

Forever Love: The Hitherto Earliest Record of Copulating Insects from the Middle Jurassic of China

Shu Li^{1,2}, Chungkun Shih¹, Chen Wang¹, Hong Pang³, Dong Ren^{1*}

1 Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, P.R. China, **2** Institute of Plant and Environmental Protection, Beijing Academy of Agriculture and Forestry Sciences, Beijing, China, **3** State Key Laboratory of Biocontrol and Institute of Entomology, Sun Yat-sen University, Guangzhou, P.R. China

Abstract

Background: Mating behaviors have been widely studied for extant insects. However, cases of mating individuals are particularly rare in the fossil record of insects, and most of them involved preservation in amber while only in rare cases found in compression fossils. This considerably limits our knowledge of mating position and genitalia orientation during the Mesozoic, and hinders our understanding of the evolution of mating behaviors in this major component of modern ecosystems.

Principal Finding: Here we report a pair of copulating froghoppers, *Anthoscytina perpetua* sp. nov., referable to the Procercopidae, from the Middle Jurassic of northeastern China. They exhibit belly-to-belly mating position as preserved, with male's aedeagus inserting into the female's bursa copulatrix. Abdominal segments 8 to 9 of male are disarticulated suggesting these segments were twisted and flexed during mating. Due to potential taphonomic effect, we cannot rule out that they might have taken side-by-side position, as in extant froghoppers. Genitalia of male and female, based on paratypes, show symmetric structures.

Conclusions/Significance: Our findings, consistent with those of extant froghoppers, indicate froghoppers' genitalic symmetry and mating position have remained static for over 165 million years.

Citation: Li S, Shih C, Wang C, Pang H, Ren D (2013) Forever Love: The Hitherto Earliest Record of Copulating Insects from the Middle Jurassic of China. PLoS ONE 8(11): e78188. doi:10.1371/journal.pone.0078188

Editor: Fabio S. Nascimento, Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Brazil

Received: May 16, 2013; **Accepted:** September 3, 2013; **Published:** November 6, 2013

Copyright: © 2013 Li et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This research is supported by the National Basic Research Program of China (973 Program) (grant 2012CB821906), the National Natural Science Foundation of China (grants 31172143, 31230065, 31272352 and 41272006), Project of Great Wall Scholar and KEY project of Beijing Municipal Commission of Education (grants KZ201310028033), and China Geological Survey (grant 1212011120115). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: rendong@mail.cnu.edu.cn

Introduction

Mating behaviors for extant insects have been studied and documented, for example, for froghoppers[1], scorpionflies[2] and planthoppers[3]. However, fossil records of unequivocal insect mating are fairly sparse. Boucot and Poinar[4] listed 33 instances of fossilized mating insects, such as fireflies, mosquitoes, plant-hoppers, leafhoppers, water striders, bees and ants, 27 of which are preserved in amber, others on compression fossils. The hitherto oldest example of copulation in fossil insects is a pair of chironomids (Diptera) discovered in Early Cretaceous amber from Lebanon [4,5].

Herein, we report a pair of well-preserved copulating froghoppers, *Anthoscytina perpetua* sp. nov., referable to the Procercopidae, from Jiulongshan Formation at the Daohugou Village in northeastern China. Procercopidae is an extinct family in the superfamily of froghoppers, Cercopoidea Leach, 1815. Froghoppers get their name because the adults hop around on plants and shrubs like tiny frogs. The nymphs of froghoppers are called spittlebugs because they cover themselves with foaming spittle, composed of tiny air bubbles trapped in secretions from their Malpighian tubules, which provides protection from predation,

parasitism and desiccation[6]. This discovery of the earliest record of copulating insects hitherto sheds light on the evolution of mating behavior in this group of insects.

Daohugou Village (N41°18'38", E119°13'20") is located in Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, northeastern China. The Jiulongshan Formation is considered to be of late Middle Jurassic age (Bathonian–Callovian boundary interval, 164–165 Ma), based on Ar-Ar and SHRIMP U-Pb dating results [7–10]. Currently, about 19 insect orders have been reported from this locality[11].

Materials and Methods

Materials

We examined more than 1200 specimens from the locality of Daohugou, Inner Mongolia, China. All fossil materials studied are housed in the fossil insect collection of the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). The extant *Cosmoscarta heros* (Fabricius) specimens are from the Insect Collection of Sun Yat-sen University, Guangzhou, China.

Methods

The specimens were examined by a LEICA MZ12.5 dissecting microscope and illustrated with the aid of a drawing tube attachment. Fossil photographs were taken by Nikon Digital Camera DXM1200C.

We follow the traditional terminologies of Cercopoidea [12] and Nel et al. [13]. Venation abbreviations used in the text and Figures: Cu, Cubitus; CuA, Cubitus Anterior; CuP, Cubitus Posterior; M, Media; MA, Media Anterior; MP, Media Posterior; Pcu, Postcubitus; R, Radius; RA, Radius Anterior; RP, Radius Posterior; ScA, Subcosta Anterior; ScP, Subcosta Posterior; m-cua, veinlet between MP and CuA, r-m; veinlet between R and M; ir, veinlet between RA and RP.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under the Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in Zoobank, the online registration system for the ICZN. The Zoobank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “[Http://zoobank.org](http://zoobank.org)”. The ISID for this publication is: urn:lsid:zoobank.org:pub:AF664AE6-A000-45B9-B9BC-6759CD0F63EE. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

Results

Systematic Palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cercopoidea Leach, 1815

Family Procercopidae Handlirsch, 1906

Genus *Anthoscytina* Hong, 1983

Type species. *Anthoscytina longa* Hong, 1983 [14] (Middle Jurassic of Haifanggou, Beipiao City, Liaoning, China).

