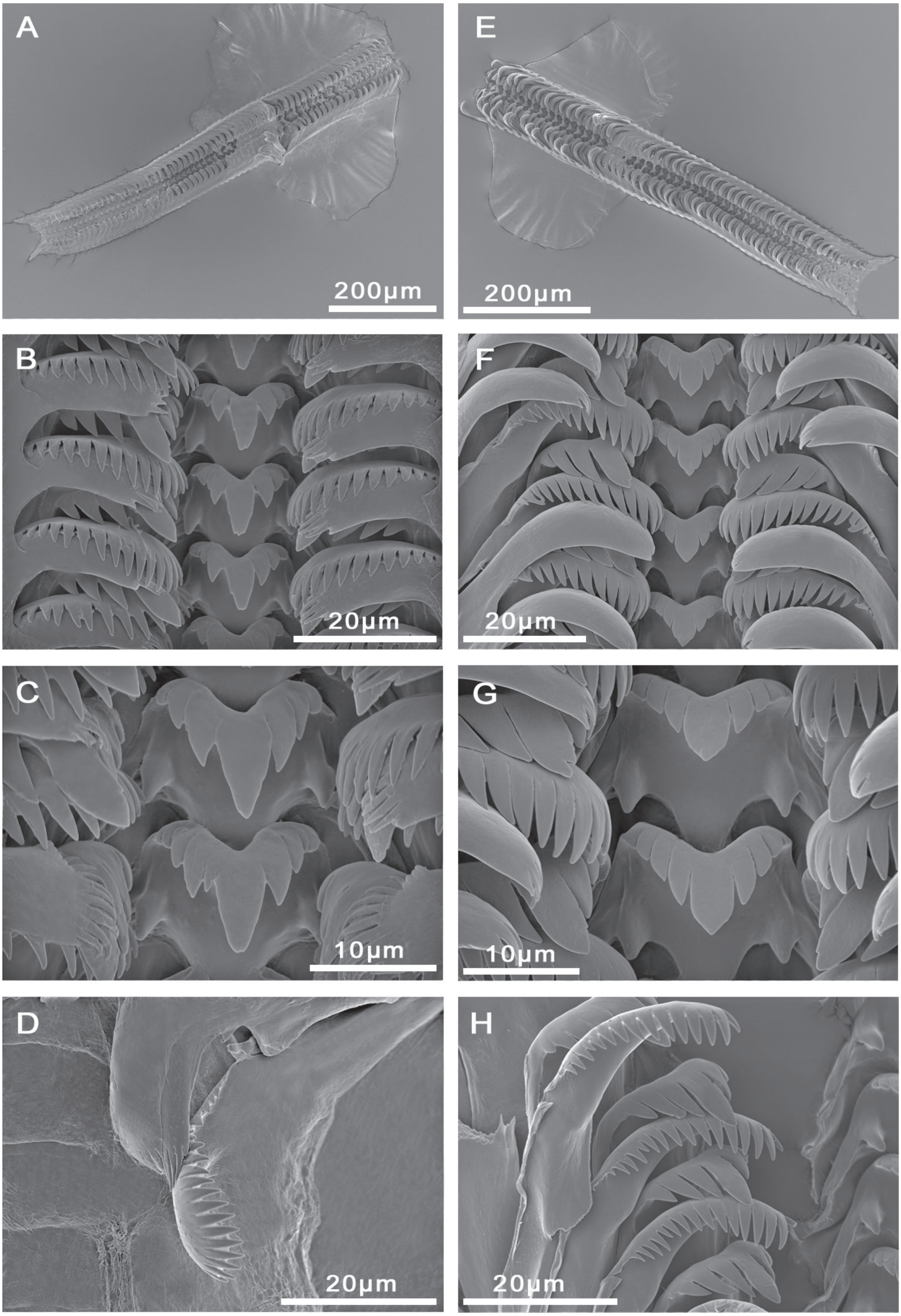

Figure 3. Radulae, **A–D** *M. bakeri*, Taghramt **E–H** *M. tingitana*, Tangier at 11 km towards Ksar es Seghir. **A, E** Radulae ribbons **B, F** Overview of rows of radulae teeth **C, G** Central tooth **D** Outer marginal tooth **H** Inner marginal and lateral teeth.

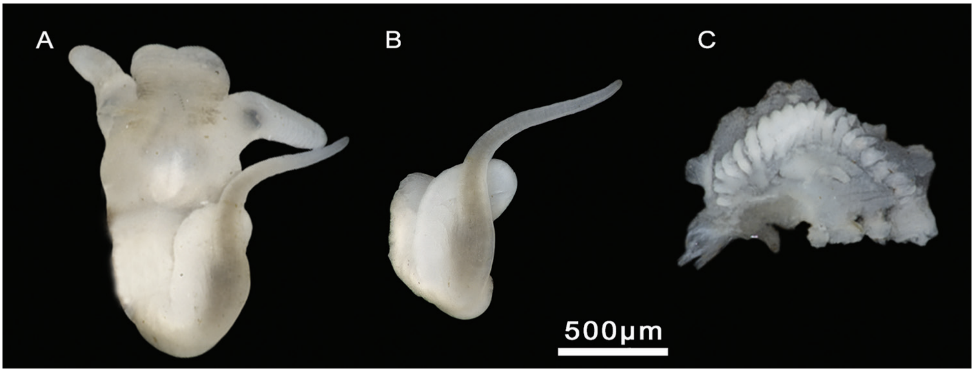

Figure 4. Male genitalia and ctenidium, *M. bakeri*, Taghramt. **A** Head with penis **B** Penis **C** Ctenidium.

almost equal in size in *M. tingitana*) and seminal receptacle (longer in *M. bakeri* than *M. tingitana*).

Ecology. See Glöer et al. (2015).

Mercuria tingitana Glöer, Boeters & Walther, 2015

Examined material. MOROCCO. Paratypes (two females): UGSB 17658, Tangier at 11 km towards Ksar es Seghir, 22/03/2014 (35°49.008'N, 5°43.643'W).

Revised diagnosis. Shell ovate-conic, whorls 4–5; periostracum greyish; body whorl large, convex, approx. three-quarters of shell length; aperture ovate and complete; umbilicus narrow, not covered by the inner lip; central radular tooth formula 4–C–4/1–1; bursa copulatrix pyriform to elongate, with a short duct; one seminal receptacle elongate, without duct; penis small, black pigmented; penial appendix as long as penis, slightly pigmented, base wide, distally positioned on inner edge of penis.

Description. Shell ovate-conic, whorls 4–5, height 2.9–3.6 mm (Figure 5A; Suppl. material 1: Table 1). Body whorl large, approx. two-thirds total shell length. Teleoconch whorls shouldered, separated by deep sutures. Periostracum greyish. Aperture ovate, complete, in contact with the body whorl; inner lip thicker than outer lip; peristome margin straight (Figure 5B). Umbilicus narrow, partially covered by the inner lip.

Operculum as for genus, brownish, whorls 2.5. Muscle attachment area oval located near the nucleus (Figure 5C, D). Radula length intermediate, approx. 600 µm long (20% total shell length), six times longer than wide, with 50–60 rows of teeth (Figure 3E; Suppl. material 1: Table 2). Central tooth formula 4–C–4/1–1; central cusps tongue-shaped. Lateral tooth formula 3–C–3; central cusp long, V-shaped (Figure 3F–H). Inner marginal teeth with 15–16 pointed cusps. Outer marginal teeth with 21–23 cusps (Suppl. material 1: Table 2).

Animal black pigmented except for neck and eye lobes. Ctenidium well-developed, with 19–23 gill filaments, occupying almost entire length of the pallial cavity. Osphradium elongate, positioned posterior to middle of ctenidium (Figure 6A). Stomach nearly as long

Figure 5. Shells and opercula, *M. tingitana*, Tangier at 11 km towards Ksar es Seghir. **A, B** Shells, **C, D** Opercula (inner, outer sides).

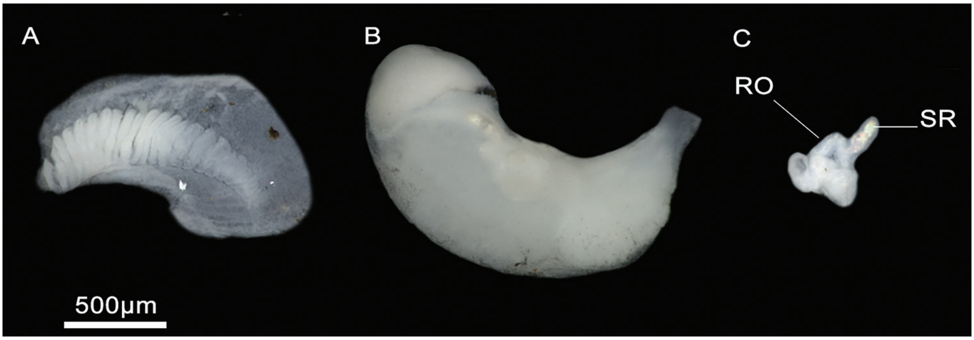

Figure 6. Ctenidium and female genitalia, *M. tingitana*, Tangier at 11 km towards Ksar es Seghir. **A** Ctenidium **B** Pallial oviduct **C** Seminal receptacle (**SR**) and renal oviduct (**RO**).

as wide; style sac slightly shorter than stomach and surrounded by an unpigmented intestine (Suppl. material 1: Table 3). Glandular oviduct approx. three times longer than wide. Capsule gland shorter and thicker than albumen gland. Renal oviduct coiled, unpigmented. Bursa copulatrix pyriform to elongate, with a short duct. Seminal receptacle small, elongate, sessile, joining renal oviduct above the insertion point with bursal duct (Figure 6B, C; Suppl. material 1: Table 4). Penis attached to central area of head. Penis and penial appendix almost equal in length. Penis black pigmented, short, and triangular. Penial appendix and base of penis unpigmented. Terminal gland small (see Glöer et al. 2015).

Distribution. Only known from the type locality.

Remarks. *Mercuria tingitana* can be distinguished from its congeners in northern Africa by its slender shell and short penis. Genetically, the closest species to *M. tingitana* is *M. bakeri*. However, both these are the most distant species to other Moroccan congeners with an uncorrected pairwise distance range of 4.7–8.5% for *M. tingitana* and of 4.7–6.8% for *M. bakeri*. *Mercuria midarensis* sp. n. and *M. emiliana* are the most genetically distant from *M. tingitana* according to COI divergences of 8.5% and 8.2%, respectively (Table 2).

Ecology. See Glöer et al. (2015).

Mercuria targouasensis Glöer, Boeters & Walther, 2015

Mercuria confusa Backhuys & Boeters, 1974: 113

Material. Examined material. MOROCCO. MHNM 18 ZTMH10, UGSB 17912, Oum Rbii Springs, N of Khenifera, 01/06/2015 (33°3.2059'N, 5°24.8797'W); MHNM 18 ZTMH11, UGSB 17955, a small ditch in Mirleft, 02/02/2015 (29°35.0167'N, 10°1.845'W).

Revised diagnosis. Shell ovate-conic, whorls 3–5; periostracum whitish; body whorl occupying more than three-quarters of total shell length; aperture ovate; umbilicus narrow, partially covered by the inner lip; operculum brownish to slightly orange; central radular tooth formula 3–C–3/1–1; bursa copulatrix elongate, with a short duct; one seminal receptacle pyriform, with a short duct; penis gradually tapering, grey; penial appendix shorter than penis, grey, base wide, medially positioned on inner edge of penis; nervous system extremely elongated (mean RPG ratio = 0.70), gently black pigmented.

Description. Shell ovate-conic, whorls 3–5, height 2.63–3.43 mm (Figure 7A–C; Suppl. material 1: Table 1). Periostracum whitish. Protoconch with two whorls, diameter ca. 600 µm; nucleus ca. 140 µm wide (Figure 7H); protoconch microsculpture granulated (Figure 7I). Teleoconch whorls convex, separated by deep sutures. Body whorl large, occupying three-quarters of total shell length. Aperture ovate, complete, in contact with the body whorl; inner lip thicker than outer lip; peristome margin straight (Figure 7D, E). Umbilicus narrow, partially covered by the inner lip.

Operculum as for genus, light orange to brown, whorls 2; muscle attachment area near nucleus (Figure 7F, G). Radula length intermediate, ca. 800 µm long (20% total shell length), seven times longer than wide, with approx. 50 rows of teeth (Fig 8A; Suppl. material 1: Table 2). Central tooth formula 3–C–3/1–1; central cusp tapered, long. Lateral teeth formula (4)3–C–3(4); central cusp wide, V-shaped (Figure 8B, D–F). Inner and outer marginal teeth having 11–15 and 14–18 cusps, respectively (Figure 8C, F).

Animal black pigmented except for pale area surrounding eye lobes and neck (Figure 9G, H). Ctenidium well-developed, with 19–25 gill filaments, occupying almost entire length of the pallial cavity. Osphradium elongate, positioned approximate middle of ctenidium (Figure 9A). Stomach nearly as long as wide; style sac slightly shorter than stomach, surrounded by an unpigmented intestine (Figure 9B; Suppl. material 1: Table 3). Glandular oviduct three times longer than wide. Capsule gland longer and thicker than

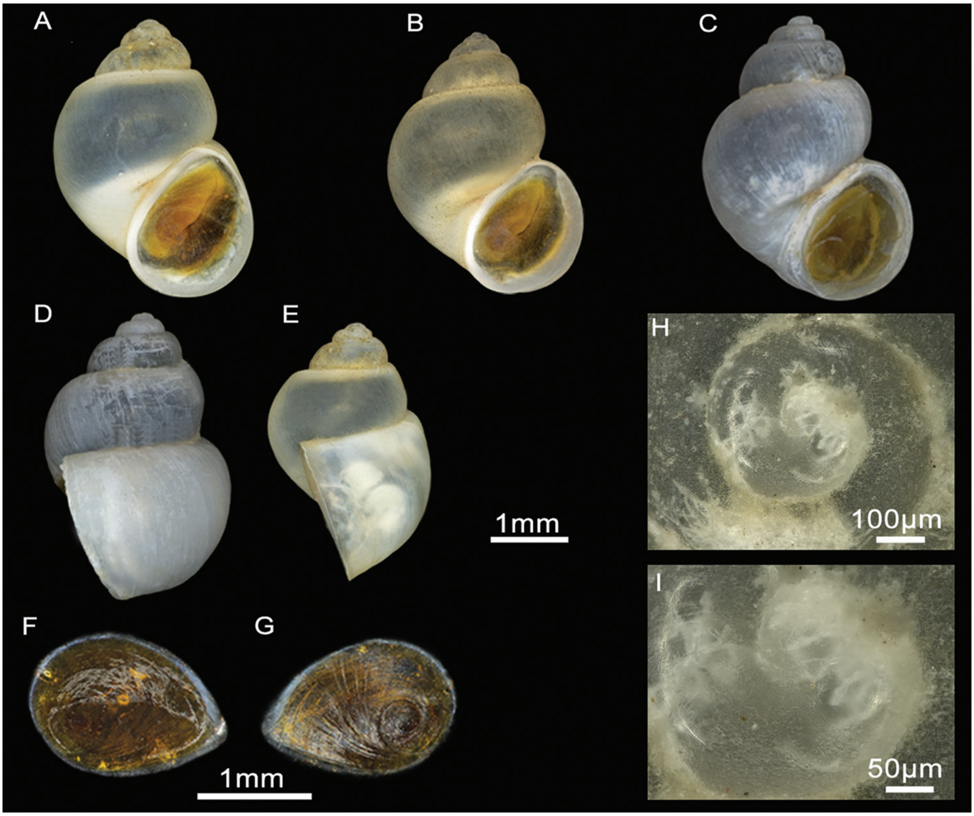

Figure 7. Shells and opercula, *M. targouasensis*. **A, B, E** Shell, Oum Rbii Springs **C, D** Shell, a small ditch in Mirleft **F, G** Opercula (inner, outer sides), Oum Rbii Springs **H, I** Protoconch and detailed microsculpture of protoconch, Oum Rbii Springs.

albumen gland. Bursa copulatrix pyriform to elongate, with a short duct. Renal oviduct unpigmented, coiled, making three loops. Seminal receptacle pyriform, with a short duct, joining renal oviduct above the insertion point with bursal duct (Figure 9D, E; Suppl. material 1: Table 4). Prostate gland bean-shaped, ca. 2.5 times longer than wide (Figure 9F; Suppl. material 1: Table 5); seminal duct entering the posterior region; pallial vas deferens emerging close to its anterior edge. Penis gradually tapering, attached to the area close to the right eye. Penial appendix slightly pigmented, shorter than penis, base wide, middle positioned on inner edge of penis. Terminal gland large, occupying the whole distal end of the appendix (Figure 9G–J; Suppl. material 1: Table 5). Nervous system gently pigmented, extremely elongated (mean RPG ratio = 0.70; Suppl. material 1: Table 6); cerebral ganglia equal in size and shape (Figure 9C).

Distribution. This species was found in coastal streams in southwestern Morocco and in a spring-fed habitat in the Middle Atlas.

Remarks. The morphological and anatomical descriptions presented here are based on specimens collected at two sites: one in the Mirleft region, 70 km from the

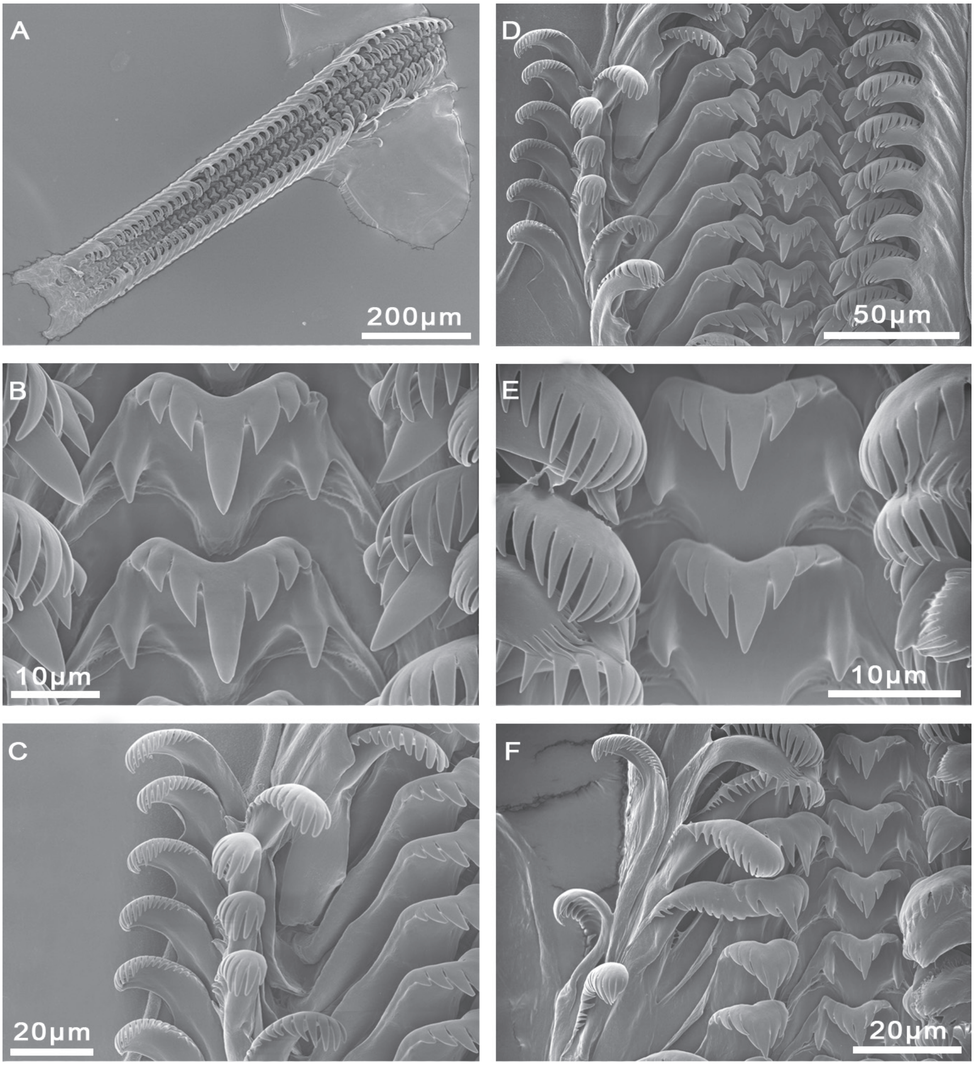

Figure 8. Radulae, *M. targouasensis*. **A–D** Oum Rbii Springs **E, F** A small ditch in Mirleft. **A** Radular ribbon **B, E** Central tooth **C, D, F** Inner marginal, outer marginal, and lateral teeth.

type locality, (i.e., ford Oued Assaka), and another, in a more remote place in the Middle Atlas Mountains. The population collected in the surroundings of Mirleft may correspond to the species *Mercuria* '*mirlheftensis*' (nomen nudum) from the same area suggested by García et al. (2010). However, the name *M.* '*mirlheftensis*' is not valid. Specimens collected in the Mirleft area resemble specimens from the type locality of *M. targouasensis* regarding the shape of the penis and prostate, and also of the female genitalia, especially bursa copulatrix shape. Based on the geographic proximity of these two localities and the similarity in shell and anatomical characters of their specimens, we assigned the population from Mirleft to *M. targouasensis*. Specimens from Oum

