Diversity of feeding and pollination strategies of Mesozoic beetles

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Summary

Beetles (order: Coleoptera) as the most diverse and successful animals on the earth, comprise about 400,000 species, constituting almost 40% of described insects and a quarter of all animal species. Beetles are normally recognized by their typical hard exoskeleton including the elytra. They are distributed in almost every terrestrial natural habitat today, with various feeding preferences. Approximately 90% of the species in Coleoptera emerged in the Mesozoic, especially during the Jurassic–Cretaceous period. At the same time, vegetation type on the earth was shifting significantly — angiosperms (flowering plants) rapidly replacing the dominating gymnosperms, an event which Charles Darwin called the "Abominable Mystery". The dramatic environmental and nutritional change could have impacted the interaction between beetles and related plant groups. The evolution of beetles may have also influenced the angiosperm radiation, e.g. through zoophilous pollination.

The studies in this thesis demonstrate the remarkable feeding strategies and ecological diversity of Mesozoic beetles. Fourteen species of seven families from Karabastau Formation, Daohugou Biota, Burmese amber and Baltic amber are described, ranging from Early Jurassic to Eocene. The co-evolution between beetles and vegetation environments is discussed. Based on the continuous fossil records of the family Mordellidae, the early evolution trend of a typical beetle-flower ecology is outlined. Hypothetically, insect pollination contributes largely to the diversity of flowering plants, and is essential to the Cretaceous radiation of angiosperms. *Angimordella burmitina* Bao, 2019 and the associated tricolpate pollens provides direct evidence of insect pollination of Cretaceous eudicots ~99 million years ago, extending the record of insect mediated angiosperm pollination at least 50 million years earlier. The great angiosperm radiation in mid-Cretaceous acted as a driving force for the replacement of earth surface vegetation. By this time, nutrition groups as gymnosperms, fern, are also changed relatively, which also imply the associated

beetle taxa. *Praezolodinus pilosus* and *Cretoptomaphagus microsoma* provide rare records of bottom forest ecosystem: an association of fern habited beetle and scavenger. Wood-borer and fungivorous beetles are abundant in Burmese amber, similar to the extant beetle species. With more and more flora and fauna inclusions discovered from Burmese amber, it is possible to draw a big picture of the Burmese forest back in. We can generally understand the forest vertical eco-components and the inner relationships of the ecosystem. The Waipoua forest could be the exant reference ecosystem. However, it should be pointed out that it is easy to underestimate the complexity of the ecosystem, when performing a comparative study of paleoecology in the future.

In this research, a variety of current techniques were applied and optimized in order to carry out detailed palynological and morphological studies, including the confocal laser microscopy (CLSM) and X-ray microtomography (micro-CT). The CLSM uses the fluorescence effect to detect the micro-structures of the study object. The micro-CT technique was used to generate a three-dimensional model, which gives a 360° vison of the sample, allowing to analyze all characters. To achieve this, amber samples need to be pre-polished until critical thickness (<1 mm). The true challenge is to optimize the visibility of the sample without causing damage to the core inclusion.

1. Introduction

1.1 The Mesozoic Era

The Mesozoic Era is geological period ranging from 252 to 66 mega-annum [Ma], preceded by the Paleozoic ("ancient life") and succeeded by the Cenozoic ("new life"). Mesozoic began in the wake of the Permian–Triassic extinction event and ended with the Cretaceous–Paleogene extinction event.

Mesozoic is an important period with significant tectonic, climate, and evolutionary events (Marshak, 2016). Compared with the vigorous orogeny (mountain-building) caused by plate convergence of the late Paleozoic, Mesozoic tectonic deformation was relatively mild. The major Mesozoic orogeny occurred in the present-day Canadian Arctic, creating the Ellesmere orogeny, the Brooks Range, the Verkhoyansk and Cherskiy Ranges in Siberia, and the Khingan Mountains in Northeast China (Hughes, 1975). This orogeny is also related to the opening of the Arctic Ocean and the subduction of the North China and Siberian cratons under the Pacific Ocean (Hughes, 1975). On the contrary, the Mesozoic featured the dramatic rifting of the supercontinent Pangaea, which gradually split into a northern continent, Laurasia, and a southern continent, Gondwana. By the end of the Mesozoic, the continents had rifted almost into their present forms, though not in their present positions. Laurasia became North America and Eurasia, while Gondwana split into South America, Africa, Australia, Antarctica and the Indian subcontinent, which collided with the Asian plate during the Cenozoic, and giving rise to the Himalayas (Ren et al., 2002; Shu et al., 2009).

Mesozoic is subdivided into three major periods:

- Triassic (~252 – 201 Ma)
- Jurassic (~201 – 145 Ma)
- Cretaceous (~145 – 66 Ma),

which are further subdivided into a number of epochs and stages.

The Triassic continental interior climate was generally hot and dry, therefore typical deposits from this time are red bed sandstones and evaporites. Pangaea's large area limited the moderating effect of the ocean. The continental climate was highly seasonal, with very hot summers and cold winters. The polar regions were apparently moist and temperate, providing habitats suitable for the development of fauna and flora (Miller and Baranyi, 2019). The Jurassic climate was tropical, much more humid than the Triassic one, and almost resembled the conditions in a preliminary rainforest in the tropical areas in Middle – Late Jurassic. These conditions paved the way for a lush vegetation to grow, slightly increasing the carbon dioxide levels, therefore creating a “greenhouse” warming of the whole earth. However, in Late Jurassic a cooling trend started which continued into the Early Cretaceous (Berriasian) (Sellwood and Valdes, 2008). Though seasonal snow may have happened farther from the poles, glaciation restricted only to high-latitude region (Huber et al., 2002). After the end of the first age of Cretaceous, likely due to the intense volcanic activities which produced large quantities of carbon dioxide, temperatures increased again and stayed almost constant until the end of the period. The cretaceous temperature gradient from the equator to the polar areas was very gentle, which implies/suggests weaker global winds that drove the ocean currents and resulted in less upwelling and more stagnant oceans than they are today (Stanley, 2004). Sediment cores show that tropical sea surface temperature may have briefly been as warm as 42 °C (108 °F), with average around 37 °C (99 °F). Meanwhile, deep ocean temperature was as much as 15 to 20 °C (27 to 36 °F) higher than that of the current (Skinner et al., 2008).

The Mesozoic period has seen a tremendous evolution of both the fauna and flora. In contrast the current terrestrial vegetation, which is dominated by angiosperms(flowering plants), the dominant terrestrial plants of that time were gymnosperms, which are vascular, cone-bearing, non-flowering plants that produce seeds without a coating, such as cycad and conifers (Wang and Ran, 2014). Angiosperms emerged and then primarily radiated sometime during the Late Jurassic–

Early Cretaceous period (Labandeira and Currano, 2013). By the end of the Cretaceous, angiosperms already dominated tree flora in many areas, although some evidence suggests that the biomass had been dominated by cycads and ferns until after the Cretaceous–Paleogene extinction (Dilcher, 1979). Mesozoic is the era of reptiles, with the dominating animals being various archosaurs: dinosaurs, pterosaurs, and aquatic reptiles such as ichthyosaurs, plesiosaurs, and mosasaurs (Hedrick and Dodson, 2020). With the tectonic and climatic changes of the late Jurassic and Cretaceous, adaptive radiation was accelerated, featured by the emergency of early birds and eutherian mammals (Holgado and Suñer, 2018). Insect diversity highly developed in Mesozoic, which may provide new insights of the Mesozoic vegetation shift (Ross, 2019; Zhang et al., 2018).

1.2 Beetles as the most successful animals

Beetles are the common names for species within the order Coleoptera (Class: Insecta). With about 400,000 species, Coleoptera is the largest of all orders, constituting almost 40% of present described insects and 25% of all known animals. Except for the oceans and the polar regions, beetles are found in almost every habitat around the world (Crowson, 1981).

The general body plan (“Bauplan”) and anatomy of beetles are quite uniform and are typical of an insect: body consists of head, thorax, abdomen and three pairs of legs (Lawrence and Ślipiński, 2005). Beetles typically have particularly hard exoskeletons including the elytra, though some (e.g. the rove beetles, Staphylinidae) have very short elytra while others (e.g. the blister beetles, Meloidae) have softer elytra. All beetles are members of the superorder Endopterygota, most of whom undergo complete metamorphosis (Beutel and Leschen, 2016). Some beetles, typically members of the families Meloidae and Rhipiphoridae undergo a hypermetamorphosis process, in which the first instar takes the form of a triungulin (Zachary H. Falin, 2002; Pinto and Bologna, 2002). The typical form of metamorphosis in beetles consists of four major stages: egg, larva, pupa, and imago or adult (Beutel and Leschen, 2016).

Coleoptera has been suggested to be monophyletic, though the classification of a large number of beetles species is problematic. The Order Coleoptera is generally classified into five suborders, represented by significant characteristics (Bouchard et al., 2011):

- Adephaga (~ 10 extant families, largely predatory beetles)
- Archostemata (4 extant families, mainly wood-eating beetles)
- Myxophaga (4 extant families, aquatic and semiaquatic beetles)
- Polyphaga (~ 90% of the beetle species, highly diversed)
- †Protocoleoptera (7 extinct families, range Early Permian–Late Albian).

Particularly, the main apomorphy for beetles in the large suborder Polyphaga lies in:

1. The hind coxa (base of the leg), which does not divide the first and second abdominal/ventral plates (known as sternites);
2. The notopleural suture (found under the pronotal shield) is not present.

Five infraorders are further divided within Polyphaga (Bouchard et al., 2011):

- Bostrichiformia
- Cucujiformia
- Elateriformia
- Scarabaeiformia
- Staphyliniformia,

which displays an enormous variety of specialization and adaptation. They have multiple interactions with their ecosystems, e.g. living and feeding on plants and fungi, leaf littering, decaying wood and flowers, breaking down animal and plant debris, and eating other small invertebrates (Peris and Rust, 2019).

Beetles are highly evolved insect groups, which is reflectedin their locomotion, communication, sociality and advanced ecology roles. Adapted to different living habits, their locomotion modes vary and the related body muscles (e.g. wings, hind legs) develop correspondingly (Bao et al., 2018c). Most beetles are solitary, but in many species and/or higher taxa conglobations, aggregations and a wide variety of parental cares are known (Brandmayr, 1992). Both their adults and larvae are the food of many predators including mammals from bats to rodents, birds, lizards, amphibians, fishes, dragonflies, robberflies, reduviid bugs, ants, other beetles, and spiders. Thus, beetles developed a variety of anti-predator adaptations to defend themselves. These include camouflage and mimicry against predators that hunt by sight, toxicity, and defensive behaviour (Poulton, 1940). A few species of beetles are ectoparasitic on mammals (e.g. *Platypsyllus castoris*, parasitises beavers *Castor* spp.) (Avenant-Oldewage, 2002). Some species of beetles (e.g. Passilidae) are intermediate hosts of mites or ticks during phoresis (Villegas-Guzmán et al., 2008).

1.3 Mesozoic beetles

The earliest Coleoptera fossil records are from Early Permian (Smith and Marcot, 2015). As a consequence of the Permian -Triassic extinction event, the fossil record of insects in Triassic is obviously scant compared with Jurassic and Cretaceous. Yet still large quantities records were found in China, Australia, Argentina, South Africa, Eastern USA and Europe (Zheng et al., 2018). Especially in Late Triassic, the diversity of beetles developed primarily, with new taxa emerging, e.g. species of the infraorders Archostemata (e.g. Ademosynidae, Schizocoleidae), species of Adephaga (e.g., Triaplidae, Trachypachidae), species of Polyphaga (e.g. Hydrophilidae, Byrrhidae, Elateroidea) are abundant in at the Babiy Kamen site in the Kuznetsk Basin (Beutel and Friedrich, 2008; Ponomarenko, 1969, 2004); species from the families Cupedidae were discovered from Lower Triassic, Madygen Suite, southwest border of Fergana valley, Osh Province, Lyaylyakskiy District (Ponomarenko, 1967).

During the Jurassic, the diversity of beetles families increased dramatically. Early herbivorous species showed primary development. The estimated divergence times suggest that most modern families of Chrysomeloidea originated during the Jurassic period (Farrell et al., 1998; Wang et al., 2014). The leaf beetles, Chrysomelidae, might have emerged in the Middle Jurassic (Wang et al., 2014). It is assumed that the ecology of Chrysomeloidea should be shifted from cycads and conifers of Early Jurassic to angiosperms of Jurassic-Cretaceous due to the angiosperm radiation (Wang et al., 2013a). Indeed, most of recent herbivorous beetles feed on angiosperms, which contributed to a doubling of herbivorous species during the Middle Jurassic (Labandeira and Sepkoski, 1993). Around the same time, early Tenebrionoidea, Scarabaeoidea and Curculionoidea appeared, indicated surface feeding strategy associated with rotten wood, fungi, lichen, moss (Gratshev and Zherikhin, 2003; Hsiao et al., 2017; Wang and Zhang, 2011). There are more than 150 important fossil sites from the Jurassic, the majority in Eastern Europe and North Asia. Outstanding sites include Solnhofen in Upper Bavaria, Germany (Ponomarenko, 1983), Karabastau formation in South Kazakhstan (Szwedo and Zyla, 2009a; Yan, 2009), the Yixian formation in Liaoning, North China, as well as the Daohugou biota and further fossil sites in Mongolia which generally belong to the Jehol Group (Wang et al., 2009)

Most of the extant beetle families appear to have arisen in the Cretaceous. The Coleoptera records discovered in Cretaceous amber inclusions are quantitively dominated (Peris et al., 2016; Peris and Rust, 2019). The diversity of Cupedidae and Archostemata decreased considerably (Ponomarenko, 1969), while the diversity of polyphaga increased tremendously, which includes 90% of extant families (Grimaldi and Engel, 2005). Staphylinidae is the most species-rich family from tropical and subtropical amber deposits, which shows a high diversity of feeding habits, covering the entire range of ecological habitats (Peris and Rust, 2019). It is supposed that the radiation of angiosperm influence on the diversity of Cretaceous Coleoptera (Faegri and Van der Pijl, 2013; Winship and Hu, 2010). However, the increase of the number of beetle families during the Cretaceous may not completely correlate with the increase of the number of angiosperm species (Labandeira and Sepkoski, 1993).

1.4 The insect-plant interaction

Taking beetles as an example, the feeding strategy and ecology of insects are quite advanced and diverse. Archostemata, normally identified as the ancestral group in Coleoptera, are characterized by a trend towards limited food uptake in the adult stage, besides, their larvae adapt to burrowing in wood (Beutel and Friedrich, 2008). The adults of Adephaga are predacious while the larvae, with only a few exceptions, possess more or less advanced preoral digestion (Beutel et al., 2019). Both the adults and larvae of Myxophaga feed on algae, while Polyphaga are primarily saprophagous, especially fungivorous (Beutel and Yavorskaya, 2019). On a macro level, except for some purely carnivorous groups, the majority of beetles and insects are associated or partially associated with flora environment. In order to study the insect-plant interactions, based on their morpho-behavioural mechanisms of food acquisitions, the related taxa are classified into Functional Feeding Groups (FFGs) (Table 1) (C. C. Labandeira, 2006; Labandeira, 2002). Basically, the FFGs can be classified as exophytic (external foliage feeding subdivided in skeletonization, hole, margin and surface feeding), endophytic (galling, leaf mining and piercing / sucking), and intermediate, that category is recognized where the arthropod herbivore is located externally but feeds on internal tissues (piercing-and-sucking, oviposition and root feeding) (Labandeira, 2013a).

Table 1. Terrestrial arthropod (insect) functional feeding groups. Based on (C. Labandeira, 2006; C. C. Labandeira, 2006; Labandeira, 2013a, 2002; Labandeira et al., 2007)

Feeding system	Functional feeding group	Examples	Tissues consumed	Earliest occurrence
Exophytic	External foliage feeding	Margin feeding, hole feeding, surface feeding, skeletonization	Epidermis, parenchyma, xylem, phloem	Middle Devonian
	Palynophagy	Whole palynomorph consumtion, puch-and-sucking of protoplasts, feeding and carrying pollen	Spores, pollen, megaspores	Middle Silurian
	Surface fluid feeding	Siphonate feeders, spongers, lappers	Secretory tissues, epidermis	Late Pensylvanian
Intermediate	Piercing and sucking	Deep-tissue feeding, mesophyll feeding, punch-and-sucking	Xylem, phloem, epidermis, parenchyma, megagametophyte endosperm tissues, integuments	Early Devonian
	Oviposition	Solitary, rows, multiple clusters	Epidermis, parenchyma, xylem, phloem, periderm	Late Pensylvanian
	Rhizophagy	(none recognized)	Epidermis, parenchyma, xylem, phloem	Middle Pensylvanian

Endophytic	Leaf mining	Serpentine mines, blotch mines, cambial mines	Epidermis, parenchyma, xylem, phloem, apical meristem, lateral meristem, intercalary meristem	Middle Triassic
	Galling	Prosoplasmic galls, histoid galls, organoid galls	Epidermis, parenchyma, xylem, phloem, collenchyma, sclerenchyma, apical meristem	Middle Devonian
	Seed predation	(none recognized)	Epidermis, megagametophyte endosperm tissues, integuments	Early Pensylvanian
	Borings	Bark borings, heartwood borings, sapwood borings, pith borings	Periderm, parenchyma, xylem, phloem, collenchyma, sclerenchyma, apical meristem, lateral meristem, intercalary meristem	Early Devonian

The fossil history of insect-plant associations can be viewed as three kinds of relatively distinct but related fossil records (Labandeira, 2018, 2010):

- · the separate plant fossil,
- · the separate animal body fossil,
- · the insect-plant association fossil record.

The first and second categories are relatively clear, based on taxonomy and phylogeny study; while the fossil records of the third category are complicated and require multi-disciplinary knowledge. The third fossil category can be further subdivided into six principal types of evidence to support and explain insect-plant associations (Labandeira, 2018):

(1) plant reproductive biology,

(2) plant damage,

(3) dispersed coprolites,

(4) insect gut contents,

(5) insect mouthparts,

(6) plant and insect taxonomic assignment to a modem descendant for which. reliable ecological data exist.

Based on strength, the above six types of evidence can be divided into direct evidences and indirect evidences (personal communication with David Peris). Direct evidences, such as insect gut contents, coprolites, plants fragments remain on insect body and mouthparts, can strongly support insect-plant associations. On the other hand, indirect evidences, e.g. insect and plant morphology and anatomy characters, plant damage, plant and insect taxonomic assignment, are less persuasive. However, when a fossil record combines both direct and indirect evidence with more details, a comprehensive explanation of the insect-plant association and ecology could be achieved (Bao et al., 2019b).

1.5 The rise of “Abominable Mystery”

The “Abominable Mystery” is used by Charles Darwin to express his wonder about the rapid radiation of angiosperms in Cretaceous (Friedman, 2009). In 1879, John Ball published an article about the origin of the flora of the European Alps, which soon drew Charles Darwin’s attention. On July 22nd, Darwin wrote about his uncertainty about the early origin and fast radiation of angiosperms in his letter to the botanist Sir Joseph Dalton Hooker. He thought, the evolution and development of every taxon should abide by the fundamental principle of going from simple to complex. Obviously, the emergency of angiosperm violates this principle, which he mentioned as the famous “abominable mystery”.

From the first macrofossil occurrence of angiosperms (Sun et al., 2002) until they took the dominance, the earth vegetation shows a big but quick transition during Jurassic–Cretaceous interval (Krassilov, 1977). Phylogenetic analysis of angiosperms shows that basal angiosperms (ANITA grade) consist of Amborellaceae, Hydatellaceae, Cabombaceae, Nymphaeaceae, Austrobaileyaceae, Trimeniaceae, Schisandraceae, and Illiciaceae developed in Early Cretaceous (Thien et al., 2009). The great angiosperm radiation, when a great diversity of angiosperms appears in the fossil record, occurred in the mid-Cretaceous (Dilcher, 1979). By the Late Cretaceous, angiosperms appear to have dominated the habitats, shaping the current earth vegetation (Sadava, 2014). Hypothetically, the large canopy-forming trees replaced conifers as the dominant trees 66 million years ago, close to the end of the Cretaceous or even later, at the beginning of the Tertiary (Sadava, 2014).

Through decades of research, the exact explanation for the rapid radiation of angiosperms is still arguable. One hypothesis is the so-called Genome Hypothesis (Simonin and Roddy, 2018). During the early Cretaceous period, only angiosperms underwent rapid genome downsizing, while genome sizes of ferns and gymnosperms remained unchanged. Smaller genomes and smaller nuclei allow for faster rates of cell division and smaller cells. Thus, species with smaller genomes can pack more and smaller cells in particular veins and stomata into a given leaf volume. Genome downsizing therefore facilitated higher rates of transpiration and photosynthesis and thus a faster rate of growth. This could have countered some of the negative physiological effects of genome duplications, facilitating increased uptake of carbon dioxide despite concurrent declines in atmospheric CO_2 concentrations, and allowed the flowering plants to outcompete other land plants.

From the view of palaeontology, the oldest flower fossil dated to the Early Cretaceous (115–125 Ma), which is related to the extant Nymphaeaceae (Friis et al., 2001). The advanced eudicot flower emerged no later than Cenomanian (Liu et al., 2018). Based on the studies of early angiosperm flower fossils and *in situ* pollen since the 1970s (Dilcher, 1979), the hypothesis that insect pollination was the dominant mode of angiosperm pollination during the Lower Cretaceous (Friis et al., 1999), with specialization increased by the angiosperm radiation (125–90 Ma) (Crepet and Nixon, 1996), is widely accepted. However, the direct evidence for Cretaceous insect-angiosperm interaction is absent. Concrning the common modern pollinators, bees (Apoidea) are rarely recorded since Cretaceous with their ancestral taxa (Poinar and Danforth, 2006), but the specimen with collected pollen are recorded only as early as Middle Eocene (Wappler et al., 2015); butterfly (Papilionoidea) records are absent before Cenozoic. The indirect evidence for early insect-angiosperm interaction is also limited, and the existing few mainly focused on floral morphology and the potential association with pollinators (Crepet and Nixon, 1998; Gandolfo et al., 2004) or the mouthpart evolution of long-proboscid insects that influenced piercing / sucking feeding strategies (Labandeira, 2010; Liu et al., 2018). However, the dramatic earth vegetation change did leave traces on the fossil records of plant-insect associations. The number of gymnosperms associated insect taxa started to decrease from Barremian (~125 Ma) and reached a stable low level by Turonian (~90 Ma). During the same period, the angiosperms associated insect taxa started to grow and reached the peak (Peris et al., 2017). The intersection of two trends caused a short-time global decrease of plant-associated diversity in total, which is called the "Aptian–Albian gap" (~125–90 Ma) (Labandeira, 2014; Wang et al., 2016). Thus, the mid-Cretaceous is also the key period for answering the palaeoecological transition of fauna taxa (Wang et al., 2013a).

2. Aim of study

2.1 The key to answering "Abominable Mystery"

Currently, Darwin's "Abominable Mystery" has come to indicate about all aspects of the origin and early evolution of flowering plants. However, indeed Darwin was deeply bothered by what he perceived to be an abrupt origin and highly accelerated rate of diversification of flowering plants in the mid-Cretaceous. Obviously, he took refuge in the possibility that a rapid diversification of flowering plants in the mid-Cretaceous might have a biological explanation involving coevolutionary interactions between pollinating insects and angiosperms. Probably, we can make breakthrough from palaeontology (palaeoentomology) aspect; try to discover the early insect taxa records which show a possible close relationship with angiosperms (e.g. feeding trace, palynology records, etc.), and use this as a shred of evidence. Before this research, this kind of evidence in Mesozoic, especially the direct pollination evidence, was completely absent. Thus, it still remains a theoretical hypothesis that there is advanced insect-angiosperm interaction during Mesozoic and due to this, insects and angiosperms both got to flourish further.

Compare with other insect groups, the Mesozoic beetles are highly diverse in ecology, especially for some polyphagan groups. Theoretically, the possible fossil materials that can support the hypothesis exist. The target material should generally match the following characters:

· Fossil records are continuous. The fossil records of the same animal group should be continuous with the range at least from Jurassic to Cretaceous, cover the angiosperm radiation and the vegetation change period (125–90 Ma).

· Morphological characters are obvious. The morphology characters of the fossil specimens should not be extremely hard to exam. Especially for the Jurassic fossil, they are mainly compressed rock fossil, detailed morphology characters may be hard to observe or damaged.

· The extant relative taxa should imply close insect-plant interaction. The relative extant taxa should give supportive reference to the ecology, which can help understand and explain the palaeoecology.

The fossil records of the beetle family Mordellidae (Coleoptera: Tenebrionoidea) apparently match for the three main requirements above. The extant Mordellidae are characterized by wedge-shaped body, expanded hind legs, wide metacoxa plate and elongated pygidium. The extant Mordellidae constitute of about 1500 species worldwide (Jackman and Lu, 2002), among the typical flower beetle, represent flower diet and generalized pollination (Yang and Ren, 1999; Beutel and Leschen, 2005).

Before this research, a certain amount of Mordellidae fossil were discovered; however, the importance of Mordellidae fossil records is not being seriously valued. The fossil records of Mesozoic mordellids are generally scarce but continues, mainly found in the Late Jurassic Karabastau Formation, Russia (Scegoleva-Barovskaja, 1929) and the Early Cretaceous Yixian Formation of China (Liu et al., 2008, 2007) without the pygidium. The Cretaceous (Albian) *Mediumiuga sinespinis* (Burgos, Spain) shares the primitive characters with modern Mordellidae, and is featured by appendix microstructures on mesotibiae and mesotarsi (Peris and Ruzzier, 2013). The Cenozoic Mordellidae are comparatively abundant, discovered in Fushun amber of the Eocene of China (Zhang and Hong, 1999), Kishenehn Fm., Eocene of Montana, USA (Huber and Greenwalt, 2011), Green River Fm., Eocene of Colorado, USA (Cockerell, 1925), Baltic amber of the Eocene Baltic gulf (Kubisz, 2003; Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013), Florissant Fm., Oligocene of Colorado, USA (Cockerell, 1907; Scudder, 1890), Rott Fm., Oligocene, Germany (Statz, 1952), Carbonate Fm., Oligocene, France (Nel, 1985), Mexican amber, Miocene, Mexico (Poinar, 1993), Olympia beds Fm., Pleistocene, Washington, USA (Ashworth and Nelson, 2014) display close similarity to the extant species and they have been traditionally assigned in the major part of the cases to *Mordella* and *Mordellistena*.

I believe the fossil records of Mordellidae could be the key factor to explain the insect-plant association in Mesozoic and the “Abominable Mystery”. Based on the newly discovered taxa and the carefully re-examination of the continuous fossil records, it will help us to understand the evolution trend of the family. The morphology change of beetles could give new insights linked to their ecology change. Besides, there could be other early flower beetle records which can be also taken as a reference during the study.

2.2 The possible beetle ecology shift while the flourish of angiosperms

As the dynamic of the earth surface vegetation changed, the flourish of angiosperms not only replaced the dominance of gymnosperm plant, but also impacted on other flora groups’ development such as tree ferns, ferns and cycadophytes. By the mid-Cretaceous, the environment formerly occupied by ferns and cycadophytes started to shift to angiosperms domination. Surprisingly, the diversity of fern dramatically increased, almost 90% of modern ferns evolved by this time (Schneider et al., 2016). The possible explanation remains unclear. Insect, including various beetle groups, probably played important roles, as some groups are closely related to particular plant groups. Based on the former summary, during the “Aptian–Albian gap”, the insect-plant association follows these shift mode (Peris et al., 2017):

(1) gymnosperm host associations that became extinct earlier in the interval, such as *zhangsolvid* flies (Ren et al., 2009);

(2) gymnosperm host associations that survived the interval and continued largely to the present, exemplified by *merothripid* thrips (Labandeira et al., 2007);

(3) gymnosperm host associations that transitioned laterally onto new angiosperm hosts, which included false blister beetles (Peris et al., 2017);

(4) new angiosperm host associations later in the interval, of which bees are an example (Wappler et al., 2015);

The new materials in this research provided new evidence to support the mentioned four modes and further discussion will up to be more complete. For instance, Cretaceous Mordellidae give new insights into early angiosperm association. Early Kateretidae records imply a shift process from gymnosperm association to angiosperm association. However, beetles are discovered in more diverse habitats with more various plant hosts, which indicated the interactions and shift dynamic are considerably more complicated than it was early assumed.

2.3 Ecology of tropical amber forest in the Cretaceous

The main Cretaceous amber deposits are all located in the northern hemisphere (Fig. 1) include Lebanon (late Barremian), Spain (early Albian), France (late Albian/early Cenomanian–Santonian), Myanmar (early Cenomanian), New Jersey (late Turonian), Russia (Taimyr, middle Santonian) and Canada (late Campanian) (Peris and Rust, 2019). The amber materials are typically found in sediments with fluvial and/or marine influence; therefore these amber-bearing deposits are thought to be mostly allochthonous accumulations (Zherikhin and Ross, 2000). It has been suggested that resin globules are commonly washed from their place of origin and concentrated in fluvial, deltaic, lacustrine or even nearshore marine environments (Penney, 2010). Regarded as the Cretaceous climate, the amber forest climate is generally characterized as nowadays tropical or subtropical. Especially for the Lebanon and Myanmar deposits, their geological setting is closer to equatorial which implies a typical tropical Cretaceous forest.

The tropical forest ecosystem is composed of complicated components, stable and with high flora and fauna diversity. This can be easily differed from Burmese amber flora and fauna inclusions. However, research in the recent years mainly focused on individual groups taxonomy and phylogeny. Few research discuss the outer picture of the whole ecosystem. Since the beetles are the most diverse and distributed fauna fossil (at least from Cretacous), they can be treated as clue to link different zone habitats, e.g. from bottom forest to top, from shore to inland, which is possibly helpful for comprehensive discussion of the amber forest as a whole.

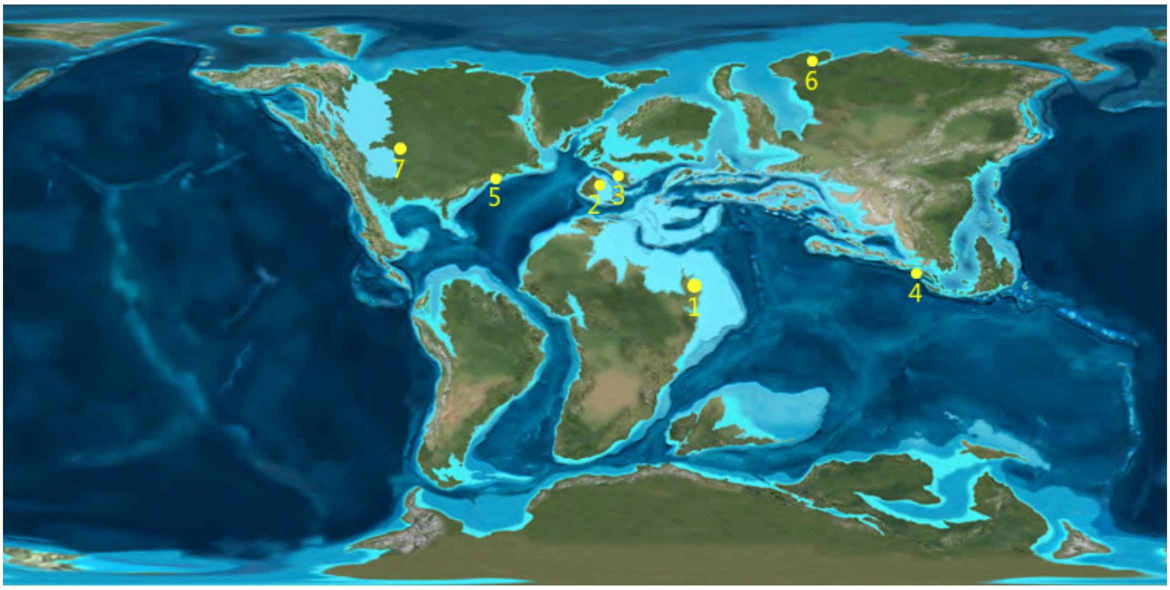

Fig. 1. Main Cretaceous amber deposits: 1. Lebanon (late Barremian), 2. Spain (early Albian), 3. France (late Albian/early Cenomanian–Santonian), 4. Myanmar (early Cenomanian), 5. New Jersey (late Turonian), 6. Russia (Taimyr, middle Santonian), 7. Canada (late Campanian). (Map source: Ron Blakey, NAU Geology)

3. Geology setting of fossil Lagerstätten

A fossil Lagerstätte is a special sedimentary deposit that exhibits extraordinary fossils with exceptional preservation. In palaeontology, two kinds of Lagerstätten were defined: Konzentrat-Lagerstätten (concentration Lagerstätten), deposits with a particular "concentration" of disarticulated organic hard parts, such as a bone bed, and Konservat-Lagerstätten (conservation Lagerstätten), deposits known for the exceptional preservation of fossilized organisms or traces (Seilacher, 1970), of which conservation Lagerstätten are more spectacular because of the special anoxic taphonomy environment, sometimes including preserved soft tissues and traces. In this research, fossils from various Konservat-Lagerstätten were checked or examined. Karabastau Formation, Daohugou biota and Yixian Formation are inorganic fossil deposits, that represent regional terrestrial sediments environment (lake, pond, bog, etc.). Daohugou biota and Yixian Formation can be considered as the compounds of Jehol Biota ecosystem with the similar sediment structures, however their fossil assemblages are quite different. Mesozoic and Cenozoic amber biota are organic fossil deposits, that represent tropical forest environments.

3.1 Karabastau Formation

The Upper Jurassic Karabastau Formation of the Karatau Range (the northwestern spur of the Tian Shan Mountains) is located near the village of Aulie (formerly called Mikhailovka), Chayan District, Chimkent Region, southern Kazakhstan (Fig. 2A). The Karabastau Formation, yielding about 18,000 insect fossils to date, abundant with vertebrate fauna (fishes, pterosaurs, amphibians and reptiles) and numerous plant fossils, is among the world’s most prolific sources of fossil insects (Rasnitsyn and Zherikhin, 2002). Based on the plant assemblages (bennettites, conifers, pteridophytes, cycadophytes, Equisetales, Caytoniales, Ginkgoales, Cycadales, and Czekanowskiales) and a spore-pollen analysis (domination of Classopolis pollen, minority with Leiotriletes-type spore and Klukisportites microrelief), the age of the Karabastau Formation may be assigned to the Upper Jurassic (Oxfordian–Kimmeridgian), i.e. circa 158–152 Ma (Kirichkova and Doludenko, 1996), but the precise age remains unclear because of the lack of a definite radiometric age.

The Karatau Range is composed of continuous rock records from Lower Proterozoic to extant. The Jurassic deposits form a narrow belt between Maly Karatau and the southern and central parts of the Bolshoy Karatau, which 2–8 km in width, stretches over 200 km from the Chokpak pass in the southeast to the valley of the Bala Turlan river in the northwest (Doludenko and Orlovskaya, 1976). The deposits consist of grey, laminate siltstones, marls, limestones and dolomites, which separate into two series by the grey or black aleurolites, with inclusions of sandstones, conglomerates and gravels (Szwedo and Zyla, 2009b). Almost all organic remains are associated with the uppermost layers of upper series with component of aleurolites, marls, limestones and dolomites (Doludenko et al., 1990).

The Karatau paleo-lake originated in the inner-mountain basin, and relatively rapidly was filled with proluvial sediments. 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 bennettita-leans, 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), significant by the water beetle Gyrinidae (Yan, 2009), the “most ancestral” extant beetle family Ommatidae (Tan et al., 2012) and ancestor flower beetle Praemodellinae (Bao et al., 2019c).

3.2 Daohugou biota and Yixian Formation

The Middle Jurassic Daohugou beds are currently known to have been distributed in a small area across the border of Ningcheng, Inner Mongolia and Lingyuan, Liaoning. Major fossil localities include the Daohugou Village, Zhujiagou, Jiangzhangzi, Wubaiding etc. (Fig. 2B). The Daohugou beds consist three lithology sequences: the lower part is mainly composed of grayish tuffs with interbedded thin and reddish shales, which had previously been misidentified as belonging to the

Tuchengzi Formation; the middle part is composed of thick grayish tuffs with interbedded thin gray or greenish tuffaceous shales; and the upper part is composed of interbedded grayish tuffs and shales, representing the main fossil abundant horizon (Wang et al., 2005). The Daohugou deposits were often folded or inverted due to strong tectonic activities. Most fossil insects from Daohugou beds 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 with 40Ar/39Ar and SHRIMP U-Pb methods 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 research, concept of rough Middle Jurassic age is preferred, 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).

Despite the Daohugou beds and Yixian Formation share high lithological similarity, their fossil assemblages are quite distinctive, significant by the absence of *Lycoptera* (iconic fish taxa in Jehol biota) in Daohugou bed (Wang et al., 2005). This probably shows they belong to the same cycle of volcanism and sedimentation although the Daohugou beds are lower than the Yixian Formation. Hypothetically, the Daohugou fossil assemblage represents the earliest evolutionary stage in Jehol Biota.

3.3 Burmese amber ("Kachin amber")

The amber from Myanmar, commonly known as Burmese amber, has a long history of excavation. The oldest record of Burmese amber comes from Siku Quanshu-Han Dynasty (~3rd century) (Kania et al., 2015); the first possible Burmese amber object was unearthed during the archaeological study of Marquis of Haihun tomb (Jiangxi, China, ~59BC) (Yang et al., 2017). Traditionally, Burmese amber plays an important role in regional economy, healthcare and art (Zhang et al., 2017). Nowadays, the commercial Burmese amber source is located in the Hukawng Valley of the Myitkyina and Upper Chindwin districts (Cruickshank and Ko, 2003; Ross, 2010; Zherikhin and Ross, 2000), which contain thirteen documented sites (Chhibber, 1934), however most of the coordinates of the locations have been lost. The deposit in Noije Bum (north of Myanmar, 20km to the southwest of Danai, Hukawng Valley, Kachin Province, "Kachin amber") (Fig. 3) was re-exploited in 1990s and became the main source for excavation (Ross et al., 2010; Xia et al., 2015), which has been regarded as one of the most important deposits for studying Cretaceous terrestrial biodiversity, more than 300 families of arthropods have been reported from this deposit (Bao et al., 2018a). Kachin amber mine was excavated for centuries, till now continuously attracted generations of researchers. The first three Kachin amber inclusion species were named in 1916; by 1999 only 45 species were identified; by the end of 2018 the total had risen to an incredible 1,192 species (Ross, 2019).

The Burma Terrane was part of a Trans-Tethyan island arc and stood at a near-equatorial southern latitude at ~95 Ma, suggesting island endemism for the Burmese amber biota (Westerweel et al., 2019). The resin chemical analysis suggests Araucaria family could be the main component of the Burmese amber forest (Ross, 2010). The surrounding matrix in Kachin amber mine consists fine-grained sedimentary rock, greyish to bluish-green, with fine fragments of volcaniclastic (Shi et al., 2012). Based on U-Pb dating of zircons, the radiometric age of Kachin amber deposit has been dated as earliest Cenomanian, Late Cretaceous, ca. 99 Ma (Shi et al., 2012). However, the true age of the amber could be slightly older due to the high roundness of the amber surface and the marine fauna inclusions (Yu et al., 2019), which indicate the re-operation process before the amber was buried into the surrounding rock matrix (Bao et al., 2018a).

3.4 Baltic amber

Baltic amber is amongst the largest and most significant of the world’s amber deposits, with numerous yield sites along the Baltic shore. It occurs primarily along the shores of the Baltic Sea in Paleogene sands dated to as early as 40 Ma ago (Kosmowska-Ceranowicz, 2005; Ritzkowski, 1997). The diagenetic history of Baltic amber from its origin until the present has been outlined by Gaigalas and Halas (2009) based on isotope analysis. The most productive amber deposit is located in the Samland Peninsula (Kaliningrad, Russia), featured by the main amber bearing sediment, the Blue Earth (a high glauconite concentration and a dark-blue clayey silt) (Kasiński and Kramarska, 2008). The Samland amber layer also extend to Poland, and thus, further Baltic amber deposits exist, such as Chłapowo, the delta of Parczew, the region of Kurpie and Polesie Lubelskie in South Poland (Kosmowska-Ceranowicz, 1997).

The Baltic amber resin source is supposed to contain several species in family Pinaceae, Araucariaceae and Sciadopityaceae, based on the morphological-anatomical analysis and resin chemical analysis (Sadowski, 2017). In the Baltic amber, animal inclusions are more abundant than plant inclusions. Especially Arthropoda are very well represented, approximately comprise 80% of all animal inclusions from Baltic amber with 539 families were hitherto described, among which Diptera represent the most abundant group of arthropods with 800 species being described, followed up by Araneae (587 species) and Hymenoptera (448 species) (Weitschat and Wichard, 2010). The flora inclusions are comparatively less numerous, approximately 130 species of plants (conifers and angiosperms) were described (Sadowski, 2017).

3.5 Dominican amber

Dominican amber is an important Cenozoic amber deposit from the Dominican Republic, dated as the Miocene. Three main sites are in yielding: La Cordillera Septentrional, in the north, and Bayaguana and Sabana de la Mar, in the east. In the northern area, the amber-bearing unit is formed of clastic rocks, washed down with sandstone fragments and other sediments that accumulated in a deltaic environment, even in water of some depth. In the eastern area, the amber is found in a sediment formation of organic-rich laminated sand, sandy clay, intercalated lignite, and as well as some solvated beds of gravel and calcarenite.

The supposed resin source for Dominican amber from the extinct tree *Hymenaea protera* (Fabaceae), indicated the tropical forest climate. Differing with Baltic amber, the Dominican amber is nearly always transparent with higher quantity of fossil inclusions.

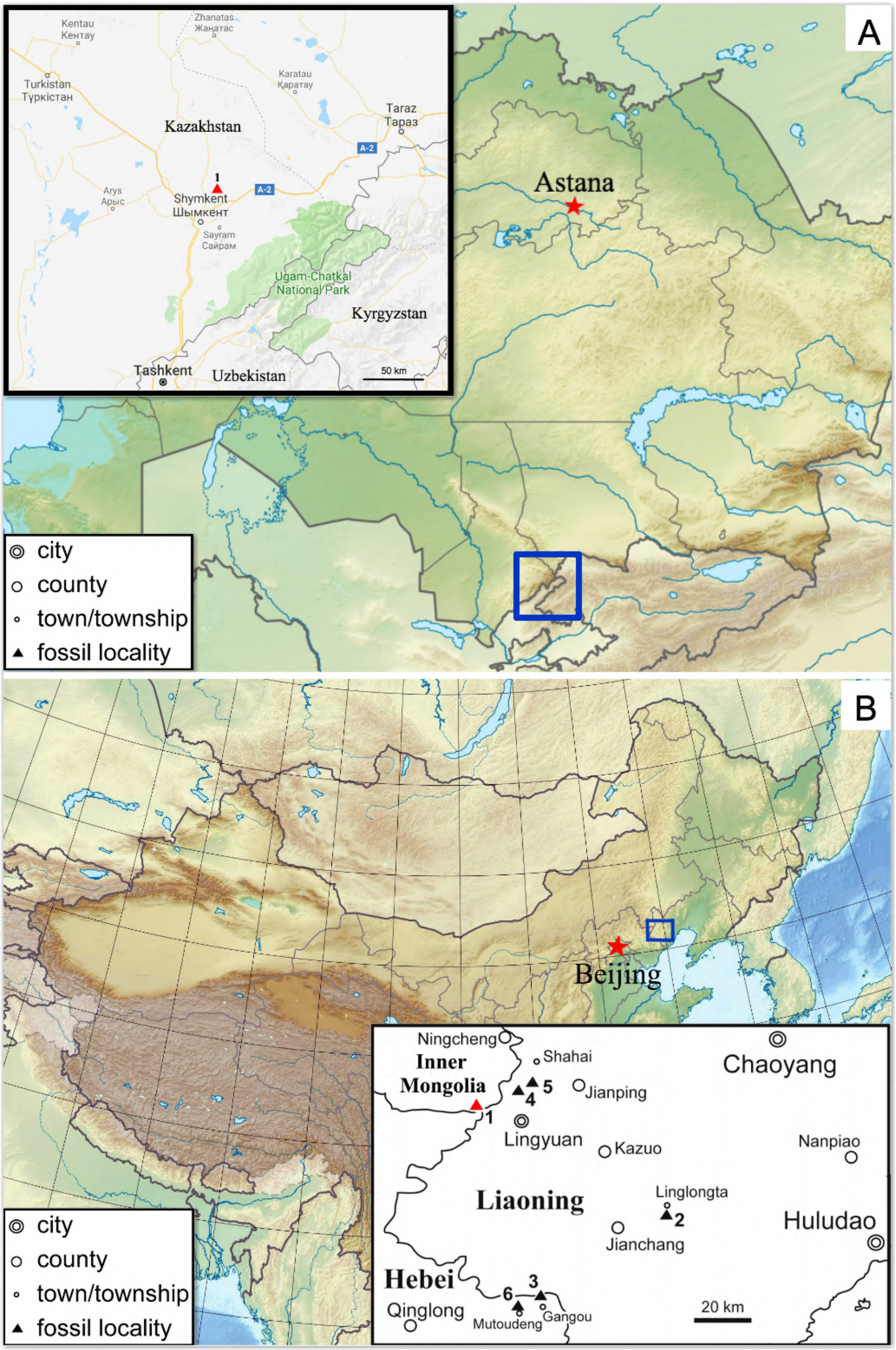

Fig.2. (A) map of the locality of Karabastau Formation in southern Kazakhstan. Highlighted area enlarged and shown in detail. 1, main fossil locality near village of Aulie. Scale bars = 50 km. (B) map of the Daohugou biota in Inner Mongolia and north-eastern China. Highlighted area enlarged and shown 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).

