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A large artematopodid beetle (Coleoptera: Elateroidea: Artematopodidae) from the Early Cretaceous of China and its systematic position

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ABSTRACT

Artematopodidae is small basal group of elateroid beetles. Definitive Mesozoic artematopodids are currently confined to the Middle Jurassic Daohugou biota. Here we report a new genus and species, *Cretobrevipogon breviantennatus* gen.et sp. nov., from the Lower Cretaceous Yixian Formation (ca. 125 Ma) in Liaoning Province, northeastern China. *Cretobrevipogon* exhibit many diagnostic features of the extant family Artematopodidae, such as paired carinae on prosternum and more importantly, an apical interlocking tongue on the ventral side of elytron. Phylogenetic analyses indicate that *Cretobrevipogon* is closely related to the Middle Jurassic *Sinobrevipogon*. They share a presumably plesiomorphic character, i.e. mesocoxal cavitiy closed by mesepimeron and anterolateral edge of metanepisternum. The discovery of a new genus from the Early Cretaceous highlights the morphological disparity and palaeodiversity of the family in the Mesozoic. Artematopodidae probably represent a relictual elateroid family that once diversified in the middle–late Mesozoic.

1. Introduction

The family Artematopodidae is small group of elateroid beetles, with approximately 70 described species in nine extant genera (Lawrence, 2005, 2010). Recent molecular-based phylogenetic analyses strongly indicate that Artematopodidae, together with Omethidae and Telegeusidae, forms the basal-most lineage of Elateroidea (Kundrata et al., 2014; McKenna et al., 2015; Zhang et al., 2018). Artematopodidae is now divided into three subfamilies: Electribiinae (*Electribius* Crowson, Mexico, Central America, Eocene Baltic amber, and Miocene Mexican amber); 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 Russian, Japan; *Macropogon* Motschulsky, North America, Asia; and *Proartematopus* Crowson, Eocene Baltic amber) (Crowson, 1973; Lawrence, 1995, 2005; 2010; Young, 2002; Wu et al., 2015). Among all elateroid beetles, adults of Artematopodidae can be readily recognized by a peculiar feature, namely a tongue-like process associated with the apicoventral region of the elytron (Lawrence, 2005).

Fossils belonging to Artematopodidae are poorly documented. Mesozoic artematopodids have recently reported from the Middle Jurassic Daohugou beds (Inner Mongolia, northeastern China). Jurassic artematopodids currently include two genera: *Sinobrevipogon* Cai et al. and *Tarsomegamerus* Zhang (Cai et al., 2015). Cai et al. (2015) also indicated that the unusual species, *Forticatinius elegans* Tan and Ren, from the Lower Cretaceous Yixian Formation is closely related to members of Artematopodidae, rather than a member of Myxophaga as originally proposed by Tan and Ren (2007). Peris et al. (2016) listed an undescribed artematopodid from the mid-Cretaceous amber from France. Cenozoic artematopodids are principally known from the upper Eocene Baltic amber (Lawrence, 2010). Two

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genera are known from this deposit: *Electribius*, with four extinct species and two extant ones and the monotypic genus *Proartematopus* (Crowson, 1973; Lawrence, 1995; Hörnschemeyer, 1998). Wu et al. (2015) reported the youngest fossil artematopodid, *Electribius palaeomexicanus* Wu et al., from the Miocene Mexican amber, and the intriguing biogeographic implication of *Electribius* was tentatively discussed. Here we report the first definitive artematopodid fossil from the Lower Cretaceous Yixian Formation (Jehol biota). The systematic position of the new genus is discussed.

2. Material and methods

Fossil material. The studied specimen, with part and counterpart, has been collected from the yellowish tuff of Jingangshan Member of Yixian Formation near Huangbanjigou Village (Fig. 1; Beipiao, Liaoning Province, northeastern China; also refer to Cai et al., 2011). This stratum (Yixian Formation) represents a typical component of the famous Jehol biota well known for yielding feathered dinosaurs, mammals, primitive birds, angiosperm plants and numerous insects (e.g., Chang, 2003). The precise age of the Yixian Formation has been indicated as circa 125 million years ago (Swisher III et al., 1999). The fossil beetle has been split through the median gap into two counterparts. Although characters of both ventral and dorsal sides are imprinted on both counterparts, one part (NIGP168714a) better preserves characters of the dorsal side, whereas the other (NIGP168714b) displays more characters of the ventral side. The holotype is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences (Nanjing, Jiangsu Province). The specimen was examined both dry (under low-angled light) and moistened with 70% alcohol (in order to improve contrast). Photographs were taken using a Zeiss Discovery V20 microscope with a digital camera attached. Extended depth of field images were digitally compiled using Helicon Focus 3.10 software, and arranged in Adobe Photoshop CS5. The nomenclatural acts established herein are registered under ZooBank LSID: urn:lsid:zoobank.org:pub:C87042E6-763C-4241-86DF-155707337F5D.

