

An exquisitely preserved harvestman (Arthropoda, Arachnida, Opiliones) from the Middle Jurassic of China

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Abstract Sclerosomatids constitute the largest family of the arachnid order Opiliones, and one of the two families commonly found in the temperate regions of the northern Hemisphere. Harvestmen have a sparse fossil record in the Mesozoic, with only two species known from the Jurassic, one of them poorly preserved and none with precise phylogenetic placement. Here we report a new fossil, *Mesobunus dunlopi* sp. nov., from the Middle Jurassic (approx. 165 Mya) of Daohugou, Inner Mongolia, China. The new species is related to another genus of the same formation, but the preservation quality and details of the penis and pedipalps allow us to place them in the extant sclerosomatid subfamilies Gagrellinae or Leiobuninae. The first recognisable fossil in this subfamily highlights morphological stasis over ca. 165 Mya and the finding of this species along with lacustrine insects suggests a life mode similar to that of some modern sclerosomatids, and a possible connection between morphological and ecological stasis.

Keywords Mesozoic · Fossil · Sclerosomatidae · Gagrellinae · Leiobuninae

Introduction

Opiliones (harvestmen or daddy-long-legs) is the third largest arachnid order, after Acari and Araneae, with ca. 6,500 described species and probably including up to 10,000 living species (Pinto-da-Rocha et al. 2007). They have an old fossil record, beginning in the Early Devonian (ca. 410 Ma), for what it is considered a member of the suborder Eupnoi (Dunlop et al. 2003a, 2003b). Recent dating using molecular sequence data suggests a Late Silurian origin of Opiliones, and a Devonian origin for the typical “daddy-long-legs” of the superfamily Phalangioidea (Giribet et al. 2010). Therefore Opiliones have been used as exemplar taxa for biogeographic study of old vicariant lineages (e.g., Boyer et al. 2007; Giribet and Kury 2007; Giribet et al. 2011; Sharma and Giribet 2011).

The arachnid fossil record is sparse throughout the whole Mesozoic period (Selden 1993), specially for the Jurassic period. The recent discovery of hundreds of new specimens of spiders from the Middle Jurassic Jiulongshan Formation (ca. 165 Ma) at Daohugou, China, however, marked a dramatic increase in information on fossil spiders of this period (Selden et al. 2008, 2011; Selden and Huang 2010). The Opiliones fossil record of the Mesozoic is also sparse, and has been reviewed in detail by Huang et al. (2009). It is currently restricted to five described species, including Eupnoi, Dyspnoi and Cyphophthalmi (Jell and Duncan 1986; Giribet and Dunlop 2005; Dunlop 2007; Poinar 2008; Huang et al. 2009).

Here we describe the third Jurassic member of the arachnid order Opiliones from the Middle Jurassic of China. The specimen, preserved in a finely laminated, pale gray tuff, as

