

# Earliest mordellid-like beetles from the Jurassic of Kazakhstan and China (Coleoptera: Tenebrionoidea)

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## ABSTRACT

Within this study the subfamily Praemordellinae is reviewed and the holotype of *Praemordella martynovi* Sczegoleva-Barovskaja, 1929 is re-described. The genera *Cretanaspis* Huang and Yang, 1999, *Mirimordella* Liu et al., 2007, *Bellimordella* Liu et al., 2008 and *Wuhua* Wang and Zhang, 2011 is attributed to Praemordellinae. One new species, *Wuhua peregrina* sp. nov., is erected based on two well-preserved specimens from the Middle Jurassic Daohugou Biota (Inner Mongolia, China). The morphological characters of Praemordellinae are given and a key to genera of Praemordellinae is presented. Praemordellinae is closely related to extant Mordellidae in having humpbacked body, strongly deflexed head, filiform antennae and pectinate tarsal claws, but it is differing in that the pygidium absent and hind femora not well developed. It is also similar to Ripiphoridae in having a convex body and simple tarsi, but differs Ripiphoridae in having filiform antennae. Praemordellinae is probably a stem group including the ancestor of Mordellidae and Ripiphoridae. Also, within this paper, the fossil record of Mordellidae is summarized.

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## 1. Introduction

The Mordellidae Latreille et al., 1802 (Tenebrionoidea Latreille et al., 1802), commonly known as tumbling flower beetles, is a relatively homogeneous group comprising about 1500 extant species worldwide (Jackman and Lu, 2002; Lawrence and Ślipiński, 2010). They are easily recognizable beetles with a wedge-shaped humpbacked body, a long pygidium (an elongated last tergum), highly developed hind coxal plates, enlarged hind femora and spiny ridges on the tibiae and tarsi of hind legs (Jackman and Lu, 2002). Adults of the species are mainly phytophagous, apparently feeding on the pollen of many different plant species, especially of umbelliferous (Apiaceae) and composite (Asteraceae) flowers (Jackman and Lu, 2002), although some species may graze on a

fungi's surface (Lawrence and Ślipiński, 2010). The larvae are primarily herbivorous feeding on a herbaceous stems, decaying wood, and fungi (Ford and Jackman, 1996; Lawrence and Ślipiński, 2010). The family includes two living subfamilies: Ctenidiinae Francisco, 1951 with only one species from South Africa, and Mordellinae Latreille et al., 1802 consisting of over 100 genera (Bouchard et al., 2011; Lawrence and Ślipiński, 2010). Additionally, an extinct subfamily Praemordellinae Sczegoleva-Barovskaja, 1929, was erected by Sczegoleva-Barovskaja (1929). Liu et al. (2007,2008) justified the adhesion of Praemordellinae as a new subfamily of Mordellidae and included some new extinct species based on their primitive characters. Praemordellinae traditionally are considered as the ancestor of the living family members.

Compared to other families of Tenebrionoidea, Mordellidae has a richer fossil record. The earliest Mordellidae was from Albian Spanish amber (tribe: Mediumiugini) (Peris and Ruzzier, 2013) with absence of pygidium and preservation of primitive legs characters. The first true Mordellidae with iconic pygidium was described from lower Cenomanian Burmese amber (Bao et al., 2019). In addition, a further 28 species are known as amber inclusions or impressions from the Paleogene of Europe

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and North America (Table 1). Some undescribed specimens come from the Late Cretaceous Burmese, New Jersey and Canadian amber (Crowson, 1981; Grimaldi et al., 2002; Grimaldi and Engel, 2005; McKellar et al., 2008). Moreover, eight mordellid-like beetles have been described (Table 2): one from the Middle Jurassic of Daohugou, China (Wang and Zhang, 2011); one from the Late Jurassic of Karatau, Kazakhstan (Scegoleva-Barovskaja, 1929), five records from the Early Cretaceous of

China (Huang and Yang, 1999; Liu et al., 2008, 2007) and one record from lower Cenomanian amber of Myanmar (Bao et al., 2018b). Fossil Mordellidae are highly important for understanding the early evolution of Tenebrionoidea, even Coleoptera, because they are usually regarded as a calibration point used for dating the molecular phylogeny of Tenebrionoidea or Coleoptera (Gunter et al., 2014; Hunt et al., 2007; Levkaničová and Bocák, 2009; McKenna and Farrell, 2009). The fossils with incorrect

