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Jurassic artematopodid beetles and their implications for the early evolution of Artematopodidae (Coleoptera)

CHEN-YANG CAI[1], JOHN F. LAWRENCE[2], ADAM ŚLIPIŃSKI[2] and DI-YING HUANG[1]

[1]State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China and [2]Australian National Insect Collection, CSIRO National Collections Australia, Canberra, Australia

Abstract. Fossil Artematopodidae are rarely collected and previously confined to middle Eocene Baltic amber. Here we report the first definitive artematopodid, *Sinobrevipogon jurassicus* **gen. et sp.n.**, from the Middle Jurassic Daohugou beds (*c*. 165 Ma) in Inner Mongolia, northeastern China. It exhibits a number of defining features of Artematopodidae, including paired carinae on prosternum and an internal apical interlocking tongue on the ventral side of each elytron. However, it differs from any modern Artematopodidae by having the mesocoxal cavitiy closed by the mesepimeron and the anterolateral edge of metanepisternum. The discovery of this new genus represents the earliest fossil record for Artematopodidae, highlighting the antiquity of the family. The systematic positions of *Forticatinius* Tan & Ren and *Tarsomegamerus* Zhang are discussed, and the latter is formally transferred to Artematopodidae. Phylogenetic relationships within Artematopodidae were investigated to elucidate the relationships between the two Jurassic genera and Recent genera. Eleven in-group taxa and two out-groups were included in a cladistic analysis based on 30 adult characters; the resulting tree recovered the family Artematopodidae in three clades: (i) *Electribius authority*, (ii) *Ctesibius* authority + *Brevipogon* authority + *Sinobrevipogon* + *Tarsomegamerus* and (iii) the remaining Recent genera, including *Allopogonia authority*.

Introduction

With approximately 70 described species in nine genera, Artematopodidae is a small family of beetles forming one of the basal lineages of Elateroidea (Hörnschemeyer, 1998; Lawrence, 2005, 2010). The family includes three subfamilies: Electribiinae (*Electribius* Crowson, Mexico, Central America, Baltic amber of northern Europe); Allopogoninae (*Allopogonia* Cockerell, California); and Artematopodinae (*Artematopus* Perty, Central and South America; *Brevipogon* Lawrence, California; *Carcinognathus* Kirsch, South America; *Ctesibius* Champion, Mexico and Central America; *Eurypogon* Motschulsky, North America, Italy, eastern Russia, China, Japan; *Macropogon* Motschulsky, North America, Asia; and *Proartematopus* Crowson, Baltic amber of northern Europe) (Crowson, 1973; Lawrence, 1995, 2005, 2010; Young, 2002). Modern artematopodids are found by sweeping and beating forest understorey foliage and very little is known of their habits (Young, 2002).

Correspondence: Di-Ying Huang, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, No.39 East Beijing Road, Nanjing 210008, China. E-mail: dyhuang@nigpas.ac.cn

There seems little doubt that species of *Eurypogon* and *Macropogon* are closely associated with and probably feed on mosses growing on boulders (Lawrence, 2010); however, *Artematopus* larvae in Brazil were reared through to the adult stage on cut-up pieces of insects (Costa *et al.*, 1985) The adult artematopodids resemble certain elaterids in superficial appearance (Fig. 1), but are easily separated from the latter by a curious feature – a tongue-like process associated with the apicoventral region of the elytron (Young, 2002; Lawrence, 2005). The family Artematopodidae was included in Dascillidae in older publications (e.g. Pic, 1914; Arnett, 1963), but it has been placed within Elateroidea based on adult and larval characters (Beutel, 1995; Lawrence *et al.*, 1995, 2011) and recent molecular studies have confirmed this placement (Kundrata *et al.*, 2014).

To date, fossil artematopodids were confined to the Middle Eocene Baltic amber (Lawrence, 2010). Two genera are known: *Electribius*, with four extinct and two Recent species, and the monotypic genus *Proartematopus* (Crowson, 1973; Lawrence, 1995; Hörnschemeyer, 1998). The inclusion of the Baltic amber species *Electrapate martynovi* Iablokov-Khnzorian

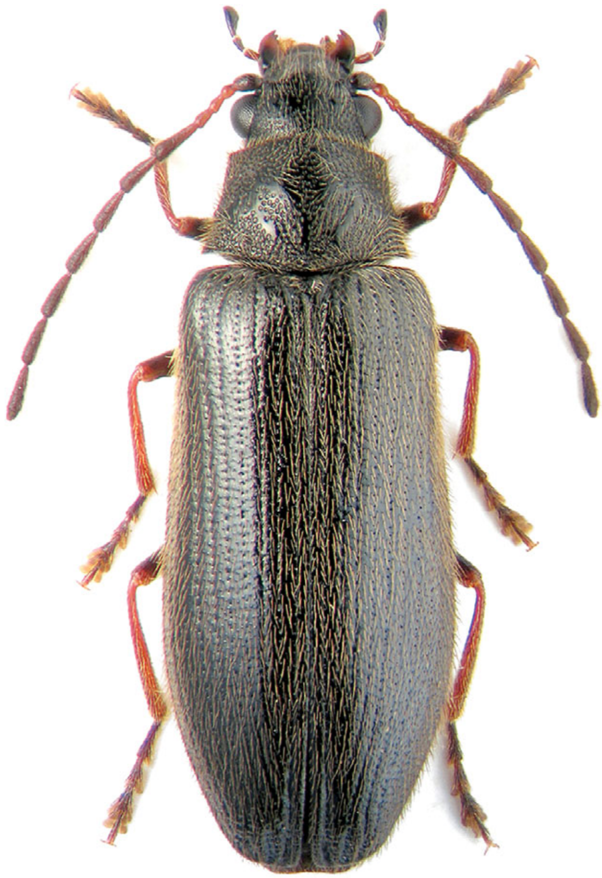

Fig. 1. An extant representative of Artematopodidae, *Macropogon pubescens* Motschulsky. Photo credit: Kirill V. Makarov.

