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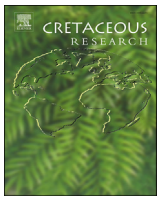

Short communication

# New *Lineaburmops* fossils (Araneae: Lagonomegopidae) with contrasting color patterns from mid-Cretaceous Kachin amber, northern Myanmar

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ABSTRACT

The fossil spider family Lagonomegopidae is widespread in the Cretaceous period, and mainly reported from mid-Cretaceous Kachin amber, northern Myanmar. Here, two new lagonomegopid species, belonging to the genus *Lineaburmops*, are described from Kachin amber: *Lineaburmops longiantepes* sp. nov. and *Lineaburmops rhombus* sp. nov., which showing similar contrasting body coloration as other *Lineaburmops* species. The compositional element of these special color patterns and their potential functions are discussed.



## 1. Introduction

Lagonomegopidae is an extraordinary extinct spider family, notable not only for their large eyes on the anterolateral corner of the carapace, but also for the relatively high diversity of species and special distribution in geologic history. To date, 33 species belonging to 21 genera, of Lagonomegopidae have been recorded. Interestingly, though lagonomegopid spiders are known only from the Cretaceous, they are widely distributed in space, having been recorded from nine different localities: Taimyr amber (Russia; Eskov and Wunderlich, 1995), Manitoban amber (Canada; Penney, 2004), New Jersey amber (USA; Penney, 2005), Kachin amber (Myanmar; Penney, 2005), Álava amber (Spain; Penney, 2006), Jordanian amber (Jordan; Kaddumi, 2007), El Soplao amber (Spain; Pérez-de la Fuente et al., 2013), San Just amber (Spain; Pérez-de la Fuente et al., 2013) and the Jinju Formation (Korea; Park et al., 2019). The variety of morphologies, both amber and non-amber occurrence and worldwide distribution of lagonomegopids indicate that lagonomegopid spiders probably had different life styles and occupied diverse habitats (Park et al., 2019; Guo et al., 2020; Wunderlich and Müller, 2021). Moreover, the fossil evidence of maternal care in lagonomegopid spiders has been reported, adult lagonomegopid females probably built and then guarded egg sacs in their retreats or nests, and the hatched spiderlings may have stayed together with their mother for some time (Guo et al., 2021).

The lagonomegopid genus *Lineaburmops*, which has been reported only from mid-Cretaceous Kachin amber, northern Myanmar, contains three species: *Lineaburmops beigeli* Wunderlich, 2015, *Lineaburmops hirsutipes* Wunderlich, 2015 and *Lineaburmops maculatus* Wunderlich, 2017. They have the following distinctive morphological characters: carapace and abdomen with longitudinal stripes composed of white setae (Wunderlich, 2015, 2017). It should be mentioned that these colors may not reflect the original colors of *Lineaburmops* spiders when they were alive, because the majority of chemical compounds related to colors are lost rapidly after death of the organism, and the original colors are easily altered or lost during fossilization (Martínez-Delclòs et al., 2004; McNamara, 2013; Cai et al., 2020). So, original colors of fossils are

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rarely shown directly, most of them are preserved as color patterns (McNamara, 2013; Vinther. 2015). Herein, two *Lineaburmops* spiders with contrasting color patterns are described from Kachin amber, providing new materials for further paleo color studies.

## 2. Materials 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). The amber-bearing deposits have been dated to the earliest Cenomanian, ~98.8 ± 0.6 Mya, based on U–Pb radiometric dating of zircons from the volcaniclastic matrix (Shi et al., 2012). The clear traces of redeposition shows that Myanmar amber was formed earlier than the surrounding rocks, and could be of mid-Cretaceous age, i.e., Cenomanian (Grimaldi and Ross, 2017). All amber 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 (see Author Statement in "Supplementary material").

Preparation and imaging methods follow Selden and 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. Amber specimens CNUARA-MA2016027 was scanned with a micro-CT SkyScan 1172, located at the Museum of Hebei University, with the following parameters: no filter, Image Pixel Size (μm) = 3.59, Source Voltage (kV) = 58, and Source Current (μA) = 153. The three-dimensional structure of CNUARA-MA2016027 was reconstructed using the software Drishti (Version 3.1). The line drawings were prepared with Adobe Illustrator CC and Adobe Photoshop CC, the images were processed by Adobe Photoshop CC. Measuring method follows Selden et al. (2016). 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); fe, femur; mt, metatarsus; pa, patella; PLE, posterior lateral eye(s); PLS, posterior lateral spinneret(s); PME, posterior median eye(s); ta, tarsus; ti, tibia.

