

## New species of *Ameletus* Eaton, 1885 from the Russian Far East with notes on *Ameletus camtschaticus* Ulmer 1927 (Ephemeroptera: Ameletidae)

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### Abstract

The male imagoes, larvae, and eggs of *Ameletus allengaensis* **sp. nov.** and *Ameletus sirotskii* **sp. nov.** from the Russian Far East are described. Based on the structure of the male genitalia, the imago and larvae of *A. allengaensis* **sp. nov.** and *A. sirotskii* **sp. nov.** are similar to those of *A. camtschaticus*, but the discovery of these new species and separation from *A. camtschaticus* were confirmed by studies of the morphology of the larvae and male imago, as well as molecular analysis. Identity of various developmental stages of the new species were confirmed by analysis of the mitochondrial gene cytochrome oxidase 1 (COI) DNA barcode, which was also used to reconstruct the phylogenetic relationships within the genus *Ameletus*. The intraspecific sequence divergence based on the Kimura-2-parameter (K2P) distance ranged from 0.0–2.5%, whereas the interspecific sequence divergence based on the K2P distance ranged from 6.2–7.9% within *A. sirotskii* **sp. nov.**, *A. allengaensis* **sp. nov.** and *A. camtschaticus*. Male imagoes of *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* can be distinguished by the size and location of small denticles on the ventral plate of the penis. The larvae of *A. allengaensis* **sp. nov.** differ from those of *A. sirotskii* **sp. nov.** by the size of gills I and II. In *A. allengaensis* **sp. nov.**, gill I is almost twice as small as gill II; in *A. sirotskii* **sp. nov.**, gill I is only slightly smaller than gill II. Both new species differ from *A. camtschaticus* by gill II, which does not have an anal rib on the anal margin.

**Key words:** mayflies, *Ameletus*, taxonomy, morphology, egg, interspecific sequence, Far East

### Introduction

Mayflies of the genus *Ameletus* Eaton, 1885 are common in the streams of the Russian Far East, where ten species have been recorded (Kluge 2007; Tiunova 2013): one Trans-Holarctic taxon, *Ameletus inopinatus inopinatus* Eaton 1887; three East Palearctic taxa, *A. inopinatus labiatus* Sinitshenkova 1981, *A. montanus rossicus* Kluge 2007, and *A. cedrensis* Sinitshenkova 1981; four East Asian continental species, *A. camtschaticus* Ulmer 1927, *A. khasanensis* Tiunova 2013, *A. montanus arlecchino* Kluge 2007, and *A. longulus* Sinitshenkova 1981; and two East Asian island species, *A. montanus montanus* Imanishi 1930 and *A. costalis* Matsumura 1931.

Extensive material of this genus has been collected for many years by the first author, and phenological analysis showed that *A. camtschaticus* adults have been encountered particularly from mid-June to August (Gorovaya 2014). However, the descriptions of the larvae of this species in Sinichenkova and Tshernova (1976) and Kluge (2007) differ, justifying the specific collection of *A. camtschaticus* larvae and adults in several areas in the Russian Far East allowing a comprehensive taxonomic review.

An integrative taxonomic approach includes morphological characters as well as a molecular analysis (Webb *et al.* 2007, Ogden *et al.* 2009). The DNA barcode corresponding to the ca 650-bp fragment of the mitochondrial gene cytochrome c oxidase I (COI) has been identified as the core of a global bio-identification system at the species level (Hebert *et al.* 2003) and has proved to be useful in mayflies (Ball *et al.* 2005; Webb *et al.* 2012; Gattolliat *et al.* 2015; Selvakumar *et al.* 2016). DNA barcodes of *Ameletus camtschaticus* were obtained and revealed important genetic distances between some populations.

Based on these data and a more detailed study of larval and adult morphology, we have identified two new species, *A. allengaensis* **sp. nov.** and *A. sirotskii* **sp. nov.**, which are described below. The description of the larvae of *A. camtschaticus* was based on specimens collected in the south eastern part of the Kamchatka Peninsula (Avacha River Basin), near to the topotype locality. The penis structures of both new species are very similar to that of *A. camtschaticus*, a brief description and illustrations of this species are therefore also presented.

The material is deposited in the collection of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia.

## Material and methods

Total genomic DNA was extracted from thorax of 45 specimens of *Ameletus camtschaticus* using the Invitrogen PureLink Genomic DNA Mini Kit and the Qiagen DNeasy Blood and Tissue Kit in compliance with the manufacturer's protocols. Approximately 650 base pairs of the COI were amplified from diluted genomic DNA by polymerase chain reaction (PCR) in a total volume of 10 µl with 5 µl of Go Taq Green Master Mix (Promega Corp, Madison, WI, USA), 0.5 µl of each primer (100 ng/µl), 3 µl of nuclease-free water and 1 µl of total DNA. The PCR thermal regime consisted of one cycle of 1 min at 94 °C; five cycles of 1 min at 94 °C, 1.5 min at 45 °C and 1.5 min at 72 °C; 35 cycles of 1 min at 94 °C, 1.5 min at 50 °C and 1 min at 72 °C; and a final cycle of 5 min at 72 °C. The primers COIF-ALT (5'-ACAAATCAYAARGAYATYGG-3') and COIR-ALT (5'-TTCAGGRTGNCCRAARAAYCA-3'), which were obtained from Mikkelsen *et al.* (2006), were used. The PCR products were bidirectionally sequenced using the BigDye Terminator v3.1 cycle kit and run on an ABI 3130xl DNA analyzer (Applied Biosystems™).

Sequences were aligned and manually edited in MEGA 7 (Kumar *et al.* 2016). Bayesian analysis was carried out using MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) by partitioning sequences for each codon position (using Partition finder 2.1.1) and running the algorithm using a mixed model. The best model of nucleotide substitution was GTR+I, F81+I and GTR+G for first, second and third positions respectively. All *Ameletus* sequences have been deposited in GenBank (KY175168 - KY175212).

## Results

The final alignment of the COI gene yielded 658 bp for *Ameletus sirotskii* **sp. nov.**, *A. allengaensis* **sp. nov.** and *A. camtschaticus*. Intraspecific sequence divergence ranged from 0.0–2.5% (Table 1) with a mean divergence value of 0.4%, which is within the normal range for mayflies (Ball *et al.* 2005). Several specimens of *A. allengaensis* **sp. nov.** and *A. camtschaticus* were from localities more than 2,000 km apart from each other, but this geographic distance was not reflected in the distance data. The intraspecific sequence divergence of *A. camtschaticus* also did not depend on the geographical location.

Interspecific sequence divergences based on K2P distance for the three species ranged from 6.2–7.9% (mean 6.9%) without overlapping with the intraspecific sequence divergences (Table 1, Fig. 1). Using GenBank data for the *Ameletus* COI (22 valid species), we found that interspecific sequence divergences ranged from 6.7% (*A. andersoni* AY326935—*A. dissitus* AY326866) to 24.7% (*A. subnotatus* JQ663260—*A. pritchardi* AY326941), and the mean value was 18.3%. According to Ball *et al.* (2005), K2P distance in *Ameletus* ranged from 6.5–24.8%.

The monophyly of *A. sirotskii* **sp. nov.**, *A. allengaensis* **sp. nov.**, and *A. camtschaticus* was strongly supported (Fig. 1). Our outgroup species (*A. montanus* Imanishi, KP970689) exhibits a mean K2P of 14.4%.

**TABLE 1.** Mean values and ranges of intraspecific sequence divergences (% difference, K2P distance) of COI MtDNA partial sequences of three *Ameletus* species.

| Species                                      | Number of sequences | Mean variation (%) | Range (%) |
|----------------------------------------------|---------------------|--------------------|-----------|
| <i>Ameletus sirotskii</i> <b>sp. nov.</b>    | 9                   | 0.2                | 0–0.8     |
| <i>Ameletus allengaensis</i> <b>sp. nov.</b> | 26                  | 0.8                | 0–2.5     |
| <i>Ameletus camtschaticus</i>                | 10                  | 0.2                | 0–0.8     |

