Zootaxa 5642 (3): 301–324
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5642.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:23B9520C-B13F-4C6F-82DD-F65A186B3449

Eggs of twelve Siberian and Far Eastern Isoperlinae (Plecoptera: Perlodidae)

VALENTINA A. TESLENKO
Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences (FSC EATB FEB RAS), 690022, Vladivostok, Russia
teslenko@biosoil.ru; https://orcid.org/0000-0002-0649-8028

Abstract

Eggs of 12 Isoperlinae species from Siberia and the Russian Far East are examined, illustrated, and described using scanning electron microscopy images for the first time. Keys for their identification are proposed and included. East-Palaearctic *Isoperla eximia* Zapekina-Dulkeit, 1975 is recorded for Japan for the first time.

Key words: stoneflies, *Isoperla*, *Kaszabia*, egg, new record, key, Siberia, Far East, Russia

Introduction

Two genera of Isoperlinae Frison, the Holarctic *Isoperla* Banks, 1906, and East Palaearctic *Kaszabia* Raušer, 1968, are known from Siberia and the Russian Far East. Currently, *Kaszabia* includes two Asian species, the mainland *K. nigricauda* (Navás, 1923) and the island *K. digitata* (Kawai, 1963), which is no longer found in Japan after its description (DeWalt *et al.* 2025). Males of both *Kaszabia* species differ from *Isoperla* in having paired lateral processes on the 3rd and 4th abdominal segments (Raušer 1968, Zwick 1973). At the same time, paired lateral processes on the abdominal tergum of males are found in four species of *Isoperla* (Nelson 1976, Maruyama & Hanada 2016, Huo & Du 2020, Chen *et al.* 2021). Further genetic research and study of the morphological features of the genital structure of males, females, eggs, and larvae will help to support or refute the validity of *Kaszabia*.

Isoperla is represented by 12 species. Only *I. obscura* (Zetterstedt, 1840) has a very wide range in the West and East Palaearctic, whereas seven species (*I. altaica* Šámal, 1939, *I. asiatica* Raušer, 1968, *I. chereshnevi*, Teslenko, 2017, *I. eximia* Zapekina-Dulkeit, 1975, *I. kozlovi* Zhiltzova, 1972, *I. lunigera* (Klapálek, 1923), *I. mongolica* Zhiltzova, 1972) are widespread in the East Palaearctic, and four (*I. flavescens* Zhiltzova & Potikha, 1986, *I. maculata* Zhiltzova, 1977, *I. ornata* Zhiltzova, 1988, *I. pseudornata* Zhiltzova, 1988) species have narrow East Asian ranges limited to the south of the Russian Far East, Korea, and/or northeastern China. Adults of the East Palaearctic species have been relatively well studied to distinguish them mainly by morphological features of the genital structures of males and females and the morphology of larvae (Zwick & Surenkhorloo 2005, Zhiltzova 1972, 1977, 1988, Potikha & Zhiltzova 1986, Teslenko 2008). At the same time, the eggs of Isoperlinae remain poorly studied, although the egg structure is one of the basic characteristics by which the species within the genus *Isoperla* are distinguished (Szczytko & Kondratieff 2015). Limited information about eggs of nine East Palaearctic species was presented by Zwick & Surenkhorloo (2005) in the revision of Mongolian Isoperlinae. The description and illustrations were based on a study of the eggs in transmitted light, so their chorion structure was difficult to determine. This paper presents the results of the investigation of egg morphology of 12 Isoperlinae species inhabiting Siberia and the Russian Far East using scanning electron microscopy (SEM).

Materials and Methods

Specimens used in the study are archived in the collection of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences (FSC EATB FEB RAS), Vladivostok, Russia. Eggs

Accepted by S. Grubbs: 14 Apr. 2025; published: 29 May 2025

were dissected from female specimens fixed in 75% ethanol and cleaned in an ultrasonic cleaner for 5–30 seconds to remove extra-chorionic membranes. Cleaned eggs were placed in 95% ethanol, air-dried, and mounted on stubs covered with double-sided tape. Stubs were carbon-coated and examined with a Zeiss Merlin SEM. Morphological terminology follows Szczytko & Kondratieff (2015).

Results

Isoperla altaica Šámal, 1939

Figs. 1–9

Material examined. Russia, Siberia: Krasnoyarsk Krai, Khakassia: 3♀, 22 km NW of Shira Lake, Bely Iyus River, 2.07.2014, coll. A. Leley; 1♂, Rastorguikha River, Selenga R. Basin, Burkalsky protected area, 23.08.2018, coll. Matafonoff; 1♂ 1♀, Altai, Tuekta River, 05.09.2021, coll. L. Yanygina.

Egg. Shape oval, symmetrical, with anterior and posterior poles broadly rounded and a concave cross-section (Figs. 5–6). Length 322–332, width at the equator of 234–239 μm (n=2). Collar well developed, with raised longitudinal wavy carinae and small transverse projections (Figs. 1, 3); base with a thickened, wavy ridge wider than the apically flanged rim, so the collar appears multi-leveled from above (Figs. 1, 3, 5). Anchor mushroom-shaped, with small globular bodies concentrated into groups of five and located in a peripheral area along the anchor edge; top of the anchor deeply embedded (Figs. 2, 4). Follicle cell impressions (FCIs) near the collar range from elongated to hexagonal (Figs. 1–2, 5). Chorion covered with hexagonal FSCs with slightly thickened elevated ridges (Figs. 1–2, 5–8); floors shallow with numerous (20) shallow pits (Figs. 1–2, 5–8). Micropyles arranged singularly in a row on follicle cell ridges near the anterior ¼ of the egg (Figs. 1–2, 6). Orifices oval and located on raised, tunnel-shaped, and relatively long sperm guides, some associated with FCI rosettes (Figs. 7–8). Eclosion line absent. The chorionic structure on an external membrane comprises hexagonal FCIs bearing scattered adhesive mushroom bodies along the perimeter of each cell (Fig. 9).

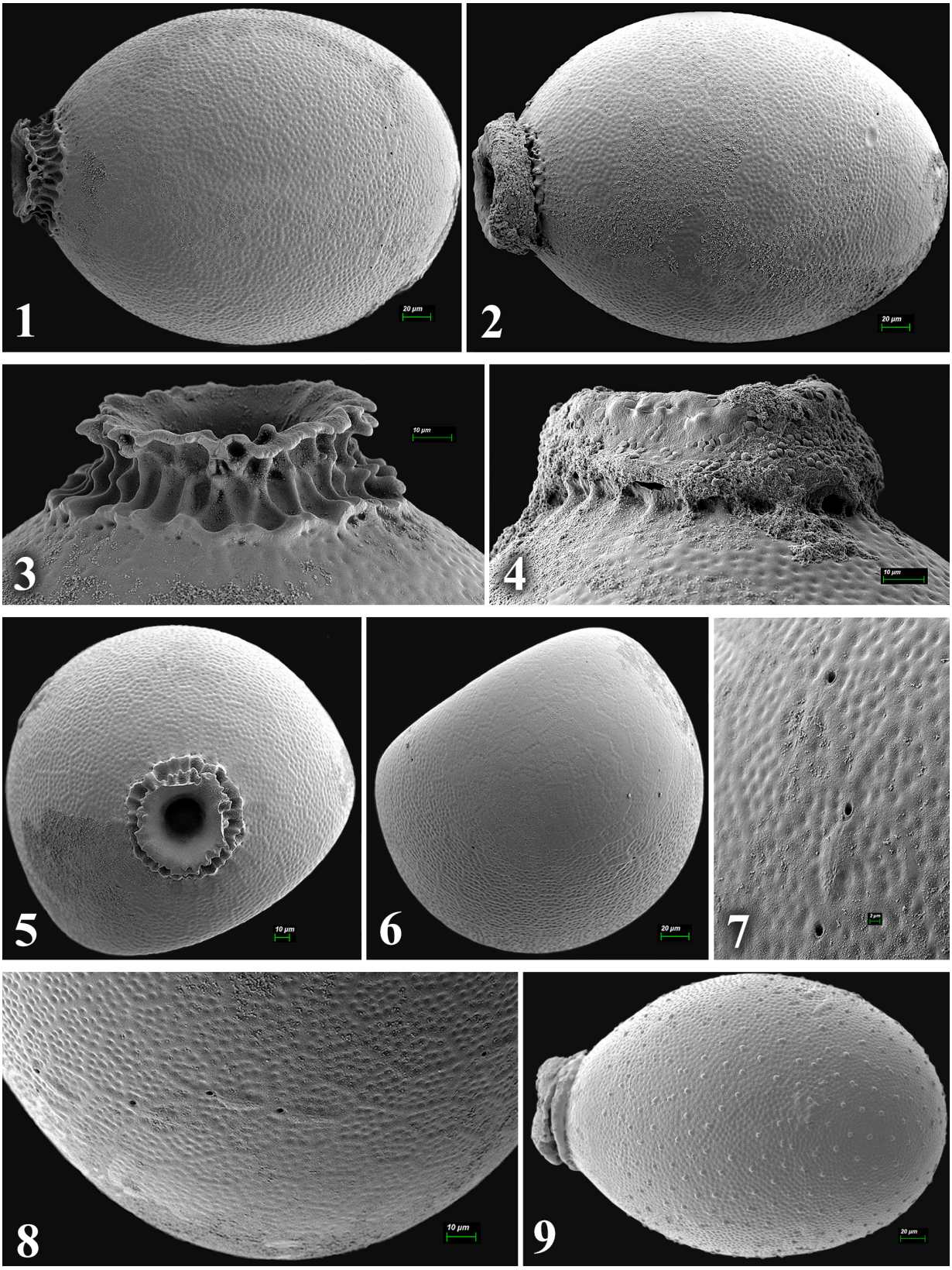
Distribution: East Palaearctic species with limited distribution in Russia, Siberia: Altai, Sayan, Transbaikalia. East Kazakhstan. Mongolia.

Remarks. *Isoperla altaica* eggs from Siberia are smaller in size than those from Mongolia (360×250 μm) and larger than those from East Kazakhstan (295×235 μm) (Zwick & Surenkhorloo 2005). Apparently, the Siberian eggs imaged here are quite mature since their chorion is completely covered by FCIs. According to the available data obtained in transmitted light, the structure of the eggs from Kazakhstan is finely punctured, whereas the chorion of Mongolian eggs is unstructured (Zwick & Surenkhorloo 2005).

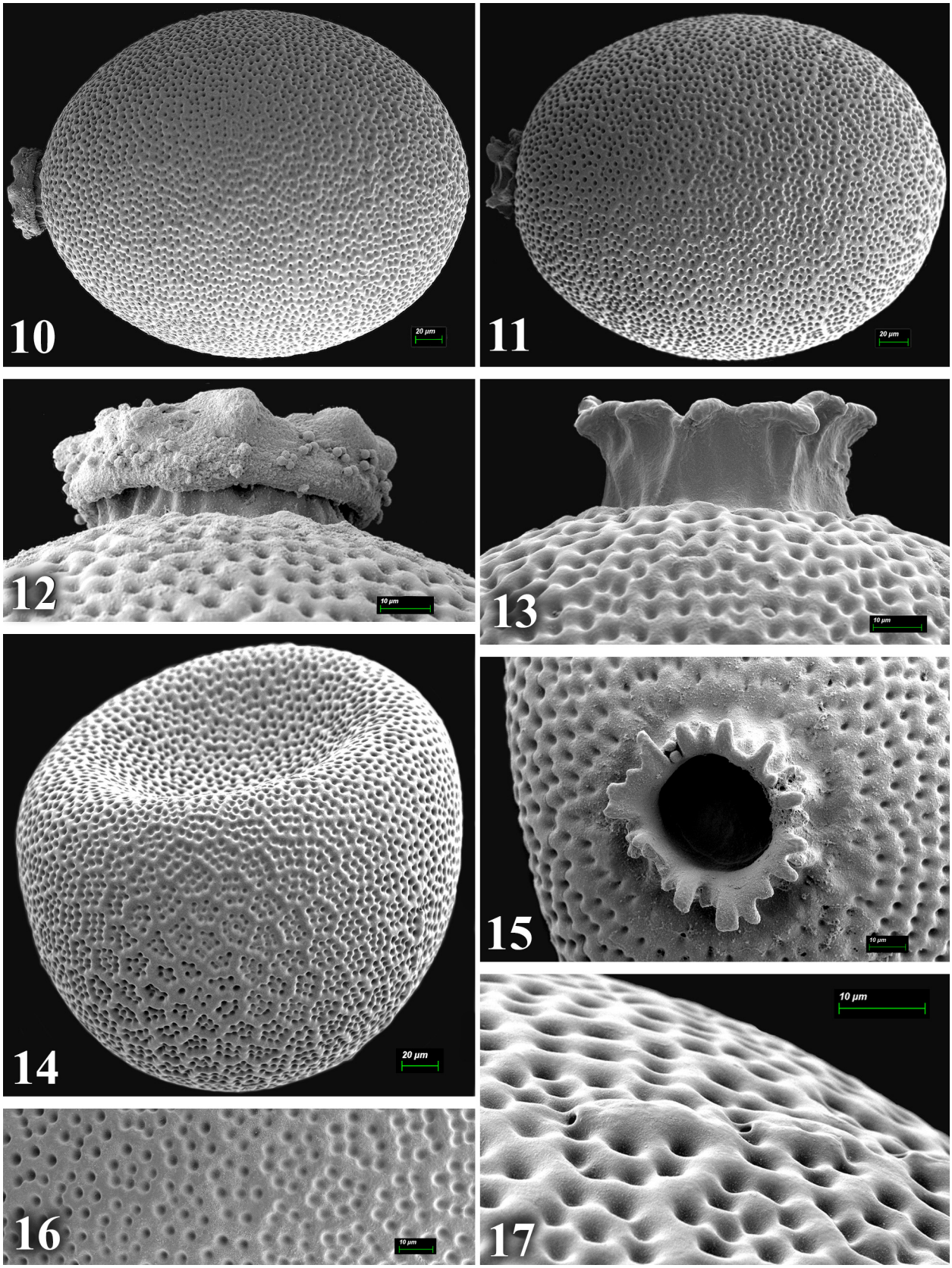
Isoperla asiatica Raušer, 1968

Figs. 10–17

Material examined. Russia, Far East, Khabarovsk Krai: 1♂, Anyuisky National Park, Gassi Lake, Anyui River basin, Amur R. basin, 4.06.2019, N. Yavorskaya; 1♀, same locality, Anyui R., Adzhu Channel, 4.06.2019, coll. N. Yavorskaya; 2♀, same locality, Solomi R., Anyui R. basin, 3.06.2019, coll. N. Yavorskaya; **Amurskaya Oblast**: 6♂ 3♀, Bol'shiye Simichi River, Bureya R. basin, Amur R. basin, 9.06.2013, coll. V. Teslenko; 1♀, Zeya River, Ovsyanka settlement, Amur R. basin, 7.07.2015, coll. T. Tiunova; 1♂ 1♀, Dikan River, near the auto bridge, 27.07.2015, coll. V. Teslenko; **Primorsky Krai:** 1♀, Lazovsky Nature Reserve, Proselochnaya River, Proselochnaya cordon, Partizanskaya R. basin, 22.05.2007, coll. O. Zorina; 2♀, same locality, Staro-Kamensky stream, near Staraya Kamenka settlement, 28.05.2004, coll. Eu. Makarchenko; 1♂ 1♀, Bolshaya Ussurka River, Ussuri R. basin, Amur R. basin, settlement Zvenigorodka, 06.08.2004, coll. V. Teslenko; 1♂ 2 ♀, Ussuri River, Kamenka village, 07.05.1993, coll. V. Teslenko; 8♂ 8 ♀, Barabashevka River, near fish factory, 30.04.2003, coll. V. Teslenko.



