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A new Early Cretaceous 'megapodagrionid' genus (Zygoptera: Coenagriomorpha) from the Jinju Formation of the Republic of Korea

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Abstract

Koreapodagrion coloratus n. gen. n. sp. represents the third known Cretaceous 'megapodagrionid' taxon and is described from the lower Albian of the Korean Peninsula. The other two were described from Barremian and Barremian–Aptian deposits from China and the Democratic People's Republic of Korea, respectively. This distribution in East Asia, suggests that the area was favorable to these damselflies during the Early Cretaceous. *Koreapodagrion coloratus* n. gen. n. sp. is characterized by a distinctive coloration pattern, colored zones on the wing membrane, and a particular wing venation, *inter alia*, characterized by an elongate pterostigma, a very long postnodal area, and IR1 with a strong curve below pterostigma. This new taxon highlights the underestimated diversity within the 'megapodagrionid' *sensu lato*.

Keywords: Insecta; Odonata; Cretaceous diversity; Jinju Formation

1. Introduction

The damselfly group 'Megapodagrionidae' is relatively common and diverse in the Cenozoic, spanning from the Paleocene to the Pliocene, but is found exclusively in the Palearctic and Nearctic regions (Azar and Nel, 2008; Zessin, 2011; Nel, 2023). Only two Mesozoic taxa are currently attributed to this group: *Cretapodagrion sibelleae* Huang, Azar and Nel, 2018, from the Lower Cretaceous (Barremian) of China, and *Phyonganpodagrion ryonsangae* So and Won, 2022 from the Lower Cretaceous (Barremian–Aptian) of the Democratic People's Republic of Korea (Huang et al., 2018; So and Won, 2022). Today, the 'family' is restricted to warm, predominantly intertropical, biotas. Most known fossil taxa were described based on wing compressions in lacustrine sediments, with body fragments being rare.

According to Dijkstra et al. (2014), the 'Megapodagrionidae' are currently considered a polyphyletic group. The former 'megapodagrionid' subfamily Argiolestinae Fraser, 1957 is now classified as a separate family Argiolestidae, though it lacks an 'unequivocally unique character available for adults' (Kalkman and Theischinger, 2013). The former 'megapodagrionid' subfamily Philosininae Ris, 1917 is also considered as a distinct family, Philosinidae, by Dijkstra et al. (2014), who

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restricted the Megapodagrionidae to the extant genera *Allopodagrion* Förster, 1910, *Megapodagrion* Selys-Longchamps, 1885, and *Teinopodagrion* De Marmels, 2001. No clear synapomorphy in wing venation characterizes these families, making it challenging to assign fossil 'megapodagrionids' to the families proposed by Dijkstra et al. (2014).

Here we describe the third Cretaceous genus and species of 'Megapodagrionidae' from the Albian of the Republic of Korea.

2. Material and methods

The specimens were collected from the lower part of the Jinju Formation at the Jeongchon section (35°07'45"N, 128°06'02"E), 5.6 km south of the city of Jinju, Republic of Korea (see Park et al., 2019). The most recent detrital zircon analysis shows that the age of the lower boundary of the Jinju Formation is 112.4 ± 1.3 Ma, while the upper boundary is 108.7 ± 0.5 Ma; hence the age of the formation can be considered as early Albian (Lee et al., 2018). The Jinju Formation likely corresponds to the latest stage of the famous Jehol Biota, as suggested by Kopylov et al. (2020, pp. 1236–1237). The fossils are preserved as a reflective carbonaceous film on different slabs of dark grey shale (e.g., Jouault and Nam, 2023; Lee et al., 2024). All the specimens are housed in the Gongju National University of Education (GNUE). The fossils were photographed with a Canon Eos 6D camera with an attached Canon EF 100 mm lens. Images were cropped and enhanced using Adobe Illustrator CC2019 and Adobe Photoshop CC2019.

The wing venation nomenclature is based on the interpretations of Nel et al. (1993) and Bechly (1996), modified from that of Riek and Kukalová-Peck (1984). Abbreviations for vein names are: AA/AP, anal vein (anterior/posterior); CuA, cubitus anterior; IR1, IR2, intercalary radial veins; MA, median anterior; MA/a, anterior branch of MA; MA/b, posterior branch of MA; MP, median posterior; N, nodus; 'O', oblique crossvein; pt, pterostigma; RA/RP, radial vein (anterior/posterior) (RP is divided into three main branches RP1, RP2, and RP3/4); RP1, RP2, RP3/4, branches of radius posterior; ScP, posterior subcostal vein; sn, subnodus.

This published work and its included nomenclatural acts are registered in ZooBank (https://www.zoobank.org, last access: 22/12/2024), with the following LSID: urn:lsid:zoobank.org:pub:B6B15FA6-7585-4757-8437-D4AE0FD37096.

