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Short communication

Two new lagonomegopid spiders (Arachnida: Araneae) from the mid-Cretaceous of Northern Myanmar, with comments on the superfamilial placement of Lagonomegopidae

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ABSTRACT

Two new lagonomegopid spiders, *Odontomegops titan* gen. et sp. nov. and Lagonomegopidae indet., are described from mid-Cretaceous Myanmar (Burmese) amber. *Odontomegops titan* gen. et sp. nov. differs from other lagonomegopids in its large body size and the presence of true teeth on the cheliceral retromargin. The two lagonomegopids described here also clarify the presence of feathery setae in this family. The superfamilial placement of Lagonomegopidae in Palpimanoidea is discussed, based on the true teeth and feathery setae.

1. Introduction

The extinct spider family Lagonomegopidae Eskov and Wunderlich, 1995, which can be easily distinguished from other spider families by the two large eyes (recognized as posterior lateral eyes; Eskov and Wunderlich, 1995; Park et al., 2019) positioned on the anterolateral flanks of the carapace, was first described from two juvenile specimens in Cretaceous (Santonian) amber from the Taimyr Peninsula, Siberia (Eskov and Wunderlich, 1995). Since then, many more species from Cretaceous amber, especially Myanmar (formerly known as Burma) amber, have been described and placed in this family. Park et al. (2019) described the first two lagonomegopid species preserved as compression fossils from the Cretaceous (Albian) Jinju Formation of Korea. At present, the family Lagonomegopidae comprises 30 species in 18 genera widespread in the Cretaceous period (Park et al., 2019, see supplemental material table 2). Of these, 19 species in 12 genera have been reported from Burmese amber.

Forster and Platnick (1984) reviewed the superfamily Palpimanoidea and expanded it to include ten families. However, subsequent phylogenetic studies supported a Palpimanoidea comprising five living families: Archaeidae C. L. Koch and Berendt, 1854, Palpimanidae Thorell, 1870, Stenochilidae Thorell, 1873, Huttoniidae Simon, 1893 and Mecysmaucheniidae Simon, 1895 (Wood et al., 2012; Wheeler et al., 2016). In addition, there are four fossil families (Spatiatoridae Petrunkevitch, 1942, Lagonomegopidae, Micropalpimanidae Wunderlich, 2008 and Vetiatoridae Wunderlich, 2017) tentatively placed in this superfamily, but their phylogenetic positions have not been tested cladistically.

Lagonomegopidae was placed in the superfamily Palpimanoidea primarily based on the presence of peg teeth and the absence of true teeth on the cheliceral promargin, as well as the trichobothrial pattern and spineless legs (Eskov and Wunderlich, 1995). Penney (2004) described a juvenile or female lagonomegopid,

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Grandoculus chemahawinensis Penney (2004), from Canadian amber, which possessed dense, hook-tipped scopulae prolaterally on the anterior metatarsus (Penney, 2004; Pérez-de la Fuente et al., 2013). Though these scopulae have a different structure from the common scopulae with spatulate tips which are present in the palpimanoid families Palpimanidae and Stenochilidae (Forster and Platnick, 1984), the two types of scopulae were hypothesized to be homologous and to support the placement of Lagonomegopidae in Palpimanoidea (Penney, 2004). However, Pérez-de la Fuente et al. (2013) considered it controversial to place Lagonomegopidae in the superfamily Palpimanoidea, based on their comparison of various characters in Lagonomegopidae and other palpimanoid families. They presumed that the lagonomegopid lineage is most likely basal or sister to other palpimanoid lineages (Pérez-de la Fuente et al., 2013).

The lagonomegopid spiders were regarded as free hunters rather than web builders due to their short legs and large eyes (Eskov and Wunderlich, 1995). Wunderlich (2015) thought that both sit-and-wait predators and active hunters existed in this family. Because most lagonomegopids are preserved in amber, they were presumed to live in arboreal habitats (Eskov and Wunderlich, 1995; Park et al., 2019). Recently, *Jinjumegops dalingwateri* Park, et al. 2019 and *Koreamegops samsiki* Park, et al. (2019) from the Jinju Formation of Korea suggested an additional cursorial life mode for lagonomegopids (Park et al., 2019).

Herein, two lagonomegopid spiders (one of them based on an exuvia) are described from Burmese amber. With a body length of >10 mm, *Odontomegops* gen. nov. is the largest lagonomegopid described to date (Park et al., 2019, supplemental table 2). These discoveries help us to observe more morphological details of lagonomegopids, and add new material for further phylogenetic study of this spider family.

2. Material and methods

The amber specimens investigated in this paper are from Tanai Village in the Hukawng Valley, Myitkyina District of Kachin State, Myanmar (Cruickshank and Ko, 2003: fig. 1; Chen et al., 2018; Lin et al., 2019; Yang et al., 2019). The amber-bearing deposits have been dated to the earliest Cenomanian, circa 98.8 ± 0.6 Ma, based on U–Pb radiometric dating of zircons from the volcaniclastic matrix (Shi et al., 2012). All specimens are deposited in the Key Lab of Insect Evolution & Environmental Changes at the College of Life Sciences, Capital Normal University, Beijing (CNUB; Dong Ren, curator).

