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Review of East Palaearctic *Elliptera* (Diptera, Limoniidae) immatures with description of a new species

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Abstract. The genus *Elliptera* Schiner, 1863 is represented by ten species worldwide, but immatures of only the European species *E. omissa* Schiner has been described so far. Molecular methods were used to associate larvae and adults for two East Asian species from South Korea. *Elliptera jacoti* Alexander and *E. zipanguensis zipanguensis* Alexander are common species in aquatic, hygropetric habitats in mountainous parts of the Korean peninsula. *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov. from Mongolia and China (Inner Mongolia) is described based on mitochondrial DNA COI gene barcode sequences and morphological characters of larvae. Larvae of all three species and pupae of *E. jacoti* are described and illustrated. Morphological characters of the larvae useful for discrimination of species are given. An identification key for East Asian larvae of the genus *Elliptera* is compiled.

Key words. Crane fly, integrative taxonomy, larva, mt COI, pupa.

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Introduction

Genus *Elliptera* Schiner, 1863 is a small group with ten species (one of them with two subspecies) of aquatic crane flies in the subfamily Limoniinae Speiser, 1909 (Diptera, Limoniidae) (Oosterbroek 2020). All species are distributed in mountainous regions. The highest diversity, six species, is recorded in western North America, two species recorded from Europe, two species from the East Palaearctic, and one species from Taiwan in the Oriental region.

Adults of *Elliptera* are among the commonest crane flies in aquatic and semiaquatic habitats in the Korean Peninsula and were taxonomically revised by Podenas & Byun (2013). Larvae, pupae and adults were collected many times during several expeditions arranged by the National Institute of Biological Resources (NIBR), Incheon, South Korea, but rearings of immatures were unsuccessful so far.

Larvae of *Elliptera* were collected only once out of over 400 sites sampled by the Mongolian Aquatic Insect Survey (MAIS) during numerous sampling expeditions in central and western Mongolia during 2003–2011. No adults were found at the site where larvae were collected, nor at any other sites in Mongolia and the adult stage of the Mongolian species remains unknown. Larvae of *Elliptera* were also collected in China (Inner Mongolia) in 2018 and no adults of this genus were found.

Little attention was given to the immature stages of the genus *Elliptera.* Descriptions and illustrations of the immature stages of *Elliptera* are available for the European species, *E. omissa* Schiner, 1863 (Mik 1886, translated description by Alexander 1920), but the illustrations failed to show detailed structure of the larval head capsule or spiracular disc which are of taxonomic importance. A photo of the larval habitat of another European species, *E. hungarica* Madarassy, 1881 is given by Kramer & Billard (2019). Rogers (1930) and Alexander (1966) described the habitat for the North American species, *E. clausa* Osten Sacken, 1877, *E. illini* Alexander, 1920 and *E. usingeri* Alexander, 1966 in detail. Immature stages of this genus develop on steep or vertical cliff faces kept wet by a thin film of water supporting algal growth (*fauna hygropetrica*) (Alexander 1920; Rogers 1930; Brindle 1967; Savchenko 1985; Reusch & Schrankel 2006; Krivosheina & Krivosheina 2011; Kramer & Billard 2019) with larvae and pupae of *E. illini* in "delicate, indefinite tubes that were concealed beneath the strands of algae or moss and the adhering silt" in tiny crevices or silt-filled pits in the rock face (Rogers 1930). At least in California, USA, these habitats are seasonal and dry completely by summer (Alexander 1966).

Larvae of crane flies can be associated with adults by rearing or with the help of molecular methods. In some cases, when larvae of several species of the same genus develop in the same habitat, or larvae cannot be kept alive in the lab until pupation, then only the use of molecular methods is reliable. The taxonomical problems of insect larvae are now easier to solve, since molecular methods are presently largely available and easy to apply (Keresztes *et al*. 2018).

Material and methods

The majority of the larvae and pupae of the genus *Elliptera* were collected by hand in South Korea (2012–2019), Mongolia (2003–2011) and China, Inner Mongolia (2018) by the senior author. For DNA extraction and mt COI DNA comparison, males of *E. jacoti* Alexander, 1925 and *E. zipanguensis zipanguensis* Alexander, 1924 and several larvae of *E. zipanguensis zipanguensis* were taken from the collection of National Institute of Biological Resources, Incheon, South Korea (NIBR). In total, 94 larvae, 3 female pupae, 14 female pupal exuviae and two males were used in this study. All examined material are preserved in 70% ethanol. The head capsules of larvae were cleared in hot, approximately 10% KOH for a few hours and temporary slides in gelatinous glycerol were made. Spiracular discs of larvae were cut off and temporary slides in gelatinous glycerol were made. Specimens were examined with an Olympus SZX10 dissecting microscope. Photographs of the general habitus of larvae, pupae and head capsules were taken with the digital camera Canon EOS 80D through a Canon MP–E 65 mm macro lens. Head capsules were traced to a drawing based on a photograph. Larvae, pupae and voucher specimens of *E. jacoti* and *E. zipanguensis zipanguensis* are deposited at the collection of NIBR. Holotype, paratypes and voucher specimens (paratypes) of new species were deposited at the collection of the Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (ANSP) and at the collection of Shenyang Agricultural University, China.

Molecular analysis was used to associate adult males with their putative larvae. A phylogenetic tree was based on molecular sequence data from DNA barcoding regions of 658 bp of the mitochondrial cytochrome c oxidase subunit I (COI) from 2 adults and 8 larvae belonging to *E. jacoti*, *E. zipanguensis zipanguensis* and the new species of *Elliptera*. DNA was extracted from larvae and adult males using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. PCR amplification was carried out using a mix of LCO-1490 and HCO-2198 primers for amplification of the standard Barcode region of COI from invertebrates. For the extraction we used whole larval and adult specimens. For PCR amplification reaction we used BCS PCR 2X Master Mix (Biocube System Inc., Republic of Korea). All of the PCR reaction mixtures had a total volume of 22 µl and 3 µl of DNA template (in the range between 1.0 to 20 ng) per reaction. Each reaction included 11 µl of Biocube System's 2X Master Mix, 1 µl of each (LCO-1490 and HCO-2198) primer (forward and reverse, 10 µM) and 8 µl of sterile distilled water. The thermocycle program for COI amplification consisted of 95°C for 3 min, 35 cycles of 95°C for 30 s, 51°C for 39 s and 72°C for 45 s with a final extension at 72°C for 5 min.

PCR products were sequenced by Macrogen Inc. (Korea) (10 sequences). Sequences were verified at the NCBI website using a Basic Local Alignment Search Tool (BLAST) of Johnson *et al*. (2008) and deposited in GenBank (accession numbers presented in Table 1). The phylogenetic tree was computed using the MrBayes ver. 3.1 software (Ronquist & Huelsenbeck 2003). Best–fit model of evolution (GTR) was selected by the software MrModeltest ver. 3.7 (Nylander 2004). The analysis was run for a total of 5 million generations and sample frequency was set to every 100th generation. The constructed phylogenetic tree was visualized in FigTree ver. 1.4.3 (Rambaut 2009). Genetic distances between examined species were calculated using the Jukes-Cantor model of substitution, as implemented in the program MEGA ver. 7.0 (Kumar *et al*. 2016). We used mt COI sequences of *Antocha nebulipennis* Alexander, 1931 as an outgroup (GenBank access number MG674214). Adult and larval associations were accepted when posterior probabilities were high and bootstrap values rose to 95–100% or clustered together in a monophyletic unit. The identified larvae were then compared morphologically to detect taxonomically informative characters.

The terminology of larval and pupal morphological features generally follows that of Oosterbroek & Theowald (1991) and Teskey (1981). Terminology of adult morphological features generally follows Cumming & Wood (2017).

