

Four new Laniatorean harvestmen (Arachnida: Opiliones) from mid-Cretaceous Burmese amber

Christian Bartel^{a,*}, Jason A. Dunlop^b, Prashant P. Sharma^c, Paul A. Selden^{d,e}, Pavel E. Tarasov^a, Dong Ren^f, Chungkun Shih^f

^a Freie Universität Berlin, Institute of Geological Sciences, Palaeontology Section, Malteserstraße 74-100, D-12249 Berlin, Germany

^b Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, D-10115 Berlin, Germany

^c University of Wisconsin-Madison, Department of Integrative Biology, 352 Birge Hall, 430 Lincoln Drive, Madison, WI 53706, USA

^d Department of Geology, University of Kansas, 1414 Naismith Drive, Lawrence, KS 66045, USA

^e Natural History Museum, Cromwell Road, London SW7 5BD, UK

^f College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

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Abstract

Four new laniatorean harvestmen specimens (Arachnida: Opiliones: Laniatores) are described from the mid-Cretaceous (upper Albian–lower Cenomanian) Burmese amber of Northern Myanmar. One is placed as *Insidiatores* indet., but is not formally named as it is probably immature. *Burmalomanius circularis* n. gen. n. sp. and *Petroburma tarsomeria* n. gen. n. sp. represent the first fossil records of the extant families Podoctidae and Petrobunidae respectively. Finally, *Mesodibunus tourinhoae* n. gen. n. sp. belongs to Epedanidae, a family previously recorded from Burmese amber. These new records bring the total number of Burmese amber laniatorean species to ten, and the total number of fossil laniatoreans to fifteen. The new finds offer additional calibration points for the Laniatores tree of life and are consistent with the hypothesis that the modern Laniatores fauna of Southeast Asia may have had Gondwanan, as opposed to a Laurasian, origins.

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Keywords: biogeography; mid-Cretaceous; fossil record; Laniatores; Southeast Asia; taxonomy

1. Introduction

Harvestmen (Arachnida: Opiliones) consist of four living suborders: Cyphophthalmi, Dyspnoi, Eupnoi, and Laniatores. The last is by far the most diverse, with over 4200 extant species out of the 6600 modern harvestmen species described to date (Kury, 2017). Laniatoreans are

also known as armoured harvestmen due to the presence of large, raptorial pedipalps combined in several groups with strongly pronounced body or leg armature in the form of spines and/or tubercles. Nevertheless, their appearance can vary significantly and species without heavy armature are also quite common. Laniatoreans are further subdivided into two infraorders based on their claw morphology. *Insidiatores* bear single claws on legs III and IV, with smaller distal branches of the claw (perhaps best exemplified by the family *Triaenonychidae*). By contrast, *Grassatores* bear two claws on legs III and IV with separate insertions. Most Laniatores are distributed in humid tropical and temperate forest regions of the world (see

* Corresponding author.

E-mail addresses: christianb@zedat.fuberlin.de (C. Bartel), jason.dunlop@mfh.berlin (J.A. Dunlop), prashant.sharma@wisc.edu (P.P. Sharma), selden@ku.edu (P.A. Selden), ptarasov@zedat.fuberlin.de (P. E. Tarasov), rendong@cnu.edu.cn (D. Ren), chungkun.shih@gmail.com (C. Shih).

e.g., [Pinto-da-Rocha et al., 2007](#) for an overview of their biology).

Compared with their high modern diversity, the number of fossil Laniatores described so far remains relatively low and consists of only twelve species. Recently, seven new taxa from the mid-Cretaceous Burmese amber of Myanmar were described ([Selden et al., 2016](#); [Bartel et al., 2021](#)). In addition to these, there is one laniatorean species in Eocene Baltic amber and four from Miocene Dominican amber (see also [Dunlop et al., 2020](#); [Bartel et al., 2021](#) and references therein). In this study, we describe another four new Laniatores from Burmese amber, three of which are recognised as new species.

2. Material and methods

Four specimens from Burmese amber were available for this study. Three originate from the private collection of Patrick Müller, and are now deposited in the Museum für Naturkunde Berlin (repository numbers 4446–4448 (see also 3. Systematic palaeontology) under the acronym MB.A. for Museum Berlin, Arthropoda), the fourth is from the fossil insect collection of the Key Laboratory of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU), Beijing, China. All specimens are moderately well preserved ([Figs. 1–6](#)), with some exceptions where body parts are missing, desiccated or covered by detritus, fractures or crystalline growth.

For the purpose of this study, all specimens were photographed immersed in water to reduce reflections using a Leica Z16 APO A stereomicroscope equipped with the software package Leica Application Suite. Image Z-stacks were composed of 15–20 images. These images were combined with Helicon Focus 6 (Method C) and corrected for brightness and contrast using Adobe Photoshop CS5.

Drawings were made using a Leica M205C stereomicroscope with a camera lucida attachment. Computer-aided illustrations were created from the camera lucida drawings following the methods of [Coleman \(2003\)](#) with Adobe Illustrator CS2 and Adobe Photoshop 6.0 using a Wacom Intuos graphic tablet. Sometimes setae or tubercles were omitted to ensure visibility of important characteristics. All measurements are in mm and are slight approximations due to the three-dimensional position of the amber specimens in the amber matrix.

The new inclusions were compared with extant Laniatores available in the collection of the Museum für Naturkunde, Berlin as well as with previously described species from Burmese amber ([Selden et al., 2016](#); [Bartel et al., 2021](#)).

2.1. Burmese amber

Burmese amber is known for its rich diversity of inclusions, currently with 2198 species in 1481 genera and

667 families ([Ross, 2022](#)). Most of these are arthropods with 2059 described species. Further species of e.g., vertebrates, plants, fungi, and protists have also been recorded. Most of the amber-bearing material derives from the Hukawng Valley in the Kachin State of northern Myanmar which consists of folded sedimentary and volcanic rocks. Within these, the amber is often found as disk-shaped clasts which are oriented parallel to the bedding ([Cruickshank and Ko, 2003](#)). Inclusions are usually dated to an upper Albian–lower Cenomanian age (e.g., [Shi et al., 2012](#); [Smith and Ross, 2018](#); [Lin et al., 2019](#); [Yu et al., 2019](#); [Zhao et al., 2020](#)). During this time, the Burma Terrane may have been part of a Trans-Tethyan island arc ([Westerweel et al., 2019](#)) with a near-equatorial southern latitude. The resin was possibly produced by trees of the family Araucariaceae, which were additionally distributed along shorelines, brackish water bays or estuaries, as a few marine specimens are recorded from Burmese amber ([Poinar et al., 2007](#); [Mao et al., 2018](#); [Smith and Ross, 2018](#)). A tropical climate with high average temperature, typical for the Cretaceous, was proposed by [Grimaldi et al. \(2002\)](#).

3. Systematic palaeontology

Abbreviations: ch, chelicerae; cl, claw; cx, coxa; ey, eye lens; fe, femur; L, length; mt, metatarsus; oc, ocularium; op, opisthosoma; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter; W, width. Average values are marked with an *.