## 3. Results

### 3.1. Systematic palaeontology

Order: Araneae Clerck, 1757.
Family: Lagonomegopidae Eskov and Wunderlich, 1995
Genus: *Lineaburmops* Wunderlich, 2015
Type species: *Lineaburmops beigeli* Wunderlich, 2015

*Lineaburmops longiantepes* Guo, Selden and Ren sp. nov (Figs. 1–2).
(urn:lsid:zoobank.org:act:386D46FE-FEC4-4E74-9B7A-36F050BDC63A)
*Holotype*: Male, specimen no. CNU-ARA-MA2016019.
*Etymology*: The genus name is the combination of the Latin words *longi* and *antepes*, meaning long forefoot, alluding to legs I and II being much longer than legs III and IV in this species.
*Locality and horizon*: Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, mid-Cretaceous.
*Diagnosis*: This new species clearly belongs to genus *Lineaburmops*, based on its longitudinal stripes on carapace and abdomen. It can easily be distinguished from other *Lineaburmops* species by: carapace with a white longitudinal stripe in the middle of the cephalic region, extending from clypeus to fovea (carapace without white stripe in the middle of cephalic region in *L. beigeli*, *L. hirsutipes* and *L. maculatus*, carapace with an almost rhomboid white patch in the centre of the cephalic region in *L. rhombus*); carapace piriform in outline (outline of carapace almost rectangular in *L. rhombus*); legs I and II much longer than legs III and IV (leg IV longest in *L. maculatus*).


**Fig. 1.** *Lineaburmops longiantepes* sp. nov. (CNU-ARA-MA2016019). A, habitus, dorsal view; B, habitus, ventral view. Scale bar represents 1 mm.

*Taphonomic features*: CNU-ARA-MA2016019: this specimen is completely preserved, while the abdomen is distorted slightly; there are many tiny granular impurities in this piece of amber.
*Description*: Body length 3.61, dark-colored, with several white regions composed of white setae on the carapace and abdomen (Fig. 1). Carapace white-colored on the lateral and posterior areas, and with a white longitudinal stripe on the middle of cephalic region, extending from clypeus to fovea. A pair of white longitudinal stripes with wave-shaped boundaries situated on the lateral sides of abdomen.
Carapace piriform in outline, length 1.66, width 0.97 at widest point, covered with short, dense, feathery setae adpressed against cuticle. Cephalic region slightly raised, with pair of anterolateral protrusions next to inner side of PME (Fig. 2A). Eight eyes; PME enormous, 0.28 in diameter, situated on anterolateral corner of carapace; PLE small, placed at lateral margin of carapace, behind PME, separated 0.40 from PME centre; AME and ALE contiguous, situated between PME and clypeal margin. Fovea small and shallow, situated at centre of thoracic region. Chelicera length 0.74, width 0.23 at base, cheliceral insertion slightly separated from mouthparts, stridulatory files absent. Cheliceral promargin and retromargin not visible. Labium ligulate, slightly longer than wide, not fused to sternum. Endites elongated, details not visible. Sternum shield shaped, covered with long setae, convex and without tubercles.
Palpal podomere lengths: fe 0.62, pa 0.27, ti 0.34, ta 0.67. Palp hairy, feathery setae present at least on cymbium. Cymbium spoon-like. Detailed structures of male palp, such as embolus and conductor, not recognizable (Fig. 2B).

