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Descriptions of new species of *Issikiomartyria* (Lepidoptera, Micropterigidae) and a new genus *Melinopteryx* gen. n. with two new species from Japan

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Abstract

Micropterigidae is considered to be the sister group of all other extant Lepidoptera. In Japan, 17 species of five genera have been recorded including three endemic genera, *Issikiomartyria* Hashimoto, 2006, *Kurokopteryx* Hashimoto, 2006 and *Neomicropteryx* Issiki, 1931, all of which are associated with the liverwort genus *Conocephalum* Hill. We discovered four new species of *Issikiomartyria* from snowy regions in Northeastern Japan, and two new species of a new genus *Melinopteryx* **gen. n.** from the subalpine zone of the Akaishi Mountain Range. All these new taxa, *I. hyperborea* **sp. n.**, *I. leptobelos* **sp. n.**, *I. catapasta* **sp. n.**, *I. trochos* **sp. n.**, *M. coruscans* **sp. n.** and *M. bilobata* **sp. n.** are also associated with *Conocephalum* liverworts. Furthermore, females of *I. akemiae* Hashimoto, 2006 and *I. plicata* Hashimoto, 2006 are described here for the first time. Our extensive surveys revealed that the fine-scale endemism of *Issikiomartyria* restricted to the fragmented area facing the Japan Sea. Keys to *Issikiomartyria* species based on the adult morphology are provided.

Introduction

Micropterigidae represents one of the branches in the first splitting event among extant Lepidoptera (Kristensen 1999, Kristensen et al. 2007). The fossil record of Micropterigidae extends to the Early Cretaceous (Whalley 1978) and likely originated during or before the Late Triassic (Zhang et al. 2013, van Eldijk et al. 2018). The Micropterigidae is a non-glossatan moth family, which along with Agathiphagidae and Heterobathmiidae are devoid of a coilable proboscis and instead retain functional mandibles which in micropterigids only are functional in the adult (Kristensen 1984, 1999, Kristensen et al. 2015, Regier et al. 2015). The Micropterigids are species-rich, comprising about 160 described species in 21 genera from all biogeographic regions (Gibbs 2010, van Nieukerken et al. 2011), including four fossil genera (Whalley 1978, Kozlov 1988, Skalski 1995, Engel and Kinzelbach 2008), and more than 100 species have been found which are still undescribed (van Nieukerken et al. 2011). The geographic ranges of the micropterigids are patchy, with a concentration of endemic genera in the Australian ecozone and the Japanese Archipelago, where four and three genera are known respectively (Gibbs 2010, 2014, Hashimoto 2006). The global diversity and high endemism of the micropterigids provide us with a wealth of opportunities for understanding of the biogeographic patterns and processes suggested by primitive moths (Gibbs 1983, 2006, Gibbs and Lees 2014) whose evolution and ecological associations largely predates the diversification of angiosperms (Imada et al. 2011).

Micropterigidae in Japan comprise 17 described species in five genera: namely, *Micropterix* Hübner, 1825, *Paramartyria* Issiki, 1931, *Neomicropteryx* Issiki, 1931, *Kurokopteryx* Hashimoto, 2006, and *Issikiomartyria* Hashimoto, 2006. *Micropterix* is a genus distributed

over the Palearctic ecozone as far as the Himalayan foothills (Lees et al. 2010); in Japan, *M. aureatella* (Scopoli, 1763) patchily inhabits Hokkaido and subalpine zones of Honshu (Issiki 1953; Hashimoto 2006, Imada et al. 2011). Among East Asian *Paramartyria,* two species are known only from Japan (Issiki 1931): *P. immaculatella* Issiki, 1931 and *P. semifasciella* Issiki, 1931. Three genera, *Neomicropteryx*, *Kurokopteryx*, and *Issikiomartyria*, are endemic to Japan and the species ranges are often restricted in small geographic areas in a strongly allopatric fashion (Hashimoto 2006, Imada et al. 2011).

All species of Japanese endemic genera, comprising at least 14 species, feed exclusively on *Conocephalum* Hill. liverworts and also seem to occupy similar ecological niches (Hashimoto 2006, Imada et al. 2011). Remarkably, the liverwort-feeding micropterigids in Japan have experienced diversification without changing host-plants, during or after the Miocene (Imada et al. 2011), which represent one of the largest radiations known to have taken place on a single host-plant genus. These *Conocephalum*-feeders are widely distributed across the major islands of Japan (i.e. Honshu, Shikoku, Kyushu) yet the species do not co-occur with one another (Imada et al. 2011).

Our thorough field surveys for molecular phylogenetic analysis have revealed that the micropterigid fauna in the Northeastern Japan is unexpectedly diverse. We reveal a new genus that inhabits an elevational zone of ca. 1500–1800 m in the Akaishi Mountain Range, which is sister to *Issikiomartyria* in the molecular phylogenetic analysis of Imada et al. (2011). In addition, we newly discovered that four new species of *Issikiomartyria* were distributed across the area ranging from the northern end of Honshu to the northern part of Yamagata Prefecture, which has not sufficiently been investigated. *Issikiomartyria* is a genus consisting of five species, and each species tends to be found from geographically fragmented areas facing the Japan Sea (Issiki 1953; Hashimoto 2006). Furthermore, we describe females of *I. akemiae* Hashimoto, 2006 and *I. plicata* Hashimoto, 2006, for the first time.

In this study, males and females of four *Issikiomartyria* species new to science and females of two known species are described. Also, a new genus is established based on two species new to science. An updated account of the distribution of micropterigids in the northeastern Japan based on the detailed additional sampling records is provided.

Methods

Adults and larvae of micropterigid moths were collected from temperate forests in Japan, and larvae were reared in plastic cases with their host-plants. A total of 226 adult pinned specimens were used for this study. For genital dissections, the whole abdomen was removed and macerated for 30 min in 10 % KOH. Residual scales and tissues were then washed in distilled water to remove KOH, immersed in 50 % ethanol and dehydrated in an ethanol series. Genitalia were then stained with 5 % chlorazol black E for 10 min, and dehydrated in a series of 70−100 % ethanol. After washing, specimens were mounted and stored in 70 % glycerol. For some specimens, to examine the wing veins, wings were removed and scales were removed by brushing in 70 % EtOH. Observation and measurements were made under an Olympus BX53F microscope at 10–40× with the aid of a micrometer scale.

All the specimens examined in this study are deposited in the following collections: National Museum of Nature and Science (NMNS), Graduate School of Human and Environmental Studies, Kyoto University (KUHE).

Terminology follows Gibbs and Kristensen (2011) and Davis and Landry (2012). Author's names are abbreviated: YI and MK stand for Yume Imada and Makoto Kato, respectively.

Taxonomy

Melinopteryx gen. n.

http://zoobank.org/54C3DAD7-B3D6-4EA7-8706-6DAFBCD57E63
Figs 1a, b, 2–7

Type species. *Melinopteryx coruscans* sp. n. by present designation.

Diagnosis. Aedeagus with three pairs of dorsal fins, a pair of lateral triangular fins, and a ventral longitudinal fin. Genital chamber with a large genital sclerite with four paddle-shaped accessory sclerites at posterior end.

Description. The generic description is based on *M. coruscans* sp. n. and *M. bilobata* sp. n.

Head capsule densely covered by microtrichia; genal area glossy and naked; most of clypeus, frons, and vertex covered with brownish yellow piliform scales. Ocelli present. Antenna moniliform, approximately as long as forewing in male, longer than in female; densely covered with fuscous piliform scales on scape and pedicel; scape the largest segment, three times longer than most basal flagellum; pedicel small, as long as most basal flagellum. SOI (Kristensen and Nielsen 1979) about 0.4. MIOI (Hirowatari 1997) about 0.5. Interocellar sulcus complete. Postinterocellar sulcus distinct. Epicranial sulcus almost absent. Temporal sulcus as a darker line. Occipital sulcus interrupted at ventro- and dorso-lateral corner. Occipus fan-shaped. Labrum approximately pentagonal, length more or less twice that of clypeus. Mandible elongate rectangular, distal edge truncated. Proximal prelabium sclerite weakly sclerotized. Labial palp 2-segmented. Maxillary palp 5-segmented.

Foretibial epiphysis absent. Antero-lateral processes of pronotum present, weakly sclerotized.

Wing venation as shown in Fig. 3A, B. Fore- and hindwings obtuse at apex, forewing with brown to purple luster, cilia shining grayish brown. Forewing with Sc forked, R1 unforked; R3 stalked with R4+5. Hindwing with a

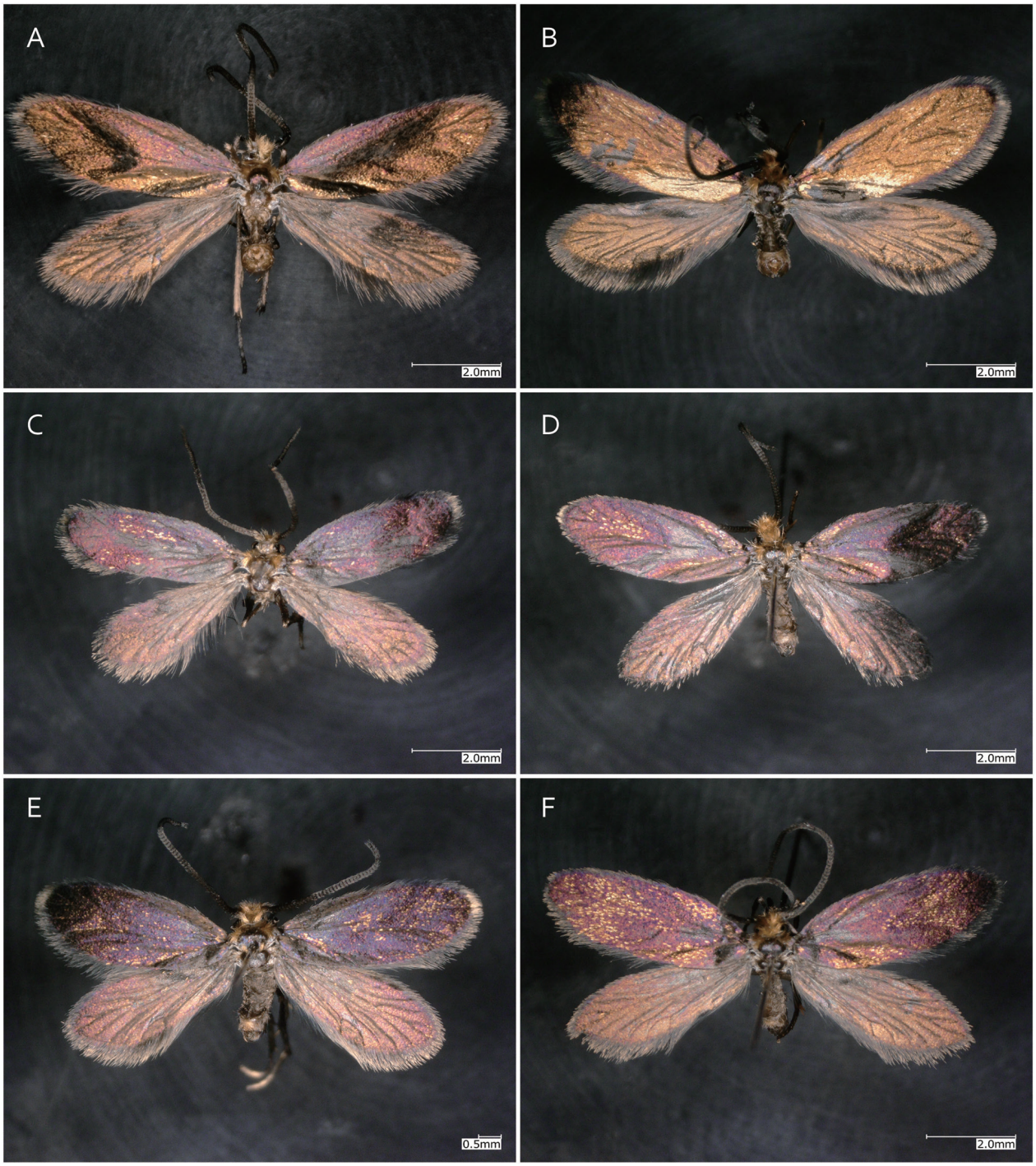

Figure 1. Habitus of adult males of *Melinopteryx* and *Issikiomartyria*. **A:** *Melinopteryx coruscans* sp. n. [holotype; MC 0204]; **B:** *M. bilobata* sp. n. [holotype: MC 0221]; **C:** *Issikiomartyria hyperborea* sp. n. [holotype: MC0252]; **D:** *I. leptobelos* sp. n. [MC 0250]; **E:** *I. catapasta* sp. n. [MC 0241]; **F:** *I. trochos* sp. n. [MC 0231]

main stem of R absent; most anterior vein of hindwing forked near terminal end (Sc1 and Sc2+R1). Abdomen grayish brown, covered with piliform and lamellar scales, scattered with dark orange piliform scales on venter and genital segments in male. Sternum V gland present; orifice of gland a narrow slit.

Male abdomen and genitalia. Sternum VIII membranous. Segment IX a complete ring, well sclerotized, with a posterior expansion dorsally. Valva triangular, broadly membranous at proximo-dorsal surface, with a proximo-ventral ridge; anterior portion fused with median plate; median plate large, roughly fan-shaped. Phallobase strongly curved, without ventral longitudinal ridge. Aedeagus stout at caudal end, with three pairs of fins dorso-medially; a pair of lateral triangular fins extending horizontally; a pair of ventral fin extending vertically; dorsal apex of aedeagus acute and ventral one slightly forked, longer than dorsal one; gonopore opening horizontally; vesica with

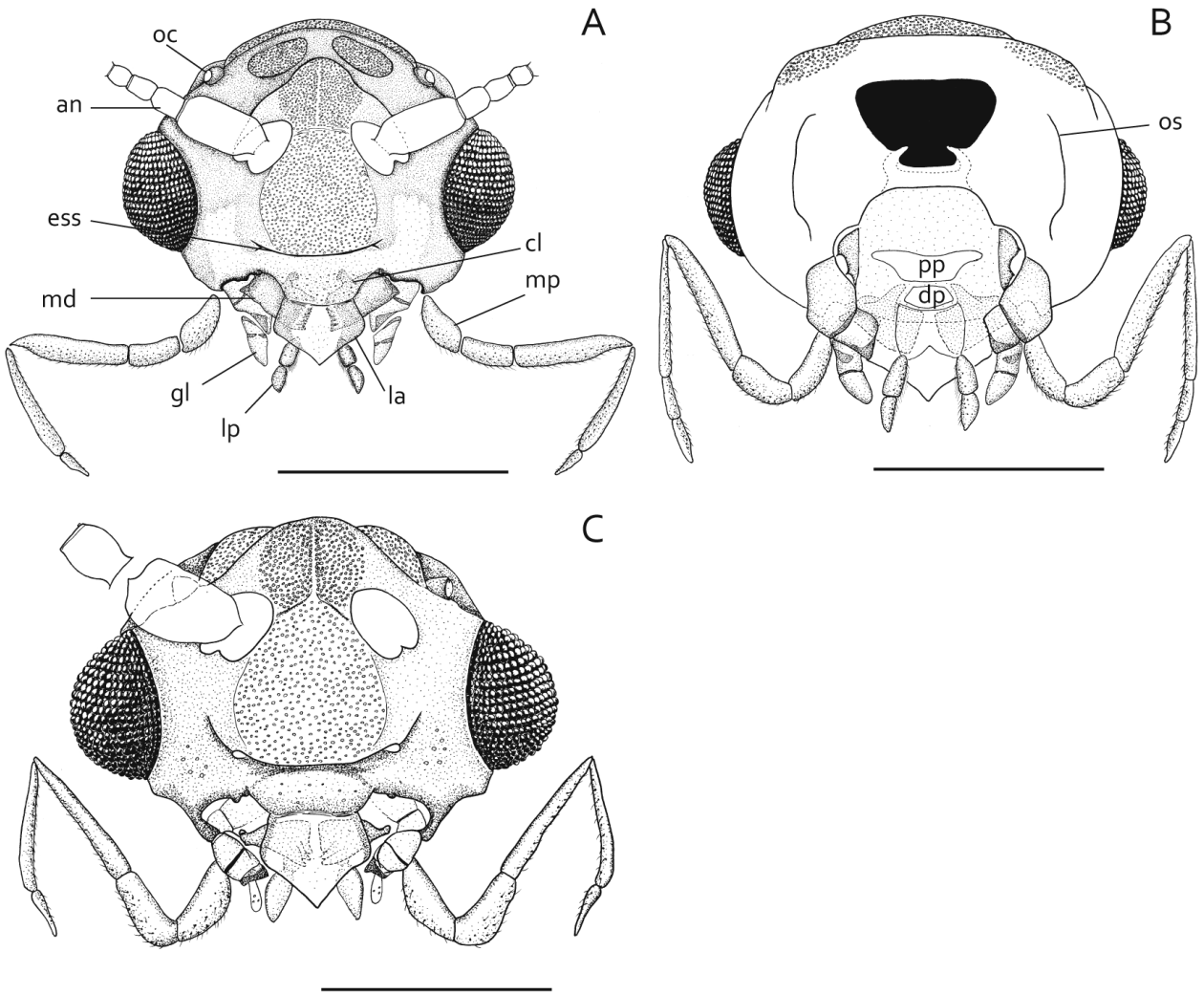

Figure 2. Adult heads of *Melinopteryx* and *Issikiomartyria*. **A:** *Melinopteryx bilobata* sp. n., frontal view; **B:** ditto, posterior view; **C:** *Issikiomartyria hyperborea* sp. n., frontal view. Abbreviations: **an** = antenna; **cl** = clypeus; **dp** = distal prelabium; **ess** = epistomal sulcus; **gl** = galea; **la** = labium; **lp** = labial palp; **md** = mandible; **mp** = mandibular palp; **oc** = ocellus; **os** = occipital sulcus; **pp** = proximal prelabium. Scale bars: 0.5 mm.

serrate minute projections. Tergum X broader than long, with a pair of long ventral plates (venter X plates) extending antero-ventrally at base of terminal processes.