Order Opiliones [Sundevall, 1833](#)

Suborder Laniatores [Thorell, 1876](#)

Remarks: All four amber specimens described here can be recognised as members of the suborder Laniatores due to the presence of a scutum magnum (carapace and the first five opisthosomal tergites are fused) or a scutum completum (carapace and tergites I–VII are fused). In Laniatores, the latter state is restricted to the family Sandokanidae ([Sharma and Giribet, 2009](#)), but is also observed in the harvestman suborder Cyphophthalmi. However, the scutum characters in combination with the relatively large and spiny pedipalps and two claws on tarsus III–IV further identify all the new fossils as laniatoreans and differentiate them from the other harvestman suborders.

Family Insidiatores indet.
([Fig. 1](#))

Remarks: MB.A. 4446 is very likely a juvenile at one of the mid-late nymphal stages, due to a very low tarsomere count (1:1:2:2), light body colouration and the absence of armature, combined with a relatively small size of 1.27 mm ([Fig. 1A](#)). Adult laniatoreans with such a reduced

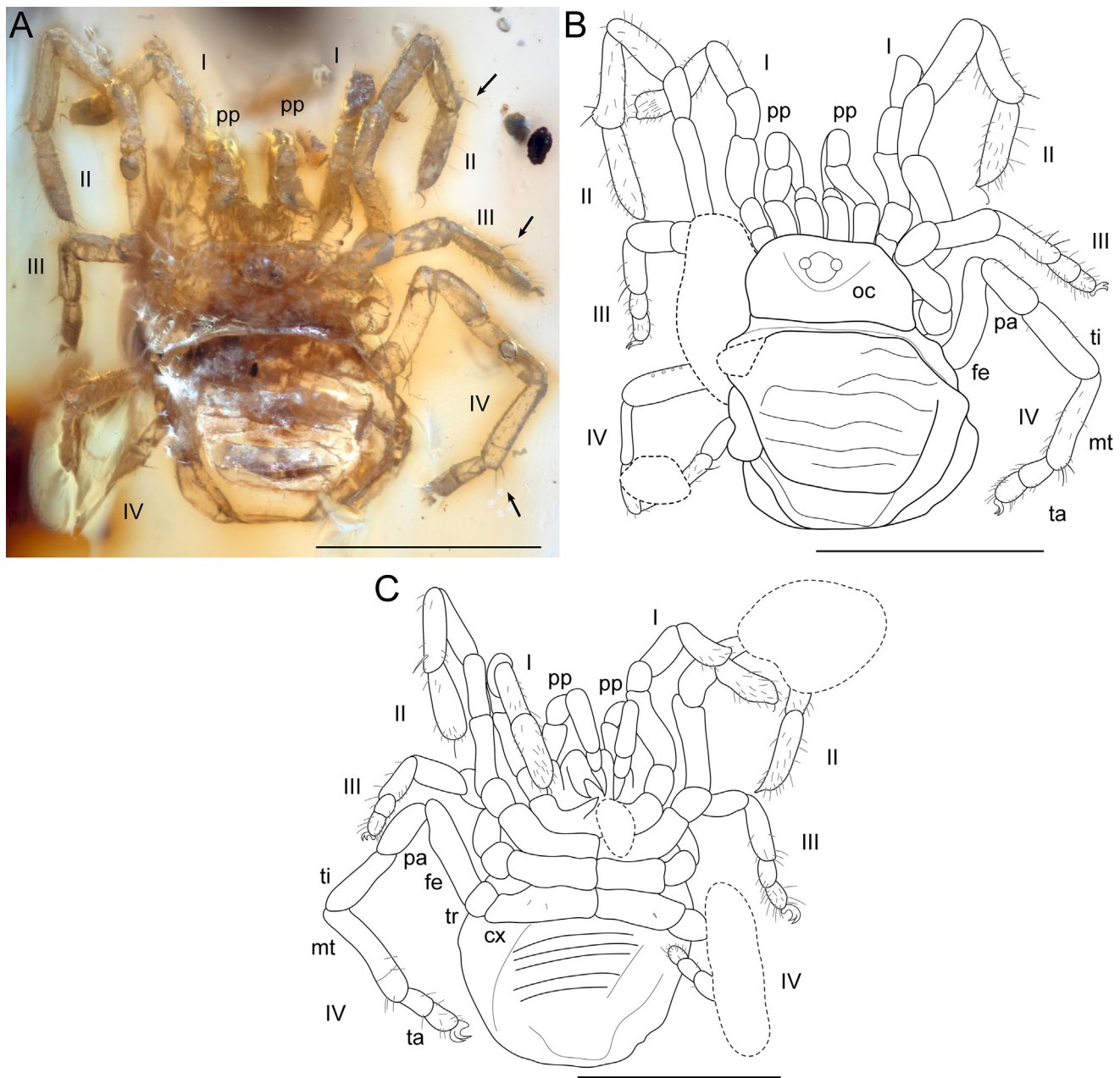


Fig. 1. *Insidiatores* indet., MB.A. 4446. (A) Dorsal overview, pairs of spines on the metatarsus are arrowed. (B) Camera lucida drawing of the same. (C) Ventral *Camera lucida* drawing. Legs numbered from I–IV. Scale bar = 1 mm.

tarsomere count like this can only be found in the family Sandokanidae. However, key characteristics of sandokanids like a swollen leg tarsus, elongated pedipalp tarsus, a scutum completum (equivocal in the fossil due to deformation of the opisthosoma) and two claws independently inserted on legs III and IV are missing. Instead, the fossil bears two simple unbranched claws on a central prong without an arolium which supports referral to the infraorder *Insidiatores* (Fig. 1B, C). This claw structure is somewhat similar to modern members of the families Cladonychiidae, Paranonychidae or Triaenonychidae, although juveniles belonging to these are sometimes characterized by complex multi-branched claws. Living

trienonychids are further characterized by a low tarsomere count in the range of 2–3 (1–2):2–4:3–4:3–4 and a high number of different claw morphologies which could indicate affinities to the fossil. It should be mentioned that Bartel and Dunlop (2019) described a much smaller juvenile *Insidiatores* possibly from the family Cladonychiidae with a comparable spine (two spines distally on metatarsus I–IV) and claw pattern which already featured strong pedipalp spination.

As most of the important characters are likely to change significantly during growth, the fossil is provisionally described as an *Insidiatores* indet. There is a high possibility that this fossil represents a novel, extinct species of

