New shore bug (Hemiptera, Heteroptera, Saldidae) from the Early Cretaceous of China with phylogenetic analyses

Weiting Zhang†, Yunzhi Yao‡, Dong Ren§

College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

† urn:lsid:zoobank.org:author:4F8C0034-AB0C-4839-B6C1-E3C164BD4CA7
‡ urn:lsid:zoobank.org:author:6286B0B0-BB05-4EFE-9D80-4E4DAFDC770C
§ urn:lsid:zoobank.org:author:D507ABBD-6BA6-43C8-A1D5-377409BD3049

Corresponding author: Yunzhi Yao (yaoyz100@gmail.com)

Academic editor: D. Shcherbakov | Received 18 May 2011 | Accepted 4 July 2011 | Published 24 September 2011

urn:lsid:zoobank.org:pub:5EBFAD3B-6F27-4324-A8AE-1A48FBBD0ECE

Citation: Zhang W, Yao Y, Ren D (2011) New shore bug (Hemiptera, Heteroptera, Saldidae) from the Early Cretaceous of China with phylogenetic analyses. In: Shcherbakov DE, Engel MS, Sharkey MJ (Eds) Advances in the Systematics of Fossil and Modern Insects: Honouring Alexandr Rasnitsyn. ZooKeys 130: 185–198. doi: 10.3897/zookeys.130.1563

Abstract
A new genus with a new species of Saldidae, Brevrimatus pulchalifer gen. et sp. n., is described and illustrated. The fossil specimen was found from the Early Cretaceous Yixian Formation of Duolun County, Inner Mongolia, China. Phylogenetic analyses within Saldidae were performed, and the results indicate B. pulchalifer gen. et sp. n. should be assigned to the subfamily Chiloxanthinae.

Keywords
Saldidae, fossil, phylogeny, Early Cretaceous, China

Introduction
The Saldidae is a small family of insects belonging to Heteroptera. About 335 extant species have been described in this cosmopolitan family (Schuh and Polhemus 2009). Most saldids are littoral, inhabiting lake shores, beaches and stream banks and they
are predaceous, feeding on small insects and decaying animal materials (Brooks and Kelton 1967).

Cobben (1959) proposed a classification of Saldidae, and divided Saldidae into three subfamilies: Aepophilinae, Chiloxanthinae and Saldinae. Schuh and Polhemus (1980) later considered the Aepophilinae to be of family rank based on their cladistic and phenetic analysis of the infraorder Leptopodomorpha. At present, Saldidae is divided into two subfamilies, Chiloxanthinae and Saldinae (Schuh and Slater 1995). The phylogenetic analyses concerning relationships within Saldidae (Polhemus 1977, Schuh and Polhemus 2009) present valuable information and conclusions.

To date, 6 incontrovertible fossil species in 3 genera have been reported: *Oligosal-dina* Statz & Wagner, 1950 with three species, *O. rottensis*, *O. rhenana* and *O. aquatilis*, found from Upper Oligocene deposits in Germany; *Propentacora froeschneri* (= *Oreokora froeschneri*) found in Miocene Latah Formation in USA (Lewis 1969); *Salda exigua* Germar & Berendt, 1856 found in Eocene Baltic amber, and *Salda littoralis* found in Recent Late Glacial clay (Jessen 1923).

However, 2 genera assigned to this group previously are not saldids. *Leptosalda chiapensis* (Cobben, 1971) from Mexico amber was assigned to the subfamily Leptosaldinae within Saldidae first, but was later transferred to Leptopodidae by Schuh and Polhemus (1980). Popov (1973) erected a subfamily Saldoniinae in Saldidae with one genus *Saldonia* and one species *S. rasnitsyni* Popov, 1973, but later (Popov 1985) transferred the genus to Archegocimicidae, synonymized Saldoniinae under Archegocimicidae, and added two more species *S. sibirica* Popov, 1985 and *S. maculata* Popov, 1985, all from the Lower or Middle Jurassic of Transbaikalia, Russia. Archegocimicidae is similar to Saldidae, and it was assigned to the infraorder Leptopodomorpha (Popov 1985, 1989, Popov et al. 1994). Polhemus (1977) thought *Saldonia* probably should be classified into Dipsocoridae based on its wing venation. Cobben (1987) didn’t consider this genus as a member of the infraorder Leptopodomorpha, but he didn’t give detailed explanation.

