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A new fossil mordellid (Coleoptera: Tenebrionoidea: Mordellidae) from the Yixian Formation of Western Liaoning Province, China

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Abstract

A new genus and species, *Mirimordella gracilicruralis* **gen.** et **sp. nov.**, in the subfamily Praemordellinae of Mordellidae, is described and illustrated based on a nearly complete fossil specimen. It is from the Yixian Formation of western Liaoning Province, NE China. The diagnosis of the subfamily Praemordellinae is emended based on this new species. Characters such as simple and linear maxillary palpi, simple claws, simple penultimate segments of fore and middle tarsi, small hind coxal plates, slender hind femora, only apical ridges on hind tibiae and tarsi, and no elongated last tergum suggest that Praemordellinae might be the precursor of modern mordellids. The resemblance between the new species and the Late Jurassic *Praemordella martynovi* indicates close relationships between them and with the tribe Stenaliini in the subfamily Mordellinae. The position of epicoxa and slender hind femur suggest that the new species may be more primitive than *Praemordella martynovi* and may indicate the age of the Yixian Formation no later than Late Jurassic.

Key words: fossil, Mordellidae, new taxon, Late Jurassic, Yixian Formation, Liaoning

Introduction

Mordellids have a distinctive wedge-shaped body. The fossil representatives of this family, especially Mesozoic ones, are infrequent. The earliest occurrence of mordellids was assigned to the Late Jurassic, for which a new genus and species was described as *Praemordella martynovi* Scegoleva-Barovskaja (1929) (Fig. 1) from the Karatau Range in Kazakhstan. To date, Early Cretaceous mordellids have been reported from two sites: Lushangfen Formation of western Beijing, China (Huang & Yang 1999) and Koonwarra Bed of Victoria, Australia (Jeel & Duncan 1986), where a new genus and species, *Cretanaspis lushangfenensis* Huang & Yang, 1999 and one poorly preserved specimen without description were reported respectively. Huang and Yang (1999) considered *Cretanaspis* as an intermediate genus between modern Mordellinae and Anaspidinae and placed it within the family Mordellidae. In addition, Wang (1993) described a mordellid-like sample from the Yixian Formation of western Liaoning Province, and established an extinct family Liaoximordellidae for it, with *Liaoximordella hongi* as the type species. The Late Cretaceous has been claimed to be a very important time in the evolutionary history of the family based on the discovery of undoubted mordellid specimens. All of these mordellids are awaiting further identification, including five specimens from Burmese amber (Grimaldi *et al.* 2002) and five from New Jersey amber (Grimaldi *et al*. 2000).

Recently we recovered the current well preserved mordellid-like fossil from the Yixian Formation. This discovery is of great interest, as this specimen is an important supplement to the record of fossil mordellids and may aid study of the origin of modern mordellids. However, the age of the Yixian Formation is still being debated and three opinions have been offered: Late Jurassic (Ren *et al*. 1997, Zheng *et al*. 2003), the transition

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from Late Jurassic to Early Cretaceous (Chen *et al*. 2004; Wang *et al.* 2004, 2005), and Early Cretaceous (Swisher *et al*. 1999, Li *et al*. 2001, Pang *et al*. 2002, Zhou *et al*. 2003). We tentatively consider the age of the Yixian Formation as Late Jurassic.

Material and methods

The specimen was examined under a Leica MZ12.5 dissecting microscope and illustrated with the aid of a camera lucida attached to the microscope. We follow Crowson (1953) and Franciscolo (1954, 1957) in considering Anaspidinae as a subfamily of Scraptiidae rather than Mordellidae, and Lawrence and Newton (1995) for systematic paleontology.

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Superfamily Tenebrionoidea Latreille, 1802

Family Mordellidae Latreille, 1802

Subfamily Praemordellinae Scegoleva-Barovskaja, 1929

Diagnosis. Praemordellinae has comprised a single species, *Praemordella martynovi*, until now. Based on the material from the Yixian Formation of western Liaoning Province, we have added one new genus and species to this subfamily. The diagnosis of Praemordellinae can be emended as follows: body wedge-shaped and arched; head deflexed strongly, constricted behind eyes to form a neck; apex of abdomen exceeding elytral apices; last tergum without prolongation; claws simple; penultimate segments of fore and middle tarsi simple; hind tibiae and tarsi only with apical ridges; hind coxae enlarged to a small but transversely elliptical plate; hind femora slender, not as enlarged as those of modern mordellids.