(Iablokoff-Khnzorian, 1962) by Lawrence (2010) is considered erroneous. Although there appears to be a pair of artematopodid-like carinae on the prosternum in the ventral view, the well-developed metakatepisternal suture crossing the discrimen and the structure of the abdominal ventrites are both not diagnostic for this family. In fact, Cobos (1963) recognized Iablokoff-Khnzorian's family Electrapatidae as a tribe within the buprestid subfamily Schizopodinae, and this was noted by Bouchard *et al.* (2011). Here we report fossils of the oldest Artematopodidae from the Middle Jurassic deposits of China. A new genus and species are described and figured, and two other probable Mesozoic artematopodid genera are discussed herein.

Material and methods

Fossil material

The fossils studied here were collected from the Jiulongshan Formation (Daohugou beds) at Daohugou, Ningcheng County, Inner Mongolia, northeastern China. The precise age of the Daohugou beds is still debated. The radiometric dating of the overlying ignimbrite studied by different researchers yielded a similar age: 164–152 Ma (Chen *et al*., 2004; Liu *et al*., 2006), a middle or early late Jurassic age. The composition of hymenopterans from Daohugou suggests that the assemblage is probably middle Jurassic (e.g. Rasnitsyn *et al*., 2006). However, Zhang (2010, 2011) suggested a middle Jurassic–early late Jurassic age based on the fact that Daohugou dipterans were similar to those from Karatau (probably Callovian–Oxfordian). The types of the new species described herein are housed in the Nanjing Institute of Geology and Palaeontology, Nanjing. The specimens were examined both dry (under low-angled light) and under 70% alcohol. Photographs were taken using a Zeiss Discovery V20 microscope with a digital camera attached. Line drawings were made under a binocular Olympus SZX7 using a camera lucida.

Phylogenetic analysis

Taxon selection

Exemplar taxa for phylogenetic analyses were selected from adult specimens only. Exemplars included: (i) two Jurassic species, *Sinobrevipogon jurassicus* **sp.n.** and *Tarsomegamerus mesozoicus* Zhang, 2005; (ii) species belonging to nine extant artematopodid genera; (iii) *Nipponocyphon nakanei* Lawrence & Yoshitomi, 2007 (Scirtidae), a member of the polyphagan superfamily Scirtoidea, and (iv) *Eulichas* Jakobson, 1913, representing the family Eulichadidae, into which *Tarsomegamerus* was placed by Kirejtshuk & Azar (2013).

In-group taxa

Allopogonia Cockerell, 1906. Data from dissection of *A. villosus* Horn. *Artematopus* Perty, 1830. Data from Crowson (1973) and dissections of several species. *Brevipogon* Lawrence, 2005. Data from Lawrence (2005) and dissections of *B. confusus* (Fall). *Carcinognathus* Kirsch, 1873. Data from Crowson (1973) and dissections of one species. *Ctesibius* Champion, 1897. Data from Lawrence (1995) taken from holotype of *C. eumolpoides* Champion. *Electribius* Crowson, 1973. Data from Crowson (1973), Lawrence (1995, 2005) and Hörnschemeyer (1998) and dissection of holotype of *E. crowsoni* Lawrence. *Eurypogon* Motschulsky, 1859. Data from Sakai (1982), Kundrata *et al.* (2013) and dissections of several species. *Macropogon* Motschulsky 1845. Data from Crowson (1973), Lawrence (2005) and dissections of several species. *Proartematopus* Crowson, 1973. Data from Crowson (1973). *Sinobrevipogon* **gen.n.** Data given below. *Tarsomegamerus* Zhang, 2005. Data from Zhang (2005) and data given below.

Out-group taxa

Nipponocyphon Lawrence & Yoshitomi, 2007. Data from Lawrence & Yoshitomi (2007) and dissection of paratype of *N. nakanei* Lawrence & Yoshitomi. *Eulichas* Jakobson, 1913. Data from Lawrence *et al*. (1995), Hájek (2007), Lawrence *et al*. (2011) and dissections of several species.

Thirty discrete morphological characters were selected and coded using the Delta editor. Morphological characters used in the phylogenetic analysis are listed in Table S1. All characters were unordered and unweighted. The data matrix is given in Table S2.

Analysis

The morphological matrix was analysed under parsimony with the program TNT (Goloboff *et al*., 2008) assigning equal and implied weights. The implied weighting analyses were aimed at minimizing the effect of homoplasy over the phylogenetic signal by using various values of concavity constant, K, ranging from 3–50. The value of K dictates the strength of the weighting against homoplastic characters, as measured by the number of additional steps required to fit the cladogram topology in question; with higher values of K weighting less strongly against the homoplasy (Goloboff, 1993). All characters were treated as nonadditive and were optimised on cladograms using unambiguous optimization in Winclada (Nixon, 2002). Gaps were treated as missing characters. The small size of the matrix enabled us to use the implicit enumeration in equal and implied weighting approaches, and it has always resulted in a single tree with the same topology irrespective of the analytical method.

