

Description of *Meloidoderita salina* sp. n. (Nematoda, Sphaeronematidae) from a micro-tidal salt marsh at Mont-Saint-Michel Bay in France

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Abstract

Meloidoderita salina sp. n. is described and illustrated from the halophytic plant *Atriplex portulacoides* L. (sea purslane) growing in a micro-tidal salt marsh in the Mont-Saint-Michel Bay in France. This new species is the first member of *Meloidoderita* Poghossian, 1966 collected from a saline environment, and is characterized by the following features: sedentary mature females having a small swollen body with a clear posterior protuberance; slightly dorsally curved stylet, 19.9 µm long, with posteriorly sloping knobs; neck region irregular in shape and twisted; well developed secretory-excretory (S–E) pore, with markedly sclerotized S–E duct running posteriorly; prominent uterus bordered by a thick hyaline wall and filled

with eggs. The adult female transforms into a cystoid. Eggs are deposited in both egg-mass and cystoid. Cystoids of *Meloidoderita salina* **sp. n.** display a unique sub-cuticular hexagonal beaded pattern.

Male without stylet, pharyngeal region degenerated, S-E duct prominent, deirids small, developed testis 97.5 µm long, spicules 18.4 µm long, cloacal opening ventrally protruded, small phasmids posterior to cloaca opening and situated at 5.9 (3.2–7.7) µm from tail end, and conical tail ending in a rounded terminus marked with one (rarely two) ventrally positioned mucro. Additionally, some young males of the new species were observed enveloped in the last J2 cuticle. Second-stage juvenile body 470 µm long, with a 16.4 µm long stylet, prominent rounded knobs set off from the shaft, hemizonid anterior and adjacent to S-E pore, small deirids located just above S-E pore level, genital primordium located at 68–77% of body length, phasmids small and located at about 19 µm from tail tip, and tail 38.7 µm long, tapering to finely pointed terminus with a finger-like projection. Phylogenetic analyses based on the nearly full length small subunit ribosomal DNA sequences of *Meloidoderita salina* **sp. n.** revealed a close relationship of the new species with *Sphaeronema alni* Turkina & Chizhov, 1986 and placed these two species sister to the rest of Criconematina.

Keywords

Atriplex portulacoides, cystoid, halophyte, hexagonal, morphology, morphometrics, nematode, new species, sea purslane, SEM, SSU rDNA, taxonomy

Introduction

Since Poghossian (1966) established the genus *Meloidoderita* Poghossian, 1966 to accommodate the new species *Meloidoderita kirjanovae* Poghossian, 1966, two other *Meloidoderita* species have been described. *Meloidoderita kirjanovae* was isolated from roots of mint (*Mentha longifolia* (L.) Huds.) from the Mergi region in Armenia. Poghossian (1966) placed *Meloidoderita* within Heteroderidae Filipjev & Schuurmans Stekhoven, 1941 (Skarbilovich, 1947) on the basis of cyst induction with a pattern of spine-like structures. Wouts and Sher (1971) considered *Meloidoderita* as *genus inquirenda* in the subfamily Heteroderinae Filipjev & Schuurmans Stekhoven, 1941. One year later Wouts (1972) reported that in the previous study, due to a lack of type material and an insufficient description, they “could not establish the exact status of the genus *Meloidoderita*”. Afterwards, after examining five females identified as *M. kirjanovae* and on the basis of the presence of a large egg-sac (gelatinous matrix), short stylet, the absence of a cyst, and pronounced galls in the observed roots, Wouts (1972) considered *Meloidoderita* as a valid genus belonging in Meloidogynidae Skarbilovich, 1959 (Wouts, 1973).

Kirjanova and Poghossian (1973) re-described *M. kirjanovae* and established a newly erected family, Meloidoderitidae, within Criconematidea Taylor, 1936 (1914) (Thorne, 1949). Moreover, Poghossian (1975) reported that the material examined by Wouts probably had been contaminated by *Meloidogyne hapla* Chitwood, 1949.

M. kirjanovae has been recorded parasitizing on *Mentha* spp. (mint and water mint) and *Utrica dioica* L. (common nettle) (Poghossian 1966, Narbaev 1969, Cohn and Mordechi 1982, Vovlas et al. 2006).

Siddiqi (1985, 2000) classified *Meloidoderita* in the subfamily Meloidoderitinae Kirjanovae & Poghossian, 1973, family Sphaeronematidae (Raski & Sher, 1952) Ger-aert, 1966, superfamily Tylenchuloidea (Skarbilovich, 1974) Raski & Siddiqui, 1975 and suborder Criconematina Siddiqi, 1980.

The second species of *Meloidoderita*, *M. safrica*, was described by Van den Berg and Spaull (1982) from soil and root samples of sugarcane (*Saccharum* hybrid) in South Africa.

Golden and Handoo (1984) described *M. polygoni* from USA. Previously, Golden (1976) and Andrews et al. (1981) reported the occurrence of a population of *Meloidoderita* sp. from roots of smartweed (*Polygonum hydropiperoides* Michx.), which was not able to infect mint and nettle.

During a nematode survey conducted in Mont-Saint-Michel Bay in France, a *Meloidoderita* population was isolated from soil and roots of the halophyte *Atriplex* (= *Halimione*) *portulacoides* (L.) Aellen. This nematode was infecting roots of sea purslane (*Atriplex portulacoides*) growing in a muddy soil salt marsh region. Preliminary morphological and molecular analyses (G. Karssen, unpublished) indicated that the population differed from all three known described species of *Meloidoderita* and represented a new species. This was the first *Meloidoderita* species collected from a salt marsh environment.

The main objectives of the present study were to: i) describe a new species of *Meloidoderita* isolated from soil and roots samples of *A. portulacoides* from a salt marsh region in France and provide a detailed morphological description based on LM and SEM; ii) characterize *Meloidoderita* species by means of small subunit rDNA sequencing; iii) determine the phylogenetic position of *Meloidoderita* within the suborder Criconematina.

Materials and methods

Collection of samples

Soil and root samples were isolated from *A. portulacoides* grown in muddy soil of a costal tidal salt marsh environment in "Le Vivier- sur- Mer" at 48°36'32"N and 1°47'00"W at Mont-Saint-Michel Bay in France.

The Mont-Saint-Michel Bay (MSMB) is a costal embayment and macro-tidal environment located on the English Channel (Southern gulf of Normandy) between the Cotentin Peninsula and the Brittany coast, in the northwestern coast of France (Detriche et al. 2011, Dubois et al. 2007). The climate is Oceanic-Breton with average annual temperature of 9°C (Costil et al. 2001). Samples were collected during the months of March, June, September, and December in 2007. The average salinity of soil in MSMB is about 34–35 g/L (3.5%). The tides cover the area where *A. portulacoides* grows about twenty times a year.

The Mont-Saint-Michel Bay is a specific ecosystem on a small geographic scale. Despite the presence of numerous ecological studies that have been applied since 1979 in MSMB, nematodes have been mostly neglected (Lefeuvre et al. 2003).

Nematode extraction and comparison

To obtain a homogenized sample of the cohesive muddy soil, we gently mixed samples in a kneading machine for 15 min. Afterwards, nematodes including juveniles, males, cystoids, and eggs, were extracted from soil samples by means of a magnesium sulphate centrifugal flotation technique (Coolen 1979).

Females were collected with two different methods: i) centrifugal flotation method (Coolen 1979) for extracting females, and ii) direct handpicking of females and egg-masses from roots with the aid of dissecting tools under a stereomicroscope. Root samples were washed with tap water under low pressure to prevent damage to the nematodes.

The *Meloidoderita* populations and a *Sphaeronema* Raski & Sher, 1952 population used for comparison are listed in Table 1.

Table 1. Host and origin of the populations of three *Meloidoderita* species and one *Sphaeronema* species which were compared with the population of *M. salina* sp. n.

Species	Host	Origin
<i>M. kirjanovae</i> (Poghossian, 1966) Kirjanova and Poghossian (1973)	<i>Mentha longifolia</i> (L.) Huds.	Megri region, Armenia
<i>M. kirjanovae</i> characterized by Golden & Handoo (1984)	<i>Mentha longifolia</i>	Mediterranean region
<i>M. kirjanovae</i> characterized by Siddiqi (1985)	<i>Mentha longifolia</i>	Armenia
<i>M. kirjanovae</i> characterized by Vovlas et al. (2006)	<i>Mentha aquatic</i> L.	Laceno Lake at Avellino, southern Italy
<i>M. safrica</i> Van den Berg & Spaull, 1982	<i>Saccharum</i> hybrid (Sugar cane)	Mposa area of Natal, South Africa
<i>M. polygona</i> Golden & Handoo, 1984	<i>Polygonum hydropiperoides</i> Michx.	Beltsville, Maryland, USA
<i>Sphaeronema alni</i> Turkina & Chizhov, 1986 (topotype population)	<i>Alnus incana</i> (L.) Moench, <i>A. glutinosa</i> L., <i>Betula pubescens</i> Ehrh.	Russia

Light and scanning electron microscopy

Specimens for light microscopy (LM) were fixed in heated (70°C) TAF (2 ml triethanolamine, 7ml formaldehyde and 91 ml distilled water (Courtney et al. 1955)), and processed to anhydrous glycerin following the method of Seinhorst (1966). Fixed specimens including second-stage juveniles, males, females, cystoids, egg-masses and eggs were mounted in a small drop of desiccated glycerin with the paraffin wax method on Cobb slides (Southey 1986).

Measurements and drawings were performed on a light microscope Olympus BH-2 equipped with Nomarski Differential Interference Contrast (DIC).

Specimens were drawn with a drawing tube, scanned and modified using Photoshop software version CS 5.1.

Light micrographs of specimens were taken with a Leica DC 300 F camera attached to a Zeiss Axio Imager M1 microscope. The original descriptions of closely related species (Table 1) were used for morphological and morphometrical comparison.

For SEM observation nematodes were fixed in 3% glutaraldehyde buffered with 0.05M phosphate buffer (pH 6.8) for 1.5 h and post-fixed with 2% osmium tetroxide for 2h at 22°C. The specimens were dehydrated in a seven-graded ethanol series of 15-25-35-50-70-95 and 100% (Wergin 1981), critical point dried with carbon dioxide, and sputter coated with a layer of 4–5 nm Pt in a dedicated preparation chamber (CT 1500 HT, Oxford Instruments). The nematodes were examined and photographed with a field emission electron microscope Jeol 6300 F, at 5 kV (Karszen 1996, 1998).

DNA Extraction, PCR-Based amplification, Cloning and Sequencing

Single nematodes (five individuals in total) were transferred to a 0.2 ml Eppendorf vial containing 25 µl of sterile water. An equal volume of lysis buffer containing 0.2 M NaCl, 0.2 M Tris-HCl (pH 8.0), 1% (vol/vol) β-mercaptoethanol, and 800 µg/ml of proteinase K was added. Lysis took place in a Thermomixer (Eppendorf, Hamburg, Germany) at 65°C and 750 rpm for 2 h followed by a 5 min incubation at 100°C (to inactive proteinase). Lysate was immediately used or stored at –20°C. SSU rDNA was amplified as two partially overlapping fragments using three universal and one nematode-specific primer (1912R). The latter was included to avoid amplification of non-target eukaryotic SSU rDNA. For the first fragments, either the primer 988F (5'-ctc aaa gat taa gcc atg c-3') or the primer 1096F (5'-ggg aat tct gga gct aat ac-3') was used in combination with the primer 1912R (5'-ttt acg gtc aga act agg g-3'). The second fragment was amplified with primers 1813F (5'-ctg cgt gag agg tga aat-3') and 2646R (5'-gct acc ttg tta cga ctt tt-3'). PCR was performed in a final volume of 25 µl containing 3 µl of 100 times-diluted crude DNA extract, 0.1 µM of each PCR primer and a ready-To-Go PCR bead (GE Healthcare, Little Chalfont, UK). The following PCR program was used: 94°C for 5 min; 5× (94°C, 30 s; 45°C, 30 s; 72°C, 70 s) followed by 35× (94°C, 30 s; 54°C, 30 s; 72°C, 70 s), and 72°C for 5 min. Gel-purified amplification products (Marligen, Ijamsville, MD) were cloned into a TOPO-TA vector (Invitrogen, Carlsbad, CA) and sent off for sequencing using standard procedures (Holterman et al. 2009). The newly generated SSU rDNA sequences were deposited at GenBank under accession numbers FJ969126 and FJ969127.

Sequence alignment

SSU rDNA-obtained sequences were aligned using the ClustalW algorithm as implemented in the program BioEdit 7.0.1 (Hall 1999). Manual improving and editing the alignment was then performed using arthropod secondary structure information (<http://www.psb.ugent.be/rRNA/secmodel/index.html>) according to Wuyts et al. (2000). Out-group taxa and those nematodes compared with the sequence of the new *Meloidoderita* were chosen in accordance with Holterman et al. (2009). The final alignment included 39 SSU rDNA sequence and contained 1883 aligned position including gaps.

Phylogenetic analyses

The phylogenetic tree was constructed using Bayesian inference (MrBayes 3.1.2 (Ronquist and Huelsenbech 2003)) and a fast maximum likelihood method (RAxML-VI-HPC v.4.0.0 (Stamatakis 2006)). Modeltest 3.06 (Posada and Crandall 1998) identified the general time reversible (GTR) model with invariable sites and a gamma-shaped distribution of substitution rates as the best substitution model. Bayesian analysis was performed with a random starting tree and four Markov chains. The programme was run for 5×10^6 generations with a sampling frequency of 1,000 generations. Two independent runs were performed for each analysis. After discarding the 'burn-in' samples of 500,000 generations, sampled trees were combined to generate a 50% majority rule consensus tree, which represents posterior probabilities.

The second phylogenetic tree was constructed with a fast maximum likelihood method. The SSU rDNA alignment was analysed at a distant server (CIPRES, <http://www.phylo.org>) running the program, RAxML-VI-HPC v.4.0.0 using the same GTR model. One hundred bootstrap replicates were performed.

Results

Meloidoderita salina sp. n.

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http://species-id.net/wiki/Meloidoderita_salina

Figs 1–8; Table 2

Measurements. *Females, males and second-stage juveniles:* See Table 2. *Embryonated eggs* ($n = 44$): Length: 102.5 ± 5.0 (94.4–112) μm ; diam.: 41.7 ± 1.9 (38.4–46.4) μm ; length/width ratio: 2.5 ± 0.2 (2.1–2.9). *Cystoids* ($n = 18$): Length: 224 ± 34.5 (176–336) μm ; Width: 187.5 ± 33.1 (145.6–280) μm ; length/width ratio: 1.2 ± 0.1 (1.0–1.7).

Description. Female. Body swollen with a small posterior protuberance, pearly white to light brown, oval to pear-shaped. Neck region distinct, irregular shaped, usually twisted, 49 to 82 μm in length (Figs 2, 8). Body cuticle thick, without annulation. Head continuous with body, without annules. Cephalic framework weakly developed, lip region flattened. Stylet well developed, with posteriorly sloping oval-shaped knobs; stylet cone longer than shaft, slightly curved dorsally, shaft cylindrical (Fig. 2C). Dorsal gland orifice (DGO) close to basal knobs; vestibule extension visible. Secretory-excretory (S-E) pore well developed with clear cuticular lobes, located posterior to the neck, about 35 (20–56)% from anterior end of body; S-E duct markedly sclerotized, running posteriorly. Pharyngeal lumen from stylet to valve of metacarpus prominent. Metacarpus usually oval-shaped, situated at the posterior part of neck region, with distinct sclerotized valve apparatus, distance from middle of metacarpus to anterior end about 58 ± 10 μm long. Posterior gland bulb extending into anterior portion of swollen body cavity. Reproductive system extending towards pharyngeal region, monodelphic,

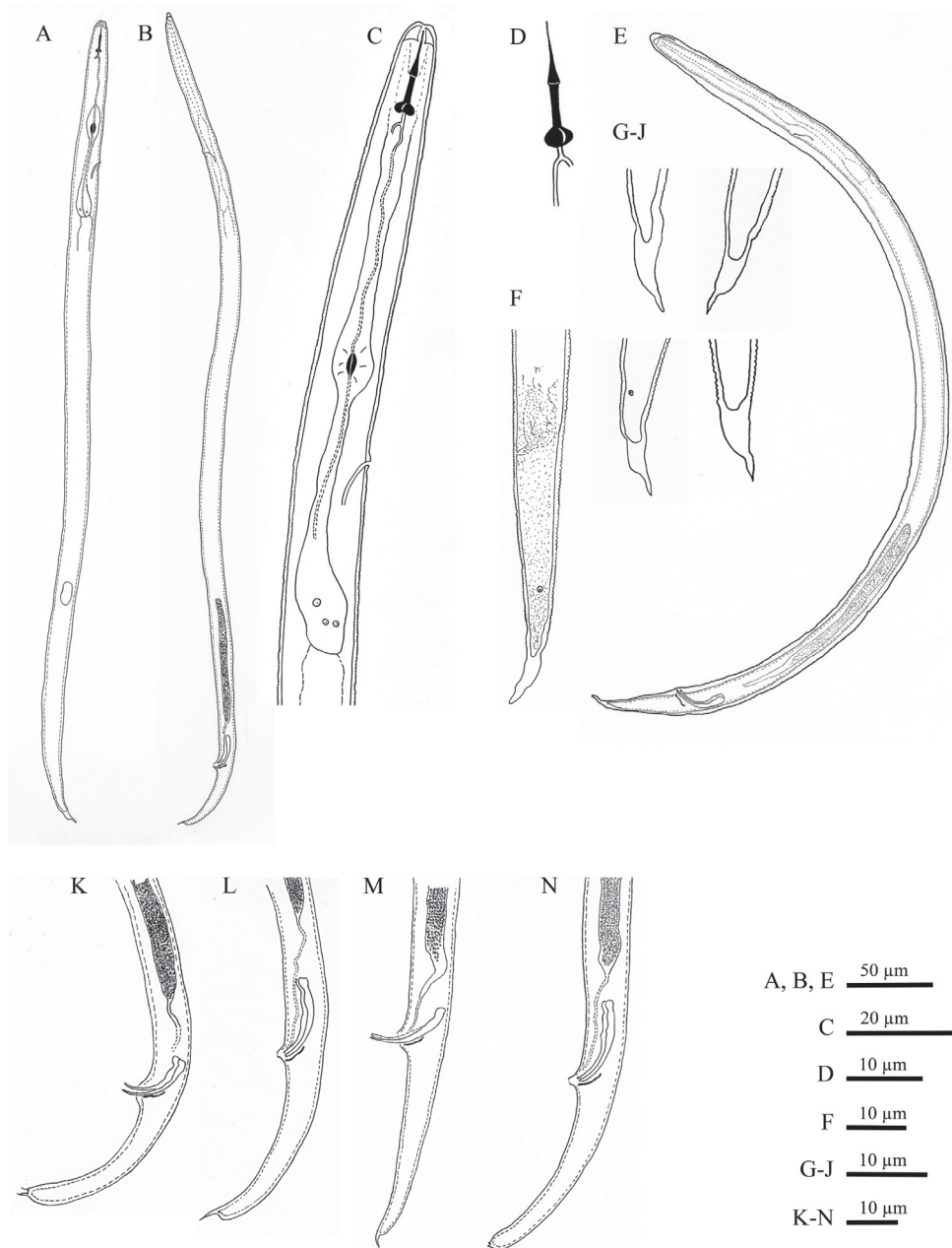


Figure 1. *Meloidoderita salina* sp. n. **A** Second-stage juvenile (J2) **B** Male **C** J2 anterior region **D** J2 stylet **E** Male within old J2 cuticle **F** J2 posterior region **G-J** J2 Tail tip **K-N** Male posterior region.

spermatheca not observed; vulva with noticeable protruding lips, positioned usually at the posterior extremity of the body, rarely subterminal. Vulval lips forming thickened and muscular area around vulval slit (vulval area). Anus faint, opening pore-like, diffi-

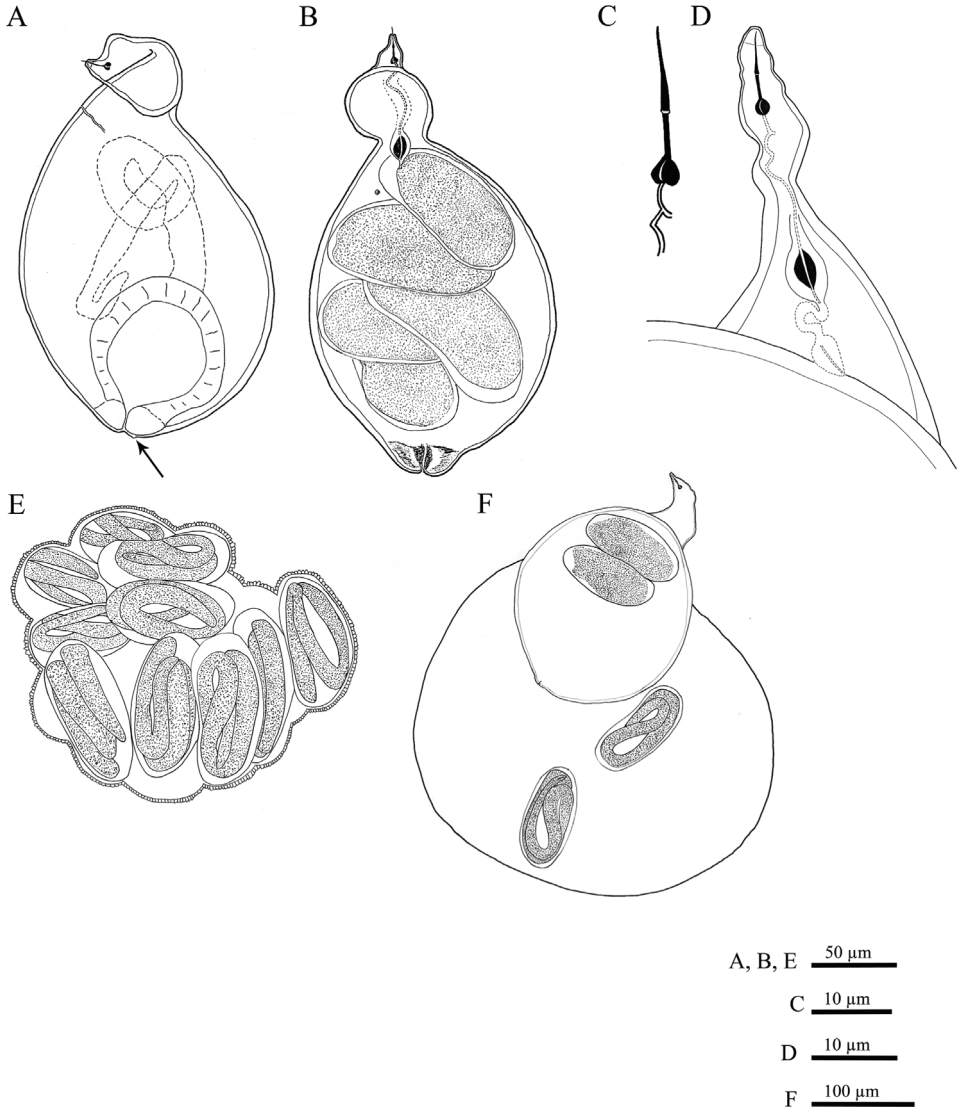


Figure 2. *Meloidoderita salina* sp. n. **A, B** Female body (arrow = anus) **C** Female stylet **D** Female neck region **E** Cystoid **F** Female with egg-mass.

cult to observe by LM, located at the base of dorsal vulval lip, apparently not functional (Figs 5E, 8C). Uterus swollen, prominent, bordered by a thick hyaline wall, becoming enlarged and filled with eggs, transforming into a cystoid within the female cuticle.

Male. Body slender, vermiform, tapering at both ends but more posteriorly, usually slightly curved ventrally at tail region. Cuticle marked by fine annulations, about 0.9 μ m wide. Young males usually still enveloped in the last cuticle of second-stage juveniles (Fig. 4D). Lateral field beginning with 2 weak lines, roughly between head end and S-E pore level, and continuing with four weak lines behind S-E pore level.



Figure 3. *Meloidoderita salina* sp. n. LM photographs of second-stage juveniles. **A** Entire body **B, C** Anterior body (arrow = DGO) **D** S-E duct adjacent to hemizonid (arrow = S-E duct) **E** Basal bulb (arrow = hemizonid) **F** Mid-body portion (arrow = primordium) **G-I** Tail (arrow = anus). Scale bars: **A** = 100 μ m **B-I** = 10 μ m.

