

A new longhorn beetle (Coleoptera: Cerambycidae) from the Early Cretaceous Jehol Biota of Western Liaoning in China



Yali Yu^{a,d}, Adam Ślipiński^b, Chris Reid^c, ChungKun Shih^a, Hong Pang^d, Dong Ren^{a,*}

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

^bCSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia

^cEntomology, Australian Museum, 6 College Street, Sydney, NSW 2010, Australia

^dState Key Laboratory of Biocontrol, Key Laboratory of Biodiversity Dynamics and Conservation of Guangdong Higher Education Institute, Sun Yat-Sen University, Guangzhou 510275, China

ARTICLE INFO

Article history:

Received 25 December 2013

Accepted in revised form 27 February 2014

Available online 24 March 2014

Keywords:

Chrysomeloidea

Mesozoic

Fossil

New genus

New species

Early Cretaceous

Yixian Formation

ABSTRACT

Pre-Cenozoic representatives of the coleopteran family Cerambycidae are practically little known. The discovery of a well-preserved fossil of longhorn beetle in the Lower Cretaceous (about 122 Ma) lacustrine deposits of the Yixian Formation in Western Liaoning, China, is the second record of Mesozoic Cerambycidae. We assign this specimen to a new genus and species, *Sinopraecipius bilobatus* gen. et sp. nov., but are unable to place it with confidence in any existing subfamily of Cerambycidae due to the insufficient morphological evidence available from the specimen.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

The longhorn beetles (family Cerambycidae) with over 30,000 described species, constitute one of the largest groups of beetles, distributed worldwide excluding Antarctica (Ślipiński and Escalona, 2013). Virtually all Cerambycidae feed on living or dead plant tissues and play a significant role in all terrestrial environments where plants are found. Cerambycid larvae often utilize damaged or dead trees for their development, and through feeding on dead wood form an important element of the saproxylic fauna.

The classical division of Cerambycidae family into 8 subfamilies, Disteniinae, Parandrinae, Spondylinae, Prioninae, Aseminae, Lepritinae, Cerambycinae and Lamiinae, was proposed by Linsley (1961) for the North American fauna and subsequently has been generally accepted. However, this classification scheme has been questioned by comparative studies of larval (Švácha and Danilevsky, 1987) and adult characters (Napp, 1994; Reid, 1995,

2000). Švácha et al. (1997) split Cerambycidae into Oxypeltidae, Vesperidae (including Anoplodermatinae), Disteniidae and Cerambycidae based mostly on larval characters. Molecular studies have not been undertaken of the major cerambycid lineages, but give some support to the reclassification of Švácha et al. (Gómez-Zurita et al., 2008).

These studies strongly suggest that Chrysomeloidea is a well-defined clade but the “cerambycid” and “chrysomelid” lineages are weakly defined with Megalopodidae and Orsodacnidae occupying somewhat transitional positions, Megalopodidae tending to belong with the cerambycid lineage and Orsodacnidae tending to belong with the chrysomelid lineage (Kuschel and May, 1990; Reid, 1995; Švácha et al., 1997; Gómez-Zurita et al., 2008).

Until very recently, the earliest Mesozoic fossils attributed to Chrysomeloidea are four genera of Protoscelidinae (Chrysomelidae) described by Medvedev (1968) from the Jurassic deposits of Karatau and *Tarsomegamerus* Zhang (2005) from Daohugou biota placed in the same subfamily. In particular *Cerambyomima* Medvedev has often been compared to Cerambycidae because of very long antennae and emarginate eyes (Grimaldi and Engel, 2005; Kuschel and May, 1990; Zhang, 2005). Legalov (2013) revised Medvedev's taxa and recognized only single genus (*Protoscelis* Medvedev) in Protoscelidinae, and moved them to Anthribidae

* Corresponding author.

E-mail addresses: yuyali2934@126.com (Y. Yu), Adam.Slipinski@csiro.au (A. Ślipiński), Chris.Reid@austmus.gov.au (C. Reid), chungkun.shih@gmail.com (C. Shih), Lshpang@mail.sysu.edu.cn (H. Pang), rendong@mail.cnu.edu.cn (D. Ren).

(Curculionoidea). *Tarsomegamerus* was subsequently removed from Chrysomelidae and placed in a new family Lasiosynidae by Kirejtshuk et al. (2010a).

Several 19th Century descriptions of putative Cerambycidae from Mesozoic deposits in United Kingdom and Germany listed in Scudder (1891) were mostly based on isolated elytra and could not be reliably identified. Very few species from that period were critically revised and included in other beetle families, e.g., *Cerambycites* Deichmüller (=Ditomoptera Germar) was placed in Coptoclavidae by Ponomarenko (1985).

Reliably identified fossils of Cerambycidae have been recorded from the Palaeogene, mainly from Baltic (Eocene) (Hagedorn, 1906; Abdullah, 1967; Vitali, 2005, 2006) and Dominican amber (Miocene) (Martins and Galileo, 1999; Vitali, 2007), and from Eocene–Oligocene shales from Florissant (Grimaldi and Engel, 2005). The Upper Jurassic *Parandrexis* Martynov (1926) described in Cerambycidae, Prioninae belongs in Cucujoidea and is currently classified in Parandrexidae (Kirejtshuk, 1994).

