

New specimens from Mid-Cretaceous Myanmar amber illuminate the phylogenetic placement of Lagonomegopidae (Arachnida: Araneae)

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New lagonomegopid spiders are described from Mid-Cretaceous Myanmar (Burmese) amber. Two new genera and species based on single specimens, *Scopomegops fax* gen. & sp. nov. and *Hiatomegops spinalis* gen. & sp. nov. are described. Two specimens belonging to *Lineaburmops beigeli* are further described. Additionally, after re-examining the holotype of *Odontomegops titan*, a detailed description of its basal ventral abdomen is added here. A phylogenetic analysis was performed to investigate the phylogenetic placement of Lagonomegopidae. A matrix of 79 morphological characters, scored for six lagonomegopid taxa and 26 non-lagonomegopid taxa, was analysed through parsimony and Bayesian phylogenetic inference. Our results recover extant Palpimanoidea as a monophyletic group and partly suggest that Lagonomegopidae is the sister-group to extant Palpimanoidea. The external sexual organs, retrolateral tibial apophysis on the male palp and tracheal spiracle in lagonomegopids are discussed.

ADDITIONAL KEYWORDS: fossil – Mesozoic – Palpimanoidea – retrolateral tibial apophysis – tracheal spiracle.

INTRODUCTION

Spiders (Araneae) are one of the most diverse animal groups and an important component of every terrestrial ecosystem, with more than 49 000 described extant species and 1300 described fossil species (Dunlop *et al.*, 2020; World Spider Catalog, 2021). Many recent phylogenetic studies, which improved our knowledge of the systematics and evolution of spiders, were based on the morphological, behavioural and molecular data of extant taxa (e.g. Griswold *et al.*, 2005; Bond *et al.*, 2014; Fernández *et al.*, 2014; Ramírez, 2014; Polotow *et al.*, 2015; Garrison *et al.*, 2016; Dimitrov *et al.*, 2017; Wheeler *et al.*, 2017; Azevedo *et al.*, 2018; Wood *et al.*, 2018; Opatova *et al.*, 2020). Extinct spider taxa have usually been used for anchoring the age of particular nodes in the phylogenetic trees depicting

relationships among extant taxa (e.g. Dimitrov *et al.*, 2013; Benavides *et al.*, 2017; Fernández *et al.*, 2018; Li & Li, 2018; Shao & Li, 2018; Magalhaes *et al.*, 2020). By contrast, only several studies used fossil spiders as terminal taxa in the phylogenetic analysis (Wood *et al.*, 2012, 2013, 2015; Wood, 2017; Selden *et al.*, 2020). Therefore, the phylogenetic placement of spider fossils is often ambiguous (Magalhaes *et al.*, 2020).

The fossil spider family Lagonomegopidae, widespread in the Cretaceous period (Park *et al.*, 2019), was deemed not to be a stem group of some extant lineage because of its highly derived morphology, and thus it was likely to represent an extinct lineage (Magalhaes *et al.*, 2020). It was incorporated into 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 & Wunderlich, 1995). However, as more and more lagonomegopids were reported, some characters weakening the support for its superfamilial placement in Palpimanoidea, such as tarsal trichobothria and feathery setae, were

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described (Penney, 2004, 2005; Guo *et al.*, 2020). The phylogenetic placement of Lagonomegopidae was thus considered controversial (Pérez-de la Fuente *et al.*, 2013; Guo *et al.*, 2020).

Forster & Platnick (1984) based an expanded superfamily Palpimanoidea, including ten families, on two cheliceral features: the presence of peg teeth on the promargin and an elevated cheliceral gland mound. But some subsequent studies did not support this expanded Palpimanoidea (Schütt, 2000; Griswold *et al.*, 2005; Rix *et al.*, 2008; Dimitrov *et al.*, 2012). Wood *et al.* (2012) performed a phylogenetic analysis using both morphological and molecular data. This total-evidence analysis resulted in a delimitation of the superfamily Palpimanoidea to contain five families: Archaeidae Koch & Berendt, 1854, Palpimanidae Thorell, 1870, Stenochilidae Thorell, 1873, Huttoniidae Simon, 1893 and Mecysmaucheniidae Simon, 1895. Although another study based on six genetic markers suggested that Palpimanoidea is paraphyletic (Wheeler *et al.*, 2017), two recent studies using transcriptomic data and DNA sequences from Ultra-Conserved Elements and exonic loci recovered a monophyletic Palpimanoidea (Fernández *et al.*, 2018; Wood *et al.*, 2018). All these recent analyses (Wood *et al.*, 2012, 2013, 2018; Wheeler *et al.*, 2017; Fernández *et al.*, 2018) considered Palpimanoidea as a possible sister-group of Entelegynae, a more diverse and derived spider group. Thus, palpimanoids are an important group for understanding spider evolution (Wood *et al.*, 2018).

Except Lagonomegopidae, there are three fossil families (Spatiatoridae Petrunkevitch, 1942, Micropalpimanidae Wunderlich, 2008 and Vetiatoridae Wunderlich, 2017) and four fossil genera (family uncertain; *Sinaranea* Selden *et al.*, 2008, *Seppo* Selden & Dunlop, 2014, *Caestaranea* Selden *et al.*, 2020 and *Onychopalpus* Selden *et al.*, 2020) placed in the superfamily Palpimanoidea. But only *Sinaranea*, *Caestaranea* and *Onychopalpus* have been analysed cladistically for their phylogenetic positions (Selden *et al.*, 2020). Fossils can have crucial implications for understanding spider evolution; indeed, detailed examination of spider fossils using modern methods is critical to better understand and interpret the phenotypic features and phylogenetic affinities of extinct taxa (Dimitrov & Hormiga, 2021). Moreover, exploring the behaviours and lifestyles of fossil taxa can provide a window into the sophisticated ecosystems in geological history (Lin *et al.*, 2019; Zhao *et al.*, 2020; Gao *et al.*, 2021), but such research focusing on fossil spiders is relatively scarce.

Herein, two new genera and species, as well as new specimens of *Lineaburmops beigeli* Wunderlich, 2015, are described from Burmese amber. A supplementary description of *Odontomegops titan* Guo & Selden, 2020 is provided after re-examining its holotype. Phylogenetic analyses based on morphological data were carried out

to test the phylogenetic placement of Lagonomegopidae. We recovered extant Palpimanoidea as a monophyletic group and our implied weighted analyses suggests that Lagonomegopidae is the sister-group to extant Palpimanoidea.

MATERIAL AND METHODS

MATERIAL AND TERMINOLOGY

The amber specimens investigated in this paper are from Tanai Village in the Hukawng Valley, Myitkyina District of Kachin State, Myanmar (Cruikshank & Ko, 2003; fig. 1). The amber-bearing deposits have been dated to the earliest Cenomanian, $c. 98.8 \pm 0.6$ Mya, based on U–Pb radiometric dating of zircons from the volcanoclastic matrix (Shi *et al.*, 2012). All specimens are housed at the fossil collection of the Key Lab of Insect Evolution & Environmental Changes, at the College of Life Sciences, Capital Normal University (CNUB; Dong Ren, curator), in Beijing, China. They were acquired by Fangyuan Xia before 2013 and donated for this study in 2015.

Preparation and imaging methods follow Selden & Penney (2017). The photographs were taken with a Nikon SMZ 25 and an attached Nikon DS-Ri 2 digital camera system, as well as a Nikon ECLIPSE Ni and an attached Nikon DS-Ri 2 digital camera system. Micro-CT scanning of specimen CNU-ARA-MA2020001 was carried out with a Micro-CT (HeliScan micro-CT, Thermos Fisher Scientific), located at the Department of Geology at the University of Kansas. The voltage of the Micro-CT scanner was 100 KV. The three-dimensional structure of the male palp of CNU-ARA-MA2020001 was reconstructed using 3D Slicer 4.10.2. The line drawings were prepared with Adobe Illustrator CS6 and Adobe Photoshop CC, the images were processed by Adobe Photoshop CC. Measuring method follows Selden *et al.* (2016); measurements of coxae and trochanters are 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); ALS, anterior lateral spinneret(s); AME, anterior median eye(s); at, anal tubercle; C, conductor; cx, coxa; ef, epigastric furrow; E, embolus; fe, femur; MA, median apophysis; mt, metatarsus; P, protrusion(s); pa, patella; PLE, posterior lateral eye(s); PLS, posterior lateral spinneret(s); PME, posterior median eye(s); PMS, posterior median spinneret(s); RTA, retrolateral tibial apophysis; ST, subtegulum; ta, tarsus; ti, tibia; tr, trochanter; ts, tracheal spiracle.

TAXON SAMPLING AND CHARACTER CHOICE

The discovery of new lagonomegopid fossils with well-preserved morphological details (Park *et al.*, 2019; Guo

et al., 2020) provided incentive for our analysis of the phylogenetic placement of Lagonomegopidae. We sampled six terminal taxa from Burmese amber (five taxa) and the Jinju Formation of Korea (one taxon) representing Lagonomegopidae. These taxa comprise adult males of four species: *Lineaburmops beigeli*, *Jinjumegops dalingwateri* Park *et al.*, 2019, *Odontomegops titan* and *Scopomegops fax*, one adult female: *Hiatomegops spinalis*, and one sub-adult male: Lagonomegopidae *indet.* described by Guo *et al.* (2020). They were selected because the specimens are well preserved and show some characters which were reported for the first time in Lagonomegopidae.

