

Mantophasmatodea now in the Jurassic

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Abstract The Mantophasmatodea is the most recently discovered insect order. The fossil records of all other ‘polyneopteran’ orders extend far in the past, but the current absence of pre-Cenozoic fossils of the Mantophasmatodea contradicts a long evolutionary history, which has to be assumed from the morphological distinctness of the group. In this paper, we report the first Mesozoic evidence of a mantophasmatodean from the Middle Jurassic of Daohugou, Inner Mongolia, China. Furthermore, the new fossil shares apomorphic characters with Cenozoic and recent Mantophasmatodea, suggesting a longer evolutionary history of this order.

Keywords Insecta · Mantophasmatodea · Middle Jurassic · Evolution · Polyneoptera · Phylogeny

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Introduction

The Mantophasmatodea, also named African rock crawlers, heelwalkers, or gladiators, is the most recently discovered order of insects (Klass et al. 2002). Extant Mantophasmatodea are known from Namibia, Tanzania, and South Africa (Picker et al. 2002; Zompro et al. 2003). While nearly all the ‘polyneopteran’ orders are known to be very ancient, with oldest records ranging at least between the Early Carboniferous to the Triassic, fossil rock crawlers are only described from the Eocene Baltic amber (Zompro 2001, 2005; Klass et al. 2002; Arillo and Engel 2006). No pre-Cenozoic insects can be attributed to this newly discovered order. The affinities of these insects were long considered controversial due to the few supporting morphological apomorphies and contradictions in molecular analyses (Klass et al. 2002; Terry and Whiting 2005; Cameron et al. 2006; Klass 2007). Mantophasmatodea have to be considered the sister group of the modern Dictyoptera (Klass et al. 2003), Mantodea (Dallai et al. 2003), Orthoptera (Tilgner 2002; Zompro 2005), Grylloblattodea (Terry and Whiting 2005; Kjer et al. 2006; Arillo and Engel 2006), or Phasmatodea (Cameron et al. 2006). Hamilton (2003) even synonymized the taxon with the Carboniferous Cnemidolestodea but Zompro (2005) convincingly rejected this opinion. Gorochov (2007) suggested, without argument, that the Mantophasmatodea could be a subgroup of the Permo-Triassic order Titanoptera. However, on the basis of the wing venation, Béthoux (2007) argued that Titanoptera belongs to the orthopteroid lineage. In conclusion, we agree with Damgaard et al. (2008, pp. 459–460) that the ‘sister-group relationship of Mantophasmatodea to Grylloblattodea or some other neopteran lineage is far from settled.’

The Palaeozoic and Mesozoic fossils that are currently included into the Grylloblattodea share no apomorphies with their modern representatives. Grylloblattodea were considered to be paraphyletic by Storozhenko (2002) who studied the fossil ‘grylloblattids’ and are not characterized by any apomorphy. The Mesozoic and Palaeozoic ‘grylloblattodea’ is a ‘waste basket’ that replaces the former polyphyletic group ‘Protorthoptera,’ and should be completely reevaluated. Until now, there was still no evidence supporting the existence of Mesozoic Grylloblattodea sensu stricto, with the same applying to the Palaeozoic and Mesozoic fossils currently attributed to the Phasmatodea, and Tilgner (2001) considered the oldest unambiguous Phasmatodea to be Cenozoic. Pre-Cenozoic fossils that have been assigned to Phasmatodea have problematic relationships (Nel et al. 2004).

The fossil reported in this paper shows several apomorphic features of the Mantophasmatodea. It comes from the Middle Jurassic (165 Mya) of Daohugou, Inner Mongolia, China, which has also yielded plants, insects, conchostracans, anostracans, spiders, salamanders, pterosaurs, and mammals (Huang et al. 2006).

Materials and methods

The female holotype (NIGP 142171) is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. It is exquisitely fossilized as part and counterpart on a slab of volcanic tuff. The exam was realized without alcohol and under alcohol.

Systematic paleontology

Order Mantophasmatodea (Klass et al. 2002)

Family Mantophasmatidae (Klass et al. 2002)

Subfamily Raptophasmatinae (Zompro 2005)

Emended diagnosis This subfamily is supposed to be uniquely Eocene (Baltic amber). The present discovery implies that its geological range is wider. The head of the Eocene Raptophasmatinae is triangular in anterior view, which is not the case in *Juramantophasma*; thus, this character has to be excluded from the diagnosis of the subfamily.