**Table 1**  
Fossil records of Mordellidae.

| Fossil taxa  | Age                           | Deposit   |
|--|-------------------------------|---|
| undescribed  | late Pleistocene              | Olympia beds Formation, USA (Ashworth and Nelson, 2014)   |
| <i>Mordella atrata</i>                                     | late Pleistocene              | Ziegler Reservoir, USA (Elias, 2014)  |
| <i>Mordellistena</i> sp.                                   |                               |   |
| <i>Mordella indata</i> Statz, 1952                         | Oligocene ( Chattian)         | Rott-am-Siebengebirge, Germany (Statz, 1952)  |
| <i>Mordella nigripilosa</i> Statz, 1952                    |                               |   |
| <i>Stenalia oligocenica</i> Nel, 1985                      | Oligocene (Rupelian)          | Cereste, France (Nel, 1985)   |
| undescribed  | Miocene                       | Mexican Amber (Poinar, 1993)  |
| undescribed  | Miocene                       | Dominican amber (Grimaldi and Engel, 2005)  |
| <i>Glipostena pomomarenkoi</i>                             | upper Eocene (Priabonian)     | Rovno amber, Ukraine (Odnosum and Perkovsky, 2010)  |
| Odnosum and Perkovsky, 2009                                |                               |   |
| <i>Mordella priscula</i> Cockerell, 1924                   | upper Eocene                  | Green River Formation, USA (Cockerell, 1925; Odnosum and Perkovsky, 2016)   |
| <i>Isotrilophus rasnitsyni</i> Odnosum and Perkovsky, 2016 |                               |   |
| <i>Mordella lapidicola</i> Wickham, 1909                   | middle Eocene                 | Florissant Formation, USA (Cockerell, 1907; James, 1939; Scudder, 1890; Wickham, 1913)                                |
| <i>Mordella stygia</i> Wickham, 1914                       |                               |   |
| <i>Mordellistena florissantensis</i> Wickham, 1912         |                               |   |
| <i>Mordellistena nearctica</i> Wickham, 1914               |                               |   |
| <i>Mordellistena protogaea</i> Wickham, 1914               |                               |   |
| <i>Mordellistena scudderiana</i> Wickham, 1914             |                               |   |
| <i>Mordellistena smithiana</i> Wickham, 1913               |                               |   |
| <i>Tomoxia inundata</i> Wickham, 1914                      |                               |   |
| undescribed  | middle Eocene                 | Kishenehn Formation, USA (Greenwalt et al., 2016)   |
| <i>Glipostena sergeli</i> Ermisch, 1943                    | Eocene                        | Baltic amber (Bao et al., 2018a; Engel, 2001; Ermisch, 1943; Germar, 1813; Kubisz, 2003; Perkovsky and Odnosum, 2013) |
| <i>Falsomordellistena eocenica</i> Kubisz, 2003            |                               |   |
| <i>Mordella inclusa</i> Germar, 1813                       |                               |   |
| <i>Mordella scheelei</i> Ermisch, 1941                     |                               |   |
| <i>Mordellaria friedrichi</i> Perkovsky and Odnosum, 2013  |                               |   |
| <i>Mordellistena amplicollis</i> Ermisch, 1941             |                               |   |
| <i>Mordellistena antiqua</i> Ermisch, 1941                 |                               |   |
| <i>Mordellistena goeckei</i> Ermisch, 1941                 |                               |   |
| <i>Mordellistena korschefskyi</i> Ermisch, 1941            |                               |   |
| <i>Mordellistena soror</i> Ermisch, 1941                   |                               |   |
| <i>Succimorda rubromaculata</i> Kubisz, 2001               |                               |   |
| <i>Tomoxia succinea</i> Bao, 2018                          |                               |   |
| <i>Asiamordella furvis</i> (Hong, 2002)                    | lower Eocene (Ypresian)       | Fushun amber, China (Zhang and Hong, 1999)  |
| undescribed  | Upper Cretaceous (Campanian)  | Canadian amber  |
| undescribed  | Upper Cretaceous (Turonian)   | New Jersey amber  |
| <i>Primaevomordellida burmitina</i> Bao, 2019              | Upper Cretaceous (Cenomanian) | Burmese amber (Bao et al., 2019)  |
| <i>Mediumiugini</i> Peris and Ruzzier, 2015                | Lower Cretaceous (Albian)     | Spanish amber   |
| <i>Mediumiuga sinespinis</i> Peris, 2013                   |                               |   |

**Table 2**  
Fossil records of mordellid – like species.

| Fossil taxa (traditional systematics)                     | Age              | Deposit                               |
|---|------------------|---------------------------------------|
| Unknown family  | Middle Jurassic  | Daohugou biota, Inner Mongolia, China |
| <i>Wuhua</i> sp. Wang and Zhang, 2011                     |                  |                                       |
| Mordellidae Latreille et al., 1802                        | Late Jurassic    | Karatau, Kazakhstan                   |
| Praemordellinae Scegoleva-Barovskaja, 1929                |                  |                                       |
| <i>Praemordella martynovi</i> Scegoleva-Barovskaja, 1929  |                  |                                       |
| Mordellidae Latreille et al., 1802                        | Early Cretaceous | Western Beijing, China                |
| <i>Cretamordella lushangfenensis</i> Huang and Yang, 1999 |                  |                                       |
| Mordellidae Latreille et al., 1802                        | Early Cretaceous | Yixian formation, Liaoning, China     |
| Praemordellinae Scegoleva-Barovskaja, 1929                |                  |                                       |
| <i>Mirimordella gracilicruralis</i> Liu, 2007             |                  |                                       |
| <i>Bellimordella capitulifera</i> Liu, 2008               |                  |                                       |
| <i>Bellimordella longispina</i> Liu, 2008                 |                  |                                       |
| <i>Bellimordella robusta</i> Liu, 2008                    |                  |                                       |
| Apotomouridae Bao, 2018                                   | lower Cenomanian | Burmese amber, Myanmar                |
| <i>Multispinus multispinosus</i> Bao, 2018                |                  |                                       |
| <i>Apotomoura fortiscrura</i> Bao, 2018                   |                  |                                       |

taxonomic data may have an inaccurate influence on dating results (McKenna, 2011). Recently, new specimens were collected from the Middle Jurassic Daohugou deposit, which had such detailed preservation and diagnostic characters that they have paved the way for the re-examination of the holotype of *P. martynovi*. *Praemordella martynovi* Sczegoleva-Barovskaja, 1929, from the Late Jurassic of Kazakhstan, was previously considered to be the earliest Mordellidae (Hunt et al., 2007; Liu et al., 2007). However, the original description and illustration of the type are incorrect, and some important characters of this taxon need further revision (Liu et al., 2007; Wang and Zhang, 2011). Here we re-describe the holotype of *P. martynovi*, erect a new species of *Wuhua* based on one well-preserved specimen from Daohugou, and discuss the phylogenetic position of Mesozoic mordellid-like beetles.