FIGURES 1–9. *Isoperla altaica* Šámal, 1939. Russia, Siberia, Krasnoyarsk Krai, Khakassia, Bely Iyus River, Shira Lake basin. Egg. **1.** Habitus, cleaned, without anchor, lateral. **2.** Habitus with deeply embedded, mushroom-shaped anchor lateral. **3.** Collar, longitudinal wavy ridges with small transverse projections, base with wavy ridge, lateral. **4.** Anchor with small globular bodies in a peripheral area. **5.** Posterior pole, a "multi-level" collar, a view from above. **6.** Anterior pole, micropylar row, a view from above. **7.** Oval orifices on raised, tunnel-shaped, and long sperm guides**. 8.** Chorion structure, orifices associated with FCI rosettes. **9.** Uncleaned egg, an external membrane with scattered adhesive mushroom bodies.



FIGURES 10–17. *Isoperla asiatica* Raušer, 1968. Russia, Far East, Primorsky Krai, Barabashevka River. **10.** Habitus, cleaned, with anchor, lateral. **11.** Habitus, cleaned, without anchor, lateral. **12.** Anchor, mushroom-shaped with globular bodies near the edge, lateral. **13.** Collar with irregular longitudinal ridges, lateral. **14.** Anterior pole, a view from above. **15.** Posterior pole, collar with deeply serrated rim, a view from above. **16.** Chorion structure. **17.** Micropylar row, canal tunnel-shaped, and long, floating over the orifice and slightly covering it.

Egg. Shape oval, symmetrical, with anterior and posterior poles broadly rounded and a concave cross-section (Figs. 10–11, 14); chorion thickness 2.9–5.3 μm. Length 314–346 μm, width at the equator 237–261 μm (n=6). Collar well developed, with irregular longitudinal ridges; rim deeply serrated and curved outward; collar surrounded by slightly pronounced shoulder without ring (Figs. 11, 13, 15). Anchor mushroom-shaped, with small grouped globular bodies placed along a peripheral area of the anchor edge (Figs. 10, 12). Chorion surface is rough, covered with hexagonal follicle cell impressions with thick, slightly elevated ridges (Figs. 10–11, 14, 16–17); floors with numerous (9–11) deep groove-like pits (Figs. 16–17). Eclosion line absent. Micropyles located along ridges, FCI in the anterior ¼, and faintly noticeable (Figs. 10, 14). Micropylar canals straight or slightly sloping, tunnel-shaped, and relatively long; canals raised slightly above the surface (Fig. 17). Orifices the same size as FCI pits.

Distribution. East Palaearctic species. Russia, Siberia: Altai, East Sayan, Baikal Lake basin, Transbaikalia; Far East: Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Krai, Primorsky Krai, Sakhalin Island. East Kazakhstan. Mongolia. China, Inner Mongolia Autonomous Region (Huo *et al.* 2020).

Remarks. The shape, size, and chorion structure of the egg as a whole correspond to the first description by Zwick & Surenkhorloo (2005). Egg bears a specific collar with a serrated rim; the chorion structure appears as FCI's with thick elevated ridges, their floors covered with numerous (9–11) deep groove-like pits.

Isoperla eximia Zapekina-Dulkeit, 1975

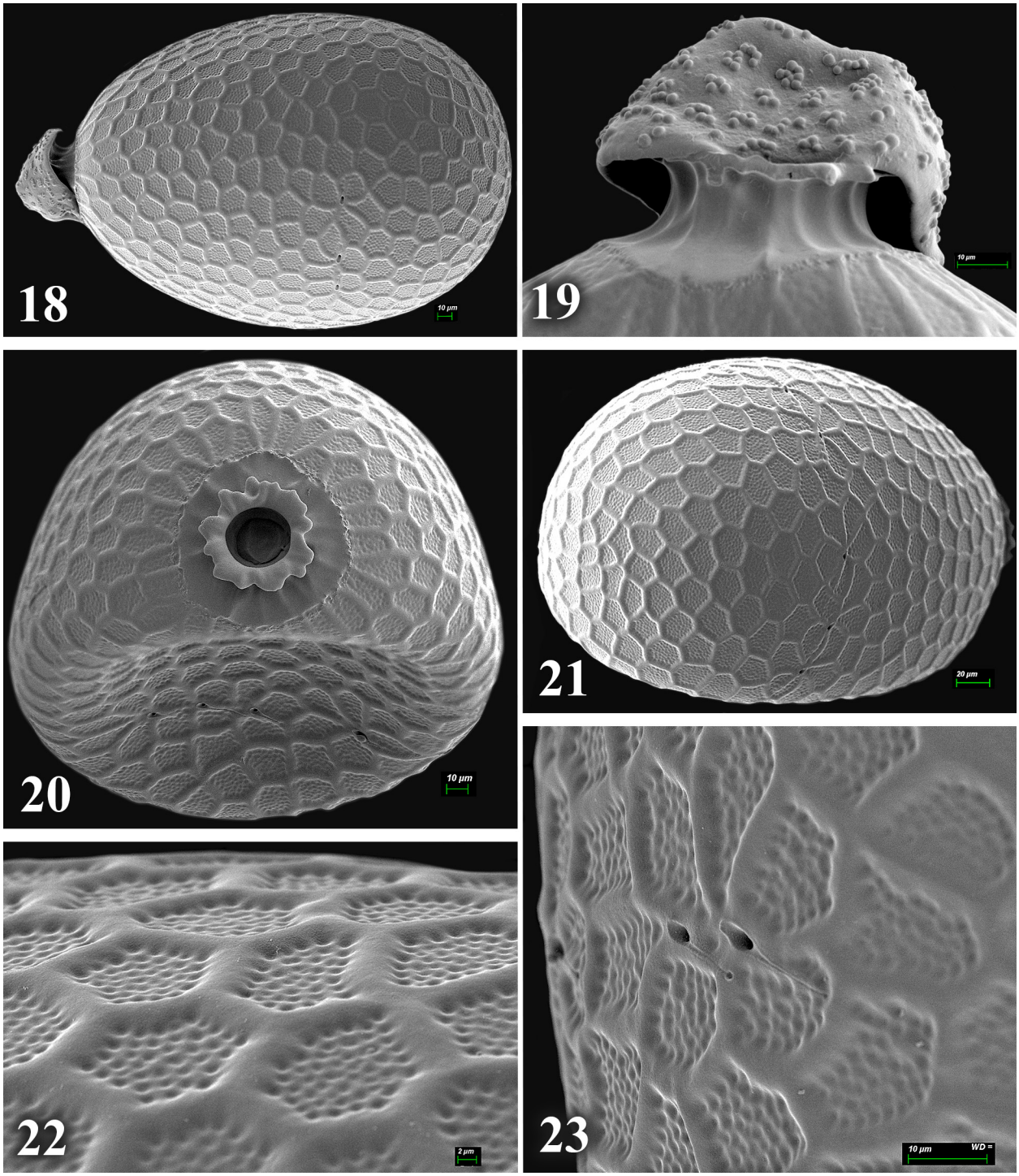
Figs. 18–27

Material examined. Russia, Far East, Khabarovsk Krai: 1♂, Bol'shaya Uda River, 18.08.2021, N. Yavorskaya; 1 L, Bol'shaya Del'ya River, 11.07.2022, coll. I. Tiunov; 1♂, Bol'shaya Del'ya River, 12.08.2022, coll. I. Tiunov; 1♂, Malaya Del'ya River, downstream, 5.08.2022, coll. I. Tiunov; **Jewish Autonomous Region**: 1 L, Nature Reserve Bastak, Bol'shoy Sorennak River, near the bridge to the Kukan, 11.07.2018, coll. T. Vshivkova; 1♂ 1♀, Kuldur River, Kuldur settlement, above the spring, Amur R. basin, 17.08.2024, coll. N. Yavorskaya; 2♀, Bastak Nature Reserve, Bastak River, Amur R. basin, 14.08.2024, coll. N. Yavorskaya. **Japan, Hokkaido:** 1♂ 1♀ 5 L, Tobetsu River, 43°28.67 N 144°17.65 E, 10.09.1995, coll. G. Kraft; 1♀, Shiretoko Pass Summmit, near Rausu, 44°3.2 N 145°6.2 E, 11.09.1995, coll. G. Kraft; 2♀, Soukippkaononai River near Shibetsu town, 43°44.4 N 144°53.6 E, 12.09.1995, coll. G. Kraft; 9♀, trib. Churui River, at bridge near Shibetsu town, 44°43.7 N 144°48.4 E, 12.09.1995, coll. G. Kraft; 1♀, 1 L, trib. Ikushina River, near Shibetsu town, 43°48.1 N 144°46.9 E, 12.09.1995, coll. G. Kraft.

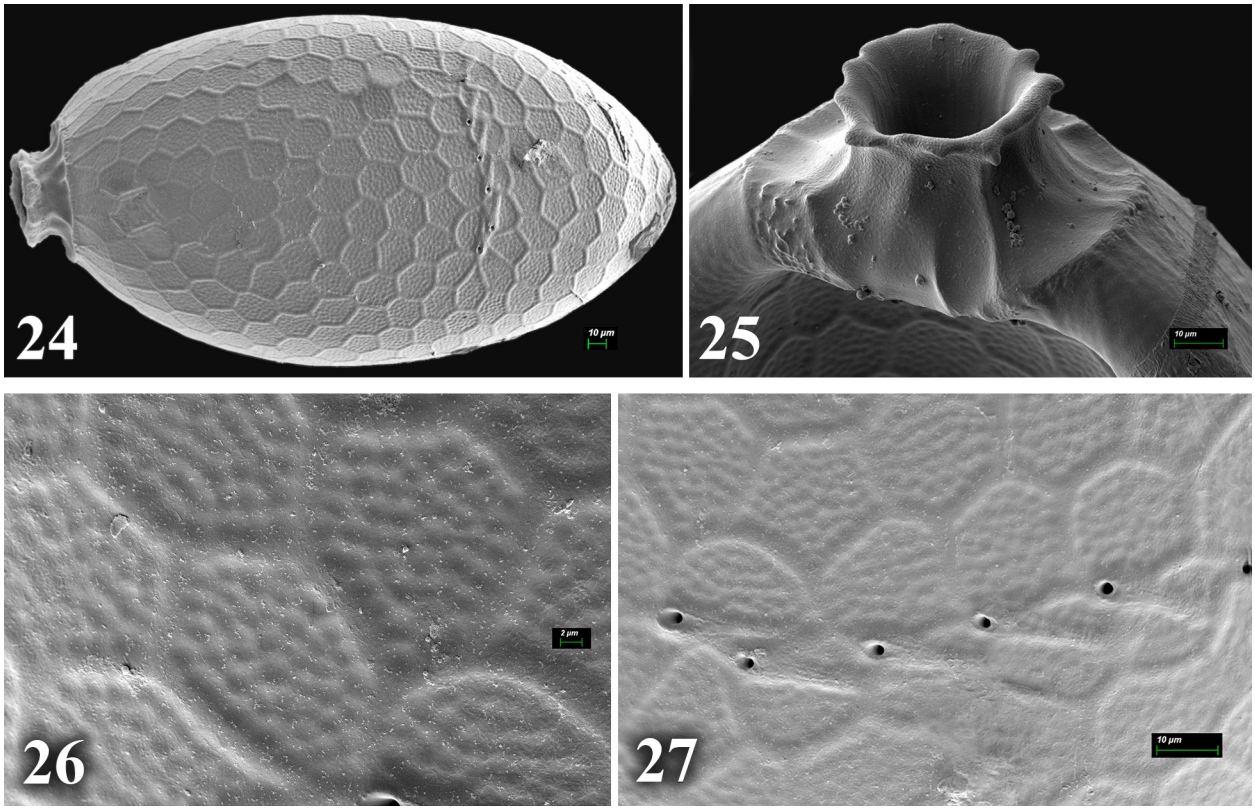
Egg. Shape oval; marginally asymmetrical, anterior pole is rounded more widely than posterior pole (Fig. 18), and a concave cross-section (Fig. 20). Length 345–349 μm, width at equator 222–227 μm (n=2). Collar well developed, with irregular longitudinal ridges and a flanged and incised rim; base of collar surrounded by a wide smooth shoulder limited by a ring (Figs. 19–20). Anchor mushroom-shaped, with small grouped globular bodies covering the entire surface of anchor evenly (Figs. 18–19). Follicle cell impressions near the collar ranged from subrectangular to hexagonal (Figs. 18, 20). Chorion covered with hexagonal FCIs with thick elevated ridges (Figs. 18, 21–23); floors with numerous (ca. 37–39) very shallow and small pits (Figs. 22–23). Micropylar row well visible along anterior ⅓ (Figs. 18, 21). Micropyles located near paired ridges and surrounded with rosettes of FCIs (Figs. 18, 21, 23). Micropylar canals straight, tunnel-shaped, and relatively long; orifices set in small oval cup-like depressions with long, smooth, slanted, and open sperm guides extending from cup rims (Figs. 18, 21, 23).

Remarks. The egg of *I. eximia* is described here for the first time. Eggs from Japan (Figs. 24–27) and the Russian Far East are similar in size (330–357 μm long, 177–207 μm wide, n=4), have a collar with a smooth shoulder at the base, limited by a raised ring (Fig. 25), and have a similar chorion structure (Figs. 26–27). The main difference between Japanese eggs is their oblong shape (Figs. 18, 24). It is possible that the shape and appearance of eggs from the Japanese population vary depending on the degree of hydration. Eggs from dried Japanese females appear almost parallel-sided and narrow.