A very recent discovery of a specimen of Cerambycidae from the Lower Cretaceous Yixian Formation (Wang et al., 2013) placed in the subfamily Prioninae constitutes the earliest known longhorn beetle so far. The chrysomeloid beetle from the same geological formation described herein is tentatively placed in Cerambycidae but its taxonomic position is not well resolved as discussed below.

2. Material and methods

The study is based on a single specimen found near a small village (Dawangzhangzi) in western Liaoning in China (Fig. 1). Dawangzhangzi is one of the most important sites of the Mesozoic Jehol Biota and is renowned for yielding rich and exquisitely preserved fauna including abundant vertebrates (e.g., primitive birds and feathered dinosaurs), gymnosperm and angiosperm plants (Sun et al., 1998, 2002; Leng and Friis, 2006), and well-preserved insects (Liu et al., 2006; Ren et al., 2010). The fossil deposits at Dawangzhangzi have been considered as the Yixian Formation,

based on both biostratigraphic and radiometric geochronologies and dated to the Early Cretaceous (Zhou et al., 2003; Kirejtshuk et al., 2010b). Some important work has established and suggested that this formation most likely to be restricted to 129.7–122.1 Ma: Barremian–early Aptian (Yang et al., 2007; Chang et al., 2009; Zhou and Wang, 2010). Recently, the palaeoclimate of this area is interpreted as cool temperate with mean air temperatures of 10 ± 4 °C (Amiot et al., 2011). The fossil-bearing horizon is considered to be the Dawangzhangzi Bed (~122 Ma, Aptian) (Dong et al., 2013) of the Yixian Formation (Fig. 2).

The specimen was examined using a Leica MZ12.5 dissecting microscope and illustrated with the aid of a drawing tube attached to the microscope. Digital photographs taken with Nikon Digital camera and the line drawings were enhanced in Adobe Photoshop CS graphic software. Beetle morphology follows Lawrence et al. (2011) and the taxonomic system used here follows that of Ślipiński et al. (2011).

3. Systematic paleontology

Order Coleoptera Linnaeus, 1758

Superfamily Chrysomeloidea Latreille, 1802

Family Cerambycidae Latreille, 1802

Subfamily unknown

Genus *Sinopraecipius* gen. nov

Type species. *Sinopraecipius bilobatus* sp. nov.

Etymology. From Latinized Greek *Sino-* (referring to China) combined with *Praecipius* (meaning that the specimen is special). Gender masculine.

Horizon and locality. Lower Cretaceous, Yixian Formation (Dawangzhangzi Bed); Dawangzhangzi Village, Songzhangzi Township, Lingyuan City, Liaoning, China.

Diagnosis. Body elongate, somewhat oval. Antennae filiform with very short scape and relatively long pedicel. Pronotum transverse with margins finely crenulate, Procoxal cavities with hypomeral