Comparisons. Praemordellinae is 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 (Franciscolo 1957). We do not believe that Praemordellinae has a true pygidium because the elongated and pointed abdomen illustrated by Scegoleva-Barovskaja (1929) is not a mere prolongation of the last terminal tergum, but the extended last few abdominal segments together. Thus Praemordellinae differs from the subfamily Ctenidiinae of Mordellidae mainly in not having flabellate antennae, not having an elongated last tergum (pygidium), and having less developed hind coxae and femora; it differs from Mordellinae mainly in not having an elongated last tergum (pygidium), having less developed hind coxae and femora, and lacking any ridges on hind tibiae and tarsi except the apical ridges. Moreover, we do not place Praemordellinae in Rhipiphoridae because the former has filiform antennae (Falin 2002). Also, we do not place it in Liaoximordellidae mainly because Praemordellinae has a wedge-shaped body, longer hind tarsi than hind tibiae, and simple, linear penultimate tarsal segments.

Key to the subfamilies of Mordellidae (modified from Franciscolo 1957)

1. Antennae of male flabellate from the 5th segment; segments 5-10 bearing at their inner side a single, very long flabellum; segment 11 as long as segments 5-10 taken together, in form of flabellum. Antennae of

females with segments 6–10 much prolonged at their inner side, but without true flabella. Galea in both sexes extremely thin, longer than one half of head. ..... subfamily Ctenidiinae Franciscolo, 1951

Antennae of both sexes filiform, moniliform or dentate, but never bearing flabellum-like appendages at their inner side. Galea in both sexes much shorter than one half of head. 2

2. Last tergum elongated to form a pygidium, hind coxae greatly enlarged to a round or square plate, hind femora developed strongly, and hind tibiae with subapical ridges in addition to apical ridges ....subfamily Mordellinae Fowler, 1912

Last tergum without elongation, hind coxae only enlarged to a small but transversely elliptical plate, hind femora slightly larger than fore and middle ones, and hind tibiae without any other ridges except apical ones ..... subfamily Praemordellinae Scegoleva-Barovskaja, 1929

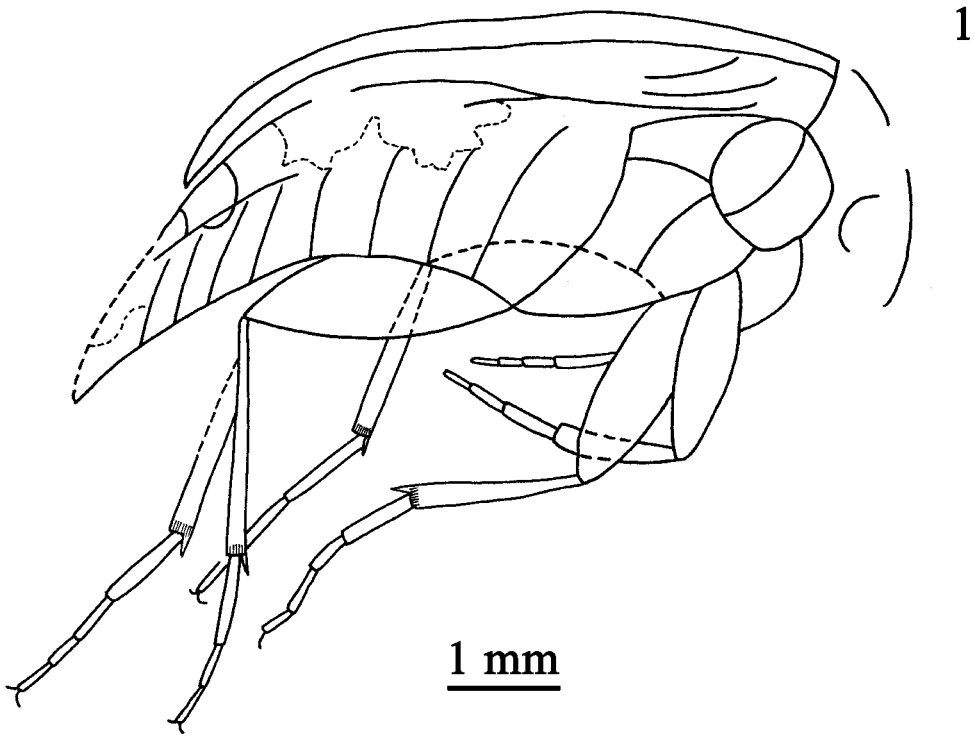


FIGURE 1. *Praemordella martynovi* redrawn from Scegoleva-Barovskaja (1929).

