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To cite this article: Yali Yu, Steven R. Davis, Chungkun Shih, Dong Ren & Hong Pang (2019) The earliest fossil record of Belidae and its implications for the early evolution of Curculionoidea (Coleoptera), *Journal of Systematic Palaeontology*, 17:24, 2105-2117, DOI: [10.1080/14772019.2019.1588401](https://doi.org/10.1080/14772019.2019.1588401)



To link to this article: <https://doi.org/10.1080/14772019.2019.1588401>

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The earliest fossil record of Belidae and its implications for the early evolution of Curculionoidea (Coleoptera)

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(Received 29 September 2017; accepted 11 February 2019)

Here we report the earliest known fossil belid, *Sinoeuglypheus daohugouensis* gen. et sp. nov., from the latest Middle Jurassic Jiulongshan Formation of north-eastern China. Extant belids are specialist herbivores feeding on gymnosperms or angiosperms, but it is likely that this new belid fed on coexisting conifers or other gymnosperms. Extant members of Belidae are predominantly distributed in the Southern Hemisphere. Therefore, this new find in the north-eastern China deposit is significant for understanding the early stages of the radiation of this group during the mid-Mesozoic, and the early evolution of Curculionoidea.

<http://zoobank.org/urn:lsid:zoobank.org:pub:2020E35D-E918-4C84-993C-20B8E4DBB671>

Keywords: Coleoptera; weevil; Middle Jurassic; Jiulongshan Formation; Daohugou; China

Introduction

Weevils in the family Belidae, with about 375 extant species in 38 genera, constitute a small and evidently relict lineage, distributed predominantly in the Southern Hemisphere (Oberprieler *et al.* 2007). Larvae of the nominate subfamily Belinae are borers in stems and logs, with those of the more primitive tribes Pachyurini and Agnesiotidini primarily found in conifers (Araucariaceae, Podocarpaceae and Cupressaceae), while Belini are present in angiosperms, especially acacias in Australia (Oberprieler *et al.* 2007). By contrast, larvae of the subfamily Oxycoryninae develop mostly in reproductive plant organs of gymnosperms (araucarians and cycads) and angiosperms, but also in stems or under bark (Marvaldi *et al.* 2006; Oberprieler *et al.* 2007). The biology of pachyurines and agnesiotidines is considered to be primitive for the clade, although not necessarily primitive for all weevils given that belids have thus far not been shown to be sister to the remainder of the superfamily. Belinae are distributed in Australia, New Zealand, New Guinea, the Solomon Islands, the Moluccas, Brazil, Argentina, Paraguay and Chile, while Oxycoryninae are known from southern Florida and Cuba to Argentina and Chile, as well as in South Africa, northern Africa, the Canary Islands, mainland and oceanic Southeast Asia, New Zealand, New

Caledonia, Hawaii and some other Pacific island groups (Marvaldi & Ferrer 2014).

The classification of Belidae has varied widely among authors (e.g. Crowson 1955; Thompson 1992; Zherikhin & Gratshev 1995). For example, some authors have considered the tribe Aglycyderini to be an independent subfamily or even family, while others have suggested Oxycoryninae (including or excluding the subtribe Allocorynina) should be removed as their own family as well. However, a close relationship between Oxycoryninae and Belinae has been well supported in phylogenetic analyses (Kuschel 1995; Marvaldi & Morrone 2000; Marvaldi *et al.* 2002; Oberprieler *et al.* 2007; McKenna *et al.* 2009) and the circumscription of these two groups into a single family has become more widely adopted.

Available fossil records of belids have been documented and summarized by different authors in recent years (Gratshev & Zherikhin 2003; Oberprieler *et al.* 2007; Soriano 2009; Legalov 2012; Oberprieler & Oberprieler 2012). We will not reiterate the list of taxa here, as some appear to be misidentified and many require re-examination prior to assignment. They have been recorded from the Upper Jurassic Karabastau Formation at Karatau, Kazakhstan (Oxfordian–Kimmeridgian, 161–151 Ma) and the Lower Cretaceous Crato Formation near Santana, Brazil (upper Aptian, 125–112 Ma) (e.g. Zherikhin & Gratshev 2004; Santos

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et al. 2007), the Yixian Formation in Liaoning, China (Barremian, 125 Ma) (Davis *et al.* 2013), the Emanra Formation along the Khetana River, Russia (Lower Cretaceous: mid-Albian, 112–100 Ma), and the La Pedrera de Rubies Formation in the Sierra del Montsec, Spain (Barremian, 130–125 Ma). Soriano (2009) summarized 18 species in nine genera from Mesozoic deposits (Soriano 2009), although *Gratshevbelus erici* actually belongs to the Rhynchitinae (SRD pers. obs.). Oberprieler & Oberprieler (2012) deemed that fossils convincingly attributable to Belidae are absent from the Mesozoic record owing to the absence of observable defining features of crown-group belids (Oberprieler *et al.* 2007). Accordingly, the Mesozoic record of Belidae may be based solely on stem groups and perhaps on taxa generally misplaced on the basis of plesiomorphies alone. As mentioned above, while the latter is more applicable to the described fossil weevil fauna, there do seem to be proper belid taxa from some of the above Mesozoic deposits. Indeed, many of them are in need of more detailed description before being placed confidently within Belidae, but it would be hasty to deem all of them as not being attributable to the clade.

The origin of Belidae was dated to *c.* 151.5 Ma, i.e. the Late Jurassic, based on a time-calibrated phylogeny for the group based on DNA sequences (McKenna & Farrell 2009; McKenna *et al.* 2009). Herein we report the discovery of a new species of Belidae dating from about 165 Ma from the Jiulongshan Formation. The discovery of this fossil in the mid-Mesozoic is of significance for understanding the early diversification of weevils, and extends the record of this family to the latter part of the Middle Jurassic, and in rough correspondence with prior divergence estimates.

Material and methods

Fossil specimen

The holotype of the species described herein, CNU-COL-NN2011122, was collected from the Jiulongshan Formation at the village of Daohugou (41°18'38"N, 119°13'20"E), Shantou Township, Ningcheng County, Inner Mongolia, China. The geological age of this deposit is considered to be latest Middle Jurassic (late Callovian) (Chen *et al.* 2004; Liu *et al.* 2004; Walker *et al.* 2013), approximately 165–164 Ma. The Jiulongshan Formation is well known for yielding feathered dinosaurs, mammals, conifers, bennettitaleans and 20 orders of insects that have contributed significantly to our understanding of the evolution of these groups (Zhang & Zheng 1987; Xu & Zhang 2005; Huang & Nel 2009; Ren *et al.* 2010; Shih *et al.* 2011; Gao *et al.* 2012; Yu *et al.* 2012). The reconstructed

palaeoenvironment indicates that this locality was a volcanic region with mountain streams and lakes (Ren *et al.* 2002) and the climate at the time was humid and warm temperate (Tan & Ren 2002).