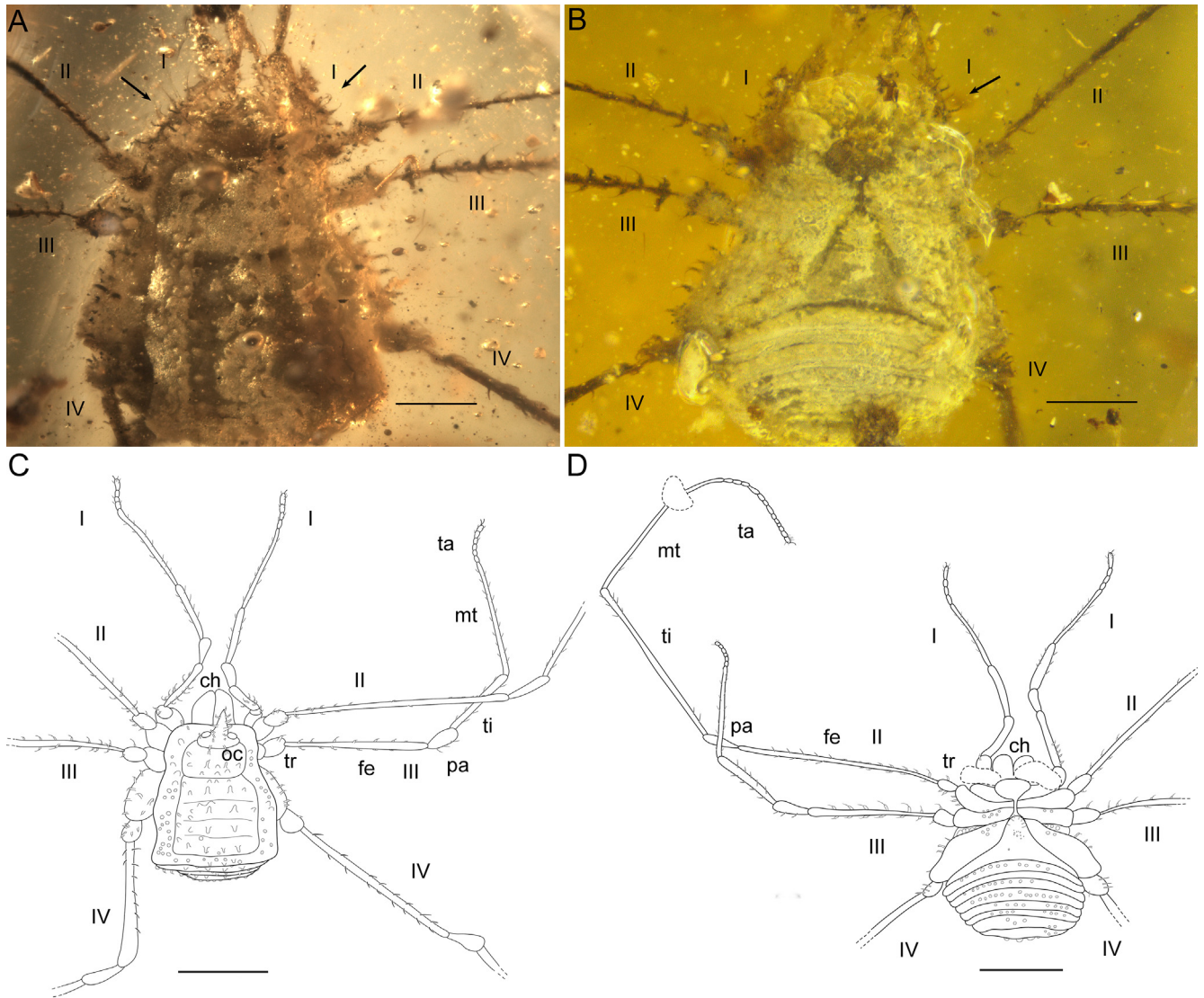


Fig. 2. *Burmalomanius circularis* n. gen. n. sp. (Podoctidae), holotype, MB.A. 4447. (A) Dorsal overview, with spination on leg I femur (arrowed). (B) Ventral overview. (C, D) Camera lucida drawing of the same without pedipalps. Legs numbered from I–IV. Scale bar: 0.5 mm for (A, B); 1 mm for (C, D).

Insidiatores, however, description of a new taxon should not be based on a juvenile. Nevertheless, we figure the specimen here in the expectation that it can be used for comparison in future studies.

Material: MB.A. 4446 (ex collection Patrick Müller, BUB3614). Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (upper Albian–lower Cenomanian).

Description: Body pear-shaped and smooth, L 1.27, anterior W 0.75, maximum posterior W 1.02. Opisthosoma strongly deformed (Fig. 1A). Ocularium slightly elevated (L 0.13, W 0.14), located near anterior border with lateral eyes. Chelicerae relatively short and slender, without armature (Fig. 1C). Chelicera proximal segment L 0.19; cheliceral hand L 0.13, with fixed and movable finger (L 0.14). Pedipalps long, thin and smooth. Pedipalp claw as long as tarsus (Fig. 1C). Pedipalp length: tr 0.17, fe

0.19, pa 0.16, ti 0.31, ta 0.12, cl 0.13, total (tr–ta) 1.08. Legs relatively short and mostly smooth (legs II and IV longest), covered with thin (sensory) setae on metatarsus and tarsus. Additionally, metatarsus I–IV bears a pair of spines distally (Fig. 1A, B). Leg IV femur covered with row of small tubercles. Tarsus I–II with one claw and not subdivided. Tarsus III–IV bear two simple unbranched claws on a central prong. Tarsal formula: 1:1:2:2. Leg length: Leg I cx 0.33, tr 0.18*, fe 0.31*, pa 0.22, ti 0.24, mt 0.29, ta 0.36, total (cx–ta) 1.93; Leg II cx 0.49, tr 0.15, fe 0.38*, pa 0.31, ti 0.36, mt 0.40, ta 0.40, total (cx–ta) 2.49; Leg III cx 0.39*, tr 0.15, fe 0.25, pa 0.32, ti 0.25, mt 0.30, ta 0.23*, total (cx–ta) 1.89; Leg IV cx 0.48, tr 0.14, fe 0.50, pa 0.31*, ti 0.39, mt 0.49*, ta 0.28, total (cx–ta) 2.59.

Ventral parts of opisthosoma equivocal.

