

New cleroid beetles from the Middle–Late Jurassic of China

JIŘÍ KOLIBÁČ and DIYING HUANG



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Four specimens of fossil beetles recorded from the Middle and Late Jurassic boundary beds of Inner Mongolia, China are assigned to the melyrid lineage of Cleroidea. Three of them are described as *Sinomelyris praedecessor* gen. et sp. nov. and constitute the earliest known representatives of the family Melyridae. The new species habitually resembles some extant beetles of the subfamily Melyrinae but it is distinctly smaller and possesses four elytral carinae, the pronotum without a pair of the dorsolateral carinae, and the tarsal claw simple. The fourth specimen *Juraniscus majeri* gen. et sp. nov., is classified as Cleroidea incertae sedis. The new species has the symmetrical antennomeres including three terminal ones, the tarsomeres 1–4 with the lobes, the tarsal claw simple, and the aedeagus with the separated parameres. It is considered to be a member of the melyrid lineage and its relations to the relevant families Mauroniscidae, Rhadalidae, Dasytidae, and Malachiidae are discussed. A complete list of fossil species in the melyrid lineage described to date is provided.

Key words: Coleoptera, Cleroidea, Melyridae, Mesozoic, Inner Mongolia, Daohugou.

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Introduction

The volcanic deposits in which the fossils described herein were found, are located close to the village of Daohugou, Wuhua Township, Ningcheng County, Inner Mongolia, north-eastern China and very near the border of the provinces of Hebei and Liaoning. The fossil assemblage, obtained from the Lagerstätte, belongs to the Yanliao Biota (Hong 1983) with an early assemblage known as the Daohugou Biota, a term introduced by Ji and Yuan (2002), the age of which has been a subject of discussion in recent decades. Invertebrate workers (e.g., Ren et al. 2010; Selden and Huang, 2010; Giribet et al. 2012) regard the strata as equivalent to the Haifanggou Formation of Liaoning, also known as the Jiulongshan Formation of Hebei, dated to as early as the latest Middle Jurassic (Callovian; 166.1–163.5±4.0 Ma) (Chen et al. 2004; Liu et al. 2004). Recently, some vertebrate palaeontologists (Ji et al. 2006) have concurred with this age, whereas others have considered the Daohugou strata possibly as late as Middle–Late Jurassic (Zhang et al. 2008; Wang and Li 2008; Evans and Wang 2009) or still later than that (for an overview of the issue see Sullivan et al. 2014). Such discussions have resulted in applying a reserved and

somewhat younger dating scale, including the Callovian and Oxfordian stages, to major palaeontological surveys in recent years (e.g., McKenna et al. 2015; Smith and Marcot 2015; Toussaint et al. 2017). Following the latest opinions based on new data from isotope geochronology (^{40}Ar – ^{39}Ar dating) (Liu et al. 2006; Yang and Li 2008; Chang et al. 2014; Huang 2019), which indicates that the lower tuff layer in the Daohugou bed was formed at 165.0±1.2 Ma (Yang and Li 2008), the current authors incline towards a somewhat older age for the strata, i.e., to the boundary of the Middle and Late Jurassic (Huang 2019). The age of the four fossil specimens described herein probably corresponds to the upper boundary of the Callovian, i.e., approximately 163 Ma.

The Yanliao Biota contains a large number of exceptionally well-preserved fossils, including e.g., insects, crustaceans, spiders, millipedes, molluscs, fishes, salamanders, lizards, pterosaurs, dinosaurs, mammals, plants, pollens, spores, and fungi (Huang 2016; Xing et al. 2016). Fossiliferous layers are distributed to the north of the Yellow River and west of Xinjiang, extending to Central Asia. Huang (2015) divided the Yanliao Biota into an early assemblage called the Daohugou biota (Shihezi Stage: Bathonian to lower Oxfordian) and a late assemblage called the Linglongta biota (Manas Stage: mid-upper Oxfordian to lower Kimmeridgian). Some fossils

Table 1. List of fossils described within the melyrid lineage of the superfamily Cleroidea. Species within particular families are ordered by age of the deposit († denotes genera containing exclusively fossil species).

Taxon/author	Locality	Age	Classification	Note
<i>Acanthocnemoides sukatshevae</i> Zherikhin, 1977†	Russia: N Siberia, Taimyr Peninsula	Cretaceous amber, Santonian	Acanthocnemidae?	
<i>Idgiaites jurrasicus</i> Liu, Ślipiński, Leschen, Ren, and Pang, 2015†	China: Inner Mongolia Daohugou	Middle Jurassic, Callovian–Oxfordian	Prionoceridae	
<i>Prionocerites tattriei</i> Lawrence, Archibald, and Ślipiński, 2008†	Canada: British Columbia	Eocene	Prionoceridae	larva
<i>Aplocheble berendti</i> Majer, 1998†	Germany	Baltic amber, Eocene–Oligocene	Rhadalidae	
<i>Aplocheble fuscipes</i> Majer, 1998†	Germany	Baltic amber, Eocene–Oligocene	Rhadalidae	
<i>Aplocheble kunowi</i> Majer, 1998†	Germany	Baltic amber, Eocene–Oligocene	Rhadalidae	
<i>Aplocheble viridiaeneus</i> Chernyshev, 2012	Russia: Kaliningrad	Baltic amber, Eocene–Oligocene	Rhadalidae	
<i>Eudasytes listriiformis</i> Wickham, 1912†	USA: Colorado	Florissant shales, upper Miocene	Dasytidae	revised by Mawdsley (1999)
<i>Eutrichopleurus miocenicus</i> (Wickham, 1912)	USA: Colorado	Florissant shales, upper Miocene	Dasytidae	revised by Mawdsley (1999)
<i>Malachius immurus</i> Wickham, 1917	USA: Colorado	Florissant shales, upper Miocene	Malachiidae	unrevised classification
<i>Colotes constantini</i> Kirejtshuk and Nel, 2008	France	Oise amber, lower Eocene	Malachiidae	
<i>Colotes impexus</i> Kirejtshuk and Nel, 2008	France	Oise amber, lower Eocene	Malachiidae	
<i>Colotes sambicus</i> Kubicz, 2001	Poland	Baltic amber, Eocene–Oligocene	Malachiidae	
<i>Protocephaloncus perkovskiyi</i> Chernyshev, 2016†	Ukraine	Rovno amber, upper Eocene	Malachiidae	
<i>Palpattalus baltiensis</i> Chernyshev, 2016†	?	Baltic amber, Eocene–Oligocene	Malachiidae	
<i>Palpattalus eocenicus</i> Chernyshev, 2016†	?	Baltic amber, Eocene–Oligocene	Malachiidae	
<i>Troglops punctatissima</i> Théobald, 1937	France	upper Miocene	Malachiidae	unrevised classification

found in the bottom section of the Daohugou bed are related to the Yaopo Formation, thus indicating that the origin of the Yanliao Biota may be traced back to older strata (Huang et al. 2015). The forests of the Daohugou biota were dominated by gymnosperm trees such as ginkgopsids, conifers, and cycads (Liu et al. 2006, 2018). The Middle Jurassic of China is characterised by the *Coniopteris–Phoenicopsis* floral assemblage (Czekanowskiales), which appeared in the mid-Early Jurassic and achieved its greatest prosperity in the Middle Jurassic, declining in the mid-Late Jurassic (ca. 155 Ma). It was followed by a series of drought events in the Northern Hemisphere. With the advent of arid climate, the Yanliao Biota declined rapidly around the middle of the Late Jurassic, while certain relict groups migrated southwards (Huang 2019).