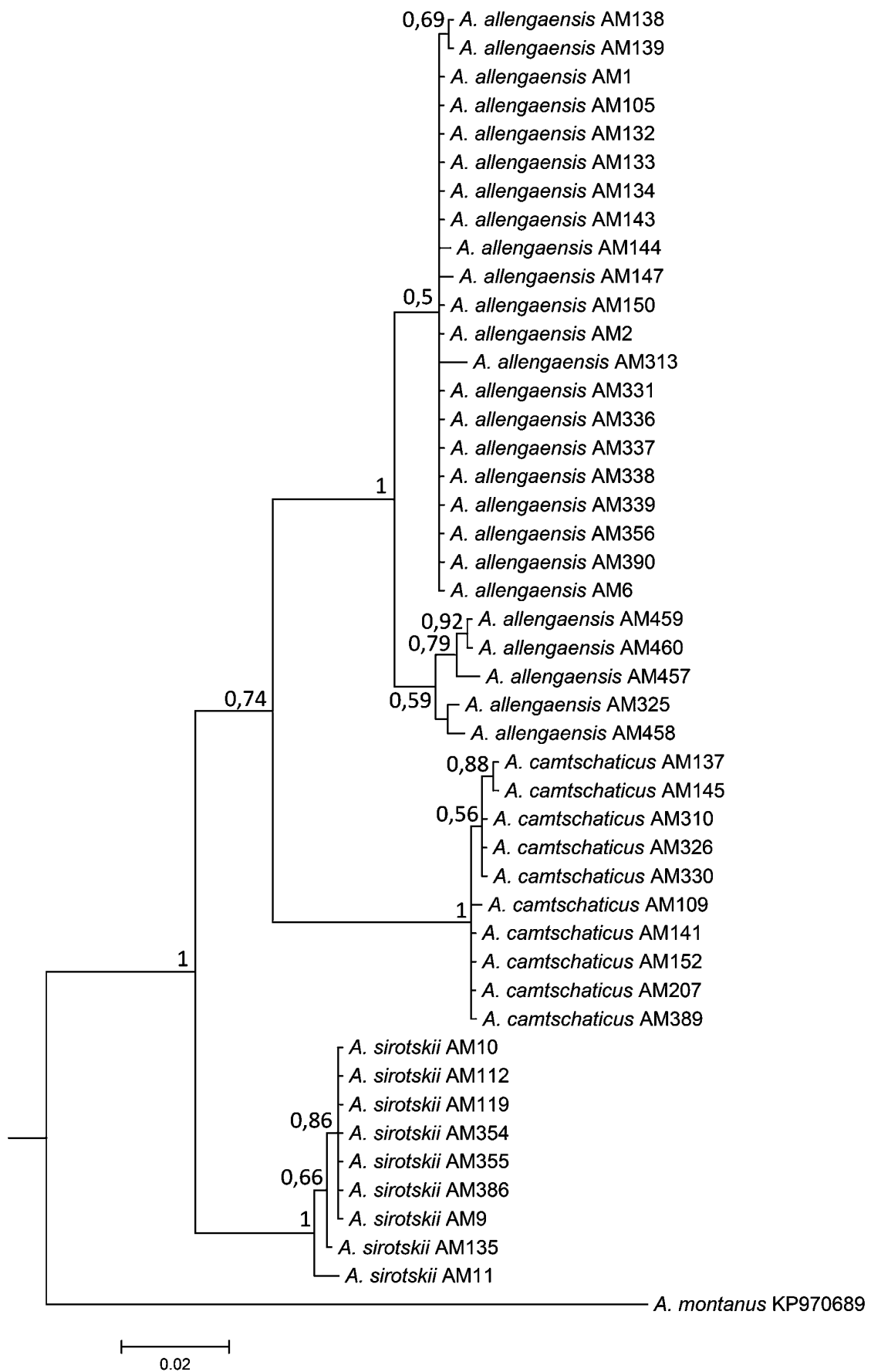


FIGURE 1.

***Ameletus allengaensis* Tiunova, sp. nov.**

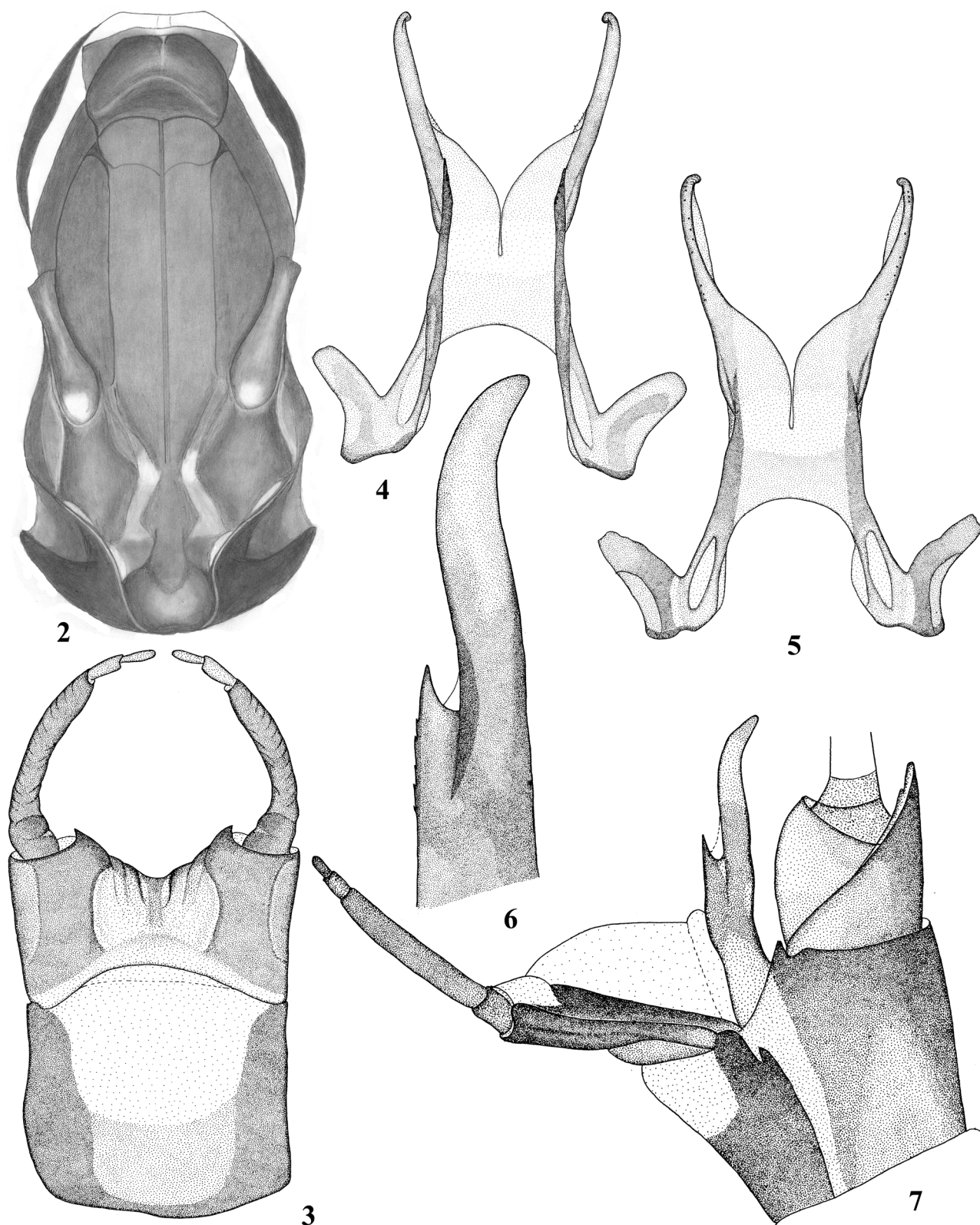
(Figs 2–31)

**Material.** **Holotype** male imago (reared from larva), **RUSSIA**, AMURSKAYA OBLAST', Zeyskii district, Allenga River, above mouth, 29.VI.2015, T. Tiunova. **Paratypes:** collected together with the holotype: 12 male and 3 female, 1 female (AM339) imagines (reared from larva); same place, 29.VI.2015, 5 male, 13 female imagines, 11 larvae, 13 larval skin, T. Tiunova.

**Other material examined.** **RUSSIA:** KHABAROVSKIY KRAY, Okhotskii district: Ul'ya River Basin, Khetana River, 08.VII.1985, 4 male and 1 female subimagines, 10 larvae, V. Zherikhin; Bulginka River, a turn on the Bulgino village, 26.VI.1999, 1 male and 2 female imagines (reared from larva), 2 male and 2 female subimagines (reared from larva), 2 larvae, T. Tiunova; same locality, 03.VII.1999, 2 larvae, T. Tiunova; Amur River Basin, Gera River, about 2 km upper Gera Lake, 26.VI.2000, 1 larva, T. Tiunova; at highway Khabarovsk–Nikolaevsk-na Amure: Yai River, bridge, 30.VI.2005, 4 larvae, T. Tiunova; Hivanda River, 1.VII.2005, 2 larvae, T. Tiunova; AMURSKAYA OBLAST': Zeya Reservoir Basin: stream, ~ 2 km below the mountain Zolotaya Sopka, at highway Zeya–Beregovoy, 20.VI.2004, 10 larvae, T. Tiunova; at highway Zeya–Verhnezeysk: Sirik River, bridge, 21.VI.2004, 12 larvae, T. Tiunova; Dess River, bridge, 21.VI.2004, 9 larvae, T. Tiunova; Artemiy stream, bridge, 21.VI.2004, 5 larvae, T. Tiunova; Palpaga River, bridge, 22.VI.2004, 3 larvae, T. Tiunova; Kiryak River, bridge, 22.VI.2004, 5 larvae, T. Tiunova; ZEYSKII RESERVE: Zeya Reservoir Basin, Bolshoi Garmakan River, about 300 m above mouth, 02.VII.2015, 2 male, 5 female imagines, 2 male, 1 female subimagines, 11 larvae, T. Tiunova; same locality, 08.VII.2015, 3 male, 13 female imagines, 6 male, 5 female subimagines, 1 larva, T. Tiunova; Zeya River Basin: Bolshaya Erakingra, 52-i km, 6.VII.2013, 7 male, 6 female imagines, 4 male, 2 female subimagines, 19 larvae, 1 larva (AM6), T. Tiunova; same locality, 09.VII.2014, 6 male, 8 female imagines, 2 female subimagines, 6 mature larvae, 1 larva (AM133), 1 larva (AM134), T. Tiunova; same locality, 3–4.VII.2015, 17 male, 13 female, 1 female (AM337) imagines (reared from larvae), 17 mature larvae, 1 larva (AM336), T. Tiunova; Bolshaya Makcha River, bridge, at highway Tynda–Zeya, 08.VII.2014, 1 male imago (AM132), T. Tiunova; same locality, 28.VI.2015, 3 larvae, 1 larva (AM331), T. Tiunova; Kamenushka River, 06.VII.2015, 11 larvae, T. Tiunova; Tynda River Basin, Allenga River, bridge, at highway Zeya–Snezhnogorsk, 07.VII.2013, 2 male, 5 female, 1 female (AM1) (reared from larvae) imagines, 34 larvae, 1 larva (AM2), T. Tiunova; same locality, 06.VII.2014, 11 larvae, 1 larva (AM105), T. Tiunova; same place, 13 larvae, 1 larva (AM325), T. Tiunova; Savushkin stream, 38 km from Zeya town, at highway Zeya–Steznogorskiy, 09.VII.2015, 13 larvae, 1 larva (AM338), 1 larva (AM356), T. Tiunova; MAGADANSKAYA OBLAST': Ola River, upper reaches, 24.VI.2013, 1 female subimago, 2 larvae, E. Khamenkova; same locality, 30.V.2014, 2 larvae, 1 larva (AM390), E. Khamenkova; same locality, 16.VI.2014, 2 larvae, 1 larva (AM143), 1 larva (AM144), 1 larva (AM147), 1 larva (AM150), E. Khamenkova; same locality, 08.VII.2014, 2 male and 1 female (reared from larvae) imagines, 1 female subimago, 1 mature larvae, E. Khamenkova; Ola River Basin, Donyshko River, 16.VI.2014, 1 larva (AM138), 1 larva (AM139), E. Khamenkova; KAMCHATKA PENINSULA, Poperechnaya River, 28.VII.2015, 3 mature larvae, 1 larva (AM313), I. Tiunov; SACHA YAKUTIYA: Timplon River Basin, Gorbyllah River, bridge, at highway Tygda–Neryungri, 30–31.VII.2010, 4 male, 2 female imagines (reared from larvae), 6 larvae, T. Tiunova; same locality, 30.VII.2016, 7 larvae, 1 larva (AM457), 1 larva (AM458), 1 larva (AM459), 1 larva (AM460), I. Reznik.