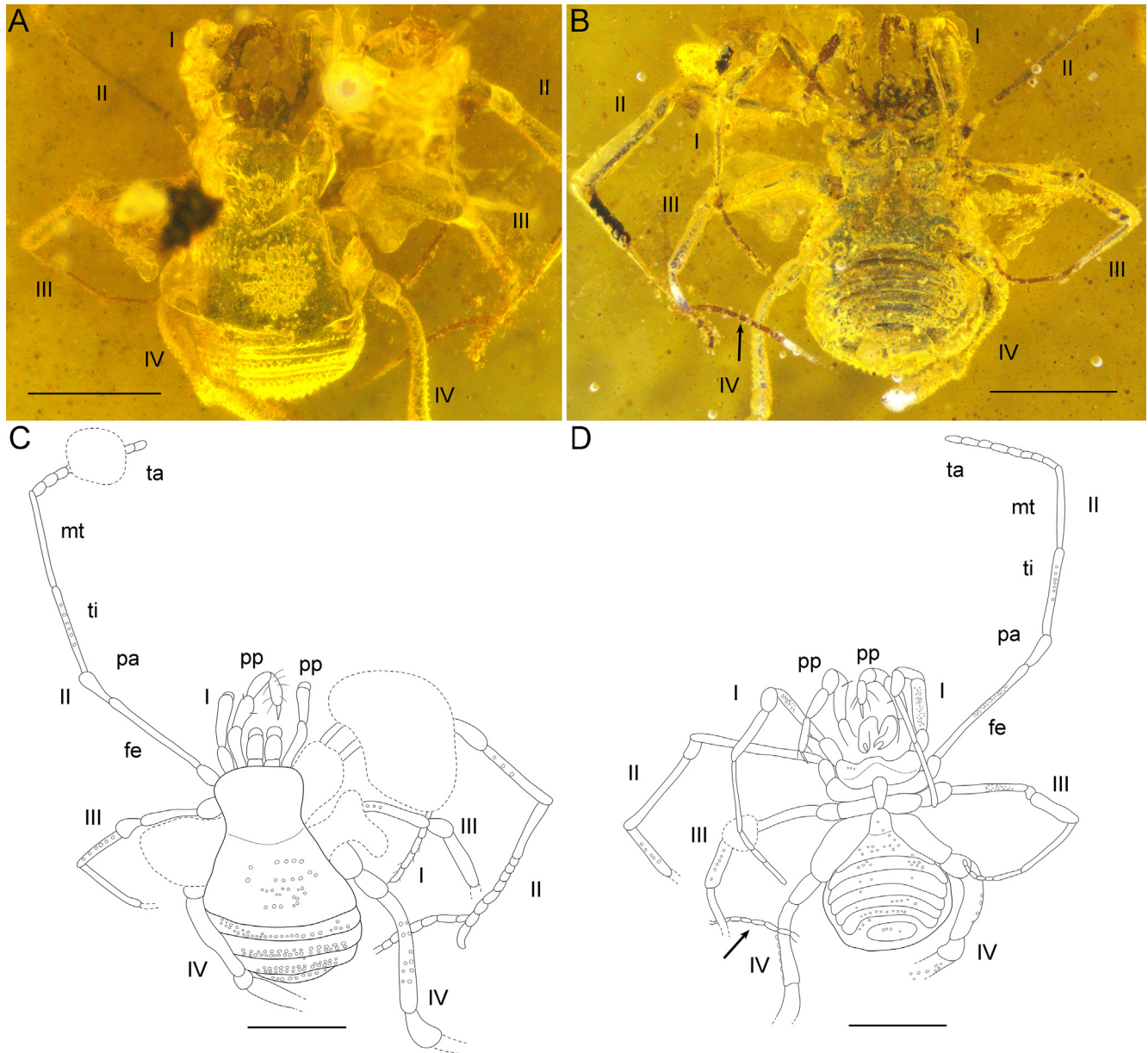


Fig. 3. *Petroburma tarsomeria* n. gen. n. sp. (Petrobunidae), holotype, MB.A. 4448. (A) Dorsal overview. (B) Ventral overview, with broken tarsus IV (arrowed). (C, D) Camera lucida drawing of the same. Legs numbered from I–IV. Scale bar = 1 mm.

Family Podoctidae Roewer, 1912

Remarks: MB.A. 4447 closely resembles modern adult females of the family Podoctidae. The subtrapezoidal habitus combined with robust body and leg armature in the form of tubercles, spines and hair-tipped tubercles (especially on the leg I femur where the hair-tipped tubercles appear more densely spaced and somewhat larger) clearly support podoctid affinities (Fig. 2A–C). In addition, some modern podoctids show strong sexual dimorphism (e.g., *Paralomanius mindanaoensis* Suzuki, 1977), with males having a larger ocularium often leaning back against the scu-

tum, longer and thickened chelicerae and/or pedipalps. The new fossil, however, bears a small ocularium with an anteriorly projecting central spine and relatively small chelicerae and pedipalps, which would be more typical for females (Fig. 2C). Extremely long legs, not greatly enlarged coxa IV and two simple claws with separated insertions visible on tarsus III further argue for a placement within Podoctidae. Modern podoctids exhibit some variability in tarsal formula, with tarsomere counts spanning the range 2–4:2–25:4–5:4–5 (Sharma et al., 2017). The fossil's discernible tarsal formula (4:13:6:?) falls within this range, with the exception of leg III. Again, the fossil's morphology

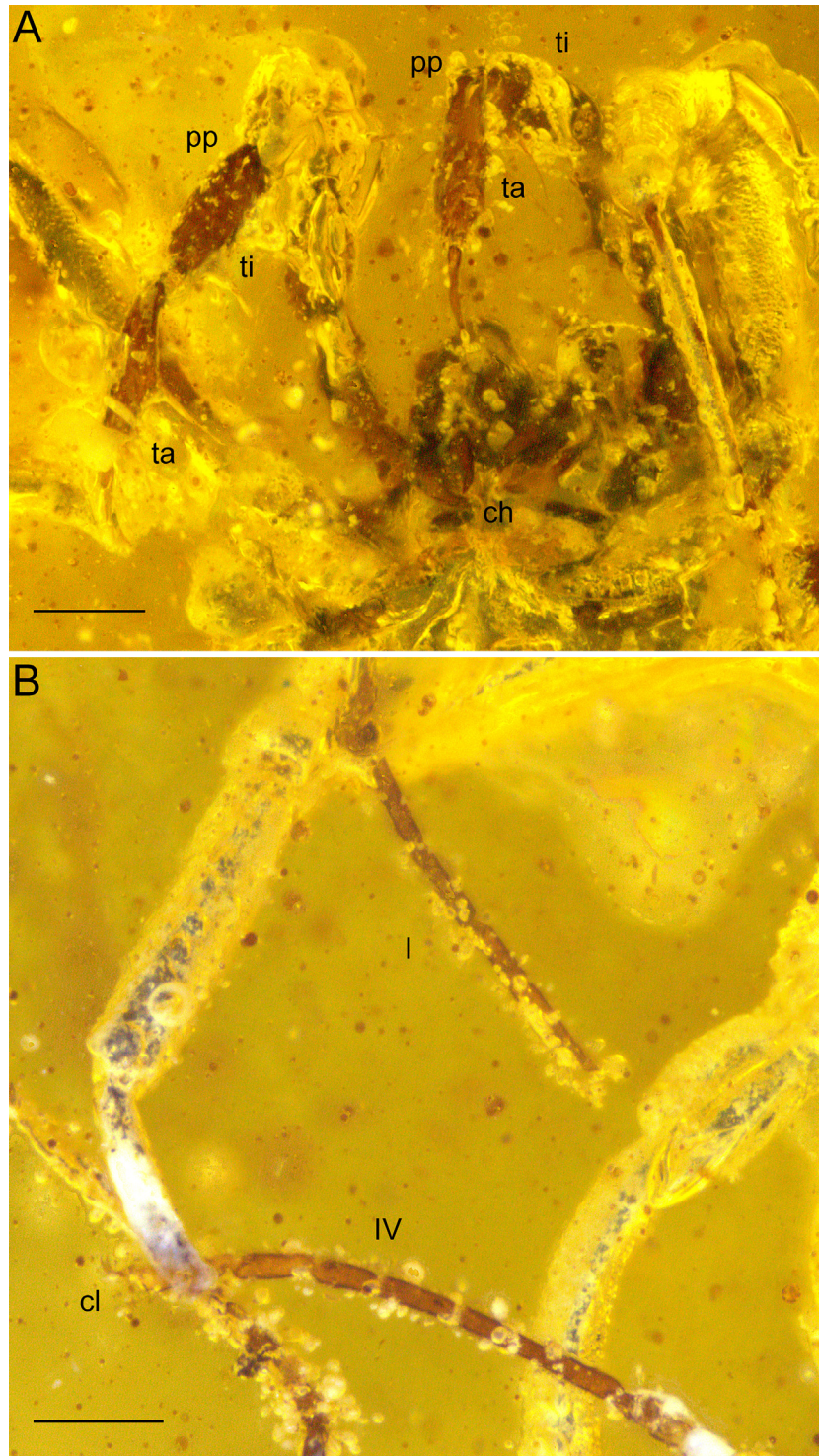


Fig. 4. Details of *Petroburma tarsomeria* n. gen. n. sp. (Petrobunidae), holotype, MB.A. 4448. (A) Pedipalps and chelicerae in ventral view. (B) Tarsus I and IV in ventral view. Legs I and IV numbered. Scale bar = 0.2 mm.

is comparable to modern females of the genus *Lomanius* Roewer, 1923 and *Paralomanius* Goodnight and Goodnight, 1948. However, based on the distinct armature of the ocularium and body, the absence of strong pedipalpal spination (modern females of *Lomanius* usually bear larger spines than what can be observed in the fossil) and

the tarsal differences, a new genus and species is proposed. The new fossil represents the oldest, and so far, only fossil record of the family Podoctidae.