Based on the plants found in the Haifanggou Formation, Zhang and Zheng (1987), Kimura et al. (1994), and Wang et al. (2006) concluded that the climate in Liaoning during the Middle Jurassic was subtropical to temperate, warm and humid. From the finding of *Phoenicopsis* in Daohugou biota, Huang et al. (2016) deduced the occurrence of deciduous forests of the temperate-warm climate growth-type in the area. On the other hand, Selden and Huang (2010), in the light of plectreurid spider records, determined the climate as comparable to modern conditions in the Caribbean islands.

The fossils of terrestrial insects in the locality are often associated with freshwater crustaceans (especially

Conchostraca, or clam shrimps). It is supposed that, during rainy periods, insects fell from vegetation into temporary pools or freshwater basins and sank to a fine-grained sediment, an ideal substrate for fossilization. However, fine volcanic ash produced by frequent volcanic activity in the region of the Yanliao Biota is believed to be the key factor in the exceptional preservation of the fossils (Huang 2016, 2019; Xing et al. 2016). The composition of Coleoptera in the locality displays extreme diversity, with beetles among the predominant insect fossils. Daohugou representatives of Cleroidea identified to date have been classified within the families Prionoceridae (Liu et al. 2015), Trogossitidae (Yu et al. 2012, 2014), and Cleridae (Kolibáč and Huang 2016). Mesozoic cleroid fossils also include two findings of the species-poor but clearly-distinguished family Thanerocleridae (Yu et al. 2017; Cai and Huang 2018) from the Burmese amber of the Cretaceous. The species-rich families Rhadalidae, Melyridae, Dasytidae, and Malachiidae are the last of larger cleroid families previously unknown from the Daohugou biota of the Mesozoic. Four species of Rhadalidae (Majer 1998), two of Dasytidae (Wickham 1912) and eight of Malachiidae (Wickham 1912, 1917; Théobald 1937; Kubicz 2001; Kirejtshuk and Nel 2008; Chernyshev 2012, 2016) have been described from the lower Oligocene to upper Eocene. (Spahr 1981a, b; Ponomarenko and Kirejtshuk 2003–2015). *Acanthocnemoides sukatshevae* Zherikhin, 1977 as yet the only described Mesozoic cleroid species, from the Albanian–

Cenomanian amber of Siberia (Zherikhin and Sukatsheva 1973; Zherikhin 1977), might belong to the melyrid lineage. However, two specimens of the latter species, well-preserved, need further study to clarify their systematic position. A detailed list of all fossil species belonging to the melyrid lineage is given in Table 1.

Here we report two fossil species of the melyrid lineage of the superfamily Cleroidea. The both present the oldest findings of the beetle group and one of them is the first Mesozoic record of the large cleroid family Melyridae.

Institutional abbreviations.—MMBC, Moravian Museum, Brno, Czech Republic; MMBC-SC, Moravian Museum, systematic collection; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:59D7E8F0-32D0-4718-919F-FF-D25A15C044

Material and methods

Four fossil specimens are well-preserved in the finely laminated, pale grey tuffaceous lacustrine deposit. They come from localities near Daohugou (for details of the locality, see Huang et al. 2006). All the material is more-or-less three-dimensionally preserved and partly covered with a dark carbon film; the counterparts were not found. Preparation consisted of separating off the tuff layers with a sharp blade. Photomicrographs of the fossils were taken with a Zeiss Discovery V20 microscope equipped with an AxioCam HSc camera, then refined in Photoshop (Adobe CS6). Body parts were measured by means of AxioVision 4.8 software. Some photographs were taken with the specimens under alcohol for better detail definition and others at lower angles of light to allow for three-dimensional acquisition. Helicon Focus 4.21 software was also used to stack certain images. All drawings were based on both photographs and the original specimens. Blurred contours are indicated by broken lines. The dorsal habitus photographs of Recent, specimens were taken by a Canon EOS 6D with an MP-E 65 mm macro lens and Leica Z16Apo. LAS 3.6.0 software was used to stack the images. Adobe CS6 (Illustrator 16.0.3 and Photoshop 13.0.1) was used for reconstruction of the both species.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Superfamily Cleroidea Latreille, 1802

Remarks.—The melyrid “stock” is a term introduced by Majer (1994a) for the cleroid families Acanthocnemidae, Mauroniscidae, Prionoceridae, Dasytidae, Melyridae, Mala-

chiidae, and Attalomimidae. Bocakova et al. (2011) presented a molecular phylogenetic analysis of the lineage, established the monophyletic Rhadalidae, and confirmed Dasytidae, Malachiidae, Melyridae, Prionoceridae, and Mauroniscidae as separate cleroid families. Recently, the comprehensive phylogeny of Cleroidea based on 4-gene analyses (Gimmel et al. 2019) has supported Rhadalidae and Mauroniscidae as the most basal clades of the melyrid lineage, a diversification of which was followed by separation of Prionoceridae and Melyridae sensu lato (incl. Dasytinae and Malachiinae). On the other hand, morphologically-based modern phylogenies (i.e., Lawrence et al. 2011), as summarized by Bouchard et al. (2011), recognise Rhadalinae, Dasytinae, and Malachiinae as subfamilies within Melyridae sensu lato. Two further related families, Attalomimidae and Gietellidae, established by Majer (1994a, b) were generally included in Malachiidae and Dasytidae respectively, although *Gietella* Constantin and Menier, 1987 has been found as a derived apterous group of Rhadalidae (Gimmel et al. 2019). Crowson (1960, 1964), Lawrence and Newton (1982), and Majer (1994a) proposed closer relationships among Acanthocnemidae, Phycosecidae, Prionoceridae, and Melyridae sensu lato. Recent molecular phylogenies of beetles (Bocak et al. 2014; McKenna et al. 2015) classify Acanthocnemidae as one of basal groups of all Cleroidea, confirm a position for Phycosecidae at the very base of the melyrid lineage, and establish Prionoceridae as actually part of the lineage (cf. Majer 1987 who proposed a relation of Prionoceridae with Cleridae). Thus, the melyrid lineage includes the families Phycosecidae, Rhadalidae, Mauroniscidae, Prionoceridae, Melyridae, Dasytidae, and Malachiidae (see Crowson 1964; Peacock 1987; Majer 1994a, 1995, 2002; Bocakova et al. 2011; Bocak et al. 2014; McKenna et al. 2015). This concept is applied throughout this paper.

