



<https://doi.org/10.11646/palaeoentomology.7.2.6>

<http://zoobank.org/urn:lsid:zoobank.org:pub:BD803C97-4B96-494A-88C1-CFEC9AD37024>

Two new long-pedipalp spiders (Araneae: Pholcochyroceridae) from mid-Cretaceous Kachin amber of northern Myanmar

YAN-MENG HOU¹, XIANG-BO GUO², PAUL A. SELDEN^{1,3,4}, LU-YU WANG^{5,*} & DONG REN^{1,*}

¹College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

²Key Laboratory of Zoological Systematics and Application, College of Life Sciences, Hebei University, Baoding 071002, China

³Department of Geology, University of Kansas, Lawrence, KS, United States

⁴Natural History Museum, London, United Kingdom

⁵Key Laboratory of Eco-environments in Three Gorges Reservoir Region (Ministry of Education), School of Life Sciences, Southwest University, Chongqing 400715, China

✉ hym19970415@163.com; <https://orcid.org/0000-0003-0059-3419>

✉ xiangboguo@126.com; <https://orcid.org/0000-0002-7074-8642>

✉ selden@ku.edu; <https://orcid.org/0000-0001-7454-4260>

✉ wangluyu1989@163.com; <https://orcid.org/0000-0002-5250-3473>

✉ rendong@mail.cnu.edu.cn; <https://orcid.org/0000-0001-8660-0901>

*Corresponding authors

Abstract

The spider genera *Longissipalpus* Wunderlich, 2015 and *Pedipalparaneus* Wunderlich, 2015 of the extinct family Pholcochyroceridae Wunderlich, 2008, are reported from mid-Cretaceous Kachin amber only. Members of both genera exhibit extremely elongated pedipalps. Here, two new species are described: *Longissipalpus albistriatus* sp. nov. and *Pedipalparaneus protumidus* sp. nov., both are endemic to Kachin amber. Detailed diagnoses and illustrations are provided, and their potential living habits are also discussed.

Keywords: *Longissipalpus*, *Pedipalparaneus*, Mesozoic, new species

Introduction

Kachin (Burmese) amber, from the Hukawng Valley in the Myitkyina region of northern Myanmar, is a part of the Myanmar Terrane. In general, Kachin amber probably originated on an island in the Tethys Archipelago before being pushed northward by the Indian Plate and colliding with Asia about 50 Myr later (Westerweel *et al.*, 2019; De Francesco Magnussen *et al.*, 2022). Based on Pb-U zircon crystal dating, the age of Kachin amber is estimated to be early Cenomanian (98.79 ± 0.62 Ma; Shi *et al.*, 2012), but the actual age might be slightly older (Mao *et al.*, 2018). The fauna and flora recorded in the amber

suggest that it was formed by resin-producing plants, such as multiple species of Araucariaceae, Cupressaceae and Sciadopityaceae (Smith & Ross, 2016; Poinar, 2018). Kachin amber contains abundant well-preserved arachnids and other terrestrial invertebrates (most of them are insects; *e.g.*, Wang *et al.*, 2022; Gu *et al.*, 2023; Yang *et al.*, 2023; Cui *et al.*, 2024; Wu *et al.*, 2024; Zhang *et al.*, 2024) and is known as a Fossil-Lagerstätte (Selden & Ren, 2017), while rare inclusion of aquatic life indicates that at least part of the amber forest is close to estuarine environments and freshwater habitats (Smith & Ross, 2016; Yu *et al.*, 2019).

Spiders are one of the most diverse groups of arthropods, with nearly 52,000 extant species in 135 families and 4,376 genera (WSC, 2024). The oldest known true spider, *Arthrolycosa* sp. B (Selden *et al.*, 2014) (Mesothelae Pocock, 1892; only a carapace remained), dates back to the Upper Carboniferous (Upper Bashkirian) of Kamensk-Shakhtinsky, Donets Basin (Russia), about 315 Myr ago (Selden *et al.*, 2014). Despite this, the fossil records of spiders are not rich, as their soft and fragile bodies are rarely preserved as fossils (Selden & Penney, 2010). But that began to change when the abundance of Kachin amber began to be studied (Selden & Ren, 2017; Magalhães *et al.*, 2020, 2021). In the last decade, a large number of new spider species from Kachin amber have been described. As of now, there are more than 300 spider species reported from the Cretaceous, about 80% of which come from Kachin amber (Dunlop *et al.*,

2023). These discoveries in Mid-Cretaceous Kachin amber provide important insights into the phylogeny of certain higher spider taxa and are of great significance for understanding the origin, early evolution, taxonomic systematics, paleoecology and paleogeography of various spider groups in the Mesozoic.

The extinct spider family Pholcochyroceridae was first described under Pholcochyrocerini Wunderlich, 2008 of the family Praeterleptonetidae Wunderlich, 2008. It was considered to be a haplogyne spider and was placed in the superfamily Dysderoidea Bristowe, 1938. The designated type genus was *Pholcochyrocer* Wunderlich, 2008 (by monotypy: *Pholcochyrocer guttulaequae* Wunderlich, 2008) (Wunderlich, 2008, 2017). Since then, the taxonomic status of this family has undergone an unstable history: 1) Wunderlich (2012) elevated the tribe Pholcochyrocerini to family status and transferred it from Dysderoidea to Leptonetoidea Simon, 1890 (based on characters such as having eight eyes, cribellate, and no retrobasal tibial spurs of the male pedipalps, *etc.*), representing the least advanced family of Leptonetoidea; 2) considering that the members of the family are cribellate and have slender articles of the male pedipalps, which differ from those of the family Praeterleptonetidae (ecribellate) and are more similar to the family Mongolarachnidae Selden, Shi & Ren, 2013 (cribellate; Jurassic), thus Wunderlich (2017) unified the two families Pholcochyroceridae and Mongolarachnidae into the superfamily Pholcochyroceroidea Wunderlich, 2008; 3) Wunderlich & Müller (2018) regarded the superfamily as entelegyne like Deinopoidea C. L. Koch, 1851 and, according to the discovered fossils in Kachin amber, the true members of the family Leptonetidae possess only six eyes and are not strongly related to the eight-eyed members of the Mongolarachnidae and Pholcochyroceratidae, so they unified the two superfamilies Pholcochyroceroidea and Deinopoidea into the pholcochyroceroid-deinopoid branch. So far, eight genera and 20 species of this family have been described and all of them are known from Kachin amber (Dunlop *et al.*, 2023). This family can be diagnosed as follows (including but not limited to): eight eyes in two rows on a wide field, lateral eyes distinctly widely spaced; basal cheliceral articles not fused; a pair of booklungs, cribellate; pedipalps and legs usually slender and spiny, three tarsal claws; bulbs attached ventrally on the cymbium and bear at least two large slender and pointed tegular apophyses, one is apparently connected with the embolus (Wunderlich, 2008, 2012, 2015; Wunderlich & Müller, 2018; Jiang *et al.*, 2020).

