

First record of harpacticoid copepods from Lake Tahoe, United States: two new species of *Attheyella* (Harpacticoida, Canthocamptidae)

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Abstract

Benthic harpacticoids were collected for the first time at Lake Tahoe, California-Nevada, United States. Two species were identified as members of the genus *Attheyella* Brady, 1880. The genus *Attheyella* comprises about 150 species within six subgenera, but only twelve species have previously been reported from North American freshwater habitats. The two new species of *Attheyella* described here have a 3-segmented endopod on P1 and 2-segmented P2–P4 endopods, the distal segment of exopod of P2–P4 has three outer spines, and the P5 has five setae on the exopod and six setae on the baseoendopod. *Attheyella* (*Attheyella*) *tahoensis* **sp. n.** most closely resembles *A. (A.) idahoensis* (Marsh, 1903) from Idaho, Montana, and Alaska (United States) and *A. (A.) namkungi* Kim, Soh & Lee, 2005 from Gosu Cave in South Korea. They differ mainly by the number of setae on the distal endopodal segment of P2–P4. In addition, intraspecific variation has been observed on the caudal rami. *Attheyella* (*Neomrazekiella*) *tessiae* **sp. n.** is characterized by the extension of P5 baseoendopod, 2-segmented endopod of female P2–P3, and naked third seta of male P5 exopod. The two new species are likely endemic to Lake Tahoe, an isolated alpine lake within the Great Basin watershed in the western United States.

Keywords

Benthic Harpacticoida, Canthocamptidae, Lake Tahoe, Nevada, California

Introduction

Lake Tahoe is a large freshwater lake in the Sierra Nevada of the United States. At a surface elevation of 1,897 m, it is located along the border between California and Nevada. Lake Tahoe is the largest alpine lake in North America. Its depth is 501 m, making it the deepest in the United States after Crater Lake (593 m). Lake Tahoe is one of the largest lakes by volume ($1.5 \times 10^{11} \text{ m}^3$) in the United States, only being exceeded by the Great Lakes. While, some basic ecological investigations have occurred in Lake Tahoe (Flint and Goldman 1975, Frantz and Cordone 1996, Vander Zanden et al. 2003), most recent investigations are focused on studies of water quality (Jassby et al. 2003), invasive species (Denton et al. 2012, Wittmann et al. 2012), and loss of native biodiversity (Caires et al. 2013). Meiobenthic (especially harpacticoid copepods) diversity has not been studied in Lake Tahoe until recently, and the ecological role of meiobenthos in Lake Tahoe remains unstudied.

During the past century, fresh water harpacticoid copepods in North America have been reported by several researchers, with checklists provided by: Wilson CB (1932; Woods Hole, Massachusetts), Coker (1934; Illinois, North Carolina and Minnesota), Reid (1996; Washington, D.C.), Hudson et al. (1998; the Great Lakes), Suárez-Morales and Reid (1998; the Yucatan peninsula), Bruno et al. (2005; Florida), and Reid and Hribar (2006; the Florida Keys). Moreover, Wilson and Yeatman (1959) and Reid and Williamson (2009) provided key to species in North American freshwater harpacticoid copepods.

Considering all studies of North American harpacticoid copepods, Canthocamptidae is the most abundant harpacticoid family on the continent (Reid and Williamson 2009) with representatives of the following 12 genera; *Attheyella* Brady, 1880, *Bryocamptus* Chappuis, 1928, *Canthocamptus* Westwood, 1836, *Cletocamptus* Schmankévitsch, 1875, *Elaphoidella* Chappuis, 1928, *Epactophanes* Mrázek, 1893, *Gulcamptus* Miura, 1969, *Heteropsyllus* Scott T., 1894, *Maraenobiotus* Mrázek, 1893, *Mesochra* Boeck, 1865, *Moraria* Scott T. & Scott A., 1893, and *Pesceus* Özdikmen, 2008 (Reid and Williamson 2009).

The genus *Attheyella* Brady, 1880 has been found in a wide range over the world (Dussart and Defaye 1990). Despite its cosmopolitan distribution, only 12 species of *Attheyella* have been reported in North America; *Attheyella* (*Attheyella*) *alaskaensis* Wilson M.S., 1958, *A. (A.) idahoensis* (Marsh, 1903), *A. (A.) obatogamensis* (Willey, 1925), *A. (Neomrazekiella) americana* (Herrick, 1884), *A. (N.) dentata* (Poggenpol, 1874), *A. (N.) dogieli* (Rylov, 1923), *A. (N.) illinoisensis* (Forbes S.A., 1876), *A. (N.) nordenskiöldii* (Lilljeborg, 1902), *A. (N.) ussuriensis* Rylov, 1933, *A. (Ryloviella) carolinensis* Chappuis, 1932, *A. (R.) pilosa* Chappuis, 1929, and *A. (R.) spinipes* Reid, 1987.

As part of ongoing efforts to understand the ecological role of meiobenthos in Lake Tahoe, harpacticoid copepods have been collected and documented here for the first time. Here, two new species of *Attheyella* from the Lakeside Beach littoral zone are described and an updated key to species of *Attheyella* in North America is provided.

Material and methods

Samples were collected from the Lakeside Beach littoral zone, 5 m water depth, on south shore of Lake Tahoe near the California-Nevada border in July 2013. Sediment samples were collected manually by SCUBA divers. Sediments were sampled with 2.9 cm inner diameter core tubes and were fixed with 70% ethanol and stained with Rose Bengal. Meiofauna was extracted from sediments by Ludox isopycnic centrifugation (Burgess 2001). Due to the coarseness of sand typical of Lake Tahoe, vortexing was replaced with gentle agitation during the Ludox extraction procedure to prevent mechanical damage to animals. Harpacticoids were sorted and enumerated under a Leica S8APO dissecting microscope, and stored in 70% ethanol.

Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a camera lucida on a Leica DM 2500 differential interference contrast microscope. Specimens were deposited at the Smithsonian National Museum of Natural History.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth thoracopod; exp (enp)-1 (2, 3) to denote the proximal (middle, distal) segment of a ramus. Scale bars in figures are indicated in μm .

Results

Order Harpacticoida Sars, 1903

Family Canthocamptidae Brady, 1880

Genus *Attheyella* Brady, 1880

Subgenus *Attheyella* (*Attheyella*) Chappuis, 1929

Attheyella (*Attheyella*) *tahoensis* sp. n.

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Figs 1–6

Type locality. The Lakeside littoral zone; 38°57'42"N, 119°57'14"W, 5 m water depth, of Lake Tahoe in California-Nevada, United States.

Material examined. Holotype: 1♀ (USNM No: 1251801) dissected on 8 slides. Paratype 2♀♀ and 1♂ (USNM No's listed in order presented in text: 1251802, 1251804, 1251803) each dissected on 6, 9 and 8 slides respectively, and 6♀♀ and 4♂♂ (USNM No's for specimens in vials (female, male): 1251805, 1251806) in 70% ethanol, vial. All from the type locality, July 2013, *leg.* J.G. Baguley.

Description. Female. Total body length 816 μm (n=6; range: 753–868 μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width measured at posterior margin of cephalic shield: 241 μm . Urosome narrower

than prosome (Fig. 1A). Posterior and lateral margins on all somites except anal somite strongly serrated (Fig. 1A–B).

Cephalothorax (Fig. 1A) bell-shaped, with saddle-shaped dorsal integumental window and some scattering sensillae on dorsal surface and along lateral margin (Fig. 1C). Pedigerous somites with sensillae on dorsal surface, serrate posteriorly as cephalothorax; pleural areas well developed. Urosome 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites.

Genital somite and first abdominal somite partly fused forming double-somite, wider than long. Genital field as in Fig. 4B. Genital apertures located anteriorly, closely set together. Copulatory pore located anteriorly between genital apertures. Seminal receptacle well developed on each side. P6 with small protuberance bearing 2 pinnate setae.

Anal somite (Figs 1D, 4C) with pair of sensilla dorsally, with well-developed rounded operculum bearing row of setules. Caudal rami (Fig. 1D–E) bottle-shaped, strongly tapering distally, about 2.5 times as long as wide, each ramus with 7 setae: setae I–II bare, short, of subequal lengths, closely set, seta III bipinnate, seta IV bare, seta V longest, seta VI bare and short, seta VII tri-articulate at base. Inner margin of each ramus with lateral concavity.

Antennule (Fig. 2A) 7-segmented. Segment 1 largest, with 1 spinular row and 1 seta. Segment 2 with 2 spinular rows around posterior and lateral margins. Segment 4 with aesthetasc fused basally to seta and set on pedestal. Armature formula: 1-[1], 2-[9], 3-[6], 4-[2+(1+ae)], 5-[1], 6-[4], 7-[8+acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 bare setae.

Antenna (Fig. 2B) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small. Allobasis elongated; spinules on abexopodal margin; with 2 long abexopodal setae. Exopod 1-segmented; with 1 inner and 3 apical pinnate setae. Endopod elongated, with strong spinules along inner margin; lateral armature consisting of 2 pinnate spines and a minute seta; distal armature consisting of 2 apically curved pinnate spines and 3 geniculate setae, the outer-most bipinnate and basally fused to an additional short seta.

Mandible (Fig. 2C–D) with well-developed gnathobase bearing 2 strong teeth and several smaller, multicuspidate teeth around distal margin and 1 pinnate spine at dorsal corner; spinules near base of palp. Palp 2-segmented, distal segment with 4 bare setae.

Maxillule (Fig. 2E). Praecoxal arthrite well developed, with 9 apical strong and transformed spines, 2 bare setae on anterior surface and, few spinules near outer margin. Coxa with cylindrical endite bearing 1 naked seta, and 1 curved spine. Basis with 2 geniculated setae and 1 bipinnate spine apically; with several spinules around inner distal margin and base of endopod. Endopod and exopod incorporated in basis and presented by 1 pinnate and 1 naked seta, and 2 naked setae, respectively.

Maxilla (Fig. 2F). Syncoxa with 2 endites each carrying apically 2 strong pinnate spines and 1 seta. Allobasis drawn out into strong, slightly curved, distally pinnate claw, accessory armature consisting of 2 bare setae with 1 tube pore. Endopod small, with 2 naked setae.

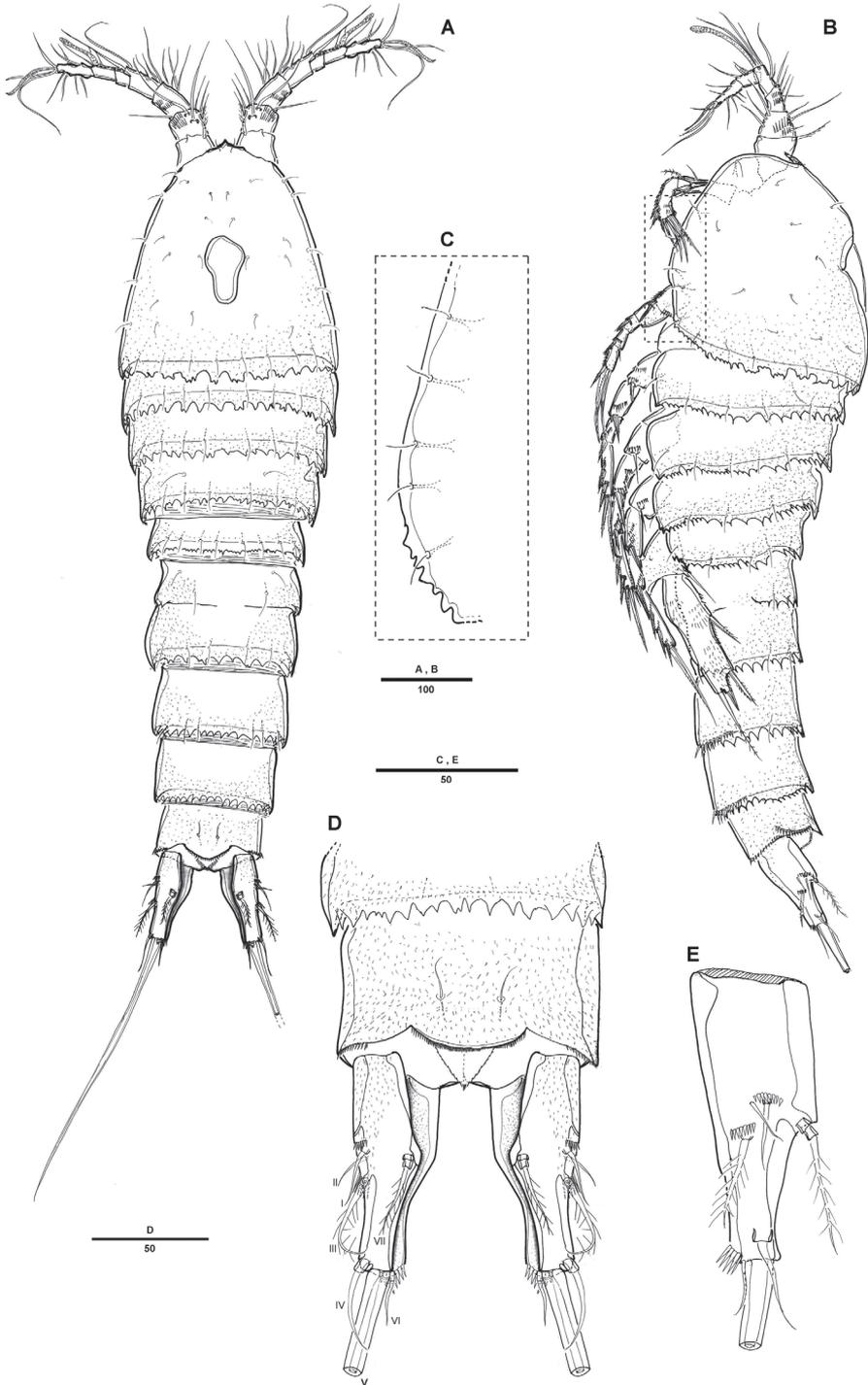


Figure 1. *Attheyella (Attheyella) tahoensis* sp. n. female: **A** habitus, dorsal **B** habitus, lateral **C** cephalothorax lateral anterior margin **D** anal somite and caudal rami, dorsal **E** caudal ramus, lateral.

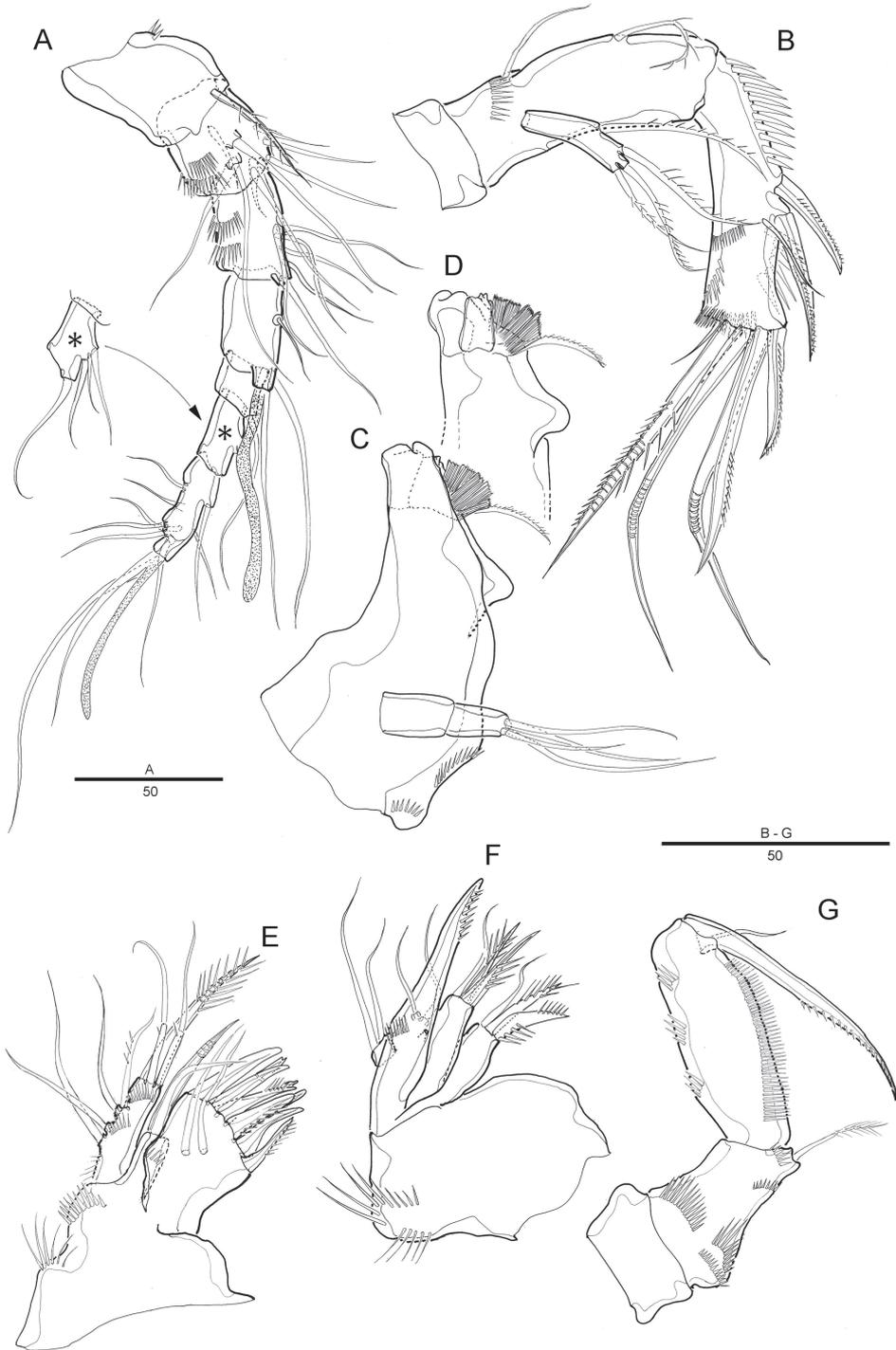


Figure 2. *Attheyella (Attheyella) taboensis* sp. n. female: **A** antennule **B** antenna **C** mandible **D** mandible, other view **E** maxillule **F** maxilla **G** maxilliped.

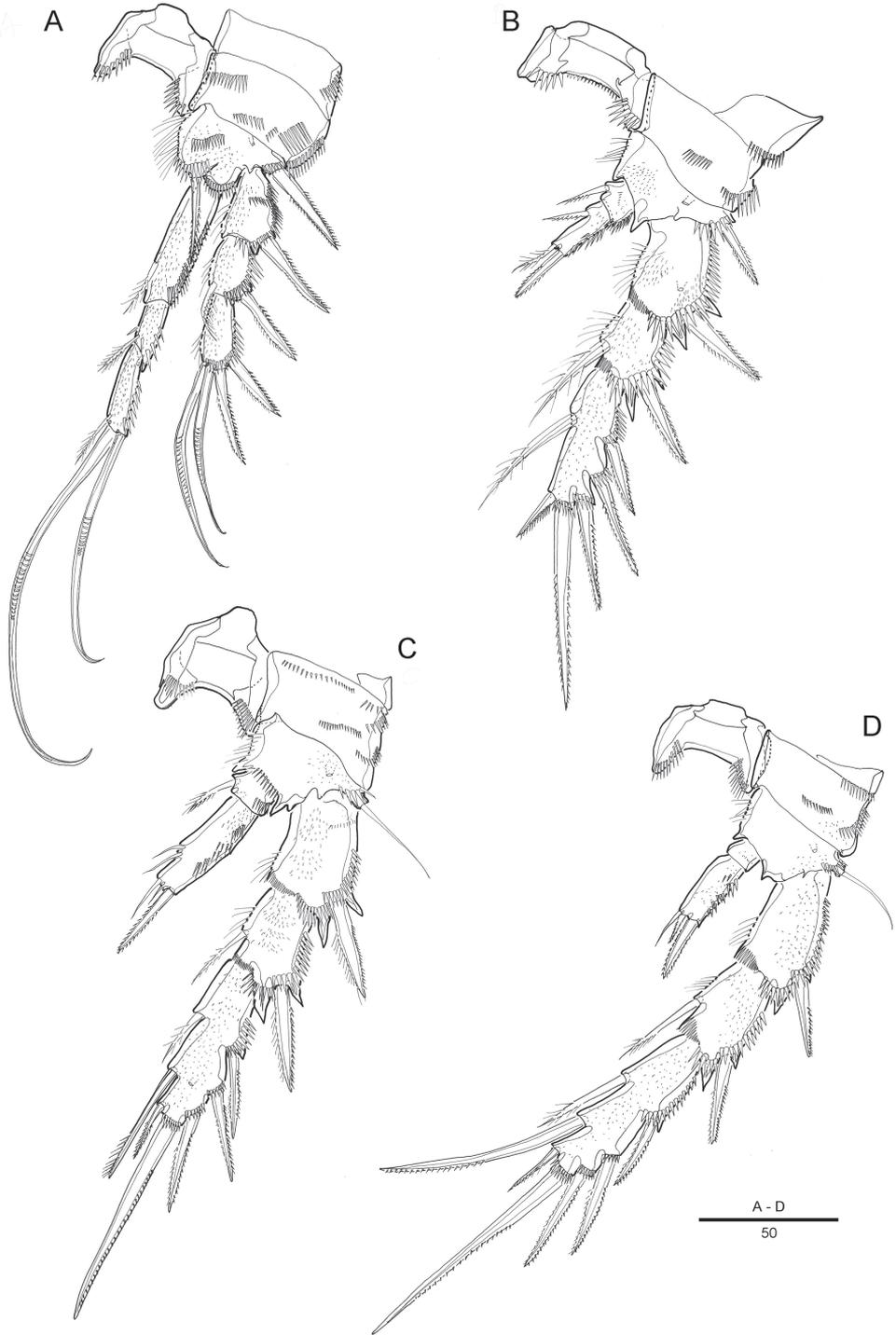


Figure 3. *Attheyella (Attheyella) taboensis* sp. n. female: **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior.

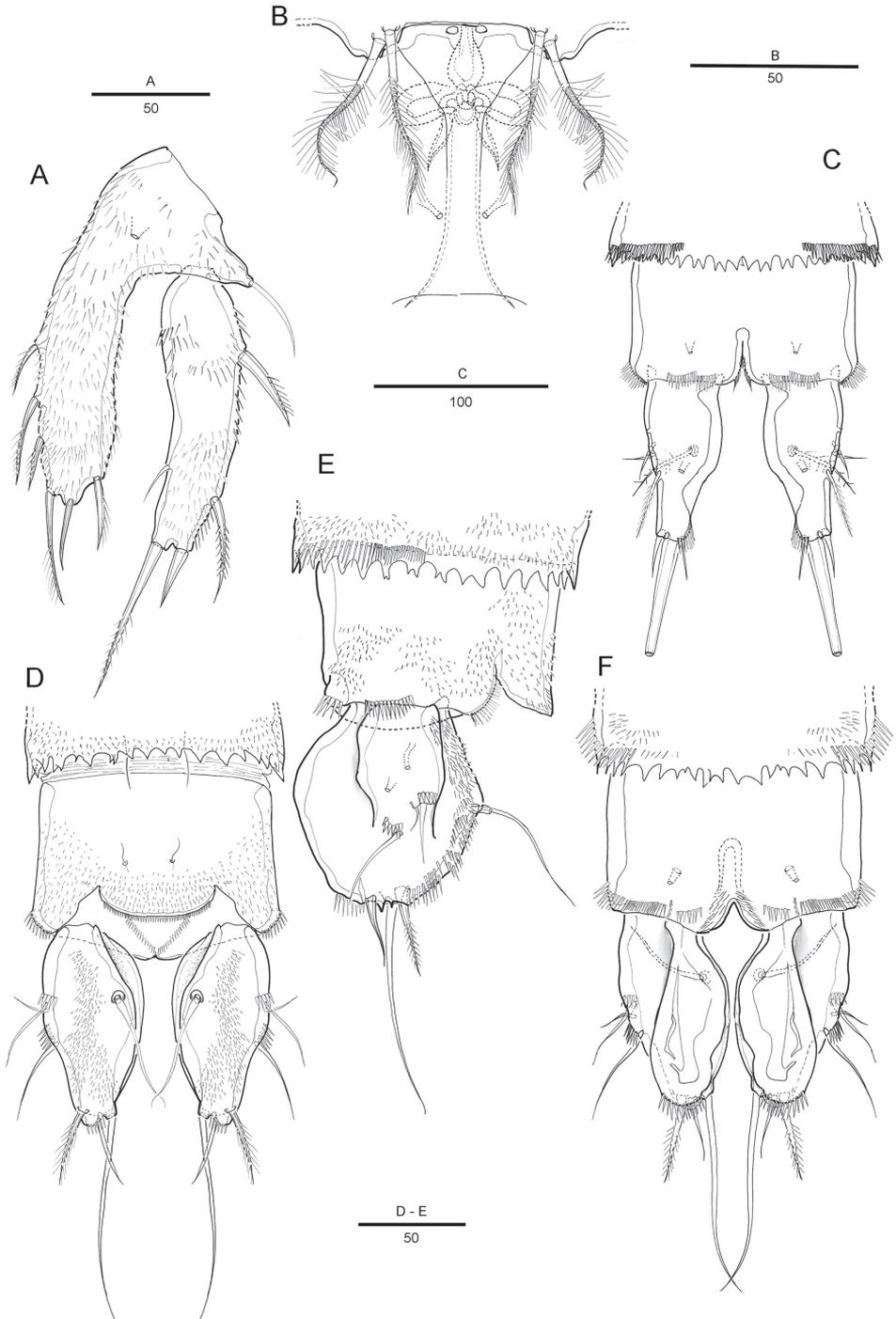


Figure 4. *Attheyella (Attheyella) taboensis* sp. n. female: **A** P5, anterior **B** genital field, ventral **C** anal somite and caudal rami, ventral **D** abnormal caudal rami, ventral **E** abnormal caudal rami, dorsal **F** abnormal caudal rami, lateral, ventral.

Maxilliped (Fig. 2G). Syncoxa with 1 plumose seta on inner distal corner. Basis with 1 row of spinules along palmar region. Endopodal segment produced into strong and distally pinnate curved claw; accessory armature consisting of 1 small seta at base.

Swimming legs 1-4 with wide intercoxal sclerite, biramous, endopods 2-segmented except for P1, exopods 3-segmented. Coxa and basis with row of spinules along outer margins as illustrated.

P1 (Fig. 3A). Praecoxa large, with longitudinal spinular row on anterior surface. Coxa large, with four spinular rows on anterior surface, and row of spinules along outer margin. Basis with strong bipinnate outer spine on outer margin and bipinnate spine on inner distal surface, with several spinules and setules as figured. Endopod 3-segmented; enp-1 about 2.1 times as long as enp-2; enp-1 with one small inner bipinnate seta on distal fourth; enp-2 with 1 bipinnate inner seta; enp-3 with 1 small pinnate seta and 2 long geniculate setae distally. Exopod 3-segmented, reaching middle of enp-2, exp-2 with 1 inner pinnate seta; exp-3 with 2 geniculate distal setae and 2 strong spinulose outer spines.

P2-P4. Coxa and basis with spinular rows along outer margin and anterior surface. Basis with pinnate spine (P2) or bare seta (P3-P4), each seta arising from a setophore.

P2 (Fig. 3B) with large coxa, ornamented with row of spinules on anterior surface, and with row of long spinules along outer margin; P2 enp-2 more than twice as long as enp-1; with 1 short, pinnate inner seta; enp-2 with 1 inner pinnate short seta, and 1 short apical seta and 1 bipinnate apical spine; exopod 3-segmented; each segment with row of spinules along outer margins; third segment about 1.8 times as long as second segment with 3 strong bipinnate outer spines, 2 apical pinnate spines, and 1 inner bipinnate seta.

P3 (Fig. 3C) with small praecoxa. Coxa nearly 1.5 times as wide as long, with 3 spinular rows on anterior surface and 2 rows of spinules along outer margin. Enp-2 about 3 times longer than enp-1; enp-2 with 2 small bare inner setae and 2 short distal naked setae and one pinnate spine.

P4 (Fig. 3D) with small and triangular praecoxa, with row of spinules on anterior surface along distal margin. Coxa with 1 row of small spinules on anterior surface and 1 spinular row along outer margin. Enp-2 2.5 times as long as enp-1; enp-2 with 1 naked seta, 1 pinnate seta and 1 spine. Spine and setal formulae as follows:

	Exopod	Endopod
P1	0.1.022	1.1.120
P2	0.1.123	1.120
P3	0.1.223	1.230
P4	0.1.223	0.030

P5 (Fig. 4A) with separate exopod and baseopod, each covered with spinules as illustrated. Baseopod longer than wide, forming short outer setophore bearing the basal seta. Endopodal lobe long and almost reaching distal margin of exopod, with 3 pinnate inner setae, 2 distal setae, and 1 pinnate outer seta. All setae pinnate and

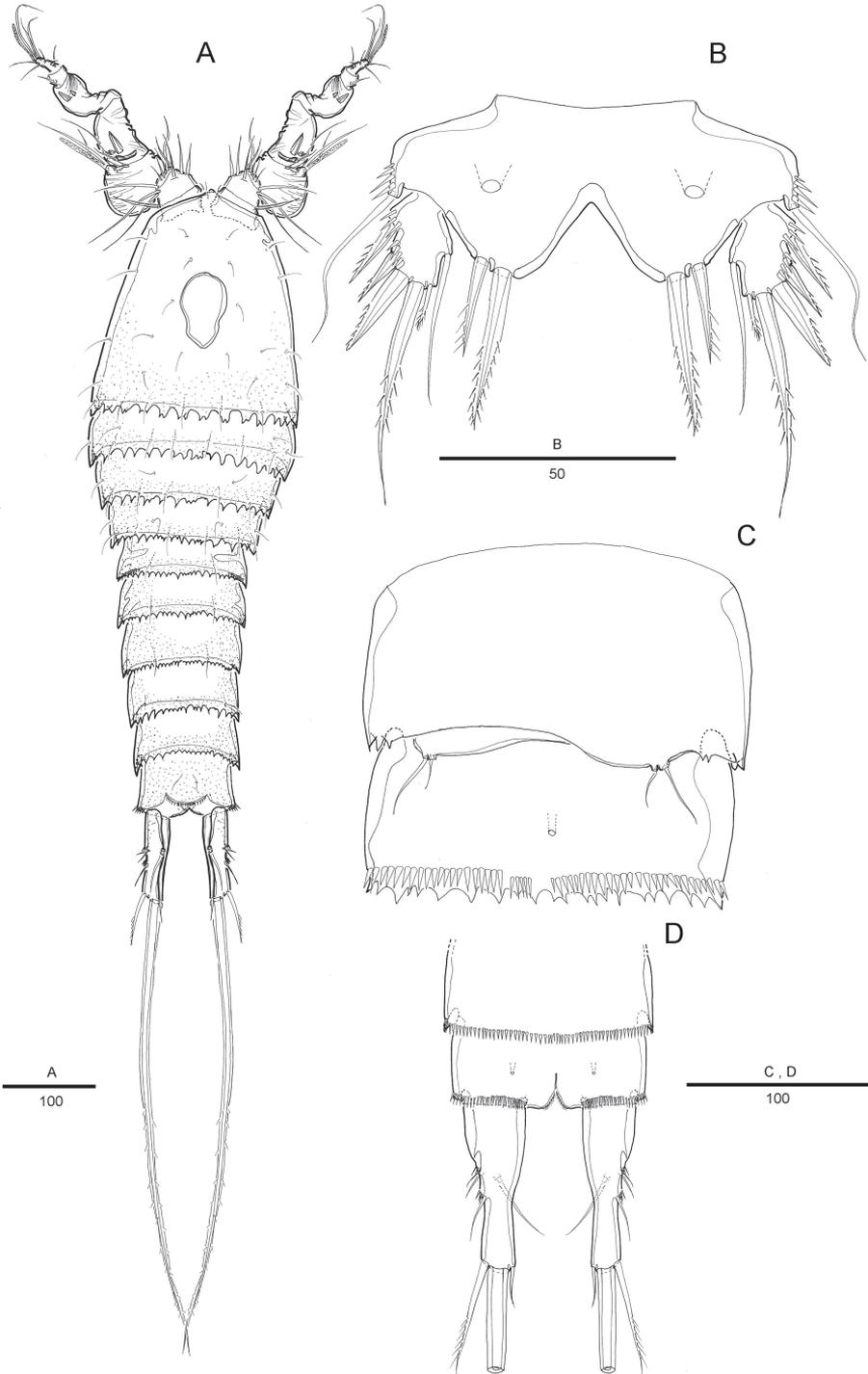


Figure 5. *Attheyella (Attheyella) taboensis* sp. n. male: **A** habitus, dorsal **B** P5, anterior **C** genital field, ventral **D** anal somite and caudal rami, ventral.

short. Secretory pore on anterior surface. Exopod elongated, 3.4 times as long as wide, with 1 short inner, 2 distal and 2 outer setae.

P6 (Fig. 4B) each with small protuberance bearing 2 plumose setae.

Description. Male. Body slightly smaller and more slender than female, habitus as in Fig. 5A. Body length 784 μm ($n=5$; range: 765-821 μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width measured at P2-bearing somite: 214 μm . Sexual dimorphism in antennule, P3-P4 endopod, P5 and P6.

Prosome (Fig. 5A) posterior margin of cephalothorax and pedigerous somites with serrated process, with integumental sensilla.

Urosome (Fig. 5A, C) 6-segmented, comprised of P5-bearing somite, genital somite, and 4 free abdominal somites. Urosomite with serrated posterior margin dorsally and ventrally.

Caudal rami (Fig. 5D) slightly more elongated than female, about 3.3 times as long as wide, seta III bare, seta IV pinnate. Inner margin of each ramus with lateral concavity.

Antennule (Fig. 6A) 10-segmented; subchirocer with geniculation between segments 5 and 6, and between segment 7 and 8. Segment 1 with a row of spinules along anterior margin. Segment 4 and 6 represented by a small sclerite. Segment 5 swollen with large bump along posterior margin. Segment 7 and 8 with 3 spinular processes from modified setae on each segment. Armature formula: 1-[1], 2-[7], 3-[9], 4-[2], 5-[5 + (1 + ae)], 6-[2], 7-[2 + 3 modified] 8-[3 modified], 9-[1], 10-[7 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 bare setae.

P3 (Fig. 6B). Exopod as in female, except for outer spine on first and second exopodal segment of P3 proportionately stronger. Endopod modified, 3-segmented; enp-1 shortest with inner pinnate seta; enp-2 with well-developed inner apophysis; enp-3 with 1 pinnate apical seta and 1 long bare seta.

P4 (Fig. 6C). Setae and spines on exopod modified, outer spine on first and second exopodal segment proportionally stronger than female. Endopod 2 with 1 pinnate seta and 2 pinnate spines and longer than those in female.

Fifth pair of legs (P5) (Fig. 5B) smaller and much shorter than female and fused medially, with no spinules. Baseoendopod with outer setophore bearing the basal seta. Endopodal lobe with 2 distal pinnate setae with large pore on anterior surface. Exopod shorter than in female, as long as wide, with 1 inner bare seta, 2 distal pinnate setae and 1 pinnate spine, and 2 outer pinnate spines.

P6 (Fig. 5C) asymmetrical, bearing 2 naked seta on a cylindrical process. On left side a lobe with two setae, on the right side a small plate with two setae.

Variability. Intraspecific variability was observed in the shape of caudal rami of female (about 20%; 6/30 observed individuals). Caudal rami (Fig. 4D-F) lamelliform and elongate, about twice as long as wide, laterally compressed, inner margin of each ramus with lateral concavity. Each ramus with 7 setae: seta III bare, seta IV bipinnate, seta V extremely reduced, seta VI bare and longer than normal.

Etymology. The species name refers to the type locality, Lake Tahoe. This is one of the largest alpine lakes in the world is known for its pristine waters and aesthetic beauty.

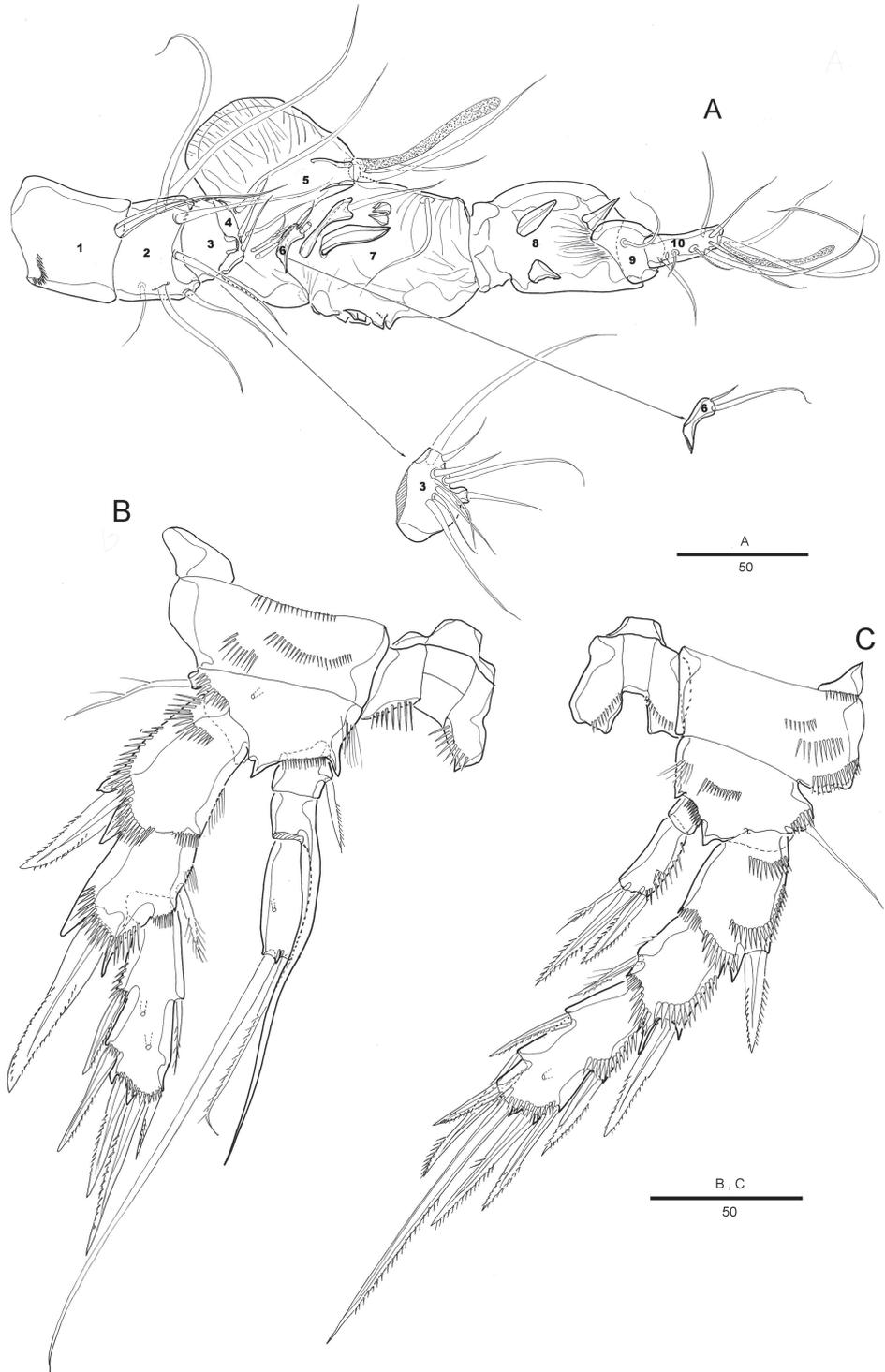


Figure 6. *Attheyella (Attheyella) tahoensis* sp. n. male: **A** antennule **B** P3, anterior **C** P4, anterior.

Subgenus *Attheyella* (*Neomrazekiella*) Ozdikmen & Pesce, 2006***Attheyella* (*Neomrazekiella*) *tessiae* sp. n.**

<http://zoobank.org/752396F3-38A4-4B57-B2C9-294B1FC888D8>

Figs 7–10

Type locality. The Lakeside littoral zone; 38°57'42"N, 119°57'14"W, 5 m water depth, of Lake Tahoe in California-Nevada, United States.

Material examined. Holotype: 1♀ (USNM No: 1251796) dissected on 9 slides, from the type locality. Paratype 1♀ and 1♂ (USNM No's listed in order presented in text: 1251797, 1251798) each dissected on 3 and 9 slides respectively, and 10♀♀ and 6♂♂ (USNM No's for specimens in vials (female, male): 1251799, 1251800) in 70% ethanol, vial. Additional samples were deposited in the first author's collection. All from the type locality, July 2013, *leg.* J. G. Baguley.

Description. Female. Total body length 660 µm (n=5; range: 635–694 µm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width measured at posterior margin of cephalic shield: 176 µm. Urosome narrower than prosome (Fig. 7A).

Cephalothorax (Fig. 7A) bell-shaped, with oval dorsal integumental window and some scattering sensillae on dorsal surface and along lateral margin. Rostrum (Fig. 7B) small and triangular, completely fused to cephalothorax and with pair of sensilla and pore near anterior margin.

Prosome with smooth posterior margins, pleural areas well developed. Body slightly constricted between each somite. All pedigerous somites with plain hyaline frill on posterior margin. Urosome 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites.

Genital double-somite as wide as long. Original segmentation marked by discontinuous internal chitinous rib laterally, completely fused ventrally. A row of spinules present on lateral side of genital field. Genital field located far anteriorly (Fig. 7C). Genital apertures paired, closely set together. Copulatory pore located anteriorly between genital apertures. Seminal receptacle well developed on each side. P6 with small protuberance bearing 2 bare unequal setae.

Anal somite (Fig. 7D–E) with well-developed rounded operculum. Surface ornamentation consisting of a pair of sensilla dorsally and a pair of pores ventrally, posterior margin with spinules ventrally and dorsally, with triangular process dorsally, anal opening with a fringe of fine setules. Caudal rami short, as long as wide, each ramus with 7 setae: setae I–II small, closely set, seta III bare, seta IV pinnate, seta V bipinnate and longest, seta VI bare, seta VII tri-articulate at base.

Antennule (Fig. 7B) 8-segmented. Segment 1 largest, with 1 spinular row around posterior margin and 1 pinnate seta. Segment 4 with aesthetasc fused basally to seta and arising from a pedestal. Armature formula: 1-[1], 2-[8], 3-[5], 4-[1+(1+ae)], 5-[1], 6-[3], 7-[2], 8-[4+acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 bare setae.

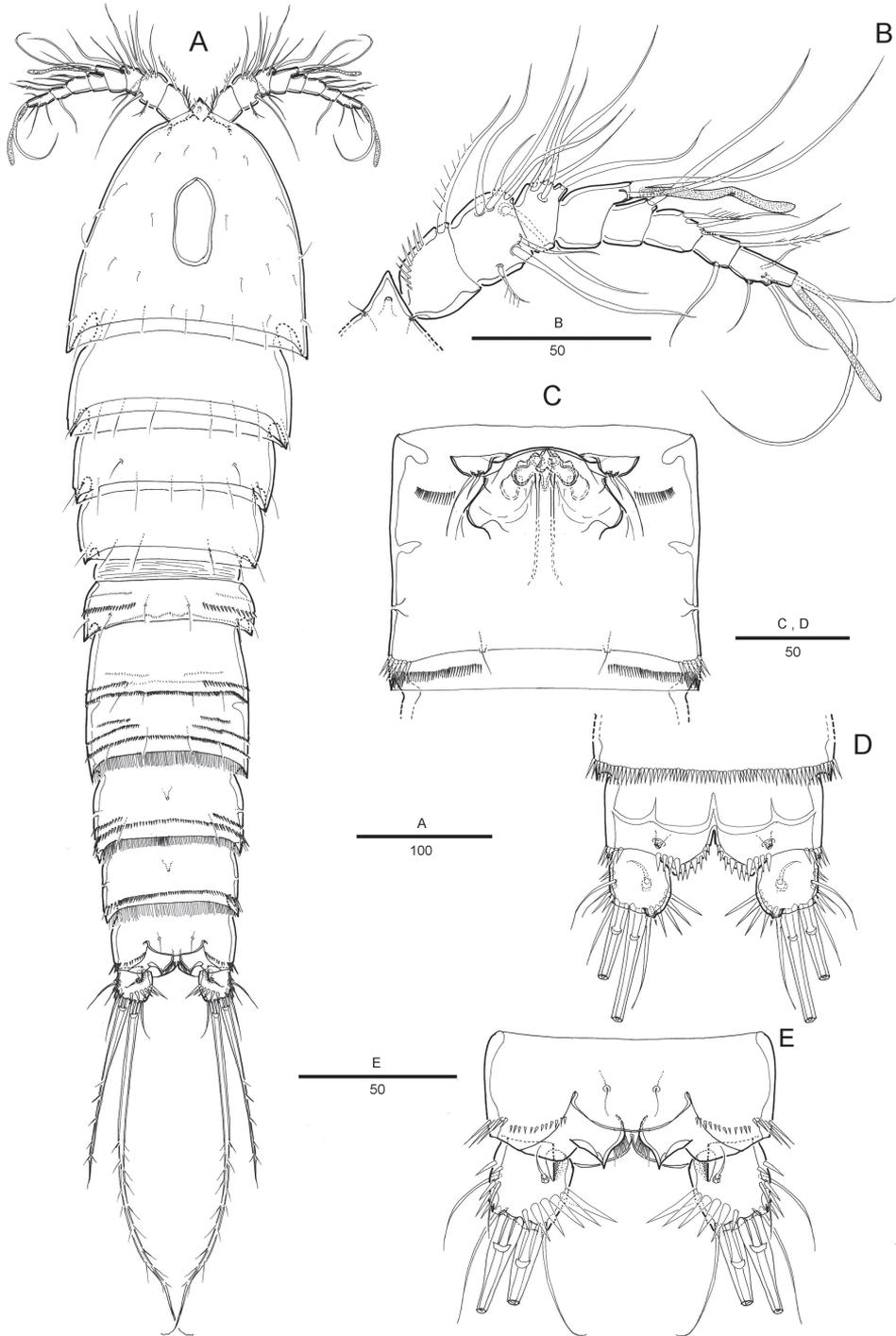


Figure 7. *Attheyella (Neomrazekiella) tessiae* sp. n. female: **A** habitus, dorsal **B** antennule **C** genital field **D** anal somite and caudal rami, ventral; **E** anal somite and caudal rami, dorsal.