Phylogenetic analyses. We scored *Cretobrevipogon breviantennatus* sp. nov. for 30 adult characters and integrated the fossil taxon along with representatives of extant and extinct genera of Artematopodidae and two scirtoid outgroups (basal-most polyphagan families as suggested by molecular-based phylogenies, McKenna et al., 2015; Zhang et al., 2018). All selected characters were derived from Cai et al. (2015). Exemplar taxa for phylogenetic analyses were selected from adults only, since larvae remains largely unknown. Exemplars included: 1) Two fossil species: *Sinobrevipogon jurassicus* Cai et al. from the Middle Jurassic and *C. breviantennatus* from the Early Cretaceous; 2) species belonging all nine extant artematopodid genera; and 3) *Declinia relicta* Nikitsky et al. (Decliniidae) and *Nipponocyphon nakanei* Lawrence and Yoshitomi (Scirtidae) as the outgroup in the phylogenetic analyses.

Maximum parsimony analysis was conducted using TNT 1.5 (Goloboff and Catalano, 2016) using New Technology search. We used two search strategies, including equal weights and implied weights. Goloboff et al. (2018) suggested that equal-weights parsimony and model-based methods (Mk model; Lewis, 2001) seem to perform similarly, and implied weighting outperformed equal weights. As suggested in Goloboff et al. (2018), better phylogenetic results can be obtained using implied weighting under larger concavity values of K ($K = 12$). For the implied weighting analysis, we tested a concavity value of 12 and found no changes to the tree topology under the equally weighting analysis. Branch support values were estimated using 10,000 bootstrap replicates under implied weighting ($K = 12$).

Out-group taxa.
Declinia Nikitsky et al., data from Nikitsky et al. (1993), and Lawrence et al. (1995).
Nipponocyphon Lawrence and Yoshitomi, data from Lawrence and Yoshitomi (2007) and dissection of paratype of *N. nakanei.*

In-group taxa.
Allopogonia Cockerell, data from dissection of *A. villosus* Horn.
Artematopus Perty, data from Crowson (1973) and dissections of several species.
Brevipogon Lawrence, data from Lawrence (2005) and dissections of *B. confuisus* (Fall).
Carcinognathus Kirsch, data from Crowson (1973) and dissections of one species.
Ctesibius Champion, data from Lawrence (1995) taken from holotype of *C. eumolpoides* Champion.
Electribius Crowson, data from Crowson (1973), Lawrence (1995, 2005) and Hörnschemeyer (1998) and dissection of holotype of *E. crowsoni* Lawrence.

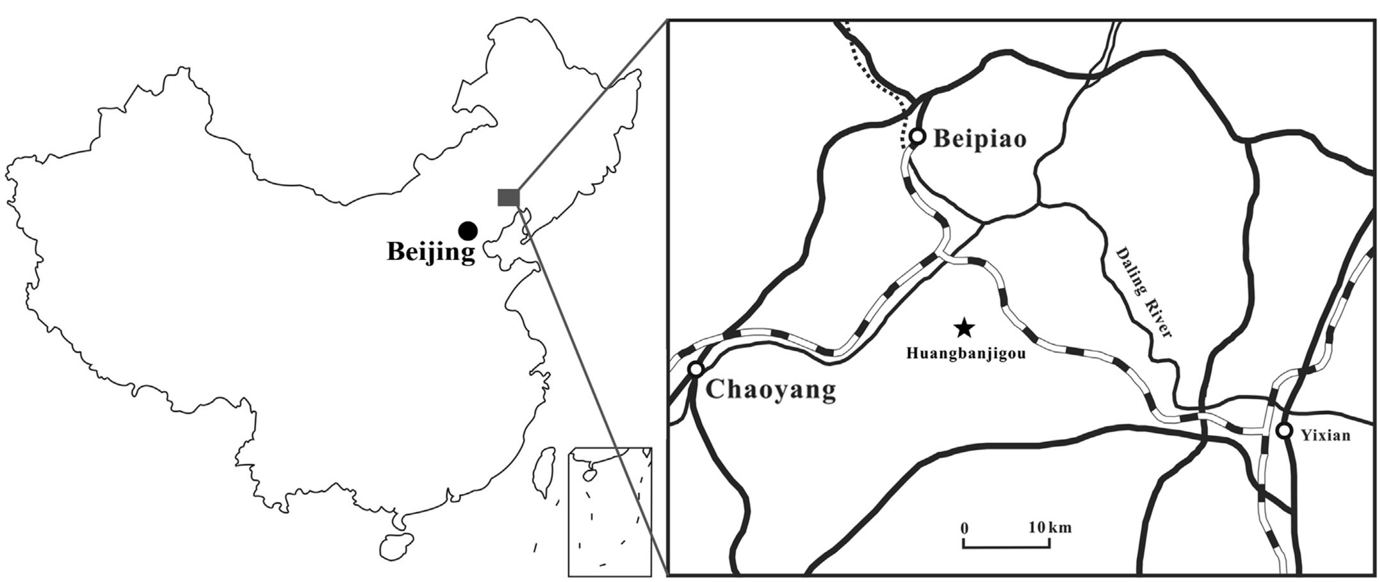

Fig. 1. Map of western Liaoning Province, with the solid star indicating the fossil locality at Huangbanjigou.