In this paper, we described a new fossil shore bug, *Brevrimatus pulchalifer* gen. et sp. n., from the Yixian Formation, Baitugou, Nanyingpan Village, Sanbeigou Town, Duolun County, Inner Mongolia, China. Xing et al. (2005) and Zhang et al. (2004), respectively, based on isotope data and abundant statistical analysis of fossils data came to the consistent opinion that the age of the Yixian Formation is Early Cretaceous. And this opinion has been accepted widely (Swisher et al. 1999, Lu 2000, Zhou et al. 2003, Fürsich et al. 2007). Here we consider the age of the Yixian Formation as the Early Cretaceous (about 125 Ma).

**Material and methods**

Our fossil specimen is deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China. It was examined with the LEICA MZ 12.5 dissecting microscope. The specimens were examined without al-
cohol and under alcohol. Photos were taken by a Nikon Digital Camera DXM1200C. Line drawings were made with Photoshop graphic software. Morphological terminology used here follows that of Schuh and Slater (1995).

The body length was measured from the apex of head to the apex of abdomen; body width, at the maximal width of body; pronotum length, along the midline; pronotum width, across the broadest part at its posterior angles; wing length, from the basal to the apex of anterior margin; wing width, at the maximal width of the wing. All measurements are in millimeters (mm).

### Systematic paleontology

| Order          | Hemiptera Linnaeus, 1758 |
|----------------|--------------------------|
| Suborder       | Heteroptera Latreille, 1810 |
| Infraorder     | Leptopodomorpha Popov, 1971 |
| Family         | Saldidae Amyot & Serville, 1843 |
| Subfamily      | Chiloxanthinae Cobben, 1959 |

**Brevrimatus gen. n.**

urn:lsid:zoobank.org:act:B57D1B53-16FE-421A-BCA6-8F3141142A84

http://species-id.net/wiki/Brevrimatus

**Type species.** Brevrimatus pulchalifer sp. n.

**Diagnosis.** Body ovate, moderate in size, macropterous. Head relatively short. Rostrum reaching to the base of hind coxae. Corium with large pale spots, medial fracture short, costal fracture of hemelytra very long, hypocostal ridge and associated secondary hypocostal ridge present on hemelytra, membrane with five closed cells. Posterior margin of female sternum VII concave along the midline. Base of ovipositor exposed.

**Etymology.** The generic name is a combination of the Latin prefix “brev-” (short) and Latin word “rimatus” (fracture), which indicated the genus with short medial fracture. Gender masculine.

**Distribution.** China.

**Brevrimatus pulchalifer sp. n.**

urn:lsid:zoobank.org:act:80999FB3-E52E-459A-8A25-46CEAF6D947E

http://species-id.net/wiki/Brevrimatus_pulchalifer

Figs 1, 2

**Type material.** Holotype, ♀, CNU-HET-ND2010334 p/c (part and counterpart).

**Type locality and horizon.** Baitugou, Nanyingpan Village, Sanbeigou Town, Duolun County, Inner Mongolia, China, Yixian Formation. Early Cretaceous.
Diagnosis. Head relatively short. The last segment of antennae slightly swollen. Corium with three large pale spots, medial fracture short, costal fracture of hemelytra very long; membrane with five cells, apex of innermost cell of membrane extending past apex of outermost cell. Posterior margin of female sternum VII extremely concave along the midline.

Description. Body ovate, about 2.4 times as long as wide.

Head 1.4 times as wide as long. Antennae slender, 4-segmented, first segment shortest, second segment longest, 1.47 times as long as the third segment, fourth segment slightly shorter than third segment. Eyes reniform, moderately protrusive, located at the posterolateral angles of the head. Ocelli round, raised slightly, ocelli separated by 1.3 times the width of an ocellus, ocelli closer to each other than to margins of eyes. Rostrum reaching to the hind coxae. Length of head subequal to the length of pronotum on midline.

