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ORIGINAL PAPER

Harvestmen (Arachnida: Opiliones) from the Middle Jurassic of China

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Abstract Harvestmen (Arachnida: Opiliones) are familiar animals in most terrestrial habitats but are rare as fossils, with only a handful of species known from each of the Palaeozoic, Mesozoic, and Cenozoic eras. Fossil harvestmen from Middle Jurassic (ca. 165 Ma) strata of Daohugou, Inner Mongolia, China, are described as *Mesobunus martensi* gen. et sp. nov. and *Daohugopilio sheari* gen. et sp. nov.; the two genera differ primarily in the relative length of their legs and details of the pedipalps. Jurassic arachnids are extremely rare and these fossils represent the first Jurassic, and only the fourth Mesozoic, record of Opiliones. These remarkably well-preserved and modern-looking fossils are assigned to the Eupnoi, whereby *M. martensi* demonstrably belongs in Sclerosomatidae. It thus represents the oldest record of a modern harvestman family and implies a high degree of evolutionary stasis among one of the most widespread and abundant groups of long-legged, round-bodied harvestmen.

Keywords Daohugou · Fossil · Inner Mongolia · Sclerosomatidae

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Introduction

Harvestmen (Opiliones) are a diverse group of arachnids with 6,411 living species (Kury 2008). They have a long, albeit sporadic, fossil record with the oldest dating from the Early Devonian (ca. 410 Ma) and already assignable to the Eupnoi (Dunlop et al. 2003)—a crown-group encompassing the classic 'daddy long-legs' type of animal. Twenty-six fossil species are currently recognized (summarized in 2007 by Dunlop (2007)) and over half of them derive from Palaeogene–Neogene ambers. These inclusions have largely been referred to extant genera and now include representatives of all four major harvestman lineages (cf. Giribet et al. 2002): i.e., Cyphophthalmi, Eupnoi, Dyspnoi, and Laniatores. Until recently, arachnid-bearing localities were particularly rare throughout the entire Mesozoic. Harvestmen from this era were originally known from only a single long-legged, small-bodied animal from the Early Cretaceous (ca. 115–118 Ma) Koonwarra beds of Australia (Jell and Duncan 1986) which the authors felt was too poorly preserved to be formally named or assigned taxonomically. The second Mesozoic example, *Halitherses grimaldii* Giribet and Dunlop 2005, was described from mid-Cretaceous (ca. 100 Ma) Burmese amber. Also long-legged, and with a large and distinctive, bilobed ocular tubercle, it was assigned to the Troguloidea of the Dyspnoi largely on the basis of its pedipalp morphology. Most recently, a cyphophthalmid was described from Burmese amber (Poinar 2008). Other putative records of Mesozoic harvestmen in the literature have been shown to be misidentifications (Giribet and Dunlop 2005). For example, unnamed forms described by Roger (1946) from Upper Cretaceous (Santonian) limestones in Sahel-Alma, Lebanon, from a fully marine setting, were studied by PAS and considered to be long-legged crustaceans, and a supposed harvestman figured by Schlüter (1978) from Cretaceous (Cenomanian) amber of the Paris and Aquitaine Basins, northwest France, is almost certainly a mite.

The Jurassic period has an extremely sparse arachnid fossil record. Reports of spiders and/or harvestmen from the famous Solnhofen locality in Germany are typically long-legged crustaceans (e.g., Polz 1975), while a putative member of the Palpigradi from the same locality is an insect (Delclòs et al. 2008). There is one reliable, but uninspiring, scorpion (Scorpiones) from near Braunschweig in Germany (Dunlop et al. 2007). Another putative scorpion from Siberia appears to be a cockroach (Fet et al. 2000). There are a handful of oribatid mites (Acari) from Sweden, Siberia, and England (Krivolutsky and Druk 1986; Selden et al. 2008a). Among spiders, there is an extinct family, Juraraneidae, and an archaeid from central Asia (Eskov 1984, 1987), a poorly preserved spider from the Middle Jurassic Jiulongshan Formation at Zhouyingzi, Hebei Province, China (Hong 1984), and an undescribed spider from Germany (Ansorge 2003). The recent recovery of hundreds of new specimens of spiders from the Middle Jurassic Jiulongshan Formation (ca. 165 Ma) at Daohugou, Ningcheng County, Inner Mongolia, northeast China, marked a dramatic increase in information on fossil spiders of this period. This new material mainly belongs to the superfamilies Deinopoidea (Uloboridae), Araneoidea, and Palpimanoidea, including archaeids (Selden et al. 2008b).