Eurypogon Motschulsky, data from Sakai (1982), Kundrata et al. (2013) and dissections of several species.
Macropogon Motschulsky, data from Crowson (1973), Lawrence (2005) and dissections of several species.
Proartematopus Crowson, data from Crowson (1973).
Sinobrevipogon jurassicus Cai et al., data from Cai et al. (2015).
Cretobrevipogon breviantennatus sp. nov., data given below.

Morphological characters and states.

1. Large, deep setose cavity beneath antennal insertion: 0, absent; 1, present.
2. Antennae in male: 0, not or weakly serrate; 1, strongly serrate.
3. Antennomere 5: 0, subequal to or only slightly longer than 4 and with similar pubescence; 1, about twice as long as 4 and with denser pubescence.
4. Antennomere 5 in male: 0, clothed mainly with decumbent or inclined hairs; 1, densely clothed with erect hairs.
5. Anterior edge of frontoclypeus: 0, more or less rounded, neither emarginate nor dentate: 1, emarginate or dentate.
6. Mandible: 0, without subapical tooth: 1, with subapical tooth.
7. Terminal maxillary palpomere: 0, not expanded and truncate or if slightly expanded widest point well before apex: 1, distinctly expanded and truncate at apex.
8. Posterior pronotal angles: 0, right, obtuse or rounded: 1, acute.
9. Pronotal disc: 0, without pair of deep, basal impressions: 1, with pair of deep, basal impressions.
10. Pronotal disc: 0, without glabrous elevations: 1, with glabrous elevations.
11. Prosternum in front of coxae: 0, simple, without paired longitudinal ridges: 1, with paired longitudinal ridges continuing anteriorly from lateral margins of prosternal process.
12. Prosternum in front of coxae: 0, without paired cavities: 1, with pair of deep cavities located at anterior ends of paired longitudinal ridges.
13. Elytral punctures: 0, forming distinct, more or less complete rows: 1, forming indistinct rows anteriorly or completely confused.
14. Sutural stria: 0, not deeply impressed at apex: 1, deeply impressed at apex.
15. Elytral apex: 0, without interlocking tongue: 1, with interlocking tongue.
16. Mesoventral cavity: 0, absent or weakly indicated, not or barely extending beyond anterior edges of mesocoxal cavities: 1, distinct and extending well beyond anterior edges of mesocoxal cavities.
17. Distance between mesocoxal cavities: 0, less than 0.25 times shortest diameter of a cavity: 1, greater than 0.25 times shortest diameter of a cavity.
18. Metanepisternum: 0, reaching lateral edge of mesocoxal cavity: 1, not reaching lateral edge of mesocoxal cavity.
19. Axillary space of metaventrite: 0, absent or very weakly developed, its lateral edge less than a fifth as long as distance between it and posterolateral edge of mesoventrite: 1, well developed, its lateral edge more than one-fourth as long as distance between it and posterolateral edge of mesoventrite.
20. Outer edge of metacoxal plate: 0, more or less expanded mesally: 1, straight.
21. Radial cell of hind wing: 0, about as long as wide: 1, at least slightly elongate.
22. Base of radial cell: 0, oblique, so that inner posterobasal angle right or obtuse: 1, straight, so that inner posterobasal angle more or less right; 2, oblique so that inner posterobasal angle is acute.
23. Membranous pad on tarsomeres 2 to 4 or 3 and 4: 0, simple or emarginate: 1, distinctly bilobed.
24. Pretarsal claws: 0, simple: 1, with basal tooth.
25. Suture between ventrites 4 and 5: 0, not or very weakly curved: 1, moderately to strongly curved at middle.
26. Sutures separating ventrites 2 from 3, 3 from 4 to 4 from 5: 0, complete: 1, incomplete at middle.
27. Ventrite 5 at midline: 0, not longer than ventrites 3 and 4 combined: 1, longer than ventrites 3 and 4 combined.
28. Ventrite 5 in male: 0, without transverse subapical groove: 1, with transverse subapical groove.
29. Ventrite 5 in male: 0, not completely covered with glandular hairs: 1, completely covered with glandular hairs.
30. Tergite IX in male: 0, apically truncate, not fused to tergite X: 1, apically emarginate, not fused to tergite X; 2, completely fused to tergite 10.

3. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758
Family: Artematopodidae, Lacordaire, 1857
Subfamily: Unknown

Genus: ***Cretobrevipogon*** gen. nov.
Type species: *Cretobrevipogon breviantennatus* sp. nov.