Pronotum transverse, 3.2 times as wide as long. Anterior and posterior margins of pronotum concave, lateral margins straight, anterior and posterior angles feebly rounded. Scutellum distinctly longer than pronotum on midline, triangular, 1.3 times as wide as long. Tarsal formula: 3–3–3. Fore tibiae about 2.0 times as long as corresponding tarsi, fore tarsomere I shortest, tarsomeres II and III almost subequal in length; mid femora 1.3 times as long as tibiae, tibiae 2.3 times as long as tarsi, tarsomere I shortest, tarsomere II slightly longer than tarsomere III; hind tibiae long, almost 1.5 times as long as hind femora, and 2.3 times as long as tarsi. Fore wing macropterous, 0.6 times as long as body; corium and membrane clearly delimited; corium with embolium;

Figure 1. Brevrimatus pulchalifer gen. et sp. n., line drawings. Holotype, CNU-HET-ND2010334 p/c. A dorsal view B ventral view. Scale bar=2 mm.
medial fracture short, 0.3 times as long as fore wing; costal fracture of hemelytra very long, reaching to the middle of the corium; venation of corium weakly indicated; membrane large, with five closed cells, cells reduced gradually from the inner to the outer. Claval commissure shorter than scutellum length at median line. Hemelytra with only slight modification for mating, the embolar region slightly thickened.

Anterior margin of female sternum VII curve; posterior margin of female sternum VII extremely concave along the midline. Base of ovipositor exposed ventrally.

**Measurements (in mm).** Body length 8.00, width 3.18. Head length 0.84, width 1.24. Antennal measurements I–IV: 0.56, 1.30, 0.92, 0.85. Interocular space of ocelli 0.12. Interocular space of eyes 0.84. Pronotum length 0.78, width 2.52. Scutellum length 1.43, width 1.78. Length fore leg: tibia 1.22, tarsomeres I–III: 0.13, 0.23, 0.23; length mid leg: femur 1.91, tibia 1.57, tarsomeres I–III: 0.18, 0.27, 0.23; length hind leg: femur 2.14, tibia 3.15, tarsomeres I–III: 0.22, 0.69, 0.52. Hemelytron length 5.14, width 1.73.

**Etymology.** The species name is a combination of the Latin prefix “pulch-” (beautiful) and Latin word “alifer” (wing), meaning beautiful wing. Gender masculine.

**Discussion**

The Leptopodomorpha consists of four extant families (Saldidae, Aepophilidae, Leptopodidae, Omaniidae) and three extinct families (Archeogocimicidae, Mesolygaeidae, Palaeoleptidae). Popov et al. (1994) synonymized Mesolygaeidae to Archegocimicidae.

---

**Figure 2. Brevrimatus pulchalifer** gen. et sp. n., photographs. Holotype, CNU-HET-ND2010334 p/c. A part and B counterpart. Scale bar=2 mm.
But herein we think it is better to treat them as two separated families, because of their distinct difference in forewing. We compared our fossil with all the families in Leptopodomorpha. The body sizes of aepophilids and omaniids are less than 2mm, while the new species reaches to 8mm, much larger than aepophilids and omaniids. In Leptopodidae, rostrum at most reaches to the base of the fore coxae, while rostrum of the new species reaches to the base of the hind coxae. Besides that, anterior margin of pronotum is distinctly narrower than head in Leptopodidae, but anterior margin of pronotum of the new species is almost as wide as head. All the extinct families from Mesozoic are contemporaneous with the new fossil species. But they are different in some characters. Nine cells present in Archegocimicidae (Handlirsch 1906–1908), and the arrangement of the cells (Popov 1985) are totally different from the new species. Fore wing of Palaeoleptidae is nearly completely coriaceous except for small membrane (Poinar and Buckley 2009), which is different from the new species with large membrane. And wing venation consists of eight cells in Palaeoleptidae, which differs from the new species with five cells. The pronotum of Mesolygaeidae is divided into two parts (Zhang 1991), but in the new species no groove present on pronotum. The structure of end of abdomen is also different between the new species and mesolygaeids. So we classified our fossil into Saldidae based on the combined characters: compound eyes large and reniform, rostrum long, posterior margin of pronotum indented, hemelytra with costal fracture, medial fracture well developed and membrane with five cells.

**Phylogenetic analysis**

The new genus possesses some typical Chiloxanthinae characters, such as costal fracture very long, female sternum VII truncate with mesal concavity and base of ovipositor exposed. On the other hand, it possesses short medial fracture as Saldinae. Therefore, we carried out phylogenetic analyses to determine the placement of our new genus.

