

A new species of *Cletocamptus* Schmankevitsch, 1875 (Copepoda, Harpacticoida, Canthocamptidae) from Rayong Province, Eastern Thailand

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Abstract

Cletocamptus thailandensis **sp. nov.** was discovered in a water body at the base of a small mountain near the Phang Rat River Delta in Rayong Province, Eastern Thailand. The new species resembles *C. goenchim* Gómez, Ingole, Sawant & Singh, 2013 and *C. koreanus* Chang, 2013, but it can be distinguished from these two species based on the armament of the endopodal lobe of the male P5, ornamentations of the abdominal segments, the caudal ramus, the male P3Endp-3, and the relative length of the aesthetasc on the fourth segment of the female antennule. According to the combinations of certain female characteristics, including the number of setae on the P3Endp-2, the relative length of the caudal ramus, the relative length of the inner apical seta on the P3Endp-2, the shape of the P5, and the number of setae on the P3Exp-2, five groups of the *Cletocamptus* species can be defined.

Keywords

Brackish water, diversity, estuary, mangrove, Southeast Asia

Introduction

Cletocamptus Schmankevitsch, 1875 has previously been considered enigmatic, as its higher taxonomic position is inconsistent, and some of its representatives exhibit a high degree of morphological variability (Gee 1999). The genus was originally placed in the family Cletodidae (e.g., Monard 1927; Lang 1936, 1948) and later in Canthocamptidae as *incertae sedis* (Por 1986). According to the shared apomorphic character of subdistal spinules on the ventral surface of the rostrum, its taxonomic position has more recently been clarified after Gómez and Yáñez-Rivera (2022) placed it, with *Cletocamptoides* (Gómez & Yáñez-Rivera, 2022) and *Amphibiperita* (Fiers & Rutledge, 1990), in the newly created subfamily Cletocamptinae of the family Canthocamptidae. Recently, 28 species has been recognized as valid, including *C. affinis* Kiefer, 1957, *C. albuquerquensis* (Herrick, 1894), *C. assimilis* Gómez & Gee, 2009, *C. axi* Mielke, 2000, *C. cecsurirensis* Gómez, Scheihing & La Barca, 2007, *C. chappuisi* Gómez, Gerber & Fuentes-Reinés, 2017, *C. confluens* (Schmeil, 1894), *C. deborahdexterae* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. dominicanus* Kiefer, 1934, *C. feei* (Shen, 1956), *C. fourchensis* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. goenchim* Gómez, Ingole, Sawant & Singh, 2013, *C. gomezi* Suárez-Morales, Barrera-Moreno & Ciro-Pérez, 2013, *C. gravihatus* (Shen & Sung, 1963), *C. koreanus* Chang, 2013, *C. levis* Gómez, 2005, *C. mongolicus* Stërba, 1968, *C. nudus* Gómez, 2005, *C. pilosus* Gómez & Gee, 2009, *C. retrogressus* Schmankevitsch, 1875, *C. samariensis* Fuentes-Reinés, Zoppi de Roa & Torres, 2015, *C. schmidtii* Mielke, 2000, *C. sinaloensis* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. spinulosus* Gómez & Gee, 2009, *C. stimpsoni* Gómez, Fleeger, Rocha-Olivares & Foltz, 2004, *C. tainoi* Gómez, Gerber & Fuentes-Reinés, 2017, *C. tertius* Gómez & Gee, 2009, and *C. trichotus* Kiefer, 1929.

From a geographical viewpoint, *Cletocamptus* is considered a cosmopolitan genus that occurs across the salinity range (Boxshall and Defaye 2008), from freshwater to hypersaline environments. It generally occurs in estuaries, coastal areas, and beach lagoons on all continents. Some species, such as *C. cecsurirensis* (> 4000 m a.s.l.) and *C. gomezi* (> 2,300 m a.s.l.), have been recorded in high-altitude water bodies (Gómez et al. 2007; Suárez-Morales et al. 2013).

During the sampling of copepods in a shallow water body at the base of a small limestone mountain located near a mangrove forest approximately 7.5 km away from the Phang Rat River Delta in Rayong Province, Thailand, a species of *Cletocamptus* was discovered. The Thai *Cletocamptus* is likely identical to *C. deitersi sensu* Tai and Song (1979), *C. goenchim*, recorded in India, and *C. koreanus*, recorded in Korea. However, because the Chinese *C. deitersi* has now been considered *species inquirendae* (Gómez et al. 2004; Gómez and Yáñez-Rivera 2022) and because some distinctive characters that distinguishes the Thai *Cletocamptus* from the Indian and Korean congeners was observed, the new species is justified and reported in this contribution. The description of its morphological characteristics and the results of a comparative study are presented.

Materials and methods

The sample was collected from standing water at the base of an isolated limestone mountain in the Gong Din Subdistrict of Rayong Province, eastern Thailand (Fig. 1) using a hand net with a mesh size of 60 μm , and stored in 4% formaldehyde. In the laboratory, the specimens were sorted under a stereomicroscope and stored in 70% ethanol. They were later transferred into glycerol after being placed in a mixture of glycerol and 70% ethanol (ratio ca. 1:10 v/v) for 30 min. Before morphological examination, specimens were completely dissected in a drop of 40% glycerol and mounted on a slide with coverslip.

The examination of body parts and ornamentations was performed under a Nikon ECLIPSE E200 compound light microscope at 1000 \times magnification. The habitus and appendages were drawn using a drawing tube attached to a compound microscope. Morphological descriptions were made based on the terminology used in Huys and Boxshall (1991). The descriptive abbreviations used in the description and figures are as follows: **ae** = aesthetasc, **I** = spine, **Endp** = endopod, **Exp** = exopod, **Endp-1 (2)** = proximal (distal) segment of the endopod of the swimming legs, **Exp-1 (2, 3)** = proximal (middle, distal) segment of the exopod of the swimming legs, **P1–P6** = first to sixth swimming legs, **Seta I–VII** = first to seventh caudal seta, **Seta I** = anterolateral accessory seta, **Seta II** = anterolateral seta, **Seta III** = postereolateral seta, **Seta IV** = outer terminal seta, **Seta V** = inner terminal seta, **Seta VI** = terminal accessory seta, and **Seta VII** = dorsal seta.

The type materials have been deposited at the Princess Maha Chakri Sirindhorn National History Museum at Prince of Songkla University, Songkhla, Thailand (PSUNHM).

Taxonomy

Order Harpacticoida G.O. Sars, 1903

Family Canthocamptidae Brady, 1880

Subfamily Cletocamptinae Gómez & Yáñez-Rivera, 2022

Genus *Cletocamptus* Schmankevitsch, 1875

Cletocamptus thailandensis sp. nov.

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Figs 2–7 (female), 8–11 (male)

Material examined. *Holotype*: THAILAND • 1 ♀ (adult), 670 μm long; Rayong Province; 12°45'52.96"N, 101°47'55.16"E, 24 m a.s.l.; 19 Jul. 2022; C. Boonyanusith leg.; hand net; completely dissected and mounted on a slide in glycerol and sealed with nail polish; PSUZC-PK2007-01. *Allotype*: THAILAND • 1 ♂ (adult), 483 μm long; 22 May 2022; other collection data as for holotype; PSUZC-PK2007-02. *Paratypes*: THAILAND • 1 ♀ (adult) and 1 ♂ (adult); same data as for holotype; PSUZC-PK2007-03 and PSUZC-PK2007-04, respectively.

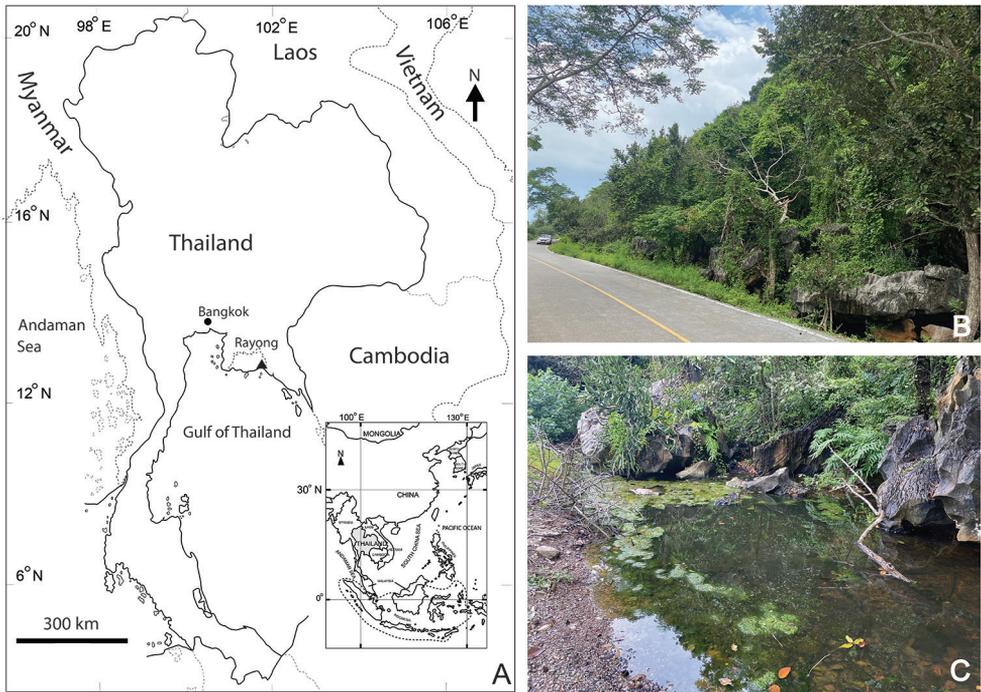


Figure 1. Geographical location and details of sampling site **A** map of Thailand and location of sampling site in Rayong province (indicated by a triangular) **B** details of the mountain in which, the specimens were collected **C** details of the type locality.

Additional material. THAILAND • 1 ♂ (adult), 1 ♀ (adult); same data as for holotype; preserved in 70% ethanol; retained in collection of the first author (CB).

Diagnosis. Female: Body fusiform. All abdominal somites with row of moderately long spinules on lateral surface. Anal operculum with two rows of spinules. Caudal ramus ca. 1.7× as long as wide, with three rows of spinules on inner margin. Antennary exopod with three setae. Mandibular palp with two setae on free segment and one seta arising nearby. Praecoxal arthrite of maxillule with moderately strong, lateral seta. P1Endp-1 reaching distal fourth of Exp-2, with inner seta. Armature complement of Exp-3 and Endp-2, from P1–P4: 4.5.6.5 and 3.3.5.2, respectively. Inner apical seta on P3Endp-3 reaching mid length of outer one. P5 with large notch between baseoendopodal lobe and exopodal one, with six marginal setae on the former and five setae on the latter. P6 reduced to small protuberance with one apical seta on peduncle. **Male:** Left and right legs of P5 fused at base, with three marginal setae on baseoendopodal lobe and four setae on exopodal one. P6 reduced to simple unarmed plate.

Description of adult female. Total body length, excluding caudal setae, ranging from 630 µm to 680 µm (mean = 655; $n = 4$). Habitus tapering posteriorly, with maximum width at posterior fourth of cephalothorax (Fig. 2A, B). Rostrum (Fig. 3A) well developed, distinct, with broad base and rounded tip; dorsal surface with pair of

sensilla; ventral surface with arch row of long spinules subdistally. Prosome ca. $1.1\times$ as long as urosome (including caudal rami), comprising cephalothorax and three free pedigerous somites (P2–P4-bearing somites). Cephalothorax ca. $1.1\times$ as long as wide and ca. $0.5\times$ as long as length of prosome, furnished with numerous pits, with numerous sensilla and with long spinules along margin dorsally and laterally (Fig. 2A, B). Dorsal and lateral surfaces of free pedigerous somites with numerous transverse rows of spinules, with stronger spinules and subdistal sensilla near posterior margin; posterior margin with long spinules.

Urosome (Figs 2A, B, 3B) comprising fifth pedigerous somite (P5-bearing somite), genital double-somite, and three free abdominal somites; lateral surface of all abdominal somites with row of moderately long spinules (Fig. 2B). Fifth pedigerous somite (first urosomite) with numerous transverse rows of spinules, with spinules and subdistal sensilla near posterior margin; posterior margin with larger spinules dorsally and long spinules laterally. Second and third urosomites fused ventrally forming genital double-somite, ca. $0.6\times$ as wide as long, with subchitinous rib representing former division of genital somite and first abdominal one and dividing genital double-somite into anterior and posterior portions; dorsal and lateral surfaces of both portions with numerous transverse rows of spinules, with spinules along margin of subchitinous rib and with hair-like spinules near posterior margin of posterior portion; ventral surface with row of spinules medially, with ventral pore beside medial row of spinules (Fig. 3B); posterior margin of double-somite with moderately long spinules. Genital field (Fig. 3B) with ovipore medially at the middle of genital double-somite. Second and third abdominal somites (fourth and fifth urosomites) with numerous transverse rows of spinules, with hair-like spinules dorsally and sensilla near posterior margin and with moderately longer spinules along posterior margin.

Anal somite (Figs 2C, 3B) with pair of dorsal sensilla in front of anal operculum, with numerous paired rows of moderately long spinules on dorsal, lateral, and ventral surfaces as shown, accompanied with two pairs of cuticular pores ventrally. Anal operculum slightly convex, with two rows of spinules.

Caudal rami (Figs 2C, D, 3B) slightly divergent, each ca. $1.7\times$ as long as wide, with seven setae; ornamentation comprised of three transverse rows of spinules on inner margin, row of spinules dorsally near distal margin, oblique row of strong spinules near insertion of seta IV, row of long spinules ventrally near insertion of seta IV and seta V, and cuticular pore near base of seta II. Seta I inserted ventro-laterally near insertion of rami; seta II and seta III inserted closely to each another at anterior third of ramus; seta IV and V, ca. 0.22 and ca. 0.58 of body length, respectively, with fracture plane in seta V; seta VI slender, inserted on inner distal corner; seta VII biarticulate, inserted at mid length of ramus medially.

Antennule (Fig. 4A) six-segmented. First segment with two rows of spinules medially. Fourth segment with aesthetasc on peduncle; aesthetasc slightly elongated, $> 45\%$ of length of aesthetasc surpassing the tip of antennule. Ultimate segment ca. $4.5\times$ as long as wide, with aesthetasc. Aesthetascs fused to seta at base. Armature formula: 1-[1], 2-[9], 3-[6], 4-[1 + (1 + ae)], 5-[1], 6-[9 + (1 + ae)].

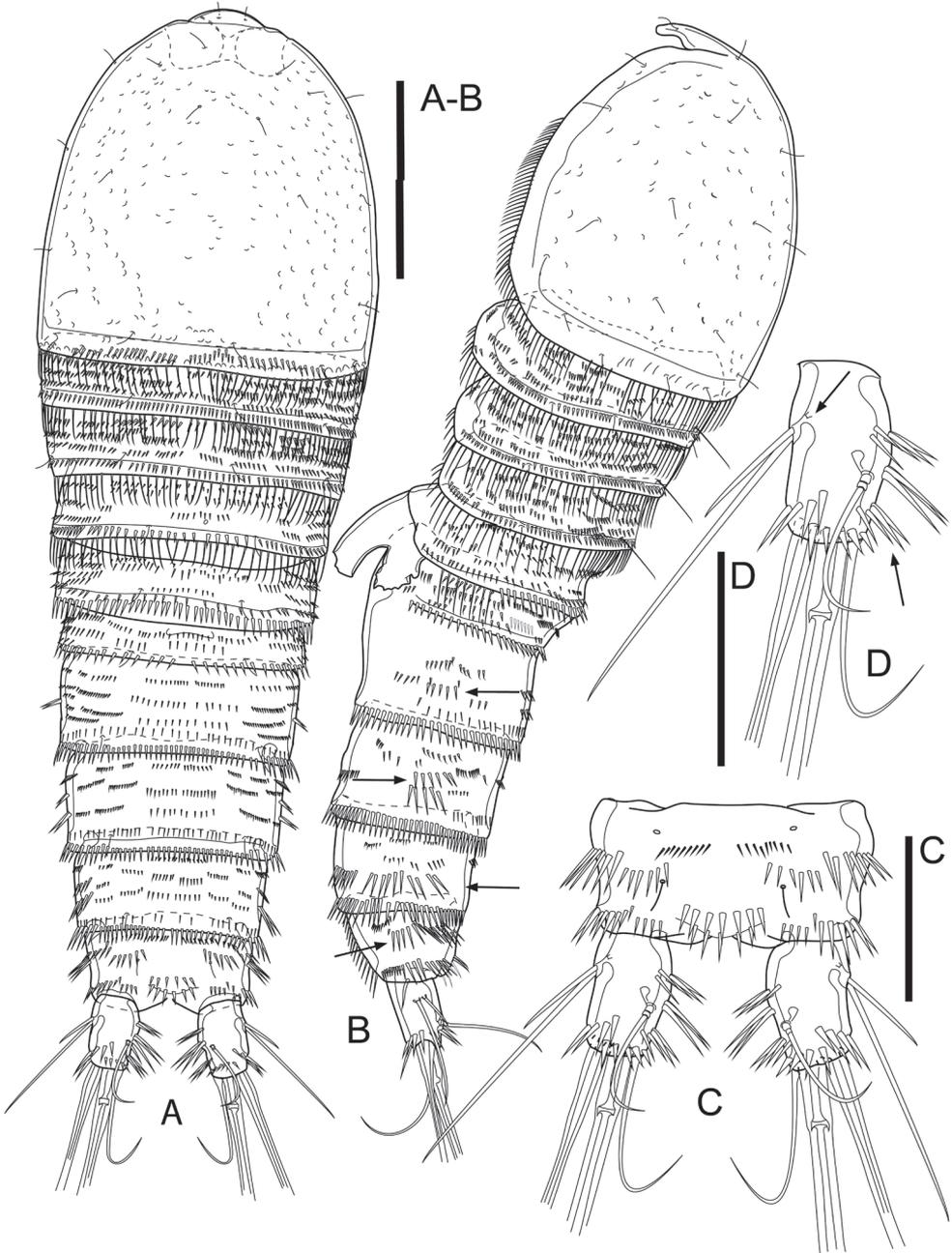


Figure 2. *Cletocamptus thailandensis* sp. nov. female, holotype **A** habitus, dorsal view **B** habitus, lateral view (Arrows indicate rows of moderately long spinules) **C** anal somite and caudal rami, dorsal view **D** caudal ramus, dorsal view (Arrows indicate cuticular pore and additional row of spinules). Scale bars: 50 μ m.

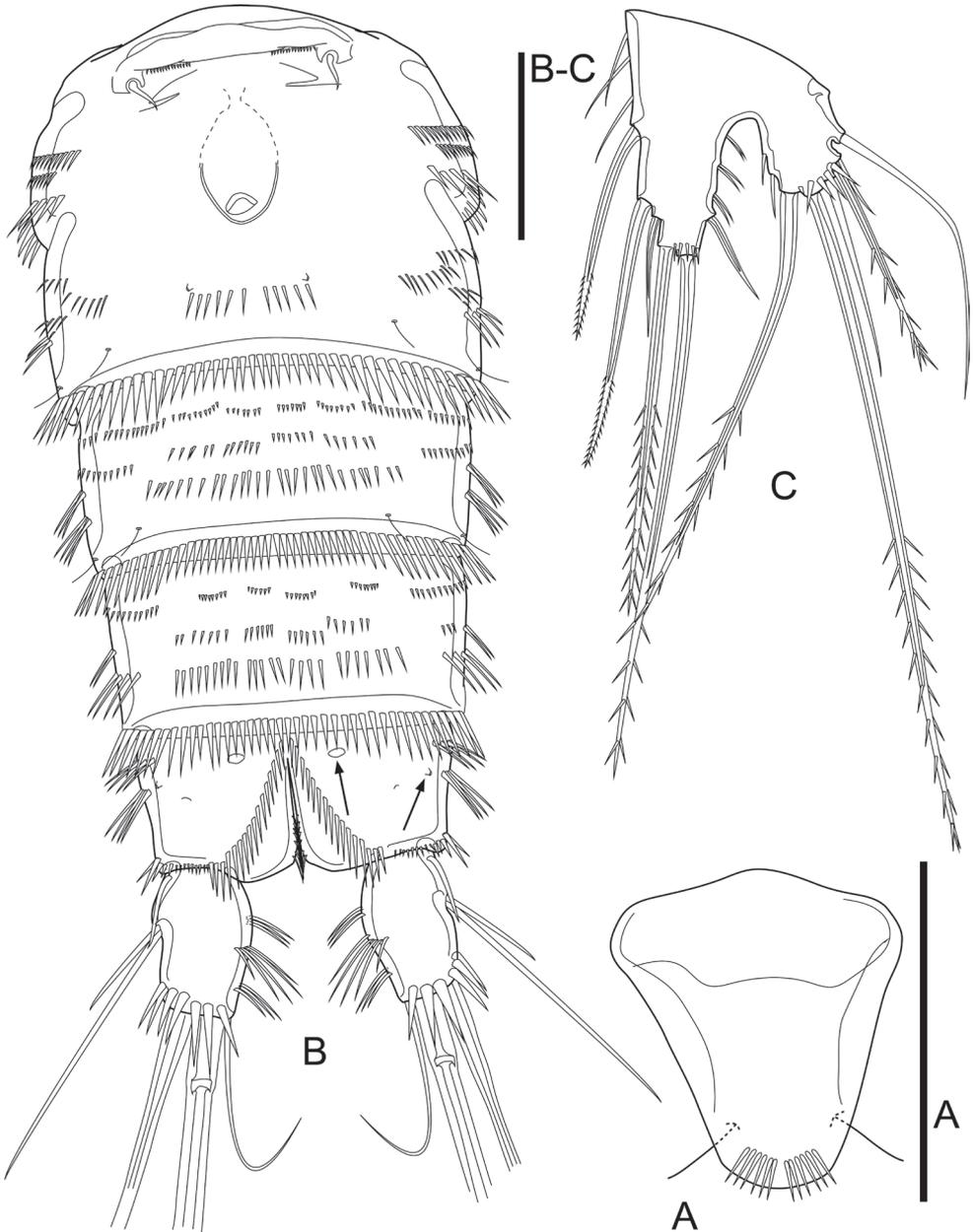


Figure 3. *Cletocamptus thailandensis* sp. nov. female, holotype **A** rostrum, ventral view **B** urosome, ventral view **C** P5. Scale bars: 50 μ m.

Antenna (Fig. 4B) biramous, comprising coxa, allobasis, one-segmented Exp, and one-segmented Endp. Coxa short, with arch row of spinules on outer margin. Allobasis with two abexopodal setae. Exp cylindrical, with few spinules subdistally and armed with one lateral seta and two apical setae (one of the apical setae short and slim).

Endp club-shaped, with one short seta and two spines medially on inner margin, and five apical setae of which two innermost ones spiniform, two median ones geniculate, outermost one spiniform with two strong spinules half-length of element and bipinnate along distal half; spinule ornamentation comprised of proximal and distal rows of strong spinules, and row of spinules distally.

Mandible (Fig. 4C) comprising sclerotized coxal gnathobase and mandibular palp. Coxal gnathobase with two arch rows of spinules as shown; cutting edge with five bicuspidate and multicuspidate teeth, with one pyriform element and pinnate, ventral seta. Mandibular palp one-segmented, with two apical setae, accompanied with one short seta inserted nearby.

Maxillule (Fig. 5A, B) comprising robust praecoxa, coxa, and basal complex, the latter composed of basis with Endp and Exp completely incorporated to the latter. Praecoxal arthrite with row of spinules on caudal surface and on lateral margin, armed with surface seta on frontal surface and nine distal elements: seven of which strong, curved spines, subdistal seta slim and pinnate, lateral seta moderately strong and pinnate. Coxa with cylindrical endite bearing two smooth apical setae, and with few spinules. Basis seemingly with three apical setae of which middle robust and pinnate. Endp and Exp completely incorporated to basis, seemingly represented by three setae each.

Maxilla (Fig. 5C) composed of syncoxa and allobasis, and Endp fully incorporated to the latter. Syncoxa with two endites, each endite armed with three elements apically, one of which slender. Allobasis drawn out into claw, with one seta basally on caudal surface. Endp completely incorporated to allobasis, represented by three smooth setae.

Maxilliped (Fig. 5D) subchelate, three-segmented, comprising syncoxa, basis, and Endp. Syncoxa with curved row of spinules on caudal surface, with one pinnate seta on inner distal corner. Basis with longitudinal row of spinules on frontal and caudal surfaces, and two transverse rows of spinules on outer margin. Endp drawn out into strong claw and armed with one minute seta near base.

P1–P4 comprised of intercoxal sclerite, praecoxa, coxa, basis, and two rami.

P1 (Fig. 6A). Intercoxal sclerite as shown, with two rows of minute spinules on each side. Praecoxa triangular, with spinules along distal margin and on outer distal corner. Coxa rectangular, with one row of spinules medially, with two oblique rows of spinules and with strong spinules on outer distal corner. Basis with integumental pore on frontal surface, with oblique row of spinules and three rows of stronger spinules of which innermost at base of inner spine, median between insertion of rami, outermost at base of Exp; armament comprising outer and inner spines, inner spine reaching distal third of Endp-1. Exp three-segmented, all segments with spinule row on outer margin and outer distal corner; Exp-1 with outer spine; Exp-2 with outer spine and inner seta; Exp-3 with four elements: innermost and inner apical ones slender. Endp two-segmented, reaching tip of Exp; Endp-1 reaching distal fourth of Exp-2, with inner seta; Endp-2 slightly longer than Endp-1, with three elements of which outer apical spiniform.

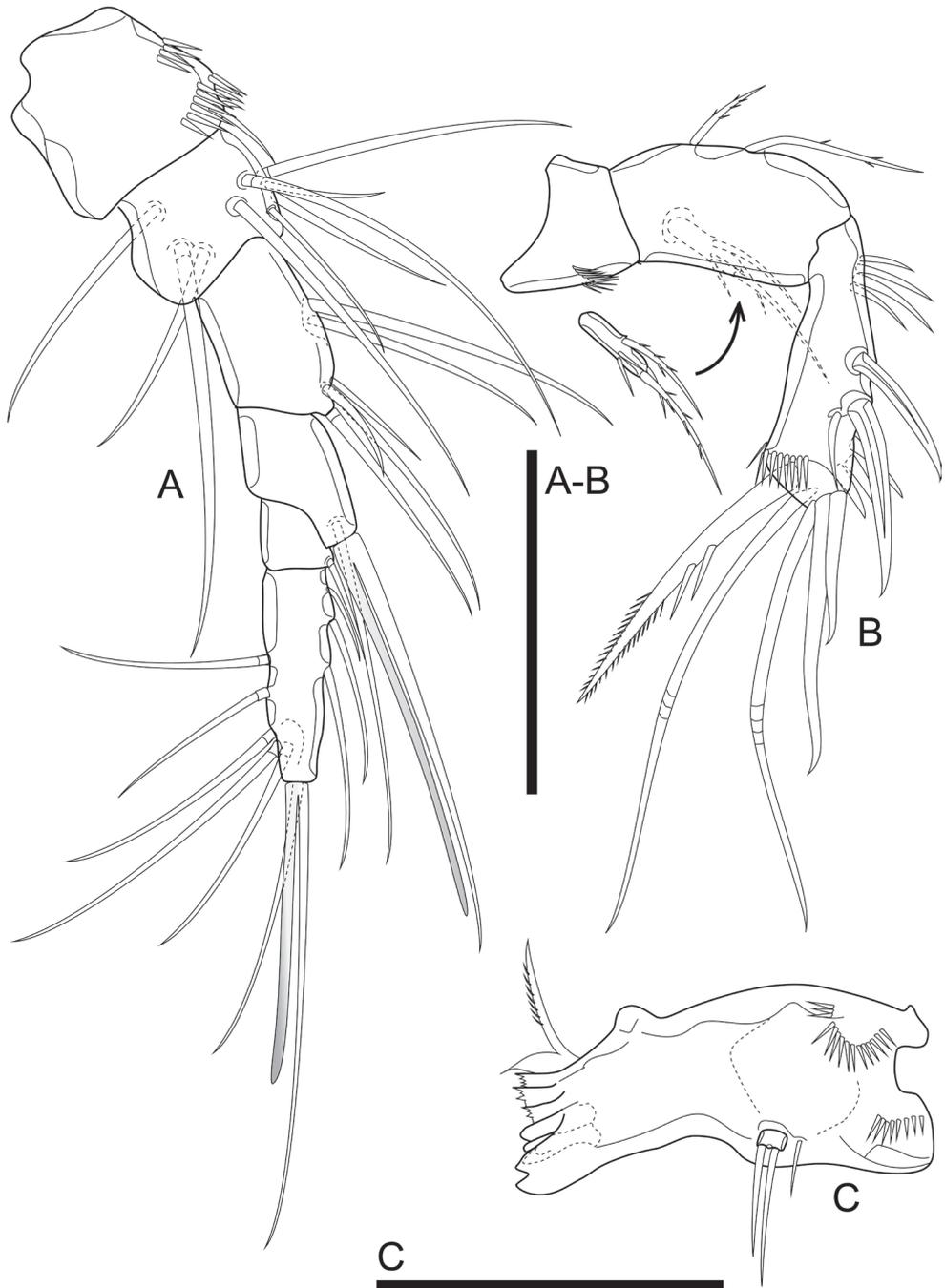


Figure 4. *Cletocampus thailandensis* sp. nov. female, holotype **A** antennule **B** antenna **C** mandible. Scale bars: 50 μ m.

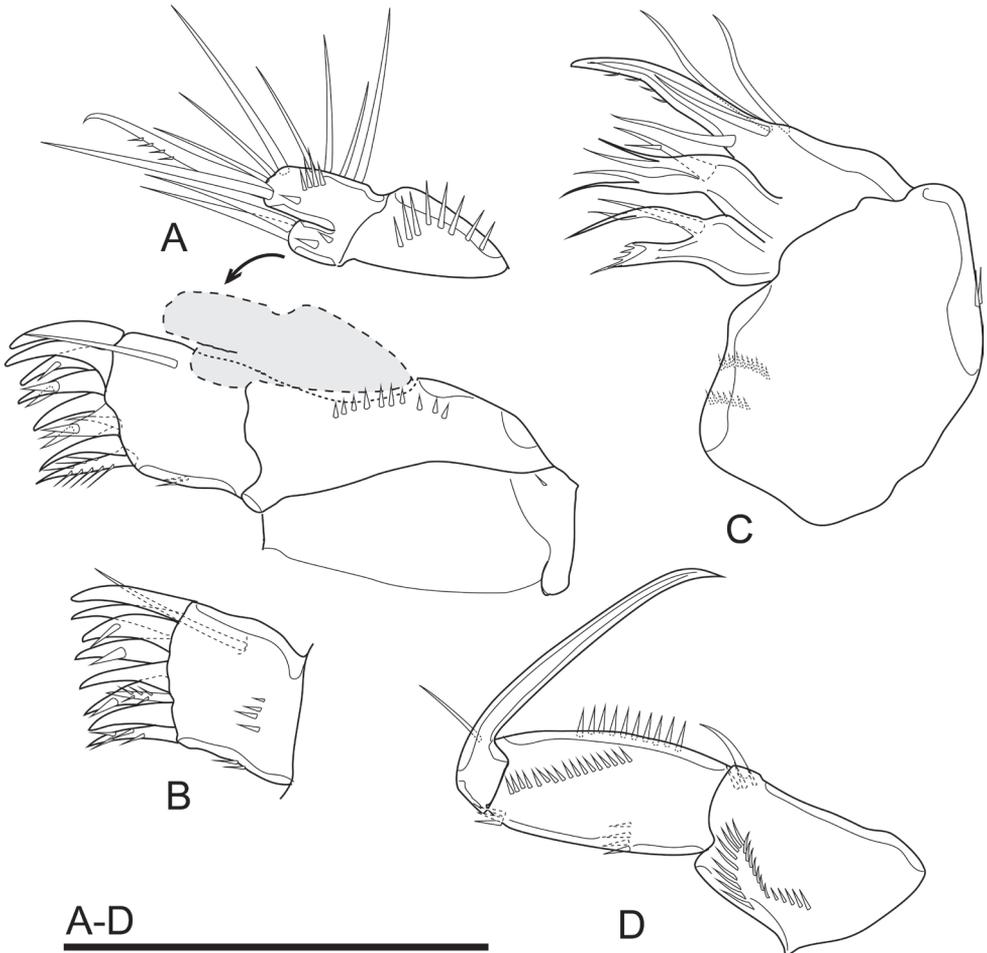


Figure 5. *Cletocamptus thailandensis* sp. nov. female, holotype **A** maxillule, frontal view **B** praecoaxal arthrite, caudal view **C** maxilla, caudal view **D** maxilliped, caudal view. Scale bar: 50 μ m.

P2 (Fig. 6B). Intercoxal sclerite as shown, bare. Praecoaxa with spinules along distal margin. Coxa with row of spinules medially and strong spinules along outer margin. Basis as that of P1 but lacking inner spine and inner distal corner; spinule row between rami with smaller spinules relative to those of P1; with medial pore proximally. Exp three-segmented, with spinule ornamentation as that of P1, additionally with row of spinule on inner distal corner of Exp-1 and Exp-2; Exp-1 with outer spine; Exp-2 with outer spine and inner seta; Exp-3 with five elements (two outer spines, two distal and one inner seta). Endp two-segmented, reaching middle of Exp-2; Endp-1 small, wider than long, with inner spinules; Endp-2 ca. 3.0 \times as long as wide, with spinule ornamentation on outer and inner margins, armed with three elements of which outer spiniform and slender.

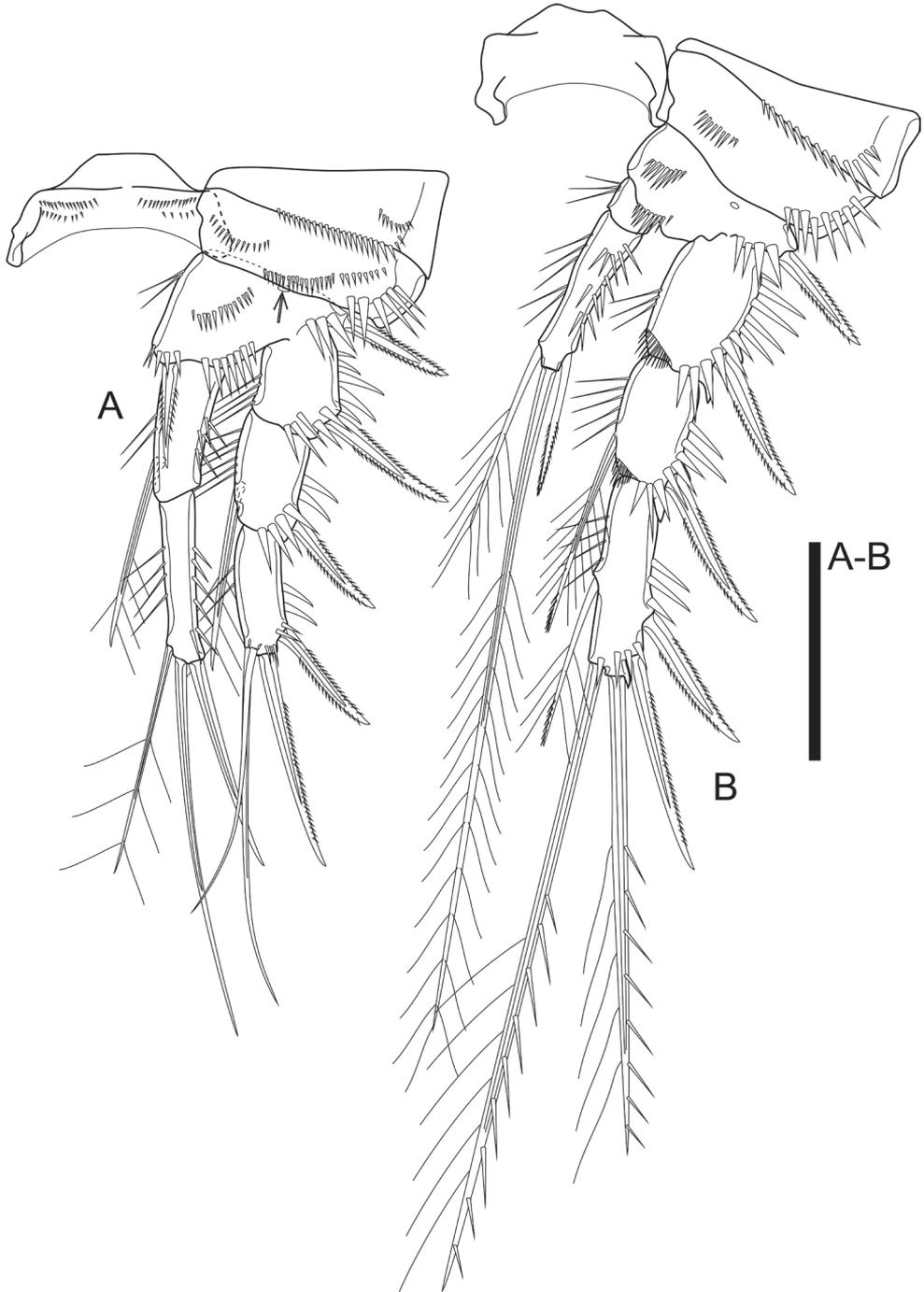


Figure 6. *Cletocamptus thailandensis* sp. nov. female, holotype **A** P1 **B** P2. Scale bar: 50 μ m.

P3 (Fig. 7A). Intercoxal sclerite, praecoxa, coxa, and basis as those of P2. Exp three-segmented; Exp-1 and Exp-2 as those of P2; Exp-3 with six elements (two outer spines, two distal and two inner seta). Endp two-segmented; Endp-1 small, wider than long, with inner spinules; Endp-2 ca. 3.5× as long as wide, armed with five elements of which outer spiniform and slender, inner apical one reaching middle of outer apical one, two inner ones subequal in length.

P4 (Fig. 7B). Intercoxal sclerite, praecoxa, coxa, and basis as those of P2. Exp three-segmented; Exp-1 and Exp-2 as those of P2; Exp-3 with five elements (two outer spines, two distal and one inner seta). Endp two-segmented; Endp-1 small, wider than long, with inner spinules; Endp-2 ca. 2.5× as long as wide, armed with two apical setae of which outer ca. 2.5× as long as inner one.

Armature formula of P1–P4 as in Table 1.

Table 1. Armature formula of P1–P4 of *Cletocamptus thailandensis* sp. nov. Arabic numerals indicate number of setae; Roman numerals indicate number of spines.

Legs	Basis	Exopod			Endopod		
		1	2	3	1	2	3
P1	I-1	I-0	I-1	I-II-1	0-1	0-II-1	
P2	I-0	I-0	I-1	II-2-1	0-0	I-1-1	
P3	I-0	I-0	I-1	II-2-2	0-0	I-2-2	
P3 (male)	I-0	I-0	I-1	II-2-2	0-0	0-0	0-2-0
P4	I-0	I-0	I-1	II-2-1	0-0	0-2-0	

P5 (Fig. 3C). Baseoendopod and Exp completely fused basally, with large notch between them; left and right legs completely separated. Baseoendopodal lobe ca. 1.5× as long as length of exopodal one, with one outer, two apical and three inner setae. Exopodal lobe with five elements accompanied with slender, outer seta of basis; relative length and characteristics of setae on both baseoendopodal and exopodal lobes as shown.

P6 (Fig. 3B) reduced to minute prominence, forming simple plate near anterior margin of genital double-somite, with row of minute spinules and one short seta on each side.

Description of adult male. Body smaller than in female. Total body length, excluding caudal setae, ranging from 483 µm to 505 µm (mean = 493; $n = 4$). Prosome ca. 1.1× as long as urosome (Fig. 8A, B). Cephalothorax slightly longer than wide, ca. 0.6× as long as length of prosome. Rostrum (Fig. 8C) well developed, distinct, narrower than that of female, with rounded tip; dorsal surface with pair of sensilla, ventral surface with arch row of long spinules subdistally. Ornamentation of cephalothorax and free prosomite as those of female.

Urosome (Figs 8A, B, 9A) six-segmented, comprising fifth pedigerous somite, genital somite and four free abdominal somites; lateral surface of all abdominal somites with row of moderately long spinules. Dorsal and lateral surfaces of fifth pedigerous somite with numerous transverse rows of spinules, with spinules and subdistal sensilla near posterior margin; posterior margin with long spinules. Genital somite with

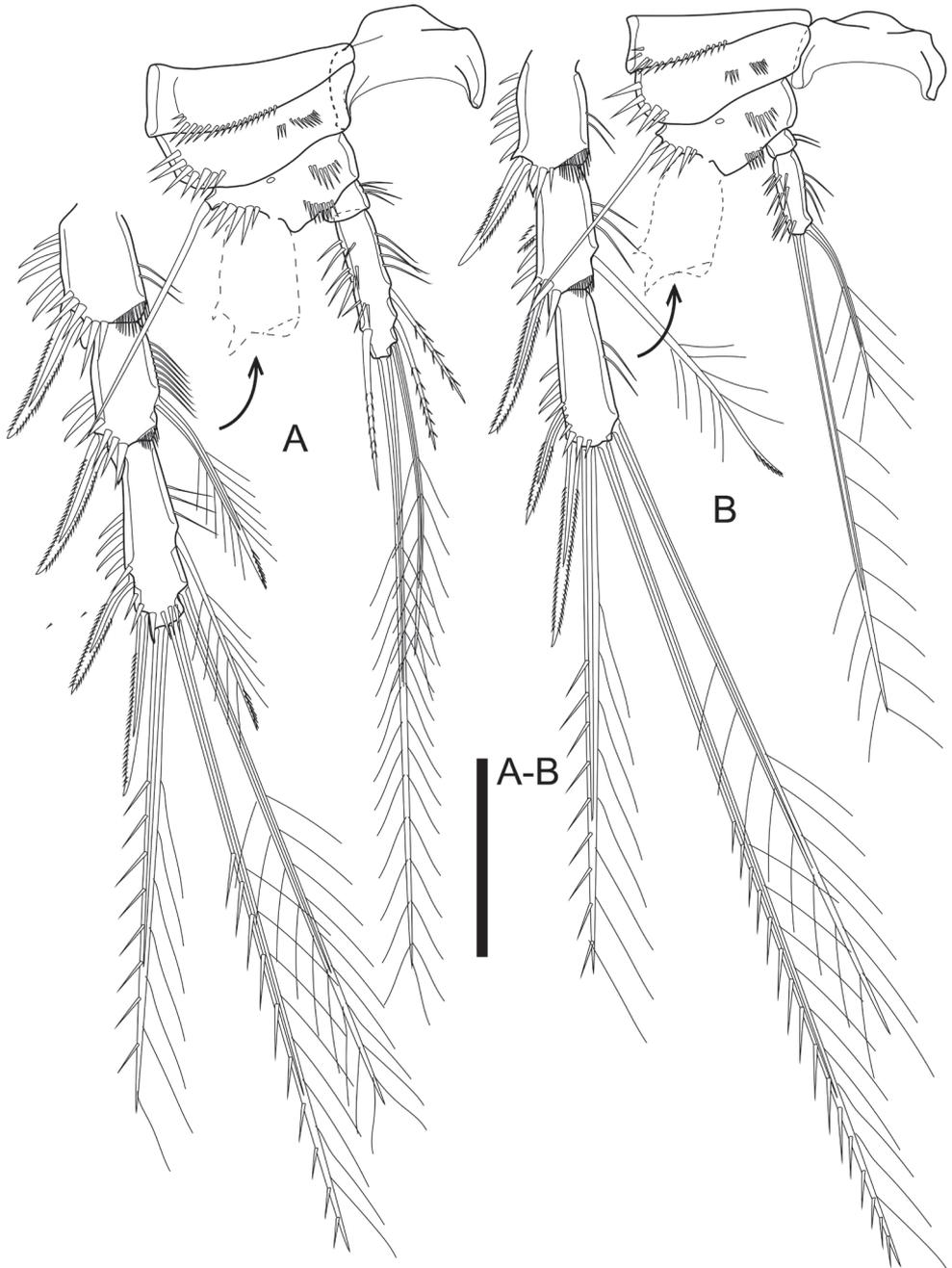


Figure 7. *Cletocampus thailandensis* sp. nov. female, holotype **A** P3 **B** P4. Scale bar: 50 μ m.

numerous transverse rows of spinules, with spinules and subdistal sensilla near posterior margin; posterior margin with larger spinules dorsally and long spinules laterally. Genital opening positioned mid-ventrally near anterior margin of genital somite (Fig. 9A).

First to third abdominal somites as those of female, but lacking hair-like spinules near posterior margin; spinule ornamentation lesser developed in comparison to those of female, each somite with three medial rows of spinules ventrally. Anal somite (Figs 8D, 9A) as that of female.

Caudal rami (Figs 8D, 9A) as that of female, but inner margin with only two transverse rows of spinules. Seta IV and V, ca. 0.26× and ca. 0.59× body length, respectively. Seta VI relatively shorter than that of female.

Antennule (Fig. 9B, C) subchirocerate, six-segmented. First segment with two rows of spinules medially. Fourth segment bulbous, with aesthetasc on peduncle. Ultimate segment with two claw-shaped extensions subdistally. Aesthetascs to seta at base. Armature formula: 1-[1], 2-[9], 3-[6], 4-[7 + (1 + ae)], 5-[1], 6-[6 + (1+ae)].

Antenna, mandible, maxillule, maxilla, and maxilliped as those of female.

P1 (Fig. 10A) as that of female, except for the projection on inner distal corner of basis.

P2 (Fig. 10B) as that of female, except for sexual dimorphic (slightly shorter and stronger) inner seta on Endp-2.

P3 (Fig. 11A) as that of female in intercoxal sclerite, praecoxa, coxa, basis, and Exp. Endp three-segmented; Endp-1 short, wider than long; Endp-2 drawn out into apophysis, with row of spinules on outer margin and on frontal surface near base of Endp-3, apophysis surpassing tip of Endp-3; Endp-3 with two apical setae.

P4 (Fig. 11B) as that of female.

Left and right legs of P5 (Fig. 10C) fused medially at base, with medial notch indicating former separation between them; baseoendopod and Exp fused basally, with large notch indicating division between baseoendopodal and exopodal lobes. Baseoendopodal lobe with three pinnate spiniform setae apically, setae subequal in length; exopodal lobe with spinules at base of outermost apical seta, armed with four elements of which three apical ones pinnate and spiniform, outermost smooth and slender. Smooth soft seta on outer margin of basis, accompanied with row of spinules at base.

P6 (Fig. 9A) reduced to simple plate, without armature and ornamentation. Posterior margin smooth.

Etymology. The species name is a noun proposed to reflect the name of the country, 'Thailand', where the new species was encountered. It is in the nominative singular, gender masculine.

Type locality. The new species was collected from a water body at the base of an isolated limestone mountain (Fig. 1A, B) that is the distalmost part of the Cha Moon-Cha Mao Mountain Range in the Gong Din Subdistrict, Klaeng District, Rayong Province, Eastern Thailand. The coordinates of the type locality are 12°45'52.96"N, 101°47'55.16"E. The mountain is located beside a monastery known in Thai as 'Wat Tham Rakang Thong' (Tham Rakang Thong Monastery). The mountain and the water body are surrounded by a manmade concrete road (Fig. 1C), which separates the mountain and the monastery from the mangrove forests. The water is ca. 20 cm in depth and transparent with a brown color. The bottom of the water body is covered

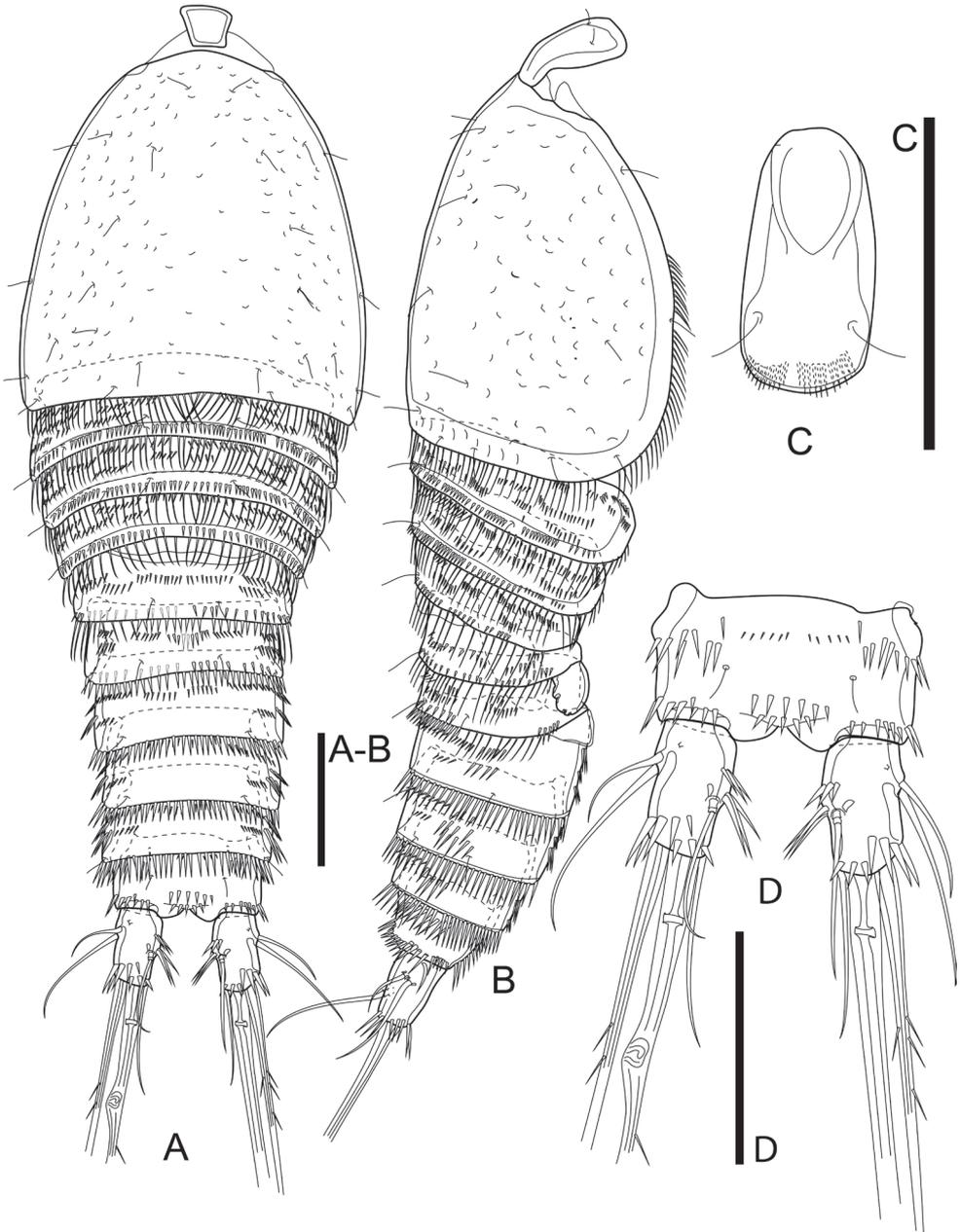


Figure 8. *Cletocamptus thailandensis* sp. nov. male, allotype **A** habitus, dorsal view **B** habitus, lateral view **C** rostrum, frontal view **D** anal somite and caudal rami, dorsal view. Scale bars: 50 μm .

by leaf litter and filamentous algae. On the first sampling occasion, the temperature was 27.4 °C, the pH was 5.48, and the dissolved oxygen level was 5.5 mg L⁻¹. The water electroconductivity and total dissolved solids were higher than 3,999 $\mu\text{S cm}^{-1}$

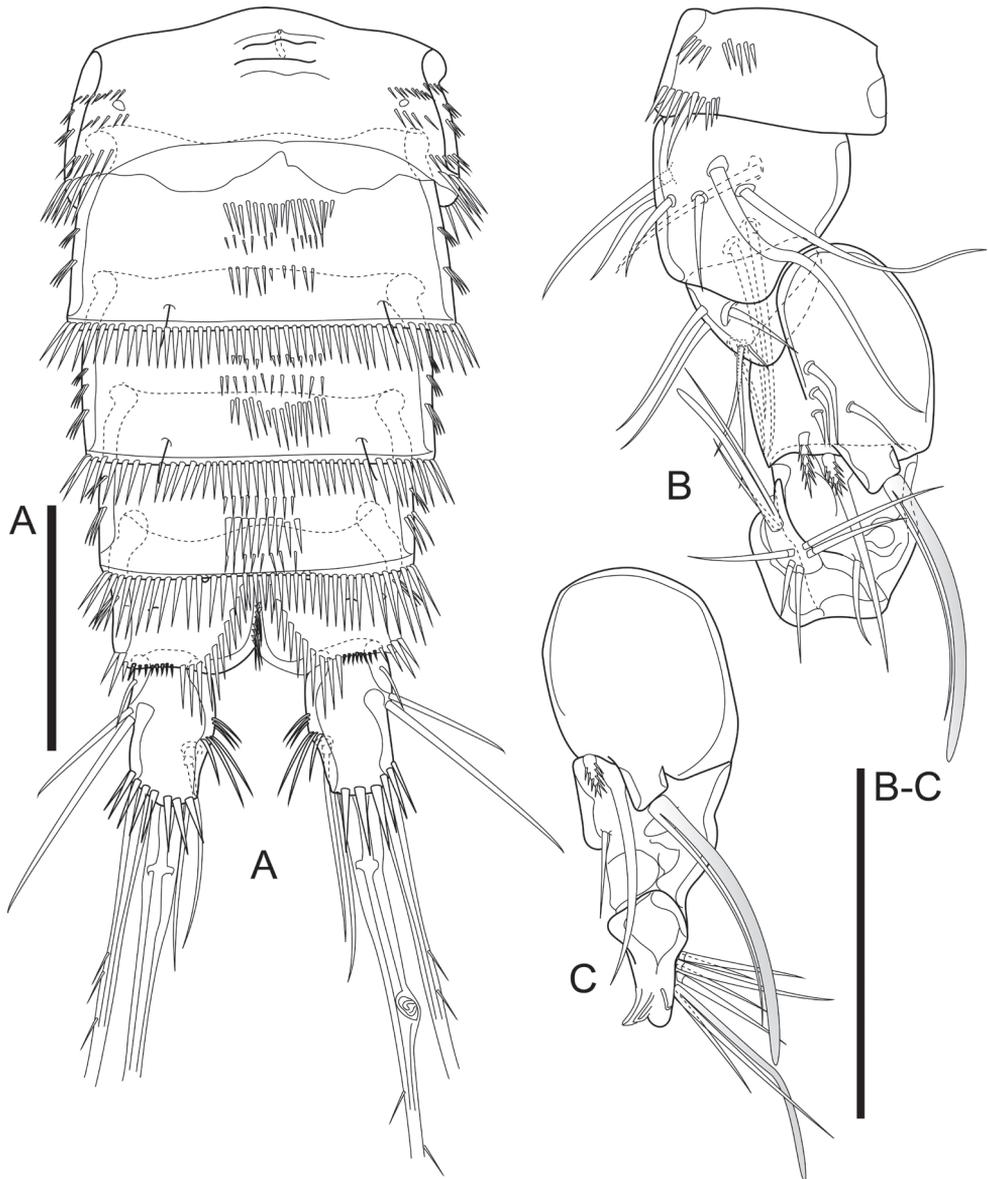


Figure 9. *Cletocamptus thailandensis* sp. nov. male, allotype (**A**, **B**); paratype (**C**) **A** urosome, ventral view **B** antennule **C** segments 4–6 of antennule. Scale bars: 50 μ m.

and 2,000 ppm, respectively. On the second occasion, the temperature was 30.0 °C, the pH was 6.53, the electroconductivity was 2,158 μ S cm^{-1} , and the total dissolved solids were 1,080 ppm. The new species was collected with other zooplankton species, such as *Phyllognathopus paludosus* (Mrazek, 1893), *Mesocyclops ogunnus* Onabamiro, 1957 (the most dominant), *Apocyclops borneoensis* Lindberg, 1954, *Tropocyclops* sp., *Nitokra* sp., the rotifer of the genus *Testudinella* Bory de St. Vincent, 1822, the clad-

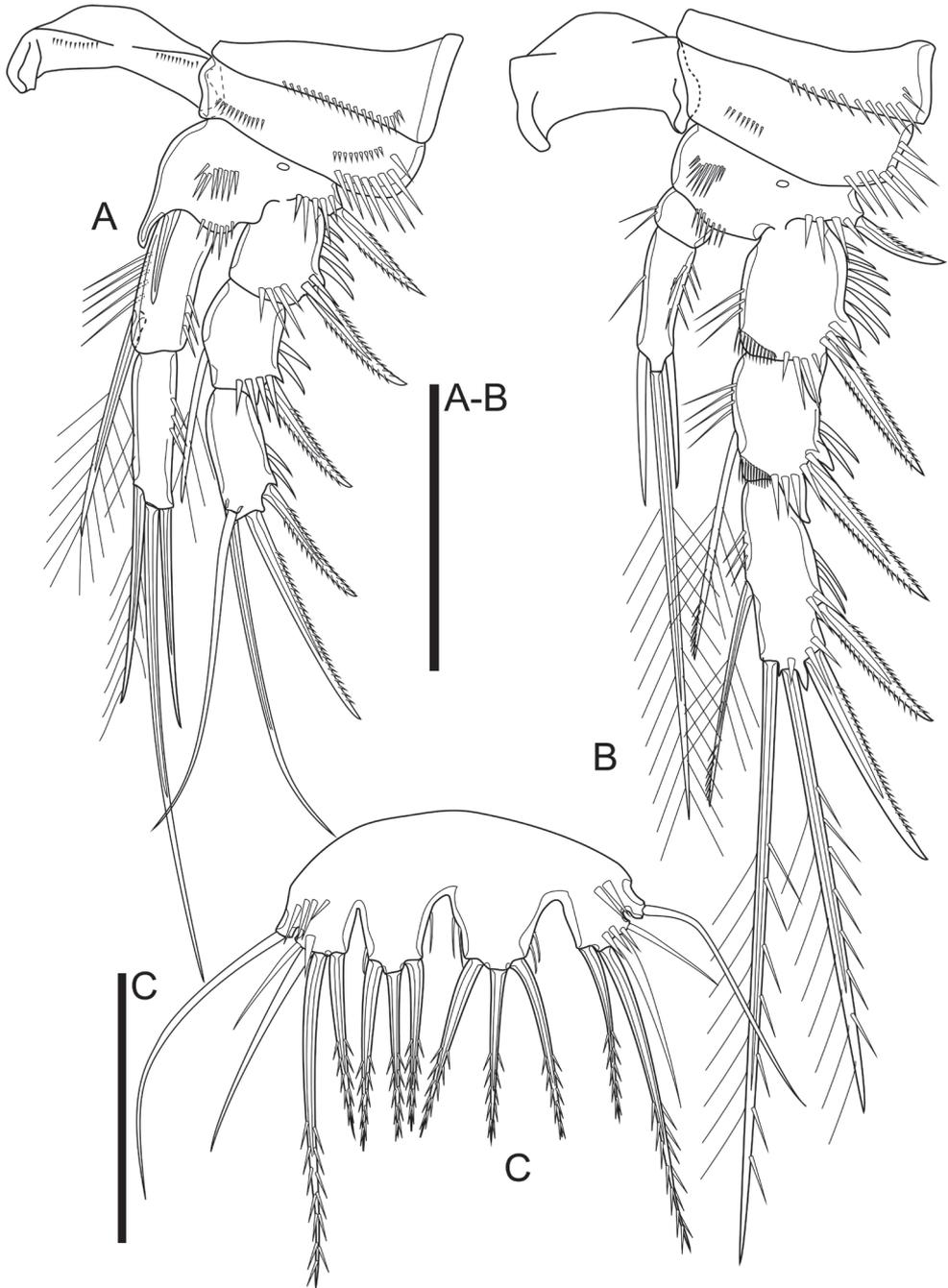


Figure 10. *Cletocamptus thailandensis* sp. nov. male, allotype **A** P1 **B** P2 **C** P5. Scale bars: 50 μ m.

oceran of the genus *Leberis* Smirnov, 1989, and ostracods. Aquatic insects belonging to the order Ephemeroptera and the family Chironomidae were also observed.

Distribution. The species has been known from the type locality only.

Remarks

The new species was assigned to the genus *Cletocamptus* because of the combination of the following characteristics:

1. a sexually dimorphic rostrum with subdistal ventral spinules,
2. a cephalothorax and prosomite with long spinules along the posterior margin,
3. a sexually dimorphic outer spine on the P2Endp-2,
4. the genital and first abdominal somites being completely fused ventrally, forming a genital double-somite with the dorsal subchitinous rib on the dorsal and lateral surfaces.

The genus has now been placed in the subfamily Cletocamptinae of the family Canthocamptidae, along with *Cletocamptoides* and *Amphibiperita* (Gómez and Yáñez-Rivera 2022). Among these three genera, *Cletocamptus* is the sister group of *Cletocamptoides*, according to phylogenetic research (Gómez and Yáñez-Rivera 2022). The new species and other *Cletocamptus* can be distinguished from *Cletocamptoides* by the following characteristics:

1. the absence of a somatic constriction between the somite,
2. the presence of long spinules on the posterior margin of the cephalothorax and prosomite,
3. the reduced mandibular palp bearing, at most two setae on the free segment and one seta nearby (as opposed to three setae on one well-developed segment),
4. the P4 with two-segmented Endp (reduced to one segment in *Cletocamptoides*).

Recently, 28 species of *Cletocamptus* have been validated. In the valid species, five groups of species can be defined based on the combination of the following female characteristics: the number of setae on the P3Endp-2, the relative length of the caudal ramus, the relative length of the inner apical seta on the P3Endp-2, the shape of the P5, and the number of setae on the P3Exp-3 (Table 2). The first group is composed of *C. albuquerqueensis*, *C. dominicanus*, *C. tainoi*, *C. confluens*, *C. chappuisi*, and *C. trichotus*, which bear relatively long caudal rami ($> 2\times$ as long as wide), P3Endp-2 with five setae, P3Endp-2 with inner apical seta reaching the middle of the outer one, P5 exopodal lobe highly fused to the baseoendopodal lobe in the P5 of both males and females (baseoendopodal and exopodal lobes separated by small notch), and P3Exp-3 with five setae. In many species, the P1Endp-1 is relatively short, reaching the middle of Exp-2 at most, and the caudal seta IV and V are fused at the base. The second group comprises *C. pilosus* and *C. retrogressus*, which bear relatively long caudal rami ($> 2\times$ as long as wide), P3Endp-2 with five setae, P3Exp-3 with six setae, and P5 with a large notch between the exopodal and baseoendopodal lobes in both males and females. The inner apical seta of P3Endp-2 reaches the middle of the outer one in *C. retrogressus*, but it is shorter in *C. pilosus*. Furthermore, caudal seta IV and V are fused at the base in the former but separated in the latter. The third group is composed of *C. gomezi*, *C. mongolicus*, *C. feei*, *C. gravihatus*, and *C. affinis*, which, in general, bear relatively long caudal rami ($> 2\times$ as long as wide), P3Endp-2 with short inner apical seta not reaching the middle of the outer

one, P5 with a large notch between the exopodal and baseoendopodal lobes in both males and females, and P3Exp-3 with five setae. In this group, a reduction of either the number or the length of the inner seta of the P3Endp-2 was observed, resulting in variations in the number of setae on the P3Endp-2. In *C. gomezi*, *C. mongolicus*, *C. gravih hiatus* and *C. affinis*, there are five setae, whereas there are four in *C. feei*. Even if the number of inner setae is not reduced, the inner and inner apical seta are relatively shorter than those of most species of the first and the second groups. The fourth group is composed of *C. stimpsoni*, *C. goenchim*, and *C. koreanus*, which bear relatively short caudal rami (generally, ca. 1.5–1.7× as long as wide), P3Endp-2 with five setae, P3Endp-2 with an inner apical seta reaching the middle of the outer one (except in *C. stimpsoni*), P5 with a large notch between the exopodal and baseoendopodal lobes in both males and females, and P3Exp-3 with six setae. It has been found that P1Endp-1 reaches the distal margin of the Exp-2. The last group comprises *C. assimilis*, *C. axi*, *C. cecsurirensis*, *C. deborahdexterae*, *C. fourchensis*, *C. levis*, *C. nudus*, *C. samariensis*, *C. schmidt*, *C. sinaloensis*, *C. spinulosus*, and *C. tertius*, which, in general, bear relatively short caudal rami (mostly ca. 1.5× as long as wide), P3Endp-2 with three setae, P3Endp-2 with an inner apical seta not reaching the middle of the outer one (except *C. spinulosus*), P5 with a large notch between the exopodal and baseoendopodal lobes in both males and females, and P3Exp-3 with six setae in *C. nudus*, *C. samariensis*, and *C. schmidt* but five in the rest. In this group, the P1Endp-1 is relatively short, reaching the middle of Exp-2 at most, and the lateral seta of the praecoxal arthrite of the maxillule is robust and spinulose in many species, including *C. assimilis*, *C. axi*, *C. cecsurirensis*, *C. deborahdexterae*, *C. fourchensis*, *C. levis*, *C. nudus*, *C. samariensis*, *C. schmidt*, *C. sinaloensis*, and *C. tertius*. Only *C. spinulosus* has slender seta.

Table 2. Comparison of characters among five groups of species of the genus *Cletocamptus*. The superscripts indicate the feature that is less common in the group, and the species possessing it is listed in the note below the table.

Characters	Species group 1	Species group 2	Species group 3	Species group 4	Species group 5
Female					
1. Relative length of the caudal ramus	ca. 3–4 or 2 ^A	ca. 2 ^A or 3 ^B	ca. 3 or 2 ^A	ca. 1.5–1.7	ca. 1.5–1.7 or ca. 1.1 ^C or 2 ^A or 3 ^B
2. Caudal seta IV and V	Fused at base or separated ^D	Fused at base ^E or separated ^D	Separated	Separated	Separated
3. Armature formula of number of setae/spines on P2–P4Endp-2	3.5.2 or 3.3.2 ^F or 4.5.2 ^G	4.5.2	3.5.2 or 4.5.2 ^H or 3.4.2 ^I	3.5.2	3.3.2
4. Armature formula of number of setae/spines on P2–P4Exp-3	5.5.4	5.6.5	5.5.4 or 5.5.5 ^J	5.6.5	5.5.4 or 5.6.5 ^K
5. Length ratio of inner apical seta and outer apical seta of P3Endp-2	ca. 0.6–0.8	ca. 0.3–0.8	ca. 0.2	ca. 0.5–0.6	ca. 0.3–0.5
6. Notch between exopodal and baseoendopodal lobes	Small and shallow	Large	Large	Large	Large
Male					
7. Number of setae/spines on P2Endp-2	3	4	3 or 4 ^L	3	3
8. Endp-2 and Endp-3 of P3	Fused	Separated	Separated	Separated	Separated
9. Modification of P3Exp-1 in comparing to that of female	Elongated or not elongated ^M	Elongated or not elongated ^M	Slightly elongated	Not elongated	Elongated or not elongated ^M

Note: ^A = in *C. dominicanus*, *C. trichotus*, *C. pilosus*, *C. gomezi*, *C. axi*, and *C. schmidt*. ^B = in *C. retrogressus*, *C. tertius* and *C. spinulosus*. ^C = in *C. cecsurirensis*. ^D = in *C. trichotus* and *C. pilosus*. ^E = in *C. retrogressus*. ^F = in *C. confluentis*. ^G = in *C. trichotus*. ^H and ^L = in *C. gomezi*. ^I and ^J = in *C. feei*. ^K = in *C. nudus*, *C. samariensis*, and *C. schmidt*. ^M = in *C. dominicanus*, *C. retrogressus*, *C. nudus*, *C. samariensis*, and *C. schmidt*.

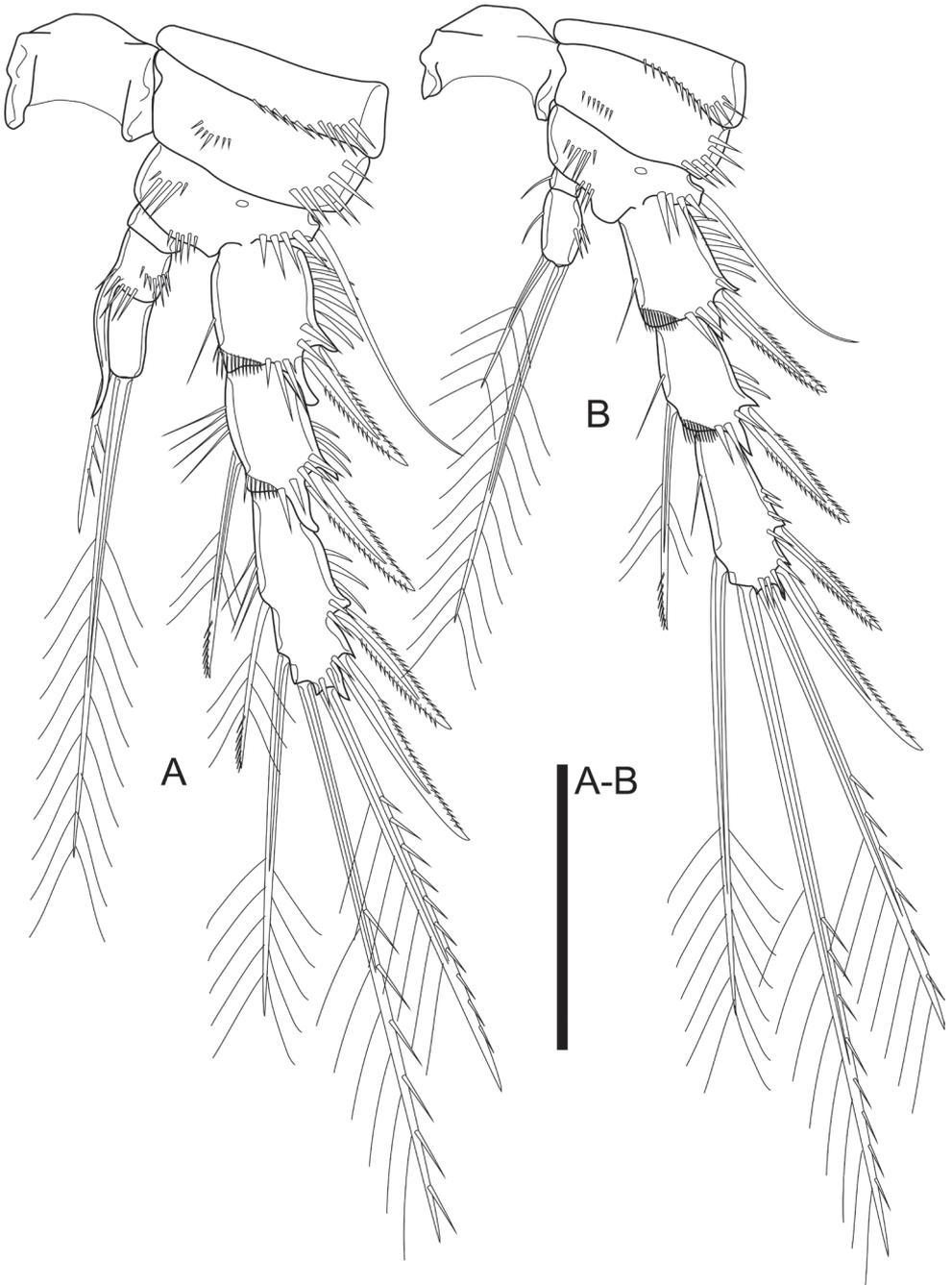


Figure 11. *Cletocamptus thailandensis* sp. nov. male, allotype **A** P3 **B** P4. Scale bar: 50 μ m.

Based on the above criteria, the new species belongs to the fourth group, and its most closely related species are *C. koreanus* and *C. goenchim*, corresponding to their geographical distribution. According to the characteristic of the relative length of the inner apical seta on P3Endp-2, *C. pilosus* and *C. stimpsoni* could be included in the third group. However, the setae on P3Exp-3 are more numerous in *C. pilosus* and *C. stimpsoni* (with six setae) than in the third group (with five setae). Furthermore, as the reduction of the inner seta and inner apical seta on P3Endp-2 is commonly observed in the members of the third group, the reduction in length of the inner apical seta is probably convergent among *C. pilosus*, *C. stimpsoni*, and the members of the third group.

Previously, *C. koreanus* and *C. goenchim* were described in Korea and India, respectively (Chang 2013; Gómez et al. 2013). The new species and the two above-mentioned ones share several characteristics, including the length ratio of Endp-1 and Endp-2 of P1, the relative length of P1Endp and P1Exp, the integumental ornamentation of the cephalothorax, the armament and ornamentations of P1–P4 in both sexes and the female P5, the ornamentation of the anal operculum, the relative length of the caudal ramus, the number of abexopodal setae on the antennary allobasis, the number of setae on the antennary exopod and mandibular palp, and the shape of the lateral seta on the praecoxal arthrite of the maxillule. However, based on the author's knowledge, there is no characteristic unique to these three Asian *Cletocamptus*.

A finely detailed examination showed that the new species can be distinguished from *C. koreanus* and *C. goenchim*. The exopodal lobe of the male P5 of the new species has four elements, whereas it has three elements in *C. koreanus* and *C. goenchim*. The lateral surface of all abdominal segments is ornamented with a row of moderate long spinules in the new species, which are absent in *C. koreanus* and *C. goenchim*. Between the caudal dorsal seta VII and the row of spinules near the caudal seta VI of the females, there is an additional row of spinules on the inner margin that is absent in *C. koreanus* and *C. goenchim*. The aesthetasc on the fourth segment of the female antennule is relatively longer in the new species, with ca. 45% of the length of the aesthetasc surpassing the tip of the antennule, whereas it is relatively shorter in *C. koreanus* and *C. goenchim*, where less than 40% of the length of the aesthetasc surpasses the tip of the antennule. The new species lacks the spinular row at the base of the basal outer seta of the female P5 that is present in *C. koreanus* and *C. goenchim*. There are few spinules at the base of the basal outer seta of the male P5 in the new species and *C. koreanus*, but they are absent in *C. goenchim*. Furthermore, there are spinule rows on the frontal surface of the male P3Endp-2 that are absent in *C. koreanus* and *C. goenchim*.

Key to the female of *Cletocamptus*

The description of *C. chappuisi* was done, based only on the male by Chappuis (1933) and Gómez et al. (2017). So, it was not included in this key. However, it would be suggested that *C. chappuisi* belongs to the species group 1, according to the chaetotaxies of P2–P4Endp-2 and P2–P4Exp-3, along with the shape and chaetotaxy of caudal rami.