Head continuous with body, rounded-conoid, without annules and separated lips, distinct but weak cephalic framework present; amphidial apertures slit-like, angled, adjacent to oral opening surrounded by a small elevated oral disc (Fig. 7B). Pharyngeal region degenerated except for the posterior bulb, no stylet observed. S-E pore well developed, adjacent to hemizonid. S-E duct strongly sclerotized anteriorly (Fig. 4E). Deirids small, located just above S-E pore level (Fig. 7C). Monorchic, outstretched, testis well developed, with small vas deferens about 6 μ m long. Spicules paired, equal, not fused, arcuate, with rounded manubrium. Gubernaculum slightly curved. Cloacal

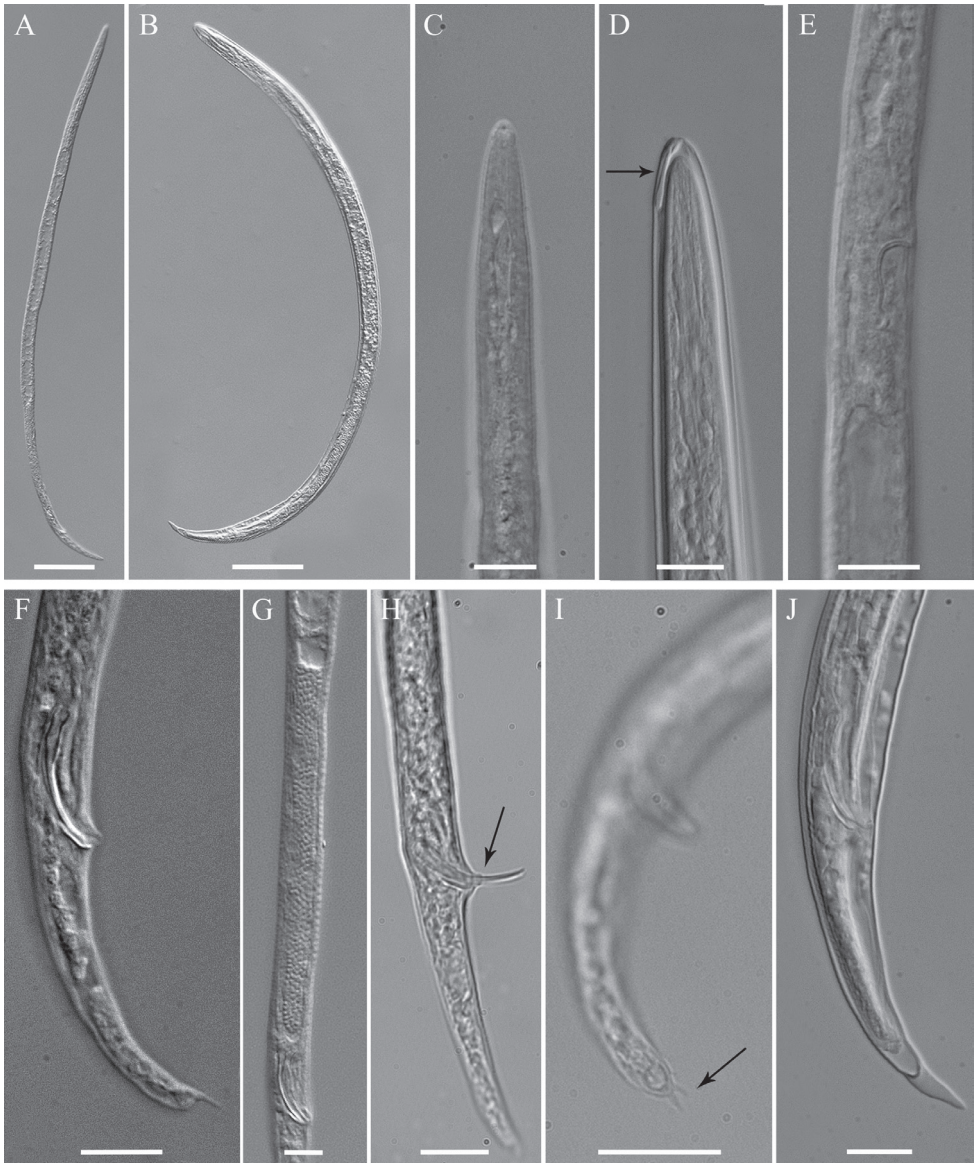


Figure 4. *Meloidoderita salina* sp. n. LM photographs of males. **A** Entire body **B** Male within the second-stage juvenile (J2) cuticle **C** Anterior body **D** Anterior body of male within the old cuticle of J2 (arrow = anterior portion of J2 stylet) **E** S-E duct **F** Posterior region **G** Testis **H** Spicule and cloacal tube (arrow) **I** Tail tip (arrow = mucron) **J** Posterior end of male within the old cuticle of J2. Scale bars: **A, B** = 50 μ m **C–J** = 10 μ m.

tube about 2 μ m long. Bursa-like structure visible by SEM (Fig. 7E). Phasmids small, posterior to cloacal opening. Tail conical, tapering to rounded terminus, marked with one or rarely two mucrones; if two are present, ventral mucro usually smaller; terminal mucro positioned ventrally, length 0.6–3.2 μ m (Fig. 1K–N).

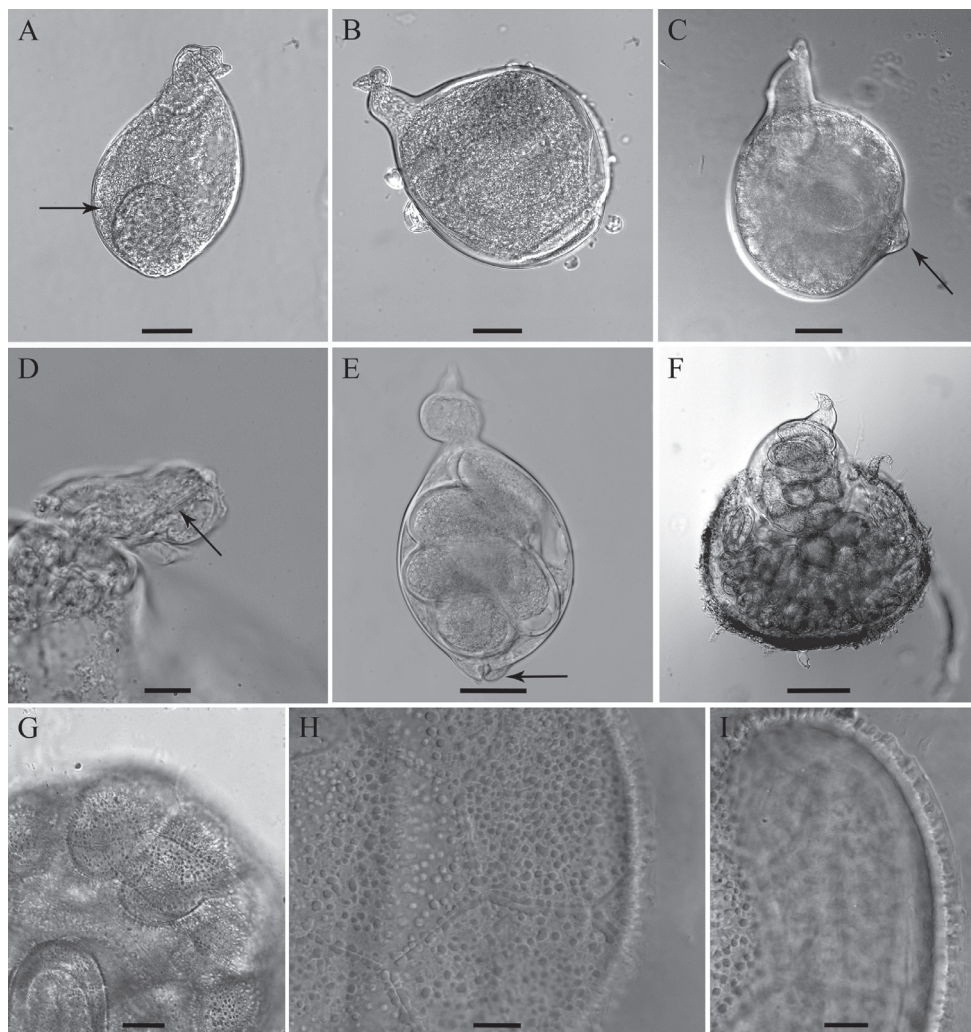


Figure 5. *Meloidoderita salina* sp. n. LM photographs of females. **A, B** Entire body (arrow = uterus) **C** Sub-terminal protruded vulva (arrow) **D** Head region (arrow = stylet) **E** Entire body (arrow = vulva) **F** Female surrounded by egg-mass **G** Cystoid **H, I** Hexagonal beaded pattern. Scale bars: **F**= 100 μm **A-C, E** = 50 μm **D, G-I** = 10 μm .

Second-stage juvenile. Body slender, vermiform, tapering at both ends but more so posteriorly, slightly ventrally curved at tail region; cuticle with fine annulations, annules about 1 μm wide. Lateral field with two visible outer lines in some specimens; in SEM, lateral field starts with three lines about 30 μm from head at neck region, four lines at 20%, and five lines at 33% of body length. Head continuous with body, rounded-conoid with slightly elevated concave oral disc, with distinct but relatively weak cephalic framework, without annules; two open slit-like amphidial apertures adjacent to slightly elevated concave oral disc surrounding the oral aperture, as visible by SEM (Fig. 6A). Lips not visible as distinct structures. Stylet well developed; cone

tapering towards fine point; shaft straight; knobs rounded, prominent, sloping slightly posteriorly, set off from shaft (Fig. 1D). DGO close to stylet base. Metacarpus slightly elongated, with weak valves. S-E pore posterior and adjacent to hemizonid, located at isthmus level; hemizonid 2–3 annules long (Fig. 3D). Isthmus slender, distinct. Pharyngeal glands slightly overlapping intestine ventrolaterally. Deirids small, located just above S-E pore level. Genital primordium located posteriorly at 68–77% of body length. Anus small, weakly developed, obscure by LM, pore-like (Fig. 6E). Phasmids small, difficult to observe by LM, located at about 19 μm from tail tip. Tail conical, slightly curved ventrally, tapering to finely pointed terminus, with finger-like projection. Hyaline tail part clearly delimited anteriorly (Fig. 3G–I).

Cystoid. Irregularly spherical to oval, filled with embryonated and non-embryonated eggs. Colour ranging from light in young cystoids to brown in older cystoid bodies. Body wall thickness 5.3 ± 1.2 (3.2–8.3) μm , containing bead-like outgrowths, displaying a specific sub-cuticular hexagonal beaded pattern (Figs 5, 8).

Egg mass. Females and cystoids usually completely surrounded by a gelatinous matrix (egg-mass) measuring about 316 ± 71.0 μm in length and 275 ± 54.0 μm in diameter (Fig. 5F).

Eggs. Oblong, translucent, egg shell without any visible markings, enveloped in a gelatinous matrix or within a cystoid.

Type host and locality. Collected from rhizosphere and roots of the salt marsh halophytic shrub *Atriplex portulacoides* L. (= *Halimione portulacoides* (L.) Aell.), the most abundant species in ungrazed European salt marshes (Bouchard et al. 1998), growing in cohesive muddy soil of the macro-tidal salt marshes of ‘Le Vivier-sur-Mer’ at 48°36'32"N latitude and 1°47'00"W longitude at Mont-Saint-Michel bay, France.

Type material. Holotype female (slide WT 3591) and paratypes (second-stage juveniles, females, cystoids and males) (slides WT 3592–WT 3595) deposited in the Wageningen Nematode Collection (WaNeCo), Wageningen, The Netherlands. Additional second-stage juvenile, female, cystoid and male paratypes deposited at each of the following collections: Biology Department, Gent University, Gent, Belgium; Central Science Laboratory (CSL), Sand Hutton, York, UK.

Etymology. The specific epithet refers to salty soil (saline environment) and is derived from the Latin word sal or salis meaning “salt”.

Diagnosis and relationships. *Meloidoderita salina* sp. n. is characterized by sedentary mature females having a small swollen body with a clear posterior protuberance, stylet 19.9 (19–22) μm long, stylet cone slightly curved dorsally and longer than shaft, with posteriorly sloping knobs, neck region irregular in shape and twisted, well developed S-E pore, prominent uterus bordered by a thick hyaline wall and filled with eggs. *M. salina* sp. n. is further distinguished by the cystoid having a unique sub-cuticular hexagonal beaded pattern.

Male without stylet, pharyngeal region degenerated, S-E duct prominent, spicules 18.4 (15.3–21.1) μm long, deirids just above S-E pore level, small phasmids posteriorly to cloaca opening and situated at 5.9 (3.2–7.7) μm from tail end, conical tail ending in a rounded terminus with one (rarely two) ventrally positioned mucro.

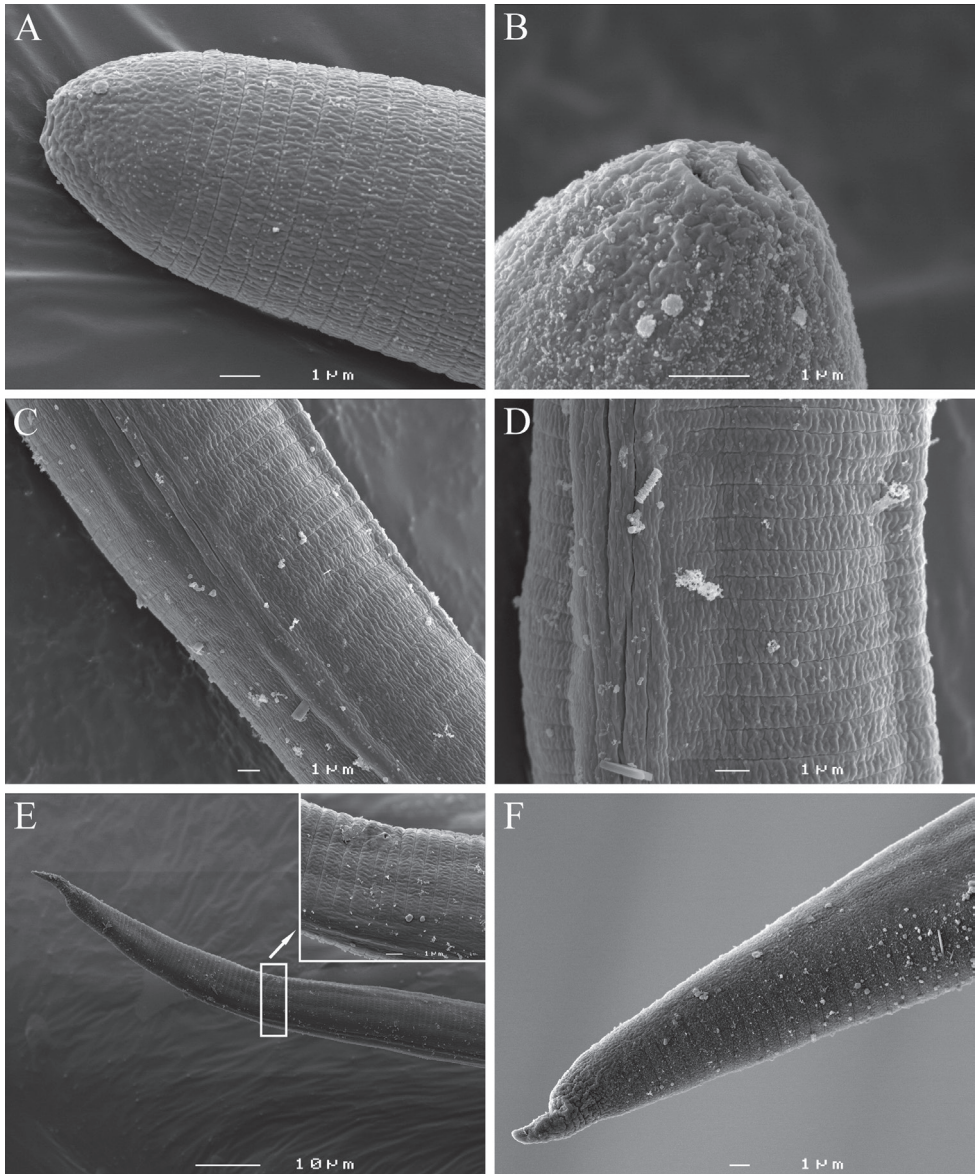


Figure 6. *Meloidoderita salina* sp. n. SEM photographs of second-stage juveniles. **A** Lateral view of head region **B** Amphids **C** Lateral field at 30 μm from anterior end **D** Lateral field at 33% of body length **E** Posterior region (arrow = anus) **F** Lateral view of tail region.

Second-stage juvenile body is 470 (419–496) μm long, with a 16.4 (14.7–17.3) μm long developed stylet, prominent rounded knobs set off from the shaft, hemizonid anterior and adjacent to S-E pore, tail 38.7 (33.9–44.2) μm long tapering to a finely pointed terminus with a finger-like projection.

On the basis of morphology, the female of *M. salina* sp. n. resembles other species of the genus (*M. kirjanovae*, *M. safrica* and *M. polygona*) in the shape of the neck region

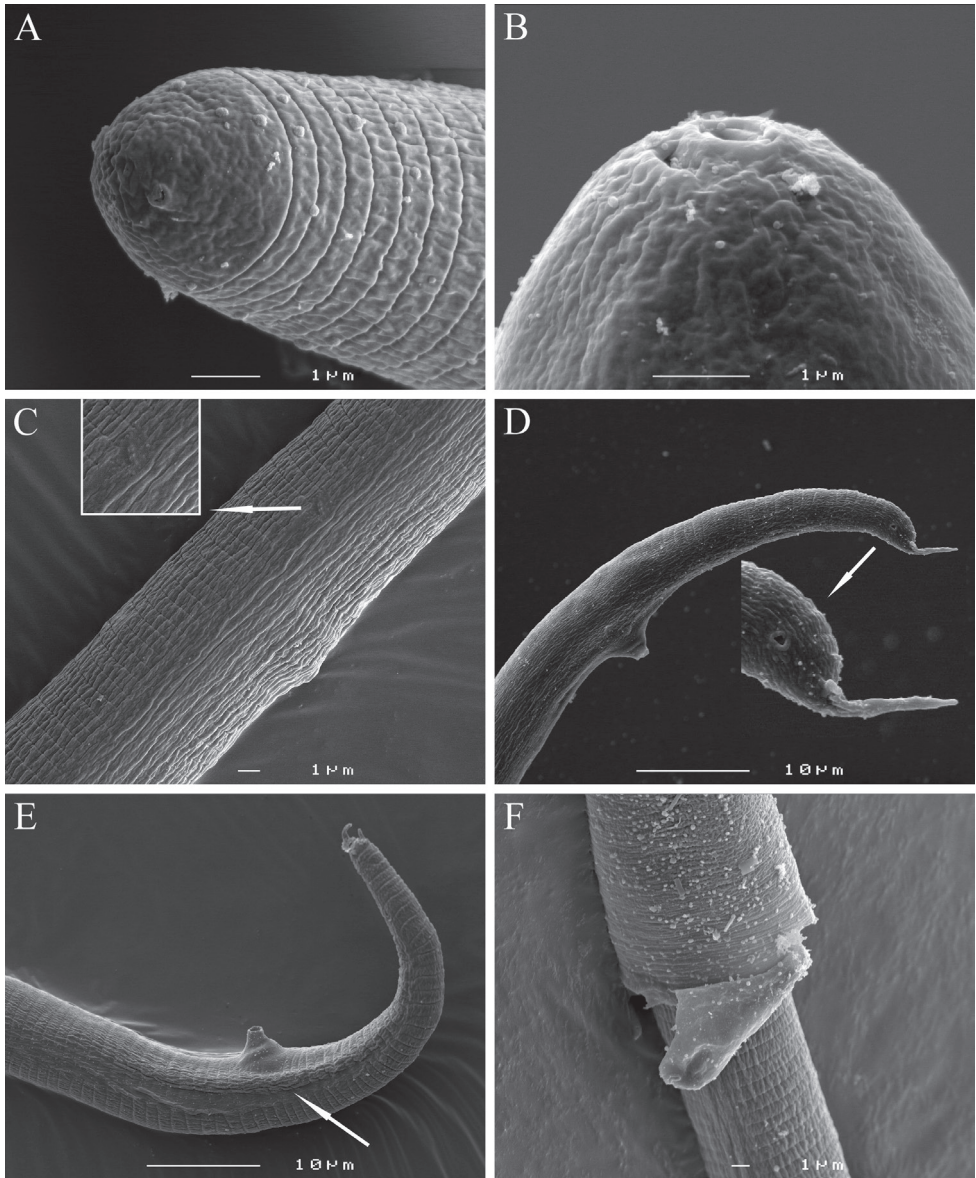


Figure 7. *Meloidoderita salina* sp. n. SEM photographs of male. **A, B** Head region **C** Lateral field at S-E pore level (arrow = deirid) **D** Lateral view of tail region (arrow = phasmid) **E** Tail region (arrow = bursa-like structure) **F** Young male within the second-stage juvenile's old cuticle.

(twisted, irregular and variable in size), the shape of the vulva (protruded), and the shape of the uterus (prominent, with large cells and a thick wall). Males of the four species are similar in lack of a stylet, degenerated pharyngeal region, the shape of the spicules (arcuate), the shape of the cloacal opening (ventrally protruded), and the shape of the tail (slightly curved ventrally, ending in a terminal mucro). Second-stage juveniles

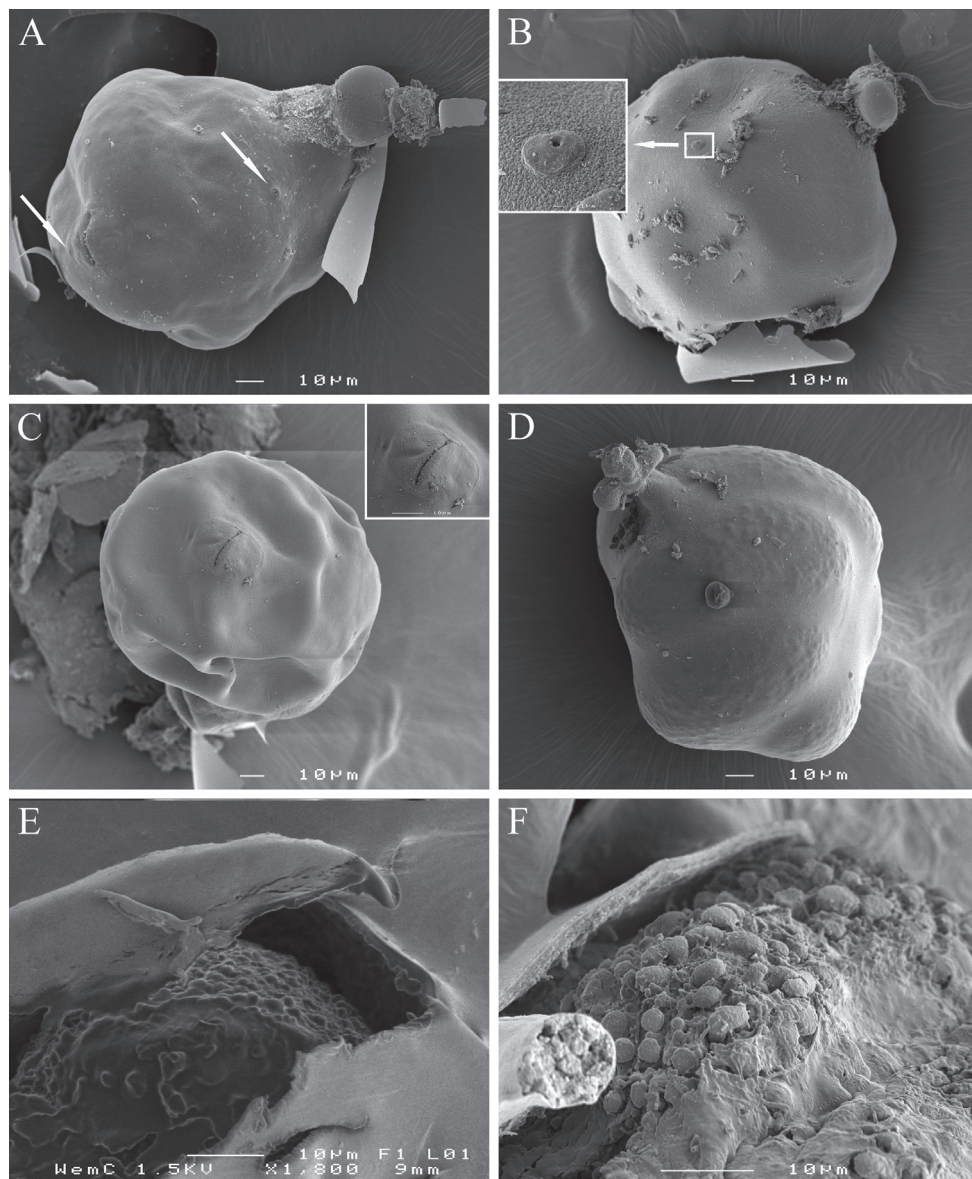


Figure 8. *Meloidoderita salina* sp. n. SEM photographs of female and cystoid. **A** Female body (arrows = S-E pore, anus) **B** Female body (arrow = S-E pore surrounded by cuticular lobes) **C** Vulva and anus **D** Young cystoid with irregular shaped neck region and surface displaying a beaded pattern **E** Sub-cuticular beaded pattern **F** Detail of surface markings in cystoid.

have a continuous head region, weakly sclerotized cephalic framework, similar shape of the tail (conically tapering to a pointed terminus, often with a finger-like terminal mucro), obscure anus, and position of hemizonid (anterior and adjacent to S-E pore).

Meloidoderita salina sp. n. differs from the previously described species by a smaller female body, a longer J2 body, the male with a longer body length and (except *M. kir-*

Table 2. Morphometrics of *Meloidoderita salina* sp. n. All measurements are in μm and in the form: mean \pm SD (range).