3. Systematic palaeontology

Class Insecta Linnæus, 1758
Order Odonata Fabricius, 1793
Suborder Zygoptera Selys-Longchamps, 1854
Family 'Megapodagrionidae' Calvert, 1913 (*sensu lato*)

Genus *Koreapodagrion* n. gen.

LSID: urn:lsid:zoobank.org:act:546C6C2D-1B8C-4764-A834-7AD4DE1F483F.
Type species: *Koreapodagrion coloratus* n. sp.
Etymology: The genus name is a combination of Korea, the originating country of the material, and '-podagrion' often used in the name of Megapodagrionidae genera. Gender masculine.
Diagnosis: Wing venation characters only. Wings with basal part hyaline, two transverse dark zones separated by a hyaline one in distal two-thirds of wing; pterostigma elongate, covering six cells or more; basal side of pterostigma weakly oblique; postnodal area very long; IR1 with a strong curve below pterostigma, with two rows of cells between it and RP1; vein MA/b making a rather acute angle with posterior side of discoidal cell.

Koreapodagrion coloratus n. sp.
(Figs. 1–3)

LSID: urn:lsid:zoobank.org:act:EEEC81D0-1D0D-4DD5-8D01-988D94A954EA.
Etymology: Named after the colored wings.
Material: Holotype GNUE211014/GNUE211013; paratypes GNUE211010/GNUE211018, GNUE211011/GNUE211017, GNUE211012/GNUE211015; all housed in the Gongju National University of Education, Gongju, Republic of Korea.
Locality and horizon: Jinju Formation, Jeongchon section, near the city of Jinju, Republic of Korea; lower Albian, Lower Cretaceous.
Diagnosis: As for the genus.
Description:

Holotype (GNUE211014/GNUE211013). Wing incomplete with base up to MA/b missing, with two large colored transverse zones situated between nodus and half of postnodal area and basad pterostigma up to wing apex, wing base and a broad transverse zone hyaline in-between. Preserved wing length 21.4 mm, maximum width 6.2 mm; distance from base to nodus unknown; from MA/b to nodus 3.0 mm, from nodus to pterostigma 11.6 mm, from pterostigma to wing apex 3.2 mm; pterostigma sclerotized, 2.6 mm long, 0.6 mm wide, covering up to six cells; pterostigmal brace aligned with basal side of pterostigma, but weakly oblique; distal side of pterostigma slightly more oblique than basal side; 18–19 postnodal crossveins between nodus and pterostigma, almost aligned with corresponding postsubnodals; 16–17 postsubnodal crossveins; subnodus and nodal brace weakly oblique; distal side (MA/b) of discoidal cell distinctly oblique; subdiscoidal cell well defined, separated from AP by one cell; base of RP3/4 basad subnodus, at 1.3 mm from subnodus; base of IR2 at almost same level of subnodus; RP2 originating five cells distad subnodus; IR1 strongly curved distally, originating four cells distad base of RP2; two rows of cells between IR1 and RP1; IR2 slightly zigzagged; 2–5 rows of cells between IR1 and RP2, 2–3 rows of cells between RP2 and IR2, IR2 and RP3/4, RP3/4 and MA/a, MA/a and