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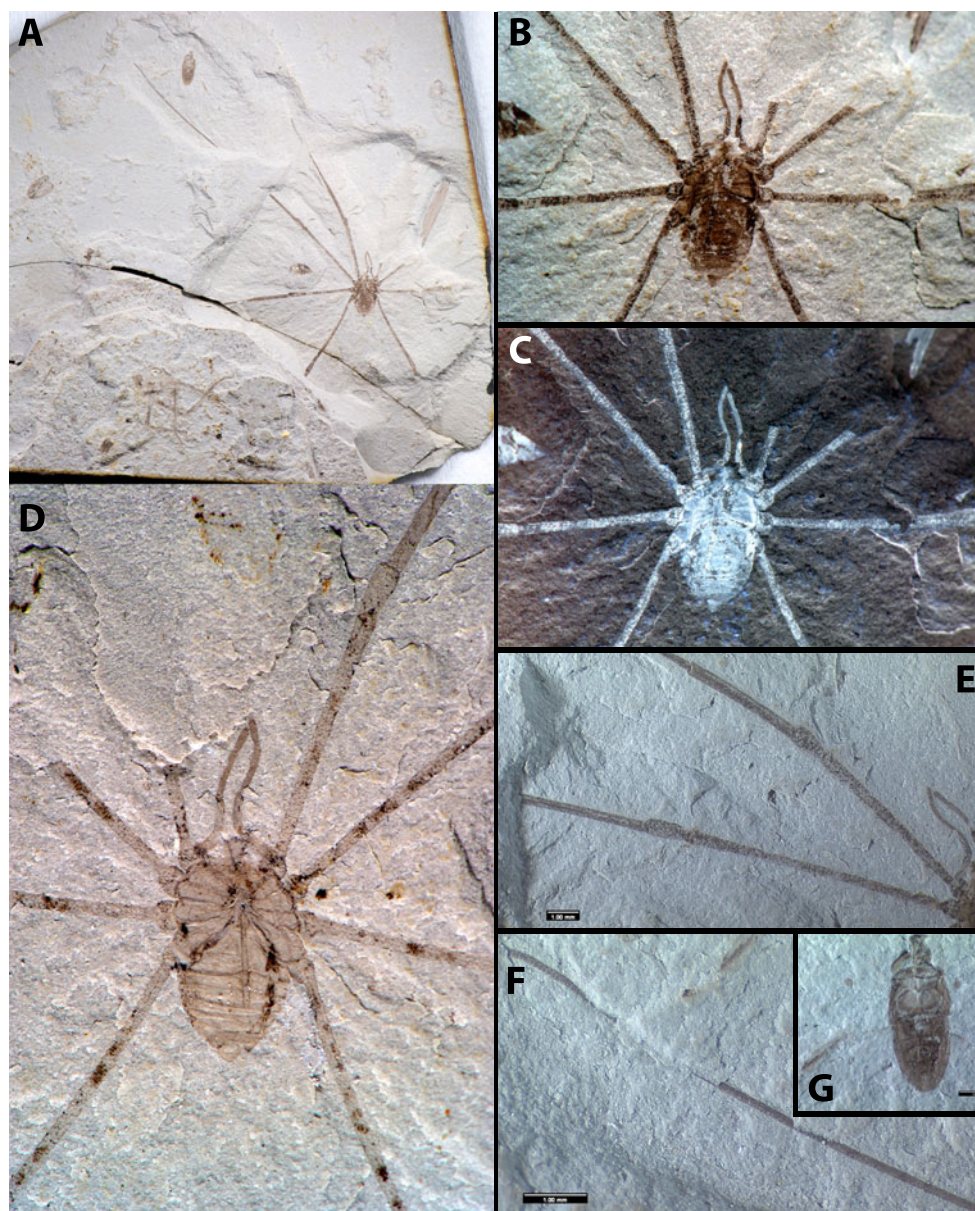
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part and counterpart is a member of the Eupnoi clade Phalangioidea, family Sclerosomatidae, subfamily Gagrellinae or Leiobuninae.

Materials and methods

The new fossil (Figs. 1a–h), part and counterpart, was studied and photographed dry under low-angle light in a stereomicroscope. Images were manipulated in Adobe Photoshop, by inverting colour, which revealed additional cuticular structures (Figs. 1b,c). All measurements are in millimetres and were made from the photographs generated with Automontage.

Fig. 1 a–g Photographs of holotype, CNU-OPI-NN2008001 p/c. **a** Dorsal view (part) of whole tuff piece. **b** Dorsal view of body. **c** Same view with inverted coloration in Photoshop to highlight cuticular structures. **d** Ventral view (counterpart) of body. **e** Left legs I and II, proximal region. **f** Distal region of left leg II. **g** Nepomorpha. Bars e–g 1 mm



Species concepts in fossils are by nature more restricted than those applicable to living organisms for many obvious reasons. Here we use the criterion of diagnosability for recognizing species (Nixon and Wheeler 1990; Davis and Nixon 1992), but with the limitation of knowing that a single specimen is studied, and thus choose only those characters that would diagnose species of living Opiliones.

Geological setting

The Jiulongshan Formation is a lacustrine sequence that crops out in Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, Northeastern China (41°19.532' N, 119° 14.589' E) (Ren et al. 2002). The section at Daohugou is

