



## Short communication

## The oldest armoured harvestman (Arachnida: Opiliones: Laniatores), from Upper Cretaceous Myanmar amber

Paul A. Selden<sup>a, b, c, \*</sup>, Jason A. Dunlop<sup>d</sup>, Gonzalo Giribet<sup>c, e</sup>, Weiwei Zhang<sup>f</sup>, Dong Ren<sup>a, \*\*</sup><sup>a</sup> College of Life Sciences, Capital Normal University, Beijing 100048, People's Republic of China<sup>b</sup> Department of Geology and Paleontological Institute, University of Kansas, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA<sup>c</sup> The Natural History Museum, Cromwell Road, London SW7 5BD, UK<sup>d</sup> Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, Berlin 10115, Germany<sup>e</sup> Museum of Comparative Zoology & Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA<sup>f</sup> PO Box 4680, Chongqing 400015, People's Republic of China

## ARTICLE INFO

## Article history:

Received 5 February 2016

Received in revised form

5 May 2016

Accepted in revised form 8 May 2016

Available online 10 May 2016

## Keywords:

Burmese amber

Cenomanian

Epedanoidea

Grassatores

## ABSTRACT

The oldest laniatorean harvestman, *Petrobunoides sharmai* gen. et sp. nov. (Opiliones: Laniatores) is described, from the Upper Cretaceous (lowermost Cenomanian) amber of Myanmar. This is the first fossil Laniatores recovered from Southeast Asia, which is placed in the extant family Epedanidae. It is also the first fossil known within the superfamily Epedanoidea; a relatively derived clade of Laniatores restricted to Southeast Asia today. At ca. 99 Ma, this new amber inclusion is substantially older than the previous oldest record of a member of Laniatores from Baltic amber (ca. 44–49 Ma); however, given the Palaeozoic age of Laniatores implied by molecular data, the new record from Burmese amber is probably still too young for constraining or calibrating the date of cladogenesis for total group Laniatores. Nevertheless, it provides a much better constraint for Epedanoidea, adding the first useful laniatorean fossil to provide an internal calibration point for a clade of Grassatores.

© 2016 Elsevier Ltd. All rights reserved.

## 1. Introduction

Harvestmen (Arachnida: Opiliones) are currently divided into five suborders: Cyphophthalmi, Tetrophthalmi (extinct), Eupnoi, Dyspnoi, and Laniatores. Of these, laniatoreans are the most diverse encompassing almost two-thirds of the recorded species (4212 from 6616; Kury, 2015). Laniatores express a range of morphologies (Sharma and Giribet, 2011). Some are rather squat, short-legged and dull in colour. Others can be brightly patterned, and may show distinct enlargement of the chelicerae, pedipalps and/or fourth pair of legs. The hind legs and body may be ornamented with arrays of defensive spines or tubercles. This gives some species a truly bizarre appearance and leads to the common name of armoured harvestmen.

Despite their modern diversity, fossil Laniatores are very rare (five known species; see Cokendolpher and Poinar, 1998) and restricted to Eocene and Miocene deposits. Dominican amber (Miocene, ca. 16 Ma) has yielded three described species: *Philacarus hispaniolensis* Cokendolpher & Poinar, 1992 is currently unplaced at the family level; *Pellobunus proavus* Cokendolpher, 1987 and *Hummelinckiolus silhavyi* Cokendolpher & Poinar, 1998 belong to Samoidae, a family found today across the Neotropical, Afrotropical and Australasian regions. There is also a record of an undescribed possible *Kimula* (Kimulidae) from the same amber in Cokendolpher & Poinar (1992), but the species has not been formally described. Somewhat older is *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854) from Baltic amber (Eocene, ca. 45–49 Ma). Originally described in the Neotropical genus *Gonyleptes* Kirby, 1819, this placement seemed intuitively unlikely. Starega (1976) transferred it to *Scotolemon* Lucas, 1860 (Phalangodidae) and it was eventually referred to a new (extinct) genus *Proholoscotolemon* Ubick & Dunlop, 2005 (Cladonychiidae). These authors concluded that the Baltic amber laniatorean was probably closely related to the southern European genus *Holoscotolemon* Roewer, 1915.

In recent years, intensive efforts have been made to resolve laniatorean phylogeny (reviewed by Giribet and Sharma, 2015), and

\* Corresponding author. Department of Geology and Paleontological Institute, University of Kansas, 1475 Jayhawk Boulevard, Lawrence, KS 66045, USA.

\*\* Corresponding author. College of Life Sciences, Capital Normal University, Beijing 100048, People's Republic of China.

E-mail addresses: [selden@ku.edu](mailto:selden@ku.edu) (P.A. Selden), [Jason.Dunlop@mfn-berlin.de](mailto:Jason.Dunlop@mfn-berlin.de) (J.A. Dunlop), [giribet@oeb.harvard.edu](mailto:giribet@oeb.harvard.edu) (G. Giribet), [zhangweiwei@insectnet.cn](mailto:zhangweiwei@insectnet.cn) (W. Zhang), [rendong@mail.cnu.edu.cn](mailto:rendong@mail.cnu.edu.cn) (D. Ren).

to date the likely origins of the group. For example, Giribet et al.'s (2010) molecular tree suggested that Laniatores should have appeared by the Carboniferous. Other studies have yielded similar or younger dates (see Discussion), although the Eocene age of the Baltic amber Laniatores restricts its usefulness as a calibration point in work of this nature. Sharma and Giribet (2011, p. 125) noted that harvestmen are an ancient and morphologically quite conservative group, thus *Proholoscotolemon nemastomoides* is probably too young realistically to constrain the oldest age of its respective family and/or superfamily. Older records would be advantageous and, here, we describe a new genus and species of armoured harvestman from the Burmese amber of Myanmar (Late Cretaceous, ca. 99 Ma) which we refer to the Asian family Epedanidae. This is the oldest Laniatores to date and doubles the stratigraphic range of the group. It is also of considerable biogeographical interest as the first Laniatores fossil representative to be sampled from Southeast Asia and from Epedanoidea.

