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Integrative taxonomy of the *Capnia cordata* species group (Plecoptera: Capniidae)

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Abstract. The *Capnia cordata* species group (Plecoptera: Capniidae) is reviewed based on an integrative taxonomic approach that combines morphological and molecular methods. Within this group, two species are described as new to science: *C.* s. lat. *bispina* Cao & Li sp. nov. from Qinghai Province and *C.* s. lat. *huanglong* Cao & Li sp. nov. from Sichuan Province. Both are illustrated and compared with related taxa, and keys for both males and females of the species group are provided. The known localities of the *C. cordata* species group are mapped. Additionally, a phylogenetic analysis based on *Cox*1 sequence was conducted involving 14 species of the Capniidae family, supporting the distinctness of this species group.

Keywords. *Capnia* s. lat. *bispina* sp. nov., *Capnia* s. lat. *huanglong* sp. nov., winter stonefly.

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Introduction

The genus *Capnia* Pictet, 1841 is the most species-rich genus of the winter stonefly family Capniidae Banks, 1900. It contains nearly 120 species distributed throughout the Holarctic and Oriental realms, including 13 valid species from China (Shen *et al.* 2021; DeWalt *et al.* 2025). However, *Capnia* is likely a polyphyletic assemblage. Under a strict interpretation (s. str.), the diagnosis identifies only seven species as forming a monophyletic clade with the type species (Murányi *et al.* 2014). The remaining species

currently classified within *Capnia* should be considered as *Capnia* s. lat. and warrant reclassification into other genera.

Within the *Capnia* s. lat., one of the lineages believed to be monophyletic is the *C. cordata* species group, according to Zhiltzova (2001). The group was characterized by a combination of features including an entire and elongated male epiproct, a posteromedial process on male tergum IX, and the presence of a vesicle on male sternum IX. This group includes closely related species distributed in the high mountains of Asia. The first five species were described from the Central and Eastern Himalayas (Kimmins 1946). During the next decades, a further four species were described from the Western and Central Himalayas (Jewett 1958, 1975; Harper 1977), although two of these were later considered to be junior subjective synonyms of existing species (Zwick & Sivec 1980). Meanwhile, four species were also described from other ranges of the Hindukush, Pamir and the Tien Shan (Zhiltzova 1969, 1974). Finally, five new species and further two unassociated females have been described from northwestern and southwestern China during the last 15 years (Li & Yang 2009; Li *et al.* 2011; Chen & Du 2017a, 2017b; Chen & Song 2019; Shen *et al.* 2021). Hitherto, the *C. cordata* species group is composed of 16 valid species with 8 being reported from China (Zhiltzova 2001; Murányi *et al.* 2014; Chen & Song 2019) (as shown in Table 1).

In this paper, we redefine the *C. cordata* species group, describe two new species from Qinghai and Sichuan provinces of China, give a key for both males and females of the group, and depict their distribution on a map.

Material and methods

All adults were collected by handpicking or sweeping and preserved in 75% ethanol. The male terminalia were cleared in 10% NaOH. Types and other specimens used in this study are deposited in the Entomological Museum of China Agricultural University, Beijing (CAU), and the Henan Institute of Science and Technology, Xinxiang (HIST), China. Specimens were examined with a Leica S8APO dissecting microscope and the color photographs were made with the aid of Imaging Source CCD attached to a Leica S8APO camera. Further color illustrations were made with the aid of a Leica M205FA dissecting microscope attached with a digital camera. Drawings were made on the basis of color photos, while examining the NaOH cleared structures. The SEM photographs were taken by an FEI Quanta2000 scanning electron microscope. The morphological terminology follows that of Murányi *et al.* (2014). The standard map (Fig. 1) was downloaded from the Ministry of Natural Resources, People's Republic of China (http://bzdt.ch.mnr.gov.cn/; map number GS (2016)2938) and was used as a base for the distribution maps.

We used the Cytochrome c oxidase subunit I (*Cox*1) as a marker for our phylogenetic analyses. Total genomic DNA was extracted from the head, legs and thoracic of the specimens using the TIANamp Genomic DNA Kit (Tiangen Biotechnology, Beijing, China) according to the manufacturer's instructions and stored at -20°C until used for PCR. For PCR, we amplified the DNA barcode region of the *Cox*1 gene using 5'-GGTCWACWAATCATAAAGATATTGG-3' (LCO1490) and 5'-TAAACTTCWGGRTGWCAAARAATCA-3' (HCO2198) (Folmer *et al.* 1994). PCRs were performed using T100TM (Bio-RAD, USA) with a reaction volume of 25 µL PCR reaction mixes included 14.5 µL of ultrapure water, 5 µL of Taq buffer, 1 µL of each primer (0.01 mM), 2 µL of each dNTP (0.05 mM), 0.5 µL of Easy Taq polymerase, and 1 µL of DNA template. Thermal cycling consisted of initial denaturation at 95°C for 30 s, 40 amplification cycles of 95°C/30 s, 40–60°C/50 s, 65°C/60 s, followed by a final extension at 65°C for 10 min. The amplification products were checked through 1% agarose gel electrophoresis, and bidirectional sequencing was performed at Sangon Biotech (Shanghai, China). All sequences were deposited at GenBank (access numbers for the barcode region of *Cox*1 are in Table 2). The phylogenetic analysis included the newly determined sequences, as well as sequences obtained from GenBank. We used *Zwicknia bifrons* (Newman, 1838)

Table 1. World list of the *C. cordata* species group.

Number	Species	Distribution
1	*C*. s. lat. *ansobiensis* Zhiltzova, 1974	Tajikistan
2	*C*. s. lat. *badakhshanica* Zhiltzova, 197	Tajikistan
3	*C*. s. lat. *bilobat*a Chen & Song, 2019	China: Shaanxi
4	*C*. s. lat. *bispina* Cao & Li sp. nov.	China: Qinghai
5	*C*. s. lat. *cordata* Kimmins, 1947	Nepal; China: Xizang
6	*C*. s. lat. *hingstoni* Kimmins, 1947	Indian: Sikkim
7	*C*. s. lat. *huanglong* Cao & Li sp. nov.	China: Sichuan
8	*C*. s. lat. *manii* Jewett, 1958	India: Himachal Pradesh; Pakistan
9	*C*. s. lat. *montana* Kimmins, 1947	India: Sikkim; Nepal
10	*C*. s. lat. *montivaga* Kimmins, 1947	China: Xizang
11	*C*. s. lat. *oblata* Chen & Du, 2017	China: Yunnan
12	*C*. s. lat. *prolongata* Zhiltzova, 1969	Kazakhstan, Kyrgyzstan, Tajikistan
13	*C*. s. lat. *shugnanica* Zhiltzova, 1974	Tajikistan
14	*C*. s. lat. *qilianshana* Li & Yang, 2009	China: Gansu, Qinghai
15	*C*. s. lat. *tibetana* Kimmins, 1947	China: Xizang
16	*C*. s. lat. *triangulipennis* Jewett, 1975	Nepal
17	*C*. s. lat. *xiei* Chen & Du, 2017	China: Qinghai
18	*C*. s. lat. *yunnana* Li & Yang, 2011	China: Yunnan

as an outgroup. Phylogenetic trees were constructed by the maximum likelihood (ML) method in IQ-TREE web server (http://iqtree.cibiv.univie.ac.at/) assessed with molecular dataset. In order to receive a robust estimate of the entities, three approaches were applied to the *Cox*1 data both separately and in concatenation, as follows: Assemble Species by Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.* 2021), Automatic Partitioning (ASAP; Puillandre *et al.* 2021), Bayesian Poisson Tree Processes (bPTP; Zhang *et al.* 2013). For ABGD and ASAP, we used the online platforms https://bioinfo.mnhn.fr/abi/public/abgd and https://bioinfo.mnhn.fr/abi/public/asap respectively, using the Kimura Two-Parameter (K2P) model (Kimura 1980). For the bPTP, we used the online platforms https://species.h-its.org.

Table 2. List of specimens of the *Capnia* s. lat. *C. cordata* group used for phylogenetic analysis. Species studied, isolate numbers, sex, location and GenBank accessions.

Species	Isolate	Sex	Province	Coordinates	Accession
C. yunnana Li & Yang, 2011	T68	♀	Tibet Sejilashan Zhongshan Zhan	94.6032° E, 29.6100° N	PQ469706
C. bispina Cao & Li sp. nov.	T86	♂	Qinghai Province Datong County	101.6018° E, 36.9158° N	PQ469707
C. bispina	T87	♀	Qinghai Province Datong County	101.6018° E, 36.9158° N	PQ469708
C. qilianshana Li & Yang, 2009	T90	♀	Qinghai Province Menyuan County	102.5331° E, 37.1339° N	PQ469709
C. oblata Chen & Du, 2017	T92	♀	Qinghai Province Qilian County	99.9503° E, 38.1442° N	PQ499489
C. qilianshana	T7	♂	Gansu Province Zhangye City	99.5722° E, 38.8011° N	PQ469710
C. bilobata Chen & Song, 2019	T134	♂	Shaanxi Province Huyi Zhongnan Mt	108.6486°E, 33.8981°N	PQ469711
C. bilobata	T138	♀	Shaanxi Province Huyi Zhongnan Mt	108.6486° E, 33.8981° N	PQ469712
Capnia sp.	T5	♀	Tibet Autonomous Region Sejilashan	94.6031° E, 29.6100° N	PQ499488

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Plecoptera Burmeister, 1839
Family Capniidae Banks, 1900

Genus ***Capnia*** Pictet, 1841

Capnia Pictet, 1841: 116.

Type species

Capnia nigra (Pictet, 1833).

Diagnosis

Additionally, the entirely setose main epiproct sclerite is unique and will easily distinguish it from all other males in the species group.

Definition of the *Capnia* s. lat. *cordata* species group

Diagnosis

Both the male and female are macropterous, the forewing having a curved A1 and R1 and a quadrangular cubital cell (Fig. 3). The mesothoracic postfurcasternum is separated from the furcasternum and furcasternal pit (Murányi *et al.* 2014: fig. 53). The male epiproct has a large basal sclerite that is weakly divided from the smaller laterobasal sclerites. The main epiproct sclerite is laterally entire and fully divided on the ventral surface. The caudal setae are absent and the inner sclerite is weak but long. The epiproct tip lacks an eversible crest (Murányi *et al.* 2014: figs 11–12). The male paraprocts are long and widely separated at the apex (Murányi *et al.* 2014: fig. 26). The fusion plate is long and narrow, the small

retractoral plate not fused (Murányi *et al.* 2014: fig. 37). The male tergum IX has a single posteromedial process that lacks scales or a sensilla basiconica. Tergum X is subdivided and posteriorly connected. A vesicle is usually present on the sternum IX and the subgenital plate is divided from sternum and tergum IX (Figs 4, 10). The female subgenital plate is large and its lateral portions are often weakly sclerotized. The posterior lobe is distinct and variable with the lateral and anterior sclerites being distinct. The inner sclerite and postgenital plate are lacking (Fig. 8).