Character	Female		Male Paratypes	J2 Paratypes
	Holotype	Paratypes		
n	-	43	21	27
L	286	260 \pm 34 (186–358)	469 \pm 28 (416–522)	471 \pm 19 (419–496)
a	1.8	1.3 \pm 0.2 (0.9–1.8)	40.0 \pm 2.8 (35.0–45.0)	30.4 \pm 1.1 (28.2–32.5)
b	-	-	4.1 \pm 0.4 (3.3–4.8)	3.7 \pm 0.2 (3.4–4.3)
c	-	-	12.9 \pm 1.4 (11.1–15.9)	12.2 \pm 0.9 (9.9–13.9)
c'	-	-	3.9 \pm 0.5 (2.5–4.6)	4.2 \pm 0.2 (4.0–4.3)
Greatest body diam.	152	206 \pm 37 (126–320)	11.8 \pm 0.8 (10.9–13.4)	15.5 \pm 0.5 (14.1–16.0)
Body diam. At excretory pore	-	-	10.4 \pm 1.1 (7.7–12.8)	14.4 \pm 0.5 (13.4–15.4)
Body diam. at anus or cloacal opening	-	-	9.6 \pm 0.9 (7.0–10.9)	9.2 \pm 0.6 (8.3–10.9)
Head region height	-	-	2.2 \pm 0.3 (1.9–2.6)	4.0 \pm 0.2 (3.8–4.5)
Head region diam.	-	-	3.7 \pm 0.4 (3.2–4.5)	7.0 \pm 0.4 (6.4–7.7)
Stylet length	19.2	19.9 \pm 0.7 (19.0–22.0)	-	16.4 \pm 0.5 (14.7–17.3)
Stylet cone	12	11.6 \pm 0.6 (10.5–12.8)	-	-
Stylet shaft	-	-	-	5.1 \pm 0.3 (4.5–5.8)
Stylet knob height	2.6	3.0 \pm 0.4 (2.6–4.0)	-	2.6 \pm 0.2 (1.9–3.2)
Stylet knob width	3.2	3.7 \pm 0.5 (3.2–5.0)	-	3.7 \pm 0.2 (3.2–3.8)
Ant. end to knobs base	-	-	-	18.4 \pm 0.4 (17.3–19.2)
DGO	3.2	3.3 \pm 0.5 (2.5–4.0)	-	2.4 \pm 0.4 (1.9–3.2)
Ant. end to metacarpus	42.9	-	-	65 \pm 1.2 (63–67)
Metacarpus valve length	16.0	15.8 \pm 0.9 (15.0–17.9)	-	-
Metacarpus valve width	8.9	8.5 \pm 0.8 (7.7–10.0)	-	-
Pharynx length	-	-	115 \pm 13 (90–138)	126 \pm 7 (111–144)
Ant. end to excretory pore	74	92 \pm 22.1 (55–125)	82 \pm 5.5 (74–96)	87 \pm 3.0 (77–93)
Ant. end to genital primordium	-	-	-	340 \pm 20 (305–371)

Character	Female		Male Paratypes	J2 Paratypes
	Holotype	Paratypes		
Genital promordium to posterior end	-	-	-	131 ± 12 (105–150)
Genital primordium length	-	-	-	13.0 ± 1.3 (9.6–15.4)
Genital primordium width	-	-	-	6.8 ± 1.0 (4.5–9.0)
Tail length	-	-	36.6 ± 3.8 (27.5–41.6)	38.7 ± 2.5 (33.9–44.2)
Hyaline tail terminus	-	-	-	8.1 ± 1.0 (6.4–9.6)
Phasmid to posterior end	-	-	5.9 ± 1.5 (3.2–7.7)	-
Spicule length	-	-	18.4 ± 1.8 (15.4–21.1)	-
Gubernaculum length	-	-	5.3 ± 0.5 (4.5–6.4)	-
Testis	-	-	98 ± 21.9 (62–137)	-
Vulva slit length	20.4	19.5 ± 1.4 (16.0–22.5)	-	-
Vulva-anus	16.0	17.3 ± 2.6 (13.4–23.0)	-	-
Vulva area length	-	41.0 ± 4.9 (32.0–54)	-	-
Vulva area diam.	-	32.4 ± 3.7 (25.6–40.0)	-	-
Cuticle thickness	3.2	5.0 ± 1.4 (2.5–7.7)	-	-
(Excretory pore/L)*100	-	-	17.5 ± 0.8 (16.2–18.9)	18.6 ± 0.8 (17.1–20.6)
Genital primordium % of body length	-	-	-	72.1 ± 2.6 (68.2–77.2)
Hyaline % of tail length	-	-	-	21.0 ± 3.0 (15.1–26.3)

janovae described by Poghossian (1975)) by the present of a bursa-like structure, and by having a smaller cystoid body with a unique body cuticle surface pattern (displaying a hexagonal beaded pattern *vs* a spine-like structure in *M. kirjanovae*, *M. polygona* and *M. safrica*). It also differs from them in known hosts and the saline habitat.

The new species differs in other characters from *M. kirjanovae* by females having a longer stylet length and a much shorter distance from anus to vulval slit. Male differs from those characterized by Golden & Handoo (1984), and Vovlas et al. (2006) by having longer spicules length (15.4–21.1 *vs* 13.4–16.1, and 13–15 µm, respectively), and by a lateral field with 2–4 *vs* 3 incisures, and 4 incisures in *M. kirjanovae* as re-described by Kirjanova & Poghossian (1973). The second-stage juvenile of *M. salina* sp. n. differs from *M. kirjanovae* characterized by Golden & Handoo (1984), Sidiqi (1985) and Vovlas et al. (2006) in having a longer stylet (14.7–17.3 *vs* 12.9–14,

12–14, and 12–15 μm , respectively), lateral field (with 3–5 *vs* 3 incisures), a shorter hyaline tail with 6.4–9.6 μm long *vs* 8.1–13.3 μm long in those reported by Golden & Handoo (1984), 9–14 μm long in Siddiqi (1985), and 14–15 μm long in those of *M. kirjanovae* re-described by Kirjanova & Poghossian (1973). Second-stage juveniles also differ from those reported by Golden & Handoo (1984) and Vovlas et al. (2006) by a shorter tail (33.9–44.1 *vs* 38–51, and 41–50 μm , respectively).

M. salina sp. n. differs from *M. safrica* by the female having DGO closer to base of stylet (2.5–4.0 *vs* 8.1–22.1 μm), shorter distance from vulval slit to anus (13.4–23.0 *vs* 22.4–24.3 μm), by the male having a shorter testis (62–137 *vs* 190–319 μm), and by the J2 having a longer distance from anterior end to base of pharynx (111–144 *vs* 51.8–75.4 μm).

It differs from *M. polygona* females having a longer stylet (19.0–22.0 *vs* 15.0–17.4 μm), shorter distance from vulval slit to the anus (13.4–23.0 *vs* 32.0–86 μm), and a shorter vulval slit (16.0–22.5 *vs* 22.0–34.0 μm), and by the male without stylet *vs* visible anterior stylet part, a shorter tail (27.5–41.6 *vs* 32.0–56).

The new species is morphologically close related to the genus *Sphaeronema*, particularly to *Sphaeronema alni* Turkina & Chizhov, 1986. According to their observed phylogenetic relationships, they form together a highly supported clade. The absence of a cystoid stage in *Sphaeronema* is the most important differences compared to *Meloidoderita*. Additionally *M. salina* sp. n. differs from *S. alni* by females having a head region continuous with body *vs* head cap set off from neck and the lip region lacking annulations *vs* 2 annuli. The second-stage juveniles has a tail conically tapering to a pointed terminus, often with a finger-like projection, whereas in *S. alni* the tail tapers gradually to a finely rounded terminus.

Molecular characterization and phylogenetic position of *M. salina* sp. n.

The nearly complete rDNA sequence length of SSU rDNA obtained for *M. salina* sp. n. (GenBank FJ969126 and FJ969127) both spanned 1728 bp. A local alignment (1883 aligned position) included 39 nearly full length SSU rDNA sequences from related taxa and representatives of the genus *Ecphyadophora* were selected as outgroup. The SSU rDNA sequence analysis and the gene tree represented by the Bayesian and RAxML trees (Fig. 9) revealed a robust sister relationship between the new species and *Sphaeronema alni* within the Criconematina, and the two combined were positioned at the basal part of the local tree. The phylogenetic position of the suborder Criconematina has been analyzed several times (Subbotin 2005, Vovlas et al. 2006, Holterman et al. 2009, van Megen et al. 2009, Palomares-Ruis et al. 2010). However, for conclusive statements on the positioning of this genus among the Criconematina, more rDNA sequence from representatives of the genus *Meloidoderita* are required. Further phylogenetic analyses using SSU rDNA and more taxon sampling are needed to infer intra-generic relationships and the position of *M. salina* sp. n. within the Criconematina.

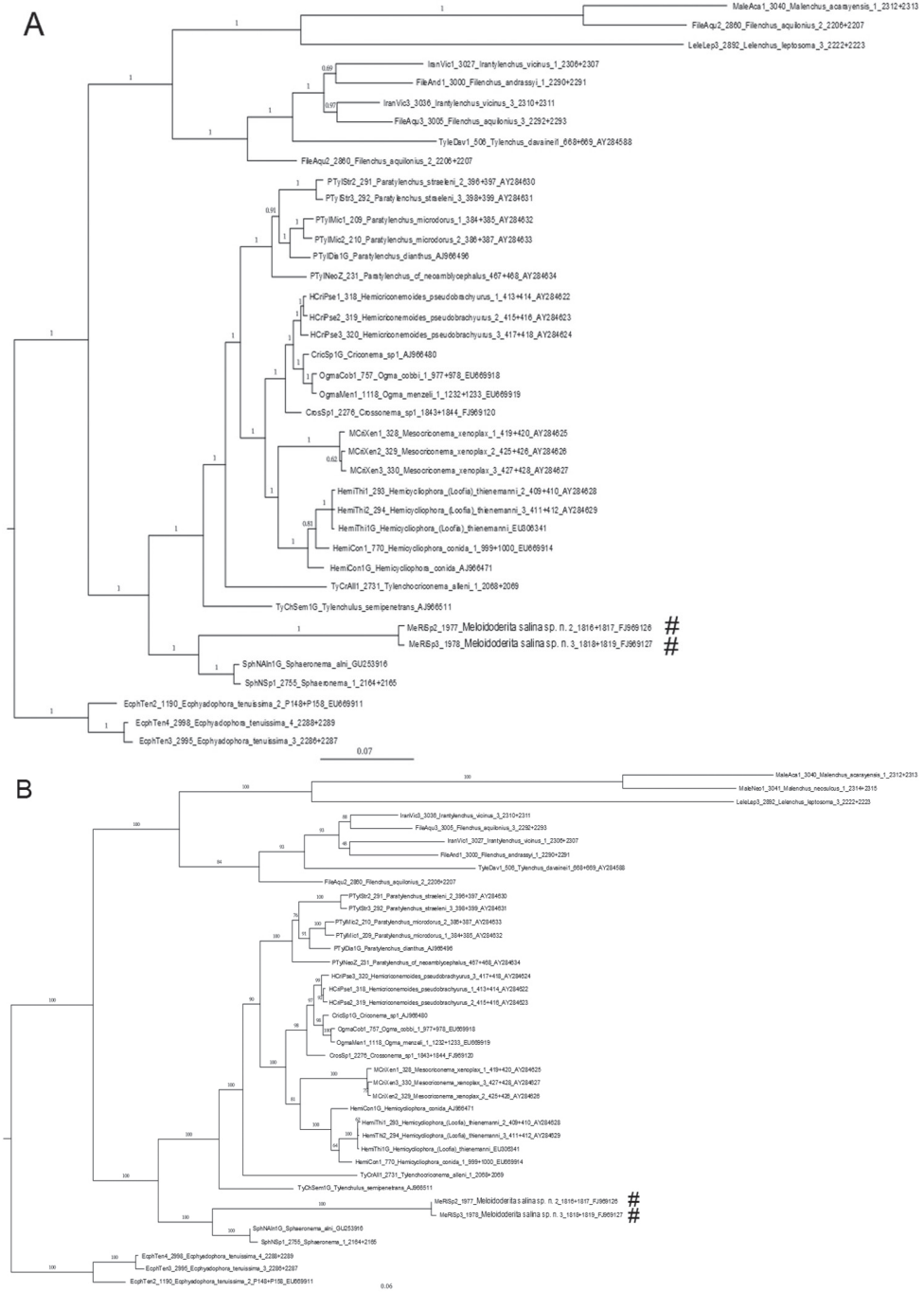


Figure 9. Phylogenetic relationships as inferred from nearly full length of SSU rDNA sequence using GTR + I + G model. Dataset obtained sequences were aligned with the ClustalW algorithm. Numbers near the nodes indicate posterior probabilities in the Bayesian tree (A) and ML tree (B) as implemented in the program BioEdit 7.0.1. Newly generated SSU rDNA sequences are labeled with a (#).

Discussion

M. salina sp. n. was described from a salt marsh area at Mont-Saint-Michel Bay in France, parasitizing the halophyte plant *Atriplex portulacoides*. On average, this area has a salinity of about 34–35g/L which usually increases after submersion by the tides. The presence of a well sclerotized S-E duct is a noticeable character, especially in adult males and matured females of *M. salina* sp. n. which could be correlated with their saline environment and their halophytic host plant. The presence of a strongly sclerotized S-E duct has been also reported in the genus *Halenchus* N.A. Cobb in M.N. Cobb, 1933 as the only known marine Tylenchomorpha. The genus *Halenchus* with three species is exclusively marine parasitic nematode which produces galls on sea algae (Siddiqi, 2000). The “widened and sclerotized excretory duct, exclusively marine, and parasitic on sea algae” are the key characters that have been applied by Siddiqi (2000) in support of the subfamily Halenchinae with its single genus *Halenchus* in Anguinidae Nicoll, 1935 (1926). Considering the sclerotization of S-E duct in both *Meloidoderita salina* sp. n. and *Halenchus*, more physiological studies will probably clarify the role of this structure in these genera.

Spiegel and Cohn (1985) and Vovlas et al. (2006) reported secretion of gelatinous matrix from the vulva slit in *M. kirjanovae*. Vovlas et al. (2006) considered it as a discriminating character for differentiation between “*M. kirjanovae* and that of other tylenchulids such as *Tylenchulus* and *Trophonema* which secrete the gelatinous matrix from the secretory-excretory pore”. They discussed that “this physiological characteristic may confirm the result of phylogenetic analysis” as inferred by Subbotin et al. (2005, 2006) and Sturhan and Geraert (2005), who studied the phylogeny of Tylenchuloidea. Nevertheless, no evidence (e.g. the presence of the vulval glands) was observed to support their opinion regarding formation of the gelatinous matrix. In *M. salina* sp. n. the S-E pore is a well-developed structure connected to a markedly sclerotized duct running posteriorly. It is possible that this prominent structure could be also involved in the production of the gelatinous matrix.

Poghossian (1966) classified *Meloidoderita* under the family Heteroderidae. However, some years later Kirjanova & Poghossian (1973) established the new family Meloidoderitidae to accommodate *Meloidoderita*, and placed it within the superfamily Criconematoidea. Siddiqi (1985, 2000) proposed the new subfamily Meloidoderitinae to accommodate its single genus, namely *Meloidoderita* and the type species *M. kirjanovae*, under the family Sphaeronematidae and the suborder Criconematina on the basis of “the lack of the neck; uterine walls form a protective cystoid body for eggs” (Siddiqi 2000).

Siddiqi (2000) described the genus *Meloidoderita* as mature females with a swollen body, without neck or tail, and males without bursa. Andrassy (2007) also described the *Meloidoderita* adult female as “without neck”. Regardless, Kirjanova and Poghossian (1973), Van den Berg and Spaull (1982), and Golden and Handoo (1984) who reported the presence of an irregularly shaped neck region modified by root tissue and influenced by the cellular root structures. We also observed in *M. salina* sp. n. females a well-defined and twisted neck region (Figs 5, 8).

Siddiqi (2000) described the family Sphaeronematidae as “ectoparasite” in which the juveniles “attack and feed on roots ectoparasitically”. However, it was Siddiqi who wrote in 1985: “*Meloidoderita kirjanovae* is reported to be endoparasitic in *Mentha longifolia* roots, becoming secondarily exposed as the growing female ruptures the root epidermis”. Andrassy (2007) also defined the genus *Meloidoderita* as “ectoparasitic” nematodes. In addition to Cohn and Mordechai (1982) and Andrews et al. (1981) who reported *M. kirjanovae* and *Meloidoderita* sp. respectively as semi-endoparasitic, Vovlas et al. (2006) recently reported, “Severe infections of *M. kirjanovae* were detected on young roots of *Mentha aquatica*. Adult females of *M. kirjanovae* protruded from the surface of all infected root segments occurring individually or in clusters, but did not cause distortion of the entire root diameter. Eggs were laid in a gelatinous matrix regularly protruding from the root surface but cystoid body was often located within the root cortex”. Andrews et al. (1981) reported that juveniles migrated intracellularly through the cortex. Further studies are needed to examine the biology, life-cycle and histopathology of *Meloidoderita* sp. and to clarify their parasitic behavior.

Cohen & Mordechai (1982), while studying the biology of *M. kirjanovae*, observed several males attached to or enveloped by old second-stage juveniles cuticle. They reported that it “could obviously be identified as offspring of the particular female beneath the egg-mass, rather than having migrated from outside. Furthermore, often more than one molting cuticle was present at the same time, indicating that development of juveniles into adult males was a relatively short process and apparently did not necessitate feeding on the host tissues”. These enveloped males in second-stage juveniles cuticle have been reported by Van den Berg and Spaul (1982). In the present study these enveloped males were also described and we did not observe any J3 or J4 male stages.

In the classification scheme proposed by Siddiqi (2000) the suborder Criconematina was described as “phasmids absent”. Andrassy (2007) has also emphasized that “the absence of phasmids” is one of “the main distinguishing characteristics of this suborder”.

Recently Sturhan & Geraert (2005) assessed the presence of phasmids in Tylenchulidae. They observed phasmid-like structures in *Sphaeronema*, *Meloidoderita*, *Tylenchulus*, *Trophotylenchulus*. However, they did not find phasmids in examined species of Criconematidae, *Hemicycliophora* sp., *Paratylenchus*, *Cacopaurus* and *Tylenchocriconema*. Our observation (LM and SEM) confirmed the presence of phasmids in both juveniles and males of *Meloidoderita salina* sp. n.

Phylogenetic studies done by Subbotin (2005, 2006) Vovlas et al. (2006) Palomares-Ruis et al. (2010) and our phylogenetic analysis showed that *Meloidoderita* together with *Sphaeronema* form a clade and are placed as stem taxa at the base of the Criconematina phylogenetic trees. These morphological observations and molecular studies show that the lack of phasmids in other taxa of Criconematina could be considered as an apomorphic character (Sturhan & Geraert, 2005). Hence, within Criconematina those taxa without phasmids could be probably defined by the autapomorphism of the absence of phasmids.

Based on the distribution of the type host *Atriplex portulacoides* in tidal salt marshes in France, it may be expected that *M. salina* sp. n. is more widely distributed in West-

European salt marshes. Sturhan and Geraert (2005) reported an unknown *Meloidoderita* sp. and also an undescribed *Sphaeronema* species isolated from *Atriplex portulacoides*, both from northern Germany. We suggest further sampling along the North Sea coast (France, Belgium, Germany and UK) to characterize the distribution of this species.

Human consumption is currently one of the most important aspects for cultivation of *Atriplex* spp. It has a salty taste when it is eaten raw or cooked, and is presently served in luxury restaurants. *Atriplex portulacoides* has an important role in primary production, and in the food web in salt marsh ecosystems (Bouchard et al. 1998, Neves et al. 2007, 2008). *Atriplex* spp. is also used for other agricultural and environmental aspects such as dune stabilization, land reclamation, or as livestock fodder and ornamental plant (Aronson 1986, Khan et al. 2000, Daoud et al. 2001). The effect of *M. salina* sp. n. on the host plant *Atriplex portulacoides* is unknown and needs to be studied.

It is interesting to report that during this study we found a unique sub-cuticular hexagonal beaded pattern in the cystoids of *M. salina* sp. n. This specific pattern can be seen on the surface of the cystoid and displays symmetrical hexagons (Figs 5H & I, 8D–F). This pattern reported in this study is probably the first to be observed among all the identified species of nematodes so far.

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References

- Andrassy I (2007) Free-living nematodes of Hungary (Nematoda errantia). II. *Pedozoologica Hungarica* 4. Budapest, Hungary, Hungarian Natural History Museum and Systematic Research Group of the Hungarian Academy of Sciences, 496 pp.
- Andrews SW, Krusberg LR, Golden AM (1981) The host range, life-cycle and host-parasite relationships of *Meloidoderita* sp. *Nematologica* 27: 146–159. doi: 10.1163/187529281X00205
- Aronson J (1989) HALOPH a data base of salt tolerant plants of the world. Office of arid land studies, the University of Arizona, Tucson, Arizona-USA.
- Bouchard V, Crech V, Lefeuvre J, Bertru G, Mariotti, A (1998) Fate of plant detritus in a European salt marsh dominated by *Atriplex portulacoides* (L.) Aellen. *Hydrobiologia* 373–374: 75–87. doi: 10.1023/A:1017026430513
- Chitwood BG (1949) Root-knot nematodes, part I. A revision of the genus *Meloidogyne* Goeldi, 1887. *Proceedings of Helminthological Society of Washington* 16: 90–104.
- Chitwood BG (1933) A revised classification of the Nematoda. *The Journal of Parasitology* 20: 131.
- Chitwood BG (1937) A revised classification of the Nematoda. In: Anon. (Ed) *Papers on Helminthology, 30 year jubileum KJ Skrjabin*. Moscow, All-Union Lenin Academy of Agricultural Sciences, 69– 80.

- Cobb NA in Cobb MV (1933) New nemic genera and species, with taxonomic notes. The Journal of Parasitology 20: 81–94. doi: 10.2307/3272166
- Cohn E, Mordechai M (1982) Biology and host-parasite relations of a species of *Meloidoderita* (Nematoda: Criconematoidea). Revue de Nematologie 5: 247–256.
- Coolen WA (1979) Methods for extraction of *Meloidogyne* spp. and other nematodes from roots and soil. In: Lamberti F, Taylor CE (Eds) Root-knot nematodes (*Meloidogyne* species) Systematics, biology and control. New York, NY, USA, Academic Press, 317–329.
- Costil K, Dussart GBJ, Daguzan J (2001) Biodiversity of aquatic gastropods in the Mont St-Michel basin (France) in relation to salinity and drying of habitats. Biodiversity and conservation 10: 1–18. doi: 10.1023/A:1016670708413
- Courtney WD, Polley D, Miller VL (1955) TAF, an improved fixative in nematode technique. Plant Disease Reporter 39: 570–571.
- Daoud S, Harrouni MC, Bengueddour R (2001) Biomass production and ion composition of some halophytes irrigated with different seawater dilutions. First International Conference on Saltwater Intrusion and Costal Aquifers Monitoring, Modeling, and Management. Essaouira, Morocco.
- Detriche S, Susperregui AS, Feunteun E, Lefeuvre JC, Jigorel A, (2011) Interannual (1999–2005) morphodynamic evolution of macro-tidal salt marshes in Mont-Saint-Michel Bay (France). Continental Shelf Research 31: 611–630. doi: 10.1016/j.csr.2010.12.015
- Dubois S, Comtet T, Retiere C, Thiebaut E (2007) Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. Marine Ecology progress Series 346: 243–254. doi: 10.3354/meps07011
- Filipjev IN, Schuurmans Stekhoven JH, Jr (1941) A Manual of Agricultural Helminthology. EJ Brill, Leiden, Netherlands, 878 pp.
- Geraert E (1966) The systematic position of the families Tylenchulidae and Criconematidae. Nematologica 12: 362–368. doi: 10.1163/187529266X00842
- Golden AM (1976) First occurrence and morphology of a *Meloidoderita* species in the United States. Journal of Nematology 8: 286.
- Golden AM, Handoo ZA (1984) Description of *Meloidoderita polygona* n. sp. (Nematoda: Meloidoderitidae) from USA and Observations on *M. kirjanovae* from Israel and USSR. Journal of Nematology 16: 265–282.
- Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.
- Holterman M, Karssen G, van den Elsen S, van Megen H, Bakker J, Helder J (2009) Small sub-unit rDNA-based phylogeny of the Tylenchida sheds light on relationships among some high-impact plant-parasitic nematodes and the evolution of plant feeding. Phytopathology 99: 227–235. doi: 10.1094/PHYTO-99-3-0227
- Karssen G (1996) Description of *Meloidogyne fallax* n. sp. (Nematoda: Heteroderidae), a root-knot nematode from The Netherlands. Fundamental and Applied Nematology 19: 593–599.
- Karssen G, van Aelst A, van der Putten WH (1998) *Meloidogyne duytsi* n. sp. (Nematoda: Heteroderidae), a root-knot nematode from Dutch coastal foredunes. Fundamental and Applied Nematology 21: 299–306.