**Description.** **Male imago** (in alcohol). Length (mm): body 12.9–14.0; forewings 11.5–12.7; cerci 12.3–16.0. **Head:** upper portion of the eyes grey; lower portion dirty grey. **Thorax:** Medioscutum and submedioscutum dark brown; median longitudinal suture narrow and dark (Fig. 2). Sublateroscutum dark brown. Scutellum dark brown; scuto-scutellar impression brown or light brown with light lateral margins. Posterior scutellum protuberance dark brown with narrow white spot near the posterior lateral margin. Anteronotal protuberance dark brown; anterolateral sides dark. Forelegs dark brown or dirty brown; middle and hind legs yellowish or brownish; tarsal segments slightly darker. Length (mm) of foreleg segments: femora 2.3–2.4; tibia 2.0–2.3; tarsal segments 0.5–0.6, 1.3–1.5, 1.3–1.4, 0.9–1.0, and 0.5–0.6. Wings brownish, hyaline; all veins brown with lighter crossveins; pterostigma milky. **Abdomen:** tergum I dark; terga II–VI brownish or dirty brownish with lateral margins and posterolateral corners dark brown at the posterior margin (Figs 8–9); in the first third of terga, a wide brown strip that connects with dark lateral angles; a pair of brownish oblique stripes medially; terga VII–VIII with dark brown posterolateral corners and posterior margins; tergum IX dark brown (Fig. 9). Sternum I dark brown; sternum II–III brown; sternum IV–VII





FIGURES 2–7.



**FIGURES 8–10.**





FIGURES 11–12.

brownish; sterna VIII–IX with two brownish oblique stripes and a pair of brown dots in the middle part of the anterior margin; sterna VII–VIII white with brownish stripes in the middle area; sterna II–IV with a pair of brown oblique stripes and spots near the anterior margin; sterna V–VIII with brown ganglionic markings (Fig. 10). Styliger white and well-contrasted medially with dark brown lateral margins (Fig. 3). First segment of forceps dark brown, sometimes lighter in the distal part; second and third segments light brown or brownish (Fig. 3). Lateral margin of penis lobes rounded and bent medially (Figs 4–5); each ventral plate bears large and long apical pointed denticle (Figs 6–7, 11–12), outer edge with several very small denticles, which are evenly located far from each other (Figs 6, 11–12); the first small denticle is located far from base of main denticles (Figs 6, 12). Cerci brown with dark brown joints of segments and pale tips.

**Female imago.** Length (mm): body 13.0–14.3; forewings 13.0–13.7; cerci 11.0–15.0. **Head:** eyes blackish and tinged grey. Base of the median and lateral ocelli delineated black; antennae brown at the base with remainder part pale. Space between the eyes white with blackish pigmentation. **Thorax:** Pronotum brown with white granular coating; mesonotum brown; anteronotal protuberance with white median longitudinal suture; posterior margin of mesonotum with a pair of wide and curved white stripes exciting the scuto-scutellar impression, the inner edge of the posterior scutal protuberance and the base of the submedioscutum; sublateroscutum with pairs of dark and white spots. Forelegs brown; middle and hind legs light brown or yellowish. Wings hyaline; all veins brown. **Abdomen:** Colour of terga as in the male (Fig. 13). Sterna light brown, lateral margins pale; sterna IV–VII with brown ganglionic maculation; sternum VII brown with pale middle area; sterna VIII–IX brown with diffuse white pigmentation. Subgenital plate brown with a deep incision. Cerci brownish; joints of segments brown.

**Mature larva.** Length (mm): body 11.5–14.2; cerci 4.2–6.3. **Head:** Brown with pale triangular spot from the median ocellus to the anterior margin of the clypeus (Fig. 14). Antennae brown at the base, tips pale. Labrum

(length 0.8–0.86 that of the width) light brown with a wide, brown, nearly rectangular spot that does not reach the anterior margin (Figs 14, 16); spot sometimes almost black with an extended anterior margin with a mushroom shape. Clypeus brown, lateral sides pale (Figs 14, 16). First denticle incisor of the left mandible largest, the fourth smallest, the second nearly equal to the third (Fig. 17); third denticle incisor of the right mandible widest (Fig. 18). Labium whitish, shown in Fig. 19. **Thorax:** pronotum and mesonotum brown with contrasting pale and light brown stripes and spots (Fig. 15). Legs light brown; femur of all legs light brown with brown spots near the joints of segments and a pale spot near the posterior margin (Figs 15, 20); tibia brown; tarsus light brown in the middle and



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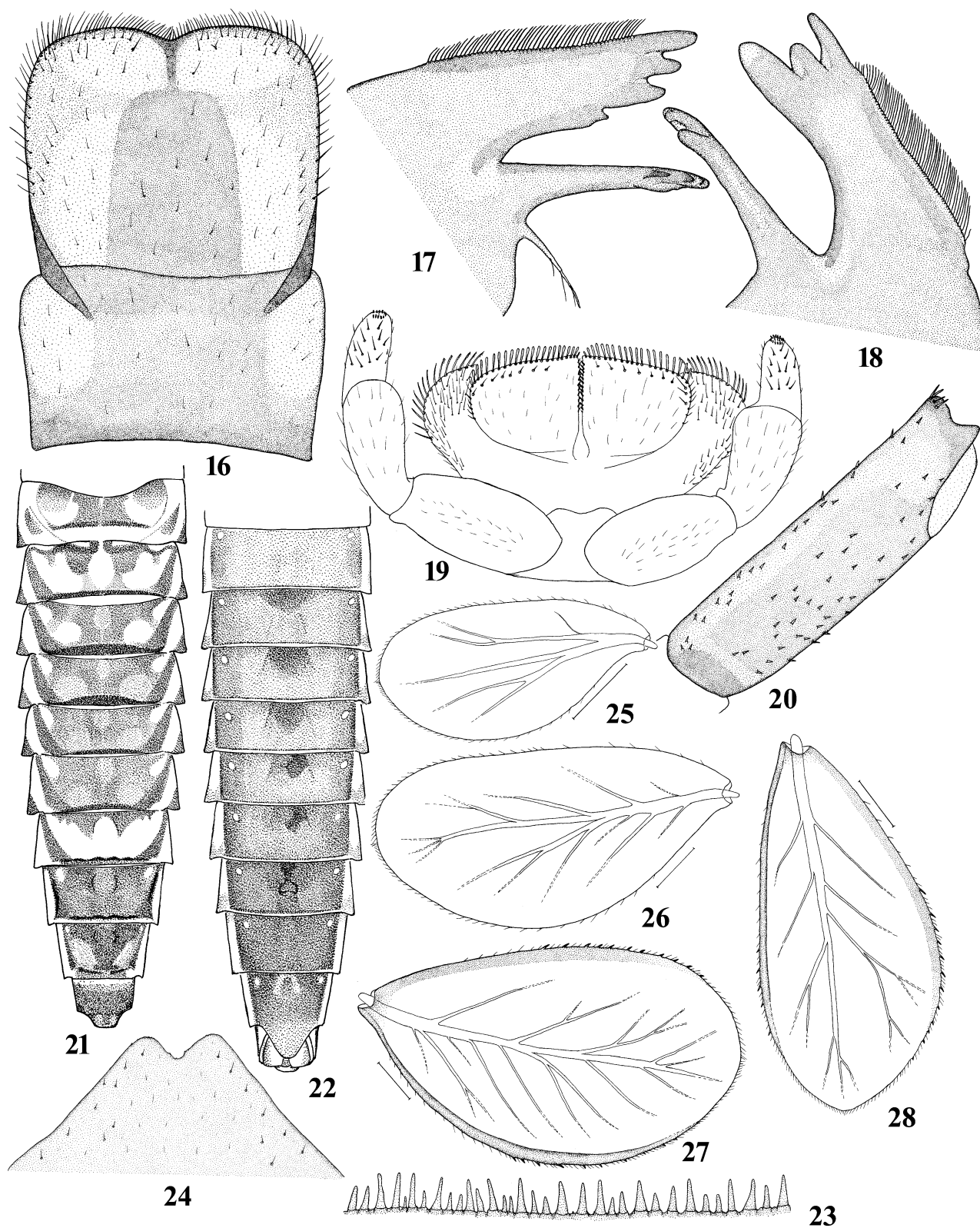
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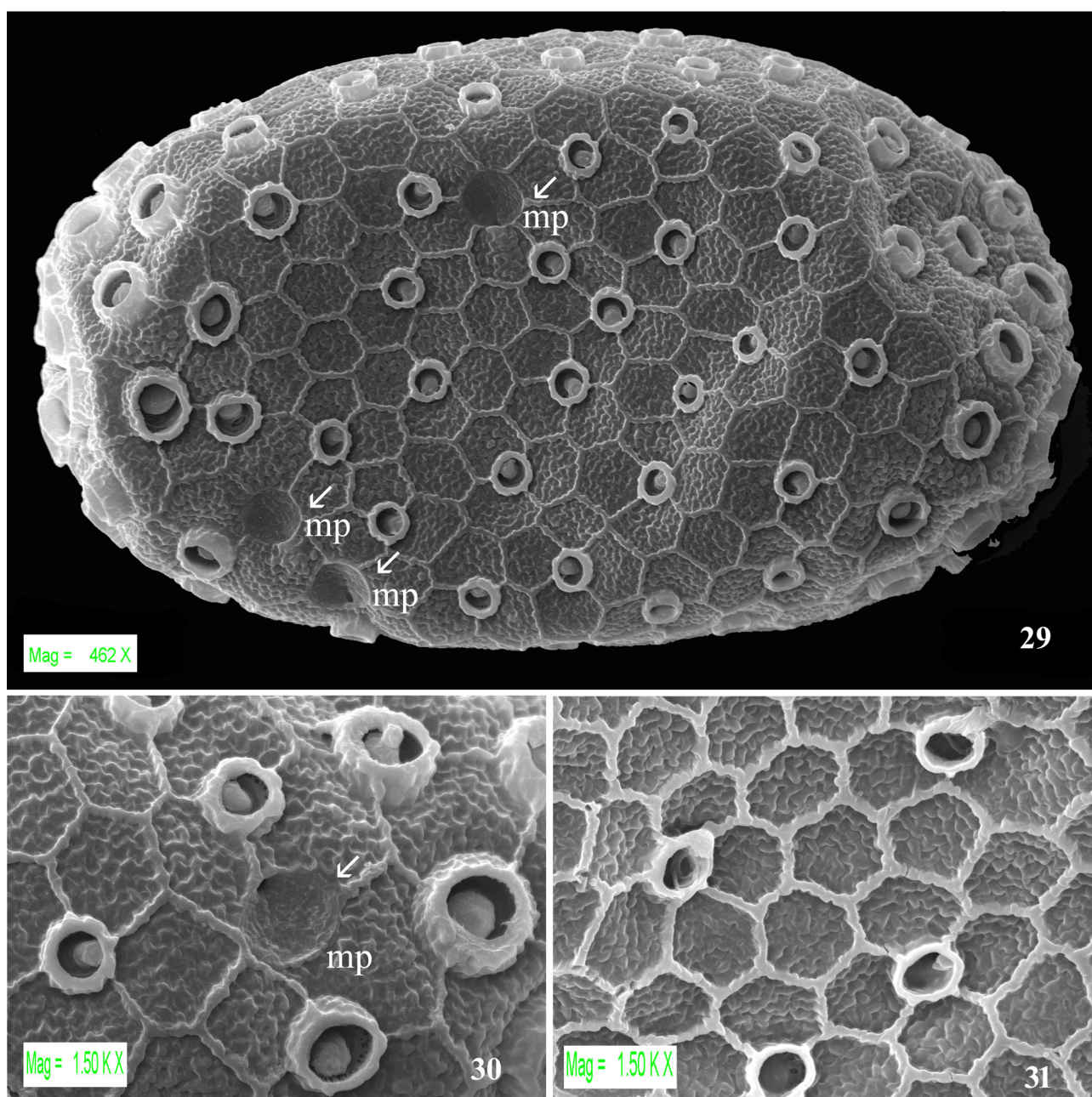
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FIGURES 13–15.