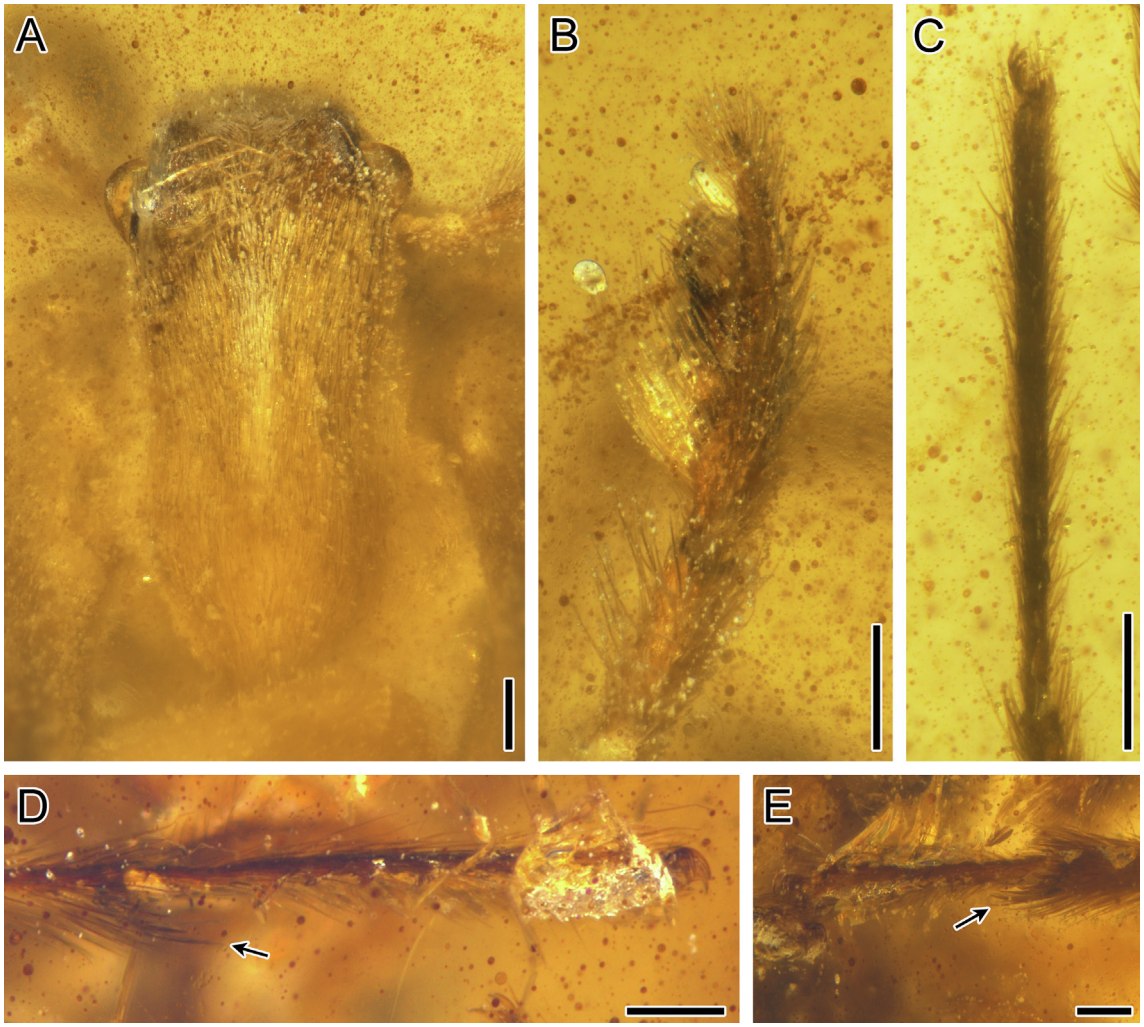


**Fig. 2.** *Lineaburmops longiantepes* sp. nov. (CNU-ARA-MA2016019). A, carapace, dorsal view; B, right male palp and palpal patella, lateral view; C, tarsus of right leg II, lateral view; D, tarsus of right leg IV, showing preening comb on distal metatarsus ventrally (arrow); E, tarsus of left leg III, showing preening comb on distal metatarsus ventrally (arrow). Scale bar represents 0.2 mm (A–C), 0.1 mm (D, E).

Legs hairy, feathery setae at least present on femur. Leg formula I > II > IV > III: leg I fe 2.52, pa 0.64, ti 2.90, mt 2.44, ta 1.17; leg II fe 2.66, pa 0.65, ti 2.65, mt 1.97, ta 0.89; leg III fe 1.46, pa 0.49, ti 1.21, mt 0.88, ta 0.47; leg IV fe 2.13, pa 0.55, ti 1.54, mt 1.10, ta 0.57. Legs I and II much longer than legs III and IV; metatarsus distinctly longer than tarsus. Metatarsus and tarsus without scopulae (Fig. 2C). Distal preening comb composed by 7–8 short macrosetae, present on metatarsus of posterior legs ventrally (Figs. 2D, E). Trichobothria present on tibia, metatarsus and tarsus. Three tarsal claws, paired claws with teeth, median claw hook-like.

Abdomen ovoid, length 2.03, width not measurable, densely covered with short setae. Spinnerets not recognizable.

*Lineaburmops rhombus* Guo, Selden and Ren sp. nov (Figs. 3–4). (urn:lsid:zoobank.org:act:864211A5-C47D-4671-ACAD-47CA45353F05)

*Holotype*: Male, specimen no. CNU-ARA-MA2016027.