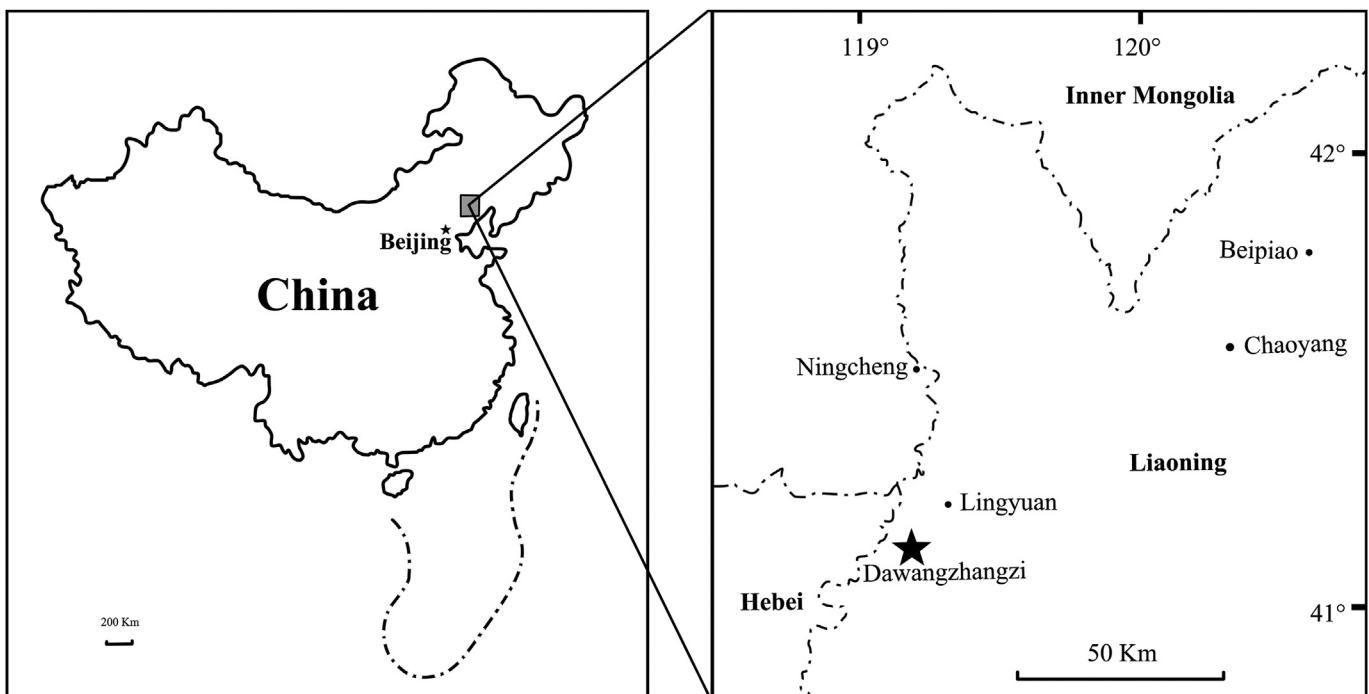


Fig. 1. Map showing the fossil locality.

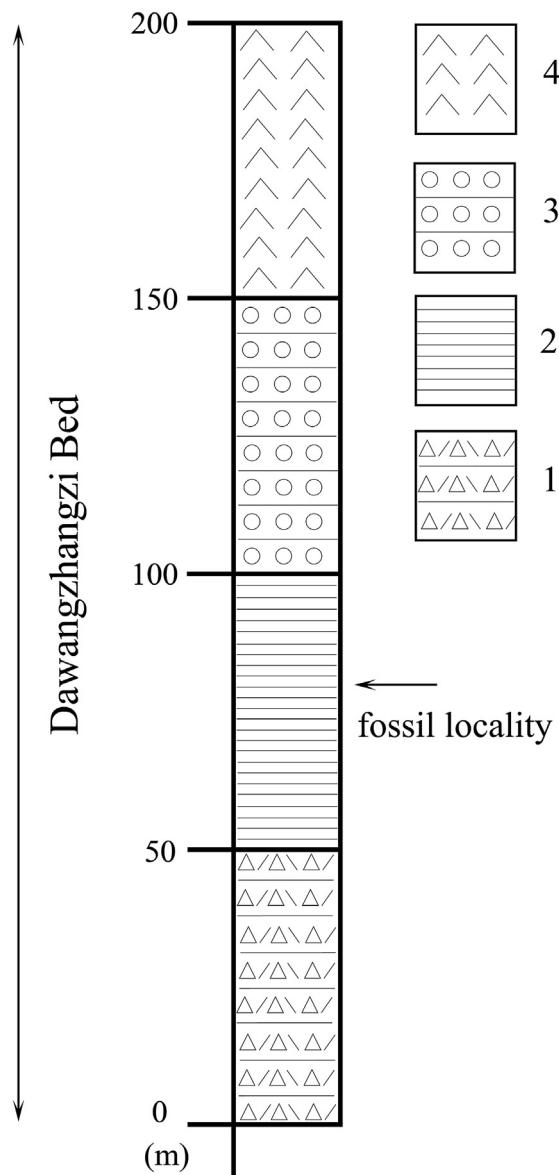


Fig. 2. Stratigraphic column measured at the Yixian Formation near Dawangzhangzi Village, Songzhangzi Township, Lingyuan City (Modified from Ji et al., 2004). 1. Gray-white tuffaceous breccia, tuffaceous sandstone/siltstone (50.0 m); 2. Yellow-brown tuffaceous siltstone, shale (50.0 m); 3. Gray-white tuffaceous sandy conglomerate (50.0 m); 4. Gray-green trachyte porphyry.

lobes posteriorly closing or almost closing the cavities. Mesocoxae apparently rather narrowly separated. Elytra with very pointed apices and dense punctures. Protibia and mesotibia with paired apical spurs. Tarsi pseudotetramerous.

Comparison. The new genus differs from known recent Cerambycidae in having very short scape and relatively long pedicel combined with very pointed apices of elytra. *Sinopraecipius* is distinguished from the Mesozoic *Cretoprionus* Wang et al. in having: (1) strongly emarginated eyes; (2) simple, not serrate antennae; (3) pronotum transverse, 1.5 times wider than long, without coarse punctures; the lateral pronotal margins crenulate but without dentate lateral carina; anterior edge relatively weakly concave anteriorly; (4) scutellum relatively triangular; (5) elytra with very pointed apices, widest at anterior fourth, slightly wider

than pronotum; (6) protibia and mesotibia with two longitudinal rows of short setae and paired apical spurs; tarsomere 5 longer than 1.

Sinopraecipius bilobatus sp. nov.
(Figs. 3–5)

Etymology. Specific epithet is derived from the Latin adjective *bilobatus* and refers to the bilobed tarsomeres.