Etymology. The genus-group name is a combination of *Creto*-, referring to "Cretaceous", and the extant genus *Brevipogon*; it is masculine in gender. The genus is registered under LSID urn:lsid:zoobank.org:act:B17F7D49-3B02-4D35-B2E0-17B7088E65C9.
Diagnosis. Very large (ca. 13.2 mm long), elongate oval. Antennae short, slightly serrate. Pronotum with complete lateral carinae, and acute posterior pronotal angles; prosternum long, with a pair of distinct longitudinal carinae in front of procoxae. Elytra regularly striate, with apical interlocking tongue on the ventral side of each elytron. Prosternal process narrow, slightly widened towards apex. Mesocoxae moderately widely separated; mesocoxal cavitiy closed by the mesepimeron and the anterolateral edge of metanepisternum. Metacoxae excavate, with narrow but complete coxal plates. Abdomen with five visible ventrites; ventrite 1 shortest, much shorter than ventrite 2; ventrite 5 long, slightly shorter than ventrites 3 and 4 combined. Sutures between all abdominal ventrites distinctly curved; suture between ventrites 4 and 5 very strongly curved anteriorly.

Cretobrevipogon breviantennatus sp. nov. (Figs. 2 and 3).

Etymology. Derived from a combination of the Latin adjectives *brevis* and *antennatus*, meaning with short antennae. The species is registered under LSID urn:lsid:zoobank.org:act:94FB9B00-0999-4B02-A536-7D229A444550.
Material. Holotype, NIGP168714a,b, with part and counterpart. The holotype is a nearly completely preserved adult beetle, with both dorsal and ventral characters visible. Some mouthpart structures (e.g., maxillary and labial palpi) and metatarsi are not preserved.
Occurrence. Lower Cretaceous Yixian Formation (ca. 125 Ma, Barremian–Aptian; Swisher III et al., 1999); Huangbanjigou of Beipiao City, Liaoning Province, northeastern China.
Diagnosis. As for the genus (*vide supra*).
Description. Body very large, 13.2 mm long; about 2.5 times as long as wide. Densely and finely setose and punctate.

Head (Fig. 3A) small, much narrower than pronotum, 1.52 mm long and 1.76 mm wide; apparently not declined, slightly narrowed from posterior margins of eyes towards base. Eyes (Fig. 3A) well developed, slightly protuberant, located anteriorly. Antennal insertions located at anterolateral edges of head, slightly in front of eyes, widely separated. Subantennal groove absent. Anterior edge of frontoclypeus rounded. Antennae (Fig. 3B) 11-segmented,

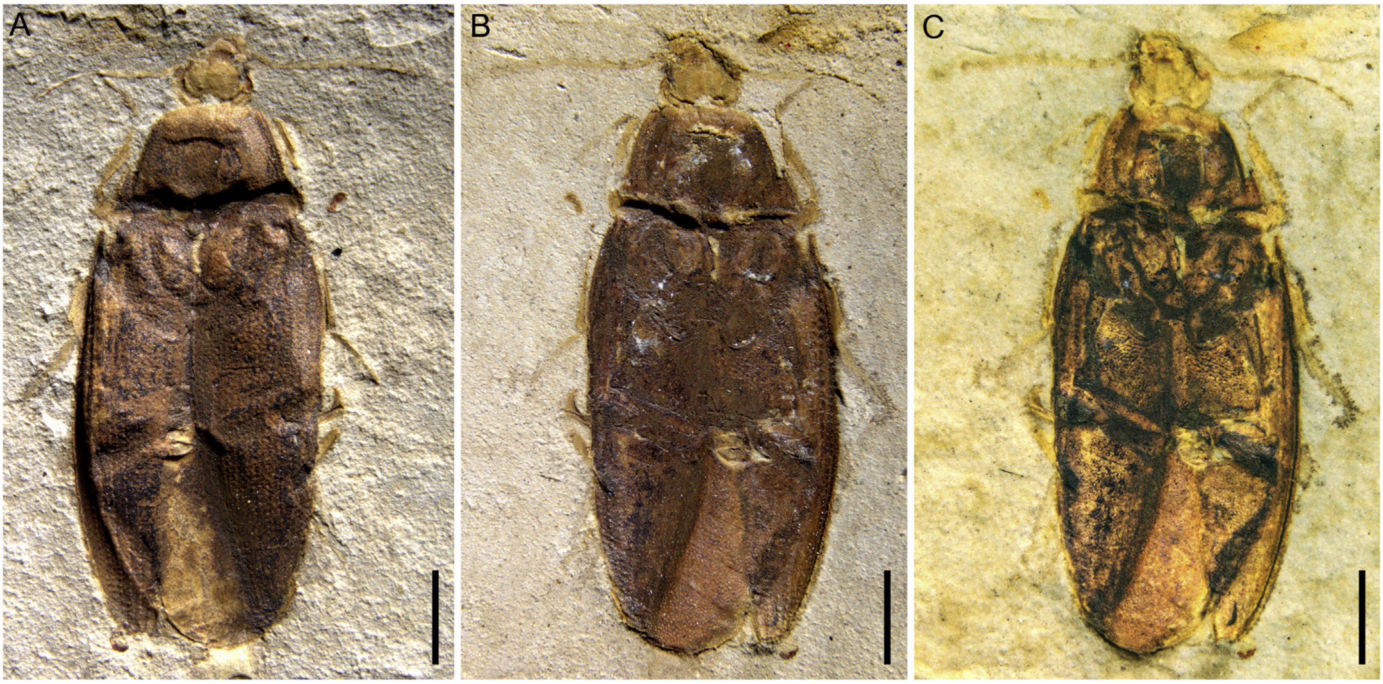

Fig. 2. Microphotographs of holotype (NIGP168714a,b) of *Cretobrevipogon breviantennatus* gen. et sp. nov., from Lower Cretaceous Yixian Formation (Liaoning Province, northeastern China). A. NIGP168714a, part, under low-angled light, mainly showing dorsal view; B. NIGP168714b, counterpart, under low-angled light, mainly showing ventral view; C. same as B, moistened with 70% alcohol. Scale bars: 2 mm.