Female abdomen and genitalia. Segment IX forming a complete ring, strongly sclerotized, with a dorso-lateral concavity, without lateral protrusion. Segment X composed by lateral sclerites and one or two dorsal sclerotized plates; lateral sclerites simple, broader than long, having digitate projections with an apical seta at terminal inner margin. Corpus bursae large, globular, membranous, with signa composed of three or four sclerites near caudal end. Genital chamber with a large sclerite (genital sclerite) and a few tiny sclerites; genital sclerite deeply furcated posteriorly into four paddle-shaped accessory sclerites.

Remarks. The genetic distance between *Melinopteryx coruscans* sp. n. (labelled as '*Issikiomartyria*' sp. in Imada et al. 2011) and its sister clade *Issikiomartyria* spp. (6.3 ± 0.9%, based on the Kimura 2-parameter model) was almost as large as the intergeneric COI divergence among other Japanese micropterigid genera (for example, 7.8 ± 0.1% between *Neomicropteryx* and *Kurokopteryx*), indicated by Imada et al. (2011). *Melinopteryx* has a 2-segmented labial palp, while 1-segmented in *Issikiomartyria*, except for *I. bisegmentata* Hashimoto, 2006 which is 2-segmented. *Melinopteryx* is characteristic in its aedeagus with three pairs of dorsal fins, a pair of lateral triangular fins, a ventral longitudinal fin or protrusion extending vertically in the male. In female, a large sclerite with more than four accessory sclerites in genital chamber is also unique in *Melinopteryx*. Fore- and hindwing without a radial cell and large bulbous corpus bursae in female are shared with *Issikiomartyria*.

Etymology. The genus name is a compound noun derived from the Greek words transliterated into Latin, "melinos" (honey-color) and "pteryx" (wing), referring to the adult wing color of the species of this genus. The gender is feminine.

***Melinopteryx coruscans* sp. n.**

http://zoobank.org/EB7BCFF1-B58E-4896-ADF1-C1674D21016A
Figs 1a, 3, 4, 5
Japanese name: to-o-yama-takane-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂collected by MK on 29.VII.2007 at Shirabiso-touge (1800m), Iida-shi, Nagano Pref (Fig. 19:1), NMNS.

Paratypes: JAPAN [HONSHU] 13♂1♀ collected by MK on 29.VII.2007 at same locality as holotype, KUHE.

Additional materials: JAPAN [HONSHU] 1♀ emerged on 9.VI.2014 from a larva collected by YI on 27.IV.2014 at same locality as holotype, KUHE; 1♂1♀ collected by MK on 13.VII.2009 at Irisawai (1115m), Ohshika-mura, Nagano Pref (Fig. 19:2), KUHE.

Type locality. Japan, Nagano Pref: Shirabiso-touge (Honshu).

Diagnosis. Aedeagus with a pair of ventral longitudinal fins, extending more than half of aedeagal length; female corpus bursae with two forms of signa consisting of two semicircular sclerite and a long rectangular sclerite.

Description. Head dark brown, naked and glossy on both sides, sparsely covered with brownish yellow piliform scales with dark yellow scales on vertex. Antenna about same length of forewing in male, about 4/5 in female; with 67 (60–74) flagellomeres in males (n=7). Labial palp 2-segmented. Thorax grayish brown, sparsely covered with purple and brownish gold scales on prothorax with blue metallic scales, with dark yellow piliform scales on tegula. Forewing with brownish purple luster tinged with coppery, densely covered with golden luster over basal half of dorsum; cilia grayish brown, pale yellow on apex; ventral surface glossy grayish purple. Forewing length 5.1 mm (4.8–6.0, n=8) and 5.1 mm (n=1) in male and female, respectively. Hindwing glossy brownish purple scattered with piliform scales on basal half; cilia grayish brown; ventral surface same as forewing. Abdomen sparsely covered with grayish brown piliform scales.

Male abdomen and genitalia (Fig. 4). Mid-dorsal length of segment IX ring about 1/6 of ventral length. Valva with obtuse apex, with a very small proximo-ventral ridge; inner ventral margin broad without concavity. Aedeagus with a ventral longitudinal fin extending vertically more than half of aedeagal length; three pairs of dorsal fins present; a pair of lateral triangular fins extending horizontally. Tergum X with longitudinal convex at medial part, with a pair of triangular lobes disto-dorsally.

Female abdomen and genitalia (Fig. 5). Segment IX ring strongly sclerotized, deeply concave dorso-laterally; mid-dorsal length about 1/3–1/2 of mid-ventral length, without lateral protrusion. Dorsal plate between segment X sclerites large, well sclerotized. Corpus bursae membranous, bulbous; signa consisting of two semicircular sclerites and a ribbon-shaped sclerite. Genital chamber armed with a large sclerite with four bar-shaped accessory sclerites.

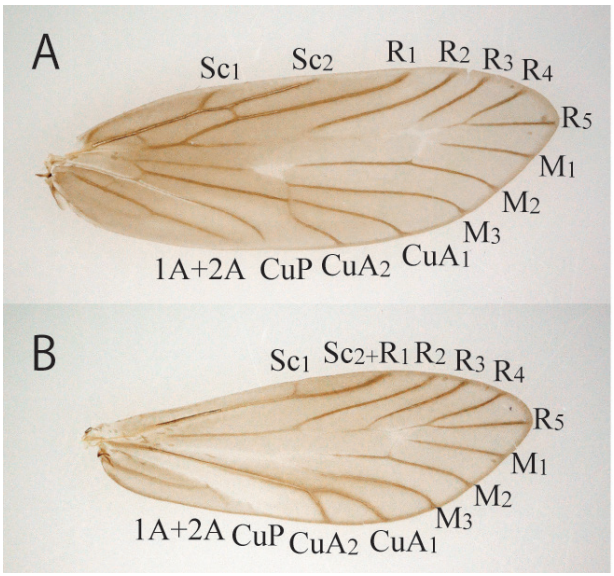

Figure 3. Adult wings of *Melinopteryx coruscans* sp. n. **A:** right forewing; **B:** right hindwing.

Variations. Geographic variation is recognizable between individuals in the populations at Irisawai and Shirabiso-touge. In the populations of Irisawai, the proximal portion of the male tergum X is stouter and much more developed than that of Shirabiso-touge; wing color tinged with strongly purplish scales at Irisawai population, whereas wing color of the individuals at Shirabiso-touge tend to be more tinged with coppery and golden scales.

Remarks. *Melinopteryx coruscans* sp. n. is distinguished from *M. bilobata* sp. n. based on the following character states: aedeagus with a ventral longitudinal fin extending more than half of aedeagal length; female segment X with a rectangular plate of dorsal sclerites; corpus bursae with two different forms of signa consisting of a pair of semicircular sclerites and a ribbon-shaped sclerite. This species corresponds to " '*Issikiomartyria*' sp." in Imada et al. (2011).

Etymology. The specific name is a participle in the nominative singular from the Latin word "coruscans", which stands for flashing.

Distribution. The Western mountain range of the Akaishi Mountain Range of Japan (Honshu: Nagano Pref.).

Bionomics. There is a single generation per year; however, there may be one generation per two years in some populations at high elevation, where larvae exhibit two significantly different size during the same period of time. The habitat is the peak or valley of sub-alpine forests at approximately 1100–1820 m of the Akaishi Mountain

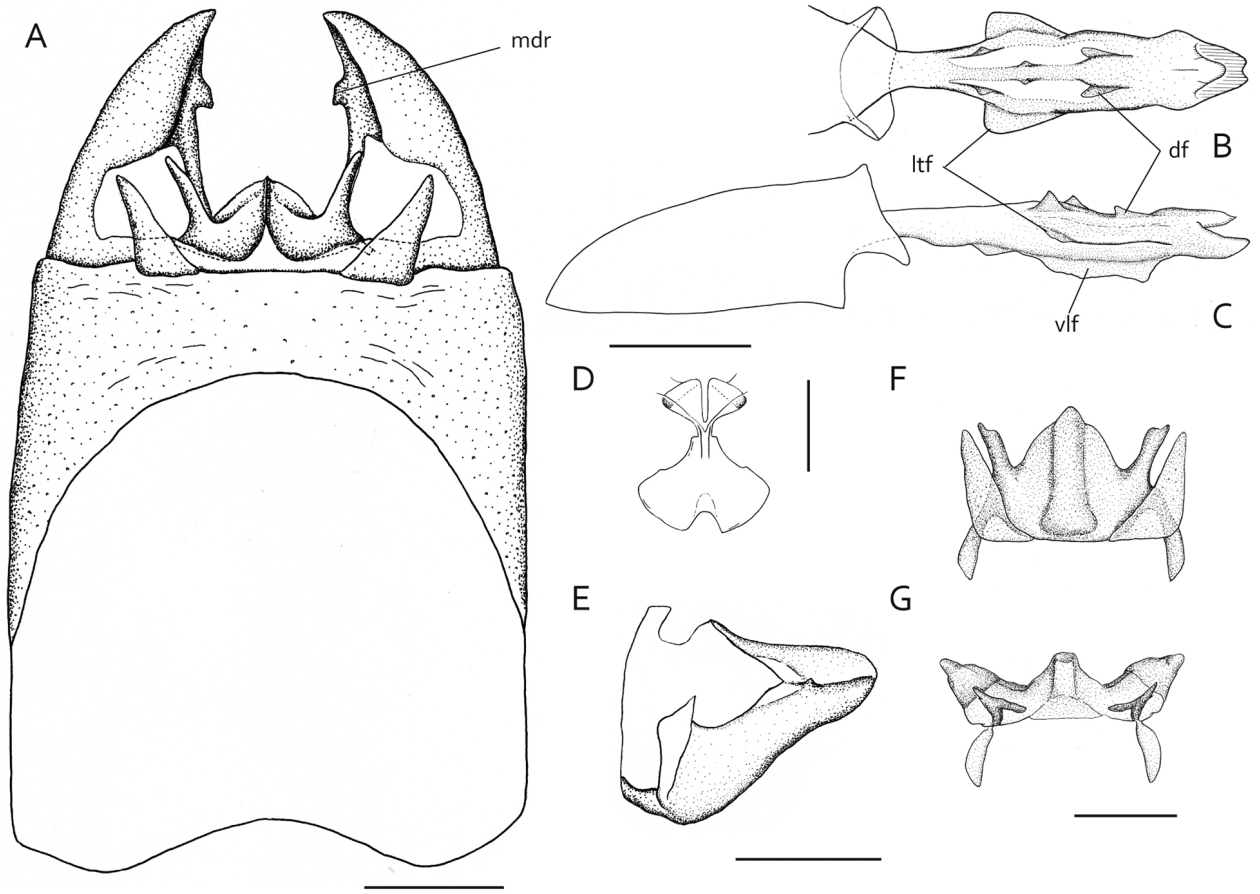

Figure 4. Male genitalia of *Melinopteryx coruscans* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** median plate; **E:** left valva, inner view; **F:** tergum X and venter X plate, dorsal view; **G:** ditto, oblique view; **H:** genital capsule, lateral view. Abbreviations: **df** =dorsal fin; **ltf** = lateral triangular fin; **mdr** = mid-dorsal ridge; **vlf** = ventral longitudinal fin. Scale bars: 0.2 mm.

Range of Japan. The dominant arboreal species of their habitat are *Tsuga diversifolia* (Maxim.) Mast., *Abies veitchii* Lindl., and *Picea jezoensis* (Sieb. & Zucc.) Carriére var. *hondoensis* (Mayr) Rehde (Pinaceae). The larvae feed on the thalli of *Conocephalum* liverworts.

Melinopteryx bilobata sp. n.

http://zoobank.org/17C1F904-9FD2-4A5A-82AB-8CE02B7C7E58
Figs 1b, 2a, b, 6, 7
Japanese name: ikawa-takane-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂ collected by YI on 3.VII.2016 at Ikawa-touge (1559m), Tatsuno-cho, Shizuoka Pref (Fig. 19: 3), NMNS.

Paratypes: JAPAN [HONSHU] 5♂1♀ collected by T. Kato on 10.VII.2016 at same locality as holotype, NMNS.

Additional materials: JAPAN [HONSHU] 1♂ emerged on 15.VI.2015 from larva collected by MK on 10.V.2015 at same locality as holotype, NMNS; 10♂ collected by YI on 3.VII.2016 at same locality, KUHE.

Type locality. Japan, Shizuoka Pref: Ushikubi-touge (Honshu).

Diagnosis. Aedeagus with a short ventral fin in male genitalia; female segment X with two reduced lobes of dorsal sclerite.

Description. Head dark brown, naked and glossy on both sides, sparsely covered with brownish yellow piliform scales with dark yellow scales on vertex. Antenna slightly longer than forewing in male; with 67 (64–73) flagellomeres in males (n=8). Labial palp 2-segmented. Thorax grayish brown, sparsely covered with purple and brownish gold scales on prothorax with blue metallic scales, with dark yellow piliform scales on tegula. Legs covered with glossy fuscous scales. Forewing with brownish purple luster tinged with coppery, densely covered with golden luster over basal half of dorsum; cilia grayish brown, pale yellow on apex; ventral surface glossy grayish purple. Forewing length 4.9 mm (4.6–5.0, n=10) in male. Hindwing glossy brownish purple scattered with piliform scales on basal half; cilia grayish brown; ventral surface same as forewing. Abdomen sparsely covered with grayish brown piliform scales.

Male abdomen and genitalia (Fig. 6). Mid-dorsal length of segment IX ring about 1/5 of ventral length.

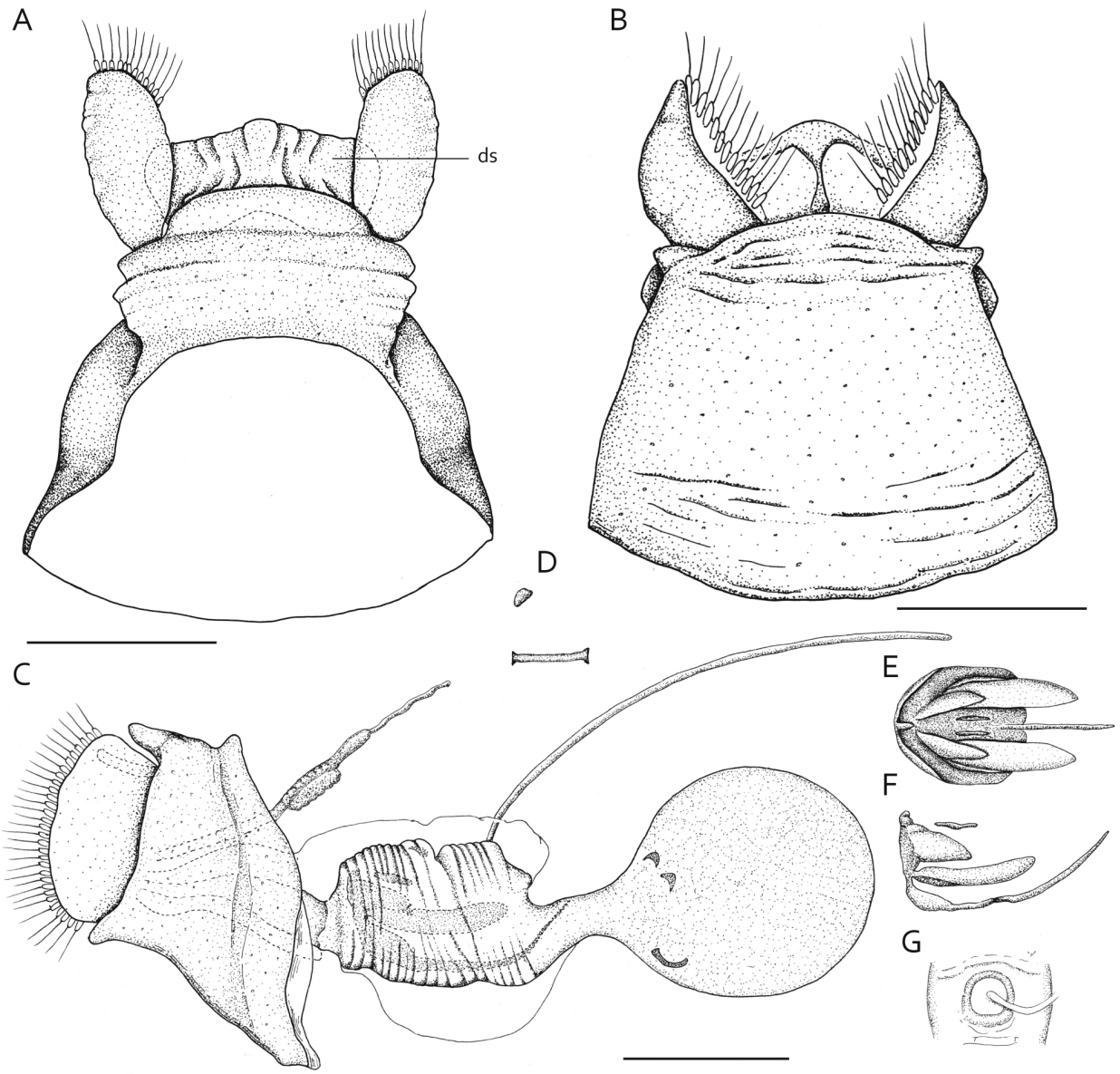

Figure 5. Female genitalia of *Melinopteryx coruscans* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** signa; **E:** genital sclerite, dorsal view; **F:** ditto, lateral view; **G:** arising part of ductus spermathecae, dorsal view. Abbreviation: **ds** = dorsal sclerite. Scale bars: 0.2 mm.