Type material. Holotype. Sex unknown. A well-preserved body with elytra, antenna and three pairs of legs. No. CNU-COL-LB201101 P/C, part and counterpart (Fig. 3A, B), deposited in the Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University in Beijing, China.

Diagnosis. As for the genus by monotypy.

Description. Body elongate, somewhat oval with filiform antennae reaching apices of elytra; elytra completely covering pygidium. Dorsal vestiture and sculpture not clearly visible.

Head trapezoidal, slightly narrower than pronotum; frontoclypeal suture not visible (Fig. 4A, D). Eyes large, emarginate but only partially visible. Possible sinusoidal groove anterior to eye and posterior to antennal base. Mandible about 0.5 times as long as head, robust and falciform, blunt; apex simple with subapical tooth. Maxillae and labium not visible. Antenna 11-segmented, inserted near the base of mandibles, as long as body length; scape stout, about as long as broad, pedicel slightly shorter and distinctly narrower than scape, antennomere 3 elongate, three times as long wide, antennomere 11 distinctly shorter than 10. Apices of antennomeres unspined (Figs. 4E and 5A, B).

Pronotum transverse, 1.5 times wider than long, broadest at middle with sides arcuate between angles, margins finely crenulate without distinct lateral carina. Anterior angles weakly acute and weakly projecting anteriorly, posterior angles right angled and not projecting. Disc without apparent impressions or tubercles, with row of pits along right margin; anterior edge concave anteriorly, posterior edge slightly convex not margined (Figs. 3A, 4A and 5A, B).

Prosternum in front of coxae distinctly longer than coxal longitudinal diameter with transverse groove or fold between notosternal sutures; procoxal cavities transversely oval with hypomeral lobes posteriorly closing or almost closing the cavities; prosternal process rather broad and parallel-sided but partially damaged. Procoxae transverse, globular or weakly conical, the right coxa is damaged and displaced posteriorly but the left coxa is in place; protrochantin not visible (Figs. 3A, 4A and 5A, B).

Scutellum triangular or trapezoidal, posterior edge arcuate. Mesoventrite long, flat and concave anteromedially. Mesocoxae weakly projecting and ovate-triangular, apparently rather narrowly separated; mesocoxal cavities partly closed laterally by mesanepisternum and mesepimeron; mesotrochantin small but exposed; metanepisternum narrow, attenuate posteriorly, with curved groove in anterior corner (Figs. 3A, 4A and 5A, B).

Elytra about 1.6 times as long as combined width, widest at anterior fourth, then distinctly narrowing and acute apically; surfaces without puncture-rows but with small, rounded and dense punctures; epipleuron narrow at base, absent or not visible in apical half (Figs. 3A, 4B, C and 5B). Wings apparently absent.

Legs long with robust femora; tibiae straight, distinctly widened apically; protibia and mesotibia with two longitudinal rows of short setae and paired apical spurs. Tarsi pseudotetramerous with tarsomeres 2 and 3 broad, flattened and probably bilobed, tarsomere 5 longer than 1, terminated by pair of slightly divergent, simple claws; empodium not visible (Figs. 3A, C, D, E and 5A).



Fig. 3. *Sinopraecipius bilobatus* gen. et sp. nov., photographs of holotype. A, part CNU-COL-LB2011101P; B, counterpart CNU-COL-LL2011101C; C, left front and mid tarsi; D, right front and mid tarsi; E, right hind tarsus. (A–B, Scale bars = 5 mm. C–D, Scale bars = 1 mm).

Abdomen with five ventrites; ventrite 5 apparently longest and rounded apically. Pygidium (tergite VII) visible between elytral apices (Figs. 3 and 5A).

Measurements (in mm). Body length 20.35, width across elytra 8.65; head length 2.87, head width 3.43; pronotum length 4.30, pronotum maximum width 6.53, width at anterior angles 4.76, width at posterior angles 4.82; elytra length 13.78, elytra width 8.55; abdomen length 7.60, ventrite 1 length 1.86, ventrite 2 length 1.21, lengths of ventrites 3 and 4 1.15, ventrite 5 length 1.65; pygidium length, 0.96, pygidium width at base, 0.54. Relative lengths of antennomeres: 0.8: 0.5: 1.5: 1.2: 1.4: 1.3: 1.4: 1.3: 1.3: 1.3: 0.9.

4. Discussion

The short antennal pedicel in otherwise long antennae, the lack of notopleural sutures, two prominent tibial spurs and

pseudotetramerous tarsi suggest the placement of *Sinopraecipius* gen. sp. in the Chrysomeloidea, but the laterally inserted antennae and overall body features of *Sinopraecipius* are also reminiscent of *Cerambyomima* placed as a junior synonym of *Protoscelis* in Anthribidae (Curculionoidea) by Legalov (2013). Based on description and illustrations in Legalov (2013) *Sinopraecipius* differs from *Protoscelis* in having antenna without the club, pronotum without transverse line along base, procoxal cavities externally open or very narrowly closed, elytra confusedly punctured without striae and tibia without apical spurs.

