

New data on the taxonomy, systematics, and phylogeny of the tribe Boreoheptagyiini Brundin (Diptera: Chironomidae: Diamesinae)

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Abstract

A multilocus phylogeny of the tribe Boreoheptagyiini was reconstructed using nuclear (18S, 28S, and CAD4) and mitochondrial (COI5P, COI3P, and COII) genes. Species delimitation using ASAP analysis of DNA barcodes identified 22 molecular operational taxonomic units (mOTUs), which were congruent with morphological species hypotheses. Based on robust phylogenetic and morphological evidence, we formally propose the transfer of the genus *Sasayusurika* Makarchenko, including *S. nigatana* (Tokunaga), from the tribe Diamesini to the tribe Boreoheptagyiini. To maintain monophyly, the genera *Palatovia* Makarchenko et Semenchenko and *Kaluginia* Makarchenko are downgraded to subgeneric rank within the genus *Boreoheptagya* Brundin. Furthermore, *Boreoheptagya kurobebrevis* (Sasa et Okazawa, 1992) and *B. unica* Makarchenko were reclassified to the subgenus *Kaluginia* Makarchenko, and *B. zhengi* Lin et Liu, 2021 to the subgenus *Shilovia* Makarchenko. In this regard, the new structure of the Boreoheptagyiini tribe with all its taxa, their diagnosis based on morphological data, keys, descriptions, and redescrptions for adult males as well as for immature stages of the studied species, are presented. In this revision, two new species, *Boreoheptagya* (s. str.) *elbursica* **sp. nov.** and *B.* (s. str.) *serratosioi* **sp. nov.** are also described.

These taxonomic revisions provide a more stable and phylogenetically consistent classification for the Boreoheptagyiini tribe.

Key words: Diptera, Chironomidae, Diamesinae, Boreoheptagyiini, taxonomy, DNA barcoding

Introduction

Tribe Boreoheptagyiini and genus *Boreoheptagya*, were erected by Brundin (1966) for the Holarctic species of the genus *Heptagya* Philippi. Currently, the genus *Boreoheptagya* Brundin includes 27 valid species, with the only *B. lurida* (Garrett) from the Nearctic region (Oliver *et al.* 1990; Ashe & O'Connor 2009) and the majority of species recorded from the Palaearctic and Oriental regions (Serra-Tosio 1983, 1989; Endo 2002; Makarchenko *et al.* 2008; Ashe & O'Connor 2009; Yamamoto & Yamamoto 2014; Rossaro 2017; Makarchenko *et al.* 2020a; Lin *et al.* 2021).

After the fundamental work of Brundin (1966), Serra-Tosio (1989) undertook a comprehensive study of the taxonomy of *Boreoheptagya*. He revised the European and North American species into three stages of development, published descriptions and identification keys for 7 species adult males, 8 species pupae, and 9 species larvae. All other studies, including ours, were limited to descriptions of new and redescrptions of little-known species of the genus, and only based on adult males, ignoring pupae and larvae, although they used an integrative method with DNA barcoding (Makarchenko *et al.* 2008, Makarchenko *et al.* 2020a; Lin *et al.* 2021). DNA barcoding has been successfully applied to solving taxonomic problems within the tribe Boreoheptagyiini, including biodiversity assessment, species delimitation, life-stage association, and range determination (Makarchenko *et al.* 2017,

Makarchenko *et al.* 2018, Makarchenko *et al.* 2020a–c, Lin *et al.* 2021). Using an integrative method, we concluded that the tribe Boreoheptagyiini should be expanded so that in addition to the *Boreoheptagya*, to include at least three more genera, namely *Kaluginia* Makarchenko, *Shilovia* Makarchenko, and *Palatovia* Makarchenko et Semenchko (Makarchenko *et al.* 2017, 2018, 2020a). DNA barcoding has also enabled the definitive identification of *Palatovia lorestanica* Makarchenko et Semenchko, *Boreoheptagya iranica* Makarchenko, *B. joeli* Makarchenko, and *B. sarymsactyensis* Makarchenko (Makarchenko *et al.* 2020c), as well as *Shilovia xinhuaewangi* Makarchenko et Semenchko, *S. yakovlevi* Makarchenko et Semenchko, and *S. rara* Makarchenko (Makarchenko *et al.* 2020b). Furthermore, it facilitated the separation of morphologically similar populations of *Kaluginia lebetiformis* Makarchenko, 1987 from South Korea and the Amur River basin into two distinct subspecies (Makarchenko *et al.* 2020a).

A recent multilocus phylogenetic reconstruction confirmed the monophyly of the tribe and the sister relationship between the genera *Palatovia* and *Kaluginia*. However, the genus *Boreoheptagya* was found to be paraphyletic with respect to *Shilovia*, leading to the latter being downgraded to subgeneric rank (Semenchenko *et al.* 2024). Unfortunately, most *Boreoheptagya* specimens in that study were represented by larvae or pupae and remained undescribed at the species level. Furthermore, numerous previously described species were missing from the analysis. The present study expands and refines these results by incorporating new taxa and increasing taxonomic coverage to consolidate the molecular phylogeny and DNA barcode database for the tribe. Additionally, we revise the taxonomic status of *Palatovia* and *Kaluginia* using a multilocus phylogeny approach integrated with the morphological analysis of pupa and larva.

The main aims of this work are as follows.

1. To reconstruct the phylogenetic relationships within the tribe by incorporating all currently available sequences into a multilocus framework.
2. To perform species delimitation using DNA barcodes (COI5P) and establish intra- and interspecific genetic distances for all recognized species.
3. To carry out a taxonomic revision of the Boreoheptagyiini tribe using an integrative method by obtaining molecular genetics and morphological data, including from a scanning electron microscope.

Materials and methods

The adults and preimaginal stages of chironomids were preserved in 70% ethanol for further study of morphology and in 96% ethanol for DNA barcoding. The material was slide-mounted in polyvinyl lactophenol. The morphological terminology and abbreviations used below generally follow Sæther (1980). For some structures of the hypopygium, however, the terminology of Hansen & Cook (1976) and Oliver (1989) is used. The photographs were taken using an Axio Lab.A1 (Karl Zeiss) microscope with an AxioCam ERc5s digital camera and an Olympus SZX16 stereomicroscope with an Olympus DP74 digital camera, and then stacked using Helicon Focus software. The final illustrations were post-processed for contrast and brightness using Adobe Photoshop software.

To examine the shape and size of the cephalic outgrowths, the armament of the anterior and posterior prolegs, and the tergal microrelief of larvae, the specimens were passed through a graded ethanol series, dehydrated in acetone, critical-point dried, mounted on aluminum stubs with double-sided adhesive tape, and sputter-coated with gold using a Polaron PS 100 sputter coater. All SEM observations were performed on a Vega3 Tescan scanning electron microscope at the Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences (RAS), Moscow. Scanning electron microscope photographs in text are marked with the SEM symbol.

Holotypes and paratypes of the new species, as well as all other material, are deposited in the Bioresource Collection (reg. number 2797657) of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia (FSCEATB FEB RAS).

Total genomic DNA was extracted from the whole body using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) or the PureLink Genomic DNA Mini Kit (Invitrogen Corp., Carlsbad, CA) following the manufacturer's protocols, with DNA eluted in 70–100 µl. Subsequent molecular procedures depended on the gene set targeted for each specimen. To ensure robust support for phylogenetic nodes, we used nearly complete sequences of the nuclear ribosomal genes 18S and 28S, and a fragment of the protein-coding gene CAD4. Mitochondrial markers included COI5P, COI3P, and COII. In this study, we sequenced 18 specimens for this full dataset (though COI5P for some had

been sequenced previously). An additional 15 specimens of the tribe Boreoheptagiini with the complete six-gene set were included from Semenchenko *et al.* (2024). All molecular protocols—including DNA extraction, primer sets, PCR conditions, amplicon visualization, purification, and sequencing—followed the methods described by Semenchenko *et al.* (2024).

An additional 21 specimens were sequenced in this study specifically for COI5P DNA barcodes using Folmer *et al.* (1994) primers (LCO1490 and HCO2198). Detailed laboratory protocols and primer sequences are provided in Semenchenko *et al.* (2024) and Makarchenko *et al.* (2022, 2023a, 2024). DNA barcoding enabled us to refine intraspecific distances, expand known species ranges, and associate different life stages.

To ensure the stability of the phylogenetic position of each clade, we included 1 to 3 representative individuals per molecular species for which the full six-gene dataset was available (see above). For specimens with only DNA barcodes, missing genes were coded as missing data. The exceptions were *Boreoheptagya alulasetosa*, *B. brevitarsis*, *B. kurobebrevis*, and *B. zhengi*, for which only mitogenomes are available; for these taxa, COI and COII were used, while nuclear markers were treated as missing (Lin *et al.* 2022). Members of the tribes Heptagiini and Diamesini and subfamily Protanypodinae were selected as outgroups, following Cranston *et al.* (2012) and Semenchenko *et al.* (2024).

Comprehensive information for each specimen—including taxonomic identity, voucher ID, life stage, sex, geographic coordinates, and GenBank accession numbers—is provided in Supplementary Table S1. This table specifies the original references for sequences retrieved from previous studies; notably, all newly generated sequences produced for this study are highlighted in bold.

Species delimitation was performed using the distance-based approach ASAP (Assemble Species by Automatic Partitioning; Puillandre *et al.* 2021) to independently test morphological species hypotheses. The analysis was based on the COI5P barcode dataset using Kimura 2-parameter (K2P) distances. We evaluated the partitioning schemes based on the ASAP score, where the lowest score indicates the most parsimonious delimitation. This approach allowed us to identify molecular operational taxonomic units (MOTUs) and compare them with our morphological identifications.

Phylogenetic reconstruction was performed using IQTree3 (Wong *et al.* 2025) with a partitioned analysis approach. To find the optimal partitioning scheme and substitution models, we used the built-in ModelFinder Plus algorithm with the partition merging option (-m MFP+MERGE; Kalyaanamoorthy *et al.* 2017). Branch support was assessed using 100,000 replicates of both the SH-like approximate likelihood ratio test (SH-aLRT) and the Ultrafast Bootstrap (UFB) (Hoang *et al.* 2018). The resulting phylogenetic tree was visualized in FigTree v.1.4.4 and further edited for publication in Adobe Illustrator. To verify topological stability and test for long-branch attraction artifacts, supplementary control runs were performed using Bayesian Inference in MrBayes v3.2.7 (Ronquist *et al.* 2012), using identical partitioning schemes for 10 million generations with a 25% burn-in.

Molecular results and discussion

In this study, molecular analysis was conducted using two complementary strategies: a six-gene dataset to provide robust phylogenetic backbone support, and DNA barcodes (COI5P) to assess intraspecific distances, range expansion, and life-stage associations. This dataset included 18 newly sequenced specimens with full gene sets and additional 21 specimens only with DNA barcodes. To ensure a comprehensive review of the tribe Boreoheptagiini, all sequences available in public databases as of March 2026 were included in the analysis (see Supplementary Table S1).

Phylogenetic relationships and taxonomic revision

The results of the Maximum Likelihood (ML) analysis are presented in Figure 1. The tree was rooted using members of the subfamily Protanypodinae, which formed a distinct lineage according to Semenchenko *et al.* (2024). Two subsequent lineages diverging from the common Diamesinae stem correspond to the tribes Heptagiini (SH-aLRT = 100%, UFB = 100%) and Diamesini (SH-aLRT = 90.6%, UFB = 90%), which is consistent with the Cranston *et al.* (2012) and Semenchenko *et al.* (2024).

Sasayusurika nigatana is recovered within the Boreoheptagiini clade with maximum support (SH-aLRT = 100%, UFB = 100%). The current placement of the genus *Sasayusurika* within the Diamesini is inconsistent with

the recovered topology and renders the tribe Boreoheptagiini paraphyletic. Given the robust molecular evidence and shared larval synapomorphies (see below), we hereby transfer the genus *Sasayusurika* (including its type species *S. nigatana*) from the tribe Diamesini to the tribe Boreoheptagiini.

To test whether the basal placement of *Sasayusurika* was biased by long-branch attraction (LBA, Bergsten 2005), we performed supplementary outgroup-extraction analyses (not shown). Removal of the Protanypodinae and the tribes Heptagiini and other Diamesini in both IQ-TREE 3 and MrBayes under midpoint rooting consistently recovered *Sasayusurika* as a stable sister lineage to the remaining Boreoheptagiini, proving that its phylogenetic position is driven by a genuine evolutionary signal rather than an LBA artifact.

The remaining members of the tribe Boreoheptagiini diverged into two major, well-supported clades (SH-aLRT = 100, UFB = 100). The first clade comprises five molecular operational taxonomic units (MOTUs, after ASAP analyses) representing several genera and species: *Palatovia lorestanica*, *Boreoheptagya iranica*, both subspecies of *Kaluginia* (*K. lebetiformis koreana* and *K. l. lebetiformis*), the recently identified species *K. wangi* and *B. kurobebrevis*.

While this topology is generally consistent with the multilocus phylogeny of Semchenko *et al.* (2024), the inclusion of new taxa provides critical insights into the tribal relationships. Notably, *B. iranica* was recovered as sister to *P. lorestanica* with high support (SH-aLRT = 99.1, UFB = 100). This relationship was previously suggested based only on COI barcodes, but with negligible support (BPP = 0.73, ML-BS = 51; Makarchenko *et al.* 2020c). Our six-gene dataset confirms this sister relationship; however, *B. iranica* lacks the morphological characters typical of *Palatovia* (Makarchenko *et al.* 2020c).

The recovered phylogenetic position of *B. iranica* nested within the *Palatovia* + *Kaluginia* clade renders the genus *Boreoheptagya* paraphyletic. High nodal support (SH-aLRT = 99.1, UFB = 100) for this topology demonstrates that the current generic boundaries of *Palatovia* and *Kaluginia* are phylogenetically untenable.

To rigorously test whether this systematic paraphyly was driven exclusively by the volatile position of *B. iranica*, we performed a supplementary control analysis by completely omitting this taxon from the dataset (not shown). In its absence, both IQ-Tree 3 and MrBayes successfully recovered *Palatovia* and *Kaluginia* as distinct monophyletic sister lineages forming a well-supported basal clade to the remaining *Boreoheptagya* s. str. However, despite this conditional monophyly, isolating *B. iranica* as incertae sedis to preserve independent generic statuses was rejected. Such an approach merely masks the genuine evolutionary transitions within the tribe and creates an unstable systematic framework for accommodating intermediate West Asian lineages. Therefore, retaining them as subgenera remains the most robust and parsimonious solution.

To resolve this paraphyly and establish a stable monophyletic classification, we hereby synonymize the genera *Palatovia* and *Kaluginia* with *Boreoheptagya*, formally downgrading them to subgeneric rank: *Boreoheptagya* (*Palatovia*) **stat. nov.** (including single species *P. lorestanica*) and *Boreoheptagya* (*Kaluginia*) **stat. nov.** (including two species, *K. lebetiformis* and *K. wangi*). This taxonomic act is further corroborated by synapomorphic characters of the immature stages (see below), which provide a morphological basis for the unified genus *Boreoheptagya*.

The species *B. kurobebrevis* exhibits a notable phylogenetic position. Despite the absence of nuclear markers, the use of mitogenomic data (including COI5P, COI3P, and COII) provided moderate support (SH-aLRT = 75.4, UFB = 96) for a sister relationship between *B. kurobebrevis* and *K. wangi*.

However, the conspecificity of the specimens from China (Lin *et al.* 2021, 2022) and the type material from Japan (Sasa & Okazawa 1992) remains uncertain. Our phylogenetic and morphological data (see below) suggest that the Chinese specimens of *B. kurobebrevis* belong to the subgenus *Kaluginia*. We emphasize that DNA barcodes from the Japanese type material are required before a formal transfer of the entire species to this subgenus can be finalized.

The second major clade includes the remaining species of the genus *Boreoheptagya* s. str., as well as members of the subgenus *Shilovia*, which was recently downgraded to subgeneric rank (Semchenko *et al.* 2024). While the overall topology is consistent with previous phylogenies, our study incorporates several new taxa, nomenclatural updates, and significantly expanded sampling for most species.

The Chinese species *B. joeli* was recovered as the first diverging lineage within this clade (SH-aLRT = 100, UFB = 100), consistent with previous results (Makarchenko *et al.* 2020c). This was followed by a poorly supported clade including *Boreoheptagya* sp. 7 from Kazakhstan and Iran. Although only larvae and mature male pupae are available for this taxon, its phylogenetic position is distinct.

Sister to this lineage are *B. serratosioi* **sp. nov.** from India (previously referred to as *Boreoheptagya* sp. 4 by

Semenchenko *et al.* 2024) and *B. alulasetosa* from China (Lin *et al.* 2021, 2022). The low support for this clade is likely due to the lack of nuclear markers for *B. alulasetosa*, which appears to have weakened the phylogenetic signal.

The clade comprising the three species of the subgenus *Shilovia* received support only from the SH-aLRT analysis (98.3%). Within this group, *B. zhengi* (Lin *et al.* 2021) was integrated based on mitochondrial data. Both morphological evidence (see below) and our phylogenetic results support the formal transfer of *B. zhengi* to the subgenus *Shilovia*.

Boreoheptagya sarymsactyensis, described from Kazakhstan, was found to be conspecific with *Boreoheptagya* sp. 4 from Semenchenko *et al.* (2024). It is recovered as a sister (SH-aLRT = 74.1, UFB = 74) to *B. brevitarsis* from China. Notably, the specimens from Iran previously identified as *B. brevitarsis* represent a distinct species according to both the ASAP analysis and its position on the tree. Based on this, as well as the morphological differences of the imago, pupa, and larva, we describe from Iran a new species *B. elbursica* **sp. nov.** Since *B. brevitarsis* was originally described from Japan, DNA barcodes from the type locality are essential for comparing populations of *B. brevitarsis* from China and the new species from Iran.

The lineages designated as *Boreoheptagya* sp. 1, sp. 2, and sp. 3 remain consistent with Semenchenko *et al.* (2024). These are represented by larvae or pupae from Kyrgyzstan, Georgia, and Russia; formal descriptions await the collection of adult males. For *Boreoheptagya* sp. 3, three new individuals were added, including one with a complete six-gene dataset.

A single adult male from Iran, designated here as *Boreoheptagya* sp. 6, represents another distinct lineage. Its phylogenetic position suggests it may represent an undescribed species restricted to the Middle East.

Finally, *B. legeri* and *B. aff. legeri* were recovered as sister species (clade not supported). Although morphologically similar, they represent distinct MOTUs according to the ASAP results. The sequences for *B. aff. legeri*, consisting only of DNA barcodes, are reported here for the first time. We also expanded the known range of *B. legeri* by adding four new individuals, including the first records from the Karachay-Cherkessia Republic.

Inter and intraspecific distances

The average intraspecific K2P distance for the COI5P barcode region, calculated for species represented by two or more individuals, was 0.54%. The highest intraspecific variation was observed in *B. sarymsactyensis* (1.22%), *B. aff. legeri* (1.13%), and *B. brevitarsis* from Iran (1.01%). In contrast, no intraspecific variation (0%) was detected in *Sasayusurika nigatana*, *B. (Shilovia) rara*, and *B. iranica*, where all sampled individuals shared a single haplotype.

The average interspecific distance within the genus *Boreoheptagya*—including the subgenera *Shilovia*, *Palatovia*, and *Kaluginia*, but excluding *Sasayusurika nigatana*—was 12.49%. The minimum interspecific distances were recorded between *Shilovia xinhuaewangi* and *S. yakovlevi* (4.46%), and between *Boreoheptagya* sp. 2 and *Boreoheptagya* sp. 3 (4.81%). Such distance values are close to or correspond to the minimum interspecific threshold for Diamesinae (Montagna *et al.* 2016; Makarchenko *et al.* 2023b; Semenchenko & Makarchenko 2025), which is typically around 5% K2P and can slightly decrease to 4.46% in the subgenus *Shilovia* (Makarchenko *et al.* 2020b). All other species pairs exceeded a 6% distance threshold, confirming their status as distinct molecular entities.

Species Delimitation (ASAP)

The ASAP analysis of the COI5P barcode dataset (alignment length: 658 bp) was used to independently test the morphological species hypotheses for the tribe Boreoheptagyiini. The best partitioning scheme, characterized by the lowest ASAP score of 3.5 (p-value = 6.37e-04), identified 22 distinct molecular operational taxonomic units (MOTUs) (Fig. 1).

This primary partition was defined by a threshold K2P distance of 2.87%. This molecular boundary effectively separated all recognized species within the tribe, including newly sequenced taxa such as *Sasayusurika nigatana*, *Boreoheptagya* sp. 7, and *B. aff. legeri*. The identified MOTUs showed perfect congruence with the phylogenetic tree topology and morphological identifications. Alternative partitioning schemes suggesting 25 or 23 MOTUs were rejected due to higher ASAP scores (5.0 and 5.5, respectively), confirming that the 22-species model is the most robust and parsimonious interpretation of the genetic data for this group.

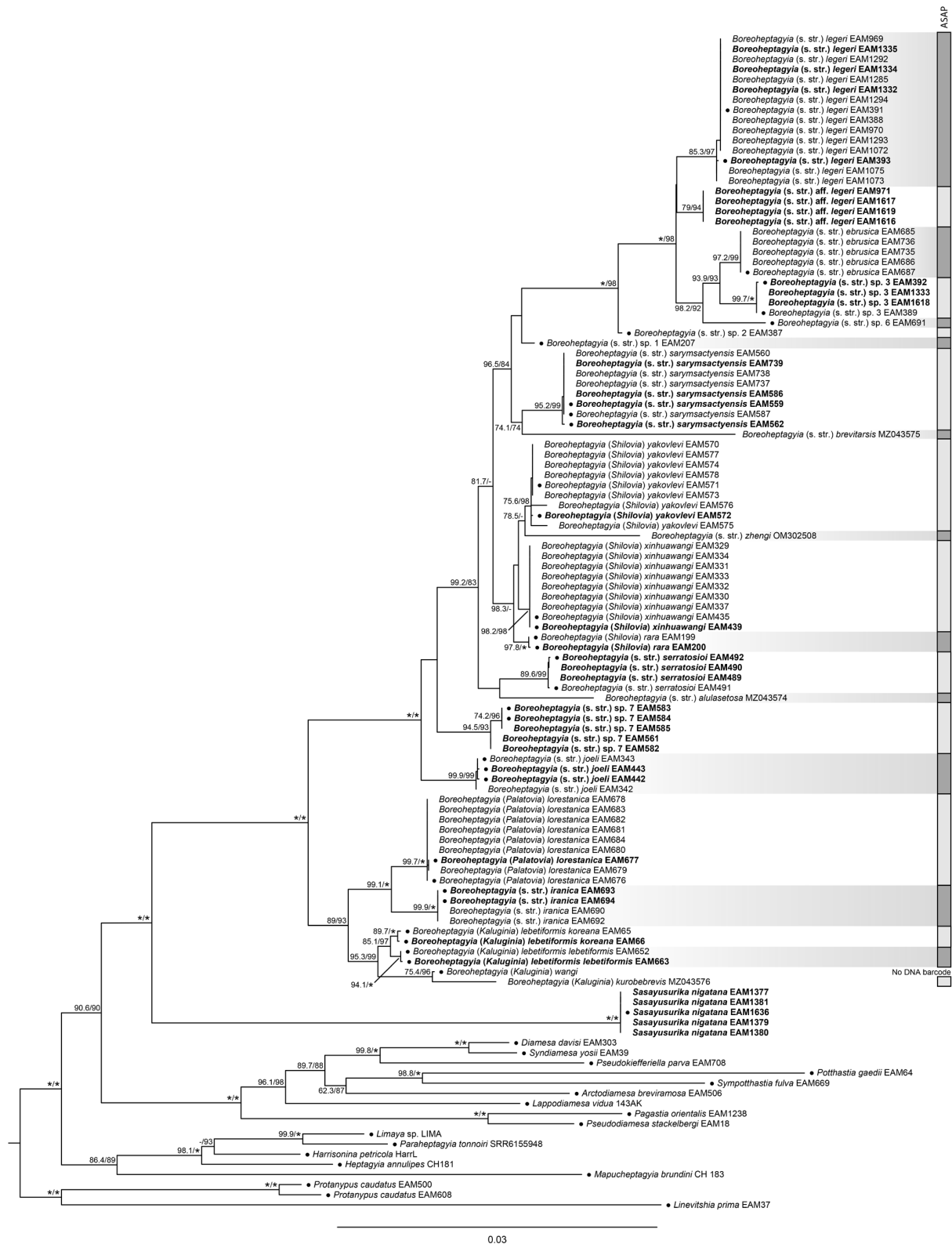


FIGURE 1. Maximum likelihood phylogenetic tree of the tribe Boreoheptagiini based on the combined analysis of six genes (18S, 28S, CAD4, COI5P, COI3P, and COII). Numbers at nodes indicate SH-aLRT support (%) and ultrafast bootstrap (UFB) values $\geq 70\%$. Specimen names in bold indicate new molecular data generated in this study (including new barcodes and additional markers for previously barcoded specimens). The black circle symbol (●) following a specimen ID denotes individuals for which the complete four-six gene dataset was obtained. Vertical colored bars on the right represent molecular species boundaries as delimited by the ASAP analysis (K2P distance). Outgroups include members of the tribes Heptagiini and Diamesini, as well as the subfamily Protanypodinae. Scale bar: 0.03 substitutions per site.

Taxonomic review of the tribe Boreoheptagiini Brundin by morphology

As mentioned above, as a result of the analysis of the obtained molecular genetic data, the structure of the tribes Diamesini and Boreoheptagiini has changed. Thus, the genus *Sasayusurika* was transferred from the first tribe to the tribe Boreoheptagiini, and the rank of the genera *Shilovia*, *Kaluginia* and *Palatovia* included in it was lowered to subgenera of the genus *Boreoheptagyia*. In this regard, below we present the new structure of the Boreoheptagiini tribe with all its taxa, their diagnosis based on morphological data, keys, descriptions and redescrptions (if need) for adult males as well as for immature stages of studied species. Also we point out some problems in the systematics of individual taxa.

Key to the genera and subgenera of the Boreoheptagiini tribe

Adult males

1. Antenna with 13 flagellomeres and well-developed plume; AR more than 2.5. Fourth tarsomere proximally cylindrical but with laterally extended adhesive pads distally. Wing with cross-vein MCu connecting posterior end of RM and fork FCu; R₄₊₅ almost devoid of setae except distally. Total length 6.0–7.8 mm, wing length 3.2–4.9 mm genus *Sasayusurika* Makarchenko
- Antenna with 5–13 flagellomeres and reduced plume (Figs 22–30); AR less than 0.82. Fourth tarsomere cordiform or cylindrical, without laterally extended adhesive pads. Wing without cross-vein MCu connecting RM and FCu; R₄₊₅ with setae. Total length 1.5–4.3 mm, wing length 1.6–2.6 mm. genus *Boreoheptagyia* Brundin 2
2. Vertex with a pair of conical frontal tubercles (Fig. 123). Antenna with 5–13 flagellomeres; pedicel bare. Acrostichals long, beginning near antepnotum and extending to near scutellum (Figs 31–32). Tarsomere 4 cordiform, shorter than tarsomere 5. Mid leg with pseudospurs on tarsomere 1; hind leg with pseudospurs on tarsomeres 1 and 2. Tergite IX broadly emarginated posteriorly, with or without small anal point on dorsal surface; aedeagal lobe membranous; gonocoxite simple with flat median field (Figs 55–56) subgenus *Boreoheptagyia* s. str.
- Vertex without frontal tubercles and not with the above combination of the characters 3
3. Antenna with 5–7 flagellomeres (Figs 24–25); pedicel with setae. R₂₊₃ reduced, clearly visible only in basal part (Figs 41–42); FCu distal to MCu. Acrostichals beginning near the antepnotum and extending near the middle of the mesonotum (Figs 33–35). Tarsomere 4 cordiform, shorter than tarsomere 5. Hypopygium with round-triangular or small, sometimes reduced anal point as well as without anal point; gonocoxite with small basal protuberance; gonostylus scoop-shaped with inner lobe bearing 5–6 megasetae as well as simple with twisted angle and stout megasetae at apex (Figs 57–59) subgenus *Kaluginia* Makarchenko
- Antenna with 5–6 flagellomeres (usually 5); pedicel bare. R₂₊₃ absent; FCu proximal to RM. Acrostichals beginning near the antepnotum and extending to near the scutellum. Tarsomere 4 cylindrical, shorter than tarsomere 5. Hypopygium without anal point. 4
4. Scutum covered with macrotrichia. Postnotum densely covered with aculeiform macrotrichia. Acrostichals in one row, short; dorsocentrals short and sparse, situated in two groups only in the anterior part of the mesonotum (Fig. 36). Fore, mid, and hind legs with pseudospurs on tarsomere 1. Hypopygium: tergite IX almost rectangular or inverted trapezoid; aedeagal lobe strongly sclerotized with complex structure (apex nose- or beak-shaped); gonocoxite with median volsella bearing short lobe basally; transverse sternapodeme narrow and triangular, with rounded apex; gonostylus wide basally, gradually tapering to rounded apex, with long setae along edges and several megasetae subapically subgenus *Palatovia* Makarchenko et Semenchenko
- Scutum bare. Postnotum with or without setae (Fig. 39), but without dense aculeiform macrotrichia. Acrostichals in 1–3 rows; dorsocentrals in 2–4 rows, extending along mesonotum (Figs 37–38). Fore, mid, and hind legs with pseudospurs on tarsomere 1. Hypopygium: tergite IX wide, with concave or almost straight posterior edge, covered with numerous very short setae; gonocoxite with long apical projection (“heel”) densely covered with long thin setae (this heel posterior to gonostylus 0.35–0.63 times as long as gonostylus); inferior volsella in form of tubercle densely covered with macrotrichiae and setae; aedeagal lobe weakly sclerotized, apical part hooked or fingerlike; gonostylus simple, almost straight or curved, distally with a tooth and short megaseta subgenus *Shilovia* Makarchenko

Pupae

1. Total length up to 6.8 mm. Frontal apotome with low tubercles (Fig. 9). Thoracic horn candle-shaped and consists of two parts: basal part large and wide, not sclerotized and semitransparent, apical part short, well sclerotized and finger-shaped (Figs 11–12). Pupae free-living, without special nest cases genus *Sasayusurika* Makarchenko
- Total length up to 4 mm. Frontal apotome with small conical spine-like tubercles (Fig. 79), sometimes with pair of long setae. Thoracic horn small, triangular, strongly sclerotized covered with short setae, sometimes with longitudinal groove (Figs 65, 80–81, 110, 180). Apophyses usually absent, poorly developed, but sometimes well developed. Pupae enclosed in gelatinous nest cases. genus *Boreoheptagyia* Brundin 2

2. Frontal apotome with conical spine-like tubercles and pair of long setae (Fig. 63)subgenus *Kaluginia* Makarchenko
- Frontal apotome only with conical tubercles. 3
3. Thoracic horn with longitudinal groove (Fig. 180) subgenus *Shilovia* Makarchenko
- Thoracic horn without longitudinal groove 4
4. Apophyses well developed (Fig. 161). Anal lobe with 1 dark brown median setae (Fig. 160).
- subgenus *Palatovia* Makarchenko et Semenchenko
- Apophyses absent or poor developed.subgenus *Boreoheptagyia* s. str.