Genus *Mirimordella* gen. nov.

Type species: *Mirimordella gracilicruralis* sp. nov.

Etymology. From the Latin prefix *miri-*, strange, and the genus *Mordella* Linnaeus 1758; gender feminine.

Species included. Holotype species only.

Diagnosis. Maxillary palpi linear, last segment without distinct enlargement. Scutellum long, triangular or rectangular. Elytra arched, sharply tapering on apical 1/3; apex pointed. Epicoxa present in front of hind coxal plate and immediately juxtaposed to metepisternum. Hind tibiae expanded apically, with oblique truncate apex, as long as femora; hind tarsi longer than tibiae. Abdomen with 5 visible abdominal segments.

Comparisons. We assign this new genus to Praemordellinae based on agreement with the revised diagnosis of the subfamily. This new genus and the genus *Praemordella* share many characters including the wedge-shaped body, the body size, the sharply narrowing elytra, the pointed apex of elytra, and the abdomen extended beyond elytra, the hind coxae and femora less enlarged than modern mordellids, the apical ridges only on hind tibiae and tarsi, the simple penultimate segments of fore and middle tarsi, and simple claws.

However, the new genus can be distinguished from *Praemordella* by the following: 5 visible abdominal segments, less developed hind femora, hind tarsi longer than tibiae, apices of hind tibiae oblique, tarsal formula 5-5-4, and presence of epicoxa anterior to hind coxal plate and immediately juxtaposed to metepisternum. This new genus differs from the genus *Cretanaspis* (Mordellinae) in the following: 5 visible abdominal segments, penultimate segments of fore and middle tarsi simple, hind tarsi longer than tibiae, and apices of hind tibiae oblique.

***Mirimordella gracilicruralis* sp. nov.**
Fig. 2A–B

Holotype. No. CNU-C-LB2006201, an impression of a nearly complete mordellid in ventrolateral position rotated 10° towards the right side, with the left side fully and the right side partially exposed. It is housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Science, Capital Normal University, Beijing, China (CNUB; Ren Dong, Curator).

Locality and horizon. Yixian Formation, Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, NE China.

Etymology. From the Latin prefix *gracil-* for being slim and Latin *cruralis* for leg, together referring to the relatively slim legs.

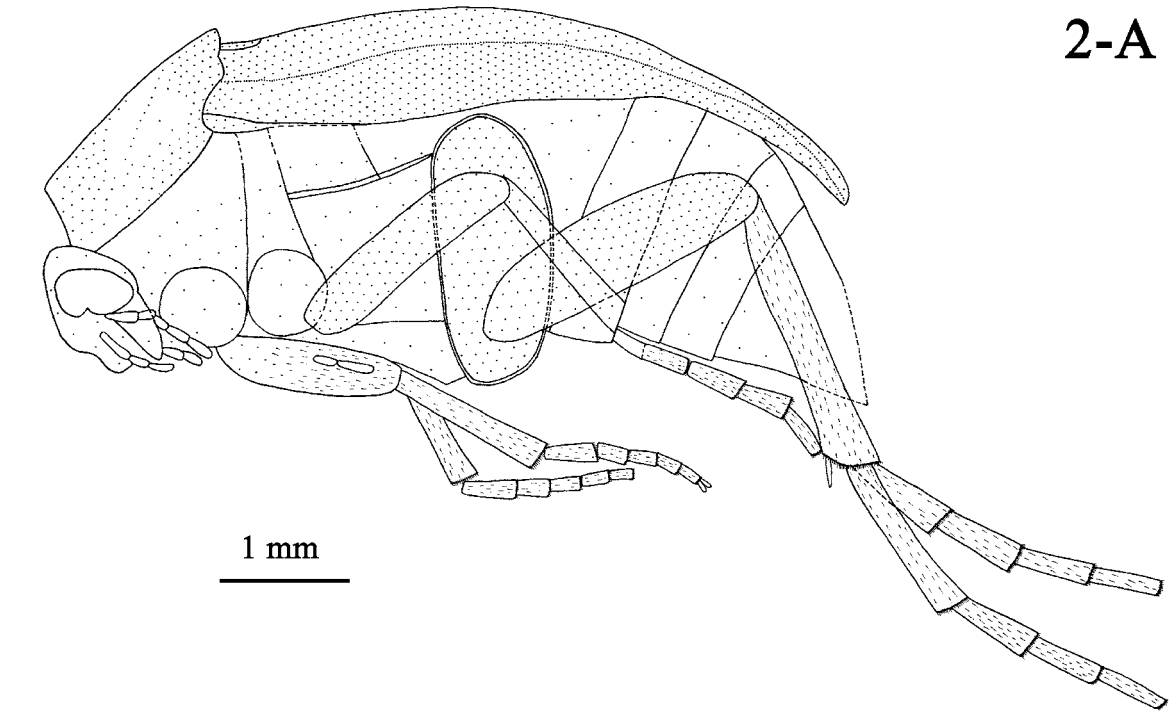
Diagnosis. In addition to the diagnosis for the subfamily and genus, the species can be diagnosed as follows: head small; eyes elongated oval, not reaching occiput; temporal angles and margins present; elytra with some longitudinal folds; elytral epipleuron small but present.