- 1 P5 exopodal and baseoendopodal lobes highly fused, barely separated by small shallow notch or without notch; caudal rami ca. 3–4× as long as wide (ca. 2× as long as wide in some species); caudal seta IV and V fused at base or separated; P2–P4Endp-2 with 3 or 4, 5, 2 elements (= setae and spines), respectively; P2–P4Exp-3 with 5, 5, 4 elements, respectively; P3Endp-2 with inner apical seta reaching or surpassing middle of outer apical seta, species group 1 **2**
- P5 with large notch between exopodal and baseoendopodal lobes; caudal rami relatively short, generally ca. 1.1–2× as long as wide (> 3× as long as wide in some species); caudal seta IV and V fused at base or separated **6**
- 2 A2Exp with 3 setae **3**
- A2Exp with 1 setae **4**
- 3 Caudal seta IV and V fused at base; P2Endp-2 with 3 elements *C. albuquerquensis*
- Caudal seta IV and V separated; P2Endp-2 with 4 elements *C. trichotus*
- 4 Mandible with 2 setae on palp and 1 seta arising nearby *C. tainoi*
- Mandible with 3 setae on palp **5**
- 5 Caudal rami ca. 2× as long as wide; exopodal and baseoendopodal lobes with 5 and 6 marginal setae, respectively *C. dominicanus*
- Caudal rami ca. 3× as long as wide; exopodal and baseoendopodal lobes with 4 and 6 marginal setae, respectively *C. confluens*
- 6 P2–P4Endp-2 with 4, 5, 2 elements, respectively; P2–P4Exp-3 with 5, 6, 5 elements, respectively; P1 with Endp surpassing tip of Exp, species group 2 **7**
- P2–P4Endp-2 with 3 or 4, 4 or 5, 2 elements, respectively; P2–P4Exp-3 with 5, 5, 4 or 5 elements, respectively; relative length of caudal rami ca. 2–3× as long as wide; inner apical seta on P3Endp-2 relatively short, doing not surpass proximal sixth of outer apical seta, species group 3 **8**
- P2–P4Endp-2 with 3, 5, 2 elements, respectively; P2–P4Exp-3 with 5, 6, 5 elements, respectively; relative length of caudal rami ca. 1.5–1.7× as long as wide; P3Endp-2 with inner apical seta surpassing proximal third of outer apical seta and generally reaching middle of outer apical seta; P1 with Endp-1 subequal in length to Endp-2, species group 4 **12**
- P2–P4Endp-2 with 3, 3, 2 elements, respectively; P2–P4Exp-3 with 5, 5, 4 or 5, 6, 5 elements, respectively; inner apical seta on P3Endp-2 reaching proximal third of outer apical seta at most (reaching middle of outer apical seta in some species); P1 with Endp-1 shorter than Endp-2, species group 5 **15**
- 7 Caudal seta IV and V fused at base; caudal rami 2.5× as long as wide; P1 with Endp-1 longer than Endp-2 *C. retrogressus*
- Caudal seta IV and V separated; caudal rami at most 2× as long as wide; P1 with Endp-1 shorter than Endp-2 *C. pilosus*
- 8 P1Endp-1 with inner seta **9**
- P1Endp-1 without inner seta **10**
- 9 P2–P4Endp-2 with 4, 5, 2 elements, respectively *C. gomezi*
- P2–P4Endp-2 with 3, 5, 2 elements, respectively *C. affinis*

- 10 P2–P4Endp-2 with 3, 4, 2 elements, respectively..... *C. feei*
 – P2–P4Endp-2 with 3, 5, 2 elements, respectively..... 11
- 11 Antennule six-segmented *C. mongolicus*
 – Antennule seven-segmented *C. gravibiatus*
- 12 Inner apical seta on P3Endp-2 reduced, doing not reach the proximal fourth of outer apical seta; posterior margin of cephalic shield and prosomite 2–3 with short spinules; mandible with 2 setae on palp only..... *C. stimpsoni*
 – Inner apical seta on P3Endp-2 normally develops, reaching middle of outer apical seta; posterior margin of cephalic shield and prosomite 2–3 with long spinules; mandible with 2 setae on palp and 1 seta arising near palp 13
- 13 Caudal rami with 4 transverse rows of spinules on inner margin; lateral surfaces of third and fourth urosomites (second and third abdominal somites) with transverse rows of moderately long spinules (these spinules as long as those of medial spinule row on ventral surface); female P5 without spinule row at base of basal seta..... *C. thailandensis* sp. nov.
 – Caudal rami with 3 transverse rows of spinules on inner margin; lateral surfaces of third and fourth urosomites without transverse rows of moderately long spinules; female P5 with spinule row at the base of basal seta 14
- 14 Maxilliped with basis ca. 3× as long as wide, posteriormost spinule row on ventral surface of fourth urosomite continuous..... *C. koreanus*
 – Maxilliped with basis ca. 2.5× as long as wide; posteriormost spinule row on ventral surface of fourth urosomite medially interrupted..... *C. goenchim*
- 15 P2–P4Exp-3 with 5, 6, 5 elements, respectively 16
 – P2–P4Exp-3 with 5, 5, 4 elements, respectively 18
- 16 Anal operculum without spinule on distal margin..... *C. nodus*
 – Anal operculum with spinule on distal margin..... 17
- 17 Mandible with 2 setae on palp only *C. samariensis*
 – Mandible with 2 setae on palp and 1 short seta arising nearby *C. schmidt*
- 18 Anal operculum without spinule on distal margin..... *C. fourchensis*
 – Anal operculum with spinules on distal margin..... 19
- 19 Caudal rami ca. 3× as long as wide..... 20
 – Caudal rami ca. 1.1–2× as long as wide..... 21
- 20 Posterior margin of cephalic shield with long spinule dorsally and laterally; lateral seta on praecoxal arthrite strong; P6 with 3 setae..... *C. tertius*
 – Posterior margin of cephalic shield with small spinules laterally, bare or with few spinules dorsally; lateral seta on praecoxal arthrite slender; P6 with 2 setae..... *C. spinulosus*
- 21 Caudal rami ca. 1.1× as long as wide..... *C. cecsurirensis*
 – Caudal rami ca. 1.5–1.6× as long as wide..... 22
 – Caudal rami ca. 1.7–2× as long as wide..... 24
- 22 A2Exp with 2 setae; P6 with 1 seta; anal operculum with two rows of strong spinules..... *C. sinaloensis*
 – A2Exp with 3 setae; P6 with 1 or 2 setae..... 23

- 23 P6 with 1 seta; Cephalic shield with long spinules along lateral margin, with or without smaller spinules along posterior-dorsal and dorso-lateral margin (smaller spinules shorter than those of second and third prosomites *C. deborahdexterae*
 – P6 with 2 setae; Cephalic shield with long spinules along posterior margin dorsally and laterally..... *C. levis*
- 24 Caudal rami with transverse row of strong spinules on medial margin *C. axi*
 – Caudal rami without transverse row of strong spinules on medial margin *C. assimilis*

Key to the male of *Cletocamptus*

- 1 P5 exopodal and baseoendopodal lobes, barely separated by small shallow notch or without notch; caudal rami ca. 3–4× as long as wide (ca. 2× as long as wide in some species); caudal seta IV and V fused at base or separated; P2–P4Endp-2 with 3 or 4, 5, 2 elements, respectively; P2–P4Exp-3 with 5, 5, 4 elements, respectively; P3Endp-2 and Endp-3 fused, species group 1 2
 – P5 with large notch between exopodal and baseoendopodal lobes; caudal rami relatively short, generally ca. 1.1–2× as long as wide ($\geq 3\times$ as long as wide in some species); caudal seta IV and V fused at base or separated; P3Endp-2 and Endp-3 separated 7
- 2 A2Exp with 3 setae 3
 – A2Exp with 1 setae 4
- 3 Caudal seta IV and V fused at base; P3Endp-3 with inner apical seta ca. 2× as long as outer apical one..... *C. albuquerqueensis*
 – Caudal seta IV and V separated; two apical setae on P3Endp-3 subequal in length *C. trichotus*
- 4 Anal operculum without spinule on distal margin..... *C. chappuisi*
 – Anal operculum with spinule on distal margin 5
- 5 Mandible with 3 setae on palp 6
 – Mandible with 2 setae on palp and 1 seta arising nearby *C. tainoi*
- 6 Caudal rami ca. 4× as long as wide; P3Endp-2 modified, with 2 strong dentiform projections; P5 exopodal lobe with 3 marginal setae *C. confluens*
 – Caudal rami ca. 2 times as long as wide; P3 with Endp-2 fused to Endp-3, with apophysis; P5 exopodal lobe with 4 marginal setae..... *C. dominicanus*
- 7 Caudal rami ca. 2–3× as long as wide; P2Endp-2 with 4 elements; P2–P4Exp-3 with 5, 6, 5 elements, respectively, P1Endp surpassing Exp; P1 with Endp-1 unequal in length to Endp-2, species group 2 8
 – Caudal rami ca. 3× as long as wide (ca. 2× as long as wide in some species); P2Endp-2 with 3 or 4 elements; P2–P4Exp-3 with 5, 5, 4 elements, respectively; P1 with Endp-1 longer or subequal in length to Endp-2, species group 3..... 9
 – Caudal rami ca. 1.5–1.7× as long as wide; P2Endp-2 with 3 or 4 elements; P2–P4Exp-3 with 5, 6, 5 elements, respectively; P1 with Endp-1 subequal in length to Endp-2, species group 4..... 13

- Caudal rami ca. 1.1–1.7× as long as wide (2 or 3× as long as wide in some species); P2Endp-2 with 3 elements; P2–P4Exp-3 with 5, 6, 5 or 5, 5, 4 elements, respectively; P1 with Endp-1 shorter than Endp-2, species group 5 **16**
- 8 Caudal seta IV and V fused at base; caudal rami at least 2.5× as long as wide; P1 with Endp-2 longer than Endp-1 *C. retrogressus*
- Caudal seta IV and V separated; caudal rami ca. 2× as long as wide; P1 with Endp-2 shorter than Endp-1 *C. pilosus*
- 9 Caudal rami with 7 setae *C. mongolicus*
- Caudal rami with 6 setae **10**
- 10 P2Endp-2 with 4 elements *C. gomezi*
- P2Endp-2 with 3 elements **11**
- 11 P1Endp-1 with inner seta *C. affinis*
- P1Endp-1 without inner seta **12**
- 12 P3Endp-3 with inner seta surpassing tip of apophysis *C. feei*
- P3Endp-3 with inner seta doing not surpass tip of apophysis *C. gravihatus*
- 13 P2Endp-2 with 4 elements; mandible with 2 setae on palp only *C. stimpsoni*
- P3Endp-2 with 3 elements; mandible with 2 setae on palp and 1 seta arising nearby **14**
- 14 P5 exopodal lobe with 4 marginal setae *C. thailandensis* sp. nov.
- P5 exopodal lobe with 3 marginal setae **15**
- 15 Baseoendopodal lobe with 4 setae, or often 3 or 4 setae asymmetrically *C. koreanus*
- Baseoendopodal lobe with 3 setae consistently *C. goenchim*
- 16 P2–P4Exp-3 with 5, 6, 5 elements, respectively; P3Exp curved; P3Exp-1 elongated, comparing to that of female **17**
- P2–P4Exp-3 with 5, 5, 4 elements, respectively; P3Exp straight; P3Exp-1 similar to that of female **19**
- 17 Anal operculum without spinule on distal margin; Left and right P5 distinct *C. nodus*
- Anal operculum with spinule on distal margin **18**
- 18 Mandible with 2 setae on palp and lacking seta arising nearby *C. samariensis*
- Mandible with 2 setae on palp and 1 short seta arising nearby *C. schmidti*
- 19 Caudal rami at least 3× as long as wide **20**
- Caudal rami ca. 1.1–2× as long as wide **21**
- 20 Medial element on P1 basis spiniform; lateral seta on praecoxal arthrite strong; outer spine on P2Endp-2 strongly curved and robust; lateral seta on A2Exp reduced, shorter than outer apical seta *C. tertius*
- Medial element on P1 basis setiform; lateral seta on praecoxal arthrite slender; outer spine on P2Endp-2 slightly curved and thin; lateral seta on A2Exp normal developed, as long as outer apical seta *C. spinulosus*
- 21 Left and right P5 distinct *C. cecsurirensis*
- Left and right P5 fused **22**
- 22 Caudal rami ca. 1.5–1.7× as long as wide **23**
- Caudal rami ca. 2× as long as wide *C. axi*

- 23 A2Exp with 2 setae; fifth urosomite without medial row of moderately long spinules..... *C. sinaloensis*
- A2Exp with 3 setae; fifth urosomite with medial row of moderately long spinules24
- 24 Posterior margin of cephalic shield with few small spinules dorsally, with long spinules laterally..... *C. levis*
- Posterior margin of cephalic shield with long spinules dorsally and laterally.....25
- 25 P5 exopodal lobe with longest seta ca. 7× as long as the outermost seta; outer spine on P2Endp-2 strongly curved and robust..... *C. fourchensis*
- P5 exopodal lobe with longest seta ca. 2.9× as long as the outermost seta *C. deborahdexterae*

Discussion

Among the representatives of the genus *Cletocamptus*, *C. deitersi* is the most problematic in that it expresses a high degree of morphological variation (Gómez et al. 2004). The species has so far been recorded in North and Central America, as well as in India, China, Ethiopia, Hawaii, Australia, Iran, and Malaysia (see the list of references in Gómez et al. 2004). However, recent molecular and morphological studies have proved that *C. deitersi* is a mixture of different species (Rocha-Olivares et al. 2001; Gómez et al. 2004, 2007; Gómez and Gee 2009), and its cosmopolitan distribution is the result of the insufficient description and inadequate illustration of Richard's original description of the species separation of *C. deitersi*. Recently, it has been recognized as *species inquirendae* (Gómez et al. 2004). In Asia, Ranga Reddy and Radhakrishna (1979) reported *C. deitersi* in India without a description or any comments on the morphology of the specimens, while Tai and Song (1979) reported it in China, with a short description of the female. Gómez et al. (2013) pointed out that Ranga Reddy and Radhakrishna (1979) identified the Indian specimens on the basis of the revision of Lang (1948) and the description of Hamond (1973), who reported the presence of *C. deitersi* in Australia. Gómez et al. (2013) also argued that the female P3 of the Australian *C. deitersi* is likely similar to that of *C. brehmi*, which has been considered by Chappuis (1933) and Kiefer (1936) as a synonym of *C. deitersi*. Based on the viewpoint of Gómez et al. (2013), the new species shows a close affinity to the Indian *C. deitersi* in having five setae on its P3Endp-2. However, we found that Kiefer's (1936) and Hamond's (1973) *C. deitersi* share the presence of four setae on the exopodal lobe of the female P5, which is different from that of the Thai *Cletocamptus*. Based on the illustrations of Daday (1902) and Chappuis (1934) adopted by Lang (1948), the new species differs from Daday's (1902) *C. deitersi*, as the inner apical seta of the female P3Endp-2 does not reach the middle of the outer apical one in the latter but reaches the middle of the inner one in the new species. We believe that Daday's (1902) *C. deitersi* is morphologically related to the member of the third group of valid species because it has a short inner apical seta on the P3Endp-2 and a relatively long caudal ramus. Furthermore, whereas the outer spine of the male P2Endp-2 is straight and slim in the new species, it is curved and shortened in Chappuis's (1934) *C. deitersi*. The curved

and shortened spine of the male P2Endp-2 of Chappuis's (1934) *C. deitersi* seems similar to that of *C. levis*, *C. fourchensis*, *C. sinaloensis*, and *C. goenchim*.

The type locality is the water body at the base of an isolated limestone mountain. Within it, two microhabitats could be defined: a submerged filamentous algal mat and an area of leaf litter. A greater number of specimens was collected from the filamentous algal mat, indicating the habitat preference of the aerated zone of the new species. It seems like that of *C. gomezi*, which is absent in the sandy bottom but present in the filamentous algal mat of *Ruppia maritima* L. and *Chara* sp. (Suárez-Morales et al. 2013).

The global distribution and the high degree of polymorphism of *C. deitersi* have previously been mentioned. Gómez et al. (2004), however, suggested that it is because of the high degree of intraspecific variability of *Cletocamptus* species and the morphologically similar among the specimens attributed to *C. deitersi*. After the molecular study of the American and Mexican specimens confirmed the hypothesis of several authors, showing clearly that different species had been identified as *C. deitersi* (Rocha-Olivares et al. 2001), it has recently been accepted that *C. deitersi* is a species complex, consists of morphologically indistinguishable sibling species, that cannot be differentiated, based on Richard's original description (Gómez et al. 2004). Because the description of such records was done on the conservative features with which they are insufficient for species separation (see list of contributions in Gómez et al. 2004), several records of *C. deitersi* around the globe have now been considered *species inquirenda* (Gómez et al. 2004). Many new species have later been elevated for the specimens previously identified as *C. deitersi* (e.g., Gómez et al. 2004; Gómez 2005; Gómez and Gee 2009). However, as morphological differences can occur between the partial populations of a cosmopolitan species (Mielke 2000a, b), and information about the variability of the genuine *C. deitersi* remains unknown, it raises doubt about whether they are independent species or subspecies. So, the knowledge of the variability and the full description of the genuine *C. deitersi* from the type locality is needed for further taxonomic work on the status clarification of *C. deitersi*, as well as the recently described species.

Acknowledgements

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A new genus of *Textricini* Lehtinen, 1967 (Araneae, Agelenidae) from Anatolia

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Abstract

Türkiye is known to have the highest diversity of the spider family Agelenidae in the Western Palaearctic and the highest diversity of the subfamily Ageleninae globally. The new agelenid genus *Anatextrix* **gen. nov.** (Ageleninae, *Textricini*) and its type species, *A. spectabilis* **sp. nov.** (♂♀; Mersin and Adana provinces, southern Türkiye), are described. A key to all four genera of *Textricini* is provided.

Keywords

Ageleninae, Aranei, dichotomous key, new species, Türkiye

Introduction

Agelenidae C.L. Koch, 1837 is a large family of spiders currently comprising 1374 extant species in 91 genera distributed worldwide (WSC 2023). According to Lehtinen (1967), two subfamilies – Ageleninae C.L. Koch, 1837 and Coelotinae F.O. Pickard-Cambridge, 1893 – can be recognized within Agelenidae, with the former comprising the following tribes: Agelenopsini Lehtinen, 1967 (Nearctic and Neotropical), Agelenini C.L. Koch, 1837 (Holarctic and Afrotropical), Tegenariini Lehtinen, 1967 (primarily Palaearctic), and *Textricini* Lehtinen, 1967 (Western Palaearctic). *Textricini*,

the smallest tribe and the focus of this paper, is primarily distributed in the Mediterranean region (WSC 2023). Several new species of this tribe have been described over the past few years, including five from the Maghreb (Bosmans et al. 2022) and one from Anatolia (Dimitrov 2022).

Recently, we had the opportunity to examine specimens of a new species of *Textricini* from Türkiye. This species displays a series of interesting characters, including a strongly modified palpal femur bearing several processes or outgrowths, which is a unique trait in the whole family. Based on a comparison with other genera of *Textricini*, we decided that this undescribed species also represents a new genus. In this paper, both the new genus and species are described, and a key to all four genera of *Textricini* is provided.

Materials and methods

The samples were collected with pitfall trapping and hand aspirator and preserved in 70% ethanol. Specimens were photographed using a Canon EOS 7D camera attached to an Olympus SZX16 stereomicroscope at the Zoological Museum of the University of Turku. Digital images were montaged using Combine ZP and edited using CorelDraw. Illustrations of internal genitalia were made after clearing and cleaning the epigyne in a 10% KOH aqueous solution, followed by a few minutes of treatment in Chlorazol Black. Lengths of leg segments were measured on the dorsal side and are listed as: total length (femur, patella, tibia, metatarsus, tarsus). All measurements are in millimetres (mm). Spination formula follows Bolzern et al. (2008, 2009).

Abbreviations

Eyes: **ALE** – anterior lateral eye, **AME** – anterior median eye, **PLE** – posterior lateral eye, **PME** – posterior median eye.

Spination: **d** – dorsal, **Fe** – femur, **Mt** – metatarsus, **Pa** – patella, **pl** – prolateral, **rl** – retrolateral, **Ti** – tibia, **v** – ventral.

Male palp: **Bd** – dorsal branch of the conductor, **Ca** – anterior arm of the conductor, **Cf** – cymbial fold, **Cp** – posterior arm of the conductor, **Db** – distal bulge, **Eb** – base of the embolus, **Kt** – ventral keel, **Pb** – proximal bulge, **Pt** – prolateral apophysis, **Rt** – retrolateral apophysis, **So** – stump-like outgrowth, **Sp** – spine-like outgrowth, **St** – subtegulum, **Te** – tegulum, **Va** – ventral apophysis.

Epigyne: **Cd** – copulatory duct, **Fd** – fertilization duct, **Oc** – copulatory opening, **Re** – receptacle, **Se** – septum.

Depositories

AZMM Alaşehir Zoological Museum of Manisa Celal Bayar University, Türkiye (E.A. Yağmur).

ZMUT Zoological Museum of the University of Turku, Finland (V. Vahtera).

ZMUU Zoological Museum of the Bursa Uludağ University, Türkiye (R.S. Kaya).

Taxonomy

Family Agelenidae C.L. Koch, 1837

Subfamily Ageleninae C.L. Koch, 1837

Tribe Tetricini Lehtinen, 1967

Diagnosis. Species considered in Tetricini have a very long terminal segment of the posterior lateral spinnerets (Fig. 1C), and a strongly recurved posterior eye row (vs procurved in Agelenini, straight in Tegenariini). Furthermore, males of Tetricini species lack a tegular (= median) apophysis (vs present in all other agelenids; also see Discussion). For other characters, see Lehtinen (1967) and Bolzern et al. (2010, 2013).

Composition. Thirty species in four genera: *Anatextrix* gen. nov. (one species), *Lycosoides* Lucas, 1846 (14 species), *Maimuna* Lehtinen, 1967 (eight species), and *Textrix* Sundevall, 1833 (seven species).

Key to the genera

This key is primarily based on the characters of the generotypes: *Lycosoides coarctata* (Dufour, 1831), *Maimuna vestita* (C.L. Koch, 1841), and *Textrix denticulata* (Olivier, 1789).

- | | | |
|---|--|---------------------------------------|
| 1 | Male | 2 |
| – | Female | 5 |
| 2 | Femur, patella and tibia with apophyses; tibia with prolateral apophysis; cymbium with prolateral fold (Figs 2A, 4A) | <i>Anatextrix</i> gen. nov. |
| – | Femur without apophyses or only with minor modifications; prolateral tibial apophysis and prolateral cymbial fold are lacking..... | 3 |
| 3 | Palpal patella modified: swollen with one retrolateral apophysis (Fig. 8A, D) | <i>Lycosoides</i> Lucas, 1846 |
| – | Palpal patella not modified..... | 4 |
| 4 | Posterior arm of the conductor with two branches, one branch directed dorsally (<i>Bd</i>) and partly hiding cymbium; prolateral arm as large as tibia (Fig. 8B, E)..... | <i>Maimuna</i> Lehtinen, 1967 |
| – | Conductor different (Fig. 8C, F)..... | <i>Textrix</i> Sundevall, 1833 |
| 5 | Epigyne with scape and distinct, deep fovea..... | <i>Textrix</i> |
| – | Epigyne without scape and deep fovea | 6 |
| 6 | Epigyne with stripe-like septum..... | <i>Anatextrix</i> gen. nov. |
| – | Epigyne without septum..... | 7 |
| 7 | Epigyne with anterior hood and anchor-like median plate; receptacles located meso-laterally..... | <i>Lycosoides</i> |
| – | Hood absent; receptacles located posteriorly and spaced by ca two diameters of each | <i>Maimuna</i> |

Genus *Anatextrix* gen. nov.

<https://zoobank.org/3E23C193-9504-47BF-B38A-DDE6BAE44DEE>

Type species. *Anatextrix spectabilis* sp. nov.

Etymology. The generic epithet is a combination of Anatolia and *Textrix*; gender feminine.

Diagnosis. The new genus differs from all other genera of Textricini by having a strongly modified male palpal femur with two outgrowths and two bulges (vs one or none), presence of the palpal prolateral tibial apophysis (*Pt*) and the cymbial prolateral fold (*Cf*) (vs lacking), the straight mesal part of the embolic base (vs round) (cf. Figs 2A, 4A, 8A–F), and by having a thin septum in the epigyne (vs absent). Furthermore, the female of *Anatextrix spectabilis* sp. nov. differs from those of *Textrix* by having no epigynal fovea and scape (vs present). From the females of the two other genera, the female of this species differs by the anterior position of the receptacles (vs mesal or posterior).

Description. Same as for the type species.

Composition. Only the type species.

Distribution. Same as for the type species.

***Anatextrix spectabilis* sp. nov.**

<https://zoobank.org/A95490E1-44D5-411A-BFF0-17B6E3F877AD>

Figs 1A–C, 2A–E, 3A–E, 4A–D, 5A–C, 6A–C, 7A–G

Type material. *Holotype* ♂ (ZMUU), TÜRKIYE: **Mersin Province:** Erdemli district, 36°44'N, 34°09'E, 960 m a.s.l., 18.07.2015, hand collection (E.A. Yağmur). *Paratypes:* 1♂2♀ (ZMUT), same data as for the holotype; 1♂17♀ (ZMUU), same data as for the holotype; **Adana Province:** 2♂12♀ (ZMUU), Pozantı district, 37°25'58"N, 34°55'11"E, 1396 m a.s.l., 27.09.2018, hand collection (R.S. Kaya and E.A. Yağmur); 2♂2♀ (AZMM), same locality, 31.10.2017–02.04.2018, pitfall traps, (E.A. Yağmur); 8♂3♀ (ZMUU), same locality, 31.10.2017–02.04.2018, pitfall traps, (E.A. Yağmur); 15♂6♀ (ZMUU), same locality, 04.08.2018–19.07.2019, pitfall traps, (E.A. Yağmur).

Etymology. The specific epithet is a Latin adjective meaning “remarkable”.

Diagnosis. Same as for the genus.

Description. Male (Holotype). Habitus as in Fig. 1B. Total length 6.55. Carapace 3.57 long, 1.22 wide at pars cephalica, 2.37 wide at pars thoracica. Eye sizes: AME: 0.11, ALE: 0.15, PME: 0.22, PLE: 0.16. Carapace, sternum, labium, and maxillae light brown; carapace with darker submedian bands. Chelicerae light reddish brown, each with 3 pro- and 2 retromarginal teeth. Legs yellowish brown, with annulations. Abdomen dorsally dark greyish with lighter foliate pattern, light greyish ventrally. Spinnerets light greyish, darker basally (Fig. 1C). Measurements of legs: I: 7.48 (2.00, 0.90, 1.53, 1.95, 1.10), II: 7.75 (2.15, 0.89, 1.53, 2.00, 1.18), III: 7.78 (2.00, 0.93, 1.60, 2.20, 1.05), IV: 9.64 (2.55, 0.84, 1.95, 2.97, 1.33). Spination is given in Table 1.



Figure 1. *Anatextrix spectabilis* sp. nov. **A** female habitus, dorsal view **B** male habitus, dorsal view **C** spinnerets of the male, lateral view. Scale bars: 0.2 mm, unless stated otherwise.

Table 1. Spination of legs of *Anatextrix spectabilis* sp. nov. The letter “p” indicates paired spines.

		Fe	Pa	Ti	Mt
		d-pl-rl	d-pl-rl	d-pl-rl-v	pl-rl-v
I	♂	3-1-1	2-1-1	1-2-1-1+2p	1-1-3p
	♀	3-1-1	2-1-1	1-2-1-1+1p	2-2-2p
II	♂	3-1-1	2-1-1	1-2-1-1+1p	2-2-3p
	♀	3-1-1	2-1-1	1-2-1-1+1p	2-2-3p
III	♂	3-1-1	2-1-1	1-2-2-1+1p	3-2-3p
	♀	3-1-1	2-1-1	1-2-3-3p	3-3-3p
IV	♂	3-1-1	2-1-1	2-2-2-2+1p	3-3-3p
	♀	3-1-1	2-1-1	2-2-2-2+1p	3-3-3p

Palp as in Figs 2A–E, 3A–E, 4A–D, 5A–C, 6A–C; femur relatively short (ca 3× longer than wide, 1.5× shorter than cymbium) and strongly modified: slightly bent, with proximal (*Pb*) and distal (*Db*) bulges and 2 outgrowths: spine-like (*Sp*) and

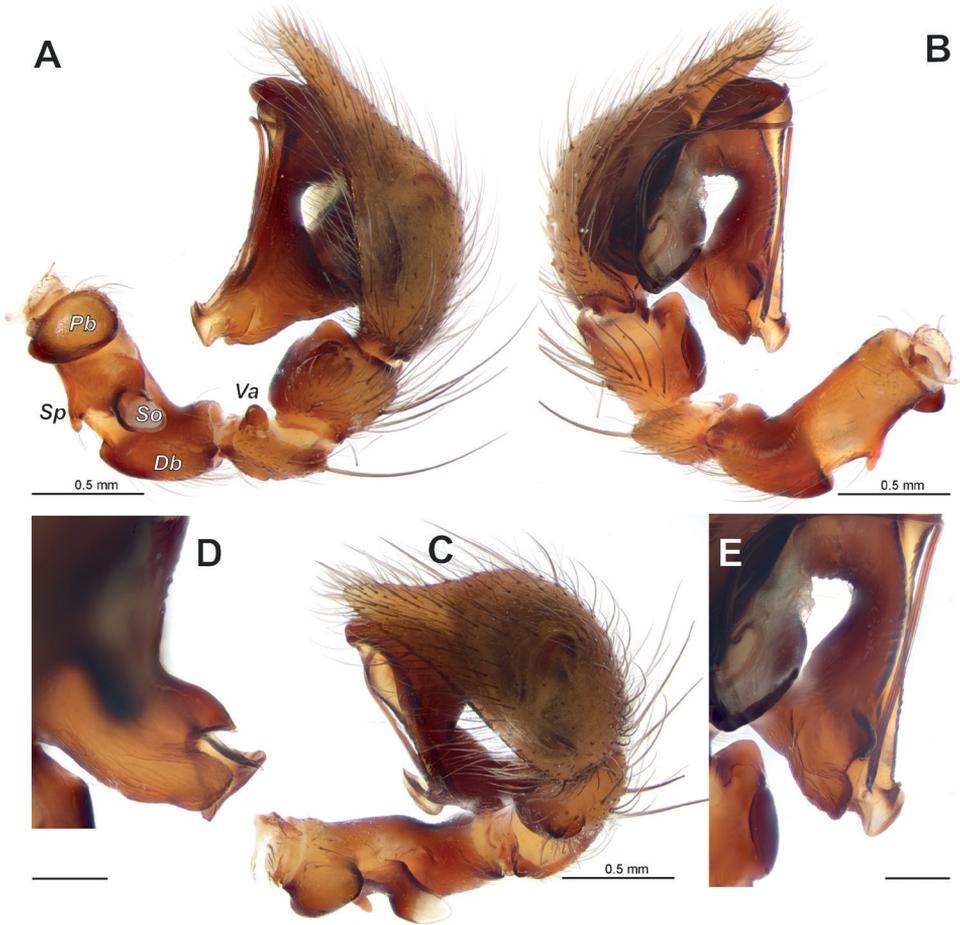


Figure 2. Male palp of *Anateatrix spectabilis* sp. nov. **A–C** full palp, retrolateral, prolateral and retrodorsal views **D, E** details of the embolus and the posterior arm of the conductor, prodorsal and prolateral views. Scale bars: 0.2 mm, unless stated otherwise. Abbreviations: *Db* – distal bulge, *Pb* – proximal bulge, *So* – stump-like outgrowth, *Sp* – spine-like outgrowth, *Va* – ventral apophysis.

larger stump-like (*So*). Patella short, wider than long, with ventral apophysis (*Va*). Tibia slightly wider than long in retrolateral view, with retrolateral (*Rt*) conical apophysis directed laterally, ventral keel (*Kt*) and prolateral apophysis (*Pt*). Cymbium droplet-shaped, ca 1.7× longer than wide, with small baso-prolateral fold (*Cf*). Subtegulum (*St*) round, hidden by tegulum and conductor. Tegulum (*Te*) small, round, hidden by conductor and embolus base. Conductor very large, ca 0.7× shorter than cymbium; anterior and posterior parts extending over tegulum; anterior arm (*Ca*) as long as wide, posterior arm (*Cp*) more than 2× longer than wide; posterior part of posterior arm very broad and extending ventrally; tip of posterior arm trifurcate. Embolus proper originates at about 8 o'clock position and terminates at about 5 o'clock position; base of embolus (*Eb*) not rounded: mesal part straight, prolateral part bent on right angle.

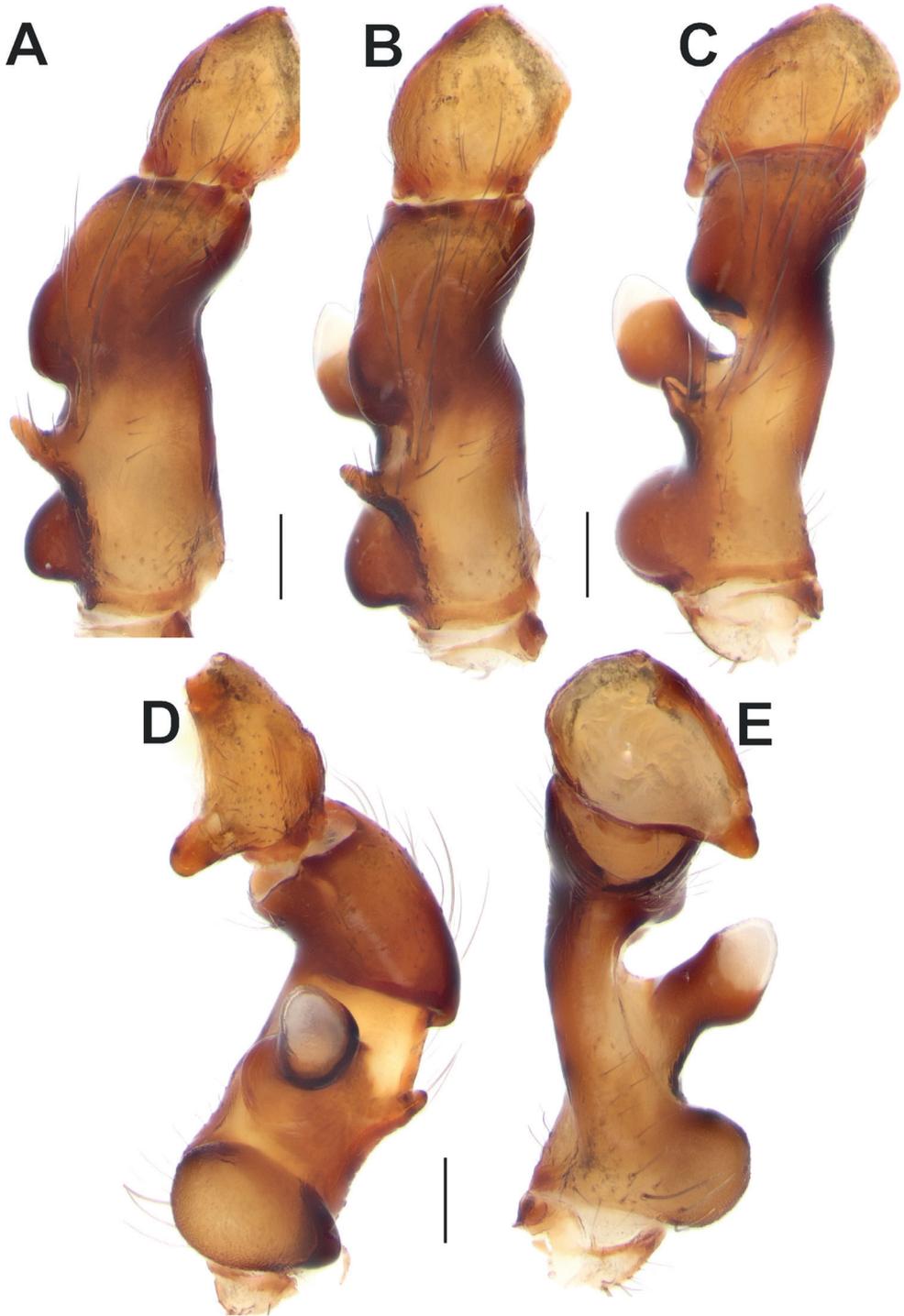


Figure 3. Male palpal femur and patella of *Anatetrix spectabilis* sp. nov. **A** prolateral view **B** prodorsal view **C** dorsal view **D** retrolateral view **E** ventral view. Scale bars: 0.2 mm.

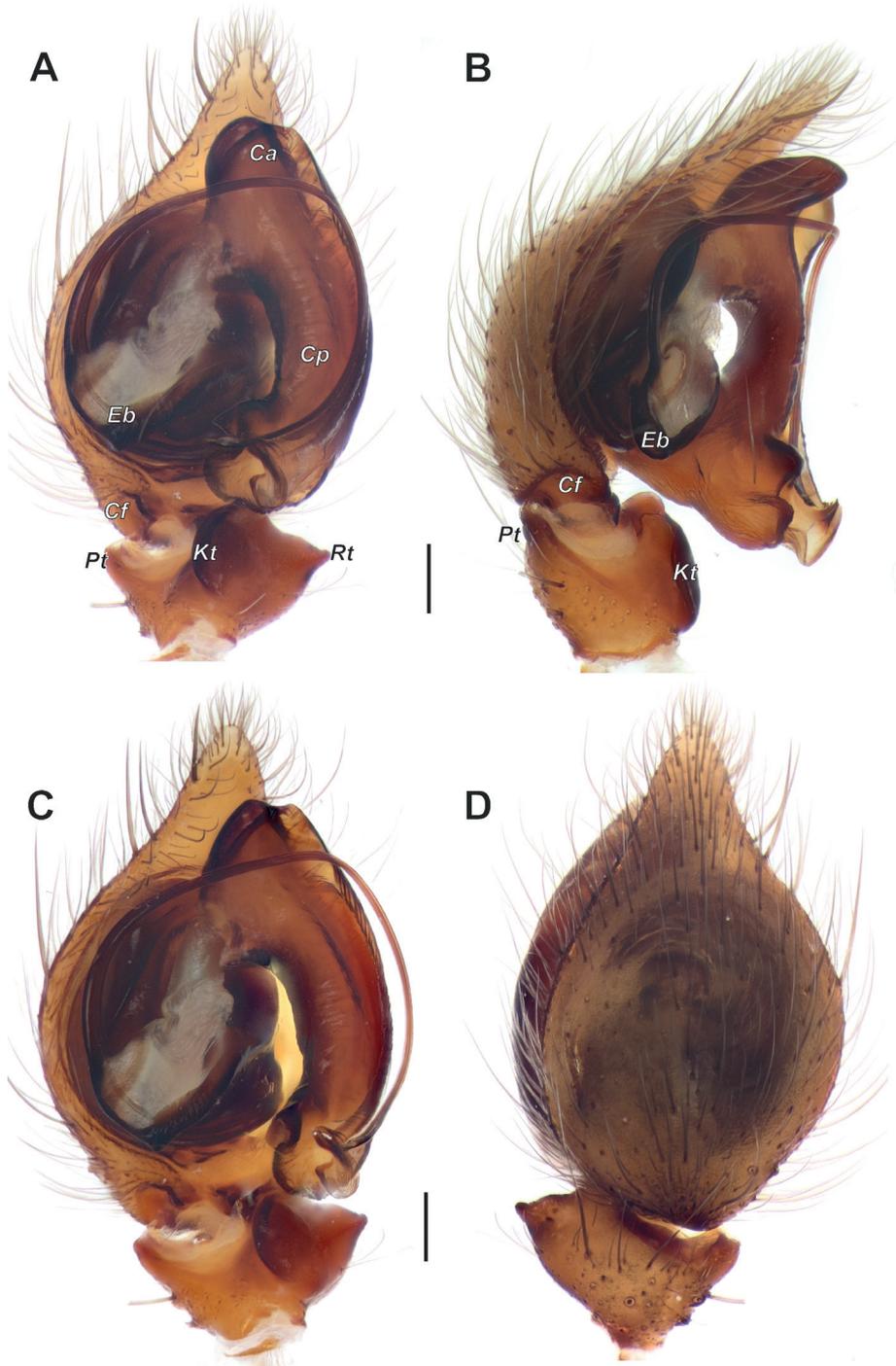


Figure 4. Male palp of *Anateatrix spectabilis* sp. nov. **A** ventral view **B** prolateral view **C** proventral view **D** dorsal view. Scale bars: 0.2 mm. Abbreviations: *Ca* – anterior arm of the conductor, *Cp* – posterior arm of the conductor, *Cf* – cymbial fold, *Eb* – base of the embolus, *Kt* – ventral keel, *Pt* – prolateral apophysis, *Rt* – retrolateral apophysis.

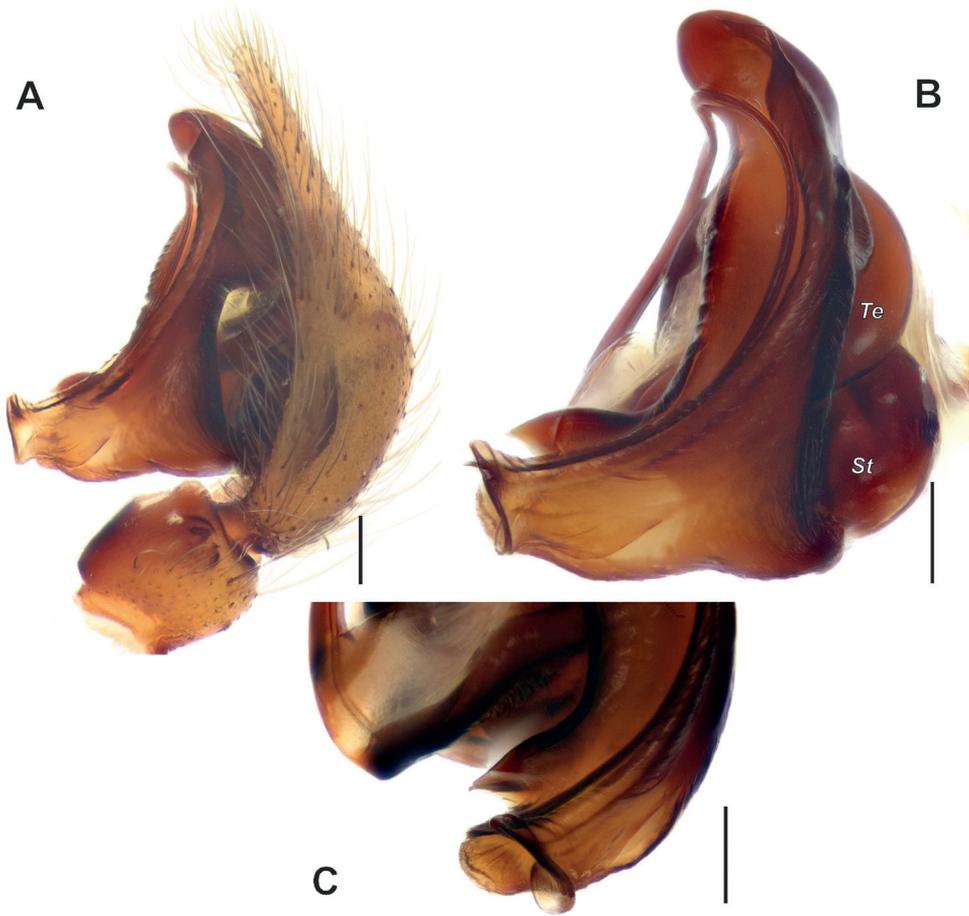


Figure 5. Male palp of *Anateatrix spectabilis* sp. nov. **A** retrolateral view **B** dissected bulb, retrolateral view **C** details of the embolus and the posterior arm of the conductor, anteroventral view. Scale bars: 0.2 mm. Abbreviations: *St* – subtegulum, *Te* – tegulum.

Female (Paratype, ZMUT). Habitus as in Fig. 1A. Total length 6.75. Carapace 2.95 long, 1.16 wide at pars cephalica, 2.97 wide at pars thoracica. Eye sizes: AME: 0.10, ALE: 0.15, PME: 0.22, PLE: 0.14. Coloration generally as in male, except for darker submedian bands on carapace and more distinct annulations on legs. Measurements of legs: I: 6.55 (1.80, 0.87, 1.30, 1.58, 1.00), II: 6.73 (1.87, 0.93, 1.30, 1.57, 1.06), III: 6.98 (1.90, 0.90, 1.33, 1.85, 1.00), IV: 9.05 (2.29, 1.04, 1.92, 2.60, 1.20). Spination is given in Table 1.

Epigyne as in Fig. 7A–G; epigynal plate 1.6× wider than long; fovea lacking depression, weakly sclerotized with thin septum (*Se*), anterior part delimited by well sclerotized margin, posterior part delimited by weakly sclerotized margins; septum not covered by setae; copulatory openings (*Oc*) located on posterior margin on both sides of septum; copulatory ducts (*Cd*) fused, forming a rectangular plate ca 2× longer than wide (Fig. 7G); receptacles (*Re*) small, suboval, located anteriorly and separated by ca one length of each; fertilization ducts (*Fd*) short and small.

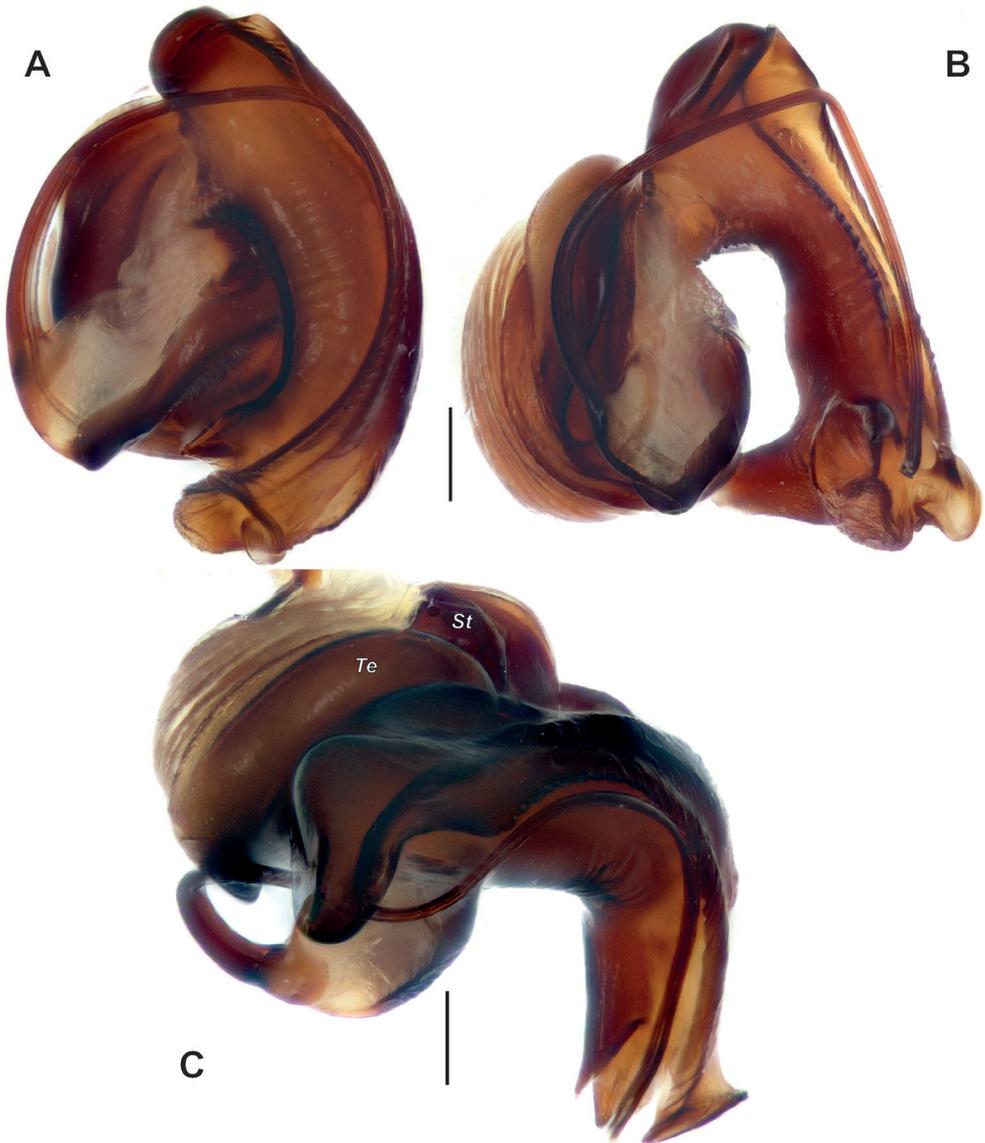


Figure 6. Dissected bulb of *Anateatrix spectabilis* sp. nov. **A** ventral view **B** prolateral view **C** anterior view. Scale bars: 0.2 mm. Abbreviations: *St* – subtegulum, *Te* – tegulum.

Natural history. The specimens were collected off their funnel-webs constructed under the stones or within shrubs and crevices in the soil. The habitat is a typical maquis shrubland dominated by *Quercus* L. (Fagaceae) and *Pinus* L. (Pinaceae) at Erdemli (Mersin), while it is dominated by *Abies* Mill. (Pinaceae) at Pozantı (Adana).

Distribution. Known only from the provinces of Mersin and Adana, southern Türkiye.

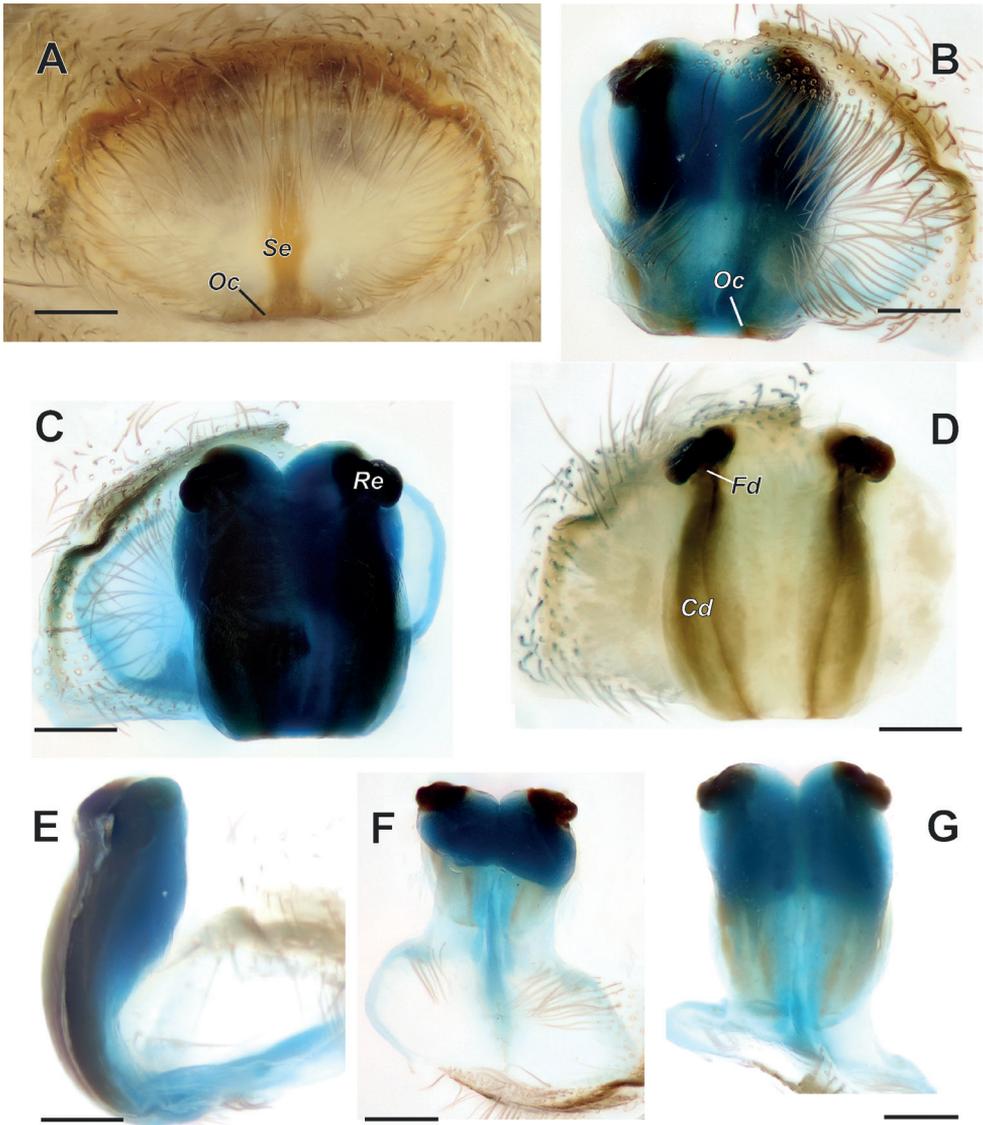


Figure 7. Epigyne of *Anateatrix spectabilis* sp. nov. **A** intact, ventral view **B, G** macerated, ventral view **C, D** vulva, dorsal view **E, F** same, lateral and anterior views. Scale bars: 0.2 mm. Abbreviations: *Cd* – copulatory duct, *Fd* – fertilization duct, *Oc* – copulatory opening, *Re* – receptacle, *Se* – septum.

Discussion

In this paper, a new genus and species of Textricini are described from southern Türkiye. Since many species of Textricini have characteristics that differ from the type species of the genera in which they are currently classified, this tribe, as a whole, needs to be revised. Furthermore, both *Lycosoides* and *Textrix* comprise species that show consider-

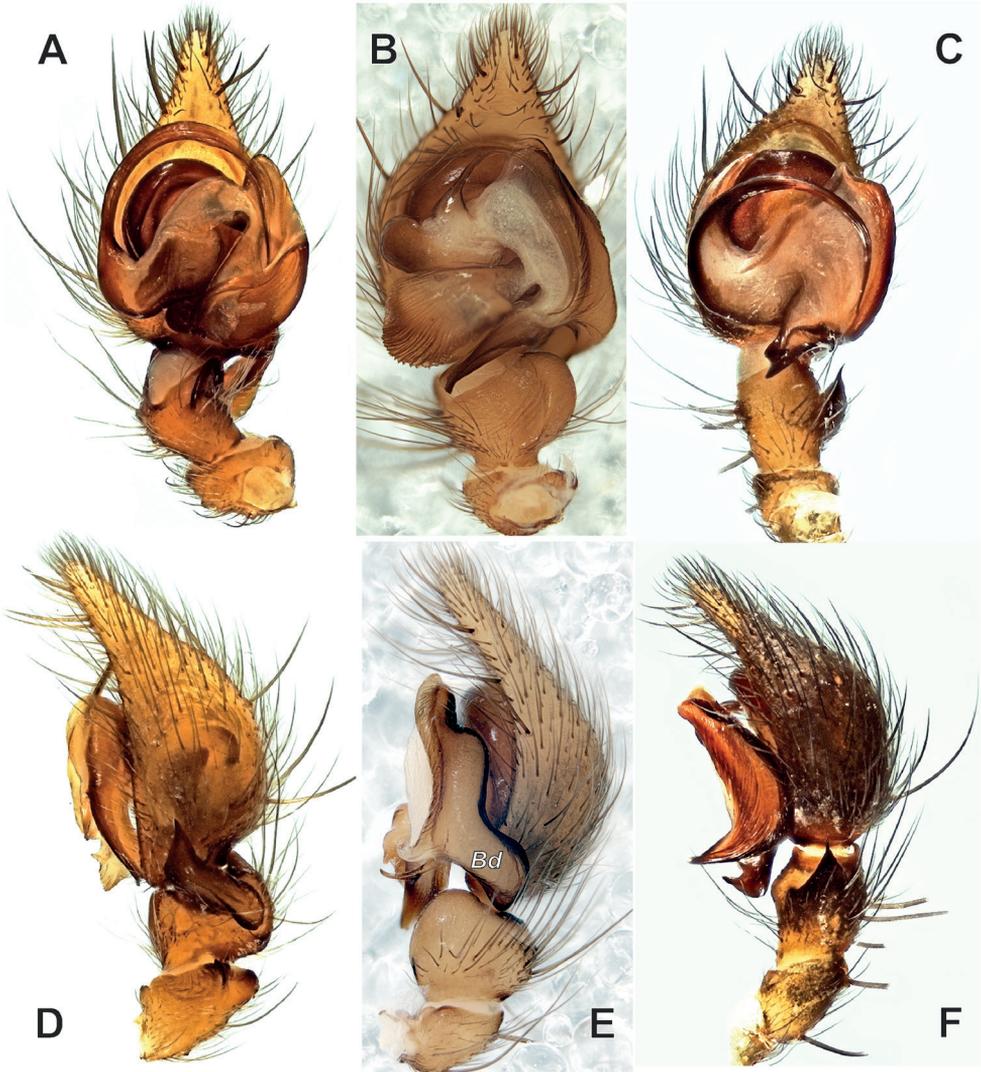


Figure 8. Male palps of the type species of three genera belonging to Tetricini: *Lycosoides coarctata* (A, D), *Maimuna vestita* (B, E) and *Tetricus denticulata* (C, F) A–C ventral view D–F retrolateral view A, C, D, F courtesy of P. Oger B, E from Dimitrov (2022), courtesy of D. Dimitrov. Abbreviation: Bd – dorsal branch of the conductor.

able differences in the conformation of their copulatory organs, and, thus, might be misclassified. This is most likely why de Blauwe (1980) considered all Tetricini species known at that time to belong to *Tetricus*.

The terminology of one particular palpal sclerite in *Maimuna* has been controversial: Lehtinen (1967) suggested that a tegular (= median) apophysis is lacking (i.e., “totally reduced”) in species of this genus, which was not followed by Levy (1996), Bolzern et al. (2013), and Dimitrov (2022). It became evident in our examination of

the expanded bulbs that all species of *Maimuna* indeed lack a tegular apophysis, as the structure that the aforementioned authors considered as the “median apophysis” arises from the conductor, not the tegulum.

Agelenidae is relatively well studied in Türkiye due to several regional revisions and other taxonomic and faunistic contributions (e.g., Brignoli 1972, 1978a, b; Kaya et al. 2010; Danışman and Karanfil 2015; Danışman et al. 2016; Topçu and Demircan 2018; Dimitrov 2022). Currently, there are 72 species in 16 genera of Agelenidae known from Türkiye (Danışman et al. 2022; present paper), which is considerably higher than what is known from, for example, Iran (25 species in seven genera; Zamani and Marusik 2019, 2020), the entire Caucasus (36 species in 11 genera; Otto 2022), Greece (48 species in 12 genera; Nentwig et al. 2023), Bulgaria (43 species in 11 genera; Nentwig et al. 2023), Italy (58 species in 14 genera; Nentwig et al. 2023), France (41 species in 13 genera; Nentwig et al. 2023), and Spain (41 species in 13 genera; Nentwig et al. 2023). Indeed, in terms of the diversity of agelenids in the Palaearctic, Türkiye is only second to China (>445 species in 35 genera; Li 2020). It is noteworthy that Türkiye houses the highest number of Ageleninae species globally.

Although most of the Turkish agelenids belong to Tegenariini (including 19 endemic species), Tetricini is also relatively diverse in this country (i.e., eight species in all four known genera, including one endemic genus and two endemic species; Danışman et al. 2022; present paper). As it has been mentioned earlier, members of this tribe are primarily distributed in the Mediterranean region. The only exceptions are *Lycosoides lehtineni* Marusik & Guseinov, 2003 from Azerbaijan and *Tetricix nigromarginata* Strand, 1906 from Ethiopia, although both are known only from females and the latter is most likely misclassified (Strand 1906, 1908; Marusik and Guseinov 2003).

Despite the relatively well-explored status of the Turkish agelenids, new species and records are still found regularly. Most likely there are many interesting species of Agelenidae in this country that are currently undiscovered, as it is evidenced by the remarkable new genus described in this paper. Hopefully, a more complete picture of the diversity of this family in Türkiye can be achieved once the lesser explored habitats (e.g., caves) and regions (e.g., eastern Türkiye) are systematically surveyed.

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A new species of Bush frog (Anura, Rhacophoridae, *Raorchestes*) from southeastern Yunnan, China

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Abstract

In this study, based on morphological and molecular data, a new bush frog species is described from Yunnan, China. Eleven samples of *Raorchestes malipoensis* **sp. nov.** were collected from Malipo County, southeastern Yunnan. This species can be distinguished from other congeners by a combination of 13 morphological characters. Phylogenetic analyses based on the 16S rRNA gene indicate that these individuals form a monophyletic group, and genetic divergence between this clade and its closest relatives is higher than 3.1%, which is comparable to the divergence between recognized *Raorchestes* species. The discovery of this new species suggests that additional extensive surveys in the southeastern Yunnan would yield more amphibian lineages yet unknown to science.

Keywords

Kurixalus gryllus, *Raorchestes gryllus*, *Raorchestes malipoensis* sp. nov., taxonomy

* These authors contributed equally.

Introduction

The genus *Raorchestes* Biju, Shouche, Dubois, Dutta & Bossuyt, 2010 belongs to the family Rhacophoridae Hoffman, 1932. It includes bush frogs with adult size ranging from 10.0 mm to 50.5 mm (Priti et al. 2016). They are distinguished by the presence of a transparent/translucent vocal sac, the absence of vomerine teeth, and direct development without free swimming tadpoles (Seshadri et al. 2012). The genus *Raorchestes* currently contains 74 species, ranging from the southern tip of the Indian Peninsula to northeastern India, Indo-China, and southwestern China (Frost 2021): most are from south and Southeast Asia including southern India to Nepal, Myanmar, Thailand, Laos, southern China, Vietnam, and West Malaysia. Of the 74 recognized species, seven species have been originally described from China: *Raorchestes longchuanensis* (Yang & Li, 1978), *R. menglaensis* (Kou, 1990), *R. andersoni* (Anderson, 1927), *R. cangyuanensis* (Wu et al., 2019), *R. dulongensis* (Wu et al., 2021), *R. hillisi* (Jiang et al., 2020), and *R. huanglianshan* (Jiang et al., 2020). Detailed ecological data is not available for the species reported in China except for *R. longchuanensis*, for which Yan et al. (2021) reported the breeding mode.

Many *Raorchestes* species from the region were described with few diagnostic characters and limited morphological data, which hampers the identification of these small-sized bush frogs (Jiang et al. 2020). In addition, the taxonomy of *Raorchestes gryllus* is under dispute. It was originally described as *Philautus gryllus* Smith, 1924, from Langbian Peaks, southern Vietnam. Biju et al. (2010) classified this species into *Raorchestes* according to the 16S sequences from Pac Ban, Tuyen Quang, northern Vietnam, and recently Poyarkov et al. (2021) suggested a transfer to *Kurixalus* based on morphological and molecular data of specimens from the type locality (Langbian, southern Vietnam).

In this work we studied specimens allocated to *Raorchestes* from Malipo County. This county is located in the southeast of Yunnan Province, and lies on the China-Vietnam border where few herpetological investigations have been conducted. During the fieldwork, we collected 11 specimens of a small-sized bush frog that could be assigned to the genus *Raorchestes* based on morphological and molecular evidence. Phylogenetically, these specimens were grouped together with a misidentified “*R. gryllus*” from Pac Ban, Tuyen Quang, northern Vietnam. However, considering that the type locality of *Philautus gryllus*, Langbian Plateau, is 1200 km far from the China-Vietnam border and that obvious morphological differences exist between *Philautus gryllus* and the lineage consisting of individuals from China-Vietnam border region, we consider that these specimens represent a new species that we formally describe here.

Materials and methods

Sampling

Fieldwork was conducted at Malipo County, Yunnan Province, China (23.182°N, 104.78°E, elevation 1496 m). Six specimens were collected on 7 May 2019 (Figs 1, 2) and another five specimens were collected on 22 July 2020. Specimens were collected by hand

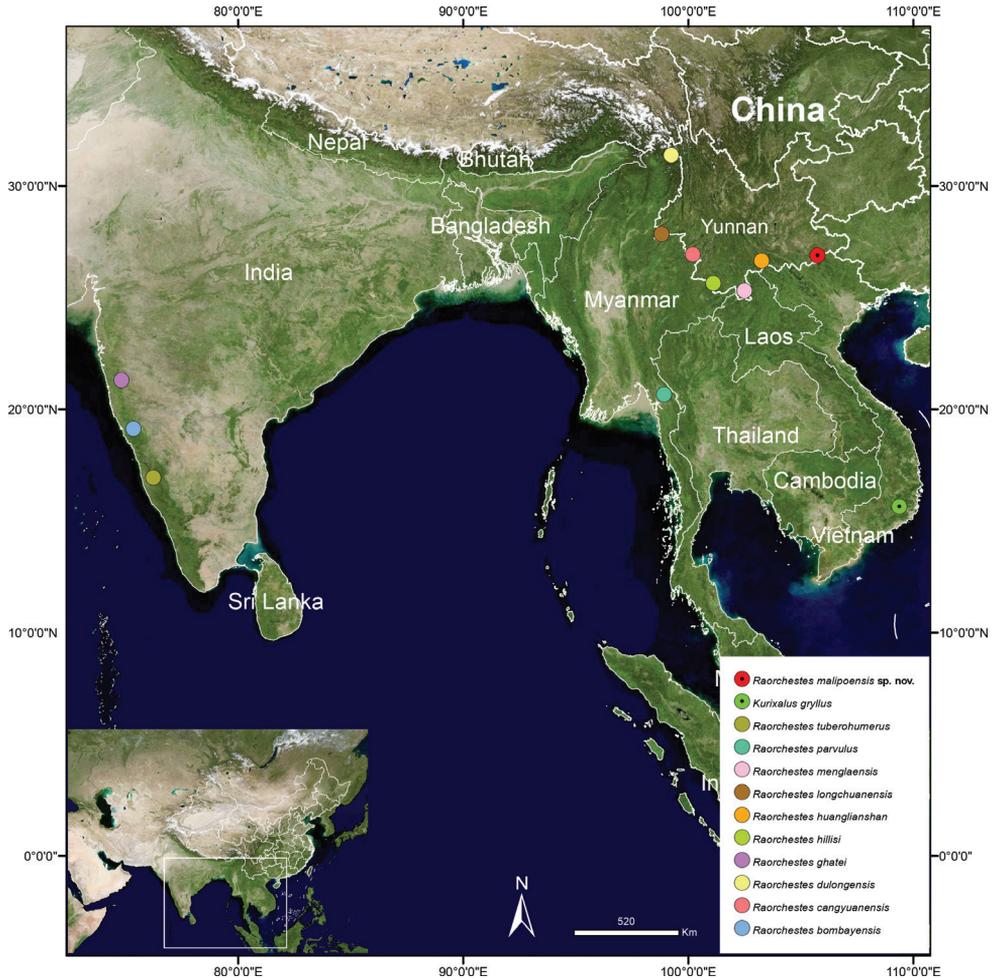


Figure 1. The type locality of *Raorchestes malipoensis* sp. nov., its closest relatives, and also *Kurixalus gryllus* (previously *Raorchestes gryllus*).

and subsequently euthanized with 20% ethanol following standard euthanasia protocols for amphibians. Liver or muscle tissues were taken from the specimens and preserved in 95% ethanol before fixing them in 75% ethanol. Voucher specimens SWFU 3110, SWFU 3113, SWFU 3114, SWFU 3116, SWFU 3111, and SWFU 3112 were deposited at Southwest Forestry University (SWFU). GXNU 000338, GXNU 000339, GXNU 000340, GXNU 000341, GXNU 000342 were deposited at Guangxi Normal University (GXNU).

Morphology and morphometrics

All the measurements were made with slide calipers to the nearest 0.1 mm. Morphological terminology and measurement methods followed Fei et al. (2009). The morphological characters include: snout-vent length (SVL); head length (HL); head width



Figure 2. Habitat at the type locality of *Raorchestes malipoensis* sp. nov., Malipo County, Yunnan Province, 23.182°N, 104.78°E, elevation 1496 m, China.

(HW); snout length (SL); internarial distance (INS); interorbital distance (IOS); eye horizontal diameter (EHD); maximum width of upper eyelid (UEW); tympanum diameter (TD); forelimb and hand length (FAHL); width of lower arm (LAW); hand length (HAL); femur length (FML); tibia length (TBL); length of tarsus and foot (TFL); foot length (FOL); tibia width (TBW); and femur width (FMW). Morphological measurements of the specimens are given in Table 1. Males and females (breeding individuals) were identified based on the presence or absence of an external single subgular vocal sac. Comparative morphological data of congeneric species were taken from previous studies and are presented in Table 2.

DNA sequencing and analyses of sequences

Total DNA was extracted using a commercial tissue DNA isolation kit (Chenlu Biotech, China). For seven specimens in this study, the mitochondrial gene 16S ribosomal RNA (16S rRNA) gene was sequenced. The fragments of 16S rRNA were amplified using primers 16Sar-L (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr-H (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi et al. 1991). Polymerase chain reactions (PCR) amplifications were performed in a 25 µl reaction volume with an initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 1 min, 51 °C for 1 min, 72 °C for 1 min, and a final extension at 72 °C for 10 min. The

Table 1. Measurements (mm) of adult specimens in the type series of *Raorchestes malipoensis* sp. nov. Abbreviations defined in the Materials and methods.

Sex	Males (n = 4)			Females (n = 2)		Males (n = 3)			Females (n = 2)		
	Catalog No.	SWFU 3110	SWFU 3113	SWFU 3114	SWFU 3116	SWFU 3111	SWFU 3112	GXNU 000338	GXNU 000339	GXNU 000341	GXNU 000340
SVL	17.1	17.0	16.5	14.7	19.3	19.0	17.5	17.7	17.3	18.7	18.3
HL	5.7	5.8	6.3	5.2	6.5	7.9	5.9	6.4	5.7	6.3	6.7
HW	7.7	7.5	8.2	5.5	8.2	7.9	6.5	6.8	6.4	7	7
SL	2.5	2.6	1.8	2.5	2.9	2.6	2	2.6	2.4	2.5	2.2
INS	1.5	2.2	2.2	2.0	2.2	2.1	2.2	2.1	2.3	2.2	2
IOS	2.7	2.7	2.9	2.9	3.2	2.9	2.9	2.6	2.9	2.7	2.9
UEW	1.2	1.2	1.9	1.4	1.6	1.7	1.6	1.3	1.4	1.4	1.7
EHD	2.2	2.1	2.1	2.6	2.6	2.8	2.4	2.6	2.4	2.5	2.2
TD	1.4	1.4	1.5	1.3	1.1	1.5	1.2	1.5	1.4	1.6	1.4
FAHL	9.3	9.3	8.8	7.0	8.6	9.6	7.8	8.2	7.2	7.3	7.1
HAL	5.6	5.6	5.3	4.2	5.2	5.6	5.3	5.2	5.3	4.6	5.4
LAW	1.7	2.0	1.6	1.3	1.4	1.6	1.5	1.2	1.6	1.3	1.3
TBL	9.1	8.7	8.4	7.5	9.1	9.2	9	8.8	8	8.7	8.8
FML	7.5	9.2	8.3	7.1	8.0	10.2	7.5	8	7.5	8.2	7.9
TBW	2.1	2.6	1.8	1.5	2.0	2.8	1.7	1.7	1.8	1.8	1.9
TFL	9.8	10.9	10.6	8.8	10.0	11.8	10.8	11	10.1	9.6	10.7

Table 2. The source of morphological data for *Raorchestes* species used in this study.

ID	<i>Raorchestes</i> species	Literature
3	<i>Raorchestes ghatei</i> Padhye, Sayyed, Jadhav, & Dahanukar, 2013	Padhye et al. 2013
4	<i>Raorchestes parvulus</i> (Boulenger, 1893)	Bossuyt and Dubois 2001
5	<i>Raorchestes cangyuanensis</i> Wu, Suwannapoom, Xu, Murphy, & Che, 2019	Wu et al. 2019
6	<i>Raorchestes longchuanensis</i> (Yang & Li, 1978)	Al-Razi et al. 2020 b; Yang and Li 1978
7	<i>Raorchestes menglaensis</i> (Kou, 1990)	Jiang et al. 2020
8	<i>Raorchestes hillisi</i> Jiang Ren, Guo, Wang & Li, 2020	Jiang et al. 2020
9	<i>Raorchestes huanglianshan</i> Jiang, Wang, Ren, & Li, 2020	Jiang et al. 2020
10	<i>Raorchestes dulongensis</i> Wu, Liu, Gao, Wang, Li, Zhou, Yuan, & Che, 2021	Wu et al. 2021
11	<i>Raorchestes andersoni</i> (Ahl, 1927)	Bossuyt and Dubois 2001
12	<i>Raorchestes rezakhani</i> Al-Razi, Maria, & Muzaffar, 2020	Al-Razi et al. 2020 a
13	<i>Raorchestes annandalii</i> (Boulenger, 1906)	Che et al. 2020

PCR products were sequenced using an ABI 3730 automated sequencer. To study the phylogenetic relationships among *Raorchestes* species, matrilineal genealogies were reconstructed based on the 16S fragment. Fifty-two sequences of *Raorchestes* and representative outgroups (Jiang et al. 2020) were downloaded from GenBank (Table 3). The dataset was checked by eye and manually adjusted using MEGA 6.0 with default settings (Tamura et al. 2013), and the alignment was checked by eye and adjusted manually. JMODELTEST v. 2.1.7 (Darrriba et al. 2012) was used to select an appropriate nucleotide substitution model for Bayesian Inference (**BI**). The GTR+G+I model was chosen as the best-fit model following the Bayesian information criterion (BIC; Posada 2008). Bayesian analysis was performed using MrBayes 3.2 (Ronquist et al. 2012). For BI analyses, the Monte Carlo Markov chain length was run for 120,000,000 genera-

Table 3. Information on voucher numbers, GenBank accession numbers, and localities of specimens used in this study; for collections and their abbreviations see Material and methods.