Other included species. *A. reducta* (Becker-Migdisova, 1949) [15] (Lower Jurassic of Kyzyl-Kiya, Kyrgyzstan); *A. daica* Shcherbakov, 1988 [16] (Upper Jurassic–Lower Cretaceous, Glushkovo Formation of Chita, Siberia, Russia); *A. parallelica* Ren, Lu, et Guo, 1995 [17] (Middle Jurassic of Zhouyingzi, Hebei, China); and *A. aphthosa* Ren, Yin, et Dou, 1998 [18] (Lower Cretaceous, Yixian Formation of Beipiao, China); and *A. perpetua* Li, Shih et Ren, sp. nov.

Anthoscytina perpetua Li, Shih et Ren, sp. nov. (Figs. 1–4)
urn:lsid:zoobank.org:act:7DDCC368-3CBA-4815-9DA1-762AC77DE6DE

Diagnosis. Forewing slender, RA simple (vs. 2–4 branches in *A. reducta*, *A. daica* and *A. parallelica*); M branching into MA and MP at distal fifth of wing (vs. at 3/4 of wing in *A. longa*); CuA₁ twice as long as CuA₂ (vs. 1.5 times as long as CuA₂ in *A. longa*); crossvein ir at level of crossvein r-m, apical of the crossvein m-cua (vs. ir directly distal to other veinlets in *A. aphthosa*). Hind wing with crossvein r-m between MA and RP, slightly distal to bifurcation of M.

Description. Body 15–17 mm long including forewings in repose (Figs. 1A, 2A, E, 3); head narrower than pronotum, with declivous inflated clypeus; eyes ovoid, antenna with 4

segments visible (Fig. 2C); postclypeus swollen, about 0.9 mm long, and 0.3 mm wide, with distinct transverse grooves; rostrum very long, well extending beyond middle coxae, about 2.4 mm long. Pronotum greatly expanded, 2 times as long as vertex at mid length; mesonotum and scutellum about 1.43 mm long. Hind tibia with 1 lateral spine (Figs. 2D, 3B).

Forewing elongate, length 13.2–15.3 mm, width 3.5–4.3 mm, length/width ratio 3.2–4.3, based on holotype, allotype (Fig. 2B) and paratypes listed in the referred material (Fig. 3). ScA terminating at running to costal margin, ScP arched and fusing with R at basal 1/7 of wing length. R branching into RA and RP at basal 2/5 of wing length. RA simple, a sinuous crossvein ir between RA and RP at basal 8/9 of wing length. RP with 1–2 branches at basal 9/10 of wing length. Crossvein r-m meeting RP at the same point of crossvein ir. M branching into MA and MP at basal 5/6 of wing length. A crossvein m-cua between M and CuA₁. Crossvein ir at level of crossvein r-m, apical of crossvein m-cua. Stem Cu bifurcating into CuA and CuP at wing base. CuA curving anteriorly and meeting M, then bending posteriorly, CuA branching into CuA₁ and CuA₂ at basal 2/3 of wing length. Middle part of CuA₁ curving anteriorly. CuA₁ twice as long as CuA₂. CuP straight, reaching posterior margin at the same point as CuA₂, about 3/4 of wing length, forming a long clavus. Vein Pcu slightly curved, ending at about midpoint of wing. Fore wing membrane with granules. Posterior part of membrane infuscate.

Hind wing partly preserved in paratype CNU-HEM-NN2010003 (Figs. 1E, 3E). Vein M with 2 branches, crossvein r-m between MA and RP, slightly distal to bifurcation of M. CuA₁ connecting with M by a crossvein m-cua basal to bifurcation of M.

Male genitalia: Pygofer symmetrical in lateral view (clearly preserved), approximately 2 times as long as broad, posterior margin gently produced caudad in lateral view; accommodating anal tube at the apex (Figs. 1C, D, 4A–C). Segments 8 to 9 disarticulated from segment 7. Aedeagus elongate, tubular, when copulating inserted inside the bursa copulatrix of the female, shaft of aedeagus with external sclerotization from base to turning point, with one apical spine and phallosome pin-like (Figs. 1C, D). Gonostyli of paratypes CNU-HEM-NN2010014 and CNU-HEM-NN2010236 symmetrical, short and broad, fused with pygofer at base (Figs. 3A, D, 4A, C).

Female genitalia: Anal tube elongate, apical margin concave in lateral view. Valvulae not visible in copulating female (Figs. 1A, C, D, 2E–G). In the paratypes of female specimens (Figs. 4D–H), valvulae symmetrical almost rectangular, sclerotized plates in lateral view, but in dorsal view with some distinct hairs on the cauda (IX tergite) (Figs. 2F, G).

Etymology. From the Latin *perpet*, eternal love, in reference to this everlasting copulation.

Holotype. CNU-HEM-NN2012002 p/c (male) (Figs. 1, 2)

Referred material. Allotype: CNU-HEM-NN2012003p/c (female) (Figs. 1, 2); paratypes: males, CNU-HEM-NN2010014, CNU-HEM-NN201049, CNU-HEM-NN2010236, CNU-HEM-NN2010247; females, CNU-HEM-NN2010003, CNU-HEM-NN2010006, CNU-HEM-NN2010010, CNU-HEM-NN2010035 p/c, CNU-HEM-NN2010042, CNU-HEM-NN2010046, CNU-HEM-NN2010078, CNU-HEM-NN2010221, CNU-HEM-NN2010243. (Figs. 3, 4)

Locality and age. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China. Jiulongshan Formation, late Middle Jurassic, the Callovian–Bathonian boundary.