The photographs were taken with a Nikon SMZ 25 and an attached Nikon DS-Ri 2 digital camera system. The line drawings were prepared with Adobe Illustrator CS6, the images were processed by Adobe Photoshop CC. Measuring method follows Selden et al. (2016); measurements of coxae and trochanters are rather imprecise and uninformative. All measurements are in mm.

Leg formula indicates the length of each leg relative to the others, longest to shortest. Abbreviations: I, II, III, IV, leg numbers; ALE, anterior lateral eye(s); AME, anterior median eye(s); ch, chelicera; cx, coxa; ef, epigastric furrow; en, endite; f, fovea; fe, femur; fo, folium; lb, labium; mt, metatarsus; op, opisthosoma; pa, patella; Pd, pedipalp; PLE, posterior lateral eye(s); PME, posterior median eye(s); st, sternum; ta, tarsus; ti, tibia; tr, trochanter.

3. Systematic palaeontology

Order Araneae Clerck, 1757
Family Lagonomegopidae Eskov and Wunderlich, 1995

Emended diagnosis. Chelicera with several peg teeth on promargin; true teeth present or absent on retromargin. Carapace with a pair of large posterior median eyes situated on anterolateral corner, other eyes tiny. Endites subtriangular, directed across the labium, almost meeting at the midline. Trichobothria present on leg tibia and metatarsus. Three tarsal claws, unpaired claw hook-like. Six spinnerets. Female palpal tarsi lacking a claw.

Genus ***Odontomegops*** Guo and Selden, gen. nov.
(urn:lsid:zoobank.org:act:1961987C-2CE0-4D0E-8AEE-81E02DF5E6E6).

Etymology. The genus name is a combination of Greek *odonto* (meaning teeth) referring to the true teeth on the cheliceral retromargin and *mega-ops* (meaning large eyes), a common suffix for lagonomegopid spiders. The name is masculine.
Type and only species. Odontomegops titan Guo and Selden sp. nov.
Diagnosis. Large lagonomegopid (>10 mm body length); fovea present; cheliceral insertion distinctly separated from mouthparts in vertical plane; chelicera with peg teeth on promargin, and true teeth on retromargin; legs long and densely hairy, no legs enlarged, metatarsus distinctly longer than tarsus; feathery setae and hair-like bristles present.
Remarks. The new genus described here clearly belongs to Lagonomegopidae, based on the large eyes situated anterolaterally on the carapace which is the typical character of this family. *Odontomegops* gen. nov. is different from all other lagonomegopid genera by the following characters: large body size; relatively long legs and true teeth on cheliceral retromargin.

The new genus is most similar to another lagonomegopid genus, *Lagonoburmops* Wunderlich, 2012, from Burmese amber, due to the large body size and hairy legs. But *Odontomegops* gen. nov. differs from *Lagonoburmops* in these characters: feathery setae present on carapace, pedipalp, legs and opisthosoma; hair-like bristles present on all podomeres of legs; leg I much longer than body length (the ratio of fe + pa + ti + mt of leg I to body length is 2.17 *vs.* 1.31 in *Lagonoburmops plumosus* Wunderlich, 2012, the type species of *Lagonoburmops*); and metatarsus much longer than tarsus in anterior legs (mt/ta ratio 4.59 *vs.* 2.00 in *L. plumosus*) (Wunderlich, 2012). Furthermore, *Odontomegops* gen. nov. can be distinguished from *Lagonoburmops* by true teeth on the cheliceral retromargin, but we must point out that this character is not fully resolved in *Lagonoburmops* according to Wunderlich's description: “at least 7 long cheliceral “peg teeth”, further teeth unknown (probably absent)”. We tried to clarify this by checking photographs of the holotype of *L. plumosus*, courtesy of Dr. Axel Christian (curator of the Senckenberg Museum für Naturkunde, Görlitz), but failed. Restudy of the holotype of *L. plumosus* will be helpful to solve this problem.

Odontomegops titan Guo and Selden gen. et sp. nov
(Figs. 1A–D; 2A–I.)
(urn:lsid:zoobank.org:act:6D1D3BC3–7BF4–42F0-A08D-D15169AB090D)
Xia et al., (2015): 171 (as large spider)

Diagnosis. As for the genus.
Etymology. The specific epithet is the Greek term *titan* (a race of giant gods in Greek mythology), referring to the large body size.
Type material. Holotype, CNU-ARA-MA2019001, an adult male. A picture of this specimen has already been published (Xia et al., 2015, photo on page 171), but it has not been described or named formally. This specimen is relatively well preserved, although the opisthosoma and some leg podomeres are broken. The opisthosoma is somewhat ground ventrally; the spinnerets and anal tubercle are not preserved. The right legs are more damaged than those on the left, only two stumps consisting of tarsus, metatarsus and part of tibia remain. Based on the positions and the length ratios of tarsus to metatarsus of the two stumps, they are

interpreted as parts of right leg I/II and leg III/IV respectively (Fig. 1A–D). Moreover, there are some impurities around the spider, a crack near the femur of left leg III, a beetle near the metatarsus of left leg I, and a groove on the surface of the amber.