## 2. Materials and methods

The holotype and only known specimen of the new species comes from Burmese amber, which originates from the mine on Noije Bum hill, near Tanai Village (26°21'33.41"N, 96°43'11.88"E) in the Hukawng Valley of northern Myanmar. The type specimen, currently housed in the Key Lab of Insect Evolution and Environmental Changes at the College of Life Sciences, Capital Normal University, Beijing (CNU), will be eventually deposited in the Three Gorges Entomological Museum, Chongqing (specimen available for study by contacting DR or WZ). A summary of the geological setting of the Burmese amber can be found in Ross et al. (2010, and references therein), and Shi et al.'s (2012) U–Pb zircon dating constrained this amber to a maximum age of  $98.79 \pm 0.62$  Ma, which is Upper Cretaceous (lowermost Cenomanian). Two harvestmen have already been described from Burmese amber and more await formal description. *Halitherses grimaldii* Giribet & Dunlop, 2005 belongs to the suborder Dyspnoi and was recently raised to its own family (Dunlop et al., 2016). *Palaeosiro burmanicum* Poinar, 2008 belongs to Cyphophthalmi and was originally placed in the European/North American family Sironidae before being transferred to the Southeast Asian family Stylocellidae by Giribet et al. (2012).

The specimen is preserved in a cabochon of amber, subcircular in outline and about 13 mm in diameter, along with many small bubbles and a various fragments of organic detritus, some of which obscure the morphology, especially on the ventral side (Figs. 1C, 2G). Tiny bubbles trapped among setae on the tarsi somewhat obscure the tarsomeres (Fig. 3C, D); nevertheless, studying from different angles assures that their counts are accurate. Bubbles also obscure the mouthparts and are present between some coxae and ventral segments (Fig. 2G). Because of the obscuring bubbles and debris, in order to get a complete view of the animal, it was observed, drawn, and photographed (as necessary) from different angles and with different lighting. The body and most of the appendages are preserved in three dimensions, but the leg trochanters are, oddly, compressed and diaphanous.

The specimen was studied and photographed using Leica M165C and M205C stereomicroscopes with Canon EOS 5D MkII and MkIII cameras attached. Photographs were captured using DSLR Assistant software ([www.kaasoft.com](http://www.kaasoft.com)) on an Apple MacBook Pro computer. Photographs were taken under incident and/or transmitted illumination, as appropriate. Sharper focus was achieved by merging a stack of images using Photoshop CC (see Selden, 2014 for details). Final drawings were made from the photographs and pencil drawings made with a camera lucida attachment to the M205C microscope with Autodesk Graphic ([www.graphic.com](http://www.graphic.com)). Note that,

due to the three-dimensional nature of amber-preserved specimens, appendage measurements are difficult to obtain because podomeres may lie at an angle to the viewer. Hence, contrary to the usual practice for compression fossils in which measurements of left and right appendages are averaged, the larger of these two measurements is recorded. Even so, measurements of appendages must be considered as approximate. All measurements are in mm.

Abbreviations: I, II, III, IV leg numbers; a op, anal operculum; cx, coxa; fe, femur; L, length; l + c, labium and coxapophyses; mt, metatarsus; oc, ocularium; pa, patella; Pd, pedipalp; ta, tarsus; ti, tibia; tr, trochanter; W, width.

