

<https://doi.org/10.70590/ice.2024.01.11>  
<http://zoobank.org/urn:lsid:zoobank.org:pub:E4FB4B07-C6D7-4C0D-B4F8-68683417CD6C>

## ● First discovery of snow scorpionflies (Mecoptera: Boreidae) from China

Ji-Shen WANG<sup>1\*</sup> & Liang-Jie JIA<sup>2</sup>

College of Agriculture and Biological Science, Dali University, Dali 671003, Yunnan Province, China

<sup>1</sup> <https://orcid.org/0000-0002-0188-0228>; [wangjishen826@gmail.com](mailto:wangjishen826@gmail.com)

<sup>2</sup> <https://orcid.org/0009-0003-2568-9983>; [1471766293@qq.com](mailto:1471766293@qq.com)

\*Corresponding author

**Abstract:** Snow scorpionflies are notable for their unusual activity during the cold winter months as adults. Although widely distributed in boreal or high-altitude areas of the Palearctic and Nearctic Regions, their presence in China has not been documented until now. This paper reports the first discovery of three species of snow scorpionflies, *Boreus altaicus* Nikolajev, 2015, *B. beybienkoi* Tarbinsky, 1962, and *B. transiliensis* Nikolajev, 1998 from Xinjiang Uygur Autonomous Region, northwestern China, and provides new insights into their morphology and biology. These discoveries increase the number of known Mecoptera families in China from three to four.

**Keywords:** Altay, *Boreus*, morphology, Ili, immature stages, new records, winter insects

## ● 雪蝎蛉（长翅目：雪蝎蛉科）在中国的首次发现

王吉申\* & 贾亮杰

农学与生物科学学院，大理大学，大理 671003，云南省，中国

\*通讯作者

**摘要：**雪蝎蛉因其成虫不同寻常地在寒冷的冬季月份中活动而得名。虽然在古北区和新北区的北部和高海拔地域有广泛的分布，它们此前还未在中国被记录到。本文报道三种雪蝎蛉——阿尔泰雪蝎蛉 *Boreus altaicus* Nikolajev, 2015、贝氏雪蝎蛉 *B. beybienkoi* Tarbinsky, 1962 和伊犁雪蝎蛉 *B. transiliensis* Nikolajev, 1998 在中国西北部新疆维吾尔自治区的首次发现，并补充其形态学和生物学信息。这些发现将中国已知长翅目昆虫科的数量从三个提升为四个。

**关键词：**阿勒泰，雪蝎蛉属，形态学，伊犁，未成熟阶段，新记录，冬季昆虫

**Citation:** Wang J-S & Jia L-J 2024: First discovery of snow scorpionflies (Mecoptera: Boreidae) from China. *The Indochina Entomologist*, 1 (11): 75–93. [王吉申 & 贾亮杰 2024: 雪蝎蛉（长翅目：雪蝎蛉科）在中国的首次发现. 中南半岛昆虫学家, 1 (11): 75–93.]  
<https://doi.org/10.70590/ice.2024.01.11>

Accepted by Cheng-Bin WANG: 8.XI.2024; published online: 9.XI.2024

Copyright Ji-Shen WANG & Liang-Jie Jia. This is an open access article distributed under the terms of the Creative Commons Attribution License (CCBY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

The family Boreidae belong to the holometabolous order Mecoptera, and are commonly known as snow scorpionflies due to their unusual activity during the cold winter months as adults (Dunford & Somma 2008; Bicha 2018; Beutel *et al.* 2019a, b). The name originated from Βορέας (Boréas), the Greek god associated with the cold north wind, storms, and winter (Penny 1977). This cold-tolerance, enabled by the antifreezing agents in their body fluids (Vanin *et al.* 2008; Hågvar 2010), is similar to that found in the ice crawlers (Grylloblattodea), the snow flea (Collembola: *Hypogastrura nivicola* (Fitch, 1846)), the snow flies (Diptera: Tipulidae: genus *Chionea*), the winter stoneflies (Plecoptera: Capniidae and Taeniopterygidae), and the Tasmanian snow scorpionflies (Mecoptera: Apteropanorpidae). The adults can jump using both their middle and hindlegs, in contrast to the fleas (Siphonaptera), which rely solely on their hindlegs for jumping (Burrows 2011).

The adults usually bear an elongated rostrum formed from the clypeus, labrum, genae, and maxillo-labium, resembling that of the Panorpidae (Wang & Hua 2021, 2022). They are flightless, the wings of males are modified as slender hooks serving to grasp the female during copulation, while those of females being mostly reduced and flap-like (Beutel *et al.* 2019a, b). The females have their eighth to eleventh abdominal segments and cerci modified into a secondary ovipositor (except for *Caurinus* spp., Sikes & Stockbridge 2013; Beutel *et al.* 2019a, b). The larvae are scarabaeiform or curculioniform and lack abdominal appendages (Cooper 1974; Fabian *et al.* 2015; Beutel *et al.* 2019a, b), unlike those of Bittacidae and Panorpidae (Wang & Hua 2022). The larvae and adults typically feed on mosses and liverworts (Palmer 2010; Glime 2017; Beutel *et al.* 2019a), and the adults also consume fluids of dead arthropods (Withycombe 1922). Differing from most members of Mecoptera, which possess a sperm pump in males for liquid ejaculation (Grimaldi & Engel 2005), snow scorpionflies transfer sperm by means of a spermatophore (Mickoleit 1974; Russell 1979a).

Thirty-three extant species in the family can be assigned into two subfamilies: the Boreinae and the Caurininae, based on some primitive characters of the latter such as the extremely short rostrum and the undeveloped secondary ovipositor in females (Beutel *et al.* 2019a; Beutel & Friedrich 2019). The Boreinae contain two genera: *Boreus* Latreille, 1816 (29 spp. widely distributed in the northern Nearctic and Palearctic Regions) and *Hesperoboreus* Penny, 1977 (two spp. restricted to western North America), while the Caurininae comprise only one genus, *Caurinus* Russel, 1979 (2 spp. found from Oregon, Washington, and Alaska of North America). The earliest known members of snow scorpionflies belonged to the genus †*Palaeoboreus* (2 spp.) discovered from the Upper Jurassic of Mongolia and the Lower Cretaceous of Transbaykalia, Russia (Sukatsheva & Rasnitsyn 1992). They lack a long rostrum, resembling members in the Caurininae, but possess a secondary ovipositor similar to that of the extant Boreinae members (Sukatsheva & Rasnitsyn 1992; Grimaldi & Engel 2005).

The Boreidae have long been considered a key group in resolving one of the major phylogenetic puzzles of Antliophora (scorpionflies, fleas and true flies): whether the Mecoptera is monophyletic (Misof *et al.* 2014) or paraphyletic (Whiting 2002; Whiting *et al.* 2008; Wiegmann *et al.* 2009)? A sister-group relationship between Boreidae and Siphonaptera was supported by both morphological and molecular data, rendering Mecoptera paraphyletic (Whiting 2002; Whiting *et al.* 2008; Wiegmann *et al.* 2009; Beutel & Friedrich 2019). However, other authors challenged this view and suggested that the family †Aneuretopsychidae characterized by siphonate mouthparts, were likely the sister group of fleas (Huang *et al.* 2012; Zhu *et al.* 2015). Some recent studies (Meusemann 2020; Tihelka *et al.* 2020) suggested that the closest relatives of fleas are the relic family Nannochoristidae. Despite ongoing disputes, the paraphyly of Mecoptera has been consistently supported in most recent studies (Whiting 2002; Grimaldi & Engel 2005; Meusemann 2020; Tihelka *et al.* 2020; Zhao *et al.* 2020), and the fleas may no longer be considered a separate insect order (Tihelka *et al.* 2020). Therefore, traits such as small size (typically 1–4 mm), compressed body shape, reduced wings, and long legs adapted for jumping were either independently evolved or inherited from a common ancestor shared by snow scorpionflies and fleas.