With reference to previous phylogenetic analyses of Araneomorphae (Griswold *et al.*, 2005; Wood *et al.*, 2012), we sampled an additional 26 non-lagonomegopid taxa representing the major Araneae clades, with the most basal spider family Liphistiidae and mygalomorph family Antrodiaetidae as the outgroups. Five living families of Palpimanoidea (Wood *et al.*, 2012; Wheeler *et al.*, 2017; Fernández *et al.*, 2018), as well as *Mimetus* Hentz, 1832 and *Pararchaea* Forster, 1955, which have peg teeth on the cheliceral promargin but belong to the superfamily Araneoidea (Wood *et al.*, 2012; Garrison *et al.*, 2016; Wheeler *et al.*, 2017; Fernández *et al.*, 2018), were included in this study.

Sixty-seven characters were extracted from previous analyses (Griswold *et al.*, 2005; Wood *et al.*, 2012) and 12 new characters were added for this analysis. Character states of non-lagonomegopid spiders were scored using data from other studies (Forster & Platnick, 1984; Griswold, 1990; Wesolowska, 1999; Griswold *et al.*, 2005; Hendrixson & Bond, 2007; Wood *et al.*, 2012; Ramírez, 2014; Murphy & Roberts, 2015; Xu *et al.*, 2015), as well as from SEM images acquired from other arachnology labs as part of the NSF Assembling the Tree of Life – Spiders project (<http://www.morphbank.net>). MESQUITE v.3.6 (Maddison & Maddison, 2019) was used to assemble the character matrix. These characters were coded as unordered. Inapplicable and unknown characters were respectively coded as ‘-’ and ‘?’ . Descriptions of character states are given in the Supporting Information (File S1). All the taxa used can be found in the Supporting Information (File S2). The data matrix is given in the Supporting Information (Files S2, S3).

PHYLOGENETIC ANALYSIS

Phylogenetic analyses were carried out using maximum parsimony and Bayesian methods. The optimal trees under the parsimony criterion were sought in TNT v.1.5 (Goloboff *et al.*, 2008a; Goloboff & Catalano, 2016) using the traditional search option under the following parameters: tree bisection reconnection (TBR) branch-swapping algorithm with 1000 replications saving 100 trees per replicate. Searches were performed under equal weights and implied weights (Goloboff, 1993; Goloboff

et al., 2008b). In our implied weights analysis, we used the methodology proposed by Mirande (2009) to set the value of concavity constant K , which determines how strongly the analysis will weigh against homoplasy. The TNT script developed by Mirande (2009: appendices S3, S4) was used (script commands `aaa 2 16 50 95 7`) to find the most fit trees under a wide range of K values. The best trees under different values of K were compared using SPR distances, the most stable tree had the highest average SPR similarity, which defined the best K value (Goloboff, 2008). Clade support was estimated within TNT through symmetric resampling (Goloboff *et al.*, 2003; absolute frequencies, change probability 33%, 1000 replicates) and by Bremer (1994) support (using a script that comes with the TNT package). The characters were mapped in WinClada (Nixon, 2002).

Bayesian analyses were performed in MrBayes v.3.2.7 (Ronquist & Huelsenbeck, 2003; Ronquist *et al.*, 2012) using a NEXUS file (including MrBayes’ commands) provided by Selden *et al.* (2020: supplementary data). The analysis employed the Lewis (2001) discrete (morphology) model. Two runs of four chains, three of which were heated, were run for a total of 5 000 000 generations, with sampling every 500 generations and the first 25% discarded as burn-in. A majority-rule consensus tree was computed with posterior probabilities for each node.

RESULTS

PHYLOGENETIC RESULTS

The equal weights analysis found 50 most parsimonious trees with 214 steps [consistency index (CI) = 41, retention index (RI) = 62]. The strict consensus of these trees (Supporting Information, Fig. S1) was unresolved regarding the relationships within Araneomorphae. The Bayesian analysis had a similar result (Supporting Information, Fig. S2). Extant Palpimanoidea were recovered as a monophyletic group with high posterior probabilities (0.99) in our Bayesian analysis, as well as the parsimony analysis under equal weights. These two analyses recovered a monophyletic Lagonomegopidae, but neither of them resolved its phylogenetic placement.

The consensus trees obtained in the implied weights analysis with $K = 3.505, 4.075, 4.793, 5.727, 6.991, 8.795, 11.585$, which shared identical topological structures, were the ones with the highest average SPR similarity (Table 1). Analysis under a K value of 3.505 resulted in ten most fit trees with 214 steps (CI = 41, RI = 62), the strict consensus tree was used as our working hypothesis tree (Fig. 1). Symmetric resampling and Bremer support values of each nodes, as well as the sensitivity (*sensu* Giribet, 2003) to weighting regimes, are shown in this tree. The preferred tree with characters marked for exploring synapomorphies can be found in the Supporting

Table 1. Average similarity between trees calculated through SPR distances. The trees with the highest average similarity with the remaining trees are in bold

	<i>K</i>	Average SPR similarity
k1	1.432	0.811
k2	1.615	0.811
k3	1.822	0.811
k4	2.060	0.811
k5	2.336	0.897
k6	2.659	0.897
k7	3.043	0.897
k8	3.505	0.915
k9	4.075	0.915
k10	4.793	0.915
k11	5.727	0.915
k12	6.991	0.915
k13	8.795	0.915
k14	11.585	0.915
k15	16.466	0.887
k16	27.205	0.887

Information (Fig. S3). Although the relationships within Lagonomegopidae are not resolved, this analysis also recovered Lagonomegopidae as a monophyletic group. A monophyletic extant Palpimanoidea is recovered here as the sister-group of Lagonomegopidae. But this clade, Lagonomegopidae + extant Palpimanoidea, has low supports (symmetric resampling = 20; Bremer support = 0.02) and only shares three homoplastic synapomorphies (characters 19, 20, 58). Entelegynae is also recovered as a monophyletic group but with low support (symmetric resampling = 22; Bremer support = 0.02). Entelegynae and the clade of Lagonomegopidae + extant Palpimanoidea are recovered as sister-groups, sharing three synapomorphies (characters 7, 47, 76). In addition, this analysis recovered both Araneoidea and the RTA clade as monophyletic but with low support.

SYSTEMATIC PALAEOLOGY

ORDER ARANEAE CLERCK, 1757

FAMILY LAGONOMEGOPIDAE ESKOV & WUNDERLICH, 1995

GENUS *SCOPOMEGOPS* GUO ET AL. **gen. nov.**

Zoobank registration: urn:lsid:zoobank.org:act:A8809BE3-D927-432B-9C04-0AC83C27391F

Etymology: The genus name is the combination of *scopa*, broom in Latin, after the clustered clavate spicules on the palpal retrolateral tibial apophysis (RTA), and the Greek suffix -μεγόψ, magnification, from *Lagonomegops*, type genus of the family. The name is masculine.

Type species: *Scopomegops fax* sp. nov.

Diagnosis: Male palpal tibia with a small apophysis on the distal retrolateral surface, several clustered clavate spicules situated on the top of retrolateral apophysis; leg metatarsus distinctly much longer than tarsus.

Remarks: CNU-ARA-MA2020001 is an adult male. It can be easily distinguished from other male lagonomegopids by the apophysis on the distal retrolateral surface of the male palpal tibia. It cannot be included in the two lagonomegopid genera (*Lagonoburmops* Wunderlich, 2012 and *Picturmegops* Wunderlich, 2015) comprised only of female specimens, because of: carapace piriform in outline, much longer than wide (carapace distinctly narrowed posteriorly, slightly wider than long in *Picturmegops*); leg setae not long and dense (legs densely covered with long setae in *Lagonoburmops*). Conspecific spiders have some morphological differences at different developmental stages (Foelix, 2011). It is difficult to judge whether an adult male and a juvenile are the same species, especially in fossils. Therefore, we have erected a new genus *Scopomegops* based on CNU-ARA-MA2020001.

Besides *Scopomegops*, seven species belonging to five genera of Lagonomegopidae are known to have one or more apophyses on the male palpal tibia. In *Albiburmops annulipes* Wunderlich, 2017, the carapace length is equal to its width, whereas the carapace is distinctly much longer than wide in *Scopomegops*. In *Archaelagonops propinquus* Wunderlich, 2015 and *Archaelagonops scorsum* Wunderlich, 2015, the palpal tibia bears two apophyses, whereas there is only one in *Scopomegops*. In *Cymbiolagonops cymbiocalcar* Wunderlich, 2015, the palpal tibia bears a divided apophysis, whereas the RTA is undivided in *Scopomegops*. In *Parviburmops bigibber* Wunderlich, 2017, the tibial apophysis is situated on the ventral surface, but is on the retrolateral surface in *Scopomegops*. In *Paxillomegops longipes* Wunderlich, 2015 and *Paxillomegops brevipes* Wunderlich, 2015, the palpal tibia bears numerous short peg bristles, which are lacking in *Scopomegops*.