## 2. Geological setting

The holotype of *Praemordella martynovi* was collected from the Upper Jurassic Karabastau Formation of the Karatau Range near the village of Aulie (formerly called Mikhailovka), Chayan District, Chimkent Region, southern Kazakhstan (Fig. 1A). The Karabastau Formation, yielding about 18,000 insect fossils to date, is among the world's most prolific sources of fossil insects (Rasnitsyn and Zherikhin, 2002). The deposits consist of grey, laminate siltstones, marls, limestones and dolomites, and almost all organic remains are from the uppermost layers (Szwedo and Zyla, 2009). The Karatau paleo-lake originated in the inner-mountain basin, and relatively rapidly was filled with proluvial sediments. Its age is probably Callovian–Kimmeridgian based on the analysis of plant and spore-pollen assemblages (Kirichkova and Doludenko, 1996), but the precise age remains unclear because of the lack of a definite radiometric age. The water in the lake was characterized by high hardness and relatively high salinity, and the paleoclimate was dry (Ponomarenko et al., 2005). Preserved in this deposit there are abundant fishes, insects, and diverse plants including bennettitaleans, cycads, conifers, and ferns (Doludenko and Orlovskaya, 1976). The insects from Karatau are preserved as organic remains in dark grey siltstone. These insects have been intensively studied during the past eighty years and include 19 orders and several thousand species. Among them, the Coleoptera is the most diverse group and comprises approximately half of all the fossil insects from Karatau (Yan, 2009).

The two other specimens come from the Middle Jurassic Daohugou beds of Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia of China (Fig. 1B). The Daohugou deposit, consisting of grey tuff, tuffaceous siltstone, and mudstone is now considered to be one of the most important insects deposit. Most fossil insects from Daohugou are preserved as organic remains on the surface of grey tuffaceous siltstones, usually in such impeccable detail that even fine setae can be discerned on tiny specimens (Wang et al., 2009). The radiometric dating of the underlying and overlying ignimbrite suggested that the Daohugou biota occurred at an interval from 168 Ma to 152 Ma (Liu et al., 2006), a Middle Jurassic or early Late Jurassic age. In this paper, we adopted the rough Middle Jurassic age, which was supported by most palaeontologists based on the analysis of fossil plants, conchostracans, bivalves, and insects (Jiang, 2006; Rasnitsyn et al., 2006; Ren et al., 2002; Shen et al., 2003; Zhou et al., 2007). The paleoclimate in Daohugou during the mid-Jurassic times was warm temperate, and the flora was dominated by Bennettitales, Filicales, Pinales, Ginkgoales, and Coniferales (Pott et al., 2012; Zhang, 2006). The coleopteran assemblage is the most diverse group in this fauna and more than 10 families have been described and a plethora of fossils (especially Polyphaga) await further description (see a summary in Kirejtshuk et al., 2010).

## 3. Materials and methods

The specimens were examined dry and under alcohol, using a Nikon SMZ1000 stereomicroscope. Photographs were prepared using a digital camera (DXM1200) connected to the stereomicroscope, and line drawings were readjusted on photographs using image-editing software (CorelDRAW X4 and Adobe Photoshop CS). In drawings, dashed lines indicate faintly seen and hypothesized missing parts. All measurements in the description are given in millimetres.

The specimen PIN is deposited at the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; specimen CNU-C-NN2007203 at the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China; and specimen NIGP154954 at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

## 4. Systematic paleontology

Order Coleoptera Linnaeus, 1758

Superfamily Tenebrionoidea Latreille et al., 1802

Family Mordellidae Latreille et al., 1802

Subfamily Praemordellinae Sczegoleva-Barovskaja, 1929

[Praemordellinae] Sczegoleva-Barovskaya, 1929, Comptes Rendus de l'Académie des Sciences de l'URSS 27–29. – Liu et al., 2007, Zootaxa 1415, 49–56. – Liu et al., 2008, Cretaceous Research 29, 445–450. – Bouchard et al., 2011, Zookeys 88, 389. – Liu et al., 2015, Journal of Environmental Entomology 37, 866: [stem: *Praemordell*-].

Praemordellidae Wang, 1993, Acta Geologica Sinica, 67, 86–94.

Type genus. *Praemordella* Sczegoleva-Barovskaja, 1929, by original designation.