composed of grey tuffaceous sandstone and sandy mudstone. The palaeoenvironment reconstructed for this locality is a volcanic region with mountain streams and lakes (Ren et al. 2002), the latter justified by the presence of several *Nepomorpha* fossils (Ren et al. 2010; Fig. 1h). Daohugou has provided abundant and diverse arthropod fauna composed of complete specimens of other arachnids such as Araneae (Selden et al. 2008, 2011; Selden and Huang 2010) and other species of Opiliones (Huang et al. 2009). The Daohugou deposits have also yielded plants, insects, freshwater conchostracans (Zhang and Shen 1987), anostracans, salamanders, dinosaurs, pterosaurs, and mammals (see Ren et al. 2010). Surrounding Gymnosperm forests were dominated by Ginkgopsida (*Ginkgoites*, *Ginkgo Baiera*, *Czekanowskia*, *Phoenicopsis*), Coniferopsida (*Pityophyllum*, *Rhipidiocladus*, *Elatocladus*, *Schizolepis*, *Podozamites*), Lycoposida (*Lycopodites*, *Selaginellites*), Sphenopsida (*Equisetum*), Filicopsida (*Todites*, *Coniopteris*) and Cycadopsida (*Anomozamites*) (Mi et al. 1996). All these paleontological data have been interpreted as indicating humid and warm-temperate climate (Ren et al. 2010).

The accurate Ar-Ar and SHRIMP U-Pb dating shows that the age of intermediate-acid volcanic rocks overlying the Daohugou fossil-bearing beds is about 164–165 Mya, and that the age of this fossil-bearing beds is older than or equal to 165 Mya (Chen et al. 2004). Combined with the above-mentioned composition of insect fauna and conchostracans, the age of the Daohugou biota is Middle Jurassic (Bathonian - Callovian boundary) (Ren et al. 2002; Gao and Ren 2006; Ren et al. 2010).

Results

Systematic paleontology

Order Opiliones Sundevall, 1833

Suborder Eupnoi Hansen & Sørensen, 1904

Superfamily Phalangioidea Latreille, 1802

Family Sclerosomatidae Simon, 1879

Subfamily Gagrellinae Thorell, 1889 or Leiobuninae Banks, 1893

Genus *Mesobunus* Huang et al., 2009

Mesobunus dunlopi sp. nov.

Etymology The species is named after Jason Dunlop, colleague and friend who has contributed enormously to Opiliones palaeontology, among many other arachnid groups.

Holotype CNU-OPI-NN2008001 p/c in the College of Life Sciences, Capital Normal University, Beijing; adult male. No other specimens known.

Diagnosis Tibial inner apophysis of pedipalp not present. Corona analis present. Penis (Fig. 2c,d) as in extant species of Gagrellinae and Leiobuninae. Penis shaft long, five times the length of winglets, with straight contour, constricted only at the height of glans; glans and stylus area very conspicuous. Winglets conspicuous, longer than wide, with truncate contour. Compared to *Mesobunus martensi* Huang, Selden & Dunlop, 2009, *M. dunlopi* sp. nov. is similar in size, but patellae are shorter and pedipalps are much more slender, with all articles of equivalent width. *Mesobunus martensi* shows conspicuous enlarged chelicerae, inflated palps (femur and patella) with slender tibia and tarsus, and rudiments of corona analis, in addition to longer legs than *M. dunlopi* sp. nov. *Daohugopilio sheari* Huang et al. 2009

