



A diverse new spider (Araneae) fauna from the Jinju Formation, Cretaceous (Albian) of Korea

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A collection of spiders from the Cretaceous (Albian) Jinju Formation of Korea is described. These finds increase the number of known spiders from the Jinju Formation from one to 11. There is considerable diversity of mygalomorphs and araneomorphs, including palpimanoids (including lagonomegopids), as well as cribellate and ecribellate entelegynes. Such diversity among so few specimens hints that an even greater range of families will come to light as more specimens are discovered in the future. The first non-amber Lagonomegopidae are described, with the first preservation of a spider eye tapetum in the fossil record, providing evidence for lagonomegopid enlarged eyes being posterior medians. The female-biased sex ratio of lagonomegopids is discussed and it is concluded that the bias is fortuitous.

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Introduction

Spiders form one of the most diverse animal groups in terrestrial ecosystems, yet fossilized spiders are rare due to the fragility of their soft bodies. Nevertheless, a fair number of studies, especially since the 1990s, have produced reliable data for understanding their diversity over geological time (Selden & Penney 2010; Penney & Selden 2011). Numerous discoveries of fossilized spiders preserved in amber are not only the commonest sources of known diversity from the Early Cretaceous onward, but also the sources of detailed morphological information due to the exquisite preservation. In contrast, non-amber spider fossils generally show limited details of morphology, compared to the amber fossils, but could provide pre-Cretaceous information about arachnids, including the earliest evolutionary history of spiders (e.g. Garwood *et al.* 2016). Moreover, the fossil record preserved in amber could be biased towards the groups that had an arboreal habitat or behavioural features that enabled resin entrapment, while non-amber fossils could provide a less biased fossil record of spiders.

The Lower Cretaceous Jinju Formation is the most fossiliferous formation of the Gyeongsang Supergroup,

Korea. The remains of diverse fossils from this formation include: plants, bivalves, arthropods, fishes, and dinosaur and pterosaur teeth. Fossil spores and pollen were reported by D. K. Choi (1985) and D. K. Choi & Park (1987). Trace fossils, such as arthropod tracks, turtle tracks and dinosaur tracks, are also common (J. Y. Kim & Pickerill 2002; J. Y. Kim *et al.* 2005; J. Y. Kim & Lockley 2016); recently, D.-C. Lee (2017) reported the new ichnogenus *Radialimbricatus* from the formation, with arthropods, cnidarians and annelids being the candidates for the trace maker. Paik (2005) reported stromatolite-caddisfly bioherms. However, by far the most common fossils from the Jinju Formation are arthropods, such as ostracods (B.-D. Choi & Huh 2016; B.-D. Choi *et al.* 2018), conchostracans (S.-O. Park & Chang 1998), isopods (T.-Y. Park *et al.* 2012) and insects (Engel *et al.* 2002, 2006; Baek & Yang 2004; T.-Y. Park *et al.* 2013; Nam & Kim 2016), although understanding the full diversity of them is far from complete. A recent addition to the arthropod fossil list of the Jinju Formation is a fossil spider (Selden *et al.* 2012). A single specimen of *Korearachne jinju* Selden *et al.*, 2012 was preserved in a dark grey shale slab with albuiform fish, dipteran insects and possible

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crustacean fragments. Since the specimen lacked some key features including the opisthosoma, the familial assignment of this genus remained unresolved. Apart from this single specimen of *Korearachne jinju*, no more spider fossils from the Jinju Formation have been discovered until now, and the diversity of the Cretaceous spiders of Korea has remained unsatisfactorily understood.

Here, we describe a spider fauna which consists of seven different species from the Lower Cretaceous Jinju Formation. Together with *Korearachne jinju*, the new spider species in this study will fill in the post-Aptian spider fossil record in East Asia, which has been largely unknown, due to the lack of post-Aptian fossiliferous strata in China. Interestingly, the fauna includes the first lagonomegopid spiders preserved outside amber, extending palaeoecological aspects of this Cretaceous spider family. Lagonomegopidae Eskov & Wunderlich, 1995 is known to be highly diverse, with a worldwide distribution in the Cretaceous Period (Pérez-de la Fuente *et al.* 2013), but they were hitherto only known from inclusions in amber, providing limited aspect for their ecology. Lagonomegopids bear two large eyes positioned on the anterolateral flanks of the carapace, which is a unique feature of this family (Pérez-de la Fuente *et al.* 2013). The laterally positioned large eyes of lagonomegopids were originally described as posterior median

eyes (Eskov & Wunderlich 1995) but, subsequently, Wunderlich (2015) suggested that they are anterior median eyes, referring to the eye positions in the allegedly closely related families Micropalpimanidae Wunderlich, 2008 and Archaeidae C. L. Koch & Berendt, 1854. Another interesting feature of lagonomegopids is the rarity of adult male specimens; Pérez-de la Fuente *et al.* (2013) suggested two explanations for this: (1) the taphonomic bias of amber inclusions by which smaller specimens have a greater chance to be trapped, or (2) a truly female-biased sex ratio, possibly due to parthenogenesis. The female-biased sex ratio of lagonomegopids is discussed and we conclude that the bias is fortuitous.

Geological setting

The Cretaceous Gyeongsang Supergroup is distributed in the south-eastern part of the Korean Peninsula (Fig. 1). The succession consists of non-marine sedimentary sequences with some volcanic component. The presence of albuiform fish fossils (see Selden *et al.* 2012) and occurrence of *Archaeoniscus* isopod fossils (T.-Y. Park *et al.* 2012) might suggest a marine connection to the basin for this succession. However, the other, overwhelming occurrences of terrestrial fossils, such as

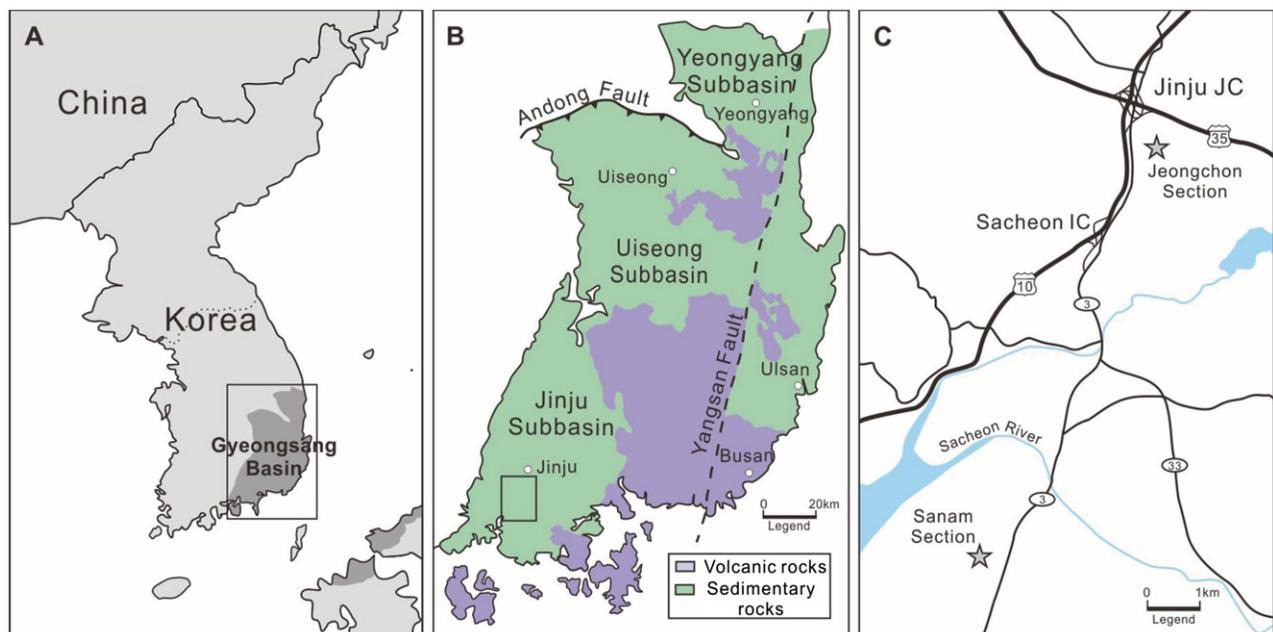


Figure 1. Locality map of the study area. **A**, distribution of Cretaceous sedimentary basins around the Korean Peninsula; rectangular area is magnified in **B**. **B**, simplified geological map of the Gyeongsang Arc System; the sedimentary rocks represent the Gyeongsang Backarc Basin, while the volcanic rocks represent the Gyeongsang Volcanic Arc; rectangular area is magnified in **C** (modified from Chough & Sohn 2010; the displacement by the Yangsan Fault has been recovered). **C**, road map of the study area showing the two fossil localities (stars).

plants (J. H. Kim & Lee 2014; J. H. Kim *et al.* 2016), ostracods (B.-D. Choi & Huh 2016; B.-D. Choi *et al.* 2018), freshwater molluscs (Yang 1976, 1979) and pollen (D. K. Choi 1985; D. K. Choi & Park 1987), indicate that the basin was largely non-marine. The fossil evidence conforms to the interpretation of the Gyeongsang Supergroup as a non-marine back-arc basin deposit by Chough & Sohn (2010): the back-arc basin (the Gyeongsang Backarc Basin) provided fluvio-lacustrine environments, situated west of the Gyeongsang Volcanic Arc which was formed by the subduction of the proto-Pacific (Izanagi) plate under the Asian continent. Accordingly, the occurrence of the isopod *Archaeoniscus* from the Gyeongsang Basin was interpreted as the first occurrence of this genus in a freshwater environment (T.-Y. Park *et al.* 2012).

Due to differences in lithology and geographical distribution, the Gyeongsang Backarc Basin is subdivided into the Jinju, Uiseong and Yeongyang sub-basins (Fig. 1). The stratigraphy in the Jinju Sub-basin is relatively simple; its age spans the Hauterivian to Campanian, and consists of the Nakdong Formation, Hasandong Formation, Jinju Formation, Chilgok Formation, Silla Conglomerate, Haman Formation, Gusandong Tuff and Jindong Formation, in ascending order (Chough & Sohn 2010). Of these, the lower three formations, Nakdong, Hasandong and Jinju, are collectively called the Sindong Group. The Jinju Formation is 1000 to 1800 m thick, mainly comprising grey to black shale intercalated by packets of sandstones, and is interpreted to have been deposited in a fluvio-lacustrine environment (Chough & Sohn 2010).

The exact age of the Jinju Formation remained debated until recently. Palynological data suggested that the Sindong Group is late Neocomian (Hauterivian and Barremian) in age (D. K. Choi 1985; D. K. Choi & Park 1987; Yi *et al.* 1994), while recent geochronological data from detrital zircons suggested younger ages. T.-H. Lee *et al.* (2010) constrained the age of the Jinju Formation to between 112.4 ± 1.3 Ma and 110.4 ± 2.0 Ma, which is latest Aptian to early Albian. Y. I. Lee *et al.* (2010) reported the youngest detrital zircon age of 106.0 ± 1.9 Ma from the formation, which is middle Albian. Taking this together with the geochronological data of the underlying and overlying formations, Kang & Paik (2013) suggested an early to middle Albian age for the Jinju Formation.

Material and methods

Material

A total of 10 spider specimens (five of which consist of part and counterpart) from the Jinju Formation are

described in this study. All but two of the specimens are deposited in the palaeontological collections of the Korea Polar Research Institute, with registration numbers prefixed by KOPRIF (KOPRIF7011–7018), while the other two specimens are housed in the Biseulsan Fossil Museum with registration numbers prefixed by DBFM (DBFM 00054, 00061). All spider specimens described here come from the black shale of the Jinju Formation at two different localities in the Jinju Sub-basin: the Jeongchon section ($35^{\circ}07'45''\text{N}$ $128^{\circ}06'02''\text{E}$) and the Sanam sections ($35^{\circ}03'59.42''\text{N}$ $128^{\circ}04'7.03''\text{E}$) (Fig. 1). Both sections were being excavated when the fossils were collected, and are now covered and inaccessible. Before it was covered in 2017, a c. 43 m succession of black shales intercalated by thick sandstone of the Jinju Formation was exposed in the Jeongchon section. The black shale of this section produced various fossils, including plants, fishes, bivalves, ostracods, conchostracans, isopods and insects (Fig. 2). The most common fossils from this section are insects, with c. 3000 specimens collected. Of these, T.-Y. Park *et al.* (2013) reported nymphs of the aquatic coleopteran *Coptoclava* Ping, 1928, and Nam & Kim (2016) documented nymphs and imago fragments of the odonatan *Hemeriscopis* Pritykina, 1977. Not much information is available on the Jinju Formation at the Sanam section, which has been covered since 2010. Six spider specimens were collected from the Jeongchon Section (KOPRIF7011–7016), and the other four specimens were recovered from the Sanam Section (KOPRIF7017–7018, DBFM 00054, DBFM 00061). Of the four specimens from the Sanam section, two specimens were donated by Mr Samsik Lee (KOPRIF7017–7018).

Methods

The spiders (Figs 3–14) are preserved in slabs of finely laminated, very dark grey shale with associated insects and crustaceans on some slabs. The specimens were studied immersed in 70% ethanol under a Leica M205C microscope and photographed with a Canon 5D MkII camera attached. Drawings were made from photographs using Autodesk Graphic (www.graphic.com).

Measurements of paired organs are averages of left and right of part and counterpart, i.e. maximally four measurements if all are preserved. Measurements were made only of complete podomeres, except where marked with \geq which is a minimum measurement of an incomplete podomere; measurements of coxae and trochanters are rather imprecise and uninformative. Length/width ratios are provided for carapace, opisthosoma, sternum and femora. Chelicera lengths include the fang. Leg total lengths are given as femur–tarsus; tarsus lengths include the claw. Leg formula (e.g. I > II > IV > III) indicates the length of each leg relative to the others, longest to shortest. Total



Figure 2. An outcrop view and the columnar section of the Jeongchon Section. **A**, an outcrop view image taken in 2012, showing the fossiliferous dark shale; **B**, columnar section of the Jinju Formation, exposed at the Jeonchon Section, with fossil occurrences. Note that the spider fossils for this study were collected from the lower part of the exposed interval.

body length includes chelicerae and anal tubercle; cheliceral length includes fang; tarsal length includes claws.