Affinities

The *Cox*1 based molecular analyses well support both the monophyly of the group, and its distinction from *Capnia* s. str. (Murányi *et al.* 2014). It deserves definition as a new genus, as it will be described in the ongoing genus level revision of the Capniidae being conducted by Dávid Murányi. Morphologically, males are closely related to the genus *Zwicknia* Murányi, 2014, though molecular analyses do not suggest a close relationship (Murányi *et al.* 2014). The species of *Zwicknia* differ by the presence of a distinct eversible crest on the apicolaterally divided main epiproct sclerite; alternatively, the *C. cordata* group lacks the eversible crest. Females of the *cordata* group are distinctive among Palaearctic Capniidae by the distinct posterior lobe of the large but usually laterally weakly sclerotized subgenital plate, combined with the lack of an inner sclerite of the vaginal complex, a normal anal field of the hind wing, and a quadrangular cubital cell of the forewing. The larva is known only for two species (Zwick & Sivec 1980; Rehman *et al.* 2022); the tuft of hairs on the tip of the galea (Zwick & Sivec 1980) is a possible distinctive character for the group.

Distribution

Members of the *C. cordata* group are distributed in High Asia, where they are the most common and diverse Capniidae. Species are known from the Tien Shan, Hindukush, Pamir, Himalayas and the eastern ranges, sloping from the Qinghai-Tibet Plateau (Fig. 1). The morphologically similar *Zwicknia* has a mainly West Palaearctic distribution, extending eastwards to the Central Asian high mountains. This distribution pattern elucidates the geographically vicariant relationship between *Zwicknia* and the *C. ordata* group.

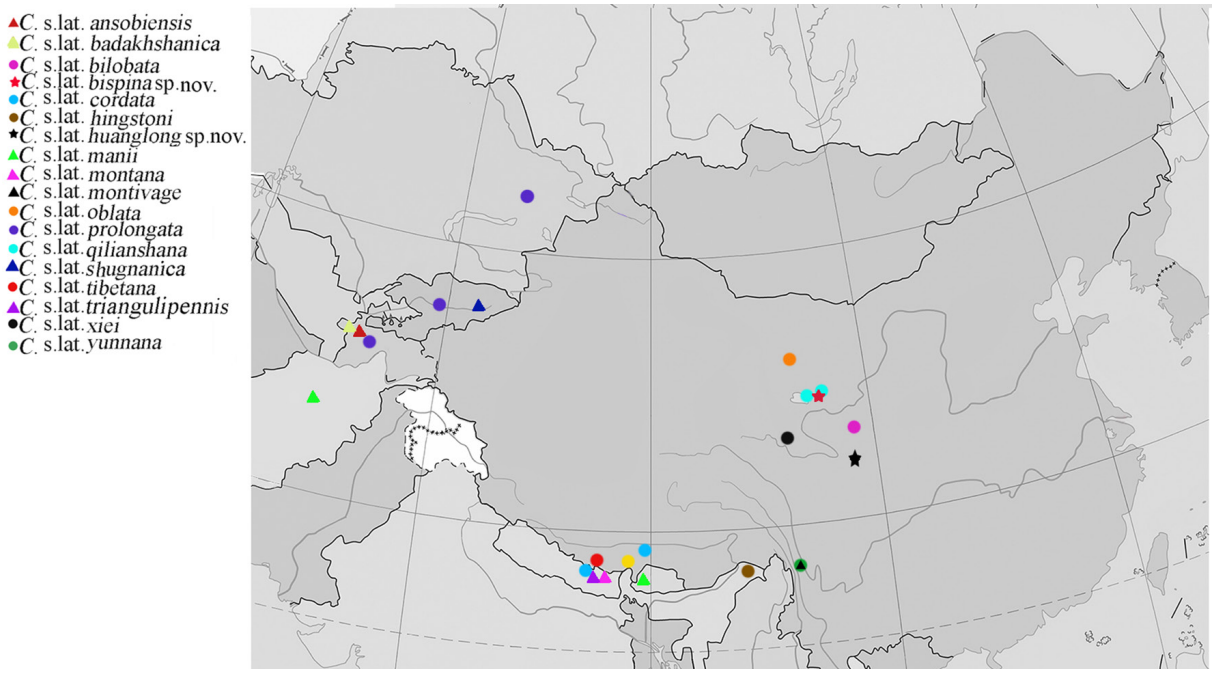

Fig. 1. Distribution of the *Capnia cordata* species group.

Capnia s. lat. ***bispina*** Cao & Li sp. nov.
urn:lsid:zoobank.org:act:B54BC6B4-681D-4ECA-833B-192955B1B8C7
Figs 1–8, 11A–B, 12A–C, 13–14

Diagnosis

The male of this new species differs markedly from that of most other members of the *C. cordata* species group by its caudally projecting posteromedial process of tergum IX ending in two acute spines.

Etymology

The specific epithet '*bispina*' is derived from Latin '*bi*' (meaning 'two' or 'double') and '*spina*' (meaning 'spine' or 'thorn') in reference to the two apical spines of the posteromedial process of male tergum IX. Use as a noun, gender feminine.

Type material

Holotype

CHINA • ♂; Qinghai Province, Xining City, Datong County, Niangniang Mountain; 36°54′56.81″ N, 101°36′10.51″ E; 2864 m a.s.l.; 17 Mar. 2021; Wei-Hai Li and Fan-Bin Kong leg.; HIST.

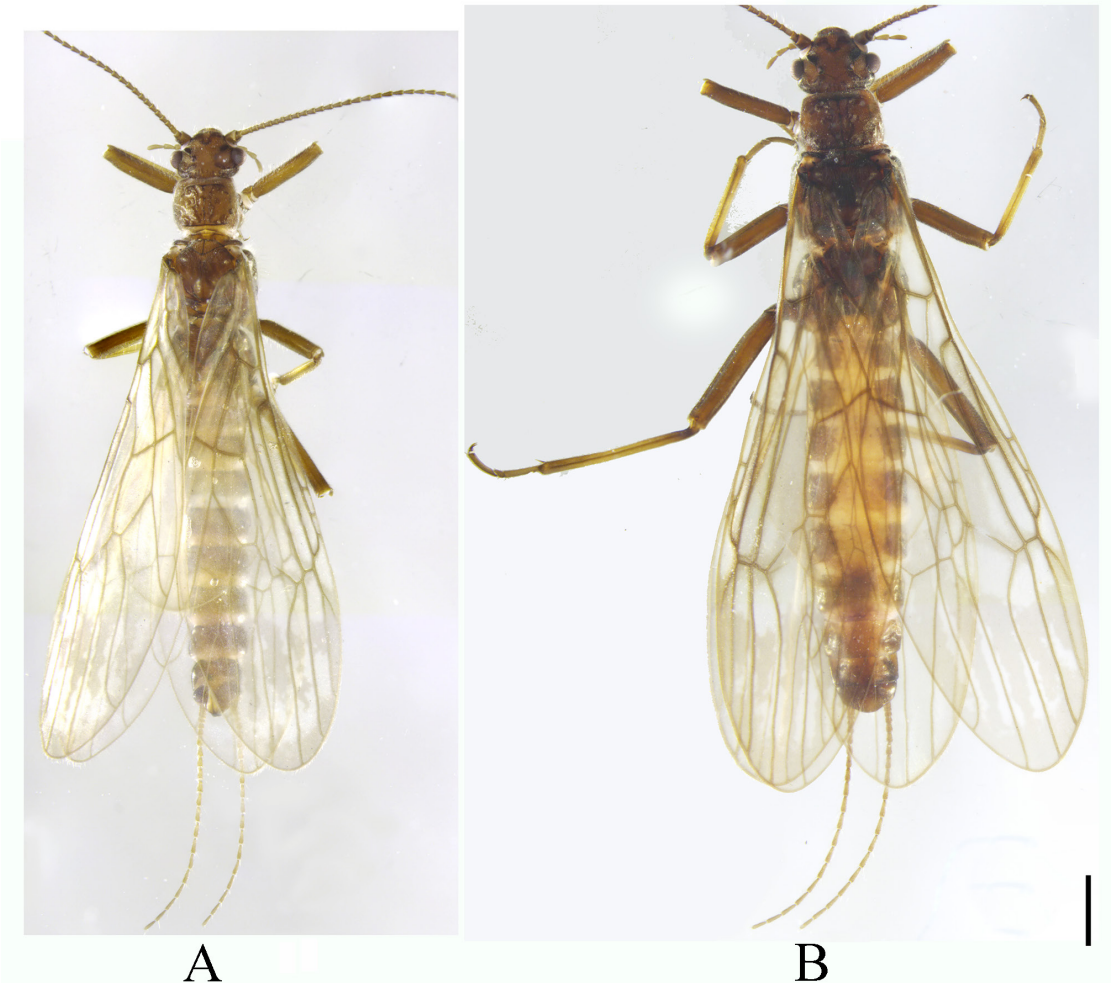

Fig. 2. *Capnia* s. lat. *bispina* Cao & Li sp. nov. **A**. Holotype, ♂ (HIST), habitus, dorsal view. **B**. Paratype, ♀ (HIST), habitus, dorsal view. Scale bar = 1 mm.

Paratypes

CHINA • 9 ♂♂, 5 ♀♀; same data as for holotype; HIST.

Description

Male

Adult habitus (Fig. 2). Body generally dark brown. Body length 9.1–9.3 mm. Forewing length 8.8–9.0 mm, hindwing length 7.0–7.2 mm (N = 10). Macropterous. Wing venation typical for species group. Forewing mottled, dark band in distal third, light band basal to it, other clouds of pigmentation. Head slightly wider than pronotum, with three ocelli, M-line and tentorial callosities dark brown. Antennae and palpi brown to dark brown. Pronotum trapezoid with dark rugosities, corner obtuse. Legs brown; tibiae lighter. Cerci with 17–18 slightly clubbed segments, each with apical whorl of long hairs.