SCOPOMEGOPS FAX GUO ET AL. **sp. nov.**

(FIG. 2)

Zoobank registration: urn:lsid:zoobank.org:act:A897B322-B55F-4652-AF1C-FAD42209F78C

Etymology: The specific name is the Latin noun *fax*, meaning torch, referring to the shape of the male palp.

Holotype: Male, specimen no. CNU-ARA-MA2020001.

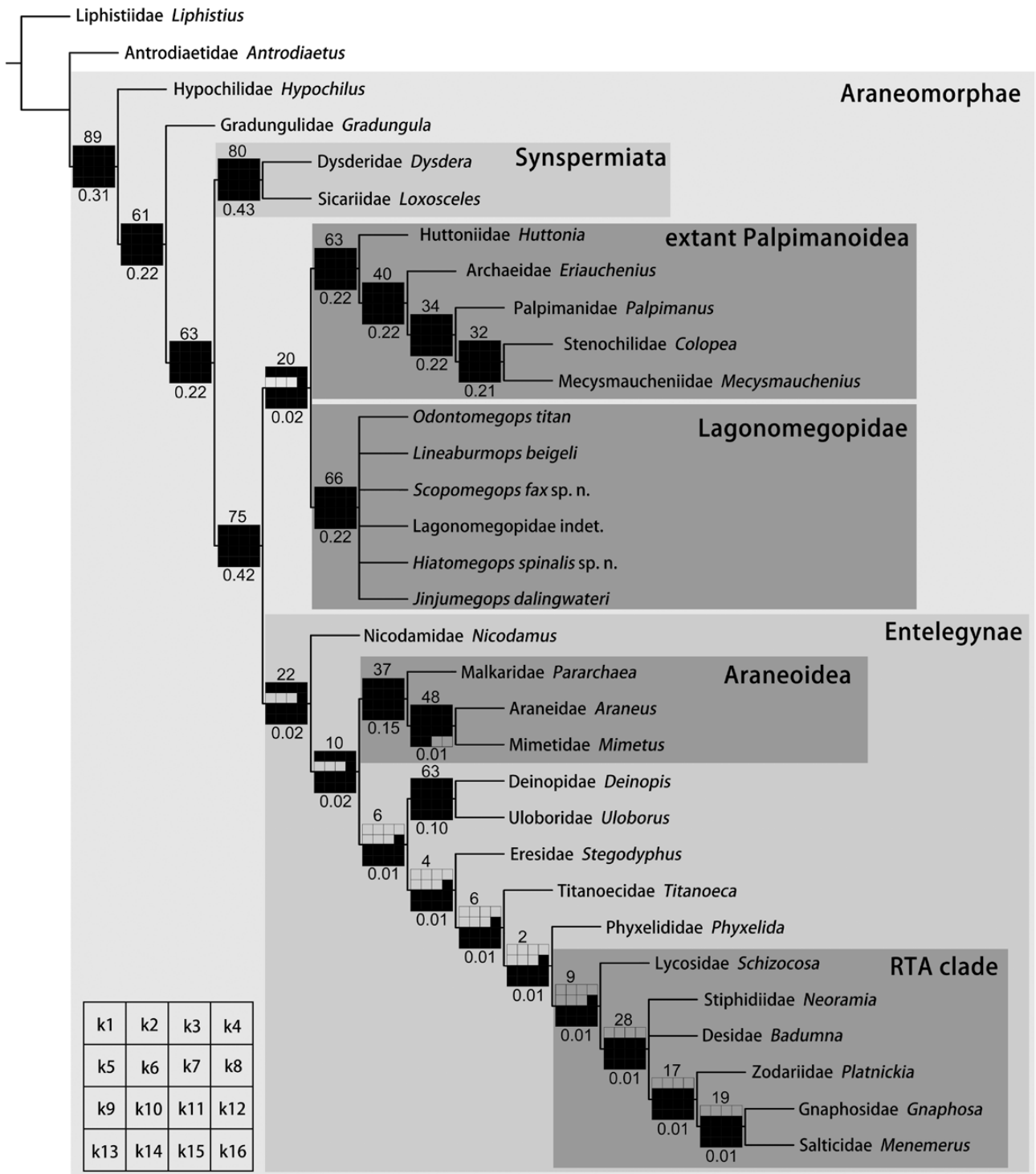


Figure 1. Strict consensus of ten trees obtained under implied weights analysis with *K* values of 3.505 (topology identical to *K* values of 4.075, 4.793, 5.727, 6.991, 8.795 and 11.585). Symmetric resampling values are shown above branches, Bremer supports below branches. Sensitivity to weighting regimes: black squares are recovered topologies, white squares are unrecovered topologies.

Locality and horizon: Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, Mid-Cretaceous.

Diagnosis: As for the genus.

Taphonomic features: CNU-ARA-MA2020001: femur, patella, tibia, metatarsus, tarsus of left leg II and metatarsus, tarsus of right leg I are missing; left leg I, caused by developmental malformation or autotomy, is much smaller than right leg I; the abdomen is compressed; there is a large bubble on the left side of the abdomen, and several small bubbles around the spider. A thrips near the left leg IV is present as a syninclusion.

Description: Body length 4.97, carapace light-coloured medially, dark-coloured laterally, a pair of indistinct dark longitudinal stripes on abdomen dorsally. Carapace piriform in outline, length 2.44, width 1.54 at widest point, covered with short, dense, feathery setae pressed flat against the cuticle. Cephalic region of carapace slightly raised, with a pair of distinct protrusions beneath the inner side of PME (Fig. 2G). Fovea oval, shallow, situated in the centre of carapace, next to the posterior margin of cephalic region. Eight eyes present; PME enormous, 0.43 in diameter, situated on anterolateral corner of carapace; PLE small, placed at the mediolateral margin of cephalic region, separated 0.50 from the PME centre; AME and ALE contiguous, situated between the PME and the clypeal margin (Fig. 2G). Chelicera length 0.96, and width 0.36 at base, cheliceral insertion close to mouthparts, stridulatory files absent. Fang length 0.33. Chelicera with about six peg teeth on promargin (Fig. 2C); retromargin unrecognizable. Labium ligulate, longer than wide, not fused to sternum. Endites elongated, converging and meeting in midline; apex and prolateral margin of endites brushy with dense setae; serrula as a single row of teeth. Sternum shield shaped, covered with setae, slightly convex and without tubercles.

Palpal podomere lengths: fe 1.01, pa 0.40, ti 0.43, ta 0.98. Palp hairy, feathery setae at least present on tibia. Tibia with at least three dorsal trichobothria in a single row; a small apophysis present on the distal retrolateral surface of tibia, several clustered clavate spicules situated on the top of retrolateral apophysis (Fig. 2D, H). Male palp torch-like, cymbium elongate; embolus curved, slightly embraced by the long sheet conductor; median apophysis horn-like; subtegulum round, with a distally curved apophysis (Fig. 2I–L; File S4).

Legs long but no legs enlarged; metatarsus distinctly much longer than tarsus in all legs. Leg formula II > I > IV > III: leg I cx 0.64, tr 0.11, fe 2.81, pa 0.92, ti > 2.69; leg II cx 0.60, tr 0.11, fe 2.95, pa 0.84, ti 3.42, mt 2.42, ta 0.87; leg III cx 0.60, tr

0.10, fe 1.94, pa 0.65, ti 1.92, mt 1.13, ta 0.63; leg IV cx 0.65, tr 0.12, fe 2.51, pa 0.77, ti 2.28, mt 2.01, ta 0.82. Metatarsus and tarsus without scopulae. Distal preening comb composed of eight short macrosetae, present on metatarsus of posterior legs ventrally (Fig. 2E, F). Feathery setae at least present on all tibia. Tibiae with about 14, metatarsi with about ten, tarsi with about ten trichobothria (Fig. 2E, F). Three tarsal claws, paired claws with about four to five teeth, distal two teeth distinctly larger than others, median claw hook-like. Abdomen length 2.17, width > 0.66, densely covered with short setae. Four spinnerets visible, details unrecognizable.

Remarks: Holotype with left leg I much smaller than right leg I. It was caused by developmental malformation or autotomy. Autotomy is a voluntary act allowing most spiders to amputate one of their own legs to escape from a perilous situation. Although the lost legs can be replaced by new ones regenerated after the next moult, these are usually smaller, and need further moults to grow into normal size (Foelix, 2011).

GENUS *HIATOMEGOPS* GUO ET AL. **gen. nov.**

Zoobank registration: urn:lsid:zoobank.org:act:F0561F03-E69D-45E6-A7FB-4A4D3BFEC6EE

Etymology: The genus name is the combination of *hiatus*, opening in Latin, after the broad tracheal spiracle behind the epigastric furrow, and *Lagonomegops*, type genus of the family, from Greek -μεγόψ, magnification. The name is masculine.