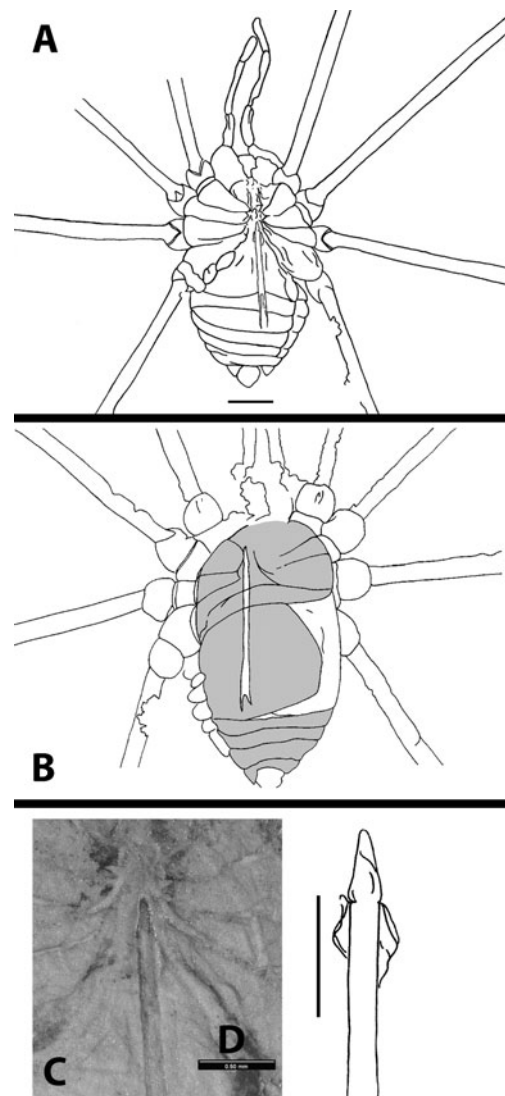


Fig. 2 a–d Illustrations of holotype, CNU-OPI-NN2008001 p/c. **a** Line drawing, ventral view (counterpart) of body. **b** Line drawing, dorsal view (part) of body. **c** Detail of penis. **d** Line drawing, penis. Bars **a** 1 mm; **c,d** 0.5 mm

(Huang et al. 2009) is poorly preserved, but it is a smaller species difficult to compare morphologically.

Description Body oval in outline, length 5.01, width 2.78. Eye mound not visible, but with a cuticular hole in the anterior of dorsal carapace where the eye mound may have been located. Front of carapace with poorly preserved cuticle, and only anterior border of margin of carapace preserved, but with two missing pieces of cuticle, especially visible with inverted image (Fig. 1d). Without conspicuous visible ornamentation or setae. Dorsal and ventral sclerites recognizable. Second prosomal tergite present between carapace and opisthosomal dorsal scutum, slightly larger than in *Mesobunus martensi*. Opisthosomal dorsal scutum subrectangular, lateral outline straight, rounded anteriorly and posteriorly. Free tergites I–III evident. Genital operculum subtriangular, with each border slightly curved inwards, large, longer than wide. A similar type of subtriangular genital operculum is found in the other Jurassic Eupnoi genus *Daohugopilio*. Sternites IX–XIV of similar size and shape, sternite X slightly larger than others, anterior and posterior margins almost straight. Two lateral triangular pieces present at each side of round anal operculum are rudiments of corona analis (present in several New World species of Gagrellinae; Tourinho and Kury 2001; Tourinho 2007b).

Pedipalps slender and very long, up to 2.8 mm, of a length comparable to half body length, without any conspicuous armature. Femur not well preserved. Patella of same size as tibia; granules and apophyses not visible. Patellar apophyses are present in most living species of Gagrellinae as well as in *M. martensi* and *Daohugopilio sheari*, although they can be very small or inconspicuous in some cases. Tibial inner apophysis not present. Proventral row of denticles on palpal tarsus not observed. Tarsus half the size of tibia. Chelicera not visible, perhaps detached.

Legs Measurements of Femur/Patella for left legs I–III, and right leg IV: 5.79/1.17, 8.52/1.16, 6.00/1.28, 7.54/1.33; leg formula (2,431). Coxae large and robust, larger than in *M. martensi*, spines, granules and apophyses not visible on femora, patellae or tibiae. Only the proximal part of the metatarsi III is preserved. One nodule in leg IV, assumed by irregularities in the femora of legs IV (see remarks for further explanations). Coxae IV larger than I–III.

Penis 2.2 mm in length Shaft long and narrow, five times the length of winglets; glans triangular shaped (Fig. 2c, d). Winglets rounded trapezoidal, developed lamina, moderately expanded laterally, and not very prolonged longitudinally.

Discussion

Taxonomic position

According to current taxonomy, there are two characters that would allow taxonomic placement for this fossil, the penis and the nodules of the femora of leg IV. The penis of sclerosomatids can possess developed winglets with internal structures that play a role in sexual selection and thus in species reproduction. The presence of developed saccular winglets in the penis is supposedly a plesiomorphic feature found only in Gagrellinae and Leiobuninae. Although some Gagrellinae and derived Leiobuninae (*lanceolata* group) can lack sacs, no member of any other subfamilies or families have the developed saccular winglets. The absence of such sacs may have important implications in mating behaviour (Shultz 2005; Macías-Ordóñez et al. 2010). *Mesobunus dunlopi* sp. nov. clearly shows the winglets forming a developed sac (Fig. 2c,d), therefore discarding an affinity to Gyiinae, Sclerosomatinae, the *Metopilio* group or *Dicranopalpus*. It also allows the position of *Mesobunus martensi*, for which the penis was not as well preserved, to be refined.

