



Research article

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The first fossil wedge-shaped beetle (Coleoptera, Ripiphoridae) from the middle Jurassic of China

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Abstract. A new species of Ripiphoridae Gemminger & Harold, 1870, *Archaeoripiphorus nuwa* gen. et sp. nov., is described and illustrated from a well-preserved impression fossil from the Middle Jurassic Jiulongshan Formation collected at Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China, representing the oldest documented occurrence of the Ripiphoridae described from the Mesozoic era. It shares several characters belonging to two basal ripiphorid subfamilies (Pelecotominae and Ptilophorinae), but it cannot be attributed to either of them and is herein placed as Subfamily *incertae sedis*. An overall similarity between *Archaeoripiphorus* gen. nov. and Recent Pelecotominae and the occurrence of wood-boring beetles in the same Formation implies a similar parasitoid host preference in xylophagous beetles for *A. nuwa* gen. et sp. nov., putting a spotlight on a potential host-parasitoid relationship in the Mesozoic.

Keywords. Coleoptera, Ripiphoridae, new fossil taxa, conjecture of natural history, Middle Jurassic.

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Introduction

Beetles are the most diverse and successful organisms, well adapted to various habitats and comprising a major part of animal biodiversity on Earth. They are also abundant and speciose in the fossil record.

The research on fossil Coleoptera was initiated in the early part of the 20th century (e.g., Handlirsch 1906–1908); in China, work on Mesozoic fossil Coleoptera has progressed well in the past 30 years and over 200 species have been described (Tan *et al.* 2010). Among these fossil beetles, studies of fossil tenebrionoids are relatively few, including some species of Tenebrionidae, Mordellidae and Liaoximordellidae (Wang 1993; Huang & Yang 1999; Liu *et al.* 2007, 2008; Wang & Zhang 2011; Chang *et al.* 2016).

Ripiphoridae Gemminger & Harold, 1870, also known as wedge-shaped beetles because of the wedge-shaped, humped and tapered body, are traditionally divided into 6 subfamilies: Pelecotominae, Micholaeminae, Ptilophorinae, Hemirhipidiinae, Ripidiinae, and Ripiphorinae (Lawrence & Newton 1995). Lawrence *et al.* (2010) followed Falin (2003), treating Micholaeminae as part of Pelecotominae and transferring some genera of Pelecotominae to Ptilophorinae. The subfamilial classification of Falin (2003) was also followed by Batelka (2012) although Falin's study remains unpublished. Ripiphoridae includes more than 400 species in 38 genera and 5 subfamilies widely distributed worldwide (Lawrence *et al.* 2010). Lacordaire (1859) placed the family Ripiphoridae next to Mordellidae, and such a relationship was also discussed and suggested by Selander (1957), Franciscolo (1962), Crowson (1995) and Falin (2002). In contrast, several authors linked Ripiphoridae to Meloidae based on some adult and larval characters (Forbes 1926; Böving & Craighead 1931; Beutel & Friedrich 2005). Recently, some molecular phylogenetic studies have given some new insights into the phylogenetic position of Ripiphoridae. Gunter *et al.* (2014) used six genes to resolve family-level phylogenies of Tenebrionoidea. The results of Maximum Likelihood and Bayesian analysis supported that Ripiphoridae is sister to Mordellidae and the monophyly of the clade Ripiphoridae + Mordellidae. However, Ripiphoridae was presented as a paraphyletic group in the resultant ML tree and Bayesian tree. The same relationship was also presented in Kergoat *et al.* (2014) by using four mitochondrial gene fragments and four nuclear fragments in their phylogenetic analysis. McKenna *et al.* (2015) reconstructed a comprehensive phylogeny of beetles based on DNA sequence data from eight nuclear genes and the result provided good support for a monophyletic group including Stenotrachelidae, Lymexylidae, Aderidae, Anthicidae, Meloidae, Mordellidae and Ripiphoridae, which is in a basal position within Tenebrionoidea. Nevertheless, Mordellidae and Ripiphoridae were not recovered as sister groups, and Ripiphoridae was not even monophyletic on the ML tree. Batelka *et al.* (2016a) performed a comprehensive molecular phylogenetic analysis of Ripiphoridae, which was inferred from rRNA and mtDNA markers and for 23 taxa in 4 subfamilies. Ripiphoridae was still not recovered as a monophyletic group, with Mordellidae forming a terminal lineage within a paraphyletic Ripiphoridae. The clade Ripiphoridae + Mordellidae is in a basal position within Tenebrionoidea. It suggested that ripiphorid lineages gradually split basally to Mordellidae and refuted the previous hypotheses on the relationship between Meloidae and Ripiphoridae.