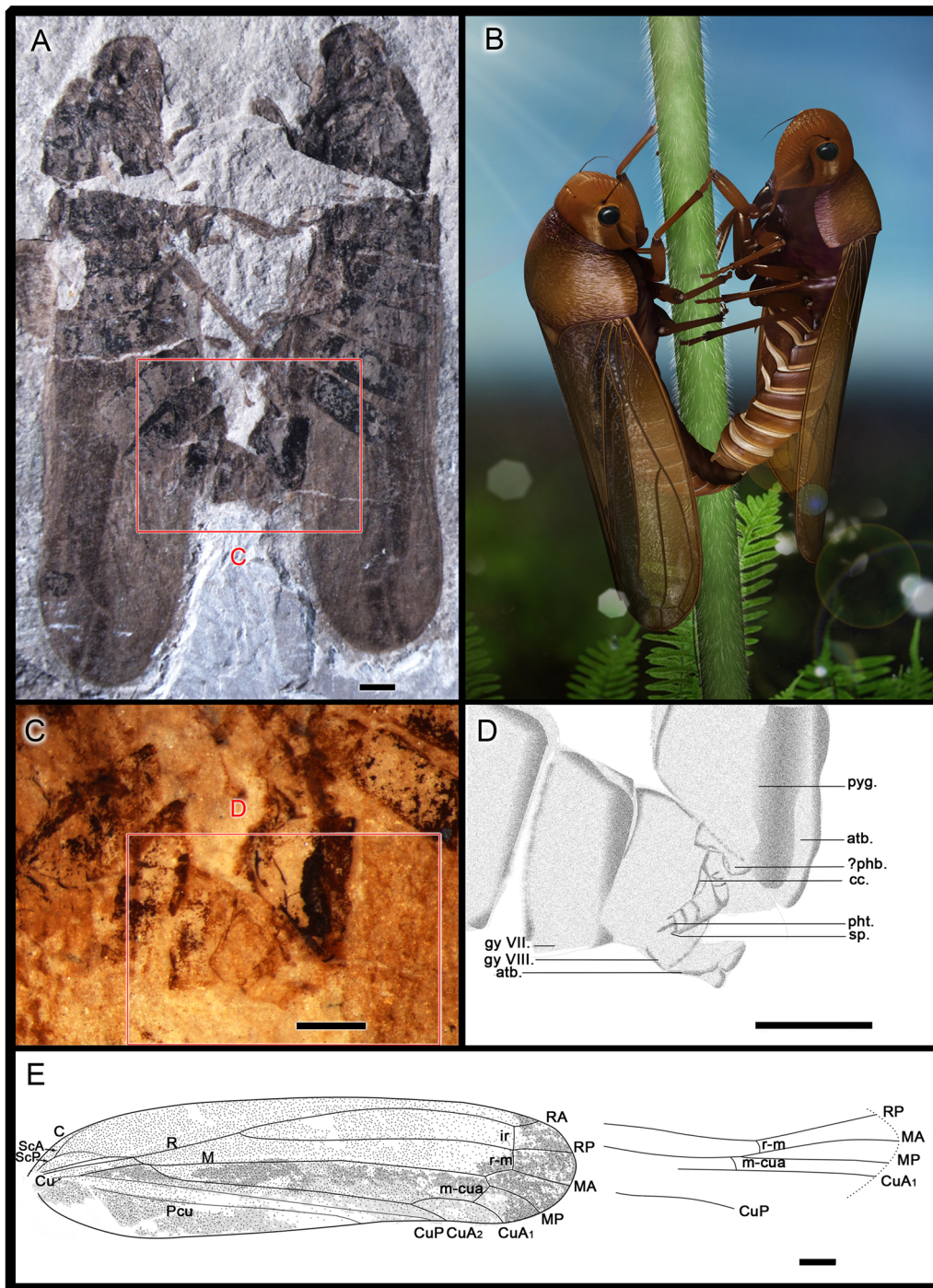


Figure 1. *Anthoscytina perpetua* Li, Shih et Ren, sp. nov. A–D, holotype. male, on the right (CNU-HEM-NN2012002 p) and allotype. female, on the left (CNU-HEM-NN2012003 p). **A**, photograph of habitus. **B**, 3-D ecological reconstruction. **C**, photograph of male and female genitalia in copulation, under alcohol. **D**, interpretative drawing of **C**. **E**, paratype. CNU-HEM-NN2010003, interpretative drawings of venations of the forewing and hind wing. pyg., pygofer; atb., anal tube; phb., phallobase; cc., corpus connective; pht., phallorema; sp., sclerotized process; gy., gonapophyses. Scale bars = 1 mm (**A**, **C**, **D**, **E**).
doi:10.1371/journal.pone.0078188.g001

Discussion

The superfamily of froghoppers Cercopoidea Leach, 1815 comprises approximately 3000 described species distributed in five extant families. Following Wang et al. [19], a tentative reconstruction of the phylogenetic relationships within the

Cercopoidea is proposed in Fig. 5. Although fossil records of Cercopoidea are lacking during the Late Cretaceous, Wang et al. have hypothesized that extant families, with the earliest fossil records from Paleocene, evolved from Procercopidae[19].

On the mating pair, the male's aedeagus is inserted inside the bursa copulatrix of the female. The shaft of aedeagus has external