In this paper, we describe the first ever Jurassic harvestmen, which represent only the fourth, and oldest, Mesozoic record of Opiliones. The two examples are very well preserved and include details such as setae, claws, and genitalia. They differ sufficiently in their limb and body proportions that we consider them to represent distinct genera. Both fossils are referred here to Eupnoi and closely resemble extant genera in their gross morphology. One can even be placed with confidence in the family Sclerosomatidae.

Materials and methods

The specimens come from a finely laminated, pale gray tuff near Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China (41°19.532′ N, 119° 14.589′ E). The Daohugou deposits (see Ren et al. (2002) for details) consist of gray tuff, tuffaceous siltstones, and mudstones, indicative of lacustrine conditions in a volcanic region, and have also yielded plants, insects, conchostracans, anostracans, spiders, salamanders, theropod dinosaurs, pterosaurs, and mammals. A Middle Jurassic age for the Daohugou assemblage has been proposed most recently, based on the composition of the insect fauna (e.g., Ren et al. 2002; Huang et al. 2006), conchostracans (Shen et al. 2003), and isotopic dating (Chen et al. 2004; Liu et al. 2004).

The material comprises part and counterpart of both holotype (and only known) specimens of these two new genera. Both are almost complete harvestmen showing predominantly ventral views, but with dorsal structures superimposed on the ventral parts of *Mesobunus*. The specimens are preserved as external molds with much adhering, minutely fragmented, dark material (this appears to be a replacement of the original organic matter).

On some leg podomeres of *Mesobunus*, there appear to be joints where they would not occur in comparison to living opilionids, e.g., on right femur 4 and left basitarsus 3. There is segmentation of the tarsi, as expected, and the apparent joints on more proximal podomeres are not pseudoarticulations (see below). Furthermore, the measurements of the podomeres of left and right legs of a pair are not always as close as would be expected, even allowing for accuracy errors and normal preservational artifacts, e.g., the femora of legs 2 and the basitarsi and tarsi of legs 3. Since harvestmen do not re-grow their legs after autospasy (Gnaspini and Hara 2007), leg asymmetry cannot be explained by regeneration. Moreover, the number of tarsomeres varies somewhat on the left and right sides of the same pair. The best explanation of the differences in leg length and the apparent jointing on podomeres where it would not be expected is that the rock has suffered some compression which has caused some long podomeres to telescope: some to shorten and others to lengthen. Proximally, on the femora of leg 4 in *Mesobunus*, there are apparent thickenings with a granular texture; we considered these as possible pseudoarticulatory nodules (which would concur with a placement in Scleromatidae: Gagrellinae), but their unusual texture and left–right asymmetry suggest they are probably artifacts.

Preparation was carried out using a sharp knife. The material was studied using Leica MZ16A and M205C stereomicroscopes and photographed and drawn using Leica digital cameras and drawing tubes attached to these microscopes. Morphological terminology follows Shultz (2000). All measurements are in millimeters. Measurements of structures for which left and right and/or part and counterpart are preserved are given as the mean of all measurements, except for the legs (see above).

Abbreviations: leg formula (e.g., 1234) longest to shortest; a op, anal operculum; bt, basitarsus; car, carapace; ch, chelicera; cx, coxa; d sc, dorsal scutum; fe, femur; g op, genital operculum; mp, metapeltidium; o t, ocular tubercle; pa, patella; Pd, pedipalp; s, sternite; t, tergite; ta, tarsus; ti, tibia.

Systematic paleontology

Order Opiliones Sundevall, 1833
Suborder Eupnoi Hansen and Sørensen, 1904
Family Sclerosomatidae Simon, 1879

Remarks Specimen NIGP 141509a, b (Figs. 1–3) can be assigned to Sclerosomatidae on the basis of the extremely elongate legs (Fig. 1), a single tarsal apotele, a pediform pedipalp, and, particularly, the fusion of the first five opisthosomal tergites into a single dorsal plate, the *scutum parvum* (Fig. 2a, e), which is characteristic for this family (Tourinho 2007). In other eupnoid families, all dorsal tergites are either all fused together and strongly sclerotized (Monoscutidae) or fused together and more leathery with little external segmentation (Phalangiidae, Neopilionidae). Protolophidae has the first five areas of the opisthosoma fused, but usually with prominent humps, while Caddidae can be excluded because these are very small harvestmen (max. 3 mm) with proportionally massive eyes. Should the thickenings near the base of fourth femora be real, and not artifacts, then these could be interpreted as pseudoarticulatory nodules and suggest a placement in the subfamily Gagrellinae (Tourinho 2007). We note that there is no consensus opinion regarding the phylogeny of Opiliones, so our determinations are based on recent literature (Giribet et al. 2002; Kury 2008); conversely, it would be unwise to suggest changes to harvestmen phylogeny based on fossils, though the specimens described here do not provide evidence for any novel hypotheses.