Fossil ripiphorid taxa are rare, and most species were described from Cenozoic ambers (Kaupp *et al.* 2001). Mesozoic taxa include two species from the Burmese amber (upper Cretaceous) and two from French Albo-Cenomanian ambers (mid Cretaceous) (Cockerell 1917; Perrichot *et al.* 2004; Falin & Engel 2010; Batelka *et al.* 2016b). In the present paper, we describe a new genus and species of Ripiphoridae based on an individual preserved in the Middle Jurassic Jiulongshan Formation of Daohugou, which is composed of grey tuffaceous sandstone and sandy mudstone; the paleoenvironment is considered to have been a volcanic region with mountain streams and lakes (Ren & Krzeminski 2002). The new genus shares several characters belonging to two Recent subfamilies (Pelecotominae and Ptilophorinae), but it cannot be attributed to either of them (see Discussion section for details). It represents the oldest fossil record for this family. We also discuss the possible natural history of this new species.

Material and methods

The sole specimen is derived from impression fossil deposits in the Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. The type specimen is deposited at the Key

Laboratory of Insect Evolution & Environmental Changes, Capital Normal University in Beijing, China. The specimen was observed using a Nikon SMZ1270 stereo microscope. Photographs were taken using a Nikon DXM1200C digital camera and drawings prepared with a pen on a sheet of tracing paper covered on a copied figure to suitable size. Digital photographs were enhanced with Adobe Photoshop CS3 graphic software. The photographs of *Trigonodera tokejii* (Nomura & Nakane, 1959) were taken at the Hokkaido University Museum (Sapporo, Japan). The morphological terminology used follows Batelka (2009) and Lawrence *et al.* (2010). The subfamilial classification follows Falin (2003) and Lawrence *et al.* (2010).

The measurements were taken as follows: (1) body length was measured from anterior margin of clypeus to the apex of elytra; width across the greatest part of elytra; (2) head length was measured from anterior margin of clypeus to posterior margin of occiput; (3) eye diameter is the greatest width of eyes; (4) antenna length was measured from the first to the last visible antennomere; (5) thorax length was the greatest length of pronotum. Absolute measurements are indicated in millimeters (mm).

Results

Systematic paleontology

Class Hexapoda Blainville, 1816
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Tenebrionoidea Latreille, 1802
Family Ripiphoridae Gemminger & Harold, 1870
Subfamily Unknown (*incertae sedis*)

Genus *Archaeoripiphorus* Hsiao, Yu & Deng gen. nov.
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Type species

Archaeoripiphorus nuwa gen. et sp. nov.

Diagnosis

Body large-sized (about 15–16 mm); head elongate, abruptly constricted posteriorly to form broad neck; eyes oval, shallowly emarginate, distinctly separated from each other; antennae 11-segmented, antennomeres IV to X rectangular or trapezoidal and antennomere XI with pointed apex; terminal maxillary palpomere elongate securiform, not modified, about 4.0 times as long as minimum width; pronotum almost triangular, trilobed at base; elytra complete, covering entire abdomen; abdomen with five ventrites; protibiae nearly as long as protarsi; apices of tibiae without spiniform seta; claws pectinate, at least in mid and hind legs.

Etymology

The generic name is derived from the type genus of Ripiphoridae, *Ripiphorus* and the prefix *Archaeo-*, indicating ancient. Gender masculine.

Archaeoripiphorus nuwa Hsiao, Yu & Deng sp. nov.

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Figs 1–4

Diagnosis

As for the genus (*vide supra*). In particular this species resembles the extant ptilophorine species, *Trigonodera tokejii* (Nomura & Nakane, 1959) in general appearance (Fig. 5), from which it differs by



Fig. 1. *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov., holotype, habitus, dorsal view. Scale bar = 5.0 mm. Photograph of dry specimen.