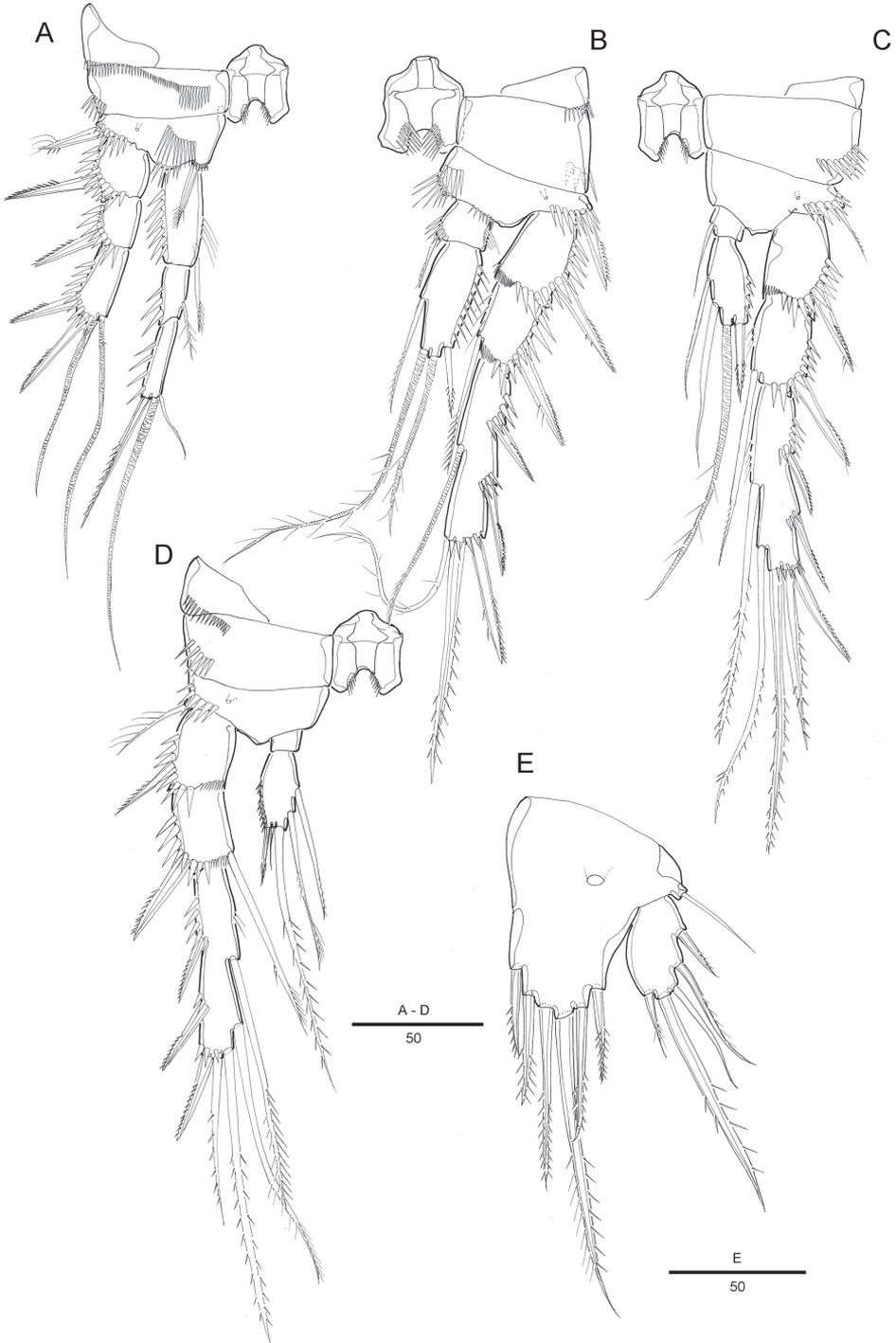


Figure 8. *Attheyella* (*Neomrazekiella*) *tessiae* sp. n. female: **A** P1, anterior **B** P2, anterior **C** P3, anterior **D** P4, anterior **E** P5, anterior.

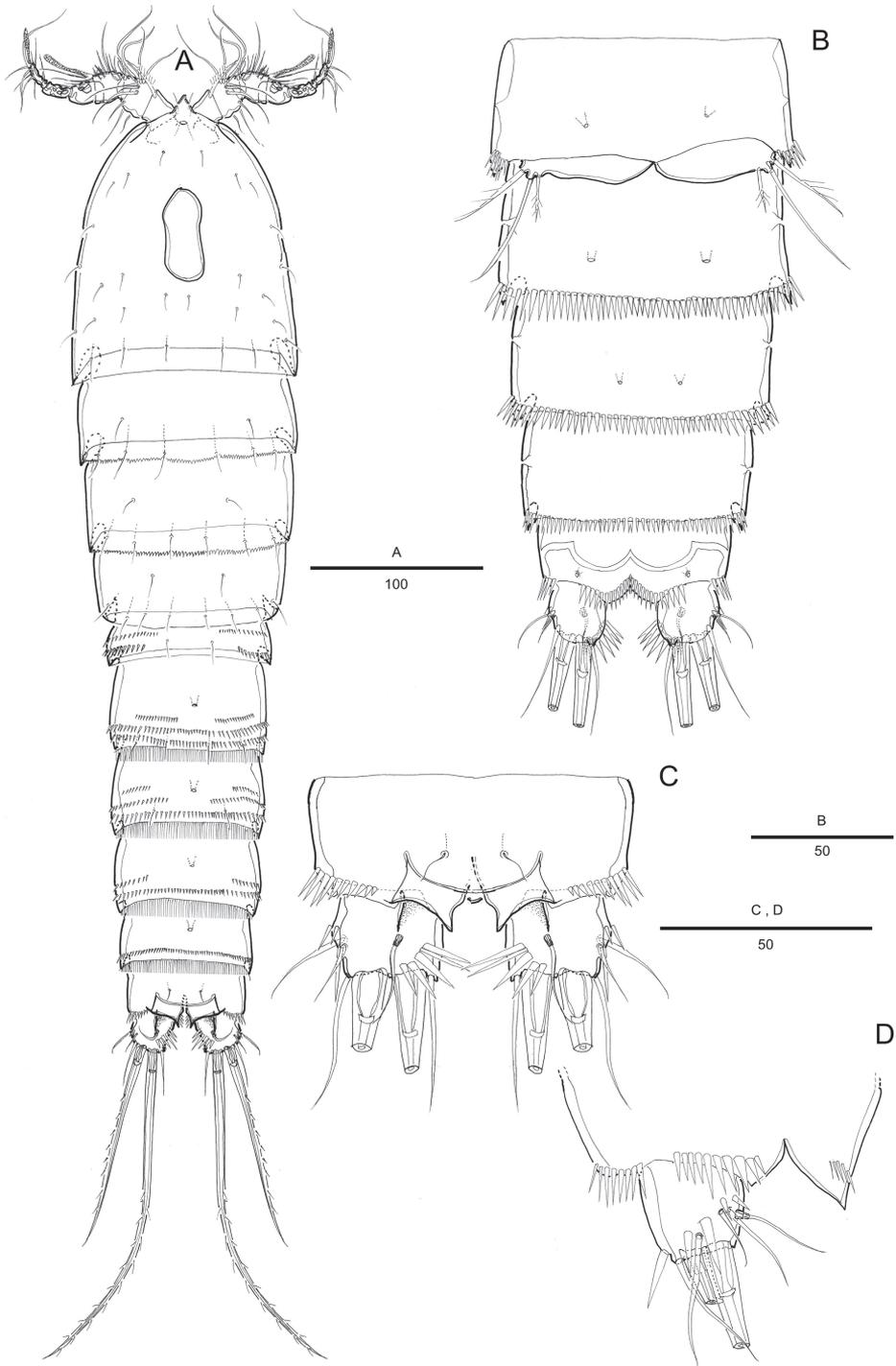


Figure 9. *Attheyella (Neomrazeikiella) tessiae* sp. n. male: **A** habitus, dorsal **B** Urosome (excluding P5-bearing somite), ventral **C** anal somite and caudal rami, dorsal; **E** anal somite and caudal ramus, lateral.

Antenna, mandible, maxillule, maxilla, and maxilliped as in *A. (A.) tahoensis* sp. n.

P1 (Fig. 8A) with well-developed coxa with spinular row on anterior surface. Basis with setules along outer margin and anterior surface, with pinnate outer and inner spines. Endopod 3-segmented, 1.3 times as long as exopod; enp-1 longer than enp-2, with one inner pinnate seta; enp-2 with 1 bipinnate inner seta; enp-3 with a small inner seta, and 1 long geniculate seta and 1 pinnate seta distally. Exopod 3-segmented, reaching end of enp-2, exopodal segments with strong spinules along outer margin and outer distal corner; exp-3 with 2 geniculate distal setae and 2 strong spinulose outer spines.

P2 (Fig. 8B) with small triangular praecoxa, with row of spinules on anterior surface along distal margin. Coxa nearly 1.5 times as wide as long, ornamented with row of long spinules along outer margin; Basis with outer pinnate spine; P2 enp-2 more than twice as long as enp-1; with 1 short, pinnate inner seta; enp-2 with 1 inner pinnate seta, and 2 distal bipinnate setae and 1 bipinnate outer seta; exopod 3-segmented; each segment with row of spinules along outer margins; third segment about 2.3 times as long as second segment with 3 bipinnate outer spines, 1 apical pinnate spines and 1 plumose seta, and 1 inner long bipinnate seta.

P3 (Fig. 8C) with small praecoxa. Coxa nearly 1.5 times as wide as long, with row of spinules along outer margin. Basis with outer pinnate seta and spinular row along outer margin. Endopod-1 with 1 bare inner seta; enp-2 with 2 inner naked setae, and 1 pinnate seta and short distal spine; exp-3 about twice as long as second segment with 3 bipinnate outer spines, 2 apical pinnate spines and 2 long bipinnate inner setae.

P4 (Fig. 8D) with small and triangular praecoxa. Coxa with spinular row along outer margin. Enp-2 with 2 inner pinnate setae, and 3 pinnate setae, the innermost longest; exp-3 with 3 bipinnate outer spines, 2 apical pinnate setae and 2 long bipinnate inner setae. Spine and setal formulae as follows:

	Exopod	Endopod
P1	0.0.022	1.1.120
P2	0.1.123	1.121
P3	0.1.223	1.220
P4	0.1.223	0.230

P5 (Fig. 8E). Baseoendopod forming short, outer setophore bearing the basal seta. Endopodal lobe trapezoidal, with 2 pinnate inner setae, 2 distal setae, and 2 pinnate outer seta; all setae of different length and apical outermost is the longest. A secretory pore on anterior surface. Exopod twice as long as wide, with one short inner, 2 distal (innermost longest) and 2 outer setae, all pinnate.

Description. Male (Fig. 9A). Body smaller and more slender than female. Body length 564 μm (n=6; range: 509–613 μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width measured at P2-bearing somite: 131 μm . Sexual dimorphism in antennule, P3-P4 endopod, P5 and P6.

Cephalothorax (Fig. 9A) with smooth posterior margin, with integumental sensilla. Urosome (Fig. 9B–D) 6-segmented, comprised of P5-bearing somite, genital

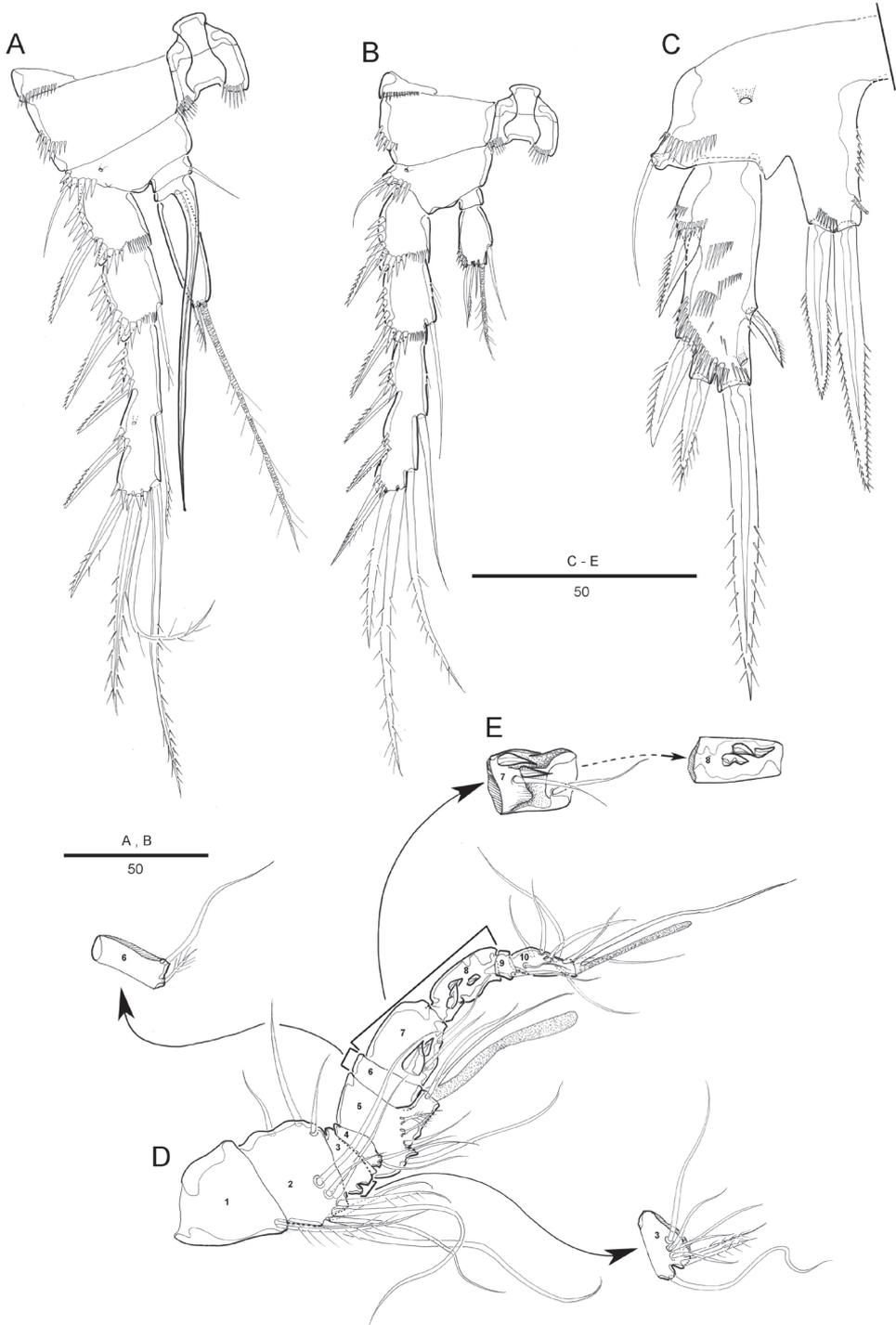


Figure 10. *Attheyella* (*Neomrazekiella*) *tessiae* sp. n. male: **A** P3, anterior **B** P4, anterior **C** P5, anterior **D** antennule **E** seventh and eighth segments of antennule, other view.

somite, and 4 free abdominal somites. Urosomites with spinules along posterior margin dorsally and ventrally. Anal somite with inner process on lateral margin.

Antennule (Fig. 10D–E) 10-segmented; subchirocer with geniculation between segments 7 and 8. Segment 2 largest. Segment 5 not swollen. Aesthetasc on segments 5 and 10. Some elements on segments 7 and 8. Armature formula: 1-[1], 2-[10], 3-[8], 4-[2], 5-[6 + (1 + ae)], 6-[2], 7-[2 + 2 modified] 8-[3 modified], 9-[1], 10-[7 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 bare setae.

P3 (Fig. 10A). Setae on exopod modified. Endopod modified, 3-segmented; enp-1 with inner seta; enp-2 with well-developed inner apophysis; enp-3 with 2 apical setae.

P4 (Fig. 10B). Exp-3 setae modified. Enp-2 with 1 inner and 3 distal setae.

Fifth pair of legs (P5) (Fig. 10C) fused medially. Baseoendopod with outer setophore bearing the basal seta. Endopodal lobe with 2 distal pinnate setae, the outmost longest, large pore on anterior surface. Exopod about 2.6 times as long as wide, with 1 outer and 1 outer distal pinnate setae of similar length, 2 pinnate distal setae, the innermost longest, and a small outer pinnate seta.

P6 (Fig. 9B) asymmetrical, bearing 1 pinnate outer, 1 long naked and 1 short bi-pinnate inner setae on a cylindrical process, apically.

Etymology. The species name refers to Tahoe Tessie, a cryptozoological creature which supposedly resides in Lake Tahoe. While some claim to have seen the mythical Tahoe Tessie, none until now have seen these non-mythical microscopic creatures of the sand.

Discussion

The family Canthocamptidae is the largest family of Harpacticoida found in freshwater habitats, and can be found in rivers, streams, ponds, lakes, and wetland, and even in hot springs, glacial melt water and damp moss (Boxshall and Halsey 2004). Canthocamptidae is in need of revision because several genera have high species diversity and many species exhibit wide variation, the widest variability recorded for freshwater Harpacticoida. Additionally, many species are incompletely described, often with major features such as A2 exopod setation and the setal formula for P2–P4 being unknown (Wells 2007).

The genus *Attheyella* Brady, 1880 is a genus of Canthocamptidae, and is cosmopolitan in distribution at the generic level (Boxshall and Halsey 2004). *Attheyella* is highly diverse, with more than 150 species, and is divided into six subgenera: *Attheyella*, *Canthosella*, *Chappuisiella*, *Delachauxiella*, *Neomrazekiella*, and *Ryloviella*. The genus *Attheyella* is also in need of revision because the species boundaries are not clear due to high variability in number of characters (Reid and Williamson 2009).

Both new species are placed in the genus *Attheyella* because of the following diagnostic features: small rostrum, P1 with 3-segmented rami, 2-segmented endopod of P2–P3 in female, and 3-segmented P3 in males.

In 1876, Forbes S.A. reported the freshwater harpacticoid copepod *Canthocamptus illinoisensis* from Normal, Illinois, which is represented as *Attheyella* (*Neomrazekiella*) *il-*

linoisensis. Since then, several new species were added, and the genus *Attheyella* in North America currently includes 3 subgenera (*Attheyella*, *Neomrazekiella*, *Ryloviella*) and 12 species. Wilson and Yeatman (1959) and Reid and Williamson (2009) provided a key to the species of the genus *Attheyella* from North America. The accepted species are: *Attheyella* (*Attheyella*) *alaskaensis*, *A. (A.) idahoensis*, *A. (A.) obatogamensis*, *A. (Neomrazekiella) americana*, *A. (N.) dentata*, *A. (N.) dogieli*, *A. (N.) illinoisensis*, *A. (N.) nordenskioldii*, *A. (N.) ussuriensis*, *A. (Ryloviella) carolinensis*, *A. (R.) pilosa*, and *A. (R.) spinipes*.

Attheyella (*Attheyella*) *tahoensis* sp. n. clearly belongs to the subgenus *Attheyella* given the elongate exopod and baseopod of P5, about equally wide, baseopod reaching near the end of exopod in female, and male P3 exopod-2 with enlarged outer spine reaching to end of exopod. *Attheyella* (*A.*) *tahoensis* sp. n. is closely related to the North American *A. (A.) idahoensis* (Marsh, 1903) and *A. (A.) namkungi* Kim, Soh and Lee, 2005 from South Korea, with seta formula of the female P4 exopod, and concave shape of caudal rami without a process. However, *A. (A.) tahoensis* sp. n. can readily be distinguished from its congeners by the number of setae on P2–P4. *A. (A.) idahoensis* has 4, 5 and 3 setae on distal segment of P2–P4 endopod, whereas *A. (A.) tahoensis* sp. n. has 3, 4 and 5 setae, respectively. Additionally, *A. (A.) namkungi* has 3, 4 and 2 setae on the distal endopod of P2–P4.

Morphological variation and abnormality are common in harpacticoid copepods. In the present study, intraspecific variation of *A. (A.) tahoensis* sp. n. has been recorded, with some specimens having variations on the shape and armature of the caudal rami (about 20% of total observed specimens). In the most commonly observed condition, caudal rami are about 2.5 times as long as wide, bottle-shaped, strongly tapering distally. In the less common morphological variant, caudal rami are about twice as long as wide, laterally compressed, with the inner margin of each ramus having lateral concavity.

In numerous instances, the morphological variation or deformity occurred due to environmental factors such as water pollution. However, some studies suggest that variation in caudal rami may be caused by interspecific competition. For example, Ishida (1994) reported high proportions of caudal rami variation in *Attheyella* (*Attheyella*) *nakaii* (Chappuis, 1927), and suggested that it played a role in sexual segregation due to sympatric distribution with *Attheyella* (*Attheyella*) *yesoensis* Ishida, 1993. Certainly, morphological variation in other harpacticoid species has led to discoveries of concomitant genetic differences and presumed cryptic speciation (Garlitska et al. 2012).

Attheyella (*Neomrazekiella*) *tessiae* sp. n. is placed in the subgenus *Neomrazekiella* on account of the following combination of characters: prosome with smooth posterior margins, female P5 endopodal lobe triangular, basal expansion wider than exopod, with six setae, male P5 not produced into narrow prolongation, P3 spine of exopod 2 not greatly enlarged in male. *A. (N.) tessiae* sp. n. can be clearly distinguished from other members of the subgenus *Neomrazekiella* by the 2-segmented endopods of female P2–P3, P5 baseopod produced to middle of exopod segment in female, and naked third seta of the male P5 exopod.

This investigation marks the first record of meiobenthos, and more specifically, of harpacticoid copepods, in Lake Tahoe. The newly described *A. (A.) tahoensis* sp.

n. and *A. (N.) tessiae* sp. n. are likely endemic to Lake Tahoe. A total of 10 endemic macrobenthos have previously been identified in Lake Tahoe (summarized by Caires et al. 2013), so it is reasonable to hypothesize that several species of meiobenthos also evolved in this ecosystem. Expanded sampling in the western United States, and beyond, will be necessary to validate the endemism of these species.

Together with newly described *A. (A.) tahoensis* sp. n. and *A. (N.) tessiae* sp. n., the three subgenera and fourteen species currently recognized as valid in the genus *Attheyella* from North America can be identified with the specific key given below. It is amended from Wilson and Yeatman (1959) and Reid and Williamson (2009).

Key to the species of the genus *Attheyella* from North America

- 1 Female P5 both exopod and baseoendopod elongate, of nearly same width, baseoendopod reaching nearly to end of exopod **subgenus *Attheyella*...2**
- Female P5 baseoendopod much wider than exopod..... **5**
- 2 Caudal ramus inner margin smoothly tapering or concave, without a process... **3**
- Female caudal ramus with prominent, acute, haired inner process; male caudal ramus with smaller, smooth inner process.. ***A. (A.) obatogamensis* (Willey, 1925)**
- 3 Caudal ramus narrowed distally, the apex truncate **4**
- Caudal ramus hardly at all narrowed distally, the apex rounded..... ***A. (A.) alaskaensis* M.S. Wilson, 1958**
- 4 Female antennule 8-segmented, P2–P4 endopod-2 with 4, 5, and 3 setae, respectively ***A. (A.) idahoensis* (Marsh, 1903)**
- Female antennule 7-segmented, P2–P4 endopod-2 with 3, 4, and 5 setae, respectively ***A. (A.) tahoensis* sp. n.**
- 5 Female P5 baseoendopod with 3 to 5 setae; caudal rami of both sexes similar, and body segments coarsely serrate **subgenus *Ryloviella*...6**
- Female P5 baseoendopod with 6 setae; caudal rami of both sexes different, and body segments weakly serrate or smooth **subgenus *Neomrazekiella*...8**
- 6 All or most setae on P1 - P5 slender..... **7**
- Setae on P1 - P5 short, stout, spiniform..... ***A. (R.) spinipes* Reid, 1987**
- 7 P5 exopod about 2 times as long as wide; female P5 baseoendopod with 3 or 4 setae; caudal ramus with 2 or more longitudinal rows of spinules ***A. (R.) carolinensis* Chappuis, 1932**
- P5 exopod about 1.5 times as long as wide; female P5 baseoendopod with 5 (rarely 4) setae; caudal ramus with 2 or 3 oblique inner rows of hairs..... ***A. (R.) pilosa* Chappuis, 1929**
- 8 Female P2–P3 endopods usually 3-segmented; female P5 endopodal lobe produced to middle of exopod segment or beyond; male P5 exopod seta 3 naked, more slender than other setae **9**
- Female P2–P3 endopods usually 2-segmented; female P5 endopodal lobe hardly at all produced; male P5 exopod seta 3 usually similar to other setae **10**

- Female P2–P3 endopods 2-segmented; female P5 endopodal lobe reaching distal margin of exopod; male P5 exopod seta 3 naked... *A. (N.) tessiae* sp. n.
- 9 Female caudal ramus, distal half of outer margin strongly constricted, and outer apical seta outbent at base; male P4 exp3 outer distal and apical spines strongly curved *A. (N.) nordenskioldii* (Lilljeborg, 1902)
- Female caudal ramus, outer margin evenly rounded, and base of outer apical seta straight; male P4 exp3 outer distal and apical spines straight
.....*A. (N.) illinoisensis* (S. A. Forbes, 1876)
- 10 Caudal ramus, lateral setae inserted next to each other **11**
- Caudal ramus, insertions of lateral setae well separated **12**
- 11 Female P5 baseoendopod with 6 normal setae; caudal ramus, outer distal corner with rounded sclerotized flange overlying bases of apical setae
.....*A. (N.) dogieli* (Rylov, 1923)
- P5 baseoendopod with 6 slender spiniform setae, all of them completely fused with baseoendopod; caudal ramus, outer distal corner with only a few spinules.....*A. (N.) ussuriensis* Rylov, 1933
- 12 Caudal ramus about as long as anal somite, smoothly tapering, dorsal surface with prominent subquadrate or crescentic sclerotization distal to dorsal seta
.....*A. (N.) dentata* (Poggenpol, 1874)
- Caudal ramus about 1/2 length of anal somite, outer distal margin constricted, dorsal surface with no special structure.... *A. (N.) americana* (Herrick, 1884)

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A taxonomic study of *Ooctonus* (Hymenoptera, Mymaridae) from Heilongjiang, China

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Abstract

Five species of *Ooctonus* Haliday (Hymenoptera, Mymaridae) from Heilongjiang Province, China, are reviewed. One species, *O. huberi* sp. n., is described as new, and four species, *O. orientalis* Doutt, *O. saturn* Triapitsyn, *O. sublaevis* Förster and *O. vulgatus* Haliday are reported as new to China. A key to the females of the 10 described Chinese species is given. All the specimens are deposited in the insect collections of Northeast Forestry University, China.

Keywords

Chalcidoidea, Mymaridae, *Ooctonus*, taxonomy, new species, China

Introduction

Ooctonus currently contains 36 described species: one in the Australian region (Perkins 1905), 12 in the Palearctic region, five in the Oriental region (Triapitsyn 2010), 14 species in the Nearctic region including three also distributed in the Palearctic region (Huber 2012), three in the Afrotropical region (Huber et al. 2010), and four in the Neotropical region (Huber 2013). Here we describe a new species, record 4 others for the first time from northeast China, and provide a key to females of the 10 *Ooctonus* species known from China.

Materials and methods

Twenty-three specimens (19 females and 4 males) of *Ooctonus* were collected in Heilongjiang Province, northeast China by sweeping, Malaise traps (MT) or yellow pan traps (YPT). Specimens were dissected and mounted in Canada balsam on slides following the method described by Noyes (1982) and modified for Mymaridae by Huber (1988). Photographs were taken with a digital CCD camera attached to an Olympus BX51 compound microscope, and most measurements were made from slide-mounted specimens using an eye-piece reticle. Total body length excluding ovipositor was measured with an eye-piece reticle from alcohol-preserved specimens before being dissected. All measurements are given in micrometers (μm). Triapitsyn (2010) and Huber (2012) should be consulted for depositories of type specimens, hosts, and literature references to species described from Palaearctic, Oriental, and Nearctic regions. Morphological terminology and abbreviations are those of Huber (2012). All the specimens listed below are deposited in Northeast Forestry University, Harbin, China (NEFU).

Key to the females of *Ooctonus* species in China

- 1 Metacoxa yellowish or brown, different in color from mesosoma 2
- Metacoxa dark brown or black, almost same color as mesosoma 9
- 2 Frenum (Figs 27, 34) smooth medially, reticulate at lateral borders, sometimes also at anterior and posterior margins 3
- Frenum (Figs 5, 13, 19) entirely reticulate, sometimes only faintly so 4
- 3 Funicle with 2 mps on fl_5 and fl_6 ; propodeum (Fig. 27) with median areole well separated from metascutellum by fairly long median carina, but the median carina often incomplete, not extending to anterior margin of propodeum, or almost absent *O. sublaevis*
- Funicle without mps on fl_5 and fl_6 ; propodeum (Fig. 34) with median areole abutting metascutellum; the median carina absent and replaced by the two carinae forming inner margin of dorsolateral areoles *O. vulgatus*
- 4 Mesoscutum (Figs 13, 19) with median longitudinal groove, the groove sometimes very short at posterior margin or extending about 0.7 \times length of mesoscutum 5
- Mesoscutum (Figs 4, 34) without median longitudinal groove 6
- 5 Funicle with 2 mps on fl_5 and fl_6 ; plica (Fig. 13) bifurcate anteriorly with a long lateral and long medial arm *O. orientalis*
- Funicle without mps on fl_5 and fl_6 ; plica (Fig. 19) bifurcate anteriorly with a short lateral and short medial arm *O. saturn*
- 6 Clava with 8 mps *O. insignis* Haliday
- Clava with 7 mps 7
- 7 Funicle without mps on fl_6 *O. notatus* Walker
- Funicle with 1 or 2 mps on fl_6 8

- 8 Propodeum with median areole separated from metascutellum by median carina; plica with an anterior bifurcation; mesosoma yellow; ovipositor relatively long, at least 1.1× as long as metatibia ***O. novickyi* Soyka**
– Propodeum (Fig. 5) with median areole abutting metascutellum; the median carina absent and replaced by the two carinae forming inner margin of dorso-lateral areoles; plica without an anterior bifurcation; mesosoma dark brown; ovipositor relatively short, at most 0.9× as long as metatibia ***O. huberi***
- 9 Body length about 1 300 µm; mesoscutum without median longitudinal groove or at most with very short one ***O. himalayus* Subba Rao**
– Body length about 2 600 µm; mesoscutum with long median longitudinal groove (at least 0.5× length of mesoscutum) ***O. sinensis* Subba Rao**

Taxonomy

***Ooctonus huberi* Bai, Jin & Li, sp. n.**

<http://zoobank.org/9E177EE9-7AD7-4FB2-B8A1-57A71D8B23F4>

Figs 1–11

Holotype. ♀ (NEFU) Harbin City, Maoershan Town, Mt. Maoershan, 700m. 18.VIII. 2014, Cheng-De Li, Hai-Feng Bai, Xiang-Xiang Jin, YPT.

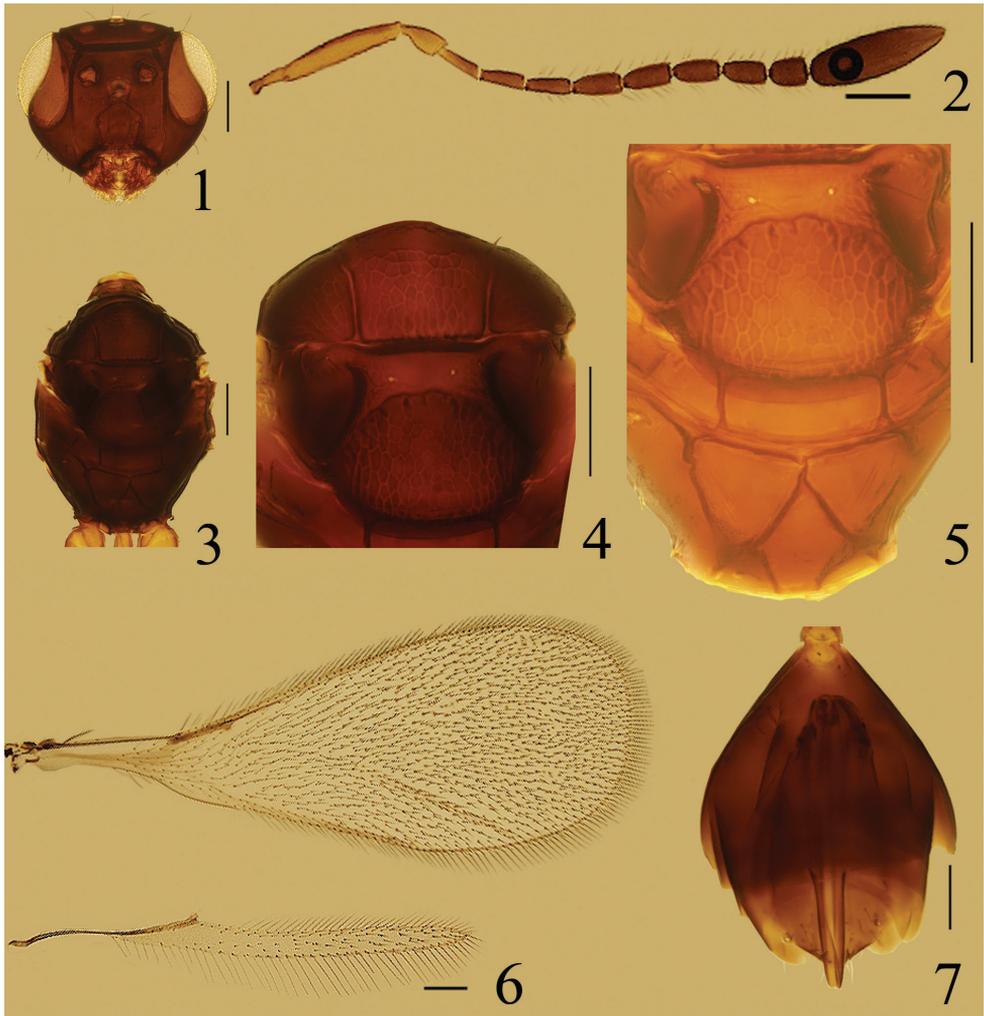
Paratypes. 3 females, 2 males. Harbin City, Maoershan Town: Jianlagou. 4–17.VIII. 2014, Cheng-De Li, Hai-Feng Bai, Chao Zhang, Zhi-Guang Wu (2 ♀ ♀, NEFU), MT; same data as holotype (2 ♂ ♂, NEFU); Laoyeling. 16–29.VIII. 2013, Cheng-De Li, Hai-Feng Bai (1 ♀, NEFU), MT.

Diagnosis. Funicle (Fig. 2) with 2 mps at least on fl_4 – fl_8 and 7 mps on clava; mesoscutum (Fig. 4) without median longitudinal groove; frenum (Figs 4, 5) entirely reticulate; propodeum (Fig. 5) with median areole abutting metascutellum; the median carina absent and replaced by the two carinae forming inner margin of dorsolateral areoles; plica without an anterior bifurcation; petiole 3.54–4.05× as long as wide; ovipositor (Fig. 7) slightly exerted, about 0.9× as long as gaster, and 0.86–0.90× as long as metatibia.

Ooctonus huberi sp. n. runs to *O. novickyi* in Triapitsyn's key (2010), and the differences are shown in the key above. The new species is also similar to *O. lokomotiv*. Both species have 1 mps sometimes on fl_3 and 2 mps on fl_4 – fl_8 and have reticulation on mesoscutum and frenum, but *O. huberi* sp. n. differs from the latter by having 7 mps on the clava (8 mps in *O. lokomotiv*); petiole 3.54–4.05× as long as wide (2.6–3.3× in *O. lokomotiv*); and ovipositor 0.86–0.90× as long as metatibia (1.2–1.4× in *O. lokomotiv*).

Description. Female. Body length 1240–1380. Head and mesosoma dark brown, metasoma brown; scape and pedicel mostly yellow except dorsally dark brown; fl_1 brown, remainder of funicle dark brown; petiole and legs yellow except apical tarsomere brown.

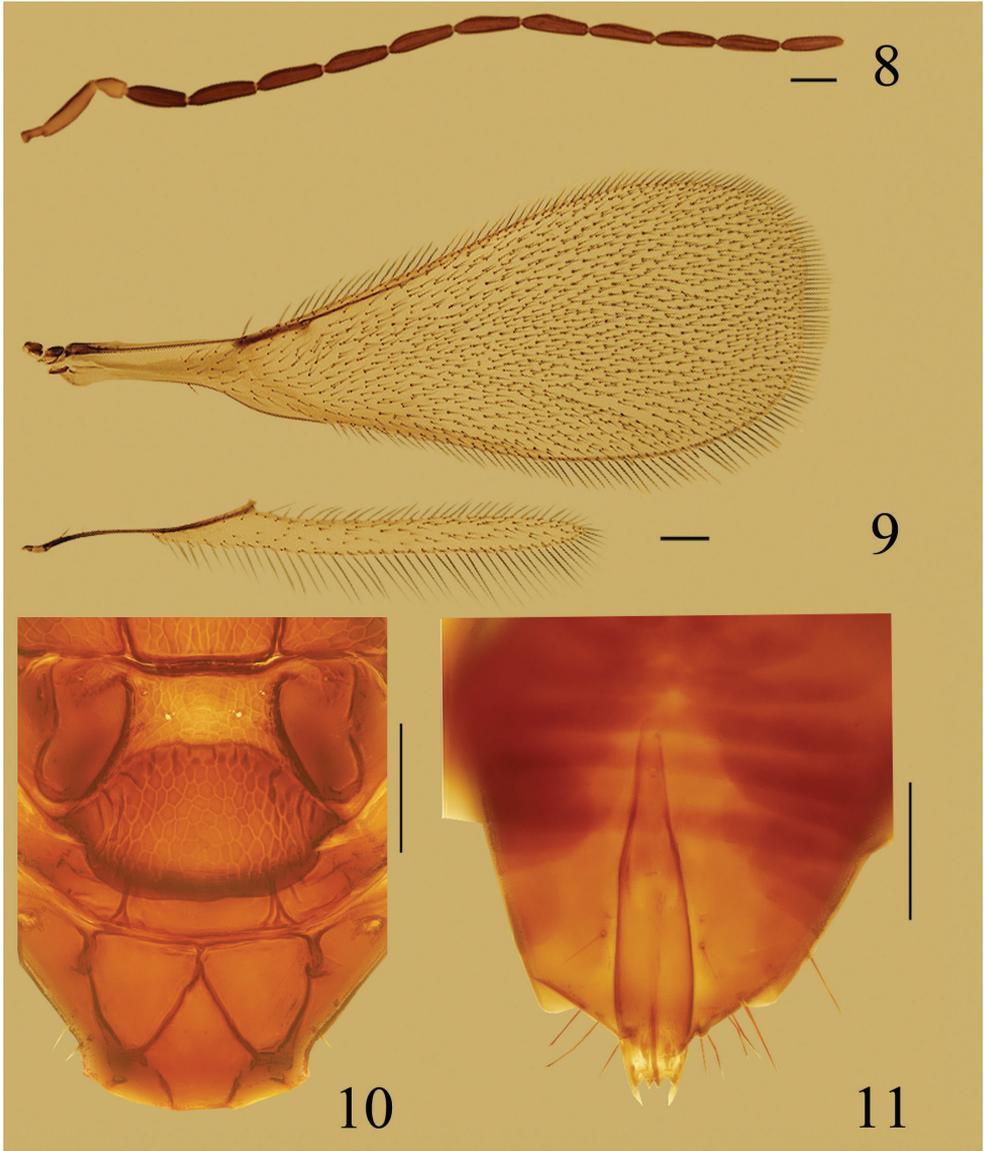
Head. Head (Fig. 1) width 396–406. Vertex without stemmaticum. Mid ocellus diameter 29–31. Vertex with conspicuous reticulate sculpture; face with faint, inconspicuous reticulate sculpture.



Figures 1–7. *Ooctonus huberi* sp. n., holotype female (Jianlagou): **1** head, dorsal **2** antenna **3** mesosoma, dorsal **4** mesoscutum and scutellum, dorsal **5** frenum and propodeum, dorsal **6** wings **7** gaster, dorsal. Scale bars = 100 μ m.

Antenna. Antenna (Fig. 2) with scape 4.61–5.25 \times as long as wide, slightly longitudinally striate; pedicel slightly longer than fl₁; funicle with 2 mps on fl₄–fl₈ and 7 mps on clava, and sometimes fl₃ with 1 mps on one antenna. Clava 3.17–3.31 \times as long as wide, slightly longer than fl₆–fl₈ together. Measurements (length/width): radicle 53, scape 199–204/ 38–43, pedicel 65–72/ 36–38, fl₁ 60–72/ 22–24, fl₂ 70–79/ 24–26, fl₃ 72–77/ 26–29, fl₄ 77–82/ 29–34, fl₅ 77–79/ 31–36, fl₆ 72–77/ 31–36, fl₇ 70–79/ 36–38, fl₈ 58–65/ 43–46, clava 221–240/ 70–74.

Mesosoma. Mesosoma (Fig. 3) with pronotum weakly sculptured. Mid lobe of mesoscutum (Fig. 4) with meshes raised; scutellar setae long, extending posterior to



Figures 8–11. *Ooctonus huberi* sp. n., paratype male (Jianlagou): **8** antenna **9** wings **10** posterior part of mesoscutum to propodeum, dorsal **11** genitalia. Scale bars = 100 μ m.

medially concave frenal line; frenum 0.69–0.75 \times mesoscutellum length and entirely reticulate. Metanotum with metascutellum smooth. Propodeum (Fig. 5) smooth between carinae and its anterior margin with a stub slightly lateral to lateral margin of metascutellum; median areole abutting metascutellum; the median carina absent and replaced by the two carinae forming inner margin of dorsolateral areoles; plica almost straight, extending almost to anterior margin of propodeum just medial to stub, without an anterior bifurcation but with a slight curved thickening posterior to the stub.

Wings. Fore wing (Fig. 6) length 1415–1512, width 512–585, length/width 2.57–2.76, longest marginal setae 77–84, 0.13–0.15× as long as greatest wing width. Marginal vein length 125–132. Hind wing (Fig. 6) length 1049–1122, width 67–70, length/width 16–17, longest marginal setae 122–125.

Metasoma. Petiole 3.54–4.05× as long as wide, 1.35–1.38× as long as metacoxa, shorter than metacoxa + metatrochantellus. Gaster (Fig. 7) with ovipositor length 455–485, slightly exerted, 0.89–0.91× as long as gaster, and 0.86–0.90× as long as metatibia (515–525).

Male. Body length 1230–1310. Mid ocellus diameter 29–31. Antenna (Fig. 8). Measurements, length: radicle 48–50, scape 139–144, pedicel 60–70, fl₁ 125, fl₂ 137–144, fl₃ 142–144, fl₄ 134–139, fl₅ 142, fl₆ 137–142, fl₇ 137–142, fl₈ 134–139, fl₉ 130, fl₁₀ 132–137, fl₁₁ 134–142. Total flagellar length 1537–1561. Fl₆ length/width 4.21–4.38, with 7 mps. Fore wing (Fig. 9) length 1463–1512, width 561–585, length/width 2.50–2.70, longest marginal setae 89–101, 0.15–0.18× as long as greatest wing width. Hind wing (Fig. 9) length 1073–1122, width 72, length/width 14.91–15.58, longest marginal setae 132–134, 1.83–1.87× as long as greatest wing width.

Host. Unknown.

Etymology. This species is named in honor of JT Huber, of the Canadian Forest Service, Ottawa, Canada.

***Ooctonus orientalis* Doult, 1961**

Figs 12–15

Triapitsyn 2010: 36–40 (redescription, primary type data, distribution).

Specimens examined. 3 ♀ ♀. Harbin City, Maoershan Town: Laoyeling. 10–11.VI. 2013, Xiang-Xiang Jin, Si-Zhu Liu, Chao Zhang, sweeping (1 ♀); Laoshan. 12–14.VI. 2013, Xiang-Xiang Jin, Si-Zhu Liu, Chao Zhang, YPT (1 ♀); Jianlagou. 19.VII. 2014, Cheng-De Li, Hai-Feng Bai, Xiang-Xiang Jin, Yan Gao, YPT (1 ♀).

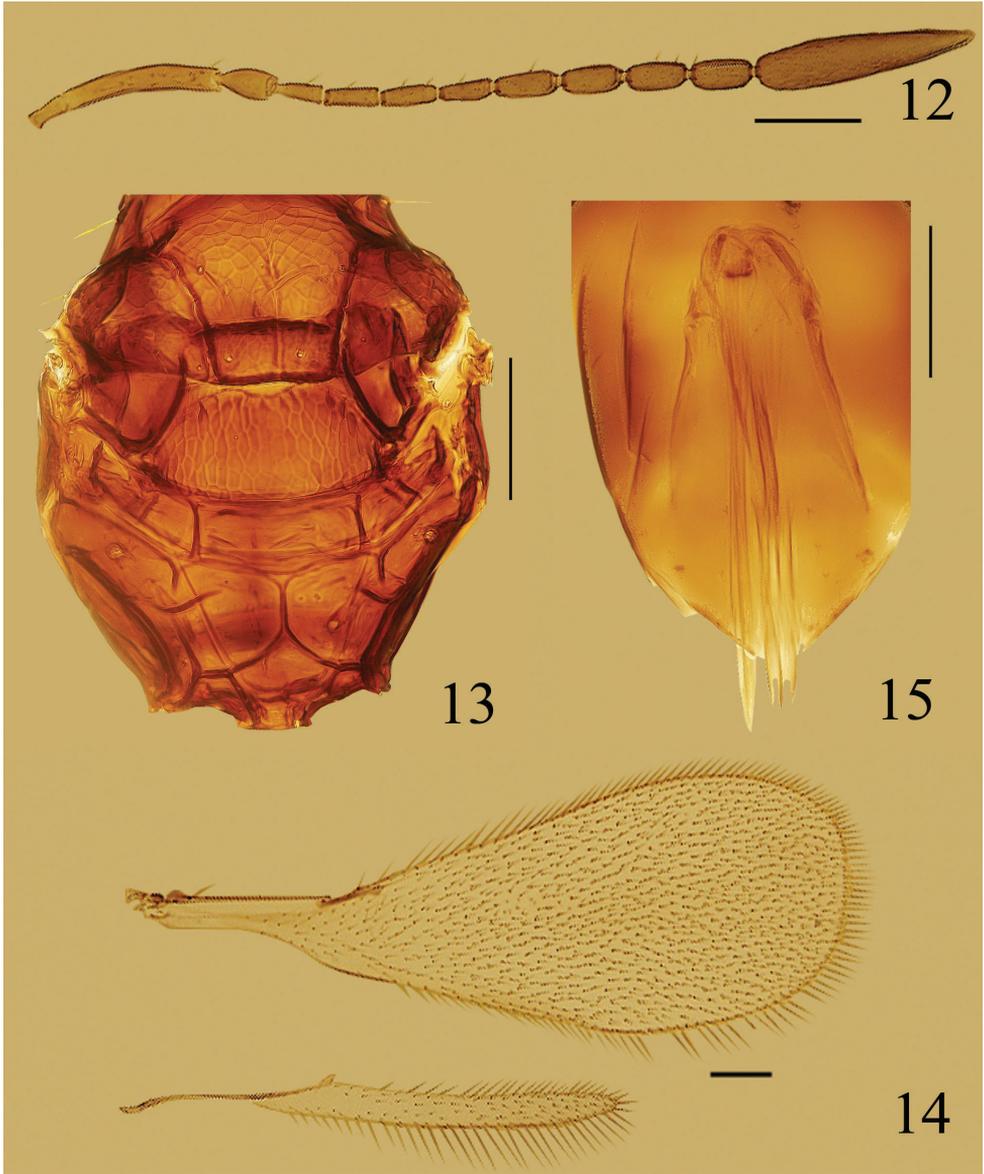
Diagnosis. Funicle (Fig. 12) usually with 2 mps on fl₅–fl₈ and 7 mps on clava; mesoscutum (Fig. 13) with median longitudinal groove, the groove sometimes very short at posterior margin of mesoscutum or extending about 0.7× length of mesoscutum; frenum entirely reticulate; propodeum (Fig. 13) with median areole separated from metascutellum by long median carina; plica bifurcate anteriorly with a long lateral and shorter medial arm.

***Ooctonus saturn* Triapitsyn, 2010**

Figs 16–24

Triapitsyn 2010: 36–40 (description, type data, distribution).