- Khan MA, Ungar IA, Showalter AM (2000) Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii* var. *stocksii*. *Annals of Botany* 85: 225–232. doi: 10.1006/anbo.1999.1022
- Kirjanova ES, Poghossian EE (1973) A redescription of *Meloidoderita kirjanovae* Poghossian, 1966 (Nematoda; Meloidoderitidae, fam. n.). (In Russian). *Parazitologiya* 7: 280–285.
- Lefeuvre JC, Laffaille P, Feunteun E, Bouchard V, Radureau A (2003) Biodiversity in salt marshes: from patrimonial value to ecosystem functioning. The case study of the Mont-Saint-Michel bay. *Comptes Rendus Biologies* 326: 125–131. doi: 10.1016/S1631-0691(03)00049-0
- Narbaev ZN (1969) [Forms of root nematodes from genera *Heterodera* and *Meloidoderita* in Uzbekistan]. *Mater. Nauchn. Knof., Vses. Obshch. Gel'mintol. AN SSSR, Moscow* 1: 195–200.
- Neves JP, Ferreira LF, Simoes, MP, Gazarini LC (2007) Primary Production and Nutrient Content in Two Salt Marsh Species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Southern Portugal. *Estuaries and Coasts* 30: 459–468. doi: 10.1007/BF02819392
- Neves JP, Ferreira LFP, Vaz MM, Gazarini LC (2008) Gas exchange in the salt marsh species *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L. in Southern Portugal. *Acta Physiologiae Plantarum* 30: 91–97. doi: 10.1007/s11738-007-0094-6
- Nicoll W (1935) Rhabditida. Anguinidae. VI. *Vermes, Zoological Record* 72:105.
- Palomares-Rius JE, Vovlas N, Subbotin SA, Troccoli A, Cantalapiedra-Navarrete C, Liebanas G, Chizhov VN, Landa BB, Castillo P (2010) Molecular and morphological characterization on *Sphaeronema alni* Turkina & Chizhov, 1986 (Nematoda: Sphaeronematidae) from Spain compared with a topotype population from Russia. *Nematology* 12: 649–659. doi: 10.1163/138855410X489338
- Poghossian EE (1966) A new genus and species of nematode of the family Heteroderidae from the Armenian SSR (Nematoda). (Transl. from Russian.) *Dan Reports of the Academy of Sciences of the Armenian SSR* 47: 117–123.
- Poghossian EE (1975) Description of the male of *Meloidoderita kirjanovae* Poghossian, 1966 (Nematoda: Meloidoderitidae). (Transl. from Russian) *Akademi Nauka Armyanskoi SSR* 60: 252–255.
- Posada D, Crandall KA (1998) MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818. doi: 10.1093/bioinformatics/14.9.817
- Raski DJ, Sher SA (1952) *Sphaeronema californicum*, nov. gen. nov. spec., (Criconematidae: Sphaeronematinae, nov. subfam.) an endoparasite of the roots of certain plants. *Proceedings of Helminthological Society of Washington* 19: 77–80.
- Raski DJ, Siddiqui IA (1975) *Tylenchocriconema alleni* n. g., n. sp. from Guatemala (Tylenchocriconematidae n. fam.; Tylenchocricinematoida n. superfam.; Nematoda). *Journal of Nematology* 7: 247–251.
- Raski DJ (1962) Paratylenchidae n. fam. With description of five new species of *Gracilacus* n. g. and an emendation of *Cacopaurus* Thorne, 1943, *Paratylenchus* Micoletzky, 1922 and *Criconematidae* Thorne, 1943. *Proceedings of Helminthological Society of Washington* 29: 189–207.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. doi: 10.1093/bioinformatics/btg180

- Seinhorst JW (1966) Killing nematodes for taxonomic study with hot f.a. 4:1. *Nematologica* 12: 178. doi: 10.1163/187529266X00239
- Siddiqi, MR (1980) Taxonomy of the plant nematode superfamily Hemicycliophoroidea, with a proposal for Criconematina, new suborder. *Revue de Nematologie* 3: 179–199.
- Siddiqi MR (1985) *Meloidoderita kirjanovae*. C.I.H. Descriptions of plant-parasitic nematodes. St. Albans, UK, Commonwealth Agricultural Bureaux, Set 8, No. 113, 2 pp.
- Siddiqi MR (2000) Tylenchida parasites of plants and insects, 2nd edition. Wallingford, UK, CABI Publishing, 833 pp. doi: 10.1079/9780851992020.0000
- Skarbilovich TS (1947) Revision of the systematics of the nematode family Anguilluliniidae Baylis and Daubney, 1926. *Doklady Akademii Nauk, SSR* 57: 303–308.
- Skarbilovich TS (1959) On the structure and systematics of nematodes order Tylenchida Thorne, 1949. *Acta Parasitologica Polonica* 7: 117–132.
- Southey JF (Ed) (1986). Laboratory methods for work with plant and soil nematodes. ADAS, Harpenden laboratory, Harpenden, Herts, UK vii + 202 pp.
- Spiegel Y, Cohn E (1985) Chitin is present in gelatinous matrix of *Meloidogyne*. *Revue de Nematologie* 8: 184–186.
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. doi: 10.1093/bioinformatics/btl446
- Sturhan D, Geraert E (2005) Phasmids in Tylenchulidae (Tylenchida: Criconematoidea). *Nematology* 7: 249–252. doi: 10.1163/1568541054879593
- Subbotin SA, Vovlas N, Crozzoli R, Sturhan D, Lamberti F, Moens, M, Baldwin JG (2005) Phylogeny of Criconematina Siddiqi, 1980 (Nematoda: Tylenchida) based on morphology and D2-D3 expansion segments of the 28S-rRNA gene sequences with application of a secondary structure model. *Nematology* 7: 927–944. doi: 10.1163/156854105776186307
- Subbotin SA, Sturhan D, Chizhov VN, Vovlas N, Baldwin JG (2006) Phylogenetic analysis of Tylenchida Thorne, 1949 as inferred from D2 and D3 expansion fragments of the 28S rRNA gene sequences. *Nematology* 8: 455–474. doi: 10.1163/156854106778493420
- Taylor, AL (1936) The genera and species of the Criconematinae, a sub-family of the Anguilluliniidae (Nematoda). *Transactions of American Microscopical Society* 55: 391–421. doi: 10.2307/3222522
- Thorne G (1949) On the classification of the Tylenchida, new order (Nematoda, Phasmidia). *Proceeding of the Helminthological Society of Washington* 16: 37–73.
- Turkina AY, Chizhov VN (1986) Two new species of nematodes (Tylenchida) parasitizing the grey alder. *Zoologichesky Zhurnal* 65: 620–624.
- Van den Berg E, Spaull VW (1982) A new *Meloidoderita* species on sugar cane in South Africa (Nematoda: Meloidoderitidae). *Phytophylactica* 14: 205–213.
- van Megen H, van den Elsen S, Holterman M, Karssen G, Mooyman P, Bongers T, Holo-vachov O, Bakker J, Helder J (2009) A phylogenetic tree of nematodes based on about 1200 full-length small subunit ribosomal DNA sequences. *Nematology* 11: 927–950. doi: 10.1163/156854109X456862
- Vovlas N, Landa BB, Liebanas G, Handoo ZA, Subbotin SA, Castillo P (2006) Characterization of the cystoid nematode *Meloidoderita kirjanovae* (Nematoda: Sphaeronematidae) from South Italy. *Journal of Nematology* 38: 376–382.
- Wergin WP (1981) Scanning electron microscopic techniques and application for use in nematology. In: Zuckerman BM, Rohde RA (Eds) Plant parasitic nematodes. Vol. 3, London, UK, Academic Press, 175–204.

- Wouts WM, Sher SA (1971) The genera of the Subfamily Heteroderinae (Nematoda: Tylenchoidea) with a description of two new genera. *Journal of Nematology* 3: 129–144.
- Wouts WM (1972) A revision of the family Heteroderidae (Nematoda: Tylenchoidea).
1. The family Heteroderidae and its subfamilies. *Nematologica* 18: 439–446. doi: 10.1163/187529272X00034
- Wouts WM (1973) A revision of the family Heteroderidae (Nematoda: Tylenchoidea). II. The subfamily Meloidoderinae. *Nematologica* 19: 218–235. doi: 10.1163/187529273X00349
- Wuyts J, de Rijk P, van de Peer Y, Pison G, Rousseeuw P, de Wachter R (2000) Comparative analysis of more than 3,000 sequences reveals the existence of two pseudoknots in area V4 of eukaryotic small subunit ribosomal RNA. *Nucleic Acids Research* 28: 4698–4708. doi: 10.1093/nar/28.23.4698

A revised key to the Neotropical cleptoparasitic anthidiine genera (Hymenoptera, Megachilinae) with notes and description of the male of *Rhynostelis* Moure & Urban

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Abstract

Rhynostelis Moure & Urban is a monotypic cleptoparasitic neotropical anthidiine genus currently known from two females. Herein, we describe and illustrate for the first time the male and its genitalia and it is confirmed that *Rhynostelis* parasitizes nests of *Eufriesea*. An identification key to the genera of cleptoparasitic anthidiine from the Neotropical region is also presented.

Keywords

Anthidiini, Brazil, cleptoparasitism, host, taxonomy

Introduction

Cleptoparasitism is a common behavior among species of Anthidiini and presumably evolved multiple times within the tribe (Gonzalez et al. 2012). This condition is currently known in eleven genera worldwide, seven of which occur in the neotropical region, *Austrostelis* Michener & Griswold, 1994; *Dolichostelis* Parker & Bohart, 1979;

Heterostelis Timberlake, 1941; *Hoplostelis* Dominique, 1898; *Rhynostelis* Moure & Urban, 1995; *Stelis* Panzer, 1806; and the recently described *Melostelis* Urban, 2011, which is known from a single female from the Amazon (Michener 2007, Moure & Urban, 2007). In the classification proposed by Michener (2007), *Austrostelis*, *Hoplostelis* and *Stelis* are treated as genera, with remaining taxa treated as subgenera. In this contribution, all taxa are treated at the generic level, according to the classification of Urban and Moure (2007).

Little is known about the biology of these cleptoparasitic bees. In some genera, as *Hoplostelis* and *Dolichostelis*, the female enters the nest of a host and kills its eggs and/or larvae. In other groups, such as *Stelis*, the female lays her eggs on the nest while still open and the young larva has mandibles adapted to kill the host egg or larva (Michener 2007). Cleptoparasitic Anthidiini mostly parasitizes other Anthidiini, but they can also parasitize other Megachilinae genera well as Euglossini (Apinae). *Austrostelis* was recorded by Zanella and Ferreira (2005) from a nest of *Epanthidium tigrinum* (Schrottky, 1905); *Hoplostelis* is known to parasitize the orchid bee *Euglossa cordata* (Linnaeus, 1758) (Bennett 1966); *Dolichostelis* is cleptoparasitic in nests of *Megachile* Latreille, 1802, probably of the subgenus *M.* (*Chelostomoides*) Robertson, 1901 (Parker and Bohart 1979); *Stelis* parasitizes several genera of Megachilinae: *Anthidiellum* Cockerell, 1904, *Anthidium* Fabricius, 1804, *Ashmeadiella* Cockerell, 1897, *Chelostoma* Latreille, 1809, *Heriades* Spinola, 1808, *Hoplitis* Klug, 1807, *Megachile* Latreille, 1802 and *Osmia* Panzer, 1806 (Michener 2007); *Heterostelis* is known to parasitize species of *Trachusa* Panzer, 1804 (Thorp 1966 and Michener 2007).

Rhynostelis consists of a single species, *R. multiplicata* (Smith, 1879), which is known from two female specimens collected on the State of Amazonas, Brazil. Herein, we present an updated diagnosis of *Rhynostelis*, describe and illustrate the male of *R. multiplicata* and, based on two specimens collected from a trap-nest, we record the orchid bee *Eufriesea laniventris* (Ducke, 1902) as its host. A key to all neotropical cleptoparasitic anthidiine genera is also provide.

Material and methods

Morphological terminology follows Michener (2007) and that for mandibles Michener and Fraser (1978). Measurements are given in millimeters and were taken using an ocular micrometer on a stereoscopic microscope Leica MZ125. Total length was measured in lateral view, from the head to the apex of metasoma; length of forewing was measured at the anterior margin, from the costal sclerite to the wing apex. The illustrations were obtained with a Leica DFC 500 digital camera attached to the stereoscopic microscope Leica MZ 16 and combined with the software AUTO-MONTAGE PRO. All material used in this study is deposited in the Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil (DZUP).

Taxonomy

Rhynostelis Moure & Urban, 1995

<http://species-id.net/wiki/Rhynostelis>

Figs 1–7, 15, 17

Rhynostelis Moure & Urban, 1995: 297.

Hoplostelis (*Rhynostelis*) Michener, 2007: 518.

Male description. Diagnosis. Mandibles with only apical tooth elongated, upper distal angle rounded (Fig. 2); clypeus protuberant, with a basal tubercle at middle; supra-clypeal area protuberant (Fig. 1); scutum and scutellum bigibbous; axillae and dorso-ventral area of mesepisternum gibbous (Figs 3, 5); distal tergum short and sinuous at middle (Fig. 6); sternum sixth with laminar rounded, lateral projections.

Description. Mandibles with distal margin almost straight, only with apical tooth elongated; upper distal angle slightly marked, condylar carina elevated and strongly laminated, slightly wider at base (Fig. 2). Clypeus protuberant with median basal tubercle elongated, extended in low irregular carina in basal half, apex depressed without projections, not exceeding labrum, covered by many long hairs. Labrum weakly bilobed near clypeal base. Supraclypeal area with wide, somewhat flat median carina; frons with long, well marked carina. Juxtantennal carina laminated, ventrally short, not arising at base of antennal sockets and extending upward (Fig. 1). Scutum and scutellum bigibbous; axillae gibbous; base of propodeum with irregular foveae (Fig. 3, 5). Omaulus lamellate, almost extending ventrally; mesepisternum with gibbous area near mesocoxal cavity. Fore and middle tibiae with midapical spine on outer surface (Fig. 15); arolia present. Fifth and sixth terga with transverse, median low carina; sixth tergum with apical projection at middle; distal tergum slightly emarginated at apex (Fig. 6). Second sternum enlarged, with apex weakly emarginated at middle, with long pilosity at apex; third to fifth sterna with dense apical pilosity, laterally with longer and curved hairs; sixth sternum with distal margin almost straight, with large, angled, laminar, lateral projections subapically.

Genitalia. Gonostylus slightly longer than penis valves; apical half with dense and long pilosity on inner margin; apex rounded, laterally slightly convex. Gonobase incomplete dorsally, only visible laterally (Fig. 7).

Comments. Moure and Urban (1995) mentioned that the base of the propodeum in *Rhynostelis* lacks foveae. Michener (2007), also pointed out this feature as one of the characteristics that separates *Rhynostelis* from *Hoplostelis*. However, a re-examination of *Rhynostelis* specimens revealed the presence of irregular fovea in the base of its propodeum, which are difficult to see due the shiny yellow integument. Michener (2007) considered *Rhynostelis* as a subgenus of *Hoplostelis* and in his key, the male agrees with the female by the characters he listed, except for the absence of foveae in the base of propodeum, as commented above. The male of *Hoplostelis* further differs from *Rhynostelis* by the following combination of characters: three

strong mandibular teeth and two basal depressions near the articulation of the head; omaulus carinate only in the dorsal one-half or one-third; sixth sternum with narrow lateral projections and without gibbous mesosoma.

***Rhynostelis multiplicata* (Smith, 1879)**

http://species-id.net/wiki/Rhynostelis_multiplicata

Figs 1–7, 15, 17

Anthidium multiplicatum Smith, 1879: 87.

Rhynostelis multiplicata; Moure and Urban 1995: 298.

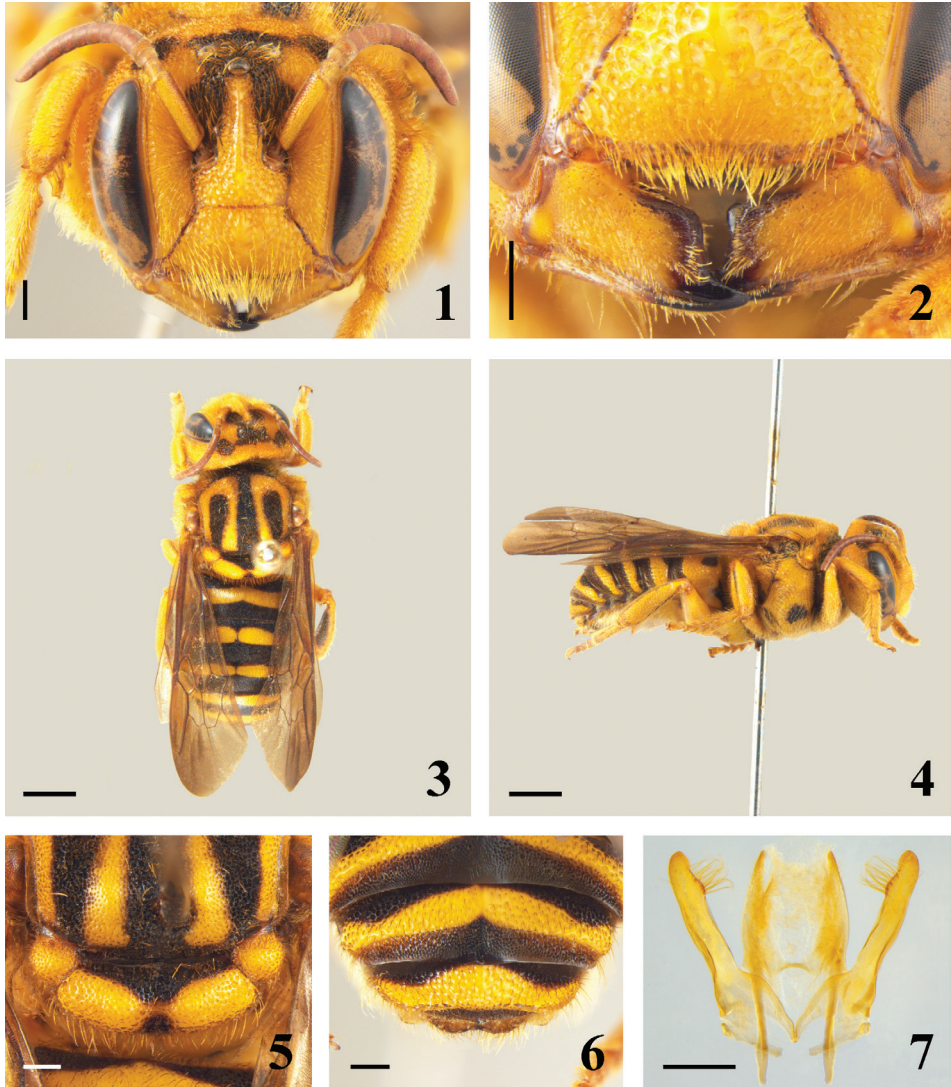
Hoplostelis (Rhynostelis) multiplicata; Michener 2007: 518.

Diagnosis. Integument black, with wide yellow areas in both sexes. Scutum with a large, reverse U-shaped macula; scutellum almost totally yellow; axillae yellow and all terga with yellow bands (Figs 3, 4). Male and female with protuberant clypeus.

Male description. Approximate body length 13.29; forewing length 10.45; head width 4.02; head length 3.67; eye length 2.55. Head integument yellow except: distal margin of mandible and apical tooth black; labrum blackened; frons black, bands above superior margin of antennal sockets extending to vertex, including ocelli and finely attached with black spot above compound eyes. Antennae with ventral face of pedicel darkish yellow, remaining segments light brown; dorsal face with scape and pedicel light brown and flagellum amber (Figs 1, 2). Pronotal lobe yellow; scutum black with large reverse U-shaped yellow maculae; scutellum with on yellow gibbous area joined medially by fine yellow band; axillae yellow; metanotum brown and propodeum yellow. Mesepisternum and metepisternum yellow; mesepisternum with discal black spot, metepisternum with ventral area black. Tegula amber and wing membrane brown. Legs almost totally yellow; middle tibiae with internal darkish area and hind tibiae with large internal darkish area (Figs 3, 4, 5). Terga black; basal tergum with yellow band slightly angled at middle; second to fourth with large yellow band, slightly narrower and slightly interrupted medially; fifth tergum with yellow band emarginated at middle on posterior margin; sixth tergum with yellow band, wider medially; distal tergum with subapical yellow band and blackish margin (Fig. 6). Two basal sterna yellow, with large translucent margin; third to fifth yellow with black infumated area on apical half; sixth sternum with large median black apical spot.

Pubescence. Light yellow with predominantly short hairs (less than ocellus diameter). Pilosity longer and denser among ocelli, above antennal sockets and clypeus apex. Hairs of mesepisternum little longer than mesoscutum, curved on scutellum and propodeum. Fore leg with coxa and trochanter covered by dense pilosity. Third to fifth sterna with apical dense and long slight curved hairs.

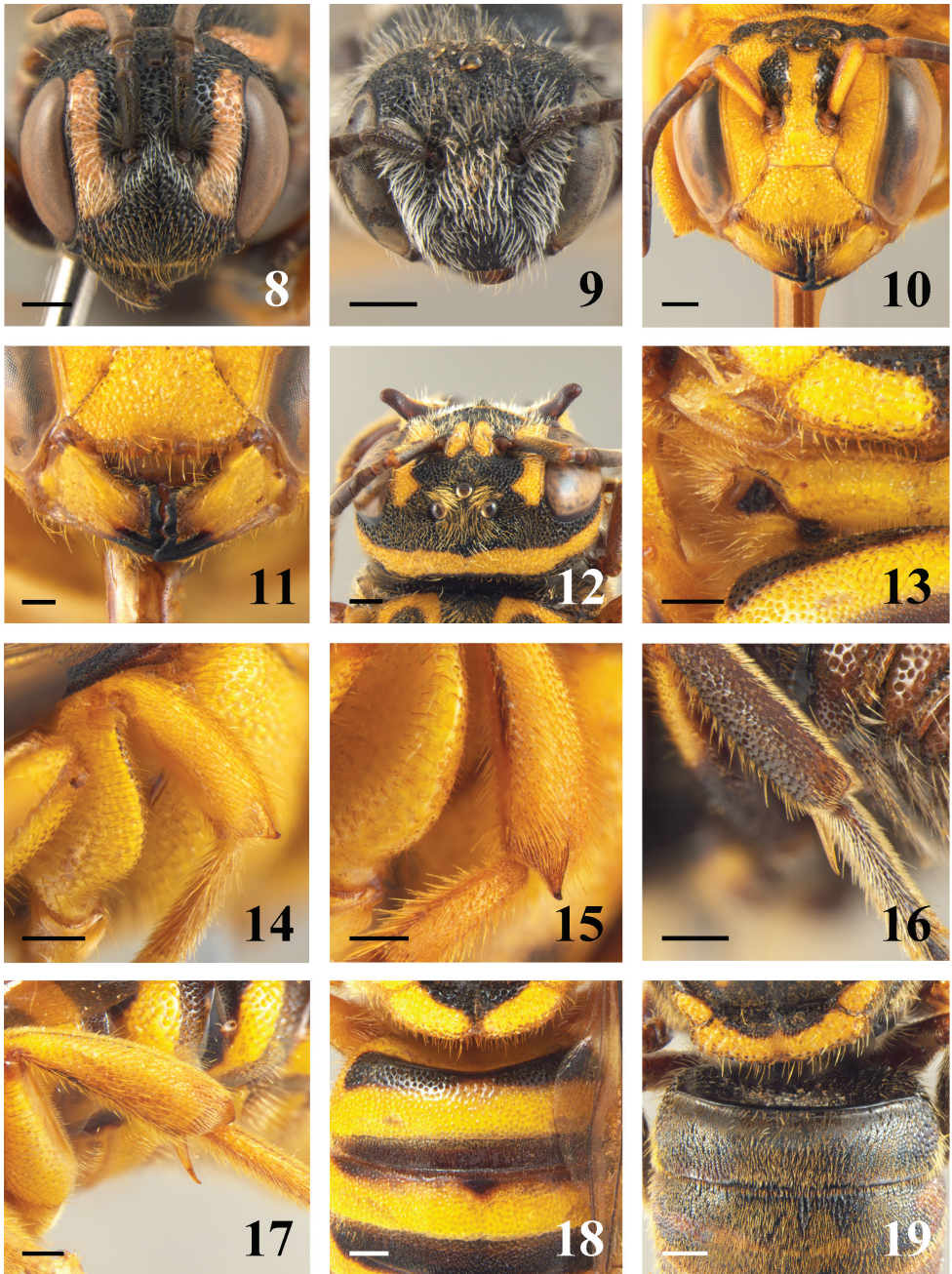
Sculpturing. Head finely punctate with sparser punctures on clypeal protuberance and at supraclypeal area. Mandibles with punctures smaller than that of head. Mesoscutum with integument microreticulated, punctures deeper than head. Gibbous area



Figures 1–7. Male of *Rhynostelis multiplicata*. **1** head in frontal view **2** detail of mandibles **3** dorsal view **4** lateral view **5** detail of scutellum **6** apex of metasoma **7** male genitalia in dorsal view. Scale line = 0.5 mm (Figures 1–2, 5–7). Scale line = 2.0 mm (Figures 3–4).

of mesepisternum with larger and sparser punctures; distance between punctures at least half width a puncture diameter. Punctures of terga fine and shallow; punctures on yellow bands larger and sparser than those on black areas.

Material examined. BRAZIL, *Pará*, Belém: one male, “IPEAN [Instituto de Pesquisas e Experimentação Agropecuária do Norte, Belém] / 105-2 / EU” (DZUP); and one female “IPEAN / 105-1/ EU” (DZUP). *Amazonas*, Manaus: one female “Proj. DBFF.WWF/ Manaus-AM/ Brasil 04/11/89 / M. B. V. Garcia (DZUP).