The specimen was examined using a Leica MZ165C dissecting microscope and illustrated with the aid of a drawing tube attachment, and digital photographs were taken with a Leica DFC500 digital camera (Wetzlar, Germany) attached to a Leica MZ165C microscope. Line drawings were enhanced in Adobe Photoshop CS software. Morphological terminology follows Lawrence *et al.* (2011).

Environmental scanning electron microscopy (SEM) was performed at low vacuum with the uncoated specimen using a Zeiss EVO60 EP-SEM.

Phylogenetic analysis

For the phylogenetic analysis based on morphological characters, the belid matrix from Anderson & Marvaldi (2013) was adopted and modified for inclusion of this fossil taxon to obtain an approximate placement (see that publication for character information). The morphological character matrix (Supplemental material) was edited in WinClada (Nixon 2000) and analysed in NONA (Goloboff 1993). The analysis used the ratchet search algorithm (Nixon 1999), sampling 45 characters (equally weighted) for 5000 ratchet iterations using two simultaneous threads.

Morphological characters

As mentioned, the characters and character matrix of Anderson & Marvaldi (2013) were used and modified for the inclusion of the new fossil taxon. Only the characters that were visible in the fossil, and therefore coded, are listed below, and the character states of *Sinoeuglypheus daohugouensis* gen. et sp. nov. are shown in the Supplemental data matrix. All other characters can be found in the above publication.

Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758

Superfamily **Curculionoidea** Latreille, 1802

Family **Belidae** Schönherr, 1826

Subfamily incertae sedis

Genus ***Sinoeuglypheus*** Yu, Davis & Shih gen. nov.

Type species. *Sinoeuglypheus daohugouensis* sp. nov.

Diagnosis. Rostrum projecting anteriorly and fairly straight, only slightly curved, slightly longer than head

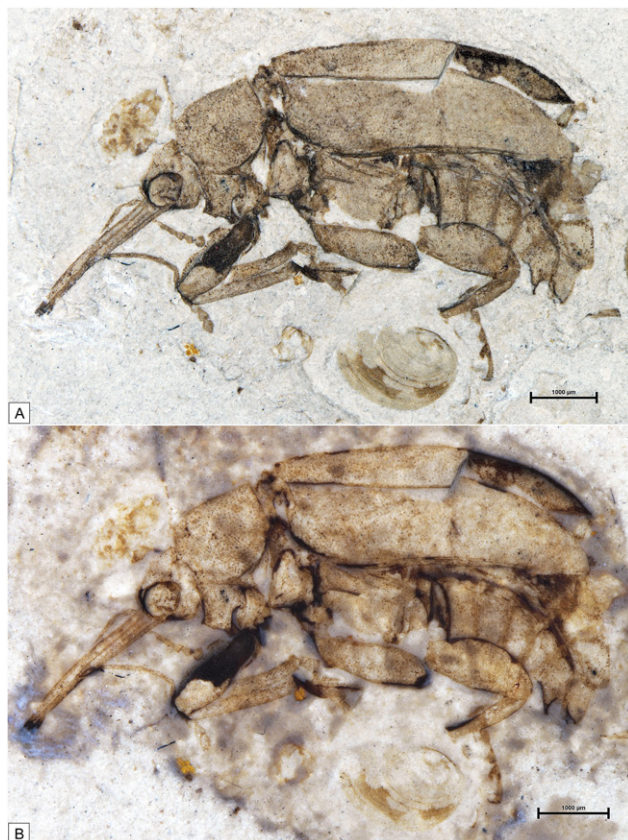


Figure 1. *Sinoeuglypheus daohugouensis* gen. et sp. nov. **A**, photomicrograph of dry specimen; **B**, photomicrograph of specimen wetted with 100% ethanol. Scale bars = 1000 µm.

and prothorax combined; antennae inserted approximately at mid-length of rostrum; antennae with loose club; flagellomere I elongated, *c.* length of scape and pedicel combined. Compound eyes round, apparently bulging. Pronotal surface densely and coarsely punctate; postero-medial margin of prothorax with small knob. Elytra with dense covering of short setae and small punctures irregularly arranged (not arranged into striae); basal margin weakly flanged. Lateral margins of ventrites with complete submarginal carinae for fastening of elytra to abdomen. Fore tibiae with outer longitudinal carina; inner apical tibial brush present. At least tarsomere III lobed; II perhaps shallowly lobed.

Etymology. The new generic name is formed of the Latinized Greek prefix *sino-* (referring to China), combined with *euglypheus* (from Greek, meaning that the taxon is well preserved). The gender is masculine.

Remarks. While scutellary striae on the elytra are not visible in this specimen due to its preservation

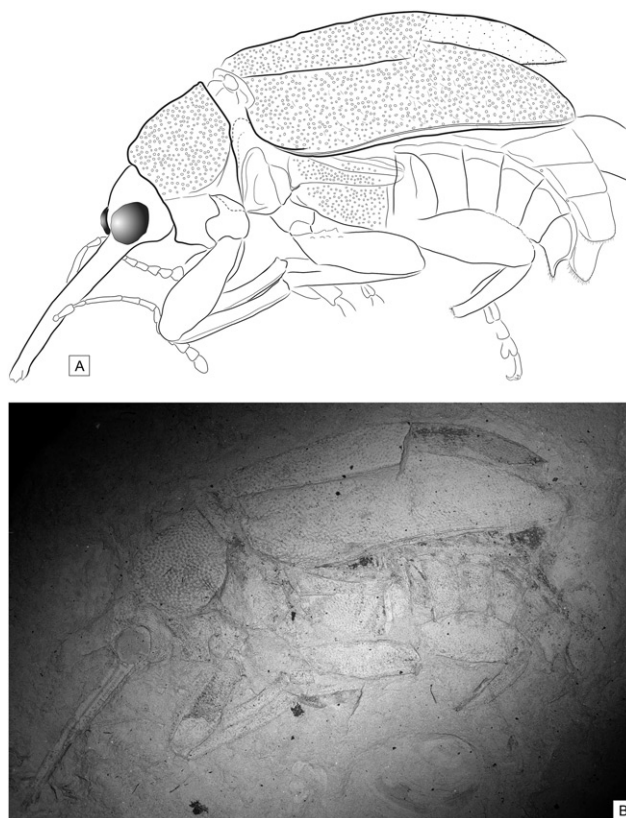


Figure 2. *Sinoeuglypheus daohugouensis* gen. et sp. nov. **A**, illustration of specimen; **B**, scanning electron micrograph of entire specimen.

