

The first orthopteran fossils from the Lower Cretaceous (Albian) Jinju Formation of Korea: Ethological implications for elcanids

Do-Yoon Kim ^a, Mirinae Lee ^b, Gi-Soo Nam ^{c, **}, Tae-Yoon S. Park ^{b, *}

^a Department of Life Science, Sogang University, Seoul, 04107, Republic of Korea

^b Division of Earth Sciences, Korea Polar Research Institute, Incheon, 21990, Republic of Korea

^c Gongju National University of Education, Gongju, Chungcheongnam-do 32553, Republic of Korea

ARTICLE INFO

Article history:

Received 23 November 2020

Received in revised form

14 February 2021

Accepted in revised form 30 March 2021

Available online 8 April 2021

Keywords:

Jinju Formation

Elcanidae

WDS analysis

Pterostigma

Spur

Tridactyloidea

ABSTRACT

The lower Albian Jinju Formation has produced various fossils of invertebrates. Of them, insect fossils have remained understudied, and especially, orthopteran fossils have never been described from the Jinju Formation. Here we report a new species of the Elcanidae (Orthoptera: Elcanoidea), *Panorpidium spica* sp. nov. based on three specimens from the Jinju Formation. Notably, we have applied Wavelength Dispersive Spectrometer (WDS) analysis for the first time on insect fossils, and discovered that the carbon elemental maps are helpful in recognizing crucial morphology. The presence of pterostigmata in forewing supports that elcanids evolved a unique flight mechanism distinct from other extant orthopterans. Based on a detailed morphological comparison with the paddles of the extant tridactylids, it is inferred that the leaf-shaped spurs on the metatibiae of elcanids were used for jumping on the water, although other possible functions cannot be ruled out. Diving into the water and jumping on the water surface must have been an effective way of escaping from predators, both for the flightless nymphs and the short-range flying adults.

© 2021 Elsevier Ltd. All rights reserved.

1. Introduction

The Cretaceous Gyeongsang Supergroup, Korea, spanning from the Hauterivian to the Santonian, is known to produce diverse fossils and traces. Especially the lower Albian Jinju Formation has produced abundant trace fossils and body fossils. The trackways reported from the Jinju Formation are of non-avian dinosaurs (Kim et al., 2012a; Kim et al., 2018a; Kim et al., 2018b), birds (Lockley et al., 2012; Kim et al., 2012b), lizards (Kim et al., 2017a), turtles (Kim and Lockley, 2016), frogs (Kim et al., 2019), and mammals (Kim et al., 2017b). Vertebrate body fossils are relatively uncommon, which include fishes (Yabumoto and Yang, 2000; Yabumoto et al., 2006; Kim et al., 2014), teeth of pterosaurs and non-avian dinosaurs (Yun et al., 2007). Along with vertebrate fossils and trackways, the Jinju Formation produces fossils of various kinds of invertebrates which must have been a food source for small vertebrates in the Cretaceous. Examples of invertebrate fossils include

insects (Engel et al., 2002; Engel et al., 2006; Baek and Yang 2004; Park et al., 2013; Nam and Kim 2016; Khramov et al., 2020; Sohn et al., 2019), spiders (Selden et al., 2012; Park et al., 2019), isopods (Park et al., 2012), ostracods (Paik et al., 1988; Choi, 1990; Choi and Huh, 2016; Choi et al., 2018), and conchostracans (Park and Chang, 1998). Of them, despite the abundance and high diversity, insect fossils have remained extremely understudied, and especially, to date, orthopteran fossil has not been documented from the Jinju Formation.

Within the Order Orthoptera, the phylogenetic position of the extinct superfamily Elcanoidea remains unsettled; they are considered to belong to the Suborder Ensifera (Zessin, 1987; Kukalová-Peck, 1991; Carpenter, 1992; Gorochov, 1995; Gorochov et al., 2006), or treated as a sister group to the Suborder Caelifera (Béthoux and Nel, 2002), while Gorochov and Rasnitsyn (2002) even proposed a possibility of being a sister group to all other orthopterans. The Elcanoidea is divided into two families, Elcanidae and Permelcanidae (Grimaldi and Engel, 2005; Gorochov et al., 2006; Fang et al., 2018b). The Permelcanidae includes six species of three genera, known from the Lower Permian to the Lower Triassic (Tillyard, 1937; Sharov, 1968), while the Elcanidae contains more than 50 species belonging to fifteen genera usually from the

* Corresponding author.

** Corresponding author.

E-mail addresses: nks33@hanmail.net (G.-S. Nam), typark@kopri.re.kr (T.-Y.S. Park).

Mesozoic (Gorochov et al., 2006; Cigliano et al., 2018). The elcanid fossils occur from the Upper Triassic to the Cretaceous of Europe, Asia, North and South America (Sharov, 1968; Martins-Neto, 1991; Ansoorge, 2003; Gorochov et al., 2006; Peñalver and Grimaldi, 2010; Fang et al., 2015). Recently, a single forewing from the Paleogene of France was assigned to a new species of the Elcanidae, which suggests a possibility of elcanids having survived the Cretaceous–Paleogene extinction (Schubnel et al., 2020). Although a growing number of the Cretaceous elcanid fossils are being documented from the Burmese amber and the Jehol Biota (Poinar et al., 2007; Heads, 2009; Peñalver and Grimaldi, 2010; Fang et al., 2015; Fang et al., 2018a; Tian et al., 2019a; Kocárek, 2020), their detailed morphology still remains incompletely understood.

This study describes a new species of the elcanid genus *Panorpidium* Westwood, 1854, based on three specimens collected from the Lower Cretaceous (Albian) Jinju Formation. In order to fully appreciate the fossil morphology, we have used wavelength dispersive X-ray spectrometers (WDS), which marks the first application to insect fossils. The new specimens provide critical information on elcanid features, such as pterostigma in the wings and well-preserved spurs in the hind legs. Especially, we compare the spurs to the paddles and spurs in the hind legs of the extant tridactylid orthopterans, the pygmy mole crickets, which will help understand the function of the spurs in elcanids.

2. Material and methods

Three specimens for this study 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 early Albian (Lee et al., 2018). The fossils are preserved as reflective carbonaceous film on different slabs of dark grey shale. The specimens are housed in the Gongju National University of Education, with registration numbers GNUE212001, GNUE212002, and GNUE212003.

The fossils were immersed in 70% ethanol and photographed by a Leica M205C microscope equipped with a Leica DFC550 camera. Different parts of the specimens were photographed and then the images were stitched in Adobe Photoshop CS6. The JEOL JXA-8530F field emission electron probe microanalyzer (FE-EPMA) at the Korea Polar Research Institute, equipped with five wavelength dispersive X-ray spectrometers (WDS) and energy dispersive X-ray spectrometers (EDS) was used for X-ray elemental maps of carbon. The maps were acquired from an acceleration voltage of 20 kV, beam current of 200 nA, beam size of 5–8 μm , dwell time of 10–12 ms, and step size of 5–8 μm . Each raw data of X-ray elemental maps was processed for brightness, contrast and pseudo-colouring by ImageJ to enhance visibility. The specimens were coated by gold for mapping using a Cressington 108 Auto sputter coater with 10 mA for 80 s. Drawings were made from photographs and X-ray carbon elemental images, using photo-editing and painting software: PaintTool SAI (<http://detstwo.com/sai/>) and CLIP STUDIO PAINT (<https://www.clipstudio.net/en/>).

Wing venation nomenclature follows Béthoux and Nel (2001, 2002). Abbreviations of wing venation nomenclatures are: CP, posterior costa; ScA, ScP, anterior, posterior subcosta; R, radius; RA, RP, anterior, posterior radius; MA, MP, anterior, posterior media; CuA, CuP, anterior, posterior cubitus; CuPa α , the anterior branch of first posterior cubitus; CuPa β , the posterior branch of first posterior cubitus; CuPb, the second posterior cubitus; 1A, anterior anal vein.

Anatomical terminology for body structure follows Storozhenko et al. (2015), but also refers to Peñalver and Grimaldi (2010) and

Fang et al. (2018a) to describe the exceptional tibia structure of elcanids. Corresponding abbreviations of Anatomical terminology for body are: as, apical spur; cl, claws; cr, cercus; ds1–3, 1–3rd dorsal spur; dv, dorsal valves of ovipositor; epp, epiproct; sgp, subgenital plate; st, sternites; t8–10, 8–10th tergites; ta1–3, 1–3rd tarsomeres; tb, tibia; vs, ventral spines; vv, ventral valves of ovipositor.

3. Systematic palaeontology

Order Orthoptera Olivier, 1789

Superfamily Elcanoidea Handlirsch, 1908

Family Elcanidae Handlirsch, 1908

Subfamily Elcaninae Handlirsch, 1908

Genus *Panorpidium* Westwood, 1854

Type species: *Panorpidium tessellatum* Westwood, 1854

Included species. Type species *Panorpidium tessellatum* Westwood, 1854; *P. angustior* Handlirsch, 1939; *P. beyrichi* Giebel, 1856; *P. bimaculatum* Gorochov, Jarzembowski & Coram, 2006; *P. deichmuelleri* Handlirsch, 1908; *P. geinitzi* Geinitz, 1880; *P. lata* Sharov, 1968; *P. liasinum* Giebel, 1856; *P. lithophilum* Germar, 1842; *P. longicorne* Handlirsch, 1908; *P. magnum* Handlirsch, 1908; *P. medium* Handlirsch, 1908; *P. mesostenum* Handlirsch, 1939; *P. minimum* Handlirsch, 1908; *P. minutum* Sharov, 1968; *P. oppenheimi* Handlirsch, 1908; *P. parvum* Gorochov, Jarzembowski & Coram, 2006; *P. phyllophorum* Handlirsch, 1908; *P. proximum* Gorochov, Jarzembowski & Coram, 2006; *P. reticulatum* Handlirsch, 1939; *P. sibiricum* Sharov, 1968; *P. westwoodi* (Handlirsch, 1908); *P. yixianensis* Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015; and possibly *P. parvum* Gorochov, Jarzembowski and Coram, 2006.

Panorpidium spica sp. nov.

(urn:lsid:zoobank.org:act:C2E51899-1280-4C38-98A7-DDC649EFE5FC).

Materials. Holotype, well-preserved female with incomplete head, GNUE212001 (Figs. 2, 3 and 4A–D); Paratype, sex unknown, head and posterior abdomen incomplete, GNUE212002, (Figs. 4A–D and 5E–F); sex unknown, Forewing overlapped with hindwings, GNUE212003 (Figs. 4E–F and 5G).