Results

Phylogenetic analysis

Bayesian phylogenetic analysis grouped eight sequences of larvae and two sequences of adults into three well-supported clades, which allowed South Korean larval specimens to be associated with their putative adults (Fig. 1). Larval specimens from Mongolia and China formed a separate clade. We found no more sequences of genus *Elliptera* in Barcode of Life Data Systems (BOLD) and GenBank genetic

Table 1. Pairwise genetic distance for COI gene sequences between East Asian *Elliptera* Schiner, 1863 species (calculated in MEGA7 using Jukes-Cantor model of substitution algorithm). Abbreviations: CF01 = *E. jacoti* Alexander, 1925, larva, GenBank accession no. MT233405; CF02 = *E. zipanguensis zipanguensis*, Alexander, 1924, larva, GenBank accession no.MT233406; CF03 = *E. zipanguensis zipanguensis*, larva, GenBank accession no. MT233407; CF04 = *E. zipanguensis zipanguensis*, larva, GenBank accession no. MT233408; CF05 = *E. zipanguensis zipanguensis*, larva, GenBank accession no. MT233409; CF06 = *E. zipanguensis zipanguensis*, larva, GenBank accession no. MT233410; CF07 = *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov., larva, GenBank accession no. MT233411; CF08 = *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov., larva, GenBank accession no. MT233412; CF09 = *E. jacoti*, ♂, GenBank accession no. MT233413; CF10 = *E. zipanguensis zipanguensis*, ♂, GenBank accession no. MT233414.

Species	CF01	CF02	CF03	CF04	CF05	CF06	CF07	CF08	CF09
CF01									
CF02	10.4								
CF03	10.4	0							
CF04	10.4	0	0						
CF05	10.4	0	0	0					
CF06	10.4	0	0	0	0				
CF07	8.5	9.6	9.6	9.6	9,6	9.6			
CF08	8.5	9.6	9.6	9.6	9.6	9.6	0.7		
CF09	0.9	10.2	10.2	10.2	10.2	10.2	8.1	8.1	
CF10	10.4	0.55	0.55	0.55	0.55	0.5	9.5	9.5	10.2

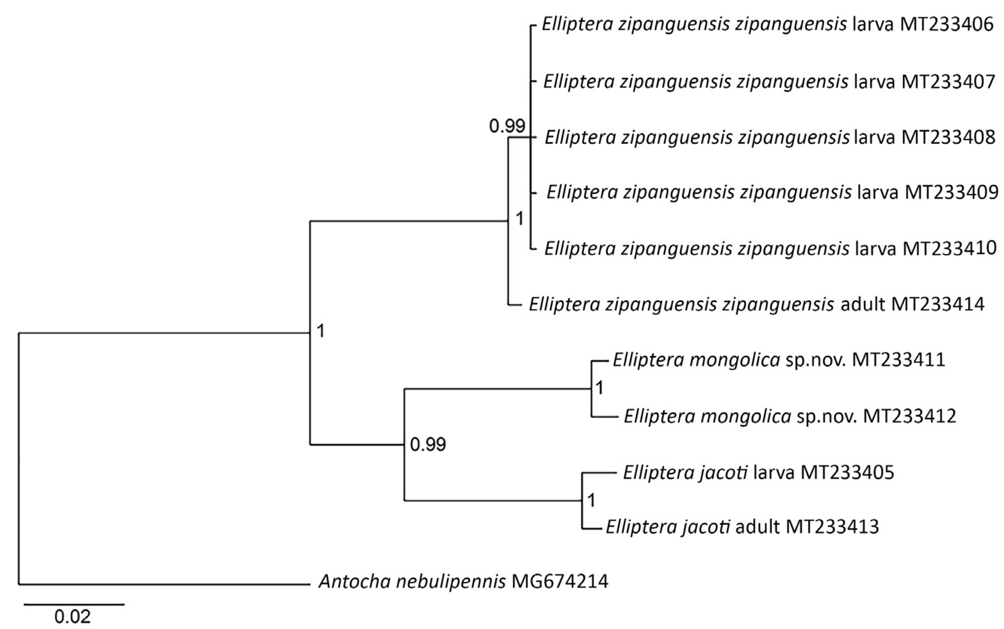

Fig. 1. Bayesian phylogenetic tree constructed using mitochondrial CO I gene sequences of East Asian *Elliptera* Schiner, 1863 species with *Antocha nebulipennis* Alexander, 1931 as outgroup. Posterior probabilities are indicated in the tree. Species names, developing stages and GenBank accession numbers are given in Table 1.

sequence databases, so this phylogenetic tree was based only on our material. The pairwise genetic distances between all three *Elliptera* species ranged from 8.5% between *E. jacoti* and the new *Elliptera* species to 10.4% between *E. jacoti* and *E. zipanguensis zipanguensis* (Table 1). Genetic distance between Mongolian and Chinese larval specimens is 0.7%, which clearly confirms that the larval specimens from China and Mongolia belongs to the same species, notwithstanding the great distance separating localities where the larvae were collected.

Taxonomy

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Infraorder Tipulomorpha Rohdendorf, 1961
Family Limoniidae Speiser, 1909
Subfamily Limoniinae Speiser, 1909
Tribe Antochini Savchenko, 1989

Genus ***Elliptera*** Schiner, 1863

Elliptera Schiner, 1863: 222.

Elliptera – Edwards 1938: 20, 49. — Lackschewitz & Pagast 1942: 56, 60. — Ishida 1956: 124, 145. — Savchenko & Krivolutskaya 1976: 111, 113. — Savchenko 1983: 105; 1985: 17; 1989: 280. — Podenas & Byun 2013: 177. — Kato & Tachi 2019: 1.

Type species

Elliptera omissa Schiner, 1863.

Description

Adults are brown, sometimes yellowish gray, medium-sized crane flies with body length 4.0–9.0 mm. Antennal flagellum beaded. Mesonotal prescutum without tuberculate pits and pseudosutural foveae. Wing unpatterned or at most with darkening along cord, vein *Sc* long and nearly reaching branching point of *Rs*; *sc-r* before base of *Rs*; radial sector long and straight, situated very close to *R* and nearly parallel to it; R_2 indistinct, slightly beyond fork of *Rs*; discal cell open due to the atrophy of basal part of M_3; *m-cu* close to the branching point of *M*; anal angle widely rounded. Male terminalia large with transverse ninth tergum, elongate gonocoxite bearing two terminal gonostyles, and straight and short aedeagus. Ovipositor elongate and sclerotized with strongly raised apex of cercus.

Larva depressed dorsoventrally. Head capsule heavily sclerotized, with complete hypostoma. Frons fused with internolateralia, which are considerably shorter than externolateralia. Abdominal segments II–VII with dorsal and ventral creeping welts. Spiracular field surrounded by four lobes.

Pupa with large, ear-shaped pronotal horns. Sheaths of legs reaching sixth abdominal segment. Abdomen with dorsal and ventral transverse rows of spines.

Savchenko (1989) placed the genus *Elliptera* into the tribe Antochini based only on adult characters. Phylogenetic relationships of the family Limoniidae, including *Elliptera,* based on larval and pupal characters were analyzed by Oosterbroek & Theowald (1991), using a nonquantitative analysis. The final tree placed *Elliptera* as the sister group to the unresolved *Atypophthalmus*-*Discobola* lineage based on the presence of larval creeping welts on abdominal segments 2–4 in these genera, with the genus *Antocha* Osten Sacken, 1860 placed as sister group to the rest of the Limoniinae based on a weak synapomorphic character of oblong-shaped, obliquely placed spiracles (spiracles lost in *Antocha*).

Key to the East Palaearctic larvae of the genus *Elliptera*

1. Darker sclerotization only along margins of the spiracular field of the lateral lobe (Fig. 14H–I) ....***Elliptera zipanguensis zipanguensis*** Alexander, 1924 (Japan, North and South Koreas, Russian Far East)
– Darker sclerotization covering almost the entire spiracular field of the lateral lobe (Figs 3A–B, 8B, D) 2

2. Hypostoma with nine teeth (Fig. 2I) .... ***Elliptera mongolica*** Podeniene, Podenas & Gelhaus sp. nov. (China, Mongolia)
– Hypostoma with eleven teeth (Fig. 7G) ....***Elliptera jacoti*** Alexander, 1925 (China, North and South Koreas, West Siberia and Far East of Russia)

Elliptera mongolica Podeniene, Podenas & Gelhaus sp. nov.
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Figs 2–5

Diagnosis

Body length reaching up to 14.5 mm. Head capsule heavily sclerotized. Hypostoma with nine teeth. Abdominal segments II–VII with dorsal and ventral creeping welts. Spiracular disc surrounded by four lobes, with lateral pair of lobes almost entirely sclerotized.

Etymology

The specific epithet is a noun 'mongol' with Latin suffix 'ica', referring to the distribution of the new species.