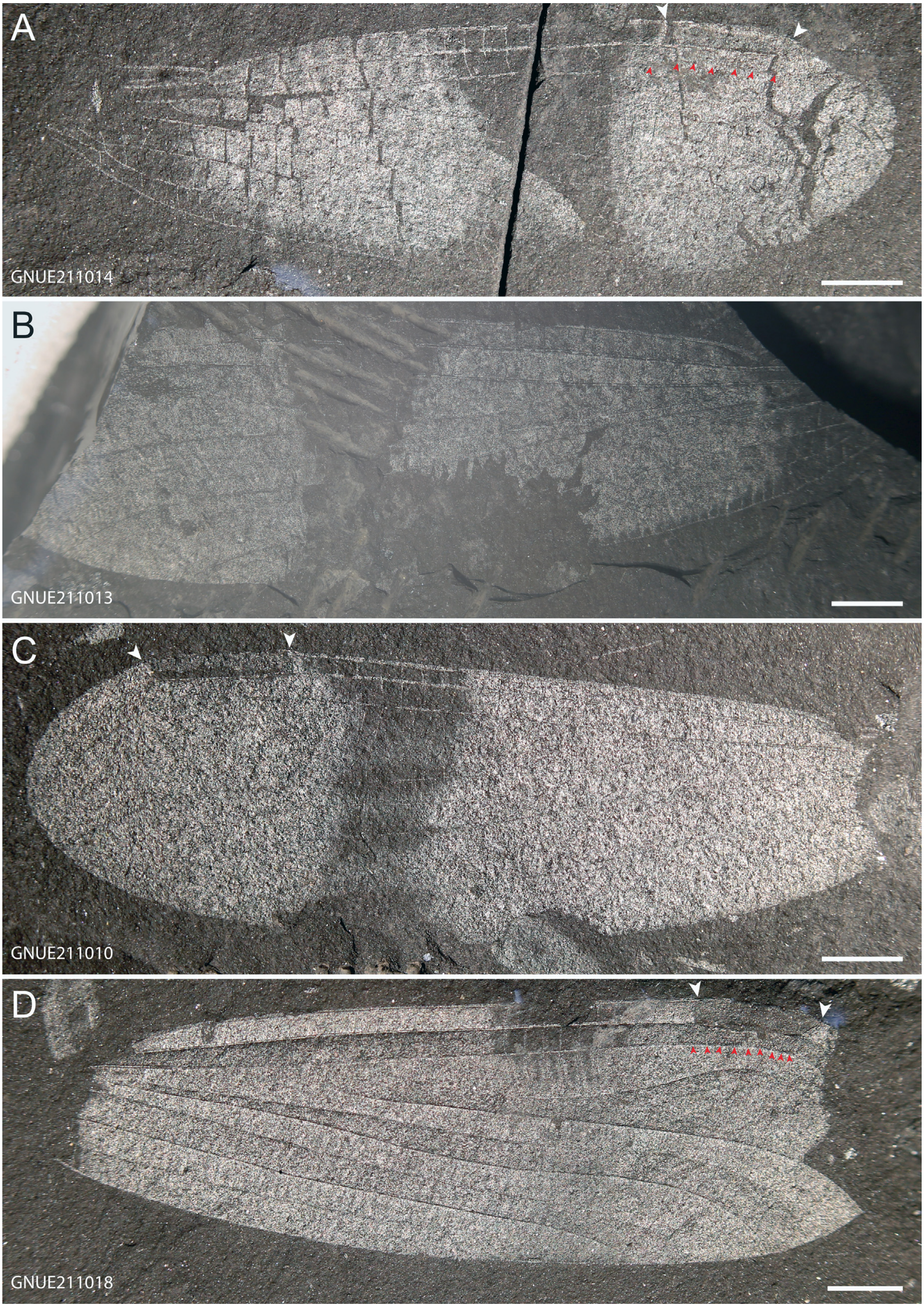

Fig. 1. *Koreapodagrion coloratus* n. gen. n. sp., Jinju Formation, Albian, Republic of Korea. (A) Holotype GNUE211014 (part, white arrows pointing at the limits of the pterostima, red arrows pointing at the limits of cells below the pterostigma). (B) Holotype GNUE211013 (counterpart). (C) Paratype GNUE211010 (part, white arrows pointing at the limits of the pterostima). (D) Paratype GNUE211018 (counterpart, white arrows pointing at the limits of the pterostima, red arrows pointing at the limits of cells below the pterostigma). Scale bars = 2 mm.

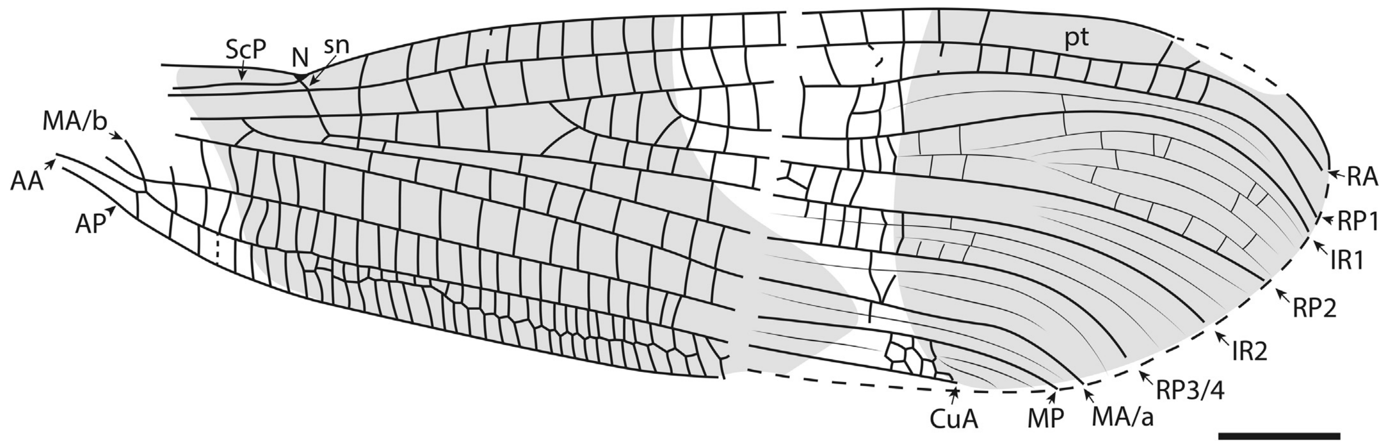

Fig. 2. *Koreapodagrion coloratus* n. gen. n. sp., Jinju Formation, Albian, Republic of Korea, holotype GNUE211014. Interpretative drawing of the wing venation with names of veins and diagnostic structures labelled. Scale bar = 2 mm.