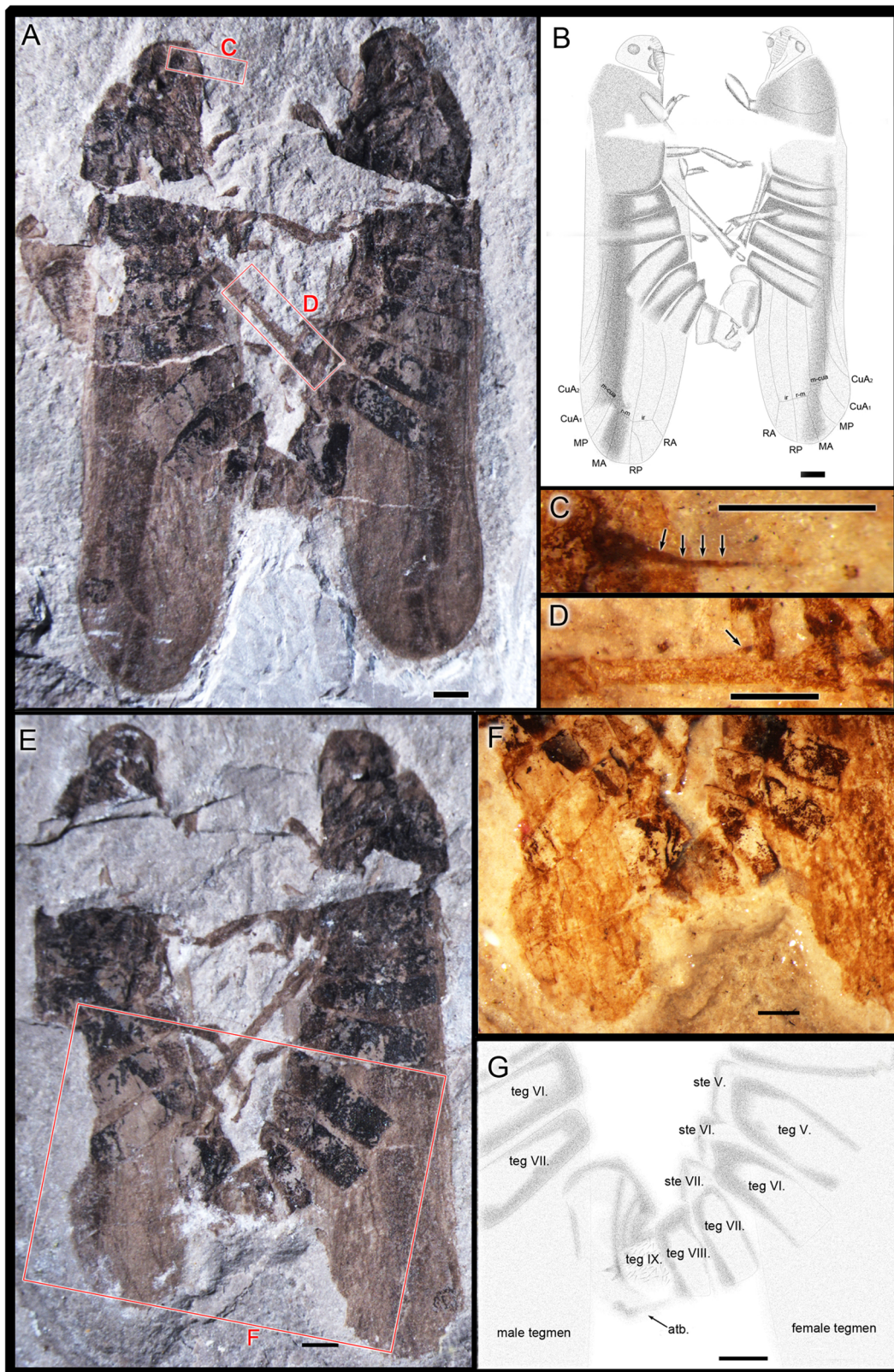


Figure 2. *Anthoscytina perpetua* Li, Shih et Ren, sp. nov. A–B, holotype. (CNU-HEM-NN2012002 p, male, on the right) and allotype (CNU-HEM-NN2012003 p, female, on the left). **A**, photograph of habitus. **B**, interpretative drawing. **C–D**, paratype. CNU-HEM-NN2010003 p. **C**, photograph of antenna, under alcohol. **D**, photograph of hindleg, under alcohol. **E–F**, holotype. (CNU-HEM-NN2012002 c, male, on the left) and allotype (CNU-HEM-NN2012003 c, female, on the right). **E**, photograph of habitus. **F**, photograph of male and female genitalia in copulation, under alcohol. **G**, interpretative drawing of male and female genitalia in copulation. teg., tergite; ste., sternite; atb., anal tube. Scale bars = 1 mm for all. doi:10.1371/journal.pone.0078188.g002