Snow scorpionflies have been widely recorded from boreal or high-altitude regions in Europe (Beutel *et al.* 2019a, b; Dvořák *et al.* 2022), North America (Penny 1977; Beutel *et al.* 2019a, b), Central Asia (Kazakhstan,

Kyrgyzstan and Tajikistan (Tarbinsky 1962; Nikolajev 1998, 2003, 2015, 2018; Gabdullina & Nikolajev 2015), Russian Far East (Navás 1926; Martynova 1954; Plutenko 1985), and Japan (Hokkaido, Hori & Morimoto 1996). However, they lack any reliable records from China, where three families of Mecoptera, the Bittacidae, the Panorpididae, and the Panorpodidae have been documented (Wang & Hua 2022). In fact, some scholars (Chou & Hua 1999; Gabdullina & Nikolajev 2015; Nikolajev 2003, 2018) have suggested a strong likelihood of discovering these insects in China, as its northern regions, including Xinjiang in the northwest, and Heilongjiang, Jilin and Liaoning in the northeast, fall within the appropriate latitude range and offer a diverse array of habitats well-suited to the snow scorpionflies, such as coniferous forests, mesic deciduous woodlands, dry pine forests, grasslands, shrub-steppe, and tundra (Beutel *et al.* 2019a, b).

The species *Boreus beybienkoi* Tarbinsky, 1962, and *B. transiliensis* Nikolajev, 1998, were originally discovered on the northern slope of the Alatau Ridge along the border of Kyrgyzstan and Kazakhstan (Tarbinsky 1962; Nikolajev 1998). They were subsequently recorded at additional localities in eastern and southeastern Kazakhstan, as well as in Tajikistan (Nicolajev 1998, 2003, 2015, 2018; Gabdullina & Nikolajev 2015). These sites are located near the Ili Kazakh Autonomous Prefecture, linked to the latter by the Tianshan Mountains and the Ili Valley, indicating a strong likelihood of their occurrence in the Chinese part of the Ili Valley and the Tianshan Mountains. Similarly, the Altay Mountains linking the Katon-Karagay National Nature Park (northeastern Kazakhstan) and the Altay Prefecture (northwestern Xinjiang, China) suggest the possibility of discovering *B. altaicus* Nikolajev, 2015 from the latter (Gabdullina & Nikolajev 2015).

In the spring and autumn of 2024, expeditions led by the authors were conducted with the aim of discovering snow scorpionflies in Xinjiang. Fortunately, a series of immature stages and adults of snow scorpionflies were successfully collected from several localities, and identified as three species, i.e., *B. altaicus*, *B. beybienkoi*, and *B. transiliensis*. We herein provide detailed illustrations and descriptions of both the adults and immature stages, along with notes on their biological aspects.

## Material and methods

All the specimens examined in this study are deposited in the Biological Science Museum, Dali University (BMDU). Adult snow scorpionflies were caught by the first and the second author and preserved in 95% ethanol. Photographs were taken with an Apple iPhone 14 smartphone (Fig. 1), and a Canon EOS R5 mirrorless digital camera in conjunction with a Canon MP-E 65 mm f/2.8 1–5× macro lens (the others). A pair of Yongnuo YN-560 IV Flash Speedlites were used as the light source. All pictures were adjusted and grouped with Adobe Photoshop CC. The terminology follows Penny (1977) and Beutel *et al.* (2019a, b).

## Taxonomy

**Family Boreidae Latreille, 1816** 雪蝎蛉科

**Subfamily Boreinae, Latreille, 1816** 雪蝎蛉亚科

**Genus *Boreus* Latreille, 1816** 雪蝎蛉属

***Boreus altaicus* Nikolajev, 2015 in Gabdullina & Nikolajev 2015** 阿尔泰雪蝎蛉

Figs 2–4; 9A–F

**Specimens examined.** 50♂50♀ adults, CHINA, Xinjiang Uygur Autonomous Region [新疆维吾尔自治区]: Altay Prefecture [阿勒泰地区], Burqin County [布尔津县], southern slope of the Altay Mountains, grassland scattered with various rocks and boulders (Fig. 1A & B), 48°19'15.19"N, 87°6'44.51"E, 1500 m, 28.X.2024, leg. Liang-Jie Jia & Ji-Shen Wang; 1 egg, 39 larvae, 1 male pupa, same data, in compact moss (mostly *Grimmia* sp.) rhizoids.

**Measurements** (mm). Adults: male body length 2.80–4.30 (n = 50), female body length 3.50–5.80 (n = 50); egg: length 0.56, width 0.32 (n = 1); larvae: 1st instar, head length 0.52–0.53, width 0.41–0.42, body length 1.40–

1.60 (n = 3); 2nd instar, head length 0.60–0.62, width 0.50–0.52, body length 2.20–2.65 (n = 4); 3rd instar, head length 0.86–0.88, width 0.71–0.73, body length 3.80–4.60 (n = 26); 4th instar: head length 1.00–1.03, width 0.84–0.86, body length 4.80–5.50 (n = 6); male pupa: body length 4.76 (n = 1).



**FIGURE 1.** Habitats of snow scorpionflies: **A, B** habitats of *Boreus altaicus* Nikolajev, 2015, the Altay Mountains **C, D** habitats of *B. beybienkoi* Tarbinsky, 1962, the Ili Valley **E, F** habitats of *B. transiliensis* Nikolajev, 1998, the Wusun Mountains **G** the second author searches for *B. transiliensis* among the moss cushions **H** the first author photographs snow scorpionflies on the snow. Red arrows denote precise locations where the insects were found.

*Adults.* This species can be recognized by the black body color (Fig. 2), the pronotum lacking long bristles (Figs 2 & 9A, B), the strongly protruded apex (hood) of male epandrium (= tergite IX, Fig. 9C), the convex apex of male hypandrium (= sternite IX, Fig. 9D), and the slender female cerci (Figs 2 & 9E, F).