Larvae of fourth instar

1. Large sized, up to 10.7 mm. Dorsal surface of head without tubercles. Antenna without pedestal. Premandible wide in distal part, with 1 tooth and strong, simple lateral spine (Fig. 15). Seta subdentalis of mandible narrow and long (Fig. 18). Seta interna absent. Mentum with 1 median and 6 pairs of lateral teeth; median tooth in 4 times as wide as first lateral tooth (Fig. 17). Both sides of maxilla with numerous long fantail situated setae (Fig. 19). Body without multipointed spines. Procercus not longer than wide, bearing 10 anal setae; lateral setae situate near procercus on the body (Fig. 21). Supraanal setae stronggenus *Sasayusurika* Makarchenko
- Medium sized, up to 8 mm long. Dorsal surface of head with some tubercles, ranging in shape from long angular tubercles to low protrusions; tubercles with or without setae (Figs 88–89, 106, 118). Antenna borne on short pedestal which with inner or sometimes outer processes (Figs 92, 145, 188). Premandible apically broad with 6–8 blunt teeth; lateral spine apically branched or plumose (Fig. 190). Seta subdentalis of mandible long and narrow, extending beyond apex of third inner tooth or minuscule, curved, not even reaching the tip of the last tooth (Fig. 150). Seta interna present, consisting of 10–18 simple to weakly serrate branches. Mentum with 1 or 2 median and 5–9 pairs of lateral teeth; median teeth (or tooth) are almost as wide as the first lateral teeth (Figs 91, 146). Maxilla with long fantail situated setae only from one side. Body with multipointed spines. Dorsum of thorax and abdomen with minute, closely set simple-, double- or multi-pointed spines usually forming regular pattern on thorax and 2 transverse bands on each abdominal segment (Fig. 144)
- genus *Boreoheptagyia* Brundin

Comment for keys. It is not feasible to create keys for the identification of *Boreoheptagyia* subgenera based on larvae, because this stage exhibits a high degree of morphological similarity, making it difficult to distinguish between subgenera.

Review of the Boreoheptagyiini tribe's composition

Genus *Sasayusurika* Makarchenko, stat. nov.

Sasayusurika Makarchenko, 1993: 118.

Sasayusurika Makarchenko; Sæther *et al.* 2000: 149; Willassen 2007: 315; Ashe & O'Connor 2009: 309; Makarchenko & Endo 2009: 67; Sæther & Andersen 2013: 155; Yamamoto & Yamamoto 2014: 250; Cranston & Tang 2024: 177.

Type of genus: *Sasayusurika aenigmata* Makarchenko, 1993 [= *Diamesa* (*Psilodiamesa*) *nigatana* Tokunaga, 1936], by original designation and monotype.

Generic diagnosis (emended)

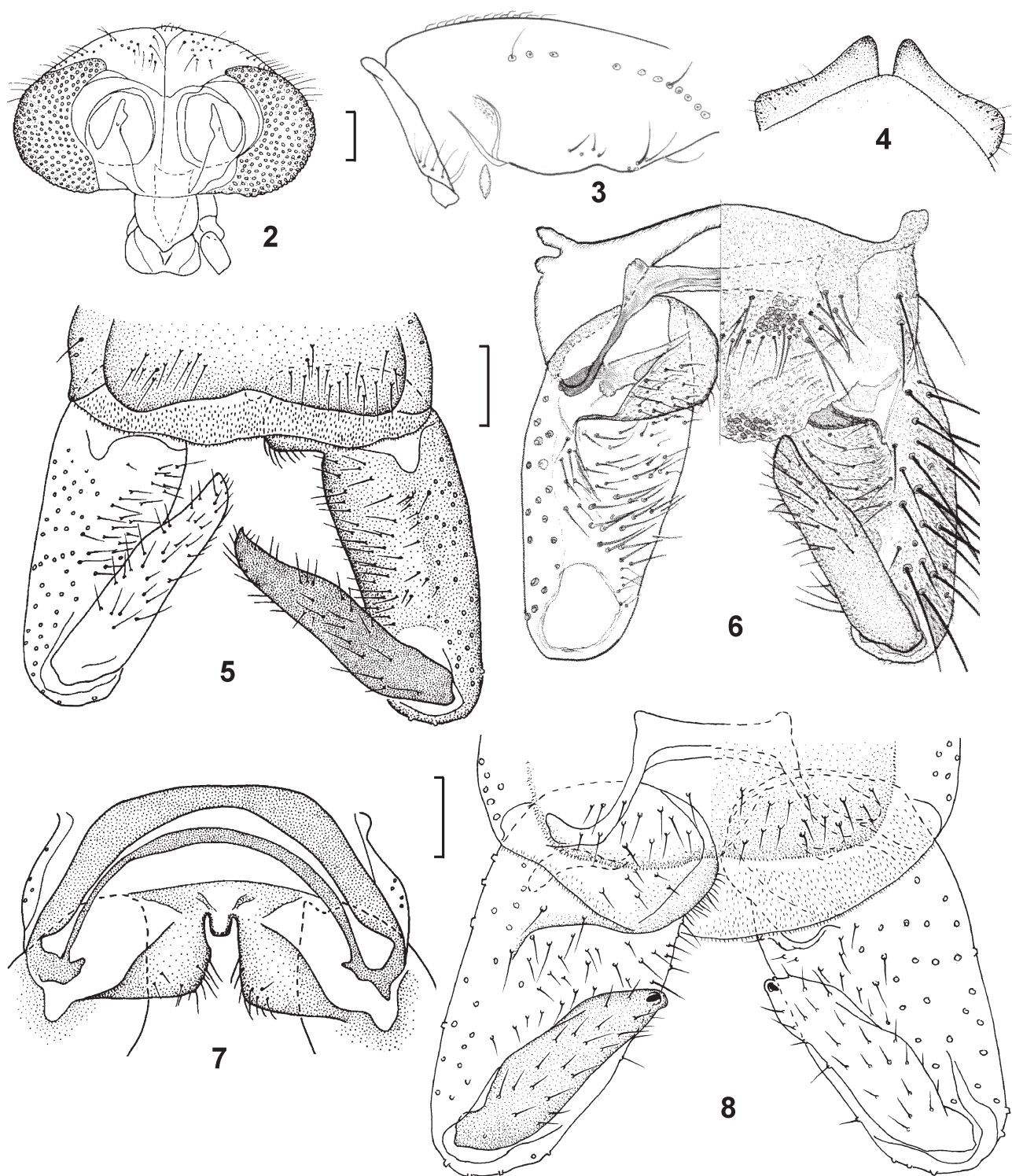
Based on the material from the East Palaearctic and Oriental Region, the generic diagnosis given by Makarchenko (1993), Willassen (2007), Makarchenko & Endo (2009), Sæther & Andersen (2013) should be emended as follows.

Adult male. Total length 6.0–7.8 mm. Wing length 3.2–4.9 mm.

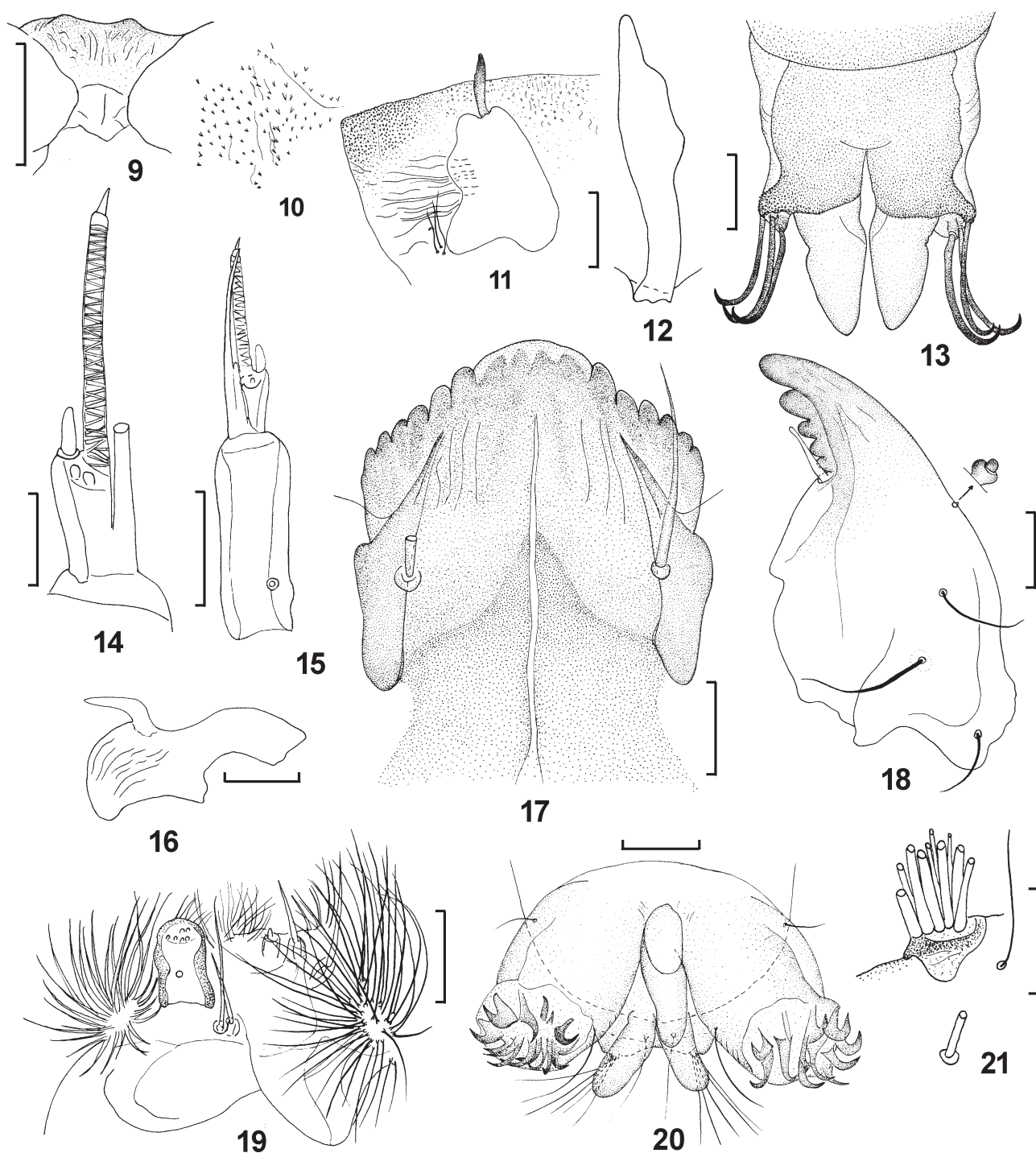
Head. Eyes slightly projecting dorsomedially, bare to very weakly pubescent (Fig. 2). Antenna with 13 flagellomeres and well-developed plume; pedicel with 4–6 setae; terminal flagellomere with 1 subapical seta; AR 2.52–3.0. Third palpomere in distal part with sensilla capitata. Clypeus without setae.

Thorax. Antepronotal lobes separated medially by U shaped notch (Fig. 4). Scutum with 11–15 acrostichals distributed posterior approximately to level of third dorsocentral seta (Fig. 3). Dorsocentrals 10–21, uniserial; prealars 10–14; supraalars 1–3; scutellars *ca* 50–70.

Wing. Wing membrane without setae, but with coarse microtrichia. R_{4+5} almost devoid of setae except distally. Posterior end of RM and fork FCu interconnected by cross-vein MCu. FCu proximal of RM. Squama with fringe of numerous setae in two rows; alula without setae.



FIGURES 2–8. The adult male of *Sasayusurika nigatana* (Tokunaga) from Japan (2, 4–5, 7), the Indian Himalaya (3, 6), and China (8). 2. head. 3. pronotum and mesonotum, lateral view. 4. pronotum, dorsal view. 5–6, 8. hypopygium, dorsal view. 7. basal part of gonocoxite. Scale bars: 50 μ m. Figs 2, 4–5, 7 after Makarchenko 1993; Figs 3 & 6 after Willassen 2007; Fig. 8 after Sun *et al.* 2019.



FIGURES 9–21. The pupa (9–13) and larva (14–21) of *Sasayusurika nigatana* (Tokunaga). 9. frontal apotoma. 10. small spines of anterior part of thorax. 11. anterior part of thorax with thoracic horn. 12. apical part of thoracic horn. 13. anal segment of male. 14. distal part of antenna. 15. antenna. 16. premandible. 17. mentum. 18. mandible. 19. maxilla. 20. anal segment with posterior parapods and anal papillae, from below. 21. procercus and lateral setae. Scale bars are as follows: Figs 12, 14–20 μm , Figs 13, 20–21—200 μm , Figs 9–11, 15–19—50 μm . Figs 8–21 after Makarchenko & Endo 2009.

Legs. Hind tibia with comb of setae. All fourth tarsi cylindrical proximally, but with laterally extended adhesive pads distally.

Hypopygium (Figs 5–8). Tergite IX narrow, without anal point. Transverse sternapodeme low, trapezoidal, arched with fairly straight anterior margin and anterolateral projections. Basal plate of gonocoxite rounded with

dense microtrichia and relatively weak setae. Medial field poorly delineated from rest of gonocoxite. Gonostylus reaching almost to basal plate, more or less parallel-sided at base and tapering about halfway towards apex, darker than gonocoxite; apical megaseta short. HR 1.5.

Pupa. Total length up to 6.8 mm. Exuviae brownish-grey or brown.

Cephalothorax. Frontal apotome without setae but with a pair of low tubercles (Fig. 9). Anteprenotum with 1 median and 1 lateral anteprenotals. Dorsocentrals reduced. Thorax intensive granulated by small spines in anterodorsal part, smooth in anterolateral

part and not so intensive granulated in middle and posteriodorsal parts; thoracic horn candle-shaped and consists of two parts: basal part large and wide, not sclerotized and semitransparent, apical part short, well sclerotized and finger-shaped; three precorneals present (Figs 10–12).

Abdomen. Tergites and sternites I–VIII and anal lobes uniformly covered by shagreen of small spinules. Tergites and sternites without posterior transverse row of large spines.

Segment I with 2 pairs of short hair-like lateral setae; segments II–VIII with 4 pairs of short hair-like lateral setae. Dorsal muscle marks bare. Anal lobe with 3 strong and long anal macrosetae which situated in anal-lateral angles of lobe and in distal part declinated; median setae and apical tubercle absent. Male genital sac extended beyond anal lobe, female genital sac not reaching apex of lobe (Fig. 13).

Larva. Total length 8.5–10.7 mm.

Antenna. With 5 segments; third annulated segment at least in 3 times longer than second, fourth and fifth segments very short. Style less than 1/3 length of segment 3. Lauterborn organs shorter and style longer than third segment (Figs 14–15).

Labrum. S_{I–IV} setae simple and seta-like. Labral lamellae consisting of long, narrow, spine-like lobes. Pecten epipharyngis consisting of 5 long rounded scales. Premandible wide in distal part, with 1 tooth and strong, simple lateral spine (Fig. 16).

Mandible. Apical tooth shorter than combined width of four inner teeth. Seta subdentalis narrow and long. Seta interna absent. Median part of outer margin with small sensilla (Fig. 18).

Mentum. With 1 median and 6 pairs of lateral teeth; median tooth in 4 times as wide as first lateral tooth; median tooth slightly lighter in color than remaining brownish lateral teeth. Ventromental plate elongate and narrow. Setae submenti strong and arising closer to mentum than to postoccipital margin (Fig. 17).

Maxilla. Palp longer than wide. Seta maxillaris simple. Both sides of maxilla with numerous long fantail situated setae (Fig. 19).

Abdomen. Anterior and posterior parapods separate, each bearing apical crown of long narrow claws (Fig. 20). Procercus not longer than wide, bearing 10 anal setae, without lateral setae; lateral setae situate near procercus on the body (Fig. 21). Supraanal setae strong. Body setae dark and distinct good visible.

Remarks. The genus occupied a separate position in the subfamily Diamesinae, primarily due to the original structure of the immature stages, namely the pupa, which has an original thoracic horn in the shape of a candle. No representative of the subfamily has such a thoracic horn. On the other hand, the larva has the same structure of antennae and subdental seta of mandible of the lower jaw as all Boreoheptagyini. These diagnostic features, to some extent, and in addition to genetic data, justify the transfer of the genus to the Boreoheptagyini tribe.

The composition of the genus *Sasayusurika* Makarchenko

Sasayusurika nigatana (Tokunaga)

Diamesa (*Psilodiamesa*) *nigatana* Tokunaga, 1936: 537.

Sasayusurika aenigmata Makarchenko, 1993: 119; Sæther *et al.* 2000: 149; Willassen 2007: 316.

Sasayusurika nigatana (Tokunaga, 1936); Ashe & O'Connor 2009: 309; Makarchenko & Endo 2009: 67; Yamamoto & Yamamoto 2014: 250; Sun *et al.* 2019: 547; Cranston & Tang 2024: 177.

Distribution. Known from Japan, India, and Oriental China.

Genus *Boreoheptagyia* Brundin

Heptagyia auct., partim

Heptagyia auct., partim

Boreoheptagyia Brundin, 1966 : 420; Makarchenko 1985: 37, 2006: 257; Serra-Tosio 1989: 135; Sæther *et al.* 2000: 222.

Neopodonomus Chaudhuri *et* Ghosh, 1981: 373.

Toyamadiamesa Sasa, 1994 : 49.

Type of genus: *Heptagyia* [= *Heptagyia*] *rugosa* Saunders, 1930, by original designation.

Diagnosis of the genus *Boreoheptagyia* Brundin

Based on the material from the East Palaearctic and Oriental Region, the generic diagnosis given by Brundin (1966), Serra-Tosio (1989), Oliver (1983, 1986, 1989), Sæther & Andersen (2013) and our data should be emended as follows.

Adult male. Total length 1.4–4.3 mm, wing length 1.6–2.6 mm.

Head. Frontal tubercles on vertex either present as a pair of conical projections (in the nominate subgenus) or absent. Eyes bare or pubescent, not extended dorsomedially (or slightly extended in *Boreoheptagyia* s. str.). Antennae with reduced plume; terminal flagellomere short, club-shaped, bearing 1–3 subapical setae. Number of flagellomeres varies from 5 to 13. Antennal ratio (AR) less than 0.82. Pedicel bare or with some setae.

Wing. Wing membrane with coarse punctation, without macrotrichiae. Anal lobe of wing from right-angled to moderately developed. Costa moderately extended.

Legs. Tarsomere 4 cordiform or cylindrical, but always shorter than tarsomere 5; pseudospurs (thick spinules) present on tarsomere 1 of mid and hind legs in most subgenera, but may be absent on hind legs.

Hypopygium variable: tergite IX with or without anal point; gonostylus simple or scoop-shaped.

Pupa. Small, up to 4 mm long. Exuviae light to yellow-brown.

Cephalothorax. Frontal apotome with small conical cephalic tubercles, sometimes with pair of long setae (Figs 63, 79, 156). Thorax with 2 median and 2 lateral anteprenotals, dorsally wrinkled, in the anterior half it is dorsally and dorsolaterally granulated, dorsolaterally also with small spines (Figs 82, 84–85). Thoracic horn small, triangular, strongly sclerotized, usually covered with short hair-like setae (Figs 65, 110, 163, 180). Three precorneals and 2 dorsocentrals present; supraalar not seen. All thoracic setae small, often difficult to see. Fore and mid leg sheaths straight, directed posteriorly; hind leg sheath recurved under posterior part of wing sheath; tips of each leg sheath moderately extended posterior to apex of wing sheath with apices of fore and mid leg sheaths slightly curved laterally.

Abdomen. Tergite I often without shagreen; II–VIII with median and lateral shagreen; IX with or without anteromedian shagreen. Sternites without shagreen or with very delicate shagreen of small spinules, which is visible only under high magnification of a microscope (Figs 87, 115, 168). Tergites and sternites without posterior spines. Apophyses, with rare exceptions, are not developed.

Abdominal setation: Tergites I–VII with 5 D setae; VIII with 1 D seta. Segments I–VIII with 4 simple, ventral L setae. Sternites I–VII with 4 V setae; VIII with 1 V seta.

Anal lobe broad with truncated apex and flange-like lateral margins; 3 strong, apically hooked anal macrosetae present on lateral margin of lobe; 1–2 dorsomedial and 1 ventromedial setae present; fringe and apical tubercle absent. Male genital sac broad, strongly extending beyond anal lobe and sometimes apex curved (Figs 83, 160).

Pupae enclosed in gelatinous nest cases which with double wall; external wall thick, gelatinous, convex dorsally, oval; internal wall of pupal case very thin, hyaline, parchmentlike, closely and completely surrounding pupal body; larval skin retained on posterior segments of pupa, being enclosed within the parchmentlike sack together with pupa (Figs 128–129).

Larva. Medium sized, up to 8 mm long.

Dorsal surface of head. With some tubercles, ranging in shape from long angular tubercles to low protrusions (Figs 88–89, 97, 106, 145, 187, 195); tubercles with or without setae.

Antenna. With 5 segments; annulated segment 3 often longer than second, and fourth very short. Style and Lauterborn organs less than half the length of segment 3. Borne on short pedestal; pedestal often with inner and outer processes (Figs 88–89, 90, 92).

Labrum. S_I seta-like; S_{II} simple, often narrow leaf-shaped (Fig. 147). Labral lamellae consisting of 2 broad pectinate lobes. Pecten epipharyngis consisting of 5 broad, elongate, apically blunt scales. Chaetulae laterales

covered by pecten epipharyngis. Premandible apically broad with 6–8 blunt teeth; lateral spine apically branched or plumose (Fig. 93).

Mandible. Apical tooth partly dorsal to and subequal in size to first inner tooth; 4 inner teeth present. Seta subdentalis often curved, extending beyond apex of third inner tooth and often reaches the top of the apical tooth, apically pointed but sometimes it is minuscule, curved, not even reaching the tip of the last tooth (Figs 96, 109, 150, 172). Seta interna consisting of 10–24 simple to weakly serrate branches.

Mentum. Narrow with 1 or 2 median and 6–9 pairs of lateral teeth; convex with teeth decreasing in size from median to lateral or truncated with 4–6 teeth across apex subequal in size and larger than teeth along sides (Figs 91, 108, 146, 175). Ventromental plate elongate and narrow. Setae submenti arising closer to mentum than to postoccipital margin.

Maxilla. Palp with a lateral sensillum divided into 5–6 pointed lamellae. Chaetulae of palpiger setose. Lamellae of galea setose.

Body. Anterior parapods fused, apically divided into 2 lobes, with each lobe bearing circle of claws. Posterior parapods partly fused basally, each bearing circle of claws (Fig. 100). Anal end bent ventrally. Procercus very short, often absent; 6–8 short anal setae present (Figs 121, 154, 179). Two pairs of anal tubules present; shorter than posterior parapods; 1 tubule directed distoventrally, often extending ventrally to posterior parapods. Dorsum of thorax and abdomen with minute, closely set simple-, double- or multi-pointed spines usually forming regular pattern on thorax and 2 transverse bands on each abdominal segment (Figs 99, 117, 144, 177). The sculpture of the surface of the thorax and abdominal tergites can be varied - reticulated, honeycombed, tuberculate, etc. (Figs 97, 119, 178, 196).

The composition of the genus *Boreoheptagyia*

The genus includes four subgenera: *Boreoheptagyia* s. str., *Kaluginia*, *Palatovia* and *Shilovia*.

Subgenus *Boreoheptagyia* s. str.

Type of subgenus: *Heptagyia* [= *Heptagyia*] *rugosa* Saunders, 1930, by original designation.

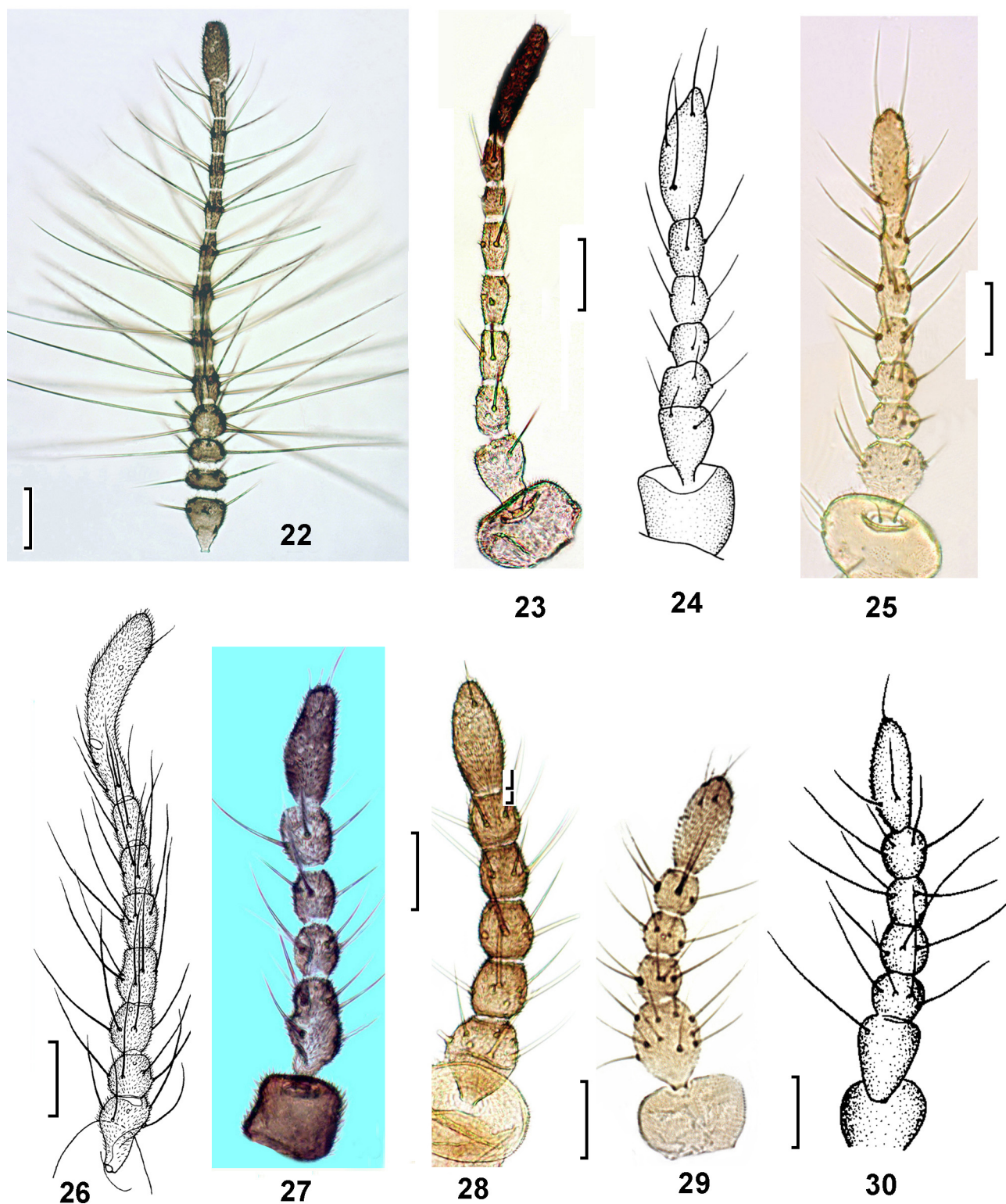
Subgeneric diagnosis

Adult male. Head. Eye bare or pubescent, slightly or not extended dorsomedially. Temporal setae numerous, consisting of inner and outer verticals, postorbitals and frontals; orbitals absent. Vertex with pair of conical frontal tubercles, sometimes with setae.

