

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

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## ABSTRACT

One new family, six new genera and six new species of laniatorean harvestmen (Arachnida: Opiliones: Laniatores) from the mid-Cretaceous (Cenomanian, ca. 99 Ma) Burmese amber of Northern Myanmar are described. *Ellenbergellus tuberculatus* gen. et sp. nov. is the first fossil assignable to the extant family Tithaeidae. *Mesokanus oehmkuhnlei* gen. et sp. nov. is the first fossil assignable to the newly described family Mesokanidae fam. nov. *Biungulus xiai* gen. et sp. nov. and *Gigantochelone nilsi* gen. et sp. nov. are referred to Epedanidae, a family previously recorded in Burmese amber. *Protopyramidops nalae* gen. et sp. nov. is the first fossil potentially assignable to the extant family Pyramidopidae. Finally, *Palaeobeloniscus thilolebi* gen. et sp. nov. is the first fossil assignable to the extant family Beloniscidae. These records offer new mid-Cretaceous constraints for the origins of four modern families and suggest that the Burmese amber forests hosted a fairly diverse fauna of laniatorean harvestmen which mostly belonged to lineages still present in Southeast Asia today.

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## 1. Introduction

Laniatores (Arachnida: Opiliones) is one of four living suborders of the harvestmen, and represents a diverse arachnid group with more than 4200 living species (Kury, 2017). They are found throughout the world in warmer latitudes and can have a striking and sometimes colourful appearance. They are sometimes referred to as armoured harvestmen, being characterized by an often robust body ornamented with spines and/or tubercles, raptorial pedipalps and enlarged sexually dimorphic chelicerae in many groups (e.g. Pinto da Rocha et al., 2007). Despite their modern diversity their fossil record remains poorly known, with only six fossil species described to date. The youngest come from Miocene Dominican Republic amber (ca. 16 Ma) and comprise *Philacarus hispaniolensis*

Cokendolpher and Poinar, 1992, which is of uncertain familial affinities, a fossil assigned to *Kimula* sp. (Kimulidae) in Cokendolpher and Poinar (1992), and two fossils in the family Samoidae: *Pellobunus proavus* Cokendolpher, 1987 and *Hummelinckiolus silhavyi* Cokendolpher and Poinar, 1998. The next oldest is *Proholoscotolemon nemastomoides* (Koch and Berendt, 1854) from Eocene Baltic amber, (ca. 44–49 Ma) which belongs in the family Cladonychiidae. The Mesozoic currently yields only a single fossil laniatorean, *Petrobunoides sharmai* Selden et al., 2016 from the mid-Cretaceous Burmese amber of Myanmar (ca. 99 Ma). It was placed in the family Epedanidae by Selden et al. (2016).

Harvestmen have been an exemplary group for integrating fossil calibration points into phylogenies of living species (e.g. Giribet et al., 2010; Garwood et al., 2011, 2014; Hedin et al., 2012; Sharma and Giribet, 2011). A challenge here has been the lack of Palaeozoic records for both Laniatores and another suborder, Cyphophthalmi, both of which are predicted to have been present in the Devonian or Carboniferous based on multilocus molecular dating analyses. Several authors used different approaches to estimate laniatorean origination dates (Fernández et al., 2017;

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Sharma and Giribet 2011, 2014). In most of these previous works Mesozoic Laniatores fossils were not available as calibration points. Sharma and Giribet (2014) proposed an Early Devonian diversification age (410.3 Ma) for non-synthetonychiid laniatores using total evidence dating, an Early Carboniferous age (329.7 Ma) using node dating of a phylogenetic supermatrix, and an Early Permian age (282.4 Ma) using node dating combining morphology and molecules. These dates imply a gap of 310–180 million years between the estimated origin of laniatores and their first appearance in the fossil record (Selden et al., 2016). Phylogenomic estimation of divergence times based on an uncorrelated gamma clock model recovered a younger age for Laniatores in the Late Jurassic, but with uninformatively large confidence intervals spanning 150 Ma (Fernández et al., 2017).

Here we describe seven new Laniatores specimens from Burmese amber, six of which are recognised as new species, thus doubling the number of fossil species in this suborder. Most of them belong to families found today in Southeast Asia and include two new species in Epedanidae, as well as the first formal fossil records of the families Tithaeidae, Pyramidopidae, Beloniscidae and the newly described extinct group Mesokanidae fam. nov. Our data suggest that the Burmese amber forests hosted a diverse assemblage of laniatores in the mid-Cretaceous of Southeast Asia. Although they are probably still much too young to resolve the Palaeozoic origination dates of modern Laniatores clades, they offer several new calibration points for the harvestman Tree of Life and constrain the origins of families whose geographic provincialism underpin biogeographic investigations.

## 2. Material and methods

Seven specimens were available; see also Bartel (2019) for details. Four come from the private collection of Patrick Müller, one from the collection of Sieghard Ellenberger and one from the collection of Christoph Öhm-Kühnle. All have now been deposited in the arthropod palaeontology collection of the Museum für Naturkunde Berlin, with repository numbers 4308–4313 (see also below) under the acronym MB.A for Museum Berlin, Arthropoda. The other specimen comes from the collection of Xia Fangyuan and had already been deposited in the fossil insect collection of the Key Lab of Insect Evolution and Environmental Changes, at the College of Life Sciences, Capital Normal University (CNU) Beijing, China.

All material is generally well preserved (Figs 1–9), with some exceptions where body parts are covered by bubbles, detritus, fractures or crystalline growth. All specimens were immersed in water and photographed using a Leica Z16 APO A stereomicroscope equipped with the software package Leica Application Suite which was used to generate stacks of about 15–20 images. These were combined with Helicon Focus 6 and edited for brightness and contrast using Adobe Photoshop CS5 to ensure that all parts of the specimens are visible. Drawings were made on 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. Setae or tubercles were sometimes omitted to ensure visibility of important characteristics. All measurements are in mm, with occasional deviations in measured lengths due to the three-dimensional position of the amber specimens in the matrix. Average values are marked with asterisks. The inclusions were compared with extant Laniatores in the collection of the Museum für Naturkunde Berlin and the University of Wisconsin-Madison as well as the type of the previously described Burmese amber species *Petrobunoides sharmai* held in the Capital Normal University Beijing under the repository number BU-002036.

### 2.1. Burmese amber

Burmese amber or ‘Burmite’ has been mined for over two millennia in northern Myanmar. Most of the modern inclusion-bearing material derives from the Hukawng Valley. These deposits have yielded many well-preserved insect fossils (e.g. Chen et al., 2019; Gao et al., 2019; Lin et al., 2019; Zhao et al., 2019). For an overview of the deposit with particular reference to arachnids see Selden & Ren (2017). A lower Cenomanian age of  $98.79 \pm 0.62$  Ma was proposed by Shi et al. (2012) based on U–Pb dating of zircons. Bivalve borings in Burmese amber investigated by Smith & Ross (2018) and the recent discovery of an ammonite tapped in amber (Yu et al., 2019) confirm a lower Cenomanian or perhaps upper Albian age. The Cretaceous is known as one of the warmest periods and therefore characterized by a tropical climate with average temperatures over 30 °C in some areas (Grimaldi et al., 2002). The resin was possibly produced by trees of the families Araucariaceae and Taxodiaceae (Smith & Ross, 2018). These were probably distributed along a shoreline given the discovery of marine animals (see above) as well as the more typical terrestrial arthropods and vertebrates. Burmese amber from northern Myanmar has proved to be a remarkably diverse window into the mid-Cretaceous of Southeast Asia. So far 1303 species in 954 genera and 559 families have been described. Arthropods are the most common group with 1223 known species in 881 genera and 508 families (Ross, 2019).

## 3. Systematic palaeontology

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

**Remarks.** The fossils described here can all be referred to Laniatores due to the presence of a *scutum magnum*, in which the carapace and first five opisthosomal tergites are fused, or a *scutum completum* in which dorsal tergites I–VII are fused. The *scutum magnum* condition is expressed in all laniatores, apart from the family Sandozanidae (Sharma and Giribet, 2009) which has a *scutum completum*, as do two of the new fossils described here (see below). The large and often spiny pedipalps and two claws on tarsi III–IV seen in all the fossils further distinguish them from members of other harvestmen suborders. Somatic characters used to diagnose specimens consist of the overall habitus, ocularium (eye tubercle), chelicerae, pedipalps, and legs. Strong sexual dimorphism, intraspecific variability and ontogenetic differences within laniatores (see Discussion) are further impediments to classification. Given these challenges the familial affinities proposed here are in some cases tentative, and in general we favour a conservative approach towards the creation of new taxa.

Family Tithaeidae Sharma and Giribet, 2011

**Remarks.** MB.A. 4308 (Fig. 1A–D) is interpreted as an adult because of its relatively high tarsomere count and the absence of typical juvenile structures like an arolium on tarsi III and IV (Šilhavý, 1946; Muñoz-Cuevas, 1971). The habitus of this specimen’s body, pedipalps, and chelicerae resembles the Southeast Asian families Petrobunidae and Tithaeidae, which share a pear-shaped body, armed pedipalps, relatively small chelicerae and two simple claws on tarsi III–IV. Petrobunidae can be excluded due to the absence of the following characters: a median ocularial tubercle, arcuate femur III, and a possible sexually dimorphic leg IV (with an enlarged, often spined trochanter in males). A large ocularium close to the anterior margin in the fossil (Fig. 1C) resembles the condition in a few living species of Tithaeidae; e.g. *Tithaeus rubidus* (Suzuki, 1969) formerly in *Metatithaeus*, but see Schmidt et al. (2019). They usually bear a

low ocularium far removed from the anterior margin (Sharma and Giribet, 2011; Schmidt et al., 2019), in addition to a leg-to-body length ratio close to that observed in the specimen. Furthermore, Petrobunidae have a count of three tarsomeres in leg I, whereas Tithaeidae have a count of five tarsomeres like the amber fossil (Fig. 1C: inset). Given that most somatic characters are consistent with modern members of Tithaeidae the fossil is placed here and represents the oldest record of the family.

Genus *Ellenbergellus* gen. nov.

urn:lsid:zoobank.org:act:C7050192-1D64-4799-8DF4-632B85CF5409.

*Type species. Ellenbergellus tuberculatus* gen. et sp. nov.

*Etymology.* Named after Sieghard Ellenberger, who kindly donated the holotype from his private collection to the Museum für Naturkunde, Berlin. Gender masculine.

*Diagnosis.* Body pear-shaped, dorsal segments fused into *scutum magnum*. Mesotergum and opisthosomal tergites armed with belts of tubercles at the posterior boundary of each segment. Ocularium large, dome-like, lacking spines or ornamentation, located near anterior margin of prosoma. Chelicerae small and unarmed. Pedipalps short but robust, with spinose trochanter and patella, at least three large ventral setiferous tubercles on femur, and three pairs of setiferous tubercles on tibia and tarsus. Pedipalpal claw longer than tarsus. Legs moderately long (leg II longest) and somewhat granulated, especially on ventral surfaces of trochanters, femora and patellae. Tarsi III–IV with simple double claws.