Definitions of setae, macrosetae, spines and bristles are given in Selden *et al.* (2016); peg teeth are small macrosetae present on the pro- and/or retromargin of the chelicera in palpimanoid, mimetid and pararchaeine malakarid spiders, whereas true teeth (unsocketed) occur in other spiders (Forster & Platnick 1984).

Anatomical abbreviations

I, II, III, IV: leg numbers; **a s**: anterior spinneret; **a t**: anal tubercle; **cal**: calamistrum; **car**: carapace; **cx**: coxa; **e f**: epigastric furrow; **f**: fovea; **fe**: femur; **L**: length; **lb**: labium; **m**: maxilla; **mt**: metatarsus; **op**: opisthosoma; **pa**: patella; **Pd**: pedipalp; **s**: sigillum; **sp**: spinneret(s); **st**: sternum; **ta**: tarsus; **ti**: tibia; **tr**: trochanter; **t s**: tracheal spiracle; **W**: width.

Institutional abbreviations

DBFM: Biseulsan Fossil Museum, Yong-ri, Yuga-eup, Dalseong-gun, Daegu, Republic of Korea; **KOPRI**: Korea Polar Research Institute, Yeonsu-gu, Incheon, Republic of Korea.

Systematic palaeontology

Order **Araneae** Clerck, 1757
Suborder **Opisthothelae** Pocock, 1892

Infraorder **Mygalomorphae** Pocock, 1892
Fam., gen. et sp. indet.

(Fig. 4)

Material. DBFM 00054.

Stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Sanam Section.

Remarks. This specimen is one of the largest fossils in the collection (Fig. 3), with a leg span approaching 20 mm. It is preserved showing mainly dorsal features, and the carapace is displaced to the right, presumably during compaction of the sediment. Some ventral features are discernible by impression through the dorsal cuticle, e.g. a cheliceral fang and the clot of matrix at the base of the spinnerets (Fig. 4). As in DBFM 00061, there are reflective vermiform marks along parts of the body and legs, which could be tool marks, or possibly organic decay structures. The carapace is short and wide, with distinct furrows and a large fovea. A region to the anterior is confusing, but estimating from the position of the pedipalp femora and the existence of a short, thin cheliceral fang permits the interpretation of this region as consisting of the chelicerae and maxillae (Fig. 4B). The pedipalps are rather long and the distal podomeres are somewhat swollen, although other organisms overlying the specimen rather confuse this region. A possible bulb is present on the right side (? in Fig. 4B), hence this specimen is interpreted as an adult

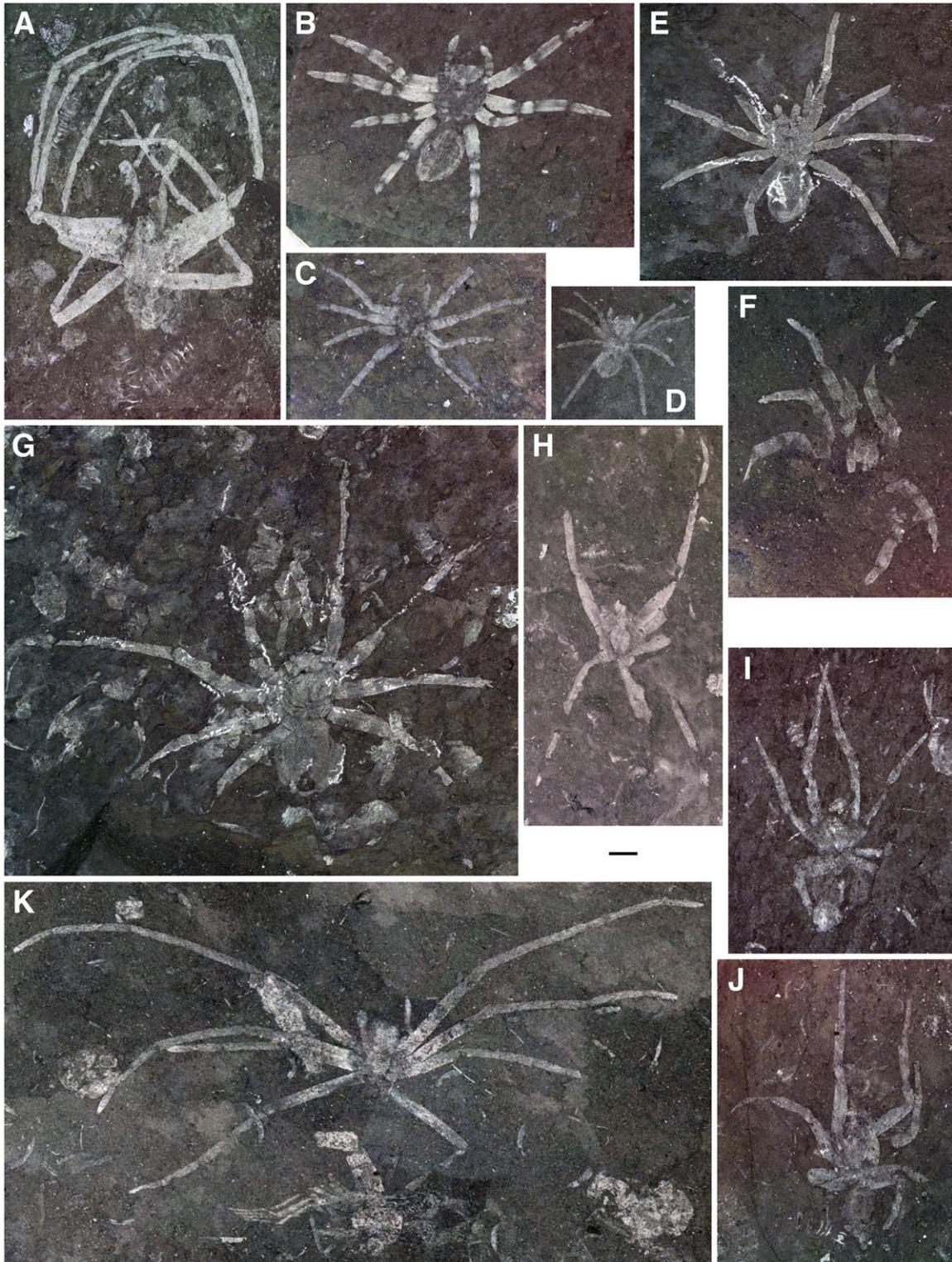


Figure 3. Diversity of Jinju Formation spiders. This figure illustrates all known specimens at the same scale; if part and counterpart are present, these are shown superimposed. **A**, *Jinjumegops dalingwateri* gen. et sp. nov., KOPRIF7014a,b. **B**, *Koreamegops samsiki* gen. et sp. nov., KOPRIF7011a,b. **C**, *Koreamegops samsiki* gen. et sp. nov., KOPRIF7012a,b. **D**, *Koreamegops samsiki* gen. et sp. nov., KOPRIF7017a,b. **E**, *Palpimanoidea incertae sedis*, DBFM 00061. **F**, Cribellate Entelegynae species 1, KOPRIF7016. **G**, *Mygalomorphae incertae sedis*, DBFM 00054. **H**, *Araneomorphae incertae sedis*, KOPRIF7018a,b. **I**, Cribellate Entelegynae species 2, KOPRIF7013. **J**, Cribellate Entelegynae species 2, KOPRIF7015. **K**, *Korearachne jinju* Selden *et al.* 2012. Scale bar =1 mm.

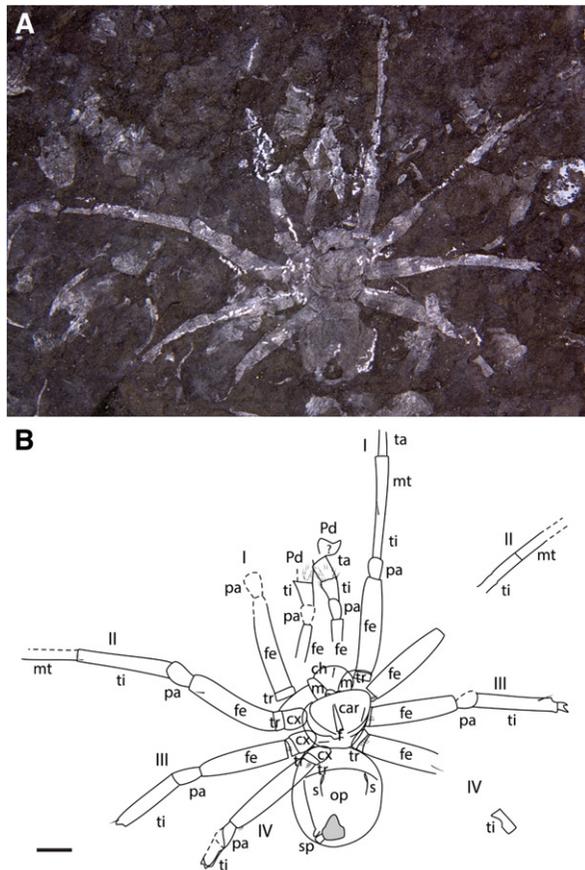


Figure 4. Mygalomorphae *incertae sedis*, DBFM 00054. **A**, photograph; **B**, explanatory drawing. Scale bar = 1 mm.

male. The distal parts of most legs are missing; podomere lengths are difficult to discern but where obvious on one side (e.g. left leg II), the opposite side can be extrapolated. The legs are almost equal in length (judging from the lengths of the femora), and tibiae are slightly longer than femora. The opisthosoma is subcircular in outline (so was likely subspherical in life), and bears a pair of sigilla about one-third of the length of the abdomen from its anterior border. A clot of matrix obscures the spinneret region, but there is no evidence for elongated spinnerets.

A number of features suggest this spider belongs in the Mygalomorphae. The wide, short carapace with large fovea (presumably deep in life) and strong furrows is reminiscent of numerous mygalomorph families. The orthognath fang is a clear indicator of this infraorder. The long pedipalps, elongate maxillae, and legs subequal in length are also mygalomorph features. The patellae are, however, relatively short (but these are not well preserved). Dorsal abdominal sigilla are present in some spider families, including mygalomorphs, e.g. Idiopidae Simon, 1889 (e.g. Raven & Wishart 2005; Rix *et al.*

2018), Nemesiidae Simon, 1889 (e.g. Siliwal *et al.* 2015), and Hexathelidae Simon, 1892 (e.g. Gray 2010). However, there are insufficient diagnostic features present on the fossil to be able to identify to which mygalomorph family it belongs.

Description. Spider covered in setation, few macrosetae on legs. Body L 4.36 mm. Carapace wider than long, with distinctive procurved furrows radiating laterally from large fovea situated near rear of carapace, demarcating large cephalic area which bears large median furrow (Fig. 4), L 1.56, W 2.03, L/W ratio 0.77. Chelicerae correct, bearing thin fang directed backwards (orthognath). Maxilla longer than wide, L 0.62 mm, W 0.36 mm, L/W ratio 1.68. Pedipalp long, fe-ta length ~3.57 mm (~3.84 mm including possible bulb). Legs approximately equal in length, leg formula (based on femur length) $IV \geq I \geq II \geq III$; tibiae longer than femora; curved bristles distally on trochanters. Podomere lengths: Leg I fe 2.66 mm, pa 0.64 mm, ti 2.90 mm; Leg II cx 0.67 mm, tr 0.21 mm, fe 2.64 mm, pa 0.74 mm, ti 2.60 mm; Leg III cx 0.66 mm, tr 0.20 mm, fe 2.47 mm, pa 0.76 mm, ti 2.14 mm; Leg IV cx 0.51 mm, tr 0.20 mm, fe 2.75 mm, pa 0.68 mm. Opisthosoma subcircular in outline, hirsute, bearing pair of elongate, teardrop shaped sigilla *c.* two-thirds length from anterior border (Fig. 4), L 2.91 mm, W 2.59 mm, L/W ratio 1.12.

Infraorder Araneomorphae Smith, 1902

Araneomorphae *incertae sedis*

Fam., gen. et sp. indet.

(Fig. 5)

Material. KOPRIF7018a,b.

Stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Sanam Section.

Remarks. This specimen is preserved as part and counterpart, showing the ventral side. Only leg I (left on part) is complete; parts of legs II and IV are preserved, but little of leg III or the pedipalp. The opisthosoma is preserved as an elongate mark but, since the lateral edges are not visible, its true shape is unknown. No calamistrum is visible, so it is assumed that this is not a cribellate spider. The subelliptical shape of the sternum, with only slight scalloping, is reminiscent of free-running spiders such as Anyphaenidae Bertkau, 1878, Clubionidae Wagner, 1887 and Gnaphosidae Pocock, 1898. However, these spiders bear conspicuous scopulae or claw tufts on the tarsi, which are absent from the fossil. It is not possible to identify this spider further than as Araneomorphae *incertae sedis*.