For the phylogenetic analyses, we selected three extant genera from Chiloxanthinae, five extant genera from Saldinae, our new fossil genus, and an unambiguous fossil species *Oligosaldina aquatilis* as in-group. Following previous studies (Polhemus 1977, Schuh and Polhemus 1980, 2009), we chose representatives from the family Leptopodidae (*Patapius thaiensis* Cobben, 1968) and Aepophilidae (*Aepophilus bonnairei* Siguenor, 1879) as our out-group taxa. The 12 taxa that we chose for these phylogenetic analyses are listed in Table 1. We carried out phylogenetic analyses respectively with the fossil taxon *O. aquatilis* and without this fossil taxon.

Most character information of the extent taxa was extracted from literatures (Cobben 1959, 1969, Drake 1961, Cobben and Polhemus 1966, Polhemus and Evans 1969, Polhemus 1972, 1977, 1991, Cobben 1980, King and Fordy 1984, Chen and Zheng 1987, Vinokurov 2005, 2009, Schuh and Polhemus 2009). The descriptions for the 17 characters and character states are listed in the Appendix. All characters were treated as unordered and weighted equally. A maximum parsimony analysis of the character matrix (Table 2) edited by NDE (Nexus Data Editor) version 0.5.0 (Page 2001), was
performing on NONA (Goloboff 1998), using the Multiple TBR+TBR search strategy, options set to hold 10000 trees, 1000 replications with 100 starting tree replication. The unambiguous characters were mapped by WinClada (Nixon 2000).

**Phylogenetic results**

For the phylogenetic analyses excluding fossil species *O. aquatilis*, we got two equally most parsimonious trees (Fig. 3A, B), with the following main characteristics: tree

**Table 1.** Taxa included in the phylogenetic analysis (*: only included when we carried out phylogenetic analysis with *Oligosaldina aquatilis*)

| Family       | Subfamily | Tribe       | Species                                      |
|--------------|-----------|-------------|----------------------------------------------|
| out-group    | Leptopodidae |            | *Patapius thaiensis* Cobben, 1968          |
|              | Aepophilidae |            | *Aepophilus bonnairei* Signoret, 1879       |
| in-group     | Saldidae   | Saldini     | *Salda lugubris* (Say, 1832)                |
|              |            |             | *Teloleuca altaica* Vinokurov, 2009         |
|              |            | Saldoidini  | *Saldula montana* Cobben, 1966              |
|              |            |             | *Calacanthia sichuanicus* Chen & Zheng, 1987|
|              |            | Saldunculini| *Salduncula swezeyi* (Usinger, 1946)         |

**Table 2.** Matrix of 17 characters and the 12 taxa used for phylogenetic analysis (*: only included when we carried out phylogenetic analysis with *Oligosaldina aquatilis*)

| Taxon/Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|----------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Patapius thaiensis* | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Aepophilus bonnairei* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *Salda lugubris* | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Teloleuca altaica* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Saldula montana* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Calacanthia sichuanicus* | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Salduncula swezeyi* | 2 | ? | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Chiloxanthus pilosus* | 2 | ? | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Pentacora ligata* | 1 | 2 | 0 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Paralosalda innova* | 2 | 2 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Brevrimatus pulchalifer* gen. et sp. n. | 2 | 2 | ? | 1 | 0 | 1 | 2 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? |
| *Oligosaldina aquatilis* | ? | 2 | 0 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

The table contains a matrix of 17 characters and 12 taxa used for phylogenetic analysis. The characters are mapped to the taxa, and the presence or absence of the character is indicated by a 1 or 0, respectively. The table includes the following taxa: *Patapius thaiensis*, *Aepophilus bonnairei*, *Salda lugubris*, *Teloleuca altaica*, *Saldula montana*, *Calacanthia sichuanicus*, *Salduncula swezeyi*, *Chiloxanthus pilosus*, *Pentacora ligata*, *Paralosalda innova*, *Brevrimatus pulchalifer* gen. et sp. n., and *Oligosaldina aquatilis*.
length = 28, consistency index (CI) = 82, retention index (RI) = 87. The strict consensus tree is shown in Figure 3C. Phylogenetic results indicate Saldidae is a monophyletic group, which is supported by four synapomorphies: posterior pronotal margin indented distinctly (Character 4:1); eversible glands present posterolaterally between sterna VI and VII (Character 9:1); eggs with aeropyles (Character 15:1); larval organ present (Character 16:1). Some synapomorphic characters, such as apicolateral sclerotized structures of penis present (Character 13:1) and filum gonopori coiled one to four times, like a watch-spring (Character 14:1) supported the monophyly of the subfamily Saldinae. Chiloxanthinae with our fossil species included is a monophyletic group, which is supported by four synapomorphies: five well defined cells in membrane (Character 6:1); medial fracture long (Character 8:2); female subgenital plate truncate with concavity along the midline (Character 11:2); base of ovipositor exposed (Character 12:1). In summary, phylogenetic results suggest our new fossil genus is in Chiloxanthinae and short medial fracture was treated as a reversal character.