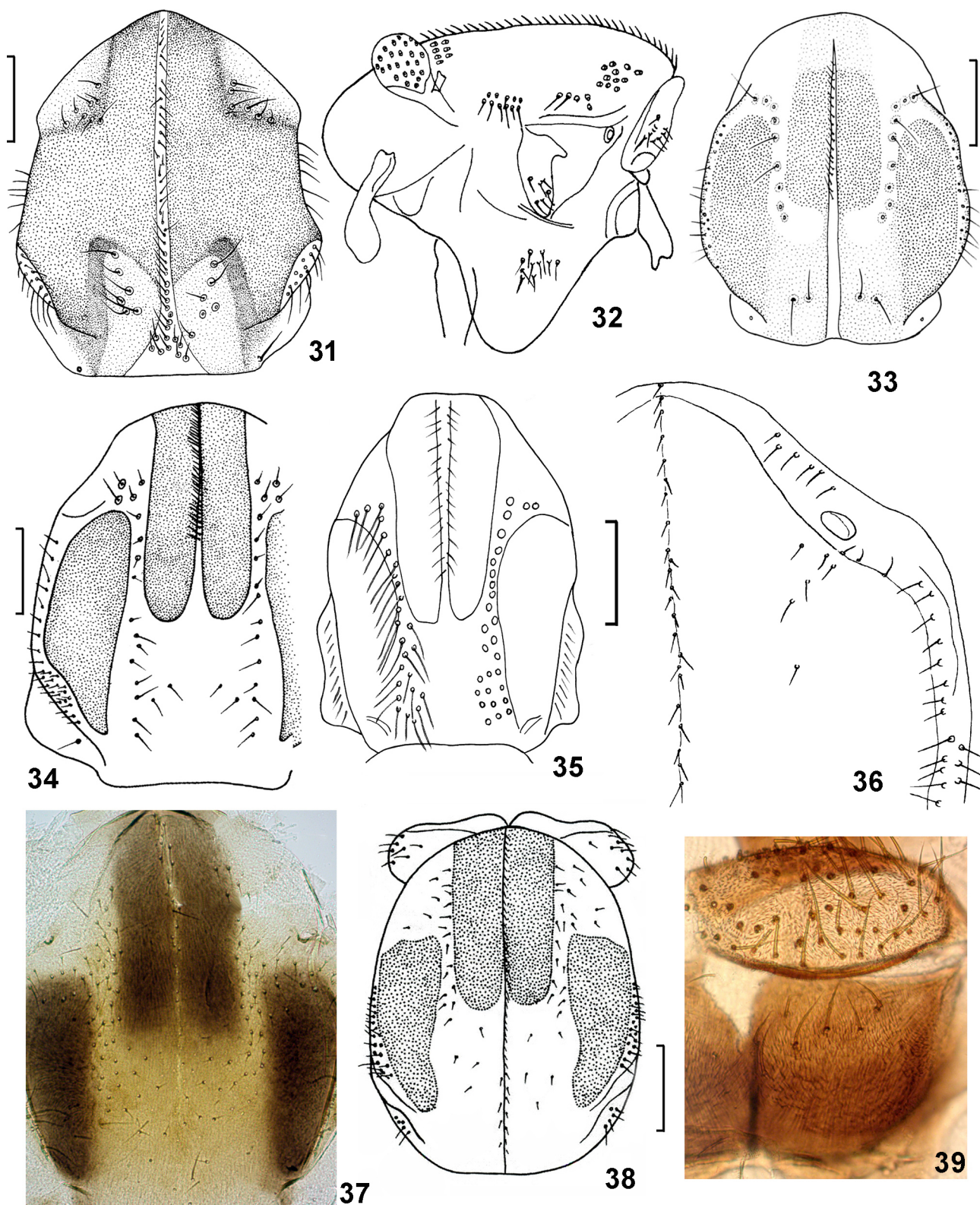
Antenna. Distinctive with reduced plume and short club-shaped terminal flagellomere; sometimes antenna female-like in appearance. Scape and pedicel bare. Flagellum with 5–13 flagellomeres; terminal flagellomere with 1–3 subapical setae (Figs 22–23, 26). AR of antenna with 5–8 flagellomeres is 0.15–0.82; with 13 flagellomeres—0.11–0.22.

Thorax. Anteprenotal lobes in contact to widely separated medially; dorsal anteprenotals present or absent; ventral anteprenotals present, sometimes extending on to middle part of lobe. Scutum broad, low, sometimes extended over anteprenotal notch, and covered with well-developed setae. Acrostichals long, beginning near anteprenotum and extending to near scutellum, sometimes diverging near scutellum; dorsocentrals in 1–3 rows as well as in 2 groups (near scutellum and on humeral area) or in one group in humeral area only; prealars extending anterior to level of median anepisternum II, sometimes to parapsidal suture; scutellum covered with setae; preepisternum and MAII with or without setae (Figs 31, 38).

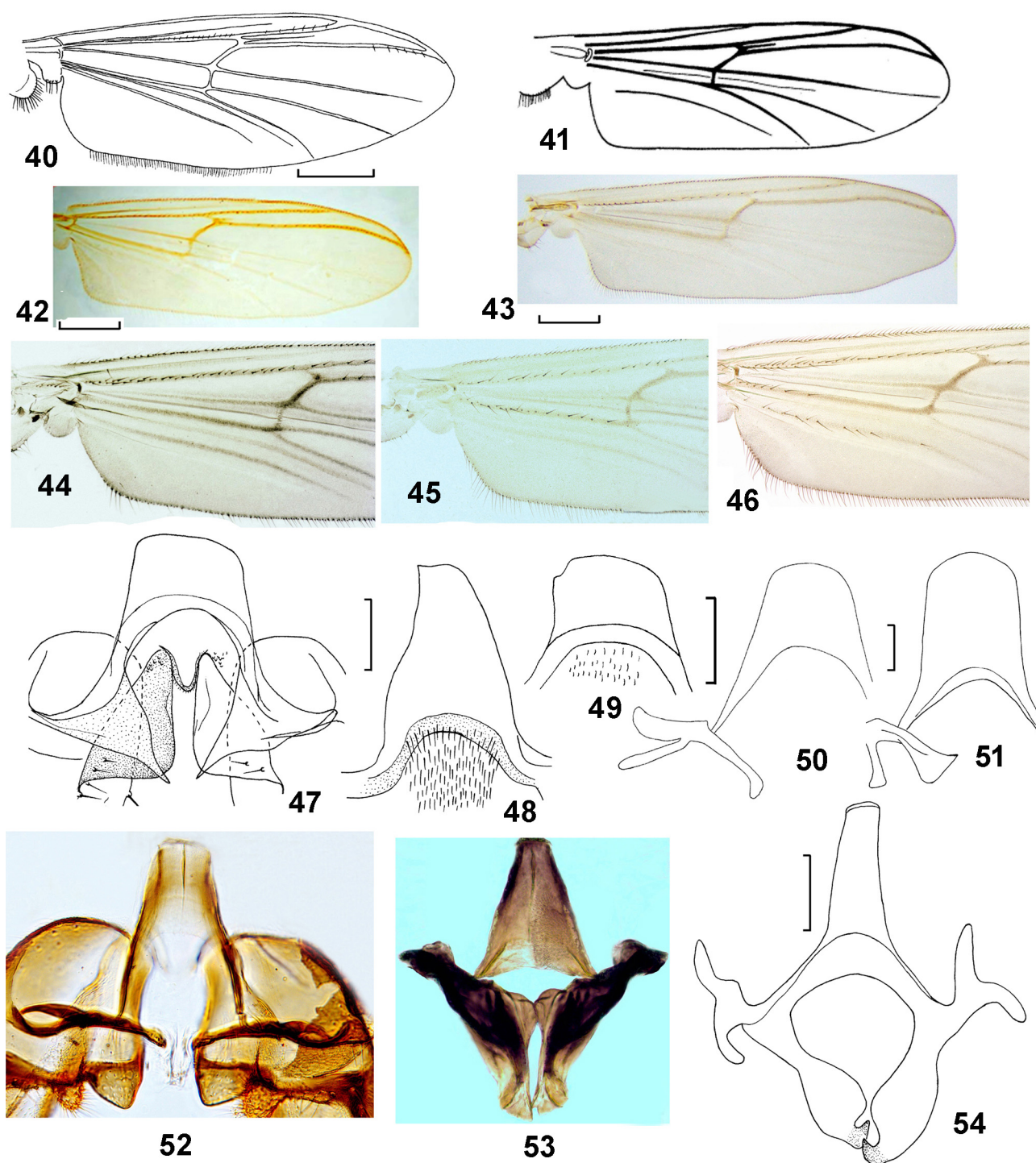
Wing. Membrane without setae and with very coarse punctation. Anal lobe right angled to slightly produced. Costa moderately produced; RM faint, ending before or in costa about 1/3 of distance from R, to R₄₊₅; FCu proximal to distal to RM. R₄₊₅ with setae. R₂₊₃ developed. Squama fully fringed (Fig. 40).



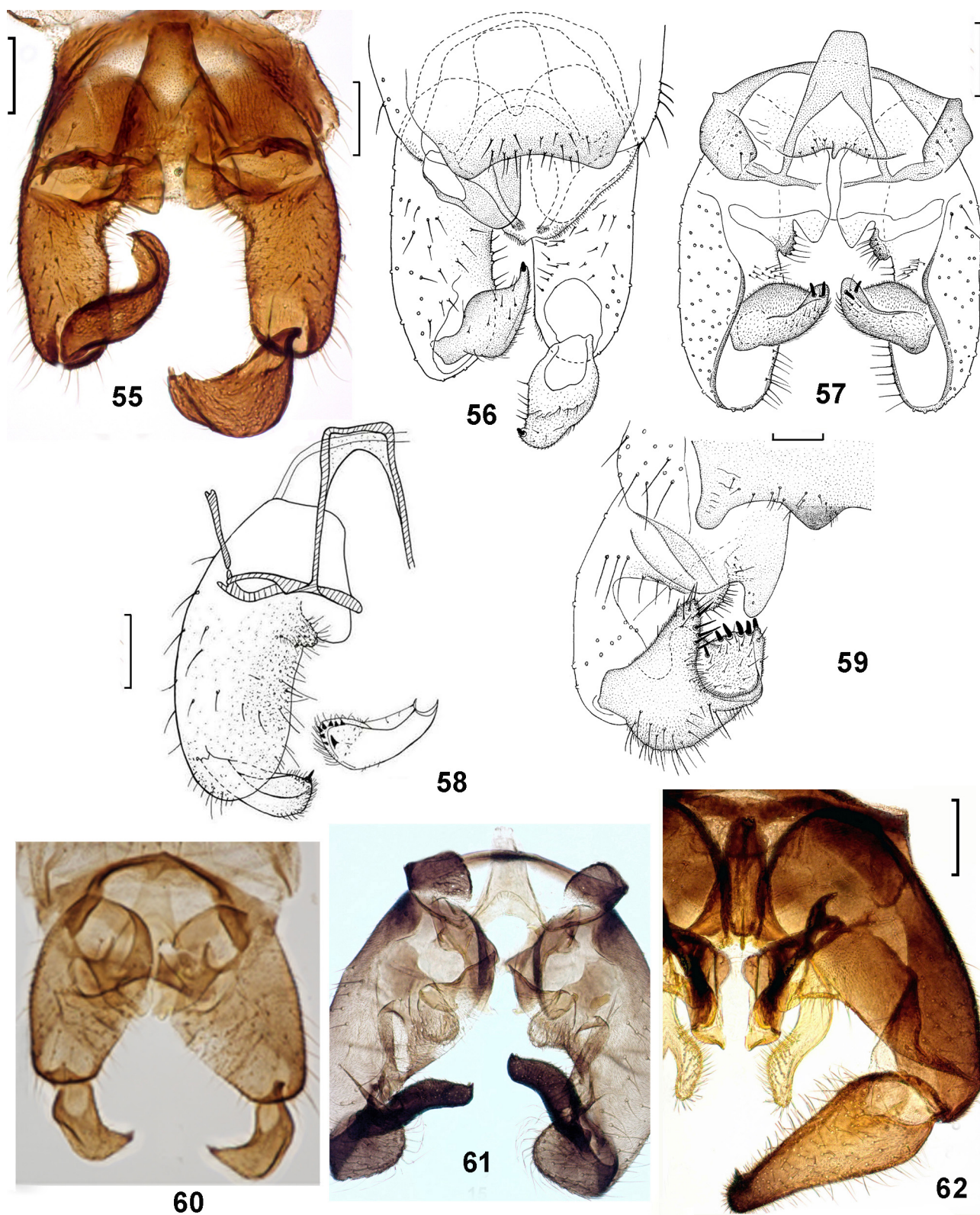
FIGURES 22–30. Antennae of Boreoheptagyini adult males. 22. *Boreoheptagia* (s. str.) *iranica* Makarchenko. 23. *B.* (s. str.) *joeli* Makarchenko. k 24. *B.* (*Kaluginia*) *unica* Makarchenko. 25. *B.* (*K.*) *lebetiformis lebetiformis* Makarchenko. 26. *B.* (s. str.) *nepalensis* Makarchenko *et* Endo. 27. *B.* (*Palatovia*) *lorestanica* Makarchenko *et* Semenchenko. 28. *B.* (*Shilovia*) *xinhuawangi* Makarchenko *et* Semenchenko. 29. *B.* (*S.*) *rara* Makarchenko. 30. *B.* (s. str.) *tibetica* Makarchenko *et* Wang. Scale bars: 50 μ m. Figs 22–23, 27 after Makarchenko *et al.* 2020c; Fig. 24 after Makarchenko 1994; Fig. 25 after Makarchenko *et al.* 2018; Fig. 26 after Makarchenko *et al.* 2008; Figs 28–29 after Makarchenko *et al.* 2020b; Fig. 30 after Makarchenko *et al.* 1996.



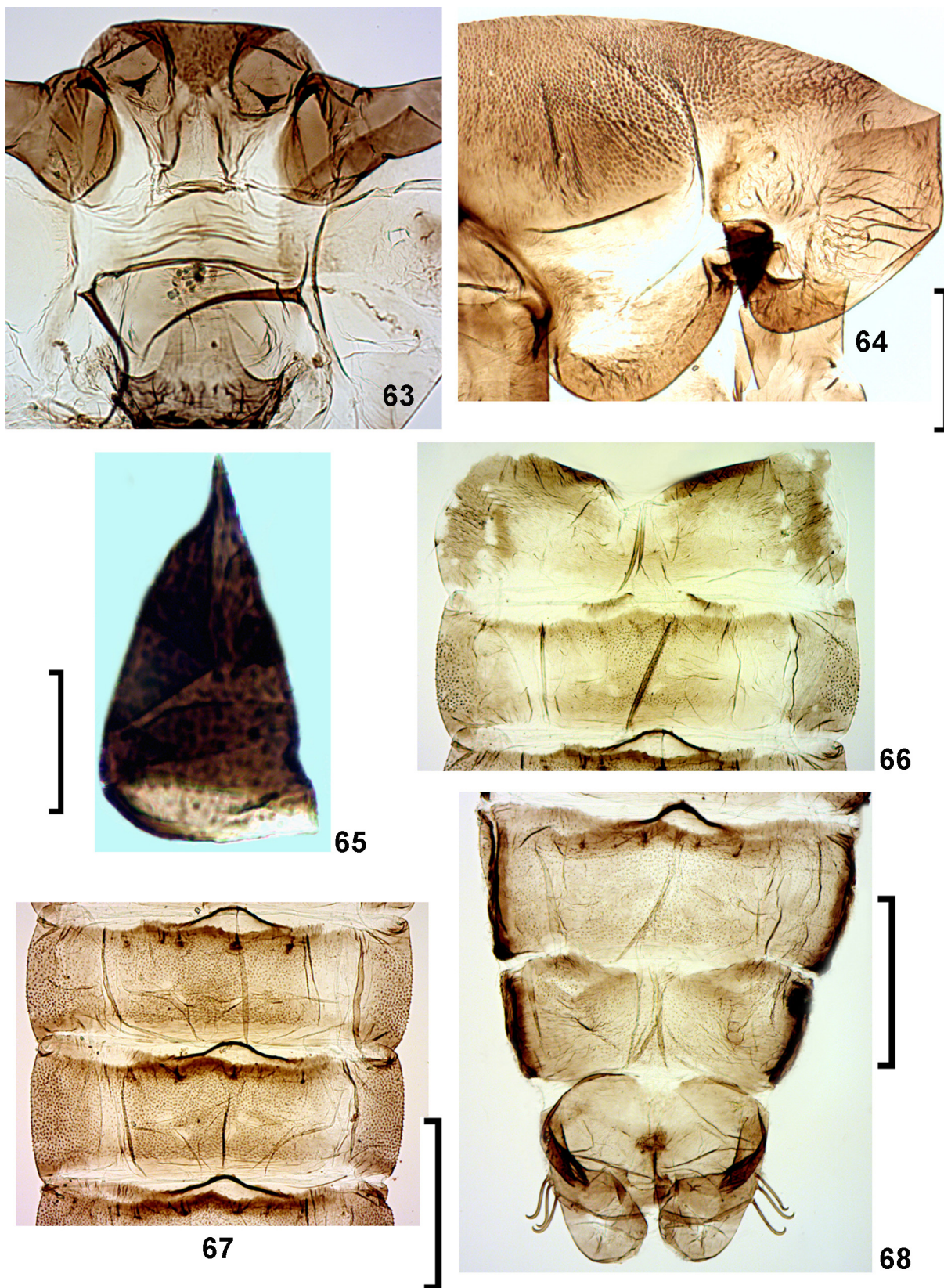
FIGURES 31–39. Parts of thorax of Boreoheptagyini adult males. 31. Scutum in dorsal view of *Boreoheptagyia* (s. str.) *nepalensis* Makarchenko *et* Endo. 32. thorax of *B.* (s. str.) *sasai* Makarchenko *et* Endo in lateral view. 33. *B.* (*Kaluginia*) *unica* Makarchenko. 34. *B.* (*K.*) *lebetiformis lebetiformis* Makarchenko. 35. *B.* (*K.*) *kurobebrevis* (Sasa *et* Okazawa). 36. *B.* (*Palatovia*) *lorestanica* Makarchenko *et* Semenchenko. 37. *B.* (*Shilovia*) *yakovlevi* Makarchenko *et* Semenchenko. 38. anteprenotum and scutum of *B.* (*S.*) *rara* Makarchenko. 39. scutellum and postnotum of *B.* (*S.*) *xinhuwangi* Makarchenko *et* Semenchenko. Scale bars: 200 µm. Fig. 31–32 after Makarchenko *et al.* 2008; Fig. 33 after Makarchenko 1994; Fig. 34 after Makarchenko *et al.* 2018; Fig. 35 after Sasa & Okazawa 1992; Fig. 36 after Makarchenko *et al.* 2020c; Figs 37–39 after Makarchenko *et al.* 2020b.



FIGURES 40–54. Wings (40–46), skeleton (47–54) and transverse sternapodeme (48–51) of Boreoheptagyini adult males. 40. *Boreoheptagyia* (s. str.) *nepalensis* Makarchenko *et* Endo. 41. *B. (K.) lebetiformis* Makarchenko. 42. *B. (K.) kurobebrevis* (Sasa *et* Okazawa). 43, 53. *B. (Palatovia) lorestanica* Makarchenko *et* Semenchenko. 44. *B. (S.) yakovlevi* Makarchenko *et* Semenchenko. 45. *B. (Shilovia) xinhuaewangi* Makarchenko *et* Semenchenko. 46, 54. *B. (S.) rara* Makarchenko. 47. *B. (s. str.) brevitarsis* (Tokunaga). 48. *B. (s. str.) joeli* Makarchenko. 49. *B. (s. str.) sarymsactyensis* Makarchenko. 50–51. *B. (K.) lebetiformis* Makarchenko. 52. *B. (K.) wangi* Song *et* Qi. Scale bars: 50 μ m. Fig. 40 after Makarchenko *et al.* 2008; Fig. 41, 50–51 after Makarchenko *et al.* 2018; Fig. 42 after Sasa & Okazawa 1992; Figs. 43, 53, 47–49 after Makarchenko *et al.* 2020c; Figs. 44–46, 54 after Makarchenko *et al.* 2020b; Fig. 52 after Song *et al.* 2026.



FIGURES 55–62. Hypopygium of Boreoheptagyini adult males. 55. *Boreoheptagyia* (s. str.) *monticola* Serra-Tosio. 56. *B.* (s. str.) *alulasetosa* Makarchenko, Wu et Wang. 57. *B.* (*Kaluginia*) *unica* Makarchenko. 58. *B.* (*K.*) *wangi* Song et Qi. 59. *B.* (*K.*) *lebetiformis*. 60. *B.* (*Shilovia*) *zhengi* Lin et Liu. 61. *B.* (*S.*) *xinhuawang*i Makarchenko et Semenchenko. 62. *B.* (*Palatovia*) *lorestanica* Makarchenko et Semenchenko. Scale bars: 50 μ m. Fig. 56 after Makarchenko et al. 2008; Fig. 57 after Makarchenko 1994; Fig. 58 after Song et al. 2026; Fig. 59 after Makarchenko et al. 2018; Fig. 60 after Lin et al. 2021; Fig. 61 after Makarchenko et al. 2020b; Fig. 62 after Makarchenko et al. 2020c.



FIGURES 63–68. Pupa of *Kaluginia lebetiformis lebetiformis* Makarchenko. 63. frontal apotome and ocular field. 64. anterior part of thorax, lateral view. 65. thoracic horn. 66. tergites I–II. 67. tergites II–IV. 68. tergites VII–VIII and anal segment. FS—frontal setae. Figs 63–68 after Makarchenko *et al.* 2020a. Scale bars are as follows: Figs 63–64, 66–68—200 µm, Fig. 65—50 µm.

Legs. Tibiae with or without light coloured ring; spurs comparatively short, usually not longer than width of tibial apex. Fore leg without pseudospurs; mid leg with pseudospurs on tarsomere 1; hind leg with pseudospurs on tarsomeres 1 and 2; tarsomere 1 of hind leg with or without sensilla chaetica. Tarsomere 4 cordiform, shorter than tarsomere 5.

Hypopygium (Figs 55–56, 73, 103). Tergite IX broadly emarginated posteriorly, with or without small anal point on dorsal surface. Phallapodeme weakly sclerotized; aedeagal lobe membranous, sometimes with spines or setae (Figs 47–49). Gonocoxite simple with flat median field.

Key to the species of subgenus *Boreoheptagyia* s. str.

Adult males

1. Antenna with 5 flagellomeres. Tergite IX with a small anal point. Gonocoxites with, at their base and on their ventral side, a tuft of long setae directed backwards. Setae of the proximo-superior margin of the gonostylus spine-shaped *B. (s. str.) lurida* (Garrett)
- Antenna with more than 5 flagellomeres. Tergite IX without anal point. Gonocoxites without tuft of long setae at their base. None of the setae of the gonostylus spine-shaped 2
2. Antenna with 12–13 flagellomeres 3
- Antenna with 6–9 flagellomeres 18
3. Antenna with 12 flagellomeres 4
- Antenna with 13 flagellomeres 5
4. Gonostylus with large rounded-triangular wing-like lobe along the outer edge (Moubayed 1992, Fig. 7). AR 0.26–0.27 *B. (s. str.) phoenicia* Moubayed
- Gonostylus without wing-like lobe along the outer edge, greatly enlarged in its basal half, covered with microtrichiae and fine, rather long setae (Serra-Tosio 1989, Figs 7, 9). AR 0.13. *B. (s. str.) alpicola* Serra-Tosio
5. Dc setae are grouped only in anterior part of mesonotum 6
- Dc setae in two groups, anterior and posterior or in one row 9
6. Eyes hairy. Transverse sternapodeme low, wide and trapezoidal (Serra-Tosio 1989, Figs 24, 26). *B. (s. str.) dasyops* Serra-Tosio
- Eyes bare or pubescence. Transverse sternapodeme different shape. 7
7. Ac setae length < 60 μ . AR 0.09 *B. (s. str.) monticola* Serra-Tosio
- Ac setae length > 60 μ . AR 0.13–0.15 8
8. Prealars 12. Aedeagal lobe with some distal teeth (Makarchenko *et al.* 2008, Fig. 8) *B. ambigua* Makarchenko, Wu et Wang
- Prealars 1–4. Aedeagal lobe without teeth (Makarchenko *et al.* 2008, Fig. 12) *B. xinglongiensis* Makarchenko, Wu et Wang
9. Dc setae in one row 10
- Dc setae in two groups, anterior and posterior 11
10. Basal plate of gonocoxite rounded or triangular-rounded, rather wide. Transverse sternapodeme tall, with chopped apex (Makarchenko *et al.* 2020c, Fig. 19) *B. (s. str.) iranica* Makarchenko
- Basal plate of gonocoxite rounded at the end, rather narrow. Transverse sternapodeme in the form of narrow, pigmented blade (Serra-Tosio 1989, Fig. 87) *B. (s. str.) rugosa* (Sounders)
11. Alula with 3–4 setae. Gonostylus short and inflated, with very short, narrow apical part; apical part of aedeagal lobe with many small spinules (Makarchenko *et al.* 2008, Figs 1–2) *B. (s. str.) alulasetosa* Makarchenko, Wu et Wang
- Alula bare. Gonostylus and aedeagal lobe different 12
12. Transverse sternapodeme in distal part with field of small spinules 13
- Transverse sternapodeme without small spinules in distal part 14
13. Preepisternum and median anepisternum II with setae. Scutellars 58–62. Gonostylus with wide median part and short narrow apical part (Makarchenko *et al.* 2008, Fig. 32) *B. (s. str.) sasai* Makarchenko et Endo
- Setae only on preepisternum. Scutellars 119–124. Gonostylus wrinkled, slightly curved (Makarchenko *et al.* 2020c, Fig. 45) *B. (s. str.) sarymsactyensis* Makarchenko
14. AR 0.21–0.22. Transverse sternapodeme high trapezoidal. Aedeagal lobe is thin and rod-shaped (Serra-Tosio 1983, Fig. 13) *B. (s. str.) rotunda* Serra-Tosio
- AR 0.14–0.18. Transverse sternapodeme and aedeagal lobe different shape 15
15. Setae on preepisternum present. Transverse sternapodeme broad-bladed. Aedeagal lobe transparent, with indistinct outline (Fig. 103) *B. (s. str.) legeri* (Goetghebuer)
- Setae on preepisternum absent. Transverse sternapodeme different shape. Aedeagal lobe triangular or with wide basal 1/3 and thin rod-shape distal part 16
16. Aedeagal with wide basal 1/3 and thin rod-shape distal part (Fig. 125) *B. (s. str.) serratosioi* sp. nov.
- Aedeagal lobe triangular 17

17. Aedeagal lobe narrowly triangular, dagger-shaped (Fig. 74). *B. (s. str.) elbursica* **sp. nov.**
- Aedeagal lobe widely triangular (Makarchenko *et al.* 2008, Fig. 19) *B. (s. str.) brevitarsis* (Tokunaga)
18. Antenna with 6 flagellomeres 19
- Antenna with 8 flagellomeres 20
19. Hypopygium with a median pointed aedeagal lobe, knob-like, heavily sclerotized inferior volsella, gonostylus enlarged at basis (Rossaro 2017, Fig. 1H) *B. (s. str.) ortladamellica* Rossaro
- The aedeagal lobe is narrowly triangular Inferior volsella reduced. Gonostylus curved and widest in basal 1/3 (Makarchenko *et al.* 1996, Fig. 1) *B. (s. str.) tibetica* Makarchenko et Wang
20. Aedeagal lobe weakly sclerotized, apical part smooth. Gonostylus narrow, slightly curved, without megaseta (Makarchenko *et al.* 2008, Fig. 25) *B. (s. str.) nepalensis* Makarchenko et Endo
- Gonostylus with megaseta 21
21. Gonostylus bilobate, inner lobe covered with numerous setae and 1 apical megaseta; outer lobe wide and without setae (Makarchenko *et al.* 2020c, Fig. 18) *B. (s. str.) joeli* Makarchenko
- Gonostylus simple, greatly enlarged, covered with microtrichiae and fine, fairly long setae; setae on the inferodistal margin and distal tip shorter and sturdier, shaped like small spines; three claws at the tip of each gonostylus (Serra-Tosio 1989, Figs 16–17) *B. (s. str.) cinctipes* (Edwards)

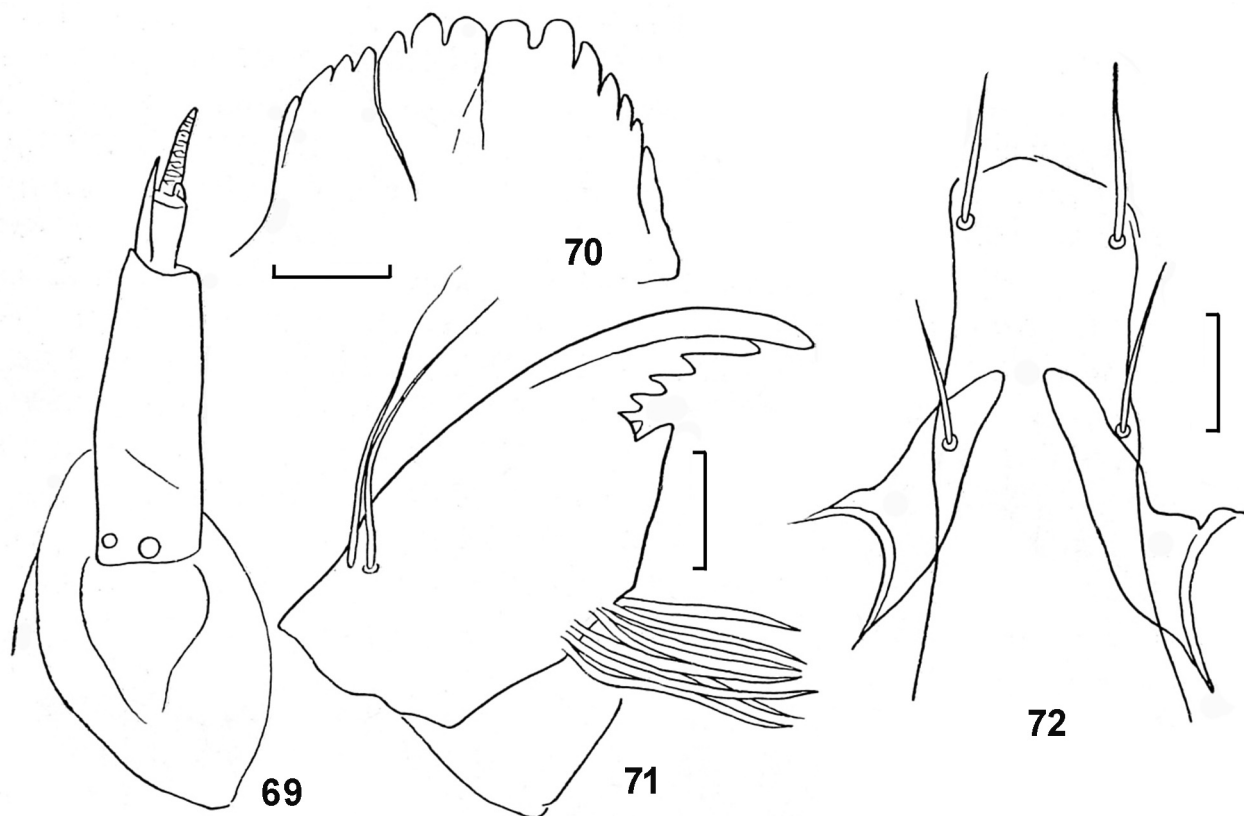
The composition of the subgenus *Boreoheptagyia* s. str.