Phylogenetic assessment of Jurassic artematopodids

In the single cladogram resulting from the dataset and analysis described above (Fig. 6), the family Artematopodidae is monophyletic, including the two fossil genera *Sinobrevipogon* and *Tarsomegamerus*, but excluding the genus *Eulichas* (Eulichadidae). Within the family, three clades are supported: (i) *Electribius*, (ii) (*Sinobrevipogon* + *Tarsomegamerus*) + (*Brevipogon* + *Ctesibius*), and (iii) (*Artematopus* + (*Carcinognathus* + *Proartematopus*)) + (*Allopogonia* (*Eurypogon* + *Macropogon*)). The inclusion of *Tarsomegamerus* in this family, exclusive of *Eulichas,* contradicts statements by Kirejtshuk & Azar (2013) that the former genus should be transferred tentatively to Eulichadidae. The genus *Electribius*, represented in both the Oligocene and Recent faunas, was placed by Crowson (1973) in a subfamily Ctesibiinae, along with the Mexican genus *Ctesibius*, but Lawrence (1995) placed *Electribius* in a separate subfamily and reduced Ctesibiinae to tribal rank within Artematopodinae, along with Allopogonini, Macropogonini and Artematopodini. In a later work, Lawrence (2005) recognized both Electribiinae and Allopogoninae as subfamilies and within Artematopodinae, and both *Ctesibius* and a new genus *Brevipogon* were placed outside the main artematopodinae clade (Macropogonini + Artematopodini) in two cladograms based on a cladistic analysis of 34 adult characters. The present analysis based on both fossil and Recent genera does not support the position of *Allopogonia*, which here forms part of the macropogonine clade, but does support the sister group relationship of *Ctesibius* and *Brevipogon* in one of Lawrence's two cladograms. *Sinobrevipogon* and *Tarsomegamerus* form a clade sister to the modern ctesibiine clade, and not to the bulk of Recent taxa, as might be expected given their age (see Discussion).

Systematic palaeontology

Family: Artematopodidae Lacordaire, 1857
Subfamily *incertae sedis*

Genus: *Sinobrevipogon* gen.n.

Type species. Sinobrevipogon jurassicus **sp.n.**, designated here.

Diagnosis. Moderately large, elongate oval, densely setose. Eyes relatively large, laterally protruding. Antennae long, 11-segmented, slightly serrate. Pronotum transverse, with complete lateral carinae; prosternum with a pair of longitudinal carinae in front of procoxae. Elytra striate, densely setose, with apical interlocking tongue on the ventral side of each elytron. Prosternal process relatively wide, subparallel-sided. Protrochantins exposed. Mesocoxae moderately widely separated; mesocoxal cavity closed by the mesepimeron and the anteromesal edge of metanepisternum. Metacoxae excavate, with narrow but complete coxal plates. Meso- and metatarsi five-segmented, metatarsomeres 1 and 2 elongate, tarsomeres 3 and 4 lobed. Abdominal ventrite 1 short, much shorter than ventrite 2; ventrite 5 very long, longer than ventrites 3 and 4 combined. Sutures between all abdominal ventrites more or less curved; suture between ventrites 4 and 5 very strongly curved anteriorly.

Etymology. The genus-group name is a combination of *Sino*-, meaning 'China', and the genus *Brevipogon*; it is masculine in gender.

Sinobrevipogon jurassicus sp.n.

(Figs 2–4)

Material. Holotype, NIGP160704; paratypes, NIGP160705, NIGP160706. The holotype is a nearly completely preserved adult beetle, with both dorsal and ventral characters (including hindwings) visible. The paratype NIGP160705 displays mainly ventral and some dorsal aspects visible. NIGP160706 shows mainly dorsal and a few ventral (abdominal ventrites) aspects of the beetle, with palpi, coxal cavities, and legs not preserved.

Occurrence. Middle Jurassic Jiulongshan Formation; Daohugou, Ningcheng County, Inner Mongolia, northeastern China.

Diagnosis. As for the genus (*vide supra*).

Description. Body moderate, 6.20–6.50 mm long. Densely clothed with recumbent hairs.

Head narrower than pronotum, 0.76 mm long, 1.26 mm wide; not declined, not constricted posteriorly. Posterior edge with a pair of vertical impressions. Frontal region usually not declined. Eye well developed, slightly protuberant, entire. Antennal insertion located at anterolateral edges of head, slightly in front of eye, widely separated and exposed. Subantennal groove absent.