(which would exclude placement in Caridae, Brentidae or Curculionidae), several features of Belidae are present and visible. These characters include the irregularly arranged punctures on the elytra (Figs 1, 2), the elongated first flagellomere of the antennae (Figs 1, 2, 4), the outer longitudinal carina (Figs 1, 3) and apical setal brush (Fig. 3C) on the fore tibiae, the wide prothoracic cavity for reception of the procoxa (Figs 1, 2, 5A, E, F), the form of the meso- and metathoracic episterna and epimera (Figs 1, 7A, B, E, 8), the small flange along the elytral basal margin (Figs 1, 2), and lateral carinae on the abdominal ventrites (Figs 9A, C, 10). Although some Belinae possess narrow to closed procoxal cavities (Fig. 5B), similar to most Nemonychidae (Fig. 5C, D), the latter do not have modified posterolateral prothoracic margins. Nemonychidae also have lateral carinae on the abdominal ventrites (Fig. 9B), but these are weaker and incomplete compared to those in Belinae (Fig. 9A). It is noted that although the lateral procoxal cavity appears to be widely open, the certainty of this state cannot be confirmed due to some distortion that is evident in the specimen and overlying matrix. The rough

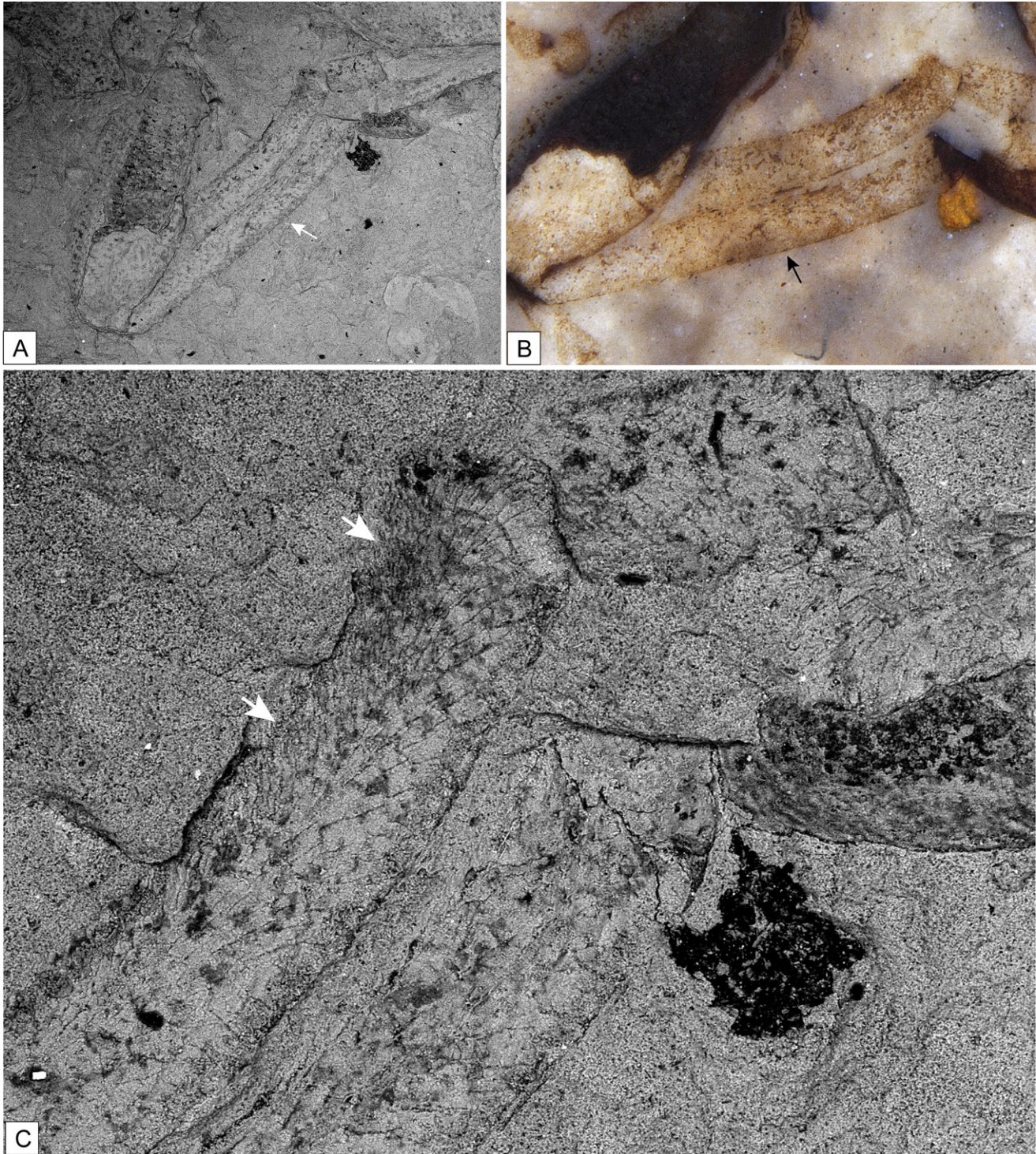


Figure 3. **A**, scanning electron microscopy (SEM) image of the forelegs, showing the outer longitudinal carina of the tibiae; **B**, photomicrograph (using ethanol-wetted specimen) of the forelegs, showing the outer longitudinal carina of the tibiae; **C**, SEM image of the protibiae, showing the dense setal brush along the inner apical margin of the tibia.

texture of the cuticle also is finely preserved on most of the specimen, as is visible from the SEM. A roughly textured, rugose area is particularly visible on the left profemur.

Among belids, species of the subfamily Oxycoryninae have antennae that are inserted at the base of the rostrum and the prothorax is often strongly laterally carinate, traits not present in the current fossil.