Abdomen (Figs 2A, 4–7, 11A–B, 12A–B). Tergum I medially divided, terga II–IV subdivided by anteromedial membranous portion; antecosta medially divided on terga III and X, medially indent but entire on terga VI–IX (Fig. 11B). Terga IV–IX laterally with paired longitudinal patch and pair of spots. Tergum IX strongly sclerotized, posterior edge indenting laterad to posteromedial process, process slightly raised and extending to anterior margins of tergum X, 1/5 × as wide as segment, falciform in shape and bilobed apically. Tergum X subdivided by evenly rounded anteromedial indentation (Figs 4–5).

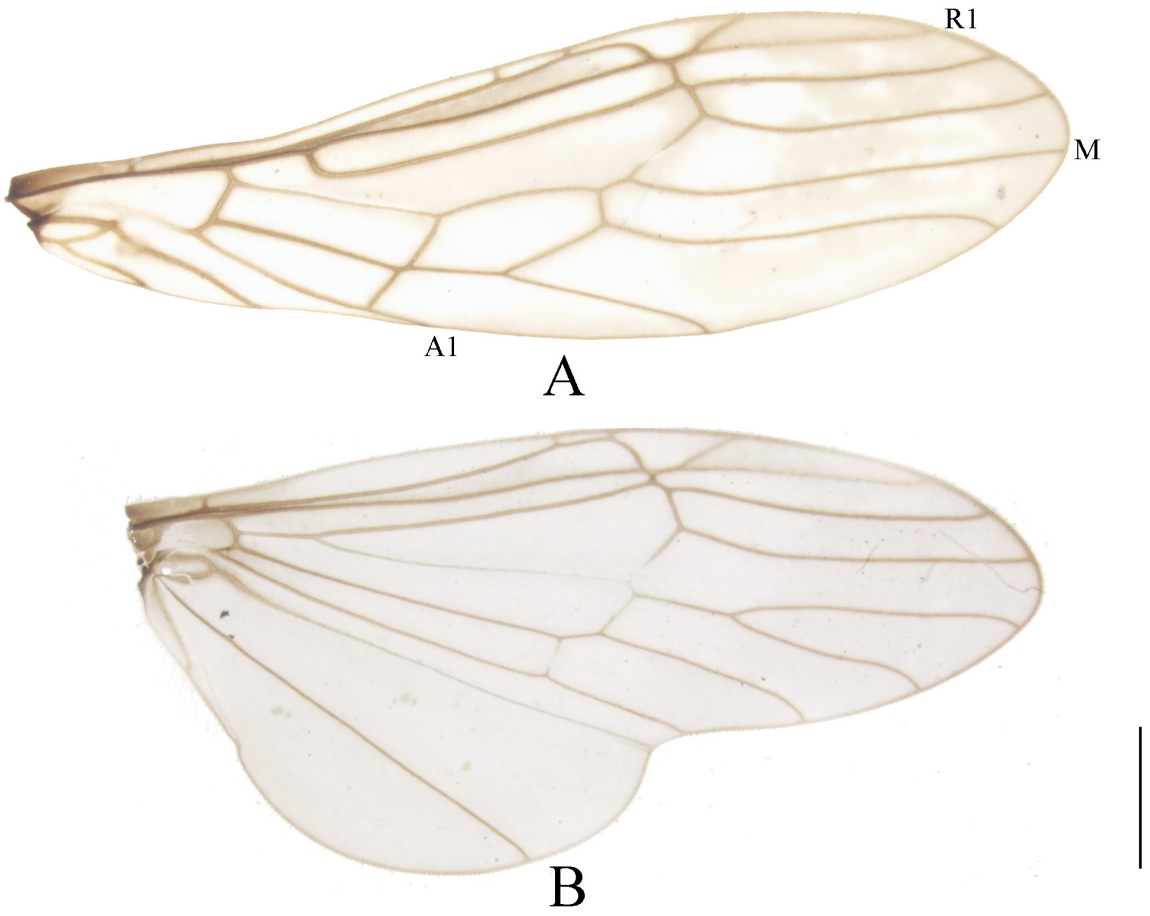

Fig. 3. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♂, holotype (HIST). **A**. Forewing, dorsal view. **B**. Hindwing, dorsal view. Abbreviations: A1 = first anal vein; M = Media Vein; R1 = first radial vein. Scale bar = 1 mm.

Sternum I entire and unmodified; sternum II with posterior sclerite not fused with anterior and lateral sclerites, sternum III with posterior sclerite not fused with anterior sclerites; sterna IV–VIII with anterior and lateral sclerites fused with posterior sclerite. Sternum IX fused with tergum IX anterolaterally (Fig. 11B); subgenital plate divided from other sclerites and tongue-shaped, with darkly sclerotized lateral margins; vesicle very large and covered with dense long hairs, rounded and wider than long. Short basal stalk, extending over ½ of subgenital plate (Fig. 4B). Paraprocts with long and wide apex, fusion plate long and narrow (Fig. 5B). Epiproct consist of large basal sclerite fused with relatively large, triangular basolateral sclerites; main epiproct sclerite 0.35 mm in length, long and widely triangular in dorsal view, dorsal edge convex while ventral edge convex in lateral view but apical third slightly dilated then abruptly narrowed into sharp, slightly downcurved apex. Dorsal division of main epiproct sclerite straight and narrow, only slightly opens after NaOH treatment; basal portion slightly darker, with delicate keel laterobasally; basal fork relatively large, fused with laterobasal sclerites; apex sharply pointed in both lateral and dorsal aspects (Figs 5, 12A–B); sclerite covered with dense setae on its dorsal and lateral surface, setae slightly shorter on basal portion and not similar to caudal setae of other Capniidae, sensillae occur on apex; inner sclerite long but thin and indistinct (Figs 6–7).

Female

Adult habitus (Fig. 2B). Body length 10.5–10.6 mm. Forewing length 9.2–9.3 mm, hindwing length 8.2–8.3 mm. Habitus generally similar to male.

Abdomen (Figs 8, 11A, 12C). Terga I–VIII divided by wide median membranous area, each marked with pair of small dark spots; tergum IX with pair of anterior indentations, tergum X entire. Sternum I

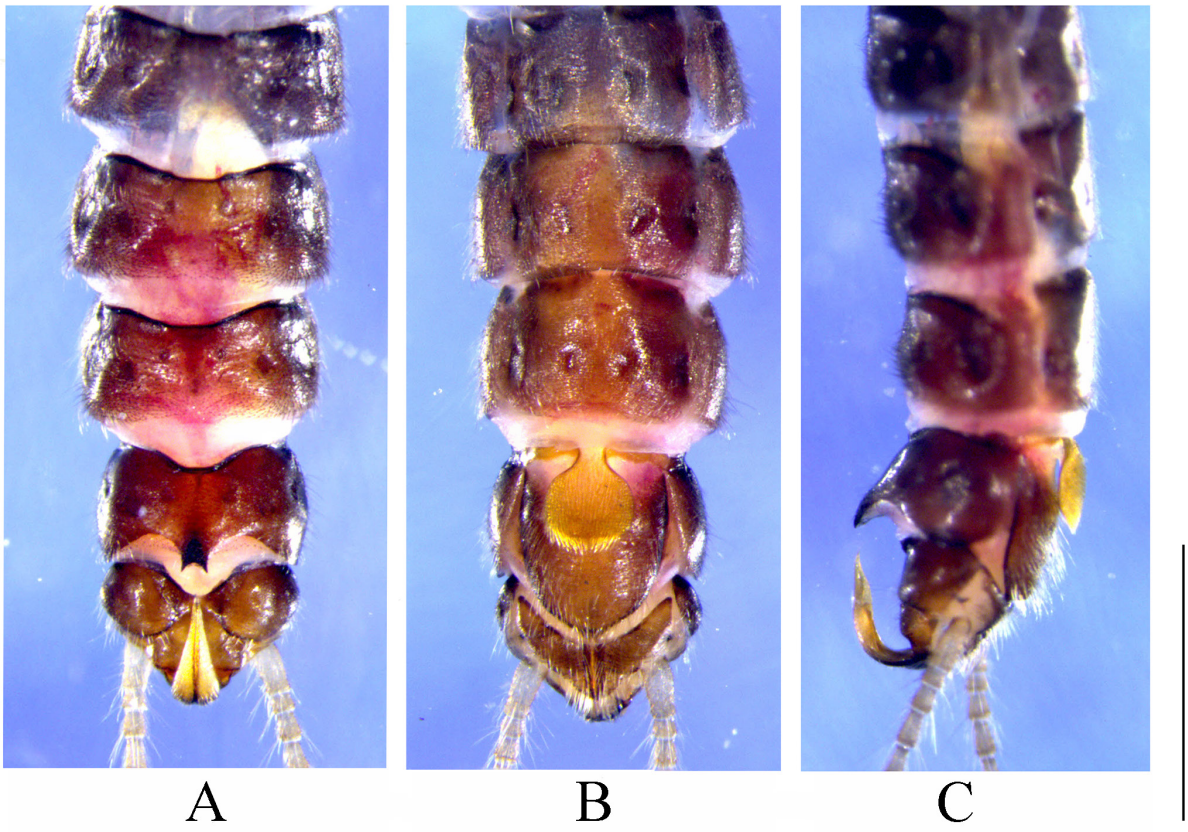

Fig. 4. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♂, holotype (HIST). **A**. Terminalia, dorsal view. **B**. Terminalia, ventral view. **C**. Terminalia, lateral view. Scale bar = 1 mm.

entire and unmodified; sterna II–VI with anterior sclerites not fused with posterior sclerite and lateral sclerites lacking, sternum VII with anterior sclerites not fused with posterior sclerite but small lateral sclerites present and fused (Figs 8A, C, 11A). Anterior sclerites of sternum VIII quadrangular, fused with subgenital plate. Subgenital plate wide trapezoidal, covering most of sternum (Fig. 12C), flat in lateral