Family Melyridae Leach, 1815

Subfamily Melyrinae Leach, 1815

Genus *Sinomelyris* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:CF56C67A-FD59-42CC-A38F-3ABC467C0D99

Type species: *Sinomelyris praedecessor* sp. nov.; by monotypy, see below.

Etymology: From the Latin *sina*, referring to China, and the nominotypical genus *Melyris*, associated the name with the family Melyridae. Masculine in gender.

Diagnosis.—As for the type species by monotypy.

Sinomelyris praedecessor sp. nov.

Figs. 1, 2A, 4A.

ZooBank LSID: urn:lsid:zoobank.org:act:5A512392-F673-480C-ADBB-52916821AB66

Etymology: From a Latin *praedecessor*, ancestor.

Type material: Holotype: NIGP168476 (Fig. 1B); sex unknown, counterpart absent; perfect dorsal side of specimen preserved, elytra open, meso- and metathorax and abdomen visible. Paratypes: NIGP168477 (Fig. 1A); sex unknown, counterpart absent; perfect dorsal side of specimen preserved, elytra partly open, antennae missing, legs partly

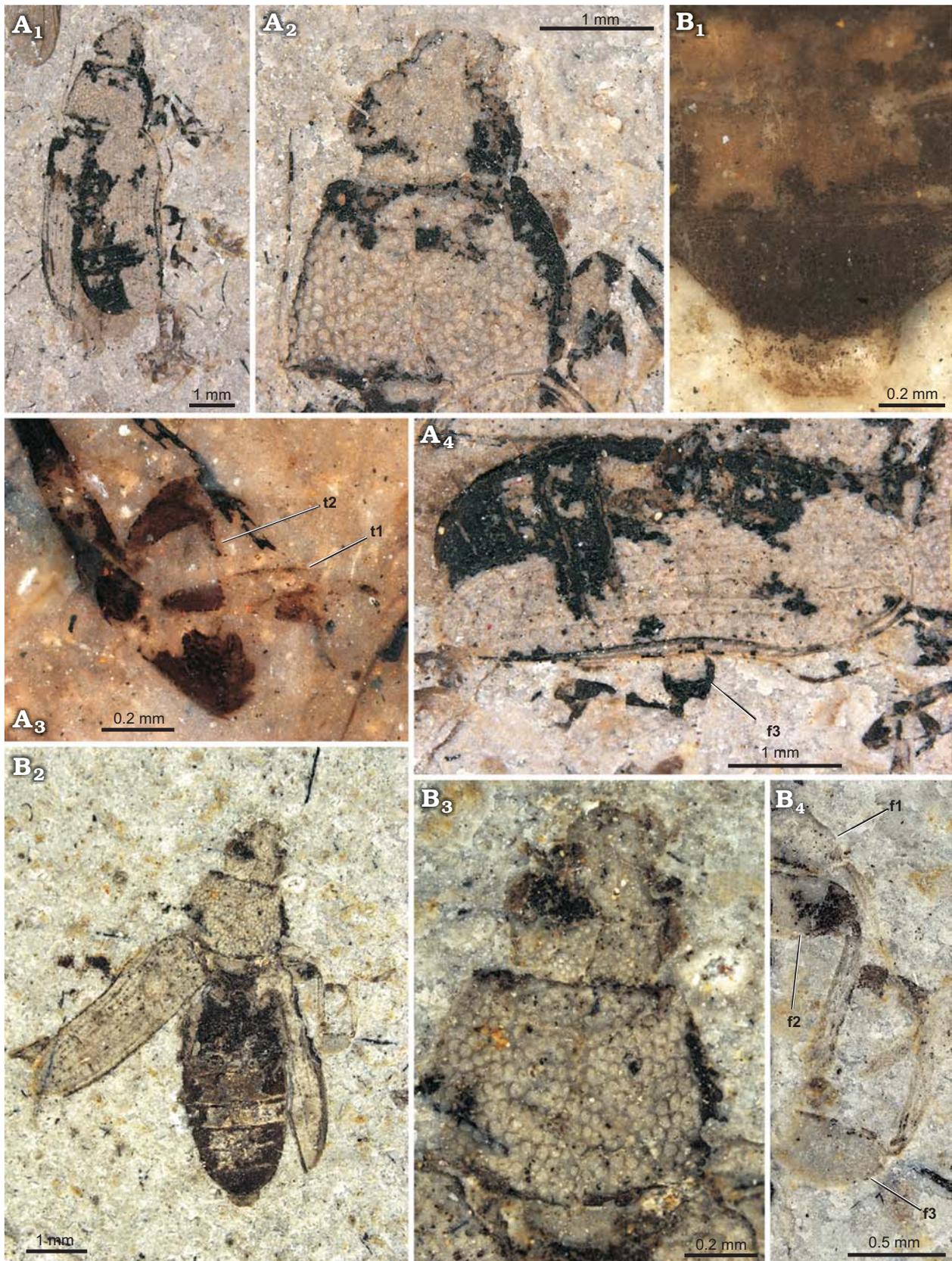


Fig. 1. Melyrid beetle *Sinomelyris praedecessor* gen. et sp. nov. from the Middle Jurassic Haifanggou Formation of Daohugou Village, Inner Mongolia, China. **A.** Paratype, NIGP168477; dorsal habitus (A₁), pronotum and head dorsally (A₂), detail of front and middle legs (A₃), right elytron and hind leg dorsally (A₄). **B.** Holotype, NIGP168476; abdominal apex dorsally (B₁), dorsal habitus (B₂), pronotum and head dorsally (B₃), detail of front, middle and hind legs (B₄). Abbreviations: f1–3, femora of 1st to 3rd pair of legs; t1–2, tarsi of 1st to 2nd pair of legs.

visible; NIGP168478 (Fig. 2A); sex unknown, counterpart absent; perfect dorsal side of specimen preserved incl. fragment of antenna. All from the type locality.

Type locality: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Haifangou Formation, Callovian, Middle Jurassic.