MP, and below CuA; area between IR1 and RP2 relatively broad; no lestine oblique vein 'O' between RP2 and IR2; MA/a weakly zigzagged distally; a tendency to form only one row of cells basally in area between MP and CuA; MP straight, not distally zigzagged; CuA very long, zigzagged in its distal part (due to crossveination pattern); probably no secondary antenodal crossvein distad Ax2, but arculus and Ax2 not preserved.

Paratypes: Specimen (GNUE211010/GNUE211018). Wing incomplete with base up to MA/b missing, with two large transverse zones situated between nodus and half of postnodal area and basad pterostigma up to wing apex, wing base and a broad transverse zone hyaline in-between narrower than in the holotype. Preserved wing length 22.6 mm, maximum width 6.8 mm; distance from base to nodus unknown; from MA/b to nodus about 3.2 mm, from nodus to pterostigma 13.6 mm, from pterostigma to wing apex about 4 mm; pterostigma sclerotized, 3.5 mm long, 0.65 mm wide, covering up to eight cells; pterostigmal brace aligned with basal side of pterostigma, but weakly oblique; distal side of pterostigma slightly more oblique than basal side; 20–21 postnodal crossveins between nodus and pterostigma, almost aligned with corresponding postsubnodals; 20 postsubnodal crossveins; subnodus and nodal brace weakly oblique; distal side (MA/b) of discoidal cell distinctly oblique; subdiscoidal cell well-defined, separated from AP by one cell; base of RP3/4 basad subnodus; base of IR2 at almost same level of subnodus; RP2 originating five cells distad subnodus; IR1 strongly curved distally, originating four cells distad that of RP2; two rows of cells between IR1 and RP1; IR2 slightly zigzagged; 2–3 rows of cells between IR1 and RP2, RP2 and IR2, IR2 and RP3/4, RP3/4 and MA/a, MA/a and MP, and below CuA; area between IR1 and RP2 relatively broad; no lestine oblique vein 'O' between RP2 and IR2; MA/a weakly zigzagged distally; a tendency to form only one row of cells in area between MP and CuA; MP straight, not distally zigzagged; distal side of discoidal cell not oblique; CuA very long, zigzagged in its distal part.

Specimen (GNUE211011/GNUE211017). Wing incomplete with base up to MA/b missing, with two large transverse zones situated between nodus and half of postnodal area and basad pterostigma up to wing apex, wing base and a broad transverse zone hyaline in-between narrower than in the holotype. Preserved wing length 21.5 mm, maximum width 6.8 mm; distance from base to nodus unknown; from nodus to pterostigma 10.4 mm, from pterostigma to wing apex 4 mm; pterostigma sclerotized, 3.5 mm long, 0.7 mm wide, covering up to eight cells.

Specimen (GNUE211012/GNUE211015). Wing incomplete, preserved wing length 18 mm, maximum width 6 mm; distance from nodus to wing apex 16.6 mm; distance from nodus to pterostigma 11.7 mm, pterostigma 2.5 mm long, 0.55 mm wide.

Remarks: One additional specimen (GNUE211094; costal part of postnodal area of a wing) (Fig. 4) probably belongs to the same genus because the coloration and venation patterns of the preserved parts are very similar to that of *Koreapodagrion coloratus* n. sp., in particular the courses of the branches of the radius posterior. It differs from the latter in the presence of at least about 28 postnodal crossveins versus 16–20 in *K. coloratus*. However, the lack of information on the pterostigma and the other regions of the wing hinders us from creating a new species for this fossil. Length of fragment 17.8 mm; a colored zone between nodus up to 10.7 mm distally, a second one 3.6 mm distally.