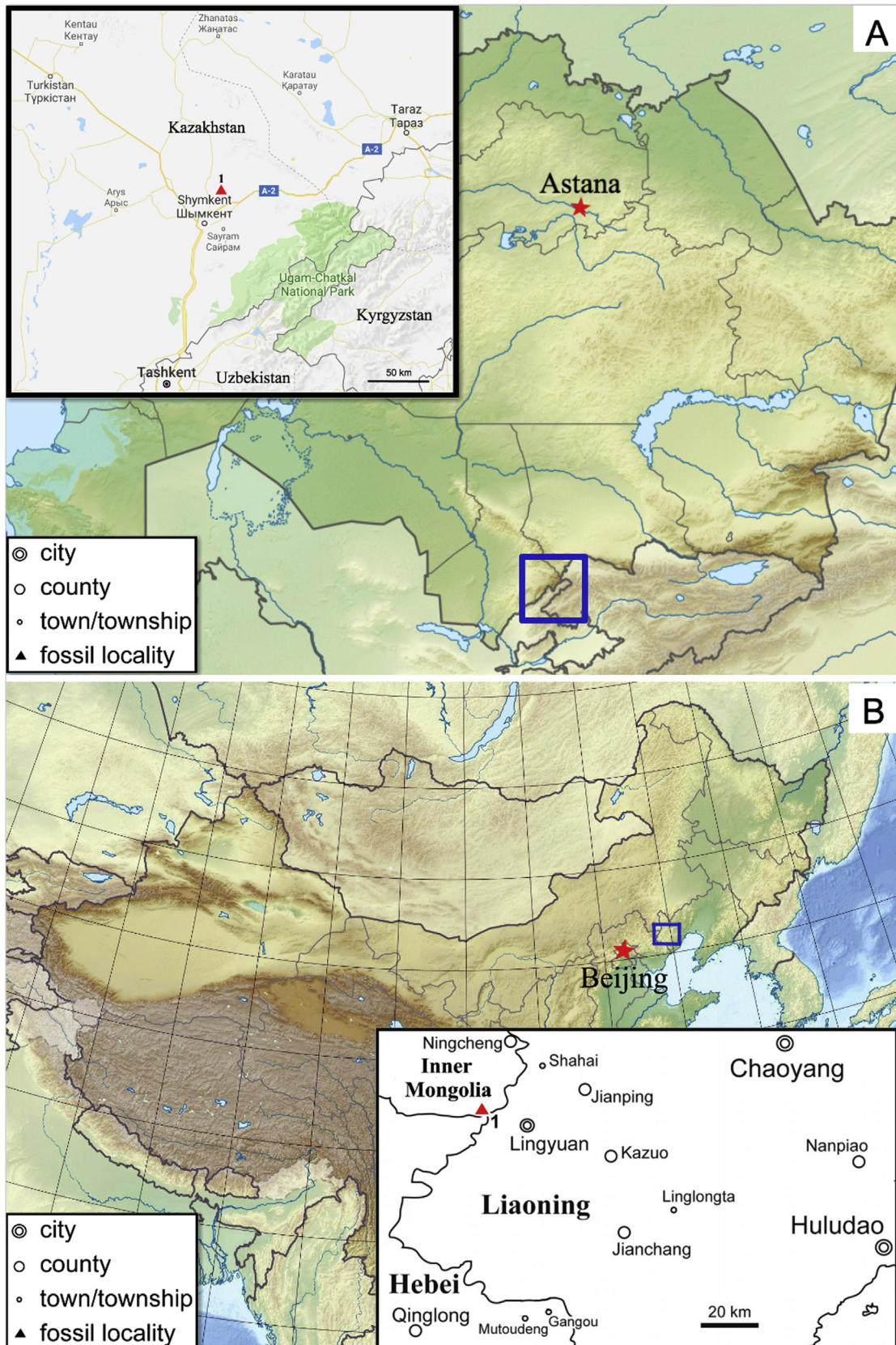
*Emended diagnosis.* Body wedge-shaped, arched, with fine pubescence. Antennae filiform, inserted in front of eyes; maxillary palpi linear, last segment with slight enlargement. Eyes ovate, not reaching occiput, head deflexed strongly, constricted behind eyes to form a neck; hind coxae enlarged to a small but transversely elliptical plate; hind femora slender, not as enlarged as those of modern mordellids; hind tibiae longer than hind femur; penultimate tarsal segments simple; tarsal claws pectinate; last tergite without prolongation.

*Composition.* Five genera: the type genus *Praemordella* Sczegoleva-Barovskaja, 1929; *Wuhua* Wang and Zhang, 2011 (Middle Jurassic; Daohugou deposits of China); *Cretanaspis* Huang and Yang, 1999 (Early Cretaceous; Lushangfen Formation of China); *Mirimordella* Liu et al., 2007 and *Bellimordella* Liu et al., 2008 (Early Cretaceous; Yixian Formation of China).

*Remarks.* Two “Mordellidae” fossils from the Lower Cretaceous of Australia and Spain respectively probably belong to this family (Jell and Duncan, 1986; Soriano et al., 2007).

Key to genera of Praemordellinae

- 1 Hind coxae with width/length ratio about 3  
     ..... 2  
   – Hind coxae strongly enlarged, width/length ratio < 2.5  
     ..... 3
- 2 Hind tibiae longer than hind tarsi, with oblique truncate apex.  
     .....  
     ..... *Wuhua* Wang & Zhang  
   – Hind tibiae shorter than hind tarsi, with straight truncate apex  
     .....  
     ..... *Praemordella* Sczegoleva-Barovskaja
3. Hind tibiae much longer than hind tarsi; hind apical spur longer than 1st tarsomere  
     .....  
     ..... *Cretanaspis* Huang & Yang



**Fig. 1.** (A) map of the locality of Karabastau Formation in southern Kazakhstan. Highlighted area enlarged and shown in detail. 1, main fossil locality near village of Aulie. Scale bars = 50 km. (B) map of the Daohugou biota in Inner Mongolia and north-eastern China. Highlighted area enlarged and shown in detail. 1, Daohugou locality. Scale bars = 20 km. Research materials collected from the localities with red triangle mark. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

- Hind tibiae shorter than hind tarsi; hind apical spur shorter than 1st tarsomere . . . . . 4
- 4 Elytra curved; hind tibiae with oblique truncate apex . . . . .  
 . . . . . *Mirimordella* Liu, Lu & Ren
- Elytra flat; hind tibiae with straight truncate apex . . . . .  
 . . . . . *Bellimordella* Liu, Zhao & Ren

Genus *Praemordella* *Scegoleva-Barovskaja*, 1929

Type species. *Praemordella martynovi* *Scegoleva-Barovskaja*, 1929. Monotypy.