The following features in combination suggest placement in Cerambycidae *sensu lato*, rather than Orsodacnidae or Chrysomelidae.

Body size. A body length of 20 mm is rarely attained by Chrysomelidae (Hispinae, Sagrinae) but it is common in Cerambycidae. However *Janbechynea* Monrós in Orsodacnidae reaches 17 mm.



Fig. 4. *Sinopraecipius bilobatus* gen. et sp. nov., photographs of holotype. A, head, prothorax and pterothorax, ventral; B, pterothorax and abdomen, ventral; C, apical part of elytron, dorsal; D, head dorsal; E, antenna. Scale bars = 1 mm (A–B, photographs with alcohol on the specimen).

Antennae. The antennae are massive in *Sinopraecipius*, as long as body, with broad oval scape, short pedicel and elongate flagellomeres, slightly expanded at apices. This antennal structure is typical of Cerambycidae, although the scape is usually more elongate, but is rare in Chrysomelidae (similar but proportionately

smaller in Sagrinae) and absent in Orsodacnidae (antennomeres short, of similar size) and Megalopodidae.

Antennal insertions. The identification of the sockets is problematical in this specimen. It appears that the antennae are inserted laterally, with the eye apparently curved dorso-ventrally around

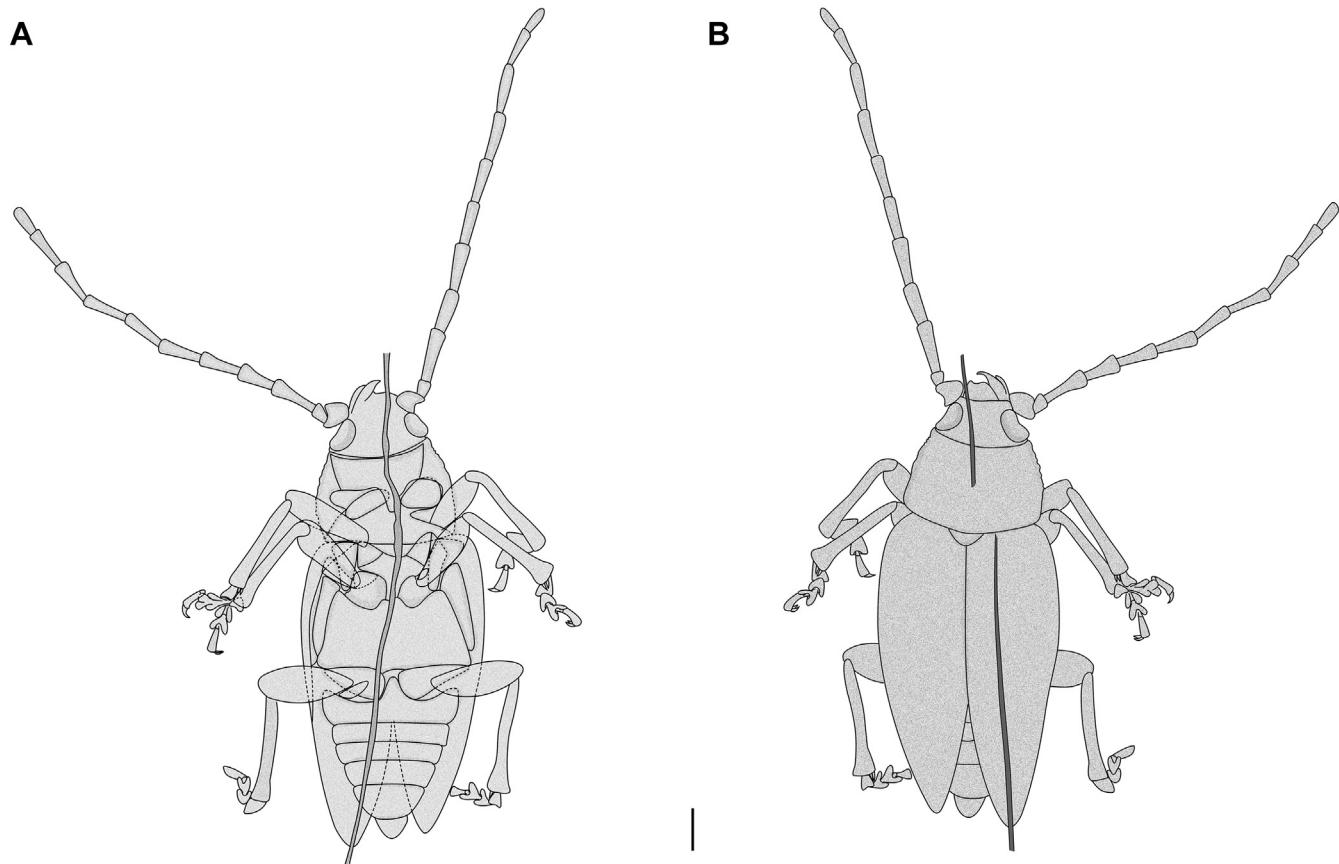


Fig. 5. *Sinopraecipius bilobatus* gen. et sp. nov., reconstruction illustrations of holotype. A, ventral view; B, dorsal view. Scale bars = 2 mm.

the socket. Laterally placed antennae inserted next to the eyes are found in some Cerambycidae, Orsodacnidae and Chrysomelidae.