*Ellenbergellus tuberculatus* gen. et sp. nov.

urn:lsid:zoobank.org:act:861A3729-3D48-4053-879E-2ADAEEECF02.

*Holotype.* MB.A. 4308, ex coll. Sieghard Ellenberger.

*Type-locality.* Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

*Etymology.* The specific epithet, derived from the Latin “*tuberculum*”, (hump, protuberance, or swelling), refers to the ornamentation of the opisthosoma.

*Diagnosis.* As for the genus.

*Description.* Body pear-shaped and covered with white dots, which may be preservational artefacts, L (length) 2.22, anterior W (width) 1.18, maximum posterior W 1.70. Dorsal segments fused into *scutum magnum*. Prosoma slightly granulated. Opisthosomal region covered by rows of tubercles at the posterior boundary of each segment (Fig. 1A and C). Large, smooth, dome-shaped ocularium located near anterior margin of prosoma (L 0.33, W 0.41), eye lenses not visible. Chelicerae small and only visible in dorsal view. Chelicera proximal segment L 0.41\*, smooth and projecting forward. Pedipalps relatively short, robust and partly desiccated. Pedipalpal trochanter with one large spine, femur with three large and one small setiferous tubercles ventrally, patella with at least one spine, tibia with at least three pairs of large setiferous tubercles and one small setiferous tubercle, tarsus with three pairs of setiferous tubercles. Armature is only visible on the right and more desiccated pedipalp in dorsal view. Pedipalp claw longer than tarsus and slightly curved. Pedipalp lengths: tr 0.22, fe 0.37, pa 0.17, ti 0.21, ta 0.17, cl 0.30, total (tr-ta) 1.14. Legs smooth except for granulation on patella, femur and trochanter, especially on the ventral side. Coxae triangular and partly visible in dorsal view. Coxa II bears a small projecting apophysis. Tarsi covered by small setae and subdivided into tarsomeres with one claw on tarsi I–II and two claws with two separate insertions on tarsi III–IV (Fig. 1A, inset). Tarsal formula: 5–6: 8–10: 5: 6. Leg lengths: Leg I tr 0.18, fe 0.74, pa 0.52, ti 0.54, mt 0.46\*, ta 0.59\*, total (tr-ta) 3.03; Leg II tr 0.22, fe 1.37, pa 0.52, ti 0.89, mt 1.07, ta 1.11, total (tr-ta) 5.18; Leg III tr 0.22, fe 0.63, pa 0.37, ti 0.67, mt 0.70\*, ta 0.67, total

(tr-ta) 3.26; Leg IV tr 0.29, fe 0.96, pa 0.44, ti 0.85, mt 1.22, ta 0.81, total (tr-ta) 4.57.

Ventral region partly obscured by crystalline growths. Genital operculum subtriangular, closed, typical of most Laniatores. Sternites 4–9 tuberculate, each with recurved anterior and posterior borders; widths: 4, 1.65; 5, 1.50; 6, 1.42; 7, 1.29; 8, 1.08; 9, 0.83. Anal operculum sub-elliptical and tuberculate, L 0.09, W 0.42.

Family Mesokanidae fam. nov.

urn:lsid:zoobank.org:act:EDBC8770-C257-4503-930F-A187B237FC62.

*Etymology.* Refers to the modern family Sandokanidae Özdikmen & Kury, 2007 and the Mesozoic record of the fossil.

*Diagnosis.* Dorsal tergites fused into scutum completum. Opisthosoma smooth, divided into at least five tergal elements, all separated by a median groove. Ocularium low, located near anterior margin, with large lateral eyes. Chelicerae small and slender. Pedipalps relatively long, without armature. Pedipalp tarsus elongated. Legs relatively short and smooth, with a tarsomere count of 3:4:4:5. Tarsi III–IV bearing two simple Y-shaped claws with single insertion.

*Remarks.* MB.A. 4309 (Figs. 2A–D and 3A–B) can easily be distinguished from the other amber laniatores by the presence of a *scutum completum* (Fig. 2A and C) which is only found today among laniatores in members of the Southeast Asian family Sandokanidae. The habitus of this fossil, particularly the body and unadorned pedipalps with an elongated tarsus (Fig. 2B) are similar to those of extant Sandokanidae. However, the legs of the fossil differ by a higher tarsomere count (3:4:4:5), whereas sandokanids have a reduced tarsomere count in the range from 1–2: 1–2: 1–3: 1–3. The synapomorphic swollen feet (tarsi), found in all living sandokanid genera, is also missing in the fossil. Additionally, sandokanids, as members of the infraorder Grassatores, have tarsi III–IV bearing two claws with separate insertions (Sharma & Giribet, 2009; Gainett et al., 2018). The fossil described here appears to have two simple, Y-shaped claws possibly with a single insertion (Fig. 3B), which is a typical character for the other laniatores infraorder Insidiatores. Nevertheless, we cannot exclude the possibility that the claw morphology observed in MB.A. 4309 is an artefact of preservation. Given that important characteristics (i.e. a *scutum completum* combined with the tarsomere count and claw morphology alluded to above) do not fit in a modern family we propose the establishment of a new family, Mesokanidae fam. nov. as a possible stem-group to Sandokanidae.

Genus *Mesokanus* gen. nov.

urn:lsid:zoobank.org:act:D6D8C40C-0822-47DD-B22E-729A24EAE53D.

*Type and only species. Mesokanus oehmkuehnlei* gen. et sp. nov (by monotypy).

*Etymology.* Refers to the family name Mesokanidae.

*Diagnosis.* As for the family.

*Mesokanus oehmkuehnlei* gen. et sp. nov.

urn:lsid:zoobank.org:act:D32DBD32-03CE-4A35-894A-D4758B9495E0.

*Holotype.* MB.A. 4309, ex coll. Christoph Öhm-Kühnle.

*Type-locality.* Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

*Etymology.* After Christoph Öhm-Kühnle, who kindly donated the holotype from his private collection to the Museum für Naturkunde, Berlin. Gender masculine.

*Diagnosis.* As for the family.

*Description.* Body pear-shaped, L 2.40, anterior W 1.11, maximum posterior W 2.10. Prosoma partly obscured by a planar fracture.



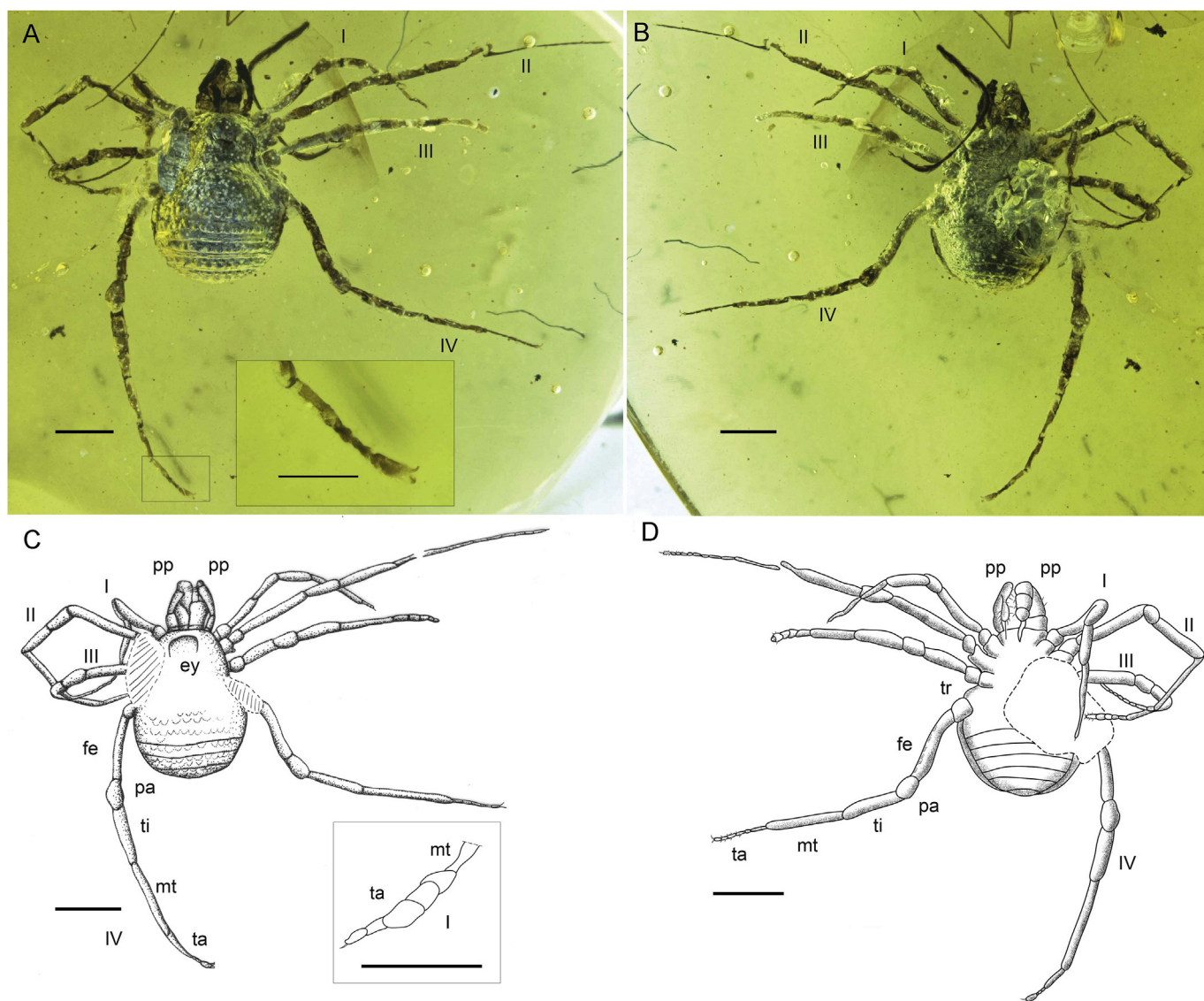
Anterior prosomal region slightly granulated. Dorsal tergites fused into *scutum completum*. Opisthosoma smooth, divided into at least five tergal elements, all uniquely separated by a median groove (Fig. 2A and C). Ocularium low (L 0.17, W 0.24), located near anterior margin. Ocularium bears a small horn between large lateral eyes. Chelicerae small and slender. Chelicera proximal segment L 0.65, smooth and projecting forward; cheliceral hand L 0.20, with fixed and movable fingers (L 0.15). Pedipalps long and smooth (without large spines) except for trochanter and femur which are covered with numerous short thickened setae. Pedipalpal claw shorter than elongated tarsus, slightly curved and slender. Pedipalp lengths: tr 0.11\*, fe 0.53\*, pa 0.40\*, ti 0.30, ta 0.67, cl 0.15, total (tr-ta) 2.01. Legs relatively short (leg IV longest) covered ventrally with thickened setae on the coxae and femora whereas the remaining podomeres are covered with thin (sensory) setae. Leg II bears large raptorial spine ventrally on femur (Fig. 2C). Coxae partly visible in dorsal view. Coxae I–II showing large apophyses prolaterally. Tarsi subdivided into tarsomeres with one claw on tarsi I–II and two simple Y-shaped claws with a single insertion on tarsi III–IV (Fig. 3B).