Description. Spider covered in fine setation, numerous macrosetae on all legs. Body L 4.22 mm. Carapace L

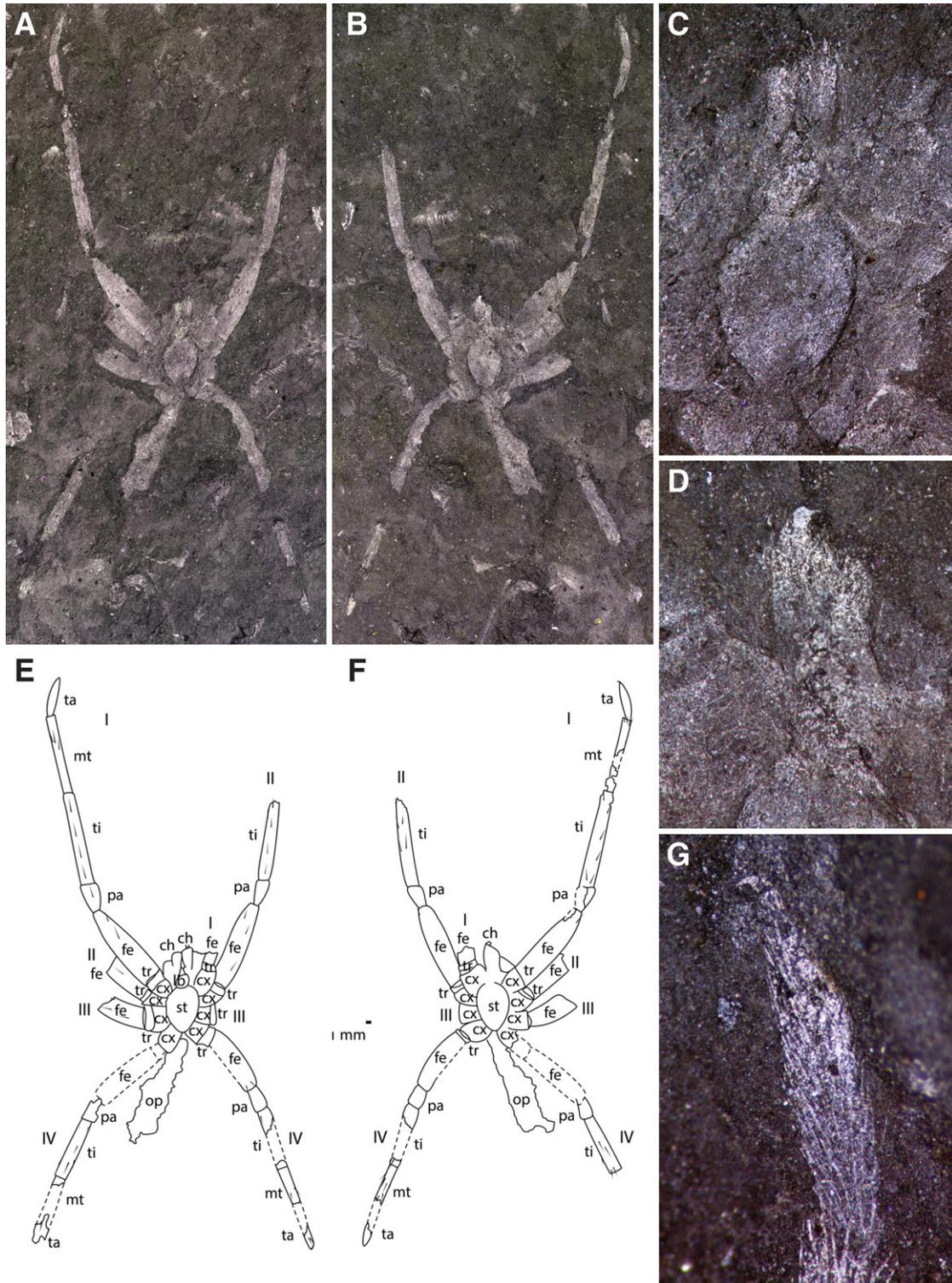


Figure 5. *Araneomorphae incertae sedis*, KOPRIF7018a,b. **A**, photograph of part; **B**, photograph of counterpart; **C**, ventral prosoma of part, showing sternum, labium and chelicerae; **D**, counterpart, left chelicera showing base of fang and left coxa I showing long, fine setae; **E**, explanatory drawing of part; **F**, explanatory drawing of counterpart; **G**, right tarsus I of counterpart, showing pectinate claw. Scale bar =1 mm.

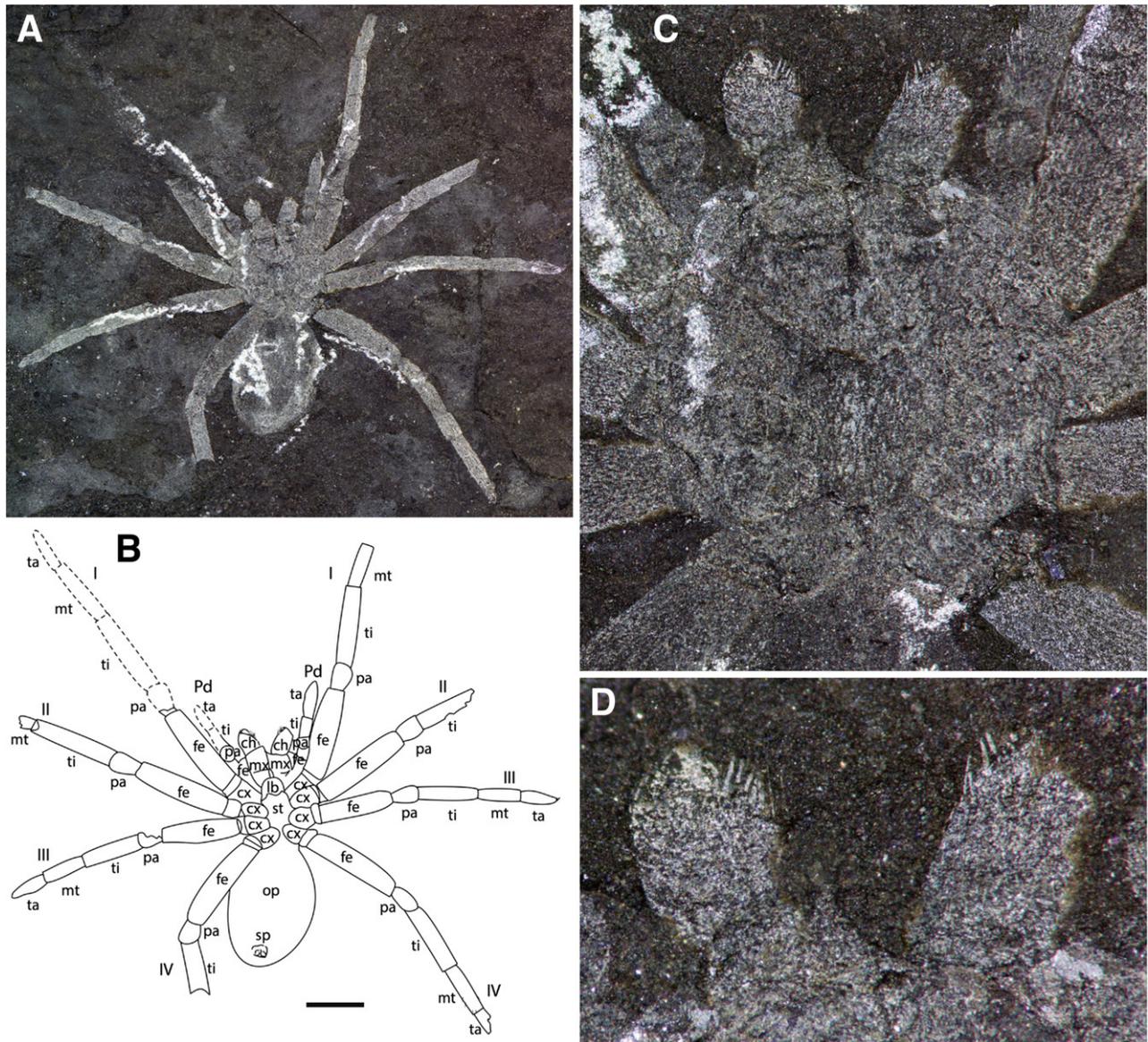


Figure 6. *Palpimanoidea incertae sedis*, DBFM 00061. **A**, photograph; **B**, explanatory drawing; **C**, ventral prosoma, showing sternum, labium, maxillae, coxae and chelicerae; **D**, chelicerae showing peg teeth. Scale bar = 1 mm.

1.99 mm. Sternum subelliptical, about twice as long as wide: L 0.99 mm, W 0.68 mm, L/W ratio 1.45, lateral edge slightly scalloped, not produced between coxae IV. Labium somewhat pentagonal, about as long as wide: L 0.27 mm, W 0.28 mm, L/W ratio 0.96, appears thickened anteriorly. Chelicera short, L 0.63 mm. Leg formula (approximated) I > II > IV > III; leg IV nearly three-quarters length of leg I; tibiae longer than metatarsi. Long, fine setae on coxa I (Fig. 5D); at least one pectinate claw on tarsus I (Fig. 5G), lacking claw tufts or scopulae. Podomere lengths: Leg I fe 1.83 mm, pa 0.57 mm, ti 2.00 mm, mt 1.59 mm, ta 0.83 mm, total fe-ta 6.82 mm (fe-ti 4.39 mm); Leg II fe 1.78 mm, pa

0.53 mm, ti 1.86 mm (total fe-ti 4.17 mm); Leg IV fe 1.37 mm, pa 0.45 mm, ti 1.28 mm, mt 1.03 mm, ta 0.76 mm, total fe-ta 4.90 mm (fe-ti 3.11 mm). Opisthosoma L 2.40 mm.

CY spigot clade Wheeler *et al.*, 2017

Superfamily **Palpimanoidea** Thorell, 1870 *sensu* Wood *et al.*, (2012)

Remarks. Palpimanoids are ecribellate spiders which share a combination of non-exclusive characters (see Wood *et al.* 2012, appendix 3). The most notable morphological characters seen in the fossils are the chelicerae peg teeth, on both pro- and retromargins and

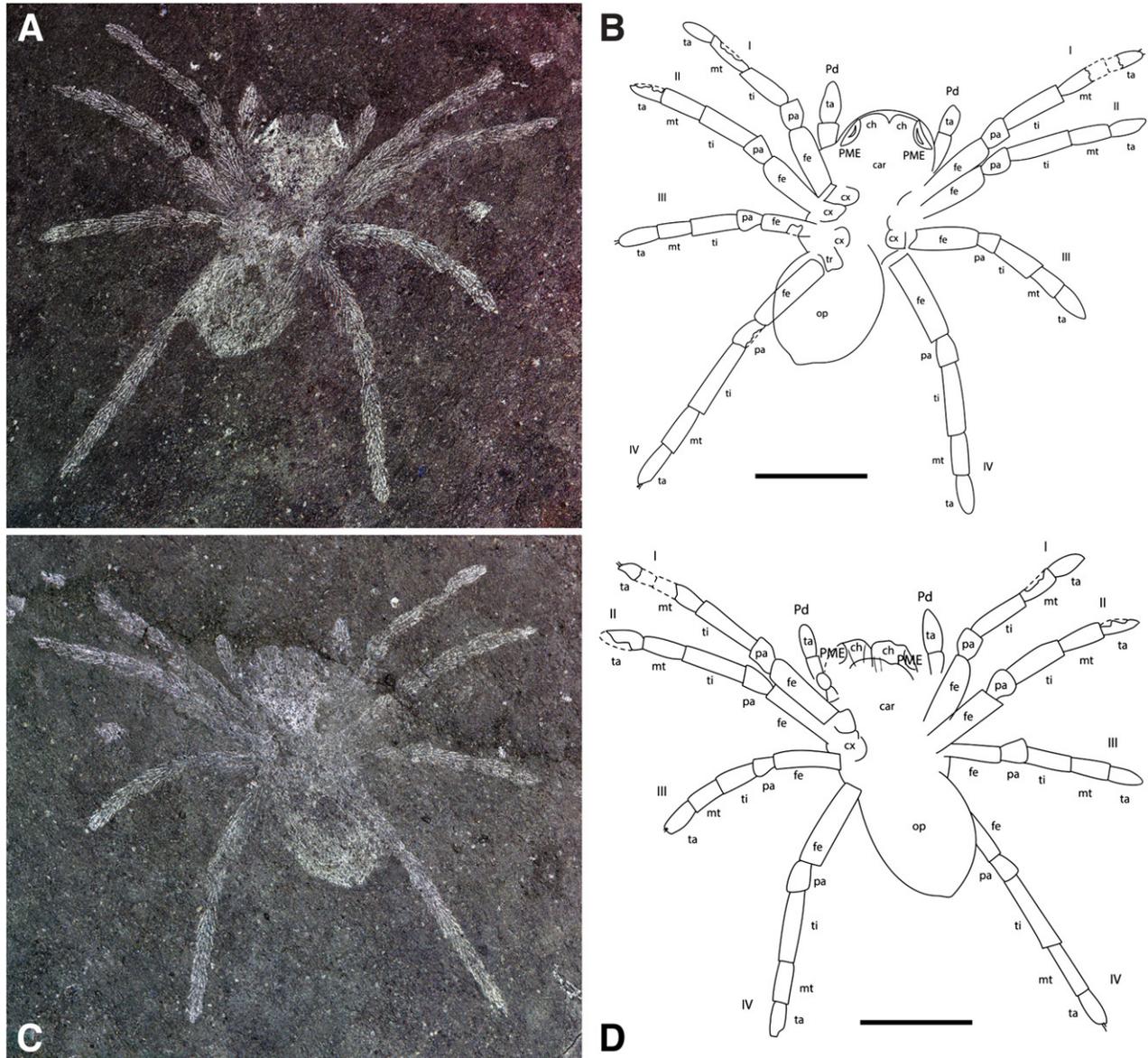


Figure 7. *Koreamegops samsiki* gen. et sp. nov., paratype specimen KOPRIF7017a,b. **A**, photograph of part; **B**, explanatory drawing of part; **C**, photograph of counterpart; **D**, explanatory drawing of counterpart. Scale bars = 1 mm.

clustered near the fang tip, the scopulae of spatulate setae on the tibia-tarsus of leg I, and the elevated cephalic region of the carapace. In the most recent molecular systematic analyses, Dimitrov *et al.* (2017), Wheeler *et al.* 2017, Fernández *et al.* (2018) and Wood *et al.* (2018) recovered the superfamily as sister to the Entelegynae. The clade currently encompasses the families Archaeidae Koch & Berendt, 1854, Huttoniidae Simon, 1893, Mecysmaucheniidae Simon, 1895, Palpimanidae Thorell, 1870 and Stenochilidae Thorell, 1873, and the extinct Lagonomegopidae Eskov & Wunderlich, 1995, Spatiatoridae Petrunkevitch, 1942,

Micropalpimanidae Wunderlich, 2008 and Vetiatoridae Wunderlich, 2015.