## 3. Systematic paleontology

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

Infraorder Grassatores Kury, 2002

Superfamily Epedanoidea Sørensen, 1886

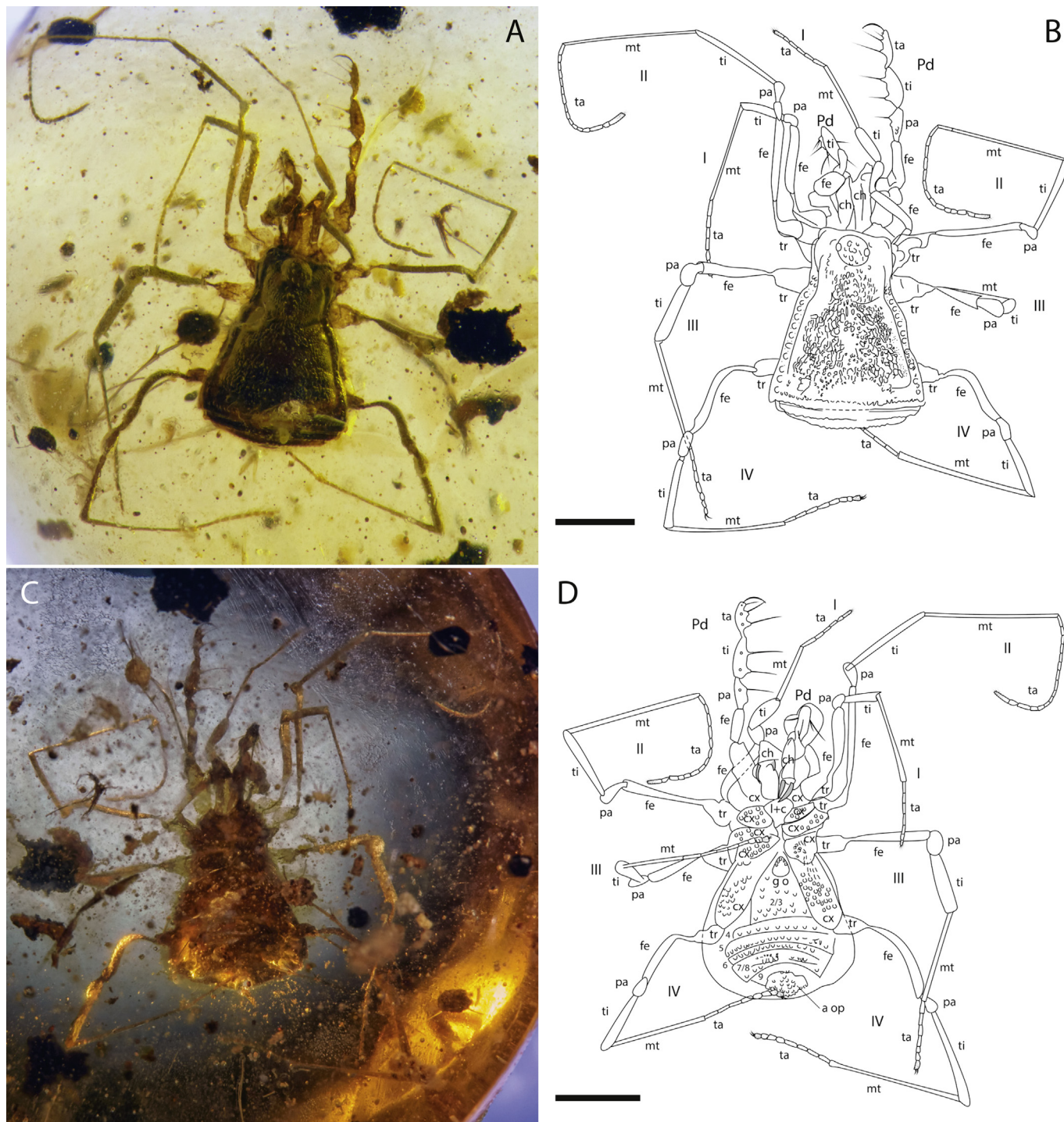
Family Epedanidae Sørensen, 1886

**Remarks.** With some exceptions (e.g. the Southeast Asian Sandoakanidae), Laniatores typically express the *scutum magnum* condition, in which the carapace and first five opisthosomal tergites are fused into a single dorsal plate. They also have the apomorphy of strongly raptorial pedipalps used for prey capture. Both characters are clearly present in the new fossil (Fig. 1) and confirm its status as the oldest member of Laniatores. The suborder is conventionally divided into eight superfamilies and about thirty families (summarized in Kury, 2015). Many authors recognize a split into two infraorders: Insidiatores and the more diverse Grassatores. Although recent phylogenetic analyses based on a few molecular markers have tended to recover Insidiatores as paraphyletic (Giribet and Sharma, 2015), recent phylogenomic work clearly shows reciprocal monophyly of both clades (R. Fernández, P. Sharma & G. Giribet, unpublished results). Grassatores can be defined on the apomorphy of two tarsal claws on legs III and IV (Sharma and Giribet, 2011). Legs III and IV of the new fossil reveal such paired claws and thus support its referral to Grassatores.

Given the demonstrated low vagility and landmass fidelity of Opiliones (e.g., Giribet and Kury, 2007), we would expect the affinities of this amber inclusion to lie with one of the families currently found in Southeast Asia. However, taxa from other regions should not automatically be excluded and, as a precedent, we note that Burmese amber hosts Ricinulei (Wunderlich, 2012), which are today restricted to West Africa and the Americas (e.g., Fernández and Giribet, 2015). The habitus of the new fossil is similar to some members of Assamiidae, a family distributed today in Africa, Australia, Papua New Guinea and Southeast Asia. Characters consistent with Assamiidae (as defined by Kury, 2007), include a dorsal scutum which is wider in the opisthosomal region, a granular scutum (seen in at least some living species), grooves defining discrete areas on the mesotergum, a weakly armoured ocular tubercle, ventromesal and ventroectal spines on the patella, tibia and tarsus of the pedipalp, and the lack of armament on the rather smooth legs. However, key assamiid characters such as a ventral row of tubercles on the pedipalp femur, or the typical chelicerae of adult assamiids, very short, often tucked closely against the anterior carapace, and the relatively short pedipalps in turn wrap or cross over them, are not seen in the new fossil and argues against affinities with this family. The eyes of Assamiidae are also usually much closer together on a small ocularium.