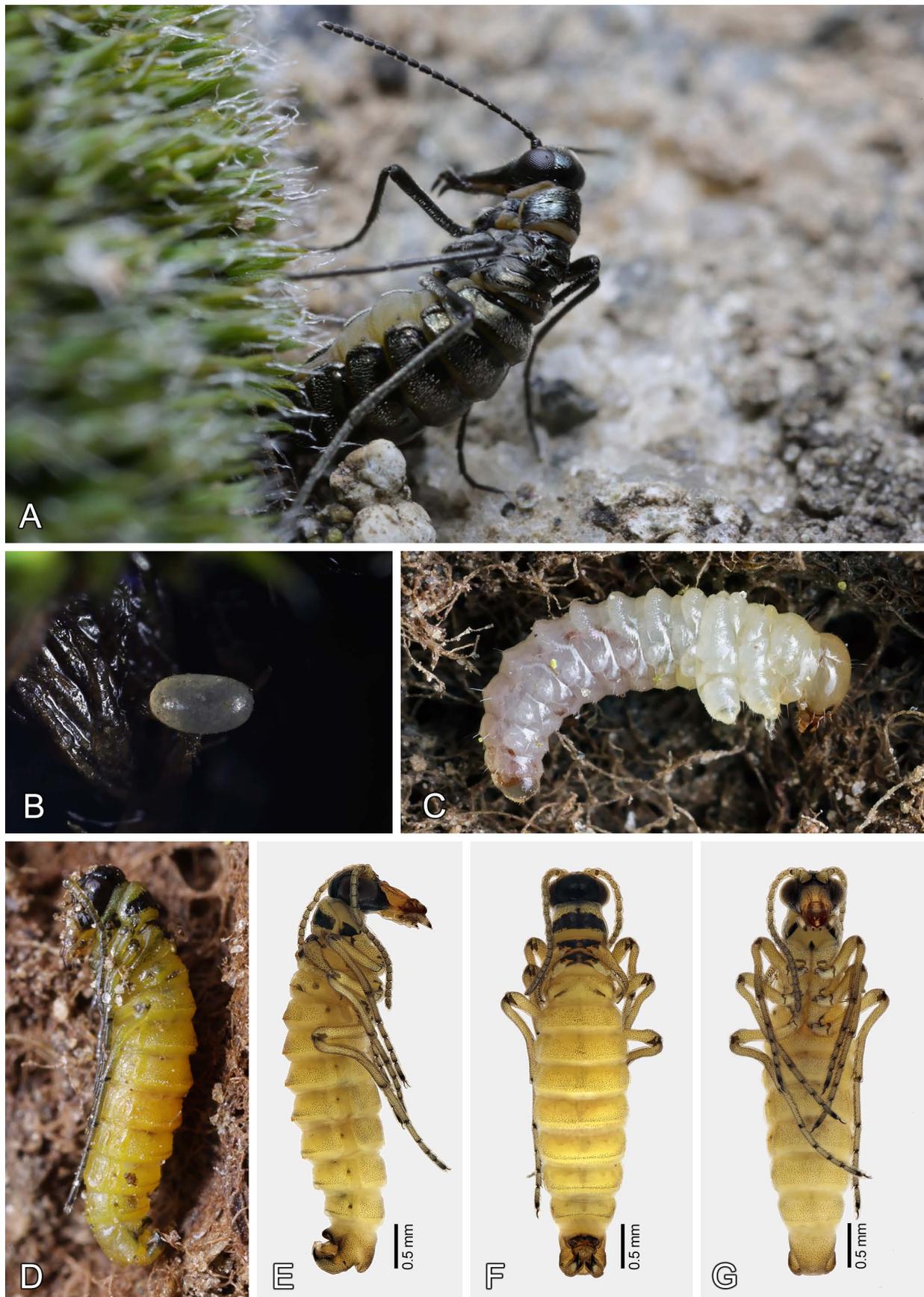


**FIGURE 2.** Adults of *Boreus altaicus* Nikolajev, 2015: **A** male **B** female **C** a mating pair.

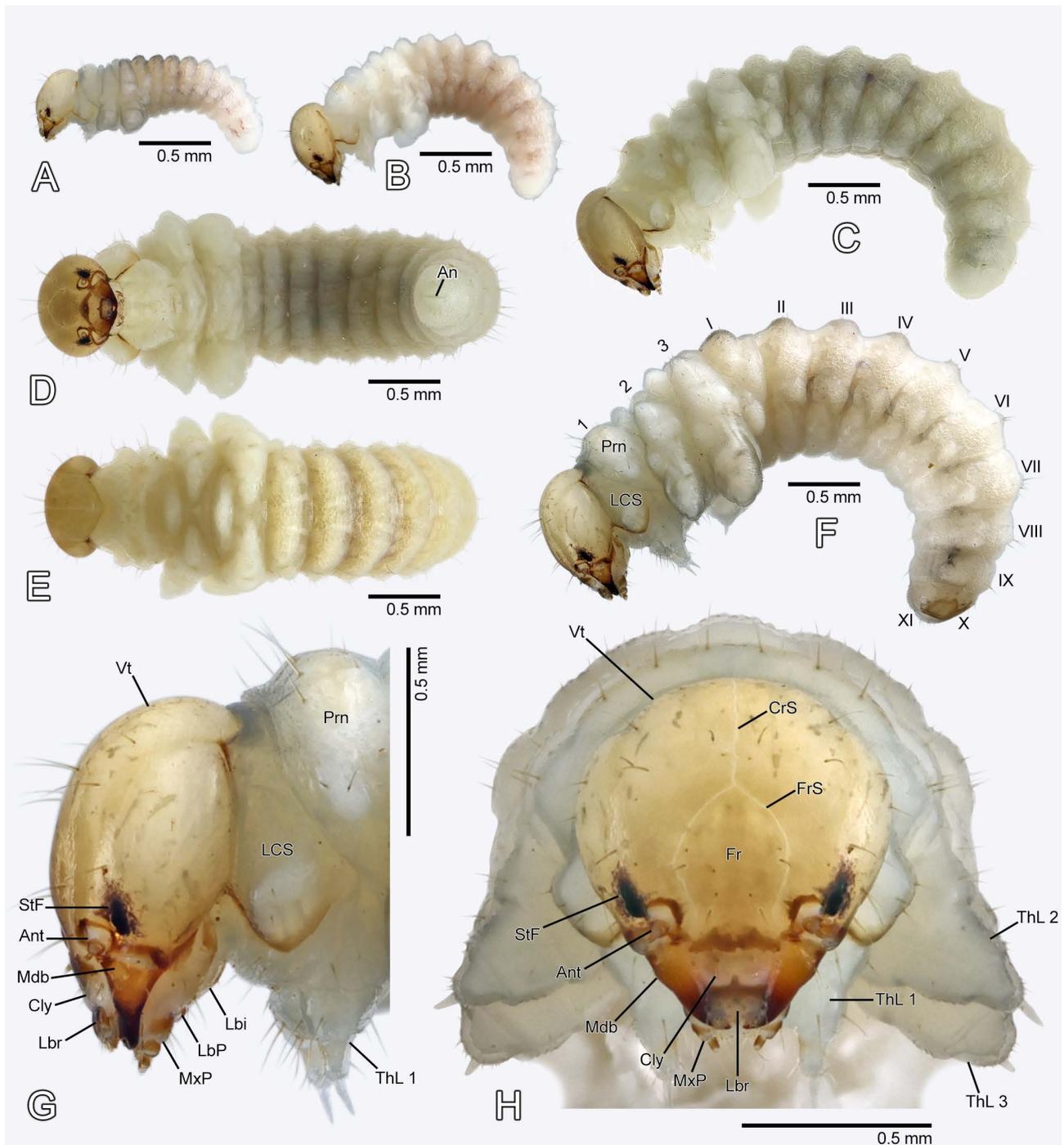
*Immature stages.* The egg (Fig. 3B) is pale white in color and ellipsoidal in shape when freshly laid.

The 1st instar larva (Fig. 4A) is pale white, except for the brown head capsule, dark mandibles, and black stemmata field. The larva is typically scarabaeiform with a distinctly sclerotized orthognathous head and an unsclerotized postcephalic body. The larva abdomen is distinctly curved in a C-shape. The 2nd (Fig. 4B), 3rd (Figs 3C & 4C–E) and 4th instar larvae (Fig. 4F–H) are similar to the 1st instar larva.

The following descriptions are mainly based on the 4th instar larvae (Fig. 4F–H). The head capsule is slightly compressed along the antero-posterior axis (Fig. 4G) and nearly rounded in frontal view. The coronal and frontal sutures form a reversed Y-shape, while the frontal sutures slightly converged towards clypeus (Fig. 4H). Three stemmata are present on each side of the head capsule, but are difficult to observe due to the dense aggregation of black pigment in the stemmata field. The antennae are very short and two-segmented. Two brown patterns are present at the junctions between the frons and clypeus, and between the clypeus and labrum. The dorsal pattern is subtriangular with irregular margins and a notch at the dorsal corner, while the ventral pattern is subtrapezoidal with



**FIGURE 3.** Oviposition and immature stages of *B. altaicus*: **A** female deposits eggs by inserting her secondary ovipositor into the moss cushion **B** egg **C** 3rd instar larva **D** male pupa, lateral view **E–G** male pupa (in alcohol), lateral, dorsal, and ventral views.



**FIGURE 4.** Larvae of *B. altaicus*: **A** 1st instar larva, lateral view **B** 2nd instar larva, lateral view **C–E** 3rd instar larva, lateral, ventral, and dorsal views **F** 4th instar larva, lateral view **G & H** head and thorax of 4th instar larva, lateral and frontal views. **Annotations:** **An** anus **Ant** antenna **Cly** clypeus **CrS** coronal suture **Fr** frons **FrS** frontal suture **Lbi** labium **Lbr** labrum **LCS** lateral cervical sclerite **Mdb** mandible **MxP** maxillial palp **Prn** pronotum **StF** stemmata field **ThL** thoracic leg **Vt** vertex. The thoracic segments are denoted by Arabic numerals, and the abdominal segments by Roman numerals.

a distinct median protrusion dorsally. These patterns can also be observed in other instars (Fig. 4D). The stout mandibles and fused maxillo-labial complex are similar to those of other species of *Boreus*. Setae on head capsule distinctly longer than stemmata field. The lateral cervical sclerites are strongly hardened along their ventral margin. The thorax and abdomen are weakly sclerotized with deep folds. The pronotum bears a row of long setae along

anterior margin. The thoracic and abdominal spiracles are very small and indistinct. The three-segmented thoracic legs are well-developed, with the short and thin foreleg shifted mesally and directing ventrally, while the longer, thicker middle- and hindlegs are directed ventrolaterally. Long setae are present on the coxae and femora of legs 1 (Fig. 4G). Numerous peg-like denticles are found on the posterior surface of the coxae and femora of legs 2 and 3 (Fig. 4H). The abdomen is devoid of appendages and composed of ten distinct segments and a very short terminal segment XI. The anus is a longitudinal split at the end of segment XI.