Palpimanoidea incertae sedis

Fam., gen. et sp. indet.

(Fig. 6)

Material. DBFM 00061, immature female?

Stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, c. 106–112 Ma), Sanam Section.

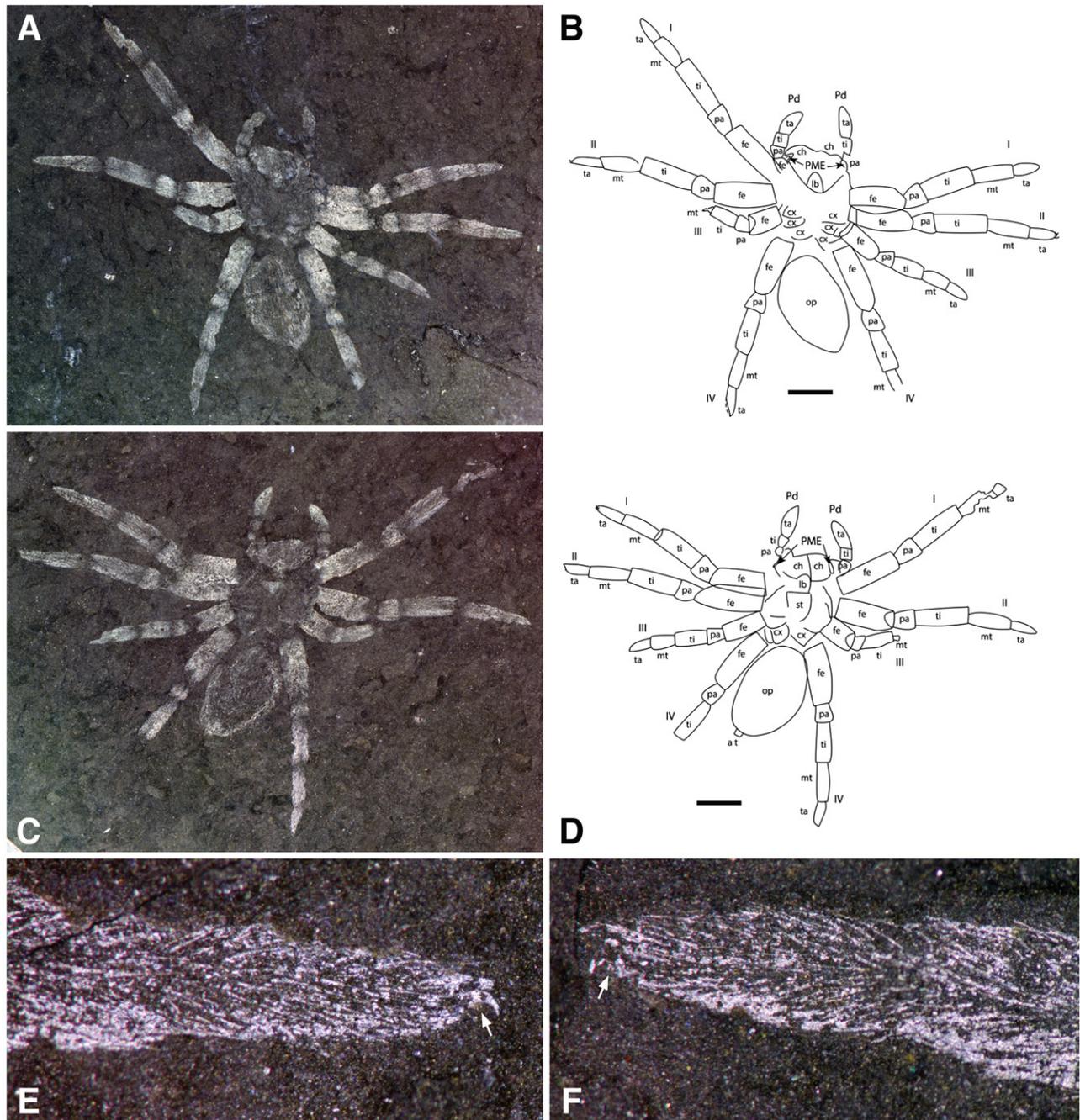


Figure 8. *Koreamegops samsiki* gen. et sp. nov., holotype specimen KOPRIF7011a,b. **A**, photograph of part, apparent leg banding results from decreased setation at podomere proximal boundaries; **B**, explanatory drawing of part; **C**, photograph of counterpart; **D**, explanatory drawing of counterpart; **E**, close-up view of left leg II tarsus of part, arrow indicates tiny teeth on proximal part of paired claw; **F**, close-up view of right leg II tarsus of part, arrow indicates tiny teeth on proximal part of paired claw. Scale bars = 1 mm.

Remarks. The preservation is similar to that of the other spiders in the Jinju Formation except that leg II on the left side is seen only as faint marks beyond the base of the patella. As in DBFM 00054, there are reflective vermiform marks along parts of the body and legs, which could be tool marks, or possibly organic decay structures. The spider is preserved ventral side

up, so the sternum is visible but not the carapace. The chelicerae appear to be rather short and perfect, whereas the maxillae are large (Fig. 6). It is possible that what appear to be large maxillae are actually basal extensions of the chelicerae, although a distinct angle at the base of the chelicera, approximately at the edge of the carapace, argues against this interpretation. The spinneret region is

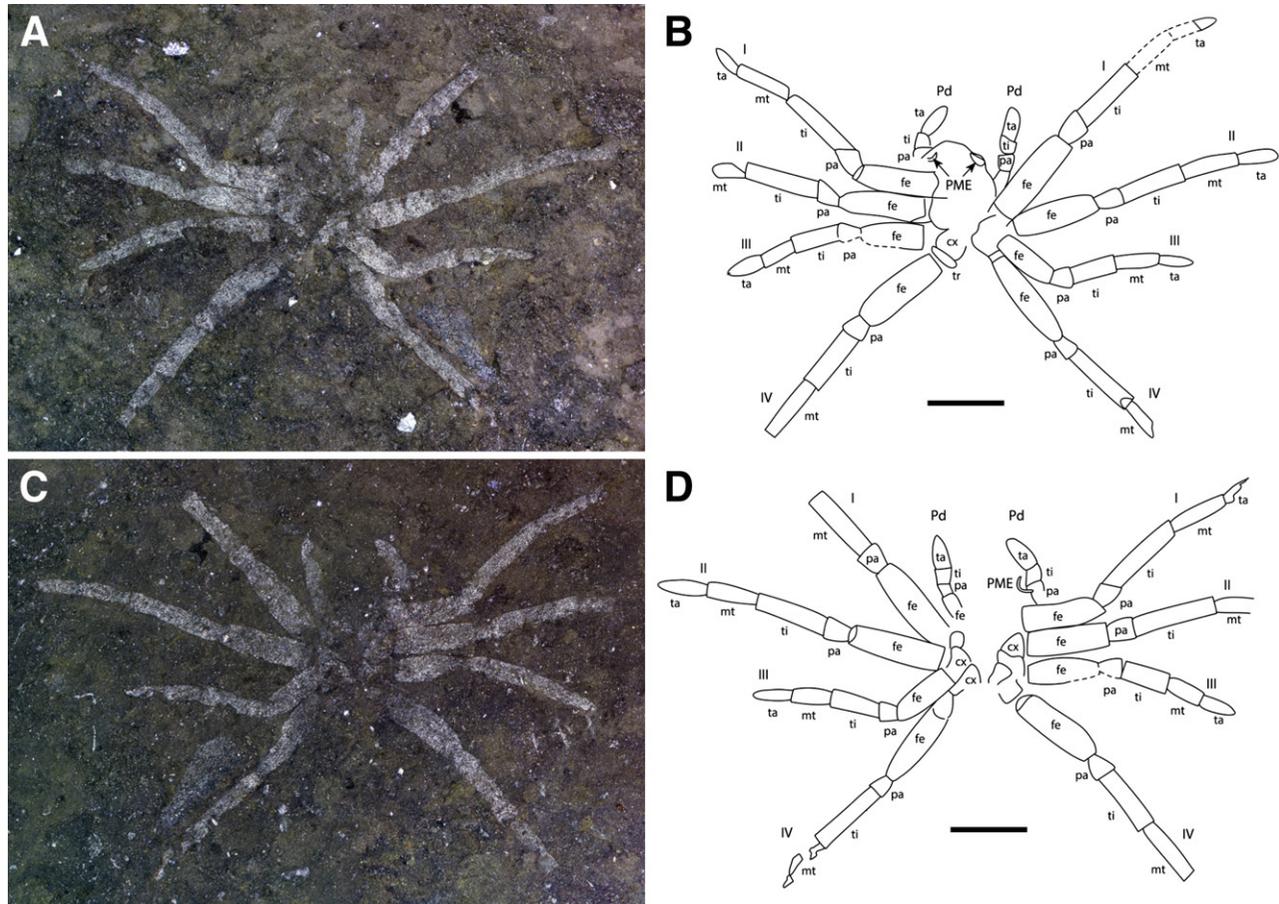


Figure 9. *Koreamegops samsiki* gen. et sp. nov., paratype specimen KOPRIF7012a,b. **A**, photograph of part; **B**, explanatory drawing of part; **C**, photograph of counterpart; **D**, explanatory drawing of counterpart. Scale bars = 1 mm.

compact and subterminal: no spinnerets can be seen extending beyond the posterior margin of the opisthosoma. Indeed, only two, small spinnerets can be discerned, and such an arrangement of few, small spinnerets is typical of palpimanoids.

Specimen DBFM 00061 belongs in this superfamily on account of its possession of peg teeth on the chelicerae, the lack of macrosetae on the legs, and the reduced number of spinnerets. It cannot be an archaeid because of the short chelicerae, nor a palpimanid because of the lack of body sclerotization and enlarged femora. It does not resemble *Mecysmaucheniidae* nor *Lagonomegopidae* (see below), and the sternum is unlike that in *Stenochilidae*. *Spatiatoridae*, *Micropalpimanidae* and *Vetiatoridae* are extinct families known from amber. It is not possible to assign DBFM 00061 to a palpimanoid family, so it is recorded here as *Palpimanoidea incertae sedis*.

Description. Entire spider covered in coarse setation; no macrosetae on legs except few on distal edge of mt. Body L 4.14 mm. Sternum *c.* 1.3× longer than wide: L 0.66 mm, W 0.50 mm, L/W ratio 1.31, scalloped lateral

margins around coxae (Fig. 6C). Labium slightly wider than long: L 0.30 mm, W 0.39 mm, L/W ratio 0.78. Chelicera L 0.48 mm, W 0.30 mm, L/W ratio 1.65), bearing peg teeth (Fig. 6D). Maxilla large, longer than wide: L 0.54 mm, W 0.36 mm, L/W ratio 1.65. Leg formula (based on fe-ti) II > I > IV > III; legs not elongated, relatively short compared to body length (longest leg ~1.33× body L). Podomere lengths: Pedipalp fe 0.66 mm, pa 0.23 mm, ti 0.39 mm, ta 0.57 mm, total fe-ta 1.85 mm; Leg I fe 1.57 mm, pa 0.53 mm, ti 1.42 mm, mt 1.16 mm, ta 0.73 mm, total fe-ta 5.41 mm, fe-ti 3.52 mm (NB: mt and ta L determined from faint traces on left side); Leg II fe 1.65 mm, pa 0.47 mm, ti 1.50 mm, total fe-ti 3.62 mm; Leg III fe 1.30 mm, pa 0.45 mm, ti 1.05 mm, mt 0.74 mm, ta 0.67 mm, total fe-ta 4.20 mm, fe-ti 2.79 mm; Leg IV fe 1.66 mm, pa 0.47 mm, ti 1.20 mm, mt 0.90 mm, total fe-ti 3.34 mm. No spatulate setae visible on leg I mt. Opisthosoma suboval in outline, about twice as long as wide: L 2.20 mm, W 1.49 mm, L/W ratio 1.47; spinnerets subterminal in position, in a compact group; only two spinnerets visible.