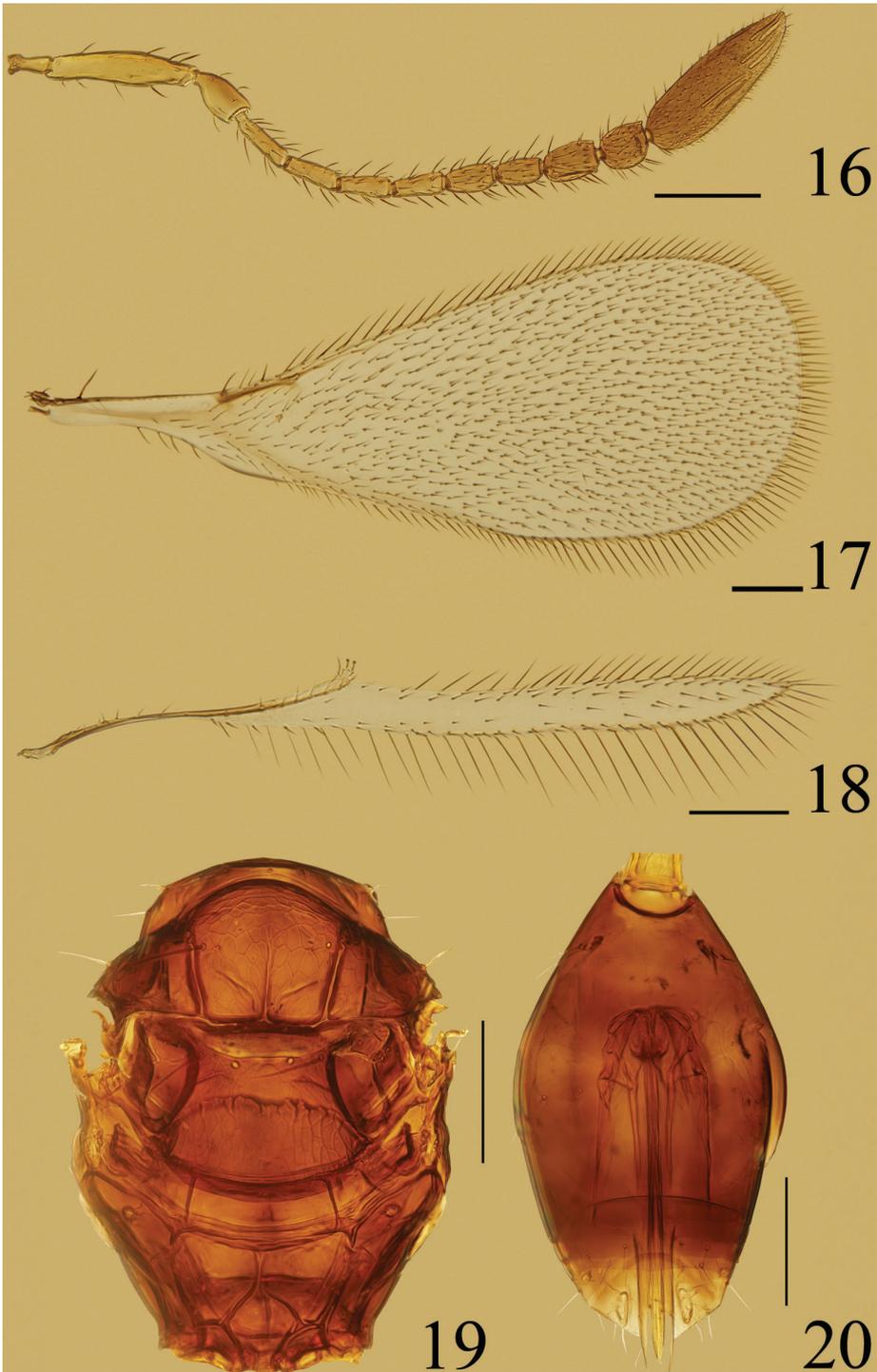
Specimens examined. 7 ♀ ♀, 2 ♂ ♂. Harbin City, Maoershan Town: Jianlagou. 1–17.VI. 2014, Cheng-De Li, Hai-Feng Bai, Ye Chen, Chao Zhang, MT (3 ♀ ♀);



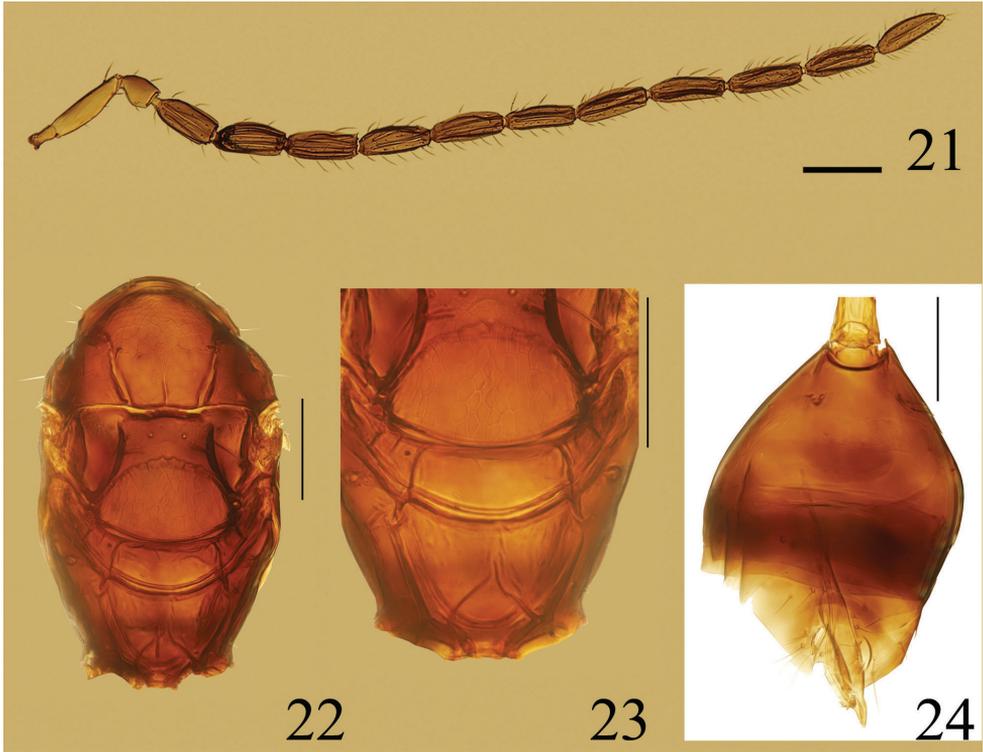
Figures 12–15. *Ooctonus orientalis*, female (Laoyeling): **12** antenna **13** part of mesosoma, dorsal **14** wings **15** ovipositor. Scale bars = 100 μ m.

Jianlagou. 4.VIII. 2014, Cheng-De Li, Hai-Feng Bai, Xiang-Xiang Jin, Yan Gao, sweeping (1 ♀); Laoshan. 12–14.VI. 2013, Xiang-Xiang Jin, Si-Zhu Liu, Chao Zhang, YPT (1 ♀); Jianlagou. 17.VI. 2014, Cheng-De Li, Hai-Feng Bai, Ye Chen, Chao Zhang, YPT (2 ♀ ♀, 2 ♂ ♂).

Diagnosis. Funicle (Fig. 16) with 2 mps on fl_7 and fl_8 and 7 mps on clava; mesoscutum (Fig. 19) with median longitudinal groove, the groove sometimes very short



Figures 16–20. *Ooctonus saturn*, female (Jianlagou): **16** antenna **17** fore wing **18** hind wing **19** mesosoma, dorsal **20** gaster. Scale bars = 100 μ m.



Figures 21–24. *Ooctonus saturn*, male (Jianlagou): **21** antenna **22** mesosoma, dorsal **23** part of mesosoma, dorsal, **24** gaster. Scale bars = 100 μm .

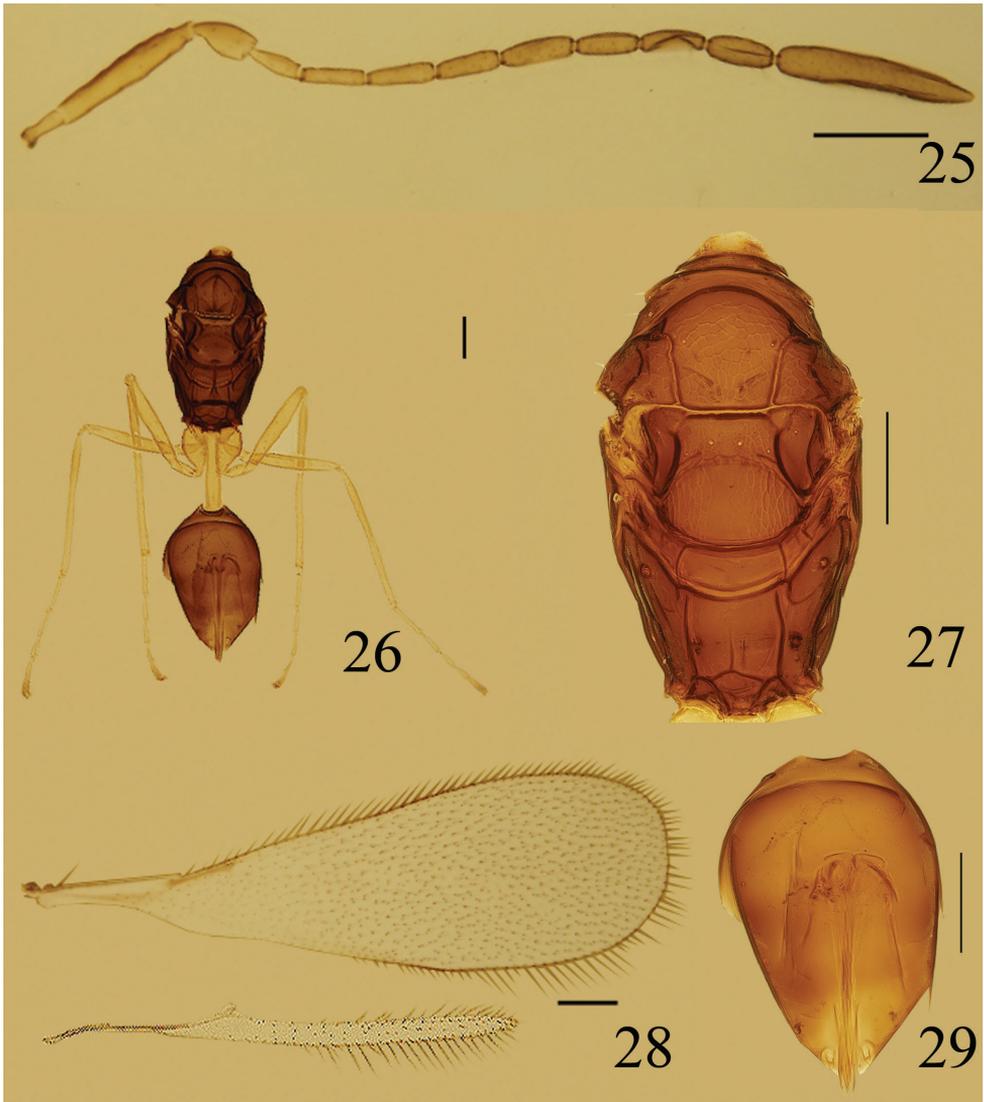
at posterior margin of mesoscutum or extending about $0.5\times$ length of mesoscutum; frenum entirely reticulate; propodeum (Fig. 15) with median areole separated from metascutellum by median carina; plica with a short bifurcation anteriorly.

Ooctonus sublaevis Förster, 1847

Figs 25–29

Specimens examined. 4 ♀ ♀: Harbin City, Maershan Town, Laoyeling. 10–11. VI. 2013, Xiang-Xiang Jin, Si-Zhu Liu, Chao Zhang, sweeping (1 ♀); Yichun City, Wuying Town, Fenglin Natural Reserve. 3–4.VII. 2013, Guo-Hao Zu, Hui Geng, Si-Zhu Liu, Yang Peng, sweeping (3 ♀ ♀).

Diagnosis. Funicle (Fig. 25) usually with 2 mps on fl_5 – fl_8 (occasionally fl_6 with just 1 mps) and 7 mps on clava; mesoscutum (Fig. 27) usually without median longitudinal groove, rarely with a very short groove; frenum with weak reticulate sculpture; propodeum (Fig. 27) with median areole well separated from metascutellum by fairly long median carina, but the median carina often incomplete, not extending to anterior margin of propodeum, or almost absent; plica straight or slightly curved outward and not divided anterodorsally.



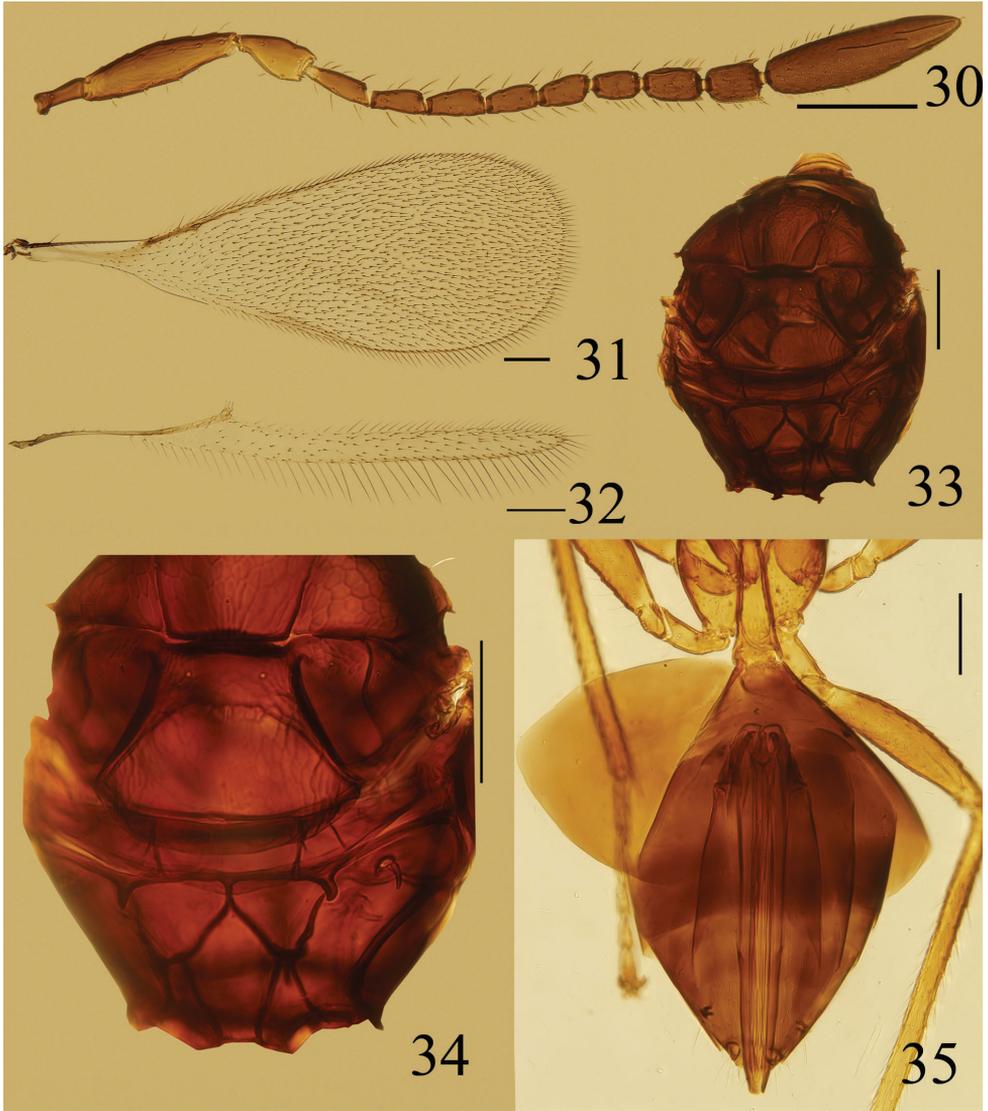
Figures 25–29. *Ooctonus sublaevis*, female (Fenglin Natural Reserve): **25** antenna **26** body, dorsal **27** mesosoma, dorsal **28** wings **29** gaster. Scale bars = 100 μm .

Ooctonus vulgatus Haliday, 1833

Figs 30–35

Specimen examined. 1 ♀. Harbin City, Maoershan Town, Laoyeling. 17.VI. 2014, Cheng-De Li, Hai-Feng Bai, Guo-Hao Zu, Ye Chen, sweeping.

Diagnosis. Funicle (Fig. 30) with 2 mps on fl_7 and fl_8 and 7 mps on clava; mesoscutum (Fig. 33) without median longitudinal groove; frenum mostly smooth,



Figures 30–35. *Ooctonus vulgatus*, female (Laoyeling): **30** antenna **31** fore wing **32** hind wing **33** mesosoma, dorsal **34** posterior part of mesoscutum to propodeum, dorsal **35** gaster. Scale bars = 100 μ m.

except for obscure sculpture at lateral borders and sometimes also at anterior margin; propodeum (Fig. 34) with median areole abutting metascutellum; the median carina absent and replaced by the two carinae forming inner margin of dorsolateral areoles; plica almost straight and not divided anterodorsally, ending just anterior and medial to stub.

Acknowledgements

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Temnothorax crasecundus sp. n. – a cryptic Eurocaucasian ant species (Hymenoptera, Formicidae) discovered by Nest Centroid Clustering

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Abstract

The paper integrates two independent studies of numeric morphology-based alpha-taxonomy of the cryptic ant species *Temnothorax crassispinus* (Karavajev, 1926) and *T. crasecundus* sp. n. conducted by different investigators, using different equipment, considering different character combinations and evaluating different samples. Samples investigated included 603 individual workers from 203 nests – thereof 104 nest samples measured by Seifert and 99 by Csösz. The material originated from Europe, Asia Minor and Caucasia. There was a very strong interspecific overlap in any of the 29 shape characters recorded and subjective expert determination failed in many cases. Primary classification hypotheses were formed by the exploratory data analysis Nest Centroid (NC) clustering and corrected to final species hypotheses by an iterative linear discriminant analysis algorithm. The evaluation of Seifert's and Csösz's data sets arrived at fully congruent conclusions. NC-Ward and NC-K-means clustering disagreed from the final species hypothesis in only 1.9 and 1.9% of the samples in Seifert's data set and by 1.1 and 2.1% in Csösz's data set which is a strong argument for heterospecificity. The type series of *T. crassispinus* and *T. crasecundus* sp. n. were allocated to different clusters with $p = 0.9851$ and $p = 0.9912$ respectively. The type series of the junior synonym *T. slavonicus* (Seifert, 1995) was allocated to the *T. crassispinus* cluster with $p = 0.9927$. *T. crasecundus* sp. n. and *T. crassispinus* are parapatric species with a long contact zone stretching from the Peloponnisos peninsula across Bulgaria northeast to the southern Ukraine. There is no indication for occurrence of interspecifically mixed nests or intraspecific polymorphism. However, a significant reduction of interspecific morphological distance at sites with syntopic occurrence of both species indicates local hybridization. The results are discussed within the context of the Pragmatic Species Concept of Seifert (2014). The taxonomic description and a differential diagnosis of *T. crasecundus* sp. n. are given.

Keywords

Numeric morphology-based alpha-taxonomy, Pragmatic Species Concept, parapatric species, hybridization, intraspecific dimorphism

Introduction

The small Formicoxenine ants *Temnothorax nylanderi* (Förster, 1850) and *T. crassispinus* (Karavajev, 1926) are dominant elements of the forest floor fauna of European temperate woodland biomes. They have repeatedly stood in the focus of thorough studies after Seifert (1995) presented evidence of their distinctness. In that paper he treated the two entities as subspecies: *Leptothorax nylanderi nylanderi* (Förster, 1850) and *Leptothorax nylanderi slavonicus* Seifert, 1995. He concluded that they spread from an Ibero-Italian and Balkan Pleistocene refuge respectively and have met in Germany along a 900-kilometers-long front line latest during the Atlantic (about 7500 years before present). In the years 1990–2000, this front-line ran in northeast Germany over Anklam-Krakow am See-Osterburg-Burg-Aken-Leipzig-Grimma-Freiberg and in south Germany over Pegnitz-Ingolstadt-München. After objections against the use of the subspecies concept (pers. comm. of Barry Bolton to Seifert in 1995), both entities were treated and named as parapatric species (Seifert 1996). Based on geographic and morphological indications, Radchenko (2000) later supposed a junior synonymy of *Leptothorax slavonicus* with *L. crassispinus* Karavajev, 1926. After getting access to the type series of *L. crassispinus* kept in the museum of Kiev, Seifert (2007) confirmed Radchenko's view and transferred the species to the genus *Temnothorax* Mayr, 1861 in agreement with the new genus-level classification of Bolton (2003).

According to mtDNA data (Pusch et al. 2006), the splitting of *T. nylanderi* and *T. crassispinus* in separate glacial refuges should have occurred already in Early Pleistocene \pm 1.4 Myr b.p. if 2.0% sequence divergence correspond to 1 Myr. These refuge areas probably have been used with similar topography and migration routes during all glaciations since then. A very low within-species mtDNA sequence divergence (0.14% in *T. nylanderi* and 0.29% in *T. crassispinus*) indicates a rapid postglacial spreading.

Frequent hybridization of *T. nylanderi* and *T. crassispinus* along the front-line in Germany has been shown (Pusch et al. 2006) or made credible (Seifert 1995). The depth of the front zone is not larger than 25 km while the east-west extension of both species' range is 3600 km at least. Despite some 7500 years of contact, the genomic integrity of the species and the clear-cut parapatric separation has been maintained by apparently two factors: (a) there is a significant selection against hybrid genotypes – hybrid gynes are smaller and show a strongly reduced fertility (Pusch et al. 2006) and (b) mating flights are short-ranged and there is no long-range postmating dispersal of gynes (Plateaux 1986, Foitzik and Heinze 2001).

Very early it became obvious to the senior author (Seifert) that there existed a third cryptic entity of the *T. nylanderi* complex in the Balkans, Asia Minor and Caucasus that may occur syntopic with *T. crassispinus*. These preliminary investigations, how-

ever, came to a complete standstill after three rejections of research funding proposals in the years 2007–2009. More recently, the junior author (Csösz) could investigate further material from the Balkans and Asia Minor. Csösz's data considerably improved the knowledge about the relations of the two species in the contact zone. We fuse in this paper the independent approaches of two investigators to a broad basis of evidence for the existence of the new cryptic species *T. crasecundus* sp. n. which is a sibling species of *T. crassispinus*. The contact situation is comparable to that found in *T. nylanderii* and *T. crassispinus*. *T. crasecundus* sp. n. and *T. crassispinus* are parapatric – the front line in Greece and Bulgaria is known and predicted to run diagonally through Romania and Moldova.

T. crasecundus sp. n. and *T. crassispinus* are truly cryptic species. Each of the 29 investigated shape characters and absolute size show a considerable interspecific overlap even in nest sample means and much more so on individual level. Furthermore, there is no clear signal provided by pigmentation and overall phenotypic impression. Both authors, having a long experience in identification of *Temnothorax* ants by simple eye inspection, are able to make a fair subjective guess on the species identity in a good number of samples but fail in many others. Both species thus fully fit the definition of cryptic species by Seifert (2009): "...species which are not safely separable by primary visual or acoustic perception of an expert. This reflects the immediate sense of the word and restricts the term to the truly cryptic cases – i.e., to species not safely separable by training of innate pathways of the human cognitive system."

Morphology is essential to establish the link between species delimitation and Linnean nomenclature (Franz 2005, Brower 2006, Schlick-Steiner et al. 2007, Steiner et al. 2009). Allocation of taxonomic names to cryptic species is only possible via direct investigation of type specimens – in our case, 90-years old types of some 2.7 millimeters-long ants and other still older museum specimens have to be evaluated. Degradation of DNA is very likely and the success even of advanced methods of DNA analysis unpredictable. A curator of a museum collection should not allow destructive DNA sampling from a type specimen of a small insect and there is no doubt that next generation sequencing in our 600 dry mounts would be enormously costly and time-consuming. Much more practicable are non-destructive, advanced methods of morphological clustering. The methodology of numeric morphology-based alpha-taxonomy (NUMOBAT, Seifert 2009) in ants experienced a fast evolution during the last years. It started with hypothesis-driven analyses of conventional linear morphometrics (Seifert 2005). Later, explorative analyses of more complex data sets (Seifert et al. 2009, Seifert 2011) and geometric morphometrics (Bagherian et al. 2012, Seifert et al. 2014) were added to the toolbox. The most recent methodological improvement is Nest-Centroid clustering (NC clustering, Seifert et al. 2013). NC clustering is a high-resolution explorative data analysis applicable to any group of eusocial organisms or to any cohesive biological system providing repeats of definitely conspecific elements.

In this paper, we firstly present our argumentation why *T. crasecundus* sp. n. has a separate species status and why local hybridization is no argument against heterospecificity. Then we give the formal description of the new species.

Material and methods

Material

A total of 203 nest samples with 603 individual workers of both species was investigated – 104 samples by Seifert and 99 by Csösz. Only one nest series, the type series of *T. crassispinus* (Karavajev, 1926), was investigated by both Csösz and Seifert. Though genetically representing the same nest population we treated these two samples as operationally different because of the deviating character systems of the investigators and their different individual selection of workers from the type series.

Temnothorax crassispinus

A total of 119 nest samples originated from the following countries: Austria 13, Bosnia 2, Bulgaria 7, Czechia 3, Germany 39, Greece 24, Hungary 8, Italy 2, Macedonia 3, Moldova 2, Poland 5, Serbia 1, Slovenia 4 and Ukraine 7 samples. A detailed account of the samples is given in the following under the sequence site, date in the format yyyy.mm.dd, sample No [latitude in decimal format, longitude in decimal format, altitude].

AUSTRIA: Arnoldstein, 1994.06.03, [46.550 N, 13.704 E, 570 m]; Bad Vöslau, pre 1980 [47.967 N, 16.222 E, 250 m]; Einöd-0.5 km N, 1994.08.05, No 40 [48.318 N, 15.732 E, 250 m]; Göttlesbrunn, 1955.08.25, [48.058 N, 16.738 E, 170 m]; Innsbruck, Kalvarienberg, 1994.08.05, No H2 [47.283 N, 11.435 E, 630 m]; Innsbruck, 1944.04.02 [47.266 N, 11.408 E, 580 m]; Kärnten: Gösselsdorfer See, 1994.08 [46.566 N, 14.618 E, 680 m]; Paudorf-1 km N, 1994.07.13, No 41, g82 [48.358 N, 15.618 E, 350 m]; Roppen-1 km E, 1994.07.04, No 207 [47.223 N, 10.831 E, 730 m]; Seebenstein: Türkensturz, pre 1970 [47.679 N, 16.136 E, 540 m]; Wachau: Spitz-5 km NW, 1990.07.01, No 2774 [48.392 N, 15.358 E, 400 m]; Wellersdorf-2 km NW, 1994.07.11 [46.567 N, 14.169 E, 770 m]. **BOSNIA:** Golubic-10 km N, 1989.09.15, No 51, 56 [44.768 N, 15.929 E, 400 m]. **BULGARIA:** Kokalyane-3 km E, 2009.06.06, No 080, 1033, 1035 [42.579 N, 23.434 E, 650 m]; Vitosha: Vladaya district, 2004, No 590, 856 [42.630 N, 23.205 E, 930 m]; Vitosha: Zheleznitsa- 1 km N, 2009.06.06, No 1009 [42.546 N, 23.365 E, 1000 m]; Vratehansica Planina: Vratsa-5 km S, 2009.06.07, No 1074 [43.137 N, 23.591 E, 1000 m]. **CZECHIA:** Masovice-3.7 km S, 1997.09.18, No 227 [48.824 N, 15.977 E, 285 m]; Strelna-0.5 km E, 1993.09.28, No 02, 03 [50.667 N, 13.755 E, 350 m]. **GERMANY:** Abensberg-10 km E, 2000.09.05, No AB1, AB2 [48.812 N, 11.969 E, 425 m]; Adlersberg- 0.5 km W, 2000.09.06, No AD/M6, AD/M7 [49.042 N, 12.004 E, 453 m]; Altenhain-1 km NW, 1994.06, No 07, 08 [51.299 N, 12.685 E, 15 m]; Berching, 2001.09, No 1, 3 [49.115 N, 11.444 E, 410 m]; Berzdorf, 1981.04.07 [51.055 N, 14.886 E, 274 m]; Berzdorf, 1993.03.19, No g31 [51.055 N, 14.886 E, 274 m]; Genthin-3.6 km S, 1994.06, No 6, 8, 04 [52.375 N, 12.150 E, 39 m]; Glesien-1.6 km W, 1994.06, No 3, 5 [51.445 N, 12.205 E, 122 m]; Hohburg-1 km S, 1993.06.19, No g77 [51.405 N, 12.799 E, 170

m]; Koldenhof, 2000.11.02, No-000074 [53.330 N, 13.340 E, 119 m]; Kühren-1 km W, 1993, No 94 [51.875 N, 11.978 E, 58 m]; Löbauer Berg, 1983.07.13 [51.089 N, 14.692 E, 392 m]; Meissen, Bosel, 1982.06.09, No 303 [51.138 N, 13.514 E, 170 m]; Mertitz, 2001.06.25 [51.177 N, 13.321 E, 138 m]; Obergruna-1 km S, 1993.04.12, No 59, 145 [51.005 N, 13.316 E, 285 m]; Ponholz-2 km SE, 2000.09.06, No P10, P11 [49.151 N, 12.119 E, 399 m]; Quolsdorf-2.8 km NE, 1992.04.06 [51.402 N, 14.872 E, 115 m]; Serrahn, 2000.05.04, No 000036, 17 [53.670 N, 12.350 E, 62 m]; Steffenhagener Heide, 2007.04.27 [54.110 N, 13.295 E, 7 m]; Technitz-1.2 km WNW, 1994.06, No 1, 6, 8 [51.130 N, 13.051 W, 165 m]; Trebsen-2.1 km SW, 1994, No 02, 03, 08, 09, 44 [51.272 N, 12.697 E, 165 m]; Uchtsprunge-0.5 km S, 1995, No 10 [52.534 N, 11.605 E, 75 m]. **GREECE:** Chelmos, 1994.06.04, No 1394 [37.987 N, 22.198 E, 2000 m]; Kalamata-20 km E, 1994.06.01, No 1348, 1349 [37.080 N, 22.280 E, 1250 m]; Kastanitsa-4 km SW; 2000.04.22, No 20 [37.280 N, 22.670 E, 1300 m]; Konitsa-5 km N, 1996.05.23, No 355 [40.108 N, 20.764 E, 550 m]; Levidi-10 km S, 2000.04.27, No 118, 119, 137 [37.630 N, 22.280 E, 1700 m]; Meliana vic., 1996.05.21, No 024 [39.361 N, 20.787 E, 700 m]; Parnon Mts., 2011.04.26, No 117, 145 [37.270 N, 22.610 E, 1650 m]; Sitena vic., 2000.04.05, No 56 [37.300 N, 22.650 E, 1000 m]; Sitena-3 km W, 2000.04.25-66, 071,079 [37.300 N, 22.600 E, 1700 m]; Sparti-20 km SW, 2000.04.29, No 150b, 150c [36.970 N, 22.350 E, 1950 m]; Taigetos Oros, 2011.04.30, No 305 [36.948 N, 22.377 E, 1500 m]; Tripolis-15 km NNW, 2011.04.29, No 214, 221 [37.629 N, 22.302 E, 1000 m]; Tripolis-22 km NNW, 2011.04.29, No 234, 238 [37.654 N, 22.268 E, 1600 m]; Vamvakou-3 km SE, 2011.04.26, No 162 [37.22 N, 22.59 E, 1300 m]; Vitina-5 km NE, 2011.04.29, No 261 [37.681 N, 22.208 E, 1000 m]. **HUNGARY:** Budapest, 1909.05.21 [47.543 N, 18.966 E, 250 m]; Csillebérc, 2004.05.30, No 397 [47.500 N, 18.959 E, 400 m]; Hatvan, 2011.03.12, No 432, 433 [47.673 N, 19.647 E, 200 m]; Isaszeg, 2011.04.02, No 437 [47.535 N, 19.397 E, 200 m]; Pécs (leg. Kaufmann), pre 1945 [46.104 N, 18.245 E, 200 m]; Vérteskozma, 2009.04.30, No 411 [46.459 N, 18.432 E, 350 m]. **ITALY:** Villa Santina, 1989.09.18, No 03, 04 [46.403 N, 12.844 E, 460 m]. **MACEDONIA:** Jacupitsa, 2009.06.19, No 001 [41.418 N, 21.416 E, 1300 m]; Konopishte, 2009.06.19, No 003 [41.248 N, 22.079 E, 672 m]; Lukovo, 2009.06.16, No 004 [41.366 N, 20.606 E, 590 m]. **MOLDOVA:** Vall du Berlad (Barlad Valley), pre 1930, No 1, 2 [47 N, 28 E, 70 m]. **POLAND:** Kielce: Pongrac [50.83 N, 20.66 E, 300 m]; Osiecznica-3 km W, 1994.04.09, No 85, 104 [51.344 N, 15.379 E, 187 m]; Wolin: Wapnica-3.5 km E, 2006, No 46, 79 [53.883 N, 14.485 E, 35]. **SERBIA:** Sremska Kamenica, 1971.05.02 [45.22 N, 18.44 E, 300 m]. **SLOVENIA:** Knezac, 1989.09.17, No 10, 11 [45.619 N, 14.250 E, 615 m]; Postojna-12 km W, 1997.05.29, No 401 [45.778 N, 14.062 E, 900 m]; Novo Mesto, 2007.05.29, No WL16 [45.811 N, 15.169 E, 200 m]. **UKRAINE:** Cherkassy: Kanev Nat. Res. [49.711 N, 31.477 E, 220 m]; Donetzk, S riv. Donetz, 1982.07.16 [47.9 N, 37.8, 120 m]; Golosseyev, pre 1926 [50.5 N, 30.5 E, 140 m]; Kiev vic., 1988.07.08 [50.5 N, 30.5 E, 140 m]; Pervomajsk, 1998.06.10 [48.044 N, 30.859 E, 100 m]; Pisch, 2004.06.10 [51.071 N, 21.003 E, 170 m].

***Temnothorax crasecundus* sp. n.**

A total of 84 nest samples originated from the following countries: Armenia 1, Bulgaria 31, Georgia 6, Greece 15, Romania 4, Russia 2, Turkey 21 and Ukraine 4 samples. A detailed account of the samples is given in the following.

ARMENIA: Armenia: without site, 1986.06.11 [40 N, 45 E, 1600 m]. **BULGARIA:** Arkutino, 1978.08.01 [42.33 N, 27.77 E, 15 m]; Bistrits-1 km N, 2009.06.06, No 1004 [42.594 N, 23.363 E, 400 m]; Dobrostan, 1982.09.12-55 [41.93 N, 24.88 E, 1500 m]; Dospat-2SW, 2009.06.10, No 1203 [41.634 N, 24.149 E, 1300 m]; German Monastery, 2004.05, No 467, 470 [42.602 N, 23.434 E, 800 m]; Harsovo-1 km SE, 2009.06.09, No 1130, 1130/1, 1131 [41.458 N, 23.390 E, 200 m]; Kiten, 2011.04.29, No 373 [42.238 N, 27.772 E, 27 m]; Kokalyane-3 km E, 2009.06.06, No 079 [42.579 N, 23.434 E, 650 m]; Malko Tarnovo: Propada, 2009.07.26, No 370 [41.982 N, 27.492 E, 385 m]; Malko Tarnovo: Brashlyan 2009.08.22, No 374 [42.044 N, 27.427 E, 340 m]; Mladezhko, 2009.08.21, No 366 [42.152 N, 27.362 E, 220 m]; Novakovo-2 km SE, 2009.06.12, No 1299 [41.887 N, 25.099 E, 400 m]; Obsor, 1981.08.01 [42.82 N, 27.86 E, 50 m]; Pasarel-1 km NW, 2009.06.06, No 070, 078 [42.594 N, 23.362 E, 770 m]; Peshtera, 2008.05.25, No 369 [42.297 N, 24.299 E, 580 m]; Pirin Mts.: Rozen-8 km N, 1982.09.05, No 0, 396 [41.60 N, 23.45 E, 1400 m]; Plovdiv, 1977.05.27 [42.14 N, 24.72 E, 200 m]; Sofia: Borisova Park 1, 2004, No 841 [42.680 N, 23.342 E, 596]; Sofia: Borisova Park 2, 2004, No 509, 558 [42.678 N, 23.351 E, 586]; Sofia: Lozenetz distr., 2004, No 709 [42.666 N, 23.312 E, 620 m]; Tsaparevo-2 km S, 2009.06.09, No 1168 [41.612 N, 23.097 E, 800 m]; Vitoshka: Vladaya distr., 2004, No 596, 854 [42.630 N, 23.205 E, 930 m]; Zeleznitza-1 km N, 2009.06.06, No 043, 047 [42.539 N, 23.367 E, 1000 m]. **GEORGIA:** Abastumani-1.4 km W, 2013.09.17, No GEOII-70, GEOII-71, GEOII-72 [41.758 N, 42.817 E, 1532 m]; Daba-0.26 km E, 2010.08 [41.811 N, 43.452 E, 1030 m]; Pizunda, 1984.08.11 [43.153 N, 40.342 E, 17 m]; Sedaseni-Kloster, 2004.07.28 [41.871 N, 44.768 E, 1150 m]. **GREECE:** Karitza-6 km W, 1998.04.04 [39.840 N, 22.710 E, 750 m]; Kastanitza-6 km W, 1998.04.04 [37.28 N, 22.67 E, 1300 m]; Kosmas-2 km SW, 2000.04.26, No 93, 96, 098 [37.080 N, 22.730 E, 1100 m]; Levidi-10 km S, 2000.04.27, No 132 [37.630 N, 22.280 E, 1700 m]; Litohoro-3 km W, 1996.05.13 [40.080 N, 22.450 E, 1200 m]; Litohoro-7 km W, 1996.05.13, No 187 [40.112 N, 22.480 E, 600 m]; Parnon Mts., 2011.04.26, No 152 [37.27 N, 22.61 E, 1650 m]; Sitena-3 km W, 2000.04.25, No 62, 71a [37.300 N, 22.600 E, 1700 m]; Sparti-20 km SW, 2000.04.25, No 149 [36.97 N, 22.35 E, 1950 m]; Stagira, 2011.04.09, No 027 [40.531 N, 23.720 E, 585 m]; Taigetos Oros, 2011.04.30, No 302, 311 [36.948 N, 22.377 E, 1500 m]. **ROMANIA:** Comana: Vlasca, pre 1935, No 1, 2 [43.90 N, 28.31 E, 130 m]; Dobrogea: Babadag, 2005.06.02, No 105, 106 [44.857 N, 28.691 E, 100 m]. **RUSSIA:** Gelendzhik-5 km SSE, 2006.06.04, No 249 [44.48 N, 38.145 E, 150 m]; Obilnoje, 2006.06.08, No 219 [44.207 N, 43.538 E, 240 m]. **TURKEY:** Aydogdu-5 km SW, No 1147, 1157, 1158 [40.714 N, 42.495 E, 1500 m]; Cat-2 km S, 2012.07.02, No 046 [39.418 N, 35.957 E, 1550 m]; Demir-

köy, 2009.07.06, No 474, 476 [41.818 N, 27.814 E, 170 m]; Erzincan-25 km SE, 2012.07.13, No 179 [39.661 N, 39.734 E, 1200 m]; Eskishir-Sögüt, 2003.05.10, No 162 [39.550 N, 30.130 E, 966 m]; Ispir-10 km NW, 1993.07.01, No 1197 [40.585 N, 40.852 E, 1700 m]; Mahya hill, 2005.05.30, No 472 [41.771 N, 27.638 E, 820 m]; Mezraa vic., 2012.07.11, No 153, 159 [39.378 N, 39.805 E, 1300 m]; Ordu-25 km NW, 2012.07.21, No 396 [41.064 N, 37.711 E, 400 m]; Ordu-40 km WSW, 2012.07.21, No 402 [40.719 N, 37.622 E, 1000 m]; Posof-3 km E, 2012.07.17, No 303 [41.414 N, 42.762 E, 1500 m]; Pülümür vic., 2012.07.11, No 159 [39.482 N, 39.890 E, 1600 m]; Seydiler-7 km N, 2012.07.23, No 495 [41.694 N, 33.718 E, 1200 m]; Sögüt vic., 2003.05.10, No 166 [39.570 N, 30.13 E, 1050 m]; Tortum-15 km E: Kirecli Gecidi, 2012.07.13, No 205 [40.353 N, 41.704 E, 2400 m]; Tortum-45 km NNE, 2012.07.11, No 217 [40.325 N, 41.572 E, 1600 m]; Ulu Dag: Sogukpinar, 1993.07.05, No 1230 [40.055 N, 29.120 E, 750 m]. **UKRAINE:** Agarmis, 1980.09.29 [45.252 N, 35.025 E, 600 m]; Armiansk, 1985.05.04 [46.107 N, 33.693 E, 15 m]; Krasnolesye, 1980.09.12 [44.952 N, 34.102 E, 100 m]; Simferopol, 1995.08.13, No 826 [44.938 N, 34.099 E, 300 m].

Type material

***Leptothorax nylanderi* var. *crassispina* Karavajev, 1926**

The type series, stored in Shmalhausen Institute of Zoology Kiev and certainly representing a nest sample, is labeled “Kiev: Golosejev (Karavajev No 3057)”. Three syntype workers were investigated by Seifert and seven syntype workers by Csösz.

***Leptothorax nylanderi slavonicus* Seifert, 1995**

The paratypes, seven workers on the same pin and originating from the nest that contained the queen holotype, are labeled “Kr. Görlitz, 19.3.1993, Schönau-Berzdorf, Hutberg, g31”, „*Leptothorax n. slavonicus* Seifert”, “Paratypes”. Four paratypes of this sample were investigated by Seifert. Material is stored in Senckenberg Museum of Natural History Görlitz. Csösz investigated four worker paratypes of another nest series from the type locality, labelled “Germany, Kr. Görlitz, Hutberg Schönau-Berzdorf, 19.03.1993 Seifert”.

***Temnothorax crasecundus* sp. n.**

The worker holotype is labelled “BUL: 42.6785°N, 23.3508°E Sofia, 586 m, Borisova gradina Park, Part 2 V.Antonova 2004.05-509” and “Holotype *Temnothorax crasecundus* Seifert & Csösz”. Four worker paratypes, two males and two gynes from

the holotype nest are mounted on two other pins and carry the same collecting data label and “Paratypes *Temnothorax crasecundus* Seifert & Csöz”. A second series with five worker paratypes on two pins is labeled “BUL: 42.6797°N, 23.3417°E Sofia, 596 m, Borisova gradina Park, Part 1 V.Antonova 2004.05-841” and “Paratypes *Temnothorax crasecundus* Seifert & Csöz”. These two type series are stored in Senckenberg Museum of Natural History Görlitz. A third paratype series containing three workers on the same pin, is labelled “Bulgaria_28: East Rhodopes, 2 km SE Novakovo 25 km SE. Asenovgrad, 1299, 400mH, 41°53'12"N, 25°5'55"E, 12.06.2009, Leg A Schulz”, “ANTWEB CASENT 0906045” and is stored in the Hungarian Museum of Natural History Budapest.

Methods

The senior and junior author performed two independent investigations of worker ant morphology, considering different character combinations and using different microscopic equipment. Seifert recorded 18 and Csöz 22 primary morphometric characters. In bilaterally developed characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and fully dried specimens. Measurements of body parts always refer to real cuticular surface and not to the diffuse pubescence surface.

Equipment and measurement procedures of Seifert

Seifert used for spatial adjustment of specimens a pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0 planapochromatic objective (resolution 1050 lines/mm) at magnifications of 120–384×. The mean relative measuring error over all magnifications was 0.3%. A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light-cables, providing 30°-inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarized-light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52% of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field.

Equipment and measurement procedures of Csöz

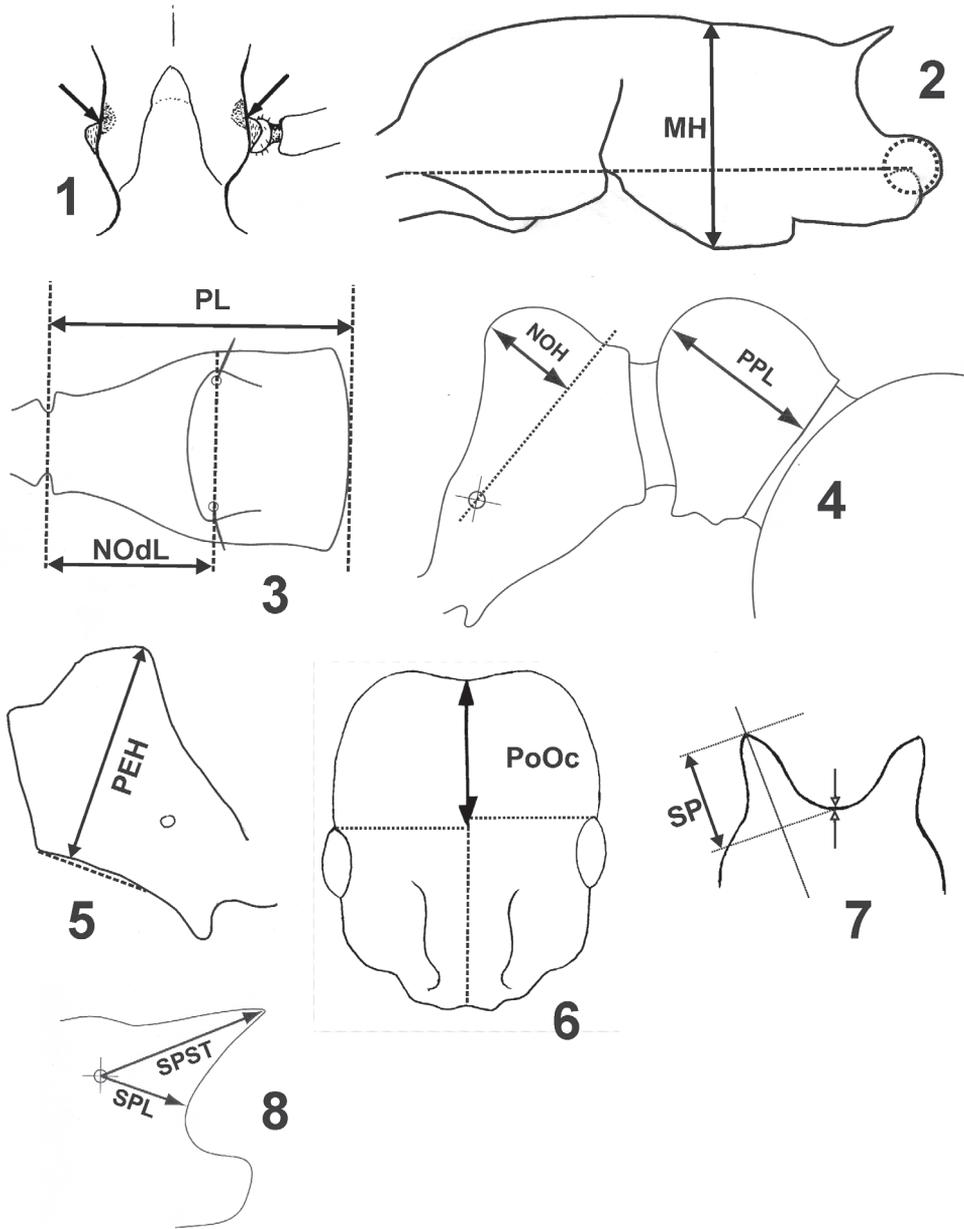
Measurements were made using a pin-holding stage, permitting rotations around X, Y, and Z axes. An Olympus SZX9 stereomicroscope was used at a magnification of 150× for each character, allowing a precision of $\pm 2 \mu\text{m}$.

The morphometric characters

29 morphometric characters were investigated – ten of these by both authors. We give the character definitions in alphabetic order. In square brackets is indicated who investigated a character.