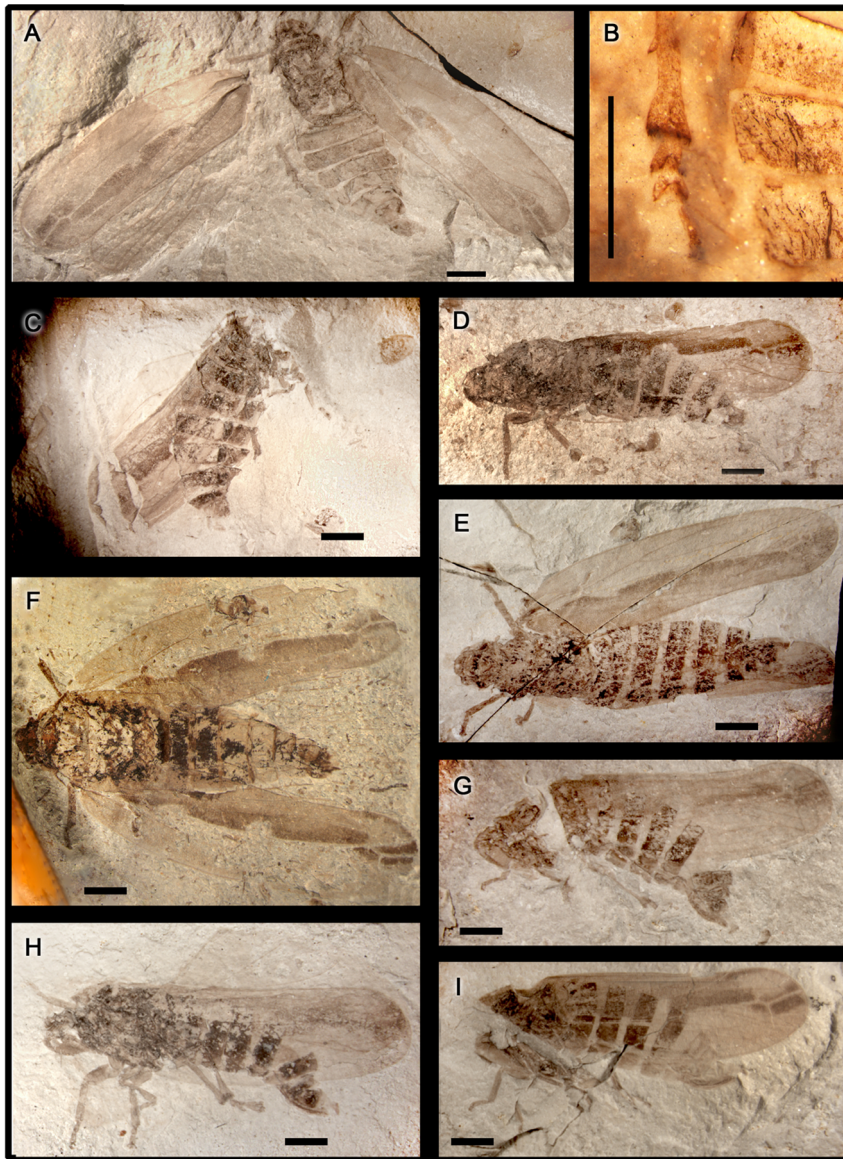


Figure 3. *Anthoscytina perpetua* Li, Shih et Ren, sp. nov. **A–I**, photographs of paratype specimens: **A**, CNU-HEM-NN2010014, male. **B**, hind leg with a lateral spine, under alcohol, CNU-HEM-NN2010014. **C**, CNU-HEM-NN2010247, male. **D**, CNU-HEM-NN2010236, male. **E**, CNU-HEM-NN2010003, female. **F**, CNU-HEM-NN2010006, female. **G**, CNU-HEM-NN2010035p, female. **H**, CNU-HEM-NN2010046p, female. **I**, CNU-HEM-NN2010042, female. Scale bars = 2 mm for all.

doi:10.1371/journal.pone.0078188.g003

sclerotization from base to turning point, with an apical spine and a pin-like phallotreme (Figs. 1C, D). Abdominal segments 8 and 9 of the male are disarticulated (Figs. 1A, C, 2E–G), suggesting that these segments might have been twisted and flexed during mating. The female’s valvulae are not visible on the fossils, but anal tube is distinctly elongate and apical margin concave. As shown by representative paratypes in Figs. 4A–G, male and female genitalia are symmetrical. The copulating pair exhibit belly-to-belly mating position as preserved. However, due to the potential taphonomic effect, we cannot rule out that they might have taken a side-by-side position when alive, as do extant froghopper taxa [1,6,20].

Mating positions and the evolution of asymmetric insect genitalia have been reviewed by Huber et al [21] and further

reported by Huber [22]. Huber et al. proposed that the female-above mating position is plesiomorphic for Neoptera. The next process involves a change of positions to male-above, belly-to-belly, or side-by-side, in which the male’s genitalia actually contact the female from below as in a female-above position. These positions presumably allow a better control for the males during mating. In most of these positions, both females and males have symmetric genitalia, except for the cases that the side of approach becomes fixed (“one-sided position”), genitalia become asymmetric. For end-to-end and belly-to-belly positions, insects usually rotate the abdomen or the genitalia by 180 degree [21]. Genital asymmetry is a recurring phenomenon in insect morphology and current data suggest that it has arisen multiple times independently in several neopteran orders [22].