FIGURES 16–28.



FIGURES 29–31.

dark brown at the edges; claws dark brown. Foreleg (mm): femur 1.6–2.0; tibia 0.9–1.0; and tarsus 1.0–1.2. Middle leg: femur 1.5–2.0; tibia 1.0–1.1; and tarsus 0.9–1.2. Hind leg: femur 1.5–2.0; tibia 1.0–1.1; and tarsus 1.0–1.2. **Abdomen:** Brown with contrasting pale maculation (Figs 15, 21); terga I–VI with oblique white stripe on the sides and brown posterolateral corners; tergum I with a pair of white semilunar spots; posterior margin white; anterolateral corners white; tergum II with a pair of white spots of indefinite shape and a large oval white spot in the middle; tergum III with a pair of drop-shaped spots near the anterolateral corners and a pair of round spots in the posterior part; terga IV–VI with colour similar to tergum III but fainter; tergum VII with a white spot in the form of a maple leaf; tergum VIII brown with a pair of drop-shaped spots near the anterior margin; tergum IX with a pair of large white spots near the posterior margin, which sometimes merge along the posterior margin into a single spot; tergum X brown or dark brown with a white anterior area (Fig. 21); all terga with a row of long and short spines along of posterior margin (Fig. 23). Sterna brown or dark brown (Fig. 22); sterna I–IX with pale lateral margins and a pair of small white spots near the anterolateral corners; sternum I pale; sterna II–V with a large

blackish spot in the centre near the anterior margins; sterna VI–VII with blackish ganglionic markings; sternum VIII dark brown; sternum IX (female) with a pair of pale stripes centrally, near the anterior margin and a deep incision (Fig. 24). Gills white; gills I and II without anal rib (Figs 25, 26); gill I nearly two times smaller than gill II, width 0.50 of length; gill II: width 0.48 of length; gills III–VII with anal rib on the margins; gills III–VI with rounded distal margins and width 0.52–0.56 of length (Fig. 27); gill VII narrower and slightly smaller than gill VI, with width 0.49 of length (Fig. 28). Cerci brownish with dark band at the middle part (Fig. 15).

**Eggs.** General shape elliptical with a length of 189–208  $\mu\text{m}$  and a width of 105–121  $\mu\text{m}$  (Fig. 29). Chorionic surface covered with large-mesh, regular pentagonal cells; each cell with a wrinkled bottom (Figs 30, 31); borders of cells solid, relatively high; each four or five cells united by one small round knob that evenly covers the whole egg surface; large and round knobs arranged on both poles, smaller knobs centrally (Fig. 29). Micropyles located in the subequatorial area (Fig. 29); sperm guide round, micropylar rim absent; sperm guide well apparent (Fig. 30).

**Etymology.** The name refers to the type locality, the Allenga River, where the types were collected.

**Distribution and biology.** Russian Far East: Khabarovskiy Kray, Amurskaya and Magadanskaya Oblast', Sacha Yakutiya. According our observations, the period of emergence of the adults continues from 20 June to 30 July.

### *Ameletus sirotskii* Tiunova, sp. nov.

(Figs 32–58)

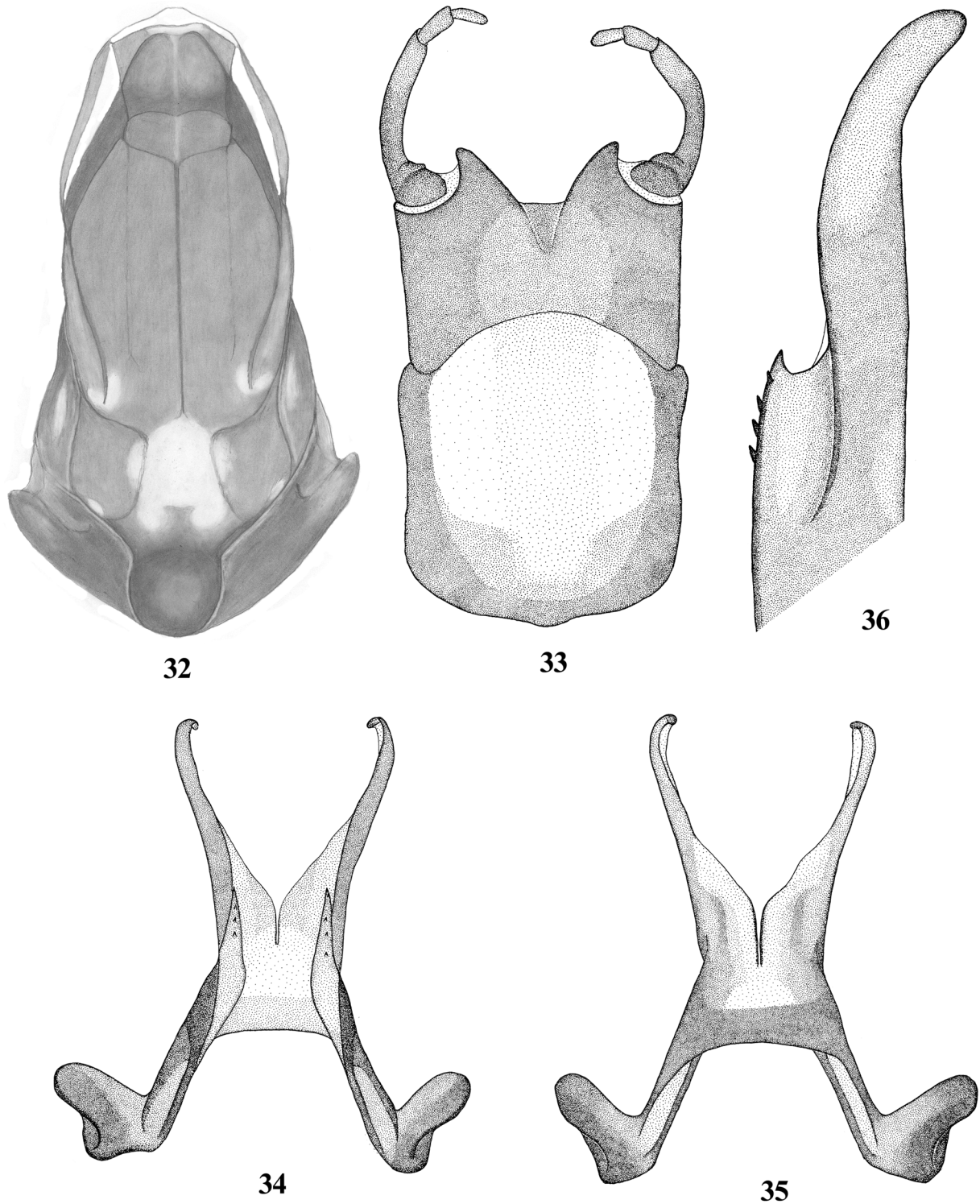
**Material.** **Holotype** male imago (reared from larva), **RUSSIA**, AMURSKAYA OBLAST', Zeyskii district, Bolshoi Garmakan River, about 300 m above mouth, 08.VII.2015, T. Tiunova. **Paratypes:** collected together with the holotype: 4 male, and 1 female imagines (reared from larva), 9 mature larva; same locality, 23.VI.2004, 1 larvae, T. Tiunova; same locality, 02.VII.2013, 18 mature larvae, T. Tiunova; same locality, 07.VII.2013, 4 larvae, 1 larva (AM10), T. Tiunova; same locality, 7.VII.2014, 1 female subimago (reared from larva), T. Tiunova; same locality, 02.VII.2015, 8 larvae, T. Tiunova.