Genus *Juramantophasma* gen. n.

Type species *Juramantophasma sinica* sp. n.

Diagnosis The insect was diagnosed as Raptophasmatinae, with head round in an anterior aspect; mandibles armed with strong teeth, especially the right one; sclerotized elongate dorsal process of third tarsomere spine-like; both female cerci and paraprocts hook-like; pronotum more or

less rounded and mesonotum shorter than wide; metanotum with postero-lateral angles; hind legs distinctly not saltatorial; arolium large, projecting beyond claws; pro- and mesofemora lacking definite, prominent spines; profemora with small granulae; and ventro-apical spines absent on tibiae.

Juramantophasma differs from *Raptophasma* in its profemora with small granulae, instead of being with only small bristles, and in the round head, which is triangular in *Raptophasma*. *Praedatophasma* (Zompro et al. 2002) has also a round head but differs from *Juramantophasma* in the presence of spines on the body and of ventral spines on the prothoracic tibiae (Zompro et al. 2002).

Etymology Genus named after *Jura* and *Mantophasma*.

Juramantophasma sinica sp. n.

Material Only the holotype was included (NIGP 142171a, b). This specimen is a nearly complete adult female in dorsal–ventral compression that split in the median section of the insect. Thus, we designate 142171a as the part preserved with head structures and postabdominal appendages and 142171b as the counterpart with thorax and most parts of the legs (Fig. 1a–l).

Locality and age Middle Jurassic Jiulongshan Formation at Daohugou, Ningcheng County, Inner Mongolia, Northeast China.

Etymology The species was named after the Latin name for China.

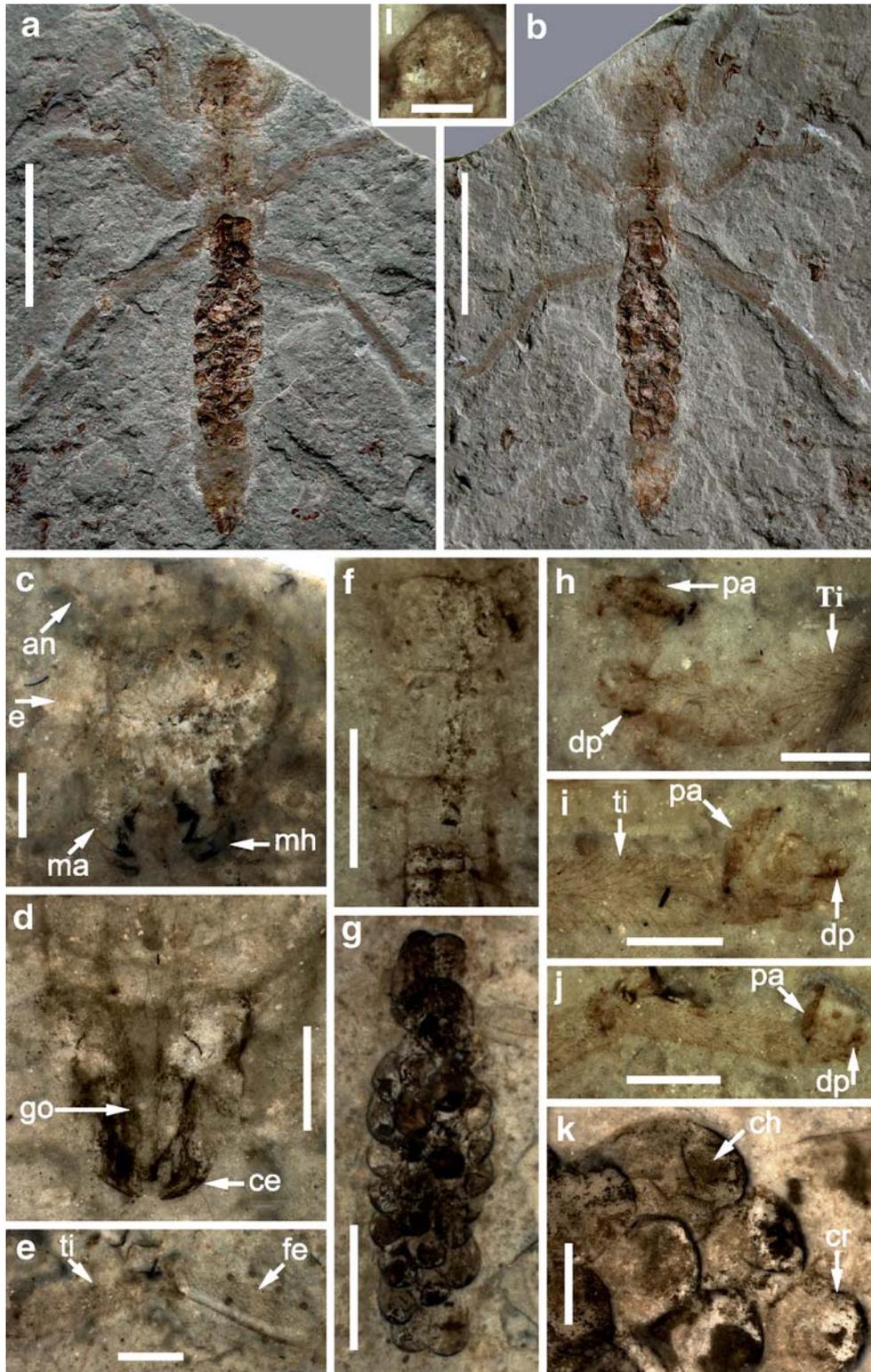
Diagnosis The insect was diagnosed as for genus.