Tarsal formula: 3: 4: 4: 5. Leg lengths: Leg I tr 0.26, fe 0.36\*, pa 0.39, ti 0.55, mt 0.72, ta 0.46, total (tr-ta) 2.74; Leg II tr 0.38, fe 0.80, pa 0.51, ti 0.83, mt 1.04, ta 0.60\*, total (tr-ta) 4.16; Leg III pa 0.22\*, ti 0.52, mt 0.93, ta 0.44, total (pa-ta) 2.11; Leg IV tr 0.22, fe 1.17\*, pa 0.64, ti 0.72, mt 1.34, ta 0.43, total (tr-ta) 4.52.

Genital operculum subtriangular, located between coxae IV (L 0.28, W 0.24). Sternite 2/3 trapezoidal broadening from genital operculum to distal ends of coxae IV. Sternites 4 to 9 each with recurved anterior and posterior borders; width: 4, 1.81\*; 5, 1.94\*; 6, 1.80\*; 7, 1.46\*; 8, 1.17\*; 9, 0.80\*, respectively. Anal operculum smooth and sub-elliptical in outline, L 0.19, W 0.50\*.

Laniatores indet.

**Remarks.** MB.A. 4310 (Fig. 4A–D) is a juvenile Laniatores, due to the presence of a very low tarsomere count (1:1:2:2) and an arolium on claws III–IV (Fig. 4B: inset). The slightly elevated ocularium, mostly smooth pedipalps and small chelicerae support sandokanid affinities, as does the presence of a *scutum completum* (Fig. 4A). However, the presence of an arolium and the long and strongly spined



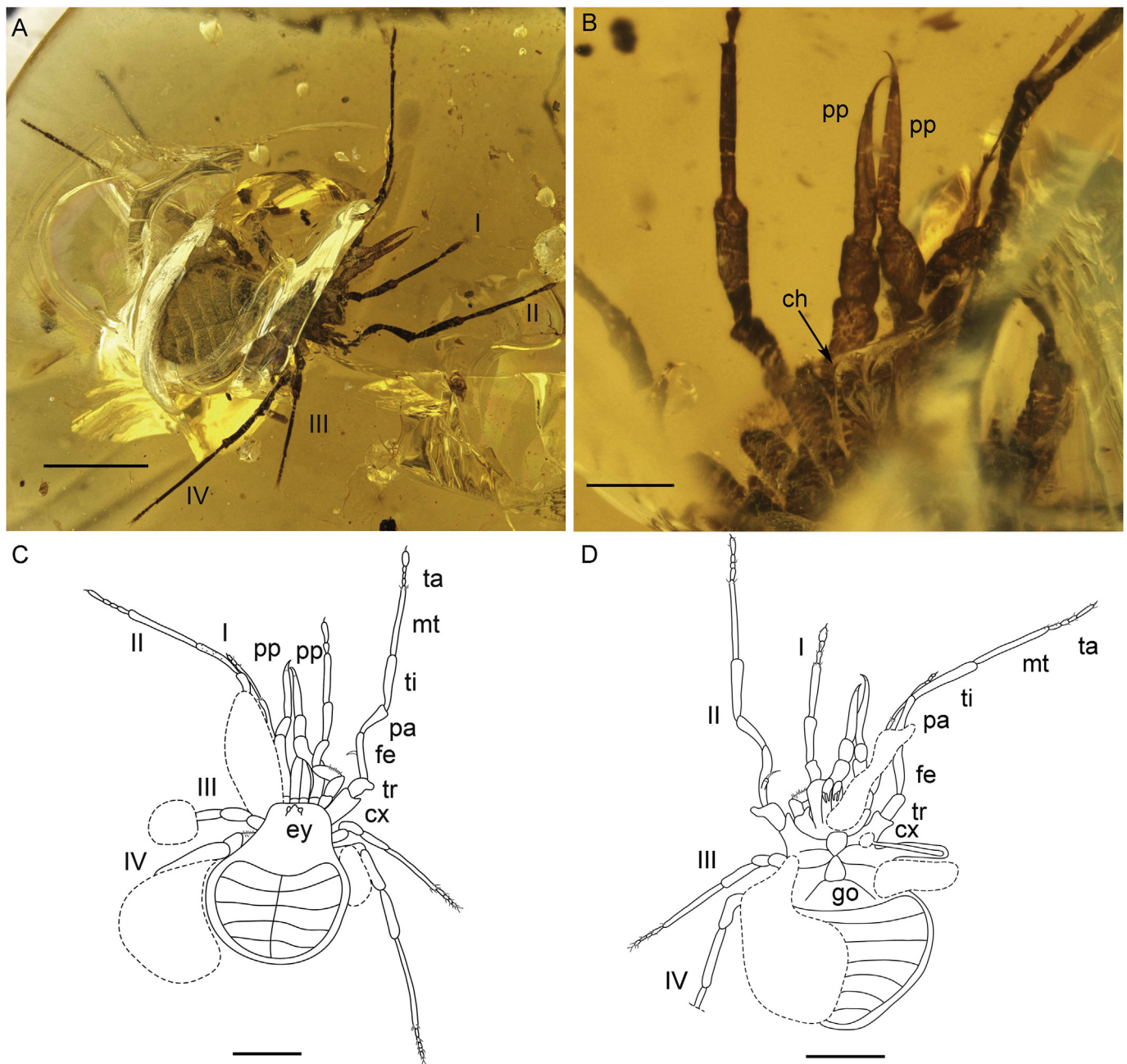
**Fig. 1.** *Ellenbergellus tuberculatus* gen. et sp. nov. (Tithaeidae), holotype: MB.A. 4308. A. Dorsal overview; inset shows claws of leg IV. B. Ventral overview. C–D. Camera lucida drawings of the same; inset shows leg I tarsomeres. Abbreviations: ey, eyes; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm (insets 0.5 mm).

legs (Fig. 4B and D) are not known from modern (adult) sandokanids, which mostly express short, stout and smooth legs. Formal assignment of the fossil to a given family is difficult as most of the characters could change during growth. This enigmatic specimen is described and figured here for completeness.

**Material.** MB.A. 4310, ex coll. Patrick Müller BUB2198. From Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

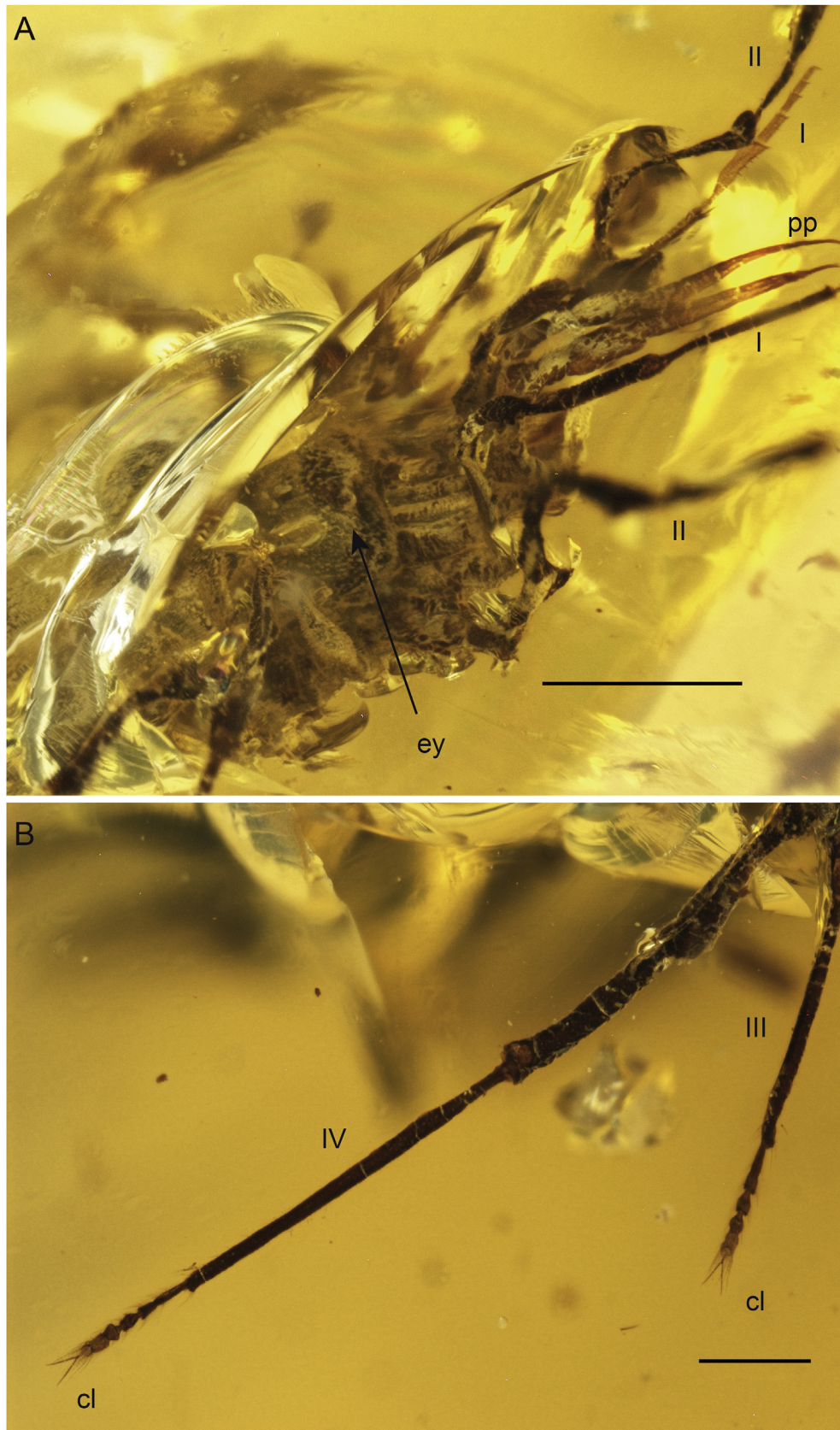
**Description.** Body pear-shaped and completely smooth, L 1.26\*, anterior W 1.00, maximum posterior W 1.44. Dorsal tergites I–VIII are fused into a *scutum completum*, with a single opisthosomal plate and several grooves. Ocularium slightly elevated (L 0.12, W 0.25), located near the anterior border. Eyes lateral on ocularium. Middle

of ocularium bears few small setae. Chelicerae short and robust, without spines. Chelicera proximal segment L 0.35; cheliceral hand L 0.15 with plate-like fixed and movable finger (L 0.17). Movable fingers show grooves on inner margin. Pedipalps long, robust and covered with few tubercles and smaller setae. Tibiae bearing large cone-shaped apophysis, proximal. Pedipalp claw sickle-shaped and longer than tarsus. Pedipalp length: tr 0.18, fe 0.34, pa 0.15, ti 0.11, ta 0.15, cl 0.32, total (tr–ta) 0.93. Legs long (leg IV longest) and from femora completely covered with tubercles and spiny setae. Coxae and trochanters mostly smooth, with sparse tubercles or larger spines on coxae II–III. Tarsi not subdivided except tarsi III and IV. Tarsi I and II with one claw, Tarsi III and IV with two claws and an arolium between them (Fig. 4D: inset). Tarsal formula: 1:1:2:2. Leg