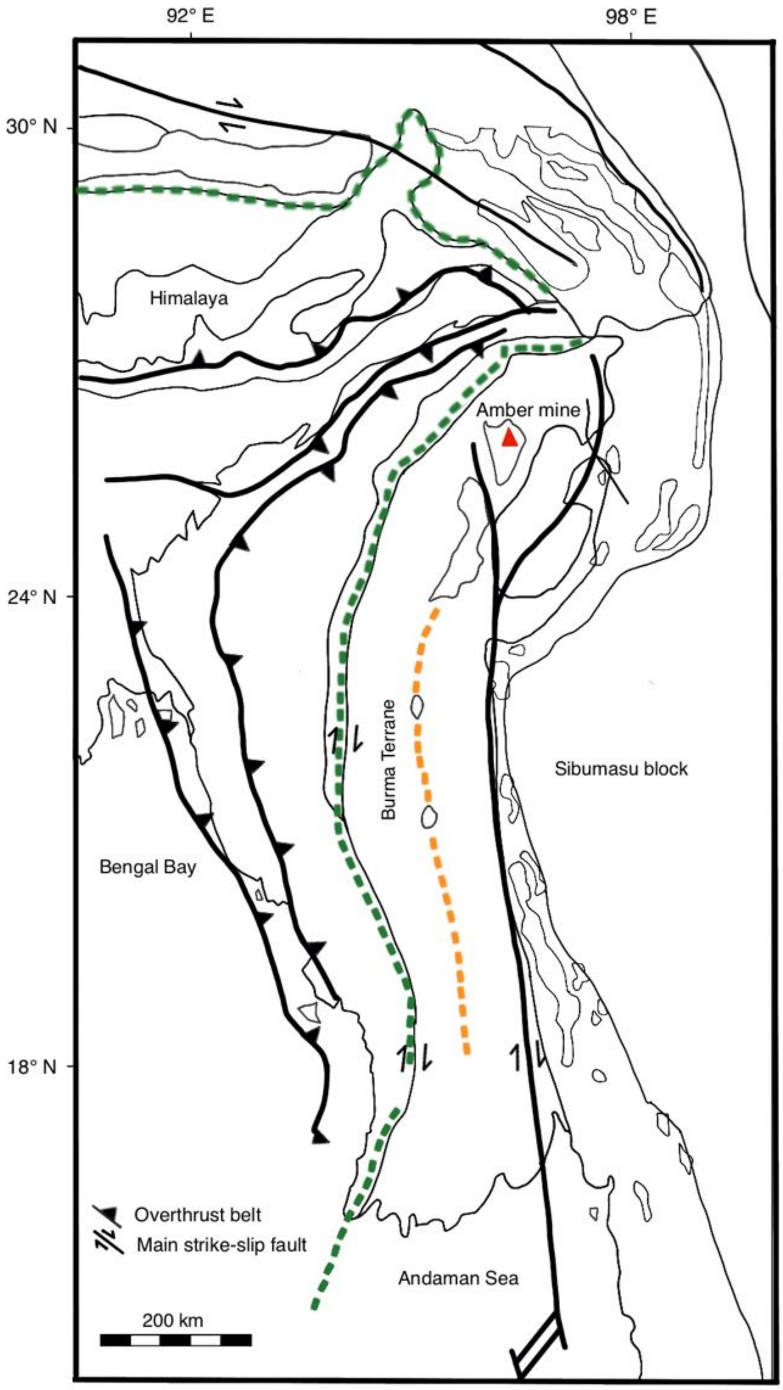

Fig. 3. Regional geology of Myanmar and the locality indication of amber mine in Kachin, northern Myanmar.

4. Material and methods

4.1 Investigated specimens

The research materials are stored and investigated in different institutions and organizations (Table 2). The rock fossils materials included Daohugou Biota fossil, Yixian Formation fossil and Karabastau Formation fossil. The amber materials were discovered from Northern Myanmar, Baltic Sea regions, Ethiopia and Dominican Republic. For reference, collections of extant beetle fauna from Naturhistorisches Museum, Vienna, Austria and Museum Alexander König, Bonn, Germany were examined.

Table 2. Examined materials for this thesis.

Institution/Organization	**Collection**
Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences (NIGPAS), China	Daohugou Biota fossil, Yixian Formation fossil, Burmese amber
Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia	Karabastau Formation fossil
Laboratory-Museum of Amber Inclusions, Gdansk University, Poland	Baltic amber, Ethiopia amber
Lingpoge Shanghai Museum, China	Burmese amber, Baltic amber, Dominian amber
Shiguangnian Tengchong Museum, China	Burmese amber, Dominican amber
Eurofossil Nuremberg, Germany	Dominican amber
Naturhistorisches Museum, Vienna, Austria	Coleoptera collection
Museum Alexander König, Bonn, Germany	Coleoptera collection

The revised holotype in this research should keep the original identification number in the original institution. The newly described holotype and paratype are permanently preserved with unique identification number in related institution. The related published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The not officially published work is temporary mark with LSID urn: lsid: zoobank.org: act:XXXXX.

4.2 Preparation, microscopy and imaging

The Daohugou Biota fossils and Yixian Formation fossils were excavated autonomously from the Lagerstätte through variable mechanical methods. Amber samples were excavated by local labors, then transferred to specific laboratory for further preparation, observing and imaging.

4.2.1 Lab preparation

The imbedding rock matrix for Daohugou biota and Yixian Formation fossils are clean sedimented shale. General cleaning process could be accomplished with distilled water. Air scriber HW-322 was applied for detailed restoration, which can maximally protect the material from fragmentation in process of preparation.

Before observation, amber materials need go through a series of preparation processes. Firstly, the thin surface surrounding rock matrix needs to be removed by centrifuge which may take 3–5 days depending on the hardness of materials. The inclusions of the preliminary prepared amber samples are visible to the naked eye or to the simple optical stereo microscope, which are ready for the primary taxonomy study. For the selected materials through the primary observation, advanced detail preparation will be proceeded. Buehler ISOMET mechanical saw was applied to cut and shape the amber samples into a good observation form. The rotating speed of saw and the counterweight can be adjusted due to the amber samples. For polishing the amber surface, Buehler surface operation system was applied. The roughness degree of CarbiMet & MicroCut abrasive paper varies from grit size 400 (P800)-1000 (P2500), which can be used to decrease progressively in practice. The finest abrasive media is MasterPolish™ suspension of high purity alumina and silica gel, which should be used together with velvet disc, achieve polish grade till 0.05μm.

The particular shaped and partially damaged amber samples could be embedded and stabilized in artificial adhesives (Araldite®). Following the protocol by Nascimbene and Silverstein (2000), the artificial resin matrix produced by a mixture of high-grade Epoxy resin (EPO-TEK 301-2, Part A) and hardener (EPO-TEK 301-2, Part B). To avoid numerous air bubbles occurring during the mixing process, the air was released by placing the container for a short time into a vacuum drying oven (VO 200, with pump module PM 200) until a vacuum of 50 mbar was reached. The target amber specimen was glued into a chamber of silicon ice cube mould. The injected volume of glue liquid should be adjusted perfectly in case the specimens ‘floating up’ in the mould during the embedding process. Under a fume hood, the epoxy resin-hardener mix was added to each chamber containing an amber specimen by a plastic pipette, covering the entire amber piece at least 1–2 mm above the upper facet. After that, the silicon mould was set into the vacuum chamber (adjust vacuum to 50 mbar) and remained there for at least 15 minutes to ensure that the epoxy permeated the entire amber specimen. Air bubbles which remained in the epoxy resin were removed with a needle afterwards. For further operation, the mould that contains all embedded specimens was placed into a fume hood for at least 3–5 days, air-dry. Later, the well-embedded amber samples could be taken out from mould and repeated with the cutting and polishing process.

4.2.2 Optical photomicrography

Stereo zoom microscope is the key equipment to observe the micro world, which provides a 3-dimensional or "stereo" image when looking through the microscope. Stereo zoom microscopes allow quick zoom from low to high magnification. Using a stereo zoom microscope makes it simple to view a sample in the entire field of view, then focus and zoom in on a particular part of interest. Stereo microscope magnification is calculated by multiplying several variables including: eyepiece magnification, built-in objective lens (or zoom) magnification and auxiliary lens magnification. Zeiss AXIO Zoom V16 microscope system at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences (NIGPAS), China, Leica M205 A microscope system and the Leica Application Suite (LAS Version 4.7) at Laboratory-Museum of Amber Inclusions, Gdansk University, Poland, Zeiss AXIO Zoom V16 microscope system and ZEN application University of Bonn, Germany were applied during research. For observing amber specimens, incident and transmitted light were used simultaneously in most instances. Each image was digitally stacked with 40−50 individual focal planes, produced with the software Helicon Focus 6 (http://www.heliconsoft.com) or Zeiss software ZEN for better illustration of the three-dimensional structures. Variable colour lens and syrup or liquid paraffin can improve the image quality. For observing rock fossils, Nikon SMZ1000 stereomicroscope with external digital camera (DXM1200) at the State Key Laboratory of Palaeobiology and Stratigraphy, NIGPAS, China was applied with only incident light.

High magnification optical microscope was used for observing particular micro objects in amber samples, e.g. pollens, spores and other micro inclusions. Amber specimens must be polished till ultimate thickness (<0.5mm) and set into slice. When applying the objective 40x, 60x, cedarwood oil, liquid paraffin or glycerol must be used as observation media.

4.2.3 Confocal laser scanning microscopy

Confocal laser scanning microscopy (CLSM) is an optical imaging technique for increasing optical resolution and contrast of a micrograph using a spatial pinhole to block out-of-focus light in image formation. Confocal microscopy provides the capacity for direct, noninvasive, serial optical sectioning of intact, thick, living specimens with a minimum of sample preparation as well as a marginal improvement in lateral resolution compared to wide-field microscopy. CLSM makes it possible to protect the amber material and meanwhile observe the detail structures of inclusions. Especially for detecting pollen and spore inclusions, light produced by fluorescence very close to the focal plane can be detected, the image's optical resolution, particularly in the sample depth direction, is much better than that of wide-field microscopes. Photomicrographs in research normally with green-black background were taken using a CLSM Zeiss LSM710 system with laser wavelength 488 nm (Laser module LGK 7812 ML5) at the State Key Laboratory of Palaeobiology and Stratigraphy, NIGPAS, China. Based on the diameter and thickness of amber specimen, two objectives (“Plan-Neofluar” 20X/0.50 M27 and “Plan-Apochromat” 63X/1.40 Oil DIC M27) were applied. AxioVision 4.0 modules with the software AxioVision Rel. 4.8.2 were used to produce high resolution images.

4.2.4 X-ray micro-computed tomography

X-ray micro-computed tomography uses x-rays to create cross-sections of a physical object that can be used to recreate a virtual model (3D model) without destroying the original object. Comparing the medical X-ray tomography, the X-ray micro-computed tomography is a closed X-ray system, in which X-ray shielding is put around the scanner. Target object was placed on the spiral table, digital detectors with small pixel pitches and micro-focus x-ray tubes were employed to yield in high resolution images. In order to perform a three-dimension reconstruction of the insect inclusion in amber samples, the fossils were scanned at the micro-CT laboratory of NIGPAS, using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, 3D-XRM uses CCD-based objectives to achieve higher spatial resolution. Based on the size of the fossil specimen, a charge-coupled device (CCD) and 4X objective was used, providing variable isotropic voxel sizes (μm, see figure captions) with the help of geometric magnification. During the scan, the acceleration voltage for the X-ray source was 50 kV (power 4W), and a thin filter (LE3) was used to avoid beam hardening artefacts. To improve signal-to-noise ratio, 3000 projections over 360° were collected, and the exposure time for different projection was 2–5s (see figure captions). Volume data processing was performed using software VGStudio Max (version 3.0, Volume Graphics, Heidelberg, Germany) and the ASTRA toolbox *.

* The ASTRA Toolbox is a MATLAB toolbox of high-performance GPU primitives for 2D and 3D tomography, from 2009–2014 developed by iMinds-Vision Lab, University of Antwerp and since 2014 jointly developed by iMinds-VisionLab, UAntwerpen and CWI, Amsterdam. The toolbox supports parallel, fan, and cone beam, with highly flexible source/detector positioning. A large number of reconstruction algorithms are available, including FBP, ART, SIRT, SART, CGLS.

4.2.5 Synchrotron X-ray microtomography

Synchrotron tomography provides a way for visualising the three-dimensional interior structure of real objects non-destructively and with a high spatial resolution. This allows the detailed microstructural analysis of many different kinds of materials. Synchrotron x-ray tomography is based on the detection of either the attenuation or the phase shift of the beam transmitted through a sample. While radiography measures images for a single orientation of the sample, tomography measures images for many different angular positions. This results in a set of projections, which can be used to reconstruct two-dimensional layers or slices through the object. By stacking these slices together, it is possible to visualise the structure in three dimensions. In recent years, synchrotron-based X-ray microtomography (SR-µCT) has become an important technique to examine fossil insects in amber (Soriano et al., 2010; van de Kamp et al., 2014), which allows a non-destructive visualization of amber inclusions without distracting particles or reflections and even facilitates the examination of internal anatomical characters. In comparison with X-ray micro-computed tomography, theoretically synchrotron-based X-ray beams provide the following advantages: the very high intensity of the source yields images with a high signal-to-noise ratio on short time-scales, which enables fast radiographic investigations. The beam can be easily monochromatic. This allows correlations between attenuation values and the chemical constituents of the sample. The option to vary the energy of the radiation enables the investigation of objects with very different absorption coefficients within the same measuring environment. The high parallelism of the beam limits imaging artefacts. The high beam coherence can be used for phase contrast imaging and holotomography, which provide much higher image contrast. However, practically it is truly impossible to predict the degree of preservation of an insect by the outer shape of the inclusion, which caused the scanning result very much varies. Besides, a careful scanning and examination process remains serious time-consuming. Even if SR-µCT is often described as being non-destructive, it should be noticed that intense synchrotron-based X-rays – and in particular the polychromatic radiation employed for high-throughput experiments – usually results in browning of the amber, lasts for couple of months (van de Kamp et al., 2014). Thus, Synchrotron based X-ray microtomography of amber inclusions is still in its infancy. Large comprehensive studies on the different kinds of amber materials are demanded.

4.3 Permanent storage

The permanent storage of rock fossils is comparatively simple due to the properties of rock: good water resistance, pressure resistance and oxidation resistance. The research materials should be set into sample box with cotton or other soft issue in the bottom, then placed in the collection cabinet with clear identified label.

The amber specimen could be temporarily stored in mini sealed sample box in order to be re-examined easily. Some amber specimens exhibited deep fissures and cracks that even extended to the inclusion, which may facilitate deterioration of the amber inclusions, destabilizes the entire specimen and also impairs the optimal view of the inclusion (Bisulca et al., 2012; Nascimbene and Silverstein, 2000; Pastorelli, 2009). Thus, a perfect protection measures are required for permanent storage. The amber specimens which reached ultimate thickness (< 0.5mm) can be assembled into slice with coverslip and stored at moderate temperature and humidity. The amber specimens that embedded into artificial adhesives (see 4.2.1) can be carefully placed into moderate sized sample box and sealed.

5. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Superfamily Tenebrionoidea Latreille, 1802

Family Mordellidae Latreille, 1802

Subfamily Praemordellinae Scegoleva-Barovskaja, 1929 (Scegoleva-Barovskaja, 1929)

[Praemordellinae] Scegoleva-Barovskaya, 1929, Comptes Rendus del'Academie des. Sci. 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* Scegoleva-Barovskaja, 1929, by original designation.

Diagnosis (emended). 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* Scegoleva-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* Scegoleva-Barovskaja

3. Hind tibiae much longer than hind tarsi; hind apical spur longer than 1st tarsomere... ... ... …………....*Cretanaspis* Huang&Yang

– 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.

Diagnosis (revised). 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. 4)

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.

Type material. Holotype PIN (reference numbers with PIN for the collection in Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia), 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.

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.

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 taphonomical condition also occurs in some other beetles. For example, the last few abdominal segments of a tenebrionoid beetle (CNU-C-NN2007203) (reference numbers with CNU for the collection in the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China) were extended from the abdomen, making this part appear to be a pointed “pygidium” (Fig. 6.).

Genus *Wuhua* Wang and Zhang, 2011

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

Diagnosis (revised). 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 *Wuhua peregrina* sp. nov., both from the Middle Jurassic of Daohugou, China.

Wuhua peregrina sp. nov.

(Figs. 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 *Wuhua jurassica* in having a larger body, shorter pronotum, and tarsomere I shorter than tarsomeres II-IV of hind tarsi.

Type material. Holotype NIGP154954 (reference numbers with NIGP for collection of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing), a complete beetle in lateral position (with the right side fully exposed).

Locality and horizon. Middle Jurassic; Daohugou deposits (41° 180’ N, 119 °130’ E), Wuhua Town, Ningcheng County, Chifeng City, Inner Mongolia, China.

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

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.

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.

Family Mordellidae Latreille, 1802

Subfamily Apotomourinae Bao, 2019

[Apotomouridae] Bao, 2018, Cretaceous Research, 91: 14–19

LSID urn: lsid: zoobank.org: act:086C7E0B-E0C2-490B-B836-D6140 F6AD82E

Diagnosis. Body small, length 1.2–2.5 mm, wedge-shaped; color from dark brown to black. Head strongly declined. Pygidium completely reduced. Fore- and middle legs obviously shorter than hind legs. Metafemora well developed, strongly enlarged. Comb-like setae widely preserved on the posterior metatibiae. Sclerotic spines preserved in the ventral metatibiae and metatarsi. Claws small, b-cleft.

Etymology. Apotomos (Greek) - short; oura (Greek) - tail. Apotomourinae is referring to the short body shape, without last sterna elongation.

Genus *Multispinus* Bao, 2018

LSID urn: lsid: zoobank.org: act:4BD5B958-B109-4E39-A683-570B 6BBDB5EF

Type species. *Multispinus multispinosus* Bao, 2018

Diagnosis. Body small, wedge-shaped, size 2.20 mm -2.50 mm; shape smooth, streamlined, color dark brown to black. Head large, declined. Pygidium reduced. Fore and mid legs slender and shorter than the hind legs. Metafemora strong and enlarged, sclerotic spines or comb-like setae widely preserved on the metatibiae and metatarsi. Claws small with 2 spines.

Etymology. Multispinus (Latin) - many spines, referring to the character of hind legs.

Multispinus multispinosus Bao, 2018.

(Fig. 7-8.)

LSID urn: lsid: zoobank.org: act: CEB1A8FE-92EB-47DD-9BA8-848 99D95D3B0

Diagnosis. As for the genus.

Type material. Holotype NIGP168210 and paratype NIGP168211, NIGP168212 are adult specimens; holotype male, paratype sex unknown.

Etymology. As for the genus, different suffix for species name.

Description. All measurements in mm.

The body length of holotype NIGP168210 is 2.27, of paratype NIGP168211 is 2.50 and paratype NIGP168212 is 2.35; wedge-shaped, widest at base of prothorax, slightly narrowed anteriorly and strongly narrowed posteriorly. Lateral view, body curled up with slightly convex abdomen.

Head large, triangular in frontal view, strongly declined, as wide as apex of thorax, abruptly constricted behind eyes to form a narrow neck which is concealed by pronotum; hypognathous. Occipital region with transverse carina that adjoin anterior edge of pronotum. Eyes lateral, large, well developed, shape oval, entirely emarginated, finely faceted, interfacetal setae reduced. Antennae are about half-length of the body; filiform; consist of 11 antennomeres, covered with short setae. Clypeus distinct; labrum prominent; maxillary palpi long with four visible palpomeres, apical palpomere slightly expanded, scalene.

Pronotum length 0.52 in holotype, narrowed in front, as wide as elytra at base, widest posteriorly; shape irregular, sides moderately curved; surface rugose-punctate. Lateral pronotal carinae complete, simple, without raised margin or bead. Prosternum short, concave. Mesosternum about twice the length of prosternum, carinate; mesocoxae small. Metasternum large, about three times length of prosternum; metacoxae very large, flat, contiguous. Scutellar shield small, posteriorly narrowly rounded. Elytra length 1.58 in holotype, narrowed behind, exceeding the body, surface rugose-punctate; margin fold up slightly. Legs well developed; hind legs longer and stouter than fore and mid legs. Trochanter joint strongly oblique with base of femur in contact with coxa. Metafemora enlarged for jumping. Metatibiae slender, with large spurs preserved by side; slightly expanded posteriorly with terminal comb-like setae. Tarsal formula 5-5-4, tarsomeres compressed, slender. Spurs preserved in the inner surface of the first tarsomere; comb-like setae preserved in the same position of 2nd to 4th tarsomeres. Claws very small, cleft; terminal sharp, with 2 short spines.

Abdomen with five sterna, with slightly sclerotized spines on the posterior margin of I-IV sterna, V sternum distinctly narrowed posteriorly, sutures distinct; pygidium reduced; surface micro- rugose. Male genitalia are visible in holotype specimen, short.

Remarks. Due to the surrounding amber matrix, the specimen appears dark-brown to black in color, without patterns and spots on scutellum and elytra. Setae are well developed, from head until the terminal abdomen; neatly toward posterior direction. Wings folded and rolled under elytra.

Multispinus parvus Bao, 2020

(Fig. 9.)

LSID urn: lsid: zoobank. org: act: 8DCC3478-F601-47A7-A88A-8B920129A330

Differential diagnosis. *Multispinus parvus* different from Multispinus multispinosus by: (1) body much smaller, (2) pronotum shape special, anterior rounded, posterior wide, with two bends; (3) 6 pairs of short spines preserved in ventral metatibiae.

Type material. Holotype NIGP171284, male.

Etymology. Parvus (Latin) - small.

Description. All measurements in mm.

Holotype NIGP171284, body very small, length 1.21, wedge-shape, widest in posterior pronotum, body slightly narrower anterior and posterior; laterally curved, C-shape. Body colour from dark brown to black, without patterns.

Head small, rounded triangular in frontal view; narrowest posterior, as wide as anterior pronotum; hypognathous. Eyes lateral, large, well-developed, shape oval, finely faceted, interfacial setae well developed. Antennae short, less than half body length; serrate-filiform. Clypeus distinct; maxillary palpi moderated with four palpomeres, apical palpomere expanded, securiform.

Pronotum length 0.14, widest at the base 0.44, anterior rounded, posterior wide with two bends. Scutellum shield length 0.07, width 0.09, triangular. Elytra not exceed abdomen, length 1.12, widest at anterior 0.42, surface almost smooth, with very fine setae; hind wing transparent, hided under elytra.

Metaepistena long, irregular rectangular, preserved with fine setae. Metacoxae enlarged formed metacoxal plate; trochanter oblique. Metafemora enlarged, numerous tiny spines preserved posterior. Metatibiae slim, long; comb-like setae preserved posterior. Tarsi form 5-5-4, slim. Metatibiae and metatarsi without any ridge. Ventral metatibiae preserved 6 pairs sclerotic tiny spines. Ventral metatarsus I preserved long and short fine spines; ventral metatarsus II-IV preserved short setae; comb-like setae preserved in each posterior metatarsus. Length metatarsi: 0.19, 0.10, 0.07, 0.10. Claw simple, b-cleft.

Abdomen with 1-5 five sterna, narrowed posteriorly, surface micro-rugose, length 0.11, 0.08, 0.07, 0.05, 0.15, very fine setae preserved between sternites. Pygidium distinct, aedeagus partially exposed.

Genus *Apotomoura* Bao, 2018

LSID urn: lsid: zoobank. org: act: BF540A74-B2B7-47A7-B78B-D04 83C8A000E

Type species. *Apotomoura fortiscrura* Bao, 2018

Diagnosis. Body usually very small, wedge-shaped, size 1.50 mm to 1.70 mm; shape smooth, streamlined, normally curved; thorax big; color black. Head large, lying flush to thorax. Abdomen sterna contracted; pygidium reduced. Fore and mid legs slender and shorter than the hind legs. Metafemora strong and enlarged; metatibiae and metatarsi short and strong; 3-4 sclerotic spines preserved on the metatibiae and the first tarsomere. Claw small.

Etymology. Apotomos (Greek) - short, oura (Greek) - tail, referring to the short body.

Apotomoura fortiscrura Bao, 2018

(Fig. 10.)

LSID urn: lsid: zoobank. org: act:47D094F1-939A-4481-8F87-5EE C011FBAEC

Diagnosis. As for the genus.

Type material. Holotype NIGP168213 and paratype NIGP168214 are adult specimens, sex unknown.

Etymology. Fortis (Latin) - strong, scrura (Latin) - legs, referring to the morphological character.

Description. All measurements in mm.

The body length of holotype NIGP168213 is 1.69; of paratype NIGP168214 is 1.64; wedge-shaped, widest at posterior base of prothorax, slightly narrowed anteriorly and posteriorly. Lateral view, body strongly curled upwards; thorax inflated conspicuously; hind legs very large and stretched.

Head large, oval in frontal view, strongly declined, as wide as apex of thorax, sharply constricted behind eyes, hypognathous; surface rugose-punctate, with short setae covered widely. Eyes lateral, large, well developed, shape oval, entirely emarginated, finely faceted, interfacetal setae well developed. Antennae short, not extending beyond thorax; serrate-filiform; antennomeres triangular to oval. Clypeus distinct; maxillary palpi moderated with four palpomeres, apical palpomere expanded, securiform.

Pronotum length 0.51 in holotype, narrowed in front, as wide as elytra at base, widest posteriorly; surface smooth; shape irregular, margin without fold or setae. Prosternum abbreviated, metasternum large. Metacoxae very large, flat, contiguous. Scutellar shield small, triangular, posteriorly narrowed. Elytra highly curled, narrowed behind, surface rugose-punctate; margin smooth. Hind legs longer and stouter than fore and mid legs. Trochanter reduced. Metafemora strongly enlarged; metatibiae short but strong, with 3-4 tiny spurs preserved by side; comb-like setae preserved by the posterior terminal. Tarsal formula 5-5-4, tarsomeres compressed, shorter and stronger compared with *Multispinus multispinosus*; all tibiae and tarsi with distinct apical ridges; 3-4 tiny spurs preserved by side of the first tarsomere; a pair of short setae preserved at the posterior margin of each tarsomere, no comb-like setae. Claws very small.

Abdomen with five sterna, narrowed posteriorly, surface micro- rugose, sutures distinct; pygidium distinct.

Remarks. Specimen color black or dark brown. The preserving posture of all the specimens are similar, highly curled and hind legs extended. Body setae short and less dense. Wings folded and rolled under elytra.

Family Mordellidae Latreille, 1802

Subfamily Mordellinae Latreille, 1802

Tribe Raynoldsiellini Franciscolo, 1957

Diagnosis (emended). Tribe Raynoldsiellini Franciscolo, 1957 represented by only one extant monotypic genus, *Reynoldsiella parallela* Ray, 1930, recorded hitherto only from Venezuela. The most important differential character for Raynoldsiellini Franciscolo, 1957 is metatibiae without any kind of ridges, including the subapical one (Franciscolo, 1957; Peris and Ruzzier, 2013).

Primaevomordellida Bao, 2019

LSID urn: lsid: zoobank.org: act:5CC9AB4D-97B1-4F73-8412- 9C0F68453EF7

Type species. *Primaevomordellida burmitina* Bao, 2019

Diagnosis. *Primaevomordellida* differs from *Reynoldsiella* mainly based on the following characters: (1) eyes small, glabrous; (2) metafemora not greatly enlarged; (3) subapical spurs on metatibiae long, about half length of metatibiae; (4) pygidium sharply elongated, length ratio between pygidium and hypopygidium 4:1; (5) branches of right genital parameron with equal length.

Etymology. Primaevo (Latin) - primaevus, means original; primaevomordellida refers to the first true pintail beetle.

Primaevomordellida burmitina Bao, 2019
(Figs. 11-12)
LSID urn: lsid: zoobank.org: act:5BBB6443-3582-4E0B-94F8- 7066CF4AC45A

Diagnosis. As for the genus.

Type material. Holotype NIGP168789 (Male) and paratype NIGP168790 (sex undetermined).

Etymology. Burmitina (Latin), related to mineralogical name burmite.

Description. Dimensions: holotype NIGP168789 is 3.0 mm in length, of the paratype NIGP168790 is 2.9 mm (pygidium excluded); body profile typically mordelloid, slightly arched in lateral view. General colour of the body integuments black, except for the orange anterior legs.

Head: head large, almost as the prothoracic width, strongly declined; eyes lateral, moderately small, finely faceted and glabrous, not reaching occiput. Occipital region wide and flat, matching perfectly with the anterior edge of pronotum. Antennae comparatively short, filiform and feebly serrate; antennomeres covered of setae. Apical palpomere securiform.

Prothorax: pronotum trapezoid in dorsal view, slightly narrowed in front and as wide as elytra at base; disc of the pronotum smooth and covered of short and dense recumbent hairs. Anterior legs simple; tibiae slender and linear, tarsus with all the five segments feebly dilated; tarsomere one to four bearing short spines at the detail margin; apical spurs on pro tibia present.

Meso and metathorax: scutellum triangular. Elytra, in dorsal view, subparallel at the humeri, gradually curving up to apex proximity; integuments covered with by fine setae. Metaepistena typically mordelloid, of the Mordellistena-type.

Coxal plate expanded, widely rounded at the posterior margin, typically mordelloid; trochanter reduced.

Metafemora laterally compressed and feebly expanded. Meta- tibiae elongated, subconical, with obliquely truncated apexes; metatibiae missing of any kind of ridge including the sub apical one; apical margin of hind tibiae bearing comb-like setae; ventral side of metatibiae and metatarsomeres presenting fine spine-like setae; Apical spurs on posterior tibiae present, equal in size and

approximately half of length of metatibiae. Tarsal formula 5-5-4; pro- and mesotarsomeres cylindrical, slightly dorso-ventrally compresses, onlychium instead apically on the fourth tarsomere; metatarsi laterally compressed, slender, presenting comb-like setae at the apical margin; length ratio of the four hind tarsomeres 3:2:1:1. Claws small and bi-cleft.

Abdomen: visible abdominal sternites with length ratio 3:3:3:4:8. Pygidium subconical, elongated and pointed at apex; pygidium length about four times the hypopygidium. Genital organs of holotype partially exposed. Apical part of penis visible, pointed.

Remarks. The holotype and paratype shows natural black or deep brown colour on elytra. Fine setae are well developed on the beetle body (including legs, antennae), dorsally and ventrally, regularly in a posterior direction. The amber matrix is not clear, contains a large amount of organic impurities.

Family Mordellidae Latreille, 1802

Subfamily Mordellinae Latreille, 1802

Tribe Mordellini Seidlitz, 1875

Genus *Tomoxia* Costa, 1854

Type species. *Tomoxia bucephala* Costa, 1854.

Diagnosis (emended). The diagnostic characters for the genus Tomoxia when compared to the other members of the tribe Mordellini are: (1) eyes finely granulated; (2) scutellum quadrilateral or irregular shaped; (3) hind tibia with a fine dorsal ridge and a lateral ridge; basal tarsomere of hindleg also with a fine dorsal ridge (Franciscolo, 1965; Jackman and Lu, 2001; Liljeblad, 1945; Smith, 1882)

Tomoxia succinea Bao, 2019

(Fig.13-14.)

LSIDurn:lsid:zoobank. org:act:0E01A684-3C9E-4C43-82CF-82180FFDC9CC.

Diagnosis (emended). The differential specific diagnosis for *Tomoxia succinea* is: (1) the length to width ratio of the pronotum is 1:2, slightly narrower than the elytra at base; (2) the length ratio between the last abdominal sternum and pygidium is 1:4; (3) the length ratio of the hind tarsomeres is 2:1:1:1; (4) the form of the scutellum is transitional, ranging from triangular to quadrilateral.

Type material. Holotype 5715 and paratype 5743 (reference ID for the collection of the Laboratory-Museum of Amber Inclusions, Gdansk University), adult specimens; sex unknown.

Locality and horizon. Eocene Baltic amber. Mine located in territory of Republic of Poland.

Etymology. From succinum, Latin for amber.

Description. All measurements in mm.

The body length of the holotype is 2.6, that of the paratype is 2.9; edge-shaped, widest at base of prothorax, much narrower posteriorly, lying in lateral view, curled up with a slightly convex abdomen.

Head rather large, almost of prothoracic width, finely punctured; eyes large, ellipsoidal, finely faceted and granulated, apparently not reaching occiput, hairy. Antennae long, filiform. Mouthpart is invisible due to preservation. Pronotum trapezoidal or quadrilateral from dorsal view, length to width ratio 1:2, slightly narrower than elytra at base. Anterior lobe moderate, not distinctly narrow, slightly protruding inwards, anterior angles not visible from above; lateral margins gradually curved from anterior to posterior angles; posterior margin sinuate, posterior lobe slightly protruding backwards. Scutellum irregular quadrilateral. Elytra elongated, cuneate; sculpture reticulate with rather obvious and fine punctures; leather luster, lateral margin rounded and smooth; posterior margin narrow and rounded, not sharp. Mesothorax and metathorax enlarged, flat, covered by fine setae. Middle tibiae as long as first three segments of same pair of legs; hind tibiae with a fine but obvious dor- sal ridge and a lateral ridge close to subapical side. Basal tarsomere of hindleg also with fine dorsal ridge; last two tarsomeres of hindleg slightly longer, length ratio of four hind tarsomeres 2:1:1:1; pair of subapical spines preserved on each tarsomere. Five abdominal sterna with length ratio 3:2:2:2:4, compact and neatly connected, no appendix struc- ture between each. Pygidium elongated and pointed; length ratio between last abdominal sternum and pygidium is 1:4.

Remarks. The holotype has an unusual leathery shiny gloss; the paratype has a natural black color pattern on the elytra. The beetle cuticle is punctured, setae are well developed on the body, dorsally and ventrally, regularly in a posterior direction. Genital structure is not clear due to the preservation. Paratype body surface covered by fine white layer, which is typical for Baltic amber inclusions due to the effect of the air during preservation.

Family Mordellidae Latreille, 1802

Subfamily Mordellinae Latreille, 1802

Genus *Angimordella* Bao, 2019

LSID urn:lsid:zoobank.org:act:D31C312B- 218A-47EC-A427-53ED39FE1926

Type species. *Angimordella burmitina* Bao, 2019

Diagnosis. Body small, with pronotum and elytra with wrinkles or ridges dorsally; antennae serrate; meso- and meta-tibiae without any kind of ridge including sub-apical one; pygidium not well developed, shorter than 1/2 of last abdominal sternite.

Etymology. The generic name is derived from the Latin prefix “angi” (referring to angiosperm) and the genus *Mordella* Linnaeus.

Angimordella burmitina Bao, 2019

(Fig. 15-16.)

LSID urn:lsid:zoobank.org:act:46B77E87-5047–49B4- B29A-448D0B41CA9D

Diagnosis. As for genus.

Type material. Holotype. NIGP171315 (Fig. 15), a complete beetle with left side visible but its right side covered by abundant micro-bubbles. A thrip is near the maxillary palpi of the beetle on the left side. Numerous pollen grains distributed on and around beetle body.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific name is derived from Latin “Burmitina”, referring to the mineralogical name of Burmese amber.

Description. All measurements in mm.

Body strongly convex, wedge-shaped, widest near based of prothorax, slightly narrowed anteriorly and posteriorly (Fig. 15A and B). Body length 4.25; ratio of body length to greatest body width 3:2. Head length 0.51, large, transverse, strongly declined, with mouthparts directly posteriorly; compound eyes finely faceted and glabrous. Occipital region wide, surface with wrinkles and hairs, matching perfectly with anterior edge of pronotum. Antennae comparatively short, with 7 visible antennomeres, obviously serrate (Fig. 15D), covered with hairs. Maxillary palp length 0.38; apical maxillary palpomere length 0.18, securiform, strongly enlarged.

Pronotum length 1.11, slightly narrowed anteriorly, widest posteriorly, as wide as elytra at base, lateral margin slightly curved; pronotum disc with ridges and covered by short and dense recumbent hairs (Fig. 15C). Elytra length 2.46, approximately 2.5 times as long as pronotum, covering all abdominal segments, with slight surface relief, gradually curving up to apex proximity; integuments covered with fine hairs. Fore legs simple, tibiae slender. Mesotibiae and mesotarsi simple, long and slender. Metaepistena long, rectangular. Metacoxae greatly enlarged with rounded posterior margin, extending laterally to meet elytra, widely rounded at posterior margin; trochanter oblique. Metafemora length 0.80, laterally compressed and greatly expanded, more than 4 times wider than mesofemora. Metatibiae length 0.74, blade shaped, about same length as metafemora with obliquely truncated apexes; metatibiae without any kind of ridge including sub apical one; apical margin of hind tibiae bearing comb-like setae; ventral side of metatibiae and metatarsomeres with fine spine-like setae; apical spurs on metatibiae absent. Metatarsi laterally compressed, comparatively sturdy, with comb-like setae on apical margin and apical spurs on posterior margin, spiny on inner margins (Fig. 15F); length of four metatarsomeres 0.50, 0.30, 0.18, 0.16, ratio 5:3:2:2. Claws small and bi-cleft. Abdomen distinctly narrowed posteriorly, with five free ventrites. Ventrites 1−5 length 0.16, 0.16, 0.15, 0.12, 0.26, ratio 1:1:1:1:2 (Fig. 15E). Hairs present on abdomen, slightly elongated between sternites. Pygidium very short, 0.18 long.

Remarks. *Angimordella burmitina* can be attributed to the subfamily Mordellinae by the following characters: wedge-shaped body, enlarged last segment of maxillary palpi; metacoxae greatly enlarged forming a rounded plate; metafemora expanded and well developed; and pygidium very short. It resembles Primaevomordellida burmitina Bao, 2019 from Burmese amber in the absence of ridge on metatibiae and metatarsi, but differs from the latter in having a short-pointed pygidium. It is also similar to Mediumiuga sinespinis Peris and Ruzzier, 2013 from late Albian Spanish amber in having a very short pygidium and ventrally spiny metatibiae and metatarsi, but differs from the latter in the absence of ridge on metatibiae and metatarsi.

Pollen Descriptions. There are at least 62 pollen grains (from only the visible left side of the beetle) in the amber in total, of which 24 pollen grains aggregate into two small clusters near the abdominal end of the mordellid (Fig. 16A). Pollen grains in the amber are retitricolpate and highly uniform in morphology (Fig. 16B, C and H). The shape of the grain is approximately oblate spheroidal, 25.56 μm (30.95−22.08 μm) × 16.49 μm (20.68−13.93 μm) in equatorial view (based on measurement of the 27 best preserved pollen grains; Table 3). The colpi are long, wide and deep and extend to the pole. The exine is moderately thick, approximately 1 μm. The lumina are small, evenly spaced and approximately 0.5 μm in diameter. The pollen clump shape is irregular, and the pollen grains are well preserved (Fig. 16F and G), indicating that they are natural floral remains rather than coprolites (Winship and Hu, 2010). These pollen grains can be confidently attributed to the eudicot monophyletic group (true dicotyledons), members of which are distinguished from all other angiosperms by their tricolpate pollen structure (Halbritter et al., 2018; Judd and Olmstead, 2004).

Table 3. Length and width measurements of pollen grains.

Length (μm)	Width (μm)
22.50	14.31

25.83	17.92
27.54	19.29
23.80	20.01
23.06	16.36
23.90	16.46
24.44	16.17
22.08	20.68
23.60	16.86
22.75	15.91
27.05	17.06
30.95	15.90
22.55	18.17
27.13	18.57
24.98	17.39
28.40	15.38
26.95	15.77
25.11	14.53
28.89	18.31
27.12	14.42
29.83	19.39
23.98	14.05
25.79	14.33
22.24	15.01
25.71	14.40
23.41	13.93
30.58	14.80

Note: Pollen length is the maximum value between two polar points, and pollen width is the maximum value of the equatorial zone.

Family Tenebrionidae Latreille, 1802

Subfamily Zolodininae Watt, 1975

Type genus Zolodinus Blanchard, 1853

Praezolodinus gen. nov.

LSID urn: lsid: zoobank.org: act:XXXXX

Type species. *Praezolodinus pilosus* gen. et sp. nov.

Diagnosis. (1) Body small, elongated, completely covered with long erect and shorter suberect setae (or pubescence) dorsally and punctured setae ventrally, (2) antennae long and slender, 11-antennomeres, 3-segments club, (3) mandibular mola with fine and long pubescence, (4) apical maxillary palpomere securiform, slightly enlarged, (5) pronotum big, quadrilateral, lateral angle sharp (<90°), distinct, (6) elytra not strong convex, with rounded humeral angles, with more than 10 striae of circular punctures, with scutellary striole, (7) procoxal cavities not closed externally; prosternal process convex, (8) mesocoxae with exposed trochantins, (9) meso- and meta coxal cavities closed laterally by meso- and metasterna, (10) tibiae and tarsi slender, with numerous with sclerotized short spines and setae apically and parallel-sided; penultimate tarsomere not lobed; claws simple, (11) abdomen 5-sternites, punctured, intersegmental membranes absent, (12) aedeagus inverted, pimeloid type.

Etymology. Prae - Latin prefix, meaning "before". Praezolodinus refers the ancient Zolodinus.

Praezolodinus pilosus sp. nov.

(Fig. 17.)

LSID urn: lsid: zoobank.org: act:XXXXX

Diagnosis. As for the genus Praezolodinus gen. nov.

Type material. Holotype NIGP001, male, a complete beetle covered by abundant micro-bubbles, preserved together with a small leiodid beetle. Unknown plant fragments remain.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. Pilosus -Latin, meaning “hairy”, refers to the surface with abundance pubescence and setae.

Description. All measurements in mm.

Body elongated, slightly convex dorsally; unicolorous dark brown, total length 4.20 (Fig. 17A). Head prognathous; eyes large, transverse, oval, slightly prominent, not convergence in the middle of head; antennae 11-antennomeres, filiform, moderately long, length 1.40, evenly covered with sparse, erect to semi-erect simple pubescence; antennal insertion not concealed; antennomere 1 enlarged, antennomeres 2–8 elongate, subequal in length, antennomeres 9–11 slightly dilated apically, formed club, antennomere 11 spindle-shaped (Fig. 17B); labrum free; apical maxillary palpomere securiform, wider than preceding ones, narrowly truncate apically with sparse setae; process of galea brush-like (Fig. 17B); mandibular mola with fine and long pubescence; labial palp 2-segments, short, narrowed. Pronotum irregular quadrilateral, length 1.02, widest in middle, 1.20. Lateral slightly arcuate, exceed anteriorly and posterity, with comparatively long and dense pubescence; apex posteriorly concave, rounded; base posteriorly convex, rounded; anterolateral angle sharp, distinct, posterolateral angle sharp, distinct; disc flattened, lateral curved up, without impressions; pronotal punctation minute and dense, punctures sparser on disc than lateral; disc sparsely covered with dark erect very short setae. Prothoracic hypomera covered with short erect setae; prosternum punctured, prosternal process convex, tenebrionid type; procoxae externally open; procoxal cavities not closed behind. Elytra elongate-oval, length 2.42 (Fig. 17C), convex dorsally, terminal sharp narrowed; humeri rounded; each elytron with numerous striae (more than 5) of dot punctures, undulate; lateral margin with long pubescence, length ca. 0.2, dorsum with short semierect setae. meso- and metaventrite with delicate, moderately sparse punctation; meso- and metaepisternum with small and distinctly denser punctures; covered with short, fine semierect setae, gradually narrowing posteriorly. Legs long, slender, covered with sparse setae. Procoxal cavities closed. Mesotrochantin exposed. Mesocoxae oval, longitudinal; metacoxae narrowly oval, transverse; all coxae distinctly not contiguous; meso- and meta coxal cavities closed laterally by meso- and metasterna (Fig. 17E). Femora slender, without appendix structure, metafomora length 0.91, distinctly longer than mesofemora. Tibiae slender and straight, parallel-sided with sclerotized short spines and setae, slightly shorter than femora, apically with numerous short spines (more than 4). Tarsi form 5-5-4, almost the same length of tibiae, with dense setation on parallel side and sclerotized short spines apically; penultimate tarsomere not bilobed or widened, shortest compare with other tarsomeres. Protarsomere 1-5 length: 0.07, 0.06, 0.07, 0.06, 0.17. Mesotarsomere 1-5 length: 0.14, 0.08, 0.08, 0.06, 0.15. Metatarsomere 1-4 length: 0.22, 0.09, 0.08, 0.17. Claws thin, free, simple, bi-cleft. Abdomen 5-segments (Fig. 17D), sternites 1-3 connate, sternites 4-5 flexible and movable, ventral with fine setae (sternites 4-5 denser), intersegmental membranes absent or nor exposed between sternites 3–5; length sternites 1-5: 0.26, 0.36, 0.28, 0.18, 0.21. Genitals complete exposed, length 0.83; phallus with sclerotized arms; aedeagus inverted, pointed, pimeloid type (Fig. 17F).

Remarks. Darkling beetle is the common name of the large family of beetles Tenebrionidae. The number of species in the Tenebrionidae is estimated at more than 20,000 and the family is cosmopolitan in distribution. Most species are generalistic omnivores, and feed on decaying leaves, rotting wood, fresh plant matter, dead insects, and fungi as larvae and adults (Bouchard et al., 2005). *Praezolodinus pilosus* gen. et sp. nov. assigned to the tenebrionid subfamily Zolodininae based on the following characters: tarsal formula 5-5-4 (general feature of tenebrionoid

Coleoptera); trochanters all of heteromeroid type; procoxal cavities not closed; aedeagus inverted; elytra with more than 10 striae; mandibular mola with fine appendix structure; trochantins exposed; penultimate tarsal segments simple not lobed; tarsal claws simple.

Subfamily Zolodininae hitherto includes two genera *Tanylypa* Pascoe, 1869 (Tasmania), *Zolodinus* Blanchard, 1853 (New Zealand). *Praezolodinus* gen. nov. is distinguished by body not glabrous, preserved with numerous setae or pubescence; prothorax width ≥ length; mandibular mola with pubescence.