Boreoheptagyia (s. str.) *accomodata* (Pankratova)

Figs 69–72

Heptagyia accomodata Pankratova, 1950: 165; 1970: 67.

Boreoheptagyia accomodata (Pankratova); Serra-Tosio 1989: 137; Ashe & o'Connor 2009: 264.



FIGURES 69–72. Larva of *Boreoheptagyia* (s. str.) *accomodata* (Pankratova). 69. antenna. 70. Mentum. 71. mandible. 72. head tubercles. Scale bars: 50 µm. Figs 69–72 after Pankratova 1970.

Diagnostic characters. The larva is dark, 6–7 mm long. The spines on the dorsal side of the body form a cross-shaped pattern, the frontal sclerite is wrinkled at the back. The processes of the genal sclerites are high, curved forward, their ends converging above the frontal sclerite as in *B. (s. str.) cinctipes*. There are no processes at the base

of the antennae. The mandibles have light, elongated terminal teeth; the seta under the eubicae is light, spiny; the inner seta consists of approximately 12 equal branches, plumose on one side, extending from a common base. In the middle of the submentum there are 4 rounded teeth, 6 pairs of lateral teeth.

Characteristics of this species are very reminiscent of the larva of *B. (s. str.) legeri* and *B. (s. str.) cinctipes*.

Remarks. Species was described in Russian (Pankratova 1970) and known only by larva. In connection with this, we found it appropriate to provide a brief diagnosis of this species, which may be useful in further research into the taxonomy of the subgenus.

Distribution. Tajikistan.

***Boreoheptagyia (s. str.) alpicola* Serra-Tosio**

Boreoheptagyia alpicola Serra-Tosio, 1989: 138; Ashe & O'Connor 2009: 264.

Distribution. France.

***Boreoheptagyia (s. str.) alulasetosa* Makarchenko, Wu et Wang**

Boreoheptagyia alulasetosa Makarchenko, Wu et Wang in Makarchenko, Endo, Wu & Wang 2008: 2; Ashe & O'Connor 2009: 264.

Distribution. China (Sichuan, Yunnan).

***Boreoheptagyia (s. str.) ambigua* Makarchenko, Wu et Wang**

Boreoheptagyia ambigua Makarchenko, Wu et Wang in Makarchenko, Endo, Wu & Wang 2008: 4; Ashe & O'Connor 2009: 264.

Distribution. China (Sichuan).

***Boreoheptagyia (s. str.) brevitarsis* (Tokunaga, 1936)**

Prodiamesa (Monodiamesa) brevitarsis Tokunaga, 1936: 528.

Heptagyia brevitarsis (Tokunaga); Tokunaga 1939: 302; Sasa & Kikuchi 1995: 207.

Boreoheptagyia brevitarsis (Tokunaga); Serra-Tosio 1989: 140; Endo 2002: 12; Makarchenko *et al.* 2008: 6; Ashe & O'Connor 2009: 264; Yamamoto & Yamamoto 2014: 246; Makarchenko *et al.* 2020c: 101; Lin *et al.* 2021: 196.

Boreoheptagyia brevitarsis (Tokunaga); Makarchenko 1981: 89, 1985: 38, 2006: 259 misidentifications.

Boreoheptagyia kurobeia Sasa et Okazawa, 1992; Endo 2002.

Remarks. The male of *B. (s. str.) brevitarsis* was described by Tokunaga (1936) from Japan and redescribed by Makarchenko *et al.* (2008), with notice that this species is known only from Japan, all other records from China (Lin *et al.* 2021) and the Russian Far East should be revised.

Distribution. Japan (Hokkaido, Honshu, Kyushu);?China.

***Boreoheptagyia (s. str.) cinctipes* (Edwards)**

Boreoheptagyia cinctipes Edwards, 1928: 4; Ashe & O'Connor 2009: 264.

Distribution. Corsica, France, Italy.

***Boreoheptagyia (s. str.) dasyops* Serra-Tosio**

Boreoheptagyia dasyops Serra-Tosio, 1989:145; Ashe & O'Connor 2009: 265.

Distribution. France.

***Boreoheptagyia (s. str.) joeli* Makarchenko**

Boreoheptagyia joeli Makarchenko, 2020c: 96.

Distribution. China (Xinjiang Uygur Autonomous Region).

***Boreoheptagyia (s. str.) eburnea* (Tokunaga, 1937)**

Heptagyia eburnea Tokunaga, 1937: 60;

Boreoheptagyia eburnea (Tokunaga); Ashe & O'Connor 2009: 265; Yamamoto & Yamamoto 2014: 246.

Remarks. The species was described and known only by the adult female.

Distribution. Japan (Honshu).

***Boreoheptagyia* (s. str.) *elbursica* Makarchenko, Semenchenko et Palatov, sp. nov.**

urn:lsid:zoobank.org:act:AEFDD7A1-CC14-4922-8366-A8AD3C315F0C

(Figs 73–96)

Type material. Holotype: pharate adult male, IRAN: Mazandaran Province, near Bimak Village, Iranian Plateau, near Elburze Mountains, head of Gelenrud River, alt. 1987 m a.s.l., 36.304600 N, 51.834783 E, 26.06.2019, leg. D. Palatov. Paratypes: 4 pharate males (mature pupae), 3 pupae, 10 larvae, the same data as holotype.

Derivatio nominis. The species name *elbursica* comes from the Elburze Mountains range in northern Iran, where it was collected.

Description

Pharate adult male (n = 3). Total length 2.0–2.9 mm.

Coloration: Head brown to dark brown. Antenna yellowish to brown. Thorax brown to dark brown. Abdomen brown or brownish.

Head. Frontal tubercles semi-oval, 48 µm long and 12–16 µm wide, covered with macrotrichiae and with 1 setae, 36–40 µm long. Temporal setae including 5–8 frontals, 15 outer verticals, without inner verticals. Clypeus with 7–9 setae. Antenna with 13 flagellomeres, antennal plumose reduced; pedicel without setae. Lengths (µm) of flagellomeres 1–13 (n = 1): 52 : 28 : 32 : 40 : 44 : 48 : 44 : 48 : 52 : 48 : 40 : 40 : 88. The number of setae on flagellomeres 1–13 and their length (in brackets, µm) : 3 (40–60) : 4 (48–72) : 4 (192–208) : 5 (192–216) : 6 (216–269) : 5 (168–216) : 4 (192–208) : 4 (120–185) : 4 (112–128) : 4 (80–108) : 4 (69–112) : 4 (32–64) : 5 (24–52). AR 0.17–0.18. Lengths (µm) of palpomeres 1–5 (n = 1): 32 : 48 : 84 : 60 : 92. Head width/palp length 1.5.

Thorax. Covered with macrotrichiae. Anteprenotum with 7–8 lateral setae. Acrostichals 27–32, 24–60 µm long, in 1 row in anterior half and in 2 rows posterior; dorsocentrals 13–22, 48–52 µm long, in anterior and posterior groups; prealars 24–27, 36–64 µm long; supraalars 2–4. Scutellum with ca 50 setae.

Wings and legs impossible to observe and measure. Anal lobe of wing well developed, rounded. Alula without setae. Squama with 28 setae in 1–2 rows, 40–80 µm long. LR₁ 0.48.

Hypopygium (Figs 73–78). Tergite IX with 25–27 setae, 16–20 µm long. Laterosternite IX with 5–7 setae, 28–40 µm long. Transverse sternapodeme 28–44 µm wide (Figs 74, 77–78). Aedeagal lobe weakly sclerotized, narrowly triangular, dagger-shaped, 84 µm long (Fig. 74). Gonocoxite 140–152 µm long. Gonostylus 80–92 µm long, short ending with a short megaseta (Figs 73, 75–76). HR 1.52–2.0.

Pupa (n = 4). Total length 2.4–2.6 mm. Cephalothorax dark brown to black, abdomen greenish-brown. Exuviae brownish.

Cephalothorax. Frontal apotome with dark brown to black, spine-shape cephalic tubercles, 12–16 µm long (Fig. 79). Thorax is dorsally wrinkled, in the anterior half it is dorsally and dorsolaterally granulated, dorsolaterally also with small spines (Figs 82, 84–85). Thoracic horn strongly sclerotized, from dark brown to black, triangular, 48–80 µm long, 32–44 µm wide, covered with hair-like setae (Figs 80–81). Pc₁ 44–48 µm, Pc₂ 40–44 µm, Pc₃ 12–16 µm; 2 lateral anteprenotals, 24–40 µm long are present, median anteprenotals and dorsocentrals are absent.

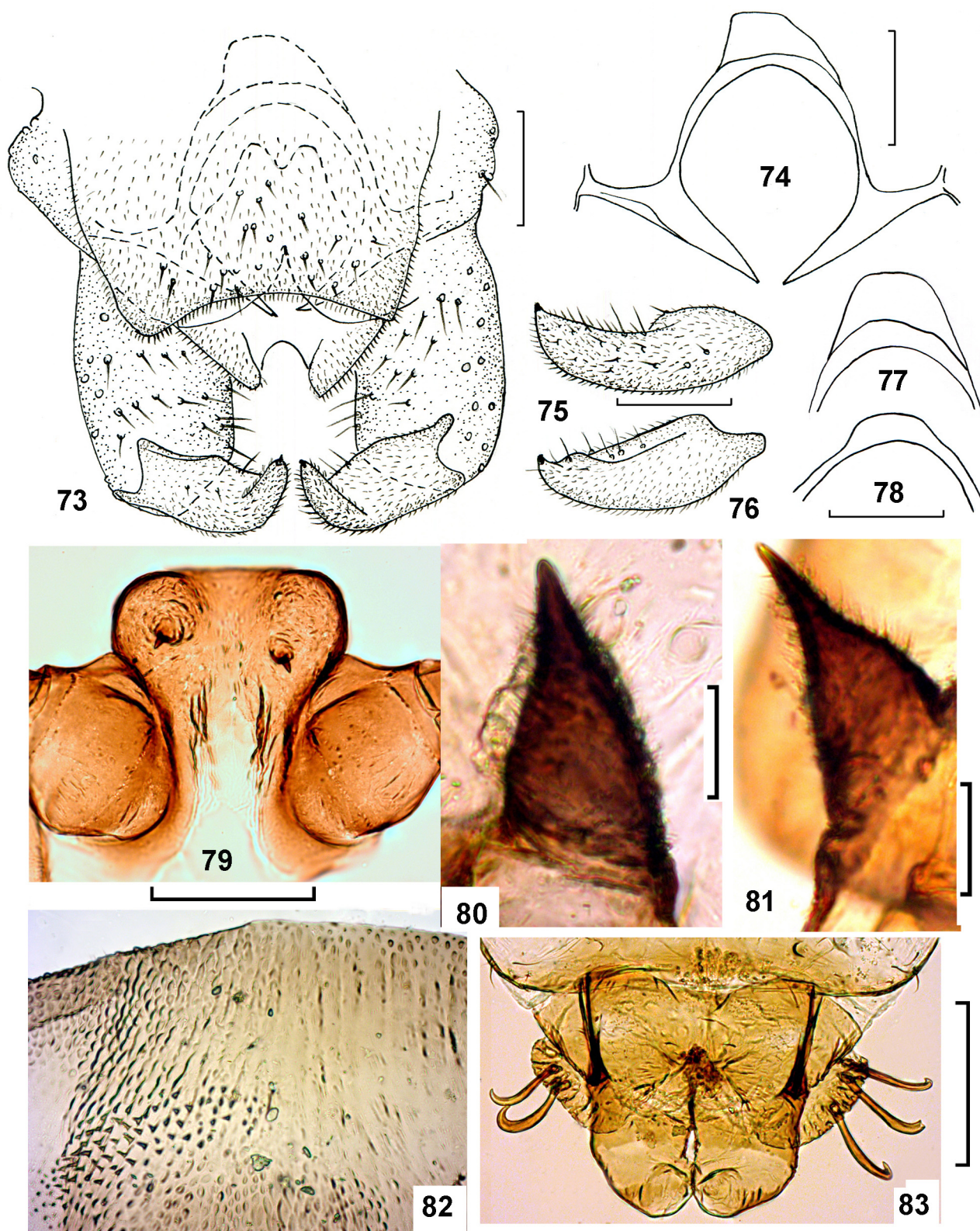
Abdomen. Tergite I in anterior 1/3 with fine shagreen of spinules; tergites II–VIII with fine shagreen in middle part, sometimes in anterior or posterior parts (Fig. 86). Sternites with very fine shagreen of spinules (Fig. 87). Tergites and sternites without posterior spines. Apophyses not developed. Segments I–VII with 4 pairs of hairlike lateral setae, 24–56 µm long; segment VIII with 4 pairs of lateral setae, 32–48 µm long. Anal lobe broad, with 3 strong, apically hooked anal macrosetae, 72–92 µm long. Male genital sac broad, strongly extended beyond the anal lobe, and apex curved dorsally (Fig. 83).

Larva of fourth instar (n = 5). Greenish, greenish-brown, brownish. Total length 3.5 mm.

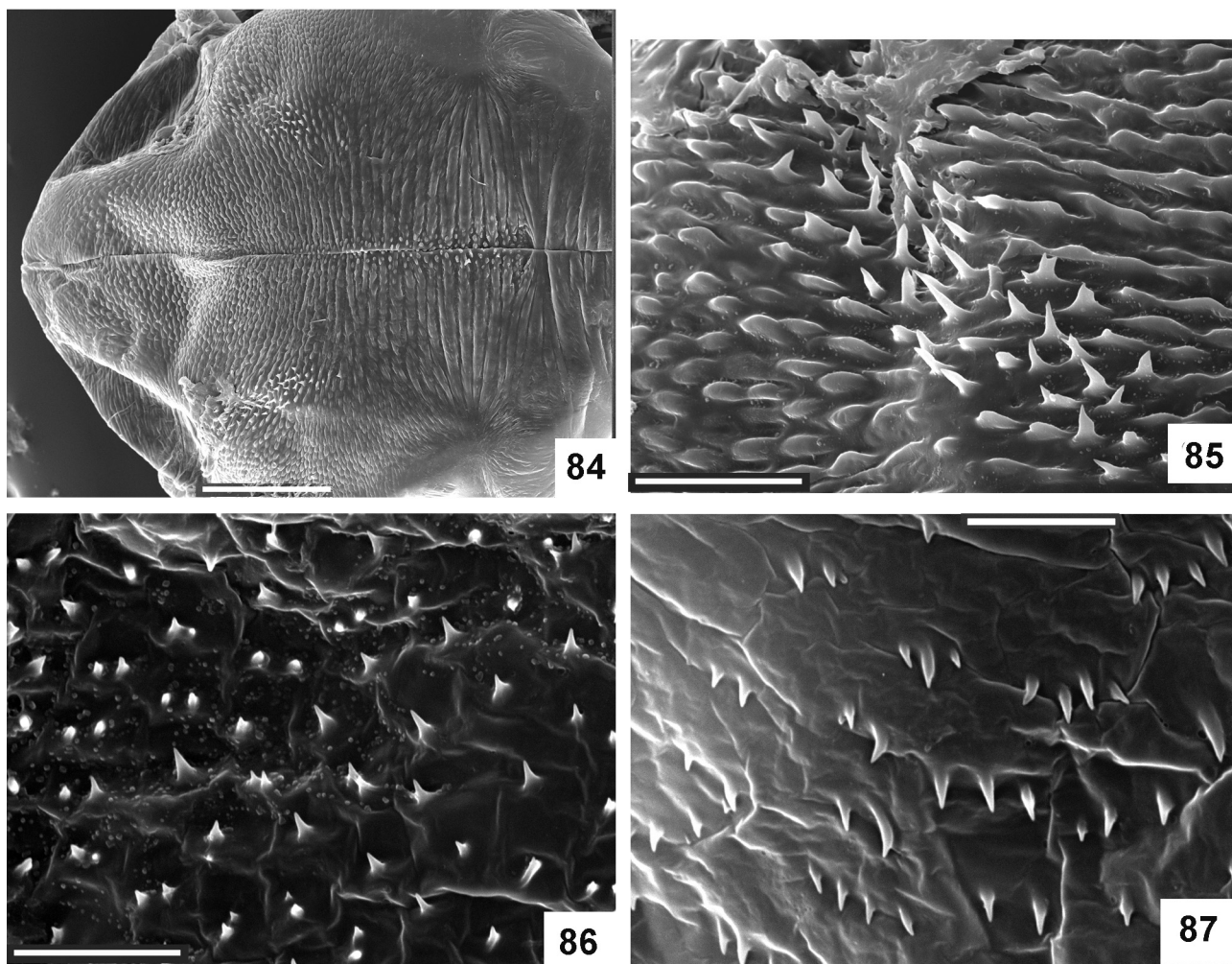
Head. Brownish-yellow, 377–361 µm long, 295 µm wide. Dorsally with yellow triangular pair tubercles, 84–92 µm long (Figs 88–89, 97). Postoccipital margin dark brown to black. Dorsal setae S₁–S₅ dark brown and strong, 49–85 µm long.

Antenna. Dark brown to black, with 5 segments, length of 1–5 segments (in µm)—80–89 : 16–18 : 16–21 : 2–4 : 3–4. Blade ending approximately one-third or half of segment 3; style, 7 µm long and lauterborn organs, 3 µm long on apex of segment 2; large ring organ in basal ¼ of segment 1 (Figs 94–95); AR 1.9–2.1. Antennal pedestal with outer and inner dark brown to black processes, 40–52 and 44–64 µm long respectively (Figs 88–89, 90, 92).

Labrum. S_I seta-like; S_{II} simple and wide. Pecten epipharyngis consisting of 5 broad, elongate, apically blunt scales. Premandible apically broad with 6 blunt teeth, lateral spine apically plumose (Fig. 93).



FIGURES 73–83. Adult male (73–78) and pupa (79–83) of *Boreoheptagyia* (s. str.) *elbursica* **sp. nov.** 73. hypopygium, dorsal view. 74. transverse sternapodeme and aedeagal lobes. 75–76. gonostylus in various positions. 77–78. transverse sternapodeme. 79. cephalic tubercles. 80–81. thoracic horn. 82. anterior part of thorax, lateral view (light microscope). 83. anal segment. Scale bars are as follows: Figs 73–78, 80–81—50 μ m, Figs 79, 82–83—200 μ m.



FIGURES 84–87. Pupa of *Boreoheptagyia* (s. str.) *elbursica* **sp. nov.** (SEM). 84. surface sculpture of thorax, dorsal view. 85. granulations and spines of thorax. 86. spines of tergite II. 87. spines of sternite VI. Scale bars are as follows: Fig. 84—250 μ m, Figs 85–86—50 μ m, Fig. 87—50 μ m.

Mandible with 5 teeth, apical tooth yellow, other teeth dark brown; seta subdentalis curved, extending apex of apical tooth, apically pointed; seta interna consisting of 15–17 simple to weakly serrate branches (Fig. 96).

Mentum. With 2 median and 7 pairs of lateral teeth; median tooth and 2 pairs of lateral teeth subequal in size and little wider than other lateral teeth. Ventromental plates elongate and narrow (Fig. 91).

Abdomen. Procercus reduced, with 6 anal setae, 104–116 μ m long (Figs 98, 100).

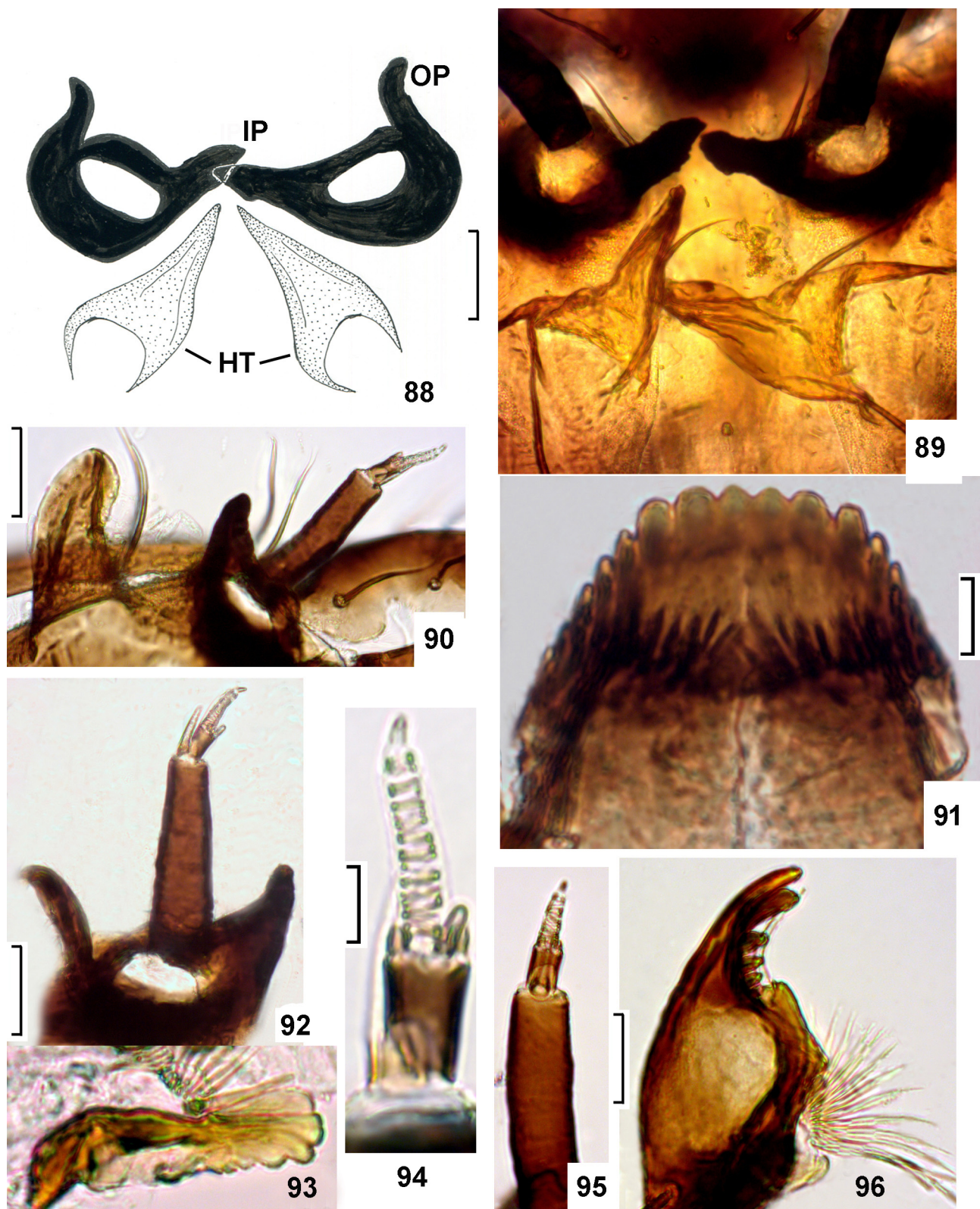
Diagnostic characters. Male of *B.* (s. str.) *elbursica* **sp. nov.** is closely related to *B.* (s. str.) *brevitarsis* (Tokunaga) but is well separated from later by the shape of the aedeagal lobe of male, which is narrowly triangular, dagger-shaped while aedeagal lobe of *B.* (s. str.) *brevitarsis* is widely triangular. Larva of a new species with 2 middle and 7 pairs of lateral teeth of mentum. *B.* (s. str.) *brevitarsis* with 1 middle and 7 pairs of lateral teeth.

Distribution. Known only from the type locality in the Iranian Plateau, near the Elburze Mountains.