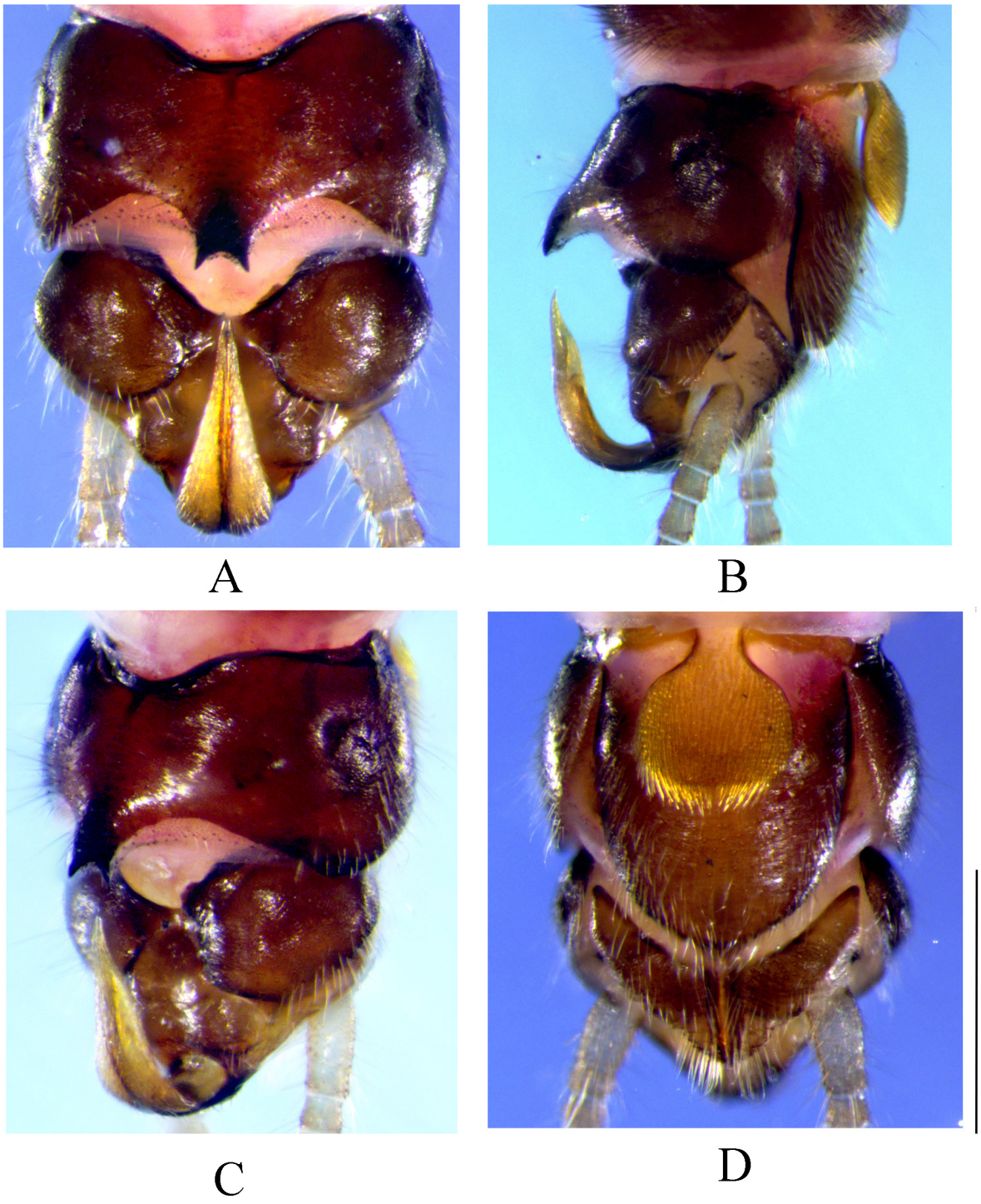

Fig. 5. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♂, holotype (HIST). **A**. Terminalia, dorsal view. **B**. Terminalia, lateral view. **C**. Terminalia, oblique lateral view. **D**. Terminalia, ventral view. Scale bar = 0.5 mm.

view; evenly sclerotized, setation lacking from medial portion and posterior lobe; posterior lobe less wide than ⅓ of subgenital plate width, not further lobed but expanded laterad with sharp, triangular portions. Lateral sclerites bean-shaped and bald, not fused with subgenital plate nor with tergum VIII. Postgenital plate and inner vaginal sclerite lacking. Sternum IX with wavy anterior edge, not fused with tergum IX; paraprocts triangular (Fig. 8B).

Distribution

China: Qinghai Province, Datong County. Adults were collected in mid-March, emerging from a slow to moderately fast flowing, small headwater tributary of the Datong River, its streambed consisting of large boulders and gravel (Fig. 13).

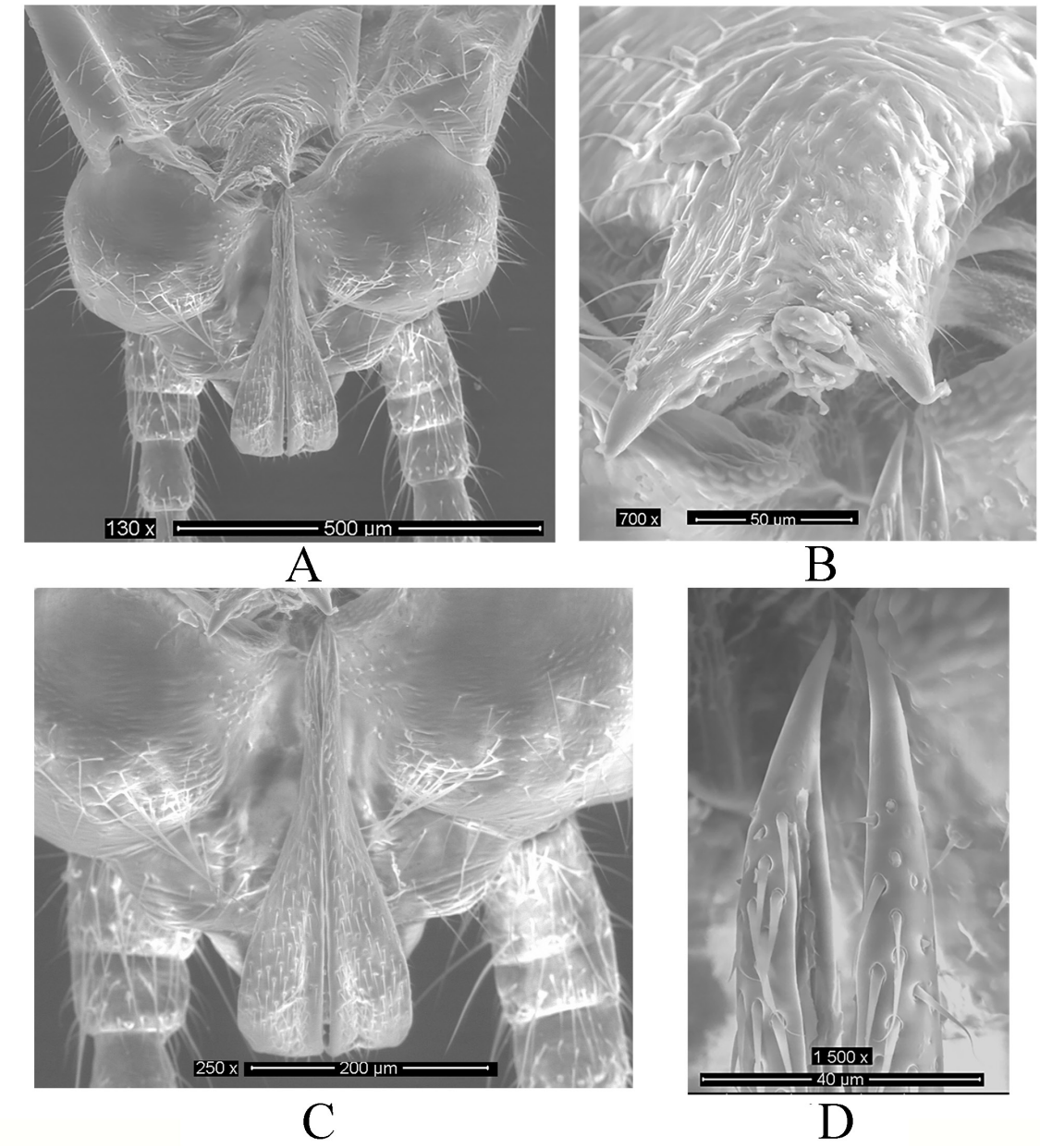

Fig. 6. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♂, paratype (HIST). **A**. Terminalia, dorsal view. **B**. Process of tergum IX, dorsal view. **C**. Epiproct, dorsal view. **D**. Epiproct, apically, dorsal view.

Remarks

Only *C.* s. lat. *bilobata* Chen & Song, 2019 and *C.* s. lat. *badakhshanica* Zhiltzova, 1974 share a similar tergum IX process, but in *C.* s. lat. *bilobata*, it is wider and bilobed without apical spines and in *C.* s. lat. *badakhshanica*, it is shorter and smaller. The entirely setose main epiproct sclerite is unique in the species group, also easily distinguishing the male. The female of *C.* s. lat. *bispina* Cao & Li sp. nov. appears the closest to *C.* s. lat. *qilianshana* Li & Yang, 2009 and *C.* s. lat. *yunnana* Li & Yang, 2011, sharing a similar narrow posterior lobe of the subgenital plate that is expanded lateral with triangular portions. However, the evenly sclerotized subgenital plate easily distinguishes the female from those two species.