Description The female holotype was 34 mm long. The hypognathous head covered with fine fur-like setae, 5.1 mm long and 4.4 mm wide; large eyes, 1.7 mm long and

Fig. 1 *Juramantophasma sinica* gen. and sp. n., holotype Nigpas 142171a–b. **a** General habitus of part. **b** General habitus of counterpart. **c** Details of head under alcohol (142171a) showing antenna, eyes, mandibles, and maxillary hooks. **d** Female postabdominal appendages of 142171a, showing ovipositor, cerci, and paraprocts. **e** Enlargement of right middle leg of 142171a, showing setae arrangements of femora and tibia. **f** Enlargement of thorax (142171b), showing pronotum, mesonotum, and metanotum. **g** 142171a, showing arrangements of eggs. **h** Details of left hind tarsi of 142171b, showing euplantulae of tarsomeres, dorsal process of third tarsomere and pretarsal arolium with dorsal setae rows. **i** Details of right hind tarsi of 142171b, showing dorsal process of third tarsomere and pretarsal arolium. **j** Details of right middle tarsi of 142171b, showing dorsal process of third tarsomere and pretarsal arolia. **k** Enlargement of **g**, showing details of eggs. **l** Enlargement of **g**, showing small points within circular ridge of eggs. *an* antenna, *ce* cercus, *ch* chorion, *cr* circular ridge, *dp* dorsal process of third tarsomere, *e* eye, *fe* femur, *ma* mandible, *mh* maxillary hook, *go* gonapophyse 8 of ovipositor, *pa* pretarsal arolium, *ti* tibia. Scale bars 10 mm in **a** and **b**, 2 mm in **e** and **j**, 1 mm in **c**, **d**, **f**, **i**, **k**; 500 μ m in **l**

1.3 mm wide, but no visible ocelli (Fig. 1a–b); antennae filiform, with basal five antennomeres preserved; large scape, 0.8 mm long; pedicel, 0.25 mm long; first flagellomere, 0.95 mm long; second flagellomere, 0.8 mm long; both mandibles with three strong teeth but not symmetrical; left

mandible stronger, broader, and with larger teeth than the right one, with apical tooth and first marginal tooth relatively sharp, second marginal tooth very blunt; right mandible armed with a sharper apical tooth, first marginal tooth similar to left one, second marginal tooth smaller than



left one, with a nearly orthogonal tip; all teeth bearing clear cutting margins, a topmost ridge visible in all teeth of the right mandible; maxillary hooks (laciniae) with two apical teeth; and an apical maxillary hook distinctly larger than the second (Fig. 1c).