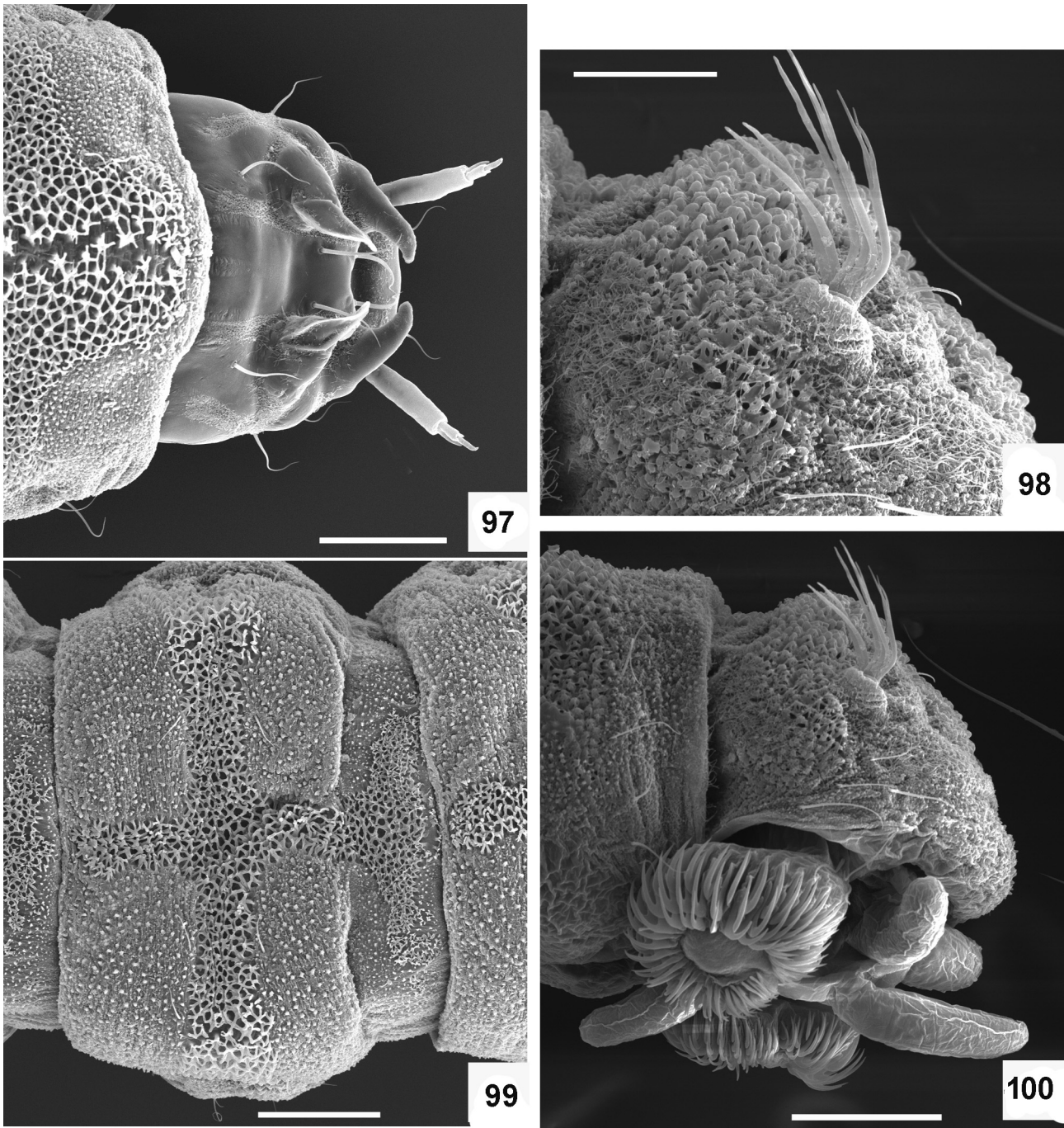
***Boreoheptagyia* (s. str.) *iranica* Makarchenko**

Boreoheptagyia iranica Makarchenko, 2020c: 99.

Distribution. Iran.



FIGURES 88–96. Larva of *Boreoheptagyia* (s. str.) *elbursica* **sp. nov.** 88–89. head tubercles, outer and inner processes of antennal pedestal, dorsally. 90. head tubercle and inner process of antennal pedestal, laterally. 91. Mentum. 92. antenna with outer and inner processes, laterally. 93. premandible. 94. flagellomeres 2–5. 95. Antenna. 96. mandible. HT—head tubercles, IP—inner process, OP—outer process of antennal pedestal. Scale bar: 50 μ m.



FIGURES 97–100. Larva of *Boreoheptagyia* (s. str.) *elbursica* sp. nov. (SEM). 97. head capsule and segment I, dorsally. 98. last abdominal segment with procercus. 99. surface sculpture of tergite IV. 100. last abdominal segment with procercus, papille and posterior parapods. Scale bars are as follows: Figs 97, 99–100—100 μ m, Fig. 98—50 μ m.

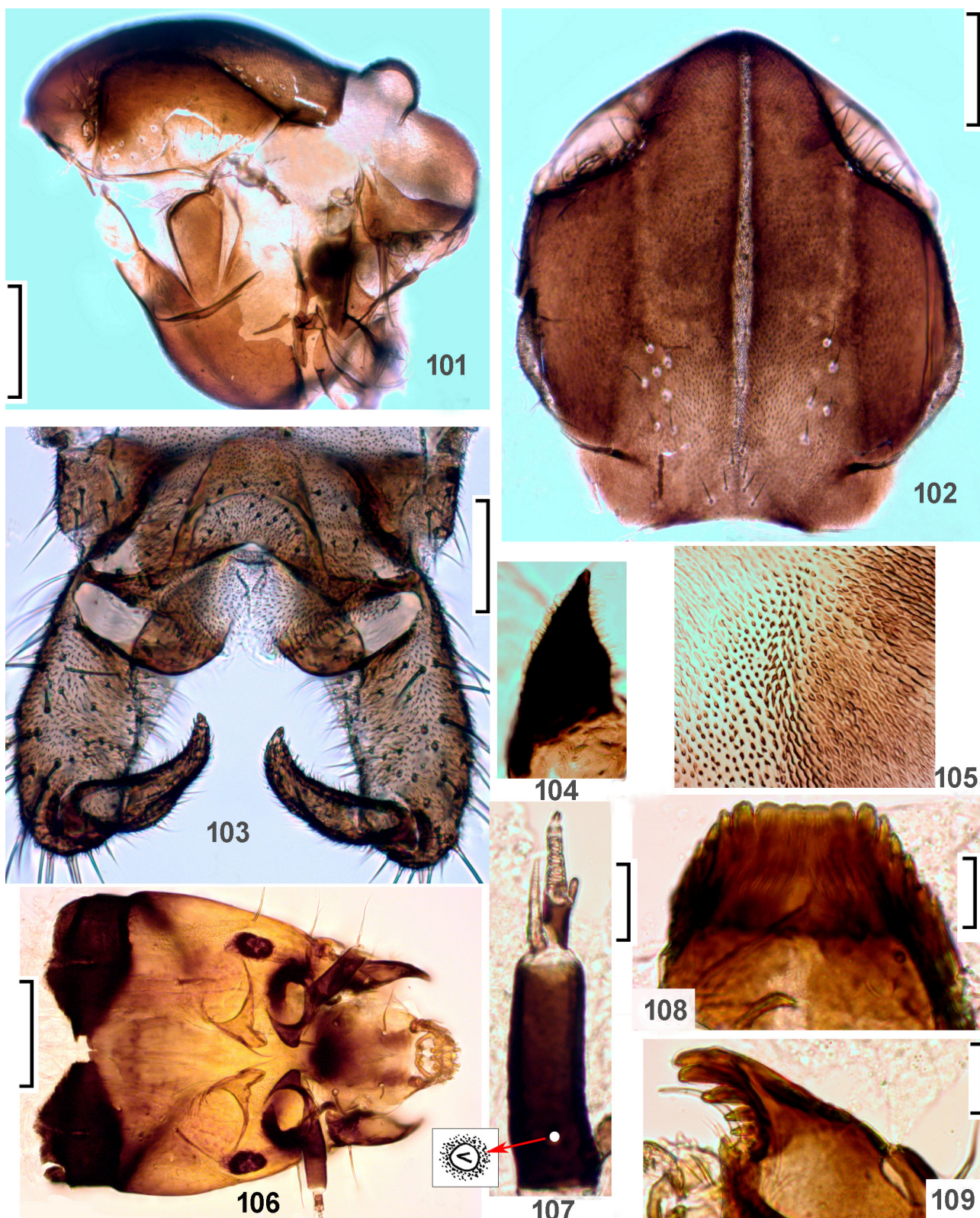
***Boreoheptagyia* (s. str.) *legeri* (Goetghebuer, 1933)**
(Figs 101–121)

Protanypus legeri Goetghebuer, 1933: 357.

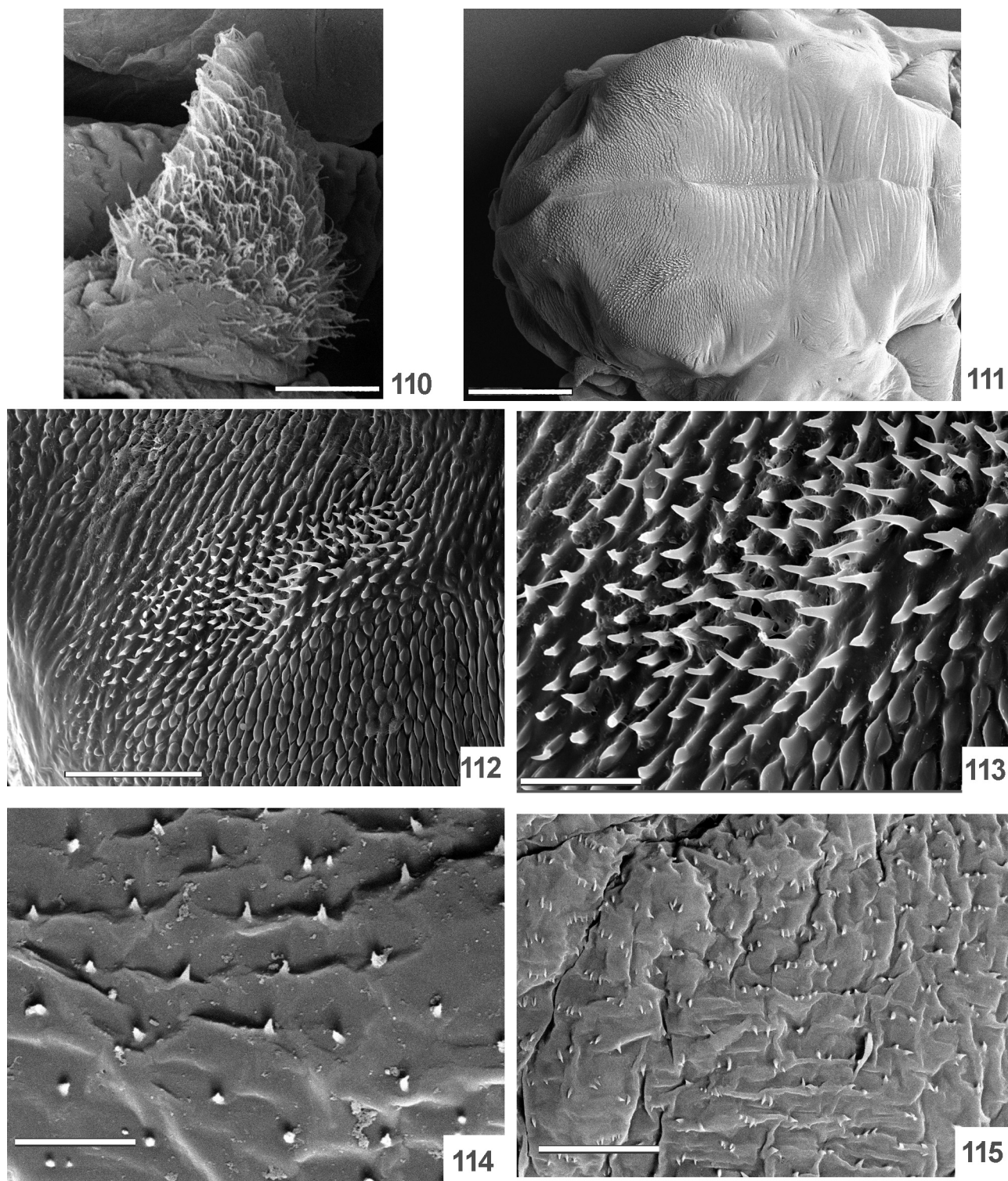
Heptagia (and *Heptagyia*) *legeri* (Goetghebuer); Goetghebuer 1939: 22; Pagast 1947: 564.

Heptagia (and *Heptagyia*) *punctulata* Goetghebuer 1934: 357; Goetghebuer 1939: 22; Mayer 1935: 158; Thienemann 1944: 568; Pagast 1947: 564; Bertrand & Grenier 1949: 30; Pankratova 1970: 64.

Boreoheptagyia legeri (Goetghebuer); Brundin 1966: 421; Lehmann 1971: 475; Säwedal 1982: 5–7; Serra-Tosio 1989: 149; Ashe & O'Connor 2009: 265; Ergović *et al.* 2023: 132.



FIGURES 101–109. Adult male (101–103), pupa (104–105) and larva (106–109) of *Boreoheptagyia* (s. str.) *legeri* (Goetghebuer). 101. thorax laterally. 102. scutum dorsally. 103. hypopygium. 104. thoracic horn. 105. anterior part of scutum (light microscope). 106. head, dorsal view. 107. antenna. 108. mentum. 109. mandible. Scale bars are as follows: Figs 101–102—200 μm , Figs 103–105, 107–109—50 μm , Fig. 106—100 μm .



FIGURES 110–115. Pupa of *Boreoheptagyia* (s. str.) *legeri* (Goetghebuer) (SEM). 110. thoracic horn. 111. thorax, dorsal view. 112. surface sculpture of thorax. 113. spines and granulations of thorax, lateral view. 114. spines of tergite V. 115. spines of sternite V. Scale bars are as follows: Figs 110, 113–115—50 μ m, Fig. 111—250 μ m, Fig. 112—100 μ m.

Material examined. 1 larva, RUSSIA: Republic of North Ossetia-Alania, Alagirsky District, Caucasus Mountains, Terek River basin, Tsejdon River, 42.79266 N, 43.920051 E, 24.VII.2021, leg. D. Palatov; 1 pupa, 1 larva, Republic of Dagestan, Tlyaratinsky District. Caucasus Mountains, Sulak River basin, right tribunary of Dzhurmut River, 41.898002 N, 46.654012 E, 12.VIII.2021, leg. D. Palatov; 1 pharate adult male, 3 larvae, Republic of Kabardino-

Balkaria, Chereksky district. Caucasus Mountains, Terek River basin, Cherek Bezengiiskij River, 43.105747 N, 43.131731 E, leg. D. Palatov; 2 mature pupae (males), 2 larvae, Karachay-Cherkess Republic, Zelenchuksky District. Khyzgora River, 200 m upstream from the mouth, 43.631303 N, 41.386717 E, 9.IV.2023, leg. D. Palatov; 1 pupa, 2 larvae, REPUBLIC OF ABKHAZIA: Gulripshi District. Caucasus Mountains, Kodor River basin, Dzhangal River near mouth of Shakuran River, 43.028589 N, 41.334719 E, 2.II.2018, leg. D. Palatov.

Description

Pharate adult male (n = 4). Total length 2.0–2.6 mm.

Coloration. Head and thorax brown to dark brown. Abdomen brown or brownish.

Head. Frontal tubercles semi-oval, 28–32 μm long, covered with macrotrichiae and with 1 setae, 36 μm long. Temporal setae including 5–8 frontals, 15 outer verticals, without inner verticals. Clypeus with 10 setae. Antenna with 13 flagellomeres, antennal plumose reduced; pedicel without setae. Lengths (μm) of flagellomeres 1–13 (n = 1): 64 : 32 : 28 : 40 : 48 : 50 : 52 : 56 : 56 : 52 : 50 : 50 : 50. AR 0.19. Lengths (μm) of palpomeres 1–5 (n = 1): 32 : 48 : 84 : 60 : 92. Head width/palp length 1.5.

Thorax. Covered with macrotrichiae. Anteprenotum with 6–7 lateral setae, 48–60 μm long. Acrostichals 28–36, 40–52 μm long, in 1 row in anterior half and in 2 rows posterior; dorsocentrals 7–18, 40–52 μm long, in anterior and posterior groups; prealars 16–23, 40–48 μm long; supraalars 2 (Figs 101–102). Scutellum with ca 43–50 setae.

Wing. Wing length 2.0–2.6 mm. R and R_1 with 18 setae, R_{4+5} with 4 setae in distal part. R_{2+3} poorly visible. Anal lobe well developed. Squama with 44 setae, 72–96 μm long, RM/MCu 2.47.

Legs. Spur of fore tibia 44 μm long; spurs of mid tibia 40 μm and 44 μm long; of hind tibia 60 μm and 44 μm long. Hind tibial comb with 12–13 spines. Lengths and proportions of leg segments as in Table 1.

TABLE 1. Lengths (in μm) and proportions of leg segments of *Boreoheptagyia* (s. str.) *legeri* (Goetghebuer), male (n = 1).

	fe	ti	ta ₁	ta ₂	ta ₃	ta ₄	ta ₅	LR	BV	SV	BR
P ₁	607	804	361	213	115	82	98	0.45	3.12	3.91	1.17
P ₂	787	787	353	230	131	66	98	0.45	2.08	4.46	1.33
P ₃	804	968	525	558	139	66	115	0.54	4.59	3.38	2.0

Hypopygium (Fig. 103). Tergite IX without anal point, with 29–30 setae, 12–18 μm long. Laterosternite IX with 8 setae, 20–40 μm long. Transverse sternapodeme broad-bladed, 88 μm length and 80 μm wide. Aedeagal lobe weakly sclerotized, narrowly triangular, narrow basally, widening toward the middle and tapering distally, 80–96 μm long. Gonocoxite 198 μm long. Gonostylus 100–104 μm long, narrow, slightly curved, gradually narrowing, covered with microtrichiae, bearing quite a number of fine setae and short megaseta. HR 1.8–1.9.

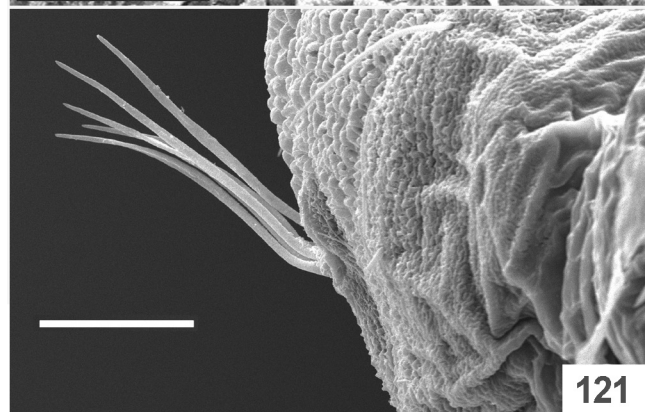
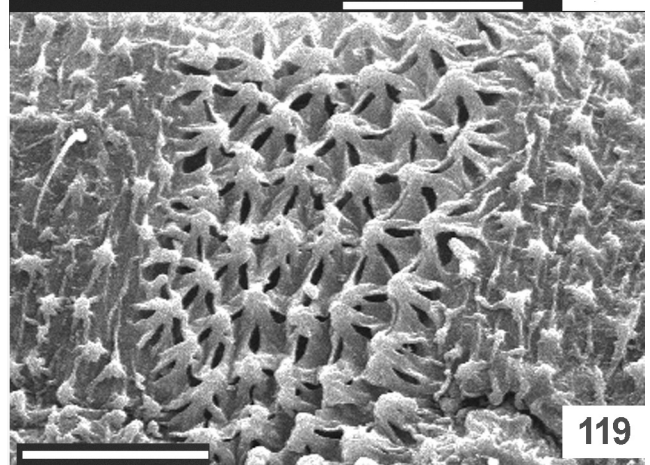
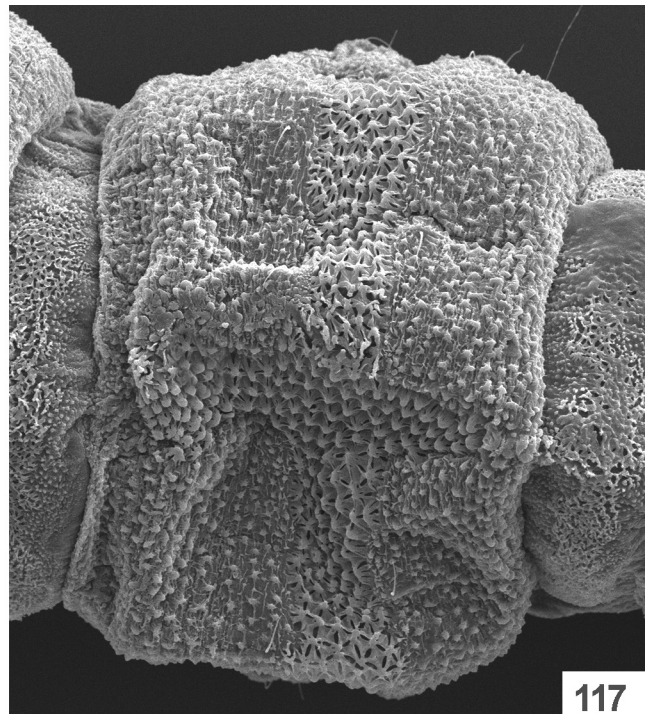
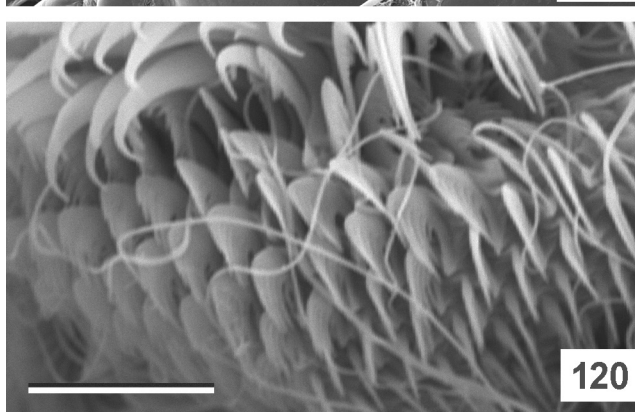
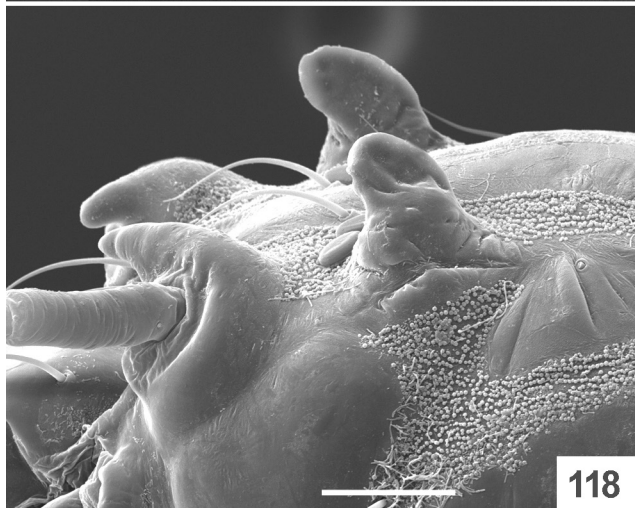
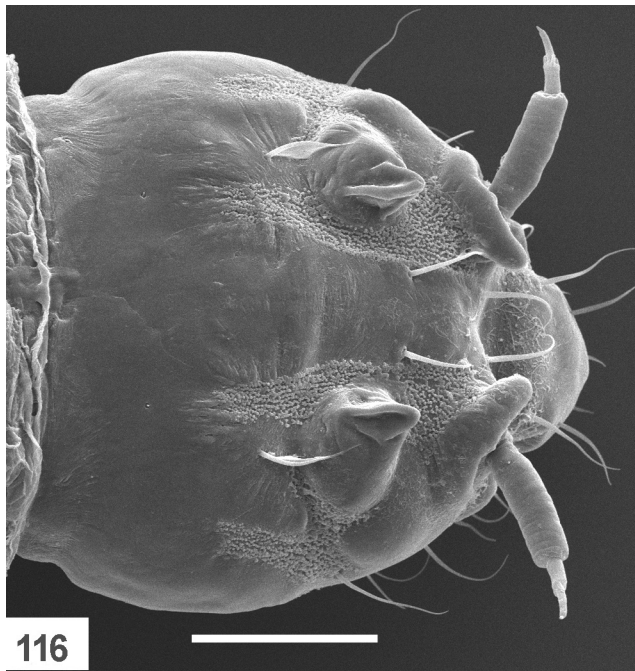
Pupa (n = 6). Total length 2.0–3.4 mm. Cephalothorax dark brown to black, abdomen brown, greenish-brown. Exuviae grayish.

Cephalothorax. Frontal apotome with black, spine-shape cephalic tubercles, 16–20 μm long. The posterior two-thirds of the thorax are wrinkled dorsally and dorsolaterally and almost without granulation. The anterior third is heavily granulated dorsally and dorsolaterally and bears spinules dorsolaterally. (Figs 105, 111–113). Thoracic horn strongly sclerotized, from dark brown to black, triangular, 84–120 μm long, 44–64 μm wide at the base, covered with hair-like setae (Figs 104, 110). Pc₁ 84–92 μm , Pc₂ 68–72 μm , Pc₃ 80–84 μm ; 2 lateral anteprenotals, 36–40 μm long are present, median anteprenotals and dorsocentrals usually are absent but sometimes 1 dorsocentrals, 16 μm long, is present.

Abdomen. Tergite I in anterior 1/3 with fine shagreen of spinules; tergites II–VIII with fine shagreen in middle part, sometimes in anterior or posterior parts (Fig. 114). Sternites with very delicate shagreen spinules, which are sparsely located. Tergites and sternites without posterior spines. Apophyses not developed. Segment I with 2 pairs of hair-like lateral setae, 16–20 μm long; segments II–VIII with 4 pairs of lateral setae, 40–68 μm long. Anal lobe broad, with 3 strong, apically hooked anal macrosetae, 100–148 μm long. Male genital sac broad, strongly extended beyond anal lobe.

Larva of fourth instar (n = 5). Greenish, greenish-brown. Total length 3.3–5.5 mm.

Head. Brown, dark brown, 410 μm long, 344 μm wide. Dorsally with triangular pair tubercles, 40–48 μm long (Figs 106, 116, 118). Dorsal setae S₁–S₅ dark brown and strong, 60–68 μm long.



FIGURES 116–121. Larva of *Boreoheptagyia* (s. str.) *legeri* (Goetghebuer). 116. head capsule, dorsal view. 117. surface sculpture of tergite V. 118. head tubercles and inner processes of antennal pedestal. 119. surface sculpture of abdominal segments. 120. hooks of posterior parapods. 121. posterior abdominal segment with procercus. Scale bars are as follows: Figs 116–117—100 μm , Figs 118–119, 121—50 μm , Fig. 120—20 μm .

Antenna. Dark brown to black, with 5 segments, length of 1–5 segments (in μm)—71–77 : 18–20 : 18–21 : 2–3 : 3–4. Blade, 21–23 μm long, ending approximately one-third or half of segment 3; style, 7 μm long and lauterborn organs, 3 μm long on apex of segment 2; large ring organ in basal $\frac{1}{4}$ of segment 1, with triangle spine inside (Fig. 107); AR 1.65–1.67. Antennal pedestal with outer and inner dark brown to black processes, 60–68 and 20–24 μm long respectively (Figs 106, 116, 118).

Labrum. S_I seta-like, 13–18 μm long; S_{II} simple and wide, 18–20 μm long. Pecten epipharyngis consisting of 5 broad, elongate, apically blunt scales. Premandible apically broad, with 6 blunt teeth.

Mandible. With 5 dark brown teeth; seta subdentalis curved, extending apex of apical tooth, apically pointed; seta interna consisting of 15–20 weakly serrate branches (Fig. 109).

Mentum. With 2 median and 7–8 pairs of lateral teeth; median tooth and 2 pairs of lateral teeth subequal in size and little wider other lateral teeth. Ventromental plates elongate and narrow (Fig. 108).

Abdomen. The sculpture of the surface of the thorax and abdomen tergites consists of spines grouped into tubercles resembling small volcanoes (Figs 117, 119). Posterior parapodes with sickle-shaped hooks of three types (Fig. 120). Procercus reduced, with 6 anal setae, 88–112 μm long (Fig. 121).

Distribution. A widespread Palearctic species.

Boreoheptagyia* (s. str.) aff. *legeri

Material examined. 1 pupa, RUSSIA: Republic of North Ossetia-Alania, Alagirsky District, Caucasus Mountains, Terek River basin, Sadon River near of Galon Village, 42.853506 N, 43.994131 E, 09.10.2020, leg. D. Palatov; 2 mature pupae, the same data, except

Republic of Dagestan, Dokuzparinsky District, mouth of the Seldy River, northern part, alt. 2282 m a.s.l., 41.279886 N, 47.844925 E, 21.08.2024, leg. D. Palatov.

Remarks. The pupa of this species is morphologically indistinguishable from *B.* (s. str.) *legeri* and, together with other species isolated using DNA barcoding (*Boreoheptagyia* (s. str.) sp. 1, *Boreoheptagyia* (s. str.) sp. 2 should for now be placed in the *B.* (s. str.) *legeri* group species.

Distribution. Known from North Caucasus.

***Boreoheptagyia* (s. str.) *lurida* (Garrett)**

Diamesa lurida Garrett, 1925: 6.

Diamesa (*Psilodiamesa*) *lurida* Garrett; Johannsen 1926: 205; Saunders 1928: 261.

Heptagyia lurida (Garrett); Edwards 1931: 265; Thienemann & Mayer 1933: 9; Thienemann 1934: 8, 1944: 568; Johannsen 1937: 29; Pagast 1947: 564; Sublette 1967: 300.

Boreoheptagyia lurida (Garrett); Brundin 1966: 421; Oliver 1983: 125; Serra-Tosio 1989: 155; Ashe & O'Connor 2009: 265.

Distribution. North America (Canada, USA).

***Boreoheptagyia* (s. str.) *monticola* (Serra-Tosio)**

Heptagyia monticola Serra-Tosio, 1964: 47.

Boreoheptagyia monticola (Serra-Tosio); Fittkau & Reiss, 1978 : 411; Serra-Tosio 1989: 157; Ashe & O'Connor 2009: 265.

Boreoheptagyia ? *monticola* (Serra-Tosio); Säwedä 1982: 4.

Distribution. Known from France, Switzerland, North Macedonia.