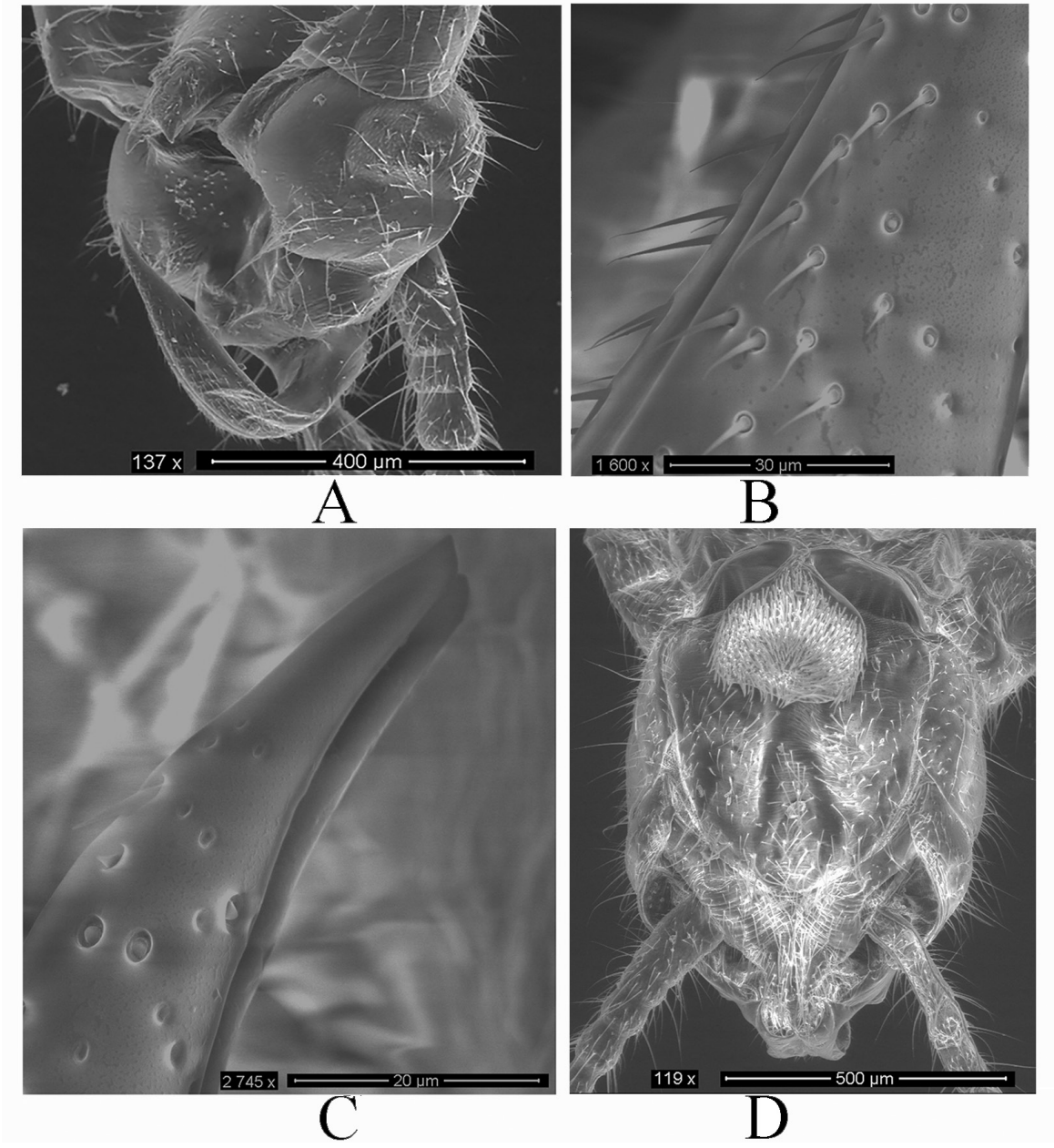

Fig. 7. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♂, paratype (HIST). **A**. Terminalia, dorsolateral view. **B.** Partial region of the main epiproct with sensilla basiconica, dorsolateral view. **C**. Apical of the main epiproct, dorsolateral view. **D**. Terminalia, ventral view.

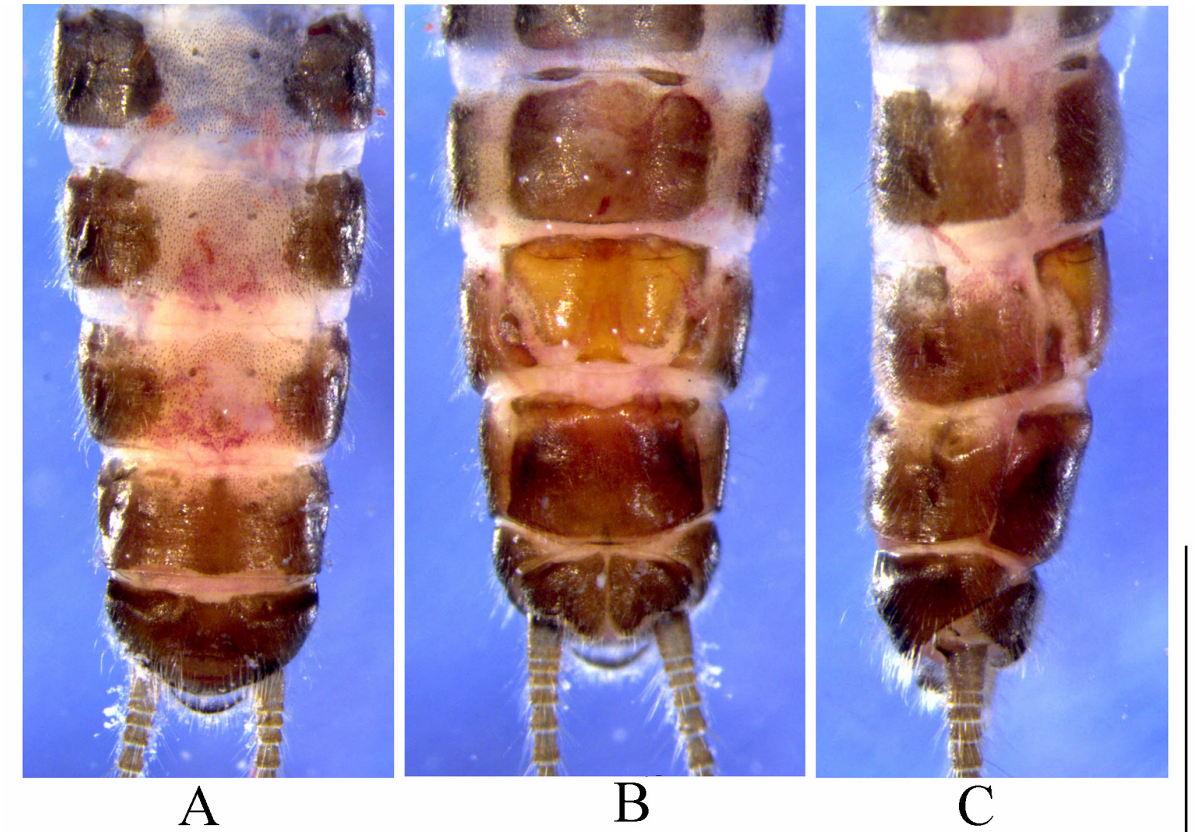

Fig. 8. *Capnia* s. lat. *bispina* Cao & Li sp. nov., ♀, paratype (HIST). **A**. Terminalia, dorsal view. **B**. Terminalia, ventral view. **C**. Terminalia, lateral view. Scale bar = 1 mm.

C. s. lat. ***huanglong*** Cao & Li sp. nov.
urn:lsid:zoobank.org:act:91C439D8-907B-4E78-9024-9F824A83837D
Figs 1, 9–10, 11C,12D–E

Diagnosis

The male of this new species differs markedly from that of most other members of the *C. cordata* species group by its straight process of tergum IX and the long and narrow triangular epiproct sclerite with the ventral and dorsal edges slightly but evenly convex in lateral view.

Etymology

The specific epithet '*huanglong*' is derived from the Huanglong Scenic Spot, where the new species was found and probably restricted to these places and the nearby ranges. Used as a noun, gender neutral.

Material examined

Holotype

CHINA • ♂; Sichuan Province, Aba Tibetan and Qiang Autonomous Prefecture, Songpan County, Huanglong Scenic Spot; 103°49′32.52″ E, 32°44′55.68″ N; 3550 m a.s.l.; 2 Aug. 2011; Si-Pei Liu and Wei-Hai Li leg.; HIST.

Description

Male

Adult habitus (Figs 2–3). Body generally dark brown. Body length 8.9 mm. Forewing length 10.3 mm, hindwing length 8.0 mm. Macropterous. Wing venation typical for species group. Head slightly wider than pronotum, with three pale and small ocelli, M-line and tentorial callosities dark brown. Antennae and palpi brown. Pronotum trapezoid with dark rugosities, corner obtuse. Legs brown; femora darker. Cerci with clubbed segments, each with apical whorl of long hairs; apical part of cerci broken in holotype.

Abdomen (Figs 9A, 10, 11C, 12D–E). Terga I–IV medially divided by membranous portion; antecosta medially divided on terga II–IV and X, medially indenting but entire on terga V–IX; short, medial longitudinal band projecting from antecosta on terga VIII–IX. Tergum IX strongly sclerotized, posterior edge nearly straight in dorsal view, process elevated and triangular in lateral view, with two small sclerotized teeth projecting into small membranous patch. Tergum X subdivided by widely rounded anteromedial indentation. Sternum I entire and unmodified; sternum II with anterior sclerites not fused with posterior sclerite, lateral sclerites lacking; sterna III–VIII with anterior and lateral sclerites, all fused with posterior sclerite (Fig. 11C). Sternum IX fused with tergum IX anterolaterally; subgenital plate divided from other sclerites and subtriangular, with darkly sclerotized lateral margins; vesicle elliptical and medium-sized, covered with numerous long hairs, posteriorly reaching ⅓ of subgenital plate. Paraprocts with long and wide apex, fusion plate long and narrow (Fig. 10). Epiproct consists of large basal sclerite fused with small, triangular laterobasal sclerites; main epiproct sclerite 0.6 mm in length, long and narrowly triangular in dorsal view, both ventral and dorsal edge slightly but evenly convex in lateral view. Dorsal division of main epiproct sclerite slightly dilated in apical third, widely opens after NaOH treatment; basal portion darkly sclerotized with raised subtriangular structure in dorsal aspect; basal fork small, fused with laterobasal sclerites; apex pointed but its tip blunt in both lateral and dorsal aspects; sclerite bald besides few apical sensillae; inner sclerite long but thin and indistinct (Figs 10, 12D–E).

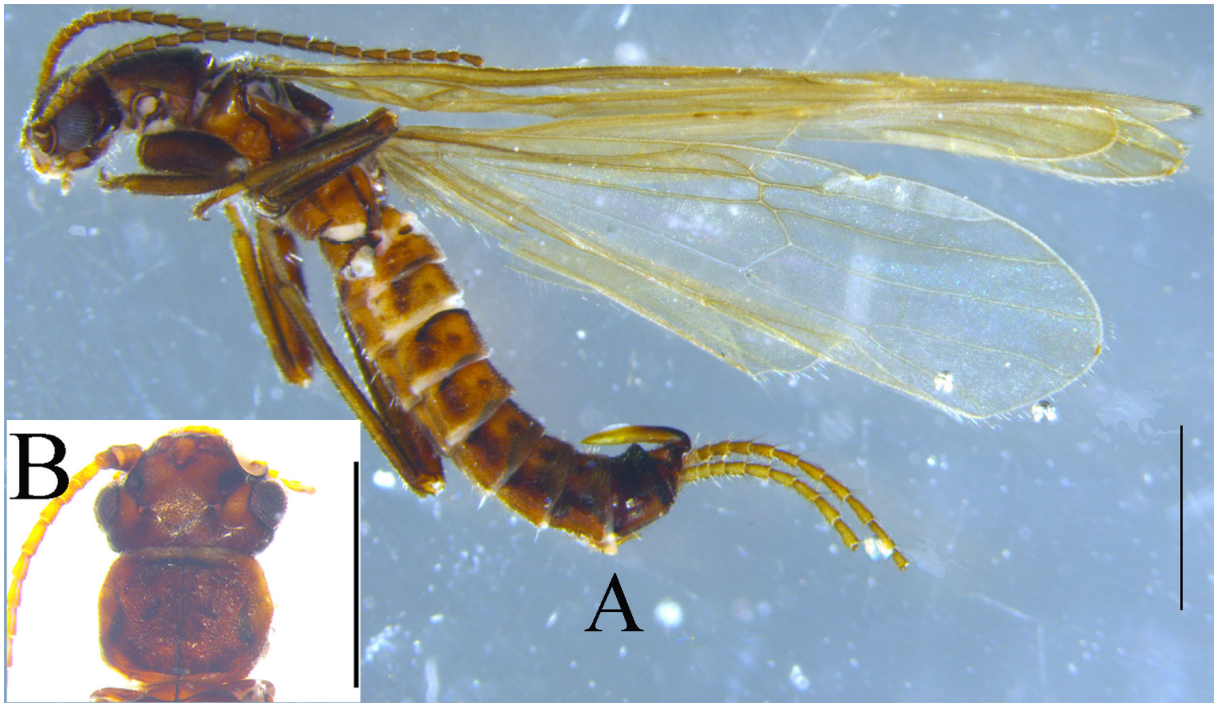

Fig. 9. *Capnia* s. lat. *huanglong* Cao & Li sp. nov., ♂, holotype (HIST). **A**. Habitus, lateral view. **B.** Head, dorsal view. Scale bar = 1 mm.