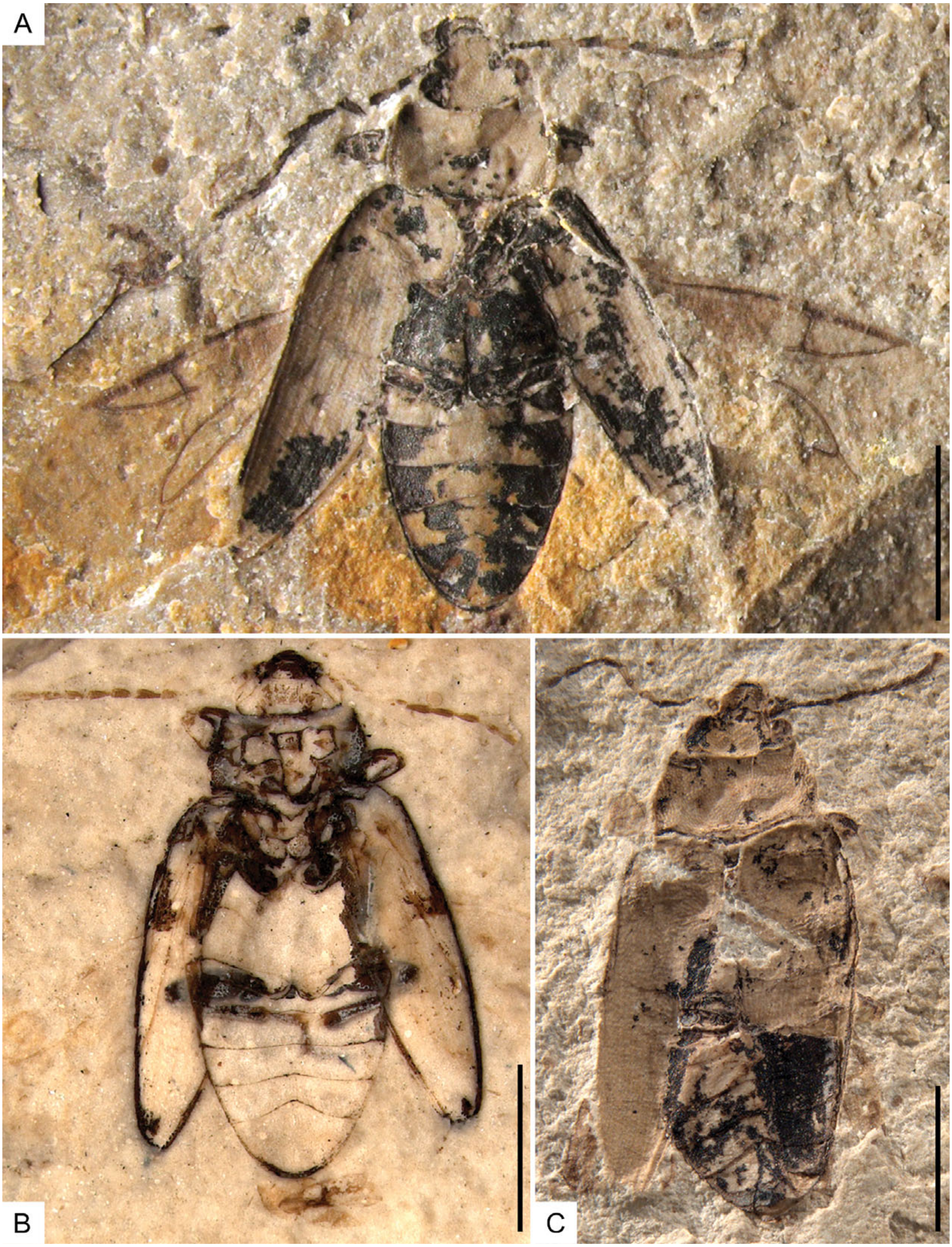

Fig. 2. General habitus of *Sinobrevipogon jurassicus* **gen. et sp.n.** (A) Holotype, NIGP160704. (B) Paratype, NIGP160705. (C) Paratype, NIGP160706. (A, C) Under low-angled light; (C) moistened with 70% alcohol. Scale bars: 2 mm.