Most subfamilies of Tenebrionidae are recovered as paraphyletic (Kergoat et al., 2014). The relationships and higher taxonomy of Tenebrionidae remains problematic. Two broad evolutionary lineages, tentyrioid lineage and tenebrionoid lineage, are recognized within the Tenebrionidae based on structure of the mouthparts and male genitalia and on the occurrence of abdominal defensive glands (Doyen and Lawrence, 1979). Based on the adult character of inverted aedeagus and the absence of abdominal defensive glands, Zolodininae indicate close relation with Pimeliinae; therefore, represent the tentyrioid lineage (Watt, 1974). However, larva of *Zolodinus* suggest a relationship to the tenebrionoid lineage (Doyen and Lawrence, 1979). Molecular analyses supported that the family Tenebrionidae is made of three major lineages, namely “pimelioid”, “lagrioid” and “tenebrionoid”, of those Pimeliinae among the most basal taxa (Kergoat et al., 2014). The extant Pimeliinae distributed widely in all biogeographic realm, and Zolodininae only be found in New Zealand and Tasmania (Lawrence and Ślipiński, 2013). The discovery of *P. pilosus* may imply the Laurasia origin of this lineage.

Spore microfossil. Numerous spores (30-40 µm in length) compactly preserved near the thorax and on the aedeagus terminal of tenebrionid beetle. Spores monolete, outline in equatorial view bean-shaped, surface densely covered by verrucae of irregular shape, polygonal. Verrucatosporites-type. Many genera of spores from ferns are characterized by kidney-shaped grains with a single elongate monolete scar.

Monolete spores are common in seven families of pteridophytes (Aspleniaceae, Blechnaceae, Dryopteridaceae, Gleicheniaceae, Lomariopsidaceae, Polypodiaceae and Thelypteridaceae). Species of Gleicheniaceae and Thelypteridaceae discovered from Burmese amber (Regalado et al., 2018; Schmidt et al., 2016). The Verrucatosporites-type is quite common within the family Polypodicaeae (Van Uffelen, 1991).

Family Leiodidae Fleming, 1821
Subfamily Cholevinae Kirby, 1837
Tribe Ptomaphagini Jeannel, 1911
Type genus Ptomaphagus Hellwig, 1795

Cretoptomaphagus gen. nov.
LSID urn: lsid: zoobank.org: act:XXXXX

Type species. *Cretoptomaphagus microsoma* gen. et sp. nov.

Diagnosis. (1) small body size (1.35 mm); (2) apical maxillary palpomere elongate, subcylindrical and distinctly narrowed just after its base; (3) protibia weakly bent distally; (4) metaventral carina extending posteriorly from the lateral edge of mesocoxal cavity.

Etymology. The generic name Cretoptomaphagus is a combination of the prefix Creto-, referring to the Cretaceous, and Ptomaphagus Illiger, type genus of Ptomaphagini.

Cretoptomaphagus microsoma sp. nov.
(Figs.18-19.)
LSID urn: lsid: zoobank.org: act:XXXXX

Diagnosis. As for the genus *Cretoptomaphagus* gen. nov.

Type material. Holotype NIGP001, gender unknown.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific epithet derives from the Greek 'mikros' (= small), and 'soma' (= body), and alludes to the small size of the beetle.

Description. All measurements in mm.

Body length ca 1.35. Form compact and elongated oval; moderately convex. Body color dark brown, mouthparts yellowish brown (Fig. 18A). Exposed part of the head delimited posteriorly by an occipital carina, its contour firmly connected with anterior edge of pronotum (Fig. 18B); dorsal surface covered with short setae. Ocelli are absent. Compound eyes located on the posterolateral area of the head capsule; moderately sized, with convex surface and numerous ommatidia; the anterior edge is evenly rounded while the posterior margin is slightly convex, almost straight, and delimited by a postocular ridge (Fig. 18B). Antennal insertion visible from above, foramen facing anterolaterally. Antenna length 0.54, with 11 antennomeres; scapus, pedicellus and antonnomere 3 elongated and subcylindrical; scapus longer than pedicellus, which in turn is longer than antennomere 3, all of them of subequal width (Fig. 19B-C). Remaining antennomeres wider than long. Antennomeres 7–11 compose an indistinct club (Fig. 19B-C). Antennomere 7, 9 and 10 large and cupola-shaped; antennomere 8 distinctly shortened. Antennomere 11 elongate and subconical apically (Fig. 19B-C). All antennomeres are densely covered with setae; some longer setae are distributed close to the distal border of the antennomeres 7, 9, and 10; antennomere 11 with some long setae inserted laterally at the base of the subconical part, and also at the apex (Fig. 19C). Antennal periarticular gutter not visible. Maxillary palp with four palpomeres. Palpomere I very short; palpomere II cylindrical, almost twice as long as palpomere I; palpomere III elongate, distinctly widening distally and almost four times longer than palpomere II; palpomere IV elongate, subcylindrical and thinner just after its base (so that the upper margin seems slightly concave), slightly longer than palpomere III (Fig. 19D). Palpomere III covered by setae, palpomere IV with no apparent setae. Labium with apical palpomere slightly longer than the subapical one, and slightly shorter than the basal palpomere (Fig. 19D). Pronotum densely pubescent, without any apparent pattern of setal distribution; anterorateral angle rounded, posterolateral angle acute. Elytra densely pubescent, with parallel rows of transverse strigae along which the setae are aligned (Fig. 19C, arrows). Metathoracic wings present (Fig. 18A). Mesothoracic pleural suture approximately transverse (Fig. 18C-E). Mesepimeron trapezoidal; posterior margin transverse; posteromesal corner forming an acute angle (Fig. 18C-E). Metanepisternum visible. Metathoracic anapleural suture visible. A metaventral carina extends posteriorly from the lateral edge of mesocoxal cavity, reaching approximately the midlength between the posterior edge of the metaventrite and the lateral edge of the mesocoxal cavity (Fig. 18C-E). Procoxae subconical, extending over the mesoventrite in ventral view (Fig. 19A). Profemur flattend, fairly broad proximally and slightly narrowing distally; the distal half of its margin opposed to the tibia is slightly concave. Protibia cylindrical, slightly widening distally; apical portion weakly bent, causing a slight concavity at the distal extension of the outer tibial margin (Fig. 19E, arrow; while the inner tibial margin, in turn, is slightly convex in its distal extension); only an apical spur is visible ventrally. Protarsus composed of five tarsomeres (Fig. 19F); the four proximal tarsomeres expanded laterally; ventral surface with a dense vestiture of tenent setae; terminal tarsomere almost as long as tarsomeres 2-4 combined, bearing a pair of claws at apex. Middle legs longer than forelegs. Mesocoxa weakly projecting beyond the ventral surface of the pterothorax. Mesofemur with lateral edges slightly diverging at the basal third, and then gradually converging toward apex. Mesotibia cylindrical, subtly curved, and slightly widening distally; surface with short, suberect spines sparsely distributed; mesotibial apex armed with a crown of regularly-sized spines; two apical spurs are visible ventrally

(Fig. 19A, G). Mesotarsus composed of five slender tarsomeres without ventral tenant setae; at least the basal tarsomere with a few short spines protruding at the ventral apex; terminal tarsomere with apical claw (Fig. 19G). Hind legs longer than middle legs (Fig. 19A). Mesofemur flattened, with subparallel edges at the basal half. Mesotibia straight. Other morphological aspects of the hind leg are otherwise very similar to those of the middle leg (Fig. 19G, H). All legs pubescent. Abdomen with six visible ventrites densely setose.

Remarks. Family Leiodidae included around 3800 described species found worldwide, adults and larvae of these beetles generally feed on fungi in rotting plant or animal remains (Peck and Newton, 2017). *Cretoptomaphagus microsoma* is attributed to Leiodidae based on the characteristic interrupted five-segmented antennal club – i.e., the second club antennomere is smaller than the first and third – a synapomorphy of the family (Newton, 2016). Leiodidae is currently subdivided into six subfamilies. Cholevinae, the most diverse, has been sustained as monophyletic based on its typical cephalic configuration, with the posterodorsal contour of the exposed part of the head capsule abutting with the anterior pronotal edge, both appearing firmly connected (Antunes-Carvalho et al., 2019). This synapomorphic feature is found in *C. microsoma*, supporting its inclusion in Cholevinae. An additional synapomorphy of this subfamily is the presence of a genal fold covering the posterior face of the compound eyes (Antunes-Carvalho et al., 2019, 2017), a feature apparently also presents in the leiodid fossil.

Cretoptomaphagus microsoma is placed in Ptomaphagini by having a distinctly narrowed apical maxillary palpomere, one of the derived characters that supports the monophyly of this tribe (Antunes-Carvalho et al., 2019). A unique synapomorphy of Ptomaphagini is the V-shaped depression at the distal extension of the unguitractor plate(Antunes-Carvalho and Gnaspini, 2016), a very small feature that cannot be observed in the fossil. In contrast to the pubescent apical maxillary palpomere generally found in Cholevinae, members of Ptomaphagini retain as a plesiomorphic trait a distal maxillary palpomere mostly glabrous (Antunes-Carvalho et al., 2019). The same condition is shared by *C. microssoma*. Other traits that characterize the tribe – and were detected in the fossil – include the metaventral carina, a regular crown of spines at the tibial apex, protarsi laterally expanded in males, and dorsal surface of elytra with parallel rows of transverse strigae (with the pubescence aligned below them).

Ptomaphagini presently comprises three subtribes, Baryodirina, Ptomaphagina and Ptomaphaginina. The monotypic Baryodirina was described based on a single female of *Baryodirus* from Gunung Mulu, Malaysia (Perreau, 2000). Its peculiar morphology includes tetramerous protarsi, dual setation on the pronotal and elytral surface, and a strongly developed median longitudinal carina, features that easily separate *Baryodirus* from other Ptomaphagini including *C. microsoma*. The other subtribes are distinguished from each other by the presence of a row of spines along the external margin of the protibia in Ptomaphaginina, a trait also present in *Baryodirus*, but lacking in Ptomaphagina (Newton, 1998; Perreau, 2000). The external row of spines was not detected in the protibia of *C. microsoma*. The mutual monophyly of Ptomaphagina and Ptomaphaginina was recently suggested, even though weakly supported and only if *Baryodirus* was excluded from the analysis; when added, *Baryodirus* was nested inside Ptomaphaginina (Antunes-Carvalho et al., 2019). Derived features that sustained each subtribe cannot be confirmed in *C. microsoma*.

Ptomaphagina encompasses eight extant genera with members distributed in Holarctic, Neotropical and Oriental regions (Perreau, 2000). Features of the antenna and maxillary palp tentatively suggest an affinity of the fossil with *Ptomaphagus* (Holarctic, Neotropical and Oriental) and *Adelopsis* (Neotropical), the most diverse genera of Ptomaphagini. *Cretoptomaphagus microsoma* distinguishes from other Ptomaphagina by its very small size and protibial bent distally. However, due to the limited variation in external morphology, the discussions on generic relationships and the single phylogenetic study focused on the tribe are dominated by genitalic characters (e.g., (Gnaspini, 1996; Peck, 1973). Additionally, the access to external characters is limited in the fossil, and those of the genitalia are presently unavailable for study. This scenario makes it challenging to infer the phylogenetic position of *C. microsoma* within Ptomaphagina.

Family Anthicidae Latreille, 1819
Subfamily Tomoderinae Bonadona, 1961
Genus Pseudotomoderus Pic, 1892

Type species. *Pseudotomoderus compressicollis* Motschulsky, 1839

Diagnosis (emended). (1) pronotum lacking distinct apical rim or collar, (2) distinct lateral antebasal constriction present on pronotum, (3) metacoxae broadly separated, (4) intercoxal projection rounded, (5) elytra flattened, humeri obsolete, subangular.

Pseudotomoderus burmitina sp. nov.
(Fig. 20.)
LSID urn: lsid: zoobank.org: act:XXXXX

Differential diagnosis. (1) body small, (2) elytra elongated, flattened, subquadrate, with angle marked humeral (shoulder form), (3) elytra less dense punctured, (4) aedeagus long, apical sharp pointed.

Type material. Holotype NIGP002, a complete beetle covered by numerous micro-bubbles.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. The specific name is derived from Latin “Burmitina”, referring to the mineralogical name of Burmese amber.

Description. All measurements in mm.

Male. Body very small, total length 1.64, head, thorax and abdomen clearly divided, uniformly brownish to dark brown, numerous black dots preserved on elytra, no other colour patterns.

Head smooth, dorsally flattened, length 0.21, width 0.36. Eyes large, prominent, subcircular, not collide in the middle frons, truncate opposite the insertions of antennae. Dorsal surface with very fine punctures, pubescence very sparse and inconspicuous. Antennae comparatively long, clavate, length 0.71, 11-antenomeres, extending to base of elytra; basal antennomere long; 2nd – 4th antennomere slender, 5th – 10th antennomere oval to triangular, wider than preceding ones, 11th antennomere elongate, asymmetrically triangular, apical pointed, as long as antennomeres 9th –10th combined. Mandible small; terminal maxillary palpomere slightly expanded, subangular on inner margin, finely faceted.

Pronotum width 0.40, length 0.32, smooth dorsally with very fine punctures, wider than head; ant-like shape, anterior sharply narrowed, width anterior lobe 0.18; posterior strongly constricted formed bottleneck shape contact with elytra, width anterior lobe 0.24; evenly rounded on lateral margins. Scutellum very small, triangular.

Elytra flattened, elongate, each elytron subquadrate, length 1.11, width in the middle 0.71. Humeri obsolete, subangular, shoulder form. Punctures widely preserved on elytra surface, irregularly arranged into more than 6 rows on each elytron, deeper and dense in anterior. Pubescence sparse, appressed, directed posteriorly.

Ventral body smooth, with very fine and sparse setae. Mesosternum small and short. Metacoxae broadly separated by moderately rounded intercoxal projection. Legs slender, smooth; tibiae and tarsi with very fine setae; tarsi form 5-5-4. Metatarsomeres slender and bilobate; length metafemur 0.34, metatibiae 0.37, metatarsomeres 0.18, 0.07, 0.05, 0.06. Claws simple, rather long.

Abdomen smooth, lateral margin with sparse but comparatively long pubescence, 5-segements. Length abdominal segments, 0.17, 0.14, 0.12, 0.11, 0.11. A very short pygidium hided. Aedeagus exposed, length 0.17, apical pointed.

Superfamily Cucujoidea Latreille, 1802

Family Kateretidae Kirby, 1837

Genus *Magnipolliniretes* gen. nov.

LSID urn: lsid: zoobank.org: act:XXXXX

Type species. *Magnipolliniretes burmites* gen. et. sp. nov.

Differential diagnosis. (1) Body size bigger, > 4mm. (2) Elytra shortened, but exceed 40% of body length, leaving two last abdominal segments exposed, (3) Numerous punctured striae on each elytron. (4) Maxilla with galea and lacinia long, narrow, curved inward near distal end. (5) 4th pro-, meso- and meta- tarsomere shortened, obviously compared with 5th tarsomere.

Etymology. Magni (Latin) – big, Pollini- (Latin), from the Latin ‘pollinis’, referring to the English ‘pollen’; -retes, the usual suffix for generic names in the family Kateretidae.

Magnipolliniretes burmites gen. et. sp. nov.

LSID urn: lsid: zoobank.org: act:XXXXX

Diagnosis. As for genus.

Type material. Holotype. NIGP003, a complete beetle with partial ventral compressed. Numerous grains attached to the body.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. Burmite (Latin) – Burmese amber.

Description. All measurements in mm.

Length 4.2. Body oblong oval, flattened. Dorsum with recumbent pubescence. Head prognathous, not abruptly constricted posteriorly. Eyes finely faceted, moderately convex. Antennae length 0.90, 11- antennomere with loose 3-segmented club (antennomere 9-11); antennomere 1 elongated oval, length 0.11; antennomere 2-8, length ca. 0.07, subcylindral; antennomere 9-11, length ca. 0.08, cup shaped, prolonged and enlarged with fine pubescence, formed club. Antennal insertions exposed; subantennal grooves and subantennal ridges absent. Labrum free, transverse. Mandibles well developed, length 0.75, high sclerotized, moderately curved. Maxilla with galea and lacinia long, narrow, curved inward near distal end; lacinia with pointed apex and group of setae on outer edge prior to apex, Maxillary palp 4-segments, terminal palpomere securiform, wider than preceding ones, narrowly truncate apically with sparse pubescence. 2nd segment of labial palp cup shaped, narrowed, elongated.

Pronotum length 1.06, width in middle 1.30 as wide as elytra, nearly rectangular, sides slightly arcuate; lateral carinae complete, simple; anterior angles obtusely angulate; posterior angles broadly rounded.

Elytra shortened, length 1.60, width in middle 1.37; leaving pygidium and part of preceding abdominal tergum exposed, truncate apically; transversely strigose; scutellary striole absent; scutellum shield small, triangular; numerous punctured striae on each elytron.

Prosternite anterior with fine pubescence. Procoxal cavities transverse, externally open. Mesosterna completely bordered anteriorly. Metasterna flat. Metacoxae transverse, widely separated. Femur slender, tibiae typically widened posteriorly; lateral edges with short setae; two tibial spurs present; tarsi 5-5-5, tarsomeres 1–3 bilobed, with densely setose pads; tarsomere 4 shortened, setae preserved parallel-side and apical. Length protarsomeres 1-5: 0.11, 0.08, 0.06, 0.03, 0.19; length mesotarsomeres 1-5: 0.09, 0.05, 0.06, 0.04, 0.18; length metatarsomeres 1-5: 0.11, 0.10, 0.08, 0.05, 0.24. claws simple, bi-cleft.

Abdomen with five ventrites, exceed elytra, ventral surface with very fine and short setae, posterior ventrite with sparse pubescence. Pygidium oblique transverse.

Remarks. Color varies from black to dark brown based on light. Ventral structure partially compressed, difficult to observe. Structure detail shows under CLSM.

The numerous pollen grains show high similarities to several basal angiosperms (ANITA group, ANITA stands for Amborella, Nymphaeales, Illiciales, Trimeniaceae and Austrobaileya), especially the nymphaealean plants. The earliest fossil record of nymphaealean plants dated as Early Cretaceous (Friis et al., 2011). The earliest Nymphaeaceae pollen record is from the Maastrichtian Edmonton Formation (Alberta, Canada) (Srivastava, 1969), characterized by monosulcate, elliptical and retipilate to reticulate pollen ornamentation. The grains preserved in NIGP003 is approximately oblate spheroidal, 54.75 μm (63.22–47.01 μm) × 44.33 μm (52.59–38.76 μm) (based on measurement of the 10 best preserved grains) in equatorial view. Monosulcate; colpi long, wide, deep and extend to the pole. Exine moderately thick, ~1.5 μm. Ornamentation very simple or hard to observe.

Superfamily Lymexyloidea Fleming, 1821

Family Lymexylidae Fleming, 1821

Subfamily Atractocerinae Laporte, 1840

Type Genus *Urtea* Paulus, 2004

Diagnosis (emended). Genus *Urtea* is distinguished from other atractocerines by the following combination of characters: (1) body small, narrow and elongated (~12-16 mm); (2) head large, wider than pronotum; (3) eyes large, occupy entire frons, contiguous anteriorly; (4) antenna long, slender, filiform, surface with short setae; (5) pronotum anteriorly narrow; (6) scutellum, width < length; (7) elytron subquadrate, length / width ratio ca. 4:1; (8) hindwings well developed, C+Sc+R, r-m, M+Cu present; (9) metacoxae long, oblique, cone-shaped, together with trochanter formed X-shape symmetrically.

Type species. *Urtea graeca* Paulus, 2004

Urtea orientem sp. nov.

LSID urn: lsid: zoobank.org: act:XXXXX

Diagnosis. The new species differs from *Urtea graeca* with the characters: (1) eyes smaller, dorsum neck area behind the eyes comparatively wide; (2) 11th antennomere triangular, apically pointed; (3) pronotum nearly rectangular, narrower at anterior and posterior; (4) scutellum narrow, irregular shield shape, width < length, with small black pattern near median.

Type material. Holotype. NIGP004, a complete specimen. Bubbles accumulated below the abdomen terminal. A small Diptera above the dorsum.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. Orientem (Latin) – oriental, referring to the discovery region.

Description. Measurements in mm.

Male. Body length 13.3, elongated, narrowly parallel sided, moderately dorsoventrally flattened. Head, pronotum and elytra surface leathery, preserved with tiny setae. Body brownish to yellowish, no colored patterns or textures.

Head large, broadly oval, slightly vertical, wider than pronotum, width 1.11. Eyes very large, irregular oval, occupying extensive parts of head surface, frontal nearly convergence formed a suture. Dorsum neck area behind the eyes comparatively wide, Raractocerus-type. Antennae long, 1.40; filiform, with numerous setae. 11 antennomeres, 1st and 2nd antennomeres thick, 3rd - 10th antennomeres has general elongated form, but continuously shortened, 11th antennomere triangular, apically pointed. Mandibles small. Maxillary palpus 4-segmented; 4th palpomere highly modified into palp organ.

Pronotum nearly inverted trapezoidal, brownish, matt; length 1.00, anterior protruding, narrow, width 0.42, biggest width 0.90, posterior width 0.67, lateral margin slightly curved. A fully developed longitudinal lines throughout in the middle. Scutellum very small, subquadrate or shield shape, length longer than width (length 0.35, width 0.29), with tiny blackish patterns.

Elytra shorter than 1/5 of body length, narrow at the base, each elytron subquadrate, length 2.08, width in the middle 0.60; dorsum simple, brownish, matt. Hindwings exposed, marginal C+Sc+R vein well developed, r-m crossvein present, conspicuous; M+Cu fork present.

Prothoax narrow, cervicalia large, prosternum diminished. Mesosternum small. Metasternum long, narrow. Markedly modified metacoxae elongated and oblique, together with trochanter formed X-shape structure, Urtea-type. Legs slender, thin, with very short setae on surface, tarsi form 5-5-5, claws simple.

Abdomen long, flattened dorsoventrally, sternites subquadrate. Abdominal segment II-VII ventrally leathery, nearly rectangular. VIII tergite very small, telescoped inside VII. Aedeagus exposed. Median lobe exposed, narrow; lateral lobe thick.

Type material. Paratype. NIGP005, a complete specimen. Bubbles distributed ventrally. Numerous fungi spore grains associated with beetle.

Description. All measurements in mm.

Sex unknown. Body length 11.5, elongated, narrowly parallel sided, dorsoventrally flattened. Head, pronotum and elytra surface leathery, preserved with tiny setae. Body brownish, numerous colored dots on ventral abdomen and elytra.

Head large, broadly oval, flattened, wider than pronotum, width 1.03. Eyes very large, irregular oval, occupying extensive parts of head surface, frontal nearly convergence formed a suture. Dorsum neck area behind the eyes wide, Raractocerus-type. Antennae long, 1.03, filiform, 11 antennomeres, terminal antennomere triangular, apically pointed. 4th palpomere highly modified into palp organ, highly expanded.

Pronotum nearly rectangular, brownish, matt; length 1.00, anterior protruding, narrow, width 0.44, biggest width 0.85, posterior sharply narrowed, width 0.41, lateral margin slightly curved, with two dark colored lineal pattern, lateral posterior margin slightly extended. A fully developed longitudinal lines throughout in the middle, blackish. Scutellum very small, posterior sharply narrowed, shield shape, length longer than width (length 0.43, width 0.31), with two symmetrical tiny blackish patterns near the median.

Elytra shorter than 1/5 of body length, narrow at the base, each elytron subquadrate, length 1.80, width in the middle 0.48; dorsum simple, brownish, matt, anterior with numerous blackish dots. Hindwings exposed, marginal C+Sc+R vein well developed, r-m crossvein present; M+Cu fork present.

Prothoax narrow. Mesosternum small. Metasternum long, narrow, with very fine and dense setae. Metacoxae distinctively modified, elongated and oblique, Urtea-type. Legs slender, thin, with very short setae on surface; posterior tibiae spurs preserved, tarsi form 5-5-5, claws simple.

Abdomen long, flattened dorsoventrally, sternites subquadrate. Abdominal segment II-VII ventrally leathery, with very fine surface setae, nearly rectangular. Genitalia hided.

Remarks. Family Lymexylidae also known as ship-timber beetles, are the sole member of the superfamily Lymexyloidea (Wheeler, 1986). Genus *Urtea* including only one species *Urtea graeca* Paulus, 2004 distributed in eastern Europe (Paulus, 2004). *Urtea orientem* sp. nov. shows similarity to Raractocerus with vertical head position and eyes form. However, the distinctly modified metacoxae, shield shape scutellum (width < length) and anteriorly narrowed protonum assigned it to *Urtea*.

Urtea orientem sp. nov. easily separated with another Cretaceous genus Vetaractocerus with bigger body size, shorter elytra, present of M+Cu, scutellum shape and metacoxae shape.

Superfamily Scarabaeoidea Latreille, 1802

Family † Passalopalpidae Boucher and Bai, 2016

Type genus Passalopalpus Boucher and Bai, 2016

Colorpassalopalpus gen. nov.

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Type species *Colorpassalopalpus coloratum* gen. et sp. nov.

Differential diagnosis. Characters distinguished with Passalopalpus: (1) Mandibles powerful, surface smooth, with 4 strong teeth, basal teeth obviously small; (2) maxillary palps exceeding 3/4 length the lateral edges of mandibles; (3) lateral pronotum covered with setae of uneven lengths, very long anteriorly and short posteriorly; (4) protibiae well developed, with 6 sclerotized teeth, with more than 10 pairs long setae; (5) abdominal sternites II-VI with short setae on the lateral margin, VII-VIII with long setae on the lateral margin, mediotergite VIII apex with plentiful very long setae; (6) elytra shinning and rainbow colourful.

Etymology. Color, shortened for coloratum (Latin), means colour.

Colorpassalopalpus coloratum sp. nov.

(Fig. x.)

LSID urn: lsid: zoobank.org: act:XXXXX

Diagnosis. As for the genus Colorpassalopalpus gen. nov.

Type material. Holotype NIGP006, sex unknown, a complete beetle attached by numerous mites on ventral and dorsal body. A small sized beetle preserved alongside holotype, same species.

Horizon and locality. Mid-Cretaceous (approximately 99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Etymology. See etymology for genus *Colorpassalopalpus*.

Description. All measurements in mm.

Macropterous. Habitus depressed, widely pubescent, elongated and narrow, except widened elytra. Colour of body and legs dark brown or black ventral and dorsal, elytra shinning and colourful. Body length:7.54; greatest width: 2.65 over middle elytra; smallest width: 1.35 over middle pronotum.

Head frontal border, on half concave, thin and with long and spaced setae; sides prominent; external angles powerful and thick, apex curved and thorny upward, forming anterior angles of head. Clypeus exposed, wider than the labrum. Labrum large, narrower on base, anterior border convex. Medio- and laterofrontal areas large, concave; anterior mediofrontal area glabrous; laterofrontal areas, anteriorly with long and scattered setae, posteriorly with a tuft of very long and dense setae close to supra-ocular ridges. Posterior mediofrontal area concave as previously, but forming a narrow cavity with a dense tuft of setae, most of them very long. Lateropostfrontal areas convex; integument smooth, with setae in tufts less dense and less long than previously. Postfrontal area glabrous, with light anteroposterior lines on almost all width. Latero-ocular pit large and deep, connecting eye and supra-ocular ridge, with numerous short to very long setae. Eyes globulous, exceeding head width. Ocular canthus rather short and narrow; apex obtuse shorter than eye. Postocular pits obsolete, with small and scattered setae. Antennae with 9 antennomeres, rather long; scape long and curved. Antennomeres VII-IX formed clubs, length: 0.29, 0.40, 0.39, thick, convex down, with numerous minute but prominent setae; antennomeres I-VI slender and smooth, length: 0.27, 0.09, 0.07, 0.07, 0.06, 0.06, with a pair long setae on II-VI each and numerous short setae. Mandibles powerful and regularly waisted; inner lobes with 4 strong teeth, conical, on same plan with comparable development and conformation; basal teeth obviously small, proximal tooth higher and longer; smooth. Ligula small, covered with setae. Maxillae with long and straight maxillary palps of 4 articles, exceeding 3/4 length the lateral edges of mandibles, smooth; galea very developed, long and straight, with numerous, strong and long setae almost everywhere. Mentum large, trapezoid; disk somewhat convex; no lateral pits; integument almost smooth, except very short and spaced setae. Submentum large, with numerous punctuations and rather long setae almost everywhere. Hypostomal processes wide and long, hairless and smooth.

Pronotum thin, narrow and elongated, quadrilateral, length 1.86, biggest width at posterior, 1.51. Anterior border weakly concave; anterior angles well rounded; sides slightly concave on half of median length; marginal groove obsolete, except close to posterior apex; posterior border regularly rounded, incised in middle; dorsodiscal integument glabrous, finely granulous throughout, but irregular. Lateral pronotum covered with setae of uneven lengths, very long anteriorly and short posteriorly. Ventral with numerous short setae.

Elytra thin, little sclerotized, length, narrow on the base, then clearly widened on postmedian part, length 4.09; anterior border concave, with sharp edge and long, thick and scattered setae up to included calli. Elytron hairless, with more than 5 striates, not punctuated, little deep and wide, more or less parallel; interstriae smooth or almost, slightly convex. Elytron margin covered with fine and dense setae of very uneven lengths. Apex rounded, thin, very concave at junction of elytra, where last abdominal sternites clearly exposed dorsally. Hindwings hided.

Procoxal fosse very large and oval. Mesocoxal pit small and oval. Metacoxae external, very large. Legs long and rather slender, tarsi form 5-5-5. Profemora short and very wide on the base; mesofemora narrow and elongated; metafemora of intermediate conformation with the previous, rather thickset. Protibiae comparatively strong; outer face slightly curved, with 6 sclerotized teeth, with more than 10 pairs long setae, inner face with fine and dense setae like brush, more some distal setae; tarsal pit long, with not thorny and very slanted margin. Mesotibiae less expanded than protibiae, with numerous pairs long setae. Metatibiae finer and longer than mesotibiae; setae more numerous; apical forks and spolons very well developed. Tarsomeres 5 articles; I-IV fine, elongated and pointed, with 2 pairs long setae on the lower and upper faces, more some scattered shorter setae; V expanded, more elongated, with 4 pairs long setae. Claws long, thin and strongly hooked, thickened on the lower face, only with short setae on surface. Abdomen long and wide, 7 visible sternites, complete II-VII and mediotergite VIII, length: 0.26, 0.25, 0.37, 0.32, 0.26, 0.18, 0.13. Abdominal sternites II-VI with short setae on the lateral margin; VII-VIII with long setae on the lateral margin. Terminate mediotergite VIII exposed dorsally, exceeding the apex of elytra and with plentiful very long setae. Reproductive organs not clear visible.

Fig. 4. *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.

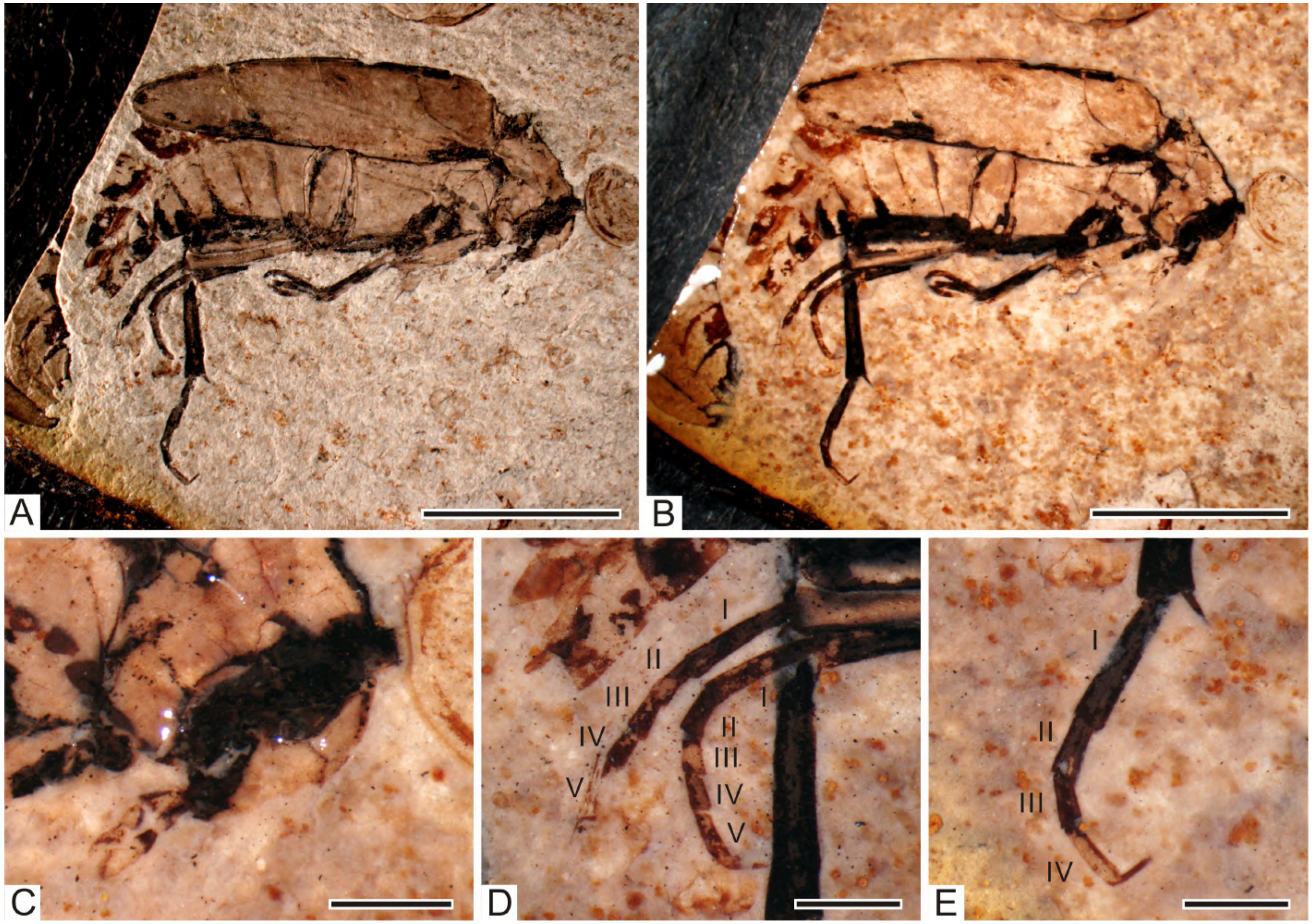

Fig. 5. *Wuhua peregrine*, NIGP154954, holotype. A–B Body. The specimen was photographed dry A and under alcohol B. C, Head. D, Tarsus of middle leg. E, Tarsus of hind leg. Scale bars = 5 mm in A–B; 1 mm in C–E.

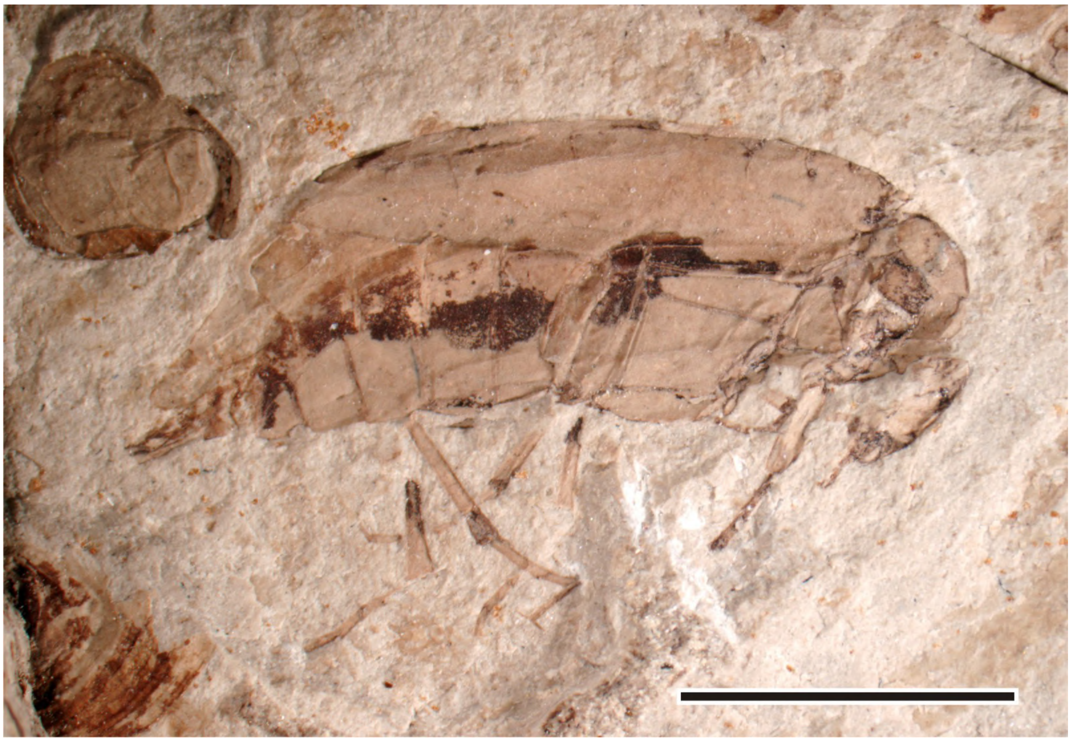

Fig. 6. A tenebrionoid beetle, CNU-C-NN2007203. Scale bar = 5 mm.

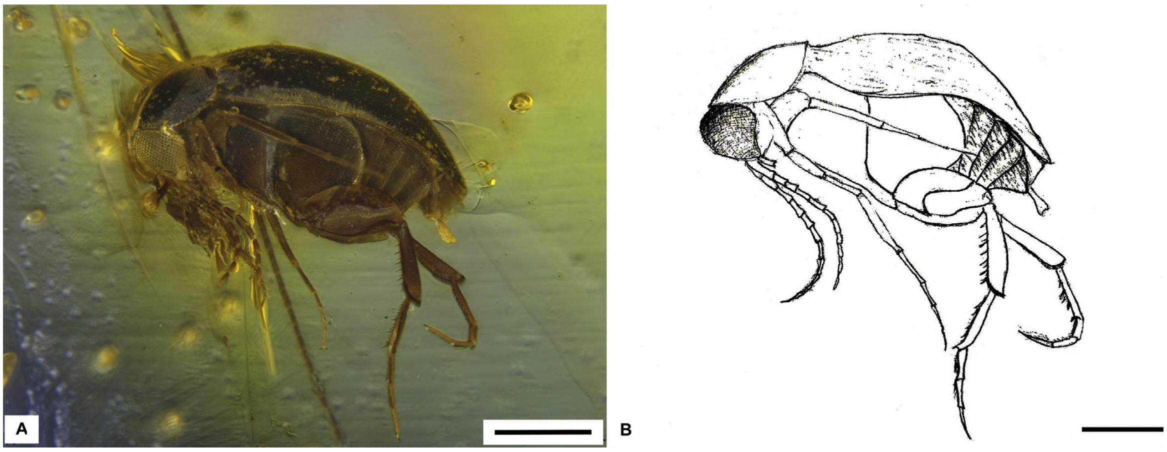

Fig. 7. *Multispinus multispinosus*, general view, holotype NIGP168210. A. microscope photo, lateral view. B. Hand drawing. Scale bars 0.5 mm.

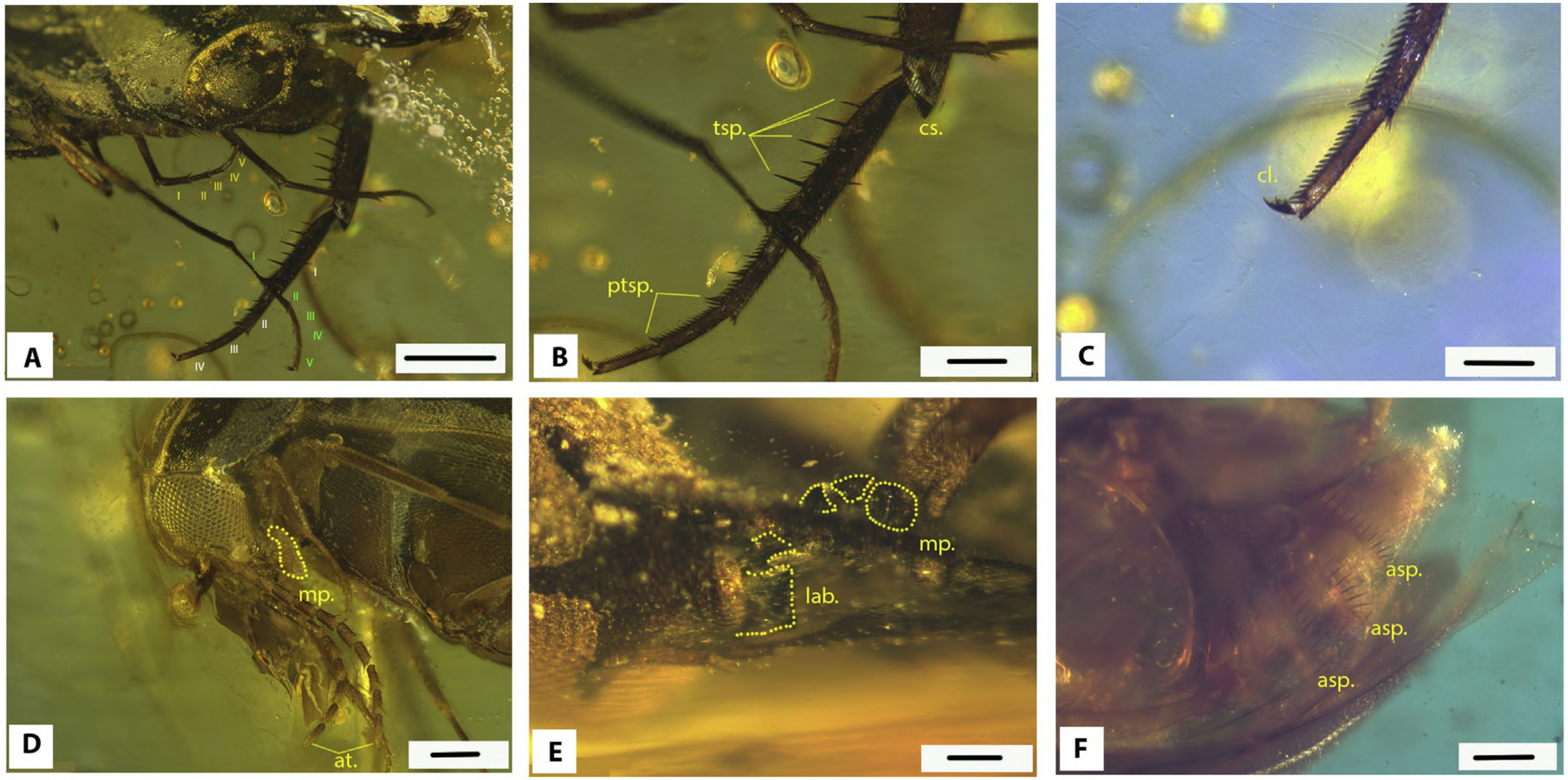

Fig. 8. *Multispinus multispinosus* details. A-C. Details of leg structure, paratype NIGP168211. A. Tarsal formula 5-5-4. I-V, tarsal segment number. B. Spines and setae structure. tsp.- tarsal spine, ptsp.-posterior margin tarsal spine, cs.-comb-like setae on posterior margin of metatibiae. C. Claws. cl.- claws, with 2 spines. D, E. Head and mouthpart structures, holotype NIGP168210. mp.- maxillary palpi. at.- antennae. lab.- labrum. F. Spines preserved in posteriors margin of abdominal sterna, specimen NIGP168212. asp.- abdominal spines. Scale bars 0.1 mm.

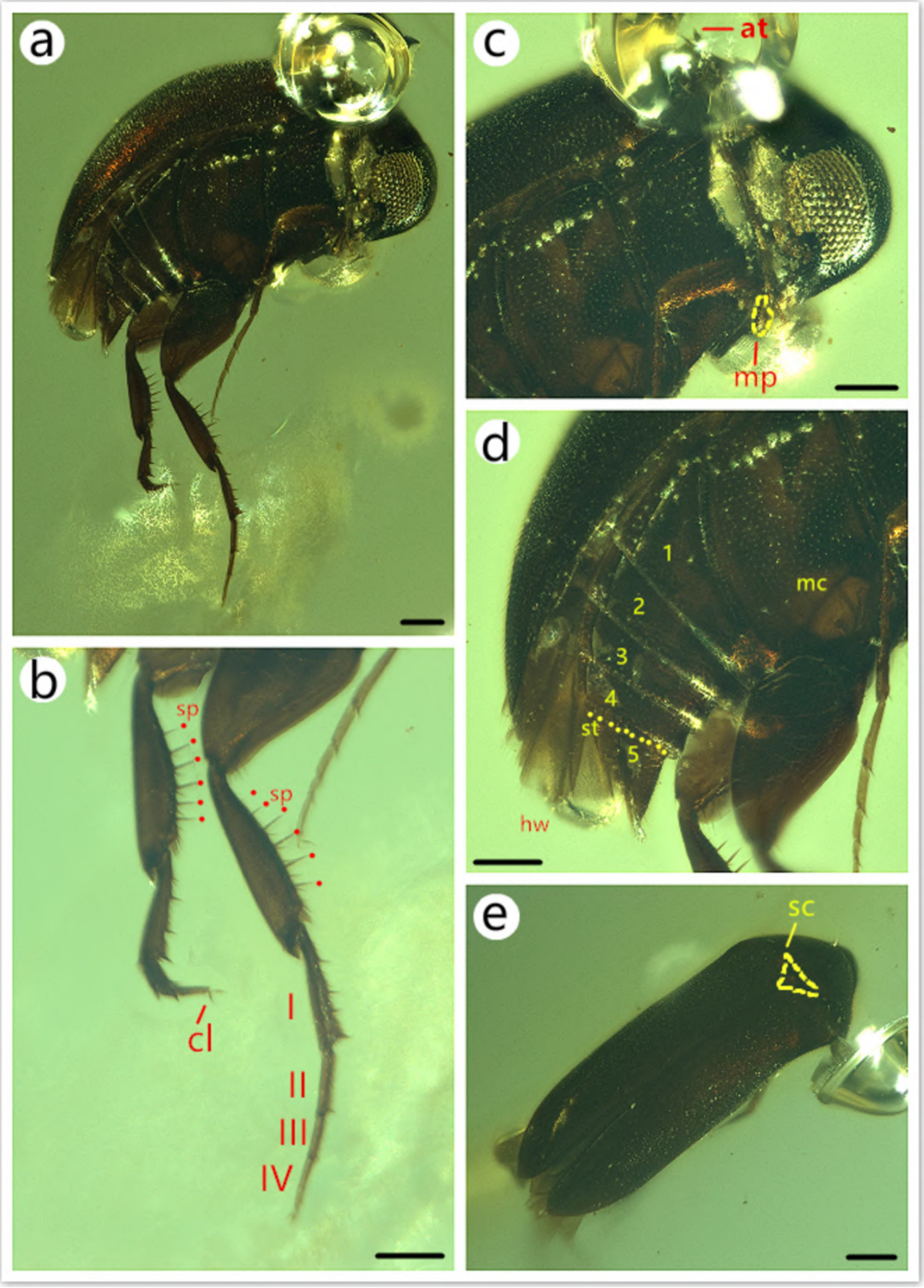

Fig. 9. *Multispinus parvus* a. lateral view; b. details of hind legs, I−IV represent 1st to 4th metatarsomeres, metatibiae spines pointed by red dots; c. details of head and thorax; d. details of metathorax and abdomen, 1–5 represent 1st to 5th sternites, a row of fine setae between 4th and 5th sternites pointed by yellow dots; e. dorsal view. Abbrevia- tions: at. antennae; cl. claw; hw. hind wings; mc. metacoxal plate; mp. maxillary palp; sc. scutellum; sp. spines on metatibiae; st. setae. Scale bars = 0.1 mm.