Locality and horizon. Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Description. Body length 11.98. Carapace piriform in outline, length 6.26, width 4.21 at widest point, height 2.18, covered with short, dense, feathery setae pressed flat against the cuticle. Cephalic region of carapace slightly raised, with two subtriangular dark patches on the posterior and middle parts, and dark ring around PME. Fovea a longitudinal ellipse, depressed, situated in the centre of carapace, next to the posterior margin of cephalic region. Thoracic region flat, with six dark stripes pointing from fovea toward the coxae of legs. Eight eyes present; PME enormous, 0.78 in diameter, situated on anterolateral corner of carapace; PLE small,

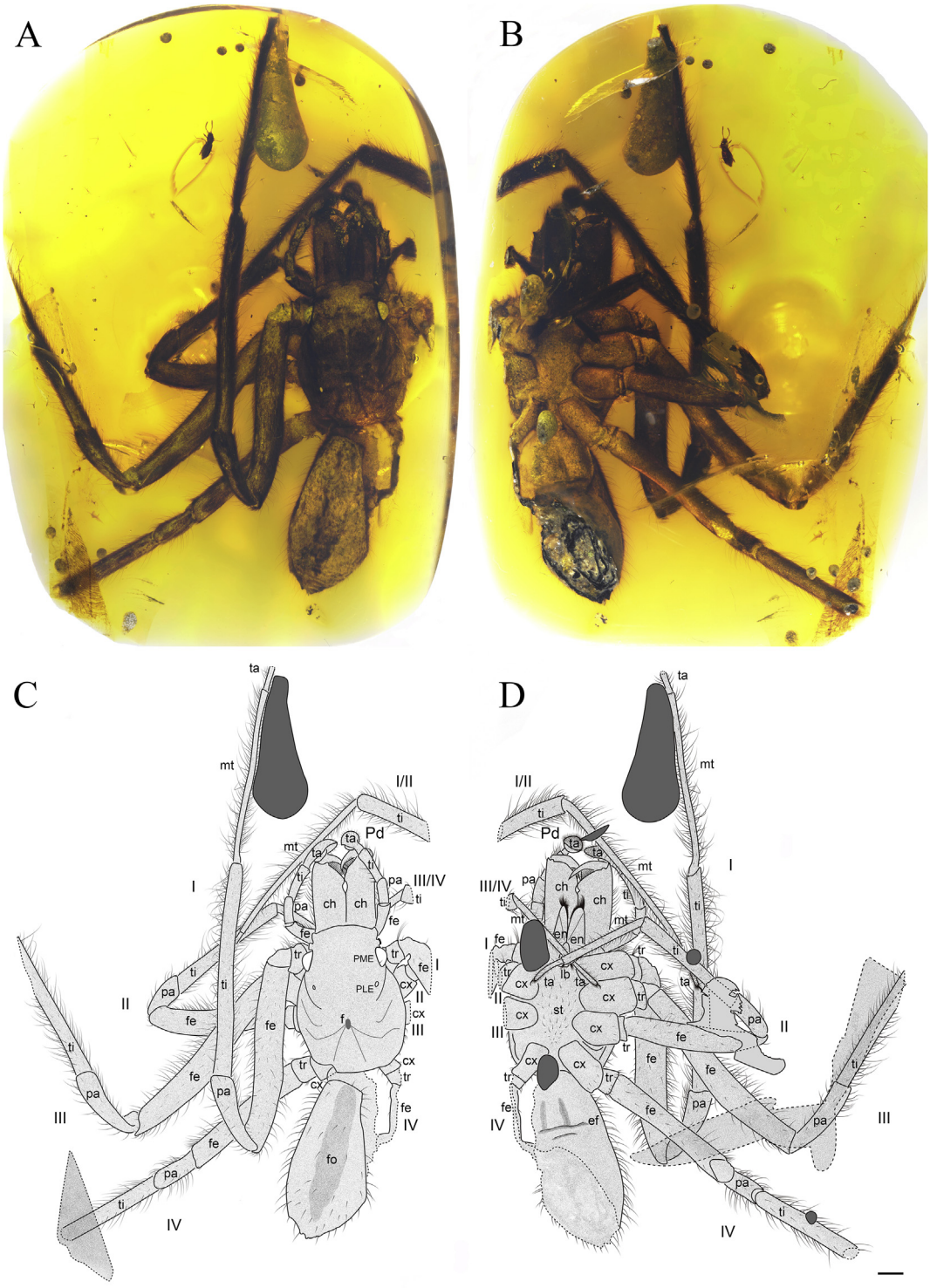

Fig. 1. *Odontomegops titan* gen. et sp. nov. (CNU-ARA-MA2019001). A, dorsal view; B, ventral view; C, explanatory drawing of A; D, explanatory drawing of B, dark gray areas are impurities. Scale bar represents 1 mm.