Type material

Holotype

MONGOLIA • larva (in alcohol); Tov Aimag, Mongonmorit Soum, Zuun Baydlag Gol, downstream, 15 km SW of Mongonmorit; 48°06.49′ N, 108°22.04′ E; 1475 m a.s.l.; 14 Jul. 2011; V. Podeniene leg.; MAIS #2011071402; ANSP-ENT-146962.

Paratypes

MONGOLIA • 22 larvae (in alcohol); same collection data as for preceding; GenBank: MT233411; ANSP.

CHINA • 11 larvae (in alcohol); Inner Mongolia, Chifeng, Bailin Youqi, Sai Hanwula Reserve; 44°15.06′ N, 118°19.54′ E; 1165 m a.s.l.; 10 Jul. 2018; V. Podeniene leg; Shenyang Agricultural University; GenBank: MT233412; ANSP.

Description

Larva

Measurements. Length 11.6–14.5 mm, width 1.7–2.0 mm.

Body. Cylindrical, dark brown, hairs on dorsal and ventral sides darker than on lateral side. Abdominal segments II–VII divided into anterior and posterior parts, anterior part with dorsal and ventral creeping welts (Fig. 2A–C). Creeping welts with dark brown spines, arranged into transverse rows. All thoracic and abdominal segments I–II shorter than wider. Abdominal segments III–VIII approximately as long as wide. Pale circular area present on dorsum of all segments except the prothorax (Fig. 2B).

Head. Length 1.20–1.25 mm, width 1.10–1.20 mm. Head capsule oval, heavily sclerotized and slightly reduced (Fig. 2D). Frontal suture absent, dorsal suture reaching to about the middle of head capsule (Fig. 2D), hypostoma complete (Fig. 2I). Labrum wide with numerous sensory structures: short seta, middle-long seta and three sensory pegs in the middle of anterior part (Fig. 2E). A narrow sclerotized band situated anterior to sensory structures. Anterior part and sides of labrum as well as epipharynx covered with numerous short hairs. Clypeus fused with labrum and bears wide sclerotized plate anteriorly (Fig. 2E). Frons separated from clypeus and fused with internolateralia, which are considerably shorter than externolateralia; four long setae located on each side of the anterior margin of frons, one seta below the base of antenna, a pair of sensory pits in the middle of anterior part, caudal end of frons–internolateralia very wide and arched (Fig. 2D–E). Basal antennomere cylindrical, more than twice as long as wide, with two long setae and a few very short sensory structures apically; apical segment short, cylindrical; sensory pit located at the base of basal segment (Fig. 2E). Mandible conus-shaped, with two large apical teeth, both similar in shape and size (Fig. 2F), first ventral tooth triangular, second ventral and basal teeth blunt; single well developed sharp tooth on dorsal side; two long setae at the base of mandible (on outer margin). Maxilla well developed (Fig. 2G); outer lobe (stipes) and inner lobe (galea fused with lacinia) large and similar in size. Outer lobe: two-thirds sclerotized, apical part and outer margin covered by long setae; button shaped apical papilla with sensory structures on the apex and small papilla next to it. Inner lobe: basal part sclerotized; long and short sensory papillae on apical part; apical part and inner margin covered with short setae. Cardo large, wedge shaped with sensory pit near outer margin of sclerite. Hypopharynx arched, sclerotized and toothless. Prementum dentated (four large teeth in the middle and two small similar in size teeth on both sides) (Fig. 2H). Hypostoma with nine anterior teeth, the middle tooth most prominent (Fig. 2I).

Anal division. Spiracular field surrounded by four lobes, ventral lobe twice as long as lateral lobe (Fig. 3A–B). Lateral lobe as long as wide, almost entirely sclerotized except the middle part, three medium-long setae located along the outer margin of lobe. Ventral lobe twice as long as wide at the base with dark U–shaped sclerite, ventral branch of each lobe fused with its opposing sclerite to form continuous line. Dark spot situated at base of each lobe below spiracle (missing in some specimens). Two long setae and one medium-long seta located at the apical part of lobe; one medium-long seta on the outer margin of lobe. A pair of sensory pit located on dorsal margin of spiracular field. Spiracular field fringed with long firm setae, longest around the apical part of each lobe. Spiracles large, oblong, placed obliquely and inclined dorsally (Fig. 3A–B). Anal field consists of two pairs of conical, white, fleshy anal papillae (Fig. 2C).

Pupal and adult stages unknown.

Habitat

Larvae were found on accumulated mud on river boulders in Mongolia (Fig. 4). Larvae in China were found on accumulated mud on spring boulders. Some of them (in both localities) made cases from mosses (Fig. 5).

Distribution

Currently known only from Mongolia and Inner Mongolia (China).

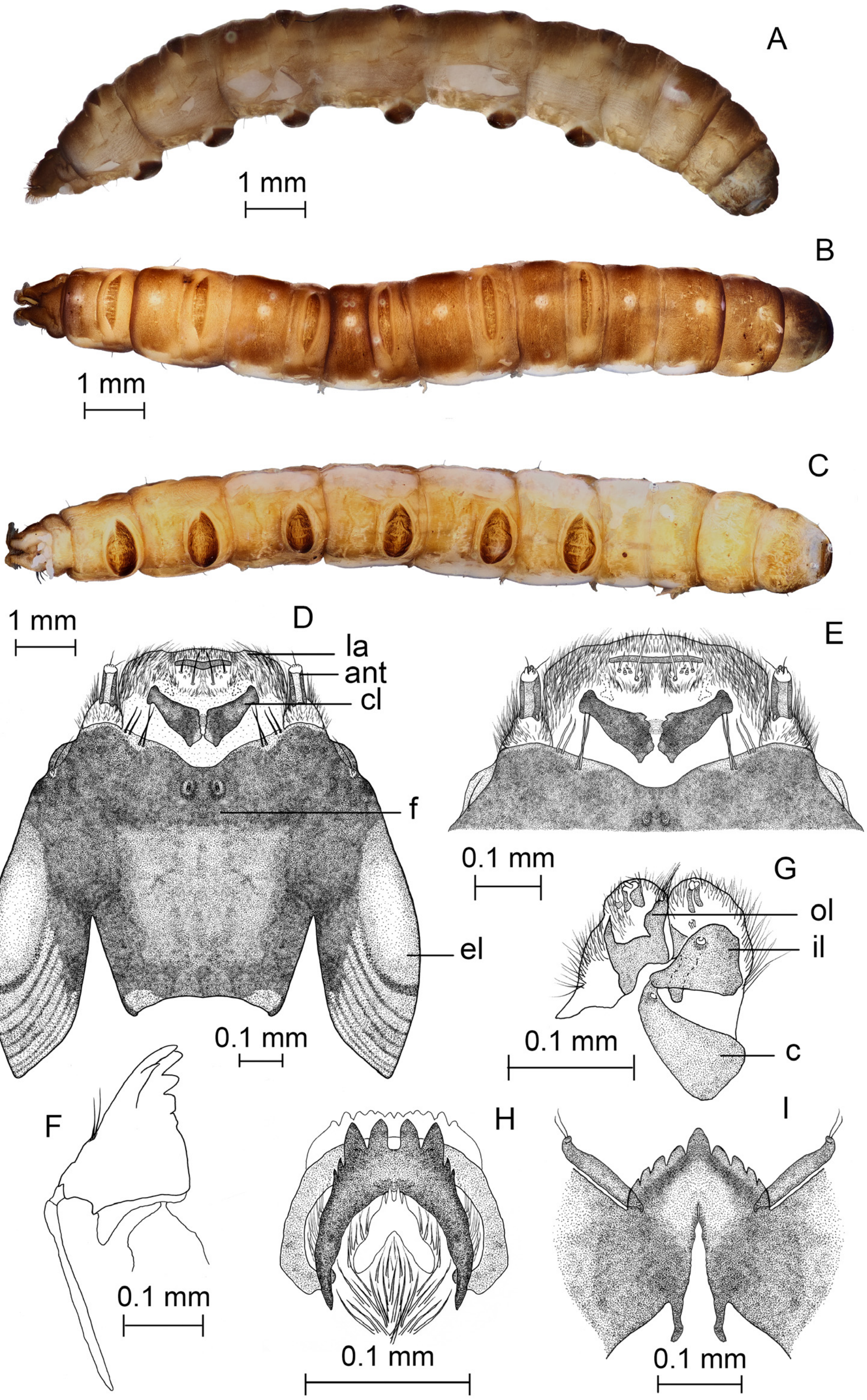

Fig. 2. Larva of *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov., paratype (ANSP). **A**–**C**. General view. **A**. Lateral aspect. **B**. Dorsal aspect. **C**. Ventral aspect. **D**. General view of head capsule, dorsal aspect. **E**. Labrum, clypeus and antennae. **F**. Right mandible, dorsal view. **G**. Right maxilla, ventral view. **H**. Hypopharynx and prementum. **I**. Hypostoma. Abbreviations: ant = antenna; c = cardo; cl = clypeus; el = externolateralia; f = frons; il = inner lobe; la = labrum; ol = outer lobe.