Sharma and Giribet (2011) recognized a putative Epedanoidea clade encompassing five Southeast Asian families, two of which were proposed as new in that paper. Of these, Podoctidae is



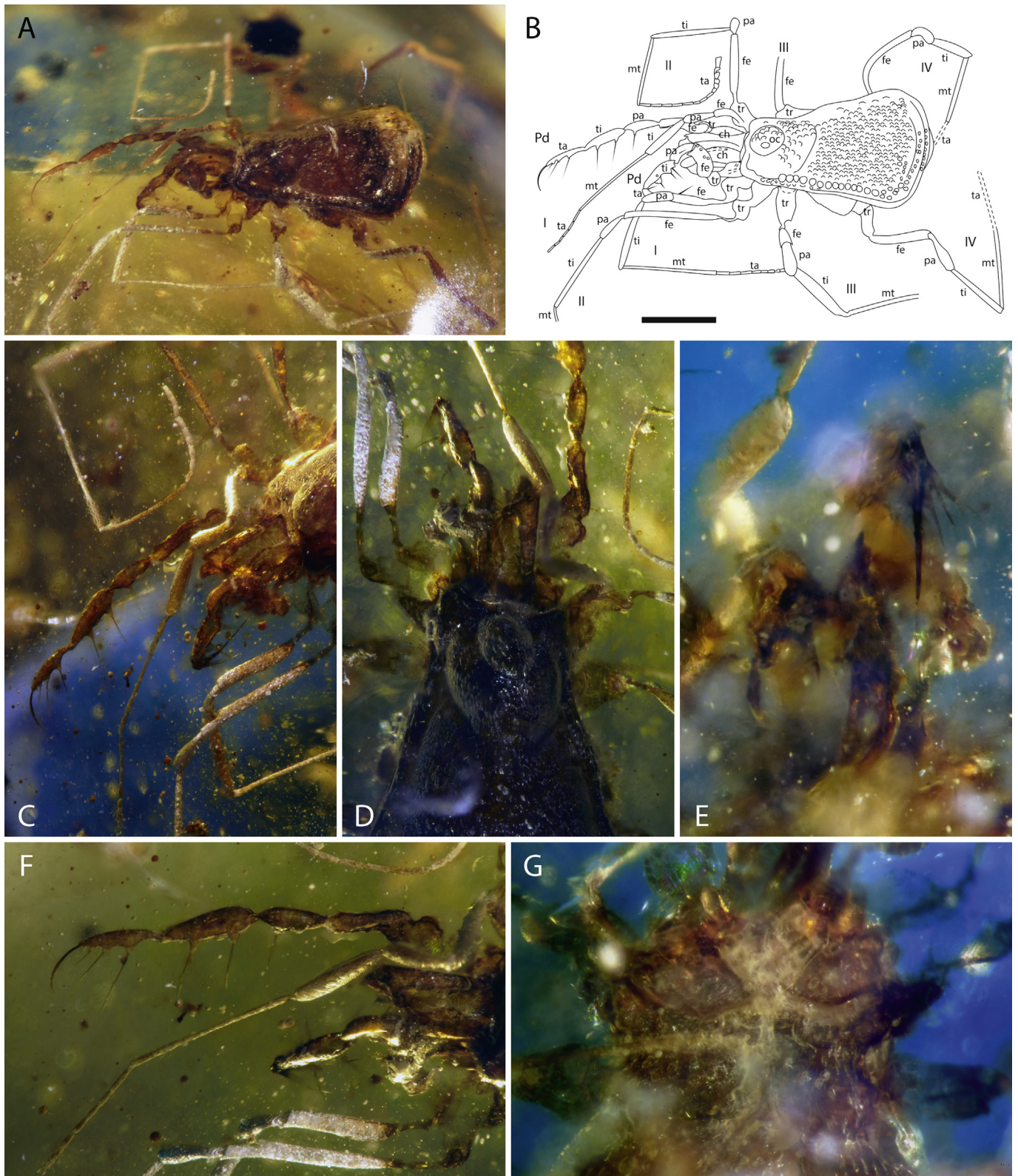


**Fig. 1.** *Petrobunoides sharmai* gen. et sp. nov. from Late Cretaceous Myanmar amber. Holotype BU-002036. A, Dorsal view, see Fig. 1B for explanation; B, Explanatory drawing, dorsal view; C, Ventral view, see Fig. 1D for explanation; D, Explanatory drawing, ventral view, grey areas are cheliceral fingers, circles on left pedipalp mark spines directed upward. Scale bars represent 1 mm.

characterized by powerful dorsal and ventral spines on the first pair of legs and a reduced tarsal count. In our fossil this leg is smooth. The habitus of this fossil is wholly inconsistent with the unusual family Sandakanidae which has fairly short, stubby legs, enlarged chelicerae, a *scutum completum* (i.e. all dorsal tergites are fused) and a reduced tarsal count. The general habitus and *scutum magnum* of the fossil are similar to the conditions seen in the two epedanoid families Tithaeidae and Petrobunidae. Furthermore, the