Species	Voucher No.	GenBank No.	Locality	Resource
Ingroup				
<i>Raorchestes malipoensis</i> sp. nov.	SWFU 3110	ON128247	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	SWFU 3111	ON128241	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	ROM 30288	GQ285674	Pac Ban, Tuyen Quang, Vietnam	Li et al. 2009
<i>Raorchestes malipoensis</i> sp. nov.	GXNU 000338	ON128246	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	GXNU 000339	ON128245	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	GXNU 000340	ON128244	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	GXNU 000341	ON128243	Malipo, Yunnan, China	This study
<i>Raorchestes malipoensis</i> sp. nov.	GXNU 000342	ON128242	Malipo, Yunnan, China	This study
<i>Raorchestes dulongensis</i>	KIZ 035082	MW537814	Qinlangdang, Yunnan, China	Wu et al. 2021
<i>Raorchestes hillisi</i>	CIB 116331	MT488411	Xiding, Yunnan, China	Jiang et al. 2020
<i>Raorchestes longchuanensis</i>	KIZ 048468	MN475870	Unknown	Wu et al. 2019
<i>Raorchestes parvulus</i>	LSUHC:11118	MH590201	Gunung Stong, Kelantan, Malaysia	Chan et al. 2018
<i>Raorchestes menglaensis</i>	CIB 116349	MT488410	Menglun, Yunnan, China	Jiang et al. 2020
<i>Raorchestes huanglianshan</i>	CIB 116365	MT488414	Lvchun, Yunnan, China	Jiang et al. 2020
<i>Raorchestes cangyuanensis</i>	KIZ 015855	MN475866	Cangyuanensis, Yunnan, China	Wu et al. 2019
<i>Raorchestes tuberothumerus</i>	CESF 148	JX092697	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes bombayensis</i>	CESF 1010	JX092657	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes ghatei</i>	AGCZRL	KF366391	Western Ghats, India	Padhye et al. 2013
	Amphibia 128			
<i>Raorchestes griet</i>	CESF 073	JX092654	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes coonoorensis</i>	CESF 439	JX092716	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes charius</i>	CESF 132	JX092691	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes marki</i>	CESF 467	JX092719	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes indigo</i>	CESF 138	KM596557	Kudremukh Massif, Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes emeraldii</i>	CESF 1365	KM596556	Valparai plateau, Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes ponmudi</i>	CESF 063	JX092651	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes aureus</i>	CESF 1164	KM596540	Malabar, Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes montanus</i>	CESF 130	KM596552	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes timmiens</i>	CESF 438	JX092715	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes primarrunfi</i>	CESF 442	KM596575	Nilgiri Massif, Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes signatus</i>	Unknown	AY141841	Sri Lanka	Meeegaskumbura et al. 2002
<i>Raorchestes chromasynchyisi</i>	CESF 1127	JX092667	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes chotta</i>	CESF 1003	JX092656	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes nerostagona</i>	CESF 1061	JX092661	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes kadalarensis</i>	CESF 1766	JX092701	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes agasthyaensis</i>	CESF 492	JX092723	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes travancoricus</i>	CESF 473	JX092721	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes luteolus</i>	CESF 1012	JX092659	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes beddomii</i>	CESF 072	JX092653	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes theuerkaufi</i>	CESF 1342	JX092693	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes munnarensis</i>	CESF 094	JX092655	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes anili</i>	CESF 386	JX092708	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes respplendens</i>	CESF 1258	JX092683	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes dubois</i>	CESF 114	JX092668	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes kakachi</i>	CESF 1385	KM596558	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes katikatti</i>	CESF 444	JX092718	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes sushili</i>	CESF 1259	JX092684	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes flavioocularis</i>	CESF 1252	KM596549	Manalar Plateau, Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes ochlandrae</i>	CESF 1111	JX092666	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes manohari</i>	CESF 1187	JX092674	Western Ghats, India	Vijayakumar et al. 2014

Species	Voucher No.	GenBank No.	Locality	Resource
<i>Raorchestes uthamani</i>	CESF 483	JX092722	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes chlorosomma</i>	FB-2008c	EU450017	Munnar, Idukki, Kerala, India	Biju and Bossuyt 2009
<i>Raorchestes crustai</i>	CESF 1199	JX092677	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes graminirupes</i>	CESF 044	JX092649	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes johnceei</i>	CESF 1236	JX092679	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes glandulosus</i>	CESF 1080	JX092665	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes jayanami</i>	CESF 1260	JX092686	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes bobingeri</i>	CESF 1238	JX092680	Western Ghats, India	Vijayakumar et al. 2014
<i>Raorchestes akroparallagi</i>	CESF 061	JX092650	Western Ghats, India	Vijayakumar et al. 2014
Outgroup				
<i>Philautus abditus</i>	ROM 33145	GQ285673	Krong Pa, Gia Lai, Vietnam	Li et al. 2009

Table 4. Uncorrected pairwise sequence divergence (%) among 16S ribosomal RNA mtDNA sequences, including *R. malipoensis* sp. nov., *R. dulongensis*, *R. hillisi*, *R. longchuanensis*, *R. menglaensis*, *R. huanglianshan*, *R. cangyuanensis*, *R. parvulus*, *R. bombayensis*, *R. tuberothumerus*, and *R. ghatei* as shown in phylogenetic tree presented in Fig. 3.

Species	1	2	3	4	5	6	7	8	9	10
<i>R. malipoensis</i> sp. nov.										
<i>R. bombayensis</i>	4.5									
<i>R. tuberothumerus</i>	4.8	2.0								
<i>R. ghatei</i>	4.5	4.2	4.0							
<i>R. parvulus</i>	5.9	5.1	5.9	5.4						
<i>R. cangyuanensis</i>	5.7	6.6	6.8	5.6	7.1					
<i>R. longchuanensis</i>	3.1	4.7	4.9	4.0	4.0	5.6				
<i>R. menglaensis</i>	5.2	4.2	4.9	5.7	2.0	5.9	4.7			
<i>R. hillisi</i>	4.3	4.9	5.2	4.3	6.1	6.3	4.2	5.4		
<i>R. huanglianshan</i>	6.0	6.1	6.4	5.2	4.5	6.8	5.4	4.5	5.4	
<i>R. dulongensis</i>	5.2	6.1	6.4	5.0	6.6	6.6	4.2	6.2	3.3	5.7

Taxonomic account

Raorchestes malipoensis sp. nov.

<https://zoobank.org/0DCF253A-45E1-4354-9C6B-AA44E7C6C309>

Fig. 4, Table 1

“*Pseudophilautus gryllus*” (Li et al. 2009).

“*Raorchestes gryllus*” (Biju et al. 2010).

Holotype. GXNU 000339, adult male, collected from Malipo County, Yunnan Province (23.182°N, 104.78°E, elevation 1496 m) on 22 July 2020 by Shuo Liu.

Paratypes. SWFU 3110, SWFU 3113, SWFU 3114, SWFU 3116, GXNU 000338, GXNU 000341 (six adult males), SWFU 3111, SWFU 3112, GXNU 000340, GXNU 000342 (four adult females), collected at the same locality as the holotype on 22 July 2020 by Xiaolong Liu and Shuo Liu.

Diagnosis. The genus *Raorchestes* is a group of small frogs, diagnosed primarily on the basis of an adult snout-vent length between 15 and 45 mm; vomerine teeth absent; large gular pouch transparent while calling; nocturnally active; direct development without free-swimming tadpoles in all species for which the development is known (Biju et al. 2010). Although the mode of development in the new species remains unknown, *R. malipoensis* sp. nov. is placed in the genus *Raorchestes* due to the combination of following characters: small body size, vomerine teeth absent, single translucent external subgular vocal sac present, and tips of all fingers and toes expanded into discs with circum-marginal grooves. The new species is distinguished from geographically and molecularly relevant congeners by the following combination of characters: (1) very small body size (males SVL 14.6–17.7 mm, $n = 7$; females SVL 18.3–19.3 mm, $n = 4$); (2) head wider than long; (3) tympanum small, supratympanic fold distinct; (4) tips of all fingers and toes yellow; (5) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); (6) inner and outer metacarpal tubercle indistinct; (7) heels not meeting when limbs held at right angles to body; (8) tibiotarsal articulation reaching anterior border of eye when hindlimb is stretched alongside of body; (9) iris golden brown; (10) nuptial pad small and milky white; (11) inner metatarsal tubercle rounded, outer metatarsal tubercle absent; (12) fingers and toes having lateral dermal fringe; and (13) interorbital distance larger than eye horizontal diameter.

Description of the holotype. Adult male (Fig. 4), body size small (SVL 17.7 mm); head wider than long (HL 6.4 mm; HW 6.8 mm); top of head relatively flat; snout rounded in profile, projecting beyond lower jaw; snout length almost equal to interorbital distance at narrowest point (SL 2.6 mm; IOS 2.6 mm); the canthus rostralis rounded, loreal region slightly concave; tympanum small (TD 1.5 mm); internarial distance wider than maximum width of upper eyelid (INS 2.1 mm; UEW 1.3 mm); nostril slightly closer to tip of snout than to anterior corner of eyes; tongue pyriform, with a deep notch at posterior tip; vomerine teeth absent; pineal ocellus absent; eyes moderately large (EHD 2.6 mm) and protruding, pupil horizontal; supratympanic fold distinct, from posterior corner of eye to above insertion of arm.

Forelimbs fairly robust (FAHL 8.2 mm); relative finger lengths: I < II < IV < III, tips of all four fingers expanded into discs with circum-marginal grooves; all fingers with lateral dermal fringes on both sides; subarticular tubercles distinct, rounded; supernumerary tubercles absent; no webbing between fingers; inner and outer metacarpal tubercle indistinct; nuptial pad is small and milky white on dorsal surface of the first finger.

Foot long and relatively robust (TFL 11 mm), longer than tibia length (TBL 8.8 mm); relative toe lengths: I < II < V < III < IV; tips of toes with discs having circum-marginal grooves, toe discs smaller than finger discs; all toes with lateral dermal fringes on both sides; subarticular tubercles distinct, rounded; supernumerary tubercles absent; webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); inner metatarsal tubercle rounded, outer metatarsal tubercle absent.

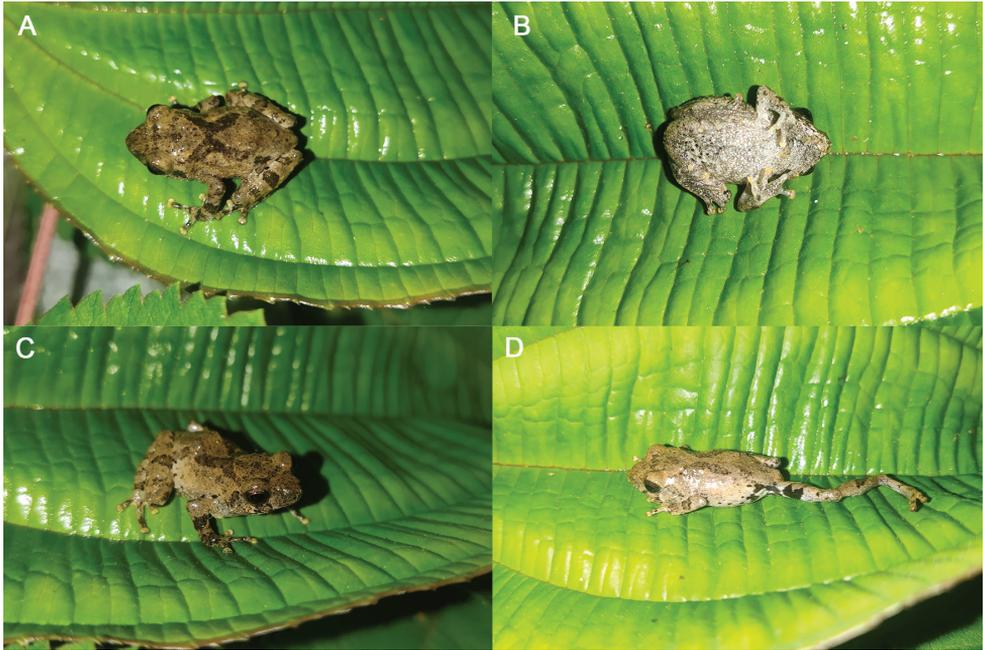


Figure 4. Holotype (GXNU 000339) of *Raorchestes malipoensis* sp. nov. in life.

Dorsal surfaces of head, body, forelimbs, thighs, and tibia rough with small granules; upper eyelid with several small granules; throat, chest, and ventral surfaces of forelimbs smooth; abdomen, ventral side of thigh, and area around vent with granules; dorsolateral folds absent.

Coloration of holotype in life. For coloration of the holotype in life see Fig. 4. Dorsal surface beige, with pale brown band between eyes; dorsal surface with a dark brown X-shaped marking; pale brown interorbital rectangle between eyes; upper and lower lips with white and black dots; supratympanic fold pale brown; iris golden brown; dorsal parts of arms and legs with dark brown crossbars that align; crotch with a distinct black patch bordering large creamy white plaque below the black patch near the groin; dorsal thigh beige with one brown crossbar when leg is bent in resting position; ventral surface body and beige, and area around vent with small black spots; discs of fingers and toes yellow.

Coloration in alcohol. After preservation in alcohol, the general pattern did not change. Dorsal color changed to grayish brown, the blotches or spots blackish brown, discs on the fingers become pale gray similar to the body color, ventral side become whiter (Fig. 5).

Etymology. The specific epithet is named for the type locality, Malipo County, Yunnan Province, China. We suggest “Malipo Bush Frog” as its English common name, and “Ma Li Po Guan Shu Wa (麻栗坡灌树蛙)” as its Chinese common name.

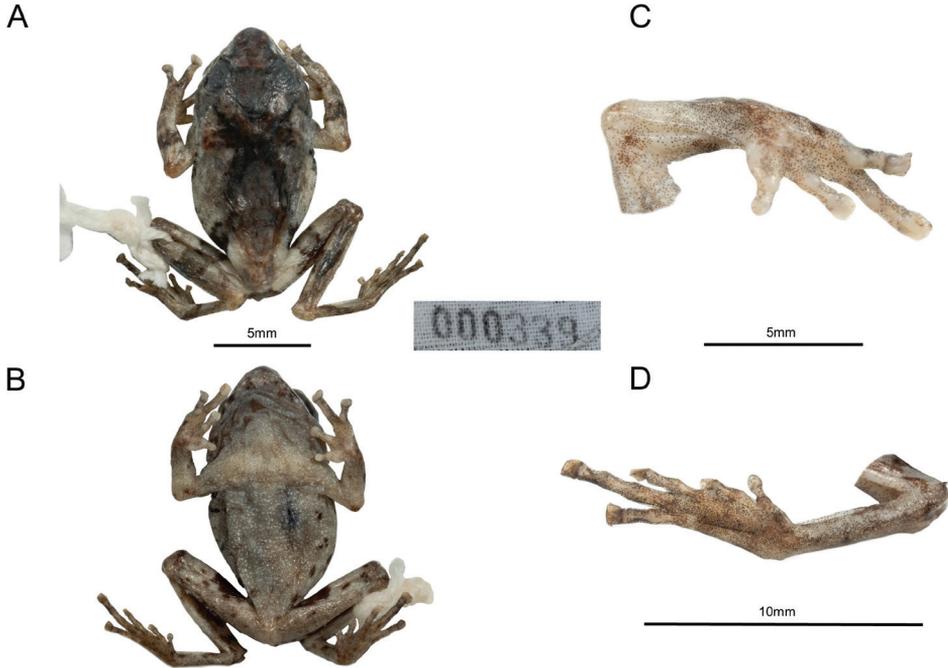


Figure 5. Holotype (GXNU 000339) of *Raorchestes malipoensis* sp. nov. in preservative, showing **A** dorsal view **B** ventral view **C** ventral view of hand **D** ventral view of foot.

Distribution. Currently known from the type locality, Malipo County (Fig. 1), Yunnan Province, China and Pac Ban, Tuyen Quang, in north of Vietnam.

Variation. The measurements are given in Table 1. GXNU 000338 has large black spots on dorsal side and GXNU000342 has distinctly darker ground color on dorsal side.

Comparisons. Rather than comparing *R. malipoensis* sp. nov. to all known *Raorchestes*, we focus on our morphological comparison with phylogenetically closely related taxa and species without genetic data in adjacent countries (Table 5).

The new species differs from *R. menglaensis* by 1) tubercles absent along the outer side of the forearm and foot; (2) head wider than long; (3) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); (4) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); (5) lateral dermal fringe present (6) inner and outer metacarpal tubercle indistinct; (7) outer metatarsal tubercle absent; and (8) relative toe lengths: I < II < V < III < IV (vs. a series of tubercles along the outer side of the forearm and foot; head length and head width are approximately the same; tympanum indistinct; webbing formula (II 1 – 2 III 1 – 2^{1/2} IV 2^{1/2}–1 V); lateral dermal fringe present; inner and outer metatarsal tubercle present; outer metatarsal tubercle present; relative toe lengths: III \approx V, or V > III).

Table 5. Comparison of *R. malipoensis* sp. nov. with phylogenetically closely related taxa or those with no genetic data in surrounding countries. “–” means unknown.

Species	<i>R. menglaensis</i>	<i>R. parvulus</i>	<i>R. dulongensis</i>	<i>R. hillisi</i>	<i>R. huanglianshan</i>	<i>R. cangyuanensis</i>
SVL of adult males (in mm)	14.6–17.7, <i>n</i> = 7	–	15.0–19.0, <i>n</i> = 3	14.5–17.7, <i>n</i> = 3	17.0–19.6, <i>n</i> = 11	16.1–19.0 mm, <i>n</i> = 3
SVL of adult females (in mm)	18.3–19.3, <i>n</i> = 4	23.6, <i>n</i> = 1	–	17.5, <i>n</i> = 1	21.5, <i>n</i> = 1	–
SVL of adult (in mm)	14.6–19.3, <i>n</i> = 11	23.6, <i>n</i> = 1	15.0–19.0, <i>n</i> = 3	14.5–17.7, <i>n</i> = 4	17.0–21.5, <i>n</i> = 4	16.1–19.0 mm, <i>n</i> = 3
IOS/EHD	IOS > EHD, or IOS = EHD	IOS < EHD	IOS < EHD	IOS < EHD	IOS > EHD, or IOS = EHD	IOS < EHD
HDW/HDL	HDW > HDL	HDW > HDL	HDW < HDL	HDW < HDL	HDW > HDL	HDW > HDL
Tympanum	Distinct	Distinct	Distinct	Distinct	Distinct	Indistinct
Nuptial pad	Small and milky white	–	Absent	Present	Present	Reddish nuptial pad
Toe web	I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V	Webbing present, medium	Rudimentary web	II 1 – 2 III 1 – 2 ^{1/2} IV 2 ^{1/2} – 1 V	II 1 – 2 III 1 – 2 – IV 2 – 1 V	Rudimentary web
Lateral dermal fringe	Present	–	–	Present	Absent	Present
Disc color	Yellow	Not orange in life	Greyish or orange	–	Orange	Orange
Inner metacarpal tubercle	Indistinct	Present	Present	Indistinct	Indistinct	–
Outer metacarpal tubercle	Indistinct	Present	Present	Indistinct	Indistinct	–
Inner metatarsal tubercle	Round	Present	Round	Round	Round	Round
Outer metatarsal tubercle	Absent	Absent	Absent	Absent	Absent	Absent
Relative toe lengths	I < II < V < III < IV	I < II < V < III < IV	I < II < V < III < IV	I < II < III < V < IV	I < II < III < V < IV	I < II < V < III < IV
Range	Malipo, Yunnan, China and the north of Vietnam	Indochina Peninsula and peninsular Malaysia	Gongshan, Yunnan, China	Menghai, Yunnan, China	Lvxuan, Yunnan, China	Cangyuan, Yunnan, China

Table 5. Continued.

Species	<i>R. ghatei</i>	<i>R. rezabihani</i>	<i>R. annandali</i>	<i>R. bombayensis</i>	<i>R. ruberohumerus</i>	<i>R. longchuanensis</i>	<i>R. andersoni</i>
SVL of adult males (in mm)	19.1–25.5, <i>n</i> = 9	18.8–19.0 mm, <i>n</i> = 4	–	30 mm, <i>n</i> = –	17.4–18.2 mm, <i>n</i> = 3	21.4–23.9 mm, <i>n</i> = 5	13.5–24.0 mm, <i>n</i> = 2
SVL of adult females (in mm)	15.4–29.8, <i>n</i> = 13	–	17.0 mm, <i>n</i> = 1	–	–	–	–
SVL of adult (in mm)	15.4–29.8, <i>n</i> = 22	18.8–19.0 mm, <i>n</i> = 4	17.0 mm, <i>n</i> = 1	30 mm, <i>n</i> = –	17.4–18.2 mm, <i>n</i> = 3	21.4–23.9 mm, <i>n</i> = 5	13.5–24.0 mm, <i>n</i> = 2
IOS/EHD	–	IOS < EHD	IOS > EHD, or IOS = EHD	–	IOS > EHD, or IOS = EHD	IOS > EHD	IOS < EHD
HDW/HDL	HDW > HDL	HDW > HDL	HDW < HDL	–	HDW > HDL	HDW ≈ HDL	HDW > HDL
Tympanum	Indistinct	Indistinct	Distinct	Indistinct	Indistinct	Distinct	Distinct
Nuptial pad	Absent	Absent	–	–	–	Present	–
Toe web	I 2–2 II 2–2½ III 2–3 IV 2½–2 V	I 2–2 II 1¾–2 III 1½–3 IV 2¾–2 V	Rudimentary web	1/3 webbing	Rudimentary web	1/4 webbing	1/3 webbing
Lateral dermal fringe	Present	Absent	Present	–	–	–	–
Disc color	–	Reddish or whitish	–	–	–	Reddish, orange, or whitish	orange
Inner metacarpal tubercle	–	Absent	Present	–	–	Present	Present
Outer metacarpal tubercle	–	Absent	Present	–	–	Present	Present
Inner metatarsal tubercle	Round	Absent	Absent	–	Present	Present	Present
Outer metatarsal tubercle	Absent	Absent	Absent	–	Absent	Absent	Absent
Relative toe lengths	I < II < V = III < IV	I < II < V < III < IV	I < II < V = III < IV	–	I < II ≤ V < III < IV	III ≈ V	I < II < III = V < IV
Range	Western Ghats, India	Northeastern Bangladesh	Himalayas and northeastern India	Western Ghats, India	Western Ghats, India	Yunnan, China and Lai Chau, Vietnam	India, North Myanmar, Tibet and Yunnan, China

The new species differs from *R. parvulus* by (1) smaller female body size (females 18.3–19.3 mm, $n = 4$); (2) interorbital distance larger than eye horizontal diameter; and (3) inner and outer metacarpal tubercle indistinct; (vs. female 23.6 mm, $n = 1$; interorbital distance smaller than eye horizontal diameter; inner and outer metacarpal tubercle present).

The new species differs from *R. dulongensis* by (1) head wider than long; (2) interorbital distance larger than eye horizontal diameter; (3) nuptial pad present; (4) yellow disc; and (5) inner and outer metacarpal tubercle indistinct (vs. head smaller than long; interorbital distance smaller than eye horizontal diameter; nuptial pad absent; greyish or orange disc; inner and outer metacarpal tubercle indistinct present).

The new species differs from *R. hillisi* by (1) larger female body size (females 18.3–19.3 mm, $n = 4$); (2) head wider than long; (3) interorbital distance larger than eye horizontal diameter; (4) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); and (5) and relative toe lengths: I < II < V < III < IV (vs. female 17.5 mm, $n = 1$; head longer than wider; interorbital distance smaller than eye horizontal diameter; webbing formula (II 1–2 III 1–2^{1/2} IV 2^{1/2}–1 V); relative toe lengths: I < II < III < V < IV).

The new species differs from *R. huanglianshan* by (1) smaller female body size (females 18.3–19.3 mm, $n = 4$); (2) lateral dermal fringe present; (3) yellow disc; (4) webbing formula (II 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); and (5) relative toe lengths: I < II < V < III < IV (vs. female 21.5 mm, $n = 1$; lateral dermal fringe absent; orange disc; fingers and toes lacking lateral dermal fringe; webbing formula (II 1–2 III 1 – 2 – IV 2 – 1 V); relative toe lengths: I < II < III < V < IV).

The new species differs from *R. cangyuanensis* by (1) interorbital distance larger than eye horizontal diameter; (2) nuptial pad small and milky white; and (3) yellow discs (vs. interorbital distance smaller than eye horizontal diameter; reddish nuptial pad at the base of first finger; orange disc).

The new species differs from *R. ghatei* by (1) smaller body size (males 14.6–17.7 mm, $n = 7$; females 18.3–19.3 mm, $n = 4$); (2) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); (3) nuptial pad present; (4) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); and (5) relative toe lengths: I < II < V < III < IV (vs. males 19.1–25.5 mm, $n = 9$; females 15.4–29.8 mm, $n = 13$; tympanum indistinct; nuptial pad absent; webbing formula (I 2 – 2 II 2 – 2½ III 2– 3 IV 2½ – 2 V); relative toe lengths: I < II < V = III < IV).

The new species differs from *R. rezakhani* by (1) smaller male body size (males 14.6–17.7 mm, $n = 7$); (2) interorbital distance larger than eye horizontal diameter; (3) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); (4) nuptial pad present; (5) lateral dermal fringe present; (6) yellow disc; (7) inner and outer metacarpal tubercle indistinct; (8) inner metatarsal tubercle round; and (9) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V) (vs. males 18.8–19.0 mm; interorbital distance smaller than eye horizontal diameter; tympanum indistinct; nuptial pad absent; lateral dermal fringe absent; reddish or whitish; inner and outer metacarpal tubercle absent; inner metatarsal tubercle absent; webbing formula (I 2 – 2 II 1¾ – 2 III 1½ – 3 IV 2¾ – 2 V).

The new species differs from *R. annandalii* by (1) head wider than long; and (2) relative toe lengths: $I < II < V < III < IV$ (vs. head longer than wide; relative toe lengths: $I < II < V = III < IV$).

The new species differs from *R. bombayensis* by (1) smaller body size (males 14.6–17.7 mm, $n = 7$; females 18.3–19.3 mm, $n = 4$); (2) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); and (3) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V) (vs. 30 mm, $n = 1$; tympanum indistinct; 1/3 webbing between toes).

The new species differs from *R. tuberothumerus* by (1) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); and (2) relative toe lengths: $I < II < V < III < IV$ (vs. tympanum indistinct; relative toe lengths: $I < II \leq V < III < IV$).

The new species differs from *R. longchuanensis* by (1) smaller male body size (males 14.6–17.7 mm, $n = 7$); (2) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); and (3) yellow disc (vs. males 21.4–23.9 mm, $n = 5$; 1/4 webbing between toes; reddish, orange, or whitish disc).

The new species differs from *R. andersoni* by (1) interorbital distance larger than eye horizontal diameter; (2) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); (3) yellow disc; and (4) relative toe lengths: $I < II < V < III < IV$ (vs. interorbital distance smaller than eye horizontal diameter; 1/3 webbing between toes; orange disc; relative toe lengths: $I < II < III = V < IV$).

Discussion

Recently, Poyarkov et al. (2021) placed *Philautus gryllus* in the genus *Kurixalus* based on unpublished molecular evidence and a study of type materials. In this study, the sample previously identified as *R. gryllus* from northern Vietnam (voucher number: ROM 30288) nests in the clade of *R. malipoensis* sp. nov. without distinct genetic divergence (Table 4), indicating that they are likely conspecific (Table 4). Morphologically, *Raorchestes malipoensis* sp. nov. is obviously distinguishable from *K. gryllus* as described by Smith (1924; Table 6) by (1) smaller body size 14.6–19.3 mm, $n = 11$; (2) tympanum distinct (TD 1.1–1.6 mm, $n = 11$); (3) webbing formula (I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V); (4) no webbing between fingers; (5) outer metatarsal tubercle absent (vs. 25.0–27.0 mm, $n = 3$; tympanum distinct; toes a little more than half webbed; fingers free except for a rudiment of a web between the two outer; outer metatarsal tubercle separated for approximately two-thirds of their length). Therefore, we consider that *Raorchestes malipoensis* sp. nov. is not conspecific with *K. gryllus* and the record of *R. gryllus* (ROM 30288) from northern Vietnam should be revised to *R. malipoensis* sp. nov. We also suggest that the taxonomic status of other records of *R. gryllus* from Vietnam and Laos need further examinations.

In recent years, many new species have been found along the border between China and Vietnam, such as *Odorrana geminata* (Bain et al., 2009), *Tylosotriton zieglerei* (Nishikawa et al., 2013), *Leptobranchella feii* (Chen et al., 2020), *Amolops shihaitaoi* (Wang et al., 2022), and *Theloderma hekouense* (Du et al., 2022). Tropical montane forests in the

Table 6. Morphological comparison between *Raorchestes malipoensis* sp. nov. and *Kurixalus gryllus* (Smith, 1924).

Character	Species	
	<i>Raorchestes malipoensis</i> sp. nov. (n = 11)	<i>Kurixalus gryllus</i> (n = 3)
SVL	14.6–19.3 mm	25.0–27.0 mm,
HL	5.2–7.9 mm	8.0–9.5 mm
HW	5.5–8.2 mm	10.0–11.0 mm
EHD	2.1–2.8 mm	3.0–3.5 mm
SL	1.8–2.9 mm	4–4.5 mm
HAL	4.2–5.6 mm	7.5–8.5 mm
TBL	7.5–9.2 mm	12–13 mm
TD	1.1–1.6 mm n = 11	tympanum indistinct
Tubercles along forearm and foot	absent	present
Web of toes	I 2 – 2 II 2 – 2 III 2 – 3 IV 3 – 2 V	toes a little more than half webbed
Web of fingers	no webbing between fingers	fingers free except for a rudiment of a web between the two outer fingers
Metatarsal tubercle	inner metatarsal tubercle rounded, outer metatarsal tubercle absent	a small inner metatarsal tubercle
Coloration	dorsal surface beige, with pale brown and dark brown spots, an individual having large black spots on its body surface	dorsal color with pale or dark brown, green, yellow, or grey, many individuals had a bright green patch on the snout, and patches of similar color on the knees and round the vent

border region between China and Vietnam are known to harbor a high level of species richness and local endemism (Sterling et al. 2006). One of the main reasons assumed to be responsible for this richness is the greater environmental heterogeneity observed in the montane regions as opposed to the lowland regions, allowing for a larger number of habitats to be occupied by species (Keller et al. 2009). It is expected that more new species from this region would be discovered, and further studies are required to accurately determine the species richness of tree frogs in China-Vietnam border region. Due to historical reasons, herpetological surveys of this region had been scarce, but considering the biogeographical interest of the region it is important to facilitate collaborative research to comprehensively understand herpetofaunal diversity, community composition, and species range limits around the region in order to better protect them and their environment in the face of global warming and habitat destruction.

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A review of *Eupholidoptera* (Orthoptera, Tettigoniidae) from Crete, Gavdos, Gavdopoula, and Andikithira

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Abstract

Being nocturnal, hiding in prickly bushes and shrubs during the day, *Eupholidoptera* species in Crete and its neighbouring islands are easily overlooked, and until now our knowledge about their distribution was based on some thirty sightings across 11 species. In this paper results are presented of a study of *Eupholidoptera* specimens collected between 1987 and 2020 by hand-catches and pitfall and fermenting traps on the Greek islands of Crete, Gavdos, Gavdopoula, and Andikithira. Diagnostic features of all known species are presented and illustrated with stacked images. An updated key to all species is provided. *Eupholidoptera francisae* Tilmans & Odé, **sp. nov.** from Andikithira and southwestern Crete and *Eupholidoptera marietheresae* Willemse & Kotitsa, **sp. nov.** from Mt. Dikti are described. Female *E. cretica*, *E. gemellata*, and *E. mariannae* are described, and the female of *E. astyla* is redescribed. Bioacoustics for *E. francisae* Tilmans & Odé, **sp. nov.**, *E. giuliae*, and *E. jacquelinae* are presented for the first time. *Eupholidoptera smyrnensis* is reported for the first time from Crete. A substantial amount of new distribution data for *Eupholidoptera* species on Crete is presented. The current distribution pattern and first analyses of phylogeny based on molecular data of *Eupholidoptera* species on Crete are discussed in relation to paleogeographical events.

Keywords

Bioacoustics, faunistics, Greece, new species, phylogeography, systematics, traps

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Introduction

Eupholidoptera is a Mediterranean bush-cricket genus with 54 species belonging to the tribe Pholidopterini (Çiplak et al. 2021). It is distributed from southern France to Turkey and the Middle East (Çiplak et al. 2009). Most species are found in Greece and Turkey, each country listing more than 20 species. With an amazing eleven species, Crete, with its satellite islands, forms a hotspot for *Eupholidoptera* in Greece. Besides mesophytic vegetation, *Eupholidoptera* species are often associated with maquis and phrygana vegetation. This also applies to Crete where *Eupholidoptera* species live in thorny, spiny shrubs and bushes. These can be tall shrubs like *Rubus* and *Calicotome* on which they can be found sunbathing in the early morning, as well as low shrubs like *Sarcopoterium*. *Eupholidoptera* are nocturnal, hiding during the day inside shrubs and bushes. Males start singing late in the afternoon. The spiny and dense vegetation and the overall nocturnal activity pattern make it quite challenging to actually see *Eupholidoptera* during the day, let alone to collect them. In addition, *Eupholidoptera* can only be found during certain parts of the summer season. In lowlands, adult *Eupholidoptera* appear in May or early June and disappear again late July or August whereas at higher altitudes adults appear from late June onwards and may be found up to October. Table 1 presents the total number of all locations published up to now for *Eupholidoptera* species from Crete and its satellite islands. Because of the limited number of known locations, little was known in detail about distribution patterns of *Eupholidoptera* species in Crete. Previously known locations presented in Table 1 and Fig. 1 (blue dots) suggest that *Eupholidoptera* species are restricted to specific altitudinal ranges and absent from large parts of Crete, especially some lowland areas. Based on published locations and known threats, all Cretan species of *Eupholidoptera* were assessed in one of the IUCN threatened categories in 2016 (Hochkirch et al. 2016). In order to gain a better understanding of distribution patterns of *Eupholidoptera* as well as their phenology and habitat preferences, Crete and the islands of Andikithira (32 km northwest of Crete) and Gavdos (36.5 km south of southwestern Crete) were visited by the Dutch and German authors on various occasions between 1987 and 2020. In the same period and parallel to the efforts to collect *Eupholidoptera* using hand catches, *Eupholidoptera* species have also been trapped exten-

Table 1. Published record of *Eupholidoptera* species from Crete and Gavdos.

Species	Number of locations	Altitude (m)	Reference
<i>E. annamariae</i>	2	50–200	Nadig 1985; Çiplak et al. 2009
<i>E. astyla</i>	10	800–1850	Ramme 1927; Çiplak et al. 2009
<i>E. cretica</i>	1	not indicated	Ramme 1951
<i>E. feri</i>	1	1100	Willemse and Heller 2001
<i>E. forcipata</i>	3	1700–1850	Willemse and Kruseman 1976; Çiplak et al. 2009
<i>E. gemellata</i>	1	1650	Willemse and Kruseman 1976
<i>E. giuliae</i>	3	0–175	Massa 1999; Çiplak et al. 2009
<i>E. jacquelinae</i>	1	50	Tilmans 2002; Çiplak et al. 2009
<i>E. latens</i>	7	500–1800	Willemse and Kruseman 1976; Çiplak et al. 2009
<i>E. mariannae</i>	4 ⁽¹⁾	500–700	Willemse and Heller 2001; Ramme 1927
<i>E. pallipes</i>	1	1600–1800	Willemse and Kruseman 1976

¹: includes two locations of paratypes described by Ramme (1927) under *E. astyla*.

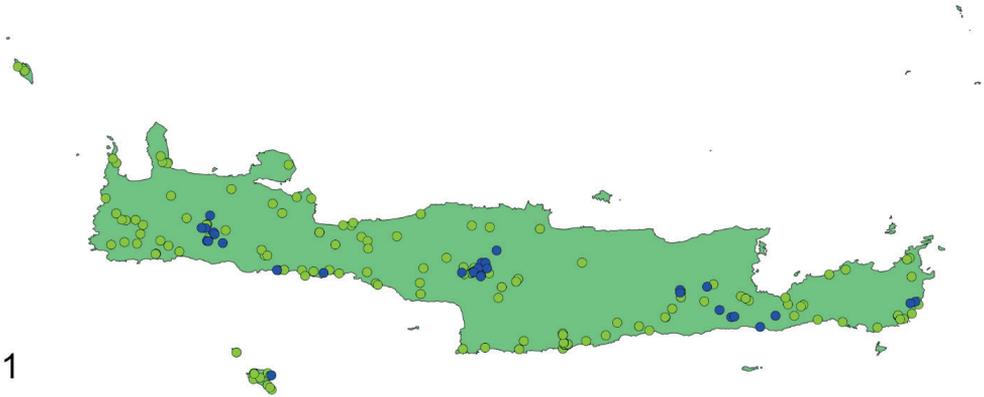


Figure 1. Occurrence records *Eupholidoptera* from Crete, Gavdos, Gavdopoula, and Andikithira. Blue dots: published locations; green dots: new locations.

sively as by-catch in pitfall and fermenting traps, across Crete and its satellite islands. This paper summarises the systematic and faunistic results based on specimens collected between 1987 and 2020. An updated key is presented. For each species, diagnostic features are given illustrated with stacked images, supplemented with a differential diagnosis and updated information on distribution, habitat, and phenology. In addition, comments are made on morphological variation found in the specimens studied.

Materials and methods

Hand catches

Hand catches included scanning larger shrubs (*Rubus*, *Calicotome*) in the morning to check for sunbathing individuals, walking through a terrain, and checking for individuals hiding in spiny bushes during the day. Additionally, singing males can be located

using audio equipment late in the afternoon and in combination with a (head) light in the first half of the night. Specimens were killed using ethylacetate or potassium cyanide, eviscerated, the belly filled with cotton wool, and airdried.

Rearing

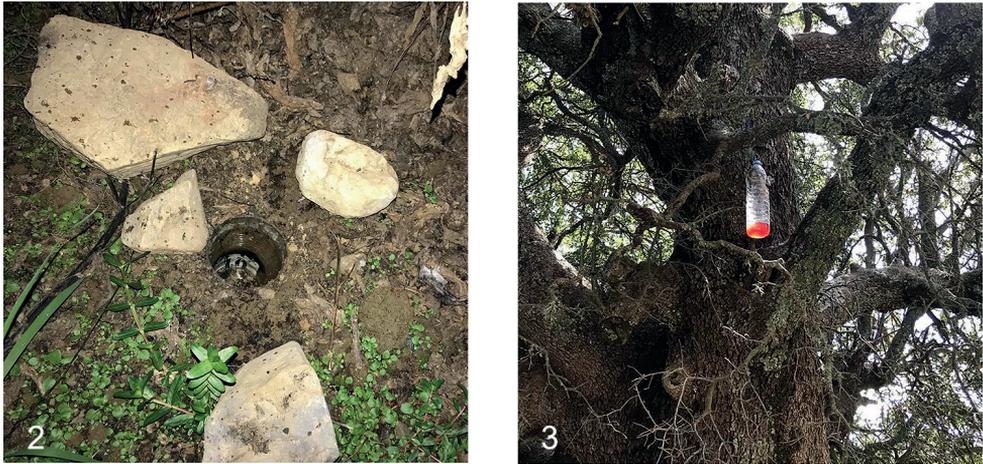
Specimens found as nymphs were reared to adults. For this, cylindrical plastic containers with small twigs were used and nymphs were fed with oat flakes. In some cases, however, very young nymphs that, based on their dark colour pattern, were assumed to be *Eupholidoptera* turned out to belong to different genera (for instance *Incertana* Zeuner, 1941).

Traps

The traps were part of MSc and PhD studies aimed at the epigeal fauna of Crete and environmental monitoring programs, carried out by the Natural History Museum of the University of Crete (Trichas et al. 2008). The main research goals of those studies were at first the description of diversity, phenology, and biogeography of several ground-dwelling beetle families (Carabidae, Tenebrionidae, Staphylinidae, etc.), while in the middle of the 1990s, Gnaphosidae and other ground spider families were added, and in the late 2000s chilopods, diplopods, and isopods were included. Details on trap protocols (active time of trapping, years, trap dimensions, chemicals, etc.) and trap efficiency are discussed in publications linked to these and other studies (Trichas et al. 2008; Kaltsas and Simaiakis 2012; Kaltsas et al. 2013; Salata et al. 2020).

Two types of traps were used, pitfall traps dug into the soil and fermenting traps placed higher up in the vegetation.

Pitfall traps (Fig. 2) used between 1988 and 2019 consisted of standardised sized cups (9.5 cm diameter, 12 cm depth) placed in a standardised pattern (15 per sampling station, stations always of homogenous biotope appearance) (Trichas et al. 2008; Kaltsas et al. 2013). Ethylene glycol was used as a killing/preserving agent being replaced by undiluted propylene glycol during the last ten years. Occasionally, a small quantity of attractants like vinegar, or surface tension reducers like liquid soap, were used. Traps were placed as far away as possible from visible ant nests, as ants tend to gather in masses in the container cups, preventing many of the targeted arthropods to be successfully caught. Sampling stations were active for one-year-round (occasionally with an additional two months in the next year) and were sampled bimonthly (Kaltsas and Simaiakis 2012), six (or seven) times in total. At elevations above 1500 m on the mountains, which were covered with snow from November or December till late April of the next year, usually only three samples per year were collected. For instance, traps set in April were emptied and refilled with propylene glycol in June, emptied and refilled again in August, etc., all year round. Locations with pitfall stations were usually remote from each other, as the biogeography of Crete was always one of the experimental targets. The numbers of *Eupholidoptera* specimens recovered from the contents of a single trapping event were usually fewer than ten, but quite regularly traps contained



Figures 2, 3. Traps **2** pitfall trap **3** fermenting trap.

several dozens of specimens. The highest numbers recorded in a single trapping event were 189 specimens of *E. astyla* and 513 specimens of *E. annamariae*.

Fermenting traps (Fig. 3) were only used between March 2018 and August 2019 primarily aimed at saproxylic beetles. Not all sampling stations were active for the entire duration of the study. In total, 24 stations around Crete were sampled (Bolanakis 2019; Bolanakis and Trichas 2019). The fermenting traps consisted of plastic water bottles (1.5 L) with an entrance hole in the top half containing a mix of alcoholic ingredients, sugars and some preservative (as in Galford 1980; Nageleisen and Bouget 2009). The mix that lured the *Eupholidoptera* specimens consisted of vinegar, sugar, salt, alcohol, yeast, glucose and rotten banana (Bolanakis 2019). Ingredients were stirred manually until the sugar and salt were dissolved and 0.2–0.3 L of the mix was poured in each bottle. Bottles were hanged inside the foliage and tied on tree or bush branches with a string. Trap stations were revisited every one or two months to replace traps and take the collected samples, after adding pure alcohol, to the laboratory (Bolanakis 2019). *Eupholidoptera* were collected in fermenting traps at nine different locations. With the exception of one trap placed in a *Pinus* forest which collected 28 specimen of *E. mariannae* in a six-week period, only few specimens (fewer than five) were found in fermenting traps.

Storage medium

Specimens collected by hand were dried and pinned. Specimens caught by traps are stored in 70% alcohol except for a few which, after examination, were pinned. For the storage medium for each of the examined specimens see Suppl. material 2.

DNA samples

Part of the DNA samples used for phylogenetic analysis derived from right mid legs from specimens collected in 2014, 2017, and 2019 (see Suppl. material 2). Additional

DNA samples were taken from specimens collected in pitfall traps and from dried, pinned specimens. Most specimens collected by pitfall traps did not yield good quality DNA due to the age of the samples, the collection method (deceased specimens stayed in the traps for weeks without ethanol and DNA-degrading agents such as vinegar before collection), and preservation (specimens were stored in room temperature). Dried, hand-picked samples had a better success rate than pitfall and fermenting trap catches. Still, some older dry samples (mainly collected before 2004) failed to yield good quality DNA results, especially regarding mitochondrial DNA, which is more prone to degradation compared to nuclear DNA.

DNA isolation and amplification

DNA was extracted from femoral muscles of *Eupholidoptera* specimens that were preserved either in alcohol (75% or 95%) or dry mounted. For recent and well-preserved specimens, a standard protocol for DNA isolation using ethanol precipitation was used. For dry-mounted and old, alcohol-preserved specimens from pitfall and fermenting traps DNA-isolation kits were used (Qiagen DNeasy Blood & Tissue Kits and Invitrogen purelink genomic DNA mini kit) following the manufacturers' instructions.

Sequence data for one protein-coding mitochondrial gene (NADH dehydrogenase subunit 2 – NADH2) and one non-coding nuclear region (the internal transcribed spacers 1 and 2 together with the 5.8S rDNA gene in-between – ITS) were used. For amplification of NADH2 the primers used were TM-J210 AATTAA-GCTAATGGGTTTCATACCC (forward) and TW-N1284 AYAGCTTTGAARGYT-ATTAGTTT (reverse) (Simon et al. 2006). The ITS fragment was amplified with the primers WeekF TAGAGGAAGTAAAAGTCG (forward) and WeekR GCT-TAAATTCAGCGG (reverse) (Weekers et al. 2001) "schema": "<https://github.com/citation-style-language/schema/raw/master/csl-citation.json>".

Polymerase chain reactions were performed using Thermo Scientific DreamTaq Hot Start Master Mix according to the manufacturer's instructions. Temperature cycling for the NADH2 followed Chobanov et al. (2017), with adaptations for hot-start PCR and slight adjustments, as follows: initial step at 95 °C for 5 min, followed by 35 cycles of denaturation (95 °C for 50 sec), annealing (51 °C for 40 sec), and elongation (72 °C for 80 sec), with a final elongation step at 72 °C for 15 min. Temperature cycling for the ITS fragment followed the protocol by Ullrich et al. (2010).

Additional sequences for both loci were obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

Phylogenetic analyses

Obtained sequences were trimmed, assembled, and visually checked using Codon-Code Aligner v. 8.0.2 (CodonCode, Dedham, MA, USA). All protein-coding sequences were checked for numt possibility and unique haplotypes were selected using DAMBE 7.2.152 (Xia, 2018). Sequence alignments were performed in MEGA-X (Kumar et al. 2018) using the MUSCLE algorithm. The protein-coding sequenc-

es were checked for saturation and the two loci were concatenated using DAMBE 7.2.152. Nucleotide-substitution models for all codon positions of the NADH2 and a single partition of the ITS were estimated with Partition Finder 2.1.1 (Lanfear et al. 2016) under the corrected Akaike information criterion and implemented in subsequent phylogenetic analyses.

Bayesian inference (BI) phylogenetic analysis was performed on the concatenated dataset (NADH2 + ITS) using Mr. Bayes v. 3.2.7 (Ronquist and Huelsenbeck 2003), with four simulations of Markov chains and 4×10^6 generations sampling each 100th tree. Stationary distribution of the MCMC parameters was checked with Tracer ver. 1.7.1 (Rambaut et al. 2018) multivariate visualization, demographic trajectory reconstruction, conditional posterior distribution summary, and more. Tracer is open-source and available at <http://beast.community/tracer>. The first 25% of trees were excluded as burn-in. Results were visualized in FigTree 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Geographical coordinates

Coordinates are presented in decimal degrees (DD) and may therefore differ from collecting labels that use degrees, minutes and seconds or degrees and minutes (DMS). For locations for which no coordinates were available Google Earth has been used in which case coordinates have been placed between square brackets “[]”.

Dissection of titillators

Titillators, once removed, were cleared in a KOH solution and fixed with glue on a small board, pinned under the specimen or in case of *E. latens* from Rhodopos, transferred to glycerol (Aspöck 1971).

Bioacoustics

For song recordings several digital recorder systems (digital tape, solid state memory and computer hard disk) and microphones were used. Usually a frequency response better than 50–20,000 Hz were achieved. Most recordings were made indoors in a lab or room, in the evening or night, using (partly) open containers, frequently housed in an anechoic cupboard, with the microphone at 3–15 cm distance. The air temperature during recording in room or studio was between 15 °C and 27 °C. We did not attempt to correct for the possible body temperature of the animals, which may well have been below or above the measured room temperature. Specific data for the individual recordings can be found in Suppl. material 3.

Song analysis of the digital recordings has been performed using Wavelab software (www.steinberg.net). Oscillograms have been prepared using Praat software (www.praat.org).

Bioacoustic terminology: calling song – the song produced by an isolated male; syllable – the sound produced by one opening-and-closing movement of the tegmina;

hemisyllable – the sound produced by the opening or closing movement of the tegmina; syllable period – period from one syllable beginning to the next. Syllable repetition rate – the number of syllables produced per second.

Photography

For stacked images, a Zeiss SteREO Discovery V20 stereomicroscope was used, combined with a Zeiss AxioCam MRc5 microscope camera. The habitus photographs were taken with a NIKON D5600 with a sigma 105 mm macrolens and a Canon EOS 5D digital camera using a Canon zoom lens EF 28–90 mm F 4–5.6 with three combined Hama Close-Up lenses 1, 2 + 4×.

Measurements

Figs 4–7 illustrate how measurements of body parts were taken, and the results are presented in Tables 6, 7. As bodies tend to be more or less swollen when kept in alcohol or shrunken after having been kept in spirit, measurements of body size tend to show a larger variation than, for instance, those of the pronotum or hind femur.

Specimens

A list summarising all known localities, specimens, and repositories is presented in Suppl. material 1. Specimens examined to describe new species or the female sex are also mentioned in the taxonomic treatment. Suppl. material 2 lists all specimens studied for this paper including details about their use for field or stacked images, DNA, sound recording, and measurements.



Figures 4–7. Measurements **4** body length **5** pronotum length **6** hind femur length and width **7** ovipositor length.

Repositories and acronyms

- BMNH** British Museum of Natural History, London, UK;
CH collection Klaus-Gerhard Heller, Triesdorf, Germany;
CMUP collection Bruno Massa, University of Palermo, Palermo, Italy;
CT collection Jos Tilmans, Wassenberg-Rothenbach, Germany;
IBER Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria;
MfNB Museum für Naturkunde, Berlin, Germany;
MHNG Natural History Museum Geneva, Switzerland;
NHMC Natural History Museum Crete, University of Crete, Iraklion, Greece;
obs. observation (specimen not collected);
RMNH Naturalis Biodiversity Center, Leiden, The Netherlands.

Results

Table 2 and Fig. 1 summarise new locations for *Eupholidoptera* from Crete and its adjoining islands discovered between 1987 and 2020 as presented in this paper. Apart from two species new to science and the first records of *E. smyrnensis* from Crete, the total number of records increased fivefold, largely due to the bycatches from the trapping program.

Table 2. Published and unpublished records (period 1987–2020) of *Eupholidoptera* from Crete and adjoining islands.

	Altitudinal range (m)	Published locations (Table 1)	Tilmans 1987–2019	Trapping program 1987–2019	Oddé 2014	Observations 2012–2020	Heller 2016	Willemse and Zacharopoulou 2017	Chobanov et al. 2018	Tilmans and Willemse 2019	Total
<i>E. annamariae</i>	5–550	2	5	3	0	0	0	2	2	0	14
<i>E. astyla</i>	5–1850	10	6	24	0	0	1	3	1	0	45
<i>E. cretica</i>	1165–1234	1	0	4	0	0	0	0	0	0	5
<i>E. feri</i>	1100	1	0	0	0	0	0	0	0	0	1
<i>E. forcipata</i>	1350–2225	3	2	3	0	0	0	0	0	0	8
<i>E. francisae</i> sp. nov.	1–835	0	2	1	0	0	0	2	2	9	16
<i>E. gemellata</i>	1650–1910	1	0	1	0	0	0	0	0	0	2
<i>E. giuliae</i>	0–525	3	4	9	0	7	1	3	1	4	32
<i>E. jacqueliniae</i>	30–270	1	0	8	0	1	0	0	0	0	10
<i>E. latens</i>	20–1815	7	3	4	1	0	1	1	2	2	21
<i>E. mariannae</i>	0–1475	4	2	9	0	0	0	2	0	0	17
<i>E. mariethesae</i> sp. nov.	1715	0	0	1	0	0	0	0	0	0	1
<i>E. pallipes</i>	1600–2440	1	0	1	0	1	0	0	0	0	3
<i>E. smyrnensis</i>	25–340	0	0	1	0	0	0	1	0	1	3
Total		34	23	69	1	9	3	14	8	16	178



Figures 8–10. Colour pattern abdomen from above **8** *Eupholidoptera smyrnensis* ♀ Makrigiannis RMNH.INS152908 **9** *Eupholidoptera gemellata* ♀ Mt. Idi FC1651 RMNH.INS1141844 **10** *Eupholidoptera astyla* ♂ Krotos RMNH5086990.

Key to *Eupholidoptera* species from Crete, Gavdos, Gavdopoula, and Andikithira

- 1 Frons with tiger-pattern (Fig. 11); hind margin of abdominal tergites at the centre with tiny black dot (Fig. 8); male cercus with basal tooth (Fig. 111); hind margin of female subgenital plate forming two narrowly pointed lobes (Fig. 39) (west and central Crete)..... *smyrnensis*
- Frons with isolated dark spots or black crossband (Figs 12–24); abdominal tergite unicolourous, hind margin without a central black dot (Fig. 10) or with black edge (Fig. 9); male cercus unarmed or with subbasal tooth (Figs 112–125); hind margin of female subgenital plate different (Figs 40–52) **2**
- 2 Females..... **3**
- Males..... **15**
- 3 Subgenital plate with pair of elongate concavities divided by median ridge, apical lobes touching (Fig. 46) (Lasithi) *annamariae*
- Subgenital plate convex or proximally concave or with pits, apical lobes separated (Figs 40–45, 47–52)..... **4**
- 4 Gavdos or Gavdopoula *jacquelinae*
- Crete or Andikithira **5**
- 5 Subgenital plate wider to much wider than long (Figs 40, 42, 45, 50, 51).... **6**
- Subgenital plate as wide as long or elongated (Figs 41, 43, 44, 47–49, 52) **10**
- 6 Hind margin of subgenital plate with wide and deep median excision (Fig. 42) (Mt. Lefka) *cretica*
- Hind margin of subgenital plate differently formed (Figs 40, 45, 50, 51)..... **7**
- 7 Hind margin of subgenital plate medially concave, without excision (Fig. 40) (Mt. Idi) *gemellata*
- Hind margin of subgenital plate with distinct excision (Figs 45, 50, 51) **8**

- 8 Subgenital plate with apical lobes rounded (Fig. 45), in profile its apex (measured in a straight line parallel to the ovipositor) not reaching or surpassing proximal half of gonangulum (Fig. 67) (Andikithira and Chania) (in some females from Chania the subgenital plate is as wide as long or even elongated; see Taxonomic treatment and Discussion).....***francisae* sp. nov.**
- Subgenital plate with apical lobes pointed (Figs 50, 51), in profile its apex (measured in a straight line parallel to the ovipositor) reaching or surpassing distal half of gonangulum (Fig. 68) (Mt. Idi or Mt. Dikti).....**9**
- 9 Subgenital plate 2.0× wider than long, proximal pits small, widely separated (Fig. 50) (Mt. Idi).....***forcipata***
- Subgenital plate 1.4× wider than long, proximal pits large, closer to each other (Fig. 51) (Mt. Dikti)..... ***marietheresae* sp. nov.**
- 10 Front of head with large black patches (Fig. 13) (Mt. Lefka).....***pallipes***
- Front of head with black dots (Figs 15–17, 19–21)..... **11**
- 11 Apex subgenital plate in profile (measured in a straight line parallel to the ovipositor) not reaching or surpassing proximal half of gonangulum (Fig. 67) (Chania)***francisae* sp. nov.**
- Apex subgenital plate in profile (measured in a straight line parallel to the ovipositor) reaching or surpassing distal half of gonangulum (Fig. 68) **12**
- 12 Subgenital plate proximally convex, flattened or slightly concave (Fig. 47)....
.....***astyla***
- Subgenital plate proximally with one wide or two separate pits (Figs 43, 44, 48, 49)..... **13**
- 13 Apical lobes of subgenital plate not well produced, rectangular (Fig. 43); black patch front half pronotal disc absent, small or large, if present hind edge acutely V to U-shaped (Fig. 29)***latens***
- Apical lobes of subgenital plate more produced, rectangular to acute (Figs 44, 48, 49); front half pronotal disc with black patch, its hind edge widely V-shaped to transverse (Figs 30, 34, 35) **14**
- 14 Subgenital plate proximally with two distinct pits separated by a median keel (Fig. 44); central black patch front half pronotal disc well delimited by pale edges, hind margin widely V-shaped (Fig. 30) (Chania and Rethimno)..... ***giuliae***
- Subgenital plate proximally with a single or two pits (Figs 48, 49); front half pronotal disc mostly black, hind margin transverse (Figs 34, 35) (west and central Lasithi including Mt. Dikti)..... ***mariannae***
- (Mt. Dikti, Katharo plains)..... ***feri***
- 15 Styli pointing backwards (Figs 169–171, 179–181) **16**
- Styli pointing downward or inward (Figs 172–178)..... **21**
- 16 Cercus with subbasal side tooth (Figs 112, 113); subgenital plate with a short curved spine at base of each stylus (Figs 169, 170)..... **17**
- Cercus unarmed (Figs 114, 123–125); subgenital plate without spines (Figs 171, 179, 180) or with a very long straight spine at base of each stylus (Fig. 181)..... **18**

- 17 Pronotum pale (Fig. 27); apical arms titillator completely fused, tip rounded at either side with a tiny thorn (Fig. 184) (Mt. Lefka).....***pallipes***
- Pronotum with black band or patches (Fig. 26); apical arms fused, in apical quart split, tip truncated, unarmed (Fig. 183) (Mt. Idi).....***gemellata***
- 18 Styli very long, 5–6× longer than wide (Figs 171, 181).....**19**
- Styli short, 2× longer than wide (Figs 179, 180).....**20**
- 19 Subgenital plate with long spine at base of stylus (Fig. 181); apical arms titillators separate in apical half (Fig. 197); anal tergite with hind margin with two large triangular extensions with V-shaped medial excision (Fig. 96) (Gavdos and Gavdopoula).....***jacquelinae***
- Subgenital plate without a spine at base of stylus (Fig. 171); apical arms titillators separate in apical quarter (Fig. 185); anal tergite with hind margin forming two small, widely separated, triangular lobes (Fig. 86) (Mt. Lefka).....***cretica***
- 20 Hind margin of anal tergite from the cercus downward straight, side flaps gradually narrowing (Fig. 94); cerci narrower, 4–5× longer than wide, straight or very weakly curved inward (Fig. 123); apical arms titillator ending in two evenly curved, slender hooks (Fig. 195) (Mt. Idi).....***forcipata***
- Hind margin of anal tergite from the cercus downward S-curved, side flaps first widening before narrowing (Fig. 95); cerci wider, 3–4× longer than wide, curved inward (Fig. 124); apical arms titillator ending in two very slender curved hooks, near the apex curved inward (Fig. 196) (Mt. Dikti).....***marietheresae* sp. nov.**
- 21 Anal tergite distally extended into two very long, spined hooks pointing downward (Fig. 90); apical arms titillator narrow, completely fused ending in needle shaped tip, pointing barely left or right (Figs 190, 206) (Lasithi)....***annamariae***
- Anal tergite distally extended into short pointed lobes (Figs 87–89, 91–93); apical arms titillator in basal half wide or widening (Figs 186–189, 202–205) or narrow but tips not completely fused (Figs 191–194, 207–209).....**22**
- 22 Pointed lobes of anal tergite close together (Figs 91–93).....**23**
- Pointed lobes of anal tergite widely separated (Figs 87–89).....**25**
- 23 Cercus unarmed (Fig. 120); apical arms titillator strongly asymmetrical (Figs 191, 207) (central Crete).....***astyla***
- Cercus with subbasal side tooth (Figs 121, 122); apical arms titillator asymmetrical or barely so (Figs 193, 194, 208, 209) (east Crete).....**24**
- 24 Cercus conical (Fig. 121); pointed lobes anal tergite pointing backward (Fig. 92); (Katharo plain, Mt. Dikti).....***feri***
- Cercus flattened and widened proximally (Fig. 122); pointed lobes of anal tergite pointing forward (Fig. 93) (west and central Lasithi including Mt. Dikti).....***mariannae***
- 25 Subgenital plate as wide as long (Fig. 145) with styli pointing inward (Fig. 173) (in Chania and Apokoronas subgenital plates are longer with styli pointing downwards; see species treatment and discussion).....***giuliae***
- Subgenital plate elongate, tapering toward the apex (Figs 144, 146) with styli pointing downward (Figs 172, 174).....**26**

- 26 Tips apical lobes subgenital plate with a tooth (Figs 146, 160, 174) (on Andikithira tooth always present, in west and southwest Chania tooth sometimes missing or only on one apical lobe present), subgenital plate much longer than wide (mean ratio length-width 1.66).....*francisae* sp. nov.
- Tips apical lobes subgenital plate always without a tooth (Figs 144, 158, 172), subgenital plate longer than wide (mean ratio length-width 1.44) (north and central Chania)*latens*

Taxonomic treatment (species in alphabetical order)

The taxonomic treatment contains short diagnostics, illustrated with stacked images, for all species until now reported from Crete and its adjoining islands. New taxa as well as previously unknown sexes are described in more detail.

Eupholidoptera annamariae Nadig, 1985

Figs 18, 32, 46, 60, 76, 90, 104, 118, 119, 133, 147, 161, 175, 190, 206, 240, 254, 256, 259, Tables 1, 2, 5–7, 10, Suppl. materials 1–4

Eupholidoptera annamariae Nadig 1985: 329.

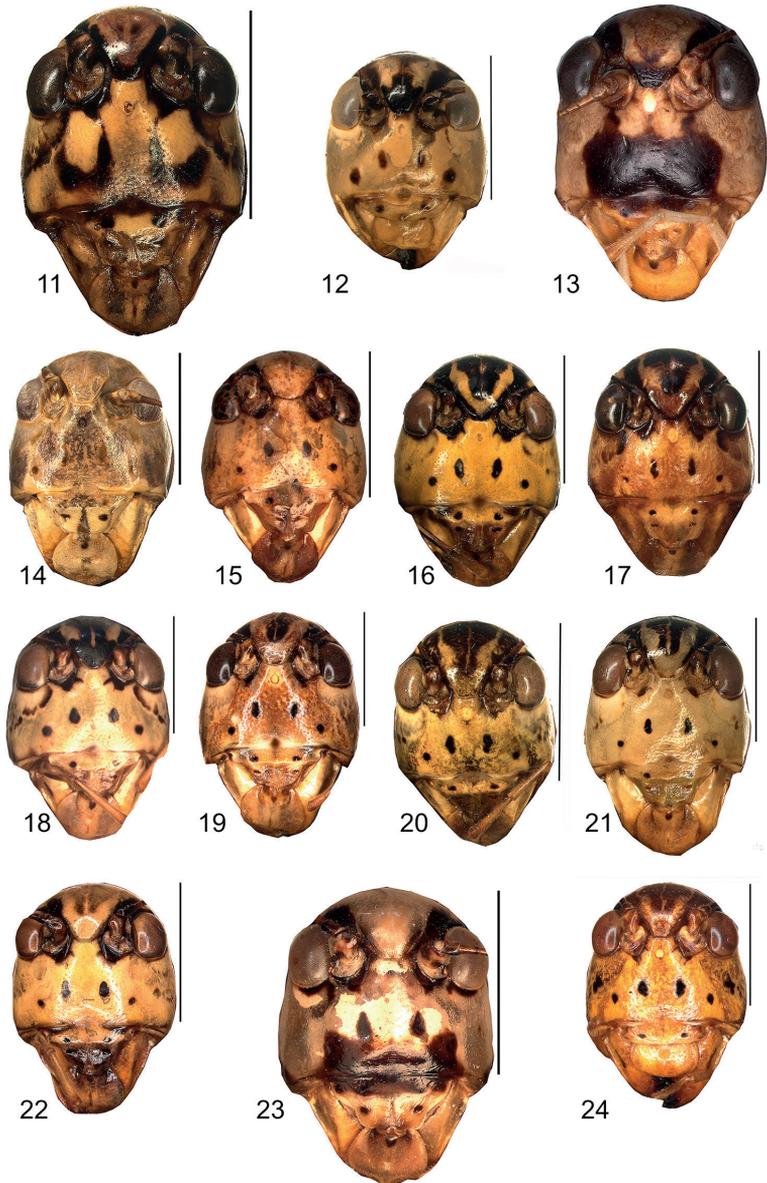
Morphological description. Nadig 1985: 329.

Bioacoustics. Çiplak et al. 2009: 27, 54.

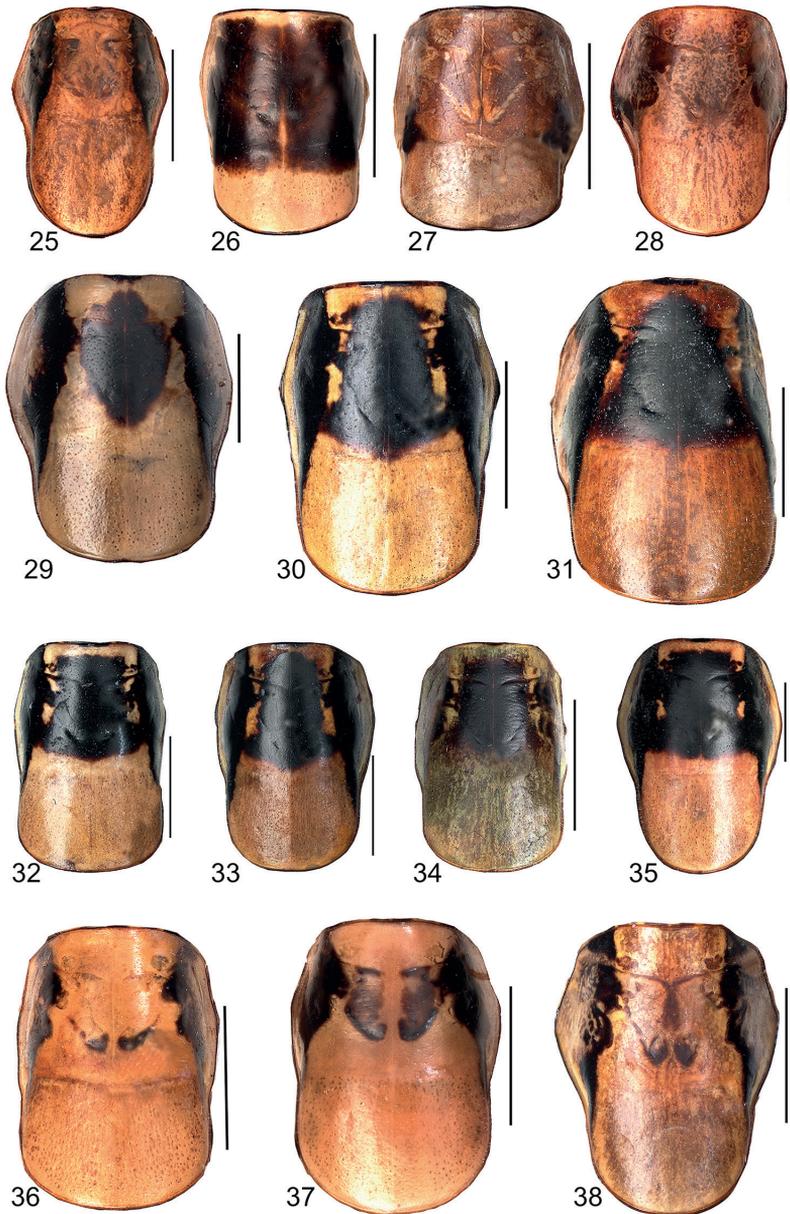
Examined specimens. 1 ♂, 1 ♀ (**paratypes**); 23 ♂, 24 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 18) pale with black dots; frontal half of pronotal disc (Fig. 32) predominantly black sharply transversely delineated from pale rear half. Male (Fig. 240) – stridulatory file with 109 teeth (89 in Nadig 1985) (including proximal and distal ones), density of teeth in middle two thirds of the file 19 teeth per mm; anal tergite (Figs 76, 90, 104) with hind margin medially strongly bent downward forming two very long, curved teeth covered with small denticles pointing downward and slightly outward; cerci (Figs 118, 133) unarmed, 5× longer than wide, basal half cylindrical, apical half conical, slightly curved inward halfway subtly widened, in profile straight; subgenital plate (Figs 147, 161) wider than long, widest halfway, sides widely rimmed, in profile strongly upturned, pointing upward, tip apical lobes rounded, spineless, excised along one third of length; styli (Fig. 175) short, ca. one third as long as cerci, 1.5–2.0× longer than wide, inserted ventrally just proximal of tip of apical lobe, pointing downward; titillator (Figs 190, 206) slightly asymmetrical, apical arms strong, narrow, fused along entire length, smooth, evenly curved, apically narrowed toward needle shaped tip, pointing somewhat left or right. Female – subgenital plate (Figs 46, 60) circular to transverse oval with central longitudinal hump, adjoined by deep grooves, apical lobes touching, hind margin medially excised along one quarter to one third of length, in profile deltoid, with deep ventral groove, tip obtuse angular.

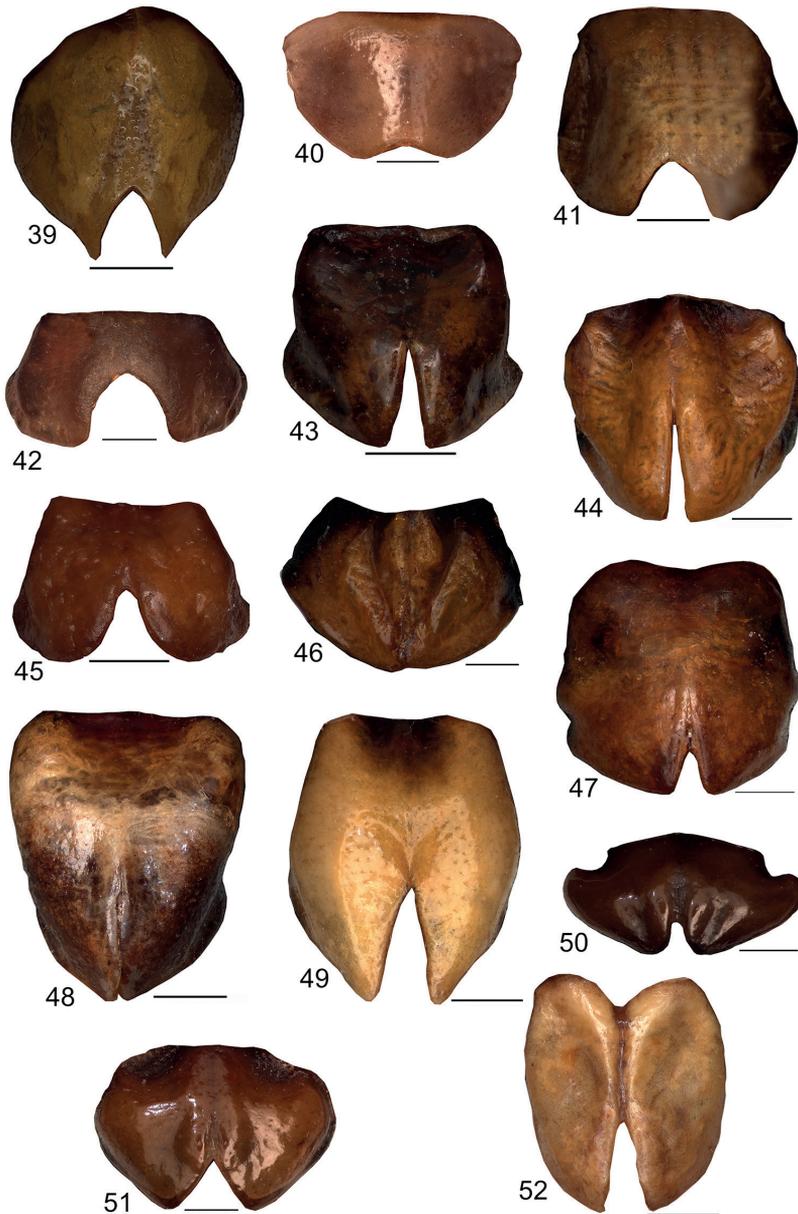
Measurements. See Tables 6, 7.



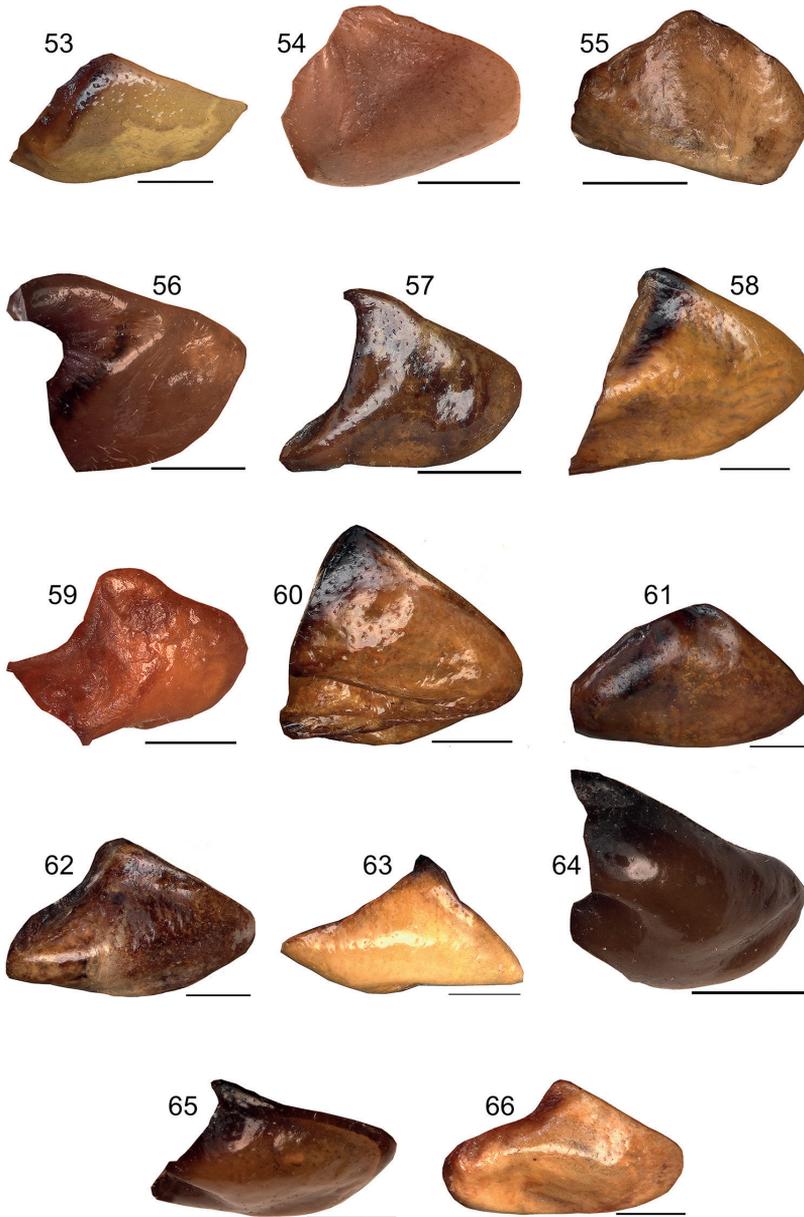
Figures 11–24. Colour pattern of head, frontal view **11** *Eupholidoptera smyrnensis* ♀ Makrigiannis RMNH5014918 **12** *Eupholidoptera gemellata* ♂ Mt. Idhi RMNH.INS1141843 **13** *Eupholidoptera pallipes* ♂ paratype Mt. Lefka RMNH.INS1105313 **14** *Eupholidoptera cretica* ♂ Mt. Lefka, Omalos RMNH.INS114838 **15** *Eupholidoptera latens* ♀ Mt. Lefka, Kalergi CT1987.047.04 **16** *Eupholidoptera giuliae* ♂ Argoules CT1995.011.18 **17** *Eupholidoptera francisae* sp. nov. ♀ allotype Andikithira CT 2002.004.11 **18** *Eupholidoptera annamariae* ♀ Kato Zakros CT1995.020.03 **19** *Eupholidoptera astyla* ♀ Ano Vianonos CT1987.024.03 **20** *Eupholidoptera feri* ♂ holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **21** *Eupholidoptera mariannae* ♀ Ag. Ioannis RMNH.5014906 **22** *Eupholidoptera forcipata* ♂ Mt. Idhi CT1987.044.03 **23** *Eupholidoptera marietheresae* sp. nov. ♂ paratype Mt. Dikti, FC1606 CT2000.096.01 **24** *Eupholidoptera jacquelineae* ♂ holotype Gavdos CT2000.005.02. Scale bars: 5 mm.