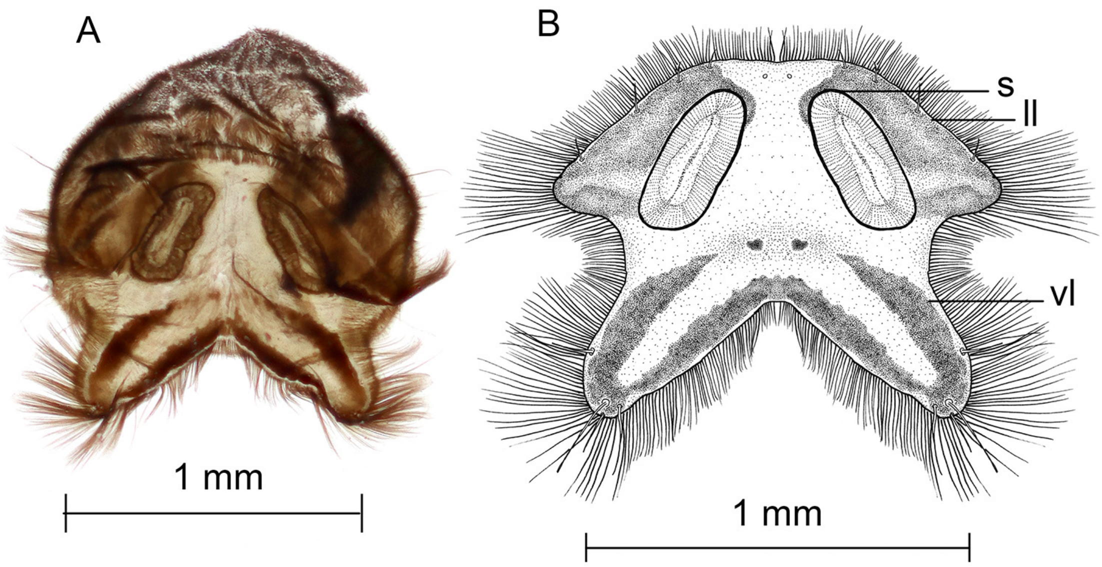

Fig. 3. Larva of *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov., paratype (ANSP) **A**. Spiracular field. **B**. Spiracular field. Abbreviations: ll = lateral lobe; s = spiracle; vl = ventral lobe.

Fig. 4. Type locality of *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov.

Fig. 5. Larva of *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov., paratype (ANSP), in case.

Elliptera jacoti Alexander, 1925
Figs 6–12

Diagnosis

Adult (Fig. 6)

Brown sparsely pruinose species with body 4.2–8.7 mm long, wing 8.8–16.1 mm long. Head black, antenna 16-segmented, 1.4–2.4 mm long, flagellomeres strongly dilated at about two thirds of length, with distinct apical pedicels, apical flagellomere longer than preceding segment. Verticils approximately as long as respective segments. Mesonotal prescutum brown without stripes. Pleuron brown, covered with gray pruinosity. Wing tinged with brown, stigma indistinct, cord surrounded by dark band. Male wing with widened distal part of cell *sc*, thus tip of wing is blunt and widely rounded, distal part of cell *sc* not widened in female. Cell r_3 distally strongly widened in both sexes. Discal cell missing, *m-cu* some distance before branching point of *M*. Haltere with dark brown knob and yellowish base of stem. Coxae yellow with testaceous bases. Legs generally brown with slightly darkened tips of femur, tibia and distal segments of tarsus. Abdomen brownish dorsally, light brown ventrally. Male genitalia rusty brown, ninth tergite with blunt lateral lobe, gonostyles long and narrow. Ovipositor with narrow cercus, distal part of which slightly raised.

Larva

Body length reaching up to 12.5 mm. Head capsule heavily sclerotized. Hypostoma with eleven anterior teeth. Abdominal segments II–VII with dorsal and ventral creeping welts. Spiracular disc surrounded by four lobes, with lateral pair of lobes almost entirely sclerotized.

Pupa

Body length reaching up to 8 mm. Abdomen yellowish white, head, thorax, wings, legs and terminal segment light brown. Pronotal horns large, flattened, ear shaped, anterior and posterior end widely curved inwards. Sheath of cerci long, sclerotized and directed upward, sheath of valvae reach only half length of sheath of cerci.

Material examined

SOUTH KOREA • 25 last instar larvae, 10 third instar larvae, 3 ♀♀ pupae, 14 ♀♀ pupae exuviae (in ethanol); Gyeongsangbuk-do, Gyeongju-si, Yangbuk-myeon, Janghang-ri; 35°45.74′ N, 129°21.84′ E; 333 m a.s.l.; 28 May 2016 (1); Podeniene leg.; GenBank: MT233405; NIBR • 4 last instar larvae (in ethanol); Jeollabuk-do, Namwon-si, Sannae-myeon, Ipseok-ri; 35°24.61′ N, 127°38.84′ E; 319 m a.s.l.; 11 May 2013; V. Podeniene leg.; NIBR • 1 ♂ (in ethanol); Gyeonggi-do, Yangju-si, Jangheung-myeon, Gyohyeon-ri, Doiryung Valley, Bukhansan National Park; 37°41.42′ N, 126°59.38′ E; 242 m a.s.l.; 16 Oct. 2018 (2); H.–Y. Seo, S. Podenas leg.; S. Podenas det.; GenBank: MT233413; NIBR.

Description

Larva

Measurements. Length 9.5–12.5 mm, width 1.6–1.7 mm. In general similar to that of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov.

Body. Cylindrical, yellowish brown, hairs on dorsal and ventral sides darker than on lateral side. Abdominal segments II–VII divided into anterior and posterior parts, anterior part with dorsal and ventral creeping welts (Fig. 7A–C). Creeping welts with dark brown spines, arranged into transverse rows. All thoracic and abdominal segments I–II shorter than wider. Abdominal segments III–VIII approximately as long as wide. Pale circular area present on dorsum of all segments except the first thoracic segment (Fig. 7B).

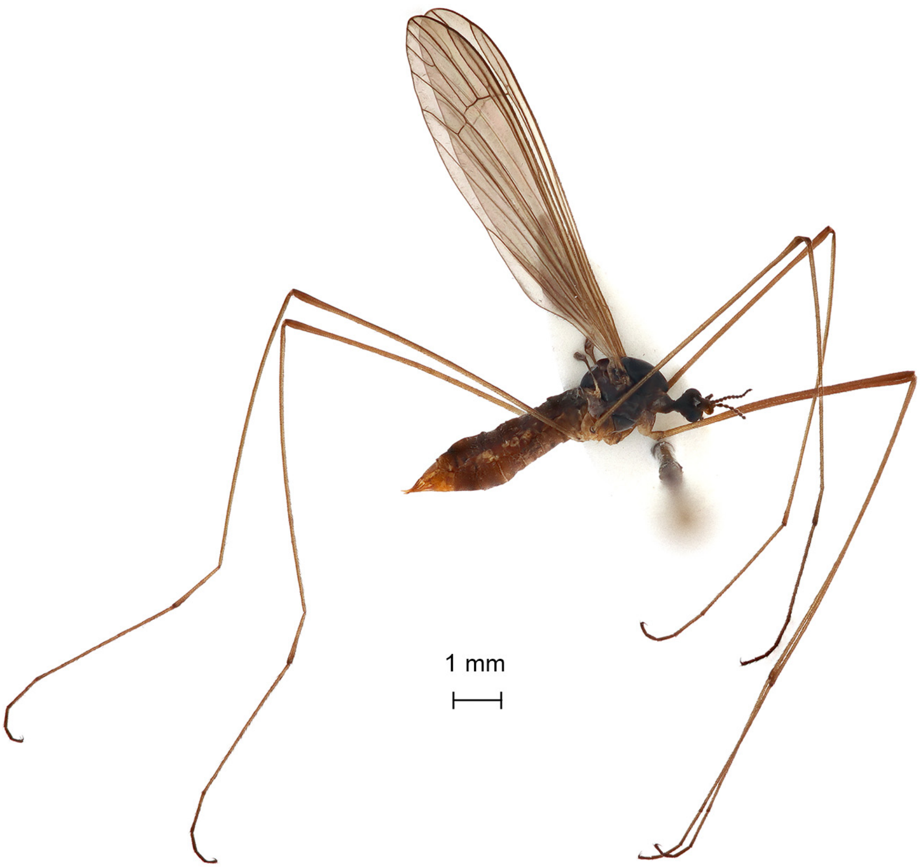

Fig. 6. Female of *Elliptera jacoti* Alexander, 1925 (NIBR).