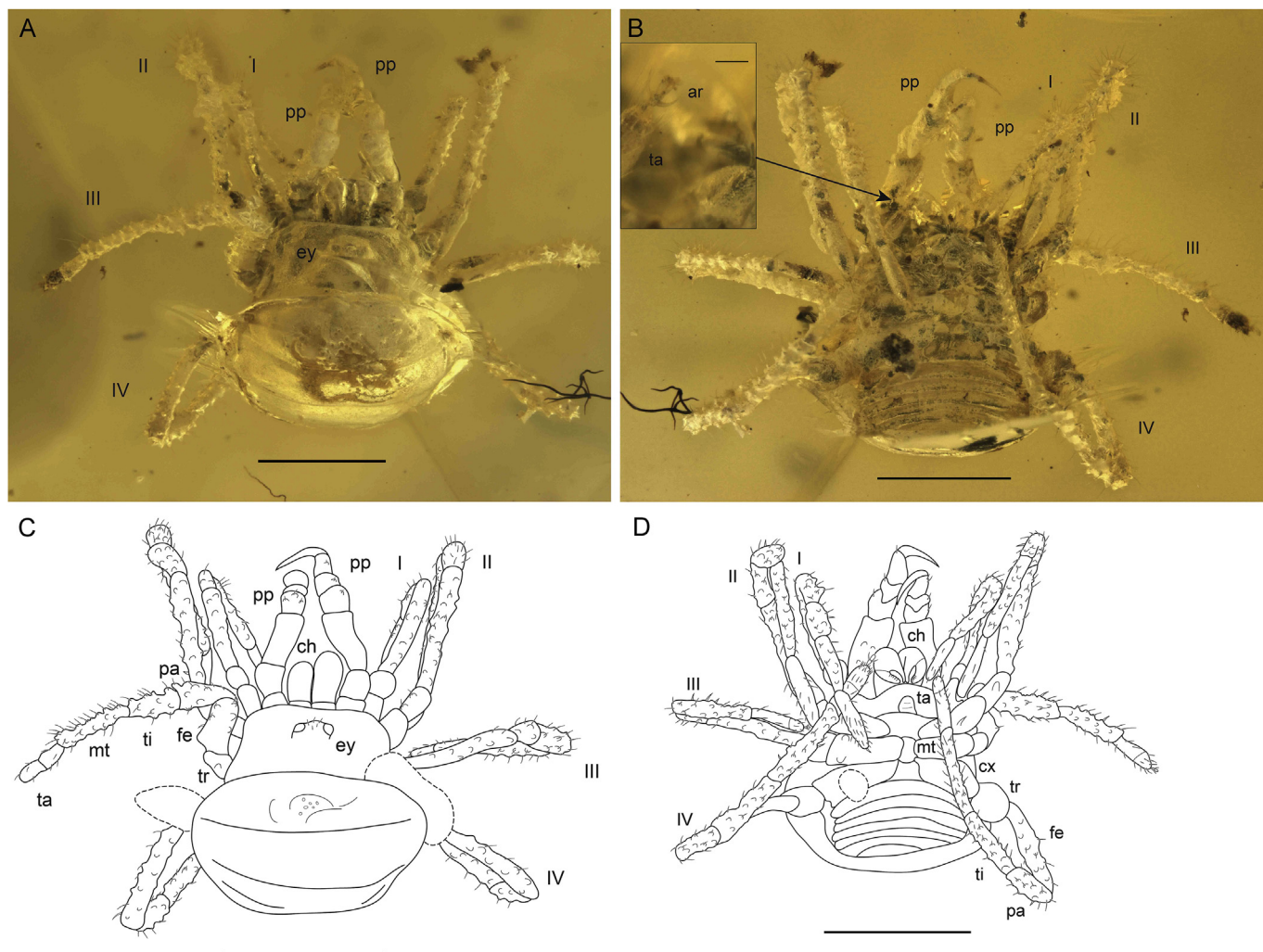


**Fig. 2.** *Mesokanus oehmkuehnei* gen. et sp. nov. (Mesokanidae fam. nov.), holotype: MB.A. 4309. A. dorsal overview. B. Ventral details of the chelicerae and pedipalps. C–D. Camera lucida drawings of dorsal and ventral surfaces. Abbreviations: ch, chelicerae; cx, coxa; ey, eyes; fe, femur; go, genital operculum; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm (A, C–D) and 0.5 mm (B).





**Fig. 3.** Details of *Mesokanus oehmkuehnei* gen. et sp. nov. (Mesokanidae fam. nov.), holotype: MB.A. 4309. A. Dorso-lateral view including eyes. B. Legs III and IV with their claws. Abbreviations: cl, claw; ey, eyes; pp, pedipalps; legs numbered from I–IV. Scale bars equal 1 mm (A) and 0.5 mm (B).



**Fig. 4.** Laniatores indet., MB.A. 4310. A. dorsal overview. B. Ventral overview; inset shows arolium on leg IV. C–D. Camera lucida drawings of the same. Abbreviations: ar, arolium; ch, chelicerae; cx, coxa; ey, eyes; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm.

lengths: Leg I cx 0.18\*, tr 0.15, fe 0.55\*, pa 0.20\*, ti 0.25, mt 0.38, ta 0.44, total (cx–ta) 2.15; Leg II cx 0.50, tr 0.22, fe 0.75, pa 0.21, ti 0.21\*, mt 0.63, ta 0.48, total (cx–ta) 3.00; Leg III cx 0.50, tr 0.12, fe 0.60\*, pa 0.27, ti 0.32, mt 0.48, ta 0.3, total (cx–ta) 2.59; Leg IV cx 0.54, tr 0.20, fe 0.63, pa 0.34, ti 0.49, mt 0.60, ta 0.36, total (cx–ta) 3.16.

Genital operculum rounded, located between coxae III (L 0.18, W 0.10). Sternite 2/3 sub-trapezoidal broadening from genital operculum to distal ends of coxae IV. Sternites 4 to 9 each with slightly recurved anterior and posterior borders, width: 4, 0.95; 5, 0.92; 6, 0.92; 7, 0.92; 8, 0.85; 9, 0.65, respectively. Anal operculum elliptical, L 0.08, W 0.43.

Family Epedanidae Sørensen, 1886.

**Remarks.** CNU-SPI-MA 2015014 (Fig. 5A–D) is an adult, as inferred from its high tarsomere count, especially on leg II (thirteen tarsomeres: Fig. 5C). Pedipalps lacking strong armature, the small chelicerae and the absence of large body processes suggest that this is a female. In general, this fossil is very unusual compared to most modern Asian Laniatores families (e.g. Assamiidae, Epedanidae, Podoctidae), which are often heavily armed with megaspines or tubercles. By contrast, the amber fossil bears only sparse spines or thorns (Fig. 5A–C) and additional granulation. Nevertheless, the

spine between the eyes, the elongate pedipalps, and the unique claw pattern (Fig. 5D: claws III and IV differ markedly from one another) support referral to Epedanidae. This family is known for its extremely diverse tarsal claws (Kury, 2007) including sometimes secondary mesal processes as observed in claw IV of the fossil (Fig. 5D). Furthermore, members of the epedanid subfamily Dibuninae bear separated eye lenses far removed from the anterior margin together with very long pedipalps and legs, whereas members of other subfamilies additionally exhibit spines between the eyes (Pinto-da-Rocha and Giribet, 2007). These characteristics are consistent with the amber fossil. For the reasons given above, the fossil is placed in Epedanidae and represents the second record of the family from Burmese amber following the laniatores described by Selden et al. (2016).

Genus *Biungulus* gen. nov.

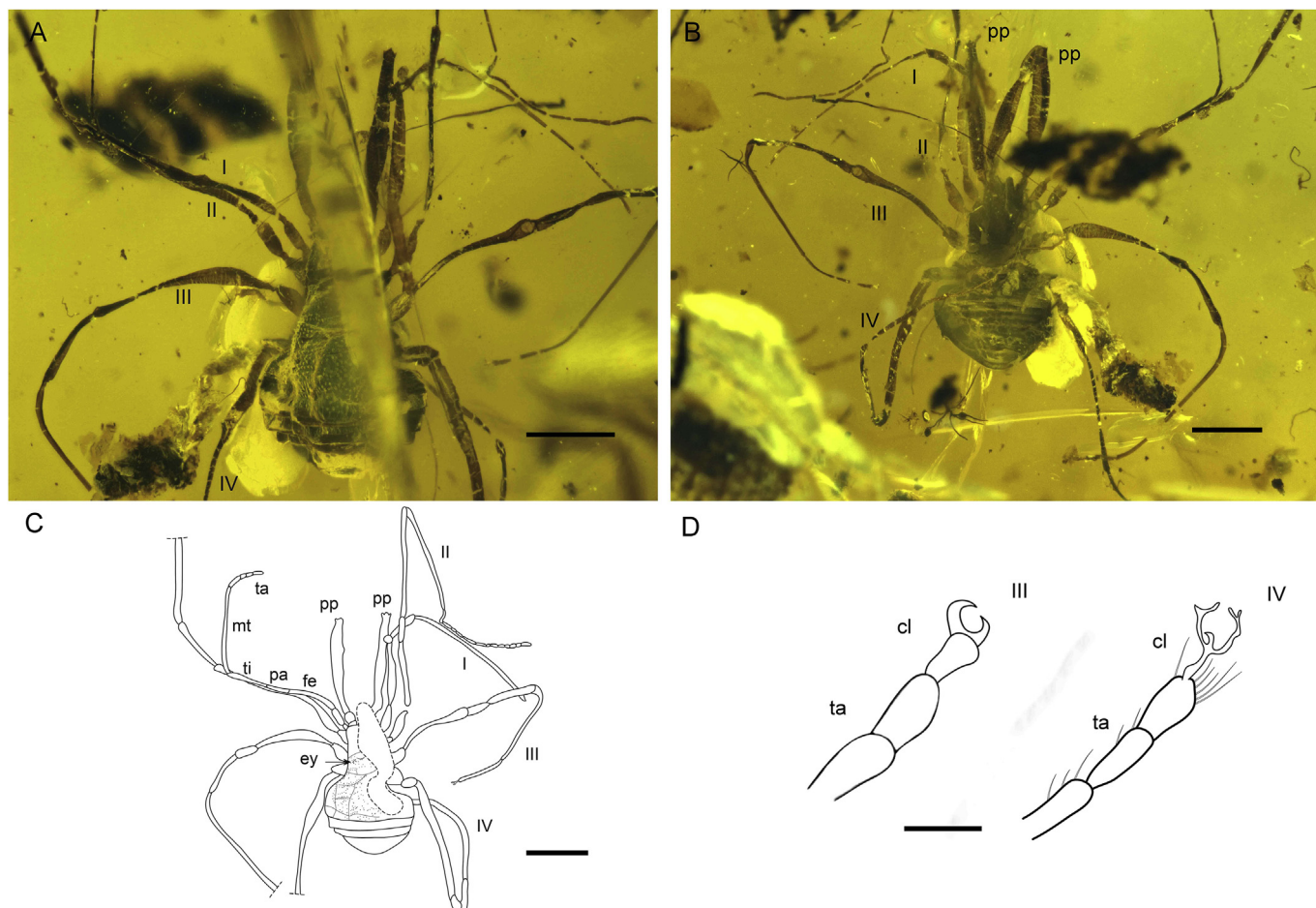
urn:lsid:zoobank.org:act:AAE0D689-D064-4A80-920B-6F5530230FC3.