Type species: *Hiatomegops spinalis* sp. nov.

Diagnosis: Palpal tibia and tarsus with several dorsal trichobothria; leg metatarsus slightly longer than tarsus; broad tracheal spiracle situated on postgastric area behind epigastric furrow.

Remarks: Finding a fossil spider species in which both males and females have been described is rare. Among 19 reported genera in Lagonomegopidae, only *Archaelagonops* Wunderlich, 2012 is known from both male and female specimens. The two female specimens, which were subsequently included in *Archaelagonops* (erected on a male specimen originally), lack sufficient evidence to belong in that genus (Wunderlich, 2012, 2015). In general, female spiders are a larger size than conspecific males. Four lagonomegopid species, *Lineaburmops beigeli*, *Lineaburmops maculatus* Wunderlich, 2015, *Parviburmops brevipalpus* Wunderlich, 2015 and *Planimegops parvus* Wunderlich, 2017, comprised only

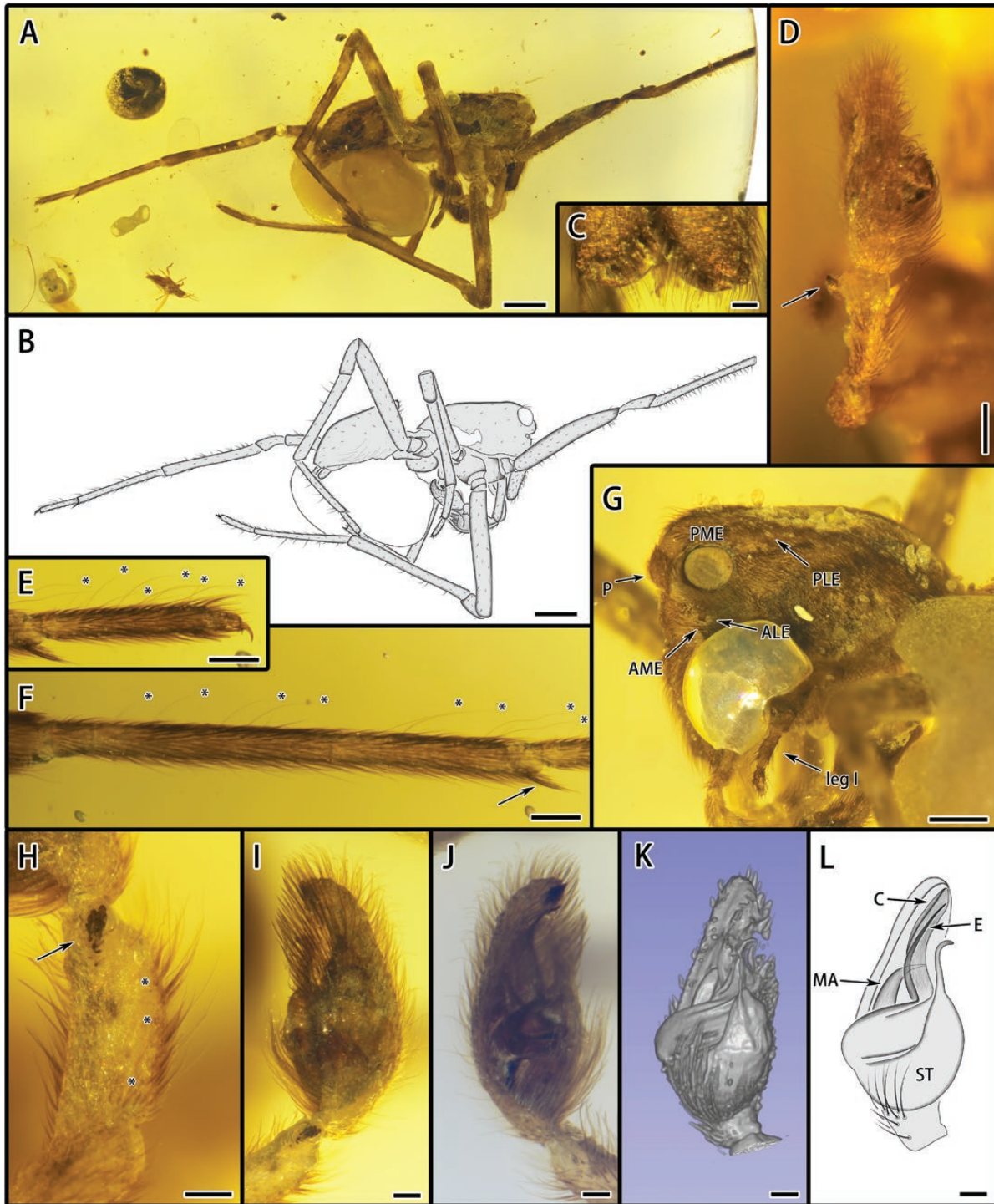


Figure 2. *Scopomegops fax*, holotype CNU-ARA-MA2020001: A, habitus, lateral view; B, schematic drawing of lateral habitus; C, distal part of chelicerae, dorsal view, showing peg teeth; D, tibia and male palp of right pedipalp, dorsal view, showing retrolateral tibial apophysis (arrow); E, tarsus of left leg IV, lateral view, showing trichobothria (asterisks); F, metatarsus of left leg IV, lateral view, showing trichobothria (asterisks) and preening comb (arrow); G, cephalothorax, lateral view, showing eyes and abnormal left leg I; H, tibia of left pedipalp, lateral view, showing trichobothria (asterisks) and retrolateral tibial apophysis (arrow); I, left male palp, retrolateral view; J, left male palp, ventral view; K, 3D CT reconstruction of left male palp, ventral view; L, reconstruction of left male palp, ventral view. Scale bars represent 1 mm (A, B) 0.5 mm (G), 0.2 mm (D, E, F) and 0.1 mm (C, H, I, J, K, L).

of male specimens, were described as having a similar or smaller size with CNU-ARA-MA2020002, an adult female. CNU-ARA-MA2020002 can be distinguished from them by: carapace without white patch (carapace with distinct white patches in *Lineaburmops beigeli* and *Lineaburmops maculatus*); carapace much longer than wide (carapace length equal with width in *Parviburmops brevivalpus*); cephalic region of carapace with a pair of anterolateral protrusions next to the inner side of PME (protrusions absent in *Planimegops parvus*). We erected a new genus *Hiatomegops* based on CNU-ARA-MA2020002. *Hiatomegops* can be distinguished from the other two lagonomegopid genera (*Lagonoburmops* and *Picturmegops*) comprised only of female specimens by: body length 2.89 (body length about 8.00 in *Lagonoburmops*); carapace piriform in outline, much longer than wide (carapace distinctly narrowed posteriorly, slightly wider than long in *Picturmegops*); carapace without a stripe (carapace with distinct stripes in *Picturmegops*); metatarsus of leg I slightly longer than tarsus (metatarsus of leg I about two times longer than tarsus in *Lagonoburmops*).

In addition, the holotypes of *Grandoculus chemahawinensis* Penney, 2004, *?Lagonomegops cor* Pérez-de la Fuente et al., 2013, *Soplaogonomegops unzuei* Pérez-de la Fuente et al., 2013, *Spinomegops aragonensis* Pérez-de la Fuente et al., 2013 and *Spinomegops arcanus* Pérez-de la Fuente et al., 2013 were identified as ‘juvenile or adult female’ (Penney, 2004; Pérez-de la Fuente et al., 2013). *Hiatomegops* can be easily separated from these by: carapace piriform in outline, without neck (carapace heart-shaped when viewed from above in *?Lagonomegops cor*; cephalic region constricted in a neck, with narrowest point medially in *Soplaogonomegops unzuei*), fovea small oval, deeply depressed (fovea absent in *Spinomegops aragonensis* and *Spinomegops arcanus*), leg I not enlarged, metatarsus and tarsus without scopulae (leg I distinctly longer and more robust than the others, metatarsus and tarsus with scopulae hairs in *Grandoculus chemahawinensis*).

***HIATOMEGOPS SPINALIS* GUO ET AL. sp. nov.**

(FIG. 3)

Zoobank registration: urn:lsid:zoobank.org:act:9168FFD9-29C1-4158-878B-D29E71594D41

Etymology: The specific name is the Latin adjective *spinalis*, meaning with spine(s), referring to the long macrosetae on the distal prolateral surface of palpal tibia.

Holotype: Female, specimen no. CNU-ARA-MA2020002.

Locality and horizon: Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, Mid-Cretaceous.

Diagnosis: As for the genus.

Taphonomic features: CNU-ARA-MA2020002: completely preserved; many bubbles and impurities are present around the spider. Parts of insect legs are present as syninclusions.