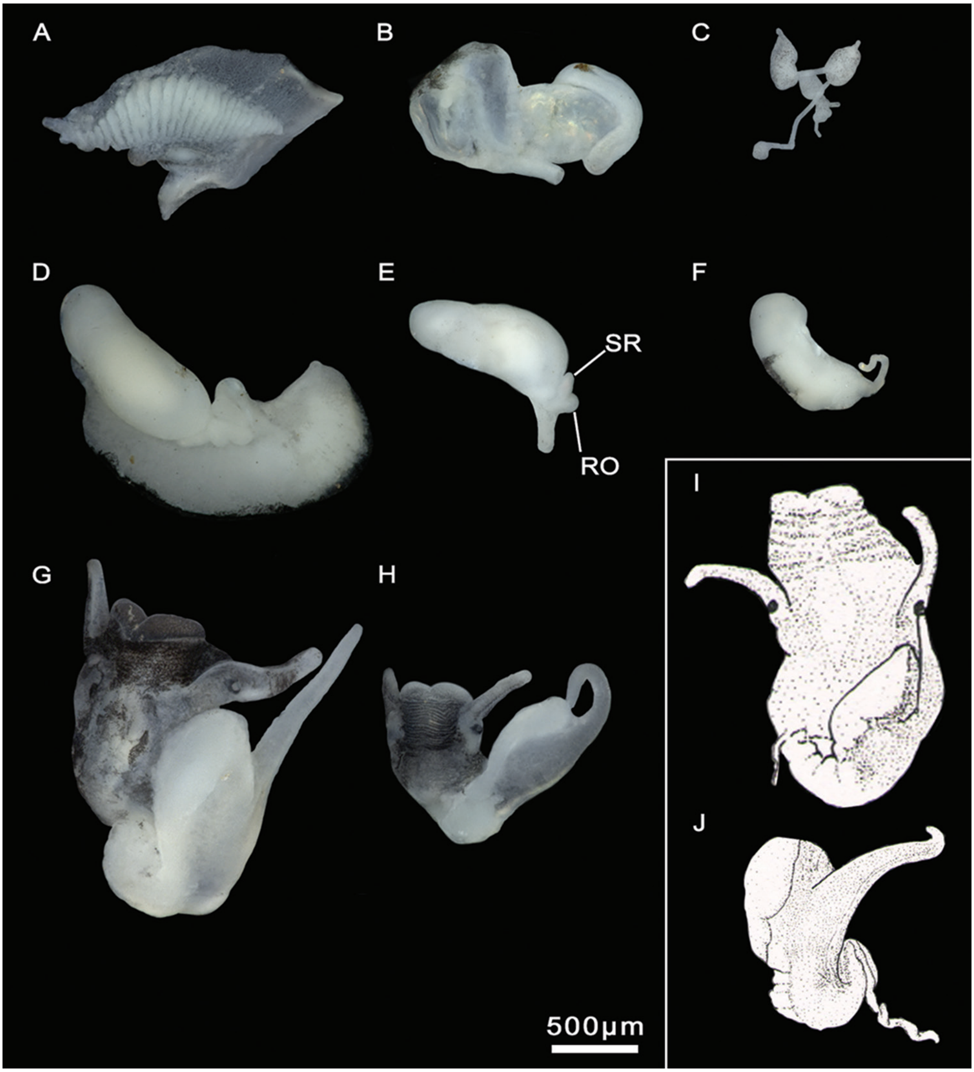

Figure 9. Anatomical structures, *M. targouasensis*. **A–F, H** A small ditch in Mirleft **G, I–J** Oum Rbii Springs. **A** Ctenidium **B** Stomach **C** Partial nervous system **D** Pallial oviduct **E** Bursa copulatrix and seminal receptacle **F** Prostate gland **G, H** Head with penis **I, J** Head and penis drawings. **RO** renal oviduct **SR** seminal receptacle.

Rbii (Middle Atlas) were also tentatively assigned to this species based on shell and morphological similarities and a short genetic distance (1.3%) between this and the Mirleft population. However, this assignment needs confirmation in future systematic studies on *Mercuria*, which should include these and other Mediterranean species.

Mercuria targouasensis and *M. midarensis* sp. n. are sister species and differ molecularly by 2.1%–3.4% (mean sequence divergence 2.8%). The two species are close in shell dimensions but differ in other shell features such as the relative size of the body whorl (larger in *M. targouasensis*) or the umbilicus (wider in *M. midarensis* sp. n.). They also differ anatomically; *Mercuria midarensis* sp. n. has typically a strap-like penis, 2.5 times longer than head length, a small penial appendix with narrow insertion into the penis, and an elongate bursa copulatrix, whereas in *M. targouasensis*, the penis is more often gradually tapering, equal or 1.5 times longer than head length, the penial appendix is larger with a wider insertion, and the bursa copulatrix is pyriform to elongate. These two species also differ in the number of cusps on radular teeth (Suppl. material 1: Table 2).

Ecology. In the new localities of *M. targouasensis*, this species was found attached to stones in a saltwater spring in the Middle Atlas (ca. 1,200 m a.s.l. altitude, and 37.9 PSU, practical salinity unit) and in the sediment of a ditch in the region of Mirleft cohabiting with *Melanopsis praemorsa*.

***Mercuria midarensis* sp. n.**

http://zoobank.org/C15971DC-9513-4AC8-B7E5-D74D0EFF8644

Type material. Holotype, MNCN 15.05/200019H (Ethanol 80%), a small ditch 7 km from Midar, Northern Morocco, 34°54.5795'N, 3°34.0292'W, 03/06/2015, leg. K.B., M.G., D.D., T.H. Paratypes MNCN 15.05/200019P, UGSB 17921, and MHNM 18 ZTMH12 (from the same lot).

Other material. MOROCCO. MHNM 18 ZTMH20, UGSB 17921, UGSB 17922, a small ditch 7 km from Midar, 03/06/2015 (34°54.5795'N, 3°34.0292'W); MHNM 18 ZTMH13, UGSB 19933, Selouan River, S of Nador, 30/04/2016 (35°4.6117'N, 2°55.485'W); MHNM 18 ZTMH14, UGSB 19939, Ouzej River, Al Aaroui, 30/04/2016, (35°0.3634'N, 2°59.5133'W); UGSB 19935, Cherarba ponds W of Saidia, 28/04/2016 (35°6.3116'N, 2°20.75'W); MHNM 18 ZTMH15, UGSB 19934, Izerouan River, 20 km W of Nador, 12/05/2015 (35°9.8333'N, 3°6.6'W); MHNM 18 ZTMH16, UGSB 19940, Mariouari River, 30/04/2016 (35°18.36'N, 2°58.6483'W); MHNM 18 ZTMH17, UGSB 19938, Messoussate River, Selouan, 02/05/2016 (35°3.81'N, 2°54.383'W). SPAIN. MHNM 18 ZTMH18, UGSB 19937, Rio de Oro, Melilla, 18/05/2015, (35°17.2483'N, 2°56.6283'W).

Diagnosis. Shell ovate-conic, whorls 4–5; periostracum whitish; body whorl large, convex, occupying more than three-quarters of total shell length; aperture ovate, complete; umbilicus narrow, not covered by the inner lip; protoconch microsculpture granulated; operculum dark orange to dark brown; central radular tooth formula (3)4–C–4(3)/1–1; bursa copulatrix elongate, with a short duct; one seminal receptacle elongate without duct; penis gradually tapering to strap-like, light to dark grey pigmented; penial appendix similarly pigmented, shorter than penis, base wide, medially positioned on inner edge of penis; nervous system extremely elongated (mean RPG ratio = 0.70), slightly pigmented.

Description. Shell ovate-conic, whorls 4–5, height 3–4.7 mm (Figure 10A–J; Suppl. material 1: Table 1). Periostracum whitish. Protoconch ca. 400 µm wide, whorls

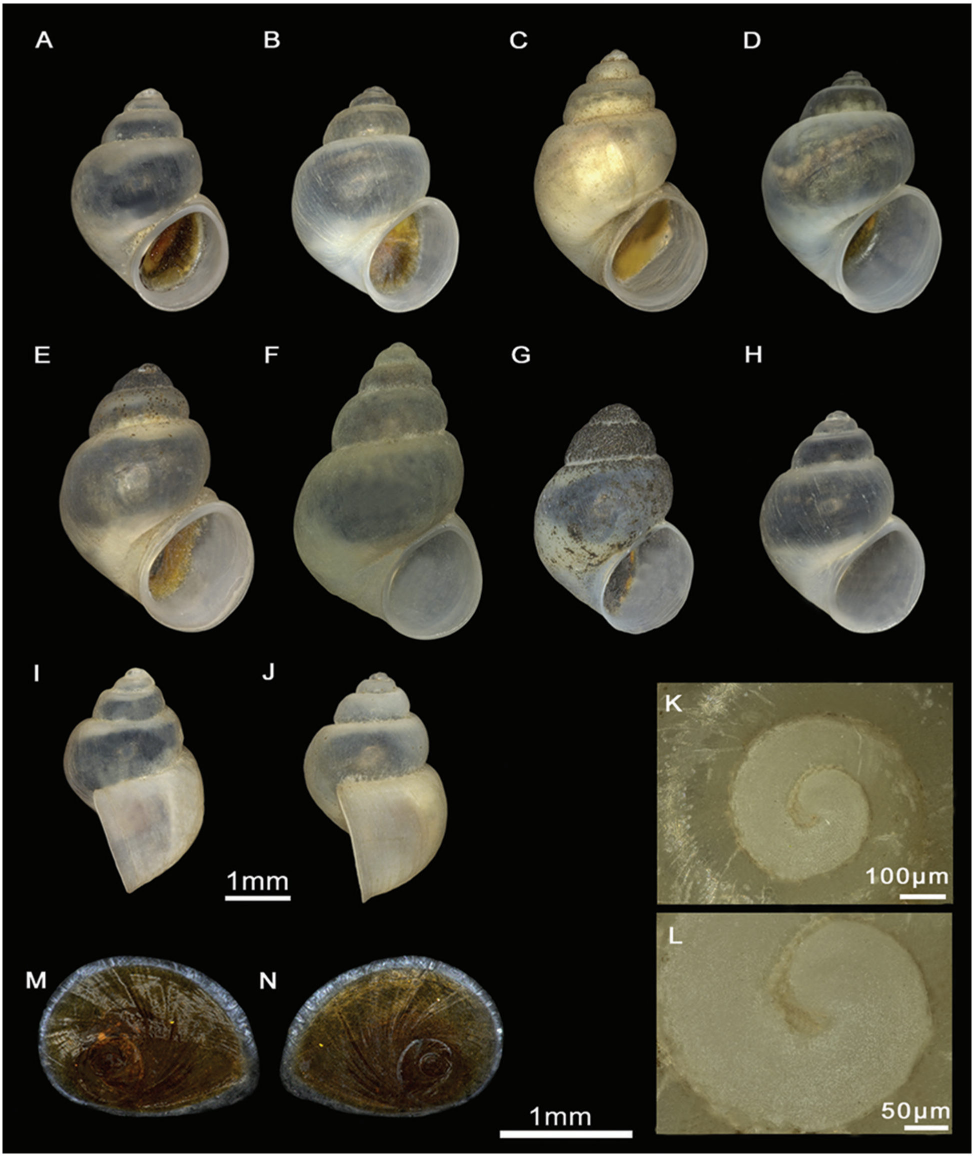

Figure 10. Shells and opercula, *M. midarensis* sp. n. **A, I** Holotype MNCN 15.05/200019H **B** Shell, a small ditch 7 km from Midar **C** Shell, Selouan River **D** Shell, Ouzej River **E** Shell, Cherarba ponds **F** Shell, Mariouari River **G** Shell, Rio de Oro **H** Shell, Izerouan River **M, N** Opercula (inner, outer sides), a small ditch 7 km from Midar **K, L** Protoconch and detailed microsculpture of protoconch, Selouan River.

1.5; nucleus ca. 125 μm wide; protoconch microsculpture granulated (Figure 10K–L). Teleoconch whorls shouldered, separated by deep sutures. Body whorl large, occupying three-quarters of total shell length. Aperture ovate, complete, sometimes in contact with the body whorl; inner lip thicker than outer lip; peristome margin straight (Figure 10I–J). Umbilicus narrow, not covered by the inner lip.

Operculum as for genus, dark orange to dark brown, surrounded by a thin and transparent border, whorls 2, muscle attachment area oval and located near the nucleus (Figure 10M–N). Radula length intermediate, ca. 900 µm long (23% total shell length), 7.5 times longer than wide (Figure 11A, F; Suppl. material 1: Table 2); 53–67 rows of teeth. Central tooth formula (3)4–C–4(3)/1–1; central cusp V-shaped, long (Figure 11B–D, G–I). Lateral tooth formula (2)3–C–3(2); central cusp tongue-shaped (Figure 11J). Inner marginal teeth with 12–14 long, pointed, cusps. Outer marginal teeth bearing 18–20 cusps (Figure 11E–J, Suppl. material 1: Table 2).

Head and tentacles dark brown pigmented; eye lobes and snout margin unpigmented; pigmentation lighter on neck (Figure 12G–H). Ctenidium well developed, with 21–26 gill filaments, occupying most of pallial cavity. Osphradium elongate, positioned opposite middle of the ctenidium (Figure 12A). Stomach slightly longer than wide; style sac shorter than stomach, surrounded by an unpigmented intestine (Figure 12B, Suppl. material 1: Table 3). Glandular oviduct from two to three times longer than wide. Albumen gland shorter than capsule gland. Bursa copulatrix elongate, from two to three times longer than wide. Bursal duct very short. Renal oviduct unpigmented, coiled. Seminal receptacle elongate, without duct (Figure 12D–F, J, Suppl. material 1: Table 4). Prostate gland bean-shaped, approx. two times longer than wide (Figure 12I). Seminal duct entering the posterior region and pallial vas deferens emerging close to its anterior edge. Penis gradually tapering to strap-like, attached well behind right eye, base large and slightly pigmented. Penis tapering, light grey pigmented. Penial appendix light grey, shorter than penis, two times longer than wide, base wide, medially positioned on inner edge of penis (Figure 12G–H, K–L; Suppl. material 1: Table 5). Terminal gland large, occupying the whole distal end of the appendix. Nervous system slightly pigmented, extremely elongated (mean RPG ratio 0.70; Suppl. material 1: Table 6); cerebral ganglia almost equal in size and shape (Figure 12C).

Etymology. This species is named *midarensis* after Midar, the nearby city where this species was collected for first time.

Distribution. *Mercuria midarensis* sp. n. is distributed mostly in spring-fed and riverine habitats of northeastern Morocco and the surroundings of the Spanish city of Melilla.

Remarks. The mean uncorrected sequence divergence within *Mercuria midarensis* was 1.8%, ranging from 0%–3.4%. Despite their geographic proximity, *M. midarensis* populations were genetically resolved into two geographically separate groups: the northern populations, i.e. those from the Mariouari River, Rio de Oro, and Izerouan River basins; and the southern ones, i.e. ditch in Midar (type locality), Selouan River, Ouzej River, and Cherarba Ponds. Although mean genetic distances between these two groups of populations were relatively high ranging from 2.6% to 3.4% for COI, we found no consistent morphological differences to consider them distinct. However, we did observe shell variability within each group. For most localities, shell length mostly ranged from 3.0 mm to 4.5 mm, with the body whorl occupying 75–82% total shell length. As exceptions, specimens from the Mariouari and Selouan river basins had larger shells (4.0–5.5 mm and 3.6–4.8 mm, respectively) and a body whorl occupying 60–75% total shell length (Figure 10C, F). Although female genitalia morphology and

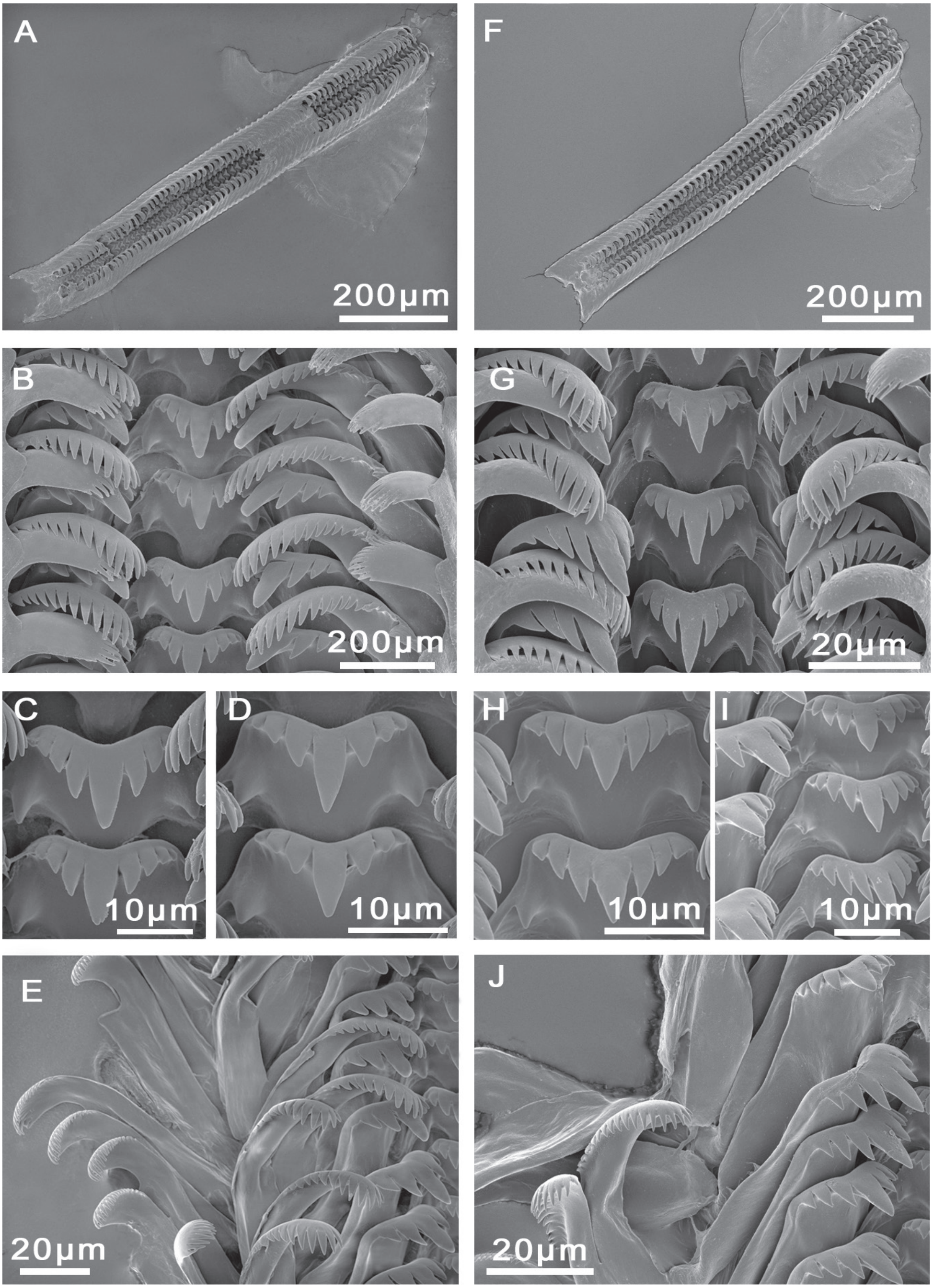

Figure 11. Radulae, *M. midarensis* sp. n. **A–D** Selouan River **E** A small ditch 7 km from Midar **F, H–J** Rio de Oro **G** Izerouan River. **A, F** Radulae ribbons **B, G** Overview of rows of radulae teeth **C, D, H, I** Central tooth **E, J** Inner marginal, outer marginal, and lateral teeth.