Figures 8–19. 8–10 head in frontal view of female. 8 *Dolichostelis louisae* 9 *Stelis lateralis* 10 *Melostelis amazonensis* 11 details of mandibles of *Melostelis amazonensis* 12 vertex of *Hoplostelis bilineolata* 13 fovea of propodeum of *Melostelis amazonensis* 14–15 middle tibia of female 14 *Melostelis amazonensis* 15 *Rhynostelis multiplicata* 16–17 hind tibia of female 16 *Hoplostelis bilineolata* 17 *Rhynostelis multiplicata* 18–19 details of first tergum of metasoma of female 18 *Melostelis amazonensis* 19 *Hoplostelis bilineolata*. Scale line = 0.5 mm (Figures 8–19).

Remarks on the female from Pará. Approximate body length 16.13; forewing length 12.38; head width 4.90; length head 4.16, eye length 3.18. Integument predominantly yellow. The female differs from the male as follows: black maculae on vertex and frons larger than in male. All terga with yellow bands; basal tergum with complete band; second and third terga with bands slightly interrupted at middle; fourth tergum with band interrupted anteriorly only at middle, fifth tergum with band interrupted only posteriorly at middle; sixth tergum with subapical band and blackish margin. All sterna yellow; distal sternum with medioapical spot and black margin. The female collected in Manaus is a little smaller than the female from Belém and the integument of the head is darker and with irregular macula. Such differences in color might be caused by some chemical product used during collection or preservation.

Host records. Urban & Moure (1995) commented that one female of *R. multiplicata* emerged from a test-tube placed on a termite nest where an orchid bee was previously seen (possible *Eufriesea pulchra* (Smith, 1854)). However, the record of the host was never confirmed. The specimens from Belém studied herein emerged from one nest of *Eufriesea laniventris* (Ducke, 1902), (DZUP), according the identification of Dr. Gabriel A. R. Melo. Thus, the cleptoparasitism of *R. multiplicata* on orchid bees of the genus *Eufriesea* is confirmed.

Identification key to the neotropical cleptoparasitic genera of Anthidiini

- 1 Juxtantennal carina absent; middle tibia with two widely separated apical spines.....**2**
- Juxtantennal carina present; middle tibia with one apical spine, or subapical carina.....**4**
- 2(1) Hind tibia with subapical spine near posterior margin, sometimes completely hidden by dense hairs; hind basitarsus with carina along inner dorsal angle, separated from margin by a longitudinal depression..... *Heterostelis*
- Hind tibia without subapical spine; hind basitarsus without carina.....**3**
- 3(1) Anterior surface of mesepisternum with punctures sparser than on lateral surface; omaulus carinate; interalveolar area short and protuberant (Fig. 8). Male: third sternum with pair of translucent lobes; fourth sternum with two median projections *Dolichostelis*
- Mesepisternum uniformly punctate; omaular carina absent; interalveolar area flat (Fig. 9). Male: third sternum not modified and fourth sternum with a setose medioapical projection..... *Stelis*
- 4(1) Body relatively elongated; small-sized species. Integument coarsely punctate; pilosity between ocelli not differentiated from remaining areas of head..... *Austrostelis*
- Body robust, metasoma almost globose, large species (Fig. 3, 4). Integument with fine to moderate-sized punctures; pilosity among ocelli longer than in remaining areas of head (Fig. 12)..... **5**

- 5(4) Scutellum laterally with laminate distal margin, with punctures at least twice as larger as those on scutum; hind tibia without flat apical projection on outer surface (Fig. 16); basal tergum with transverse carina (Fig. 19) ***Hoplostelis***
- Scutellum without laminate projection, with punctures about as large as those on scutum; hind tibia with flat apical projection on outer surface (more developed in females) (Fig. 17); basal tergum without carina (Fig. 18) **6**
- 6(5) Frons not carinate; clypeus without basal tubercle and with two apical projections (Fig. 10). Mesosoma not gibbous; postspiracular fovea drop-shaped, microreticulated, coarsely punctuate and with irregular alveoli (Fig. 13). Female: mandible without bifurcated condylar carina and without protuberance near anterior articulation (Fig. 11); fore and middle tibiae with apical spine as long as half width of median ocellus diameter (Fig. 14) ... ***Melostelis***
- Frons carinate; clypeus with basomedian tubercle and without apical projections (Fig. 1). Scutum and scutellum bigibbous (Fig. 5); postspiracular fovea rectangular and with regular alveoli. Female: mandible with bifurcated condylar carina elevated and with protuberance near anterior articulation; fore and middle tibiae with apical spine as long as a diameter of median ocellus (Fig. 15)..... ***Rhynostelis***

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References

- Bennett F D (1966) Notes on the biology of *Stelis (Odontostelis) bilineolata* (Spinola), a parasite of *Euglossa cordata* (Linnaeus). Journal of the New York Entomological Society 74: 72–79.
- Gonzalez VH, Griswold T, Praz CJ and Danforth BN (2012) Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. Systematic Entomology 37: 261–286. doi: /10.1111/j.1365-3113.2012.00620.x
- Michener CD (2007) The Bees of the World [2nd Edition]. Johns Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., + 20 pls.
- Michener CD, Fraser A (1978) A comparative anatomical study of mandibular structure in bees. The University of Kansas Science Bulletin 51: 463–482.

- Moure JS, Urban, D (1995) [1994] *Rhynostelis*, gen. n. e notas sobre *Hoplostelis* Dominique (Hymenoptera, Apoidea, Megachilidae). *Revista Brasileira de Zoologia* 11: 297–302. doi: 10.1590/S0101-81751994000200014
- Parker FD, Bohart G E (1979) *Dolichostelis*, a new genus of parasitic bees. *Journal of the Kansas Entomological Society* 52: 138–153.
- Thorp RW (1966) A synopsis of the genus *Heterostelis* Timberlake. *Journal of the Kansas Entomological Society* 39: 131–146.
- Urban D, Moure JS (2007) Anthidini. In: Moure JS, Urban D, Melo GAR (Eds) *Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region*. Curitiba: Sociedade Brasileira de Entomologia, 875–913. Also available at: www.moure.cria.org.br/catalogue
- Urban D (2011) *Melostelis* gen. nov., espécies novas e notas complementares sobre Anthidiini (Hymenoptera, Apidae). *Revista Brasileira de Entomologia* 55(2): 219–225. doi: 10.1590/S0085-56262011005000013
- Zanella FCV, Ferreira AG (2005) Registro de Hospedeiro de *Austrostelis* Michener & Griswold (Hymenoptera: Megachilidae) e de sua Ocorrência na Caatinga. *Neotropical Entomology* 34(5): 857–858. doi: 10.1590/S1519-566X2005000500022

Species of the genus *Lamachus* Förster (Hymenoptera, Ichneumonidae) parasitizing diprionid sawflies (Hymenoptera, Diprionidae) with descriptions of two new species and a key to Chinese species

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Abstract

Four species of the genus *Lamachus* Förster 1869 belonging to the tribe Mesoleiini of the subfamily Ctenopelmatinae (Hymenoptera, Ichneumonidae) are reported from China. Two of them are new to science, *L. nigrus* Li, Sheng & Sun, **sp. n.** and *L. rufiabdominalis* Li, Sheng & Sun, **sp. n.** were reared from *Neodiprion huizeensis* Xiao & Zhou, in Guizhou Province of the Oriental part of China. The biology of *L. rufiabdominalis* is described. A key to the species of *Lamachus* known from China is provided.

Keywords

Ctenopelmatinae, *Lamachus*, new species, parasitoid, Diprionidae, *Neodiprion huizeensis*, *Diprion jingyuanensis*, biology

Introduction

Lamachus Förster 1869, belonging to the subfamily Ctenopelmatinae of Ichneumonidae (Hymenoptera), comprises 24 described species (Yu et al. 2012), of which four are known from the Eastern Palearctic, 14 from the Western Palearctic and six from the Nearctic. Hitherto, most hosts of this genus are sawflies of the families Diprionidae and Tenthredinidae, including *Diprion* Schrank, *Neodiprion* Rohwer, *Gilpinia* Benson and *Pristiphora* Latreille (Cushman 1937, 1939; Finlayson and Finlayson 1958; Meyer 1936, Morris et al. 1937; Price and Tripp 1972; Townes 1970; Uchida 1955; Yu et al. 1997).

Two species of *Lamachus* Förster have been known in China (Sheng and Sun 2007; Li et al. 2012): *Lamachus gilpiniae* Uchida, parasitizing *Diprion jingyuanensis* Xiao & Zhang (Hymenoptera, Diprionidae) (Li et al. 2012), found in Shanxi Province, China, which is a parasitoid of *Gilpinia tohi* Takeuchi (Hymenoptera, Diprionidae) in Japan (Uchida 1955); and *L. sheni* Sheng & Sun 2007, from Henan Province, China.

In the last four years the first author has been researching web-spinning and leaf-rolling sawflies in China, and has reared large numbers of ichneumonids. New discoveries will be reported successively. In this article, two new species of *Lamachus* are reported.

Materials and methods

Materials used were collected using the following methods.

Rearing parasitoids. Cocoons of sawflies were collected under the naturally heavily infested trees in Weining County (26°54'N, 104°13'E, elevation 2000 to 2200 m), Guizhou Province, and stored individually in glass tubes (100 mm long and 15 mm in diameter) with a piece of filter paper dipped in distilled water (to prevent desiccation), plugged with absorbent cotton, and maintained in the laboratory at room temperature. The emerged insects were collected daily.

Direct collection. Specimens were collected using entomological sweep nets in the forests, where the trees were naturally heavily infested by sawflies.

Images of whole insects were taken using a CANON Power Shot A650 IS. Other images were taken using a Cool SNAP 3CCD attached to a Zeiss Discovery V8 Stereomicroscope and captured with QCapture Pro version 5.1. Morphological terminology is based on Gauld (1991). Wing vein nomenclature is based on Ross (1936) and the terminology of Mason (1986, 1990).

Type specimens are deposited in the Insect Museum, General Station of Forest Pest Management (GSFPM), State Forestry Administration, P. R. China.

Descriptions

Genus *Lamachus* Förster, 1869
<http://species-id.net/wiki/Lamachus>

Lamachus Förster, 1869. Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens, 25(1868): 206. Type species: *Tryphon lophyrum* Hartig.

Diagnosis. Clypeus small, almost flat or weakly convex. Upper tooth of mandible slightly longer than or equal to lower tooth. Notaulus absent, or short and weak. Propodeal carinae weak or absent. Areolet present. Fore wing with vein 1cu-a distal of 1/M by about 0.25 times length of 1cu-a. Hind wing vein 1-cu longer than cu-a. Glymma present. Median dorsal carina of first tergum weak; dorsolateral carina complete. Setae of female genital plate slanted backward.

Key to species of *Lamachus* known in China

- 1 Median longitudinal carina of propodeum distinct. Median dorsal carina of first tergum distinct. Upper tooth of mandible as long as lower tooth..... *L. gilpiniae* Uchida
- Median longitudinal carina of propodeum absent (Figs 4, 11). Median dorsal carina of first tergum incomplete or absent. Upper tooth of mandible slightly longer than lower tooth **2**
- 2 Third to fifth terga red (Fig. 7). First tergum 2.5 times as long as apical width. Second tergum 0.8 times as long as apical width (Fig. 12). Antenna with 46–48 flagellomeres *L. rufiabdominalis* Li, Sheng & Sun, sp. n.
- All terga black. First tergum 1.4 or 2.1 times as long as apical width. Second tergum 0.6 or 1.1 times as long as apical width. Antenna with 38(39) to 40 flagellomeres **3**
- 3 First tergum 2.1 times as long as apical width, median dorsal carina absent. Second tergum 1.1 times as long as apical width. Scutellum and postscutellum black. Basal 0.7 of hind tibia white *L. sheni* Sheng & Sun
- First tergum 1.4 times as long as apical width, basal portion of median dorsal carina present. Second tergum 0.6 times as long as apical width (Fig. 6). Lateral and apical portions of scutellum and entire postscutellum yellow. Hind tibia black *L. nigrus* Li, Sheng & Sun, sp. n.

***Lamachus nigrus* Li, Sheng & Sun, sp. n.**

urn:lsid:zoobank.org:act:02E9E94E-0D92-43FB-8A87-64F6138A2687

http://species-id.net/wiki/Lamachus_nigrus

Figures 1–6

Etymology. The specific name is derived from the body being entirely black.

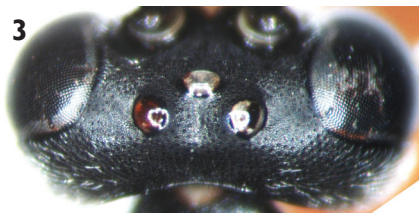
Types. *Holotype*, female, CHINA: Weining, Guizhou Province, 13 March 2012, leg. Tao Li, Mao-Ling Sheng. *Paratypes*: 7 females and 5 males, CHINA: Weining, Guizhou Province, 8 to 24 March 2012, leg. Tao Li, Mao-Ling Sheng.

Diagnosis. Malar space 0.4 to 0.5 times as long as basal width of mandible. Postocellar line approximately 1.5 to 1.6 times as long as ocular-ocellar line. Antenna with 39 to 40 flagellomeres. Fore wing with vein 1cu-a distal of 1/M by about 0.5 times length of 1cu-a. Vein 2-Cu approximately 1.5 times as long as 2cu-a. Hind wing vein 1-cu about 1.5 times as long as cu-a. First tergum 1.4 times as long as apical width. Abdomen entirely black.

Description. Female (Fig. 1). Body length 8.0 to 10.0 mm. Fore wing length 7.5 to 9.0 mm.

Head. Inner eye orbits weakly concave at level of antennal insertions. Face (Fig. 2) 1.6 to 1.7 times as wide as long, with dense punctures, upper center margin with weak longitudinal wrinkles. Clypeus approximately flat and smooth, with sparse setae, 2.0 times as wide as long; central part of apical margin distinctly concave. Mandible smooth, with weak punctures, upper tooth slightly longer than lower tooth. Malar space with fine leathery texture, 0.4 to 0.5 times as long as basal width of mandible. Gena with evenly dense punctures. Posterior part of vertex (Fig. 3) with texture as that of gena. Ocellar triangle with fine leathery texture, with weak median longitudinal groove. Postocellar line about 1.5 to 1.6 times as long as ocular-ocellar line. Frons approximately flat, with texture as that of face, lower portion concave at antennal areas. Antenna with 39 to 40 flagellomeres, ratio of length from first to fifth flagellomeres: 9.0:5.0:4.5:4.5:4.0. Occipital carina complete.

Mesosoma. Anterior portion of pronotum with fine leathery texture and dense punctures; median portion with short transverse wrinkles; upper posterior portion with dense punctures. Mesoscutum evenly convex, with texture as that of upper posterior portion of pronotum. Notaulus evident on anterior half of mesoscutum. Scutoscutellar groove wide, with weak longitudinal wrinkles. Scutellum evenly convex, with sparse punctures, larger than those of mesoscutum. Postscutellum transverse, punctures denser than on scutellum. Mesopleuron (Fig. 5) evenly convex, with punctures as scutellum. Epicnemial carina weak, 0.5 times as long as mesopleuron. Speculum with fine leathery texture. Metapleuron convex, with dense punctures and fine wrinkles. Submetapleural carinae complete. All tibiae with distinct pegs. Ratio of length of hind tarsomeres 1:2:3:4:5 is 25.0:11.0:7.0:4.0:6.0. Fore wing with vein 1cu-a distal of 1/M by about 0.5 times length of 1cu-a. Vein 2-Cu approximately 1.5 times as long as 2cu-a. Fore wing with stalked triangular areolet. Vein 3rs-m distinctly longer than 2rs-m. Areolet receiving vein 2m-cu approximately at lower-posterior angle. Hind wing vein 1-cu about 1.5 times as long as cu-a. Propodeum (Fig. 4) evenly convex, without areas, with texture as that of mesoscutum. Pleural carina distinct. Propodeal spiracle approximately circular, located at anterior 0.3 of propodeum.



Figures 1–6. *Lamachus nigrus* Li, Sheng & Sun, sp. n. Holotype. Female **1** Body, lateral view **2** Head, anterior view **3** Head, dorsal view **4** Propodeum **5** Mesopleuron **6** Terga 2 to 3, dorsal view.

Metasoma. First tergum 1.4 times as long as apical width, with fine granulose texture. Basal portion of median dorsal carinae present. Spiracle circular, at middle of first tergum. Second tergum (Fig. 6) approximately 0.6 times as long as apical width, with texture as that of first tergum. Thyridium present. Third tergum (Fig. 6) and following terga slightly compressed, with fine leathery texture and dense small punctures. Ovipositor sheath approximately 0.3 times apical depth of metasoma. Ovipositor with dorsal notch. Basal portion of ovipositor very wide, apically portion distinctly slender.

Color (Fig. 1). Black, except the following. Median portion of face, clypeus, mandible except black teeth, ventral portion of fore coxa, median portion of subalar ridge, hind corner of pronotum, lateral and apical portions of scutellum, postscutellum, yellow. Maxillary and labial palpi blackish brown. Anterior portion of fore femur, tibia, tarsomeres, basal half of mid tibia, yellowish brown. Apical portion of mid tibia and tarsus blackish brown. Wing membrane brownish hyaline. Pterostigma and veins brownish black.

Male. Body length about 7.0 to 9.0 mm. Fore wing length about 6.0 to 7.0 mm. Antenna with 37 to 39 flagellomeres. Median and lower lateral portions of face, clypeus, mandible (teeth black), maxillary palp, anterior portion of fore coxa, hind corner of pronotum, subalar ridge, basal portion of notaulus, lateral fleck of scutellum, postscutellum, yellow. Labial palp, pterostigma, veins, blackish brown. Fore (except median portion of tibia blackish brown, first to fourth tarsomeres yellowish brown) and mid legs dark brown.

Host. *Neodiprion huizeensis* Xiao & Zhou (Hymenoptera: Diprionidae).

Host plant. *Pinus armandi* Franch. (Pinaceae).

Biology. The mature larva forms a cocoon inside host's cocoon and outside the body of the host larva.

Remarks. This new species is similar to *Lamachus gilpiniae* but can be distinguished from the latter by the following combination of characters: upper tooth of mandible longer than lower tooth; postocellar line approximately 1.5 to 1.6 times as long as ocular-ocellar line; median longitudinal carina of propodeum absent; first tergum 1.4 times as long as apical width; second tergum 0.6 times as long as apical width. *Lamachus gilpiniae*: upper tooth of mandible as long as lower tooth; postocellar line approximately as long as ocular-ocellar line; median longitudinal carina of propodeum distinct; first tergum 1.7 times as long as apical width; second tergum 0.7 to 0.8 times as long as apical width.

***Lamachus rufiabdominalis* Li, Sheng & Sun, sp. n.**

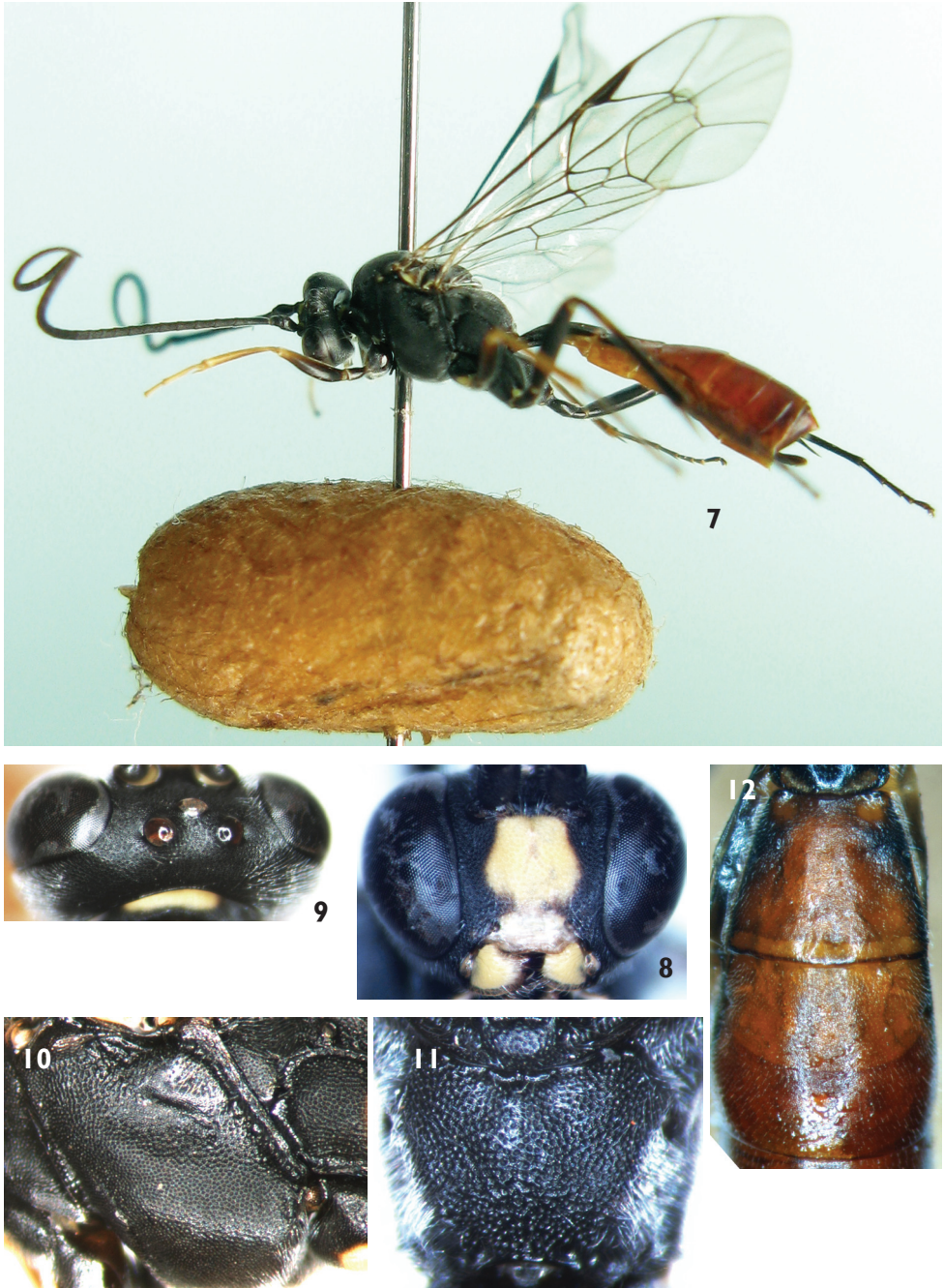
urn:lsid:zoobank.org:act:8FE1BA4D-4DD7-436F-B9FA-A06AC082D196

http://species-id.net/wiki/Lamachus_rufiabdominalis

Figures 7–15

Etymology. The specific name is derived from the red metasoma.

Types. *Holotype*, female, CHINA: Weining, Guizhou Province, 14 March 2012, leg. Tao Li, Mao-Ling Sheng. *Paratypes*: 51 females and 26 males, CHINA: Weining, Guizhou Province, 3 March to 15 April 2012, leg. Tao Li, Mao-Ling Sheng.



Figures 7–12. *Lamachus rufiabdominalis* Li, Sheng & Sun, sp. n. Holotype. Female **7** Body, lateral view **8** Head, anterior view **9** Head, dorsal view **10** Mesopleuron **11** Propodeum **12** Terga 2 to 3, dorsal view.

Diagnosis. Malar space 0.5 times as long as basal width of mandible. Postocellar line as long as ocular-ocellar line. Antenna with 46 to 48 flagellomeres. Fore wing with vein 1cu-a slightly distal of 1/M. Vein 2-Cu approximately as long as 2cu-a. Hind wing vein 1-cu about as long as cu-a. First tergum 2.5 times as long as apical width. Median and apical portions of second tergum, third to fifth terga red.

Description. Female (Fig. 7). Body length 7.0 to 10.0 mm. Fore wing length 7.0 to 9.0 mm.

Head. Inner eye orbits weakly concave at level of antennal insertions. Face (Fig. 8) 0.9 times as wide as long, with dense punctures, upper center with median longitudinal groove. Clypeus smooth, weakly convex at basal portion, 2.5 times as wide as long; apical portion distinctly concave, with fine wrinkles. Mandible smooth, with fine punctures, upper tooth slightly longer than lower tooth. Malar space with fine leathery texture and dense punctures, 0.5 times as long as basal width of mandible. Gena with texture as that of malar space. Vertex (Fig. 9) smooth, with fine leathery texture. Ocellar triangle weakly convex. Postocellar line about equal to ocular-ocellar line. Middle portion of frons evenly convex, with texture as that of vertex. Lateral portion of frons evenly concave. Antenna with 46 to 48 flagellomeres, ratio of length from first to fifth flagellomeres: 10.0:6.0:6.0:6.0:5.0. Occipital carina complete.