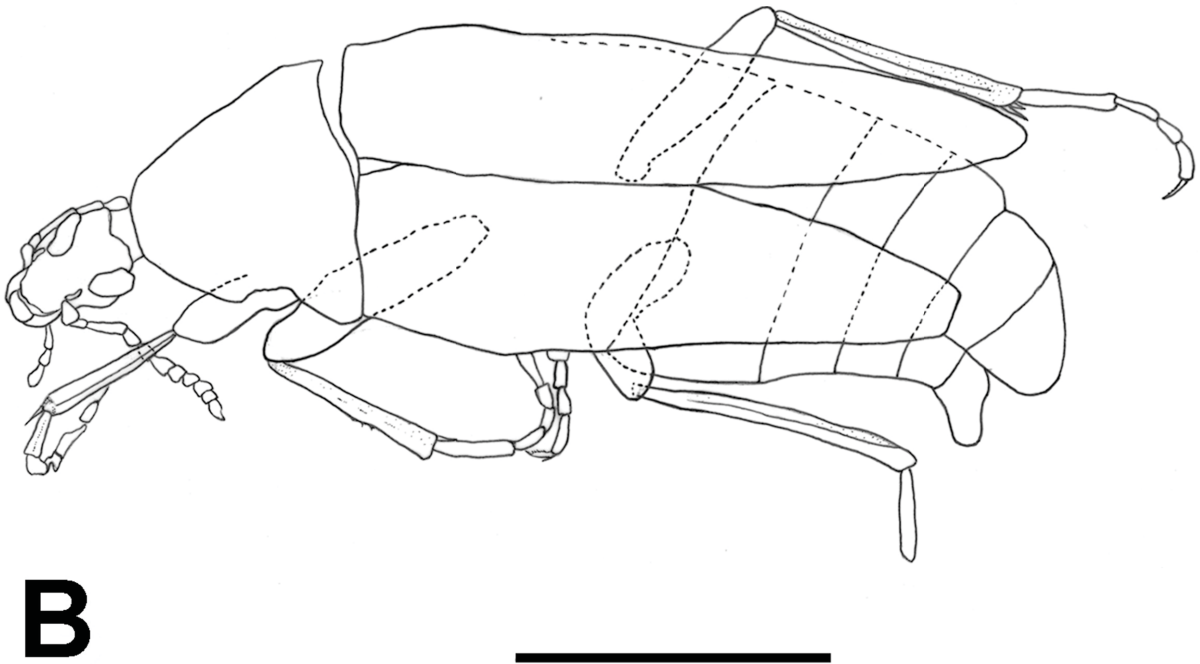


Fig. 2. *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov., holotype. **A.** Photograph of complete specimen. **B.** Habitus drawing. Scale bars = 5.0 mm.

its shorter antennae and terminal maxillary palpomere, wider pronotum anteriorly, shorter elytra, and tibial edges without spiniform seta apically.

Etymology

The specific name honors the great goddess in the ancient Chinese mythology, Nüwa, who created mankind and saved humanity from a major catastrophe by using the five-colored stones to repair the damage to the pillar of heaven caused by the water god, Gonggong.

Type material

Holotype

CHINA: nearly complete specimen in dorsal position; sex unknown (CNU-C-NN-2006841).