Description: Body length 2.89, carapace and legs dark-coloured, abdomen light-coloured, with an indistinct median dorsal stripe (Fig. 3A, B). Carapace piriform in outline, length 1.30, width 0.87 at widest point, covered with short, dense, feathery setae pressed flat against the cuticle (Fig. 3A). Cephalic region of carapace slightly raised, with a pair of anterolateral protrusions next to the inner side of PME (Fig. 3E). Fovea small oval, deeply depressed, situated in the centre of carapace, next to the posterior margin of cephalic region (Fig. 3A). Eight eyes present; PME enormous, 0.26 in diameter, situated on anterolateral corner of carapace; PLE small, placed at the mediolateral margin of cephalic region, separated 0.31 from the PME centre; AME and ALE contiguous, situated between the PME and the clypeal margin. Chelicera length 0.62, width 0.27 at base, cheliceral insertion close to mouthparts, stridulatory files absent. Fang length 0.22. Chelicera with about six peg teeth on promargin (Fig. 3E), retromargin not visible. Labium ligulate, slightly longer than wide, not fused to sternum. Endites elongated, converging and meeting in midline; serrula as a single row of teeth. Sternum shield shaped, covered with setae, convex and without tubercles.

Palpal podomere lengths: fe 0.34, pa 0.17, ti 0.24, ta 0.45. Palp hairy; tibia and tarsus with several dorsal trichobothria; tibia with a long macrosetae on the distal prolateral surface (Fig. 3F). Palpal claw absent.

Legs hairy, no legs enlarged; metatarsus slightly longer than tarsus. Leg formula II > I > IV > III: leg I cx 0.23, tr 0.07, fe 0.90, pa 0.47, ti 0.76, mt 0.64, ta 0.49; leg II cx 0.26, tr 0.07, fe 0.98, pa 0.40, ti 0.93, mt 0.63, ta 0.46; leg III cx 0.27, tr 0.07, fe 0.80, pa 0.36, ti 0.58, mt 0.47, ta 0.42; leg IV cx 0.33, tr 0.09, fe 0.93, pa 0.33, ti 0.73, mt 0.67, ta 0.47. Metatarsus and tarsus without scopulae. Distal preening comb composed of seven to ten short macrosetae, present on metatarsus of posterior legs ventrally. Feathery setae at least present on femur and patella of leg II. Tibiae with about ten, metatarsi with about six, tarsi with about six trichobothria in at least two rows. Three tarsal claws, paired claws with three to five teeth, median claw hook-like.

Abdomen ovoid, length 1.33, width 0.89, densely covered with short, feathery setae. Female genitalia

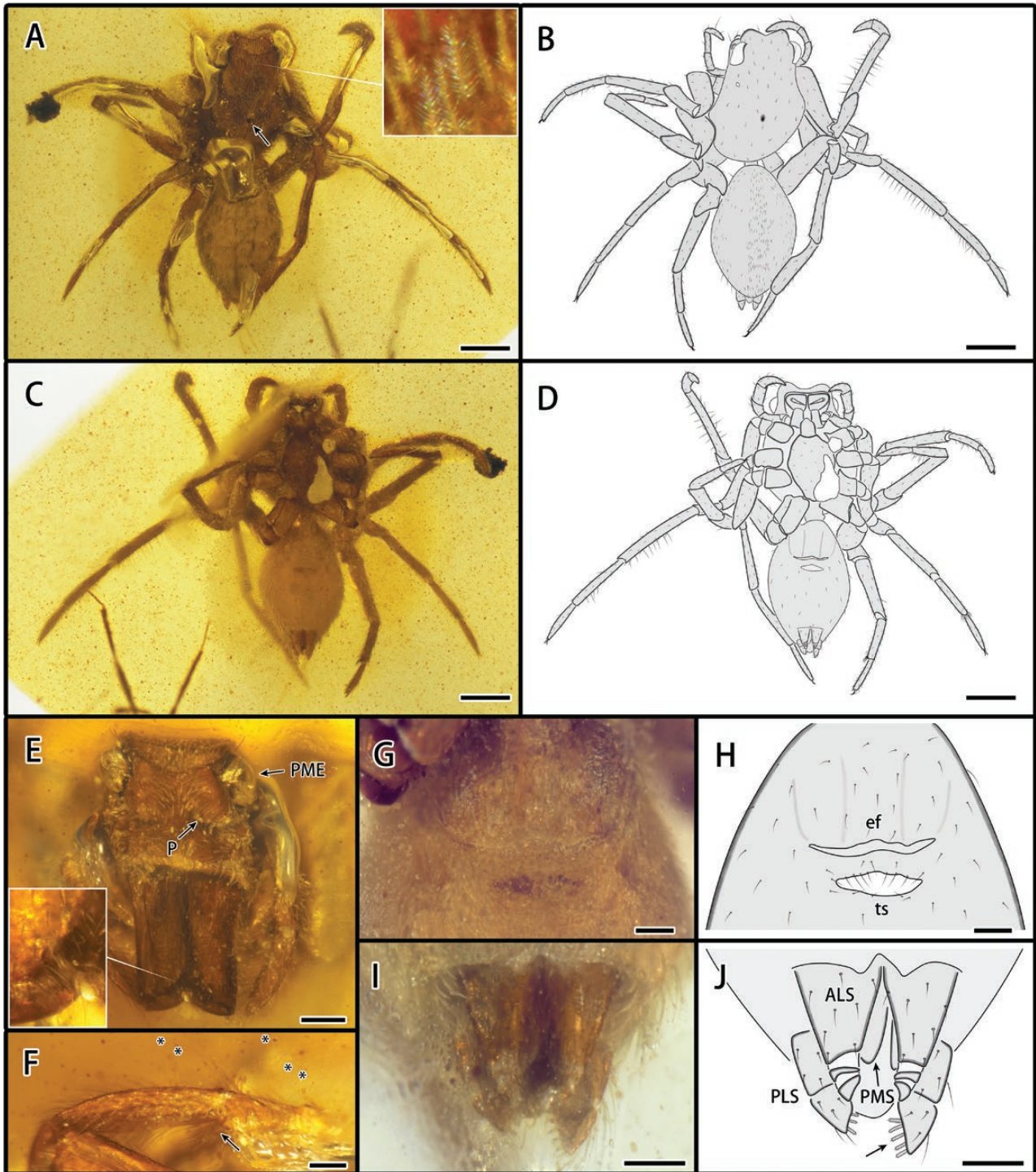


Figure 3. *Hiatomegops spinalis*, holotype CNU-ARA-MA2020002: A, habitus, dorsal view, showing fovea (arrow) and feathery setae (magnified at the top right) on carapace; B, schematic drawing of dorsal habitus; C, habitus, ventral view; D, schematic drawing of ventral habitus; E, cephalothorax, anterior view, showing peg teeth (magnified at the bottom left); F, tibia and tarsus of right pedipalp, lateral view, showing trichobothria (asterisks) and long macrosetae (arrow); G, basal part of abdomen, ventral view, showing female genitalia and tracheal spiracle; H, schematic drawing of basal ventral abdomen; I, spinnerets, ventral view; J, schematic drawing of spinnerets, showing spigots (lower arrow). Scale bars represent 0.5 mm (A, B, C, D), 0.2 mm (E) and 0.1 mm (F, G, H, I, J).

simple, epigyne absent. A broad subovoid opening, interpreted as tracheal spiracle, situated on the postgastric area behind the epigastric furrow (Fig. 3G, H). Six spinnerets; ALS with three segments, basal segment much longer than others; PLS about as large as ALS, with two segments, distal segment almost as the equal length with basal segment; retrolateral surface of distal segment with a series of large spigots (Fig. 3I, J).

Remarks: Lagonomegopidae was once thought to have a female-biased sex ratio (Pérez-de la Fuente *et al.*, 2013), but as more and more male lagonomegopids are found and described, this issue was resolved (Park *et al.*, 2019). The well-preserved female genitalia of CNU-ARA-MA2020002 shows that it is an unequivocal adult female.

GENUS *LINEABURMOPS* WUNDERLICH, 2015

Type species: *Lineaburmops beigeli* Wunderlich, 2015.

LINEABURMOPS BEIGELI WUNDERLICH, 2015

(FIGS 4, 5)

Wunderlich (2015): 255–256, figs 236, 237, photos 104, 105.

Material: Two adult males, specimen nos CNU-ARA-MA2020003 and CNU-ARA-MA2020004.

Locality and horizon: Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, Mid-Cretaceous.

Taphonomic features: CNU-ARA-MA2020003: the pedicel and abdomen are somewhat broken; metatarsus, tarsus of left leg I, II and patella of left leg IV are missing; there are a few bubbles and impurities around the spider. A thrips near the tibia of left leg III is present as a syninclusion. CNU-ARA-MA2020004: the tarsus of left leg IV is incomplete, tarsal claws are missing; and there are many impurities and cracks around the spider.

Description: Body length 2.98–3.08, dark-coloured, with a subtriangular white patch on clypeus, a pair of reniform white patches on the thoracic region and a pair of white longitudinal stripes on the abdomen dorsally (Figs 4A, B, 5F). Carapace length 1.57–1.59, width 0.96–0.99 at widest point, covered with short, dense, feathery setae pressed flat against the cuticle. Cephalic region of carapace slightly raised, with a pair of anterolateral protrusions next to the inner side of PME. Neck present between cephalic and thoracic regions, slightly narrower than cephalic region.