The two genera of long-pedipalp spiders, *Longissipalpus* and *Pedipalparaneus*, were originally placed in Longissipalpinae Wunderlich, 2015 and Pedipalparaneinae Wunderlich, 2015, respectively, in the family Mongolarachnidae. Wunderlich & Müller

(2021) suggested that the extremely long articles of the male pedipalps may well be a basic character of the family Pholcochyroceridae, and therefore considered that all known genera of long-pedipalp spiders in Kachin amber belong to Pholcochyroceridae, and transferred the above two genera from Mongolarachnidae to Pholcochyroceridae. This eventually resulted in the removal of Mongolarachnidae from the Kachin amber family list. The main difference between the two genera is the trait of the pedipalps (patella almost as long as the tibia in *Longissipalpus*, while the patella is distinctly shorter than the tibia in *Pedipalparaneus*) (Wunderlich & Müller, 2021). Up to now, there are six species of *Longissipalpus* and only one species of *Pedipalparaneus*, *Pedipalparaneus seldeni* Wunderlich, 2015. Herein, two pholcochyrocerid spiders (one of them based on two pieces of amber) are described from Kachin amber, which not only help us to observe more morphological details of pholcochyrocerids, but also provide new materials for further phylogenetic studies of this spider family.

Material and methods

Three specimens are described here, two of which are deposited in the Key Lab of Insect Evolution and Environmental Changes at the College of Life Sciences, Capital Normal University, Beijing (CNUB; Dong Ren, curator), the other one is deposited in the Collection of Spiders, School of Life Sciences, Southwest University, Chongqing, China (SWUC).

All specimens were examined, photographed and measured with a Nikon SMZ 25 stereomicroscope and an attached Nikon DS-Ri 2 digital camera system, photos were stacked using Helicon Focus 7 and the line drawings were prepared with the Inkscape software (v. 1.0.2.0). All images were edited and formatted using Adobe Photoshop 2022.

All measurements are in mm. Pedipalp measurements are shown as: total length (femur, patella, tibia, cymbium); leg measurements are shown as: total length (femur, patella, tibia, metatarsus, tarsus). Leg formula indicates the length of each leg relative to the others, from longest to shortest. Terminology of morphological characters follows Penney & Selden (2002), Wunderlich (2015), Selden *et al.* (2016) and Guo *et al.* (2020). 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; bl—booklung; C—conductor; ca—calamistrum; ch—chelicera; cr—cribellum; Cy—cymbium; E—embolus; EC—embolus + conductor; ef—epigastric furrow; en—endite; fe—femur; fg—fang; L—left; lb—labium; MOA—median ocular area; pa—

patella; Pd—pedipalp; PLE—posterior lateral eye(s); pls—posterior lateral spinneret(s); PME—posterior median eye(s); pms—posterior median spinneret(s); R—right; st, sternum; T—tegulum; TA—tegular apophysis; TAL—tegular apophysis distal part length; ti—tibia; tr—trochanter; TW—tegular width.

Systematic palaeontology

Order Araneae Clerck, 1757

Infraorder Araneomorphae Smith, 1902

Family †Pholcochyroceridae Wunderlich, 2008

Genus †*Longissipalpus* Wunderlich, 2015

Type species. *Longissipalpus minor* Wunderlich, 2015

Longissipalpus albistriatus Hou, Wang & Ren sp. nov. (Figs 1–3)

Type material. Holotype ♂ (CNU-ARA-MA2016014), Kachin amber (Fig. 1A, B). The specimen is preserved in a nearly translucent piece of amber, only a few impurities scattered around the spider. This spider is relatively well preserved, except for a few incomplete legs. Overall, the right legs are more damaged than the left. Right tarsus I is completely missing, and only the base of the metatarsus remains; left leg I is abnormally black, the base of femur is obscured by a small piece of leaf residue, the basal-prolateral of metatarsus is slightly ground, the claw is not visible; right leg II is almost entirely missing, with only the coxa, trochanter, and part of the femur remaining; right patella III is missing; the tarsi of each leg IV are missing, and the metatarsi are partially preserved. Holotype deposited in CNUB.

Paratype 1 ♂ (SWUC-MA001), Kachin amber (Fig. 3A, B). Although the specimen is well preserved, the left legs are covered by a large impurity, resulting in part of left femur I and almost the entire left leg II are not visible. A crack near the middle of right femur I; right femur and tibia IV incomplete, patella missing. Both bulbs are hidden by bubbles and are slightly deformed. There are also two large and some small impurities in front of the spider. The sternum is hidden by some emulsion and the abdomen is deformed. No biotic syninclusions.

Etymology. The specific name is derived from a combination of the Latin word “*albus*” and “*striatus*”, meaning white and striate, respectively, which refers to the presence of white stripes on the carapace.

Diagnosis. The new species resembles *Longissipalpus impudicus* Wunderlich, 2021 in having extremely long (over body length) and spiny palpal femur, but differs by

genital characters (e.g., TAL approximately $1.50\times$ vs. $1.00\times$ longer than TW in retrolateral view; cymbium bearing four straight strong setae retrobasally in the new species, while absent in latter; cf. Figs 2G, 3F with fig. 89 in Wunderlich & Müller, 2021), larger body size (i.e., body length min. 3.85 mm vs. 2.80 mm) and slender pedipalps (e.g., palpal femur length min. 6.89 mm vs. 4.50 mm and $2.46\text{--}2.77\times$ vs. $2.37\times$ longer than tibia). It also can be distinguished from *L. minor*, *L. major* and *L. cochlea* by the presence of strong setae of palpal tibia retroapically (cf. Figs 2G, H, 3F with figs 187, 189 in Wunderlich, 2015 and figs 125, 126 in Wunderlich, 2017), the trait of palpal femur (the new species with min. four spines, while absent in latter three), larger body size (i.e., body length max. 2.70 mm in latter three) and slender appendages (e.g., palpal femur length max. 2.50 mm and femur I min. $9.83\times$ vs. max. $9.50\times$ longer than broad in latter three); from *L. magnus* and *L. aliter* by lacking a clavate tegular apophysis (cf. Figs 2G, H, 3F with fig. 127 in Wunderlich, 2017 and fig. 90d in Wunderlich & Müller, 2021).

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

Description. Male (holotype): generally yellowish brown. Entire body well covered with dense setae, pedipalps and legs extremely slender and with spines and hair-like bristles (Fig. 1).

Prosoma (Fig. 2A, B): carapace height/length ratio 0.43, hairs short, with stripes; fovea distinct, deep and longitudinal, situated in center of carapace; cephalic region slightly raised (Fig. 2A). Ocular area with long curved setae; eight eyes in two wide rows, all deformed, anterior medians largest, posterior median eyes widely spaced, lateral eyes slightly close together. Clypeus high and fairly concave (Fig. 2B). Chelicera covered with setae, retromargin with two true teeth; posterior surface with a pair of bow-shaped setae apically; fangs long, apparently labidognath. Endite elongated, serrula in a single row (Fig. 2B).