**Revised diagnosis.** Elytra flat, tapering on apical 1/3; hind coxae transversely enlarged to form an elliptical plate, width/length ratio about 3; hind tibiae expanded apically, shorter than hind tarsi, with straight truncate apex. It is most closely related to *Wuhua* in having the flat elytra, wide hind coxae, but differs from *Wuhua* in having the hind tibiae shorter than hind tarsi, with straight truncate apex. It is different from *Mirimordella* in having the flat elytra, wide hind coxae, middle coxae distant from fore coxae, and hind tibiae with straight truncate apex; from *Bellimordella* in possessing the wide hind coxae; from *Cretanaspis* in having the hind tibiae much longer than hind tarsi, and hind apical spur longer than 1st tarsomere.

**Type horizon and locality.** Karabastau Formation, Upper Jurassic; village of Aulie, Chayan District, Chimkent Region, southern Kazakhstan.

*Praemordella martynovi* *Scegoleva-Barovskaja*, 1929 (Figs. 2–3A)

**Diagnosis.** Body moderate sized (length about 9 mm). Pronotum strongly convex, about one-fourth of elytra length. Middle tarsal ratio 10:4:4:3:3. Hind tarsi slightly longer than hind tibiae, tarsal ratio 10:5:4:4.

**Description.** Body medium-sized, elongate. Head strongly deflexed and deformed, eyes large, ovate, about 0.5 times as long as head. Pronotum strongly convex, 0.25 times as long as elytra; lateral sides rounded. Scutellum not visible. Metepisternum long, narrow, broad anteriorly.

All tibiae and tarsi with distinct apical ridges. Fore femora slightly longer than tibiae, fore tibiae slightly increasing in width apically; apical spur not visible; fore tarsi with basal 2 segments preserved. Middle femora as long as tibiae, longer than fore ones; two subequal apical spurs simple, 1/3 as long as tarsomere I; middle tarsi 1.2 times as long as middle tibiae, tarsal ratio 10:4:4:3:3. Hind coxae transversely enlarged to form an elliptical plate, which is slightly shorter and wider than the hind femora; width/length ratio 3:1; hind femora wider and longer than fore or middle ones; hind tibiae 1.1 times longer than femora, slightly increasing in width apically; two apical spurs visible, about 1/4 as long as tarsomere I; hind tarsi 1.1 times as long as hind tibiae, tarsal ratio 10:5:4:4.

Abdomen with 5 visible segments, sharply tapering towards apex from segment III. Segment I slightly longer than the other segments; segment 3 shortest; segment V extended beyond elytra; last tergite without prolongation, as sclerotized as its ventrites.

**Measurements** (mm). Body length 6.5 (from front edge of head to tip of elytra). Head length 1.0. Fore leg length: femur 1.3; tibia 1.2; tarsomeres 1–2 0.65, 0.31. Middle leg length: femur 1.6; tibia 1.6, tibial spur 0.27; tarsomeres 1–5 0.80, 0.33, 0.32, 0.24, 0.24. Hind leg length: coxae 0.57; femur 1.9; tibia 2.2, tibial spur 0.22; tarsomeres 1–4 1.04, 0.52, 0.40, 0.40; tarsal claws 0.30. Pronotum length 1.2. Length of abdominal segments 1–5 0.56, 0.52, 0.32, 0.60, 0.52. Elytral length 5.5.

**Type material.** Holotype PIN, a beetle with head deformed in a lateral position (with the right side fully exposed).

**Locality and horizon.** Late Jurassic Karabastau Formation; village of Aulie, Chayan District, Chimkent Region, southern Kazakhstan.

**Remarks.** The type specimen does not have a true pygidium because the elongated and pointed abdomen illustrated by *Scegoleva-Barovskaja* (1929) is not a prolongation of the last terminal tergite, but the last few abdominal segments extended together. A similar taphonomic condition also occurs in some other beetles. For example, the last few abdominal segments of a tenebrionoid beetle (CNU-C-NN2007203) were extended from the abdomen, making this part appear to be a pointed “pygidium” (Fig. 4).

Genus *Wuhua* Wang and Zhang, 2011

Type species. *Wuhua jurassica* Wang and Zhang, 2011.

**Revised diagnosis.** Antennae filiform, as long as pronotum. Elytra tapering on apical 1/3, apex individually rounded; middle coxae separated from each other, distant from fore coxae; hind coxae transversely enlarged to form an elliptical plate, width/length ratio 3:1; hind tibiae expanded apically, longer than hind tarsi, with oblique truncate apex. *Wuhua* differs from *Praemordella Scegoleva-Barovskaja*, 1929 in having hind tibiae longer than hind tarsi, with oblique truncate apex; differs from *Mirimordella* in possessing flat elytra with rounded apex, middle coxae distant from fore coxae, wide hind coxae, and longer hind tibiae with straight truncate apex; differs from *Bellimordella* in having middle coxae distant from fore coxae and hind coxae wide; and distinctly different from *Cretanaspis* in having the longer hind tarsi, and the hind apical spur shorter than 1st tarsomere.

**Type horizon and locality.** Middle Jurassic Daohugou deposits; Wuhua Town, Ningcheng County, Chifeng City, Inner Mongolia, China.

**Composition.** Two species: *Wuhua jurassica* Wang and Zhang, 2011 and *W. peregrina* sp. nov., both from the Middle Jurassic of Daohugou, China.

*Wuhua peregrina* sp. nov.

(Figs. 3B, 5)

**Diagnosis.** Body large (length about 12 mm). Pronotum short, about one-fourth of elytra length. Hind tarsi slightly shorter than hind tibiae, tarsal ratio 5:2:2:2. It differs from *W. jurassica* in having a larger body, shorter pronotum, and tarsomere I shorter than tarsomeres II–IV of hind tarsi.