**Other material examined.** **RUSSIA:** KHABAROVSKIY KRAY: Okhotskii district, Staryi Vodozabor stream, 03.VII.1999, 7 larvae, T. Tiunova; Malyi Marekan River, about 500 m above mouth, 06.VII.1999, 8 larvae, T. Tiunova; Ayno-Maisky district, Uyka River, ~ 1 km above mouth, 26.VII.1999, 2 larvae, T. Tiunova; AMURSKAYA OBLAST': Zeyskii reserve: Malyi Garmakan River, about 200 m above mouth, 02.VII.2013, 13 larvae, 1 larva (AM9), 1 larva (AM11), T. Tiunova; same locality, 7.VII.2014, 19 larvae, 1 larva (AM112), 1 larva (AM119), T. Tiunova; same locality, 08.VII.2015, 12 larvae, T. Tiunova; Bolshaya Erakingra River, 52-i km from Zeya, bridge, at highway Zeya–Beregovoy, 06.VII.2013, 19 larvae, T. Tiunova; same locality, 09.VII.2014, 1 female imago (reared from larva), 1 female subimago, 9 mature larvae, 1 larva (AM135), T. Tiunova; same locality, 04.VII.2015, 6 mature larvae, T. Tiunova; Shirokovka River, ~ 300 m above mouth, 2.VII.2013, 9 larvae, T. Tiunova; same locality, 07.VII.2014, 7 larvae, T. Tiunova; Kamenushka River, bridge, at highway Zeya–Beregovoy, 06.VII.2015, 23 larvae, T. Tiunova; Zeya River Basin: Dess River, bridge, at highway Zeya–Verhnezeysk, 21.VI.2004, 2 larvae, T. Tiunova; Gulik River, upper reaches, bridge, at highway Zeya–Verhnezeysk, 06.VII.2013, 12 larvae, T. Tiunova; Tynda River Basin, Allenga River, bridge, at highway Zeya–Snezhnogorsk, 14.VII.2012, 4 larvae, T. Tiunova; same locality, 0.7.VII.2013, 10 larvae, T. Tiunova; Allenga River, above mouth, 29.VI.2015, 6 larvae, 3 larval skin, T. Tiunova; Savushkin stream, 38 km from Zeya, at highway Zeya–Steznogorskiy, 09.VII.2015, 13 larvae, 1 larva (AM354), 1 larva (AM355), 1 larva (AM386), T. Tiunova; MAGADANSKAYA OBLAST', Ola River, upper reaches, 24.VI.2013, 3 larvae, E. Khamenkova.

**Description.** *Male imago* (in alcohol). Length (mm): body 9.7–10.5; forewings 9.7–10.0; cerci 10.5–12.0.

**Head:** upper portion of the eyes brownish; lower portion dirty grey. Medial and lateral ocelli white. **Thorax:** Medioscutum and submedioscutum dark brown; median longitudinal suture narrow and dark (Fig. 32). Scutellum dark brown; scuto-scutellar impression white. Posterior scutal protuberance and anteronotal protuberance dark brown. Femur of forelegs light brown or brown; tibia and tarsal segments dark brown; middle and hind legs from brownish to yellowish, tarsal segments slightly darker. Length (mm) of foreleg segments: femora 1.9–2.0; tibia 1.7–1.9; tarsal segments 0.5–0.6, 1.0–1.3, 1.0–1.2, 0.8, and 0.4–0.5. Wings brownish, hyaline; all veins brown with light brown crossveins. **Abdomen:** terga brown, opaque, posterior margins dark brown (Fig. 37); tergum I dark brown or dark; terga II–VI with a pair of brownish oblique stripes located medially; tergum VII–IX light brown with dark brown lateral corner. Sterna brownish or whitish, opaque; sternum I brown; sternum II light brown;

sterna III–VI whitish; sterna III–V with two brownish, oblique stripes and a pair of brown dots in the middle part of the anterior margin; sterna VII–VIII with brownish middle area; sternum IX white, all margins are bordered with dark brown (Fig. 38). Styliger and first segment of forceps dark brown, darker than other segments (Fig. 33). Penis lobes light brown on inner sides and brown on the outer side; penis lobes rounded laterally and curved medially (Figs 34, 35); each ventral plate of penis bears large and wide apically pointed denticle (Figs 36, 40), the outer edge with few small denticles (Figs 39, 40); the first small denticle located near the base of apical denticle (Fig. 40). Cerci brown with darker joints and light brown tips.



**FIGURES 32–36.**





**FIGURES 37–38.**

**Female imago.** Length (mm): body 7.6–9.5; forewings 8.2–9.5; cerci 8.7–10.0. **Head:** Blackish; eyes black. Medial and lateral ocelli contoured by black; antennae brownish with pale tips. **Thorax:** Pronotum brownish with pale posterior margin. Medioscutum and submedioscutum brown; medioparapsidal suture light brown; anteronotal protuberance and scutellum brown; scuto-scutellar impression pale. Forelegs brown; middle and hind legs yellowish, joints brown. Wings hyaline: all veins brown. **Abdomen:** Terga brownish; posterior margins and posterolateral corners darker. Sterna pale; sterna I–II and VII–VIII dirty pale. Subgenital plate brownish without incision. Cerci brownish, tips pale.



FIGURES 39–40.

**Mature larva.** Length (mm): body 9.0–11.2; cerci 3.6–5.2. **Head:** Brown (Fig. 42). Antennae light brown. Labrum (length 0.82 that of width) brown with an oval pale spot bordering brown stripe (Figs 42, 43); lateral margins dark; distal area pale. Basal part of clypeus dark brown (Figs 42, 43). First denticle incisor of the left mandible nearly equal to the second (Fig. 44); third denticle of the right incisor nearly equal to the first (Fig. 41). Labium white, shown in Fig. 46. **Thorax:** Pronotum and mesonotum light brown or brown with pale median strip (Fig. 41). Pronotum with dark brown anterior margin and pale lateral sides. Mesonotum contrasting, with light and dark streaks and spots (Fig. 41). Legs brownish; foreleg slightly darker than middle and hind legs. Femur of foreleg with long pale stripe near outer margin (Fig. 47); femur of the middle and hind legs with a broad pale spot in distal part. Foreleg (mm): femur 1.2–1.5; tibia 0.6–0.9; and tarsus 0.8–1.0. Middle leg: femur 1.2–1.4; tibia 0.7–0.9; and tarsus 0.7–1.0. Hind leg: femur 1.2–1.5; tibia 0.6–0.9; and tarsus 0.7–1.0. **Abdomen:** Terga I–VII brown with dark posterior margins and white lateral sides (Figs 41, 48); terga I–VII with a pair of pale elongated spots connected at midline and with oval pale spot medially; terga VIII–IX with white posterior area and wide white middle stripe; all terga with almost regular row of spines (Fig. 50). Sterna brownish with white lateral margins (Fig. 49); sterna I–II lighter than others; sterna II–VI with a pair of small dark spots on the anterolateral corners; sterna VII–IX with a pair of small white spots on the antero-lateral corners; sterna VI–VIII without ganglionic marking; abdominal sternum IX (female) with a shallow incision (Fig. 51). Gills white; gills I and II small without an anal rib (Figs 52, 53); gill I only slightly smaller than gill II: width 0.44 of length; gill II: width 0.43 of length; gills III–VII with an anal rib on the margins (Figs 54, 55); gills III–VI with rounded distal margins (Fig. 54) and width 0.50–0.54 of length; gill VII narrower with a pointed tip and slightly smaller than gill VI: width 0.39 of length (Fig. 55). Basal quarter of cerci yellowish, more distally brown, than yellowish, tips brown (Fig. 41); joints of each segment darker.