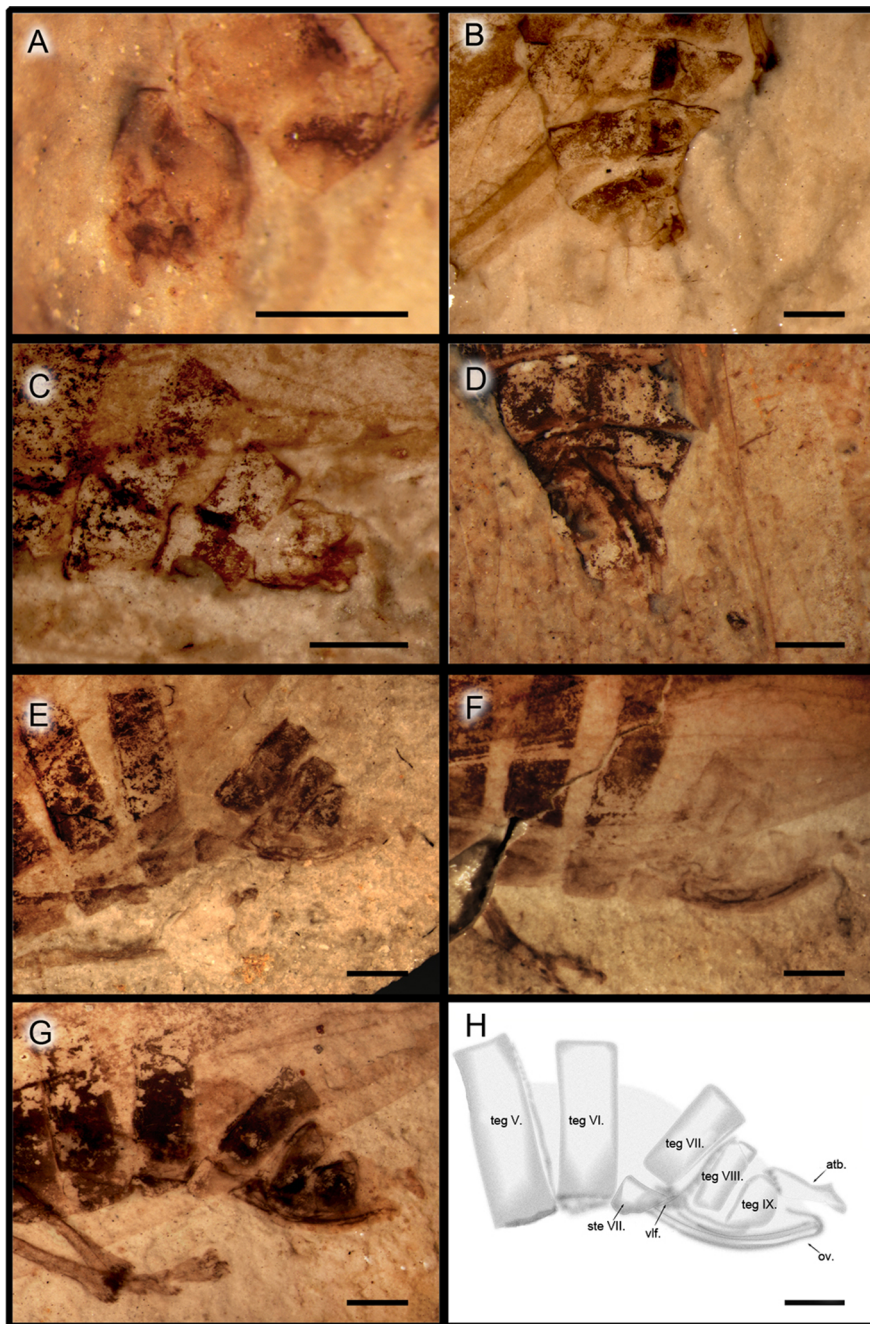


Figure 4. *Anthoscytina perpetua* Li, Shih et Ren, sp. nov. A-G photographs of paratype specimens: **A**, CNU-HEM-NN2010014, male genitalia, dorsal view. **B**, CNU-HEM-NN2010247c male genitalia, ventrolateral view. **C**, CNU-HEM-NN2010236, male genitalia, dorsolateral view. **D**, CNU-HEM-NN2010006p, female genitalia, dorsal view. **E**, CNU-HEM-NN2010035p, female genitalia, lateral view. **F**, CNU-HEM-NN2010042, female genitalia, lateral view. **G**, CNU-HEM-NN2010046p, female genitalia, lateral view. **H**, CNU-HEM-NN2010046p, interpretative drawing of female genitalia in G. teg., tergite; atb., anal tube; ste., sternite; vlf., valvifer; ov., valvula of ovipositor. Scale bars = 1 mm for all. doi:10.1371/journal.pone.0078188.g004

Extant froghoppers, both males and females, have symmetric genitalia [21,23–25]. The genitalia of a representative extant froghopper of *Cosmoscarta heros* (Fabricius) are shown in Figs. 6B–F. The male aedeagus curves upward dorsally (Figs. 6D, E), indicating that the male rotates and flexes its terminalia during side-by-side (or belly-to-belly) mating. In the CNU’s extensive collection of more than 200 thousand insect

fossils, a very high number of froghopper fossils, about 1200, suggest that froghoppers were abundant in their eco-systems. As observed in some 200 specimens with well-preserved structures of male and female genitalia, the genitalia of females and males were symmetrical in *A. perpetua* sp. nov., as shown by representative three male and four female paratypes in Figs. 3A–I, 4A–G. A single mating fossil from such a high