placed at the mediolateral margin of cephalic region, separated 1.25 from the PME centre; AME and ALE contiguous, AME placed below ALE, with both situated on a projection between the PME and the clypeal margin (Fig. 2D). Clypeus width 2.88, height 0.48. Chelicera length 3.72, and width 1.28 at base, slightly anteriorly directed, with depression on prolateral surface; cheliceral insertion distinctly separated from mouthparts in vertical plane (Fig. 2D). Chelicera covered with setae, with subtriangular dark patch dorsally. Fang length 1.55. Chelicera with more than thirty peg teeth on promargin, and 3–4 (right chelicera with 3, left chelicera with 4) true teeth on retromargin (Fig. 2B, C). Cheliceral stridulatory files absent. Labium partly visible, likely subtriangular, longer than wide, not fused to sternum (Fig. 2F). Endites elongated, subtriangular, converging and meeting in midline, with ridged apophysis near prolateral margin ventrally; apex and prolateral margin of endites brushy with dense setae increasing in length distally (Fig. 2D, F); serrula as a single row of teeth. Sternum shield shaped, covered with setae, not convex and without tubercles.

Pedipalp podomere lengths: fe 2.54, pa 0.98, ti 1.49, ta 1.82. Pedipalp hairy, feathery setae present on femur, patella, tibia and base of tarsus. Tibia with three dorsal trichobothria in a single row. Cymbium length 1.43, width 0.82. Pedipalp bulb small, occupying about half length of cymbium. Detailed structures, such as embolus and conductor, not recognizable (Fig. 2E).

Legs long and densely hairy, no legs enlarged, metatarsus distinctly much longer than tarsus. Leg formula 2143 (based on the length of femur): left leg I cx 2.06, tr 0.38, fe 7.45, pa 3.15, ti 8.23, mt 7.15; left leg II cx 2.19, tr 0.49, fe 9.10, pa 3.09; left leg III cx 1.86, tr 0.29, fe 5.70, pa 2.10, ti 4.83, mt 3.81, ta 1.38; left leg IV cx 1.91, tr 0.68, fe 5.96, pa 2.17; right leg I/II mt 7.66, ta 1.67; right leg III/IV mt 3.50, ta 1.27. Absence of scopulae on metatarsus or tarsus I + II. Left metatarsus III and right metatarsus III/IV with distal preening comb ventrally (Fig. 2I). Feathery setae present on coxa, femur, patella and the base of tibia. Hair-like and elongated bristles present on all podomeres of legs. Numerous trichobothria dorsally on all tibiae, metatarsi and tarsi, shorter than bristles (Fig. 2G, H, I). Three tarsal claws, paired claws with three teeth, median claw hook-like.

Opisthosoma subovoid, length as preserved 6.46, width 3.31, densely covered with short feathery setae (Fig. 2A) and long sparse bristles. Opisthosoma with indistinct median dorsal folium occupying about one third width of dorsum. Epigastric plate with a pair of longitudinal grooves, epigastric furrow long, a shout transverse groove situated on the postgastric area behind the epigastric furrow. Spinnerets and anal tubercle not visible.

Lagonomegopidae indet (Figs. 3A–B; 4A–I.)

Material. CNU-ARA-MA2019002, the exuvia of a sub-adult male. This specimen is somewhat broken, and there are some impurities