*Etymology*: The specific name is the Latin word *rhombus*, referring to the almost rhomboid white patch in the centre of the cephalic region.

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

*Diagnosis*: This new species clearly belongs to genus *Lineaburmops*, based on its longitudinal stripes on carapace and abdomen. It can easily be distinguished from other *Lineaburmops* species by: carapace with an almost rhomboid white patch in the centre of the cephalic region (carapace without white stripe in the middle of the cephalic region in *L. beigeli*, *L. hirsutipes* and *L. maculatus*, carapace with a white longitudinal stripe in the middle of the cephalic region in *L. longiantepes*); clypeus with an almost V-shaped white patch between AME and the clypeal margin (clypeus with a subtriangular white patch in *L. beigeli*, a transverse band of white setae present on the clypeus in *L. hirsutipes*); carapace almost rectangular in outline (outline of carapace piriform in *L. hirsutipes* and *L. longiantepes*).

*Taphonomic features*: CNU-ARA-MA2016027: this specimen is relatively well preserved, while the abdomen is distorted slightly and some leg podomeres are broken; metatarsus and tarsus of left leg I, tarsus of right leg I and patella of right leg IV are totally missing; there are several bubbles and impurities around the spider.

*Description*: Body length 3.97, dark-colored, with several white regions composed of white setae on carapace and abdomen (Fig. 3). Carapace white-colored on lateral areas, with almost rhomboid