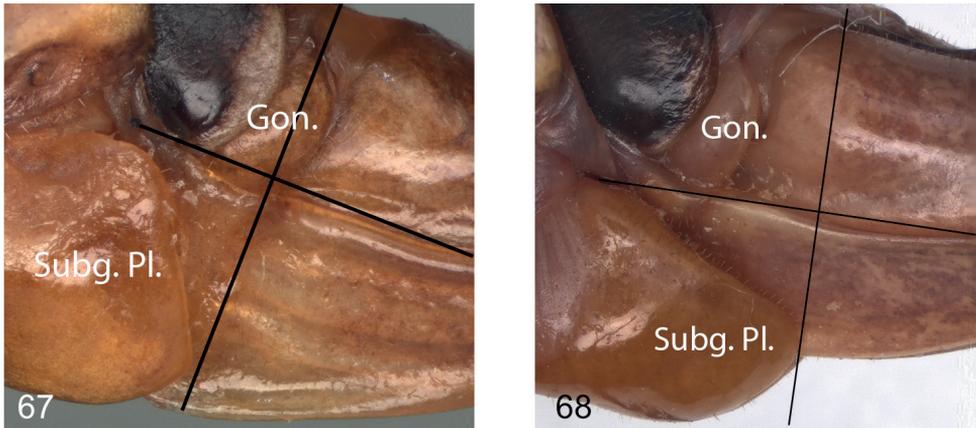
Figures 25–38. Colour pattern of pronotum, dorsal view **25** *Eupholidoptera smyrnensis* ♂ Makri-
giannis RMNH.INS152909 **26** *Eupholidoptera gemellata* ♂ Mt. Idhi, Amariou RMNH.INS1141843
27 *Eupholidoptera pallipes* ♂ paratype Mt. Lefka RMNH.INS1105313 **28** *Eupholidoptera cretica* ♂ Mt.
Lefka, Omalos RMNH.INS1141838 **29** *Eupholidoptera latens* ♂ Rhodopos CH8236 **30** *Eupholidoptera*
giuliae Chora Sfakion ♂ CT2000.014.10 **31** *Eupholidoptera francisae* sp. nov. ♂ holotype Andikithira
CT2002.004.04 **32** *Eupholidoptera annamariae* ♂ Kato Zakros CT2000.030.04 **33** *Eupholidoptera astyla*
♂ Krotos RMNH.INS1141819 **34** *Eupholidoptera feri* ♂ holotype Mt. Dikti, Katharo plain RMNH.
INS1105297 **35** *Eupholidoptera mariannae* ♀ Kalavros RMNH.5086974 **36** *Eupholidoptera forcipata*
♂ Mt. Idhi CT1987.044.03 **37** *Eupholidoptera marietheresae* sp. nov. ♂ holotype Mt. Dikti RMNH.
INS1141850 **38** *Eupholidoptera jacquelineae* ♂ holotype Gavdos CT2000.005.02. Scale bars: 5 mm.



Figures 39–52. Female subgenital plate in ventral view **39** *Eupholidoptera smyrnensis* Makrigiannis RMNH.5014918 **40** *Eupholidoptera gemellata* Mt. Idhi, FC1602 CT2000.095.02 **41** *Eupholidoptera pal-lipes* allotype Mt. Lefka RMNH.INS1105312 **42** *Eupholidoptera cretica* Mt. Lefka, Omalos RMNH.INS1141837 **43** *Eupholidoptera latens* Mt. Lefka, Kalergi CT1987.047.04 **44** *Eupholidoptera giuliae* Argoules CT1995.011.03 **45** *Eupholidoptera francisae* sp. nov. allotype Andikithira CT2002.004.11 **46** *Eupholidoptera annamariae* Kato Zakros CT1995.020.03 **47** *Eupholidoptera astyla* Krotos RMNH.INS1141820 **48** *Eupholidoptera feri* allotype Mt. Dikti, Katharo plain RMNH.INS1105298 **49** *Eupholidoptera mariannae* Kalavros RMNH5014912 **50** *Eupholidoptera forcipata* Mt. Idhi, FC1602 RMNH.INS1141845 **51** *Eupholidoptera marietheresae* sp. nov. allotype Mt. Dikti RMNH.INS1141849 **52** *Eupholidoptera jacquelineae* Gavdos allotype CT2001.004.13. Scale bars: 1 mm.



Figures 53–66. Female subgenital plate in lateral view **53** *Eupholidoptera smyrnensis* Makrigiannis RMNH.5014918 **54** *Eupholidoptera gemellata* Mt. Idhi, FC1602 CT2000.095.02 **55** *Eupholidoptera pal-lipes* allotype Mt. Lefka RMNH.INS1105312 **56** *Eupholidoptera cretica* Mt. Lefka, Omalos RMNH.INS1141837 **57** *Eupholidoptera latens* Mt. Lefka, Kalergi CT1987.047.04 **58** *Eupholidoptera giuliae* Argoules CT1995.011.03 **59** *Eupholidoptera francisae* sp. nov. allotype Andikithira CT2002.004.11 **60** *Eupholidoptera annamariae* Kato Zakros CT1995.020.03 **61** *Eupholidoptera astyla* Krotos RMNH.INS1141820 **62** *Eupholidoptera feri* allotype Mt. Dikti, Katharo plain RMNH.INS1105298 **63** *Eupholidoptera mariannae* Kalavros RMNH5014912 **64** *Eupholidoptera forcipata* Mt. Idhi, FC1602 RMNH.INS1141845 **65** *Eupholidoptera marietheresae* sp. nov. allotype Mt. Dikti RMNH.INS1141849 **66** *Eupholidoptera jacquelineae* allotype Gavdos CT2001.004.13. Scale bars: 1 mm.

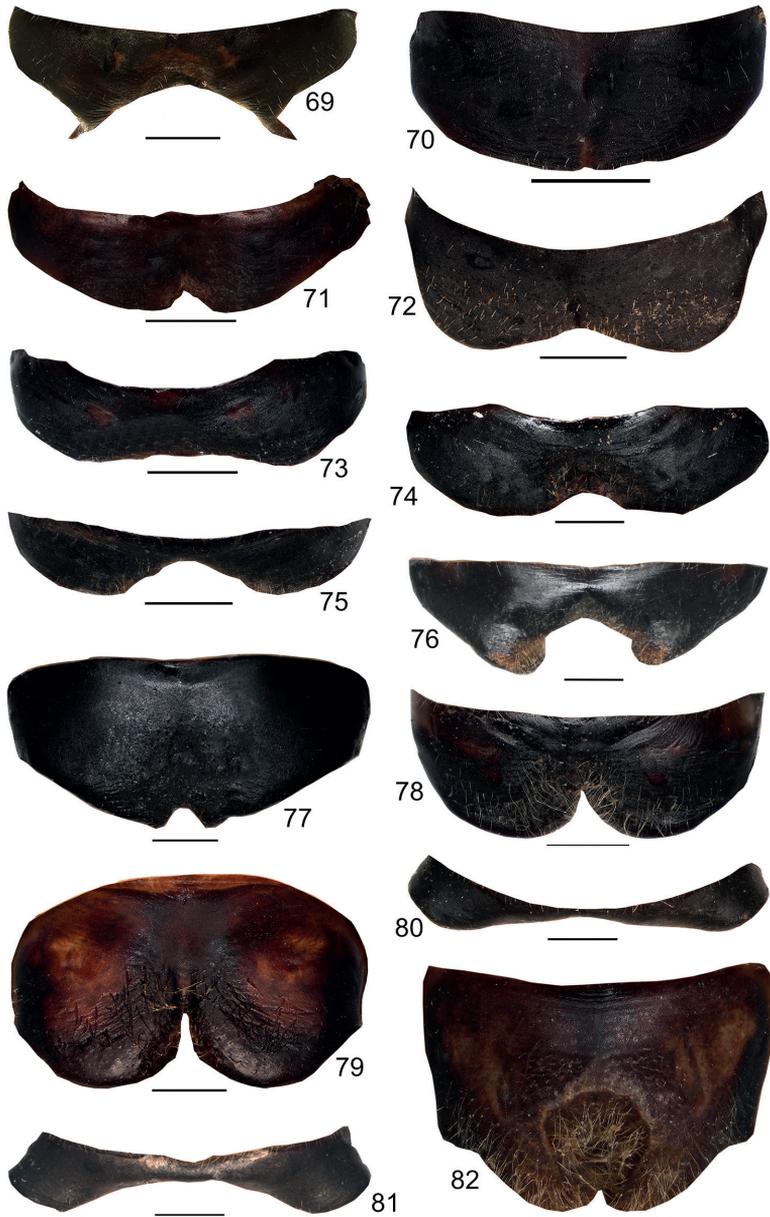


Figures 67, 68. Female subgenital plate in lateral view **67** *Eupholidoptera francisae* sp. nov. Anidhroi CT2001.002.07 **68** *Eupholidoptera latens* Prases DC-Ott000512.

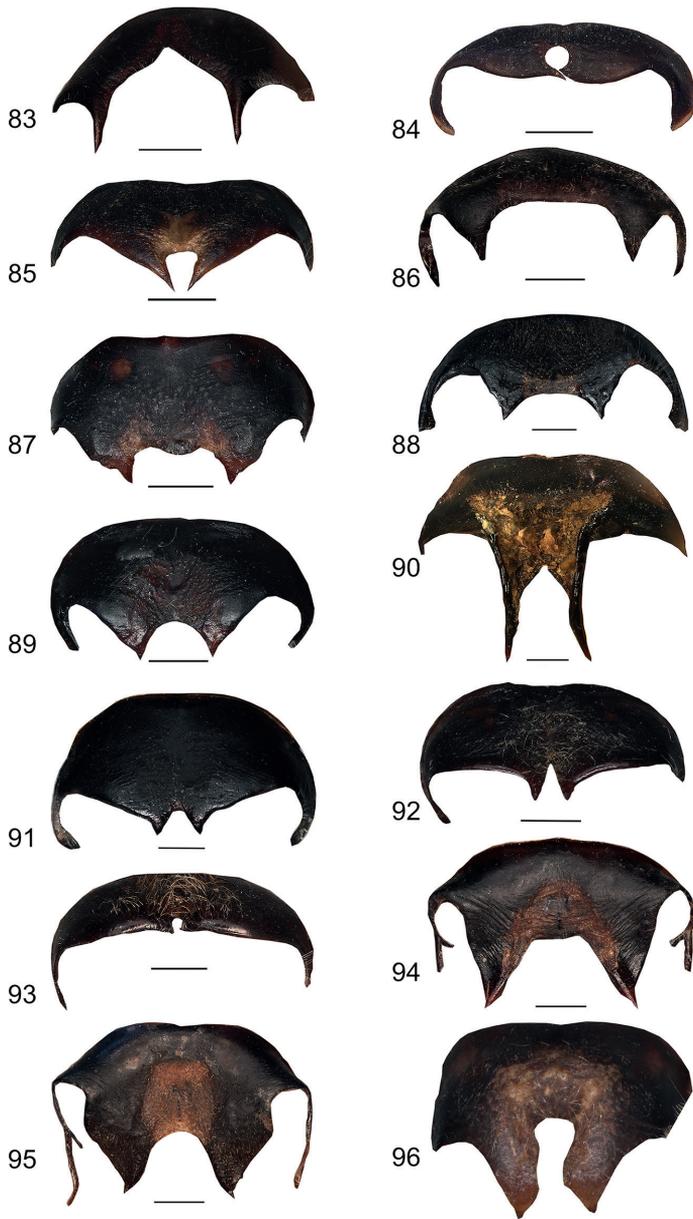
Bioacoustics. Based upon the sound recordings of 6 specimens (53 syllables measured), the song of *E. annamariae*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. annamariae*, the syllable duration is ~ 160 ms. In the present recordings, the syllable repetition rate is very low. Published records (Çiplak et al. 2009) show a syllable duration of ~ 128 ms at 25 °C and a syllable repetition rate of 1/s at maximum. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera annamariae* see Suppl. material 3.

Variation. The colour pattern and genitalia in *E. annamariae* in the specimens studied show little variation with one exception. In one of four males collected along the northern coast of Lasithi, west of Sitia, near Xerokampos the cerci showed a clearly developed inner tooth, halfway the cercus (Fig. 119). Other morphological traits in this aberrant male as well as in the other three males from Xerokampos fitted *E. annamariae*. The cercus with a side tooth is considered an anomaly. It is noteworthy that the location where the aberrant male of *E. annamariae* was found is the north-western most location of *E. annamariae* only some 5 km away from Kalavros where *E. mariannae* was found.

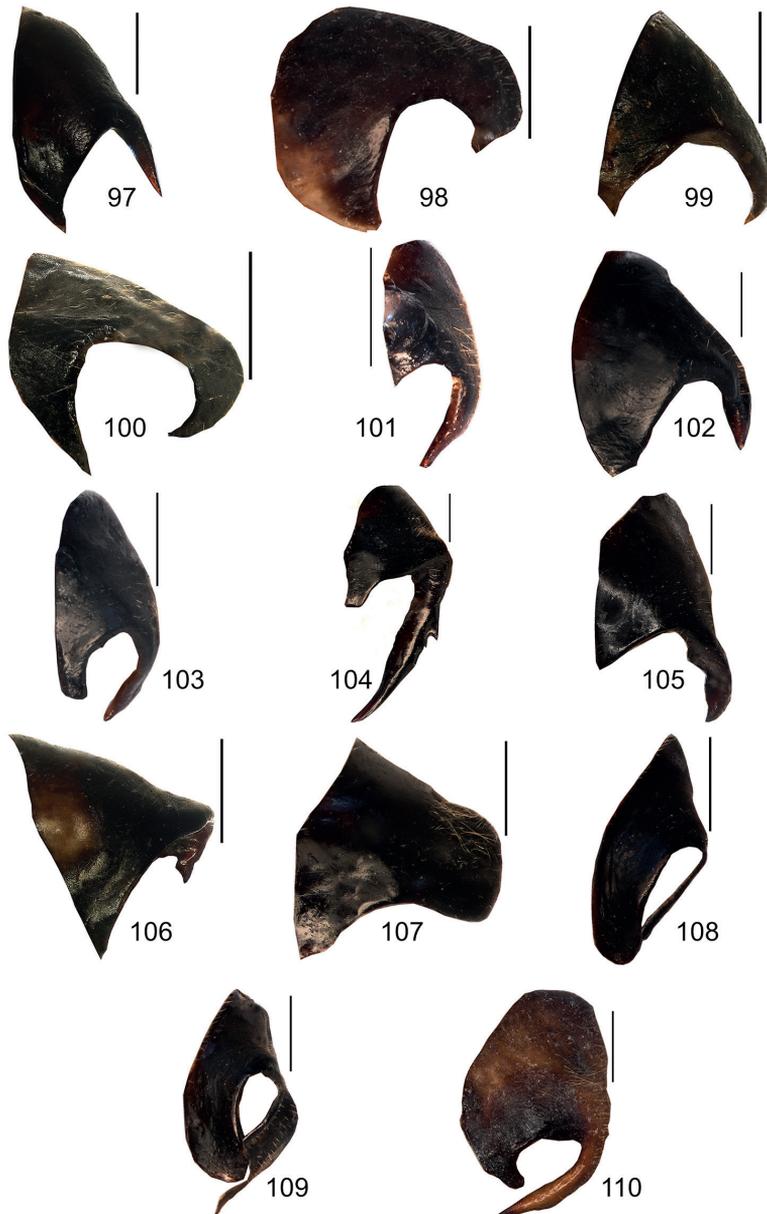
Differential diagnosis. Males differ from congenetics in the anal tergite (Figs 76, 90, 104) with the uniquely shaped long, curved spined teeth pointing downward and inward, in the stout, unarmed almost straight cercus (Figs 118, 133), in the wide, upturned subgenital plate (Figs 147, 161) lacking spines, pre-apically inserted with short, downward pointing styli (Fig. 175) and in the narrow, completely fused slightly asymmetrical apical arms of the titillator (Figs 190, 206). Females distinctly differ in the subgenital plate (Figs 46, 60) with a central hump bordered by deep and wide semi-circular grooves. From all Cretan *Eupholidoptera* species, the black part in the anterior half of the pronotum is most pronounced in *E. annamariae*. For more details differentiating *E. annamariae* from other Cretan *Eupholidoptera* see Table 5.



Figures 69–82. Male anal tergite in dorsal view **69** *Eupholidoptera smyrnensis* Makrigrigiannis RMNH. INS152909 **70** *Eupholidoptera gemellata* holotype Mt. Idhi RMNH.INS1105300 **71** *Eupholidoptera pal-lipes* paratype Mt. Lefka RMNH.INS1105313 **72** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **73** *Eupholidoptera latens* Mt. Lefka, Kalergi CT2003.009.01 **74** *Eupholidop-tera giuliae* Chora Sfakion CT2000.024.04 **75** *Eupholidoptera francisae* sp. nov. holotype Andikithira CT2002.004.04 **76** *Eupholidoptera annamariae* Kato Zakros CT2000.030.04 **77** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **78** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS 1105297 **79** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **80** *Eupholidoptera for-cipata* Mt. Idhi CT1987.044.01 **81** *Eupholidoptera marietheresae* sp. nov. paratype Mt. Dikti FC1606 CT2000.096.01 **82** *Eupholidoptera jacquelineae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



Figures 83–96. Male anal tergites in caudal view **83** *Eupholidoptera smyrnensis* Makrigrigiannis RMNH.INS152909 **84** *Eupholidoptera gemellata* Mt. Idhi CT2000.095.01 **85** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105314 **86** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **87** *Eupholidoptera latens* Mt. Lefka, Kalergi CT2003.009.01 **88** *Eupholidoptera giuliae* Chora Sfakion CT2000.014.01 **89** *Eupholidoptera francisae* sp. nov. paratype Andikithira CT2002.004.02 **90** *Eupholidoptera annamariae* Kato Zakros CT2000.030.01 **91** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **92** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **93** *Eupholidoptera mariannae* Prina FC17798 RMNH.INS1141840 **94** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.01 **95** *Eupholidoptera marietheresae* sp. nov. paratype Mt. Dikti FC1606 CT2000.096.01 **96** *Eupholidoptera jacquelineae* paratype Gavdos NHMC2001.004.12. Scale bars: 1 mm.



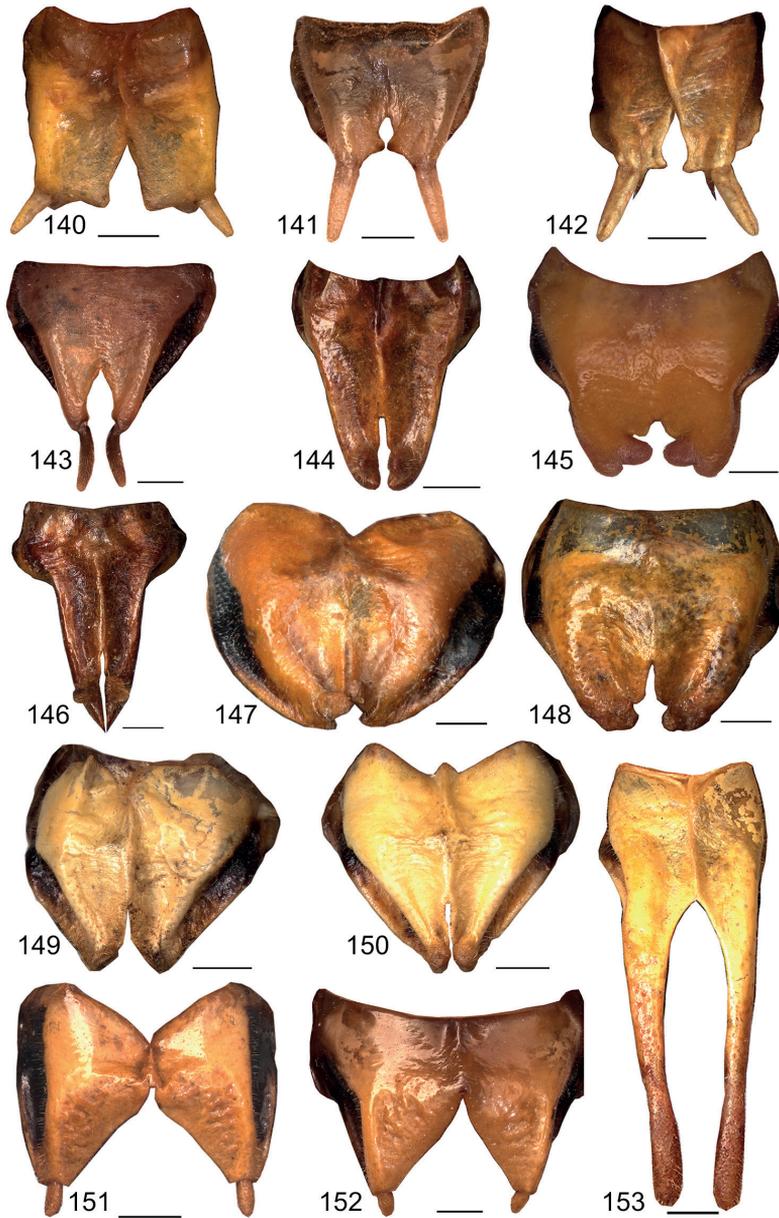
Figures 97–110. Male anal tergites in lateral view **97** *Eupholidoptera smyrnensis* Makrigiannis RMNH5087053 **98** *Eupholidoptera gemellata* Mt. Idhi CT2000.095.01 **99** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105314 **100** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **101** *Eupholidoptera latens* Mt. Lefka, Kalergi CT1987.047.01 **102** *Eupholidoptera giuliae* Argoules CT1995.011.11 **103** *Eupholidoptera francisae* sp. nov. paratype Andikithira CT2002.004.02 **104** *Eupholidoptera annamariae* Kato Zakros CT2000.030.03 **105** *Eupholidoptera astyla* Ano Vianonos CT1995.024.01 **106** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **107** *Eupholidoptera mariannae* Kalavros CT2017.029.01 **108** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.01 **109** *Eupholidoptera marietheresae* sp. nov. paratype Mt. Dikti FC1606 CT2000.096.01 **110** *Eupholidoptera jacquelineae* Gavdopoula CT1996.019.01. Scale bars: 1 mm.



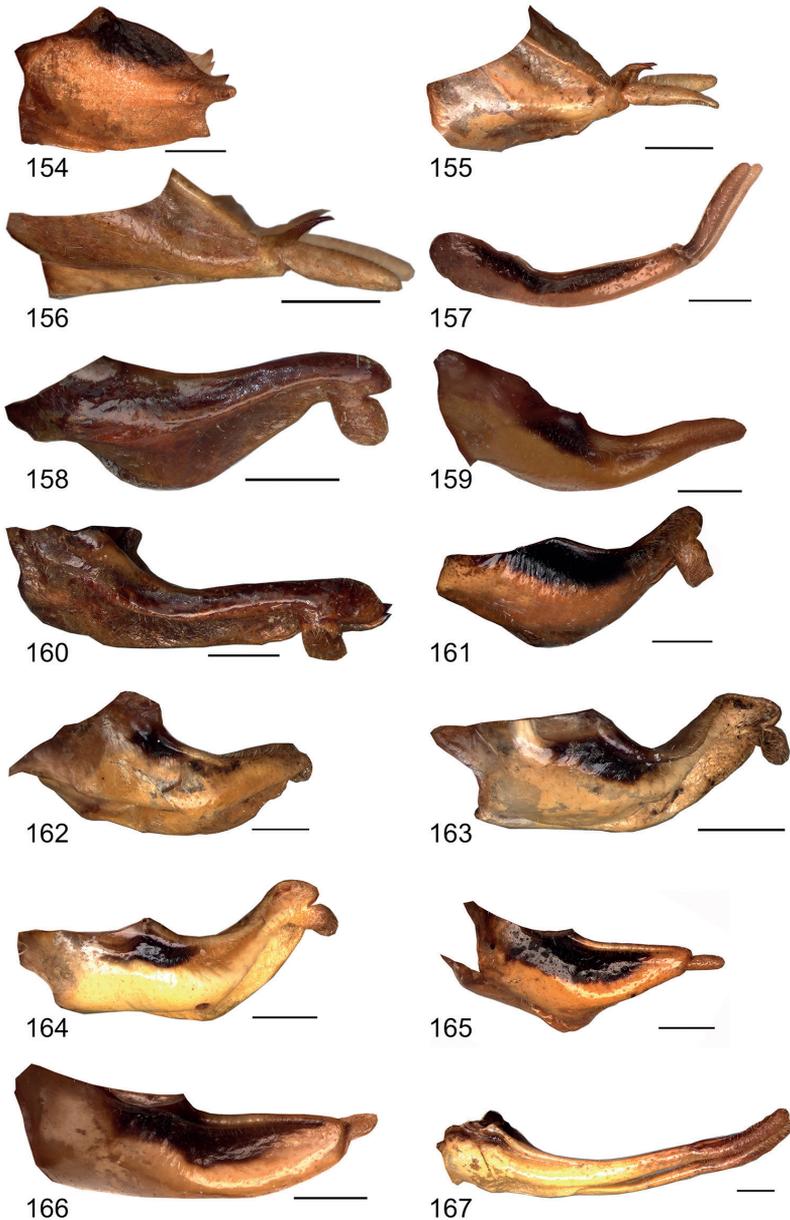
Figures 111–125. Male cercus in dorsal view **111** *Eupholidoptera smyrnensis* Makrigiannis RMNH5087053 **112** *Eupholidoptera gemellata* Mt. Idhi FC1651 RMNH.INS1141843 **113** *Eupholidoptera pallipes* Mt. Lefka paratype RMNH.INS1105314 **114** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **115** *Eupholidoptera latens* Xiloskalo IBER DC-Orr000558 **116** *Eupholidoptera giuliae* Chora Sfakion CT2000.014.02 **117** *Eupholidoptera francisae* sp. nov. holotype Andikithira CT2002.004.04 **118** *Eupholidoptera annamariae* Kato Zakros CT2000.030.03 **119** *Eupholidoptera annamariae* Xerokampos, male with anomalous cercus, IBER DC-Orr000565 **120** *Eupholidoptera astyla* Ierapetra MfN s.n. **121** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **122** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **123** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.01 **124** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH.INS1141850 **125** *Eupholidoptera jacquelineae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



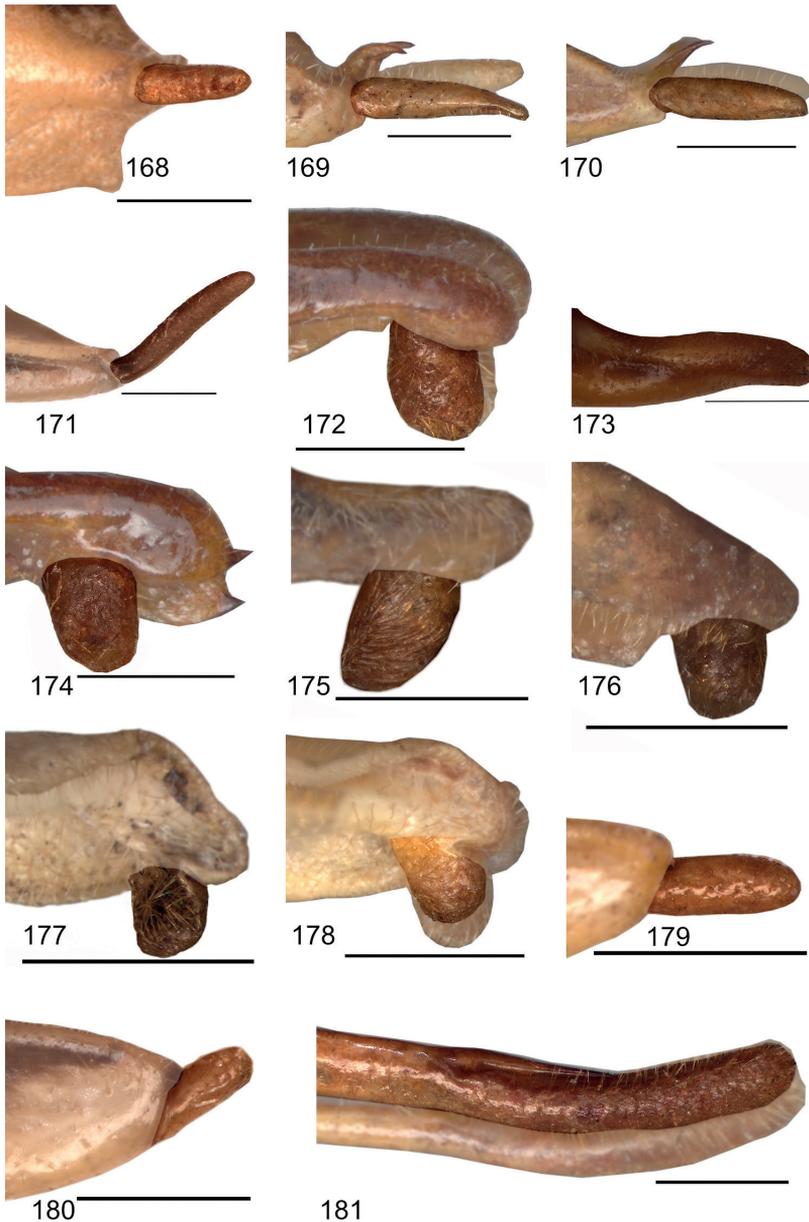
Figures 126–139. Male cercus in lateral view **126** *Eupholidoptera smyrnensis* Makrigiannis RMNH.5087053 **127** *Eupholidoptera gemellata* Mt. Idhi FC1651 RMNH.INS1141843 **128** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105314 **129** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **130** *Eupholidoptera latens* Mt. Lefka Kalergi CT2003.009.01 **131** *Eupholidoptera giuliae* Chora Sfakion CT2000.024.04 **132** *Eupholidoptera francisae* paratype sp. nov. Andikithira CT2002.004.08 **133** *Eupholidoptera annamariae* Kato Zakros CT1995.020.02 **134** *Eupholidoptera astyla* paratype Ierapetra MfN s.n. **135** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **136** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **137** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.01 **138** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH.INS1141850 **139** *Eupholidoptera jacquelinae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



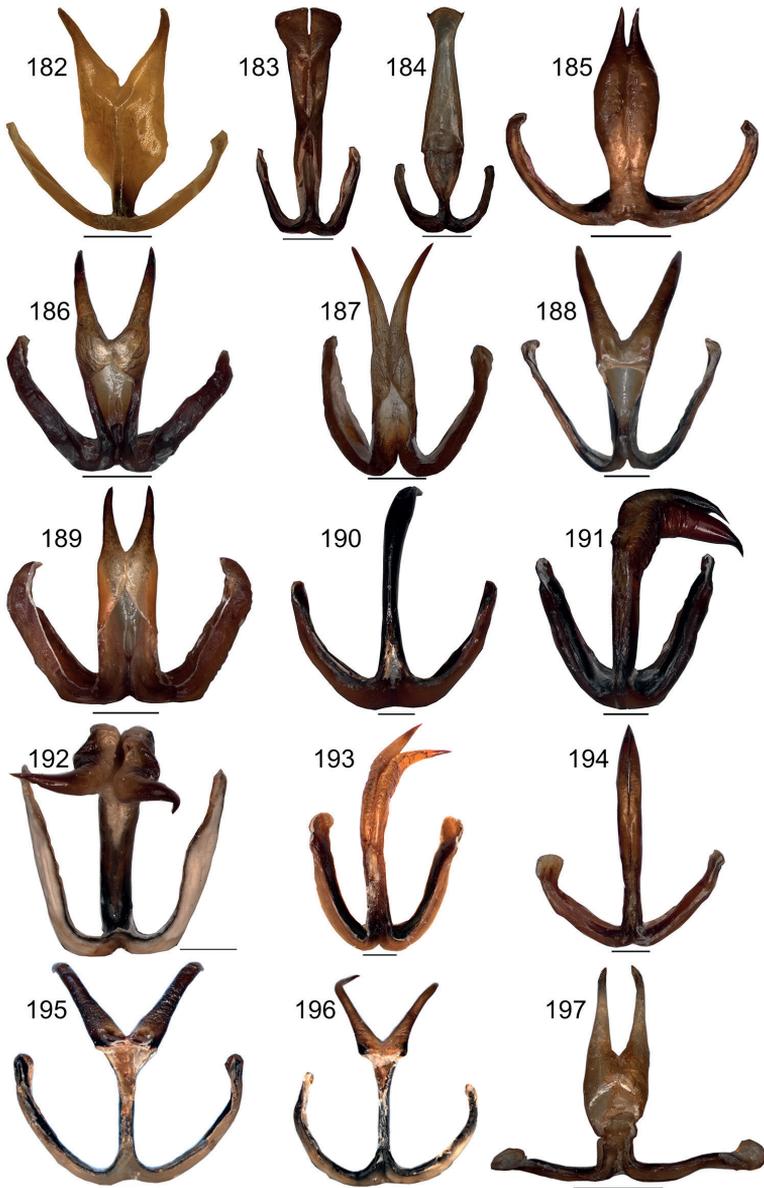
Figures 140–153. Male subgenital plate in ventral view **140** *Eupholidoptera smyrnensis* Lagkada RMNH 5106270 **141** *Eupholidoptera gemellata* Mt. Idhi FC1651 RMNH.INS1141843 **142** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105313 **143** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **144** *Eupholidoptera latens* Mt. Lefka Kalergi CT1987.047.02 **145** *Eupholidoptera giuliae* Skaloti IBER DC-Ort000564 **146** *Eupholidoptera francisae* sp. nov. holotype Andikithira CT2002.004.04 **147** *Eupholidoptera annamariae* Kato Zakros CT2000.030.04 **148** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **149** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **150** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **151** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.03 **152** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH.INS1141850 **153** *Eupholidoptera jacquelineae* holotype Gavdos 2000.005.02. Scale bars: 1 mm.



Figures 154–167. Male subgenital plate in lateral view **154** *Eupholidoptera smyrnensis* Lagkada RMNH. INS152909 **155** *Eupholidoptera gemellata* holotype Mt. Idhi RMNH.INS1105300 **156** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105313 **157** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 (RMNH.INS1141838 **158** *Eupholidoptera latens* Mt. Lefka Kalergi CT2003.009.01 **159** *Eupholidoptera giuliae* Skaloti IBER DC-Ort000564 **160** *Eupholidoptera francisae* sp. nov. holotype Andikithira CT2002.004.04 **161** *Eupholidoptera annamariae* Kato Zakros CT2000.030.04 **162** *Eupholidoptera astyla* Krotos RMNH5086992 **163** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **164** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **165** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.03 **166** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH. INS1141850 **167** *Eupholidoptera jacquelineae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



Figures 168–181. Male stylus in lateral view **168** *Eupholidoptera smyrnensis* Makrigrigiannis RMNH. INS152909 **169** *Eupholidoptera gemellata* holotype Mt. Idhi RMNH.INS1105300 **170** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105313 **171** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **172** *Eupholidoptera latens* Mt. Lefka Kalergi CT2003.009.01 **173** *Eupholidoptera giuliae* Skaloti IBER DC-Ort000564 **174** *Eupholidoptera francisae* sp. nov. paratype Andikithira CT2002.004.08 **175** *Eupholidoptera annamariae* Kato Zakros CT2000.030.04 **176** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **177** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **178** *Eupholidoptera mariannae* holotype Anatoli RMNH.INS1105311 **179** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.03 **180** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH.INS1141850 **181** *Eupholidoptera jacquelineae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



Figures 182–197. Male titillator in ventral view **182** *Eupholidoptera smyrnensis* Makrigrigiannis RMNH5087053 **183** *Eupholidoptera gemellata* Mt. Idhi Amariou FC1651 RMNH.INS1141843 **184** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105314 **185** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **186** *Eupholidoptera latens* Mt. Lefka Kalergi CT2003.009.01 **187** *Eupholidoptera latens* Rhodopos CH 8236 **188** *Eupholidoptera giuliae* Argoules CT1995.011.11 **189** *Eupholidoptera francisae* sp. nov. paratype Andikithira CT2002.004.08 **190** *Eupholidoptera annamariae* Kato Zakros CT2000.030.01 **191** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **192** *Eupholidoptera astyla* Kofinas FC460 RMNH.INS1141836 **193** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **194** *Eupholidoptera mariannae* paratype Malles CH2906A **195** *Eupholidoptera forcipata* Mt. Idhi CT2019.047.01 **196** *Eupholidoptera marietheresae* sp. nov. paratype Mt. Dikti FC1606 CT2000.096.01 **197** *Eupholidoptera jacquelineae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.



Figures 198–212. Male titillator in lateral view **198** *Eupholidoptera smyrnensis* Makrigiannis RMNH5087053 **199** *Eupholidoptera gemellata* Mt. Idhi Amariou FC1651 RMNH.INS1141843 **200** *Eupholidoptera pallipes* paratype Mt. Lefka RMNH.INS1105314 **201** *Eupholidoptera cretica* Mt. Lefka, Omalos FC17807 RMNH.INS1141838 **202** *Eupholidoptera latens* Mt. Lefka Kalergi CT2003.009.01 **203** *Eupholidoptera latens* Rhodopos CH 8236 **204** *Eupholidoptera giuliae* Argoules CT1995.011.11 **205** *Eupholidoptera francisae* sp. nov. paratype Andikithira CT2002.004.08 **206** *Eupholidoptera annamariae* Kato Zakros CT2000.030.01 **207** *Eupholidoptera astyla* Krotos RMNH.INS1141819 **208** *Eupholidoptera feri* holotype Mt. Dikti, Katharo plain RMNH.INS1105297 **209** *Eupholidoptera mariannae* Kalavros CT2017.029.01 **210** *Eupholidoptera forcipata* Mt. Idhi CT1987.044.01 **211** *Eupholidoptera marietheresae* sp. nov. holotype Mt. Dikti FC1606 RMNH.INS1141850 **212** *Eupholidoptera jacuelinae* holotype Gavdos CT2000.005.02. Scale bars: 1 mm.

Distribution. The species was described from Kato Zakros along the eastern coast of Crete. After its original finding it was collected again in the same area between Kato Zakros and Zakros (Çiplak et al. 2009). New data presented here show that the range extends from the southeastern coast east of Kalo Nero Bay along the entire east coast up into the northernmost peninsular and along the northern coast westward up to and beyond Sitia (Fig. 254). It is still unclear if the species also occurs more inland east of the Koutsouras-Sitia road. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The species has been found in sparse phrygana between sea level and 550 m in dry open terrains with bare ground, covered with small spiny or thorny shrublets in which it hides during the day. The species was also found in a pitfall trap in sand dunes near Xerokampos along the southeastern coast.

Phenology. Hand catches of this species were made between end of May and mid-August (25/05–15/08). This roughly coincides with the period during which the species was caught in pitfall traps. Still their presence may be more prolonged into August or up to October as a trap sampled 12 October 2000 and set 6 August still contained nine adults.

Eupholidoptera astyla (Ramme, 1927)

Figs 10, 19, 33, 47, 61, 77, 91, 105, 120, 134, 148, 162, 176, 191, 192, 207, 213, 224, 225, 241, 254, 256, 259, Tables 1, 2, 5–7, 9, 10, Suppl. materials 1–4

Pholidoptera astyla Ramme 1927: 133.

Eupholidoptera astyla (Ramme, 1927); Ramme 1951: 198.

Morphological description. Ramme 1927: 133; 1939: 100; Harz 1969: 377.

Bioacoustics. Çiplak et al. 2009: 27, 54–55.

Examined specimens. 1 ♂ (paratype); 81 ♂, 59 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 19) pale with black dots; frontal half of pronotal disc (Fig. 33) with more or less extensive black patch, border with pale rear half transverse or V-shaped. Male (Fig. 241) – stridulatory file with 101–105 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 22–24 teeth per mm; anal tergite (Figs 77, 91, 105) with hind margin toward middle forming two small pointed teeth separated by a short narrow V-shaped excision, tips pointing downwards; cerci (Figs 120, 134) unarmed, 5–7× longer than wide, weakly conical, weakly curved inward in basal half, in profile straight; subgenital plate (Figs 148, 162) wider than long, widest halfway, sides rimmed, in profile upturned, tip apical lobes narrowly truncate, spineless, at inner side emarginate with V-shaped excision along one fifth of length; styli (Fig. 176) minute, circular, inserted ventrally, proximal of tip of apical lobe, pointing inward to downward; titillator (Figs 191, 207) asymmetrical, apical arms widening from base, halfway splitting into two strongly thickened, flattened and wrinkled arms, forming wide to almost straight angle ending into two very strong curved spine-like teeth, pointing left or right.

Redescription of female. In 1927 *E. astyla* was described based on a single male from Naxos and three females and the male abdomen from Crete (Ramme 1927).

According to Willemse and Heller (2001) the presence of *E. astyla* on Naxos is doubtful. An extensive search on Naxos in June 2019 by the first author only revealed *E. smyrnensis* at midlevel altitudes in the north-eastern part of the island but no other *Eupholidoptera* species. Willemse and Heller (2001) indicated that the *E. astyla* females listed in the original description (Ramme 1927: 134) from Ierapetra, Anatoli, and Kato Chorio could in fact belong to *E. mariannae* which they described in their paper from this area. In 2001 female *E. mariannae* were not known and this assumption could neither be confirmed nor denied. Based on the discovery of male and female *E. mariannae* in neighbouring locations near Kavousi and Kalavros, opportunity has been taken to re-examine paratypes used by Ramme (1927) in his description of *E. astyla* and compare them with female *E. astyla* and *E. mariannae* described in this paper. Unfortunately, the female from “Jerapetra” could not be located in the MfNB. Comparison of the subgenital plates (Figs 214, 215) revealed that females from Kato Chorio and Anatoli resemble female *E. mariannae* from Kalavros and Kavousi rather than *E. astyla*. This implies that Ramme based his description of female *E. astyla* on female *E. mariannae*. Consequently female *E. astyla* has still not been described and is redescribed here based on specimens from Rethimno and Iraklion.

Description. Female. Examined specimens. 11 ♀: RETHIMNO: Idhi Mt., Idhaio Andro -1987.041.02 (CT); Idhi Mt., Ski-centre – 1987.046.03 (CT); Nea Kria Vrissi, 2 km NW – 2000.016.04 (CT); IRAKLION: Ano Viannos, 3 km SE – 1995.024.03 (CT), RMNH.5014909 (RMNH), RMNH.5086970 (RMNH), RMNH 5086971 (RMNH); Krotos, 0.5 km N – RMNH.INS1141820 (RMNH); Marathos – RMNH.5086989 (RMNH); Mournia, 3 km SW – 2001.008.04 (CT); Tsoutsouros, 6 km NNW – 1995.014.03 (CT). For more details see Suppl. material 2.

General appearance (Figs 224, 225) and colouration as male. First abdominal segment dorsally black, laterally lighter; remaining segments dorsally yellowish brown, sides lighter coloured, last segment completely black. Elytra in dorsal view covered by



Figures 213–215. *Eupholidoptera astyla* paratypes **213** titillator in dorsal view *Eupholidoptera astyla* ♂ paratype Ierapetra s.n. **214** subgenital plate in ventral view *Eupholidoptera mariannae* ♀ Anatoli s.n. [paratype of *Eupholidoptera astyla*] **215** *Eupholidoptera mariannae* ♀ Kato Chorio s.n. [paratype of *Eupholidoptera astyla*].

pronotum, in profile barely protruding, light coloured. Cercus short, conical tapering, more so in apical third toward a pointed tip, straight to slightly upturned in profile, straight to slightly curved inward in dorsal view, covered with pale short and long hairs. Subgenital plate (Figs 47, 61) oblong, greatest width halfway or in distal quarter, in ventral view convex, proximally flattened to slight depressed, halfway on side with or without a (in-)distinct bulge, surface shiny, smooth with dispersed hairs, hind margin converging gradually from halfway or more abruptly in distal quarter, with medial V-shaped excision along one third of length, corners rectangular to sharp-angled, in profile triangular to trapezoid with a more or less distinct dorsal depression, lower edge straight distally slightly upturned, tip obtuse angular. Ovipositor almost straight to slightly upcurved, 1.5–2.0× longer than pronotum.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of two specimens (20 syllables measured), the song of *E. astyla*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. astyla*, the syllable duration is ~ 120 ms, with a syllable rate up to ~ 1/s. Published records (Çiplak et al. 2009) show a syllable duration of ~ 166 ms at 25 °C and a syllable repetition rate of less than 1/s. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera astyla* see Suppl. material 3.

Variation. High altitude specimens are smaller than specimens found at lower altitudes. Variation in black and pale colour patterns seem linked to individuals rather than to populations. Cercus more or less slender and more or less bent inward. Medial excision anal tergite V- to U-shaped, adjoining teeth aligned with dorsal surface pointing distally or bent downward, pointing downward. Subgenital plate more or less compact, in profile, lower margin evenly rounded or with an angle halfway. Styli minute to small, in the west and north pointing inward, toward the south and east pointing downward, exceptionally also outward. In some males from Asterousia Mt. (central-south Crete), styli were lacking almost completely. Titillator can be more or less compact, apical arms parallel or slightly divergent, apical teeth gradually or suddenly and more strongly pointed, pointing right or left. Two males (of 34) collected in pitfall traps near Kofinas along the south coast showed an almost symmetrical titillator, the two apical arms pointing in opposite directions (Fig. 192). In other characters these two males fully matched *E. astyla*, as did all other males from Kofinas. The symmetrical titillators are considered individual anomalies. The shape of the female subgenital plate varies: in the west and at higher altitudes on Mts. Idi and Dikti being plump with a short median excision, toward the east changing to oblong more distinctly acutely bilobed with a deeper excision, resembling those of *E. feri* and *E. mariannae*.

Differential diagnosis. Males differ from congenics in the strongly asymmetrical, thickened and wrinkled apical arms of the titillator (Figs 191, 207) pointing left or right, in the narrow V-shaped excision in the anal tergite (Figs 77, 91, 105) with tips pointing downward, in the slender, unarmed weakly inward curved cerci (Figs 120, 134), in the wide, upturned, spineless subgenital plate (Figs 148, 162) and

in the minute, pre-apically inserted styli pointing downward (Fig. 176). Females differ in the oblong subgenital plate (Figs 47, 61), proximally convex with a short excision. In the southeast toward Lasithi female subgenital plates are longer, the apical lobes on both sides of the medial excision more pointed, resembling *E. mariannae*. In colouration, particularly the anterior half of the pronotum *E. astyla* resembles *E. annamariae*, *E. feri*, *E. giuliae*, and *E. mariannae*. For more details differentiating *E. astyla* from other Cretan *Eupholidoptera* see Table 5.

Distribution. From the Cretan species of *Eupholidoptera*, *E. astyla* has the widest range. Current data indicate its range covers large parts of central Crete, stretching from central and eastern Rethimno to western Lasithi, from Skaleta east of the city of Rethimno in the northwest to Ierapetra along the southern coast in the southeast (Fig. 254). Despite the additional localities presented here, the exact boundaries in the west, where it meets *E. giuliae*, and in the east, where it meets *E. mariannae* and *E. feri*, are not clear. Current information suggests *E. astyla* to be absent from large parts of the central lowlands south of Iraklion and the northern coastal region east of Iraklion but this certainly requires additional investigation. Opportunity was taken to examine (and photograph) the male mentioned by Ramme (1927) in his description of *E. astyla* of which only the last part of the abdomen was left. Based on the shape of the titillator (Fig. 213) this male clearly belongs to *E. astyla*. The label of this male only states “Jerapetra”. It is not clear whether the name “Jerapetra” actually refers to the town Ierapetra or the district. Either way, assuming the label is correct, the presence in Ierapetra indicates there is an area west of Ierapetra where both *E. astyla* and *E. mariannae* may occur together (Fig. 254). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The species habitats cover a wide altitudinal range: from sea level along the northern and southern coast to 1550–1800 m on Mt. Idi and Mt. Dikti. Pitfall traps that caught *E. astyla* were placed in sparse to dense phrygana, maquis and areas dominated by pine trees.

Phenology. Hand catches indicate adults can be found from early May onward at lower altitudes up to the end of August at higher altitudes. Pitfall trap catches indicate that especially at higher altitudes the species can be found at least up to the second half of September or even early October.

Eupholidoptera cretica Ramme, 1951

Figs 14, 28, 42, 56, 72, 86, 100, 114, 129, 143, 157, 171, 185, 201, 226, 227, 255, Tables 1, 2, 5–7, 9, 10, Suppl. materials 1, 2

Eupholidoptera cretica Ramme, 1951: 202.

Morphological description. Ramme 1951: 202.

Remark. *Eupholidoptera cretica* was described after a single male, collected 13 June 1942 by K. Zimmermann. This, most likely, is the mammologist who worked on the mammals of Crete and published a review of his observations including a map

(Zimmermann et al. 1953). As collecting location for the specimen Ramme (1951) mentioned “Sanmaria” [sic]. Samaria is the name used both for the gorge as well as the hamlet in the gorge ca. 4 km inland at 340 m altitude. Extensive searches in 2000, 2011, and 2019 around Agia Roumeli, the coastal village at the entrance of the gorge and the Samaria gorge itself were unsuccessful. Likewise visits to the Omalos plain above the Samaria gorge in 1991 (Heller), 2003 and 2004 (Tilmans) failed to find the species. Then the species appeared to have been trapped in fermenting traps placed in bushes at 1200 m on the southeastern-most flanks of Mt. Lefka above the villages of Anopoli and Limnia in 1991 and again on the Omalos plateau just above the Samaria gorge in 2019. Only few specimens were caught. A single undamaged male and female have been used to make stacked images, present diagnostic features for the male and describe the female.

Examined specimens. 1 ♂, 2 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 14) pale with black dots; pronotum (Fig. 28) pale with more or less distinct black spots in centre of disc and along rear edge of side flap. Male – stridulatory file with 107 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 32 teeth per mm; anal tergite (Figs 72, 86, 100) with hind margin forming two widely separated triangular lobes pointing backward and downward with pointed tip; cerci (Figs 114, 129) unarmed, 5× longer than wide, basal half cylindrical, apical half conical, strongly curved inward, in profile straight; subgenital plate (Figs 143, 157) as slightly wider than long, proximally widest, apically gradually narrowing, sides partly rimmed, in profile very weakly upturned, pointing backward, tip apical lobes narrowly truncate, spineless, with wide V-shaped excision along one third of length; styli (Fig. 171) long, 0.6× as long as cerci, 6× longer than wide, cylindrical, inserted at inner tip of apical lobe, pointing backward and upward; titillator (Figs 185, 201) symmetrical, apical arms from base widening, in apical half narrowing again, swollen, fused except for straight tooth-like apical fifth part, in profile weakly S-shaped hardly widened in basal half, somewhat dilated in swollen apical half.

Description. Female. Examined specimens. 2♀: CHANIA: Lefka Mt., above Omalos – RMNH.INS1141837 (RMNH); Lefka Mt., Sfakion above Anopoli – 2005.060.01 (CT) (for details see Suppl. material 2).

General appearance (Figs 226, 227) and colouration as male. Elytra in dorsal view covered by pronotum, in profile barely protruding, light coloured. Cerci relatively long, as long as subgenital plate, slightly bent inward and upward, conical, gradually narrowing toward slender pointed tip. Subgenital plate (Figs 42, 56) distinctly wider than long, greatest width in distal half, in ventral view medially convex, laterally flattened, halfway forming distinct bulge, surface dull, smooth with dispersed hairs, hind margin with very wide U-shape excision reaching along a quarter to halfway, corners rectangular, in profile rhomboid to deltoid with a distinct depression in apical and dorsal corner, lower edge strongly convex, tip obtuse angular. Ovipositor in proximal two thirds straight, apical third slightly curved upward, 2× longer than pronotum.

Measurements. See Tables 6, 7.

Bioacoustics. The song of this species has not yet been recorded.

Differential diagnosis. Males differ from congenetics in the stout, unarmed, inward curved cercus (Figs 114, 129), in the widely separated triangular lobes of the anal tergite with tips pointing backward and downward (Figs 72, 86, 100), in the subgenital plate (Figs 143, 157) gradually narrowing into truncate and spineless tips, in the very long, apically inserted backward and upward pointing styli (Fig. 171) and the widened apical arms of the titillator (Figs 185, 201) fused except for two short straight teeth in apical fifth. Females differ in the wide, convex, subgenital plate (Figs 42, 56), the hind margin medially with a very wide and deep excision. In colouration *E. cretica* is one of the few Cretan *Eupholidoptera* species with no or only minute black marking on the pronotal disc. For more details differentiating *E. cretica* from other Cretan *Eupholidoptera* see Table 5.

Distribution. Besides the type location which is not exactly traceable, only known from two spots on Mt. Lefka, one in northwest near the Omalos plateau and Samaria gorge and a second along the southeastern slopes above the villages of Anopoli and Limnia (Fig. 255). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The area around the Omalos plateau where the species was trapped is described as *Cupressus* forest. The species has been trapped in fermenting traps placed above the ground in shrubs, indicating *E. cretica* like *E. smyrnensis*, *E. mariannae* as well as *E. jacquelinae* but contrary to most other Cretan species, actually lives in such shrubs and not in small prickly bushes on the ground.

Phenology. Still very little is known. The first male was caught on 13 June 1942. Specimens being caught in traps were found in traps operative between 31 July and 19 October. The recorded altitudes where the species was found are between 1165 m and 1235 m.

Eupholidoptera feri Koçak & Kemal, 2010

Figs 20, 34, 48, 62, 78, 92, 106, 121, 135, 149, 163, 177, 193, 208, 255, 259, Tables 1, 2, 5–7, 10, Suppl. materials 1–3

Eupholidoptera rammei Willemse & Heller, 2001: 333.

Eupholidoptera feri Koçak & Kemal, 2010: 7.

Morphological description. Willemse and Heller 2001: 333–339.

Bioacoustics. Willemse and Heller 2001: 335, fig. 52 [as *E. rammei*]; Çiplak et al. 2009: fig. 234 [as *E. rammei*].

Examined specimens. Holotype, allotype (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 20) pale with black dots; frontal half of pronotal disc (Fig. 34) with extensive central black patch, border with pale rear half transverse to V-shaped. Male – stridulatory file with 100 teeth (Çiplak et al. 2009) (including proximal and distal ones), density of teeth in middle two thirds of

the file 22–24 teeth per mm; anal tergite (Figs 78, 92, 106) with hind margin medially forming two small pointed teeth pointing downward, separated by a short narrow V-shaped excision; cerci (Figs 121, 135) armed, inner margin with short side-tooth at one third of length pointing inward, 5× longer than wide, basal half cylindrical, apical half conical, straight, in profile slightly upturned in apical third; subgenital plate (Figs 149, 163) slightly wider than long, widest in proximal third, sides widely rimmed, in profile upturned, tip apical lobes narrowly truncate, spineless, with slit-like excision along one fifth of length; styli (Fig. 177) minute, circular, flat, inserted at inner side of apical lobes, just proximal of tip, pointing downward; titillator (Figs 193, 208) slightly asymmetrical, greater part apical arms fused, in apical half transversely wrinkled diverging into two spines pointing sideways in different angles, in profile narrow, halfway slightly wider, curved upward, in apical half stronger so. Female – subgenital plate (Figs 48, 62) longer than wide, widest in proximal third, convex, proximally concave, apical lobes touching, tips acute with median excision along one third of length, in profile triangular.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of 1 specimen (10 syllables measured), the song of *E. feri*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. The syllable duration is ~ 271 ms, recorded at 15 °C, with a syllable rate up to ~ 1/s. Published records (Çiplak et al. 2009), based upon the same sound recording and after correction for the low temperature, show a syllable duration of ~ 121 ms at 25 °C and a syllable repetition rate of ~ 1/s at maximum. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera feri* see Suppl. material 3.

Differential diagnosis. Males differ from congenetics in the stout, cylindrical cerci (Figs 121, 135) with a subbasal inner side tooth, in the anal tergite (Figs 78, 92, 106) medially not extended, bent downward with very narrow V-shaped excision, tips pointing downward, in the wide, upturned, spineless subgenital plate (Figs 149, 163) with minute, pre-apically inserted styli (Fig. 177) pointing downward and the narrow asymmetrical apical arms of the titillator (Figs 193, 208). Females differ in the elongated and proximally concave subgenital plate (Figs 48, 62), its apical lobes touching with an excision along one third of the length. In colouration the species resembles *E. annamariae*, *E. astyla*, and *E. mariannae*. For more details differentiating *E. feri* from other Cretan *Eupholidoptera* see Table 5.

Distribution. Only known from the Katharo plain in the eastern offshoots of Mt. Dikti, in the western part of the Lasithi district (Fig. 255). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The type specimens were collected 1–2 m high in a *Quercus* shrub in the Katharo plain, part of which is used for cultivation (vineyards), the rest consists of bare grounds.

Phenology. The Katharo plain lies at an altitude of 1100 m. The type specimens were collected in late August.

***Eupholidoptera forcipata* Willemse & Kruseman, 1976**

Figs 22, 36, 50, 64, 80, 94, 108, 123, 137, 151, 165, 179, 195, 210, 255, 259, Tables 1, 2, 5–7, 9, 10, Suppl. materials 1–3

Eupholidoptera forcipata Willemse & Kruseman, 1976: 131.

Morphological description. Willemse and Kruseman 1976: 131–134.

Bioacoustics. Çiplak et al. 2009: 27, 51, 54.

Examined specimens. Holotype, allotype, 8 ♂, 9 ♀ (paratypes); 12 ♂, 5 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 22) pale with black dots; pronotal disc (Fig. 36) pale with central black marking resembling an open “W” or frontal half with larger central black patch, border with pale rear half transverse or V-shaped; Male – stridulatory file with 193 teeth (190 in Çiplak et al. 2009) (including proximal and distal ones), density of teeth in middle two thirds of the file 36 teeth per mm (33 in Çiplak et al. 2009); anal tergite (Figs 80, 94, 108) narrow, distally strongly bent and extended downward forming two apical lobes ending in strong teeth pointing downward and slightly outward separated by a wide, deep excision; cerci (Figs 123, 137) unarmed, 4× longer than wide, basal half cylindrical, apical half conical straight, inner margin sinuate with minute bulge halfway, in profile slightly upturned in apical half; subgenital plate (Figs 151, 165) wider than long, widest halfway, sides widely rimmed, in profile upturned, tip apical lobes narrowly truncate, spineless, forming very wide V-shaped excision reaching halfway; styli (Fig. 179) short, 0.3 as long as cerci, 2× longer than wide, cylindrical, inserted at tip of apical lobes pointing backwards; titillator (Figs 195, 210) symmetrical, basal half apical arms fused, narrow, stalk-like, halfway widening, swollen, diverging into two evenly curved, slender hooks, in profile in basal half narrowing apically, wide angled with apical hooks, reaching or extending above anal tergite. Female – subgenital plate (Figs 50, 64) twice as wide as long, widest halfway, proximally with two distinct, widely separated pit-like concavities, apical lobes with depression, tips rounded, separated by U-shaped excision along one quarter of length, in profile oblong, lower edge distally strongly upcurved, tip truncated.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of one specimen (30 syllables measured), the song of *E. forcipata*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. forcipata*, the syllable duration is ~ 525 ms, with a syllable rate up to somewhat less than 1/s. The syllable duration easily discerns the song of this species from the other known songs of *Eupholidoptera* from Crete. Published records (Çiplak et al. 2009) show a syllable duration of ~ 425 ms and a syllable repetition rate far lower than 1/s. For details of sound recordings of *Eupholidoptera forcipata* see Suppl. material 3.

Differential diagnosis. Males differ from congeners in the pointed backward and downward extended widened apical lobes of the anal tergite (Figs 80, 94, 108)

with tips pointing downward and slightly outward, in the wide upturned, spineless subgenital plate (Figs 151, 165) with a very wide V-shaped excision, in short, apically inserted styli (Fig. 179) pointing backward, in the stout, straight cerci (Figs 123, 137) with a minute bulge on the inner margin and the symmetrical apical arms of the titillator (Figs 195, 210), in basal half fused and narrow, in apical half strongly diverging hooks. Females differ in the very wide subgenital plate (Figs 50, 64), proximally with two concavities, tips rounded with U-shaped excision along quarter of the length. *Eupholidoptera forcipata* closely resembles *E. marietheresae* sp. nov. but male *E. forcipata* differ from male *E. marietheresae* sp. nov. in the straight hind margin of the anal tergite (compare Fig. 94 with Fig. 95), slimmer cercus (compare Fig. 123 with Fig. 124) and the apical arms of the titillator being straight in basal half and gradually upcurved in apical half (compare Fig. 195 with Fig. 196). In female *E. forcipata* the subgenital plate is shorter and the proximal pits being placed further apart than in *E. marietheresae* sp. nov. (compare Fig. 50 with Fig. 51). In colouration particularly the anterior half of the pronotum *E. forcipata* lacks extensive black markings or patches. For more details differentiating *E. forcipata* from other Cretan *Eupholidoptera* see Table 5.

Distribution. Only known from higher altitudes on Mt. Psiloritis, central Crete (Fig. 255). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The species lives at high altitudes in subalpine phrygana in low prickly bushes (e.g., *Astragalus*) in which it hides during the day.

Phenology. The species occurs between 1350 m and 2225 m. Adults have been collected by hand at the end of July and during the first half of August. Trap catches indicate they are still active up to September and possibly October.

***Eupholidoptera francisae* Tilmans & Odé, sp. nov.**

<https://zoobank.org/6A1CA984-AD9D-4472-A6C3-3B8CF2100492>

Figs 17, 31, 45, 59, 67, 75, 89, 103, 117, 132, 146, 160, 174, 189, 205, 216–218, 228–231, 243–246, 254, 256–259, Tables 2–8, 10, Suppl. materials 1–4

Remark. The *Eupholidoptera* populations present on the island of Andikithira and in the area of western-southwestern Chania in Crete not only proved to differ from the geographically nearest other taxa of the genus: *Eupholidoptera spinigera*, restricted to the island of Kithira, and *Eupholidoptera latens* from northern and central Chania, but also from all its other congenics. This new taxon is described below. For arguments to assign the *Eupholidoptera* populations of Andikithira and western/southwestern Chania populations as one single new taxon see under Discussion.

Examined specimens. Type specimens. ♂ **holotype** (2002.004.04) (CT), ♀ **allotype** (2002.004.11) (CT), both labeled: HELLAS, Andikithira, 150 m, 9.V.2002/3 km S.E.S. Potamos/WGS 84 35°51.996'N, 023°18.114'E/legnt. J.M. Tilmans and J.F.R. Tilmans-Smid.

Paratypes. 8 ♂ & 5 ♀ (CT), 1 ♂ & 1 ♀ (NHMC), 1 ♂ & 1 ♀ (RMNH): same location and date as holotype; further paratypes 2 ♀ (CT): HELLAS, Andikith-

ira, 50 m, 9.V.2002/0,6 km S.E.S. Potamos/WGS84 35°52.600'N, 023°17.426'E/legnt. J.M. Tilmans & J.F.R. Tilmans-Smid; 1 ♂ & 2 ♀ (CT): HELLAS, Andikithira, 50 m, 27.V.2008/0,6 km S.E.S. Potamos/WGS84 35°52.605'N, 023°17.439'E/legnt. J.M. Tilmans & J.F.R. Tilmans-Smid; 1 ♂ & 2 ♀ (RMNH): Greece – Crete (Chania): Ag. Paraskevi (Elafonisos-Maniatiana)/445 m; 17.VI.2019; 35.285645°N, 23.588774°E/leg. L. Willemse & J. Tilmans; 1 ♀ (RMNH): Greece – Crete (Chania): 1 km NE of Anidhroi/385 m; 21.VI.2017; 35.255925°N, 23.737376°E/leg. L. Willemse & P. Zacharopoulou; 6 ♂ & 2 ♀ (CT): HELLAS, nomos Khania, 300 m/3 km E. Anidhroi, 27–29.IV.2001/35°15.288'N, 23°44.157'E/leg. J.M. Tilmans & J.F.R. Tilmans-Smid; 1 ♂ (CT), 2 ♂ & 1 ♀ (RMNH): Greece – Crete (Chania): 1 km N of Chondros/485 m; 16.VI.2019; 35.322094°N, 23.685799°E/leg. L. Willemse & J. Tilmans; 1 ♂ & 1 ♀ (RMNH): Greece – Crete (Chania): Elos/480 m; 16.VI.2019; 35.367374°N, 23.637676°E/leg. L. Willemse & J. Tilmans; 1 ♀ (CT), 1 ♀ (RMNH): Greece – Crete (Chania): 0.5 km W of Kamaria/345 m; 18.VI.2019; 35.282516°N, 23.778568°E/leg. L. Willemse & J. Tilmans; 1 ♀ (RMNH): 1 km S of Livadas/225 m; 18.VI.2019; 35.263004°N, 23.814722°E/leg. L. Willemse & J. Tilmans; 1 ♂ (IBER): Louchio, 0.5 km (35.3691°N, 23.6244°E) 665 m, 23/05/2018 Chobanov, D., Iorgu, I. & Borissov, S. 1 ♂ IBER; 1 ♂ 2 ♀ (RMNH): Greece – Crete (Chania); Maroulia, Ano Sfinari – Kostogiannides/715 m; 19.VI.2017; 35.390335°N, 23.605317°E/leg. L. Willemse & P. Zacharopoulou; 2 ♂ & 2 ♀ (CT), 3 ♂ & 4 ♀ (RMNH): Greece – Crete (Chania): Psariana-Aligi/420 m; 17.VI.2019; 35.351833°N, 23.694208°E/leg. L. Willemse & J. Tilmans; 1 ♂ & 1 ♀ (CT), 2 ♂ & 1 ♀ (RMNH): Greece – Crete (Chania): 1 km S of Sarakina/305 m; 16.VI.2019; 35.289181°N, 23.674417°E/leg. L. Willemse & J. Tilmans; 2 ♀ (IBER): Sfinari (35.4407°N, 23.5704°E) 1m, 23/05/2018 Chobanov, D., Iorgu, I. & Borissov, S.; 1 ♂ (CT), 1 ♂ & 1 ♀ (RMNH): Greece – Crete (Chania): just N of Strovles/420 m; 16.VI.2019; 35.368656°N, 23.669718°E/leg. L. Willemse & J. Tilmans; 1 ♂ (RMNH): Greece – Crete (Chania): 0.5 km N of Temenia/835 m; 17.VI.2019; 35.299652°N, 23.751684°E/leg. L. Willemse & J. Tilmans; 1 ♂ 1 ♀ (CT), 1 ♂ 2 ♀ (NHMC), 1 ♀ (RMNH): Greece – Crete (Rethimno): 1 km SE of Piso Moni Preveli/20 m; 12.VII.1997; 35.1518°N, 24.4725°E/leg. P. Lymberakis. (for details see Suppl. material 2).

Description. Male. General appearance (Figs 228, 229), elytra and legs as type species of genus, *E. chabrieri*.

Pronotum (Fig. 31) dorsally slightly flattened.

Forewing: stridulatory file left elytron consists of 96–138 teeth, shortest distance between proximal and distal end 3.0–3.9 mm, density of teeth in middle two thirds of the file 27–34 teeth per mm.

Anal tergite (Figs 75, 89, 103) apically strongly curved downward with round dorsomedian depression; posterior margin with wide, concave, moderately deep rounded (in many specimens semi-circular), median excision, bordered by two sharply toothed processes laterally, directed downward.

Cerci (Figs 117, 132) long, slender, 6–7× longer than greatest width, cylindrical with golden-coloured short and long hairs, without any tooth, slightly bent inwards.

Table 3. Measurements (in mm) and biometrics of male *E. latens* and *E. francisae*.

Males	<i>Euph. latens</i>	<i>Euph. francisae</i>	<i>Euph. francisae</i> only Andikithira	<i>Euph. francisae</i> only Chania
length body	<i>n</i> = 9	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	18.9–27.1	19.0–28.8	20.9–28.3	19.0–28.8
mean ± SD	22.4 ± 2.58	24.1 ± 2.66	25.6 ± 2.58	23.5 ± 2.50
length pronotum	<i>n</i> = 9	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	8.4–9.9	8.0–10.7	9.0–10.7	8.0–10.4
mean ± SD	9.1 ± 0.53	9.5 ± 0.65	10.0 ± 0.53	9.3 ± 0.59
length hind femur	<i>n</i> = 13	<i>n</i> = 37	<i>n</i> = 10	<i>n</i> = 27
min. – max.	17.0–22.7	19.0–23.1	19.0–22.8	19.7–23.1
mean ± SD	19.3 ± 2.28	21.1 ± 0.93	20.7 ± 1.10	21.2 ± 0.83
width hind femur	<i>n</i> = 13	<i>n</i> = 37	<i>n</i> = 10	<i>n</i> = 27
min. – max.	3.9–4.8	3.7–4.9	4.0–4.6	3.7–4.9
mean ± SD	4.3 ± 0.23	4.3 ± 0.25	4.4 ± 0.18	4.3 ± 0.27
ratio length-width hind femur	<i>n</i> = 13	<i>n</i> = 37	<i>n</i> = 10	<i>n</i> = 27
min. – max.	4.14–5.28	4.47–5.49	4.52–5.07	4.47–5.49
mean ± SD	4.53 ± 0.37	4.88 ± 0.25	4.74 ± 0.16	4.93 ± 0.26
length subg. plate	<i>n</i> = 12	<i>n</i> = 34	<i>n</i> = 11	<i>n</i> = 23
min. – max.	3.75–6.30	4.25–5.90	5.35–5.90	4.25–5.80
mean ± SD	4.45 ± 0.74	5.08 ± 0.49	5.57 ± 0.17	4.85 ± 0.41
width subg. plate	<i>n</i> = 12	<i>n</i> = 34	<i>n</i> = 11	<i>n</i> = 23
min. – max.	2.20–5.00	2.00–3.85	2.95–3.85	2.00–3.75
mean ± SD	3.21 ± 0.78	3.13 ± 0.48	3.43 ± 0.32	2.99 ± 0.48
ratio length-width subg. plate	<i>n</i> = 12	<i>n</i> = 34	<i>n</i> = 11	<i>n</i> = 23
min. – max.	0.84–2.05	1.13–2.44	1.48–1.90	1.13–2.44
mean ± SD	1.44 ± 0.32	1.66 ± 0.30	1.63 ± 0.15	1.67 ± 0.35
length incision subg. plate	<i>n</i> = 12	<i>n</i> = 32	<i>n</i> = 11	<i>n</i> = 21
min. – max.	1.15–1.60	1.20–1.90	1.50–1.85	1.20–1.90
mean ± SD	1.33 ± 0.15	1.53 ± 0.21	1.67 ± 0.13	1.46 ± 0.21

Subgenital plate (Figs 146, 160) very large, longer than wide, strikingly elongated, lateral margins swollen, ventrally with a median keel; basal third wide, then suddenly (strongly) incurved to the median part with in many specimens nearly parallel lateral margins; in apical third strongly tapering, hind margin distinctly medially excised over the whole length of the apical third, apical lobes laterally flattened, the apex round spatulate with a well-defined, slightly upwards-pointing, curved tooth at the lower end; in profile pointing backward. Styli (Fig. 174) short, thick, 1.1–1.6× longer than wide, downwardly directed in lateral view, inserted quite far before apex of apical lobe.

Titillator (Figs 189, 205) moderately sized; basal parts extending, strongly curved in the direction of the apical arms; fused part of apical arms broad at base not widening to the beginning of the unfused part of the apical arms; unfused part of apical arms hook-like, parallel or diverging and in lateral view in a 35–50 degrees angle curved upward to dorsum, wide at basis and evenly narrowing to tip; fused part of apical arms as long to longer than unfused part.

Colouration (in living specimens): general colouration in Andikithiran specimens dark brown (in several specimens chestnut brown) (Fig. 243), in Chania specimens green to light brown (Fig. 245). Head: frontal part below antennae and

Table 4. Measurements (in mm) and biometrics of female *E. latens* and *E. francisae*.

Females	<i>Euph. latens</i>	<i>Euph. francisae</i>	<i>Euph. francisae</i> only Andikithira	<i>Euph. francisae</i> only Chania
length body	<i>n</i> = 8	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	17.5–23.3	19.5–31.5	23.7–31.5	19.5–26.9
mean ± SD	20.3 ± 2.32	24.1 ± 2.43	26.3 ± 1.93	23.2 ± 1.98
length pronotum	<i>n</i> = 8	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	8.1–9.4	8.5–10.5	8.5–10.5	8.6–10.4
mean ± SD	8.7 ± 0.46	9.6 ± 0.56	9.8 ± 0.65	9.5 ± 0.49
length ovipositor	<i>n</i> = 8	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	13.8–16.4	13.8–19.3	15.8–18.7	13.8–19.3
mean ± SD	14.9 ± 0.76	16.6 ± 1.38	17.5 ± 0.89	16.2 ± 1.39
ratio length ovip. pronot.	<i>n</i> = 8	<i>n</i> = 38	<i>n</i> = 11	<i>n</i> = 27
min. – max.	1.64–1.79	1.52–1.99	1.61–1.99	1.52–1.91
mean ± SD	1.72 ± 0.05	1.73 ± 0.11	1.79 ± 0.12	1.71 ± 0.11
length hind femur	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 11	<i>n</i> = 26
min. – max.	17.1–22.9	20.9–24.9	20.0–21.7	20.9–24.9
mean ± SD	18.8 ± 1.93	22.2 ± 1.04	21.2 ± 0.61	22.6 ± 0.90
width hind femur	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 11	<i>n</i> = 26
min. – max.	3.9–4.8	4.1–5.1	4.1–4.7	4.1–5.1
mean ± SD	4.3 ± 0.27	4.5 ± 0.24	4.5 ± 0.20	4.5 ± 0.25
ratio length-width hind femur	<i>n</i> = 9	<i>n</i> = 37	<i>n</i> = 11	<i>n</i> = 26
min. – max.	3.98–4.77	4.55–5.62	4.55–5.02	4.60–5.62
mean ± SD	4.40 ± 0.25	4.93 ± 0.28	4.76 ± 0.17	5.00 ± 0.28
length subg. plate	<i>n</i> = 9	<i>n</i> = 35	<i>n</i> = 11	<i>n</i> = 24
min. – max.	2.10–3.75	1.75–2.70	1.90–2.60	1.75–2.70
mean ± SD	2.68 ± 0.51	2.19 ± 0.23	2.18 ± 0.25	2.19 ± 0.23
width subg. plate	<i>n</i> = 9	<i>n</i> = 35	<i>n</i> = 11	<i>n</i> = 24
min. – max.	2.10–3.20	1.95–3.40	2.20–3.40	1.95–2.90
mean ± SD	2.62 ± 0.39	2.53 ± 0.41	2.93 ± 0.39	2.34 ± 0.27
ratio length-width subg. plate	<i>n</i> = 9	<i>n</i> = 35	<i>n</i> = 11	<i>n</i> = 24
min. – max.	0.86–1.44	0.59–1.23	0.59–1.00	0.75–1.23
mean ± SD	1.03 ± 0.17	0.89 ± 0.15	0.76 ± 0.14	0.95 ± 0.12
length incision subg. plate	<i>n</i> = 9	<i>n</i> = 35	<i>n</i> = 11	<i>n</i> = 24
min. – max.	1.15–1.70	0.90–1.60	0.90–1.25	0.95–1.60
mean ± SD	1.32 ± 0.18	1.16 ± 0.16	1.08 ± 0.12	1.20 ± 0.17

eyes in Andikithiran specimens creamy yellow-brownish with two larger inner and two smaller outer dark brown spots (Fig. 17) and often brownish speckled below the eyes, in Chania specimens bright green and likewise arranged and sized spots in black; border of frons with (lighter coloured) clypeus with dark transverse patches; upper part around eyes and antennal sockets black; behind both eyes and antennae two black bands separated from each other by a yellowish median line; occiput with black marking often provided with a thin lighter median line. Pronotum: dorsum dark brown-chestnut brown (Andikithira) to greenish or yellowish brown and often mottled (Chania) in first half with more (Andikithira) (Fig. 31) or less (Chania) extensive black marking; lateral lobes in upper part with black, ventrally not sharply delimited, longitudinal band, lower part pronotal lobes brownish to pinkish (Andikithira), green or yellow-white (Chania); in many specimens lower margin pronotal lobes in metazona yellowish. Elytra: visible parts not covered by the pronotum black or dark brown, covered part

(lighter) brownish. Abdomen: first tergite dorsally black, other tergites completely dark brown to chestnut brown (Andikithira) or green to brownish often dorsally lighter coloured (Chania) and on both islands abdominal tergites sometimes mottled, anal tergite completely black; abdominal sternites pinkish brown (Andikithira) or yellowish brown (Chania). Cercus and subgenital plate: same (general) colour as body. Titillator: basal parts and unfused part of apical arms same colour as body, fused part of apical arms lighter coloured. Legs: same colour as body; fore and middle legs with many blackish to brownish stripes, spots, and markings; hind femur in the basal half dorsally with a longitudinal black to brownish stripe and also laterally on the outside in the middle part of its length; hind knees black.