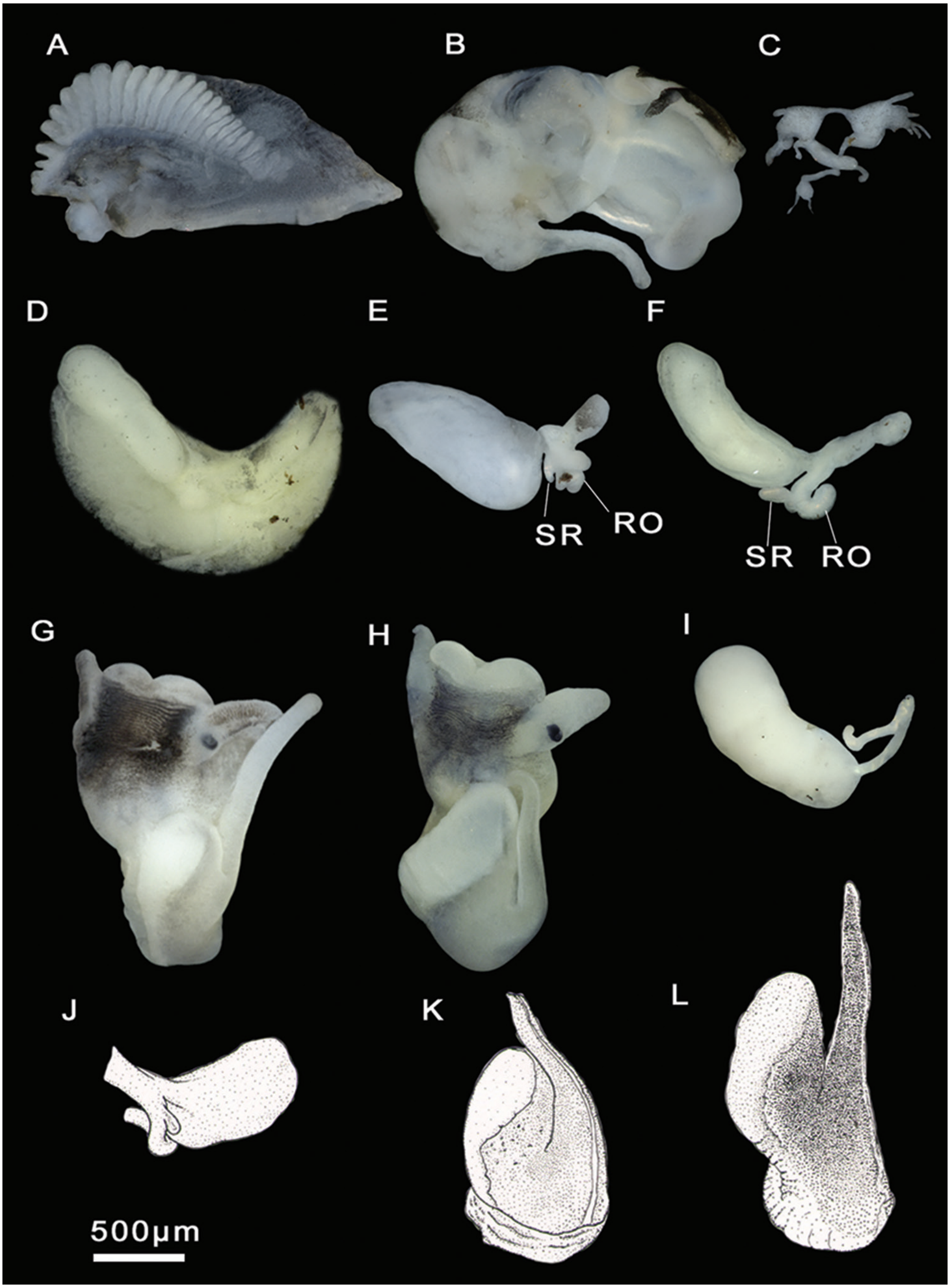

Figure 12. Anatomical structures, *M. midarensis* sp. n. **A–C, E, G, I, K–L** a small ditch 7 km from Midar **D** Ouzej River **F** Rio de Oro **H** Selouan River. **A** Ctenidium **B** Stomach **C** Partial nervous system **D** Pallial oviduct **E, F** Bursa copulatrix and seminal receptacle **J** Bursa copulatrix drawing **G, H** Head with penis **I** Prostate gland **K, L** Penis drawings. **RO** renal oviduct **SR** seminal receptacle.

morphometry were similar in all populations of the species, we detected variability in penis shape and size. Both the southern populations and the population from the Rio de Oro basin (within the northern group) are characterized by a long penis (2.1–3.2 mm), 2 to 3 times longer than the appendix and 1.5 to 3 times longer than the head. In contrast, northern populations have a shorter penis (0.6–2.1 mm), which is 2.6 to 4 times longer than the appendix. Moreover, in the population from the Izerouan River basin, the penis is 1.4 to 1.8 times longer than the head while it is shorter than the head in the population from the Mariouari River basin.

Mercuria bakeri and *M. tingitana* have more elongate, tall-spired shells than most of the populations of *M. midarensis* sp. n., except for specimens from the Mariouari and Selouan rivers. *Mercuria midarensis* sp. n. differs from *M. bakeri* in its shorter seminal receptacle, shorter bursal duct, and larger penial appendix, and from *M. tingitana* in its longer seminal receptacle, larger penis, and fewer cusps on the radular teeth. The mean genetic distance between *M. bakeri* and *M. midarensis* sp. n. was 6.8% while between the latter and *M. tingitana* it was 8.5%.

Ecology. Most specimens were found in small ditches or river tributaries attached to stones or simply in the sediment. *Mercuria midarensis* sp. n. co-occurs with other gastropod species such as *Melanopsis praemorsa*, *Galba truncatula*, *Ancylus fluviatilis*, and *Physella acuta*.

Mercuria tensiftensis sp. n.

http://zoobank.org/42E0CFAF-0F49-48AB-BFC8-9323FEB6996D

Type material. Holotype, MNCN 15.05/200018H (ethanol 80%), a ditch in Sidi Bouzid, Chichaoua, Morocco, 31°29.6133'N, 8°47.1116'W, 28/11/2015, K.B., M.G. Paratypes MNCN 15.05/200018P, UGSB 17910, and MHNM 18 ZTMH4 (from the same lot).

Other material. MOROCCO. MHNM 18 ZTMH19, UGSB 17910, ditch in Sidi Bouzid, Chichaoua, 28/11/2015 (31°29.6133'N, 8°47.1116'W); MHNM 18 ZTMH5, UGSB 17914, a pond near Lahjar Spring, Essaouira, 28/11/2015 (31°38.7583'N, 9°35.0983'W); MHNM 18 ZTMH6, UGSB 17918, ditch in Haddada Bouzerktoun, Essaouira, 28/11/2015 (31°37.95'N, 9°35.0983'W); MHNM 18 ZTMH7, UGSB 19944, ditch in Agadir N'tachraft, 34 km S of Marrakesh, 20/02/2017 (31°23.0917'N, 8°7.353'W); MHNM 18 ZTMH8, UGSB 19945, a spring near Lalla Takerkoust dam, 34 km S of Marrakesh, 20/02/2017 (31°22.5491'N, 8°7.638'W); MHNM 18 ZTMH9, UGSB 19946, Talkount, 80 km E of Marrakesh, 21/02/2017 (31°40.5775'N, 7°16.0298'W).

Diagnosis. Shell ovate-conic, whorls 4–5; periostracum whitish, exceptionally yellowish; body whorl large, convex, occupying approx. two-thirds of total shell length; umbilicus narrow, not covered by the inner lip; aperture ovate; protoconch microsculpture grooved; central radula tooth formula (5)4–C–4(5)/1–1; bursa copulatrix elongate, with a short duct; one seminal receptacle elongate, with a short duct; penis

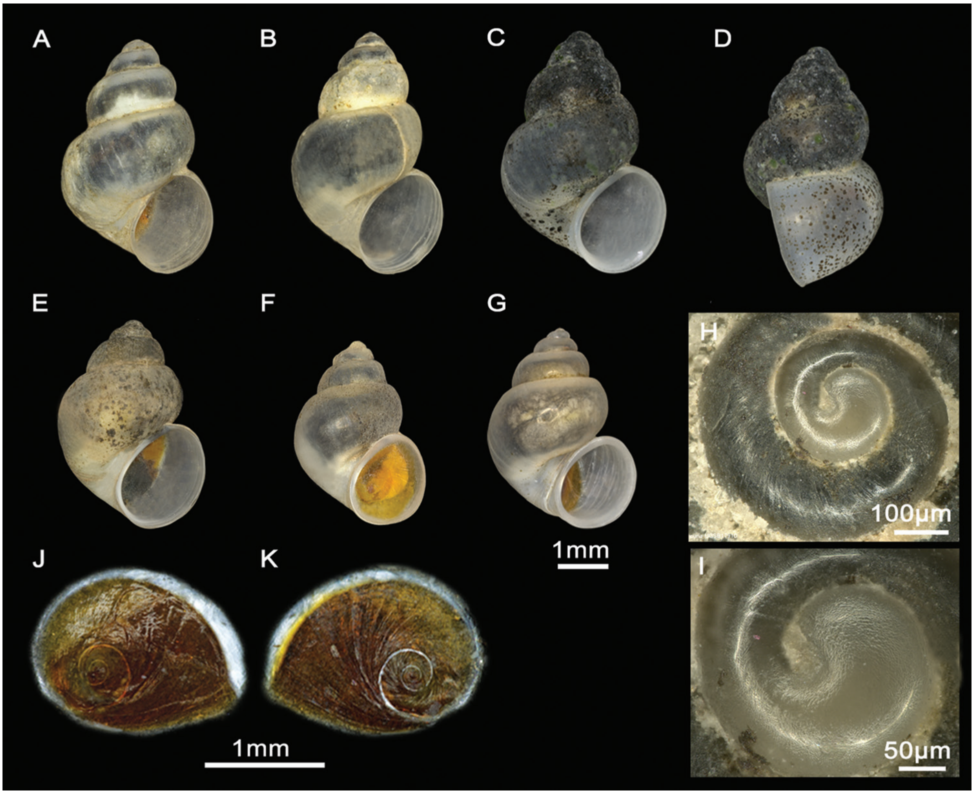

Figure 13. Shells and opercula, *M. tensiftensis* sp. n. **A** Holotype MNCN 15.05/200018H, **B** Shell, ditch in Sidi Bouzid **C, D** Shell, ditch in Agadir N'tachraft **E** Shell, ditch in Talkount **F** Shell, a pond near Lahjar Spring **G** Shell, a spring near Lalla Takerkoust dam **J, K** Opercula (inner, outer sides), ditch in Agadir N'tachraft **H, I** Protoconch and detailed microsculpture of protoconch, ditch in Agadir N'tachraft.

gradually tapering; penial appendix dark pigmented, rectangular, shorter than penis, base narrow and black pigmented, medially positioned on inner edge of penis; nervous system elongated (mean RPG ratio = 0.64), slightly pigmented.

Description. Shell ovate-conic, whorls 4–5, height 3–5.1 mm (Figure 13A–G; Suppl. material 1: Table 1). Periostracum whitish. Protoconch ca. 400 µm wide, whorls 1.5; nucleus ca. 125 µm wide (Figure 13H); protoconch microsculpture grooved (Figure 13I). Teleoconch whorls convex, with deep sutures. Body whorl large, occupying approx. two-thirds of total shell length. Aperture ovate, often attached to body whorl on the top; inner lip thicker than outer lip; peristome margin straight narrow (Figure 13D). Umbilicus narrow, not covered by the inner lip.

Operculum as for genus, orange to brownish, about two whorls; muscle attachment area oval and located near the nucleus (Figure 13J–K). Radula length intermediate, ca. 900 µm long (25% total shell length), approx. eight times longer than wide; approx. 60 rows of teeth (Figure 14A). Central tooth formula (5)4–C–4(5)/1–1; central cusp V-shaped (Figure 14B, D, E). Lateral tooth formula (4)3–C–3(4); central cusp

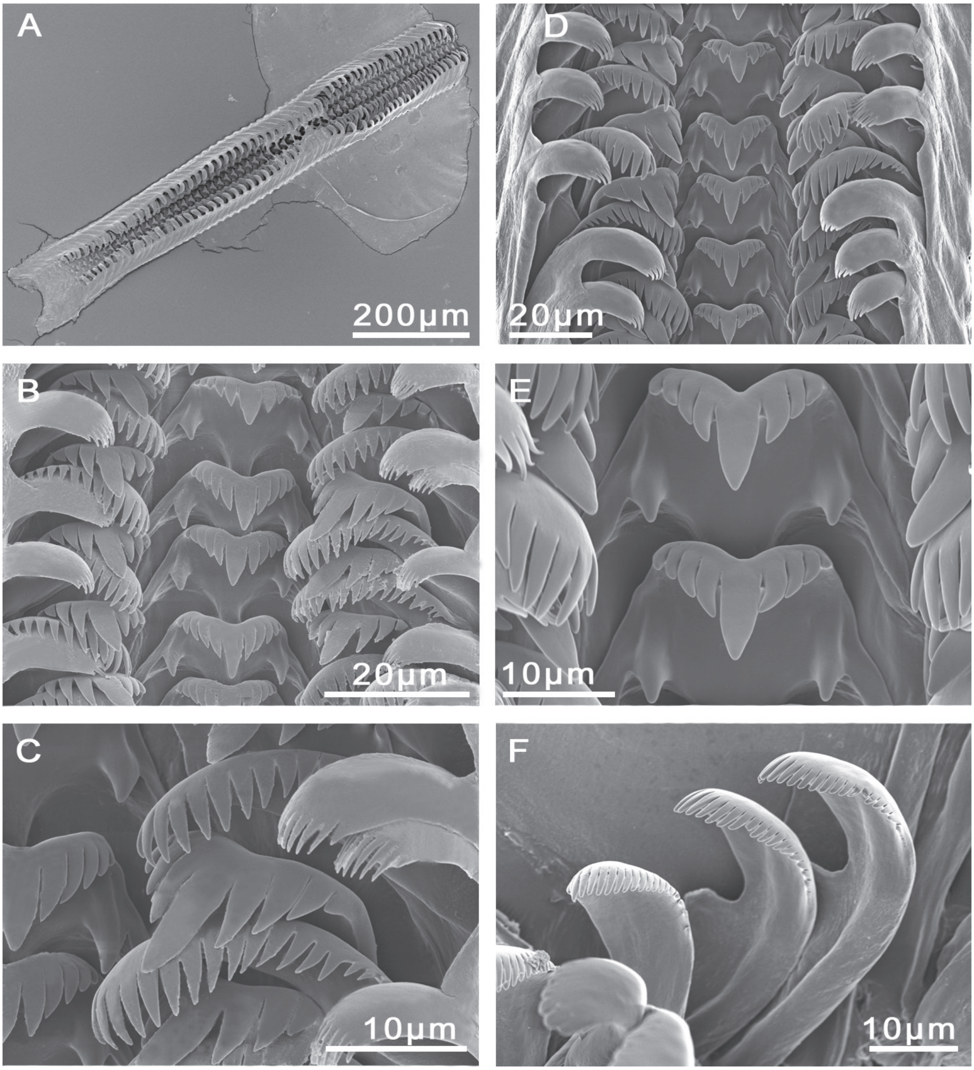

Figure 14. Radulae, *M. tensiftensis* sp. n. **A, E** a spring near Lalla Takerkoust dam **B, C** a pond near Lahjar Spring **D, F** ditch in Sidi Bouzid. **A** Radular ribbon **B, D** Rows of radular teeth **C** Lateral tooth and inner marginal teeth **E** Central tooth **F** Outer marginal teeth.

long, tongue-shaped (Figure 14B–C). Inner marginal teeth bearing 13–16 cusps and outer marginal with 15–21 cusps (Figure 14D, F; Suppl. material 1: Table 2).

Animal darkly pigmented except for neck and tentacles (Figure 15G). Ctenidium well-developed, with 23–27 gill filaments, occupying nearly entire length of pallial cavity. Osphradium elongate, positioned opposite middle of ctenidium (Figure 15A). Stomach slightly longer than wide, with two chambers almost equal in size; style sac longer than wide, surrounded by unpigmented intestine (Figure 15B; Suppl. material 1: Table 3). Glandular oviduct approx. three times as long as wide. Albumen gland

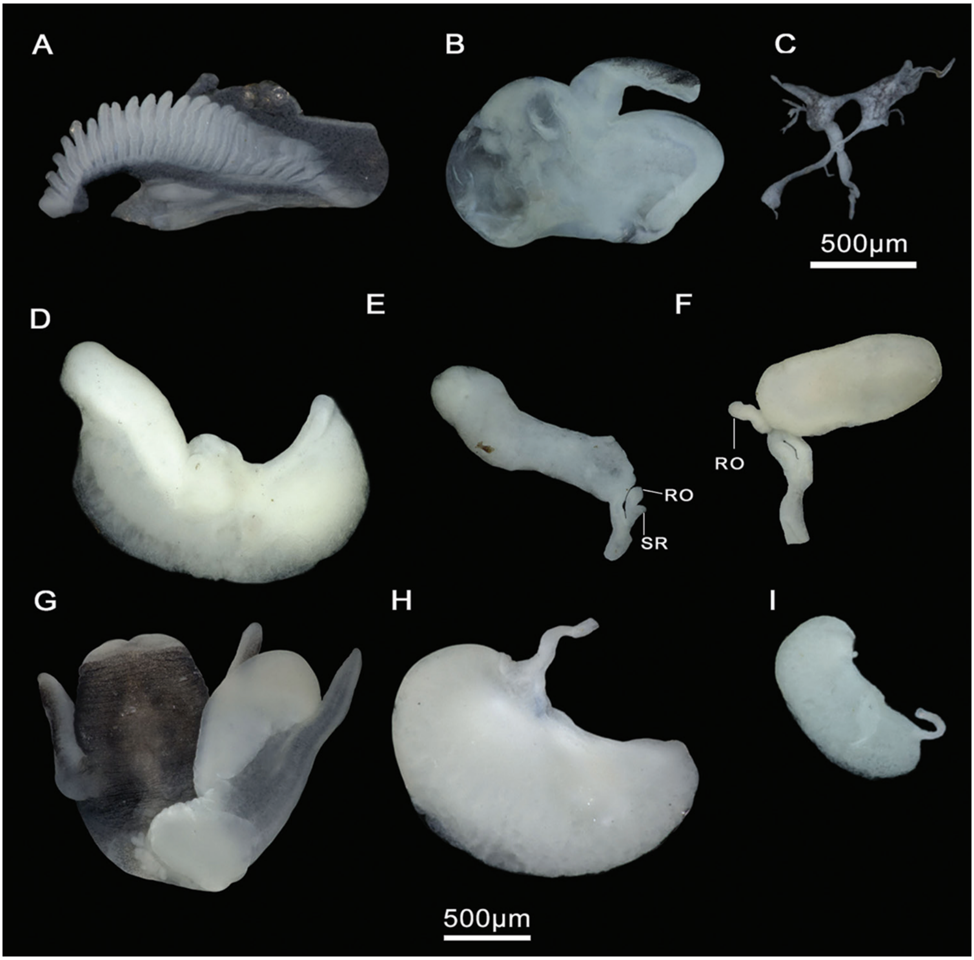

Figure 15. Anatomical structures, *M. tensiftensis* sp. n. **A, D, E, G, H** ditch in Sidi Bouzid **B, F, I** a pond near Lahjar Spring **C** a spring near Lalla Takerkoust dam. **A** Ctenidium **B** Stomach **C** Partial nervous system **D** Pallial oviduct **E, F** Bursa copulatrix and seminal receptacle **G** Head with penis **H, I** Prostate gland. **RO** renal oviduct **SR** seminal receptacle.

longer than capsule gland (Figure 15D–F). Bursa copulatrix elongate, two to three times longer than wide, with a duct shorter than bursal length. Renal oviduct unpigmented, coiled, making 2–3 loops. Seminal receptacle elongate, with a short duct, joining renal oviduct just above the insertion point with bursal duct (Figure 15E–F; Suppl. material 1: Table 4). Prostate gland approx. two times longer than wide, bean-shaped; seminal duct entering the posterior region; pallial vas deferens emerging close to its anterior edge. Penis gradually tapering, attached to the area close to the right eye. Penis dark pigmented, tapering. Penial appendix dark pigmented, shorter than penis, base narrow, medially position on inner edge of penis. Terminal gland occupying the whole distal end of the appendix (Figure 15G–I; Suppl. material 1: Table 5). Nervous system with black granules, elongate (mean RPG ratio 0.64; Suppl. material 1: Table 6); cerebral ganglia approx. equal in size; ganglia darker than connectives and commissures (Figure 15C).

Etymology. The name *tensiftensis* refers to the hydrological basin (Tensift) where this species was collected.

Distribution. This species was found in ponds, springs, and ditches in proximal localities of the Tensift River basin in northwestern Morocco.

Remarks. Shells of this species vary in size (2.4–5.1 mm shell height) and, accordingly, two morphotypes can be distinguished in all populations. One morphotype comprises small to medium-sized shells (2.4–4.0 mm shell height), with slightly shouldered spire whorls and a thick aperture. This morphotype is found in Lahjar, Talkount, and Lalla Takerkoust with an average shell length of 3.5 mm. The second larger group (4.0–5.1 mm shell height) comprises shells with five sloping spire whorls and a thin aperture. This morphotype is well represented in the populations from Sidi Bouzid Springs and Agadir N'tachraft with an average shell length of 4.1 mm. Despite this morphological variation within the species, the estimated genetic distance was 0% for COI.

Two morphotypes of male reproductive organs were also observed in dissected specimens. The most represented is that with a long penis, large appendix, and large prostate gland (localities of Lahjar near Essaouira, Sidi Bouzid, and Lalla Takerkoust dam). However, other dissected males showed a smaller retracted penis and a small degraded prostate gland (localities of Agadir N'tachraft and Talkount). We observed that this second group of males contained parasites known to cause castration in host snails (Lim and Heyneman 1972, Combes and Cheng 1986, Mouahid and Mone 1990, Ashby and Gupta 2014) and propose this as the cause of such variation (see Figure 16). According to our observations in parasitized specimens of different populations, male and female genitalia seem more affected than other organs.