slightly serrate from antennomere 5, short, extending posteriorly slightly beyond posterior margin of pronotum; antennomere 1 long, broad; antennomere 2 longer than wide, shorter than antennomere 1; antennomre 3 elongate, longer than antennomere 2; antennomere 4 slightly shorter and narrower than 3; antennomeres 5–10 each slightly serrate, clothed with short hairs, each not less than twice as long as wide; antennomere 11 elongate. Mandible acute, with small teeth.

Pronotum (Fig. 3A) slightly transverse, 2.48 mm long and 3.93 mm wide; widest at base; sides slightly curved; base narrower than elytral bases; lateral pronotal carinae complete; anterior angles obtuse; posterior pronotal angles strongly acute (Fig. 3A); posterior edge bisinuate; disc densely punctate. Prosternum (Fig. 3A) very long, in front of coxae much longer than mid length of procoxal cavity; with paired, subparallel carinae, without pits at anterior ends of paired carinae. Prosternal process complete, narrow. Procoxae (Fig. 3A) transverse. Procoxal cavities (Fig. 3A) strongly transverse, moderately widely separated, externally open. Scutellar shield (Fig. 3F) well developed, longer than wide, posteriorly rounded.

Elytra (Fig. 3F) complete, 9.10 mm long, each 2.61 mm wide; about 3.7 times as long as pronotum; punctation distinctly seriate, with about eleven distinct puncture rows, punctures large; apices rounded, each with elongate ventrally interlocking tongue (Fig. 3E); epipleura very narrow, complete. Mesoventrite (Fig. 3C) very small, short; anterior edge with paired, strongly declined procoxal rests (Fig. 3C); discrimen present but incomplete; mesoventral cavity oblique. Mesocoxae not projecting. Mesotrochantins exposed. Mesocoxal cavities (Fig. 3C) moderately widely separated, slightly transverse, partly closed by mesepimeron and metanepisternum. Metaventrite (Fig. 3C) large, moderately convex; discrimen (Fig. 3C) long; transverse (katepisternal) suture almost complete; exposed portion of metanepisternum (Fig. 3C) elongate, broader anteriorly. Metacoxae transverse, contiguous, extending laterally to meet elytra (Fig. 2C), metacoxal plates weakly developed, but complete.

Legs moderately long. Pro- and mesotarsi with five tarsomeres; protarsomere 5 longest. Hind wing apparently present, with subtriangular radial cell.

Abdomen (Fig. 3D) broad, with five connate ventrites, the sutures between ventrites visible, sinuate with anterior mesal curvature increasing posteriorly; suture between ventrites 4 and 5 very strongly curved (Fig. 3D). Ventrite 1 much shorter than 2, without postcoxal lines; intercoxal process acute. Ventrites 2, 3 and 4 almost in same length. Ventrite 5 slightly shorter than ventrites 3 and 4 combined. Aedeagus exposed.

Remarks. The new genus *Cretobrevipogon* can be firmly placed in the extant elateroid family Artematopodidae as evidenced by a combination of following characters: the presence of paired carinae on prosternum and an internal, apical interlocking tongue on the ventral side of each elytron (Lawrence, 2010). The elytral interlocking tongue also independently occurs in some members of the family Byrrhidae, which differ in many other characters from Artematopodidae (Cai et al., 2015). Additionally, many other features are also indicative of such a familial assignment, including slightly serrate antennae, transverse pronotum, slightly excavate metacoxae with narrow metacoxal plates, and strongly curved sutures between abdominal ventrites 4 and 5.

4. Discussion

Artematopodidae currently includes three subfamilies: Electribiinae, Allopogoninae and Artematopodinae (Lawrence, 2005; Lawrence, 2010). *Cretobrevipogon* can be separated from the genus *Electribius*, the sole genus of Electribiinae, by lacking cavities beneath antennal insertion and transverse groove connecting paired cavities on pronotum; from Allopogoninae (represented by one genus *Allopogonia*) by the presence of distinct paired carinae on prosternum (Lawrence, 2010). *Cretobrevipogon* shares the most similarities with members of the Artematopodinae, such as the