Valva with a small proximo-ventral ridge; inner ventral margin broad without concavity; apical end obtuse. Aedeagus with a ventral protrusion at base; with three pairs of short dorsal fins; with a pair of small, lateral triangular fins extending horizontally. Tergum X with squarish medial part, with a pair of spines disto-dorsally.

Female abdomen and genitalia (Fig. 7). Segment IX ring strongly sclerotized, shallowly concave dorso-laterally; mid-dorsal length about 1/2 of mid-ventral length, without lateral protrusion. Segment X consisting of a pair of lateral sclerites and two dorsal sclerotized plates; dorsal plates small, well sclerotized, being behind dorsal side of segment IX. Corpus bursae membranous, bulbous, possessing four semicircular signa. Genital chamber armed with a large sclerite with four plate-shaped accessory sclerites.

Remarks. *Melinopteryx bilobata* sp. n. is distinguished from *M. coruscans* sp. n. based on the following characteristics: aedeagus with a ventral protrusion at base; female segment X with a pair of small dorsal sclerites.

Etymology. The specific name is a compound adjective in the nominative singular from the Latin words, "bi-" (two) and "lobatus" (having diminutive lobes), referring to a pair of small dorsal sclerites of the female genitalia (Fig. 7).

Distribution. The Eastern mountain range of the Akaishi Mountain Range of Japan (Honshu: Shizuoka Pref.).

Bionomics. The larvae feed on the thalli of *Conocephalum conicum* (L.) Dum. The habitat is a forest path along the mountain ridge of sub-alpine or cool-temperate for-

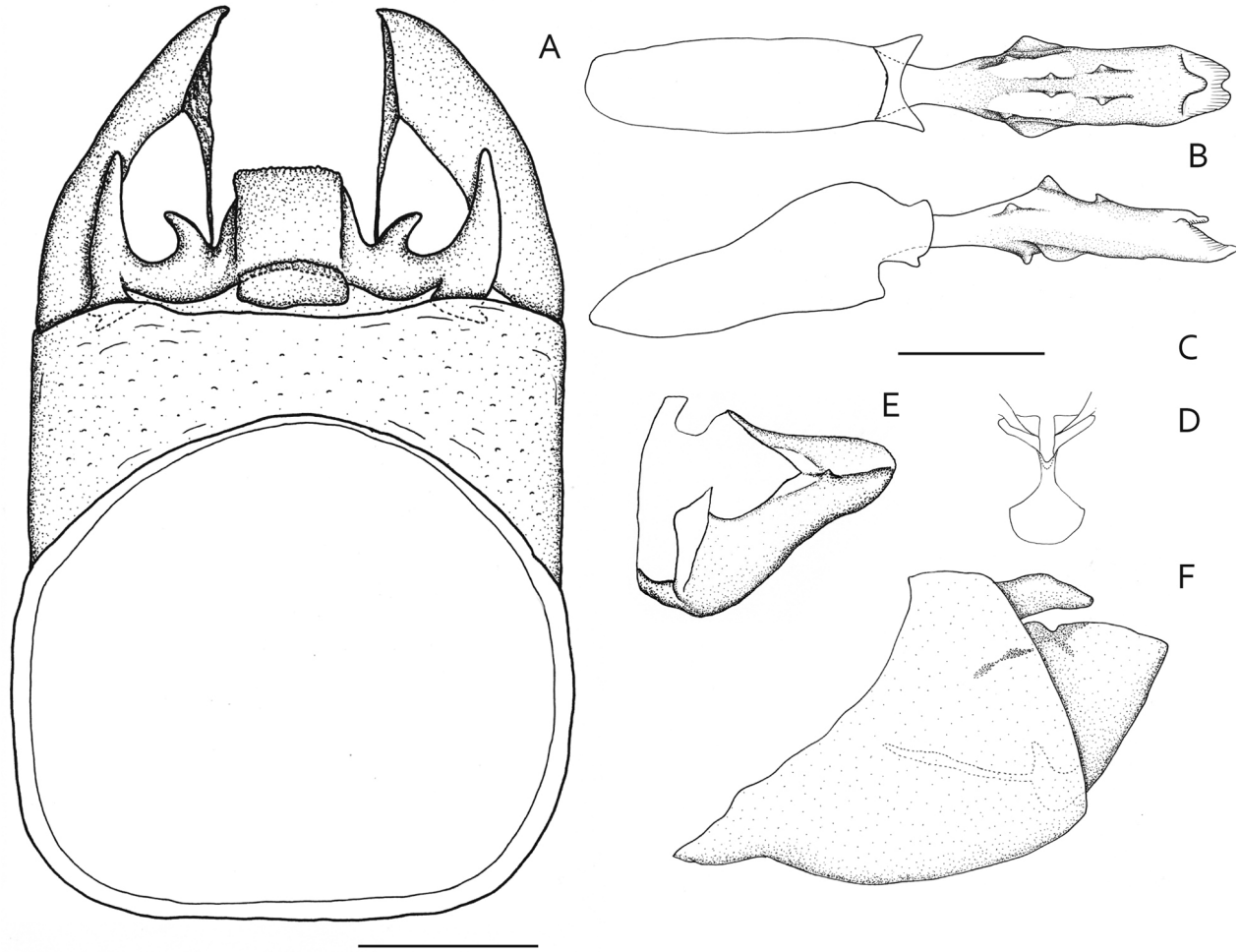

Figure 6. Male genitalia of *Melinopteryx bilobata* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** median plate; **E:** left valva, inner view; **F:** genitalia capsule, lateral view; **G:** ditto, ventral view. Scale bars: 0.2 mm.

ests at approximately 1500 m of the Akaishi Mountain Range of Japan, where *Fagus crenata* Blume (Fagaceae) and *Abies firma* (Sieb. & Zucc.) (Pinaceae) dominate.

Genus *Issikiomartyria* Hashimoto, 2006

Type species. *Neomicropteryx nudata* Issiki, 1953, fixed by original designation.

Diagnosis. Aedeagus with two pairs of dorsal fins.

Description. The generic description is based on *I. nudata* (Issiki, 1953), *I. akemiae*, *I. plicata*, *I. distincta* Hashimoto, 2006, *I. bisegmentata*, *I. hyperborea* sp. n., *I. leptobelos* sp. n., *I. catapasta* sp. n., *I. trochos* sp. n., and on the previous studies on this group (Issiki 1953, Hashimoto 2006).

Head capsule densely covered by microtrichia, apart from genal area where glossy and naked; most of clypeus, frons, and vertex covered with brownish yellow piliform scales. Ocelli present. Antenna moniliform, approximately as long as forewing in male, longer than in female; scape the largest segment, twice longer than most basal flagellum; pedicel bulbous, larger than most basal flagellum; basal one or two flagellomeres cylindrical. SOI about 0.4. MIOI about 0.5. Interocellar sulcus almost complete. Postinterocellar sulcus distinct. Epicranial sulcus distinct between occipital foramen and postinterocellar sulcus, being as a short distance anterior to interocellar sulcus. Temporal sulcus as a darker line. Occipital sulcus almost complete, but slightly indistinct on dorso-lateral corner. Occipus fan-shaped. Mandibular teeth greatly reduced. Labial palp 1- or 2-segmented. Maxillary palp 5-segmented. Proximal prelabium obscure. Foretibial epiphysis absent. Antero-lateral processes of pronotum present, strongly sclerotized. Fore- and hindwings obtuse at apex, forewing with brown to purple luster, without any distinct maculation. Forewing with R1 unforked; R3 stalked with R4+5. Hindwing with a main stem of R absent; most anterior vein of hindwing forked near terminal end (Sc1 and Sc2 + R1). Sternum V gland present; orifice of gland a narrow slit.

Male abdomen and genitalia. Sternum VIII membranous. Segment IX a complete ring, well sclerotized, with a posterior expansion dorsally; posterior margin gradually expanded from dorsum to venter. Valva triangular, broadly

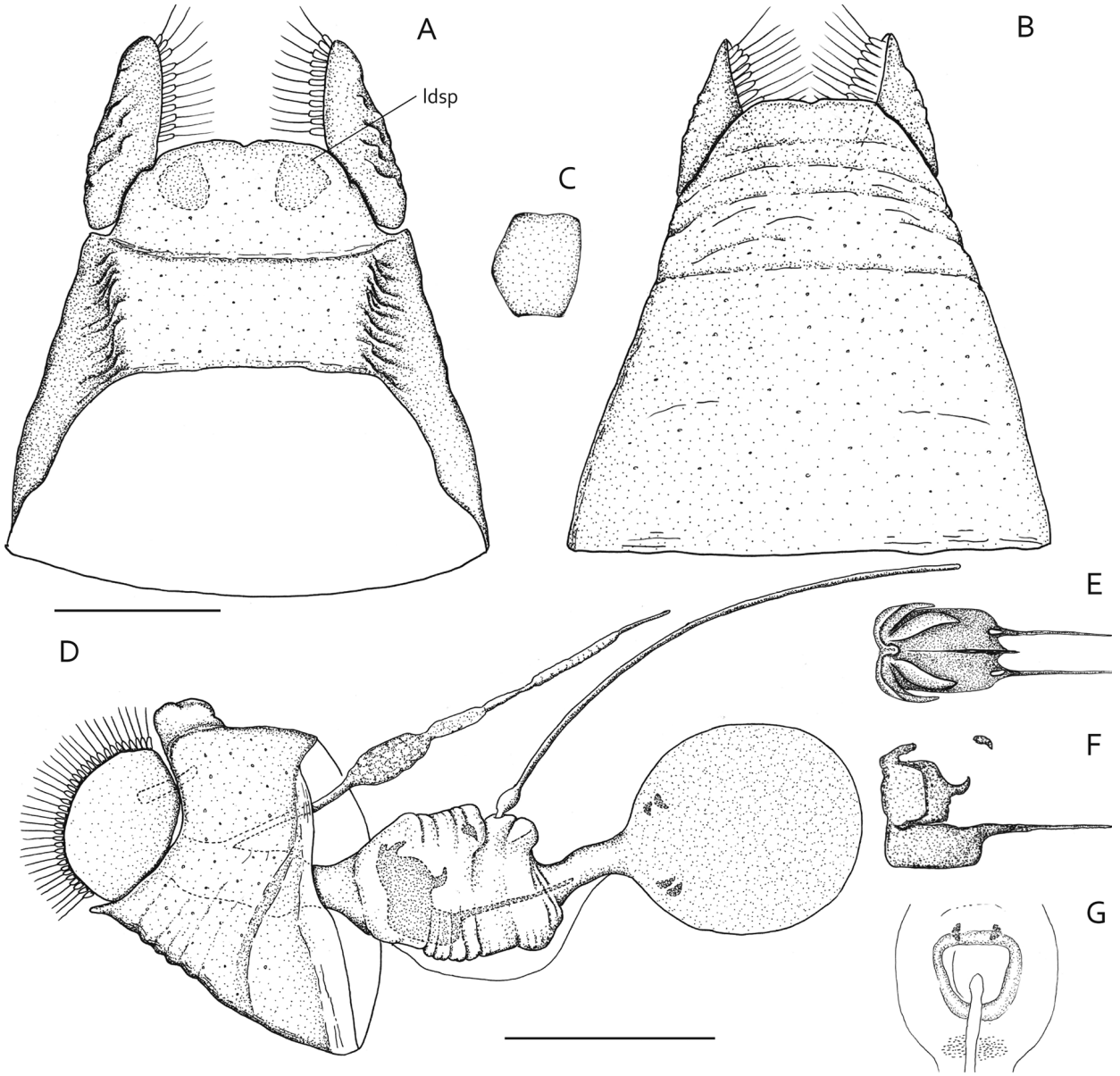

Figure 7. Female genitalia of *Melinopteryx bilobata* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** a lobe of dorsal sclerotized plate of Segment X, dorsal view; **D:** female genitalia, lateral view; **E:** genital sclerite, dorsal view; **F:** ditto, lateral view; **G:** arising part of ductus spermathecae, dorsal view. Scale bars: 0.2 mm. Abbreviation: **ldsp** = two lobes of dorsal sclerotized plate of segment X.

membranous at inner surface, with a proximo-ventral ridge whose anterior portion fused with median plate; median plate large, roughly fan-shaped. Phallobase strongly curved, with or without longitudinal ventral ridge(s) on midline. Aedeagus with acute apex, ventrally forked slightly at caudal end; with two pairs of basal fins dorso-medially and a pair of lateral triangular fins; gonopore opening horizontally; vesica with serrate minute projections. Tergum X, broader than long, with a pair of long ventral plates (venter X plates) extending antero-ventrally at base of terminal processes.

Female abdomen and genitalia. Segment IX forming a complete ring, strongly sclerotized; anterior margin gradually expanded anteriorly from dorsum to venter; mid-dorsal length generally shorter than 2/5 of mid-ventral length; laterally protruded in some species. Segment X consisting of a pair of lateral sclerites and a dorsal sclerotized plate; lateral sclerites simple, broader than long, with digitate projections having an apical seta at terminal inner margin. Corpus bursae large, globular, membraneous, with signa composed of four sclerites. Ductus spermathecae arising from a hexagonal or round concavity. Genital chamber with small sclerite(s).

Comparative Remarks. The following characters are regarded as synapomorphies of *Issikiomartyia*: aedeagus with two pairs of hornlike dorsal projections and without any protrusion vertically in male: sclerite in female genital chamber greatly reduced.

***Issikiomartyria hyperborea* sp. n.**

http://zoobank.org/823D926C-6B02-452A-A2CD-0F4B76A62337

Figs 1c, 8, 9

Japanese name: tsugaru-issiki-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂ emerged on 24.V.2012 from larva collected by T. Kato on 4.V.2012 at Tairadate (240m), Sotogahama-machi, Aomori Pref (Fig. 19:4), NMNS.

Paratype: JAPAN [HONSHU] 1♀ emerged on 24.V.2012 from larva collected by MK on 24.V.2012 at same locality, NMNS.

Additional materials: JAPAN [HONSHU] 1♀ emerged on 24.V.2014 from larva collected by YI on 10.V.2014 at same locality, KUHE.

Type locality. Japan, Aomori Pref: Tairadate (Honshu).

Diagnosis. Aedeagus with a pair of lateral triangular fins arising from ventral margin, extending horizontally. Female segment IX with a strong concavity extending from lateral to ventral sides.

Description. Head dark brown, naked and glossy on both sides, sparsely covered with yellow piliform scales with dark yellow scales on vertex. Antenna slightly longer than forewing in male; densely covered with fuscous piliform scales on scape and pedicel. Labial palp 1-segmented. Forewing length 3.8 mm (n=1) and 3.9 mm (n=1) in male and female.

Male abdomen and genitalia (Fig. 8). Mid-dorsal length of segment IX ring about 1/4 of ventral length. Valva sharply tapered apically, with a tiny proximo-ventral ridge whose anterior portion fused with median plate. Aedeagus with a pair of short distal fins and a pair of longer, proximal fins extending vertically, arising from dorsal side; a pair of lateral triangular fins ventrally-oriented, extending horizontally. Tergum X with a small medial part; shorter than half of valva; with a pair of spines disto-dorsally.