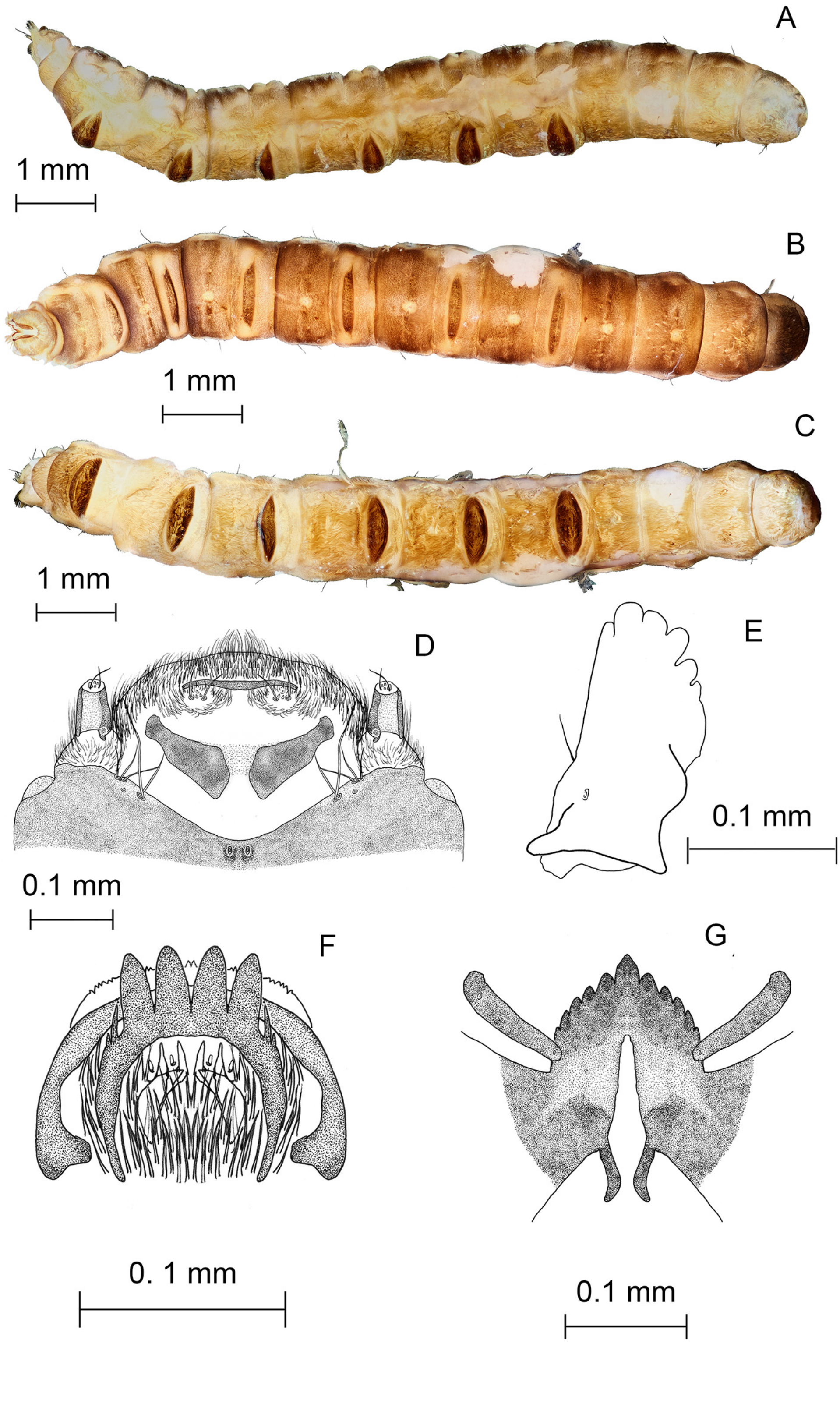

Fig. 7. Larva of *Elliptera jacoti* Alexander, 1925 (NIBR). **A**–**C**. General view. **A**. Lateral aspect. **B**. Dorsal aspect. **C**. Ventral aspect. **D**. Labrum, clypeus and antennae. **E**. Right mandible, dorsal view. **F**. Hypopharynx and prementum. **G**. Hypostoma.

Head. Length 1.00–1.05 mm, width 0.90 mm. In general similar to that of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. Differences were noticed in arrangement of sensory structures on labrum and frons, shape of mandible, number of teeth on hypostoma and prementum. Labrum bears two long setae and three sensory pegs on each side in the middle of anterior part (Fig. 7D). One long, three medium-long setae and sensory pit located on anterior margin of frons (Fig. 7D). Mandible conus-shaped, with two large, blunt apical teeth, similar in shape and size (Fig. 7E), first ventral tooth is the largest, second ventral tooth blunt, basal teeth triangular. Dorsal tooth small and blunt. Prementum has four median large teeth with one smaller tooth on each side (Fig. 7F). Hypostoma bears 11 teeth, the middle tooth most prominent (Fig. 7G).

Anal division. Spiracular field surrounded by four lobes, ventral and lateral lobes similar in length (Fig. 8B, D). Lateral lobe as long as wide, almost completely sclerotized, except small area in middle. Four medium-length setae located along the outer margin of lobe. Ventral lobe twice as long as width at base with dark U-shaped sclerite, ventral branches fused medially to form a complete line. Two long setae and three medium-length setae located at the apex. Paired medium-length setae and sensory pits located on dorsal margin of spiracular field. Spiracular field fringed with long firm setae, longest around apical margins of lobes. Each spiracle large, oblong, placed obliquely and inclined dorsally (Fig. 8A–B, D). Anal field consists of two pairs of conical, white, fleshy anal papillae (Fig. 8C).