**Type species.** *Biungulus xiai* gen. et sp. nov., designated herein.

**Etymology.** Named from the Latin words *bi-* (two) and *ungulus* (claw), which refer to the different claws found on legs III and IV.

**Diagnosis.** Body pear-shaped, dorsal segments fused into scutum magnum plus three short opisthosomal tergites. Prosoma and





**Fig. 5.** *Biungulus xiai* gen. et sp. nov. (Epedanidae), holotype: CNU-SPI-MA 2015014. A. Dorsal overview. B. Ventral overview. C. Camera lucida drawing. D. Detailed comparative drawings of claws III and IV. Abbreviations: cl, claw; ey, eyes; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; legs numbered from I–IV. Scale bars equal 1 mm (A–C) and 0.1 mm (D).

anterior opisthosoma strongly granulated. Ocularium small, far removed from anterior margin with a sickle-shaped spine on top. Chelicerae unarmed, very small and slender. Pedipalps very long and granulated with sparse needle-like spines on the tarsi and femora. Pedipalpal claw much shorter than tarsus, robust and curved. Legs very long (leg II longest) and smooth. Tarsi subdivided into tarsomeres with one claw on tarsi I–II; two claws with single insertion on tarsus III; and one claw with two secondary processes, one mesal and one ectal, on tarsus IV (Fig. 5D). Tarsal formula: 4:13:4:4. Leg lengths: Leg I tr 0.31, fe 0.79, pa 0.36, ti 0.66, mt 1.41, ta 0.61, total (tr–ta) 4.14; Leg II tr 0.25, fe 1.82, pa 0.44, ti 1.79, mt 1.72, ta 1.70, total (tr–ta) 7.72; Leg III tr 0.34, fe 1.23, pa 0.38, ti 0.74, mt 1.44, ta 0.80, total (tr–ta) 4.93; Leg IV tr 0.24, fe 1.92, pa 0.25, ti 0.56, mt 1.52\*, ta 1.37\*, total (tr–ta) 6.11.

***Biungulus xiai* gen. et sp. nov.**

urn:lsid:zoobank.org:act:EBC86159-8527-4161-A513-01D1D3F8002B.

**Holotype.** CNU-SPI-MA 2015014, ex coll. Xia Fangyuan.

**Type-locality.** Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

**Etymology.** After Xia Fangyuan, who kindly donated the specimen to the Capital Normal University Beijing, China. Gender masculine. **Diagnosis.** As for the genus.

**Description.** Body pear-shaped, L 2.13, anterior W 0.61, maximum posterior W 1.42. Dorsal segments fused into *scutum magnum* with three visible and relatively smooth opisthosomal tergites. Prosoma and anterior opisthosoma strongly granulated. Ocularium small, far removed from anterior margin with a sickle-shaped spine on top. Chelicerae smooth, very small and slender. Pedipalps very long and

granulated with sparse needle-like spines on the tarsi and femora (Fig. 5A–C). Tips of the femora also bear some short tubercles. Pedipalpal claw much shorter than tarsus, robust and curved. Pedipalpal length: tr 0.17, fe 1.53, pa 0.82, ti ?, ta 1.18, total (tr–ta) 3.92. Legs very long (leg II longest) and smooth. Tarsi subdivided into tarsomeres with one claw on tarsi I–II; two claws with single insertion on tarsus III; and one claw with two secondary processes, one mesal and one ectal, on tarsus IV (Fig. 5D). Tarsal formula: 4:13:4:4. Leg lengths: Leg I tr 0.31, fe 0.79, pa 0.36, ti 0.66, mt 1.41, ta 0.61, total (tr–ta) 4.14; Leg II tr 0.25, fe 1.82, pa 0.44, ti 1.79, mt 1.72, ta 1.70, total (tr–ta) 7.72; Leg III tr 0.34, fe 1.23, pa 0.38, ti 0.74, mt 1.44, ta 0.80, total (tr–ta) 4.93; Leg IV tr 0.24, fe 1.92, pa 0.25, ti 0.56, mt 1.52\*, ta 1.37\*, total (tr–ta) 6.11.

Ventral prosomal region strongly desiccated. Opisthosomal sternites 4–9 each with straight anterior and posterior borders; width: 4, 1.64; 5, 1.58; 6, 1.53; 7, 1.50; 8, 1.39; 9, 1.03. Anal operculum subtrapezoidal in outline, L 0.19, W 0.55.

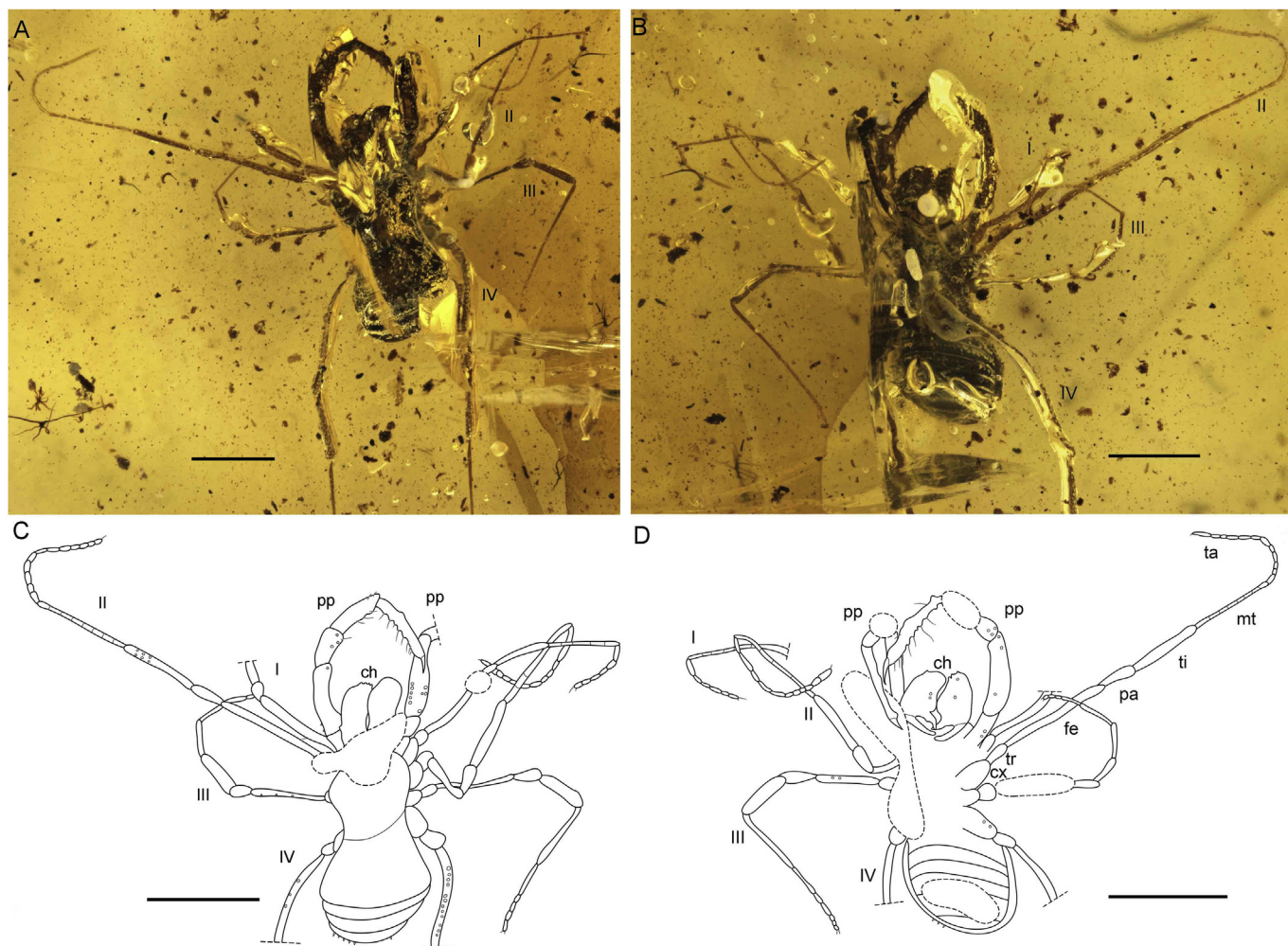
**Genus *Gigantocheles* gen. nov.**

urn:lsid:zoobank.org:act:B646BD1C-8DEC-4977-8E33-AA56E82FDEDE.

**Type species.** *Gigantocheles nilsi* gen. et sp. nov, designated herein.

**Etymology.** Named for its very large chelicerae.





**Fig. 6.** *Gigantocheles nilsi* gen. et sp. nov. (Epedanidae), holotype: MB.A. 4311. A. Dorsal overview. B. Ventral overview. C–D. Camera lucida drawings of the same. Abbreviations: ch, chelicerae; cx, coxa; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 1 mm.

**Diagnosis.** Body hourglass-shaped and slightly tuberculate, dorsally. Dorsal segments fused into *scutum magnum* and three visible opisthosomal tergites. Chelicerae very large, robust and covered with tubercles and rows of spines, with dentition visible on the cheliceral hand. Fixed and movable finger elongated. Pedipalps very long. Trochanters, patellae and femora tuberculate, with few thorns. Tarsi and tibiae bearing several long, needle-like spines. Pedipalp claw much shorter than tarsus, slightly curved. Legs very long (leg II longest) and tuberculate. Metatarsi II subdivided into 8 pseudosegments. Tarsi III bear two simple claws with two separate insertions. Sternites covered with row of tubercles.

**Remarks.** MB.A. 4311 (Fig. 6A–D) is probably a male as it has very large chelicerae and pedipalps and a high tarsomere count (Fig. 6C–D). The habitus clearly links this species to modern representatives of the Southeast Asian family Epedanidae. This family exhibits large, somewhat spiny, and often sexually dimorphic chelicerae with a curved mobile digit that does not meet the second digit's ventral margin when closed; long, spinose pedipalps with a tarsal claw as long as the tarsus; and elongate legs with a high tarsomere count. The specimen is clearly not an assamiid; a family in which enlarged chelicerae also sometimes occur. In Assamiidae, pedipalps tend to be relatively short with respect to the chelicerae and are characterized by a row of small tubercles on the ventral surface of the pedipalpal femur, giving it a serrated appearance.

MB.A. 4311's appearance clearly supports a referral to Epedanidae, as the third representative of this family from Burmese amber.