Distribution. East Palaearctic. Russia, Siberia: Altai, Sayan, Transbaikalia; Far East: Southern Yakutia, Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Region, Primorsky Krai, Sakhalin, and South Kuril Isles. East Kazakhstan (Devyatkov 2022). Mongolia. China (Changbai Mountain and Jilin Province) (Wang *et al.* 2018, Chen *et al.* 2019). *Isoperla eximia* is recorded from Japan (Hokkaido) for the first time.



FIGURES 18–23. *Isoperla eximia* Zapekina-Dulkeit, 1975. Russia, Far East, Jewish Autonomous Region, Kuldur River, Amur R. basin. **18.** Habitus, with anchor and micropylar row, lateral. **19.** Collar and mushroom-shaped anchor with grouped globular bodies, covered anchor evenly, lateral. **20.** Posterior pole, collar with wide smooth shoulder limited by ring, a view from above. **21.** Anterior pole, micropylar row, orifices surrounded with rosettes of FCI, view from above and lateral. **22.** Chorion structure. **23.** Orifices, setting in small oval cup-like depressions with long, smooth, and open sperm guides extending from cup rims, sperm guides slanted, lateral.



FIGURES 24–27. *Isoperla eximia* Zapekina-Dulkeit, 1975. Japan, Hokkaido, Churui River basin, near Shibetsu town. **24.** Habitus, with collar and micropylar row, lateral. **25.** Collar with wide shoulder and ring. **26**. Chorion structure. 27. Micropylar row, orifices, sperm guides, lateral.

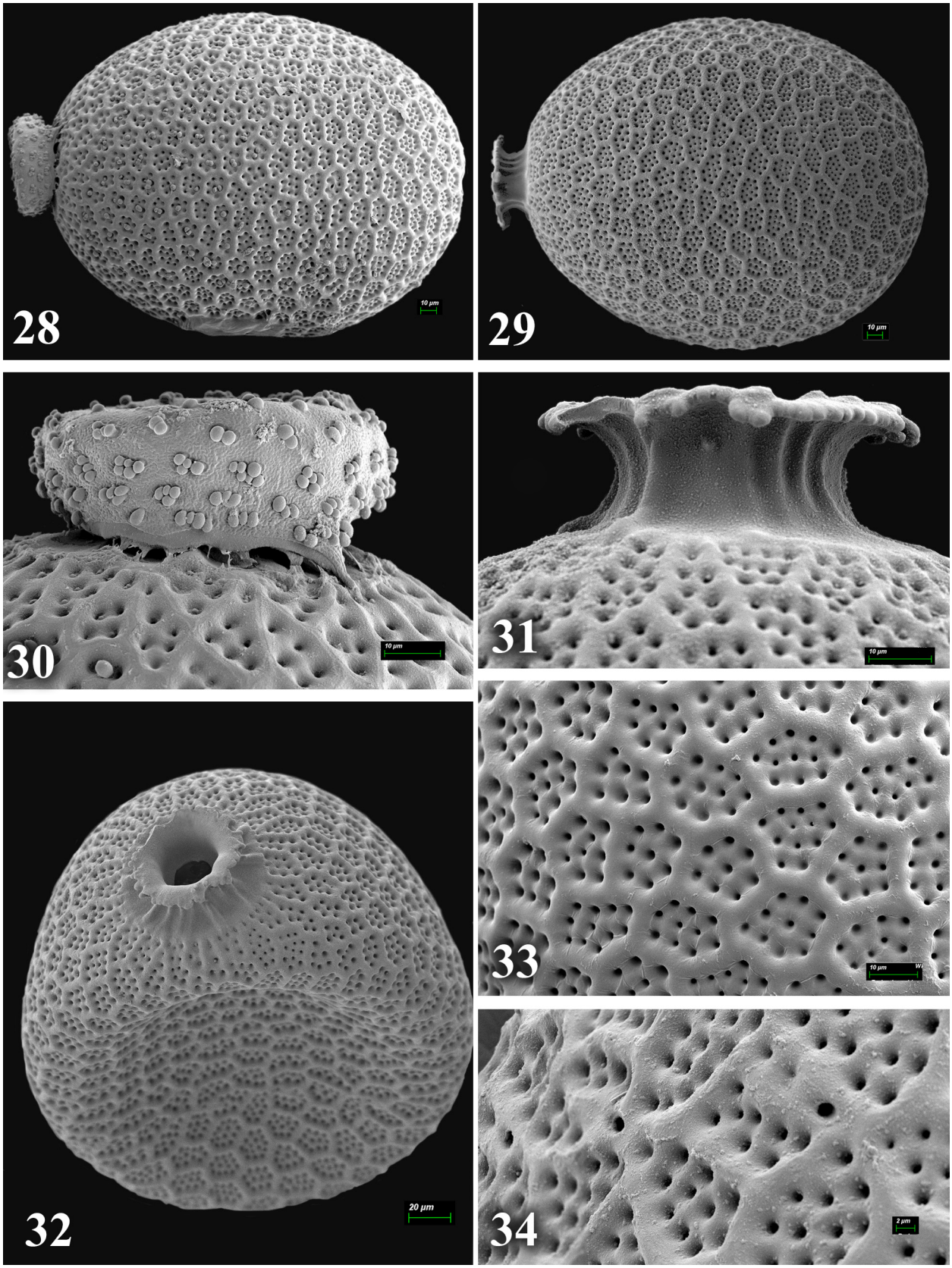
Isoperla flavescens Zhiltzova & Potikha, 1986 (in Potikha & Zhiltzova 1986)

Figs. 28–34

Material examined. Russia, Far East, Khabarovsk Krai: 1♂, Anyuisky National Park, Tormasu River, Anyui R. basin, Amur R. basin, 21.06.2018, coll. N. Yavorskaya; **Primorsky Krai:** 7♂ 7♀, Lazovka River, Partizanskaya R. basin, below the pass, under the bridge, 13.06.1998, coll. V. Teslenko; 9♀, Malinovka River, Ussuri R. basin, Amur R. basin, 10 km above the Pozhiga village, highway, 16.06.1998, coll. V. Teslenko.

Egg. The egg of *I. flavescens* is described here for the first time. Shape oval, symmetrical with anterior and posterior poles broadly rounded (Figs. 28–29) and a concave cross-section (Fig. 32). Length of 287–302 µm and a width at the equator of 200–217 µm (n=4). Collar well developed, with irregular longitudinal ridges extending onto the shoulder; shoulder contoured with a ring; rim incised and flanged (Figs. 29, 31–32). Anchor mushroom-shaped, with small grouped globular bodies covering the entire surface of the anchor evenly (Figs. 28, 30). FCIs near collar range from pentagonal to hexagonal (Fig. 32). Chorion covered with hexagonal FCIs with thick elevated ridges (Figs. 28–29, 32–34); floors covered with deep pits, their number not exceeding 9–13 (Figs. 33–34). Micropylar row visible near anterior ¼ (Fig. 29). Micropyles located near ridges and surrounded with rosettes of FCIs (Figs. 29, 34). Micropylar canals smaller than in other species; orifices and sperm guides weakly visible (Fig. 34).

Distribution. East Asian species with limited distribution in the south of the Russian Far East (Jewish Autonomous Region, Khabarovsk Krai, and Primorsky Krai). South Korea (Kim *et al.* 1998). China (Changbai Mountains) (Huo *et al.* 2022).



FIGURES 28–34. *Isoperla flavescens* Zhiltzova & Potikha, 1986. Russia, Far East, Primorsky Krai, Lazovka River, Partizanskaya R. basin. Egg, cleaned. **28.** Habitus, with anchor, lateral. **29.** Habitus with collar, micropylar row, and rosettes, lateral. **30.** Mushroom-shaped anchor with small globular bodies, lateral**. 31**. Collar with irregular longitudinal ridges, rim incised, and flanged, lateral. **32.** Collar, longitudinal ridges extending onto the shoulder with a ring, view from above. **33**. Chorion structure. **34**. Orifices and weakly visible sperm guides.

***Isoperla kozlovi* Zhiltzova, 1972**
Figs. 35–40

Material examined. Russia, Far East, Amurskaya Oblast: 5♂ 15♀, Bureya River, Amur R. basin, Novobureysk settlement, 27.06.2013, coll. V. Teslenko; 16♂ 19♀, Bureya River, Novobureysk settlement, above Podoshva island, 28.06.2013, coll. V. Teslenko; Khabarovsk Krai: 10♂ 17♀, Bikin River, Amur R. basin, 300 m below the bridge, Vladivostok-Khabarovsk highway, 18.06.2000, coll. T. Tiunova; **Prymorsky Krai:** 1♂, Razdolnaya River, Zagorodnoye settlement, 08.06.2019, coll. E. Gorovaya.

Egg. Rhombus-shaped, uniformly tapered toward the anterior and posterior poles, with a cross-shaped ridge along the anterior ⅓; posterior pole cross-section triangular, with three distinct longitudinal ridges; anterior pole quadrangular with four longitudinal ridges; anterior end of egg is convex (Figs. 35, 37, 38). Length 269–290 μm, width widest at ⅓ from the anterior pole of 173–177 μm, thickness 2.4 μm (n=2). Collar well developed, with short longitudinal ridges and a narrow flanged and slightly wavy rim; base covered with a mesh of empty cells of a smoothed triangular shape directed into interior of egg (Figs. 36–37, 39). Anchor mushroom-shaped, covered with small, globular bodies larger than other species (Fig. 36). Chorion near collar smooth, ranging downward from pentagonal to hexagonal FCIs with thick and elevated ridges; floors flat with numerous (ca. 19–29) punctations (Figs. 37–38). Eclosion line absent. Micropylar row visible near the anterior ⅓ of egg (Fig. 35). Micropyles scattered in groups of 3 on FCI ridges and surrounded by rosettes of FCIs; orifices set in small oval cup-like depressions with short sperm guides (Fig. 40).

Distribution. East Palaearctic species. Russia, West Siberia, West Altai, Sayan, Baikal Lake basin, Transbaikalia; Far East: Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Region, Primorsky Krai. East Kazakhstan (Devyatkov 2022). Mongolia. China, Northeast, including Changbai Mountain, Jilin Province (Chen *et al.* 2021). South Korea (Hwang & Muranyi 2020).

Remarks. The original description of the egg indicates one of the diagnostic features—the shape of the collar. Collar with a few subdued meshes, edge simple, base smoothly bulging into interior of egg (Zwick & Surenkhorloo 2005).

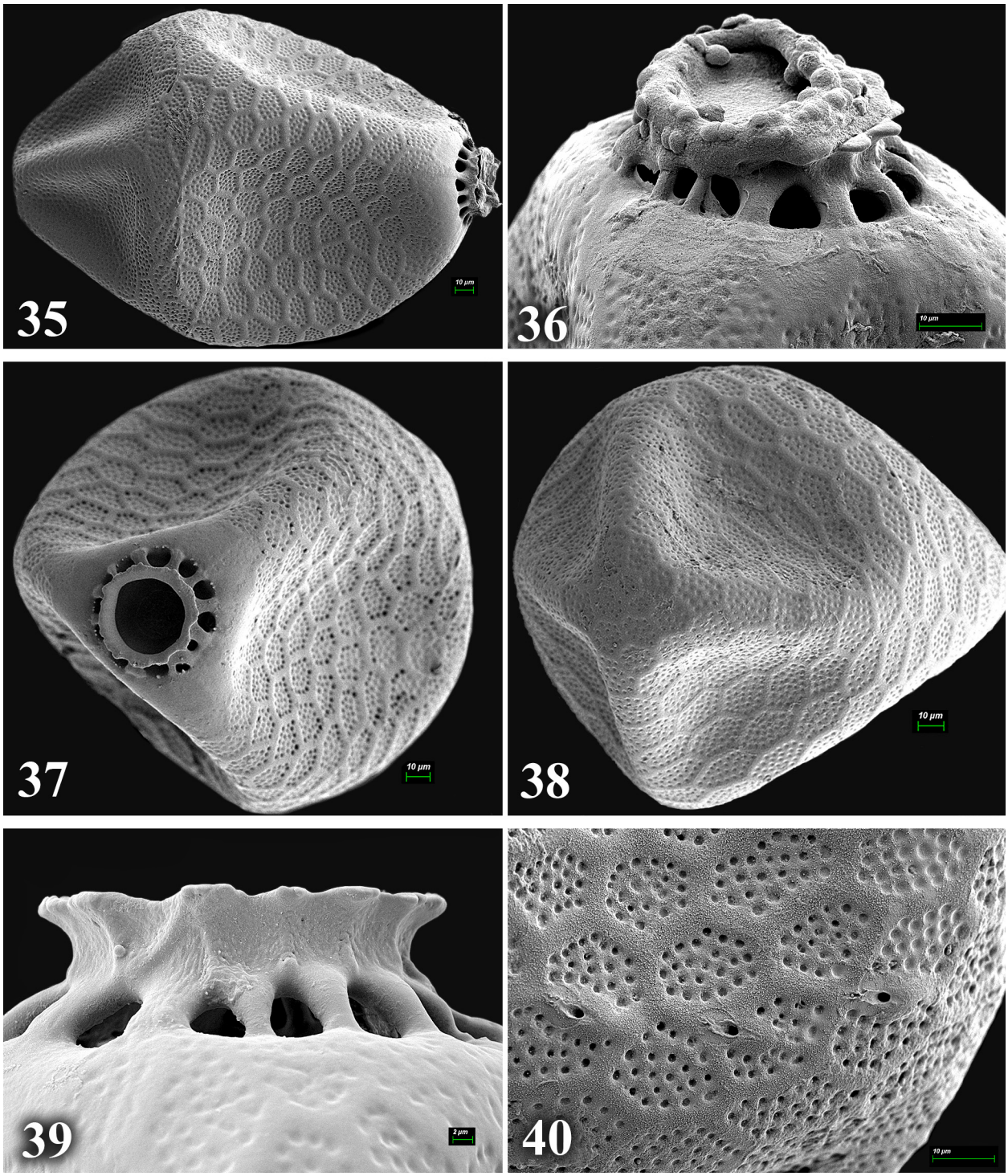
***Isoperla lunigera* (Klapálek, 1923)**
Figs. 41–47

Material examined. Russia, Far East, Amurskaya Oblast: 1♂ 2♀, Dikan River, Bureya R. basin, Amur R. basin, 1 km below auto bridge, 5 km from Novobureisk settlement, 10.07.2015, coll. T. Tiunova; Khabarovsk Krai: 1♂, Komsomolsk Nature Reserve, Bitki River, Udyl Lake, 13.07.2021, coll. N. Yavorskaya; **Jewish Autonomous Region:** 1♀, Bastak Nature Reserve, Scorpion's Lair Stream, 29.07.2022, coll. T. Vshivkova; **Primorsky Krai:** 4♂ 3♀, Ussuri River, Amur R. basin, Stepanovka village, 26.06.1988, coll. V. Teslenko; 3♂ 4♀, Ussuri River, Kamenka village, 5.07.1993, coll. V. Teslenko; 1♂ 9♀, Shumnaya River, Ussuri R. basin, Shumny settlement, 29.06.2017, coll. V. Lyubarets.