Etymology. Derived from the binary star ‘Spica’, the α Virginis, referring to the two spots on the forewing.

Type horizon and locality. Jinju Formation, lower Albian, at the Jeongchon section (35°07'45"N, 128°06'02"E), 5.6 km south of the city of Jinju, Republic of Korea (Fig. 1).

Diagnosis. Forewing medium sized; area of ScA narrow; area of ScP wider than ScA with four branches ending at the anterior margin; RA and RP forked near middle point of ScP; narrow MP situated relatively proximal; S-shaped curved CuA + CuPa α and M; slightly widened width of the area between 1A and CuPb; two large and round spots present, through which MA branches and some RP branches run.

General Description. Head to tip of wing 18.4–22.7 mm long (except antennae segment).

Head: incompletely preserved, narrow and elongate; mandible thick, but gathered sharp; enlarged antennal scape segments.

Thorax: Lateral lobes of large saddle-shaped pronotum with posterior prolongation, prolonged area two times longer than unprolongated area, coloured stripe around lower and posterior margin (present in the paratype specimen GNUE212002). Prothoracic and mesothoracic legs long (Fig. 3C); tibia relatively wider than other leg segments with a longitudinal inner groove in center; coxa short, cylindrical shape; protarsus slender with row of tiny spines; mesotarsus preserved with three tarsomeres; ta1 long with

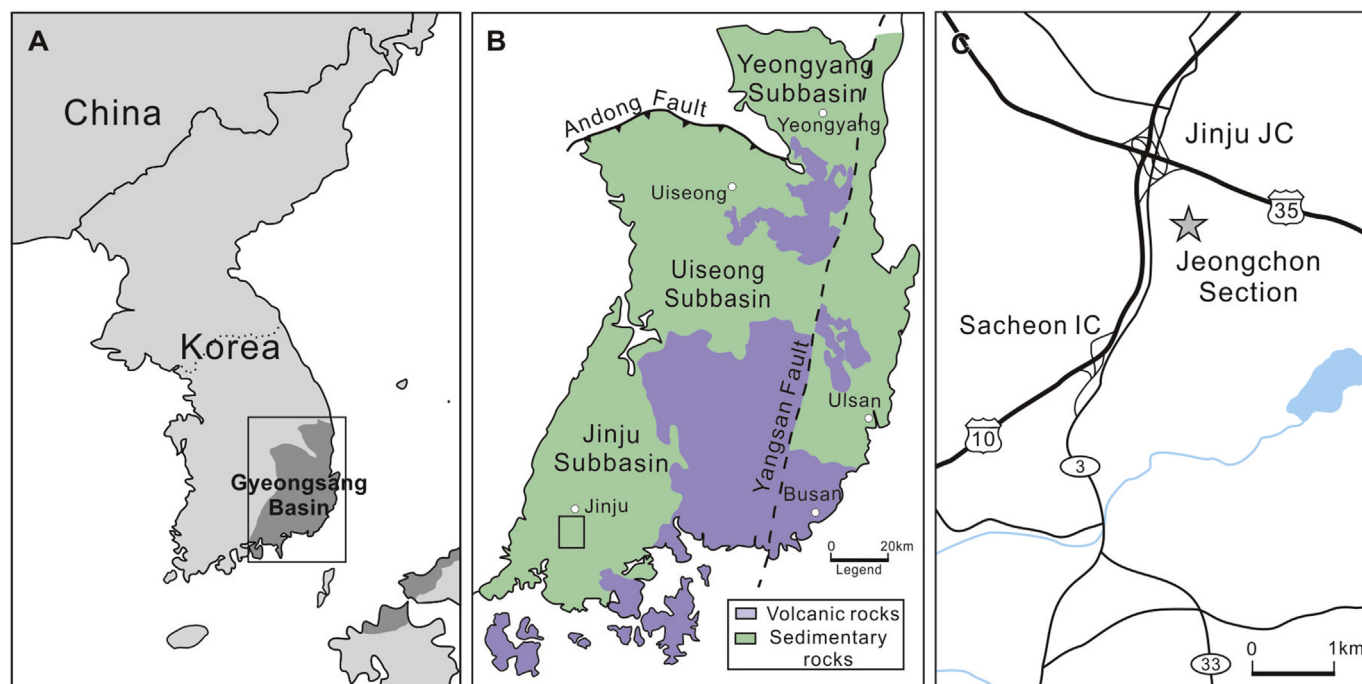


Fig. 1. Location map of the Jeongchon section (modified from Park et al., 2019). **A.** Location of the Gyeongsang Basin; the rectangular area is magnified in **B.** **B.** Distribution of the sedimentary rocks and volcanic rocks in the Gyeongsang Basin. **C.** Road map of the study area showing the fossil locality (star).

rows of tiny spines with an apical spine; ta2 very short with a stout conical spine; ta3 longest, simple; claws well-developed. Metathoracic legs well-developed (Figs. 3D and 4B); metacoxa small, rounded triangle; metafemur very long and thick, with short and denser setulae on dorsal surface, two stripes across the knee and femur; hind knee robust, semi-lunar processes prominent on the dorsal edge; metatibia long (Figs. 2B,E, 3E and 4B), flat and relatively wide, two dorsal rows of tiny spines, three pairs of articulated leaf-like subapical dorsal spurs, long apical spurs developed; metatarsus long with three tarsomeres; ta1 longest with row of spines, ta2 very short with a stout conical spine, ta3 long; claws well-developed.

Abdomen (Figs. 2E–G and 3B): tenth tergite short, narrow, triangular; cerci long, slender, unsegmented; subgenital plate short; ovipositor long but not reaching the forewing end, gently recurved, 9.8 mm long (from the tip to the base).

Wing: Forewing macropterous, relatively medium size with rounded and pointed apex, long and narrow, 14.9–18.6 mm long and 2.8–3.1 mm wide at midlength. Costal area long and narrow; CP reaching anterior margin at 1/4 of forewing, with numerous branchlets; area of ScA narrow, branches reaching anterior margin at one third of forewing; area of ScP wider than ScA, branches reaching anterior margin before half of forewing; stem of R long and strong, forked into RA and RP near middle point of ScP area; basal stem of R thick and strong; RA long, close to anterior margin with numerous oblique branches reaching anterior margin close to apex; RP with seven to eight comb-like branches with more branches near apex; area between RA and RP narrow with 13–14 crossveins; MA branched into MA1 and MA2, MA1 branched close to diverging RA and RP, MA2 branched near the ending point of ScA; MP narrow, starting before middle of ScA area in anterior margin with more than five to six crossveins reaching CuA + CuPa α ; CuA + CuPa α starting near the end point of ScP, reaching posterior margin; CuPa β , CuPb and 1A fused with each other, reaching posterior margin at one third of forewing; area between 1A and posterior margin filled with partly oblique crossveins; area between RA and

margin coloured like pterostigma with four short extensions to the area between RP and RA, connected with a colouration of the apex; two large and round spots in region of RP and MA branches, some spots in area between 1A, CuPa β and stem of R. Hindwing shorter than forewing with more rounded apex.

Holotype. GNUE212001 (Figs. 2, 3 and 5A–D); head to tip of wing 22.7 mm long (except antennae segment), well-preserved body with ovipositor, forewing overlapped by other wings, dorsal part of abdomen, and metafemurs.

Head: The proximal to dorsal part of the head, a few segment of antennae partially preserved. 1.1 mm wide, 2.0 mm high.

Thorax: Lateral lobe 5.0 mm long, 3.2 mm high. Prothoracic leg: Both profemurs not preserved; left tibia 2.3 mm long, right tibia >1.4 mm long (inaccuracy of proximal extremities); only proximal part of ta1 preserved, left tarsus with short spines, left tarsus >0.6 mm long and right tarsus >0.4 mm long. Mesothoracic leg: Both mesofemurs not well-preserved; left tibia 2.1 mm long, right tibia >1.5 mm long (only preserved middle part); first segment of mesotarsus had short spines; left tarsus complete with three tarsomeres and a claw, ta1 0.8 mm long (except the spine), conical form ta2 0.2 mm long excluding the spine, ta3 1.1 mm long, claw 0.5 mm long; conical form ta2 including the spine 0.5 mm long; right tarsus >0.7 mm long (some proximal part preserved). Metathoracic leg: Distal half part of right femur hidden by abdomen, left femur 8.3 mm long and 2.2 mm wide at thickest section, setulae preserved on dorsal surface; both tibiae retaining incomplete two pairs subapical dorsal spurs; left tibia 9.0 mm long and 0.5 wide, ds1 1.2 mm long and 0.2 mm wide, ds2 1.1 mm long and 0.3 mm wide, two apical spurs preserved, 0.6 mm long and 1.2 mm long; right tibia >8.8 mm long and 0.5 wide, ds1 1.0 mm long and 0.3 mm wide, ds2 >0.9 mm long and >0.3 mm wide (proximal part incomplete), an apical spur preserved, 1.5 mm long; left tarsus nearly completed but some part of ta2, t3, tarsomeres and claws incomplete, ta1 2.6 mm long (except vs), ta2 >0.2 mm long, ta3 >0.7 mm long, claws >3 mm; right tarsus nearly complete but proximal part of ta1