Female. General appearance (Figs 230, 231) as in male. Elytra completely covered by pronotum, only in some females scarcely protruding laterally.

Cercus short, conical with golden coloured short and long hairs, nearly straight, tapering apically; tip pointed, slightly bent inwards.

Subgenital plate (Figs 45, 59) in ventral view generally wider than long; hind margin rounded, medially with a broadly rounded wide V-shaped excision half as long as the subgenital plate; basis concave with a shallow medial longitudinal ridge; in profile short triangular, apex rounded and not reaching or surpassing the proximal half of the gonangulum (Fig. 67).

Ovipositor nearly straight, only slightly upcurved near its apex, 1.5 to almost 2.0× longer than pronotum.

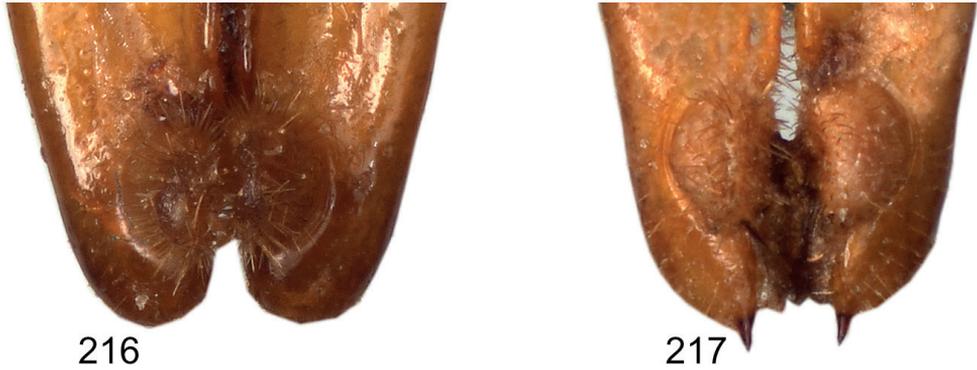
Colouration generally as in male (Figs 244, 246). Black marking of pronotum dorsally in prozona in most females less extensive as in males. First abdominal segment black; cercus, subgenital plate and ovipositor same colour as body (Andikithira) or yellowish brown with tip of ovipositor darker brown and laterally its medial part greyish brown.

Morphological variation found in *E. francisae* sp. nov. is elaborated in the Discussion.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of 15 specimens (153 syllables), the song of *E. francisae* sp. nov., as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. francisae* sp. nov., the syllable duration is ~ 188 ms (Fig. 218). In the present recordings, the syllable repetition rate is slower than 0,5/s. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera francisae* sp. nov. see Suppl. material 3.

Variation. Within this new taxon, specimens from Andikithira are, as stated earlier, quite uniform in their morphological traits and colouration, while the populations on Crete incorporate more variation as the morphometric analyses in Tables 3, 4 show. For the males this is especially the case in the presence/absence of tiny spines at the tip of the subgenital plate (compare Figs 216, 217), the ratio length-width hind femur, the ratio length-width subgenital plate, the length of the incision of the subgenital plate. The females show most variation in the ratio length-width hind femur. Looking at the differences between the populations of Andikithira and those of west-



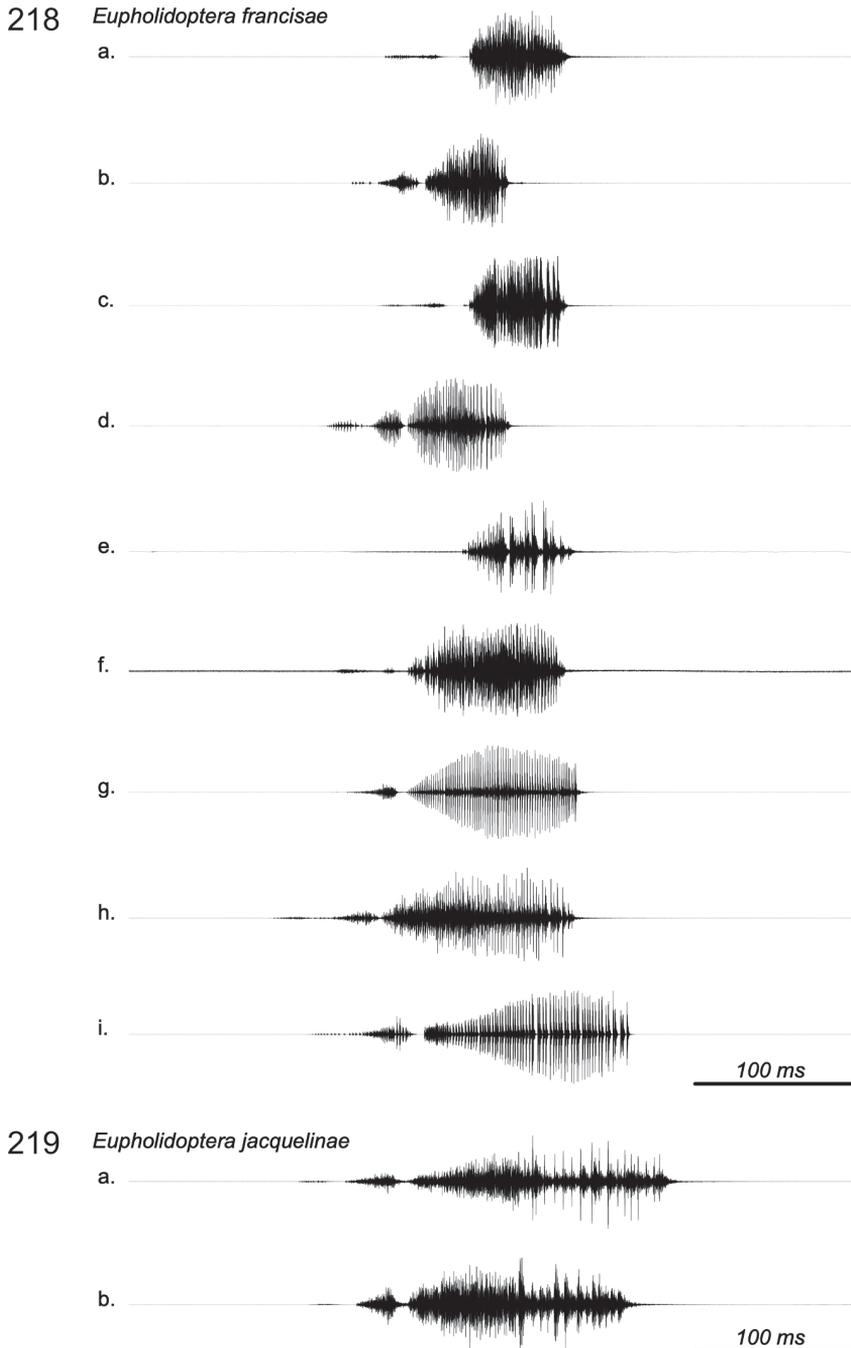
Figures 216, 217. Tip of male subgenital plate in ventral view **216** *Eupholidoptera francisae* sp. nov. paratype Anidhroi CT2001.002.01 **217** *Eupholidoptera francisae* sp. nov. paratype Anidhroi CT2001.002.0.

ern/southwestern Crete, the males and females of Andikithira in general have a larger body length and pronotum length; the males of Andikithira also possess a subgenital plate that is longer and wider than in those from Chania; the females of Andikithira have a subgenital plate that generally is wider than in those from Chania. Moreover, in females from Chania the length of the median incision of the hind margin of the subgenital plate is longer.

Differential diagnosis. The new species differs from all the other species of the genus by the shape of the strikingly elongated male subgenital plate. Within the *E. prasi-na* group (male cerci of most taxa possess no tooth) the new species belongs to the *E. latens* subgroup as its preapically situated short styli are downward directed in lateral view. *Eupholidoptera francisae* sp. nov. seems most related to *E. latens* by the shape and proportions of the male subgenital plate with the apical lobes provided with a tooth at its tip, the proportions of the stylus, the shape of the titillator and the ratio height-length of the hind femur (see Tables 6, 7 for measurements). A phylogeny based on molecular data also clearly separates *E. francisae* from *E. latens* (see discussion).

The male subgenital plate of *E. francisae* sp. nov. (Figs 146, 160) is larger and more elongated than in *E. latens* (Figs 144, 158). The stylus of *E. francisae* sp. nov. is 1.5× longer than wide, while in *E. latens* it is 2–3× longer than wide. The fused parts of the apical arms of the titillator of *E. francisae* sp. nov. (Fig. 189) are broad at base, not widening to the beginning of the unfused part, while in *E. latens* (Figs 186, 187) they are narrow at base and clearly widening to the beginning of the unfused part. The unfused part of the apical arms of the titillator of *E. francisae* sp. nov. is not spine-like, straight and only slightly to moderately curved upward to the dorsum. In contrast, in *E. latens* the unfused part is spine-like and in most specimens strongly hooked upward to the dorsum.

The females of *E. francisae* sp. nov. differ from the other taxa in the genus by the shape and proportions of the subgenital plate (Figs 45, 59). It can be distinguished from females of *E. latens* by the fact that in ventral view the incision of the



Figures 218, 219. Oscillograms of *Eupholidoptera* **218** Single syllables of nine specimens of *E. francisae* sp. nov., timescale 500 ms and temperature 25–27.7 °C **a** 2002.004.10 **b** 2002.004.09 **c** 2002.004.08 **d** 2002.004.07 **e** 2002.004.04 **f** 2002.004.07 **g** RMNH.5087052 **h** 2001.002.02 **i** RMNH.5106281 **219** single syllables of one specimen of *E. jacquelinae*, timescale 500 ms and temperature 23.9–24.5 °C **a, b** 2001.004.12.

hind margin is shaped in the form of a wide V, instead of slit-like or narrowly V-shaped as in *E. latens*; in profile the apex of the female subgenital plate of *E. francisae* sp. nov. does not reach or surpass the proximal half of the gonangulum, while in *E. latens* the apex reaches the distal half of the gonangulum or even surpasses it. For more details differentiating *E. francisae* sp. nov. from other Cretan Eupholidoptera, see Table 5.

Distribution. This new taxon has been found on the island of Andikithira situated some 32 km NW of Crete and also in the western and southwestern part of Chania in western Crete (Fig. 254). Andikithira is a geographically isolated island halfway between the island of Kithira in the northwest and Crete in the southeast. It is a small, dry, and stony island (20.43 km²) rising to not more than 378 meters above sea level. The island has only few tens of residents and is hardly visited by tourists.

In Chania populations of *E. francisae* sp. nov. have been encountered west and southwest from the line of Gramvousa peninsula (northwest coast) to Livadas (near the south coast and situated 3–4 km west of the famous Samaria Gorge). Worth mentioning is also the fact that several males and females of *E. francisae* sp. nov. were caught in 1997 in a pitfall trap near Piso Moni Preveli. This location a long way to the east along the southern coast of the Rethimno region is ~ 60 km (in a straight line) east of Livadas. Piso Moni Preveli is also situated near the eastern (sic!) boundary of *E. giuliae*. Why *E. francisae* sp. nov. occurs here and has not been found on intermediate locations is puzzling. A revisit to this location to confirm its presence is necessary to rule out a mistake of mislabelling. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. On Andikithira the species was found in phrygana and garrigue that cover a significant part of the entire island. Most specimens were collected as nymphs in *Sarcopoterium spinosum* that is present all over the island. The collecting sites are situated 50–150 m above sea level. But this species probably is present from sea level to the highest points of the island wherever phrygana and garrigue formations are present. On one of the collecting sites on Andikithira the new species was found together with the first specimen of *Rhacocleis andikithirensis* (Tilmans et al. 2016). On both collecting sites on Andikithira also *Poecilimon cretensis* or a new taxon closely linked to it (pers. obs.) was present. In southwestern Chania *E. francisae* sp. nov. was not only found in low prickly shrublets in phrygana, but also frequently on tall shrubs of blackberry (*Rubus*).

Etymology. Named in honour of Mrs. Francis Smid-Elbers, the late mother-in-law of the second author. Together with her husband Jacques Smid, she enthusiastically collected many interesting Orthoptera specimens in Greece, also from Crete. For instance, the paratype male and female of *E. giuliae* from 2.5 km E. of Argoules.

Phenology. On Andikithira most specimens were collected as nymphs becoming adult in the period 22 May–10 June. In Chania collected nymphs became adult in the period 26 May–6 June and adults were collected in the period 23 May–21 June. Adults of *Eupholidoptera francisae* sp. nov. can thus be encountered from the end of May throughout June to July and possibly even later.

***Eupholidoptera gemellata* Willemse & Kruseman, 1976**

Figs 12, 26, 40, 54, 70, 84, 98, 112, 127, 141, 155, 169, 183, 199, 232, 233, 255, Tables 1, 2, 5–7, 9, 10, Suppl. materials 1, 2

Eupholidoptera gemellata Willemse & Kruseman, 1976: 136.

Morphological description. Willemse and Kruseman 1976: 137.

Remark. The species was described after a single male was collected in 1973. Pitfall catches made in 2000–2001 at Mt. Psiloritis at 1950 m above Lochria and Agia Marina caught 11 males and 8 females. Opportunity is taken here to describe the female and illustrate important morphological structures with stacked images.

Examined specimens. Holotype, 3 ♂, 2 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 12) pale with two larger and two smaller dark dots; pronotal disc (Fig. 26) pale with irregular small or large black patches or largely blackish, posterior quarter to third pale; narrow band along anterior margin fourth to ninth abdominal tergites black. Male – stridulatory file with 101 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 22 teeth per mm; anal tergite (Figs 70, 84, 98) wide, distally bend downward centrally forming two inward pointing, overlapping, spines separated by short circular excision; cerci (Figs 112, 127) 4–5× longer than wide, conical, straight in profile and dorsal view, armed with inward curved inner sub-basal rectangular sidetooth; subgenital plate (Figs 141, 155) ca. as wide as long, proximally widest, sides rimmed except in apical quarter, in profile, narrowing, straight, pointing backward, tip apical lobes widely truncate with a protuberance on the inner margin and strong upward and backward pointing curved spine at base of stylus, with V-shaped excision along one third of total length; styli (Fig. 169) long, more than half as long as cerci, 3× longer than wide, conical, inserted at tip of apical lobe, pointing backwards; titillator (Figs 183, 199) symmetrical, weakly sclerotised, basal arms short, apical arms fused, in apical quart widened and split, tip truncate, unarmed in profile S-shaped from base to tip equally wide.

Description. Female. Examined specimens. 2 ♀: RETHIMNO: Psiloritis, above Lochria, FC1602 1♀ RMNH.INS1141844 (RMNH) 1♀ 2000.095.02 (CT). For more details, see Suppl. material 2.

General appearance and size as male (Figs 232, 233). Colouration as male. In dorsal view wings covered by pronotum, in profile hardly visible, light coloured. Cercus short, conical, slightly more than half as long as subgenital plate, straight in profile and in dorsal view, conical, tapering in apical third toward a pointed tip, densely covered with pale short and long hairs. Subgenital plate (Figs 50, 54) wider than long, in profile triangular, in ventral view trapezoid, basally widest, hind margin medially with wide shallow excision; surface basally and centrally convex, laterally flattened, thinly covered with hairs; ovipositor proximal two thirds straight, apical third slightly curved upward, 1.4–1.9× longer than pronotum.

Measurements. See Tables 6, 7.

Bioacoustics. The song of this species has not yet been recorded.

Differential diagnosis. Males differ from congeners in the stout, straight cercus (Figs 112, 127) with sub-basal rectangular side-tooth, in the subgenital plate (Figs 141, 155) narrowing into a truncate tip with upward and backward pointing spines, the inner margin of the excision with a protuberance, in the long, apically inserted styli (Fig. 169) pointing backward, in the anal tergite (Figs 70, 84, 98), medially bent downward forming a small circular excision adjoined by two partly overlapping, inward pointing spines and in the titillator (Figs 183, 199) with short basal arms and fused and adjoined apical arms with widened and truncated tip. Females differ in the wide, convexly rounded subgenital plate (Figs 50, 54), hind margin centrally with wide shallow excision. *Eupholidoptera gemellata* closely resembles *E. pallipes* but males differ in the apical arms of the titillator apically not being fused in *E. gemellata* (Fig. 183) and fused with small lateral spinelets in *E. pallipes* (Fig. 184). Females of both species differ in the shape and the hind margin of the subgenital plate (compare Fig. 40 with Fig. 41). In colouration *E. gemellata* is easily recognisable by the head with larger frontal black dots, the extensive blackening of the pronotal disc and narrow anterior transverse black band in the abdominal tergites. For more details differentiating *E. gemellata* from other Cretan *Eupholidoptera* see Table 5.

Distribution. The holotype was collected on Mt. Idi at 1650 m near the spring of Skaronero. Additional specimens collected in pitfall traps at a site northwest of Skaronero at 1950 m above Lochria between 15 September 2000 and 12 June 2001 (Fig. 255). For a complete list of localities, specimens, and repositories see Suppl. material 1.

Habitat. Rocky mountain slopes with phrygana.

Phenology. The holotype was collected at 1650 m on 28 July. The pitfalls that trapped the species were positioned at 1910 m and emptied on 15 September and 30 October 2000, and again on 12 June 2001.

Eupholidoptera giuliae Massa, 1999

Figs 16, 30, 44, 58, 74, 88, 102, 116, 131, 145, 159, 173, 188, 204, 220–223, 247, 248, 254, 256–259, Tables 1, 2, 5–10, Suppl. material 1–4

Eupholidoptera giuliae Massa, 1999: 72.

Morphological description. Massa 1999: 72–75; Willemse and Heller 2001: figs 8, 16, 23, 30, 45.

Examined specimens. 2 ♂, 1 ♀ (paratypes); 52 ♂, 30 ♀ (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 16) pale with black dots; frontal half of pronotal disc (Fig. 30) with extensive central black patch not reaching sides, border with pale rear half diffuse or distinct V-shaped. Male (Fig. 247) – stridulatory file with 106 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 23 teeth per mm; anal tergite (Figs 74, 88, 102) wide, centrally depressed, distally bend downward forming two pointed lobes pointing downward and slightly outward separated by wide excision; cerci (Figs 116, 131) unarmed,

5–6× longer than wide, basal half cylindrical, apical half conical almost straight to slightly curved inward, in profile straight; subgenital plate (Figs 145, 159) wider than long, widest in proximal third, sides rimmed in proximal half, in profile upturned, pointing upward, tip apical lobes rounded, spineless, at inner side emarginate with V-shaped excision along one seventh of length; styli (Fig. 173) minute, square to circular, as long as wide, inserted at internal margin of apical lobes proximal of tip, pointing inward to slightly downward; titillator (Figs 188, 204) symmetrical, apical arms proximally fused, halfway to two thirds diverging into two parallel or divergent, smooth hooks, in profile basal half distinctly wider than in ventral or dorsal view, halfway recurved, forming wide angle with beak-like evenly, weakly curved spines. Female (Fig. 248) – subgenital plate (Figs 44, 58) generally as long as wide, widest in proximal third, proximally with two distinct, dark-coloured concavities separated by a median ridge, tip apical lobes acute, rounded, separated by slit-like medial excision along one third to half the length, in profile triangular, ventrally and in proximal upper corner depressed.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of 5 specimens (50 syllables measured), the song of *E. giuliae* – as in all species of *Eupholidoptera* – consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. giuliae*, the syllable duration is ~ 199 ms, with a syllable rate up to ~ 1/s. There are no published descriptions of the song of this species. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera giuliae* see Suppl. material 3.

Variation. Along the south coast and more to the northeast up toward the town of Rethimno males show little variation in cerci, anal tergite, subgenital plate or titillator. Styli are small, mostly pointing inward but in some specimens somewhat downward. In the titillator the two apical arms are mostly divergent but sometimes almost parallel and close to each other. It is unclear whether such variation is structural, the result of the drying up process after killing or the age of the specimen in number of days after the final moult. Toward the northwest, in the municipalities of Chania and Apokoronas, male subgenital plates (Fig. 220) are longer than wide with long styli pointing downward (Fig. 221) resembling the subgenital plate in *E. latens*. A unique feature found in males from this area are the teeth bordering the medial excision in the hind margin of the anal tergite (Fig. 222) which are distinctly longer than in other areas. Notwithstanding differences in the subgenital plate and anal tergite, populations from Chania and Apokoronas have been assigned to *E. giuliae* because the titillator with its slender apical arms and long apical hooks (Fig. 223) perfectly fits this species. The morphological variation in *E. giuliae*, its geographical pattern and links to *E. latens*, are further elaborated in the discussion.

Differential diagnosis. Males differ from congeners in the wide, upturned, spineless subgenital plate (Figs 145, 159) with styli (Fig. 173) inserted at the inner margin of apical lobes pointing inward to slightly downward, in the anal tergite



Figures 220–223. Male terminalia *Eupholidoptera giuliae* complex **220** subgenital plate in ventral view Drapanos RMNH.5086980 **221** styli in lateral view Skloka CT2019.022.01 **222** anal tergite in caudal view Skloka CT2019.022.01 **223** titillator in lateral view Skloka CT2019.022.01 Scale bars: 1 mm.

(Figs 74, 88, 102) medially bent downward forming two widely separated lobes with tips pointing downward and slightly outward, in the slender, weakly inward bent, unarmed cerci (Figs 116, 131) and in the stout apical arms of the titillator (Figs 188, 204), fused in basal half, separated into two strong, long, parallel to diverging curved hooks. Females differ in the elongated subgenital plate (Figs 44, 58), proximally with two distinct concavities, apical lobes with slit-like excision along one third to half the length. In colouration, the amount of black shown by *E. giuliae* is intermediate between overall pale coloured species such as *E. cretica*, *E. jacquelineae* and *E. smyrnensis* and dark coloured species like *E. annamariae*, *E. astyla*, or *E. mariannae*. For more details differentiating *E. giuliae* from other Cretan *Eupholidoptera*, see Table 5.

Distribution. The species was described from Chora Sfakion and a site 2.5 km east of Argoules along the southwestern coast of Crete (Massa 1999; Çiplak et al. 2009). Additional data gathered over the past years indicate that *E. giuliae* occurs from the eastern part of the Chania regional unit to the western part of the Rethimno regional unit not only along the southern coast but across the island up to the northern coast (Fig. 254). The westernmost find of *E. giuliae* just south of Chania town is quite close to the easternmost find of *E. latens* from Lakki. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. Based on current data *E. giuliae* is a lowland species occurring from sea level up to some 500 m. It has been found in a variety of habitats ranging from very dry phrygana covered hills and *Quercus* forest, to rather wet lush vegetations including ferns.

Phenology. Adults of this species have been collected by hand from 10 May to 24 June. This is also the period during which most pitfall catches were made but at least in one instance *E. giuliae* adults were caught in a trap that had been set 20 August. This indicates that although adults may appear early in the season and may be most numerous in June, they can still be found until late August.

***Eupholidoptera jacquelineae* Tilmans, 2002**

Figs 24, 38, 52, 66, 82, 96, 110, 125, 139, 153, 167, 181, 197, 212, 219, 242, 254, 256, 259, Tables 1, 2, 5–7, 10, Suppl. material 1–4

Eupholidoptera jacquelineae Tilmans, 2002: 157.

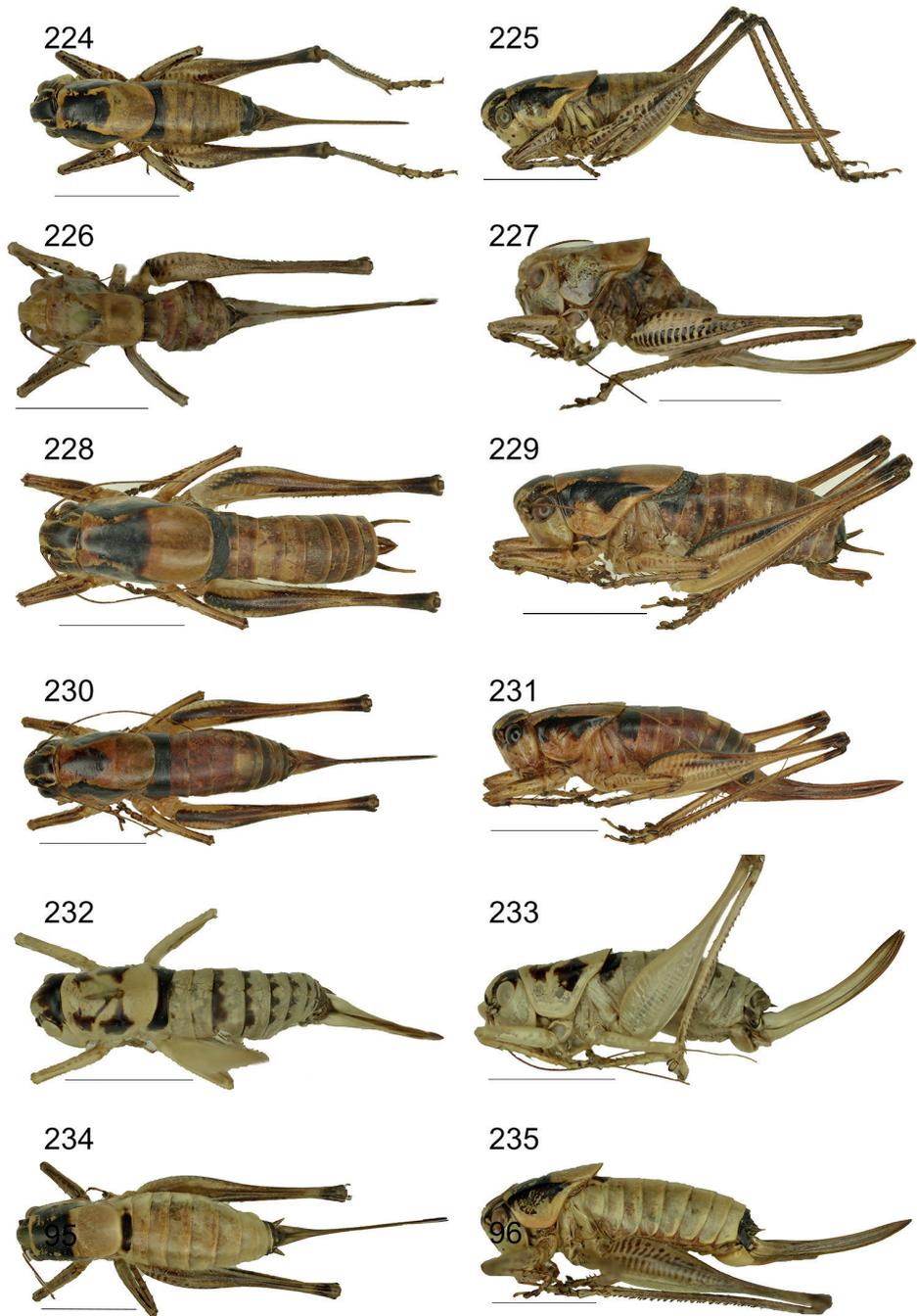
Morphological description. Tilmans 2002: 157.

Examined specimens. **Holotype, allotype**, 2 ♂ (paratypes); 4 ♂, 6 ♀ (for details see Suppl. material 2).

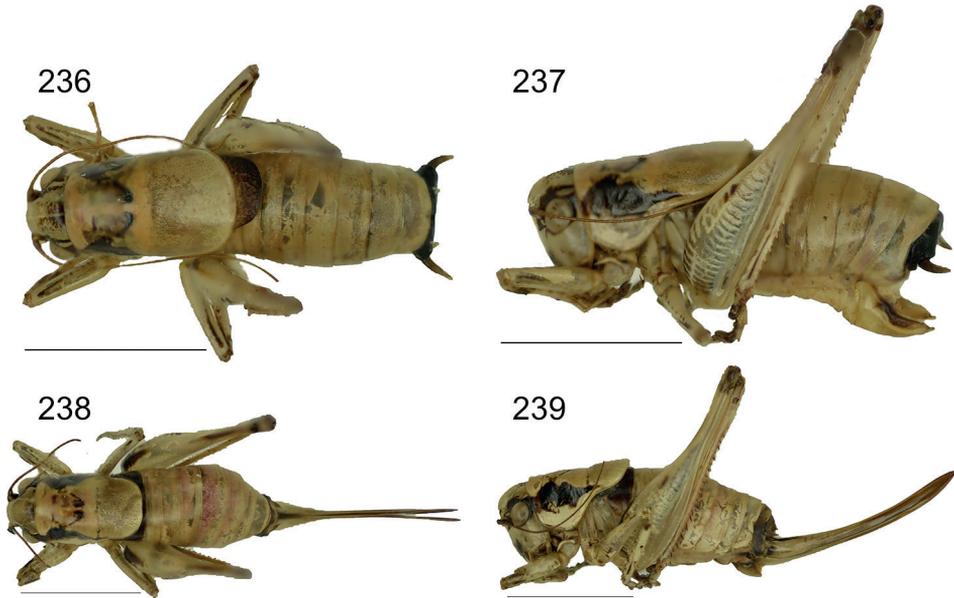
Diagnostics features. Frontal part of head (Fig. 24) pale with black dots. Pronotal dorsum (Fig. 38) brown to yellow, orange-brown flush with dark brown markings in middle of prozona, metazona yellow with brown flush, pronotal lateral lobes with black dorsal fascia, in prozona not sharply delimited ventrally and strongly narrowing posteriorly, rest of pronotal lateral lobes yellow with vague brown marks except for broad bright yellow margin in metazona; elytra area near the fore margin white, other parts black; anal tergite black, other tergites in living specimens brownish to olive-green; subgenital plate from cream white to bright yellow. Male – stridulatory file left elytron (paratype 2001.004.12): length 4.4 mm, width 0.1 mm, total number of teeth (including proximal and distal ones) 144, density of teeth in middle two thirds of the file 29 teeth per mm; cercus (Figs 125, 139) slender, 8–9× longer than wide, without any tooth, slightly bent inwards; subgenital plate (Figs 153, 167) in ventral view convex, remarkably slender with well-defined median keel and next to it on both sides a depression; strongly elongated apical lobes that (faintly discernible) pass into long styli that form an extension of the lobes; apex of the apical lobes dorsally armed with a sharp spine that covers the basis of the stylus (Fig. 181); anal tergite (Figs 82, 96, 110) in dorsal view with a round dorsomedian depression, in caudal view posterior margin triangularly extended ventrally with V-shaped medial excision, strongly curved frontally, provided with an apical tooth on either side, surface of processes with transverse wrinkles, depression and processes densely covered with golden-coloured hairs; titillator (Figs 197, 212) small, with basal parts extending, weakly curved laterally, apical parts fused, slightly swollen in basal half with medial depression, divided in apical half, from the narrow basis widening up to middle of basis half, from there narrowing apically, tips simply pointed, parallel, surface with transverse wrinkles, in lateral view moderately curved dorsally. Female (Fig. 242) – subgenital plate (Figs 52, 66) varying from longer than wide to somewhat wider than long, slightly impressed on both sides of median groove, in some females with transverse faint wrinkles, hind margin obliquely convergent toward a triangular, median excision along one third of total length, apical lobes diverging with narrowly posterior angles, lateral sides slightly impressed.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of one specimen, the song of *E. jacquelineae*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. jacquelineae*, the syllable duration is ~ 231 ms (Fig. 219). In the present two recordings, the syllable repetition rate is slower than 1/s. Although the recordings do not



Figures 224–235. Habitus *Eupholidoptera* spp. in dorsal and lateral view **224, 225** *Eupholidoptera astyla* ♀ Mt. Idhi CT1987.046.03 **226, 227** *Eupholidoptera cretica* ♀ Mt. Lefka Omalos FC17807 RMNH.INS1141837 **228, 229** *Eupholidoptera francisae* sp. nov. ♂ holotype Andikithira CT2002.004.04 **230, 231** *Eupholidoptera francisae* sp. nov. ♀ allotype Andikithira CT2002.004.11 **232, 233** *Eupholidoptera gemellata* ♀ Mt. Idhi FC1651 RMNH.INS1141844 **234, 235** *Eupholidoptera mariannae* ♀ Ag. Ioannis RMNH5014906 1844. Scale bars: 10 mm.



Figures 236–239. Habitus *Eupholidoptera marietheresae* sp. nov. in dorsal and lateral view **236, 237** ♂ holotype Mt. Dikti FC1606 RMNH.INS1141850 **238, 239** ♀ allotype Mt. Dikti FC1606 RMNH.INS1141849. Scale bars: 10 mm.

permit detailed analysis, it seems that the first part of the closing hemisyllable contains a more densely series of teeth impacts and the second part a more loosely series. This would suggest the closing movement initially is fast but ends slowly. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera jacquelineae* see Suppl. material 3.

Variation. For the description of *E. jacquelineae* in 2002 only three males and one female from Gavdos were available. At present more specimens are at hand, also from the islet of Gavdopoula. We compared seven males (5 from Gavdos and 2 from Gavdopoula) and seven females (also 5 from Gavdos and 2 from Gavdopoula). The males, compared with the holotype, show no differences in colour, marking, last abdominal tergite, subgenital plate with styli, cercus, or titillator (from three males). The females, however, compared to the allotype, show some variation in marking and the form of the subgenital plate. Most of the females show more black markings on the lateral lobes of the pronotum than the allotype, but even then, less markings than in the males. A bit more than half of the females studied possesses a subgenital plate that is not longer than wide as in the allotype, but as long as wide or even a little bit wider than long. In one female from Gavdos and one of Gavdopoula the median groove of the subgenital plate fades away toward the basis. In a small number of the females the subgenital plate show faint transverse wrinkles.

Differential diagnosis. Male *E. jacquelineae* is differentiated from all other (Cretan) *Eupholidoptera* by its uniquely shaped, strongly elongated apical lobes of the subgenital plate (Figs 153, 167) armed with a long apical spine that dorsally covers the basis of



Figures 240–246. Field images *Eupholidoptera* spp. Crete **240** *Eupholidoptera annamariae* ♂ Kata Zakros CT1995.0530 **241** *Eupholidoptera astyla* ♂ Mt. Idhi CT2004.08.14 **242** *Eupholidoptera jacquelinae* ♀ Gavdos **243** *Eupholidoptera francisae* sp. nov. ♂ paratype Andikithira CT2002.004.07 **244** *Eupholidoptera francisae* sp. nov. ♀ paratype Andikithira CT2002.004.12 **245** *Eupholidoptera francisae* ♂ paratype Maroulia RMNH5087052 **246** *Eupholidoptera francisae* ♀ paratype Maroulia RMNH5014917.

the long styli that form an extension of the lobes. Females differ in the subgenital plate (Figs 52, 66), that is a bit longer than wide to a little wider than long combined with a medial incision of its hind margin measuring more than one third of the length of the subgenital plate. In colouration *E. jacquelinae* is one of the Cretan *Eupholidoptera* species with no or only minute black marking on the pronotal disc. For more details differentiating *E. jacquelinae* from other Cretan *Eupholidoptera* see Table 5.

Distribution. Restricted to the islets of Gavdos and Gavdopoula, south of western Crete (Fig. 254). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The habitats where the species was found consists of rocky ground with sparse vegetation of low trees (*Pinus brutia*), thorny shrubs and smaller plants as well as sand dunes with *Pistacia*, *Juniperus*, and *Tamarix*. The male specimens of *E. jacquelinae*



Figures 247–253. Field images *Eupholidoptera* spp. Crete **247** *Eupholidoptera giuliae* ♂ Prasies RMNH5087051 **248** *Eupholidoptera giuliae* ♀ Rethymnon RMNH5014921 **249** *Eupholidoptera latens* ♂ Kolympari RMNH553681 **250** *Eupholidoptera mariannae* ♂ Kalavros RMNH5014907 **251** *Eupholidoptera mariannae* ♀ Ag. Ioannis RMNH5014906 **252** *Eupholidoptera pallipes* ♀ below Pakhnes **253** *Eupholidoptera smyrnensis* ♂ Makrigiannis RMNH5087053.

were collected by hand on bushes of *Erica manipuliflora*, *Pistacia*, *Tamarix*, and *Pinus* but not on prickly bushes like *Juniperus* or *Sarcopoterium spinosum*, a spiny shrublet very common on Crete but much less so on Gavdos. The females however were found hiding under the low spiny shrubs of *Euphorbia acanthothamnus*. Trap catches on Gavdos and Gavdopoula recorded the species between 8 and 270 m.

Phenology. The holotype male together with a paratype male was collected on 11 June at 50 m. The allotype female together with another paratype male was collected as nymph in the period 30 April to 2 May, becoming adult 25 May. Additional females were collected on 5 August. Specimens were found in traps emptied between mid-March and mid-November.

***Eupholidoptera latens* Willemse & Kruseman, 1976**

Figs 15, 29, 43, 57, 68, 73, 87, 101, 115, 130, 144, 158, 172, 186, 187, 202, 203, 249, 254, 256–259, Tables 1–10, Suppl. materials 1–4

Eupholidoptera latens Willemse & Kruseman, 1976: 134.

Morphological description. Willemse and Kruseman 1976: 134, 135.

Bioacoustics. Çiplak et al. 2009: 27, 51, 54, 55.

Examined specimens. Holotype, allotype, 4 ♂, 3f (paratypes); 12 ♂, 7 ♀ (for details see Suppl. material 2).

Diagnostics features. Frons (Fig. 15) pale with black dots; pronotal disc (Fig. 29) rarely completely pale, mostly frontal half with more or less well defined black central patch, border with pale rear half. V-shaped. Male (Fig. 249) – stridulatory file with 108–123 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 26–31 teeth per mm; anal tergite (Figs 73, 87, 101) centrally depressed, distally bend downward, forming two lobes with teeth like apex pointing downward, separated by wide excision; cerci (Figs 115, 130) unarmed, 6–7× longer than wide, in basal half conical, in apical half cylindrical, slightly curved inward in basal half, in profile straight to weakly upturned; subgenital plate (Figs 144, 158) longer than wide, widest in proximal third, tapering and distinctly narrower in distal two thirds, sides rimmed in proximal third, in profile pointing backward, tip apical lobes rounded, spineless, with narrow median excision along one quarter of length its proximal half narrower; styli (Fig. 172) short, one quarter as long as cerci, 2–3× longer than wide, round or flattened, inserted at ventral side of apical lobes, proximal of tip, pointing downward; titillator (Figs 186, 187, 202, 203) symmetrical, apical arms fused, parallel to slightly widening toward apical third inflated, diverging into two straight diverging hook-like teeth, in profile basal two thirds parallel, in second third swollen forming wide angle with two weakly upward curved hook-like teeth. Female – subgenital plate (Figs 43, 57) generally slightly wider than long, proximally with two concavities separated by keel, tip apical lobes rectangular, rounded, with slit-like to narrow V-shaped excision reaching one third to halfway, in profile rhomboid, upper distal angle rectangularly rounded.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of nine specimens (49 syllables measured), the song of *E. latens*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. latens*, the syllable duration is ~ 228 ms, with a syllable rate up to ~ 1/s. Published records (Çiplak et al. 2009) show a syllable duration of ~ 161 ms and a syllable repetition rate of ~ 0.5/s at maximum. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera latens* see Suppl. material 3.

Variation. *Eupholidoptera latens* is restricted to the northern and central Chania region in western Crete. The cerci and anal tergite show little variation across its range.

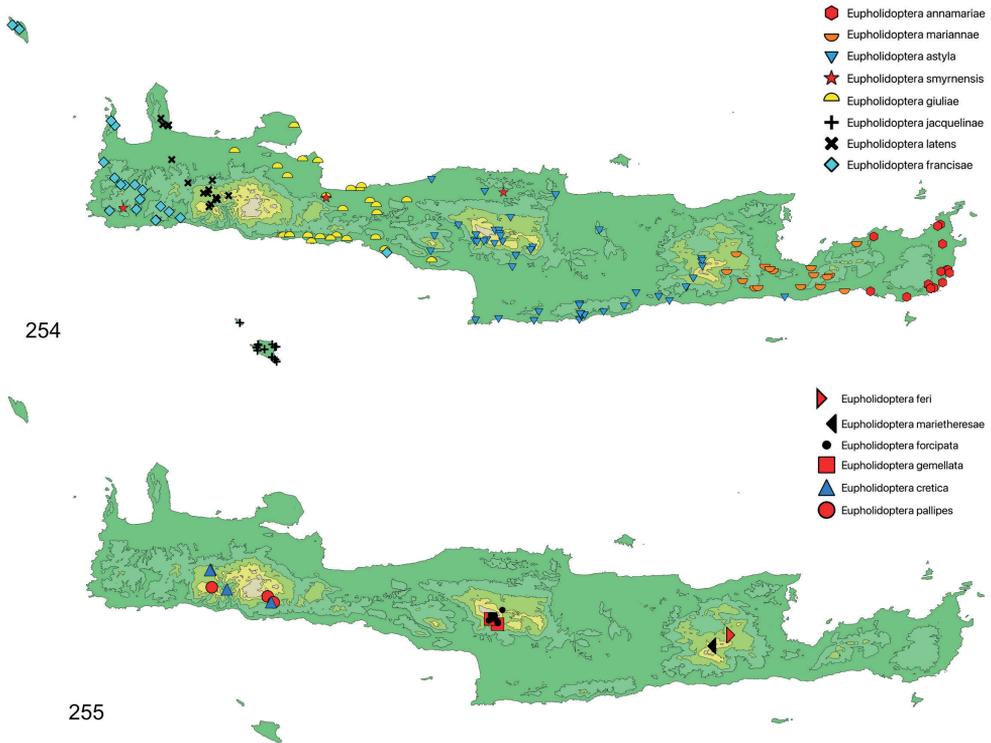
Titillators in males from the Rodopou peninsula (Figs 187, 203) are relatively slender, with longer apical hooks, being intermediate between *E. latens* and *E. giuliae*. In males, morphological variation is most pronounced in the subgenital plates. In males from Kolympari, Rodhopos, and Kato Kefalia in central and northern Chania, as well as in the outlier found in Rethimno the subgenital plate is clearly more slender than in the populations of the Lefka area, the transition between the wide basal part and the narrow apical part generally being more distinct. The morphological variation found in *E. latens*, *E. giuliae*, and *E. francisae* sp. nov. is further elaborated in the discussion.

Differential diagnosis. Males differ from congenetics in the stout apical arms of the titillator (Figs 186, 187, 202, 203), fused in basal half, separated into two strong, short, parallel or diverging curved hooks in the elongated, in the slender subgenital plate (Figs 144, 158) narrowing at one third of the length, the apical lobes without a teeth at its apex and with short styli (Fig. 172), inserted pre-apically pointing downward, the anal tergite (Figs 73, 87, 101) medially bent downwards forming two widely separated lobes with short pointed tips pointing downward and in the slender, unarmed, weakly inward and upward bent cerci (Figs 115, 130). *Eupholidoptera latens* most closely resembles *E. francisae* sp. nov. but differs in the shape of the subgenital plate (compare Fig. 144 with Fig. 146), the length-width ratio of styli, the shape of the titillator (compare Figs 186, 187 with Fig. 189), body size and the ratio height-length of the hind femur (see Tables 3, 4 for measurements). Females differ in the subgenital plates (Figs 43, 57) being as long as wide, proximally with two concavities, slit-like to narrow V-shaped excision between the apical lobes reaching halfway. They can be distinguished from females of *E. francisae* by the fact that in ventral view the incision of the hind margin in *E. francisae* is shaped in the form of a wide V; in profile the apex of the female subgenital plate in *E. latens* reaches the distal half of the gonangulum or surpasses it (Fig. 68) while in *E. francisae* it does not reach or surpass the proximal half of the gonangulum (Fig. 67). In colouration, the amount of black shown by *E. latens* is intermediate between overall pale coloured species like *E. cretica*, *E. jacquelineae* and *E. smyrnensis* and dark-coloured species like *E. annamariae*, *E. astyla*, or *E. mariannae*. For more details differentiating *E. latens* from other Cretan *Eupholidoptera* see Table 5.

Distribution. The species was discovered in 1973 at high altitudes on Mt. Lefka, western Crete and published records from this species originated only from this mountain and its foothills (Lakki). Specimens collected between 2016 and 2019 indicate the species also occurs at low altitudes in the northern and northeastern parts of Chania region (Fig. 254). To the east the distribution area of *E. latens* borders to but is separated from *E. giuliae*. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The species occupies habitats from sea level to alpine regions between 1600 and 1800 m on Mt. Lefka. It hides in low prickly shrublets in the phrygana while at lower altitudes it was also found on shrubs of blackberry (*Rubus*) or gorse (*Ulex*).

Phenology. At low altitudes adults appear around mid-May, at mid-level elevations toward the end of May or early June whereas at high altitudes it may take to the second half of July before the first adults appear.



Figures 254, 255. Distribution maps *Eupholidoptera* Crete and adjacent islands **254** lowland species **255** highland species.

Eupholidoptera mariannae Willemse & Heller, 2001

Figs 21, 35, 49, 63, 79, 93, 107, 122, 136, 150, 164, 178, 194, 209, 214, 215, 234, 235, 250, 251, 254, 256, 259, Tables 1, 2, 5–7, 10, Suppl. materials 1–4

Eupholidoptera mariannae Willemse & Heller, 2001: Willemse et al. 2018: figs 946, 947. Morphological description. Willemse and Heller 2001: 329–331.

Bioacoustics. Willemse and Heller 2001: 331; Çiplak et al. 2009: 27, 54, 55.

Examined specimens. Holotype, 1 ♂ (paratype); 8 ♂, 15 ♀ (for details see Suppl. material 2).

Diagnostic features. Frons (Fig. 21) pale with black dots; frontal half of pronotal disc (Fig. 35) predominantly black sharply with transverse rarely a V-shaped border with pale rear half; elytra black, veins and cross-veins more or less extensively yellow. Male (Fig. 250) – stridulatory file with 89–105 teeth (90 in Çiplak et al. 2009) (including proximal and distal ones), density of teeth in middle two thirds of the file 18–23 teeth per mm (18–20 in Çiplak et al. 2009); anal tergite (Figs 79, 93, 107) very wide, bilobed, lobes separated by groove, distally bend downward, centrally forming two teeth pointing forward separated by narrow, densely haired pits; cerci (Figs 122, 136)

3× longer than wide, proximally wide, flattened, strongly narrowing in second third, apical third cylindrical, pointing outward, in profile bent upward, armed with short, strong inner side-tooth at ca. one fifth of length; subgenital plate (Figs 150, 164) as wide as long, widest in proximal third, sides rimmed, in profile pointing upward and backward, tip apical lobes rounded, spineless, with slit-like excision along one fifth of length; styli (Fig. 178) minute, flat or depressed, inserted at ventral side of apical lobes, proximal of tip, pointing downward; titillator (Fig. 194, 209) slightly asymmetrical, apical arms strongly sclerotised, narrow, except for very tip, fused along entire length, smooth, needle shaped tip pointing somewhat laterad, in profile narrow, middle third slightly wider evenly upward curved.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of two specimens (20 syllables measured), the song of *E. mariannae*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. mariannae*, the syllable duration is ~ 172 ms. In the present recordings, the syllable repetition rate is very low. Published records (Çiplak et al. 2009) show a syllable duration of ~ 123 ms and a syllable repetition rate of 1/s at maximum. The song may most likely be confused with the other species of *Eupholidoptera* in Crete, except *E. smyrnensis* and *E. forcipata*. For details of sound recordings of *Eupholidoptera mariannae* see Suppl. material 3.

Variation. Apical arms of the titillator in most specimens are fused, in some they become apically somewhat separated. The central pits in the anal tergite may be more or less well developed and more or less densely haired.

Description of female. Examined specimens. 15 ♀: LASITHI: Agios Ioannis – RMNH.5014906 (RMNH); Anatoli – s.n. [paratype of *E. astyla* Ramme 1927] (MfNB); Kalavros -2017.029.02 (CT) RMNH.5014912, RMNH. 5086974 (RMNH); Katharo plain, 1 km NE FC17787 – RMNH.INS1124470, RMNH. INS1124471 (RMNH); Kato Chorion s.n. [paratype of *E. astyla* Ramme 1927] (MfNB); Kavousi – 1999.029.02 (CT), RMNH.INS1141830 (RMNH); Koutsouras – 2002.007.05 (CT); Prina, 0.5 km N FC17798 – 2019.061.02 (CT), RMNH. INS1141839 (RMNH); Mt. Thrypti – 2019.032.01 (CT), FC25104 RMNH. INS1124469 (RMNH). (For details see Suppl. material 2).

General appearance and colouration as male (Figs 234, 235, 251). First abdominal segment dorsally darkened, in one female black; second segment may also be somewhat darkened. Fore wings covered by pronotum, in profile barely protruding, pale coloured.

Cercus short, conical hardly tapering but for apical third which is distinctly narrower, tip pointed, slightly upturned in profile, straight in dorsal view, covered with pale short and long hairs.

Subgenital plate (Figs 49, 63) longer than wide, mitre-shaped, in profile triangular; hind margin toward middle forming two distinct pointed apical lobes, separated by a deep and wide excision along one third of length; dorsal margin usually at least partly visible in the apical half as a protruding edge or bulge, in profile the apical half straight, the basal half straight except for the proximal part which is concave; ventral side proxi-

Table 5. Diagnostic characters and character-states for *Eupholidoptera* species from Crete, Andikithira, Gavdos, and Gavdopoula.

Structure	1			2			3		4				5		6				7			
Character	a	b	c	a	b	c	a	b	a	b	c	d	a	b	a	b	c	d	a	b	c	d
Species																						
<i>annamariae</i>	1	3	1	2	2	2	2	1	1	2	1	1	1	1	2	1	1	1	1-3	2	1	1
<i>astyla</i>	1	3	1	1	1	1	3	1	1	1	1	1	1	1	3	1	3	1	3-4	2	1	1
<i>cretica</i>	1	1	1	1	3	3	2	1	1	2	1	1	3	2	1	1	2	2	1	3	2	1
<i>feri</i>	1	3	1	1	1	1	2	3	1	1	1	1	1	1	2	1	2	1	4	2	1	2
<i>forcipata</i>	1	1	1	2	3	1	1	1	1-2	3	1	1	2	2	1	1	3	1	1	1	2	3
<i>francisae</i>	1	2	1	1	2	1	3	1	3	2	1	1	1	1	1	1	3	2	1-3	3	2	2-3
<i>gemellata</i>	3	3	3	1	1	2	2	3	1-3	2	2	2	2	2	1	2	2	2	1	1	2	1
<i>giuliae</i>	1	2	1	1	2	1	3	1	1-3	1	1	1	1	3	1	1	3	2	2-4	3	1	3
<i>jacquelineae</i>	1	1	1	2	2	1	3	1	3	3	2	1	3	2	1	1	3	2	3-4	3	1	1
<i>latens</i>	1	2	1	1	2	1	3	1	(1)-3	2	1	1	2	1	1	1	3	2	2	3	1	2-3
<i>mariannae</i>	1	3	1	1	1	3	1	3	2	1	1	1	1	1	2	1	3	1	3-4	2	1	2-3
<i>marietheresae</i>	3	1	1	2	3	1	1	1	1	3	1	1	2	2	1	1	3	1	1	2	2	3
<i>pallipes</i>	3	3	3	1	1	2	2	3	2	2	2	2	2	2	1	2	1	2	2	1	2	1
<i>smymensis</i>	2	1	2	1	3	1	1	2	2	3	3	2	2	2	1	1	3	2	3	2	2	1
1. Male and Female colouration																						
a. frons	1. dots (Fig. 12); 2. mosaic (Fig. 11); 3. black patch (Fig. 13)																					
b. pronotal disc	1. pale (Fig. 28); 2. small patch (Fig. 29); 3. large patch (Fig. 32)																					
c. abdomen	1. pale (Fig.10); 2. black dot (Fig. 8); 3. black edge (Fig. 9)																					
2. Male anal tergite																						
a. extended backwards	1. not/hardly; 2. distinctly																					
b. excision tips	1. narrow; 2. intermediate; 3. wide																					
c. direction tips	1. downward; 2. inward; 3. forward																					
3. Male cercus																						
a. length-width ratio	1. < 5; 2. 5-6.5; 3. > 6.5																					
b. side tooth	1. missing; 2. basal; 3. sub-basal																					
4. Male subgenital plate																						
a. length-width ratio	1. < 1; 2. ca. 1; 3. > 1																					
b. length excision-total length ratio	1. 0.1-0.25; 2. 0.3-0.4; 3. 0.5-0.6																					
c. spine	1. absent; 2. one; 3. two																					
d. protuberance	1. absent; 2. present																					
5. Male styli																						
a. length-width ratio	1. 1.0-2.0; 2.0-3.0; 3. > 4.0																					
b. direction	1. downward; 2. backward; 3. inward																					
6. Male titillator																						
a. symmetry	1. symmetrical; 2. subsymmetrical; 3. asymmetrical																					
b. basal arms	1. long; 2. short																					
c. apical arms	1. merged; 2. largely merged; 3. free for > 1/3																					
d. apical arms	1. basal half stalk-like; 2. basal half wide																					
7. Female subgenital plate																						
a. length-width ratio	1. < 0.75; 2. 0.75-0.90; 3. 0.90-1.10; 4. >1.10																					
b. length excision-total length ratio	1. < 0.25; 2. 0.25-0.33; 3. > 0.33																					
c. medial excision	1. narrow; 2. wide																					
d. proximally	1. convex; 2. concave; 3. with 2 concavities																					

mally with two dark coloured concavities separated by a more or less distinct keel, the apical half flattened to shallowly depressed with a median keel, surface smooth without wrinkles, with dispersed hairs.

Ovipositor almost straight, apically slightly upcurved, 1.4–2.2× longer than pronotum.

Differential diagnosis. Males differ from congeners in the stout, upturned, proximally flattened cercus, pointing outward (Figs 122, 136), sub-basally armed with short strong inner tooth, in the anal tergite (Figs 79, 93, 107) medially not extended, bent downward with very narrow V-shaped excision, tips pointing forward, in the wide, upturned, spineless subgenital plate (Figs 150, 164) with minute, pre-apically inserted styli (Fig. 178) pointing downward and in the barely asymmetrical, narrow, fused apical arms of the titillator (Figs 194, 209). Females differ from congeners in the elongated subgenital plate (Figs 49, 63) proximally with two concavities, apical lobes pointed, separated by wide excision, as deep as one third of the length. In colouration, the amount of black shown, *E. mariannae* together with *E. annamariae*, *E. astyla*, *E. feri*, and *E. francisae* sp. nov. belongs to the darkest coloured species. For more details differentiating *E. mariannae* from other Cretan *Eupholidoptera* see Table 5.

Distribution. The species was described from southwestern Lasithi. Recent findings indicate its distribution area also includes western central Lasithi from the eastern slopes of Mt. Dikti eastward up to Kalavros in the north and Koutsouras in the south (Fig. 254). In the east there seems to be no overlap with *E. annamariae* although near Kalavros and Xerokampos both species were found within 5 km of each other. *Eupholidoptera mariannae* and *E. astyla* may overlap in the Ierapetra area but up to now co-occurrence could not be confirmed. In the northwest, *E. mariannae* was also found in the Katharo plain where *E. feri* was discovered. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. The altitudinal range of *E. mariannae* is considerable. It ranges from sea level where it was found near Koutsouras, to 1475 m, the highest altitude at which it was found on Mt. Thrypti. The type series was found inside open pine forest and groups of planted olive trees. Near Kalavros the species was found on open hill slopes with quite a dense vegetation of small shrubs interspersed with taller shrubs. Near Kavousi (Pacheia Amos) the species was trapped on a hill covered by phrygana. Around Malles and Anadoli individual males were heard singing on the branches of olive trees a few meters above the ground.

Phenology. At low altitudes adults can be found already in early May, at higher altitudes starting from 300–700 m up to 1475 m, adults appear in June or July and have been caught until the end of September and mid-October.

***Eupholidoptera marietheresae* Willemse & Kotitsa, sp. nov.**

<https://zoobank.org/8119FA55-0B62-4158-8323-C64A5E307A9F>

Figs 23, 37, 51, 65, 81, 95, 109, 124, 138, 152, 166, 180, 196, 211, 236–239, 255, 256, Tables 2, 5–7, 9, 10, Suppl. materials 1, 2, 4

Remark. Pitfall catches collected on Mt. Dikti at a site above the Limnakaro plateau trapped a total of 127 specimens of *Eupholidoptera* which at first glance were identified as *E. forcipata*. Closer examination however revealed differences with *E. forcipata* based on which a species new to science is described here.

Examined specimens. Type locality. GREECE, Crete, Lasithi, Dikti Mt., above Limnakaro plateau, SE of Ag. Anastasi mountain refuge, SW Spathi Madharas, 35.1107°N, 25.4779°E, 1715 m

Type specimens. Holotype ♂, RMNH.INS1141850, **allotype** ♀, RMNH.INS1141849. Both pinned (from alcohol) with original label: "Dikti Mt., above Limnakaro plateau, SE of Ag. Anastasi mountain refuge, SW Spathi Madharas. FC1606"; FC1606 operated between 05/08/2000–02/10/2000 (RMNH)

Paratypes. 1 ♂ RMNH.INS11418546 (pinned from alcohol), 1 ♂ RMNH.INS1124467 (alcohol), 3 ♀ RMNH.INS1141847, RMNH.INS1141848, RMNH.INS1141849 (pinned from alcohol), 1 ♀ RMNH.INS1124468 (alcohol) (RMNH); 2 ♂ 2000.096.01, 2000.096.03 2 ♀ 2000.096.02, 2000.096.04 (pinned from alcohol (CT), same location and date as holotype (for details see Suppl. material 2).

Additional specimens (not examined). 40 ♂, 37 ♀ in alcohol (NHMC) LASITHI: Dikti Mt., above Limnakaro plateau, SE of Ag. Anastasi mountain refuge, SW Spathi Madharas, 35.1107°N, 25.4779°E, 1715 m, FC1606, 05/08/2000–02/10/2000; 17 ♂, 24 ♀ in alcohol (NHMC) same as holotype, FC1536 12/05/2000–05/08/2000; 2 ♀ in alcohol (NHMC) same as holotype, FC1655 02/10/2000–09/01/2001.

Description. Male. General appearance (Figs 236, 237) as type species *E. chabrieri*, more compact. Pronotum hardly widening posteriorly, metazona relatively short, hind margin slightly convex. Legs short and thick, hind femur 1.7–1.9× as long as pronotum (2.0–2.2 in *E. chabrieri*), mid and hind femur ventrally unarmed.

Stridulatory file with 211–216 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 37–42 teeth per mm.

Anal tergite (Figs 81, 95, 109) in dorsal view narrow in the middle, laterally widening, in the middle folded downward, centrally forming large pale coloured hairy patch in the centre, laterally with striae, hind margin somewhat swollen, from the ventro-lateral corner folded around cerci, extending straight down- and inward, toward the middle forming two wide downward pointing lobes with toothlike tip separated by a wide excision.

Cercus (Figs 124, 138) compact, unarmed, conical, weakly and gradually curved inward in basal half, in profile slightly upturned, 4× as long as the greatest width.

Subgenital plate (Figs 152, 166) very compact, 1.5× wider than long, widest at one third of the length, proximal margin slight concave; in profile compact, lower margin straight ca. halfway bent upward, hardly narrowing apically, apical part pointing upward in situ covering last abdominal segment; ventral surface with a strong median keel, proximal half depressed next to the keel, halfway transversely depressed, apical half divided into two flattened triangular lobes, tip straight truncated, without a spine, surface irregularly gibbose, laterally with straight rod-like protuberances; lateral margin in ventral view a folded back rim, thickened near the base, apically disappearing under the rod-like protuberances, in profile straight with a proximal nod; posterior margin with a very wide V-shaped median excision along more than half the total length, edges straight toward the middle weak convex. Styli (Fig. 180) short, 2× longer than wide, conical, inserted at the tip of the apical lobes pointing backward and upward.

Titillator (Figs 196, 211) symmetrical, apical arms in dorsal/ventral view in lower half narrow, almost stalk-like apically widening, swollen, two apical arms diverging

into two very long and slender hooks, smooth except for some wrinkles, near the apex curved inward; in profile stalk like basal half weakly S-curved, transition with apical half distinct, apical hooks evenly curved backward and upward, reaching or extending above the anal tergite.

General colouration (based on specimens kept in alcohol) yellowish brown. Head with the frontal part below antennae and eyes pale with two black dots (Fig. 23), the lower part frons and upper part clypeus with large transverse black patch, upper part around the eyes and antennal sockets black, occiput behind the eyes and in the middle with black patches. Pronotal disc (Fig. 37) pale yellowish with central black markings at best resembling an open “W” or frontal half with large central black patch forming transverse or V-shaped border with pale rear half; lateral lobes with wide black dorsal fascia, not sharply delineated ventrally, posteriorly narrowing not reaching the hind margin. Elytra black. Fore and middle legs with few black dots and stripes, concentrated around the knee. Hind femur dorsally with black basal patch and apical black stripe, outer side near the base with or without a series of transverse stripes, pre- and post-genicular part black. Anal tergite black, subgenital plate laterally below the dorsal margin black.

Female. General appearance (Figs 238, 239) as male. Elytra clearly visible in profile. Cercus conical, hairy, bent inward, narrowing in apical fifth, apex pointed. Subgenital plate (Figs 51, 65) shiny, smooth with very few hairs, 1.5× wider than long, greatest width in proximal third; in ventral view, convex with a median ridge, proximally with two distinct, dark coloured concavities, apically flattened, hind margin with a wide acute V-shaped median excision along one third of the length, corners obtuse rectangular; in profile oblong, ventrally with a distinct basal depression and more shallow apical depression, lower edge convex, distally upturned, tip obtuse angular. Ovipositor 2.0–2.4× as long as pronotum, straight, in apical quart weakly upturned. Colouration as the male, transverse black patch at the transition between frons and clypeus more pronounced; elytra pale; first abdominal segment black.

Measurements. See Tables 6, 7.

Bioacoustics. The song of this species has not yet been recorded.

Differential diagnosis. Males differ from congeners in the pointed back- and downwardly extended widened lobes of the anal tergite (Figs 81, 95, 109) with tips pointing downward and slightly outward, in the wide upturned, spineless subgenital plate (Figs 152, 166) with a very wide V-shaped excision, in the short, apically inserted styli (Fig. 180) pointing backward, in the stout, weakly inward curved cerci (Figs 124, 138) and the symmetrical apical arms of the titillator (Figs 196, 211), in basal half fused and narrow, in apical half strongly diverging hooks. Females differ from congeners in the very wide subgenital plate (Figs 51, 65), proximally with two concavities, tips rounded with U-shaped excision along quarter of the length. *Eupholidoptera marietheresae* sp. nov. closely resembles *E. forcipata* but differs in the male by the thin, apically incurved apical arms of the titillator, the compact weakly incurved cercus lacking the subtle bulge halfway the inner side and the anal tergite with wider downward expansion combined with a narrower excision and in the female in a more elongated subgenital plate, with the proximal pits being close together. In colouration, *E. marietheresae* sp. nov. differs from all Cretan congeners except *E. pallipes* in the

large transverse black patch on the lower part of the frons. For more details differentiating *E. marietheresae* sp. nov. from other Cretan Eupholidoptera see Table 5.

Distribution. Only known from a single location on Mt. Dikti above the Limnakaro plateau where the species was trapped in pitfall traps (Fig. 255). For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. Mountain slopes at 1700 m in phrygana vegetation.

Phenology. Pitfall traps in which the species was found were checked irregularly. Based on the three catching periods, adults can be found prior to early August up to at least early October.

Etymology. The species is named in honour of Marie-Therèse Willemse-Dresen (1929–2017) wife and lifelong companion of Fer Willemse who contributed a large part of his entomological career to the study of the Orthoptera fauna of Greece, describing 40 species new to science from Greece, including four Cretan species of Eupholidoptera. In his last, and most challenging, paper on *Chorthippus* (*Glyptobothrus*) from Greece (Willemse et al. 2009) he wrote in the acknowledgements:

“This publication would not have been possible without help from my family. My wife’s patience and tolerance to my single-minded enthusiasm was almost boundless. Both the long hours spent during our travels in seemingly dull and uninteresting areas, as well as at home recording and studying have been accepted without much ado. For that I owe her an enormous amount of gratitude.”

It is in this spirit that we pay a tribute to Marie-Therèse. The fact that *E. marietheresae* sp. nov. is found on the same mountain and in the vicinity of *E. feri*, a species named after Fer Willemse, is making it even more appropriate.

***Eupholidoptera pallipes* Willemse & Kruseman, 1976**

Figs 9, 13, 27, 41, 55, 71, 85, 99, 113, 128, 142, 156, 170, 184, 200, 252 255, Tables 1, 2, 5–7, 10, Suppl. materials 1, 2

Eupholidoptera pallipes Willemse & Kruseman, 1976: 135.

Morphological description. Willemse and Kruseman 1976: 135, 136.

Examined specimens. Holotype, allotype, 5 ♂ (paratypes) (for details see Suppl. material 2).

Diagnostic features. Frontal part of head (Fig. 13) pale with two large black patches joined or not into a transverse band; pronotum (Fig. 27) pale except for small black patch in the rear of the side flap; abdomen pale, proximal margins tergites black. Male – stridulatory file with 94 teeth (including proximal and distal ones), density of teeth in middle two thirds of the file 22 teeth per mm; anal tergite (Figs 71, 85, 99) wide with central groove, distally bend downward, forming two spines pointing downward and inward almost touching each other separated by rectangular excision; cerci (Figs 113, 128) 5× longer than wide, cylindrical, central third conical, weakly curved inward and upward, armed with sharply pointed inward curved sub-basal tooth; subgenital plate (Figs 142, 156) as wide as long, proximally widest, sides rimmed al-

Table 6. Measurements (in mm), ratios, and biometrics of male *Eupholidoptera*.

Males	Body length	Pronotum length	Hind femur length	Hind femur width	Ratio length-width hind femur	Number of teeth
<i>annamariae</i>	<i>n</i> = 23	<i>n</i> = 23	<i>n</i> = 23	<i>n</i> = 23	<i>n</i> = 23	<i>n</i> = 1
mean ± SD	28.3±2.1	11.3±0.5	21.3±0.8	4.8±0.2	4.43±0.16	
min. – max.	25.0–32.2	10.5–13.1	19.6–22.8	4.4–5.1	4.16–4.81	109
<i>astyla</i>	<i>n</i> = 79	<i>n</i> = 79	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 2
mean ± SD	25.5±2.4	9.9±1.0	19.5±2.0	4.5±0.4	4.34±0.17	
min. – max.	21.0–30.8	8.2–12.2	16.2–23.0	3.9–5.3	3.77–4.74	101–105
<i>cretica</i>	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	
min. – max.	21.7	8.8	22.1	4.4	5.04	107
<i>feri</i>	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	
min. – max.	26.8	8.8	18.6	4.0	4.61	100
<i>forcipata</i>	<i>n</i> = 20	<i>n</i> = 20	<i>n</i> = 20	<i>n</i> = 20	<i>n</i> = 20	<i>n</i> = 1
mean ± SD	23.4±1.6	9.5±0.5	17.8±0.7	4.3±0.2	4.18±0.11	
min. – max.	20.8–26.7	8.6–10.5	16.6–19.6	4.0–4.7	3.96–4.43	193
<i>francisae</i>	<i>n</i> = 38	<i>n</i> = 38	<i>n</i> = 37	<i>n</i> = 37	<i>n</i> = 37	<i>n</i> = 19
mean ± SD	24.1±2.7	9.5±0.7	21.1±0.9	4.3±0.3	4.88±0.25	119±10.3
min. – max.	19.0–28.8	8.0–10.7	19.0–23.1	3.7–4.9	4.47–5.49	96–138
<i>gemellata</i>	<i>n</i> = 3	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 4	<i>n</i> = 1
mean ± SD	21.1±3.9	7.4±0.3	17.1±0.2	4.0±0.1	4.32±0.10	
min. – max.	16.8–24.2	7.0–7.7	16.8–17.3	3.9–4.1	4.17–4.45	101
<i>giuliae</i>	<i>n</i> = 52	<i>n</i> = 52	<i>n</i> = 52	<i>n</i> = 52	<i>n</i> = 52	<i>n</i> = 1
mean ± SD	24.5±3.2	10.2±0.5	21.7±0.8	4.7±0.2	4.66±0.24	
min. – max.	17.2–30.2	9.1–11.4	20.0–23.8	4.0–5.0	4.26–5.43	106
<i>jacquelineae</i>	<i>n</i> = 6	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 1
mean ± SD	27.4±2.5	10.6±0.3	24.8±1.1	4.8±0.2	5.14±0.36	
min. – max.	25.3–32.1	10.2–11.2	23.8–26.4	4.4–5.1	4.86–5.98	144
<i>latens</i>	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 13	<i>n</i> = 4
mean ± SD	22.4±2.6	9.1±0.5	19.3±2.3	4.3±0.2	4.53±0.37	113±7.1
min. – max.	18.9–27.1	8.4–9.9	17.0–22.7	3.9–4.8	4.14–5.28	108–123
<i>mariannae</i>	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 4
mean ± SD	24.4±2.2	10.1±0.4	21.2±0.9	4.6±0.3	4.65±0.17	
min. – max.	21.5–28.9	9.5–10.9	19.8–22.3	4.2–4.9	4.36–5.00	89–105
<i>marietheresae</i>	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 2
mean ± SD	24.9±2.7	9.4±0.6	17.1±0.6	4.0±0.2	4.30±0.14	
min. – max.	21.4–28.5	8.9–10.3	16.4–18.1	3.8–4.2	4.04–4.45	211–213
<i>pallipes</i>	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 1
mean ± SD	20.3±1.0	7.7±0.3	16.9±0.6	4.1±0.1	4.18±0.13	
min. – max.	19.3–21.9	7.4–8.1	16.5–18.0	3.9–4.2	3.92–4.32	94
<i>smymensis</i>	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 1
mean ± SD	20.2±1.6	9.8±0.4	23.3±0.6	4.5±0.1	5.24±0.19	
min. – max.	17.5–22.6	9.5–10.3	22.4–24.0	4.3–4.6	4.92–5.48	100

most up to apex, in profile distally narrowing, straight, pointing backward, tip apical lobes truncate with protuberance on the inner margin and strong upward and backward pointing curved spine at base of stylus, with V-shaped excision along one third of total length; styli (Fig. 170) long, more than half as long as cerci, 3× longer than wide, cylindrical, inserted at tip of apical lobes, pointing backward and outward; titillator (Figs 184, 200) symmetrical, weakly sclerotised, basal arms short, apical arms completely fused, widening in basal third, gradually narrowing in apical two thirds, near

Table 7. Measurements (in mm), ratios, and biometrics of female *Eupholidoptera*.

Females	Body length	Pronotum length	Hind femur length	Hind femur width	Ratio length-width hind femur	Ovipositor length	Ratio length ovipositor-length pronotum
<i>annamariae</i>	<i>n</i> = 24	<i>n</i> = 24	<i>n</i> = 24	<i>n</i> = 24	<i>n</i> = 24	<i>n</i> = 24	<i>n</i> = 24
mean ± SD	25.6±2.6	10.8±0.5	21.7±0.6	4.9±0.2	4.48±0.14	19.0±1.1	1.76±0.09
min. – max.	21.7–32.2	10.2–12.1	20.4–22.8	4.6–5.2	4.20–4.81	17.0–21.2	1.63–2.05
<i>astyla</i>	<i>n</i> = 59	<i>n</i> = 59	<i>n</i> = 59	<i>n</i> = 59	<i>n</i> = 59	<i>n</i> = 59	<i>n</i> = 59
mean ± SD	23.8±2.8	9.6±1.1	20.1±2.1	4.5±0.4	4.41±0.19	17.3±1.9	1.80±0.13
min. – max.	17.8–30.7	7.9–11.9	16.8–23.8	3.8–5.2	3.77–4.89	14.0–20.9	1.42–2.16
<i>cretica</i>	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
min. – max.	22.2–24.2	9.1–9.6	21.4–22.4	4.6–4.9	4.36–4.87	18.1–18.2	1.86–1.99
<i>feri</i>	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
min. – max.	27.8	9.6	21.7	4.9	4.43	16.1	1.67
<i>forcipata</i>	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14
mean ± SD	24.2±2.7	9.5±0.8	19.0±1.9	4.4±0.4	4.38±0.27	17.9±0.8	1.90±0.14
min. – max.	21.6–30.8	8.3–11.00	16.6–22.8	4.0–5.3	3.96–5.04	16.7–19.6	1.63–2.12
<i>francisae</i>	<i>n</i> = 38	<i>n</i> = 38	<i>n</i> = 37	<i>n</i> = 37	<i>n</i> = 37	<i>n</i> = 38	<i>n</i> = 38
mean ± SD	24.1±2.4	9.6±0.6	22.2±1.0	4.5±0.2	4.93±0.28	16.6±1.4	1.73±0.11
min. – max.	19.5–31.5	8.5–10.5	20.9–24.9	4.1–5.1	4.55–5.62	13.8–19.3	1.52–1.99
<i>gemellata</i>	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 2
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
min. – max.	20.5–22.1	7.4–10.0	16.5–22.4	4.2–4.6	3.93–4.92	13.8–14.2	1.42–1.86
<i>giuliae</i>	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 30	<i>n</i> = 30
mean ± SD	24.2±2.7	10.3±0.4	22.3±0.9	4.8±0.2	4.65±0.19	17.7±1.5	1.73±0.15
min. – max.	18.7–29.8	9.4–10.9	21.1–24.2	4.5–5.4	4.38–5.13	15.7–21.2	1.45–2.12
<i>jacquelineae</i>	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7	<i>n</i> = 7
mean ± SD	28.3±2.9	10.6±0.4	26.2±0.8	5.3±0.1	4.96±0.16	20.3±0.9	1.91±0.09
min. – max.	24.9–33.6	10.2–11.1	25.2–27.5	5.1–5.4	4.74–5.29	19.4–21.8	1.76–2.04
<i>latens</i>	<i>n</i> = 8	<i>n</i> = 8	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 8	<i>n</i> = 8
mean ± SD	20.3±2.3	98.7±0.5	18.8±1.9	4.3±0.3	4.40±0.25	14.9±0.8	1.72±0.05
min. – max.	17.5–23.3	8.1–9.4	17.1–22.9	3.9–4.8	3.98–4.77	13.8–16.4	1.64–1.79
<i>mariannae</i>	<i>n</i> = 15	<i>n</i> = 15	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 14	<i>n</i> = 15	<i>n</i> = 15
mean ± SD	22.4±2.8	8.9±1.0	19.0±2.4	4.3±0.3	4.43±0.27	15.9±1.2	1.80±0.22
min. – max.	19.1–27.5	7.5–10.3	16.5–22.8	3.9–4.9	3.92–4.74	13.6–17.5	1.41–2.23
<i>marietheresae</i>	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6
mean ± SD	23.6±3.3	8.3±0.7	18.5±2.1	4.2±0.2	4.36±0.39	17.9±1.1	2.15±0.14
min. – max.	20.5–28.8	7.4–9.5	16.6–22.6	3.9–4.4	3.95–5.16	15.9–18.9	1.98–2.38
<i>pallipes</i>	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1	<i>n</i> = 1
mean ± SD	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
min. – max.	21.7	9.5	23.8	4.6	5.23	13.5	1.43
<i>smyrnsis</i>	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5	<i>n</i> = 5
mean ± SD	20.0±1.8	9.9±0.3	23.6±0.9	4.6±0.1	5.18±0.18	17.6±0.8	1.78±0.12
min. – max.	17.5–22.6	9.5–10.3	22.4–24.7	4.4–4.7	4.92–5.48	16.6–18.6	1.61–1.96

tip widening again, tip rounded at either side with a tiny thorn, in profile equally wide, straight, in apical half weakly curved upward. Female (Fig. 252) – subgenital plate (Figs 41, 55) as long as wide, proximally convex, apical lobes rectangularly rounded separated by wide concave median excision along quarter of total length, in profile rhomboid, apically truncate, upper angle widely rounded.