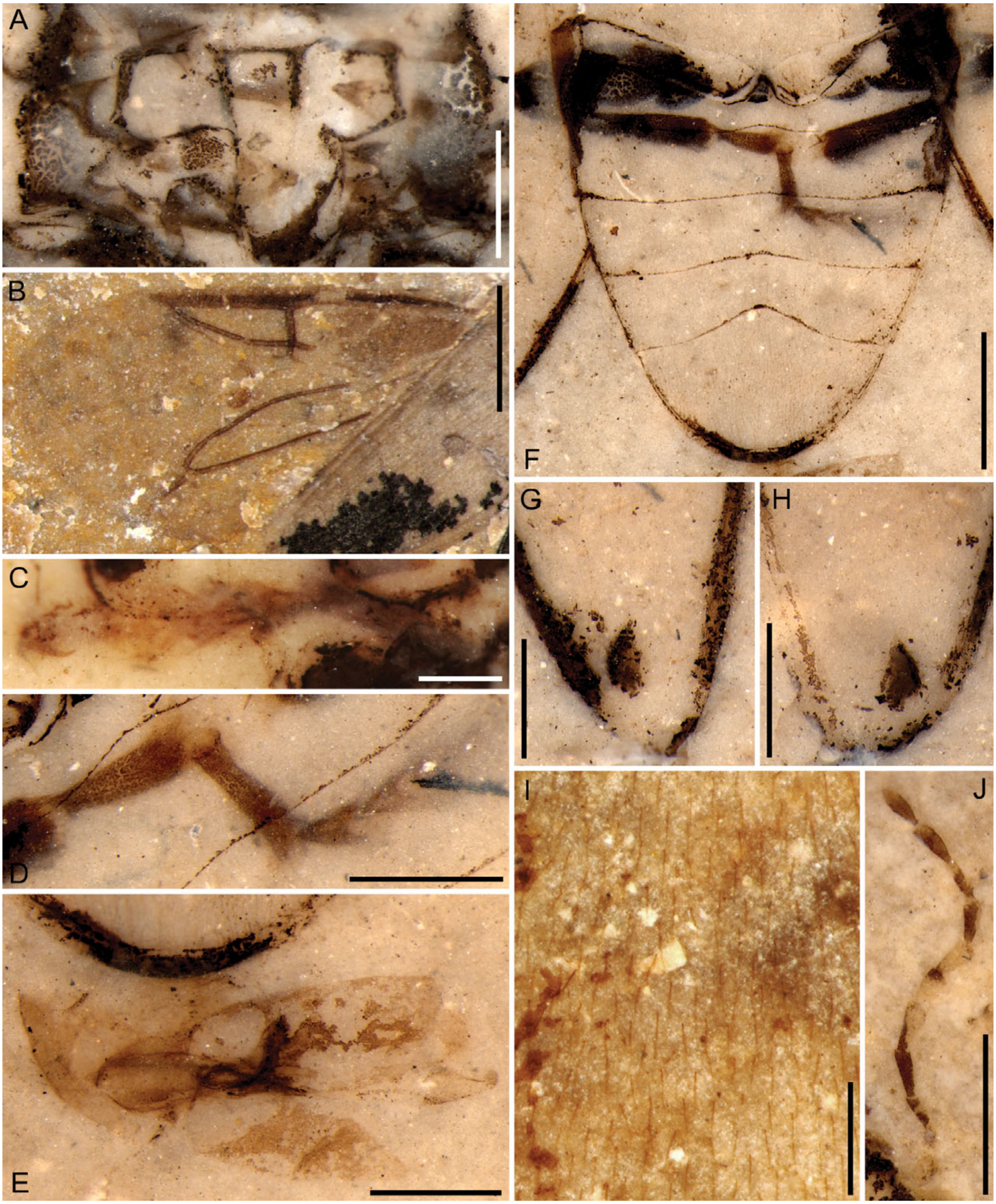

Fig. 3. Enlargements of *Sinobrevipogon jurassicus* **gen. et sp.n.** (A) Details of prothorax, showing the paired carinae on prosternum, paratype, NIGP160705. (B) Left hind wing of holotype. (C) Right mesotarsus, NIGP160705. (D) Left metatarsus of paratype (NIGP160705), showing lobed tarsomeres 3 and 4. (E) Enlargement of the exposed trilobate aedeagus, NIGP160705. (F) Abdomen of NIGP160705. (G, H) Apex of elytron, showing apical interlocking tongue on ventral side of elytron, NIGP160705. (I) Enlargement of fine and dense setae on elytron, holotype. (J) Left antenna of paratype, showing slightly serrate antennomeres, NIGP160706. Scale bars: 1 mm (B, F, G); 200 µm (C, I); 500 µm in others.

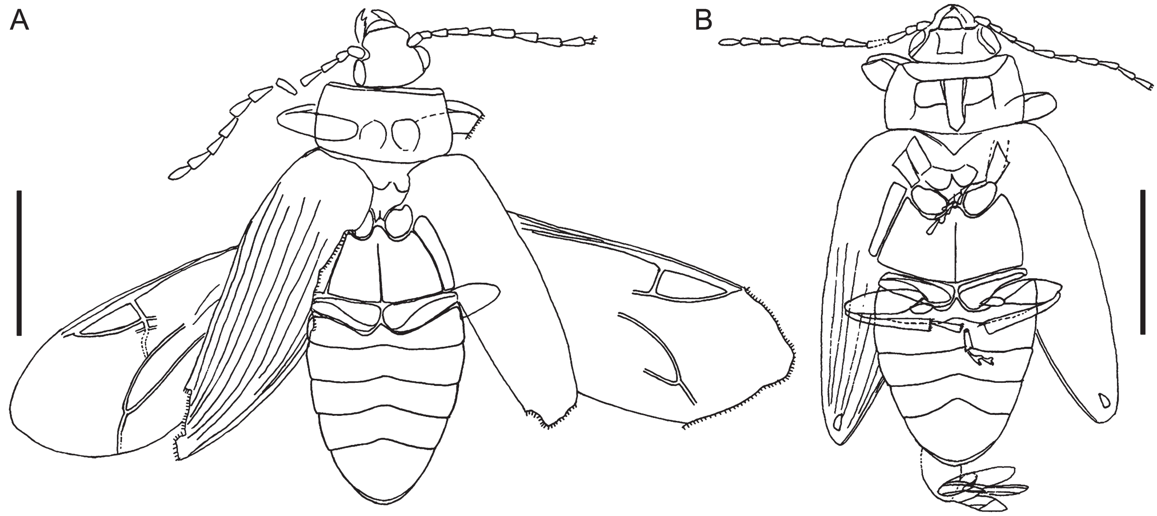

Fig. 4. Line drawings of *Sinobrevipogon jurassicus* **gen. et sp.n.** (A) Holotype, NIGP160704. (B) Paratype, NIGP160705. Scale bars: 2 mm.

Frontoclypeal suture absent. Anterior edge of frontoclypeus rounded. Antenna (Fig. 3J) 11-segmented, slightly serrate, long, extending posteriorly to metaventrite; antennomere 1 long, broad; antennomere 2 longer than wide, narrower than antennomere 1; antennomere 3 elongate; antennomere 4 elongate, slightly longer than 3; antennomeres 5–10 each slightly serrate, clothed with dense short hairs, each >2× as long as wide; antennomere 11 elongate, fusiform. Mandible acute. Gular sutures widely separated.

Pronotum transverse, 0.92 mm long, 1.84 mm wide, 0.5× as long as wide; widest at base; sides slightly curved; base slightly narrower than elytral bases; lateral pronotal carinae complete; anterior angles nearly right; posterior angles slightly acute; posterior edge bisinuate; disc densely setose. Prosternum (Fig. 3A) in front of coxae longer than mid length of procoxal cavity; with paired, slightly oblique carinae, without deep pits at anterior ends of paired carinae. Prosternal process complete, more or less parallel-sided. Procoxa transverse, protrochantin exposed. Procoxal cavities strongly transverse, moderately widely separated, externally open. Scutellar shield well developed, longer than wide, posteriorly broadly rounded. Elytron complete, 4.26 mm long, each 1.28 mm wide; 4.63× as long as pronotum; punctation distinctly seriate, with about ten distinct puncture rows, punctures apparently very large; densely setose (Fig. 3I); apex rounded, with ventrally interlocking tongue, which is more or less semicircular (Fig. 3G, H); epipleuron very narrow, complete. Mesoventrite very short; anterior edge with paired, strongly declined procoxal rests; discrimen present but incomplete; mesoventral cavity small, oblique. Mesocoxa not projecting. Mesotrochantin exposed. Mesocoxal cavities moderately widely separated, slightly transverse, partly closed by mesepimeron and metanepisternum. Metaventrite long, moderately convex; discrimen moderately long; transverse (katepisternal) suture almost complete, located close to posterior edge of metaventrite; exposed portion of metanepisternum elongate, broader anteriorly. Metacoxa transverse, contiguous, extending laterally to meet elytron, plates weakly developed, but complete; metatrochanter oval-shaped, moderate; metafemur robust; metatibia slender, gradually dilated to apex, longer than metafemur, with two simple small spurs at apex. Hindwing present (Fig. 3B), radial cell 1.9× as long as wide at base, inner basal angle almost right. Legs moderately long; metatarsus (Fig. 3D) five-segmented, tarsomere 1 elongate, gradually dilated to apex, as long as antennomere 2; tarsomere 2 narrower than 1; tarsomeres 3–4 each ventrally lobed.