Frontal grooves. The interocular surface of the head on this fossil appears to be dorsal, lacking deep facial grooves present in chrysomelid subfamilies Sagrinae and Criocerinae. *Frontoclypeal suture* is apparently lacking in the fossil, as in many Cerambycidae or Chrysomelidae but not in Orsodacnidae or Megalopodidae.

Mandible. The mandible is robust in the fossil but it is damaged and difficult to interpret. It appears to have single apical tooth that agrees with most of the basal lineages of Chrysomeloidea, excluding some Lamiinae.

Pronotum. The pronotum is broad, almost as broad as elytra at base. The size ratio is typical of many prionine and cerambycine Cerambycidae and several Chrysomelidae, but not Sagrinae. The anterior angles of the pronotum are slightly projecting, as in some Prioninae, Aulacoscelidinae, and several Chrysomelidae but not Sagrinae. The sides of the pronotum are crenulate without obvious lateral carina, as in many Cerambycidae or Megalopodidae but not in Orsodacnidae and only in a few Chrysomelidae (Cryptocephalinae, Eumolpinae, Galerucinae).

Prosternum. The venter of the prothorax shows a long prosternal anterior field with a transverse fold or groove. This feature is lacking in Orsodacnidae, Megalopodidae and Chrysomelidae but common in Cerambycidae. The hypomeral lobe (postcoxal process) is narrow but closes or almost closes the procoxal cavity. The prosternal process appears to be narrow, parallel-sided and not expanded at apex. The protrochantin appears to be concealed. This combination of features enclosing the coxal cavity and a concealed trochantin is common in Cerambycidae but much less common in Chrysomelidae, Megalopodidae or Orsodacnidae which have always visible trochantins.

Mesothorax. The anterior field of the mesoventrite is long and flat (without transverse folds or rests), similar to Orsodacnidae and Cerambycidae, but rarely found in Megalopodidae or Chrysomelidae.

Elytra. The elytra are unusual, with apparently tapering apices with the surface densely micropunctate and lacking obvious striae, including a sutural stria. The epipleuron is narrow at base and may be absent at the apex. *Janbechynea* in Aulacoscelidinae is similar, but with the upper margin of the epipleuron entirely absent. Less similar are Palophaginae (but the elytra only feebly taper), or some flightless Cerambycidae, Lamiinae (such as *Xyloteles* White), but with distinct sutural stria, sparse punctures and rounded elytral apex. Recently eclosed beetles may also have pointed elytra, but they are foreshortened and wrinkled. The wings appear to be absent. No trace of wing venation is present in this fossil. Lack of wings may partly explain the curiously shaped elytra, although the metaventrite is elongate as in normally winged beetles.

Legs. The femora are moderately robust and of equal size on all legs. In Palophaginae and many Cerambycidae the femora are much more gracile, while other megalopodids and Sagrinae have enlarged hind femora. The tibiae are simple, straight-edged with only a slight apical expansion. Two prominent spurs are present at the tibial apex, each one about half as long as apical tibial width. The tibiae appear to lack the elongate ridges of Aulacoscelidines and some Chrysomelidae. Paired tibial spurs are rare in Chrysomelidae (absent from most subfamilies) but common in Orsodacnidae, Megalopodidae and Cerambycidae. The tarsi are relatively short and broad, especially the second tarsomere. Similar tarsi are found in Megalopodines (but not Palophaginae), some Orsodacnidae, some Cerambycidae (especially Prioninae and flightless species), and widely in Chrysomelidae.

In sum, we believe that the evidence weakly supports placement in Cerambycidae rather than Megalopodidae, Orsodacnidae or Chrysomelidae.

Based on available characters that can be observed on the fossil we can diagnose *Sinopraecipius* as not belonging to Disteniidae or Lamiinae because of simple tibiae devoid of apparent antennal cleaners or to Spondylidinae and Parandrinae because of long filiform antennae and broadly expanded tarsomeres. We cannot exclude it from the other subfamilies of Cerambycidae but a relatively long prosternum and mesoventrite, weak crenulations of the lateral pronotal margins and the shape of metanepisterna are similar to many members of Cerambycinae.

5. Conclusions

The record of Mesozoic Cerambycidae *Sinopraecipius bilobatus* gen. et sp. nov., has many characters same as the extant cerambycids to support its placement in Cerambycidae. But, *S. bilobatus* has several different characters when compared with extant cerambycids. Furthermore, placement of *S. bilobatus* with confidence in a specific subfamily of Cerambycidae is not possible, because of insufficient evidence preserved and different characters of various subfamilies present in *S. bilobatus*. This unique combination of characters provides us a glimpse of the early evolutionary history of cerambycids. However, due to very limited fossil record of Cerambycidae, it is not feasible to conduct phylogenetic analyses. It is proposed that some of these characters might have been plesiomorphies for ancient Cerambycidae, while changes and development of these and other characters might have resulted in taxa of various subfamilies in the subsequent evolutionary process.