Female abdomen and genitalia (Fig. 9). Segment IX ring strongly sclerotized, concave both at lateral and ventral sides; mid-dorsal length about 2/5 of ventral length. Dorsal plate between segment X sclerites large, well sclerotized, enlarged dorso-caudally. Corpus bursae large, globular, membranous,

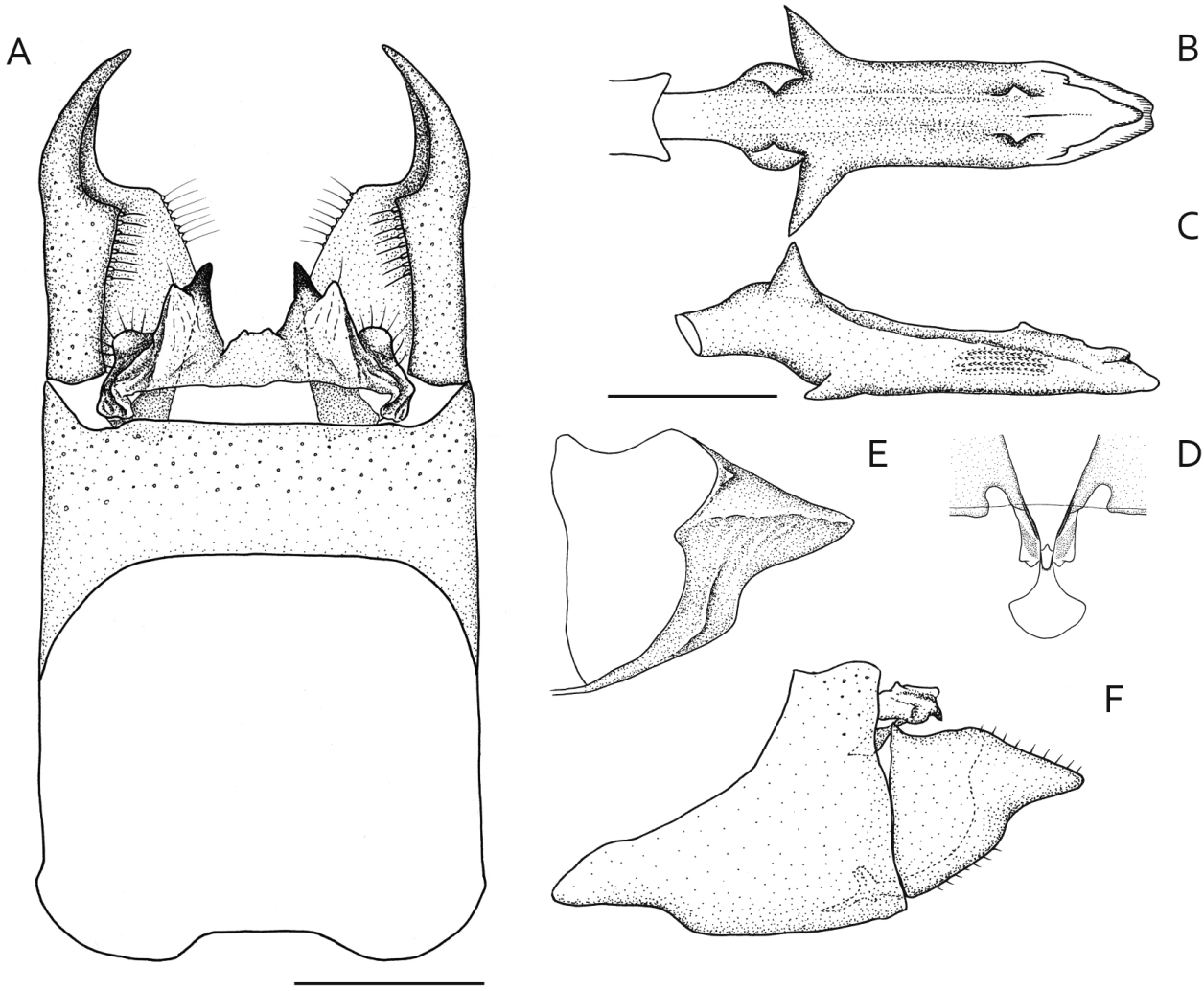

Figure 8. Male genitalia of *Issikiomartyria hyperborea* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** median plate; **E:** left valva, inner view; **F:** genital capsule, lateral view. Scale bars: 0.2 mm.

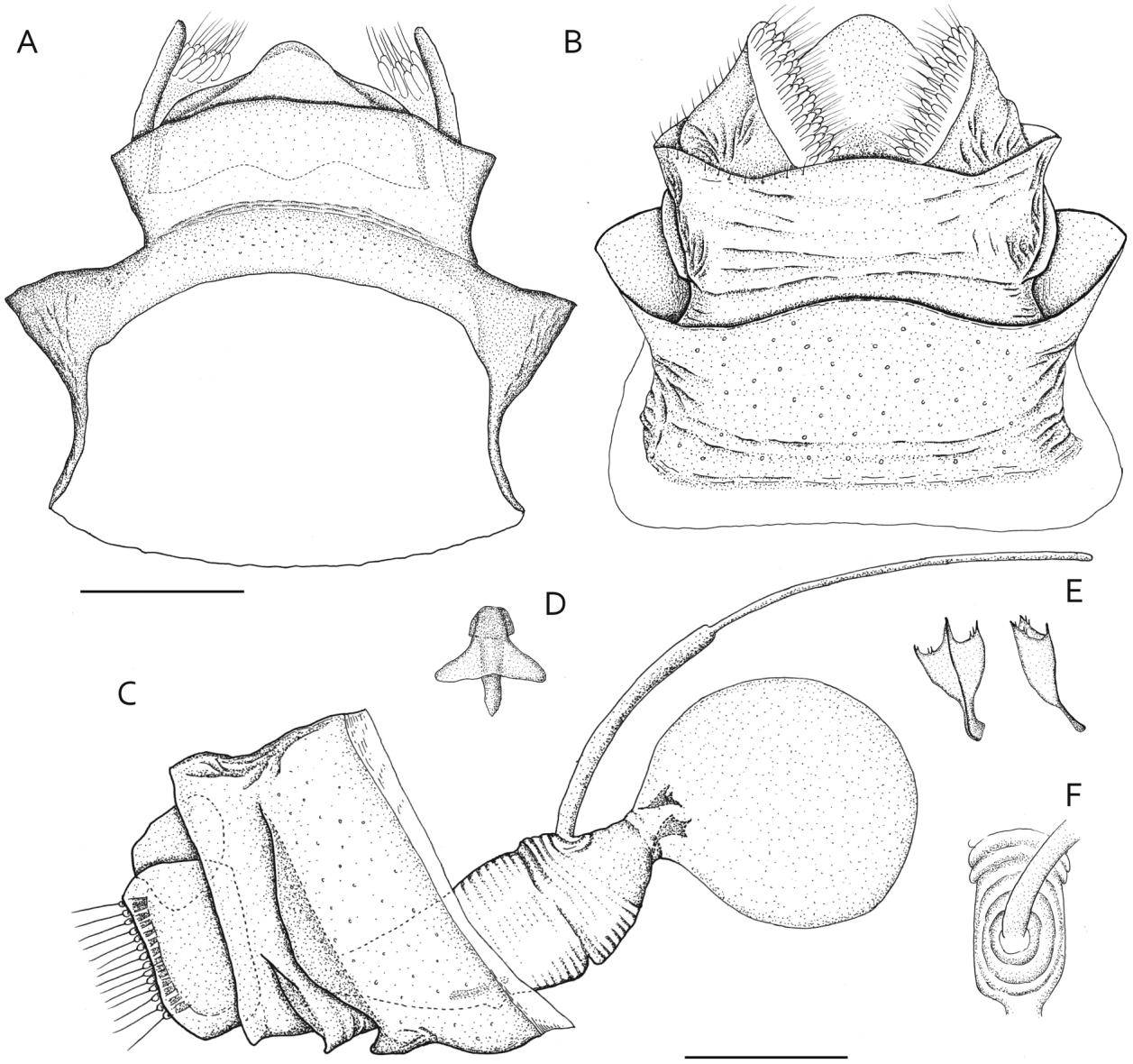

Figure 9. Female genitalia of *Issikiomartyria hyperborea* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** genital sclerite; **E:** signa; **F:** arising part of ductus spermathecae, dorsal view. Scale bars: 0.2 mm.

with signa composed of four tridenta-form sclerites near proximal end. Ductus spermathecae arising from a round concavity. Genital chamber with a small, triangular sclerite.

Remarks. *Issikiomartyria hyperborea* sp. n. is distinguishable from the known *Issikiomartyria* species by the following characters. In the male, aedeagus with a pair of latero-basal fins arising from ventral side. In the female, segment IX with a deep concavity extending from lateral to ventral sides; dorsal sclerite of segment X convex vertically in the middle.

Etymology. The specific name is an adjective in the nominative singular derived from the Greek word transliterated into Latin, "hyperboreus", indicating the mythical people of Greek mythology who lived "Beyond the North Wind".

Distribution. This species has only been found from Tsugaru peninsula of Japan (Fig. 14:1; Honshu: Aomori Pref).

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*. The locality is a forest path along a stream in the cool-temperate forests at approximately 250 m of Tsugaru peninsula, where *Fagus crenata* and *Quercus crispula* Blume (Fagaceae) dominate.

Issikiomartyria leptobelos sp. n.

http://zoobank.org/28714D8E-2B21-482F-B372-CFCF435FCFC4

Figs 1d, 10, 11

Japanese name: shirakami-issiki-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂ collected by YI on 15.VI.2015 at Hachimori (100 m), Happo-cho, Akita Pref (Fig. 19:5), NMNS.

Paratype: JAPAN [HONSHU] 9♂2♀ collected by YI on 15.VI.2015 at same locality, NMNS.

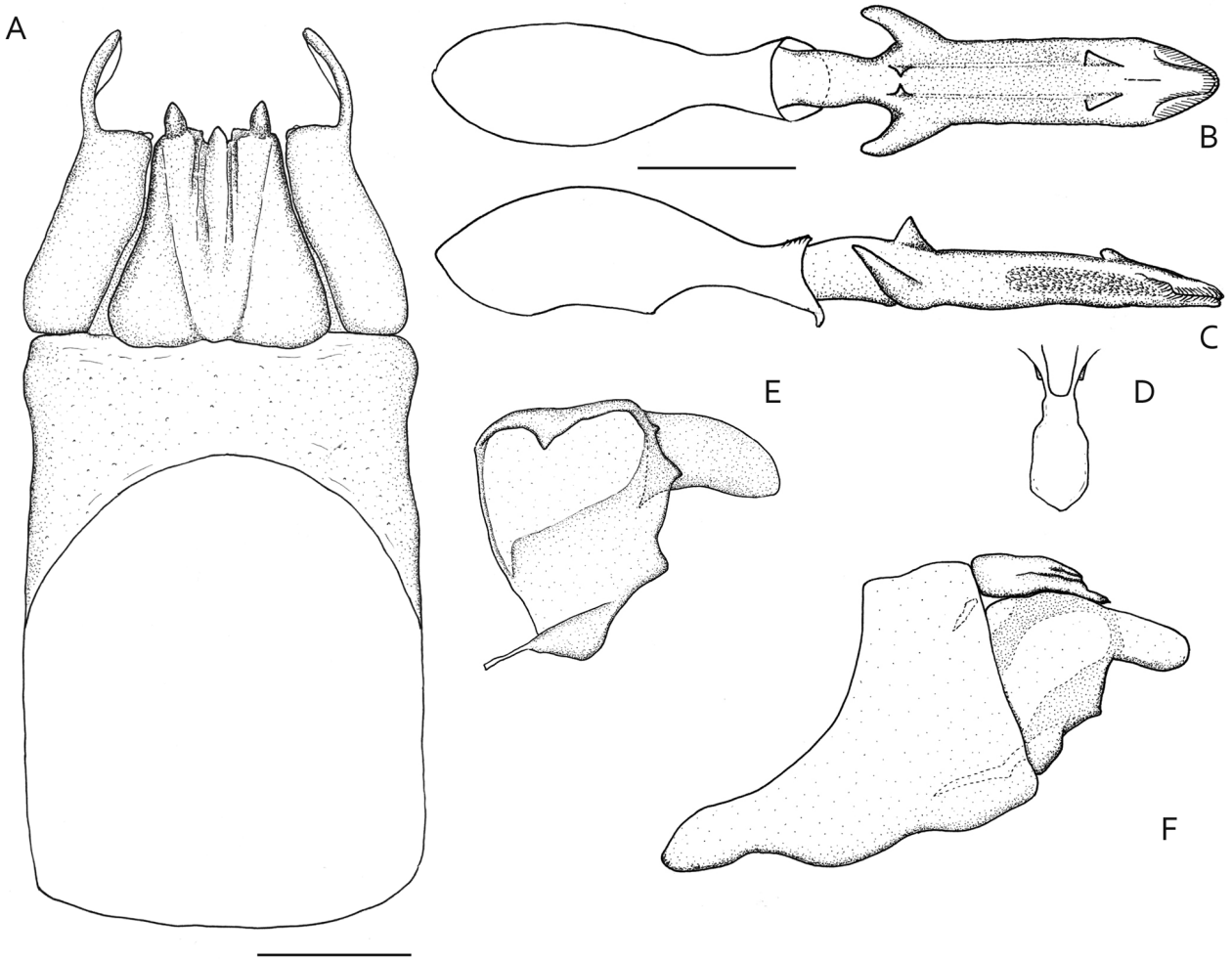

Figure 10. Male genitalia of *Issikiomartyria leptobelos* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** median plate; **E:** left valva, inner view; **F:** genital capsule, lateral view. Scale bars: 0.2 mm.

Type locality. Japan, Akita Pref: Hachimori (Honshu).

Diagnosis. Apical part of valva digitiform. Tergum X longer than 3/4 of valva.

Description. Head dark brown, naked and glossy on both sides, sparsely covered with yellow piliform scales with dark yellow scales on vertex. Antenna longer than forewing in male; with 56 (45–61) flagellomeres in males (n=5). Labial palp 1-segmented. Forewing length 4.5 mm (4.0–4.7, n=9) in male.

Male abdomen and genitalia (Fig. 10). Mid-dorsal length of segment IX ring about 1/4 of ventral length. Valva with digitiform, elongated apex; with a tiny proximo-ventral ridge. Aedeagus straight, with two pairs of dorsal fins: a pair of shorter, distal fins and a pair of longer proximal fins extending vertically; with a pair of lateral triangular fins extending upwards. Tergum X with squarish medial part, longer than 3/4 of valva; with a pair of protrusions disto-dorsally.

Female abdomen and genitalia (Fig. 11). Segment IX forming a complete ring, strongly sclerotized; strongly concave dorso-laterally. Segment X consisting of a pair of lateral sclerites and a dorsal sclerotized plate: lateral sclerite simple, broader than long; dorsal sclerite rounded at apex. Corpus bursae large, globular, membranous, with signa composed of four sclerites near proximal end. Ductus spermathecae arising from a round concavity. Genital chamber with a small, umbrella-shaped sclerite.

Remarks. *Issikiomartyria leptobelos* sp. n. is unique in valva with the digitiform apex in the male. This species is most similar to *I. hyperborea* sp. n., but can be distinguished by the segment IX without a concavity at lateral and ventral sides in the female.

Etymology. The specific name is a compound noun in apposition derived from the Greek words transliterated into Latin, “leptos” (fine) and “belos” (divine, arrow), referring to the digitiform valva of this species.

Distribution. This species has only been found from Hachimori-cho (Honshu: Akita Pref).

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*. The locality is a forest path along a stream in the cool-temperate forests at 100–340 m.

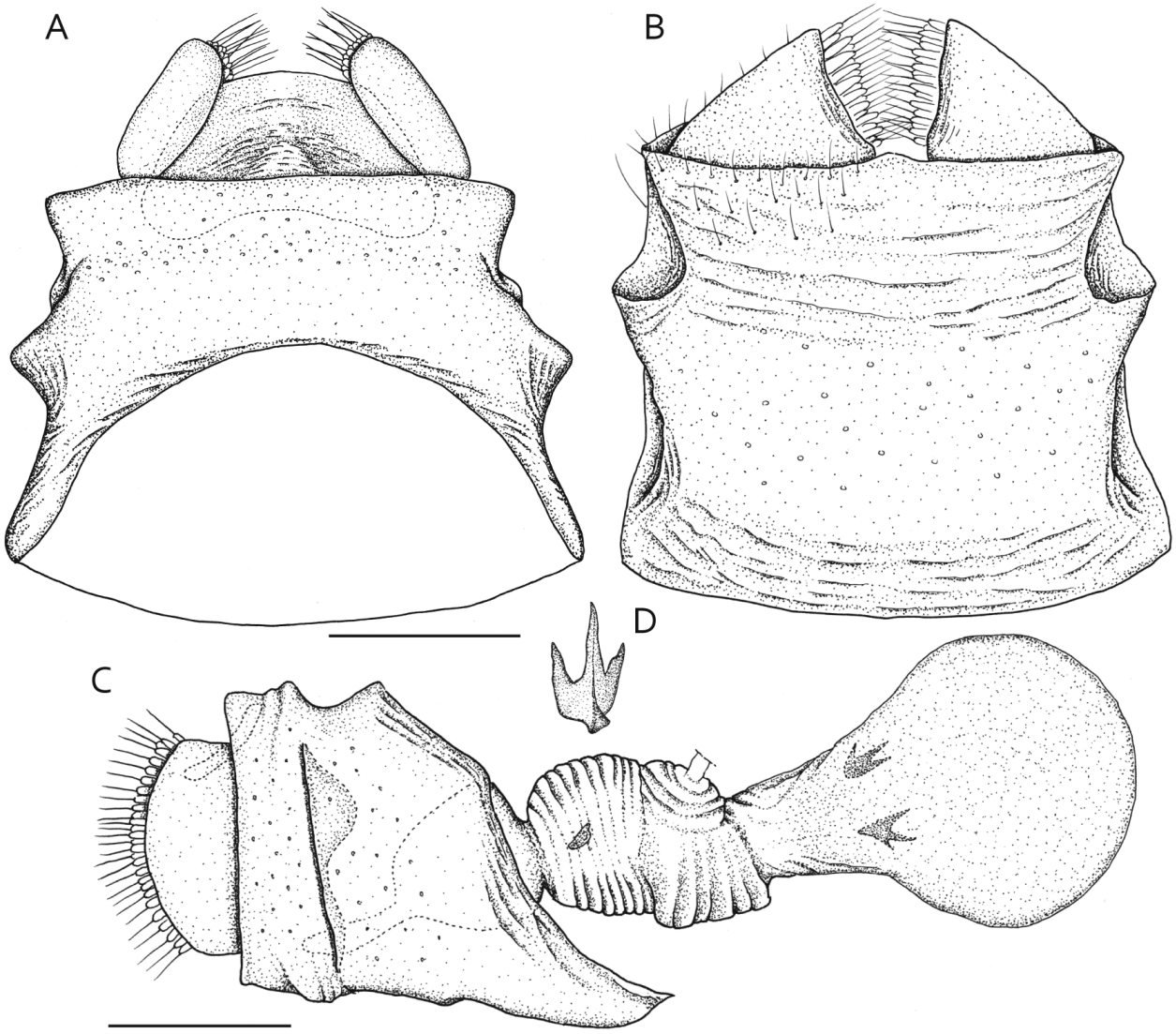

Figure 11. Female genitalia of *Issikiomartyria leptobelos* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** signa. Scale bars: 0.2 mm.