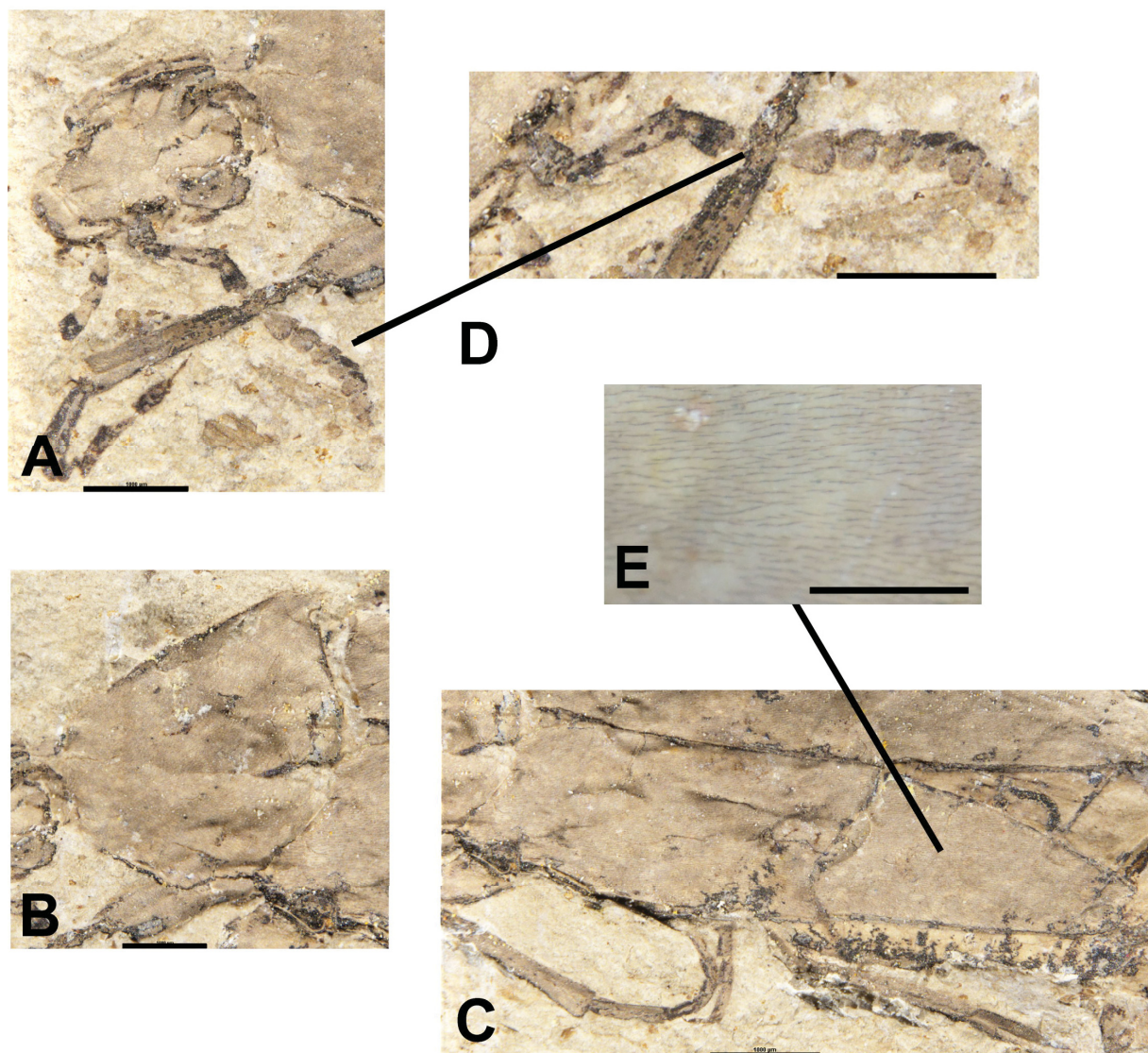


Fig. 3. *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov., holotype. **A.** Head. **B.** Prothorax. **C.** Elytron. **D.** Antenna. **E.** Photograph of the surface of the body. Scale bars: A–C = 1.0 mm; D = 0.1 mm; E = 0.5 mm. The black arrows indicate the magnified portions.

Type locality

CHINA: NE China, Daohugou, Shantou Township, Ningcheng County, Inner Mongolia.

Type horizon

Jiulongshan Formation, Middle Jurassic, about 165 Ma (Gao & Ren 2006).

Description

BODY (Figs 1–2). Length 15.5 mm, width 5.0 mm, head length 2.0 mm, antennal length 3.4 mm, pronotum length 3.5 mm, pronotum width 4.0 mm, elytra length 10.0 mm. Surface densely covered with fine pubescence (Fig. 3E).

HEAD (Fig. 3A). Small and elongate, abruptly constricted posteriorly to form broad neck; surface sparsely punctate. Eyes oval, shallowly emarginate, distinctly separated from each other, ratio of eye diameter to interocular space 1.00:1.65; surface finely faceted. Frontoclypeal suture indistinct. Apical margin of clypeus slightly sinuate. Labrum rounded, subquadrate. Terminal maxillary palpomere elongate securiform, about 4.0 times as long as minimum width. Antennal insertions widely separated, exposed from above. Antennae 11-segmented. Scape and pedicel very short, antennomere III strongly elongate, IV to X rectangular or trapezoidal, antennomere XI with pointed apex (Fig. 3D). Length ratio of antennomeres as follows: 1.20:1.00:2.30:1.35:1.20:1.35:1.10:0.90:0.90:0.90:1.45.