The thorax (Fig. 1f) is covered with fine short setae elongate 11.0 mm long; pronotum, 3.5 mm long and 4.5 mm wide, more or less rounded rather than square, with slightly protruding anterior and posterior margins and arched lateral margins; mesonotum trapezoidal, distinctly shorter than wide, 3.2 mm long, 4.8 mm wide; metanotum rectangular, distinctly shorter than wide, 3.3 mm long and 4.0 mm wide, with small postero-lateral angles pointed backward.

The legs are covered with fine setae (Fig. 1e); all coxae protruding laterally due to taphonomic compression, mid coxae larger than hind ones; anterior margins in wave shape with a dense row of setae; hind coxae with rather straight anterior margins and a row of dense setae; trochanters smaller than coxae, fore- and mid-trochanters more or less triangular, fore trochanters smallest, hind trochanters more rounded, setae on trochanters arranged in bands; fore femora, 5.4 mm long and 2.2 mm wide; fore tibia, 5.3 mm long; mid femora, 4.5 mm long and 1.7 mm wide; tibia, 3.9 mm long; hind femora, 6.0 mm long and 1.5 mm wide; tibia, 7.0 mm long; tibiae with inner side lacking hair but limited by two rows of long setae, and outer side covered with small setae; femora with inner side without hair and limited by two rows of small setae, median part without hairs, and outer side setose, basal part without setae; sclerotized elongate dorsal process of third tarsomere spine-like, slightly curved, but not pointed apically; four basal tarsomeres bearing very large euplantulae; arolia of all legs fan-like, very large, and broad (Fig. 1h–j), those of the forelegs the smallest, mid-legs the largest; ten dorsal processes, each process armed with a long seta; claws hook-shaped and sharp near apex in all legs, very large in fore legs; all tarsi rather short, in hind legs first tarsomere broadest and longest, first to fourth tarsomeres gradually shorter and narrower, fifth tarsomere elongate but shorter than the first one, with increased width.

Abdomen is 21 mm long and 5 mm wide, filled by 28 visible eggs (approximately 3.3 mm long and 1.6 mm wide), anterior most part of abdomen with only two rows of eggs, middle part with four rows of eggs, posterior part with three rows of eggs (Fig. 1k–l); apex of abdomen very well preserved, with all structures clearly visible; last abdominal tergum lobe-like; second last tergum narrower but longer than third last, with distinct postero-lateral angles; third last tergum very short, shortest in its median section; a thin but sclerotized gonapophyse 8 of ovipositor almost covered by last abdominal tergum, with tapering shape and a cut tip, armed with

marginal hair pointed inner and backward; cerci one-segmented, hooked, with a strong base, posterior section abruptly thinner and more or less incurved; two hooked, sharp, incurved at apex, and strong structures are visible between the cerci, but they are shorter than them. They probably correspond to the gonoplasts IX ‘gl9’ sensu Klass et al. (2003; Fig. 1d).

Discussion

The general body shape and leg structures of this insect correspond to those of a ‘Polyneoptera.’ Because it has unsegmented cerci, the fossil could not be considered to belong to any extant group of Grylloblattodea, which have segmented cerci. Even the few fossil taxa currently attributed to the Grylloblattodea, with preserved body structures, have multi-segmented cerci (i.e., *Blattogryllidae* Rasnitsyn 1976). Among Hexapoda with unsegmented cerci, the presence of large mandibles excludes the *Diplura*. The plesiomorphic condition of five-segmented tarsi of *Juramantophasma* is present not only in the Mantophasmatodea but also in the Mesozoic Dermaptera, whereas all recent representatives of the other ‘polyneopteran’ orders have unsegmented cerci.

Juramantophasma exhibits several characters currently considered as apomorphies of the Mantophasmatodea, i.e., a third tarsomere with a sclerotized elongated dorsal process; enlarged and fan-like pretarsal arolia with a clearly visible row of dorsal setae, identical to those of the modern *Mantophasma zephyra* (Zompro et al. 2002, as figured in Klass et al. 2002 and Beutel and Gorb 2006, Fig. 3b); last tarsomere making a right angle with the others, keeping it up in the air; female gonoplasts (valves 3) short and claw-shaped; and egg with a circular ridge. All of these characters are completely different from those of the modern Phasmatodea, Grylloblattodea (see Zompro 2001; Beutel and Gorb 2001 and 2006, Fig. 4), and Dermaptera (see Haas and Gorb 2004), which exclude affinities with these insects.