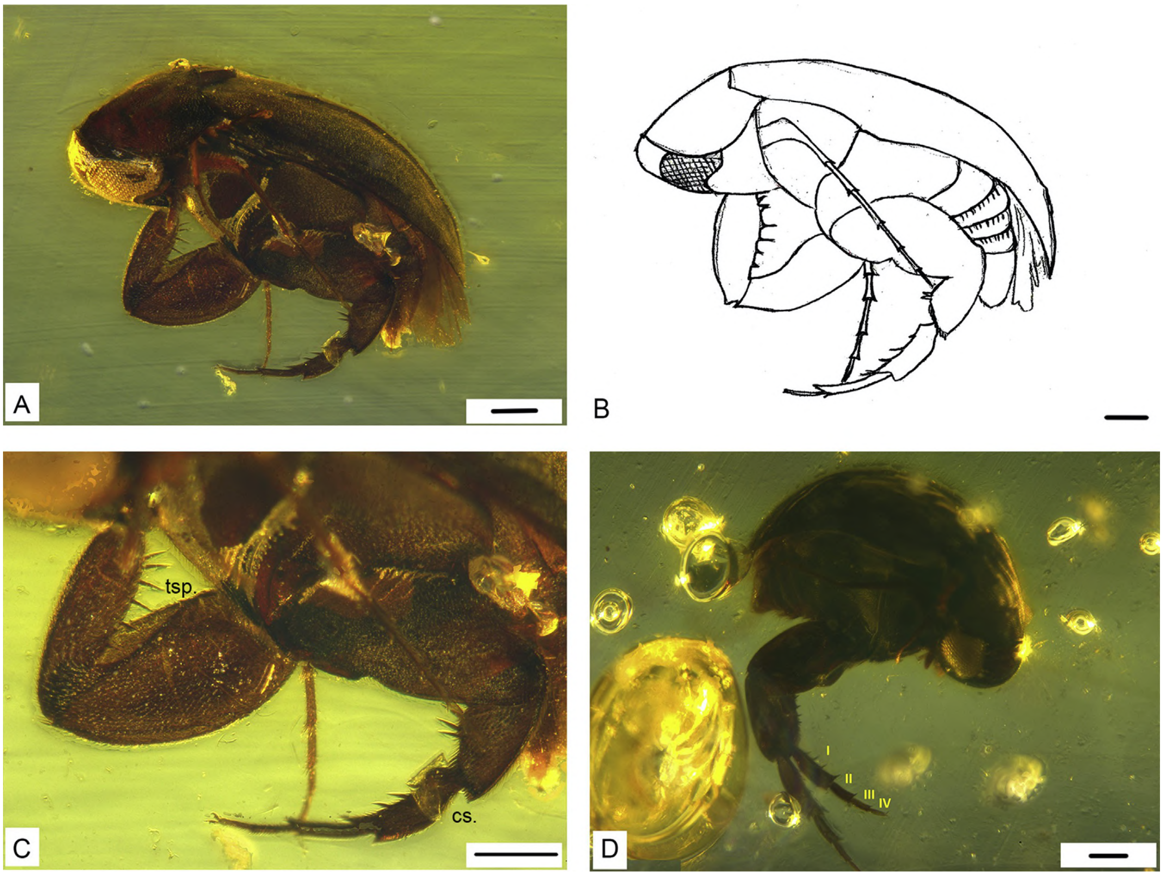

Fig. 10. A, B. *Apotomoura fortiscrura* general view, holotype NIGP168213. A. microscope photo, lateral view. B. Hand drawing. C. Spines and setae structure, holotype NIGP168213. tsp.- tibiae spine, cs.-comb-like setae on posterior margin of tibiae. D. Tarsal formula, hind tarsi 4 segments, paratype NIGP168214. I-IV, tarsal segment number. Scale bars 0.2 mm.

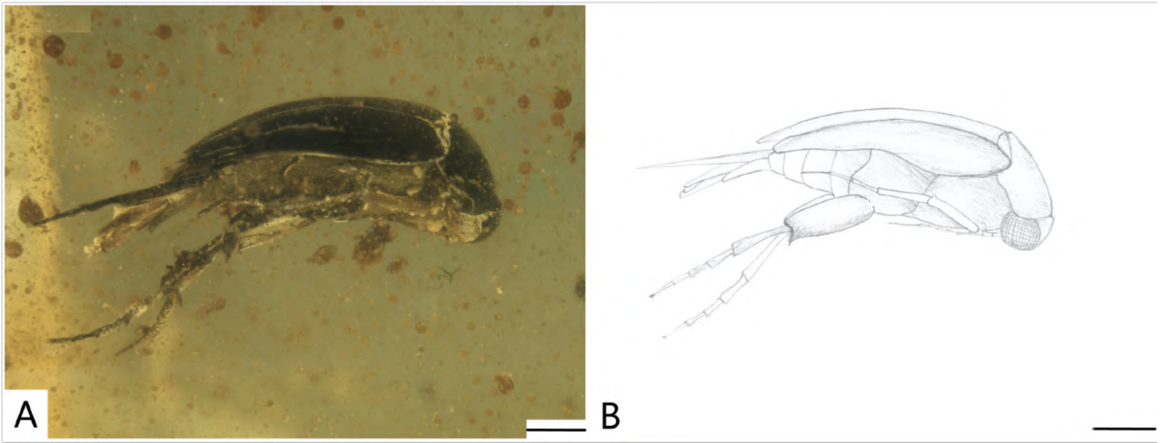

Fig. 11. *Primaevomordellida burmitina* general view, holotype NIGP168789. A. microscope photo, lateral view. B. Hand drawing. Scale bars 0.4 mm.

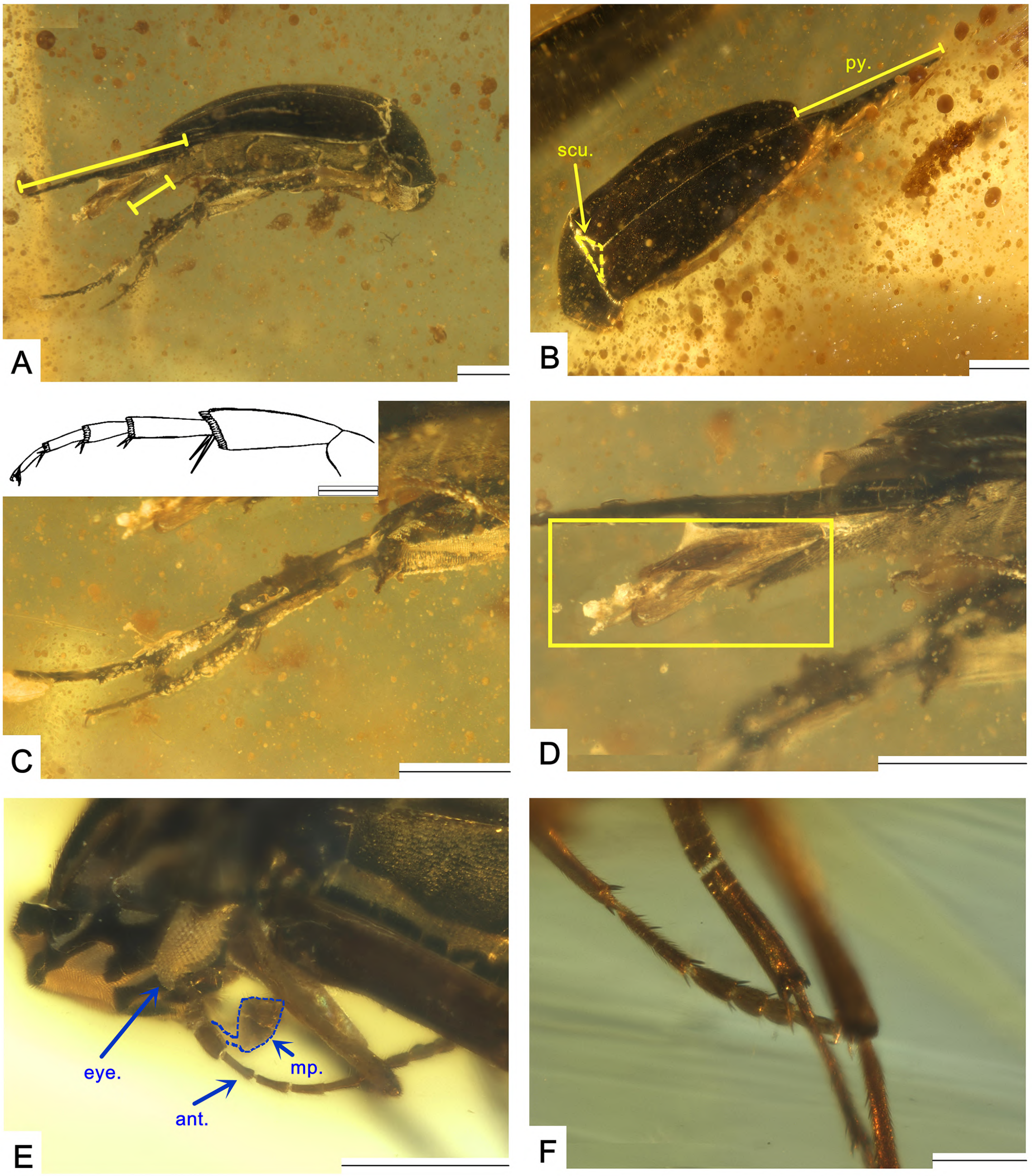

Fig. 12. Body structures of *Primaevomordellida burmitina*. A. Lateral view, length of pygidium and last abdominal segment are indicated. B. Dorsal view, scu.- scutellum, py.- pygidium. C. hind leg structures, hand drawing is highlighted. D. Genital organ highlighted. E. Detail structures of head and mouthpart. eye.- eyes, ant.- antennae, mp.- maxillary palpus. F. Fore legs structures. A-D from holotype NIGP168789, E-F from paratype NIGP168790. Scale bar A-E 0.4 mm, F. 0.2 mm.

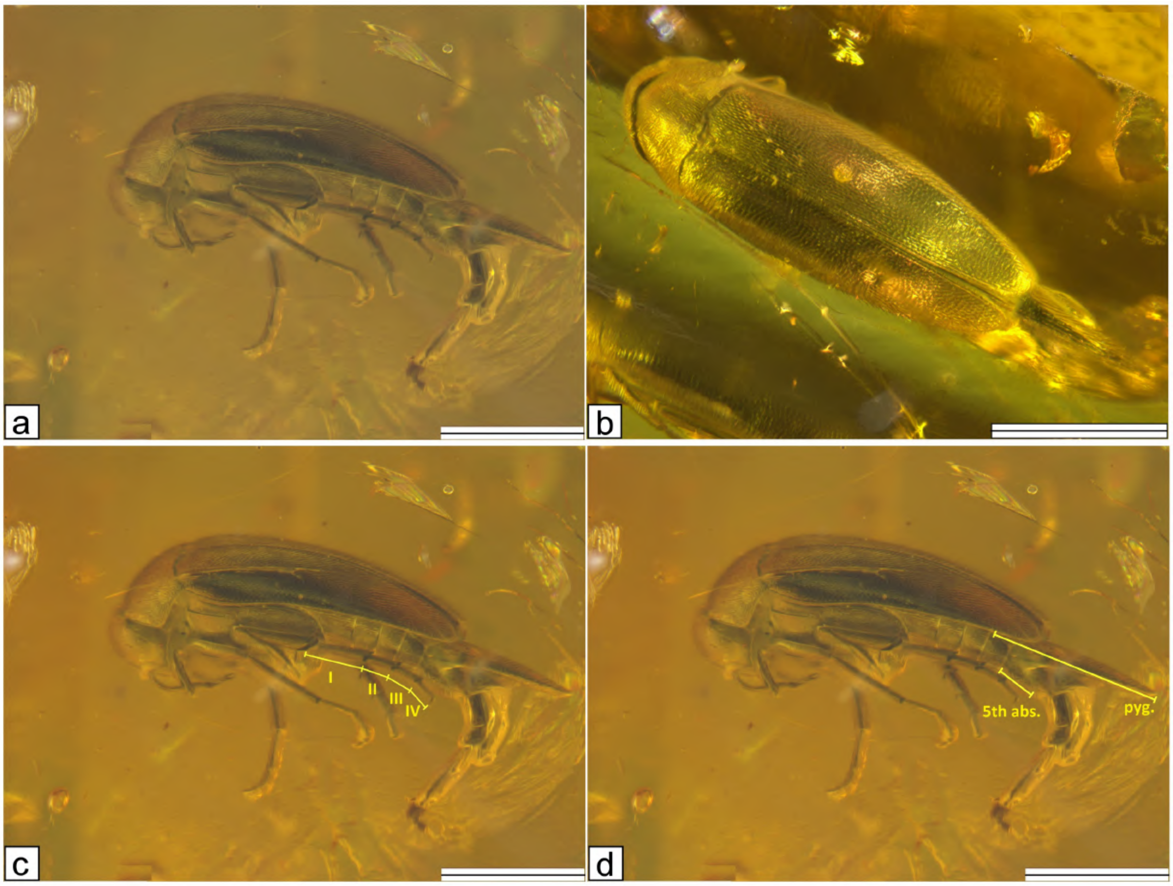

Fig. 13. Holotype of *Tomoxia succinea*. a Lateral view. b Dorsal view. c I–IV: 1st to 4th hind tarsomeres; length ratio 2:1:1:1. d 5th abs. the 5th abdominal sternum, pyg. pygidium, length ratio 1:4. Scale bar: 1 mm

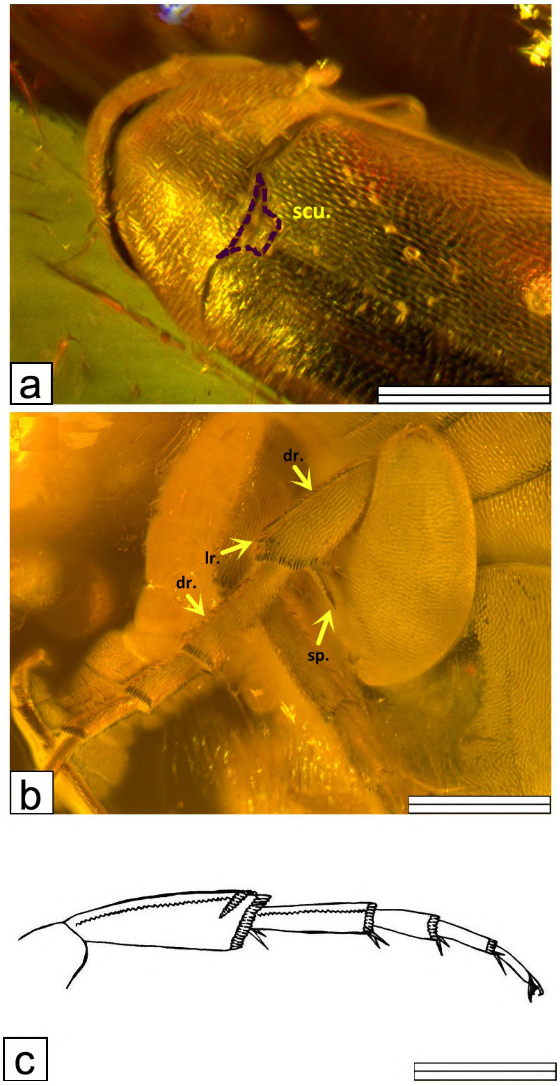

Fig. 14. Detailed morphological structures. a Highlighted scutellum shape (holotype). scu. scutellum. b Detailed hind leg structures (paratype). dr. fine dorsal ridge, lr. lateral ridge, sp. subapical spines on tibia and tarsomere. c Schematic drawing of hind tibia and tarsi. Scale bar: 0.5 mm

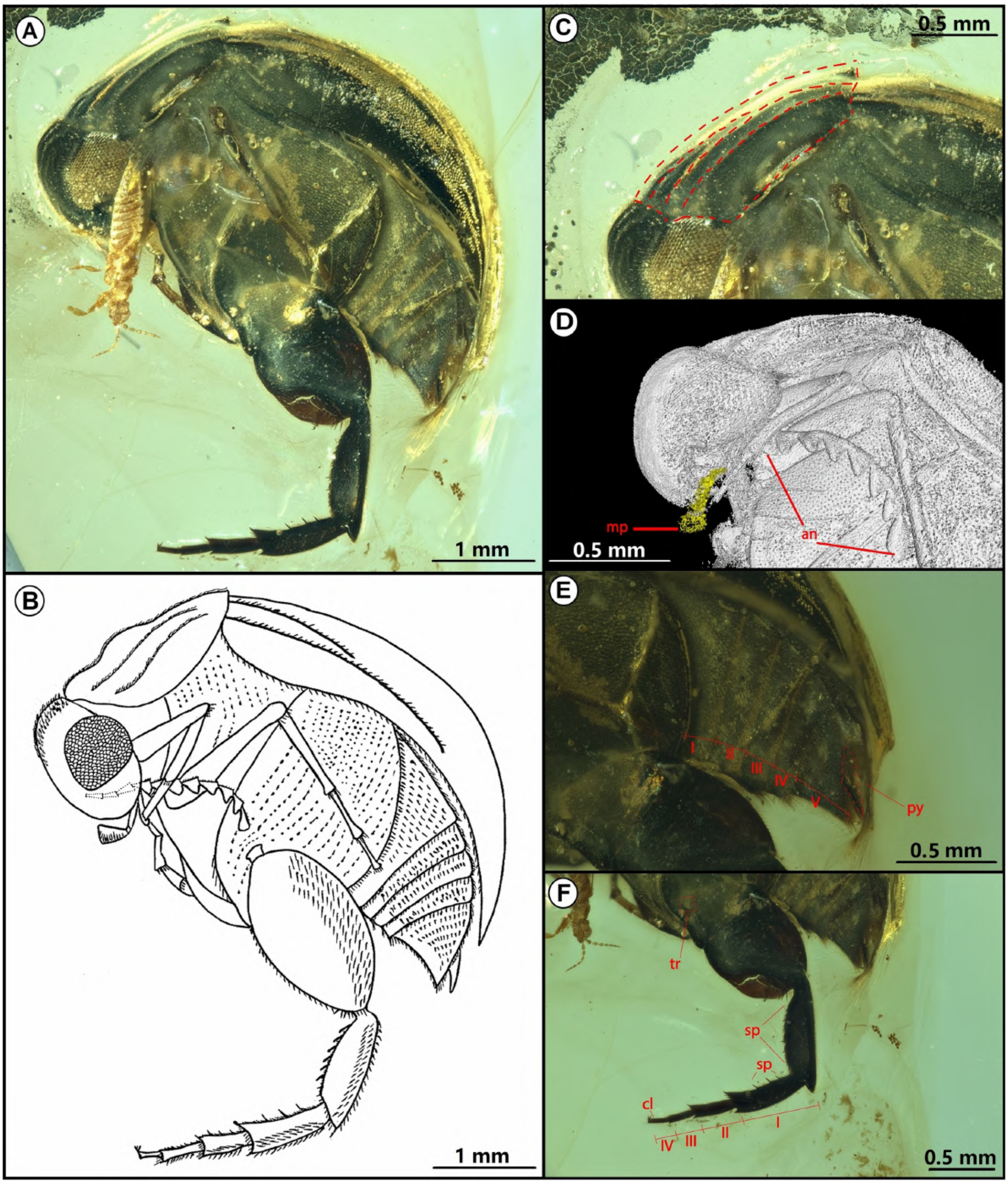

Fig. 15. Cretaceous tumbling flower beetle Angimordella burmitina. (A) Habitus. (B) drawing. (C) Prothorax and pronotum highlighted by red dashed lines. (D) Microtomographic reconstruction of the head. Maxillary palpi highlighted in yellow. (E) Abdomen, I–IV represent 1st to 5th abdominal ventrites. (F) Hind leg, I–IV represent 1st to 4th metatarsomeres. an, antennae; cl, claw; mp, maxillary palp; py, pygidium; sp, spines on metatibiae and metatarsi; tr, trochanter.

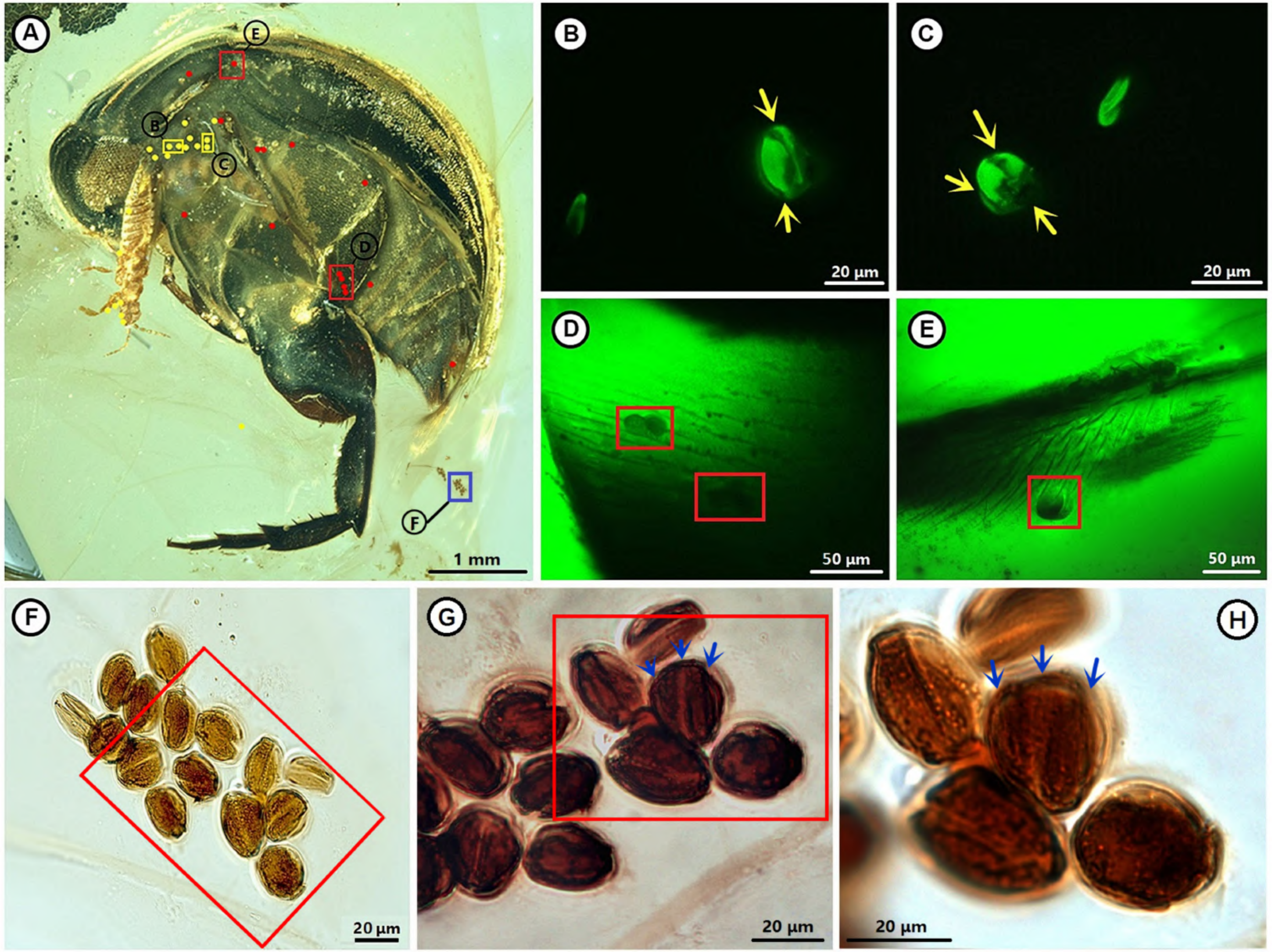

Fig. 16. *Angimordella burmitina* and tricolpate pollen grains. (*A*) Habitus. Pollen grains attached to the body are indicated by red dots, unattached are indicated by yellow dots, clumped pollens are indicated by blue squares. *B*−*H* locations are highlighted in *A*. (*B* and *C*) Pollen grains near the body. Yellow arrows point to colpi. (*D* and *E*) Pollen grains on the body. (*F*−*H*) Clumped pollen grains. G and H focus on the pollens that at the right side of the clump in *F* with different magnification and rotation angle. Blue arrows point to colpi.

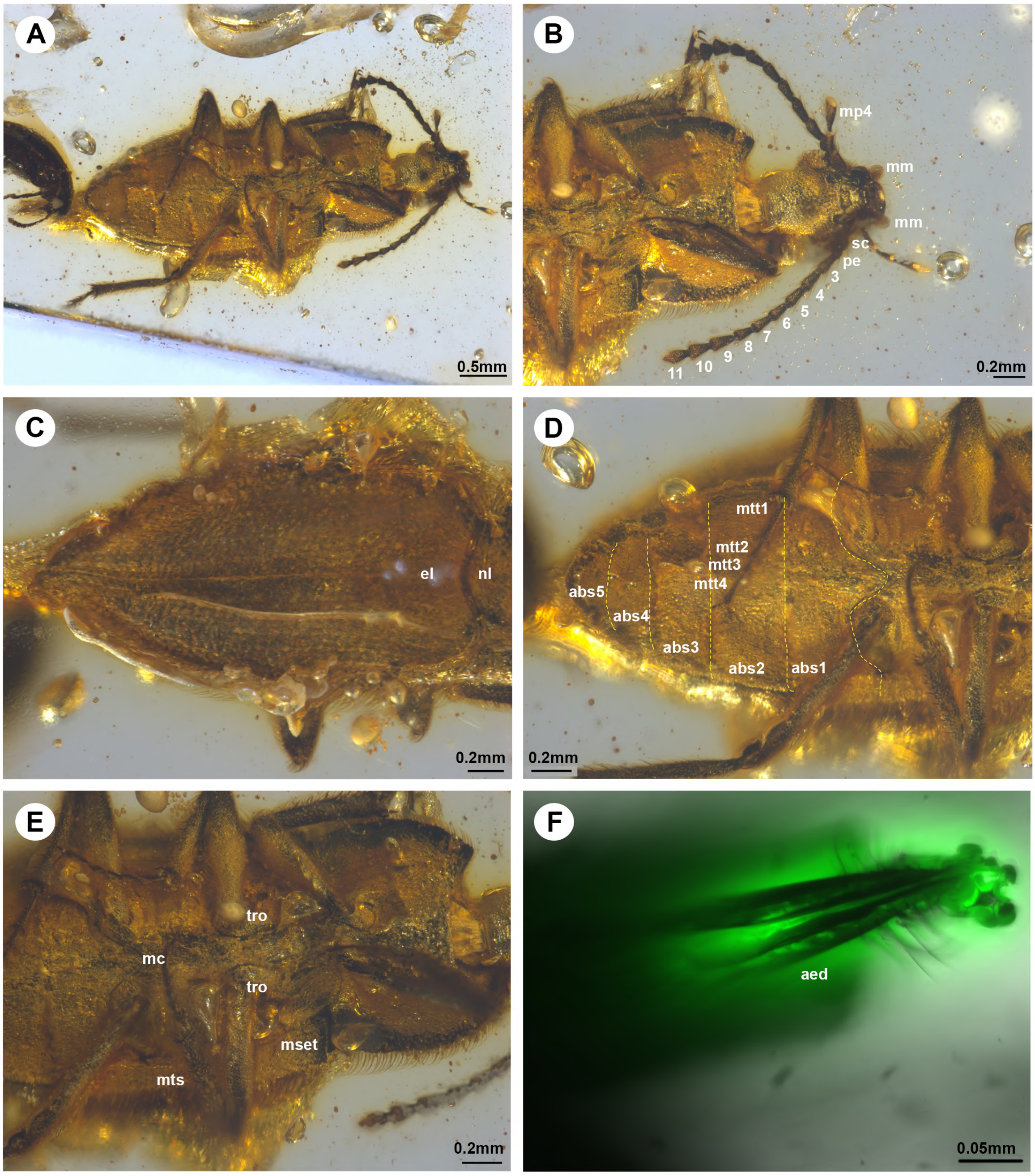

Fig. 17. A-F. *Praezolodinus pilosus* gen. et sp. nov. 3-11, antennomeres 3-11; abs 1-5, abdominal sternites 1-5; aed, aedeagus; el, elytron; mc, metacoxae; mm, mandibular mola; mp4, maxillary palpomere 4; mset, mesepisternum; mts, metasterna; mtt1-4, metatarsomere 1-4; n1, pronotum; pe, pedicellus; sc, scapus; tro, trochantins;

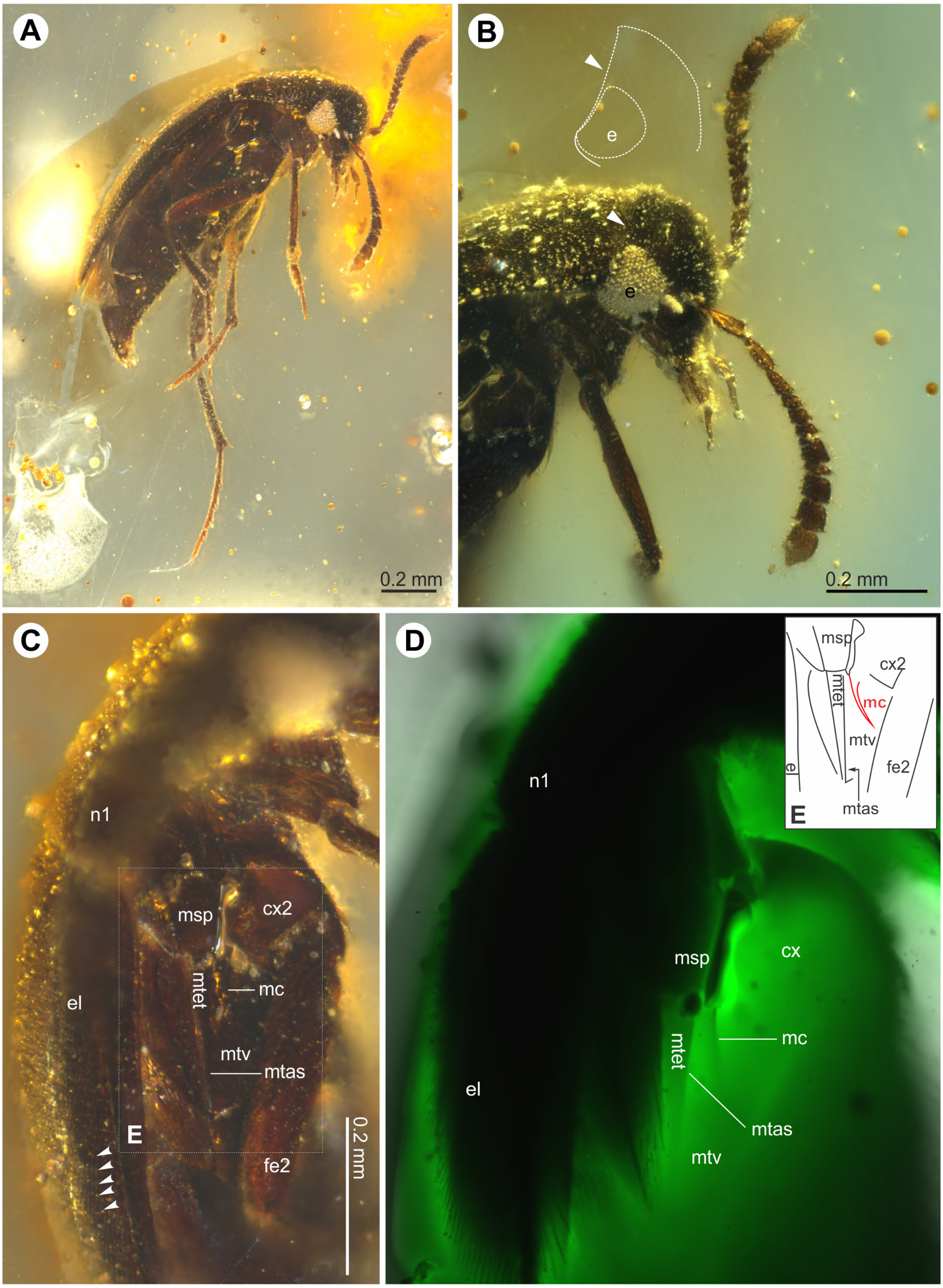

Fig. 18. A-E. *Cretoptomaphagus microsoma* gen. et sp. nov. cx2, mesocoxa; el, elytron; fe2, mesofemur; mc; metaventral carina; msp, mesepimeron; mtas, metathoracic anapleural suture; mtet, metanepisternum; mtv, metaventrite; n1, pronotum.

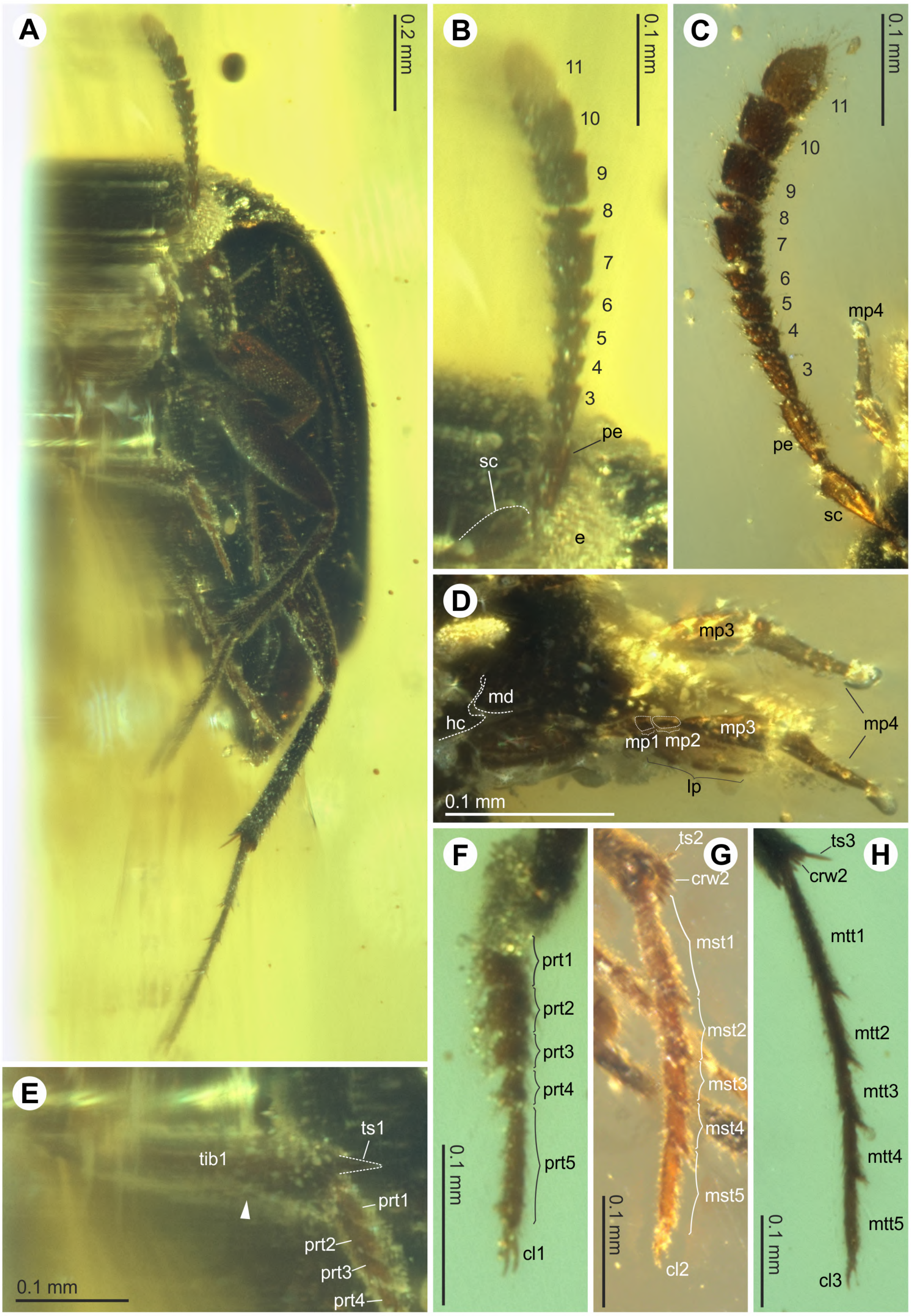

Fig. 19. A-H. *Cretoptomaphagus microsoma* gen. et sp.nov. 3-11, antennomeres 3-11; cl1-3, pro-/meso-/metatarsal claw; hc, head capsule; lp, labial palp; md, mandible; mp1-4, maxillary palpomere 1-4; mst1-5, mesotarsomere 1-5; mtt1-5, metatarsomere 1-5; pe, pedicellus; prt1-5, protarsomere 1-5; sc, scapus; tib1, protibia; ts1-3, pro-/meso-/metatibial spur.

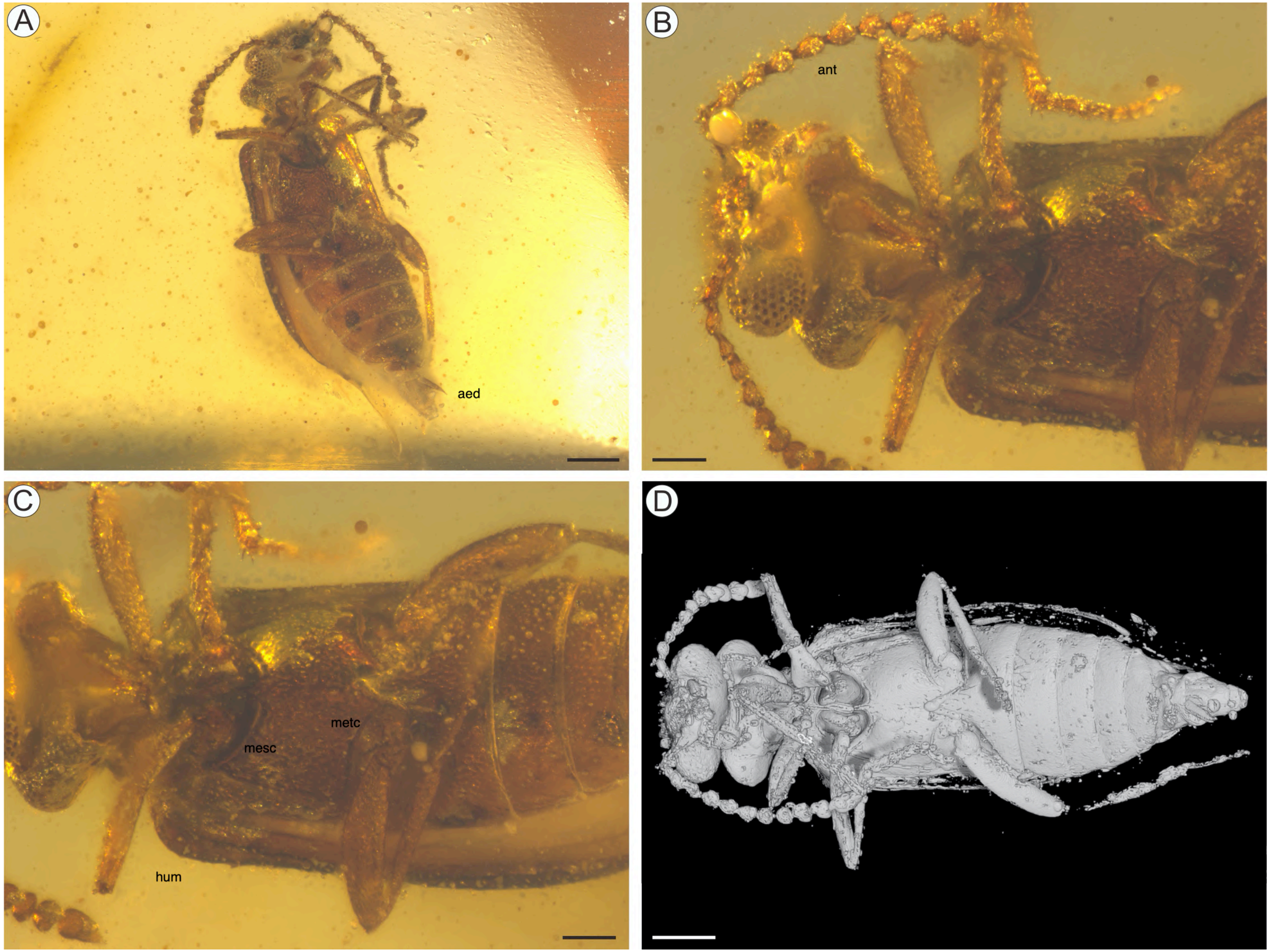

Fig. 20. A-D. *Pseudotomoderus burmitina* sp. nov. A. Habitus. B and C. Morphology detail. D. 3-dimentional reconstruction based on micro-CT scan data (4× objective, isotropic voxel sizes 2.07 µm, acceleration voltage for the X-ray 50 kV (power 4W)). aed, aedeagus; ant, antennae; hum, humeri; mesc, mesocoxa; metc, metacoxa. Scale A-D = 0.2 mm.

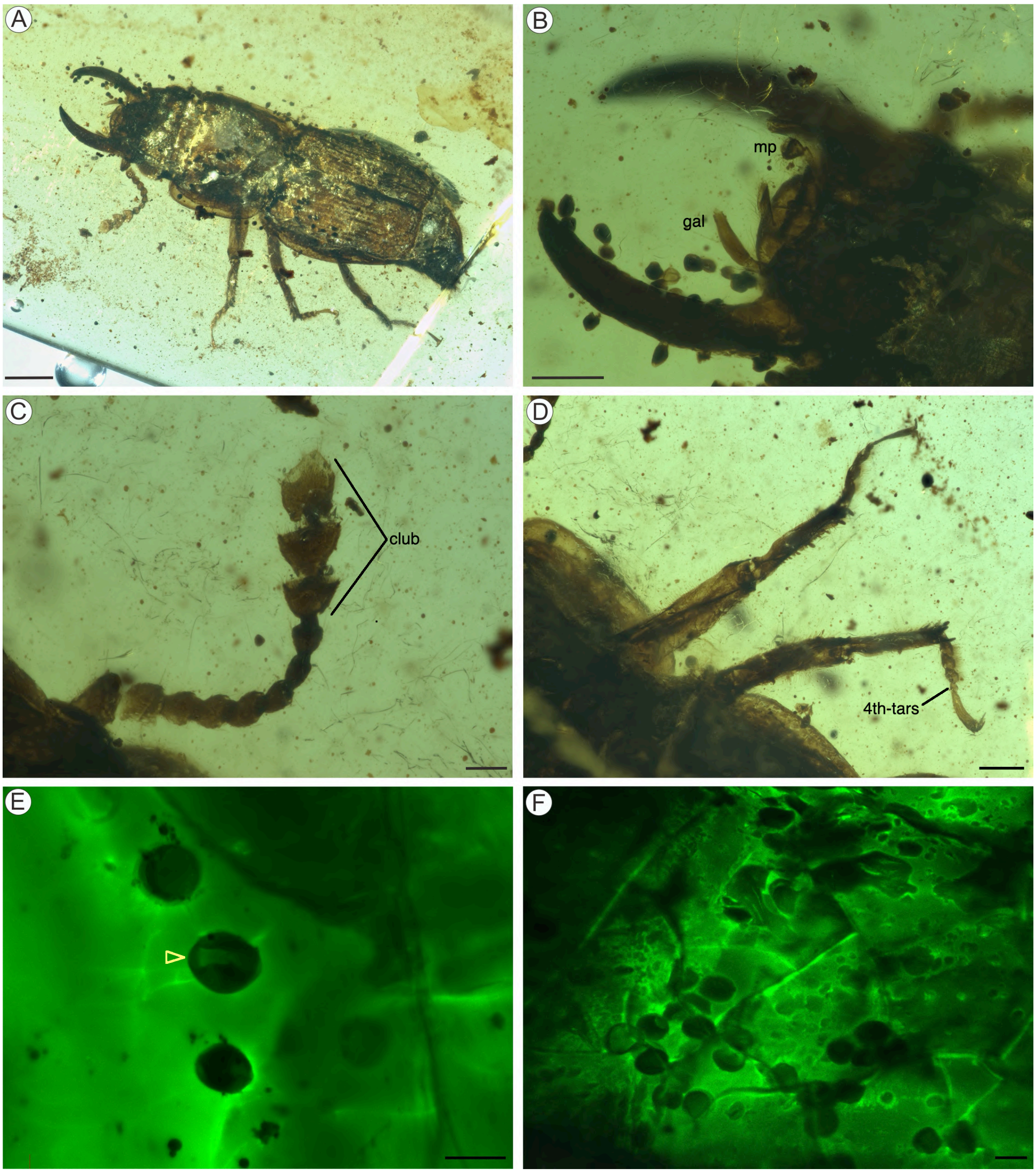

Fig. 21. A-F. *Magnipolliniretes burmites* gen. et. sp. nov. A. Habitus. B-D. Morphology detail. E and F. Pollen grain attached, monosulcate marked by yellow arrow. club, antennae club; gal, galea; mp, maxillary palpi; 4th-tars, 4th tarsomere. Scale A= 0.5mm B and D = 0.2mm, C = 0.1mm, E and F = 50 µm.