4. Discussion

These wings have a series of characters that justify placing them within the same genus, if not species. Notably, the distal two-thirds of the wings are broad and elongate, with a high density of cells; postnodal crossveins are numerous; the pterostigma is very long, covering more than six cells; the IR1 vein curves sharply below the pterostigma; two rows of cells are present between CuA and the posterior margin of the wing; the base of RP3/4 is positioned one cell

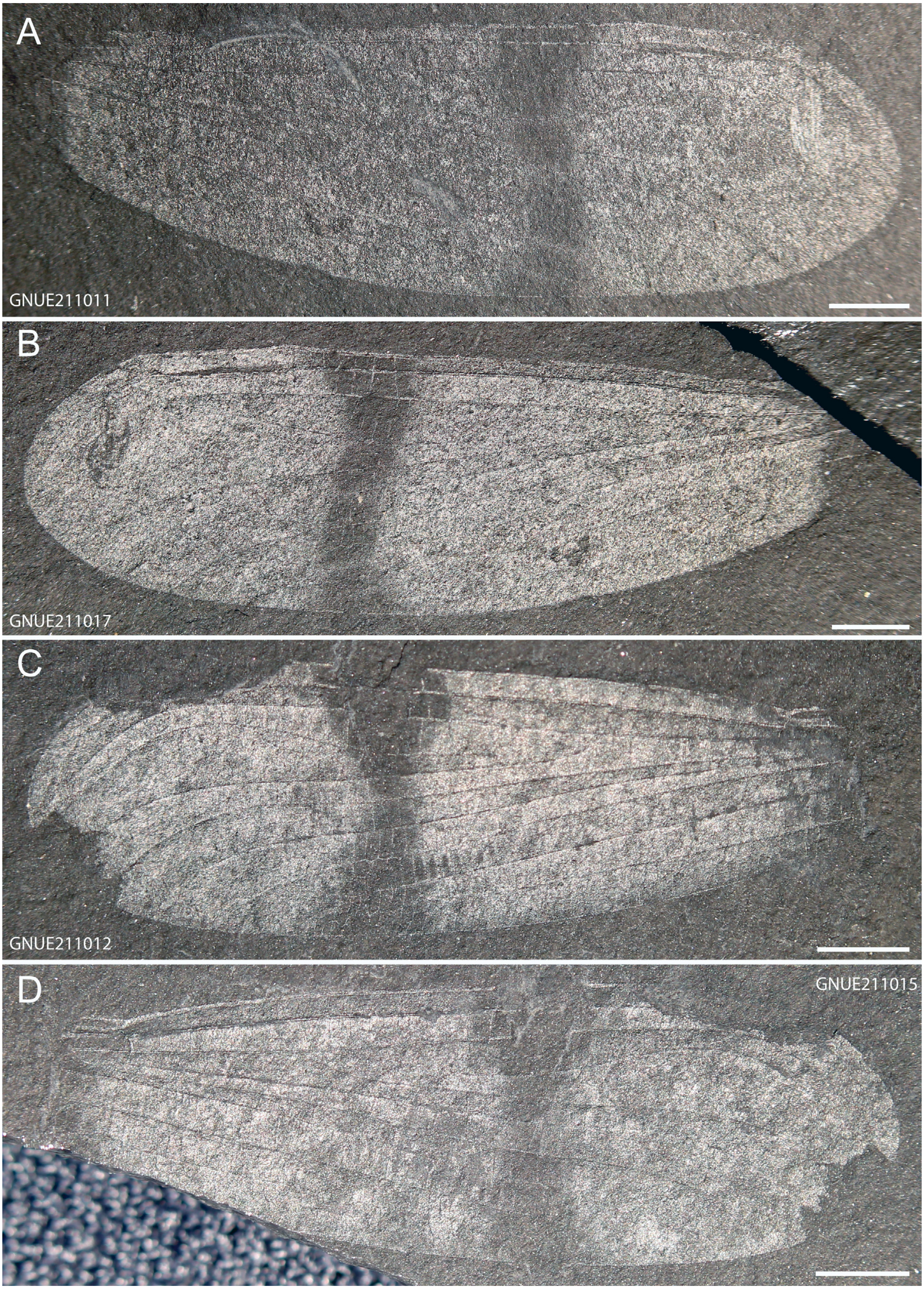

Fig. 3. *Koreapodagrion coloratus* n. gen. n. sp., Jinju Formation, Albian, Republic of Korea. (A) Paratype GNUE211011 (part). (B) Paratype GNUE211017 (counterpart). (C) Paratype GNUE211012 (part). (D) Paratype GNUE211015 (counterpart). Scale bars = 2 mm.

Fig. 4. Additional specimen of Odonata likely belonging to the new taxon (GNUE211094), Jinju Formation, Albian, Republic of Korea. Scale bar = 2 mm.

basad the subnodus; the base of IR2 is located below the subnodus; the base of RP2 is located far distad the subnodus; the main veins are nearly along most of their length but curve near the posterior margin of the wing; the wing have hyaline (transparent) base, with two large, more distal colored zones separated by a mid-section hyaline zone located between the nodus and pterostigma.

