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Short communication

A new species of Elcaninae (Orthoptera, Elcanidae) from the Lower Cretaceous Yixian Formation at Liutiaogou, Inner Mongolia, NE China, and its morphological implications

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ABSTRACT

Two adult females of Elcanidae (Orthoptera: Elcanoidea) from the Lower Cretaceous Yixian Formation of China are described as a new species, *Probaisselcana euryptera* sp. nov. The new materials have both wings and body structures well preserved. The new species differs from all other Elcaninae species in forewing venation and body features. The new specimens provide more morphological information of body structures of elcanids. The function of their flattened metatibial spurs is discussed.

1. Introduction

Elcanid-form insects constitute an extinct and special group in the Orthoptera which was traditionally assigned into two families, Permelcanidae and Elcanidae (Grimaldi and Engel, 2005). These insects share the long, filiform antennae and exerted ovipositors with ensiferans (Sharov, 1968; Poinar et al., 2007; Peñalver and Grimaldi, 2010), but also have similar forewing venation with caeliferans (Béthoux and Nel, 2002). However, due to their rare and fragmented fossil record, the systematic position of this group remains a subject of debate. They have been considered to be a clade close to all other orthopterans (Gorochov and Rasnitsyn, 2002), or attributed to the Ensifera (Kukalová-Peck, 1991; Gorochov, 1995; Gorochov et al., 2006), or the Elcanidae resloved as a sister group of caeliferan in a cladistic analysis by Béthoux and Nel (2002). Obviously, more discoveries with fine structures preserved are helpful to clarifying the phylogenetic relationship of this group.

Until now, Elcanidae have been reported to contain more than forty species from the Upper Triassic to the Cretaceous in Europe, Asia, North and South America (Handlirsch, 1906; Sharov, 1968; Martins-Neto, 1991; Gorochov et al., 2006; Poinar et al., 2007; Peñalver and Grimaldi, 2010; Fang et al., 2015; Fang et al., 2018a, b). These species fall into 13 genera and two subfamilies, Archelcaninae and Elcaninae, after the revision by Gorochov et al. (2006). In China, abundant orthopterans (mainly belonging to the Hagloidea) have been reported from the famous Jehol Biota, especially Yixian Formation (Hong, 1982; Zhang, 1993; Meng and Ren, 2006; Gu et al., 2010; Wang et al., 2013), but only two species, *Panorpidium yixianensis* Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Li and Liu, 2015 (attributed to Elcaninae) and *Jeholelcana yanensis* Fang, Heads, Wang, Zhang and Wang, 2018 (attributed to Archelcaninae), have been described from Yixian Formation (Fang et al., 2015; Fang et al., 2018a). Unfortunately, these records lack well-preserved body structures, such as head, abdomen and ovipositor. Here, we described a new species of *Probaissclcana* Gorochov, 1989 based on two female specimens. These new materials, with fine body structures preserved, improve our knowledge of the Cretaceous elcanids.

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2. Materials and methods

The two specimens described in this contribution were collected from the Lower Cretaceous of Yixian Formation at Liutiaogou Village, Ningcheng County, Chifeng City, Inner Mongolia (Liu and Huang, 2019: fig. 2). The fossils are preserved in yellow silty shale (Wang et al., 2012). The age is approximately 129.7–122.1 Ma (Barremian to early Aptian) (Chang et al., 2009; Yan et al., 2012; Ren et al., 2010, 2019).

The specimens were examined with a Nikon SMZ 25 microscope, and photographed with a Nikon DS-Ri 2 digital camera system. Line drawings were prepared by using Adobe Illustrator CC and Adobe Photoshop CC graphics software. The specimens are deposited in the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University (CNU), Beijing, China.

Wing venation followed the interpretation proposed by Béthoux & Nel (2001, 2002). Corresponding abbreviations are: CP, posterior costa; ScA, ScP, anterior, posterior subcosta; RA, RP, anterior, posterior radius; MA, MP, anterior, posterior media; CuA, CuP, anterior, posterior cubitus; CuPaα, the anterior branch of first posterior cubitus; CuPaβ, the posterior branch of first posterior cubitus; CuPb, the second posterior cubitus; AA1, anterior anal vein. Meanwhile, the metatibia morphology follows Fang et al. (2018a), ds, dorsal subapical spur; asp, apical spur.

3. Systematic palaeontology

Order Orthoptera Olivier, 1789
Family Elcanidae Handlirsch, (1906)
Subfamily Elcaninae Handlirsch, (1906)

Genus ***Probaisselcana*** Gorochov, 1989
Type species: *Probaisselcana karatavica* (Sharov, 1968)

Emended diagnosis. Forewing medium or large size, ScA with relatively few branches, two longitudinal branches between basal part of RP and CuA+CuPaα, area between MP and posterior wing margin narrow and relatively short, divided by short crossveins, CuPaβ, CuPb, and AA1 fused with each other distally, anal area filled with regular or irregular reticulated veins.
Included species. Probaisselcana karatavica (Sharov, 1968) (Upper Jurassic, Kazakhstan) and *P. cretacea* Gorochov, Jarzembowski & Coram, 2006 (Lower Cretaceous, East Sussex, England).