The male pupa is greenish yellow with darkened head, pronotum, and genitalia. Two pairs of wing cases are much shorter than the adult wings and curve laterocaudally to enclose the meso- and metathorax. It is denticous and exarate, with free antennae and legs (Fig. 3D–G).

**Biological notes.** The immature stages were collected from the rhizoids of compact mosses (*Grimmia* sp.) growing on rock surface and in crevices within open grasslands during late autumn (Fig. 1A, B). The larvae reside in a small chamber characterized by smooth, well-defined walls. When unearthed and exposed to bright light, they slowly retreat deeper into the moss rhizoids, clumsily maneuvering with their head, thoracic legs and abdomen.

The mating of *B. altaicus* exhibits a typical rapine posture in Boreinae: the male carries the female on his back while locking her forefemora using his hook-like wings (Fig. 2C). A female was observed depositing eggs by inserting her secondary ovipositor through the boundary of the moss cushion (Fig. 3A).

**Distribution.** Kazakhstan (Katon-Karagay) and China (Xinjiang: Burqin).

### *Boreus beybienkoi* Tarbinsky, 1962 贝氏雪蝎蛉

Figs 5; 9G–L

**Specimens examined.** 3♂11♀ adults, CHINA, Xinjiang Uygur Autonomous Region [新疆维吾尔自治区]: Ili Kazakh Autonomous Prefecture [伊犁哈萨克自治州], Nilka County [尼勒克县], 43°39'10.09"N, 82°14'4.29"E, 980 m, arid steppe (Fig. 1C), leg. Liang-Jie Jia & Ji-Shen Wang; 4♂11♀ adults, Yining County [伊宁县], 43°48'31.94"N, 81°55'22.63"E, 860 m, 02.XI.2024, arid steppe (Fig. 1D), leg. Liang-Jie Jia & Ji-Shen Wang.

**Measurements** (mm). Adults: male body length 2.35–2.50 (n = 7), female body length 3.50–4.00 (n = 22).

**Adults.** This species can be recognized by the dark brown color of body including legs (Fig. 5), the pronotum with erecting, long and thick bristles along anterior and posterior margin (Figs 5 & 9G, H), the slightly convex apex of male hypandrium (Fig. 9J), and the short and stout female secondary ovipositor (Fig. 9K, L).

**Biological notes.** In contrast to its alpine and subalpine congeners, this species likely prefers lower elevations, including mountains and plains below 1000 m. The severe arid conditions in the low-mountains and steppes (Fig. 1C, D) provide limited humidity, making it challenging for mosses to thrive. Only scattered colonies of *Syntrichia* species were found in the rock crevices on northern slopes, where small communities of *B. beybienkoi* can be observed crawling and hopping on and around *Syntrichia* sp. (Fig. 5A, B). No immature stages have been obtained for this species.

The mating is similar to the other *Boreus* species in a “carrying-locking” posture (Fig. 5C).

**Distribution.** Kazakhstan (Arkharly Pass, Chu-Ili Range, Dzungarian Alatau, Ili Valley, Kurdai Pass, Kapchagay Reservoir), Kyrgyzstan (Bishkek, Kyrgyz Alatau), Tajikistan (Kondara Gorge in the Gissar Range), and China (Xinjiang: Ili Valley).



FIGURE 5. Adults of *Boreus beybienkoi* Tarbinsky, 1962: A male B female C a mating pair.

***Boreus transiliensis* Nikolajev, 1998 伊犁雪蝎蛉**

Figs 6–8; 9M–R

**Specimens examined.** 25♂20♀ adults, CHINA, Xinjiang Uygur Autonomous Region [新疆维吾尔自治区]: Ili Kazakh Autonomous Prefecture [伊犁哈萨克自治州], Qapqal Xibe Autonomous County [察布查尔锡伯自治县], northern slope of the Wusun Mountains [乌孙山] (a small range in the Tianshan Mountains [天山]), grassland with scattered rocks (Fig. 1E), 43°30'2.92"N, 81°7'0.55"E, 1700 m, 25.X.2024, leg. Liang-Jie Jia & Ji-Shen Wang; 7 larvae, same locality, 23.IV.2024, in compact moss (mostly *Grimmia* sp.) rhizoids (Fig. 7B, C), leg. Ji-Shen Wang; 1 egg, 78 larvae, 9♂2♀ pupae, same data except 25.X.2024, leg. Liang-Jie Jia & Ji-Shen Wang.

7♂7♀ adults, forest edge with scattered rocks (Fig. 1F), 43°30'34.58"N, 81°13'40.02"E, 1840 m, approximately 8 km east of the previous site, 25.X.2024, leg. Liang-Jie Jia & Ji-Shen Wang.

4♂4♀ adults, 1730 m, CHINA, Xinjiang Uygur Autonomous Region [新疆维吾尔自治区]: Tacheng (Tarbagatay)

Prefecture [塔城地区], Usu City [乌苏市], northern slope of the Borohoro Mountains [博罗科努山], steppe near the Anjihai River [安集海河], 44° 0'39.75"N, 84°59'20.32"E, 1730 m, 30.X.2024, leg. Liang-Jie Jia & Ji-Shen Wang.

**Measurements** (mm). Adults: male body length 2.6–3.0 (n = 36); female body length 3.8–4.5 (n = 31); egg: length 0.48, width 0.29 mm (n = 1); larvae: 1st instar, head length 0.38–0.40, width 0.34–0.35 (n = 11); 2nd instar, head length 0.46–0.48, width 0.41–0.42 (n = 24); 3rd instar, head length 0.80–0.82, width 0.71–0.73 (n = 43); 4th instar, head length 0.90–0.94, width 0.81–0.82 (n = 7); male pupae body length 3.2–3.8 (n = 9); female pupae body length 4.5–4.7 (n = 2).

**Adults.** This species can be recognized by the yellowish-brown body with strong bronze gloss (Fig. 6), and the pronotum with much shorter and thinner bristles (Figs 6 & 9M, N) than that of *B. beybienkoi*, although in some individuals these bristles are extremely short or nearly absent. The apex of the male hypandrium is broad and somewhat truncated (Fig. 9P). The female secondary ovipositor is slender, with a length approximately 4.8 times its width at the middle (Figs 6B–E & 9Q, R), whereas in *B. beybienkoi*, the ratio is approximately 3.4 times (Figs 5B, C & 9K, L).

**Immature stages.** The egg (Fig. 7A) is pale white in color and ellipsoidal in shape when freshly laid. The larvae of all four instars can be remarkably differentiated from those of *B. altaicus* by the following characters: 1) much shorter setae on head capsule and anterior margin of pronotum (Fig. 8F–H vs. Fig. 4F–H); 2) less conspicuous frontal and coronal sutures (Fig. 8H vs. Fig. 4H); and 3) clypeus lacking brown patterns in anterior and posterior portions (Fig. 8H vs. Fig. 4H).

The male pupae (Fig. 7D) are similar to those of *B. altaicus* (Fig. C–F). The female pupae (Fig. 7E) are similar to the male ones with longer body, much shorter wing cases, and elongated terminalia (containing secondary ovipositor).

**Biological notes.** Eggs, all four larval instars, pupae, and adults of *B. transiliensis* were collected simultaneously in late autumn, indicating an irregular cycle of oviposition, molting, pupation, and emergence for this species (similarly, *B. altaicus*). When ready to emerge, the pupae vigorously open and close their mandibles, twisting their bodies through moss rhizoids to reach the surface, where they complete eclosion with their terminalia anchored in the moss (Fig. 7F). Notably, the presence of snow scorpionflies can be traced by the whitish exuviae (Fig. 7G), which remain attached to the mosses even after the adults have departed. The presence of strongly sclerotized mandible cases serves as a distinctive characteristic for their recognition. The teneral adults are initially light greenish-yellow (Fig. 7H) and develop full coloration within approximately half a day.