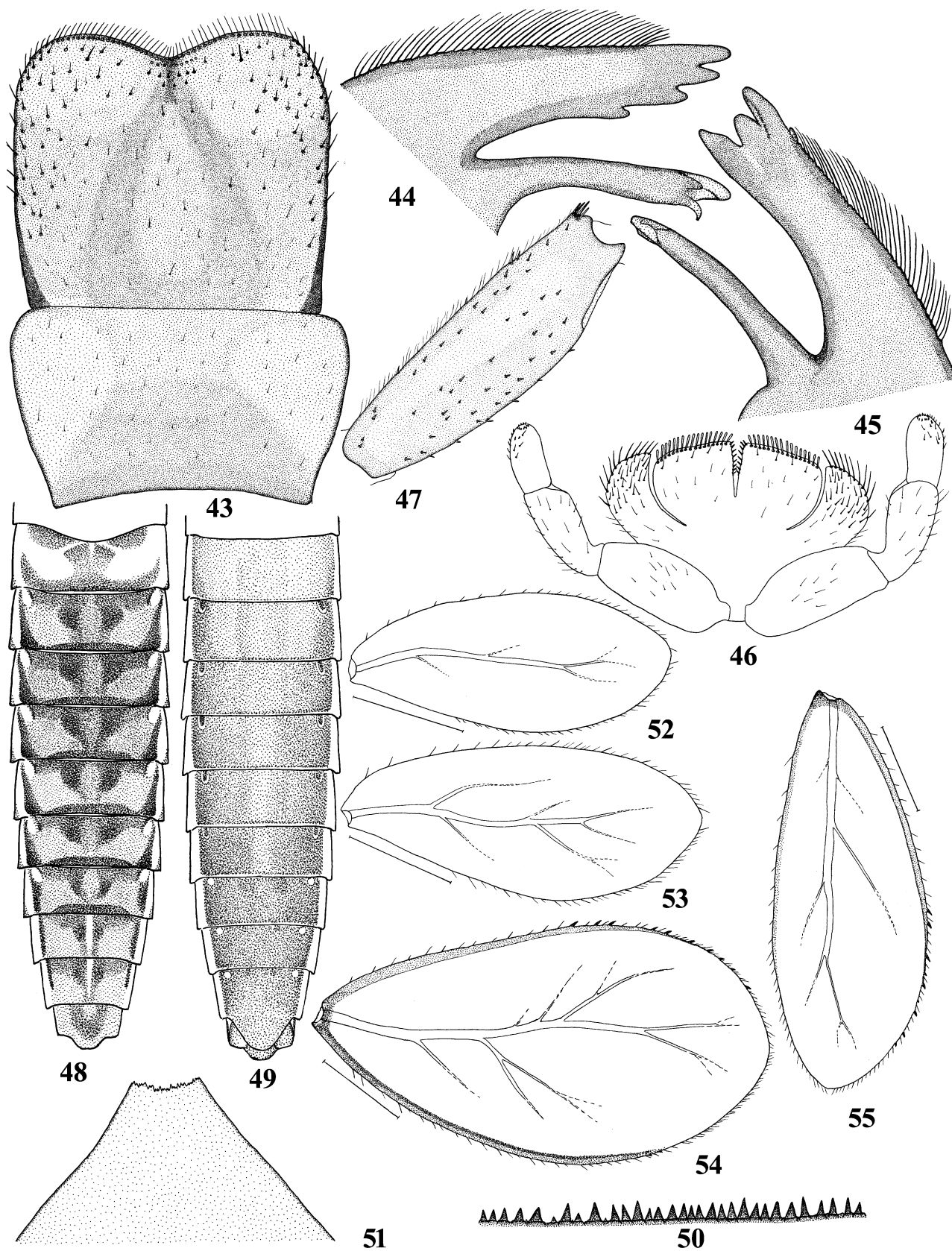
**Eggs.** General shape ellipsoidal with a length of 176–202  $\mu\text{m}$  and a width of 105–128  $\mu\text{m}$  (Fig. 56). Chorionic surface covered with large-mesh regular pentagonal cells; each cell with a wavy bottom; borders of cells solid, relatively high; every four cells united by one small round knob, that evenly covers the whole egg; large and round knobs arranged on both poles (Fig. 56). Micropyles located in the equatorial area; sperm guide round, well apparent; micropylar rim absent (Fig. 58).

**Etymology.** The species is named in memory of the Far Eastern hydroecologist Sergey Egorovich Sirotsky, who for a long time was investigator of the Far Eastern Rivers.

**Distribution and biology.** Russian Far East: Khabarovskiy Kray, Amurskaya and Magadanskaya Oblast'. Adult emergence period from the middle July to the 10 August.

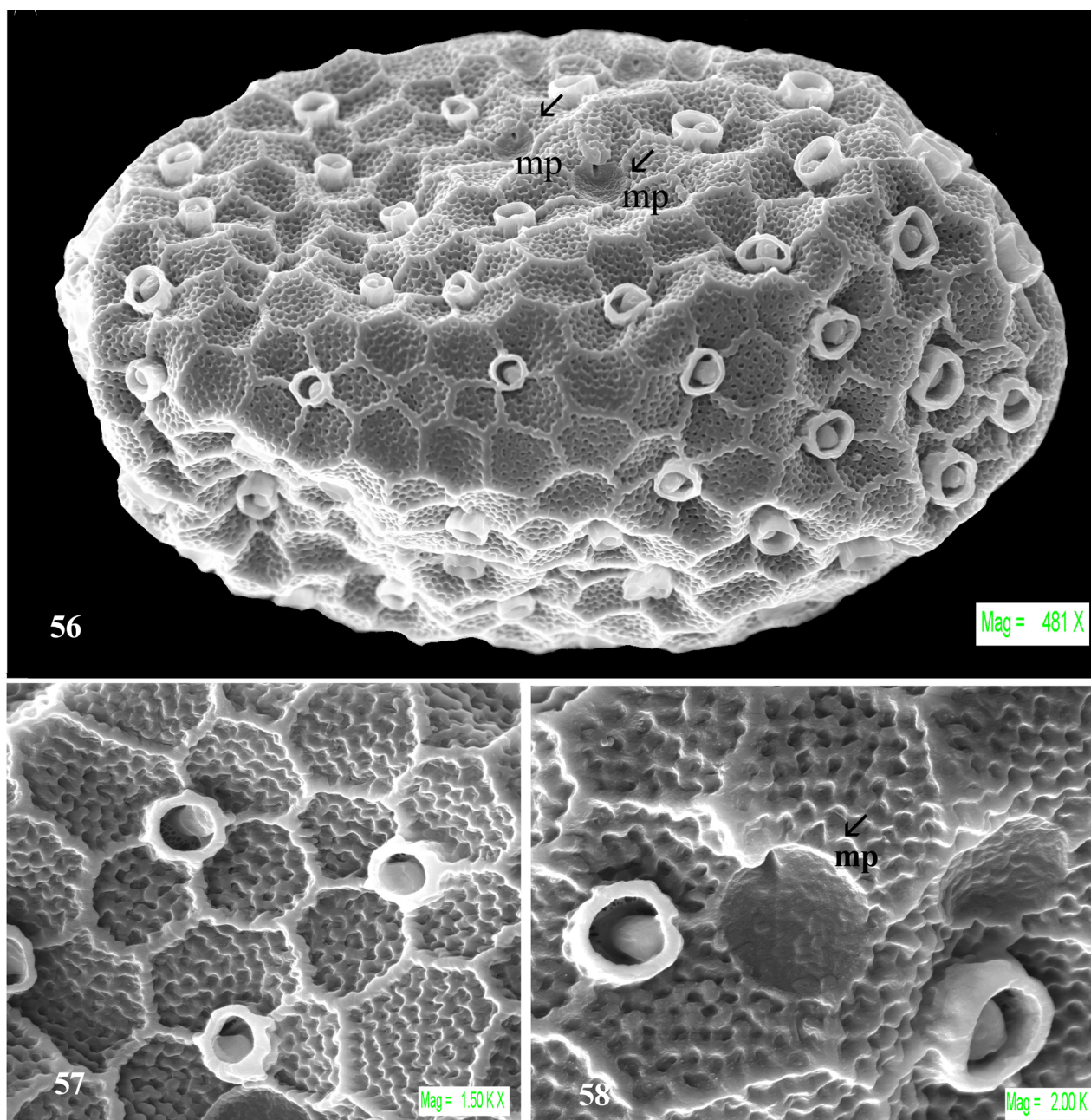


FIGURES 41–42.



FIGURES 43–50.





FIGURES 56–58.