Fovea absent. Eight eyes present; PME enormous, 0.17 in diameter, situated on anterolateral corner of carapace; PLE small, placed at the mediolateral margin of cephalic region, separated 0.25 from the PME centre; AME and ALE contiguous, situated between the PME and the clypeal margin. Chelicera length 0.58 and width 0.29 at base, cheliceral insertion distinctly separated from mouthparts, stridulatory files absent. Fang length 0.19. Chelicera with about eight peg teeth on promargin (Fig. 4C); retromargin not visible. Labium subtriangular, slightly longer than wide, not fused to sternum. Endites elongated, converging but not meeting in midline; serrula as a single row of teeth. Sternum covered with setae, convex and without tubercles.

Palpal podomere lengths: fe 0.51, pa 0.18, ti 0.27, ta 0.67. Palp hairy, feathery setae at least present on tarsus. Tibia with three dorsal trichobothria in a single row (Fig. 5A). Cymbium elongate, finger-like distally (Fig. 5A). Detailed structures of male palp, such as embolus and conductor, not recognizable.

Legs long but no legs enlarged; metatarsus distinctly much longer than tarsus in anterior legs; metatarsus slightly longer than tarsus in posterior legs. Leg formula I > II > IV > III: leg I cx 0.31, tr 0.07, fe 1.47–1.58, pa 0.34, ti 1.44–1.60, mt 1.10–1.16, ta 0.66–0.75; leg II cx 0.37, tr 0.07, fe 1.49–1.53, pa 0.31–0.37, ti 1.43–1.45, mt 1.08–1.11, ta 0.66–0.71; leg III cx 0.24–0.28, tr 0.06, fe 1.14–1.17, pa 0.30–0.32, ti 1.02–1.14, mt 0.67–0.69, ta 0.50–0.57; leg IV cx 0.29–0.31, tr 0.08, fe 1.46–1.51, pa 0.32–0.35, ti 1.28–1.42, mt 0.83–0.86, ta 0.64–0.67. Metatarsus and tarsus without scopulae. Distal preening comb composed of six to eight short macrosetae, present on metatarsus of posterior legs ventrally (Fig. 5C). Feathery setae at least present on femur, patella, tibia and metatarsus (Fig. 5B). Tibiae at least with five, metatarsi at least with six, tarsi at least with nine trichobothria (Fig. 5C, D). Three tarsal claws, paired claws with five to eight teeth, median claw hook-like. Serrate accessory claw setae near the median claw present at least on left leg III (Fig. 5E).

Abdomen ovoid, length 1.27–1.34, width 0.65–0.68, densely covered with short feathery setae. Spinnerets and anal tubercle encircled by a quadrate glabrous band. Four spinnerets visible. ALS with two segments, distal segment much smaller than basal segment; PLS about as large as ALS, details not visible (Fig. 4E, F).

Remarks: These two specimens can be assigned to *Lineaburmops beigeli*, the type species of genus *Lineaburmops*, by the following characters: the shape and placement of white patches on carapace and abdomen; the length of the podomeres.

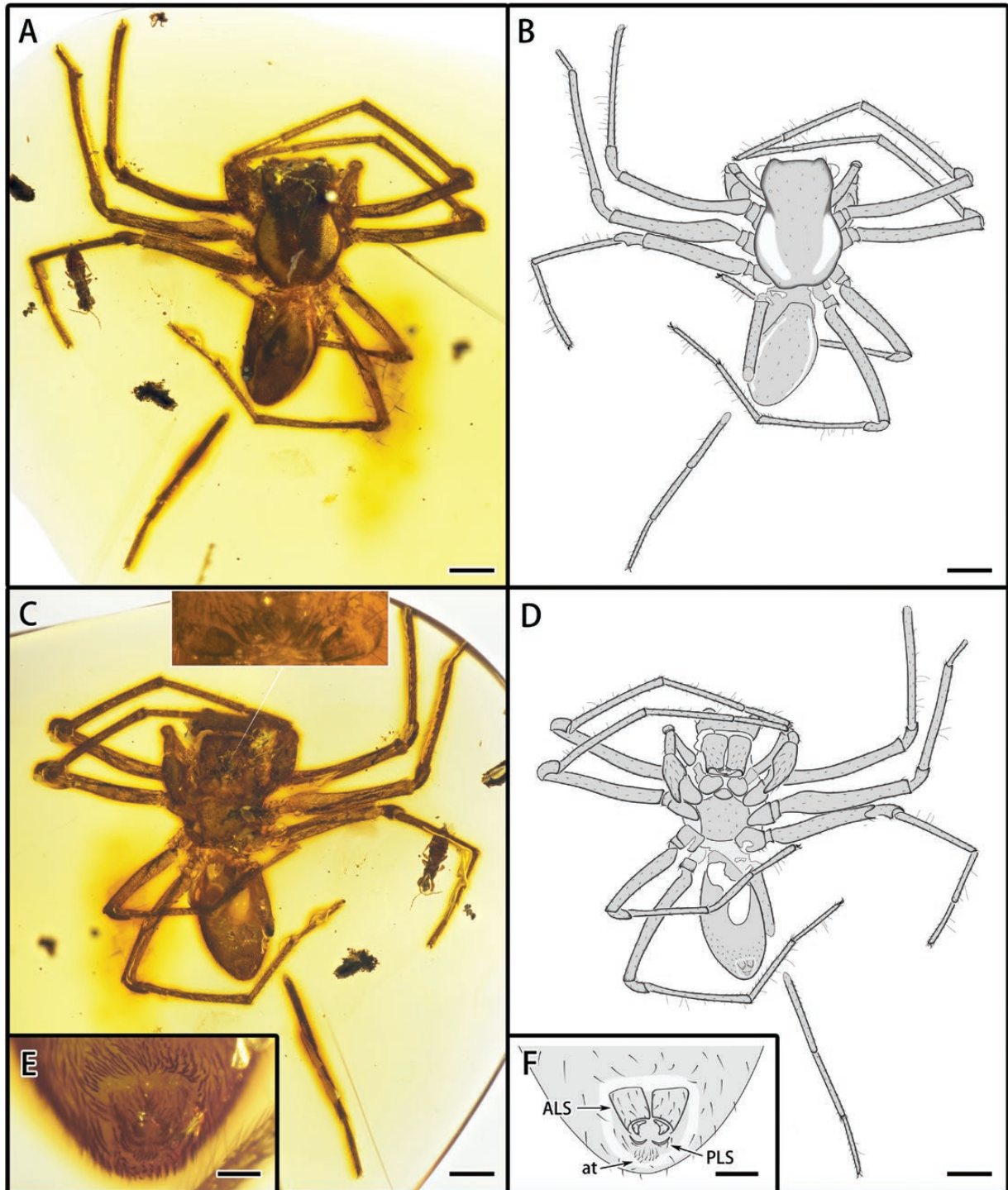


Figure 4. *Lineaburmops beigeli*; CNU-ARA-MA2020003: A, habitus, dorsal view; B, schematic drawing of dorsal habitus; C, habitus, ventral view, showing peg teeth (magnified at the top); D, schematic drawing of ventral habitus; E, distal part of abdomen, ventral view, showing spinnerets and anal tubercle; F, schematic drawing of distal ventral abdomen. Scale bars represent 0.5 mm (A, B, C, D) and 0.1 mm (E, F).