Several stages of the mating behavior of *B. transiliensis* have been observed in this study. Initially, the male attempts to grasp one of the female's legs using his copulatory apparatus, specifically, a pair of gonostyli. Once the female is secured, the male holds her between his hook-like wings and abdomen, attempting to rotate her body to achieve genital coupling (Fig. 6C). After successful coupling, the male releases his grip on the female once their genitalia are firmly interlocked (Fig. 6D). Subsequently, the female lowers her body and draws up her antennae, head, and legs, while the male uses his hook-like wings to grasp her forefemora (Fig. 6E). They then maintain this "carrying-locking" posture for several hours, with the female remaining mostly immobile while the male is able to walk and hop around freely. If disturbed, the male momentarily releases his wing grip and then re-establishes it if their genitalia remain interlocked.

Expeditions were also conducted in the nearby spruce forests (Fig. 1F), but no individuals were found in the moss mats. This is likely due to the loose structure of the mosses found beneath forest canopies, which may harbor more predators and lose moisture too rapidly (Penny 1977; Glime 2017).

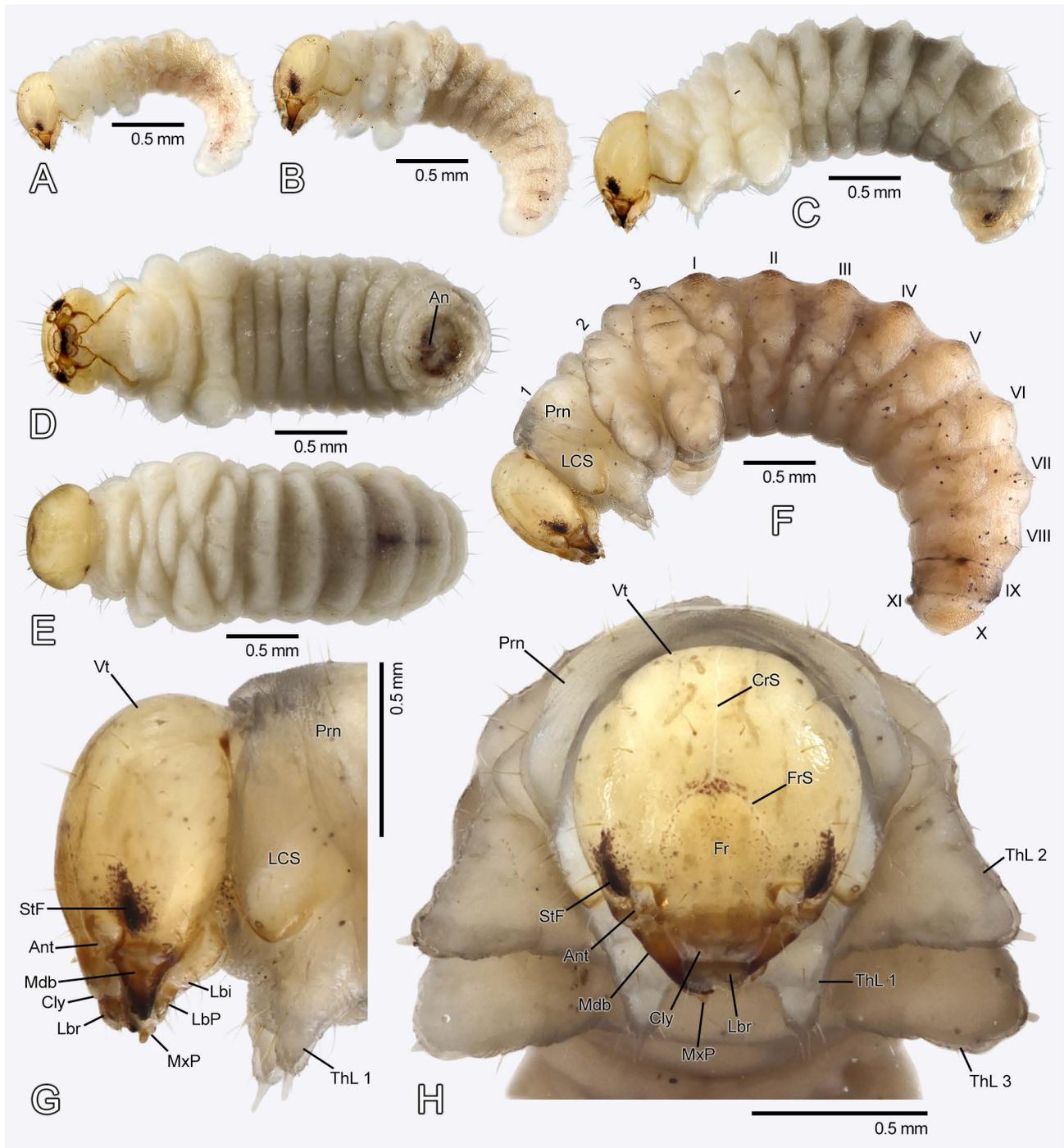
**Distribution.** Kazakhstan (Zailiysky Alatau, also spelt as Trans-Ili Alatau) and China (Xinjiang: Borohoro and Wusun Mountains).



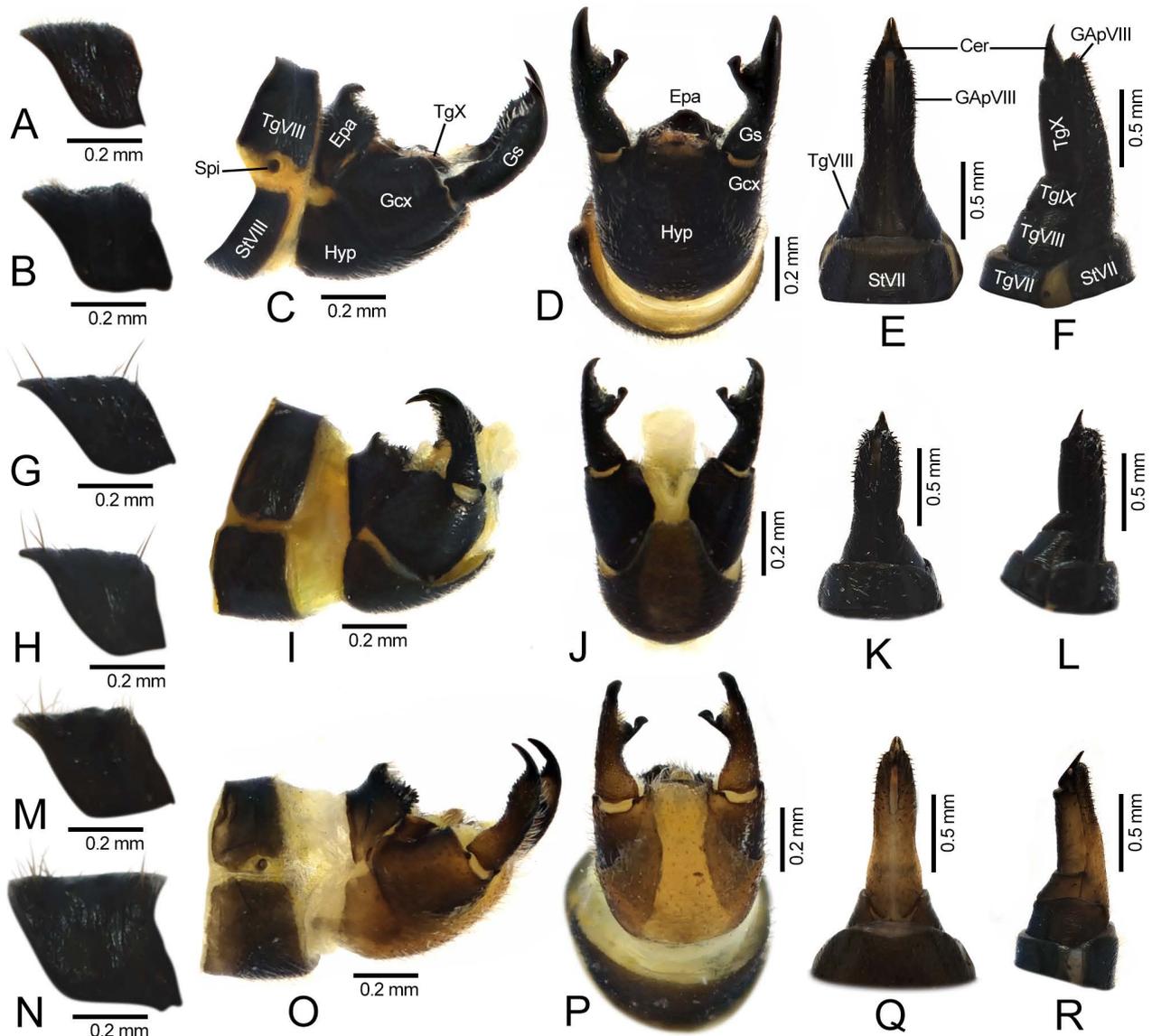
**FIGURE 6.** Adults of *Boreus transiliensis* Nikolajev, 1998: **A** male **B** female **C** male holds female between wings and abdomen **D** male releases hold on female after genital coupling **E** male uses his wings to lock the female's forefemora, while she draws her antennae, head, and legs close to her body.