***Gigantocheles nilsi* gen. et sp. nov.**

urn:lsid:zoobank.org:act:006019DD-7973-4488-8673-3D6BA8EA1610.

**Holotype.** MB.A. 4311, ex coll. Patrick Müller, BUB3115.

**Type-locality.** Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

**Etymology.** Named after the son, Nils, of Patrick Müller, who made this material available for study. Gender masculine.

**Diagnosis.** As for the genus.

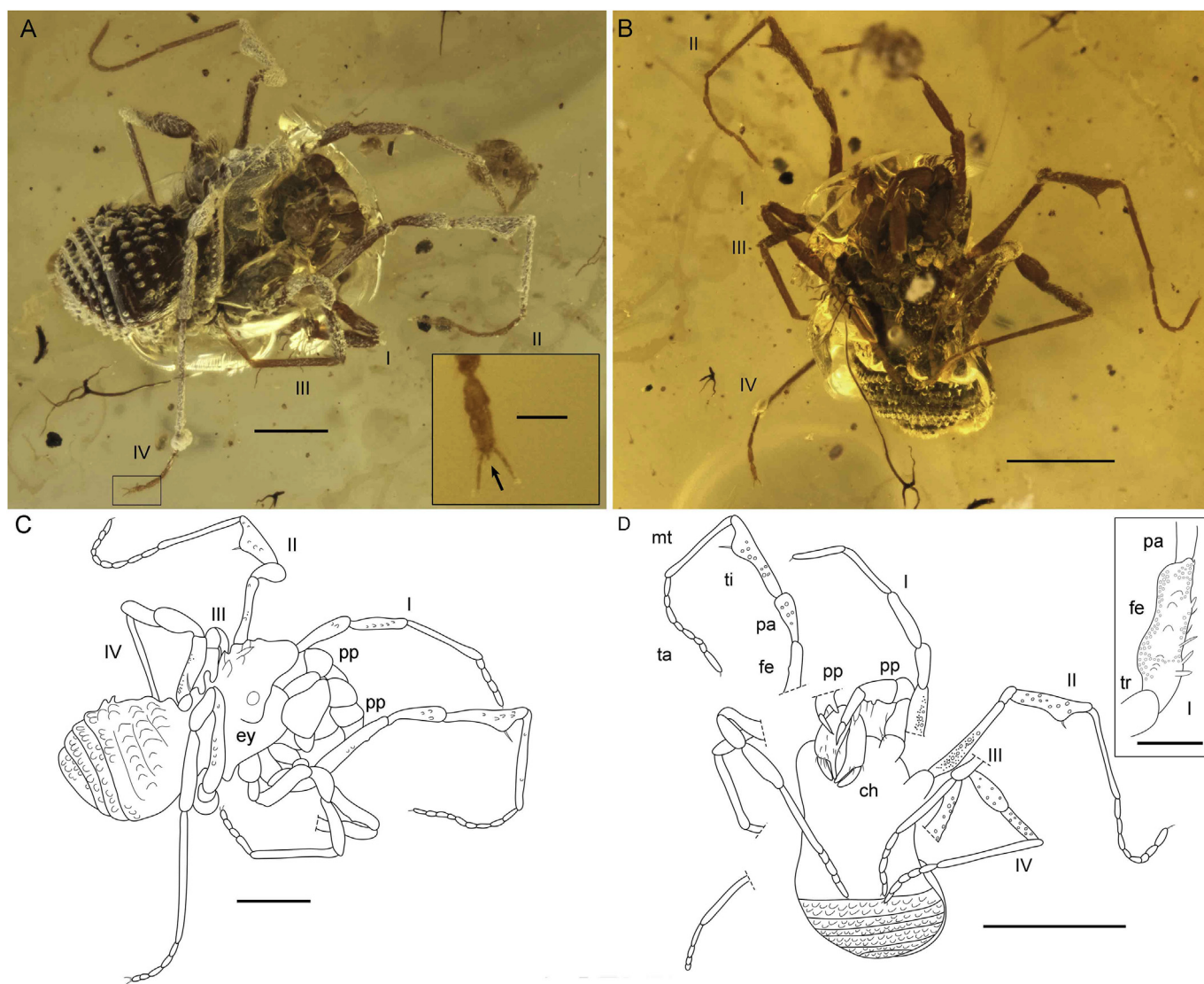
**Description.** Body hourglass-shaped (Fig. 6C) and dorsally somewhat tuberculate, L 1.63, anterior W 0.71, maximum posterior W 0.98. Dorsal segments fused into *scutum magnum* plus three opisthosomal tergites. Last tergite covered with small spines. Prosoma and opisthosoma separated by a narrowing. Anterior prosomal region and ocularium obscured by crystalline growths. Chelicerae very large and robust (Fig. 6D). Chelicera proximal segment L 0.62; cheliceral hand L 0.45 covered with tubercles, rows of spines and thorns, bears elongated fixed and movable finger (L 0.24). Pedipalps very long (Fig. 6A and C). Trochanters, patellae and femora tuberculate, with a few thorns. Tarsi and tibiae bearing several long needle-like spines. Pedipalp claw much shorter than tarsus, slightly

curved. Pedipalp length: tr 0.17, fe 0.64, pa 0.33, ti 0.47, ta 0.62, cl 0.15, total (tr–ta) 2.23. Legs very long (leg II longest) and tuberculate. Leg IV equivocal from the metatarsus. Leg coxae partly visible in dorsal view. Metatarsi II subdivided into at least eight pseudo-segments (Fig. 6C–D). Tarsi I–III additionally subdivided into tarsomeres, with one claw on tarsi I–II and two simple claws on tarsi III. Tarsal formula: 6:12:5:?. Leg length: Leg I cx 0.20, tr 0.11, fe 0.57, pa 0.27, ti 0.49, mt 0.64, ta 0.54, total (cx–ta) 2.82; Leg II cx 0.30, tr 0.20, fe 0.96, pa 0.30, ti 0.62, mt 0.70, ta 1.01, total (cx–ta) 4.09; Leg III cx 0.17, tr 0.14, fe 0.69, pa 0.28, ti 0.44, mt 0.61, ta 0.64, total (cx–ta) 2.97; Leg IV cx 0.33, tr 0.19, fe 1.05\*, pa 0.36, ti 0.83. Ventral prosomal region partially obscured by fractures and bubbles. Opisthosomal sternites 4 to 9 each with curved anterior and posterior borders; width: 4, 1.15; 5, 1.11; 6, 1.09; 7, 1.09; 8, 0.97; 9, 0.75. At least sternites 4 to 7 are each covered with row of tubercles. Anal operculum sub-trapezoidal, L 0.09, W 0.44.

Family Pyramidopidae Sharma et al., 2011.

**Remarks.** MB.A. 4312 (Fig. 7A–D) is probably an adult, having large pedipalps and chelicerae, and a high tarsal formula (4: 8–9: 4–5:

5). In addition, the swollen and armed tibia II (Fig. 7D) suggests that this specimen is a male. The habitus resembles members of modern families such as Podoctidae and Pyramidopidae, due to the presence of a large dome-like ocularium at the anterior margin (Fig. 7C). The fossil also shares this affinity with the modern species *Ausulus minutus* Roewer, 1927 Fig. 1, which was erroneously described as a phalangodid. Podoctidae are known for their large number of morphological synapomorphies like a cheliceral comb often found on the fixed and movable fingers, chained tubercular ridges on the dorsal scutum, an interocular mound and a strongly spined leg I femur found in most species (Sharma et al., 2017; Kury and Machado, 2018). All of these characters are absent from the amber fossil, therefore Podoctidae can be excluded. The form of the chelicerae (Fig. 7D), the tarsal formula within a range from 3–5: 5–20: 4–5: 5–6, the armature of the ocularium, the opisthosomal rows of tubercles and the swelling of tibia II as observed in the amber fossil are consistent with members of the family Pyramidopidae. However, in extant species the pedipalps are covered with megaspines, whereas the fossil bears smaller spines and setiferous tubercles on the pedipalps. The oversized coxae IV,



**Fig. 7.** *Protopyramidops nalaе* gen. et sp. nov. (Pyramidopidae), holotype MB.A. 4312. A. Dorso-lateral overview; inset shows claws IV with arrowed tarsal process. B. Ventral overview. C–D. Camera lucida drawings of the same; inset shows leg spination on femur I. Abbreviations: ch, chelicerae; ey, eyes; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; legs numbered from I–IV. Scale bars equal 1 mm (A), 0.1 mm (inset A) and 0.25 mm (inset D).



typical for many modern specimens, is also missing in the fossil (Sharma et al., 2011). On balance, the specimen is provisionally placed in Pyramidopidae.

Genus **Protopyramidops** gen. nov.

urn:lsid:zoobank.org:act:D496C611-02BE-4C5F-AC8A-011B57FCDC9A.

*Type species.* *Protopyramidops nalae* gen. et sp. nov., designated herein.

*Etymology.* From the Greek ‘proto’ (first or earliest), combined with the modern genus *Pyramidops*.

*Diagnosis.* Body pear-shaped, dorsal segments fused into *scutum magnum* with three short opisthosomal tergites. Opisthosomal region covered by rows of large tubercles. Prosomal region dominated by very large ocularium forming a horn, with scale-like processes on top. Chelicerae long and robust, covered by sparse setae, especially on cheliceral hand. Pedipalps robust, relatively long and covered mostly by setiferous tubercles and few spines. Pedipalp claw shorter than tarsus and slightly curved. Legs long (leg II longest) and tuberculate. Leg I bears 4–5 small spines on femora.

Tibiae II triangular and swollen distally, bearing a large ventral spine. Tarsi III–IV with tarsal process and two simple claws, with two separate insertions. Sternites 4 to 8 and anal operculum densely covered with rows of tubercles.

***Protopyramidops nalae*** gen. et sp. nov.

urn:lsid:zoobank.org:act:FE96641D-E347-428F-972A-D12AA09D55C1.