**Description.** Body elongate, with short pubescence. Head strongly deflexed, constricted behind eyes, with a clear occipital protrusion. Maxillary palpi linear, with 3 complete segments visible; length ratio from base to apex 3:2:3, with terminal one distinctly enlarged. Eyes large, ovate, about 0.5 times as long as head. Mouth-parts not clearly visible. Antennae inserted in front of eyes: one antenna with only distal 5 antennomeres visible. Pronotum strongly convex, widened posteriorly, slightly longer than head; basal angles acute; base straight. Scutellum small, sharply pointed posteriorly. Epipleuron narrow, extending apically on 1/3 of basal elytra. Metepisternum long, narrow, broad anteriorly.

All tibiae and tarsi with distinct apical ridges; tarsi simple; claws pectinate. Fore coxae conical, fore tibiae slightly increasing in width apically; fore tarsi 0.8 times as long as fore tibiae, tarsal ratio 10:7:6:6:8. Middle coxae almost triangular; middle trochanters small; middle femora slightly shorter than tibiae; apical spurs simple, 1/4 as long as tarsomere I; middle tarsi slightly longer than middle tibiae, tarsal ratio 9:4:4:4:5. Hind coxae transversely enlarged to form an elliptical plate; width/length ratio 3:1; hind trochanters small; hind femora wider and longer than middle one; hind tibiae slightly longer than femora, 1.2 times as long as hind tarsi, slightly increasing in width apically; one apical spur visible, curved, 1/4 as long as tarsomere I; hind tarsi with tarsal ratio 5:2:2:2.

Abdomen with 5 visible segments, sharply tapering towards apex from segment III. Segment I slightly longer than the other segments; segments 2–5 subequal in length; last tergite without prolongation, as sclerotized as its ventrites.



Fig. 2. *Praemordella martynovi* Scegoleva-Barovskaja, 1929, PIN, holotype. (A) Body. (B) Tarsus of hind leg. (C) Tarsus of middle leg. Scale bars = 2 mm in (A); 1 mm in (B–C).

**Measurements (mm).** Body length 11.5 (from front edge of head to tip of elytra). Head length 2.1. Eye length 1.0. Fore leg length: tibia 1.6; tarsomeres 1–5 0.67, 0.47, 0.40, 0.40, 0.54. Middle leg length: femur 2.7; tibia 3.1, tibial spur 0.28; tarsomeres 1–5 1.16, 0.54, 0.50, 0.54, 0.67; tarsal claws 0.47. Hind leg length: coxae 0.81; femur 3.0; tibia 3.8, tibial spur 0.75; tarsomeres 1–4 1.39, 0.54, 0.54, 0.60; tarsal claws 0.40. Pronotum length 2.2. Scutellum

length: 0.7. Length of abdominal segments 1–5 1.08, 0.81, 0.81, 0.81, 0.94. Elytral length 9.3.

**Type material.** Holotype NIGP154954, a complete beetle in lateral position (with the right side fully exposed).

**Locality and horizon.** Middle Jurassic; Daohugou deposits (41°18' N, 119°13' E), Wuhua Town, Ningcheng County, Chifeng City, Inner Mongolia, China.

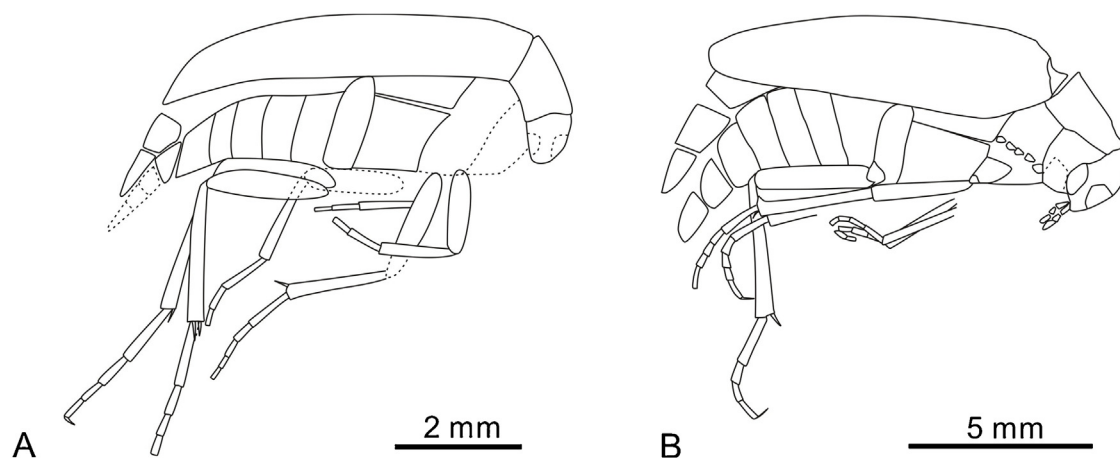


Fig. 3. (A) *Praemordella martynovi* Scegoleva-Barovskaja, 1929, PIN, holotype. (B) *Wuhua peregrine* sp. nov., NIGP154954, holotype.



Fig. 4. A tenebrionoid beetle, CNU-C-NN2007203. Scale bar = 5 mm.