- CL** [Csösz & Seifert]: maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of hind vertex and/or clypeus reduce CL.
- CS** [Seifert]: cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.
- CSb** [Csösz]: cephalic size; the arithmetic mean of CL and CWb.
- CW** [Seifert]: maximum cephalic width; the maximum is found in *Temnothorax* and *Leptothorax* usually across and including the eyes, exceptionally posterior of the eyes.
- CWb** [Csösz]: maximum width of head capsule, measured just posterior of the eyes.
- EL** [Csösz]: maximum diameter of the eye.
- EYE** [Seifert]: eye-size index: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye is divided by CS, i.e. $EYE = (EL + EW) / (CL + CW)$. All structurally visible ommatidia are considered.
- FRS** [Csösz & Seifert]: distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus (arrows in Fig. 1). If these dorsal lamellae do not laterally surpass the frontal carinae, the deepest point of scape corner pits may be taken as reference line. These pits take up the inner corner of scape base when the scape is fully switched caudad and produce a dark triangular shadow (spotted area in Fig.1) in the lateral frontal lobes immediately posterior of the dorsal lamellae of scape joint capsule.
- MGr** [Seifert]: depth of metanotal groove or depression, measured from the tangent connecting the dorsalmost points of promesonotum and propodeum; here given as per cent ratio of CS.
- MH** [Seifert]: in workers: with mesosoma in lateral view and measured orthogonal to “longitudinal mesosomal axis”, MH is the longest measurable *section* line of mesosoma at mesopleural level (not height above all). “Longitudinal mesosomal axis” in lateral view is defined as straight line from the centre of propodeal lobe (centre of circus in Fig.2) to the border point between anterior pronotal shield and propleuron. In gynes it is the longest section line directed perpendicular to the straight dorsal profile line of mesosoma (formed by mesonotum and scutellum). The lower measuring point is usually the lowest part of mesopleuron.
- ML** [Csösz & Seifert]: in workers: mesosoma length from caudalmost point of propodeal lobe to transition point between anterior pronotal slope and anterior propodeal shield (preferentially measured in lateral view; if the transition point is not well defined, use dorsal view and take the centre of the dark-shaded borderline between pronotal slope and pronotal shield as anterior reference

- point). In gynes: length from caudalmost point of propodeal lobe to the most distant point of steep anterior pronotal face.
- MW** [Csösz & Seifert]: maximum mesosoma width; this is in workers pronotal width, in gynes it is measured anteriorly of the tegulae.
- NOdL** [Csösz]: Anterior length of petiole measured in dorsal view. Distance from the (centre of anteriormost seta pit on the petiolar node to the level of the constriction of articulation condyle with propodeum (Fig. 3). Measuring requires a change of focus from above (seta pit) to below (constriction). Dorsal view is achieved when the dorsalmost point of anterior petiolar peduncle at the level of its strongest constriction and the dorsalmost point of caudal petiolar margin are in the same focal level.
- NOH** [Csösz]: Maximum height of the petiolar node, measured in lateral view from the uppermost point of the petiolar node perpendicular to a reference line set from the petiolar spiracle to the imaginary midpoint of the transition between the caudal slope and the caudal cylinder of the petiole (Fig. 4).
- NOL** [Csösz]: Length of the petiolar node, measured in lateral view from petiolar spiracle to dorso-caudal corner of caudal cylinder. Do not erroneously take as reference point the dorso-caudal corner of the helcium, which is sometimes visible.
- PEH** [Csösz & Seifert]: maximum petiole height. The chord (dashed line in Fig. 5) of ventral petiolar profile at node level is the reference line perpendicular to which the maximum height of petiole is measured.
- PEL** [Seifert]: diagonal petiolar length in lateral view; measured from anterior corner of subpetiolar process to dorsocaudal corner of caudal cylinder.
- PEW** [Csösz & Seifert]: maximum width of petiole.
- PL** [Csösz]: Total petiole length measured in dorsal view; distance between the dorsalmost point of caudal petiolar margin and the dorsalmost point of anterior petiolar peduncle at the transversal level of its strongest constriction. Positioning of petiole as in NOdL (Fig. 3).
- PoOc** [Csösz & Seifert]: postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL. Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin. Note that many heads are asymmetric and average the left and right postocular distance (Fig. 6).
- PPH** [Csösz]: Maximum height of the postpetiole in lateral view measured perpendicularly to a line defined by the linear section of the segment border between dorsal and ventral petiolar sclerite.
- PPL** [Csösz]: Maximum length of the postpetiole measured in lateral view perpendicular to the straight section of lateral postpetiolar margin (Fig. 4).
- PPW** [Csösz & Seifert]: maximum width of postpetiole.
- SL** [Csösz & Seifert]: maximum straight line scape length excluding the articular condyle as arithmetic mean of both scapes.
- SP** [Seifert]: maximum length of propodeal spines; measured in dorsofrontal view along the long axis of the spine, from spine tip to a line, orthogonal to the long axis, that touches the bottom of the interspinal meniscus (Fig. 7). This mode



Figures 1–8. Explanation of morphometric characters.

of measuring is less ambiguous than other methods but it results in some spine length in species with reduced spines.

SPL [Csösz]: Minimum distance between the center of propodeal spiracle and the margin of subspinal excavation measured with both end points positioned in the same focal level (Fig. 8).

- SPBA** [Csösz & Seifert]: the smallest distance of the lateral margins of the spines at their base. This should be measured in dorsofrontal view, since the wider parts of the ventral propodeum do not interfere with the measurement in this position. If the lateral margins of spines diverge continuously from the tip to the base, a smallest distance at base is not defined. In this case, SPBA is measured at the level of the bottom of the interspinal meniscus.
- SPST** [Csösz & Seifert]: distance between the centre of propodeal stigma and spine tip. The stigma centre refers to the midpoint defined by the outer cuticular ring but not to the centre of real stigma opening that may be positioned eccentrically.
- SPTI** [Csösz & Seifert]: the distance of spine tips in dorsal view; if spine tips are rounded or truncated, the centres of spine tips are taken as reference points.
- SPWI** [Csösz]: Maximum distance between outer margins of spines; measured in same position as SPBA.

Explorative and supervised data analyses and classification methods

The delimitation of the cryptic species was done by an interaction of Nest-Centroid Clustering (NC clustering) and a confirmative linear discriminant analysis (LDA). NC Clustering was run both as hierarchical NC-Ward clustering and non-hierarchical NC-K-means clustering. These methods were described in more detail by Seifert et al. (2013) who also provided a script written in R and freely available under the GNU / GPL license from the following website: <http://sourceforge.net/projects/agnesclustering/>.

The same mathematical procedures were applied for the data sets of Seifert and Csösz. NC-Ward clustering was run first to indicate the putative number of K main clusters. In the second step NC-K-Means was performed with the setting of K classes suggested by NC-Ward. Classifications being coincident between the hierarchical and non-hierarchical clustering formed the hypothesis for the controlling LDA that was subsequently run. Samples with classifications disagreeing between NC-Ward and NC-K-means were run in this LDA as wild-cards. The final classification (“final species hypothesis”) was established by the LDA in the iterative procedure described by Seifert et al. (2013). There remained no undecided cases independent which posterior probabilities they had. LDA and ANOVA tests were performed with the software package SPSS 15.0.

Results and discussion

Separation of the *Temnothorax nylanderi* species complex from other *Temnothorax* species

The W Palaearctic species of the *Temnothorax nylanderi* species complex – *T. nylanderi*, *T. crassispinus* and *T. crasecundus* sp. n. – can be separated from other species of the region by the following character combination.

- (1) Head short, mean index CL/CW only 1.053–1.063.
- (2) Whole dorsum of vertex regularly and continuously longitudinally carinulate, shining surface areas are absent or restricted to a narrow median stripe.
- (3) Metanotal depression always visible, at least suggested.
- (4) Antennal club and femora never with a blackish pigmentation.
- (5) Petiole in lateral view rather high and with a weakly concave frontal face; the anterior profiles of node and peduncle form an angle of about 150–155° whereas anterior and dorsal profiles of node form an angle of 90–105°. Dorsal profile of node steeply sloping down to caudal cylinder. The profiles of this slope and of the caudal cylinder form an angle of about 140°.
- (6) Propodeal spines acute, deviating from longitudinal axis of mesosoma by 32–42° and moderately long, SP/CS 0.200–0.260, SPST/CS 0.253–0.356.

Convincing clustering of the cryptic species

In the data set of Seifert and considering all 18 characters, NC Ward clustering provided a clear separation of the cryptic species in two main branches (Fig. 9). Accordingly, NC-K-means was run with $K=2$. The classifications of both NC-Ward and NC-K-means differed in 7.7% of samples. These samples were set as wild-cards in the controlling LDA. The final species hypothesis was determined in the iterative process described by Seifert et al. (2013). Both NC-Ward (Fig. 9) and NC-K-means clustering disagreed from the final species hypothesis in only 1.9% of samples. Character reduction by a stepwise LDA did not result in an improvement. The type series of *T. crassispinus* and *T. slavonicus* were allocated to the same cluster with $p=0.9766$ and $p=0.9858$ respectively while the holotype series of *T. crasecundus* sp. n. was allocated to the other cluster with $p=0.9912$.

The results were similar in the data set of Csösz, considering all 22 characters and following the same procedure. The classifications of NC-Ward and NC-K-means differed in 11.1% of samples. NC-Ward disagreed from the final species hypothesis in 11.1% and NC-K-means in 3.1% of samples. A character reduction by a stepwise LDA, again performed iteratively, improved the classification result significantly. NC-Ward disagreed from the final species hypothesis in only 2.1% (Fig. 10) and NC-K-means in only 1.1% of samples when the ten characters CSb, CL/CWb, FRS/CSb, SL/CSb, ML/CSb, NOL/CSb, SPST/CSb, SPLV, PPW/CSb and SPWI/CSb are considered. The type series of *T. crassispinus* and the paratype series of *T. slavonicus* were allocated to the same cluster with $p=0.9937$ and $p=0.9996$ respectively while the third paratype series of *T. crasecundus* sp. n. from Bulgaria: Novakovo was allocated to the other cluster with $p=0.9950$.

We consider the congruent results of two independent investigations and investigators and the low disagreement of 1.1–2.1% between the classifications of exploratory data analyses with the final species hypothesis as a strong argument for heterospecificity of *T. crasecundus* sp. n. and *T. crassispinus*. This interpretation is supported by the coincidence of phenotyping with a clear-cut parapatric distribution (Fig. 11) and the rejection of intraspecific dimorphism (see below).

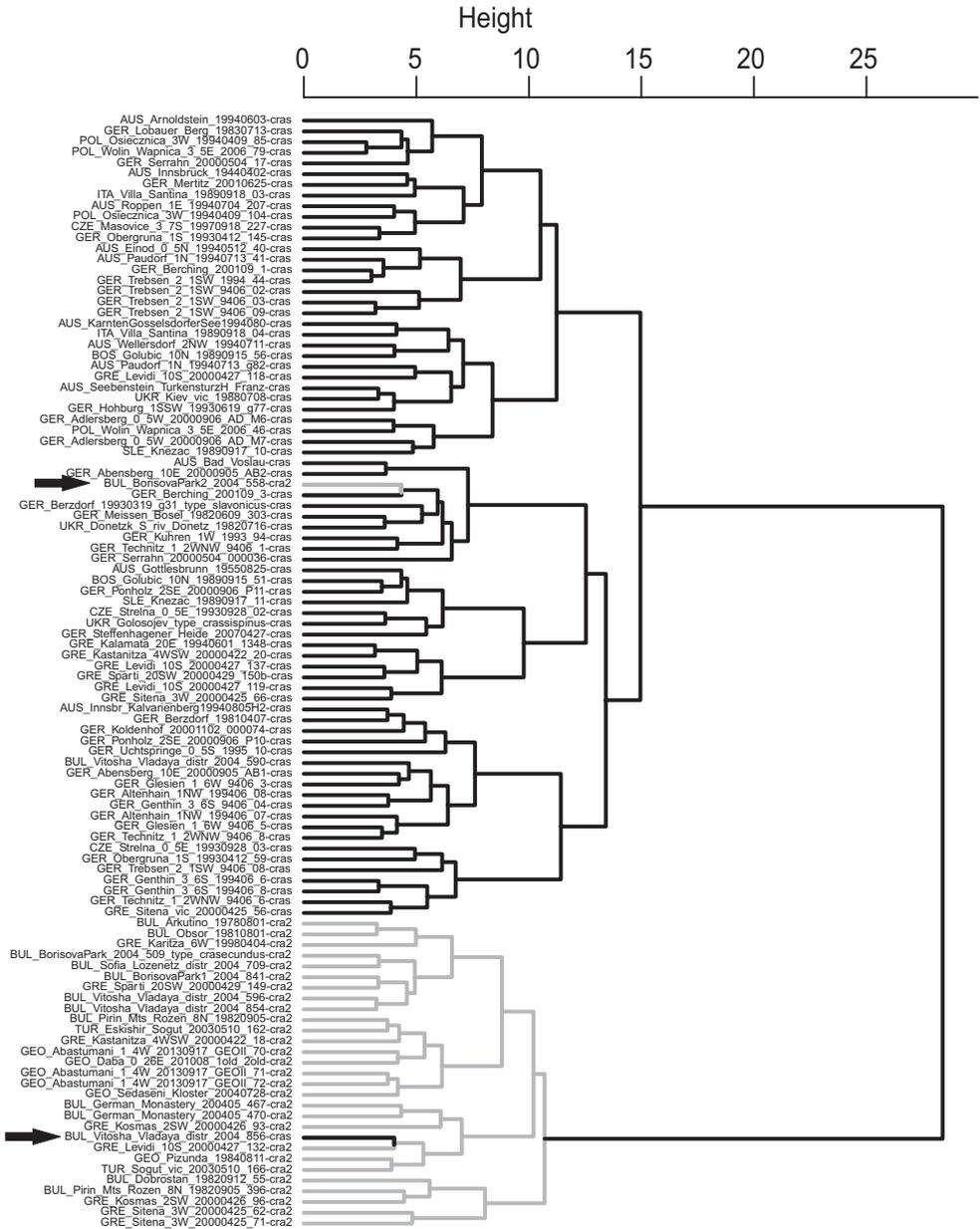


Figure 9. *Temnothorax crasecundus* sp. n. (grey branch) and *T. crassispinus* (black branch). NC-Ward clustering. Data set of Seifert: 104 nest samples investigated and 18 characters considered. Arrows point to samples clustered in disagreement with the final species hypothesis.

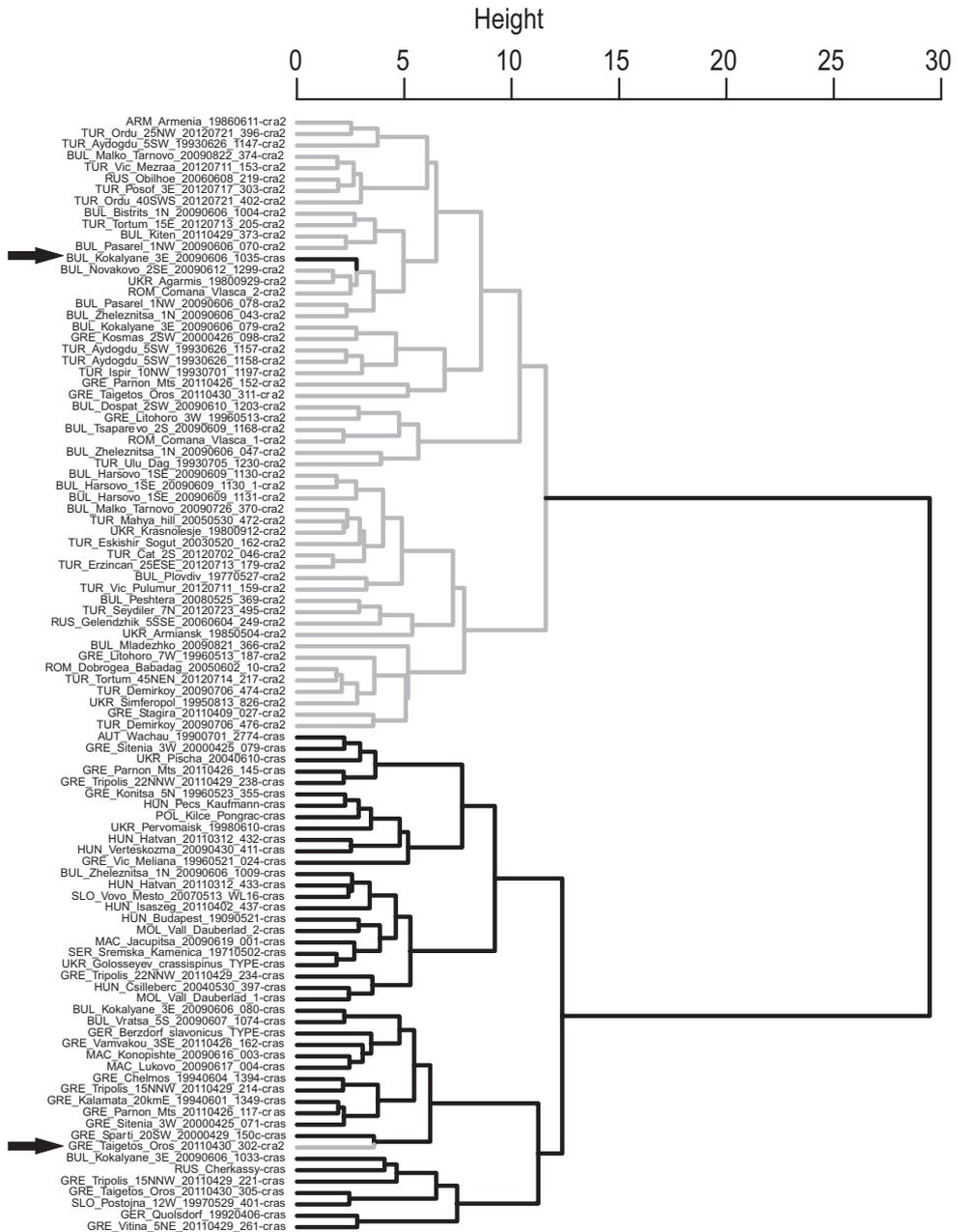


Figure 10. *Temnothorax crasecundus* sp. n. (grey branch) and *T. crassispinus* (black branch). NC-Ward clustering. Data set of Csöz: 99 nest samples and 10 characters considered. Arrows point to samples clustered in disagreement with the final species hypothesis. Figs 1 and 2 sum up to 203 different samples.



Figure 11. *Temnothorax crasecundus* sp. n. [black rectangles] and *T. crassispinus* [white rhombs]. The parapatric distribution is clearly shown.

Evolutionary divergence, local hybridization and heterospecificity

Seifert et al. (2013) reported an impressive performance of NC clustering in the separation of cryptic species but they also showed a significant weakness of this methodology if substantial numbers of hybrids are in a sample. In five data sets with a mean percentage of 18.9% hybrids, four of these did not involve cryptic species, the average agreement of NC-Ward and NC-K-means clustering with the LDA vector indication was reduced to 87.6%. They also stated that the best phenotypical identification of hybrids is given by their position along an interspecific vector (examples in Kulmuni et al. 2010; Seifert et al. 2010; Steiner et al. 2011; Bagherian et al. 2012). LDA vectors in particular are rather robust against the fluctuating nature of characters in hybrids. The larger the agreement of NC-clustering with the position along an interspecific LDA vector appears, the lower is the probability that hybrids are in the data set.

We achieved an agreement of 97.9–98.9% between the final species hypothesis and four different cluster analyses. This indicates a significant evolutionary divergence and could indicate that no or very few hybrids are present in our data set. Yet, the present problem is more difficult because extremely similar species are involved which prevents a reliable phenotypic identification of a particular hybrid sample. A broader statistic approach is needed. Accordingly, we compare the positions of samples along the interspecific LDA vector (i) from the potential contact zone, (ii) from the allopat-

Table 1. Distance of the sample means of *Temnothorax crassispinus* and *T. crasecundus* sp. n. from the zero point of the interspecific discriminant vector. The ANOVA data are placed in the line between the compared data sets.

	Distance from zero
Potential contact zone (total 84, <i>crassispinus</i> 34, <i>crasecundus</i> 50)	1.6173 ± 1.0000 [0.1186,3.8912]
ANOVA [F, p]	0.370, 0.543
Allopatric zones (total 119, <i>crassispinus</i> 85, <i>crasecundus</i> 34)	1.6941 ± 0.7906 [0.0326,3.4717]
ANOVA [F, p]	11.267, 0.001
Syntopic sites (total 31, <i>crassispinus</i> 18, <i>crasecundus</i> 13)	1.1465 ± 0.8740 [0.1186,3.4894]
ANOVA [F, p]	12.383, 0.001
Potential contact zone without syntopic sites (total 53, <i>crassispinus</i> 16, <i>crasecundus</i> 37)	1.8927 ± 0.9727 [0.1258,3.8912]

ric zones and (iii) from sites with established syntopic occurrence of both species. Reduced interspecific distances in contact zones are an indication that hybridization could have occurred. We consider the territories of Greece, Bulgaria, Romania and Moldova to form the potential contact zone (Fig. 11).

There is only a very weak, insignificant reduction of the distance from the zero point of the discriminant vector in samples from the potential contact zone compared to those from the allopatric zones (Tab. 1). However, there is a highly significant distance reduction in 31 samples from the nine Bulgarian and Greek sites with established syntopic occurrence of both species. This is in our opinion a strong suggestion of local hybridization and possibly also of introgression. We have determined all 203 samples following a YES/ NO decision but four samples, this is 2% of the whole material, are suspected to represent F1 hybrids or backcrosses of F1 hybrids with a parental species. However, as mentioned above, our phenotypical identification system does not allow a reliable identification of hybrids because few samples with discriminant values close to zero are also found in the allopatric ranges of both species where hybridization is impossible (Table 1).

We conclude that *T. crassispinus* and *T. crasecundus* sp. n. are a pair of cryptic, parapatric species showing hybridization in the contact zone. We follow here the Pragmatic Species Concept of Seifert (2014) which allows local hybridization and even weak introgression between species as long as they are separable over their whole range in the vast majority of samples. Seifert formulated his concept in several sentences: “A species is a cluster of organisms which passed a threshold of evolutionary divergence. Divergence is determined by one or several operational criteria described by an adequate numerics. A single conclusive operational criterion is sufficient. Conflicts between operational criteria require an evolutionary explanation. Thresholds for each operational criterion are fixed by consensus among the experts of a discipline under the principle of avoiding over-splitting. Clusters must not be the expression of intraspecific polymorphism.”

Seifert proposed as operational criterion for the discipline “multivariate investigation of ant worker morphology” and as a remedy against over-splitting that at least 97% of the classifications by exploratory data analyses should agree with the classifications by linear discriminant analyses that form the final species hypothesis. However, 4% disagreement

or 96% confirmation seem to be a more reasonable threshold when considering the performance of the two most powerful methods of NC-clustering, NC-K-Means and NC-Ward, in the separation of 74 cryptic ant species (Table 1 in Seifert et al. 2013).

The consequences of threshold decisions may be illustrated by an example. Over many years we studied the situation in the Mediterranean *Temnothorax lichtensteini* complex and intended to accept three species: the largely western entity *T. lichtensteini* (Bondroit, 1918), a second, largely eastern, semipatric entity (provisionally designated by Seifert (2007) in his key as “*T. lichtensteini* sp. 2”) and a third entity restricted to southern Balkans. Csösz et al. (2013) showed that a linear discriminant analysis could separate all three clusters. Yet, the agreement between NC-clustering and the LDA was only 92% in the second entity but 100% in the third entity. As a consequence, a taxonomic naming of the second entity was suspended whereas the third one was described as the new species *T. laconicus* Csösz et al. 2013. It is possible that multisource taxonomy, in particular application of adequate nuDNA markers, could lead to other conclusions in case of the second entity.

We want to emphasize in this context that hybridization and reticulate evolution is a matter of fact in the living nature around us (reviewed, e.g., in Abbott et al. 2013). Exemplary groups in animals are ducks (Phillips 1915, 1921), redstarts (Ertan 2002) or butterflies (Mavárez et al. 2006, Kronforst 2008). Ants are no exception: as much as 18% of the Central European ant species are credibly shown to hybridize (Pearson 1983, Seifert 1984, Douwes and Stille 1991, Seifert 1999, 2006, Seifert et al. 2010, Kulmuni et al. 2010, Steiner et al. 2011, Van der Have et al. 2011, Bagherian et al. 2012, Seifert 2013). A workable species concept has to recognize this. Alternatively, a taxonomist considering the term “reproductive isolation” in its genuine meaning of an impenetrable barrier would have to synonymize a big portion of taxa currently considered by any taxonomist as well-separable species.

Finally we address the question if our two entities might represent an intraspecific dimorphism instead of representing different species by considering geographic distribution and the frequency and distribution of supposedly mixed nests in the sympatric and allopatric zones. Frequencies of discrete morphs provided by the gene pool of a single species may show steep geographic gradients - remind alone of the famous text book example of the Peppered Moth *Biston betularia* (e.g., Cook 2003). However, the clear-cut parapatric partitioning as in our case is not known for morphs. This is the primary, zoogeographic argument against intraspecific polymorphism. Considering the 84 nest samples from the sympatric area from Greece north to Moldova and accepting only classifications with posterior probabilities of $p > 0.90$, we found only two nests (=2.4%) putatively containing both *T. crassispinus* and *T. crasecundus* workers morphs whereas 97.6% contained pure samples of either species. According to these two arguments, we consider intraspecific dimorphism with panmictic behavior as extremely unlikely. Even more, these two putatively mixed nests in the sympatric zone could represent hybrids or misidentifications rather than indicating mixtures of pure phenotypes. A small percentage of misidentification is always expectable in a large material of 203 samples with 603 workers and becomes obvious in a third “mixed”

sample from near Hohburg / Saxony. This site is deeply within the *T. crassispinus* range and some 1350 km away from the next site of *T. crasecundus* sp. n. – occurrence of a mixed nest should be impossible there.

Species description

Temnothorax crasecundus sp. n.

<http://zoobank.org/9C3131DE-FCCE-4078-A0BB-2BFC68EBA7B5>

Etymology. In the provisional internal naming system of the senior author the new species had been designated over the years as “*Temnothorax crassispinus* sp. 2”. The taxonomic name, composed of “cra” (first syllable of *crassispinus*) and “secundus” (= the second), intends to indicate both this history and the close relationship.

Type material. See above under “Material”.

Description of the worker caste. All morphometric data given in the following verbal description are arithmetic means of 256 worker individuals calculated by fusing Seifert’s and Csösz’s data sets. Harmonization of the different data sets has been performed by the function $CW = 1.0791 * CWb$.

Worker (Tables 2, 3; Figs 12–14; compare with photos of *T. crassispinus* type in Figs 15–17): Medium-sized species (CS 641 μ m, ML 760 μ m). Head weakly elongated but significantly more than in *T. crassispinus* (CL/CW 1.069 vs. 1.055, CL/CWb 1.153 vs. 1.139). Head in dorsal aspect with strongly convex postocular sides, convex genae and straight posterior margin. Eyes with a moderate distance from posterior margin of vertex (PoOc/CL 0.391) and medium-sized in terms of the genus but significantly smaller than in *T. crassispinus* (EYE/CS 0.210 vs. 0.216). Scape moderately long (SL/CS 0.762, SL/CSb 0.793) and with variable pubescence: with the scape directed caudad, pubescence is appressed to decumbent (0–15°) at inner margin and more subdecumbent (30°) at outer margin. Frontal carinae rather distant (FRS/CS 0.361), their median part more or less parallel. Sculpture on central vertex regularly longitudinally carinulate. A transversal line between the frontal carinae, positioned immediately posterior of the frontal triangle, crosses 21–23 carinulae. A small longitudinal zone on median vertex occasionally without sculpture and shining. Lateral vertex and head with a more irregular sculpture, being a mixture of microreticulate and rugulose structures. Antennal sockets on shining ground surrounded by 7–8 concentric rugulae. Clypeus between sagittal level of frontal carinae rather smooth but with 5–8 longitudinal carinulae. Frontal triangle with very delicate microsculpture and 0–4 longitudinal carinulae.

Mesosoma moderately wide (MW/CS 0.608) and metanotal depression always developed (MpGr/CS 2.1%). Propodeal spines rather long and acute but distinctly shorter than in *T. crassispinus* (SPST/CS 0.283 vs. 0.322). Distance of their bases and tips rather large but significantly smaller than in *T. crassispinus* (SPBA/CS 0.286 vs. 0.300, SPTI/CS 0.324 vs. 0.353), spine tips slightly curving inwards. Direction of

Table 2. Data set of Seifert; nest sample means of morphometric data of the workers of the cryptic species *T. crasecundus* sp. n. and *T. crassispinus* (Karavajev, 1926). Arrangement of data: arithmetic mean \pm standard deviation [minimum, maximum]. F values and significance levels p are from an univariate ANOVA; the F values of the most separating characters are given in heavy type.

	<i>T. crasecundus</i> sp. n. (n=29)	ANOVA F, p	<i>T. crassispinus</i> (n=75)
CS	641 \pm 36 [594,713]	0.02, n.s.	645 \pm 30 [556,713]
CL/CW	1.065 \pm 0.014 [1.038,1.087]	16.90, 0.000	1.053 \pm 0.013 [1.013,1.081]
SL/CS	0.767 \pm 0.011 [0.741,0.786]	1.38, n.s.	0.764 \pm 0.013 [0.734,0.790]
PoOc/CL	0.395 \pm 0.007 [0.380,0.406]	3.63, n.s.	0.392 \pm 0.007 [0.373,0.405]
EYE/CS	0.210 \pm 0.005 [0.201,0.219]	29.22, 0.000	0.216 \pm 0.005 [0.207,0.233]
FRS/CS	0.361 \pm 0.008 [0.344,0.376]	2.48, n.s.	0.364 \pm 0.008 [0.345,0.386]
SPBA/CS	0.280 \pm 0.010 [0.252,0.297]	26.53, 0.000	0.294 \pm 0.012 [0.268,0.322]
SPTI/CS	0.325 \pm 0.014 [0.295,0.347]	75.95 , 0.000	0.350 \pm 0.013 [0.324,0.377]
SPST/CS	0.285 \pm 0.014 [0.250,0.308]	179.20 , 0.000	0.323 \pm 0.014 [0.286,0.354]
SP/CS	0.218 \pm 0.015 [0.188,0.246]	202.63 , 0.000	0.260 \pm 0.012 [0.232,0.290]
PEW/CS	0.253 \pm 0.007 [0.242,0.270]	6.76, 0.011	0.258 \pm 0.008 [0.239,0.275]
PPW/CS	0.353 \pm 0.010 [0.335,0.375]	24.77, 0.000	0.367 \pm 0.013 [0.331,0.395]
PEH/CS	0.357 \pm 0.008 [0.343,0.374]	14.22, 0.000	0.364 \pm 0.009 [0.343,0.391]
PEL/CS	0.472 \pm 0.011 [0.452,0.497]	7.41, 0.008	0.479 \pm 0.013 [0.446,0.508]
ML/CS	1.187 \pm 0.016 [1.158,1.221]	0.08, n.s.	1.188 \pm 0.015 [1.156,1.239]
MW/CS	0.605 \pm 0.010 [0.580,0.628]	3.68, n.s.	0.600 \pm 0.011 [0.780,0.626]
MH/CS	0.524 \pm 0.011 [0.500,0.547]	11.93, 0.001	0.532 \pm 0.012 [0.507,0.566]
MPGR/CS	2.10 \pm 0.56 [1.31,3.41]	0.25, n.s.	2.04 \pm 0.49 [1.07,3.23]

spines in lateral view deviating from longitudinal axis of mesosoma by 26–29°. Mesosoma irregularly microreticulate-rugulose with few superimposed longitudinal rugae on promesonotum. Metapleuron more regularly longitudinally carinate-rugose.

Petiole in lateral view rather high and with a weakly concave frontal face; the anterior profiles of node and peduncle form an angle of about 150–155° whereas anterior and dorsal profiles of node form an angle of 90–105°. Dorsal profile of node weakly convex or nearly straight and moderately long, steeply sloping down to caudal cylinder. The profiles of this slope and of the caudal cylinder form an angle of about 140°. Whole surface of petiolar and postpetiolar nodes microreticulate with a mesh width of 9–13 μ m. Two longitudinal rugae typically demarcate the margin of dorsal petiolar plane while the sides of petiolar tergites are stabilized by one longitudinal carina/ruga on each side.

Overall body color dirty yellow to light brown with a strong yellowish component. Mesosoma, appendages, waist and basis of first gaster tergite usually lighter yellow to dirty yellow. Head dorsum and the posterior surfaces of gaster tergites usually darker, generally yellowish brown. Lighter heads occur.

A more simple means for species delimitation. There is considerable overlap in each of the 29 shape characters and absolute size (Tables 2 and 3) and a much larger one on individual level (data not shown). This excludes a simple separation of

Table 3. Data set of Csösz; nest sample means of morphometric data of the workers of the cryptic species *T. crasecundus* sp. n. and *T. crassispinus* (Karavajev, 1926). Arrangement of data: arithmetic mean ± standard deviation [minimum, maximum]. F values and significance levels p are from an univariate ANOVA; the F values of the most separating characters are given in heavy type.

	<i>T. crasecundus</i> sp. n. (n=55)	ANOVA F, p	<i>T. crassispinus</i> (n=44)
CSb	614 ± 37 [539,718]	1.73, n.s.	623 ± 36 [544,688]
CL/CWb	1.155 ± 0.018 [1.120,1.196]	14.03, 0.000	1.140 ± 0.021 [1.082,1.180]
SL/CSb	0.791 ± 0.013 [0.763,0.836]	6.40, 0.013	0.784 ± 0.013 [0.756,0.811]
PoOc/CL	0.390 ± 0.007 [0.379,0.405]	0.00, n.s.	0.390 ± 0.007 [0.370,0.410]
EL/CSb	0.255 ± 0.007 [0.236,0.279]	0.71, n.s.	0.256 ± 0.005 [0.247,0.268]
FRS/CSb	0.375 ± 0.008 [0.358,0.397]	1.57, n.s.	0.377 ± 0.008 [0.362,0.400]
MW/CSb	0.630 ± 0.010 [0.610,0.662]	1.37, n.s.	0.627 ± 0.017 [0.590,0.678]
ML/CSb	1.227 ± 0.017 [1.193,1.268]	1.01, n.s.	1.223 ± 0.023 [1.183,1.303]
SPBA/CSb	0.298 ± 0.012 [0.277,0.321]	32.89, 0.000	0.312 ± 0.013 [0.282,0.339]
SPTI/CSb	0.333 ± 0.016 [0.300,0.384]	96.86 , 0.000	0.365 ± 0.016 [0.332,0.397]
SPWI/CSb	0.352 ± 0.018 [0.295,0.405]	110.18 , 0.000	0.388 ± 0.016 [0.355,0.422]
SPST/CSb	0.289 ± 0.015 [0.253,0.319]	220.08 , 0.000	0.330 ± 0.011 [0.298,0.356]
SPL/CSb	0.162 ± 0.006 [0.149,0.175]	17.06, 0.000	0.157 ± 0.008 [0.137,0.175]
PEW/CSb	0.269 ± 0.008 [0.252,0.288]	10.18, 0.002	0.275 ± 0.011 [0.255,0.317]
PEH/CSb	0.372 ± 0.009 [0.354,0.398]	7.88, 0.006	0.377 ± 0.009 [0.361,0.400]
NOH/CSb	0.169 ± 0.007 [0.156,0.202]	29.11, 0.000	0.177 ± 0.007 [0.164,0.189]
NOL/CSb	0.254 ± 0.010 [0.232,0.274]	4.68, 0.033	0.258 ± 0.008 [0.237,0.275]
NODL/CSb	0.296 ± 0.014 [0.266,0.318]	0.02, n.s.	0.295 ± 0.017 [0.267,0.340]
PPW/CSb	0.368 ± 0.009 [0.348,0.387]	19.17, 0.000	0.377 ± 0.012 [0.348,0.405]
PPH/CSb	0.350 ± 0.008 [0.335,0.368]	7.74, 0.007	0.356 ± 0.011 [0.340,0.384]
PPL/CSb	0.255 ± 0.009 [0.234,0.273]	1.04, n.s.	0.257 ± 0.008 [0.236,0.272]
PL/CSb [%]	0.413 ± 0.011 [0.383,0.434]	5.74, 0.019	0.419 ± 0.013 [0.393,0.454]

T. crasecundus sp. n. and *T. crassispinus* by single characters. The complex species delimitation procedures presented above require much training of the investigator and a high-quality optical equipment. Even then, data recording for a single nest sample composed of three workers needs 100–120 minutes. In order to allow a practitioner of biodiversity or ecosystem research a more easy approach to the problem, we developed a more simplified determination rule using six absolute measurements. With all measurements given in mm, the discriminant

$$D(6) = 22.058*PoOc+17.640*SL-66.166*SPST+38.233*MW-28.926*PPW-35.873*SPTI-1.797$$

classified 203 nest samples with an error of 3.4%. Samples with an arithmetic mean of $D(6) < 0$ are determined as *T. crassispinus* and those with larger values as *T. crasecundus* sp. n. With PoOc, SL and SPST being recorded bilaterally, a trained investigator needs for the resulting nine measurements about 15 minutes per individual.



Figure 12. *Temnothorax crasecundus* sp. n. Head of holotype.



Figure 13. *Temnothorax crasecundus* sp. n. Lateral aspect of holotype.



Figure 14. *Temnothorax crasecundus* sp. n. Dorsal aspect of holotype.



Figure 15. *Temnothorax crassispinus* (Karavajev). Head of a syntype.



Figure 16. *Temnothorax crassispinus* (Karavajev). Lateral aspect of a syntype.

The most simple means for separation of *T. crasecundus* from *T. nylanderi* is geography: the shortest distance between a site of both species is 1000 km and a closing of this broad gap is prevented by habitat saturation of the omnipresent, highly competitive *T. crassispinus*. A rather simple phenotypical species delimitation is possible using three absolute measurements. With all measurements given in mm, the discriminant

$$D(3) = 129.53 \cdot SPBA - 120.88 \cdot PPW + 133.8 \cdot MpGR + 4.446$$

classified 87 nest samples with an error of 3.4%. Samples with an arithmetic mean of $D(3) < 0.64$ are determined as *T. nylanderi* and those with larger values as *T. crasecundus* sp. n.

Zoogeography and biology. The present zoogeography (Fig. 11) suggests that *T. crasecundus* sp. n. survived the last glaciation in an Aegean / West Anatolian arboreal refuge centre near to sea level. The refuge of *T. crassispinus* should have been situated rather close to that area in the lowlands of the West Balkans along the eastern Adria and was divided from the *T. crasecundus* sp. n. refuge by the Dinaric and Greek mountains. Unhindered by its competing sibling species, there was probably



Figure 17. *Temnothorax crassispinus* (Karavajev). Dorsal aspect of a syntype.

a fast postglacial spreading of *T. crasecundus* sp. n. to the north and northeast over Bulgaria, Romania, Moldova and the southern Ukraine to Caucasia and to the east over Asia Minor to Transcaucasia. Spreading to the west was blocked by a front-line confrontation with *T. crassispinus* – the underlying mechanisms stabilizing this parapatry are probably comparable to those along the Central European front line between *T. nylanderi* and *T. crassispinus* (Pusch et al. 2006). Postglacial spreading of *T. crassispinus* was rapid in northern and northeastern direction. The southern limit of its distribution in the Ukraine and south Russia coincides with the southern border of the natural range of the woodland steppe (Bohn et al. 2000). Despite a larger distance of its Pleistocene refuge from wintercold continental areas of European Russia, *T. crassispinus* obviously arrived here before *T. crasecundus*. This colonization advantage is probably explained by a higher freezing resistance: the most wintercold known site in *T. crassispinus* near Kazan / Russia has a mean January temperature of -13°C and that of *T. crasecundus* near Erzurum / East Anatolia one of -10.5°C (climatic data from www.weather-and-climate.com). Biology and ecology of *T. crasecundus* sp. n. are not studied in detail. Nests were found on ground of deciduous or coniferous forests in microspaces such as hollow acorns, nuts, rotten twigs or galls. Nest populations are monogynous.

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Revision of the genus *Exaesiopus* Reichardt, 1926 (Coleoptera, Histeridae, Sapriniinae)

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Abstract

The genus *Exaesiopus* Reichardt, 1926 is revised herein. It now contains seven species; one new combination is proposed: *Pachylopus glaucus* = *Exaesiopus glaucus* (Bickhardt, 1914), **comb. n.**, and one species is described as new: *Exaesiopus therondi* **sp. n.** from Afghanistan. Subspecies *E. grossipes berberus* Peyerimhoff, 1936 is sunk in synonymy with *E. grossipes* (Marseul, 1855), **syn. n.** Lectotypes and paralectotypes, respectively, for *Saprinus grossipes* Marseul, 1855, *Exaesiopus grossipes berberus* Peyerimhoff, 1936 and a neotype for *Pachylopus glaucus* Bickhardt, 1914 are designated. *Exaesiopus grossipes* is re-described; other species are provided with diagnostic descriptions and supplemented by SEM micrographs, colour images, and line drawings of their male genitalia. A key to species is given. *Exaesiopus glaucus* (Bickhardt, 1914) is newly recorded from the Republic of South Africa; *Exaesiopus torvus* Reichardt, 1926 is new to Uzbekistan and Russia; *Exaesiopus atrovirens* Reichardt, 1926 is new to Ukraine and Tajikistan; and *Exaesiopus henoni* (Schmidt, 1896) is new to Libya and Djibouti.

Keywords

Exaesiopus, revision, Coleoptera, Histeridae, Sapriniinae, Palearctic and Afrotropical Regions

Introduction

The genus *Exaesiopus* was erected by Reichardt (1926) based on the species *Saprinus grossipes* Marseul, 1855. Reichardt (1926) mainly used the presence of prosternal vestiture as the discriminating character from the presumably closely related genus *Hypocaccus*

C. Thomson, 1867. In the same paper he described two further species from ex-Soviet Middle Asia, *E. torvus* and *E. atrovirens*, and combined the species *Pachylopus henoni* Schmidt, 1896 into *Exaesiopus*. Peyerimhoff (1936), based on the elytral punctuation, split the species *Exaesiopus grossipes* into two subspecies: *E. grossipes grossipes* from the northern shore of the Mediterranean Sea and South Europe, and *E. grossipes berberus* from North Africa (Algeria, Tunisia). Théron (1964) added an additional species, *E. laevis* from Somalia, to the genus. Lackner (2010) included a diagnosis and a brief discussion of the monophyly of *Exaesiopus* in his Review of the Palaearctic Genera of Sapriniinae (Histeridae), without having examined the Somali species. In the discussion pertaining to *Exaesiopus* I mentioned that the genus is most likely non-monophyletic and its relationship to the genus *Hypocaccus* should be the focus of future studies. The single synapomorphy of Old World *Exaesiopus* (ciliate pronotal hypomeron) is prone to parallelism and shared with at least two Nearctic species of *Hypocaccus*. The present revision of the genus is therefore meant to act chiefly as a tool for identifying *Hypocaccus*-like Sapriniinae species with ciliate pleura and sterna from the Old World. These are grouped here under the currently valid genus *Exaesiopus*; however, a worldwide review and phylogenetic study of all *Hypocaccus*-like taxa is a prerequisite for a sound classification of this difficult group of beetles. During the years 2009–2014 I have had the opportunity to examine many rare Sapriniinae taxa, including *E. laevis* from Somalia and *Hypocaccus* (*Hypocaccus*) *glaucus* (Bickhardt) from Namibia. The results of these examinations are presented below. This work presents another contribution to ongoing revisionary work on the genera of the subfamily Sapriniinae (Lackner 2009a–c, 2010, 2011a, b; Lackner 2012; Lackner 2013a, b; Lackner and Gomy 2013; Lackner 2014a, b, c, d; Lackner and Tishechkin 2014; Tishechkin and Lackner 2012).

Material and methods

All dry-mounted specimens were relaxed in warm water for several hours or overnight, depending on the body size. After removal from their original cards, the beetles were side-mounted on triangular points and observed under a Nikon 102 stereoscopic microscope with diffused light. Some structures were studied using methods described by Ôhara (1994): the head and male genitalia were macerated in a hot 10% KOH solution for about 15 minutes, cleared in 80% alcohol, macerated in lactic acid with fuchsine, incubated at 60 °C for two hours, and subsequently transferred into a mixture of glacial acetic acid 1 part and methyl salicylate 1 part heated at 60 °C for 15 minutes and cleared in xylene. Specimens were then observed in α -terpineol in a small glass dish. Digital photographs of the male terminalia, mouthparts and antenna were taken by a Nikon 4500 Coolpix camera and edited in Adobe Photoshop CS4. Based on the photographs or direct observations, the genitalia were drawn using a light-box Hakuba klv-7000. SEM photographs were taken with a JSM 6301F microscope at the laboratory of Faculty of Agriculture, Hokkaido University, Sapporo, Japan as well as at the Laboratory of the Electron Microscopy at the Faculty of Biology, Charles University,

Prague, Czech Republic. Colour images were produced by F. Slamka (Bratislava, Slovakia). All available specimens were measured with an ocular micrometre. Beetle terminology follows that of Ôhara (1994) and Lackner (2010). Separate lines of the same label are demarcated by a slash (/). The following acronyms of museums and private collections are used throughout the text:

CAS	Collection Alexander Sokolov, Moscow, Russia;
CYG	Collection Yves Gomy, Nevers, France;
NHM	The Natural History Museum, London, United Kingdom (R. Booth);
MNHN	Muséum National d'Histoire Naturelle, Paris, France (A. Taghavian);
ZMHUB	Museum für Naturkunde, Leibnitz Gesellschaft, Berlin, Germany (B. Jaeger);
MSNM	Museo Civico di Storia Naturale, Milano, Italy (F. Rigato);
NCB	Naturalis Biodiversity Centre, Leiden, Netherlands (B. Brugge);
TLAN	Tomáš Lackner collection, temporarily housed at Naturalis Biodiversity Centre, Leiden, Netherlands;
TMSA	Transvaal Museum of Natural History, Pretoria, Republic of South Africa (R. Müller);
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (B. Kataev).

Abbreviations of morphological measurements follow Ôhara (1994) and are used throughout the text as follows:

APW	Width between anterior angles of pronotum
EL	Length of elytron along sutural line
EW	Maximal width between outer margins of elytra
PEL	Length between anterior angles of pronotum and apices of elytra
PPW	Width between posterior angles of pronotum.

Taxonomy

Exaesiopus Reichardt, 1926

Exaesiopus Reichardt 1926: 14. Type species *Saprinus grossipes* Marseul, 1855, original designation.

Exaesiopus: Reichardt (1941): 156, 329; Peyerimhoff (1936): 226; Kryzhanovskij and Reichardt (1976): 112, 232; Mazur and Kaszab (1980): 7, 61; Vienna (1980): 117, 195; Mazur (1984): 101; Mazur (1997): 263; Yélamos (2002): 245, 338; Mazur (2004): 92; Lackner (2010): 63, 111; Mazur (2011): 210.

Diagnosis. Although the genus has been recently diagnosed (Lackner 2010: 111), it requires modification to accommodate the newly examined species *E. laevis*, the newly

included *E. glaucus* (Bickhardt), and the newly described *E. therondi*. Body in most species strongly convex, especially dorsally; cuticle light to dark brown to almost black, in several species with (feeble) green lustre. Clypeus anteriorly elevated (Fig. 4); frontal stria carinate (Fig. 2); frons with several chevrons, occasionally surrounded by numerous tiny rugae (Fig. 2); pronotal hypomeron setose (Fig. 55). Elytra in most species with punctation; in all species striate; pleura and sterna furnished with short setae (Fig. 41). Prosternum with both sets of striae complete, and occasionally with weakly impressed prosternal foveae (Fig. 6). Protibia with 2–3 (large) teeth topped by triangular denticle; protibial spur in most species inconspicuous (apparently absent); metafemora thickened; metatibiae triangularly dilated and thickened (except for *E. glaucus*).