Description. Form wedge-shaped, elongate, arched, broadest behind base of pronotum. Elytra, middle femora, hind femora, and hind tibiae darker than the rest. Body, elytra, tibiae and tarsi with short pubescence. Head small, strongly deflexed, apparently constricted behind eyes to form a neck. Eyes of medium size, transversely elongated oval, not reaching occiput, slightly emarginated behind antennae. Temple distinct, with temporal angles and margins present. Labrum slightly bilobed or concave in the middle. Mandibles long and triangular from ventrolateral view. Maxillary palpi linear, with 3 visible segments, length ratio of the base segment to the terminal one 15: 8: 9, terminal one without enlargement. Antennae filiform, inserted in front of eyes, as long as or slightly longer than pronotum.

Pronotum 1.5 times as long as head; sides nearly parallel on anterior 3/4; basal angles acute, base arcuate, basal lobe short and rounded. Scutellum long, triangular or rectangular, obtusely pointed posteriorly.

Elytra arched, with some longitudinal folds, 3 times as long as pronotum, broadest from anterior 2/5 to 3/5, subparallel on anterior 2/3, sharply tapering caudad on apical 1/3, apex pointed. Epipleuron small, distinct on anterior 1/15 of elytra, extending apically to 1/5 of elytra. Metepisternum short, elongate rectangular. Epicoxa triangular, immediately juxtaposed to metepisternum, anterior to hind coxal plate, not separated by hind coxal plates as modern mordellids.

All tibiae and tarsi with distinct apical ridges; penultimate segments of fore and middle tarsi simple, not bilobed; claws paired, simple, not dentate. Fore and middle coxae close to each other, distant from hind coxae. Fore coxae rounded, fore trochanters invisible, fore femora slightly longer than tibiae, fore tibiae slightly increasing in width apically, fore tarsi as long as femora, length ratio of tarsi 1 to 5 8:5:5:4:4. Middle coxae rounded; middle trochanters not visible; middle femora longer than fore ones, as long as tibiae; first tarsal segment invisible, apical 4 tarsal segments of the same length. Hind coxae transversely enlarged to form an elliptical plate, small and narrow, slightly shorter and 1.5 times as broad as hind femora; hind trochanters invisible; hind femora broader and longer than fore or middle ones; hind tibiae as long as femora, slightly increasing in width apically, with oblique apices; only one apical spur visible, 1/5 as long as tarsal segment 1; hind tarsi 1.5 times as long as tibiae, length ratio of tarsi 1 to 4 15:7:6:6.