Mesosoma. Anterior portion of pronotum with fine leathery texture and dense punctures; upper part of median portion with weak wrinkles; lower part of median portion with dense punctures; upper posterior portion with dense punctures. Mesoscutum evenly convex, with dense punctures. Notaulus weak. Scutoscutellar groove wide, with weak longitudinal wrinkles. Scutellum evenly convex, with texture as that of mesoscutum. Postscutellum transverse, punctures finer than on scutellum. Middle and lower portions of mesopleuron (Fig. 10) convex, with texture as that of mesoscutum. Upper portion of mesopleuron with rough punctures. Speculum small, with fine granulose texture. Lower portion of speculum weakly concave. Metapleuron evenly convex, with texture as that of mesopleuron. Submetapleural carina complete. Ratio of length of hind tarsomeres 1:2:3:4:5 is 10.0:5.0:3.5:2.0:2.0. Fore wing with vein 1cu-a weakly outside of 1/M. Vein 2-Cu approximately as long as 2cu-a. Fore wing with stalked triangular areolet. Vein 3rs-m distinct longer than 2rs-m. Areolet receiving vein 2m-cu approximately at lower-posterior angle. Hind wing vein 1-cu about as long as cu-a. Propodeum (Fig. 11) evenly convex, without areas, with texture as that of mesoscutum. Propodeal spiracle circular, located at about anterior 0.3 of propodeum.

Metasoma. First tergum 2.5 times as long as apical width, with fine leathery texture and sparsely punctate. Spiracle circular, small, located at middle of first tergum. Dorsolateral carina complete posterior to spiracle. Ventrolateral carina complete. Second tergum (Fig. 12) approximately 0.8 times as long as apical width, with texture as that of first tergum and apical portion sparsely punctate. Thyridium circular. Ovipositor sheath approximately 0.3 times as long as hind tibia. Ovipositor with dorsal notch. Basal portion of ovipositor very wide. Apical portion distinctly slender.

Color (Fig. 7). Black, except the following. Middle portion of face (width of fleck 0.75 times as long as that of face in holotype, width of fleck 0.60 to 0.86 times as long as



Figures 13–15. *Lamachus rufabdominalis* Li, Sheng & Sun, sp. n. **13** Larva **14,15** Pupa.

width of face among individuals), clypeus, mandible except black teeth, front portion of fore coxa and first trochanter, part of anterior of mid coxa, hind corner of pronotum, fleck of propodeum, yellowish green. Anterior side of fore femur, tibia and tarsus, apical portion of mid femur, tibia and tarsus, yellowish brown. Hind tibia entirely black, or subbasally with a small, indistinctly yellowish spot. Central and apical portion of second tergum, third to fifth terga, red. Pterostigma and veins brownish black. Wings brownish hyaline.

Male. Body length about 7.0 to 9.0 mm. Fore wing length about 5.0 to 7.0 mm. Antenna with 48 flagellomeres. Face, coxa and front portion of trochanters of fore leg, coxa and front portion of trochanters of mid leg, yellowish green. Hind tibia entirely black. Other characteristics as for female.

Host. *Neodiprion huizeensis* Xiao & Zhou (Hymenoptera: Diprionidae).

Host plant. *Pinus armandi* Franch. (Pinaceae).

Remarks. This new species is similar to *L. iwatai* Momoi 1962, but can be distinguished from the latter by the following combination of characters: first tergum 2.5 times as long as apical width; hind tarsomere 4 as long as tarsomere 5; inner orbit, malar space and mesoscutum entirely black. *L. iwatai*: first tergum 1.7 times as long as apical width; hind tarsomere 4 shorter than tarsomere 5; inner orbit, malar space, a median spot of mesoscutum, yellow.

Biology. *Lamachus rufiabdominalis* is an endoparasitoid of *N. huizeensis* larvae. The mature larva of *L. rufiabdominalis* is cream-colored (Fig. 13), the color changing continuously as development continues. The body of the pupa is yellowish white, compound eyes and ocelli, red. After four days, the compound eyes became black, ocelli changed to reddish brown and the teeth red (Fig. 14). One day later, the ventral profile of the mesothorax, anterior portion of median lobe and lateral portion of lateral lobe of mesoscutum, were brown. After two days, the median portion of the face and mandible (teeth, blackish brown) were yellowish white, femur yellowish brown, most of the first tergum (except apically reddish brown) were blackish brown, second and third terga yellowish brown with reddish marks. The body was black, antenna blackish brown, median portion of face and basal portion of mandible yellowish green, femora yellowish brown, second and third terga red when the pupa was mature (Fig. 15). Of 78 adults of *Lamachus rufiabdominalis* that emerged from cocoons of *N. huizeensis*, the female to male ratio was 2.1:1. The parasitism rates of *N. huizeensis* by *L. rufiabdominalis* were 1.2% to 1.3%. Adults of *L. rufiabdominalis* emerged between 3rd and 30th March under laboratory conditions.

***Lamachus gilpiniae* Uchida, 1955**

http://species-id.net/wiki/Lamachus_gilpiniae

Figure 16

Lamachus gilpiniae Uchida, 1955. Insecta Matsumurana, 19: 3.

Specimens examined. 2 females, CHINA: Taiyuan, Shanxi Province, 22 September 2009. 2 females, CHINA: Taiyuan, Shanxi Province, 25 May to 1 June 2010, Mao-Ling Sheng; 1 male, CHINA: Taiyuan, Shanxi Province, 26 July 2010, Tao Li.



Figure 16. *Lamachus gilpiniae* Uchida, 1955. Female. Body, lateral view.

Host. *Diprion jingyuanensis* Xiao & Zhang, *Gilpinia tobi* Takeuchi (Hymenoptera: Diprionidae) (Uchida 1955; Li et al. 2012).

Host plant. *Pinus tabulaeformis* Carr. (Pinaceae).

***Lamachus sheni* Sheng & Sun, 2007**

http://species-id.net/wiki/Lamachus_sheni

Figure 17

Lamachus sheni Sheng & Sun, 2007. Acta Zootaxonomica Sinica, 32(4):959.

Specimens examined. 2 females, CHINA: Neixiang National Natural Reserve, Henan Province, 10 May 2006, Xiao-Cheng Shen.

Host. Unknown.



Figure 17. *Lamachus sheni* Sheng & Sun, 2007. Holotype. Female. Body, lateral view.

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References

- Cushman RA (1937) New Japanese Ichneumonidae parasite on pine sawflies. *Insecta Matsumurana* 12: 32–38.
- Cushman RA (1939) New Ichneumon-flies parasitic on the hemlock sawfly (*Neodiprion tsugae* Middleton). *Journal of the Washington Academy of Sciences* 29: 391–402.
- Förster A (1869) Synopsis der Familien und Gattungen der Ichneumonen. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens* 25(1868): 135–221.
- Gauld ID (1991) The Ichneumonidae of Costa Rica, 1. Introduction, keys to subfamilies, and keys to the species of the lower Pimpliform subfamilies Rhyssinae, Poemeniinae, Acaenitinae and Cylloceriinae. *Memoirs of the American Entomological Institute* 47: 1–589.

- Li T, Sheng ML, Zou QC (2012) A new Chinese record species of Ichneumonidae (Hymenoptera) parasitizing *Diprion jingyuanensis*. *Acta Zootaxonomica Sinica* 37(2): 463–465.
- Mason WRM (1986) Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. *Proceedings of the Entomological Society of Washington* 88: 1–7.
- Mason WRM (1990) Cubitus posterior in Hymenoptera. *Proceedings of the Entomological Society of Washington* 92: 93–97.
- Meyer NF (1936) Parasitic Hymenoptera in the family Ichneumonidae of the USSR and adjacent countries. Part 5. Tryphoninae. *Opredeliteli Faune SSSR* 21(5): 1–340.
- Momoi S (1962) Descriptions of four Ichneumonidflies parasitic on insect pests of coniferous trees. *Science Reports of the Hyogo University of Agriculture* 5(2): 49–52.
- Ross HH (1936) The ancestry and wing venation of the Hymenoptera. *Annals of the Entomological Society of America* 29: 99–111.
- Sheng ML, Sun SP (2007) Discovery of the genus *Lamachus* Förster (Hymenoptera: Ichneumonidae) in China with description of a new species. *Acta Zootaxonomica Sinica* 32(4): 959–961.
- Townes HK (1970) The genera of Ichneumonidae, Part 3. *Memoirs of the American Entomological Institute* 13(1969): 1–307.
- Uchida T (1955) Neue oder wenig bekannte Schmarotzer der Nadelholz-Blattwespen nebst einem neuen sekundären Schmarotzer. *Insecta Matsumurana* 19(1/2): 1–8.
- Yu DS, Horstmann K (1997) A catalogue of world Ichneumonidae (Hymenoptera). *Memoirs of the American Entomological Institute* 58: 1–1558.
- Yu DS, van Achterberg C, Horstmann K (2012) *Taxapad 2012 – World Ichneumonoidae 2011. Taxonomy, Biology, Morphology and Distribution. On USB Flash drive. Ottawa, Ontario, Canada. www.taxapad.com*

A new species of *Bembidion* (*Ecuadion*) from Ecuador (Coleoptera, Carabidae, Bembidiini), with a key to members of the *georgeballi* species group

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Abstract

A new species of ground beetle, *Bembidion ricei*, is described from the Andes mountains of Ecuador east of Quito. It belongs to the *georgeballi* species group of subgenus *Ecuadion*, and is most similar to *B. georgeballi*. A key to the species of the group is provided.

Keywords

Bembidion, Trechinae, Bembidiini, DNA, morphology, taxonomy, systematics

Introduction

Ecuadion is a diverse subgenus of *Bembidion* restricted to higher elevations in South and Central America (Erwin 1982; Moret and Toledano 2002; Toledano 2008; Vigna Taglianti and Toledano 2008). Adult beetles range in length from 2.2 to 6.1 mm; they are generally shades of brown, either uniform or with various patterns, a few spe-

cies having metallic reflections. Unlike many other *Bembidion*, most *Ecuadion* are not closely associated with shores of bodies of water; they inhabit the leaf litter of cloud forests (e.g., *B. georgeballi* Toledano, *B. onorei* Moret and Toledano, *B. andersoni* Toledano), or run on clay cliffs along roadsides (e.g., *B. agonoides* Vigna Taglianti and Toledano, *B. chimbazonum* Bates, *B. walterrossii* Toledano), or inhabit open high-elevation grasslands (e.g., *B. humboldti* Moret and Toledano, *B. guamani* Moret and Toledano, *B. chimbazonum* Bates, *B. cotopaxi* Moret and Toledano).

In Toledano's (2008) study on the Northern Andean fauna of *Bembidion*, he illustrated (his Figure 21) a single female belonging to the *georgeballi* species group from Rio Chalpi, Ecuador, noting that it was similar to *B. georgeballi* but that it may represent a separate species; the decision about its status was postponed until males could be discovered. In 2010, the senior author and colleagues collected specimens of this form from the same region from which Toledano's specimen originated. The larger series and characteristics of the male genitalia indicate that this form is a species distinct from *B. georgeballi*, and it is here described, and compared to other members of the *georgeballi* group.

Methods

Several hundred specimens of *Ecuadion* were examined as part of this study, including 50 specimens of *B. georgeballi* and 16 specimens of *B. ricei*, n. sp. Specimens came from or have been deposited in the collections listed below. Each collection's listing begins with the coden used in the text.

BMNH The Natural History Museum, London

CTVR Luca Toledano Collection, Verona, Italy

MNHN Muséum National d'Histoire Naturelle, Paris

OSAC Oregon State Arthropod Collection, Oregon State University, Corvallis

QCAZ Catholic University of Ecuador, Quito

USNM National Museum of Natural History, Smithsonian Institution, Washington

Methods of specimen preparation for morphological work, and terms used, are given in Maddison (1993; 2008). Measurements for Apparent Body Length (ABL) are from apex of the labrum to apex of the longer elytron.

Photographs of body parts were taken with a Leica Z6 and JVC KY-F75U camera. For pronotal, elytral, and genitalic images, a stack of photographs at different focal planes was taken using Microvision's Cartograph software; these photographs were then merged using the PMax procedure in Zerene Systems's Zerene Stacker; the images thus potentially have some artifacts caused by the merging algorithm.

Sequences of 28S ribosomal DNA and cytochrome oxidase I genes were obtained using the protocols given in Maddison (2012), and deposited in GenBank with accession numbers JX971116 and JX971117.

Common morphological features and composition of the *georgeballi* species group

Among *Ecuadion*, adults of the *georgeballi* group are characterized by convex elytral intervals, with deep and complete elytral striae, and with elytra reddish or with yellowish markings (Toledano 2008). There are five known species in the group, four of which are restricted to Ecuador (Fig. 1), the fifth in Venezuela:

- B. georgeballi* Toledano [Ecuador]
- B. ricei* Maddison and Toledano [Ecuador]
- B. pierrei* Toledano [Ecuador]
- B. cosangaense* Toledano [Ecuador]
- B. guaramacal* Toledano [Venezuela]

Species identification and description

- 1 Elytra reddish, unicolorous; if with a faint, slightly darker spot, then with a pale rufous pronotum (see Toledano 2008: Fig. 24) **2**
- Elytra with a mottled testaceous and brown pattern, pronotum darker, at least centrally (Fig. 2) **3**
- 2 Pronotum piceous-black, narrower (pronotal width/length = 1.17 to 1.20), elytra reddish, unicolorous; Ecuador ***B. cosangaense***
- Pronotum rufous, wider (pronotal width/length = 1.32 to 1.33), elytra reddish, sometimes with a faint, slightly darker spot; Venezuela... ***B. guaramacal***
- 3 Posterior lateral seta and carina of pronotum both absent, pronotum more constricted at hind angles (Fig. 3B) ***B. georgeballi***
- Posterior lateral seta and carina of pronotum both present, pronotum less constricted at hind angles (e.g., Fig. 3A) **4**
- 4 Microsculpture absent from elytra in males and females; elytral striae 3 and 4 connected in front of the anterior discal seta (see Fig. 2A and 4A); elytral intervals notably convex ***B. ricei* sp. n.**
- Isodiametric microsculpture on the whole dorsal surface in males and females; elytral striae normal; elytral intervals only slightly convex.... ***B. pierrei***

***Bembidion ricei* Maddison & Toledano, sp. n.**

urn:lsid:zoobank.org:act:A72AE0D9-3325-427C-B59B-E0B02507CA9B

http://species-id.net/wiki/Bembidion_ricei

Holotype. Adult male, with three labels: “ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S 78.0852°W, 26.x.2010. DRM 10.159. W.P. & D.R. Maddison, M. Reyes”, “David R. Maddison DNA2653 DNA Voucher [printed on pale green paper]”, and “HOLOTYPE *Bembidion ricei* Maddison & Toledano [printed on red paper]”.

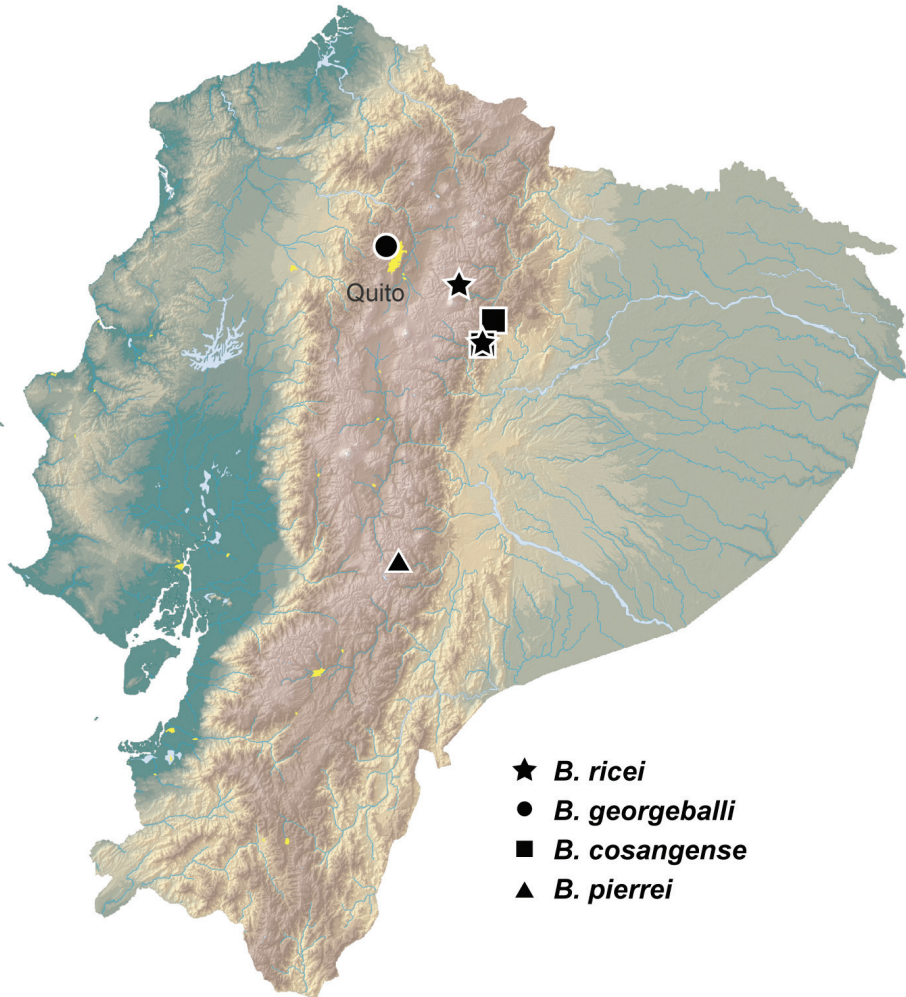


Figure 1. Geographic distribution of known members of the *georgeballi* species group in Ecuador. Base map modified from Chirico and Warner (2005).

Specimen to be deposited at QCAZ; temporarily in OSAC. Genitalia in glycerine in vial pinned beneath specimen. GenBank accession numbers of DNA sequences from the holotype: JX971116 (28S ribosomal DNA) and JX971117 (cytochrome oxidase I).

Paratypes. Six males and nine females from: ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W, 26.x.2010 & 8.xi.2010 (11 exx., OSAC, BMNH, MNHN); ECUADOR: Napo: Papallacta, 2750 m, Rio Chalpi, 8.xi.1985 (1 ex., CTVR); ECUADOR: Napo: Rio Guango (=Rio Huango), 2730m, 0.3758°S, 78.0748°W, 26.x.2010 (2 exx., OSAC); ECUADOR: Napo: Sierrazul (Hacienda Aragon) 10 km W of Cosanga, 2250m, 3–4.vi.1993, 00°44'08"S, 077°53'50"W (1 ex., USNM).

Type locality. ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W.

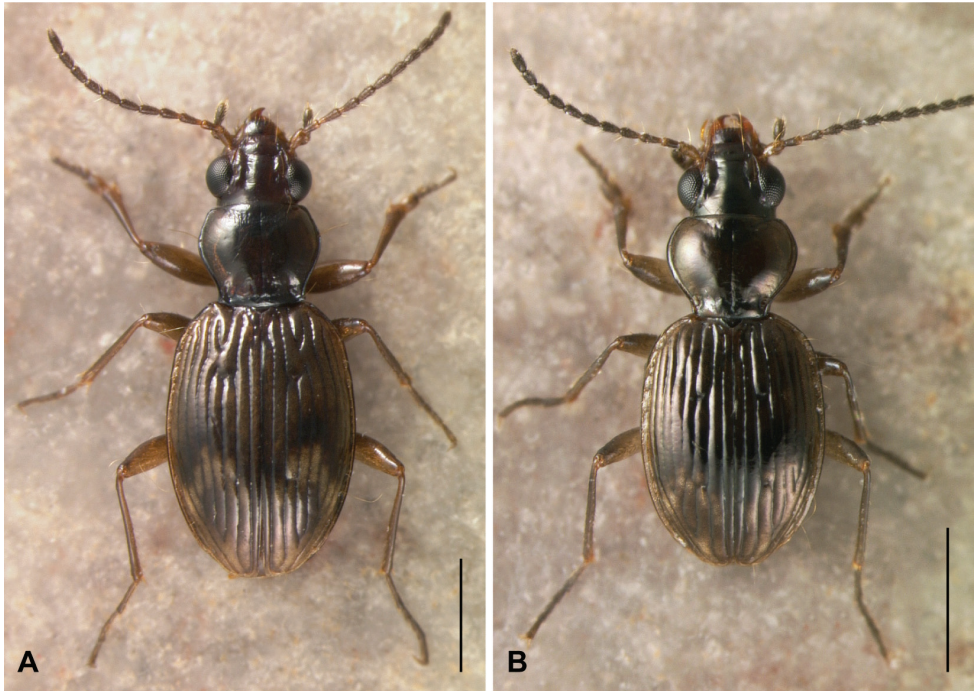


Figure 2. Habitus of male *B. ricei* and *B. georgeballi*. Scale bar is 1 mm. **A** *B. ricei* (ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W, D.R. Maddison voucher V100622) **B** *B. georgeballi* (ECUADOR: Pichincha: Quebrada Lozada, on road to Res. Yanacocha, 3460m, 0.1105°S, 78.5642°W, voucher V100658).

Derivation of specific epithet. It gives us great pleasure to name this species after the late Harold Edward Rice, a passionate butterfly collector and active member of the Pacific Northwest lepidopterist community, and friend to the senior author. Through Harold's generosity, systematic entomology is well supported at Oregon State University. The fund he established paid for the expedition that yielded most of the known specimens of *B. ricei*, including the holotype.

Diagnosis. A shiny, medium-sized *Bembidion* (*Ecuadion*) with convex elytral intervals, and with a mottled pattern of light and dark on the elytra (as in Fig. 2A); adults have a seta at the hind corner of the pronotum, and lack elytral microsculpture in both males and females. Stria 3 and stria 4 are joined together and interrupted in front of the anterior discal seta (ed3; Fig. 2A, 4A); the striae are otherwise complete, and deeply engraved. This combination of characteristics is distinct within the genus.

Brown, with lateral margins of pronotum paler brown in most specimens, and with elytra having a pale apex, and a pale transverse preapical region surrounded by darker brown (Fig. 2A); the region adjacent to ed3 is also slightly darker. Prothorax with sinuate lateral margin, hind angles about 90°, and with a posterior lateral carina (Fig. 3A). Elytral striae deep, complete, although with striae 3 and 4 joined together and interrupted in front of ed3 (Fig. 4A) in all 16 specimens examined; elytral intervals

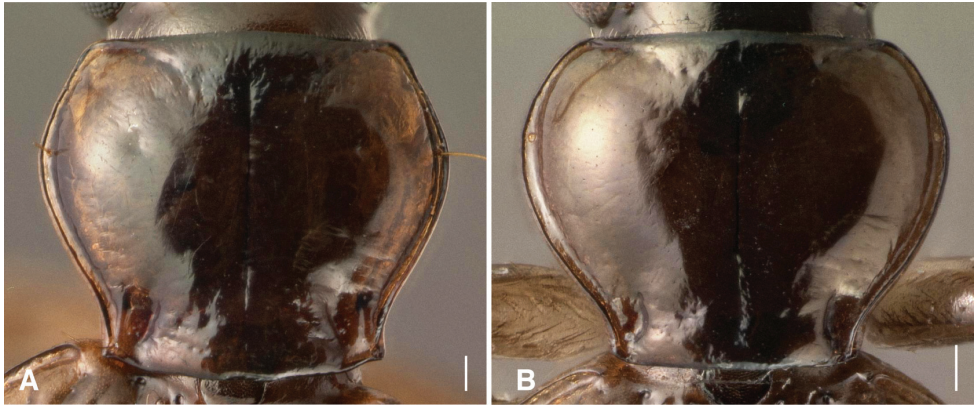


Figure 3. Pronota of male *B. ricei* and *B. georgeballi*. Scale bar is 0.1 mm. **A** *B. ricei* (ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S 78.0852°W, D.R. Maddison voucher V100677) **B** *B. georgeballi* (ECUADOR: Pichincha: Quebrada Lozada, on road to Res. Yanacocha, 3460m, 0.1105°S, 78.5642°W, voucher V100658).

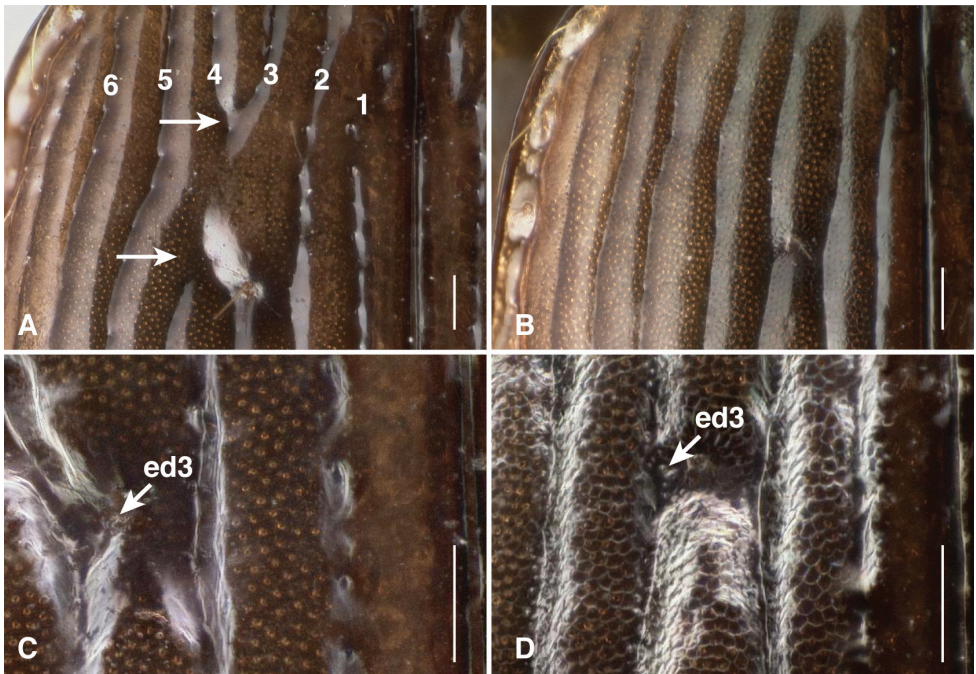


Figure 4. Elytra of *B. ricei* (A & C, from ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W) and *B. georgeballi* (B & D, from ECUADOR: Pichincha: Quebrada Lozada, on road to Res. Yanacocha, 3460m, 0.1105°S 78.5642°W). Scale bar is 0.1 mm. **A** *B. ricei* male (D.R. Maddison voucher V100656), showing joining of striae 3 and 4 (indicated by arrows), with subsequent gap in each stria (between arrows); illuminated by two diffuse lateral lights **B** *B. georgeballi* female (voucher V100676); illuminated by two diffuse lateral lights **C** *B. ricei* female (voucher V100675), illuminated by a ring light **D** *B. georgeballi* female (voucher V100676), illuminated by a ring light.