Pedipalp (Fig. 2G, H): densely covered by hairs; femur, patella and tibia extremely long and slender, femur longest, $1.82\times$ longer than body and with four long spines dorsally; patella longer than tibia; tibia slightly curved, without spines but bearing four or five curved strong setae retroapically; cymbium small, protruding dorsally, bearing long hairs especially apically, four straight strong setae present retrobasally, prolateral margin with a row of bristles covering bulbs; bulbs attached ventrally to the cymbium, bearing a long, thin, bent and directed forward tegular apophysis (could be a secondary conductor); embolus thin, screw-shaped and pointed, attached and guided by a thick conductor.

Opisthosoma: elongated and subovoid (height/length ratio 0.49), densely covered by hairs, with scattered black

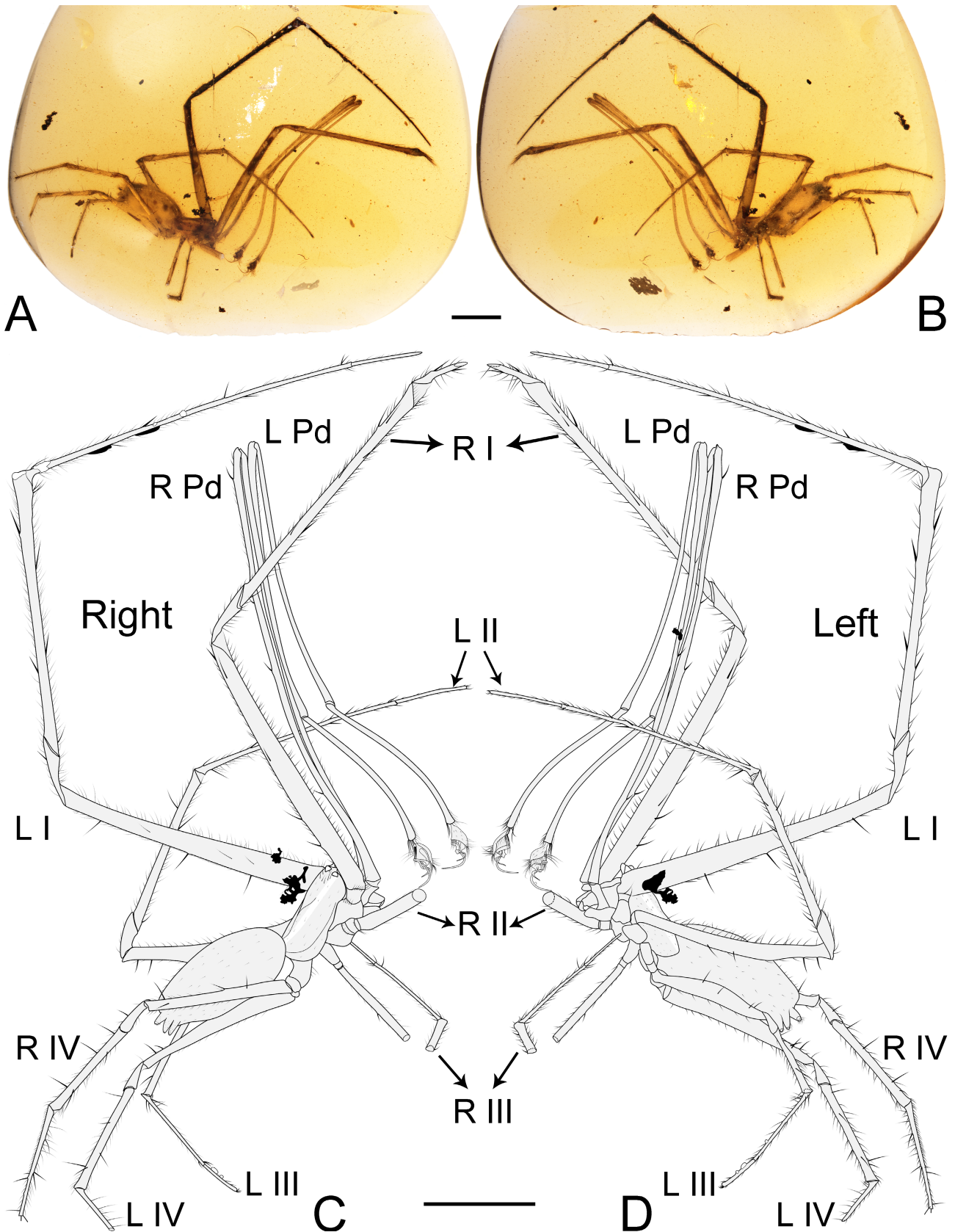


FIGURE 1. *Longissipalpus albistriatus* sp. nov., holotype male (CNU-ARA-MA2016014). **A**, Right lateral view. **B**, Left lateral view. **C**, Line drawing of **A**. **D**, Line drawing of **B**, black areas are impurities. Scale bars: 2 mm. Abbreviations: I, II, III, IV—leg numbers; L—left; Pd—pedipalp; R—right.