**Etymology.** Specific epithet is from the Latin word “*peregrine*”, meaning strange.

## 5. Discussion

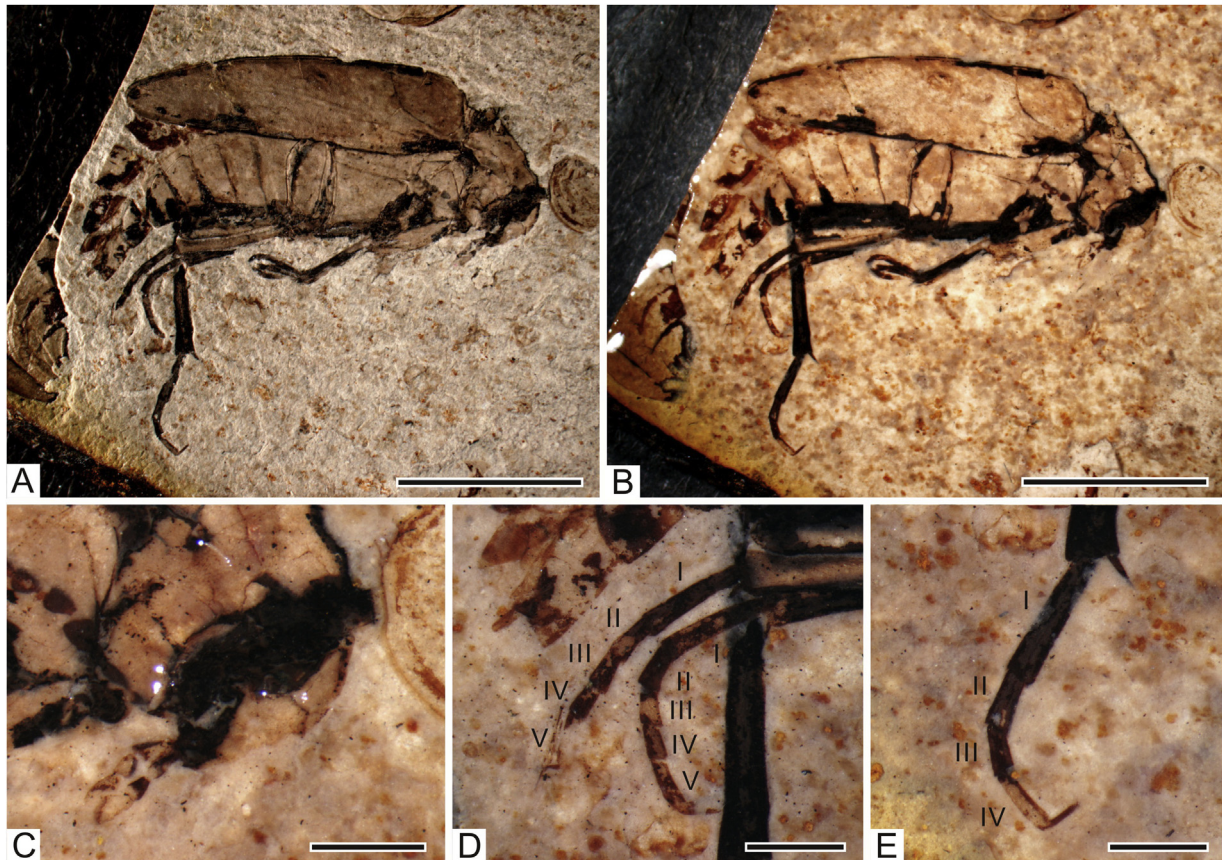
### 5.1. Praemordellinae (Polyphaga: Tenebrionoidea)

Praemordellinae remains a subfamily in Mordellidae but differs from most families within Tenebrionoidea in the following characters: body convex; head strongly deflexed, not retracted into prothorax; antennae filiform and tarsi simple. It is similar to extant Mordellidae in having the humpbacked body, strongly deflexed head, filiform antennae and pectinate tarsal claws, but distinctly different in the absence of the pygidium, hind femora not well developed, and absence of the preapical ridges on the hind tibiae. Praemordellinae is similar to Ripiphoridae in having the convex body and simple tarsi, but differs from the latter in having filiform antennae. It also resembles Scaptiidae in having the filiform antennae, and humpbacked body, but differs in having pectinate tarsal claws (simple in Scaptiidae), and penultimate tarsal segments simple (distinctly lobed in Scaptiidae). Furthermore, Praemordellinae is different from Meloidae in having the humpbacked body with middle coxae separated from each other; and different from Tetratomidae because the latter has the short, triangular, slightly deflexed head.

The monotypic family Liaoximordellidae (type species *Liaoximordella hongii*) was established by Wang, 1993 based on a nearly complete, dorsoventrally compressed specimen from the Lower Cretaceous Yixian Formation of western Liaoning, China (Wang, 1993). Currently *L. hongii* is regarded as a basal member of the Mordellidae based on the following four characters (Wang, 1993): basal and apical segments of the antennae are shorter than middle ones; head and pronotum are large, broader than long; legs are slender with distinct tibial spurs; pygidium is present. The first three characters are not autapomorphies of Mordellidae, and can be found in some Tenebrionoidea groups, such as Melandryidae and Scaptiidae (Wang, 1993). Judging from the photograph, *L. hongii* does not have an elongate and pointed terminal tergite. Its last abdominal segment is just extruded, and this taphonomical deformation is common in dorsoventrally compressed beetles (e.g., figs. 5–8 in Kirejtshuk et al., 2010; figs. 8–10 in Nikolajev et al., 2011). Huang and Yang (1999) suggested that it was a primitive representative of Ripiphoridae. However, *L. hongii* is distinguished from typical Ripiphoridae in having filiform antennae, and no distinct characters show its close relationship with Ripiphoridae. Additionally, some Tenebrionidae beetles were known from the same horizon (Kirejtshuk et al., 2012). *L. hongii* may be a representative of Tenebrionidae, and more clear evidence is needed to resolve this taxonomic issue.