Acknowledgments

We are grateful to Chenyang Cai, Hermes Escalona, John F. Lawrence, Rolf Oberprieler and Petr Švácha, for valuable discussions and opinions on the systematic position of this fossil. John F. Lawrence has revised a draft of the paper providing many important suggestions. We are also greatly thankful to Alexander G. Kirejtshuk and Huali Chang for their early work.

This research was supported by the National Basic Research Program of China (973 Program) (Grant 2012CB821906), the National Natural Science Foundation of China (Grants 31230065, 41272006), Great Wall Scholar and KEY project of Beijing Municipal Commission of Education (Grant KZ201310028033), Program for Changjiang Scholars and Innovative Research Team in University (IRT13081) to D. Ren and the Australian Biological Resources Study (ABRS) to A. Slipinski and C. Reid.

References

- Abdullah, M., 1967. *Palaeoasemum crowsoni* and *P. duffyi*, a new genus and two new species of the Asemini (Coleoptera, Cerambycidae) from the Baltic amber. Deutsche entomologische Zeitschrift (new series) 14 (1–2), 147–151.
- Amiot, R., Wang, X., Zhou, Z.H., Wang, X.L., Buffetaut, E., Lécuverd, C., Ding, Z.L., Fluteau, F., Hibino, T., Nusuhashi, N., Mo, J.Y., Suteethorn, V., Wang, Y.Q., Xu, X., Zhang, F.S., 2011. Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climate. Proceedings of the National Academy of Sciences of the United States of America 108, 5179–5183.
- Chang, S.C., Zhang, H.C., Renne, P.R., Fang, Y., 2009. High-precision $^{40}\text{Ar}/^{39}\text{Ar}$ age for the Jehol Biota. Palaeogeography, Palaeoclimatology, Palaeoecology 280, 94–104.
- Dong, L.P., Roček, Z., Wang, Y., Jones, M.E.H., 2013. Anurans from the Lower Cretaceous Jehol Group of Western Liaoning, China. PLOS ONE 8 (7), e69723. <http://dx.doi.org/10.1371/journal.pone.0069723>.
- Gómez-Zurita, J., Hunt, T., Vogler, A.P., 2008. Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). Cladistics 24 (1), 34–50.
- Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, Cambridge, 755 pp.
- Hagedorn, M., 1906. Borkenfafer des baltischen Bernsteins. Schriften der physikalisch-ökonomischen Gesellschaft zu Koenigsberg in Preussen 47, 115–121.
- Ji, Q., Chen, W., Wang, W.L., Jin, X.C., Zhang, J.P., Liu, Y.Q., Zhang, H., Yao, P.Y., Ji, S.A., Yuan, C.X., Zhang, Y., You, H.L., 2004. Mesozoic Jehol Biota of Western Liaoning, China. Geological Publishing House, Beijing, 226 pp.
- Kirejtshuk, A.G., 1994. Parandrexidae fam. nov., Jurassic beetles of the infraorder Cucujiformia (Coleoptera, Polyphaga). Paleontologicheskii Zhurnal 28, 57–64.
- Kirejtshuk, A.G., Chang, H.L., Ren, D., Shih, C.K., 2010a. Family Lasiosynidae n. fam., new palaeoendemic Mesozoic family from the infraorder Elateriformia (Coleoptera: Polyphaga). Annales de la Société entomologique de France (n.s.) 46, 67–87.
- Kirejtshuk, A.G., Ponomarenko, A.G., Prokin, A.A., Chang, H.L., Nikolajev, G.V., Ren, D., 2010b. Current knowledge of Mesozoic Coleoptera from Daohugou and Liaoning (Northeast China). Acta Geologica Sinica (English Edition) 48, 783–792.
- Kuschel, G., May, B.M., 1990. Pallophaginae, a new subfamily for leaf-beetles, feeding as adult and larva on Araucarian pollen in Australia (Coleoptera: Megalopodidae). Invertebrate Taxonomy 3, 697–719.
- Lawrence, J.F., Ślipiński, A., Seago, A.E., Thayer, M.K., Newton, A.F., Marvaldi, A.E., 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici (Warszawa) 61, 1–217.
- Legalov, A.A., 2013. Review of the family Anthribidae (Coleoptera) from the Jurassic of Karatau: subfamily Protoscelinae. Genus *Protoscelis* Medvedev. Paleontological Journal 47 (3), 292–302.
- Leng, Q., Friis, E.M., 2006. Angiosperm leaves associated with *Sinocarpus* infructescences from the Yixian Formation (mid-Early Cretaceous) of NE China. Plant Systematics and Evolution 262 (3–4), 173–187.
- Linsley, E.G., 1961. The Cerambycidae of North America. Part I. Introduction. University of California Publications in Entomology 18, 1–97.
- Liu, Y.S., Ren, D., Sinitshenkova, N.D., Shih, C.K., 2006. Three new stoneflies (Insecta: Plecoptera) from the Yixian Formation of Liaoning, China. Acta Geologica Sinica 82 (2), 249–256.