For the phylogenetic analysis including fossil species *O. aquatilis*, we got one most parsimonious tree (Fig. 3D), tree length = 28, CI = 82, RI = 88. The monophyly of Saldidae is supported by four synapomorphies (Character 4:1, 9:1, 15:1 and 16:1) as the results above. In this phylogenetic result, besides Character 13:1 and Character

Figure 3. Phylogeny of Saldidae. A, B the most parsimonious trees based on 11 taxa and 17 characters. C the strict consensus tree based on 11 taxa and 17 characters D the most parsimonious trees based on 12 taxa and 17 characters. (●) non-homoplasious; (○) homoplasious.
14:1, short costal fracture of hemelytra (Character 7:1) supports the monophyly of the subfamily Saldinae. Five well defined cells in membrane (Character 6:1) indicate that our new genus should be in the branch of Chiloxanthinae. Therefore, both of the phylogenetic analyses suggest our fossil species should be classified into Chiloxanthinae.

Comparison with Chiloxanthinae indicates the new fossil species differs from other extant chiloxanthines in its short medial fracture. Besides this character, the boundary between corium and membrane is not clear in *Enalosalda*, which is different from *Brevirimatus* gen. n. with clear boundary. *Paralosalda* has four membrane cells, which is different from *Brevirimatus* gen. n. with five cells. Embolar modification of female is well developed in *Pentacora*, but in *Brevirimatus* gen. n. the embolar region is slightly thickened. Sublateral cell of membrane is shortest in *Chiloxanthus*, which differs from *Brevirimatus* gen. n. with the lateralmost cell is shortest. We further compared it with other fossil Saldidae. The arrangement of the cells of *Brevirimatus* gen. n. is similar to that of *Oligosaldina*, but lateralmost cell of membrane is distinctly smaller than that of *Oligosaldina*. Long costal fracture is present on *Brevirimatus* gen. n., but absent on *Oligosaldina*. A deep furrow is present in the pronotum of *Oligosaldina*, while it is absent in our new genus. *Propentacora* contains five closed cells in the wing membrane, but the corial vein of *Propentacora* appears to continue between the third and fourth membrane cells, which is different from the new genus. *Brevirimatus* gen. n. is distinctly different from *Salda*, which can be seen in phylogenetic result. Comparing our fossils with the fossil species *Salda exigua*, we can separate them in the following characters: *Brevirimatus* gen. n. possesses five closed cells in the forewing membrane, while *S. exigua* has three closed cells and rostrum of *Brevirimatus* gen. n. reaches to the base of hind coxae, while in *S. exigua*, rostrum just reaches to the fore coxae. Therefore *Brevirimatus* gen. n. is different from all other fossil genera. In geological age, all of the previously recorded fossil saldids are from Cenozoic. So far, *Brevirimatus* gen. n. found in the Lower Cretaceous sedimentary stratum is the oldest saldid.

Acknowledgements

We make a grateful acknowledgement for Alexandr Rasnitsyn’s contribution to paleoentomology. We sincerely thank Dr. Nikolai N. Vinokurov (Institute for Biological Problems of Cryolithozone, Siberian Branch, Russian Academy of Sciences), Ganyang Zhang (Entomology Department, University of California) and Hui Liu (Entomological Laboratory, Faculty of Agriculture, Kyushu University) for sending papers to us. Thanks to Dr. Shih ChungKun (College of Life Science, Capital Normal University) for his improvement of our manuscript, and to two anonymous reviewers and the editor for constructive comments. This research was supported by grants from the National Natural Science Foundation of China (No. 40872022, 31071964, 30800095), Nature Science Foundation of Beijing (No. 5082002), Beijing Talented Scholar Program Foundation (No. 20081D050160092) and the PHR20090509 Project of Beijing Municipal Commission of Education.
References

Brooks AR, Kelton LA (1967) Aquatic and semiaquatic Heteroptera of Alberta, Saskatchewan, and Manitoba (Hemiptera). Memoirs of the Entomological Society of Canada 51: 1–92. doi: 10.4039/entm9951fv

Chen PP, Zheng LY (1987) A new species and some new records of shore bug from China (Hemiptera: Saldidae). Acta Zootaxonomica Sinica 12 (4): 393–397.