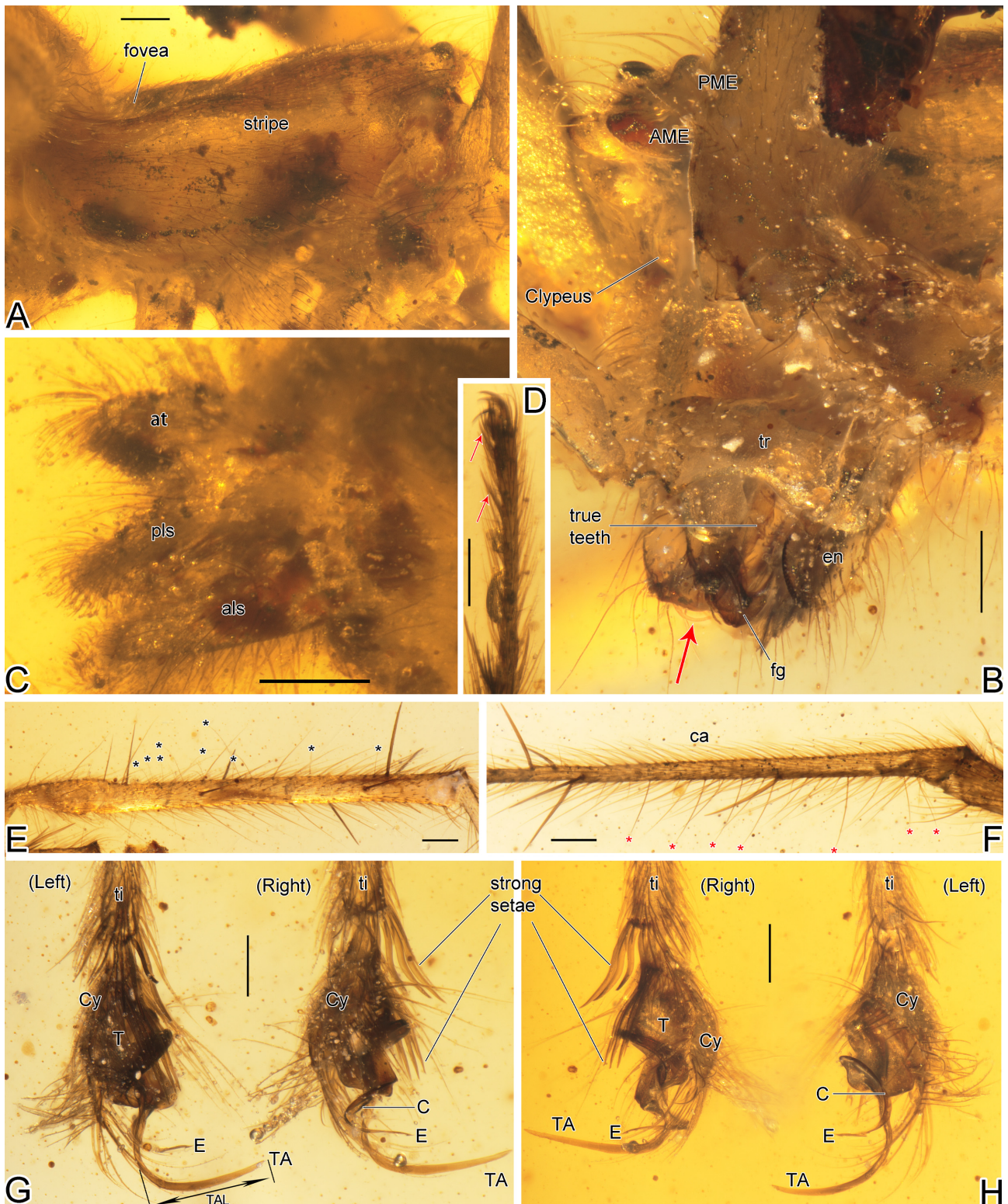


FIGURE 2. *Longissipalpus albistriatus* sp. nov., holotype male (CNU-ARA-MA2016014). **A**, Prosoma, right lateral view. **B**, Ocular area and chelicera, left lateral view, red arrow points at a bow-shaped seta. **C**, Spinnerets, right lateral view. **D**, Left tarsus III, retrolateral view, red arrows point to spines. **E**, Left patella and tibia IV, prolateral view, showing trichobothria on tibia dorsally (black asterisks). **F**, Right metatarsus IV, prolateral view, showing a row of vertical bristles (red asterisks). **G**, Left palpal organ, retrolateral view and right palpal organ, prolateral view. **H**, Right palpal organ, retrolateral view and left palpal organ, prolateral view. Scale bars: 0.2 mm. Abbreviations: als—anterior lateral spinneret(s); AME—anterior median eye(s); at—anal tubercle; C—conductor; ca—calamistrum; Cy—cymbium; E—embolus; en—endite; fg—fang; pls—posterior lateral spinneret(s); PME—posterior median eye(s); T—tegulum; TA—tegular apophysis; TAL—tegular apophysis distal part length; ti—tibia; tr—trochanter.