The family Apotomouridae has recently erected and it includes two species *Multispinus multispinosus* and *Apotomoura fortiscrura* from Burmese amber (lower Cenomanian, ca. 99 Ma) (Bao et al., 2018b). The retractile wedge-shaped body and tarsal formula 5-5-4 placed Apotomouridae in Tenebrionoidea. Apotomouridae shares similarities with Mordellidae in body shape, antennae shape, ventrite numbers, etc., but the absence of pygidium, the coxae form and complex appendix structures on hind legs make it difficult to assign with Mordellidae. The absence of pygidium also applies for Praemordellinae, whereas Apotomouridae shows more detail structures e.g. ventrite setae, hind femora spines and tibiae spines, indicating an adaption for the late Cretaceous environment.

Liu et al. (2007) indicated that “Praemordellinae” could be placed in Mordellidae on the following characters: tarsal formula is 5-5-4; body is wedge-shaped, elongate and arched, with fine pubescence; head is deflexed, constricted behind the eyes to form a neck; abdomen extends beyond elytra. These characters are not autapomorphies of Mordellidae, and all can be found in the Ripiphoridae and Scaptiidae. Primitive characters of Praemordellinae indicate that this group could arise earlier than the relative extant taxa, and furthermore could consist ancestors of



**Fig. 5.** *Wuhua peregrine* sp. nov., NIGP154954, holotype. (A–B) Body. The specimen was photographed dry (A) and under alcohol (B). (C) Head. (D) Tarsus of middle leg. (E) Tarsus of hind leg. Scale bars = 5 mm in (A–B); 1 mm in (C–E).

Mordellidae, Ripiphoridae and Apotomouridae. Extant Mordellidae is a well-supported monophyletic group, defined by the pointed pygidium, strongly enlarged metacoxae, and spiny subapical ridges on the metatibia and metatarsus (Franciscolo, 1957; Jackman and Lu, 2002; Lawrence and Ślipiński, 2010). To complete a well-supported cladistic analysis, more robust morphological data are needed for fossils and some important morphological characters must be re-examined. With current data, the phylogenetic analysis may be premature.

### 5.2. Mesozoic Tenebrionoidea

The Mesozoic records of Tenebrionoidea are quite abundant, dominated by Burmese amber species that are increasing each year (Batelka et al., 2018). The relationship between basal taxa in Tenebrionoidea like Mordellidae, Ripiphoridae has been argued for a long time. Crowson (1955) indicated close relationships between the scaptiids and mordellids, but later he suggests a tenebrionoid lineage consisting of Melandryidae, Mordellidae + Ripiphoridae and Scaptiidae (Crowson, 1966). Lawrence (1982) suggested a slightly different group, placing Tetratomidae, Melandryidae, Mordellidae and Ripiphoridae into a single assemblage. The ripiphorid-mordellid relationship is also supported by Franciscolo (1957, 2000) based on the similarities of Ctenidiinae and some Ripiphoridae. However, it was questioned by Švácha (1994) with the preliminary comparative observations on the larvae of *Pelecotoma fennica* (Ripiphoridae: Pelecotominae) and various mordellids. In recent studies, molecular analyses also supported the sister-group relationship between the Ripiphoridae and Mordellidae, and further indicated this lineage is probably a

primitive group (Batelka et al., 2016; Hunt et al., 2007; Levkaničová and Bocák, 2009; Zhang et al., 2018). Despite the widespread opinion considering Mordellidae closely related to the Ripiphoridae, their phylogenetic relationships with other families of Tenebrionoidea remain unclear (Falın, 2002). However, the up-to-date knowledge supported a clade of Mordellidae + Ripiphoridae sister to all remaining Tenebrionoidea and Lymexylidae (Batelka et al., 2016). The adult characters show that Praemordellinae is closely related to Mordellidae, Ripiphoridae and the fossil family Apotomouridae, and thus probably is a stem group including the ancestor of these families. However, further elucidation of phylogenetic position of Praemordellinae will require additional study of tenebrionoid phylogeny.

### 5.3. Paleocology

Modern Mordellidae have the most common jumping adaption of adult beetles, in which case the hind coxae are much enlarged (Crowson, 1981). When disturbed or captured the adults kick with their hind legs which make them bounce quickly (Jackman and Lu, 2002). The elongated last tergite (pygidium) in extant mordellids is useful for keeping balance, and its appearance is associated with the jumping ability (Franciscolo, 1954, 1957; Liu et al., 2007). Jurassic Praemordellinae had wide hind coxae and slender femora, and the absence of pygidium. They probably had a weak ability to jump and tumble. Some Early Cretaceous Praemordellinae species (e. g. *Cretamordella lushangfenensis* Huang and Yang, 1999) had developed enlarged hind coxae and longer femora, which suggests an improvement of jumping ability. It was not until the mid-Cretaceous, when true mordellids appeared, indicated by the



strongly enlarged hind coxae and well-developed pygidium, which display no major morphological differences from modern mordellids (Bao et al., 2019; Grimaldi, 2000; Grimaldi et al., 2002). Although the great improvement of jumping ability of Mordellidae seems to co-occur with the rise of angiosperms in the mid-Cretaceous, the specialization is not directly related to the evolution of angiosperms (Wang et al., 2013). The ability to jump is a particularly interesting predator avoidance behaviour that has been shown to be very effective (Ge et al., 2011). Therefore, the formation of jumping legs of Mordellidae probably results from the intense predation pressure from newly-evolved insectivorous animals which diversified during the Early Cretaceous, such as small feathered theropods, primitive mammals, and early birds (e.g. Luo, 2007; Zhou, 2006). In addition, the presence of the jumping mechanism of Mordellidae may reinforce the greater diversification rate, as with the flea beetles (Ge et al., 2011). A better understanding of the phenomenon awaits further study of more Cretaceous mordellid-like beetles.

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