Diagnosis.—Relatively small species (body length 6.2–6.8 mm); body bare; pronotum with single pair of carinae; anterior corners of prothorax obtuse; each elytron with four carinae; tarsomere 1 approximately as long as tarsomere 2 in all pairs of legs; tarsal claw simple.

Description.—*Body length* (from elytral apex to clypeus): holotype 6.2 mm, paratypes 6.8 and 6.4 mm. For other measurements of visible body parts see Table 2.

Coloration and sculpture: body elongate, rather flat; entire dorsal surface either unicolorous or each elytron with two colour patches, in anterior and posterior thirds. Head coarsely, densely punctate (punctures touch one another; interspaces not larger than half of puncture diameter, mostly reduced to border between neighbouring punctures); pubescence not observed. Pronotum very coarsely and densely punctate (interspaces less than diameter of punctures, most of which touch one another); punctures much larger than those on head, their floors flat, rounded or polygonal in shape; some punctures with short seta growing from the centre. Elytron very coarsely sculptured; punctures large, irregularly shaped, touching one another without distinct interspaces; dorsal surface including humeral margin bare, elytron without pubescence. Ventral surface, antenna and legs without coarse punctation or distinct sculpture and without pubescence.

Head: frons distinctly flat; clypeus distinct, extended anteriorly but frontoclypeal suture absent; antennal socket visible from above; eye relatively large (space between eyes approximately two times as wide as eye diameter), distinctly elevated, not emarginate, elliptic, finely faceted; head distinctly narrowed behind eyes.

Mouthparts: labrum oblong, not emarginate anteriorly; mandible robust, apical tooth acuminate.

Antenna: scape robust, as large as three following antennomeres together; antennomeres progressively dilated from fourth one (only 8 antennomeres recognised in the paratype NIGP168478); whole antenna would be approximately as long as head.

Prothorax: pronotum transverse, approximately 1.4–1.6 times as wide as long; anterior margin straight, not emarginate, anterior corners not projecting, rounded; lateral edge present, evenly rounded; carina along lateral margin of pronotum absent; sides of posterior margin of pronotum sinuate.

Mesothorax: mesonotum transverse; mesocoxal cavities narrowly separated. Each elytron with four distinctly elevated carinae, suture also elevated; interspaces between carinae with two or three rows of punctures.

Metathorax: metaventre flat and wide, weakly transverse, narrowed towards anterior portion; discriminial line (discrimen) conspicuous along whole length; metacoxal cavities narrowly separated. Membranous wing fully developed.

Legs: mesocoxae oval, metacoxae extended to lateral margin of metathorax; femora weakly clavate; tibiae without row of spines along outer margin, apical spines not observed; tarsomere 1 conspicuous, approximately as long as tarsomere 2; tarsomere 4 approximately as long as 3; tarsomere 5 as

Table 2. Measurements (in mm) of visible body parts in *Sinomelyris praedecessor* gen. et sp. nov.

Measurement		NIGP168476 (holotype)	NIGP168477 (paratype)	NIGP168478 (paratype)
Body	length (elytral apex to clypeus)	6.23	6.76	6.38
	maximum width	2.05	~ 2.6	2.18
Head	length (base to clypeus)	–	–	0.95
	maximum width (including eyes)	1.10	1.26	1.19
	minimum width (between eyes)	–	–	0.68
Eye (longitudinal diameter)		–	–	0.45
Antenna (scape to pedicel)		–	–	0.28
Pronotum	length	1.36	1.38	1.45
	minimum width	1.72	2.25	2.06
	approx. anterior width	–	1.36	–
	approx. posterior width	–	1.82	–
Mesoventrite length		~ 0.6	–	–
Metaventre length		~ 0.9	–	–
Elytron	width (at base)	1.02	1.12	1.09
	maximum width	1.21	1.32	1.09
	maximum length	3.65	4.35	3.90
Metatibia length		1.00	–	–
Metafemur length		0.67	–	–
Metatarsus length (including claw)		0.83	–	–
Metatarsal claw length		0.18	–	–
Abdominal ventrites 1–5		2.01	–	–

long as, or slightly longer than, 1–4 combined; tarsal lobes absent but ventral side of tarsomeres setose; claws large, without denticles; empodium probably small (not observed in well-preserved metatarsus of paratype NIGP168477); tarsal formula unknown, metatarsi 5-segmented.

Abdomen: five ventrites distinctly visible; pygidium (sex unknown) nearly straight along apical margin.

Remarks.—Habitus as well as body size in the monotypic genus similar to that of extant melyrids of the subfamily Melyrinae (or Melyrini sensu Bouchard et al. 2011), such as, for example, *Melyris* Fabricius, 1775 or *Falsomelyris* Pic, 1913 (Fig. 3A₁, B₂). Pronotum with posterior (basal) margin sinuate at the sides (cf. Figs. 2A₂, 3A); punctation of head and pronotum composed of very large punctures with flat floors and a short seta at centre (a pattern denoted as the granular punctation by Kolibáč and Huang [2016]; cf. Figs. 1A₂, B₃, 3B₁); elytron with sharp, distinct carinae (cf. Figs. 1A₄, B₂, 3B₂); elytral sculpture very coarse, irregular, resembling extant members of *Melyris*; fifth tarsomere as long as tarsomeres 1–4 together; tarsal claw simple, without denticles, as in *Melyrodes* Gorham, 1882 (Majer 1994a; Constantin 2008). The two carinae running along lateral margins of pronotum in most of the extant species of *Melyris* (Fig. 3A₂) absent in the fossils as well as in *Chalchas* Blanchard, 1845, and other melyrines. Antennomeres from fourth to eighth progressively dilated (Fig. 2A₁); in the extant melyrines antenna serrate from fourth antennomere.

Stratigraphic and geographic range.—NE China: Inner Mongolia, Daohugou; Middle Jurassic, Callovian.

Superfamily Cleroidea Leach, 1815

Melyrid lineage, family indet.

Remarks.—As explained below, the new species is a member of the melyrid lineage but it cannot be unambiguously classified within one of the families Mauroniscidae, Rhadalidae, Dasytidae, and Malachiidae. Therefore, the new species is formally classified as Cleroidea incertae sedis.

Genus *Juraniscus* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:ECBE11A9-9E38-4D59-AAC2-9774EADDEF2DD

Type species: *Juraniscus majeri* sp. nov., by monotypy, see below.

Etymology: A combination of *Jura-*, referring to the Jurassic period, and the *-niscus* derived from the generic name *Mauroniscus*, the genus that, of all the extant melyrid lineage members, resembles the new fossil genus the most. Masculine in gender.

Diagnosis.—As for the type species by monotypy.

Juraniscus majeri sp. nov.

Figs. 2B, 4B.