Issikiomartyria catapasta sp. n.

http://zoobank.org/55CCF04A-D282-4619-B886-535EB184527C
Figs 1e, 12, 13
Japanese name: ani-issiki-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂ collected by YI on 21.VI.2015 at Tachimata-keikoku (620 m), Kitaakita-shi, Akita Pref (Fig. 19:6), NMNS.

Paratypes: JAPAN [HONSHU] 1♀ collected by YI on 13.VI.2016 at same locality as holotype (Fig. 19:6), NMNS.

Additional materials: JAPAN [HONSHU] 3♂ collected by YI on 21.VI.2015 at same locality as holotype, KUHE; 3♂ 1♀ collected by YI on 13.VI.2016 at same locality, KUHE; 1♂ collected by YI on 14.VI.2016 at Mt. Moriyoshi (380 m), Kitaakita-shi, Akita Pref (Fig. 19:7), KUHE.

Type locality. Japan, Akita Pref: Tachimata-keikoku (Honshu).

Diagnosis. Middle portion of tergum X in male undeveloped, approximately half of lateral portions. Female genital chamber with numerous sclerites at proximo-dorsally.

Description. Head dark brown, naked and glossy on both sides, sparsely covered with yellow piliform scales with dark yellow scales on vertex. Antenna longer than forewing in male, with 60 flagellomeres in female (n=1). Labial palp 1-segmented. Forewing length 4.3 mm (4.1–4.6, n=9) in male.

Male abdomen and genitalia (Fig. 12). Mid-dorsal length of segment IX ring about 1/4 of ventral length. Valva with elongated apex; with a very small proximo-ventral ridge. Aedeagus with two pairs of dorsal ridges: a pair of shorter distal fins and a pair of longer proximal fins extending vertically; with a pair of lateral triangular fins extending upwards. Tergum X with squarish medial part, with a pair of triangular lobes disto-dorsally.

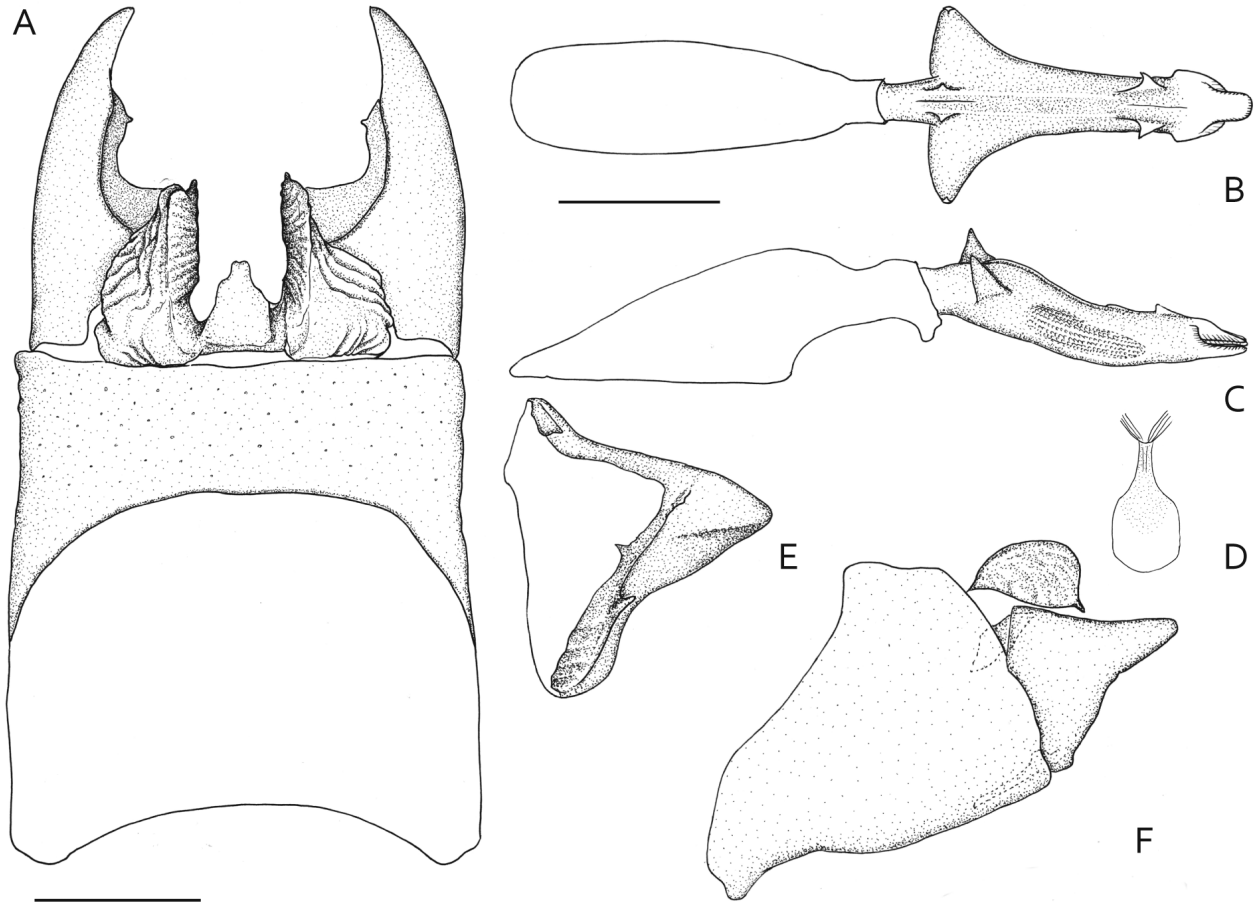

Figure 12. Male genitalia of *Issikiomartyria catapasta* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** median plate; **E:** left valva, inner view; **F:** genitalia capsule, lateral view. Scale bars: 0.2 mm.

Female abdomen and genitalia (Fig. 13). Segment IX forming a complete ring, strongly sclerotized; with a pair of dorso-lateral protrusions near base. Segment X consisting of a pair of lateral sclerites and a dorsal sclerotized plate; dorsal sclerite longer than width, projected upward at caudal end. Corpus bursae large, globular, membranous, with long narrow neck region anteriorly; with signa composed of four saggitate sclerites near proximal end. Ductus spermathecae arising from a round concavity. Genital chamber with numerous tiny sclerites dorsally and a large, fan-shaped sclerite ventrally.

Remarks. *Issikiomartyria catapasta* sp. n. is most similar to *I. trochos* sp. n. in that lateral parts of tergum X extending dorsally, but can be distinguished by the following traits: two basal pairs of dorsal and lateral aedeagal fins closer to each other; numerous tiny sclerites scattered dorsally in female genital chamber; corpus bursae without tiny sclerites.

Etymology. The specific name is a noun in the genitive singular derived from a Latin word, "catapastus" (patchwork), referring to the numerous tiny sclerites in the female genital chamber of this species (Fig. 13).

Distribution. This species has only been found from Kitaakita-shi (Honshu: Akita Pref).

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*. The localities are forest paths along mountain streams of cool-temperate forests at 380–620 m, where *Fagus crenata* Blume (Fagaceae), *Pterocarya rhoifolia* Sieb. Et Zucc. (Junglandaceae) and *Aesculus turbinate* Blume (Sapindaceae) predominately occur.

Issikiomartyria trochos sp. n.

http://zoobank.org/6D2D9E1C-04D0-405B-A00A-5F4E965C8654
Figs 1f, 14, 15
Japanese name: waga-issiki-kobane

Material examined. Holotype: JAPAN [HONSHU] 1♂ collected by YI on 19.VI.2015 at Mahirudake-rindou (410 m), Nishiwaga-cho, Iwate Pref (Fig. 19:8), NMNS.

Paratypes: JAPAN [HONSHU] 3♂1♀ collected by YI on 19.VI.2015 at same as holotype locality, NMNS.

Additional materials: 1♂ collected by YI on 11.VI.2016 at Kodera-keikoku (580 m), Ohemachi, Yamagata Pref (Fig. 19:9), KUHE; 2♂ collected by YI on 12.VI.2016

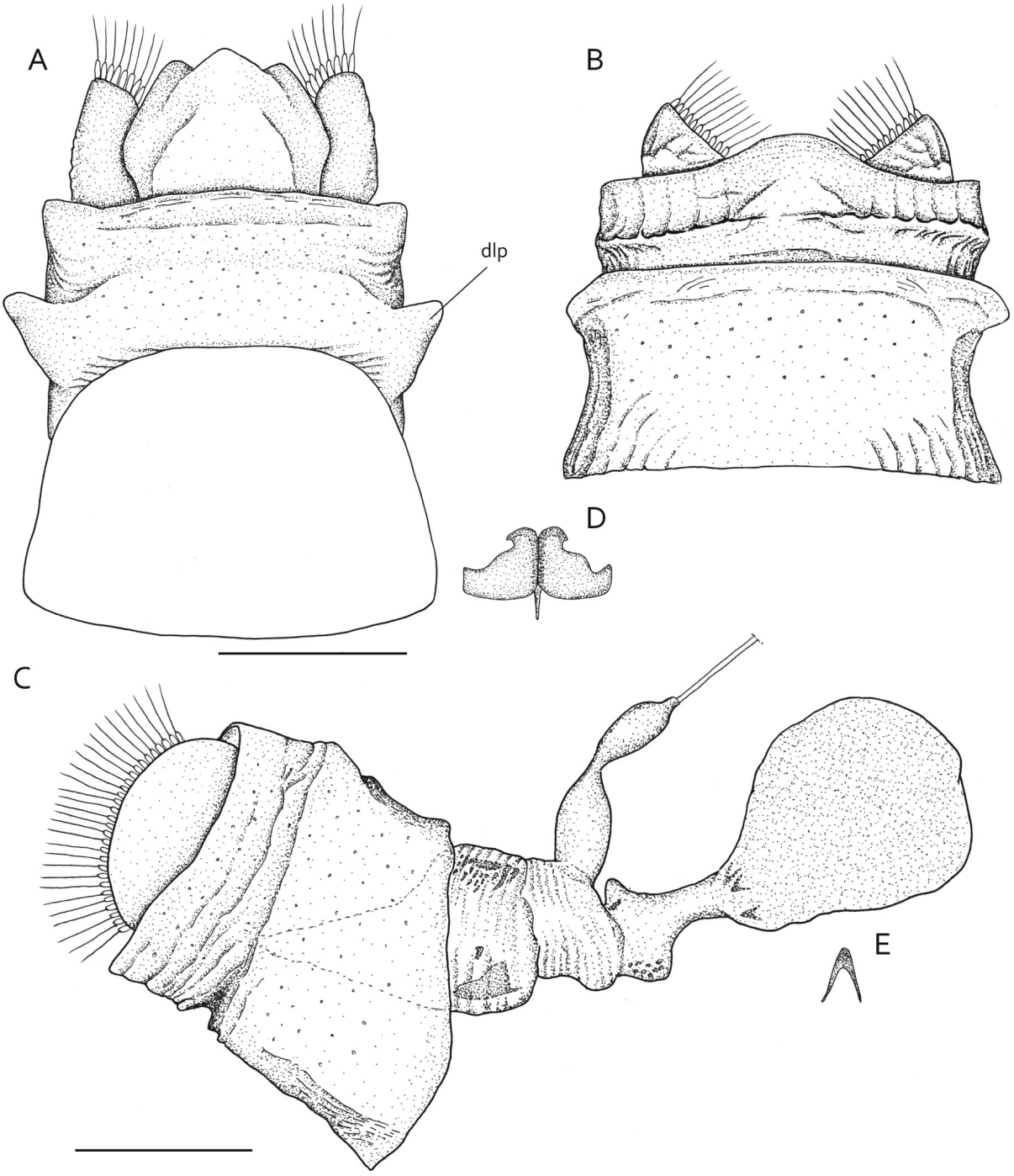

Figure 13. Female genitalia of *Issikiomartyria catapasta* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** genital sclerite; **E:** signa. Abbreviation: **dlp** = dorso-lateral protrusion. Scale bars: 0.2 mm.

at Aosawa Sakata-shi, tunnel (340 m), Yamagata Pref (Fig. 19:10), KUHE.

Type locality. Japan, Iwate Pref: Mahirudake-rindou (Honshu).

Diagnosis. Male tergum X with middle portion as large as lateral portions, lateral portions extending dorsally. Female corpus bursae with tiny sclerites on membrane surface near caudal end.

Description. Head dark brown, naked and glossy on both side, sparsely covered with yellow piliform scales with dark yellow scales on vertex. Antenna longer than forewing in male; with 62 (61–65) flagellomeres in males (n= 3). Labial palp 1-segmented. Forewing length 4.4 mm (4.2–4.7, n=8) in male.

Male abdomen and genitalia (Fig. 14). Mid-dorsal length of segment IX ring about 1/4 of ventral length. Valva with a proximo-ventral ridge; inner ventral margin broad without concavity. Aedeagus with two pairs of dorsal ridges: a pair

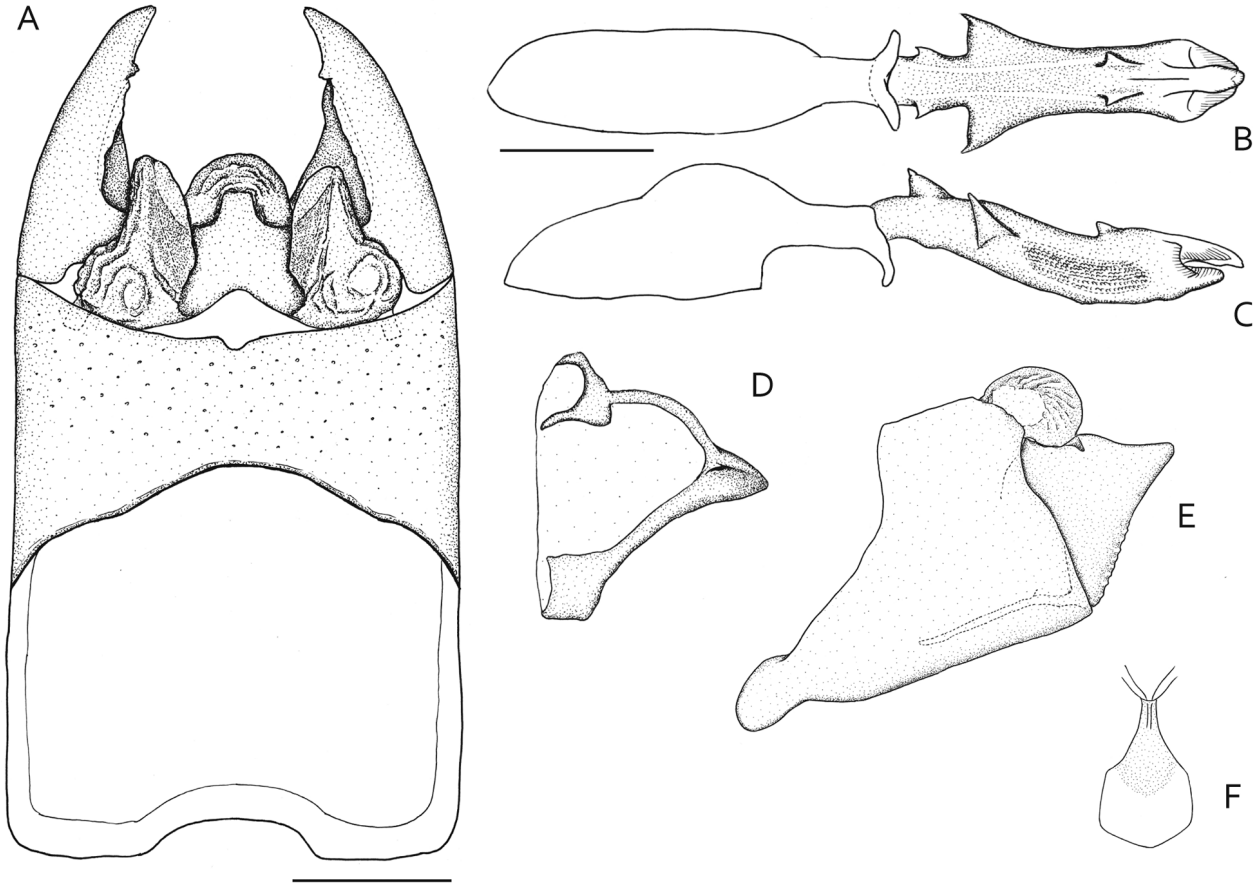

Figure 14. Male genitalia of *Issikiomartyria trochos* sp. n. [holotype]. **A:** genitalia capsule, dorsal view; **B:** phallus, dorsal view; **C:** ditto, lateral view; **D:** left valva, inner view; **E:** genitalia capsule, lateral view; **F:** median plate. Scale bars: 0.2 mm.

of shorter distal fins and a pair of longer proximal fins oriented about proximal quarter of aedeagal length, extending upwards; with a pair of lateral triangular fins extending horizontally. Tergum X with developed medial part, as large as lateral portions; lateral portions expanded dorsally.

Female abdomen and genitalia (Fig. 15). Segment IX forming a complete ring, strongly sclerotized; with a pair of dorso-lateral protrusions near base. Segment X consisting of a pair of lateral sclerites and a dorsal sclerotized plate; dorsal plate almost rectangular, slightly projected in middle. Corpus bursae large, globular, membranous, with long narrow neck region anteriorly; membrane surface with tiny sclerites scattered near caudal end; with signa composed of four saggitate sclerites near proximal end. Ductus spermathecae arising from a round concavity. Genital chamber smooth without sclerites, and a large fan-shaped sclerite ventrally.

Remarks. *Issikiomartyria trochos* sp. n. is most similar to *I. catapasta* sp. n. in that lateral parts of tergum X extending dorsally, but can be distinguished by the following traits: dorso- and latero-basal aedeagal fins separated from each other; female genital chamber without small sclerites; corpus bursae with tiny sclerites on membrane surface near caudal end.