Cobben RH (1959) Notes on the classification of Saldidae with the description of a new species from Spain. Zoologische Mededelingen 36 (22): 303–316.

Cobben RH (1969) A new species of Leptopodidae from Thailand (Hemiptera-Heteroptera). Pacific Insects 10 (3–4): 529–533.

Cobben RH (1971) A fossil shore bug from the Tertiary amber of Chiapas Mexico (Heteroptera, Saldidae). University of California Publications in Entomology 63: 49–56.

Cobben RH (1980) On some species of Pentacora, with the description of a new species from Australia (Heteroptera, Saldidae). Zoologische Mededelingen 55: 115–126.

Cobben RH (1987) New African Leptopodomorpha (Heteroptera: Saldidae, Omaniidae, Leptopodidae), with an annotated checklist of Saldidae from Africa. I. New species of the genus Saldula (Saldidae). Revue de Zoologie Africaine 100: 399–421.

Cobben RH, Polhemus JT (1966) African Saldidae in the Snow Entomological Museum (Hemiptera). Journal of the Kansas Entomological Society 39 (3): 382–396

Drake CJ (1961) Insects of Micronesia Hemiptera Saldidae. Insects of Micronesia 7 (6): 287–305.

Fürsich TF, Sha JG, Jiang BY, Pan YH (2007) High resolution palaeoecological and taphonomic analysis of Early Cretaceous lake biota, western Liaoning (NE-China). Palaeogeography, Palaeoclimatology, Palaeoecology 253: 434–457.

Goloboff PA (1998) NONA, Version 2.0. Program and Documentation. American Museum of Natural History, New York.

Handlirsch A (1906–1908) Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Wilhelm Engelmann, Leipzig, 1430 pp.

Jessen K (1923) A submerged peat-bog in the harbour of Rungsted and changes of sea-level in the sound in the late-glacial period. Dansk Geologisk Forening 6 (14): 1–18.

King PE, Fordy MR (1984) Observations on Aepophilus bonnairei (Signoret) (Saldidae: Heteroptera) an intertidal insect of rocky shores. Zoological Journal of the Linnean Society 80: 231–238. doi: 10.1111/j.1096-3642.1984.tb01975.x

Lewis SE (1969) Fossil Insects of the Latah Formation (Miocene) of Eastern Washington and Northern Idaho. Northwest Science 41 (3): 99–115.

Lu CH (2000) The age and disintegration of Yixian Formation. Liaoning geology 17 (1): 51–56 [in Chinese with English abstract]

Nixon KC (2000) WinClada, Version 0.9.99.60. Program.

Page RDM (2001) Nexus Data Editor for Windows, version 0.5.0.