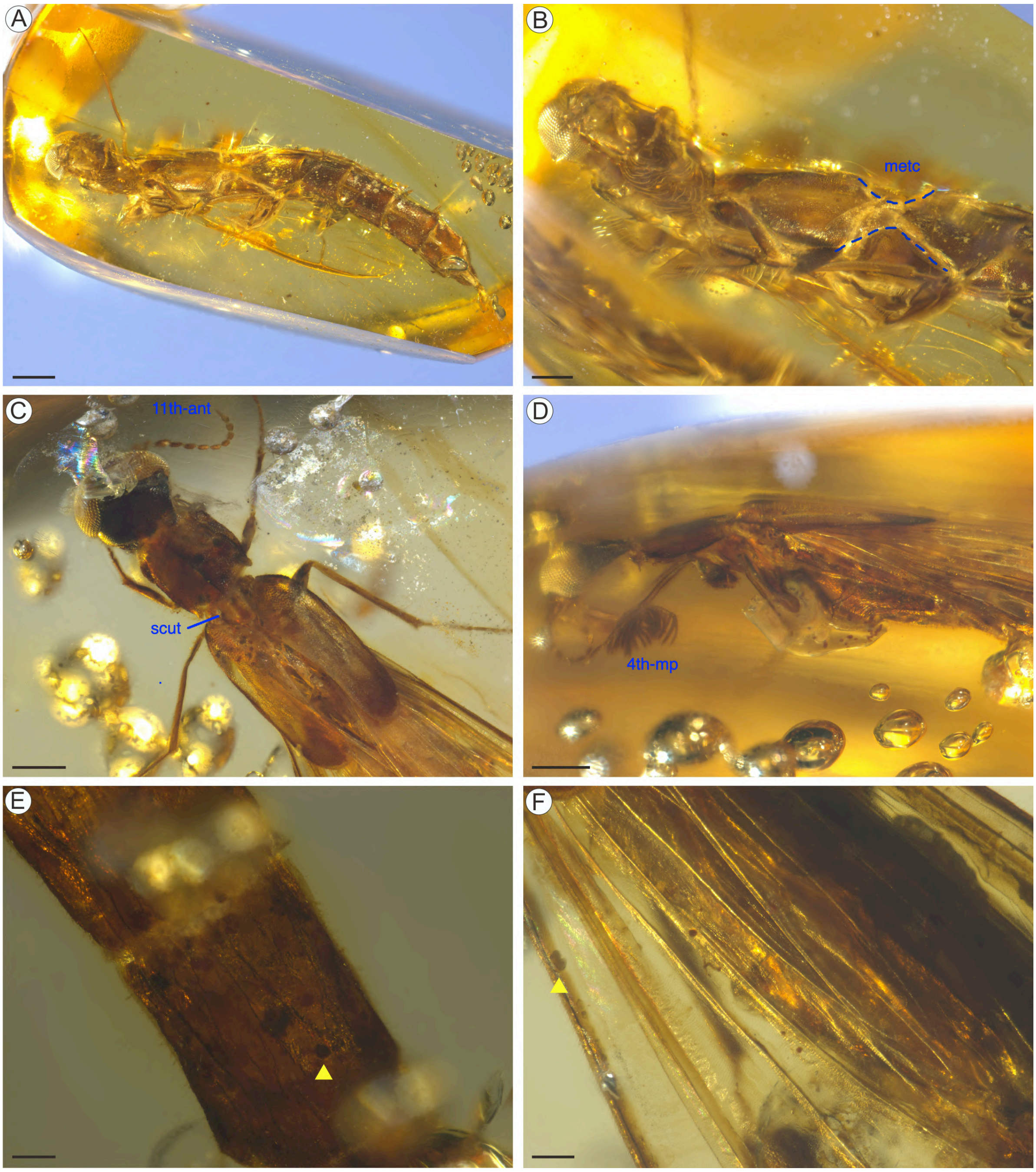

Fig. 22. A-B. *Urtea orientem* sp. nov. Holotype. NIGP004. C-F. *Urtea orientem* sp. nov. Paratype. NIGP005. metc, metacoxa; scut, scutellum; 4th-mp, 4th maxillary palpomere; 11th-ant, 11th antennomere. Suspected fungi spores are marked by yellow arrow. Scale A=1 mm, B-D = 0.5 mm, E and F = 0.2 mm.

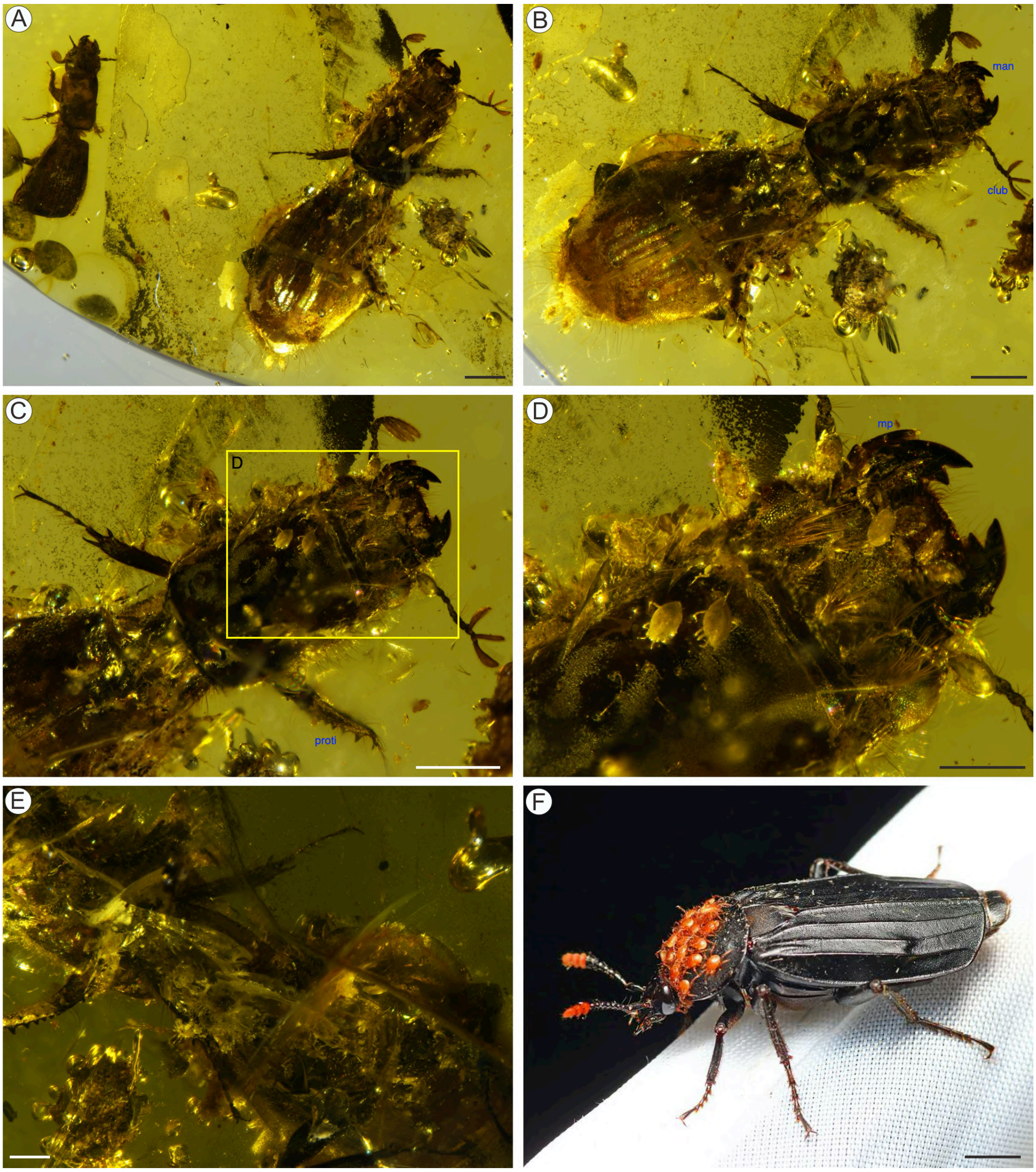

Fig. 23. A-E. *Colorpassalopalpus coloratum* gen. et. sp. nov. with mites associated dorsoventrally. F. Silphidae sp. (extant) present typical mite phoresis scenario. club, antennae club; man, mandibles; mp, maxillary palpi; proti, protibiae. Scale A-C = 1 mm, D and E = 0.5 mm, F = 1 mm.

6. Discussion

6.1 Mordellidae and Mesozoic Tenebrionoidea

Mordellidae is emended into four subfamilies (†, extinct taxa):

· † Praemordellidae,

· † Apotomourinae,

· Mordellinae,

· Ctenidiinae.

Except Ctenidiinae that includes only one species *Ctenidia mordelloides* without fossil records, Praemordellidae, Apotomourinae, Mordellinae have high species diversity and fossil records are abundant.

Praemordellinae was emended as a subfamily of Mordellidae but differs from most families within Tenebrionoidea in the combination of following characters: body convex; head strongly deflexed, not retracted into prothorax; antennae filiform and tarsi simple. It is similar to extant subfamily Mordellinae in having the humpbacked body, strongly deflexed head, filiform antennae and pectinate tarsal claws, but distinctly differs with most of extant mordellids beetle 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 Scraptiidae in having the filiform antennae, and humpbacked body, but differs in having pectinate tarsal claws (simple in Scraptiidae), and penultimate tarsal segments simple (distinctly lobed in Scraptiidae). Furthermore, Praemordellinae is different from Meloidae in having the humpbacked body with middle coxae separated from each other; and from Tetratomidae because the latter has the short, triangular, slightly deflexed head.

Apotomourinae was originally established as the family Apotomouridae (Bao et al., 2018c), now is emended as the subfamily Apotomourinae, including 2 genera 3 species, all from mid-Cretaceous Burmese amber. The identified characteristic of Apotomourinae are coincided with majority of extant mordellids, such as: humpbacked body, wedge-shape, short antennae, elytra not exceed abdomen, hind legs well developed, metacoxa specialized as metacoxal plate. The differential characters of Apotomourinae are: pygidium absence, completely not developed, body with usually with appendix structures (e.g. setae, spines). The non-completely-developed pygidium is also significant in Praemordellinae (Bao et al., 2019c). The Mordellinae species *Mediumiuga sinespinis* Peris, 2013 discovered in Cretaceous Spanish amber preserved with not complete developed pygidium (Peris and Ruzzier, 2013). The Mordellinae species from Cretaceous Burmese amber *Primaevomordellida burmitina* Bao, 2019 preserved with an elongated pygidium as majority of extant mordellids (Bao et al., 2019a). Thus, the development of pygidium has varied degree inside family Mordellidae. It is an apomorphy between subfamilies within Mordellidae, rather apomorphy between Mordellidae and other families. The common but obvious characters of extant Mordellidae (Mordellinae) are diversity of ridges on metatibiae and metatarsi, such as apical-subapical ridges, dorsal-lateral ridges (Jackman and Lu, 2002), which is not common in Apotomourinae. The species of Apotomourinae are with complicated setae and spines structures on legs instead of ridges. *M. sinespinis* Peris, 2013 are preserved with both ridges and advanced setae and spines which indicated *M. sinespinis* could be a transition species between Apotomourinae and Mordellinae. The thorax and coxa structure values importantly in Coleoptera taxonomy (Beutel and Friedrich, 2005); such as the specialized metacoxal plate is an important apomorphy for differentiation of Mordellidae and related groups (e.g. Ripiphoridae, Meloidae) (Hsiao *et al.*, 2017). This structure is clearly examined in Apotomourinae, which made it hard to be established as a single family.

Mordellinae species originated from the Cretaceous and displayed a high diversification. Six tribes, Raynoldsiellini, Conaliini, Mordellini, Mordellistenini, Mediumiugini and Stenaliini are included in subfamily Mordellinae, with a distinctive evolutionary trend of the hind leg structures (Jackman and Lu, 2002; Peris and Ruzzier, 2013). The suspected earliest record *Liaoximordella hongi* Wang, 1993, is a nearly complete, dorsoventrally compressed specimen from the Lower Cretaceous Yixian Formation of western Liaoning, China (Wang, 1993), the correct classification still needs to be discussed and the holotype may be lost. The first true Mordellinae species is *Primaevomordellida burmitina* Bao, 2019, which is described from Cretaceous Burmese amber (Bao et al., 2019a). The filiform antennae, the Mordellistena-type episterna and the elongated pygidium place *P. burmitina* into Mordellinae undoubtedly and the simple hind leg structure without appendix structures assignes it to the basal tribe Raynoldsiellini. Compared to the only extant species *Reynoldsiella parallela* (basal Mordellinae), *P. burmitina* shows similarities to species of tribe Mordellini and Mordellistenini, including the dilatation of antennae starts from the 5th antennomere, which occurs in almost all Mordellini species; the 4th segment of the maxillary palpus is expanded, securiform, which is typical in genus Mordella; the scutellum shape is triangular which is common for most of Mordellini and Mordellistenini species, while for *Reynoldsiella parallela* this is exactly semicircular; the pygidium is obviously elongated, narrow and sharp-pointed, similar with the genus *Mordellapygium* (Franciscolo, 1957; Jackman and Lu, 2002). In Cenozoic, Mordellinae rapidly diversified with the significant development of ridges structure on metatibiae and metatarsi. The most abundant records are from Baltic amber, with in total 6 genera 12 species (Bao et al., 2018b) (Table 4)

Table 4. List of fossil records of Mordellidae found in Baltic amber. The extinct fossil taxa are marked by †.

Species	**Deposit department**
Falsomordellistena eocenica †	ISEA Krakow collection

Glipostena ponomarenkoi †	Klesov locality (SIZC K collection), Rovno Amber
Glipostena sergeli	Hoffeins/Deutsches Entomologisches Institut collection
Mordellistena amplicollis	Hoffeins/Deutsches Entomologisches Institut collection
Mordellistena antiqua	Scheele collection, University of Hamburg
Mordellistena goeckei	Scheele collection, University of Hamburg
Mordellistena korschefskyi	Hoffeins/Deutsches Entomologisches Institut collection
Mordellistena soror	Hoffeins/Deutsches Entomologisches Institut collection
Mordella inclusa	Halle collection
Mordella scheelei	Scheele collection, University of Hamburg
Mordella sp.	Hoffeins/Deutsches Entomologisches Institut collection
Mordellaria friedrichi †	Schmalhausen Institute of Zoology SIZC collection
Tomoxia succinum sp. nov.†	Laboratory-Museum of Amber Inclusions, Gdansk University

The Mesozoic records of Tenebrionoidea are quite abundant, dominated by Burmese amber species and the total species amount increases each year (Batelka et al., 2018). The Early Mesozoic Tenebrionoidea are mainly discovered in Karabastau Formation (Kazakhstan), Daohugou Biota (Inner Mongolia, China) and Yixian Formation (Liaoning, China) (Wang et al., 2013b). The earliest Ripiphoridae *Archaeoripiphorus nuwa* Hsiao, 2017 discovered from Daohugou biota, shows high similarities in body morphology and taphonomy condition with Praemordellinae (Hsiao et al., 2017). *Liaoximordella hongi* Wang, 1993 (Yixian Formation) 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 length; 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 Scraptiidae (Wang, 1993). Evaluating based on the photograph, *L. hongi* does not have an elongated 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. hongi* is distinguished from typical Ripiphoridae in having filiform antennae. These evidences indicated the Ripiphoridae and Mordellidae may share a common origin. Besides, some of the extant Mordellidae species show typical rhipiphoroid traits, e.g. the only one species *Ctenidia mordelloides* in Ctenidiinae and *Ideorhipistena occipitalis* Franciscolo, 2000. Though *I. occipitalis* definitely fits within the ground plan of Mordellidae, it superficially resembles *Rhipistena* Sharp (Rhipiphoridae, subfam. Pelecotominae) probably as a result of convergence (Franciscolo, 2000).

The phylogeny relationships between basal taxa in Tenebrionoidea like Mordellidae, Ripiphoridae has been argued for a long time. Crowson (1955) indicated close relationships between the scraptiids and mordellids, but later he suggested a tenebrionoid lineage consisting of Melandryidae, Mordellidae + Ripiphoridae and Scraptiidae (Crowson, 1966). Lawrence, (1982) suggested a slightly different group, placing Tetratomidae, Melandryidae, Mordellidae and Ripiphoridae into a single assemblage. The sister group relationship Mordellidae + Ripiphoridae is also supported by Franciscolo (2000, 1957) based on the similarities of Ctenidiinae and some Ripiphoridae, but Falin (2003) argued about the monophyly of Ripiphoridae. It was also 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 (Zachary H Falin, 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 Apotomourinae, and thus probably is a stem group including the ancestor of these families (Bao et al., 2019c). However, further elucidation of phylogenetic position of Praemordellinae will require additional study of tenebrionoid phylogeny.

6.2 Beetle-angiosperm associations

Beetles are among the most important pollinators of flowering plants, especially basal angiosperms (Thien et al., 2009), and they are also thought to be among the earliest insect visitors and pollinators of angiosperms (Bernhardt, 2000). Especially five main groups of polyphagan beetle Tenebrionoidea, Scarabaeoidea, Curculionoidea, Cucujoidea and Chrysomeloidea, spanning the key period of angiosperms development in the Jurassic-Cretaceous; the extant species of these five beetle groups are important pollinators of basal angiosperms today, suggesting that their ecological association with angiosperms probably formed as early as Jurassic-Cretaceous, thus provided important clues to explore the coevolutionary processes between beetles and angiosperms (Wang et al., 2013b).

Tenebrionoidea

Tenebrionoidea is morphologically distinguished group. Adult tenebrionoids have an aedeagus of heteromeroid condition, trochanterofemoral articulations oblique, and tarsal formulae of 5-5-4, 4-4-4, 3-4-4 or rarely 3-3-3 (Lawrence et al., 2010).

Mordellidae is among the basal taxa of Tenebrionoidea (see 6.1). The extant Mordellidae body length ranges from 1.5 to 15 mm, can achieve irregular tumbling movements to escape from predator and feeding on flower corolla. The meta-trochanter-femur (thighs and surrounding rings of the third leg pair) has a great capacity of free rotation which increased the jumping ability (Burrows, 2006; Ge et al., 2011; Konez et al., 2008; Reuter, 1995). The elongated pygidium can enhance the ability of keeping balance and self-thumbing. Praemordellinae dated as early as Upper Jurassic, further developed till Early Cretaceous, clearly before the initial rise of angiosperms. The specimens of Praemordellinae are normally over 10 mm, characterized by body flatten, hind leg not well-developed, pygidium absence, indicated a surface vegetation uptake (e.g. fungi, lichen, moss, plant debris). In mid-Cretaceous (Cenomanian) Burmese amber, Mordellidae diversity was high, mainly including species in Apotomourinae and Mordellinae. The body size is usually small, *Multispinus parvus*, 1.2 mm, *Multispinus multispinosus*, 2.2–2.5 mm, *Apotomoura fortiscrura*, 1.5–1.7 mm, *Primaevomordellida burmitina*, 2.9–3.0 mm, *Angimordella burmitina*, 4.2mm, with curve body, very well-developed legs and complex appendix structures (e.g. setae, spines), which indicated the similar fly and jump mechanism as extant mordellids, and implied the potential angiosperms related ecology. The early flower inclusions in Burmese amber are also abundant, usually with well-developed nectar and five petals, the diameter of corolla not exceed 5mm (Liu et al., 2018; Poinar and Chambers, 2005), which matched with the mordellids body size. *Angimordella burmitina* has the typical Mordella-type apical maxillary palpomere, which is enlarged and securiform (Franciscolo, 1957). This specialized modification of the maxillary palpomere has been known to aid collecting and most likely transporting pollen grains (Krenn et al., 2005; Wang et al., 2013b). *A. burmitina* has fine hair; the spacing and height of these hair influence the ability of the hair to carry pollen grains (Santos et al., 2019). Accordingly, the hair on the beetle’s thorax and abdominal sternites are distinctly longer than 30 μm, and the spacing between the hair is consistent with the width of the coexistent pollen grains (~20 µm) and is well-adapted for holding and transporting pollen grains (Santos et al., 2019). It is important to note that *A. burmitina* is covered by abundant tricolpate pollen grains that are mainly distributed on the thorax and abdomen. The tricolpate pollen grains found in Burmese amber exhibit remarkable zoophilous pollination features including their reticulate surface (Fig. 16H) and presence of pollen clumping, thus providing more evidence to support beetle-mediated pollination. The prior earliest direct evidence of insect pollination of angiosperms was reported from several pollen-collection bees from the middle Eocene of Eckfeld and Messel (48 and 45 Ma, respectively) in Germany (Wappler et al., 2015). This finding thereby extends the known geological range of direct evidence of insect pollination of angiosperms by at least 50 million years (Fig. 24).

Fig.24. Ecological reconstruction of *A. burmitina*. These tumbling flower beetles are feeding on eudicot flowers. The color and morphology of flowers are artistic only.

The small flower visiting beetles Anthicidae (common name "ant-like flower beetles") also appeared in the Burmese amber, *Pseudotomoderus burmitina*.

Anthicidae are classified by heads constrict just in front of the pronotum, forming a neck, and the posterior end of the pronotum is usually narrow as well. Legs and antennae are slender, heightening the ant-like appearance, and the body is sparsely covered with setae (Chandler, 2002). Adult beetles are omnivorous, are known to consume small arthropods, pollen, fungi, and whatever else they can find. Larvae are either omnivorous, predators, or fungus-eaters (Telnov, 2010). The extant *Pseudotomoderus* species are usually common ground dwellers, live in litter and rotten wood (Telnov and Ghahari, 2018). However, the relationship between subfamily Tomoderinae and Lemodinae are ambiguous. *Pseudotomoderus burmitina* preserved primitive characters which indicated its basal phylogeny statue. The setae and maxillary palpi of *P. burmitina* are similar to taxa that are closely related to the pollen feeding group.

Curculionoidea

Beetles belonging to the superfamily Curculionoidea are commonly called weevils, usually small (less than 6 mm in length), and herbivorous, some species are serious pests of agricultural crops. They are easily recognizable by a rostrum or snout projecting forward and downward from the head, with mandibles or jaws positioned at the rostral tip (Thompson, 1992). The oldest weevils, belonging to the Nemonychidae, occur in the Upper Jurassic of Karabastau formation, Central Asia (Oberprieler et al., 2007). Abundant weevils were recorded from the Lower Cretaceous of Russia, Spain, China and Brazil (Davis et al., 2013; Soriano et al., 2006).

Cucujoidea

Cucujoidea includes some fungus beetles and a diversity of lineages of "bark beetles" unrelated to the "true" bark beetles (Scolytinae), which are weevils (superfamily Curculionoidea). Early Cucujoidea emerged from the Middle Jurassic of

China represented the enigmatic family Boganiidae, currently known from Gondwanan localities in South Africa, Australia and New Caledonia, suggested to be a potential cycads pollinator (Liu et al., 2018). The Cretaceous Cucujoidea shows high diversity, especially from the amber fossils. The Kateretidae are a small family of beetles within the Cucujoidea with about 95 species described in 14 genera (Cline and Audisio, 2010). Adult Kateretidae feed on angiosperm flowers and their shortened elytra which expose some abdominal segments, so that Kateretidae are commonly termed the short-winged flower beetles (Jelínek and Cline, 2011). The Kateretidae records in Cretaceous are quite abundant. *Lebanoretes andelmani* Kirejtshuk and Azar, 2008 is the oldest species from Early Cretaceous Lebanese amber (Kirejtshuk and Azar, 2008), *Furcalabratum burmanicum* Poinar and Brown, 2018, *Eoceniretes antiquus* Peris, 2019, *Cretaretes minimus* Peris 2019 are from the mid-Cretaceous Kachin amber (Peris and Jelínek, 2020; Poinar and Brown, 2018). *Cretaretes minimus* is described based on 41 fossil beetle specimens together in one piece of fossil resin and *Eoceniretes antiquus* is also described based on 41 fossil beetle specimens together in another piece of amber sample, shows early eusociality, which is also common for some extant Kateretidae (Cline and Audisio, 2010). *Magnipolliniretes burmites* was newly described from Burmese amber, shows significantly bigger body size than other Burmese amber species. Numerous pollen grains associate with the *M. burmites,* accumulate on dorsal elytra and mouthpart. The pollen grains are suspected to belong to early nymphaealean plants: monosulcate, colpi long and wide, exine moderately thick, ornamentation very simple. The *M. burmites* maxilla with galea and lacinia long, narrow, curved inward near distal end; lacinia with pointed apex and group of setae on outer edge prior to apex, terminal palpomere securiform, wider than preceding ones, narrowly truncate apically with sparse pubescence. Pollen grains particularly accumulated around the mouthpart, indicated a food up taking scenario. However, the monosulcate pollen with very simple ornamentation are not the typical zoophilous pollination pollen (Hu et al., 2008). The nymphaealean plants are normally water living angiosperms, the taphonomical condition are particular and different from terrestrial taphonomy (Bao et al., 2018a). The resin embedding process of this specimens should fit in a very particular situation: fast and big quantity resin falling; very calm transportation and second embedding procedure (Bao et al., 2018a).

Scarabaeoidea and Chrysomeloidea

Scarabaeoidea (scarab beetles) is a cosmopolitan monophyletic superfamily comprising around 35,000 described species (Grebennikov and Scholtz, 2004). A recent molecular analysis suggests that most scarab families may have originated in the Cretaceous (McKenna and Farrell, 2009), significantly before the mid-Cretaceous angiosperm radiation, probably during the Middle–Late Jurassic. Almost all species of extant Chrysomeloidea are phytophagous, and most phytophagous Chrysomeloidea feed on angiosperms (Farrell et al., 1998). Their great diversity has been commonly attributed to co-radiation with early angiosperms (Farrell and Sequeira, 2004; Farrell et al., 1998; Reid, 2000; Wilf et al., 2000). The Chrysomeloidea diversified around this time, feeding on a wide array of plant hosts from cycads and conifers to angiosperms. Based on the observations of pollination systems of the most basal angiosperms, (ANITA group), two families, Scarabaeidae and Chrysomelidae, are pollinators of extant Nymphaeaceae (Bernhardt, 2000; Bernhardt et al., 2003). However, there is still lack of direct evidence to prove their Mesozoic origin of angiosperm mutualism.

6.3 Beetle-gymnosperm association

Only two fossil species of beetles have been recorded as hypothetical gymnosperm pollinators in the fossil record; both are from the Cretaceous ambers (Cai et al., 2018; Peris et al., 2017). *Cretoparacucujus cycadophilus* Cai, 2018 from family Boganiidae, recently described from Myanmar amber alongside cycad pollen. Cycads, unlike modern wind-pollinated gymnosperm conifers and Ginkgo, are unusually pollinated by insects. The extant species of family Boganiidae includes pollinator species for both angiosperms and gymnosperms (Cai et al., 2018; Escalona et al., 2015). *C. cycadophilus* is supposed to prove the early cycad pollination behavior found in Boganiidae at least since the Cretaceous. *Darwinylus marcosi* Peris, 2017 of Oedemeridae described in association with gymnosperm-like pollen grains from Albian Spanish amber. Oedemeridae larvae are currently found in decaying wood, but adults interact almost exclusively with flowering plants (Abtahi et al., 2012; Carrel et al., 1986). The *D. marcosi* hypothetically indicates a gymnosperm-to-angiosperm host transition for this beetle family, which is a new evolutionary pattern for ancient pollination (Peris et al., 2017). However, hypotheses based on these two specimens seem not to be enough robust. Firstly, the pollen grain association are not directly attached to the beetle body which indicates that the pollen grains are higly likely imbedded in the resin in accident, especially for *C. cycadophilus*. Secondly, the logical reasoning about both *C. cycadophilus* and *D. marcosi* ecology are flawed. A modem descendant Boganiidae does not fully support the paleoecology of *C. cycadophilus*. The pollen grains associated with *D. marcosi* not necessarily belong to gymnosperms, which may mislead the conclusion about their pollination mode.

Until now, direct evidence of other Cretaceous insect pollination supports insect-gymnosperm pollination, such as that involving thrips (Peñalver et al., 2012), true flies (Peñalver et al., 2015), and scorpionflies (Lin et al., 2019). These insect-gymnosperm mutualisms achieved through liquid sucking feeding strategy with specialized long-proboscid mouthparts. Recently, the early evolution of long-proboscid mouthparts insect has been outlined by the detail study of family Aneuretopsychidae whose mouthparts are vital to deciphering the early evolution of Mesopsychoidea and putatively the origin of fleas (Siphonaptera) (Zhao et al., 2020). The phylogenetic analysis provides robust evidence for the debated monophyly of

Mesopsychoidea that suggested the long-proboscid condition has most likely evolved once in Mesopsychoidea, independently from fleas, and further revealed the variety and complexity of mid-Cretaceous pollinating insects (Zhao et al., 2020).

6.4 Other beetle ecology in Cretaceous amber (fern association, scavenger, fungivorous, wood-borer, algae eater)

Ferns (Polypodiopsida) are an important member of Earth's vascular plants (Christenhusz and Byng, 2016). Spores of polypod ferns often form sporangia with enclosures. When met with the perfect situation, spores escape from the sporangia and disperse by wind or water (Rost et al., 2006). The spores in the amber specimen NIGP001 compactly preserved near the tenebrionid beetle without enclosure, support *in-situ* preservation rather than random embedding (Dilcher, 1979; Hu et al., 2008). The extant Tenebrionidae are very diverse with various habitats, including under stone environments, leaf litter, dry rotted wood, tree trunks and in soil, feeding on living plant tissue, dead plant tissue, ferns, lichens, fungi and flowers (Watt, 1992). The body of *Praezolodinus pilosus* is elongated and completely covered with different lengths of pubescence or setae dorsally and ventrally. The mouthparts are specialized, with mandibular mola with fine and long pubescence and a slightly enlarged securiform apical maxillary palpomere, which probably increased the chance to detect and collect spores or plant fragments (Labandeira, 2013b, 1997). Extant leiodid beetles included Cholevinae are mostly scavengers, commonly seen in forest litter, soil and other environments with availability of humus, carrion, dung and similar decaying organic matter (Newton, 2016). This scenario could be interpreted as an indirect support for the taphonomic environment. The combination of morphological analyses of beetles and fern spores provide evidence to support the scenario of bottom forest environment. The feeding or pollination relationship between *P. pilosus* and Polypodicaeae are not conclusive, because detailed gut contents analysis or direct feeding evidence are missing (Bao et al., 2019b; Labandeira, 2013c). However, this specimen provides a rare opportunity to understand the lower layer fern habitat in Cretaceous Burmese amber forest based on the association of herbivorous beetles, scavengers and fern remains.

In general, ferns are more widespread than angiosperms (Smith, 1972) and most of the extant Polypodiales evolved concurrently with angiosperms in the Cretaceous (Schneider et al., 2004). Therefore, both non-phytophagous and phytophagous insects would have had as much evolutionary time available to switch from other food sources to ferns or to angiosperms (Hendrix, 1980). However, the evidence of insect-fern interaction in the Mesozoic is truly scarce. One influential factor could be the morphological complexity of the host plant, as ferns lack complex reproductive structures, which has a huge impact on their plant architecture and causes reduction of biomass (Lawton, 1983). The second factor could be the bio-chemical composition. Compared to angiosperms, ferns lack alkaloids and biflavonyl (Burger, 1971; Markham, 2013), but contain tannins, ecdysones, thiaminase factors and cyanogenic glycosides (Lawton, 1976; Srivastava et al., 1997), which increase self-defensive effects and forced potential insect groups to change host plants passively.

Based on the Mesozoic beetle fossil, mainly from amber inclusions, saproxylicity was the most common feeding strategy for these fossil beetles. More specifically, fungivorous species appear to dominate (Peris and Rust, 2019). The body size of saproxylic beetle from Cretaceous amber is normally small, probably is specific for fungivorous diet. Based on the Cretaceous Staphylinidae species, Cai et al., (2017) pointed out the mouthparts of early oxyporines, including enlarged mandibles and greatly enlarged apical labial palpomeres with dense specialized sensory organs, match those of modern taxa and suggest that they had a mushroom feeding biology. Ambrosia beetles, wood-boring beetles which live in nutritional mutualism with ambrosia fungi, commonly include species of the weevil subfamilies Platypodinae and Scolytinae (Hulcr and Stelinski, 2017). However, mutualistic symbiosis with fungi or yeast-bacteria complex have been also observed in Lymexylidae (Batra, 1967; Francke-Grosmann, 1967; Lawrence, 2010; Wheeler, 1986). Adult Lymexylidae live free only for some days; they are found in decaying wood, under bark, or on tree trunks, while larvae are wood-borers (Young, 2002). Egg laying takes place on the outside of suitable host trees, in bark crevices, or under bark scales by means of a long ovipositor (Francke-Grosmann, 1967). Once the eggs are deposited, females deposit with them a sticky matrix with the fungal spores carrying in mycangia near the end of the ovipositor (Young, 2002). First instar larvae bore usually straight into the wood, but can also form false surface galleries in special cases. Larvae carry the fungal spores into the wood on their bodies and ambrosia fungi grew in the galleries; larvae apparently feed primarily on the fungi. *Urtea orientem* is described from Burmese amber with adult holotype NIGP004 and paratype NIGP005. The morphology of *U. orientem* are similar to the extant relative in eastern Europe, which indicated a wood-boring habitat. The suspected fungi spores are preserved on the wings and abdomen of paratype NIGP005. This could indicate Lymexylidae developed the similar mutualistic symbiosis with fungi at least from mid-Cretaceous.

6.5 The tropical amber forest ecosystem in Cretaceous

Due to the recent research, the Burmese amber forest has been thought of as the most species rich tropical-subtropical near-shore rainforest in the Cretaceous, dominated by Araucaria trees (Ross et al., 2010; Yu et al., 2019). The modern forest normally has four levels horizonal combination, from down to up: surface nutrition, herbs, short shrubs, high wooden trees (Eduard Linsenmair et al., 2013). The Burmese amber forest supposed to have the prototype of this mode. The surface nutrition included moss, lichens, plant debris, associate with scavengers and humus uptakes. Ferns and short herbaceous angiosperms compose the second level. However, the biomass of herbaceous angiosperms is yet not competitive with ferns (Augusto et al., 2014; Schmidt et al., 2016; Smith, 1972). The third level vegetation may be ambiguous, as the development of angiosperm height is hard to estimate. The high wooden trees are dominated by Araucariaceae, which is also the main resin producer. Whereas, it is hard to deny the high wooden angiosperm tree also had developed during this period (Augusto et al., 2014). The inclusions from Burmese amber are not only terrestrial, but marine ammonite (Yu et al., 2019), water ostracod (Xing et al., 2018), which indicated forests are extended close to the sea shore and have considerable salt and alkali resistance.

Based on the research of New Jersey amber using ^{13}C- enriched carbon isotope signatures, Mckellar et al., (2011) pointed the wood-boring insect attack may enhanced production of resin. However, this hypothesis is not strongly supported by Burmese amber wood-boring beetles. The wood-borer beetles in Burmese amber should not be the selective force driving the evolution of resin production during the Cretaceous, as many species in the family may feed also on decaying wood and fungi without affecting living trees (Peris et al., 2019).

The complexity of insect behaviour is another aspect to show the advancement of Cretaceous amber forest. A species of extinct beetle family Passalopalpidae Boucher, 2016, *Colorpassalopalpus coloratum*, is preserved with numerous mites on ventral and dorsal body, as an early evidence of phoresis. Mites or ticks use phoresis as a strategy for dispersal, which means mite (the phoretic) attaches itself to another animal (the host) solely for the purpose of traveling. Phoresis is regarded as an important adaption for avoiding inbreeding and escaping from habitat deterioration. The phoretic mites are thought to be a transition mode between free living and complete parasite, with high diversity in morphology, behaviour, phoresis season and host selection, which indicated the diversity of their final host choice. Indeed, the possible host, dinosaur and early bird, discovered from Burmese amber supported the miniaturization which benefit for increasing mobility and expantion of territory (Peñalver et al., 2017; Xing et al., 2017, 2020). Passalopalpidae and their extant relative Passalidae are sister group, indicating a high degree of sociality (Boucher et al., 2016). The earliest eusociality of cockroaches and Staphylinidae beetle is conserved in termites. The complex adaptive mechanisms permit these animals to integrate into societies and to exploit their controlled physical conditions and plentiful resources, as well as to garner protection inside termite nests (Cai et al., 2017a; Vršanský et al., 2019a, 2019b).

Based on the flora characteristics, Poinar and Buckley (2008) pointed out the ecological similarity between the Burmese amber forest and the Waipoua kauri forest in Northern New Zealand. The Waipoua forest is the only virgin Agathis (Araucariaceae) forest in the world today and comprises a mixed dense ecosystem of flowering plants, ferns, lycopods and mosses (McGregor, 1948). *Praezolodinus pilosus* is assigned to subfamily Zolodininae, which is currently only distributed in New Zealand (Watt, 1992, 1974), Passalidae are currently distributed in Australia (Ulyshen, 2018). This could be an additional support for such similarity from an entomological perspective. However, to accurately reconstruct the Cenomanian amber forest palaeoecology, there needs to be an integration of terrestrial and oceanic influence, paleoclimatologic and atmospheric factors, and deep research of flora and fauna inclusion. Thus, further work is awaiting.

7. Conclusions

New studies presented in this thesis showed a remarkable feeding strategy and ecology diversity of Mesozoic beetles. Fourteen species from 7 families were described from Karabastau Formation, Daohugou biota, Burmese amber and Baltic amber, range from Early Jurassic to Eocene. The mechanism of interaction between beetles and vegetation environment is discussed. Based on the continuous fossil records of family Mordellidae, four subfamilies were emended, which indicated the early evolution trend of a typical flower beetle ecology. Insect pollination of flowering plants (angiosperms) is responsible for the majority of the world's flowering plant diversity and is key to the Cretaceous radiation of angiosperms. *Angimordella burmitina* Bao, 2019 and the associated tricolpate pollens provided direct evidence of insect pollination of Cretaceous angiosperms, extending the range of insect-angiosperm pollination association by at least 50 million years indicating that specialized insect pollination modes were present in eudicots at least 99 million years ago. The great angiosperm radiation in mid-Cretaceous acts as dynamic for earth surface vegetation replacement. By this time, nutrition groups as gymnosperms, ferns, are also changed relatively, which also imply the associated beetle taxa. With more and more flora and fauna inclusions discovered from Burmese amber, it is possible to draw a big picture of the Burmese amber forest. We can generally understand the forest vertical eco-components and discuss about the inner relations of the ecosystem. The extant Waipoua forest could be the ecosystem reference in reality. However, we must be aware that it is easy to underestimate the complexity of ecosystem, when performing comparative study of paleoecology in the future.

8. Outlook

8.1 Taxonomy and phylogeny study

Taking in consideration only currently found Mesozoic fossil Lagerstätte, still enormous amout of work remains about fauna and flora taxonomy and phylogeny. For example, there only about 20% insect from Burmese amber were described so far (personal communication with Bo Wang). The basic taxonomy and phylogeny work are still urgently required. Especially for the mid-Cretaceous fossil deposits, the entomology records showed great increasing during the angiosperm radiation. Surely, the co-evolution between insect and plant needs to be further investigated.

8.2 Detail study of geological background of amber deposit

The geological setting of amber deposit has been questioned for decades. The correct knowledge of geological background of amber deposit can help understand the paleotopography and taphonomic process, further indicate more information about paleoclimate and environment change. The embedding environment of amber is different from a normal sedimented process. In order to accurately analyse the chronology age of amber, it would be best if isotope method was applied. However, this require particular surrounding rock matrix, consisting igneous rock (e.g. tuff), which is not common for all amber Lagerstätte.

8.3 Cretaceous macroecology study

During mid-Cretaceous, angiosperm fast radiation led to their domination and replacement of gymnosperm in earth vegetation. However, based on the resin chemical analysis of Tilin amber (uppermost Campanian ~72.1 Ma, western Myanmar), gymnosperms still dominated the Late Cretaceous forest wood flora. Besides, the fern diversity did not decrease by the time angiosperm replace their niche. The change of other nutrition (moss, fungi, lichen) is still under investigation. The component difference between Cretaceous amber forest and non-amber forest are also obvious. In the future, a comprehensive study about the macroecology of Cretaceous forest as a whole may answer the reason of each partially eco-change. Necessarily, the extant ecosystem should act as a reference.

8.4 The comparative study Cretaceous island-continental environments

Taking Burmese amber as an expample, we believe it is a Cretaceous sea-shore tropical forest, indicated a near equatorial island environments. In contrast, the Jehol biota, (e.g. Yixian Formation) presented an inland lagoon sediment environment.

Based on this, a further comparative study of Cretaceous island-continental environments could be proceeded, which should be helpful to comprehensively understand the Middle Mesozoic (Jurassic-Cretaceous) paleoclimate.

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Declaration about personal contributions to the papers included in this thesis

1. Tong Bao. 2020. A new small-bodied Mordellid beetle (Coleoptera: Mordellidae) from mid-Cretaceous Burmese amber and taxonomic revision. Acta Palaeontologica Sinica, 59(1). doi:10.19800/j.cnki.aps.2020.01.13
Personal contribution ca. 100 %.
T.B. designed research; T.B. performed research; T.B. analyzed data; T.B. wrote the paper; T.B. collected and prepared the fossil material.

2. Tong Bao, Bo Wang, Jianguo Li, and David Dilcher, 2019, Pollination of Cretaceous flowers. Proc. Natl. Acad. Sci. U. S. A., 116 (49) 24707-24711. doi:10.1073/pnas.1916186116.
Personal contribution ca. 70 %.
B.W. and D.D. designed research; T.B., B.W., J.L., and D.D. performed research; B.W. contributed new reagents/analytic tools; T.B., B.W., and D.D. analyzed data; T.B., B.W., J.L., and D.D. wrote the paper; T.B. and B.W. collected and prepared the fossil material.

3. Tong Bao, Xuesong Zhang, Katarzyna S. Walczyńska, Bo Wang, and Jes Rust. 2019. Earliest mordellid- like beetles from the Jurassic of Kazakhstan and China (Coleoptera: Tenebrionoidea). Proceedings of the Geologists' Association 130: 247–256. doi:10.1016/j.pgeola.2019.02.002.
Personal contribution ca. 80 %.
T.B., X.Z., and B.W. designed research; T.B., K.W., B.W., and J.R. performed research; T.B. and K.W. analyzed data; T.B., K.W., and B.W. wrote the paper; T.B., X.Z., and B.W. collected and prepared the fossil material.

4. Tong Bao, Katarzyna S. Walczyńska, Samantha Moody, Bo Wang, and Jes Rust. 2019. The first true Mordellidae (Coleoptera: Tenebrionoidea) from lower

Cenomanian amber of Myanmar. Cretaceous Research 93: 60–65.
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Personal contribution ca. 80 %.
T.B. and B.W. designed research; T.B., K.W., B.W., and J.R. performed research; T.B., and K.W. analyzed data; T.B., K.W., S.M., and B.W. wrote the paper; T.B. and B.W. collected and prepared the fossil material.

5. Tong Bao, Katarzyna Walczyńska, Samantha Moody, Bo Wang and Jes Rust, 2018. New family Apotomouridae fam. nov. (Coleoptera: Tenebrionoidea) from lower Cenomanian amber of Myanmar. Cretaceous Research，91: 14-19.
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Personal contribution ca. 80 %.
T.B. and B.W. designed research; T.B., K.W., B.W., and J.R. performed research; T.B., and K.W. analyzed data; T.B., K.W., S.M., and B.W. wrote the paper; T.B. and B.W. collected and prepared the fossil material.

6. Tong Bao, Katarzyna S Walczyńska, Błażej Bojarski, Ed Jarzembowski, Bo Wang, and Jes Rust. 2018. A new species of tumbling flower beetle (Coleoptera: Mordellidae) from Baltic amber. PalZ 1: 3. doi:10.1007/s12542-018-0434
Personal contribution ca. 80 %.
T.B. designed research; T.B., K.W., B.B., E.J., B.W., and J.R. performed research; T.B., K.W., and B.B. analyzed data; T.B., K.W., B.B., and E.J. wrote the paper; T.B. and B.W. collected and prepared the fossil material.

7. David Peris, Tong Bao, Bastian Mähler and Keith Philips. 2019. A morphologically unique species of Ptinidae (Coleoptera) and the first found in mid-Cretaceous Kachin amber (Myanmar). Journal of Systematic Palaeontology.
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Personal contribution ca. 10 %.

D.P. designed research; D.P., T.B., B.M., and K.P. performed research; D.P. analyzed data; D.P., T.B., B.M., and K.P. wrote the paper; D.P., and T.B. collected and prepared the fossil material.