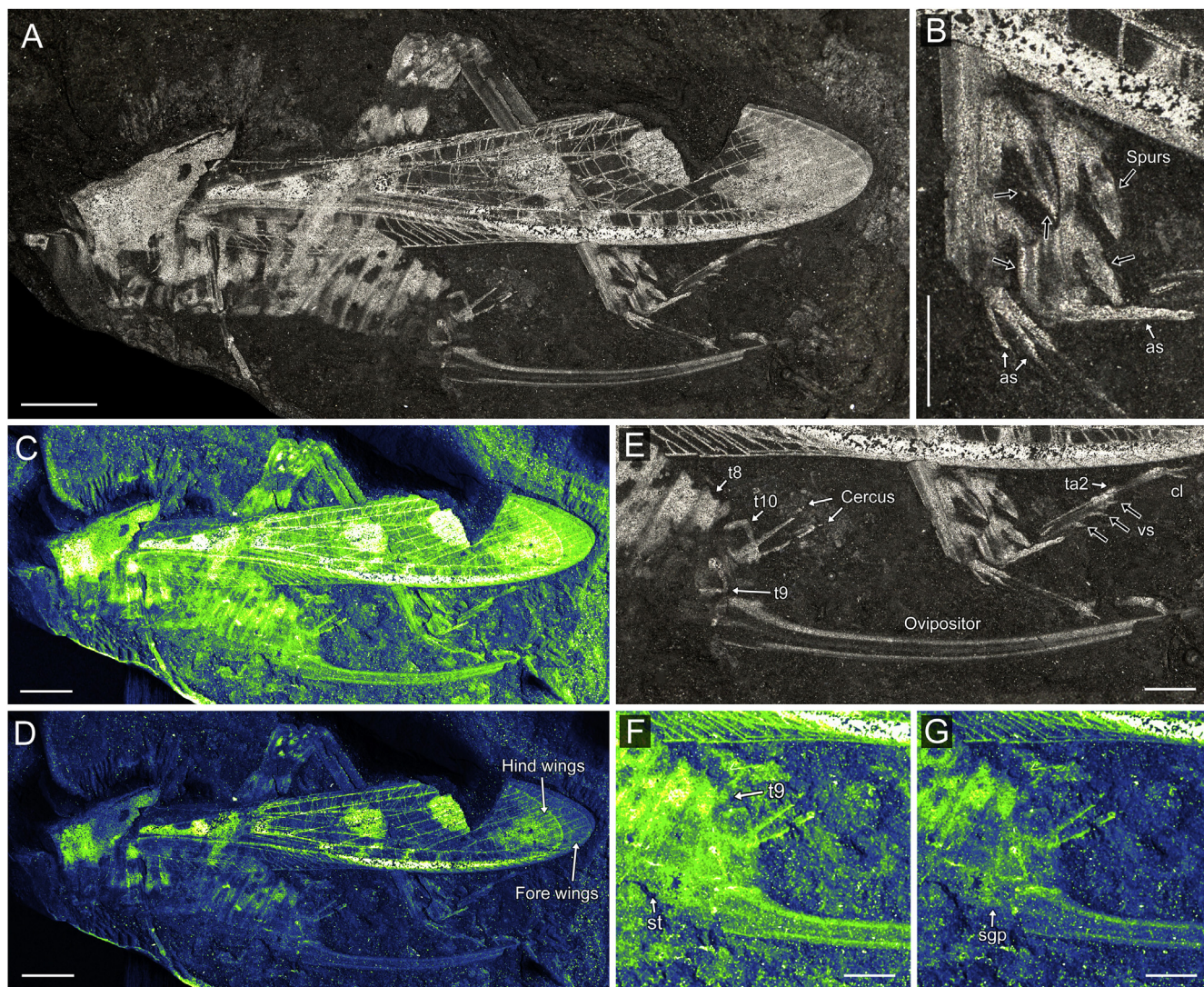


Fig. 2. The holotype of *Panorpium spica* sp. nov., GNUE212001. **A.** Overview, **B.** Magnified image of the distal part of metatibiae showing details of the spurs, **C–D.** Carbon elemental maps from Wavelength Dispersive Spectrometer (WDS) analyses, emphasizing lower concentration parts and higher concentration parts, respectively, **E.** Magnified image of the apex of the abdomen showing detailed ovipositor structures, **F–G.** Carbon elemental maps of the apex of the abdomen, emphasizing lower concentration parts and higher concentration parts, respectively. Abbreviations: as, apical spur; cl, claws; sgp, subgenital plate; st, sternites; t8–10, eight to tenth tergites; ta2, second tarsomeres; vs, ventral spines. Scale bars for A, C and D are 2 mm; B, E, F, and G are 1 mm.

incomplete, ta1 >2.6 mm long (except vs), ta2 0.2 mm long except a spine, ta3 1.0 mm long, claws 0.6 mm, 0.5 mm long each other.

Abdomen: Abdomal segments well-exposed, detached tergites and sternites show several segments, apex part of abdomen preserved; dorsal part of ninth tergite incomplete; tenth tergite triangular; cerci nearly preserved but apical parts broken by fragments; left cercus 1.6 mm long, right cercus >1.4 mm long; subgenital plate preserved weakly (recognizable in the WDS carbon elemental map), small in profile; ovipositor 9.8 mm long (measured from the tip to the base), base 0.7 mm wide, tip 0.2 mm wide.

Wing: Partially incomplete near the MA area; forewing 18.6 mm long and 3.1 mm wide at midlength; CP preserved at least 9 oblique branches, several proximal branches pectinate, reaching margin; ScA with four branches ending in anterior margin; two crossveins preserved between CP and ScA; ScP with four branches ending in anterior margin, six cross-vein preserved between ScA and ScP; RA preserved at least 21 short oblique branches, two proximal branches pectinate; fourteen crossveins preserved between RA and RP; RP with seven longitudinal branches which are pectinate,

reaching margin, some branches incompletely preserved; one crossvein preserved between RP and MA1; six crossveins preserved between MP and CuA + CuPaz; distal part of MA branches not preserved.

Paratypes. GNUE212002 (Figs. 4A–D and 5E–F). Smaller than the holotype, head to tip of wing 18.4 mm long, head and apex of abdomen incomplete, forewing overlapped by the other forewing, hind wings, metafemurs and metatarsus.

Head: Preserved in anterior view, incomplete dorsal part; frons weakly preserved; each mandible 1.2 mm long.

Thorax: Lateral lobe 3.6 mm long, 2.4 mm high, stripe around lower and posterior margin preserved. Prothoracic leg: Incompletely preserved, right tibia and proximal part of ta1 saved inaccurately; right tibia >1.1 mm long, ta1 > 0.6 mm. Mesothoracic leg: Incompletely preserved. Metathoracic leg: Both femurs obliquely overlapped with metacoxae, right femur 6.7 mm long and 1.8 mm wide at thickest section, left femur 6.5 mm long and >1.5 mm wide at thickest section; right tibia >3.6 mm long, folded in femur, with fragment of three parts subapical spur and a row of tiny spines at

dorsal; left tibia >3.6 mm long, overlapped by wings only partially but preserved fragments of subapical spur and two rows of tiny spines at dorsal margin; both tarsi not preserved.

Abdomen: Three abdominal segments preserved, but ventral part incomplete.

Wing: Apex of wing partially incomplete; forewing >14.3 mm long and 2.5 mm wide at midlength; at least ten oblique branches preserved in middle of CP; ScA branches unpreserved; one crossvein preserved between CP and ScA; ScP with four branches ending in anterior margin; RA preserved at least twenty short oblique branches; fourteen crossveins between RA and RP; RP with six longitudinal branches which are pectinate, reaching margin, distal part of RP branches incomplete; four crossveins preserved between RP and MA1; five crossveins preserved between MP and CuA + CuPa α .

GNUE212003 (Figs. 4E–F and 5G): Only overlapped wings; forewing 14.9 mm long and 2.8 mm wide at midlength; CP preserved at least eight oblique branches; ScA with three branches reaching anterior margin; four crossveins preserved between CP and ScA; ScP four branches reaching anterior margin; incomplete colourations present around RA branches; thirteen crossveins preserved between RA and RP; RP with seven longitudinal branches which are pectinate, reaching margin; one crossvein preserved between RP and MA1; six crossveins preserved between MP and CuA + CuPa α . **Remarks.** These three specimens can be easily recognized by the presence of two large and round spots, and the colouration in the apex area in the forewings. The forewing with narrowed area between RA and RP, fused distal parts of CuPa β , CuPb, and 1A indicate that these specimens belong to Elcaninae. The presence of three longitudinal branches between the basal part of RP and CuA + CuPa α (Fig. 5D), and the converging and fusion of distal parts of