Abdomen (Fig. 3F) broad, with five apparently connate ventrites, the sutures between them obvious, sinuate with anterior mesal curvature increasing posteriorly; suture between ventrites 4 and 5 very strongly curved. Ventrite 1 much shorter than 2, without postcoxal lines; intercoxal process angulate. Ventrites 2 and 3 almost in same length. Ventrite 4 shortest medially. Ventrite 5 longer than ventrites 3 and 4 combined. Aedeagus (Fig. 3E) exposed, trilobate, symmetrical; parameres individually articulated. Penis undivided (without dorsal and ventral lobes), with short anterior struts.

Etymology. Derived from Jurassic, the age of the fossil.

Discussion

Sinobrevipogon **gen.n.** is placed in the modern elateroid family Artematopodidae based on the paired carinae on the prosternum (Fig. 5E) and the presence of an internal, apical interlocking tongue on the ventral side of each elytron (Fig. 5A, C) (Lawrence, 2010). The elytral interlocking tongue, referred to by Johnson (2002) as a laminar flange, also occurs in some members of the family Byrrhidae (Lawrence *et al.*, 2011, fig. 24C, E), which differ in many other respects from Artematopodidae. In addition, a number of other features are suggestive of this assignment, including the slightly serrate antennae, transverse pronotum, lobed tarsomeres 3 and 4, slightly excavate

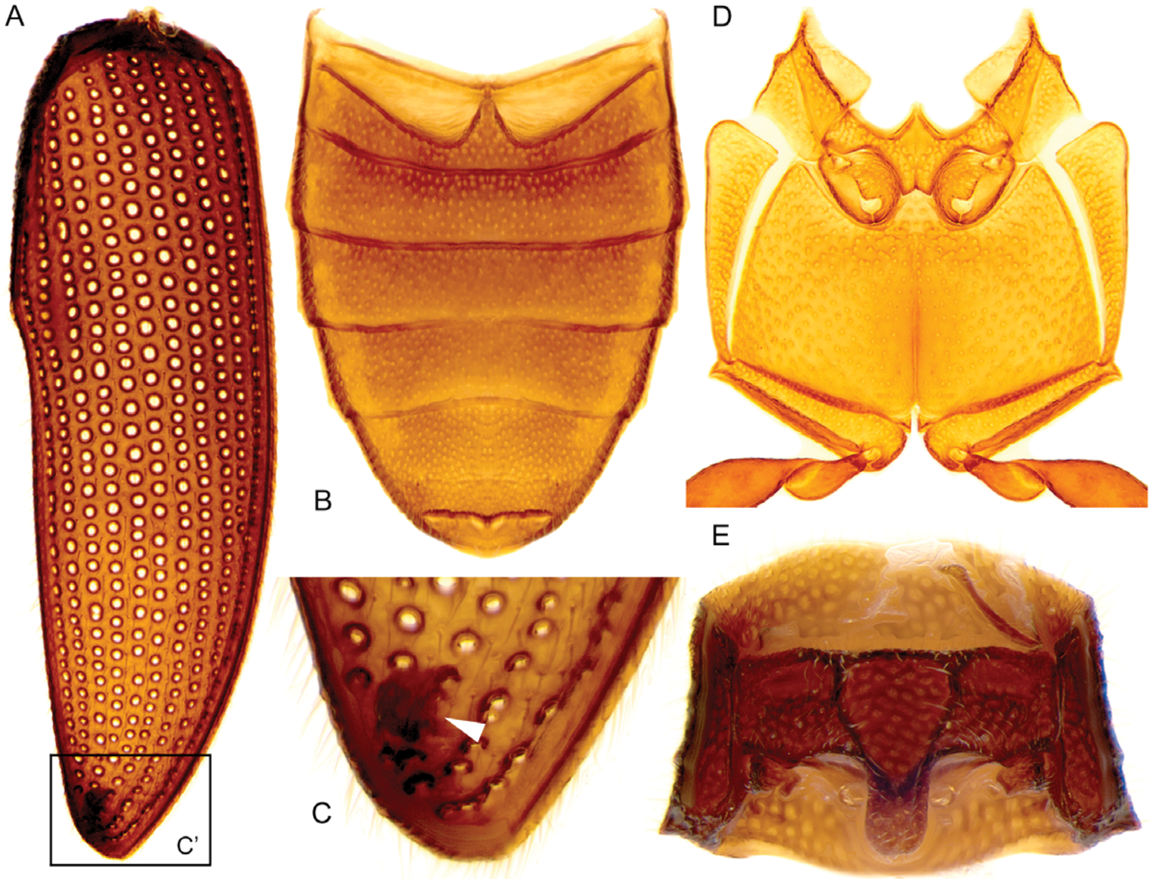

Fig. 5. Some key characters of a Recent artematopodid, *Eurypogon* sp. (A) Ventral view of right elytron. (B) Abdomen. (C) Enlargement of (A), with the internal, apical interlocking tongue on the ventral side of elytron indicated. (D) Meso- and metathorax. (E) Ventral view of prothorax, showing paired carinae on prosternum.