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·研究论文·

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白垩纪缅甸琥珀中小型花蚤一新种(鞘翅目：花蚤科)及对花蚤科的分类学修订*

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提要　根据产自缅甸北部白垩纪中期克钦琥珀中的一块小型花蚤化石标本，建立 1 新种——小多刺花蚤(*Multispinus parvus* sp. nov.)，归于花蚤科(Mordellidae)。同时，对缅甸琥珀中已发现的花蚤和泛花蚤进行了重新观察和研究，重点分析了其形态学特征并认真考虑了相关分类学依据，将短尾花蚤科(Apotomouridae)修订为花蚤科之下的短尾花蚤亚科(Mordellidae: Apotomourinae)。短尾花蚤中普遍存在的臀锥完全不发育，不可作为区分于花蚤科的衍征。白垩纪中期琥珀中发现的花蚤化石类群体型均小，这也许与白垩纪中期生态环境和栖息地被子植物花朵形态有关。

关键词　甲虫　花蚤科　缅甸琥珀　白垩纪　分类学　古生态

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A NEW SMALL-BODIED MORDELLID BEETLE (COLEOPTERA: MORDELLIDAE) FROM MID-CRETACEOUS BURMESE AMBER AND TAXONOMIC REVISION

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Abstract A new small-bodied beetle, *Multispinus parvus* sp. nov., is described from the mid-Cretaceous Burmese amber and assigned to Mordellidae (Coleoptera: Tenebrionoidea). Based on a careful re-examination of the Mordellidae and mordellid-like beetles from the Burmese amber and analysis of their morphological characters, the family Apotomouridae is reduced herein to a subfamily of Mordellidae as Apotomourinae. The absence of a pygidium in Apotomourinae cannot be regarded as a synapomorphy. All known mordellids found in the mid-Cretaceous ambers are all small in size, which may be related to the mid-Cretaceous ecological environment and the early angiosperm flower morphology in their habitat.

SYSTEMATIC PALAEONTOLOGY

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Superfamily Tenebrionoidea Latreille, 1802
Family Mordellidae Latreille, 1802
Subfamily Apotomourinae subfam. nov.
【Apotomouridae】Bao, 2018, Cretaceous Research, 91: 14–19

***Multispinus* Bao, 2018**
Type species *Multispinus multispinosus* Bao, 2018
Emended diagnosis Body small, length 1.2–2.5 mm, wedge-shaped; color from dark brown to black. Head strongly declined. Pygidium completely reduced. Fore- and middle legs obviously shorter than hind legs. Metafemora well developed, strongly enlarged. Comb-like setae widely preserved on the posterior metatibiae. Sclerotic spines preserved in the ventral metatibiae and metatarsi. Claws small, b-cleft.

***Multispinus parvus* sp. nov.**
urn:lsid:zoobank.org:act:8DCC3478-F601-47A7-A88A-8B920129A330
(Fig. 2)
Etymology *parvus,* Latin, small.
Differential diagnosis *Multispinus parvus* sp. nov. different from *Multispinus multispinosus* by: (1) body much smaller, (2) pronotum shape special, anterior rounded, posterior wide, with two bends; (3) 6 pairs of short spines preserved in ventral metatibiae.
Description Holotype NIGP171284, body very small, length 1.21 mm, wedge-shape, widest in posterior pronotum, body slightly narrower anterior and posterior; laterally curved, C-shape. Body colour from dark brown to black, without patterns.

Head small, rounded triangular in frontal view; narrowest posterior, as wide as anterior pronotum; hypognathous. Eyes lateral, large, well-developed, shape oval, finely faceted, interfacial setae well developed. Antennae short, less than half body length; serrate-filiform. Clypeus distinct; maxillary palpi moderated with four palpomeres, apical palpomere expanded, securiform.

Pronotum length 0.14 mm, widest at the base 0.44 mm, anterior rounded, posterior wide with two bends. Scutellum shield length 0.07 mm, width 0.09 mm, triangular. Elytra not exceed abdomen, length 1.12 mm, widest at anterior 0.42, surface almost smooth, with very fine setae; hind wing transparent, hided under elytra.

Metaepistena long, irregular rectangular, preserved with fine setae. Metacoxae enlarged formed metacoxal plate; trochanter oblique. Metafemora enlarged, numerous tiny spines preserved posterior. Metatibiae slim, long; comb-like setae preserved posterior. Tarsi form 5-5-4, slim. Metatibiae and metatarsi without any ridge. Ventral metatibiae preserved 6 pairs sclerotic tiny spines. Ventral metatarsus I preserved long and short fine spines; ventral metatarsus II-IV preserved short setae; comb-like setae preserved in each posterior metatarsus. Length metatarsi: 0.19 mm, 0.10 mm, 0.07 mm, 0.10 mm. Claw simple, b-cleft.

Abdomen with 1-5 five sterna, narrowed posteriorly, surface micro-rugose, length 0.11 mm, 0.08 mm, 0.07 mm, 0.05 mm, 0.15 mm, very fine setae preserved between sternites. Pygidium distinct, aedeagus partially exposed.

Key words Beetle, Mordellidae, Burmese amber, Cretaceous, taxonomy, palaeoecology

1 前言

花蚤科(Mordellidae)和短尾花蚤科(Apotomouridae)均为拟步甲总科(Tenebrionoidea)的基部类群(Hunt *et al*., 2007; McKenna and Farrell, 2009; Bao *et al*., 2018c)。花蚤，俗称针尾甲虫，绝大多数拥有完全发育的臀锥，故此得名(Jackman and Lu, 2002)；花蚤科目前含三个亚科Mordellinae, Ctenidiinae 和 Praemordellinae，其中先花蚤亚科(Praemordellinae)仅含化石种(Bao *et al*., 2019b)，而前两个亚科现生种分布广泛。花蚤科的最早化石记录为侏罗纪中晚期道虎沟生物群中的侏罗五化甲 *Wuhua jurassica* Wang, 2011，归于先花蚤亚科(Wang and Zhang, 2011)。该科在白垩纪缅甸琥珀

(Bao *et al*., 2019a)、西班牙琥珀(Peris and Ruzzier, 2013)和新泽西琥珀(Grimaldi and Engel, 2005)中均有发现，新生代波罗的海琥珀中也有大量化石种发现(Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013; Bao *et al*., 2018b)。

短尾花蚤科与花蚤科、大花蚤科形态上具有高度相似之处，显示出它们之间存在密切关系(Bao *et al*., 2018c)。但值得注意的是，短尾花蚤的臀锥完全不发育，使短尾花蚤在形态上与绝大多数花蚤科个体明显不同。而随着缅甸琥珀和其他产地中更多花蚤化石的发现，短尾花蚤的先前分类暴露出一些问题，对该类化石及其相近类群的形态学再分析和分类学修订越来越有必要。

在本次研究过程中，笔者对现有泛花蚤类化石进行了再一次细致观察分析，推敲各个形态特征的相对关系，对已有短尾花蚤的分类进行了修订，并讨论了其个体发生和生态学意义。

2 地质背景和材料

本次研究材料为缅甸硬琥珀(“burmite”，又称克钦琥珀)，产自缅甸北部克钦邦胡康河谷达奈镇附近[Zheng 等(2018)报道了缅甸中部新发现琥珀矿址(“提林琥珀”)，埋藏年代距今约 72 Ma，埋藏环境和琥珀性质与本文所讨论的材料不同]，保存于中国科学院南京地质古生物研究所。关于缅甸琥珀的最早文字记录可见《汉纪》(公元 205 年—265 年)(张一骋等, 2017)，最早的疑似缅甸琥珀实物标本出土于江西南昌海昏侯墓(约公元前 59 年)(Yang *et al*., 2017)。千百年来，缅甸琥珀在当地经济、医疗和艺术等方面扮演了重要角色。缅甸琥珀埋藏于白垩纪复理石沉积单元中，含灰绿色至蓝绿色的细粒沉积岩，具有细小的火山碎屑(Shi *et al*., 2012)。根据 U-Pb 锆石测年分析，缅甸琥珀的埋藏年代为晚白垩世早塞诺曼期(Cenomanian)，距今约 99 Ma (Shi *et al*., 2012)。然而，琥珀表面的磨圆程度和内含物中的海洋生物，表明琥珀被埋入围岩基质前有一系列再作用过程，从而揭示了缅甸琥珀的实际年代可能更老(Bao *et al*., 2018a)。

3 研究方法

研究所用琥珀标本在中国科学院南京地质古生物研究所琥珀实验室进行处理并拍照。切割和打磨使用德国产 Buehler ISOMET 系列设备，显微摄影应用配备了高清相机的蔡司体式显微镜(Zeiss Stereo Discovery AXIO Zoom V16)，图片叠加应用软件 Helicon Focus，文中所用地图由软件 R studio-2017 及其地图软件包生成，后期图像处理运用软件 Adobe Photoshop CS4。

文中所用术语和名称遵循相关文献(见 Bouchard *et al*., 2005, 2011；刘名, 2007)。本研究描述的标本已经在 ZooBank 中注册，具有唯一 ZooBank 登记码(LSID urn:lsid:zoobank.org:pub:AD5E35A2-7F2D-4ACB-BD86-D27D9BD1918D)。新建种的 LSID 编号将在系统古生物学部分体现。

4 系统古生物学

昆虫纲 Insecta Linnaeus, 1758
鞘翅目 Coleoptera Linnaeus, 1758
拟步甲总科 Tenebrionoidea Latreille, 1802
花蚤科 Mordellidae Latreille, 1802
短尾花蚤亚科(新亚科) Apotomourinae subfam. nov.

2018 Apotomouridae, Bao, Cretaceous Research, 91: 14－19.

亚科特征(修订) 虫体小，楔形。身体前部可伸缩，身体常呈 C 型；鞘翅短；臀椎完全消失；腹部 5 节，1 至 4 节末端(两腹节交界处)有一列刚毛；跗节 5-5-4 型。触角短，不超过体长一半，11 节，丝状。下颚须 4 节，末节膨大。后足发育完全，基节特化为基节板，股节粗壮，胫节和跗节附有硬化短刺。头部、前胸背板、鞘翅、腹节和腿的表面均有细短刚毛。爪小，简单，二裂。

多刺花蚤属 *Multispinus* Bao, 2018

模式种 多刺花蚤 *Multispinus multispinosus* Bao, 2018

属征(修订) 虫体小，体长 1.2—2.5 mm；流线型；深棕色至黑色。头极向后下收缩。臀锥完全

不发育。前足和中足明显比后足短，纤细。后足股节强烈膨大，胫节末端有梳状端距；胫节和跗节内侧有硬化刺(刚毛)；爪二裂。

小多刺花蚤(新种)　*Multispinus parvus* sp. nov.

urn:lsid:zoobank.org:act:8DCC3478-F601- 47A7- A88A-8B920129A330

(图 1)

词源　*parvus*，拉丁语，意为“小”。

正模　NIGP171284，雄性，保存完整，头部上方和口器处各有一气泡。

种征　虫体极小。触角短，不超过体长 1/2，各节长度类似。前胸背板前缘与侧缘形成半圆，后缘宽二弯状。颈极短，不可见。胫节内侧有六对硬质小刺，呈 V 型。

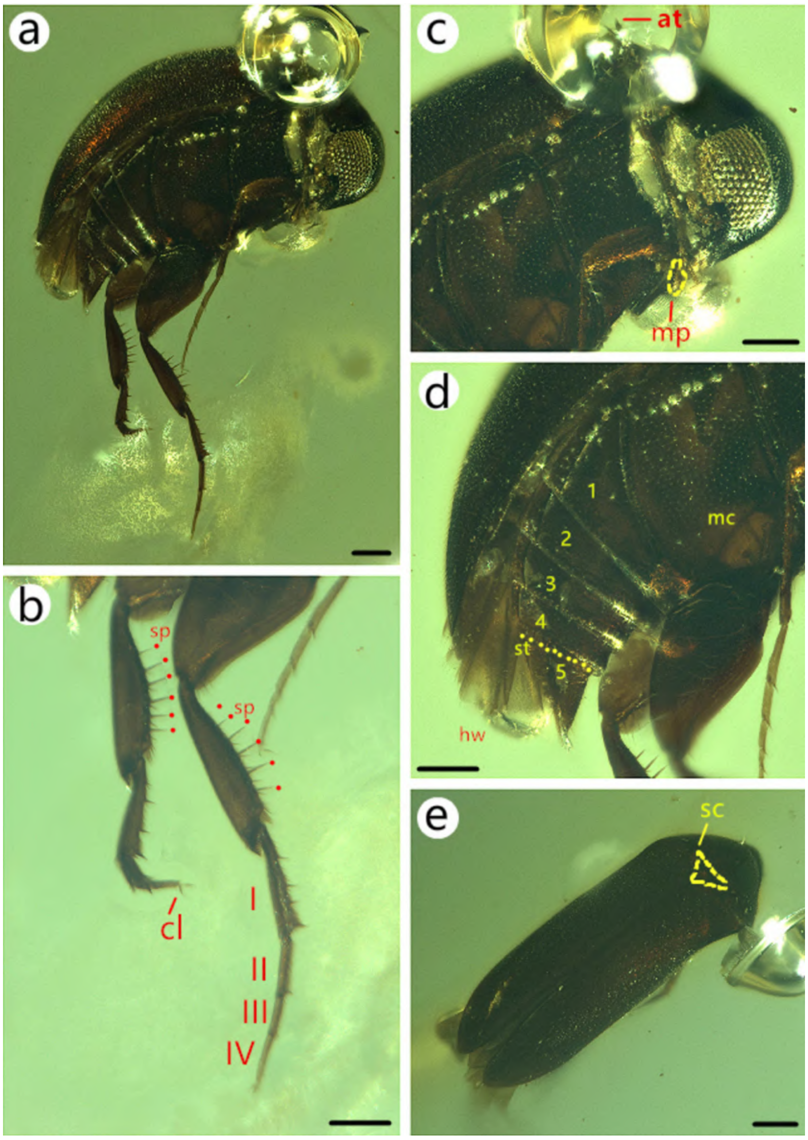

图 1　小多刺花蚤(新种)

Fig. 1　*Multispinus parvus* sp. nov.

a. 全身侧面观; b. 后足细节, I—IV 代表第 1 至第 4 跗节，红点标示胫节内侧的六对刺; c. 身体前部(头和胸部)细节; d. 后胸和腹部细节, 1—5 代表第 1 至第 5 腹节，黄点标示第 4 和第 5 腹节之间的一排细刚毛; e. 全身背面观。缩略语: at. 触角; cl. 爪; hw. 后翅; mc. 后基节板; mp. 下颚须; sc. 中胸小盾片; sp. 胫节内侧的刺; st. 刚毛。比例尺 = 0.1 mm。

a. lateral view; b. details of hind legs, I–IV represent 1st to 4th metatarsomeres, metatibiae spines pointed by red dots; c. details of head and thorax; d. details of metathorax and abdomen, 1–5 represent 1st to 5th sternites, a row of fine setae between 4th and 5th sternites pointed by yellow dots; e. dorsal view. Abbreviations: at. antennae; cl. claw; hw. hind wings; mc. metacoxal plate; mp. maxillary palp; sc. scutellum; sp. spines on metatibiae; st. setae. Scale bars = 0.1 mm.

描述 正模标本 NIGP171284, 体型极小, 体长 1.21 mm, 楔形, 身体最宽处位于前胸背板基部; 身体前端与末端均有不同程度的收缩, 流线型。侧面观, 身体卷曲, 呈 C 型。虫体颜色于琥珀中呈深棕至黑色, 无花斑。

头小, 正面观呈倒三角形, 基部最窄, 与前胸背板前缘同宽, 下口式。额区窄, 后头宽, 表面附有短刚毛。复眼一对, 侧置, 大, 完全发育, 具边框, 微多面型小眼面, 椭圆形, 边缘有刚毛, 于后头处不相接。触角短, 不及身长 1/2, 丝状。上唇突出; 下颚须末节膨大, 斧状。

前胸背板长 0.14 mm, 宽(基部最宽处)0.44 mm, 侧缘及前缘组合呈半圆状, 后缘宽二弯状。中胸小盾片长 0.07 mm, 宽 0.09 mm, 倒三角形。鞘翅一对, 不长于腹部, 长 1.12 mm, 宽(前部最宽处)0.42 mm, 表面近光滑, 有刻点及极短刚毛; 后翅透明, 膜质, 藏于鞘翅下。

足三对, 分别着生于前胸、中胸和后胸, 跗节 5-5-4 型。后胸前侧片窄, 不等四边形, 表面有小粒及极短刚毛; 后胸腹板宽阔, 表面有小粒及极短刚毛。后足基节特化为基节板, 膨大; 转节突出; 股节强烈膨大, 末端与胫节连接处有若干小刺; 胫节细长, 内侧弓型弯曲, 末端略扩大, 具端距, 数量多, 呈梳状; 跗节细长, 端部具爪, 无齿, 二裂。后足胫节与跗节表面无脊; 胫节内侧有六对硬质小刺, 呈 V 型; 跗节第一节内侧有长短两种小刺, 交互排布; 跗节第二节至第四节仅有短刺(或短刚毛); 每节跗节末端具有硬化端距。四节跗节长度依次为: 0.19 mm, 0.10 mm, 0.07 mm, 0.10 mm。

腹部 1—5 节可见腹板, 长度依次为: 0.11 mm, 0.08 mm, 0.07 mm, 0.05 mm, 0.15 mm, 腹板间有稀疏短刚毛一列, 腹板表面附有小粒及极短刚毛; 臀锥完全不发育。阳茎部分伸出。

种间差异 新种小多刺花蚤 *Multispinus parvus* sp. nov.与多刺花蚤 *Multispinus multispinosus* 相比: 1)虫体明显小; 2)前胸背板形状特殊, 侧缘及前缘组合呈半圆状, 后缘宽二弯状; 3)胫节内侧仅有六对硬质小刺, 呈 V 型。

产地与层位 缅甸联邦共和国克钦邦达奈镇, 缅甸硬琥珀原矿; 上白垩统塞诺曼阶底部(～99 Ma)。

5 讨 论

5.1 分类学修订

短尾花蚤由科(Apotomouridae)修订为花蚤科下的亚科(Mordellidae: Apotomourinae), 现包括 2 属 3 种, 均发现于白垩纪缅甸琥珀。短尾花蚤亚科的鉴定特征大部分吻合花蚤科的特征, 如: 身体蜷缩、楔形; 触角短; 鞘翅不超过腹节; 后足发达; 后足基节特化为基节板。该亚科明显异于绝大多数花蚤的特征为: 臀锥完全不发育; 身体多附属结构, 如刚毛, 刺等。臀锥完全不发育亦可见于侏罗纪先花蚤亚科(Mordellidae: Praemordellinae)(Bao *et al*., 2019b), 于白垩纪西班牙琥珀中发现的 *Mediumiuga sinespinis* Peris, 2013 表现为臀锥极不完全发育 (Peris and Ruzzier, 2013), 于缅甸琥珀中发现的 *Primaevomordellida burmitina* Bao, 2019 则与绝大多数现生花蚤一样臀锥非常发育 (Bao *et al*., 2019a)。这表明花蚤科内不同种类的臀锥发育程度呈极大多样性, 故此特征非科间鉴定衍征。现生花蚤各属种间, 后足胫节和跗节上的脊结构呈现多样性, 如端脊、亚端脊、侧脊、背脊(Jackman and Lu, 2002)。短尾花蚤亚科各属种均不具此特征, 但具有较发达的刺或刚毛附属结构, 而 *M. sinespinis* 兼具刚毛和脊, 故 *M. sinespinis* 可能为短尾花蚤亚科与其他花蚤的中间过渡种, 足的附属结构为短尾花蚤亚科衍征。一般来说, 甲虫胸部及其基节结构特征具有重要的分类学意义(Beutel and Friedrich, 2005), 如后基节特化为基节板为花蚤科区别于其他相邻分支(大花蚤科, 芫菁科等)的重要特征(Hsiao *et al*., 2017)。此特征在短尾花蚤亚科表现清晰, 故很难将短尾花蚤独立建新科。

分子系统发生学分析表明, 花蚤和大花蚤存在姐妹群关系(Mordellidae + Ripiphoridae)(Kergoat *et al*., 2014), 但 Falin (2003)指出大花蚤科的单系缺乏有力支持。短尾花蚤亚科作为花蚤科中的原始化石类群, 与先花蚤亚科一样, 具有许多原始大花蚤的特征。这也说明了拟步总科(Tenebrionoidea)的基部类群分类仍模糊, 尚需进一步研究。

5. 2　个体发生学和古生态学

现生花蚤科个体大小范围 1.5—15 mm (Jackman and Lu, 2002)。小多刺花蚤 *Multispinus parvus* 体长 1.2 mm, 属于花蚤科中体型最小的类群之一。相比其他缅甸琥珀中的花蚤类群(*Multispinus multispinosus*, 2.2—2.5 mm; *Apotomoura fortiscrura*, 1.5—1.7 mm; *Primaevomordellida burmitina*, 2.9—3.0 mm), 小多刺花蚤体型也明显小。事实上, 迄今白垩纪琥珀中发现的花蚤体型均小, 未见体长超过 5 mm 的个体。与此相比, 先花蚤亚科各属种体型明显大, 体长约 10 mm。但身体形态上, 先花蚤亚科与其他花蚤明显不同, 表现为: 后足细长, 不膨大; 身体平展, 不强烈蜷曲。这可能揭示了先花蚤亚科与其他花蚤取食策略和生态环境的不同(Wang *et al*., 2013; Bao *et al*., 2018c)。短尾花蚤与现生绝大多数花蚤一样, 具有发达的后足和蜷曲的体型, 据此推测其可能具有相似的飞行、跳跃动作(黄迪颖、杨俊, 1999) 和花冠取食行为(Franciscolo, 1957)。白垩纪中期被子植物出现并快速辐射, 从而影响陆生昆虫等同样快速协同进化与辐射, 是陆地生命进化中生物学上最重要的时期之一(Dilcher, 2000; Benton, 2010)。缅甸琥珀中发现的被子植物花朵均不具有大型花冠, 不形成花序, 多数呈小型、简单五瓣花状(Poinar, 2017; Liu *et al*., 2018), 这与访花花蚤类甲虫的小体型吻合。由此设想, 白垩纪被子植物与访花昆虫类群可能存在协同进化, 相互影响。

6　结　论

白垩纪中期缅甸琥珀中发现花蚤科一新种, 命名为小多刺花蚤 *Multispinus parvus* sp. nov.。短尾花蚤科被重新修订为花蚤科下的亚科——短尾花蚤亚科。白垩纪中期被子植物处于快速发展期, 花朵结构不甚发达, 或许可从协同进化角度解释这一时期花蚤类甲虫的普遍小型化现象。

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Pollination of Cretaceous flowers

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Insect pollination of flowering plants (angiosperms) is responsible for the majority of the world's flowering plant diversity and is key to the Cretaceous radiation of angiosperms. Although both insects and angiosperms were common by the mid-Cretaceous, direct fossil evidence of insect pollination is lacking. Direct evidence of Cretaceous insect pollination is associated with insect-gymnosperm pollination. Here, we report a specialized beetle-angiosperm pollination mode from mid-Cretaceous Burmese amber (99 mega-annum [Ma]) in which a tumbling flower beetle (Mordellidae), *Angimordella burmitina* gen. et sp. nov., has many tricolpate pollen grains attached. *A. burmitina* exhibits several specialized body structures for flower-visiting behavior including its body shape and pollen-feeding mouthparts revealed by X-ray microcomputed tomography (micro-CT). The tricolpate pollen in the amber belongs to the eudicots that comprise the majority of extant angiosperm species. These pollen grains exhibit zoophilous pollination attributes including their ornamentation, size, and clumping characteristics. Tricolpate pollen grains attached to the beetle's hairs are revealed by confocal laser scanning microscopy, which is a powerful tool for investigating pollen in amber. Our findings provide direct evidence of insect pollination of Cretaceous angiosperms, extending the range insect-angiosperm pollination association by at least 50 million years. Our results support the hypothesis that specialized insect pollination modes were present in eudicots 99 million years ago.

amber | insect | angiosperm | pollen | paleoecology

Angiosperms, flowering plants, are the most diverse group of land plants (1). The earliest unequivocal pollen and macrofossils of angiosperms are generally thought to date from the early Hauterivian (~130 Ma) and early Aptian (~125 Ma), respectively, (2, 3) despite claims based on other fossils and molecular analyses (1, 4, 5). The apparently rapid and tremendous evolutionary diversification of angiosperms during the Cretaceous was the great "abominable mystery" mentioned by Darwin and continues to be an active and sometimes a controversial area of research (6–8). Insect pollination (entomophily) is generally considered to be a key contributor to the Cretaceous radiation of angiosperms (9–12). It is generally thought to be the dominant pollination mode of angiosperms during the early mid-Cretaceous with specialization increasing during the angiosperm radiation, supported by basal flower morphology, palynological data, and phylogenetic inferences (8, 13–15). Some Cretaceous insects are palynivores of angiosperms based on their pollen- or nectar-feeding mouthparts (16, 17), gut contents (18), or coprolites (19). However, a palynivore is not equivalent to a pollinator. Only direct evidence (pollen-carrying behavior and pollen-feeding mouthparts) can provide unambiguous demonstration of ancient insect pollination. Until now, direct evidence of Cretaceous insect pollination supports insect-gymnosperm pollination, such as that involving thrips (20), true flies (21), beetles (22, 23), and scorpionflies (17). Although both insects and angiosperms were common during the mid-Cretaceous, direct evidence for Cretaceous insect-angiosperm pollination mode has been absent.

The Coleoptera (beetles) constitute almost 1-4th of all animal species on Earth (24) and are among the most prominent pollinators of angiosperms (25, 26). More than 77,000 beetle species are estimated to visit flowers (27). Among these flower-visiting beetles, Mordellidae (tumbling flower beetles) is one of the most species-rich families, and adults are easily recognized by their humpbacked body, deflexed head, pointed abdomen, and stout hind legs (28, 29). The majority of extant adult mordellids feed on angiosperm pollen (28, 29). Cretaceous mordellids have been hypothesized to be angiosperm pollinators, but direct evidence was lacking (30).

We report a species of Mordellidae from mid-Cretaceous Burmese amber (see *Systematic Descriptions and Notes*). We used optical microscopy, confocal laser scanning microscopy (CLSM), and X-ray microcomputed tomography (micro-CT) to reveal the morphology of the pollen and beetle mouthparts. Multiple lines of evidence, including pollen-feeding mouthparts, pollen-carrying hairs on the body, and zoophilous pollination attributes of these tricolpate pollen, strongly support a specialized beetle-angiosperm pollination mode. This is the earliest direct evidence of insect pollination of angiosperms.

Discussion

Angimordella burmitina exhibit a series of specialized body structures related to its flower-visiting behavior, similar to its modern counterparts, which feed on various angiosperm pollen (28, 29). It has the *Mordella*-type apical maxillary palpomere, which is enlarged and securiform (31). This maxillary palpomere is blocked by a thrip,

Significance

Since Darwin, insect pollination was thought to be a key contributor to the Cretaceous radiation of angiosperms. Both insects and angiosperms were common during the mid-Cretaceous, but direct evidence for a Cretaceous insect-angiosperm pollination mode was until now absent. Here, we report a specialized beetle-angiosperm pollination mode preserved in Burmese amber where a tumbling flower beetle is carrying tricolpate pollen grains that belongs to the eudicots that comprise the majority of extant angiosperm species. Our study provides direct evidence of insect pollination of Cretaceous flowers, which is further supported by the flower-visiting body shape, specialized pollen-feeding mouthparts, and zoophilous pollen grains. These findings demonstrate that insect pollination of flowering plants was well established 99 million years ago.

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The authors declare no competing interest.

Data deposition: The data supporting the findings of this study have been deposited in the Figshare database (https://doi.org/10.6084/m9.figshare.10025825).

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but the palpomere shape is revealed by micro-CT (Fig. 1; see Movie S1 for detailed account). This specialized modification of the maxillary palpomere has been known to aid collecting and most likely transporting pollen grains (30, 32). *A. burmitina* has a curved and laterally compressed body with a strongly declined head, allowing for flexibility when feeding inside the flower (31). Its hind legs are well developed, with enlarged metacoxa and metafemora and spiny metatibiae and metatarsi, which make it easier to move on the corolla and from one flower to another (33). Moreover, *A. burmitina* has fine hairs; the spacing and height of these hairs influence the ability of the hairs to carry pollen grains (34) (Fig. 2 *D* and *E*). Accordingly, the hairs on the beetle's thorax and abdominal sternites are distinctly longer than 30 μm, and the spacing between the hairs is consistent with the width of the coexistent pollen grains (~20 μm) and is well-adapted for holding and transporting pollen grains (34).

It is important to note that *A. burmitina* is covered by abundant tricolpate pollen grains that are mainly distributed on the thorax and abdomen (Fig. 2*A*). Tricolpate pollen is both the defining and most important character of the eudicots. The eudicots comprise ~75% of extant angiosperm species (35). The earliest fossil record of tricolpate pollen is ~125 million years old, slightly older than the earliest eudicot macrofossil (36). By 99 million years ago (Burmese amber age), tricolpate pollen had become widespread worldwide (5, 37–39) and eudicot macrofossils are reported from Burmese amber (e.g., refs. 40 and 41). Many Cretaceous plants with tricolpate pollen are animal-pollinated and characterized by their ornamentation, size (10–300 μm), and clumping characteristics (15). Small angiosperm pollen grains in amber, especially those buried under insect body hairs, are often not visible under optical microscopy and, thus, could be easily overlooked. In this study, the pollen grains between body hairs were detected by confocal laser scanning microscopy (CLSM), which takes advantage of pollen fluorescence, which contrasts with the surrounding dark insect cuticle (41) (Fig. 2 *D* and *E*). The tricolpate pollen grains found in Burmese amber exhibit remarkable zoophilous pollination features including their reticulate surface (Fig. 2*H*) and presence of pollen clumping (Fig. 2*F*), thus providing more evidence to support beetle-mediated pollination. Interestingly, only one type of pollen was found on this beetle. This could reflect that there were not very many different types of flowers during the mid-Cretaceous or that the insect visited only one type of flower before it was trapped in the amber.

Mordellidae, comprising ~1,500 extant species worldwide, are among the most basal group of Tenebrionoidea based on morphological analysis and molecular data (24, 42, 43). Although

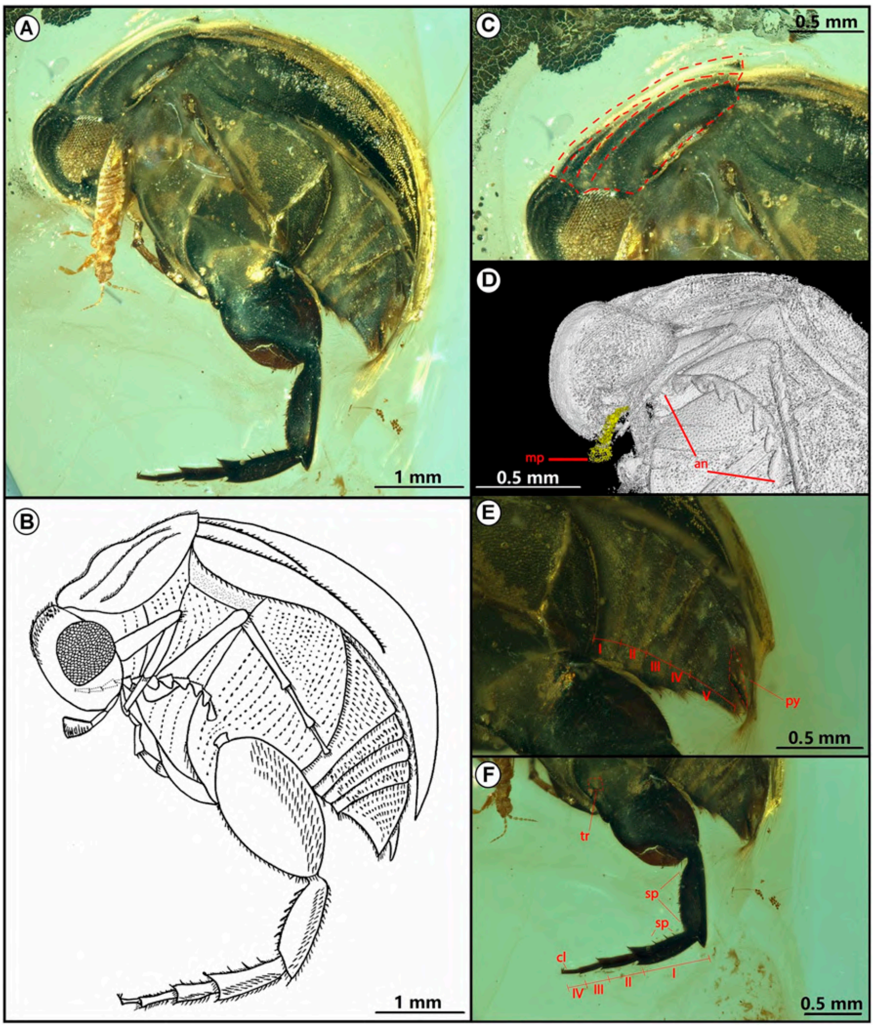

Fig. 1. Cretaceous tumbling flower beetle *A. burmitina*. (*A*) Habitus. (*B*) Drawing. (*C*) Prothorax and pronotum highlighted by red dashed lines. (*D*) Microtomographic reconstruction of the head. Maxillary palpi highlighted in yellow. (*E*) Abdomen, I–IV represent first to fifth abdominal ventrites. (*F*) Hind leg, I–IV represent first to fourth metatarsomeres. an, antennae; cl, claw; mp, maxillary palp; py, pygidium; sp, spines on metatibiae and metatarsi; tr, trochanter.

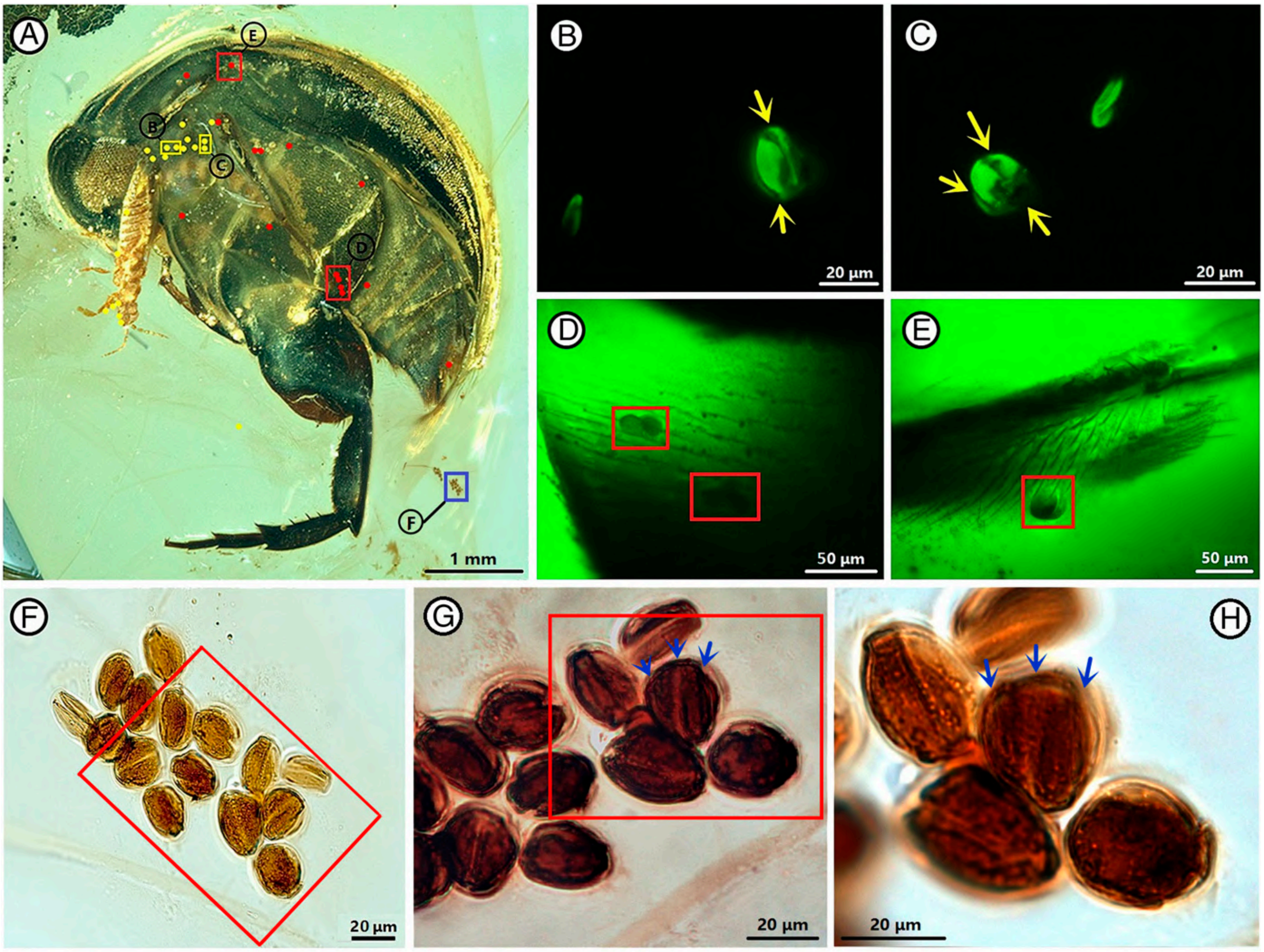

Fig. 2. *A. burmitina* and tricolpate pollen grains. (*A*) Habitus. Pollen grains attached to the body are indicated by red dots, unattached are indicated by yellow dots, clumped pollen are indicated by blue squares. (*B–H*) Locations are highlighted in *A*. (*B* and *C*) Pollen grains near the body. Yellow arrows point to colpi. (*D* and *E*) Pollen grains on the body. (*F–H*) Clumped pollen grains. (*G* and *H*) Locations are highlighted in *F* and *G*, respectively. Blue arrows point to colpi.

mordellid-like beetles are reported from the Middle-Late Jurassic of China and Kazakhstan, the earliest true mordellids (extant subfamily) are known from the mid-Cretaceous Spanish and Burmese amber (44). *A. burmitina* is among the earliest true mordellids and indicates that mordellid-angiosperm pollination mutualisms have been present since at least 99 million years ago (Fig. 3). These mutualisms may be an important driver for the radiation of true mordellids.

This study provides direct evidence of Cretaceous insect pollination of angiosperms, which is strongly supported by the flower-visiting body shape, specialized pollen-feeding mouthparts, and zoophilous pollen grains attached to the body. The prior earliest direct evidence of insect pollination of angiosperms was reported from several pollen-collection bees from the middle Eocene of Eckfeld and Messel (48 and 45 Ma, respectively) in Germany (45). Our finding thereby extends the known geological range of direct evidence of insect pollination of angiosperm by at least 50 million years.

Systematic Descriptions and Notes

Family Mordellidae Latreille, 1802.
Subfamily Mordellinae Latreille, 1802.
Angimordella burmitina gen. et sp. nov.

Etymology. The generic name is derived from the Latin prefix "angi" (referring to angiosperm) and the genus *Mordella* Linnaeus. The specific name is derived from Latin "Burmitina," referring to the mineralogical name of Burmese amber.

Holotype. NIGP171315 (Fig. 1), a complete beetle with left side visible but its right side covered by abundant microbubbles. A thrip is near the maxillary palpi of the beetle on the left side.

Horizon and Locality. Mid-Cretaceous (~99 Ma); Burmese amber, from the Hukawng Valley, Kachin State, Myanmar.

Diagnosis. Body small, with pronotum and elytra with wrinkles or ridges dorsally; antennae serrate; mesotibiae and metatibiae without any kind of ridge including subapical one; pygidium not well developed, shorter than 1/2 of last abdominal sternite.

Description. Body strongly convex, wedge-shaped, widest near base of prothorax, slightly narrowed anteriorly and posteriorly (Fig. 1 *A* and *B*). Body length 4.25 mm; ratio of body length to greatest body width 3:2. Head length 0.51 mm, large, transverse, strongly declined, with mouthparts directly posteriorly; compound eyes finely faceted and glabrous. Occipital region wide, surface with wrinkles and hairs, matching perfectly with anterior edge of

Fig. 3. Ecological reconstruction of *A. burmitina*. These tumbling flower beetles are feeding on eudicot flowers. The color and morphology of flowers are artistic only.

pronotum. Antennae comparatively short, with 7 visible antennomeres, obviously serrate (Fig. 1*D*), covered with hairs. Maxillary palp length 0.38 mm; apical maxillary palpomere length 0.18 mm, securiform, strongly enlarged.

Pronotum length 1.11 mm, slightly narrowed anteriorly, widest posteriorly, as wide as elytra at base, lateral margin slightly curved; pronotum disk with ridges and covered by short and dense recumbent hairs (Fig. 1*C*). Elytra length 2.46 mm, ~2.5 times as long as pronotum, covering all abdominal segments, with slight surface relief, gradually curving up to apex proximity; integuments covered with fine hairs. Forelegs simple, tibiae slender. Mesotibiae and mesotarsi simple, long and slender. Metaepistena long, rectangular. Metacoxae greatly enlarged with rounded posterior margin, extending laterally to meet elytra, widely rounded at posterior margin; trochanter oblique. Metafemora length 0.80 mm, laterally compressed and greatly expanded, more than 4 times wider than mesofemora. Metatibiae length 0.74 mm, blade shaped, about same length as metafemora with obliquely truncated apexes; metatibiae without any kind of ridge including subapical one; apical margin of hind tibiae bearing comb-like setae; ventral side of metatibiae and metatarsomeres with fine spine-like setae; apical spurs on metatibiae absent. Metatarsi laterally compressed, comparatively sturdy, with comb-like setae on apical margin and apical spurs on posterior margin, spiny on inner margins (Fig. 1*F*); length of four metatarsomeres 0.50 mm, 0.30 mm, 0.18 mm, 0.16 mm, ratio 5:3:2:2. Claws small and bicleft. Abdomen distinctly narrowed posteriorly, with 5 free ventrites. Ventrites 1–5 length 0.16 mm, 0.16 mm, 0.15 mm, 0.12 mm, 0.26 mm, ratio 1:1:1:1:2 (Fig. 1*E*). Hairs present on abdomen, slightly elongated between sternites. Pygidium very short, 0.18 mm long.

Remarks. *A. burmitina* can be attributed to the subfamily Mordellinae by the following characters: wedge-shaped body, enlarged last segment of maxillary palpi; metacoxae greatly enlarged forming a rounded plate; metafemora expanded and well developed; and pygidium very short. It resembles *Primaevomordellida burmitina* Bao et al. 2019 from Burmese amber (46) in the absence of ridge on metatibiae and metatarsi but differs from the latter in having a short pointed pygidium. It is also similar to *Mediumiuga sinespinis* Peris & Ruzzier, 2013 from late Albian Spanish amber (47) in having a very short pygidium and ventrally spiny metatibiae and metatarsi but differs from the latter in the absence of ridge on metatibiae and metatarsi.

Pollen Descriptions. There are at least 62 pollen grains (from only the visible left side of the beetle) in the amber in total, of which 24 pollen grains aggregate into two small clusters near the abdominal end of the mordellid (Fig. 2*A*). Pollen grains in the amber are retitricolpate and highly uniform in morphology (Fig. 2 *B*, *C*, and *H*). The shape of the grain is approximately oblate spheroidal, 25.56 μm (30.95–22.08 μm) × 16.49 μm (20.68–13.93 μm) in equatorial view (based on measurement of the 27 best preserved pollen grains; *SI Appendix*, Table S1). The colpi are long, wide, and deep and extend to the pole. The exine is moderately thick, ~1 μm. The lumina are small, evenly spaced, and ~0.5 μm in diameter. The pollen clump shape is irregular, and the pollen grains are well preserved (Fig. 2 *F* and *G*), indicating that they are natural floral remains rather than coprolites (48). These pollen grains can be confidently attributed to the eudicot monophyletic group (true dicotyledons), members of which are distinguished from all other angiosperms by their tricolpate pollen structure (49, 50). We did not assign the pollen to a taxon given the nature of this microscopic method conducted within amber.

Materials and Methods

Materials. The amber piece came from an amber mine near Noije Bum Village, Danai Town in northern Myanmar. The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 million years (51), which is also supported by the ammonite trapped in the amber (52). The specimen (NIGP171315) is deposited in the Nanjing Institute of Geology and Paleontology (NIGPAS), Chinese Academy of Sciences.

Optical Photomicrography. Photographs were taken using a Zeiss AXIO Zoom V16 microscope system at the State Key Laboratory of Paleobiology and Stratigraphy, NIGPAS. Incident and transmitted light were used simultaneously in most instances. Each image was digitally stacked with 40–50 individual focal planes, produced with the software Helicon Focus 6 (https://www.heliconsoft.com/) for better illustration of the 3-dimensional (3D) structures.

Confocal Laser Scanning Microscopy. Photomicrographs with green background were taken using a CLSM Zeiss LSM710 system with laser wavelength 488 nm (Laser module LGK 7812 ML5) at the State Key Laboratory of Paleobiology and Stratigraphy, NIGPAS. Based on the diameter and thickness of amber specimen, 2 objectives (“Plan-Neofluar” 20×/0.50 M27 and “Plan-Apochromat” 63×/1.40 Oil DIC M27) were applied. AxioVision 4.0 modules with the software AxioVision Rel. 4.8.2 were used to produce high-resolution images.

X-ray Microcomputed Tomography. To 3-dimensionally reconstruct the beetle, we scanned the fossil at the micro-CT laboratory of NIGPAS, using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, 3D-XRM uses charge-coupled device (CCD)-based objectives to achieve higher spatial resolution. Based on the size of the fossil specimen, a CCD and 4× objective was used, providing isotropic voxel sizes of 3.43 μm with the help of geometric magnification. During the scan, the acceleration voltage for the X-ray source was 50 kV (power 4W), and a thin filter (LE3) was used to avoid beam hardening artifacts. To improve signal-to-noise ratio, 3,000 projections over 360° were collected, and the exposure time for each projection was 5 s. Volume data processing was performed using software VGStudio Max (version 3.0, Volume Graphics, Heidelberg, Germany).