Genus *Burmalomanius* n. gen.

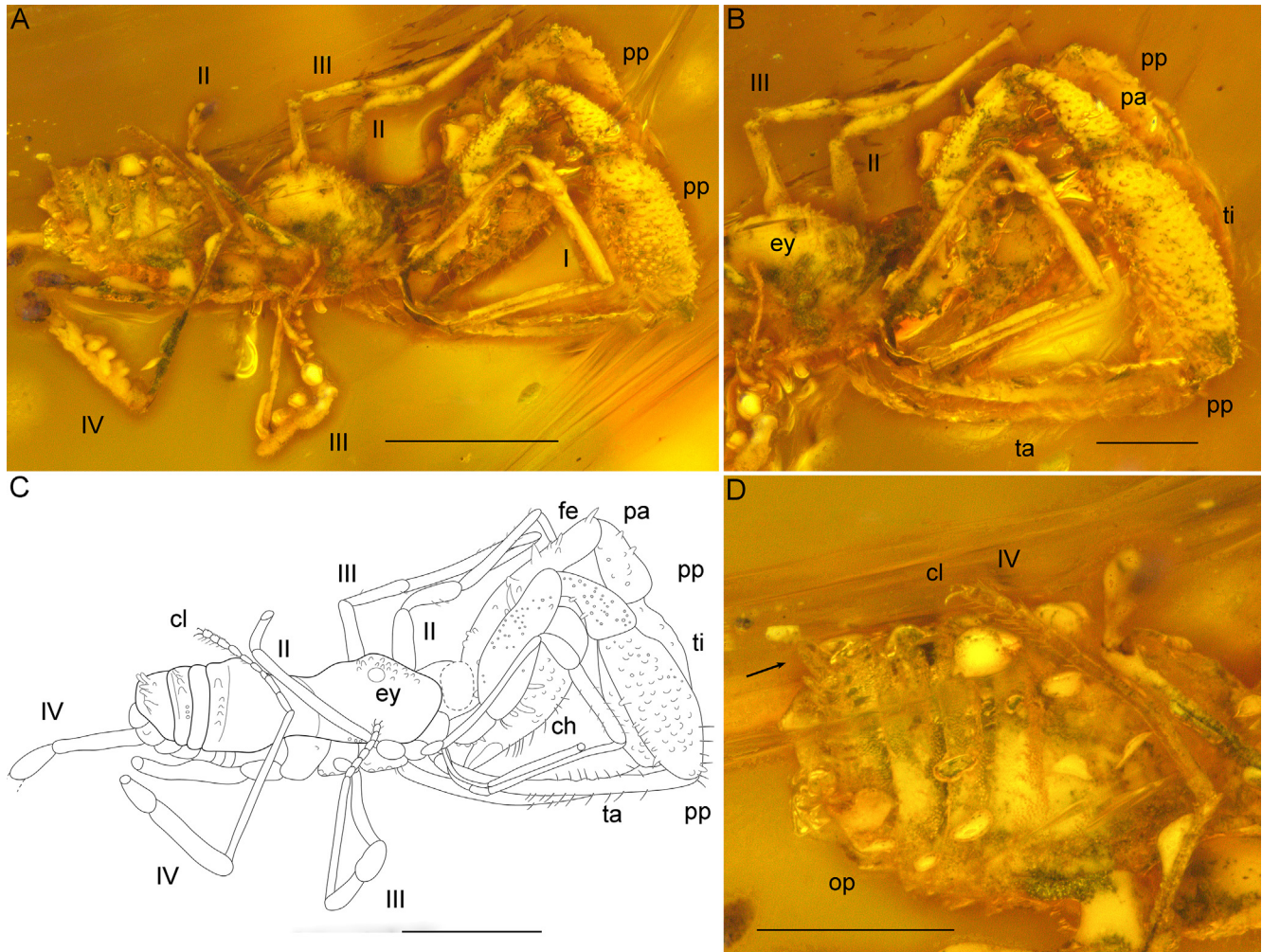


Fig. 5. *Mesodibunus tourinhoae* n. gen. n. sp. (Epedanidae), holotype, CNU-SPI-MA 2015013. (A) Dorso-lateral overview. (B) Details of the prosoma and pedipalps in dorso-lateral view. (C) Camera lucida drawing of (A). (D) Details of the opisthosoma, with large tubercles on the last tergite (arrowed) and tarsus IV. Legs numbered from I–IV. Scale bar: 1 mm for (A, C); 0.5 mm for (B, D).

LSID: urn:lsid:zoobank.org:act:42A0488C-2655-466D-97B8-DF608568581.

Etymology: Named after the Burma Terrane, combined with the modern genus *Lomanius*. Gender masculine.

Type species: *Burmalomanus circularis* n. gen. n. sp., monotypic.

Diagnosis: Body subtrapezoidal, covered with numerous tubercles and spines. Dorsal segments fused into scutum magnum. Ocularium in females armed with large central spine bearing additional pairs of hair-tipped tubercles. Pedipalps relatively small and slender covered with needle-like spines. Legs elongate with hair-tipped tubercles on coxa, trochanter and femur. Femur I in particular densely covered with somewhat larger and circularly arranged hair-tipped tubercles. Tarsus III with simple and separately inserted double claws. Female genital operculum bears small spines and tubercles.

Burmalomanus circularis n. gen. n. sp.

(Fig. 2)

LSID: urn:lsid:zoobank.org:act:22069539-47C2-45EA-9BD1-B18B30B9BDD7.

Etymology: Named for its circular arranged hair-tipped tubercles, especially on the leg I femur. Gender masculine.

Holotype: MB.A. 4447 (ex collection Patrick Müller, BUB3630). Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (upper Albian–lower Cenomanian).

Diagnosis: As for the genus.