Measurements. See Tables 6, 7.

Bioacoustics. The song of this species has not yet been recorded.

Differential diagnosis. Males differ from congeners in the stout, straight cerci (Figs 113, 128) with a sub-basal rectangular side-tooth, in the subgenital plate (Figs 142, 156) narrowing into truncate tips with an upward and backward pointing spine, a protuberance on the inner margin of the excision, in the long, apically inserted, backward pointing styli (Fig. 170), in the anal tergite (Figs 71, 85, 99), medially bent downward forming an excision adjoined by two inward and downward pointing spines and in the titillator (Figs 184, 200) with short basal arms and completely fused apical arms, apically widened, tip rounded at either side with a tiny thorn. Females differ from congeners in the subgenital plate (Figs 41, 55), as long as wide, convex hind margin centrally with wide excision a deep as quarter of the length. *Eupholidoptera pallipes* closely resembles *E. gemellata* but males differ in the apical arms of the titillator apically being fused in *E. pallipes* (Figs 184, 200), its tip with a tiny lateral thorn, in *E. gemellata* (Figs 183, 199) being adjoined the tip being bare. Females of both species differ in the shape and the hind margin of the subgenital plate (compare Figs 40, 41). In colouration *E. pallipes* differs from congeners, except *E. gemellata*, in the general pale colouration in particular of the legs and the narrow anterior transverse black band in the abdominal tergites (Fig. 9). For more details differentiating *E. pallipes* from other Cretan *Eupholidoptera* see Table 5.

Distribution. The type series was collected in 1973 on Mt. Lefka at the saddle of Linoseli above Xyloskalo between 1600 m and 1800 m. Additional specimens were collected in pitfall traps operated in the summer of 1991 more to the east on Mt. Lefka above Limnia (Fig. 255). On 13 October 2017 a female was photographed just below the Pakhnes peak at 2440 m. For a complete list of localities, specimens and repositories see Suppl. material 1.

Habitat. Rocky mountain slopes with phrygana between 1600 and 2440 m.

Phenology. The type series was collected 5 August 1973. Pitfalls above Limnia trapped adults between early August and early September and during the entire month of October whereas a trap operated between early June and early July only contained nymphs.

Eupholidoptera smyrnensis (Brunner von Wattenwyl, 1882)

Figs 8, 11, 25, 39, 53, 69, 83, 97, 111, 126, 140, 154, 168, 182, 198, 253, 254, 256, 259, Tables 2, 5–7, 9, 10, Suppl. materials 1–4

Thamnotrizon smyrnensis Brunner von Wattenwyl, 1882: 336.

Olythoscelis smyrnensis (Brunner von Wattenwyl, 1882): Bolivar 1899: 601.

Pholidoptera smyrnensis (Brunner von Wattenwyl, 1882): Ebner 1919: 157.

Eupholidoptera smyrnensis (Brunner von Wattenwyl, 1882): Ramme 1951: 198.

Morphological description. Brunner von Wattenwyl 1882: 336; Willemse 1980: 59.

Bioacoustics. Heller 1988: 132; Çiplak et al. 2009: 27, 54.

Examined specimens. 9 ♂, 5 ♀ (for details see Suppl. material 2).

Diagnostics features. Frontal part of head (Fig. 11) pale, dark spots enlarged and merged into a mosaic pattern; pronotal disc (Fig. 25) completely pale chestnut brown;

abdomen pale, each tergite with tiny central dot on hind margin. Male (Fig. 253) – stridulatory file with 78 teeth (including proximal and distal ones) (Çiplak et al. 2009 report a stridulatory file with 100 teeth), density of teeth in middle two thirds of the file 19 teeth per mm; anal tergite (Figs 69, 83, 97) oblong, distally bend downward forming two strong spines pointing downward, separated by a very wide semi-ellipsoid excision; cerci (Figs 111, 126) 3× longer than wide, basal half conical, apical half cylindrical, curved inward, in profile straight, armed with strong basal inner side-tooth; subgenital plate (Figs 140, 154) ca. as wide as long, halfway widest, sides unrimmed, in profile distally narrowing, straight, pointing backward, tip apical lobes emarginate with protuberance at inner margin and two small upward pointing teeth, with V-shaped median excision along half the total length; styli (Fig. 168) long, one third as long as cerci, 2–3× longer than wide, cylindrical, inserted at ventro-outer tip of apical lobes, pointing distad and outward; titillator (Figs 182, 198) symmetrical, apical arms mostly fused, from narrow base plate-like expanded, apically divided into two long parallel or diverging spines, in profile moderately upcurved. Female – subgenital plate (Figs 39, 53) as long as wide, in ventral view strongly convex, hind margin converging to two pointed apical lobes separated by wide V-shaped excision a third to a quarter as deep as the total length, in profile triangular, upper and lower margin converging to a pointed apex.

Measurements. See Tables 6, 7.

Bioacoustics. Based upon the sound recordings of one specimen (10 syllables measured) from Crete, the song of *E. smyrnensis*, as in all species of *Eupholidoptera*, consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In *E. smyrnensis*, the syllable duration is ~ 40 ms, the shortest in Cretan *Eupholidoptera*. In the present recordings, the syllable repetition rate is 2/s at maximum. The song is also characterised by syllables that are produced in compact series of 3–10s followed by a longer silence after which another series follows. The first few syllables in a series are weaker than the following ones. This pattern has so far not been found in other species of *Eupholidoptera* in Crete. Recordings from other Greek Islands (Rhodes and Naxos) and published by Çiplak et al. (2009) show a comparable syllable duration (35–45 ms) and repetition rate (2–3/s). For details of sound recordings of *Eupholidoptera smyrnensis* from Crete see Suppl. material 3.

Differential diagnosis. Males differ from congenics in the stout, inward curved cerci (Figs 111, 126) with a strong basal side-tooth, in the subgenital plate (Figs 140, 154) slightly narrowing, tips with two small upward pointing teeth, the inner margin of the excision with a protuberance, in the long, apically inserted, backward pointing styli (Fig. 168), in the anal tergite (Figs 69, 83, 97) medially bend downward forming two strong, widely separated, downward pointing spines and in the fused wing-like expanded basal part of the apical arms of the titillator (Figs 182, 198), apically divided into two long parallel or diverging spines. Females differ from congenics in the strongly convex subgenital plate (Figs 39, 53) with narrow, acute apical lobes, hind margin with wide excision as deep as a quarter or third of the length. In colouration *E. smyrnensis* differs from its Cretan congenics in the black dots on the frons of the head merged into a mosaic pattern (Fig. 11), the unicolourous pale pronotal disc and

a tiny central black dot along the hind margin of the abdominal tergites (Fig. 8). For more details differentiating *E. smyrnensis* from other Cretan *Eupholidoptera* see Table 5.

Distribution. *Eupholidoptera smyrnensis* is one of the most widespread species of the genus. Its range covers western Anatolia and the southern Balkan (southern Bulgaria, southeastern Republic of North Macedonia, and north-western Greece) (Çiplak et al. 2009). Beside mainland Greece it has also been reported from a number of Aegean islands to the north (Thasos, Limnos), east (Samos, Nisyros, and Rhodes) as well as Evvoia (Monnerat et al. 1999: 65) and more to south from the Cyclades islands of Tzia (Willemse and Willemse 2008) and Naxos (unpublished data 2019). Much to our surprise, a single large population was discovered in 2017 in a small neglected patch of agricultural land full of blackberries (*Rubus*) amidst olive orchards southeast of Doxaro and west of the hamlet of Makrigiannis, central Crete in the lowlands south of the Taleon Mts. The species was collected again in 2019 in the southwestern most corner of Crete near the village of Lagkadas. Furthermore, pitfall catches from 1996 and 1997 revealed the presence of the species near Kavallios at the edge of Limni Kourna (Fig. 254). Cretan *E. smyrnensis* are smaller than mainland *E. smyrnensis*, but overall colour pattern and shapes of cercus, anal tergite, subgenital plate, and titillator fit with *E. smyrnensis* from other parts of Greece. For a complete list of localities, specimens, and repositories see Suppl. material 1.

Habitat. Although on the Greek mainland *E. smyrnensis* is found up to 1200 m, in Crete, it has only been found between 25 m and 340 m. Unlike most other *Eupholidoptera* species in Crete, *E. smyrnensis* is not found in spiny shrubs on the ground but lives in taller spiny bushes like blackberries (*Rubus*).

Phenology. Based on hand and pitfall catches *E. smyrnensis* becomes adult in June and near Limni Kourna adults have still been trapped after 20 August, probably being active well into September and possibly October.

Phylogenetic analysis

The aligned concatenated dataset, which consisted of 1684 bp including 375 variable and 292 parsimony informative sites, involved ten ingroup and two outgroup taxa (respectively 36 ingroup and two outgroup haplotypes). The NADH2 fragment consisted of 855 bp including 353 variable and 279 parsimony informative sites, and the ITS had 829 bp with gaps, with 22 variable and 13 parsimony-informative sites. No numt signs were detected in alignments of protein-coding sequences, and the saturation tests did not show signs of significant saturation. Best substitution models for the partitioned dataset were as follows: NADH2, positions 1 and 2 – gamma, position 3 – gamma+ invariable sites; ITS – proportion of invariable sites.

Our phylogenetic analysis provided well resolved phylogeny of the studied taxa, showing strong support for all nodes (Fig. 256).

The taxa *E. latens*, *E. giuliae*, *E. francisae*, and *E. astyla* form a monophyletic lineage that splits into two major clades. The first clade contains all specimens occurring in western and southwestern Chania and Andikithira, showing very low genetic distances to each other (see also Fig. 258: yellow dots). The second clade is formed by three

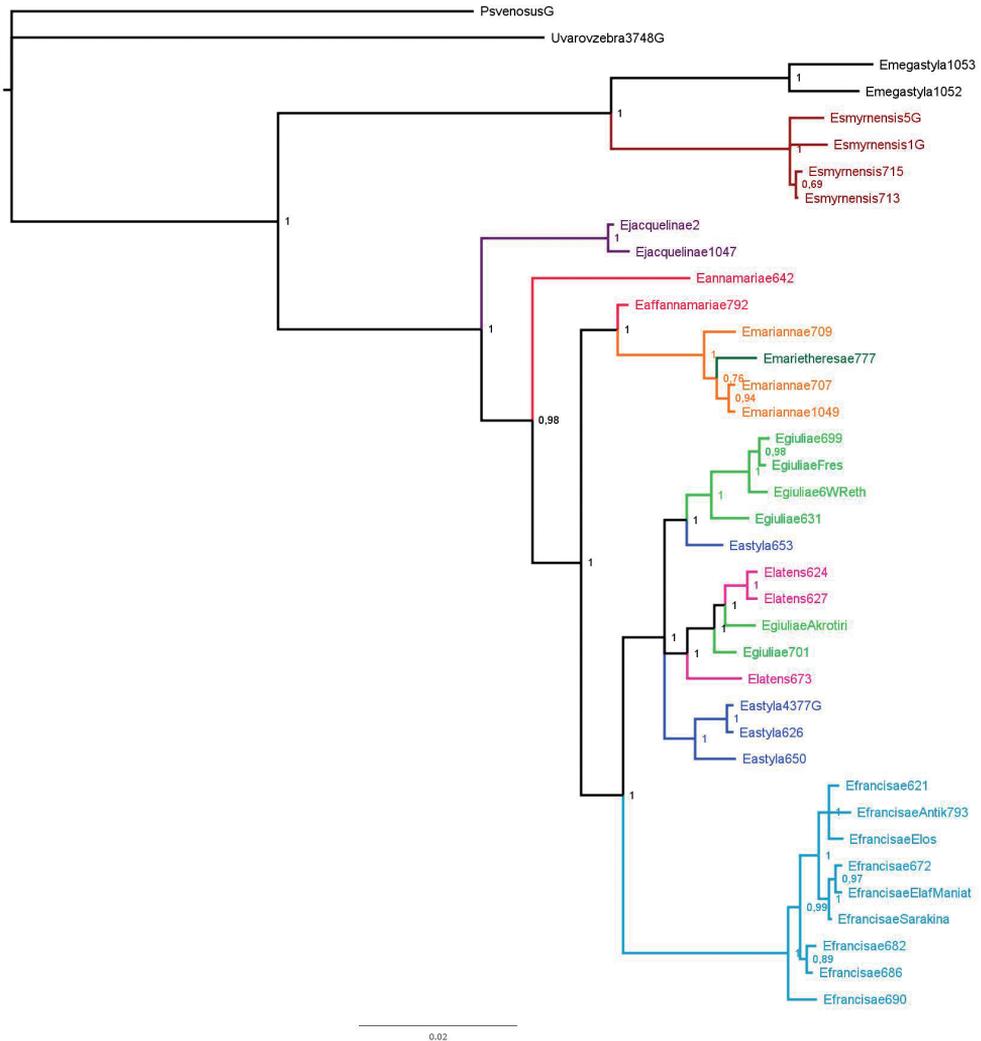


Figure 256. Bayesian inference phylogenetic tree of *Eupholidoptera* of Crete, Andikithira and Gavdos, including two outgroups and congeners from the Greek and Turkish mainlands, based on a 1684bp concatenated alignment of the NADH2 + ITS fragments. Node values at branches show node support with BI posterior probabilities. Different colours correspond to the different morphological species. See Suppl. material 4 for details of the specimens and Suppl. material 5 for details of NADH2 and ITS sequences.

sub-clades: (1) most of *E. giuliae* samples (Fig. 258: dark blue dots), (2) *E. latens* s.str. (Fig. 258: purple dots) + some *E. giuliae* samples (Fig. 258: light blue dots), and (3) the *E. astyla* samples.

Some Cretan species appear to be paraphyletic: *E. marietheresae* is nested within *E. mariannae* despite their large morphological differences; an *E. annamariae* specimen found at the boundary of the *E. annamariae* and *E. mariannae* distributions appears to be more closely related to *E. mariannae* than to *E. annamariae*, despite its distinct morphology; and an *E. astyla* specimen is more closely related to *E. giuliae* than to other *E. astyla*s.

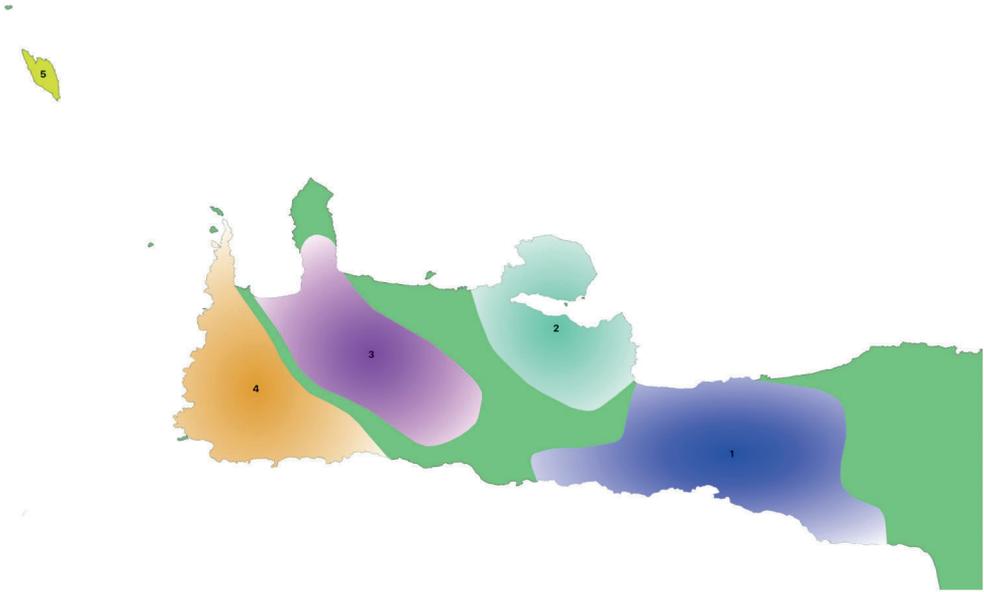


Figure 257. The *Eupholidoptera giuliae-latens-francisae* complex: geographic distribution of five morphological entities in the *Eupholidoptera giuliae-latens-francisae* complex: (1) eastern Chania + western Rethimno (*E. giuliae*), (2) northeastern Chania including Akrotiri peninsula (atypical *E. giuliae*), (3) northern and central Chania (*E. latens*), (4) western and southwestern Chania (*E. francisae*), (5) Andikithira (*E. francisae*).

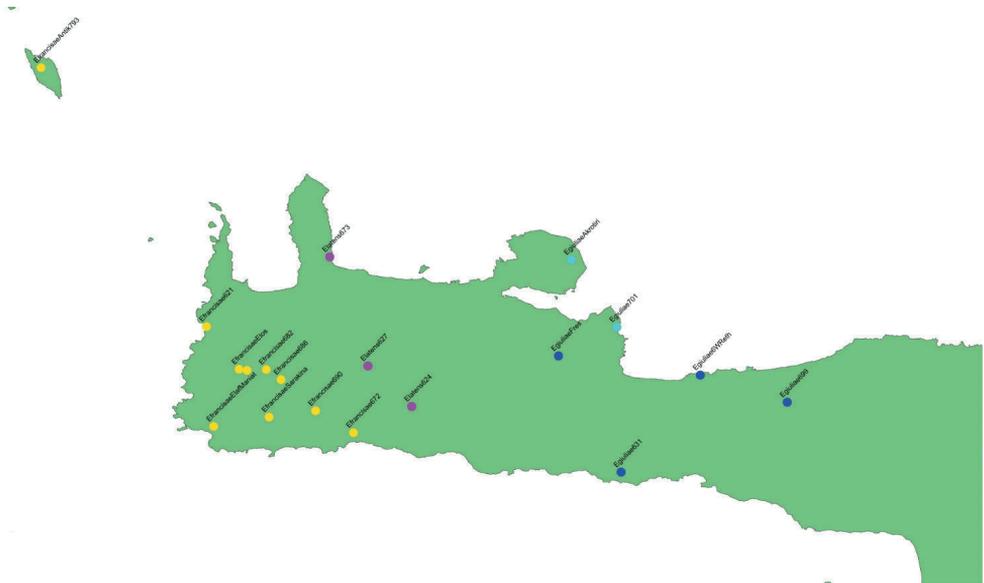


Figure 258. Distribution results genetic analysis: geographic pattern of analysis of genetic data of *Eupholidoptera* populations in western Crete. yellow dots: *E. francisae*, purple dots: *E. latens*, blue dots: *E. giuliae*, light blue dots: atypical *E. giuliae*.

The position of *E. marietheresae* inside the *E. mariannae* clade is an interesting observation, given their distinct morphological differences. Additional study is required, including the incorporation of *E. forcipata* sequences in the phylogenetic tree (the species morphologically closest to *E. marietheresae*), of more *E. marietheresae* specimens, and additional molecular (mostly nuclear) markers, in order to decipher the relationship between these species. Here it should be mentioned that the molecular results from Çiplak et al. (2021, 2022) do not support all hypotheses. From the few species studied there they suggest a relationship ((*latens*, *forcipata*)+(*giuliae*, *astyla*)), with a split between both groups ~ 2.5 Mya (Çiplak et al. 2022).

Eupholidoptera jacquelineae, the endemic of the island of Gavdos, is the basalmost taxon of the Cretan clade. The only non-endemic *Eupholidoptera* on Crete, *E. smyrnensis*, is nested firmly within conspecifics from Anatolia. It should be noted that the nuclear fragment (ITS) showed very low interspecific variability. As a result, the topography of the concatenated tree is mostly influenced by the mitochondrial gene NADH2.

Discussion

Together with western and southern Anatolia, Crete is a biodiversity hotspot for *Eupholidoptera* (Çiplak et al. 2009, 2010). This publication adds to the systematics, taxonomy, and faunistics of the genus in Crete and adjacent islands. For all species many new specimens, sound recordings, and distribution data have become available. This made it possible to describe all known species in detail, among which are two new species. The distribution patterns resulting from the new data confirmed disjunct distribution areas between some species but also provided evidence for the sympatric occurrence of others, and differences in altitudinal preferences became more evident. New data allowed for a better assessment of both infraspecific and intraspecific variation. This in turn led to questions about the species concept and potential evolutionary driving forces behind the present variation. These and other aspects of *Eupholidoptera* from Crete and adjoining islands are discussed in more detail below.

The *E. latens*–*E. giuliae*–*E. francisae* complex

The current study revealed that based on morphological traits *E. giuliae*, *E. latens* and *E. francisae* may share a complex phylogeographical relationship.

Based on the shape of the anal tergite, subgenital plate, stylus and titillator of the male, five subgroups can be distinguished in western Crete and Andikithira (Table 8, Fig. 257). The first subgroup is found along coastal areas in the municipality of Sfakia in the southeastern part of Chania extending east into southern Rethimni and reaching northwards across the island to the region around the town of Rethimni (Fig. 257: area 1). Males are characterised by a wide central excision in the hind margin of the anal tergite bordered by short teeth, a wide subgenital plate with short inward pointing styli and compact apical arms of the titillator ending in long hooks. This group matches the

Table 8. Morphological differences across the *E. latens*-*E. giuliae*-*E. francisae* complex (see Fig. 257).

Subgroups	Anal tergite excision-teeth	Subgenital plate	Styli	Titillator
1. Eastern Chania + western Rethimni	wide-short	compact	short-inward	compact – long hooks
2. Northeastern Chania incl. Akrotiri	narrow-long	intermediate	long-downward	slender – long hooks
3. Northern and central Chania	wide-short	slender	long-downward	compact – short hooks
4. Western and southwestern Chania	narrow-short	very slender	short to long, downward	compact – short hooks
5. Andikithira	narrow-short	extremely slender	short, downward	compact – short hooks

description of *E. giuliae*. Populations in the municipalities of Chania and Apokoronas in the North (Drapanos, Garipa, Skloka) (Fig. 257: area 2) form a second subgroup. Males differ from the first group in the narrow excision in the hind margin of the anal tergite bordered by long teeth, the slimmer subgenital plate with long downward pointing styli and slender apical arms of the titillator. From the five subgroups, females in this region are atypical for *E. giuliae*, when compared to the first subgroup, in having slender subgenital plates which are distinctly longer than wide. Morphological characters in the third subgroup match the description presented for *E. latens*. It occurs at higher elevations on Mt. Lefka and in mid-level elevations and lowlands in the municipality of Platanias (Kolympari, Rodhopos, Prases, and Kato Kefalia) in central and northern Chania (Fig. 257: area 3). It is characterised by the wide central excision in the hind margin of the anal tergite bordered by short teeth, a slender subgenital plate with short to long downward pointing styli and compact apical arms of the titillator with short hooks. Populations found in the western and southwestern part of the Chania region, southwest from the line Gramvousa peninsula on the northwest coast to Livadas near the south coast (Fig. 257: area 4), form the fourth subgroup. They show some similarities with *E. latens* but differ in the very slender subgenital plate with apical lobes which in little more than half of the specimens carry a tiny spine at one or both tips. The populations in the fourth region very closely resemble *Eupholidoptera* populations found on Andikithira (Fig. 257: area 5) which possess an extremely slender subgenital plate with the tip of the apical lobes always provided with a spine, forming the fifth subgroup.

Following the above pattern, populations in the western and southwestern corner of Crete (subgroup 4) represent a genetically well-outlined lineage, sharing the nuclear ITS fragment and its mitochondrial genome with the population on Andikithira (subgroup 5) (genetic distances of the nuclear internal transcribed spacers show very low variation among *Eupholidoptera*). The two islands have been isolated since the beginning of the Pleistocene (2.6 Mya), with only a narrow length of sea separating them during the Last Glacial Maximum (Lykousis 2009; Simaiakis et al. 2017; Fassoulas 2018; Bailey et al. 2022). This, combined with the small but stable morphological differences between the two isolated lineages and the deep marine strait between Crete and Andikithira suggest that the *Eupholidoptera* populations of Crete and Andikithira, have been isolated for a considerable length of time. The populations on Andikithira are morphologically very uniform with very little variation whereas populations from western and southwestern Chania show considerable morphological variation even within a single population.

The reason for this could be the isolation of the Andikithira population, which did not permit genetic flow between it and other *Eupholidoptera* populations. This would lead to low genetic variability within the island of Andikithira, and, therefore, uniform morphological traits. A founder effect could have also taken place on the island with similar results. On the contrary, the populations from western and southwestern Chania were less isolated from each other and maintained a high genetic variability, that lead to the morphological diversity observed today. Interspecific gene exchange with populations of neighbouring taxa such as *E. giuliae* could have also taken place.

Based on the molecular results and the low morphological differences between populations from Andikithira and western and southwestern Chania (subgroups 4 and 5 in Table 8, Fig. 257), the decision was made to assign the populations from both areas, although closely related to *E. latens*, to *E. francisae* sp. nov.

The second clade may be regarded as a monophyletic mitochondrially-defined species complex of three subclades – the typical *E. giuliae* (morph-group 1), a clade formed by morph-groups 2 and 3, and a clade formed by *E. astyla* samples. The very low genetic mitochondrial distances between morphologically well outlined taxa (i.e., *E. astyla* and the rest) may point to former population crises (bottlenecks), where mitochondrial genome was shared between two or more taxa. At the same time, genetic drift caused by genetic bottlenecks may have contributed to unique characteristics (for instance, the peculiar shape of the titillators in *E. astyla*). On the other hand, the existence of specimens with symmetrical titillators and the intermixture of a tentatively identified female of *E. astyla* within the *E. giuliae* s.str. subclade (Fig. 256), calls for possible hybridisation in zones of syntopic occurrences.

An alternative scenario of the systematics of this western species complex may be proposed. Since the clade of morph-groups 2 and 3 show intermediate and variable morphology between specimens of *E. francisae* (morph-group 4) and *E. giuliae* (morph-group 1), and they intermix at the phylogenetic tree, those populations may represent a hybridogenic lineage of two formerly partially speciated taxa or may still be in the ‘grey zone’ of their evolutionary differentiation where they can either become distinct taxa or merge back into a common genetic pool in future.

The above scenario may not be unique and could be expected in other sibling species of Cretan *Eupholidoptera* that express intermediate or variable morphological characters (e.g., *E. mariannae* and *E. annamariae*). As results based on morphology and genetics are not unequivocal and boundaries do not match, as yet no taxonomic decision has been taken for morph-groups 1, 2, and 3. For the time being, both the eastern groups (morph-groups 1 and 2) have been assigned to *E. giuliae*, whereas the central group (morph-group 3) matches *E. latens*.

Titillators

The diversity of male insect genitalia is well known (Simmons 2014). They are even considered as “the most variable and divergent of all morphological structures”. In *Eupholidoptera* mainly four different parts are involved: cercus, titillator, subgenital plate and last abdominal tergite. In the Cretan species all these structures vary between

the species, but the most variable ones are the titillators. While the other three structures seem to be connected with some kind of fit between male and female genitalic organs, the function of the titillators remained unclear for a long time because they are typically concealed within the abdomen during copulation. Just recently, Wulff et al. (2017) demonstrated by in vivo X-ray cineradiography in the related *Roeseliana roeselii* that the titillator is moved rhythmically during mating. The authors assume that it is “initially used for stimulation” and perhaps later also involved in spermatophore transfer. In *Eupholidoptera* rhythmical movements of the titillator have also been observed (Dagmar von Helversen, pers. comm., probably before 2000), possibly visible externally due to its large size. The rapid evolution in shape may occur under sexual selection (see Simmons 2014; Wulff et al. 2017) and *Eupholidoptera* may be an interesting study object where species-specific differences of varying magnitude in size, curvature and symmetry can be found.

Asymmetry

Although in some orders of insects, asymmetry of genitalia is the ground plan, in most insects, including Orthoptera, it is very rare (Huber et al. 2007). In Cretan *Eupholidoptera* asymmetric titillators are found in *E. annamariae*, *E. feri* and by far the most evident example is *E. astyla*. In male *E. astyla* titillators are antisymmetric asymmetric, a quite unique and rare feature (Schilthuizen 2013). Of 13 males studied, the tip of the titillator is pointing to the right in 8, and to the left in 5 males. This category of asymmetry has been coined “pure antisymmetry”. Sexual selection has played a crucial role in the evolution of insect genital asymmetry (Huber et al. 2007; Huber 2020) via the route of mating positions. Available data strongly corroborate a correlation between morphological asymmetry and one-sided mating positions, whereas symmetric genitalia allow for random-side positions. The few images available on *Eupholidoptera* mating indicate that their mating position is end-to-end with the heads of the male and female pointing in opposite directions, that of the male pointing to the female ovipositor. It would be interesting to know whether in *E. astyla* mating positions differ from those in *Eupholidoptera* species with symmetric genitalia. In this context it is striking that the titillator in two male *E. astyla* from the Asterousia Mts (Fig. 192) was symmetrical. None of the 30 other specimens trapped at the same site showed this anomaly.

Bioacoustics

The song of *Eupholidoptera* is quite uniform throughout the genus and is even considered a not very reliable character for discerning species (Çiplak et al. 2009). It consists of isolated syllables produced in long series with the opening hemisyllable much shorter and weaker than the closing hemisyllable. In some cases, the opening hemisyllable is partly or not visible in the recordings, which may be a character of the song of a specimen. It may, on the other hand, also reflect the quality of the sound recording. In the known Cretan species, syllable duration is between 40 ms and 600 ms (Fig. 259). During active singing the syllable repetition rate may be as fast as 2/s but is often much

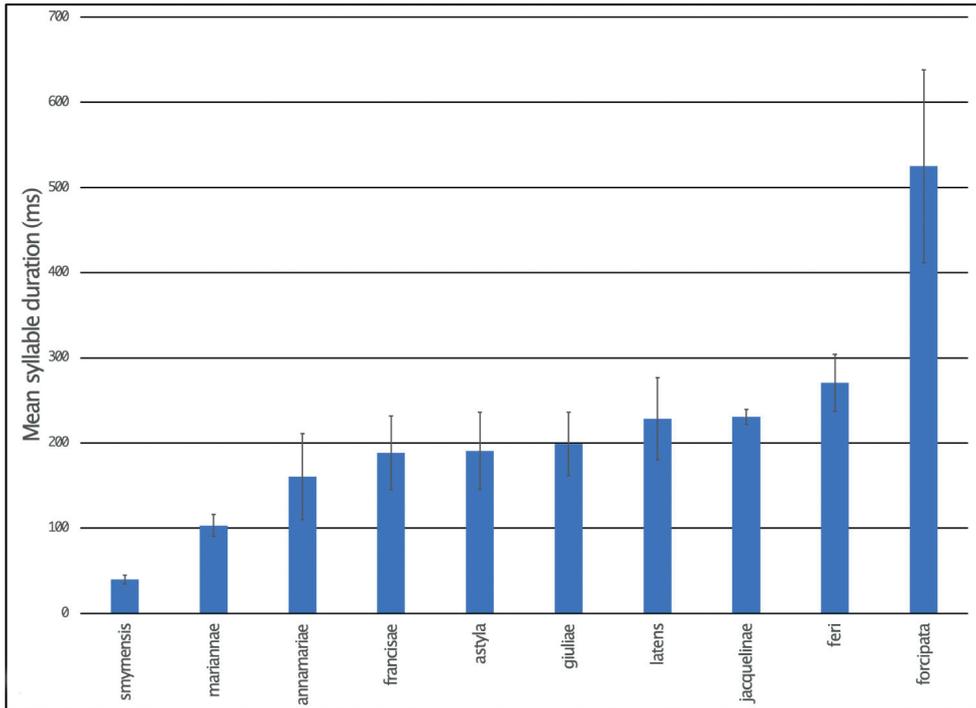


Figure 259. Mean syllable duration in recorded species from Crete (incl. Gavdos and Andikithira). See Suppl. material 3 for measurements per recorded specimen.

slower. In the best available recordings, single tooth impacts may be visible in the closing hemisyllable, each corresponding with one tooth on the stridulatory file.

In quite some recordings it is not easy to clearly discern the opening hemisyllable, leaving discussion whether it is just weak and may be not well recorded or it is absent, with no sound produced during this wing movement. As a main character of the species' song may be the duration of the syllable, the absence of the opening hemisyllable in some recordings or specimens accounts for inaccurate measurements of this song character. The same holds for the effect of temperature on the duration of syllables, which may last twice as long with temperatures differing only as little as 2–5 °C. This adds to the fact that in many cases not so many specimens and not so much time (actively) singing has been available to us to compare the song of the species thoroughly. Bioacoustic measurements presented in Fig. 259 include all measurements regardless of their quality or ambient temperature. Fig. 259 shows that *E. smyrnensis* and *E. forcipata* produce a song with a syllable duration clearly different from all other Cretan species analysed. When considering the relatively small differences in syllable duration in the other species these could be species-specific but could also be explained by differences in temperature during the recording or the low number of recordings. No statistical analysis has been performed and no attempt has been undertaken to correct for differences in temperature. Within

the species that show morphological variation throughout their range (*E. giuliae*, *E. francisae*, and *E. latens*) no variation in song characters could be found. Between the morphologically related *E. latens* and *E. francisae* no systematic difference in song characters could be demonstrated. Maybe a larger number of standardised sound recordings (especially standardised for temperature) may yield in more systematic differences between taxa.

Most Cretan species of *Eupholidoptera* are allopatric and a female will only hear the calling song of conspecific males. The syllable duration between most Cretan species is largely overlapping and not distinctive (but long for *Eupholidoptera* in general; Çiplak et al. 2009) and differences in morphology fit into the conclusion by Heller (2006) that regarding differentiation of allopatric populations, changes in calling songs seem to appear more slowly than changes in morphology. In some locations Cretan species of *Eupholidoptera* occur sympatrically (Table 9). Interestingly, nine out of ten sympatric occurrences detected included a species with an unusual song pattern, either *E. smyrnensis* with shorter syllables than all others or *E. forcipata* (respectively, the similar *E. marietheresae* sp. nov. with probably similar songs) with distinctly longer syllables than all others (see Fig. 259). Besides *E. latens*, the 10th example included *E. cretica* for which the calling song is not yet recorded. Obvious song differences between sympatric *Eupholidoptera* species were also listed in Çiplak et al. (2009). If male calling songs in two sympatric species differ this of course helps females to locate conspecific males. Concerning the evolution of these differences, the Cretan recordings of the wide-spread *E. smyrnensis* do not differ from recordings made elsewhere in its range so the species has obviously not changed its song when coming to Crete. In contrast, the extraordinarily long syllables of *E. forcipata* may be an important factor allowing the co-existence with other Cretan *Eupholidoptera*.

Geographical distribution

Findings presented here, collected over the past 30 years, show that the known distribution range for five *Eupholidoptera* species in Crete (*E. annamariae*, *E. astyla*, *E. giuliae*, *E. latens*, and *E. mariannae*) is larger than previously known (Fig. 254).

Table 9. Examples of syntopic occurrences of *Eupholidoptera* species in Crete.

Trap no.	Coll. date	Location	GPS Coordinates	Alt. (m)	Species 1	Species 2
FC111	30/10/1996	Limni Kourna	35.3269, 24.2790	25	<i>giuliae</i>	<i>smyrnensis</i>
FC495	10/07/1997	Limni Kourna	35.3269, 24.2790	25	<i>giuliae</i>	<i>smyrnensis</i>
FC70	20/08/1996	Limni Kourna	35.3269, 24.2790	25	<i>giuliae</i>	<i>smyrnensis</i>
FC1536	05/08/2000	Dikti Mt.	35.1107, 25.4779	1715	<i>astyla</i>	<i>marietheresae</i> sp. nov.
FC1606	02/10/2000	Dikti Mt.	35.1107, 25.4779	1715	<i>astyla</i>	<i>marietheresae</i> sp. nov.
FC1655	09/01/2001	Dikti Mt.	35.1107, 25.4779	1715	<i>astyla</i>	<i>marietheresae</i> sp. nov.
FC1602	15/09/2000	Idi Mt.	35.1973, 24.7920	1910	<i>forcipata</i>	<i>gemellata</i>
FC1651	30/10/2000	Idi Mt.	35.1973, 24.7920	1910	<i>forcipata</i>	<i>gemellata</i>
FC1916	12/06/2001	Idi Mt.	35.1973, 24.7920	1910	<i>forcipata</i>	<i>gemellata</i>
FC17807	19/10/2018	Lefka Mt.	35.3524, 23.9050	1200	<i>cretica</i>	<i>latens</i>

Eupholidoptera has now been found in most areas of Crete, occurring nearly everywhere on the island. Up to now *Eupholidoptera* has been overlooked at low altitudes due to its early appearance. For instance, recent findings of *E. latens* indicate that at lower altitudes animals are already adult at the beginning of May, while in the mountains adults only appear at the end of July or early August.

Altitudinal preferences

Of the 14 species of *Eupholidoptera* treated in this paper, six species have only been found at higher altitudes (above 1000 m): *E. pallipes*, *E. cretica*, *E. gemellata*, *E. forcipata*, *E. marietheresae* sp. nov., and *E. feri*, five species are restricted to lower altitudes (below ca. 500 m): *E. francisae* sp. nov., *E. giuliae*, *E. jacquelinae*, *E. annamariae*, and *E. smyrnensis*, whereas data presented here indicate that *E. astyla*, *E. latens*, and *E. marianae* are found across a wide altitudinal range from sea level to higher altitudes.

Traps

Pitfall traps are widely used to monitor ground dwelling invertebrates. For Orthoptera trapping results provide a contradictory picture (Schirmel et al. 2010). Tomar et al. (2017) compared bioacoustics and pitfall traps to monitor the Ensifera in suburban Delhi, India. In this study bioacoustics resulted in more species, but fewer specimens compared to pitfall traps. Differences were explained in the way bioacoustics (active) and pitfall traps (passive) operated and in possible microhabitat preferences, which affect pitfall trap results. The fact that quite a number of *Eupholidoptera* species (and other bush-cricket and cricket genera for that matter) across Crete have been trapped in pitfall traps (often in large numbers), is a strong indication that during the night their natural behaviour includes walking over the ground. This applies to species found in phrygana, inhabiting low prickly bushes. Some species like *E. cretica* and *E. marianae* were caught using fermenting traps that hung from trees and tall bushes indicating these species prefer to live in higher shrubs and trees in which they probably hide during the day. Summarising, the results presented here for trap catches provide a strong indication that traps may provide a valuable addition to monitoring techniques used for Orthoptera in general and *Eupholidoptera* in particular.

Sympatry

Little information was available on the sympatric occurrences of different *Eupholidoptera* species. The syntopic occurrence of *latens/pallipes* on Mt. Lefka and *gemellata/forcipata* on Mt. Idi was conjectured but not proven. Çiplak et al. (2009) describe the syntopic (and synchronic singing, unpublished) occurrence of *astyla* and *forcipata* on Mt. Idi. Results from pitfall catches provide further proof of syntopic occurrences. Of a total of some 150 pitfall events (location + collecting date), ten events at four separate locations resulted in two *Eupholidoptera* species ending up in the same trap (Table 9).

However, one must bear in mind that the period between activating the traps and collecting the accumulated specimens was at least two months. Therefore, it cannot be ruled out that despite the sympatry, species do not (completely) overlap in their phenology or daily activity patterns. Interestingly, in nine of the ten trapping events a species with unusual song pattern is involved, either *smyrnensis* with shorter syllables than all others or *forcipata* (respectively the similar *marietheresae* sp. nov. with probably similar song) with distinctly longer syllables than all others (see Fig. 259). It would probably be interesting to study their coexistence in more detail by an intense field survey with observations of interspecific behaviour.

Conservation status

Recently, a Red List for all European Orthoptera species has been compiled, including the *Eupholidoptera* species of Crete (Hochkirch et al. 2016). Except for *E. smyrnensis*, all Cretan species are classified as threatened (Critically Endangered, Endangered, or Vulnerable) (Table 10). Based on the information presented in this publication the status for widespread species like *E. astyla*, *E. giuliae*, *E. latens*, and *E. annamariae* is likely to change to Least Concern. For other species with a (very) restricted area of occurrence, the Red List Status is expected not to change, underpinning the necessity to protect the habitats of these species. The two new species still have to be assessed. Most likely *E. francisae* will be evaluated as Least Concern based on its geographic range and *E. marietheresae* as Vulnerable based on its very restricted geographic range.

Citizen scientists and observations

To further close the gaps in our knowledge, observations made during excursions by tourists in Crete can be very useful especially if these are uploaded to online platforms

Table 10. Current IUCN Red List Status for *Eupholidoptera* species of Crete and adjacent islands.

Species	Common name	IUCN RLA status*
<i>E. annamariae</i>	Annamaria's Marbled Bush-cricket	VU
<i>E. astyla</i>	Mount Ida Marbled Bush-cricket	EN
<i>E. cretica</i>	Cretan Marbled Bush-cricket	VU
<i>E. feri</i>	Fer's Marbled Bush-cricket	CR
<i>E. forcipata</i>	Idi Marbled Bush-cricket	VU
<i>E. francisae</i> sp. nov.	Francis's Marbled Bush-cricket	Not Evaluated
<i>E. gemellata</i>	Skaronero Marbled Bush-cricket	VU
<i>E. giuliae</i>	Giulia's Marbled Bush-cricket	VU
<i>E. jacquelineae</i>	Jacqueline's Marbled Bush-cricket	VU
<i>E. latens</i>	Hidden Marbled Bush-cricket	VU
<i>E. marianna</i>	Marianne's Marbled Bush-cricket	VU
<i>E. marietheresae</i> sp. nov.	Marietherese's Marbled Bush-cricket	Not Evaluated
<i>E. pallipes</i>	Pale-legged Marbled Bush-cricket	VU
<i>E. smyrnensis</i>	Smyrna Marbled Bush-cricket	LC

*: CR – Critically Endangered, EN – Endangered, VU – Vulnerable, LC – Least Concern.

like iNaturalist and Observation.org. This paper includes nine observations on *Eupholidoptera* from Crete (Suppl. material 1), which based on images were assigned to *E. giuliae* (7), *E. pallipes* (1), and *E. jacquelineae* (1). The importance of social media and citizen science cannot be emphasised enough. They may help to solve systematic puzzles like in the case of the Australian pygmy grasshoppers (Skejo et al. 2020). However, one must bear in mind that in case of *Eupholidoptera*, species are nocturnal and less likely to be observed during the day, and that caution is advised when identifying species from photos, since important diagnostic characters might not be visible.

Phylogeography

Fourteen species of *Eupholidoptera* in the Cretan area is a remarkable gathering of taxa, albeit not unique across various invertebrate orders. Other examples include for instance *Dendarus* (Coleoptera: Tenebrionidae) with 13 species (Trichas 2008), *Mastus* (Gastropoda: Enidae) with 16 species (Parmakelis et al. 2005) and *Albinaria* (Gastropoda: Clausiliidae) with 31 species (Welter-Schultes 2010). Although the taxonomy in *Albinaria* (Dimopoulou et al. 2017) and *Dendarus* (Trichas et al. 2020) is still a matter of debate, these large numbers of unique endemic taxa are indicative of the isolation and “speciation dynamics” of Crete.

This high concentration of endemic species of *Eupholidoptera*, and especially the presence of some primitive representatives (*E. gemellata*, *E. pallipes*), has led previous researchers to propose the southeastern Aegean plate, possibly including Crete, as the origin place of the last common ancestor of *Eupholidoptera* (Çiplak et al. 2009, 2010). Phylogenetic analyses by Çiplak et al. (2021, 2022) based on molecular markers confirmed this hypothesis, suggesting that *Eupholidoptera* split from its closest relative (*Parapholidoptera*) 12 Mya, during the Serravallian. The last common ancestor of *Eupholidoptera* was dated to the Tortonian during the regression of the Mid-Aegean Trench (12–9 Mya), in an area around south Anatolia and Crete. This ancestor probably possessed a larger range that was split due to the Aegean tectonic movements, and then later dispersed to the rest of Greece and the Balkans (Çiplak et al. 2022).

Of the fourteen species of *Eupholidoptera* only one, *E. smyrnensis*, has a large distribution area. The finding of *Eupholidoptera smyrnensis* on Crete adds new information to the phylogeography of the *Eupholidoptera chabrieri* group of species as presented by Çiplak et al. (2010). Studies with genetic markers should elucidate whether *E. smyrnensis* reinvaded Crete using terrestrial corridors that existed during the Messinian Salinity Crisis (5.96–5.33 Mya) or whether its presence is linked to recent (human?) introduction. According to Çiplak et al. (2022) the branch with *E. smyrnensis* separated from the other studied Cretan *Eupholidoptera* species ~ 8 Mya.

Only one *Eupholidoptera* species is not found on Crete itself but restricted to surrounding islands. Gavdos and the small islet of Gavdopoula are home to *E. jacquelineae*. The islands are surrounded by a fairly extensive shelf that was exposed above sea level during Mio-Pliocene but were never connected to Crete during the Quaternary (2.58 Mya up to now) (Kasapidis et al. 2005; Sakellariou and Galanidou 2015). Estimates

of the isolation of Gavdos and Gavdopoula from Crete range from 2.4 to 4.8 Mya, depending on author (Anastasakis 1987; Van Hinsbergen and Meulenkaamp 2006; Broggi 2015; Poulakakis et al. 2015; Fassoulas 2018). Despite their long isolation, lineages of various terrestrial groups found on Gavdos and Gavdopoula are heavily influenced by the Cretan terrestrial counterparts. Examples are the land-snail genus *Mastus* (Welter-Schultes 2000; Parmakelis et al. 2005), beetle genera like *Dendarus* (Trichas et al. 2020) and *Drilus* (Kundrata et al. 2015), as well as the scorpion *Mesobuthus* (Parmakelis et al. 2006), where the populations on Gavdos and Gavdopoula are Pleistocene descendants from Cretan terrestrial taxa. Given the amount of diversification of *E. jacquelineae*, only an old vicariant event (somewhere between 2.4 and 4.8 Mya) or a quite old dispersal scenario (towards the upper half of Pleistocene) could explain the presence of the ancestors of *E. jacquelineae* on Gavdos and Gavdopoula. But one must have in mind that both explanations seek for closest relatives on the Cretan land, while so far, they are found only more remotely (Tilmans 2002). A more complete phylogeny of all Cretan *Eupholidoptera* taxa with several genetic markers, better time estimations and a more precise evaluation of the relationships between them, could provide more definitive insights on the *E. jacquelineae* origin and its relationship with the other Cretan taxa.

Another interesting phylogeographical matter is that of *Eupholidoptera francisae* occurring on the island of Andikithira (32 km NW of western Crete) and in the extreme western/southwestern part of Crete. The faunal affinities between Andikithira and W. Crete and their biogeographical implications in the area, have a long story of theories and debates, starting from “Boettger’s line” (between Kithira and Andikithira) and the Peloponnese-Kithira-Andikithira-Crete relations (Boettger 1894; Gittenberger 1990; Gittenberger and Goodfriend 1993). These authors, based on the distributions of terrestrial gastropods, concluded that Andikithira was not connected to Kithira or to Crete during the entire Pleistocene which at the time these papers were published was considered to have started ~ 1,8 Mya ago. Sfenthourakis (1993), in an analysis of the isopod fauna of Andikithira (plus the surrounding satellite islets of Pori and Poreti), postulated older connections between Andikithira and Crete, but also disconnections and reconnections with both Kithira and Crete during the Pliocene/Pleistocene. All of the above authors, more or less agree that the geological separation between Kithira and Andikithira is a very old one, that between Andikithira and Crete younger, and the one between Kithira and the Peloponnese Peninsula the youngest (Gittenberger and Goodfriend 1993). Moreover, a recent discovery of a unique lizard species on the small Andikithira satellite islets of Pori and Poreti (*Podarcis levendis* Lymberakis et al., 2008), is also indicative of the amount of time isolation of the small Andikithira archipelago, although does not elucidate the Andikithira-Crete geological relationship. Similarly, *Dendarus antikythereensis* from Andikithira and Pori islet is very closely related to *D. graecus* from Crete, but again, not informative enough on the Andikithira-Crete relationship (Trichas et al. 2020). Both taxa were interpreted as long-distance dispersals from their Cycladic (central Aegean) ancestors to Andikithira and Crete respectively. From a geological/paleogeographic point of view it seems very probable that there were no solid land connections between Andikithira and Crete at least for the last 2 Mya, but many authors (e.g., Lykousis 2009) postulate very narrow sea strait be-

Table 11. Cretan invertebrate and vertebrate monophyletic lineages and time of divergence of East-West clades.

Taxon	Order	Number of subclades	Diverged approximately at	Reference
<i>Cyrtocarenum cunicularium</i>	Araneae	2	3.3 Mya	Kornilios et al. (2016)
<i>Poecilimon cretensis</i>	Orthoptera	2	0.6 – 1.2 Mya	Borissov et al. (2020)
<i>Thaumetopoea wilkinsoni</i>	Lepidoptera	2	< 1 Mya	Petsopoulos et al. (2018)
<i>Reticulitermes</i>	Blattodea	4	< 1 Mya	Fig. 2B in Velonà et al. (2010)
<i>Carabus banoni</i>	Coleoptera	2	1.47 Mya	Vlachopoulos et al. (pers. Comm.)
<i>Podarcis cretensis</i>	Squamata	2	5.42 – 4.36 Mya	Psonis et al. (2021)*

*: but see also Kyriazi et al. 2013; Spilani et al. 2019 for much smaller divergence time estimations for *Podarcis cretensis* east-west clades, 2.9–0.48 Mya.

tween Andikithira and Crete, at the period of Late Pleistocene (480–350 Kya). Given the amount of geological isolation of Andikithira and the genetical characteristics of the two populations of *E. francisae* on Andikithira and W. Crete, we can only speculate on a dispersal event from western/southwestern Crete to Andikithira, with the Late Pleistocene period as a good candidate for that event.

One more important question is, what caused the diversification of the 11 endemic *Eupholidoptera* species restricted to Crete itself and what factors contributed to their current distribution patterns? Although phylogeographic studies over the past 30 years revealed two major geological events that contributed to the diversification in the Aegean – the formation of the mid-Aegean trench (MAT) at the end of the Miocene (12–9 Mya) that separated Crete from the west Aegean and Anatolia, and the final isolation of Crete from Peloponnisos after the Messinian Salinity Crisis (MSC, 5.33 Mya) – solid evidence of exact patterns of diversification via in situ speciation within individual islands in the Aegean, i.e. Crete, remains still scarce (Poulakakis et al. 2015).

Several studies on monophyletic lineages of invertebrates and vertebrates (Table 11) in Crete using mitochondrial and nuclear markers indicate the existence of two major east-west clades and possible subclades, depending on the age of the arrival of the taxon in question. Pliocene paleogeography contributed to these well separated east-west units in many animal groups that arrived (or left?) on that south Ägäis piece of land after the Zanclean Flood (Krijgsman et al. 1999; Blanc 2002; Lymberakis and Poulakakis 2010).

East-west divergences are also evident in Cretan *Eupholidoptera* lineages, but the question whether the species found in Crete and the adjacent islands are polyphyletic as concluded by Çiplak et al. (2010) or, apart from *E. smyrnensis*, are monophyletic still needs a more definite answer. The study of 2010 did not use any molecular data but only morphological traits and song data, while the most recent molecular study (Çiplak et al. 2022) covers only four Cretan taxa (*E. forcipata*, *E. giuliae*, an unidentified species which is most likely *E. latens*, and *E. astyla*, in addition to *E. smyrnensis*). Lastly, the phylogenetic tree presented here does not include some crucial taxa such as *E. gemellata*, *E. pallipes*, *E. cretica*, and *E. forcipata* which, according to Çiplak et al. (2010), are the most distinct morphologically and are placed in clades distant from the rest of the Cretan taxa. Additional samplings of these rare species will provide a clearer picture on the monophyly of the Eupholidoptera of Crete.

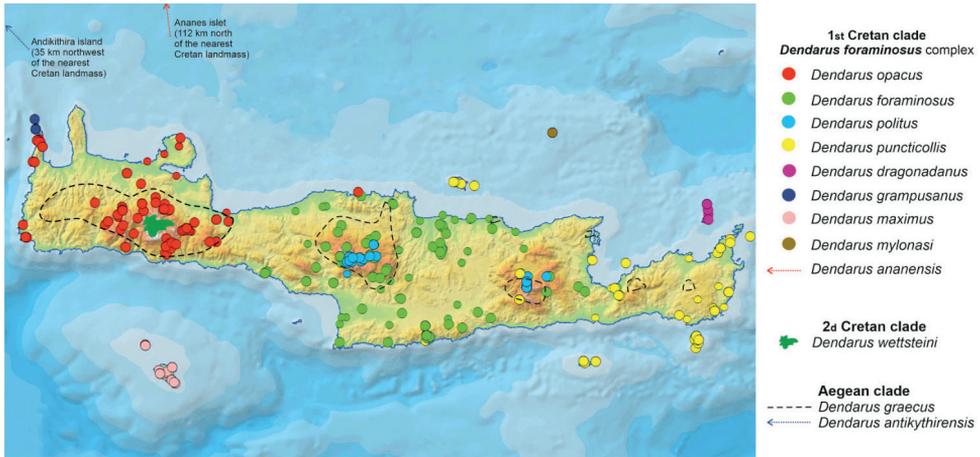


Figure 260. Distribution pattern of Cretan *Dendarus* taxa (Coleoptera), map visualised from data obtained from Trichas et al. (2020) and Trichas (2008).

An example of another polyphyletic genus under investigation on Crete is *Dendarus* (Coleoptera: Tenebrionidae) that consists of three distinct lineages on the island (two mitochondrial, one nuclear gene locus, and 61 morphological characters; Trichas et al. 2020) and includes 13 species. Distribution patterns in wingless *Dendarus* darkling beetles (Fig. 260) are quite similar in some extend to those found in *Eupholidoptera*. They share, for instance, high mountain taxa with similar distributions as *E. forcipata*, *E. gemellata*, and *E. pallipes* (*D. politus* and *D. wettsteini* are distributed on the same mountaintops, Fig. 260), as well as lowland species, with *E. astyla* most strikingly similar in distribution to *D. foraminosus*. *Eupholidoptera giuliae* occupies only west Cretan lowlands much like *D. opacus*. Also, *E. jacqueliniae* is distributed on both Gavdos and Gavdopoula islets, exactly as *Dendarus maximus* does, while the morphologically distinguishable number of taxa in the area is almost the same. Is there any ground to consider a similar number of different lineages, too? Given the new findings of *E. smyrnensis* populations on Crete, one can speculate even on six different groups at least on Crete mainland alone, but how many clades do we have? Are the west (*E. latens*+*E. giuliae*+*E. francisae*+*E. cretica*), central/central-east (*E. astyla*+*E. forcipata*+*E. marietheresae*), and east groups (*E. annamariae*+*E. mariannae*+*E. feri*) monophyletic like the *Dendarus foraminosus* complex? Are *E. pallipes*+*E. gemellata*, like *Dendarus wettsteini*, relictual equivalents and is *E. smyrnensis* a recent Aegean dispersal (much like *Dendarus graecus*)? Or are we facing a totally different range of evolutionary events? Along with the interrelations between groups, it would be interesting to investigate further the depth and time of divergence between lowland and high-altitude taxa in each group, i.e., how deep is the distance between *E. astyla* and *E. forcipata* (and when did they diverge)? Are the timings of divergence of Pleistocene age or even shallower? Answering all these questions raised by the unique diversity and complicated distribution patterns of *Eupholidoptera* in Crete requires a thorough phylogenetic/phylogeographic study.

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Supplementary material 1

List of localities, specimens, and repositories of *Eupholidoptera* from Crete, Gavdos, Gavdopoula, and Andikithira

Authors: Luc Willemse, Jos Tilmans, Nefeli Kotitsa, Apostolos Trichas, Klaus-Gerhard Heller, Dragan Chobanov, Baudewijn Odé

Data type: occurrence data (excel document)

Explanation note: The table contains all published and unpublished localities, specimens collected and their repositories for all *Eupholidoptera* species from Crete and its satellite islands known to the authors.

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Link: <https://doi.org/10.3897/zookeys.1151.97514.suppl1>

Supplementary material 2

Examined specimens

Authors: Luc Willemse, Jos Tilmans, Nefeli Kotitsa, Apostolos Trichas, Klaus-Gerhard Heller, Dragan Chobanov, Baudewijn Odé

Data type: specimen studied (excel document)

Explanation note: This table lists examined specimens with an indication of how they are stored (D: dry pinned; W: in alcohol), whether they have been measured (mm), photographed (image), sampled for DNA analysis (DNA), or audio recorded (audio). Abbreviations used: √: done; S: stacked images(s); F: field image from life specimen; H: habitus image from collection specimen; FC: trap. For more details of location and trap see Suppl. material 1. Specimens are arranged in alphabetical order of species and within species on region and location.

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Link: <https://doi.org/10.3897/zookeys.1151.97514.suppl2>

Supplementary material 3

Sound recordings and song data

Authors: Baudewijn Odé, Jos Tilmans, Klaus-Gerhard Heller

Data type: bioacoustic recordings (excel document)

Explanation note: table with detailed information on sound recordings and song data.

The tab sound recordings summarises details of sound recordings of *Eupholidoptera* species from Crete, Andikithira, and Gavdos. Recordings are in the collection of Jos Tilmans, Baudewijn Odé, and Klaus-Gerhard Heller. The tab song details provides information about the ambient temperature and mean syllable duration for individual specimen.

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Link: <https://doi.org/10.3897/zookeys.1151.97514.suppl3>

Supplementary material 4

Details of specimens used in phylogenetic analysis

Authors: Nefeli Kotitsa, Dragan Chobanov

Data type: table (excel document)

Explanation note: Details of specimens used for the Bayesian inference phylogenetic tree of 9 *Eupholidoptera* species from Crete, Andikithira, and Gavdos (see Figs 256, 258).

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Link: <https://doi.org/10.3897/zookeys.1151.97514.suppl4>

Supplementary material 5

NADH2__ITIS_sequences

Authors: Nefeli Kotitsa, Dragan Chobanov

Data type: table (excel document)

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Helminth and protozoan parasites of subterranean rodents (Chordata, Mammalia, Rodentia) of the world

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Abstract

Published studies and ten new unpublished records included herein reveal that approximately 174 species of endoparasites (helminths and protozoans) are known from 65 of 163 species of rodents that occupy the subterranean ecotope globally. Of those, 94 endoparasite species were originally described from these rodents. A total of 282 host-parasite associations are summarized from four major zoogeographic regions including Ethiopian, Palearctic/Oriental, Nearctic, and Neotropical. Thirty-four parasite records from the literature have been identified to only the level of the genus. In this summary, ten new records have been added, and the most current taxonomic status of each parasite species is noted. Interestingly, there are no data on endoparasites from more than 68% of described subterranean rodents, which indicates that discovery and documentation are at an early stage and must continue.

Keywords

Bathyergidae, Cricetidae, Ctenomyidae, Endoparasite, Geomyidae, Heterocephalidae, Octodontidae, Spalacidae

Introduction

Subterranean rodents are animals adapted to live underground with minimal dependency on surface resources. They exhibit numerous adaptations to maintain their life activities in this niche including almost no externally visible neck, small eyes and ears,

short legs, and very loose skin with soft fur that enables them to turn in their burrows with ease (Maser et al. 1981; Lacey et al. 2000). Conditions within the burrow systems are characterized by complete darkness, constant temperatures, relative humidity of 100% with low levels of air circulation, elevated carbon dioxide levels, and usually closed tunnels.

In contrast to mammals that live on the surface of the soil, subterranean rodents are completely acclimated to live in complex burrow systems below the surface. These animals have the capability to dig burrow systems through many types of friable soils (Lessa et al. 2008). The underground habitat has been invaded by rodents utilizing specialized digging methods in all zoogeographic regions of the world. However, rodents with the ability to dig tunnels underground by utilizing strong digging limbs as well as other morphological and physiological traits occur in all zoogeographic regions except Australia and Antarctica and adaptations by non-phylogenetically related groups to a subterranean existence are considered a product of convergent evolution (Losos 2011). Approximately 40% of the 6,500 mammal species of the world are rodents. Even though only 6.5% of all rodent species occupy the subterranean ecotope, these mammals play an essential part of the ecology in the areas in which they live, functioning as biological plows, cycling the earth, changing the landscape, promoting plant growth and ecological succession, and playing a critical role in cycling carbon and other nutrients through the soil. In the order Rodentia, a total of 163 extant subterranean species across 23 genera, within seven families, has been recognized with distributions throughout all continents except Antarctica and Australia (see Table 1) (Van Daele et al. 2007; Wilson et al. 2016, 2017).

Based on macroevolutionary patterns derived from the study of the fossil record, subterranean rodent species diversity has appeared to have oscillated since early Oligocene time [ca. 36 million years ago, (mya)]. The Geomyidae Bonaparte, 1845 and the Bathyergidae Waterhouse, 1841 have the greatest diversity among all subterranean rodent families relative to the number of genera found throughout evolutionary time and identified thus far as fossil taxa (Cook et al. 2000). Fluctuation cycles in diversification, known as taxon pulses (Erwin 1985) appear to have been driven by local, regional, and global climate oscillations, and explained by the Stockholm Paradigm, which seeks to provide an understanding of the evolution of host-parasite/pathogen systems via the evolutionary process of species diversification following mass extinctions (Brooks et al. 2019).

Ethiopian subterranean rodents

Subterranean rodents in the Ethiopian zoogeographic region are represented by twenty species in seven genera across three families (Heterocephalidae, Bathyergidae, and Spalacidae) including *Heterocephalus* Rüppell, 1842, *Heliophobius* Peters, 1846, *Bathyergus* Illiger, 1811, *Georchus* Illiger, 1811, *Cryptomys* Gray, 1864, *Fukomys* Kock et al., 2006, and *Tachyoryctes* Rüppell, 1835 (see Landry 1957; Patterson and Upham 2014; Wilson et al. 2016).

Table I. List of subterranean rodents. NA = Nearctic, Nt = Neotropical, E = Ethiopian, P = Palearctic, O = Oriental.

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region						
Castorimorpha	Geomorpha	Geomyidae	Geomyinae	Thomomyini	1	<i>Thomomys atrovarius</i> J. A. Allen, 1898	NA	NA					
					2	<i>Thomomys bottae</i> (Eydoux & Gervais, 1836)	NA	NA					
					3	<i>Thomomys bulbivorus</i> (Richardson, 1829)	NA	NA					
					4	<i>Thomomys clusius</i> Coues, 1875	NA	NA					
					5	<i>Thomomys idahoensis</i> Merriam, 1901	NA	NA					
					6	<i>Thomomys mazama</i> Merriam, 1897	NA	NA					
					7	<i>Thomomys monticola</i> J. A. Allen, 1893	NA	NA					
					8	<i>Thomomys nayarensis</i> Mathis et al., 2013	NA	NA					
					9	<i>Thomomys sheldoni</i> Bailey, 1915	NA	NA					
					10	<i>Thomomys talpoides</i> (Richardson, 1828)	NA	NA					
					11	<i>Thomomys townsendii</i> (Bachman, 1839)	NA	NA					
					12	<i>Thomomys umbrinus</i> (Richardson, 1829)	NA	NA					
				Geomyini	13	<i>Geomys arenarius</i> Merriam, 1895	NA	NA					
					14	<i>Geomys attwateri</i> Merriam, 1895	NA	NA					
					15	<i>Geomys breviceps</i> Baird, 1855	NA	NA					
					16	<i>Geomys bursarius</i> (Shaw, 1800)	NA	NA					
					17	<i>Geomys jugassicularis</i> Hooper, 1940	NA	NA					
					18	<i>Geomys knoxjonesi</i> Baker & Genoways, 1975	NA	NA					
					19	<i>Geomys lutescens</i> Merriam, 1890	NA	NA					
					20	<i>Geomys personatus</i> True, 1889	NA	NA					
					21	<i>Geomys pinetis</i> Rafinesque, 1817	Nt	Nt					
					22	<i>Geomys streckeri</i> Davis, 1943	NA	NA					
					23	<i>Geomys texensis</i> Merriam, 1895	NA	NA					
					24	<i>Geomys tropicalis</i> Goldman, 1915	NA	NA					
					25	<i>Zygoeomys trichopus</i> Merriam, 1895	Nt	Nt					
					26	<i>Orthogeomys grandis</i> (Thomas, 1893)	NA	Nt					
Castorimorpha	Geomorpha	Geomyidae	Geomyinae	Geomyini	27	<i>Heterogeomys cavator</i> (Bangs, 1902)	Nt	Nt					
					28	<i>Heterogeomys cherriei</i> (J. A. Allen, 1893)	Nt	Nt					
					29	<i>Heterogeomys dariensis</i> (Goldman, 1912)	Nt	Nt					
					30	<i>Heterogeomys heterodus</i> (Peters, 1865)	Nt	Nt					
					31	<i>Heterogeomys hispidus</i> (Le Conte, 1852)	Nt	Nt					
					32	<i>Heterogeomys lanius</i> Elliot, 1905	Nt	Nt					
					33	<i>Heterogeomys underwoodi</i> Osgood, 1931	Nt	Nt					
					34	<i>Pappogeomys bulleri</i> (Thomas, 1892)	Nt	Nt					
					35	<i>Cratogeomys castanops</i> (Baird, 1852)	NA	Nt					
					36	<i>Cratogeomys fulvescens</i> Merriam, 1895	NA	Nt					
					37	<i>Cratogeomys fumosus</i> (Merriam, 1892)	Nt	Nt					
					38	<i>Cratogeomys goldmani</i> (Merriam, 1895)	NA	Nt					
					39	<i>Cratogeomys merriami</i> (Thomas, 1893)	Nt	Nt					
					40	<i>Cratogeomys perotensis</i> Merriam, 1895	NA	Nt					
					41	<i>Cratogeomys planiceps</i> (Merriam, 1895)	NA	Nt					
					Hystricomorpha	Hystriognathi	Ctenomyidae			42	<i>Ctenomys andersoni</i> Gardner et al., 2014	Nt	Nt
										43	<i>Ctenomys argentinus</i> J. R. Contreras & Berry, 1982	Nt	Nt
										44	<i>Ctenomys australis</i> Rusconi, 1934	Nt	Nt
										45	<i>Ctenomys azarae</i> Thomas, 1903	Nt	Nt
										46	<i>Ctenomys bergi</i> Thomas, 1902	Nt	Nt
										47	<i>Ctenomys bicolor</i> Miranda-Ribeiro, 1914	Nt	Nt
										48	<i>Ctenomys boliviensis</i> Waterhouse, 1848	Nt	Nt
										49	<i>Ctenomys bonettoi</i> J. R. Contreras & Berry, 1982	Nt	Nt
										50	<i>Ctenomys brasiliensis</i> de Blainville, 1826	Nt	Nt
										51	<i>Ctenomys colburni</i> J. A. Allen, 1903	Nt	Nt
										52	<i>Ctenomys coludo</i> Thomas, 1920	Nt	Nt
										52	<i>Ctenomys coludo</i> Thomas, 1920	Nt	Nt
53	<i>Ctenomys conoveri</i> Osgood, 1946	Nt	Nt										

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region
Hystricomorpha	Histricognathi	Ctenomyidae			54	<i>Ctenomys coihaiquensis</i> Kelt & Gallardo, 1994	Nt Nt
			55	<i>Ctenomys dorbignyi</i> Contreras & Contreras, 1984	Nt Nt		
			56	<i>Ctenomys dorsalis</i> Thomas, 1900	Nt Nt		
			57	<i>Ctenomys emilianus</i> Thomas & S. Leger, 1926	Nt Nt		
			58	<i>Ctenomys erikacuellarae</i> Gardner et al., 2014	Nt Nt		
			59	<i>Ctenomys famosus</i> Thomas, 1920	Nt Nt		
			60	<i>Ctenomys flamarioni</i> Travi, 1981	Nt Nt		
			61	<i>Ctenomys fodax</i> Thomas, 1910	Nt Nt		
			62	<i>Ctenomys fochi</i> Thomas, 1919	Nt Nt		
			63	<i>Ctenomys frater</i> Thomas, 1902	Nt Nt		
			64	<i>Ctenomys fulvus</i> Philippi, 1860	Nt Nt		
			65	<i>Ctenomys goodfellowi</i> Thomas, 1921	Nt Nt		
			66	<i>Ctenomys haigi</i> Thomas, 1919	Nt Nt		
			67	<i>Ctenomys ibicuiensis</i> Freitas et al., 2012	Nt Nt		
			68	<i>Ctenomys jobannis</i> Thomas, 1921	Nt Nt		
			69	<i>Ctenomys juris</i> Thomas, 1920	Nt Nt		
			70	<i>Ctenomys knighti</i> Thomas, 1919	Nt Nt		
			71	<i>Ctenomys lami</i> Freitas, 2001	Nt Nt		
			72	<i>Ctenomys latro</i> Thomas, 1918	Nt Nt		
			73	<i>Ctenomys lessai</i> Gardner et al., 2014	Nt Nt		
			74	<i>Ctenomys leucodon</i> Waterhouse, 1848	Nt Nt		
			75	<i>Ctenomys lewisi</i> Thomas, 1926	Nt Nt		
			76	<i>Ctenomys magellanicus</i> Bennett, 1836	Nt Nt		
			77	<i>Ctenomys mariafarelli</i> Azurduy, 2005	Nt Nt		
			78	<i>Ctenomys maulinus</i> Philippi, 1872	Nt Nt		
			79	<i>Ctenomys mendocinus</i> Philippi, 1869	Nt Nt		
			80	<i>Ctenomys minutus</i> Nehring, 1887	Nt Nt		
			81	<i>Ctenomys nattereri</i> Wagner, 1848	Nt Nt		
			82	<i>Ctenomys occultus</i> Thomas, 1920	Nt Nt		
			83	<i>Ctenomys opimus</i> Wagner, 1848	Nt Nt		
			84	<i>Ctenomys osvaldoreigi</i> J. R. Contreras, 1985	Nt Nt		
			85	<i>Ctenomys paraguayensis</i> J. R. Contreras, 2000	Nt Nt		
			86	<i>Ctenomys pearsoni</i> Lessa & Langguth, 1983	Nt Nt		
			87	<i>Ctenomys perrensi</i> Thomas, 1896	Nt Nt		
			88	<i>Ctenomys peruanus</i> Sanborn & Pearson, 1947	Nt Nt		
			89	<i>Ctenomys pilarensis</i> J. R. Contreras, 1993	Nt Nt		
			90	<i>Ctenomys pontifex</i> Thomas, 1918	Nt Nt		
			91	<i>Ctenomys porteusi</i> Thomas, 1916	Nt Nt		
			92	<i>Ctenomys pundti</i> Nehring, 1900	Nt Nt		
			93	<i>Ctenomys rionegrensis</i> Langguth & Abella, 1970	Nt Nt		
			94	<i>Ctenomys roigi</i> J. R. Contreras, 1988	Nt Nt		
			95	<i>Ctenomys rondoni</i> Miranda-Ribeiro, 1914	Nt Nt		
			96	<i>Ctenomys rosendopascuali</i> J. R. Contreras, 1995	Nt Nt		
			97	<i>Ctenomys talarum</i> Thomas, 1898	Nt Nt		
			98	<i>Ctenomys torquatus</i> Lichtenstein, 1830	Nt Nt		
			99	<i>Ctenomys tuconax</i> Thomas, 1925	Nt Nt		
			100	<i>Ctenomys tucumanus</i> Thomas, 1900	Nt Nt		
			101	<i>Ctenomys tulduco</i> Thomas, 1921	Nt Nt		
			102	<i>Ctenomys saltarius</i> Thomas, 1912	Nt Nt		
			103	<i>Ctenomys scagliai</i> J. R. Contreras, 1999	Nt Nt		
			104	<i>Ctenomys sericeus</i> J. A. Allen, 1903	Nt Nt		
			105	<i>Ctenomys sociabilis</i> Pearson & Christie, 1985	Nt Nt		
			106	<i>Ctenomys steinbachi</i> Thomas, 1907	Nt Nt		
			107	<i>Ctenomys validus</i> J. R. Contreras et al., 1977	Nt Nt		
			108	<i>Ctenomys viperinus</i> Thomas, 1926	Nt Nt		
			109	<i>Ctenomys yatesi</i> Gardner et al., 2014	Nt Nt		
			110	<i>Ctenomys yolandae</i> J. R. Contreras & Berry, 1984	Nt Nt		

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region							
Hystricomorpha	Histicognathi	Ocotodontidae			111	<i>Spalacopus cyanus</i> (Molina, 1782)	Nr	Nr						
			Heterocephalidae			112	<i>Heterocephalus glaber</i> Rüppell, 1842	E	E					
				Bathyergidae			113	<i>Heliophobius argenteocinereus</i> Peters, 1846	E	E				
					114	<i>Bathyergus janetta</i> Thomas & Schwann, 1904	E	E						
					115	<i>Bathyergus suillus</i> (Schreber, 1782)	E	E						
					116	<i>Georchys capensis</i> (Pallas, 1778)	E	E						
					117	<i>Cryptomys hottentotus</i> (Lesson, 1826)	E	E						
					118	<i>Fukomys amatus</i> (Wroughton, 1907)	E	E						
					119	<i>Fukomys anselli</i> (Burda et al., 1999)	E	E						
					120	<i>Fukomys bocagei</i> (de Winton, 1897)	E	E						
					121	<i>Fukomys damarensis</i> (Ogilby, 1838)	E	E						
					122	<i>Fukomys darlingi</i> (Thomas 1895)	E	E						
					123	<i>Fukomys foxi</i> (Thomas, 1911)	E	E						
					124	<i>Fukomys kafuensis</i> (Burda et al., 1999)	E	E						
					125	<i>Fukomys mechowii</i> (Peters, 1881)	E	E						
					126	<i>Fukomys ochraceocinereus</i> (Heuglin, 1846)	E	E						
					127	<i>Fukomys vandevoestijneae</i> Van Daele et al., 2013	E	E						
					128	<i>Fukomys whytei</i> (Thomas, 1897)	E	E						
					129	<i>Fukomys zechi</i> (Matschie, 1900)	E	E						
		Myomorpha			Cricetidae	Arvicolinae	Prometheomyini	130	<i>Prometheomys schaposchnikowi</i> Satunin, 1901	P	P			
								Ellobiusini	131	<i>Ellobius alaiicus</i> Vorontsov et al., 1969	P	P		
									132	<i>Ellobius fuscocapillus</i> (Blyth, 1843)	P	P		
									133	<i>Ellobius lutescens</i> Thomas, 1897	P	P		
									134	<i>Ellobius talpinus</i> (Pallas, 1770)	P	P		
									135	<i>Ellobius tancrei</i> Blasius, 1884	P	P		
									Spalacidae	Myospalacinae	136	<i>Myospalax armandii</i> (Milne-Edwards, 1867)	P	P
											137	<i>Myospalax aspalax</i> (Pallas, 1776)	P	P
											138	<i>Myospalax epsilanus</i> Thomas, 1912	P	P
				139							<i>Myospalax myospalax</i> (Laxmann, 1773)	P	P	
140	<i>Myospalax psilurus</i> (Milne-Edwards, 1874)			P		P								
141	<i>Eospalax baileyi</i> (Thomas, 1911)			P		P								
142	<i>Eospalax cansus</i> (Lyon, 1907)			P		P								
143	<i>Eospalax fontanierii</i> (Milne-Edwards, 1867)			P		P								
144	<i>Eospalax rothschildi</i> (Thomas, 1911)			P		P								
145	<i>Eospalax rufescens</i> (J. A. Allen, 1909)			P		P								
Rhizomyinae	Rhizomyini			146		<i>Eospalax smithii</i> (Thomas, 1911)	P	P						
				147		<i>Rhizomys pruinosus</i> (Blyth, 1851)	P	O						
				148		<i>Rhizomys sinensis</i> Gray, 1831	P	O						
				149		<i>Rhizomys sumatrensis</i> (Raffles, 1821)	O	O						
				150		<i>Cannomys bodius</i> (Hodgson, 1841)	O	O						
				Tachyoryctini		151	<i>Tachyoryctes macrocephalus</i> (Rüppell, 1842)	E	E					
						152	<i>Tachyoryctes splendens</i> (Rüppell, 1835)	E	E					
				Spalacinae			153	<i>Spalax antiquus</i> Méhely, 1909	P	P				
							154	<i>Spalax arenarius</i> Reshetnik, 1939	P	P				
							155	<i>Spalax giganteus</i> Nehring, 1898	P	P				
	156					<i>Spalax graecus</i> Nehring, 1898	P	P						
	157					<i>Spalax istricus</i> Méhely, 1909	P	P						
	158					<i>Spalax microphthalmus</i> Gldenstdt, 1770	P	P						
	159					<i>Spalax uralensis</i> Tiflov & Usov, 1939	P	P						
	160	<i>Spalax zemni</i> (Erleben, 1777)	P		P									
	161	<i>Nannospalax ehrenbergi</i> Nehring, 1898	P		P									
	162	<i>Nannospalax leucodon</i> (Nordmann, 1840)	P		P									
	163	<i>Nannospalax xanthodon</i> (Nordmann, 1840)	P	P										

Nearctic subterranean rodents

Species of the family Geomyidae are endemic to the Nearctic and northern Neotropics and are known collectively as pocket gophers due to presence of fur-lined cheek pouches in all species. They are a monophyletic group of subterranean rodents that share common ancestry with rodents of the family Heteromyidae (Wilson et al. 2016). Pocket gophers inhabit a wide geographic range, extending from a northernmost limit in southwest and south-central Canada through the central and western United States, southeast into central Florida, and south into Mexico and through Central America into Panama and near the Rio Atrato in northern Colombia (Hall 1981; Alberico 1990; Solari et al. 2013). As in most subterranean rodents, pocket gophers are fusiform in shape, having a naked and sensitive tail (they can run backwards as fast as they can forwards, using their tail as a rear-guide sensor (Gardner, pers. obs.)). They have small pinnae, loose skin, and their fur-lined cheek pouches are used only for food transport (Howard and Childs 1959; Maser et al. 1981; Hafner 1982; Honeycutt and Williams 1982; Hafner et al. 1994). The family consists of seven extant genera and 41 species (Wilson et al. 2016). The genus *Thomomys* Wied-Niewied, 1839, has 12 species and many subspecies, making this genus the most speciose of the family Geomyidae (see Patton 2005).