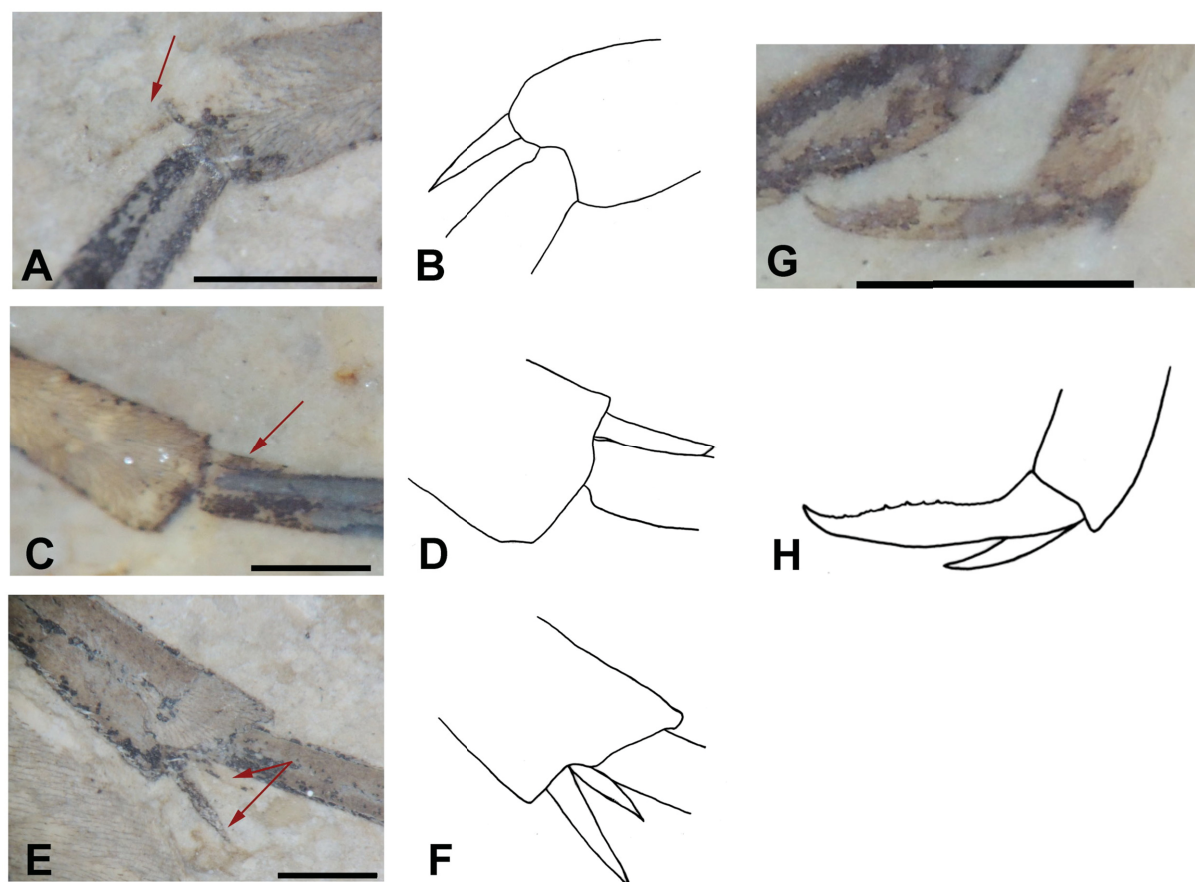


Fig. 4. *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov., holotype. **A–F.** Tibial spurs (indicated by the red arrows). **A–B.** Fore leg. **C–D.** Mid leg. **E–F.** Hind leg. **G–H.** Tarsal claw of mid leg. A, C, E, G. Photographs. B, D, F, H. Hand drawings. Scale bars: 0.5 mm.

PROTHORAX (Fig. 3B). Almost triangular, about 0.88 times as long as wide, slightly narrower than elytra at base, tapering anteriorly; anterior margin truncate and straight; anterior angles rounded and indistinct, posterior margin trilobed, with posterior angles moderately protruding and obtuse; dorsal surface densely punctate. Scutellar shield minute, angulate apically.

ELYTRA (Fig. 3C). About 2 times as long as wide, lateral sides slightly narrowing posteriorly; surface densely and regularly punctate. Abdomen with five tergites and ventrites.

LEGS. Long and slender; tibiae moderately widening apically, without spiniform seta at apices, tibial spur formula 1-1-2 (Fig. 4A–F); tarsi slender, tarsal formula 5-5-4; tarsus nearly as long as tibiae in fore and mid legs, slightly shorter than tibiae in hind legs; tarsomeres cylindrical, hind tarsomere I slightly longer than tarsomeres II and III combined. Claws slightly pectinate (Figs 4G–H).