Etymology. The specific name is a noun in apposition from the Greek word, "trochos" (wheel, disk), referring to the unusually extended form of tergum X of this species.

Distribution. This species has been found from the northern part of the main island of Japan (Honshu: Yamagata Pref.).

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*. The habitat is a forest path along mountain streams of cool-temperate forests at 340–595 m, where *Fagus crenata* and *Quercus crispula* dominate.

Issikiomartyria akemiae Hashimoto, 2006

Fig. 16

Issikiomartyria akemiae Hashimoto, 2006: 70, fig. 20.

Material examined. Lectotype: JAPAN [HONSHU] 5♂1♀ collected by MK on 8.VI.2009 at Kiyotsu-kyo, Niigata Pref (Fig. 19: 11), NMNS.

Description (based on female). Head dark brown, naked and glossy on both side, sparsely covered with yellow pili-

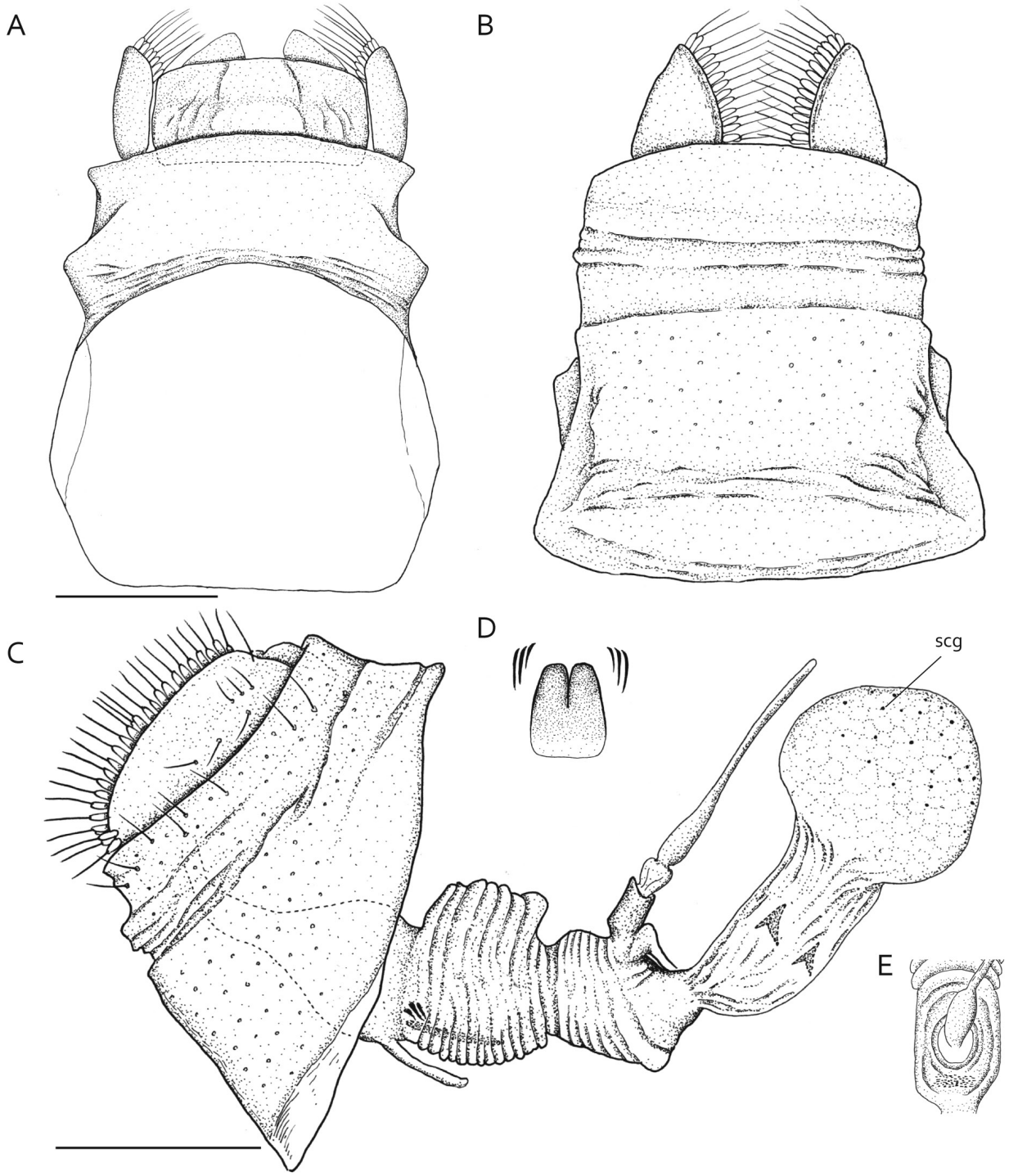

Figure 15. Female genitalia of *Issikiomartyria trochos* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** genital sclerite; **E:** arising part of ductus spermathecae, dorsal view. Scale bars: 0.2 mm. Abbreviation: **scg** = sclerotized granules of corpus bursae.

form scales with dark yellow scales on vertex. Antenna longer than forewing in male. Labial palp 1-segmented.

Female abdomen and genitalia (Fig. 16). Segment IX forming a complete ring, strongly sclerotized, without lateral concavity. Segment X consisting of a pair of lateral sclerites and a dorsal sclerotized plate; lateral sclerites simple, as broad as long, with digitate projections having an apical seta at terminal inner margin. Corpus bursae large, membranous, with long narrow neck region anteriorly; with signa composed of four tridenta-form sclerites around neck region. Ductus spermathecae arising from a round concavity, forked in middle. Genital chamber with numerous tiny sclerites dorsally and a large fan-shaped sclerite ventrally.

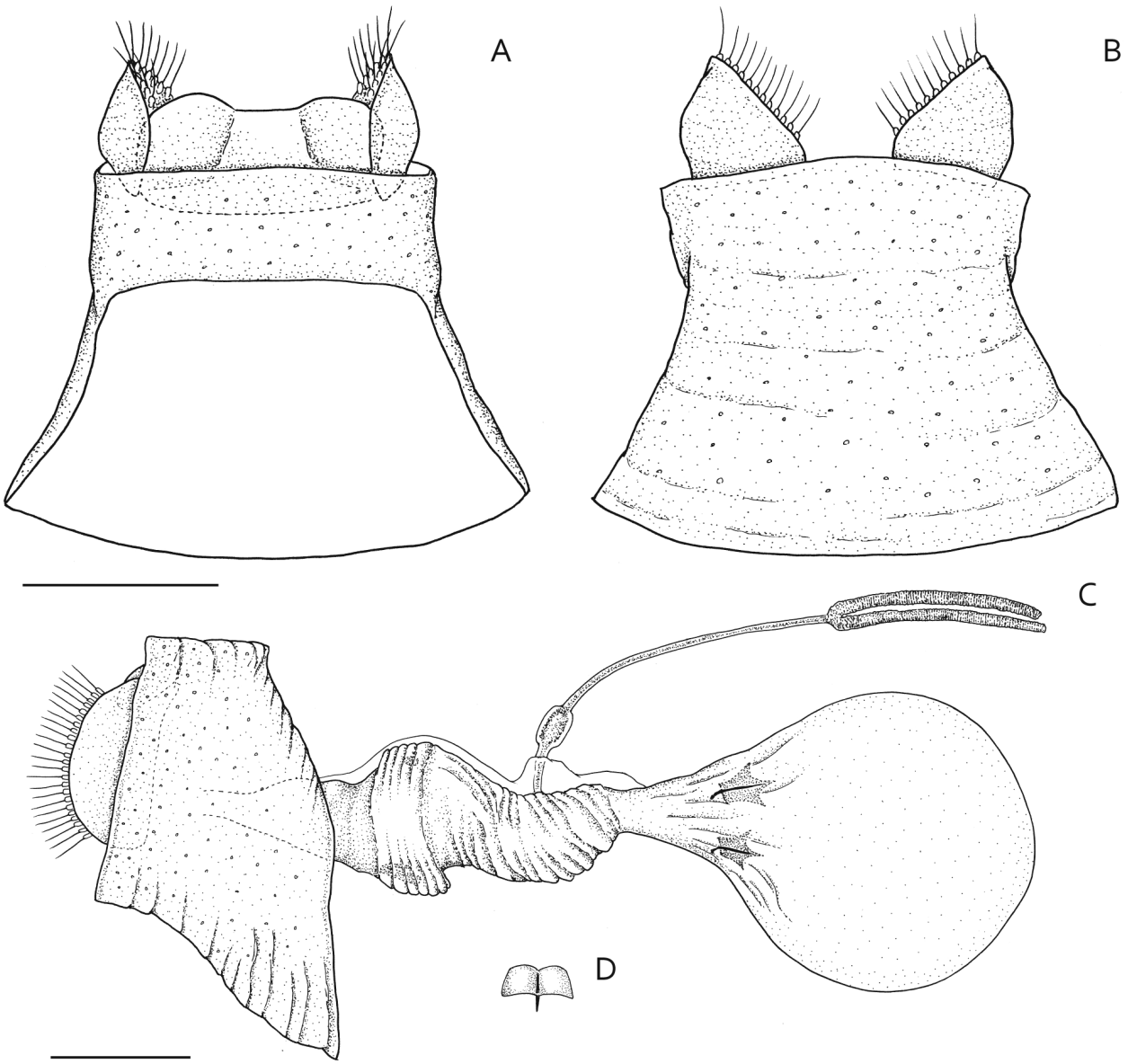

Figure 16. Female genitalia of *Issikiomartyria akemiae* **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** genital sclerite. Scale bars: 0.2 mm.

Remarks. *I. akemiae* can be distinguished by female genitalia having the ductus spermathecae forked in the middle.

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*.

Issikiomartyria plicata Hashimoto, 2006

Fig. 17

Issikiomartyria plicata Hashimoto, 2006: 71, fig. 21.

Materials examined. Lectotype: JAPAN [HONSHU] 11♂2♀ collected by MK, YI on 8.VI.2009 at Amamizukoshi (495m), Matsunoyama-cho, Niigata Pref (Fig. 19:12), NMNS.

Additional materials: JAPAN [HONSHU] 2♂ collected by YI on 14.V.2008 at Shimooritateurasa, Uonuma-shi, Niigata Pref (Fig. 19:13); 11♂ collected by YI on 27.VI.2011 at Komanoyu (370m), Uonuma-shi, Niigata Pref (Fig. 19:14); 1 larva collected by YI on 13.VI.2011 at Sagurigawa-dam, Uonuma-shi, Niigata Pref (Fig. 19:15); 11♂2♀ collected by MK on 8.VI.2009 at Nishinomae, Matsunoyama-cho, Niigata Pref (Fig. 19:16); 3♂3♀ collected as larvae by YI on 6.XII.2010 at same locality; 3♂1♀ collected by YI on 13.VI.2011 at Mizunashi, Matsunoyama-cho, Niigata Pref (Fig. 19:17).

Description (based on female). Head dark brown, naked and glossy on both side, sparsely covered with yellow piliform scales with dark yellow scales on vertex. Antenna longer than forewing in male. Labial palp 1-segmented.

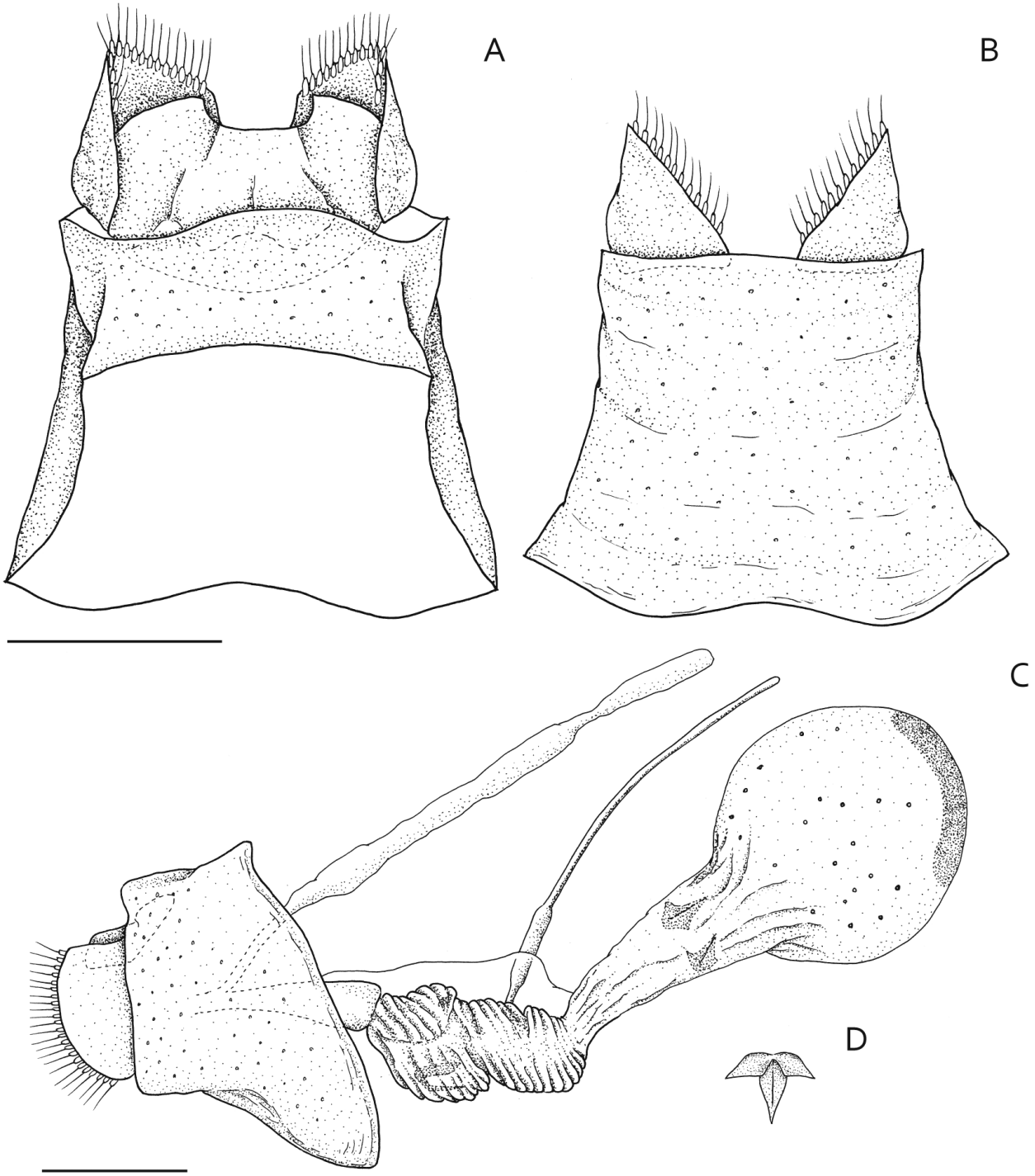

Figure 17. Female genitalia of *Issikiomartyria plicata* sp. n. [paratype]. **A:** genitalia capsule, dorsal view; **B:** ditto, ventral view; **C:** female genitalia, lateral view; **D:** genital sclerite. Scale bars: 0.2 mm.

Female abdomen and genitalia (Fig. 17). Segment IX forming a complete ring, strongly sclerotized; concave dorso-laterally. Segment X consisting of lateral sclerites and a dorsal sclerotized plate; lateral sclerites simple, as broad as long, with digitate projections having an apical seta at terminal inner margin. Corpus bursae large, membranous, with long narrow neck region anteriorly; with signa composed of four fan-shaped sclerites at distal of neck region; distal end densely sclerotized. Ductus spermathecae arising from a round concavity. Genital chamber with a sclerite ventrally.

Remarks. *I. plicata* can be distinguished from other species of *Issikiomartyria* based on the female genitalia in that having densely sclerotized zone at distal end of corpus bursae.

Bionomics. Larvae feed on the thalli of *Conocephalum conicum*.