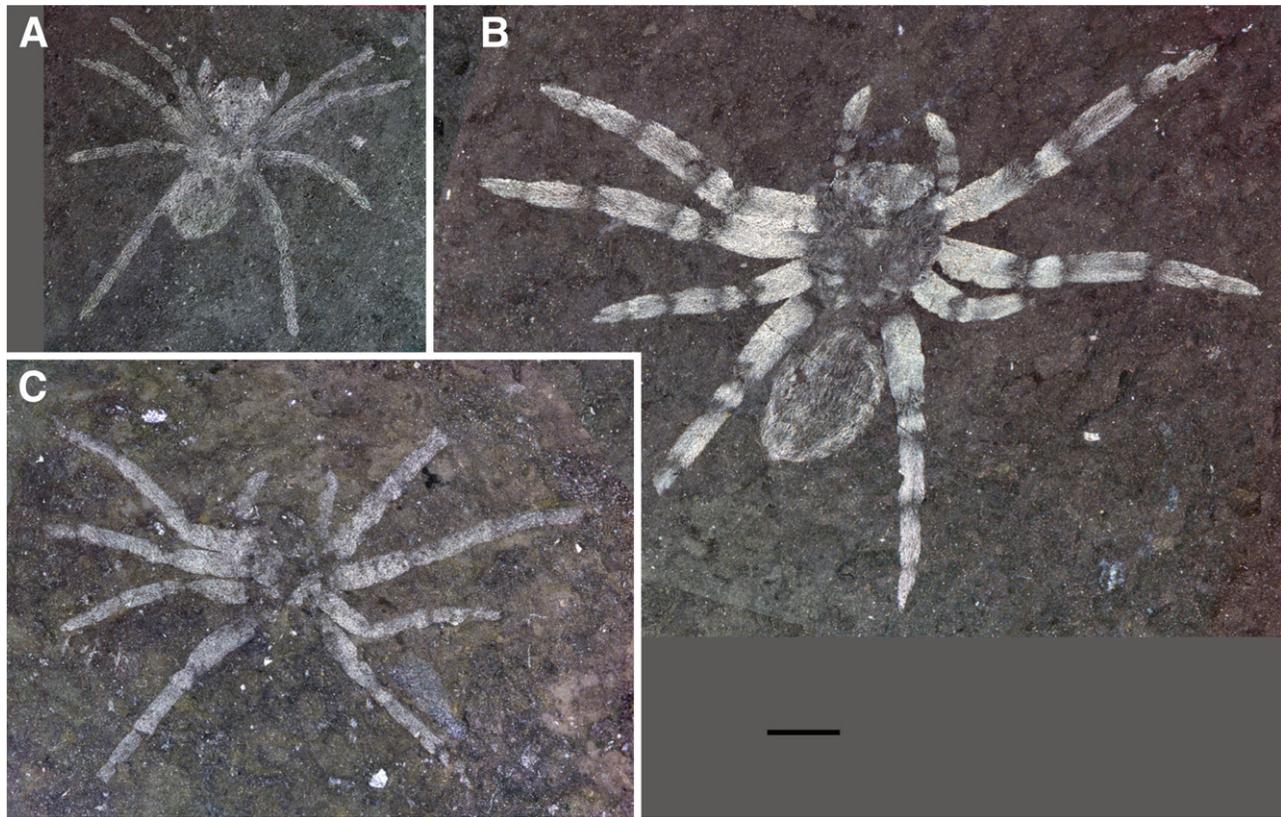


Figure 10. *Koreamegops samsiki* gen. et sp. nov., photographs of all three type specimens, with part and counterpart superimposed, to scale. **A**, paratype specimen KOPRIF7017a,b; **B**, holotype specimen KOPRIF7011a,b; **C**, paratype specimen KOPRIF7012a,b. Scale bar = 1 mm.

Family **Lagonomegopidae** Eskov & Wunderlich, 1995

Remarks. The extinct family Lagonomegopidae was erected by Eskov & Wunderlich (1995) for some unusual, juvenile spiders in Cretaceous Siberian amber. These were the first Mesozoic amber spiders to be described (Penney 2005). The characteristic feature of these spiders is the enlarged eye situated laterally on the carapace; the generic name is derived from the Greek for large (*mega*), eyes (*ops*) and situated on the flanks (*lagono*). Modern spider families with a greatly enlarged pair of eyes include the Salticidae and Deinopidae (see Morehouse *et al.* 2017, fig. 2); in these families, however, the enlarged eyes are situated at the front of the carapace, for forward viewing. Lagonomegopidae were placed in Palpimanoidea on the basis of their possession of peg teeth on the chelicerae and lack of spines on the legs.

Two juvenile specimens of the type and only known species, *Lagonomegops sukatchevae* Eskov & Wunderlich (1995), were described from Cretaceous (Santonian) amber from Taimyr, Siberia. Since then, a great many more lagonomegopid species have been described, all from Cretaceous amber (Supplemental material Table 2).

The new genus and species described here are thus the first record of the family outside of amber preservation.

The family Lagonomegopidae was diagnosed by Eskov & Wunderlich (1995, pp. 97–98) thus:

“Small ecribellate araneomorph spiders. Carapace convex, evenly rounded so that head region merges into thorax, its surface with long sparse protruding setae; fovea indistinct. Eight (or six?) eyes in three rows; PME [posterior median eyes] very large, in flank positions at anterior corners of carapace. Chelicerae moderately long, its promargin with peg-teeth, true teeth absent; lateral stridulatory ridges absent. Endites directed across labium, meeting at midline; serrula as a single row of teeth; labium free, regularly triangular. Sternum scutiform, with long protruding setae; coxae IV widely separated. Abdomen ovate, with six spinnerets, without sclerotization. Legs nearly spineless, with neither calamistrum nor scopulae, clothed with plumose hairs. Tarsi with three claws and without onychium; superior claws with a single row of teeth and inferior claw seems to be bare. No trichobothria on tarsi, a single subdistal trichobothrium on metatarsi, two subdistal on tibiae I and II. Genitalia of both sexes still unknown.”

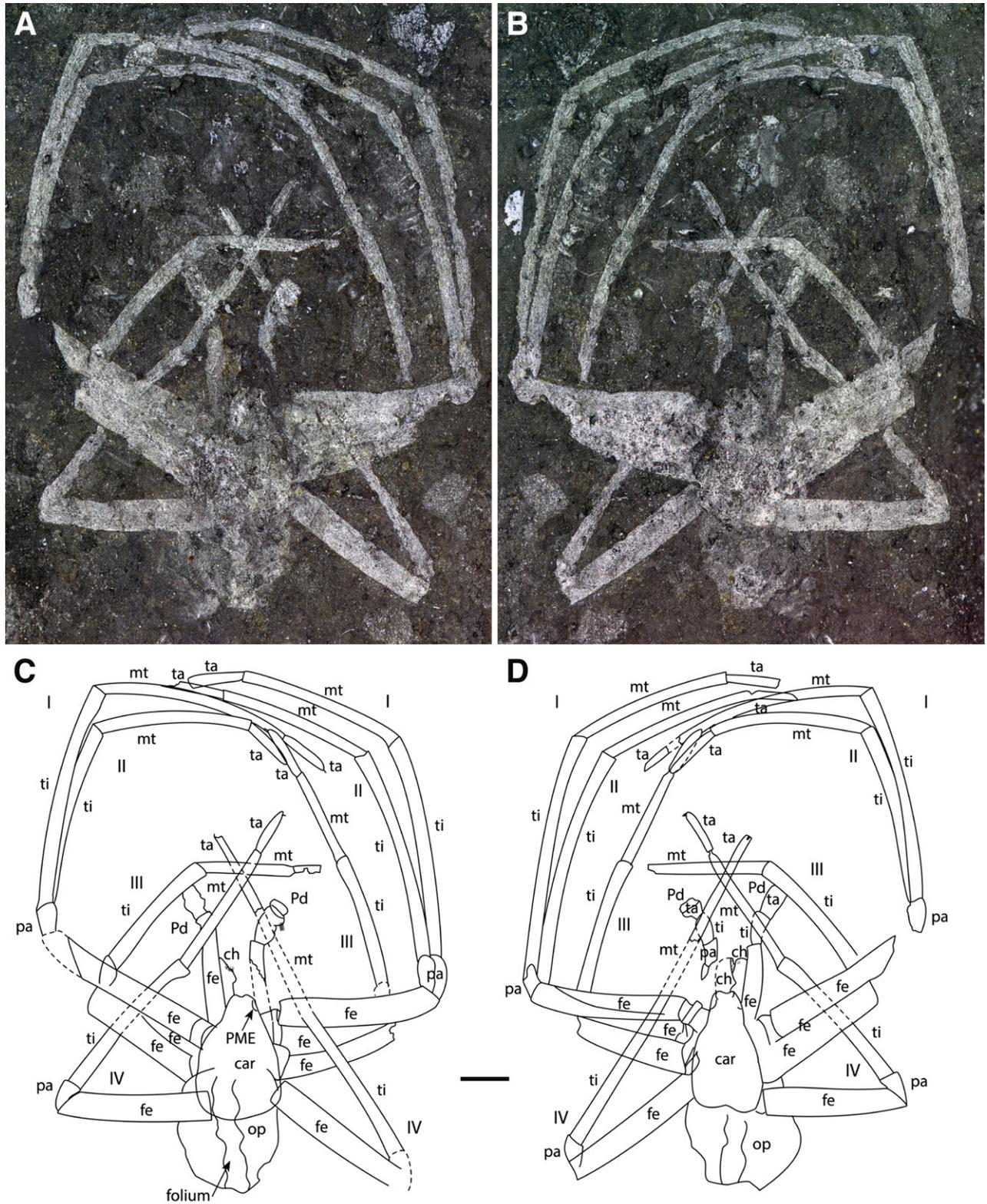


Figure 11. *Jinjumegops dalingwateri* gen. et sp. nov. KOPRIF7014a,b. **A**, part; **B**, counterpart; **C**, explanatory drawing of part; **D**, explanatory drawing of counterpart. Scale bar = 1 mm.

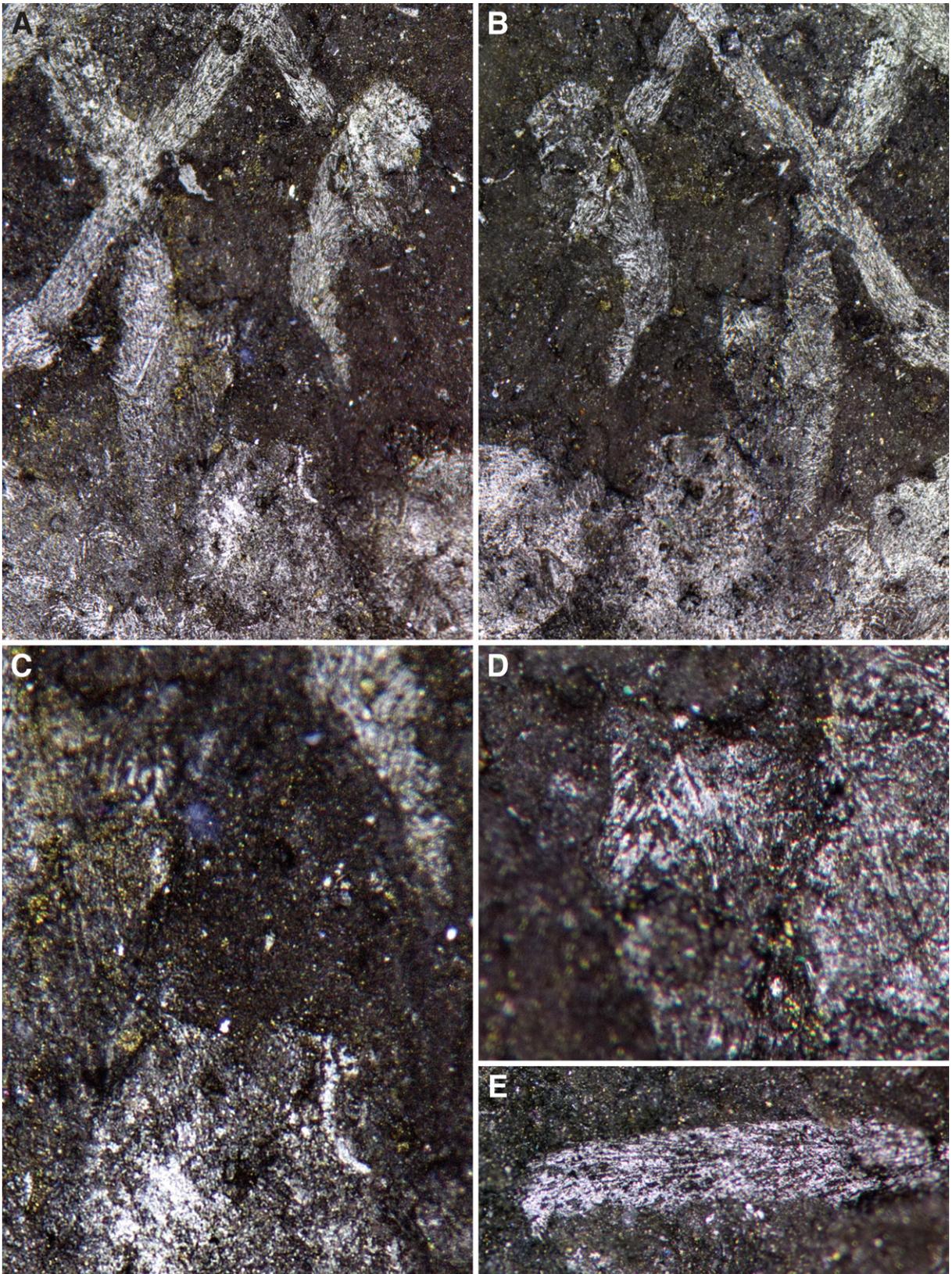


Figure 12. *Jinjumegops dalingwateri* gen. et sp. nov. KOPRIF7014a,b. **A**, part, detail of anterior carapace, chelicerae and pedipalps; **B**, counterpart, detail of anterior carapace, chelicerae and pedipalps; **C**, part, detail of anterior part of carapace showing right PME tapetum (bottom right) and cheliceral peg teeth (top left); **D**, counterpart, cheliceral peg teeth; **E**, counterpart, right tarsus IV, showing pectinate claw. See Figure 10C, D for explanatory drawings and scale.