***Ameletus camtschaticus* Ulmer, 1927**

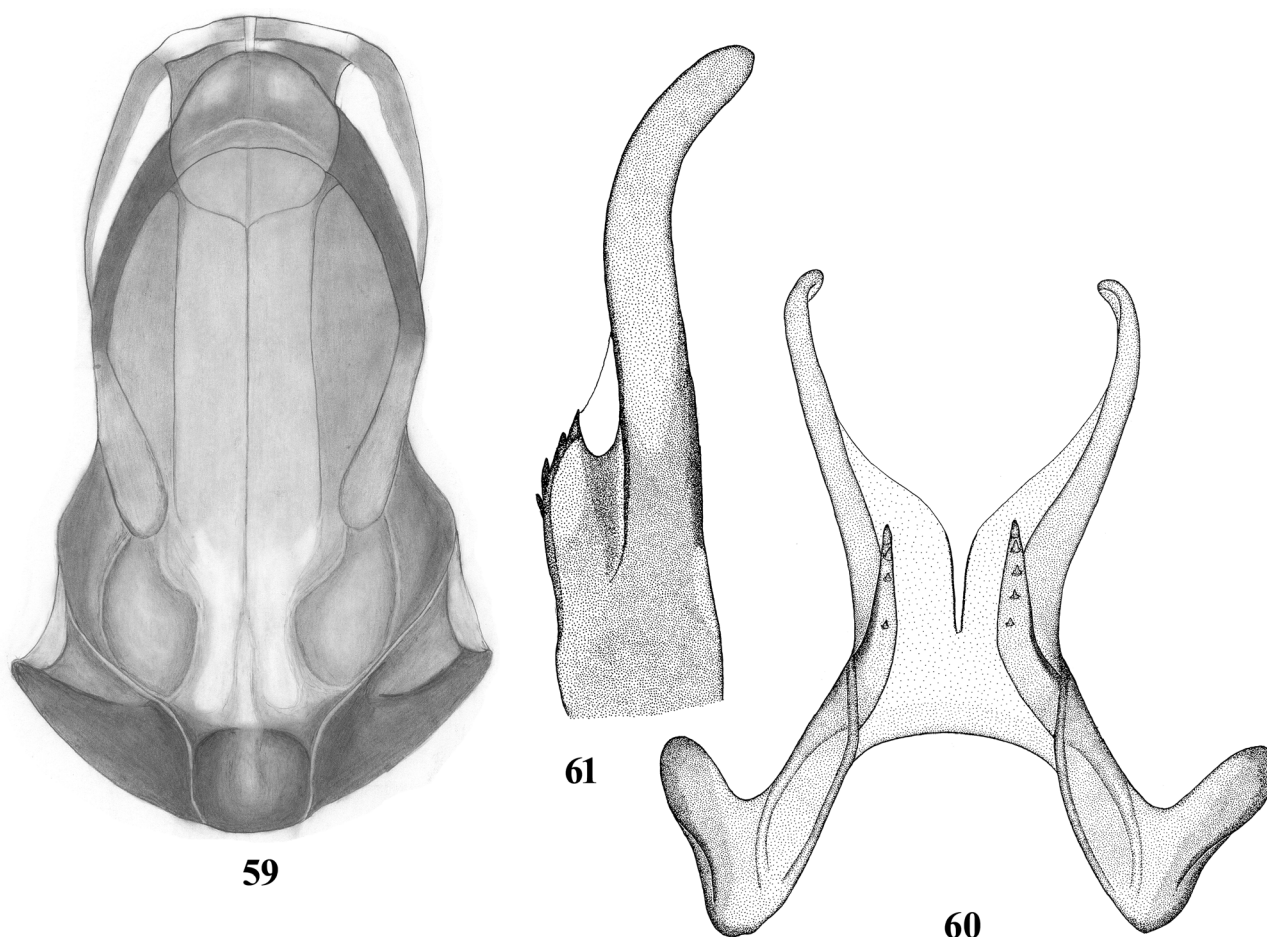
(Figs 59–78)

*Ameletus camtschaticus* Ulmer, 1927: 12, figs 10–12 [description; male imago]; Sinitshenkova & Tshernova, 1976: 13, figs 3–9 [complementary description; male subimago, larva]; Kluge, 2004: fig. 11A–D [figures of male imago genitalia]; Kluge, 2007: 251 [short description of larva, male genitalia and egg];

*Ameletus pilatus* Sinitshenkova, 1981:73, fig. 1 [description; larva]; Tshernova *et al.*, 1986: 126, figs 57: 7–8 [key; male imago]; Kluge, 1995: 10 [types observation; junior synonym].

**Material. RUSSIA:** KHABAROVSKIY KRAY, Okhotskii district: Bulginka River, near Bulgino village, 05.VIII.1998, 2 mature larvae, T. Tiunova; spring without name near Mount Three Brothers, ~ 3 km from the Okhotsk, 21.VIII.1998, 1 male imago (reared from larva), 3 mature larvae, T. Tiunova; Ul'ya River, 3 km upper

mouth, 08.VIII.1989, 1 male imago, V. Zherikhin; Ayano-Maiskiy district: Badzhalskiy Reserve, Lantar' River Basin, Uluykan River, about 100 m above the mouth, 29.VII.1999, 2 larvae, T. Tiunova; Sarafanovka River, 8 km from Ayan village, 02.VIII.1999, 2 male imagines (reared from larva), T. Tiunova; Maya River, 2 km lower Nel'kan village, 5–8.VIII.1999, 1 male imago (reared from larva), 2 larvae, T. Tiunova; Elgandzhya River, upper reaches, 13.VII.2003, 7 young larvae, T. Tiunova; AMURSKAYA OBLAST': Tynda River Basin, Allenga River, bridge, at highway Zeya–Snezhnogorsk, 5–7.VII.2013, 2 larvae, T. Tiunova; same locality, 06.VII.2014, 1 larva, 1 larva (AM109), T. Tiunova; Allenga River, upper mouth, 29.VI.2015, 1 larva, 1 larva (AM326), T. Tiunova; Tynda River, 500 m upper mouth of Allenga River, 30.VI.2015, 1 larva (AM330), T. Tiunova; Zeyskii reserve, Bolshaya Erakingra River, 52-i km from Zeya, bridge, at highway Zeya–Beregovoy, 06.VII.2013, 2 larvae, T. Tiunova; MAGADANSKAYA OBLAST', Ola River Basin: Donishko River, upper reaches of Ola River, 16.VI.2014, 1 larva (AM137), E. Khamenkova; Ola River, upper reaches, 130–137 km, 29.IV.2014, 2 young larvae, 1 larva (AM152), E. Khamenkova; same locality, 30.V.2014, 2 young larvae, 1 larva (AM389), 1 larva (AM141), E. Khamenkova; same locality, 16.VI.2014, 3 young larvae, 1 larva (AM145), E. Khamenkova; KAMCHATSKI KRAI: Kamchatka Peninsula: Chimstina River, 07.IX .2014, 1 young larva (AM207), I. Tiunov; Avacha River Basin, Ozernaya River, 28.VII.2014, 1 mature larva (AM310), I. Tiunov; SAKHA YAKUTIYA, Timpiton River Basin, Duray River, bridge, at highway Neryungri–Yakutsk, 02.VIII.2006, 1 larva, T. Tiunova.



FIGURES 59–61.

**Description. Male imago** (in alcohol). Length (mm): body 10.5–11.4; forewings 8.6–10.6; cerci 12.3. **Head:** Upper portion of the eyes brownish; lower portion blackish. **Thorax:** Medioscutum and submedioscutum light brown; median longitudinal suture narrow and brown. Anteronotal protuberance and sublateroscutum brown. Scutellum brown; scuto-scutellar impression pale. Posterior scutle protuberance brown. Parascutellum dark (Fig. 59). Forelegs brown tinged dark; femur of middle and hind legs from yellowish to brownish, joints and tarsal segments slightly darker. Length (mm) of foreleg segments: femora 1.7–1.9; tibia 1.6–1.8; tarsal segments 0.4–0.5,

1.1–1.3, 1.0–1.2, 0.8–1.0, and 0.5. Wings hyaline: all veins brown. **Abdomen:** Terga I–II and VII dirty brown; terga III–VI brownish or dirty brownish, lateral margins darker. Sterna brownish. Styli white and well contrasted medially with dark brown lateral margins. First segment of the forceps dark brown, sometimes lighter in the distal part; second and third segments light brown or brownish. Penis lobes brown proximally and light brown distally (Figs 60, 61); penis lobes rounded laterally and bent medially (Fig. 60); each ventral plate bears a large pointed apically denticle and several smaller subapical denticles (Figs 61–63); the first small denticle is located at the base of main denticle (Figs 61, 63). Cerci brown with dark brown joints and pale tips.



FIGURES 62–63.

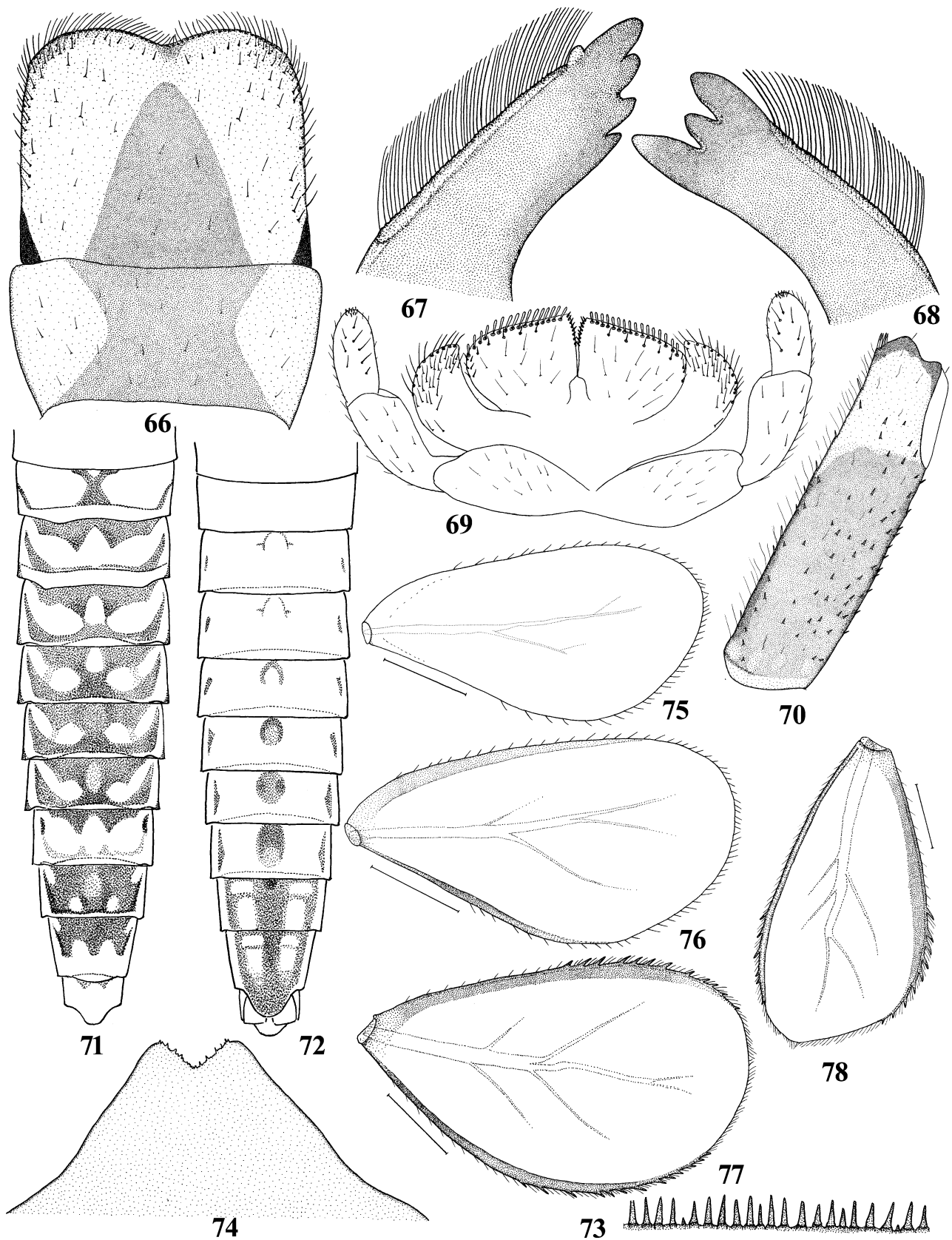
**Mature larva.** Length (mm): body 7.8–11.3; cerci 3.3–5.5. **Head:** Brown with a pale triangular spot from the median ocellus to the anterior margin of the clypeus and a pale median stripe between the eyes (Fig. 64). Antennae brownish with pale tips. Labrum (length 0.8–0.83 that of the width) pale with a wide brown triangular spot not reaching the anterior margin (Figs 64, 66); this spot well expressed in young larvae, but may have a rectangular shape in mature larvae. Clypeus brown laterally (Fig. 66). First denticle incisor of the left mandible largest, the fourth smallest, the second equal to the third (Fig. 67); incisor of the right mandible with a wide third denticle longer than the first (Fig. 68). Labium whitish, shown in Fig. 69. **Thorax:** Pronotum and mesonotum brown with contrasting white stripes and spots (Fig. 65). Femur of the forelegs white with a large brown spot located near the anterior margin and extending to the ventral cleft; posterior margin brown (Fig. 70); femur of middle and hind legs with a brown spot medially; tibia of all legs brown in the anterior half and pale posteriorly; tarsus light brown in the middle and dark brown at edges; claws dark brown. Foreleg (mm): femur 1.2–1.8; tibia 0.7–1.0; and tarsus 0.9–1.2.