Figure 5. Male aedeagus. Scale bar is 0.1 mm. **A** *B. ricei* (ECUADOR: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W, D.R. Maddison voucher V100656) **B** *B. georgeballi* (ECUADOR: Pichincha: Campamento Pichán, 3350m, 0.1093°S 78.5728°W, D.R. Maddison voucher V100657).

convex. Microsculpture absent from the pronotum and elytra in both sexes. Aedeagus as in Fig. 5A. ABL 3.9–4.1mm, n=6.

One of the more unusual aspects of these *Bembidion*, shared with some other *Ecuadion*, including males of *B. georgeballi*, is the amber-like clarity of the elytra. The elytra are similar to clear lacquer in places, allowing bright microsculpture dots from the *undersurface* of the elytra to be visible dorsally (see pale dots in Fig. 4C).

The only other *Ecuadion* with yellow and brown mottled elytra, and with complete striae and convex elytral intervals, are *B. georgeballi* and *B. pierrei* (Toledano 2008). *B. ricei* is most similar to *B. georgeballi*, sharing more convex elytral intervals, and pale lateral regions of the pronotum in most specimens. Specimens differ in being larger (ABL 3.9–4.1mm in *B. ricei*, 2.9–3.4mm in *B. georgeballi*), with a less constricted posterior margin of the pronotum (compare Fig. 3A to 3B). The posterior lateral seta



Figure 6. Type locality of *Bembidion ricei*, at Ecuador: Napo: Rio Chalpi Grande, 2800m, 0.3645°S, 78.0852°W. Specimens were found in damp leaf litter under rocks that had previously been at the site marked by the arrow; this is a small tributary of the Rio Chalpi Grande, within 4m of that river. Several *Andinodontis muellermotzfeldi* Toledano and Erwin were found within a meter of the *B. ricei* habitat; *B. (Ecuadorion) sanctaemarthae* Darlington was common about 2–4m away, along the upper banks of the main river. One of the other known localities was along the same small creek, but upstream, in a more shaded area, and further away from the shore (about 1–2m from the water), among damp leaf litter and rocks.

and carina of the pronotum are present (absent in *B. georgeballi*). *B. ricei* specimens have striae 3 and 4 joined and interrupted in front of discal seta ed3 (Fig. 4A). Microsculpture is lacking from the dorsal surface of the elytra in both males and females of *B. ricei*, and thus they are very shiny (Fig. 4A, C); in *B. georgeballi*, males lack elytral microsculpture, but females have evident isodiametric microsculpture throughout the elytra (Fig. 4B, D). In addition, the male aedeagus of *B. ricei* has larger and darker sclerotized regions on the internal sac (Fig. 5A). *B. georgeballi* is currently known only from 3350–3550m on the slopes of Volcán Guagua Pichincha west of Quito (Fig. 1).

From *B. pierrei*, *B. ricei* can be distinguished by having striae 3 and 4 joined, and lacking microsculpture on the elytra (*B. pierrei* has isodiametric microsculpture throughout the elytra in both males and females). *B. pierrei* also lacks the transparent, lacquer-like elytral regions of *B. ricei*. *B. pierrei* is known from the province of Chimborazo, far south of the localities of known localities of *B. ricei* (Fig. 1).

Geographic distribution. *B. ricei* occurs in the province of Napo between 2250m and 2800m in the Andes of Ecuador, east of Quito (Fig. 1). Most specimens have been found a few kilometers east of Papallacta along two tributaries of the Rio Papallacta; a single female has been found along a tributary of the Rio Jondachi south of Cosanga and west of La Merced de Jondachi.

Habitat. Found among leaf litter and under rocks in moist areas near small streams in montane forest (Fig. 6). Specimens were found during daytime in leaf litter under rocks or by scratching open leaf litter.

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We are very thankful to all those who helped with a collecting expedition to Ecuador during which most of the type series of *B. ricei* and numerous other *Ecuadion* were collected. Mauricio Vega arranged many details of the trip, including the relevant collecting and export permits; Wayne Maddison, Marco Reyes, and Mauricio Vega accompanied the senior author into the field and helped collect the specimens.

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References

- Chirico PG, Warner MB (2005) Topography and Landforms of Ecuador. U.S. Geological Survey Data Series 136, http://geology.er.usgs.gov/eespteam/terrainmodeling/images/large/ecuador_srtm_low.pdf [accessed 4 October 2012]
- Erwin TL (1982) Small terrestrial ground-beetles of Central America (Carabidae: Bembidiina and Anillina). *Proceedings of the California Academy of Sciences* 42: 455–496.
- Maddison DR (1993) Systematics of the Holarctic beetle subgenus *Bracteon* and related *Bembidion* (Coleoptera: Carabidae). *Bulletin of the Museum of Comparative Zoology* 153: 143–299.
- Maddison DR (2008) Systematics of the North American beetle subgenus *Pseudoperiphys* (Coleoptera: Carabidae: *Bembidion*) based upon morphological, chromosomal, and molecular data. *Annals of Carnegie Museum* 77: 147–193. doi: 10.2992/0097-4463-77.1.147
- Maddison DR (2012) Phylogeny of *Bembidion* and related ground beetles (Coleoptera: Carabidae: Trechinae: Bembidiini: Bembidiina). *Molecular Phylogenetics and Evolution* 63: 533–576. doi: 10.1016/j.ympev.2012.01.015

- Moret P, Toledano L (2002) *Ecuadion*, nouveau sous-genre de *Bembidion* Latreille, 1802 du páramo équatorien (Coleoptera, Carabidae, Bembidiini). Bollettino del Museo Civico di Storia Naturale di Venezia 53: 155–205.
- Toledano L (2008) Systematic notes on the Bembidiina of the northern Andes with particular reference to the fauna of Ecuador (Coleoptera, Carabidae). Memoirs on Biodiversity 1: 81–130.
- Vigna Taglianti A, Toledano L (2008) *Bembidion (Ecuadion) agonooides* n. sp. from Ecuador (Coleoptera, Carabidae, Bembidiina). Memoirs on Biodiversity 1: 77–80.

Corrections to *Agrilus* related species–group names in the world catalogue of Bellamy and new substitute names for *Agrilus* species–group homonyms

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Abstract

The work treats 52 species–group names related to genus *Agrilus* incorrectly cited in the world catalogue of Bellamy (2008). The name *dimorphus* Théry, 1941 from the genus *Aphanisticus* and *mulleri* Théry, 1925 from the genus *Australodraco* are also treated. Four primary or secondary homonyms are replaced by substitute names. Most of the proposed changes refer to the availability, validity, spelling and authorship of the names. The following new nomenclatural acts are proposed: Four new substitute names for homonyms: *gola* Jendek for *filiformis* Gory & Laporte, 1839 not Herbst, 1801; *luksi* Obenberger, 1936 for *modicus* Kerremans, 1892 not Solier, 1833; *thomsoni* Jendek for *impressipennis* Thomson not Uhler, 1855; *walkerianus* Jendek (*Aphanisticus*) for *sulcicollis* Walker not Lacordaire, 1835. New synonyms: *turei* Curletti, 2002 is an objective synonym of *thurei* Curletti, 1996. Lectotype designations: A lectotype is designated for *Agrilus dualaocola* Obenberger, 1923.

Keywords

Coleoptera, Buprestidae, *Agrilus*, *Aphanisticus*, *Australodraco*, new synonyms, new substitute names, lectotype designation

Introduction

In 2008–2009, a monumental catalogue on world buprestid beetles was published by Chuck L. Bellamy. The major part of the Volume 4 (Bellamy 2008) is devoted to the genus *Agrilus*.

This work is aimed to clarify and correct some taxonomic and nomenclatural problems published in the catalogue. The term *Agrilus* related species–group names means names originally or subsequently assigned to the genus *Agrilus*.

All data were checked from original publications rather than to rely on data published in the Zoological Records. The vast majority of treated taxa belongs to *Agrilus*, but some taxa of other genera are also influenced (see Abstract).

In the course of work, several *Agrilus* species–group names were found primary or secondary homonyms. These names are replaced by substitute names in the separate section.

Treated names are cited alphabetically. Each name has the corrected status in parenthesis with its generic assignment if other than *Agrilus*. Pages where and how a taxon is listed in Bellamy (2008) is cited on the second line. The treatment of each case is stated in the last paragraph.

Corrections to the Bellamy's catalog

acutipennis Horn (unavailable name)

Pages 2216, 2258 – cited as an available synonym of *olivaceoniger* Fisher, 1928 on page 2216 and *quadriimpressus* on page 2258.

Remark. Horn (1891) did not propose the name as new, he cited *acutipennis* Mannerheim, 1837. The name *acutipennis* Horn is an unavailable name introduced by Fisher (1928).

aenescens Kerremans, 1903 (valid name)

Page 1953 – cited as a synonym of *aenescentellus* Obenberger, 1936c.

Remark. The name *aenescentellus* Obenberger, 1936c was proposed as a replacement name for *aenescens* Kerremans, 1903 not Shilsky, 1888. Because the name *aenescens* Shilsky is unavailable (see Jendek 2002b), the name *aenescentellus* Obenberger is an unnecessary replacement name and junior objective synonym of *aenescens* Kerremans.

agadiensis Théry, 1910 (valid name)

Page 2050 – cited as a synonym of *cupriventris* Gory & Laporte, 1839

Remark. The name *agadiensis* Théry, 1910 was cited by Curletti (1993) as a valid name of species. This latest taxonomic act has been omitted.

atriplicis Escalera (unavailable synonym of *rabaticus* Théry, 1930)

Page 2261 – cited as available synonym of *rabaticus*

Remark. Escalera (1914) did not propose the name as new, he cited Abeille as the author. The name *atriplicis* Escalera is an unavailable name introduced in the synonymy of *A. rabaticus* by Obenberger, 1936a.

bandanus Obenberger, 1933 (unavailable synonym of *sulphurifer* Burmeister, 1872)

Page 2318 – cited as available synonym of *sulphurifer*

Remark. The name *bandanus* Obenberger, 1933 was proposed for an aberration, which is an unavailable name (ICZN, Article 45.6.2).

bayeri Obenberger, 1935d (synonym of *sinensis splendidicollis* Fairmaire, 1889)

Page 2294 – cited as *bayeri*; synonym of *sinensis splendidicollis*

Remark. Original spelling of this patronymic name is *bayeri* (dedicated to Prof. E. Bayer) not *beyeri* which is incorrect subsequent spelling.

bolamanus Kerremans (unavailable synonym of *buraicus* Obenberger, 1928)

Page 2010 – cited as available synonym of *buraicus*

Remark. Kerremans (1914) did not propose the name as new, he cited *Agrilus bolamanus* Kerremans 1906. The name *bolamanus* Kerremans, 1914 not Kerremans, 1906 is an unavailable name introduced in the synonymy of *A. buraicus* by Obenberger (1928).

borrei Kerremans (unavailable synonym of *deborrei* Dugès, 1891)

Page 2059 – cited as available synonym of *deborrei*

Remark. Kerremans (1892a) did not propose the name as new, he misspelled *Agrilus deborrei* Dugès, 1891. The name *borrei* Kerremans is an unavailable name introduced in the synonymy of *A. deborrei* by Waterhouse (1897).

caliginulus Obenberger, 1935e (valid name)

Page 2012 – cited as *calliginulus*

Remark. Original spelling of the name is *caliginulus* not *calliginulus* which is incorrect subsequent spelling.

cameroni Bellamy, 1999 (unavailable name)

Page 2012 – cited as valid name for species

Remark. The name *cameroni* Bellamy, 1999 was proposed as a new replacement name for *dimorphus* Théry, 1941, which was supposed to be preoccupied by *dimorphus* Obenberger, 1923. Théry (1941), however, did not propose *dimorphus* in *Agrilus* but in *Aphanisticus* so the replacement was unnecessary. The names *Agrilus dimorphus* Théry and *Agrilus cameroni* Bellamy are unavailable names. See also notes at *dimorphus* Théry, 1941.

camerounensis Obenberger (unavailable name)

Page 2012 – cited as *cameroonensis* and valid name for species

Remark. The name *camerounensis* Obenberger, 1931 is listed as a valid name of species but I failed to find original publication neither by Obenberger or anybody else. The name *camerounensis* Obenberger is an unavailable name introduced by Curletti (1993) .

capicola Kerremans, 1898 (valid name)

Page 2013 – cited as *capicolus*

Remark. Original spelling of the name is *capicola* not *capicolus*. The name *is to be treated as a noun in apposition to the name of its genus* as ruled by ICZN (Article 31.2.2). The name *capicolus* is an incorrect subsequent spelling.

coeruleoniger Fisher, 1929 (valid name) Page 2032 – cited as *coeruleonigra*

Remark. Original spelling of the name is *coeruleonigra*. The ending has to be changed to *coeruleoniger* to agree with the genus gender. This is a mandatory change ruled by ICZN (Article 34.2).

confusulan Obenberger, 1935a (unavailable synonym of *grandis* Gory & Laporte, 1839) Page 2115 – cited as *confusulus* and unavailable synonym of *grandis*

Remark. Original spelling of this unavailable name proposed for an aberration is *confusulan*.

coronifrons Obenberger, 1931a (valid name)

Page 2227 – cited as a synonym of *patricius*

Remark. I failed to trace any author who proposed the synonymisation of the names *patricius* Obenberger, 1931a and *coronifrons* Obenberger, 1931a. The last use of both names was that of Curletti (1998b) who cited them as valid names for species.

cyaneus Olivier (unavailable synonym of *viridis* Linné, 1758) Page 2354 – cited as available synonym of *viridis*

Remark. Olivier (1790a) did not propose the name as new, he cited *Buprestis cyanea* Fabricius, 1775. The name *cyaneus* Olivier is an unavailable name introduced in the synonymy of *A. viridis* by Schönherr (1817).

dicalis Kerremans (unavailable synonym of *dualis* Kerremans, 1903)

Page 2069 – cited as valid name for species.

Remark. Kerremans never proposed the name *dicalis*. This name was introduced by Obenberger (1936) who misspelled the name *dualis* Kerremans, 1903. This lapse was repeated by Blackwelder (1944) and later by Bellamy (2008). The name *dicalis* Kerremans is an unavailable synonym of *dualis* Kerremans, 1903.

dimorphus Théry, 1941 (*Aphanisticus*; valid name for species)

Page 2012, 2395 – cited as a synonym of *cameroni* Bellamy, 1999 in *Agrilus* on page 2012 and as a valid name for species in *Aphanisticus* on page 2395.

Remark. The name *dimorphus* Théry, 1941 is a valid name for species in *Aphanisticus*. See also remarks at the name *cameroni* Bellamy, 1989.

dualaecola Obenberger, 1923 (synonym of *roscidinus* Obenberger, 1923)

Page 2268, 2310 – cited as a synonym of *roscidinus* on page 2268 and synonym of *subcurtulus* on page 2310.

Remark. Curletti (1993) examined 3 syntypes of *Agrilus roscidinus* subspecies *dualaecola* Obenberger, 1923 in National Museum, Prague, Czech Republic (NMPC) and found out that they belong to two different taxa. He treated the name *dualaecola* as a junior subjective synonym of *aterrimus* Kerremans, 1909 based on

two female syntypes as well as a synonym of *roscidinus* Obenberger, 1923 based on a single male syntype. Bellamy followed this approach and cited the *dualaecola* also as a synonym of two different names (see above). In order to preserve the stability of nomenclature by fixing the status of the specimen as the sole name-bearing type of a particular nominal taxon, I designate herein the male syntype of *Agrilus roscidinus* subspecies *dualaecola* Obenberger, 1923 preserved in NMPC as a lectotype. The name *dualaecola* Obenberger, 1923 is a junior subjective synonym of *roscidinus* Obenberger, 1923.

cyanophilus Schaefer, 1946 (unavailable synonym of *suworovi* Obenberger, 1935)

Page 2320–2321, 2358 – cited as unavailable synonym of *suworovi* on Page 2320 and as *cyanophila* an unavailable synonym of *viridis* on Page 2358

Remark. The name *cyanophila* Schaefer, 1946 was proposed for an aberration. The name with the correct ending *cyanophilus* is an unavailable synonym of *suworovi* Obenberger, 1935 (see also Jendek 2002a).

enriquei Murria Beltrán & Murria Beltrán, 2007 (valid name) Page 2083 – cited as *enriquei*

Remark. Original spelling of this patronymic name is *enriquei* (dedicated to Enrique Murria Beltrán) not *enriquei* which is incorrect subsequent spelling.

escalerai Obenberger, 1921 (valid name) Page 2084 – cited as *escaleri*

Remark. Original spelling of this patronymic name is *escalerai* (dedicated to Escalera) not *escaleri* which is incorrect subsequent spelling.

ferrugineoguttatus Gory & Laporte (unavailable synonym of *discolor* Fåhraeus, 1851)

Page 2072 – cited as available synonym of *discolor*

Remark. Gory and Laporte (1839) did not propose the name as new, they cited *Agrilus ferrugineoguttatus* Herbst, 1801. The name *ferrugineoguttatus* Gory & Laporte is an unavailable name introduced in the synonymy of *A. discolor* by Fåhraeus (1851).

fulgidicollis Obenberger, 1935 (unavailable name)

Page 2328 – cited as available synonym of *thoracicus*

Remark. Obenberger (1935c) proposed a replacement name *fulgidicollis* for non-existing name *fulgidicollis* Fisher not Dejean. The name *fulgidicollis* Obenberger is an unavailable name with no relation to the name *thoracicus* Gory & Laporte, 1839, as erroneously stated by Moore Rodriguez (1985).

goryi Saunders, 1871 (valid name)

Page 2118 – cited as valid name proposed as a replacement name

Remark. The name *goryi* Saunders, 1871 is a name proposed by indication to the bibliographic reference of Laporte and Gory (1839) (see ICZN Article 12.2) and not a proposal of a new replacement name.

guerryi Obenberger, 1933 (valid name)

Page 2118 – cited as *guercyi*

Remark. Original spelling of this patronymic name is *guerryi* (dedicated to Guerry) not *guerrcyi* which is an incorrect subsequent spelling.

ingnoratus Obenberger, 1924 (unavailable synonym of *ribbei* Kiesenwetter, 1879)

Page 2266 – cited as available synonym of *ribbei*

Remark. Obenberger (1924) described an *Agrilus* which name was spelled as *ingnoratus* on page 44 and *ignoratus* on pages 45 and 46. Precedence of the name *ignoratus* was fixed by Obenberger (1926) as the first reviser (ICZN Article 24.2.4). The name *ingnoratus* is an incorrect original spelling and unavailable name (ICZN Article 32.4)].

insulicola Kerremans, 1912 (valid name)

Page 2141 – cited as *insulicolus*

Remark. Original spelling of this name is *insulicola* not *insulicolus*. The name *is to be treated as a noun in apposition to the name of its genus* as ruled by ICZN (Article 31.2.2). The name *insulicolus* is an incorrect subsequent spelling.

javicola Fisher, 1935 (valid name)

Page 2146 – cited as *javicolus*

Remark. Original spelling of this name is *javicola* not *javicolus*. The name *is to be treated as a noun in apposition to the name of its genus* as ruled by ICZN (Article 31.2.2). The name *javicolus* is an incorrect subsequent spelling.

kachovskii Obenberger, 1935e (valid name)

Page 2148 – cited as *kackovskii*

Remark. Original spelling of this patronymic name is *kachovskii* (dedicated to Kachovski) not *kackovskii* which is incorrect subsequent spelling.

linearis Panzer (unavailable synonym of *viridis* Linné, 1758)

Page 2354 – cited as available synonym of *viridis*

Remark. Panzer (1806) did not propose the name as new, he cited *Buprestis linearis* Fabricius, 1792. The name *linearis* Panzer is an unavailable name introduced in the synonymy of *A. viridis* by Kiesenwetter (1857).

mucronatus Gory & Laporte (unavailable synonym of *goryi* Saunders, 1871)

Page 2110 – cited as available synonym of *goryi*

Remark. Gory and Laporte (1839) did not propose the name as new, they cited *Agrilus mucronatus* Klug, 1825. The name *mucronatus* Gory & Laporte is an unavailable name introduced in the synonymy of *A. goryi* by Saunders (1871).

muscarinus Baudon (unavailable synonym of *muscarius* Kerremans, 1895)

Page 2196 – cited as available synonym of *muscarius*

Remark. Baudon (1960) did not propose the name as new, he misspelled *Agrilus muscarius* Kerremans, 1895. The name *muscarinus* Baudon is an unavailable name introduced in the synonymy of *A. muscarius* by Descarpentries and Villiers (1963).

mulleri Théry, 1925 (*Australodraco*; valid name)

Page 2369 – cited as *muelleri*

Remark. Original spelling of this patronymic name is *mulleri* (dedicated to Franklin Müller) not *mülleri* which would authorized the mandatory change of *ü* to *ue* (ICZN, Article 32.5.2). The name *muelleri* is an incorrect subsequent spelling.

novicus Westhoff (unavailable synonym of *viridis* Linné, 1758)

Page 2356 – cited as available synonym of *viridis*

Remark. Westhoff (1881) did not propose the name as new, he misspelled the name *novicus* Ratzeburg, 1837. The name *novicus* Westhoff is an unavailable name introduced in the synonymy of *A. viridis* by Obenberger (1936a).

otini Théry, 1934 (synonym of *lukuledianus* Kerremans, 1907)

Page 2172 – cited as subspecies of *lukuledianus*

Remark. The act of Curletti (1993) who cited *otini* Théry, 1934 as a junior synonym of *lukuledianus* Kerremans, 1907 was overlooked.

parapupala Curletti, 1998a (valid name)

Page 2225 – cited as *parapupalus*

Remark. Curletti (1998a) proposed the new species name *Agrilus parapupala* in order to stress its similarity with *A. pupala* Obenberger, 1935e. The name *parapupalus* is an incorrect subsequent spelling. See also *pupala*.

patrizii Théry, 1927 (valid name)

Page 2227 – cited as *patrizzii*

Remark. Original spelling of this name is *patrizii* not *patrizzii* which is an incorrect subsequent spelling.

politus Weiss (unavailable synonym of *cuprescens* Ménétrés, 1832)

Pages 2048, 2356 – cited as unavailable synonym of *cuprescens* on page 2048 and as unavailable synonym of *viridis* on page 2356

The unavailable name *politus* cited by Weiss (1914) is a misidentification of *A. cuprescens* not *A. viridis* (Linné, 1758).

pseudroberti Fleischer, 1934 (unavailable synonym of *cyanescens* Ratzeburg, 1837)

Page 2055 – cited as *pseudoroberti*; unavailable synonym of *cyanescens*

Remark. The original spelling of this unavailable name proposed by Fleischer (1934) for an aberration is *pseudroberti* not *pseudoroberti*.

pupal Obenberger, 1935e (valid name)

Page 2255 – cited as *pupalus*

Remark. Original spelling of the name is *pupal* not *pupalus*. Following the ICZN, Article 31.2.2., the name is to be treated as a noun in apposition and original spelling is to be retained. The *pupalus* is incorrect subsequent spelling. See also *parapupal*.

pygaera Obenberger (unavailable name)

Page 2257 – cited as valid name of species

Remark. Obenberger (1931b) did not propose *pygaera* in the genus *Agrilus* but in *Anthaxia*. Ferreira (1963) erroneously cites the name in *Agrilus*. Bellamy (2008) followed the lapse of Ferreira. The name *Agrilus pygaera* Obenberger is an unavailable name.

pyri Blanchard, 1845 (available synonym of *sinuatus* Olivier, 1790b)

Page 2296 – cited as unavailable synonym of *sinuatus*

Remark. Blanchard (1845) cited name *pyri* without characters but the species is illustrated on the Plate 9, Fig 15. According the ICZN Article 12.2.7, the name published before 1931 without characters but associated with an illustration of the taxon being named is an available name.

rugiplumbeus Cobos, 1964 (valid name)

Page 2274 – cited as *rugiplumbus*

Remark. Original spelling of this name is *rugiplumbeus* not *rugiplumbus* that is incorrect subsequent spelling.

shamyl Obenberger, 1922 (subspecies of *lineola* Kiesenwetter, 1857)

Page 2167 – cited as *shamyi*; subspecies of *lineola*

Remark. Original spelling of the name is *shamyl* not *shamyi* which is an incorrect subsequent spelling.

sibiricola Obenberger, 1924 (synonym of *laticornis* Illiger, 1803)

Page 2291 – cited as *sibiricolus*

Remark. Original spelling of this name is *sibiricola* not *sibiricolus*. The name is to be treated as a noun in apposition to the name of its genus as ruled by ICZN (Article 31.2.2). The name *sibiricolus* is an incorrect subsequent spelling.

spiniger Gory & Laporte, 1839 (available synonym of *spinamajor* Chevrolat, 1838)

Page 2302 – cited as unavailable synonym of *spinamajor*

Remark. Gory and Laporte (1839) proposed *spiniger* as a name for new species. The name is junior secondary homonym to *spiniger* Eschscholtz, 1822. Lacordaire (1857) put it to the synonymy of *Agrilus spinamajor* Chevrolat, 1838.

sulcifer Bétis (unavailable synonym of *hyperici* Creutzer, 1799)

Page 2130 – cited as available synonym of *hyperici*

Remark. Bétis (1908) did not propose the name as new, he cited *Agrilus sulcifer* Abeille de Perrin, 1895. The name *sulcifer* Bétis is an unavailable name introduced in the synonymy of *A. hyperici* by Schaefer (1949).

thurei Curletti, 1996 (valid name) correct original spelling

Page 2337 – cited as a synonym of *turei*

Remark. The name *thurei* Curletti, 1996 was originally dedicated to A. Thure which follows from the *derivatio nominis* as well as from the name of collector cited on the labels of type specimens. The name was changed by Curletti (2002) to *turei* based on the fact that the verified name orthography is *Ture* not *Thure*.