Mesobunus martensi gen. et sp. nov. (Figs. 1–3)

Diagnosis Sclerosomatid with a prominent subtriangular patellar apophysis mesodistally on the pedipalp; second cheliceral article with flange parallel to the long axis of the deutomerite near its basal articulation.

Etymology Combination of the Mesozoic era and the suffix -*bunus* widely used for Recent long-legged opilionid genera. The specific epithet is after Professor Jochen Martens (Mainz, Germany) on the occasion of his recent retirement and in recognition of his extensive work on extant East Asian harvestmen.

Type material, locality, and horizon Holotype and only known specimen, part (141509a) and counterpart (141509b), deposited in the Nanjing Institute of Geology and Palaeontology, from Middle Jurassic Jiulongshan Formation, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Description Body oval in outline; length 4.78, max. width 3.23. Without strong ornament in the form of spines or tubercles, but with tiny setae on leg coxae and genital operculum, rather sparse setae on rest of abdomen, long setae on chelicerae and basal parts of pedipalps. Femora with short but rather strong spines, patellae with tiny setae,

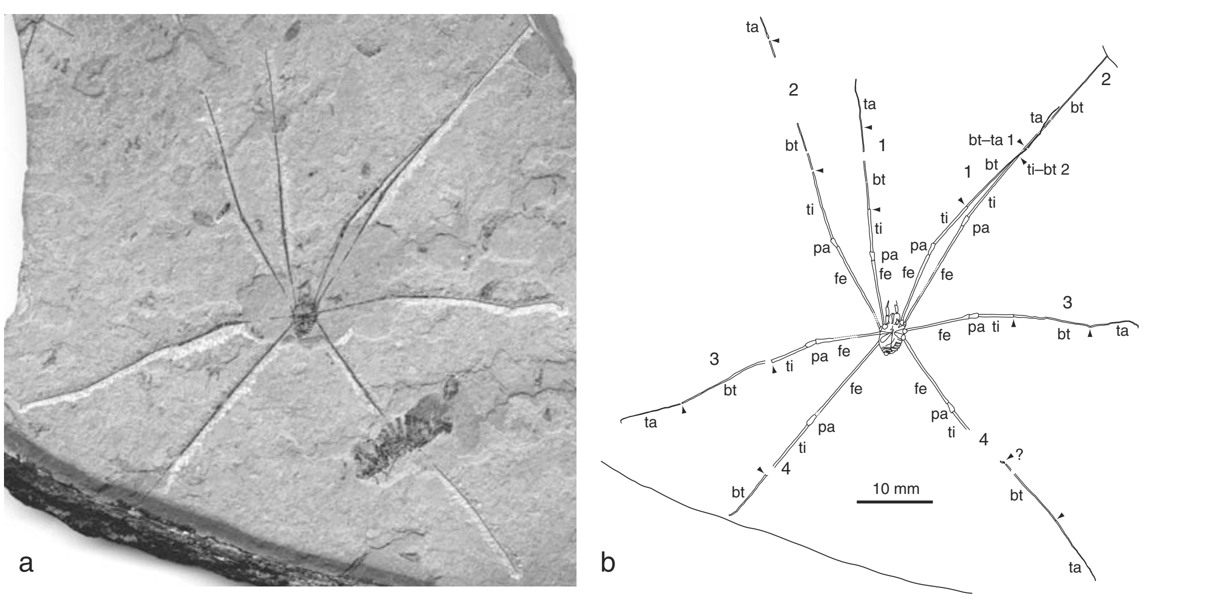

Fig. 1 *Mesobunus martensi* (NIGP 141509a). **a** Holotype part, dorsal view of whole specimen. **b** Explanatory drawing to accompany **a**