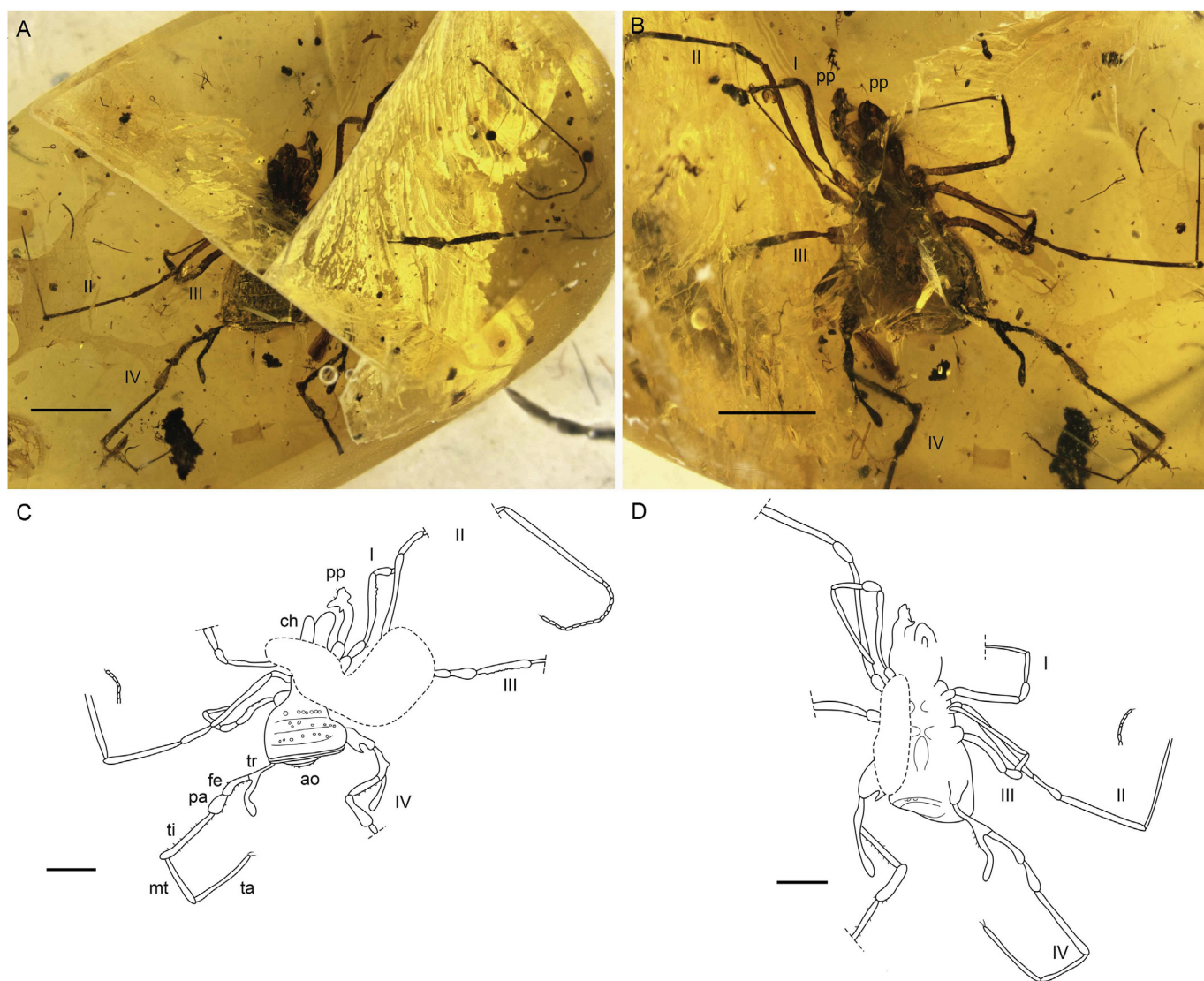
*Etymology.* Named after the daughter, Nala, of Patrick Müller who made this material available for study. Gender feminine.

*Diagnosis.* As for the genus.

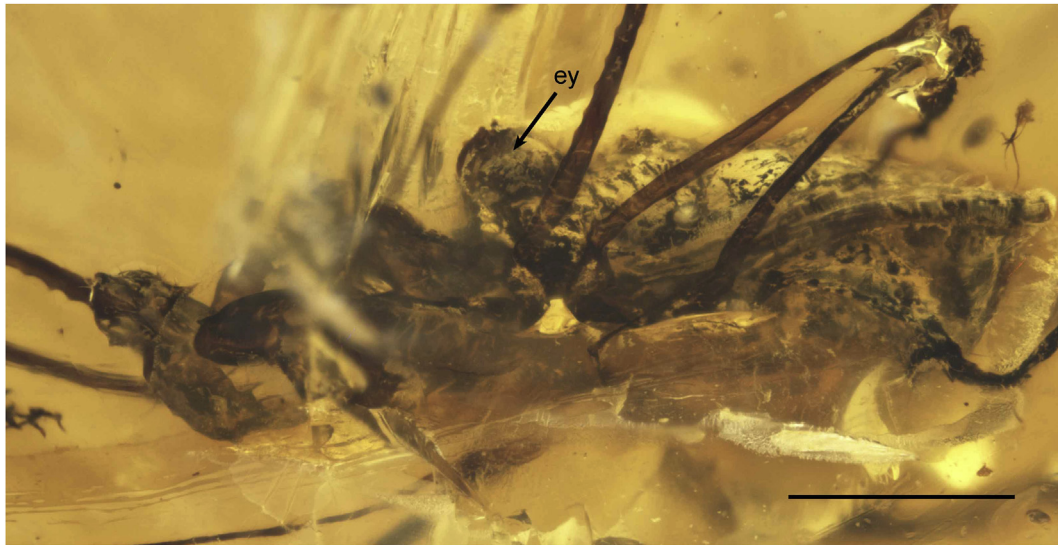
*Holotype.* MB.A. 4312, ex coll. Patrick Müller, BUB3112.

*Type-locality.* Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

*Description.* Body pear-shaped, L 1.44, anterior W 0.64, maximum posterior W 1.02. Dorsal segments fused into *scutum magnum* with three short opisthosomal tergites. Opisthosomal region covered by rows of large tubercles, especially along marginal borders of last three tergites. Prosomal region dominated by very large ocularium forming a horn, with scale-like processes on top (L 0.61, W 0.44).



**Fig. 8.** *Palaeobeloniscus thilolebi* gen. et sp. nov. (Beloniscidae), holotype MB.A. 4313. A. Dorsal overview. B. Ventral overview. C–D. Camera lucida drawings of the same. Abbreviations: ao, anal operculum; ch, chelicerae; fe, femur; mt, metatarsus; pa, patella; pp, pedipalps; ta, tarsus; ti, tibia; tr, trochanter; legs numbered from I–IV. Scale bars equal 2 mm (A, B) and 1 mm (C, D).



**Fig. 9.** *Palaeobeloniscus thilolebi* gen. et sp. nov. (Beloniscidae), holotype MB.A. 4313. Lateral overview of body, including the elevated and rounded ocularium (arrowed). Abbreviation: ey, eye lens. Scale bar equals 1 mm.

Eye lenses at base of horn in lateral position (Fig. 7A and C). Chelicerae long and robust. Chelicera proximal segment obscured by crystalline growths; cheliceral hand L 0.40 covered by sparse setae, with smooth fixed and movable finger (L 0.21). Pedipalps robust, relatively long. Pedipalp femur with four large setiferous tubercles ventrally, patellae smooth, tibiae with at least two large setiferous tubercles and tarsi with at least one large and one small pair of spines. Pedipalp claw shorter than tarsus and slightly curved. Pedipalp length: tr 0.13, fe 0.45\*, pa 0.16, ti 0.23, ta 0.27, total (tr–ta) 1.24. Legs long (leg II longest) and tuberculate. Femora granulated on ventral side with 4–5 additional smaller spines on leg I. Tibiae II triangular and swollen distally, bearing a large ventral spine (Fig. 7B and D). Tarsi subdivided into tarsomeres, with one claw on tarsi I–II and two claws with two separate insertions on tarsi III–IV. Claw-like tarsal process located between the two claws on tarsi IV. Tarsal formula: 4: 8–9: 4–5: 5. Leg length: Leg I fe 0.45, pa 0.33, ti 0.41, mt 0.50, ta 0.28, total (fe–ta) 1.97; Leg II tr 0.17, fe 0.82, pa 0.38, ti 0.62, mt 0.57, ta 0.78, total (tr–ta) 3.34; Leg III tr 0.09\*, fe 0.50, pa 0.19, ti 0.28, mt 0.56, ta 0.30, total (tr–ta) 1.92; Leg IV tr 0.09\*, fe 0.56, pa 0.37, ti 0.57, mt 0.74, ta 0.45, total (tr–ta) 2.78. Ventral prosomal region obscured by bubbles and detritus. Opisthosomal sternites 4 to 8 each with relatively straight anterior and posterior borders; width: 4, 0.97; 5, 0.96; 6, 0.90; 7, 0.77; 8, 0.52, respectively. Sternites are densely covered with rows of tubercles. Anal operculum sub-elliptical and also covered with rows of tubercles, L 0.05, W 0.30.

Family Beloniscidae Kury et al., 2019.

**Remarks.** MB.A. 4313 (Figs. 8A–D and 9) appears to be an adult male beloniscid, as inferred from its trapezoidal, dorsoventrally flattened body, the high tarsomere count, the recurved femur IV, the processes of trochanter IV, and the relative size of the raptorial pedipalps. Characteristic here are the large apophyses on the leg IV trochanter (Fig. 8A and C), which, together with this habitus, can be found in several modern American and Asian families including Cosmetidae, Cranidae, Gonyleptidae, Phalangodidae, and Assamiidae. Of these, cosmetids are characterized by a low ocularium, located in the middle of the prosoma, relatively small chelicerae, and mostly smooth, spoon-shaped pedipalps. These characters are absent in the amber specimen. Cranoids have large, strongly spined pedipalps and a typical large apophysis at the posterior margin of

the spiracular area, which cannot be observed in the fossil. Gonyleptid harvestmen are especially known for their highly variable apophyses on leg IV. However, the prosoma is much narrower than the opisthosoma and the chelicerae are very small in relation to body size. These characters strongly argue against a referral to Gonyleptoidea, and in a wider sense the presence of a Neotropical family in Cretaceous Asian amber would be surprising. Large leg apophyses are not typical for Phalangodidae, but they are known from species like *Texella spiniperca* Ubick and Briggs, 1992. An elevated ocularium, located at the anterior margin, large chelicerae and the armature of the body, as found in most phalangodids, would be consistent with the fossil. However, the pedipalps of phalangodids are invariably covered with many megaspines and the tarsal formula is much lower compared to the amber specimen (Pinto-da-Rocha and Giribet, 2007). Assamiidae includes lineages resembling the habitus of the fossil (specifically, the subfamily Mysoreinae), but this family is distinguished by relatively small palps with a denticulate ventral margin of the palpal femur—the large palps of the fossil rule out placement in Assamiidae. Within the recently recognized family Beloniscidae, the recurved apophyses of trochanter IV and antero-posterior compaction of the free tergites observed in the fossil are comparable to these features in the males of extant species like *Beloniscus albimarginatus*.

Genus *Palaeobeloniscus* gen. nov.

urn:lsid:zoobank.org:act:8BCF60C2-AF68-40BB-BDD5-14421582BC7A.

**Type species.** *Palaeobeloniscus thilolebi* gen. et sp. nov., designated herein.

**Etymology.** Refers to the discovery of the first laniatorean from Burmese amber which shows similarities to the modern family Beloniscidae.

**Diagnosis.** Body pear-shaped, covered dorsally with spines and rows of tubercles, and dorsoventrally compressed into ovular shape. Dorsal segments fused into *scutum magnum* plus three very short opisthosomal tergites. Mesotergum partially subdivided by grooves. Ocularium elevated and rounded, located at anterior margin. Chelicerae large and robust. Pedipalps long, covered with small setae and few large spines. Legs very long (leg II longest), slender and mostly smooth. Some podomeres are covered with small tubercles or small spines, especially leg IV. Very large,



distinctive paddle-shaped mesal apophyses on leg IV trochanter. Coxae IV enlarged with an additional small apophysis. Tarsi III–IV bear two simple claws, with two separate insertions. Ventral opisthosomal sternites covered with rows of small tubercles.