Differential diagnosis. Members of *Exaesiopus* are generally morphologically most similar to the Old World species of the genus *Hypocaccus*, differing from them chiefly by the setose pronotal hypomeron, strongly convex body, thickened metafemora and triangularly dilated and thickened metatibiae. In North America, however, there are at least two species of *Hypocaccus* (*H. propensus* (Casey, 1893) and *H. servilis* Casey, 1893) that are characterized by the presence of hypomeral setae.

Biology. *Exaesiopus* species are almost exclusively found in sandy soils, beach dunes, river sands, and are also found in sandy areas further inland (e.g. Sahara desert). Morphologically they are well adapted to their fossorial habits. Species are often collected on rotting biological matter, e.g. under faeces, dead fish etc., and are occasionally found under coastal wrack or by shore washing. The middle Asian *E. atrovirens* and *E. torvus* are sometimes found burrowing under *Tamarix*. The biology of *E. laevis* and *E. therondi* is unknown, the latter has been found inside the stomach of Kentish plover (*Charadrius alexandrinus* L. (Aves)).

Distribution. Genus *Exaesiopus* has a generally circum-Mediterranean-Caspian-Turanian distribution, most westerly occurring on the Canary Islands, reaching Afghanistan in the east. Its members have also been collected in the Sahara desert (Laghouat, Algeria), reaching as far east as northern Somalia (*E. laevis*) or Djibouti (*E. benoni*). *Exaesiopus glaucus* is known only from the Republic of South Africa and Namibia.

Exaesiopus grossipes (Marseul, 1855)

Figs 1–34

Saprinus grossipes Marseul 1855: 718, t. XX, fig. 153; Schmidt (1885): 315.

Saprinus rugicollis Schmidt 1890: 19 (*nomen nudum*, given as synonym).

Pachylopus grossipes: Schmidt (1896): 296; G. Müller (1931): 102.

Hypocaccus grossipes: Ganglbauer (1899): 393.

Styphrus grossipes: Jakobson (1911): 651.

Exaesiopus grossipes Reichardt (1926): 16; Reichardt (1941): 329, 330, fig. 117; Peyerimhoff (1936): 227; Kryzhanovskij and Reichardt (1976): 232, Figs 455–458; Vienna (1980): 196, fig. 69; Mazur and Kaszab (1980): 61, Figs 31, 34 D, E, F; Mazur (1984): 101; Mazur (1997): 263; Yélamos (2002): 338, Figs 12E, 161G,

169, 170A; Mazur (2004): 92; Lackner (2010): 112, Figs 19, 54, 89, 118, 339–359; Mazur (2011): 210.

Exaesiopus grossipes berberus Peyerimhoff 1936: 227 – **syn. n.**

Type locality. Spain, France: Bayeux, Marseille.

Type material examined. *Saprinus grossipes*: Lectotype, present designation, sex undetermined, pinned, right mesotibia, left mesotarsus, both hind legs missing, with the following labels: “153 / Saprinus / grossipes / m / Marseille / Barage?” (round illegible label, written); followed by: “MUSEUM PARIS / COLL. / DE MARSEUL 1890” (printed); followed by: “TYPE” (red-printed label); followed by: “Saprinus grossipes / Marseul, 1855 / LECTOTYPE 2014 / des. T. Lackner” (red label, written).

Exaesiopus grossipes berberus: Lectotype, ♀, side-mounted on a triangular point, final two metatarsomeres on right hind leg missing, with the following labels: “Laghouat” (written); followed by: “Coll. Hénon / T Théry” (written); followed by: “Saprinus / grossipes berberus / Peyerimhoff / TYPE” (written); followed by: “Exaesiopus / grossipes berberus / Peyerimhoff, 1936 / LECTOTYPE / des. T. Lackner 2014” (red label, written) (MNHN). Paralectotypes, 2 ♂♂, both mounted on a single pin on triangular mounting points with extracted genitalia, with the following label: “Bône” (written); followed by: “Coll. Hénon / T Théry” (written); followed by: “Sapr. grossipes / berberus Peyerimh / TYPE” (written); followed by: “Exaesiopus / grossipes berberus / Peyerimhoff, 1936 / PARALECTOTYPE / des. T. Lackner 2014” (red label, written) (MNHN).

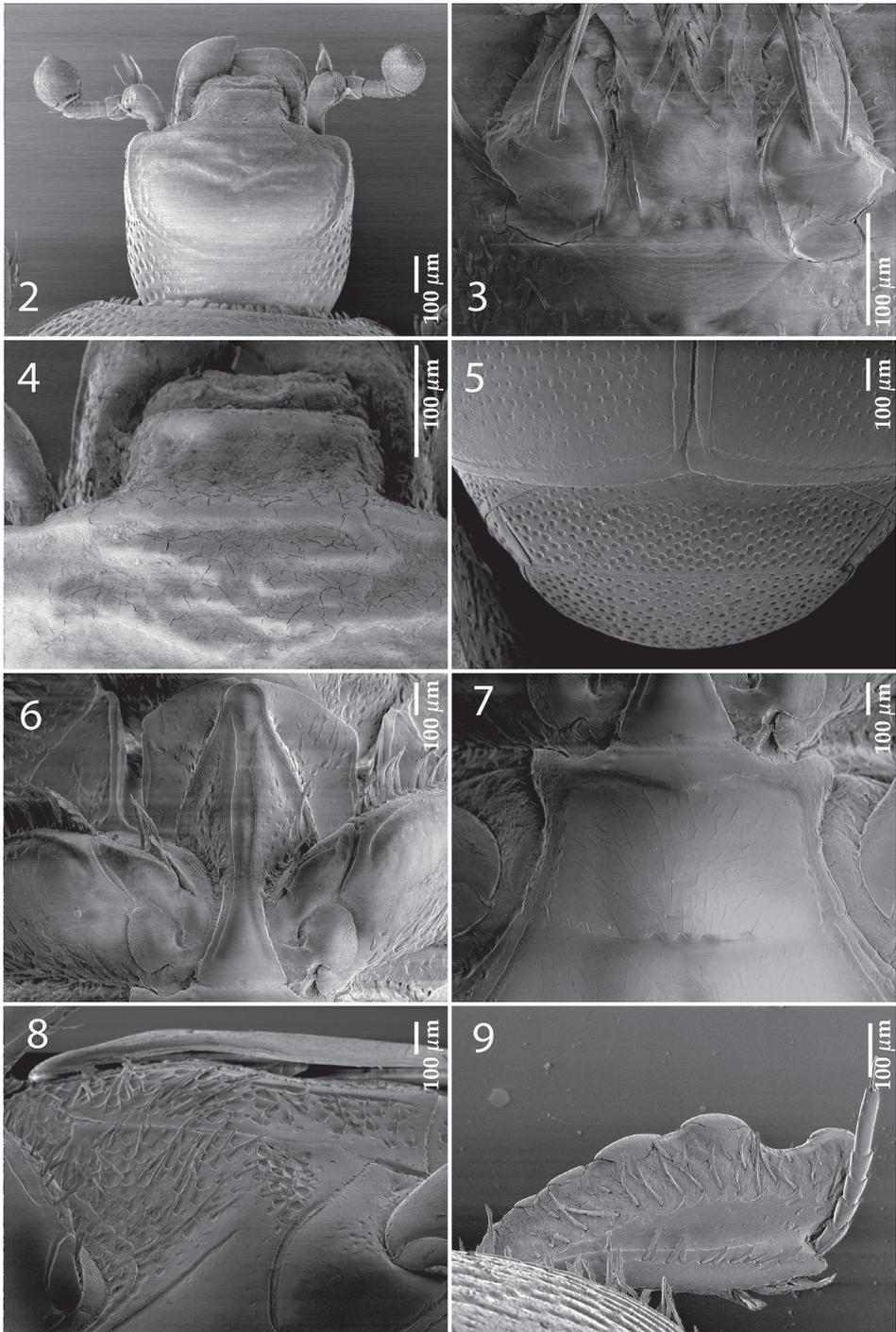
Note. Peyerimhoff (1936: 227) distinguished the subspecies *E. g. berberus* from the nominotypical one based on elytral punctation that should cover almost the entire elytral disc basally and laterally up to the second dorsal elytral stria. Among the three specimens that he furnished with type labels, however, only the female from Laghouat (Algeria) exhibits these characteristics; the two males from Bône [=Annaba, Algeria] have their apical half (approximately) impunctate and the punctation of their elytral discs terminates in third elytral stria. Therefore, a female from Laghouat has been selected for the Lectotype. Peyerimhoff (1936: 227) himself did not specify which specimen(s) belonged to the type series; he listed several localities with his extremely brief diagnosis of the new subspecies. Both Laghouat and Bône [=Annaba] were among the listed localities.

Additional material examined. BULGARIA: 1 ♀, Asenovgrad, vi.1963, A. Olexa leg. (TLAN); 1 spec., Nessebar, 30.v.1996, O. Majzlan leg. (TLAN); 1 spec., Kazanlak, vi. 1963, A. Olexa leg. (TLAN); 1 spec., Plovdiv, Rektořík leg. (TLAN); 1 ♂, Newrokop, 19.vi.1938, leg. Hlinikowski (TLAN); 1 spec., SW Bulgaria, 2 km N Gara Pirin, 11.-12.vi. 1983, leg. Hieke (NCB). BOSNIA-HERZEGOVINA: 1 ♀, Mostar, V. Zoufal leg. (ZMHUB). MACEDONIA: 2 specs., 5 km E of Velandovo, 31.v.1992, P. Zahradník leg. (TLAN). SLOVAKIA: 1 ♂, 1 ♀ + 1 spec., Čenkov, 24.vi. 1987, V. Kubáň lgt. (TLAN); 1 spec., ibid, but, 29.v.1993, T. Růžička leg. (TLAN); 2 specs., Kameničná-Balvány 8174c, 13.vii.2000, O. Majzlan leg. (TLAN). SERBIA: 1 spec., Veliko Gradište, 2.ix.1955, Stančić leg. (TLAN); 1 spec., Vranje, 4.vi.1968, collector



Figure 1. *Exaesiopus grossipes* (Marseul, 1855) habitus.

unknown (TLAN). ITALY: 1 ♀, Piemont, coll. Bickhardt (MNHN); 1 ♂, Torino, coll. Fea (MNHN); 1 ♂ + 1 ♀, Lagnola (?), xi. 1910, Sekera leg. (TLAN); 1 spec., PO, Fiume, Piacenza, 2.vi.1963, leg. P. Ratti (NCB); 1 spec., Veneto, Caorle, v. 1999, Clereau leg. (CAS); 2 ♂♂ + 1 ♀, Ponferrada, Paganetti (ZMHUB). FRANCE: 1 ♂, Bouches-du-Rhône, Les Saintes-Maries-de-la-Mer, 18.iv.1978, P. Queney leg. (CYG); 1 ♀, Charente Maritime, île de Ré, viii.1978 (P. Queney leg. (CYG); 1 ♂ + 1 ♀, Gard, Le Grau-du-Roi, 31.viii.1947, J. Théron leg. (CYG); 4 ♂♂ + 1 ♀, Gironde, Soulac, 12.iv.1890, E. Giraud leg. (CYG); 1 ♀, idem, but 6.vii.1975, G. Tempère leg. (CYG); 1 ♀, Manche, Portbail, beach, 22.vi.1955, H. Chevin leg. (CYG); 1 ♂, Pyrénées, (CYG); 1 ♂, Montelimar, 7.v.1912, Laboissere leg. (MNHN); 1 ♀, Plouharnel, 1878, no further data (MNHN); 5 specs., Bretagne, Nicolas, no further data (MNHN); 1 ex., Var, Nice, flooding, v. 1951 (MNHN); 3 specs., Grande Coté, Royau, v. 1918, Chobaut & R. Lebon (MNHN); 1 spec., Aveyron, Millau, 6.iv.1960, Fages lgt. (MNHN); 2 specs., Ile de Ré, coll. Bonnaire, no further data (MNHN); 3 specs., La Rochelle d'Orbigny, no further data (MNHN); 4 specs., Carcassonne, no further



Figures 2–9. *Exaesiopus grossipes* (Marseul, 1855) **2** head, dorsal view **3** mentum, ventral view **4** clypeus **5** propygidium + pygidium **6** prosternum **7** mesoventrite **8** lateral disc of metaventrite + metepisternum **9** protibia, dorsal view.

data (MNHN); 2 specs., Pluharnel, dept. de Morbihan, no further data (MNHN); 2 specs., St. Jean de Monts, P. Sirguy (MNHN); 1 spec., Agen, 30.v.1908, G. Nicolas (MNHN); 2 specs., Toulouse, Col. D. Grenier (MNHN); 1 spec., Grau du Roi, 11.iv.1955, J. Théron leg. (MNHN); 2 specs., *ibid*, but 2.ii.1938, J. Théron leg. (MNHN); 1 spec., *ibid*, but 10.ix.1948, J. Théron leg. (MNHN); 1 spec., *ibid*, but 19.v.1970, J. Théron leg. (MNHN); 1 spec., *ibid*, but 15.v.1951, J. Théron leg. (MNHN); 1 spec., *ibid*, but 1.x.1949, J. Théron leg. (MNHN); 2 specs., *ibid*, but 9.iii.1940, J. Théron leg. (MNHN); 2 specs., Pont du Gard, 3.iii.1927, J. Théron leg. (MNHN); 2 specs., *ibid*, but 29.v.1928, J. Théron leg. (MNHN); 2 specs., *ibid*, but 22.ix.1931, J. Théron leg. (MNHN); 1 spec., Camargue, St. Maries, 9.x.1928, L. Puel leg. (MNHN); 5 specs., Vendée, St. Jean de Monts, vi.1926, P. Sirguy leg. (NCB); 2 ♂♂ + 1 ♀, *ibid*, but MNHN; 1 spec., Morgat, Brittany, no further data (BMNH); 2 specs., France, no further data (BMNH); 1 spec., Erqny, Côtes du Nord, H.D. Preston leg. (BMNH); 1 spec., Provence, no further data (BMNH); 3 specs., St. Jean de Monts (Vendée), P. Sirguy leg., 1926 (BMNH); 1 spec., Manche, Utah Beach, 6.vi.[19]64; 1 spec., Beziers, no further data (BMNH) 1 spec., *ibid* but ZMHUB; 1 spec., Grau du Roi, 29.iii.1943, J. Théron leg. (ZIN); 1 spec., Lyon, in Rhône, no data or collector (ZIN). HUNGARY: 1 spec., Hungary, no further data (BMNH); 1 ♂, Jarabzásállás, 30.v.1971, P. Polák leg. (TLAN); 1 ♂, Dunakeszi, no further data (ZMHUB). SPAIN: 1 spec., Valencia, no further data (MNHN). IRAQ: 1 spec., Mesopotamia, Millingen, no further data (BMNH); 1 ♀, Mesopotamia, no further data (ZMHUB). RUSSIA: 1 spec., Volgogradskaya obl., Tsimlya, 27.vii.1894, collector unknown (ZIN). UKRAINE: 1 spec., Stan. Luganskaya, Lugansk okr., 17.vi.1928, collector unknown (ZIN); 2 ♀♀, Khersonskaya oblast, Alyoshki, Dneprovskij uezd, 26.v.1926, D. Znojko leg.; 2 specs., *ibid*, but 19.v.1929, N. Kostenko leg.; 1 spec., Khersonskaya oblast, Burkutskie plavni [zapovednik], 17.v.1929, N. Kostenko leg.; 1 spec., ditto, but Kazach village, 7.vi.1928, N. Kostenko leg. (all exs. ZIN). GREECE: 1 spec., Peloponese occid., Epitalion, Alfios River, nr. Pyrgos, 13.iv.1995, T. Kopecký leg. (TLAN); 1 ♀, Pirgos, 1.v.1971, leg. Wewalka leg. (TLAN); 1 spec., Peloponesus, Xylokatron, 22.v.1962, H. Pochon leg. (MNHN); 1 spec., Thessalia, no further data (ZMHUB). MOROCCO: 1 ♀, Tauorirt, 10.iii.1993, G. Chavanon leg. (CYG); 1 ♂, Morocco centr., Moyen Atlas, Aguelmame Azegza lake, 22.–26.vi.1998, T. Lackner leg. (TLAN); 1 spec., Ouarzazate prov., Oued Draa River valley, Agdz env., N 30.40.52 W 006.25.08, 29.iii.2011, in human faeces, A. Gusakov leg. (CAS); 1 ♂, Beni Ounif near Figuig, 11.v.1944, Barbier leg. (MNHN). TUNISIA: 1 ♂, Medjez el Bab, v.1935, R. Demoffys leg. (CYG); 1 ♂, Gabès, v. 1944, R. Demoffys leg. (CYG); 1 spec., Zarzia, 5.–11.v.1977, M.A. Hielkema leg. (NCB). 1 ♀, Tunis, i–ii.1882, G. & L. Doria leg. (ZMHUB); 1 spec., Hammamet mer., 25.iii.–4.iv.1992, A. Pütz leg.; 2 ♀♀, 1 ♂ & 1 spec., 6–11.vi.1982, Kairuan, A. Olexa leg. (TLAN). ALGERIA: 1 ♀, Bona [=Bône?], Desbr., no further data (ZMHUB); 2 ♂ + 1 ♀, Oued Sebaou near Tizi-Ouzou, 25.vi.1908, collector unknown (MNHN); 2 ♀♀, Aïn Sefra, v. 1936, collector unknown (MNHN); 1 ♂, *ibid*, but coll. Bonnaire (MNHN); 1 ♀, Bou-Ktoub, S of Oran, Déchouat leg. (MNHN); 1 ♀, Biskra, v. 1885, L. Bleuse leg. (MNHN);

1 ♀, Bou-Saada, no further data (MNHN); 1 ♀, south of Oran, no further data (MNHN) 1 ♂ + 1 ♀, Colomb-Béchar, 1912, P. Germain leg. (MNHN).

Redescription. Although this species has been recently re-described by the author (Lackner 2010: 112–116), I prefer to repeat this re-description here for the reason that the following species are morphologically rather similar to *E. grossipes*. Those species are consequently provided only with diagnostic descriptions outlining their respective differences.

Body length: PEL: 2.10–2.75 mm; APW: 0.825–1.00 mm; PPW: 1.625–2.25 mm; EL: 1.25–2.00 mm; EW: 1.875–2.50 mm.

Body (Fig. 1) oval, convex, cuticle light to dark brown, sometimes with feeble bronze or greenish metallic tinge; legs, mouthparts and antennae rufopiceous.

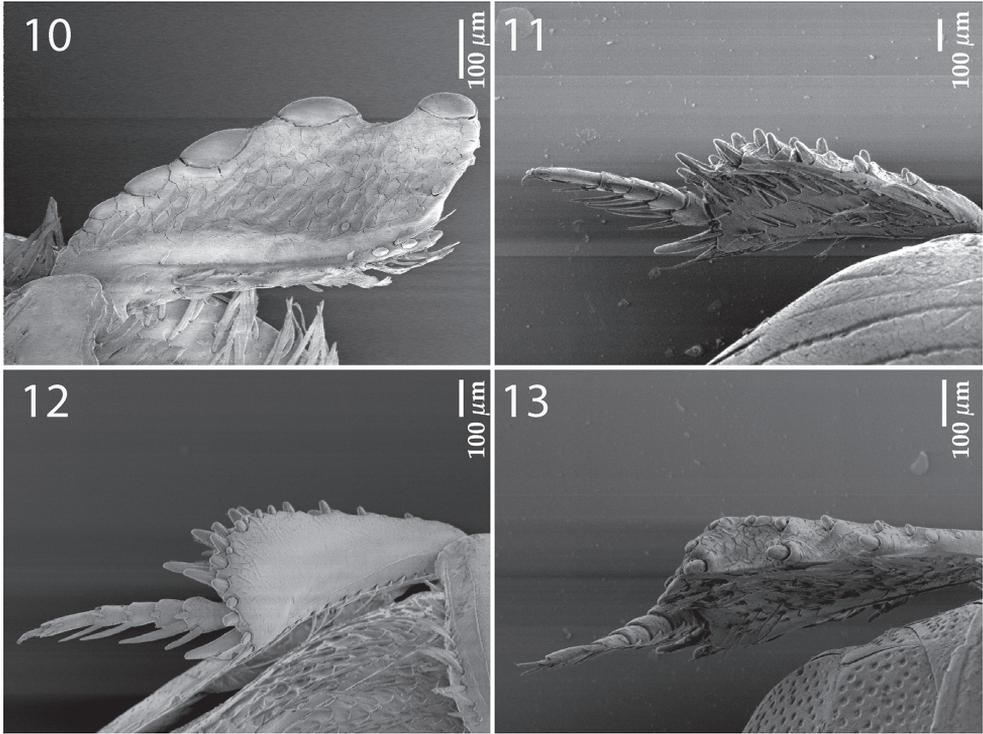
Antennal scape with few short setae; club (Fig. 2) round, entire surface with thick short yellow sensilla intermingled with sparse slightly longer setae; sensory structures of the antennal club (Fig. 14) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts: mandibles (Fig. 15) stout, outer margin slightly curved; mandibular apex bluntly pointed; sub-apical tooth of left mandible large, almost perpendicular; labrum (Fig. 16) sparsely punctate, shallowly depressed medially, two labral pits present, two labral setae arising from each; epipharynx almost completely hidden under labral fold; terminal labial palpomere elongated, its width less than half its length; mentum (Fig. 3) square-shaped, with deep antero-median notch; anterior margin with few long setae, lateral margins with single row of sparse shorter ramose setae; cardo of maxilla with few short setae on lateral margin; stipes triangular, with three much longer setae; terminal maxillary palpomere somewhat thickened, its width less than half its length, about twice as long as penultimate.

Clypeus (Fig. 4) rectangular, almost smooth, can be slightly rugose, anterior margin elevated, clypeus depressed medially; frontal stria well impressed, almost straight (sometimes somewhat curved outwardly), carinate, continued as carinate supraorbital and postorbital striae; frons with two to several irregularly shaped carinate transverse rugae or chevrons; eyes flattened, inconspicuous from above.

Pronotal sides slightly convergent forwards; apical angles blunt; marginal stria complete; pronotal disc convex, with round dense punctation, forming transverse rugae laterally, postero-median part of disc usually smooth, at times entire disc punctate (punctation can also stop short of lateral pronotal margin); pronotal base with a double row of round dense punctures; pronotal hypomeron with amber setae; scutellum small, visible.

Elytral humeri slightly prominent, elytra broad, almost as broad as long at its widest point; elytral epipleura with microscopic punctures, almost smooth; marginal epipleural stria complete; marginal elytral stria deeply impressed, continued as well impressed apical elytral stria; regular row of round punctures present along elytral marginal stria. Humeral elytral stria weakly impressed on basal third, sometimes doubled; inner subhumeral stria present medially, deep and rather long, rarely joining marginal elytral stria; elytra with four dorsal punctate elytral striae 1–4, all striae approximately reaching elytral half



Figures 10–13. *Exaesiopus grossipes* (Marseul, 1855) **10** protibia, ventral view **11** mesotibia, dorsal view **12** ditto, ventral view **13** metatibia, dorsal view.

apically (occasionally slightly surpassing it), fourth elytral stria basally connected with sutural elytral stria; sutural stria deeply punctured, apically joining apical elytral stria. Elytral punctation variable, often confined to apical half of elytra, along elytral suture reaching almost anterior third of elytral disc, punctures regular and deep, separated by about half to their own diameter, occasionally (often in specimens from North Africa) covering most part of elytral disc (elytral flanks and humeri almost always smooth).

Propygidium (Fig. 5) almost completely exposed, long, covered with coarse and dense regular punctation; punctation of pygidium (Fig. 5) sparser and finer, punctures separated by about 1–3 times their diameter.

Anterior margin of median portion of prosternum (Fig. 6) regularly rounded; prosternal foveae weakly to well impressed, small and often indiscernible under conventional binocular microscope; prosternal process slightly to deeply concave, dorsally impunctate, laterally substrigulate-punctate, few microscopic setae present; carinal prosternal striae divergent between procoxae, subparallel, vaguely united in front, at times obliterated on their anterior third; lateral prosternal striae well impressed, carinate, convergent anteriorly, united in front of apices of carinal prosternal striae.

Mesoventral disc (Fig. 7) somewhat convex, almost smooth, slightly wider than long; meso-metaventral sutural stria well impressed, with several accompanying punc-

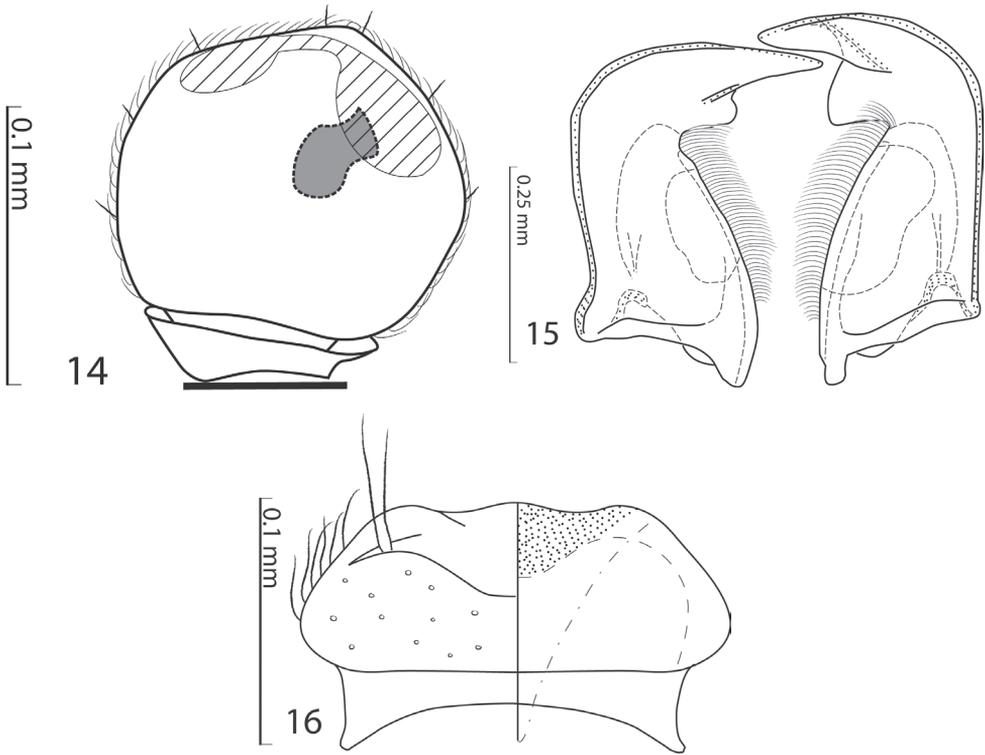
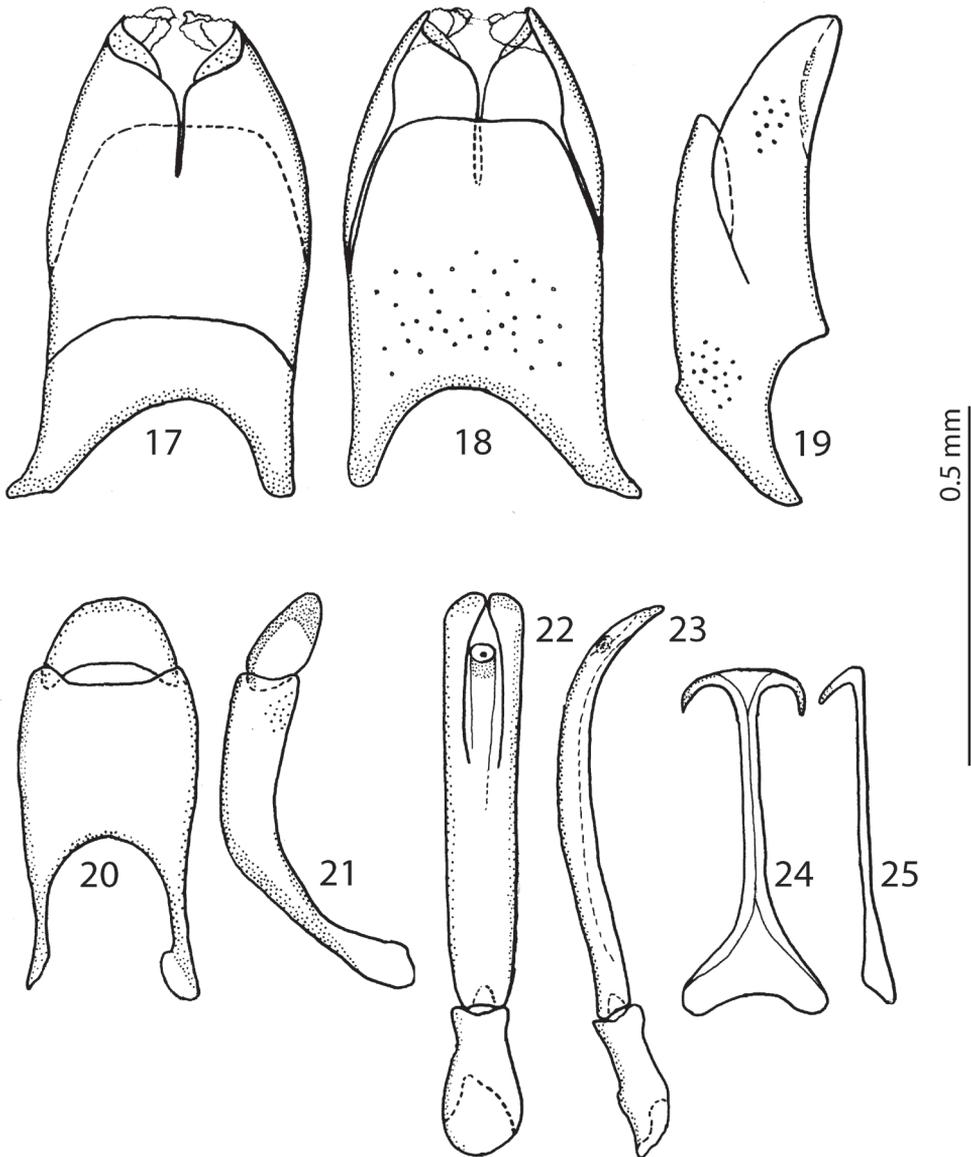


Figure 14–16. **14** *Exaesiopus grossipes* (Marseul, 1855) sensory structures of the antenna **15** mandibles, dorsal view **16** labrum, left half depicting dorsum; right half depicting underside.

tures; intercoxal disc of metaventricle with longitudinal depression in male, smooth, basally with irregular sparse shallow fine punctures; lateral metaventral stria (Fig. 8) well impressed, carinate, obliquely arcuate, apically almost reaching metacoxa; lateral disc of metaventricle concave, with shallow setiferous punctures of various sizes, separated by approximately their own diameter; metepisternum with even denser and coarser punctation and setae, on apical third + metepimeron punctation much finer and sparser; metepisternal stria deeply impressed, present on metepimeron and approximately apical third of metepisternum.

Intercoxal disc of first abdominal sternite almost completely striate laterally; disc almost smooth, with sparse punctures along apical margin; lateral portion of disc of all visible abdominal sternites with short setae.

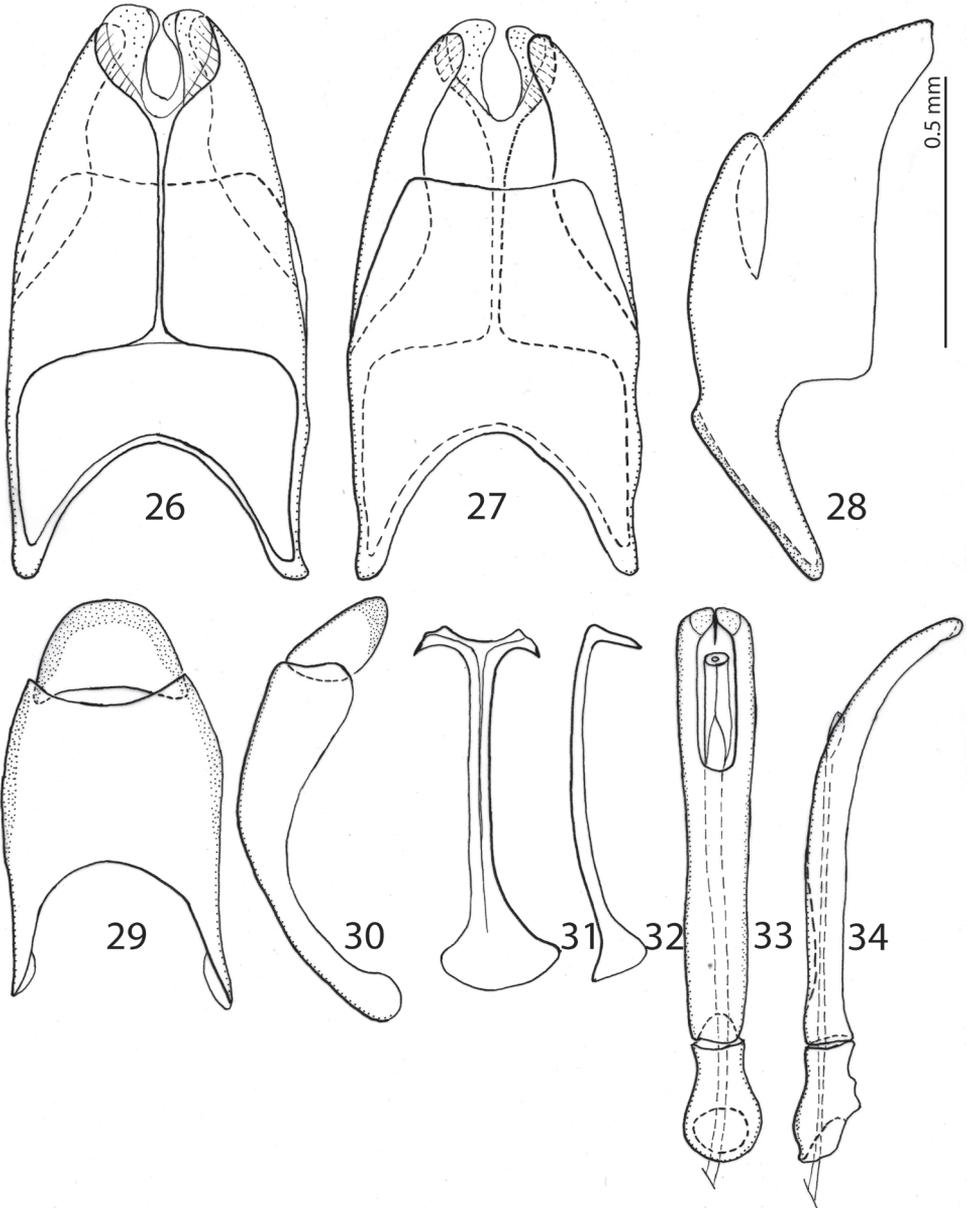
Protibia (Fig. 9) on outer margin with two to three low teeth, topped with triangular to rounded (blunt, if worn) denticle followed by two inconspicuous rounded denticles; setae of outer row sparse, moderately long; setae of median row shorter than those of outer row, sparse; anterior protibial stria shortened apically; protibial groove shallow; protibial spur (Fig. 10) minuscule, growing out from apical margin of protibia; outer part of posterior surface of protibia (Fig. 10) obscurely variolate, vaguely separated from comparatively narrower median part, posterior protibial stria complete,



Figures 17–25. *Exaesiopus grossipes* (Marseul, 1855) from Bulgaria, 8th sternite and tergite, **17** ventral view **18** ditto, dorsal view **19** ditto, lateral view **20** 9th + 10th tergites, dorsal view **21** ditto, lateral view **22** aedeagus, dorsal view **23** ditto, lateral view **24** spiculum gastrale, ventral view **25** ditto, lateral view.

terminating in two minute inner posterior denticles; inner margin of protibia with double row of short dense ramose setae.

Mesotibia (Fig. 11) moderately dilated and thickened, outer margin with two rows of sparse short denticles; setae of outer row well sclerotized, comparatively short; setae of median row shorter and sparser, covering most of posterior surface;



Figures 26–34. *Exaesiopus grossipes* (Marseul, 1855) from Tunisia, 8th sternite and tergite, **26** ventral view **27** ditto, dorsal view **28** ditto, lateral view **29** 9th + 10th tergites, dorsal view **30** ditto, lateral view **31** spiculum gastrale, ventral view **32** ditto, lateral view **33** aedeagus, dorsal view **34** ditto, lateral view.

posterior mesotibial stria vaguely impressed, shortened apically; mesotibial spur stout, prominent and long; anterior face of mesotibia (Fig. 12) smooth; anterior mesotibial stria shortened apically; claws of last tarsomere bent, shortened, shorter than half its length.

Metatibia (Fig. 13) triangularly dilated and thickened apically; outer margin with four widely-spaced short rounded denticles, a single row of tiny sparse rounded denticles present dorsally on thickened anterior face of metatibia; setae of intermedian row shorter and denser, cover almost the entire posterior face of metatibia; otherwise metatibia similar to mesotibia.

Male genitalia. Eighth sternite (Figs 17–18) on apical half longitudinally separated medially, with tiny asetose vela, eighth sternite and tergite fused laterally (Fig. 19). Ninth tergite (Figs 20–21) apically with faint emargination; basally deeply emarginated; tenth tergite (Fig. 20) apically outwardly arcuate, basally faintly inwardly arcuate. Spiculum gastrale (Figs 24–25) typical for the subfamily representing the most common type with ‘head’ and ‘tail’ (sensu Caterino & Tishechkin, 2013); ‘tail’ cordate, ‘head’ with two narrow, curved arms. Aedeagus (Figs 22–23) tube-like, slender, basal piece of aedeagus rather short, ratio of its length : length of parameres 1:3.5; parameres fused along their basal two-thirds, aedeagus slightly curved ventrad (Fig. 23).

Differential diagnosis. *Exaesiopus grossipes* differs from the three species *E. heboni*, *E. therondi* and *E. laevis* chiefly by the shape of its protibia, which is on its outer margin furnished with three low teeth topped by triangular or rounded denticles (Figs 9, 10), whereas the three other mentioned species have their protibia furnished with two large teeth topped by triangular denticles on outer margin (Figs 61, 79 & 114). From *E. atrovirens* and *E. glaucus* it differs chiefly by the absence of a green metallic hue of the dorsum (compare Figs 1 with 73 & 98); from *E. glaucus* it differs furthermore by thickened and dilated metatibia (compare Figs 13 with 106). On the other hand, some specimens of *E. grossipes* (especially from N. Africa that formerly belonged to the subspecies *berberus*) can resemble the specimens of Middle-Asian *E. torvus* by their densely punctate dorsum. These specimens differ, however, from *E. torvus* by their respective male genitalia (compare Figs 17–34 with 64–72) and the less punctate pronotal disc (see also Key to the species for details, below). Most specimens of *E. grossipes*, however (especially those from the northern shore of the Mediterranean Sea and South Europe) have distinctly less punctate dorsum than the specimens of *E. torvus*.

Biology. This species is found on the beach under coastal wrack as well as further away from the waterfront, almost exclusively on sandy soil. Beetles can be found under rotting fish, excrements or buried under vegetation.

Distribution. Known from the Canary Islands, Morocco, Algeria, Tunisia, Libya, Spain, France, Italy, Greece, Bosnia and Herzegovina, Macedonia, Bulgaria, Russia, Serbia, Slovenia, Ukraine, Slovakia, Hungary, Austria, Iraq.

Remarks. A variable species, covering vast area from the Canary Islands in the west to Iraq in the east. Its external morphology as well as male genitalia exhibit a certain degree of variation (compare Figs 17–25 and 26–34), but I find it difficult to discern discrete states among the variation and prefer to lump all examined specimens under the same species.

***Exaesiopus henoni* (Schmidt, 1896)**

Figs 35–54

Pachylopus henoni Schmidt 1896: 206*Saprinus henoni*: Bickhardt 1910: 106.*Exaesiopus henoni*: Mazur (1984): 101; (1997): 264; (2004): 92; (2011): 210.**Type locality.** Aïn Sefra, Algeria.

Type material examined. Lectotype, ♀, side-mounted on triangular point, left metatarsus missing, with the following labels: “♀” (printed); followed by: “henoni m / Aïn Sefra” (written); followed by: “coll Schmidt- / Bickhardt” (printed); followed by: “Pachylopus / henoni Schmidt / Coll. Schmidt-Bickhardt” (printed); followed by: “LECTOTYPE / N. Dégallier” (red label, printed) (ZMHUB). 1 ♂ paralectotype, with the following labels: “Aïn Sefra / Hénon” (printed); followed by: “Pachylopus / Henoni / Schm. Type” (written); followed by: “PARA- / LECTOTYPE / N. Dégallier” (printed) (BMNH). 1 ♀, paralectotype, with the following labels: “Aïn Sefra / Hénon” (printed); followed by: “Pachylopus / Henoni / Cotype ‘96 Sch.” (written); followed by: “PARA- / LECTOTYPE / N. Dégallier” (printed) (BMNH); Paralectotypes: 1 ♂ & 4 specs., with the following labels: “Aïn-Sefra / Hénon” (printed); followed by: “Museum Paris / ex coll. / P. de Peyerimhoff” (printed); followed by: “PARA - / LECTOTYPE / N. Dégallier” (red label, printed) (MNHN).

1 Syntype, ♀, side-mounted on a triangular point, with the following labels: “♀” (printed); followed by: “Type” (brick-red label, printed); followed by: “Aïn-Sefra / HÉNON” (printed); followed by: “Pachylopus / Henoni typ” (written); followed by: “Pachylopus / henoni Schmidt / Coll. Schmidt-Bickhardt” (printed); 1 Syntype, ♀, side-mounted on a triangular point, with the following labels: “♀” (printed); followed by: “Type” (brick-red label, printed); followed by: “Aïn-Sefra / HÉNON” (printed); followed by: “Pachylopus / Henoni m” (written); followed by: “coll. J. Schmidt” (printed); followed by: “Pachylopus / henoni Schmidt / Coll. Schmidt-Bickhardt” (printed); 1 Syntype, ♀, side-mounted on a triangular point, with the following labels: “♀” (printed); followed by: “Type” (brick-red label, printed); followed by: “Aïn-Sefra / HÉNON” (printed); followed by: “Pachylopus / Henoni m” (written); followed by: “Pachylopus / henoni Schmidt / Coll. Schmidt-Bickhardt” (printed) (all syntypes ZMHUB).

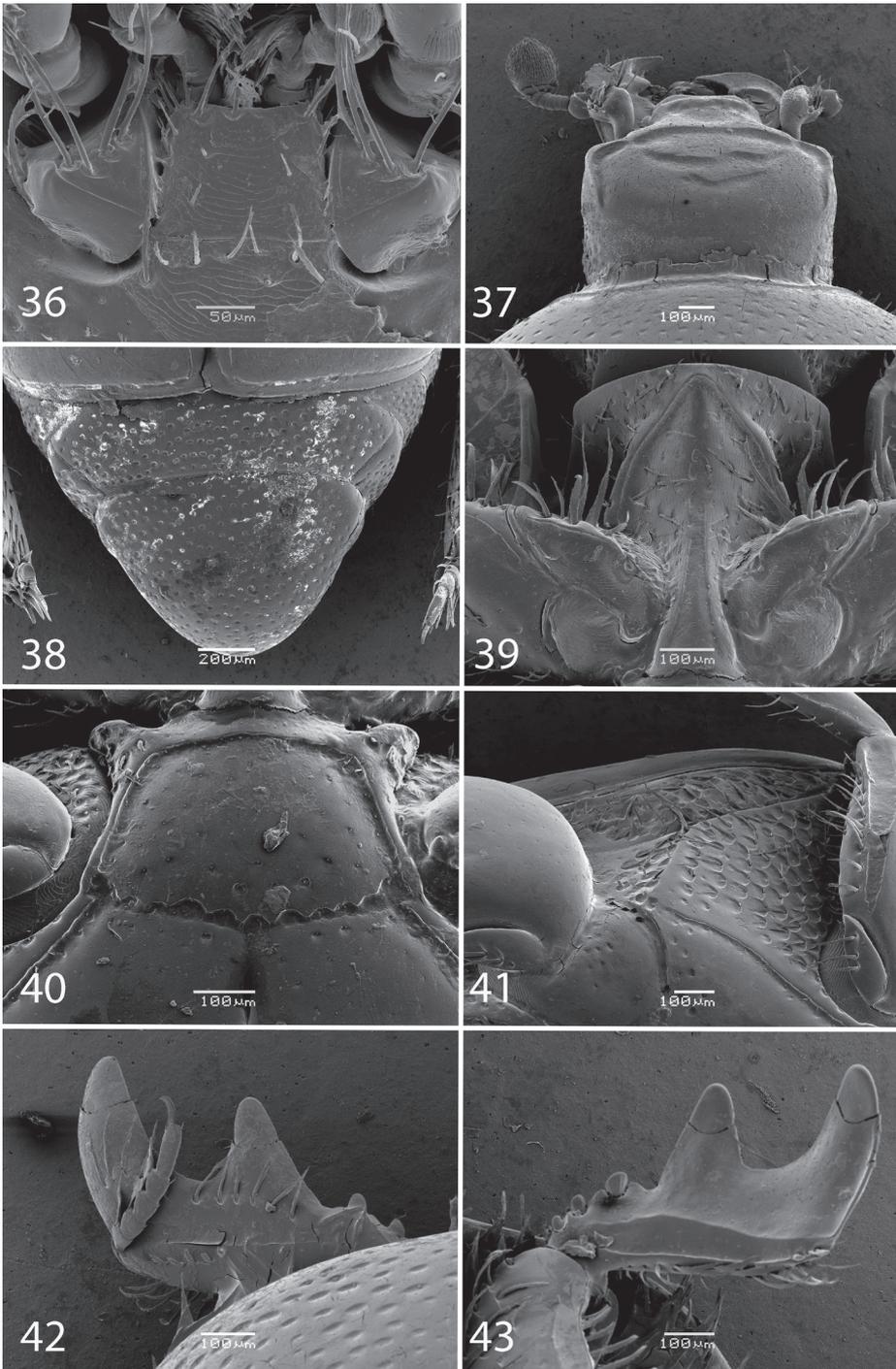
Additional material examined. ALGERIA: 1 spec., Mraier, D. de Constantine, coll. de Vauloger (ZIN); 4 ♂♂ + 1 ♀ + 3 specs., Aïn Sefra, Hénon (MNHN); 1 spec., idem, but, v-vi.1896, L. Bleuse leg. (MNHN); 1 ♂ + ♀, idem, but CYG; 3 specs., Colomb-Béchar, 27.iv.1923, J. Théron leg. (MNHN); 1 spec., ibid, but 30.iv.1923 (MNHN); 2 specs., Mraier, D. de Constantine, Vauloger (MNHN); 1 spec., Biskra, Dr. H.J. Veth leg. (NCB); 3 specs., Aïn Sefra, 26.iv.1987, A. Olexa (TLAN); 1 ♀, ibid, but 25.–27.iv.1987, D. Král leg. DJIBOUTI: 1 ♀, As-Eyla, viii.1976 (NCB). LIBYA: 1 spec., Tripolitania, Wadi Sofeggin, 21.–23.v.1963, no collector (MNHN).