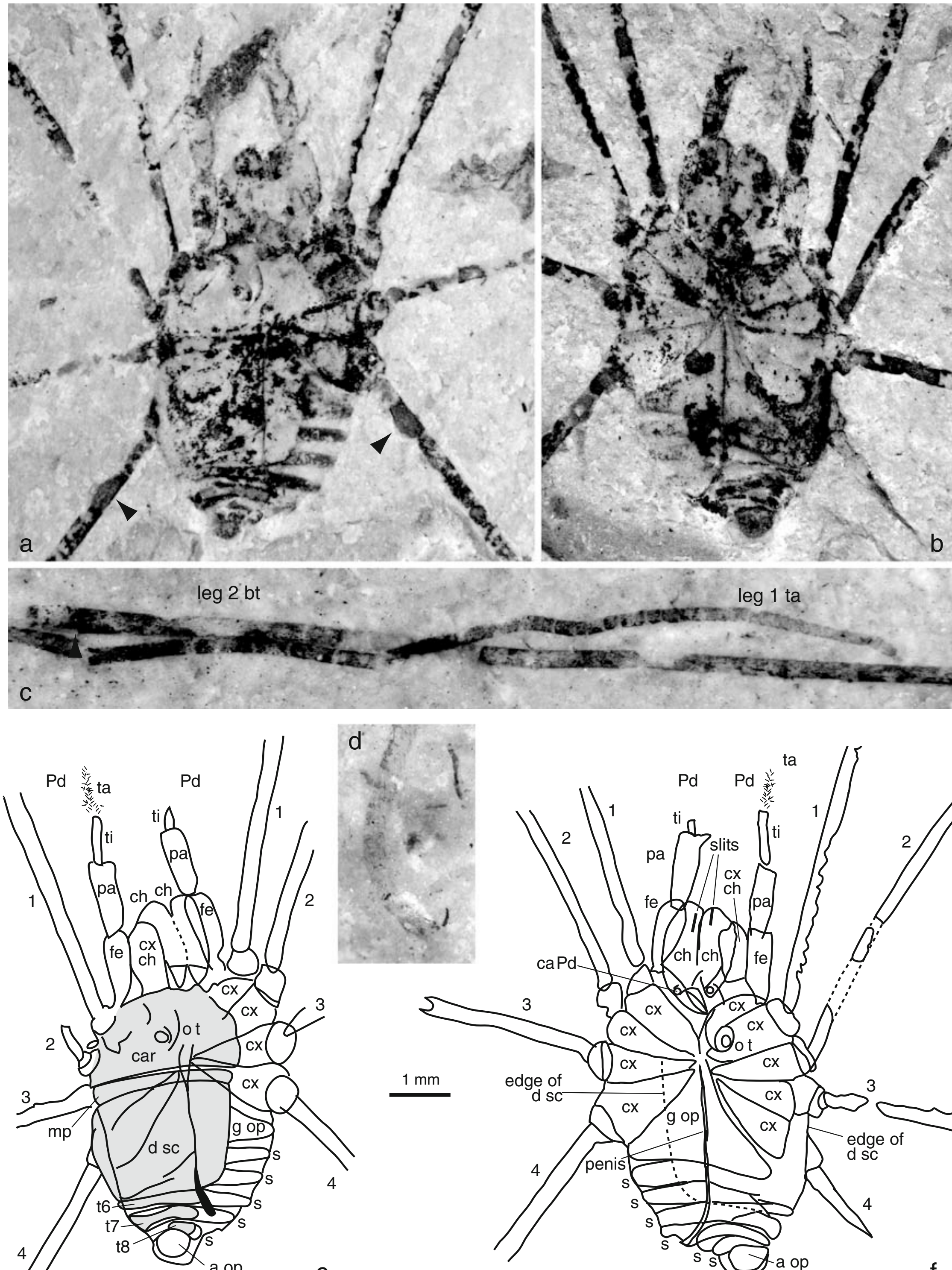

Fig. 2 *Mesobunus martensi* (NIGP 141509a,b). **a** Holotype part, dorsal view of body; *arrowheads* point to apparent proximal thickenings (probably artifacts). **b** Holotype counterpart, ventral view of body. **c** Detail of basitarsus of right leg 2 alongside tarsus of right leg 1; *arrowhead* marks proximal joint of tarsus 1 (see Fig. 1b for location and scale), showing general preservation, cuticle ornament, and tarsomeres. **d** Detail of distal part of left leg 3 tarsus showing tarsomeres and apotele. **e** Explanatory drawing to accompany **a**. **f** Explanatory drawing to accompany **b**; note that slits are external molds of flanges in life