Poinar G, Buckley R (2009) Palaeoleptus burmanicus n. gen., n. sp., an Early Cretaceous shore bug (Hemiptera: Palaeoleptidae n. fam.) in Burmese amber. Cretaceous Research 30: 1000–1004. doi: 10.1016/j.cretres.2009.03.003
Polhemus JT (1972) Notes concerning Mexican Saldidae including the description of two new species (Hemiptera). Great Basin Naturalist 32: 137–153
Polhemus JT (1977) The biology and systematics of the Saldidae of Mexico and middle America. PhD thesis, Boulder: University of Colorado.
Polhemus JT (1991) Three new species of Salduncula Brown from the Malay Archipelago, with the key to the known species (Heteroptera: Saldidae). Raffles Bulletin of Zoology 39 (1): 153–160.
Polhemus JT, Evans WG (1969) A new genus of intertidal Saldidae from the Eastern Tropical Pacific with notes on its biology (Hemiptera). Pacific Insects 11 (3–4): 571–578.
Polhemus JT, Chapman HC (1979) Family Saldidae/Shore Bugs. In: Menke AS (Ed) The semi-aquatic and aquatic Hemiptera of California (Heteroptera: Hemiptera). Bulletin of the California Insect Survey 21. University of California Press, Berkeley, California, 16–33.
Popov YuA (1971) The historical development of Hemiptera infraorder Nepomorpha (Heteroptera). Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR 129: 1–230 [in Russian]
Popov YuA (1973) The first discovery of the hemipteran family Saldidae (Heteroptera) in the Mesozoic of Siberia. Doklady Akademii Nauk SSSR 209: 703–705 [in Russian]
Popov YuA (1985) Jurassic bugs and Coleorrhyncha of southern Siberia and western Mongolia. In: Rasnitsyn AP (Ed), Jurassic insects of Siberia and Mongolia, Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR 211: 28–47 [in Russian]
Popov YuA (1989) Some aspects of systematic of Leptopodoidea. Acta Biologica Silesiana 13 (30): 63–68.
Popov YuA, Dolling WR, Whalley PES (1994) British Upper Triassic and Lower Jurassic Heteroptera and Coleorrhyncha (Insecta: Hemiptera). Genus 5 (4): 307–347.
Statz G., Wagner E (1950) Geocorisae (Landwanzen) aus den Oberoligocäner Ablagerungen von Rott. Palaeontographica (abt. A) 98: 97–136.
Schuh RT, Slater JA (1995) True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History. Cornell University Press, Ithaca, New York, 336 pp.
Schuh RT, Polhemus JT (1980) Analysis of taxonomic congruence among morphological, ecological, and biogeographic data sets for the Leptopodomorpha (Hemiptera). Systematic Zoology 29 (1): 1–26. doi: 10.2307/2412623
Schuh RT, Polhemus JT (2009) Revision and analysis of Pseudosaldula Cobben (Insecta: Hemiptera: Saldidae): a group with a classic Andean distribution. Bulletin of the American Museum of Natural History 323: 1–102. doi: 10.1206/323.1
Swisher CC, Wang YQ, Wang XL, Xu X, Wang Y (1999) Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400: 58–61. doi: 10.1038/21872
Vinokurov NN (2005) A review of the shore-bug genus Chiloxanthus Reut. (Heteroptera, Saldidae) in the fauna of Russia and adjacent countries. Entomological Review 85 (2): 118–130.
Vinokurov NN (2009) A review of species of the genus Téloleuca (Heteroptera, Saldidae) in the fauna of Russia and adjacent territories. Entomological Review 89 (9): 1092–1103. doi: 10.1134/S0013873809090115
Xing DH, Sun CL, Sun YW, Zhang LD, Peng YD, Chen SW (2005) New knowledge on Yixian Formation. Acta geoscientica sinica 26 (1): 25–30 [in Chinese with English abstract]
Appendix

List of characters and character states used in phylogenetic analysis

**Distance between ocelli:** equal to width of ocellus (0); less than width of ocellus (1); more than width of ocellus (2). [We treat this character inapplicable in Aepophilidae that doesn’t have ocellus.]

**Rostrum reaches to:** fore coxae (0); middle coxae (1); hind coxae (2). [Rostrum of Leptopodidae is very short, reaching to fore coxae at most. Rostrum of Saldidae is relatively long, reaching to middle coxae or hind coxae. Rostrum of *B. pulchalifer* sp. n. and *O. aquatilis* reaches to hind coxae. Long rostrum is the primitive character (Popov 1971).]

**Postclypeus:** absent (0); present (1). [Postclypeus present in *S. lugubris, T. altaica, S. montana, C. sichuanicus*. This character cannot be identified in our fossil specimen. In other groups postclypeus is absent.]

**Posterior pronotal margin:** non-indented (0); indented distinctly (1). [Posterior pronotal margin nearly straight in Aepophilidae, so we treat this character in Aepophilidae as non-indented. Posterior pronotal margin of Saldidae is demonstrated briefly in Figure 4A showing the indented posterior pronotal margin and Leptopodidae in Figure 4B showing the non-indented posterior pronotal margin. This character is considered as the synapomorphy for Saldidae.]