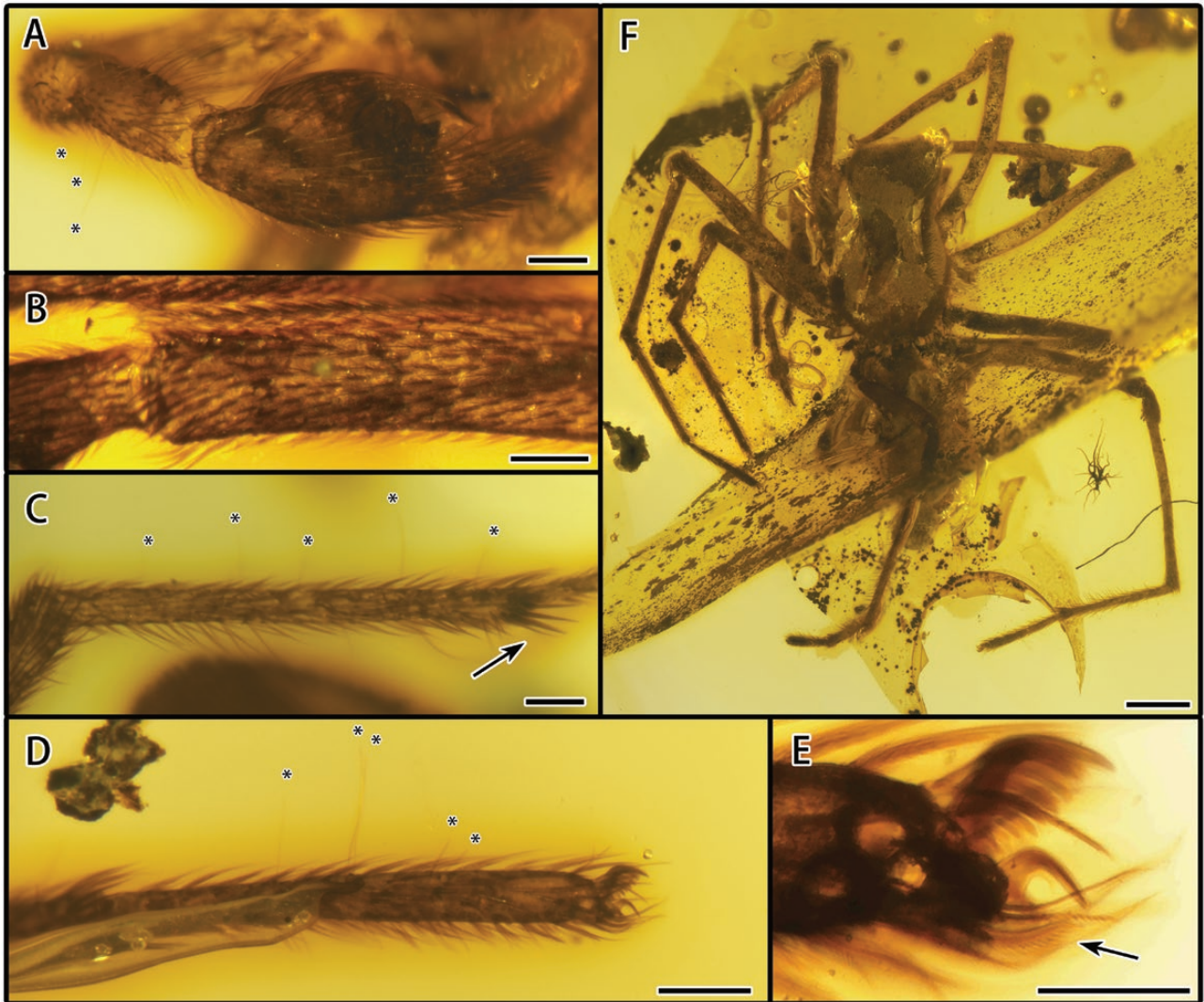


Figure 5. *Lineaburmops beigeli*; CNU-ARA-MA2020003: A, tibia and male palp of right pedipalp, dorsal view, showing trichobothria (asterisks); B, distal femur of left leg III, lateral view, showing feathery setae; C, metatarsus of right leg IV, lateral view, showing trichobothria (asterisks) and preening comb (arrow); D, tarsus of left leg III, lateral view, showing trichobothria (asterisks); E, distal tarsus of left leg III, lateral view, showing claws and serrate accessory claw setae (arrow). CNU-ARA-MA2020004: F, overall habitus, dorsal view. Scale bars represent 0.5 mm (F), 0.1 mm (A, B, C, D) and 0.05 mm (E).

GENUS *ODONTOMEGOPS* GUO & SELDEN, 2020

Type species: *Odontomegops titan* Guo & Selden, 2020.

ODONTOMEGOPS TITAN GUO & SELDEN, 2020

(FIG. 6)

Guo *et al.* (2020): 2–4, figs 1, 2.

Material: Male, specimen no. CNU-ARA-MA2019001 (holotype).

Locality and horizon: Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, Mid-Cretaceous.

Description: See Guo *et al.* (2020). Epigastric plate with more than 30 epiandrous spigots scattered along median margin of epigastric furrow (Fig. 6C). Tracheal

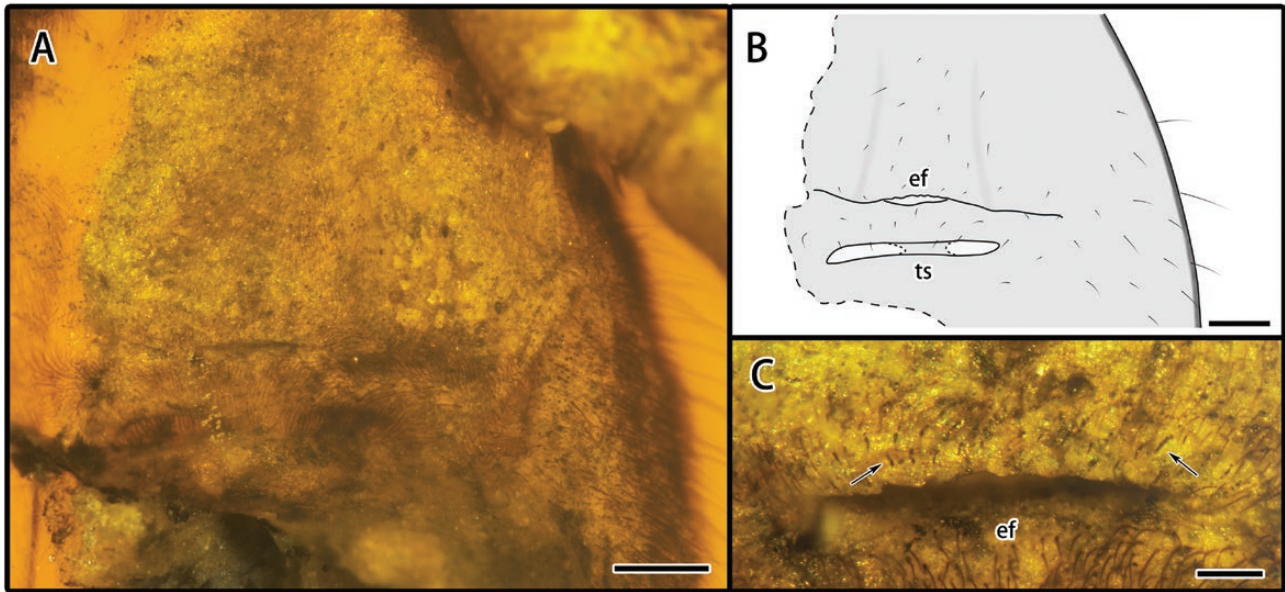


Figure 6. *Odontomegops titan*; holotype CNU-ARA-MA2019001: A, basal part of abdomen, ventral view, showing male genitalia and tracheal spiracle; B, schematic drawing of basal ventral abdomen; C, male genitalia, ventral view, showing epigastric furrow and epiandrous spigots (arrows). Scale bars represent 0.5 mm (A, B) and 0.1 mm (C).

spiracle broad, situated on postgastric area behind epigastric furrow, immediately dividing internally into two tracheae (Fig. 6A, B).

Remarks: After regrinding and repolishing the holotype of *Odontomegops titan*, the male genitalia and tracheal spiracle are now shown clearly. They differ from the single, broad opening in *Hiatomegops spinalis* (Fig. 3G, H), in that two small openings are situated on the postgastric area behind the epigastric furrow in *Odontomegops titan* (Fig. 6A, B). We interpret the abdomen of CNU-ARA-MA2019001 as being somewhat modified and broken, thus exposing the internal part of the tracheal spiracle. Hence, we interpret the posterior respiratory system of *Odontomegops titan* as a single, broad tracheal spiracle, which immediately divides internally into two smaller tracheae.

DISCUSSION

PHYLOGENETIC PLACEMENT OF LAGONOMEGOPIDAE

In our analysis, a monophyletic Lagonomegopidae is recovered but with the interfamilial relationships unclear, because the characters used here are selected for resolving the relationships among higher groups instead of lagonomegopid genera or species. The main lagonomegopid synapomorphies are: PME larger than all other eyes (character 3) and positioned on the anterolateral flanks of the carapace (character 4).

Large PME also appear independently in Deinopidae Koch, 1850 and Lycosidae Sundevall, 1833 in this study, but these are not positioned in the anterolateral flanks of the carapace. Moreover, some of the potential synapomorphies with homoplasy supporting this clade are the presence of tarsal trichobothria (character 52), leg metatarsus with three or more trichobothria (character 54) and the presence of feathery setae (character 57).

Consistent with the results of previous analyses (Wood *et al.*, 2012, 2013, 2018; Fernández *et al.*, 2018; Selden *et al.*, 2020), extant Palpimanoidea, including five families, is recovered as monophyletic in the present study. The synapomorphies shared by extant palpimanoid families have been discussed before (Wood *et al.*, 2012: appendix 3). Phylogenetic relationships among extant palpimanoid families are still unstable; the previous studies (Wood *et al.*, 2012, 2013, 2018; Fernández *et al.*, 2018; Selden *et al.*, 2020) and our analysis have yielded mixed results. It should be noted, especially, that only the analysis performed by Wood *et al.* (2018) was designed for examining relationships among palpimanoids, whereas other studies, including ours, focused on different issues.