Following the ICZN (Article 32.4): the original spelling of a name is the “correct original spelling”, unless it is demonstrably incorrect as provided in Article 32.5. The Article 32.5 requires clear evidence of an inadvertent error in the original publication itself without recourse to any external source of information. The publication of Curletti (1996) itself doesn’t provide such an evidence of an inadvertent error. The case is further intricate by the fact that Bellamy (2008) cited the original spelling of the name (*thurei*) as a synonym of the emended name (*turei*). If the nomenclatural act of Curletti (1996) had been a justified emendation then the emended name (*turei*) would have to take the authorship and date of the original publication (ICZN Article 19.2); and the incorrect original spelling sensu Curletti (*thurei*) would have no separate availability (Article 32.4).

The best solution for the stability of the nomenclature is the reversal to original state by following the ICZN Article 32.5. The name *thurei* Curletti, 1996 is a correct original spelling and the name *turei* Curletti, 2002 an unjustified emendation and available synonym of *thurei*.

turei Curletti, 2002 (available synonym of *thurei* Curletti, 1996) unjustified emendation

Page 2337 – cited as valid name

Remark. See comments at *thurei* above.

viridis Seidlitz (unavailable synonym of *cuprescens* Ménériés, 1832)

Pages 2047, 2356 – cited as unavailable synonym of *cuprescens* on page 2047 and unavailable synonym of *viridis* on page 2356

Remark. Seidlitz (1888) did not propose the name as new, he cited *Agrilus viridis* Linné, 1758. The name *viridis* Seidlitz is an unavailable name introduced by Obenberger (1935b) as a synonym of *rubicola* Abeille de Perrin, 1897, which is currently a synonym of *cuprescens* Ménériés, 1832.

zanthoxylumi Li Meng Lou, 1989 (valid name)

Page 2367 – Zhang and Wang are cited as authors.

Remark. The authorship of the name has been changed several times. Jendek & Grebennikov (2011) stated that Li Meng Lou (1989) is the first who established the name by presenting characters (ICZN, Article 13.1.1).

Substitute names for primary homonyms in the genus *Agrilus*

lukesi Obenberger, 1936b new substitute name

Remark. The name *modicus* Kerremans, 1892b is replaced by its synonym *lukesi* Obenberger, 1936b due to primary homonymy with *modicus* Solier, 1833 (recently in *Paragrilus*).

thomsoni Jendek new replacement name

Remark. The name is *impressipennis* Thomson, 1879 is replaced by a new replacement name *thomsoni* Jendek due to primary homonymy with *impressipennis* Uhler, 1855 (currently synonym of *fallax* Say, 1833).

Etymology: The name is patronymic and dedicated to Thomson.

walkerianus Jendek (*Aphanisticus*) new replacement name

Remark. The name *sulcicollis* Walker, 1858 (recently in *Aphanisticus*) is replaced by a new replacement name *walkerianus* Jendek due to primary homonymy with *sulcicollis* Lacordaire, 1835.

Etymology: The name is patronymic and dedicated to Walker.

Substitute name for secondary homonyms in the genus *Agrilus*

gola Jendek new replacement name

Remark. The name *filiformis* Gory & Laporte, 1839 (originally proposed in *Agrilus*) is replaced by a new replacement name *gola* Jendek due to primary homonymy with *filiformis* Herbst, 1801 (originally proposed in *Buprestis*; currently synonym of *viridis* Linné, 1758).

Etymology: The name is derived from the first two letters of the names Gory and Laporte.

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References

- Abeille de Perrin E (1895) Buprestides paléarctiques réputés nouveaux. Annales de la Société Entomologique de France 64: 116–126.
- Abeille de Perrin E (1897) Notes sur les Buprestides paléarctiques (Suite). Revue d'Entomologie 16: 1–33.
- Baudon A (1960) Contribution à l'étude des Buprestides du Laos. Annales de la Faculté des Sciences de Saïgon 1960: 217–233.

- Bellamy CL (1999) Nomenclatural notes in Buprestidae (Coleoptera). *Folia Heyrovskyana* 7(1): 1–11.
- Bellamy CL (2008) A world catalogue and bibliography of the jewel beetles (Coleoptera: Buprestoidea). Volume 4, *Agrilinae: Agrilina through Trachyini*. Pensoft, Sofia, 1932–2684.
- Bétis L (1908) Synopsis des Coléoptères du Var. Draguignan, Imprimerie Latil Freres, 971 pp.
- Blackwelder RE (1944) Checklist of the coleopterous insects of Mexico, Central America, The West Indies, and South America. United States National Museum, Bulletin 185(2): 189–341.
- Blanchard F (1845) Histoire naturelle des insectes : leurs moeurs, leurs métamorphoses, et leur classification ou traite elementaire d'entomologie. Tome Second, F. Savy, Paris, 524 pp.
- Burmeister HCC (1872) Buprestidae Argentini, Uebersicht der Prachtkäfer des La Plata-Gebietes. *Stettiner Entomologische Zeitung* 33: 367–387.
- Chevrolat LAA (1838) Centurie de Buprestides. *Silbermann's Revue Entomologique*, Strasbourg and Paris, 5: 41–110.
- Cobos A (1964) Nuevas especies de Buprestidae (Coleoptera) de Nueva Guinea. *Annali del Museo Civico di Storia Naturale di Genova* 75: 197–212.
- Creutzer C (1799) *Entomologische Versuche*. Karl Schaumburg und Comp., Wien, 142 pp.
- Curletti G (1993) First contribution to the revision of the genus *Agrilus* of the Ethiopic region (Coleoptera, Buprestidae). Introduction – Checklist – First synonymies – New Subgenera. *Lambillionea* 93: 421–444.
- Curletti G (1996) Nuovi taxa Africani del gen. *Agrilus* Curtis, 1825. VI. (Coleoptera: Buprestidae). *Elytron*, Barcelona 10: 123–134.
- Curletti G (1998a) Nuovi *Agrilus* delle regioni Africane e delle penisola Arabica (Coleoptera, Buprestidae). *Rivista Piemontese di Storia Naturale* 19: 89–149.
- Curletti G (1998b) Notes on metatarsal morphology in the genus *Agrilus* and proposed redefinition of its subgenera in afrotropical region (Coleoptera Buprestidae). *Bolletino della Società entomologica italiana* 130(2): 125–134.
- Curletti G (2002) Contribution a la connaissance des Agrilini de Cote d'Ivoire (Coleoptera: Buprestidae). *Lambillionea* 102: 43–64.
- Descarpentries A, Villiers A (1963) Catalogue raisonné des Buprestidae d'Indochine. II. Agrilini, genre *Agrilus* (2e partie). *Revue française d'Entomologie* 30(2): 104–119.
- Dugès DE (1891) Descripcion de coleopteros indigenas. *La Naturaleza Serie 2*, 2: 1–38.
- Escalera MM de la (1914) Los Coleópteros de Marruecos. *Trabajos del Museo Nacional de Ciencias Naturales, Madrid Serie Zoológica* 11: 1–553.
- Eschscholtz JF (1822) *Entomographien*. Erste Lieferung. G. Reimer, Berlin, 128 pp.
- Fabricius JC (1775) *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensburgi et Lipsiae, Libraria Kortii, 832 pp.
- Fabricius JC (1792) *Entomologia systematica emendata et aucta, secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. Tom. I. Pars II, Hafniae, Christ. Gottl. Proft. 538 pp. doi: 10.5962/bhl.title.36532
- Fairmaire L (1889) Descriptions de Coléoptères de l'Indo-Chine. *Annales de la Société Entomologique de France* 6(8): 333–378.
- Fähræus OI (1851) [New buprestid taxa]. In: Boheman CH (Ed.) *Insecta Caffrariae annis 1838–1845 a J. H. Wahlberg collecta, amici auxilio suffultus*. Pars I. Fascic. II. Coleoptera. (Buprestides, Elaterides, Cebriionites, Rhipicerides, Cyphonides, Lycides, Lampy-

- rides, Telephorides, Malyrides, Clerii, Terediles, Ptiniores, Palpatores, Silphales, Histeres, Scaphidilia, Nitidulariae, Cryptophagidae, Byrrhii, Dermestini, Parnidae, Hydrophyllidae) Holmiae, Norstedtiana, 299–374.
- Ferreira MC (1963) Catálogo dos Coleópteros de Moçambique. Revista de Entomologia de Moçambique 6(1): 1–532.
- Fisher WS (1928) A revision of the North American species of the buprestid beetles belonging to the genus *Agrilus*. Bulletin of the United States National Museum 145: 1–347. doi: 10.5479/si.03629236.145.1
- Fisher WS (1929) New species of buprestid beetles from Costa Rica. Proceedings of the United States National Museum No. 2803, 76(6): 1–20.
- Fisher WS (1935) New species of Buprestidae from Java (Col.). Treubia 15(1): 27–48.
- Fleischer A (1934) Přehled brouků fauny Československé republiky. Zvláštní otisk z Časopisu Moravského Musea Zemského, ročník 25–27. Akciová Moravská knihtiskárna, Brno, 483 pp. [in Czech]
- Gory HL, Laporte de Castelnau FL (1839) Histoire naturelle et iconographie des insectes coléoptères, publiée par monographies séparées. Suite aux buprestides. Tome II, P. Duménil, Paris. [genera paged separately]
- Herbst JFW (1801) Natursystem aller bekannten in- und ausländischen Insekten, als eine Fortsetzung der Büffonschen Naturgeschichte. Der Käfer. Neunter Theil. Buchhandlung des Geh. Commerzien-Raths Bauti, Berlin, 344 pp.
- Horn GH (1891) The species of *Agrilus* of Boreal America. Transactions of the American Entomological Society 18: 277–366.
- ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition, adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, 306 pp.
- Illiger JCW (1803) Verzeichniss der in Portugall einheimischen Käfer. Erste Lieferung. Magazin für Insektenkunde, Braunschweig 2: 186–258.
- Jendek E (2002a) Taxonomic and nomenclatural notes on *Agrilus suvorovi* Obenberger (Coleoptera: Buprestidae: Agrilinae). Zootaxa 52: 1–8.
- Jendek E (2002b) Nomenclatural and taxonomic notes on *Agrilus ater* (Linné), *A. biguttatus* (Fabricius) and *A. subauratus* Gebler (Coleoptera: Buprestidae: Agrilinae). Zootaxa 120: 1–12.
- Jendek E, Grebennikov V (2011) *Agrilus* (Coleoptera, Buprestidae) of East Asia. Prague, Jan Farkač, 362 pp.
- Kerremans C (1892a) Catalogue synonymique des Buprestides decrits de 1758 à 1890. Séance du 5 septembre 1891. Mémoires de la Société Entomologique de Belgique 1: 1–304.
- Kerremans C (1892b) Viaggio di Leonardo Fea in Birmania e regioni vicine. XLIX. Buprestides. Annali del Museo Civico di Storia Naturale di Genova Serie 2, 12(32): 809–832.
- Kerremans C (1895) Buprestides Indo-Malais. Deuxième partie. Annales de la Société Entomologique de Belgique 39: 192–224.
- Kerremans C (1898) Buprestides du Congo et des régions voisines. Annales de la Société Entomologique de Belgique 42: 271–329.

- Kerremans C (1903) Coleoptera Serricornia. Fam. Buprestidae, Fasc. 12b, 12c, 12d. In: Wytsman P (Ed.) Genera Insectorum. Tome II, Fascicules XII–XIV. Verteneuil & Desmet, Bruxelles, 49–338.
- Kerremans C (1906) Buprestides recueillis par Mr. L. Fea dans l’Afrique occidentale. Annali del Museo Civico di Storia Naturale di Genova Serie 3, 2(42): 406–411.
- Kerremans C (1907) Buprestides de l’Est Africain allemand. Annales de la Société Entomologique de Belgique 51: 60–67.
- Kerremans C (1909) Catalogues raisonnés de la Faune Entomologique du Congo Belge. Coleoptera, fam. Buprestidae. Annales du Musée du Congo Belge Zool. ser. III, tome I, fasc. 2, 1–44.
- Kerremans C (1912) H. Sauter’s Formosa–Ausbeute. Buprestiden. Archiv für Naturgeschichte 78, Abteilung A, Heft 7: 203–209.
- Kerremans C (1914) Buprestidae. In: Voyage de Ch. Alluad et R. Jeannel en Afrique orientale (1911–1912). Résultats scientifiques, Memoire No. 28, Coleoptera VI, Libraire A. Schulz, Paris, 207–246.
- Kiesenwetter H von (1857) Buprestidae, Eucnemidae, Bogen 1–11, Naturgeschichte der Insecten Deutschlands begonnen von Dr. W. F. Erichson, fortgesetzt von Prof. Dr. H. Schaum, Dr. G. Kraatz und H. v. Kiesenwetter. Erste Abtheilung Coleoptera. Vierter Band. Berlin, Nicolaische Verlagsbuchhandlung (G. Parthey), 1–178.
- Klug JCF (1825) Entomologiae Brasiliae specimen alterum, sistens insectorum coleopterorum nondum descriptorum centuriam. Nova Acta Physico–Medica Academiae Caesareae Leopoldino–Carolinae, Naturae curiosum, Bonnae Tomus duodecimus seu decadis secundae tomus secundus, 419–476.
- Lacordaire MT (1835) [The volume on Beetles]. In: Boisduval JBA, Lacordaire MT (Eds) Faune entomologique des environs de Paris, ou species général des insectes qui se trouvent dans un rayon de quinze a vingt lieues aux alentours de Paris. Tome premier. Méquignon–Marvis, Paris, 103–696.
- Lacordaire MT (1857) Histoire naturelle des insectes. Genera des coléoptères ou exposé méthodique de critique de tous les genres proposés jusqu’ici dans cet ordre d’insectes. Tome quatrième contenant les familles des buprestides, throschides, eucnémides, élatérides, cébrionides, cérophytides, rhipicérides, dascyllides, malacodermes, clérides, lyméxylones, cupésides, ptiniores, bostrichides et cissides. Libraire encyclopédique de Roret, Paris, 554 pp.
- Li Meng Lou (1989) *Agrilus zanthoxylumi*. In: Lou LM, Min CZ, Xin WP (Eds) Growth and pest control of *Zanthoxylum bungeanum* Maxim. Xi’an, Shaanxi Science & Technology Press, 60–63.
- Linné C von (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Holmiae, Impensis Direct. Laurentii Salvii, 824 pp. doi: 10.5962/bhl.title.542
- Mannerheim CG von (1837) Enumeration des Buprestides, et description de quelques nouvelles espèces de cette tribu de la famille des Sternoxes, de la collection de M. Le Comte Mannerheim. Bulletin de la Société Impériale des Naturalistes de Moscou 10: 1–126.
- Ménétriés E (1832) Catalogue raisonné des objets de Zoologie recueillis dans un voyage au Caucase et jusqu’aux frontières actuelles de la Perse. L’Imprimerie de l’Académie Impériale des Sciences, St. Pétersbourg, 271 pp.

- Moore Rodriguez T (1985) Aporte al conocimiento de los Buprestidos de Chile (Coleoptera–Buprestidae) Segunda Nota. Revista Chilena de Entomología 12: 113–139.
- Murria Beltrán F, Murria Beltrán Á (2007) Descripción de una nueva especie del género *Agrilus* Curtis, 1825, de España (Coleoptera, Buprestidae, Agrilinae). Boletín de la SEA, Sociedad Entomológica Aragonesa, Zaragoza No 40: 179–181.
- Obenberger J (1921) Buprestides nouveaux de Fernando Poo et de la Guinée espagnole. Travaux del Museo Nacional de Ciencias Naturales, Madrid Serie Zoológica 45: 1–16.
- Obenberger J (1922) De novis Buprestidarum regionis palaearticae speciebus II. Časopis Československé Společnosti Entomologické 19: 18–29, 66–71.
- Obenberger J (1923) Eine Serie neuer Buprestidenarten. Tijdschrift voor Entomologie 66: 1–32.
- Obenberger J. (1924) Symbolae ad specierum regionis palaearticae Buprestidarum cognitionem. Jubilejný Sborník Československé Společnosti Entomologické 1924: 6–59.
- Obenberger J (1926) Buprestidae, p. 620–663, In: Winkler A (Ed) Catalogus Coleopterorum regionis palaearticae. Pars 6, A. Winkler, Wien, 625–752.
- Obenberger J (1928) Sur les Buprestides recueillis par MM. Alluaud et Jeannel dans la region de Kilimandjaro (Col., Bupr.). Revue sbírky krasců, nalezených. Alluaudem a Jeannelem na Kilimandžaru. Acta Entomologica Musei Nationalis Pragae 6: 3–28.
- Obenberger J (1931a) Agrilenstudien I. (Col. Bupr.). Entomologisches Nachrichtenblatt 5(3): 54–71.
- Obenberger J (1931b) Studien über die aethiopischen Buprestiden II. Folia Zoologica et Hydrobiologica 3(1): 84–127.
- Obenberger J (1933) Několik poznámek o krascích. Quelques notes et rectification sur les Buprestides (Col.). Časopis Československé Společnosti Entomologické 30: 13–17.
- Obenberger J (1935a) De regionis aethiopicae speciebus generis Agrili novis (Col. Bupr.). Nové druhy krasců z rodu *Agrilus* z aethiopické oblasti (Col. Bupr.). Acta Entomologica Musei Nationalis Pragae 13: 149–210.
- Obenberger J (1935b) Catalogue raisonné des Buprestides de Bulgarie. III Partie. Bulletin des Institutions Royales d'Histoire Naturelle, Sofia 8: 23–96.
- Obenberger J (1935c) Synonymia Agrilorum (Col. Bupr.) II. Časopis Československé Společnosti Entomologické 32: 121–121.
- Obenberger J (1935d) De regionis palaearticae generis Agrili speciebus novis (Col. Bupr.). O nových palaeartických druzích krasců z rodu *Agrilus*. Časopis Československé Společnosti Entomologické 32: 161–171.
- Obenberger J (1935e) De generis Agrilis Africae speciebus novis (Col. Bupr.). Folia Zoologica et Hydrobiologica 8: 191–226.
- Obenberger J (1936a) Buprestidae V. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Volumen XIII, Pars 152, Verlag für Naturwissenschaften, W. Junk, Gravenhage, 935–1246.
- Obenberger J (1936b) De speciebus novis palaearticae generis *Agrilus* (Col. Bupr.). Nové palaeartické druhy rodu *Agrilus* (Col. Bupr.). Časopis Československé Společnosti Entomologické 33: 104–118.
- Obenberger J (1936c) Synonymia Agrilorum (Col. Bupr.) II. Časopis Československé Společnosti Entomologické 33: 91–92.

- Olivier AG (1790a) Encyclopedie méthodique. Histoire naturelle. Insectes. Tome cinquieme. Part 1, Paris, Panckoucke, 1–368.
- Olivier AG (1790b) Entomologie, ou histoire naturelle des insectes, avec leurs caractères généraux et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coléoptères. Tome second. Paris, De l'Imprimerie de Baudouin, Imprimeur de l'Assemblée Nationale, Genera No. 9–33. [paged separately]
- Panzer GWF (1806) Fauna Insectorum Germaniae initia oder Deutschlands Insecten. Heft 101, Nürnberg, Felsecker, 24 pp.
- Ratzeburg JTC (1837) Die Forst-Insecten oder Abbildung und Beschreibung der in den Wäldern Preussens und der Nachbarstaaten als schädlich oder nützlich bekannt gewordenen Insekten. In systematischer Folge und mit besonderer Rücksicht auf die Vertilgung der Schädlichen. Erster Theil. Die Käfer. Berlin, Nicolai Buchhandlung, Druckerei der Königlich Akademie der Wissenschaften, 202 pp.
- Saunders E (1871) Catalogus Buprestidarum Synonymicus et Systematicus. London, E. W. Janson, 171 pp.
- Say T (1825) Descriptions of new American species of the genera *Buprestis*, *Trachys* and *Elater*. Annals of the Lyceum of New York 1, 249–268.
- Say T (1833) Descriptions of new species of North American insects, and observations on some of the species already described. New Harmony, Indiana, 58–73.
- Schaefer L (1946) Formes nouvelles de Buprestides. Bulletin mensuel de la Société Linnéenne de Lyon 6: 71–73.
- Schaefer L (1949) Les Buprestides de France. Tableaux analytiques des Coléoptères de la faune franco-rhénane. France, Rhénane, Belgique, Hollande, Valais, Corse. Famille LVI. Miscellanea Entomologica Supplément, 511 pp, 28 pls.
- Schilsky FJ (1888) Beitrag zur Kenntnis der deutschen Käferfauna. Deutsche Entomologische Zeitschrift 32: 177–190.
- Schönherr CJ (1817) Synonymia Insectorum, oder Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum etc. geordnet. Eleutherata oder Käfer. Erster Band. Dritter Theil. Hispa – Molorchus. Upsala, Em. Bruzelius, 506 pp.
- Seidlitz GCM (1888) Fauna Transsylvanica. Die Kaefer (Coleoptera) Siebenbürgens. 1.–2. Lieferung, Königsberg, Hartungsche Verlagsdruckerei, I–XL [introduction and families] + 1–48 [genera] + 1–240 [species] pp.
- Solier AJJ (1833) Essai sur les Buprestides. Annales de la Société Entomologique de France 2: 261–316.
- Théry A (1910) Voyage de M. Ch. Alluaud au Soudan Égyptien (Nil Bleu) (1905–1906). Buprestidae (Col.). Annales de la Société Entomologique de France 79(3): 370–376.
- Théry A (1925) Wissenschaftliche Ergebnisse der Bearbeitung der Coleopteren-Sammlung von Franklin Müller (Beitrag II). Buprestides. Entomologische Mitteilungen 14(2): 162–165.
- Théry A (1927) Buprestides de la Somalie Italienne récolts par le Marquis Patrizi. Annali del Museo Civico di Storia Naturale di Genova 52: 239–245.
- Théry A (1930) Études sur les Buprestides de l'Afrique du nord. Mémoires de la Société des Sciences Naturelles du Maroc 19 (1928): 1–586.
- Théry A (1934) Contributions a l'étude de la faune de Mozambique. Voyage de M. P. Lesne (1928–1929). 15e note, Coléoptères, Buprestides. Memórias e Estudos do Museu Zoológico de Universidade de Coimbra (1) 77: 1–31.

- Théry A (1941) Notes on the Buprestidae (Coleoptera) of East Africa. Journal of the East Africa and Uganda Natural History Society 15: 91–153.
- Thomson J (1879) Typi buprestidarum musaei Thomsoniani. Appendix 1a. Paris, E. Deyrolle, 87 pp.
- Uhler PR (1855) Descriptions of a few species of Coleoptera supposed to be new. Proceedings of the Academy of Natural Sciences of Philadelphia 7: 415–418.
- Walker F (1858) Characters of some apparently undescribed Ceylon Insects. Annals and Magazine of Natural History, Third series, Vol. 2: 280–286.
- Waterhouse CO (1897) Biologia Centrali–Americana, Insecta, Coleoptera, Vol. III. Part 1, Serricornia, Buprestidae, Appendix. Fam. Buprestidae, 663–666.
- Weiss HB (1914) *Agrilus politus* Say infesting roses. Journal of Economic Entomology 7: 251, 438–440.
- Westhoff F (1881) Die Käfer Westfalens. I. Abtheilung. Bonn, Max Cohen & Sohn (Fr. Cohen). Verhandlungen des naturhistorischen Vereins der preussischen Rheinlande und Westfalens, Bonn Supplement, 38, Vierte Folge: 8. Jahrgang, XXVIII + 323 pp.