**Forewing:** macroptery or submacroptery (0); semibrachypterus moderately or strongly (1); brachyptery (2). [Wing polymorphism occurs in Saldidae. Wing pattern can be separated into five categories based on the reduction of the membrane of fore wing (Cobben 1980). The membrane of Aepophilidae completely reduced, so it is brachyptery. *C. sichuanicus* with the semibrachypterous forewing.]

**Cells:** Four well defined cells in membrane (0); five well defined cells in membrane (1). [In Aepophilidae, forewing greatly reduced, in form of pads without membrane, so we treated this character inapplicable in this family. Usually, Saldinae have four cells and Chiloxanthinae have five cells, but the distinction in hemelytral cells between the Saldinae and Chiloxanthinae is not constant (Polhemus and Chapman 1979). The fossil species, *B. pulchalifer* sp. n. and *O. aquatilis* have five cells.]

**Costal fracture of hemelytra:** absent (0); present, short (1); present, very long (2). [Costal fracture length is a stable character within subfamily. Saldinae usually
possesses short costal fracture and Chiloxanthinae usually possesses long costal fracture. Polhemus (1977) consider the long costal fracture in Chiloxanthinae to be a derived character providing a synapomorphy for the group. Costal fracture is absent in *P. thaiensis*, *A. bonneirei* and *O. aquatilis*. Costal fracture in our fossil species, *B. pulchalifer* sp. n., is long.

**Medial fracture:** absent (0); present, short (1); present, very long (2). [Long medial fracture reaches at least to level of posterior end of claval suture, and short medial fracture not reaches anteriorly more than half the distance from costal fracture to posterior end of claval suture (Schuh and Slater 1995). Medial fracture is absent in *A. bonneirei*. In *P. thaiensis*, *B. pulchalifer* sp. n. and members of Saldinae, medial fracture is short. *C. pilosus*, *P. ligata* and *P. innova* have long medial fracture.]

**Eversible glands:** absent (0); present posterolaterally between sterna VI and VII (1). [Saldidae has paired abdominal eversible glands with their openings locating between sterna VI and VII. Eversible glands is absent in Leptopodidae and Aepophilidae. This structure is unknown in *B. pulchalifer* sp. n. and *O. aquatilis*. Eversible glands is considered to be a apomorphic character in Saldidae (Polhemus 1977).]

**Sclerite adjacent to eversible gland:** present (0); absent (1). [This sclerite is present in Saldinae, but absent in Chiloxanthinae.]

**Female subgenital plate:** truncate without concavity along the midline (0); triangular, posterior margin of produced caudad along the midline (1); truncate with concave along the midline (2). [In *A. bonneirei* female subgenital plate just like a normal abdominal sternite. Subgenital plate is truncate with concave along the midline is found in the members of Chiloxanthinae and *B. pulchalifer* sp. n. as Figure 4C. Subgenital plate is triangular in Saldinae as Figure 4D.]

**Base of ovipositor:** hidden by posterior medial prolongation of subgenital plate (0); exposed (1). [The base of ovipositor is hidden in Aepophilidae and Saldinae, but
exposed in Chiloxanthinae and *B. pulchalifer* sp. n. The exposed ovipositor is considered a derived character (Polhemus 1977])

**Apicolateral sclerotized structures of penis:** absent (0), present (1). [This structure absent in Aepophilidae and Chiloxanthinae, but present in Saldinae.]

**Filum gonopori:** base of penis-filum not curled or at most forming one closed ring (0); filum gonopori coiled one to four times, like a watch-spring (1). [Base of penis-filum not curled in Leptopodidae and Aepophilidae, and coiled less than one ring in Chiloxanthinae. In Saldinae, base of penis-filum like a watch-spring.]

**Eggs:** without aeropyles (0); with aeropyles (1). [Eggs with aeropyles is regarded as a synapomorphy for Saldidae.]

**Larval organ:** absent (0); present (1). [Larval organ is absent in Leptopodidae and Aepophilidae, *S. lugubris* and *T. altaica*. Larval organ present in *S. montana*, *C. sichuanicus*, *C. pilosus*, *P. ligata*, *P. innova*. Larval organ present in most members of Saldidae. The absence condition in Saldini is presumed to be the secondary lost (Polhemus 1977).]

**Larval organ:** larval organ lateral, adjacent to spiracle (0); larval organ located medially, some distance from the spiracle (1). [In Saldinae, larval organ when present adjacent to spiracle, while the later condition occurred in Chiloxanthinae.]