Palaearctic subterranean rodents

Thirty-two species of subterranean rodents of seven genera in two families, including Cricetidae Fischer, 1817, and Spalacidae Gray, 1821, occur in the Palaearctic region. Those include *Prometheomys* Satunin, 1901, and *Ellobius* Fischer, 1814, in the family Cricetidae, which includes the subfamily Arvicolinae Gray, 1821. The genera *Myospalax* Laxmann, 1769, *Eospalax* Allen, 1938, *Rhizomys* Gray, 1831, *Cannomys* Thomas, 1915, *Spalax* Guldenstaedt, 1770, and *Nannospalax* (Nordmann, 1840) are in the family Spalacidae which includes the subfamilies Myospalacinae Lilljeborg, 1866, Rhizomyinae Winge, 1887, and Spalacinae Gray, 1821. Among all subterranean forms of the Rodentia, those occurring in the Palaearctic region have the most extensive geographic distribution. Based on fossil evidence, the first known subterranean species of rodents appeared in the early Pliocene of Asia (Repenning 1984; Repenning et al. 1990). *Rhizomys pruinosus* (Blyth, 1851) and *Rhizomys sinensis* Gray, 1831 occur in the Palaearctic and Oriental zoogeographic regions. At the current time, only two species of subterranean rodents are known from the Oriental region, and those include *Rhizomys sumatrensis* (Raffles, 1821) and *Cannomys bodius* (Hodgson, 1841).

Neotropical subterranean rodents

The Neotropical subterranean rodents are represented by two hystricognath Caviomorph families, the Ctenomyidae Lesson, 1842 and Octodontidae Waterhouse, 1839. The family Ctenomyidae currently includes only species in the genus *Ctenomys* Blainville, 1826 which are known as the tuco-tucos, with approximately 69 described

species. These rodents occur in suitable habitats with a geographic distribution from southern Peru and southwestern Brazil south to Tierra de Fuego through Chile, Argentina, Bolivia, Paraguay, and Uruguay (Reig et al. 1990; Gardner et al. 2014). The fossil record indicates that species that can be allocated to the family Ctenomyidae originated ca. 10 mya (Cook et al. 2000), with rapid diversification in the genus *Ctenomys* commencing at ca. 3 mya (Parada et al. 2011). Interestingly, the single subterranean species in the Octodontidae which are the sister taxon of the Ctenomyidae includes the monotypic *Spalacopus cyanus* (Molina, 1782) and these occur only in central Chile.

Endoparasites

Our analysis shows that endoparasites have been found and reported from fewer than 40% of known species of subterranean rodents world-wide. There are several factors that could potentially explain this lack of reported data as researchers face several challenges when trapping subterranean rodents; without prior training, just finding and then determining active subterranean mammal burrow mounds is difficult. There could be thousands of burrow mounds, but researchers need acute field expertise to identify freshly dug burrows to capture these animals. Moreover, setting subterranean rodent traps is labor intensive and time-consuming, demanding lots of patience, physical strength, and luck.

Another problem is that sampling of species of subterranean rodents has not been systematically carried out and most collecting was done over time that was rather scattered and sporadic, and very few collections included parasites in their investigations. Many previous studies have failed to record comprehensive data during their collections of mammals and other vertebrates, discarding the internal organs of collected mammals without further examination. This practice resulted in significant gaps in parasite data with black holes regarding their faunas of both ecto- and endoparasites. Parasites discovered in research projects contain vital information about themselves and their host life history, consisting of information that we cannot ignore. The work presented here represents a synthesis of all available literature on the endoparasites of subterranean rodents of the world, as such, some references and works may have been missed, but we hope that this list provides a starting point for other researchers interested in this area of study.

Materials and methods

The current checklist was created by accumulating all published references arranged in a chronologically ordered tabular form representing globally each continent. The taxonomic status of each host and parasite species are up to date and represent the most current classifications. Most of the early literature was located in the reprint library of the H.W. Manter Laboratory of Parasitology in the University of Nebraska State Museum. Some of the literature was obtained from the Digital Commons at

University of Nebraska-Lincoln Libraries while several rare international references were obtained through interlibrary loan. For new records presented herein, some samples were collected during the field Parasitology class in western Nebraska and others were included from field work by S.L. Gardner in the 1980's the 1990's and earlier. Except for a few instances that we detail in the results, we used the original taxonomic names of both the hosts and parasites as published in the original literature. Throughout this paper, we used the zoogeographic terminology first established by Wallace (1876) (Rueda et al. 2013).

Results

Literature review

Ethiopian subterranean rodent endoparasites

See graphical summary in Fig. 1 and endoparasite diversity list in Table 2.

Diesing (1864) reported the first helminth parasite species from a subterranean rodent host, where *Taenia spalacis* (Diesing, 1864) was reported from *Georychus capensis* (Pallas, 1779) collected from Port Natal, South Africa.

Ortlepp (1939) described three new nematode species from the Cape dune mole-rat, *Bathyergus suillus* (Schreber, 1782) (Bathyergidae: Rodentia) collected from Strandfontein and Cape Town, South Africa including: *Libyostrogylus bathyergi* Ortlepp, 1939, *Longistriata bathyergi*, and *Mammalakis macrospiculum* (see Ortlepp 1939; Inglis 1991). These represent the first known reports of parasitic nematodes from African subterranean rodents. Interestingly, all these species have been reclassified into different genera and are currently known as *Paralibyostrogylus bathyergi*, *Ortleppstrongylus bathyergi*, and *Mammalakis macrospiculum*, (see De Graaff 1964; Lutermann and Bennett 2012).

Fain (1956) reported *Taenia brauni* Setti, 1897, from *Tachyoryctes splendens* (Rüppell, 1835) collected in Ruanda-Urundi, East Africa. After a period of several years, De Graaff (1964) mentioned that in a personal communication that he had with Ortlepp an unidentified tapeworm was obtained by Ortlepp from *Bathyergus suillus*, collected at Houtbay, near Cape Town. Also, De Graaff (1964) wrote that Ortlepp told him that he found cysts of an unidentified species of *Echinococcus* Rudolphi, 1801 obtained from the muscles of the abdominal cavity as well as liver of *G. capensis* collected at Wynberg, near Cape Town, South Africa (Hüttner and Romig 2009).

Levine and Ivens (1965) described the first coccidian parasite, *Eimeria heterocephali* from the mucosal epithelial cells of the cecum of a *Heterocephalus glaber* specimen collected at Somaliland or Kenya, South Africa.

Schmidt and Canaris (1968) reported *Ascarops africana* (Sandground, 1933) from *Tachyoryctes macrocephalus* (Rüppell, 1842) collected from Njoro, Kenya, East Africa.

Several years later, De Graaff (1981) reported *Inermicapsifer madagascariensis* (Davaine, 1870) from the Common mole-rat, *Cryptomys hottentotus* (Lesson, 1826) (Bathyergidae: Hystricomorpha), collected from Shingwedzi, South Africa.

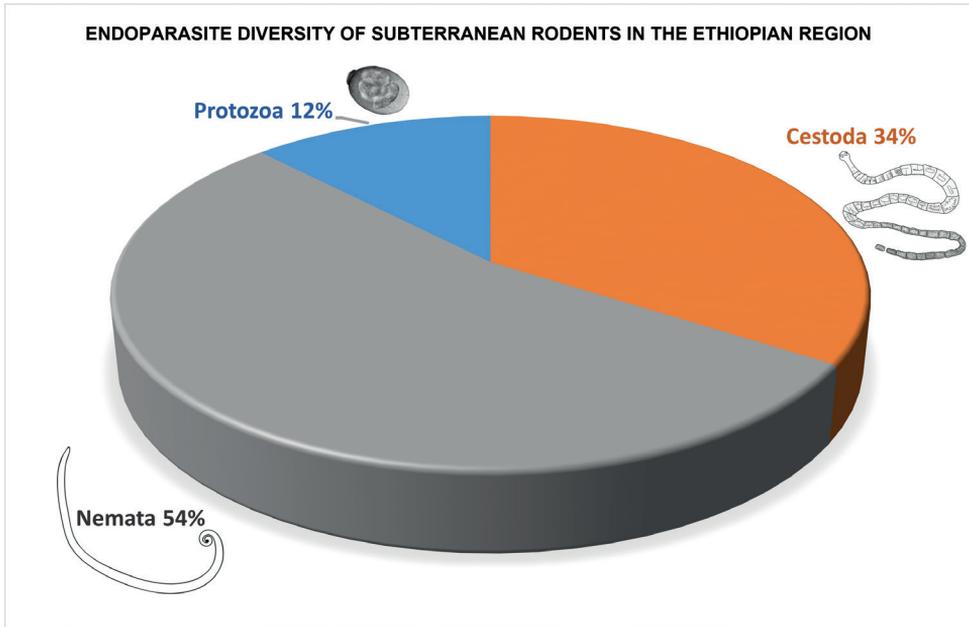


Figure 1. Pie diagram representing percentage taxon composition of the higher classification of endoparasite diversity found infecting subterranean rodents from the Ethiopian zoogeographic region derived from records in the literature published from 1864 through 2018. The Nemata are the most speciose representing 54% of the total endoparasite fauna, followed by Cestoda (34%), and Protozoa (12%).

Scharff et al. (1997) reported *Inermicapsifer madagascariensis* from the small intestine, and *Protospirura muricola* (Geddes, 1916) from the colon of *Fukomys kafuensis* (Burda et al., 1999) collected from Itezhi-Tezhi, Zambia. They also found an unidentified species of *Calodium* Moravec, 1982 (syn. *Capillaria* Zeder, 1800) (eggs only), *I. madagascariensis*, and an unknown *Raillietina* Fuhrman, 1920, from the small intestine, and *P. muricola* from the abdominal cavity of *Fukomys mechowii* (Peters, 1881) collected from Ndole, Zambia. The discovery of *P. muricola* in the abdominal cavity was probably a result of these nematodes moving from the stomach during or after the necropsy event of the individual *F. mechowii* mentioned.

Koudela et al. (2000) described *Eimeria burdai*, as a new species of coccidian from the subterranean African silvery mole-rat, *Heliophobius argenteocinereus* Peters, 1846, collected from Lubalashi Province, central Zambia.

Baruš et al. (2003) studied the relative concentration of heavy metals in helminth parasites; several Silvery mole-rats, *H. argenteocinereus*, were necropsied for their internal parasite tissues collected from the Blantyre-Limbe region of Malawi, southeastern Africa. As a result, two species of helminths were found, including *Inermicapsifer arvicanthidis* (Kofend, 1917) and *Protospirura muricola*, and these specimens were later examined for four heavy metal elements (cadmium, copper, lead, and zinc), and compared against the liver and muscle tissues of their hosts. The same species of parasites from these same hosts were reported by Tenora et al. (2003).

Table 2. Endoparasite species diversity of Ethiopian subterranean rodents and their known original hosts. Authorities are given for parasite and host species.

Host species	Parasite species	References
<i>Bathyergus suillus</i> (Schreber, 1782)	<i>Mammalakis macrospiculum</i> (Ortlepp, 1939)	Lutermann et al. 2012
	<i>Ortleppstrongylus bathyergi</i> Ortlepp, 1939	De Graaff 1964
	<i>Paralibyostrongylus bathyergi</i> (Ortlepp, 1939)	Lutermann et al. 2012
	<i>Rodentolepis</i> Spasskii, 1954	Lutermann et al. 2012
	<i>Taenia</i> Linnaeus, 1758	Lutermann et al. 2012
	<i>Trichostrongylus</i> Looss, 1905	De Graaff 1964
	<i>Trichuris</i> Roederer, 1761	Lutermann et al. 2012
<i>Cryptomys hottentotus</i> (Lesson, 1826)	<i>Ascarops africana</i> (Sandground, 1933)	Lutermann et al. 2013
	<i>Heligmonina</i> Baylis, 1928	Viljoen et al. 2011
	<i>Inermicapsifer madagascariensis</i> (Davaine, 1870)	De Graaff 1981
	<i>Mammalakis macrospiculum</i> (Ortlepp, 1939)	Archer et al. 2017
	<i>Mathevotaenia</i> Akhumyan, 1946	Viljoen et al. 2011
	<i>Neoheligionella</i> Durette-Desset, 1971	Archer et al. 2017
	<i>Protospirura</i> Seurat, 1914	Viljoen et al. 2011
	<i>Raillietina</i> Fuhrman, 1920	Lutermann et al. 2013
	<i>Trichuris</i> Roederer, 1761	Archer et al. 2017
	<i>Hexametra</i> Travassos, 1920	Lutermann et al. 2018
<i>Fukomys anselli</i> (Burda et al., 1999)	<i>Inermicapsifer</i> Janicki, 1910	Lutermann et al. 2018
	<i>Mammalakis zambiensis</i> Junker et al., 2017	Junker et al. 2017
	<i>Protospirura muricola</i> (Gedoelst, 1916)	Lutermann et al. 2018
	<i>Protospirura numidica</i> Seurat, 1914	Lutermann et al. 2018
	<i>Protospirura</i> Seurat, 1914	Lutermann et al. 2018
	<i>Rodentolepis</i> cf. <i>microstoma</i> (Dujardin, 1945)	Lutermann et al. 2018
	<i>Inermicapsifer madagascariensis</i> (Davaine, 1870)	Scharff et al. 1997
<i>Fukomys kafuensis</i> (Burda et al., 1999)	<i>Protospirura muricola</i> (Gedoelst, 1916)	Scharff et al. 1997
	<i>Capillaria</i> Zeder, 1800	Scharff et al. 1997
<i>Fukomys mechowii</i> (Peters, 1881)	<i>Inermicapsifer madagascariensis</i> (Davaine, 1870)	Scharff et al. 1997
	<i>Protospirura muricola</i> (Gedoelst, 1916)	Scharff et al. 1997
	<i>Raillietina</i> Fuhrman, 1920	Scharff et al. 1997
<i>Georchus capensis</i> (Pallas, 1778)	<i>Coenurus spalacis</i> Diesing, 1864	Diesing 1864
	<i>Echinococcus</i> Rudolphi, 1801	De Graaff 1964; Hüttner and Romig 2009
	<i>Trichuris</i> Roederer, 1761	Lutermann et al. 2012
<i>Heliophobius argenteocinereus</i> Peters, 1846	<i>Eimeria burdai</i> Koudela et al., 2000	Koudela et al. 2000
	<i>Eimeria heliophobii</i> Modrý et al., 2005	Modrý et al. 2005
	<i>Eimeria nafuko</i> Modrý et al., 2005	Modrý et al. 2005
	<i>Eimeria yamikamiae</i> Modrý et al., 2005	Modrý et al. 2005
	<i>Inermicapsifer arvicanthidis</i> (Kofend, 1917)	Baruš et al. 2003; Tenora et al. 2003
	<i>Protospirura muricola</i> (Gedoelst, 1916)	Baruš et al. 2003; Tenora et al. 2003
<i>Heterocephalus glaber</i> Rüppell, 1842	<i>Eimeria heterocephali</i> Levine & Ivens, 1965	Levine and Ivens 1965
<i>Tachyoryctes splendens</i> (Rüppell, 1835)	<i>Taenia brauni</i> Setti, 1897	Fain 1956
<i>Tachyoryctes macrocephalus</i> (Rüppell, 1842)	<i>Ascarops africana</i> (Sandground, 1933)	Schmidt and Canaris 1968

Modrý et al. (2005) described three new species of *Eimeria* from the Silvery mole-rat *H. argenteocinereus* from Malawi, including: *Eimeria heliophobii*, *E. nafuko*, and *E. yamikamiae* extracted from the fecal samples from the host specimens.

Viljoen et al. (2011), in an ecological study of the role of host traits, season, and group size on parasite burdens in a cooperative breeding mammal, captured 87 individual mole-rats were from the Tshwane region of South Africa in different seasons. Three helminths that were not identified to the species level were obtained from

the small intestine of *Cryptomys hottentotus*, including *Heligmonina* sp. Baylis, 1928, *Mathevotaenia* sp. Akhumyan, 1946, and *Protospirura* sp. Seurat, 1914.

Lutermann and Bennett (2012), during a year-long joint research and eradication project for *Bathyergus suillus* at Cape Town International Airport, Cape Town, South Africa, found these rodents infected with three species of nematodes, including: *Mammalakis macrospiculum*, *Paralibyostrogylus bathyergi*, and *Trichuris* sp. Roederer, 1761, and two species of tapeworms, *Rodentolepis* sp. Spasskii, 1954, and *Taenia* sp. Linnaeus, 1758.

Just one year later, Lutermann et al. (2013), during the study on energetic benefits and costs of parasitism in a cooperative mammal identified *Raillietina* sp., and *Ascarops africana* from the small intestine of *Cryptomys hottentotus* collected from KwaZulu-Natal, South Africa.

Archer et al. (2017), in a seasonal comparative study between two Common mole-rat populations found *Mammalakis macrospiculum*, *Neoheligmonella* Durette-Desset, 1971, and *Trichuris* sp. in *Cryptomys hottentotus* collected from two different habitats, including an arid site, 25 km outside of Kamieskroon, the Northern Cape and a mesic site near Darling, western Cape, South Africa.

Junker et al. (2017) described a new species of ascaridid nematode, *Mammalakis zambiensis* acquired from the large intestine and cecum of Ansell's mole-rat, *Fukomys anselli* (Burda et al., 1999), captured from west of Lusaka at Mukulaikwa Farm Block, Zambia.

Lutermann et al. (2018) reported the following gastrointestinal parasites from Ansell's mole-rat, *F. anselli* in Zambia. Those include *Hexametra* sp. Travassos, 1920, *Inermicapsifer* sp. Janicki, 1910, *Protospirura muricola*, *Protospirura numidica* Seurat, 1914, and *Rodentolepis* cf. *microstoma* (Dujardin, 1945).

Palaearctic subterranean rodent endoparasites

See graphical summary in Fig. 2 and endoparasite list in Table 3.

Interestingly, even though helminthology began in Europe (the western Palaearctic) in the late 1800's with the work of Leuckart, it was not until the 1920's when Schulz (1927) described the first two species of helminth parasites from two species of subterranean rodents from the Palaearctic region. First, *Physocephalus ellobii* Schulz, 1927 was found from the stomach of *Ellobius tancrei* Blasius, 1884 collected from Kotlyrevsky, the northern Caucasus region of Russia. Second, *Gongylonema longispiculum spalacis* Schulz, 1927 was described as the first subspecies found under the mucous membrane of the stomach of *Spalax microphthalmus* Gldenstdt, 1770 collected from the village Kurichya Kosa near the Don River region north of the coast of the Sea of Azov, Russia. Soon after, Marcu (1930) described *Mammalakis spalacis* Marcu, 1930 also obtained from *S. microphthalmus* collected from Romania.

Somewhat later, Schulz and Aloyan (1950), described *Ascaris spalacis* Schulz & Aloyan, 1950 from Lesser mole-rat, *Nannospalax leucodon* (Nordmann, 1840). Kirshenblat collected the materials included in the description from near the small towns of

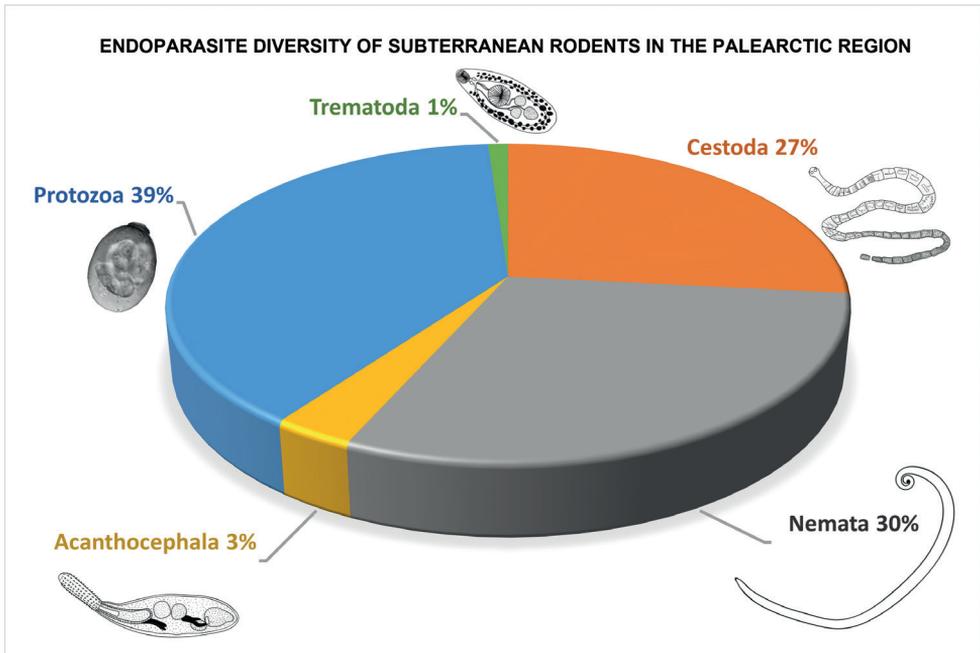


Figure 2. Pie chart showing percentage of infection summary of the higher-level classification of endoparasite diversity among Palearctic subterranean rodents derived from a survey of published records from 1927 through 2022. Protozoa constitute the greatest diversity of endoparasites accounting for 39% of the total parasite species recovered followed by Nemata (30%), Cestoda (27%), Acanthocephala (3%), and the Trematoda coming in at only 1%.

Amamla and Chandura, of the Spitakskii and Akhalkalakskii regions of Armenia, in 1947. All these nematode samples were found from the small intestines of the hosts, necropsied by Aloyan in 1948.

Petrov and Potechina (1953) described *Trichuris spalacis* from *S. microphthalmus* collected from an unspecified locality in Ukraine.

Razumova (1957) reported the following helminth parasites found in specimens of the Long-clawed mole vole, *Prometheomys schaposchnikowi* Satunin, 1901, captured from Ossetia, Russia. These include *Dicrocoelium dendriticum* (Rudolphi, 1819), *Heligmosomum halli* (Schulz, 1926), *Microcephaloides* Haukisalmi et al., 2008, *Taenia polyacantha* Leuckart, 1856, and *Hydatigera* (syn. *Taenia*) *taeniaeformis* (Batsch, 1786).

Tokobaev (1960) reported the collection of *Ellobius talpinus* (Pallas, 1770) from the Kyrgyz Republic and found larvae of *Echinococcus multilocularis* from the liver. In the same report, he reported *Aprostatanrya macrocephala* Douthitt, 1915, from the small intestine and larvae of *Mesocostoides* Vaillant, 1863 from the body cavity, liver, and small intestines. In work on mole voles just a short time later, Zanina and Tokobaev (1962) reported *Catenotaenia pusilla* Goeze, 1782, *Hymenolepis diminuta* Rudolphi,

1819, *Moniliformis moniliformis* Bremser, 1811, and *Hydatigera* (syn. *Taenia*) *taeniaeformis* (Batsch, 1786) from *E. talpinus* collected in Tajikistan.

Andreiko (1963) reported that from 1959 through 1962, 70 Lesser mole-rats, (*Nannospalax leucodon*) collected from the central part of Moldova, Romania had the following helminths: *Mammalakis spalacis* from the cecum, *Taenia straminea* (Goeze, 1782) Spasskii, 1954 and unidentified species of *Aprostotandrya* Kirshenblat, 1938 from the small intestine. In addition, she described *Heligmosomum moldovenis* Andreiko, 1963 from the small intestine of *N. leucodon*.

Kozlov and Yangolenko (1963) described *Ganguleterakis spalaxi* Kozlov & Yangolenko, 1963 from *Spalax microphthalmus* collected from Ukraine.

Kirshenblat (1965) described a new species of nematode *Heligmosomum spalacis* from the small intestine of the mole-rat *Spalax graecus* Nehring, 1898 collected from Chernivtsi, Ukraine.

Levine and Ivens (1965) described two species of *Eimeria* Fischer, 1814 from the Northern mole vole, including: *Ellobius kazakhstanensis* Levine & Ivens, 1965, and *Ellobius talpini* Levine & Ivens, 1965 from the fecal of *Ellobius talpinus* collected from Kazakhstan.

Musaev and Veisov (1963) described *Eimeria lutescenae* Musaev & Veisov, 1963 from *Ellobius lutescens* Thomas, 1897 from Nakhichevanskaia, Azerbaijan. In addition, two *Eimeria* (Schneider, 1875) species were reported with their descriptions, including: *Eimeria ellobii* Svanbaev, 1965 and *Eimeria tadshikistanica* Veisov, 1964 from *Ellobius talpinus* collected from Tajikistan.

Shaykenov and Mahmutov (1968) reported *Echinococcus multilocularis* found in *Myospalax myospalax* (Laxmann, 1773) collected from eastern Kazakhstan. This record is considered a new intermediate host for this tapeworm. Also in the same year, Mézszáros (1968) reported the occurrence of *Heligmosomum spalacis* recovered from the Lesser mole-rat, *Nannospalax leucodon*, collected from Hungary.

Murai (1968) recorded the Lesser mole-rat, *N. leucodon*, as a new host of *Moniliformis moniliformis*. The acanthocephalid parasite was extracted from the small intestines of two individuals of Lesser mole-rats. Also, *Heligmosomum spalacis* was found in the host. The study has conducted near Hajdubagos village, Hajdu-Bihar, in Hungary.

Nadtochii (1970), during a study of helminth parasites of rodents in far eastern Russia, the author described *Heligmosomum myospalaxi* Nadtochii, 1970 obtained from the small intestine of *Myospalax myospalax* collected from the seashore of eastern Russia.

Wertheim and Nevo (1971), during a study of helminths of birds and mammals from Israel recovered several species of helminth parasites from the Middle East blind mole-rat, *Nannospalax ehrenbergi* Nehring, 1898 including *Ganguleterakis spalaxi*, *Gongylonema longispiculum* Schulz, 1927, *Trichuris muris* (Schränk, 1788), and one unidentified nematode in the genus *Heligmonella* Mönnig, 1927. They also described *Heligmonina nevoi* Wertheim & Nevo, 1971 from the same host species.

Sharpilo (1973) described *Longistriata spalacis* from the small intestine of Lesser mole-rat, *Nannospalax leucodon*. He reported that this nematode species was also found from *Spalax arenarius* Reshetnik, 1939, and *Spalax microphthalmus*. These specimens were all collected from Ukraine.

Table 3. Endoparasite species diversity of Palearctic subterranean rodents and their known original hosts. Authorities are given for parasite and host species.

Host species	Parasite species	References
<i>Cannomys bodius</i> (Hodgson, 1841)	<i>Hymenolepis diminuta</i> (Rudolphi, 1819)	Malsawmtluangi and Tandon 2009
<i>Ellobius fuscicapillus</i> (Blyth, 1843)	<i>Syphacia obvelata</i> (Rudolphi, 1802)	Arzamani et al. 2017
<i>Ellobius lutescens</i> Thomas, 1897	<i>Eimeria lutescens</i> Musaev & Veisov, 1963	Musaev and Veisov 1965a
<i>Ellobius talpinus</i> (Pallas, 1770)	<i>Aprostandrya macrocephala</i> Douthitt, 1915	Tokobaev 1960
	<i>Catenotaenia pusilla</i> Goeze, 1782	Zanina and Tokobaev 1962a
	<i>Echinococcus multilocularis</i> Leuckart, 1863	Tokobaev 1960
	<i>Eimeria ellobii</i> Swanbaev, 1965	Musaev and Veisov 1965a
	<i>Eimeria kazakhstanensis</i> Levine, 1965	Levine and Ivens 1965
	<i>Eimeria tadshikistanica</i> Veisov, 1964	Musaev and Veisov 1965a
	<i>Eimeria talpini</i> Levine, 1965	Levine and Ivens 1965
	<i>Hymenolepis diminuta</i> (Rudolphi, 1819)	Zanina and Tokobaev 1962a
	<i>Mesocestoides</i> Vaillant, 1863	Tokobaev 1960
	<i>Moniliformis moniliformis</i> Bremser, 1811	Zanina and Tokobaev 1962a
	<i>Nomadolepis ellobii</i> Makarikov et al., 2010	Makarikov et al. 2010
	<i>Physocephalus ellobii</i> Schulz, 1927	Schultz 1927
	<i>Hydatigera</i> (syn. <i>Taenia</i>) <i>taeniaeformis</i> (Batsch, 1786)	Zanina and Tokobaev 1962a
<i>Ellobius tancrei</i> Blasius, 1884	<i>Arostrilepis batsaikhani</i> Dursahinhan et al., 2022	Dursahinhan et al. 2022
	<i>Echinococcus multilocularis</i> Leuckart, 1863	Afonso et al. 2015
<i>Eospalax baileyi</i> (Thomas, 1911)	<i>Eimeria baileyi</i> Cao et al., 2014	Cao et al. 2014
	<i>Eimeria fani</i> Cao et al., 2014	Cao et al. 2014
	<i>Eimeria menyuanensis</i> Cao et al., 2014	Cao et al. 2014
	<i>Eimeria myospalacensis</i> Cao et al., 2014	Cao et al. 2014
	<i>Ransomus qinghaiensis</i> Ming et al., 2004	Ming et al. 2004
	<i>Versteria</i> (syn. <i>Taenia</i>) <i>mustelae</i> Gmelin, 1790	Zhao, et al. 2014
<i>Eospalax fontanierii</i> (Milne-Edwards, 1867)	<i>Echinococcus multilocularis</i> Leuckart, 1863	Craig 2006
	<i>Heligmoptera giraudouxi</i> Elias et al., 2002	Elias, et al. 2002
	<i>Heligmoptera querei</i> Elias et al., 2002	Elias, et al. 2002
<i>Myospalax myospalax</i> (Laxmann, 1773)	<i>Echinococcus multilocularis</i> Leuckart, 1863	Shaykenov and Mahmutov 1968
	<i>Heligmoptera sibirica</i> Shakhmatova, 1990	Shakhmatova 1990
	<i>Heligmosomum myospalaxi</i> Nadtochiĭ, 1970	Nadtochiĭ 1970
	<i>Hymenolepis rymzhanovi</i> Makarikov & Tkach, 2013	Makarikov and Tkach 2013
	<i>Moniliformis clarki</i> (Ward, 1917)	Vlasenko and Krivopalov 2017
	<i>Paranoplocephala</i> Lühe, 1910	Vlasenko and Krivopalov 2017
	<i>Versteria mustelae</i> (Gmelin, 1790)	Vlasenko and Krivopalov 2017
<i>Myospalax psilurus</i> (Milne-Edwards, 1874)	<i>Ascarops strongylina</i> (Rudolphi, 1819)	Ganzorig et al. 1999
<i>Nannospalax ehrenbergi</i> Nehring, 1898	<i>Eimeria adiyamanensis</i> Sayin, 1980	Sayin 1980
	<i>Eimeria anzanensis</i> Couch et al, 1993	Couch et al. 1993
	<i>Eimeria carmelensis</i> Couch et al, 1993	Couch et al. 1993
	<i>Eimeria celebii</i> Sayin, 1980	Sayin 1980
	<i>Eimeria haranica</i> Sayin, 1980	Sayin 1980
	<i>Eimeria marasensis</i> Sayin, 1980	Sayin 1980
	<i>Eimeria microspalacis</i> Golemansky & Darawish, 1992	Golemansky and Darwish 1992
	<i>Eimeria oytuni</i> Sayin, 1980	Sayin 1980
	<i>Eimeria spalacensis</i> Couch et al, 1993	Couch et al. 1993
	<i>Eimeria torosicum</i> Sayin, 1980	Sayin 1980
	<i>Eimeria urfensis</i> Sayin, 1980	Sayin 1980
	<i>Ganguleterakis spalaxi</i> Kozlov & Yangolenko, 1963	Wertheim and Nevo 1971
	<i>Gongylonema longispiculum</i> Schulz, 1927	Wertheim and Nevo 1971
	<i>Heligmonella</i> Mönnig, 1927	Wertheim and Nevo 1971
	<i>Heligmonina nevoi</i> Wertheim & Nevo, 1971	Wertheim and Nevo 1971
	<i>Isopora spalacensis</i> Couch et al, 1993	Couch et al. 1993
	<i>Microcephaloides nevoi</i> (Fair et al., 1990) Haukisalmi 2009	Fair et al. 1990; Haukisalmi 2009
	<i>Trichuris muris</i> (Schränk, 1788)	Wertheim and Nevo 1971

Host species	Parasite species	References
<i>Nannospalax leucodon</i> (Nordmann, 1840)	<i>Aprostatandrya</i> Kirshenblat, 1938	Andreiko 1963a
	<i>Ascaris spalacis</i> Shults & Aloyan, 1950	Shults and Aloyan 1950
	<i>Coenurus parviuncinatus</i> Kirschenblatt, 1939	Kornushin and Sharpilo 1986
	<i>Eimeria celebii</i> Sayin, 1980	Nalbantoğlu et al. 2010
	<i>Eimeria elliptica</i> Sayin et al., 1977	Sayin et al. 1977
	<i>Eimeria lalahanensis</i> Sayin, et al., 1977	Sayin et al. 1977
	<i>Eimeria leucodonica</i> Veisov, 1975	Veisov 1975
	<i>Eimeria maralikiensis</i> Veisov, 1975	Veisov 1975
	<i>Eimeria oytuni</i> Sayin, 1980	Nalbantoğlu et al. 2010
	<i>Eimeria spalacis</i> Sayin et al., 1977	Sayin et al. 1977
	<i>Eimeria talikiensis</i> Veisov, 1975	Veisov 1975
	<i>Eimeria torosicum</i> Sayin, 1980	Nalbantoğlu et al. 2010
	<i>Eimeria turkmenica</i> Sayin et al., 1977	Sayin et al. 1977
	<i>Eimeria tuzdili</i> Sayin, et al., 1977	Sayin et al. 1977
	<i>Heligmosomum spalacis</i> Kirschenblat, 1965	Mészáros 1968
	<i>Heligmosomum moldovensis</i> Andreiko, 1963	Andreiko 1963a
	<i>Isospora anaticum</i> Sayin, et al., 1977	Sayin et al. 1977
	<i>Longistriata spalacis</i> Sharpilo, 1973	Sharpilo 1973a
	<i>Mammalakis spalacis</i> Marcu, 1930	Andreiko 1963a
	<i>Moniliformis moniliformis</i> Bremser, 1811	Murai 1968
<i>Taenia straminea</i> (Goeze, 1782) Spasskii 1954	Andreiko 1963a	
<i>Prometheomys schaposchnikowi</i> Satunin, 1901	<i>Dicrocoelium dendriticum</i> (Rudolphi, 1819)	Razumova 1957
	<i>Heligmosomum halli</i> (Schulz, 1926)	Razumova 1957
	<i>Microcephaloides</i> Haukisalmi et al., 2008	Razumova 1957
	<i>Taenia polyacantha</i> Leuckart, 1856	Razumova 1957
	<i>Hydatigera</i> (syn. <i>Taenia</i>) <i>taeniaeformis</i> (Batsch, 1786)	Razumova 1957
	<i>Mammalakis spumosa</i> (Schneider, 1866)	Chaisiri et al. 2017
<i>Rhizomys pruinosus</i> (Blyth, 1851)	<i>Cryptosporidium occultus</i> Kvač, 2018	Wei et al. 2019
	<i>Cryptosporidium parvum</i> Tzyzer, 1912	Wei et al. 2019
<i>Rhizomys sinensis</i> Gray, 1831	<i>Longistriata spalacis</i> Sharpilo, 1973	Sharpilo 1973a
<i>Spalax arenarius</i> Reshetnik, 1939	<i>Heligmosomum spalacis</i> Kirschenblat, 1965	Kirschenblat 1965a
<i>Spalax graecus</i> Nehring, 1898	<i>Ganguletenakis spalaxi</i> Kozlov & Yangolenko, 1963	Kozlov and Yangolenko 1963a
<i>Spalax microphthalmus</i> GÜldenstädt, 1770	<i>Gongyloinema longispiculum spalacis</i> Schulz, 1927	Schultz 1927
	<i>Longistriata spalacis</i> Sharpilo, 1973	Sharpilo 1973a
	<i>Mammalakis spalacis</i> Marcu, 1930	Marcu 1930
	<i>Hydatigera</i> (syn. <i>Taenia</i>) <i>taeniaeformis</i> (Batsch, 1786)	Sharpilo 1976
	<i>Trichuris spalacis</i> (Petrov & Potechina, 1953)	Petrov and Potechina 1953

Sharpilo (1976), during a study of helminth parasites of rodent fauna in Ukraine, reported *Hydatigera* (syn. *Taenia*) *taeniaeformis* from *Spalax microphthalmus*.

Veisov (1975) described three new species of coccidia of the genus *Eimeria* Schneider, 1875 from *Nannospalax leucodon*, including *Eimeria maralikiensis* Veisov, 1975 and *Eimeria talikiensis* Veisov, 1975 collected from Talnisk and Maralik Aniisk regions, Armenian, also, describing *Eimeria leucodonica* Veisov, 1975 from the Talnisk region only.

Sayin et al. (1977), during a survey of Lesser mole-rats, *Nannospalax leucodon*, in Lalahan district in Ankara, Turkey, described six new species of coccidia in the genus *Eimeria* Schneider, 1875 including *E. elliptica* Sayin et al., 1977, *E. lalahanensis* Sayin et al., 1977, *E. spalacis* Sayin et al., 1977, *E. turkmenica* Sayin et al., 1977, *E. tuzdili* Sayin et al., 1977, and *Isospora anaticum* Sayin et al., 1977.

Sayın (1980), during a survey conducted from 1976 through 1978, studied 41 individuals of the Middle East blind mole-rats, *Nannospalax ehrenbergi*, from Urfa, Adiyaman, and Maras provinces in Turkey. As a result, seven new species of coccidia of the genus *Eimeria* Schneider, 1875 were described. Those include *E. adiyamanensis* Sayın, 1980, *E. celebii* Sayın, 1980, *E. haranica* Sayın, 1980, *E. marasensis* Sayın, 1980, *E. oytuni* Sayın, 1980, *E. torosicum* Sayın, 1980, and *E. urfensis* Sayın, 1980.

Korniushin and Sharpilo (1986) reported a larval *Taenia* which they reported as *Coenurus parviuncinatus* Kirschenblatt, 1939 obtained from *Nannospalax leucodon* collected from Armenia.

Fair et al. (1990) described a new species of tapeworm, *Microcephaloides nevoi* Fair et al., 1990 from the Middle East blind mole-rat *Nannospalax ehrenbergi* in Masada, Golan Heights, Israel. This species has been redescribed by Haukisalmi (2009).

Shakhmatova (1990) described *Heligmoptera sibirica* Shakhmatova, 1990 found from the Siberian zokor, *Myospalax myospalax*, collected from the Gorno-Altai autonomous region of Russia.

Golemansky and Darwish (1992) described *Eimeria microspalacis* Golemansky & Darwish, 1992 from the Middle East blind mole-rat, *Nannospalax ehrenbergi*, collected from the regions of Damascus and Latakia, western Syria.

Couch et al. (1993) described four coccidian parasites obtained from the Middle East blind mole-rat, *Nannospalax ehrenbergi*, collected from 12 different localities in Israel including *Eimeria anzanensis* Couch et al., 1993, *E. carmelensis* Couch et al., 1993, *E. spalacensis* Couch et al., 1993, and *Isospora spalacensis* Couch et al., 1993.

Ganzorig et al. (1999) redescribed *Ascarops strongylina* (Rudolphi, 1819) from the Transbaikal zokor, *Myospalax psilurus* (Milne-Edwards, 1874) collected from near the Halh Gol River, Dornod province, eastern Mongolia.

Elias et al. (2002), during a joint program of French, British, and China on echinococcosis screening in Zhang County, China (Gansu), two new species of *Heligmoptera* Nadtochiy, 1977 were described from the small intestines of the Chinese zokor, *Eospalax fontanierii* (Milne-Edwards, 1867) including: *Heligmoptera giraudouxi* Elias & Durette-Desset, 2002, and *Heligmoptera querei* Elias & Durette-Desset, 2002 with the new description of the genus.

More recently in China, Ming et al. (2004) described *Ransomus qinghaiensis* Ming et al., 2004 from the cecum of the Plateau zokor, *Eospalax baileyi* (Thomas, 1911) collected from Qilian County, Qinghai province.

Craig (2006), in a survey and epidemiological assessment of human alveolar echinococcosis in 33 provinces of China, listed the Chinese zokor, *Eospalax fontanierii* as one of the intermediate hosts of *Echinococcus multilocularis*.

Malsawmtluangi and Tandon (2009) reported *Hymenolepis diminuta* attained from the Lesser bamboo rat, *Cannomys bodius* (Hodgson, 1841) collected from Mizoram, northeast India.

Nalbantoğlu et al. (2010) reported three species of coccidia acquired from the feces of the Lesser mole-rat, *Nannospalax leucodon*, collected from the Eryaman district of Ankara, Turkey. Those are *Eimeria celebii*, *E. oytuni* Sayın, 1980, and *E. torosicum* Say-

in, 1980. In the same year, Makarikov et al. (2010) described the cestode *Nomadolepis ellobii* Makarikov et al., 2010, simultaneously establishing a new genus for the tapeworm that was obtained from the small intestine of the Northern mole vole, *Ellobius talpinus*, collected from southwestern Siberia, Russia.

Soon after, Makarikov and Tkach (2013) described *Hymenolepis rymzhanovi* Makarikov & Tkach, 2013 from the small intestine of the Siberian zokor, *Myospalax myospalax* collected from eastern Kazakhstan.

Cao et al. (2014) described four new species of *Eimeria* from the Plateau zokor, *Eospalax baileyi*, collected from Haibei area, Qinghai Province, China. The parasites include *Eimeria baileyi* Cao et al., 2014, *Eimeria fani* Cao et al., 2014, *Eimeria menyuanensis* Cao et al., 2014, and *Eimeria myospalacensis* Cao et al., 2014. In the same year, Zhao et al. (2014) identified *Versteria* (syn. *Taenia*) *mustelae* (Gmelin, 1790) using DNA sequencing of larval cysts found in the Plateau zokor, *Eospalax baileyi* collected from Datong County, east of Qinghai province, China. In this study, no data were provided on number of individuals infected.

Afonso et al. (2015) reported *Echinococcus multilocularis* from the livers of Eastern mole voles, *Ellobius tancrei* which acts as the intermediate host for this cestode, collected from Sary Mogol, Alay valley, Kyrgyzstan. The authors also noted that the definitive hosts were local domestic dogs, whose feces were examined for *E. multilocularis*. The parasite samples from the dogs were genetically identical to those found in the intermediate host.

In 2017, a flurry of activity resulted from workers in the field. Vlasenko and Krivopalov (2017) reported *Moniliformis clarki* (Ward, 1917), *Paranoplocephala* Lühe, 1910 and larvae of *Versteria mustelae* (Gmelin, 1790) from *Myospalax myospalax* collected from the southern Tomsk region, Russia. Then, Arzamani et al. (2017) reported *Syphacia obvelata* (Rudolphi, 1802) (probably a misidentification as *S. obvelata* occurs only in species of *Mus*) obtained in the Southern mole vole, *Ellobius fuscocapillus* (Blyth, 1843), collected from north Khorasan province of northeast Iran. Finally in 2017, Chaisiri et al. (2017), during an ecological study of host-parasite associations, reported *Mammalakis spumosa* (Schneider, 1866) from *Rhizomys pruinosus* in Cambodia.

Wei et al. (2019) reported *Cryptosporidium parvum* Tyzzer, 1912 and *C. occultus* Kváč, 2018 found in the Chinese bamboo rat, *Rhizomys sinensis*, collected from south-central China.

Dursahinhan et al. (2022) described *Arostrilepis batsaikhani* from the Zaisan mole vole, *Ellobius tancrei* collected from Baitag Bogd, Hovd province, western Mongolia.

Endoparasites of Nearctic and northern Neotropical subterranean rodents

See graphical summary in Fig. 3 and endoparasite list Table 4.

Leidy in (1857), at a meeting of the Academy of Natural Sciences of Philadelphia, displayed some warbles taken from an evidently incapacitated pocket gopher by the side of the road, identified as *T. borealis* [probably a synonym of *T. talpoides*] near

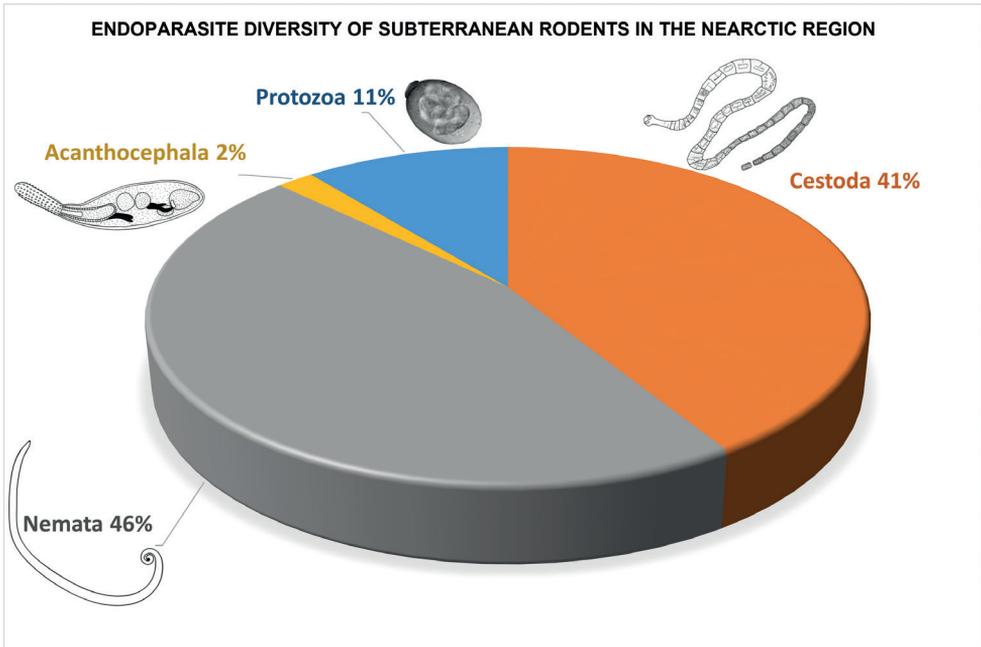


Figure 3. Percentage taxon composition pie diagram of the higher classification of endoparasite diversity occurring in Nearctic subterranean rodents (Family Geomyidae) derived from literature records published from 1857 through 2020. Among these endoparasites, the Nemata represent 46% of the species found followed by Cestoda (41%), Protozoa (11%), and Acanthocephala at just 2%.

the Bridger's pass summit of the Rocky Mountains. This record represents the first known report of an endoparasite from a member of the rodent family Geomyidae. Soon after the groundbreaking work by Leidy, Charles Wardell Stiles (1895) reported the first helminth parasite from a geomyid when he described *Pseudocittotaenia praecoquis* (Stiles, 1895) from *Geomys bursarius* (Shaw, 1800) collected near Ames, Iowa (Stiles, 1897).

Hall (1912) reported on the parasite fauna of Colorado and recorded several nematodes and some unidentified cestodes from *Thomomys fessor* J.A. Allen (probably a syn. of *T. talpoides*). Soon after, Herman Douthitt (1915) described four new species of anoplocephalid cestodes from pocket gophers collected from the central United States. *Anoplocephaloides variabilis* (Douthitt, 1915), *A. infrequens* (Douthitt, 1915), and *Andrya macrocephala* Douthitt, 1915 were all described from specimens taken from *G. bursarius* collected from Illinois, Minnesota, and North Dakota. *Monoecocestus anoplocephaloides* (Douthitt, 1915) was described from some specimens taken from *Geomys breviceps* Baird collected near Norman, Oklahoma. Douthitt (1915) also reported one unidentified species of *Oöchoristica* Luhe, 1898, and one immature form of *Cittotaenia*, now known as *Pseudocittotaenia*, Tenora, 1976 from *G. bursarius*. Douthitt (1915) also reported numerous individuals of eight different species of *Hymenolepis* from two species of pocket gophers including: *G. bursarius* collected in Illinois,

Wisconsin, Minnesota, North Dakota, and Manitoba, Canada; *G. breviceps* collected in Oklahoma and Texas; and *Geomys personatus* True, collected in Texas.

Hall (1916) described the following nematodes from *Thomomys fessor* J. A. Allen [syn. *T. talpoides* (Richardson, 1828)]: *Trichuris fessor* Hall, 1916, from specimens collected near both Crested Butte and Livermore, Colorado and *Vexillata vexillata* (Hall, 1916) from gophers collected from mountain meadows near Livermore, Colorado. These nematodes were described from the same material that Hall (1912) had previously studied. Additionally, the nematode *Protospirura ascaroidea* Hall, 1916 was described from specimens recovered from the stomachs of *Geomys bursarius* collected near Norman, Oklahoma by Herman Douthitt and sent to MC Hall for study.

Skidmore (1929) described a species of Coccidia named *Eimeria geomydis* Skidmore, 1929 from the intestinal tract of *Geomys bursarius* Shaw, collected near Lincoln, Nebraska while Dikmans (1932) reported *Capillaria* (syn. *Calodium*) *hepaticum* (Bancroft, 1893) as a parasite of *Thomomys fessor* (syn. *T. talpoides*) collected in the Medicine Bow Mountains of Wyoming. In that same year, English (1932) examined 161 specimens of *Geomys bursarius* collected in Brazos County, Texas and found 23 infected with the stomach nematode *Protospirura ascaroidea* Hall, 1916, and eight infected with an unknown species of *Hymenolepis*.

Hubbell and Goff (1939) reported *Mastophorus muris ascaroides* (Gmelin, 1790) to occur commonly in the stomach of *Geomys* sp. (most likely *G. pinetis*) collected near Leesburg, Lake County, Florida.

McIntosh (1941) described *Catenotaenia linsdalei* McIntosh, 1941 from *Thomomys bottae bottae* (Eydoux & Gervais, 1836) collected near Monterey, California on the Hastings Natural History Reservation.

Caballero and Cerecero (1943) described *Vexillata convoluta* from the small intestine of the Merriam's pocket gopher, *Cratogeomys merriami* (Thomas, 1893), collected from the state of Michoacan, Mexico.

Chandler (1945) redescribed *Trichuris fessor* Hall, 1916 from *Thomomys bottae bottae* from specimens collected on the Hastings Natural History Reservation near Monterey, California. This was the first good description of the eggs of *T. fessor*, and the first report of *T. fessor* from *T. bottae*. In the same year during an ecological study of the small mammals collected from Northrup Canyon in eastern Washington State, Rankin (1945) recorded *Hymenolepis diminuta* (Rudolphi, 1819) from *Thomomys talpoides*, see discussion below. The next year, Wenrich (1946) recorded a species of *Monocercomonoides* Travis, 1932 as a cecal commensal (flagellate) of Bottae's pocket gopher, *Thomomys bottae*.

Tryon (1947) reported both cestodes and nematodes in *Thomomys talpoides* from Montana, with most of his field work occurring in the Bridger Mountains. Less than one percent of the gophers necropsied contained an unidentified species of cestode. Nematodes identified as belonging to the family Trichuridae were found in 100% of the pocket gophers examined for endoparasites. In areas of low pocket gopher density, the prevalence of infection was low (approximately 10%); however, in areas of high gopher density, the prevalence of infection approached 80%. Tryon (1947) speculated that the young

Table 4. Endoparasite species diversity of Nearctic and Neotropical regions of subterranean rodents in the family Geomyidae and their known hosts. Authorities are given for parasite and host species. The new host-parasite associations recorded in this work are denoted by ‘Present study’ in bold.

Host species	Parasite species	References
<i>Cratogeomys castanops</i> (Baird, 1852)	<i>Calodium americanum</i> (Read, 1949)	Present study
	<i>Eimeria geomydis</i> Skidmore, 1929	Present study
	<i>Monoecocestus</i> sp. Beddard, 1914	Present study
<i>Cratogeomys merriami</i> (Thomas, 1893)	<i>Vexillata convoluta</i> Caballero & Cerecero, 1943	Present study
	<i>Paraspidodera uncinata</i> Travassos, 1914	Lamothe-Argumedo et al. 1997
<i>Cratogeomys planiceps</i> (Merriam, 1895)	<i>Vexillata convoluta</i> Caballero & Cerecero, 1943	Caballero and Cerecero 1943
	<i>Hymenolepis cratogeomyos</i> Gardner et al., 2020	Gardner et al. 2020
<i>Geomys attwateri</i> Merriam, 1895	<i>Monoecocestus centroovarium</i> Dronen et al., 1994	Dronen et al. 1994
	<i>Protospirura ascaroidea</i> Hall, 1916	LeBrasseur 2017
<i>Geomys breviceps</i> Baird, 1855	<i>Vexillata geomyos</i> Falcón-Ordaz et al., 2006	Falcón-Ordaz et al. 2006
	<i>Eimeria geomydis</i> Skidmore, 1929	Upton et al. 1992
	<i>Litosomoides westi</i> Gardner & Schmidt, 1986	Pitts et al. 2000
<i>Geomys bursarius</i> (Shaw, 1800)	<i>Monoecocestus anoplocephaloides</i> (Douthitt, 1915)	Douthitt 1915
	<i>Protospirura ascaroidea</i> Hall, 1916	Hall 1916; English 1932
<i>Geomys bursarius</i> (Shaw, 1800)	<i>Andrya macrocephala</i> Douthitt, 1915	Douthitt 1915; Hansen 1950; Ubelaker and Downhower 1965; Bartel and Gardner 2000
	<i>Anoplocephaloides infrequens</i> (Douthitt, 1915)	Douthitt 1915; Ubelaker and Downhower 1965; Bartel and Gardner 2000; Rausch 1976
	<i>Anoplocephaloides variabilis</i> (Douthitt, 1915)	Douthitt 1915; Rausch 1976
	<i>Calodium americanum</i> (Read, 1949)	Bartel and Gardner 2000
	<i>Calodium hepaticum</i> (Bancroft, 1893)	Ubelaker and Downhower 1965
	<i>Cittotaenia perplexa</i> Stiles, 1897	Burnham 1953
	<i>Eimeria geomydis</i> Skidmore, 1929	Skidmore 1929; Levine and Ivens 1965
	<i>Hymenolepis diminuta</i> (Rudolphi, 1819)	Burnham 1953
	<i>Hymenolepis geomydis</i> Gardner & Schmidt, 1988	Gardner and Schmidt 1988
	<i>Hymenolepis weldensis</i> Gardner & Schmidt, 1988	Gardner and Schmidt 1988; Bartel and Gardner 2000; Haukisalmi et al. 2010
	<i>Litomosia filaria</i> (Beneden, 1873)	Burnham 1953
	<i>Litosomoides westi</i> Gardner & Schmidt, 1986	Gardner and Schmidt 1986
	<i>Moniliformis clarki</i> (Ward, 1917)	Bartel and Gardner 2000
	<i>Monocercomonoides</i> Travis, 1932	Rissky 1962
	<i>Monoecocestus anoplocephaloides</i> (Douthitt, 1915)	Burnham 1953
	<i>Oochoristica</i> Lühse, 1898	Douthitt 1915
	<i>Ostertagia</i> Ransom, 1907	Burnham 1953
	<i>Paranoplocephala infrequens</i> (Douthitt, 1915)	Ubelaker and Downhower 1965
	<i>Physaloptera limbata</i> Leidy, 1856	Bartel and Gardner 2000
	<i>Protospirura ascaroidea</i> Hall, 1916	English 1932; LeBrasseur 2017
	<i>Protospirura muris ascaroides</i> (Hall, 1916)	Burnham 1953
	<i>Pseudocittotaenia praeoquis</i> (Stiles, 1895)	Stiles 1895
	<i>Ransomus rodentorum</i> Hall, 1916	Bartel and Gardner 2000
<i>Geomys jugossicularis</i> Hooper, 1940	<i>Anoplocephaloides variabilis</i> (Douthitt, 1915)	Present study
<i>Geomys lutescens</i> Merriam, 1890	<i>Hymenolepis weldensis</i> Gardner & Schmidt, 1988	Gardner et al. 2020
	<i>Litosomoides westi</i> Gardner & Schmidt, 1986	Present study
	<i>Physaloptera limbata</i> Leidy, 1856	Present study
	<i>Ransomus rodentorum</i> Hall, 1916	Present study
<i>Geomys personatus</i> True, 1889	<i>Monoecocestus anoplocephaloides</i> (Douthitt, 1915)	Burnham 1953
	<i>Litosomoides westi</i> Gardner & Schmidt, 1986	Pitts et al. 2000
<i>Geomys pinetis</i> Rafinesque, 1817	<i>Protospirura ascaroidea</i> Hall, 1916	LeBrasseur 2017
	<i>Mastophorus muris ascaroides</i> (Gmelin, 1790)	Hubbell and Goff 1939
<i>Geomys texensis</i> Merriam, 1895	<i>Eimeria geomydis</i> Skidmore, 1929	Upton et al. 1992
	<i>Hymenolepis</i> Weinland, 1858	LeBrasseur 2017
	<i>Protospirura ascaroidea</i> Hall, 1916	LeBrasseur 2017
<i>Heterogeomys heterodus</i> (Peter, 1865)	<i>Hobergia irazuensis</i> Gardner et al., 2020	Gardner et al. 2020
<i>Orthogeomys grandis</i> (Thomas, 1893)	<i>Eimeria orthogeomys</i> Lainson, 1968	Lainson 1968

Host species	Parasite species	References	
<i>Thomomys bottae</i> (Eydoux & Gervais, 1836)	<i>Arostrilepis horrida</i> (von Linstow, 1901)	Schiller 1952; Voge 1955; Gardner 1985	
	<i>Catenotaenia dendritica</i> (Goeze, 1782)	Voge 1955	
	<i>Catenotaenia linsdalei</i> McIntosh, 1941	McIntosh 1941	
	<i>Eimeria thomomysis</i> Levine et al., 1957	Levine et al. 1957; Levine and Ivens 1965	
	<i>Helignosomoides thomomys</i> Gardner & Jasmer, 1983	Gardner and Jasmer 1983	
	<i>Hymenolepis citelli</i> (McLeod, 1933)	Voge 1955; Jasmer 1980	
	<i>Litomosoides thomomydis</i> Gardner, 1986	Gardner and Schmidt 1986	
	<i>Monocercomonoides</i> Travis, 1932	Gardner and Jasmer 1983	
	<i>Monoecocestus anoplocephaloides</i> (Douthitt, 1915)	Hansen 1950	
	<i>Ransomus rodentorum</i> Hall, 1916	Jasmer 1980	
	<i>Trichuris fossor</i> Hall, 1916	Jasmer 1980; Douglas 1969	
<i>Thomomys bulbivorus</i> (Richardson, 1829)	<i>Arostrilepis horrida</i> (von Linstow, 1901)	Gardner 1985	
	<i>Arostrilepis schilleri</i> Makarikov et al., 2012	Makarikov et al. 2012	
	<i>Helignosomoides thomomys</i> Gardner & Jasmer, 1983	Gardner 1985; Gardner and Jasmer 1983	
	<i>Hymenolepis tualatinensis</i> Gardner, 1985	Gardner 1985	
<i>Thomomys clusius</i> Coues, 1875	<i>Ransomus rodentorum</i> Hall, 1916	Gardner 1985	
	<i>Trichuris fossor</i> Hall, 1916	Gardner 1985	
		Present study	
<i>Thomomys monticola</i> J. A. Allen, 1893	<i>Arostrilepis horrida</i> (von Linstow, 1901)	Howard and Childs 1959	
	<i>Trichuris Roederer</i> , 1761	Ingles 1952	
<i>Thomomys talpoides</i> (Richardson, 1828)	<i>Andrya macrocephala</i> Douthitt, 1915	Rausch and Schiller 1949	
	<i>Anoplocephaloides infrequens</i> (Douthitt, 1915)	Frandsen and Grundmann 1961; Todd et al. 1971	
	<i>Anoplocephaloides variabilis</i> (Douthitt, 1915)	Rausch 1976; Frandsen and Grundmann 1961; Todd et al. 1971; Lubinsky 1957	
	<i>Arostrilepis horrida</i> (von Linstow, 1901)	Grundmann, et al. 1976; Frandsen and Grundmann 1961	
	<i>Ascaris laevis</i> Leidy, 1856	Grundmann et al. 1976; Frandsen and Grundmann 1961	
	<i>Calodium hepaticum</i> (Bancroft, 1893)	Ubelaker and Downhower 1965; Lubinsky 1957; Dikmans 1932; Tryon 1947; Lubinsky 1956; Rausch 1961; Tryon and Cunningham 1968	
	<i>Catenotaenia linsdalei</i> McIntosh, 1941	Todd et al. 1971	
	<i>Eimeria fitzgeraldi</i> Todd & Tryon, 1970	Todd et al. 1971; Todd and Tryon 1970	
	<i>Eimeria jemezi</i> Wilber et al., 1994	Wilber et al. 1994	
	<i>Eimeria thomomysis</i> Levine et al., 1957	Levine and Ivens 1965; Levine et al. 1957	
	<i>Hymenandrya thomomysis</i> Smith, 1954	Smith 1954	
	<i>Hymenolepis citelli</i> (McLeod, 1933)	Frandsen and Grundmann 1961	
	<i>Hymenolepis diminuta</i> (Rudolphi, 1819)	Rankin 1945	
	<i>Litomosoides carinii</i> (Travassos, 1919)	Lubinsky 1957	
	<i>Litomosoides thomomydis</i> Gardner, 1986	Gardner and Schmidt 1986	
	<i>Nippostrongylus muris</i> (Yokogawa, 1920)	Frandsen and Grundmann 1961	
	<i>Protospirura ascaroidea</i> Hall, 1916	Todd et al. 1971	
	<i>Pseudocittotaenia glandularis</i> Beveridge, 1978	Beveridge 1978	
	<i>Pseudocittotaenia praeoquis</i> (Stiles, 1985)	Grundmann et al. 1976; Frandsen and Grundmann 1961; Smith 1951	
	<i>Ransomus rodentorum</i> Hall, 1916	Grundmann et al. 1976; Frandsen and Grundmann 1961	
	<i>Trichuris fossor</i> Hall, 1916	Hall 1916; Grundmann et al. 1976; Frandsen and Grundmann 1961; Lubinsky 1957; Todd and Lepp 1972	
	<i>Verstera mustelae</i> (Gmelin, 1790)	Lubinsky 1957	
	<i>Vexillata vexillata</i> (Hall, 1916)	Todd et al. 1971	
	<i>Thomomys umbrinus</i> (Richardson, 1829)	<i>Arostrilepis horrida</i> (von Linstow, 1901)	Frandsen and Grundmann 1961
		<i>Ascaris laevis</i> Leidy, 1856	Frandsen and Grundmann 1961
		<i>Hymenolepis citelli</i> (McLeod, 1933)	Frandsen and Grundmann 1961
		<i>Moniliformis clarki</i> (Ward, 1917)	Frandsen and Grundmann 1961
<i>Paruterina candelabraria</i> (Goeze, 1782)		Frandsen and Grundmann 1961	
<i>Ransomus rodentorum</i> Hall, 1916		Frandsen and Grundmann 1961	
<i>Trichuris fossor</i> Hall, 1916	Frandsen and Grundmann 1961		

gophers became infected before leaving the parental burrows, and by August, the prevalence of infection for the young pocket gophers was ca. 50%. Nematodes, probably of the genus *Protospirura* were found in the stomachs of some gophers, with as many as 42 in an individual pocket gopher's stomach. Concerning the presence of warbles in the pocket gophers examined during the study, Tryon stated "only 15 out of over a thousand animals examined showed warbles. Of these, ten were juveniles indicating that they may be above ground more than the adults, probably during migration from the parental burrows."

Rausch and Schiller (1949), during a study of cestodes of the genus *Andrya* Raillet, 1893, mentioned *Andrya macrocephala* Douthitt, 1915 as occurring in *Thomomys talpoides tenellus* Goldman from the Jackson Hole Wildlife Park in Wyoming.

Hansen (1950), during a study of the tapeworms of rodents, recorded *Andrya macrocephala* Douthitt, 1915 as occurring in 5 of 5 *Geomys bursarius* examined with up to 12 cestodes per host. Hansen (1950) also recorded *Monoecocestus anoplocephaloides* (Douthitt, 1915) from *Thomomys bottae* collected in the region of Sacramento, California. Interestingly, this cestode has not since been reported from any members of the genus *Thomomys*.

Smith (1951), in a study of the cestodes of *Thomomys talpoides* collected from Carbon County, Wyoming, reported the following cestodes: *Pseudocittotaenia praecoquis* (Stiles, 1895) from the small intestine; *P. megasacca* (Smith, 1951) also from the small intestine (see below for clarification of the taxonomy of these two species). Smith (1951) also included a list of the cestodes reported from pocket gophers up to that time and attempted to clarify the taxonomic relationships between *Schizotaenia* Janicki, 1904 and *Monoecocestus* Beddard, 1914.

Ingles (1952) reported *Trichuris* sp. (probably *T. fossor*) as a common parasite of the cecum of *Thomomys monticola* J. A. Allen, 1893. All specimens that Ingles examined came from an elevation of ca. 7,000 feet in the Sierra Nevada of California. In the same year, Everett Schiller (1952), in a study of the morphological variation in *Hymenolepis* (syn. *Arostrilepis*) *horrida* (von Linstow, 1901) reported *Thomomys bottae* from near O'Neals California as a host.

Burnham (1953), during a study of the parasites of *Geomys bursarius*, collected from four counties in Oklahoma reported the following species of parasites: *Protospirura muris ascaroides* (Hall, 1916) (syn. *Mastophorus muris*) from the stomachs of 18 hosts; *Litomosa filaria* Beneden, 1897 from the pleural cavities of 19 gophers (this is probably a misidentification, see discussion below regarding the filarioid nematodes of pocket gophers); *Ostertagia* sp. from the stomachs of five gophers; *Hymenolepis diminuta* (Rudolphi, 1819) from the small intestines of ten hosts (see discussion below for clarification of the problem concerning *H. diminuta* in geomyids); *Monoecocestus anoplocephaloides* (Douthitt, 1915) from 25 hosts, with a range of infection of 1–100 worms per host; and *Cittotaenia perplexa* Stiles, 1897 from two gophers.

Soon after, Smith (1954) described *Hymenandrya thomomyis* from the small intestine of *Thomomys talpoides* collected in Colorado and in this same publication, he recommended that *Catenotaenia linsdalei* McIntosh, 1941 be considered a synonym of *C. dendritica* (Goeze, 1782) Janicki 1904.

Voge (1955) in a catalogue of the cestode parasites of California mammals, listed *Catenotaenia dendritica* (Goeze, 1782), *Hymenolepis citelli* (McLeod, 1933), and an unidentified species of *Hymenolepis* from *T. bottae*.

The next year, Voge (1956), in a list of the nematode parasites of California mammals, reported *Trichuris fossor* Hall, 1916 as a parasite of *T. bottae* and in the same year, Lubinsky (1956) reported *Calodium* (syn. *Capillaria*) *hepaticum* from *T. talpoides* in Alberta, Canada. Soon after, continuing his work on small mammals, Lubinsky (1957) in a list of the helminth parasites of rodents from Alberta included the following as parasites of *Thomomys talpoides*: *Versteria* (syn. *Taenia*) *mustelae* (larvae) from the mesenteries, lungs, liver, and kidneys of gophers collected in northern and middle Alberta; *Anoplocephaloides variabilis* (Douthitt, 1915) recovered from the colon (which is a doubtful location for a cestode) from six localities in middle and southern Alberta; *Calodium* (syn. *Capillaria*) *hepaticum* from the livers of gophers collected from central and southern Alberta; *Trichuris fossor* from the cecum of gophers collected from central Alberta; *Protospirura ascaroidea* Hall, 1916 from the stomachs of gophers from middle Alberta; *Litomosoides carinii* (Travassos, 1919) from the coelom of pocket gophers from middle and southern Alberta. In the same year, Levine, et al. (1957) described *Eimeria thomomysis* from specimens of *T. bottae* collected in the Grand Canyon of Arizona.

Howard and Childs (1959) during a study of the ecology of *Thomomys monticola* reported *Hymenolepis horrida* (von Linstow, 1901) to occur commonly in adult pocket gophers. They stated, "Most of the adults had several tapeworms (*Hymenolepis horrida*), and one animal had 108 immature tapeworms with short strobila. None of the five juvenile gophers examined had tapeworms." Based on recent work by Dursahinhan et al. (2022), it appears now that the species identified as *H. horrida* may be referred to the genus *Arostrilepis*.

Frandsen and Grundmann (1960) discussed the geographic distribution of *Trichuris fossor* Hall, 1916 and *Ransomus rodentorum* Hall, 1916 from *Thomomys talpoides* and *T. umbrinus* in the Lake Bonneville basin of Utah. They speculated that the distribution of these two species of nematodes in *Thomomys* sp. in this area supports the contention that competition occurred between the two species of pocket gophers resulting in the present-day distribution patterns of the pocket gophers and their respective helminths.

Rausch (1961) reported *Calodium* (syn. *Capillaria*) *hepaticum* from *Thomomys talpoides tenellus* Goldman from near Moran, Wyoming, collected in June of 1948 and Frandsen and Grundmann (1961) reported the following helminth parasite species from several subspecies of both Northern pocket gopher, *Thomomys talpoides*, and the Southern pocket gopher *Thomomys umbrinus* (Richardson, 1829). These species include *Ascaris laevis* Leidy, 1856, *Hymenolepis citelli*, *Ransomus rodentorum*, and *Trichuris fossor*. However, *Anoplocephaloides infrequens* (Douthitt, 1915), *A. variabilis* (Douthitt, 1915), *Pseudocittotaenia praecoquis* (Stiles, 1985), *Arostrilepis horrida*, and *Nippostrongylus muris* (Yokogawa, 1920) have been reported from *T. talpoides*. In addition, *Paruterina candelabraria* (Goeze, 1781) and *Moniliformis clarki* are only reported from *T. umbrinus*.

Stock (1962) reported three males and one female of the nematode *Ransomus rodentorum* from the caeca of two specimens of *Thomomys talpoides fossor*, collected at the junction of Dry Gulch and the Gunnison River, Colorado, at ca. 7,400 feet altitude.

Rissky (1962) reported *Monocercomonoides* from the cecum of the Plains pocket gopher, *Geomys bursarius*, collected from Clay County, South Dakota.

Ubelaker and Downhower (1965) in a study of the endo and ectoparasites of *Geomys bursarius* in Kansas, reported *Calodium* (syn. *Capillaria*) *hepaticum* from the cecum of a single pocket gopher and *Andrya macrocephala* Douthitt, 1915 and *Anoplocephaloides infrequens* (Douthitt, 1915) were found to occur in seven and six of the pocket gophers examined, respectively.

Lainson (1968), during a parasitological study in El Cayo District British Honduras, a new species of coccidian parasite (*Eimeria orthogeomyos*) was described from the Giant pocket gopher, *Orthogeomys grandis* (Thomas, 1893) collected from Baking Pot, El Cayo District, Central America (Lainson, 1968).

Tryon and Cunningham (1968) in a study of *Thomomys talpoides* along an altitudinal transect in the Beartooth Mountains of Wyoming reported *Calodium* (syn. *Capillaria*) *hepaticum* from the livers of 5%, 37%, and 8% of the gophers from the Alpine, the Canadian, and the transition life zones, respectively.

Douglas (1969) studied the ecology of the pocket gophers of Mesa Verde, Colorado. He reported *Trichuris fossor* Hall, 1916 and *Cuterebra* cf. *cyanelia* (bot fly larvae) from *Thomomys bottae aureus* Douglas (1969) stated that, “Of the gophers infected with bot fly larvae, the highest prevalence of infection occurred during September, with no gophers carrying larvae during the spring.” Douglas (1969) also stated “Specimens of Cestoda currently are being studied and will be reported elsewhere.” To our knowledge, no report has ever been published.

Todd and Tryon (1970) described *Eimeria fitzgeraldi* Todd & Tryon, 1970 from *Thomomys talpoides* collected from the Beartooth Mountains, Park County Wyoming. Oocysts were recovered from the feces of two of ten juvenile males and one of 31 adult females (pocket gophers).