metacoxae with metacoxal plates narrow and complete, and the strongly curved sutures between abdominal ventrites 4 and 5. There are currently three subfamilies recognized in the Artematopodidae: Electribiinae, Allopogoninae and Artematopodinae (Lawrence, 2005, 2010). Among the three subfamilies, the new genus is separated from the Electribiinae by lacking cavities beneath antennal insertion and a transverse groove connecting paired cavities on pronotum, and from Allopogoninae (*Allopogonia*) by the presence of distinct paired carinae on prosternum and very slightly serrate antennae. It appears that *Sinobrevipogon* shares most similarities with members of Artematopodinae, such as the presence of paired longitudinal carinae continuous with lateral margins of the prosternal intercoxal process and slightly serrate antennomeres, which are more than twice as long as wide (e.g. Lawrence, 2005). There are six modern genera included in Artematopodinae. *Sinobrevipogon* differs from the Neotropical genera *Artematopus* and *Carcinognathus* by the absence of pits at anterior ends of paired carinae on prosternum and by the different structure of the frontoclypeus. It differs from *Eurypogon* and *Macropogon* by relatively long antennomeres 2 and 3, complete and well-defined lateral pronotal carinae, and the strongly curved sutures between ventrites 4 and 5 (Fig. 5B); it differs from *Ctesibius* by the proportions of the abdominal ventrites and distinctly striate elytra. The Jurassic *Sinobrevipogon* **gen.n.** is most similar to the Recent *Brevipogon* in general habitus. They share the elongate-oval body shape, absence of pits at the anterior ends of paired prosternal carinae, the striate elytra and the recumbent elytral hairs. However, *Sinobrevipogon* **gen.n.** is distinguished from the latter by normal (not lobed) tarsomeres 1 and 2 and by much more strongly curved sutures between ventrites 4 and 5. In addition, the new genus differs from the extinct (Eocene) genus *Protartematopus* Crowson by its general habitus, including slender, slightly serrate antennae and strongly curved sutures between ventrites 4 and 5. In addition to the unusual combination of characters mentioned above in *Sinobrevipogon* **gen.n.**, this genus has a remarkable distinctive feature that is not found in any modern artematopodid, namely, the fact that the mesocoxal cavity is partly closed by both mesepimeron and metanepisternum. The mesocoxal cavitiy in all other artematopodids is closed laterally by the mesepimeron, whereas the mesanepisternum is at least slightly removed from the edge of the cavity (Fig. 5D). This feature is very rare among modern families of polyphagan beetles. It occurs in the suborder Archostemata (e.g. Hörnschemeyer,

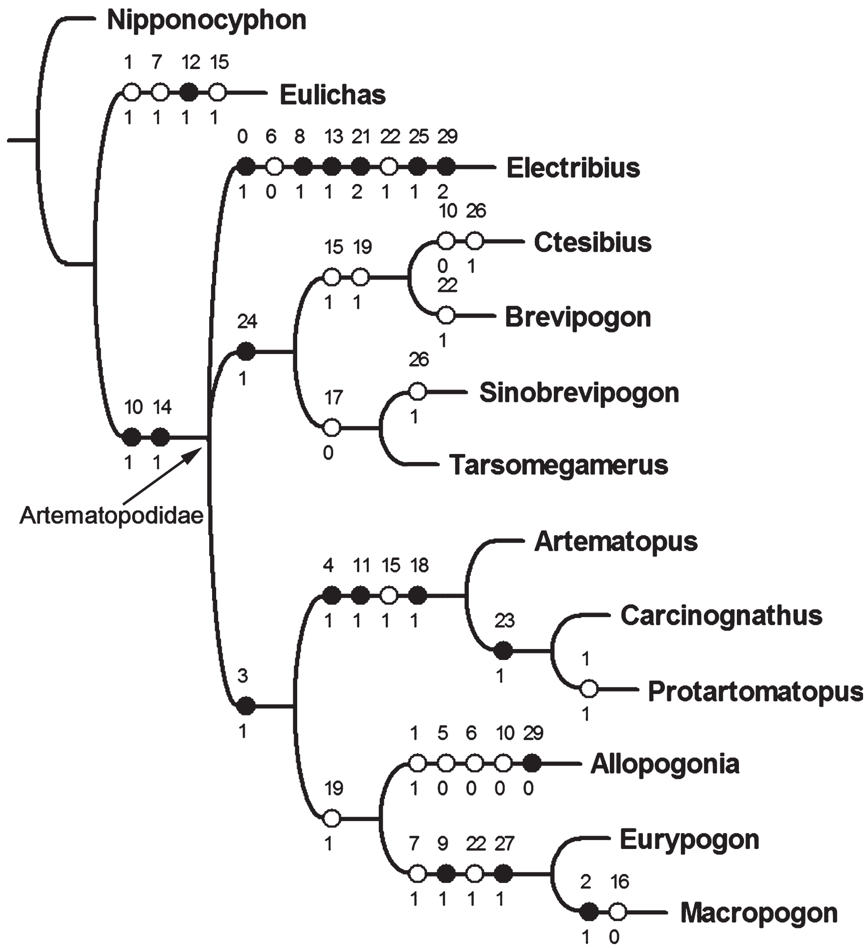

Fig. 6. Phylogenetic reconstructions of Artematopodidae: a tree with characters mapped on branches using unambiguous optimization in Winclada.