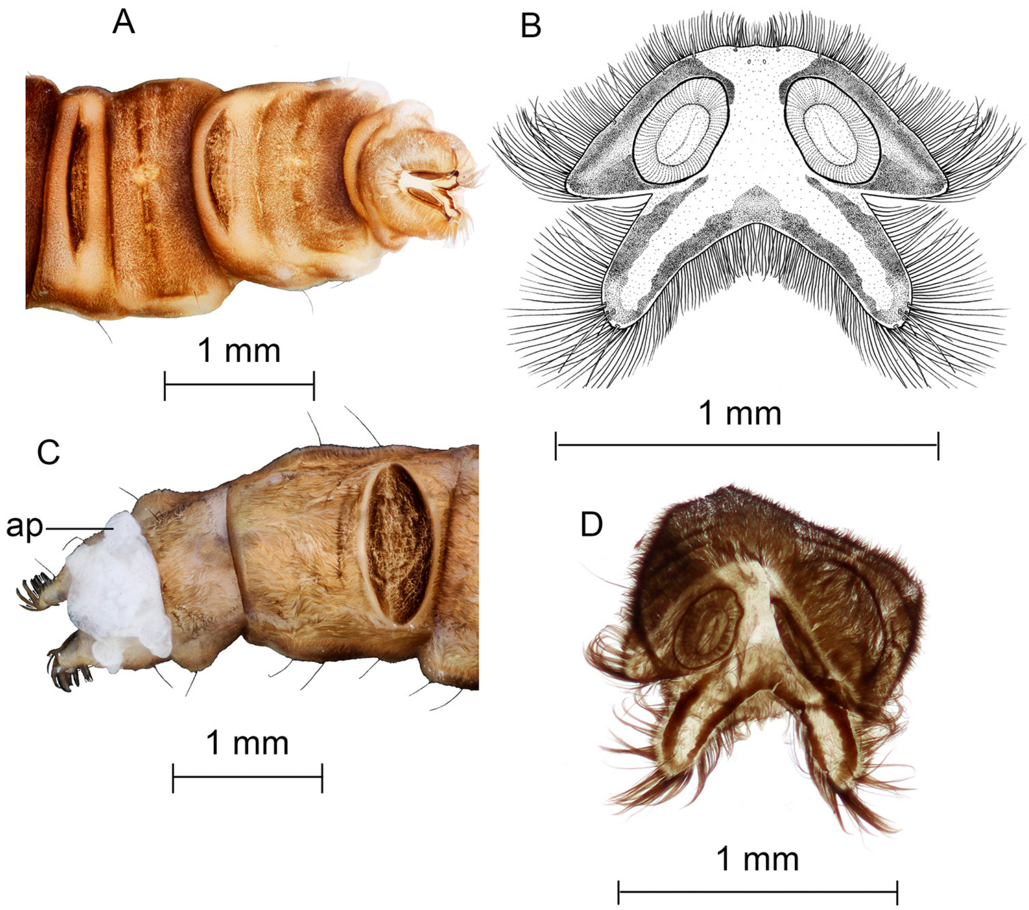

Fig. 8. Larva of *Elliptera jacoti* Alexander, 1925 (NIBR). **A**. Terminal segment, dorsal view. **B**. Spiracular field. **C**. Terminal segment, ventral view. **D**. Spiracular field. Abbreviations: ap = anal papilla.

Pupa

MEASUREMENTS. Female pupa 6.1–8.0 mm long, 1.4–1.5 mm wide. Abdomen yellowish white (Figs 9A–C). Head, thorax, wings, legs and terminal segment light brown, darker than abdomen. Male pupa unknown.

HEAD. Cephalic crest absent, surface smooth (Fig. 9D). Antennal sheath short, only slightly extending beyond wing base (Fig. 9D). Labrum rectangular with bluntly rounded apex (Fig. 9B), labial lobe triangular. Maxillary palp broad, transversal.

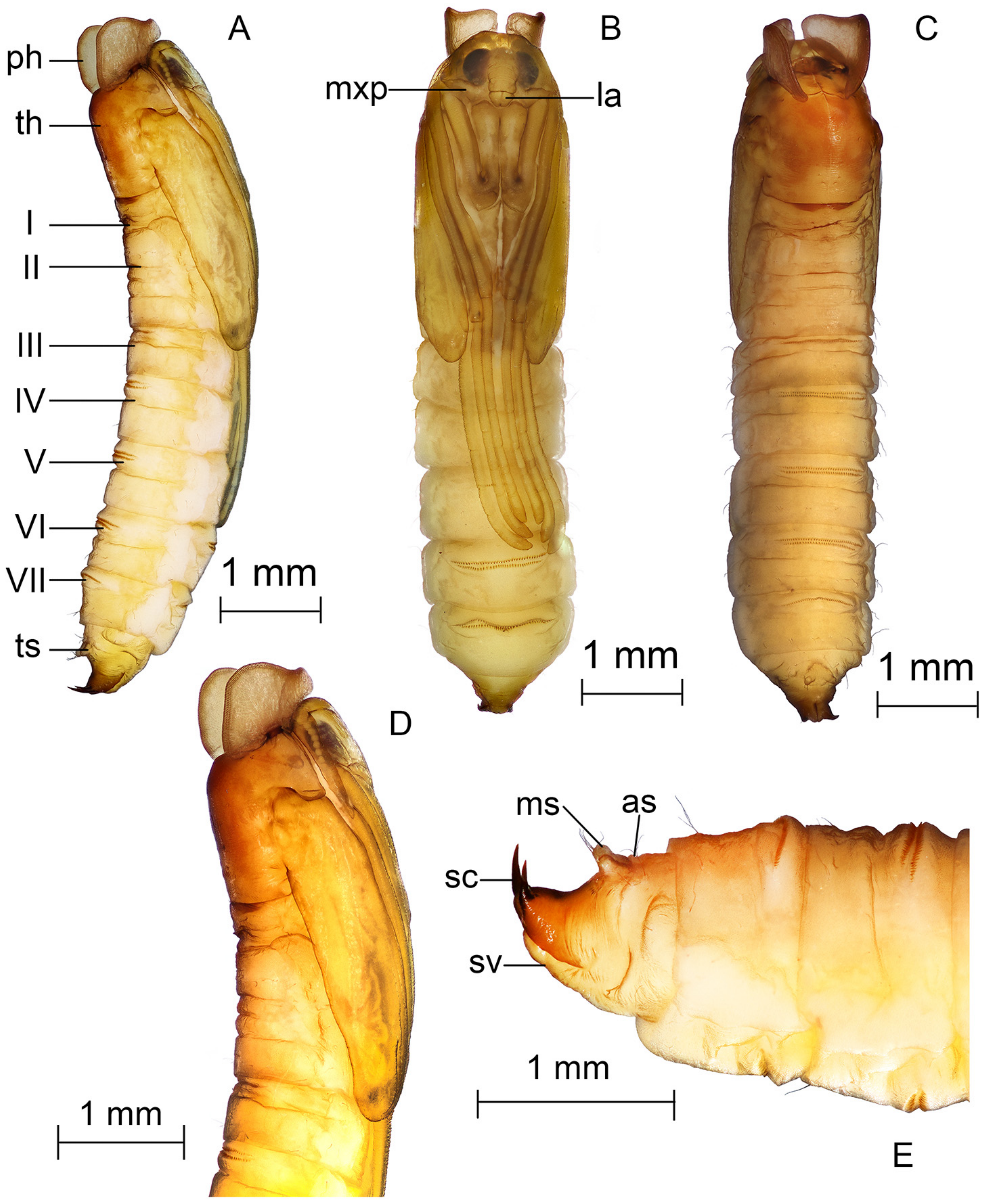

Fig. 9. Female pupa of *Elliptera jacoti* Alexander, 1925 (NIBR). **A**–**C**. General view. **A**. Lateral aspect. **B**. Ventral aspect. **C**. Dorsal aspect. **D**. Head and thorax, lateral view. **E**. Terminal segment, lateral view. Abbreviations: as = anterodorsal spine; la = labrum; ms = mediodorsal spine; mxp = maxilar palp; ph = pronotal horn; sc = sheath of cerci; sv = sheath of valva; th = thorax; ts = terminal segment; I–VII = abdominal segments.

Fig. 10. Habitat of larvae and pupae of *Elliptera jacoti* Alexander, 1925.

Fig. 11. Cases of larvae of *Elliptera jacoti* Alexander, 1925.

THORAX. Pronotal horn large, flattened, ear shaped, anterior and posterior ends widely curved inwards (Fig. 9C). Outer margin of horn entirely covered with numerous tubercles (Fig. 9D). Dorsum of thorax smooth. Apex of wing reaches ⅓ of third abdominal segment (Fig. 9A–B). Legs reach anterior third of sixth abdominal segment. The innermost pair of legs shortest, the outermost pair longest (Fig. 9B).

ABDOMEN. Abdominal segments III–VI divided into anterior and posterior parts (Fig. 9A–C). Anterior part of dorsum of segments IV–VI with two transversal rows of spines (Fig. 9A) with segments III and VII with a single row of spines. Posterior part of segments III–VII with row of setae (five clusters composed of two setae each) (Fig. 9C), segments laterally with four to five long setae (Fig. 9A). Venter of abdominal segments VI–VII with two transversal rows of spines (Fig. 9B). Surface of abdominal segments smooth. Spiracles absent. Terminal segment slightly elongate (Fig. 9E). Sheath of cerci long, sclerotized and directed upward. Sheath of valvae reach only half length of sheath of cerci, not sclerotized. Mediodorsal spine well developed, triangular with rounded apex. A few long setae located on apex of both mediodorsal and anterodorsal spines.

Habitat

Larvae develop on vertical cliff surfaces kept wet by a film of water supporting algal growth (*fauna hygropetrica*) (Fig. 10). Larvae usually make cases from silt (Fig. 11). Pupae can make cases from mosses and algae (Fig. 12).

Distribution

Recorded from China, North and South Koreas, West Siberia and the Far East of Russia.

Fig. 12. Pupal exuviae of *Elliptera jacoti* Alexander, 1925 in case (NIBR).