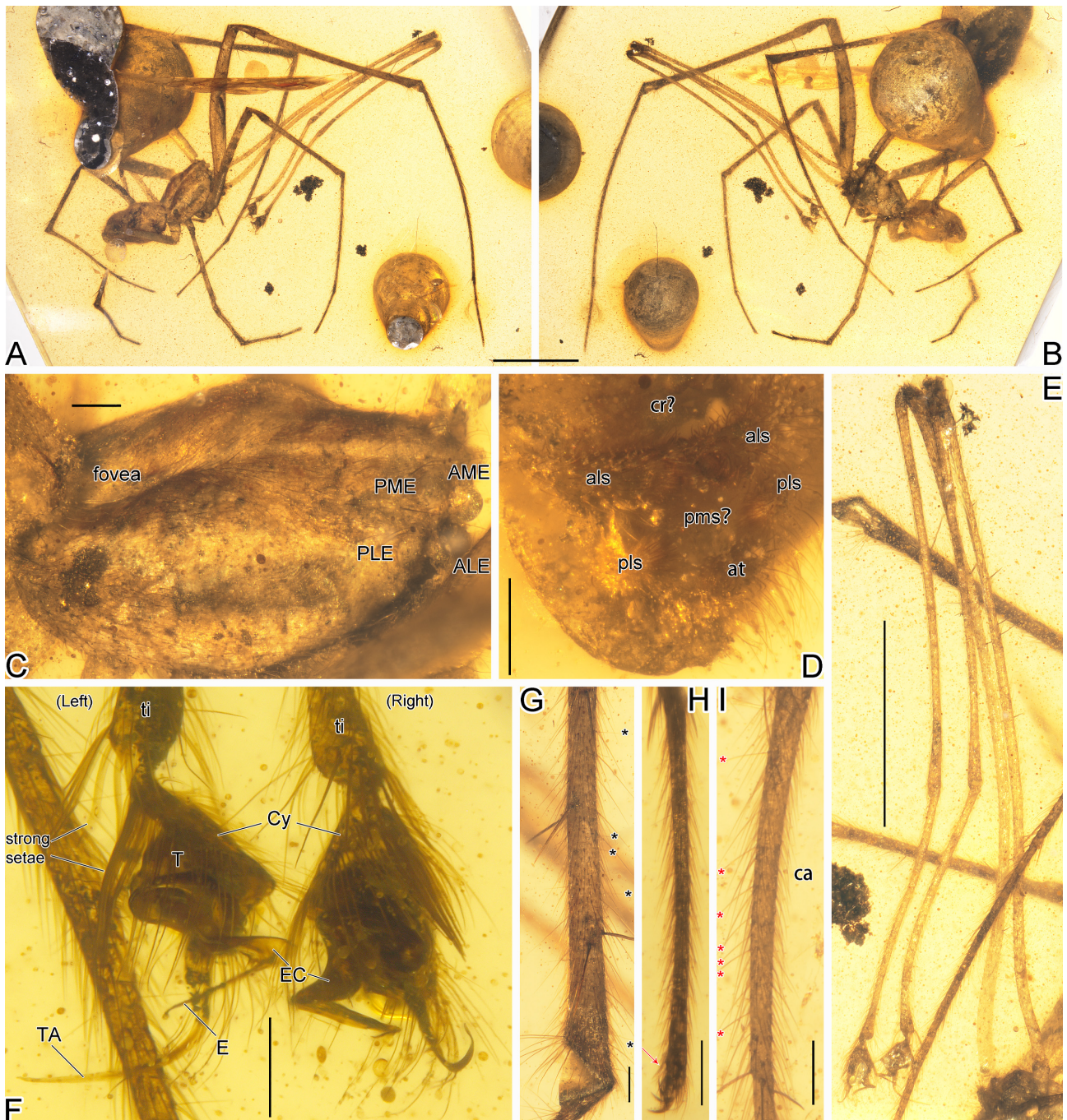


FIGURE 3. *Longissipalpus albistriatus* sp. nov., paratype male (SWUC-MA001). **A**, Right lateral view. **B**, Left lateral view. **C**, Prosoma, right lateral view. **D**, Spinnerets, ventral view. **E**, Pedipalps, lateral view. **F**, Left palp organ, prolateral view and right palp organ, retrolateral view. **G**, Right tibia I, retrolateral view, showing trichobothria dorsally (black asterisks). **H**, Right tarsus II, retrolateral view, red arrow points to spine. **I**, Left metatarsus IV, prolateral view, showing a row of vertical bristles (red asterisks). Scale bars: 0.2 mm. Abbreviations: ALE—anterior lateral eye(s); als—anterior lateral spinneret(s); AME—anterior median eye(s); at—anal tubercle; ca—calamistrum; cr—cribellum; Cy—cymbium; E—embolus; EC—embolus + conductor; PLE—posterior lateral eye(s); pls—posterior lateral spinneret(s); PME—posterior median eye(s); pms—posterior median spinneret(s); T—tegulum; TA—tegular apophysis; ti—tibia.

spots and patches. At least two pairs of spinnerets well developed; anal tubercle large (Fig. 2C). Cribellum most probably present (according to the existence of a calamistrum).

Legs (Fig. 2D–F): extremely long and densely hairy, leg formula I/II/IV/III, femur I slightly thick; spines numerous, but absent on all coxae, trochanters and all ventral femora; spines at apex of metatarsi forming a

ring (Fig. 2D); a row of bristles present on basal-ventral of all metatarsi (as pectunculus) (Fig. 2F); numerous trichobothria dorsally on all tibiae, metatarsi and tarsi (Fig. 2E); calamistrum uniseriate, present on metatarsi IV and longer than half of the length of the article (Fig. 2F). Three tarsal claws, paired claws uniseriate, with three or four teeth, median claw hook-like, without serrate accessory claw setae but with one or three spines ventral-apically (Fig. 2D).

Measurements (in mm). Body length 4.68; carapace 1.84 length, 0.79 height; opisthosoma 2.84 length, 1.38 height. MOA 0.23 length; clypeus 0.14 height; chelicera 0.84 length; endite 0.49 length. Left pedipalp 17.56 (8.50, 5.44, 3.07, 0.55), left leg I—(5.40, 1.28, 4.96, 6.49, -), leg II 12.81 (3.73, 0.86, 3.05, 3.77, 1.40), leg III 6.39 (2.23, 0.55, 1.22, 1.70, 0.69), leg IV—(3.10, 0.57, 1.96, -, -); right pedipalp 17.59 (8.54, 5.03, 3.47, 0.55), right leg I—(5.57, 1.10, 5.01, -, -), leg III—(-, -, -, 1.75, 0.72), leg IV—(3.00, 0.62, 2.13, 2.42, -).

Male (paratype). Habitus as in Fig. 3A, B. Mostly same as holotype, but a little smaller (possibly due to the deformed abdomen); white stripe visible along midline of carapace (Fig. 3C). Palpal femur with seven or eight spines dorsally; bulbs deformed (Fig. 3E, F). Legs extremely long and densely hairy; spines numerous, but absent on all coxae, trochanters and all ventral femora; calamistrum uniseriate, present on metatarsi IV and longer than half of the length of the article; three tarsal claws (Fig. 3G–I). Three pairs of spinnerets deformed (PMS small, difficult to observe), anteriors widely spaced; anal tubercle large; cribellum most probably exists (Fig. 3D). Body length 3.85; prosoma 1.86 length; opisthosoma (deformed) 1.99 length. Eyes: PME 0.15, PLE 0.11, AME-ALE 0.23, PME-PLA 0.25, ALE-PLA 0.13, MOA 0.17 length. Chelicera 0.71 length. Left pedipalp 13.87 (6.89, 3.94, 2.65, 0.39), left leg I 16.6 (4.32, 0.91, 4.13, 5.29, 1.95), leg II—(2.77, -, -, -, 1.21), leg III 5.48 (1.85, 0.61, 1.07, 1.25, 0.70), leg IV 8.00 (2.46, 0.55, 1.66, 2.40, 0.93); right pedipalp 13.81 (6.89, 3.96, 2.55, 0.41), right leg I—(4.52, 0.95, 4.53, 5.71, -), leg II 11.11 (3.23, 0.74, 2.55, 3.35, 1.24), leg III 5.38 (2.06, 0.49, 1.15, 1.10, 0.58), leg IV—(-, -, -, 1.93, 0.80).

Remarks. *Longissipalpus albistriatus* sp. nov. is the largest known species of the genus, the body length (max. 4.68 mm) exceeds that of *L. magnus* Wunderlich, 2015, and the length of the pedipalps is up to 17.59 mm. Characters such as highly uniform male genitalia (e.g., distal part of tegular apophysis extremely prolonged; embolus spiral and attached by a thick conductor; cymbium with four strong setae retrobasally), extremely elongated pedipalps and striped carapace link the two type specimens together. The body length and number of palpal femur spines of the two specimens are slightly different, which may be that the deformed abdomen of the paratype specimen due to

preservation is obvious, resulting in a small body length measurement; the common intraspecific variation results in fewer palpal femur spines in holotype specimens, so the number of spines is not suitable as a diagnostic character of the new species.

Genus †*Pedipalparaneus* Wunderlich, 2015

Type species. *Pedipalparaneus seldeni* Wunderlich, 2015

Pedipalparaneus protumidus Hou, Wang & Ren sp. nov.

(Figs 4, 5)

Type material. Holotype ♂ (CNU-ARA-MA2016255), Kachin amber (Fig. 5A, B). The specimen is preserved in a piece of amber piece approximately 20.00 mm in length. The amber is clean and transparent inside, with few impurities except for a few small bubbles, and no biotic syninclusions. The spider is located at the upper right of the amber (dorsal view) and is relatively well preserved, but some features are not visible. The left legs are almost intact, except for the missing tarsus IV. The right legs are much more damaged than the left, and there is no complete leg: all the coxae and trochanters are seriously ground; only about half of the tibia (refer to the left tibia I) and its basal articles are preserved in the right leg I; the base of the right femur II is ground, and parts of the tibia and metatarsus are missing, leaving a floating tarsus; only parts of the femur, patella and tarsus of the right leg III are preserved; the right femur IV is ground basally, and the claw is not visible. Pedicel is slightly deformed. Holotype deposited in CNUB.

Etymology. The specific name is derived from the Latin word “*protumidus*”, meaning bossed, which refers to the chelicera with a distinct lateral condyle.