Mercuria tensiftensis sp. n. is characterized by its long shell (the longest shells among Moroccan *Mercuria* species) and its large and gradually tapering penis with a terminal gland occupying the entire distal end of the penial appendix. The new species differs from *M. midarensis* sp. n. in its shorter penis (two times vs. three times longer than appendix in *M. tensiftensis* sp. n. and *M. midarensis* sp. n., respectively) (Suppl. material 1: Table 5), from *M. targouasensis* in its more elongate bursa copulatrix (Suppl. material 1: Table 4) and from *M. similis* in its longer shell and its larger and longer penis. These morphological and anatomical differences were supported by molecular data. Hence, the mean genetic distance between *M. tensiftensis* sp. n. and *M. similis* was 6.4% and between the former and *M. targouasensis* and *M. midarensis* sp. n. were 6.0% and 6.9%, respectively.

Ecology. *Mercuria tensiftensis* sp. n. was found in ditches used for irrigation, springs, and ponds, attached to stones or dead branches in the water. Most of these localities, including the type one, are small water bodies under risk of desiccation or destruction. Co-occurring species were *Galba truncatula*, *Melanopsis praemorsa*, and *Physella acuta*.

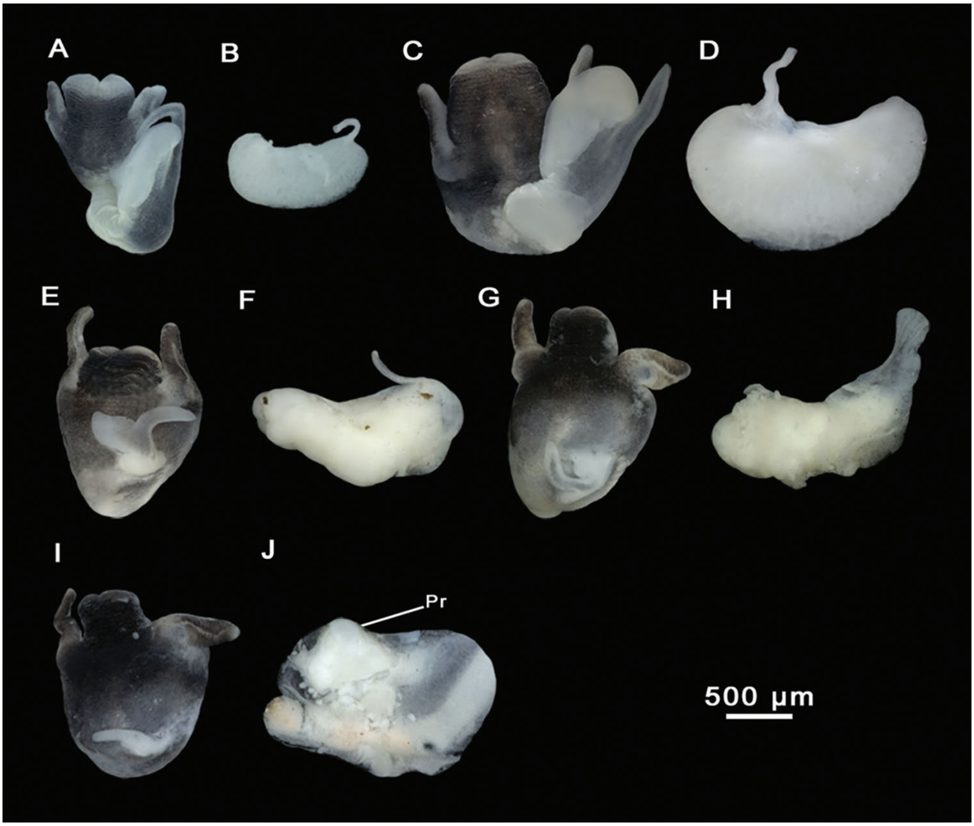

Figure 16. Head and prostate glands of non-parasitized and parasitized males, *M. tensiftensis* sp. n. **A, B** Non-parasitized male, a spring near Lalla Takerkoust dam **C, D** Non-parasitized male, ditch in Sidi Bouzid **E, F** Parasitized male, ditch in Sidi Bouzid **G–J** Parasitized males, ditch in Agadir N'tachraft. **Pr** prostate gland.

Discussion

This study provides the first molecular phylogenetic data on congeners of the genus *Mercuria* along with taxonomic descriptions of previously unknown anatomical structures for this genus such as the radula or nervous system. By integrating both molecular and morphological data, we extended the morphological information available for the three previously identified *Mercuria* species from Morocco (Glöer et al. 2015), described two new species from this region, and revealed phylogenetic relationships between these species and the European *M. emiliana* and *M. similis*. All species were recovered as independent entities in our phylogenetic inference (Figure 2) and ABGD analyses, including the European species with an uncorrected p-distance of 7.7% between them. These findings contradict previous studies (Girardi 2004, Gargominy et al. 2011, Boeters and Falkner 2017) in which the populations of *M. emiliana* studied by Boeters (1988) were synonymized with *M. similis* and the populations of *M. emiliana* described by Paladilhe (1866) were included within the genus *Pseudamnicola* Paulucci, 1878. Our molecular study revealed that sequences of *M. emiliana* available in GenBank (Table 1) were genetically distant from both the species *M. similis* and those of the genus *Pseudamnicola* (Table 2). Furthermore, according to these genetic results, neither the species *M. similis* nor *M. emiliana* were detected among our hydrobiid populations collected in Morocco. However, only genetic surveys and anatomical examinations of specimens from the type localities of both species will help resolve this taxonomic controversy. Since our genetic analyses included specimens collected from different sites than the type localities, we are unable to confirm or reject this synonymy.

In contrast with the low sequence divergence found among populations of *Mercuria tensiftensis* sp. n. (0% divergence), a higher mtDNA variation within *M. midarensis* sp. n. and *M. targouasensis* (0%–3.4% and 0%–1.3% divergence, respectively) was observed. Although an understanding of the biogeographical splitting processes of these species is beyond the scope of this study, we associate these wide ranges of sequence divergence within the latter two species with the high tectonic activity of the Rif and Atlas regions. Our data also point to remarkable morphological and anatomical variation within *Mercuria* species (e.g., within *M. tensiftensis* sp. n.), especially in shell shape and size, and penis and radula features, which may have been caused not only by adaptation (genetic or plastic) but also by seasonality and parasitism.

Shell growth differentially influenced by environmental conditions could result in different morphotypes within a species (Urdy et al. 2010). This has been recently shown for the freshwater gastropod species *Potamopyrgus antipodarum* (Gray, 1843) (Kistner and Dybdahl 2014; Verhaegen et al. 2018). Thus, given that *M. tensiftensis* sp. n. and *M. midarensis* sp. n. were found in a wide spectrum of habitat types, variation in shell shape and size within these species could be a response to variable conditions. A potential adaptive value of morphological variation within *Mercuria* species should be better evaluated in further common garden studies (see, for instance, Verhaegen et al. 2018). Lengths of the penis and the penial appendix were shown, however, to vary within *Mercuria* species according to the sexual maturity of the individuals, regardless of shell size. Holyoak et al. (2017) observed that most males across different populations of the species *M. tachoensis* (Frauenfeld, 1865) presented larger penial appendices from November to May, likely coinciding with their annual reproductive period. Another factor that can mislead taxonomists about intrinsic anatomical variation is the presence of parasites. We found that parasitized males of *M. tensiftensis* sp. n. had a smaller penis and prostate gland than non-parasitized ones. Indeed, several studies have shown that some parasites may lead to castration of the host mollusc (Lim and Heyneman 1972, Combes and Cheng 1986, Mouahid and Mone 1990, Ashby and Gupta 2014).

All these sources of variability suggest that the most efficient approach to delimit and identify *Mercuria* species is the integrated analysis of morphological descriptions and genetic data. Accordingly, when delimiting the species of this genus, intraspecific morphological differentiation of *Mercuria* species should be treated with caution and additionally assessed through molecular evidence.

Uncorrected pairwise distances between the *Mercuria* species examined here ranged from 2.8% to 8.5% with an average of 6.3%, which is lower than averages described for other spring hydrobiids, such as *Corrosella* Boeters, 1970 (5.3–12% average 9% in Delicado et al. 2013) or *Pyrgulopsis* Call & Pilsbry, 1883 (2.8–11.2% in Hershler et al. 2003), though higher than among species of the brackish-water genus *Hydrobia* Hartman, 1821 (average of 4.5%, Wilke et al. 2000). Note that genetic distances between *Mercuria* species are more comparable to those calculated for the genus *Pseudamnicola* (0.5–10% average 6.7% in Delicado et al. 2015), which could be attributed to their similar habitat preferences (i.e., small lowland rivers and streams). This common ecological pattern is suggested by numerous records of these co-occurring genera in Algeria (Glöer et al. 2010), Malta (Glöer et al. 2015), Spain (Boeters 1988), and Morocco (present study). However, although most of the *Mercuria* populations from Morocco were found in low-lying areas, some populations inhabited the Atlas Mountains, indicating a wide habitat range for this genus. Additional field surveys and comprehensive species descriptions are needed to further investigate the diversity of *Mercuria* species and their habitat types in the Mediterranean and Atlantic regions.

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Supplementary material 1

Table 1–6

Authors: Khadija Boulaassafer, Mohamed Ghamizi, Diana Delicado

Data type: measurement

Explanation note: Measurements recorded for the shell, radula, ctenidium, osphradium, digestive system, female and male genitalia, and nervous system in the *Mercuria* species examined.

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RESEARCH ARTICLE

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Four new species of *Lesticus* (Carabidae, Pterostichinae) from China and supplementary comments on the genus

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Abstract

The genus *Lesticus* in China was studied, with descriptions of four new species: *L. auripennis* **sp. n.** (Guangdong: Nanling, 24.93°N, 112.09°E); *L. bii* **sp. n.** (Xizang: Mêdog, 29.32°N, 95.34°E); *L. xiaodongi* **sp. n.** (Yunnan: Yingjiang, 24.71°N, 97.58°E); and *L. violaceous* **sp. n.** (Yunnan: Yingjiang, 24.71°N, 97.58°E). One new synonym is proposed: *L. dubius* Dubault, Lassalle & Roux, is a junior synonym of *L. solidus* Roux & Shi. An improved key and a catalogue accommodating all known Chinese *Lesticus* species are provided. Species relationships and the evolution of endophallic and other characters are preliminarily discussed.

Keywords

Trigonostomina, beetle, key, new species, endophallus, character evolution

Introduction

Lesticus Dejean belongs to the subtribe Trigonostomina (Carabidae: Pterostichinae) which includes six genera having an Oriental-Australasian distribution. This subtribe can be easily recognized by the very short and wide mentum tooth. *Lesticus* can be distinguished from other genera in the subtribe by the following character combination: first antennomere shorter than the sum of the following three segments; long antennae reaching the elytral base; labrum apex straight with six equally placed setae; terminal labial palpomere truncated at the apex; mentum not notably shortened; scutellar striae complete.

In China, species diversity of *Lesticus* is highest in tropical regions, especially Yunnan Province, but one species (*L. magnus*) is primarily distributed in northern China. Some species are widely distributed (e.g. *L. auricollis*) or locally abundant (e.g. *L. rotundatus*), while others are rare within a very narrow distribution (e.g. *L. ater*). *Lesticus* beetles tend to prefer mountain tropical or subtropical primary forests in China, having mainly nocturnal and ground-dwelling habits. Most specimens were collected under shelters, by pitfall trap, or on dirt paths during the night.

Before the present investigation, a total of 15 *Lesticus* species had been recorded in China (Roux et al. 2016), with most of them described in the past 10 years. But species determination is still difficult because some species are superficially similar to others, both from external and male genital (except endophallic) characters, and others are very rare in collections. Moreover, in the published keys (Roux and Shi 2011, Roux et al. 2016), some distinguishing characters were infraspecifically variable (e.g. pronotal basal punctations, body size) or ambiguously defined (e.g. pronotal shape, dorsal color).

In recent expeditions to southern China (W. Yunnan, S. Xizang, Guangdong), four very rare and narrowly distributed new species of *Lesticus* were collected. Aside from these, more new species are expected to be discovered in southern China, because some undetermined female specimens were present as well. When studying the new species, we found that the male endophallic characters have very important taxonomical value, both for systematics and species identification. Thus, we studied the male endophallus for all available Chinese species and a few from other countries. As a result, part of the endophallic character evolution in *Lesticus* was revealed, as well as some of the species relationships. Moreover, we found that the male holotype of *L. dubius* is very similar to, and sympatric with, *L. solidus* (only females known), and their main differences (elytra more expanded in *L. solidus*) are in fact sexual differences.

The primary purpose of the present paper is to provide an improved key and checklist with geographical distributions for all known Chinese species, to describe four new species, and to propose one new synonym. Thus, the known Chinese *Lesticus* fauna now totals 18 species with 14 of them endemic to China. For all the new species, complete descriptions, illustrations and distribution maps are provided, particularly with the addition of endophallic characters. Additionally, the evolution of endophallic characters and species relationships of *Lesticus* are briefly discussed, with four main endophallic types defined, and the present three subgenera of *Lesticus* rejected. An improved catalogue of *Lesticus* from China with new province records is presented as well.

Materials and methods

This work was based primarily on examination of specimens from China. The majority of specimens examined, including all types of new species, are deposited in the collection of the Institute of Zoology, Chinese Academy of Science, Beijing, China (**IZAS**). Collections cited in the present paper are indicated by the following abbreviations:

CCCC	Collection of Changchin Chen, Tianjin, China
CDW	Collection of David Wrase, Berlin, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museunm für Naturkunde der Humboldt- Universität zu Berlin, Berlin, Germany
NHMB	Naturhistorisches Museum, Basel, Switzerland
NMNS	National Museum of Natural Science, Taiwan, China
NMPC	Národní Muzeum Přírodovědecké Muzeum, Prague, Czech Republic
SCAU	South China Agriculture University, Guangzhou, China
ZMUM	Zoological Museum, Moscow State University, Moscow, Russia

The length of metepisternum was measured along its outer margin; the basal width was measured along its oblique basal margin (Figs 7, 18). When describing the endophallus, all lobes were named based on their location in the basic type (Type 1) as defined in the Discussion; for the derived types, lobes were named according to homology inferences rather than actual locations. Other terms used and methods of measurement, preparation of figures, dissection and endophallus everting procedures mainly follow our previous work (Shi and Liang 2015).

Key to Chinese species of *Lesticus*

1 Metepisternum short and wide, length less than or subequal to its basal width (Fig. 9) **2**

– Metepisternum long and narrow, length much greater (more than 1.3 times) than its basal width (Fig. 23).......... 7

2 Odd intervals raised, distinctly wider than even ones; S.E. Xizang.... ***L. bii* sp. n.**

– Odd intervals normal, same level and width as even ones.......... **3**

3 Propleuron, metepisternum and pronotal basal fovea completely glabrous; lateral margins straight before posterior angles; apex of median lobe strongly truncated; S. Yunnan .... ***L. ater* Roux & Shi**

– Metepisternum with at least a few coarse punctations; propleuron punctated or glabrous; pronotal basal rugose or punctated, although sometimes very finely; lateral margins slightly sinuate before posterior angles; apex of median lobe rounded or less truncated **4**

4 Pronotal basal fovea very shallow, with very fine wrinkles and punctures; median lobe of aedeagus more or less expanded ventrally; other provinces....... **5**

– Pronotal basal fovea moderately deep, distinctly punctated; median lobe of aedeagus straight ventrally; Fujian.......... **6**

5 Dorsal side almost uniformly black, elytra black or with very weak purple metallic lustre; median lobe of aedeagus strongly expanded ventrally; Yunnan, Guangxi .... ***L. perniger*** **Roux & Shi**

– Dorsal side distinctly bicolored: head and pronotum black, elytra with strong metallic lustre, purple or green; median lobe of aedeagus slightly expanded ventrally; Guangdong .... ***L. auripennis*** **sp. n.**

6 Pronotal basal fovea with coarser punctures; aedeagus apex more rounded; northern Fujian .... ***L. fukiensis*** **Jedlička**

– Pronotal basal fovea with finer punctures; aedeagus apex slightly truncated; southern Fujian.. ***L. wrasei*** **Dubault et al.**

7 Pronotum somewhat metallic, green, cupreous or purple **8**

– Pronotum completely black, without metallic lustre **15**

8 Propleuron and metepisternum glabrous or with sparse and fine punctures **9**

– Propleuron and metepisternum coarsely and densely punctated **10**

9 Pronotum with strong metallic lustre; basal fovea nearly glabrous, with very fine punctures or wrinkles at most; smaller species, 21–23 mm .... ***L. chalcothorax*** **(Chaudoir)**

– Pronotum with very faint metallic lustre; basal fovea coarsely punctated; larger species, 24–29 mm .... ***L. praestans*** **(Chaudoir)**

10 Basal fovea densely punctated, punctures also present on middle region of pronotum base; median lobe of aedeagus markedly expanded ventrally .... ***L. rotundatus*** **Roux & Shi**

– Pronotum basal fovea glabrous or punctated, without puncture on middle region of pronotum base; median lobe of aedeagus nearly straight ventrally **11**

11 Pronotum lateral margins somewhat sinuate before posterior angles; posterior angles forming an obtuse angle; Yunnan **12**

– Pronotum lateral margins completely straight before posterior angles; posterior angles obtusely rounded; other provinces **13**

12 Pronotum lateral margins strongly sinuate before posterior angles; posterior angles pointed a little outwards; pronotum metallic green, elytra blue .... ***L. xiaodongi*** **sp. n.**

– Pronotum lateral margins slightly sinuate before posterior angles; posterior angles not pointed; pronotum metallic bluish violet, elytra violet .... ***L. violaceous*** **sp. n.**

13 Pronotal basal fovea distinctly punctated; pronotum green; Guangxi .... ***L. deuvei*** **Dubault & Roux**

– Pronotal basal fovea nearly glabrous, with very fine punctures or wrinkles at most; pronotum cupreous-green; other provinces **14**

14 Elytral striae punctate relatively coarser; median lobe of aedeagus indistinctly constricted at basal third, apical orifice larger; China Mainland .... ***L. auricollis*** **Tschitschérine**

– Elytral striae punctated relatively finer; median lobe of aedeagus markedly constricted at basal third, apical orifice smaller; Taiwan... ***L. taiwanicus*** **Roux & Shi**

15 Pronotal basal fovea glabrous, with very fine wrinkles at most; propleuron anterior half with sparse punctures..**16**

– Pronotal basal fovea with dense punctures and wrinkles; propleuron anterior half with dense punctures **17**

16 Elytra completely black, not metallic; pronotal lateral margins slightly sinuate before posterior angles; posterior angles pointed a little outwards; smaller species, 25–27 mm; Yunnan .... ***L. tristis*** **Roux & Shi**

– Elytra with very faint purple metallic lustre; pronotal lateral margins straight before posterior angles; posterior angles completely rounded; larger species, 28–32 mm; Guangxi .... ***L. solidus*** **Roux & Shi**

17 Pronotal basal fovea deeper, with coarse punctures; lateral margin less sinuate before posterior angles; smaller species, 20–27 mm; China Mainland, Korea, Japan ....***L. magnus*** **(Motschulsky)**

– Pronotal basal fovea shallower, with fine punctures; lateral margin more sinuate before posterior angles; larger species, 27–30 mm; Taiwan....................... .... ***L. sauteri*** **Kuntzan**

Lesticus auripennis **sp. n.**

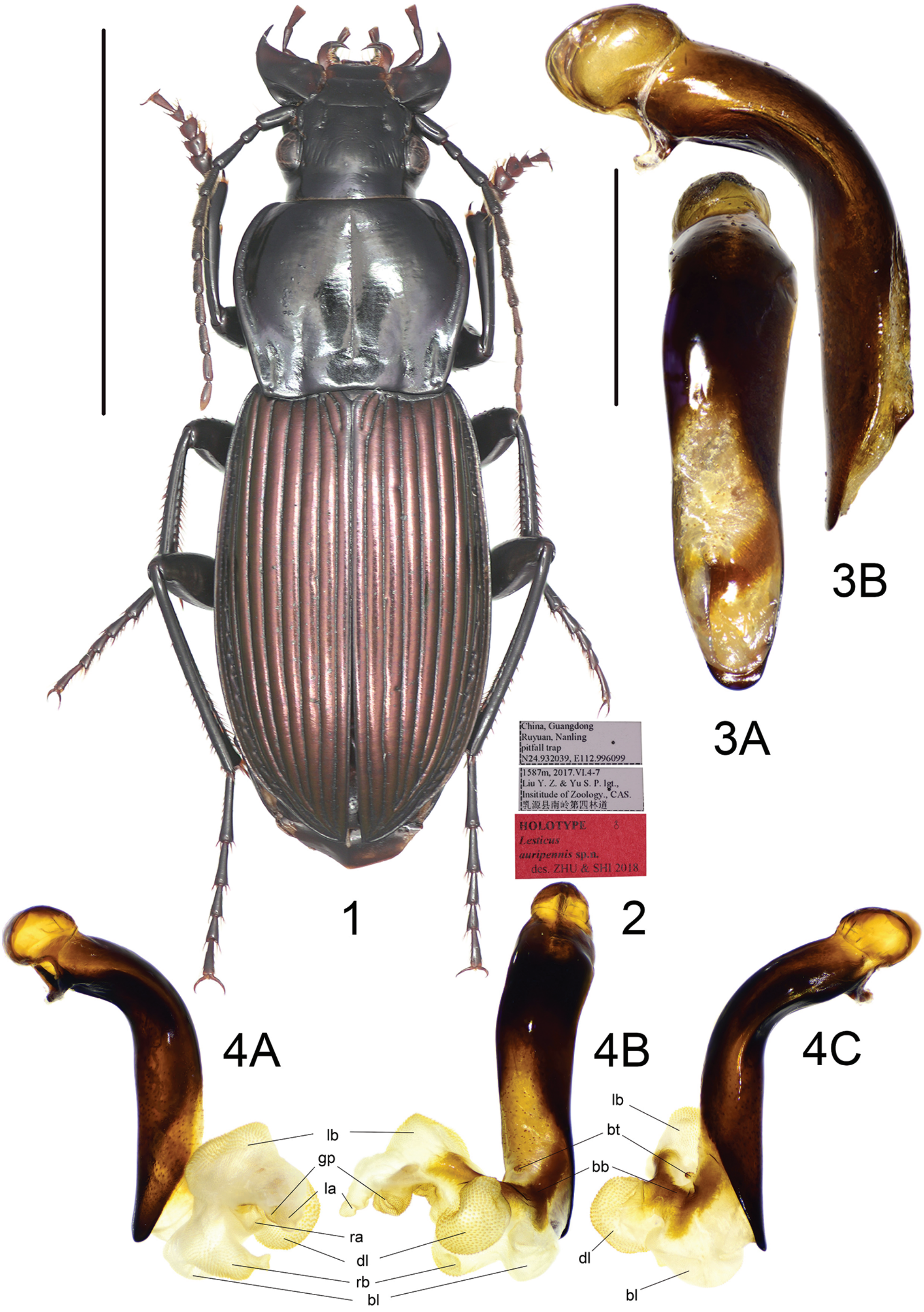
http://zoobank.org/1C717FB3-A47E-4CB3-A620-D0DD18202CE4
Figs 1–4

Type locality. China, Guangdong: Nanling (24.93°N, 112.99°E), altitude 1587 m.