The specimen GNUE211014 has a very broad hyaline zone, whereas in the other specimens, this zone is narrower or appears restricted to the postnodal and postsubnodal areas (see GNUE211018). These observations suggest three distinct coloration patterns, which could correspond to different species, fore- and hind wings differences, or sexual dimorphism within the same species (Jouault et al., 2022). Given the uncertainty, we propose recognizing a single species with three 'morphs' representing different coloration patterns. The holotype, chosen as the most complete specimen, is GNUE211014.

These wings exhibit some similarities with both the Whetwhetaksidae Archibald et al., 2021 and the Dysagrionidae Cockerell, 1908, based on the following characters: wing large and broad, elongate pterostigma, no oblique crossvein 'O', and bases of RP3/4 and IR2 near nodus and subnodus. The very long pterostigma, six to seven times as long as wide, resembles the 'pterostigma at least seven times as long as it is wide' (up to 10 times in some species) of the Whetwhetaksidae. However, in the Whetwhetaksidae, the distal side MA/b in the discoidal cell forms a very open angle with its posterior side, unlike in specimen GNUE211014 (Archibald et al., 2021; Simonsen et al., 2022).

Some Sieblosiidae Handlirsch, 1907 (e.g., *Oligolestes*) also have distal side MA/b in the discoidal cell forming an acute angle with the posterior side, similar to what is observed in GNUE211014. However, in these species, the distal side MA/b more commonly forms a very open angle with the posterior side or even adopts an inverted orientation. The Sieblosiidae also have very long pterostigmata. However, they differ from the specimens present here owing to their oblique vein 'O', and the bases of RP3/4 and IR2 located midway between arculus and nodus. Therefore, we consider affinities between the new specimens and this family highly unlikely.

All taxa currently classified within the Dysagrionidae, except *Furagrion* Petrulevičius et al., 2008, have a distal side MA/b of the discoidal cell that forms a very open angle with its posterior side, or of inverted orientation. Originally, *Furagrion* was placed in the 'Megapodagrionidae' by Petrulevičius et al. (2008), but Archibald et al. (2021) reclassified it in the Dysagrionidae, arguing that it 'satisfies all wing character states of the diagnosis' they provided for the family. They indicated that the 'distal side of the quadrangle of *Furagrion* is not much longer than the proximal side as it is in many dysagrionids, it is still longer', and considered this character critical.

However, the trait of a 'distal side MA/b of the discoidal cell longer than the basal one' is found in many Zygoptera families (e.g., Lestidae, Coenagrionidae, Megapodagrionidae), and has no diagnostic value. Archibald et al. (2021) proposed two other characters in their diagnosis of the Dysagrionidae: 'distal-posterior angle [of quadrangle] oblique', and 'proximal-anterior angle usually about 90°'. The first trait lacks precision, as the defining feature for the group should be the degree of opening between MA/b and the posterior side of the quadrangle, rather than the general obliquity. Similarly, the trait of a 'proximal-anterior angle usually about 90°' is insufficiently distinctive, as this is a common feature in many other Zygoptera (Münz, 1919).

More reliable diagnostic characters for the Dysagrionidae are: 'distal side MA/b of the discoidal cell making a very open angle with its posterior side, or of inverted orientation' and 'angle between MA/b and anterior side of the discoidal cell close to 90°'. *Furagrion* does not share either of these two features. Another issue with assigning *Furagrion* to the Dysagrionidae is its comparatively narrow cubital area. However, this trait is also seen in the Cretaceous dysagrionine genus *Congqingia*, which otherwise has both diagnostic features of the discoidal cell mentioned above. Consequently, we exclude the genus *Furagrion* from the Dysagrionidae and restore it into the 'Megapodagrionidae' *sensu lato*. The new fossil wings do not align with the characteristics of Dysagrionidae, particularly regarding the structure of the discoidal cell, as discussed above.

The fossils also cannot be placed within the Caloptera Belyshev and Haritonov, 1983, as they lack the synapomorphies of this clade — midfork recessed basally to a position between 12% and 26% of wing length, and pterostigmal brace vein obsolete (Bechly, 2016). Extant Caloptera typically have the bases of the veins RP3/4 and IR2 positioned midway between the arculus and nodus or closer to the arculus. Only the Thaumatoneuridae Fraser, 1957 have RP3/4 and IR2 bases located near the nodus, similar to the new fossils. However, the new fossils differ from the representatives of this family by the presence of a distinct pterostigmal brace and a very long pterostigma.

The absence of the oblique crossvein 'O', the well-aligned postnodal and postsubnodal crossveins, and the bases of the veins RP3/4 and IR2 located at the level of the nodus and subnodus strongly suggest affinities with the Coenagrionomorpha Bechly, 1996. Additionally, these fossils display a characteristic tendency of this group: the formation of pseudo-transverse veins in the distal part of the wing, resulting from the alignment of the crossvein rows between the costal and hind margin beyond the nodus level.