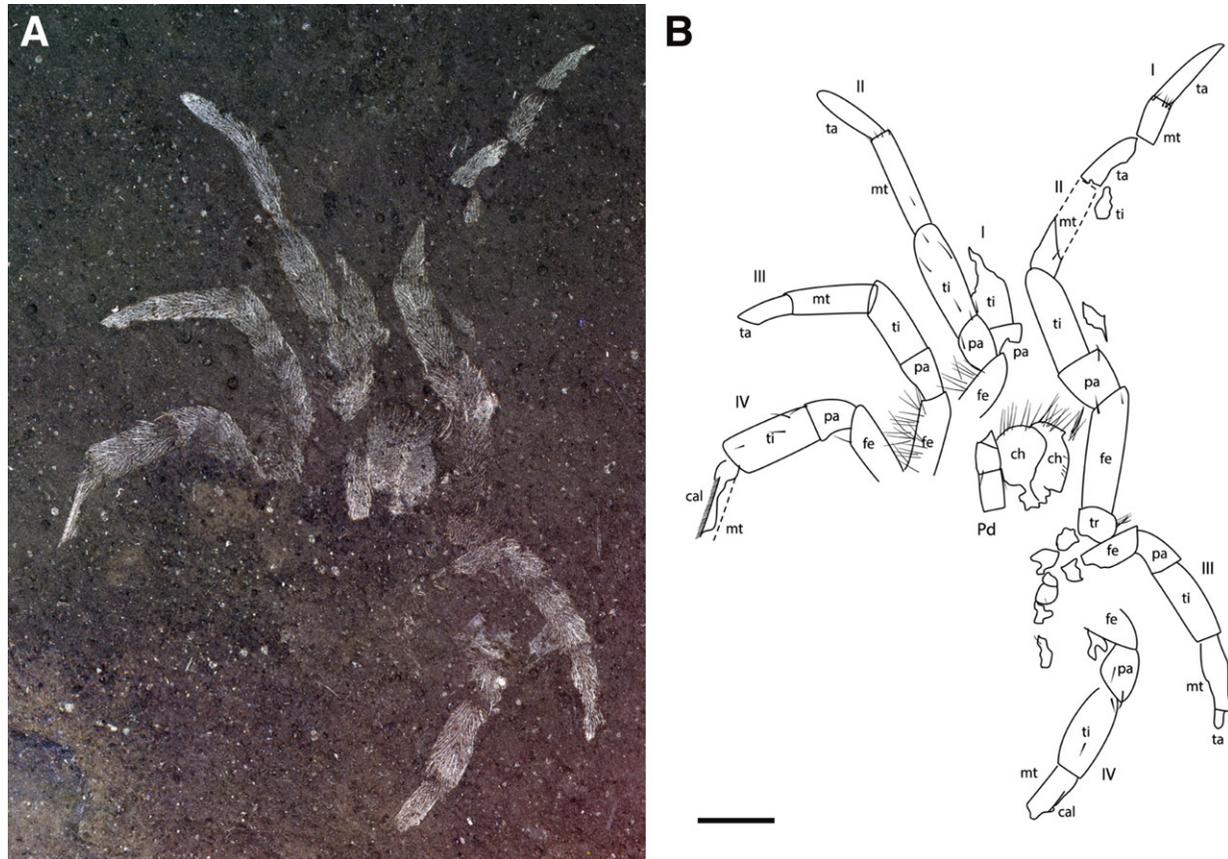


Figure 13. Cribellate Entelegynae species 1. KOPRIF7016. **A**, photograph; **B**, explanatory drawing. Scale bar = 1 mm.

Wunderlich (2008) emended this diagnosis, decreasing the eye count and adding some additional information from newly described genera: “6 (*Lagonomegops* and *Zarqagonomegops*) or 4 eyes (the remaining genera)” ... “clypeus with a pair of bulging structures (low humps)” ... “prolateral spatulate hairs of legs I–II absent (but thin and pointed hairs may be present, in *Grandoculus* Penney, 2004); leg bristles usually absent but a single dorsal-distal femoral bristle may exist and few more thin bristle (or hairs?) may exist”. In a further emendation, Wunderlich (2008, p. 198) was able to include adult male pedipalp characters for the first time: “The ♂-pedipalpus is only – and insufficiently – known from the genera *Myanlagonops* and *Archaelagonops*; it has long and slender articles and a very long cymbium which includes/hides parts of the small and not protruding bulbus”.

The family diagnosis was further emended by Pérez-de la Fuente *et al.* (2013, p. 534):

“Minute to small spiders (1 to nearly 5 mm). Cheliceral foramen absent. Chelicerae bearing several pointed, relatively short peg teeth (up to five) on the unguis. Carapace with two anterolateral protrusions, where a

pair of large eyes (tentatively interpreted as the PME) are placed. Endites subtriangular, directed across the labium, almost meeting at the midline, with serrula as a single row of teeth. Labium subtriangular, wider than long. Sternum shield-like, without marginal projections between or at the middle of coxae. Six spinnerets. Several tibial trichobothria present, with the subdistal metatarsal trichobothria longest. Three tarsal claws, unpaired claw hook-like. Female palpal tarsi lacking a claw.”

The diagnosis was revised further by Wunderlich (2015, p. 238):

“Existence of several tarsal as well as several metatarsal trichobothria usually in an irregular row, 8 eyes (probably a less number [sic] in certain taxa after the loss of the posterior lateral eyes) in four rows, peculiar long and wide eye field with huge anterior median eyes in a lateral position at the prosomal margin which are directed more sideways, remaining eyes tiny, clypeus bearing usually a pair of humps (weakly developed and almost absent e.g. in *Paxillomegops* and *Picturmegops*), diastema/foramen existing or absent. Leg bristles: probably basically existence of few – e. g. femoral bristles in certain taxa.”

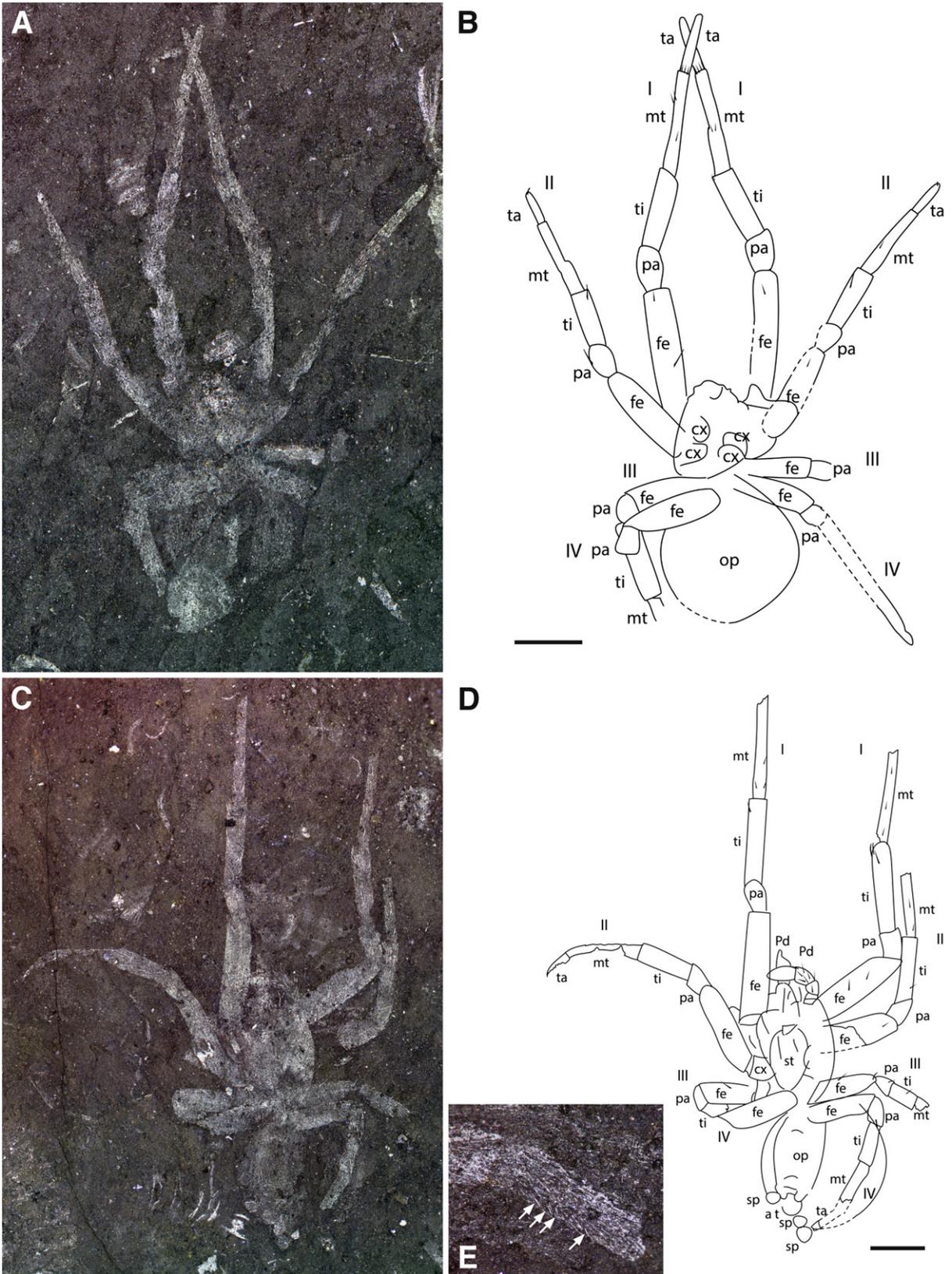


Figure 14. Cribellate Entelegynae species 2. **A**, KOPRIF7013, photograph; **B**, explanatory drawing of **A**; **C**, KOPRIF7015, photograph; **D**, explanatory drawing of **C**; **E**, detail of KOPRIF7015 right leg IV metatarsus showing dorsal depression and ventral stubby macrosetae (arrowed). Scale bars = 1 mm.

Note that, in this emendation, Wunderlich (2015) considered the large eyes to be anterior median eyes (AME) rather than PME. In the original diagnosis of Eskov & Wunderlich (1995) the large eyes were presumed to be PME; this view was followed, tentatively, by Pérez-de la Fuente *et al.* (2013), but Wunderlich (2015) considered them to be AME (see Discussion). The identification of lagonomegopids as palpimanoids was recognized from the start, by Eskov & Wunderlich (1995), on the basis of their possession of peg teeth and the absence of true teeth on the cheliceral promargin, and the relatively spineless legs.

***Koreamegops* gen. nov.**

Diagnosis. Small lagonomegopid (< 5 mm body length) with legs I, II, IV subequal in length, about as long as body, lacking macrosetae; length of leg tarsi between 0.75× and 1× length of metatarsi; ventral coxal surfaces densely covered in long setae.

Type species. *Koreamegops samsiki* sp. nov.

Etymology. A combination of ‘Korea’ and the Greek *mega-ops* meaning large eyes.

Remarks. The new genus described here can be identified as a lagonomegopid on the basis of its enormous lateral eyes on the carapace (recognized here as PME), and the lack of macrosetae on the legs. Other characters present in the new genus which are in accordance with Lagonomegopidae include: small size (< 5 mm body length); dense covering of plumose setae (the setae are presumed to be plumose because they appear quite coarse in comparison with those of most other spiders in this collection); shield-shaped sternum; legs short and stout; leg tarsi with three claws, median claw hook shaped, no onychium, claw tufts or scopulae; pedipalp tarsus lacking claw; and long, forwardly directed setae on head region of carapace.

The new genus differs from *Lagonomegops* in that the leg tarsi are shorter than the metatarsi (ta/mt ratio 0.77–0.93). Note that Penney (2005) distinguished *L. americanus* from the type species *L. sukatchevae* partly on the basis of its tarsi being longer than the metatarsi, yet in their description of the holotype Eskov & Wunderlich (1995, p. 99) stated: “tarsi distinctly longer than metatarsi”, with a ta/mt ratio of 1.65. It differs from *Grandoculus* Penney, 2004 in that leg I is not longer and more robust than the other legs, it lacks scopulae on leg I, and it does not show elongate chelicerae (Penney 2011).

The new genus is quite close in morphology to *Burlagonomegops* Penney, 2005 (see also Penney 2006;

Pérez-de la Fuente *et al.* 2013), in that the carapace is distinctly longer than wide and the legs are short; however, the length of the carapace in *Burlagonomegops* is particularly due to the elongated and constructed cephalic region, quite unlike that in *Koreamegops*. *Burlagonomegops* is also characterized by the presence of numerous trichobothria and spines on the legs, which the new genus does not possess (it is possible that the lack of trichobothria in the new fossil may be due to its preservation). It is impossible to compare *Zarqanomegops* Kaddumi, 2007 because it is a small juvenile lacking distinct characters; Wunderlich (2008) suggested it might be congeneric with *Lagonomegops*.

The legs of *Archaelagonops* Wunderlich, 2012 are rather longer than the body, the carapace is a different shape from that of the new genus, and the legs show many trichobothria (Wunderlich 2015). In *Lagonoburmops* Wunderlich, 2012, the tarsi are distinctly shorter than the metatarsi (*c.* half the length), whereas the tarsi are only a little shorter than the metatarsi in the new genus. In *Myanlagonops* Wunderlich, 2012, the legs are slender and the carapace 1.5× wider than long.

The new genus differs from *Spinomegops* Pérez-de la Fuente *et al.* 2013 by lacking erect bristles on the distal metatarsi and tarsi of legs I and II, and from *Soplaogonomegops* Pérez-de la Fuente *et al.* 2013 in lacking an elongated neck to the carapace caput region.

The legs of *Cymbiolagonops* Wunderlich, 2015 are much longer than the body and slender. *Lineaburmops* Wunderlich, 2015 has legs longer than the body, but is diagnosed based on the bands of white hairs on the carapace and opisthosoma. Neither character is consistent with the new genus; the adult male of *L. maculatus* Wunderlich, 2017 is smaller than the immatures of the new genus. Similarly, the legs of *Parviburmops* Wunderlich, 2015 are longer than the body, which is also quite small in the adult male. The legs in the species of *Paxillomegops* Wunderlich, 2015 are longer than the body, even the species *P. brevipes* Wunderlich, 2015. *Picturmegops* Wunderlich, 2015 is a prettily marked genus, with distinctively long patellae of legs I and II; in these respects, it differs from the new genus. The monotypic adult males *Albiburmops annulipes* Wunderlich, 2017 and *Planimegops parvus* Wunderlich, 2017 are smaller than the immatures of the new genus, and their legs are longer than the body.

***Koreamegops samsiki* sp. nov.**
(Figs 7–10)

Derivation of name. Named in honour of the collector, Samsik Lee, who generously donated the specimens for this study.

Material. Holotype: subadult male, KOPRIF7011a,b. Paratypes: juvenile males, KOPRIF7017a,b, KOPRIF7012a,b.

Type stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Jeongchon Section (holotype) or Sanam Section (paratypes).