***Boreoheptagyia* (s. str.) *nepalensis* Makarchenko et Endo**

Boreoheptagyia nepalensis Makarchenko et Endo in Makarchenko, Endo, Wu & Wang, 2008: 9; Ashe & O'Connor 2009: 266.

Distribution. Nepal.

***Boreoheptagyia* (s. str.) *nipponica* (Tokunaga)**

Heptagyia nipponica Tokunaga, 1937: 58; Ashe & O'Connor 2009: 266; Yamamoto & Yamamoto 2014: 247.

Remarks. The species was described and known only by the adult female.

Distribution. Japan (Honshu).

***Boreoheptagyia* (s. str.) *ortladamellica* Rossaro**

Boreoheptagyia ortladamellica Rossaro, 2017: 80.

Distribution. Italian Alps.

***Boreoheptagyia* (s. str.) *phoenicia* Moubayed**

Boreoheptagyia phoenicia Moubayed, 1993: 187; Ashe & O'Connor 2009: 266.

Distribution. Lebanon.

***Boreoheptagyia* (s. str.) *rotunda* Serra-Tosio**

Boreoheptagyia rotunda Serra-Tosio, 1983: 23, 1989: 163; Ashe & O'Connor 2009: 266.

Distribution. Nepal.

***Boreoheptagyia* (s. str.) *rugosa* (Sounders)**

Heptagyia rugosa Saunders, 1930: 209; Goetghebuer 1932: 186; Thienemann & Mayer 1933: 9; Johannsen 1937: 29; Goetghebuer 1939: 23; Thienemann 1944: 568; Pagast 1947: 564; Pankratova 1970: 64.

Boreoheptagyia rugosa (Saunders); Brundin 1966: 420; Fittkau & Reiss 1978: 411; Serra-Tosio 1989: 164; Ashe & O'Connor 2009: 266.

Distribution. Palaearctic.

***Boreoheptagyia* (s. str.) *sarymsactyensis* Makarchenko**

Boreoheptagyia sarymsactyensis Makarchenko, 2020c: 103.

Distribution. Kazakhstan.

***Boreoheptagyia* (s. str.) *sasai* Makarchenko et Endo**

Boreoheptagyia sasai Makarchenko et Endo in Makarchenko, Endo, Wu & Wang, 2008: 11; Ashe & O'Connor 2009: 266; Yamamoto & Yamamoto 2014: 247.

Distribution. Japan (Hokkaido), Russian Far East.

***Boreoheptagyia* (s. str.) *serratosioi* Makarchenko, Semenchenko *et* Palatov, sp. nov.**

urn:lsid:zoobank.org:act:B27141F3-CFCC-4E7B-A38A-4D946D584312

(Figs 122–154)

Type material. Holotype: 1 pharate adult male, INDIA: Uttarakhand, Chamoli District, Alaknanda River near the Nayachutii Village, alt. 1924 m a.s.l., 30.64395 N, 79.53365 E, 10.V.2018, leg. D. Palatov. Paratypes: 2 pharate males, 12 pupae, 14 larvae, the same data as holotype.

Derivatio nominis. The species is named in honor and memory of French chironomidologist Dr. Bernard Serra-Tosio (1937–2021), who was the leading expert on the taxonomy and systematics of Diamesinae.

Description

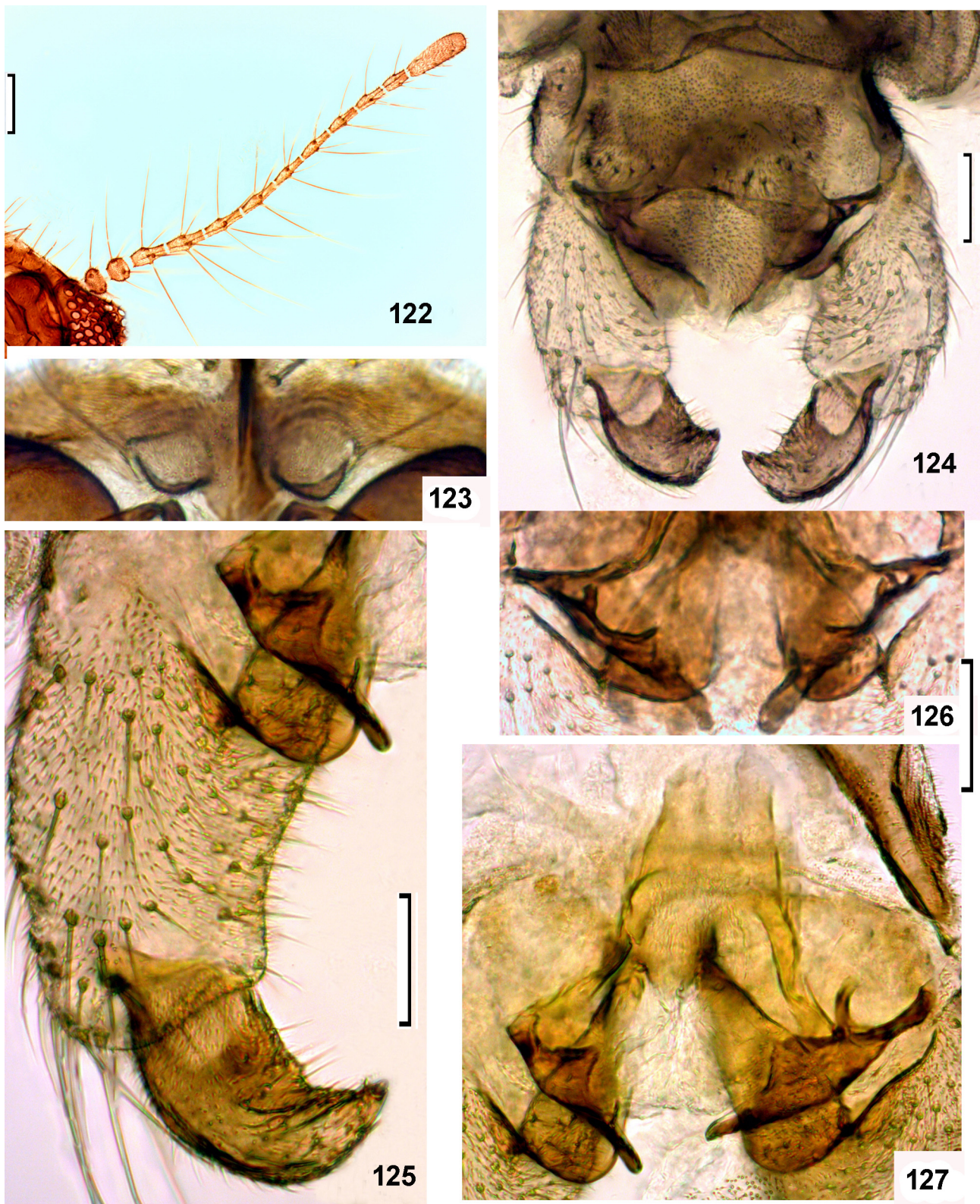
Pharate adult male (n = 2). Total length 2.4–2.8 mm.

Coloration. Head brown to dark brown. Antenna yellowish to brown. Thorax brown to dark brown. Abdomen and legs brownish to dark brown.

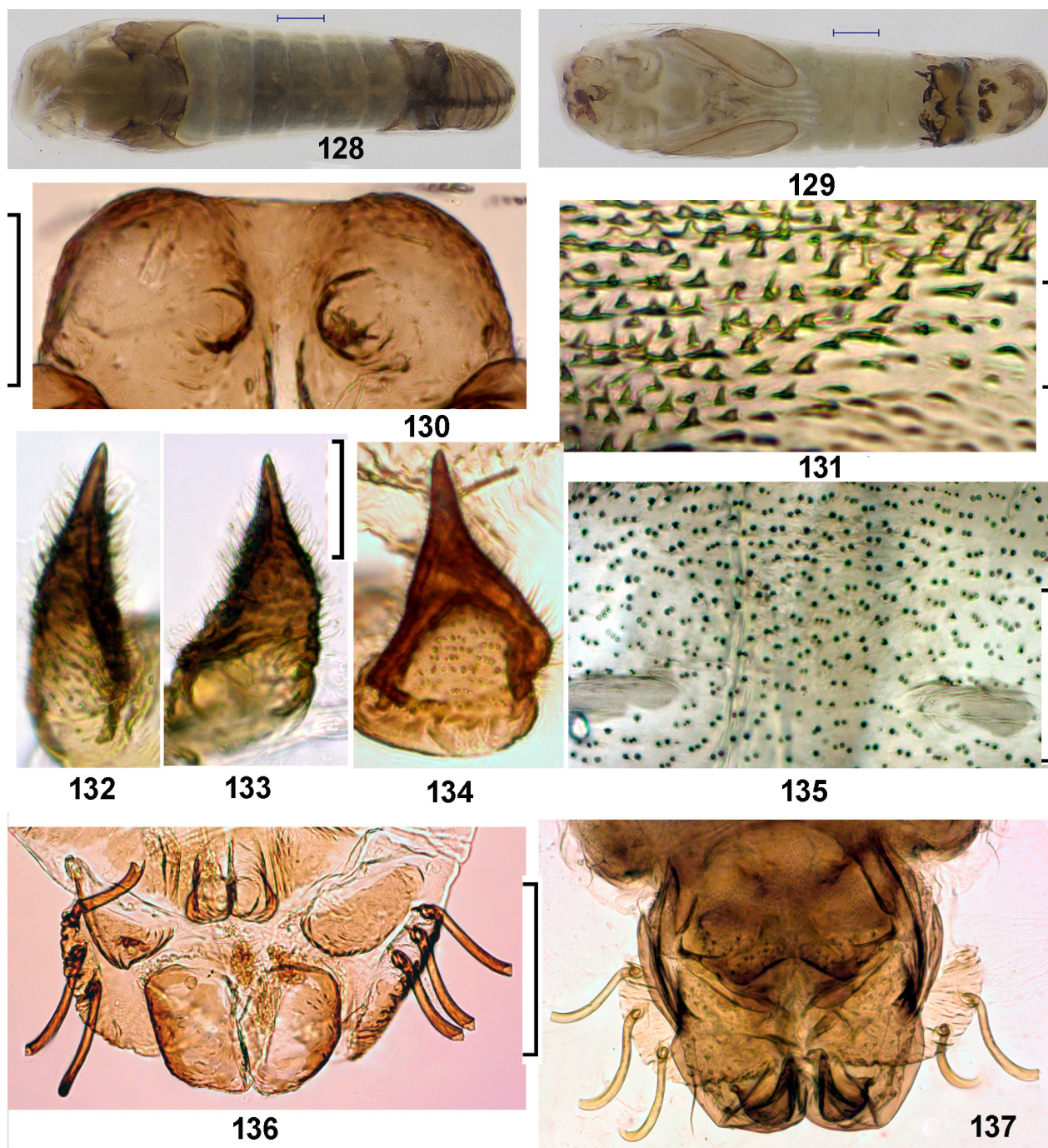
Head. Frontal tubercles semi-oval, 28 µm wide, 12 µm high, covered with macrotrichiae and with one seta, 42–52 µm long at the edge (Fig. 123). Temporal setae including 5–6 frontals, 15–17 outer verticals, without inner verticals. Clypeus with 10 setae, 44–72 µm long.

Antenna with 13 flagellomeres, antennal plumose reduced (Fig.122); pedicel without setae. Lengths (µm) of flagellomeres 1–13 (n = 1): 24 : 28 : 28 : 28 : 44 : 48 : 48 : 52 : 40 : 40 : 44 : 34 : 76. The number of setae on flagellomeres 2–13 and their length (in brackets, µm) : 3 (48–80) : 4 (60–108) : 4 (80–148) : 4 (48–120) : 3 (80–136) : 3 (80–136) : 3 (68–140) : 3 (60–124) : 4 (40–60) : 3 (40–60) : 3 (32–40) : 3 (20–24). AR 0.18. Lengths (µm) of palpomeres 1–5 (n = 1): 32 : 52 : 76 : 44 : 88. Head width/palp length 1.57.

Thorax. Covered with macrotrichiae. Anteprepronotum with 6–7 lateral setae. Acrostichals 22; dorsocentrals 19–20, in anterior and posterior groups; prealars 23 in 2 groups. Scutellum with *ca* 55 setae. Length of acrostichals, dorsocentrals, prealars and scutellars respectively (µm): 40–48 : 48–52 : 56–72 : 60–72.



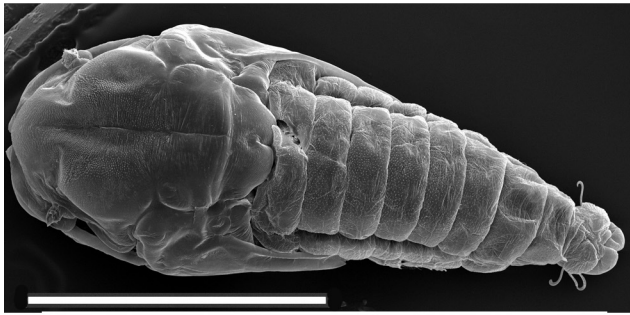
FIGURES 122–127. Adult male of *Boreoheptagyia* (s. str.) *serratosioi* **sp. nov.** 122. antenna. 123. frontal tubercles. 124. hypopygium, dorsal view. 125. part hypopygium with aedeagal lobe and basal plate. 126. aedeagal lobes. 127. skeleton. Scale bars are as follows: Fig. 122—100 μm , Fig. 124—50 μm , Figs 125–127—20 μm .



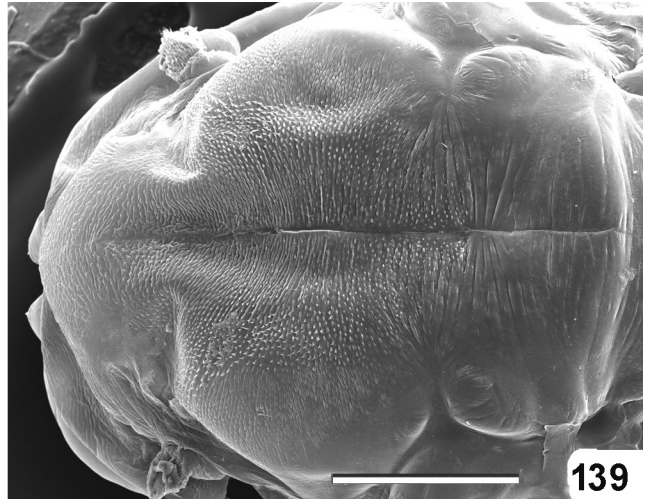
FIGURES 128–137. Pupa of *Boreoheptagyia* (s. str.) *serratosioi* **sp. nov.** 128. total view in dorsal position 129. total view in ventral position. 130. cepalic tubercles of frontal apotoma. 131. anterior part of scutum. 132–134. thoracic horn. 135. spinules of tergal shagreen. 136. anal segment of female. 137. the same of male. Scale bars are as follows: Figs 128–129—200 μ m, Figs 132–134—20 μ m, Figs 130,135–137—100 μ m, Figs 131—50 μ m.

Wings and *legs* difficult to observe in details and measure. Anal lobe of wing well developed, rounded. Alula without setae. Squama with 21 setae in 1–2 rows, 60–72 μ m long. Spurs of hind tibia 28 μ m and 44 μ m long. Hind tibial comb with 16 setae.

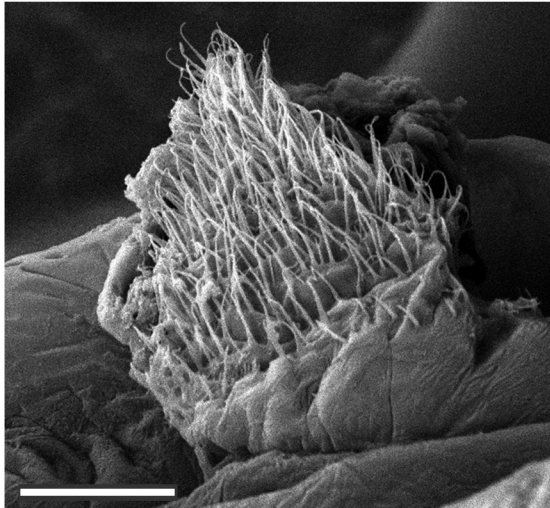
Hypopygium (Figs 124–127). Tergite IX with 9–24 setae, length 60–110 μ m. Laterosternite IX with 3–11 setae. Transverse sternapodeme 33–73 μ m wide. Aedeagal lobe weakly sclerotized, apical part of aedeagal lobe with many small spinules. Gonocoxite 155–218 μ m long. Gonostylus 68–103 μ m long, short and “inflate”, with wide median part and a short narrow apical part, ending with a short megaseta. HR 2.04–2.76.



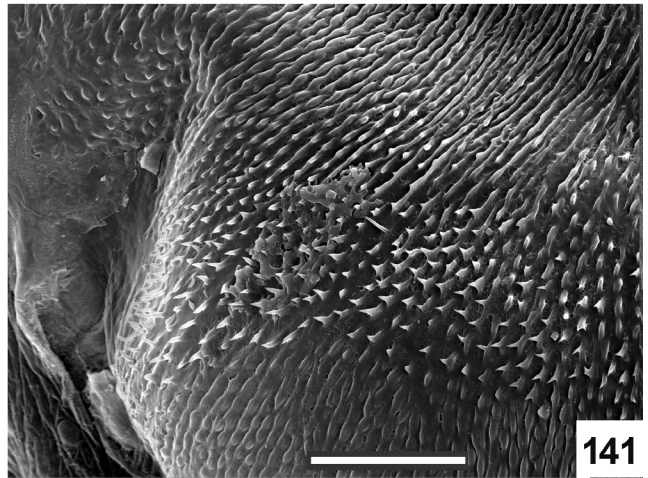
138



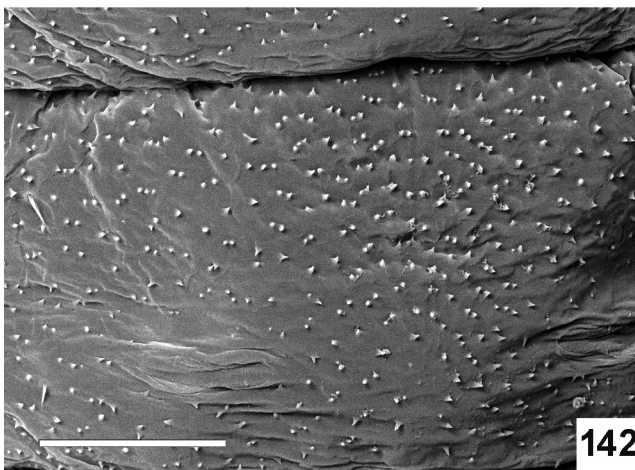
139



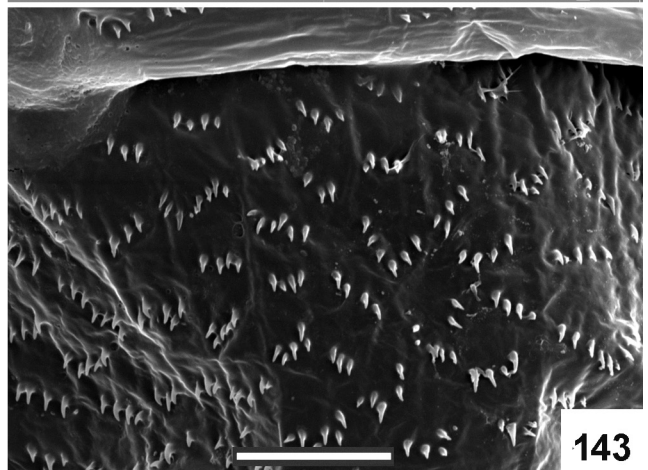
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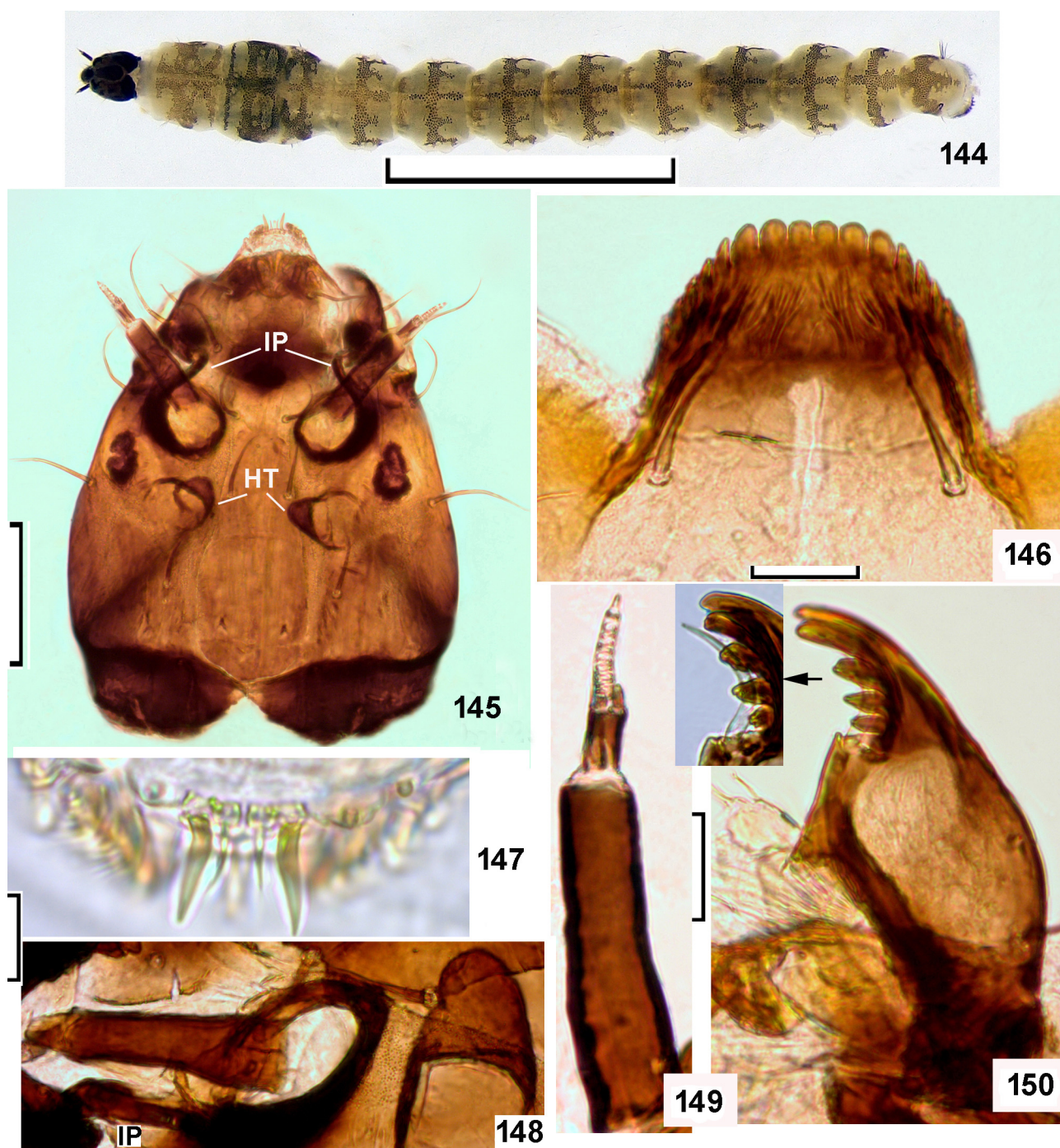
FIGURES 138–143. Pupa of *Boreoheptagyia* (s. str.) *serratosioi* **sp. nov.** (SEM). 138. total view of pupa dorsally. 139. thorax dorsally. 140. thoracic horn. 141. surface sculpture of thorax. 142. surface sculpture of tergite V. 143. surface sculpture of sternite VI. Scale bars are as follows: Fig. 138—300 μm , Fig. 139—250 μm ; Figs 140, 143—50 μm ; Figs 141–142—100 μm .

Pupa ($n = 4$) (Fig. 138). Total length 2.2–2.3 mm. Cephalothorax dark brown to black, abdomen greenish-brown. Exuviae grayish. Thoracic horn black or dark brown.

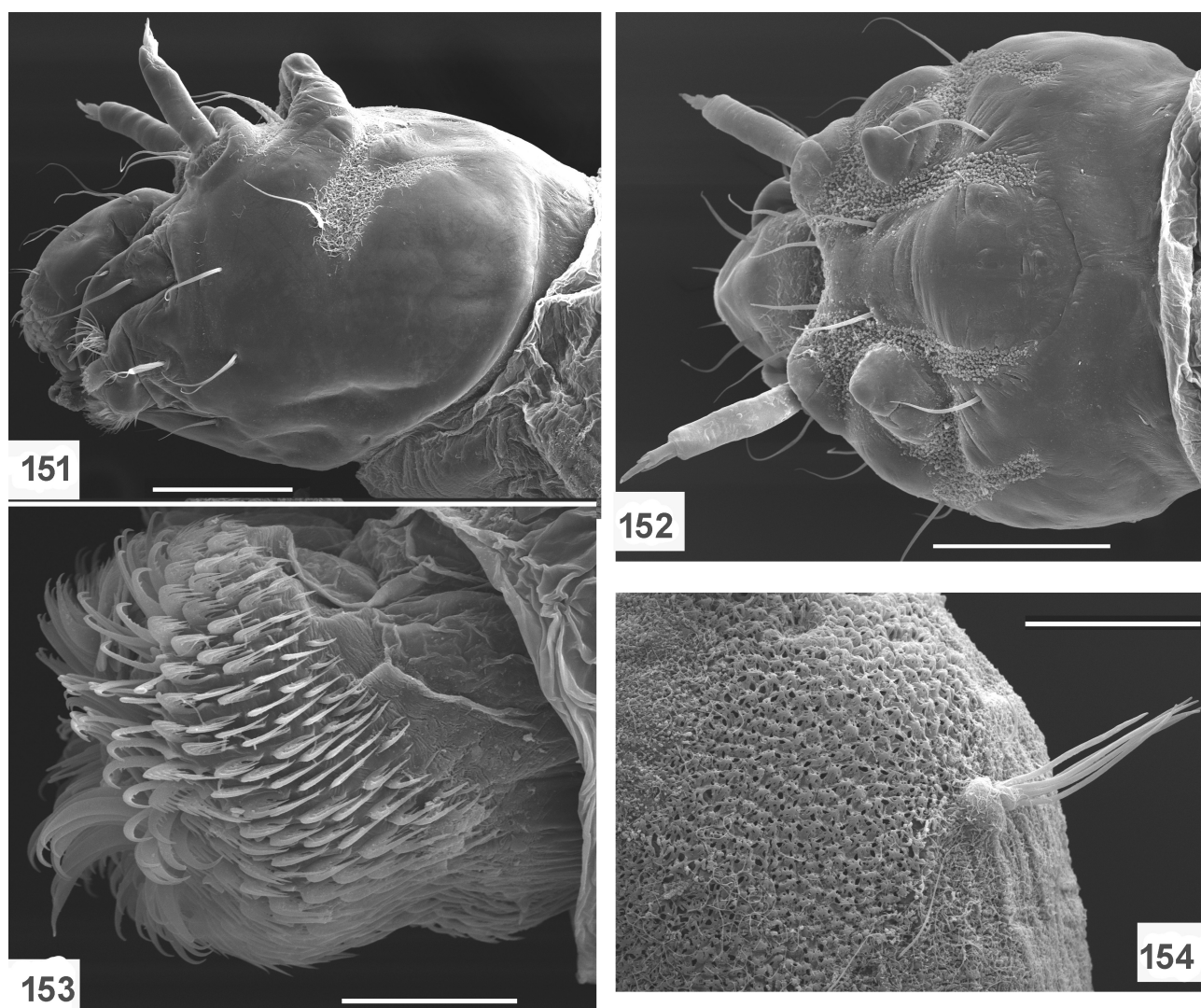
Cephalothorax. Frontal apotome with black, spine-shape cephalic tubercles, 16 μm long (Fig. 130). The anterior two-thirds of the thorax are heavily granulated dorsally and dorsolaterally, and have small spines dorsolaterally in the middle; the posterior third is only wrinkled, without granulation (Figs 139, 141). Thoracic horn triangular, 64–80

μm long, 32–48 μm wide at the base, with a spire-shaped top and covered with hair-like setae (Figs 132–134, 140). Pc_1 52 μm , Pc_2 16–36 μm , Pc_3 56–60 μm ; 2 lateral anteprenotals, 28–48 μm long, are present, median anteprenotals and dorsocentrals are absent.

Abdomen. Tergite I in anterior 1/3 with fine shagreen of spinules; tergites II–VIII with fine shagreen in the middle part, sometimes in the anterior or posterior parts (Fig. 135, 142). Sternites with very delicate shagreen spinules, which are sparsely located (Fig. 143). Tergites and sternites without posterior spines. Apophyses not developed. Segment I with 2 pairs of hair-like lateral setae, 28–40 μm long; segments II–VII with 4 pairs of lateral setae 12–40 μm long; segment VIII with 4 pairs of lateral setae, 12–20 μm long. Anal lobe broad, with 3 strong, apically hooked anal macrosetae, 80–92 μm long (Figs 136–137). Male genital sac broad, strongly extended beyond anal lobe (Fig. 137).