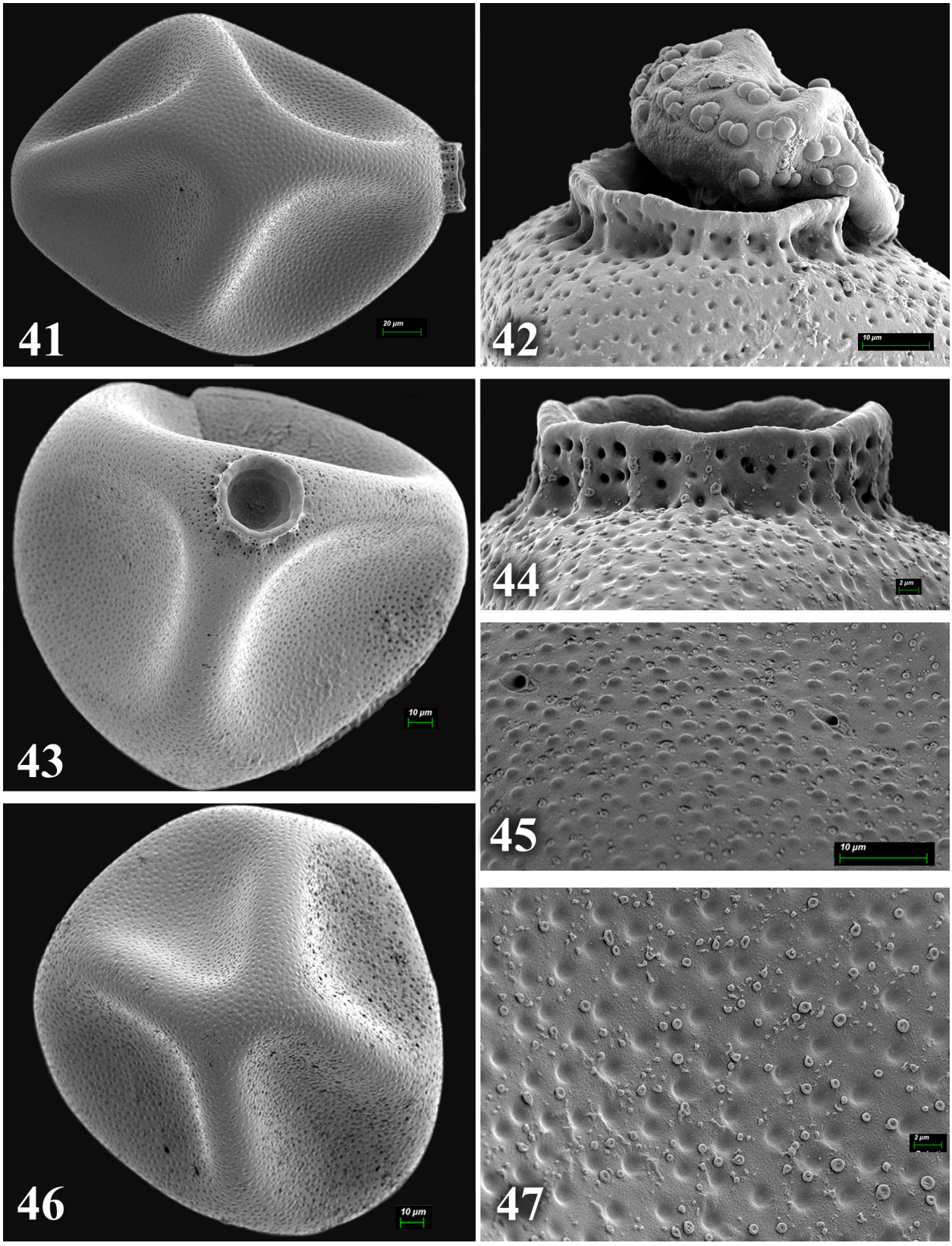
Egg. Rhombus-shaped, tapered toward the anterior and posterior poles; cross-shaped ridge present medially; posterior pole triangular in cross-section, with a distinct cross-shaped ridge on each side; anterior pole is quadrangular with four longitudinal ridges; anterior apex is convex (Figs. 41, 43, 46). Length 217–236 μm, maximum width medially 174–182 μm (n=2). Collar low, longitudinal ridges short, their bases well visible dorsally (Figs. 42–44); collar sides between ridges covered with empty pits extending to rim, rim narrow and slightly wavy apically (Figs. 42, 44). Anchor mushroom-shaped and covered with globular bodies scattered in groups of 2 or 3, globular bodies larger than other species (Fig. 42). Chorionic surface covered with numerous, very shallow punctuations; hexagonal FCIs not visible, eclosion line absent (Figs. 44–45, 47). In addition to shallow punctations, there are small and tiny donut-shaped rounded knobs present on the chorion surface (Figs. 45, 47). Micropyles are positioned singularly or in a row of 3 near the anterior ⅓ of the egg (Fig. 41); orifices set in small oval cup-like depressions, and sperm guides are long and thin, weakly visible (Fig. 45).

Distribution. East Palaearctic species. Russia, Siberia: Altai, Sayan, Baikal Lake basin, Transbaikalia; Far East: Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Region, Primorsky Krai. East Kazakhstan (Devyatkov 2022). Mongolia. China (Zhu *et al.* 2007).

Remarks. In addition to the dimensions and characteristics of the chorion structure, the original description of the collar by Zwick & Surenkhorloo (2005) generally corresponds to the results obtained here by SEM.



FIGURES 35–40. *Isoperla kozlovi* Zhiltzova, 1972. Russia, Far East, Amurskaya Oblast, Bureya River, Amur R. basin, Novobureysk settlement. Egg, cleaned. **35.** Habitus, with micropylar row, orifices surrounded by rosettes, lateral. **36.** Anchor and collar, lateral. **37.** Posterior pole with mesh collar, view from above. **38**. Anterior pole, convex, view from above. **39**. Mesh of the collar, lateral. **40.** Orifices in small oval depressions with short sperm guides.



FIGURES 41–47. *Isoperla lunigera* (Klapálek, 1923). Russia, Far East, Primorsky Krai, Ussuri River, near Stepanovka village, Amur River basin. Egg. **41.** Habitus, lateral. **42.** Anchor and collar, lateral. **43.** Posterior pole with collar, view from above. **44.** Collar, low, with empty pits between low longitudinal ridges, extending to rim. **45.** Orifices in small oval depressions and sperm guides. **46.** Anterior pole with convex apex, view from above. **47.** Chorion structure with shallow punctations and tiny donut-shaped rounded knobs.

Isoperla maculata Zhiltzova, 1977

Figs. 48–55

Material examined. Russia, Far East, Khabarovsk Krai: 1♂, Anyuisky National Park, Bira Channel, Amur R. basin, 19.06.2018, coll. N. Yavorskaya; 9♂ 11♀, Anyuisky National Park, Anyui River, Nilo Chanell, at light, Amur R. basin, 23.07.2018, coll. Ev. Makarchenko; **Primorsky Krai:** 1♂, Barabashevka River, above the fish factory, 24.06.2021, coll. T. Tiunova; 1♂ 4♀, Ryazanovka River, cordon, 9.06.1998, coll. V. Lyubarets; 7♂ 9♀, Barabashevka River, near the fish factory, 9.06.2003, coll. V. Teslenko; 5♂ 4♀, Artemovka River near the Mnogoudobnoye settlement, 14.07.2002, coll. V. Lyubarets; 1♂ 2♀, Shumnaya River, Shumny settlement, Ussuri R. basin, Amur R. basin, 29.06.2017, coll. V. Lyubarets; 2♀, Lazovka River, Lazo settlement, Partizanskaya R. basin, 22.08.2006, coll. Shokhrin.

Egg. The egg of *I. maculata* is described here for the first time. Shape oblong, with a wide diameter closer to the posterior pole; a cross-shaped ridge near the equator dividing the anterior and posterior poles; posterior pole triangular in cross-section with an indistinct cross-shaped ridge on each side; anterior pole quadrangular in cross-section with four longitudinal ridges and apex slightly concave (Figs. 48–51). Length 269 µm, maximum width nearer to posterior pole 165 µm (n=1). Collar well developed, elevated with irregular and raised longitudinal ridges, rim widely flanged, wavy apically (Figs. 49–50, 54). Anchor mushroom-shaped, globular bodies concentrated into groups of 2–5, located mainly in a peripheral area along the anchor edge and top of the anchor deeply embedded (Figs. 48, 53). Chorion covered with hexagonal FCIs with thickened, elevated, and raised ridges and numerous (12–20) deep pits (Figs. 49, 55). Micropyles small, poorly distinguishable due to their similar size to the pits in hexagonal FCIs and arranged singularly in a row on follicle cell ridges near anterior ⅓ of the egg (Fig. 55). Orifices round and located on raised horizontal, tunnel-shaped relatively long sperm guides laterally; sperm guides weakly visible and unassociated with FCI rossetes (Figs. 52, 55). Eclosion line absent.

Distribution. East Asian species with limited distribution in the south of the Russian Far East, including the Jewish Autonomous Region, Khabarovsk Krai, and Primorsky Krai.

Isoperla mongolica Zhiltzova, 1972

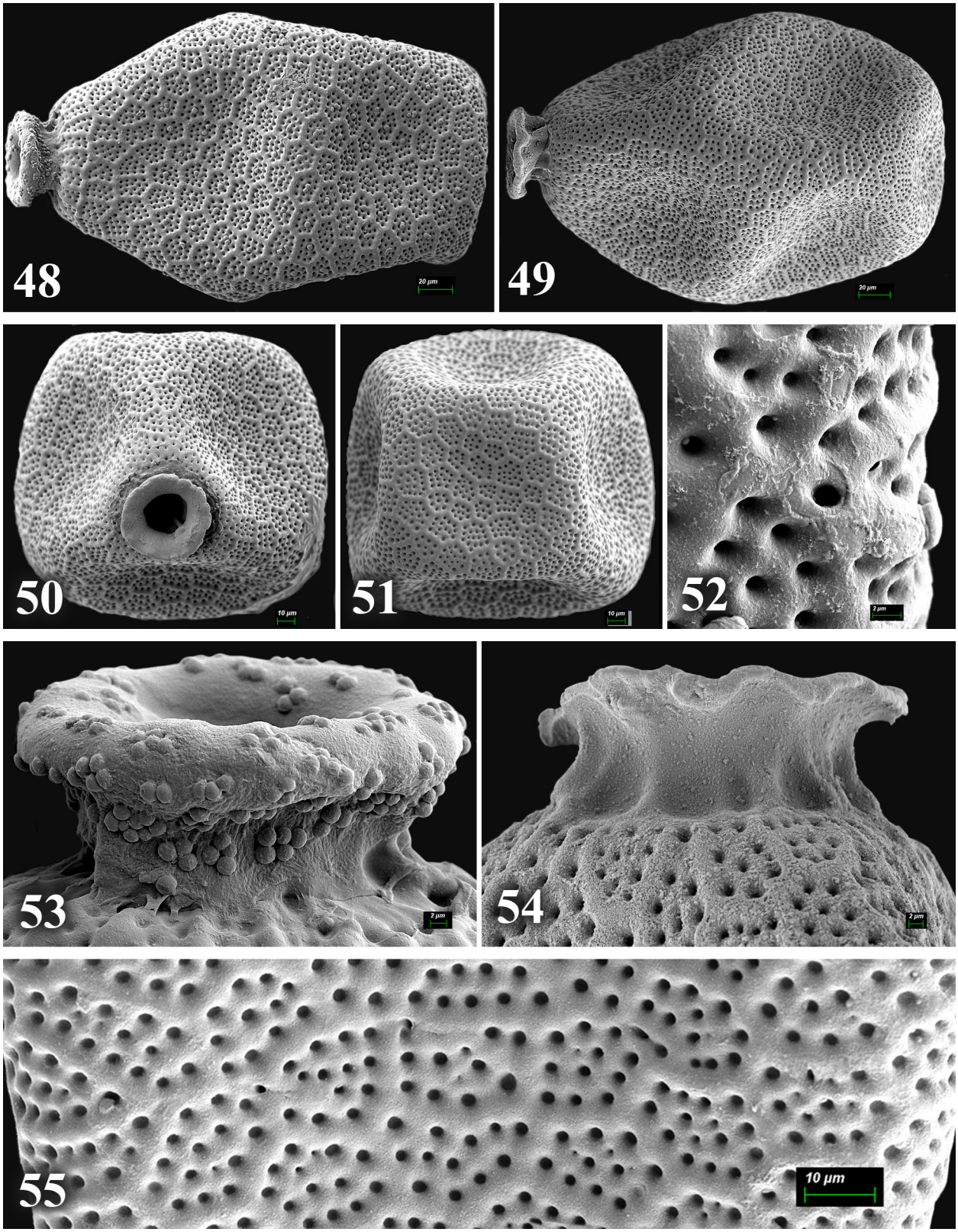
Figs. 56–62

Material examined: Russia, Siberia, Krasnojarsky Krai, Khakassia: 1♀, 50 km NW of Shira Lake, Black Iyus River, 4.07.2014, coll. A. Leley; Transbaikalia: 1♂, Rastorguikha River, Selenga R. Basin, Burkalsky protected area, 23.08.2018, coll. Matafonoff; **Altai Republic:** 1♂, 1♀, Tuekta River, Ob River basin, 05.09.2021, coll. L. Yanygina. **Mongolia, Arkhangai Aimak, Onder-Ulaan, Tsakhir:** 2♀, Cenlnt gol. 48° 07 N 100 °22 E, 2100 m above sea level, 10–13.05.1997, coll. Yu. Marusik.