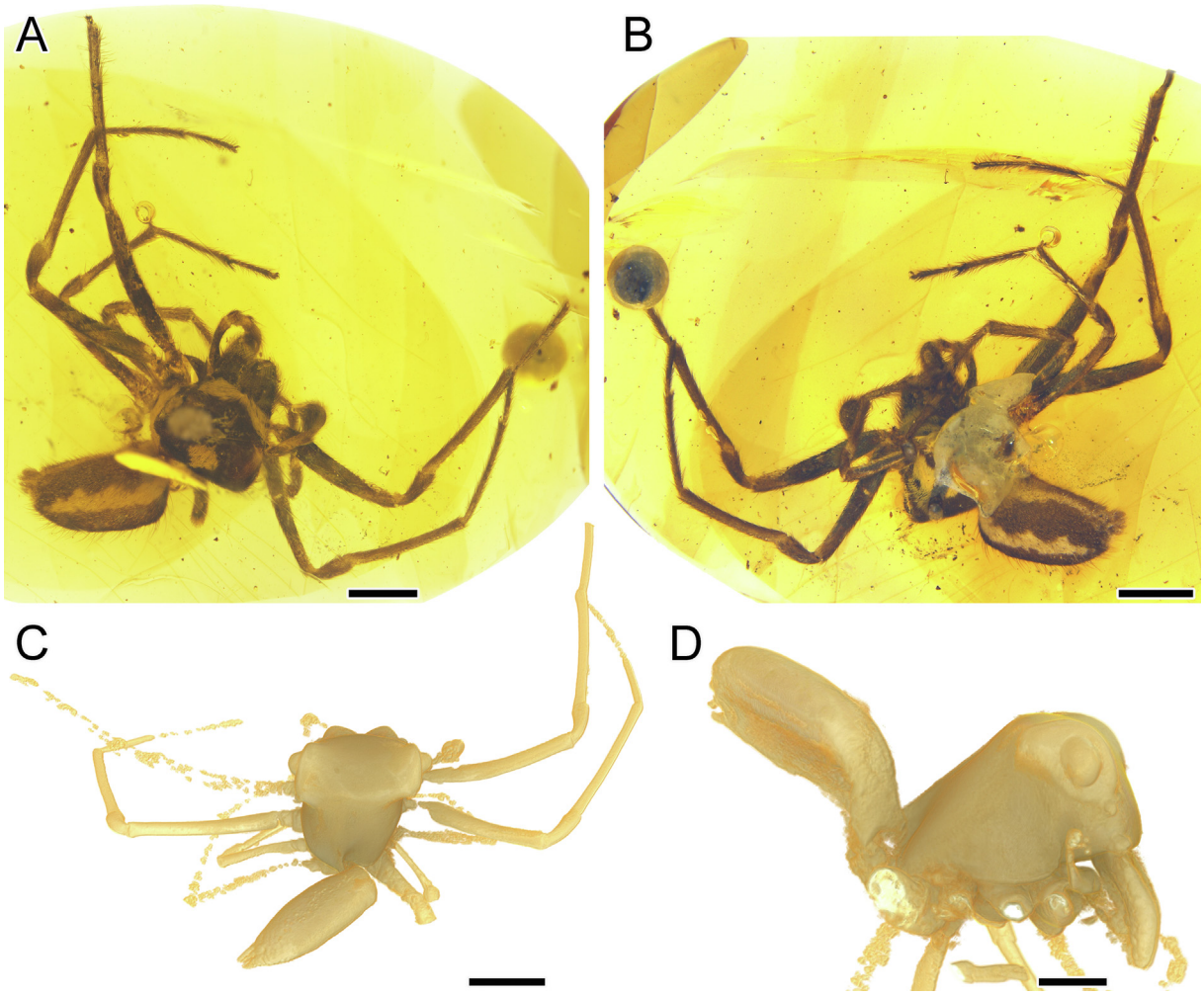


**Fig. 3.** *Lineaburmops rhombus* sp. nov. (CNU-ARA-MA2016027). A, habitus, anterior dorsal view; B, habitus, posterior ventral view; C, three-dimensional CT reconstruction, habitus, dorsal view; D, three-dimensional CT reconstruction, cephalothorax and abdomen, lateral view. Scale bar represents 1 mm (A–C), 0.5 mm (D).

white patch in centre of cephalic region (Fig. 4A). Clypeus with almost V-shaped white patch between AME and clypeal margin, and pair of small subtriangular white patches near PME (Fig. 4B). Dorsal and ventral surfaces of abdomen each with pair of white longitudinal stripes; dorsal stripes wider than ventral ones, with straight boundaries on inner sides and wave-shaped boundaries on outer sides; boundaries of ventral stripes straight.

Carapace almost rectangular in outline, length 1.82, width 1.67 at widest point, covered with short, dense, feathery setae adpressed against cuticle. Cephalic region raised slightly, anterolateral corner protruded distinctly. Eight eyes present; PME enormous, 0.30 in diameter, situated on anterolateral corner of carapace; PLE small, at posterior margin of cephalic anterolateral protrusions, separated 0.34 from PME centre; AME and ALE contiguous, situated between PME and clypeal margin (Figs. 4A, C). Fovea small, shallow, situated in centre of carapace. Chelicera length 0.88, width 0.56 at base, cheliceral insertion slightly separated from mouthparts (Fig. 3D), stridulatory files absent. Chelicera with at least eight peg teeth on promargin, retromargin not visible. Details of labium, endites and sternum not recognizable.

Palpal podomere lengths: fe 0.84, pa 0.29, ti 0.39, ta 0.81. Palp hairy, tibia with six dorsal trichobothria in two rows. Cymbium spoon-like. Detailed structures of male palp, such as embolus and conductor, not recognizable.

Legs hairy, feathery setae at least present on femur, patella and tibia. Leg formula I > II > IV > III: leg I fe 2.07, pa 0.69, ti 1.88; leg II fe 1.88, pa 0.64, ti 1.81, mt 1.55, ta 0.78; leg III fe 1.23, pa 0.43, ti 0.82, mt 0.67, ta 0.47; leg IV fe 1.86, pa 0.47, ti 1.19, mt 1.21, ta 0.61. Metatarsus slightly longer than tarsus in leg III, metatarsus almost more than two times longer than tarsus in leg II and IV. Metatarsus and tarsus without scopulae (Fig. 4E). Distal preening comb composed by 5–6 short macrosetae, present on metatarsus of posterior legs ventrally (Fig. 4F). Tibia with at least ten, metatarsus with at least eight, tarsus with at least eight trichobothria. Three tarsal claws, paired claws with 7–8 teeth, median claw hook-like.

Abdomen ovoid, length 2.15, width 0.67, densely covered with short feathery setae (Fig. 4D) and long sparse bristles. Four spinnerets visible. ALS slightly larger than PLS, details not recognizable.