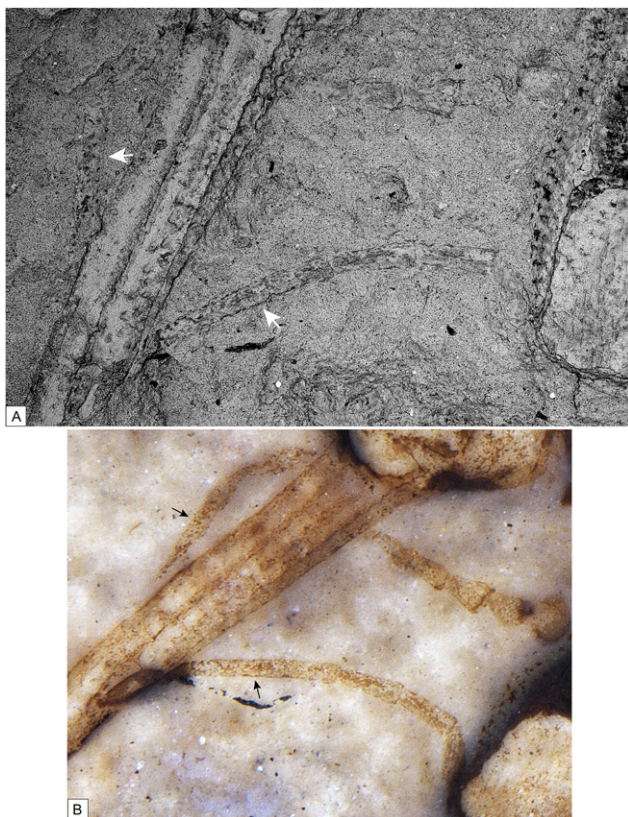


Figure 4. **A**, scanning electron micrograph of part of rostrum and antennae, showing elongated first flagellomeres; **B**, photomicrograph (using ethanol wetted specimen) of part of rostrum and antennae, showing elongated first flagellomeres.

Sinoeuglypheus daohugouensis Yu, Davis & Shih
sp. nov.
(Figs 1, 2)

Holotype. CNU-COL-NN2011122, sex unknown. Body length (including head and rostrum) *c.* 8.2 mm, as measured from apex of visible rostrum to posterior reach of abdomen in specimen. A well-preserved body with complete elytra, antennae and all pairs of legs is housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), Beijing, China.

Horizon and locality. Latest Middle Jurassic, Jiulongshan Formation, Daohugou, Shantou Township, Ningcheng County, Inner Mongolia, north-eastern China.

Diagnosis. As for the genus (see above).

Etymology. The specific epithet is based on the type locality, the village of Daohugou.

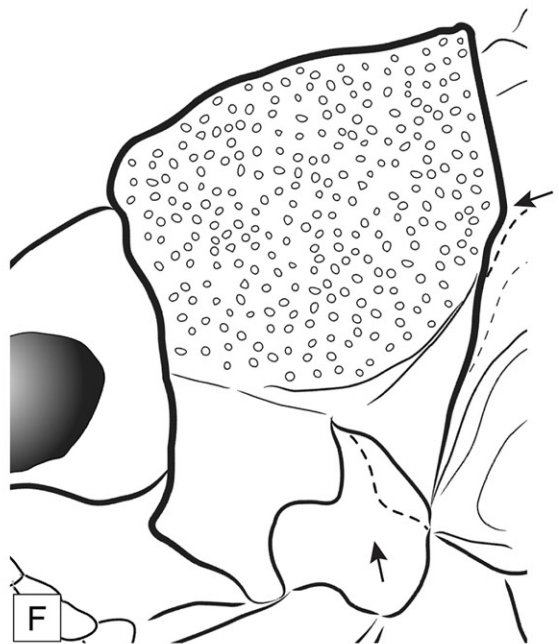
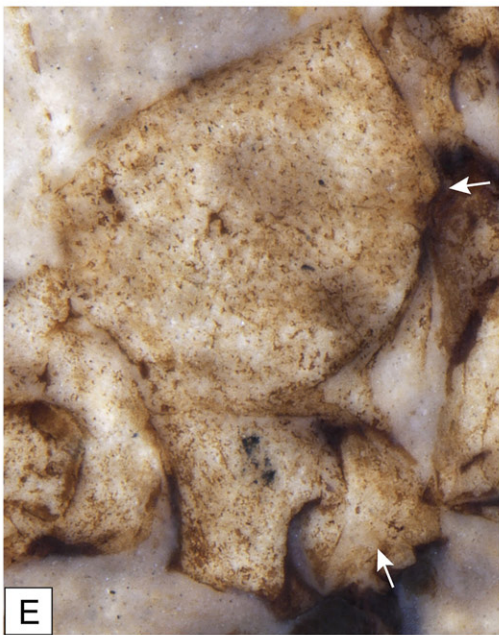
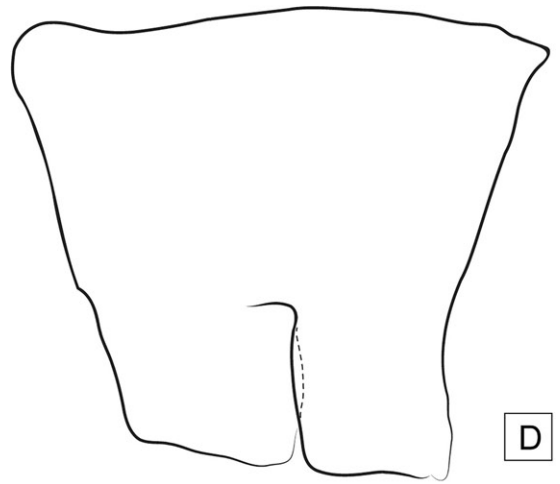
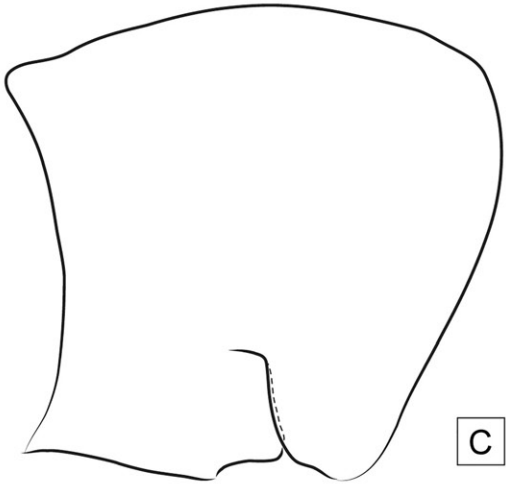
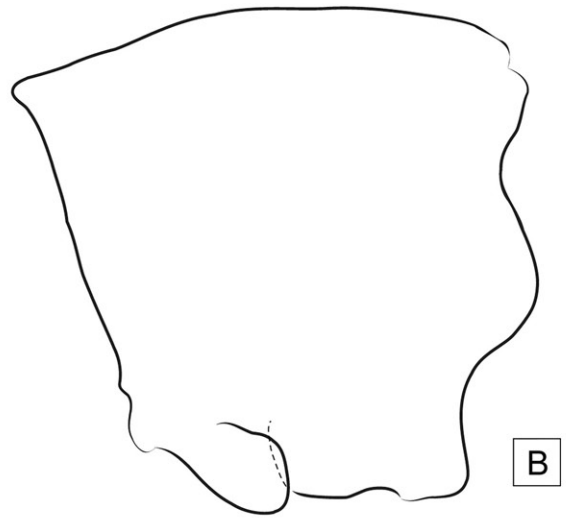
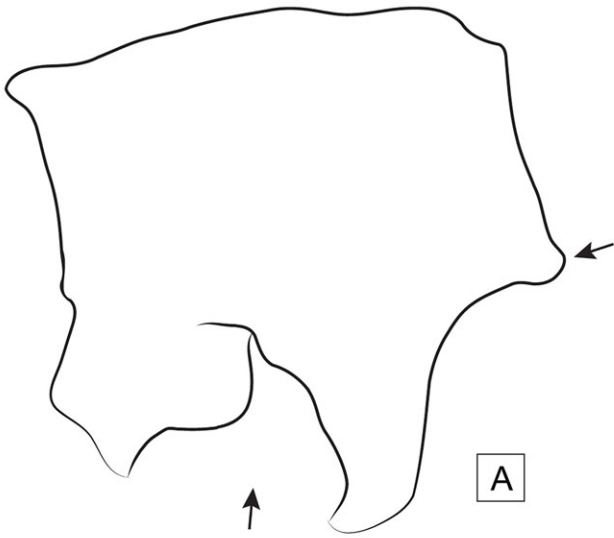
Description. Rostrum longer than head + prothorax, thin, subcylindrical, slightly curved downward, narrowing towards apex and possibly slightly expanding apically; inserted near middle of head; head bulging dorsally between eyes; labrum unclear. Compound eyes anterolateral, sub-rotund and entire, apparently strongly protuberant and well separated, anterior margin close to base of rostrum. Antennae with 11 articles, moderately long, slender; inserted at approximate middle of rostrum, perhaps slightly anterior to middle, reaching slightly beyond anterior margin of prothorax; with weak 3-article club; scape slightly longer than pedicel; the first flagellomere about $2\times$ length of pedicel.