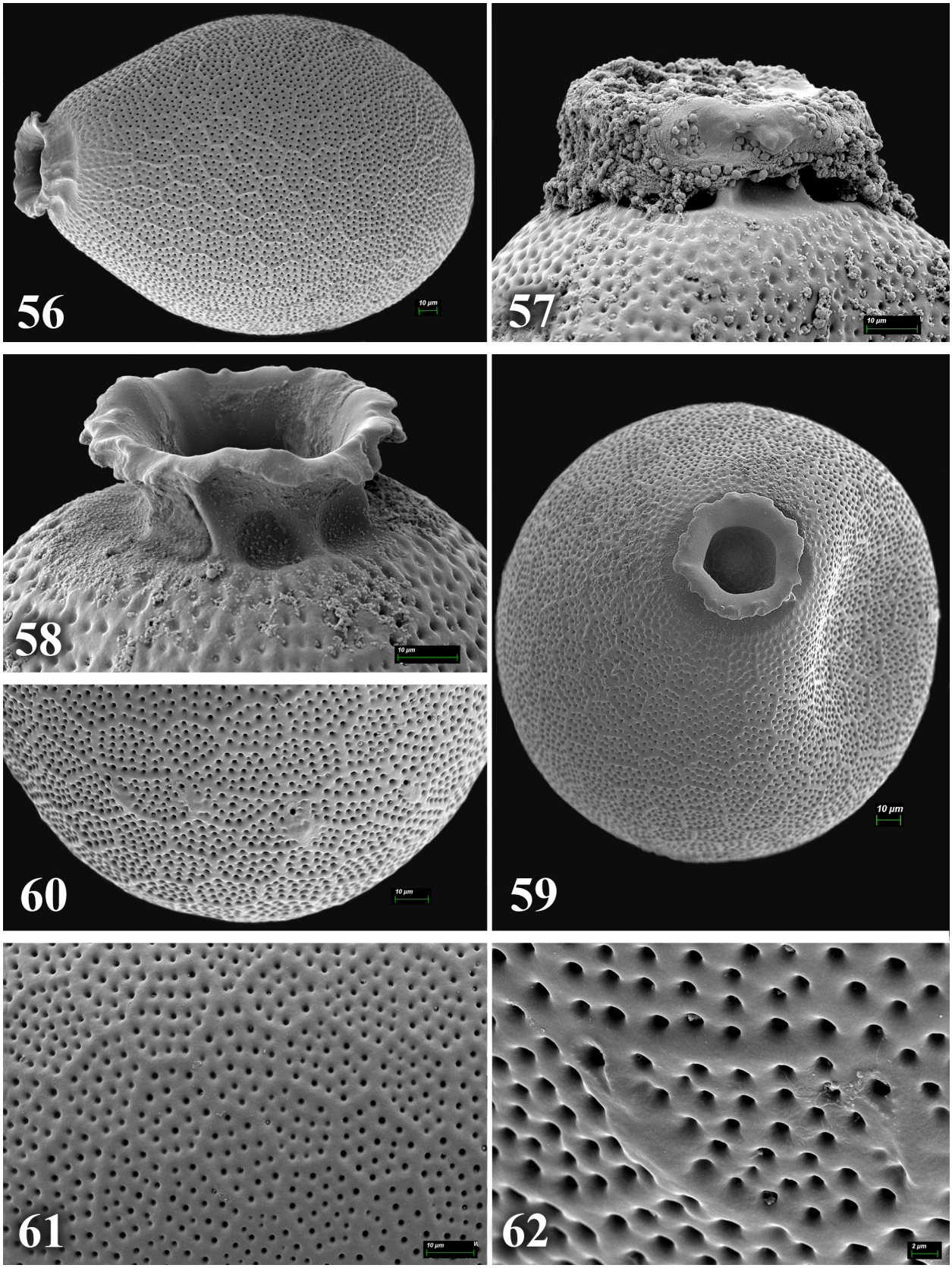
Egg. Shape oval, marginally asymmetrical with posterior pole narrower than anterior pole, anterior pole widely rounded, cross-section concave (Figs. 56, 59). Length 229–260 µm, width at the equatorial region 175–182 µm (n=4). Collar well developed, elevated with irregular longitudinal ridges; base of collar deeply embedded and surrounded by a narrow smooth shoulder; rim flanged and wavy apically (Figs. 56, 58–59). Anchor mushroom-shaped, with small globular bodies concentrated into groups of 2–5 located mainly in a peripheral area along the anchor edge (Fig. 57). Follicular cells near the collar ranged from pentagonal to hexagonal (Fig. 56). Chorion covered with hexagonal FCIs with thickened, slightly elevated ridges and numerous (12–20) deep pits (Figs. 60–62). Micropyles positioned singularly along one row on follicle cell ridges near the anterior ⅓ (Fig. 60). Orifices set in small, oval, cup-like depressions; sperm guides tunnel-shaped and relatively long and wider than ridges and are associated with FCI rosettes (Figs. 56, 60–62). Eclosion line absent.

Distribution. East Palaearctic species originally described from Mongolia (Onon River basin). The species is also known from Russia in the rivers of East and West Siberia, including Altai, the Baikal Reserve, and the Selenga River Basin. East Kazakhstan (Devyatkov 2022).

Remarks. The original description clearly indicates the size and shape of the egg, as well as the chorion structure with deep, large pits and their unclear location in polygonal fields (Zwick & Surenkhorloo 2005). The collar and anchor were also described, which generally corresponds to the SEM results presented here.



FIGURES 48–55. *Isoperla maculata* Zhiltzova, 1977. Russia, Far East, Khabarovsk Krai, Anyuisky National Park, Anyui River, Nilo Chanell, Amur R. basin. Egg. **48.** Uncleaned, habitus with anchor, extrachorion layer with mushroom bodies over FCIs, lateral. **49.** Cleaned, habitus with collar lateral. **50.** Posterior pole, collar rim view from above. **51.** Anterior pole with concave apex. **52.** Orifice round, lateral. **53.** Anchor with globular bodies, lateral. **54.** Collar with irregular and raised longitudinal ridges, lateral. **55.** Micropyle row on raised, tunnel-shaped, and relatively long and weakly visible sperm guides; chorion structure, and orifices, lateral.



FIGURES 56–62. *Isoperla mongolica* Zhiltzova, 1972. Russia, West Siberia, Altai Republic, Tuekta River, Ob River basin. Egg. **56.** Habitus lateral. **57.** Anchor with globular bodies, lateral. **58.** Collar, lateral. **59.** Posterior pole with collar, view from above. **60.** Anterior pole, chorion structure, micropylar row, orifices surrounded by rosettes, lateral. **61.** Chorion structure thickened, slightly elevated ridges, and numerous deep pits. **62.** Orifices in small, oval, cup-like depressions, sperm guides are tunnel-shaped and wider than ridges.

Isoperla obscura (Zetterstedt, 1840)

Figs. 63–70

Material examined: Russia, Siberia, Republic of Buryatiya: 6♂ 3♀, Selenga River, 6 km from the Selenga Pulp Mill, 5.06.2007, coll. N. Bazova; 2♂ 1♀, Selenga River, Tologoy Rock, 09.07.2007, coll. N. Bazova; 7♂ 5♀, Chikoy River, settlement Povorot, Selenga R. basin, 8.06.2009, coll. N. Bazova; 15♂ 17♀, Selenga River, settlement Tataurovo, 1.07.2009, coll. N. Bazova; 22♂ 16♀, Selenga River, above confluence with Chikoy River, railway bridge, 3.07.2009, coll. A. Basov and N. Basova; **Far East, Yakutiya**: 4♂ 5♀ 4L, Aldan River, Lena R. basin, 10–13.08.1987, coll. V. Bogatov; **Amurskaya Oblast:** 12♀, Zeya River, Amur R. basin, Ovsyanka settlement, 3.07.2013, coll. V. Teslenko; 2♀, Zeya River, upstream, near Mazanovo settlement, Amur R. basin, 5.08.2006, coll. T. Tiunov; 6♀, Zeya River, near Krasnoyarovo settlement, 24.06.2004, coll. V. Teslenko; 4♂ 2♀, Zeysky Nature Reserve, Gramatukha River, Zeya River basin, 9.09.2007, coll. E. Makarchenko; 6♂ 25♀, Zeya River, mouth, Blagoveshchensk, 22.06.1997, coll. T. Arefina; 5♂ 7♀, Zeya River, Alekseyevka-Alexandrovka settlement, Amur R. basin, 8.07.2013, coll. V. Teslenko; **Khabarovsk Krai:** 1♀, Bureya River, 10 km below the mouth of the Urgal River, Amur R. basin, 18.07. 2003, coll. T. Tiunova; 3♀, Tunguska River, near Danilovka settlement, Amur R. basin, 26.06.2007, coll. V. Teslenko; 3♂, 6L, Amur River, Susanino settlement, 23–26.06.2000, coll. T. Tiunova; 2♀, Amur River, Zimmermanovka settlement, 18.06.2005, coll. T. Tiunova; 1♂ 1♀, stream without name in Amur R. basin, 2.07.2006, coll. N. Yavorskaya; **Chukotka Autonomous Okrug**: 1♀, Anadyr River basin, 31.07.1982, coll. I. Chereshnev.

Egg. Shape oval, marginally asymmetrical with the posterior pole narrower than anterior one, which is widely rounded, cross-section concave (Figs. 63–64). Length 232–246 µm, width at equator 165–171 µm (n=3), chorion thickness 2.6 µm. Collar well developed, elevated with irregular and raised longitudinal ridges; base of collar embedded; ring around collar base short and slightly rough; rim flanged and wavy apically (Figs. 63, 65). Anchor mushroom-shaped with globular bodies concentrated into groups of 2–5, mainly in a peripheral area along the anchor edge (Figs. 64, 66). Chorion structure with faintly visible hexagonal FCIs and ridges; chorionic surface smooth, evenly covered with numerous, small, and deep pits (Figs. 63–64, 67–69). Micropyles arranged singularly along one row near the anterior ⅓ of the egg and grouped in threes (Figs. 63, 67). Orifices present in oval, cup-like depressions; sperm guides are tunnel-shaped and visible (Fig. 69); in the Far Eastern population, the chorion is smooth without punctations around the orifices (Fig. 70). Eclosion line absent.

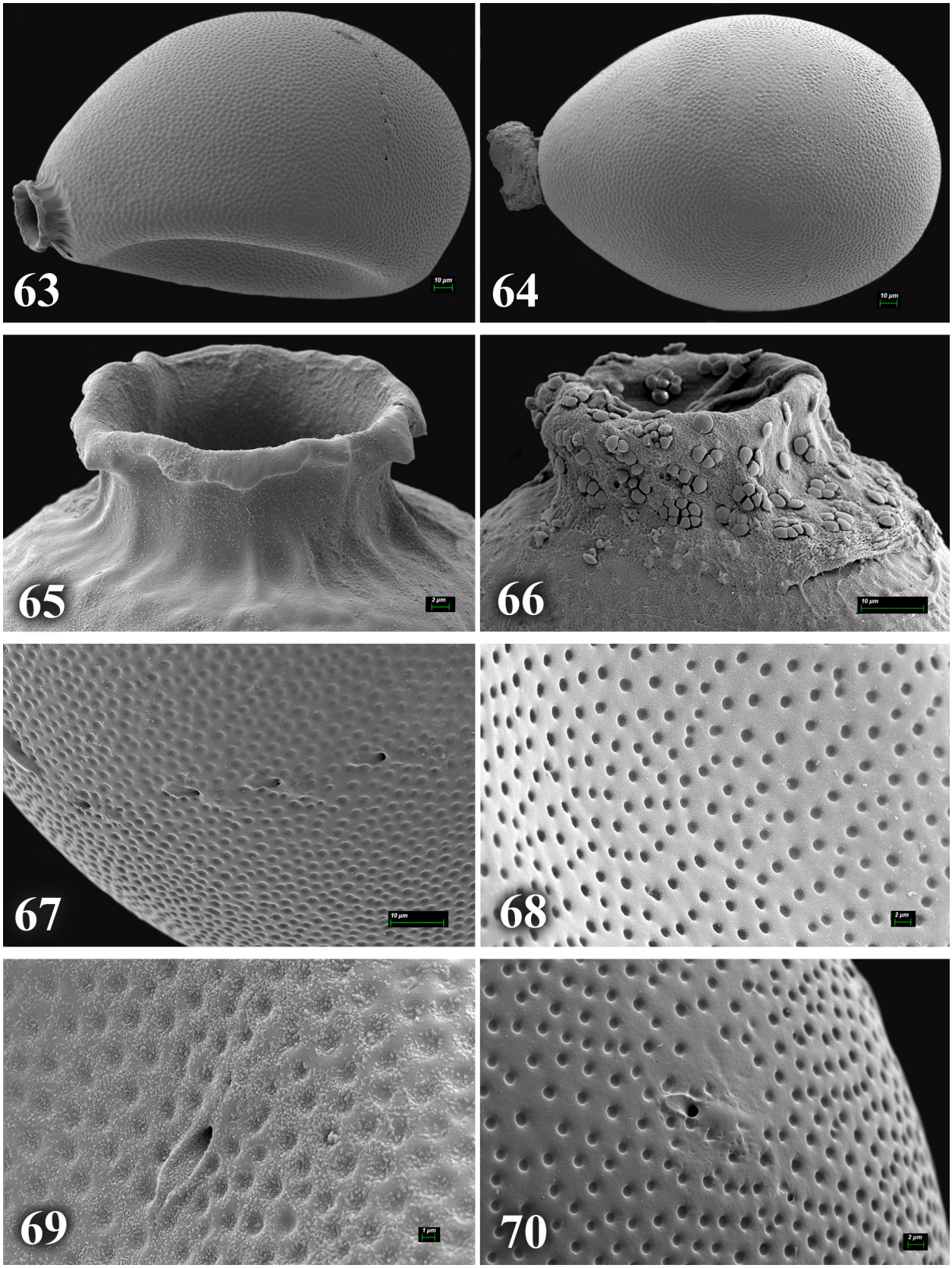
Distribution. Transpalaearctic species was originally described from Lapponia (Umensis ad Umenaes, Sweden) and found in streams and large rivers in the northern part of the Palaearctic Region. Europe: Norway, Finland, Austria, Switzerland, France, Germany, Italy, and very rarely in the Balkan Region, including Croatia. Bulgaria. Russia: North-East, Komi Republic, and Nenets Autonomous Okrug; Asia, Siberia: Krasnojarski Krai, Altai, Sayan, and Transbaikalia; Far East: Southern Yakutia, Magadanskaya Oblast, Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Krai, Primorsky Krai, and Chukotka Autonomous Okrug. East Kazakhstan (Devyatkov 2022). Mongolia.