**FIGURE 7.** Immature stages and eclosion of *B. transiliensis*: **A** egg **B–C** 3rd instar larva **D** male pupa **E** female pupa **F** female eclosion **G** exuviae **H** teneral male.



**FIGURE 8.** Larvae of *B. transiliensis*: **A** 1st instar larva, lateral view **B** 2nd instar larva, lateral view **C–E** 3rd instar larva, lateral, ventral, and dorsal views **F** 4th instar larva, lateral view **G & H** head and thorax of 4th instar larva, lateral and frontal views. Annotations: **An** anus **Ant** antenna **Cly** clypeus **CrS** coronal suture **Fr** frons **FrS** frontal suture **Lbi** labium **Lbr** labrum **LCS** lateral cervical sclerite **Mdb** mandible **MxP** maxillial palp **Prn** pronotum **StF** stemmata field **ThL** thoracic leg **Vt** vertex. The thoracic segments are denoted by Arabic numerals, and the abdominal segments by Roman numerals.



**FIGURE 9.** Character comparisons among *Boreus* spp.: A–F *B. altaicus* G–L *B. beybienkoi* M–R *B. transiliensis* A, G & M male pronotum, lateral view B, H & N female pronotum, lateral view C, I & O male genitalia, lateral view D, J & P male genitalia, caudal view E, K & Q female genitalia, ventral view F, L & R female genitalia, lateral view. Annotations: **Cer** cercus **Epa** epandrium (= tergite IX) **GAPVIII** genital appendage VIII **Gcx** gonocoxite **Gs** gonostylus **Hyp** hypandrium (= sternite IX) **StVII** sternite VII **Spi** spiracle **TgVII** tergite VII (and so forth for other segments).

## Discussion

The discovery of Boreidae in Xinjiang, northwestern China is consistent with their preference for cold habitats characterized by regular winter snowfall. Situated in the northeastern part of arid Central Asia, the Ili Valley and its surrounding mountains form a trumpet shape that narrows from west to east while gradually rising in elevation, and they receive relatively abundant precipitation brought by the prevailing westerly winds (Ye *et al.* 2000; Liu *et al.* 2023). Similarly, the precipitation in the Altay Mountains is significantly higher than the surrounding areas in the arid Central Asia. Consequently, these regions harbor a rich diversity and abundance of mosses, including those in the genera *Barbula*, *Brachythecium*, *Bryum*, *Callicladium*, *Claopodium*, *Dicranum*, *Grimmia*, *Hypnum*, *Ptychostomum*, *Rhytidium*, *Rhynchostegium*, *Syntrichia*, and *Weissia*, which may offer suitable microhabitats and

plentiful food sources for the snow scorpionflies. However, due to the limited scope of our observations, we are currently unable to determine the complete dietary range of these species, with the exception of *Grimmia* sp. (*B. altaicus* and *B. transiliensis*) and *Syntrichia* sp. (*B. beybienkoi*), in which the examined larvae and adults were found.

The snow scorpionfly *B. beybienkoi*, together with *B. talassicola* Nikolajev, 1998, can be differentiated from other Central Asian species (*B. altaicus*, *B. transiliensis*, and *B. vlasovi* Martynova, 1954) by the presence of long bristles on the anterior and posterior margins of the pronotum (Fig. 9G, H). By the pronotal bristles being black, *B. beybienkoi* can further be separated from *B. talassicola*, which bears white bristles (Nikolajev 1998, 2003, 2015, 2018; Gabdullina & Nikolajev 2015). Up to date, *B. beybienkoi* is likely the most widespread Central Asian species, reported from many locations in the Alatau Ridge of Kyrgyzstan, southern foothills of the Dzhungar Alatau, the Ili valley, the Chu-Ili Mountains of Kazakhstan (Tarbinsky 1962; Nikolajev 1998, 2003, 2015, 2018; Gabdullina & Nikolajev 2015), the Gissar Range of Tajikistan, and in this study, the Ili Valley of Xinjiang, China.

Due to their limited dispersal capacity—partly influenced by wing reduction and dependence on host mosses—some snow scorpionfly species exhibit highly diversified morphological traits and genetic structures, leading to distinct regional forms and even cryptic species (Kreithner 2001; Zangl *et al.* 2021; Strohmeier 2023). The numbers, lengths, and colors of these pronotal bristles show considerable variation in *B. beybienkoi* and *B. transiliensis*, and perhaps in *P. talassicola*. For example, in the specimens identified as *B. transiliensis* in this study, the bristles can be long, medium, short, or nearly absent across different individuals (Figs 6 & 9G, H), although none are as black and thick as those found in *B. beybienkoi*. Additionally, the specimens of *B. beybienkoi* from Kazakhstan bear long black bristles on both the pronotum and forewings (see Fig. 9 in Gabdullina & Nikolajev 2015), whereas in the specimens from the Ili Valley reported in this study, long black bristles are present only on the pronotum (Fig. 5). It is suspected that *B. beybienkoi*, *B. talassicola*, and *B. transiliensis* may represent a single, yet polymorphic species exhibiting significant geographical variation (GV Nikolajev, unpublished data). However, resolving this question is currently not possible due to the lack of specimens from a broader geographical range. Despite this, the genitalia show significant differences among these species, particularly in the morphology of the male epandrium and the basal lobe of the gonostyli (Fig. 9C, D, I, J, O, P). The female secondary ovipositor is much slender in *B. altaicus* and *B. transiliensis* than in *B. beybienkoi* (Fig. 9E, F, K, L, Q, R).

The immature stages of snow scorpionflies have been described for only a few species (Withycombe 1922; Penny 1977; Cooper 1974; Russell 1979a, 1982; Byers 1987; Fabian *et al.* 2015). According to Withycombe (1922) and Cooper (1974), snow scorpionfly larvae typically undergo four instars. In this study, we acquired four distinct head capsule size ranges in *B. altaicus* and *B. transiliensis*, corresponding to four instars. In contrast to the univoltine *Caurinus* spp. (Beutel *et al.* 2019a), members of *Boreus* and *Hesperoboreus* undergo a two-year life cycle (Beutel *et al.* 2019b). This could explain the co-occurrence of all the four instars that we observed simultaneously. The scarabaeiform larvae of *B. altaicus* and *B. transiliensis* resemble those of *B. brumalis* Fitch, 1847, *B. coloradensis* Byers, 1955, *B. hyemalis* (Linnaeus, 1767), *B. westwoodi* Hagen, 1866, *H. notoperates* (Cooper, 1972), and *H. brevicaudus* (Byers, 1961) in having three-segmented thoracic legs. In contrast, the thoracic legs of the curculioniform larvae of *Caurinus* are greatly reduced and consist of only a single segment (Fabian *et al.* 2015; Beutel *et al.* 2019a).

These discoveries increase the known number of Mecoptera families in China from three (i.e. Bittacidae, Panorpididae and Panorpididae, Wang & Hua 2022) to four.