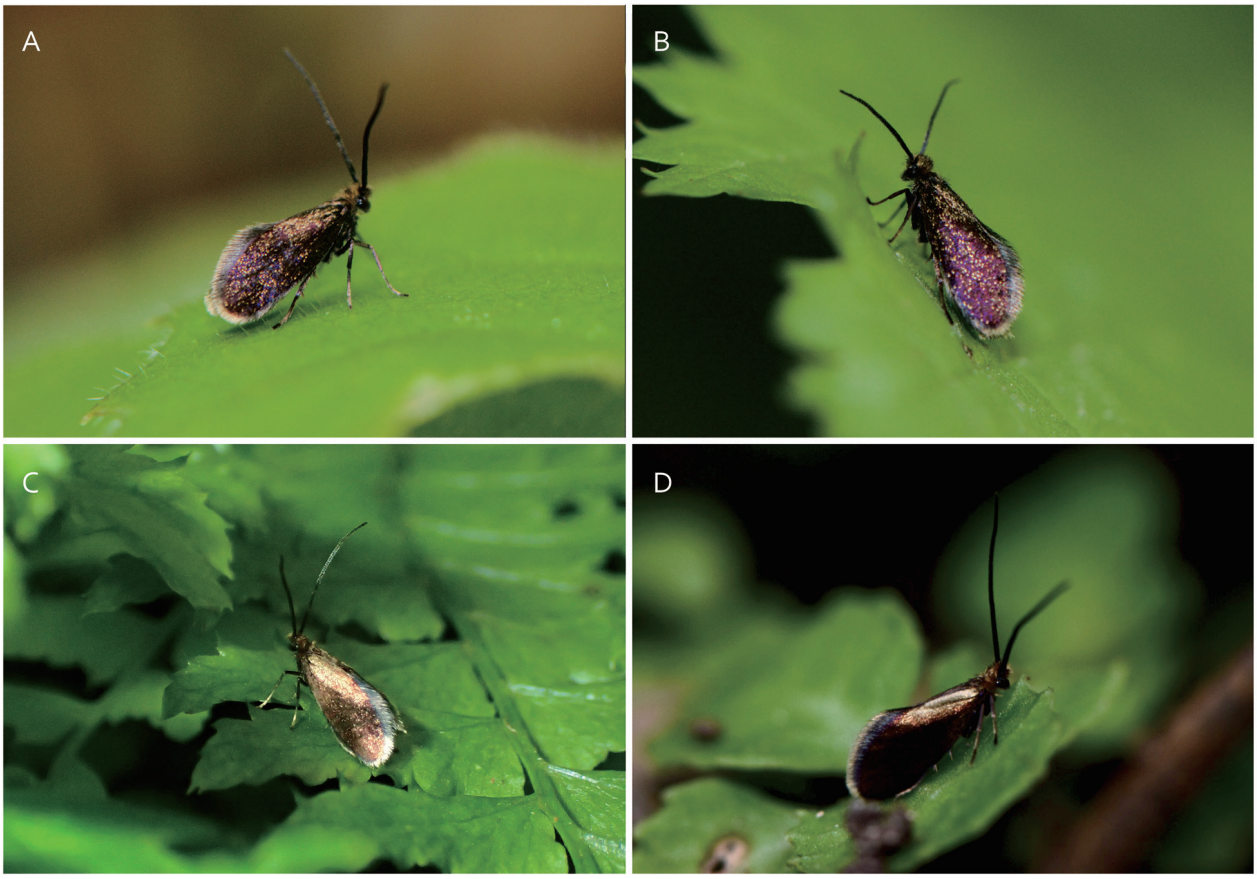

Figure 18. Ecology. **A:** *Issikiomartyria catapasta* sp. n. at Tachimata-keikoku, Akita Pref; **B:** *I. trochos* sp. n. at Jintsu-kyo, Yamagata Pref; **C:** *I. trochos* sp. n. at Mahirudake-rindo, Iwate Pref; **D:** *Melinopteryx bilobata* sp. n. at Ushikubi-touge, Shizuoka Pref.

Key to the Japanese genera of Micropterigidae (modified from Hashimoto 2006)

1 Forewing with RI vein deeply bifurcate, except for *Austromartyria porphyrodes* Turner, 1932.....Southern Hemisphere genera
– Forewing with RI vein unforked (rarely shallowly bifurcate as an individual variation) ..... (Northern Hemisphere genera)...2
2 Fore- and hindwings with an acute apex; hindwing usually with a complete stem vein of RI ..... *Micropterix*
– Fore- and hindwings with an obtusely round apex; hindwing with an incomplete stem vein of RI 3
3 Head covered with yellow or orange piliform scales 4
– Head covered with black piliform scales..... 8
4 Foretibia with epiphysis 5
– Foretibia without epiphysis 6
5 Fore- and hindwings with a radial cell; aedeagus with about 20 to 50 minute serrate projections; female segment X without a dorsal sclerite ..... *Paramartyria*
– Fore- and hindwings without a radial cell; aedeagus with a few minute serrate projections; female segment X with a dorsal sclerite .....*Palaeomicroides* Issiki, 1931
6 Fore- and hindwings without a radial cell..... 7
– Fore-and hindwings with a radial cell 8
7 Pedicel as large as the most basal flagellum; labial palp developed, 2-segmented; aedeagus with three pairs of dorsal ridges, a pair of lateral triangular fins, a ventral longitudinal fin extended vertically ..... *Melinopteryx* gen. n.
– Pedicel twice as large as the most basal flagellum; labial palp weakly developed, usually 1-segmented (except for *I. bisegmentata*); aedeagus with two pairs of dorsal ridges and a pair of lateral triangular fins, without ventral fins ..... *Issikiomartyria*
8 A basal stalk of each flagellomere distinct; aedeagus divided into dorsal and ventral branches; corpus bursae large, with four distinct tridentaform signa .....*Epimartyria* Walsingham, 1898
– A basal stalk of each flagellomere distinct; aedeagus not divided; corpus bursae small, with or without four minute signa.....*Vietomartyria* Hashimoto & Mey, 2000
9 Forewing slender; valva with a costal long projection curved ventro-mesally; aedeagus without dorsal and ventral longitudinal ridges; female segment X without a dorsal sclerotized plate ..... *Kurokopteryx*
– Forewing rather broad and oval; valva without such a long projection; aedeagus with dorsal and ventral longitudinal ridges; female segment X with a dorsal sclerotized plate.....*Neomicropteryx*

Key to *Issikiomartyria* species based on male genitalia

1 Valva with digitiform apex; tergum X longer than 3/4 of valva ..... *I. leptobelos* sp. n.
– Valva gradually tapering toward apex; tergum X shorter than 3/4 of valva 2
2 Tergum X with a pair of lateral flanges or protrusions exerted vertically; aedeagus with broad, triangular latero-basal fins 3
– Tergum X without lateral flanges; aedeagus with narrow latero-basal fins 4
3 A pair of latero-basal fins of aedeagus acute at base, arising from ventral side ..... *I. hyperborea* sp. n.
– A pair of latero-basal fins of aedeagus broad at base, arising from lateral side 5
4 Valva with a mid-dorsal ridge; aedeagus with a pair of lateral triangular fins at or near middle 6
– Valva without mid-dorsal ridge; aedeagus with a pair of lateral triangular fins near terminal end ..... *I. bisegmentata*
5 Valva with a mid-dorsal ridge; middle portion of tergum X smaller than lateral portion; dorso- and latero-basal aedeagal fins and flanges close to each other ..... *I. catapasta* sp. n.
– Valva without mid-dorsal ridge; middle portion of tergum X almost same size as lateral portion; dorso- and latero-basal aedeagal fins and flanges separated from each other ..... *I. trochos* sp. n.
6 Dorso-basal margin of valva strongly expanded posteriorly; a mid-dorsal ridge of valva a thin plate expanding ventro-mesally; dorso- and latero-basal aedeagal fins rather broadly separated from each other; lateral triangular fins of aedeagus small ..... *I. distincta*
– Dorso-basal margin of valva not expanded; a mid-dorsal ridge of valva either hornlike or a rather thick plate; dorso- and latero-basal aedeagal ridges close to each other; lateral triangular fins of aedeagus relatively large 7
7 A mid-dorsal ridge of valva a thick plate, rounded; phallobase without a longitudinal ventral ridge; proximo-lateral fins of aedeagus short, rather stout; medial part of tergum X broadly concave ..... *I. nudata*
– A mid-dorsal ridge of valva hornlike, acute ventrally; phallobase with longitudinal ventral ridges; proximo-lateral fins of aedeagus slender; medial part of tergum X not concave 8
8 Phallobase with two longitudinal short ridges running parallel each other; proximo-lateral fins of aedeagus extending antero-dorsally ..... *I. akemiae*
– Phallobase with a longitudinal ridge; proximo-lateral projections extending horizontally ..... *I. plicata*

Key to *Issikiomartyria* species based on female genitalia (female unknown in *distincta*)

1 Segment IX with a deep concavity on ventral side ..... *I. hyperborea* sp. n.
– Segment IX without concavity on ventral side 2
2 Segment IX with a dorso-lateral protrusion 3
– Segment IX without protrusion 4
3 Genital chamber with numerous small sclerites scattered; distal surface of corpus bursae smooth, without sclerotization ..... *I. catapasta* sp. n.
– Genital chamber without sclerites on dorsal side but with a large one on ventral side; corpus bursae densely covered with weakly sclerotized granules on distal surface ..... *I. trochos* sp. n.
4 Mid-dorsal length of segment IX ring shorter than 1/3 of ventral length ..... *I. leptobelos* sp. n.
– Mid-dorsal length of segment IX ring longer than 1/3 of ventral length 5
5 Distal zone of corpus bursae densely sclerotized ..... *I. plicata*
– Distal zone of corpus bursae without sclerotization 6
6 Signa composed of four reduced sclerites in corpus bursae ..... *I. nudata*
– Signa composed of four tridenta-form sclerites in corpus bursae 7
7 Sclerites in signa shallowly bifurcated; ductus spermathecae forked in middle ..... *I. akemiae*
– Sclerites in signa deeply bifurcated; ductus spermathecae without forked ..... *I. bisegmentata*

Additional sampling records of micropterigids in the Northeastern Japan

All specimens described below are stored in KUHE.

***Issikiomartyria bisegmentata* Hashimoto, 2006**

JAPAN [HONSHU] 2♂ collected by YI on 20.X.2013 at Aosawa tunnel, Sakata-shi, Yamagata Pref (Fig. 19:10); 1♀ emerged on 9.VII.2015 collected by MK on 28.VI.2015 at Okutadami dam, Uonuma-shi, Niigata Pref (Fig. 19:18); 1 larva collected by N. Yoshikawa on 9.XII.2013 at Tadami-cho, Fukushima Pref (Fig. 19:19); 2♂ emerged on 29.VI.2014 collected by YI on 17.V.2015 at Hahanaritouge, Koriyama-shi, Fukushima Pref (Fig. 19:20).

***Issikiomartyria distincta* Hashimoto, 2006**

JAPAN [HONSHU] 2 larvae collected by YI on 20.V.2013 at Shirabu-onsen, Yonezawa-shi, Yamagata Pref (Fig. 19:21); 2♂ emerged on 19.VI.2015 collected as larvae by YI on 17.V.2015 at same locality; 3♂ collected by YI on 27.VI.2015 at Goreibitsu-touge, Konan-cho, Fukushima Pref (Fig. 19:22); 1♂ collected on 17.V.2014

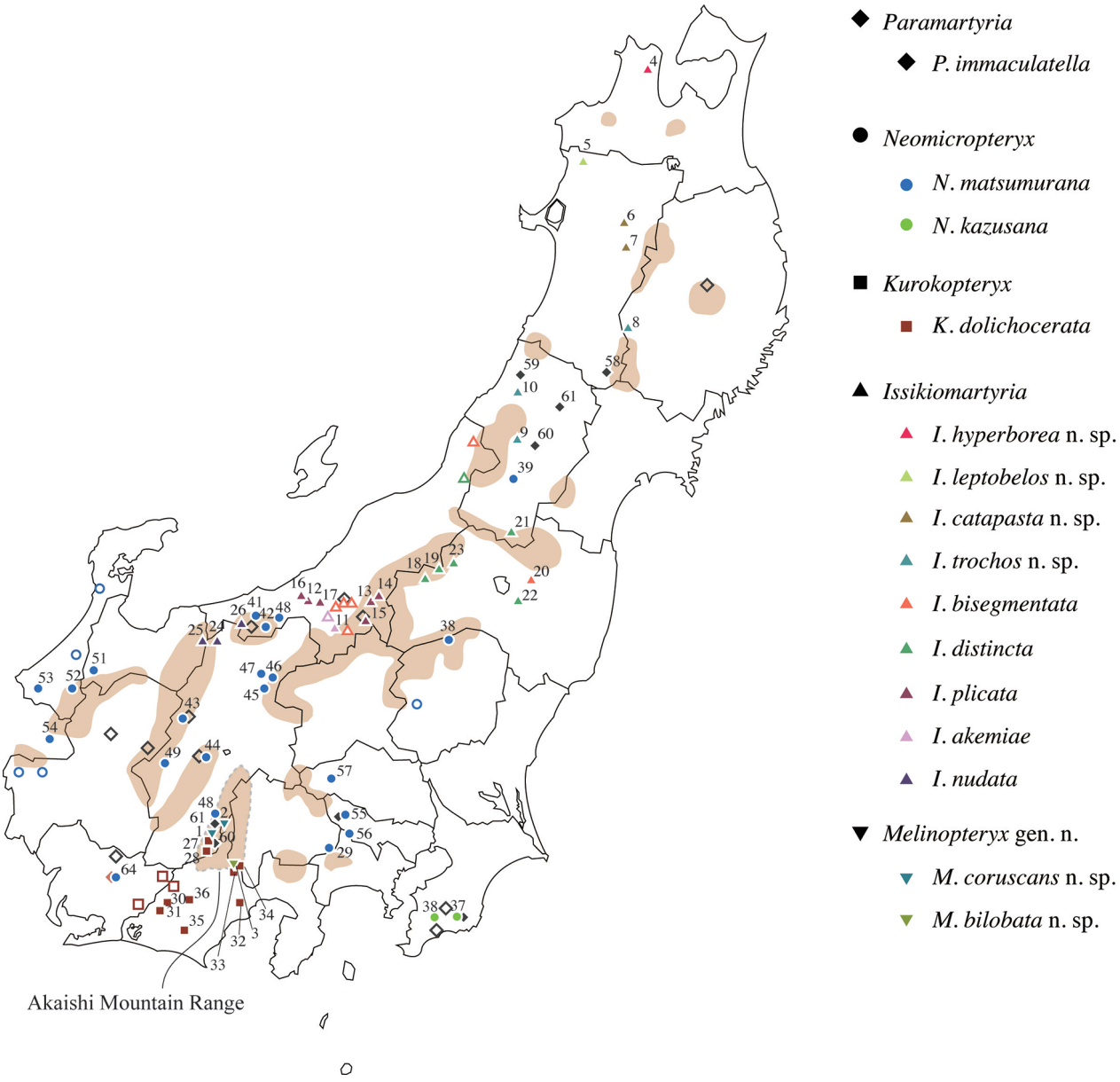

Figure 19. Locality records of micropterigid moths in the Northeastern Japan. Locality codes correspond to those in the text. Shaded are the areas higher than 1000 m elevation. Sampling records from Hashimoto (2006) are indicated as outlined symbols.

at same locality; 6♂ collected by YI on 9.VI.2016 at Kurosawa, Yanaidu-machi, Fukushima Pref (Fig. 19:23).

***Issikiomartyria nudata* Hashimoto, 2006**

JAPAN [HONSHU] 4♂ collected by MK on 14.VII.2009 at Renge-onsen, Otoigawa-shi, Niigata Pref (Fig. 19:24); 1♂ collected by MK on 11.VII.2008 at Mt.Shirouma, Hakuba-mura, Nagano Pref (Fig. 19:25); 2♂ collected by MK on 14.VII.2009 at Mt.Amakazari, Otari-mura, Nagano Pref (Fig. 19:26).

***Kurokopteryx dolichocerata* Hashimoto, 2006**

JAPAN [HONSHU] 4♂ collected by YI on 12.VI.2011 at Kashio, Ohshika-mura, Nagano Pref (Fig. 19:27); 2♂ collected as larvae by YI on 14.V.2008 at Uemura, Iida-shi, Nagano Pref (Fig. 19:28); 2 larvae collected by YI on 14.XI.2011 at same locality; 1 larva collected by MK on 17.II.2002 at Shibakawa, Fujinomiya-shi, Shizuoka Pref (Fig. 19:29); 2♂3♀ emerged on 24.IV.2009 collected as larvae by MK on 17.II.2009 at Ketagawa, Hamamatsu-shi, Shizuoka Pref (Fig. 19:30); 2♂2♀ emerged on 24.IV.2008 collected as larvae by MK on 20.IV.2008 at Shirakura-kyo, Hamamatsu-shi, Shizuoka Pref (Fig. 19:31); 1♂ emerged on 27.IV.2008 collected as larvae by MK on 21.IV.2008 at Ashikubo, Shizuoka-shi, Shizuoka Pref (Fig. 19:32); 1♀ collected by YI on 13.IV.2014 at same locality; 1♂ emerged on 15.V.2009 collected by YI on 22.IV.2009 at Kuchisakamoto Onsen, Shizuoka-shi, Shizuoka Pref (Fig. 19:33); 2♂ collected by MK on 15.VI.2008 at Umegashima Onsen, Shizuoka-shi, Shizuoka Pref (Fig. 19:34); 1♂ emerged on 30.IV.2008 collected as larvae by MK on 21.IV.2008 at Morimachi, Shizuoka Pref (Fig. 19:35); 1♂ emerged on 11.V.2008 collected as larvae by MK on

21.IV.2008 at Ishikiri, Hamamatsu-shi, Shizuoka Pref (Fig. 19:36); 1 larva collected by YI on 20.X.2015 at Uradani, Shitara-cho, Aichi Pref (Fig. 19:64).

***Neomicropteryx kazusana* Hashimoto, 1992**

JAPAN [HONSHU] 5♂ collected by MK on 14.V.2008 at Mt. Kiyosumi, Kamogawa-shi, Chiba Pref (Fig. 19:37); 2♂ emerged on 18.IV.2012 collected as larvae by MK on 24.I.2012 at Yoro-keikoku, Ichihara-shi, Chiba Pref (Fig. 15:38); 7 larvae collected by YI on 12.XI.2011 at same locality.