Remarks. The eggs of the species vary slightly in size across its wide trans-Palaearctic range. The egg size ranges from 252–268 × 169–177 µm for the Mongolian specimen to 276–289 × 194–202 µm for the Norwegian specimen (Zwick & Surenkhorloo 2005) and 232–246 × 165–171 µm in specimens from the Russian Far East. The anchor is rarely observed in eggs of the Far Eastern population. The chorion thickness was 4 µm for the Mongolian (Zwick & Surenhkorloo 2005) and 2.6 µm in the Far Eastern specimens. Minor differences were also noted in the chorion punctuations surrounding the micropyle of the eggs from Siberia (the Selenga River basin) and Far Eastern specimens (Figs. 69–70).

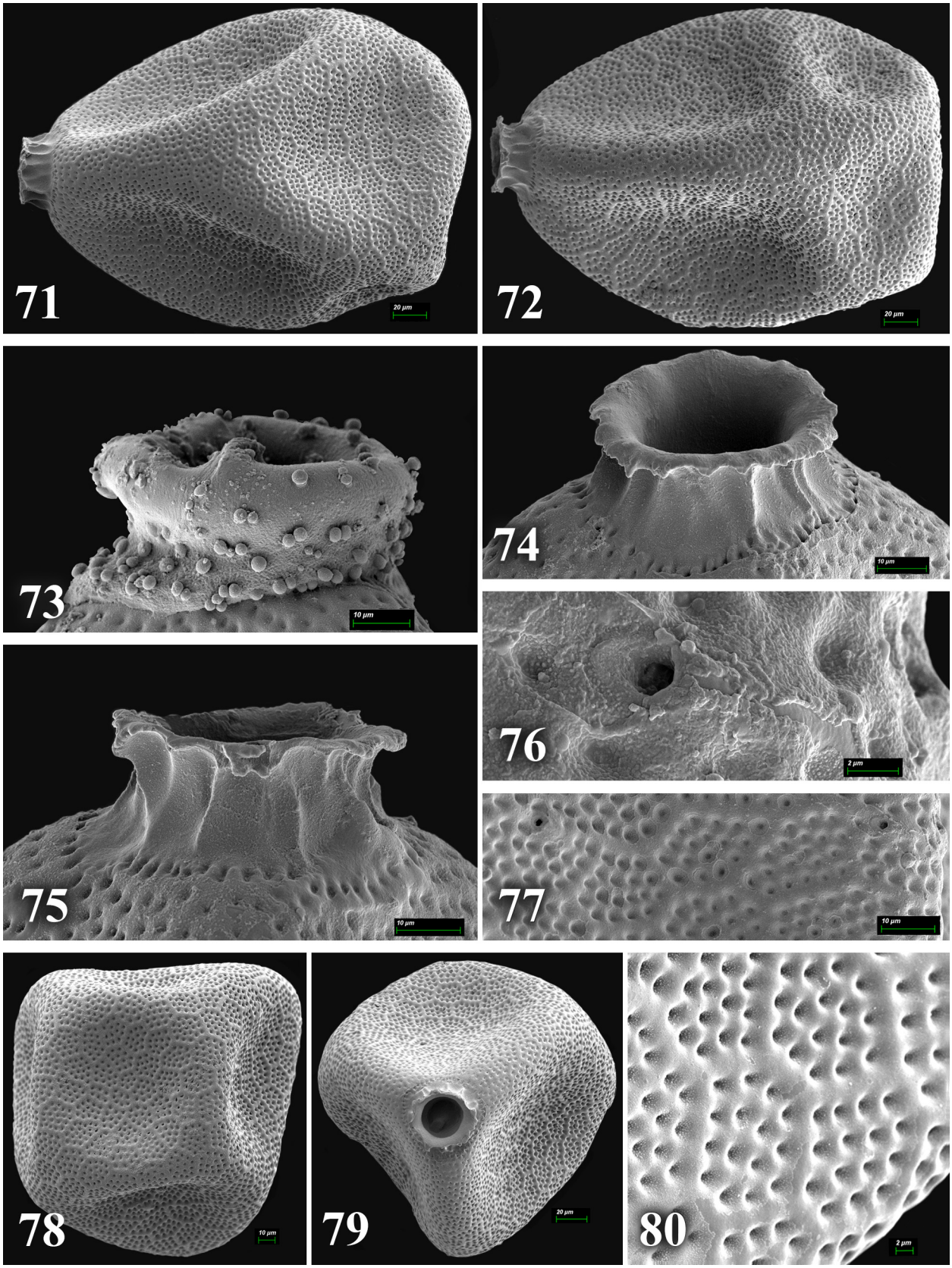
Isoperla ornata Zhiltzova, 1988

Figs. 71–80

Material examined. Russia, Far East, Primorsky Krai: 4♀, Komissarovka River, Khanka Lake basin, near Dvoryanka village, 23–25.06.1994, coll. Bulavsky; 1♀, Barabashevka River, light trap, 06.07.2021, coll. E. Gorovaya; 4♂ 4♀, Komissarovka River, Komissarovo village, 28–29.05.1998, coll. V. Teslenko; 1♂ 1♀, Tigrovaya River, opposite Khmelnitskie Shcheki, Partizanskaya R. basin, 11 06.1998, coll. V. Teslenko; 1♂ 1♀, Razdolnaya River near Fadeyevka village, 31.05.1998, coll. T. Vshivkova; 1♂, 1♀, Razdolnaya River, near the border with China, coll. T. Vshivkova; 4♂ 6♀, Shkotovka River, 25–29.05.2015, reared, V. Teslenko.



FIGURES 63–70. *Isoperla obscura* (Zetterstedt, 1840). Russia, Siberia, Republic of Buryatia, Selenga River, settlement Tataurovo. Egg, cleaned. **63.** Habitus, with collar and micropylar row, lateral. **64.** Habitus, with anchor, lateral. **65.** Collar with rough ring, lateral. **66.** Anchor plate, covered with globular bodies, lateral. **67.** Micropylar row, lateral. **68.** Chorion evenly covered with small and deep pits, lateral. **69.** Orifice in oval, cup-like depressions; sperm guides are tunnel-shaped and long. **70.** Smooth chorion without punctations around orifice, lateral.



FIGURES 71–80. *Isoperla ornata* Zhiltzova, 1988. Russia, Far East, Primorsky Krai, Shkotovka River. Egg. **71–72.** Habitus, with collar, lateral. **73.** Anchor with globular bodies, lateral. **74–75.** Collar with irregular and raised longitudinal ridges and a flanged rim, base offset with pits. **76.** Orifice in a small, oval, cup-shaped depression; sperm guide is poorly visible. **77.** Micropyles row weakly visible, orifices located singularly on follicle cell ridges. **78.** Anterior pole with concave apex, view from above. **79**. Posterior pole, with collar, view from above. **80**. Chorion structure, lateral.

Egg. The egg of *I. ornata* is described here for the first time. Egg pear-shaped, posterior ⅔ triangular in cross-section, anterior ⅓ square, with distinct cross-shaped ridges (Figs. 71–72, 78–79); anterior pole square, slightly concave (Fig. 78). Length 263–269 μm, width 181–192 μm (n=5), chorion thickness 3.1 μm. Collar well developed, elevated with irregular and raised longitudinal ridges; rim flanged, serrated, or wavy; collar base offset with pits (Figs. 74–75). Anchor mushroom-shaped, with small globular bodies concentrated into groups of 2–5 and located mainly in a peripheral area along the anchor edge, top deeply embedded and covered with single globular bodies; anchor covers the collar completely (Fig. 73). Hexagonal FCI's ridges slightly raised and thickened, floors flat with numerous (about 16) punctations (Fig. 80); eclosion line absent. Micropyles small and weakly visible, arranged singularly on follicle cell ridges near the anterior ⅓ of the egg (Fig. 77). Orifices set in small, oval, cup-shaped depressions; sperm guides poorly visible (Figs. 71–72, 77).

Distribution. East Asian species with limited distribution in the south of the Russian Far East, including the Jewish Autonomous Region, Khabarovsk Krai, and Primorsky Krai.

Isoperla pseudornata Zhiltzova, 1988

Figs. 81–89

Material examined. **Russia, Far East, Primorsky Krai:** 1♂, Barabashevka River, above the fish factory, 24.06.2021, coll. T. Tiunova; 3♂, Barabashevka River, the same place, 31.05.2004, coll. V. Teslenko; 2♂ 4♀ 3L, Barabashevka River the same place, 14–23.05.2002, coll. V. Teslenko; 5♂ 7♀, Ryazanovka River, near the hunting grounds, 10.06.2003, coll. V. Teslenko; 3♂ 2♀, Bolshaya Ussurka River, Zvenigorodka village, Ussuri R. basin, 06.08.2004, coll. V. Teslenko; 2♂ 4♀ 1L, Tigrovaya River, Partizanskaya R. basin, Khmelnitskoye settlement, 11 06.1998, coll. V. Teslenko; 2♂ 4♀, Sergeevka River, Partizanskaya R. basin, highway, under the bridge, 12.06.1998, coll. V. Teslenko.

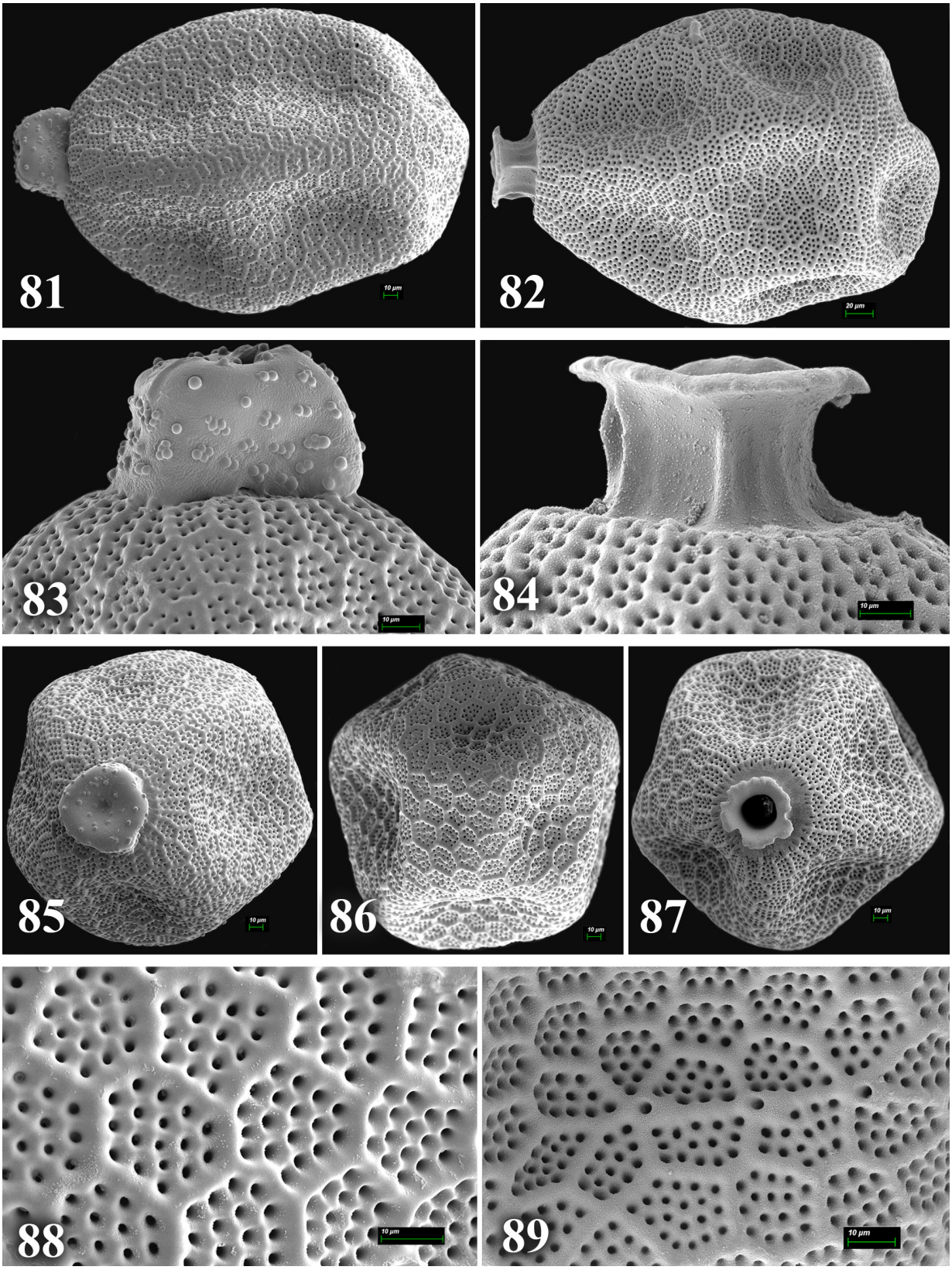
Egg. The egg of *I. pseudornata* is described here for the first time. Shape oval, sometimes pear-shaped (Figs. 81–82); cross-section pentagonal with 5 distinct longitudinal ridges; posterior and anterior poles are pentagonal, and the anterior pole is slightly concave (Figs. 85–87). Length 242–329 μm, width 203–229 μm (n=5). Collar well developed and relatively high, with irregular and raised longitudinal ridges; rim flanged, wavy at the apex; base embedded, shoulder smooth, and surrounded with a row of pits (Figs. 82, 84, 87). Anchor mushroom-shaped, with small globular bodies concentrated into groups mainly in a peripheral area along the margin's top of the anchor, shallowly embedded and covered with a few single globular bodies (Figs. 81, 83). Hexagonal FCIs well-developed, ridges wide, rose, rough, and thickened floors rough with numerous relatively deep punctations (about 14–19); eclosion line absent (Figs. 82, 88). Micropylar row clearly visible, with micropyles set on follicle cell ridges and grouped in threes near the anterior ⅓ (Fig. 82). Orifices arranged singularly on the top of FCI ridges, larger than the chorionic punctations (Fig. 89) and surrounded by polygonal rosettes; sperm guides short and thickened (Fig. 89).

Distribution. East Asian species with limited distribution in the south of the Russian Far East, Jewish Autonomous Region, Khabarovsk Krai, and Primorsky Krai.