Type material. Holotype: male (IZAS), body length = 20.4 mm, board mounted, genitalia preserved in 100% ethanol in microvial pinned under specimen, “China, Guangdong / Ruyuan, Nanling / pitfall trap / 24.932039N, 112.996099E”; “1587m, 2017.VI.4-7 / Liu Y. Z. & Yu S. P. lgt., / Insititude of Zoology., CAS.”; “HOLOTYPE♂ / *Lesticus auripennis* sp. n. / des. ZHU & SHI, 2018” [red label]. **Paratypes** (two males and six females): one male and one female (IZAS), the same data as holotype but labeled as paratype. One female (IZAS), “China, Guangdong / Ruyuan, Nanling / pitfall trap / 24.93077N, 112.994692E”; “1708m, 2017.VI.4-7 / Liu Y. Z. & Yu S. P. lgt., / Insititude of Zoology., CAS.”; “PARATYPE♂ / *Lesticus auripennis* sp. n. / des. ZHU & SHI 2018” [red label]. One male and four females (SCAU), “Guangdong, Nanling 2008 / 24.9284N, 113.0163E / 1035m, pitfall trap, Gao Lei / South China Agriculture University”; “PARATYPE♂ / *Lesticus auripennis* sp. n. / des. ZHU & SHI 2018” [red label].

Diagnosis. Pronotum completely black; elytra metallic green or purple; pronotal lateral margins slightly sinuate before posterior angles; pronotal basal fovea almost glabrous, with restricted and very fine punctures only; metepisternum short and wide, length subequal to its basal width, with coarse punctures.

Comparisons. The new species is the only one among all Chinese *Lesticus* species with black pronotum and distinctly metallic elytra. *Lesticus auripennis* sp. n. is most similar to *L. perniger* and *L. wrasei* sharing the short, wide metepisternum with coarse



China, Guangdong
Ruyuan, Nanling
pitfall trap
N24.932039, E112.996099

1587m, 2017.VI.4-7
Liu Y. Z. & Yu S. P. lgt.,
Insititude of Zoology., CAS.
乳源县南岭第四林道

HOLOTYPE ♂
Lesticus
auripennis sp.n.
des. ZHU & SHI 2018

Figures 1–4. *Lesticus auripennis* sp. n. **1** habitus of holotype (male, Guangdong, IZAS), scale bar: 10.0 mm **2** labels of holotype **3** median lobe of aedeagus (holotype) **A** dorsal view **B** left-lateral view, scale bar: 2.0 mm **4** endophallus (holotype) **A** left lateral view **B** dorsal view **C** right lateral view.

punctures; pronotal lateral margins slightly sinuate before posterior angles; pronotal basal fovea shallowly incised; elytral intervals normal. The new species is distinguishable from the latter two species by elytra metallic color, restricted and very fine pronotal basal foveal punctures and a different shape of male genitalia. Median lobe of aedeagus of the new species is very similar to that of *L. wrasei*, but different in: (1) ventral margin slightly expanded near middle (versus completely straight); (2) apex a little less truncated; (3) in dorsal view, left margin slightly sinuate near middle (versus evenly curved).

Description. Body length 19.5–23.8 mm, elytra's greatest width 7.2–8.7 mm, both sexes with similar body forms. Head, pronotum, and appendage black and shining; maxillae, labial and maxillary palpomeres, lateral sides of labrum and terminal tarsomeres reddish brown; apical half of terminal palpomere yellow; elytra with strong metallic lustre, usually purple, in some individuals green; ventral side black. Head and pronotum with isodiametric microsculpture and minute punctures; elytra with isodiametric microsculpture.

Head glabrous, without coarse punctures; short and deep frontal depressions extended posterad to middle of eyes, with five to seven shallow longitudinal wrinkles behind frontal depression; anterior margin of labrum slightly emarginate; temporae slightly tumid behind eyes; antennal apex reaching elytra basal tenth.

Pronotum wider than head, PW/HW = 1.49–1.54, a little transverse, PW/PL = 1.24–1.38; pronotum widest near middle. Lateral margins not crenulate, curved in middle, slightly sinuate before posterior angles; posterior angles obtuse, apex rounded, not pointed outwards; posterior margin a little greater than anterior margin, extended slightly backward on each side. Median line shallow but distinct, not reaching posterior margin; disc almost glabrous, with a few shallow transverse wrinkles along median line at most. Basal fovea shallow but well defined; inner groove longer, approximately one-third length of pronotum; outer groove shorter, approximately one-fifth length of pronotum; basal foveal area with very fine punctures and wrinkles along inner and outer grooves, glabrous between inner and outer grooves.

Elytra oviform, EL/EW = 1.39–1.69, gradually widened to apex, widest at posterior third approximately; basal ridge complete, gradually curved, forming a distinct obtuse angle with elytral lateral margin, humeral teeth not pointed. Intervals barely convex; striae deeply incised, with very fine and sparse punctures alongside; scutellar stria short, apex free; parascutellar pore present; third interval with three setigerous pores: first one adjacent to third stria, the other two generally close to second stria (in a male paratype, third pore close to third stria); umbilicular series on ninth interval composed of 20–22 pores evenly spaced. Hind wings very small.

Ventral side: propleuron glabrous, without puncture or wrinkle; mesopleuron with a few coarse punctures on anterior half; metepisternum short and wide, length subequal to its basal width, with sparse and coarse punctures, usually 10–20, sometimes fewer; abdominal sterna glabrous on median portion, with few coarse punctures on lateral sides of sternum II and sometimes also sternum III, and very fine wrinkles on lateral sides of all sterna.

Map 1. Distribution map for *L. auripennis* sp. n. and allied species: *L. auripennis* sp. n. (red); *L. fukiensis* Jedlicka (yellow); *L. wrasei* Dubault, Lassalle & Roux (green); *L. perniger* Roux & Shi (blue).

Legs: basal three metatarsomeres with distinct carina along almost full length of outer surface, fourth metatarsomeres with weaker carina only near base; fifth tarsomeres with 3–4 pairs of spines ventrally.

Male genitalia: median lobe of aedeagus with apical orifice opened dorsally; in lateral view, ventral margin slightly expanded in middle, apical portion straight, turned neither ventrally nor dorsally, basal portion slightly narrowed; in dorsal view, apical lamella very short, length approximately one-fourth basal width, apex rounded, slightly truncated; apical portion straight, oriented to neither left nor right. Endophallus (Fig. 4) short, extending to dorsal-left, major portion of endophallus on left-dorsal side of aedeagus when everted; gonopore (**gp**, gonopore lobe folded in Fig. 4) located at a little before apical lamella, oriented to aedeagal apex. Basal tubercle (**bt**) typical of genus; basal band (**bb**) elongated, extended from apical orifice to base of **lb**. Six distinct lobes recognized: dorsal lobe (**dl**) very large and rounded, on right-dorsal surface; one additional basal lobe (**bl**) present on basal-ventral surface, close to **dl**, large and rounded, placed near apical lamella, decorated with very fine and sparse scales; right basal lobe (**rb**) a little smaller than **dl**, close to **bl**, apex sharply pointed, apex with dense and fine scales; right apical lobe (**ra**) on ventral side of **gp**, small, decorated with fine scales; left basal lobe (**lb**) a little larger than **dl**, on dorsal-apical surface, apex with dense scales; left apical lobe (**la**) small, close to **lb**, apex sharply pointing out, decorated with fine scales.

Distribution. This species is known only in Nanling, Guangdong (Map 1). The three localities of the type series are very close together.

Etymology. The name "*auripennis*" is from Latin, "aur-" meaning colored and "pennis" meaning wing, referring to the elytra. This species is named for its distinctly metallic elytra.

Affinities. *Lesticus auripennis* sp. n. is close to *L. perniger*, *L. ater*, *L. wrasei*, and *L. fukiensis* among Chinese *Lesticus* fauna, sharing their short, wide metepisterna and similar shapes of the pronotum. Outside China, there are two other species with these characters: *L. ornatus* Dubault, Lassalle & Roux (Chiang Mai, Thailand) and *L. restrictus* Dubault, Lassalle & Roux (Shan State, Myanmar). These seven species could be recognized as one species group, which can be distinguished from other species of *Lesticus* by: (1) short, wide metepisternum, length less than or subequal to its basal width; (2) elytra third interval with two or three setigerous pores; (3) pronotum completely black, with no trace of metallic; (4) pronotum subquadrate or a little cordifrom; (5) relatively small body size, generally less than 24 mm.

Lesticus bii sp. n.

http://zoobank.org/392DF27B-155F-4FA6-B8EE-887727DCB972

Figs 5–9

Type locality. China, Xizang: Mêdog (ca. 29.32°N, 95.34°E), altitude 1500–1900 m.

Type material. Holotype: male (IZAS), body length = 17.8 mm, board mounted, genitalia dissected and glued on plastic film pinned under specimen, "Xizang, Mêdog, / 1500–1900m, 2013. / VIII.20, Bi Wenxuan"; "HOLOTYPE ♂ / *Lesticus bii* sp.n. / des. ZHU & SHI 2018" [red label]. **Paratypes** (one male and three females): one male (IZAS), "Xizang, Nyingchi, Mêdog Pari village / 1807m / 2014-VIII-9 / along road during day, Yang Xiaodong Leg. / 14Y0437 CCCC"; "PARATYPE ♂ / *Lesticus bii* sp.n. / des. ZHU & SHI 2018" [red label]. Two females (CCCC), "Xizang, Nyingchi, Mêdog / 1559m / 2016-VIII-5 / along road during night, Yang Xiaodong Leg. / 16Y CCCC"; "PARATYPE ♂ / *Lesticus bii* sp.n. / des. ZHU & SHI 2018" [red label]. One female (IZAS), "China Xizang Mêdog / Phomshen village 1850m / 2016-VII-10 / light trap, Lu Yanquan Leg. / CCCC"; "PARATYPE ♂ / *Lesticus bii* sp.n. / des. ZHU & SHI 2018" [red label].

Diagnosis. Odd intervals prominently raised but not carinate, much wider than depressed even ones; third interval without setigerous pore; pronotal lateral margins crenulate through full length; basal fovea very deep; metepisternum short and wide, length subequal to its basal width; apical lamella of aedeagus truncated, shorter than basal width, without hook.

Comparisons. This new species can be readily distinguished from all the other Chinese species of the genus by the prominently raised odd elytral intervals. There are three other species (*L. tricostatus* Chaudoir, *L. wittmeri* Morvan, and *L. cupricollis* Pouillaude) from the Himalayan region with similar elytral characters, but they are different from the new species by: pronotal lateral margins not crenulated; odd intervals carinate, of about the same width as the even ones; apical lamella hooked or much longer than its basal width. Among these three, the new species is most similar to *L. wittmeri* from Bhutan for they both have pronotal basal fovea markedly prolonged anteriorly, elytral first interval not carinate, and apical lamella unhooked.

Description. Body length 17.8–20.0 mm, elytra's greatest width 6.2–7.3 mm, both sexes with similar body form. Head, pronotum, elytra and appendages black, polished but without metallic lustre; basal antennomere, maxillae, labial and maxillary palpi, lateral sides of labrum, pro- and mesotarsomeres reddish brown; apical half of terminal labial and maxillary palpomeres yellow; ventral side black. Head, pronotum and elytra with isodiametric microsculpture and minute punctures.

Head with dense and fine punctures on vertex and occiput; vertex densely rugose, deeper and longitudinal near eyes, shallower and reticular at middle; labrum with anterior margin nearly straight; temporae slightly tumid behind eyes; antennal apex reaching elytra basal sixth.

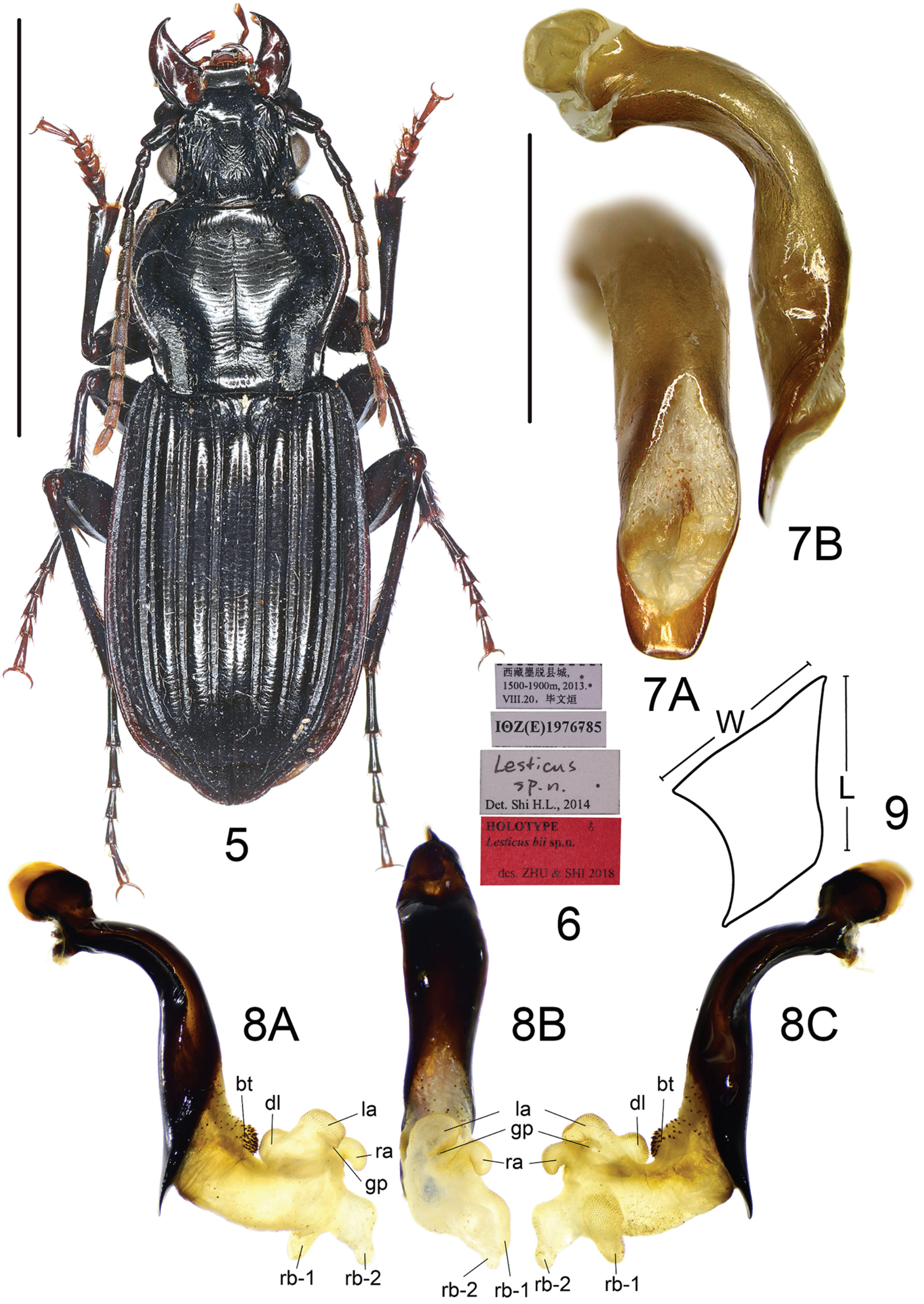
Pronotum wider than head, PW/HW = 1.38–1.44; width a little greater than median length, PW/PL = 1.13–1.21; pronotum widest near anterior third; lateral margins crenulate along full length, curved near middle, distinctly sinuate before posterior angles; posterior angles rectangular, not pointed outwards; posterior margin a little narrower than anterior margin, barely extended backward on each side, middle portion gradually concave; median line fine but a little deep, not reaching posterior margin; disc with dense transverse wrinkles alongside median line; basal fovea strongly incised, inner and outer grooves indistinct, completely fused together forming large and deep depression, extending forward beyond midpoint of pronotum, and gradually fused to widened lateral channel; basal fovea finely and densely punctated and rugose, wrinkles present on middle region of pronotal base between basal fovea.

Elytra oviform, EL/EW = 1.52–1.66, gradually widened to apex, widest near posterior third; basal ridge complete, forming indistinct obtuse angle with lateral margin, humeral teeth not pointed. Intervals with shallow transverse wrinkles; odd intervals strongly raised but not carinate, much more convex and wider, about twice width of the even ones; third interval without setigerous pore; striae deeply incised, with fine and sparse punctures alongside; scutellar stria very short, apex free; parascutellar pore on base of second interval, sometimes one additional parascutellar pore present; umbilicular series on ninth interval composed of 15–20 pores almost evenly arranged. Hind wings very small.

Ventral side: propleuron and mesopleuron with dense, fine punctures; metepisternum short and wide, length a little less than its basal width (Fig. 7), with dense, fine punctures; abdominal sterna glabrous medially, finely rugose laterally, lateral sides of sternum II and sometimes sternum III as well, finely and sparsely punctate.

Legs: basal three meso- and metatarsomeres prominently carinate along full length of outer surface, fourth tarsomeres barely carinate only near base; fifth tarsomeres with 3–4 pairs of spines ventrally.

Male genitalia: median lobe of aedeagus with apical orifice opened dorsally; in lateral view, ventral margin distinctly expanded in middle, apical portion straight,



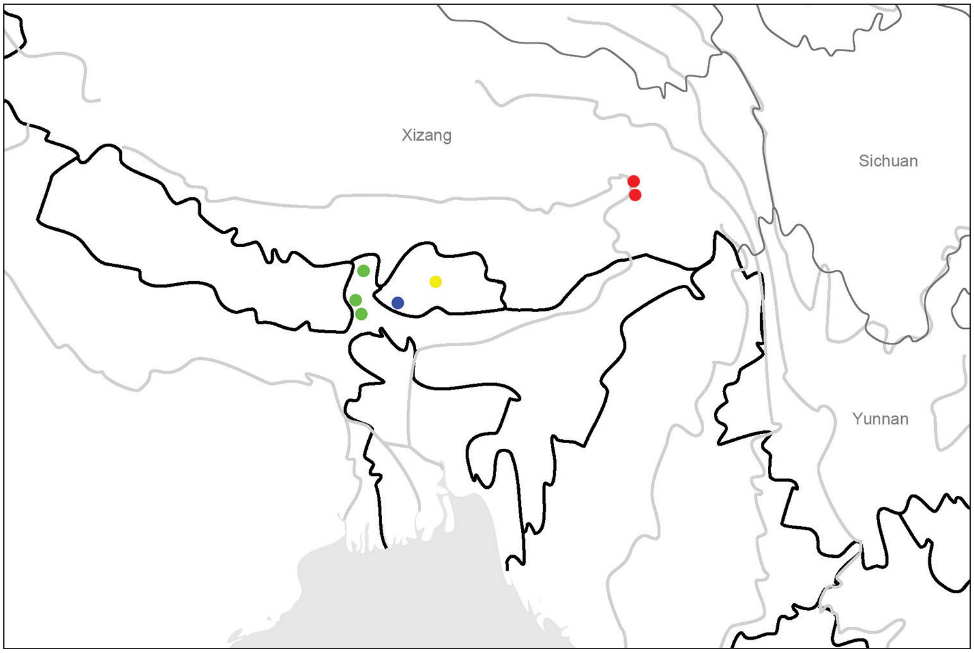
西藏墨脱县城，
1500-1900m, 2013.
VIII.20，毕文烜

IOZ(E)1976785

Lesticus
sp.n.
Det. Shi H.L., 2014

HOLOTYPE ♂
Lesticus bii sp.n.
des. ZHU & SHI 2018

Figures 5–9. *Lesticus bii* sp. n. **5** habitus of holotype (male, Xizang, IZAS), scale bar: 10.0 mm **6** labels of holotype **7** median lobe of aedeagus (holotype) **A** dorsal view **B** left-lateral view, scale bar: 2.0 mm **8** endophallus (paratype) **A** left lateral view **B** dorsal view **C** right lateral view **9** metaepisternum.