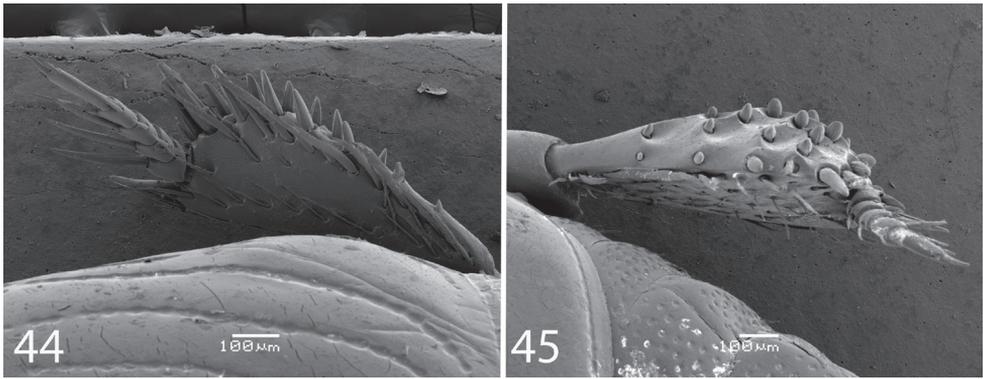
Figure 35. *Exaesiopus henoni* (Schmidt, 1896) habitus.

Diagnostic description. Body length: PEL: 2.50–2.75 mm; APW: 0.875–1.00 mm; PPW: 1.875–2.00 mm; EW: 2.125–2.20 mm; EL: 1.625–1.80 mm. Body (Fig. 35) similar to *E. grossipes*, but without any trace of metallic tinge; antennae similar to those of *E. grossipes*; sensory structures of the antennal club not examined. Mouthparts generally similar to those of *E. grossipes*; mentum (Fig. 36) sub-quadrate, feebly inwardly arcuate on anterior margin; anterior margin with several long setae, lateral margins with single row of sparse shorter ramose setae; stipes of maxilla with four setae (three in *E. grossipes*); rest of the mouthparts as in *E. grossipes*. Clypeus (Fig. 37) as in *E. grossipes*, almost smooth; frontal and supraorbital striae as in *E. grossipes*; postorbital stria missing (present in *E. grossipes*); frons with two deep chevrons.

Pronotal disc (Fig. 35) with ellipsoid to round, rather sparse punctation, punctures separated by their own to several times their diameters, postero-median part of disc always smooth, punctation stopping short of lateral pronotal margin leaving a narrow impunctate band; rest of the pronotum as in *E. grossipes*. Elytra generally as in *E. grossipes*; inner subhumeral stria shortly present medially; dorsal elytral striae for short distance surpassing elytral half; elytral punctation variable, in most specimens present only on fourth elytral interval, but can also at times be present on other elytral inter-



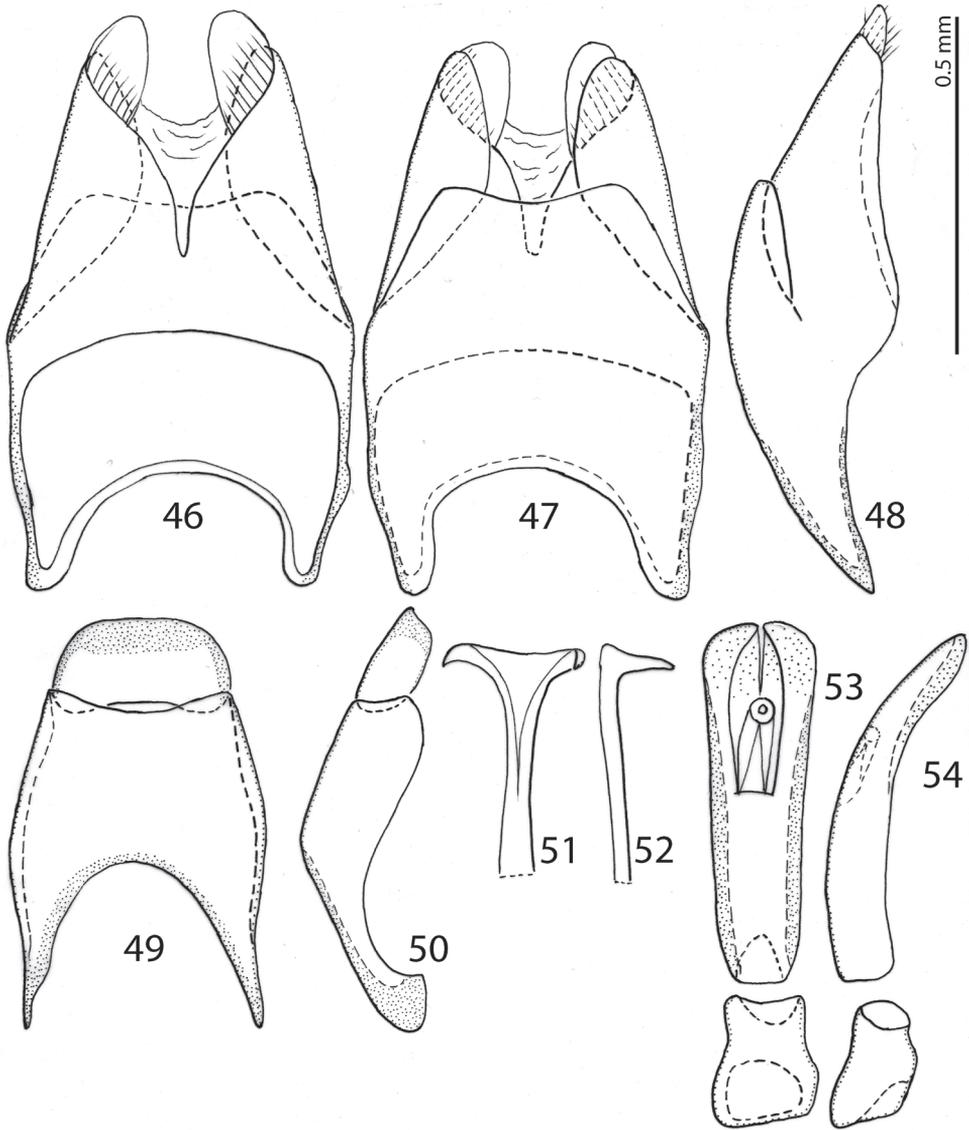
Figures 36–43. *Exaesiopus henoni* (Schmidt, 1896) **36** mentum, ventral view **37** head, dorsal view **38** propygidium and pygidium **39** prosternum **40** mesoventrite **41** lateral disc of metaventrite + metepisternum **42** protibia, dorsal view **43** ditto, ventral view.



Figures 44–45. *Exaesiopus henoni* (Schmidt, 1896) **44** mesotibia, dorsal view **45** metatibia, dorsal view.

vals (a specimen from Libya), or almost completely missing (a specimen from Algeria); along elytral suture can reach almost elytral base, punctures irregular, variously deep, separated often by several times their own diameter, elytral flanks and humeri always smooth. Propygidium (Fig. 38) and pygidium similar to those of *E. grossipes*; punctuation somewhat sparser (compare Figs 5 and 38). Prosternum (Fig. 39) generally similar to that of *E. grossipes*, but prosternal foveae very weakly impressed, often indiscernible (absent?); prosternal process deeply concave, constricted, prosternal structures and configuration of the two sets of prosternal striae similar to those of *E. grossipes*. Disc of mesoventrite (Fig. 40) almost smooth, similar to that of *E. grossipes*, but almost as long as wide; meso-metaventral sutural stria undulate; intercoxal disc of metaventrite with longitudinal depression in both sexes, more prominent in male, smooth, basally with several irregular rows of sparse punctures; lateral metaventral stria (Fig. 41) obliquely arcuate, apically almost reaching metacoaxa; lateral disc of metaventrite (Fig. 41) and metepisternum generally similar to those of *E. grossipes*, but metepisternum with denser and coarser punctuation and longer setae; metepisternal stria unrecognizable beneath setae (absent?). Intercoxal disc of first abdominal sternite as in *E. grossipes*. Protibia (Figs 42–43) on outer margin with a single massive triangular tooth, followed by another lower tooth; both teeth topped by triangular denticle followed by two-three inconspicuous rounded denticles entombed in outer protibial margin; protibial spur inconspicuous (absent?); outer part of posterior surface of protibia (Fig. 43) smooth, separated from comparatively narrower median part by a definite ridge, posterior protibial stria complete, terminating in two minuscule inner posterior denticles; inner margin of protibia with double row of long dense lamellate setae. Mesotibia (Fig. 44) as in *E. grossipes*, but denticles on outer margin longer. Metatibia (Fig. 45) even more triangularly dilated and thickened than that of *E. grossipes*; outer margin with about four strong denticles larger in size apically; dilated anterior margin dorsally with several irregular rows of scattered tiny rounded denticles.

Male genitalia. Eighth sternite (Figs 46–47) apically with a brush of sparse setae and a moderately sized velum; eighth tergite apically faintly inwardly arcuate; eighth sternite and tergite fused laterally (Fig. 48). Ninth tergite (Fig. 49) apically faintly



Figures 46–54. *Exaesiopus henoni* (Schmidt, 1896) 8th sternite and tergite, **46** ventral view **47** ditto, dorsal view **48** ditto, lateral view **49** 9th + 10th tergite, dorsal view **50** ditto, lateral view **51** spiculum gastrale, ventral view **52** ditto, lateral view **53** aedeagus, dorsal view **54** ditto, lateral view.

inwardly arcuate; tenth tergite apically rounded; spiculum gastrale (Figs 51–52) similar to that of *E. grossipes*. Aedeagus (Figs 53–54) short and stout, slightly dilated apically; apex with pseudopores; parameres fused on their apical half. Basal piece of aedeagus short; ratio basal piece : parameres approximately 1:4.

Differential diagnosis. *Exaesiopus henoni* is most similar to the species *E. laevis* and *E. therondi*, with which it shares the shape of protibia (see also Key to species for

details). From *E. therondi* it differs by sparsely punctate pronotum, frons that is devoid of tiny irregular rugae, and anterior face of protibia, which is glabrous in *E. henoni*, whereas it is obscurely variolate in *E. therondi*. From *E. laevis* it differs by punctate body (almost impunctate in *E. laevis*) and present inner subhumeral stria (absent from *E. laevis*). From the remaining species of the genus *E. henoni* differs by the shape of the protibia (see also Key to species for details).

Biology. A typical psammophile, found in sand.

Distribution. So far known only from Algeria and Morocco (Gomy et al. 2011). New to Libya and Djibouti.

Exaesiopus torvus Reichardt, 1926

Figs 55–72

Exaesiopus torvus Reichardt 1926: 17; Mazur (1984): 101; (1997): 264; (2004): 92; (2011): 210.

Type locality. Yanidarya, Kyzyl-Ordinskij Rayon, Kazakhstan.

Type material examined. Holotype, ♀ side-mounted on a triangular point, with female genitalia extracted and glued to the subsequent label with female sign, with following labels: “♀” (printed); followed by circular golden label; followed by: “Yany - Darya / perovsk u / Kyzyl-Kum / 24.iv.[1]911” (hand-written); followed by: “Type / Exaesiopus / torvus m. / A. Reichardt det.” (written-printed label); followed by: “Holotypus” (red label, printed) (ZIN).

Additional material examined. KAZAKHSTAN: 1 ♀, left bank of the river Ural, Saraichikovsk, 8.vi.1932, Lukyanovich leg.; 1 ♀ + 2 specs., left bank of Ural river, opposite of Saraychik, 8.vi.1932, Lukyanovich leg.; 1 ♂, western bank of Aral Sea, Komsomolsk na Usturyte, 31.v.1978, G. Medvedev; 1 spec., W Kazakhstan obl. [=reg.], Bilj-Agach, 4.vii.1952, L. Arnoldi (in leaf litter). (all exs. ZIN); 1 spec., 1933-102, left bank of the Ural River, Saraychik, 8.vi.[19]32, Lyukanovich (BMNH). UZ-BEKISTAN: 1 ♀, Karakum, Khiva, 3.v.1978, leg. Olexa; 1 ♂, ibid, but 1.–5.v.1979 (both exs. TLAN); RUSSIA: 1 spec., Astrakhan Region, Krasniy Yar district, near Dosang vill., 8.v.2009, A. Kovalyov leg. (CAS); 1 spec., ibid, but 14 km NE Dosang vill., barkhan [=sand dune] Tuvayak, 23-24.iv.2008, M. Smirnov leg. (CAS).

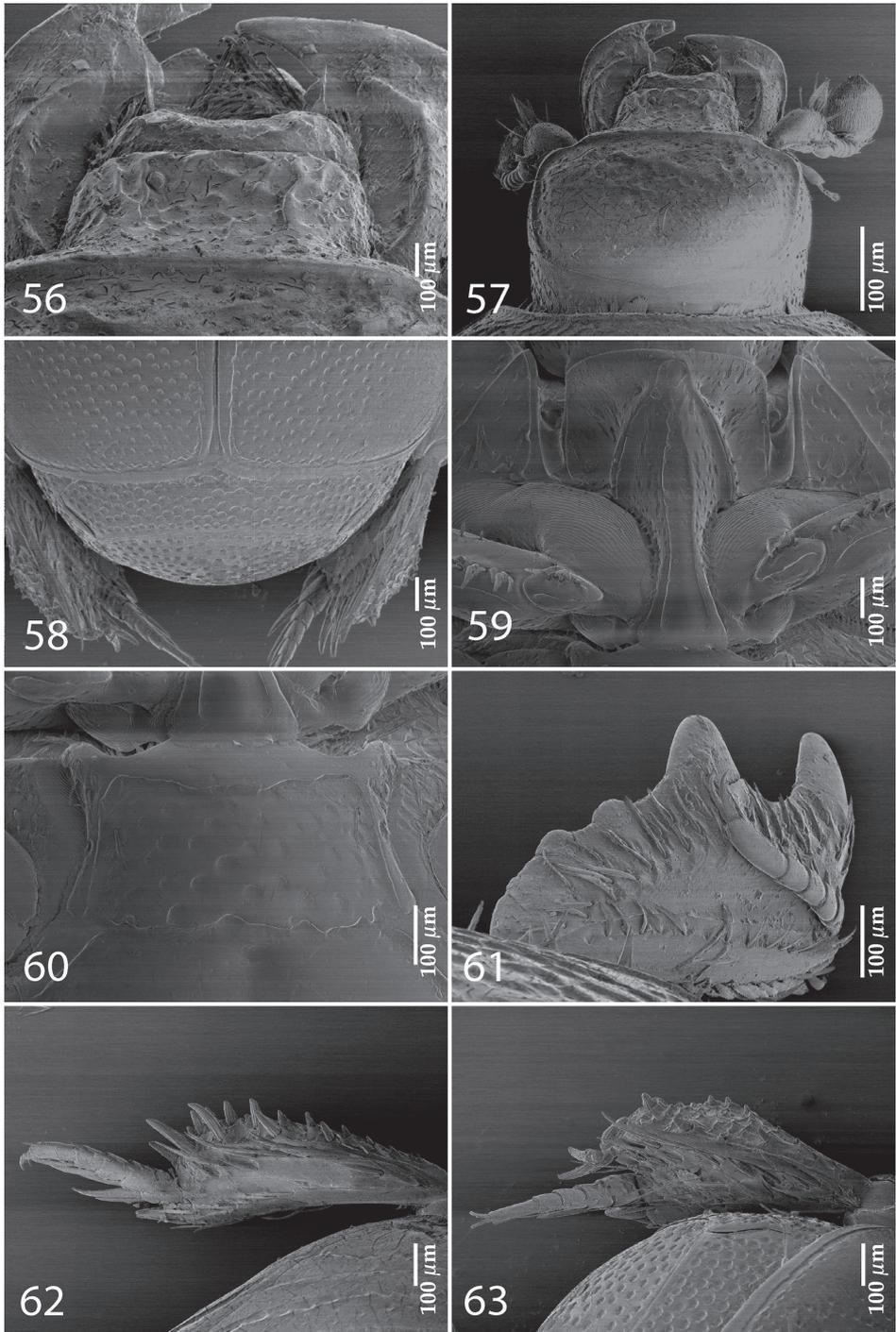
Diagnostic description. Body length: PEL: 2.15–2.575 mm; APW: 0.575–0.875 mm; PPW: 1.625–1.925 mm; EW: 1.75–2.125; EL: 1.375–1.625 mm. Body (Fig. 55) strongly convex, cuticle as in *E. grossipes*, but without metallic tinge; legs, mouthparts and antennae dark yellow to light brown. Antennae as in *E. grossipes*; sensory structures of the antennal club not examined. Mouthparts: labrum obscurely variolate, shallowly depressed medially; mentum as in *E. henoni*; rest of the mouthparts similar to those of *E. grossipes*; terminal labial and maxillary palpomeres truncate. Clypeus (Fig. 56) as in *E. grossipes*, but rugulose-lacunose; frontal, supraorbital and postorbital striae (Fig. 57) as in *E. grossipes*; frons rugose, with several irregularly shaped carinate transverse



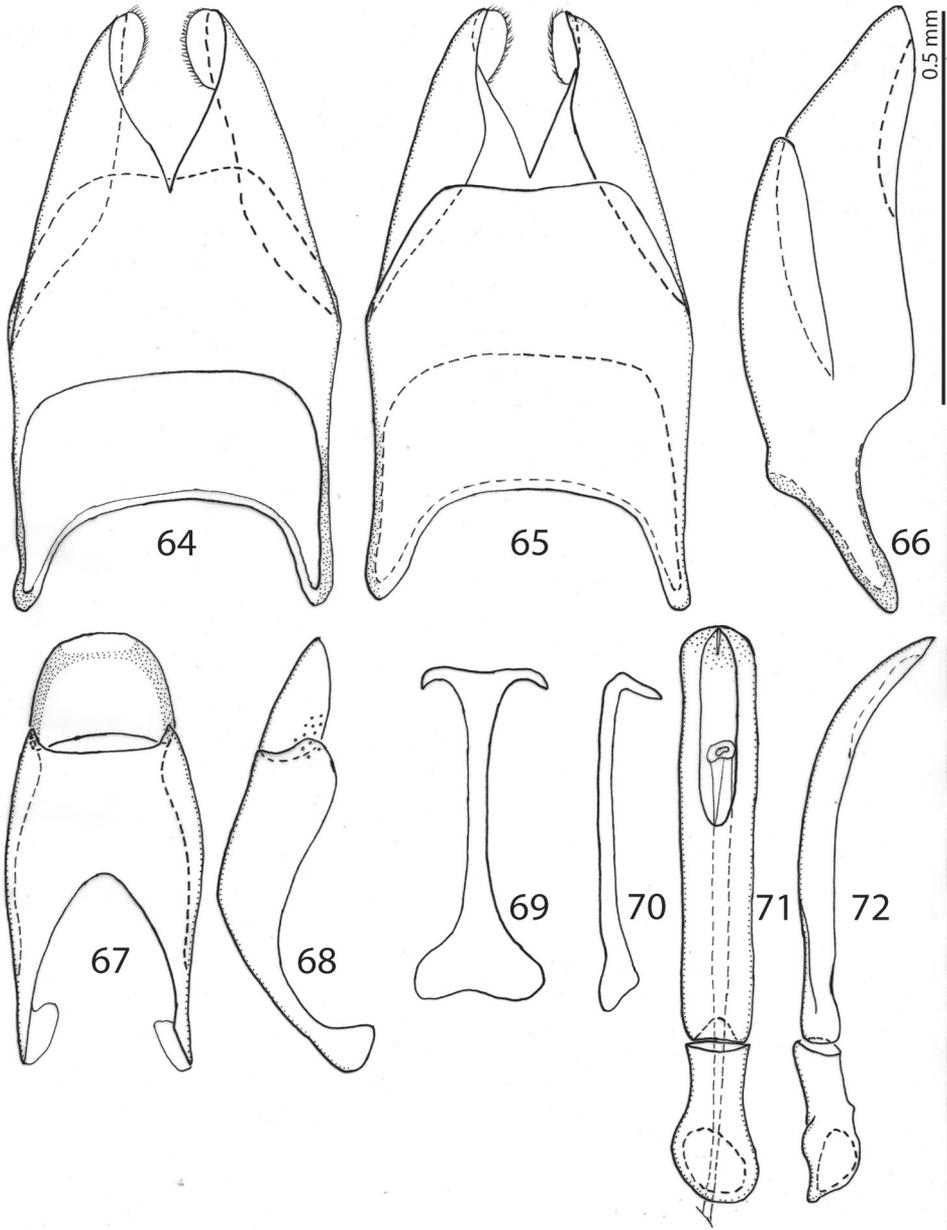
Figure 55. *Exaesiopus torvus* Reichardt, 1926 habitus.

rugae or chevrons intermingled with sparse microscopic punctures. Pronotum: pronotal disc, except for irregularly-shaped impunctate (or weakly punctate) median part entirely covered with round dense punctation, forming transverse rugae and confluent laterally, punctation reaches lateral margins; rest of pronotum as in *E. grossipes*.

Elytral humeri not particularly enlarged; inner subhumeral stria present only as a row of several punctures; elytral punctation variable, in most specimens reaching elytral base along fourth elytral interval, punctures often present in all elytral intervals, elytral flanks impunctate; punctures regular and deep, separated by about half to several times their own diameter. Propygidium (Fig. 58) and pygidium as in *E. grossipes*, but covered with denser punctation. Prosternum: prosternal foveae (Fig. 59) weakly impressed; prosternal process otherwise similar to that of *E. grossipes*. Disc of mesoventrite (Fig. 60) with scattered shallow punctures; intercoxal disc of metaventrte, lateral disc of metaventrte and metepisternum generally similar to those of *E. henoni*. Intercoxal disc of first abdominal sternite as in *E. grossipes*. Protibia (Fig. 61) more dilated than that of *E. grossipes*; on outer margin with two widely-spaced low teeth, topped by large triangular denticle followed by two low rounded denticles imbedded in outer protibial



Figures 56–63. *Exaesiopus torvus* Reichardt, 1926 **56** clypeus **57** head, dorsal view **58** propygidium + pygidium **59** prosternum **60** mesoventrite **61** protibia, dorsal view **62** mesotibia, dorsal view **63** metatibia, dorsal view.



Figures 64–72. *Exaesiopus torvus* Reichardt, 1926 8th sternite + tergite, **64** ventral view **65** ditto, dorsal view **66** ditto, lateral view **67** 9th + 10th tergites, dorsal view **68** ditto, lateral view **69** spiculum gastrale, ventral view **70** ditto, lateral view **71** aedeagus, dorsal view **72** ditto, lateral view.

margin; protibial spur inconspicuous (absent?) protibia otherwise similar to that of *E. grossipes*. Mesotibia (Fig. 62) generally similar to that of *E. grossipes*. Metatibia (Fig. 63) perhaps most triangularly dilated and thickened of all congeners; outer

margin with approximately three widely-spaced tiny denticles; inner margin with a dense row of minuscule rounded denticles; no rows of denticles present between the two rows, surface rugulose-lacunose.

Male genitalia. Eighth (Figs 64–65) sternite apically aetose, with tiny veta; eighth tergite apically faintly inwardly arcuate medially; eighth sternite and tergite fused laterally (Fig. 66). Ninth tergite (Figs 67–68) apically almost straight; tenth tergite apically outwardly arcuate, basally only faintly inwardly arcuate. Spiculum gastrale (Figs 69–70) generally similar to that of *E. grossipes*. Aedeagus (Figs 71–72) almost parallel-sided, apex with pseudopores, parameres fused along their apical half (approximately); aedeagus slightly curved ventrad from the lateral view (Fig. 72).

Differential diagnosis. Generally the most punctate species of *Exaesiopus*, which can be confused only with densely punctate specimens of *E. grossipes* from N Africa. It clearly differs from them by the punctuation of pronotum as well as male genitalia (see also Key to species for details).

Biology. Similar to that of other congeners – beetles are found in sand.

Distribution. Kazakhstan; new to Uzbekistan and Russia.

Exaesiopus atrovirens Reichardt, 1926

Figs 73–88

Exaesiopus atrovirens Reichardt 1926: 17; Mazur (1984): 101; (1997): 263; (2004): 92; (2011): 210.

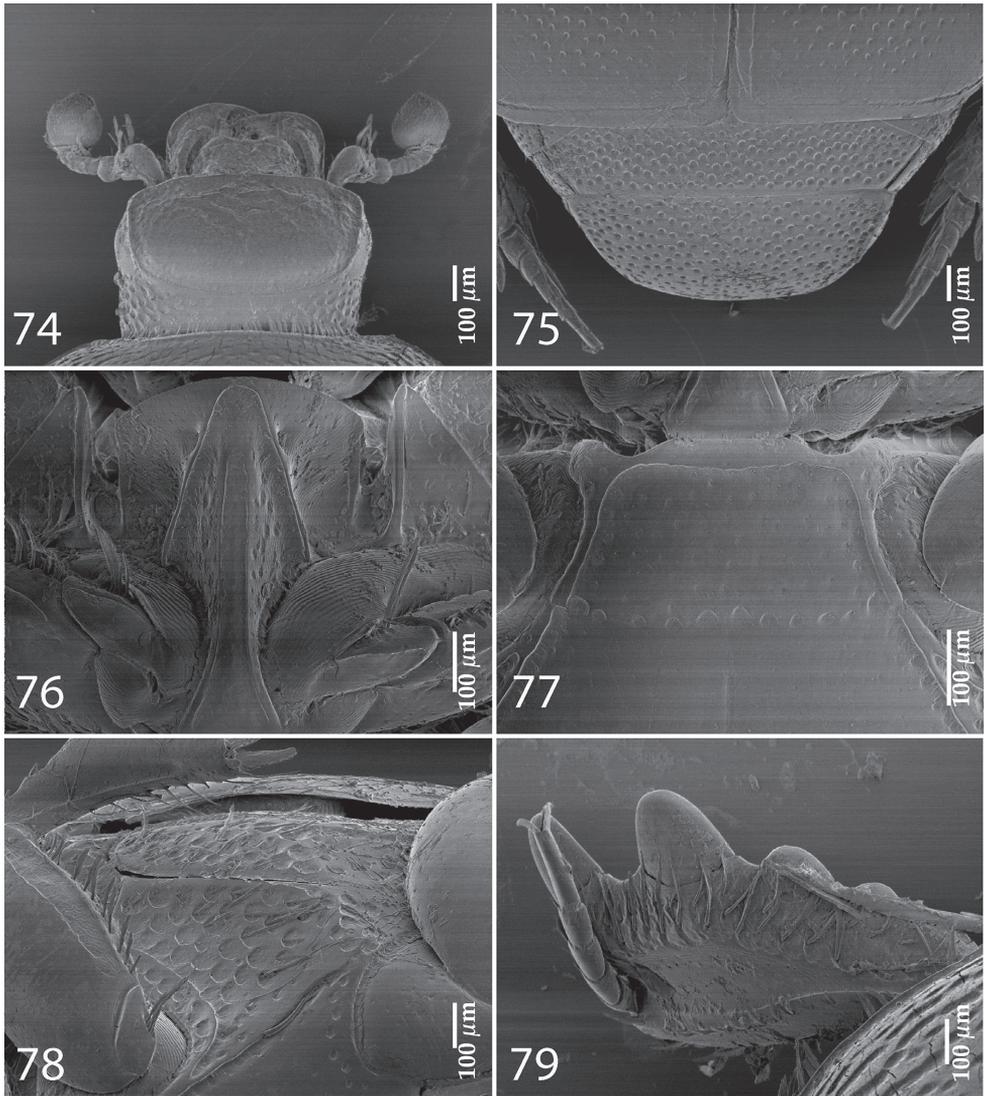
Type locality. Arys, Kazakhstan.

Type material examined. Holotype, ♂, with male genitalia extracted and glued to the subsequent label with male sign, with following labels: “♂” (printed); followed by circular golden label; followed by: “St. Arys / Tashkenskaya Zh d. / 27.v.[1]921 / na sklonach / saye, na osypyach / on the other side of the same label is written: “obryvystych kra- / yov i vypotov / soli. neredko / k reke / sb. I. Ivanov” (hand-written label on both sides); followed by: “Exaesiopus / atrovirens sp. n. / A. Reichardt det.” (written-printed label with black margin); followed by red, printed label: “Holotypus” (ZIN). Paratypes: 1 ♂ + 1 ♀, with circular golden label, followed by written label: “St. Aris / Tashkenskaya Zh. d. / I. Ivanov 27.v.[1]921”; followed by: “Exaesiopus / atrovirens sp.n. / A. Reichardt det. (printed-written); followed by red label, written: “Paratypus”; followed by: “Zoological / Institute RAS / St. Petersburg” (yellow label, printed). 1 ♂, with circular golden label, followed by written label: “Askhabad”; followed by: “Exaesiopus / atrovirens sp. n. / A. Reichardt det.” (written-printed); followed by: “Paratypus” (hand-written red label); followed by: “Zoological / Institute RAS / St. Petersburg” (yellow label, printed); followed by yellow, pencil-written label: “09-060” (added by myself); 1 spec., with circular golden label, followed by: “Caucas, further illegible”; (black-turned, formerly red label, printed-written); followed by: “Coll. / Semenov Tian-Shansky” (written-printed); followed by:



Figure 73. *Exaesiopus atrovirens* Reichardt, 1926 habitus.

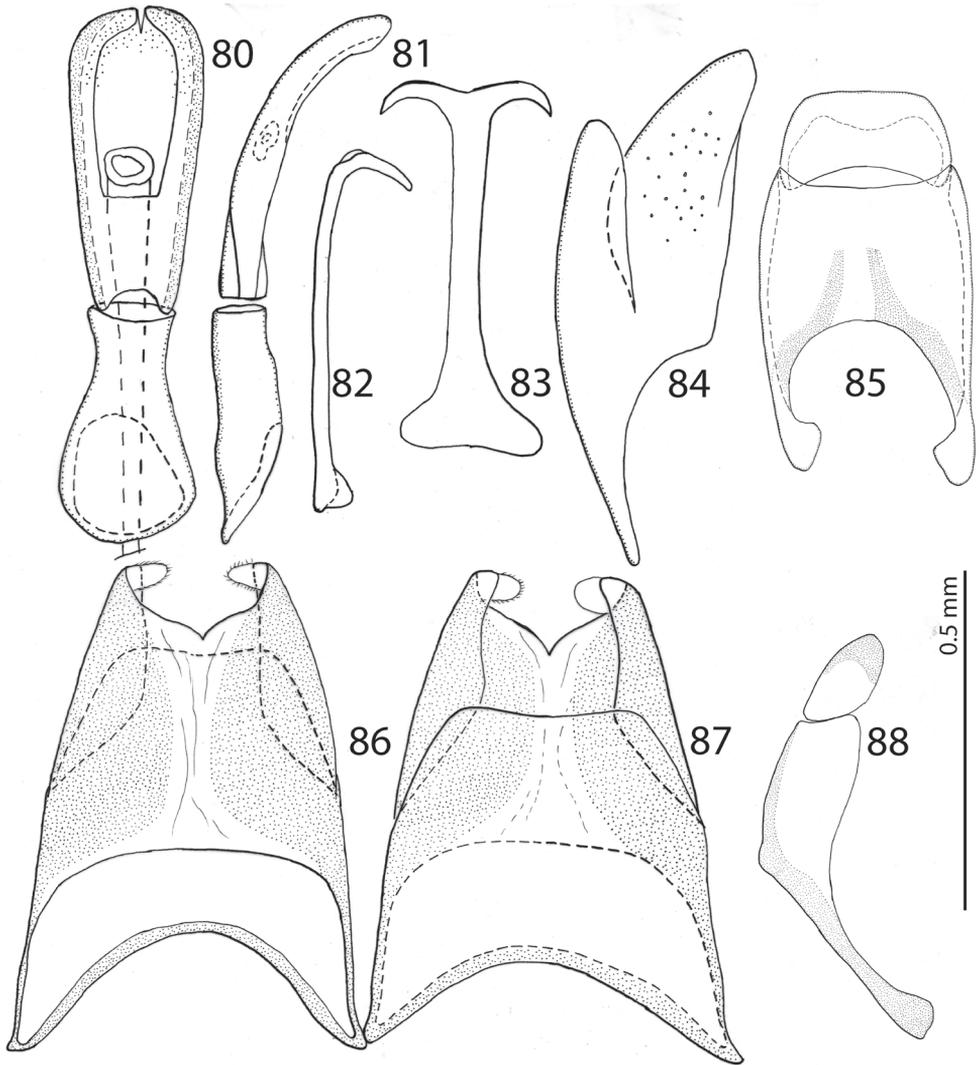
“*Exaesiopus / atrovirens* sp. n. / A. Reichardt det.” (written-printed label); followed by: “Paratypus” (hand-written red label); 1 ♂, with male genitalia extracted and glued to the subsequent label with male sign, with following labels: “♂” (printed); followed by circular golden label; followed by: “Caucasus / Coll. Kusnetzov / A. Semenov Tian-Shansky” (written-printed label); followed by: “*Exaesiopus / atrovirens* sp. n. / A. Reichardt det.” (written-printed label); followed by: “Paratypus” (hand-written red label); 1 spec., with circular golden label; followed by: “Owtshaly? / 11 mai / 1880” (written); followed by: “62” (pink label, written); followed by: “k. [=coll.] G. Siversa” (printed label in Russian); followed by: “*Saprinus / grossipes / Mrs.*” (written label); followed by: “*Exaesiopus / atrovirens* sp. n. / A. Reichardt det.” (written-printed label); followed by: “Paratypus” (hand-written red label); 1 spec., with golden circular label; followed by: “Turkestan / Sansar / Glasunov 1892” (black-margined printed label); followed by: “prope group / Hls. mit lang / Wimperhaaren / nur nicht / Akinini” (written); followed by: “k. [=coll.] A. Jacobsona” (printed); followed by: “Paratypus” (red label, written); 1 spec., with golden circular label, followed by: “St. Aris / Tashk.



Figures 74–79. *Exaesiopus atrovirens* Reichardt, 1926 head, **74** dorsal view **75** propygidium + pygidium **76** prosternum **77** mesoventrite **78** lateral disc of metaventrite + metepisternum **79** protibia, dorsal view.

[Tashkentskaya] Zhe. [iron] d. [railway] / I. Uvarov 27.v.[1]921"; followed by: "Exaesiopus / atrovirens sp. n. / A. Reichardt det." (written-printed label); followed by hand-written red label: "Paratypus"; followed by: "Zoological / Institute RAS / St. Petersburg" (yellow label, printed) (all type specimens ZIN).

Additional material examined. ARMENIA: 1 spec., Yerevan, 19.v.1938, Richter (ZIN). TAJIKISTAN: 1 ♀ & 1 spec., Pyandzh, from Khorog to Ishkashim, 6.vi.1928, Grishin leg. (ZIN); 1 spec., ibid, but BMNH. AZERBAIJAN: 1 spec.,



Figures 80–88. *Exaesiopus atrovirens* Reichardt, 1926 aedeagus, **80** dorsal view **81** ditto, lateral view **82** spiculum gastrale, lateral view **83** ditto, ventral view **84** 8th sternite + tergite, lateral view **85** 9th + 10th tergites, dorsal view **86** 8th sternite + tergite, ventral view **87** ditto, dorsal view **88** 9th + 10th tergites, lateral view.

Khudat, SE Samura, 8.vii.1913, Lyukyanovitsh leg. (ZIN); KAZAKHSTAN: 1 spec., Kazakhstan, river Ural near Kharkin, 7.v.1951, Gurjeva leg. (MNHN); 1 ♀, r. Ural near Kharkin, 13.v.1951, L. Arnoldi leg., under *Tamarix* in the sand (ZIN); 1 spec., Uralskaya obl., Kalmykov, 31.vii.1908, Borodin (ZIN); RUSSIA: 2 specs., Volgogradskaya obl. Kamyshyn, 7.v.1939, Lyubyshev leg. (ZIN); 1 ♂, Dagestan, Terekli-Mekteb, Karanogaysk. steppe, 15.v.1925, Kirichenko leg. (ZIN); 5 specs., Astrakhan Region, Krasniy Yar district, near Dosang vill., 8.v.2009, A. Kovalyov leg.

(CAS); 1 spec., *ibid*, 17.v.1998, 46°54'N, 47°54'E, K. Makarov & A.Brinyov leg (CAS). TURKEY: 1 spec., vill. Artvin, Cankurtaran Geç., 3.vi.2000, J. Mertlik leg. (TLAN); 1 spec., 21.vi.2003, Erzurum vill., ca 50 km S, Hamzalar - Hot Springs, 39°27'N, 41°07', 1935 m, Jiří Hájek & Josef Hotový leg. (TLAN); 1 spec., Adana, 1903, no further data (BMNH). IRAN: Dorahi, 16.vi.1973, collector unknown (MNHN). AFGHANISTAN: 1 ♂, Central, Gesab, 1400 m, 14.vi.1970, Kabakov leg. (ZIN). GEORGIA: 1 ♀, Mzcheta near Tbilisi, 12.–13.vi.1987, leg. Wrase & Schülke (NCB). UKRAINE: 1 spec., Kherson reg. Golaya Pristan distr. near Ribalche, 6.–9.v.1994, I. Melnik leg. (CAS).

Diagnostic description. Body length: PEL: 2.50–2.75 mm; APW: 1.00–1.10 mm; PPW: 2.00–2.25 mm; EW: 2.125–2.40 mm; EL: 1.50–1.875. Body shape (Fig. 73) as in its congeners, cuticle with greenish metallic tinge; legs, mouthparts and antennae reddish-brown. Antennae as those of *E. grossipes*; sensory structures of the antenna not examined. Mouthparts: mandibles somewhat more slender than those of *E. grossipes*; labrum with large antero-median depression, otherwise similar to that of *E. grossipes*; mentum and rest of the mouthparts likewise. Clypeus (Fig. 74) rectangular, rugose, anterior margin elevated, depressed medially; frontal, supraorbital and postorbital striae (Fig. 74) as in *E. grossipes*; frons with several irregularly shaped carinate transverse rugae intermingled with numerous tiny rugae; at times transverse rugae obliterated under numerous tiny rugae; eyes flattened, but visible from above. Pronotum as in *E. grossipes*. Elytra similar to that of *E. grossipes*; inner subhumeral stria present medially; elytral punctation, however, mostly confined to apical half of elytra, only rarely punctures present on other than fourth elytral interval. Punctuation of propygidium (Fig. 75) and pygidium similar to those of *E. grossipes*, but punctures on propygidium almost confluent. Prosternum (Fig. 76) most similar to that of *E. glaucus*, foveae small but deep; prosternal process asetose. Mesoventrite (Fig. 77) occasionally sparsely and finely punctate, otherwise similar to that of *E. glaucus*; intercoxal disc of metaventrite similar to that of *E. glaucus*; longitudinal depression in female very faint; lateral metaventral stria, rest of lateral disc of metaventrite, metepisternum + fused metepimeron (Fig. 78) most similar to those of *E. glaucus*, but the amber setae distinctly longer and denser. Intercoxal disc of first abdominal sternite most similar to that of *E. glaucus*. Protibia (Fig. 79) similar to that of *E. glaucus*, differing from it chiefly by lower teeth topped by large triangular denticle. Mesotibia and metatibia similar to those of *E. glaucus*; metatibia, however, slightly more thickened and dilated.

Male genitalia. Eighth sternite (Fig. 86–87) fused along its entire length, apically asetose, velum tiny; eighth tergite apically faintly inwardly arcuate; eighth sternite and tergite fused laterally (Fig. 84). Ninth tergite (Figs 85, 88) apically faintly inwardly arcuate; spiculum gastrale (Figs 82–83) similar to other congeners. Aedeagus (Figs 80–81) short and stout, gradually dilated anteriorly, apex with pseudopores, parameres fused along their basal two-thirds (approximately), aedeagus slightly curved ventrad (Fig. 81).

Differential diagnosis. *E. atrovirens* is most similar externally to *E. glaucus*, differing from it by longer vestiture on underside of the body, numerous irregular rugae of frons, more thickened and dilated metatibia, larger triangular denticles of protibia, and male genitalia (compare Figs 80–88 with Figs 107–113; see also Key to species for details). From the rest of the congeners it differs chiefly by its greenish metallic hue of the dorsum (other species are not metallic).

Biology. Found in sand, often under *Tamarix*.

Distribution. Known from Turkey, Russia, Armenia, Azerbaijan, Georgia, Kazakhstan, Iran, Afghanistan and Turkmenistan. New to Ukraine and Tajikistan.

Exaesiopus laevis Théron, 1964

Figs 89–97

Exaesiopus laevis Théron 1964: (3) 72; Mazur (1984): 101; Mazur (1997): 264; Mazur (2011): 210.

Type locality. Guardafui, Somalia.

Type material examined. Holotype, ♀, mounted on its side on a triangular point, right protibia missing, with printed label: “SOMALI REP. / North region”, followed by another printed label: “Guardafui / XI. 1959 / C. Hemming”; with another printed-written label: “J. Théron det., 1962 / *Exaesiopus* / *laevis* n. sp.” and a red label attached to it (printed-written): “TYPE / Esemplare / unico”; with another yellow, pencil-written label: “D08-092”, added by myself (MSNM).

Diagnostic description. Body length: PEL: 2.375 mm; APW: 0.825 mm; PPW: 1.75 mm; EL: 1.50 mm; EW: 2.00 mm.

Body (Fig. 89) without metallic tinge; legs, mouthparts and antennae light brown; antennal club amber. Antennae as in *E. grossipes*; sensory structures of the antennal club not examined. Mouthparts: mentum (Fig. 90) glabrous, sub-quadrangle, shallowly inwardly arcuate on anterior margin; anterior margin with several rather long setae intermingled with short sparse ramose setae; rest of the mouthparts as in *E. grossipes*. Clypeus and frons (Fig. 91) similar to those of *E. henoni*. Pronotum almost smooth, only laterally and behind head with vague patches of shallow sparse punctation; otherwise similar to that of *E. henoni*. Elytra: inner subhumeral stria absent; elytral disc entirely smooth. Propygidium and pygidium (Fig. 92) similar to other congeners, but only sparsely punctate, punctures separated by several times their own diameter. Prosternum (Fig. 93): prosternal foveae tiny, almost invisible; prosternal process otherwise similar to that of other congeners. Mesoventrite (Fig. 94) glabrous, about as long as wide; metaventrite smooth; lateral disc of metaventrite and metepisternum similar to those of *E. henoni*. Intercoxal disc of first abdominal sternite similar to that of *E. henoni*. Protibia (Figs 95–96) similar to that of *E. henoni*, but outer margin of teeth topped by large triangular denticles, more similar in size

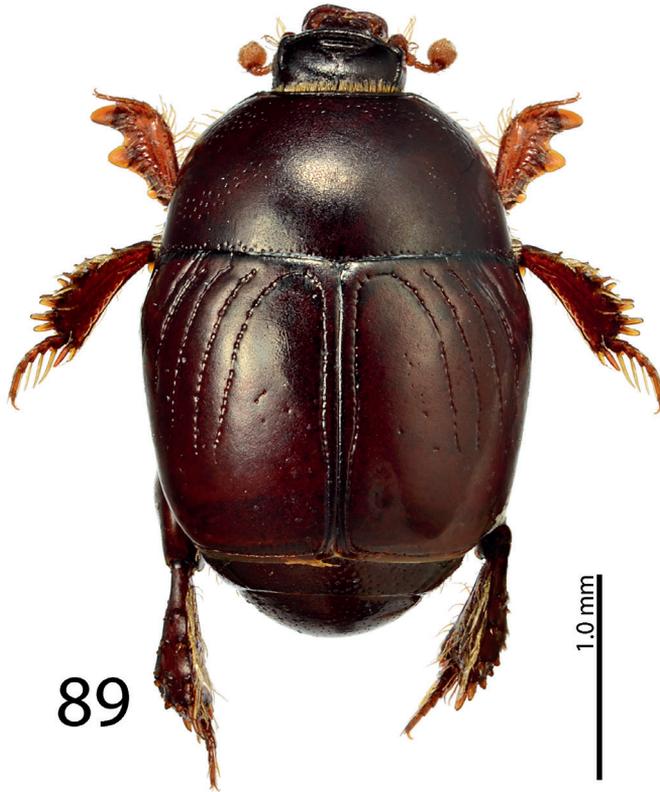


Figure 89. *Exaesiopus laevis* Théron, 1964 holotype, habitus.

than those of *E. henoni*, furthermore outer part of posterior surface of protibia of *E. laevis* obscurely variolate, whereas it is glabrous in *E. henoni*. Mesotibia generally similar to that of *E. henoni*, but denticles on outer margin shorter. Metatibia (Fig. 97) likewise generally similar to that of *E. henoni*, but denticles on outer margin more numerous.

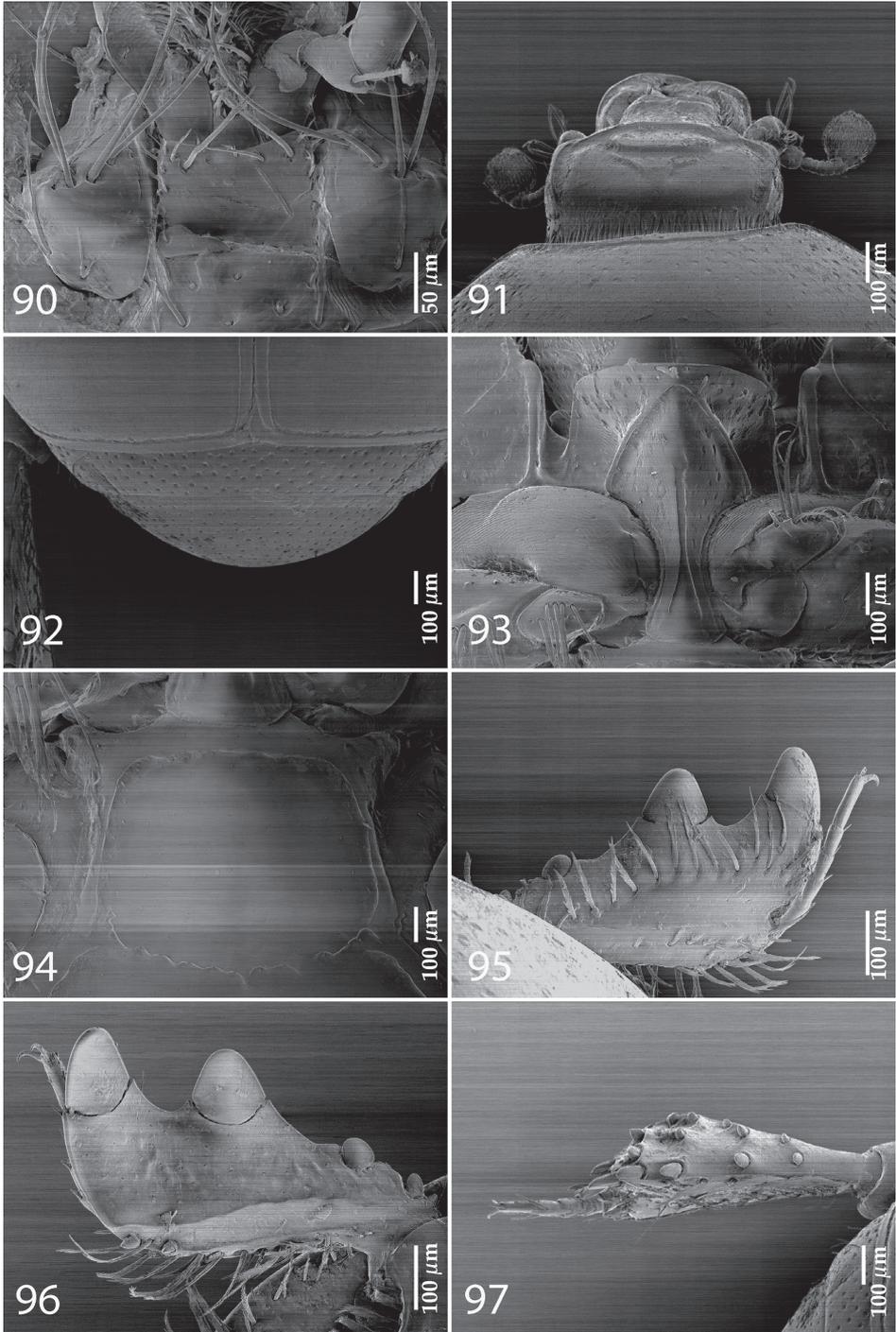
Male unavailable.