***Palaeobeloniscus thilolebi*** gen. et sp. nov.

urn:lsid:zoobank.org:act:9BA93C85-F3A3-40C6-B165-96CAAF94B536.

**Etymology.** Named after the son, Thilo, and daughter, Lebi, of Patrick Müller who made this material available for study. Gender masculine.

**Diagnosis.** As for the genus.

**Holotype.** MB.A. 4313, ex coll. Patrick Müller, BUB3114.

**Type-locality.** Burmese amber, Hukawng Valley, Myanmar. Mid-Cretaceous (lower Cenomanian).

**Description.** Body pear-shaped, L 2.23\*, anterior W 0.72\*, maximum posterior W 1.70. Prosoma partially obscured by planar fractures. Posterior prosomal region bears a few spine-like setae. Dorsal segments fused into scutum magnum with three very short opisthosomal tergites. Mesotergum partially subdivided by grooves and covered with rows of tubercles. Free tergites tuberculate. Ocularium only visible in lateral view, elevated, rounded and located at anterior margin bearing large eye lenses laterally (Fig. 9). Chelicerae large and robust. Pedipalps long but strongly desiccated. Femur covered by small setae and one large mesal thorn. Tibia bears one mesal spine. Legs very long (leg II longest), slender and mostly smooth. Some podomeres are covered with small tubercles or small spines, especially Leg IV. Very large, paddle-shaped apophyses attached to mesal side of leg IV trochanter (Fig. 8). Coxae IV large and very setose with an additional small apophysis. At least tarsi II subdivided into tarsomeres. Tarsi I–II bear one claw and tarsi IV two claws with two separate insertions. Tarsal formula: ? : 16: ? : ?. Leg length: Leg I tr 0.44, fe 1.47, pa 0.35, ti 0.63, mt 0.85\*, ta 0.85\*, total (tr–ta) 4.59; Leg II tr 0.44\*, fe 1.66, pa 0.71, ti 1.65, mt 2.56, ta 2.30, total (tr–ta) 9.32; Leg III tr 0.30\*, fe 1.10, pa 0.54, ti 1.15, mt 0.85\*, ta 0.85\*, total (tr–ta) 4.79; Leg IV tr 0.39, fe 1.20, pa 0.78, ti 1.40, mt 1.10, ta 1.46, total (tr–ta) 6.62.

Ventral region partially obscured by fractures and crystalline growth. Ventral opisthosomal sternites covered with rows of small tubercles. Anal operculum sub-elliptical, L 0.25, W 1.08.

## 4. Discussion

The discovery here of several new Laniatores in Burmese amber belonging to five different families (Tithaeidae, Epedanidae, Pyramidopidae, Beloniscidae and Mesokanidae fam. nov.) suggests that these harvestmen were a notable component of the Cretaceous arachnid fauna in the original amber forests. This is somewhat consistent with laniatorean diversity in modern tropical forest ecosystems, including Southeast Asia. Most of the Burmese amber fossils can be assigned to living families, and evidently belong to groups still largely restricted to this biogeographic province. This implies a degree of continuity in the fauna here from the mid-Cretaceous through to the present day. Sharma and Giribet (2011) identified a possible Southeast Asian laniatorean clade, albeit with limited support, including the families Epedanidae, Tithaeidae, Petrobunidae and Podoctidae; with the last of these nevertheless exhibiting signatures of transoceanic dispersal in the Indian Ocean and the South Pacific Islands (Sharma et al., 2017).

### 4.1. Palaeoecology of *Mesokanus*

The discovery of an extinct family, Mesokanidae fam. nov., in Burmese amber (Figs. 2 and 3) as a possible stem-group to

Sandokanidae is of particular note. Living sandokanids are an extraordinary group of Laniatores, easily recognizable by the presence of a *scutum completum*, a reduced tarsomere count and swollen feet. The short legs and low number of tarsomeres correlate with their ecology as ground-dwelling specimens (Sharma and Giribet, 2009). By contrast, arboricolous laniatoreans tend to have longer legs with many tarsomeres, as is seen in most of the other Burmese amber fossils described herein. Sandokanidae share many characteristics with the Opiliones suborder Cyphophthalmi, like the *scutum completum* and a reduced tarsomere count. These have evolved convergently in various groups of Opiliones, including some ground-dwelling lineages of Eupnoi and Dyspnoi, and may reflect adaptations to a similar ecological niche. Intriguingly, the Burmese amber species described here, *Mesokanus oehmkuhnlei* gen. et sp. nov., exhibits a higher tarsal formula (3:4:4:5) than sandokanids (modern *Gnomulus* and *Biantoncopus* do not exceed 2:2:3:3). This could reflect a transitional state of tarsomere reduction in the course of this family's evolutionary trajectory, from a presumably longer-legged ancestral condition with a higher tarsomere count (Garwood et al., 2014). Furthermore, the fossil bears two claws with a single insertion on legs III and IV, typical for modern members of the infraorder Insidiatores, whereas sandokanids as members of the other infraorder Grassatores bear two claws with separate insertions on legs III and IV. Short-legged Opiliones like Cyphophthalmi and Trogulidae inhabit leaf litter and are limited in vagility (Sharma and Giribet, 2011). There is one described cyphophthalmid from Burmese amber (Poinar 2008) and several more from private collections were described in the thesis of Friedrich (2015). Amber tends to trap tree-dwelling arthropods preferentially, thus it is somewhat surprising to find a relatively high number of ground-dwelling Opiliones taxa in amber. Their appearance in amber may be more related to their limited vagility rather than an arboricolous life history during the Mesozoic. Perhaps these animals became trapped in resin while waiting for prey near trees?

As noted above, one fossil (Fig. 4) is very likely a juvenile Laniatores, which shows some sandokanid affinities. Juvenile fossil harvestmen have only rarely been formally described; e.g. Bartel and Dunlop (2019) described an early instar probably belonging to the Baltic amber laniatorean genus *Proholoscotolemon* (Koch and Berendt, 1854). Complete series of postembryonic development have only been documented for a few modern harvestmen species, but several trends in ontogeny are apparent and can be compared to examples in the fossil record. The fossil described here probably represents one of the late nymphal stages, as it is relatively large (body length 1.26 mm) with an ocularium, chelicerae and pedipalps comparable to those of living adult *Gnomulus* specimens. However, the legs of the juvenile fossil are relatively long and heavily spined (Fig. 4) which differs from adults or juveniles of living sandokanids.

### 4.2. Phylogenetic and biogeographical inferences

The discovery of key Opiliones fossils (e.g., Dunlop et al., 2003; Garwood et al., 2014) has facilitated the diagnostic power of harvestmen as models for biogeography. The ancient (Palaeozoic) age of these crown-group Opiliones is demonstrative of the continuity of harvestman diversification through periods of well-characterized continental drift, particularly for the suborder Cyphophthalmi (Boyer et al., 2007; Clouse and Giribet, 2010; Giribet et al., 2012). Nevertheless, discoveries of new fossils that can be reliably assigned to existing families provides a welcome litmus test for the validity of molecular divergence time estimates. In the case of Laniatores (and specifically, Grassatores), the dearth of this group in the fossil record has hindered assessment of molecular dating for individual families exhibiting biogeographic

provincialism (e.g., Sharma et al., 2009, 2012), as well as for the basal diversification of its superfamilies (Sharma et al., 2011; Fernández et al., 2017).

A validation is provided here for Tithaeidae (Fig. 1), which was estimated to have diversified in the Mesozoic (Sharma et al., 2017; Schmidt et al., 2019). The discovery of the fossil beloniscid, like that of the tithaeid fossil, serves to support the inference of ancient provincialism among Laniatorean families.

However, a surprising discovery is the inclusion of Pyramidopidae in Burmese amber. Pyramidopids were initially described as an Afrotropical (i.e., sub-Saharan) lineage, with one relictual monotypic genus (*Maioresus*) known from the Canary Islands (Sharma et al., 2011). Through the aid of molecular phylogenetic datasets, additional relicts of Pyramidopidae with formerly erroneous systematic placements were subsequently discovered in Belize (Jarmilana pecki; Cruz López et al., 2016) and the Levant (*Haasus judaeus* and *Haasus naasane*; Aharon et al., 2019), making pyramidopids one of the few Laniatores families whose distribution spans more than one biogeographic province. The incidence of a pyramidopid in Burmese amber suggests that this family once held a much broader distribution (comparably to Biantidae or Assamiidae), but underwent regional extinctions outside of the Afrotropics. This scenario is tentative, given that Pyramidopidae remains poorly studied; future surveys of southeast Asian leaf litter fauna may yield extant members of the lineage putatively represented by *Protopyramidops nala* gen. et sp. nov.

The Burma Terrane holds a contentious position in geological reconstructions, with recent work suggesting that this terrane, which may have been an isolated island in the mid-Cretaceous (ca. 90–95 Ma), underwent collision with the northward-moving Indian Plate at ca. 60 Ma, with later collision with the Thai-Malay Peninsula/proto-Sunda Shelf (Westerweel et al., 2019). These models cast doubt about the endemism of the Cretaceous Burmese fauna, as well as their putative faunal connections to India and other fragments of Gondwana. If the Burmese Terrane was an island at the time of amber deposition, it would suggest that the taxa preserved in amber may have arrived by dispersal, either from the northward moving Indian Plate or from the Asian mainland. Given the uncertainty in these reconstructions, as well as the older diversification ages of all Laniatores families discovered in Burmese amber, we cannot rule out the possibility of short-range dispersals to this terrane. However, given the markedly poor dispersal ability of some of the Opiliones in this fauna (e.g., the Cyphophthalmi *Palaeosiro burmanicum* Poinar, 2008, and the Tithaeidae; Clouse and Giribet, 2010; Sharma et al., 2009; Stelbrink et al., 2012; Giribet et al., 2012), we consider transoceanic dispersal as an unlikely explanatory vehicle to account for the presence of these lineages in the amber. Nevertheless, in contrast to Cyphophthalmi, certain exceptional lineages of Laniatores exemplify remarkable transoceanic dispersal ability (e.g., Zalmoxidae; Podoctidae; Sharma et al., 2012, 2017). Future reconciliation of Southeast Asian geological models, in tandem with detailed biogeographic interrogations of Southeast Asian Laniatores families, will weigh heavily upon evaluating scenarios of dispersal events to and/or from the Burma Terrane in the Southeast Asian families of Laniatores.

## 5. Conclusions

Six new species of Laniatores harvestmen from five different families have been described from the Burmese amber of Northern Myanmar, implying a diverse laniatorean fauna in the mid-Cretaceous of Southeast Asia. Unpublished observations suggest that further Burmese amber Laniatores remain to be described. As well as providing important new calibration points for the

Laniatores tree of life, most of the finds here are from groups known today from Southeast Asia. All these records are informative for understanding the biogeographical origins and past distributions of laniatorean families and even genera, as well as the wider question of the degree to which Burmese amber hosts a Laurasian or Gondwanan arthropod fauna.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2020.104703>.