Dorsal surface of pronotum densely and coarsely punctate, apparently with weak lateral carinae; posterolateral margins angled or weakly knobbed. Procoxae situated between middle and posterior margin of prosternum. Mesoscutellum wider than long, with small medial convexity along posterior margin. Elytra covered with fine, dense punctures, not arranged into striae, and small dense setae.

Metafemora robust, slightly more enlarged than pro- and mesofemora; meso- and metafemora with weak dorsal crenulation; all tibiae long, narrow and nearly parallel sided; tarsi partly visible; tarsomere I longer than II, tarsomere III distinctly bilobed, tarsomere IV reduced; pretarsal claws (ungues) arched. Abdomen with five free ventrites, subequal in length.

Discussion

The flora preserved in the Jiulongshan Formation was dominated by Ginkgopsida (*Ginkgoites*, *Ginkgo*, *Baiera*, *Czekanowskia*, *Phoenicopsis*), Coniferopsida (*Pityophyllum*, *Rhipidiocladus*, *Elatocladus*, *Schizolepis*, *Podozamites*), lycopods (*Lycopodites*, *Selaginellites*), Sphenopsida (*Equisetum*), Filicopsida (*Todites*, *Coniopteris*) and Cycadopsida (*Anomozamites*) (Mi *et al.* 1996). Conifers are thought to be the ancestral hosts of crown-group Belidae (Marvaldi *et al.* 2002), and this is consistent with estimated divergence times for stem-group representatives of this family (*c.* 151.5 Ma), which predate the first appearance of definitive angiosperms (fossils 132–141 Ma [Brenner 1996], molecules 140–180 Ma [Bell *et al.* 2005]) (McKenna *et al.* 2009). It is likely that early belids were associated with gymnosperms, and potentially conifers, although this requires further testing as host shifts between stem-group belids and basal crown-group Belidae cannot be excluded as a possibility. Nonetheless, based on the available, albeit limited, evidence, one would conclude that the most likely hosts were to be found among



ancient conifers. Given that conifers are also suggested as the putative hosts of early Chrysomeloidea (Oberprieler *et al.* 2007), sister group to the Curculionoidea, it seems safe to assume for the moment that stem-group belids were found on conifers. Conifers have also been implicated as ancestral hosts for Attelabidae and Caridae, and the more basal Nemonychidae, the so-called pinecone weevils, are also found in association with gymnosperms, often pines.

Coding this new fossil within the morphological character matrix of Anderson & Marvaldi (2013) yielded an unresolved placement among beline tribes (Fig. 11). While a 50% majority-rule tree (not shown) shows a monophyletic Belinae with the fossil taxon included, the addition of missing data and homoplasies collapses this grouping in the strict consensus. The inclusion of the fossil taxon does not necessarily render Belinae an unnatural group, but more likely signifies the ancestral nature of the fossil. For example, although there is a distinct apical protibial setal brush, in which the setae within the brush region are denser than outside it, the brush setae do not appear to be as small or as dense as in extant belines. While apical tibial spurs are not clearly visible, there may be traces on the right foretibia, but this feature is too faint to indicate with any certainty. The mesonotum (Fig. 6E–G) also appears to be somewhat intermediate in form between Nemonychidae (Fig. 6C, D) and Belidae (Fig. 6A, B), such as in the protruding posterior margin of the mesonotum and the shape of the mesoscutum. The meso- and metathoracic epimera and episterna (Figs 7E, 8), although more closely resembling forms in extant Belinae (Fig. 7A, B) than in Nemonychidae (Fig. 7C, D), show some slight differences, such as in the shape of the mesepimeron. Such character variation, however, does not appear to be greater than that seen within extant Belinae and would be expected in the early diverging members of any lineage. Apparent distortion in the ventral region of the prothorax, however, challenges the structural interpretation of the lateral procoxal cavity. If it is indeed wide, then placement as an early branching beline may be appropriate. A narrow procoxal cavity would not necessarily change this interpretation, but could signify additional supporting evidence for a stem-group assignment. It should also be noted that an earlier phylogenetic analysis based on morphology (Davis 2014) and that

included the fossil taxon (labelled ‘Daohugou_belid_sp’ in the analysis), which was a larger and broader study of higher level relationships within Curculionoidea and used an entirely different set of characters, found a similar placement of the specimen within Belinae.

As mentioned in Oberprieler & Oberprieler (2012), many features useful for separating higher weevil groups are not often preserved in compression fossils. Such incomplete preservation uncovers stark difficulties in the identification of fossil weevils, in which many groups look indistinguishable when various diagnostic features are unobservable. For example, much of the confusion in the described Mesozoic fossil weevil fauna is due to the incomplete preservation of the compression fossils. At this early time in weevil evolution, compression fossils of the earliest diverging lineages are difficult to distinguish, and this is the reason behind the confusion that surrounded the eobelid lineage of Nemonychidae. Based on general external features such as leg length and width, rostral length and orientation, elytral punctuation and abdominal ventrite length, the fossil described herein has affinities with at least both Nemonychidae and Belidae. However, in this case the preservation is rather exceptional, allowing for a reasonable phylogenetic assessment based on the comparison of several morphological features ranging from head, leg and abdominal characters to the form of various thoracic sclerites.