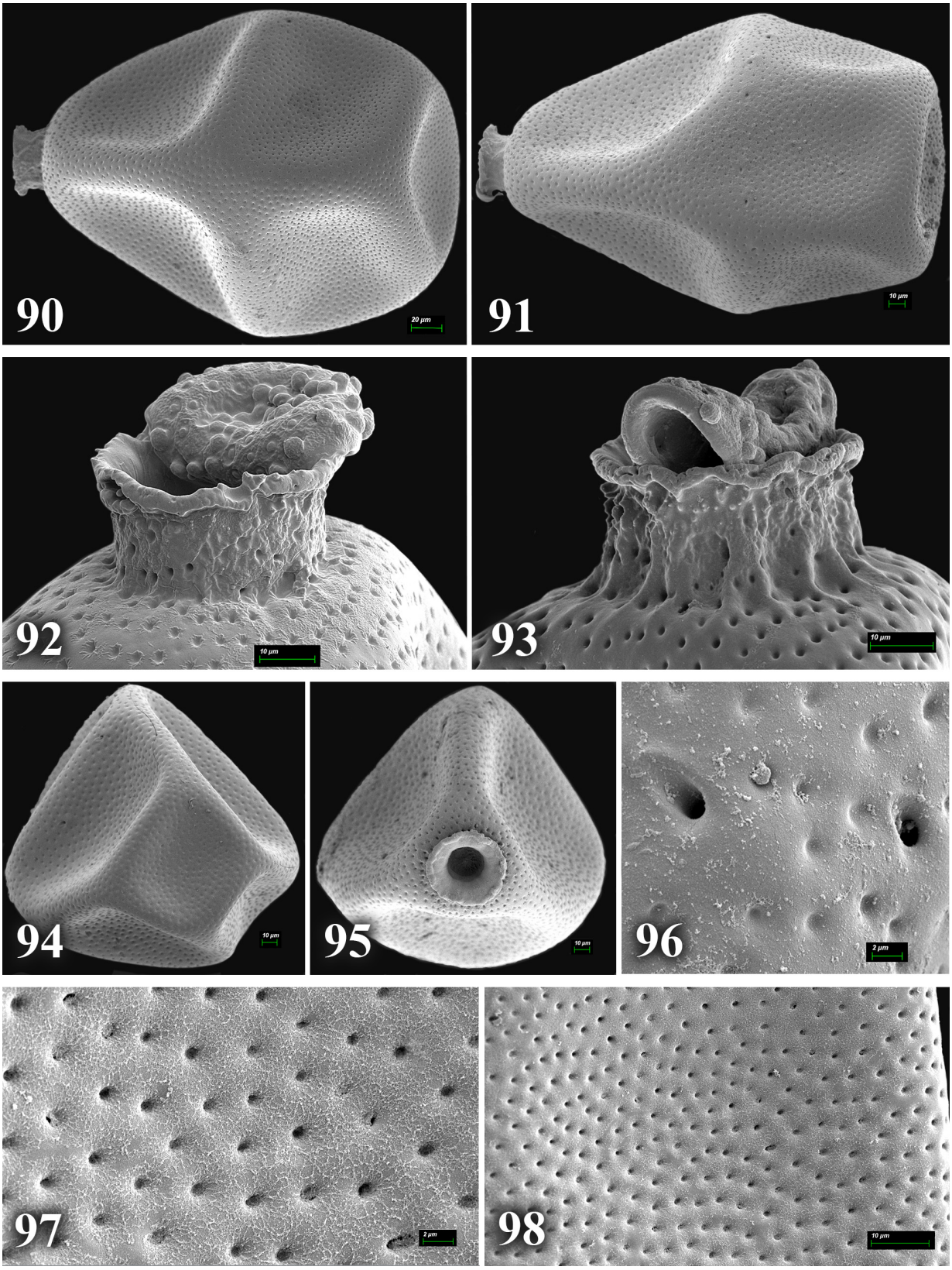
Kaszabia nigricauda (Navás, 1923)

Figs. 90–98

Material examined: **Russia, Far East, Amurskaya Oblast:** 3♂ 5♀, Norsky Nature Reserve, Nora River, cordon near Berezovoye Lake, Selemdzha-Zeya-Amur R. basins, 16.06.2004, coll. V. Teslenko; 5♂ 6♀, Tom River, under the bridge, Amur R. basin, 13.06.2004, coll. V. Teslenko; 1♀, Deya River, Bureya R. basin, Amur R. basin, 4.07.2014, coll. V. Teslenko; 3♂ 10♀, Dzhilimkur River, Zeya R. basin, Amur R. basin, high way bridge, 8.07.2013, coll. V. Teslenko; 3♀, Dikan River, under high way bridge, Bureya R. basin, Amur R. basin, 28.06.2014, coll. V. Teslenko; **Khabarovsk Krai:** 2♂ 3♀, Bolshoy In River, Tunguska R. basin, Amur R. basin, 11.06.2004, coll. V. Teslenko; 5♂ 7♀, Khekhtsirsky Nature Reserve, Beshenaya River, Amur R. basin, 10.06.2018, coll. N. Yavorskaya; **Primorsky Krai:** 2♂ 4♀, Avan River, Ussuri R. basin, Amur R. basin, 23.06.1998, coll. V. Teslenko.



FIGURES 81–89. *Isoperla pseudornata* Zhiltzova, 1988. Russia, Far East, Primorsky Krai, Ryazanovka River, near the hunting grounds**.** Egg. **81.** Habitus, with anchor and micropylar row, lateral. **82.** Habitus, with collar, lateral. **83.** Anchor with globular bodies, lateral**. 84.** Collar with irregular and raised longitudinal ridges and flanged rim. **85.** Posterior pole with shallow embedded anchor, view from above. **86.** Anterior pole with slightly concave apex, view from above. **87.** Posterior pole, with collar, smooth shoulder surrounded with a row of pits, view from above**. 88.** Chorion structure, lateral. **89.** Micropylar row, orifices located on the top of FCI ridges, sperm guides are short and thickened.



FIGURES 90–98. *Kaszabia nigricauda* (Navás, 1923). Russia, Far East, Amurskaya Oblast, Norsky Nature Reserve, Nora River, cordon near Berezovoye Lake, Selemdzha-Zeya-Amur River basins. Egg**. 90–91.** Habitus, with collar, cross-shaped ridges, and micropylar row, lateral. **92.** Anchor biscuit-shaped, flat, with large, single, globular bodies. **93.** Collar covered with pits, extending to the rim, rim flanged and wavy. **94.** Anterior pole with slightly concave apex, view from above. **95.** Posterior pole with collar, view from above. **96.** Orifices slightly elongated, sperm guides poorly visible, lateral. **97–98**. Chorion surface uniformly and densely covered with numerous small punctations.

Egg. Pear-shaped, triangular cross-section near the posterior ½; anterior ½ quadrangular with distinct cross-shaped ridges near the equator dividing anterior and posterior poles; anterior pole concave (Figs. 90–91, 94–95). Length 273–298 μm, width 175–214 μm (n=5), chorion thickness 2.8 μm. Collar relatively high with irregular longitudinal ridges, base embedded and covered with pits extending to the rim; the rim is narrow, flanged, and wavy (Figs. 92–93, 95). Anchor small, biscuit-shaped, and flat, covering only the rim; relatively large, single, globular bodies scattered over the entire anchor surface (Figs. 92–93); chorionic surface uniformly and densely covered with numerous small punctations; hexagonal FCIs not visible (Figs. 97–98). Eclosion line absent. Micropyles are scattered in groups of 3 or 4 in the subequatorial region (Figs. 90–91); orifices slightly elongated and sperm guides poorly visible (Fig. 96).

Distribution. East Palaearctic species with a broad geographical distribution in Russia from Siberia (Altai, Sayan Mountains, Baikal Lake Basin, Transbaikalia) to the Far East (Amurskaya Oblast, Jewish Autonomous Region, Khabarovsk Krai, Primorsky Krai). Kazakhstan. Mongolia. China (Huo & Du 2020)**.**

Remarks. The status of *K. nigricauda* was discussed in some detail in Huo & Du 2020. Our studies did not reveal any clear differences in the morphological features of *Isoperla* and *Kaszabia* eggs, especially since there is overlap with characteristics. It should also be noted that a comparison of the eggs of *Kaszabia* and *Isoperla* species with abdominal processes on male terga could not be carried out in full due to the lack of egg descriptions or due to the lack of SEM illustrations. The eggs of *K. nigricauda* are very similar in shape and chorion structure to the eggs of the Nearctic species *Isoperla lenati* Szczytko & Kondratieff, 2015. The main difference is the size of the collar; the collar of the *K. nigricauda* is significantly higher than that of the *I. lenati*.

According to our research, we can conclude that the eggs of *Kaszabia* are pear-shaped, the anchor is biscuit-shaped, the collar is slightly higher than in the examined *Isoperla* species, hexagonal follicle cell impressions are not visible, and the chorion is covered uniformly and densely with numerous small punctations.

Discussion

Mature eggs of Siberian and Far Eastern *Isoperla* are infrequent in the collected materials, and no mature eggs have yet to be found with females of *Isoperla chereshnevi* Teslenko, 2017. The largest known egg is *I. eximia* (length 345–349 μm, width 222–227 μm) and the smallest is of *I. lunigera* (length 217–236 μm, width 174–182 μm).

Most known Siberian and Far Eastern *Isoperlinae* have oval eggs; three species (*I. altaica*, Fig. 1; *I. asiatica*, Fig. 10; and *I. flavescens*, Fig. 28) have eggs with symmetrically rounded anterior and posterior poles; three species (*I. eximia*, Fig. 18; *I. mongolica*, Fig. 56; and *I. obscura*, Fig. 64) are distinguished by asymmetrical or unevenly rounded poles; rhombus-shaped eggs are in *I. kozlovi* (Fig. 35) and *I. lunigera* (Fig. 41), and pear-shaped or close to pear-shaped eggs are in *K. nigricauda* (Fig. 90) and *I. pseudornata* (Fig. 82). The egg cross-section is concave (*I. altaica* Fig. 6, *I. asiatica* Fig. 14, *I. flavescens* Fig. 32, *I. eximia* Fig. 20, *I. mongolica* Fig. 59, *I. obscura* Fig. 63), or multi-shaped: pentagonal (*I. pseudornata* Figs. 85–87); posterior pole triangular, anterior pole square, and concave (*I. maculata* Figs. 50–51, *I. ornata* Figs. 78–79, *K. nigricauda* Figs. 94–95); and posterior pole triangular, anterior pole quadrangular, and convex (*I. kozlovi* Figs. 35, 37–38, *I. lunigera* Figs. 41, 43, 46).

The anchor is well-developed, mainly mushroom-shaped, and covered collar completely; small grouped globular bodies cover the entire surface of the anchor evenly on eggs of *I. eximia* (Fig. 19), *I. flavescens* (Fig. 30, and *I. mongolica* (Fig. 57), or placed along a peripheral area of the anchor edge on *I. kozlovi* (Fig. 36). The top of the anchor is deeply embedded on *I. altaica* (Fig. 2), *I. maculata* (Figs. 53), and *I. ornata* (Fig. 73). The globular bodies are larger than other species on the anchor plate of *I. lunigera* (Fig. 42) and *I. kozlovi* (Fig. 36). The egg of *Kaszabia nigricauda* has a small, flat, and biscuit-shaped anchor, covering only the rim of the collar (Figs. 92–93), and relatively large, single, globular bodies scattered over the entire anchor surface.

The collar is usually well-developed, with irregular longitudinal ridges and a flanged rim. The collar's longitudinal ridges can be smooth as in *I. flavescens* Fig. 31 and *I. ornata* Figs. 74–75 or rough with small transverse projections as *I. altaica* has Figs. 1, 3, 5. The collar rim may be deeply serrated as in *I. asiatica* (Fig. 15) or wavy as *I. eximia* (Fig. 20), *I. mongolica* (Fig. 59), and *I. obscura* (Fig. 65). The collar is low in *I. lunigera* (Figs. 42, 44) and in *I. kozlovi*, where the collar base bears specific empty triangular cells (Figs. 35–37).

The FCIs are well developed with thickened walls and the chorion is covered with thickened raised reticulate ridges on I. *kozlovi* (Fig. 40), *I. eximia* (Figs. 18, 20–23), *I. flavescens* (Figs. 28–29, 32–34), *I. maculata* (Figs.

48–51, 55), *I. ornata* (Figs. 71–72, 77–78, 80), and *I. pseudornata* (Fig. 81–83, 85–89). For *I. mongolica* (Figs. 56, 60–61), *I. altaica* (Figs. 1–2, 7–8), and *I. asiatica* (Figs. 10–11, 14, 16), the ridges are slightly elevated. The FCIs are faintly visible or are absent in *I. obscura* (Figs. 63–64, 67–70), *I. lunigera* (Figs. 41, 45–47), and *K. nigricauda* (Figs. 90–91, 96–98).

Micropyles are generally located near the anterior ⅓ in a linear configuration as in *I. kozlovi* (Figs. 35, 40), *I. obscura* (Figs. 63, 67), *I. asiatica* (Figs. 10, 17), *I. eximia* (Figs. 18, 21), *I. pseudornata* (Figs. 82, 89), and *I. mongolica* (Figs. 56, 60), or grouped in 3 or 4 in the subequatorial region like on *K. nigricauda* (Figs. 90–91) or in anterior ⅓ of the egg as on *I. lunigera* (Fig. 41). However, in *I. ornata* micropyles are scattered (Fig. 77), and in *I. altaica* (Figs. 1, 7), they are positioned along a sinuous row. The eclosion line is absent in the species examined here.

The micropyle orifices are generally positioned on FCI ridges. The orifices are flush with the ridge, for example, on *I. mongolica* (Fig. 62) and *I. pseudornata* (Fig. 89). In other species, the orifices have an elongated oval lip, for example, on *I. obscura* (Fig. 67, 69–70) and *I. lunigera* (Fig. 45). Some species have sperm guides associated with the orifices; for example, *I. obscura* (Fig. 67), *I. eximia* (Figs. 24, 27), and *I. asiatica* (Fig. 17) have elongate and thick guides reminiscent of a tunnel. For *I. kozlovi* (Fig. 40) the guides are short while the orifices are set in a depression on *I. ornata* (Fig. 76) and *I. maculata* (Fig. 52).