FIGURES 144–150. Larva of *Boreoheptagyia* (s. str.) *serratosioi* sp. nov. 144. total view in dorsal position. 145. head in dorsal position. 146. mentum. 147. setae of labrum. 148. head tubercle and inner process of antennal pedestal. 149. antenna. 150. mandible. Scale bars are as follows: Fig. 144—1 mm, Fig. 145—100 μm , Figs 146–150—50 μm .



FIGURES 151–154. Larva of *Boreoheptagyia* (s. str.) *serratosioi* sp. nov. (SEM). 151. head capsule in lateral view. 152. head capsule in dorsal view. 153. hooks of posterior parapods. 154. surface sculpture of last abdominal segment with procercus. Scale bars are as follows: Figs 151–152—200 μ m; Fig. 153—50 μ m; Fig. 154—100 μ m.

Larva of fourth instar (n = 5) (Fig. 144). Greenish, greenish-brown, brownish. Total length 3.6–4.7 mm.

Head. Dark brown, 279–295 μ m long, 246–279 μ m wide. Dorsally with dark brown or yellowish brown pair tubercles, 20–62 μ m long (Figs 145, 151–152). Postoccipital margin dark brown to black. Dorsal setae S_I – S_5 dark brown and strong, 50–62 μ m long.

Antenna. Dark brown to black, with 5 segments, length of 1–5 segments (in μ m)—74–79 : 16–20 : 19–21 : 2 : 3. Blade, 23 μ m long, ending approximately 1/4 of segment 3; style, 6–8 μ m long and lauterborn organs, 3 μ m long on apex of segment 2; large ring organ in basal 1/4 of segment 1 (Fig. 149); AR 1.7–2.1. Antennal pedestal with inner dark brown to black processes, 52–57 μ m long (Figs 145, 148).

Labrum. S_I seta-like, 5–12 μ m long; S_{II} simple and wide, 15–17 μ m long (Fig. 147). Pecten epipharyngis consists of 5 broad, elongate, apically blunt scales. Premandible apically broad with 6 blunt teeth, lateral spine apically with setae.

Mandible with 5 teeth, apical tooth brownish-yellow, brown, other teeth dark brown; seta subdentalis curved, extending apex of apical tooth, apically pointed; seta interna consisting of 15–17 weakly serrate branches (Fig. 150).

Mentum. With 2 median and 7 pairs of lateral teeth; the median tooth and 2 pairs of lateral teeth subequal in size and little wider other lateral teeth. Ventromental plates elongate and narrow (Fig. 146).

Abdomen. The sculpture of the surface of abdomen tergites honeycomb-shaped (Fig. 154). Posterior parapodes

with sickle-shaped hooks of three types (Fig. 153). Procercus reduced, with 6 anal setae, 92–96 µm long (Fig. 154). Dorsal pair of anal tubules 52 µm long, ventral pair 76–80 µm long.

Diagnostic characters. Male of *B. (s. str.) serratosioi* **sp. nov.** is closely related to *B. dasyops* Serra-Tosio but is well separated from latter by alignment of dorsocentrals in anterior and posterior groups and bare eyes, which in the male of *B. (s. str.) dasyops* with microtrichiae protruding beyond the facets and dorsocentrals of scutum only in anterior group.

Distribution. Known only from its type locality in the Indian Himalayas.

***Boreoheptagyia (s. str.) similis* (Chaudhuri et Ghosh)**

Neopodonomus similis Chaudhuri et Ghosh, 1981: 373.

Boreoheptagyia similis (Chaudhuri et Ghosh); Serra-Tosio 1989: 168; Ashe & O'Connor 2009: 266.

Remarks. The pupa and larva of *B. similis* are still unknown. Original description of the male and female *Neopodonomus similis* by Chaudhuri & Ghosh (1981) clearly shows that it is in fact a chironomid belonging to the genus *Boreoheptagyia*, and therefore to the subfamily Diamesinae, not to the subfamily Podonominae as these authors believe. *B. similis* appears similar, due to its highly contrasting coloration, to the European species *B. alpicola*. However, these two species differ in the number of flagellomeres on the male's antenna: 13 flagellomeres in *B. similis*, 12 flagellomeres in *B. alpicola*.

Distribution. Known only from the Himalayas: Bhutan (Wangdi, alt. 2014 m a.s.l.).

***Boreoheptagyia (s. str.) tibetica* Makarchenko et Wang**

Boreoheptagyia tibetica Makarchenko et Wang in Makarchenko, Wang & Willassen, 1996: 825; Ashe & O'Connor 2009: 266.

Distribution. China (Tibet).

***Boreoheptagyia (s. str.) xinglongiensis* Makarchenko, Wu et Wang**

Boreoheptagyia xinglongiensis Makarchenko, Wu et Wang in Makarchenko, Endo, Wu & Wang, 2008: 15; Ashe & O'Connor 2009: 267.

Distribution. China (Sichuan).

Boreoheptagyia (s. str.) sp. 1

Material examined. 1 larva, KYRGYZSTAN: Chuy Region, Alamudun District, unnamed stream of Ala-Archa River basin, 2.5 km upper of the Ala-Archa National Park, 42.629050 N, 74.488217 E, 27.05.2016, leg. D. Palatov.

Remarks. The larva of this species is indistinguishable by morphology from *B. (s. str.) legeri*. Additional adult male and pupa material is needed for a more precise identification.

Distribution. Known only from Kyrgyzstan.

Boreoheptagyia (s. str.) sp. 2

Material examined. 1 mature pupa, REPUBLIC OF ABKHAZIA: Gulripshi District, Kodor River basin, Dzhampal River near mouth of Shakuran River, 43.028589 N, 41.334719 E, 2.02.2018, leg. D. Palatov.

Remarks. This species is indistinguishable by morphology of pupa from *B. (s. str.) legeri*. Additional adult male and larval material is needed for a more precise identification.

Distribution. Known only from the Republic of Abkhazia.

Boreoheptagyia (s. str.) sp. 3

Material examined. 1 larva, RUSSIA: Karachay-Cherkess Republic, Zelenchuksky District. Khyzgora River, 200 m upstream from the mouth, alt. 1291 m a.s.l., 43.631303 N, 41.386717 E, 09.04.2023, leg. D. Palatov. 1 larva, Republic of Dagestan, Dokuzparinsky District. Mouth of the Seldy River, northern part, alt. 2282 m a.s.l., 41.279886 N, 47.844925 E, 21.08.2024, leg. D. Palatov. 2 pupae (male and female), REPUBLIC OF ABKHAZIA, Gulripshi District, Kodor River basin, Dzhampal River near mouth of Shakuran River, 43.028589 N, 41.334719, 02.02.2018, leg. D. Palatov.

Remarks. This species is indistinguishable by the morphology of pupa and larva from *B. (s. str.) brevitarsis*. Additional adult male material is needed for a more precise identification.

Distribution. Known only from the Karachay-Cherkess Republic of Russia and the Republic of Abkhazia.

***Boreoheptagyia* (s. str.) sp. 6**

Material examined. 1 adult male, IRAN: Lorestan Province, near Cham Chit Village, Iranian Plateau, Zagros Mountains, Tenge-Kholeven River, alt. 2084 m a.s.l., 33.37895 N, 48.973567 E, 29.06.2019, leg. D. Palatov.

Remarks. This species is indistinguishable by morphology of adult male from *B. (s. str.) brevitarsis*. Additional pupa and larval material is needed for a more precise identification. Most likely the species is cryptic.

Distribution. Known only from Iran.

***Boreoheptagyia* (s. str.) sp. 7**

Material examined. 2 larvae, 2 pupae (males), KAZAKHSTAN: East Kazakhstan Region, Zaysan District. Waterfall Stream, a tributary of Bolshoe Rakhmanovskoye Lake, alt. 1820 m a.s.l., 49.523883 N 86.539083 E, 06.07.2018, leg. D. Palatov; 1 larva, the same data, except Katon-Karagay District, near Katon-Karagay village. Altai Mountains, Kurchum Range, Right tributary of Kulmes River, alt. 1113 m a.s.l., 49.166283 N, 85.633583 E, 01.07.2018, leg. D. Palatov.

Remarks. This species is indistinguishable by the morphology of adult male from *B. (s. str.) sarymsactyensis*. Additional adult male material is needed for a more precise identification. Most likely, the species is cryptic.

Distribution. Known from the East Kazakhstan Region.

Subgenus *Kaluginia* Makarchenko, stat. nov.

Kaluginia Makarchenko, 1987: 784.

Kaluginia Makarchenko; Oliver 1989: 134; Sæther *et al.* 2000: 147; Ashe & O'Connor 2009: 291.

Type of subgenus: *Kaluginia lebetiformis* Makarchenko, 1987, by original designation.

Subgeneric diagnosis

Adult male. Total length 2.42–4.3 mm. Wing length 1.68–2.6 mm.

Head. Eye bare, not extended dorsomedially. Temporal setae consisting of verticals and postorbitals. Frontal tubercles absent.

Antenna. Pedicel with setae. Flagellum with 5–7 flagellomeres; plume reduced (Figs 24–25). AR 0.28–0.82 (antenna with 5 flagellomeres), AR 0.31–0.38 (antenna with 7 flagellomeres). Terminal flagellomere with 1–2 subapical setae.

Thorax. Anteprenotal lobes narrowly joined medially; ventral anteprenotals present; dorsal ante- pronotals absent. Mesonotum is not covered macrotrichiae. Acrostichals present, beginning near anteprenotum, extending near middle of mesonotum; dorsocentrals erect and in 1–2 rows; prealars ending near parapsidal suture; supraalars 1–2, scutellars numerous (Figs 31, 33–34). Setae on Pe are not registered.

Wing. Gray, spotted. Membrane without setae, with moderate to coarse punctation. Anal lobe moderately produced. Costa extended; R_{2+3} reduced, clearly visible only in basal part; FCu distal to MCu. R_{4+5} with setae; squama fringed (Figs 41–42).

Legs. Tarsomere 4 cordiform, shorter than tarsomere 5.

Hypopygium (Figs 50–51, 57–59). Tergite IX with round-triangular dark anal point as well as reduced anal point or without it; anal-lateral corners of tergite IX can elongated in form of narrow lobes back. Transverse sternapodeme high, with rounded or straight apex (Figs 50–51). Gonocoxite with a small, basal protuberance. Basal lobe of gonocoxite is various shapes and depends on its position; in the inner half with microtrichia, along the outer margin with short setae; inferior volsella covered by setae. Gonostylus scoop-shaped; inner lobe along the margin with 5–6 megasetae and one subterminal tooth; outer lobe widely triangular, inner margin of which with strong setae (Fig. 59) or gonostylus simple, with some twisted angle, apex with some stout megasetae (Figs 57–58).

Pupa. Total length 3.7 mm. Exuviae with brown cephalothorax and brownish abdomen.

Cephalothorax. Frontal apotome without warts, with small conical cephalic tubercles. Prefrons with 2 dark brown and long frontal setae (Fig. 63).

Thorax dorsally strongly granulated in the anterior two-thirds, wrinkled in the posterior third (Fig. 64). Thoracic horn strongly sclerotized, from dark brown to black, triangular, covered with hairlike setae (Fig. 65). Three precorneals, 2 median and 2 lateral anteprenotals, 2 dorsocentrals are present.

Abdomen. Tergite I and tergite IX without shagreen. Tergites II–VIII with median and lateral shagreen of spinules, but shagreen on tergite II less intense (Figs 66–68). Sternites without shagreen. Apophyses well developed (Figs 66–67). Tergites I–VII with 5 dorsal setae, tergite VIII with 1 dorsal seta. Segment I with 2 pairs, segments II–VIII with 4 pairs of hairlike lateral setae. Anal lobe broad, with 3 strong, apically hooked anal macrosetae; also with 3 dorsomedial and 1 ventromedial setae. Male genital sac broad, strongly extended beyond anal lobe and apex curved dorsally (Fig. 68).

Larva unknown.

Key to the species and subspecies of subgenus *Kaluginia* Makarchenko

Adult males

1. Antenna with 7 flagellomeres. Tergite IX with small rounded protuberance or dark rounded triangular anal point 2
- Antenna with 5–6 flagellomeres. Anal point small, different shape or absent 3
2. Anal point like small rounded protuberance, anal-lateral corners of tergite IX not or slightly elongated
- *B. (K.) lebetiformis koreana* Makarchenko
- Anal point dark, rounded triangular and lateral corners of tergite IX elongated as narrow lobes to back (Fig. 59)
- *B. (K.) lebetiformis lebetiformis* Makarchenko
3. Anal point small triangle or like small, rounded protuberance. AR 0.29–0.49 4
- Anal point absent. AR 0.64–0.82 *B. (K.) kurobebrevis* (Sasa et Okazawa)
4. Antenna with 5 flagellomeres; AR 0.29–0.34. Gonostylus broad anteriorly and narrowing posteriorly, with some twisted angle, apex with some stout megasetae (Fig. 58) *B. (K.) wangi* Song et Qi
- Antenna with 6 flagellomeres; AR 0.49. Gonostylus widest in middle part, surface thickly covered with short spine-like setae; apical part with lobe and 2 megasetae (Fig. 57) *B. (K.) unica* Makarchenko

Composition of subgenus *Kaluginia* Makarchenko

Boreoheptagyia (Kaluginia) lebetiformis lebetiformis Makarchenko

Kaluginia lebetiformis Makarchenko, 1987: 786, 2006: 266; Oliver, 1989: 134; Ashe & Connor, 2009: 291; Makarchenko *et al.* 2018: 28 (partly).

Kaluginia lebetiformis lebetiformis Makarchenko; Makarchenko *et al.* 2020a: 21.

Distribution. This subspecies is known from Sakhalin Island, Primorye Territory and Amur River basin of the Russian Far East.

Boreoheptagyia (Kaluginia) lebetiformis koreana Makarchenko

Kaluginia lebetiformis Makarchenko, 1987; Makarchenko *et al.* 2018: 28 (partly).

Distribution. This subspecies is known only from South Korea.

Boreoheptagyia (Kaluginia) kurobebrevis (Sasa et Okazawa), **comb. nov.**

Diamesa kurobebrevis Sasa et Okazawa, 1992: 58.

Toyamadiamesa kurobebrevis Sasa & Kikuchi, 1995: 205.

Boreoheptagyia kurobebrevis (Sasa et Okazawa); Endo, 2002: 12; Makarchenko *et al.* 2008: 8; Ashe and O'Connor 2009: 265; Yamamoto & Yamamoto 2014: 247; Lin *et al.* 2021: 189.

Remarks. The species transfer to the subgenus *Kaluginia* was based on molecular and morphological data. According to the latter, males of this species exhibit the following diagnostic features of the subgenus. Frontal tubercles absent. Antenna, with 5 flagellomeres and reduced plume; pedicel with setae. Acrostichals beginning near antepnotum, extending to near middle of mesonotum. R_{2+3} reduced and good visible only in basal part.

Distribution. Known from Japan (Honshu) and China (Guizhou Province).

Boreoheptagyia (Kaluginia) wangi Song et Qi

Kaluginia wangi Song et Qi in Wang, Song, Liu & Qi, 2026: 236.

Distribution. Known from specimens collected at two localities: the type locality in the Wuyi Mountain range (Wuyishan), Fujian Province, southeastern China (one adult male), and an additional site in the Tianmu Mountains, Zhejiang Province, eastern China (two adult males).

***Boreoheptagyia (Kaluginia) unica* Makarchenko, comb. nov.**

Boreoheptagyia unica Makarchenko, 1994: 87; Ashe & O'Connor 2009: 267; Yamamoto & Yamamoto 2014: 247.

Distribution. Japan (Honshu).

Subgenus *Palatovia* Makarchenko et Semenchenko, stat. nov.

Palatovia Makarchenko et Semenchenko, 2020c: 92.

Type of subgenus: *Palatovia lorestanica* Makarchenko et Semenchenko, 2020c, by original designation.

Subgeneric diagnosis

Adult male. Small species up to 2.5 mm long, with wing length up to 1.8 mm.

Antenna. Scape and pedicel bare. Flagellum with 5 flagellomeres and reduced plume of short setae, which on flagellomeres 1–4 not more than seven setae (Fig. 27); flagellomeres 1–4 and terminal flagellomere with sensilla chaetica; terminal flagellomere with 1–3 subapical setae. Antennal ratio less than 0.50.

Head. Eye bare, not extended dorsomedially. Temporal setae numerous, consisting of inner and outer verticals, frontals, orbitals and postorbitals but some groups of setae are very difficult to be separated. Vertex without frontal tubercles. Tentorium more swollen in basal half than in distal part; microtrichia absent. Cornua of cibarial pump pointed. Palp with 5 palpomeres; palpomere 3 without sensilla capitata.

Thorax. Anteprenotal lobes in contact to widely separated medially; anteprenotals present in ventrolateral part and situated in basal 2/3 of lobe. Scutum broad, low, not extended over anteprenotal notch, and covered with macrotrichia. Acrostichals short, in one row, beginning near anteprenotum, extending and sometimes diverging to near scutellum; dorsocentrals short and sparse, situated in two groups only in anterior part of mesonotum: setae of first group in humeral area, posteriorly of humeral pit and setae of second group anteriorly of humeral pit or just posterior to anteprenotum (Fig. 36); prealars middle size, in two groups; scutellum covered with numerous setae; some supraalars and preepisternals present. Postnotum densely covered with aculeiform macrotrichia.

Wing (Fig. 43). Gray or dark grey. Membrane without setae, covered with well visible microtrichia. Anal lobe slightly reduced, angular or rounded angular. Costa slightly produced of R_{4+5} apex; R_{2+3} absent; FCu proximal to RM. MCu flows into FCu or into M_{3+4} slightly distal to FCu. R , R_1 and R_{4+5} with setae. Squama fully fringed.

Legs. Tibiae without light coloured rings; spurs comparatively short, usually not longer than width of tibial apex. Fore, mid and hind legs with pseudospurs on tarsomere 1; tarsomere 4 cylindrical, little shorter than tarsomere 5. Claws pointed apically; pulvilli as small spinules.

Hypopygium (Figs 53, 62). Tergite IX almost rectangular or in the form of an inverted trapezoid, without anal point and with numerous middle size pale setae; laterosternite IX with rounded and slightly protruding posterolateral lobes which with some setae. Aedeagal lobe strongly sclerotized with a complex structure, that is, as if several details be glued together in a dorso-ventral direction, with rounded lobe on inner side and with nose or beak shaped apex. Gonocoxite with median volsella, which in basal part bears a short lobe; basimedial setal cluster and basal plate absent. Transverse sternapodeme narrow and triangular, with rounded apex. Gonostylus with wide basal part, gradually tapering to a rounded apex, with long setae along the outer and inner edges and several megasetae in subapical part.

Pupa. See the identification key above.

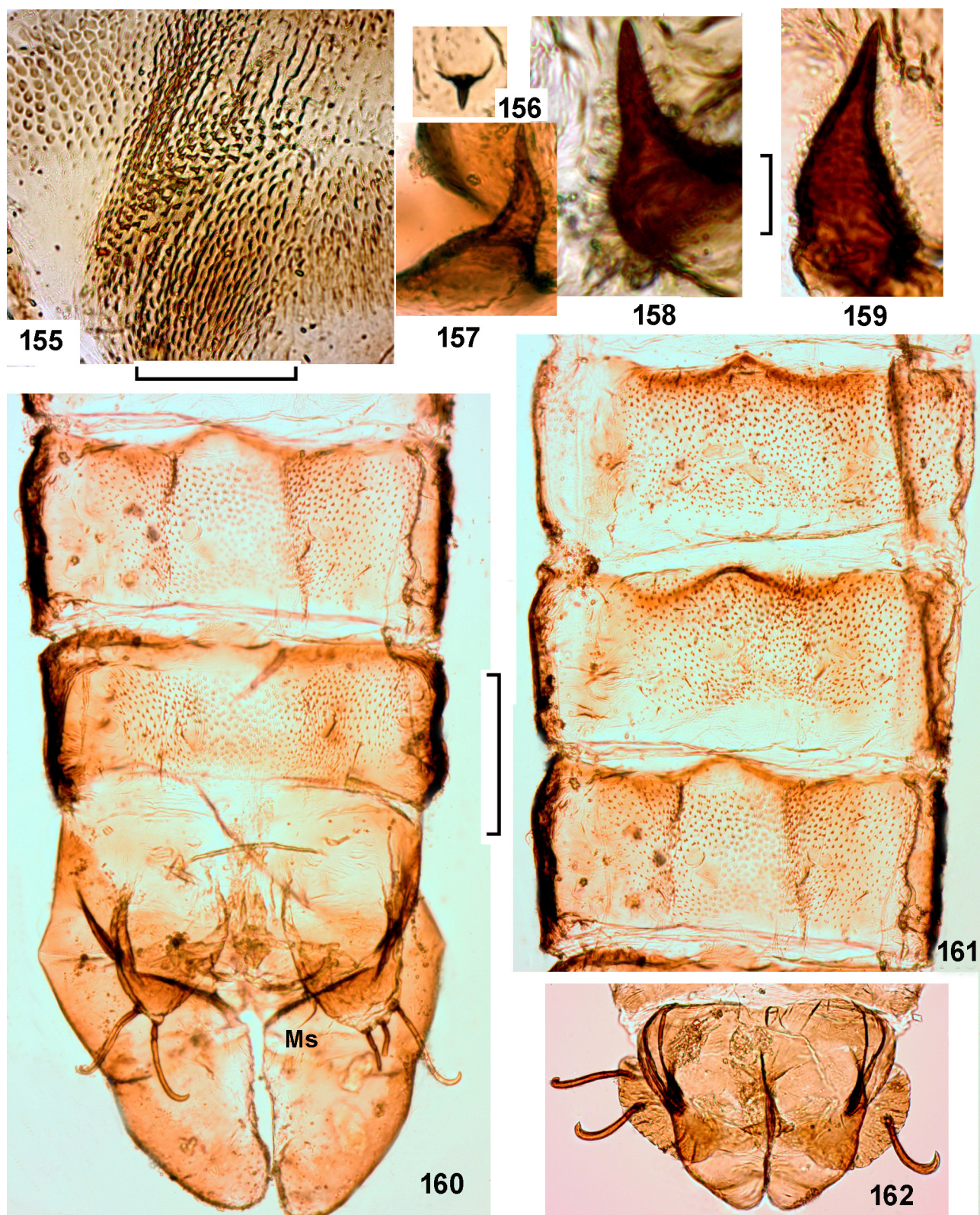
Larva of fourth instar. Due to insufficient material for analysis, it is currently impossible to prepare a diagnosis for the larvae of this subgenus.

The composition of the subgenus *Palatovia* Makarchenko et Semenchenko

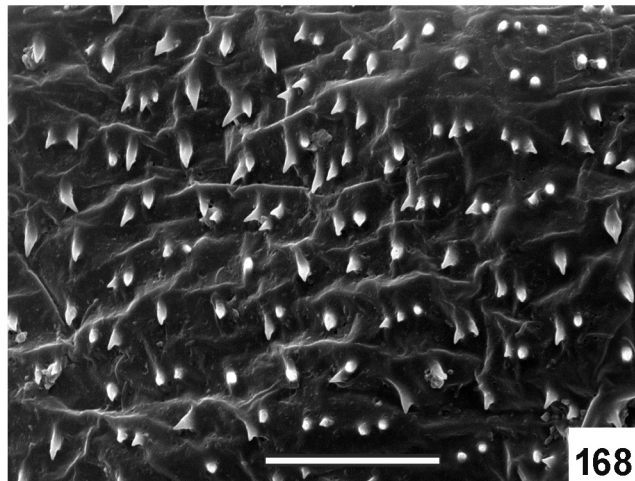
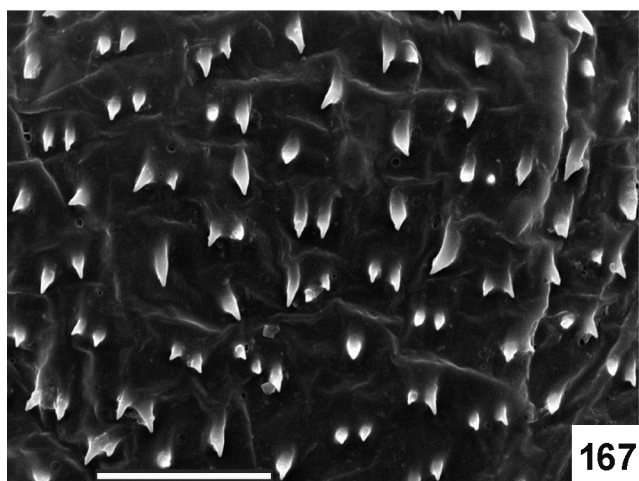
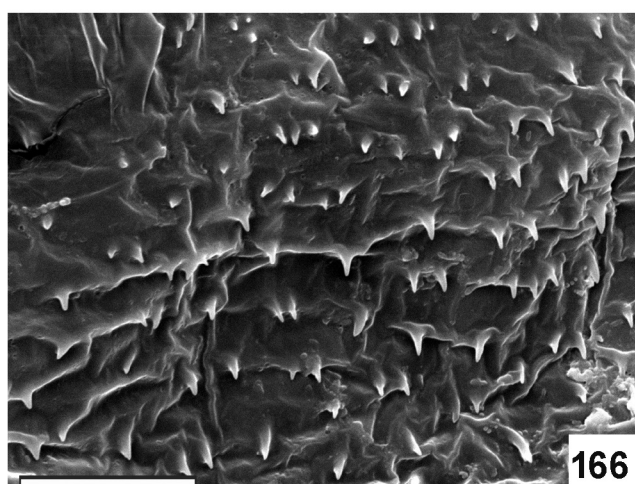
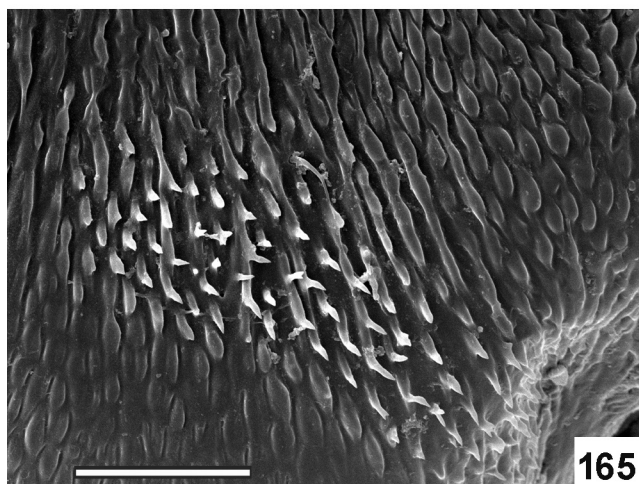
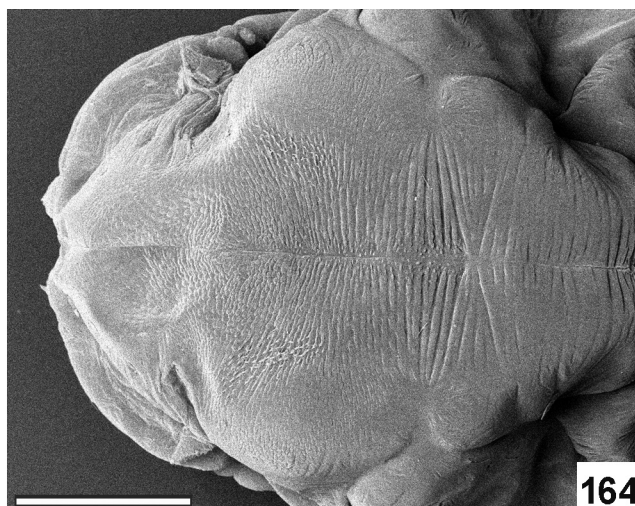
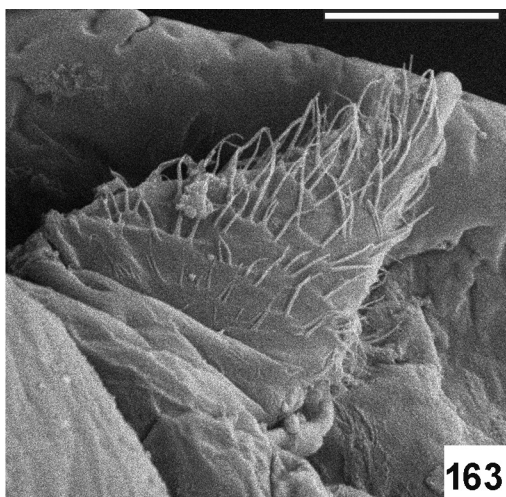
***Boreoheptagyia (Palatovia) loristanica* Makarchenko et Semenchenko, comb. nov.**

(Figs 155–179)

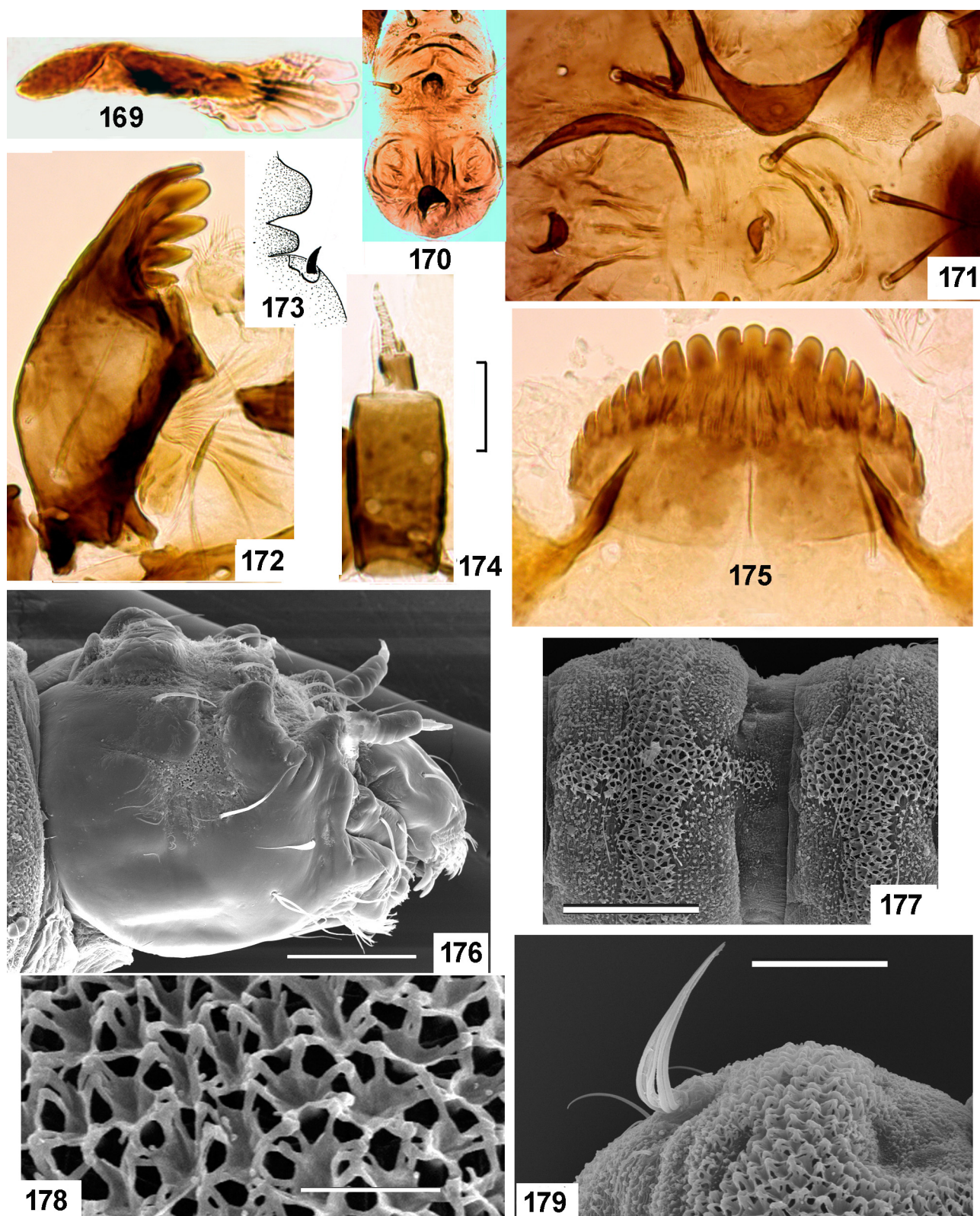
Palatovia loristanica Makarchenko et Semenchenko in Makarchenko, Semenchenko & Palatov 2020c: 94.