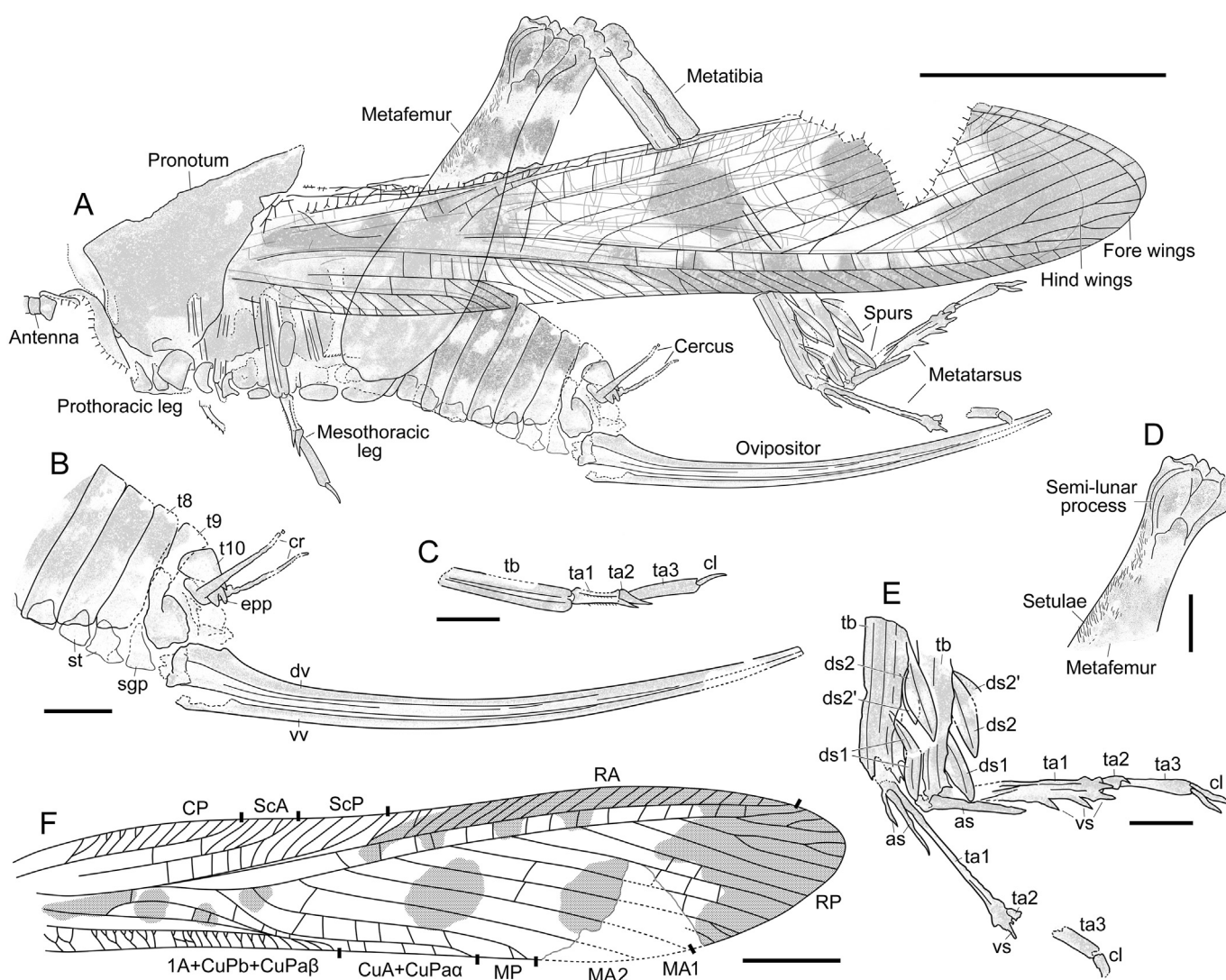


Fig. 3. Interpretive drawings of the holotype of *Panorpidium spica* sp. nov., GNUE212001. **A.** Overview, **B.** Apex of the abdomen with ovipositor structures, **C.** Mesothoracic leg, **D.** Metafemur, **E.** Distal part of metatibiae with spurs and tarsi, **F.** Forewing. Abbreviations: as, apical spur; cl, claws; cr, cercus; CP, posterior costa; CuA, CuP, anterior, posterior cubitus; CuPa α , the anterior branch of first posterior cubitus; CuPa β , the posterior branch of the first posterior cubitus; CuPb, the second posterior cubitus; ds1–2, first to second dorsal spurs; dv, dorsal valves of the ovipositor; epp, epiproct; MA, MP, anterior, posterior media; R, radius; RA, RP, anterior, posterior radius; ScA, ScP, anterior, posterior subcostal; sgp, subgenital plate; st, sternites; t8–10, eight to tenth tergites; ta1–3, first to third tarsomeres; tb, tibia; vs, ventral spines; vv, ventral valves of ovipositor; 1A, anterior anal vein. Scale bars for A is 5 mm; B, C D and E are 1 mm; F is 2 mm.

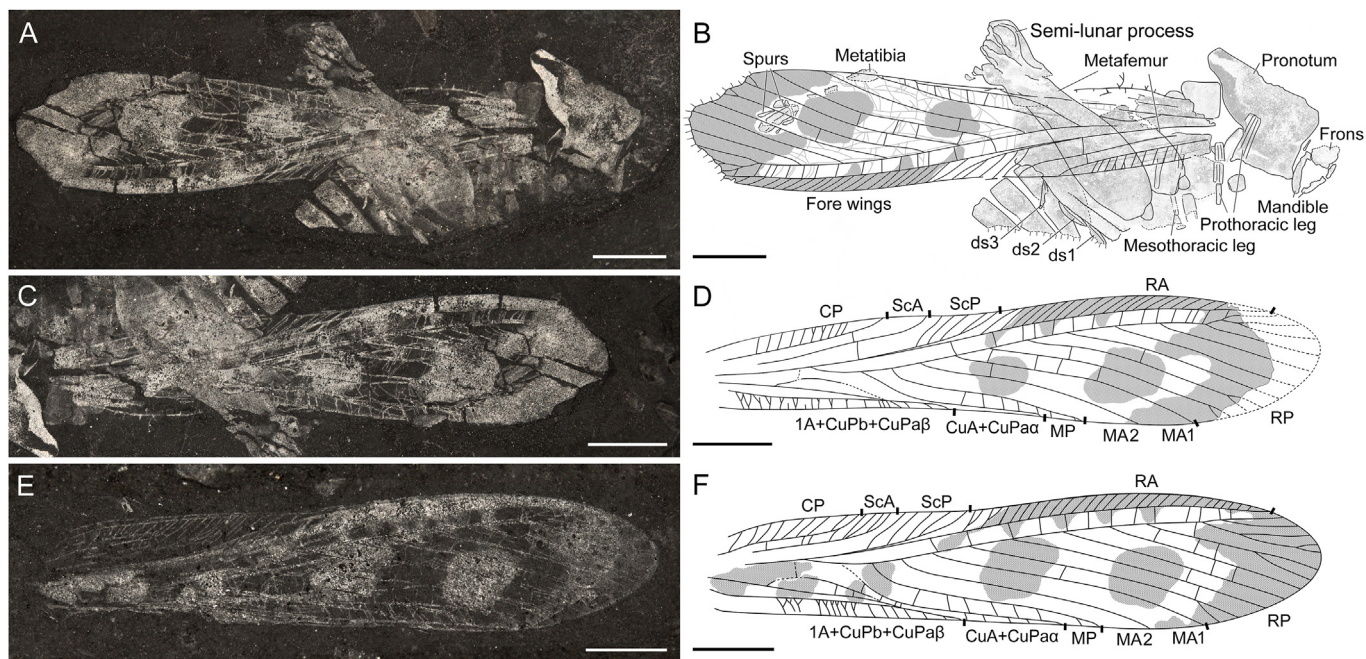


Fig. 4. Photo and interpretive drawings of the paratypes of *Panorpidium spica* sp. nov. **A–B.** Overview photo and the interpretive drawing of GNUE212002, respectively, **C–D.** Magnified images of the wing and the interpretive drawing of the forewing of GNUE212002, respectively, **E–F.** Photo and the interpretive drawing of the forewing of GNUE212003, respectively. Abbreviations: CP, posterior costa; CuA, CuP, anterior, posterior cubitus; CuPaz, the anterior branch of the first posterior cubitus; CuPaβ, the posterior branch of the first posterior cubitus; CuPb, the second posterior cubitus; ds1–3, first to third dorsal spurs; MA, MP, anterior, posterior media; R, radius; RA, RP, anterior, posterior radius; ScA, ScP, anterior, posterior subcostal; 1A, anterior anal vein. Scale bars are 2 mm.

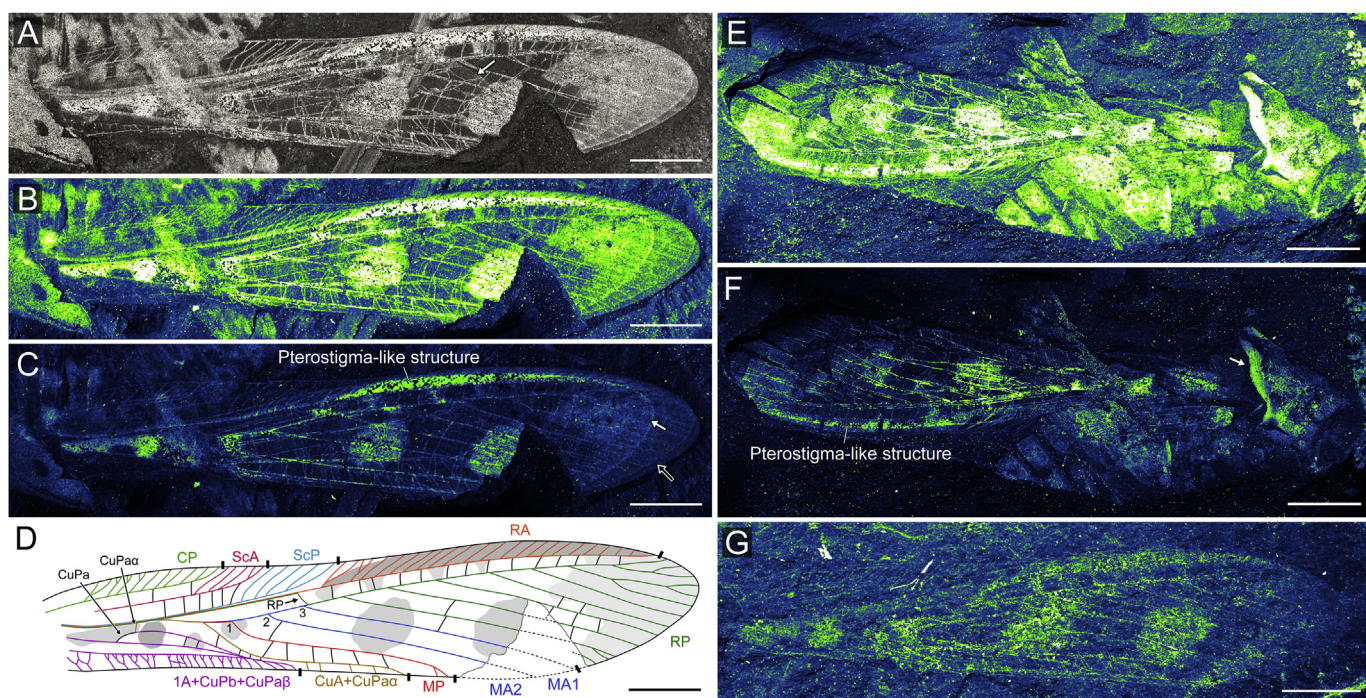


Fig. 5. Forewing morphology of *Panorpidium spica* sp. nov. **A–D.** Wings of the holotype, GNUE212001, **A.** Normal photographic image (white arrow indicates the folded anal region margin of the hind wing), **B–C.** Two carbon elemental maps, emphasizing lower concentration parts and higher concentration parts, respectively (white arrow, hind wings; black arrow, fore wings), **D.** Detailed interpretive drawing of the forewing venation and the colouration pattern, **E–G.** Carbon elemental maps of the paratypes, **E–F.** Two images of GNUE212002, emphasizing lower carbon concentration parts and higher carbon concentration parts, respectively (white arrow indicates the colouration in the margin of lateral lobes). **G.** Carbon elemental map of GNUE212003. Abbreviations: CP, posterior costa; CuA, CuP, anterior, posterior cubitus; CuPaz, the anterior branch of the first posterior cubitus; CuPaβ, the posterior branch of the first posterior cubitus; CuPb, the second posterior cubitus; MA, MP, anterior, posterior media; R, radius; RA, RP, anterior, posterior radius; ScA, ScP, anterior, posterior subcostal; 1A, anterior anal vein. Scale bars are 2 mm.