Fig. 3. Enlargements of holotype (NIGP168714a,b) of *Cretobrevipogon breviantennatus* gen. et sp. nov.; A, C and E moistened with 70% alcohol, others under low-angled light. A. head and prothorax, NIGP168714b; B. left antenna of NIGP168714b; C. ventral view of meso- and metathorax; D. ventral view of metathorax and abdomen, NIGP168714b, showing more or less curved sutures between abdominal ventrites; E. enlargement of D, showing the characteristic apical interlocking tongue on the ventral side of elytron; F. elytra, NIGP168714a, showing elytral striae. Abbreviations: a1–9, antennomeres 1–9; aest2/3, mes-/metanepisternum; ca, carina; cx1/2, pro-/mesocoxa; dis, discrimen; ely, elytron; ep2, mesepimeron; ey, eye; ilt, interlocking tongue; la, labrum; ma, mandible; msv, mesoventrite; mtv, metaventrite; pcr, procoxal rest; ppa, posterior pronotal angle; pst, prosternum; v1–5, ventrites 1–5. Scale bars: 1 mm in A–C; 2 mm in D and F; 500 μm in E.

presence of paired longitudinal carinae continuous with lateral margins of the prosternal intercoxal processand slightly serrate antennomeres. Among all six extant genera of Artematopodinae, *Cretobrevipogon* differs from the Neotropical genera *Artematopus* and *Carcinognathus* by lacking pits at anterior ends of paired carinae on prosternum. The new genus is separated from *Eurypogon* and *Macropogon* by relatively long antennomeres 2 and 3, complete lateral pronotal carinae, and the strongly curved sutures between ventrites 4 and 5; and from *Ctesibius* by the proportions of the distinctly striate elytra. Like the Middle Jurassic *Sinobrevipogon*, *Cretobrevipogon* share most morphological similarities with the extant *Brevipogon*; they share the elongate-oval body shape, absence of pits at the anterior ends of paired prosternal carinae, the striate elytra, and the recumbent hairs on elytra. It is interesting that, as in *Sinobrevipogon*, *Cretobrevipogon* also have a possibly plesiomorphic character that is not known in any modern artematopodid, namely, the mesocoxal cavity is partly closed by both mesepimeron and metanepisternum. By contrast, the mesocoxal cavitiy in all extant artematopodids is closed by the mesepimeron and almost always by a very narrow edge of the mesanepisternum. As such, *Cretobrevipogon* cannot be placed in any extant subfamily of Artematopodidae.

In order to investigate the phylogenetic position of *Cretobrevipogon*, we analyzed an integrated morphological data matrix

(Table 1) combing our fossil and representatives of all extant artematopodid genera using a parsimony approach. Using both equal weights and implied weighting implemented in TNT (version 1.5), the analyses resulted in a single tree (Fig. 4) with the same topology irrespective of the analytical method. Both results under parsimony coincided in the monophyly of the family Artematopodidae, with a relatively high supporting value (bootstrap support value = 85). The new genus *Cretobrevipogon* was recovered as a sister group to the Jurassic genus *Sinobrevipogon*, and they together sister to *Ctesibius* + *Brevipogon* (Fig. 4). The topology is nearly identical to one of the two cladograms by Lawrence (2005) based on 34 adult characters. Although the systematic position of Allopogoninae is slightly different from that in Cai et al. (2015) due to a use of different out-groups, the positions of fossil taxa appear to be stable; fossil genera form a sister group to *Ctesibius* + *Brevipogon*. *Cretobrevipogon* is closely related to the Jurassic *Sinobrevipogon*, but it differ significantly from the latter by having a very large body size (no more than 6.5 mm long in *Sinobrevipogon vs* 13.2 mm long in *Cretobrevipogon*), a much longer prosternum, much shorter antennae, and sharp posterior pronotal angles. *C. breviantennatus* also represents the largest artematopodid known to date, as the body lengths of other artematopodids are usually shorter than 10 mm (Lawrence, 2010).

Our discovery of a new compression fossil of Artematopodidae also bears some taphonomic implications. As mentioned above, Artematopodidae is characterized by a very important character, namely an apical interlocking tongue on the ventral side of each elytron (Lawrence, 2005). In extant artematopodids, this tongue-like structure is not visible from a dorsal view or even ventral view when they are in the resting position. However, the small interlocking tongue is clearly visible either in *Cretobrevipogon* or *Sinobrevipogon* (Cai et al., 2015), because these fossil beetles have been split just through the median gap of the body into two counterparts. Thus, the interlocking tongue has been impressed into the imprint which preserves most characters of the dorsal side, as shown in NIGP168714b. By contrast, the other imprint, NIGP168714a, displays not traces of the interlocking tongue, but it shows distinct striate elytra (especially under low-angled light),

Table 1
Data matrix for phylogenetic analyses.

Species/Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Declinia relicta	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nipponocyphon nakanei	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Allopogonia villosus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0
Artematopus sp.	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	1
Brevipogon confuisus	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0	1	1
Carcinognathus sp.	0	0	0	1	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	0	0	0	1
Ctesibius eumolpoides	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	0	1	0	1	0	1	1
Electribius crowsoni	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	1	1	0	0	1	2	1	0	0	1	0	0	0	2
Eurypogon sp.	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1
Macropogon sp.	0	0	1	1	0	1	1	1	0	1	1	0	0	0	1	0	0	1	0	1	1	1	1	0	0	0	0	1	0	1
Proartematopus sp.	0	1	0	?	1	?	1	0	0	0	1	?	0	0	1	?	1	1	1	0	?	1	0	1	0	0	0	0	?	?
Sinobrevipogon jurassicus	0	0	0	?	0	1	?	0	0	0	1	0	0	0	1	?	1	0	0	0	1	1	0	0	1	0	1	0	?	?
Cretobrevipogon breviantennatus	0	0	0	?	0	1	?	1	0	0	1	0	0	0	1	0	1	0	0	0	?	?	0	0	1	0	0	0	?	?