Nomenclatural Acts. This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSIDs for this publication are as follows: urn:lsid:zoobank.org:pub:2CE49289-946F-4194–904B-188A29976905; urn:lsid:zoobank.org:act:D31C312B-218A-47EC-A427-53ED39FE1926; urn:lsid:zoobank.org:act:46B77E87-5047–49B4-B29A-448D0B41CA9D.

Data Availability. The data supporting the findings of this study have been deposited in the Figshare database (53) and can be obtained upon request from the corresponding authors.

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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* Scegoleva-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.

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 Franciscolo, 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 Scegoleva-Barovskaja, 1929, was erected by Scegoleva-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)
Mordella atrata	late Pleistocene	Ziegler Reservoir, USA (Elias, 2014)
Mordellistena sp.		
Mordella indata Statz, 1952	Oligocene (Chattian)	Rott-am-Siebengebirge, Germany (Statz, 1952)
Mordella nigripilosa Statz,1952		
Stenalia oligocenica Nel, 1985	Oligocene (Rupelian)	Cereste, France (Nel, 1985)
undescribed	Miocene	Mexican Amber (Poinar, 1993)
undescribed	Miocene	Dominican amber (Grimaldi and Engel, 2005)
Glipostena ponomarenkoi Odnosum and Perkovsky, 2009	upper Eocene (Priabonian)	Rovno amber, Ukraine (Odnosum and Perkovsky, 2010)
Mordella priscula Cockerell,1924	upper Eocene	Green River Formation, USA (Cockerell, 1925; Odnosum and Perkovsky, 2016)
Isotrilophus rasnitsyni Odnosum and Perkovsky, 2016		
Mordella lapidicola Wickham, 1909	middle Eocene	Florissant Formation, USA (Cockerell, 1907; James, 1939; Scudder, 1890; Wickham, 1913)
Mordella stygia Wickham, 1914		
Mordellistena florissantensis Wickham, 1912		
Mordellistena nearctica Wickham, 1914		
Mordellistena protogaea Wickham, 1914		
Mordellistena scudderiana Wickham, 1914		
Mordellistena smithiana Wickham, 1913		
Tomoxia inundata Wickham, 1914		
undescribed	middle Eocene	Kishenehn Formation, USA (Greenwalt et al., 2016)
Glipostena sergeli Ermisch, 1943	Eocene	Baltic amber (Bao et al., 2018a; Engel, 2001; Ermisch, 1943; Germar, 1813; Kubisz, 2003; Perkovsky and Odnosum, 2013)
Falsomordellistena eocenica Kubisz, 2003		
Mordella inclusa Germar, 1813		
Mordella scheelei Ermisch, 1941		
Mordellaria friedrichi Perkovsky and Odnosum, 2013		
Mordellistena amplicollis Ermisch, 1941		
Mordellistena antiqua Ermisch, 1941		
Mordellistena goeckei Ermisch, 1941		
Mordellistena korschefskyi Ermisch, 1941		
Mordellistena soror Ermisch, 1941		
Succimorda rubromaculata Kubisz, 2001		
Tomoxia succinea Bao, 2018		
Asiamordella furvis (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
Primaevomordellida burmitina Bao, 2019	Upper Cretaceous (Cenomanian)	Burmese amber (Bao et al., 2019)
Mediumiugini Peris and Ruzzier, 2015	Lower Cretaceous (Albian)	Spanish amber
Mediumiuga sinespinis 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
Wuhua sp. Wang and Zhang, 2011		
Mordellidae Latreille et al., 1802	Late Jurassic	Karatau, Kazakhstan
Praemordellinae Scegoleva-Barovskaja, 1929		
Praemordella martynovi Scegoleva-Barovskaja, 1929		
Mordellidae Latreille et al., 1802	Early Cretaceous	Western Beijing, China
Cretamordella lushangfenensis Huang and Yang, 1999		
Mordellidae Latreille et al., 1802	Early Cretaceous	Yixian formation, Liaoning, China
Praemordellinae Scegoleva-Barovskaja, 1929		
Mirimordella gracilicruralis Liu, 2007		
Bellimordella capitulifera Liu, 2008		
Bellimordella longispina Liu, 2008		
Bellimordella robusta Liu, 2008		
Apotomouridae Bao, 2018	lower Cenomanian	Burmese amber, Myanmar
Multispinus multispinosus Bao, 2018		
Apotomoura fortiscrura 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* Scegoleva-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 Scegoleva-Barovskaja, 1929

[Praemordellinae] Ščegoleva-Barovskaya, 1929, Comptes Rendus del'Academie des. Sci. 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* Scegoleva-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* Scegoleva-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* Scegoleva-Barovskaja
3. Hind tibiae much longer than hind tarsi; hind apical spur longer than 1 st tarsomere . . . .
. . . . *Cretanaspis* Huang & Yang

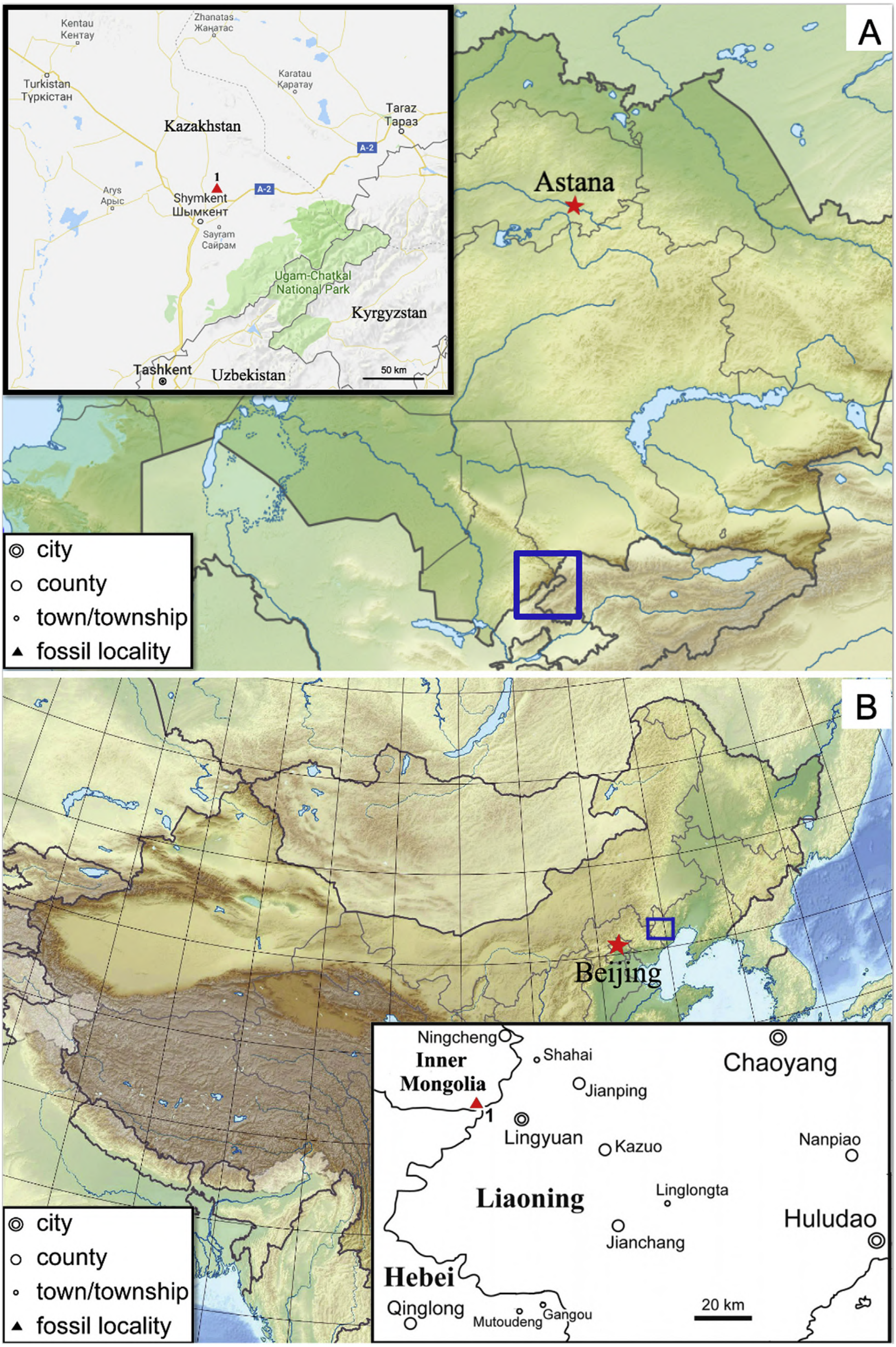

Fig. 1. (A) map of the locality of Karabastau Formation in southern Kazakhstan. Highlighted area enlarged and shown in detail. 1, main fossil locality near village of Aulie. Scale bars = 50 km. (B) map of the Daohugou biota in Inner Mongolia and north-eastern China. Highlighted area enlarged and shown 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 1 st 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 1 st 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 1 st 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.

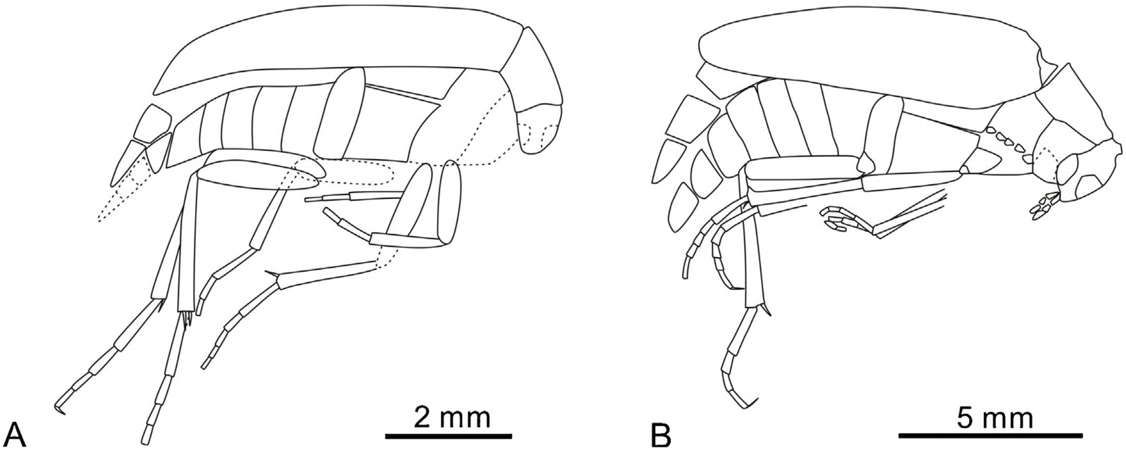

Fig. 3. (A) *Praemordella martynovi* Scegoleva-Barovskaja, 1929, PIN, holotype. (B) *Wuhua peregrine* sp. nov., NIGP154954, holotype.

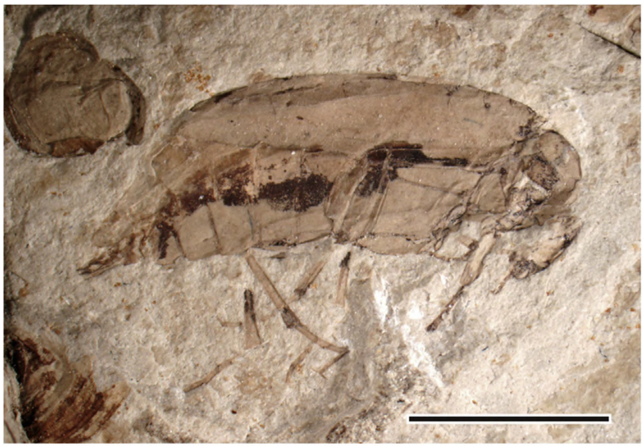

Fig. 4. A tenebrionoid beetle, CNU-C-NN2007203. Scale bar = 5 mm.

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 Scraptiidae in having the filiform antennae, and humpbacked body, but differs in having pectinate tarsal claws (simple in Scraptiidae), and penultimate tarsal segments simple (distinctly lobed in Scraptiidae). 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 hongi*) 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. hongi* 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 Scraptiidae (Wang, 1993). Judging from the photograph, *L. hongi* 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. hongi* 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. hongi* 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 Scraptiidae. Primitive characters of Praemordellinae indicate that this group could arise earlier than the relative extant taxa, and furthermore could consist ancestors of

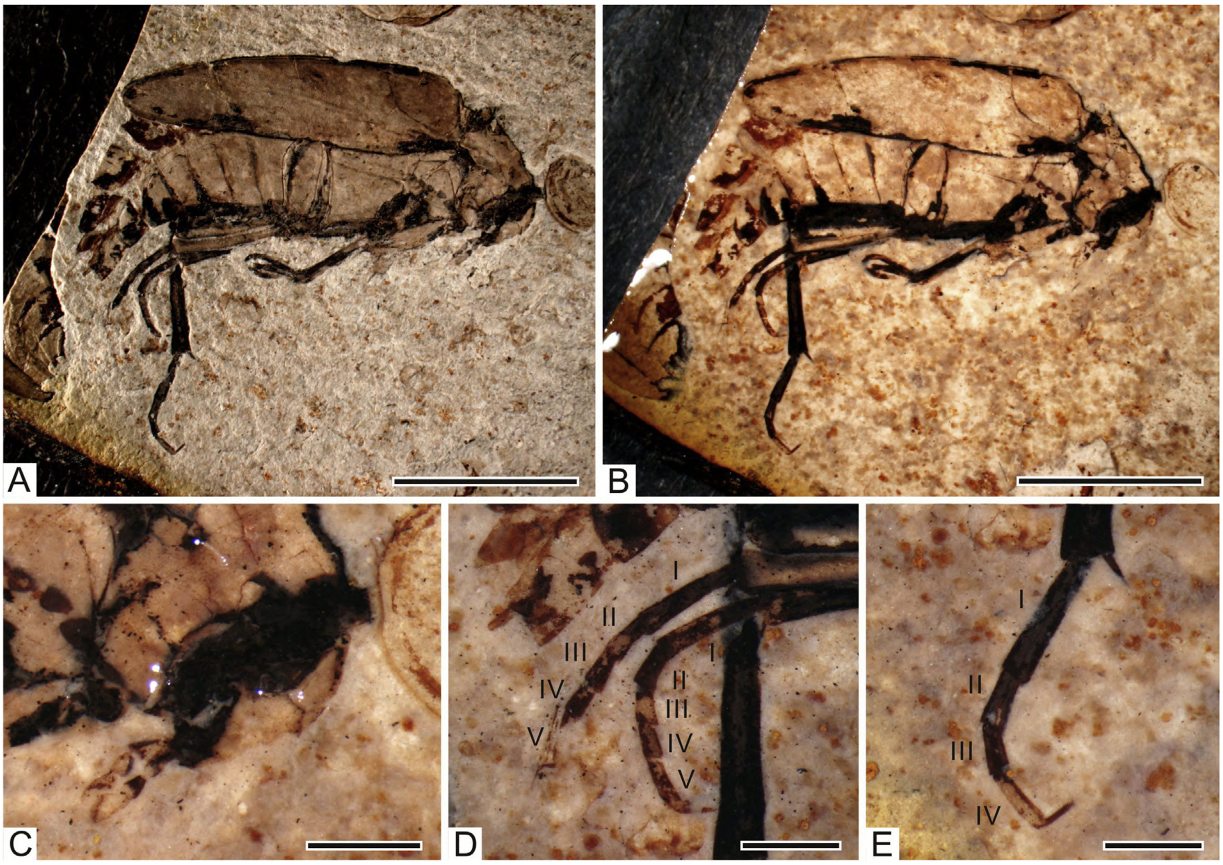

Fig. 5. *Wuhua peregrine* sp. nov., NIGP154954, holotype. (A–B) Body. The specimen was photographed dry (A) and under alcohol (B). (C) Head. (D) Tarsus of middle leg. (E) Tarsus of hind leg. Scale bars = 5 mm in (A–B); 1 mm in (C–E).

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 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 scraptiids and mordellids, but later he suggests a tenebrionoid lineage consisting of Melandryidae, Mordellidae + Ripiphoridae and Scraptiidae (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 (Falin, 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. Paleoecology

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.

Acknowledgments

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Short communication

The first true Mordellidae (Coleoptera: Tenebrionoidea) from lower Cenomanian amber of Myanmar

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ABSTRACT

Primaevomordellida burmitina gen. et sp. nov. (Coleoptera: Mordellidae) is described on the base of two well-preserved specimens from Cenomanian Burmese amber. Due to the general body plan and the preservation of elongated pygidium, it is apparently the first true pintail beetle (subfamily Mordellinae). The simple hind leg structures placed the new species into the basal tribe Raynoldsiellini; however, the comparative morphology of the new species shows advanced characters similar to tribes Mordellini and Mordellistenini. The angiosperm plant records in Burmese amber forests were reviewed and the mordellids-angiosperm interactions are discussed.

1. Introduction

The family Mordellidae, is thought to be among the most basal group of Tenebrionoidea based on molecular data (Hunt et al., 2007; McKenna and Farrell, 2009). All fossils attributable to Mordellidae refer only to Mordellinae, and Praemordellinae subfamilies, while so far there is no trace of Cteniidinae.

The Cenozoic Mordellidae discovered in Fushun amber of the Eocene of China (Zhang and Hong, 1999), Kishenehn Fm., Eocene of Montana, USA (Huber and Greenwalt, 2011), Green River Fm., Eocene of Colorado, USA (Cockerell, 1925), Baltic amber of the Eocene Baltic gulf (Kubisz, 2003; Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013), Florissant Fm., Oligocene of Colorado, USA (Scudder, 1890; Cockerell, 1907), Rott Fm., Oligocene, Germany (Statz, 1952), Carbonate Fm., Oligocene, France (Nel, 1985), Mexican amber, Miocene, Mexico (Poinar, 1993), Olympia beds Fm., Pleistocene, Washington, USA (Ashworth and Nelson, 2014) display close similarity to the extant species and they have been traditionally assigned in the major part of the cases to *Mordella* and *Mordellistena*. In comparison, the fossil records of Mesozoic mordellids are generally scarce, mainly found in the Late Jurassic Karabastau Fm, Russia (Scegoleva-Barovskaja, 1929) and the Early Cretaceous Yixian Formation of China (Liu et al., 2007, 2008). These Mesozoic mordellids have been placed into the subfamily Praemordellinae, because of the significant absence of pygidium and not-mordelloid hind legs. Mordellidae also recorded from Early Cretaceous Lebanese amber (Kirejtshuk and Azar, 2013). However, the specimen “RIH-5” is partly destroyed that made further research almost impossible.

Up to know if we exclude the suspected Mordellidae cited by Grimaldi et al. (2002), no published record and described taxa exist about Mordellidae in Burmese amber deposits. In the present paper we present and describe the first true Mordellidae; discuss comparative morphology of the new genus, additionally we reveal new knowledge concerning plant-insect interactions of the examined taxon.

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2. Materials and methods

Two specimens of Burmese amber from Hukawng Valley, Kachin Province (northern Myanmar) are stored in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing. The deposit in village Noije Bum was re-exploited in 1990s and since 2001 it has become the main source for excavation (Bao et al., 2018) (Fig. 1). The Burmese amber Lagerstätte has been dated as earliest Cenomanian, Cretaceous, ca. 99 Ma based on isotope analysis to the ash layers (Shi et al., 2012). Photomicrographs were taken using a Leica M205 A microscope system and Leica Application Suite (LAS Version 4.7) software; colour filters and agave syrup were applied to enhance the image quality. Hand drawings were created based on high-resolution images and illustrations from literature. CorelDRAW X7 (64-Bit) and Adobe Photoshop CS4 were applied for late image editing and text editing.

The familial/subfamilial classification in this paper follows that of Bouchard et al. (2005, 2011). The terminology and nomenclature follow "Handbook of Zoology" (Beutel and Leschen, 2016) and the recent research of current biology of Mordellidae (Ruzzier and Kovalev, 2016; Hsiao et al., 2018; Ruzzier, 2018). All measurements in the description are given in millimetres. This paper has been registered in ZooBank, the ICZN Official register of Zoological Nomenclature, with the unique digital ZooBank registration identifier (LSID urn: lsid: zoobank.org:pub:35AEC882-6ADC-4FBD-8A15-F83691E46379). The LSID number for the new taxa is given in the systematic paleontology section below.

3. Systematic paleontology

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Superfamily: Tenebrionoidea Latreille et al., 1802
Family: Mordellidae Latreille et al., 1802
Subfamily: Mordellinae Latreille et al., 1802
Tribe: Raynoldsiellini Franciscolo, 1957

Diagnosis. Tribe Raynoldsiellini Franciscolo, 1957 represented by only one extant monotypic genus, *Reynoldsiella parallela* Ray, 1930, recorded hitherto only from Venezuela. The most important differential character for Raynoldsiellini Franciscolo, 1957 is metatibiae without any kind of ridges, including the subapical one (Franciscolo, 1957; Peris and Ruzzier, 2013).

Primaevomordellida gen. nov.
LSID urn: lsid: zoobank.org: act:5CC9AB4D-97B1-4F73-8412-9C0F68453EF7

Type species: *Primaevomordellida burmitina* gen. et sp. nov.

Diagnosis. Primaevomordellida gen. nov. differs from *Reynoldsiella* mainly based on the following characters: (1) eyes small, glabrous; (2) metafemora not greatly enlarged; (3) subapical spurs on metatibiae long, about half length of metatibiae; (4) pygidium sharply elongated, length ratio between pygidium and hypopygidium 4:1; (5) branches of right genital parameron with equal length.

Fig. 1. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Myanmar. The border line of Republic of the Union of Myanmar is marked by yellow line. The current main source of Burmite is marked by red icon. Satellite map source from Google, scale bar 50 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Etymology. Primaevo (Latin) – primaevus, means original; primaevomordellida refers to the first true pintail beetle.

Primaevomordellida burmitina sp. nov.
(Figs. 2 and 3)

LSID urn: lsid: zoobank.org: act:5BBB6443-3582-4E0B-94F8-7066CF4AC45A

Diagnosis. As for the genus.
Type material. Holotype NIGP168789 (Male) and paratype NIGP168790 (sex undetermined) (reference numbers for collection of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing).
Etymology. Burmitina (Latin), related to mineralogical name burmite.
Description. Dimensions: holotype NIGP168789 is 3.0 mm in length, of the paratype NIGP168790 is 2.9 mm (pygidium excluded); body profile typically mordelloid, slightly arched in lateral view. General colour of the body integuments black, except for the orange anterior legs.

Head: head large, almost as the prothoracic width, strongly declined; eyes lateral, moderately small, finely faceted and glabrous, not reaching occiput. Occipital region wide and flat, matching perfectly with the anterior edge of pronotum. Antennae comparatively short, filiform and feebly serrate; antennomeres covered of setae. Apical palpomere securiform.

Prothorax: pronotum trapezoid in dorsal view, slightly narrowed in front and as wide as elytra at base; disc of the pronotum smooth and covered of short and dense recumbent hairs. Anterior legs simple; tibiae slender and linear, tarsus with all the five segments feebly dilated; tarsomere one to four bearing short spines at the detail margin; apical spurs on pro tibia present.

Meso and metathorax: scutellum triangular. Elytra, in dorsal view, subparallel at the humeri, gradually curving up to apex proximity; integuments covered with by fine setae. Metaepistena typically mordelloid, of the *Mordellistena*-type.

Coxal plate expanded, widely rounded at the posterior margin, typically mordelloid; trochanter reduced.

Metafemora laterally compressed and feebly expanded. Metatibiae elongated, subconical, with obliquely truncated apexes; metatibiae missing of any kind of ridge including the sub apical one; apical margin of hind tibiae bearing comb-like setae; ventral side of metatibiae and metatarsomeres presenting fine spine-like setae; Apical spurs on posterior tibiae present, equal in size and approximately half of length of metatibiae. Tarsal formula 5-5-4; Pro- and mesotarsomeres cylindical, slightly torso-ventrally compresses, onlychium instead apically on the fourth tarsomere; metatarsi laterally compressed, slender, presenting comb-like setae at the apical margin; length ratio of the four hind tarsomeres 3:2:1:1. Claws small and bi-cleft.

Abdomen: visible abdominal sternites with length ratio 3:3:3:4:8. Pygidium subconical, elongated and pointed at apex; pygidium length about four times the hypopygidium. Genital organs of holotype partially exposed. Apical part of penis visible, pointed.

Remarks. The holotype and paratype shows natural black or deep brown colour on elytra. Fine setae are well developed on the beetle body (including legs, antennae), dorsally and ventrally, regularly in a posterior direction. The amber matrix is not clear, contains a large amount of organic impurities.

4. Discussion

4.1. Morphology

Six tribes, Raynoldsiellini, Conaliini, Mordellini, Mordellistenini, Mediumiugini and Stenaliini are included in subfamily Mordellinae, with a distinctive evolutionary trend of the hind leg structures (Jackman and Lu, 2002; Peris and Ruzzier, 2013).

The filiform antennae, the *Mordellistena*-type episterna and the elongated pygidium place *Primaevomordellida burmitina* gen. et sp. nov. into Mordellinae undoubtedly and the simple hind leg structure without appendix structures assignes it to the basal tribe Raynoldsiellini. Compared to *Reynoldsiella parallela*, *Primaevomordellida burmitina* gen. et sp. nov. shows similarities to species of tribe Mordellini and Mordellistenini. These similarities include the dilatation of antennae starts from the 5th antennomere, which occurs in almost all Mordellini species; the 4th segment of the maxillary palpus is expanded, securiform, which is typical in genus *Mordella*; the scutellum shape is triangular which is common for most of Mordellini and Mordellistenini species, while for *Reynoldsiella parallela* this is exactly semicircular; the pygidium is obviously elongated, narrow and sharp-pointed, similar with the genus *Mordellapygium* (Franciscolo, 1957; Jackman and Lu, 2002).

The anterior tibiae have a generally linear shape in the majority of Mordellidae. The most common shape of anterior tarsus is

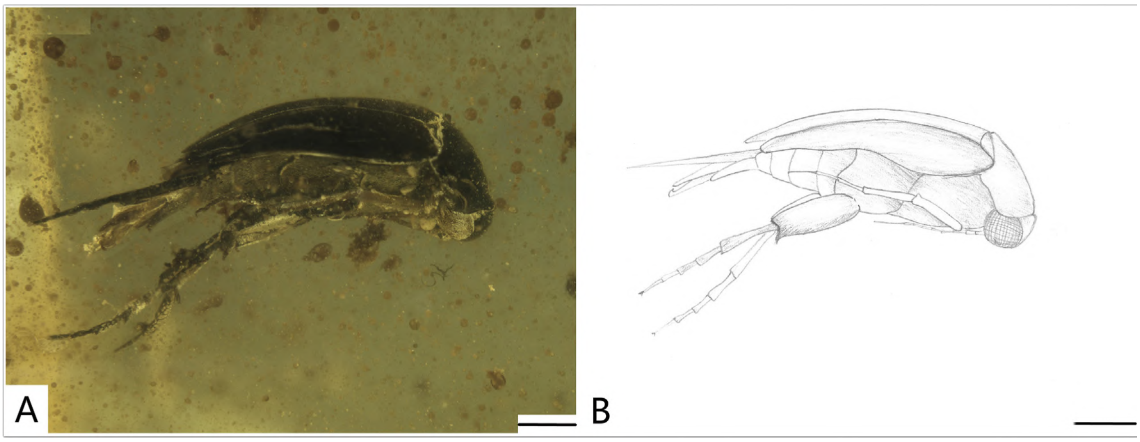

Fig. 2. *Primaevomordellida burmitina* gen. et sp. nov. general view, holotype NIGP168789. A. microscope photo, lateral view. B. Hand drawing. Scale bars 0.4 mm.

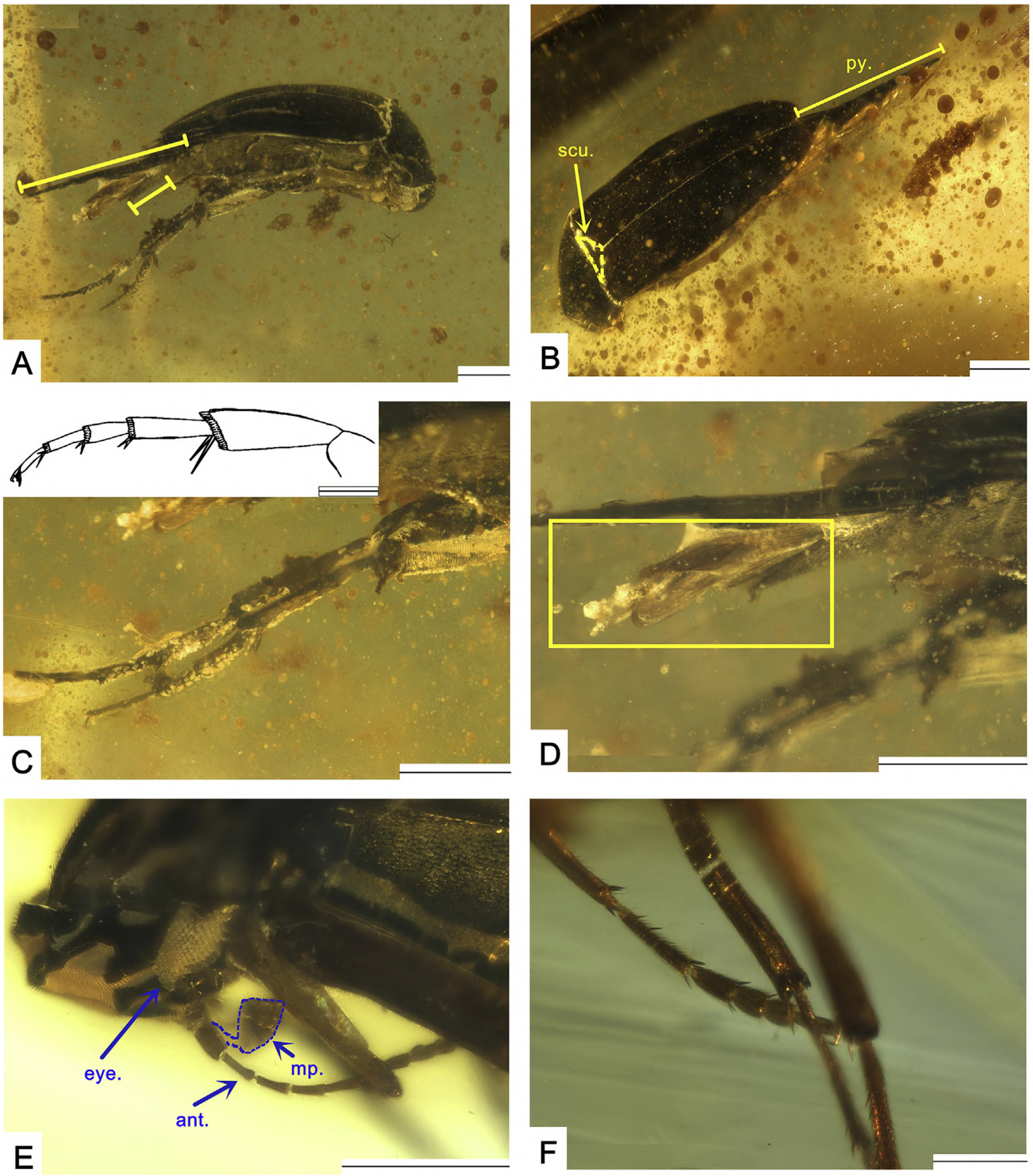

Fig. 3. Body structures of *Primaevomordellida burmitina* gen. et sp. nov. A. Lateral view, length of pygidium and last abdominal segment are indicated. B. Dorsal view, scu.- scutellum, py.- pygidium. C. hind leg structures, hand drawing is highlighted. D. Genital organ highlighted. E. Detail structures of head and mouthpart. eye.- eyes, ant.- antennae, mp.- maxillary palpus. F. Fore legs structures. A–D from holotype NIGP168789, E–F from paratype NIGP168790. Scale bar A–E 0.4 mm, F. 0.2 mm.

simple and linear with all the five segments, featured in genera *Mordella* and *Mordellistena*. These characters also applied for *Primaevomordellida burmitina* gen. et sp. nov., which differs from the Mesozoic fossil Mordellidae species *Mediumiuga sinespinis* (Spain, Cretaceous) with appendix structures on mesotibiae and mesotarsi (Peris and Ruzzier, 2013). The metafemora and metacoxae are not well developed in *Primaevomordellida burmitina* gen. et sp. nov. This character together with the absence of pygidium are the common characters for other Mesozoic mordellid or mordellid-like fossils, e.g. *Praemordella* sp. from the Jurassic of Kazakhstan (Scegoleva-Barovskaja, 1929), *Wuhua* sp. from the Jurassic of China (Wang and Zhang, 2011), as well as for *Mediumiuga sinespinis*, which made their taxonomic status doubtful.

4.2. Paleoecology

The feeding strategies of extant Mordellinae species are still under investigation. From the current knowledge, majority of Mordellinae members are featured by flower and pollen diet (Yang and Ren, 1999). They are widely distributed in all climate zones, and they have the highest species diversity in tropical regions. Larvae of mordellids usually develop in dead or decaying wood, except for few records of myrmecophilous species, life miners, stem forming species and frugivorous species; while adults are often found in warm forests or grasslands, preferring a diet of small flowers with umbel, corymb or head inflorescence (Borowiec and Kubisz, 1999). Even though the cooling trend of the last epoch of the Jurassic continued into the first age of the Cretaceous, the average temperature increased again and constantly until the end of the Cretaceous (Barron and Washington, 1982; Huber et al., 2002), which stimulated the flourish of angiosperms (Scott et al., 1960; Krassilov, 1977). Chaboureau et al. (2014) used a fully coupled climate model driven by Mesozoic paleogeographic maps to explain that climate change from arid to temperate dominance may have set the stage for the ecological expansion of flowering plants. The Cenomanian Burmese amber forests were dominated by Araucariaceae trees (Poinar et al., 2007b). Several angiosperm species have been described from Burmese amber based on flowers, represented by (1) Lauraceae species, flowers small, radial symmetry, raceme or umbel inflorescence (Poinar, 2017); (2) Cunoniaceae species, flowers small with four or five sepals and petals (Poinar and Chambers, 2017); (3) Cornaceae species, flowers small, actinomorphic (Poinar et al., 2007a); (4) Monimiaceae species, flowers small, composed of a cup-shaped perianth of 8 fused tepals arranged in one series with 8 equal subsessile (Poinar and Chambers, 2005). The flower corollas are normally small and underdeveloped, indicating the primary stage of angiosperm plant evolution. However, some flowers (undescribed) and other insect group (e.g. Diptera, Blattodea, Permopsocida) already showed clear evidence of insect - plant interactions, although it is difficult to determine which insects were actual pollinators (Santiago-Blay, 2005; Huang et al., 2016; Vršanský and Wang, 2017). According to the flower shape and living environment, it is assumed that the potential flower plant nutrition available in Burmese amber forests for *Primaevomordellida burmitina* gen. et sp. nov. was considerable. The mouthpart structures, e.g. the expanded 4th maxillary palpus segment, might have been a benefit for pollen detecting and the elongated pygidium would assist the movement along stamen. However, the underdeveloped hind legs and coxal may have impeded their jumping and flying movement and may have related to their defensive strategy, which could be a trait to other Jurassic – Cretaceous Mordellidae or mordellid-like species. For future research, with potentially better-preserved specimens, the pollen or nectar collecting structure, e.g. maniples or lacinia, should be examined in detail. The potential pollen remains, preserved on beetle body surface or in amber matrix, will also provide good evidence for Cretaceous insect-plant interactions.

5. Conclusions

The first true pintail beetle *Primaevomordellida burmitina* gen. et sp. nov. (Coleoptera: Mordellidae: Mordellinae) is described based on two specimens from Burmese amber (lower Cenomanian, ca. 99 Ma). The morphological characters of the new species suggest their taxonomic assignment to the most basal tribe of Mordellinae: Raynoldsiellini, some detailed body structures also showed similarity with advanced Mordellinae taxa, e.g. genera *Mordella* and *Mordellistena*. The common Mordellidae featured by a typical flower and pollen diet; the angiosperm fossil records prove the potential nutrition for the new species in Burmese amber forests. However, since the angiosperm plants did not dominate the Burmese amber forests and the new species retains morphological traits of other Jurassic – Cretaceous Mordellidae or mordellid-like species, the insect-plant interactions were probably at a primary stage.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2018.09.008.

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Short communication

New family Apotomouridae fam. nov. (Coleoptera: Tenebrionoidea) from lower Cenomanian amber of Myanmar

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ABSTRACT

The new family Apotomouridae fam. nov. (Coleoptera: Polyphaga: Tenebrionoidea) is described based on *Multispinus multispinosus* gen. et sp. nov. and *Apotomoura fortiscrura* gen. et. sp. nov. from Burmese amber (lower Cenomanian, ca. 99 Ma). The retractile wedge-shaped body and tarsal formula 5-5-4 placed Apotomouridae fam. nov. in Tenebrionoidea. The new family shares similarities with the Mordellidae, whereas the absence of pygidium and the combination of other microstructures assigned it more closely to the Jurassic beetle genus *Wuhua*. The morphological characters suggest the similar flower feeding style as to Mordellidae and Ripiphoridae, which represent the flower diet and pollinating strategy in the Tenebrionoidea.

1. Introduction

The Tenebrionoidea is one of the largest superfamilies in the animal kingdom with more than 34,000 described species and 29 recognized families (Lawrence and Newton, 1995; Yang and Ren, 1999; Slipinski et al., 2011; Gunter et al., 2014), with a newly described fossil family from Burmese amber, Late Cretaceous. Based on morphology, the new fossil family shows similarities to Mordellidae ("tumbling flower beetles"); however, the absence of pygidium and the combination of microstructures indicates a closer relationship to the Middle Jurassic genus *Wuhua* Wang & Zhang (Wang and Zhang, 2011).

The Mordellidae or mordellid-like fossil records from the Jurassic were represented by Praemordellidae and Liaoximordellidae (Scegoleva-Barovskaja, 1929; Wang, 1993; Liu et al., 2008, 2007). The Early Cretaceous *Mediumiuga* (Burgos, Spain) shares the primitive characters with modern Mordellidae, and is featured by appendix microstructures on mesotibiae and mesotarsi (Peris and Ruzzier, 2013). Mordellids from Baltic amber, i.e. *Glipostena ponomarenkoi* and *Mordellaria friedrichi*, are assigned to extant taxa (Alekseev, 2013; Perkovsky and Odnosum, 2013, 2009). The new fossil family is distinct within the main evolutionary trend of Mordellidae morphologically.

Tenebrionoids have a wide range of feeding strategies (Hunt et al., 2007), including herbivorous, frugivorous, saprophagous, predacious, fungivorous, root-eating, flower-eating and stem borers, in which extant Mordellidae and Ripiphoridae ("wedge-shaped beetles") represent with their flower diet and pollination (Yang and Ren, 1999; Beutel and Leschen, 2005). The morphological characters of the new family may suggest a similar feeding strategy.

2. Materials and methods

The research materials were five specimens of Burmese amber recovered from Hukawng Valley, Kachin Province in northern Myanmar (Fig. 1). The radiometric age of the Burmese amber deposit has been dated as earliest Cenomanian, Late Cretaceous, ca.

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Fig. 1. A–C. Location of recent amber mining area in the Hukawng Valley, Myitkina Province, Myanmar (modified from Kania et al., 2015).

99 Ma (Ross, 2010; Shi et al., 2012). The studied material is stored in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing. Photomicrographs were taken using a Leica M205A microscope system and Leica Application Suite (LAS Version 4.7) software; color filters and agave syrup liquid were applied to enhance the image quality. Hand drawings were based on high-resolution images; CorelDRAW X7 (64-Bit) and Adobe Photoshop CS4 were applied for late image editing and text editing.

The terminology and nomenclature in this paper follows that from Bouchard et al. (2011, 2005). This research has been registered in ZooBank, the ICZN Official register of Zoological Nomenclature, with the unique digital ZooBank registration identifier (LSID urn:lsid:zoobank.org:pub:EFBB5958-5D52-4FD4-A5A2-CFD9E0D47C21). The LSID numbers for the new taxa are listed under each new taxon name in the Systematic Palaeontology section.

All measurements in the description are in millimetres.

3. Systematic paleontology

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Superfamily: Tenebrionoidea Latreille, 1802
Family: Apotomouridae fam. nov.
LSID urn:lsid:zoobank.org:act:086C7E0B-E0C2-490B-B836-D6140F6AD82E

Type species: *Multispinus multispinosus* gen. et sp. nov. and *Apotomoura fortiscrura* gen. et sp. nov.

Diagnosis. Beetles small, wedge-shaped; fore bodies retractile, which caused the body to curl into a C-shape; elytra entire; pygidium reduced; five visible abdominal sterna, with well-developed spines preserved on the posterior margin of I-IV sterna. Antennae short, 11 antennomeres, filiform or serrate; length from moderately short to half of the body length. Maxillary palpi with four palpomeres, apical palpomere slightly expanded. Metasternum very large. Hind legs long and strong; sclerotized spines preserved on metatibiae and at least on first meta-tarsomere. Short setae widely preserved on the surface of head, pronotum, elytra, sterna and legs. Claws small and simple.

Etymology. Apotomos (Greek) – short; oura (Greek) – tail. Apotomouridae is referring to the short body shape, without last sterna elongation.

Multispinus gen. nov.
LSID urn:lsid:zoobank.org:act:4BD5B958-B109-4E39-A683-570B6BBDB5EF

Diagnosis. Body small, wedge-shaped, size 2.20 mm–2.50 mm; shape smooth, streamlined, color dark brown to black. Head large, declined. Pygidium reduced. Fore and mid legs slender and shorter than the hind legs. Metafemora strong and enlarged, sclerotic spines or comb-like setae widely preserved on the metatibiae and metatarsi. Claws small with 2 spines.

Etymology. Multispinus (Latin) – many spines, referring to the character of hind legs.

Multispinus multispinosus sp. nov. (Fig. 2–3.)
LSID urn:lsid:zoobank.org:act:CEB1A8FE-92EB-47DD-9BA8-84899D95D3B0

Diagnosis. As for the genus.

Type material. Holotype NIGP168210 and paratype NIGP168211, NIGP168212 are adult specimens; holotype male, paratype sex unknown.

Etymology. As for the genus, different suffix for species name.

Description. The body of holotype NIGP168210 is 2.27 mm long, of paratype NIGP168211 is 2.50 mm long and paratype NIGP168212 is 2.35 mm long; wedge-shaped, widest at base of prothorax, slightly narrowed anteriorly and strongly narrowed posteriorly. Lateral view, body curled up with slightly convex abdomen.

Head large, triangular in frontal view, strongly declined, as wide as apex of thorax, abruptly constricted behind eyes to form a narrow neck which is concealed by pronotum; hypognathous. Occipital region with transverse carina that adjoin anterior edge of pronotum. Eyes lateral, large, well developed, shape oval, entirely emarginated, finely faceted, interfacetal setae reduced. Antennae are about half-length of the body; filiform; consist of 11 antennomeres, covered with short setae. Clypeus distinct; labrum prominent; maxillary palpi long with four visible palpomeres, apical palpomere slightly expanded, scalene.

Pronotum is 0.52 mm long in holotype, narrowed in front, as wide as elytra at base, widest posteriorly; shape irregular, sides moderately curved; surface rugose-punctate. Lateral pronotal carinae complete, simple, without raised margin or bead. Prosternum short, concave. Mesosternum about twice the length of prosternum, carinate; mesocoxae small. Metasternum large, about three times length of prosternum; metacoxae very large, flat, contiguous. Scutellar shield small, posteriorly narrowly rounded. Elytra is 1.58 mm long in holotype, narrowed behind, exceeding the body, surface rugose-punctate; margin fold up slightly. Legs well developed; hind legs longer and stouter than fore and mid legs. Trochanter joint strongly oblique with base of femur in contact with coxa. Metafemora enlarged for jumping. Metatibiae slender, with large spurs preserved by side; slightly expanded posteriorly with terminal comb-like setae. Tarsal formula 5-5-4, tarsomeres compressed, slender. Spurs preserved in the inner surface of the first tarsomere; comb-like setae preserved in the same position of 2nd to 4th tarsomeres. Claws very small, cleft; terminal sharp, with 2 short spines.

Abdomen with five sterna, with slightly sclerotized spines on the posterior margin of I-IV sterna, V sternum distinctly narrowed posteriorly, sutures distinct; pygidium reduced; surface micro-rugose. Male genitalia are visible in holotype specimen, short.

Remarks. Due to the surrounding amber matrix, the specimen appears dark-brown to black in color, without patterns and spots on scutellum and elytra. Setae are well developed, from head until the terminal abdomen; neatly toward posterior direction. Wings folded and rolled under elytra.

Apotomoura gen. nov.
LSID urn:lsid:zoobank.org:act:BF540A74-B2B7-47A7-B78B-D0483C8A000E

Diagnosis. Body usually very small, wedge-shaped, size 1.50 mm–1.70 mm; shape smooth, streamlined, normally curved; thorax big; color black. Head large, lying flush to thorax. Abdomen sterna contracted; pygidium reduced. Fore and mid legs slender and shorter than the hind legs. Metafemora strong and enlarged; metatibiae and metatarsi short and strong; 3–4 sclerotic spines preserved on the metatibiae and the first tarsomere. Claw small.

Etymology. Apotomos (Greek) – short, oura (Greek) – tail, referring to the short body.

Apotomoura fortiscrura sp. nov. (Fig. 4.)
LSID urn:lsid:zoobank.org:act:47D094F1-939A-4481-8F87-5EEC011FBAEC

Diagnosis. As for the genus.