## Acknowledgements

The authors wish to express their sincere gratitude to Libor Dvořák (Czech Republic), Aliya U Gabdullina, Georgiy V Nikolajev (Kazakhstan), and Vladimir N Makarkin (Russia) for their great support in providing essential literature on Boreidae and assisting with species identification. The authors also wish to thank Zhi-Teng Chen for his invaluable suggestions during the manuscript revision. Special thanks go to Dr. Cheng-Bin Wang, the Editor in Chief of this journal, for facilitating the rapid and high-quality publication of this paper.

## References

- Bicha W 2018: Biodiversity of Mecoptera. In: Foottit RG & Adler PH (Eds) *Insect Biodiversity: Science and Society, II*. John Wiley & Sons, Hoboken, New Jersey, pp. 705–720.  
<https://doi.org/10.1002/9781118945582.ch23>
- Beutel RG, Friedrich F, Russell LK, Hünefeld F, Simiczyjew B, Dallai R, Fabian B & Pohl H 2019a: 2. Neomecoptera, Boreidae, Caurininae, *Caurinus*. In: Beutel RG & Friedrich F (Eds) *Handbook of Zoology. Nannomecoptera and Neomecoptera*. De Gruyter, Berlin, pp. 71–111.  
<https://doi.org/10.1515/9783110272543-002>
- Beutel RG, Russell LK, Friedrich F, Hünefeld F, Simiczyjew B, Suzuki N, Dallai R, Jandausch K & Pohl H 2019b: 3. Neomecoptera, Boreidae, Boreinae, *Boreus* and *Hesperoboreus*. In: Beutel RG & Friedrich F (Eds) *Handbook of Zoology. Nannomecoptera and Neomecoptera*. De Gruyter, Berlin, pp. 113–158.  
<https://doi.org/10.1515/9783110272543-003>
- Beutel RG & Friedrich F 2019: 4. Phylogeny. In: Beutel RG & Friedrich F (Eds) *Handbook of Zoology. Nannomecoptera and Neomecoptera*. De Gruyter, Berlin, pp. 159–161.  
<https://doi.org/10.1515/9783110272543-004>
- Burrows M 2011: Jumping mechanisms and performance of snow fleas (Mecoptera, Boreidae). *The Journal of Experimental Biology*, 214: 2362–2374.  
<https://doi.org/10.1242/jeb.056689>
- Byers GW 1987: Order Mecoptera. In: Stehr FW (Ed.) *Immature Insects, Vol. I*. Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 246–252.
- Chou I & Hua B-Z 1999: 30. Class Insecta: Order Mecoptera. In: Zheng L-Y & Gui H (Eds) *Insect Classification*. Nanjing Normal University Press, Nanjing, pp. 666–673. [周尧 & 花保祯 1999: 30. 昆虫纲: 长翅目. 见: 郑乐怡 & 归鸿 (主编) 昆虫分类. 南京师范大学出版社, 南京, pp. 666–673.]
- Cooper KW 1974: Sexual biology, chromosomes, development, life histories and parasites of *Boreus*, especially of *B. notoperates*. A Southern California *Boreus*. II. (Mecoptera: Boreidae). *Psyche*, 81: 84–120.  
<https://doi.org/10.1155/1974/48245>
- Dunford JC & Somma LA 2008: Scorpionflies (Mecoptera). In: Capinera JL (Ed.) *Encyclopedia of Entomology, 2nd Edition*. Springer Netherlands, Heidelberg, pp. 3304–3310.  
[https://doi.org/10.1007/978-1-4020-6359-6\\_4077](https://doi.org/10.1007/978-1-4020-6359-6_4077)
- Dvořák L, Mariychuk R, Manko P, Oboňa J, Krzemiński W & Godunko RJ 2022: Present knowledge on Mecoptera of Ukraine. *Zootaxa*, 5141:459–483.  
<https://doi.org/10.11646/zootaxa.5141.5.3>
- Fabian B, Russell L, Friedrich F & Beutel RG 2015: The larval cephalic morphology of the enigmatic boreid *Caurinus dectes* (Mecoptera) and its phylogenetic significance. *Arthropod Systematics & Phylogeny*, 73: 385–399.  
<https://doi.org/10.3897/asp.73.e31825>
- Gabdullina AU & Nikolajev GV 2015: A new species of the scorpion-fly of the genus *Boreus* Latreille (Mecoptera, Boreidae) from Altai Mountains, Kazakhstan. *Euroasian Entomological Journal*, 14: 32–34. [In Russian with English Abstract]
- Glime JM 2017: Terrestrial Insects: Holometabola – Mecoptera. Chapt. 12–16. In: Glime JM (Ed.) *Bryophyte Ecology. Volume 2. Bryological Interaction*. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available from: <http://digitalcommons.mtu.edu/bryophyte-ecology2/> (accessed 8.XI.2024)
- Grimaldi D & Engel MS 2005: *Evolution of the Insects*. Cambridge University Press, New York, 755 pp.
- Hågvar S 2010: A review of Fennoscandian arthropods living on and in snow. *European Journal of Entomology*, 107: 281–298.  
<https://doi.org/10.14411/eje.2010.037>
- Hori S & Morimoto K 1996: Discovery of the family Boreidae (Mecoptera) from Japan, with description of a new species. *Japanese Journal of Entomology*, 64: 75–81.
- Huang D-Y, Engel MS, Cai C-Y, Wu H & Nel A 2012: Diverse transitional giant fleas from the Mesozoic Era of China. *Nature*, 483:

201–204.