Discussion

Archaeoripiphorus gen. nov. can be placed within Tenebrionoidea based on its wedge-shaped body and characteristic 5-5-4 tarsal formula. Our described specimen shares several characters with the tenebrionoid taxon from the same Formation, *Wuhua jurassica* Wang & Zhang, 2011 (Tenebrionoidea, unknown family): oval and distinctly separated eyes, wedge-shaped body, fully developed elytra, tibial edges without spiniform seta apically and pectinate claws, but can be distinguished by its small and elongate head, elongate securiform terminal maxillary palpomere, and rectangular or trapezoidal antennomeres IV to X. *Archaeoripiphorus* gen. nov. also shares a general overall similarity to tenebrionoid members such as Mordellidae, Ripiphoridae, Melandryidae, Scaptiidae and Stenotrachelidae. The simple, unmodified

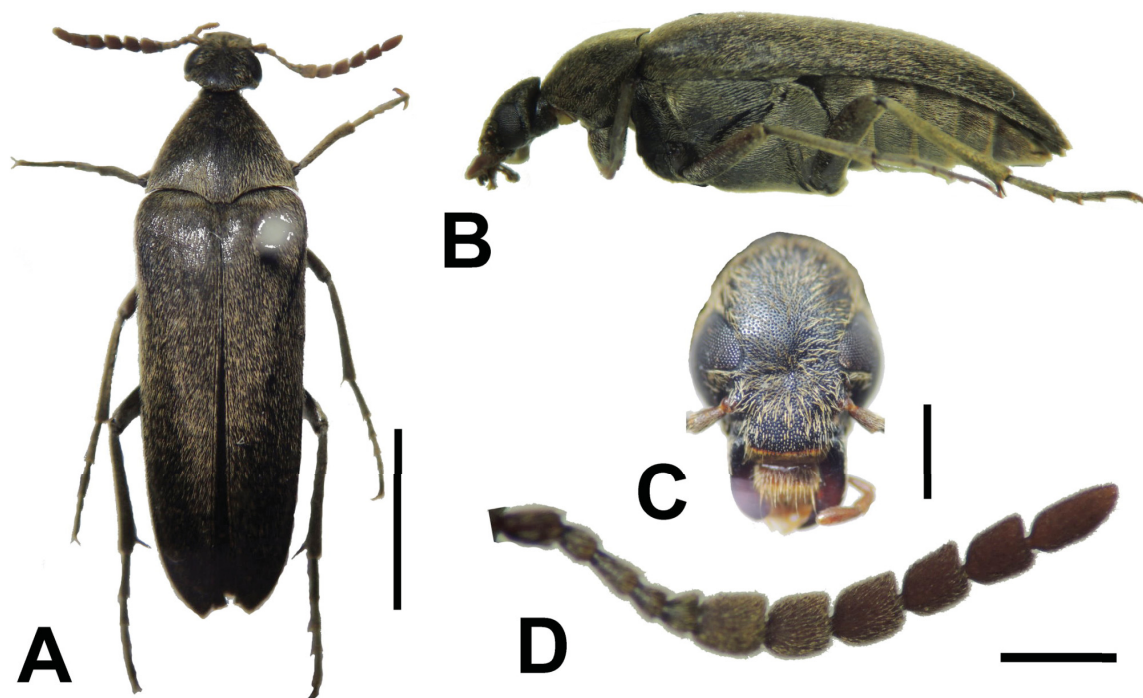


Fig. 5. An extant species of Ptilophorinae, *Trigonodera tokejii* (Nomura & Nakane, 1959). **A.** Habitus, dorsal view. **B.** Habitus, lateral view. **C.** Head, frontal view. **D.** Antenna. Scale bars: A–B = 5.0 mm; C–D = 1.0 mm.

terminal maxillary palpomere, and lack of an abdominal spine and the pulvilli of the tarsal claws suggest a placement in Ripiphoridae rather than in the above mentioned families.