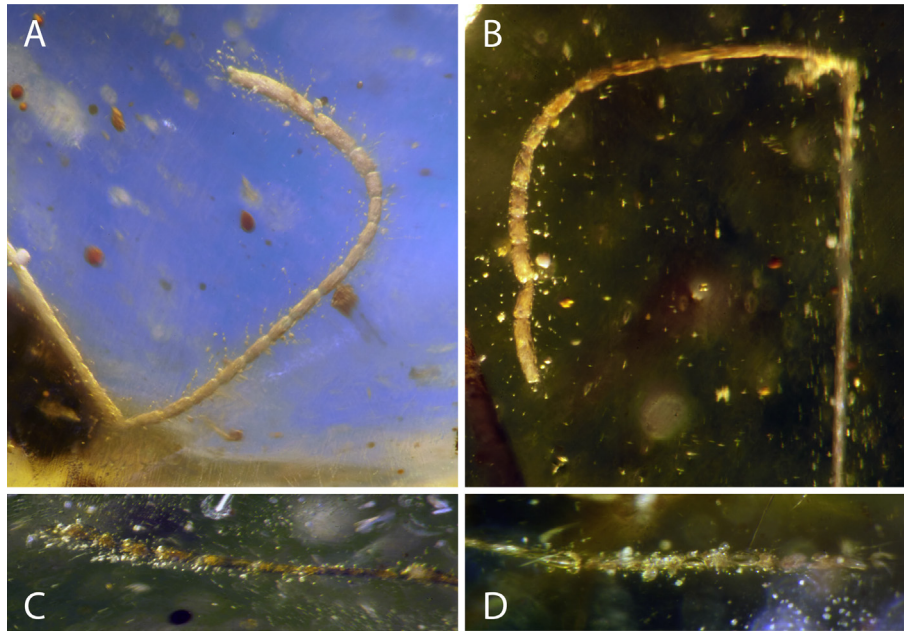
ocularium in the fossil lacks a median spine, also true for all tithaeids and some petrobunids, and femur IV is arcuate, which is similar to the condition in some members of these families. However, the fossil lacks a bulla on the chelicera, which is present in both extant families. The ocularium in the fossil reaches close to the front of the anterior margin of the carapace, but is removed from the anterior margin in Tithaeidae. Finally, the tarsal formula in the fossil differs from that in the diagnosis of both Tithaeidae and





**Fig. 2.** *Petrobunoides sharmai* gen. et sp. nov. from Late Cretaceous Myanmar amber. Holotype BU-002036. A, Left dorsolateral view, see Fig. 2B for explanation; B, Explanatory drawing, left dorsolateral view; C, Left frontal view, showing chelicerae, pedipalps, and parts of legs I and II, see Fig. 2B for explanation; D, Dorsal view of anterior, showing ocularium, chelicerae, and parts of pedipalps and anterior legs, see Fig. 1B for explanation; E, Ventral view of chelicerae and right pedipalp, see Fig. 1D for explanation; F, Dorsal view of anterior appendages, including chelicerae and right pedipalp and leg I, see Fig. 1B for explanation; G, Ventral view of anterior body, showing coxal region and right leg III tarsus, see Fig. 1D for explanation. Scale bar represents 1 mm.





**Fig. 3.** *Petrobunoides sharmai* gen. et sp. nov. from Late Cretaceous Myanmar amber. Holotype BU-002036. A, Left leg II distal metatarsus and tarsus, retrolateral view, showing setae and trapped bubbles, see Fig. 1B for explanation; B, Right leg II distal metatarsus and tarsus, prolateral view, see Fig. 1B for explanation; C, Left leg IV tarsus, retrolateral view, showing distal setae and trapped bubbles; D, Left leg III tarsus, prolateral view, showing paired terminal claws.

*Petrobunidae sensu Sharma and Giribet (2011)*. Epedanidae typically express robust chelicerae and a pedipalpal claw at least as long as the adjacent tarsus. In our fossil the chelicerae are relatively small and the pedipalp claw is shorter than the tarsus, but several other characters argue for its placement in Epedanidae, including the relatively long chelicera with the proximal segment unadorned on the dorsal surface; the elongate, raptorial pedipalps; the elongate, gracile legs with a tarsal formula consistent with Epedanidae; and the epedanid habitus with a wide ocularium and a sub-quadrilateral body. We thus place this new fossil in Epedanidae.

Our fossil also resembles in some features another clade of Laniatores that made it into Southeast Asia in the Late Cretaceous, the genus *Zalmoxis* (see Sharma and Giribet, 2012) but, again, the tarsomere count is highly divergent from the typical *zalmoxid* formula, despite now knowing that tarsal count in *Zalmoxis* is more variable than originally thought (e.g., Pérez-González et al., 2016).

#### Genus *Petrobunoides* gen. nov.

LSID urn:lsid:zoobank.org:act:A2AB6D91-F4E4-451E-A229-11F7D5D232F0

**Derivation of name.** From its superficial similarities to the extant SE Asian genus *Petrobunus* Sharma & Giribet, 2011 (Petrobunidae).

**Diagnosis.** Epedanid with a tuberculated cuticle. Body subtrapezoidal, prosomal and anterior opisthosomal segments fused into scutum magnum, followed by three short opisthosomal tergites. *Scutum magnum* with wide marginal border bearing a conspicuous row of lateroposterior tubercles and additional granulation. Dorsal prosomal region with subcircular, tuberculate ocularium (unlike Dibuninae), with median eyes on lateral surfaces of ocularium. Pedipalpal trochanter and femur robust, tuberculate, without spines; patella with single pair of spines; tibia with two pairs; tarsus with three pairs. Pedipalp claw long, almost as long as tarsus, slender and curved. Legs moderately long; leg II longest; leg IV not enlarged but with strongly curved femur bending upwards, perpendicular to the midline in life. Patellae of all legs slightly inflated. Tarsal formula: 6:16/14:7:8; Tarsi III–IV of leg with bare double claws, without scopulae (unlike Acrobuninae). Ventral

prosomal region dominated by leg coxae; leg IV coxae massive, diverging posteriorly from region of genital operculum to lateral edges of body at level of segment 5.