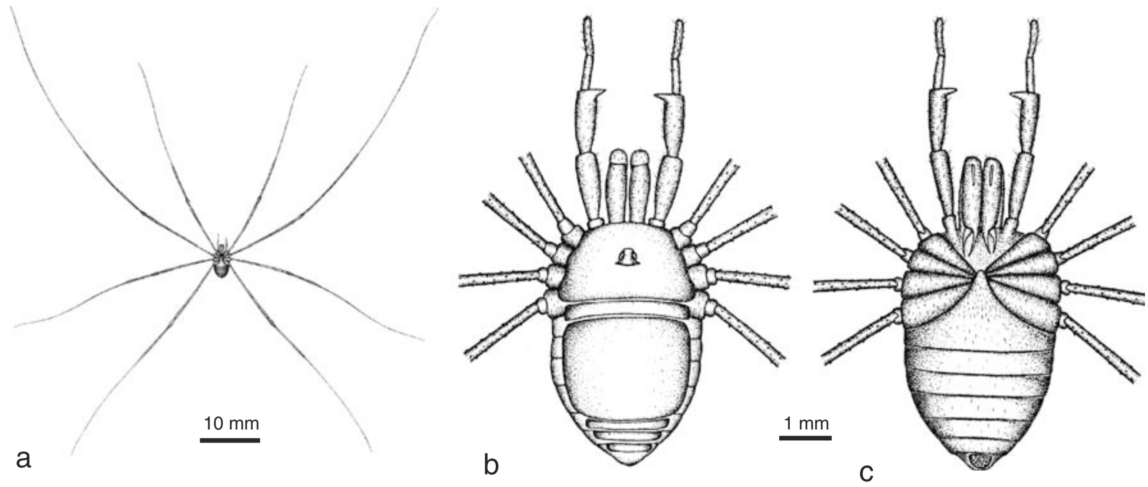

Fig. 3 *Mesobunus martensi* reconstructions. **a** Whole animal (ventral view). **b** Dorsal view of body. **c** Ventral view of body

rest of legs with denser setae. Dorsal sclerites (visible on part, Fig. 2a, e) strongly sclerotized, smooth, typical *scutum parvum* habitus: carapace approximately semicircular in outline; length 1.33, max. width (at posterior edge) 2.56. Eye tubercle located centrally on carapace (Fig. 2a, b, e, f); eye diameter c. 0.23. Free metapeltidium nearly straight (very slightly recurved) length 0.23, width 2.36. Opisthosomal dorsal scutum subrectangular; length 1.76, width 2.32. Tergites 6–8 lengths approximately 0.2; widths: tergite 6 1.47; tergite 7 1.06; tergite 8≥0.73.

Genital operculum triangular, with each border slightly curved inwards, anterior projecting forwards between leg coxae; length 1.83, width 2.46. Sternite lengths: first four c. 0.35; widths difficult to determine but narrow towards posterior; first three with straight margins, next two shorter and more procurved; two small, curved plates anterior to, and posterior and lateral to (thus surrounding) anal operculum (?*corona analis*: see Tourinho and Kury 2001, Figs. 4–6). Anal operculum finely tuberculate.

Chelicera prominent; coxa visible on left side of part and right side of counterpart (Fig. 2a, b, e, f); deutomerite ovate and setose, with tuft of setae basally (i.e., anterior with reference to body as chelicerae normally held with coxa pointing forwards and deutomerite backwards). A slit at the base of each deutomerite (visible on left and right in counterpart, Fig. 2b, f), parallel to the long axis of the deutomerite, represents a flange near the basal articulation in life (because the preservation is external mold). Apotele and fixed claw curved, tapering to acute apex. Length of deutomerite and apotele 1.92.

Pedipalp pediform, long (femur–tarsus≥4.20). Pedipalp coxae mostly hidden beneath chelicerae (Fig. 2a, b, e, f), pair of circular structures superimposed on cheliceral apoteles interpreted as pedipalp coxapophyses. Slightly inflated femur and patella; tibia and tarsus slender. Femur, patella, tibia more strongly sclerotized than tarsus, cuticle with typical ornament of minute spinules and setae; tarsus weakly sclerotized, bears only setae. Femur more setose on mesial surface. Patella bears prominent subtriangular apophysis mesodistally, mesial surface densely setose, forming a brush. Podomere lengths: femur 1.31, patella 1.27, tibia 0.90, tarsus>0.87.