Differential diagnosis. This species is most similar to *E. henoni*, from which it differs by almost impunctate pronotum (punctate in *E. henoni*), smooth elytra (punctate in *E. henoni*) and obscurely variolate posterior surface of protibia (glabrous in *E. henoni*). From the rest of *Exaesiopus* species it differs by the characters given in the Key to species (below).

Biology. Unknown, possibly similar to the congeners.

Distribution. Known only from north-extreme tip of Somalia: Guardafou.

Remarks. This species is morphologically rather similar to *E. henoni*, which is known also from the neighbouring Djibouti. The discovery of a male of *E. laevis* would help to elucidate the identities of the two respective species.



Figures 90–97. *Exaesiopus laevis* Thérond, 1964 holotype, mentum, **90** ventral view **91** holotype, head, dorsal view **92** holotype, propygidium + pygidium **93** holotype, prosternum **94** holotype, mesoventrite **95** holotype, protibia, dorsal view **96** ditto, ventral view **97** holotype, metatibia, dorsal view.

***Exaesiopus glaucus* (Bickhardt, 1914), comb. n.**

Figs 98–113

Pachylopus glaucus Bickhardt 1914: 280.*Hypocaccus (Hypocaccus) glaucus*: Mazur (1984): 94; Mazur (1997): 259; Mazur (2011): 206.**Type locality.** Gobabeb, Namibia.

Type material examined. Neotype, ♂, side-mounted on a triangular mounting point, right antennal club broken off, both terminal metatarsomeres broken off, with male genitalia mounted in Canada balsam on a separate slide under specimen, with the following labels: “S.W. Afr., Namib / Gobabeb / 23.34S–15.03E” (printed); followed by: “24.9.1974; E–Y: 376 / shore washing / leg. Endrödy-Younga” (printed); followed by: “Exaesiopus / glaucus / Bickh. / det. J. Théron” (printed-written); followed by: “D08-029” (yellow, pencil-written label, written by myself); followed by: “Pachylopus glaucus / Bickhardt, 1914 / NEOTYPE det. T. / Lackner 2014” (red label, written) (TMSA).

Note. This species has been described based on a single specimen collected in Okahandja (Namibia) (Bickhardt 1914: 280). According to the personal information by the curator of ZMHUB B. Jaeger, the specimen was deposited at the Hamburg Museum of Natural History (Germany), which has been destroyed during WWII. The type specimen of this species can thus be considered as lost and hence a Neotype is designated herein.

Additional material examined. NAMIBIA: 1 ♂ + 1 ♀, Gobabeb, 23.34S – 15.03E, 24.ix.1974, Endrödy-Younga leg., shore-washing (TMSA); 1 ♂ + 1 ♀, ibid, but MNHN; 1 ♀, Swakop River, 3 miles S of Okahandja, 7.iv.1972, floating refuse (MNHN). REPUBLIC OF SOUTH AFRICA: 1 ♂, Cape-Cedarbg, Olifants R., Boshof, 32.20S – 18.59E, 20.viii.1983, Endrödy-Younga & Penrith leg., sand banks, river (TMSA).

Diagnostic description. Body length: PEL: 2.50–2.60 mm; APW: 0.80–1.00 mm; PPW: 1.83–2.00 mm; EW: 2.00–2.18 mm; EL: 1.50–1.60 mm. Body (Fig. 98) similar to the species *E. atrovirens*, with feeble metallic tinge; legs, mouthparts and antennae light brown. Antennae as in *E. grossipes*. Mouthparts: as in *E. grossipes*; labrum with median keel-like elevation, surface anterad of it semi-circularly depressed; mentum (Fig. 99) sub-trapezoid, anterior margin without median notch, fringed with several long setae, lateral margins with single row of sparse shorter ramose setae; stipes with four setae; other mouthparts similar to those of *E. atrovirens*. Clypeus (Fig. 100) rectangular, obscurely variolate, anterior margin elevated, formed by two transverse tubercles that can occasionally be connected forming thus a ridge-like structure; clypeus and frons otherwise similar to those of *E. atrovirens*, but without numerous irregular rugae. Pronotum: sides slightly convergent on basal 3/4, strongly convergent on apical 1/4; disc with round dense punctation, laterally punctures larger in size and increasingly ellipsoid, occasionally confluent; postero-median part of disc smooth, punctation stops short of lateral pronotal margin leaving a narrow impunctate band; pronotal base with a single row of round punctures; pronotal hypomeron with short amber setae almost



Figure 98. *Exaesiopus glaucus* (Bickhardt, 1914) habitus.

invisible from dorsal view; scutellum small, visible. Elytra: humeral elytral stria well impressed on basal fourth; inner subhumeral stria present medially as a short median fragment; elytral punctation confined to apical half of elytra, along elytral suture reaches up to $2/3$ of elytral length anteriorly, punctures in most cases do not enter elytral intervals, regular and deep, separated by about their own diameter, punctation does not become denser apically; rest of elytra impunctate. Propygidium and pygidium (Fig. 101) similar to other congeners, with coarse and dense regular punctation. Prosternum (Fig. 102): prosternal foveae well impressed, rather small, but deep; prosternal process slightly concave, otherwise similar to that of other congeners. Mesoventrite (Fig. 103) slightly wider than long, almost smooth; meso-metaventral sutural stria well impressed, undulate; intercoxal disc of metaventrite with longitudinal depression in both sexes, more prominent in male, almost smooth, except for several rows of variously-sized

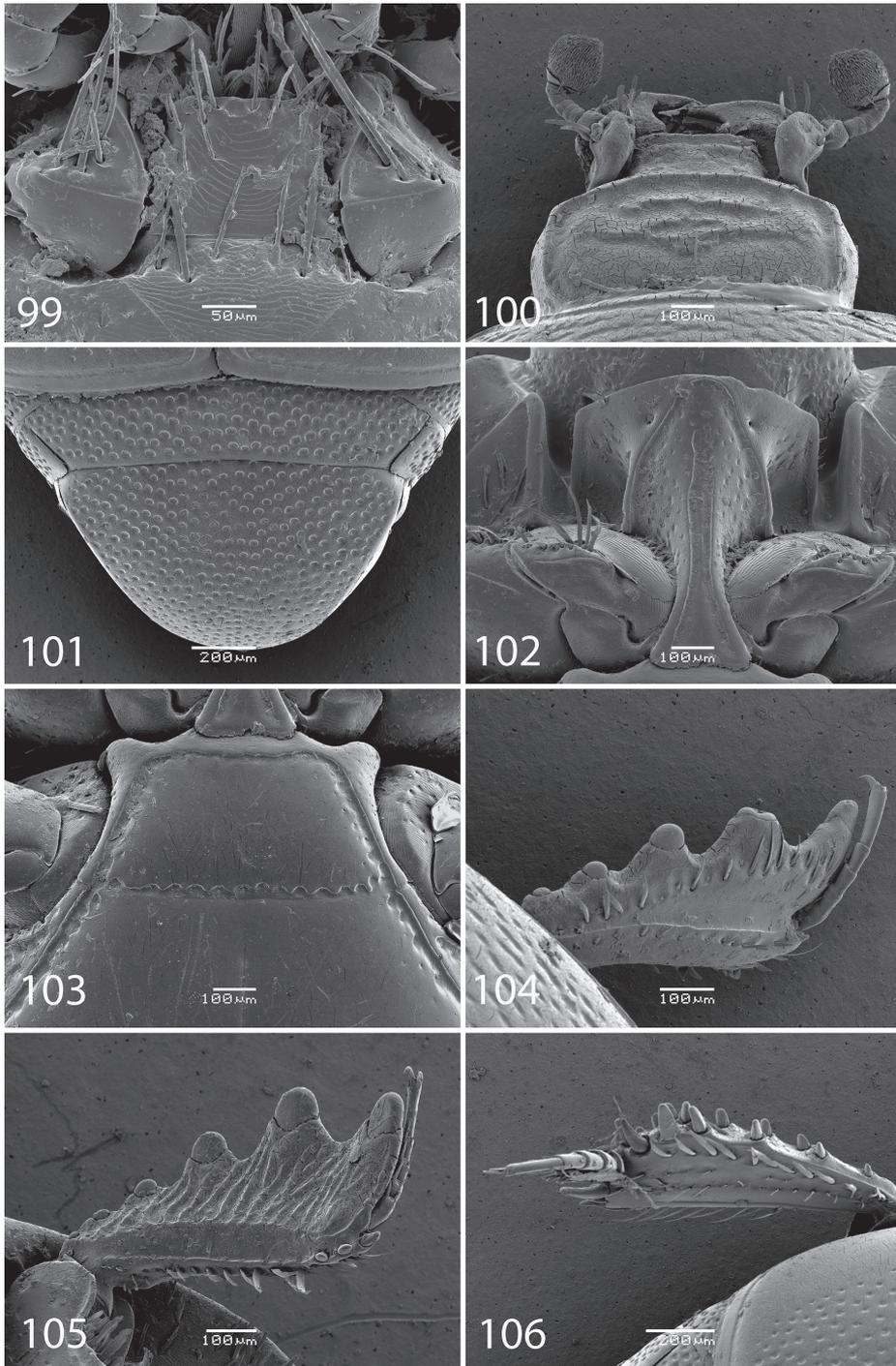
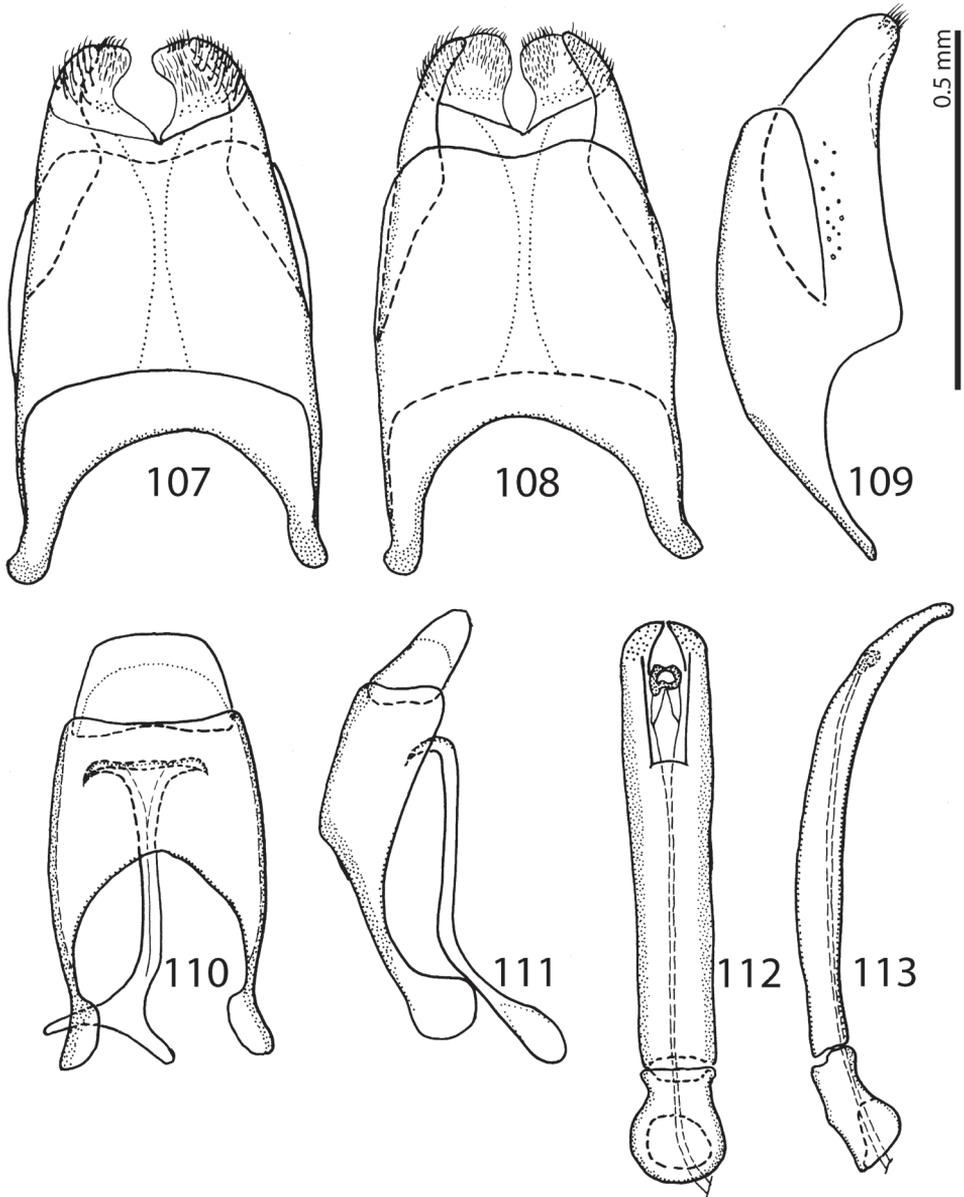


Figure 99–106. *Exaesiopus glaucus* (Bickhardt, 1914) mentum, **99** ventral view **100** head, dorsal view **101** propygidium + pygidium **102** prosternum **103** mesoventrite **104** protibia, dorsal view **105** ditto, ventral view **106** metatibia, dorsal view.



Figures 107–113. *Exaesiopus glaucus* (Bickhardt, 1914) 8th sternite + tergite, **107** ventral view **108** ditto, dorsal view **109** ditto, lateral view **110** 9th + 10th tergites dorsal view & spiculum gastrale, ventral view **111** 9th + 10th tergites & spiculum gastrale, lateral view **112** aedeagus, dorsal view **113** ditto, lateral view.

deep punctures along base; lateral metaventral stria, lateral disc of metaventricle and metepisternum similar to those of *E. henoni*. Intercostal disc of first abdominal sternite as with the rest of congeners. Protibia (Fig. 104) on outer margin with two moderately large triangular teeth, topped by rounded denticle followed by another two lower teeth

topped by small round denticle and another tiny denticle entombed in outer protibial margin; setae of outer row regular and short; setae of median row shorter than those of outer row; anterior protibial stria almost complete; protibial groove deep; protibial spur (Fig. 105) distinct but tiny, growing out from apical margin of protibia; outer part of posterior surface of protibia rugulose-lacunose, clearly separated from comparatively narrower glabrous median part; posterior protibial stria complete, terminating in two tiny inner posterior denticles; inner margin of protibia with single row of short lamellate setae. Mesotibia not particularly dilated or thickened, outer margin similar to that of *E. henoni*; posterior mesotibial stria fine, shortened apically; mesotibial spur stout, prominent and long; anterior surface of mesotibia smooth; anterior mesotibial stria shortened apically; claws of last tarsomere almost straight, their length approximately half the length of apical-most mesotarsomere. Metatibia (Fig. 106) slightly more dilated and thickened than mesotibia, but always more slender than that of the congeners; two rows of denticles on outer margin widely separated permitting for placement of another two denticles between the two rows; claws of apical-most metatarsomere shorter than half its length; otherwise metatibia similar to mesotibia. Male genitalia. Eighth sternite (Figs 107–108) entirely fused medially, apically with a setose velum; apex of eighth sternite with short dense setae. Eighth tergite apically weakly inwardly arcuate; eighth sternite and tergite fused laterally (Fig. 109). Ninth tergite (Fig. 110) on apical margin faintly inwardly arcuate; tenth tergite on apical margin regularly rounded, weakly inwardly arcuate basally. Spiculum gastrale (Figs 110–111) with typical ‘head’ and ‘tail’; aedeagus (Figs 112–113) tube-like, sub-parallel, slightly widening apically; parameres fused along their basal three-fourths, apex of aedeagus with pores; basal piece short, ratio of its length : length of parameres approximately 1:5.

Differential diagnosis. *E. glaucus* is arguably the most distinctive species of the genus differing from all other members by only slightly dilated metatibia (strongly dilated in all other species, compare Fig. 106 with e.g. 97); present and observable protibial spur (very tiny or absent in the rest of species, compare Fig. 105 with e.g. 43). Furthermore, the setae of the pronotal hypomeron are rather short and invisible from dorsal view (in all other species they are protruding from underside of the pronotum and are observable from dorsal view).

Biology. Found on a beach by the technique of shore-washing as well as on a river bank on deposited debris.

Distribution. Described from Namibia; newly recorded from the Republic of South Africa.

Remarks. The placement of this species in *Exaesiopus* must be regarded as tentative, as it differs from the rest of the members chiefly by only slightly instead of strongly dilated metatibiae. *Hypocaccus* from the Old World, however, does not contain any species with ciliate pronotal hypomera, and keeping *E. glaucus* in *Hypocaccus* would make it heterogeneous. Note that it was already Reichardt (1926) who remarked that this species should be, based on its ciliate pronotal hypomeron, moved into the genus *Exaesiopus*. Théron, in the 1960’s and 1970’s identified this species as ‘*Exaesiopus*’, rather than ‘*Hypocaccus glaucus*’.



Figure 114. *Exaesiopus therondi* sp. n. habitus, dorsal view.

***Exaesiopus therondi* sp. n.**

<http://zoobank.org/E2EBDF60-6401-43CB-B106-3EF5E926E3EF>

Figs 114–126

Type locality. Hamud-i-Sabari, Afghanistan.

Type material examined. Holotype, ♂, side-mounted on a triangular point, right hind leg missing, genitalia glued to the same mounting point as the specimen, with the following labels: “N AFGHANISTAN: / Hamud-i-Sabari / 26.iii.1949 Danish / Central Asian Expedn.” (written in black ink); followed by: “Pachylopus / sp. not in BM / J. Balfour-Browne det. / v. 1964” (written-printed); followed by: “St. No. / 7” (printed-written); followed by: “Brit. Mus. / 1964-302” (printed-written); followed by: “Ex stomach of / Charadinus a. / alexandrinus L.” (written in black ink); followed by: “Ex-



Figure 115. *Exaesiopus therondi* sp. n. head, dorsal view.



Figure 116. *Exaesiopus therondi* sp. n. propygidium + pygidium.

aesiopus / n. sp. ? / J. Théron det. 1964” (written-printed); followed by: “*Exaesiopus / therondi* n.sp. / HOLOTYPE / det. T. Lackner 2014” (red label, written) (BMNH).

Diagnostic description. Body length: PEL: 2.125 mm; APW: 0.875 mm; PPW: 1.825 mm; EW: 2.05 mm; EL: 1.55 mm. This species (Fig. 114) is externally very similar to *E. henoni*, differing from it chiefly by its densely punctate pronotum, which is furnished with two round glabrous patches amongst the punctation laterally. The structure of frons (Fig. 115) is also different; whereas *E. henoni* always possesses only two well-defined chevrons on a completely glabrous surface, *E. therondi* has its chevrons beset on all sides with irregular rugae. The punctation of propygidium and pygidium (Fig. 116) is similar to that of *E. henoni* (Fig. 38). The prosternal process (Fig. 117) of *E. therondi* is more setose than that of *E. henoni*; prosternal foveae are absent. Anterior face of profemora (Fig. 117) is covered with dense amber setae in *E. therondi*,



Figure 117. *Exaesiopus therondi* sp. n. habitus, ventral view.

whereas only several sparse short setae are present in *E. henoni*. Anterior face of protibia (Fig. 117) is rugulose-lacunose in *E. therondi* while it is glabrous in *E. henoni*. Further differences are found on male genitalia: Eighth sternite (Figs 118–119) is more slender, setae on apex are shorter; eighth sternite and tergite apically more slender (seen from lateral view; compare Figs 48 and 122). The rest of the male genitalia is markedly similar between the two species.

Differential diagnosis. *E. therondi* most resembles the Saharan species *E. henoni*, differing from it by rugulose-lacunose anterior face of protibia (glabrous in *E. henoni*), and the different structure of the frons (*E. henoni* has its frons glabrous with two chevrons whereas *E. therondi* has the chevrons surrounded by tiny rugae).

Biology. Unknown, found in a stomach of Kentish plover (*Charadrius alexandrinus* L.).

Distribution. Known only from Afghanistan: Hamud-i-Sabari.

Remarks. Although this newly described species does strongly resemble the Saharan species *E. henoni*, and it has furthermore been found in a stomach of a bird, it is unlikely that they are conspecific, given the vast geographic stretch between African Sahara and Afghanistan. If it had been consumed by a Kentish plover in Africa and

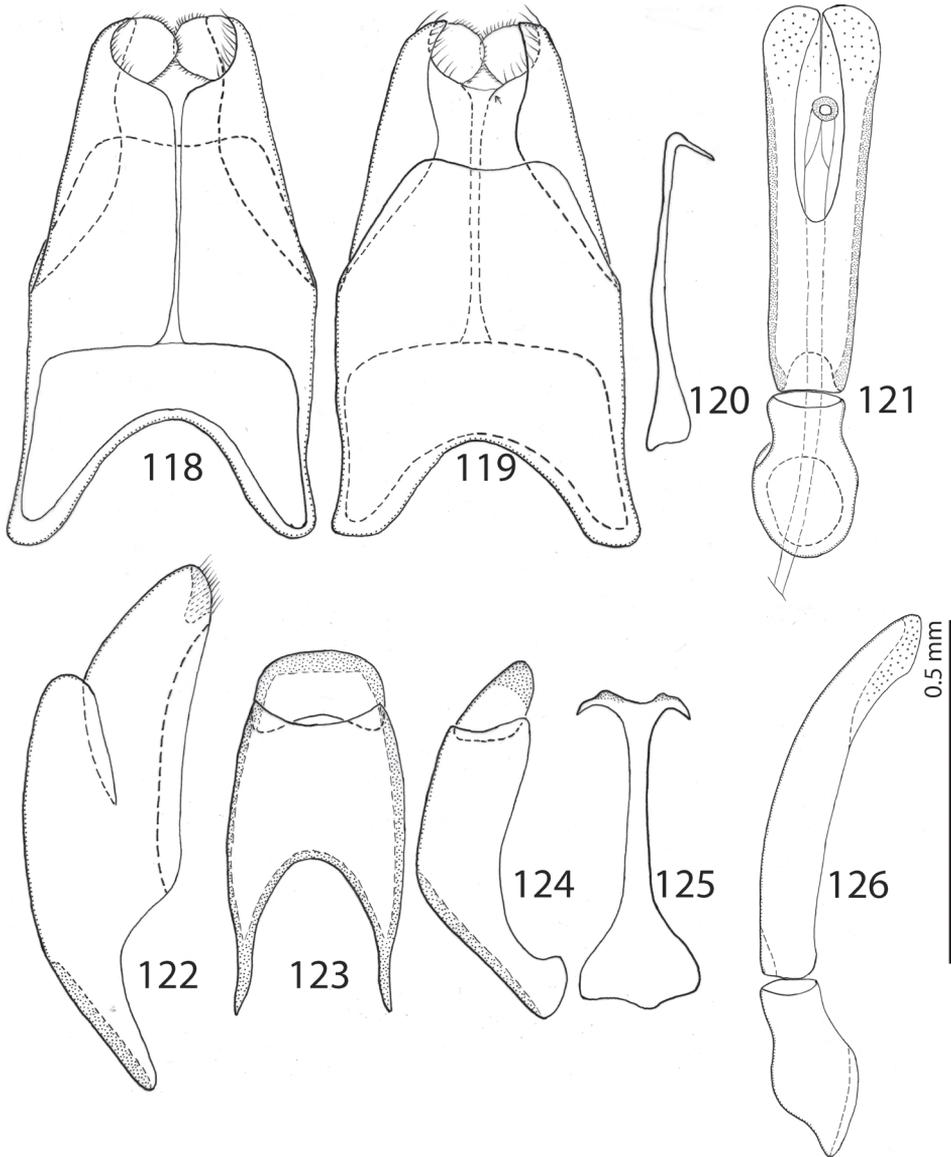


Figure 118–126. *Exaesiopus therondi* sp. n. 8th sternite + tergite, **118** ventral view **119** ditto, dorsal view **120** spiculum gastrale, lateral view **121** aedeagus, dorsal view **122** 8th sternite + tergite, lateral view **123** 9th + 10th tergites, dorsal view **124** ditto, lateral view **125** spiculum gastrale, ventral view **126** aedeagus, lateral view.

discovered in its stomach in Afghanistan it would have probably passed through the digestive tract of the bird by the time the bird migrated from the Sahara Desert to Afghanistan and would be beneath recognition at best. Instead, given the perfect shape of the insect, I consider it highly probable that the bird consumed it in Afghanistan and thus this species is an element of the Afghan fauna.

Key to the species of the genus *Exaesiopus* Reichardt, 1926

- 1 (2) Mesotibia only slightly thickened and dilated (Fig. 106); protibial spur distinct (Fig. 105); species from Namibia and the Republic of South Africa.....
.....*Exaesiopus glaucus* (Bickhardt, 1914), **comb. n.**
- 2 (1) Mesotibia strongly dilated and thickened (Fig. 97); protibial spur tiny, not easily observable to outright absent (Fig. 96), species from the Palearctic Region or Horn of Africa.
- 3 (8) Protibia with two large teeth topped by large triangular denticle followed by one to three tiny denticles entombed in outer protibial margin (Figs 43, 96, 117).
- 4 (5) Anterior face of protibia (Fig. 43) glabrous; prosternal foveae (Fig. 39) inconspicuous (absent?); species from the Sahara (Morocco, Algeria, Libya) and Djibouti..... *Exaesiopus henoni* (Schmidt, 1896)
- 5 (4) Anterior face of protibia (Figs 96, 117) obscurely variolate to rugulose lacunose; prosternal foveae tiny, but observable (Fig. 93); species from Somalia and Afghanistan.
- 6 (7) Almost completely glabrous species, with scattered faint punctation on pronotum only (Fig. 89); inner subhumeral stria absent; frons (Fig. 91) with two well-marked chevrons without additional rugae, species from extreme northern tip of Somalia.....*Exaesiopus laevis* Thérond, 1964
- 7 (6) Punctate species (Fig. 114); frons (Fig. 115) except for chevrons also with additional tiny rugae, species from Afghanistan*Exaesiopus therondi* sp. n.
- 8 (3) Protibia on outer margin with two to three low teeth topped by large triangular or rounded denticles, followed by two to three lower rounded denticles entombed in outer protibial margin (Figs 10, 61, 79).
- 9 (10) Elytral punctation mostly confined to apical third to half of elytra, never occupying all elytral intervals; species with feeble to distinct green metallic hue (Fig. 73)..... *Exaesiopus atrovirens* Reichardt, 1926
- 10 (9) Elytral punctation occasionally entering elytral intervals, in extreme cases covering entire elytral disc (Fig. 55); species without metallic hue.
- 11 (12) Punctuation of pronotum reaches pronotal margin, covering almost entire pronotal disc (Fig. 55); male genitalia: eighth tergite and sternite slightly more dilated than in the following species; aedeagus parallel-sided (Figs 64–72), species from S Russia and Middle Asia (Kazakhstan, Uzbekistan)
.....*Exaesiopus torvus* Reichardt, 1926
- 12 (11) Punctuation of pronotum does not reach pronotal margin, leaving antero-medial part of pronotum glabrous (Fig. 1); male genitalia: eighth sternite and tergite slightly more slender than in the preceding species; aedeagus on apical half slightly thickened (Figs 17–34), species from the circum-Mediterranean, Canary Islands, S Europe and Iraq.... *Exaesiopus grossipes* (Marseul, 1855)

Discussion

Exaesiopus is a taxon that is morphologically well adapted to the psammophilous and fossorial way of life by the thickened metafemora as well as dilated pro- and especially metatibiae. A setose underside of the body is common to most obligate psammophiles in Histeridae and serves as further adaptation to life in sand; setae possibly prevent tiny particles of sand entering the body cavities. Although morphologically united by at least one weak synapomorphy (ciliate pronotal hypomeron), which is possibly a parallelism shared by some *Hypocaccus* spp. from North America, the monophyly of the genus *Exaesiopus* is likely questionable. The taxonomical uncertainties between (mostly) littoral taxa *Hypocaccus*, *Exaesiopus*, *Pachylopus*, *Neopachylopus*, *Eopachylopus*, etc. lie chiefly in the morphological similarities resulting from ecological pressures causing multiple parallelisms and convergences of characters. A future phylogenetic analysis of all littoral *Hypocaccus*-like taxa should focus on characters in systems putatively independent of the environmental selection pressures; otherwise characters that are prone to homoplasies (e.g. setae, denticles, rugae, trichomes etc.) could continue to obscure true phylogenetic relationships. In the recently published phylogeny of the subfamily by the author (Lackner 2014d), which included mostly the type species of the Sapriniinae genera, the type species of *Exaesiopus* was recovered among the members of a large clade of mostly psammophilous taxa whose inter-relationships are unresolved.

Members of *Exaesiopus* are found in sandy soils or in sand over a vast geographic area rivalling perhaps only the distribution of *Xenonychus* Wollaston, 1864 (see also Lackner 2012). The distribution of *Exaesiopus* covers the area from the Canary Islands, circum-Mediterranean, South Europe, Caucasus, Iraq, Somalia, Djibouti, as far east as Afghanistan. Identity of the Somali species *E. laevis* Théron, 1964 is uncertain; the species is known from a single female only. Other related genera (sensu Lackner, 2014) e.g. the species-rich and widespread *Hypocaccus* or *Hypocacculus*, or monotypic and localized *Eopachylopus*, *Reichardtia* etc., are distributed along most of the world beaches, as well as inland sand-systems; their inter-relationships shall be the focus of future phylogenetic studies.

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Two new species of *Stenochironomus* Kieffer (Diptera, Chironomidae) from Zhejiang, China

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Abstract

Two new species of *Stenochironomus* Kieffer (Diptera: Chironomidae: Chironominae), *S. brevissimus* **sp. n.** and *S. linanensis* **sp. n.**, are described from China and the male imagines are illustrated. *S. brevissimus* **sp. n.** can be separated from the so far known species by having very short and small, spatulate superior volsella with two long setae, whereas *S. linanensis* **sp. n.** is easily separated from the other species of *Stenochironomus* by the following characters: wings transparent, body yellow, superior volsella finger-like, with nine long setae, elongated inferior volsella with four long setae and one well developed terminal spine; tergite IX with 10–15 long setae medially. A key to the males of *Stenochironomus* occurring in China is given.

Keywords

Stenochironomus, new species, key, China

Introduction

Stenochironomus Kieffer, 1919 is a species-rich genus with worldwide distribution, occurring in all biogeographical regions except in Antarctica (Cranston et al. 1989). The genus was erected by Townes in 1945 based on *Chironomus pulchripennis* (Coquillett, 1902) (Spies and Sæther 2004). The larvae are easily found mining decayed leaves or

wood in freshwater habitats ranging from small ponds and swamps to fast-flowing streams and rivers (Cranston et al. 1989). Based on the different hosts of larvae and pupae, Borkent (1984) erected two subgenera: *Stenochironomus s. str.* Kieffer (larvae and pupae mine dead submerged wood) and *Petalopholeus* Borkent (larvae and pupae mine dead submerged leaves). This subdivision has not been adopted by subsequent authors, because immature stages are known only for a few species, which makes difficult to ascribe them to any subgenus (Pinho et al. 2005, Andersen et al. 2008, Qi et al. 2008, Dantas et al. 2010, Zorina 2010). To date, there are 97 species recorded around the world: 24 species from the Palearctic Region, 17 from the Nearctic Region, 30 from the Neotropical Region, 16 from the Oriental Region, 16 from the Afrotropical Region and 4 from the Australasian Region (Qi et al. 2011, Reis et al. 2013).

Zhejiang Province is located in the Chinese central subtropical region, which has a humid monsoon climate. In Zhejiang, three species of *Stenochironomus* [*S. koreanus* Borkent, 1984, *S. nubilipennis* Yamamoto, 1981 and *S. satorui* (Tokunaga & Kuroda, 1936)] have been recorded (Wang 2000, Qi et al. 2011). In this paper, two new species of *Stenochironomus* from Zhejiang, Oriental China, are described and illustrated. A key to the males of *Stenochironomus* from China is presented.

Materials and methods

The morphological nomenclature follows Sæther (1980). Measurement methods follow Qi et al. (2012). The material examined was slide-mounted, following the procedure outlined by Sæther (1969). Specimens have been deposited in the College of Life Science, Taizhou University, China.

Abbreviations of parts measured are as follows:

AR	Antennal ration, length of 13 th / length of flagellomeres 1–12
Palpomere ratio (5th/3rd)	Length of the 5 th Palpomere / length of the 3 rd Palpomere
VR	Venarum ration, length of Cubitus (Cu) / length of Media (M)
BV	Length of (femur + tibia + ta ₁) / length of (ta ₂ + ta ₃ + ta ₄ + ta ₅)
LR	Leg ration, length of ta ₁ / length of tibia
SV	Length of (femur + tibia) / length of ta ₁
HR	Hypopygium ration, length of gonocoxite / length of gonostylus
HV	Hypopygium value, total length / length of gonostylus times ten
p₁	Fore leg
p₂	Mid leg
p₃	Hind leg
fe	femur
ti	tibia
ta₁...ta_n	tarsus ₁ ...tarsus _n
R	Radius
R₁	Radius 1 vein
R₄₊₅	Radius 4+5 vein

Taxonomy

Stenochironomus brevissimus sp. n.

<http://zoobank.org/ADC155AF-0069-4052-8907-191E35A59854>

Figs 1–10

Diagnosis. The adult male of *S. brevissimus* sp. n. can be distinguished from all other species of *Stenochironomus* by the following combination of characters: superior volsella very short and small, spatulate, with 2 long setae, elongated inferior volsella with 6 long setae, posterior margin of tergite IX with 20–22 setae and 8 spines.

Description. Male imago (n = 3). Total length 4.3–4.6 mm. Wing length 2.2–2.5 mm. Total length / wing length 1.8–1.9. Wing length / length of profemur 1.7–1.8.

Coloration. Head yellow, antenna brown. Thorax light yellow, postnotum and scutum with brown spots. Wings transparent, without any pigmentation. Abdomen and hypopygium yellow, anal point brown. Fore legs yellow with femur apically brown. Mid legs with apex and posterior basal region of femur with dark brown stripes, tibia brown, tarsomeres 1–5 yellow. Hind legs brown with femur yellow with dark brown stripes at apex.

Head (Fig. 1). AR 1.80–1.92. Temporal with 10–12 setae. Clypeus with 20–22 setae. Tentorium 173–176 mm long, 43–46 mm wide. Stipes 140–145 μm long, 10–13 μm wide. Palpomere lengths (in mm): 60–63, 60–65, 210–230, 140–150, 260–300. Palpomere ratio (5th/3rd) 1.2–1.3.

Wings (Fig. 2). VR 1.08–1.15. Brachiolum with 3–4 setae; R with 25–32 setae, R₁ with 27–30 setae, R₄₊₅ with 41–42 setae. Squama with 8–10 setae.

Thorax (Fig. 3). Dorsocentrals 12–14, acrostichals 14–16, prealars 4–5. Scutellum with 6–7 setae.

Legs (Fig. 4). Fore leg: width at apex of tibia 60–65 mm, tibia with scale 53–56 μm long, with 2–4 strong setae (Fig. 5). Mid leg: width at apex of tibia 80–83 mm, tibia with two apical spurs 40–50, 43–53 μm long. Hind leg: width at apex of tibia 70–80 mm, tibia with two apical spurs 40–50, 40–55 μm long. Mid and hind tibiae with fused combs (Figs 6–7), each comb 36–50 μm long. Lengths (in mm) and proportions of legs in Table 1.

Hypopygium (Fig. 8). Anal point 113–120 mm long, 15–20 μm wide at base, 13–15 μm wide at apex, parallel-sided, slender, apically rounded. Tergite IX with 16–17 long setae medially, posterior margin of tergite IX with 20–22 setae and 8 spines (Fig. 9). Phallapodeme 120–123 mm long; transverse sternapodeme 30–50 mm long. Gonocoxite 200–230 mm long. Superior volsella short, small and spatulate, 16–18 mm long, 20–22 mm wide, with 2 long setae (Fig. 10). Inferior volsella elongated, 190–200 mm long, with 6 long setae. Gonostylus 210–230 mm long, with 4 long setae along inner margin in distal 1/3. HR 0.95–1.00, HV 1.89–2.04.

Female, pupa and larva. Unknown.

Type material. Holotype: Male, CHINA, Zhejiang, Quzhou City, Hunan County, 19.iv.2012, leg. XL Lin, sweep net. 2 Paratypes: 2 males, same data as holotype.

Table 1. Lengths (in μm) and proportions of leg segments in *Stenochironomus brevissimus* sp. n. (n = 3).

	P ₁	P ₂	P ₃
Fe	1300–1400	1125–1200	1325–1525
Ti	1300–1500	1000–1125	1275–1400
ta ₁	1500–1600	725–800	950–1100
ta ₂	775–875	375–450	525–625
ta ₃	675–750	340–410	440–500
ta ₄	525–600	200–290	260–360
ta ₅	250–300	90–110	110–130
LR	1.07–1.15	0.71–0.73	0.74–0.79
BV	1.78–1.84	2.48–2.83	2.49–2.66
SV	1.73–1.81	2.91–2.95	2.66–2.74

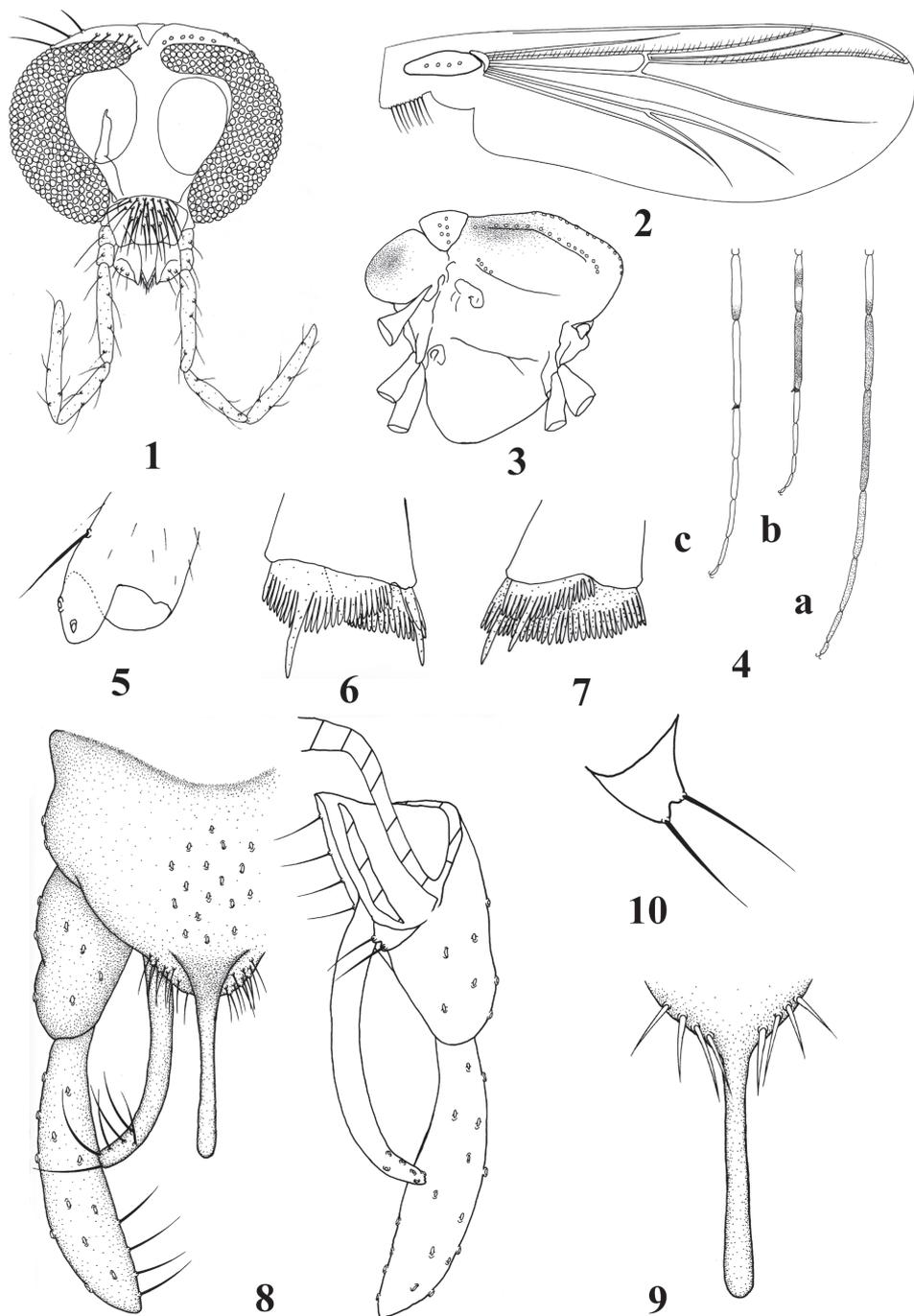
Table 2. Main differences between *S. brevissimus* sp. n., *S. hainanus* and *S. okialbus*.

	<i>S. brevissimus</i>	<i>S. hainanus</i>	<i>S. okialbus</i>
Wing	transparent, without any pigmentation	transparent, without any pigmentation	with dark bands across the middle and posterior area
Coloration	thorax light yellow, postnotum and scutum with brown spots; fore legs yellow with femur apically brown; mid legs with apex and posterior basal region of femur with dark brown stripes, tibia brown, tarsomeres 1–5 yellow; hind legs brown with femur yellow with dark brown stripes at apex	whole body yellow, without dark pigmentation	thorax yellow; fore legs yellow with femur apically brown, apex and basal region of tibia with dark brown stripes; mid legs yellow with femur apically brown; hind legs yellow with femur apically brown
Superior volsella	with 2 setae	with 3 setae	with 4 setae
Inferior volsella	with 6 setae	with 3 setae	with 4 setae and a strong terminal spine
Posterior margin of tergite IX	with 20–22 setae and 8 spines	with 16 setae	with 8 setae and 8 spines

Etymology. The specific epithet is a Latin adjective “*brevissimus*”, meaning the shortest, and refers to the superior volsella, which is the shortest in the genus.

Remarks. *S. brevissimus* sp. n. is similar to *S. hainanus* Qi, Shi & Wang, 2008 and *S. okialbus* Sasa, 1990 in having short and small superior volsella, but can separated from these species by the differences given in Table 2.

Distribution. The species is currently known only from Zhejiang Province of Oriental China.



Figures 1–10. *Stenochironomus brevisimus* sp. n., male. **1** head **2** wing **3** thorax, lateral view **4** legs coloration (a. fore leg; b. mid leg; c. hind leg) **5** fore tibial apex, ventral view **6** mid tibial apex, lateral view **7** hind tibial apex, lateral view **8** hypopygium **9** spines on posterior margin of tergite IX, ventral view **10** superior volsella.

***Stenochironomus linanensis* sp. n.**

<http://zoobank.org/F01888A4-0CA1-4041-9290-12B68CFA5BA0>

Figs 11–18

Diagnosis. The adult male of *S. linanensis* sp. n. can be distinguished from all other species of *Stenochironomus* by the following combination of characters: wings transparent, body yellow, superior volsella finger-like, with 9 long setae, elongated inferior volsella with 4 long setae and one well-developed terminal spine, tergite IX with 10–15 long setae medially.

Description. Male imago (n = 5). Total length 2.9–3.8 mm. Wing length 1.4–1.5 mm. Total length / wing length 1.98–2.41. Wing length / length of profemur 1.30–1.57.

Coloration. Head yellow. Thorax greenish yellow. Wings transparent, without any pigmentation. Abdomen yellow, hypopygium brown. Legs pale yellow.

Head (Fig. 11). AR 1.20–1.32. Temporal with 8–14 setae. Clypeus with 9–10 setae. Tentorium 153–156 mm long, 37–42 mm wide. Stipes 72–95 μm long, 5–6 μm wide. Palpomere lengths (in mm): 45–47, 28–33, 53–60, 75–90, 110–120. Palpomere ratio ($5^{\text{th}}/3^{\text{rd}}$) 2.00–2.07.

Wings (Fig. 12). VR 1.07–1.20. Brachiolum with 2 setae; R with 16–23 setae, R_1 with 17–18 setae, R_{4+5} with 22–28 setae. Squama with 5–7 setae.

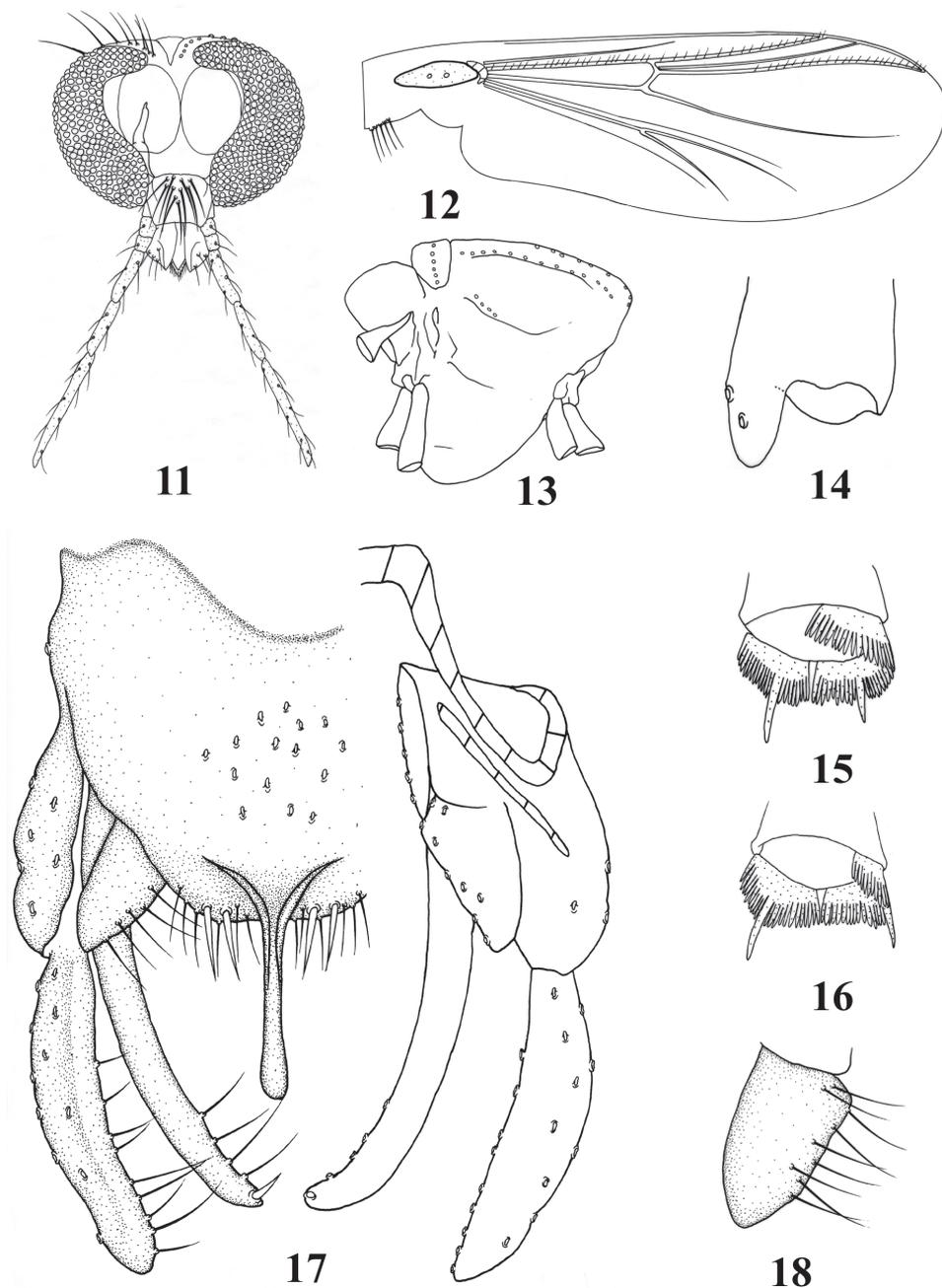
Thorax (Fig. 13). Dorsocentrals 9–13, acrostichals 9–14, prealars 4–5. Scutellum with 5–6 setae.