## 4. Discussion

A large number of living spiders are colorful; they have chemical or structural colors, arising from setae or the cuticle. Chemical colors are caused by pigments and guanine crystals in epithelial cells of spiders (Foelix, 2011), while structural colors are produced by light interference, mostly on setae with special microstructure (Foelix et al., 2013). However, spider fossils are usually monochromatic; fossil records of spiders with obvious color patterns are relatively

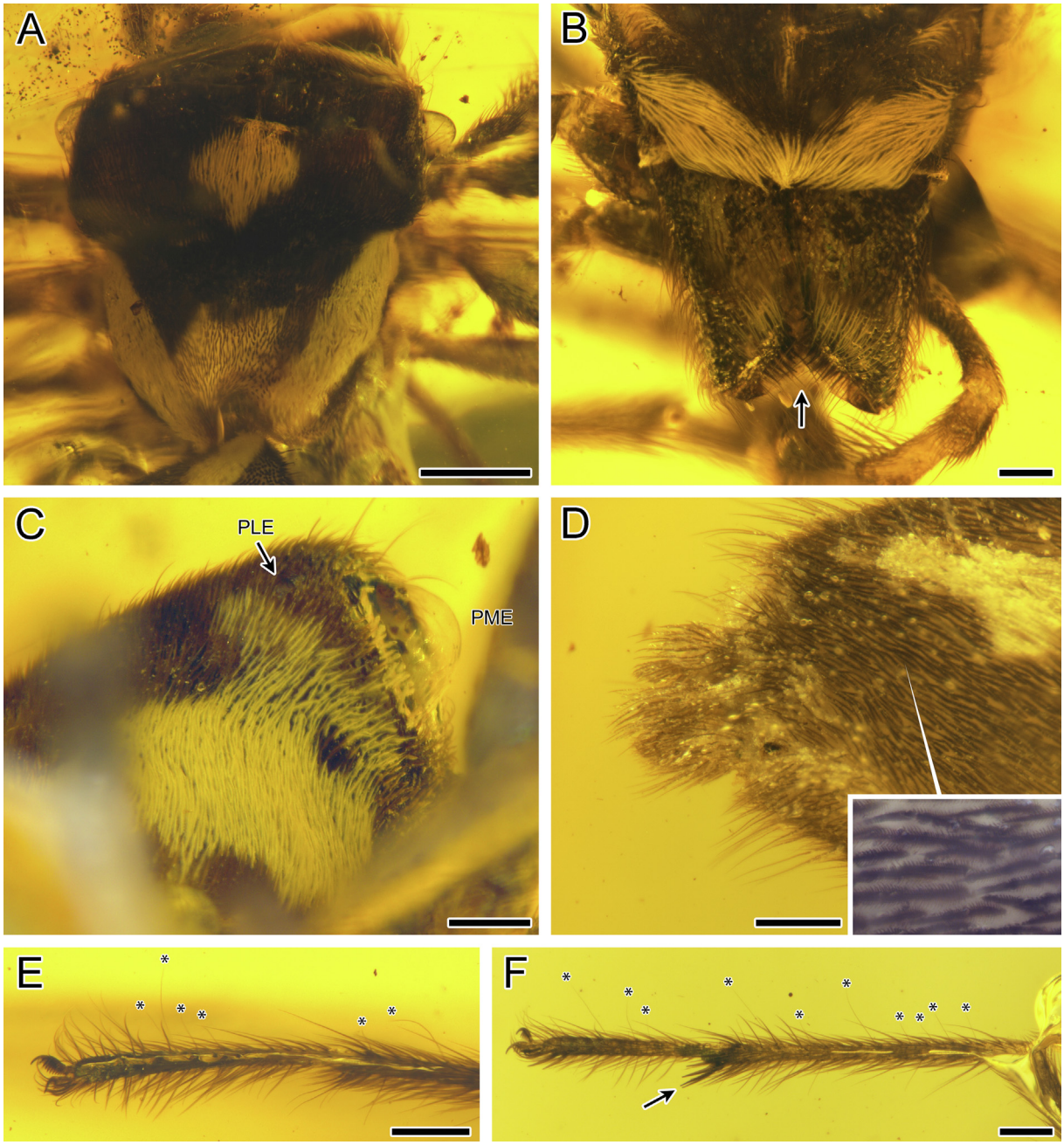


**Fig. 4.** *Lineaburmops rhombus* sp. nov. (CNU-ARA-MA2016027). A, carapace, dorsal view; B, clypeus and chelicera, anterior view, showing peg teeth (arrow); C, carapace, posterior lateral view, showing PME and PLE; D, posterior end of abdomen, lateral view, showing spinnerets and feathery setae (magnified at bottom right); E, tarsus and distal metatarsus of left leg II, showing trichobothria on tarsus and metatarsus dorsally (asterisks); F, tarsus and metatarsus of left leg III, showing trichobothria on tarsus and metatarsus dorsally (asterisks) and preening comb on distal metatarsus ventrally (arrow). Scale bar represents 0.5 mm (A), 0.2 mm (B–F).

rare and generally found in amber (Petrunkevitch, 1946; Wunderlich, 2015; Riquelme and Menéndez-Acuña, 2017; García-Villafuerte, 2020). Among these, color patterns were treated as identification traits by Wunderlich (2015). He described three lagonomegopid species with complex color patterns from mid-Cretaceous Kachin amber, and placed them in two genera, *Lineaburmops* and *Picturmegops*, based on their different color patterns. Apart from amber, some compression fossils preserve color patterns as well, for instance, leg bandings (Park et al., 2019; Downen and Selden, 2020; Martine et al., 2023).