**Type and only species.** *Petrobunoides sharmai* gen. et sp. nov., by original designation

#### *Petrobunoides sharmai* sp. nov.

Figs. 1–3

LSID urn:lsid:zoobank.org:act:3FA501F2-137E-4B1E-AAEA-C6C9092C7DA6.

**Derivation of name.** In honour of Prashant Sharma (University of Wisconsin-Madison) for his important contributions to the phylogeny of Laniatores, and for his work on harvestmen biology in general.

**Diagnosis.** As for the genus.

**Holotype.** (and only known specimen). BU-002036, from Burmese amber, Hukawng Valley, Myanmar; Upper Cretaceous (lowermost Cenomanian). The type specimen, currently housed in the Key Lab of Insect Evolution and Environmental Changes at the College of Life Sciences, Capital Normal University, Beijing (CNU), will be eventually deposited in the Three Gorges Entomological Museum, Chongqing (specimen available for study by contacting DR or WZ). **Description.** Cuticle surface tuberculate, especially pronounced on dorsal and ventral body surfaces, coxae, and proximal appendage segments (fe, pa); mostly scaly on distal parts of legs; tarsi bear numerous setae, especially distally. Body subtrapezoidal, L 2.54, W at anterior margin 1.03, maximum W (at posterior) 1.99, waisted to 1.02 about ¼ body length from anterior (Fig. 1). Prosomal and anterior opisthosomal segments fused into scutum magnum, followed by three short opisthosomal tergites. *Scutum magnum* with wide marginal border bearing conspicuous row of lateroposterior tubercles and additional granulation (Figs. 1, 2A, B). Mesotergum with faint transverse sulci posteriorly, hinting at original segmentation. Short segments behind mesotergum also tuberculate. Dorsal prosomal region bears subcircular, tuberculate ocularium (L 0.38, W 0.45), with lateral eyes (Fig. 2D).

Chelicera proximal segment (basichelicerite) L 0.87, projects forward, parallel-sided, lacking bulla; cheliceral hand L 0.59, with fixed and movable fingers (L 0.30) (Fig. 2C–F). Pedipalps raptorial, with several long, slender, needle-like inferior spines (Fig. 2A–F). Pedipalpal trochanter and femur robust, tuberculate, without spines; patella with single pair of spines; tibia with two pairs; tarsus with three pairs (two long and one short); i.e. pa mesal I, ectal I; ti mesal II, ectal II; ta mesal III, ectal III. Pedipalpal claw long, almost as long as tarsus, slender and curved; opposing distal spines of tarsus (Fig. 2C, E, F). Legs moderately long; leg II longest; leg IV not enlarged but with strongly curved femur bending upwards, perpendicular to the midline in life. Patellae of all legs slightly inflated. Metatarsi with distal calcaneus. Tarsi subdivided into tarsomeres; subterminal with basal construction, terminal rather longer and bearing a pair of claws on legs III and IV, without scopulae (Fig. 3A–D). Podomere lengths: Pd fe 0.67, pa 0.48, ti 0.58, ta 0.59 (exc. claw, L 0.38), total (fe–ta) 3.20; Leg I fe 0.86, pa 0.41, ti 0.58, mt 1.28, ta 1.01, total (fe–ta) 4.14; Leg II fe 1.45, pa 0.42, ti 1.22, mt 1.72, ta 1.79, total (fe–ta) 6.58; Leg III fe 0.91, pa 0.38, ti 0.82, mt 1.45, ta 0.92, total (fe–ta) 4.48; Leg IV fe 1.37, pa 0.34, ti 0.93, mt 1.76, ta 1.08, total (fe–ta) 5.48. Tarsal formula: 6:16/14:7:8.

Ventral prosomal region dominated by leg coxae; these strongly tuberculate, increasing in length from I to IV (L I 0.50, II 0.66, III 0.66, IV 1.32); leg IV coxae massive, diverging posteriorly from region of genital operculum to lateral edges of body at level of segment 5 (Fig. 1C, D). Subtriangular area between coxae I occupied by labium and coxapophyses (Fig. 2G). Ventral opisthosomal region with genital operculum between anteromedial corners of coxae IV, subpyriform in outline, L 0.26, W 0.25, tuberculate along anterior border. Fused segments 2/3 subtrapezoidal in outline broadening from genital operculum to distal ends of coxae IV. Segments 4 to 9 each with recurved anterior and posterior borders and row of large tubercles; widths: 4, 1.32; 5, 1.50; 6, 1.41; 7/8, 1.30; 9, 0.94. Anal operculum strongly tuberculate, transversely subelliptical in outline, L 0.36, W 0.58. Lateral rim beyond evident segmentation.