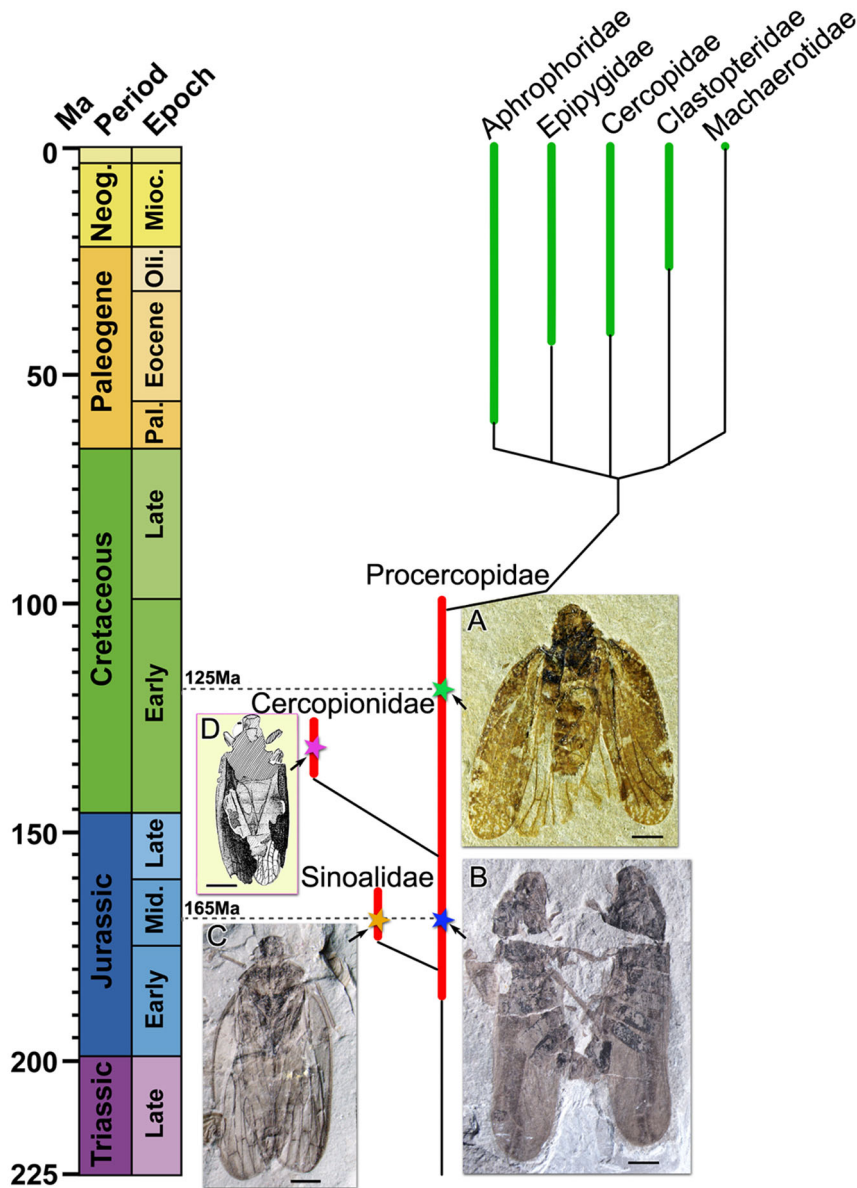


Figure 5. Tentative reconstruction of phylogenetic relationships within the Cercopoidea. Morphological data in extant and fossil taxa have been considered, as well as phylogenetic scheme of the Clypeata proposed by Wang et al. [19]. **A**, *Anthoscytina aphthosa* Ren, Yin and Dou, 1998 from the Early Cretaceous of Yixian Formation, China. **B**, *Anthoscytina perpetua* Li, Shih et Ren, sp. nov. from the Middle Jurassic of Jiulongshan Formation, China. **C**, *Jiania gracila* Wang et Szewo, 2012 from the Middle Jurassic of Jiulongshan Formation, China. **D**, *Cercopion reticulata* Hamilton, 1990 from the Early Cretaceous of Santana Formation, Brazil. Scale bars = 2 mm for all. doi:10.1371/journal.pone.0078188.g005

number of specimens clearly underscores the rarity of fossils preserving behaviors.

As already argued by Alexander [26] and supported by Huber et al. [21], all evidence suggests that a female-above position is plesiomorphic for Neoptera. It is reported that mating position of extant Cicadomorpha is side-by-side, but the tips of male and female abdomens are connected the same as in the female-above position [20, 21, 27, 28]. Twisting of the abdomen or genitalia is involved in the side-by-side and the belly-to-belly positions. The fossil pair of copulating *A. perpetua* sp. nov. show belly to belly (or side by side) position, which is consistent with the mating position of extant froghoppers (Fig. 6A). The fossil also shows that the male abdominal segments 8 to 9 disarticulated from segment 7, suggesting that during mating, the male's abdomen was twisted

and flexed after the 8th segment, as depicted in a 3-D reconstruction Fig. 1B.

Conclusions

In summary, our finding of the hitherto earliest record of copulating froghoppers, consistent with those of extant froghoppers, indicate froghoppers' genitalic symmetry and mating position have remained static for 165 million years. The evidence also confirms that symmetric genitalia are plesiomorphic for the taxon and by the Middle Jurassic, froghoppers have adopted the belly-to-belly (or side-by-side) position, which was proposed by Huber et al. [21] as the next step in the process of position changes from the basal female-above.

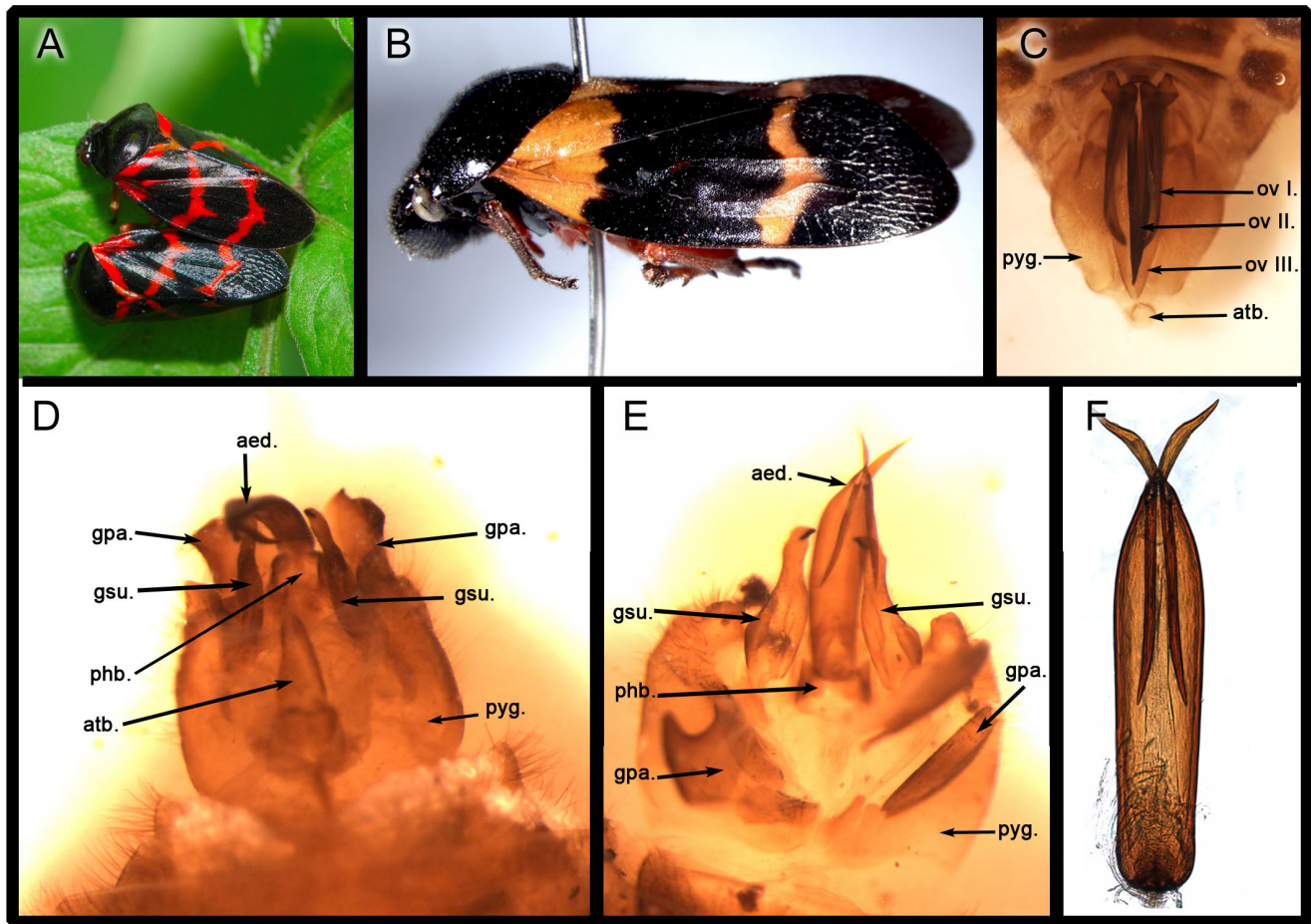


Figure 6. Mating position and genitalia of representative extant froghoppers. A, froghoppers in copulation, photo credit: Jason Shih. **B–F**, *Cosmoscarta heros* (Fabricius). **B**, lateral habitus. **C**, ovipositor ventral view. **D**, male genitalia, dorsal view. **E**, male genitalia, ventral view. **F**, aedeagus, dorsal view. pyg., pygofer; ov., valvula of ovipositor; atb., anal tube; aed., aedeagus; gsu., gonstylus; gpa., genital plates; phb., phallobase. doi:10.1371/journal.pone.0078188.g006

Acknowledgments

We are grateful to Dr. Stuart McKamey of the US Department of Agriculture for his valuable inputs and comments in improving this manuscript.