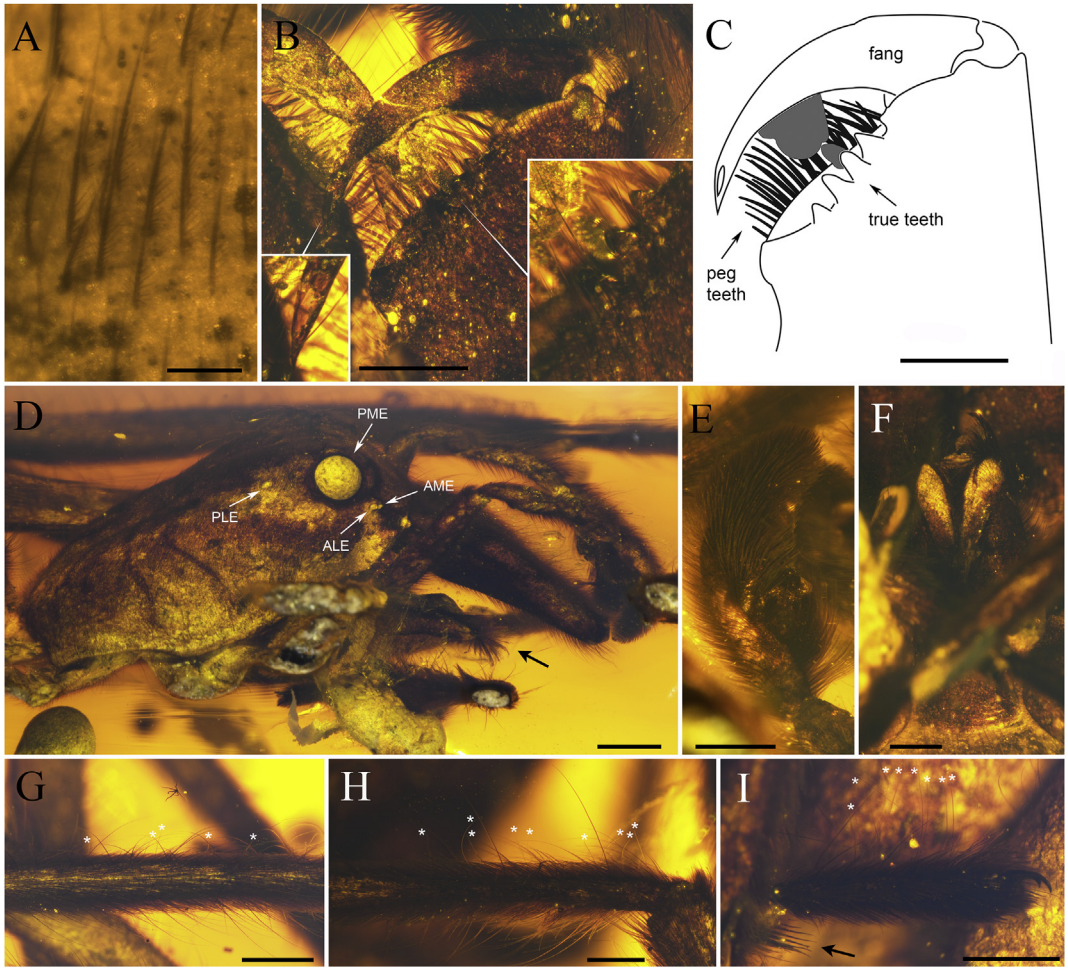

Fig. 2. *Odontomegops titan* gen. et sp. nov. (CNU-ARA-MA2019001). A, feathery setae on dorsal opisthosoma; B, left chelicera, ventral view, showing peg teeth, true teeth (magnified at the bottom right) and venom gland opening (magnified at the bottom left); C, explanatory drawing of B, dark gray areas are impurities; D, prosoma, lateral view, showing eyes (white arrows) and endites (black arrow); E, right male palp, retrolateral view; F, mouthparts, ventral view; G, middle part of left tibia I, lateral view, showing trichobothria on tibia dorsally (asterisks); H, basal part of left metatarsus III, lateral view, showing trichobothria on metatarsus dorsally (asterisks); I, right tarsus III/IV, lateral view, showing trichobothria on tarsus dorsally (asterisks) and preening comb on distal metatarsus ventrally (black arrow). Scale bars represent 1 mm (D, G), 0.5 mm (B, C, E, F, H, I) and 0.05 mm (A).

and bubbles around the spider in this piece of amber. The carapace has an irregular hole between the two large eyes. The left leg I and right leg I and II are fractured, and some of their podomeres are not preserved (Fig. 3A, B). The opisthosoma is strongly shrivelled, and a silk thread from the spinnerets can be seen being grasped by the leg claws (Fig. 4D, E). It likely shows the molting posture of this lagonomegopid spider.

Locality and horizon. Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Remarks. The empty prosoma and shrivelled opisthosoma of this specimen suggest that it is an exuvia. It is a sub-adult male, because its palpal tarsus is enlarged, but not modified into a cymbium. This specimen is placed here because of the large eyes situated anterolaterally on the carapace, and its nearly square carapace can distinguish it from other lagonomegopids with a piriform carapace. The preserved characters of CNU-ARA-MA2019002 are not clear enough for the specimen to be assigned to a particular genus among lagonomegopid spiders. It is described here because it shows feathery setae and a possible molting posture in Lagonomegopidae.

Description. Body length not measurable but >5.41. Carapace nearly square in outline, length 2.51, width 2.23 at widest point, height 1.18, covered with short, dense, white, feathery setae pressed flat against the cuticle, with several dark patches laterally. Cephalic region of carapace slightly raised. Fovea absent. Eight eyes present; PME enormous, 0.49 in diameter, situated on anterolateral corner of carapace; PLE small, placed at the lateral margin of cephalic region, separated 0.62 from the PME centre; AME and ALE contiguous, AME placed below ALE, with both situated between the PME and the clypeal margin (Fig. 4A). Clypeus width 1.80, height 0.23, with plumose setae on margin. Chelicera length 1.18, and width 0.55 at base; cheliceral insertion distinctly close to mouthparts in vertical plane (Fig. 4A). Chelicera covered with long dense setae, white feathery setae present (Fig. 4B); a distinctly elongated seta present dorsoproximally. Fang length 0.35. Chelicera with about thirteen peg teeth on promargin; retromargin not visible. Cheliceral stridulatory files absent. Labium and endites hidden. Sternum covered with setae, tubercles absent.