Diagnosis. The new species can be distinguished from the only other congener *Pedipalparaneus seldeni* Wunderlich, 2015 by having a distinctly long, thin and directed forward tegular apophysis (while short and thick in latter; cf. Fig. 5F with fig. 197 in Wunderlich, 2015 and fig. 123 in Wunderlich, 2017), smaller body size (i.e., body length 3.07 mm vs. 4.00 mm), slender pedipalps (e.g., palpal femur length 1.47–1.52 mm vs. 2.90 mm and tibia length 0.82–0.84 mm vs. 1.90 mm) and the trait of posterior eye row (almost straight vs. distinctly recurved; cf. Fig. 5C with fig. 191 in Wunderlich, 2015).

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

Description. Male (holotype): generally yellowish brown, chelicerae darker. Entire body well covered with dense setae (apparently not feathery), pedipalps and legs extremely slender and with spines. (Figs 4, 5A, B).

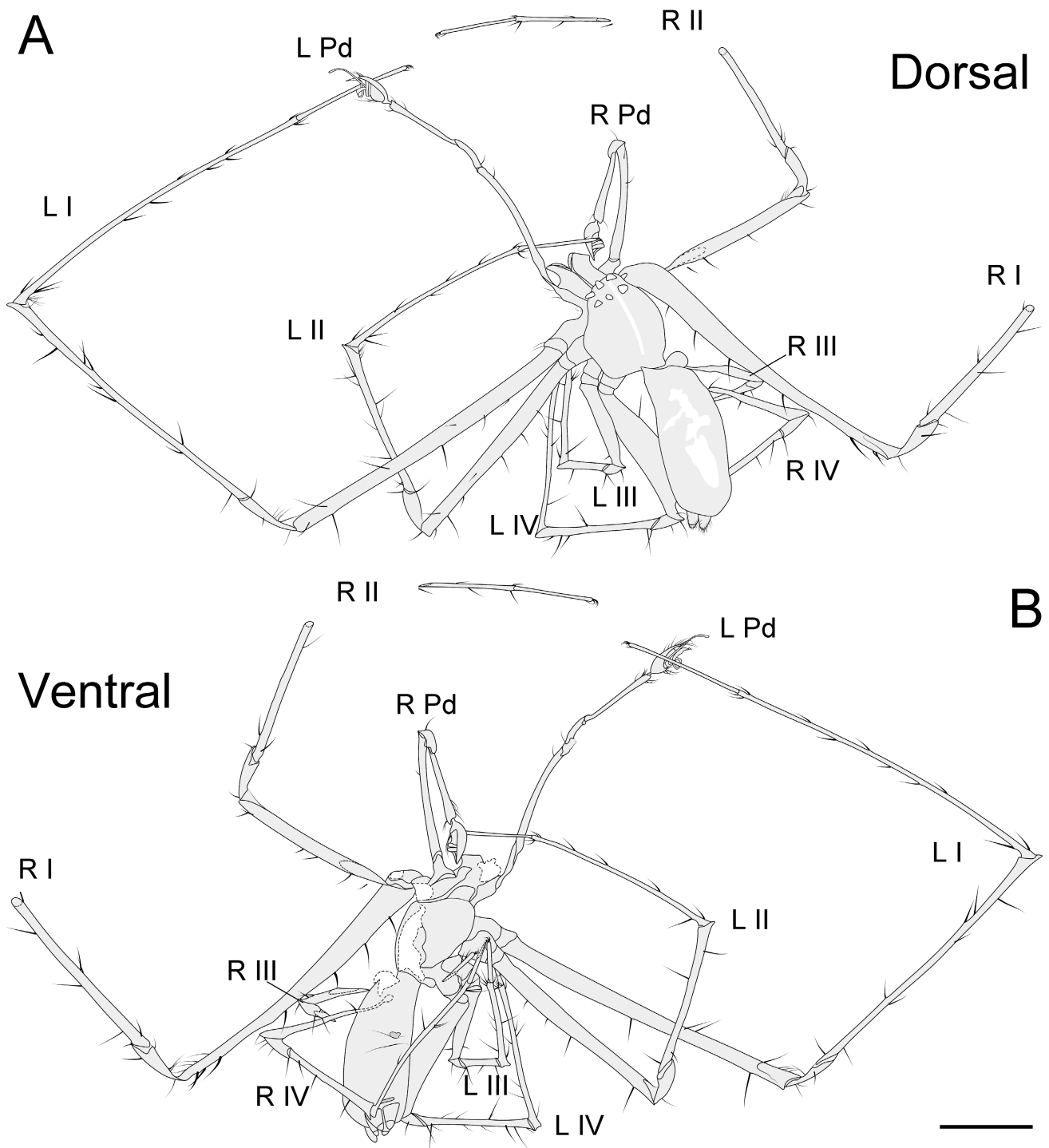


FIGURE 4. *Pedipalparaneus protumidus* sp. nov., holotype male (CNU-ARA-MA2016255). **A**, Line drawing of dorsal view. **B**, Line drawing of ventral view. Scale bar: 1 mm. Abbreviations: I, II, III, IV—leg numbers; L—left; Pd—pedipalp; R—right.

Prosoma (Fig. 5C, D): carapace width/length ratio 0.88, hairs short, with stripes; fovea indistinct. Ocular area with long curved setae; eight eyes in two wide rows, all slightly deformed, anterior median eyes probably largest, lateral eyes distinctly spaced from each other. Clypeus long and slightly concave (Fig. 5C). Chelicerae long and covered with setae, lateral condyles present; basal cheliceral articles not fused; fangs long and deformed,

teeth hidden. Endite elongated, serrula in a single row; labium nearly square, almost as long as wide and with a weak seam to the wide sternum; sternum slightly convex, posterior end protruding (Fig. 5C, D).

Pedipalp (Fig. 5F, G): densely covered by hairs; patella and tibia bear several trichobothria; femur and tibia extremely long and slender, patella distinctly shorter than tibia; femur shorter than body and slightly curved, bearing