Leg coxae subtriangular, radiating from sternal region; fourth appears largest, especially on left side of counterpart. Coxal widths (sternal apex to trochanteral joint): leg 1, 1.40, leg 2, 1.54, leg 3, 1.46, leg 4, 1.62. Trochanters typically short, hemispherical with broad base articulating with coxae in life, distal joint notched ventrally where inferior trochanter–femur articulation condyles occur, c. 0.4–0.45 long. Legs very long and slender along most of their length. Fourth femora probably without pseudoarticulatory nodules. Proximal podomeres (coxa to patella) with typical rugose cuticle with tiny spinules, patella with sparse fine setae, tibial cuticle less rugose and with setae as well as spinules, cuticle of basitarsus and tarsus rather thin, lacking spinules but with abundant setae. Basitarsal cuticle from mid-length towards distal end shows longer setae aligned parallel to long axis of podomere. Tarsomeres variable in number (see below), longer proximally (c. 0.9), becoming progressively shorter distally (Fig. 2c). Apotele thin and sickle-shaped (Fig. 2d). Leg formula 2431. Leg measurements: left 1, fe 8.68, pa 1.22, ti 5.67, bt 11.91, ta 6.50, 32 tarsomeres; total 33.98. Right 1, fe 9.39, pa 1.67, tibia 6.58, bt 11.02, ta 7.04 36 tarsomeres; total 35.70. Left 2, fe 12.10, pa 1.29, ti 9.41, bt 18.13, ta>3.42 29 tarsomeres; total>44.35. Right 2, fe 14.84, pa 1.41, ti 10.59, bt≥17.71 ta not preserved; total>44.55. Left 3, fe 8.55, pa 1.45, ti 4.99, bt 13.17, ta 8.83; total 36.99. Right 3, fe 8.51, pa 1.34, ti 4.72, bt 10.29, ta 6.40; total>31.26. Left 4, fe 12.81, pa 1.54, ti 8.59, bt>7.29, ta not preserved; total>30.23. Right 4, fe 10.22, pa 1.33, ti 9.48?, bt 10.35, ta≥9.44; total>40.82.

Penis length 3.10. Posterior part strongly curved, then almost straight from position of rear edge of dorsal scutum to anterior tip. Strongly sclerotized throughout visible length; in three parts posteriorly, single part along straight section, then broader anteriorly (where becomes undefined), reaching at least to coxa of leg 3.

A reconstruction is given in Fig. 3.

Family uncertain

Daohugopilio sheari gen. et sp. nov.

Diagnosis Opilionid with fairly short and gracile pedipalps bearing prominent inward-facing triangular apophysis at distal end of femur and stronger apophysis at distal end of patella. Leg 1 with noticeably wider proximal articles (femur–tibia) followed by a disjunct transition to the more slender distal parts of the legs (basitarsus–telotarsus).

Type material, locality, and horizon Holotype and only known specimen, part (141510a) and counterpart (141510b), deposited in the Nanjing Institute of Geology and Palaeontology, from Middle Jurassic Jiulongshan Formation, Daohugou Village, Ningcheng County, Inner Mongolia, China (Fig. 4).

Etymology A combination of Daohugou Village, from where the specimen originates, and *Opilio*, a common Recent genus of long-legged harvestman. The specific epithet is in honor of William Shear (Hampden-Sydney College, Virginia, USA) for his work on Opiliones.