ZooBank LSID: urn:lsid:zoobank.org:act:6E188F79-0922-46BE-88CB-748A6ECBA438

Etymology: Named in memory of Karel Majer (1950–2000), an eminent researcher of the melyrid lineage of Cleroidea, for his contribution to the systematics and morphology of the group.

Type material: Holotype NIGP168479; male, counterpart absent; perfect dorsal side of specimen preserved, elytra semitransparent (abdomen and metathorax partly visible).

Type locality: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Haifanggou Formation, Callovian, Middle Jurassic.

Diagnosis.—Antennomeres symmetrical including three terminal ones, progressively dilated from the fifth onwards; pronotum approximately 1.4 times as wide as long; anterior corners of pronotum weakly projecting; meso- and metatarsi with tarsomere 1 conspicuous, slightly shorter than tarsomere 2; tarsal lobes present in tarsomeres 1–4; tarsal claws without denticles.

Description.—*Body length* (from elytral apex to clypeus): 4.25 mm. For other measurements of visible body parts see Table 3.

Coloration and sculpture: body elongate, weakly convex; body surface unicolorous, without distinct colour stripes or patches, merely remnants of dark pigmentation. Head with very fine sculpture composed of round punctures; interspaces between punctures as large as puncture diameter. Pronotum with similar fine sculpture but interspaces larger than puncture diameter; pronotal punctures without seta at centre. Elytron without carinae, with sparse sculpture composed of small, round punctures; interspaces the same size as, or larger than, puncture diameter; punctation appears irregular. Body completely without pubescence, short, sparse setae observed only on tibiae and labrum.

Table 3. Measurements (in mm) of visible body parts of *Juraniscus majeri* gen. et sp. nov.

Measurement		NIGP168479 (holotype)
Complete length		5.56
Body	length (elytral apex to clypeus)	4.25
	maximum width	2.52
Head	length (base to clypeus)	~0.8
	maximum width (including eyes)	0.86
	minimum width (between eyes)	~0.5
Eye longitudinal diameter		~0.2
Antenna length		1.45
Scape length		~0.17
Pedicel length		~0.13
Pronotum	length	0.81
	maximum width	1.18
	approx. anterior width	~0.8
	approx. posterior width	~0.9
Elytron	width (at base)	0.77
	maximum width	1.26
	maximum length	2.94
Metafemur length		~0.9
Metatibia length		~0.9
Metatarsus length (including claw)		~0.8
Mesotibia length		~0.8
Mesotarsus length (including claw)		~0.6
Abdominal ventrites 1–6		~2.0

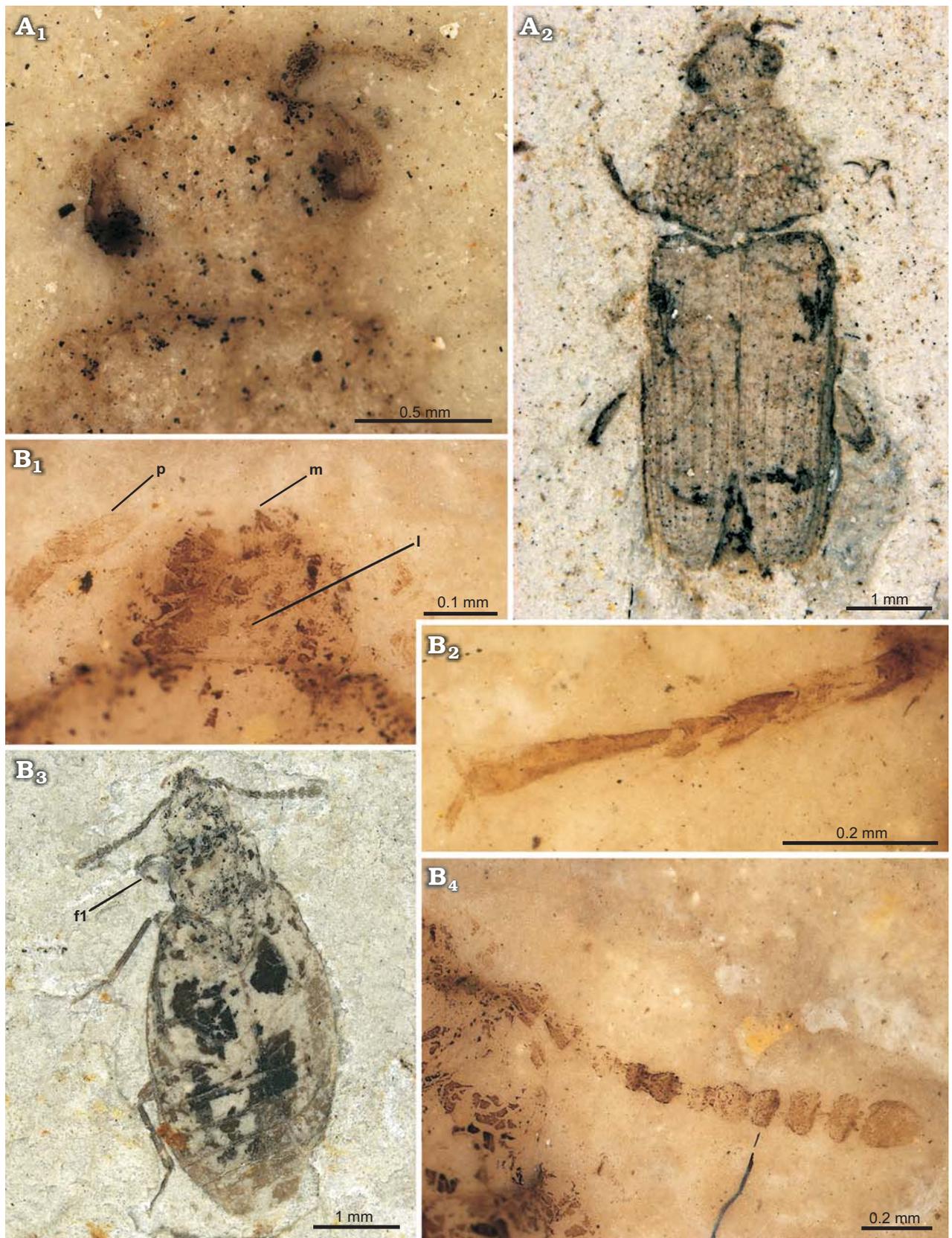


Fig. 2. Melyrid beetle *Sinomelyris praedeceptor* gen. et sp. nov. (A) and cleroid beetle *Juraniscus majeri* gen. et sp. nov. (B) from the Middle Jurassic Haifanggou Formation of Daohugou Village, Inner Mongolia, China. A. Paratype, NIGP168478; head (A₁), dorsal habitus (A₂). B. Holotype, NIGP168479; mouth parts dorsally (B₁), metatarsus dorsally (B₂), dorsal habitus (B₃), antenna dorsally (B₄). Abbreviations: fl, front femur; l, labrum; m, mandible; p, terminal palpomere of maxillary palp.