Nevertheless, Coenagrionomorpha tend to the shortening of the pterostigmata, though this is not universal. Many species within the Hypolestidae Tillyard and Fraser, 1938 and 'Megapodagrionidae' possess relatively long pterostigmata. However, Hypolestidae generally have a strongly slanting basal margin of the pterostigma and distal parts of main veins distinctly curved apically — traits that are absent in these fossils.

Affinities with the extant Coenagrioniformia Bechly, 1996 are excluded because members of this group typically have short pterostigmata, supported by only two (rarely three) crossveins beneath, and a pterostigmal brace vein that is ventrally serrated like RP1.

The new fossils share certain features with the Pseudostigmatidae Tillyard, 1917 such as rather broad wings with numerous cells. However, they differ in having a distinct pterostigmal brace and a very long pterostigma. Similarly, these fossils resemble the Cretaceous family Paracoryphagrionidae Zheng, Nel and Wang, 2018 (in Zheng et al., 2018) in their very long pterostigma and general configuration of the main veins. Yet, they differ by lacking the highly specialized crossveins present between RA and RP1, and between RP1 and IR1 (Zheng et al., 2018).

The new fossils bear the most similarities with the extant 'Megapodagrionidae' *sensu* Dijkstra et al. (2014). Shared features include a relatively long and broad pterostigma, a basal side of pterostigma and a pterostigmal brace that are not oblique, RP1 without an angle, the presence of an intercalary longitudinal vein between main veins, and the alignment of IR2 base with subnodus while the RP3/4 base is more basal, with an elongated cell between them. Other key traits are a highly oblique distal side of the discoidal cell, a long and zigzagged distal part of MA, and very long CuA and MP veins (Bechly, 1996, 2016). The fossils, however, differ from extant genera by the presence of a long intercalary longitudinal vein between IR1 and RP1 (Münz, 1919; Garrison et al., 2010).

The new fossils, with very long pterostigmata, strongly differ from the genera *Cretapodagrion* Huang, Azar and Nel, 2018, *Phyonganpodagrion* So and Won, 2022, *Eckfeldia* Petrulevičius et al., 2008, *Furagrion* Petrulevičius et al., 2008, *Morsagrion* Zessin, 2011 (Paleocene–Eocene, Denmark), *Electropodagrion* Azar and Nel, 2008 (Eocene Baltic amber), *Oligoargiolestes* Kennedy, 1925 (uppermost Eocene, UK), *Eopodagrion* Cockerell, 1921 (lowermost Oligocene, USA), *Lithagrion* Scudder, 1890 (*L. hyalinum* Scudder, 1890, lower Oligocene, USA, Lower Miocene, Kazakhstan; Fig. 5E), *Melanagrion* Cockerell, 1907 (lowermost Oligocene, USA), and *Viridiflumineagrion* Nel, 2023 (Eocene, USA), as these genera have a pterostigma covering at most three-five cells (Azar and Nel, 2008; Petrulevičius et al., 2008; Zessin, 2011; Nel, 2023).

The holotype of *Miopodagrion* Kennedy, 1925 (*M. optimum* (Cockerell, 1916), lowermost Oligocene, USA) is partially broken, preserving only the distal part of the pterostigma. Nevertheless, it differs from the new fossils by having a less acute angle between MA/b and the posterior side of the discoidal cell, and secondarily by its hyaline wings (Fig. 5A–D).

Pterostigmata nearly as long as those of the new fossils are found in *Thanetophilosina* Nel et al., 1997 (Paleocene, Menat, France) and *Cerdanyagrion* Nel et al., 1996 (Miocene, Spain) (Nel et al., 1996, 1997). While the new fossils share the presence of numerous postnodal crossveins with these taxa, they differ by having a much less oblique basal side of the pterostigma. The Miocene genus *Vulcagrion* Nel and Paicheler, 1994 also has very long pterostigmata covering numerous cells but lacks an intercalary longitudinal vein between RP1 and IR1 (Nel and Paicheler, 1994; Nel et al., 1996).

Given that two Cenozoic genera also exhibit such elongate pterostigmata, and due to the incompleteness of the new fossils, it is not possible to establish a new family for them at this time.