The discovery of a belid in the Jiulongshan Formation is significant on several levels. First, the species provides another important record of phytophagous beetles from this early insect fauna, enhancing our knowledge of the ecological community present at the time, particularly those involved in important herbivore-plant interactions. Second, the record serves as an important palaeogeographical record of occurrence for a family that is today restricted to the Southern Hemisphere but at the time of the Middle Jurassic was present in areas that correspond to today’s more northern localities. Third, despite a lack of resolution within the Belinae, the fossil appears to belong in the vicinity of this family, along the belid lineage, and displays several synapomorphies. As demonstrated by its combination of features, the specimen appears to represent either a unique, early diverging lineage within Belinae or, perhaps more plausibly, an early stem group within

Figure 5. Prothoraces of *Sinoeuglypheus daohugouensis* gen. et sp. nov. and related groups, lateral aspects. **A**, *Homalocerus lyciformis* (Belidae: Belinae), showing wide procoxal cavity and knobbed projection at the posterolateral angle of the pronotum; **B**, *Rhinotia semipunctata* (Belidae: Belinae); **C**, *Lecontellus byturoides* (Nemonychidae: Cimberidinae); **D**, *Doydirhynchus austriacus* (Nemonychidae: Cimberidinae); **E**, *Sinoeuglypheus daohugouensis* gen. et sp. nov. (Belidae: Belinae), showing a wide procoxal cavity and weakly knobbed projection at the posterolateral angle of the pronotum; **F**, illustration of E.

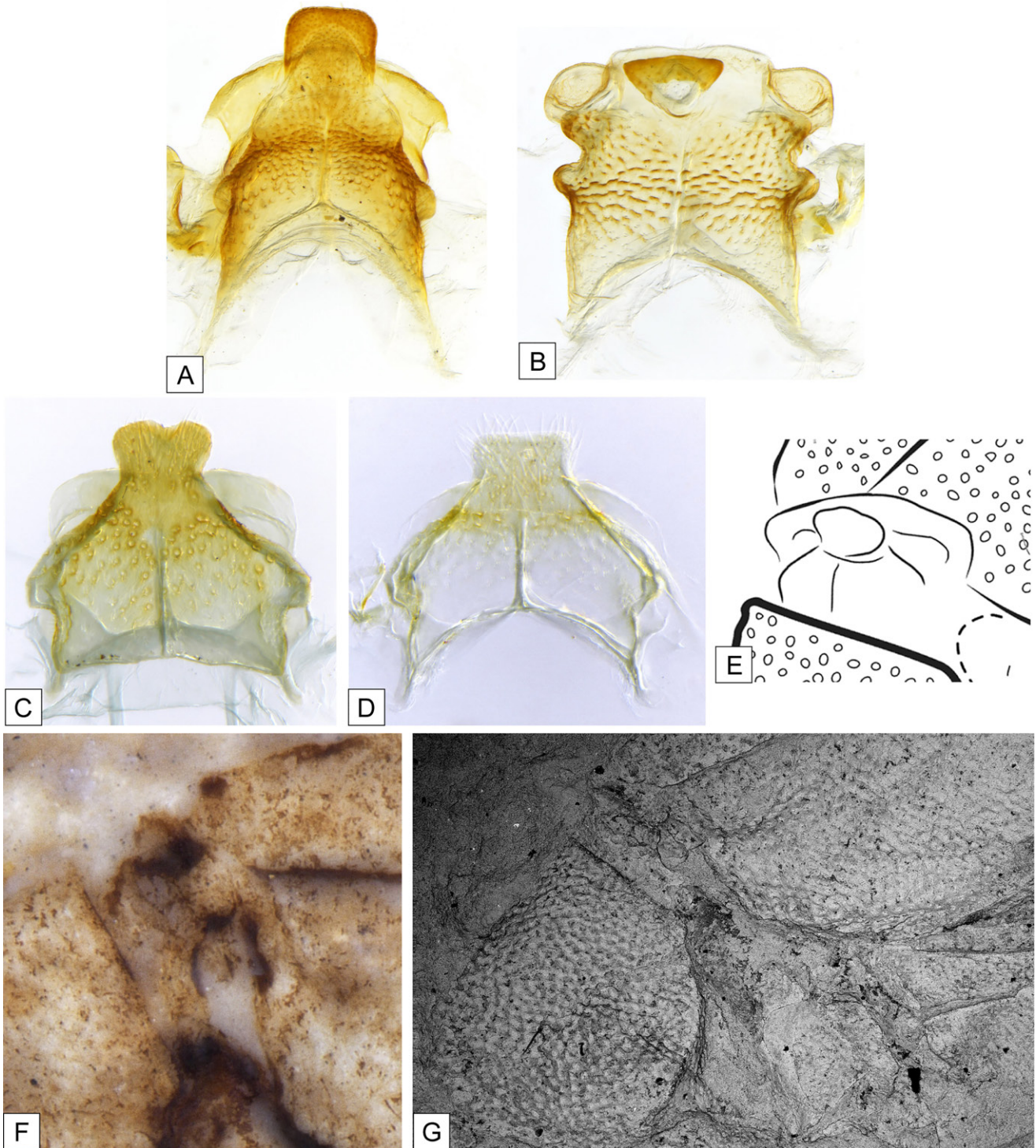


Figure 6. Mesonota of *Sinoeuglypheus daohugouensis* gen. et sp. nov. and related groups. **A**, *Homalocerus lyciformis* (Belidae: Belinae); **B**, *Rhinotia semipunctata* (Belidae: Belinae); **C**, *Lecontellus byturoides* (Nemonychidae: Cimberidinae); **D**, *Doydirhynchus austriacus* (Nemonychidae: Cimberidinae); **E**, *Sinoeuglypheus daohugouensis* gen. et sp. nov. (Belidae: Belinae), illustration of mesonotum; **F**, photomicrograph of mesonotum and surrounding area (wetted with ethanol); **G**, scanning electron micrograph of mesonotum and surrounding area.