Pedipalp podomere lengths: fe 0.94, pa 0.39, ti 0.34, ta 0.84. Tarsus enlarged, but not modified into a cymbium. Feathery setae present on femur, patella, tibia and tarsus. Tibia with six dorsal trichobothria.

Legs sturdy and hairy, no legs enlarged; metatarsus distinctly longer than tarsus in anterior legs; metatarsus and tarsus almost with equal length in posterior legs. Leg formula 2143 (based on the length of femur): leg I cx 0.47, tr 0.24, fe 2.40, pa 0.94, mt 1.31, ta 0.73; leg II cx 0.39, tr 0.23, fe 2.62, pa 1.13, ti 2.08, mt 1.24, ta 0.71; leg III cx 0.31, tr 0.25, fe 1.37, pa 0.57, ti 0.97, mt 0.48, ta 0.55; leg IV cx 0.46, tr 0.27, fe 2.27, pa 0.71, ti 1.59, mt 0.86, ta 0.77. Metatarsus and tarsus covered with dense setae, scopulae absent (Fig. 4F). Metatarsus III + IV with distal preening comb ventrally. Feathery setae (Fig. 4C) and hair-like bristles present on all podomeres of legs. Numerous trichobothria (at least two rows) dorsally on all tibiae, metatarsi and tarsi (Fig. 4G, H, I). Three tarsal claws, paired claws with two teeth, median claw hook-like.

Opisthosoma strongly shrivelled, not measurable but >2.90 long, densely covered with feathery setae. Spinnerets and anal tubercle not visible.

4. Discussion

4.1. True teeth and peg teeth

Peg teeth and true teeth (also known as denticles) are two different kinds of structures on the cheliceral promargin and retromargin. Peg teeth are modified setae and therefore are not

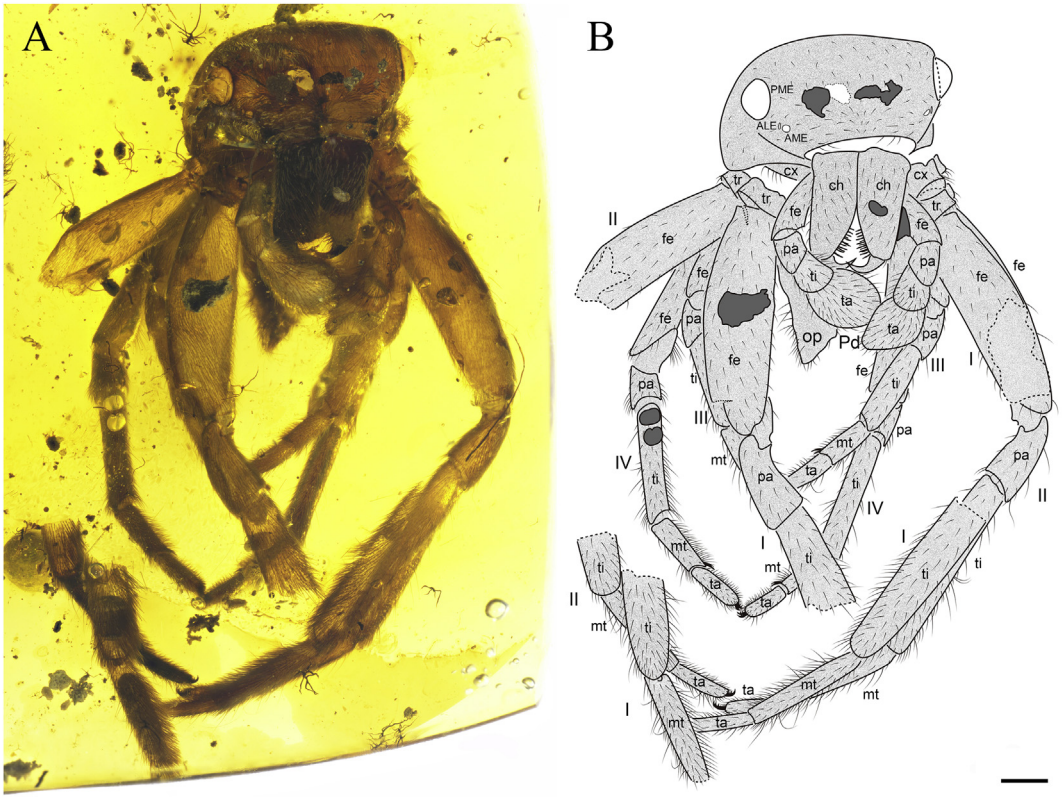

Fig. 3. Lagonomegopidae indet. (CNU-ARA-MA2019002). A, anterior view; B, explanatory drawing of A, dark gray areas are impurities. Scale bar represents 0.5 mm.