Map 2. Distribution map for *L. bii* sp. n. and allied species: *L. bii* sp. n. (red); *L. tricostatus* Chaudoir (green); *L. wittmeri* Morvan (blue); *L. cupricollis* Pouillaude (yellow).

turned neither ventrally nor dorsally, basal portion a little narrowed; in dorsal view, apical lamella short, length about half basal width, apex truncated; apical portion straight, oriented to neither left nor right. Endophallus (Fig. 8) short and straight, extending to dorsum, the inscribed angle between axes of aedeagus and endophallus about 90°; main portion of endophallus on dorsal side of aedeagus when everted; gonopore (**gp**, gonopore lobe folded in Fig. 8) located at a little before apical lamella, oriented to dorsal side of aedeagus. Basal tubercle (**bt**) much larger than in other species, very densely and heavily spined; basal band (**bb**) absent. Five distinct lobes recognized: dorsal lobe (**dl**) small, nearly rounded, almost touching **bt**; right basal lobe (**rb**) divided into two separate lobes; right basal lobe I (**rb-1**) elongated, bent to dorsal direction of endophallus, placed at right-dorsal surface, decorated with dense and fine scales; right basal lobe II (**rb-2**) close to **rl-1**, bent to apical direction of endophallus, apex pointing out to dorsal direction, without scales; right apical lobe (**ra**) small, on right side of **gp**, bent to dorsal direction of endophallus, apex curved; left basal lobe (**lb**) absent; left apical lobe (**la**) close to **dl**, on left side of **gp**, bent to apical direction of endophallus, apex a little bifid.

Distribution. This species is known only in a few localities of Xizang, Mêdog (Map 2).

Etymology. The new species is named for our friend Mr. BI Wenxuan, an excellent beetle collector, who was first to collect this rare and peculiar new species.

Affinities. *Lesticus bii* sp. n. was presumed to be close to *L. tricostatus*, *L. wittmeri*, and *L. cupricollis* for the following similarities: elytral odd intervals prominently raised;

third interval without setigerous pore; pronotal lateral margins distinctly sinuate before posterior angles; and all from the Himalayan region. Among them, the new species has more plesiomorphies than the others, such as: all odd elytral intervals not carinate, apical lamella unhooked. Moreover, *L. bii* sp. n. was considered to be associated with two other Himalayan species (*L. harmandi* Tschitschérine, and *L. holzschuhi* Straneo) for their similarities in: pronotal lateral margins crenulate and distinctly sinuate before posterior angles; large, deep basal fovea; elytral third interval without setigerous pore; short metepisternum. Another species from Northern Myanmar, *L. nigroviolaceus* Dubault, Lassalle & Roux was similar to the new species in external and male genitalia characters, although pronotal lateral margins are not crenulate and odd intervals not raised.. Thus, all seven species are assumed to be associated with and forming one species group defined by: (1) short metepisternum, length less than or subequal to its basal width; (2) elytra third interval without setigerous pore; (3) pronotal lateral margins distinctly sinuate before posterior angles, large, deep basal fovea; (4) relatively small body size, generally less than 24 mm.

***Lesticus violaceous* sp. n.**

http://zoobank.org/E7E29088-E0F3-4699-9486-4058A21CFB73
Figs 10–13

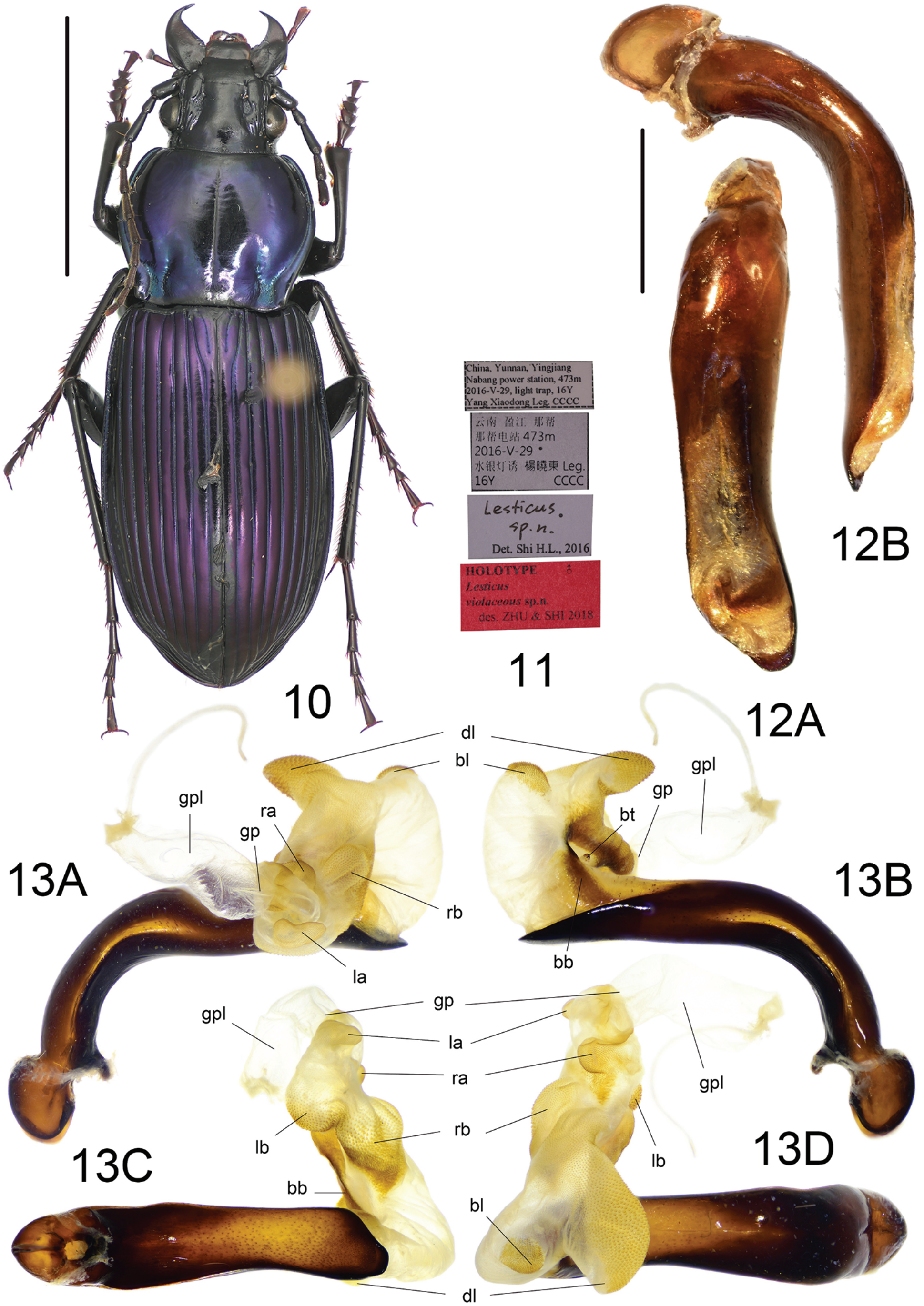
Type locality. China, Yunnan: Yingjiang, Nabang (24.71°N, 97.58°E), altitude 473 m.

Type material. Holotype: male (IZAS), body length = 25.1 mm, pin mounted, genitalia preserved in 100% ethanol in a microvial pinned under specimen, "China, Yunnan, Yingjiang / Nabang power station, 473m / 2016-V-29, light trap, 16Y / Yang Xiaodong Leg. CCCC"; "HOLOTYPE ♂ / *Lesticus violaceous* sp. n. / des. ZHU & SHI 2018" [red label].

Diagnosis. Pronotum metallic bluish violet, elytra completely violet; pronotum lateral margins slightly sinuate before posterior angles; pronotal basal fovea deep and glabrous, with very faint wrinkles; long, narrow metepisternum, length much greater than its basal width (L/W = 1.78), distinctly punctated; median lobe of aedeagus not expanded ventrally, apex markedly deflexed to right, very short apical lamella, apex a little truncated.

Comparisons. Among all *Lesticus* species from China, this new species is the only one with similar distinctly metallic color on the pronotum and elytra. From the slightly sinuate pronotal lateral margins and glabrous basal fovea, the new species is somewhat similar to *L. tristis* and *L. chalcothorax*. Besides their different color and body size, the two other species also differ from the new species in: median lobe of aedeagus distinctly expanded ventrally, apex of apical lamella more rounded.

The new species is also similar to *L. desgodinsi* from N. India and *L. episcopalis* from N. Myanmar in having a violet color on the elytra and pronotum as well as the pronotal lateral margins being somewhat sinuate before the posterior angles. Compared with the latter two species, *L. violaceous* sp. n. has less sinuate pronotal lateral



China, Yunnan, Yingjiang
Nabang power station, 473m
2016-V-29, light trap, 16Y
Yang Xiaodong Leg. CCCC

云南 盈江 那帮
那帮电站 473m
2016-V-29 •
水银灯诱 楊曉東 Leg.
16Y CCCC

Lesticus.
sp.n.
Det. Shi H.L., 2016

HOLOTYPE ♂
Lesticus
violaceous sp.n.
des. ZHU & SHI 2018

Figures 10–13. *Lesticus violaceous* sp. n. **10** habitus of holotype (male, Yunnan, IZAS), scale bar: 10.0 mm **11** labels of holotype **12** median lobe of aedeagus (holotype) **A** dorsal view **B** left-lateral view, scale bar: 2.0 mm **13** endophallus (holotype) **A** left lateral view **B** right lateral view **C** ventral view **D** dorsal view.

margins; pronotal basal fovea less punctate; and ventral margin of aedeagus straight, not expanded near middle.

Description. Body length 25.1 mm, elytra's greatest width 9.2 mm. Head black, pronotum and elytra violet, with strong metallic lustre, pronotum somewhat blue in basal fovea and lateral channel; appendages black; tarsomeres, apical antennomeres, palpomeres and lateral sides of labrum reddish brown; ventral side black, with slightly metallic violet lustre. Head and pronotum with isodiametric microsculpture and minute punctures; elytra with isodiametric microsculpture.

Head glabrous, without coarse puncture and wrinkle; frontal impressions deep, with a few fine punctures inside; anterior margin of labrum slightly emarginate; temporae not tumid behind eyes; antennal apex reaching elytra basal tenth.

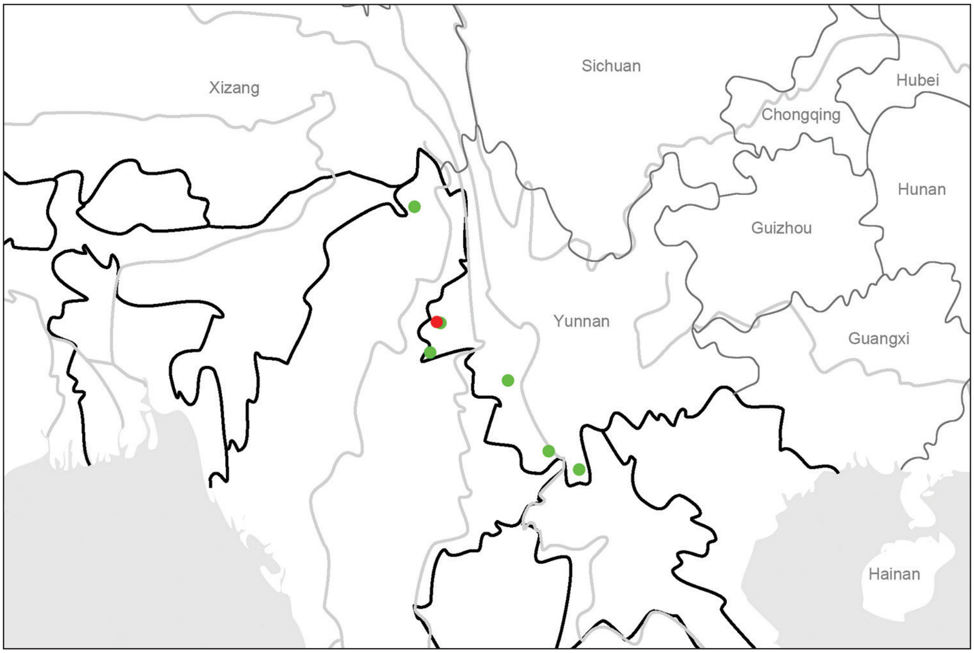
Pronotum much wider than head, PW/HW = 1.54, slightly transverse, PW/PL = 1.31, widest near middle. Lateral margins not crenulate; evenly curved at anterior two-thirds, slightly sinuate before posterior angles; posterior angles obtusely angulate, not pointed outwards; posterior margin a little narrower than anterior margin, extended slightly backward on each side. Median line deep, not reaching posterior margin; disc glabrous, without wrinkles. Basal fovea deep and narrow, inner groove nearly straight, about same length as outer one which is strongly curved, region between them deeply depressed; basal foveal area nearly glabrous, with a few very fine punctures and shallow wrinkles.

Elytra oviform, EL/EW = 1.65, gradually widened to apex, widest near posterior third; basal ridge complete, forming an indistinct obtuse angle with elytral lateral margin, humeral teeth not pointed. Intervals barely convex; striae deeply incised, with fine, sparse punctures alongside; scutellar stria long, apex free; parascutellar pore present on base of first stria; third interval with three setigerous pores: first one close to third stria, the other two close to second; umbilicular series on ninth interval composed of approximately 25 pores, sparse in middle and dense in anterior and posterior areas. Hind wings well developed.

Ventral side: propleuron with sparse, coarse punctures, a little denser on mesopleuron; long, narrow metepisternum, length much greater than its basal width (L/W = 1.78), with sparse, coarse punctures; abdominal sterna glabrous, almost impunctate, with only very shallow wrinkles on lateral sides.

Legs: basal two meso- and metatarsomeres with distinct carina only near base; fifth tarsomeres with 3–4 pairs of spines ventrally.

Male genitalia: median lobe of aedeagus with apical orifice opened dorsally; in lateral view, ventral margin straight, not expanded in middle, apical portion slightly turned dorsally before apical lamella, basal portion slightly narrowed; in dorsal view, aedeagus narrow, apical lamella very short, length approximately one-third of basal width, apex a bit truncated, apical fourth distinctly oriented to left side. Endophallus (Fig. 13) extending to dorsal-left, major portion of endophallus on left-dorsal side of aedeagus when everted; gonopore (**gp**) located at well before apical lamella, oriented to aedeagal base; gonopore lobe (**gpl**) long, a little spiral. Basal tubercle (**bt**) and basal



Map 3. Distribution map for *L. violaceous* sp. n. and allied species: *L. violaceous* sp. n. (red); *L. rotundatus* Roux & Shi (green).

band (**bb**) typical of the genus. Six distinct lobes recognized: dorsal lobe (**dl**) very large and compressed, on dorsal-right surface, pointing to base of aedeagus; one additional basal lobe (**bl**) present on basal-ventral side of **dl**, small and rounded, apex decorated with fine scales; right basal lobe (**rb**) large and wide, extended to ventral side of endophallus, surface with longitudinal impression; right apical lobe (**ra**) smaller than **rb**, rounded, at right-apical side of **rb**, at right surface of endophallus and close to **gp**; left basal lobe (**lb**) a little larger than **rb**, rounded, at ventral-apical side of **rb**, at ventral surface of endophallus; left apical lobe (**la**) small and compressed, close to left side **gp**, apex a little dilated and bifid.

Distribution. This species is known only by the holotype which was collected from Yunnan, Yingjiang, Nabang (Map 3).

Etymology. The scientific name "*violaceous*" comes from Latin, referring to the violet coloration of this new species.

Affinities. Among all Chinese *Lesticus* with the endophallus known, only *L. rotundatus* has similar male endophallic characters to the new species: endophallus strongly deflexed to left-dorsal side of aedeagus; gonopore pointed to the aedeagal base. Thus, a close relationship of these two species is possible, although they have quite different external and aedeagal characters.

***Lesticus xiaodongi* sp. n.**

http://zoobank.org/A0022926-35D1-45F0-B9DF-8DF9A490719E

Figs 14–17

Type locality. China, Yunnan: Yingjiang, Nabang (24.71°N, 97.58°E), altitude 473 m.

Type material. Holotype: male (IZAS), body length = 27.0 mm, pin mounted, genitalia preserved in 100% ethanol in a microvial pinned under specimen, "China, Yunnan, Yingjiang / Nabang power station, 473m / 2016-V-27, light trap, 16Y / Yang Xiaodong Leg. CCCC"; "HOLOTYPE ♂ / *Lesticus xiaodongi* sp. n. / des. ZHU & SHI 2018" [red label].

Diagnosis. Dorsal side bicolor: head and pronotum metallic bluish green, elytra dark metallic blue; pronotum lateral margins strongly sinuate before posterior angles; pronotal basal fovea deep, with fine punctures and wrinkles; posterior angles a little pointed; metepisternum long and narrow, length greater than its basal width (L/W = 1.35); median lobe of aedeagus slightly expanded ventrally, apical lamella very short, slightly thickened.

Comparisons. The new species can be readily distinguished from all the other known species from China by pronotal lateral margins strongly sinuate near base. From the coloration, shape of pronotum and median lobe of aedeagus slightly expanded ventrally, this new species is most similar to *L. waterhousei* Chaudoir from N.E. India and *L. peguensis* Bates from S. Myanmar. *L. waterhousei* differs in: much larger size (33–36 mm), pronotal basal fovea coarsely rugose, and apical lamella of aedeagus much longer. *Lesticus peguensis* differs in: pronotal posterior angles not pointed at all; apical lamella a little longer and not thickened.

Description. Body length 27.0mm, elytra's greatest width 9.7 mm. Dorsal side bicolor, head and pronotum metallic bluish green, elytra dark metallic blue; mouth part, clypeus, and appendages black; tarsomeres, apical antennomeres, terminal palpomeres reddish brown; ventral side black, without metallic lustre. Head, pronotum and elytra with isodiametric microsculpture and minute punctures.

Head: vertex nearly glabrous, with very fine shallow wrinkles; frontal impressions deep; coarse longitudinal wrinkles along inner margins of eyes; anterior margin of labrum distinctly emarginate; temporae not tumid behind eyes; antennal apex reaching elytra basal sixth.

Pronotum much wider than head, PW/HW = 1.52, slightly transverse, PW/PL = 1.32; widest near middle. Lateral margins not crenulate, evenly curved in middle, strongly sinuate before posterior angles; posterior angles nearly rectangular, pointed a little outward; posterior margin a little narrower than anterior, extended backward on each side. median line is deep, not reaching posterior margin; disc with very shallow transverse wrinkles alongside median line. Basal fovea deep, inner groove straight, a little longer than curved outer groove, region between them deeply depressed; basal foveal area with some fine but distinct punctures and wrinkles.

Elytra oviform, EL/EW = 1.65, gradually widened to apex, widest near posterior third; basal ridge complete, forming an indistinct obtuse angle with elytral lateral margin, humeral teeth not pointed. Intervals barely convex, striae deeply incised, with fine and dense punctures alongside; scutellar stria moderately long, apex conjoined to first stria; parascutellar pore located at base of first stria; third interval with three setigerous pores: first one close to third stria, other two close to second; umbilicular series on ninth interval composed of approximately 25 pores, sparse in middle and dense in anterior and posterior areas. Hind wings well developed.

Ventral side: propleuron and mesopleuron with dense, coarse punctures; metepisternum long and narrow, length greater than its basal width (L/W = 1.35), with sparse, coarse punctures; abdominal sterna glabrous in middle, with dense, coarse punctures on lateral sides of sternum II and sternum III, and shallow wrinkles on lateral sides of all sterna.