CuPa β , CuPb and 1A suggest that these specimens belong to the genus *Panorpidium* Westwood, 1854. With the exception of *P. bimaculatum* Gorochoy, Jarzembowski and Coram, 2006, the new species is distinguished from other Cretaceous *Panorpidium* species by the presence of the two large and round spots. Moreover, the forewing venations are different from other species: i.e., MP is more proximal than in *P. yixianensis* Fang et al., 2015 from the Yixian Formation; RA and RP forked closer to MA1 branch than first branch of RP, wider width of the area between 1A and CuPb, compared to *P. tessellatum* Westwood, 1854; narrower margin of MP area and more crossveins branches in the area between RA and RP are distinguishable from *P. sibiricum* Sharov, 1968; smaller forewing, wider ScP, narrower ScA, wider area between CuPa β and CuPb than *P. proximum*; the large forewing, several crossveins presented between RP and M. much narrower MP, wider CuA + CuPa α , wider width of the area between 1A and CuPb, and more pointed margin of apex make the new species different from *P. parvum* Gorochoy, Jarzembowski and Coram, 2006. The presence of two large round dark spots in the region of RP and MA branches is similar to *Panorpidium bimaculatum* Gorochoy, Jarzembowski and Coram, 2006, but *Panorpidium spica* sp. nov. differs in having narrower ScP, more proximally-situated divergence point of RP and RA, wider width of the area between 1A and CuPb, and the colouration of the area between RA and the margin (forming pterostigma) with four extensions towards the crossveins between RP and RA. The patterns in insect wings are for mimicry and/or camouflage, or due to sexual selection (Grimaldi and Engel, 2005; Stevens and Ruxton, 2019). Interestingly, the Middle Jurassic elcanid *Parelcana pulchmacula* Tian, Gu, Yin and Ren, 2019 also had two large and round spots in the region of RP and MA branches. It can be inferred that the presence of two round spots in the wing was a common theme in the Elcaninae with possible functions of mimicry or camouflage. Compared to the holotype, the two paratypes are relatively small, but share all key characteristics of the new species. Intraspecific variation in body and wing size is common in orthopterans (Kelly et al., 2008; Picaud and Petit 2008; Poniatowski and Fartmann, 2009; Berggren et al., 2012), including elcanids (Zessin, 1987). Given that male is usually smaller than female in orthopterans, the different size might represent sexual dimorphism.

4. Discussion

4.1. X-ray elemental maps and recognition of morphology

In a recent research on the central nervous system of the Cambrian stem euarthropod *Kerygmachela kierkegaardi* Budd, 1993, the WDS analysis was used on the fossils preserved in shale for the first time (Park et al., 2018). The present study has applied the WDS analysis on the elcanid fossils, which has turned out to be effective in recognizing wing venations, as well as other overprinted body structures. Due to overlapping with other wings or body parts, forewing venation pattern, an important criteria in insect taxonomy, is often difficult to recognize in insect fossils. In the holotype of *Panorpidium spica* sp. nov., the forewing overlaps on the other wings, dorsal part of the abdomen, and the metafemurs, hindering the recognition of the venation. The carbon maps from the WDS provide a solution to this. Different body part or structure of the holotype specimen show different carbon concentration, and the higher carbon concentration appears to be brighter in the elemental maps. For example, the apparently left forewing venations have higher carbon concentrations than the venations of the other overlapped wings, metafemurs, and abdominal structures, and thus they are brighter in the WDS carbon maps (Figs. 2C–D and

5E–F). In normal photos, identifying the forewing venations, such as ScA, ScP, CuA, and CuP, is difficult, but these venations stand out in the WDS carbon maps (Fig. 5). It was also possible to identify the branching site of the RA and the RP (Fig. 5D), which is an important generic-level diagnostic character of the Elcanidae. In a map in which lower carbon concentration areas also appear to be bright, the abdominal structures that are not distinctive in normal photographic images, such as subgenital plate and sternite, become recognizable (Fig. 2E–G).

4.2. Pterostigma in the wings

The WDS carbon maps of the *Panorpidium spica* sp. nov. show highest concentration of the carbon element near the margin of the RA area (Fig. 5C, F), which is comparable to pterostigma. The pterostigma is expanded veins or pigmented and sclerotized cuticle in a cell which is located at the anterior edge of the wing to concentrate weight and strength (Grimaldi and Engel, 2005). The concentrated mass and specialized location of pterostigma play a critical role during flight by increasing the limit of inertial pitch angle and speed at wing flapping (Norberg, 1972) or wing rotation (Ennos, 1988), or by helping control the wing vibration amplitude (Zhao et al., 2013; Song et al., 2020a). Pterostigmata are known to be present in Odonata, Zoraptera, Hymenoptera, Strepsiptera, Coleoptera, and some raphidiopterans, hemipterans and mecopterans (Kukalová-Peck, 1993). Although pterostigma is not known in extant orthopterans, its presence in the elcanids has been suggested in recent studies. Fang et al. (2018b) considered the coloured area between RA and the wing margin, filled with crossveins in *Cascadelcana virginiana* Fang et al., 2018 and *Panorpidium yixianensis* Fang et al., 2015 as pterostigma, while Kočárek (2020) reported the presence of a seemingly true pterostigma in *Elca nevelka* Kočárek, 2020 without crossvein in it. Fang et al. (2018b) and Kočárek (2020) further suggested that the presence of pterostigma structure in elcanids may have been related to a unique flight mechanism distinct from other extant orthopterans: e.g., Fang et al. (2018b) proposed a gliding mode for elcanid flight. The pterostigma-like structure of *Panorpidium spica* sp. nov. has numerous crossveins in it, which is similar to other elcanids except *Elca nevelka*. In overall, it is relatively longer and larger compared with the wing size than the pterostigmata in other insect orders, and thus must have acted as a large mass in the anterior margin. Colouration in the similar area of wing is commonly observed in the Elcanidae, and sometimes it is extended to distal part of the wing, as seen in *Panorpidium spica* sp. nov. (Zessin, 1987; Gorochoy et al., 2006; Fang et al., 2015; Tian et al., 2019a; Tian et al., 2019b). However, in the WDS carbon maps, the pterostigma-like structure can be distinguished from other extended areas by higher concentration of the element (Fig. 5C, F), which also supports that the structure was a genuine pterostigma.

4.3. Spurs in the metatibia

The well-preserved tibia of hind legs in *Panorpidium spica* sp. nov. reveals a leaf-like morphology of the spurs. The specialized spurs on metatibiae are the most distinctive feature of the Elcanidae; spurs of leaf-like, spine-like or paddle-like shapes have been documented (Sharov, 1968; Zessin, 1987; Ansoorge, 2003; Poinar et al., 2007; Peñalver and Grimaldi, 2010; Fang et al., 2015; Fang et al., 2018a; Tian et al., 2019a; Kočárek, 2020; Gu et al., 2020). Zeuner (1939) assumed that the spurs of elcanids were for swimming or preventing sinking in dry sand. For example, extant scizodactyloids have modified tarsi that secure a wide surface on the desert sand (Aydin and Khomutov, 2008; Channa and Sultana, 2013; Dawwrueng et al., 2018). However, this is not the case for

the elcanid spurs, since the spurs are located in subapical tibiae, not tarsi, and the depositional environments of the elcanids-occurring strata around the world are usually far from dry condition (e.g. Zhou et al., 2003; Paik et al., 2019; Yu et al., 2019). Kočárek (2020) proposed that elcanid spurs may have provided horizontal and vertical stabilization during flight by widely spread hind legs and had controlled the direction of flight with movable flattened structures, but other studies have supposed that given the flattened shape, elcanid spurs were related to swimming (Zeuner, 1939; Sharov, 1968; Gorochoy, 1995; Fang et al., 2015; Tian et al., 2019a; Schubnel et al., 2020).

Diving into water to escape from predators is not uncommon behavioral repertoire in the extant orthopterans (Dettner, 2019), and can be seen in tridactylids, tetrigoideans, grylloideans, and acridoideans, all of which have well-developed hind legs often ornamented with structures for swimming or evading aquatic predators (Franklin et al., 1977; Kim and Kim, 2010; Muhammad et al., 2018). Of them, tridactylids, the pygmy mole crickets, have

paddles (also referred to as natatory lamellae and spurs) on the distal part of metatibiae, which are comparable to the elcanid spurs in shape and position (Fig. 6). They usually live near water, such as pond, stream, and river, and when exposed to danger, they rapidly jump into the water (Burrows and Picker, 2010; Cao et al., 2020). After escaping from danger, they return to land by jumping repeatedly on the water using well-developed spurs and paddles on the hind legs, which become unfolded in order to increase the surface area (Fig. 6D), so that the hind legs can push the water more efficiently (Burrows and Sutton, 2012). The presence of well-developed hind legs with the semilunar process that is known to store energy for jumping (Burrows and Morris, 2001; Cofer et al., 2007) suggests that the elcanids were agile jumping insects. Thus, the relatively small bodies and the presence of dorsal spurs on the metatibiae in elcanids may have enabled them to jump at the water as tridactylids do, which must have been an effective way of escaping sudden danger from predators, such as small theropods. The depositional environment of the Jinju Formation is