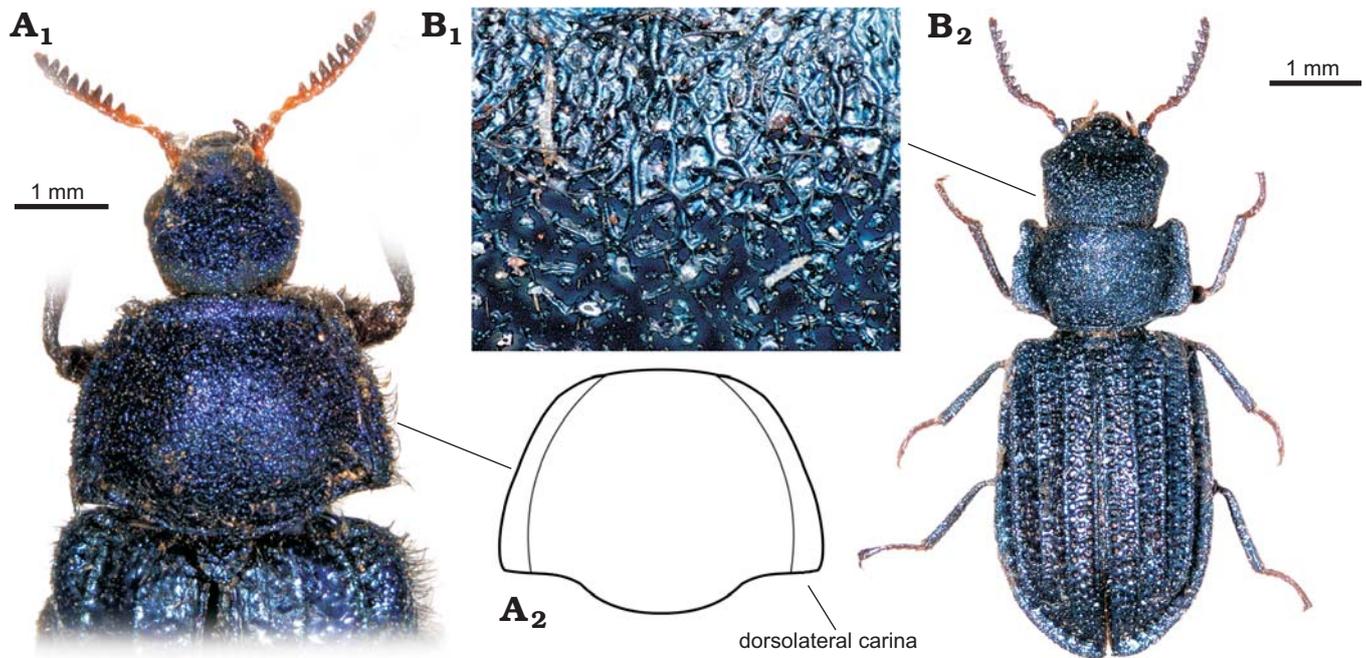


Fig. 3. Extant melyrid beetles *Melyris abdominalis* Fabricius, 1787 from Senegal and *Falsomelyris granulatus* Fabricius, 1792 (A) and from Hammoum, Algeria (B). A. MMBC-SC; base of elytra, pronotum, and head dorsally (A₁), outline of pronotum (A₂). B. MMBC-SC; detail of sculpture of head (B₁), dorsal habitus (B₂).

Head: frons flat; clypeus not extended anteriorly, distinctly separated by arcuate frontoclypeal suture; antennal socket visible from above; eye relatively large (space between eyes approximately three times eye diameter), distinctly elevated, not emarginate, elliptic, finely faceted; head inconspicuously narrowed behind eyes.

Mouthparts: mandibles medium-sized (not unidentate, slender and sharp), bidentate, acuminate; labrum oblong, weakly emarginate along anterior margin; maxillary palps 3-segmented, terminal palpomere slender, conical.

Antenna: 11-segmented; scape longer and wider than pedicel but not larger than two following antennomeres together; antennomeres symmetrical, progressively dilated from the fifth onwards; whole antenna reaches approximately as far as posterior margin of prothorax. Both antennae recognised in the fossil specimen.

Prothorax: pronotum weakly transverse, approximately 1.4 times as wide as long; anterior margin straight, not emarginate, anterior corners weakly projecting; lateral edge present, evenly rounded; carina along lateral margin of pronotum absent; posterior margin of pronotum arcuate, posterior corners conspicuous but not projecting.

Mesothorax: mesonotum transverse; mesocoxal cavities narrowly separated; membranous wing present.

Metathorax: metaventrite flat and wide, transverse; metacoxal cavities narrowly separated. Elytron with rounded humeral corner, without carinae.

Legs: mesocoxae distinctly oval, metacoxae extended to lateral margin of metathorax; femora very weakly clavate. Meso- and metatibia and meso- and metatarsus clearly visible: tibia without row of distinct spines along outer margin but with conspicuous edge along outer side; metatibia with

two apical spines (not visible in mesotibia); tarsomere 1 conspicuous, slightly shorter than tarsomere 2; tarsomere 4 approximately as long as 3; tarsomere 5 as long as 1–4 combined; tarsal lobes distinctly present in tarsomeres 1–4; claws without denticles; empodium probably small (not observed in well-preserved tarsi); tarsal formula unknown, meso- and metatarsi 5-segmented.

Abdomen: six ventrites distinctly visible; cucujoid tegmen with separated parameres present.