Female

Unknown.

Distribution

China: Sichuan Province. Presently only known from Huanglong Scenic Spot.

Fig. 10. *Capnia* s. lat. *huanglong* Cao & Li sp. nov., ♂, holotype (HIST). **A**. Terminalia, dorsal view. **B**. Terminalia, lateral view. **C**. Terminalia, ventral view. **D**. Terminalia after treatment with 10% NaOH, dorsal view. **E**. Terminalia after treatment with 10% NaOH, lateral view. **F**. Terminalia after treatment with 10% NaOH, ventral view. Scale bars: A–C = 1 mm; D–F = 0.5 mm.

Remarks

The new species is closely related to *C.* s. lat. *manii*, but can be separated by the tip of the main epiproct sclerite, which is more pointed in the latter. Furthermore, *C.* s. lat. *manii* has a vestigial ventral vesicle, in contrast to the normally developed vesicle found in the new species. The main epiproct sclerite of *C.* s. lat. *huanglong* Cao & Li sp. nov. is also different from that of other Chinese species within the *C.* s. lat. *cordata* species group: in *C.* s. lat. *yunnana*, the main epiproct sclerite has a swollen apex; in *C.* s. lat. *qilianshana*, the main epiproct sclerite has a rounded tip and its subapical area is slightly swollen; in *C.* s. lat. *oblata*, the main epiproct sclerite has a flattened apex; in *C.* s. lat. *xiei*, the main epiproct sclerite is high and has a basal bilamellar structure, while these characteristics are absent in *C.* s. lat. *huanglong*.

Molecular analysis

To characterize in detail the species limits within the *C. cordata* species group, we consider morphological characters and mitochondrial marker *Cox*1, under a phylogenetic analysis. The aligned data matrix was 651 base pairs (bp) in length. The best fit substitution model TNe+I: CO1_p1, F81+F: CO1_p2, TN+F+G4: CO1_p3 was selected for this concatenated data matrix. The Maximum Likelihood tree supported the morphological distinction of *C.* s. lat. *bispina* Cao & Li sp. nov. and the separation from the other species of the *C. cordata* species group with 100% nodal support (Fig. 14). Interspecific divergence values for *C.* s. lat. *bispina* ranged from 5.03–19.44% of genetic divergence in comparison with the other species whereas intraspecific between an associated male-female pair was only 0.31%

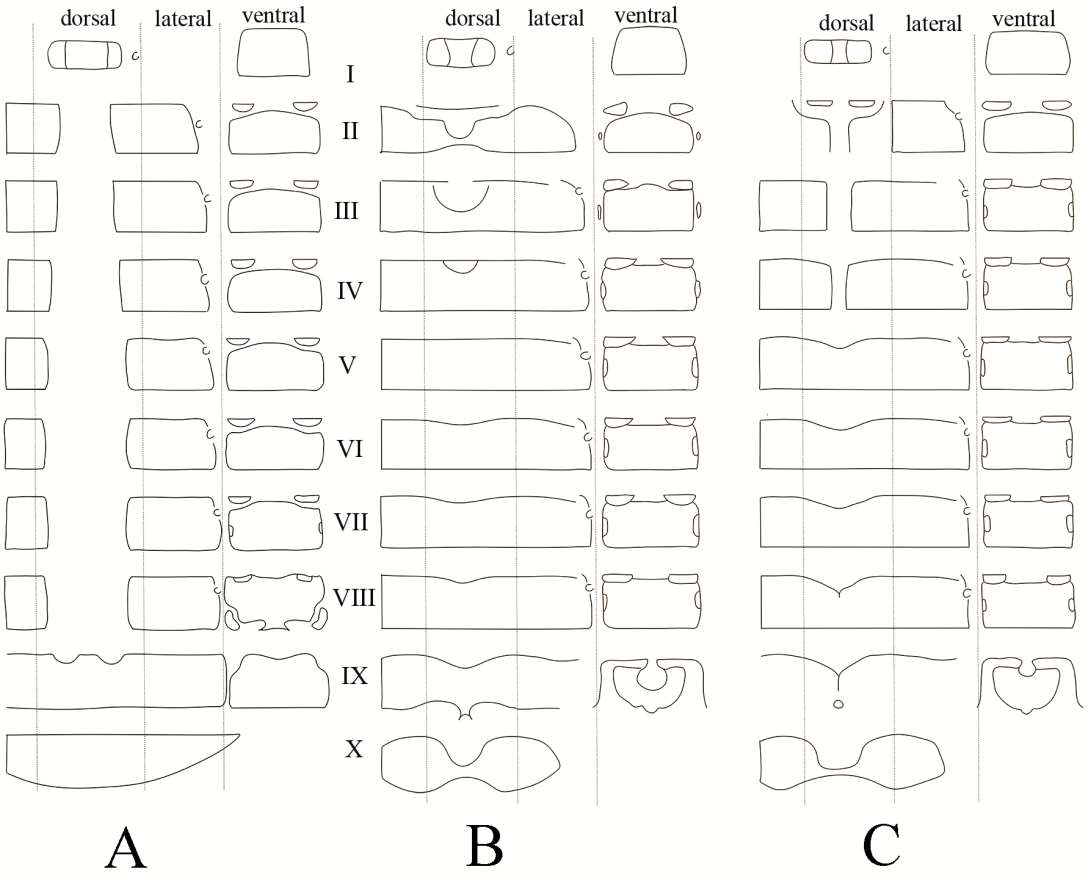

Fig. 11. Abdominal sclerites of *Capnia* s. lat. *bispina* Cao & Li sp. nov. and *Capnia* s. lat. *huanglong* Cao & Li sp. nov. **A**. *Capnia* s. lat. *bispina*, ♀, paratype (HIST). **B**. *Capnia* s. lat. *bispina*, ♂, holotype (HIST). **C**. *Capnia* s. lat. *huanglong* Cao & Li sp. nov., ♂, holotype (HIST).

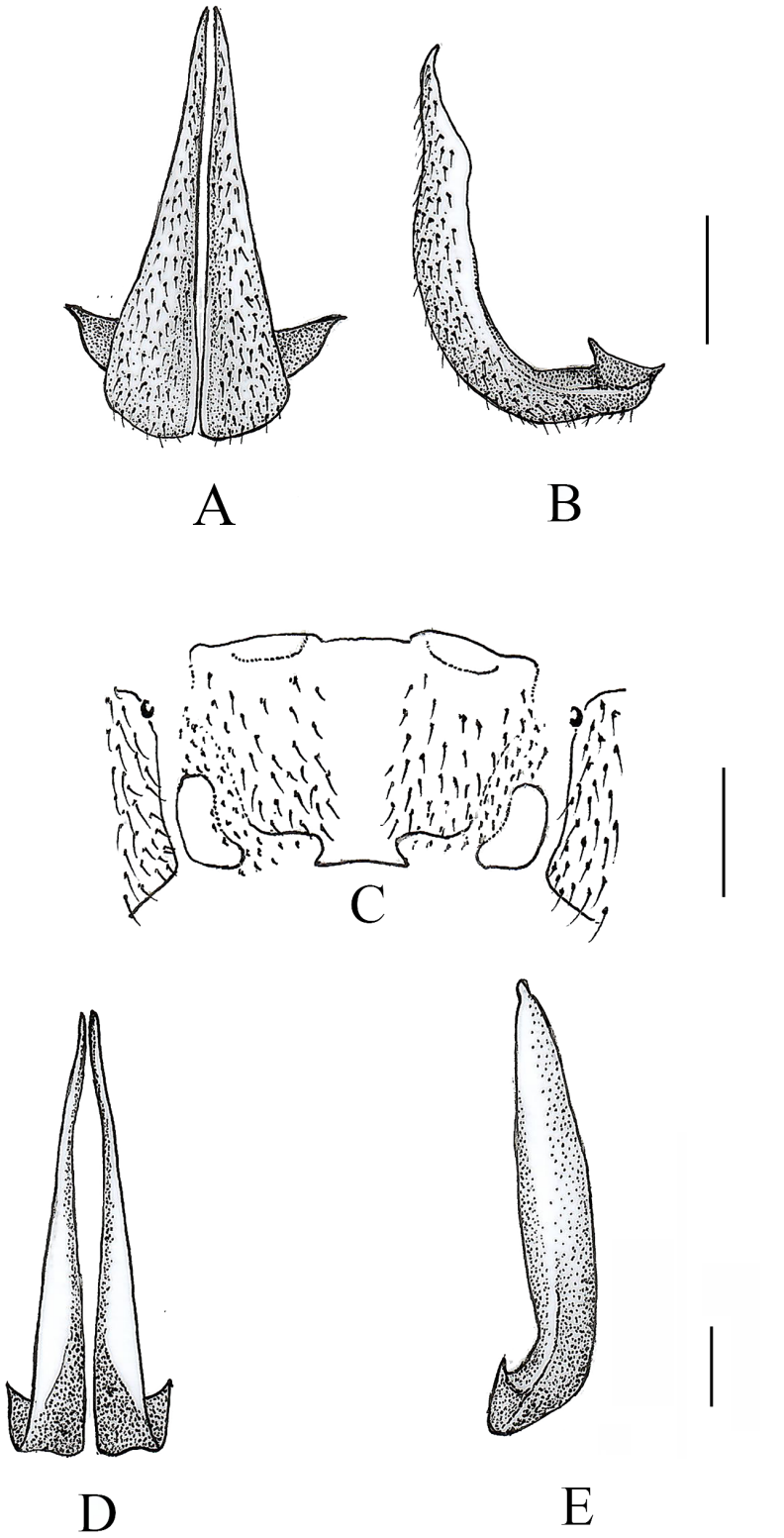

Fig. 12. A–B. Male genitalia of *Capnia* s. lat. *bispina* Cao & Li sp. nov., holotype (HIST). **A**. Dorsal view of epiproct. **B**. Lateral view of epiproct. **C**. Female terminalia of *Capnia* s. lat. *bispina*, paratype (HIST), ventral view. **D–E**. Male genitalia of *Capnia* s. lat. *huanglong* Cao & Li sp. nov., holotype (HIST). **D**. Dorsal view of epiproct. **E**. Lateral view of epiproct. Scale bar = 0.2 mm.