#### 4. Discussion

The molecular phylogeny of Giribet et al. (2010) estimated a Late Carboniferous (ca. 305 Ma) diversification date for Laniatores. A slightly older, Early Carboniferous, date (ca. 348 Ma) was obtained by Sharma and Giribet (2011), with further dates for ingroup taxa such as a putative Late Permian (ca. 249 Ma) Southeast Asian clade. A similar date of 355.5 Ma was obtained for total group Laniatores by Garwood et al. (2014). By contrast, Hedin et al. (2012) recovered a younger, Permian–Triassic date for Laniatores of 220–280 Ma. Dating problems with the latter study were discussed in detail by Sharma and Giribet (2014), who noted that total evidence dates consistently yield older estimates compared to node-based dates, which include the explicit phylogenetic placement of Palaeozoic fossils. Thus, Sharma and Giribet (2014) recovered dates for the non-synthetonychiid Laniatores of 410.3 Ma (Early Devonian) using total evidence dating, 329.7 Ma (Early Carboniferous) using node dating of a phylogenetic supermatrix, and 282.4 Ma (Early Permian) using node dating combining morphology and molecules. All of these estimates also had wide confidence intervals.

Part of the explanation for the diversity and uncertainty of these published dates may be the fact that the oldest harvestman from the Early Devonian Rhynie chert of Scotland was originally interpreted as a Eupnoi and was thus used to constrain the origins of this clade (e.g., Giribet et al., 2010; Hedin et al., 2012) at ca. 410 Ma. It was later reinterpreted as a member of the extinct

suborder Tetrophthalmi (Garwood et al., 2014), which shifts the oldest Eupnoi forward to the Carboniferous. While the suborders Eupnoi and Dyspnoi both have unequivocal Late Carboniferous records, explicitly supported by including the fossils as nodes in a cladistic analysis (Garwood et al., 2011), Cyphophthalmi and Laniatores lack records in deep time to provide equivalent calibration points. The previous constraint on Laniatores was Eocene (maximally ca. 49 Ma), which is clearly much too young, which would result in a push towards the present effect (see Giribet, 2015). Our new fossil in Burmese amber at least draws this calibration point back to the Cretaceous (ca. 99 Ma) which is also the age, and locality, of the oldest Cyphophthalmi (Poinar, 2008). Nevertheless, all the published data point towards a Palaeozoic origin of Laniatores, but as yet no fossils have been found which confirm this. Selden et al. (2016) redescribed some putative Coal Measures spiders as unusual long-bodied harvestmen which have superficial similarities with certain modern laniatorean harvestmen. However, these fossils lack demonstrable apomorphies of Laniatores such as raptorial pedipalps; thus a definitive Palaeozoic record, which would help constrain their date of cladogenesis, remains elusive. Therefore, our new fossil provides the best estimate for the much-needed internal calibration points in Laniatores.

Although too young to contribute towards dating of the total group Laniatores, the placement of *Petrobunoides sharmai* gen. et sp. nov. in the Southeast Asian family Epedanidae provides added value for future efforts to date some clades of the Laniatores tree of life. Epedanidae was estimated to originate in the Cretaceous by Sharma and Giribet (2011), and thus our new fossil provides a new internal calibration point to constrain the divergence between Epedanidae and its sister group (Petrobunidae and Podoctidae; based on an unpublished phylogenomic analysis by G. Giribet and colleagues) not far from the possible origin of the group. The new fossil thus represents a key taxon to improve a total evidence dating framework of the Laniatores tree (see Sharma and Giribet, 2014; Giribet, 2015).

#### 5. Concluding remarks

Here we describe the oldest fossil Laniatores from the Upper Cretaceous (lowermost Cenomanian) amber of Myanmar, a species that can be placed in the extant southeast Asian family Epedanidae and that more than doubles the age of the oldest Laniatores. This fossil represents the fifth described Laniatores fossil species, but by its Cretaceous age (as opposed to the available Eocene to Miocene species) and by being placed in a relatively derived Laniatores clade, Epedanoidea, the new fossil represents a key taxon to provide an internal calibration point for dating the Laniatores tree of life.

#### Acknowledgements

PAS thanks Zhipeng Zhao, Xiaodan Lin, and Chongchuan Deng (CNU, Beijing) for accompanying him to Chongqing to visit WZ, in whose collection the specimen was discovered. Prashant Sharma and an anonymous reviewer are acknowledged for constructive criticism and discussion of epedanoidean characters; the Editor is likewise acknowledged for further comments and insights that improved the manuscript. GG thanks Greg Edgecombe (NHM, London) for access to microscopes. This research is supported by the National Basic Research Program of China (973 Program) (2012CB821906), the National Natural Science Foundation of China (No. 31230065), Program for Changjiang Scholars and Innovative Research Team in University (IRT13081).