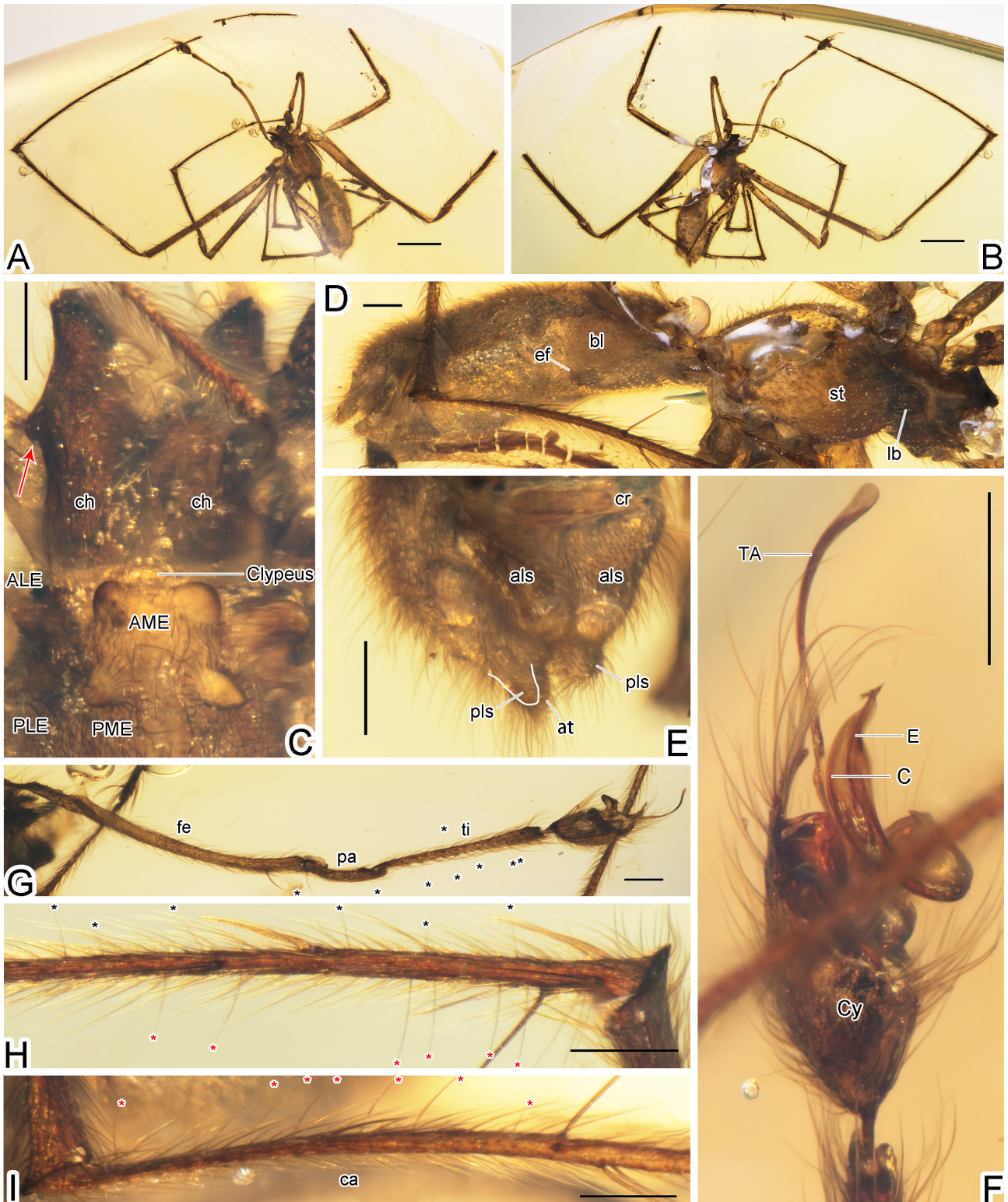


FIGURE 5. *Pedipalparaneus protumidus* sp. nov., holotype male (CNU-ARA-MA2016255). **A**, Dorsal view. **B**, Ventral view. **C**, Ocular area and chelicerae, dorsal view, red arrow points to lateral condyle. **D**, Prosoma and opisthosoma, ventral view. **E**, Spinnerets, ventral view. **F**, Left palpal organ, prolateral view. **G**, Left pedipalp, retrolateral view, showing trichobothria (black asterisks). **H**, Left metatarsus II, retrolateral view, showing trichobothria dorsally (black asterisks) and a row of vertical bristles (red asterisks). **I**, Right metatarsus IV, prolateral view, showing a row of vertical bristles (red asterisks). Scale bars: 1 mm (**A**, **B**); 0.2 mm (**C**–**I**). Abbreviations: ALE—anterior lateral eye(s); als—anterior lateral spinneret(s); AME—anterior median eye(s); at—anal tubercle; bl—booklung; C—conductor; ca—calamistrum; ch—chelicera; cr—cribellum; Cy—cymbium; E—embolus; ef—epigastric furrow; fe—femur; lb—labium; pa—patella; PLE—posterior lateral eye(s); pls—posterior lateral spinneret(s); PME—posterior median eye(s); st—sternum; TA—tegular apophysis; ti—tibia.

two long distal-dorsal spines (Fig. 5G). Cymbium small, protruding dorsally, bearing long hairs especially apically; bulbs attached ventrally to the cymbium, bearing a long, thin, bent and directed forward tegular apophysis (could be a secondary conductor); embolus thin, screw-shaped and pointed, attached and guided by a thick conductor (Fig. 5F).

Opisthosoma (Fig. 5D, E): elongated and subovoid (width/length ratio 0.47), densely covered by hairs, with white patches dorsally. Epigastric plate slightly thickened; epigastric furrow long and sclerotic, a short transverse groove situated on the postgastric area behind the epigastric furrow; one pair of booklungs (Fig. 5D). At least two pairs of spinnerets well developed; anal tubercle large; cribellum wide and undivided (Fig. 5E).

Legs (Fig. 5H, I): extremely long and densely hairy, leg formula I/II/IV/III, femur I slightly thick; spines numerous, but absent on all coxae, trochanters and all ventral femora; spines at apex of metatarsi forming a ring; a row of bristles present on basal-ventral of all metatarsi (as pectunculus); numerous trichobothria dorsally on all patellae, tibiae, metatarsi and tarsi, shorter and thinner than bristles; calamistrum uniseriate, present on metatarsi IV and longer than half of the length of the article (Fig. 5I). Three tarsal claws, paired claws uniseriate with six or seven teeth, median claw hook-like, without serrate accessory claw setae but with one or two spines ventral-apically.

Measurements (in mm). Body length 3.07; carapace 1.21 length, 1.07 width, CRW 0.71 width; opisthosoma 1.86 length, 0.88 width. Eyes: AME 0.08, ALE 0.06, PME 0.09, PLE 0.07, AME-AME 0.17, AME-ALE 0.15, ALE-ALE 0.51, PME-PME 0.23, PME-PLE 0.16, PLE-PLE 0.53, AME-PME 0.17, ALE-PLE 0.15; MOA 0.23 length. Clypeus 0.10 height; chelicera 0.62 length, 0.23 width; endite 0.39 length, 0.18 width; labium 0.23 length, 0.24 width; sternum 0.77 length, 0.62 width. Left pedipalp 3.20 (1.52, 0.42, 0.84, 0.42), left leg I 12.67 (3.56, 0.70, 3.44, 3.63, 1.34), leg II 8.41 (2.72, 0.55, 2.13, 2.16, 0.85), leg III 3.61 (1.25, 0.25, 0.72, 0.94, 0.45), leg IV—(1.99, 0.35, 1.32, 1.87, -); right pedipalp 3.07 (1.47, 0.40, 0.82, 0.38), right leg I—(3.57, 0.69, -, -, -), leg II—(-, 0.47, -, -, 0.87), leg IV—(-, 0.32, 1.19, 1.82, 0.51).