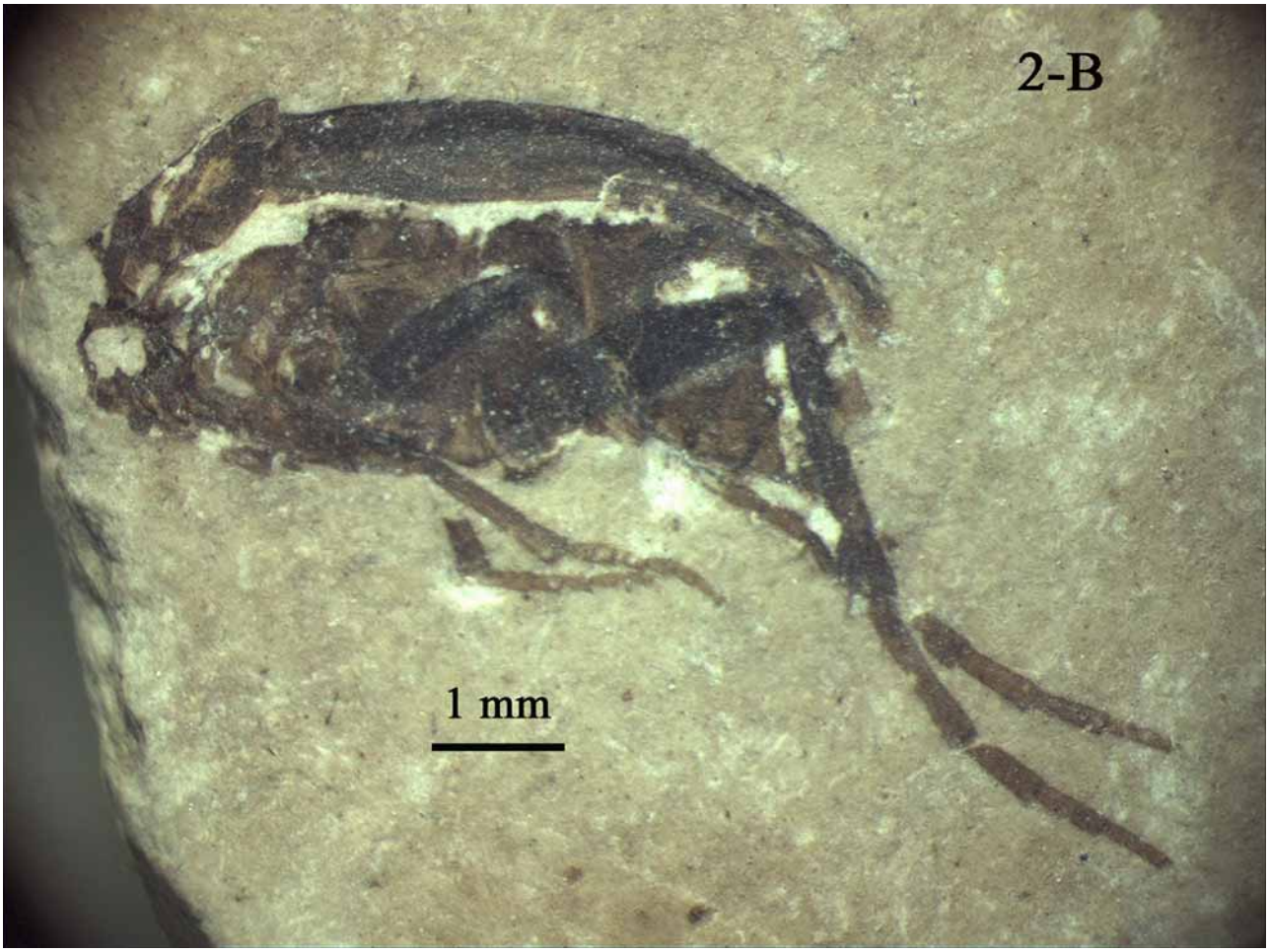


FIGURE 2. Lateral view of the holotype of *Mirimordella gracilicruralis* gen. et sp. nov. (CNU- C-LB2006201): A, line drawing; B, photograph.

Abdomen with 5 visible abdominal segments, sharply narrowing towards apex from the third visible segment, the lower half of the first visible abdominal segment mostly covered by the hind coxa and femur; last abdominal segment extending beyond elytral apex; last tergite without prolongation, less sclerotized than its sternite, partially missing its apex.

Measurement (mm). Body length: 6.2 (from front edge of head to tip of elytra). Head length: 1.2. Eye length: 0.6, width: 0.35. Mandible length: 0.5, width: 0.25. Length of maxillary palpal 1–3: 0.3, 0.16, 0.18. Fore leg length: femur 1.4; tibia 1.2; tarsal 1–5: 0.4, 0.25, 0.25, 0.2, 0.2; tarsal claws 0.1. Middle leg length: femur 2.0; tarsal 2–5 (segment 1 invisible): 0.4, 0.4, 0.4, 0.4. Hind leg length: coxa 2.0; femur 2.3; tibia 2.3, tibial spur 0.3; tarsal 1–4: 1.5, 0.7, 0.6, 0.6; width: coxa 0.85, femur 0.6, tibia 0.4. Pronotum length: 1.8. Scutellum length: 0.3. Elytra length: 5.5.