However, the subfamilial attribution of this species is difficult. Obviously, this fossil species should not be attributed to either of the morphologically derived subfamilies, Ripiphorinae and Ripidiinae, by its long and complete elytra, and unexposed wings. It also cannot be placed in Hemirhipidiinae due to its not strongly incised eyes and complete elytra. Although *Archaeoripiphorus* gen. nov. is similar to the members of Pelecotominae and Ptilophorinae by its complete elytra and shares characters with the extant genus of Ptilophorinae, *Trigonodera* (Dejean, 1834) as large-sized body and pectinate claws, it differs from Pelecotominae and Ptilophorinae in the apices of tibiae without any spiniform seta, which are terminated by clusters of strong spiniform setae (as in *Ptilophorus*) or the rim provided with dense, regular row of strong spiniform setae in both subfamilies. Furthermore, this fossil taxon can be excluded from Pelecotominae by its elongate head, rectangular or trapezoidal antennomeres IV–X, pectinate claws and protibiae nearly as long as protarsi, which is subglobular, distinctly pectinate, bidentate or rarely with irregular serration, and shorter than protarsi, respectively, in Pelecotominae. This fossil species is also different from ptilophorine taxa because of the tibial spur formula 1-1-2, which is 2-2-2 in Ptilophorinae; it is possible that the 1-1-2 tibial spur formula was caused by overlaying of one spur on another and could be an artefact of preservation and compression. In conclusion, we herein cannot determine subfamilial attribution of *Archaeoripiphorus* gen. nov. and place it as subfamily *incertae sedis*.



Fig. 6. A reconstruction of *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov., illustrating a hypothesized behavior in which the females search for damaged xylem cells, caused by larvae of xylophagous beetles, to oviposit in wood.

The biology of Ripiphoridae is diverse and quite different from their reputed relatives. Some larvae are phoretic and some are hypermetamorphic, and parasitize other insects in all known cases. The immature stages of Pelecotominae are associated with the larvae of wood-boring beetles such as Anobiidae and Cerambycidae (Hudson 1934; Watt 1983; Kuschel 1990; Švácha 1994; Falin 2002; Batelka 2005, 2009; Lawrence *et al.* 2010). It is likely that the Jurassic *Archaeoripiphorus* gen. nov. had a similar parasitism of xylophagous beetles and oviposition behavior on woods infested with wood-boring beetles (Fig. 6) based on its overall morphological similarity to extant pelecotomine species and the occurrence of Cupedidae, Elateridae, Cerophytidae and Buprestidae in the same Formation, which possibly had wood-boring larval stages (Chang *et al.* 2009a, b; Tan *et al.* 2010; Chang *et al.* 2011; Pan *et al.* 2011). On the other hand, together with the paleoenvironment at the Daohugou Village surrounded with gymnosperm forests and some angiosperms (Mi *et al.* 1996; Ren *et al.* 2010; Han *et al.* 2016; Liu & Wang 2016) and the overall morphological similarity between *Archaeoripiphorus nuwa* Hsiao, Yu & Deng gen. et sp. nov. and the extant ptilophorine species, *T. tokejii* (Nomura & Nakane, 1959) from Japan and Taiwan (Fig. 5), which can be collected by sweeping flowers and may be a pollen feeder (S. Kakizoe pers. comm.), potential pollen-feeding of *Archaeoripiphorus nuwa* gen. et sp. nov. is also suggested.

Falin (2002) indicated his doubt on the monophyly of Ripiphoridae because of the lack of a strong synapomorphy. He hypothesized an early divergence between Ripiphorinae and the ancestral lineage, then Hemirhipidiinae and Ripidiinae became the most derived sister groups and Pelecotominae was considered the most primitive subfamily, though it is possibly a non-monophyletic group. The monophyly of Ripiphoridae is also not supported in recent molecular phylogenetic studies (Gunter *et al.* 2014; Kergoat *et al.* 2014; McKenna *et al.* 2015; Batelka *et al.* 2016a). Furthermore, Batelka *et al.* (2016a) recovered paraphyletic Ripiphoridae with Mordellidae as a terminal clade and found Pelecotominae to be sister to remaining ripiphorids and mordellids, with a deep split among pelecotomines and ripiphorid lineages. Ripidiinae were regularly found within the clade Ripiphoridae + Mordellidae in a sister relationship to Ripiphorinae + Mordellidae. However, the phylogenetic signal still remains ambiguous despite denser sampling than previous studies. Hence, further phylogenetic analyses combining all fossil and extant taxa are badly needed to examine the monophyly of this family and resolve the relationships among subfamilies, which will give insight into the evolution of wedge-shaped beetles. Our new discovery of *Archaeoripiphorus nuwa* gen. et sp. nov. not only dates the existence of Ripiphoridae back to the Middle Jurassic but also provides further morphological characters for phylogenetic studies.

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