Elliptera zipanguensis zipanguensis Alexander, 1924
Figs 13–15

Diagnosis

Adult (Fig. 13)
Vein *Rs* long and straight, and very close to vein *R*, R_2 indistinct, discal cell open by the atrophy of the outer deflection of M_3, *m-cu* at branching point of *M*. Halter brownish. Frontal coxae brown frontally, whitish yellow posteriorly, middle and posterior coxae whitish yellow. Trochanters whitish yellow. Femora light brown with yellowish base. Tibiae and tarsi brown. Abdominal tergites dark brown, sternites yellowish brown, pregenital segments blackish. Male genitalia dark brown. Ninth tergite with distinct lateral lobes on posterior margin. Outer gonostylus strongly sclerotized, inner gonostylus fleshy and setose. Cercus of ovipositor short with distinctly raised and hardened apical part.

Larva
Body up to 9.2 mm long. Head capsule heavily sclerotized. Hypostoma with eleven teeth. Abdominal segments II–VII with dorsal and ventral creeping welts. Spiracular disc surrounded by four lobes with lateral lobes sclerotized only along margins.

Material examined

SOUTH KOREA • 1 larva (in ethanol); Ganngwon-do, Samcheck-ri, Gagok-myeon, Deokpungni Yongsogol; 8 Jun. 2011; H. Soh leg.; GenBank: MT233406; NIBR IN 0000499882 • 1 larva (in ethanol); same collection data as for preceding; GenBank: MT233407; NIBR IN 0000499924 • 1 larva (in ethanol); Gyeongsangbuk-do, Uiseong-gun, Anpyeong-myeon, Bakgok-ri; 7 Apr. 2012; J.O. Suk leg.;

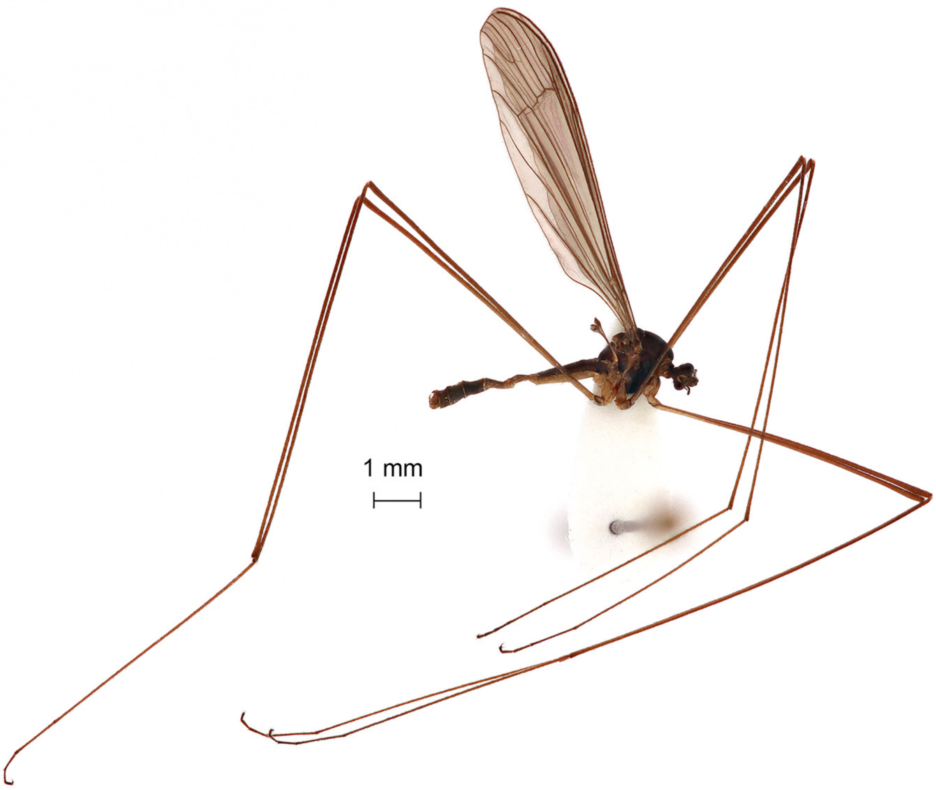

Fig. 13. Male of *Elliptera zipanguensis zipanguensis* Alexander, 1924 (NIBR).

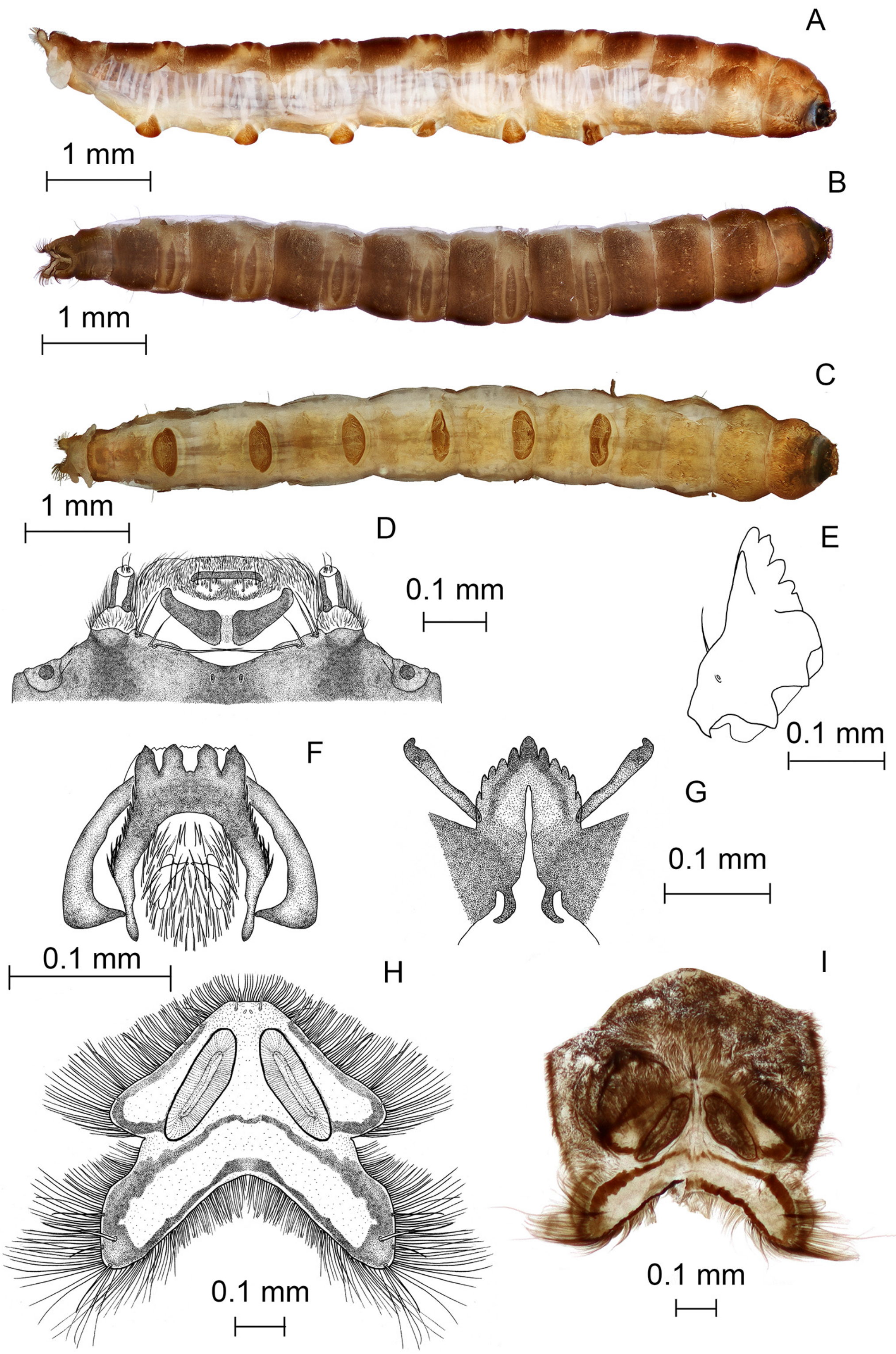

Fig. 14. Larva of *Elliptera zipanguensis zipanguensis* Alexander, 1924 (NIBR). **A**–**C**. General view. **A**. Lateral aspect. **B**. Dorsal aspect. **C**. Ventral aspect. **D**. Labrum, clypeus and antennae. **E**. Right mandible, dorsal view. **F**. Hypopharynx and prementum. **G**. Hypostoma. **H**. Spiracular field. **I**. Spiracular field.