Fig. 13. Type locality of *C.* s. lat. *bispina* Cao & Li sp. nov., upstream of Datong River.

(Table 3). Combined, this is good evidence for the validity of *C.* s. lat. *bispina* (Hebert *et al.* 2003; Zhou *et al.* 2009). Meanwhile, from the analyses we demonstrated that *C.* s. lat. *bispina* is a member of the *C. cordata* species group. Unfortunately, the specimen of *C.* s. lat. *huanglong* Cao & Li sp. nov. was 14 years old, and failed to be sequenced successfully.

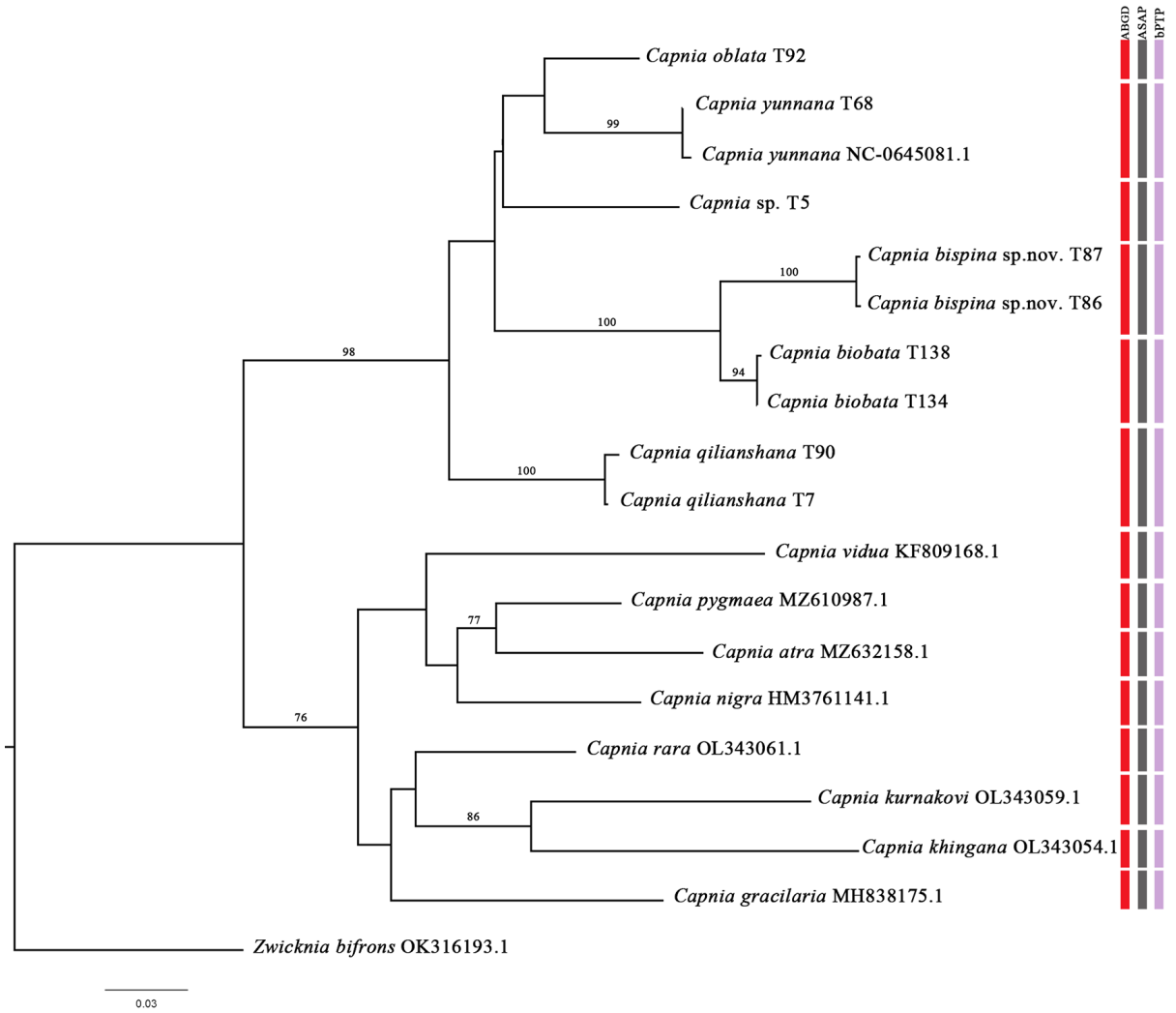

Fig. 14. Phylogenetic relationships among sequenced specimens based on a Maximum Likelihood tree analysis. Numbers at the nodes represent bootstrap values as percentages. Only nodal support values >70% are depicted on the tree. The species delimitation methods are identified by ABGD; ASAP; bPTP. The coloured bars represent the results of the species delimitation method.

Table 3. Genetic distances among sequenced specimens. Upper triangular matrix: standard deviation; lower triangular matrix: genetic distances.

	OK316193.1	T92	T90	T87	T86	T68	NC-064508.1	KF809168.1	OL343061.1	MZ610987.1	HM376114.1	OL343059.1	OL343054.1	MH838175.1	MZ632158.1	T138	T134	T7	T5
OK316193.1		0.016	0.017	0.018	0.018	0.016	0.016	0.017	0.016	0.017	0.016	0.017	0.017	0.017	0.015	0.017	0.017	0.017	0.016
T92	0.139		0.012	0.013	0.013	0.010	0.010	0.017	0.016	0.017	0.016	0.016	0.017	0.017	0.016	0.013	0.012	0.012	0.011
T90	0.150	0.085		0.014	0.014	0.012	0.012	0.018	0.015	0.016	0.016	0.016	0.017	0.015	0.017	0.014	0.014	0.003	0.013
T87	0.174	0.106	0.122		0.002	0.013	0.013	0.019	0.017	0.016	0.017	0.018	0.020	0.018	0.017	0.009	0.009	0.014	0.014
T86	0.174	0.106	0.122	0.003		0.013	0.013	0.019	0.017	0.016	0.017	0.018	0.020	0.018	0.018	0.009	0.009	0.014	0.014
T68	0.143	0.062	0.088	0.111	0.109		0.002	0.016	0.015	0.015	0.014	0.015	0.018	0.017	0.016	0.012	0.012	0.012	0.012
NC-064508.1	0.143	0.065	0.092	0.113	0.111	0.003		0.016	0.016	0.015	0.014	0.015	0.018	0.017	0.016	0.012	0.012	0.012	0.012
KF809168.1	0.157	0.168	0.170	0.192	0.194	0.156	0.156		0.017	0.014	0.016	0.016	0.016	0.017	0.016	0.019	0.018	0.018	0.019
OL343061.1	0.137	0.133	0.120	0.152	0.152	0.124	0.126	0.142		0.015	0.015	0.015	0.015	0.014	0.015	0.017	0.017	0.015	0.017
MZ610987.1	0.157	0.145	0.137	0.149	0.149	0.124	0.124	0.123	0.123		0.012	0.016	0.017	0.014	0.012	0.015	0.015	0.016	0.016
HM376114.1	0.143	0.141	0.154	0.156	0.154	0.129	0.129	0.135	0.121	0.086		0.016	0.016	0.014	0.013	0.017	0.016	0.016	0.016
OL343059.1	0.154	0.148	0.146	0.176	0.178	0.135	0.135	0.153	0.115	0.142	0.139		0.015	0.016	0.016	0.018	0.018	0.016	0.017
OL343054.1	0.155	0.157	0.155	0.186	0.184	0.167	0.169	0.146	0.121	0.150	0.138	0.130		0.017	0.016	0.019	0.019	0.018	0.018
MH838175.1	0.145	0.158	0.131	0.171	0.169	0.149	0.147	0.140	0.108	0.112	0.119	0.149	0.153		0.015	0.018	0.018	0.015	0.016
MZ632158.1	0.139	0.141	0.149	0.160	0.164	0.135	0.135	0.142	0.106	0.091	0.103	0.136	0.138	0.125		0.017	0.017	0.017	0.016
T138	0.158	0.095	0.111	0.052	0.052	0.093	0.095	0.184	0.143	0.126	0.149	0.166	0.176	0.162	0.161		0.002	0.014	0.013
T134	0.156	0.093	0.109	0.050	0.050	0.091	0.093	0.182	0.145	0.124	0.147	0.164	0.174	0.160	0.159	0.002		0.014	0.013
T7	0.146	0.081	0.006	0.118	0.118	0.085	0.088	0.168	0.122	0.135	0.153	0.152	0.157	0.130	0.147	0.107	0.106		0.013
T5	0.142	0.076	0.099	0.115	0.115	0.092	0.092	0.180	0.139	0.133	0.139	0.160	0.164	0.141	0.143	0.102	0.100	0.093	

Key to adult males of the Capnia s. lat. cordata group

Males of *C. ansobiensis* Zhiltzova, 1974*, C. montivaga* Kimmins, 1946, and *C. shugnanica* Zhiltzova, 1974 unknown.