Description: Body subtrapezoidal (Fig. 2A), L 1.78, anterior W 1.06, maximum posterior W 1.44, dorsally fused into scutum magnum with three opisthosomal tergites. Dorsal scutum subdivided into four areas, each with two large tubercles in parallel forming central longitudinal rows. Prosoma and opisthosoma strongly armed with numerous spines, tubercles and hair-tipped tubercles. Free tergites without spination or large tubercles. Ocularium elevated, armed (L 0.22, W 0.50), with lateral eyes and large central spine bearing two pairs of hair-tipped tubercles and a single upwards facing hair-tipped tubercle near the tip, located near anterior border (Fig. 2C). Chelicerae relatively small and without armature. Pedipalps rather small

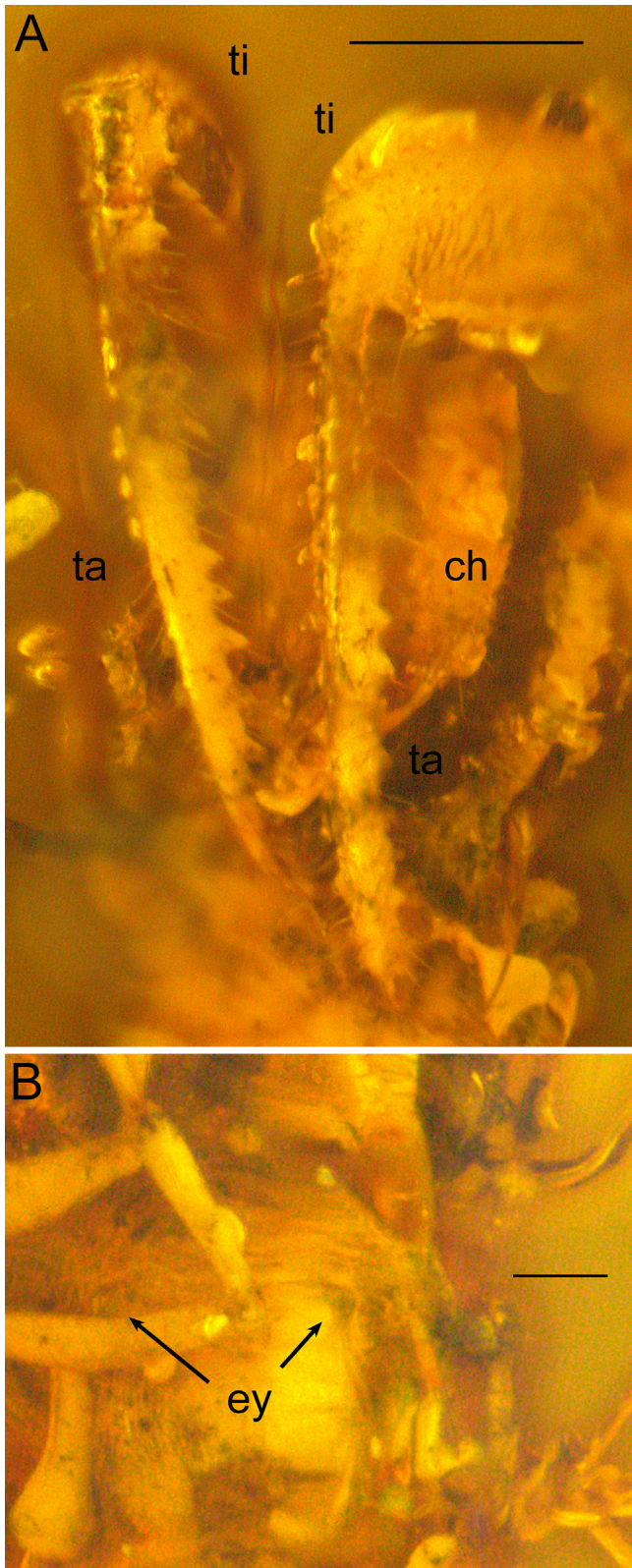


Fig. 6. Details of *Mesodibunus tourinhoae* n. gen. n. sp. (Epedanidae), holotype, CNU-SPI-MA 2015013. (A) Pedipalps and chelicerae in ventral view. (B) Prosoma in dorsal view, with eye lenses (arrowed). Scale bar: 0.5 mm for (A); 0.2 mm for (B).

and slender, covered with sparse needle-like spines and thorns. Patella covered with one larger mesal thorn, tibia with six mesal and two ectal needle-like spines, tarsus with three pairs of needle-like spines. Pedipalp claw long and curved. Legs very long (leg II longest) and strongly armed, especially on coxa, trochanter and femur with somewhat circular arranged hair-tipped tubercles (Fig. 2C, D). Patella–tarsus covered with thin (sensory) setae. Leg I femur with somewhat larger and more densely spaced hair-tipped tubercles (Fig. 2A–C). Leg coxa partly visible in dorsal view. Tarsus I–III subdivided into tarsomeres, with one claw on tarsus I–II and two simple claws on tarsus III (Fig. 2C). Tarsal formula: 4:13:6:?. Leg length: Leg I cx 0.51, tr 0.28, fe 0.64*, pa 0.25*, ti 0.65, mt 0.93*, ta 0.43, total (cx–ta) 3.69; Leg II cx 0.71, tr 0.27, fe 2.45*, pa 0.46*, ti 2.09, mt 1.37, ta 1.74, total (cx–ta) 9.09; Leg III cx 0.70, tr 0.27, fe 1.54*, pa 0.42, ti 0.87, mt 1.21*, ta 0.44, total (cx–ta) 5.45; Leg IV cx 1.14, tr 0.28, fe 2.06, pa 0.43, ti ?, mt ?, ta ?, total (cx–pa) 3.91.

Genital operculum subcircular, covered with small spines and tubercles proximally, located between coxa IV (L 0.18, W 0.20). Opisthosomal sternites 4–9 each with recurved anterior and posterior borders; widths: 4, 1.48; 5, 1.44; 6, 1.30; 7, 1.20; 8, 1.11; 9, 1.07.

At least sternites 4–8 bearing single row of tubercles. Sternites 4–6 further subdivided by a small groove (Fig. 2B).

Anal operculum sub-elliptical and tuberculate, L 0.20, W 0.68.

Family Petrobunidae Sharma and Giribet, 2011

Remarks: MB.A. 4448 almost certainly represents an adult because of its high tarsomere count and the absence of juvenile structures (e.g., an arolium) on tarsus III and IV. The fossil habitus shows similarities to living members of the families Petrobunidae and Tithaeidae, including the extinct tithaeid species *Ellenbergellus tuberculatus* Bartel, Dunlop, Sharma, Selden, Ren and Shih, 2021 recently described from Burmese amber. The latter shares with the new fossil the tuberculated opisthosoma (even though the number of tubercles is higher in the new specimen), relatively small chelicerae and pedipalps, the length of the appendages (e.g., legs) and the somewhat granulated legs with the new amber fossil (Fig. 3). The specimens differ with respect to the length of the pedipalp claw, which is shorter than the tarsus in the new specimen (Fig. 4A). This could be related to different states of preservation as the pedipalps of the holotype of *Ellenbergellus tuberculatus* were desiccated in some areas. Furthermore, the new specimen features a more curved femur IV with a higher number of tubercles and a slightly different tarsomere count on legs I, III and IV (Figs. 3A, 4B).

Significantly, the number of tarsomeres on leg I (3–4) supports referral of the new fossil to the family Petrobuni-

dae; by contrast Tithaeidae usually have 5 tarsomeres on leg I. The ocularium also appears to be more flattened in the specimen described herein. A male petrobunid can be excluded as the fossil lacks the typical sexually dimorphic oversized trochanter on leg IV and the apophyses on the opisthosomal sternites. Morphological differences between petrobunids and tithaeids are generally sparse. They are mainly distinguished by the already mentioned number of tarsomeres, the sexually dimorphic leg IV and by penis structures. As most of the above described characters are more consistent with Petrobunidae the new fossil is provisionally placed therein. Additionally, a new genus is proposed as the described combination of characters cannot be observed in any modern petrobunid representatives.

Genus *Petroburma* n. gen.

LSID: urn:lsid:zoobank.org:act:A5518446-B20E-4B49-81B1-FB554247557B.

Etymology: Refers to the modern genus *Petrobunus* and the Burma Terrane. Gender feminine.