Diagnosis. As for the genus.

Description. Measurements given in [Supplemental material Table 1](#). Entire spider covered in coarse (plumose?) setation; no macrosetae on legs; few long setae on carapace caput area ([Fig. 7](#)); ventral coxae and abdomen densely covered in long setae ([Fig. 7](#)). Body length 2.46–4.55 mm ($n=3$). Carapace *c.* 1.3× longer than wide (car L/W ratio 1.36, $n=1$). PME enormous, tapetum width *c.* 0.28 mm ($n=2$), situated on anterolateral corner of carapace, facing anterolaterally. Labium semi-elliptical, longer than wide, L 0.42 mm, W 0.36 mm (L/W ratio 1.16, $n=1$). Sternum scutiform, with straight anterior margin ([Fig. 8C, D](#)). Chelicera short, ventrally directed. Pedipalp tibia about as short as patella, tarsus slightly swollen, lacking claw. Legs I, II and IV approximately equal in size, III shorter. Legs relatively short compared to body (ratio longest leg/body length = 1.02 mm, $n=2$). Leg femora rather stout; patellae short; tibiae parallel sided; metatarsi narrowed proximally and distally, slightly longer than tarsi; tarsi suboval with talon-shaped paired claws bearing two small teeth proximally ([Fig. 8E, F](#)), hook-shaped median claw ([Fig. 8F](#)). Opisthosoma *c.* 1.3× longer than wide; anal tubercle terminal.

Jinjumegops gen. nov.

Diagnosis. Long-legged lagonomegopid (longest leg 13.64 mm, 3.3× body length); lacking macrosetae; carapace with protruding cephalic region; elongate chelicerae; opisthosoma subspherical, with dorsal folium. Differs from *Cymbiolagonops* Wunderlich, 2015 in lacking a slender pedipalp with a basally elongated cymbium.

Type species. *Jinjumegops dalingwateri* sp. nov.

Etymology. Derived from the Jinju Formation, which hosts the holotype, and Greek *mega-ops* meaning large eyes.

Remarks. The specimen is preserved with dorsal and ventral body parts superimposed, though the dorsal carapace appears to be traceable ([Fig. 11](#)). The legs are very long and preserved curled, with the femur-patella joint strongly flexed (legs I–III ~90° and leg IV ~40°). It has been shown by Downen *et al.* (2016) that spiders

preserved in freshwater (e.g. lacustrine) environments have legs extended due to osmosis, whilst those preserved in hypersaline conditions, or desiccated prior to burial, have strongly flexed legs. This is due to spider fe-pa and ti-mt joints having no extensor muscles and relying on hydraulic extension. Since all other Jinju spiders have extended legs, it is likely that *Jinjumegops* died and dried out prior to being washed into the freshwater lake.

This specimen is placed in Palpimanoidea on account of the large, porrect chelicerae bearing peg teeth, the forwardly expanded cephalic region of the carapace, and the lack of macrosetae on the legs. The chelicerae are preserved only as fragments, but a few peg teeth can be seen ([Fig. 12D](#)). The curved, reflective line seen at the anterolateral corner of the carapace is similar to those seen in *Koreamegops*, and hence is interpreted as the tapetum of a large posterior median eye. This feature places the new genus in Lagonomegopidae. The pattern of setation on the opisthosoma, in the shape of a wavy-edged folium, is also a distinctive feature of many lagonomegopids (e.g. *Archaeolagonops propinquus* Wunderlich, 2015, fig. 226, *Picturmegops signatus* Wunderlich, 2012, *Lineaburmops hirsutipes* Wunderlich, 2015, *Myanlagonops gracilipes* Wunderlich, 2012). A few species of lagonomegopids preserved in Burmese amber have long legs, e.g. *Archaeolagonops salticoides* Wunderlich, 2012, *A. scorsum* Wunderlich, 2015, *A. propinquus* Wunderlich, 2015, *Cymbiolagonops cymbiocalcar* Wunderlich, 2015, *Lineaburmops beigeli* Wunderlich, 2015, *Myanlagonops gracilipes* Wunderlich, 2012, *Paxillomegops longipes* Wunderlich, 2015, and *Planimegops parvus* Wunderlich, 2017. All of these are described from adult males, and hence can be compared to the new fossil.

To determine whether the new fossil is related to any previously described lagonomegopid, it is necessary to consider morphological similarities. Despite the descriptions of these Burmese species having long legs, only those of *Cymbiolagonops cymbiocalcar* are close in dimensions to *Jinjumegops*. *Cymbiolagonops cymbiocalcar* has a body length of 4.0 mm and its longest leg (I) is 13.30 mm; in comparison, *Jinjumegops* has a body length of 4.14 mm and its longest leg (I) is 13.64 mm. However, despite the severe deformation of the Burmese amber *Cymbiolagonops*, its pedipalp is slender and bears a distinctive tibial apophysis and a slender stalk to the cymbium (Wunderlich 2015, p. 251, figs 229, 230). Moreover, while the first leg is similar in length in the two species, the femur of *Cymbiolagonops* is longer than that of *Jinjumegops*, while the metatarsus is shorter, so the podomere proportions are dissimilar.

Hence it is unlikely that *Jinjumegops* is congeneric with the Burmese amber *Cymbiolagonops*.

Jinjumegops dalingwateri sp. nov.
(Figs 11, 12)

Derivation of name. Named in memory of John E. Dalingwater, arachnological mentor and friend to PAS at the University of Manchester 1975–2018.

Material. Holotype only, adult male, KOPRIF7014a,b.

Type stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Jeongchon Section.

Diagnosis. As for the genus.

Description. Mature male. Body covered in setae, lacking macrosetae, L 4.14 mm. Carapace L 2.56 mm, W 1.59 mm, L/W ratio 1.62, longer than wide, widest in posterior half, narrowing to protruding cephalic region, elongate fovea (dark streak in Fig. 11B), bearing large PME (Figs 11A,C, 12A,C). Chelicera long (L ~1.0 mm), with peg teeth (Fig. 12D). Pedipalp L 2.69 mm; tarsus expanded into male copulatory organ. Legs long, mainly due to elongated tibiae and metatarsi; ratio longest leg L/body L = 3.30; tibiae long, gently curved, thickened distally; metatarsi long, curved; tarsi with pectinate claws (Fig. 12E), no scopulae or claw tufts. Leg formula I > II > IV > III. Podomere lengths: Pd pa 0.54 mm, ti 0.62 mm; Leg I fe 3.41 mm, pa 0.80 mm, ti 4.69 mm, mt 3.64 mm, ta 1.10 mm, total fe-ta 13.64 mm; Leg II fe 3.29 mm, pa 0.80 mm, ti 4.00 mm, mt 3.19 mm, ta 1.19 mm, total fe-ta 12.64 mm; Leg III fe 2.41 mm, pa 0.77 mm, ti 2.74 mm, mt 1.96 mm, ta 1.15 mm, total fe-ta 8.94 mm; Leg IV fe 3.02 mm, pa 0.69 mm, ti 3.31 mm, mt, 2.76 mm, ta 0.98 mm, total fe-ta 10.75 mm. Opisthosoma L 2.60 mm, W 2.07 mm, L/W ratio 1.25, with wavy-sided median dorsal folium consisting of posteriorly directed setae occupying about one-quarter width of dorsum (Fig. 11), setae directed posteriolaterally on remainder of opisthosoma.

clade **Entelegynae** Simon, 1893

“Cribellate Entelegynae”

Remarks. The calamistrum, consisting of one or more rows of bristles on the fourth leg metatarsus of many spiders, is used to comb fine silk issuing from the cribellum, a modified pair of (anterior median) spinnerets situated in front of the true spinnerets. The cribellum/calamistrum combination occurs in all instars except those males which, on reaching adulthood, cease web production to concentrate on searching for mates. The

calamistrum was first described and illustrated by Blackwall (1833, p. 475, pl. 31), was named the calamistrum by Blackwall (1841a, p. 224), who also described the cribellum in the latter paper. The family Ciniplonidae Blackwall, 1841b was erected based on the presence of the calamistrum. Later, more spiders were included in the expanded taxon Cribellata Bertkau, 1882. However, in the twentieth century, the cribellate spiders were shown to be a paraphyletic group of araneomorphs united by the plesiomorphies of the cribellum and calamistrum (Lehtinen 1967).

Cribellate spider families, and a few which contain some cribellate genera, are scattered within the Araneomorphae, and araneomorph spiders lacking a cribellum and calamistrum are considered to have lost them. Cribellate clades include: the relatively primitive araneomorph families Hypochilidae Marx, 1888 and Filistatidae Ausserer, 1867, but not their sister group Synspermiata (Michalik & Ramírez 2014); the Austrochilidae Zapfe, 1955 and Gradungulidae Forster, 1955, but not the Palpimanoidea Thorell, 1870; among the entelegynes, the Megadictynidae Lehtinen, 1967 within the Nicodamoidea Simon, 1897, but not their sister group the Araneoidea Latreille, 1806; numerous families in the stem leading up to the RTA clade (araneomorphs with a retrolateral tibial apophysis): Eresidae Koch in Berendt, 1845, Deinopidae Koch, 1850, Oecobiidae Blackwall, 1862, Uloboridae Thorell, 1869, Titanoecidae Lehtinen, 1967, Phyxelididae Lehtinen, 1967, and Penestomidae Simon, 1903, but not the Zadariidae Thorell, 1881; within the marronoid clade, the Amaurobiidae (Amaurobiinae) Thorell, 1870, Dictynidae Pickard-Cambridge, 1871, Stiphidiidae Dalmas, 1917, and Desidae Pocock, 1895; within the Oval Calamistrum clade (Polotow *et al.* 2015) the Zoropsidae Bertkau, 1882, Ctenidae Keyserling, 1877, and Psechridae Simon, 1890; and no dionychnan families (Wheeler *et al.* 2017).

“Cribellate Entelegynae species 1”

(Fig. 13)

Material. KOPRIF7016.

Stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Jeongchon Section.

Description. Immature spider densely covered in setae; long, thin, curved setae abundant on ventral femora II and III and chelicera; macrosetae on femora, patellae, tibiae, and metatarsi (distally) of most legs (Fig. 13). Chelicera large, robust, L 1.09 mm. Legs short, stout; podomere lengths: leg II tr 0.42 mm, fe 1.53 mm, pa 0.64 mm, ti 1.33 mm, mt 1.32 mm, ta 0.97 mm, total (fe-

ta) 5.80 mm; leg III pa 0.57 mm, ti 1.05 mm, mt 1.01 mm; leg IV pa 0.59 mm, ti 1.16 mm. Metatarsus IV with almost straight, uniserial calamistrum, originating close to proximal end of podomere.

Remarks. Specimen KOPRIF7016 is a cribellate spider, as evidenced by the calamistrum present on the metatarsus of leg IV (Fig. 13). The calamistrum in the fossil is almost straight, apparently uniserial, and at least begins in a proximal position on the metatarsus, so the fossil cannot belong to the Oval Calamistrum clade. The uniserial nature suggests the spider does not belong to any modern family with a biserial calamistrum, i.e. Hypochilidae, Oecobiidae and Amaurobiidae (Amaurobiinae); however, it is possible that the disposition of the fourth metatarsus on the bedding plane might be hiding the second file of bristles. Hypochilidae are large, long-legged spiders, while oecobiids are tiny, with small chelicerae, both quite unlike the fossil. The calamistrum in filistatids is short and tripartite (Gray 1995; Murphy & Roberts 2015, pls 50–51). Cribellate spiders in the Amaurobiidae (Amaurobiinae) have a straight calamistrum, usually originating proximally on the metatarsus, so it is possible that the fossil might belong to this group. However, these spiders are fairly large and with rather longer legs than the short, stout appendages seen on the fossil, and their chelicerae are large and robust, quite unlike the characteristics of the fossil specimen.

Among families with a uniserial calamistrum, its position in Austrochilidae, Gradungulidae, Phyxelididae and Stiphidiidae is medial, in Penestomidae it is distal, while in the remaining families (Eresidae, Deinopidae, Uloboridae, Mongolarachnidae, Megadictynidae, Titanocidae, Dictynidae and Desidae) it is proximal or the full length of the metatarsus. In Uloboridae and the fossil stem-Deinopoidea from China, the calamistrum lies in a distinctive depression on the metatarsus (Opell 1979, 2001; Murphy & Roberts 2015; Joel *et al.* 2016; Selden *et al.* 2016). The depression is shallower in Deinopidae (Peters 1992; Coddington *et al.* 2012; Murphy & Roberts 2015; Joel *et al.* 2016) but the members of this family are long-legged; similarly, Mongolarachnidae Selden *et al.*, 2013 are large and long-legged. Many desids are characterized by their enlarged, porrect chelicerae which are quite unlike those seen in KOPRIF7016. In Titanocidae, the calamistrum generally starts quite far from the proximal end of the metatarsus (Murphy & Roberts 2015, pls 73–76); these spiders somewhat resemble amaurobiids in general form, which is quite unlike the fossil. Eresids have the main, linear calamistrum buried somewhat in the dense, plumose setation of the metatarsus and an additional dorsal patch of smaller calamistral setae (Miller *et al.* 2012). The calamistrum of the fossil resembles that of the Dictynidae in being uniserial, fairly straight, and occupying most of the length

of metatarsus IV starting near the proximal end (e.g. Murphy & Roberts 2015, pls 44–47). Traditional dictynids (e.g. *Dictyna* Sundevall, 1833, *Mexillia* Lehtinen, 1967 and *Mallos* Pickard-Cambridge, 1902) are fairly small, compact, cribellate spiders with a furry appearance because of their dense covering of plumose setae (Bond & Opell 1997). The fossil thus resembles these dictynids in many ways, although the presence of numerous macrosetae on the legs is an unusual feature among these genera. However, pre-Cenozoic fossil records of the RTA clade, to which Amaurobiidae, Dictynidae and Desidae belong, are rare and debated (Dunlop *et al.* 2018).