Middle leg: femur 1.2–1.8; tibia 0.7–1.0; and tarsus 0.8–1.1. Hind leg: femur 1.2–1.8; tibia 0.7–1.0; and tarsus 0.8–1.1. **Abdomen:** Colouration of the larval abdomen variable. Larvae brown with contrasting pale maculation; all terga laterally white (Fig. 71); terga II–VIII with a pair of diffuse dark oblique submedian stripes; tergum I often entirely light with an X-shaped dark spot in the middle or brown with a pair of small white spots; tergum II with wide, white transverse spot; terga III–VI with a pair of bent white spots; tergum VII almost completely pale with a brown, V-shaped stripe only at the anterior margin; tergum VIII brown with a pair of white round spots near the posterior margin; posterior half of tergum IX white; tergum X white (Fig. 71). In some larvae, the white spot on the terga diffuse with a clearly visible pair of dark oblique submedian stripes. Terga with an almost regular row of spines (Fig. 73). Sterna pale; sternum I–IX with pale lateral margins and a pair of white small spots near the anterolateral corners (Fig. 72); sternum I pale; sterna II–V with a large blackish spot in the centre near the anterior



FIGURES 64–65.



FIGURES 66–78.





**FIGURES 79–80.**





**FIGURES 81–82.**



margins; sterna VI–VII with a pair of brown stripes near the lateral sides; sterna II–IV with a diffuse brown semicircular submedian stripe; sterna V–VII with a dark round spot near the anterior margin similar to the ganglionic markings; sterna VIII–IX brown with pale spots, and sterna VII–IX sometimes almost completely dark brown; abdominal sternum IX (female) with a deep incision (Fig. 74). Gills white; gill I small without an anal rib (Fig. 75) and just slightly smaller than gill II: width 0.50 of length; gills II–VII with an anal rib on the margins (Figs 76–78); gill II: width 0.53 of length; gills III–VI with a rounded distal margin; width 0.54–0.60 of length; gill VII slightly less than gill VI: width 0.53 of length (Fig. 78). Cerci brownish with a dark band in the middle (Fig. 65).

**Distribution and biology.** Russian Far East: Khabarovskiy Kray, Amurskaya and Magadanskaya Oblast', Kamchatskiy Kray, Sakha Yakutiya. According to our data, adult emergence period from middle July to middle August.

Mature larvae and adults *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* were collected from small foothill Rivers (Figs 79–82). Water temperature in the collection periods of larvae and reared imagoes did not exceed 10°C.

**Remarks.** *Ameletus camtschaticus* was described from a single male imago collected in Petropavlovsk (Kamchatka Peninsula) in 1927 (Ulmer 1927). Sinitshenkova & Tshernova (1976) described the subimago male *A. camtschaticus* based on the similarity in the structure of the genitalia and the larvae by the similarity with adults in their size and distribution (all material was collected on the Kamchatka Peninsula). It should be noted that many of the details in the description of the larvae given in the above paper and in our description are completely consistent. The most important of which for larvae are that gill II has an anal rib, the lower edge of labrum light with a more intensely coloured medial spot with a triangle shape and a truncated apex, abdominal sternum IX with a deep incision, and the abdominal terga with contrasting pale maculation. However, the description of larvae by Kluge (2007) differs from both our description and that of Sinitshenkova & Tshernova (1976). Kluge (2007) indicated that gill II does not have an anal rib and abdominal terga are usually without contrasting pale maculation. In the present contribution, we used those specimens for which a molecular analysis was performed to describe the larvae of *A. camtschaticus*. All larvae in this group had an anal rib on gill II. Male *A. camtschaticus* imagoes were only considered in cases where they had been reared from larvae with an anal rib on gill II.

## Discussion

Based on the structure of the male imago genitalia, *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* are similar, but the male imago of *A. allengaensis* **sp. nov.** can be differentiated from *A. sirotskii* **sp. nov.** and *A. camtschaticus* by the structure of the ventral plates of the penis. The ventral plate of *A. allengaensis* **sp. nov.** bear large and long main pointed denticle and several very small denticles along the plate; the first small denticle is located far from the main denticle (Figs 6, 12). In *A. sirotskii* **sp. nov.** and *A. camtschaticus*, the small denticles on the ventral plate are larger than those of *A. allengaensis* **sp. nov.**, and the first small denticle is located near base of the large main denticle (Figs 40, 63). The male imago of *A. sirotskii* **sp. nov.** can be distinguished from *A. camtschaticus* by the location of the small denticles on the ventral plate and the size of the main denticle. In *A. sirotskii*, small denticles are arranged relatively distant from each other (Figs 36, 40), whereas, the small denticles are arranged one behind another in *A. camtschaticus* (Figs 61, 63). At the same time, the main denticle and the small denticles in *A. sirotskii* **sp. nov.** are shorter than those in *A. camtschaticus*. Male genitalia of *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* are most similar to the Nearctic species *A. tarteri* Burrows and *A. pritchardi* Zloty, but differ by the structure of the ventral plates of the penis. The ventral plate of *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* bear large and long main pointed denticle and several very small denticles along of plate, in contrast to *A. tarteri* and *A. pritchardi*, for which small denticles are located on lateral margin of main long denticle (Zloty, 1996; Zloty & Pritchard, 1997). In *A. allengaensis* **sp. nov.**, the ganglionic markings are clearly visible on sterna II–VIII (Fig. 10); in *A. camtschaticus* and *A. sirotskii* **sp. nov.** on sterna VII–VIII, (Fig. 38), *A. pritchardi* on sterna VII–VIII, and *A. tarteri* only on sternum VIII.

Based on the structure of the gills, *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, *A. camtschaticus*, *A. inopinatus inopinatus* and *A. inopinatus labiatus* can be assigned to a group of species in which gills III–VII bear an anal rib on the anal margin. The larvae of *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* differ from the larvae of *A. inopinatus inopinatus* by the presence of a dark band at the middle part of cerci (Figs

15, 41, 65), which is absent in the latter species. The larvae of *A. allengaensis* **sp. nov.**, *A. sirotskii* **sp. nov.**, and *A. camtschaticus* differ from the larvae of *A. inopinatus labiatus* in the structure of gill II, which is elongated in the latter, longer than gills III–VII (Kluge 2007). The larvae of *A. allengaensis* **sp. nov.** differ from those of *A. camtschaticus* in the structure of gill II. In *A. allengaensis* **sp. nov.**, gill II lacks an anal rib on the anal margin (Fig. 26), contrary to *A. camtschaticus* (Fig. 76). *Ameletus allengaensis* **sp. nov.** is similar to *A. sirotskii* **sp. nov.** sharing the absence of the anal rib on gill II, but these species differ based on the size of gills I and II and by the width/length ratio of gill VII. In *A. allengaensis* **sp. nov.**, gill I is almost half the size of gill II (Figs 25, 26) and the width/length ratio of gill VII is 0.49. In *A. sirotskii* **sp. nov.**, gill I is only slightly smaller than gill II (Figs 52, 53) and the width/length ratio of gill VII is 0.39. *Ameletus sirotskii* **sp. nov.** is well differentiated from *A. allengaensis* **sp. nov.** and *A. camtschaticus* by the colour of the labrum. In *A. sirotskii* **sp. nov.**, the middle area of the labrum has an oval, pale spot bordered by a brown stripe (Figs 42, 43), whereas in *A. allengaensis* **sp. nov.** the labrum has a wide, brown, nearly rectangular spot (Figs 14, 16) and in *A. camtschaticus* the labrum has a wide, brown, triangular spot (Figs 64, 66).

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