Remarks.—Habitus similar to that of Mauroniscidae (Fig. 4C), Rhadalidae, Dasytidae, and Malachiidae, with tendency to soft-bodiedness. Sparse sculpture of elytra irregular, composed of fine punctures as in members of above mentioned families. Structure of antenna (Fig. 2B₄) closely comparable with non-serrate but progressively dilated antennomeres in Mauroniscidae (e.g., *Amecomycter* Majer, 1995, *Mauroniscus* Bourgeois, 1911, *Scuromanius* Majer, 1995), Dasytidae: Danaceinae (e.g., *Danacaea* Laporte de Castelnau 1836, *Hylodanacaea* Pic, 1926), and Dasytidae: Chaetomalachiinae (e.g., *Dasytiscus* Kiesenwetter, 1859, and *Eutrix* Majer, 1996). Antennomeres from fourth or fifth distinctly asymmetrical in dasytids and weakly asymmetrical in mauroniscids (cf. Majer 1994a, 1995, 1996, 1999). Tarsomeres 1–4 with small, non-membranous lobes and long, distinct setae directed forwards as in Prionoceridae and some Dasytidae and Malachiidae. Claws simple, without denticles as in mauroniscids; membranous appendages of claws absent or not preserved. Abdomen with six ventrites as in all members of the melyrid lineage apart from Phycosecidae (ventrites I and II connate in Rhadalidae, see Peacock [1987], but their suture is clearly visible). Tegmen

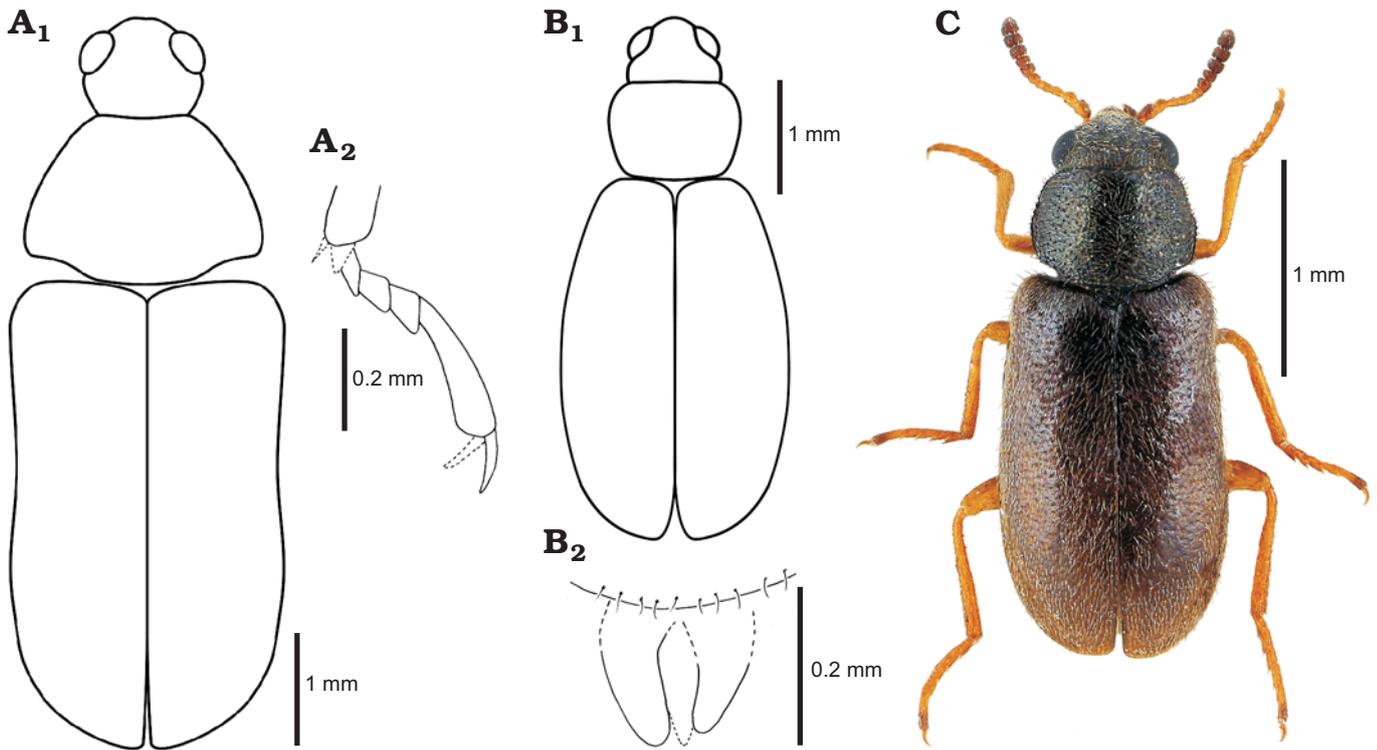


Fig. 4. Melyrid beetle *Sinomelyris praedecessor* gen. et sp. nov. (A), cleroid beetle *Juraniscus majeri* gen. et sp. nov. (B) from the Middle Jurassic, Haifanggou Formation of Daohugou Village, Inner Mongolia, China, and extant mauroniscid beetle *Mauroniscus titschacki* Pic, 1954 (C) from Cuzco, Peru. **A.** NIGP168477; reconstruction of body shape (A₁), mesotarsus laterally (A₂). **B.** NIGP168479; reconstruction of body shape (B₁), assumed apex of aedeagus dorsally (B₂). **C.** MMBC-SC, dorsal habitus.

with separated parameres as in mauroniscids (Majer 1995) and exceptionally also in dasytids (Constantin and Menier 1987; Majer 1999).

Stratigraphic and geographic range.—NE China: Inner Mongolia, Daohugou; Middle Jurassic, Callovian.

Discussion

Beetles of the melyrid lineage differ from other cleroid families in their combination of the following morphological characters: (i) head with protracted clypeus (or “clypeal area”, since the frontoclypeal suture is usually inconspicuous); (ii) eyes large, finely faceted, eleviate, not emarginate; (iii) mandible bidentate; (iv) antennomeres progressively dilated from 4th or 5th, without 3-segmented club (distinct 1-segmented club present only in Phycosecidae); (v) tarsal claws usually with denticles and membranous appendages (excepting Phycosecidae, Mauroniscidae, some Prionoceridae); (vi) elytral punctuation irregular (excepting some Phycosecidae); (vii) aedeagus inverted, consisting of a single part; (viii) parameres not separated from phallobase, usually mutually coalescent (excepting Prionoceridae, Mauroniscidae, Phycosecidae); (ix) tendency to soft-bodiedness (Bocakova et al. 2016). Both taxa described herein agree in all observed characters with such delineation of the melyrid lineage excluding inverted/uninverted position

and internal structure of the aedeagus which is not visible. Although the feature cannot be perfectly proved in fossils, the *Sinomelyris praedecessor* sp. nov. body does not show a tendency to soft-bodiedness: its elytra braced with carinae and coarsely sculptured head and pronotum seem as robust and hard as in the extant melyrids.