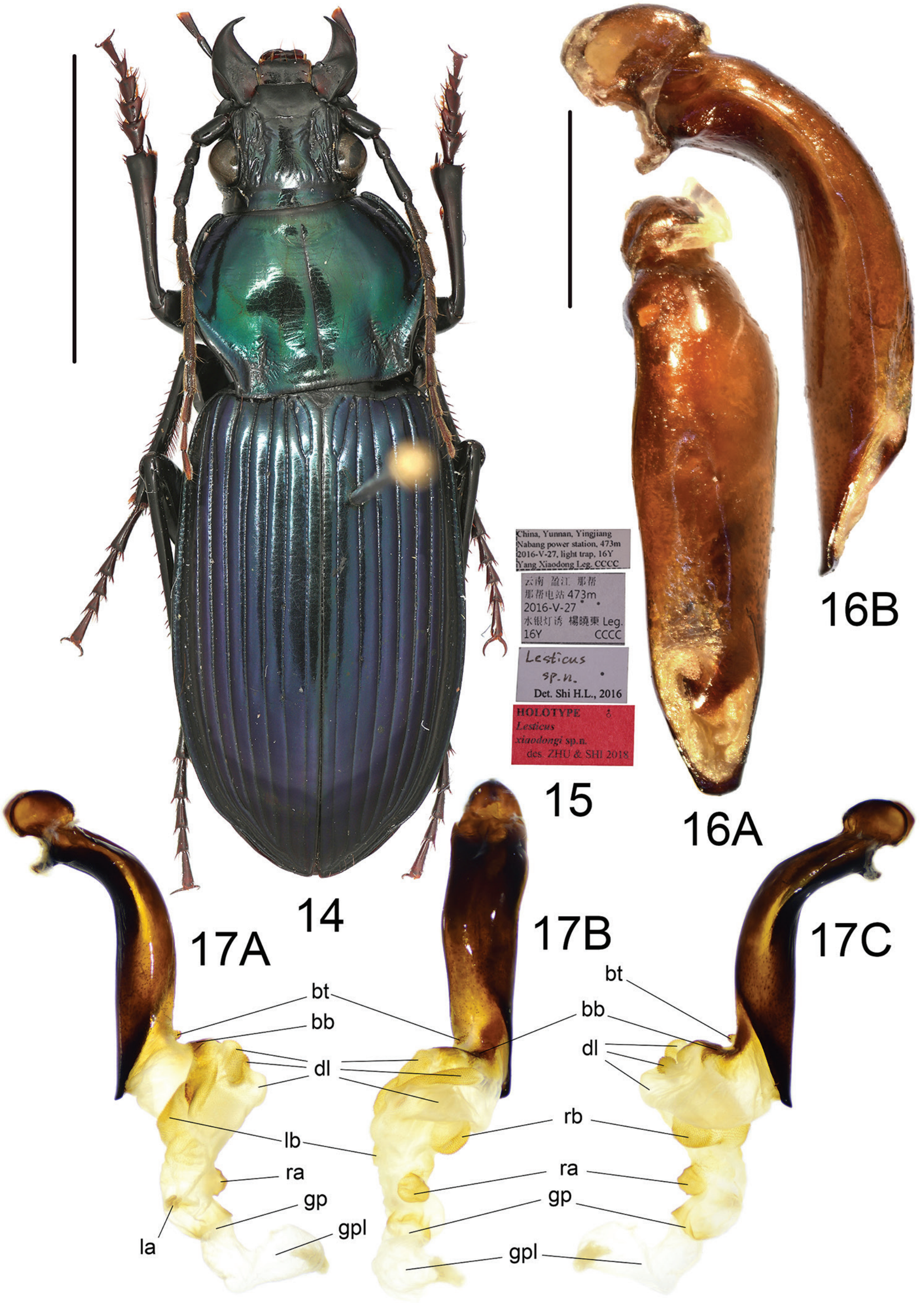
Legs: three basal metatarsomeres with distinct carina along almost the full length of outer surface, three basal mesotarsomeres, and fourth with weaker carina only near base; fifth tarsomeres with 3–4 pairs of spines ventrally.

Male genitalia: median lobe of aedeagus with apical orifice opened dorsally; in lateral view, ventral margin slightly expanded in middle, basal portion not narrowed, apical lamella slightly thickened and turned ventrally; in dorsal view, aedeagus gradually narrows from middle to apex, apical lamella very short, length approximately one-third of basal width, apex a little truncated; apical portion a little inclined to right side. Endophallus (Fig. 17) straight, extending to apex, the included angle between axes of aedeagus and endophallus about 20°; major portion of endophallus located beyond apical lamella, inclined a little to left; gonopore (**gp**) located at well beyond apical lamella, oriented to aedeagal apex; gonopore lobe (**gpl**) long, a little spiral. Basal tubercle (**bt**) typical of the genus; basal band (**bb**) short, obsolete at apex, not reaching left surface of **dl**. Five distinct lobes recognized: large dorsal lobe (**dl**), divided into three sub-lobes by longish grooves: basal one longitudinal; middle one on right side of basal one, very narrow and transverse; apical one transverse, larger than the other two, without scales; single right basal lobe (**rb**), large and rounded, on right-apical side of **dl**, decorated with dense scales; right apical lobe (**ra**) smaller than **rb**, rounded, close to **gp**; left basal lobe (**lb**) very large and flat, near apex of **bb**; left apical lobe (**la**) very small, nearly imperceptible.

Distribution. This species is known only by the holotype, which was collected from Yunnan, Yingjiang, Nabang, the same locality as the previous new species (Map 4).

Etymology. The new species is named for our friend Mr. Yang Xiaodong, who collected the holotype of this beautiful and rare new species.

Affinities. Among all Chinese *Lesticus* we studied, *L. tristis* and *L. solidus* have the most similar male endophallic characters to the new species: endophallus straight, major portion extending to apical direction of aedeagus; in lateral view, the angle between axes of endophallus and aedeagus less than 30°. Moreover, these three species all have pronotal basal fovea not well punctated, and metepisterna much longer than its basal width. This suggests a close relationship among the three species.



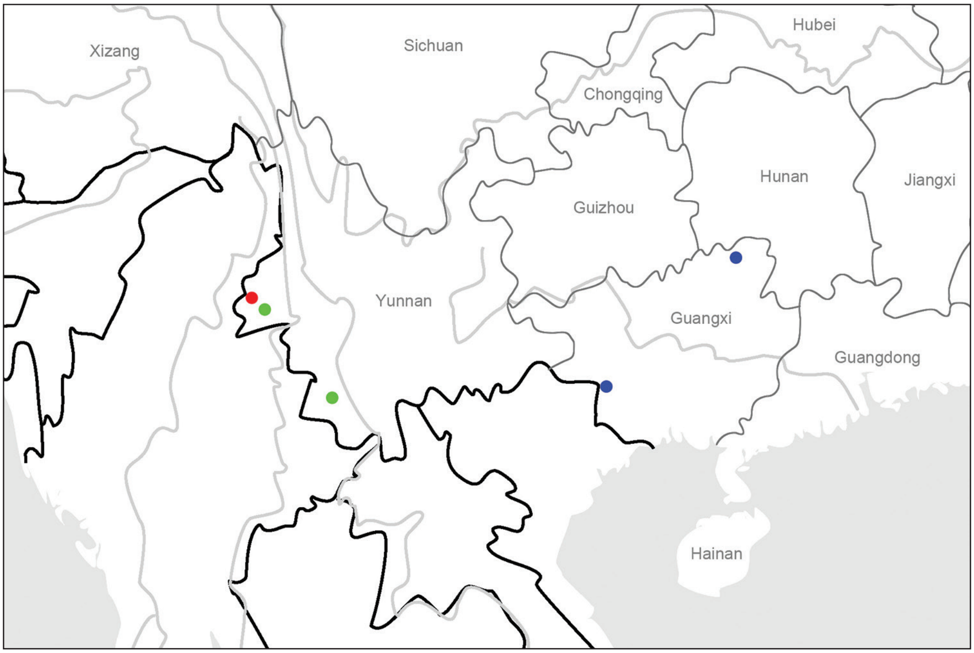
China, Yunnan, Yingjiang
Nabang power station, 473m
2016-V-27, light trap, 16Y
Yang Xiaodong Leg. CCCC

云南 盈江 那帮
那帮电站 473m
2016-V-27
水银灯诱 楊曉東 Leg.
16Y CCCC

Lesticus
sp.n.
Det. Shi H.L., 2016

HOLOTYPE ♂
Lesticus
xiaodongi sp.n.
des. ZHU & SHI 2018

Figures 14–17. *Lesticus xiaodongi* sp. n. **14** habitus of holotype (male, Yunnan, IZAS), scale bar: 10.0 mm **15** labels of holotype **16** median lobe of aedeagus (holotype) **A** dorsal view **B** left-lateral view, scale bar: 2.0 mm **17** endophallus (holotype) **A** left lateral view **B** dorsal view **C** right lateral view.



Map 4. Distribution map for *L. xiaodongi* sp. n. and allied species: *L. xiaodongi* sp. n. (red); *L. tristis* Roux & Shi (green); *L. solidus* Roux & Shi (blue)

Lesticus solidus Roux & Shi, 2011

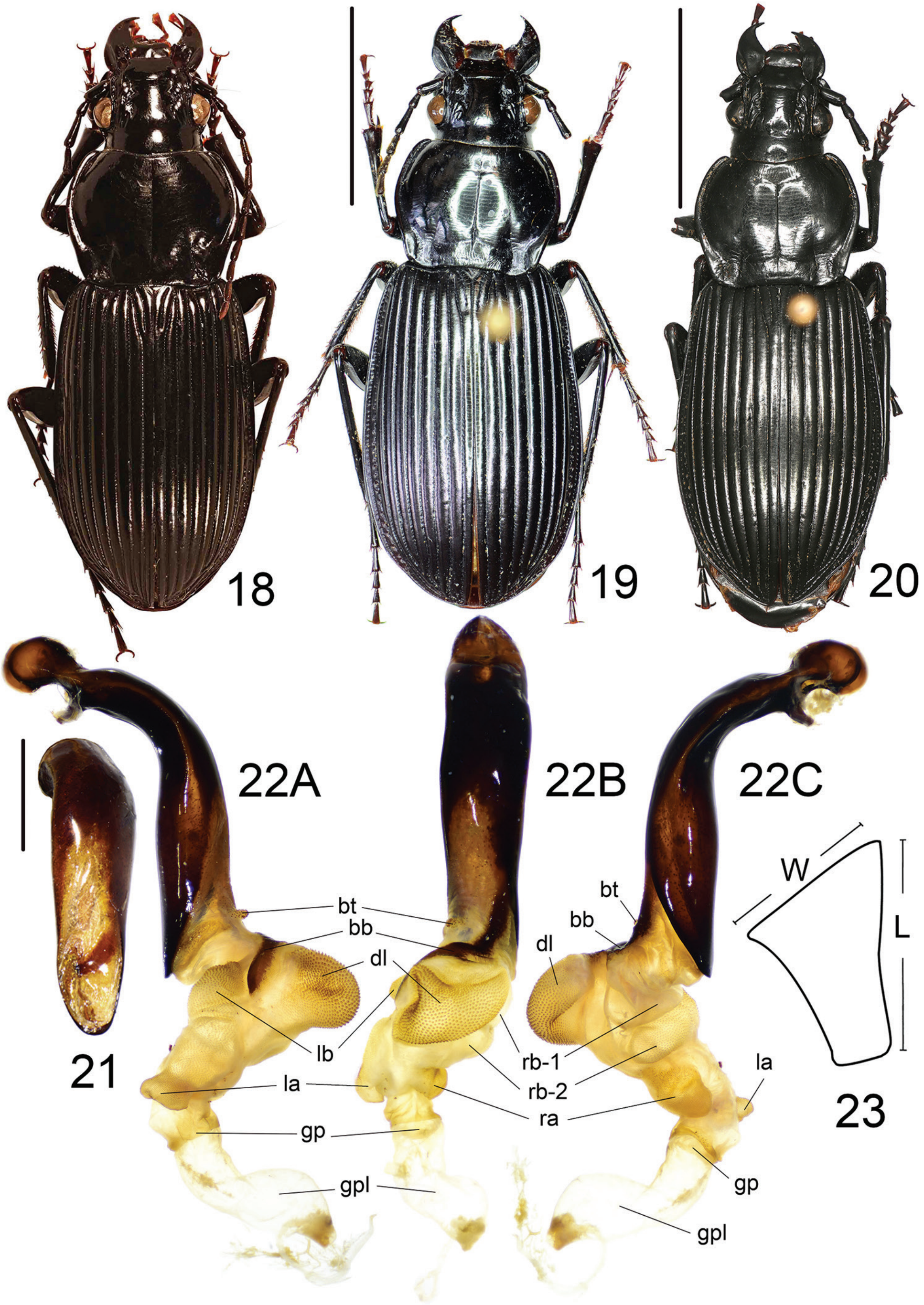
Figs 18–23

Lesticus solidus Roux & Shi, 2011: 94 (type locality: Maoershan, Guangxi, holotype in IZAS).

Synonym: *Lesticus dubius* Dubault, Lassalle & Roux, 2013: 207 (type locality: Maoershan, Guangxi, holotype in CDW). **syn. n.**

Material examined. Holotype of *L. solidus*: female (IZAS), body length = 29.1 mm, pin mounted, "Gaozhai, Maoershan Mt., / Xing'an, Guangxi, CHINA / 900m, by light trap, / 3.VIII.2005", "IOZ(E) 1891818", "HOLOTYPE♀ / *Lesticus solidus* / Roux & Shi 2011 / Des. Roux &Shi, 2011" [red label]; one male (IZAS), "Guangxi, Xing'an, Yong'an, 2009.VII.13 5-2", "IOZ(E) 1976781"; one female (IZAS), "China: Guangxi Prov, Chongzuo, Daxin county, Shuolong town, Heishuihe; 22.8194N, 106.8639E, 345m", "2016.IV.27N, on dead log; Shi H. L., Liu Y. & Liu Y. Z. lgt., Institute of Zoology., CAS.", one female (IZAS), "Guangxi Maoershan", "IOZ(E) 1976782".

Notes on synonym. *Lesticus solidus* Roux & Shi was described based on a single female from Maoershan (Guangxi, China). Two years later, *L. dubius* Dubault, Lassalle & Roux was described from exactly the same locality based on four specimens including both sexes. In the present study, we compared the female holotype of *L. solidus* (Fig. 19) and a male (Fig. 20) and found that they are perfectly in accordance with the



Figures 18–23. *Lesticus solidus* Roux & Shi. **18** holotype of *L. dubius* (male, Guangxi, MNHN) **19** holotype of *L. solidus* (female, Guangxi, IZAS), scale bar: 10.0 mm **20** habitus of a male from Guangxi, scale bar: 10.0 mm **21** median lobe of aedeagus, dorsal view, scale bar: 2.0 mm **22** endophallus **A** left lateral view **B** dorsal view **C** right lateral view **23** metaepisternum.

type locality and male genitalia illustrations (Dubault et al. 2013) of *L. dubius*. They are different only in: *L. solidus* with very faint violet lustre on elytra, and elytra more widened to apex. These differences also correspond with the original description of *L. dubius*. Among all our examined materials, the females generally exhibited elytra more widened to apex. Thus we considered it as a sexual dimorphic character. About the very faint violet lustre of *L. solidus*, it is more likely an individual variation rather than a specific character. This case is similar to head and pronotum color variations of *L. dubius* which were noted by Dubault et al. (2013). So, we herein synonymize *L. dubius* with *L. solidus*.

Supplementary descriptions on endophallus (Fig. 22): Endophallus straight, extending to apex, the angle formed by the axes of aedeagus and endophallus about 5°; major portion of endophallus located beyond apical lamella; gonopore (**gp**) located at a level well beyond apical lamella, pointing to aedeagal apex; gonopore lobe (**gpl**) long, a little spiral. Basal tubercle (**bt**) and basal band (**bb**) typical of the genus. Six distinct lobes recognized: dorsal lobe (**dl**) very large and rounded, on dorsal surface and sharply pointed out; right basal lobe (**rb**) divided into two separate lobes; right basal lobe I (**rb-1**) large and a little compressed, close to apical lamella, surface without scales; right basal lobe II (**rb-2**) a little larger than **rb-1**, rounded, at apical side of **rb-1**, decorated with sparse, fine scales; right apical lobe (**ra**) a little smaller than **rb-1**, rounded, between **rb-2** and **gp**; left basal lobe (**lb**) large and compressed, close to apex of **bb**; left apical lobe (**la**) small and compressed, pointing out sharply, at left side of **gp**.

Discussion

Lesticus is an Oriental genus with more than a hundred described species (Roux et al. 2016), and several of them have impressive metallic color. Although this genus was well defined, different species in the genus usually have similar external and male genital characters, making species determination generally difficult. Moreover, due to the limited number of available characters for systematic study, solving species relationships in *Lesticus* was never attempted before. In Pterostichini, the endophallic characters were of value for species relationships (Shi and Liang 2015). Thus, in an attempt to resolve part of the species relationships in *Lesticus*, we studied the endophallus of all available Chinese species (14 of 18 known species). Based on the comparative morphology study, preliminary conclusions on endophallic character evolution and phylogenetic considerations within *Lesticus* are presented below.

Endophallus categories in *Lesticus*

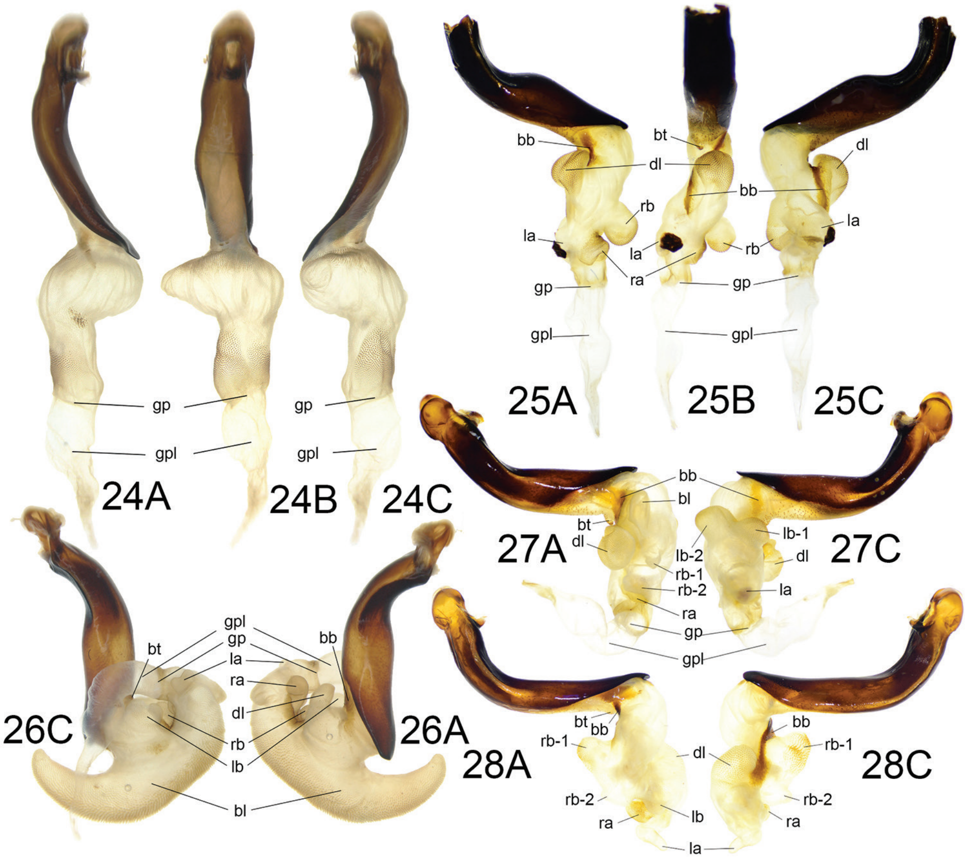
According to the materials and endophallus illustrations provided by Roux et al. (2016) that we examined, the endophallus shape is highly variable in *Lesticus*, but there are some regularities revealed. We classified here the endophallus of species studied (14 Chinese species and 19 species from other faunas) into four types, mainly based on the orientation of the gonopore and rotation or deflection of the endophallic axis.

Type I

The endophallus type I (as shown in Figs 8, 17, 22, 25 and 27) is the most common type among all examined species, and all other types can be explained as modifications based on this type. The enodphallus type I has the following character states:

Endophallic axis nearly straight; extending to genital apex, or more or less deflected to dorsum, with the angle inscribed between axes of aedeagus and endophallus (**AE-angle,** axis of endophallus was the line between midpoint of apical orifice and gonopore) between 5° and 80°; gonopore oriented to endophallic apex; major portion of endophallus located at apical, apical-dorsal or dorsal side of aedeagus. Seven groups of features recognized: (1) basal tubercle (**bt**) at the base of endophallus, generally very small, its surface with very dense scales, **bt** rarely disappearing; (2) basal band (**bb**), a long and narrow chitinized band, beginning at right margin of apical orifice, then surrounding base of **dl**, and ending at left surface of it, **bb** sometimes shortened or obsolete; (3) dorsal lobe (**dl**) on dorsal basal surface of endophallus, close to dorsal margin of aedeagus, generally large and rounded, usually the largest lobe on endophallus and decorated with very coarse scales, sometimes divided into sub-lobes or separate lobes; (4) right basal lobe (**rb**) on right basal surface of endophallus, usually divided into two separate lobes; (5) right apical lobe (**ra**) on right surface of endophallus, close to gonopore, generally much smaller than **rb**; (6) left basal lobe (**lb**) on right basal surface of endophallus, sometimes divided into two separate lobes or almost imperceptible; (7) left apical lobe (**la**) on left surface of endophallus, close to gonopore, generally much smaller than **lb**. All lobes generally decorated with scales at least on apex.