***Neomicropteryx matsumurana* Issiki, 1931**

JAPAN [HONSHU] 1♂ emerged on 20.IV.2014 from larva collected by YI on 19.X.2013 at Nogawakeikoku, Nagai-shi, Yamagata Pref (Fig. 19:39); 1♂ emerged collected as larva by YI on 20.V.2014 at Sanno-rindo, Nikko-shi, Tochigi Pref (Fig. 19:40); 1♂ collected by YI on 27.V.2014 at Mt.Yakiyama, Myoko-shi, Niigata Pref (Fig. 19:41); 1♂ collected as larva by YI on 29.IV.2014 at Myoko-kougen, Myoko-shi, Niigata Pref (Fig. 19:42); 1♂ collected by YI on 28.V.2014 at Shimashimatani, Matsumoto-shi, Nagano Pref (Fig. 19:43); 2 larvae on 7.X.2012 at Yokokawa-keikoku, Tatsuno-cho, Nagano Pref (Fig. 19:44); 1♂ collected as larva on 26.V.2014 at same locality; 1 larva on 17.X.2015 at same locality; 3 larvae collected by YI on 22.IX.2008 at Karasawanotaki, Ueda-shi, Nagano Pref (Fig. 19:45); 1 larva collected by YI on 23.IX.2008 at Zakogawa, Shigakougen, Yamauchi-machi, Nagano Pref (Fig. 19:46); 3 larvae collected by YI on 22.IX.2008 at Ohtanirindo, Suzaka-shi, Nagano Pref (Fig. 19:47); 4♂1♀ collected by MK on 11.VI.2007 at Naenataki, Myoko-shi, Nagano Pref (Fig. 19:48); 1♂ collected as larva by YI on 29.IV.2013 at same locality; 5♂ collected by MK and YI on 7.VI.2013 at Agematshu-cho, Nagano Pref (Fig. 19:49); 2 larvae collected by YI on 5.X.2012 at same locality; 6♂ collected by YI on 2.VI.2010 at Kashio, Ohshika-mura, Nagano Pref (Fig. 19:50); 2 adults collected by YI on 9.VII.2012 at same locality; 4♂ collected by MK at Bunaotouge, Nanto-shi, Toyama Pref (Fig. 19:51); 3♂ collected by MK on 3.V.2013 at Mt. Hakusan, Hakusan-shi, Ishikawa Pref (Fig. 19:52); 1♂ collected by MK as larva on 1.IX.2011 at Takedagawa, Sakai-shi, Fukui Pref (Fig. 19:53); 2 larvae collected by YI on 22.IV.2015 at Ifuriyama, Ohno-shi, Fukui Pref (Fig. 19:54); 3♂2♀ emerged on 21.IV.2016 collected as larvae by MK on 15.III.2016 at Nippara, Okutama-cho, Tokyo Metropolitan (Fig. 19:55); 2♂1♀ emerged on 9.V.2011 collected as larvae by YI on 5.IV.2011 at Kogesawa, Hachioji-shi, Tokyo Metropolitan (Fig. 19: 56); 2♂ emerged on 21.IV.2015 collected as larvae by MK on 28.XI.2014 at Okuchichibu, Chichibu-shi, Saitama Pref (Fig. 19:57); 1 larva collected by MK on 19.VIII.2002 at same locality; 2♂ emerged on 21.IV.2015 collected by MK as larvae on 28.XI.2014 at same locality.

***Paramartyria immaculatella* Issiki, 1931**

JAPAN [HONSHU] 5♂ collected by YI on 12.VI.2016 at Sanzugawa-keikoku, Yuzawa-shi, Akita Pref (Fig. 19:58); 1 larva collected by YI on 20.X.2013 at Shimoaosawa, Sakata-shi, Yamagata Pref (Fig. 19:59); 1♂ emerged on 20.IV.2014 collected as larva by YI on 19.X.2013 at Kodera-keikoku Jintsukyo, Ooema-chi, Yamagata Pref (Fig. 19:9); 1 larva collected by YI on 20.X.2013 at Onumanoukishima, Asahi-cho, Yamagata Pref (Fig. 19:60); 1 larva collected by YI on 20.X.2013 at Mt. Mokuzousan, Sakata-shi, Yamagata Pref (Fig. 19:61); 1♂ collected by YI on 7.VI.2013 at Agematsu-cho, Kiso, Nagano Pref (Fig. 19:49); 7♂ collected by YI on 12.VI.2011 at Uemura, Iida-shi, Nagano Pref (Fig. 19:28); 6 larvae feeding on *Calypogeia tosana* (Steph). Steph. (Calypogeiaceae) collected by YI on 14.XI.2011 at same locality; 1 larva collected by YI on 18.X.2015 at same locality; 1 larvae collected by YI on 19.X.2015 at Hodonooike, Iida-shi, Nagano Pref (Fig. 19:62); 1 larvae collected by YI on 18.X.2015 at Wazo, Ohshika-mura, Nagano Pref (Fig. 19:63); 2♂ collected by MK on 14.V.2008 at Mt.Kiyosumi, Kamogawa-shi, Chiba Pref (Fig. 19:37); 7 larvae feeding on *Pellia endiviifolia* (Dicks.) Dumort. (Pelliaceae) collected by YI on 12.XI.2011 at Yoro-keikoku, Ichihara-shi, Chiba Pref (Fig. 15:38); 1 larva collected by YI on 20.X.2015 at Uradani, Shitara-cho, Aichi Pref (Fig. 19:64).

Discussion on the distribution of *Issikiomartyria*

Our extensive field surveys have revealed that the distribution of *Issikiomartyria* is extended from northernmost to the central region of Honshu. *Issikiomartyria* species tend to be found from the geographically fragmented area facing the Japan Sea but not from the Pacific Ocean sides, although we conducted a census with considerable efforts throughout northeastern Honshu. The host-plant species is not likely to be the limiting factor of their distribution, because *Conocephalum* liverwort is widespread in the mainland of Japan (Imada Y and Kato M, pers. obs.). The Japan Sea side of the Japanese archipelago corresponds to the largely snow-covered area (Suzuki 1962) and harbors unique plant and animal species and it is called “Japan Sea elements” (Fukuoka 1966). The factors contributing the distribution of *Issikiomartyria* are unclear, they may be associated with heavy-snow conditions in winter.

To our knowledge, *Issikiomartyria* offers a largest example of regional diversification of insects in the northeastern Japan. Especially, it should be noted that *I. hyperborea* sp. n. may be the only insect species endemic to the Tsugaru peninsula so far known, which can be morphologically well-differenciated from the rest of *Issikiomartyria* spp. Several groups of animals represent genetic variations among the geographic populations in the northeastern Japan: terrestrial animals (Suzuki et al.

2004); *Carabus* ground beetles (Sota et al. 2001), freshwater fish (Yamamoto et al. 2004), and amphibious salamanders, *Onychodactylus nipponoborealis* (Poyarkov et al. 2012) and *Hynobius lichenatus* Boulenger, 1883 (Yoshikawa et al. 2008, Aoki et al. 2013). In addition, pronounced morphological differenciation is detected in a sinistral land snail group, *Euhadra grata* (Gude, 1900), occurring in the northeastern region. *E. grata* group consists of four morphologically distinct subspecies (Nishitani 1996, Kawana 2007), each of which range is allopatric one another. However, the geographic area where the genetic differentiations detected in these lineages are not correlated with the species ranges of *Issikiomartyria.*

Furthermore, we have discovered two species of *Melinopteryx* gen. n., *M. coruscans* sp. n. and *M. bilobata* sp. n., from highlands of the Akaishi Mountain Range. *Melinopteryx* gen. n. is sister to *Issikiomartyria* in a molecular phylogenetic analysis (Imada et al. 2011), and the species of both genera favor snowy regions of the Chubu and Tohoku regions of Japan, whereas some of the geographic populations are in proximity with either *Neomicropteryx matsumurana* or *Kurokopteryx dolichocerata*, which tend to occur in lower mountains. The species range of *M. coruscans* approximates two Japan endemic microptergid species: at the Akaishi Mountain Range, *N. matsumurana* (Fig. 19:48) and *K. dolichocerata* (Fig. 19:27,28) respectively inhabit northern and southern regions of Bunkui touge, a mountain ridge along the Median Tectonic Line, and *M. coruscans* has only been found in between narrow area higher than 1500 m. Likewise, *M. bilobata* sp. n. has been found from the southeastern area of the Akaishi Mountain Range (Fig. 19:3), where some populations of *K. dolichocerata* colonizes in adjacent but lower area (Fig. 19:33,34). Hence, this study supports prior findings that each *Conocephalum*-feeding micropterigid species belonging to the Japanese endemic micropterigid genera (*Issikiomartyria, Kurokopteryx, Neomicropteryx*) does not co-occur with one another (Hashimoto 2006, Imada et al. 2011).

The Japanese patterns of allopatry is even more extreme than that found in New Zealand *Sabatinca* yet contrasts markedly with a pattern of sympatry found in New Caledonia (Gibbs 1983; Gibbs and Lees 2014). Our study reinforces the potential research interest of Micropterigidae in differentially reflecting geological and ecological diversification processes at different spatial and temporal scales.

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References

Aoki G, Matsui M, Nishikawa K (2013) Mitochondrial cytochrome b phylogeny and historical biogeography of the Tohoku salamander, *Hynobius lichenatus* (Amphibia, Caudata). Zoological Science 30: 167–173. https://doi.org/10.2108/zsj.30.167

Davis DR, Landry J-F (2012) A review of the North American genus *Epimartyria* (Lepidoptera, Micropterigidae) with a discussion of the larval plastron. ZooKeys 183: 37–83. https://doi.org/10.3897/zookeys.183.2556

Engel MS, Kinzelbach RK (2008) A primitive moth from the earliest Eocene Fur Formation ("Mo-clay") of Denmark (Lepidoptera: Micropterigidae). Linzer biologische Beiträge 40: 1443–1448.

Fukuoka N (1966) On the distribution patterns of the so-called Japan Sea elements confined to the Japan Sea region. The Journal of Geobotany 15: 63–80. https://doi.org/10.1007/BF00218523

Gibbs GW (1983) Evolution of Micropterigidae (Lepidoptera) in the SW Pacific. GeoJournal 7: 505–510.

Gibbs GW (2006) Ghosts of Gondwana. Craig Potton Publishing, Nelson, New Zealand, 232 pp.

Gibbs GW (2010) Micropterigidae (Lepidoptera) of the Southwestern Pacific: A revision with the establishment of five new genera from Australia, New Caledonia and New Zealand. Zootaxa 2520: 1–48.

Gibbs GW (2014) Micropterigidae (Insecta: Lepidoptera). Fauna of New Zealand 72: 1–127.

Gibbs GW, Kristensen NP (2011) *Agrionympha*, the long-known South African jaw moths: a revision with descriptions of new species (Lepidoptera, Micropterigidae). Zootaxa 2764: 1–21.

Gibbs GW, Lees DC (2014) New Caledonia as an evolutionary cradle: a re-appraisal of the jaw-moth genus *Sabatinca* (Lepidoptera: Micropterigidae) and its significance for assessing the antiquity of the island's fauna. In: Guilbert É, Robillard T, Jourdan H, Grandcolas P (Eds) Zoologia Neocaledonica 8. Biodiversity studies in New Caledonia. Muséum national d'Histoire naturelle, Paris, 239-266.

Hashimoto S (2006) A taxonomic study of the family Micropterigidae (Lepidoptera, Micropterigoidea) of Japan, with the phylogenetic relationships among the Northern Hemisphere genera. Bulletin of the Kitakyushu Museum of Natural History and Human History Series A 4: 39–109.

Hirowatari T (1997) A taxonomic revision of the genus *Adela* Latreille (Lepidoptera, Adelidae) from Japan. Transactions of the Lepidopterological Society of Japan 48: 271–290.

Imada Y, Kawakita A, Kato M (2011) Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). Proceedings of the Royal Society B: Biological Sciences 278: 3026–3033. https://doi.org/10.1098/rspb.2011.0134

Issiki S (1931) On the morphology and systematics of Micropterygidae (Lepidoptera Homoneura) of Japan and Formosa, with some considerations on the Australian, European, and North American forms. Proceedings of the zoological society of London 1931:999–1039. https://doi.org/10.1111/j.1096-3642.1931.tb01052.x

Issiki S (1953) Micropterigoidea of Japan. Bulletin of the Naniwa University Series B Agricultural and Natural Science 3: 133–140.

Kawana M (2007) The world of land snails (Euhadra) in Japan. Kinmirai-sha, Nagoya, 332 pp. [In Japanese]

Kozlov MV (1988) Paleontology of lepidopterans and problems of the phylogeny of the order Papilionida. In: Panomarenko AG (Ed.)

The Mesozoic-Cenozoic crisis in the evolution of insects. Moscow, 16–69. [In Russian]

Kristensen NP (1984) Studies on the morphology and systematics of primitive Lepidoptera (Insects). Steenstrupia 10: 141–191.

Kristensen NP (1999) Lepidoptera: moths and butterflies, 1: evolution, systematics and biogeography, Handbook of zoology. Walter de Gruyter, Berlin, Germany, 501 pp.

Kristensen NP, Hilton DJ, Kallies A, Milla L, Rota J, Wahlberg N, Wilcox SA, Glatz RV, Young DA, Cocking G, Edwards T, Gibbs GW, Halsey M (2015) A new extant family of primitive moths from Kangaroo Island, Australia, and its significance for understanding early Lepidoptera evolution. Systematic Entomology 40: 5–16. https://doi.org/10.1111/syen.12115

Kristensen NP, Nielsen ES (1979) A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia 5: 69–147.

Kristensen NP, Scoble MJ, Karsholt O (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa 1668: 699–747.

Lees DC, Rougerie R, Zeller-Lukashort C, Kristensen NP (2010) DNA mini-barcodes in taxonomic assignment: a morphologically unique new homoneurous moth clade from the Indian Himalayas described in Micropterix (Lepidoptera, Micropterigidae) Zoologica Scripta 39: 642–661. https://doi.org/10.1111/j.1463-6409.2010.00447.x

Nishitani H (1996) Snails in Japan. Hiroyuki Nishitani, Kobe, 100 pp.

Poyarkov NA, Che J, Min M-S, Kuro-o M, Yan F, Li C, Iizuka K, Vieites DR (2012) Review of the systematics, morphology and distribution of Asian Clawed Salamanders, genus *Onychodactylus* (Amphibia, Caudata: Hynobiidae), with the description of four new species. Zootaxa 3465: 1–106.

Regier JC, Mitter C, Kristensen NP, Davis DR, van Nieukerken EJ, Rota J, Simonsen TJ, Mitter KT, Kawahara AY, Yen S-H, Cummings MP, Zwick A (2015) A molecular phylogeny for the oldest (nonditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life-history evolution. Systematic Entomology 40: 671–704. https://doi.org/10.1111/syen.12129

Skalski AW (1995) Study on the Lepidoptera from fossil resins. Part XI. *Baltimartyria*, a new genus for *Micropteryx proavittella* Rebel, 1936, with redescription of this species (Lepidoptera, Zeugloptera, Micropterigidae). Amber and Fossils 1: 26–37.

Sota T, Ishikawa R, Ujiie M, Kusumoto F, Vogler AP (2001) Extensive trans-species mitochondrial polymorphisms in the carabid beetles *Carabus* subgenus *Ohomopterus* caused by repeated introgressive hybridization. Molecular ecology 10: 2833–2847. https://doi.org/10.1046/j.1365-294X.2001.t01-1-01404.x

Suzuki H (1962) The classification of Japanese climates. Geographical Review of Japan (Chirigaku Hyoron) 35: 205–211. https://doi.org/10.4157/grj.35.205

Suzuki H, Yasuda SP, Sakaizumi M, Wakana S, Motokawa M, Tsuchiya K (2004) Differential geographic patterns of mitochondrial DNA variation in two sympatric species of Japanese wood mice, *Apodemus speciosus* and *A. argenteus*. Genes & Genetic Systems 79: 165–176. https://doi.org/10.1266/ggs.79.165

van Eldijk TJB, Wappler T, Strother PK, van der Weijst CMH, Rajaei H, Visscher H, van de Schootbrugge B (2018) A Triassic-Jurassic window into the evolution of Lepidoptera. Science advances 4: e1701568. https://doi.org/10.1126/sciadv.1701568

van Nieukerken EJ, Kaila L, Kitching IJ, Kristensen NP, Lees DC, Minet J, Mitter C, Mutanen M, Regier JC, Simonsen TJ, Wahlberg N, Yen S-H, Zahiri R, Adamski D, Baixeras J, Bartsch D, Bengtsson BÅ, Brown JW, Bucheli SR, Davis DR, Prins JD, Prins WD, Epstein ME, Gentili-Poole P, Gielis C, Hättenschwiler P, Hausmann A, Holloway JD, Kallies A, Karsholt O, Kawahara AY, Koster S, Kozlov MV, Lafontaine JD, Lamas G, Landry J-F, Lee S, Nuss M, Park K-T, Penz C, Rota J, Schintlmeister A, Schmidt BC, Sohn J-C, Solis MA, Tarmann GM, Warren AD, Weller S, Yakovlev RV, Zolotuhin VV, Zwick A (2011) Order Lepidoptera Linnaeus, 1758. In: Zhang Z-Q (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness 3148: 212–221.

Whalley PES (1978) New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). Annals of the Transvaal Museum 31(8): 71–86.

Yamamoto S, Morita K, Kitano S, Watanabe K, Koizumi I, Maekawa K, Takamura K (2004) Phylogeography of white-spotted Charr (*Salvelinus leucomaenis*) inferred from mitochondrial DNA sequences. Zoological Science 21: 229–240. https://doi.org/10.2108/zsj.21.229

Yoshikawa N, Matsui M, Nishikawa K, Kim J-B, Kryukov A (2008) Phylogenetic relationships and biogeography of the Japanese clawed salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), and its congener inferred from the mitochondrial cytochrome b gene. Molecular Phylogenetics and Evolution 49: 249–259. https://doi.org/10.1016/j.ympev.2008.07.016

Zhang W, Shih C, Labandeira CC, Sohn J-C, Davis DR, Santiago-Blay JA, Flint O, Ren D (2013) New Fossil Lepidoptera (Insecta: Amphiesmenoptera) from the Middle Jurassic Jiulongshan Formation of Northeastern China. PLoS ONE 8: e79500. https://doi.org/10.1371/journal.pone.0079500.t003