References

- Biedermann R (2002) Mating success in the spittlebug *Cercopis sanguinolenta* (Scopoli, 1763) (Homoptera, Cercopidae): the role of body size and mobility. *Journal of Ethology* 20: 13–18.
- Ma N, Zhong W, Hua B (2010) Genitalic morphology and copulatory mechanism of the scorpionfly *Panorpa jilinensis* (Mecoptera: Panorpidae). *Micron* 41: 931–938.
- Wang R, Liang A, Webb MD (2009) A new tropiduchid planthopper genus and species from China with descriptions of in copula genitalic structures (Hemiptera: Fulgoromorpha). *Systematic Entomology* 34: 434–442.
- Boucot AJ, Poinar Jr GO (2011) *Fossil behavior compendium*: CRC Press. 147–152.
- Boucot AJ, Babcock LE (1990) *Evolutionary paleobiology of behavior and coevolution*. 385.
- Cryan JR, Svenson GJ (2010) Family-level relationships of the spittlebugs and froghoppers (Hemiptera: Cicadomorpha: Cercopoidea). *Systematic Entomology* 35: 393–415.
- Chen W, Ji Q, Liu DY, Zhang Y, Song B, et al. (2004) Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China*: 1165–1169. (In Chinese, English summary)
- Yang W, Li SG (2004) The chronological framework of the Mesozoic volcanic rocks of Western Liaoning and its implications for the Mesozoic lithosphere thinning in Eastern China. In: *Abstracts of Symposium on National Petrology and Continental Geodynamics*, Haikou, China. 326. (In Chinese)
- Liu YQ, Liu YX, Ji SA, Yang ZQ (2006) U-Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chinese Science Bulletin* 51: 2634–2644.
- Ji Q, Liu YQ, Chen W, Ji SA, Lü JC, et al. (2005) On the geological age of Daohugou Biota. *Geol Rev* 51: 609–612. (In Chinese, English summary)
- Ren D, Shih CK (2010) *Silent Stories: Insect Fossil Treasures from Dinosaur Era of the Northeastern China*: Science Press. 13–16.
- Dworakowska I (1988) Main veins of the wings of Auchenorrhyncha (Insecta, Rhynchota: Hemelytrata). *Entomologische Abhandlungen Staatliches Museum für Tierkunde Dresden* 52: 63–108.
- Nel A, Prokop J, Nel P, Grandcolas P, Huang DY, et al. (2012) Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology* 273: 480–506.
- Hong YC (1983) *Middle Jurassic fossil insects in north China*: Beijing: Geol. Publ. House. 61–62. (In Chinese, English summary)
- Becker-Migdisova E (1949) *Mesozoic Homoptera of Central Asia*. *Trudy Paleontologicheskogo Instituta* 22: 1–20.
- Shcherbakov D (1988) New cicadas (Cicadina) from the later Mesozoic of Transbaikalia. *Paleontological Journal* 4: 52–63.
- Ren D, Lu LW, Guo ZG, Ji SA (1995) *Fauna and stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas*. Geological Publishing House, Beijing 8: 222. (In Chinese, English summary)

Author Contributions

Conceived and designed the experiments: DR. Performed the experiments: SL CW HP. Analyzed the data: SL CS HP. Wrote the paper: SL CS HP DR. Photographs and line drawings: SL CW.

18. Ren D, Yin JC, Dou WX (1998) New planthoppers and froghoppers from the Late Jurassic of northeast China. *Acta Zootaxonomica Sinica* 23: 281–288.
19. Wang B, Szwedo J, Zhang HC (2012) New Jurassic Cercopoidea from China and their evolutionary significance (Insecta: Hemiptera). *Palaeontology* 55: 1223–1243.
20. Hunt RE (1993) Role of vibrational signals in mating behavior of *Spissistilus festinus* (Homoptera: Membracidae). *Annals of the entomological Society of America* 86: 356–361.
21. Huber BA, Sinclair BJ, Schmitt M (2007) The evolution of asymmetric genitalia in spiders and insects. *Biological Reviews* 82: 647–698.
22. Huber BA (2010) Mating positions and the evolution of asymmetric insect genitalia. *Genetica* 138: 19–25.
23. Evans JW (1966) The leafhoppers and froghoppers of Australia and New Zealand (Homoptera: Cicadelloidea and Cercopoidea). Australian Museum Sydney.
24. Anufriev G, Emeljanov A (1988) Suborder Cicadinea (Auchenorrhyncha). *Opredelitel'nasekomykh Dal'nego Vostoka SSSR* 2: 12–495.
25. Hamilton KGA (2001) A new family of froghoppers from the American tropics (Hemiptera: Cercopoidea: Epipygidae). *Biodiversity* 2: 15–21.
26. Alexander RD (1964) The evolution of mating behaviour in arthropods; 78–94.
27. Weber H (1931) Homoptera. Homopterans. *Cicadina Cicadas*. *Biology of Animals in Germany*. 71–208. (In German)
28. Ansorge J (1996) Insects from the upper Lias of Pomerania (Vorpommern, northern Germany): CPress. (In German)