Sinomelyris gen. nov. is similar to the extant beetles of the genus *Melyris*, from which it can be distinguished by a unique combination of features visible in the three fossils: (i) number of elytral carinae (four instead of three), (ii) absence of pair of dorsolateral pronotal carinae and (iii) simple tarsal claws. The two latter characters can be considered plesiomorphic and are also known in other melyrids, for example *Melyrodes*. The very characteristic type of cranial and pronotal sculpture, composed of large, mutually connected flat punctures, each with a central seta growing from small tubercle (“granular punctuation”; Figs. 1B₃, 3B₁) also occurs in the *Korynetes*-group of Cleridae as well as in the earliest Middle Jurassic clerid species *Protoclerus korynetoides* Kolibáč and Huang, 2016. The structure confirms the hypothesised sister-relationship between the melyrid and clerid lineages proposed by Kolibáč and Huang (2016) and supported by a certain amount of molecular evidence (Hunt et al. 2007; Bocakova et al. 2011, 2016; Robertson et al. 2015). The evident similarity between *Sinomelyris* gen. nov. and *Melyris* indicates that the latter extant genus has changed only slightly over the course of approximately 163 Ma. In the light of the biology of more than fifty extant

species of *Melyris*, *Sinomelyris praedecessor* gen. et sp. nov. may well have been floricolous. Considering up to date palynological analysis of the Haifanggou Formation (Zhang et al. 2018) showing a dominance of gymnosperm pollen, we can suppose feeding on the pollen grains and pollination of cycads (cf. Labandeira 2010; Renner 2011; Tang et al. 2018) in *S. praedecessor* sp. nov. It has been suggested for *Palaeoboganium* Liu, Ślipiński, Lawrence, Ren, and Pang, 2017 (Liu et al. 2018) and *Parandrexia* Martynov, 1926 (Kirejtshuk 1994; Kolibáč 2012) of the same fossil assemblage as well. Melyrid larvae are predatory and tend to dwell under the bark of trees and shrubs, a mode of life similar to its relatives in Cleridae and Trogossitinae (Kolibáč 2010; Kolibáč and Leschen 2010). In modern times, Melyridae are distributed worldwide in tropical to temperate zones, except for the Oriental and Australian regions (Majer 1994a). *Melyris* and its close relative *Falsomelyris* are widespread in warm or temperate areas of Europe, northern to southern Africa, western to central Asia, and from the warm areas of North America to tropical South America. However, both genera are absent from modern Asia east of Karakoram mountains (Majer 1994a; Mayor 2007) where the fossils of *Sinomelyris praedecessor* gen. et sp. nov. were found. Wider distribution of some beetle groups in Mesozoic and their later extinction in eastern Asia have already been mentioned for example by Kolibáč and Huang (2016), Liu et al. (2018), and Yu et al. (2017). The reason why some widespread extant taxa are absent in eastern and southeastern Asia has not been explained so far, however, it is known that a large part of the Recent insect fauna of the region is of Gondwanan origin (Sklenarova et al. 2013; Kolibáč 2012; Poinar 2018). We can only presume that diversity of the original Mesozoic insect fauna of the present eastern Asia was reduced during Late Cretaceous–early Cenozoic climatic changes and intense volcanism in combination with processes which later formed Himalayas and Tibetan plateau (Briggs 2003; Karanth 2006; Raven and Axelrod 1974; Sahni 1984).

Juraniscus gen. nov. cannot be unambiguously classified within any of families of the melyrid lineage because its extant representatives, namely Mauroniscidae, Rhadalidae, Dasytidae, and Malachiidae, are similar to each other in: (i) general body shape and size, (ii) tendency to soft-bodiedness, (iii) elevate fine-faceted eye, (iv) anteriorly extended clypeal area, and (v) absence of antennal club. The broadly oval elytra, distinctly wider than the pronotum at their broadest part, occur often in Mauroniscidae (*Amecomycet* Majer, 1995, *Mecomycet* Horn, 1882) and Malachiidae (e.g., *Colotes* Erichson, 1840, *Ebaeus* Erichson, 1840, *Laius* Guérin-Méneville, 1838), sparsely in Dasytidae (e.g., *Danaceothrix* Majer, 1989) and never in Rhadalidae. Other distinguishing characters of *Juraniscus majeri* gen. et sp. nov. are in agreement with those of the mauroniscids; however, these are presumably plesiomorphic, rendering their phylogenetic value doubtful. The fossil may constitute a basal group within some of the other families mentioned above. The plesiomorphic character states are: (i) tarsal claw

simple, without denticle; (ii) dilated antennomeres symmetrical (weakly asymmetrical in Mauroniscidae, distinctly asymmetrical in other families); (iii) aedeagus, if the authors' interpretation of the fossil is correct, with separated parameres (very seldom present in Rhadalidae [*Kubanius* Majer, 1983], unknown in Dasytidae and Malachiidae). The larvae of all the four families mentioned are presumed to be predatory. They often feed on eggs of other insects or hunt for small insect larvae or adults (Kolibáč et al. 2005). Adults frequently dwell on thin branches, leaves, needles and the cones of trees and shrubs as well as the stems and leaves of herbs. They are, however, mostly floricolous, either predatory or pollinivorous or both (Crowson 1964; Peacock 1987; Kolibáč et al. 2005). Such a mode of life may also be proposed for *Juraniscus majeri* gen. et sp. nov. Extant Mauroniscidae are distributed only in North and South America while other relevant families are widespread: Rhadalidae in all biogeographical regions excluding the Austral realm, Dasytidae and Malachiidae worldwide. If *Juraniscus majeri* gen. et sp. nov. is actually a relative of the mauroniscids, a wider distribution of the beetle family in the Mesozoic may be assumed. Similar conclusions about the wider distribution of recently American cleroid groups in the past may also be drawn from findings of Mesozoic Cleridae: Epiclininae (*Wangweiella calloviana*; Inner Mongolia; Kolibáč and Huang 2016) and Thanerocleridae: Zenodosinae (*Archaeozenodosus bellus*; Myanmar; Yu et al. 2017).

Conclusions

The melyrid lineage with more than 5000 extant species forms the largest group of Cleroidea (>10 000 extant species). Although a few cleroid representatives of all major families have already been described from Mesozoic, no records from the species-rich families Rhadalidae and Melyridae *sensu lato* were hitherto known. *Sinomelyris praedecessor* gen. et sp. nov. constitutes the first Mesozoic record and earliest known representative of Melyridae. Three fossils of the species can be safely associated within the family and show surprisingly similar habitus and outer features with some extant melyrine genera (for example *Melyris* Fabricius, 1775, *Falsomelyris* Pic, 1913). Considering the biology of extant species of *Melyris*, *Sinomelyris praedecessor* gen. et sp. nov. adults may well have been floricolous, living on cycads or early flowering angiosperms. The second described cleroid beetle, *Juraniscus majeri* gen. et sp. nov., may be also associated within the melyrid lineage, however, its family assignment is not perfectly clear. Therefore the fossil is classified as Cleroidea incertae sedis although most of its outer morphological characters as well as a structure of the aedeagus are in agreement with the recent species-poor American family Mauroniscidae. Considering a distribution of the Recent Melyridae and Mauroniscidae, which are absent in eastern Asia, wider distribution of the both families in the Jurassic is supposed.

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