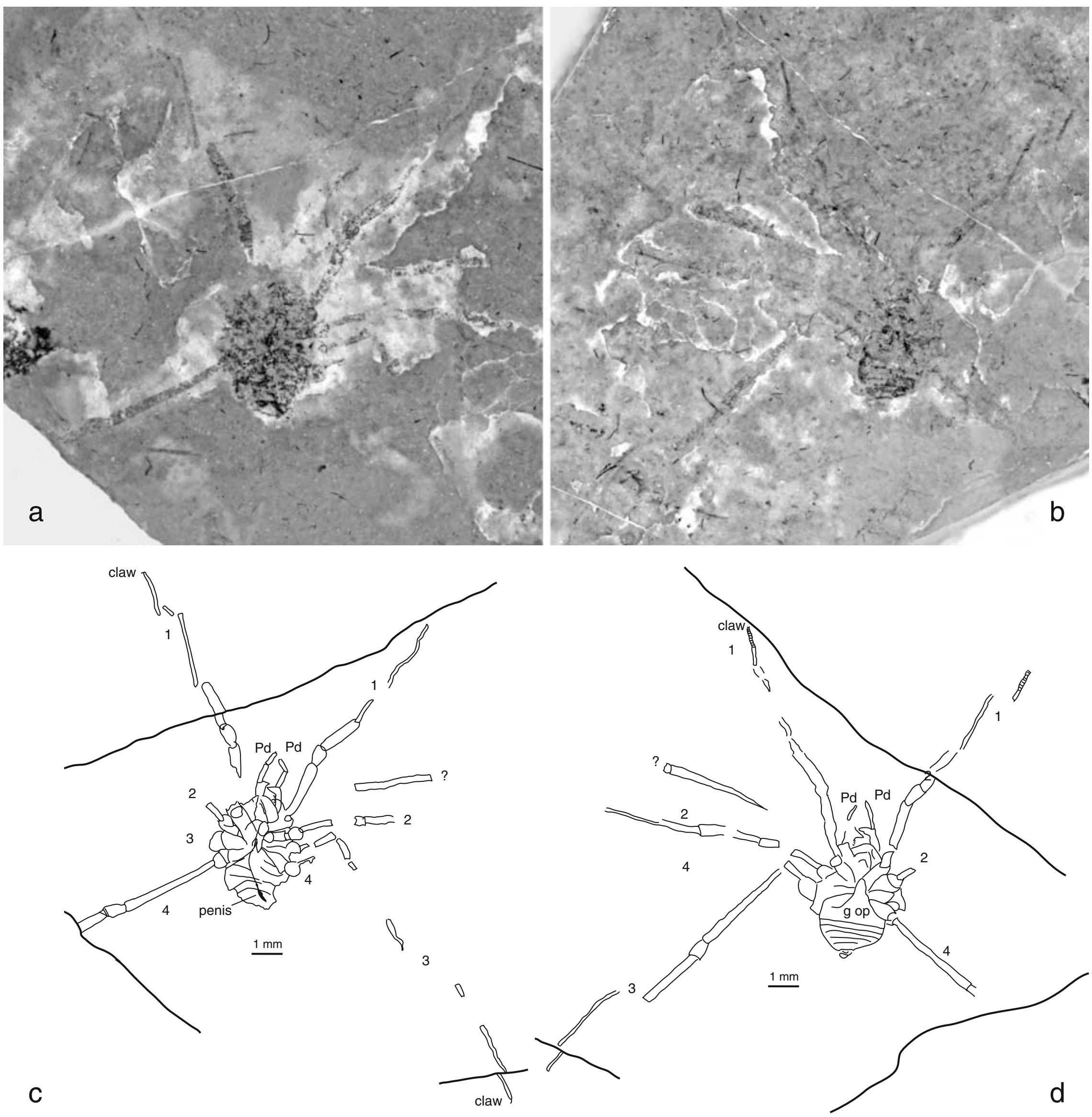

Fig. 4 *Daohugopilio sheari* (NIGP 141510a,b). **a** Holotype part, dorsal view. **b** Holotype counterpart, ventral view. **c** Explanatory drawing to accompany **a**. **d** Explanatory drawing to accompany **b**

Description Body compact, rounded–oval; length ca. 3.3, maximum width 2.6. Without strong ornament in the form of spines or tubercles. Genital operculum distinctly triangular, projecting forward between the leg coxae, followed by six short sternites. The posterior margins of the first three are more or less straight; those of the next three become more procurved. Opisthosoma ends in anal operculum, which is slightly outstanding.

Chelicerae indistinct. Pedipalps pediform, length 1.9, and fairly gracile. Femur and patella with prominent, inward-facing apophyses at their distal ends, forming a large triangular thorn. Patella and tibia with distinct brush of inward-facing setae. Leg coxae subtriangular; trochanters globose. Femora elongate, slightly curved and widening distally. Patellae bell-shaped. Tibiae, at least in leg 1, form an elongate oval. In general, proximal articles (femur–tibia) are distinctly more robust than the more distal basitarsus and telotarsus which are more slender. Telotarsus of at least leg 1 ends in at least 17 tarsomeres and a single, small, hook-shaped apotele or claw. Leg 1 article lengths: femur, 1.8; patella, 0.7; tibia, 1.9; at least 2.4 of more distal limb preserved, but articles indistinct.