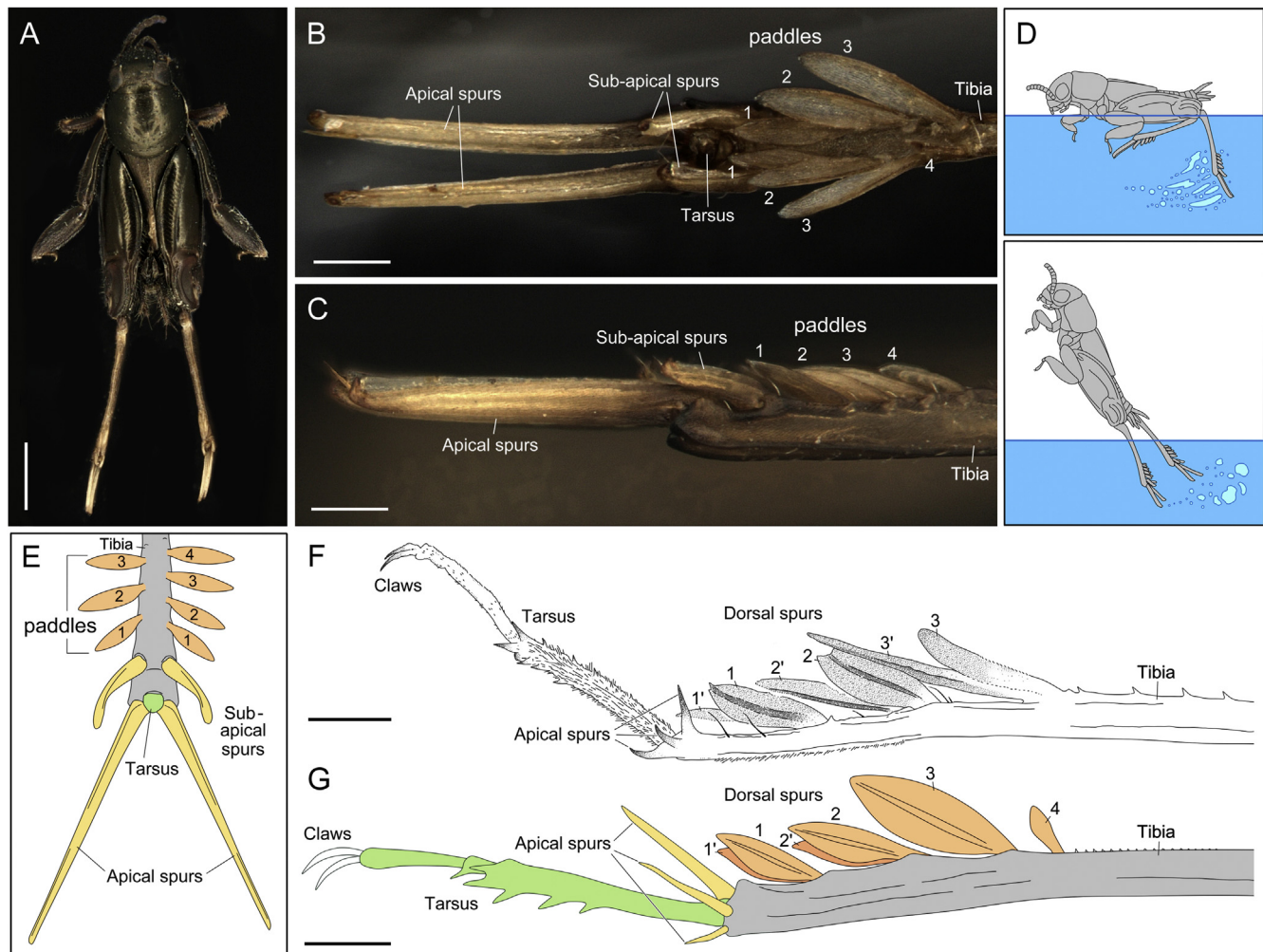


Fig. 6. Morphological comparison between the tridactylid metatibiae with paddles and the elcanid metatibiae with spurs. **A–E.** *Xya japonica* Haan, 1844 (pygmy mole cricket, collected from Guryong Falls, Jucheon-myeon, Namwon-si, Jeollabuk-do, Korea). **A–C.** Microscopic images, **A.** Dorsal view of the whole body, **B–C.** Distal part of the metathoracic leg, **B.** Dorsal view, **C.** Lateral view, **D.** Illustration of *X. japonica* jumping on water surface using paddles and spurs, drawn with reference to the jumping posture of *Xya capensis* Saussure, 1877 from Burrows and Sutton (2012), **E.** Interpretive drawing of the paddles and spurs of *X. japonica*. **F–G.** Interpretive drawings of the distal part of the elcanid metathoracic legs, **F.** Nymphal stage specimen of *Hispanelcana lopezvallei*, redrawn from Peñalver and Grimaldi (2010), **G.** Adult stage specimen (reconstruction of *Panorpidium spica* sp. nov.). Scale bars for A is 1 mm; B and C are 0.2 mm; F is 0.3 mm; G is 1 mm.



Fig. 7. Artistic reconstruction of *Panorpidium spica* sp. nov., escaping towards the water from a theropod predator (artwork by Do-Yoon Kim).

interpreted to be of large-scale lacustrine in a back-arc basin (Chough and Sohn, 2010), thus forming a suitable habitat for jumping into water as an escaping strategy (see Fig. 7).

With the exceptions of some subfamilies that are able to fly a long-distance (Uvarov, 1977; Ritchie and Pedgley 1989; Wang et al., 2014), most orthopterans repeat short-distance flights and jumps. The elcanids may also have been a short-distance flyer, so that once flew towards water, they periodically had to land on the water surface. Being equipped with the well-developed wings, they did not need to swim in the water. Rather, they would jump from the water surface right away. In many adult orthopterans, jumping is a way of launching into the air for a flight (Katz et al., 1993). In a similar sense, the spurs-assisted jumping of elcanids on the water surface must have led to launching of short-range flight.

The spurs on hind tibiae were also developed at nymphal stages of elcanids; they had leaf-like, spine-like or paddle-like shapes (Peñalver and Grimaldi, 2010; Heads et al., 2018). This indicates that spurs were already functional in the nymphal stages of elcanids (Fig. 6F). In fact, spurs must have been more useful for flightless nymphs than for the flyable adults. When attacked by predators, the flightless nymphs would jump into the water, and then repeatedly jumped or swam using metatibial spurs on water surface, eventually returning to the ground. Although they escaped from the land, water surface was not a safe haven. Fossils of several large aquatic predators are known from the Jinju Formation, such as aquatic insects, coptoclauids (Park et al., 2013) and fishes (Yabumoto and Yang, 2000; Yabumoto et al., 2006; Kim et al., 2014). Therefore, escaping to water from terrestrial predators would have been just a temporary safe strategy, so that the repeated jumping on the water surface would eventually led to landing on the ground. This behavior of flightless elcanid nymphs may have been more similar to the flightless tridactylids than the flyable elcanid adults.

There are elcanids with spine-like spurs which may have been less effective to generate a flow in water (Peñalver and Grimaldi, 2010; Kočárek, 2020). It can be inferred that they had different habitat, although it cannot be completely ruled out that, as some extant orthopterans do (Franklin et al., 1977; Brouwers and Newton 2010; Gutjahr and Souza Braga, 2018), they might have been able to swim with their spur-less hind legs. However, other possibility for the function of spurs cannot be ruled out, yet. For instance, the paddle-like spurs may have been helpful for jumping from sandy substrate, although such environments have not been inferred from the Jinju Formation. In addition, the possibility of the paddle-like spurs causing resistance during counter-moving can be also considered.

Within the Orthoptera, the presence of specialized spurs and paddles on subapical part of the metatibiae for swimming is present only in the extant tridactylids and the extinct elcanoideans. Those structures have morphological similarities in that the articulated structures of movable leaf-like shape are arranged into two rows on the dorsal side of metatibia. If the presence of such specialized spurs on metatibiae is phylogenetically meaningful, elcanoideans may have been phylogenetically close to tridactylids. Since the Tridactyloidea forms the most basal branch of the Caelifera (Song et al., 2015; Song et al., 2020b), the phylogenetic position of the Elcanoidea may have been also close to the basal position within the Orthoptera. However, the more basal group than elcanids, the Permian elcanids, did not develop spurs (Sharov, 1968), and such swimming paddles have not been observed from the Cretaceous tridactylid fossils (Heads, 2009; Poinar, 2018; Xu et al., 2020); the paddles are present in the Eocene fossil of France (Azar and Nel, 2008). Morphologically, paddles of the tridactylids are arranged asymmetrically, whereas the spurs of the elcanids are arranged symmetrically. The elcanid spurs possessed a strong rachis in the middle of leaf-shaped structure that is suitable for supporting in

the water, but it is not developed in the paddles of tridactylids. Therefore, for now, it is hard to find phylogenetic significance in the presence of specialized spurs and paddles on the metatibiae, and thus a formal phylogenetic analysis using more detailed morphological data is required for more accurate elucidation of the phylogenetic position of elcanoideans.

5. Conclusions

Panorpidium spica sp. nov. is described from the Lower Cretaceous (Albian) Jinju Formation, Korea. The Wavelength Dispersive Spectrometer (WDS) analyses have produced carbon elemental maps that are helpful in recognizing crucial features, such as pterostigma, forewing venations, and abdominal structures. The pterostigma in the wings suggest that elcanids had a unique mode of flight, distinct from extant orthopterans. The well-preserved dorsal spurs on the metatibiae are considered to have been used for jumping on the water surface, based on morphological comparison with the extant tridactylids (pygmy mole cricket). Jumping into the water must have been a useful way of escaping from the predators both for the flight-less nymphs and the short-range flying adults.

Acknowledgements

Comments on vertebrates in the illustration were provided by Minyoung Son (Seoul National University). This research was financially supported by Korea Polar Research Institute (KOPRI) project PE21060. Constructive suggestions from two anonymous reviewers and the editor significantly improved the earlier version of the manuscript.