The following characters of our fossil are further shared with the Mantophasmatodea: hypognathous head, wings absent, antennae probably long, and filiform after the shape of the preserved part, ocelli not visible, probably absent, pronotum longer than meso- and metanotum; hind legs very thin but longer than the middle and forelegs; fore femora are the widest; four basal tarsomeres very short (long in Phasmatodea, except for ground dwelling forms, e.g., *Agathemera*, some *Aschiphasmata*, *Heteropterygidae*, and *Eurycanthinae*), and bearing very large euplantulae (very small in modern Grylloblattodea); abdominal segments transverse; ovipositor elongate, nearly reaching the apex of abdomen; egg large, elongate, and a chorion with a pattern of small spots and a central gibbosity.

The phylogenetic relationships of *Juramantophasma* within the Mantophasmatodea are difficult to establish because of the lack of a phylogenetic analysis of this order based on morphological characters. The available analyses are based on molecular data only (Klass et al. 2003; Damgaard et al. 2008). We can only base our analysis on typological comparison with other Mantophasmatodea. *Juramantophasma* shares with the Mantophasmatidae (Klass et al. 2002) hind legs distinctly not saltatorial, arolium large, projecting beyond claws. The absence of ventro-apical spines on the tibiae is a difference to the Mantophasmatinae, as Zompro (2005) characterized this group on the basis of the presence of two ventro-apical spines on tibiae. *Juramantophasma* shares with the Baltic amber Raptophasmatinae (Zompro 2005), its prothoracic tibiae lacking definite ventral spines.

The mandibles of *Juramantophasma* seems to be less specialized than those of the recent Mantophasmatodea, especially the left one with three strong teeth, instead of one apical tooth well separated from two distinctly smaller teeth (Baum et al. 2007). Nevertheless, the difference is rather weak, especially with the mandibles of the recent *Mantophasma*. Unfortunately, little is known on the mandibles of the Baltic amber Mantophasmatodea. The mandibles of this Jurassic taxon look similar to those of the recent Ensifera. *Juramantophasma* was probably a predator (e.g., mandible with strong teeth; broad fore legs with strong hook-like claws) but less specialized than the recent rock crawlers, supporting Gorochov's (2006) hypothesis on the Jurassic diversification of predatory 'polyneopterous' groups that 'tried to occupy' the niches that remained empty between the extinction of the Titanoptera and the diversification of the Mantodea.

At this stage, it is not possible to infer anything on the relationships between Mantophasmatodea and the other 'polyneopterous' orders from the present discovery because *Juramantophasma* belongs to the Mantophasmatodea sensu stricto and also because of the great confusion in the systematics and phylogenetic affinities of the fossil taxa currently included in the Grylloblattodea.

Nevertheless, the present discovery of a middle Jurassic Mantophasmatodea does not fit well the assumption of Arillo and Engel (2006, p. 8) that the 'Mantophasmatodea and perhaps also their sister Grylloblattodea as they differentiated from stem-group families such as Blattogryllidae in the Jurassic or Early Cretaceous.' Mantophasmatodea are clearly much older than the middle-late Jurassic Blattogryllidae.

Juramantophasma documents that the Mantophasmatodea were present by 165 Ma ago, 120 Ma older than the previous record, and before the modern lineages of the Orthoptera are known to appear (Béthoux and Nel 2002), which contradicts the hypothesis of Tilgner (2002). This suggests that these insects could be much older

(Palaeozoic). The difficulties in resolving the phylogenetic relationships of the Mantophasmatodea within the 'Polyneoptera' are probably due to the great antiquity and rapid diversification of the latter (Whitfield and Kjer 2008).

Despite this new Mesozoic record, the Mantophasmatodea apparently remained a cryptic order in recent and past worlds, compared to the predaceous mantises that began to diversify in the Early Cretaceous (Grimaldi and Engel 2005).

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