1. Tergum IX with distinctly raised or elongated process 2
– Tergum IX with small process, raised not higher than one third of tergum height in lateral view and not overhanging the segment 4

2. Main epiproct sclerite medially swollen in lateral view; tergum IX with process raised higher than one third of tergum height in lateral view (Zhiltzova 1974: figs 7, 10) .... ***C.*** s. lat. ***badakhshanica*** Zhiltzova, 1974 (Tajikistan)
– Main epiproct sclerite not swollen in lateral view; tergum IX with process not much raised but elongated and overhanging the segment 3

3. Tergum IX with wide and bilobed process; main epiproct sclerite wavy in lateral view (Chen & Song 2019: fig. 5) ..... ***C.*** s. lat. ***bilobata*** Chen & Song, 2019 (China: Shaanxi)
– Tergum IX with narrow and spined process; main epiproct sclerite straight in lateral view (Fig. 4A, 4C) ..... ***C.*** s. lat. ***bispina*** Cao & Li sp. nov. (China: Qinghai)

4. Main epiproct sclerite with hooked, ventrally curved apex in lateral view 5
– Apex of main epiproct sclerite not curved ventrally 7

5. Apex of main epiproct sclerite blunt (Zhiltzova 1969: fig. 5) .... ***C.*** s. lat. ***prolongata*** Zhiltzova, 1969 (Kazakhstan, Kyrgyzstan, Tajikistan)
– Apex of main epiproct sclerite acute 6

6. Ventral vesicle vestigial; main epiproct sclerite slender in lateral, wider in dorsal view (Zwick & Sivec 1980: fig. 5a–c) ..... ***C.*** s. lat. ***montana*** Kimmins, 1946 (India: Sikkim; Nepal. Syn.: *C.* s. lat. *swanii* Jewett, 1975)
– Ventral vesicle present; main epiproct sclerite wider in lateral, slender in dorsal view (Kimmins 1947: fig. 9a–d) ..... ***C.*** s. lat. ***cordata*** Kimmins, 1946 (China: Xizang; Nepal)

7. Ventral edge of main epiproct sclerite straight in medial section 8
– Ventral edge of main epiproct sclerite convex in medial section 11

8. Main epiproct sclerite highest in medial portion in lateral view 9
– Main epiproct sclerite highest in apical third, just before apex 10

9. Apex of main epiproct sclerite evenly truncate (Kimmins 1947: fig. 10a) .... ***C.*** s. lat. ***tibetana*** Kimmins, 1946 (China: Xizang)
– Apex of main epiproct sclerite pointed in lateral, slightly flattened in dorsal view (Chen & Du 2017a: figs 7–8) ..... ***C.*** s. lat. ***oblata*** Chen & Du, 2017 (China: Yunnan)

10. Apex of main epiproct sclerite pointed; ventral vesicle can be vestigial (Jewett, 1975: fig. 2) .... ***C.*** s. lat. ***triangulipennis*** Jewett, 1975 (Nepal. Syn.: *C.* s. lat. *nepalensis* Harper, 1977)
– Apex of main epiproct sclerite slightly swollen; ventral vesicle present (in Chen & Du 2017a: figs 15–18) ..... ***C.*** s. lat. ***xiei*** Chen & Du, 2017 (China: Qinghai)

11. Main epiproct sclerite evenly wide before the apex in dorsal view; tergum IX only with hump (Kimmins 1947: fig. 8b, d) ..... ***C.*** s. lat. ***hingstoni*** Kimmins, 1946 (India: Sikkim)
– Main epiproct sclerite narrowing towards apical third in dorsal view; tergum IX with sclerotized process 12

12. Apex of main epiproct sclerite swollen (Li & Yang 2011: fig. 7) .... ***C.*** s. lat. ***yunnana*** Li & Yang, 2011 (China: Xizang, Yunnan)
– Apex of main epiproct sclerite not swollen 13

13. Main epiproct sclerite with apical third elliptical to rounded in dorsal view (Li & Yang 2009: fig. 5) ..... ***C.*** s. lat. ***qilianshana*** Li & Yang, 2009 (China: Gansu, Qinghai)
– Main epiproct sclerite with apical third triangular in dorsal view 14

14. Tip of main epiproct sclerite less pointed in lateral view; ventral vesicle present (Fig. 10) ....***C.*** s. lat. ***huanglong*** Cao & Li sp. nov. (China: Sichuan)
– Tip of the main epiproct sclerite more pointed in lateral view; ventral vesicle vestigial (Jewett, 1958: fig. 2, 2a) .....***C.*** s. lat. ***manii*** Jewett, 1958 (India: Himachal Pradesh; Pakistan)

Key to adult females of the Capnia s. lat. cordata group

Females of *C.* s. lat. *huanglong* Cao & Li sp. nov. and the two unnamed females sensu Li & Yang (2009) and Shen *et al.* (2021) unknown.

1. Sternum IX with separated, triangular medial sclerite (Shen *et al.* 2021: fig. 11) .... ***Capnia*** s. lat. sensu Shen *et al.* 2021 (China: Xizang)
– Sternum IX without separated medial sclerite 2

2. Subgenital plate with contrasting dark medial longitudinal area and white lateral portions 3
– Subgenital plate not contrastingly bicolored, or medial area not longitudinal dark patch 6

3. Subgenital plate medial area with four, posteriorly converging ridges (Zhiltzova 1974: fig. 3) .... ***C.*** s. lat. ***ansobiensis*** Zhiltzova, 1974 (Tajikistan)
– Subgenital plate medial area lacks ridges 4

4. Subgenital plate medial dark area widened in central portion (Zhiltzova 1974: fig. 12) ....***C.*** s. lat. ***badakhshanica*** Zhiltzova, 1974
– Subgenital plate medial dark area with nearly parallell lateral margins 5

5. Subgenital plate dark medial area posteriorly bilobed (Zhiltzova 1974: fig. 17) .... ***C.*** s. lat. ***shugnanica*** Zhiltzova, 1974 (Tajikistan)
– Subgenital plate dark medial area posteriorly rounded (Li & Yang 2009 fig. 8) .... ***Capnia*** s. lat. sensu Li & Yang 2009 (China: Sichuan)

6. Posterior lobe of subgenital plate wider than one third of width of the plate 7
– Posterior lobe of subgenital plate maximum as wide as third of width of plate 11

7. Posterior lobe of subgenital plate rounded 8
– Posterior lobe of subgenital plate weakly trilobed 9

8. Subgenital plate with anteromedial membranous portion (Chen & Du 2017a: fig. 12) .... ***C.*** s. lat. ***oblata*** Chen & Du 2017
– Subgenital plate evenly sclerotized (Kimmins 1947: fig. 8f; Chen & Du 2017a: fig. 20) .... ***C.*** s. lat. ***hingstoni*** Kimmins, 1947, *C.* s. lat. *xiei* Chen & Du 2017

9. Posterior portion of the subgenital plate folded over posterior lobe; posterior lobe expanded laterad in sharp projections (Chen & Song 2019: fig. 9) ..... ***C.*** s. lat. ***bilobata*** Chen & Song 2019
– Subgenital plate not folded over posterior lobe; posterior lobe not or only slightly expanded laterad 10

10. Central portion of posterior lobe quadrangular, lateral portions not expanded laterad (Zhiltzova 1969: 600, fig. 11) ..... ***C.*** s. lat. ***prolongate***Zhiltzova, 1969
– Central portion of posterior lobe rounded, lateral portions slightly expanded laterad (Kimmins 1947: 736, fig. 11) ..... ***C.*** s. lat. ***montana*** Kimmins, 1947

11. Posterior lobe of subgenital plate bilobed (Jewett 1975: fig. 1b) .... ***C.*** s. lat. ***triangulipennis*** Jewett, 1975
– Posterior lobe of subgenital plate not lobed but quadrangular or rounded 12

12. Posterior lobe of subgenital plate not expanded laterad, rounded or quadrangular 13
– Posterior lobe of subgenital plate expanded laterad 15

13. Posterior lobe of subgenital plate much wider than long, quadrangular (Zwick & Sivec 1980: fig. 6c) ..... ***C.*** s. lat. ***cordata*** Kimmins, 1947
– Posterior lobe of subgenital plate about as wide as long, rounded 14

14. Posterior lobe of subgenital plate widely separated from lateral sclerites (Kimmins 1947: fig. 10d) ..... ***C.*** s. lat. ***tibetana*** Kimmins, 1947
– Posterior lobe of subgenital plate set close to lateral sclerites (Jewett 1958: fig. 2b) .... ***C.*** s. lat. ***manii*** Jewett, 1958

15. Posterior lobe of subgenital plate expanded laterad with rounded portions (Kimmins 1946: fig. 11b) ..... ***C.*** s. lat. ***montivaga*** Kimmins, 1946 (China: Xizang; Nepal)
– Posterior lobe of subgenital plate expanded laterad with sharp, triangular portions 16

16. Subgenital plate evenly sclerotized ..... ***C.*** s. lat. ***bispina*** Cao & Li sp. nov.
– Subgenital plate with lightly sclerotized lateral portions 17

17. Posterior lobe of subgenital plate wider than long, posterior edge nearly straight (Rehman *et al.* 2022: fig. 11b) ..... ***C.*** s. lat. ***qilianshana*** Li and Yang, 2009
– Posterior lobe of the subgenital plate about as wide as long, posterior edge sinuous (Li *et al.* 2011: fig. 4) ..... ***C.*** s. lat.***yunnana*** Li & Yang, 2011

Discussion

Both the *Cox*1 analysis and comparative morphology support the *Capnia* s. lat. *cordata* species group as a monophyletic clade distinct from *Capnia* s. str. Our data supports its description as a new genus. That will be done as part of the ongoing genus-level revision of the Capniidae family. Distinctive characters are defined by a combination of male and female genital characters, wing venation and composition of thoracic sclerites. Morphologically, it is closely related to the vicariant genus *Zwicknia*; however, molecular analyses do not indicate a close relationship (Fig. 14).

The *C. cordata* group is restricted to the high mountains of Asia (Fig. 1). Species are known from Tien Shan (one species), Hindukush (one species), Pamir (four species), Himalayas (seven species) and the Qinghai-Tibet Plateau and its easterly sloping ranges (nine species). At present, 20 species can be distinguished (18 valid and two unnamed), and two additional species were regarded as synonyms. Further synonymy is possible, as most Himalayan species are known only from their half-century or older original descriptions. A comparative examination of the type specimens is needed to clarify these relationships. Fifteen of the 20 species are known only from females, whereas *C.* s. lat. *huanglong* Cao & Li sp. nov. is the only species known exclusively from the male.

In China, members of the group are found in the northwestern and southwestern mountainous regions, comprising a total of 12 species, including the two species described herein: *C.* s. lat. *bilobata*, *C.* s. lat. *bispina* Cao & Li sp. nov., *C.* s. lat. *cordata*, *C.* s. lat. *huanglong* Cao & Li sp. nov., *C.* s. lat. *montivaga*, *C.* s. lat. *oblata*, *C.* s. lat. *qilianshana*, *C.* s. lat. *tibetana*, *C.* s. lat. *xiei*, *C.* s. lat. *yunnana*, *C.* s. lat. sensu Li & Yang 2009 and *C.* s. lat. sensu Shen *et al.* 2021. Future explorations may uncover additional species in the vast, unstudied areas during the cold season or early spring.

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