<https://doi.org/10.1038/nature10839>

- Kreithner A 2001: Über *Boreus* - Arten aus den Alpen: Taxonomische Charakterisierung und Verbreitung (Insecta, Mecoptera, Boreidae). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck*, 88: 213–236.
- Liu P-L, Zhang S-J, Qiu M-H, Ruan Q-R, Luo J-M, Miao Y-F & Ling Z-Y 2023: Vegetation history and its links to climate change during the last 36 ka in arid Central Asia: evidence from a loess-paleosol sequence in the Eastern Ili Valley. *Frontiers in Earth Science*, 10: 1041374.  
<https://doi.org/10.3389/feart.2022.1041374>
- Martynova OM 1954: Skorpionnitsy (Mecoptera) fauny SSSR. I. *Trudy Zoologicheskogo Instituta, Akademii Nauk SSSR*, 15: 54–66. [In Russian]
- Meusemann K, Trautwein M, Friedrich F, Beutel RG, Wiegmann BM, Donath A, Podsiadlowski L, Petersen M, Niehuis O, Mayer C, Bayless KM, Shin S, Liu S-L, Hlinka O, Minh BQ, Kozlov A, Morel B, Peters RS, Bartel D, Grove S, Zhou X, Misof B & Yeates DK 2020: Are fleas highly modified Mecoptera? Phylogenetic resolution of Antliophora (Insecta: Holometabola). *BioRxiv preprint*.  
<https://doi.org/10.1101/2020.11.19.390666>
- Mickoleit G 1974: Über die Spermatophore von *Boreus westwoodi* Hagen (Insecta, Mecoptera). *Zeitschrift für Morphologie der Tiere*, 77: 271–284.  
<https://doi.org/10.1007/BF00298804>
- Misof B, Liu S-L, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG, Niehuis O, Petersen M, Izquierdo-Carrasco F, Wappler T, Rust J, Aberer AJ, Aspöck U, Aspöck H, Bartel D, Blanke A, Berger S, Böhm A, Buckley T, Calcott B, Chen J-Q, Friedrich F, Fukui M., Fujita M, Greve C, Grobe G, Gu S-C, Huang Y, Jermini LS, Kawahara AY, Krogmann L, Kubiak M, Lanfear R, Letsch H, Li Y-Y, Li Z-Y, Li J-G, Lu H-R, Machida R, Mashimo Y, Kapli P, McKenna DD, Meng G-L, Nakagaki Y, Navarrete-Heredia JL, Ott M, Ou Y-X, Pass G, Podsiadlowski L, Pohl H, von Reumont BM, Schütte K, Sekiya K, Shimizu S, Slipinski A, Stamatakis A, Song W-H, Su X, Szucsich NU, Tan M-H, Tan X-M, Tang M, Tang J-B, Timelthaler G, Tomizuka S, Trautwein M, Tong X-L, Uchifune T, Walz MG, Wiegmann BM, Wilbrandt J, Wipfler B, Wong TKF, Wu Q, Wu G-X, Xie Y-L, Yang S-Z, Yang Q, Yeates DK, Yoshizawa K, Zhang Q, Zhang R, Zhang W-W, Zhang Y-H, Zhao J, Zhou C-R, Zhou L-L, Ziesmann T, Zou S-J, Li Y-R, Xu X, Zhang Y, Yang H-M, Wang J, Wang J, Kjer KM & Zhou X 2014: Phylogenomics resolves the timing and pattern of insect evolution. *Science*, 346: 763–767.  
<https://doi.org/10.1126/science.1257570>
- Navás L 1926: Entomologische Ergebnisse der schwedischen Kamtchatka-Expedition 1920–1922. *Arkiv för Zoologi*, 18: 1–4.
- Nikolajev GV 1998: New and little-known species of insects (Mantoptera, Raphidioptera, Neuroptera, Coleoptera, Mecoptera) from Central Asia. *Vestnik KazGU. Seriya Biologicheskaya*, 5: 38–46. [In Russian with English Summary]
- Nikolajev GV 2003: The scorpion-flies of the family Boreidae (Mecoptera) in Asia. *Tethys Entomological Research*, 8: 239–248. [In Russian with English Summary]
- Nikolajev GV 2015: Problems of studying of snow scorpionflies of the genus *Boreus* Latreille, 1816 (Mecoptera: Boreidae) in Russia. *Nauchnyye Trudy Gosudarstvennogo Prirodnogo Zapovednika «Prisurskiy»*, 30(1): 195–197. [In Russian with English Abstract]
- Nikolajev GV 2018: Perspektivy izucheniya skorpionovykh mukh v Kazakhstane. In: Meldebekov AM (Ed.) *Zoological and Parasitological Studies in Kazakhstan and Neighboring Countries*. Konferentsiya, Priurochennaya k Yubileyu 90-let Instituta Zoologii, Almaty, pp. 94–97. [In Russian]
- Palmer C 2010: Diversity of feeding strategies in adult Mecoptera. *Terrestrial Arthropod Reviews*, 3: 111–128.  
<https://doi.org/10.1163/187498310X519716>
- Penny ND 1977: A systematic study of the family Boreidae (Mecoptera). *The University of Kansas Science Bulletin*, 51: 141–217.
- Plutenko AV 1985: New and little-known species of Mecoptera from the Soviet Far East. *Entomologicheskoye Obozreniye*, 1: 171–176.
- Russell LK 1979a: *A biological and systematic study of the armored Boreid, Caurinus dectes, with comparative notes on related Mecoptera*. Doctoral Dissertation, Oregon State University. Available at:  
[https://ir.library.oregonstate.edu/concern/graduate\\_thesis\\_or\\_dissertations/w37639575](https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/w37639575) (accessed 8.XI.2024)
- Russell LK 1979b: A new genus and a new species of Boreidae from Oregon (Mecoptera). *Proceedings of the Entomological Society*

- of *Washington*, 81: 22–31.
- Russell LK 1982: The life history of *Caurinus dectes* Russell, with a description of the immature stages (Mecoptera: Boreidae). *Entomologica Scandinavica*, 13: 225–235.  
<https://doi.org/10.1163/187631282X00165>
- Sikes DS & Stockbridge J 2013: Description of *Caurinus ilagu*, new species, from Prince of Wales Island, Alaska (Mecoptera, Boreidae, Caurininae). *ZooKeys*, 316: 35–53.  
<https://doi.org/10.3897/zookeys.316.5400>
- Strohmeier T 2023: *Cryptic diversity in snow scorpionflies (Boreus spp.) in relation to cuticular chemistry and geography*. Master's thesis, University of Graz. Available from: <https://unipub.uni-graz.at/obvugrhs/content/titleinfo/9276561> (accessed 8.XI.2024)
- Sukatsheva ID & Rasnitsyn AP 1992: First members of the family Boreidae (Insecta, Panorpida) from the Upper Jurassic of Mongolia and the Lower Cretaceous of Transbaykalia. *Paleontological Journal*, 26: 168–172.
- Tarbinsky SP 1962: O nakhozhenii lednichnika - *Boreus* sp. n. (Mecoptera, Boreidae) v predgoryakh Kirgizskovo Ala-too. *Sbornik Entomologicheskikh Rabot*, 1: 131–136. [In Russian]
- Tihelka E, Giacomelli M, Huang D-Y, Pisani D, Donoghue PCJ & Cai C-Y 2020: Fleas are parasitic scorpionflies. *Palaeoentomology*, 3: 641–653.  
<https://doi.org/10.11646/PALAEOENTOMOLOGY.3.6.16>
- Vanin S, Bubacco L & Beltrami M 2008: Seasonal variation of trehalose and glycerol concentrations in winter snow-active insects. *CryoLetters*, 29: 485–491.
- Wang J-S & Hua B-Z 2021: Morphological phylogeny of Panorpidae (Mecoptera: Panorpoidea). *Systematic Entomology*, 46: 526–557.  
<https://doi.org/10.1007/978-981-16-9558-2>
- Wang J-S & Hua B-Z 2022: *A Color Atlas of the Chinese Mecoptera*. Springer Nature Singapore, Singapore, 354 pp.  
<https://doi.org/10.1111/syen.12474>
- Whiting MF 2002: Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. *Zoologica Scripta*, 31: 93–104.  
<https://doi.org/10.1046/j.0300-3256.2001.00095.x>
- Whiting MF, Whiting AS, Hastriter MW & Dittmar K 2008: A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. *Cladistics*, 24: 677–707.  
<https://doi.org/10.1111/j.1096-0031.2008.00211.x>
- Wiegmann BM, Trautwein MD, Kim J-W, Cassel BK, Bertone MA, Winterton SL & Yeates DK 2009: Single-copy nuclear genes resolve the phylogeny of the holometabolous insects. *BMC Biology*, 7: 34.  
<https://doi.org/10.1186/1741-7007-7-34>
- Withycombe CL 1922: XI. On the life-history of *Boreus hyemalis* L. *Transactions of the Royal Entomological Society of London*, 69: 312–318.  
<https://doi.org/10.1111/j.1365-2311.1922.tb02813.x>
- Ye W, Dong G-R, Yuan Y-J & Ma Y-J 2000: Climate instability in the Yili region, Xinjiang during the last glaciation. *Chinese Science Bulletin*, 45: 1604–1609.  
<https://doi.org/10.1007/bf02886222>
- Zangl L, Glatzhofer E, Schmid R, Randolf S & Koblmüller S 2021: DNA barcoding of Austrian snow scorpionflies (Mecoptera, Boreidae) reveals potential cryptic diversity in *Boreus westwoodi*. *PeerJ*, 9: e11424.  
<http://doi.org/10.7717/peerj.11424>
- Zhao X-D, Wang B, Bashkuev AS, Aria C, Zhang Q-Q, Zhang H-C, Tang W-T & Engel MS 2020: Mouthpart homologies and life habits of Mesozoic long-probscid scorpionflies. *Science Advances*, 6: eaay1259.  
<https://doi.org/10.1126/sciadv.aay1259>
- Zhu Q-Y, Hastriter MW, Whiting MF & Dittmar K 2015: Fleas (Siphonaptera) are Cretaceous, and evolved with Theria. *Molecular Phylogenetics and Evolution*, 90: 129–139.  
<https://doi.org/10.1016/j.ympev.2015.04.027>

## **Additional information**

**Author contributions:** Conceptualization, Resources, Visualization, Writing-original draft: J-S Wang; Specimen collection, Writing-review and editing: J-S Wang and L-J Jia.

**Conflict of interest:** The authors have declared that no competing interests exist.

**Data availability:** All of the data that support the findings of this study are available in the main text.

**Ethical statement:** No ethical statement was reported.

**Funding:** This research was financially supported by the Starting Foundation for the High-level Talents, Dali University (grant number KY2096124040).

**Disclaimer/Publisher's Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of *ICE* and/or the editor(s). *ICE* and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.