Type material. Holotype NIGP168213 and paratype NIGP168214 are adult specimens, sex unknown.

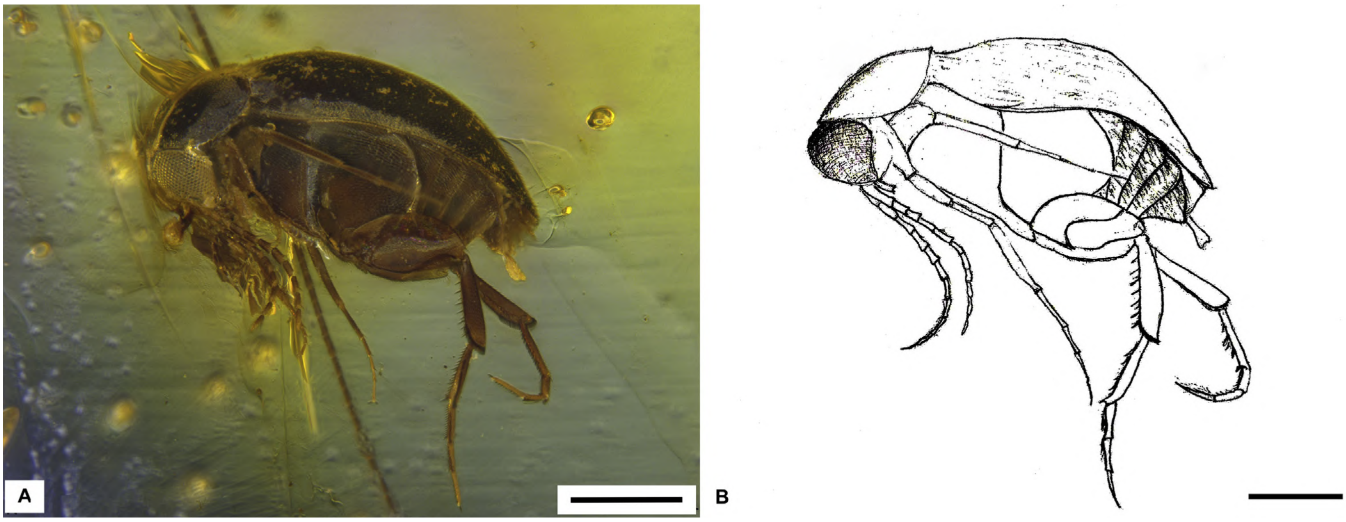

Fig. 2. *Multispinus multispinosus* gen. et sp. nov. general view, holotype NIGP168210. A. microscope photo, lateral view. B. Hand drawing. Scale bars 0.5 mm.

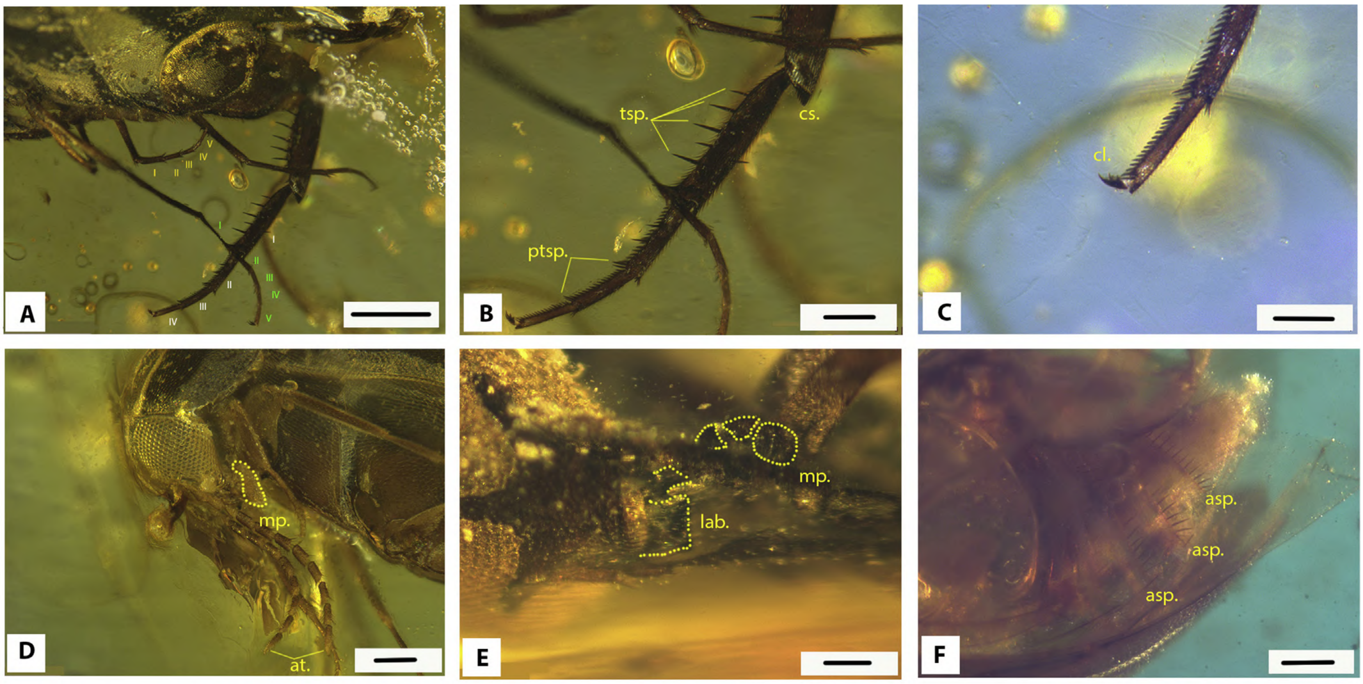

Fig. 3. *Multispinus multispinosus* gen. et sp. nov. details. A–C. Details of leg structure, paratype NIGP168211. A. Tarsal formula 5-5-4. I–V, tarsal segment number. B. Spines and setae structure. tsp.- tarsal spine, ptsp.-posterior margin tarsal spine, cs.-comb-like setae on posterior margin of metatibiae. C. Claws. cl.- claws, with 2 spines. D, E. Head and mouthpart structures, holotype NIGP168210. mp.- maxillary palpi. at.- antennae. lab.- labrum. F. Spines preserved in posteriors margin of abdominal sterna, specimen NIGP168212. asp.- abdominal spines. Scale bars 0.1 mm.

Etymology. Fortis (Latin) – strong, scrura (Latin)-legs, referring to the morphological character.

Description. The body of holotype NIGP168213 is 1.69 mm long; of paratype NIGP168214 is 1.64 mm long; wedge-shaped, widest at posterior base of prothorax, slightly narrowed anteriorly and posteriorly. Lateral view, body strongly curled upwards; thorax inflated conspicuously; hind legs very large and stretched.

Head large, oval in frontal view, strongly declined, as wide as apex of thorax, sharply constricted behind eyes, hypognathous; surface rugose-punctate, with short setae covered widely. Eyes lateral, large, well developed, shape oval, entirely emarginated, finely faceted, interfacetal setae well developed. Antennae short, not extending beyond thorax; serrate-filiform; antennomeres triangular to oval. Clypeus distinct; maxillary palpi moderated with four palpomeres, apical palpomere expanded, securiform.

Pronotum is 0.51 mm long in holotype, narrowed in front, as wide as elytra at base, widest posteriorly; surface smooth; shape irregular, margin without fold or setae. Prosternum abbreviated, metasternum large. Metacoxae very large, flat, contiguous. Scutellar shield small, triangular, posteriorly narrowed. Elytra highly curled, narrowed behind, surface rugose-punctate; margin smooth. Hind legs longer and stouter than fore and mid legs. Trochanter reduced. Metafemora strongly enlarged; metatibiae short but

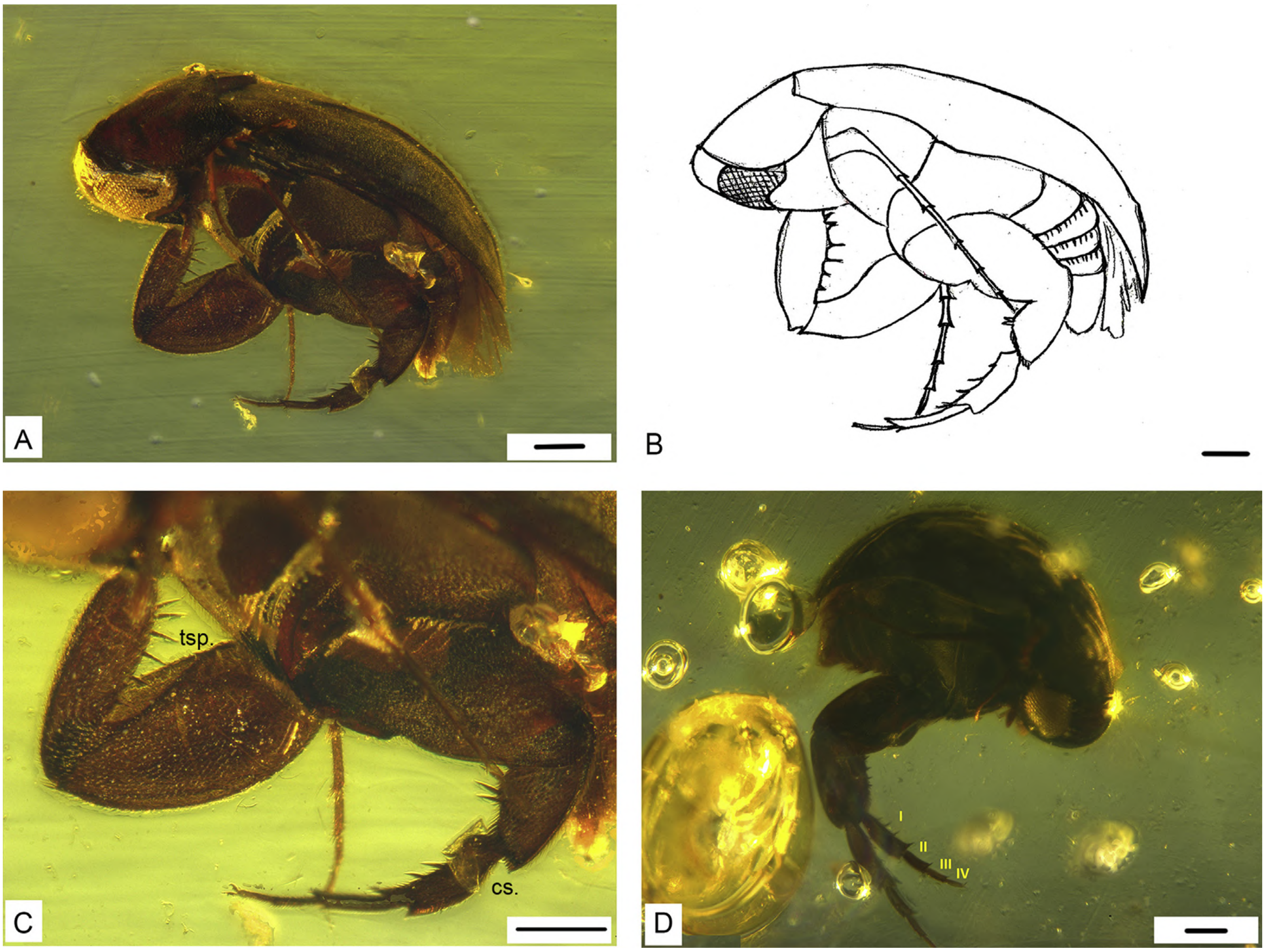

Fig. 4. A, B. *Apotomoura fortiscrura* gen. et sp. nov. general view, holotype NIGP168213. A. microscope photo, lateral view. B. Hand drawing. C. Spines and setae structure, holotype NIGP168213. tsp.- tibiae spine, cs.-comb-like setae on posterior margin of tibiae. D. Tarsal formula, hind tarsi 4 segments, paratype NIGP168214. I–IV, tarsal segment number. Scale bars 0.2 mm.

strong, with 3–4 tiny spurs preserved by side; comb-like setae preserved by the posterior terminal. Tarsal formula 5-5-4, tarsomeres compressed, shorter and stronger compared with *Multispinus multispinosus* sp. nov.; all tibiae and tarsi with distinct apical ridges; 3–4 tiny spurs preserved by side of the first tarsomere; a pair of short setae preserved at the posterior margin of each tarsomere, no comb-like setae. Claws very small.

Abdomen with five sterna, narrowed posteriorly, surface microrugose, sutures distinct; pygidium distinct.

Remarks. Specimen color black or dark brown. The preserving posture of all the specimens are similar, highly curled and hind legs extended. Body setae short and less dense. Wings folded and rolled under elytra.

4. Discussion

The retractile wedge-shaped body and tarsal formula 5-5-4 in Apotomouridae fam. nov. place it in the superfamily Tenebrionoidea (Lawrence and Newton, 1995; McHugh and Cornell, 2009; Lawrence and Ślipiński, 2013). Though the strongly convex body and enlarged hind leg indicate their similarity to the family Mordellidae (1) the absence of pygidium, (2) well-developed setae on body, (3) sclerotized spines on lateral metatibiae and between abdomen sterna, these characters in combination have never been recorded (Liljeblad, 1945; Franciscolo, 1957). These characteristics distinctly set Apotomouridae fam. nov. apart from Mordellidae and other closely related families within the Tenebrionoidea. Compared with Rhipiphoridae, the Apotomouridae fam. nov. does not show the typical bipectinate (in male) and unipectinate (in female) antennae. With the Meloidae, it does not have an elongated body and deflexed head; with the Scraptiidae, it shows more complicated tibiae and tarsal structures like spines and setae; and with the Melandryidae, its tibial spurs preserved, claws cleft, simple with spines.

A long and pointed pygidium is common for extant Mordellidae (Arthur, 1930; Lu, 1997; Jackman and Lu, 2002; Odnosum, 2010). However, for Mesozoic mordellid or mordellid-like fossil species, this character varies. Pygidiums were completely absent in the oldest Middle Jurassic Tenebrionoidea genus *Wuhua* (Wang and Zhang, 2011). The Late Jurassic species *Liaoximordella hongi* has six abdominal sterna (Wang, 1993). Another of the Late Jurassic mordellids (Mordellidae: Praemordellinae) from Yixian Fm. (China) show pointed last sternum but without obvious prolongation (Liu et al., 2008, 2007). *Mediumiuga* sp. from Early Cretaceous amber of Spain shows a very short pointed pygidium (Peris and Ruzzier, 2013). Two Eocene mordellids species from Baltic amber show typical long and pointed pygidium, both are assigned to extant genera (Ubisz, 2003; Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013). Though the formation process of amber may cause the inclusive biological tissue and organs (e.g. genitalia) to shrink or become lost (Pike, 1993; Ross et al., 2010), the abundance of Apotomouridae fam. nov. specimens and amount of Mordellidae or mordellid-like specimens that were discovered at the same amber locality supported the idea that the pygidium absence is apomorphy, not coincidence. Based on the body shape, tarsal formula 5-5-4, the absence of pygidium, and the claws formula we suggest *Wuhua* as a basal taxon of Apotomouridae fam. nov., distinct from extant and fossil Mordellidae species. The Late Cretaceous Apotomouridae fam. nov. species share some primitive characters with Mordellidae such as the slight expansion of maxillary palpi and the enlargement of the metafemur. These shared characters indicate the similar feeding strategy within Mordellidae and the its sister taxon Ripiphoridae (Zhang et al., 2018). The evolution from Jurassic mordellids and *Wuhua* to Cretaceous taxa, further on to Cenozoic taxa, highlights the possible changing of locomotion strategy from simply crawling to jump-flying (Huang and Yang Jun, 1999) and the changing of diet from surface nutrition (fungi, moss, lichen, wood, plant fragments) (Wang et al., 2013; Peris et al., 2017) to herbaceous flowers (Franciscolo, 1957).

5. Conclusions

A new family of tenebrionid beetle Apotomouridae fam. nov. (Coleoptera: Tenebrionoidea) is described based on two new genera from Burmese amber (lower Cenomanian, ca. 99 Ma). The morphological characters of the new family suggest a similar pollen feeding style like extant Mordellidae and Ripiphoridae, which reflects the angiosperm plant and insect coevolution during the Cretaceous. A comprehensive discussion about the ecological implications will be provided based on further studies.

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RESEARCH PAPER

A new species of tumbling flower beetle (Coleoptera: Mordellidae) from Baltic amber

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Abstract

A new species of tumbling flower beetle (Coleoptera: Mordellidae) *Tomoxia succinea* sp. nov. is described based on two Baltic amber specimens. The new species differs from the only extant European species of this genus, *Tomoxia bucephala* Costa, 1854, mainly in the shape of the scutellum and the length ratio of particular body parts. The fossil records of Mordellidae found in Baltic amber are summarized; their paleoecology in the Paleocene–Eocene of the Baltic region and the composition and distribution of the family Mordellidae are discussed.

Keywords Coleoptera · Mordellidae · New species · Baltic amber · Eocene · Paleoecology

Introduction

The Mordellidae Latreille, 1802 (Coleoptera: Tenebrionoidea), commonly known as tumbling flower beetles due to their irregular jumping movement, or pintail beetles on account of the special elongated posterior pygidium, include approximately 2400 extant species worldwide and only a few fossil records (Jackman and Lu 2002; Peris and Ruzzier 2013). The genus *Tomoxia* Costa, 1854 (tribe Mordellini) is represented by 52 extant species found in all zoogeographic regions except for Madagascar (Hallan 2012). *Tomoxia bucephala* Costa, 1854 is the only extant species distributed in Europe (De Jong et al. 2014).

A new *Tomoxia* species is described and identified herein, based on two Baltic amber specimens. The morphological differences and similarities between the new species and *T. bucephala* are discussed. Compared with other Mordellidae found in Baltic amber, the habitat of *Tomoxia* reflects the vegetation composition and therefore the paleoecology of the Eocene Baltic amber forest.

Material and method

The research material comprised two adult specimens in Baltic amber stored in the Laboratory-Museum of Amber Inclusions, Gdansk University, Poland. Baltic amber is amongst the largest and most significant of the world's amber deposits. It occurs primarily along the shores of the Baltic Sea in Paleogene sands dated to as early as 40 Ma ago (Ritzkowski 1997; Kosmowska-Ceranowicz 2005). The diagenetic history of Baltic amber from its origin until the present has been outlined by Gaigalas and Halas (2009) based on isotope analysis.

Photomicrographs were taken using a Leica M205 A microscope system and the Leica Application Suite (LAS

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Version 4.7) software; color filters and agave syrup were used to improve the image quality. Hand drawings and reconstruction were based on high-resolution images. CorelDRAW X7 (64 bit) and Adobe Photoshop CS4 were used for final image and text editing.

The familial/subfamilial classification employed in this paper follows that of Bouchard et al. (2005, 2011). The terminology and nomenclature follows the *Handbook of Zoology* (Beutel and Leschen 2016).

This paper has been registered in ZooBank, the ICZN official register of zoological nomenclature, with a unique digital ZooBank registration identifier (LSIDurn:lsid:zoobank.org:pub:97F1B25F-0067-456D-A024-B4A9C4B6E8ED).

All measurements given in the description below are in millimeters.

Systematic paleontology

Order **Coleoptera** Linnaeus, 1758
Suborder **Polyphaga** Emery, 1886
Superfamily **Tenebrionoidea** Latreille, 1802
Family **Mordellidae** Latreille, 1802
Tribe **Mordellini** Seidlitz, 1875

Genus ***Tomoxia*** Costa, 1854

Type species. Tomoxia bucephala Costa, 1854.

Diagnosis (emended). The diagnostic characters for the genus *Tomoxia* when compared to the other members of the tribe Mordellini are: (1) eyes finely granulated; (2) scutellum quadrilateral or irregular shaped; (3) hind tibia with a fine dorsal ridge and a lateral ridge; basal tarsomere of hindleg also with a fine dorsal ridge (Smith 1882; Liljeblad 1945; Franciscolo 1965; Jackman and Lu 2001).

Tomoxia succinea sp. nov.
Figures 1, 2

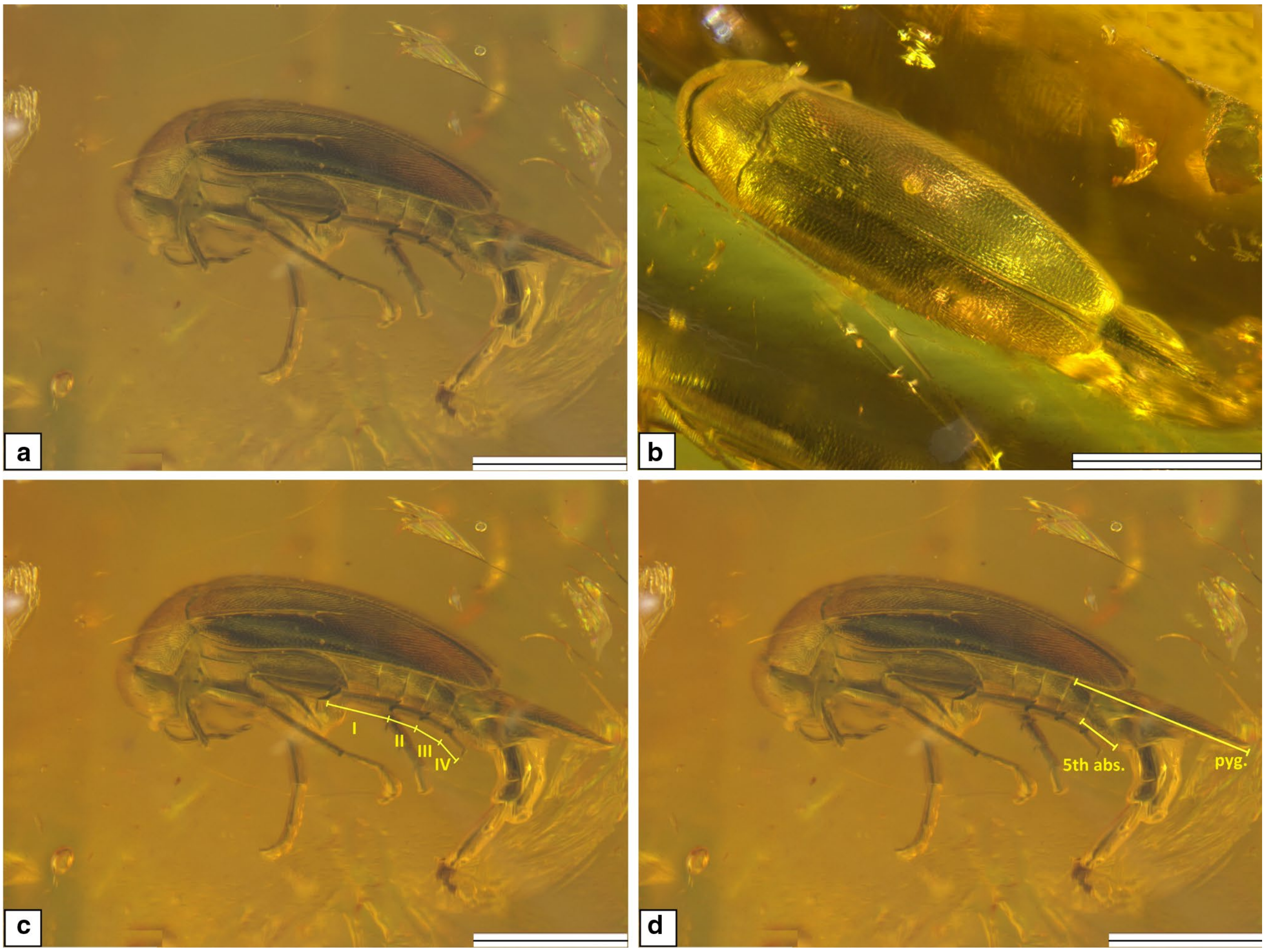

Fig. 1 Holotype of *Tomoxia succinea* sp. nov. **a** Lateral view. **b** Dorsal view. **c** I–IV: 1st to 4th hind tarsomeres; length ratio 2:1:1:1. **d** *5th abs.* the 5th abdominal sternum, *pyg.* pygidium, length ratio 1:4. Scale bar: 1 mm

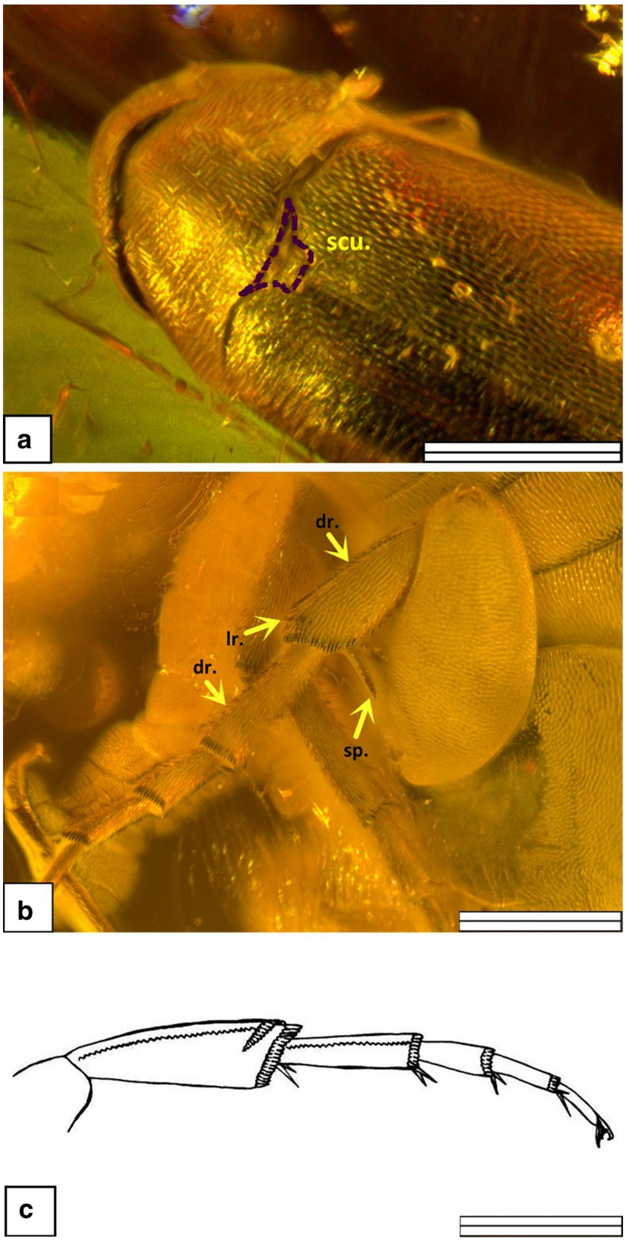

Fig. 2 Detailed morphological structures. **a** Highlighted scutellum shape (holotype). *scu.* scutellum. **b** Detailed hind leg structures (paratype). *dr.* fine dorsal ridge, *lr.* lateral ridge, *sp.* subapical spines on tibia and tarsomere. **c** Schematic drawing of hind tibia and tarsi. Scale bar: 0.5 mm

Etymology. From *succinum*, Latin for amber.

Type material. Holotype 5715 and paratype 5743 (reference ID for the collection of the Laboratory-Museum of Amber Inclusions, Gdansk University), adult specimens; sex unknown.

LSID number. LSIDurn:lsid:zoobank.org:act:0E01A684-3C9E-4C43-82CF-82180FFDC9CC.

Diagnosis (emended). The differential specific diagnosis for *Tomoxia succinea* sp. nov. is: (1) the length to width ratio of the pronotum is 1:2, slightly narrower than the elytra at base; (2) the length ratio between the last abdominal sternum and pygidium is 1:4; (3) the length ratio of the hind tarsomeres is 2:1:1:1; (4) the form of the scutellum is transitional, ranging from triangular to quadrilateral.

Description. The body of the holotype is 2.6 mm long, that of the paratype is 2.9 mm long; edge-shaped, widest at base of prothorax, much narrower posteriorly, lying in lateral view, curled up with a slightly convex abdomen.

Head rather large, almost of prothoracic width, finely punctured; eyes large, ellipsoidal, finely faceted and granulated, apparently not reaching occiput, hairy. Antennae long, filiform. Mouthpart is invisible due to preservation. Pronotum trapezoidal or quadrilateral from dorsal view, length to width ratio 1:2, slightly narrower than elytra at base. Anterior lobe moderate, not distinctly narrow, slightly protruding inwards, anterior angles not visible from above; lateral margins gradually curved from anterior to posterior angles; posterior margin sinuate, posterior lobe slightly protruding backwards. Scutellum irregular quadrilateral. Elytra elongated, cuneate; sculpture reticulate with rather obvious and fine punctures; leather luster, lateral margin rounded and smooth; posterior margin narrow and rounded, not sharp. Mesothorax and metathorax enlarged, flat, covered by fine setae. Middle tibiae as long as first three segments of same pair of legs; hind tibiae with a fine but obvious dorsal ridge and a lateral ridge close to subapical side. Basal tarsomere of hindleg also with fine dorsal ridge; last two tarsomeres of hindleg slightly longer, length ratio of four hind tarsomeres 2:1:1:1; pair of subapical spines preserved on each tarsomere. Five abdominal sterna with length ratio 3:2:2:2:4, compact and neatly connected, no appendix structure between each. Pygidium elongated and pointed; length ratio between last abdominal sternum and pygidium is 1:4.

Remarks. The holotype has an unusual leathery shiny gloss; the paratype has a natural black color pattern on the elytra. The beetle cuticle is punctured, setae are well developed on the body, dorsally and ventrally, regularly in a posterior direction. Genital structure is not clear due to the preservation. Paratype body surface covered by fine white layer, which is typical for Baltic amber inclusions due to the effect of the air during preservation.

Discussion

Worldwide, over 50 species of *Tomoxia* have been recorded. The general body plan of species in the genus *Tomoxia* does not vary significantly, which increases the difficulty associated with taxonomic studies of members of this genus and leads to unclear descriptions and classifications. For example, after a detailed review of North American Mordellidae, only four species were retained in the genus *Tomoxia* (Jackman and Lu 2001). South African (Franciscolo 1957, 1965, 1967) and North American (Liljeblad 1945) *Tomoxia* species are mainly identified based on tiny structures such as segments of the maxillary palps. Due to preservation issues, it is often difficult to study such small structures in Baltic amber specimens, so we focused on the gross morphology. Compared with the representative North American species *Tomoxia inclusa* LeConte, 1862 and *Tomoxia lineella* LeConte, 1862, *Tomoxia succinea* sp. nov. has no surface color stripe, a scutellum with a sharper outline, and slightly longer antennae. The new species differs from the closely related genera *Tomoxioda* Ermisch, 1950 and *Paratomoxioda* Ermisch, 1954 in having a fine dorsolateral ridge on the hind tibiae, posterior angles of the pronotum that are not sharp, and an anterior pronotum that is inseparably connected with the head (Horák 2007). Compared with the only European extant species *Tomoxia bucephala*, *Tomoxia succinea* sp. nov. has a longer pygidium and hind tarsi, the body shape is more cuneate than streamlined, and the scutellum has a transitional form, ranging from triangular to quadrilateral. However, the obviously wide head, finely granulated eyes, and the similarity in the type and position of the appendix structures on the hindlegs suggest a close relationship between *T. bucephala* and *T. succinea* sp. nov.

Fossils of Mordellidae found in Baltic amber are assigned to two tribes: Mordellistenini Ermisch, 1941a, b and Mordellini Seidlitz, 1875 (Germar 1813; Ermisch 1941b; Kubisz 2003; Odnosum and Perkovsky 2010; Perkovsky and Odnosum 2013) (Table 1), with comparatively high diversity observed in fossil Mordellidae species. During this study, a total of 39 mordellid specimens in the Laboratory-Museum of Amber Inclusions, Gdansk University were examined, amongst which members of the genus *Mordellistena* Costa, 1854 are the most common. The highest species richness of extant Mordellidae occurs in the tropical zone. In the subtropical and warm temperate zones, the species richness is slightly, but not considerably, lower than that in the tropical zone (Table 2). Therefore, the warm climate of Paleocene-Eocene times in the Baltic Sea region (Askin and Spicer 1995) would not have affected the total biodiversity of Mordellidae, but it could have impacted the vegetation composition and ecology (Sadowski 2017; Euro+Med PlantBase 2011). Extant members of *Mordellistena* are widely distributed across all climatic zones (Table 2). Their larvae are generally pith borers and they have a wide range of host plants, including species of Asteraceae von Berchtold and Presl, 1820, Fabaceae Lindley, 1836, Fagaceae Dumortier, 1829, Menispermaceae Jussieu, 1789, Poaceae Barnhart, 1895, Sapindaceae Jussieu, 1789, Juglandaceae de Candolle, 1818, and Tiliaceae Jussieu, 1789 (Ford and Jackman 1996; Jackman and Lu 2002). Inclusions of Fabaceae, Fagaceae, and Poaceae are not uncommon in Baltic amber (Sadowski 2017). By comparison, the larvae of *Tomoxia bucephala* normally grow in the stems of plants belonging to the genera *Populus* Linnaeus, 1753 and *Salix* Linnaeus, 1753 (family Salicaceae) (Burakowski et al. 1987; Borowiec 1996). Related Salicaceae species are very rare in Baltic amber, with only one described: *Saliciphyllum succineum* (Sadowski 2017). The presence of only three fossil records of the chrysomelid genus *Crepidodera* in Baltic amber also

Table 1 List of fossil records of Mordellidae found in Baltic amber

Species	Depository
Falsomordellistena eocenica† (Kubisz 2003)	ISEA Krakow collection
Glipostena ponomarenkoi† (Odnosum and Perkovsky 2010)	Klesov locality SIZC K collection, (Rovno amber)
Glipostena sergeli† (Ermisch 1941a)	Hoffeins/Deutsches Entomologische Institut collection
Mordellistena amplicollis† (Ermisch 1941a, b)	Hoffeins/Deutsches Entomologische Institut collection
Mordellistena antiqua† (Ermisch 1941a, b)	Scheele collection, University of Hamburg
Mordellistena goeckei† (Ermisch 1941a, b)	Scheele collection, University of Hamburg
Mordellistena korschefskyi† (Ermisch 1941a, b)	Hoffeins/Deutsches Entomologische Institut collection
Mordellistena soror† (Ermisch 1941a, b)	Hoffeins/Deutsches Entomologische Institut collection
Mordellistena sp.	Laboratory-Museum of Amber Inclusions, Gdansk University
Mordella inclusa (Germar 1813)	Halle collection
Mordella scheelei† (Ermisch 1941a, b)	Scheele collection, University of Hamburg
Mordella sp.	Hoffeins/Deutsches Entomologische Institut collection
Mordella sp.	Laboratory-Museum of Amber Inclusions, Gdansk University
Mordellaria friedrichi† (Perkovsky and Odnosum 2013)	Schmalhausen Institute of Zoology SIZC collection
Tomoxia succinea sp. nov.†	Laboratory-Museum of Amber Inclusions, Gdansk University

†The extinct fossil taxa

Table 2 Species richness of Mordellidae in different climatic zones

Regions	Genera	Species	Dominant genera
Southeast Asia	30	183	*Gilpa, Mordella, Mordellistena*
West Africa	25	62	*Mordellina, Mordellistena*
Amazon region	19	129	*Mordella, Mordellistena*
East China	14	27	*Mordella, Mordellina*
Apennines	14	120	*Mordella, Mordellistena*
Balkans	10	77	*Mordellistena*
Central Europe	13	110	*Mordella, Mordellistena*
West Europe	15	115	*Mordella, Mordellistena*
North Europe	12	99	*Mordella, Mordellistena*
Siberia	3	3	*Mordella, Mordellistena, Stenalia*
Quebec, Canada	2	3	*Mordellistena*
British Columbia, Canada	1	1	*Mordella*

Purple tropical zone, Yellow subtropical zone, Green warm temperate zone, Grey cold temperate zone

support the scarcity of Salicaceae in the Baltic amber forest, because these beetles are oligophagous—they feed on *Salix* and *Populus* species (Bukejs et al. 2016). In the Early Cenozoic, they may have subsisted on *Saliciphyllum*, like *Tomoxia* but unlike *Mordellistina*, reflecting their relative abundance.

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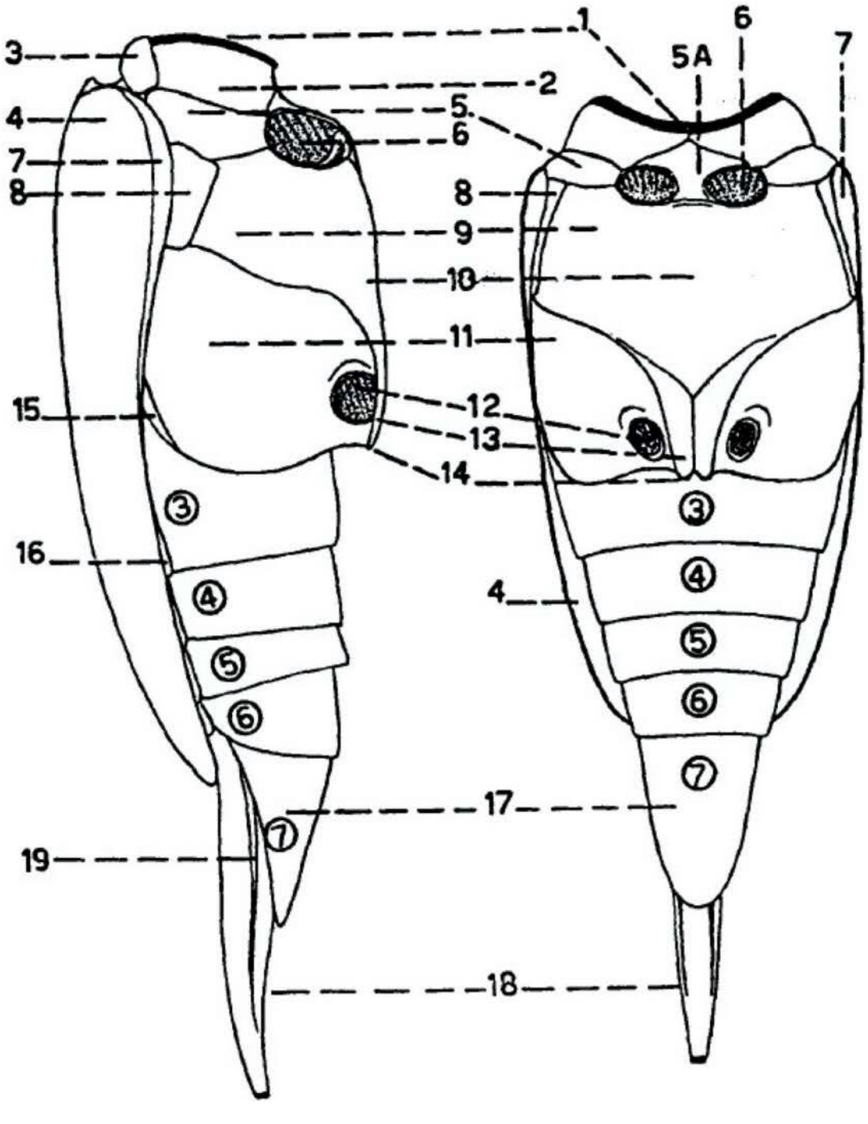
Appendix 7.

Simplified nomenclature of Coleoptera morphology (take Mordellidae as schematic example, based on Franciscolo, 1957 and Liu, 2007).



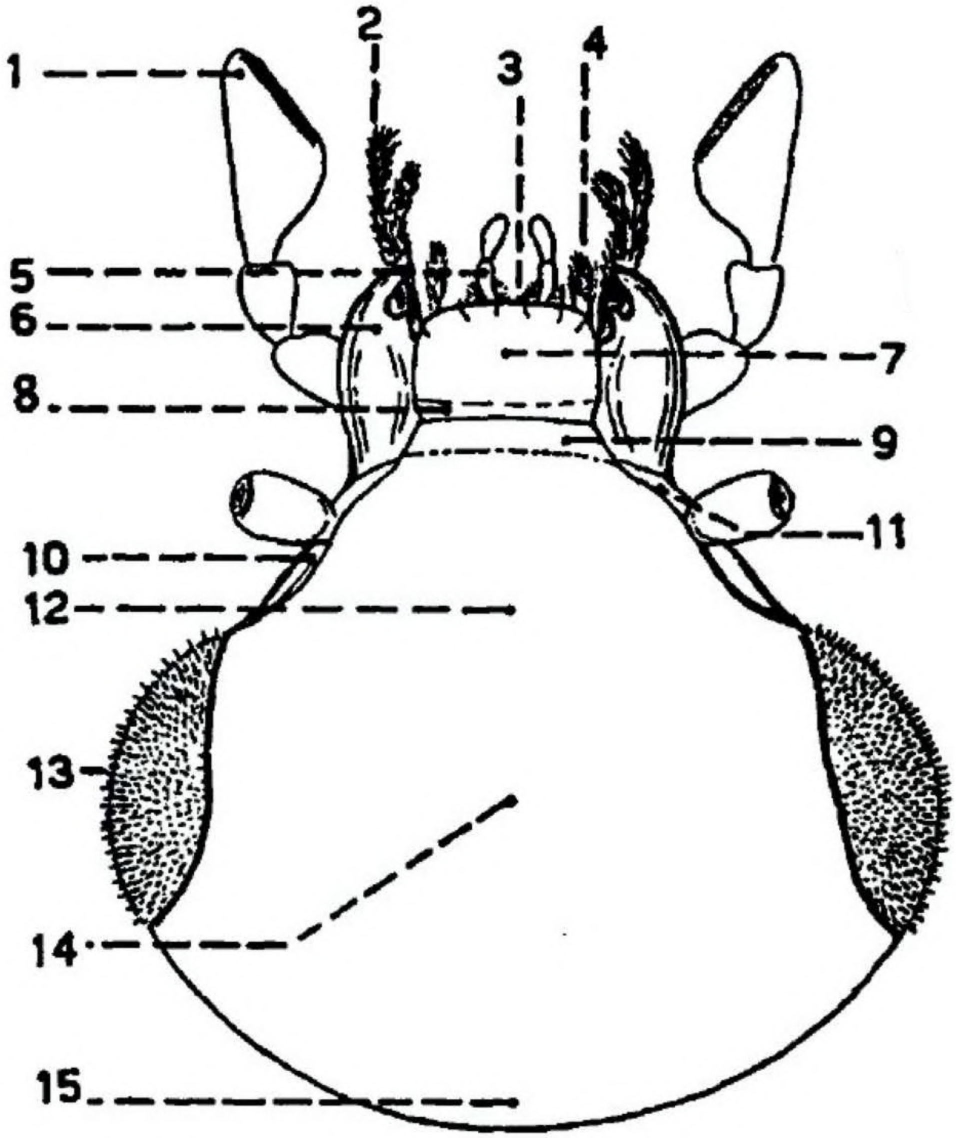
1. Anterior margin of mesosternum, the narrow marginal area of the mesosternum adjacent with the prosternum.

2. Mesoepisternum, the anterior part of the mesopleuron above the middle coxa.

3. Mesoepimere, the dorsal process of the thorax.

4. Elytron, the heavily, chitinized, frequently leathery fore wing of some insect groups protecting the soft abdomen and the membranous hind wing.

5. Mesocoxal plate, plate structure on the middle coxa.
6. Mesocoxal cavity, articular hole of the middle coxa.
7. Epipleuron, the downturning portion of the elytron.
8. Metepisternite, the anterior part of the metapleuron above the hind coxa.
9. Metasternal lobe, the lobate outgrowth on the ventral side of the metathorax together with the pleural sclerites and the pair of hind legs.
10. Metasternal plate, the plate structure of the ventral side of the metathorax together with the pleural sclerites and the pair of hind legs
11. Metacoxal plate, the plate structure of hind coxa.
12. Metacoxal cavity, the articular hole of the hind coxa.
13. Metacoxal apophyse or process, the elongate outgrowth mostly on the distal part of the hind coxa on its ventral side.
14. Apical of metacoxal apophyse or process.
15. Epicoxa, the basal leg podite, considered to form the junction between the pleuron and the thoracic dorsum.
16. Pleuron, a collective name for all the lateral plates of the thorax between the tergum and the sternum.
17. Hypopygium, the ninth abdominal sternite (sometimes the 7th to 9th) protecting the female's genital organ from below (see also genital lobe and genital plate). ③-⑦, abdominal sterna.
18. Pygidium, the tergal plate of the last abdominal segment usually between the paired anal appendages.
19. Lateral pygidial groove, a furrow inside the plates comprising the apex of the abdomen and surrounding the anus.



1. Maxillary palp, small antenna-like sensory appendage emerging from the maxilla.

2. Mandibular lobe, any lobate outgrowth on the surface of the mandible.

3. Paraglossa, the paired, rarely unpaired lobes on the anterior margin of the labium.

4. Lacinia, the paired inner lobate structures sitting on the apical margin of the maxillary stipes.

5. Labial palp, the paired sensory appendages of the labium borne on the palpiger generally consisting of three joints.

6. Mandible, the heavily chitinized, robust upper jaw in the anterior lower part of the head capsule, frequently dentate on its inner margin, used for seizing a prey or cutting up food.

7. Labium, the posterior median appendage of the mouthparts below the maxilla; it is an originally paired structure that has been secondarily fused, and sometimes has a highly modified apical margin.

8. Anteclypeus, the apical part of the clypeus separated from the postclypeus by a transverse line.

9. Postclypeus, the upper part of the clypeus, adjacent to the frons, separated from the anteclypeus by the transverse line of the clypeus.

10. Antennal groove, the broad furrow-like impression commonly found in fleas and biting lice, separating the frons from the vertex, in which the antenna may be concealed.

11. Paraclypeus, the narrow plate having separated from the two sides of the clypeus, occasionally a membranous surface.

12. Frontal area (frons), part of the head capsule that lies ventrad or anteriad of the vertex.

13. Eye, “compound eyes” made up of many units called “ommatidia”.

14. Occiput, the posterior aspect of the head.