Key to the eggs of 12 Isoperlinae species from Siberia and the Russian Far East

1 Egg shape oval with a single concavity; anterior and posterior poles similarly shaped (Figs. 5, 14, 20, 32, 59, 63) 2
- Egg shape pear-shaped or with multiple concave facets; anterior and posterior pole shape asymmetrical (Figs. 35, 41, 48, 71, 87, 90). 7
2 Chorion covered with hexagonal cell impressions and raised or elevated thickened ridges (Figs. 11, 18, 29, 56) 4
- Chorion covered with hexagonal cell impressions and faintly visible ridges (Figs. 2, 64) 3
3 Chorion covered with shallow pits (Figs. 7–8); collar multi-level with raised longitudinal wavy carinae and small transverse projections (Figs. 1, 3, 5); collar base with a thickened, wavy ridge (Fig. 3) . . . . . *I. altaica*
- Chorion evenly covered with deep pits (Figs. 68, 70); collar with irregular longitudinal carina transverse projection absent, base of collar embedded, ring short and slightly rough (Figs. 63, 65). . . . . *I. obscura*
4 Follicle cell impressions visible, walls or ridges thick and raised or elevated and strongly delineated from follicular cell floor (Figs. 18, 29). 5
- Follicle cell impressions visible, walls or ridges slightly raised or elevated and weakly delineated from follicular cell floor (Figs. 11, 56). 6
5 Collar with irregular longitudinal ridges and flanged, incised rim (Fig. 19), base of collar surrounded by wide smooth shoulder limited by ring (Fig. 20). Floor of the hexagonal FCIs areas large with numerous (ca. 37–39), shallow, and small pits (Figs. 22–23). Micropylar row well visible (Figs. 18, 21), micropyles located near paired ridges and surrounded with rosettes (Figs. 18, 21, 23). Micropylar canals tunnel-shaped and long (Fig. 21), orifices set in small oval cup-like depressions with smooth, and open sperm guides extending from cup rims, sperm guides slanted (Fig. 23) . . . . . *I. eximia*
- Collar with irregular longitudinal ridges extending onto the shoulder; shoulder is contoured with a ring; rim incised and flanged (Figs. 31–32). Floors of the hexagonal FCIs areas small, covered with deep pits (7–13) (Figs. 33–34). Micropylar row weakly visible (Figs. 28–29), micropyles located near ridges and surrounded with rosettes of FCI's (Fig. 34). Micropylar canals smaller than in other species; orifices and sperm guides are weakly visible (Fig. 34). . . . . *I. flavescens*
6 Collar rim flanged and wavy, base of collar deeply embedded and surrounded by a narrow smooth shoulder (Figs. 56, 58–59). Floors in the hexagonal FCIs bear numerous (12–20) deep pits (Figs. 61–62). Micropylar orifices set in small, oval, cup-like depressions (Fig. 62) and sperm guides tunnel-shaped and wider than ridges (Fig. 60) are associated with follicle cell impressions rosettes (Fig. 60). . . . . *I. mongolica*
- Collar rim deeply serrated and curved outward (Fig. 15), base surrounded by slightly pronounced shoulder without ring (Fig. 15). Chorion surface is rough with floor of the hexagonal follicular cell impressions with deep groove-like pits (about 11) (Figs. 16–17). Micropylar canals tunnel-shaped and relatively long; canal seems to float over the orifice and slightly covers it (Fig. 17). . . . . *I. asiatica*
7 Egg cross-section pentagonal, anterior pole slightly concave, chorion with five longitudinal ridges (Figs. 85–87). . . . . *I. pseudornata*
- Egg cross-section triangular at the posterior pole, chorion with cross-shaped ridges 8
8 Egg cross-section square at the anterior pole, and the anterior pole is convex (Figs. 38, 46). Collar low (Fig. 36, 42) 9
- Egg cross-section square at the anterior pole, anterior pole concave (Figs. 51, 78, 94). Collar raised (Figs. 54, 75, 93) 10
9 Collar base bears empty cells of a smoothed triangular shape, directed into the interior of the egg (Figs. 35–37, 39). Chorion surface with hexagonal follicular cell impressions and thick slightly elevated ridges, floors with (ca. 19–29) pits (Fig. 40). Sperm guides short (Fig. 40) . . . . . *I. kozlovi*
- Collar between longitudinal ridges covered with small pits extending to a narrow and wavy rim (Figs. 41–44). Chorion covered with numerous fine, shallow punctuations and small, donut-shaped rounded knobs, hexagonal follicle cell impressions not

visible (Figs. 45, 47, 41). Sperm guides thin, weakly visible (Fig. 45) . . . . . *I. lunigera*

10 Chorion covered uniformly and densely with numerous small punctations; hexagonal follicle cell impressions not visible (Figs 90, 97–98). Collar with relatively high irregular longitudinal ridges, base embedded, and covered with pits extending to the rim; rim is flanged and wavy (Figs. 92–93, 95). Anchor small, biscuit-shaped, and flat, covering only the rim of the collar (Figs. 92–93). Micropyles scattered in groups of 3–5 in the subequatorial region (Figs. 90–91); orifices slightly elongated, sperm guides poorly visible (Figs. 96) . . . . . *Kazsabia nigricauda*

- Egg hexagonal or pentagonal (Figs. 48, 72). Chorion with hexagonal follicle cell impressions, ridges raised and thickened (Figs. 55, 80). Collar with irregular longitudinal ridges; rim flanged, serrated, or wavy; collar base offset with pits (Figs. 54, 74). Anchor mushroom-shaped and covers the collar completely (Figs. 53, 73) 11

11 Chorion covered with hexagonal follicular cell impressions, floors with pits (about 16) (Figs. 77, 80). Micropyles small and weakly visible, arranged singularly on follicle cell ridges, orifices set in small, oval, cup-shaped depressions, sperm guides poorly visible (Fig. 77). . . . . *I. ornata*

Chorion covered with hexagonal follicular cell impressions, floors with deep pits (12–20) (Fig. 55). Micropyles small, poorly distinguishable due to their similar size to the pits in hexagonal FCIs, arranged singularly in a row on follicle cell ridges near the anterior ⅓ of the egg (Figs. 48, 55). Orifices round, located on raised horizontal, tunnel-shaped, and relatively long sperm guides laterally; sperm guides weakly visible and unassociated with FCI rosettes (Figs. 48, 55). . . . . *I. maculata*

Acknowledgements

The scanning electron micrographs were prepared with the help of Vitaliy Kazarin (*FSC EATB FEB RAS*, Vladivostok), to whom the author is very much appreciative. The author expresses sincere gratitude to Scott Grubbs (Department of Biology and Center for Biological Studies, Western Kentucky University, USA) for editorial recommendations, comments, and linguistic revision, and to Chris Verdone (North Carolina Department of Environmental Quality, Division of Water Resources, Water Sciences Section, USA) for their review, assistance in designing the illustrations, advice, and constructive suggestions, which significantly improved the manuscript. The research was carried out within the state assignment of the Ministry of Science and Higher Education of the Russian Federation (theme No. 124012400285-7).

References

Banks, N. (1906) On the perlid genus *Chloroperla*. *Entomological News*, 17, 174–175.

Chen, Z.-T., Du, S.-K. & Li, X.-T. (2021) Description of a remarkable new species of *Isoperla* (Plecoptera: Perlodidae), with supplements for *Isoperla kozlovi* Zhiltzova, 1972 from China. *Zootaxa*, 5027 (2), 160–174. https://doi.org/10.11646/zootaxa.5027.2.2

Chen, Z.-T., Song, L.-D. & Feng, W.-T. (2019) A new species of *Isoperla* (Plecoptera: Perlodidae) from the Qinling Mountains of northwestern China and notes on the Chinese species of the genus. *Zootaxa*, 4651 (2), 379–391. https://doi.org/10.11646/zootaxa.4651.2.11

Devyatkov, V.I. (2022) Materials to the stonefly fauna (Plecoptera) of East Kazakhstan. *Caucasian Entomological Bulletin*, 18 (2), 243–251. https://doi.org/10.23885/181433262022182-243251

DeWalt, R.E., Hopkins, H., Neu-Becker, U. & Stueber, G. (2025) Plecoptera Species File. Available from: https://plecoptera.speciesfile.org (accessed 03 March 2025)

Huo, Q.-B. & Du, Y.-Z. (2020) A new remarkable Isoperla species with abdominal processes from Hubei Province of Central China (Plecoptera: Perlodidae). *Zootaxa*, 4801 (3), 552–558. https://doi.org/10.11646/zootaxa.4801.3.7

Huo, Q.-B., Chen, Z.-N., Kong, X.-B. & Du, Y.-Z. (2020) New records and a confirmation of three perlodid species in China, with additional notes and images of *Rauserodes epiproctalis* (Zwick, 1997) (Plecoptera: Perlodidae). *Zootaxa*, 4808 (3), 455–474. https://doi.org/10.11646/zootaxa.4808.3.3

Huo, Q.-B., Rehman, A., Zhao, M.-Y., Yang, Y.-B., Xiang, Y.-N., Du, Y.-Z., Wang, J.-F., Murányi, D. & Teslenko, V.A. (2022) Additions to the fauna and biology of stoneflies (Plecoptera) in Taizi River Basin, Liaoning, with seven new species records to China. *Biodiversity Data Journal*, 10 (e95120), 13. https://doi.org/10.3897/BDJ.10.e95120

Hwang, J.M. & Muranyi, D. (2020) Checklist of the Korean Stoneflies (Plecoptera) with six newly recorded species. *Animal Systematics, Evolution and Diversity*, 36 (1), 46–54. https://doi.org/10.5635/ASED.2020.36.1.051

Kawai, T. (1963) A new species of the genus *Isoperla* (Plecoptera) from Echigo, Japan. *Kontyû, Tokyo Entomological Society*,

31, 61–63.
Kim, J.S., Bae, Y.J. & Zhiltzova, L.A. (1998) Bibliographic review, systematic status, and biogeographic notes on Korean and Far East Russian stoneflies (Insecta: Plecoptera) with their new Korean records. *Korean Journal of Biological Sciences*, 2 (4), 419–425.
https://doi.org/10.1080/12265071.1998.9647440
Klapálek, F. (1923) Plécoptères nouveaux. *Annales de la Société Entomologique de Belgique*, 63, 21–29.
Navás, R.P.L. (1923) Algunos insectos del Museo de París. Plecópteros. *Revista de la Academia de Ciencas Exactas, Fisicas, Quimica y Naturales de Zaragoza*, 7, 15–51.
Nelson, C.H. (1976) A new species of *Isoperla* (Plecoptera: Perlodidae) from Tennessee. *Journal of the Kansas Entomological Society*, 49, 212–214.
Maruyama, H. & Hanada, S. (2016) *A Field Guide to Japanese Aquatic Insects: Adults of Mayflies, Stoneflies, and Caddisflies*. Zenkoku Noson Kyoiku Kyokai Co., Ltd., Tokyo, 488 pp. [原色川虫図鑑 成虫編 カゲロウ.カワゲラ.トビケラ.全国農村教育協会, 東京, http://www.zennokyo.co.jp/book/musi/kw_a.html]
Potikha, E.V. & Zhiltzova, L.A. (1986) New data on the stonefly fauna (Plecoptera) of Sikhote-Alin Biosphere State Reserve. *In*: *Donnye organizmy presnykh vod Dalnego Vostoka.* Academiya Nauk SSSR, Vladivostok, pp. 48–57. [in Russian]
Raušer, J. (1968) 67. Plecoptera. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. *Entomologische Abhandlungen: Staatliches Museum für Tierkunde in Dresden*, 34 (5), 329–398, 3 tabs., 135 figs.
Šámal, J. (1939) Contribution à l'étude de la faune des Plecopteres d'Altai. *Vestnik Zoologii*, 6–7, 419–426. [in Czech and French]
Szczytko, S.W. & Kondratieff, B.C. (2015) A review of the eastern Nearctic Isoperlinae (Plecoptera: Perlodidae) with the description of twenty-two new species. *Illiesia*, 1, 1–289. Available from: http://illiesia.speciesfile.org/papers/Monographiae-of-Illiesia.pdf (accessed 14 April 2025)
Teslenko, V.A. (2008) Poorly known stonefly species, *Isoperla pseudornata* and *Kaszabia nigricauda* (Plecoptera, Perlodidae), from the Eastern Palaearctic. *Zoologocheskiy Zhurnal*, 87 (8), 1–5 [in Russian]
https://doi.org/10.1134/S0013873808050114
Teslenko, V.A. & Khamenkova, E.V. (2017) A new species of *Isoperla* Banks (Plecoptera: Perlodidae) from the northeast of the Russian Far East. *Zootaxa*, 4300 (2), 238–244.
https://doi.org/10.11646/zootaxa.4300.2.5
Wang, Y., Cao, J.J., Murányi, D. & Li, W.H. (2018) Comparison of two complete mitochondrial genomes from Perlodidae (Plecoptera: Perloidea) and the family-level phylogenetic implications of Perloidea. *Gene*, 675, 254–264.
https://doi.org/10.1016/j.gene.2018.06.093
Zapekina-Dulkeit, J.I. (1975) To the fauna of stoneflies (Plecoptera, Insecta) of rivers of the Lake Baikal basin. *Trudy Gosudarstvennogo Zapovednika "Stolby,"* 10, 199–217. [in Russian]
Zetterstedt, J.W. (1840) Family 5. Perlariae Latr. *In*: *Insecta Lapponica descripta*. Voss, Leipzig, pp. 1055–1060.
https://doi.org/10.5962/bhl.title.8242
Zhiltzova, L.A. (1972) On the fauna of stoneflies (Plecoptera) of the Mongolian People's Republic. *Nacekomye Mongolii*, 1, 113–150. [in Russian]
Zhiltzova, L.A. (1977) New species of stoneflies (Plecoptera) from Primorye Territory. *Trudy Zoologicheskogo Instituta Academii Nauk SSSR. Leningrad*, 70, 3–9. [in Russian]
Zhiltzova, L.A. (1988) New species of stoneflies (Plecoptera) of the family Perlodidae from the Soviet Far East. *In*: *Fauna, systematica, i biologiya presnovodnykh bespozvonochnykh*. Academiya Nauk SSSR, Vladivostok, pp. 7–11. [in Russian]
Zhu, J.Y., Zhang, J.H. & Wang, W. (2007) Two new record family of Plecoptera (Plecoptera: Chloroperlidae, Perlodidae) in Xinjiang. *Journal of Shihezi University (Natural Science)*, 25, 273–275.
Zwick, P. (1973) Insecta: Plecoptera Phylogenetisches System und Katalog. *Das Tierreich – Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen*, 94, 1–465.
Zwick, P. & Surenkhorloo, P. (2005) The Mongolian species of Isoperlinae (Plecoptera: Perlodidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 51 (3), 253–276.