FIGURES 155–162. Pupa of *Boreoheptagyia (Palatovia) lorestanica* Makarchenko *et* Semenchenko. 155. surface sculpture of thorax. 156. cephalic tubercle of frontal apotoma. 157–159. thoracic horn. 160. tergites VII–VIII and anal segment of male. 161. tergites III–V. 162. anal segment of female. Ms—median seta. Scale bars are as follows: Figs 155, 160–161—200 μ m, Figs 156–159—20 μ m.



FIGURES 163–168. Pupa of *Boreoheptagyia (Palatovia) lorestanica* Makarchenko *et* Semenchenko (SEM). 163. thoracic horn. 164. thorax dorsally. 165. surface sculpture of thorax. 166. surface sculpture of tergite VII. 167. surface sculpture of tergite VI. 168. surface sculpture of sternite VI. Scale bars are as follows: Figs 163, 166–168—50 μ m, Fig. 164—250 μ m, Fig. 165—100 μ m.



FIGURES 169–179. Larva of *Boreoheptagyia* (*Palatovia*) *lorestanica* Makarchenko *et* Semenchenko. 169. premandible. 170. tubercles of frontal apotome. 171. tubercles of dorsal surface of head. 172. mandible. 173. seta subdentalis. 174. Antenna. 175. mentum. 176. head capsule, from the side. 177. surface sculpture of abdominal tergites. 178. ornament of abdominal tergites. 179. surface sculpture of last abdominal segment with procercus. Scale bars are as follows: Figs 169–175—50 μm , Figs 176–179—100 μm .

Adult male. See subgeneric diagnosis above.

Pupa (n = 4). Total length 2.7–3.9 mm. Cephalothorax dark brown to black, abdomen brown, greenish-brown. Exuviae grayish.

Cephalothorax. Frontal apotome with black, spine-shape cephalic tubercles, 12–14 µm long (Fig. 156). Thorax wrinkled, in anterodorsal and lateral parts granulated in anterior half and covered with small spines dorsolaterally (Figs 155, 164–165). Thoracic horn dark brown to black, triangular, 60–80 µm long, 40–56 µm wide at the base, slightly curved, with spire-shaped top and covered with hair-like setae (Figs 157–159, 163). Pc₁ 46–48 µm, Pc₂ 48 µm, Pc₃ 20–24 µm; 2 lateral anteprenotals, 30–40 µm long are present, median anteprenotals and dorsocentrals are absent.

Abdomen. Tergite I and sternite I without shagreen of spinules. Tergites II–VIII with shagreen in middle and lateral parts (Figs 160–161, 166–167). Sternites with very delicate shagreen spinules, which is often unnoticeable (Fig. 168). Apophyses developed. Segment I with 2 pairs of hair-like lateral setae, 20–28 µm long; segments II–VIII with 4 pairs of lateral setae, length of which in µm following: L₁ 40, L₂ 16, L₃ 16, L₄ 48; lateral setae of segment VIII located in posterior corners. Anal lobe broad, with 3 strong, apically hooked anal macrosetae, 88–120 µm long and 1 dark brown median setae 56–64 µm long (Figs 160, 162). Male genital sac broad, strongly extended beyond anal lobe (Fig. 160).

Larva of fourth instar (n = 5). Brown, brownish. Total length 3.0–4.2 mm.

Head. Dark brown, 328–344 µm long, 246–279 µm wide. Dorsally with dark brown pair tubercles, 34–41 µm long (Figs 171, 176). Frontal apotoma with tubercle 23 µm long in basal part and tubercle 8 µm long in distal part (Figs 170–171). Postoccipital margin dark brown to black. Dorsal setae S_I–S₅ dark brown and strong.

Antenna. Dark brown, with 5 segments, length of 1–5 segments (in µm)—61–66 : 13 : 15–17 : 2 : 3. Blade 25 µm long, ending approximately 2/3 of segment 3; style 10 µm long and Lauterborn organs 3 µm long on apex of segment 2; 3 large ring organs, 3–5 µm diameter on basal (Fig. 174); AR 1.74–2.0. Antennal pedestal with outer dark brown to black processes, 52–57 µm long.

Labrum. S_I seta-like, 13 µm long; S_{II} simple and wide, 20 µm long. Pecten epipharyngis consisting of 5 broad, elongate, apically blunt scales. Premandible apically broad with 8 blunt teeth, lateral spine apically with setae (Fig. 169).

Mandible with 5 teeth, apical tooth narrow, brown or dark brown as well as other teeth; seta subdentalis minuscule, 5 µm long, curved, not even reaching the tip of the last tooth (Fig. 173); seta interna consisting of 12–14 weakly serrate branches (Fig. 172).

Mentum. With 1 median and 8–9 pairs of lateral teeth; median tooth and 2 pairs of lateral teeth subequal in size and a little wider other lateral teeth. Ventromental plates elongate and narrow (Fig. 175).

Abdomen. The sculpture of the surface of abdomen tergites honeycomb-shaped (Fig. 178). Procercus reduced, with 6 anal setae, 76–120 µm long (Fig. 179). Dorsal pair of anal tubules 50–60 µm long, ventral pair 70–80 µm long.

Subgenus *Shilovia* Makarchenko, stat. nov.

Shilovia Makarchenko, 1989: 137; Sæther *et al.* 2000: 134, Fig. 144; Ashe & O’Conner 2009: 292; Makarchenko *et al.* 2020b: 197.

Type of subgenus: *Shilovia rara* Makarchenko, 1989, by original designation.

Subgeneric diagnosis (emended)

Adult male. Small-sized species 1.5–2.5 mm long, with wing length 1.6–2.4 mm.

Antenna. Scape bare. Flagellum with 5–6 flagellomeres and reduced plume of short setae, which on flagellomeres 1–4 not more than 12; flagellomeres 1–4 and terminal flagellomere with sensilla chaetica; terminal flagellomere with 1–3 subapical setae (Figs 28–29). Antennal ratio 0.32–0.44.

Head. Eyes bare or pubescent, not extended dorsomedially. Temporal setae numerous, consisting of inner and outer verticals, frontals, orbitals, and postorbitals. Vertex without frontal tubercles. Tentorium narrow and long; microtrichia absent. Palp with 5 palpomeres; palpomere 3 without sensilla capitata.

Thorax. Anteprenotal lobes in contact to widely separated medially; anteprenotals present in ventrolateral part.

Scutum broad, low, not extended over anteprenotal notch, and not covered with macrotrichiae. Acrostichals short, in 1–3 rows, beginning near anteprenotum, extending to near scutellum; dorsocentrals short, in 2–4 rows, in anterior part of mesonotum reach or not reach of preanal setae, and in posterior part they are converge or not converge with acrostichal setae; prealars middle size, in 2–3 rows (Fig. 38); scutellum covered with numerous setae; some setae on MAII and also supraalars and preepisternals present. Postnotum with or without setae (Fig. 39).

Wing. Gray or dark grey. Membrane without setae, covered with good visible microtrichiae. Anal lobe slightly reduced, angular or rounded angular. Costa slightly produced of R_{4+5} apex; R_{2+3} absent; FCu proximal to RM. MCu flows into FCu or into M_{3+4} slightly distal to FCu. R , R_1 and R_{4+5} with setae; Cu and An with or without setae; squama with setae (Figs 60–61).

Legs. Tibiae with or without light coloured rings; spurs comparatively short. Fore, mid and hind legs with pseudospurs on tarsomere 1; tarsomere 4 cylindrical, shorter than tarsomere 5. Claws pointed apically; pulvilli as small spinules

Hypopygium (Figs 60–61). Tergite IX wide, with concave or almost straight posterior edge, without anal point, covered with numerous very short setae. Sternapodeme long and narrow or wide basally and narrow distally; aedeagal lobe weakly sclerotized, apical part hooked or fingerlike (Fig. 54). Gonocoxite with long apical projection (“heel”) which densely covered with long and thin setae; this “heel” posterior to gonostylus 0.35–0.63 times as long as gonostylus; inferior volsella in form of tubercle, densely covered with macrotrichiae and setae; basal lobe of gonocoxite poorly developed or reduced. Gonostylus simple, almost straight or curved in middle or distal part, in distal half covered with very short setae, on outer edge with or without rounded extension, apically with a tooth and short megaseta.

Pupa. See the identification key above.

Larva of fourth instar. Due to insufficient material for analysis, it is currently impossible to prepare a diagnosis for the larvae of this subgenus. But

Key to the species of the subgenus *Shilovia* Makarchenko

Adult males

1. Antenna with 7 flagellomeres. Preepisternum and MAII without setae. Wing membrane with microtrichiae on almost entire surface except a bare area near anal lobe. Superior volsella tongue shape with small projection. Inferior volsella finger-like. Gonostylus digging bucket-shape, with 1 megaseta at the apex (Fig. 60) *B. (S.) zhengi* Lin et Liu
- Antenna with 5–6 flagellomeres. Preepisternum and MAII with setae. Wing membrane with microtrichiae on entire surface. Superior and inferior volsellae, gonostylus, different shape 2
2. Antenna with 5 flagellomeres (Fig. 29). Legs spotted: basal 1/3 or half of femur and tibia yellow, distal 2/3 or half brown; ta_1 – ta_5 brown. Dorsocentrals in anterior part of mesonotum not reach preanal setae. Posterior margin of tergite IX concave; gonostylus in subapical part along outer edge with rounded extension; inferior volsella and basal lobe of gonocoxite present; sternapodeme long and narrow (Fig. 54) *B. (S.) rara* Makarchenko
- Antenna with 6 flagellomeres. Legs not spotted: at least basal 3/4 of femur yellowish or yellow, distal 1/4 dark brown; tibia, ta_1 – ta_5 dark brown. Dorsocentrals in anterior part of mesonotum reach preanal setae. Posterior margin of tergite IX straight or slightly concave; gonostylus another shape, in subapical part along outer edge without rounded extension; basal lobe of gonocoxite reduced; sternapodeme wide basally and narrow distally 3
3. Dorsocentrals in posterior part converge with acrostichal setae. Postnotum with setae (Fig. 39). Wing with setae on Cu and An (Fig. 45). Gonostylus length/gonostylus width 2.86–3.67 (Fig. 61) *B. (S.) xinhuaewangi* Makarchenko et Semenchenko
- Dorsocentrals in posterior part not converge with acrostichal setae (Fig. 37). Postnotum, Cu and An of wing without setae (Fig. 44). Gonostylus length/gonostylus width 5.22–7.20 *B. (S.) yakovlevi* Makarchenko et Semenchenko

Composition of subgenus *Shilovia* Makarchenko

Boreoheptagyia (*Shilovia*) *rara* Makarchenko

Shilovia rara Makarchenko, 1989: 140; Sæther *et al.* 2000: 134, Ashe & O’Connor 2009: 106; Makarchenko *et al.* 2020b: 199.

Distribution. Known from the mountains of Tajikistan (Gissar Range) and Kyrgyzstan. (Chatkal District, Tien Shan Mountains).

***Boreoheptagyia (Shilovia) yakovlevi* Makarchenko et Semenchenko**

Shilovia yakovlevi Makarchenko et Semenchenko in Makarchenko, Semenchenko & Palatov 2020b: 203.

Distribution. Known only from the type locality—Saur Mountains of East Kazakhstan

***Boreoheptagyia (Shilovia) xinhuaewangi* Makarchenko et Semenchenko**

(Figs 180–196)

Shilovia xinhuaewangi Makarchenko et Semenchenko in Makarchenko, Semenchenko & Palatov, 2020b: 202.

Adult male. See subgeneric diagnosis above.

Pupa (n = 5). Total length 3.2–3.8 mm. Cephalothorax dark brown to black, abdomen greenish-brown, brownish. Exuviae greyish.

Cephalothorax. Frontal apotome with dark brown to black, spine-shape cephalic tubercles, 16 µm long. Thorax is dorsally wrinkled, granulated dorsally and dorsolaterally in the anterior third, dorsolaterally with small elongated spines (Figs 182–184). Thoracic horn dark brown to black, triangular, with longitudinal groove, 112–120 µm long, 48–92 µm wide, covered with hair-like setae (Figs 180–181). Pc_1 20–24 µm, Pc_2 28–30 µm, Pc_3 34–40 µm; 2 lateral anteprenotals, 20–40 µm long are present.

Abdomen. Tergite I and sternite I without shagreen of spinules. Tergites II–VIII with shagreen in middle and lateral parts (Fig. 185). Sternites with very delicate shagreen spinules, which is often unnoticeable (Fig. 186). Apophyses not developed. Segments II–VIII with 3 pairs of hair-like lateral setae, 16–40 µm long. Anal lobe broad, with 3 strong, apically hooked anal macrosetae, 48–120 µm long. Male genital sac broad, strongly extended beyond anal lobe and apex curved dorsally.

Larva of fourth instar (n = 5). Greenish, greenish-brown, brownish. Total length 4.6–6.2 mm.

Head. Yellow, brownish-yellow, 394 µm long, 344–361 µm wide. Genal sclerites of the head with a pair of yellow tubercles, 112–160 µm long, widened at the base and finger-shaped distally, 16 µm wide (Figs 187–188, 195). Dorsal setae S_1 – S_5 dark brown and strong, 61–62 µm long.

Antenna. Dark brown, with 5 segments, length of 1–5 segments (in µm)—62–74 : 15–16 : 15–20 : 3–4 : 5. Blade ending approximately reaches a third of the antennal length. The second segment has two pegs, 3 and 6 µm long, on apex of segment 2; large ring organ in basal 1/4 or 1/3 of segment 1 (Fig. 194); AR 1.60–1.90. Antennal pedestal with dark brown to black outer processes, 60–64 µm long and inner processes, 12–16 µm long (Fig. 188).

Labrum. S_I seta-like, 7–10 µm long; S_{II} simple and wide, ca 16 µm long (Fig. 189). Pecten epipharyngis consisting of 5 broad, elongate, apically blunt scales. Premandible apically broad with 6–7 teeth, lateral spine apically with setae (Fig. 190).

Mandible with 5 teeth, apical tooth brownish-yellow, brown, other teeth dark brown; seta subdentalis curved, extending apex of apical tooth, apically pointed; seta interna consisting of ca. 24–35 weakly serrate branches (Figs 191–192).

Mentum. With 2 median and 7 pairs of lateral teeth; median tooth and 2 pairs of lateral teeth subequal in size and little wider other lateral teeth. Ventromental plates elongate and narrow (Fig. 193).

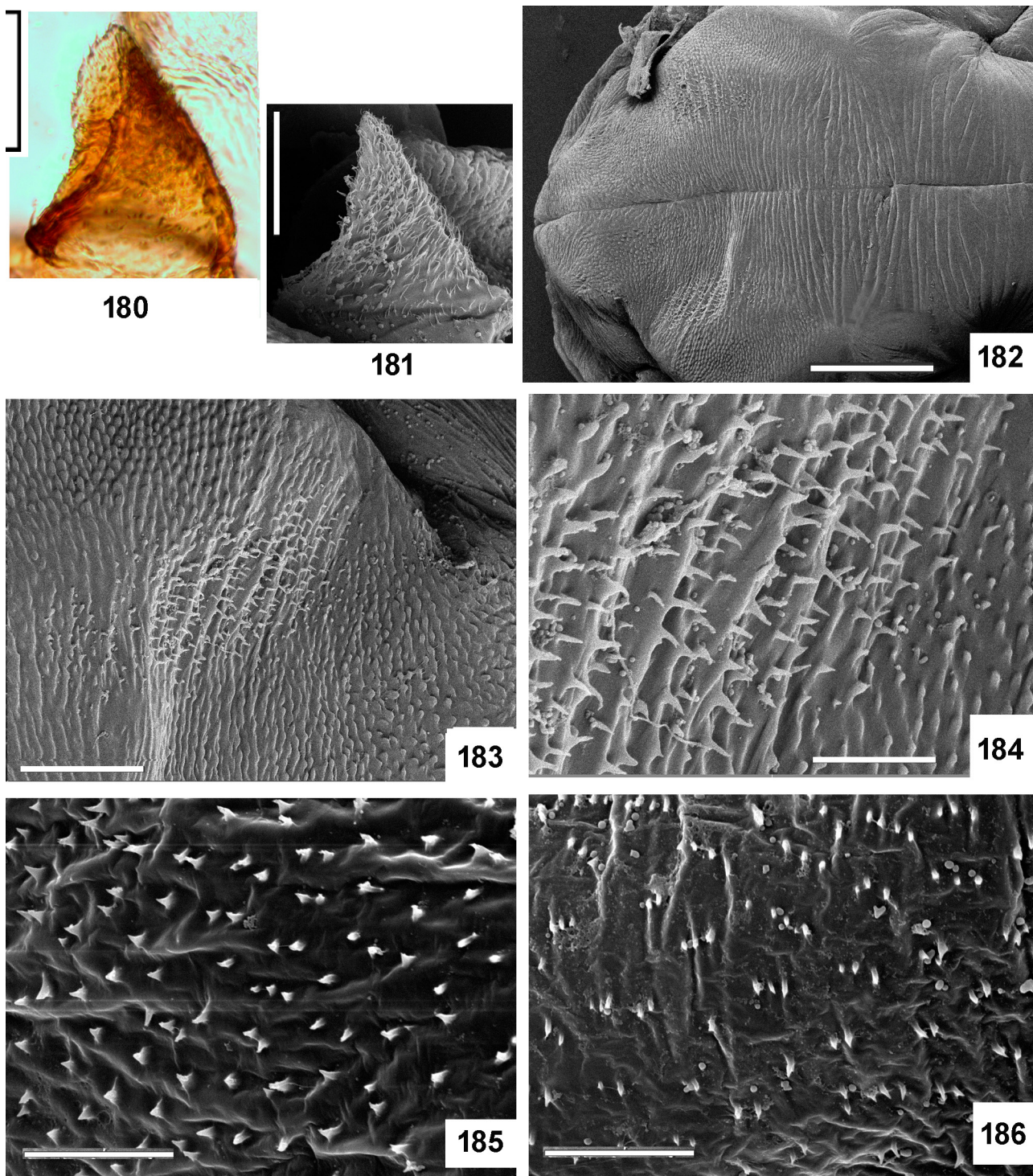
Abdomen. The sculpture of the abdominal tergites is reticulate-cellular, with dark formations at the junctions of the cells (Fig. 196). Procercus reduced, with 6 anal setae, 88–92 µm long. Dorsal pair of anal tubules little shorter of low pair.

Distribution. Known only from the type locality in Bogdo-Ula Range of Tien Shan Mountains (Xinjiang Uygur Autonomous Region, China).

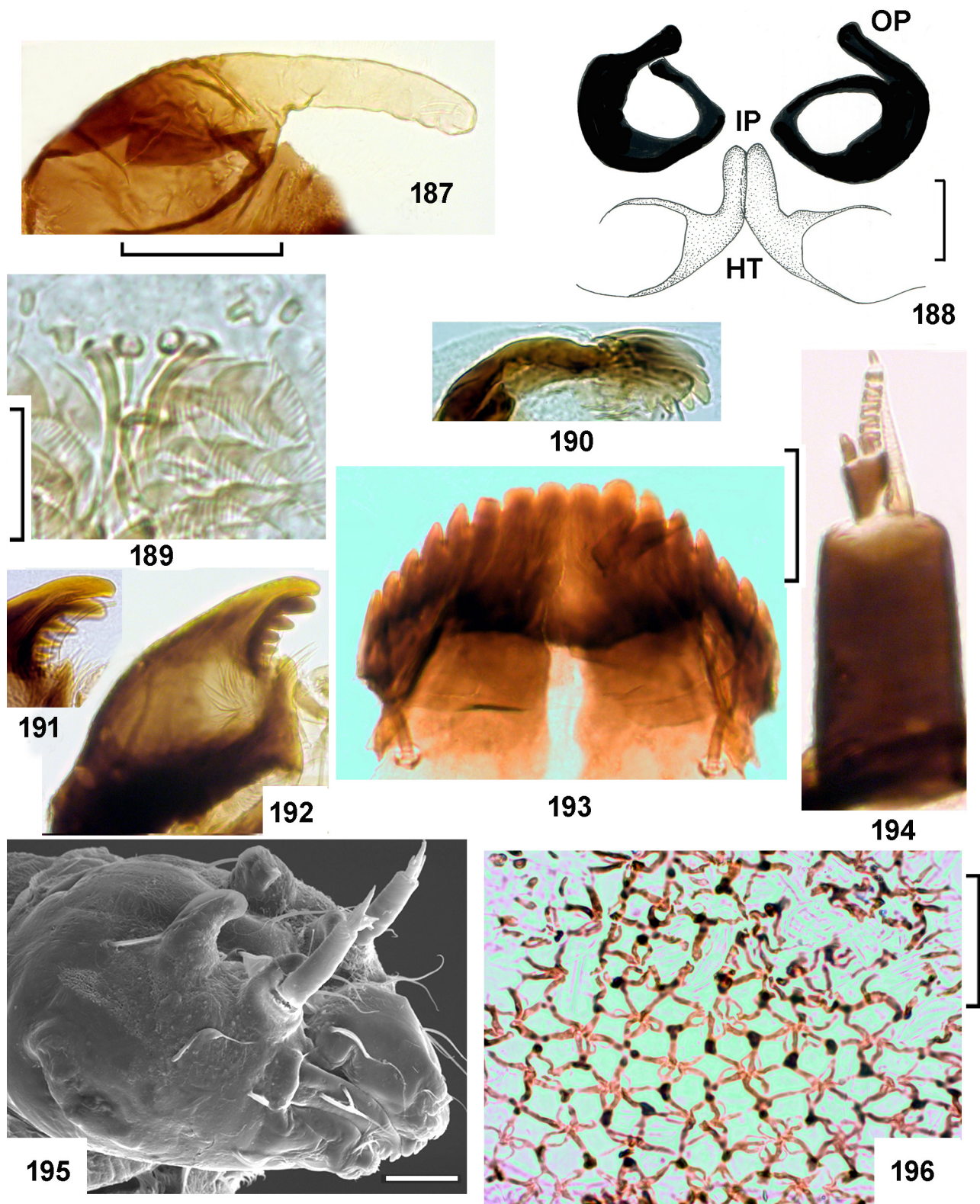
***Boreoheptagyia (Shilovia) zhengi* Lin et Liu, comb. nov.**

Boreoheptagyia zhengi Lin et Liu in Lin, Yu, Wang, Bu, Yan & Liu, 2021: 193.

Distribution. China (Yunnan).



FIGURES 180–186. Pupa of *Boreoheptagyia (Shilovia) xinhuwangi* Makarchenko *et* Semenchenko (SEM). 180–181. thoracic horn. 182. thorax dorsally. 183–184. surface sculpture of thorax. 185. surface sculpture of tergite VII. 186. surface sculpture of sternite VI. Scale bars are as follows: Figs 180–181, 186—50 μm ; Fig. 182—250 μm ; Figs 184–185—100 μm .



FIGURES 187–196. Larva of *Boreoheptagyia* (*Shilovia*) *xinhuwangi* Makarchenko *et* Semenchenko. 187. head tubercle, from the side. 188. head tubercles, outer and inner processes of antennal pedestal, dorsally. 189. setae of labrum. 190. Premandible. 191. teeth of mandible and seta subdentalis. 192. mandible. 193. mentum. 194. Antenna. 195. head, from the side. 196. surface sculpture of abdominal tergites. Designations are the same as in Figures 88–96. Scale bars are as follows: Fig. 187–193—50 μ m, Figs 189, 194—20 μ m, Fig. 195—250 μ m, Fig. 196—25 μ m.

Conclusion

This study provides the first comprehensive, integrative taxonomic revision of the tribe Boreoheptagiini by successfully synthesizing robust multi-locus molecular data (six-gene framework and COI5P DNA barcoding) with high-resolution morphological analyses.

It is generally accepted that in chironomids pupae and larvae carry stronger diagnostic characters than adult stages, and that their analysis is necessary to confirm the validity of genera and to conduct taxonomic revisions. Therefore, after obtaining molecular data for the tribe Boreoheptagiini, it was important to compare them with the results of pupal and larval morphology studies, as most genera had previously been described based only on adult males.

The use of an integrative method in determining the taxonomic structure of the tribe Boreoheptagiini was carried out for the first time, including the use of a scanning electron microscope, which allowed a more detailed study of the surface sculpture of the cephalothorax and abdomen of the pupa, as well as the head capsule and tergites of the larva.

Crucially, data obtained from the study of the morphology of preimaginal stages of development support the downgrading of the genera *Kaluginia*, *Palatovia* and *Shilovia* to subgenera, and the transfer of the genus *Sasayusurika* from Diamesini to Boreoheptagiini. Along the way, two new species, *Boreoheptagya* (s. str.) *elbursica* **sp. nov.** and *B.* (s. str.) *serratosioi* **sp. nov.**, are described by adult male, pupa and larva. Furthermore, identification keys to the genera and subgenera of the tribe Boreoheptagiini for all developmental stages, as well as keys to species of the subgenus *Boreoheptagya* s. str. based on adult males, are constructed. Finally, DNA barcodes for all available specimens of the tribe within the collection were deposited in GenBank and analyzed, establishing a highly stable, monophyletic, and practical framework for the taxonomy of this group.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

SUPPLEMENTARY TABLE S1. Taxon sampling, collection metadata, and GenBank accession numbers of the genetic markers included in the molecular phylogenetic analyses.