Discussion

Although the hind coxa of *Mirimordella gracilicruralis* is enlarged to form a coxal plate, this plate is transversely elliptical, much smaller or narrower than that of modern mordellids. In modern mordellids, this coxal plate is enlarged further to be more or less rounded or square. We use the term epicoxa to name the small triangular piece immediately juxtaposed to the metepisternum, even though its position should be behind the hind coxa and often hidden under the elytra in modern mordellids (Franciscolo 1957). It is likely that this piece was shifted caudad because of the enlargement of the hind coxae in modern mordellids. We note that all pairs of femora of the current species are slender, not as developed or enlarged as *Praemordella martynovi*. Enlarged femora may have something to do with jumping, as in some leaf beetles (Franciscolo 1957). The less enlarged femora of *Mirimordella* suggest a weaker ability to jump and tumble than *Praemordella*. In mordellids, the enlarged last segment of the maxillary palpi may aid in getting more spores or pollen and other kinds of food; the dentate claw, the subapical, dorsal-lateral ridges on the tibiae and tarsi, and the lobed penultimate segments of the fore and middle tarsi could help in crawling and staying on leaves and petals; the enlarged hind coxae could indicate better ability to jump; the pygidium may aid in keeping balance (Franciscolo 1954, 1957; Crowson 1981).

Therefore, Praemordellinae is a group with many primitive characteristics: 1) the eyes do not reach occiput; 2) the maxillary palpi are simple and linear without an enlarged terminal segment; 3) the metepisternum is short and straight at the mesosternal side; 4) the hind coxae is small but narrowly elliptical, not as developed as modern mordellids to be round or square; 5) the hind tibiae and tarsi have apical ridges only, no subapical or dorsal or lateral ridges; 6) penultimate segments of fore and middle tarsi are simple and linear, not enlarged or bilobed; 7) the claws are simple, not dentate; 8) the hind femora are slender, not as greatly developed as many modern mordellids; 9) the apices of hind tibiae are not distinctly expanded as in modern mordellids; 10) the last tergum is not elongated into a pygidium; and 11) the epicoxa is immediately juxtaposed to the metepisternum, not behind the hind coxal plate as in modern mordellids. The primitive characteristics 2, 4, 9, 10 make this new genus similar to the tribe Stenaliini in Mordellinae, suggesting a close phylogenetic relationship to modern Stenaliini and to be the precursors of modern mordellids. Members of Stenaliini are thought to be the most primitive living mordellids (Franciscolo 1957). However, the position of the epicoxa and lack of ridges except the apical ridge on hind tibiae and tarsi of the new genus make it different from Stenaliini.

The main elements of the flora in Yixian Formation were conifers and cycadophytes (Sun *et al.* 2001). Although our mordellid and the oldest known flowers, *Archaefructus*, co-existed in the Yixian Formation (Sun *et al.* 1998, 2003), *Archaefructus* is an unlikely host for our mordellid because of its aquatic characters and low frequency in the Yixian flora (Sun *et al.* 2003). Thus, the wedged-shaped body form of Mordellidae may not have evolved with the onset of angiosperms as commonly thought. The body form appears to be an

advantage for these early mordellids to feed on spores and pollination drops of conifers or other gymnosperms.

Our new species sheds new light on the age of Yixian Formation. The new genus and species, *Mirimordella gracilicruralis*, shows a strong resemblance to *Praemordella martynovi* in many characters as discussed in our comparisons. Furthermore, the 7 visible sternites and the 4-4-4 tarsal formula of *Praemordella martynovi* illustrated by Scegoleva-Barovskaja (1929) might have been the result of observational errors; such characters would be impossible in Mordellidae by the definition of the family. Other than these two differences in abdomen and tarsal formula, these two species are very similar except that the new species has an epicoxa anterior to the hind coxal plate, less developed femora, longer hind tarsi, and oblique apices of hind tibiae. The epicoxal position and slender femora suggest that the new species may be more primitive than the Late Jurassic *Praemordella martynovi*. We believe these two species have a close relationship and thus infer the age of the Yixian Formation to be no later than Late Jurassic.

Conclusions

Our new genus *Mirimordella* represents a basal group of Mordellidae based on plesiomorphic characters such as lack of other ridges except the apical ridges on hind legs, simple and linear penultimate segments of fore and middle tarsi, small hind coxal plates, slender hind femora, the anterior position of epicoxae, and lack of pygidium. It may have a close phylogenetic relationship with modern Stenaliini. The wedged-shaped body form of Mordellidae likely evolved with conifers or other gymnosperms that existed abundantly during the Late Jurassic, rather than with angiosperms as commonly thought. The great resemblance between *Mirimordella gracilicruralis* and the Late Jurassic *Praemordella martynovi* may argue for the Late Jurassic age of the Yixian Formation.

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