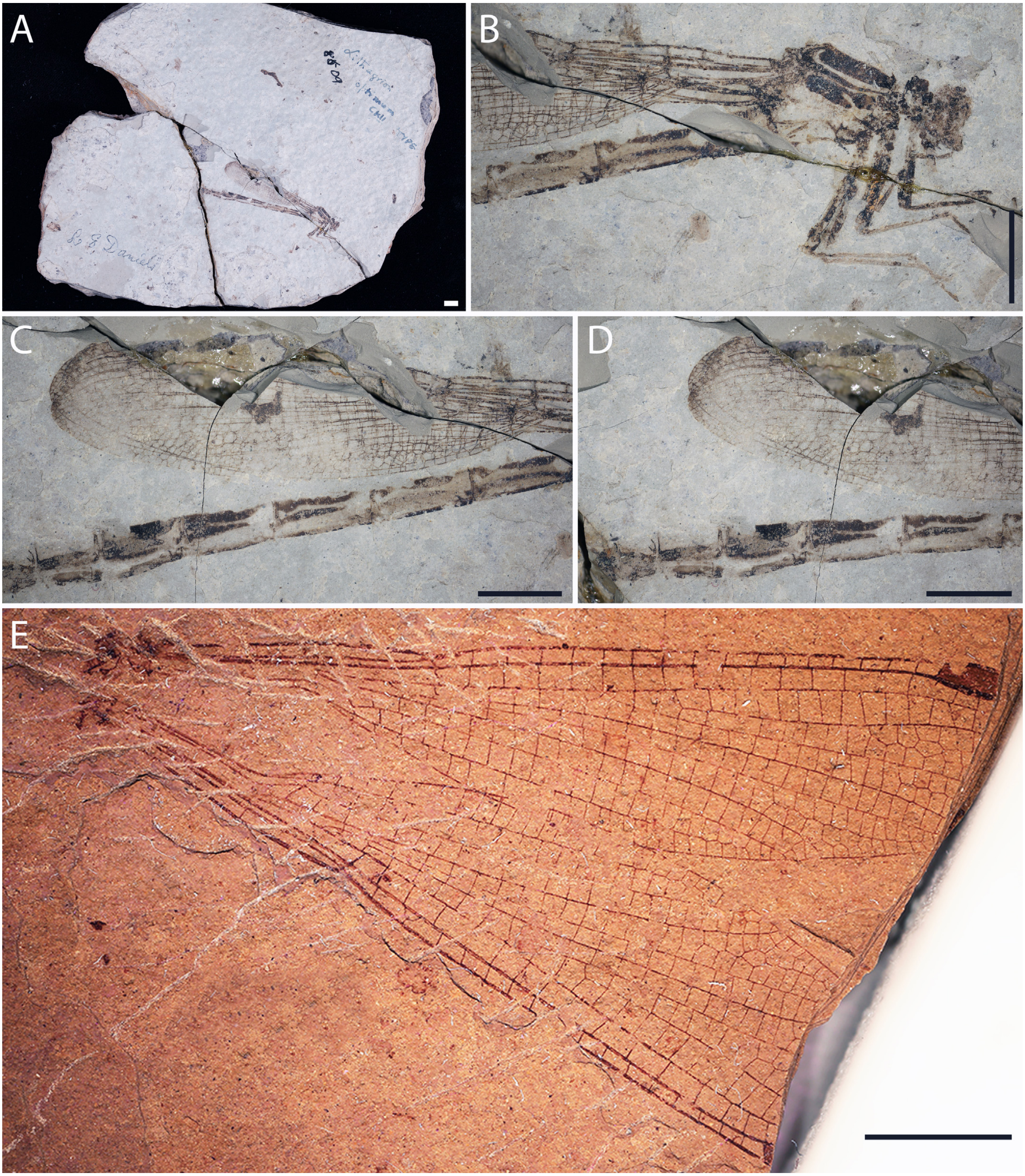

Fig. 5. Photographs of *Miopodagrion optimum* (Cockerell, 1916) (holotype UCM 8609) and *Lithagrion hyalinum* Scudder, 1890 (holotype UCM 4504). (A) Photograph of M. optimum slab. (B) Detailed view of *M. optimum* anterior part of body. (C) Detailed view of *M. optimum* mid part of body. (D) Detailed view of M. optimum posterior part of body. (E) Holotype of *L. hyalinum*. Scale bars = 5 mm.

5. Conclusion

Koreapodagrion coloratus n. gen. n. sp. is described from the Lower Cretaceous (Albian) Jinju Formation in Korea. This new species improves our understanding of Cretaceous 'megapodagrionid' diversity and their geographical distribution. During this period, 'megapodagrionids' have so far been known only from Asia, represented by two monospecific genera: *Cretapodagrion sibelleae* Huang, Azar and Nel, 2018 (Barremian, Yixian Formation, China) and *Phyonganpodagrion ryonsangae* So and Won, 2022 (Barremian/Aptian, Sinuiju Formation, Democratic People's Republic of Korea). The discovery of this new taxon suggests that the family was more diverse and thrived in the region from at least the Barremian to the Albian.

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