Remarks. The new species is cribellate, with extremely elongated pedipalps, and most importantly its palpal patella is distinctly shorter than the tibia, so it is appropriate to place it in the genus *Pedipalparaneus*. Thus, this raises questions about the original diagnosis of the genus (e.g., the opisthosoma of the new species without hair-bearing humps and femora III–IV without long ventral bristles; Wunderlich & Müller, 2021), which may be caused by interspecific differences.

Discussion

It is well known that structure often corresponds to function, and while we cannot actually see the habitat status of these extinct species nor do we know the function of these particular structures, we can analyse them through the extant taxa with similar structures (possibly convergent). Extremely elongated legs (especially leg I) and pedipalps are less common in extinct as well as extant spider taxon, such as †*Mongolarachne* Selden, Shi & Ren, 2013 in †Mongolarachnidae (see Selden *et al.*, 2011, 2013), †*Longissipalpus* and †*Pedipalparaneus* in †Pholcochyroceridae (see Wunderlich, 2015), *Cambridgea* L. Koch, 1872, *Nanocambridgea* Forster & Wilton, 1973 and *Porteria* Simon, 1904 in Desidae Pocock, 1895 (see Morrill *et al.*, 2023), *Moneta* O. Pickard-Cambridge, 1871 in Theridiidae Sundevall, 1833 (see Zhu, 1998), *Ectatosticta* Simon, 1892 in Hypochilidae Marx, 1888 (see Lin & Li, 2020; Wang *et al.*, 2021), *Gelanor* Thorell, 1869 in Mimetidae Simon, 1881 (see Benavides & Hormiga, 2016; Barrantes *et al.*, 2023) and *Epidius* Thorell, 1877 in Thomisidae Sundevall, 1833 (see Wunderlich, 2015), *etc.* Although long pedipalps are not directly associated with web-building, and both *Gelanor* and *Epidius* hunt spiders but build no capture web, almost all the extant long pedipalps or cribellate spiders (e.g., Deinopidae C. L. Koch, 1850, Psechridae Simon, 1890 and Uloboridae Thorell, 1869, *etc.*) build large capture webs, so it is presumed that spiders of *Longissipalpus* and *Pedipalparaneus* are also web-building spiders (Wunderlich & Müller, 2021). However, the three pieces of amber involved did not preserve silk webs (a questionable capture web was preserved quite near the male holotype of *P. seldeni*, but needs further study; Wunderlich, 2015), which may be related to the self-defense behavior of extant theridiids and hypochilids: these spiders actively avoid danger by falling directly from the web or hiding in a crevice when larger predators or dangerous objects touch the spider's web or body; or maybe it's just because male adults seldom weave webs and wander around in search of females, which is also common in modern spiders.

The extremely long legs I are particularly important, helping them to explore and detect prey on the web—like some pholcids (these Synspermiata spiders raise quite long and multiarticulate anterior legs like feelers, sensing changes in their surroundings and may also as a defensive behavior) (Wunderlich, 2015). The long legs are matched by extremely long pedipalps, palpal organs are very important structures that are not easily exposed, so the pedipalps may fold backward during resting and moving, as in *Ectatosticta* (Wang *et al.*, 2021; Wunderlich & Müller, 2021), and only extend when considering mating. Cannibalism is common in spiders (Schneider

& Andrade, 2011; Nentwig, 2013), and the female of the two fossil spiders involved may be quite fierce, but with the help of elongated pedipalps and legs, males can keep a greater distance while courting or mating with females, effectively reducing the risk of cannibalism; furthermore, sexual selection for male appendages length may also involve competition between males (male-male competition for females) (Hodge & Marshall, 2017; Wunderlich & Müller, 2021). In summary, the two fossil species involved lack female specimens and have extreme morphological particularity, which is difficult to associate with extant taxa. It is suggested that these species (including *Mongolarachne jurassica* (Selden, Shih & Ren, 2011)) may represent the long-legged, web-building and three-clawed cribellate primitive taxa, and considering that they are unknown from the Palaeogene, and probably became extinct at the end of the Cretaceous.

Once a fossil family is diagnosed by some unclear characters, coupled with inadequate descriptions, often leads to more confusion in the relationships between these fossil spiders (Selden & Penney, 2010; Selden & Ren, 2017). The family Pholcochyroceridae is one of them, its taxonomic status is unstable, and its internal relationships are fickle and confused (as mentioned in the introduction). Moreover, a single apomorphic character of the very diverse Pholcochyroceridae is not available, so its monophyly is difficult to acknowledge (Wunderlich & Müller, 2021). In fact, many other families of Kachin amber spiders lack clear synapomorphies, but their morphology is so bizarre and heterogeneous that it is hard to prove the relationship to extant families (Jiang *et al.*, 2020; Magalhães, 2020). Fortunately, it is advisable to incorporate fossils as terminals in the phylogenetic analysis (Giribet, 2015). Therefore, using more valuable specimens and conducting total-evidence analyses that integrate fossils and extant taxa (*e.g.*, Palpimanoidea Thorell, 1870 is a prominent example; Wood *et al.*, 2012, 2015; Wood, 2017; Wood & Wunderlich, 2023) can offer better understandings of these highly diverse early araneomorphs with ambiguous phylogenetic affinities (Magalhães, 2020). These three specimens described in our paper are extremely well preserved. They not only represent the evidence of the morphological diversity of spiders in the Cretaceous, but also show more details and new characters, such as the presence of true teeth, the distinctly undivided cribellum, and clearer spinnerets and bulbs, *etc.*, offering more morphological characteristics for the future cladistical verification of these fossil spiders.

Conclusions

Two new long-pedipalp species (three specimens were involved) belonging to the family Pholcochyroceridae,

Longissipalpus albistriatus sp. nov. and *Pedipalparaneus protumidus* sp. nov., are described from mid-Cretaceous Kachin amber, northern Myanmar. Both species, including previously reported congeners, are only based on male specimens, and they may represent primitive web-building cribellate taxa. The three well-preserved specimens demonstrate the morphological diversity of Cretaceous spiders and provide more valuable information for further phylogenetic analysis.

Acknowledgements

We are grateful to Dr Hongru Yang, Ziqiang Xu, Qi Feng, Lu Zhang and Xiao-tian Liu (Capital Normal University, Beijing, China), Dr Chi Jin (Hebei University of Engineering, Handan, China), Dr Yannan Mu and Kun Yu (Hebei University, Baoding, China) for their helpful comments, to Prof. Zhi-sheng Zhang (Southwest University, Chongqing, China) and Mr. Fangyuan Xia for donating specimens for this study. We thank the journal editor of Palaeoentomology, Prof. Diying Huang. We express our gratitude to Prof. Zhiyuan Yao, Prof. Neal Evenhuis and the anonymous reviewer for the valuable reviews of the manuscript. This research is supported by the National Natural Science Foundation of China (No. 32300364).

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