Type species: *Petroburma tarsomeria* n. gen. n. sp., monotypic.

Diagnosis: Body pear-shaped, dorsal segments fused into scutum magnum. Opisthosomal tergites armed with belts of numerous small tubercles. Chelicerae small and unarmed. Pedipalps rather short and mostly covered with needle-like spines and thorns. Pedipalp claw shorter than tarsus. Legs moderately long, granulated and with arcuate femur IV. Tarsomere count not reduced. Tarsus III–IV with simple, separately inserted double claws. Ventral opisthosoma (including the sternites) covered with tubercles.

Petroburma tarsomeria n. gen. n. sp.
(Figs. 3, 4)

LSID: urn:lsid:zoobank.org:act:7A3CC77B-0A1D-4F05-9F50-72A9473B1DAE.

Etymology: Named for its high number of tarsomeres on legs II, III and IV. Gender feminine.

Holotype: MB.A. 4448 (ex collection Patrick Müller, BUB3646). Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (upper Albian–lower Cenomanian).

Diagnosis: As for the genus.

Description: Body pear-shaped (Fig. 3A, C), L 2.16, anterior W 0.89, maximum posterior W 1.49. Dorsal segments fused into scutum magnum. Prosoma smooth. Opisthosomal region tuberculate with additional rows of tubercles at the boundary of each segment. Chelicerae small and smooth (Fig. 4A). Chelicera proximal segment L 0.32; cheliceral hand L 0.29, with fixed and movable fingers (L 0.11). Pedipalps rather short and slender. Tarsus covered with two pairs of needle-like spines, tibia with three somewhat

thicker mesal and ectal spines, patella with one mesal needle-like spine and femur bears a single mesal thorn. Pedipalpal claw shorter than tarsus and slightly curved (Fig. 4A). Pedipalp length: fe 0.46*, pa 0.22, ti 0.35, ta 0.24, cl 0.17, total (fe–ta) 1.27. Legs long and smooth, except femur, tibia and metatarsus, which are tuberculate. Femur IV arcuate. Coxa partly visible in dorsal view. Tarsus subdivided into tarsomeres with one claw on tarsus I–II and two simple claws with separate insertions on tarsus III–IV (Fig. 4B). Tarsal formula: 3–4:7+:6–7:7–8+. Leg lengths: Leg I cx 0.48, tr 0.27, fe 0.65, pa 0.24, ti 0.57, mt 0.78, ta 0.71, total (cx–ta) 3.70; Leg II cx 0.50, tr 0.23, fe 1.34, pa 0.37, ti 0.93, mt 0.88, ta 1.17, total (cx–ta) 5.42; Leg III cx 0.40, tr 0.30, fe 0.78, pa 0.27, ti 0.56, mt 0.78, ta 0.71, total (cx–ta) 3.80; Leg IV cx 0.82, tr 0.32, fe 1.19, pa 0.43, ti ?, mt ?, ta ?, total (cx–pa) 2.76.

Genital operculum subtriangular and covered with tubercles, located between coxa IV (L 0.27, W 0.22). Sternites 4–9 bearing rows of tubercles, each with recurved anterior and posterior borders; widths: 4, 1.24; 5, 1.19; 6, 1.12; 7, 1.00; 8, 0.88; 9, 0.76 (Fig. 3B, D).

Anal operculum elliptical and tuberculate, L 0.17, W 0.51.

Family Epedanidae Sørensen, 1886

Remarks: CNU-SPI-MA 2015013 is interpreted as an adult male due to its high tarsomere count and strongly developed armature. Additionally, juvenile structures on tarsus III and IV cannot be observed. The absence of a common ocularium in this amber fossil represents an interesting, and rarely developed characteristic in living laniatoreans (Figs. 5A–C, 6B). It can be observed in, for example, Biantidae, Stygnidae, Stygnommatidae, the subfamily Dibuninae of the Epedanidae, and is also known from some Samoidae and Triaenonychidae. Biantidae can be excluded for the new fossil as they often have a thin and unarmed pedipalpal femur, whereas the fossil has a large, robust and strongly armed femur (Fig. 5B, C). Stygnidae belongs to the few families bearing a tarsal process, which is lacking in the amber specimen. A scopula on tarsus III–IV, which is commonly found in Samoidae, is also absent (Fig. 5D).

By contrast, Stygnommatidae have a similar habitus to the fossil, body granulation, very large, robust and strongly armed pedipalps and chelicerae. However, the pedipalp tarsus in Stygnommatidae is often described as highly reduced with respect to the tibia, whereas the fossil has an elongated pedipalp tarsus (Fig. 6A). Additionally, the free tergites are unarmed or granulated in modern stygnommatids, while relatively large tubercles can be observed on the last free tergite in the amber specimen (Fig. 5D). The fossil further lacks the flat rectangular proximal chelicerae segment, typical for living stygnommatids. The number of tarsomeres is also somewhat different. Living Stygnommatidae have a

tarsal formula in the range of 6–8:9–14:6:6–7 (Pinto-da-Rocha and Giribet, 2007). The fossil has a tarsal formula of 5–6:?:6:8–9.

Overall most of the characteristics mentioned above, like the absence of a well-defined ocularium, greatly enlarged chelicerae and pedipalps, the armature and the tarsal formula are consistent with modern members of the epedanid subfamily Dibuninae and for this reason the fossil is provisionally placed in Epedanidae. This placement is further supported by the modern distribution of Dibuninae, as these are commonly found in Southeast Asia today. In Dibuninae the eye lenses can be more distant from each other, although we should caution that this character is known to be quite variable within this subfamily. The similarity of the new amber specimen to the previously described fossil epedanid *Gigantocheles nilsi* Bartel, Dunlop, Sharma, Selden, Ren and Shih, 2021 is also worth mentioning. Both have a comparable habitus, large chelicerae and an elongated pedipalp tarsus. The new specimen is, however, larger with a much stronger developed armature in all body parts. Sexual dimorphism in Epedanidae is mostly restricted to pedipalp spination and swollen or thickened parts of the chelicerae (Pinto-da-Rocha and Giribet, 2007). Therefore, we feel that it is unlikely that *G. nilsi* and the new fossil are merely dimorphic expressions of the same species, and a new genus and species is proposed here for the new material.

Genus *Mesodibunus* n. gen.

LSID: urn:lsid:zoobank.org:act:86FFD740-D133-49D8-B249-CBD05B490CFA.

Etymology: Refers to the modern genus *Dibunus* and the Mesozoic record of the fossil. Gender masculine.

Type species: *Mesodibunus tourinhoae* n. gen. n. sp., monotypic.

Diagnosis: Body hourglass-shaped, dorsal segments fused into *scutum magnum*. Free tergites covered with rows of large tubercles. Common ocularium absent, eye lenses separated. Chelicerae very large, robust, covered with tubercles and thick setae. Pedipalps also very long, strongly armed and robust, with enlarged tibia, elongated tarsus and very short pedipalp claw. Legs moderately long and unarmed. Tarsus III–IV with simple, separately inserted double claws.

Mesodibunus tourinhoae n. gen. n. sp.
(Figs. 5, 6)

LSID: urn:lsid:zoobank.org:act:B6A6741B-0BA0-4E81-9C78-873BCB87581B.

Etymology: In honour of Ana Lúcia Tourinho (Universidade Federal de Mato Grosso, Brazil) for her numerous contributions to the systematics and biology of Laniatores. Gender feminine.