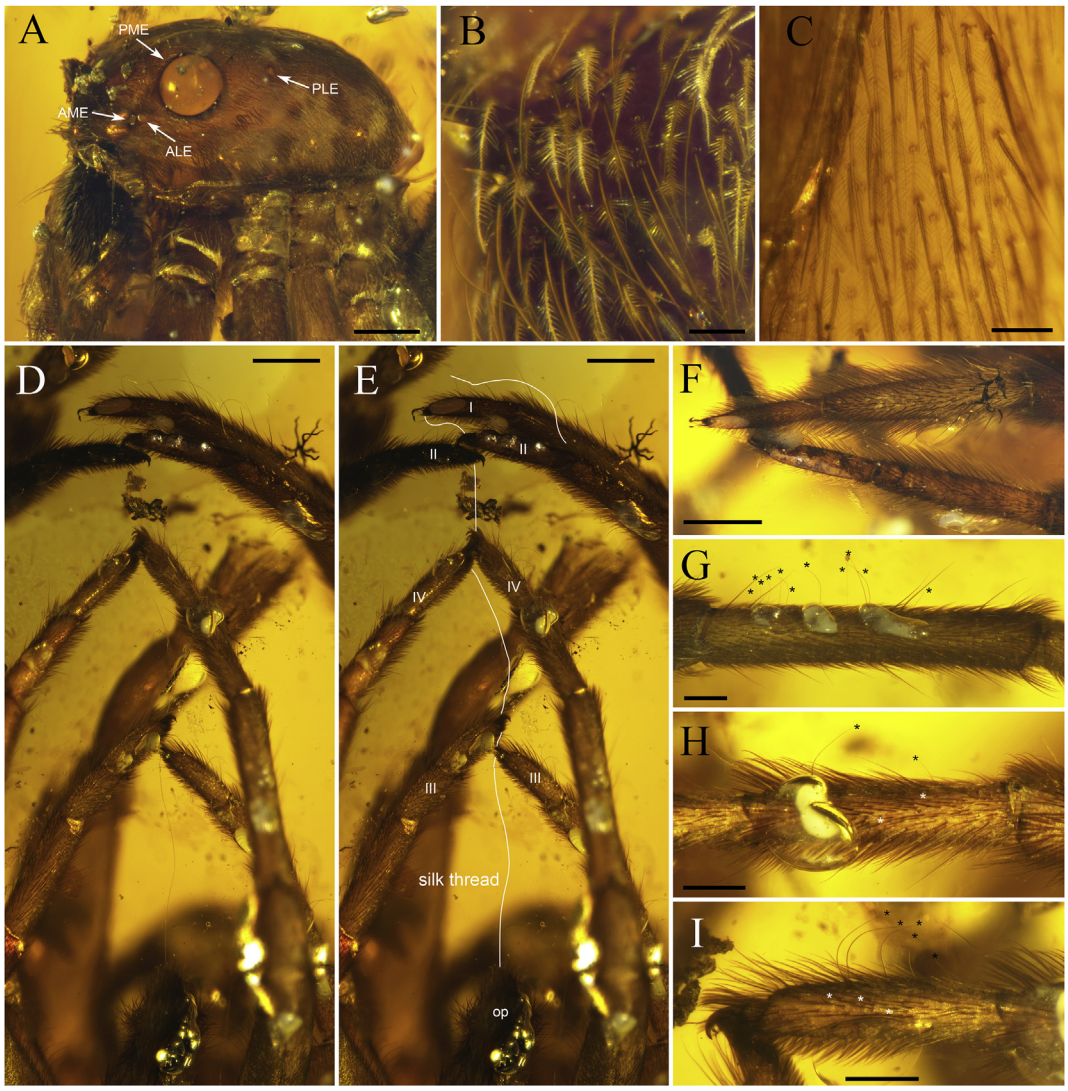

Fig. 4. Lagonomegopidae indet. (CNU-ARA-MA2019002). A, prosoma, lateral view, showing eyes (white arrows); B, feathery setae on chelicera; C, feathery setae on femur of leg; D, opisthosoma and legs, posterior view, showing silk thread; E, explanation of D, white lines represent silk thread; F, metatarsus and tarsus of leg I (the upper one) and II (the lower one), dorsal view; G, right tibia IV, lateral view, showing trichobothria on tibia dorsally (asterisks); H, left metatarsus IV, lateral view, showing trichobothria on metatarsus dorsally (asterisks); I, left tarsus IV, lateral view, showing trichobothria on tarsus dorsally (asterisks). Scale bars represent 0.5 mm (A, D, E, F), 0.2 mm (G, H, I) and 0.05 mm (B, C).