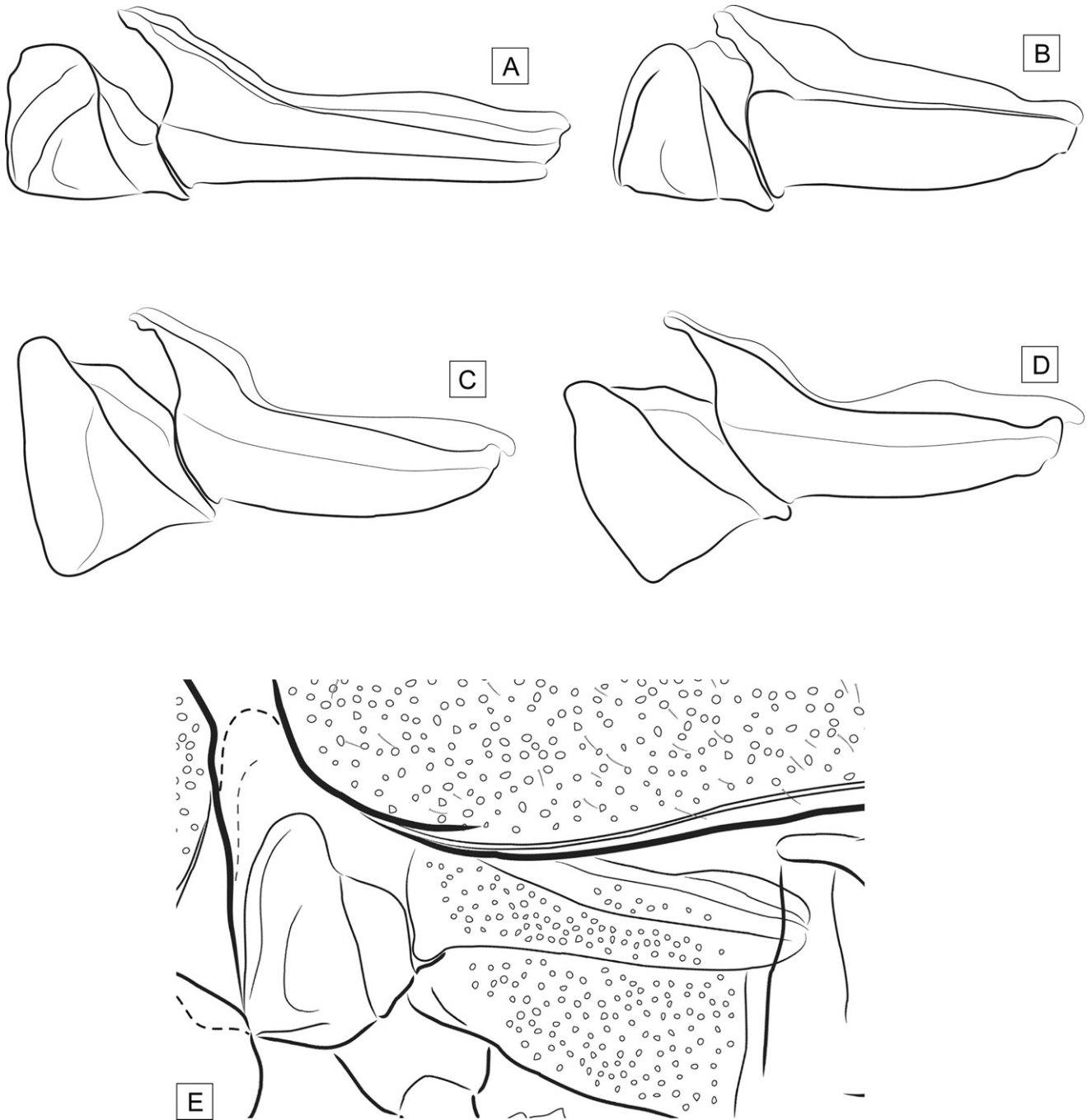


Figure 7. Meso- and metathoracic episterna and epimera of *Sinoeuglypheus daohugouensis* gen. et sp. nov. and related groups. **A**, *Homalocerus lyciformis* (Belidae: Belinae); **B**, *Rhinotia semipunctata* (Belidae: Belinae); **C**, *Lecontellus byturoides* (Nemonychidae: Cimberidinae); **D**, *Doydirhynchus austriacus* (Nemonychidae: Cimberidinae); **E**, *Sinoeuglypheus daohugouensis* gen. et sp. nov. (Belidae: Belinae), illustration of mesepisterna and metepimera.

Belidae due to the less-developed forms of several of the aforementioned synapomorphies and noted regions of challenging anatomical interpretation. It is doubtful, however, that many early stem-group belids could be

confidently differentiated from Nemonychidae in most compression fossils. A refined placement perhaps could be obtained by the inclusion of more belid genera and further examination of external characters, such as

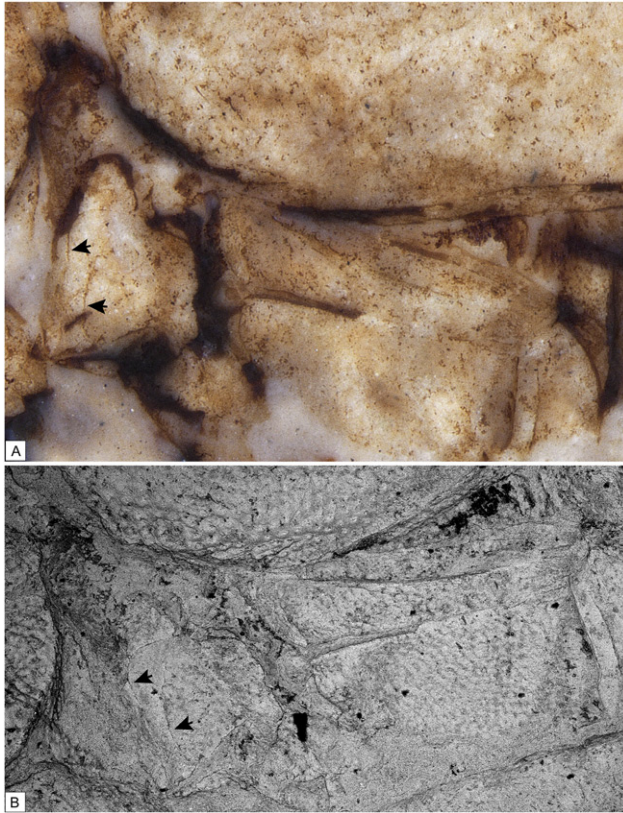


Figure 8. Meso- and metathoracic episternum and epimeron of *Sinoeuglypheus daohugouensis* gen. et sp. nov. **A**, photomicrograph of similar area as in [Figure 7E](#) of specimen (wetted with ethanol); **B**, scanning electron micrograph of similar area as in [Figure 7E](#) of specimen.

thoracic morphology, in a comparative framework. Lastly, despite the aforementioned challenges, the fossil provides an important calibration point for understanding the timing of events in the appearance of the belid lineage, extending the group back to the Middle Jurassic and slightly older than prior estimates.