References

- Ansorge, J., 2003. Insects from the lower Toarcian of middle Europe and England. *Acta Zoologica Cracoviensia* 46 (Suppl. L), 291–310.
- Aydin, G., Khomutov, A., 2008. The biology, nymphal stages, and life habits of the endemic sand dune cricket *Schizodactylus inexpectatus* (Werner, 1901) (Orthoptera: Schizodactylidae). *Turkish Journal of Zoology* 32 (4), 427–432.
- Azar, D., Nel, A., 2008. First Tridactylidae from the Eocene French amber (Insecta: Orthoptera). *Alavesia* 2, 169–175.
- Baek, K., Yang, S., 2004. Cockroaches from the Early Cretaceous of Korea (Blattaria: Mesolattinidae). *Journal of the Paleontological Society of Korea* 20, 71–98 (in Korean).
- Berggren, H., Tinnert, J., Forsman, A., 2012. Spatial sorting may explain evolutionary dynamics of wing polymorphism in pygmy grasshoppers. *Journal of Evolutionary Biology* 25 (10), 2126–2138.
- Béthoux, O., Nel, A., 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research* 10 (2), 195–198.
- Béthoux, O., Nel, A., 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. *Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov.* *Zootaxa* 96 (1), 1–88.
- Brouwers, N.C., Newton, A.C., 2010. The influence of barriers and orientation on the dispersal ability of wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae). *Journal of Insect Conservation* 14 (3), 313–317.
- Budd, G., 1993. A Cambrian gilled lobopod from Greenland. *Nature* 364 (6439), 709–711.
- Burrows, M., Morris, G., 2001. The kinematics and neural control of high-speed kicking movements in the locust. *Journal of Experimental Biology* 204 (Pt 20), 3471–3481.
- Burrows, M., Picker, M.D., 2010. Jumping mechanisms and performance of pygmy mole crickets (Orthoptera, Tridactylidae). *Journal of Experimental Biology* 213 (Pt 14), 2386–2398.
- Burrows, M., Sutton, G.P., 2012. Pygmy mole crickets jump from water. *Current Biology* 22 (23), R990–R991.
- Cao, C., Rong, H., Naveed, H., 2020. Two new species of the genus *Xya* Latreille, 1809 (Orthoptera, Tridactyloidea, Tridactylidae) from Yunnan with a key to all *Xya* species in China. *ZooKeys* 947, 103–112.
- Carpenter, F.M. (Ed.), 1992. *Treatise on Invertebrate Paleontology: Arthropoda 4. Superclass Hexapoda*. Geological Society of America.
- Channa, S.A., Sultana, R., 2013. Morphology and Burrowing Behaviour of Schizodactylus minor (Ander, 1938) (Grylloptera: Schizodactylidae: Orthoptera) of Pakistan. *Pakistan Journal of Zoology* 45 (5), 1191–1196.
- Choi, S., 1990. Some nonmarine fossils from the central part of Gyeongsang Basin, S. Korea. *Journal of the Paleontological Society of Korea* 6 (2), 165–179.
- Choi, B., Huh, M., 2016. *Mongolocypis kohi* sp. nov.: A new Early Cretaceous non-marine ostracod species from the Jinju Formation, South Korea. *Cretaceous Research* 57, 239–247.
- Choi, B., Wang, Y., Huh, M., 2018. Cypridea species (Crustacea, Ostracoda) from the Lower Cretaceous Jinju Formation of the Gyeongsang Basin, South Korea. *Palaeoworld* 27 (3), 382–391.
- Chough, S., Sohn, Y., 2010. Tectonic and sedimentary evolution of a Cretaceous continental arc-backarc system in the Korean peninsula: new view. *Earth-Science Reviews* 101 (3–4), 225–249.
- Cigliano, M., Braun, H., Eades, D., Otte, D., 2018. Orthoptera Species File. Version 5.0/5.0. <http://Orthoptera.SpeciesFile.org>. (Accessed 20 November 2020).
- Cofer, D.W., Reid, J., Zhu, Y., Cymbalyuk, G., Heitler, W.J., Edwards, D.H., 2007. Role of the semi-lunar process in locust jumping. *BMC Neuroscience* 8 (2), 1–2.
- Dawwrueng, P., Panitvong, N., Mooltham, K., Meebenjamart, P., Jaitrong, W., 2018. First record of the family Schizodactylidae (Orthoptera: Ensifera) from Thailand, with the description of a new species. *Zootaxa* 4472 (1), 60–70.
- Dettner, K., 2019. Defenses of water insects. In: Kleber, D.-C., Rhainer, G. (Eds.), *Aquatic Insects*. Springer, pp. 191–262.
- Engel, M.S., Lim, J., Baek, K., Martin, L.D., 2002. An earwig from the Lower Cretaceous of Korea (Dermaptera: Forficulina). *Journal of the Kansas Entomological Society* 75 (2), 86–90.
- Engel, M.S., Lim, J., Baek, K., 2006. Fossil snakeflies from the Early Cretaceous of southern Korea (Raphidioptera: Mesoraphidiidae). *Neues Jahrbuch für Geologie und Paläontologie-Monatshefte* Jg 2006 (4), 249–256.
- Ennos, A.R., 1988. The inertial cause of wing rotation in Diptera. *Journal of Experimental Biology* 140 (1), 161–169.
- Fang, Y., Wang, B., Zhang, H., Wang, H., Jarzembowski, E., Zheng, D., Zhang, Q., Li, S., Liu, Q., 2015. New Cretaceous Elcanidae from China and Myanmar (Insecta, Orthoptera). *Cretaceous Research* 52, 323–328.
- Fang, Y., Heads, S.W., Wang, H., Zhang, H., Wang, B., 2018a. The first Archelcaninae (Orthoptera, Elcanidae) from the Cretaceous Jehol Biota of Liaoning, China. *Cretaceous Research* 86, 129–134.
- Fang, Y., Muscente, A., Heads, S.W., Wang, B., Xiao, S., 2018b. The earliest Elcanidae (Insecta, Orthoptera) from the Upper Triassic of North America. *Journal of Paleontology* 92 (6), 1028–1034.
- Franklin, R., Jander, R., Ele, K., 1977. The coordination, mechanics and evolution of swimming by a grasshopper, *Melanoplus differentialis* (Orthoptera: Acrididae). *Journal of the Kansas Entomological Society* 50 (2), 189–199.
- Geinitz, F.E., 1880. Der Jura von Dobbartin in Mecklenburg und seine Versteinerungen. *Zeitschrift der Deutschen Geologischen Gesellschaft* Band 32 (3), 510–526.
- Germar, E.F., 1842. Beschreibung einiger neuen fossilen Insecten. In: Münster, G., Meyer, H.v. (Eds.), *Beiträge zur Petrefactenkunde*, 5. Münster's Beiträge zur Petrefactenkunde, pp. 79–89.
- Giebel, C.G., 1856. Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Bd. 2: Gliederthiere. Abt. 1: Insekten und Spinnen der Vorwelt, mit steter Berücksichtigung der lebenden Insekten und Spinnen, monographisch dargestellt. Leipzig: XVIII.
- Gorochov, A., 1995. System and evolution of the suborder Ensifera (Orthoptera). *Proceedings of the Zoological Institute, Russian Academy of Sciences* 260 (1), 3–224 (in Russian).
- Gorochov, A., Rasnitsyn, A., 2002. Superorder Gryllidea Laicharting, 1781 (= Orthopteroidea Handlirsch, 1903). *History of Insects* 293–303. Kluwer Academic Publisher, Dordrecht.
- Gorochov, A.V., Jarzembowski, E.A., Coram, R.A., 2006. Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England. *Cretaceous Research* 27 (5), 641–662.
- Grimaldi, D., Engel, M.S., Engel, M.S., Engel, M.S. (Eds.), 2005. *Evolution of the Insects*. Cambridge University Press.
- Gu, J.J., Tian, H., Wang, J., Zhang, W., Ren, D., Yue, Y., 2020. A world key to the genera of Elcanidae (Insecta, Orthoptera), with a Jurassic new genus and species of Archelcaninae from China. *ZooKeys* 954, 65–74.
- Gutjahr, A.L.N., de Souza Braga, C.E., 2018. Order Orthoptera. In: Hamada, N., Thorp, J.H., Rogers, D.C. (Eds.), *Thorp and Covich's Freshwater Invertebrates*. Elsevier, pp. 143–168.
- Haan, W. de, 1844. Bijdragen tot de kennis der Orthoptera. In: Temminck (Ed.), *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche Overzeesche Bezittingen*, vol. 2, pp. 45–248.
- Handlirsch, A. (Ed.), 1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen*. Engelmann, V.W. Publishing, Leipzig.
- Handlirsch, A., 1939. *Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. II. Teil. Annalen des naturhistorischen Museums in Wien*, 1–240.
- Heads, S.W., 2009. A new pygmy mole cricket in cretaceous amber from Burma (Orthoptera: Tridactylidae). *Denisia* 26, 75–82 (2, April 2009).
- Heads, S.W., Thomas, M.J., Wang, Y., 2018. A new genus and species of Elcanidae (Insecta: Orthoptera) from Cretaceous Burmese amber. *Zootaxa* 4527 (4), 575–580.
- Katz, S.L., Gosline, J.M., 1993. Ontogenetic scaling of jump performance in the African desert locust (*Schistocerca gregaria*). *Journal of Experimental Biology* 177 (1), 81–111.