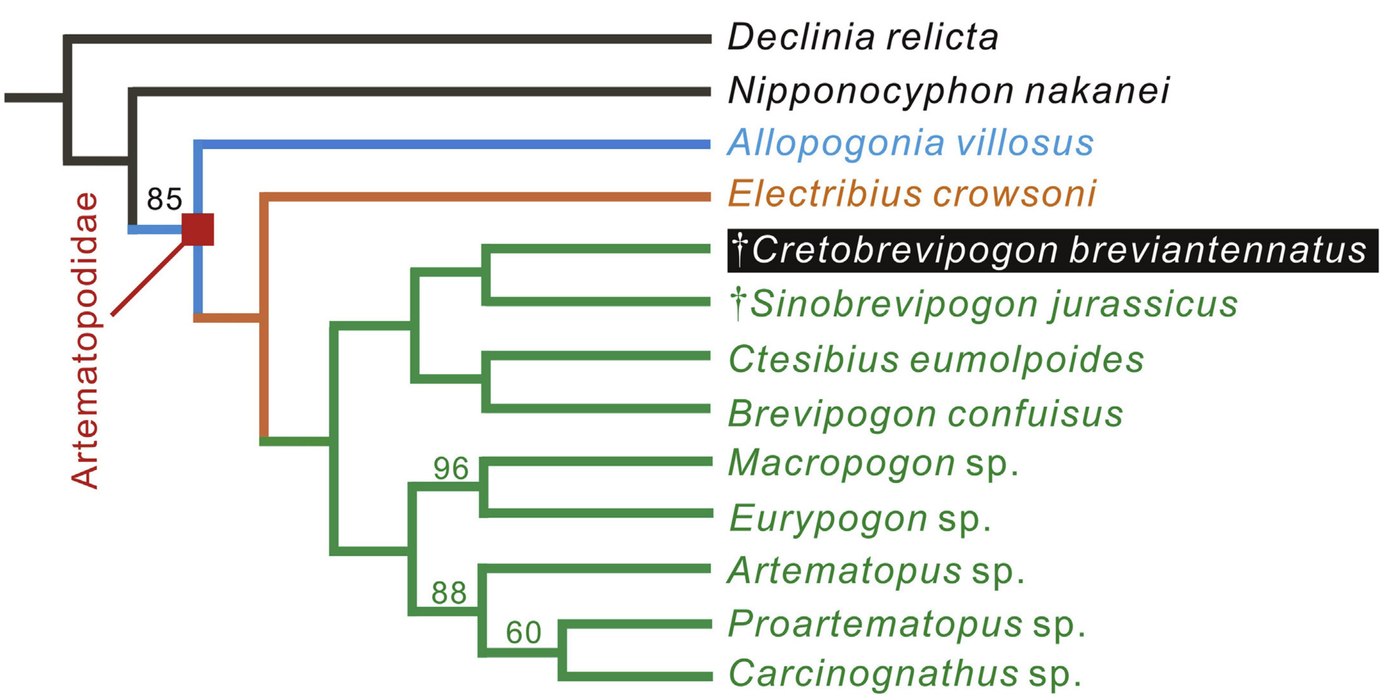

Fig. 4. Phylogenetic position of *Cretobrevipogon breviantennatus* from maximum parsimony analyses; bootstrap support values over 50% are shown on the tree (length = 45 steps, consistency index = 0.711, retention index = 0.705). Grey branches, out-group; blue branch, subfamily Allopogoninae; orange branch, subfamily Electribiinae; green branches, extant subfamily Artematopodinae and two fossil genera. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

similar to a view of the dorsal surface of the beetle. Since one of the key characters (interlocking tongue) can be preserved with fidelity in compression fossils, this may be served as a clue for discovering and recognizing new artematopodids from other fossil localities. Besides, this character can be very informative for identifying isolated beetle elytra from earlier periods, such as the Triassic, a time during which beetles mostly preserved as an isolated elytron and completely preserved ones were very rare.

5. Concluding remarks

Our discovery of *Cretobrevipogon breviantennatus* gen. et sp. nov. from the Lower Cretaceous Yixian Formation represents the first definitive representative of Artematopodidae from the Cretaceous period. Phylogenetic analyses indicated *Cretobrevipogon* as sister group to the Jurassic *Sinobrevipogon*; they share a presumably plesiomorphic character, i.e. mesocoxal cavitiy closed by mesepimeron and anterolateral edge of metanepisternum. *C. breviantennatus* possessing a very large body size and very short antenane suggests a comparatively high degree of morphological disparity of Artematopodidae in the late Mesozoic. Together with two artematopodid genera from the Middle Jurassic Daohugou beds, this find suggests that the family was much more diverse than previously documented.