## References

- Cokendolpher, J.C., 1987. A new species of fossil *Pellobunus* from Dominican Republic amber (Arachnida: Opiliones: Phalangodidae). *Caribbean Journal of Science* 22, 205–211.
- Cokendolpher, J.C., Poinar Jr., G.O., 1992. Tertiary harvestmen from Dominican Republic amber (Arachnida: Opiliones: Phalangodidae). *Bulletin of the British Arachnological Society* 9, 53–56.
- Cokendolpher, J.C., Poinar Jr., G.O., 1998. A new fossil harvestman from Dominican Republic amber (Opiliones, Samoidae, *Hummelinckiolus*). *Journal of Arachnology* 26, 9–13.
- Dunlop, J.A., Selden, P.A., Giribet, G., 2016. Penis morphology in a Burmese amber harvestman. *The Science of Nature* 103, 11–15.
- Fernández, R., Giribet, G., 2015. Unnoticed in the tropics: phylogenomic resolution of the poorly known arachnid order Ricinulei (Arachnida). *Royal Society Open Science* 2, 150065.
- Garwood, R.J., Dunlop, J.A., Giribet, G., Sutton, M.D., 2011. Anatomically modern Carboniferous harvestmen demonstrate early cladogenesis and stasis in Opiliones. *Nature Communications* 2 (444), 1–7.
- Garwood, R.J., Sharma, P.P., Dunlop, J.A., Giribet, G., 2014. A Paleozoic stem group to mite harvestmen revealed through integration of phylogenetics and development. *Current Biology* 24, 1–7.
- Giribet, G., 2015. Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zoologischer Anzeiger* 256, 96–103.
- Giribet, G., Dunlop, J.A., 2005. First identifiable Mesozoic harvestman (Opiliones: Dyspnoi) from Cretaceous Burmese amber. *Proceedings of the Royal Society B* 272, 1007–1013.
- Giribet, G., Kury, A.B., 2007. Phylogeny and biogeography. In: Pinto-da-Rocha, R., Machado, G., Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, MA, pp. 62–87.
- Giribet, G., Sharma, P.P., 2015. Evolutionary biology of harvestmen (Arachnida: Opiliones). *Annual Review of Entomology* 60, 157–175.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P., Kury, A., 2010. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* 26, 408–437.
- Giribet, G., Sharma, P.P., Benavides, L.R., Boyer, S.L., Clouse, R.M., De Bivort, B.L., Dimitrov, D., Kawauchi, G.Y., Muriene, J., Schwendinger, P.J., 2012. Evolutionary and biogeographical history of an ancient and global group of arachnids (Arachnida: Opiliones: Cyphophthalmi) with a new taxonomic arrangement. *Biological Journal of the Linnean Society* 105, 92–130.
- Hedin, M., Starrett, J., Akhter, S., Schönhöfer, A.L., Shultz, J.W., 2012. Phylogenomic resolution of Paleozoic divergences in harvestmen (Arachnida, Opiliones) via analysis of next-generation transcriptome data. *PLoS One* 7 (8), e42888. <http://dx.doi.org/10.1371/journal.pone.0042888>.
- Koch, C.L., Berendt, G.C., 1854. Die im Bernstein befindlichen Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt, G.C. (Ed.), *Die in Bernstein befindlichen organischen Reste der Vorwelt gesammelt in Verbindung mit mehreren bearbeitet und herausgegeben* 1. Nicolai, Berlin, 124 pp.
- Kury, A.B., 2007. Assamiidae Sørensen, 1884. In: Pinto-da-Rocha, R., Machado, G., Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, MA, pp. 173–176.
- Kury, A.B., 2015. Classification of Opiliones. Museu Nacional/UFRJ website. Online at: <http://www.museunacional.ufrj.br/mndi/Aracnologia/opiliones.html>.
- Pérez-González, A., Sharma, P.P., Proud, D.N., 2016. Morphological tricks and blessed genitalia: rectifying the family placement of *Fijicolana tuberculata* (Opiliones: Laniatores: Zalmoxidae). *Zootaxa* 4061, 253–260.
- Poinar Jr., G.O., 2008. *Palaeosiro burmanicum* n. gen., n. sp., a fossil Cyphophthalmi (Arachnida: Opiliones: Sironidae) in Early Cretaceous Burmese amber. In: Makarov, S.E., Dimitrijević, R.N. (Eds.), *Advances in Arachnology and Developmental Biology. Papers Dedicated to Prof. Dr. Božidar Čurčić*. Institute of Zoology, Monographs 12, Belgrade, pp. 267–274.
- Ross, A., Mellish, C., York, P., Crighton, B., 2010. Burmese amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.
- Selden, P.A., 2014. A workflow for digital photography of fossil specimens. *The Geological Curator* 10, 93–98.
- Selden, P.A., Dunlop, J.A., Garwood, R.J., 2016. Carboniferous araneomorph spiders reinterpreted as long-bodied harvestmen. *Journal of Systematic Palaeontology* 14, 127–137.
- Sharma, P.P., Giribet, G., 2011. The evolutionary and biogeographic history of the armoured harvestmen – Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). *Invertebrate Systematics* 25, 106–142.
- Sharma, P.P., Giribet, G., 2012. Out of the Neotropics: Late Cretaceous colonization of Australasia by American arthropods. *Proceedings of the Royal Society B* 279, 3501–3509.
- Sharma, P.P., Giribet, G., 2014. A revised dated phylogeny of the arachnid order Opiliones. *Frontiers in Genetics* 5, 1–13.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Staręga, W., 1976. Opiliones, Kosarze (Arachnoidea). *Panstwowe Wydawnictwo Naukowe*, Warszawa, 97 pp.
- Ubick, D., Dunlop, J.A., 2005. On the placement of the Baltic amber harvestman *Gonyleptes nemastomoides* Koch & Berendt, 1854, with notes on the phylogeny of Cladonychiidae (Opiliones, Laniatores, Travunioidea). *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe* 8, 75–82.
- Wunderlich, J., 2012. Description of the first fossil Ricinulei in amber from Burma (Myanmar), the first report of this arachnid order from the Mesozoic and from Asia, with notes on the related extinct order Trigonotarbita. *Beiträge zur Araneologie* 7, 233–244.