Acknowledgements

This study was funded by the following grants awarded to YLY: the National Natural Science Foundation of China (Grant No. 31702039) and the Fundamental Research Funds for the Central Universities (Grant No. 18lgpy55); HP: the Basic Work Special Project of the National Ministry of Science and Technology of China (2013FY111500) and key project of Science-technology basic condition platform from the Ministry of Science and Technology of the People's Republic of China (Grant No. 2005DKA21402); and to DR: the National



Figure 9. Lateral view of abdomens of *Sinoeuglypheus daohugouensis* gen. et sp. nov. and related groups, showing lateral carinae on each ventrite. **A**, *Homalocerus lyciformis* (Belidae: Belinae); **B**, *Lecontellus byturoides* (Nemonychidae: Cimberidinae); **C**, *Sinoeuglypheus daohugouensis* gen. et sp. nov. (Belidae: Belinae), photomicrograph of specimen wetted with ethanol.

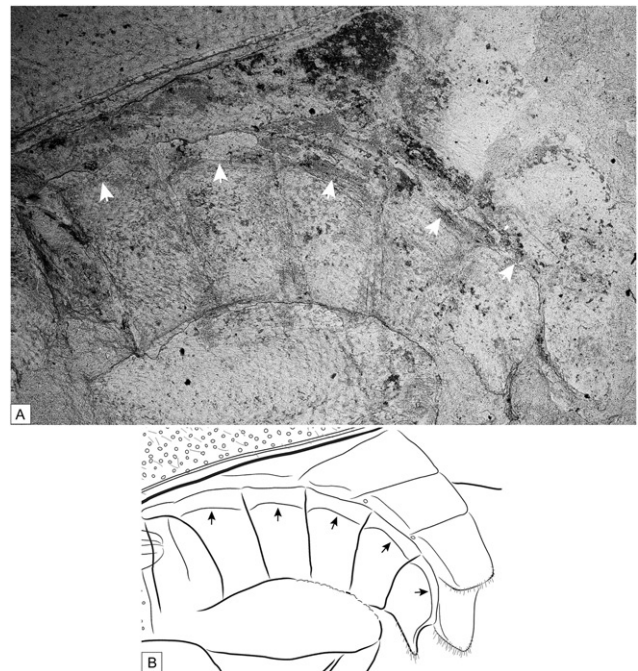


Figure 10. Lateral view of abdomen of *Sinoeuglypheus daohugouensis* gen. et sp. nov., showing lateral carinae on each ventrite. **A**, scanning electron micrograph of similar area as in [Figure 9C](#) of specimen; **B**, illustration of similar area as in [Figure 9C](#).

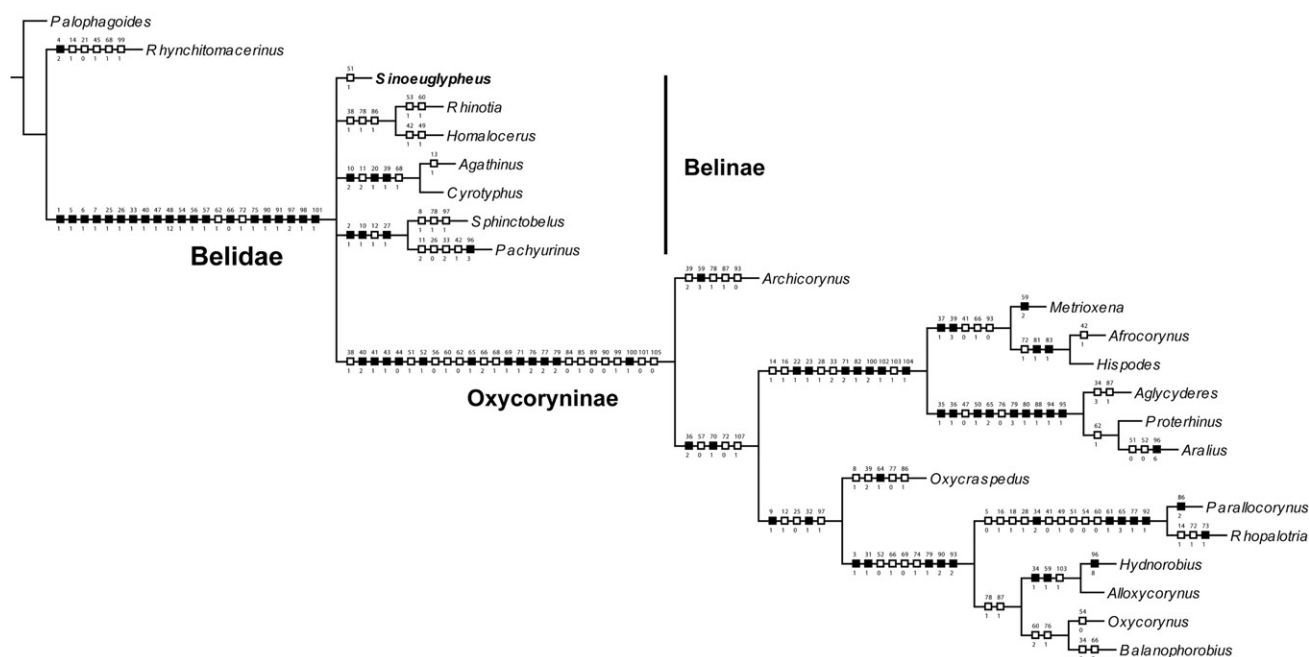


Figure 11. Strict consensus (tree length = 266 steps, consistency index [CI]=0.60, retention index [RI]=0.79) of nine most-parsimonious trees (tree length = 256 steps, CI = 0.62, RI = 0.81), showing phylogeny of Belidae with the fossil taxon included. Only unambiguous character changes are mapped (unique and homoplastic features are shown as black or white squares, respectively). The phylogenetic analysis was based on the character matrix from Anderson & Marvaldi (2013), modified for inclusion of the new fossil taxon.

Natural Science Foundation of China (Grants No. 31730087 and 41688103), the programme for Changjiang Scholars and Innovative Research Team in University (IRT-17R75) and Project of High-level Teachers in Beijing Municipal Universities (No. IDHT20180518). Partial funding was provided by NSF DEB-1110590 (to M. S. Engel, P. Cartwright and S. R. Davis) through the University of Kansas, and continued support was provided to SRD by the Gerstner and Kalbfleisch postdoctoral fellowships through the American Museum of Natural History and Richard Gilder Graduate School during the completion of this study. Much appreciation is given to two anonymous reviewers who offered constructive challenges to the interpretation of the fossil.

Supplemental material

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2019.1588401>

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Associate Editor: Vladimir Blagoderov