Lagonomegopidae is recovered as sister-group to extant Palpimanoidea in the present study, but the supports for this topology are weak and only three homoplastic synapomorphies are shared by Lagonomegopidae and extant Palpimanoidea: true teeth situated only on the retromargin of chelicera (character 19), chelicera with peg teeth (character 20) and a reduction in leg spination (character 58). Although regarded as a

homoplastic synapomorphy, character 19 is inapplicable to the members of Huttoniidae, Mecysmaucheniiidae and Stenochilidae. The presence of peg teeth on the chelicera and the spineless legs were considered as synapomorphies of Palpimanoidea in a previous study (Wood *et al.*, 2012: appendix 3). These two characters were also used by Eskov & Wunderlich (1995) to place Lagonomegopidae into Palpimanoidea. Peg teeth are not only present in palpimanoids (although absent in stenochilids), but also have evolved independently in some mimetids and malkarids; spineless legs also appear in some non-palpimanoid groups. These two characters are considered homoplastic synapomorphies shared by extant Palpimanoidea and Lagonomegopidae in this analysis.

Entelegynae is also recovered as a monophyletic group but with low support. The only non-homoplastic synapomorphy is the entelegyne female genitalia. A clade including Lagonomegopidae + extant Palpimanoidea and Entelegynae is recovered to be monophyletic with Lagonomegopidae + extant Palpimanoidea as the sister-group of Entelegynae. This clade is supported by three non-homoplastic synapomorphies: indirect eyes with canoe-shaped tapetum (character 7), tarsal organ capsulate (character 47) and spinnerets with cylindrical gland spigots (character 76), although these characters are unknown for most of lagonomegopid taxa in this study. Palpimanoidea was also considered as a possible sister-group of Entelegynae in the previous studies (Wood *et al.*, 2012, 2013, 2018; Wheeler *et al.*, 2017; Fernández *et al.*, 2018).

To explore the phylogenetic placement of Lagonomegopidae, we sampled six taxa representing this extinct family. These six representatives can cover most, but not all, characters present in Lagonomegopidae. The presence of a scopulae on leg I is an important feature in extant palpimanoid families. In Lagonomegopidae, four species (*Archaelagonops scorsum*, *Grandoculus chemahawinensis*, *Parviburmops brevialpus* and *?Paxillomegops brevipes*) have been described as having this character (Penney, 2004; Pérez-de la Fuente *et al.*, 2013; Wunderlich, 2015), but none of these were included in our study. It is important to point out that the images showing scopulae were provided only in *Grandoculus chemahawinensis* (Penney, 2004; Pérez-de la Fuente *et al.*, 2013), and these hook-tipped scopulae have a different structure from the common scopulae with spatulate tips that are present in the extant palpimanoid families (Forster & Platnick, 1984). In addition, no fossil taxa, except lagonomegopids, were included in the present study. Further phylogenetic analyses with the inclusion of more fossil spiders as terminal taxa may extend our knowledge of the evolution of the palpimanoids in the future.

EXTERNAL SEXUAL ORGANS AND APOPHYSIS ON THE RETROLATERAL SURFACE OF MALE PALPAL TIBIA (RTA)

There are two general types of female spider genitalia: haplogyne and entelegyne. Haplogyne female genitalia have only a single genital opening functioning as both copulatory duct and fertilization duct, while the entelegyne female genitalia have two different forms of ducts used for copulation and oviposition, respectively (Foelix, 2011). Corresponding to the different types of female genitalia, male palps also have various morphologies. Generally, spiders with haplogyne female genitalia have simple forms of male palps, while the ones with entelegyne female genitalia have more complex male palps (Foelix, 2011). The entelegyne female genitalia was generally considered as an identified character for Entelegynae (Wheeler *et al.*, 2017), while the haplogyne female genitalia could be found in the other spider clades. However, recent studies have suggested that the conventional model of entelegyne reproduction needs redefinition (Zhan *et al.*, 2019) and that the entelegyne condition has evolved at least six times independently within spiders (Michalik *et al.*, 2019). Anyway, the two general female genital types have played an important role in the classification and phylogeny of spiders.

The detailed morphological study on the external sexual organs of Lagonomegopidae is useful for examining its phylogenetic placement. Reconstruction of the male palp of *Scopomegops fax*, based on 3D CT data and optical images provides more information for our phylogenetic analysis. The holotype of *Hiatomegops spinalis* is one of the rare female lagonomegopid specimens, its female genitalia, without an epigynum, shows a relatively simple structure. But the criteria for determining the type of female genitalia is its interior structure, not just the presence or absence of epigynum. Hence, we considered the type of lagonomegopid female genitalia as unknown in this study.

Some spiders have apophyses on the surface of their male palpal tibia, functioning during the mating process (Coddington & Levi, 1991; Wheeler *et al.*, 2017). These apophyses come in a variety of forms and occupy different positions, and their homologies are ambiguous and controversial (Coddington, 1990; Griswold *et al.*, 2005; Ramírez, 2014). Here, we recognize that a single tibia may have apophyses on as many as four surfaces (prolateral, dorsal, retrolateral and ventral) and, therefore, divide them into four homology hypotheses in this study, following Griswold *et al.* (2005).

Retrolateral tibial apophyses (RTAs) was usually deemed as a synapomorphy that defined the RTA clade (Wheeler *et al.*, 2017), a highly diverse group, which accounted for about 45% of the known spider species. However, the RTA also appears in some other groups,

such as *Liphistius* Schiödte, 1849, *Mecysmauchenus* Forster & Platnick, 1984 and Titanoecidae Lehtinen, 1967 (Forster & Platnick, 1984; Ramírez, 2014; Xu *et al.*, 2015). In Lagonomegopidae, seven species (including *Scopomegops fax*) are known to have one or two RTAs on the male palp, which are usually small and have several clustered clavate spicules situated on the top (Wunderlich, 2015, 2017). The homology of the RTA in these different spider groups is obscure. Our analysis suggests that lagonomegopids are not closely related to the RTA clade; the similar characters, such as leg tarsal trichobothria, shared by them are possibly convergent, because they may occupy a similar niche (Penney, 2005). There is still no unambiguous fossil evidence of RTA clade spiders in the Mesozoic (Magalhaes *et al.*, 2020), although several recent studies using molecular clocks have suggested that the RTA clade had already diversified in the Mesozoic (Fernández *et al.*, 2018; Magalhaes *et al.*, 2020).

TRACHEAL SPIRACLE

Spiders are the only animal group that breathe simultaneously with book lungs and tracheae (Schmitz, 2016). Basal spiders (Mesothelae, Mygalomorphae and some basal Araneomorphae) have only book lungs situated on the second and third abdominal segments, while most modern spiders (Araneomorphae) have both book lungs and tracheae (Foelix, 2011; Schmitz, 2016). The tracheae have different relative size and pattern of distribution among various spider families (Schmitz, 2013), and a recent study indicated that tracheae evolved several times independently in Araneomorphae (Ramírez *et al.*, 2021). The tracheal spiracle is the opening of the tracheae, its number and position can be used in the classification of spiders. However, the tracheal spiracle is rarely described in fossil spiders, because it is not easy to recognize. In the holotypes of *Odontomegops titan* and *Hiatomegops spinalis*, a broad opening can be observed situated on the abdomen behind the epigastric furrow. We interpreted this opening as the tracheal spiracle based on its position and presence in both male (the holotype of *Odontomegops titan*) and female (the holotype of *Hiatomegops spinalis*) spiders.

In contrast with the tracheal spiracle, broad and placed forward in Lagonomegopidae, archaeids have two tracheal spiracles, while the other four extant palpimanoid families have a single tracheae spiracle near the spinnerets. This special tracheal spiracle is also present in Anyphaenidae Bertkau, 1878, whose members are active hunters (Ramírez, 1995; Jocqué & Dippenaar-Schoeman, 2006). The similarity in the

structure and position of the tracheal spiracle between Lagonomegopidae and Anyphaenidae suggests a similar function. So, the tracheal spiracle, broad and placed forward, developed tarsal trichobothria and large PME with a tapetum, indicate that lagonomegopids were active (possibly nocturnal) hunters, like anyphaenids. This is consistent with the posit of previous study based on the large PME and the short legs (Eskov & Wunderlich, 1995).

CONCLUSIONS

Our study is the first attempt to test the phylogenetic placement of the extinct spider family Lagonomegopidae cladistically. We reached the following conclusions: (1) Lagonomegopidae is the potential sister-group to extant Palpimanoidea; (2) although some lagonomegopids have an RTA on the male palp, our analysis suggests that they are not closely related to the RTA clade; (3) the tracheal spiracle, broad and placed forward, developed tarsal trichobothria and large PME with a tapetum, corroborate that lagonomegopids were active (possibly nocturnal) hunters. A further phylogenetic study based on a more extensive sampling (adding more fossil taxa in the analysis) may extend our knowledge of the evolution of the palpimanoids in the future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Fig. S1. Strict consensus of 50 most parsimonious trees obtained under equal weights analysis.

Fig. S2. Majority rule consensus of the trees from Bayesian analysis.

Fig. S3. The preferred tree with characters mapped on each node.

File S1. List of morphological character descriptions and character argumentations. Word file (.docx).

File S2. Matrix. Excel file (.xls).

File S3. Matrix. TNT file (.tnt).

File S4. Movie (.mp4). 3D CT reconstruction of left male palp of CNU-ARA-MA2020001.