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References

Cai, C., Huang, D., Solodovnikov, A., 2011. A new species of *Hesterniasca* (Coleoptera: Staphylinidae: Tachyporinae) from the Early Cretaceous of China with discussion of its systematic position. Insect Systematics & Evolution 42 (2), 213–220.

Cai, C., Lawrence, J.F., Ślipiński, A., Huang, D., 2015. Jurassic artematopodid beetles and their implications for the early evolution of Artematopodidae (Coleoptera). Systematic Entomology 40 (4), 779–788.

Chang, M.M., 2003. The Jehol Biota: The emergence of feathered dinosaurs, beaked birds and flowering plants. Shanghai Scientific & Technical Publishers, Shanghai, pp. 1–208.

Crowson, R.A., 1973. On a new superfamily Artematopoidea of polyphagan beetles, with the definition of two new fossil genera from the Baltic Amber. Journal of Natural History 7, 225–238.

Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238.

Goloboff, P.A., Torres, A., Arias, J.S., 2018. Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. Cladistics 38, 407–437.

Hörnschemeyer, T., 1998. New species of *Electribius* Crowson 1973 (Coleoptera: Artematopodidae) from Baltic amber. Paläontologische Zeitschrift 72, 299–306.

Kundrata, R., Bocakova, M., Bocak, L., 2013. The phylogenetic position of Artematopodidae (Coleoptera: Elateroidea), with description of the first two *Eurypogon* species from China. Contributions to Zoology 82, 199–208.

Kundrata, R., Bocakova, M., Bocak, L., 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). Molecular Phylogenetics and Evolution 76, 162–171.

Lacordaire, T., 1857. Histoire Histoire naturelle des insects – Genera des Coléoptères. Tome quatrième. Roret, Paris, 579 pp.

Lawrence, J.F., 1995. *Electribius* Crowson: alive and well in Mesoamerica, with notes on *Ctesibius* Champsion and the classification of Artematopodidae. In: Pakaluk, J., Ślipiński, S.A. (Eds.), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warsaw, pp. 411–431.

Lawrence, J.F., 2005. *Brevipogon*, a new genus of North American Artematopodidae (Coleoptera). The Coleopterists Bulletin 59, 223–236.

Lawrence, J.F., 2010. 4.2.Artematopodidae Lacordaire, 1857. In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (Eds.), Handbuchder Zoologie/Handbook of Zoology. Band/Volume IV Arthropoda: Insecta Teilband/Part 38. Coleoptera, Beetles. Volume 2. Morphology and Systematics (Polyphaga partim). W. DeGruyter, Berlin, pp. 42–47.

Lawrence, J.F., Nikitsky, N.B., Kirejtshuk, A.G., 1995. Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (*sensu lato*). In: Pakaluk, J., Ślipiński, S.A. (Eds.), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warsaw, pp. 375–410.

Lawrence, J.F., Yoshitomi, H., 2007. *Nipponocyphon*, a new genus of Japanese Scirtidae (Coleoptera) and its phylogenetic significance. Elytra, Tokyo 35, 507–527.

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50, 913–925.

Linnaeus, C., 1758. Systema Naturae per regni tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentius Salvius, Stockholm (10th revised ed.) 1: iv + 824 pp.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., McHugh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, A., Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Systematic Entomology 40, 835–880.

Nikitsky, N.B., Lawrence, J.F., Kirejtshuk, A.G., Gratshev, V.G., 1993. A new beetle family, Decliniidae fam. n., from Russian Far East and its taxonomic relationships (Coleoptera Polyphaga). Russian Entomological Journal 2, 3–10.

Peris, D., Ruzzier, E., Perrichot, V., Delclòs, X., 2016. Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. Geoscience Frontiers 7, 695–706.

Sakai, M., 1982. Occurence of the genus *Eurypogon* Motschulsky in Japan and Taiwan (Coleoptera: Artematopidae). Transactions of the Shikoku Entomological Society 16, 51–61.

Swisher III, C.C., Wang, Y.Q., Wang, X.L., Xu, X., Wang, Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400, 58–61.

Tan, J.-J., Ren, D., 2007. Two exceptionally well-preserved catiniids (Coleoptera: Archostemata: Catiniidae) from the late Mesozoic of northeastern China. Annals of the Entomological Society of America 100, 666–672.

Wu, H., Coty, D., Ding, M., 2015. First artematopodid beetle in Mexican amber and its biogeographic implications (Coleoptera, Artematopodidae). Alcheringa 39, 508–513.

Young, D.K., 2002. 53. Artematopodidae Lacordaire, 1857. In: Arnett Jr., R.H., Thomas, M.C., Skelley, P.E., Frank, J.H. (Eds.), American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida, pp. 146–147.

Zhang, S.-Q., Che, L.-H., Li, Y., Pang, H., Ślipiński, A., Zhang, P., 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. Nature Communications 9, 205. https://doi.org/10.1038/s41467-017-02644-4.