A total of 10 Chinese species have the type I endophallus: *L. solidus* Roux & Shi, *L. tristis* Roux & Shi, *L. xiaodongi* sp. n., *L. chalcothorax* (Chaudoir), *L. sauteri* Kuntzan, *L. perniger* Roux & Shi, *L. bii* sp. n., *L. deuvei* Dubault & Roux, *L. taiwanicus* Roux & Shi, *L. auricollis* Tschitschérine. Among these 10, two different forms (or subtypes) were recognized: (1) the **chalcothorax-form** (Figs 17, 23): endophallus almost straight, only slightly or not deflexed to dorsum, AE-angle 5° to 55°; gonopore at apical direction of aedeagus; **dl** very large, placed on dorsal surface; **dl** and **rb** sometimes divided; without additional basal lobe. Five Chinese species have the chalcothorax-form: *L. solidus*, *L. tristis*, *L. xiaodongi*, *L. chalcothorax*, and *L. sauteri*; (2) the **auricollis-form** (Fig. 27): endophallus markedly deflexed to dorsum, AE-angle 70° to 80°; gonopore at dorsal direction of aedeagus; **dl** placed on dorsal-right surface; **dl**, **rb** and **lb** all divided into two separate lobes; **bb** short and wide; one additional basal lobe (**bl**) present at right basal side of **dl**. Three Chinese species have the auricollis-form: *L. deuvei*, *L. taiwanicus* and *L. auricollis*.



Figures 24–28. Endophallus of species representatives. **A** left lateral view **B** dorsal view **C** right lateral view **24** *Trigonotoma lewisi* Bates from Yunnan (type I) **25** *Lesticus perniger* Roux & Shi from Yunnan (type I) **26** *Lesticus magnus* (Motschulsky) from Liaoning (type III) **27** *Lesticus auricollis* Tschitschérine from Fujian (type I) **28** *Lesticus insignis* Gestro from Sabah (type IV).

The remaining two species, *L. perniger* (Fig. 25) and *L. bii* (Fig. 8), are special within type I due to: **bt** less pointed than other species; **lb** completely absent; **rb** located well before midpoint of endophallus. But some other specialized differences might contradict their affinities: **bt** flat but very large and coarsely spined in *L. bii*; **bb** absent in *L. bii*, very long, reaching midpoint of endophallus in *L. perniger*; **la** with a heavily chitinized piece in *L. perniger*; **rb** divided into two separate lobes in *L. bii*.

Based on the endophallus illustrations provided by Roux et al. (2016), 11 species of the Chinese fauna also have an endophallus of type I. Four of them have the auricollis-form endophallus: *L. andamanensis* (Chaudoir), *L. mouhoti* (Chaudoir), *L. nubilus* Tschitschérine and *L. waterhousei* (Chaudoir); and another four have the chalcothorax-form: *L. buqueti* (Castelnau), *L. indus* (Tschitschérine), *L. kangeanensis* Dubault et al. and *L. stefanschoedli* Kirschenhofer. The remaining three species cannot be categorized as either form: *L. tricostatus* Chaudoir, *L. cupricollis* Pouillaude and

L. desgodinsi Tschitschérine. However, the former two species are clearly similar to *L. bii* sp. n. for both external and endophallic similarities. Besides *Lesticus*, some species of *Trigonotoma* (such as *T. lewisi* in Fig. 24) also have the endophallus straight and the gonopore placed well beyond the aedeagus apex (similar to the chalcothorax-form), but in *Trigonotoma* the endophallus generally has fewer or no lobes.

Type II

The endophallus type II (Figs 4, 13) with three Chinese species representatives (*L. auripennis* sp. n., *L. violaceous* sp. n. and *L. rotundatus* Roux & Shi) is characterized by: endophallic axis markedly deflexed to left, gonopore oriented to left-basal side of aedeagus; **dl** placed on right side of endophallus; one additional basal lobe (**bl**) present on basal-ventral side of dl. Among these three, *L. auripennis* is different from the other two species by: **bl** located on right surface, almost reaching midpoint of endophallus; gonopore oriented to left-apical side of aedeagus. Another species, *L. assamicus* (Kuntzen) from north India, is also known to have the type II endophallus.

Type II endophalli are well characterized by the endophallic axis markedly deflexed to left, but it seems that such a character cannot support close relationships among species with the type II endophallus. Based on other similarities among related species, we inferred that the type II endophallus might be derived from type I by the elongation of the endophallic base and deflection of the endophallic axis to the left, with *L. violaceous* and *L. rotundatus* derived from the auricollis-form, and *L. auripennis* probably from a *L. perniger*-like form.

Type III

The endophallus type III (Fig. 26) is a peculiar type only found in *L. magnus* (Motschulsky) which has a wide distribution in East Asia. It is characterized by: endophallic axis short and markedly deflexed to aedeagal base; a large conical basal lobe (**bl**) forming conspicuous ventral projection; main portion of endophallus located on dorsal side of aedeagus; gonopore oriented to ventral side. Although peculiar, type III was assumed to have transformed from the auricollis-form of type I by: endophallic apex more deflexed to basal-ventral side; all primary lobes reduced in size and restricted at dorsal margin of endophallus; the presence of a very large additional basal lobe (**bl**).

Type IV

The endophallus type IV (Fig. 28) is characterized by the endophallic axis markedly helical on the basal portion. No Chinese species has a type IV endophallus; all known species (nine) of this type are from the Malay Archipelago (Philippines, Borneo, Java). The highly specialized helix-formed endophallus and its regional distribution may suggest close relationships among species of the type IV endophallus.

Although highly specialized, the type IV endophallus was still inferred as a modified type from the type I, and homologies of all lobes can be distinguished (Fig. 28). From the chalcothorax-form of type I, type IV is assumed to be transformed by: **dl** moved to apex and deflexed to left side; endophallic base before **dl** elongated and rotated; **rb-1** enlarged and protuberant; **rb-2** generally small; **lb** obsolete; **la**, **ra**, **bb**, and **bt** similar to those in type I; main portion of endophallus located on dorsal side of aedeagus; gonopore generally oriented to basal-dorsal side.

Chinese *Lesticus* species with unknown endophallus

There are four Chinese *Lesticus* species with the endophallus unknown. Based on external and aedeagal characters, we briefly discuss here their presumed relationships and predicted endophallic types.

Lesticus fukiensis Jedlička and *L. wrasei* Dubault, Lassalle & Roux: These two species are very similar in habitus and aedeagus features and have adjacent distributions. Compared to other species from China, they are most similar to and presumed to be closely related to *L. auripennis* sp. n., sharing the short and wide metepisternum; aedeagus only slightly or not expanded ventrally; in dorsal view, apical portion of aedeagus very slightly oblique to right side (might be associated with left deflection of endophallus). Thus, these two species are hypothesized to have endophallus character states similar to the type II of *L. auripennis*.

Lesticus ater Roux & Shi: Based on the short, wide metepisternum, this species was considered as belonging to the same group of *L. perniger* (see discussion under *L. auripennis*). But from the almost impunctate ventral surface and the peculiar shape of aedeagal apex, *L. ater* is an outlier in this group and its close allies are unclear. Nevertheless, from the symmetrical aedeagal apex (in dorsal view not oblique to right or left side), *L. ater* is hypothesized to have type I endophallus similar to *L. perniger*.

Lesticus praestans (Chaudoir): This species is assumed to be close to *L. deuvei* based on their similarities in several external characters, for example: metepisternum longer than its basal width; pronotal with metallic color; basal fovea distinctly punctate. Thus, an auricollis-form endophallus is hypothesized.

Evolution of other characters

It is difficult to infer species relationships in *Lesticus* from external characters only, because only very few characters are available, and many of them have lot of variation in the genus. Similar problems were also encountered when distinguishing similar species and determining identification keys. Nevertheless, there are still some character transformations that are widely presented in *Lesticus* and important in species determination. Some of the transforming polarities seem to be clear, while others are more complex. We selected here some of the most common transformed characters in *Lesticus*, inferred their transforming polarity and preliminary evaluated their taxonomic value.

Coloration: The metallic or black pronotum is a constant character in most species and seems to have some systematic importance. The non-metallic color could be apomorphies. The head coloration always conforms with that of the pronotum, but elytra coloration should be regarded as an independent character, although in many groups it seems to have some linkage with pronotal coloration.

Punctures: The punctures of pronotal basal fovea, elytra intervals, propleuron and metepisternum are useful to distinguish similar species, but they are variable in some species. Generally, punctures on different body parts are somewhat linked, but it seems that these punctate characters have very little importance when inferring species relationships.

Pronotum shape: The pronotum shape is variable and important in identification of *Lesticus* species. Different shapes of pronotum are recognizable, among which the subquadrate shape (as in *L. magnus*) is inferred to be plesiomorphic, while round (as in *L. andamanensis*) and cordiform (as in *L. janthinus*) are apomorphies. Some species relationships might be inferred by specialized pronotal shape. For instance, the strongly cordiform pronotum may suggest a close relationship of *L. janthinus* with its allies from Indonesia.

Pronotal margin: About 13 species with quite different external appearance have crenulate pronotal lateral margins. This apomorphic character state is useful in species identification and relationship inference, but it might have homoplastic transformations also.

Elytral discal pores: Most species of the genus have three setigerous pores on elytral third interval, but some of them have only one or two pores, and a very few species have none. It is clear that three pores is plesiomorphic, and the reduced number of discal pores might support some monophyletic groups.

Elytral interval: Seven species of *Lesticus* have elytra modified by odd intervals raised, ridged or widened. This apomorphic state occurs in two groups having rather distant distributions (Himalayan Mountains and Lesser Sunda Islands) and some other characters are also different (i.e. elytral discal pores). Thus, these two groups might not be close and homoplastic transformations are inferred.

Metepisternum: The length of metepisternum has important value for species identification and the definition of some species groups. It seems that this character has distinct binary states: the shortened form (associated with reduced hind wings) with its length shorter or subequal to its basal width, and the normally longer form (associated with developed hind wings) with a length more than 1.3 times its basal width. Similar to most genera of Carabidae, the shortened metepisternum is apomorphic, and associated with the reduction of hind wings and adaptation to mountain habitat. But there seem to be several parallelisms in its character transformations.

Infra-genera taxonomy of *Lesticus*

Presently, the genus *Lesticus* is divided into three subgenera as accepted in catalogues (Lorenz 2005, Löbl and Löbl 2017). This infra-genera taxonomy comes primarily from Tschitschérine (1900) with three subgenera defined as follows: *Lesticus* s. str. (type species: *Lesticus janthinus* Dejean) have cordiform pronotum, lateral margins strongly sinuate before posterior angles; short metepisternum, the outer margin not longer than basal width. *Celistus* Tschitschérine (type species: *Triplogenius andamanensis* Chaudoir) have round pronotum, lateral margins evenly curved; short metepisternum, outer margin not longer than basal width. *Triplogenius* Chaudoir (type species: *Trigonotoma bicolor* Laporte [= *Omaseus viridicollis* Macleay]) have variable pronotum shapes, usually near quadrate; long metepisternum, outer margin distinctly longer than basal width.

However, this subgeneric system was not accepted in many important revisions (i.e. Jedlička 1962, Roux et al. 2016), and many species described later without original subgenera assignment were subsequently placed in subgenera very casually by cataloguers. For instance, two very close species, *L. auricollis* and *L. deuvei*, were assigned to different subgenera (Löbl and Löbl 2017). Moreover, many species presently assigned to *Lesticus* s. str. do not have the typical cordiform pronotum of the subgenera, and some of them even have elongated metepisternum making the definition of subgenera unclear.

In the present study, we examined all Chinese *Lesticus* species and compared them to many foreign species according to some important morphology characters. We found that in *Lesticus* the short metepisternum is not always in accordance with cordiform or round pronotum, and neither pronotum shape nor metepisternum length can support a monophyletic group inferred by the endophallic characters (see above). Both of the type species of *Lesticus* and *Triplogenius* have similar type IV endophalli which supports these two species being actually closely related. All the above evidence, object of the present infra-general taxonomy, originated with Tschitschérine (1900).

In conclusion, except the monotypic *Celistus*, the other two subgenera in the present concept are obviously not monophyletic, but an improved infra-general system cannot be proposed at this time. Thus, we suggest that it is better not to introduce subgenera in the genus *Lesticus* before a comprehensive phylogenetic study is completed.

Catalogue of *Lesticus* from China

Lesticus ater Roux & Shi, 2011

Roux and Shi 2011: 95 (Type locality: Jinping, Yunnan; Holotype in IZAS); Roux, Lassale and Dubault 2016: 356.

Chinese common name: 乌劫步甲 (Wū Jié Bù Jiǎ)

Distribution. Yunnan (Jinping).

Lesticus auricollis Tschitschérine, 1900

Tschitschérine 1900: 174 (Type locality: Bangkok; Holotype in MNHN); Kuntzen 1911: 165; Jedlička 1962: 326; Dubault et al. 2007: 217; Roux et al. 2016: 332.
Chinese common name: 金胸劫步甲 (Jīn Xiōng Jié Bù Jiǎ)
Distribution. Fujian, Jiangxi, Zhejiang, Hunan, Guangdong, Guangxi, Hainan; Thailand; Vietnam.

Lesticus auripennis sp. n.

Chinese common name: 金鞘劫步甲 (Jīn Qiào Jié Bù Jiǎ)
Distribution. Guangdong (Nanling).

Lesticus bii sp. n.

Chinese common name: 毕氏劫步甲 (Bì Shì Jié Bù Jiǎ)
Distribution. Xizang (Mêdog).

Lesticus chalcothorax (Chaudoir, 1868)

Chaudoir 1868: 153 (*Triplogenius*; Type locality: Cambodge; Lectotype in MNHN); Bates 1889a: 105 (*Triplogenius*); Kuntzen 1911: 165; Andrewes 1921: 178 (*Triplogenius*); Jedlička 1962: 327; Dubault et al. 2007: 211; Roux et al. 2016: 334.
Synonym: *Triplogenius bouqueti* Laporte de Castelnau: Bates 1889b: 276.
Synonym: *Lesticus lakhonus* Tschitschérine, 1900: 171 (Type locality: «Lakhon» [=Nakhon Phanom, Thailand]; Holotype in MNHN); Rouxet al. 2016: 334 (synonymy designation).
Chinese common name: 绿胸劫步甲 (Lǜ Xiōng Jié Bù Jiǎ)
Distribution. Jiangxi, Zhejiang, Fujian, Hunan, Guangdong, Guangxi, Guizhou, Yunnan; Myanmar; Thailand; Vietnam; Cambodia.

Lesticus deuvei Dubault & Roux, 2006

Dubault and Roux 2006: 189 (Type locality: Huaping, Guangxi; Holotype in MNHN); Roux et al. 2016: 364.
Chinese common name: 德夫劫步甲 (Dé Fū Jié Bù Jiǎ)
Distribution. Guangxi (only known from N.E. Guangxi).

Lesticus fukiensis Jedlička, 1956

Jedlička 1956: 213 (Type locality: Kuatun [=Guadun, Fujian]; Holotype in NMPC); Jedlička 1962: 323; Dubault et al. 2008: 466; Roux et al. 2016: 358.

Chinese common name: 福建劫步甲 (Fú Jiàn Jié Bù Jiǎ)

Distribution. Fujian (only known from N. Fujian).

Lesticus magnus (Motschulsky, 1860)

Motschulsky 1860: 5 (*Omaseus*; Type locality: Japan; Holotype in ZMUM); Heyden, 1879: 332 (Triplogenius); Andrewes 1933: 14 (*Pterostichus*); Jedlička 1962: 322 (misspelled as *maguus*); Roux et al. 2016: 362.

Synonym: *Omaseus ingens* Morawitz, 1863: 54 (Type locality: Jesso; Syntype in ZMUM). Chaudoir 1868: 154 (*Triplogenius*; synonym designation); Bates 1873: 284 (*Triplogenius*); Kuntzen 1911: 175.

Chinese common name: 大劫步甲 (Dà Jié Bù Jiǎ)

Distribution. Liaoning, Beijing, Hebei, Shaanxi, Gansu, Shandong, Hubei, Hunan, Jiangsu, Anhui, Jiangxi, Shanghai, Zhejiang, Sichuan; Japan; Korea.

Notes: This species was recorded from Taiwan (Jedlička 1962), but no any confirmed specimen was examined hereafter. We inferred the record from Taiwan was based on the misidentification of *L. sauteri* and excluded this regional record.

Lesticus perniger Roux & Shi, 2011

Roux and Shi 2011: 98 (Type locality: Lancang, Yunnan; Holotype in IZAS); Roux, Lassale and Dubault 2016: 352.

Chinese common name: 黑劫步甲 (Hēi Jié Bù Jiǎ)

Distribution. Yunnan; Guangxi*.

*New province record with examined materials: 1 female (SCAU), "Guangxi, Maoershan, Tongmujiang source, 1250m, 2003.8.25, TIAN M. Y.". 1 male (SNU), "China: Guangxi Prov., Lingui County, Huaping N. R., Anjiangping, 1300m, 18-VII-2011, PENG Zhong leg.". 1 male (IZAS), "China, Guangxi, Xingan, Jinshiguiyan, 1229m, 2016-VII-09 light trap, LU Y. Q. Leg. CCCC". 1 male (NHMB), "China, Guangxi Reg. Miaoershan mts., 500–1200m, south slope 26.-29.vi.1997".

Lesticus praestans (Chaudoir, 1868)

Chaudoir 1868: 154 (*Triplogenius*; Type locality: Hongkong; Lectotype in MNHN); Jedlička 1962: 323; Dubault et al. 2007: 212; Roux et al. 2016: 344.

Chinese common name: 立劫步甲 (Lì Jié Bù Jiă)

Distribution. Hongkong, Guangdong*.

*New province record with examined materials: 2 females (IZAS), “China, Guangdong, Shengzhen, Xianhu Botanical Garden, 22.58184, 114.16440 34m, 2014.5.3 N, Liang H. B., Huang X. L., Institute of Zoolgy, CAS”.

Lesticus rotundatus Roux & Shi, 2011

Roux and Shi 2011: 102 (Type locality: Shuangjiang, Yunnan; Holotype in IZAS); Roux et al. 2016: 366.

Chinese common name: 圆胸劫步甲 (Yuán Xiōng Jié Bù Jiă)

Distribution. Yunnan (Shuangjiang, Ruili, Xishuangbanna*, Yingjiang*), Myanmar* (Putao).

*New record with examined materials: 1 female (IZAS), “Guomenshan, Nabanhe, Yunnan Prov. alt. 1100m, 23-VII-2005, LI & LI leg.”. 1 female (CCCC), “13Y2013-X-12, Yunnan, Jinghong, Menglong 622m, rubber forest YANG X. D. Leg.”. 1 female (CCCC), “China, Yunnan, Yingjiang, Nabang power station, 473m, 2016-V-29, light trap, 16Y, Yang Xiaodong Leg. CCCC”. 1 male (IZAS), “Myanmar, Kachin State, Putao county, Ba aye, way to Nahteukhu. 27.3183, 97.3894, 2016.12.8 576m”.

Lesticus sauteri Kuntzen, 1911

Kuntzen 1911: 175 (Type locality: Taiwan; Syntypes in MNHU); Jedlička 1962: 322; Dubault et al. 2008: 465; Roux et al. 2016: 360.

Chinese common name: 绍氏劫步甲 (Shào Shì Jié Bù Jiă)

Distribution. Taiwan.

Lesticus solidus Roux & Shi, 2011

Roux and Shi 2011: 105 (Type locality: Xing’an, Guangxi; Holotype in IZAS); Roux et al. 2016: 350.

Synonym: *Lesticus dubius* Dubault, Lassalle & Roux, 2013: 209 (Type locality: Maoershan, Guangxi; Holotype in CDW). Roux et al. 2016: 346. **syn. n.**

Chinese common name: 壮劫步甲 (Zhuàng Jié Bù Jiă)

Distribution. Guangxi.

Lesticus taiwanicus Roux & Shi, 2011

Roux and Shi 2011: 106 (Type locality: Fushan, Taiwan; Holotype in NMNS); Roux et al. 2016: 368.

Chinese common name: 台湾劫步甲 (Tái Wān Jié Bù Jiă)

Distribution. Taiwan.

Lesticus tristis Roux & Shi, 2011

Roux and Shi 2011: 108 (Type locality: Lancang, Yunnan; Holotype in IZAS); Roux et al. 2016: 354.

Chinese common name: 暗劫步甲 (Àn Jié Bù Jiă)

Distribution. Yunnan.

Lesticus violaceous sp. n.

Chinese common name: 紫光劫步甲 (Zĭ Guāng Jié Bù Jiă)

Distribution. Yunnan (Yingjiang).

Lesticus wrasei Dubault, Lassalle & Roux, 2013

Dubault et al. 2013: 213 (Type locality: Tianbaoyan mt., Fujian; Holotype in CDW). Roux et al. 2016: 348

Chinese common name: 弗氏劫步甲 (Fú Shì Jié Bù Jiă)

Distribution. Fujian (Tianbaoyao).

Lesticus xiaodongi sp. n.

Chinese common name: 晓东劫步甲 (Xiăo Dōng Jié Bù Jiă)

Distribution. Yunnan (Yingjiang).

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