Todd et al. (1971) in a study of the endoparasites of the Northern pocket gopher (*Thomomys talpoides*) from Park County, Wyoming, reported the following species of parasites from a total of 46 specimens of *T. talpoides* examined: *Eimeria thomomysis* Levine, Ivens & Kruidenier, 1957 was found to occur in the fecal pellets of 24 of the individual gophers; *E. fitzgeraldi* Todd & Tryon, 1970 was found in the feces of two gophers; cestode cysticerci of the family Taeniidae were found in the mesenteries near the stomach and cecum of one gopher; fragments of the cestode *Catenotaenia linsdalei* McIntosh, 1941 were found in the body cavities of two animals (this is a dubious body location record); *Anoplocephaloides variabilis* (Douthitt, 1915) was present in the small intestines of 18 gophers; *A. infrequens* (Douthitt, 1915) was recovered from the small intestine of seven gophers; *Anoplocephaloides* sp. was recovered from the small intestines of 22 gophers *R. rodentorum* was found in the cecum of 34 gophers, and in the large intestine of one; *Vexillata vexillata* was recovered from the small intestines of two gophers; *Protospirura ascaroidea* was found in the stomachs of two animals;

Trichuris fossor was found in the ceca of 30 gophers; and *Calodium* (syn. *Capillaria*) *hepaticum* was recovered from the livers of 18 of the gophers examined.

Todd and Lepp (1972) redescribed *Trichuris fossor* from specimens recovered from *T. talpoides* from Park County, Wyoming.

Grundmann et al. (1976), in a paper discussing the mechanisms of parasitic helminth population regulation in rodents, listed the following parasites as occurring in *Thomomys talpoides* in Utah: *Trichuris fossor*, *Vexillata vexillata*, *Ascaris laevis* Leidy, 1856. *Hymenolepis horrida*, and *T. fossor* were reported from *T. bottae* in the same paper.

Rausch (1976) in a study of the rodent cestode genera *Paranoplocephala* Luhe, 1910 and *Anoplocephaloides* Baer, 1923 examined the type material of *Anoplocephaloides infrequens* (Douthitt, 1915) from *Geomys bursarius* collected by Douthitt in Brainerd, Minnesota, and specimens of *A. variabilis* (Douthitt, 1915) collected by Douthitt in central Illinois from *Geomys bursarius*. Also studied by Rausch (1976) were seven specimens of *A. variabilis* from *Thomomys talpoides* collected at Emerson, Manitoba, 10 km north of Prince Albert, Saskatchewan, Canada and from 5 km south of Saskatoon, Saskatchewan, Canada. Rausch (1976) stated "I also obtained it (*A. variabilis* from *T. talpoides*) in two of 11 of these rodents at Moran, Wyoming, in 1949."

Beveridge (1978) in a revision of the genus *Pseudocittotaenia* Tenora, 1976, listed the synonyms of *P. praecoquis* (Stiles, 1895) and described *P. glandularis* Beveridge, 1978 from some specimens taken from *Thomomys talpoides* in Utah by Frandsen and Grundmann (1961), and from some specimens from *T. talpoides* in Wyoming. Frandsen and Grundmann (1961) evidently misidentified *P. glandularis* Beveridge, 1978 and had determined that the specimens that they found in *T. talpoides* were *Pseudocittotaenia praecoquis* (Stiles, 1895). The specimens from the Wyoming pocket gophers were from material that Smith (1951) had mistakenly identified and redescribed as *P. praecoquis*. Beveridge (1978) also listed as synonyms: *P. megasacca* (Smith, 1951) with *P. praecoquis* (Stiles, 1895). Also reported by Beveridge (1978) and not reported elsewhere in the literature was *Pseudocittotaenia praecoquis* from *T. talpoides tenellus* Goldman, collected by Robert L. Rausch near Moran, Wyoming in June of 1948.

Jasmer (1980) in a thesis written at Humboldt State University listed the following parasites from *Thomomys bottae* (Eyndoux & Gervais): *Ransomus rodentorum*, *Trichuris fossor*, *Hymenolepis citelli*, and an unidentified species of *Heligmosomoides* Hall, 1916. He also discussed the biological characteristics and taxonomy of *R. rodentorum* (some of his specimens are now in the Manter Laboratory Parasite Collection).

Gardner and Jasmer (1983) described *Heligmosomoides thomomyos* Gardner & Jasmer, 1983 from *Thomomys bottae* (Eyndoux & Gervais) and *T. bulbivorus* (Richardson) from Humboldt County, California and Benton County, Oregon, respectively. They included some measurements and remeasurements of two other species of *Heligmosomoides*: *H. longispiculatus* (Dickmans, 1940) and *H. montanus* Durette-Desset, 1968.

Gardner (1985) described *Hymenolepis tualatinensis* from the duodenum of the Camas pocket gopher, *Thomomys bulbivorus* (Richardson, 1829) collected near the Tualatin River in the Willamette Valley of Oregon. In the report, several helminth species were documented during the study including *Arostrilepis horrida* also from the small

intestine, *Trichuris fossor* from the cecum, *Ransomus rodentorum* from the cecum, and *Heligmosomoides thomomyos* from the duodenum.

Gardner and Schmidt (1986) described *Litomosoides thomomydis* from the abdominal cavity of the Northern pocket gopher, *Thomomys talpoides*, and Botta's pocket gopher, *Thomomys bottae*, from Huerfano County, Colorado. Also, *L. westi* was described from the abdominal and pleural cavities of the Plains Pocket Gopher, *Geomys bursarius*, collected from Weld County, Colorado.

Shortly after this work, Gardner and Schmidt (1988) described two new species in the genus *Hymenolepis* Weinland, 1858, including *H. weldensis* and *H. geomydis* from the small intestines (duodenum) of the Plains pocket gopher, *Geomys bursarius*, collected from Weld County, Colorado.

Pitts et al. (1990) reported *Litomosoides westi* Gardner & Schmidt, 1986 from *Geomys personatus* True, 1889 collected from Duval and Zapata counties in Texas.

Upton et al. (1992) reported *Eimeria geomydis* Skidmore, 1929 from Baird's pocket gopher, *Geomys mericanu*, and Llano pocket gopher, *Geomys texensis* Merriam, 1895 collected from Texas.

Dronen et al. (1994) described *Monoecocestus centroovarium* found in Attwater's pocket gopher, *Geomys attwateri* Merriam, 1895 collected from Atascosa County, Texas. In the same year, Wilber et al. (1994) described *Eimeria jemezi* found in the Northern pocket gopher, *Thomomys talpoides* collected from El Cajete crater, Jemez Springs, Sandoval County, New Mexico.

Lamothe-Argumedo et al. (1997) reported *Paraspidodera merican* Travassos, 1914 from the intestine of Merriam's pocket gopher, *Cratogeomys merriami* (Thomas, 1893) first collected from Morelos, Cuernavaca, Mexico in 1984.

Pitts et al. (2000) reported the additional occurrence of the filarioid nematode, *Litomosoides westi* from the pleural cavities of Baird's pocket gopher, *Geomys mericanu* collected at the entrance of Isle, Du Boris unit, Lake Ray Roberts State Park, Denton County, Texas while *L. westi* was also documented from the pleural cavities of the Plains pocket gopher, *Geomys bursarius* captured near Aubrey, Grubbs Road, same county.

Bartel and Gardner (2000) reported the helminth parasites from the Plains pocket gopher, *Geomys bursarius*, from seven localities in the northern boundary range, Minnesota. The report includes the following: *Physaloptera limbata* Leidy, 1856 from the stomach, *Ransomus rodentorum* from the cecum and large intestine and *Calodium* (syn. *Capillaria*) *mericanum* (Read, 1949), *Anoplocephaloides infrequens*, *A. variabilis* (Douthitt, 1915), *Andrya macrocephala*, *Hymenolepis weldensis* Gardner & Schmidt, 1988 and *Moniliformis clarki* from the small intestines.

Falcón-Ordaz et al. (2006) described *Vexillata geomyos* from Attwater's pocket gopher, *Geomys attwateri* from the Welder Wildlife Refuge of San Patricio County, Texas.

Using molecular methods, Haukisalmi et al. (2010) documented *Hymenolepis weldensis* from *Geomys bursarius* collected from Illinois and Indiana.

Makarikov et al. (2012) described *Arostrilepis schilleri* obtained from the Camas pocket gopher, *Thomomys bulbivorus*, captured southeast of Corvallis, Oregon and originally reported as *H. horrida* by Gardner (1985).

LeBrasseur (2017) in an unpublished master's thesis reported a study focused on the endoparasites of four species of pocket gophers in the genus *Geomys* collected from eight counties in Texas. These host species included the Plains pocket gopher, *Geomys bursarius*, Attwater's pocket gopher, *G. attwateri* Merriam, 1895, Texas pocket gopher, *G. personatus* True, 1889, and the Central Texas pocket gopher *G. texensis* Merriam, 1895. In addition, she found an unidentified *Hymenolepis* Weinland, 1858 obtained from *G. attwateri*, *G. bursarius*, and *G. texensis* and another tapeworm, *Monoecocestus* was obtained from *G. bursarius*, and *G. texensis*. Finally, a nematode species, *Protospirura ascaroidea*, was found from all four species of *Geomys* mentioned above; the specimens were verified by HWML personnel (LeBrasseur 2017).

Gardner et al. (2020) described two new species of unarmed hymenolepidid tapeworms, including *Hobergia irazuensis* from the small intestine of *Heterogeomys heterodus* (Peters, 1865), collected from Potrero Cerrado, Cartago, Costa Rica, and *Hymenolepis cratogeomys* from the small intestine of the Volcán De Toluca pocket gopher, *Cratogeomys planiceps* (Merriam, 1895) collected from Parque Nacional Nevado de Toluca, México. Also, *H. weldensis* Gardner & Schmidt, 1988 has been documented from many individuals of *Geomys lutescens* Merriam, 1890 collected in the Sandhills, on the north side of the North Platte River near Cedar Point Biological Station in western Nebraska.

The present study reports an unidentified *Monoecocestus* sp. Beddard, 1914 (probably *M. anoplocephaloides*) from the small intestine of the Yellow-faced pocket gopher, *Cratogeomys castanops* (Baird, 1852), collected by a local landowner from Black Mesa, Oklahoma in 2016 (NP2779). *Anoplocephaloides variabilis* (Douthitt, 1915) was found from the small intestine of Hall's pocket gopher, *Geomys jugossicularis* Hooper, 1940 collected from Grama grass habitat, Keith County, Nebraska in 2016 (NP2661). Also, from 2009–2016, necropsies of *Geomys lutescens* Merriam, 1890 yielded many individuals of *Litomosoides westi* Gardner & Schmidt, 1986 from their abdominal cavities with individuals of *Ransomus rodentorum* from the cecum, and from two pocket gophers *Physaloptera limbata* Leidy, 1856 was found (NP2297, NP2298). Also, during general collecting in the area of Nebraska, we found two nematode species (*R. rodentorum*, and *T. fossor* – refer to NP1524) from the cecum of the Wyoming pocket gopher, *Thomomys clusius* Coues, 1875, collected from 5 miles east of Woods Landing, Albany County, Wyoming in 2013. All specimens mentioned in this work are deposited in the HW Manter Laboratory of Parasitology Museum collection where NP refers to the field collection number.

Endoparasites of Neotropical subterranean rodents

See graphical summary in Fig. 4 and endoparasite list Table 5.

Khalil and Vogelsang (1931) described the first helminth parasite from a subterranean host from Neotropical region, *Paraspidodera americana* Khalil & Vogelsang, 1931 from the cecum of a single individual of what they called *Ctenomys magellanicus* Bennett, 1836 collected from Carrasco near Montevideo, Uruguay in 1927. The identifica-

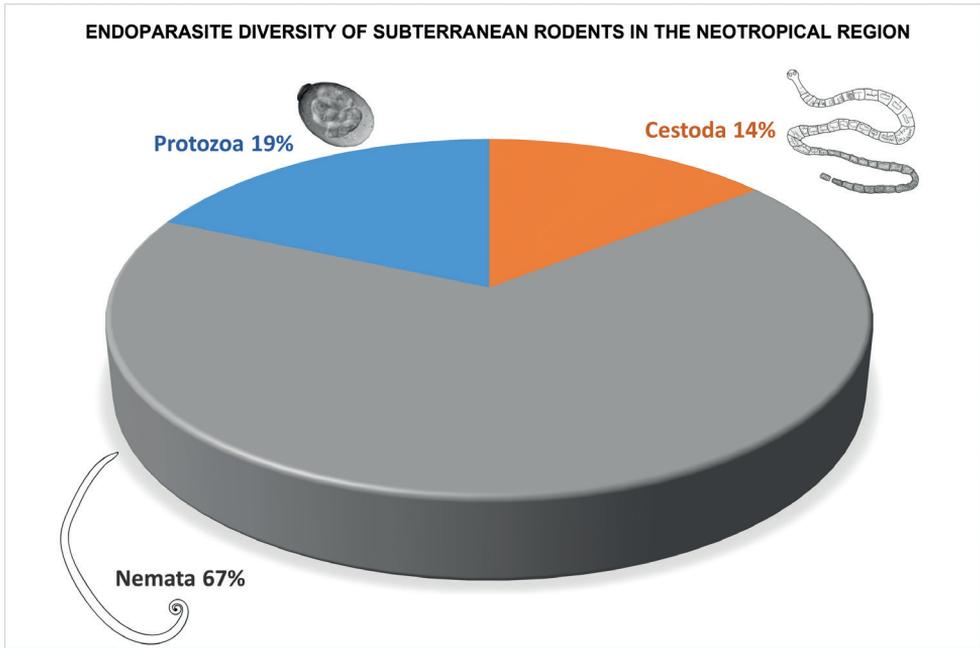


Figure 4. Percentage taxon composition of endoparasite diversity pie diagram shown by higher classification of both protozoa and helminths occurring in subterranean rodents (Family Ctenomyidae) in the southern Neotropical region. All records of parasites presented were derived from a review of the literature published from 1931 through 2021. Approximately 67% of the total endoparasite fauna of these rodents consists of Nemata, followed by Protozoa (19%), and Cestoda (14%).

tion of this mammal specimen was probably erroneous as *C. magellanicus* occurs only near the Strait of Magellan in southern Argentina). Unfortunately, no hosts or parasite specimens were deposited in any collection that we can find up to the current time.

Dollfus (1960) described *Taenia talicei* Dollfus, 1960 from the abdominal cavity of the Collared tuco-tuco, *Ctenomys torquatus* Lichtenstein, 1830, collected from Uruguay and in 1986, multistrobilate larvae of *T. talicei* were collected from several *Ctenomys opimus* at 7 km S: 4 km E. Cruce Ventilla, Oruro, Bolivia by a party from the American Museum of Natural History and the Museum of Southwestern Biology (Anderson 1997).

Olsen (1976) described *Monoecocestus torresi* obtained from the small intestine of Maule's tuco-tuco, *Ctenomys maulinus* Philippi, 1872 collected near Lonquimay, Chile. Meanwhile, Torres et al. (1976) reported *Paraspidodera uncinata* Rudolphi, 1819, and unidentified *Trichuris* are reported from Maule's tuco-tuco, *Ctenomys maulinus*, collected from Chile.

Babero and Cattán (1980) described *Graphidiodes yañezi* from the small intestine of a coruro, *Spalacopus cyanus* (Rodentia: Octodontidae), collected from near Concón, Chile.

Babero and Murua (1987) described a new species of whipworm, *Trichuris fulvi* obtained from the cecum of the Tawny tuco-tuco, *Ctenomys fulvus* Philippi, 1860, collected from San Pedro Atacama, Tarapaca province, Chile.

Lambert et al. (1988) described four new coccidian parasites in the genus *Eimeria* Schneider, 1875 recovered from the feces of the Highland tuco-tuco, *Ctenomys opimus* Wagner, 1848, trapped from several localities of the Department of Oruro, Bolivia, South America. Those species are *E. granifera* from Rancho Huancaroma, near the Rio Desaguadero, *E. montuosi*, from the north of Pomata Ayte, Rio Barros, *E. opimi*, and *E. oruroensis*, from the northeast and east of Rancho Huancaroma.

Babero and Murua (1990) described *Trichuris robusti* from the cecum and large intestine of the Tawny tuco-tuco, *Ctenomys fulvus*, collected from La Hauyca, Tarapaca province, Chile.

Gardner and Duszynski (1990), during a study on morphometric comparison of a coccidian species, *Eimeria opimi* Lambert et al., 1988, in different regions of Bolivia, the following host species were detected positive for this protozoan parasite. Those hosts include Lewis's tuco-tuco, *Ctenomys lewisi* Thomas, 1926, collected from the areas of the high-altitude region in Tarija; the Reddish tuco-tuco, *Ctenomys frater* Thomas, 1902, collected from medium latitude region of Tarija; the Conover's tuco-tuco, *Ctenomys conoveri* Osgood, 1946, collected from Chaco thorn forest area in Chuquisaca; the Bolivian tuco-tuco, *Ctenomys boliviensis* Waterhouse, 1848, and the Steinbach's tuco-tuco, *Ctenomys steinbachi* Thomas, 1907 collected from the Tropical palm/savanna region of Santa Cruz, Bolivia. In addition, the following coccidian parasites were reported from the Highland tuco-tuco, *Ctenomys opimus*. These species include *Eimeria opimi*, *E. granifera* Lambert et al., 1988, *E. oruroensis* Lambert et al., 1988, and *E. montuosi* Lambert et al., 1988 collected from the Oruro region *E. opimi* and *E. granifera* collected from the Potosi region.

Suriano and Navone (1994) described *Trichuris bursacaudata* obtained from the cecum of the Talas tuco-tuco, *Ctenomys talarum* Thomas, 1898 collected from Punta Indio, Buenos Aires, and *T. pampeana* found in the cecum of the Azara's tuco-tuco, *Ctenomys azarae* Thomas, 1903, collected from Santa Rosa, La Pampa, Argentina (Suriano and Navone 1994). However, *T. pampeana* has been redescribed from its original voucher specimens (Rossin and Malizia 2005).

Brant and Gardner (1997) described *Litomosoides andersoni* and *L. ctenomyos* from the abdominal and thoracic regions of the Highland tuco-tuco, *Ctenomys opimus*, collected from near Rancho Huancaroma, Departamento de Oruro, Bolivia.

Rossin and Malizia (2002), during a study of the relationship between helminth parasites and demographic attributes of a population, two unidentified helminth parasites were reported. Those include *Heligmostrongylus* Travassos, 1917 found in the small intestine, and *Trichuris* recovered from the cecum of the Talas tuco-tuco, *Ctenomys talarum*, collected from Necochea, Buenos Aires province, Argentina.

Rossin et al. (2004a) reported larvae of *Hydatigera* (syn. *Taenia*) *taeniaeformis* from the peritoneal cavity and liver of the Talas tuco-tuco, *Ctenomys talarum*, trapped in the

Table 5. Endoparasite species diversity from Neotropical subterranean rodents (Ctenomyidae and Octodontidae). Authorities are given for parasite and host species.

Host species	Parasite species	References
<i>Ctenomys andersoni</i> Gardner, et al., 2014	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
<i>Ctenomys australis</i> Rusconi, 1934	<i>Pudica ctenomydis</i> Rossin et al., 2006	Rossin et al. 2010a
	<i>Taenia talicei</i> Dollfus, 1960	Rossin et al. 2010b
	<i>Trichuris pampeana</i> Suriano & Navone, 1994	Rossin et al. 2010a
<i>Ctenomys azarae</i> Thomas, 1903	<i>Trichuris pampeana</i> Suriano & Navone, 1994	Suriano and Navone 1994; Rossin and Malizia 2005a
<i>Ctenomys boliviensis</i> Waterhouse, 1848	<i>Ancylostoma ctenomyos</i> Drabik & Gardner, 2019	Drabik and Gardner 2019
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys conoveri</i> Osgood, 1946	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys erikacuellarae</i> Gardner et al., 2014	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
<i>Ctenomys andersoni</i> Gardner, et al., 2014	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
<i>Ctenomys australis</i> Rusconi, 1934	<i>Pudica ctenomydis</i> Rossin et al., 2006	Rossin et al. 2010a
	<i>Taenia talicei</i> Dollfus, 1960	Rossin et al. 2010b
	<i>Trichuris pampeana</i> Suriano & Navone, 1994	Rossin et al. 2010a
<i>Ctenomys azarae</i> Thomas, 1903	<i>Trichuris pampeana</i> Suriano & Navone, 1994	Suriano and Navone 1994; Rossin and Malizia 2005a
<i>Ctenomys boliviensis</i> Waterhouse, 1848	<i>Ancylostoma ctenomyos</i> Drabik & Gardner, 2019	Drabik and Gardner 2019
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys conoveri</i> Osgood, 1946	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys erikacuellarae</i> Gardner et al., 2014	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Raillietina</i> Fuhrman, 1920	Gardner et al. 2021
<i>Ctenomys frater</i> Thomas, 1902	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys fulvus</i> Philippi, 1860	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Trichuris fulvi</i> Babero & Murua, 1987	Babero and Murua 1987
	<i>Trichuris robusti</i> Babero & Murua, 1990	Babero and Murua 1990
<i>Ctenomys lewisi</i> Thomas, 1926	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
<i>Ctenomys leucodon</i> Waterhouse, 1848	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
	<i>Pudica pujoli</i> Durette-Casset & Tcheprekoff, 1990	Gardner et al. 2021
	<i>Paraspidodera americana</i> Khalil & Vogelsang, 1931	Khalil and Vogelsang 1931
<i>Ctenomys magellanicus</i> Bennett, 1836	<i>Monoecocestus torresi</i> Olsen, 1976	Olsen 1976
<i>Ctenomys maulinus</i> Philippi, 1872	<i>Paraspidodera uncinata</i> Rudolphi, 1819	Torres et al. 1976
	<i>Trichuris</i> Roederer, 1761	Torres et al. 1976
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
<i>Ctenomys nattereri</i> Wagner, 1848	<i>Trichuris</i> Roederer, 1761	Gardner et al. 2021
<i>Ctenomys opimus</i> Wagner, 1848	<i>Eimeria granifera</i> Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	<i>Eimeria montuosi</i> Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	<i>Eimeria opimi</i> Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	<i>Eimeria oruroensis</i> Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	<i>Litosomoides andersoni</i> Brant & Gardner, 1997	Brant and Gardner 1997
	<i>Litosomoides ctenomyos</i> Brant & Gardner, 1997	Brant and Gardner 1997
	<i>Mathevotaenia</i> Akhmyan, 1946	Gardner et al. 2021, 2023
	<i>Strongyloides myopotami</i> Artigas & Pacheco, 1933	Rossin et al. 2009
<i>Ctenomys steinbachi</i> Thomas, 1907	<i>Ancylostoma ctenomyos</i> Drabik & Gardner, 2019	Drabik and Gardner 2019
	<i>Eimeria opimi</i> Lambert et al., 1988	Gardner and Duszynski 1990
	<i>Paraspidodera</i> Travassos, 1914	Gardner et al. 2021
<i>Ctenomys talarum</i> Thomas, 1898	<i>Graphidioides subterraneus</i> Rossin et al., 2005	Rossin et al. 2005b; Rossin et al. 2010b
	<i>Heligmostrongylus</i> Travassos, 1917	Rossin and Malizia 2002
	<i>Paraspidodera uncinata</i> Rudolphi, 1819	Rossin et al. 2004b; Rossin et al. 2010b
	<i>Pudica ctenomydis</i> Rossin et al., 2006	Rossin et al. 2006a; Rossin et al. 2010b
	<i>Strongyloides myopotami</i> Artigas & Pacheco, 1933	Rossin et al. 2010b; Rossin et al. 2009

Host species	Parasite species	References
<i>Ctenomys talarum</i> Thomas, 1898	<i>Hydatigera</i> (syn. <i>Taenia</i>) <i>taeniaeformis</i> Batsch, 1786	Rossin et al. 2004a
	<i>Taenia talicei</i> Dollfus, 1960	Rossin et al. 2010a; Rossin et al. 2010b
	<i>Trichostrongylus duretteae</i> Rossin et al., 2006	Rossin et al. 2006b; Rossin et al. 2010a
	<i>Trichuris</i> Roederer, 1761	Rossin and Malizia 2002; Rossin and Malizia 2005a
	<i>Trichuris bursacaudata</i> Suriano & Navone, 1994	Suriano and Navone 1994
	<i>Trichuris pampeana</i> Suriano & Navone, 1994	Rossin et al. 2010a; Rossin and Malizia 2005a
<i>Ctenomys torquatus</i> Lichtenstein, 1830	<i>Taenia talicei</i> Dollfus, 1960	Dollfus 1960
<i>Spalacopus cyanus</i> (Molina, 1782)	<i>Graphidioides yañezi</i> Babero & Cattán, 1980	Babero and Cattán 1980

urban areas of Mar de Cobo, Buenos Aires province, Argentina. These authors experimentally infected dogs with this species of tapeworm from the tucos and recovered adult cestodes.

Rossin et al. (2004b) redescribed *Paraspidodera uncinata* (Rudolphi, 1819) from a large number of specimens obtained from the cecum and large intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina.

Rossin and Malizia (2005a) redescribed *Trichuris pampeana* Suriano & Navone, 1994 found in the cecum of the Azara's tuco-tuco, *Ctenomys azarae*, collected from Santa Rosa, La Pampa province, and reported new voucher material, the Talas tuco-tuco, *C. talarum* Thomas, 1898, collected at the Necochea, coastal dunes of Buenos Aires province. Also, an unidentified *Trichuris* found in *C. talarum* collected from Buenos Aires province, Argentina was reported. Simultaneously, Rossin et al. (2005b) described *Graphidioides subterraneus* from the stomach of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Partido de Mar Chiquita, Mar del Plata, Argentina.

Continuing work on tucos, Rossin et al. (2006a) described *Pudica ctenomydis* from the small intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Partido de Mar Chiquita, Argentina. In the same year, Rossin et al. (2006b) described *Trichostrongylus duretteae* obtained from the small intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina.

Rossin et al. (2009) reported *Strongyloides myopotami* Artigas & Pacheco, 1933 found in the small intestines of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina, and from Pearson's tuco-tuco, *Ctenomys pearsoni* Lessa & Langguth, 1983, collected from Penino, Departamento de San José, Uruguay.

During an ecological study of helminth parasite infection parameters in two species of South American subterranean rodents of the genus *Ctenomys*, Rossin et al. (2010a) documented seven species of Endoparasites from two collection localities, species of hosts studied included the Southern tuco-tuco, *C. australis* Rusconi, 1934, from Necochea, Buenos Aires Province, and Talas tuco-tuco, *C. talarum* Thomas, 1898, from Mar de Cobo, Buenos Aires province, Argentina. Both species of tuco-tuco's harbored *Trichuris pampeana* in the cecum, *Pudica ctenomydis* Rossin et al., 2006 in the small intestine, and larvae of *Taenia talicei* in the abdominal cavity. Moreover, *C. talarum*

had four additional species of helminths, including *Graphidioides subterraneus* Rossin et al., 2005 in the stomach, *Paraspidodera uncinata* in the large intestine, and *Strongyloides myopotami* and *Trichostrongylus duretteae* Rossin et al., 2006 in the small intestine.

Rossin et al. (2010b) redescribed the metacestode form of *Taenia talicei* obtained from the peritoneal cavity of two tuco-tuco species including the Southern tuco-tuco, *Ctenomys australis* Rusconi, 1934, and the Talas tuco-tuco, *Ctenomys talarum*, from Necochea, Paraje Las Grutas, Buenos Aires Province in Argentina.

From Bolivia, Drabik and Gardner (2019) described *Ancylostoma ctenomyos* Drabik & Gardner, 2019 from the small intestine of the Bolivian tuco-tuco, *Ctenomys boliviensis* collected from two localities in the Department of Santa Cruz, 3.5 km west of Estación el Pailón and 2 km SSE of Santa Rosa de la Roca, and from Steinbach's tuco-tuco, *Ctenomys steinbachi* Thomas, 1907 collected from 2 km S. of Caranda by road in the Department of Santa Cruz.

Gardner et al. (2021) mentioned discovery of a new species of *Mathevotaenia* from the Highland tuco-tuco, *Ctenomys opimus*, collected in 1986 from Huancaroma, Department of Oruro, Bolivia (Gardner et al. 2023). Also from Bolivia, Gardner et al. (2021) also reported *Paraspidodera* nematodes including individuals from the cecae of Anderson's tuco-tuco, *Ctenomys andersoni* Gardner et al., 2014, the Bolivian tuco-tuco or Cajuchi, *Ctenomys boliviensis* Waterhouse, 1848, Conover's tuco-tuco, *Ctenomys conoveri* Osgood, 1946, Erica's tuco-tuco, *Ctenomys erikacuellarae* Gardner et al., 2014, the little Andean forest tuco-tuco, *Ctenomys frater* Thomas, 1902, Lessa's tuco-tuco, *Ctenomys lessai* Gardner et al., 2014, Lewis's tuco-tuco, *Ctenomys lewisi*, Steinbach's tuco-tuco, *Ctenomys steinbachi*, and Natterer's tuco-tuco, *Ctenomys nattereri* Wagner, 1848. In addition, an undescribed species of *Raillietina* was found in the small intestine of *C. erikacuellarae* collected on the experiment station grounds near Monteagudo, Bolivia and *Pudica* sp. Travassos & Darriba, 1929 was also reported from the White-toothed tuco-tuco, *Ctenomys leucodon* Waterhouse, 1848.

The present study reports that during a biodiversity survey in Bolivia in 1986, *Pudica pujoli* Durette-Desset & Tchepprakoff, 1990 was found in a single specimen of the White-toothed tuco-tuco, *Ctenomys leucodon* Waterhouse, 1848, collected from near San Andreas de Machaca, Bolivia.

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New records of water mites (Acari, Hydrachnidia) from Portugal revealed by DNA barcoding, with the description of *Atractides marizae* sp. nov.

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Abstract

This study presents the first results of DNA barcoding of water mites from Portugal. DNA barcodes were recovered from 19 water mite specimens morphologically assigned to eight species, seven of them newly reported from Portugal. Two species, *Torrenticola hispanica* (Lundblad, 1941) and *A. cultellatus* (K. Viets, 1930) were discovered more than 80 years after they were first described, and *Atractides marizae* sp. nov. is described as new for science.

Keywords

New records, new species, systematics, taxonomy

Introduction

The water mites of Portugal are still insufficiently known. Water mites of mainland Portugal and its archipelagos (Madeira and Azores) were studied by Barrois (1887, 1896), Koenike (1895), Thor (1898), Viets (1918), Lundblad (1941, 1942, 1954, 1956), and Cantallo et al. (2021, 2022). The most recent check list of water mites of Portugal and its archipelagos was published by Cantallo et al. (2022), who reported 93 hydrachnid species from 34 genera and 16 families. All of these species were exclusively identified on the basis of morphological characters, and until now there have been no studies analyzing the genetic diversity of this important but often neglected limnafaunistic group.

In recent years, the use of the mitochondrial cytochrome c oxidase subunit I (COI) gene, has proven to be a highly effective tool for delimiting and identifying water mites, in particular for recognizing species complexes with potential cryptic diversity (Martin et al. 2010; Pešić et al. 2012, 2017, 2019, 2020, 2022; Fisher et al. 2017; Pešić and Smit 2020). The use of this system, known as DNA barcoding, in recent taxonomic studies has been accelerated by the formation of worldwide databases for the storage and public identification of sequences, such as GenBank and the BOLD system (DNA Barcode of Life Data System).

In some regions, COI data on water mites has been intensively accumulated in recent years and has led to the compilation of national and regional DNA barcode libraries (e.g., Blattner et al. 2019; Pešić et al. 2021a, b; Pešić and Smit 2022). This has enabled a better assessment of the molecular diversity of water mites in specific habitats, as well as the identification of problematic species groups, resulting in the description of a number of cryptic or pseudocryptic species that would probably remain undescribed using solely classical taxonomic methods.

The main aim of this study is to enrich the existing reference library with new sequences of specimens collected in Portugal and present the taxonomic results of this collecting effort.

Materials and methods

Water mites were collected by hand netting, sorted live from other organisms and debris in the field, and immediately preserved in 96% ethanol for the purpose of the molecular analyses (see below). Water-mite specimens used for the molecular study are listed in Table 1. After DNA extraction, the specimen vouchers were stored in 96% EtOH and morphologically examined. Some of these vouchers were dissected and slide mounted in Faure's medium, while the rest was transferred to Koenike's fluid and stored in the collection of the first author. DNA sequences prepared in the course of this study were deposited in BOLD and GenBank. The DNA extracts were archived in -80°C freezers at the Centre for Biodiversity Genomics (CBG; <https://biodiversitygenomics.net>).

Table 1. Details on barcoded specimens, including data and coordinates of sampling sites, the barcode index number (^N indicates a new BIN that contains only current sequences) and associated data obtained from BOLD. DNN = distance to nearest neighbor; NN BIN = nearest neighbor BIN; NN taxonomy = species assigned to nearest neighbor BIN. BOLD data presented here was last accessed on 10 January 2023.

Species	Locality	Coordinates	Voucher Code	BOLD/GenBank Acc Nos	BIN BOLD	DNN (%)	NN BIN BOLD:	NN taxonomy
Lebertidae								
<i>Lebertia pusilla</i>	Santarém,	39.4110°N,	CCDB_39397_B06	HYDAS018-22/ OQ211647	–	–	–	–
	Caniceira	8.2615°E	CCDB_39397_C03	HYDAS027-22/ OQ211648				
Torrenticolidae								
<i>Torrenticola hispanica</i>	Santarém, Caniceira	39.4110°N, 8.2615°E	CCDB_39397_B10	HYDAS022-22/ OQ211664	^N AES2742	14.02	AEW2607	<i>Torrenticola</i> sp.
<i>Monatractides stadleri</i>	Beja, Corgo da Ponte Quebrada	37.6961°N, 8.7122°E	CCDB_39397_B05	HYDAS017-22/ OQ211649	AEU1504	8.98	AED3802	<i>Monatractides stadleri</i>
Oxididae								
<i>Oxus angustipositus</i>	Porto, Silveirinhos	41.1727°N, 8.5007°E	CCDB_39397_A06	HYDAS006-22/ OQ211652	^N AET9442	5.59	AED9576	<i>Oxus angustipositus</i>
			CCDB_39397_A08	HYDAS008-22/ OQ211651				
			CCDB_39397_A07	HYDAS007-22/ OQ211650				
Hygrobatidae								
<i>Atractides marizae</i> sp. nov.	Santarém, Caniceira	39.4110°N, 8.2615°E	CCDB_39397_B12	HYDAS024-22/ OQ211637	^N AER7878	12.98	AEN9154	<i>Atractides giustinii</i>
			CCDB_39397_C04	HYDAS028-22/ OQ211643				
			CCDB_39397_C05	HYDAS029-22/ OQ211642				
			CCDB_39397_C02	HYDAS026-22/ OQ211640				
<i>Atractides allgaier</i>	Beja, Corgo da Ponte Quebrada	37.6886°N, 8.7043°E	CCDB_39397_B02	HYDAS014-22/ OQ211639	^N AEU1287	14.58	ACS0163	<i>Atractides distans</i>
			CCDB_39397_A09	HYDAS009-22/ OQ211641				
<i>Atractides cultellatus</i>	Santarém, Caniceira	39.4110°N, 8.2615°E	CCDB_39397_B11	HYDAS023-22/ OQ211638	^N AEU1503	16.01	ADG8744	<i>Atractides rivalis</i>
Pionidae								
<i>Piona nodata</i>	Herdade do Pinheiro	38.4953°N, 8.7097°E	CCDB_39397_C06	HYDAS030-22/ OQ211655	^N AET0101	10.43	ACR9882	<i>Piona nodata</i>
			CCDB_39397_C07	HYDAS031-22/ OQ211656				
			CCDB_39397_C08	HYDAS032-22/ OQ211657				
			CCDB_39397_C09	HYDAS033-22/ OQ211653				
			CCDB_39397_C10	HYDAS034-22/ OQ211654				

Morphological nomenclature follows Gerecke et al. (2016). The genital acetabula in both sexes and the genital plate in the female were measured on both sides; therefore, their dimensions are given as a range of values, rather than a single value. The holotype and paratypes of the new species are deposited in the Naturalis Biodiversity Center in Leiden (**RMNH**).

All measurements are given in μm . The photographs of selected structures were made using the camera of a Samsung Galaxy smartphone. The following abbreviations are used: **Ac-1** = first acetabulum; **Cx-I** = first coxae; **Dgl-4** = dorsoglandularia 4; **dL** = dorsal length; **H** = height; **I-L-4-6** = fourth-sixth segments of first leg; **L** = length; **IL** = lateral length; **mL** = medial length; **P-1-P-5** = palp segment 1-5; **S-1** = proximal large ventral seta at I-L-5; **RMNH** = Naturalis Biodiversity Center, Leiden; **S-2** = distal large ventral seta at I-L-5; **Vgl-1** = ventroglandularia 1; **W** = width.

Molecular and DNA barcode analyses

The molecular analysis was conducted at the Canadian Centre for DNA Barcoding (Guelph, Ontario, Canada; CCDB; <http://ccdb.ca/>). The specimens were sequenced for the barcode region of COI using standard invertebrate DNA extraction (Ivanova et al. 2007), amplification (Ivanova and Grainger 2007a), and sequencing (Ivanova and Grainger 2007b) protocols.

DNA barcode sequences were aligned using MUSCLE alignment (Edgar 2004). Primer nucleotide sequences were removed, and chromatograms were checked for the presence of double peaks, stop codons, and frameshifts, which could indicate the amplification of nuclear mitochondrial pseudogenes. None of the DNA sequences showed evidence of pseudogenes.

Data related to each BIN, including the minimum p -distance to the nearest neighboring BIN, was estimated through BOLD. Intra- and interspecific genetic distances were calculated based on the p -distance model using MEGA X (Kumar et al. 2018). MEGA X software was used to calculate neighbour-joining (NJ) trees based on K2P distances (standard for barcoding studies) and pairwise deletion of missing data. The support for tree branches was calculated by the nonparametric bootstrap method (Felsenstein 1985) with 1000 replicates and shown next to the branches. Codon positions included were 1st+2nd+3rd+Noncoding.

Results and discussion

This study represents first DNA barcodes of water mites from Portugal with a COI barcode dataset obtained from 19 specimens and morphologically assigned to six genera (Table 1). The two species, *Torrenticola hispanica* (Lundblad, 1941) and *Attractides cultellatus* (K. Viets, 1930), which are both endemic to the Iberian Peninsula, were uploaded into the BOLD database; these contribute to the formation of a DNA barcode reference library for the reliable identification of water mite species in future studies. Moreover, one species is described as new for science, and seven species are reported as new for water-mite fauna of Portugal.

Description of new species

Family Hygrobatidae Koch, 1842

Atractides (Atractides) marizae Pešić, sp. nov.

<https://zoobank.org/97384632-7c6e-4387-9a59-d6d907670250>

Figs 1, 2A–D, 3

Type material. *Holotype* ♂ (sequenced, CCDB_39397_C02, Table 1), dissected and slide mounted (RMNH), PORTUGAL, Santarém, Caniceira stream, 39.4110°N, 8.2615°W, 25.v.2022 leg. Jovanović. *Paratypes*: 3♂, 2♀, same site and data as the holotype, 2♂, 1♀ sequenced (Table 1), 1♂ (CCDB_39397_C0) damaged (one palp and I-legs missing), 1♀ (CCDB_39397_B12) dissected and slide mounted (RMNH).

Diagnosis. Characters of the *nodipalpis*-species group (integument finely striated, muscle insertions unsclerotized; males with anteriorly and posteriorly indented genital field, P-2 with distoventral projection and ventral margin of P-4 projecting); excretory pore smooth, acetabula relatively small, arranged in an obtuse triangle.

Description. General features—Integument striated, muscle insertions unsclerotized; mediocaudal margin Cx-I strongly convex, apodemes of Cx-II in an acute angle with the median line. Excretory pore smooth; Vgl-1 not fused to Vgl-2. Palp with strong sexual dimorphism in shape of P-2 and P-4, in both sexes medial peg-like seta inserting halfway between ventral setae, seta insertions dividing ventral margin into three equal sectors. I-L-5 proximally subrectangular, distally protruding near insertion S-1, with seta S-1 slender and bluntly pointed, S-2 shorter and pointed, proximally enlarged; I-L-6 slender, curved, basally slightly thickened from the centre to the claw furrow with parallel dorsal and ventral margins (Figs 2C, 3C). **Male**—Anterior margin of genital plate with a notch and bead structure, a fine median tip projecting in a deep indentation; caudal margin with a deep indentation extending to about 1/2 L of Ac-3, Ac rounded to subtriangular, arranged in an obtuse triangle (Fig. 1B, C); ventral margin P-2 with a strongly developed distal extension, P-3 strongly concave, P-4 proximally concave, inflated near proximoventral seta. **Female**—Caudal apodemes of Cx-I +II strongly protruding, Cx-IV with well-developed apodemes at medial margins (Fig. 3A), P-2 nearly straight with a right-angled ventrodistal edge, P-3 dorsal margin slightly concave, P-4 more slender than in the male (Fig. 3B).

Measurements. Male (holotype, CCDB_39397_C02; in parentheses some measurements of paratype, CCDB_39397_C04)—Idiosoma L 559 (538), W 458 (425); maximum diameter Dgl-4, 28. Coxal shield L 344 (303); Cx-III W 388 (334); Cx-I+II mL 117 (122), Cx-I+II IL 244 (206). Genital field L/W 91(94)/129(117), L Ac-1-3: 25–28 (25–28), 23–27 (26–30), 30–31 (32–34). Ejaculatory complex L 94.

Palp—Total L 338; dL/H, dL/H ratio: P-1, 31/30, 1.05; P-2, 73/58, 1.26; P-3, 83/45, 1.83; P-4, 111/41, 2.73; P-5, 40/14, 2.8; L ratio P-2/P-4, 0.66. Gnathosoma vL 125, chelicera total L 222.

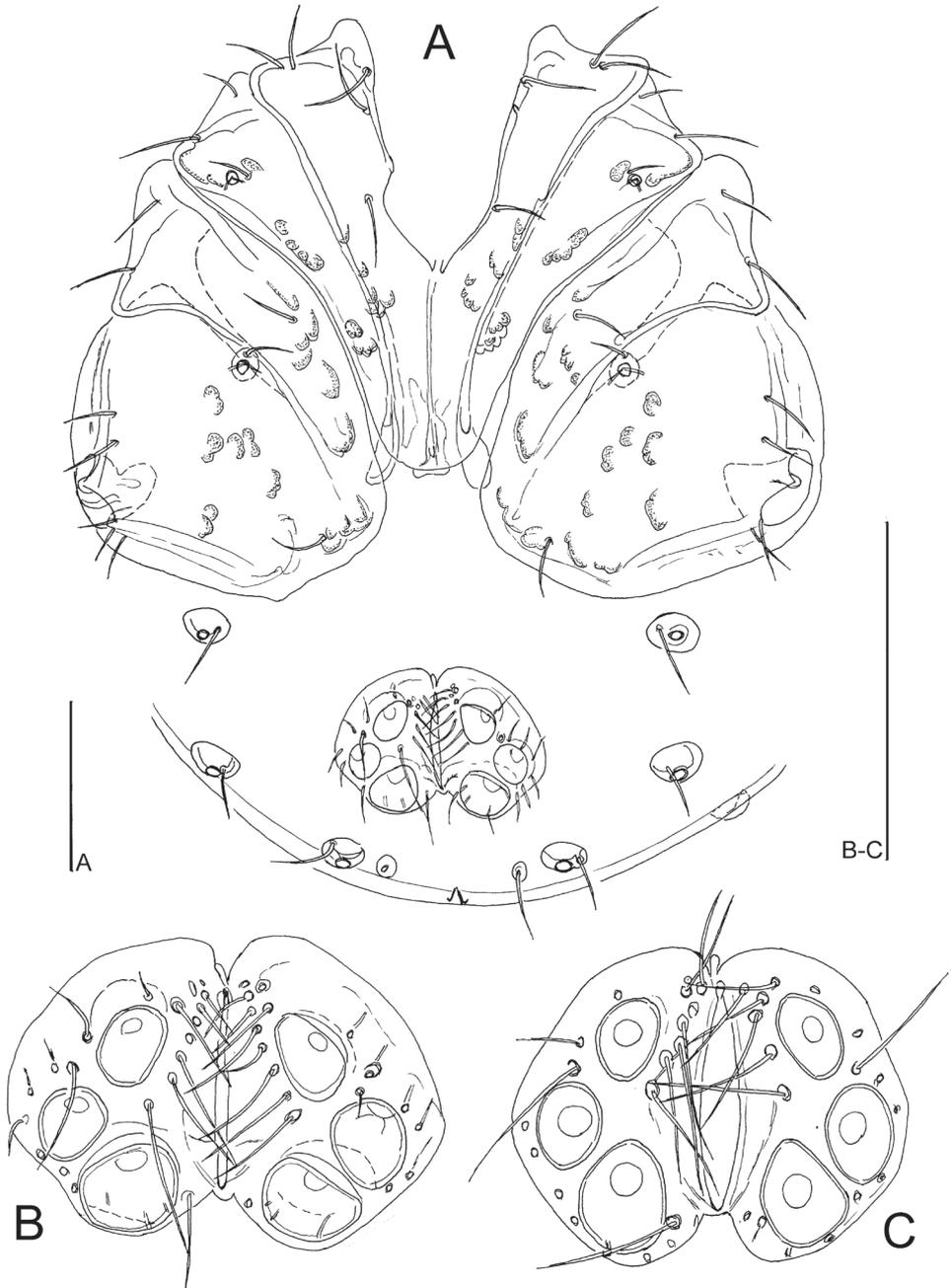


Figure 1. *Atractides marizae* nov. sp., ♂ **A, B** holotype, CCDB_39397_C02 **C** paratype, CCDB_39397_C04 **A** idiosoma in ventral view **B, C** genital field. Scale bars: 100 μ m.

Legs—I-L-5 dL 195, vL 142, dL/vL ratio 1.37, maximum H 49, dL/maximum H 3.99, S-1 L 98, L/W ratio 10.5, S-2 L 78, L/W ratio 4.99, distance S-1-2, 16, dL ratio S-1/2, 1.26; I-L-6 dL 141, central H 22, dL/central H ratio 6.46; L I-L-5/6 ratio 1.38.

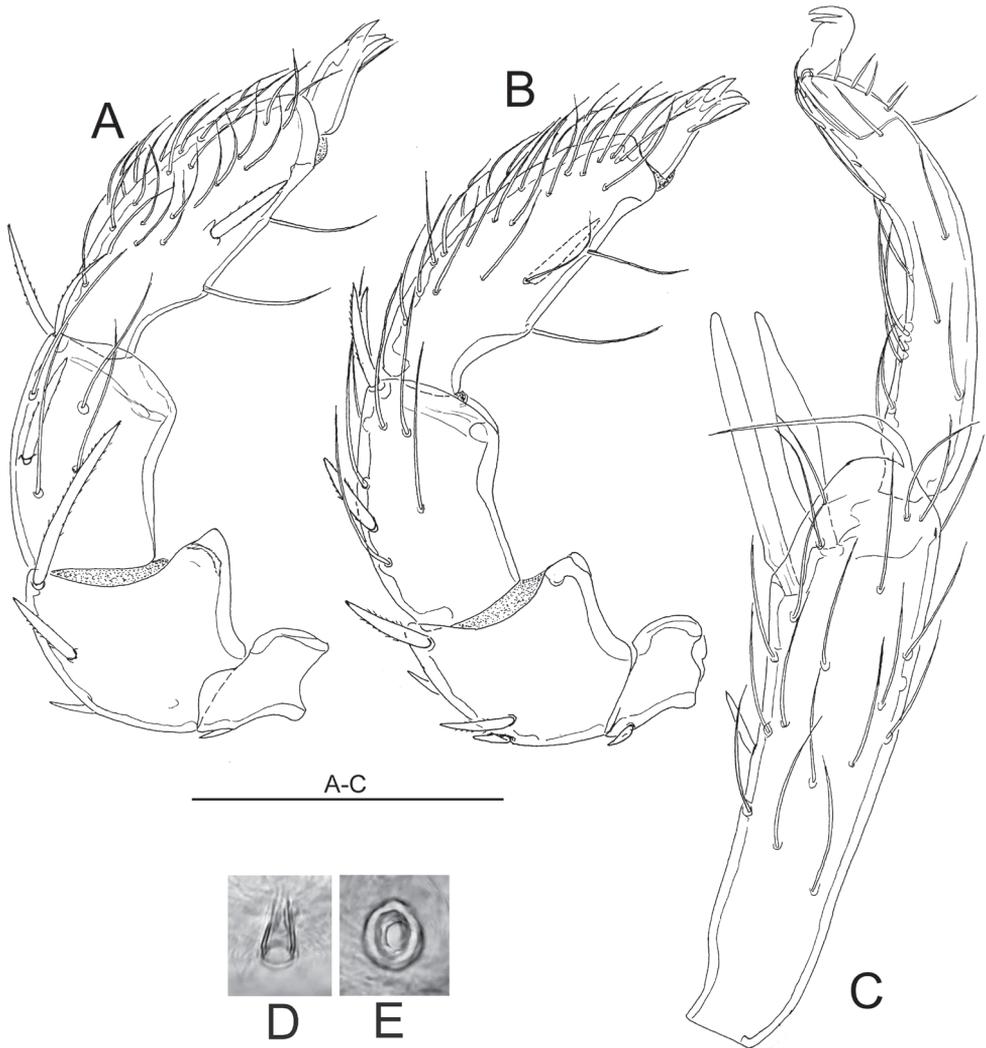


Figure 2. **A–D** *Atractides marizae* nov. sp., ♂ holotype, CCDB_39397_C02 **A** palp in medial view **B** palp in lateral view **C** I-L-5 and -6 **D** excretory pore **E** *A. ruffoi*, ♀ CCDB_39397_C02, Corsica; excretory pore. Scale bar: 100 µm.

Female (CCDB_39397_B12)–Idiosoma L 686, W 531. Coxal shield L 369; Cx-III W 466; Cx-I+II mL 122, Cx-I+II IL 263. Genital field L/W 150/167, genital plates L 122–124, pregenital sclerite 84, gonopore L 119, L Ac-1-3: 41, 39–41, 42.

Palp–Total L 454; dL/H, dL/H ratio: P-1, 38/38, 1.02; P-2, 97/64, 1.51; P-3, 127/52, 2.43; P-4, 147/36, 4.09; P-5, 45/19, 2.41; L ratio P-2/P-4, 0.66. Gnathosoma vL 158, chelicera total L 280.

Legs–I-L-5 dL 277, vL 194, dL/vL ratio 1.43, maximum H 66, dL/maximum H 4.22, S-1 L 145, L/W ratio 12.8, S-2 L 114, L/W ratio 6.1, distance S-1-2, 36, dL ratio S-1/2, 1.27; I-L-6 dL 202, central H 22, dL/central H ratio 9.22; L I-L-5/6 ratio 1.37.

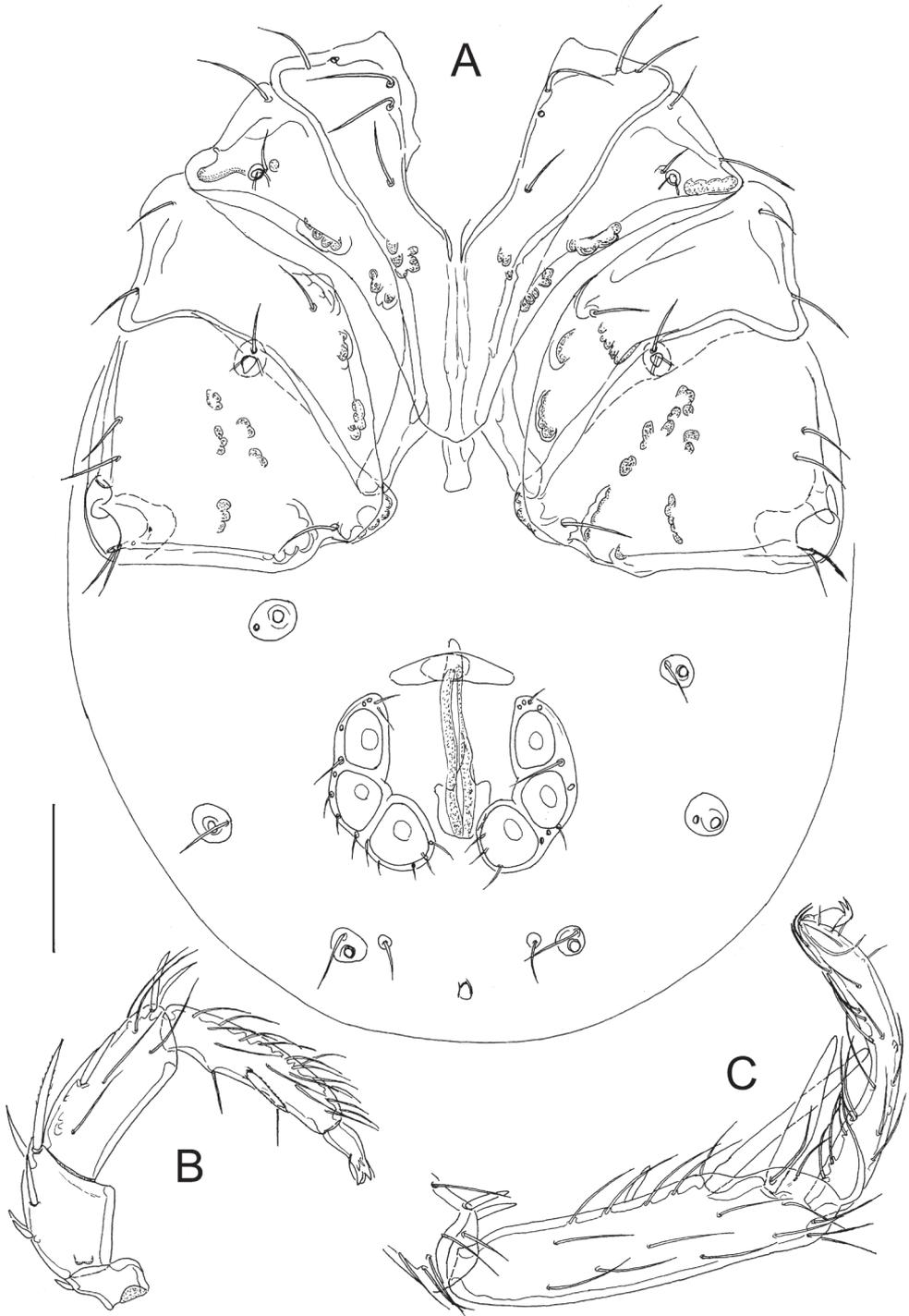


Figure 3. *Atractides marizae* nov. sp., ♀ paratype, CCDB_39397_B12 **A** idiosoma in ventral view **B** palp in medial view **C** I-L-5 and -6. Scale bar: 100 µm.

Etymology. The new species is named in honor of Marisa dos Reis Nunes, known professionally as Mariza, a famous Portuguese fado singer in the appreciation of the enjoyment her music brings to the authors.

Species delimitation using DNA-barcodes. The final alignment for species delimitation using COI sequence data comprised 674 nucleotide positions (nps) of the 175 *Atractides* specimens, morphologically assigned to 40 species listed in Suppl. material 1 and one outgroup, *Mixobates processifer* from Norway to root the tree. The NJ tree is presented in Fig. 4. The COI tree sequences retrieved from specimens of *A. marizae* sp. nov. from Portugal appeared as a sister clade of *A. ruffoi* Gerecke & Di Sabatino, 2013, a rhithrobiontic species endemic to Corsica (Gerecke and Di Sabatino 2013). The *p*-distance between the COI sequences of specimens of *A. marizae* sp. nov. from Portugal and one specimen of *A. ruffoi* from Corsica was estimated at $13.34 \pm 1.3\%$, indicating genetic separation between these two clades. The mean intraspecific divergence within the clade of new species from Portugal was relatively low (1.09 ± 0.27).

Remarks. Pešić and Smit (2022), by mistake, assigned the voucher specimen (CCDB 38559A09) of *Atractides ruffoi* from Corsica to *A. guistinii* Gerecke & Di Sabatino, 2013, a species endemic to Corsica and Sardinia. Therefore, the sequence NOVMB009-21/ON002561 deposited in BOLD/GenBank belongs to *A. ruffoi*.

Discussion. In regard to the striated integument, a characteristic “notch and bead” structure of male genital field, and the shape of the palp in the male (P-2 with distoventral projection, ventral margin of P-4 projecting), the new species resembles *A. nodipalpis* Thor, 1899, *A. robustus* (Sokolow, 1940), and *A. ruffoi*. Both sexes of *A. nodipalpis* and *A. robustus* differ by having larger acetabula in a triangular arrangement. *Atractides ruffoi* differs by the development of a sclerite at the excretory pore (Gerecke and Di Sabatino 2013).

A characteristic “notch and bead” structure of the male genital plate is found also in *A. clavipalpis* (Lundblad, 1956), which in males, differ from the new Portuguese species in having the ventral margin of P-2 distally slightly protruding and not forming a projection, and a distally club-shaped P-4 (Gerecke 2003).

Habitat. A rhithrobiont. Collected in a low-order stream, with shaded pool reaches having accumulations of leaf litter (Fig. 5).

Distribution. Portugal; only known from the type locality.

Species new for water mite fauna of Portugal

Family Lebertiidae Thor, 1900

Lebertia pusilla Koenike, 1911

Material examined. PORTUGAL, Santarém, Caniceira stream, 39.4110°N, 8.2615°W, 25.v.2022, leg. Jovanović, 2♂, 4♀, 2♀ sequenced (Table 1).

Remarks. The Portuguese specimens molecularly analyzed in this study match the description of *L. pusilla*, a species widely distributed in the Palaearctic (Di Sabatino et al. 2010). They share the presence of only one short swimming seta on II-L-5 and two

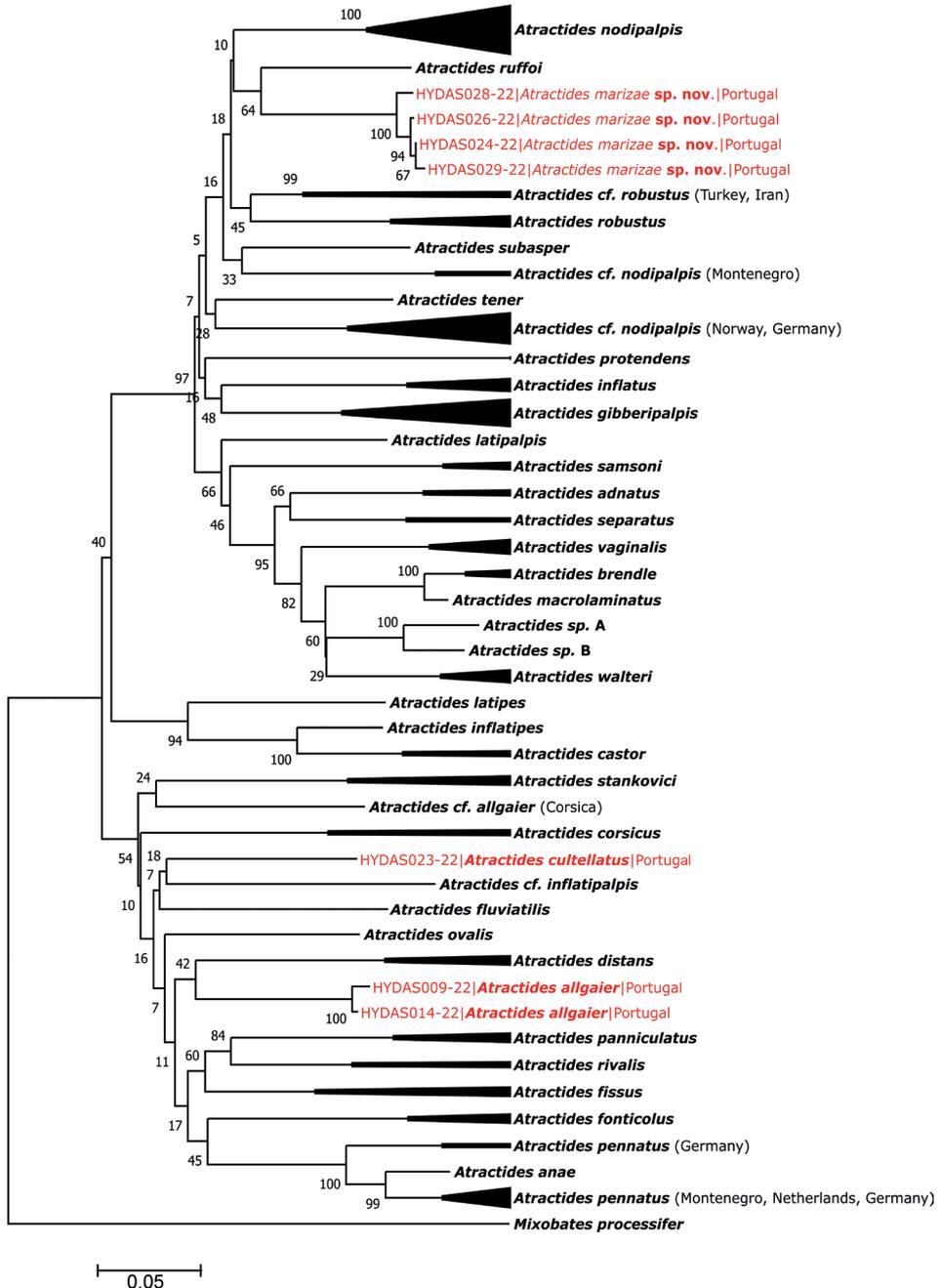


Figure 4. Neighbour-joining tree of the genus *Atractides* obtained from 175 nucleotide COI sequences.

or three swimming setae on anterior IV-L-5. It is likely that the lineage from Portugal represents a cryptic species, with a *p*-distance of 9.39–9.79% to the nearest sequence (NLACA493-15) of *L. pusilla* from the Netherlands.

Distribution. Europe.



Figure 5. Photograph of locus typicus (Caniceira stream, Santarém, Portugal) of *Atractides marizae* sp. nov. (inset). Photographs by M. Jovanović.

Family Oxidae K. Viets, 1926

Oxus (*Oxus*) aff. *angustipositus* K. Viets, 1908

Material examined. PORTUGAL, Porto, Silveirinhos stream, 41.1727°N, 8.5007°W, 25.v.2022, leg. Jovanović, 1♂, 2♀ (sequenced; Table 1).

Remarks. The Portuguese specimen molecularly analyzed in this study matches the description of *O. angustipositus*. These individuals form a unique BIN (BOLD:AET9442), with the nearest neighboring BIN being BOLD:AED9576, which consists of a specimen from Lake Ohrid, North Macedonia. The *p*-distance between the specimens from Portugal and GenBank *O. angustipositus* (Montenegro; OL870273, OL870215, OL870142, OL870101) is 8.7–9.3%; this demonstrates the need for taxonomic revision of the *O. angustipositus* complex for identifying possibly undescribed cryptic species.

Distribution. Western Palaearctic.

Family Torrenticolidae Piersig, 1902

Torrenticola (*Torrenticola*) *hispanica* (Lundblad, 1941)

Fig. 6

Material examined. PORTUGAL, Santarém, Caniceira stream, 39.4110°N, 8.2615°W, 25.v.2022, leg. Jovanović, 1♂, (sequenced; Table 1), dissected and slide mounted (RMNH).

Remarks. The Portuguese specimen molecularly analyzed in this study perfectly matches the description of *T. hispanica*, a species originally described on basis of specimens collected from a stream near Algeciras in Spain (Lundblad 1956).

Description. **Male**—Dorsal shield without a colour pattern, as shown in Fig. 6A; area of primary sclerotization of the dorsal plate with two dorsoglandularia; gnathosomal

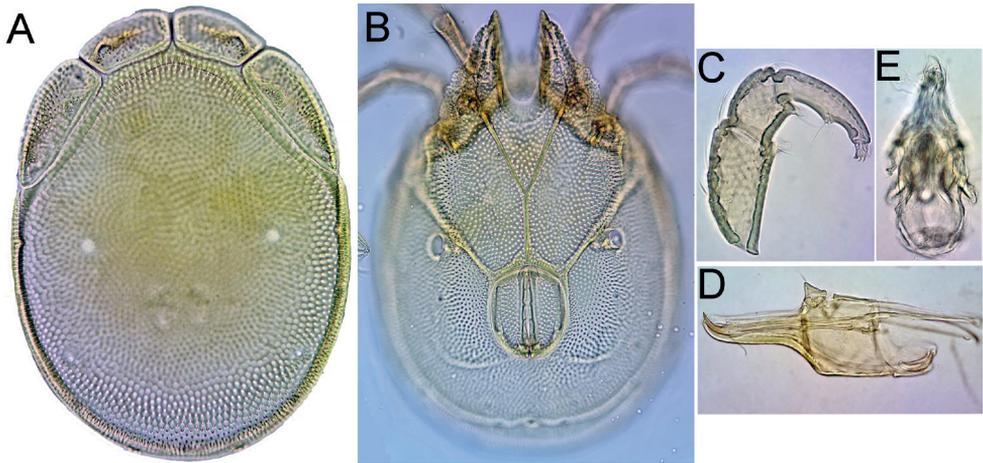


Figure 6. Selected parts of *Torrenticola hispanica*, ♂, CCDB_39397_B10 **A** dorsal shield **B** ventral shield **C** palp, lateral view (P-1 lacking) **D** gnathosoma and chelicera in lateral view **E** ejaculatory complex. Photographs by V. Pešić.

bay U-shaped, proximally rounded; Cxgl-4 subapical; suture line of Cx-IV evident, medially starting from posterior margin of genital field in a right angle to the main idiosoma axis; genital field subrectangular; ejaculatory complex conventional in shape (Fig. 6E); excretory pore located on the line of primary sclerotization; gnathosoma ventral margin curved, rostrum strongly elongated (Fig. 6D); P-2 longer than P-4; P-2 ventral margin straight, P-2 and P-3 ventrodistal protrusions blunt, laterally flattened, P-4 with a well-developed ventral tubercle bearing one longer and three shorter setae (Fig. 6C).

Measurements. (CCDB_39397_B10)–Idiosoma L 784, W 572; dorsal shield L 644, W 483, L/W ratio 1.33; dorsal plate L 598; shoulder plate L 203–206, W 75–81, L/W ratio 2.54–2.71; frontal plate L 142–147, W 70, L/W ratio 2.0–2.1; shoulder/frontal plate L 1.38–1.45. Gnathosomal bay L 172, Cx-I total L 338, Cx-I mL 164, Cx-II+III mL 128; ratio Cx-I L/Cx-II+III mL 2.64; Cx-I mL/Cx-II+III mL 1.28. Genital field L/W 159/134, ratio 1.19; distance genital field-excretory pore 113, genital field-caudal idiosoma margin 156. Palp: total L 342, dL/H, dL/H ratio: P-1, 39/31, 1.25; P-2, 114/58, 1.97; P-3, 64/51, 1.26; P-4, 106/30, 3.55; P-5, 19/13, 1.5; L ratio P-2/P-4 1.08; gnathosoma vL 337, chelicera L 400.

Distribution. Spain and Portugal.

Monatractides (Monatractides) stadleri (Walter, 1924)

Material examined. PORTUGAL, Beja, Corgo da Ponte Quebrada, stream, 37.6961°N, 8.7122°W, 23.v.2022, leg. Jovanović, 1♂ (sequenced; Table 1), gnathosoma, palps and I-legs dissected and slide mounted (dorsal and ventral shield stored in Koenike fluid).

Remarks. The Portuguese specimen molecularly analyzed in this study matches the description of *M. stadleri*, a species widely distributed in the Mediterranean region and often very frequent in lowland, running waters (Di Sabatino et al. 2010). The sequenced specimen clusters within BOLD:AEU1504, which includes two specimens of *M. stadleri* from Belgium and one specimen from Spain (identified as *Torrenticola* sp., deposited in Taxus Medio Ambiente, Spain). The *p*-distance between the latter BIN and its nearest neighbour, BOLD:AED3802, which includes specimens from Montenegro and Greece, is estimated at 8.98%. This suggests the need for taxonomic revision of the *M. stadleri* complex to identify possible undescribed cryptic species (see Pešić and Smit 2022 for a discussion).

Distribution. Central, Western, and Southern Europe.

Family Hygrobatidae Koch, 1842

Atractides (Atractides) cultellatus (K. Viets, 1930)

Fig. 7

Material examined. PORTUGAL, Santarém, Caniceira stream, 39.4110°N, 8.2615°W, 25.v.2022, leg. Jovanović, 1♀ (sequenced; Table 1), dissected and slide mounted (RMNH).

Remarks. The single female specimen from Portugal generally matches the description of *A. cultellatus*, which was originally described from a single female collected from Rio Manzanares, Spain (K. Viets, 1930). *Atractides valencianus* (K. Viets, 1930), a species originally described from Spain and later reported by Gerecke (2014) from Sardinia, resembles *A. cultellatus* in the presence of a lineated integument, a slenderer I-L-6, the more spaced sword setae of I-L-5, and Vgl-1 not fused to Vgl-2, but it differs in having P-2 completely devoid of thickening or rounding in females (Gerecke 2003).

Measurements. Female (CCDB_39397_B11)–Idiosoma L 691, W 520. Coxal shield (Fig. 7A) L 378; Cx-III W 489; Cx-I+II mL 94, Cx-I+II IL 216. Genital field L/W 163/159, genital plates L 115–118, pregenital sclerite 78, gonopore L 131, L Ac-1-3: 33–36, 28, 33. Egg maximum diameter ($n = 1$) 147. Palp (Fig. 7B): total L 354; dL/H, dL/H ratio: P-1, 36/33, 1.1; P-2, 77/51, 1.49; P-3, 95/39, 2.43; P-4, 108/31, 3.45; P-5, 38/13, 3.0; L ratio P-2/P-4, 0.71. Gnathosoma vL 119, chelicera total L 195. Legs: I-L-5 dL 229, vL 139, dL/vL ratio 1.65, maximum H 59, dL/maximum H 3.96, S-1 L 122, L/W ratio 11.1, S-2 L 102, L/W ratio 6.5, distance S-1-2, 38, dL ratio S-1/2, 1.2; I-L-6 dL 181, central H 19, dL/central H ratio 9.63; L I-L-5/6 ratio 1.27.

Distribution. Spain and Portugal.

Atractides (Atractides) allgaier Gerecke, 2003

Material examined. PORTUGAL, Beja, Corgo da Ponte Quebrada stream, 37.6886°N, 8.7043°W, 23.v.2022, leg. Jovanović, 2♀ (sequenced; see Table 1); Corgo da Ponte Quebrada stream, 37.6961°N, 8.7122°W, 23.v.2022, leg. Jovanović 1♀.

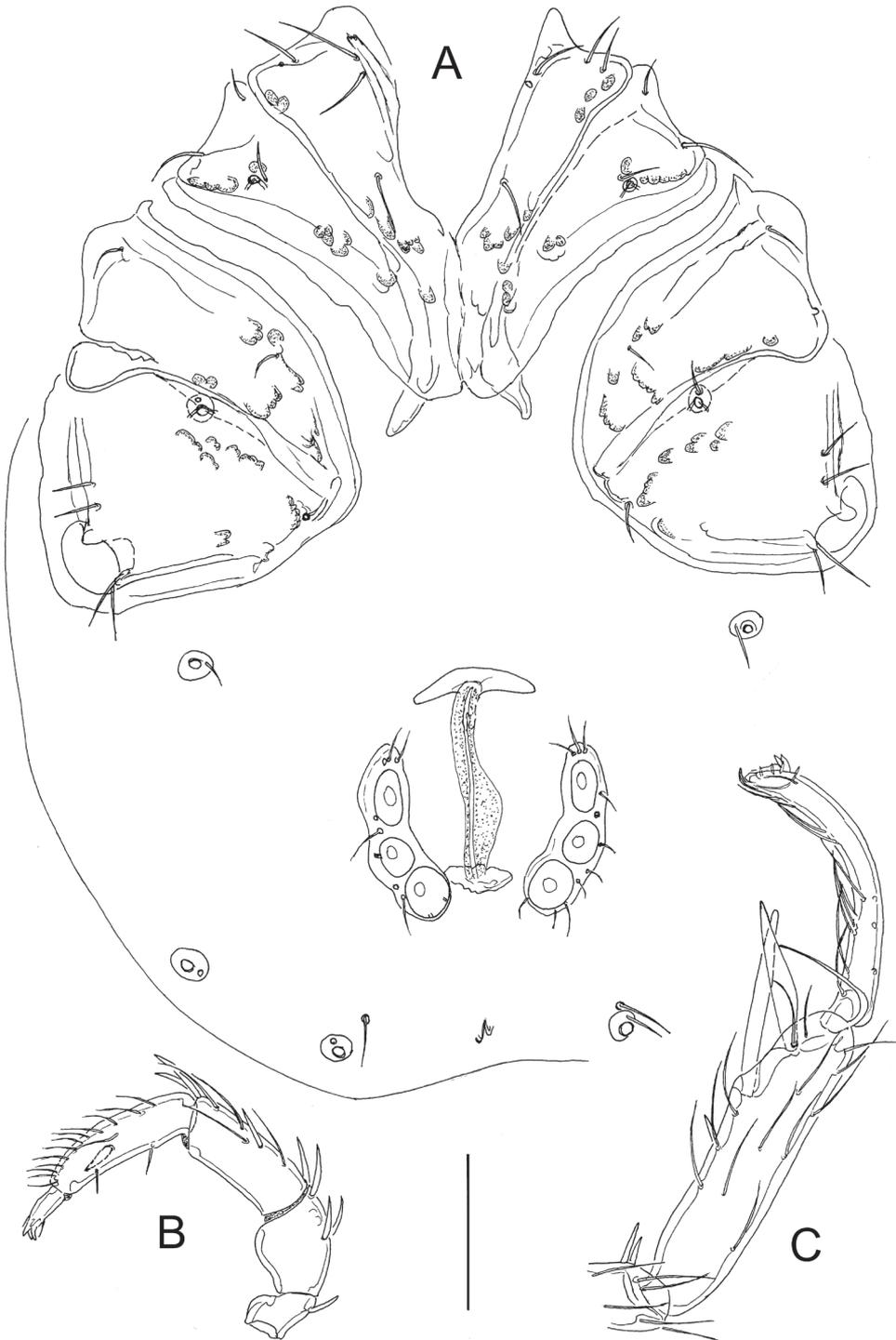


Figure 7. *Atractides cultellatus*, ♀, CCDB_39397_B11 **A** idiosoma in ventral view **B** palp in lateral view **C** I-L-5 and -6. Scale bar: 100 µm.

Remarks. Populations of this species have often been confused with those of *Atrac-tides distans* (K. Viets, 1914); see Gerecke (2003) for a discussion. Clear morphological differences, for example the presence of a lineated integument in *A. allgaier*, instead of striated one in *A. distans*, are confirmed with a large (>14%) *p*-distance between these species.

Distribution. Central, Western, and Southern Europe.

Family Pionidae Thor, 1900

Piona aff. *nodata* (Müller, 1776)

Material examined. PORTUGAL, Reserva Natural do Estuário do Sado, Herdade do Pinheiro, 38.4953°N, 8.7097°W, 10.v.2022, leg. Oliveira, 2♂, 2♀ (sequenced; Table 1).

Remarks. The Portuguese specimens molecularly analyzed in this study match description of *P. nodata*. Genetic data indicate that all examined specimens form a cluster (BOLD:AET0101) and belong to the same species. This BIN is solely composed of the Portuguese specimens; the closest neighboring BIN is that of *P. nodata* (BOLD:ACR9882) from the Netherlands. The high *p*-distance (10.45%) between these two BINs indicates that the Portuguese lineage may represent a cryptic species.

Distribution. Holarctic.

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Supplementary material I

List of *Atractides* specimens used for building the neighbour-joining (NJ) tree (Fig. 4)

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