- Martynov, A.V., 1926. To the knowledge of the fossil insects of the Jurassic states of Turkestan: V. On some forms of beetles (in Russian). Ezhegodnik Russkogo Paleontologicheskogo Obschestva 5, 1–38.
- Martins, U.R., Galileo, M.H.M., 1999. *Paleohemilophus*, a new genus of fossil Cerambycidae from Hispaniola Island (Coleoptera). Revista Brasileira de Entomologia 43 (3–4), 309–313.
- Medvedev, L.N., 1968. Polyphagous beetles from the Jurassic of Karatau (Coleoptera, Polyphaga). In: Rhodendorf, B.B. (Ed.), Jurassic insects of Karatau. Akademya Nauk SSSR (in Russian), pp. 155–165.
- Napp, D.S., 1994. Phylogenetic relationships among the subfamilies of Cerambycidae (Coleoptera, Chrysomeloidea). Revista Brasileira de Entomologia 38, 265–419.
- Ponomarenko, A.G., 1985. Fossil insects from the Tithonian "Solnhofener Plattenkalke" in the Museum of Natural History Vienna. Annalen des Naturhistorischen Museum Wien 87, 135–144.
- Reid, C.A.M., 1995. A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). In: Pakaluk, J., Ślipiński, A. (Eds.), Biology, phylogeny and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 559–631.
- Reid, C.A.M., 2000. Spilopyrinae Chapuis: a new subfamily in the Chrysomelidae and its systematic placement (Coleoptera). Invertebrate Taxonomy 14, 837–862.
- Ren, D., Shih, C.K., Gao, T.P., Yao, Y.Z., Zhao, Y.Y., 2010. Silent Stories – Insect Fossil Treasures from Dinosaur Era of the Northeastern China. Science Press, Beijing, China.
- Scudder, S.H., 1891. Index to the known fossil insects of the world including Myriapods and Arachnids. Bulletin of the United States Geological Survey 71, 1–744.
- Ślipiński, A., Escalona, H., 2013. Australian Longhorn Beetles (Coleoptera: Cerambycidae) Volume 1. Introduction and Subfamily Lamiinae. CSIRO Publishing.
- Ślipiński, A., Leschen, R.A.B., Lawrence, J.F., 2011. Order Coleoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa, 3148, pp. 203–208.
- Sun, G., Dilcher, D.L., Zheng, S.L., Zhou, Z.K., 1998. In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from Northeast China. Science 282, 1692.
- Sun, G., Ji, Q., Dilcher, D.L., Zheng, S.L., Nixon, K.C., Wang, X.W., 2002. Archæfructaceae, a new basal angiosperm family. Science 296, 899.
- Švácha, P., Danilevsky, M.L., 1987. Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part I. Acta Universitatis Carolinae – Biologica 30 (1986), 1–176.
- Švácha, P., Wang, J.J., Chen, S.C., 1997. Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). Annales de la Société Entomologique de France (N.S.) 33, 323–369.
- Vitali, F., 2005. Notes about the European fossil Lepturinae and the description of a new species (Coleoptera, Cerambycidae, Lepturinae). Lambillionea 105 (4), 530–538.
- Vitali, F., 2006. Taxonomic, biological and evolutionistic notes on the Spondylidinae included in Baltic amber (Coleoptera, Cerambycidae). Entomapeiron Paleontomology 1 (3), 29–44.
- Vitali, F., 2007. A new fossil species of *Elaphidion Audinet-Serville*, 1834 with systematic notes on the Lamiinae from Dominican amber (Coleoptera, Cerambycidae). Entomapeiron Paleontomology 2 (3), 29–39.

- Wang, B., Ma, J., McKenna, D., Yan, E.V., Zhang, H., Jarzembski, E.A., 2013. The earliest known longhorn beetle (Cerambycidae: Prioninae) and implications for the early evolution of Chrysomeloidea. *Journal of Systematic Paleontology* [Published online 09 Aug 2013]. <http://dx.doi.org/10.1080/14772019.2013.806602>.
- Yang, W., Li, S.G., Jiang, B.Y., 2007. New evidence for Cretaceous age of the feathered dinosaurs of Liaoning: Zircon U-Pb SHRIMP dating of the Yixian Formation in Sihetun, northeast China. *Cretaceous Research* 28, 177–182.
- Zhang, J.F., 2005. The first find of chrysomelids (Insecta: Coleopatra: Chrysomeloidea) from Callovian-Oxfordian Daohugou biota of China. *Geobios* 38, 856–871.
- Zhou, Z.H., Barrett, P.M., Hilton, J., 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 42, 807–814.
- Zhou, Z.H., Wang, Y., 2010. Vertebrate diversity of the Jehol Biota as compared with other lagerstätten. *China Earth Sciences* 53, 1894–1907.