homologous to true teeth, which are projections of the cheliceral cuticule (Forster and Platnick, 1984; Murphy and Roberts, 2015). True teeth play an important role in prey capture, grasping and mastication (Foelix, 2011), and peg teeth may have a similar function with true teeth. The absence of true teeth was considered a diagnostic characteristic of Lagonomegopidae by Eskov and Wunderlich (1995), when they erected this family. In the lagonomegopids described subsequently, true teeth have not been reported (Penney, 2002, 2004, 2005, 2006; Kaddumi, 2007; Wunderlich, 2012, 2015, 2017; Pérez-de la Fuente et al., 2013; Park et al., 2019). *Odontomegops titan* sp. nov. is the first lagonomegopid in which true teeth on the cheliceral retromargin are observed, in addition to the usual peg teeth on the promargin, a common feature in this family.

The presence of peg teeth and the absence of true teeth on the cheliceral promargin were considered as evidence supporting the placement of Lagonomegopidae in Palpimanoidea by Eskov and Wunderlich (1995). However, Pérez-de la Fuente et al. (2013) discussed how the presence of peg teeth may be homoplastic and thus unreliable for systematic studies, because peg teeth are present not only in palpimanoids (although absent in stenochilids) but also in some mimetids, which belong to the superfamily Araneoidea (Wheeler et al., 2016). True teeth on the cheliceral promargin are absent in palpimanoids as well as many other spider families (Jocqué and Dippenaar-Schoeman, 2006). It may be also unreliable for systematic studies.

The combination of peg teeth on the cheliceral promargin and true teeth on the retromargin, seen in *Odontomegops titan* sp. nov., is also present in some palpimanids, archaeids and mimetids (Forster and Platnick, 1984; Selden et al., 2008). Like Lagonomegopidae, not all members of Palpimanidae, Archaeidae and Mimetidae have this combination of characters, some of them have peg teeth on the cheliceral promargin but no true teeth on the retromargin (Forster and Platnick, 1984).

4.2. Feathery setae

The morphologies and distribution of diverse setae on spider bodies can provide information for spider classification and phylogenetic analysis (Griswold et al., 2005; Wood et al., 2012; Murphy and Roberts, 2015; Zakharov and Ovtsharenko, 2015). However, the functions of the various setae are poorly known, and the nomenclature is not uniform. Zakharov and Ovtsharenko (2015)

used the term “plumose setae” to cover “feathery setae” by following the concept that all types of feathery setae may be regarded as different modifications of the plumose seta type (Lehtinen, 1975). Here, to show their different morphologies, we treat plumose setae and feathery setae as two different kinds of setae. Feathery setae (Fig. 2A; 4B, C), which were called brachiate by Murphy and Roberts (2015, fig. 5), are dendritic, with lateral branches resembling the veins in a leaf; plumose setae bear abundant fine projections, generally in lines or whorls, over their entire surface (Selden et al., 2015).

Feathery setae normally lie flat on the cuticle surface, and are present in many spider families (Murphy and Roberts, 2015). Feathery setae in Lagonomegopidae were first reported in the description of *G. chemahawinensis* by Penney (2004). However, Wunderlich (2008) proposed that the feathery setae reported by Penney (2004) may actually be confused with plumose setae. In the two lagonomegopid specimens (CNU-ARA-MA2019001 and CNU-ARA-MA2019002) described here, feathery setae can be identified clearly. Moreover, feathery setae are presumably fairly widespread within this family, because this feature has also been found in a survey of 17 Burmese amber lagonomegopid specimens (out of a total of 24, ~70% of the total), which are well-preserved and deposited in the CNUB. Interestingly, feathery setae have not been reported in the five extant palpimanoid families (Forster and Platnick, 1984; Murphy and Roberts, 2015). Thus, the presence of feathery setae in Lagonomegopidae weakens support for the placement of this family in Palpimanoidea.

4.3. Habitats of lagonomegopids

CNU-ARA-MA2019002 shows a putative molting position in which the spider suspends itself by grasping a dragline with its leg claws during molting (Fig. 4D, E), such that gravity helps pull the spider out of its old skin. This suspended position is in accord with the arboreal habitats of lagonomegopids. In addition, a cursorial life mode was suggested for lagonomegopids (Park et al., 2019). The diverse habitats of lagonomegopids is in accordance with their worldwide distribution (Park et al., 2019).

5. Conclusions

Two lagonomegopid spiders, *Odontomegops titan* gen. et sp. nov., and Lagonomegopidae indet., are described from mid-Cretaceous Myanmar (Burmese) amber. They show new features of Lagonomegopidae: the presence of true teeth on the cheliceral retromargin, and the presence of feathery setae. Whilst true teeth on the retromargin are known from some other palpimanoids, feathery setae have not been described from this superfamily. So, the inclusion of Lagonomegopidae in Palpimanoidea is still controversial. The new specimens enrich our knowledge of lagonomegopid morphology and provide more information for further phylogenetic studies.

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