Legs. Fore leg: width at apex of tibia 33–47 mm, tibia with scale 33–46 μm long, with 2–3 strong setae (Fig. 14). Mid leg: width at apex of tibia 50–65 mm, tibia with two apical spurs 25–28, 30–40 μm long. Hind leg: width at apex of tibia 50–60 mm, tibia with two apical spurs 32–39, 35–40 μm long. Mid and hind tibiae with fused combs (Fig. 15–16), each comb 18–22 mm long. Lengths (in mm) and proportions of legs in Table 3.

Hypopygium (Fig. 17). Anal point 65–73 mm long, 14–20 μm wide at base, 6–8 μm wide at apex, apex of anal point slightly swollen and rounded. Tergite IX

Table 3. Lengths (in μm) and proportions of leg segments in *Stenochironomus linanensis* sp. n.

	P_1	P_2	P_3
fe	925–1075	625–700	650–725
ti	700–875	650–725	750–900
ta_1	925–1100	475–550	780–950
ta_2	500–725	200–260	400–600
ta_3	400–500	210–300	300–350
ta_4	320–400	130–200	240–300
ta_5	140–200	70–80	100–120
LR	1.25–1.32	0.73–0.75	1.04–1.06
BV	1.67–1.88	2.35–2.87	1.88–2.10
SV	1.76–1.83	2.60–2.68	1.71–1.79



Figures 11–18. *Stenochironomus linanensis* sp. n., male. **11** head **12** wing **13** thorax, lateral view **14** fore tibial apex, ventral view **15** mid tibial apex, lateral view **16** hind tibial apex, lateral view **17** hypopygium **18** superior volsella.

Table 4. Main differences between *S. linanese* sp. n., *S. macateei*, *S. maculatus* and *S. recticaudatus*.

	<i>S. linanese</i>	<i>S. macateei</i>	<i>S. maculatus</i>	<i>S. recticaudatus</i>
Wing	transparent	transparent	entire wing with pigmentation	transparent
Median setae of tergite IX	10–15	35–37	25–28	35–37
posterior margin of tergite IX	with 12–14 setae and 4 spines	with 8 setae and 6 spines	with 8 setae and 4 spines	with 14 setae and 8 spines
Anal point	apex of anal point slightly swollen and rounded	parallel-sided	apex of anal point slightly swollen and rounded	apex of anal point slightly swollen and rounded
Superior volsella	with 9 setae	with 4–5 setae	with 4–6 setae	with 6 setae
Coloration	whole body yellow, without dark pigmentation	whole body yellow, without dark pigmentation	postnotum, scutum and scutellum with dark pigmentation; other parts of body yellow	dark pigmentation entirely absent except on tarsomeres 3–5 of all legs

with 10–15 long setae medially, posterior margin of tergite IX with 12–14 setae and 4 spines. Phallapodeme 70–80 mm long; transverse sternapodeme 35–38 mm long. Gonocoxite 160–180 mm long. Superior volsella finger-like, 53–63 mm long, 25–27 mm wide, with 9 long setae (Fig. 18). Inferior volsella elongated, 160–170 mm long, with 4 long setae and one well-developed terminal spine. Gonostylus 123–170 mm long, with 9 long setae along inner margin in distal 1/2. HR 0.94–1.47, HV 1.98–2.35.

Female, pupa and larva. Unknown.

Type material. Holotype: Male, CHINA, Zhejiang, Linan City, Qingliangfeng Mountain, 16.v.2012, leg. XL Lin, sweep net. 4 Paratypes: 4 males, same data as holotype.

Etymology. The specific epithet is an adjective referring to the type locality, Linan City.

Remarks. *S. linanensis* sp. n. is similar to *S. macateei* (Malloch, 1905), *S. maculatus* Borkent, 1984 and *S. recticaudatus* Borkent, 1984 in the structure of the hypopygium and the inferior volsella with a strong terminal spine, but can be separated from these species by the differences given in Table 4.

Distribution. The species is known from Zhejiang Province of Oriental China.

Key to males of the genus *Stenochironomus* in China

- 1 Inferior volsella with a well-developed terminal spine 2
- Inferior volsella without a well-developed terminal spine 7
- 2 Wing membranes with dark pigmentation 3
- Wing membranes without any pigmentation 4
- 3 Legs almost entire brown, posterior area smoky area between veins C and M pale *S. gibbus* (Fabricius, 1805)

- Legs yellow; entire wing smoky gray ***S. maculatus* Borkent, 1984**
- 4 Apex of anal point swollen and rounded **5**
- Apex of anal point not swollen and rounded **6**
- 5 Superior volsella with 9 setae; posterior margin of tergite IX with 12–14 setae and 4 spines ***S. linanensis* sp. n.**
- Superior volsella with 4 setae; posterior margin of tergite IX with 14–16 setae ***S. koreanus* Borkent, 1984**
- 6 Posterior edge of tergite IX with 8 long setae and 6 spines; anal point parallel-sided ***S. macateei* (Malloch, 1915)**
- Posterior edge of tergite IX with 14 long setae, without any spine; anal point roughly triangular, apically pointed... ***S. mucronatus* Qi, Shi & Wang, 2008**
- 7 Wing membranes with dark pigmentation **8**
- Wings without any pigmentation or with narrow pigment areas around RM and along veins M_{3+4} and Cu_1 **10**
- 8 Abdomen and hypopygium light yellow ***S. inalemeus* Sasa, 2001**
- Abdominal tergites I–IV light yellow, tergites V–VIII light brown, hypopygium dark brown **9**
- 9 Preepisternum with brown spots; anal point slender and parallel-sided, apically rounded ***S. nubilipennis* Yamamoto, 1981**
- Preepisternum without any pigmentation; anal point slender and parallel-sided, apically pointed ***S. satorui* (Tokunaga & Kuroda, 1936)**
- 10 Posterior margin of tergite IX with spines ***S. brevissimus* sp. n.**
- Posterior margin of tergite IX without spines **11**
- 11 Entire body yellow, without dark pigmentation; wings transparent, without any pigmentation; inferior volsella with 3 long setae ***S. hainanus* Qi, Shi & Wang, 2008**
- Body yellow, with brown spots on thorax, abdomen, hypopygium and legs; wings with narrow pigment areas around RM and along veins M_{3+4} and Cu_1 ; inferior volsella with 6 long setae ***S. totifuscus* Sublette, 1960**

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Description of *Telamoptilia grewiae* sp. n. and the consequences for the definition of the genera *Telamoptilia* and *Spulerina* (Lepidoptera, Gracillariidae, Gracillariinae)

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Abstract

The new species *Telamoptilia grewiae*, reared from leafmines on *Grewia biloba* (Malvaceae) is described with details on adult and immature stages. The larval head and the pupa are described for the first time in *Telamoptilia* Kumata & Kuroko, 1988, and are illustrated with scanning electron micrographs and line drawings. Photographs of adult habitus, wing venation, male and female genitalia, as well as host plant and mines are provided. The apomorphic adult and larval characters of the new species in *Telamoptilia* are discussed in relation to the recognition of the genera *Telamoptilia* and *Spulerina* Vári, 1961.

Keywords

Lepidoptera, *Telamoptilia*, new species, immature stage, leaf miner, China

Introduction

The genus *Telamoptilia* Kumata & Kuroko, 1988 is globally represented by five species that may be found in the Oriental and African regions. The type species *T. cathedraea* (Meyrick, 1908) is geographically shared by the Oriental Region and Madagascar (De Prins and De Prins 2014). Three species are currently known from China, including *T. cathedraea*, *T. hemistacta* (Meyrick, 1924), and *T. prosacta* (Meyrick, 1918).

The larvae of *Telamoptilia* species are leaf miners. Three plant families are known as hosts for *Telamoptilia*: Malvaceae, Amaranthaceae and Convolvulaceae (De Prins and De Prins 2014). Vári (1961) briefly described the biology of *T. geyeri* (Vári, 1961). Kumata et al. (1988) described the biology and the larval body chaetotaxy of three species: *T. cathedraea*, *T. prosacta* and *T. tiliae* (Kumata & Ermolaev, 1988). However, no larval head chaetotaxy and pupal features of *Telamoptilia* have been described so far.

Telamoptilia grewiae sp. n. is associated with Malvaceae and is described in the present paper from adult external characters, male and female genitalia, wing venation and immature stages. The larval head and pupal features are described for the first time in *Telamoptilia*.

Methods

Field investigations were carried out in Mt. Baxian National Nature Reserves (40°11'N, 117°32'E), 300–600 m, Tianjin, China, from May to September in 2013 and June 2014. Leaves containing mines with larvae were placed in sealed plastic bags, or rearing containers with moist cotton. Larvae removed from mines were immersed in nearly boiling water for 30 seconds, and then were kept in 75% ethanol for morphological examination. Last instar larval skins, pupae, and exuviae were kept in 75% ethanol. Pupae in rearing containers were placed outdoors to overwinter, and were transferred into the laboratory at 20 °C on February 6, 2014. Emergence successively occurred from March 9 to early-April 2014. Adults were collected chiefly by rearing from immature stages, and occasionally by light trap.

Adult photographs were taken with a Leica M250A stereo microscope. Genitalia and wings were dissected and mounted according to the methods introduced by Li (2002), but stained with Eosin Y and/or Chlorazol Black, and the illustrations were prepared by using a Leica DM750 microscope, and refined in Photoshop® CS4 software. For scanning electron microscopy, larvae and pupae were dehydrated in gradient ethanol, dried in vacuum and coated with gold in a SCD 005 Sputter Coater (BAL-TEC), then operated with a voltage of 15 kV using Quanta 200 environmental scanning electron microscope (SEM) (FEI, Oregon). Line drawings were outlined from the photos taken by the Leica M250A stereo microscope, using path tool in Adobe Photoshop® CS4 software. Photographs of host plant, mines and a live adult were taken in the field using Canon PowerShot G10 digital camera.

Terminology of immature stages follows Davis and De Prins (2011) and De Prins et al. (2013), and that of adults follows Kumata et al. (1988). Thoracic segments I–III and abdominal segments 1–10 are abbreviated as TI–TIII and A1–A10, respectively.

All the specimens studied, including the types of the new species and the vouchered larvae and pupae, are deposited in the Insect Collection, Nankai University, Tianjin, China.

Taxonomy

Telamoptilia grewiae sp. n.

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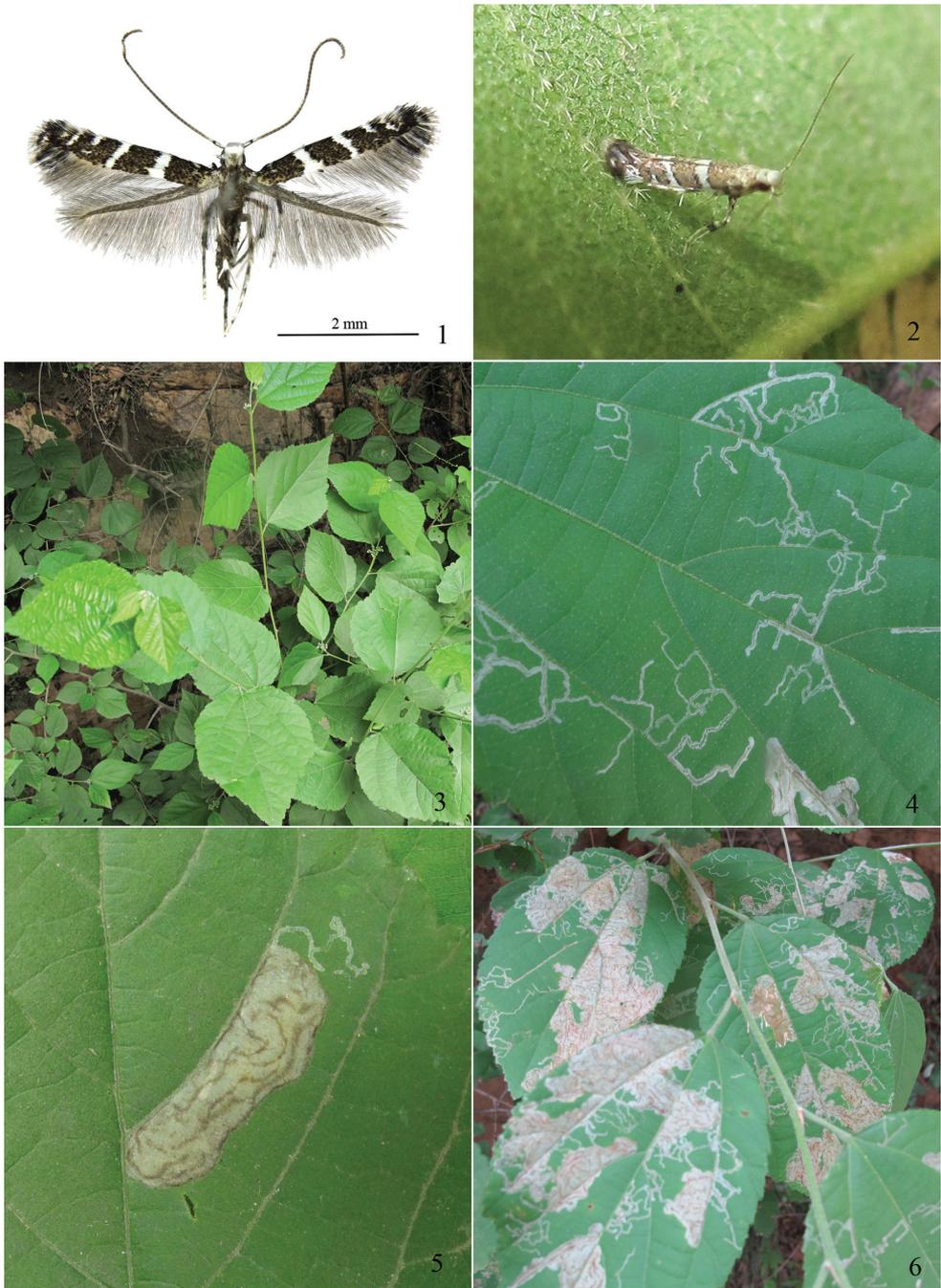
Figures 1–32

Description. Adults (Figs 1–2) with wing span 6.0–8.0 mm. Head silvery white, tinged with gray on face. Labial palpus grayish white, colored blackish gray on outer surface of distal half of second segment and before apex of third segment. Maxillary palpus white, with middle or distal half blackish fuscous. Antenna with scape white on posterior half, blackish gray on anterior half and distal portion, flap blackish gray tinged with white, as wide as scape in frontal view; flagellum silvery grayish fuscous, with each unit blackish distally. Thorax and tegula blackish gray mixed with white. Legs mostly white; foreleg with coxa blackish fuscous basally and distally, femur and tibia blackish fuscous, tarsus blackish gray distally on each except last segment; midleg with coxa blackish fuscous distally, femur blackish fuscous, except white medially and distally on dorsal surface, with ventral scale expansion blackish fuscous, tibia blackish fuscous basally and distally, white medially, tarsus white, each except last segment dotted blackish fuscous distally; hindleg with coxa blackish fuscous distally, femur blackish fuscous distally on outer surface, tibia blackish fuscous basally and distally, tarsus with basal three segments blackish fuscous distally, fourth segment dotted blackish fuscous dorso-distally. Forewing grayish fuscous to blackish fuscous; costal margin with a white spot basally at about 1/10 and one before apex, the former sometimes touching fold posteriorly, with white stria at distal 3/10 and 1/6 obliquely outward, reaching middle of wing and near termen respectively; transverse white fascia from costal 1/3 and 1/2 obliquely outward, reaching dorsal 1/2 and before end of fold respectively, edged with blackish fuscous to black scales, inner fascia wider than outer one, widened on posterior half; small white dot on distal end of M_3 , two or three small white dots along termen; apex blackish fuscous; cilia mostly blackish fuscous basally, gray distally, white adjacent to white markings, white on basal 1/4, black on median part, gray distally at apex, gray along dorsal margin. Hindwing and cilia uniformly gray.

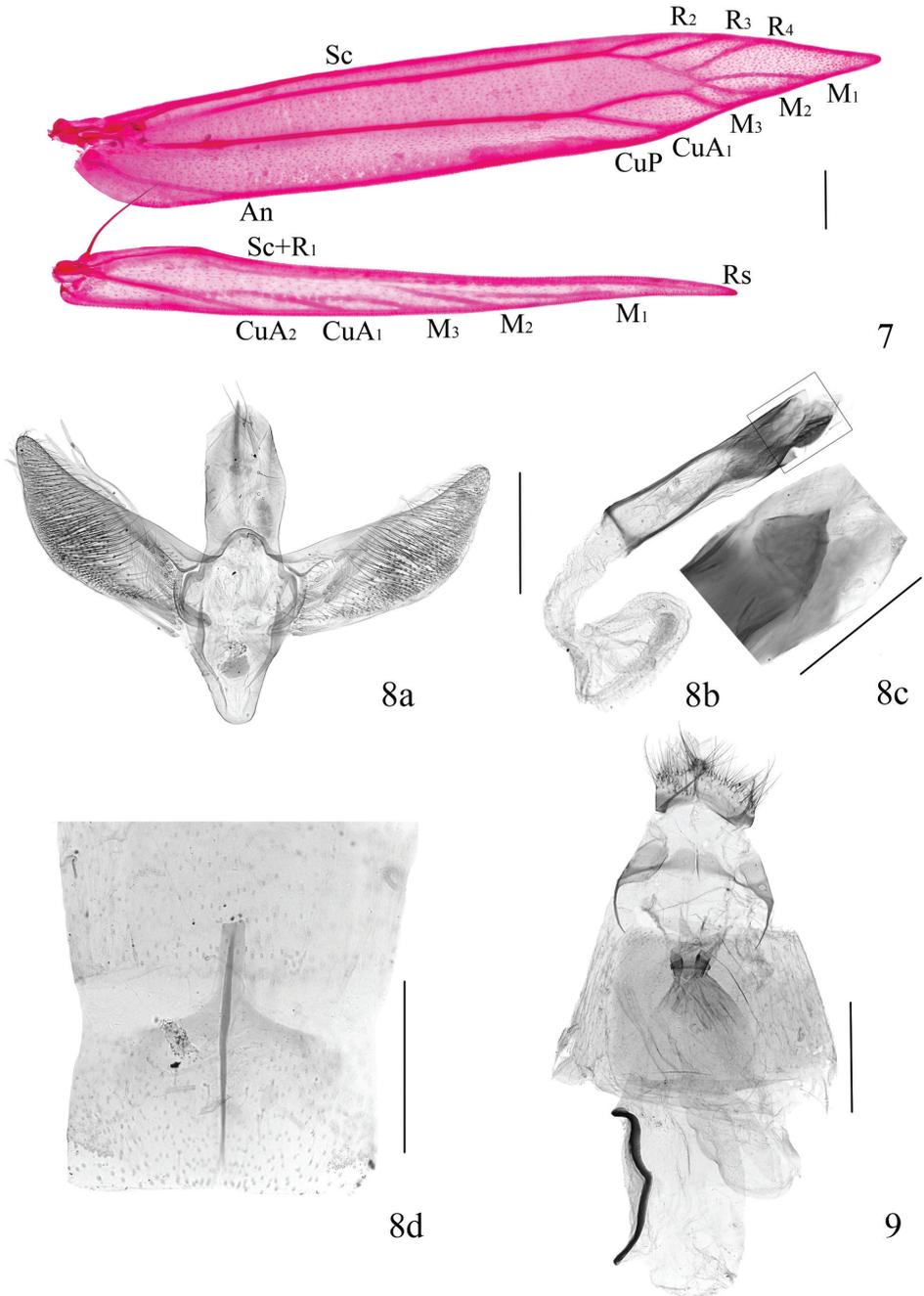
Variations. The white costal spot at about basal 1/10 is sometimes reduced to a small dot near the costa, the white costal stria at distal 3/10 is occasionally extended to unite the dot on the distal end of M_3 , the costal stria at distal 1/6 is sometimes wedge-shaped or absent, the white dot at the distal end of M_3 sometimes moves to near distal end of cell, and the small white dots along termen sometimes are absent.

Venation (Fig. 7). Forewing with R_5 totally untraceable, thus R_4 not stalked, otherwise matching the generic characters (Kumata et al. 1988), with most notably the absence of R_1 .

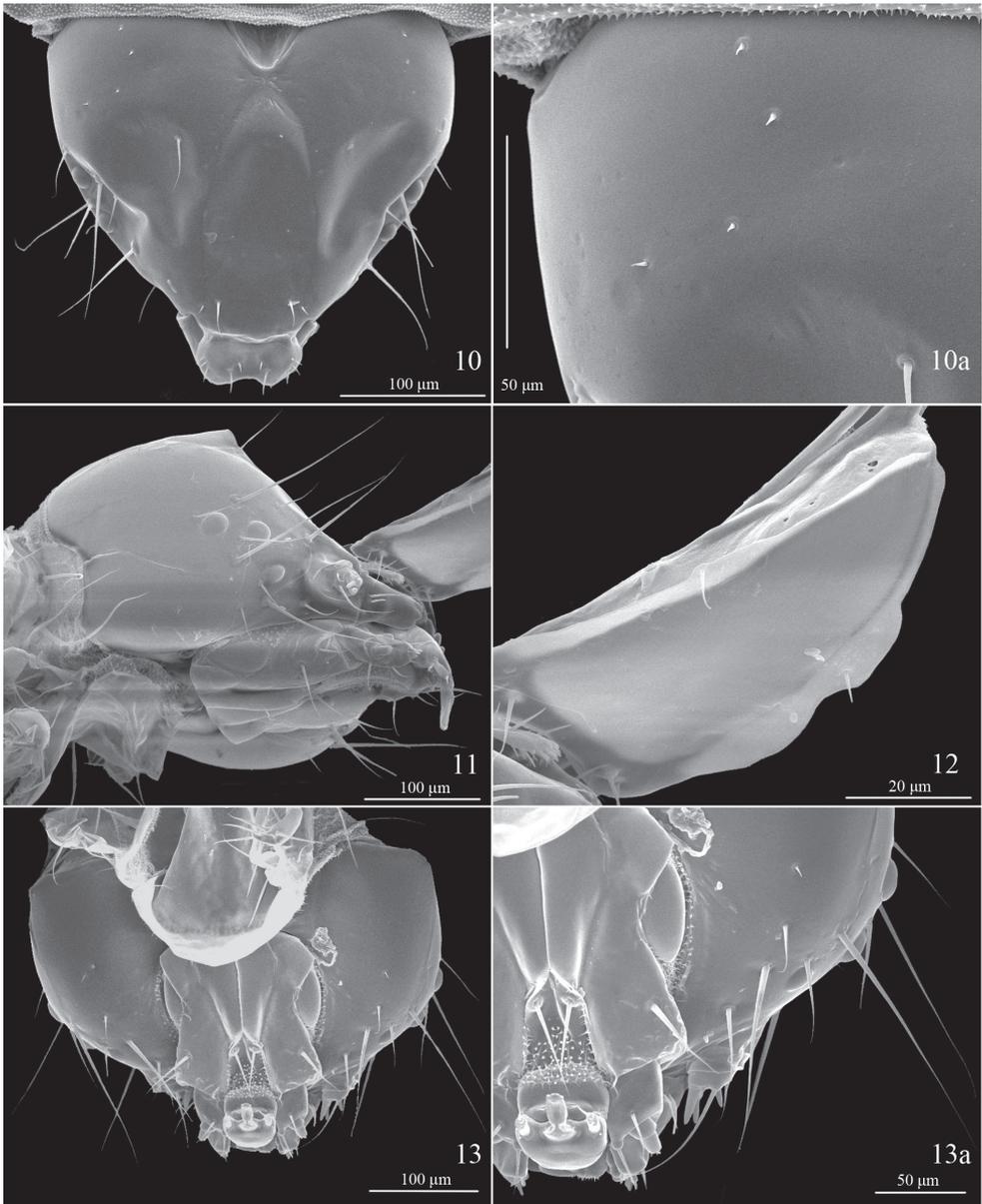
Male genitalia (Figs 8a–d). Tegumen with basal half same width, median portion slightly widened, distal half almost triangular, rounded apically; three or four long setae along lateral side. Valva 1.7 times as long as tegumen, with basal 3/4 same width, distal 1/4 apparently narrowed, bluntly pointed apically. Saccus subtriangular, rounded api-



Figures 1–6. Adult, host plant and mines of *Telamoptilia grewiae* sp. n. **1** Adult in habitus, paratype **2** Live adult **3** Host plant **4** Linear mines by early instar larvae **5** Blotch mine by later instar larva **6** Seriously damaged leaves found in September.

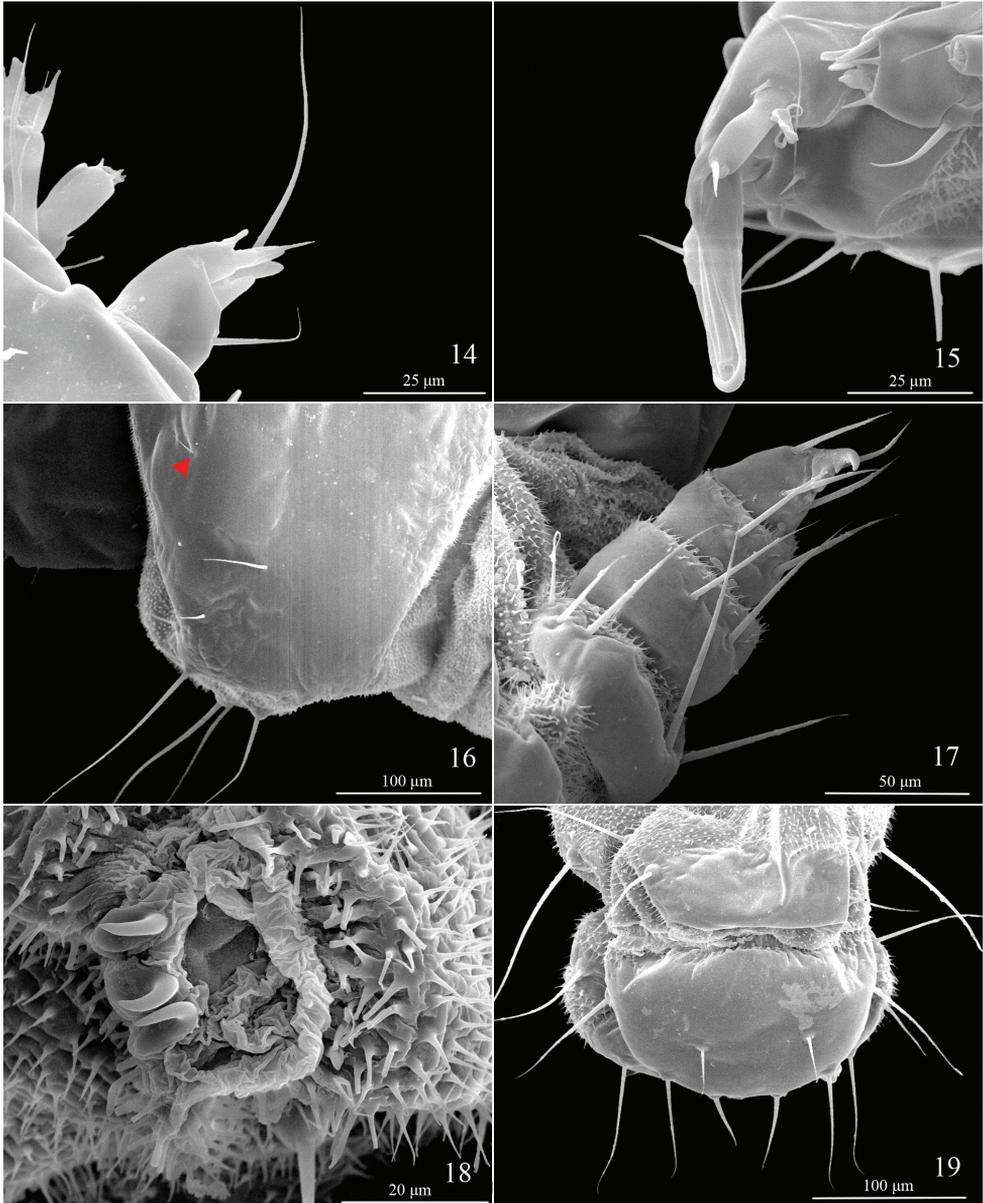


Figures 7–9. Wing venation and genitalia of *Telamoptilia grewiae* sp. n. **7** Wing venation, paratype, LTT12561W **8** Male genitalia, **8a**, male genitalia with aedeagus detached, LTT12561 **8b** aedeagus, lateral view, same slide as **8a**, **8c** close-up of the distal portion of aedeagus, indicating the triangular process, dorsal view, LTT12257, **8d**, eighth abdominal segment, paratype, same slide as **8a**, **9** Female genitalia, paratype, LTT12555 (Scales = 0.2 mm except **8c** = 0.1 mm).



Figures 10–13. Last instar larva head chaetotaxy of *Telamoptilia greviae* sp. n. **10** Dorsal view **10a** close-up of MD setae **11** Ventral-lateral view, scanned from last instar larval skin **12** Frons, frontal-lateral view, same individual as **11**, **13** Dorsal view **13a** close-up of SO and G setae.

cally. Aedeagus straight, almost as long as valva; distal half heavily sclerotized, with a triangular distal process about 1/8 length of aedeagus, pointed apically (Fig. 8c); vesica with dense spines becoming stronger towards distal (Fig. 8b). Eighth tergite with apodeme reaching posterior 1/3 of seventh segment, nearly parallel-sided (Fig. 8d).



Figures 14–19. Last instar larval characters of *Telamoptilia grewiae* sp. n. **14** Antenna **15** Mouthpart **16** Setae on prothorax shield, arrow indicating the position of XD1 **17** Thoracic leg **18** Proleg **19** A9–10, dorsal view.

Female genitalia (Fig. 9). Antrum a ring, disconnected ventrally, embed with a heavily sclerotized belt medially. Ductus bursae membranous, extremely short, not reaching anterior margin of seventh segment, wrinkled basally, without spines. Corpus bursae oval, membranous, without spines; signum slender and long, curved by 150°

medially, posterior half slightly S-shaped, anterior half curved at anterior 2/5, sometimes slightly C-shaped.

Last instar larva (Figs 10–23). Length 4.0 mm, pale green to yellowish green. Three stemmata present (Fig. 11). Spiracles on TI and A8 larger; prolegs on A3–5 each with 2–4 crochets (Fig. 18), those on A10 without crochets. (Five larvae and two last instar larval skins examined)

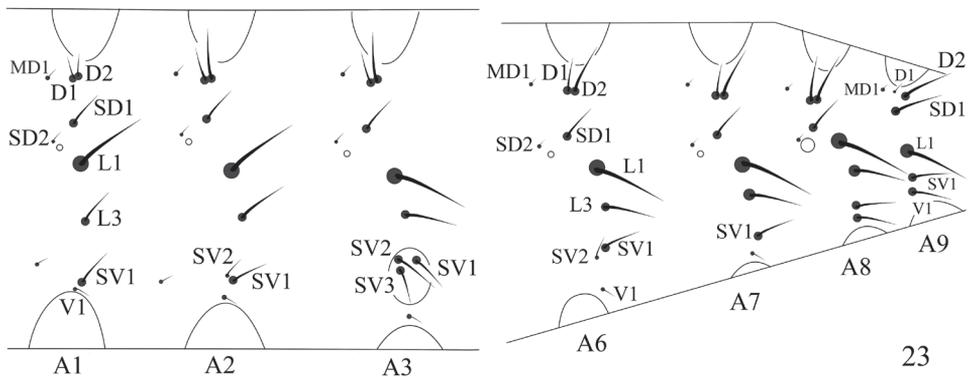
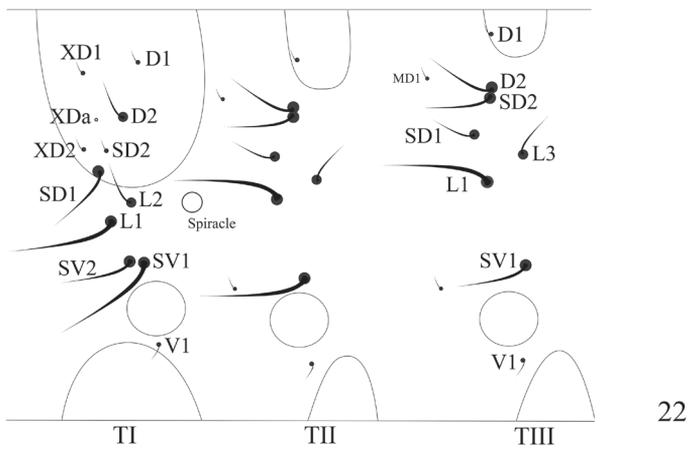
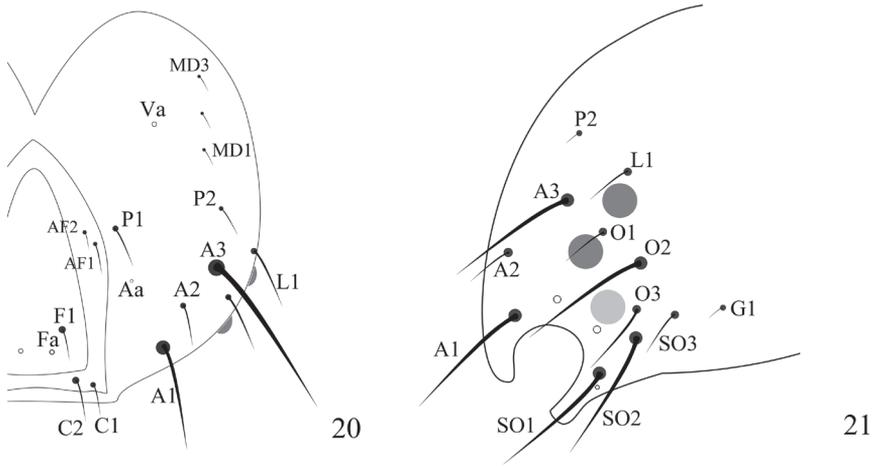
Head. Adfrontal area slightly convex above middle, AF setae placed on convexity (Fig. 12); A3 longest, followed by A1, Aa internal to half way of A2 and A3, near margin of adfrontal area; P1 lateral to AF2, near margin of adfrontal area, P2 dorsal to A3, slightly shorter than P1; three MD setae placed posterior to P2, arranged in line, Pa internal and slightly anterior to MD2; O2 longest, followed by O3; SO1 as long as SO2, SO3 shorter, SOa near SO1; G1 posterior to SO3.

Thorax. TI with XD, D, and SD setae placed on prothoracic shield, XD1 near anterior margin of prothoracic shield (Fig. 16), XDa anterior to D2, SD2 near ventral margin of prothoracic shield; L-group bisetose, L2 dorsal and posterior to L1; SV-group bisetose, sharing pinaculum. TII with D1 near anterior dorsal margin, MD1 near posterior margin of prothoracic shield, anterior to D2; SD2 close to D2, SD1 anterior and ventral to SD2; L-group bisetose, L2 absent, L3 posterior and dorsal to L1; SV-group unisetose, with a micro seta anterior to SV1. TIII similar to TII.

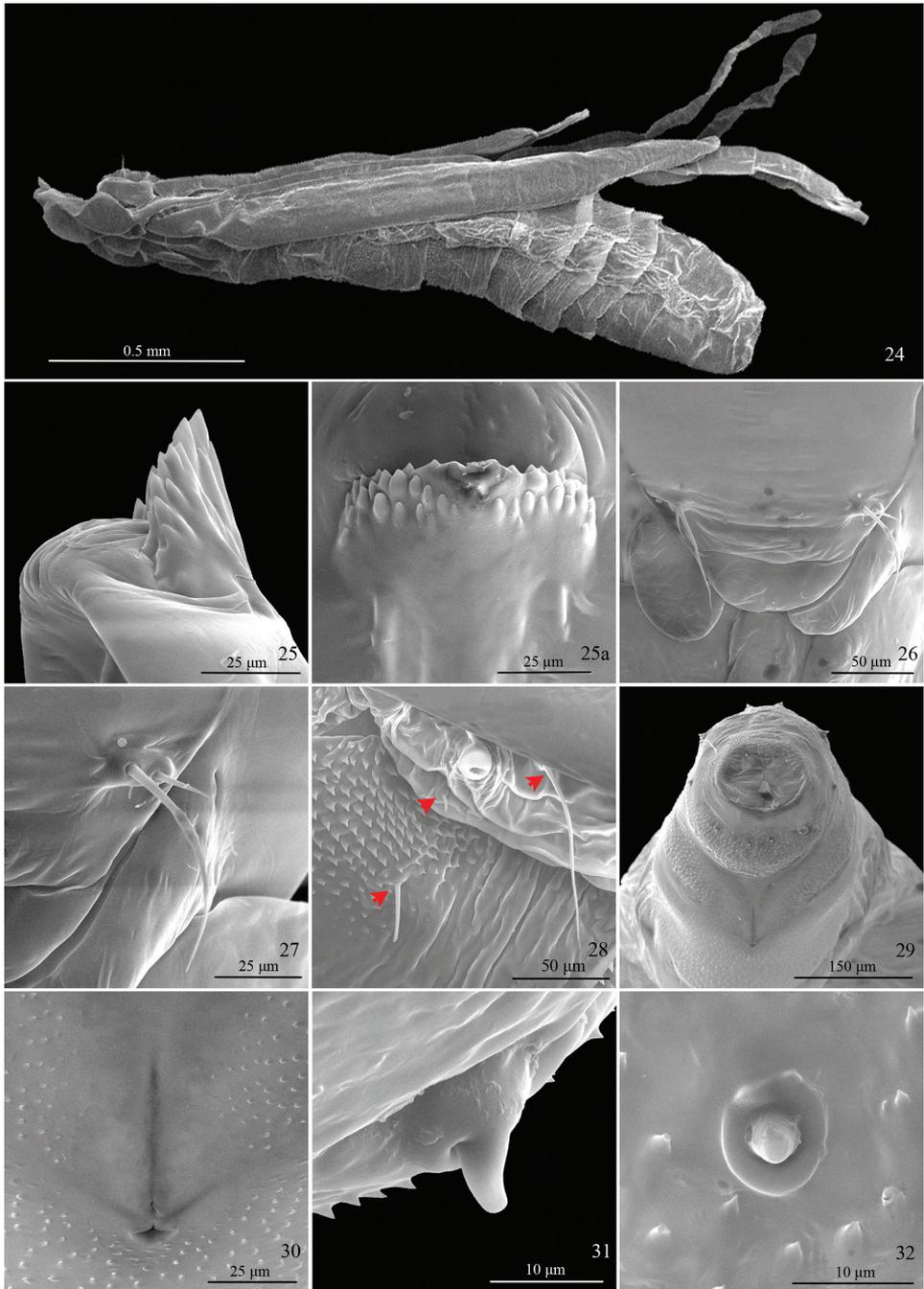
Abdomen. A1–8 with D1 and D2 closely approximated to each other, MD1 seta anterior and slightly dorsal to D1, SD1 posterior and dorsal to spiracle, SD2 shorter than SD1, anterior and dorsal to spiracle, closer to spiracle than SD1, L-group bisetose, L2 seta absent; A1 and A7–9 with SV-group unisetose, A2 and A6 bisetose, A3–5 trisetose; A9 with D1 short, MD1 seta anterior to D1, SD1 anterior and ventral to D2, as long as D2, SD1, L1, SV1 and V1 almost forming a line; A10 as shown in Fig. 19.

Pupa (Figs 24–32). Vertex with frontal process (cocoon cutter) triangular, densely covered with denticles dorsally, with 8–10 longitudinal grooves ventrally (Figs 25–25a); a pair of sensilla near base of each labial palpus, with inner sensillum three times longer than outer one (Figs 26–27); labial palpus 3.4 times longer than maxillary palpus. TII and TIII each bearing a pair of seta dorsally. A1–9 each carrying a pair of seta dorsally; A2–6 each bearing a pair of seta laterally, with one postero-ventral to spiracle, one internal to spiracle, shorter (Fig. 28); A2–10 densely covered with minute spines dorsally, which become stronger towards anterior margin on A2–7; cremaster with 9–11 denticles (Figs 29, 31–32). (Two preparations of exuviae and two pupae examined).

Diagnosis. The new species mostly resembles *T. prosacta*, especially in the male genitalia. However, it can be recognized by the male genitalia with the tegumen having 3–4 long setae on each lateral side, and the valva width does not change in the basal 3/4; in *T. prosacta*, the tegumen has 9–12 long setae on each lateral side and the valva is slightly wider at middle. In the female genitalia, *T. grewiae* sp. n. can easily be separated from all other *Telamoptilia* by the extremely short ductus bursae, not reaching the anterior margin of the seventh abdominal segment. The signum lacks a median process and is thereby more similar to signa in *Spulerina*, especially to that of *S. parthenocissi* Kumata & Kuroko, 1988, than to those in *Telamoptilia*.



Figures 20–23. Line drawings of the larval chaetotaxy of *Telamoptilia grewiae* sp. n. **20** Head, frontal view **21** Head, lateral view **22** Thoracic segments, lateral view **23** Abdominal segments, lateral view.



Figures 24–32. Pupal characters of *Telamoptilia grewiae* sp. n. **24** Pupa, lateral view **25** Frontal process (cocoon cutter), lateral view **25a** Frontal process (cocoon cutter), ventral view **26** Two pairs of sensillae on head **27** Close-up of the paired sensillae on head **28** Setae on A2, dorsal-lateral view, arrows indicating the positions of setae **29** Segments A9–10, ventral view **30** Genital orifice **31** Lateral cremaster, lateral view **32** Ventral cremaster, ventral view.

Type materials. **Holotype**, ♂, **China**: Mt. Baxian National Nature Reserves (117°33'N, 40°11'E), 300–600 m, Ji county, Tianjin, larva coll. 6-ix-2013, ex. *Grewia biloba*, emerged 9-iii-2014 (indoors), leg. Tengteng Liu. **Paratypes**: 2♂, 1♀, larva coll. 24-vi-2013, emerged 6–7-vii-2013, 1♂, 1♀, larva coll. 29-vi-2013, emerged 5-vii-2013, 4♂, 3♀, larva coll. 8-viii-2013, emerged 19–20, 22-viii-2013, 1♂, 1♀, emerged 13, 22-ix-2013, 1♂, larva coll. 12-ix-2013, emerged iv-2014 (indoors), 2♀, larva coll. 30-vi-2014, other data as holotype, genitalia slide Nos. LTT12255♀, LTT12256–7♂, LTT12261♂, LTT12555♀, LTT12556–7♂; 1♂, 300 m, 29-vi-2014, by light, leg. Kaijian Teng & Tengteng Liu, other data as holotype, genitalia slide No. LTT12561.

Non-type materials. 5 larvae, 25-vi-2013, 6-ix-2013, stored in ethanol, other data as holotype, BXS130628, BXS130942; 1 last instar larval skin, larva coll. 6-ix-2013, emerged 13-iii-2014, other data as holotype, mounted in Canada balsam, slide no. LTT1403L; 1 last instar larval skin, 24-vi-2013, stored in glycerine, other data as holotype, BXS130632; 2 pupal exuviae, 29-vi-2014, other data as holotype, mounted in Canada balsam, slide Nos. LTT1401–2L.

Host plants. *Grewia biloba* G. Don and its variety *parviflora* Hand. –Mazz. (Malvaceae). *Telamoptilia grewiae* sp. n. is thus far the only species in Gracillariinae that is known to feed on *Grewia*. The plant family Malvaceae appears to be the main host for *Telamoptilia* with now four out of six species feeding on this family (*T. tiliae* on *Tilia*, *T. cathedraea* on *Urena*, *T. geyeri* on *Pavonia*).

Distribution. China (Tianjin).

Biology. The larva mines on the upper surface of the host plant leaf. The mine begins as an epidermal silvery curved white line which soon enlarges to a whitish blotch. Yellowish-fuscous or fuscous lines can be found on the surface of the blotch. As the larva develops, the blotch usually incorporates the earlier linear mine. The last instar larva vacates the mine for pupation by chewing a semicircular opening near the margin of the blotch. No body colour transfer occurs in the full-grown larva of this species, compared to other *Telamoptilia* larvae which turn red when fully grown (Kumata et al. 1988). Some host plants can be seriously damaged by the mines in early September. Cocoons are usually found inlaid the leaf wrinkles, or occasionally in the corner of the rearing container. The cocoon is brown, with 2–3 brown minute bubbles on the surface. This species overwinters in pupa.

Etymology. The specific name is derived from the host plant genus *Grewia*, indicating the host of the new species.

Discussion

The forewing venation of *T. grewiae* sp. n. is unique within the *Acrocercops* group: R_1 and R_5 are absent, thus R_4 is not stalked with R_5 . The absence of R_1 is apomorphic for *Chrysocercops* Kumata & Kuroko, 1988 (occasionally present), *Telamoptilia* and *Spulerina* (Kumata et al. 1988, Kumata 1992). Although R_1 is also absent in *Dendrocyter* Kumata, 1978, it will not be discussed here since its status within the *Acrocercops*

group is still debatable (Kumata et al. 1988). The forewing patterns and the genitalia of *Chrysocercops* are rather different from those of *T. grewiae* sp. n. All other *Telamoptilia* and *Spulerina* have R_5 , or at least R_5 is visible distally and stalked with R_4 (Kumata et al. 1988). Currently there is not enough evidence for assigning the new species without R_5 to a new genus. A comprehensive study of more species is required for further generic definition.

Kumata et al. (1988) distinguished *Telamoptilia* from *Spulerina* by the antennal scape having a minute flap, the absence of the fan-shaped comb of the valva and the signum with median process. *Telamoptilia grewiae* sp. n. has a flap as wide as the antennal scape and a signum lacking a median process, which is most similar to *S. parthenocissi* as stated in the diagnosis section. Therefore the signum without median process is not an autapomorphy for *Spulerina* when defining *Telamoptilia* and *Spulerina*. The larval seta XD1 of *T. grewiae* sp. n. is placed near the anterior margin of the prothorax shield, which resembles that of *Spulerina* Vári, but differs from that of *Telamoptilia* that has XD1 of variable placement between D1 and D2 (Kumata et al. 1988). The fully grown larva of *Telamoptilia* and *Spulerina* changes body colour into red (Kumata et al. 1988), but colour transfer does not occur in *T. grewiae* sp. n. Consequently, the most important generic character to distinguish *Telamoptilia* from *Spulerina* is the absence of the fan-shaped comb of the valva as defined by Kumata et al. (1988), and the minute antennal scape flap and the signum with median process should be excluded for generic definition when taking *T. grewiae* sp. n. into consideration. The position of seta XD1 and the feature of larval body colour transfer vary within *Telamoptilia*, thus should not be adopted as generic characters. Considering the unique characters of *T. grewiae* sp. n., its phylogenetic relationship to other species of the genus *Telamoptilia* requires further study.

Acknowledgements

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