- Kelly, C.D., Bussiere, L.F., Gwynne, D.T., 2008. Sexual selection for male mobility in a giant insect with female-biased size dimorphism. *The American Naturalist* 172 (3), 417–423.
- Khranov, A.V., Nam, G., Vasilenko, D.V., 2020. First long-proboscid flies (Diptera: Zhangsolvidae) from the Lower Cretaceous of South Korea. *Alcheringa: An Australasian Journal of Palaeontology* 44 (1), 160–168.
- Kim, T., Kim, J., 2010. A taxonomic review of the marine littoral genus *Caconemobius* (Orthoptera: Gryllidae: Nemobiinae) in Korea. *Animal Systematics, Evolution and Diversity* 26 (1), 29–33.
- Kim, J.Y., Lockley, M., 2016. First report of turtle tracks from the Lower Cretaceous of Korea. *Cretaceous Research* 64, 1–6.
- Kim, J.Y., Lockley, M.G., Seo, S.J., Kim, K.S., Kim, S.H., Baek, K.S., 2012a. A paradise of Mesozoic birds: the world's richest and most diverse Cretaceous bird track assemblage from the Early Cretaceous Haman Formation of the Gajin tracksite, Jinju, Korea. *Ichnos* 19 (1–2), 28–42.
- Kim, J.Y., Lockley, M.G., Woo, J.D., Kim, S.H., 2012b. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of *Dromaeosauripus*. *Ichnos* 19 (1–2), 75–83.
- Kim, H., Chang, M., Wu, F., Kim, Y., 2014. A new ichthyodectiform (Pisces, Teleostei) from the Lower Cretaceous of South Korea and its paleobiogeographic implication. *Cretaceous Research* 47, 117–130.
- Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Choi, Y., 2017a. Korean trackway of a hopping, mammaliform trackmaker is first from the Cretaceous of Asia. *Cretaceous Research* 74, 188–191.
- Kim, K.S., Lockley, M.G., Lim, J.D., Pinuela, L., Xing, L., Moon, H.W., 2017b. First report of lacertiform (lizard) tracks from the Cretaceous of Asia. *Cretaceous Research* 69, 62–70.
- Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Ha, S.J., Kim, C.B., Paik, I.S., Ahn, J.H., Mun, S.C., 2018a. First reports of a distinctive theropod track assemblage from the Jinju Formation (Lower Cretaceous) of Korea provides strong correlations with China. *Cretaceous Research* 81, 26–35.
- Kim, K.S., Lim, J.D., Lockley, M.G., Xing, L., Kim, D.H., Piñuela, L., Romilio, A., Yoo, J.S., Kim, J.H., Ahn, J., 2018b. Smallest known raptor tracks suggest microraptorine activity in lakeshore setting. *Scientific Reports* 8 (1), 1–10.
- Kim, K.S., Lockley, M.G., Lim, J.D., Kim, D.H., 2019. The oldest known anuran (frog) trackways from the Jinju Formation, Lower Cretaceous, Korea. *Cretaceous Research* 96, 142–148.
- Kočárek, P., 2020. A diminutive elcanid from mid-Cretaceous Burmese amber, *Elcca nevelka* gen. et sp. nov., and the function of metatibial spurs in Elcanidae (Orthoptera). *Cretaceous Research* 116, 104574.
- Kukulová-Peck, J., 1991. Fossil history and evolution of hexapod structures. *The Insects of Australia* 1, 141–179.
- Kukulová-Peck, J., Lawrence, J.F., 1993. Evolution of the hind wing in Coleoptera. *The Canadian Entomologist* 125 (2), 181–258.
- Lee, T., Park, K., Yi, K., 2018. Nature and evolution of the Cretaceous basins in the eastern margin of Eurasia: A case study of the Gyeongsang Basin, SE Korea. *Journal of Asian Earth Sciences* 166, 19–31.
- Lockley, M.G., Lim, J., Kim, J.Y., Kim, K.S., Huh, M., Hwang, K., 2012. Tracking Korea's early birds: a review of Cretaceous avian ichnology and its implications for evolution and behavior. *Ichnos* 19 (1–2), 17–27.
- Martins Neto, R.G., 1991. Sistemática dos Ensífera insecta.(Orthopteroida) da Formação Santana (Cretáceo inferior do nordeste do Brasil) (Unpubl. Master's thesis). Instituto de Geociências, p. 304 (in Portuguese with English abstract).
- An annotated catalogue of the pygmy grasshoppers of the tribe Scelimenini Bolívar, 1887 (Orthoptera: Tetrigidae) with two new Scelimenia species from the Malay Peninsula and Sumatra. In: Muhammad, A.A., Tan, M.K., Ashikin, A.N., Azirun, M.S., Bhaskar, D., Skejo, J. (Eds.), *Zootaxa* 4485. Magnolia Press.
- Nam, K., Kim, J., 2016. Reconstruction and Paleoecological implications of Dragonfly *Hemeroscopus baissicus* Pritykina, 1977 (Hemeroscopidae) from the Lower Cretaceous Jinju Formation in the Jinju Area, Korea. *Journal of the Geological Society of Korea* 52 (2), 105–112 (in Korean with English abstract).
- Norberg, R.A., 1972. The pterostigma of insect wings an inertial regulator of wing pitch. *Journal of Comparative Physiology* 81 (1), 9–22.
- Olivier, A., 1789. *Encyclopédie méthodique, dictionnaire des insectes*, vol. 4. Pan-kouke, Paris vol. 373.
- Paik, K., Kim, Y., Huh, M., 1988. Ostracodes from the Chinju formation (Cretaceous, Non-marine) in Kyongsang Basin, Korea. *Journal of the Paleontological Society of Korea* 4 (2), 94–109.
- Paik, I., Kim, J., Kim, S., Lee, J., So, Y., Lee, H., 2019. Fossil-bearing deposits in the Jinju Formation at Jinju: Occurrences, paleoenvironments and stratigraphic implications. *Journal of the Geological Society of Korea* 55 (5), 513–530 (in Korean with English abstract).
- Park, S., Chang, K., 1998. Some Cretaceous conchostracans of Kyongsang Basin. *Journal of the Paleontological Society of Korea* 14 (2), 179–199.
- Park, T.-Y., Wilson, G.D., Lee, D., Choi, D.K., 2012. Occurrence of the Isopod *Archaeoniscus coreansis* New Species from the Lower Cretaceous Jinju Formation, Korea. *Journal of Paleontology* 86 (4), 626–640.
- Park, T.-Y.S., Kihm, J.-H., Woo, J., Park, C., Lee, W.Y., Smith, P., Harper, D.A.T., Young, F., Nielsen, A.T., Vinther, J., 2018. Brain and eyes of *Kerygmachela* reveal proto-cerebral ancestry of the panarthropod head. *Nature Communications* 9, 1–7.
- Park, T.-Y.S., Kim, Y., Nam, K., 2013. Preliminary research on the aquatic coleopteran, *Coptoclava* from the Early Cretaceous Jinju Formation. *Journal of the Geological Society of Korea* 49 (6), 617–624 (in Korean with English abstract).
- Park, T.-Y.S., Nam, K., Selden, P.A., 2019. A diverse new spider (Araneae) fauna from the Jinju Formation, Cretaceous (Albian) of Korea. *Journal of Systematic Palaeontology* 17 (15), 1271–1297.
- Latest occurrences of the Mesozoic family Elcanidae (Insecta: Orthoptera), in Cretaceous amber from Myanmar and Spain. In: Peñalver, E., Grimaldi, D.A. (Eds.), *Annales de la Société entomologique de France*. Taylor & Francis.
- Picaud, F., Petit, D., 2008. Body size, sexual dimorphism and ecological succession in grasshoppers. *Journal of Orthoptera Research* 17 (2), 177–181.
- Poinar, G., 2018. Pygmy mole crickets (Orthoptera: Tridactylidae) in Dominican and Burmese amber. *Historical Biology* 32 (2), 238–243.
- Poinar, G., Gorochov, A.V., Buckley, R., 2007. *Longiculus burmensis*, n. gen., n. sp. (Orthoptera: Elcanidae) in Burmese amber. *Proceedings of the Entomological Society of Washington* 109 (3), 649–655.
- Poniatowski, D., Fartmann, T., 2009. Experimental evidence for density-determined wing dimorphism in two bush-crickets (Ensifera: Tettigoniidae). *European Journal of Entomology* 106 (4), 599–605.
- Ritchie, M., Pedgley, D., 1989. Desert locusts cross the Atlantic. *Antenna* 13 (1), 10–12.
- de Saussure, H., 1877. *Mélanges Orthoptérologiques*, Vme fasc. Gryllides. *Memoires de la Société Physique d'Histoire Naturelle de Geneve* 25, 1–352.
- Schubnel, T., Desutter-Grandcolas, L., Garrouste, R., Hervet, S., Nel, A., 2020. Paleocene of Menat Formation, France, reveals an extraordinary diversity of orthopterans and the last known survivor of a Mesozoic Elcanidae. *Acta Palaeontologica Polonica* 65 (2), 371–385.
- Selden, P.A., Nam, K., Kim, S.H., Kim, H.J., 2012. A Fossil Spider from the Cretaceous of Korea. *Journal of Paleontology* 86 (1), 1–6.
- Song, H., Amédégnato, C., Cigliano, M.M., Desutter-Grandcolas, L., Heads, S.W., Huang, Y., Otte, D., Whiting, M.F., 2015. 300 million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics* 31 (6), 621–651.
- Sharov, A.G., 1968. Phylogeny of the Orthopteroid insects. *Akademiya Nauk SSSR Trudy Paleontologicheskogo Instituta* 118, 1–217.
- Sohn, J., Nam, G.S., Choi, S., Ren, D., 2019. New fossils of Elateridae (Insecta, Coleoptera) from Early Cretaceous Jinju Formation (South Korea) with their implications to evolutionary diversity of extinct Protagrypninae. *PloS One* 14 (12), e0225502.
- Song, Z., Tong, J., Yan, Y., Sun, J., 2020a. Effects of pterostigma structure on vibrational characteristics during flight of Asian ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae)". *Scientific Reports* 10 (1), 1–11.
- Song, H., Béthoux, O., Shin, S., Donath, A., Letsch, H., Liu, S., McKenna, D.D., Meng, G., Misof, B., Podsiadlowski, L., 2020b. Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nature Communications* 11 (1), 1–16.
- Stevens, M., Ruxton, G.D., 2019. The key role of behaviour in animal camouflage. *Biological Reviews* 94 (1), 116–134.
- Storozhenko, S.Y., Jeon, M., Kim, T. (Eds.), 2015. *Monograph of Korean Orthoptera*. National Institute of Biological Resources.
- Tian, H., Gu, J., Huang, F., Zhang, H., Ren, D., 2019a. A new species of Elcaninae (Orthoptera, Elcanidae) from the Lower Cretaceous Yixian Formation at Liutiaogou, Inner Mongolia, NE China, and its morphological implications. *Cretaceous Research* 99, 275–280.
- Tian, H., Gu, J., Yin, X.C., Ren, D., 2019b. The first Elcanidae (Orthoptera, Elcanoidea) from the Daohugou fossil bed of northeastern China. *ZooKeys* 897, 19–28.
- Tillyard, R.J., 1937. Kansas Permian insects; Part 17. The order Megaseoptera and additions to the Palaeodictyoptera, Odonata, Protoperlaria, Copeognatha, and Neuroptera. *American Journal of Science* 194, 81–110.
- Uvarov, B. (Ed.), 1977. *Grasshoppers and locusts. A handbook of general acridology* Vol. 2. Behaviour, ecology, biogeography, population dynamics. Centre for Overseas Pest Research.
- Wang, X., Fang, X., Yang, P., Jiang, X., Jiang, F., Zhao, D., Li, B., Cui, F., Wei, J., Ma, C., 2014. The locust genome provides insight into swarm formation and long-distance flight. *Nature Communications* 5, 2957.
- Westwood, J.O., 1854. Contributions to fossil entomology. *Quarterly Journal of the Geological Society* 10 (1–2), 378–396.
- Xu, C., Fang, Y., Jarzembowski, E.A., 2020. A new pygmy mole cricket (Orthoptera: Tridactylidae: Tridactylidae) from mid-Cretaceous Burmese amber. *Cretaceous Research* 111, 104371.
- Yabumoto, Y., Yang, S., 2000. The first record of the Early Cretaceous freshwater fish, *Wakinoichthys aokii*, from Korea. *Bulletin of the Kitakyushu Museum of Natural History* 19, 105–110.
- Yabumoto, Y., Yang, S., Kim, T., 2006. Early Cretaceous freshwater fishes from Japan and Korea. *Journal of the Paleontological Society of Korea* 22 (1), 119–132.
- Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences* 116 (23), 11345–11350.
- Yun, C., Baek, K., Jeong, Y., 2007. Cretaceous reptilian teeth from the Gyeongsang Basin. *Journal of the Paleontological Society of Korea* 23 (1), 27–47 (in Korean with English abstract).

- Zessin, W., 1987. Variabilität, Merkmalswandel und Phylogenie der Elcanidae im Jungpaläozoikum und Mesozoikum und die Phylogenie der Ensifera (Orthopteroidea, Ensifera). *Deutsche Entomologische Zeitschrift* 34 (1-3), 1–76 (in German with English abstract).
- Zeuner, F.E., 1939. Fossil Orthoptera Ensifera. British Museum (Natural History). British Museum Natural History, London.
- Zhao, H., Yin, Y., Zhong, Z., 2013. Arnold circulation and multi-optimal dynamic controlling mechanisms in dragonfly wings. *Acta Mechanica Solida Sinica* 26 (3), 237–244.
- Zhou, Z., Barrett, P.M., Hilton, J., 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421 (6925), 807–814.