A reconstruction is given in Fig. 5.

General discussion

As a group, harvestmen appear to exhibit a high degree of stasis. Even Palaeozoic species express the habitus of modern eupnoids (Dunlop et al. 2003; Dunlop 2007). At Middle Jurassic (c. 165 Ma), *Mesobunus* is, by some distance, the oldest harvestman that can be confidently assigned to an extant family (although, it must be pointed out, that even living eupnoids are sometimes difficult to assign to families). The gross morphology of *Mesobunus* is strongly reminiscent of modern East Asian eupnoids (see especially figures in Suzuki (1976) and Suzuki and Tsurusaki (1983)) and implies that this body plan has changed little since the Mesozoic, if not the Palaeozoic. The previous oldest records of Sclerosomatidae are Paleogene (Eocene) in age. They comprise the extant genus *Leiobunum* in Baltic amber (c. 45–50 Ma; Menge 1854) and the extinct genus *Amauropilio* from the Florissant shales (c. 34 Ma; Petrunkevitch 1922) in Colorado, USA. Other extant families first recorded from Baltic amber are Caddidae and Phalangidae (both Eupnoi), Nemastomatidae (Dyspnoi), and Cladonychidae (Laniatores) (Menge 1854; Koch and Berendt 1854). The basal family Sironidae (Cyphophthalmi) is known from Cretaceous amber of Myanmar (Poinar 2008), and there is a dubious record of Trogulidae from the Eocene shales of Geiseltal, Germany (Haupt 1956). Dominican Republic amber (Neogene: Miocene, c. 16 Ma) has yielded Kimulidae, Samoidae, and an unplaced genus (all Laniatores; Cokendolpher and Poinar 1992, 1998). Sclerosomatids today have a fairly cosmopolitan distribution (Tourinho 2007), including the Oriental region but excluding Australia, and tend to be more abundant in the northern hemisphere. *Daohugopilio* is rather modern-looking too, but lacks dorsal details and/or explicit apomorphies which would allow its familial position to be confirmed. As noted above, the Jiulongshan Formation also boasts an impressive assemblage of Middle Jurassic spiders assignable to an increasing variety of modern families (Selden et al. 2008b). As with the insects, a further study of the rich arachnid fauna of this locality is likely to reveal important data about the origins of modern family groups.

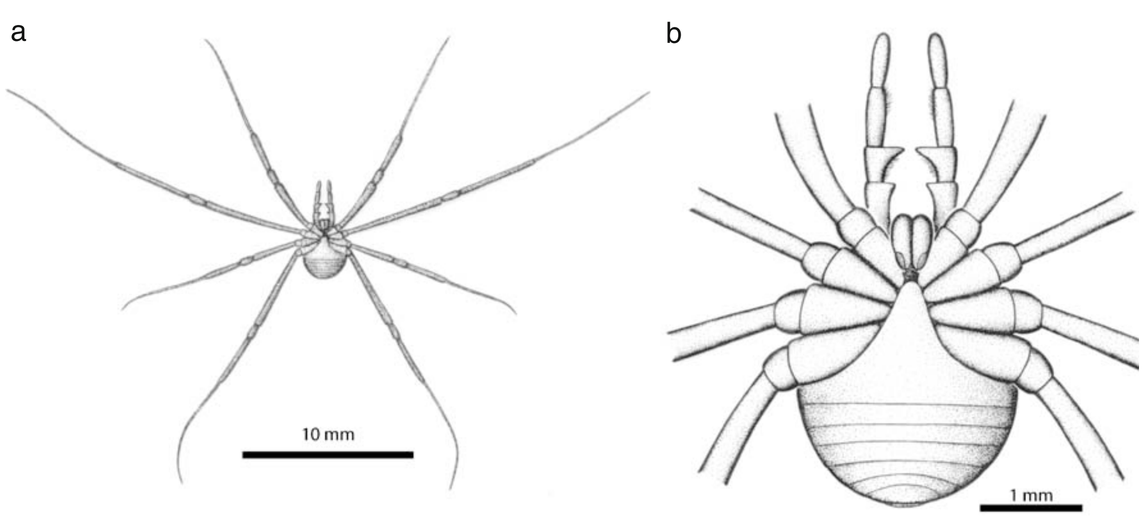

Fig. 5 *Daohugopilio sheari* reconstructions. **a** Whole animal (ventral view). **b** Ventral view of body

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