In our *Lineaburmops* fossils, body colorations are formed by the grouped distribution of white and black setae. These white and black colors probably were remnants of chemical colors rather original structural colors. Because the preservation of structural colors in amber requires rigorous conditions, tiny disturbances would make them lose original colors (Cai et al., 2020). Structural colors in spiders are usually very bright and showy, such as red, yellow, blue and even iridescence (Foelix et al., 2013; Hsiung et al., 2014, 2019). Although these fossils may not show their original colors in life, *Lineaburmops* spiders clearly had color patterns with strong visual contrast (Figs. 5A–C).

These color patterns may have functioned for camouflage or attracting prey (Wunderlich, 2015, 2017), as occurs in some living spiders (Figs. 5D, E). The coexistence of bright and dark markings on the body of *Lineaburmops* spiders may be a kind of disruptive coloration, using contrasting colors to break up the contour of the

spider, thus making them more difficult to be seen by predators (Cuthill et al., 2005; Tso, 2013; Gawryszewski, 2017). Moreover, disruptive coloration is more efficient in heterogeneous habitats, as predicted by theoretical and experimental data (Schaefer and Stobbe 2006; Stevens et al., 2006), which suggests that *Lineaburmops* spiders had a fitness for living in the complex tropical forest ecosystem of mid-Cretaceous Myanmar (Grimaldi et al., 2002). Apart from camouflage, the white marking may have had a prey attraction function as well. Behavioral experiments have shown that spiders with bright markings (e.g., white stripes and orange bands) can attract more prey than those without bright markings in some living spider groups (Lin et al., 2015; Zhang et al., 2015, 2022; Tso et al., 2016; Liao et al., 2019).

Interestingly, all *Lineaburmops* fossils reported up to now are adult males, and no female lagonomegopids with similar color patterns have been reported. One potential explanation is that the contrasting color pattern is a kind of sexual dimorphism in the genus *Lineaburmops*, and perhaps the female *Lineaburmops* have been described in other lagonomegopid genera, due to the lack of longitudinal stripes on carapace and abdomen which is considered as the typical character of the genus *Lineaburmops*. In living spiders, body coloration has been proved to play an important role as a visual signal in the mating of some diurnal and nocturnal spiders (Lim et al., 2007; Girard et al., 2011; Lin et al., 2015; Zhang et al., 2018). Lagonomegopid spiders probably have a good vision because of their huge PME. These contrasting color patterns of male *Lineaburmops* may also function in the mating context, as a result of sexual selection. Further discoveries of more *Lineaburmops* specimens, especially adult females, will help to solve this problem and contribute to clarifying the functions of color pattern in this genus. As mentioned above, we cannot exclude the hypothesis that *Lineaburmops* spiders had gorgeous structural and chemical colors when they were alive, these fossils just show what happens when the structural colors disappear and the chemical colors fade. The