Nodules have been used traditionally for distinguishing Gagrellinae from other sclerosomatids; however, recent studies have shown that this is not the case and that nodules are also present outside Gagrellinae, including species of Leiobuninae and some Phalangiidae (Tourinho 2007a). In addition, nodules are hard to distinguish even in modern specimens (Martens 1987; Tourinho and Kury 2001) and scanning electron microscopy is often required to be certain of the presence of real nodules (Tourinho and Kury 2001). Although the fossil specimen presents irregularities in the femora of legs IV, which we assume to be the nodules present in modern Gagrellinae, this cannot be ascertained with certainty, and its presence would not help resolve the systematic placement of the fossil.

The characters explored therefore discard the placement of the new fossil in certain sclerosomatid clades, but do not rule out Gagrellinae or Leiobuninae. However, the boundaries between Gagrellinae and Leiobuninae were never well established, and when penis morphology became the most important taxonomic character in sclerosomatids, the division of this group became even less clear (Starega 1976; Martens 1987; Crawford 1992; Tourinho 2007a). For example, the species of both subfamilies have been grouped in the same family, Gagrellidae by Starega (1976), the latter moved back into Phalangiidae (Martens 1987), while in his catalogue Crawford (1992) suggests that Gagrellinae, Sclerosomatinae and Gyiinae are related more closely to each other than to any of the other subfamilies included in Phalangiidae. Crawford (1992) then suggested, on the basis of genital features, that the separation of Leiobuninae and Gagrellinae was unjustified morphologically—although he

kept them separate based on zoogeographic features. Species of Gagrellinae and Leiobuninae have very similar penial morphology; additionally they share the presence of winglets, absent in species of all other subfamilies and families. Therefore the placement of this fossil species with well developed winglets in Gagrellinae/Liobuninae is well justified based on penial morphology. Nevertheless, Gagrellinae and Leiobuninae may actually not be monophyletic (Tourinho 2007a), as suggested by a recent analysis of Opiliones phylogeny including molecular data on seven sclerosomatids (Giribet et al. 2010).

The fossil record

Mesozoic fossil records of Opiliones, and that of the Jurassic period, are scarce, and thus the addition of an extraordinarily preserved harvestman from the Middle Jurassic of Inner Mongolia adds important information to this period, especially since it illustrates the stasis of the group, as already suggested for older Opiliones, and allows us to place the species within extant subfamilies Gagrellinae/Liobuninae.

Morphological stasis in Opiliones has been shown in a few modern-looking Palaeozoic species, including the well-preserved Early Devonian (~410 Ma) Rhynie Chert (Dunlop et al. 2003a, 2003b). While incomplete, these preserved internal features in three dimensions hint at an essentially modern body plan. Other Palaeozoic species, including a superficially modern-looking, long-legged fossil from the Early Carboniferous (~340 Ma) of Scotland (Dunlop and Anderson 2005), are preserved too poorly to allow an unequivocal taxonomic placement. More recently, two new species of Carboniferous (~305 Ma) harvestmen from the Montceau-Les-Mines Lagerstätte in France, found within siderite (FeCO₃) nodules and displaying three-dimensional, high-fidelity preservation, were described with the aid of high-resolution X-ray micro-tomography (μ CT) and placed phylogenetically using a cladistic analysis (Garwood et al. 2011). But then, following the Carboniferous period, well-preserved harvestmen are not recorded again until Cretaceous (~100 Ma) ambers (Giribet and Dunlop 2005).

Our specimen increases the Mesozoic diversity of Opiliones and adds additional precision to the placement of the Inner Mongolian fauna. Huang et al. (2009) argue for a similarity of *Mesobunus* to the East Asian eupnoids, but unfortunately the phylogenetic relationships and biogeographic structure of Sclerosomatidae are poorly understood, due to, among other things, its convoluted taxonomy and size, as it constitutes the largest harvestman family. Recent molecular work on Sclerosomatidae (M. Hedin and collaborators, personal communication) suggests the existence of a group of East Asian gagrellines, to which *M. dunlopi* sp. nov. may belong. However, monophyly of the currently recognised Sclerosomatidae subfamilies shows little support

in molecular analyses (Giribet et al. 2010), and the current system is in need of urgent revision. Notwithstanding this possibility, the preservation quality of the penis of *M. dunlopi* sp. nov. allows the subfamily assignment according to the current taxonomy of the group.

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