2005; Lawrence *et al.*, 2011). In addition, it is found in members of an extinct subfamily Eodromeinae Ponomarenko of the peculiar adephagan family Trachypachidae (e.g. Ponomarenko, 1977; Wang *et al.*, 2012). Yet it also occurs at least in the enigmatic modern polyphagan family Derodontidae (*Derodontus* LeConte; e.g. Ge *et al.*, 2007), in the scirtoid families Decliniidae and Scirtidae (e.g. Friedrich & Beutel, 2006), and in a few basal Staphyliniformia.

Zhang (2005) described an interesting genus *Tarsomegamerus* from the Jurassic Daohugou beds, which is in the same deposit as the one yielding type specimens of *Sinobrevipogon*. *Tarsomegamerus* was assigned to the extinct subfamily Protoscelinae of Chrysomelidae, representing the first record of chrysomeloids from the Mesozoic of China (Zhang, 2005). Kirejtshuk *et al.* (2010) transferred *Tarsomegamerus* to a palaeoendemic Mesozoic elateriform family Lasiosynidae based on the elongate radial cell of posterior wing, distinctly raised femoral plates of metacoxae, and striate elytra. However, Yan *et al.* (2013) excluded *Tarsomegamerus* from Lasiosynidae on the basis of the absence of both longitudinal and katepisternal sutures on metaventrite, the widely separated mesocoxae, small eyes, mandibles and short temples, and suggested that it seems closer to Byrrhidae or Ptilodactylidae. Yan *et al.* (2014) clarified that the tarsi of *Tarsomegamerus* are not pseudotetramerous, removed it from Lasiosynidae. Kirejtshuk & Azar (2013) transferred *Tarsomegamerus* to the subfamily Eulichadinae within the modern Eulichadidae, and suggested that *Parelateriformius* Yan & Wang is a synonym of *Tarsomegamerus*. However, it is clear that *Parelateriformius* differs from the latter by many characters, including moderately serrate antennae, absence of paired carinae on prosternum, relatively long ventrite 1, and the straight sutures between abdominal ventrites. Therefore, it is becoming more and more evident that *Tarsomegamerus* is by no means a member of subfamily Protoscelinae of Chrysomelidae. In addition, the extinct subfamily Protoscelinae from the Middle to Upper Jurassic deposits of Karatau has been transferred from Chrysomelidae to the weevil family Anthribidae (Legalov, 2013). Here we suggest that *Tarsomegamerus* actually belongs to the elateroid family Artematopodidae as supported by a number of defining characters. As shown in clearer images (moistened with alcohol) of the holotype of *Tarsomegamerus* posted online (Kirejtshuk, 2010), the characteristic paired carinae on prosternum and the apical interlocking (apparently darkened) tongue on the ventral side of elytron are clearly visible. Moreover, the slightly serrate antennae, transverse pronotum, lobed tarsomeres, slightly excavate metacoxae, and the unusual curved sutures between abdominal ventrites are all clearly visible even in the original photomicrographs and line drawings (Zhang, 2005). Many unusual features found in *Tarsomegamerus* such as paired carinae on prosternum and curved sutures between abdominal ventrites usually do not occur in the superfamily Byrrhoidea.

Tan & Ren (2007) described a very unusual species *Forticatinius elegans* Tan & Ren from the Yixian Formation (currently of Early Cretaceous age) of western Liaoning province, China. They placed the genus in an extinct archostematan family Catiniidae and suggested that it was somewhat intermediate between catiniids and primitive myxophagan beetles (Tan & Ren, 2007). Kirejtshuk *et al*. (2010) transferred the genus from Catiniidae to the cucujiform superfamily Cleroidea and suggested that it could be a junior synonym of *Nitidulina* Martynov (1926). However, *Forticatinius* is different from *Nitidulina* in a number of features, including slightly serrate antennae (slightly clubbed in *Nitidulina*), subtriangular head widest at base (head narrowed to base in *Nitidulina*), well separated mesocoxae (sub-contiguous in *Nitidulina*), ventrite 1 shorter than 2 (ventrite 1 longer than 2 in *Nitidulina*), and sutures between abdominal ventrites curved (all sutures straight in *Nitidulina*). As shown in Tan & Ren (2007: fig. 6) and Tan & Ren (2009: fig. 6.42), the slightly serrate antennae, separated mesocoxae, contiguous excavate metacoxae, short first abdominal ventrite and the typical curved sutures between abdominal ventrites are all suggestive of the polyphagan family Artematopodidae, rather than the archostematan Catiniidae. Due to the poor preservation condition of the holotype of *Forticatinius*, it is difficult to decide whether the paired carinae on prosternum and apical interlocking tongue on the ventral side of elytron are present or not. Still, we suggest that *Forticatinius* is probably a polyphagan genus and is likely close to modern Artematopodidae.

Sinobrevipogon **gen.n.** is very similar to the genus *Tarsomegamerus*; they share similar body habitus, slightly serrate antennae, paired carinae on prosternum, and curved sutures between abdominal ventrites. However, *Sinobrevipogon* **gen.n.** differs from the latter by much smaller body (14.6 mm long in *Tarsomegamerus* versus 6.23 mm long in *Sinobrevipogon* **gen.n.**), longer antennae, and much longer abdominal ventrite 5 (longer than ventrites 3 and 4 combined in *Sinobrevipogon* **gen.n.**, but shorter than 3 and 4 combined in *Tarsomegamerus*). *Sinobrevipogon* **gen.n.** is separated from *Forticatinius* by smaller body size (11.0 mm in *Forticatinius*), longer antennae, large eyes and longer ventrite 5.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12131

Table S1. Morphological character state descriptions.

Table S2. Morphological matrix.

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