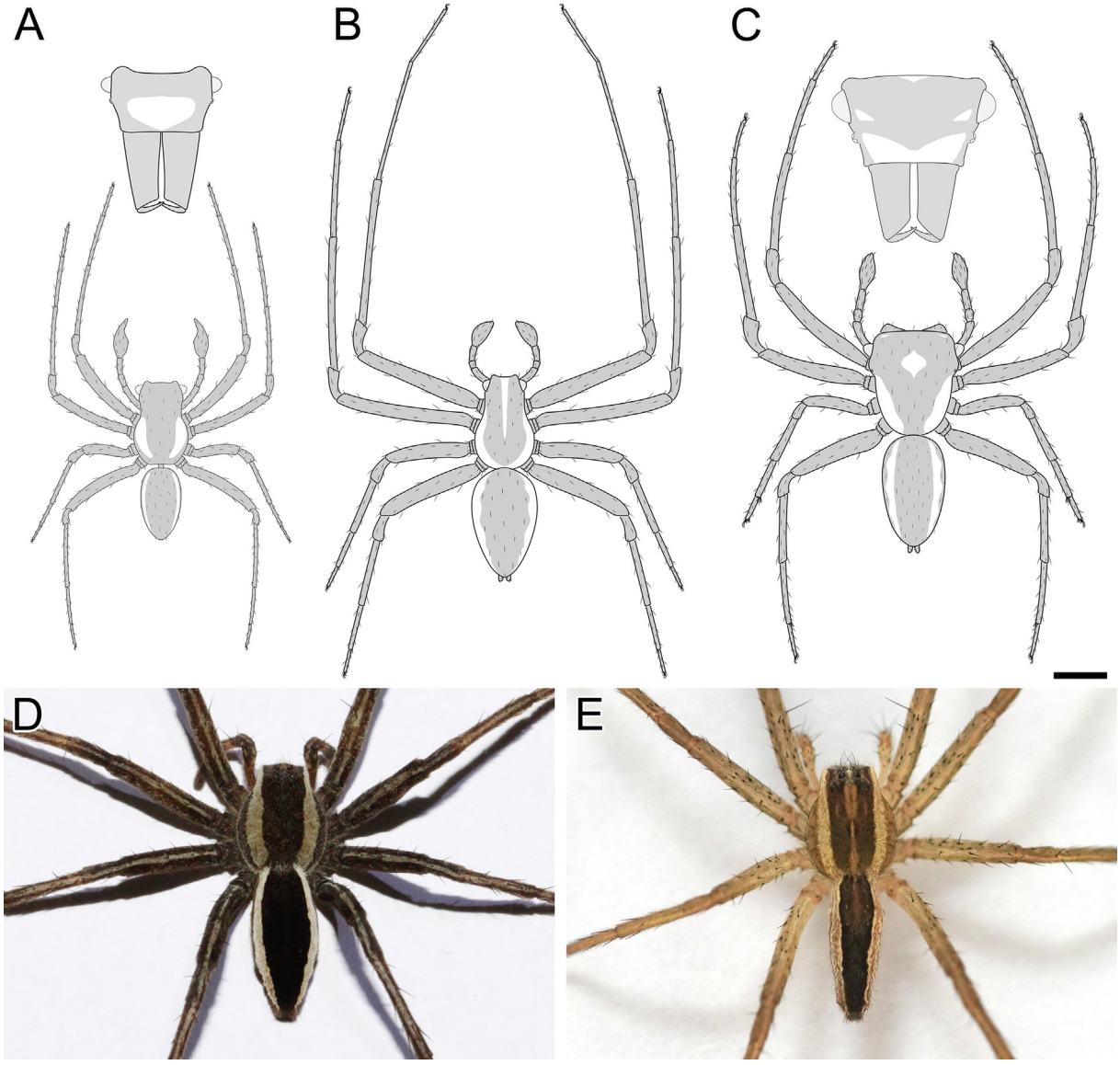


**Fig. 5.** The similar contrasting color patterns of *Lineaburmops* spiders and living pisaurid spiders. A, reconstruction of *Lineaburmops beigeli* Wunderlich, 2015, showing color pattern in dorsal (bottom) and anterior (top) view; B, reconstruction of *Lineaburmops longiantepes* sp. nov., showing color pattern in dorsal view; C, reconstruction of *Lineaburmops rhombus* sp. nov., showing color pattern in dorsal (bottom) and anterior (top) view; D, E, color patterns of two living pisaurid spiders. Scale bar represents 1 mm (A–C).

reconstruction of color in fossils has been a key topic in paleontology, these new fossils provide more materials for paleo color studies in the future.

## 5. Conclusions

Two new lagonomegopid species belonging to the genus *Lineaburmops*, *Lineaburmops longiantepes* sp. nov. and *Lineaburmops rhombus* sp. nov., are described from mid-Cretaceous Kachin amber, northern Myanmar. With the previous reported three species, all five *Lineaburmops* species are only based on male specimens, and they all have contrasting color patterns which may have functioned for camouflage, attracting prey or courtship. The new fossils enrich our knowledge of the morphological diversity of *Lineaburmops* and provide materials for further paleo color studies.

## CRediT authorship contribution statement

**Xiangbo Guo:** Conceptualization, Investigation, Methodology, Software, Writing – original draft. **Paul A. Selden:** Investigation, Writing – review & editing. **Dong Ren:** Conceptualization, Writing – review & editing. **Yiping Niu:** Methodology, Software, Writing – original draft. **Feng Zhang:** Conceptualization, Project administration, Supervision, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgments

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2024.105835.