Holotype: CNU-SPI-MA 2015013. Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (upper Albian–lower Cenomanian).

Diagnosis: As for the genus.

Description: Body hourglass-shaped, L 2.33, anterior W 0.84, maximum posterior W 1.18. Dorsal segments fused into *scutum magnum*. Prosoma mostly smooth, region around eye lenses covered with tubercles and small spines (Fig. 5A–C). Opisthosoma bears rows of smaller and larger tubercles on free tergites (tubercles become larger posteriorly). Common ocularium absent. Lateral eye lenses separated, located approximately in the first third of the prosoma (Fig. 6B). Chelicerae very large and robust, covered with tubercles and thicker setae (Fig. 5C). Chelicera proximal segment L 0.92; cheliceral hand L 0.91, with fixed and movable fingers (L 0.48). Pedipalps also very long and robust. Especially femur, patella and the enlarged tibia bearing spines, differently sized tubercles and thick setae. Pedipalpal claw much shorter than elongated tarsus (Fig. 6A). Tarsus covered with many setiferous tubercles and additional setae. Pedipalp length: tr 0.34, fe 1.16, pa 0.57, ti 1.18, ta 1.82, cl 0.25, total (tr–ta) 5.07. Legs moderately long and mostly smooth, with thin sensory setae on tarsus and few tubercles on femur and coxa. Femur IV slightly arcuate. Coxa partly visible in dorsal view. Tarsus subdivided into tarsomeres with one claw on tarsus I–II and two simple claws with separate insertions on tarsus III–IV (Fig. 5D). Tarsal formula: 5–6:?:6:8–9. Leg lengths: Leg I cx 0.48, tr 0.18, fe 1.04, pa 0.34, ti 0.66, mt 1.02, ta 0.59, total (cx–ta) 4.31; Leg II cx 0.59, tr 0.23, fe 1.12, pa 0.45, ti 1.02, mt ?, ta ?, total (cx–ti) 3.41; Leg III cx 0.41, tr 0.20, fe 1.05*, pa 0.32, ti 0.61*, mt 0.88, ta 0.43, total (cx–ta) 3.90; Leg IV cx 0.60, tr 0.25, fe 1.25*, pa 0.36, ti 0.73, mt 1.14, ta 0.83, total (cx–ta) 5.16.

Genital operculum equivocal. Sternites 4–9 smooth, each with recurved anterior and posterior borders; widths: 4, 0.93; 5, 0.91; 6, 0.89; 7, 0.86; 8, 0.79; 9, 0.75. Anal operculum subtriangular, L 0.27, W 0.70.

4. Discussion

With the discovery here of the first and oldest known records of Petrobunidae and Podoctidae, two new extant families are added to the increasingly diverse mid-Cretaceous Laniatores fauna of the Burma Terrane. Many of the Laniatores families found today in Southeast Asia have now been recorded from Burmese amber. This includes Beloniscidae, Epedanidae (including Dibuninae), Tithaeidae, Petrobunidae, Podoctidae, and the extinct Mesokanidae which may nevertheless be a possible stem-group to the extant Sandokanidae (Selden et al., 2016; Bartel et al., 2021). Therefore, the appearance of Petrobunidae and Podoctidae in Burmese amber was perhaps to be expected. Both potentially belong to a clade, the superfamily Epedanoidae, together with Epedanidae and Tithaeidae; although the group has limited stability (Sharma and Giribet, 2011; Fernández et al., 2017; Aharon et al.,

2019). Contrary to most Opiliones, Podoctidae are capable of long-range (transoceanic) dispersal as extant members of this family can be found on oceanic islands in the Indian and Pacific Ocean (Sharma et al., 2017). While it is possible that podoctids arrived on the Burma Terrane via transoceanic dispersal, a Southeast Asian ancestral area of podoctid diversification is strongly supported based on the close relationship to the other Asian families mentioned above.

Living laniatoreans of the infraorder Insidiatores, which are characterized by single claws on legs III and IV, with smaller distal branches of the claw, are not known from Southeast Asia. Many of these can be found in the surrounding areas like Japan, Australia, New Zealand, Madagascar and also in Europe or America (Derkarabetian et al., 2021). So far three fossil laniatoreans with Insidiatores affinities have been described from Burmese amber, i.e., *Mesokanus oehmkuehnei*, Laniatores indet. (Bartel et al., 2021) and Insidiatores indet. (described herein). The previously described Laniatores indet. is very likely also a juvenile Insidiatores. The claws on legs III and IV with an arolium are similar to those drawn by Briggs (1969). However, it remains unclear if the juveniles belong to Travunioidea or Triaenonychidae. The already heavy leg armature of the Laniatores indet. could indicate triaenonychid affinities. Future Burmese amber fossils of adult Insidiatores may allow a more precise placement of the two juveniles known so far and would further improve our understanding about the origin of the Burmese fauna. Triaenonychids show a clear Gondwanan and travunioidea a Laurasian distribution these days (Derkarabetian et al., 2021). Taken together, these findings suggest that members of the infraorder Insidiatores were a notable component of the Burmese amber forests during the mid-Cretaceous, with their subsequent extirpation in the equatorial belt during the Cenozoic.

Future studies on the modern southeast Asian Laniatores fauna are merited and could reveal an even richer species diversity. The best example is the recent discovery of a new and unique family of living laniatoreans in Thailand called Suthepiidae (Martens, 2020).

Protopyramidops nalaе (Pyramidopidae) was the first described Laniatores fossil with distribution of living members in the Afrotropics, and thus outside of Southeast Asia (Bartel et al., 2021). The families Pyramidopidae and Triaenonychidae have a comparable modern distribution to the arachnid order Ricinulei, which are also described from Burmese amber but apparently became extinct in Asia (see e.g., Wunderlich, 2015, 2017). This supports a Gondwanan origin for the Burmese amber fauna, which was previously suggested by authors such as Poinar (2019). His work was mainly focused on Burmese angiosperm flowers (e.g., *Tropidogyne pikei* Chambers et al., 2010 or *Palaeoanthella huangii* Poinar and Chambers, 2005) and on beetles (e.g., *Microborus inertus* Cognao and Grimaldi, 2009) with modern Neo- or Afrotropical affinities. The recent discovery of the pseudoscorpion family Ideoroncidae in Burmese amber

further argues for a Gondwanan origin of the fauna (Geißler et al., 2022). However, future research on the geology of the Burma Terrane, and its position relative to other landmasses in the mid-Cretaceous, as well as more new fossil specimens are needed to further test this hypothesis and to investigate possible dispersal events.

5. Conclusions

Three new species of fossil laniatoreans in two previously undiscovered families have been described. In all, fifteen species from this suborder and most of the modern southeast Asian families are now known from the fossil record. Our new data support the inference that the laniatorean fauna was already quite diverse, at least on the Burma Terrane, by the Cretaceous. The substantial number of untypical southeast Asian groups (Pyramidopidae, Insidiatores) indicate that the Burmese amber forests of the mid-Cretaceous hosted a more diverse Laniatores fauna than what we know from this area today. This diversity shows great potential to improve our understanding of the biogeographical origins and past distributions of laniatoreans. Nevertheless, future studies of the past and present Southeast Asian fauna and flora are needed to verify existing hypotheses.

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