GenBank: MT233408; NIBR IN 0000564371 • 1 larva (in ethanol); Gangwon-do, Pyeongchang-gun, Daegwallyeong-myeon; 1 Jul. 2011; M.J. Baek leg.; GenBank: MT233410; NIBR IN 0000564293 • 19 larvae (in ethanol); Gyeongsangnam-do, Hadong-gun, Hwagae-myeon, Beomwang-ri; 35°16.59′ N, 127°37.08′ E; 364 m a.s.l.; 24 May 2015; V. Podeniene leg.; GenBank: MT233409; NIBR • 3 larvae (in ethanol); same collection data as for preceding; 8 May 2013; V. Podeniene leg.; NIBR • 1 ♂ (in ethanol); Gangwon-do, Chuncheon-si, Dongsan-myeon, Kangwon National University Experimental Forest; 37°46.75′ N, 127°48.95′ E; 225 m a.s.l.; 9 Oct. 2018 (1); S. Podenas leg.; S. Podenas det.; GenBank: MT233414; NIBR.

Description

Larva

Measurements. Length 6.1–9.2 mm, width 1.5–1.6 mm. In general similar to that of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. and *E. jacoti*.

Body. Cylindrical, dark brown, hairs on dorsal and ventral sides darker than on lateral side. Abdominal segments II–VII divided into anterior and posterior parts, anterior part with dorsal and ventral creeping welts (Fig. 14A–C). Creeping welts with dark brown spines, arranged into transverse rows. All thoracic and first abdominal segments shorter than wider. Abdominal segments II–VIII approximately as long as wide.

Head. Length 0.90–0.94 mm, width 0.80–0.85 mm. In general similar to that of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. and *E. jacoti*. Differences were noticed in arrangement of sensory structures on labrum and frons, shape of mandible, number of teeth on hypostoma and prementum. Labrum on each side bears two medium-length setae and three sensory pegs in the middle of anterior part (Fig. 14D). One long and three medium-length setae and sensory pit located on each side along the anterior margin

Fig. 15. Habitat of larvae of *Elliptera zipanguensis zipanguensis* Alexander, 1924.

of the frons (Fig. 14D). Mandible conus-shaped, with two large apical teeth, first apical tooth blunt, second acute (Fig. 14E). First ventral tooth is similar to first apical, second ventral slightly shorter than first ventral, basal tooth smallest triangular. Dorsal tooth well developed with acute apex. Prementum has four large teeth anteriorly in the middle and numerous small acute teeth on both sides (Fig. 14F). Hypostoma with 11 teeth, the middle tooth most prominent (Fig. 14G).

Anal division. Spiracular field surrounded by four lobes, ventral lobes considerably longer than lateral lobes (Fig. 14H–I). Each lateral lobe as long as wide and posterior margin with U-shaped dark sclerite. Four medium-long setae located along the outer margin of lobe. Ventral lobe twice as long as width at the base and bears a dark U-shaped sclerite, the posterior branches fused medially into a connected line (Fig. 14H). A long seta located apically, three medium-length setae along outer margin of lobe. Two pairs of sensory pits located on dorsal margin of spiracular field. Spiracular field fringed with long firm setae, longest along the apical margins of lobes. Spiracles large, oblong, placed obliquely and inclined dorsally (Fig. 14H–I). Anal field with two pairs of conical, white, fleshy anal papillae (Fig. 14C).

Habitat

Larvae develop on vertical cliff surfaces kept wet by a film of water supporting algal growth (*fauna hygropetrica*) (Fig. 15).

Distribution

Recorded from the Far East of Russia, North and South Koreas and Japan.

Discussion

Although the larvae and pupae were described previously for *E. omissa* (Mik 1886), this paper provides the first complete descriptions and accurate illustrations for the immature stages of *Elliptera*. This is also the first new species described in Tipuloidea based on the larval stage alone. This is made possible by using an mt COI DNA-based analysis to associate adults and immature stages, and to recognize that unassociated larvae represented an undescribed species. Our study shows that *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov., *E. jacoti* and *E. zipanguensis zipanguensis* form separate clades and are separated by significant molecular distances (Table 1). Adults of *E. jacoti* and *E. zipanguensis zipanguensis* (*E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. adults remain unknown) are easily distinguished by wing and genitalic characters. Although molecular differences distinguish clearly between the three species, morphological differences between larvae of *Elliptera* are not so obvious.

Morphologically overall, larvae of the genus *Elliptera* are similar: yellowish brown body, hairs on dorsal and ventral sides darker than on lateral side, abdominal segments II–VII divided into anterior and posterior sections, and the anterior section with dorsal and ventral creeping welts. Differences between the species were noticed in the pattern on the dorsum of the larvae, sclerotization pattern of spiracular lobes and some head capsule features, most notably the number of teeth of the hypostoma. The dorsum of the body of the larva in *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. and E. *jacoti* shows single circular pale spots medially against a brown background on all abdominal segments and the last thoracic segment. The distinct spots are lacking in *E. zipanguensis zipanguensis*. The lateral spiracular lobes of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. and *E. jacoti* are almost entirely sclerotized except the very middle, while in *E. zipanguensis zipanguensis* the lateral lobe bears only a narrow U-shaped sclerite, with the rest of the lobe surface unsclerotized. The ventral lobes of *E. zipanguensis zipanguensis* bear U-shaped sclerites with both branches joined in the middle between the paired lobes. The ventral lobes of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. and *E. jacoti* have similar U-shaped sclerites but only the lower branches join in the middle to form a continuous line.

The general appearance of the larval head capsule is also similar among these three species. Differences were noticed in arrangement of sensory structures on the labrum and frons, the shape of the mandible, and the number of teeth on the hypostoma and prementum. The most significant difference and most readily observed is the number of hypostomal teeth. *Elliptera mongolica* Podeniene, Podenas & Gelhaus sp. nov. has nine teeth, while the hypostoma of *E. jacoti* and *E. zipanguensis zipanguensis* bears eleven teeth.

The larva and pupa of *E. omissa* are described and illustrated insufficiently (Mik 1886) so detailed comparisons (except general appearance) are impossible to make with the three species described in this paper. General appearances of larva and pupa of this European species is similar to that of the species described here. Of interest, the hypostoma of *E. ommissa* is illustrated with a single median tooth only (Mik 1886: fig. 4), but we suspect that the lateral teeth were obscured and not noticed. Differences were noticed in the shape of the pronotal horns of the pupae. According to Alexander (1920) the pronotal horns of *E. omissa* consist of two parts (dorsal and ventral) but that is not clearly evident in the illustrations of Mik (1886: figs 8–10). In *E. jacoti* the pronotal horns are continuous with posterior and anterior ends strongly curved inwards. The shape of the horns are different in the two species, with those of *E. ommissa* appearing much taller than wide, while those in *E. jacoti* are much wider than tall.

The habitats of the immatures and adults of *Elliptera* of eight species are known (*clausa*, *hungarica*, *illini*, *ommissa*, *usingeri*, and the three species here), and are very similar. They are found on wet vertical cliff surfaces, a specialized aquatic habitat with a thin film of water supporting lithophilous algae, includes species of *Dicranomyia* Stephens, 1829, *Geranomyia* Haliday, 1833, *Dactylolabis* Osten Sacken, 1860, *Orimarga* Osten Sacken, 1869 (all Limoniidae) and *Pedicia* Latreille, 1809 (Pediciidae) (Gelhaus & Podeniene 2019) with *Elliptera* and *Dactylobabis* appearing to be hygropetric habitat specialists at the generic level (Sinclair 1988). As such, the larval habitat of *E. mongolica* Podeniene, Podenas & Gelhaus sp. nov. on boulders in a river and spring broadens the concept of hygropetric habitat. *Elliptera* immatures live in tubes constructed from larval-produced threads, sometimes also binding mosses together, with pupation also occurring in these tubes. These habitats at least in some cases are also strongly seasonal with development occurring presumably during a short period when water is flowing, as noted by Mik (1886, as translated by Alexander 1920) in Austria, Alexander (1966) for California, USA, and Korea as well. This indicates these species spend a considerable part of the year in the desiccant-resistant egg stage.

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