Wunderlich (2008, 2011, 2015, 2017) described a number of cribellate genera from Cretaceous amber which he placed into various extant and extinct families. At present (Wunderlich 2017), these genera are distributed among the extinct Burmadietynidae Wunderlich, 2017 (*Burmadietyna* Wunderlich, 2008, *Eodeinopsis* Wunderlich, 2017, *Palaeomicromennew* Penney, 2003), Praearaneidae Wunderlich, 2017 (*Praearaneus* Wunderlich, 2017), and the extant Uloboridae (*Bicalamistrum* Wunderlich, 2015, *Burmuloborus* Wunderlich, 2008, *Furculoborus* Wunderlich, 2017, *Jerseyuloborus* Wunderlich, 2011, *Kachin* Wunderlich, 2017, *Microuloborus* Wunderlich, 2015, *Ocululoborus* Wunderlich, 2012, *Palaeomiagrammopes* Wunderlich, 2008, *Palaeoulloborus* Selden, 1990, *Paramiagrammopes* Wunderlich, 2008, *Propterkachin* Wunderlich, 2017). The calamistra are situated in a depression in Uloboridae and Praearaneidae, but not so in Burmadietynidae; however, these spiders tend to have rather long legs (Wunderlich 2008, 2015, 2017). Nevertheless, given the state of flux among Cretaceous amber cribellate families, it is possible that the fossil could be in one of these groups. In summary, the fossil KOPRIF7016 cannot be placed reliably in any family, and thus remains an *incertae sedis* cribellate entelegyne.

“Cribellate Entelegynae species 2”

(Fig. 14)

Material. KOPRIF7013 and KOPRIF7015.

Stratum and locality. Jinju Formation (mid-Cretaceous, early to middle Albian, *c.* 106–112 Ma), Jeongchon Section.

Description of KOPRIF7013. Entire spider covered in coarse setation. Body L 3.53 mm. Carapace widest in posterior half, narrowing anteriorly, L 1.41 mm, W 1.11 mm, L/W ratio 1.27. Leg formula I > II > IV > III; legs I and II relatively long; leg III short (based on *fe*). Macrosetae on femora, patellae, tibiae and metatarsi, at least of legs I and II; tarsal claws but no scopulae

present. Leg I and II tibiae rather short, metatarsi longer, basal third slightly thickened. Podomere lengths: Leg I fe 1.95 mm, pa 0.61 mm, ti 1.10 mm, mt 1.47 mm, ta 0.85 mm, total fe-ta 5.97 mm; Leg II fe 1.48 mm, pa 0.48 mm, ti 0.85 mm, mt 1.13 mm, ta 0.52 mm, total fe-ta 4.46 mm; Leg III fe 1.06 mm, pa 0.41 mm, ti 1.16 mm, total fe-mt >3.06 mm; Leg IV fe 1.29 mm, pa 0.40 mm, total fe-mt >3.74 mm. Opisthosoma subcircular in outline, about as long as wide: L 2.14 mm, W 2.00 mm, L/W ratio 1.07.

Description of KOPRIF7015. Immature male. Entire spider covered in coarse setation. Body L 4.63 mm. Carapace widest in posterior half, narrowing anteriorly, L 1.95 mm, W 1.42 mm, L/W ratio 1.37. Sternum scutiform, longer than wide, L 1.12 mm, W 0.71 mm, L/W ratio 1.57. Leg formula I > II > IV > III; legs I and II relatively long; leg III short (based on fe-ti); metatarsi longer than tibiae. Macrosetae frequent on pedipalp and all legs (Fig. 14A, B). Metatarsus IV with slight dorsal depression and possible calamistrum; row of short macrosetae at high angle to podomere length ventrally (Fig. 14A, B). Podomere lengths: Pd pa 0.22 mm, ti 0.32 mm, ta 0.52 mm; Leg I fe 1.94 mm, pa 0.59 mm, ti 1.62 mm, mt 1.90 mm (fe-ti 4.15 mm); Leg II fe 1.59 mm, pa 0.50 mm, ti 1.09 mm, mt 1.38 mm, ta 0.55 mm, total fe-ta 5.10 mm (fe-ti 3.18 mm); Leg III fe 1.11 mm, pa 0.40 mm, ti 0.54 mm (fe-ti 2.04 mm); Leg IV fe 1.36 mm, pa 0.54 mm, ti 0.75 mm, mt 0.99 mm, ta 0.62 mm, total fe-ta 4.25 mm (fe-ti 2.65 mm). Opisthosoma subcircular in outline, about as long as wide: L 2.74 mm, W 2.28 mm, L/W ratio 1.20. Spinnerets subapical, short, subspherical.

Remarks. KOPRIF7013 is not well preserved and suffers from pieces of extraneous material lying across parts of the body and legs; however, both legs I and II are preserved complete to their tarsi. KOPRIF7015 lacks tarsi on all legs except II. Both specimens lack distal parts of legs III and IV. Both specimens show an opisthosoma with a subcircular outline, and metatarsi distinctly longer than the tibiae. The more complete metatarsi of legs I and II of KOPRIF7013 show them to be slightly thickened basally. The lack of claw tufts and scopulae suggest this species does not belong to the RTA clade and was most likely a web spider. The only preserved fragment of metatarsus IV (KOPRIF2015) shows evidence of a calamistrum within a slight dorsal depression (Fig. 14E) and a row of stubby macrosetae ventrally, features which are also found in modern uloborids (e.g. Opell 1979, pl. 1). These features, together with the podomere configuration, suggest an affinity with the stem-deinopoid spiders described from the Jurassic of China (Selden *et al.* 2016).

Discussion

Lagonomegopidae

Sex ratio of lagonomegopids. With the newly documented lagonomegopids from the Jinju Formation, and recent studies, it is now possible to resolve the issue of the female-biased sex ratio of lagonomegopids raised by Pérez-de la Fuente *et al.* (2013), for which they brought up two hypotheses as mentioned above. When Pérez-de la Fuente *et al.* (2013) noted the lack of lagonomegopid males, it was based on the 24 specimens documented at that time. However, the three subsequently published monographs by Wunderlich reported both male and female lagonomegopid spiders of various sizes from Burmese amber, documenting 21 lagonomegopid species in total, and 15 new species were erected based on male spiders (Wunderlich 2012, 2015, 2017) (see Supplemental material Table 2). The body length of male lagonomegopids from Burmese amber varies from 2.7–5 mm, with a mean size of 3.67 mm. Large lagonomegopid female spiders were also documented from Burmese amber. The largest one is the holotype of *Lagonoburmops plumosus* Wunderlich, 2012, which is 8 mm long. The smallest convincing female is the holotype of *Picturmegops signatus* Wunderlich, 2015, which is 3.6 mm long. Smaller specimens (< 2.1 mm) from Spanish amber have not been confidently distinguished from juveniles, so that the holotypes of? *Lagonomegops cor*, *Soplaogonomegops unzuei*, *Spinomegops aragonensis* and *Spinomegops arcanus* are identified as ‘juvenile or adult female’ (Pérez-de la Fuente *et al.* 2013). It should be noted that Kaddumi (2007) regarded the holotype of *Zarqagonomegops wunderlichi* Kaddumi, 2007 from Jordanian amber, which is 1.7 mm long, as a juvenile female. Therefore, based on the lagonomegopid spiders documented so far, it can be concluded that both males and females of various sizes existed, and the female-biased sex ratio issue of lagonomegopids could be ascribed to an insufficient number of samples. The two male lagonomegopid spiders from the Jinju Formation in this study also corroborate this conclusion. The larger one is 4.55 mm in length although it still retains some juvenile features. The smaller one is only 2.41 mm long, which is the smallest male lagonomegopid spider so far. This shows that male lagonomegopids of various sizes existed even in non-arboreal environments.

Eyes. In their original description of the new family Lagonomegopidae, Eskov & Wunderlich (1995) considered the enormously enlarged lateral eyes of these spiders to be posterior medians. This view was held by all authors, though with little evidence, until Wunderlich (2015) proposed that they are anterior median eyes. This

supposition was based on comparison of the family with the Archaeidae C. L. Koch & Berendt, 1854 and Micropalpimanidae Wunderlich, 2008, which Wunderlich considered were closely related to the Lagonomegopidae. Wunderlich (2017) later concluded that Micropalpimanidae were not, after all, closely related to Lagonomegopidae.

AME in spiders are derived from simple ocelli, they are commonly called the principal or main eyes (Foelix 2011) (Hauptaugen: Homann 1971), while the other eyes are derived from a reduction in ancestral compound eyes (Land 1985), and are called secondary eyes (Nebenaugen: Homann 1971). The principal eyes differ from the secondary eyes in that they are everted (the rhabdomeres are directed towards the incoming light), while the secondary eyes are inverted, and light is directed to them by means of a reflective tapetum, similar to vertebrate eyes (Mark 1887; Land 1985; Barth 2011; Foelix 2011; Morehouse *et al.* 2017). The tapetum consists of guanine crystals (Mueller & Labhart 2010). In primitive spiders (mesotheles, mygalomorphs and haplogyne araneomorphs), the tapetum is a simple bowl bearing holes for the passage of the retinal cells; in more advanced entelegyne spiders the tapetum is shaped like a canoe (Mark 1887) and the retinal cells pass through a median slit. In some derived families, such as Lycosidae Sundevall, 1833, the tapetum is grate-shaped, like a grill from an oven; and a few spider families (e.g. Salticidae Blackwall, 1841b, Oxyopidae Thorell, 1870) have lost the tapetum from their secondary eyes. In most spider families showing an enlarged pair of eyes, e.g. Deinopidae, Lycosidae, Ctenidae, Oxyopidae, it is the PME, whereas salticids uniquely have enlarged AME (see Morehouse *et al.* 2017, fig. 2).

Griswold *et al.* (1999) recognized a Canoe Tapetum Clade within the Entelegynae, rooted at the node where the canoe-shaped tapetum first appeared, based on an original grouping called Higher Entelegynes by Coddington & Levi (1991) and a clade united by the same character in Platnick *et al.* (1991, fig. 311, node 73). The analysis of Griswold *et al.* (1999) excluded the Palpimanoidea, but note that members of this superfamily possess canoe-shaped tapeta (e.g. Palpimanidae: Homann 1971; Archaeidae, Huttoniidae: Griswold *et al.* 2005) and were included in Coddington & Levi's (1991) Higher Entelegynes as well as Platnick *et al.*'s (1991) clade. Nevertheless, palpimanoids were excluded from the Canoe Tapetum Clade by Coddington (2005) and in later literature (e.g. Dunlop & Penney 2011), although Griswold *et al.* (2005) failed to recover the clade in their analysis. In more recent phylogenetic analyses of Araneae (e.g. Miller *et al.* 2010; Dimitrov *et al.* 2017; Wheeler *et al.* 2017; Fernández *et al.* 2018),

Palpimanoidea is recovered as sister to a more restricted Entelegynae.

Koreamegops gen. nov. and *Jinjumegops* gen. nov., described herein, show quite remarkable preservation of a canoe-shaped tapetum in the large, lateral eyes (Figs 7–12). This is the first time that the tapetum has been described in fossil spiders. The evidence that it is the tapetum which is preserved is that other parts of the optical system are soft tissues; even the eye lens, which is derived from the cuticle, is rarely seen in non-amber fossil spiders. However, the tapetum, by its crystalline nature, is more likely to be preserved. Moreover, the shape of the structure – clearly canoe-shaped, with a median slit – corroborates this hypothesis. The presence of the tapetum indicates that these large eyes are not AME, and are most likely PME, as originally described for Lagonomegopidae.

Age and life mode of lagonomegopids. Lagonomegopids are known only from the Cretaceous: the oldest lagonomegopid species is *Zarqagonomegops wunderlichi* Kaddumi, 2007 from the Hauterivian–Barremian Jordanian amber, while the youngest species is *Grandoculus chemahawinensis* Penney, 2004 from the middle Campanian Manitoban amber. The highest diversity is known from the earliest Cenomanian, from which 22 species out of 32 known lagonomegopids have been documented, but this is likely due to the bias coming from the well-preserved fossils from Burmese amber. The presence of *Koreamegops* and *Jinjumegops* from the shale of the Jinju Formation indicates that the occurrence of lagonomegopids is not limited to amber inclusions, implying a possibility of this group occurring earlier than Hauterivian, and later than middle Campanian.

The non-amber occurrence of lagonomegopids may indicate that lagonomegopids were not limited to arboreal habitats, which are favourable for amber inclusion. The spiders in the Jinju Formation have been washed into the freshwater environment from a variety of habitats. Thus, an additional, cursorial life mode is suggested for lagonomegopids. The characteristic large eyes (PME) of lagonomegopids may have played a similar role to large eyes (AME) of salticids. The cursorial life mode is in accordance with the worldwide distribution of lagonomegopids, which spans North America, Europe, Middle East, South-east Asia and East Asia (see Supplemental material Table 1).

Post-Aptian spider diversity of East Asia

The Mesozoic spider fossil record of East Asia largely depends on the Middle Jurassic tuffaceous Daohugou deposits and the Lower Cretaceous (Barremian–Aptian)

tuffaceous mudstone of the Jehol biota of China. To date, five spider species have been formally described from the Daohugou deposits (Selden *et al.* 2008, 2011, 2013, 2016; Selden & Huang 2010), while eight species have been reported from the Jehol biota (Chang 2004; Selden *et al.* 2016; note: seven of these may be unreliable, see Dunlop *et al.* 2018), together with numerous insect fossils. However, a post-Aptian Mesozoic spider fossil record is absent in China due to the lack of fossiliferous strata.

Together with the previously reported *Korearachne jinju* Selden *et al.* 2012, the seven species documented in this study reveal a relatively diverse spider fauna of the Jinju Formation. The total of eight species of the Jinju Formation indicates that the Mesozoic spider diversity in East Asia did not decrease in post-Aptian time.

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Supplemental data

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