Probaisselcana euryptera sp. nov. Tian, Gu and Ren
(Figs. 1–3)

Materials. Holotype, female, CNU-ORT-NL2011035 (Figs. 1, 2).
Paratype, female, CNU-ORT-NL2016048PC (Fig. 3).
Etymology. From the Latin "eury-" for wide and "-pterus" for alary spurs, refers to its long and wide leaf-like spurs on metatibia.
Horizon and locality—Both of the specimens are collected from the Yixian Formation, Lower Cretaceous (Barremian–lower Aptian),

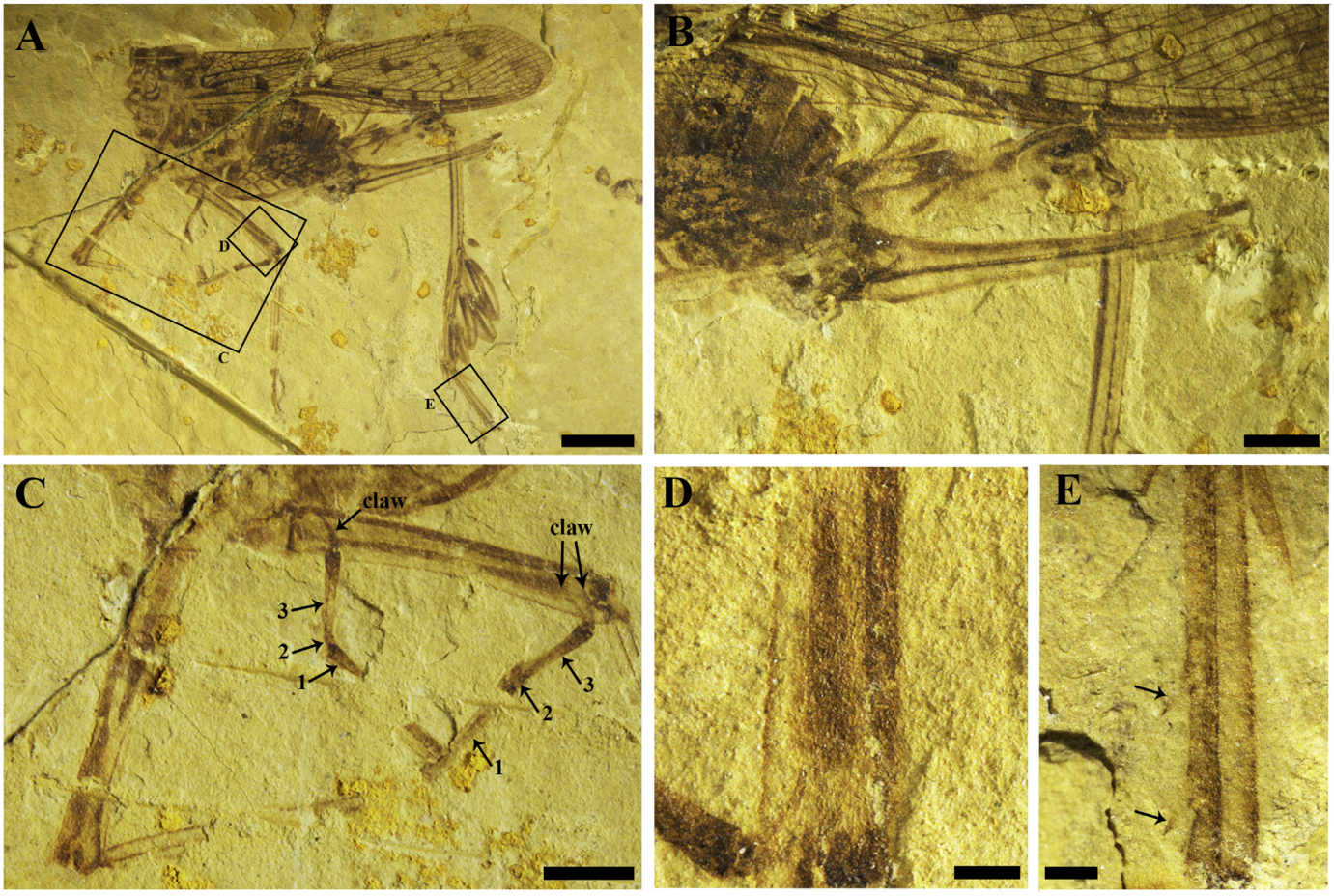

Fig. 1. *Probaisselcana euryptera* sp. nov., holotype, CNU-ORT-NL2011035. A. Photo of habitus, B. Photo of ovipositor, C. Details of fore legs, D. dense and short setae on distal part of profemur, E. spines on distal part of metabasitarsus. Scale bar for A = 5 mm; B and C = 2 mm; D and E = 0.5 mm.

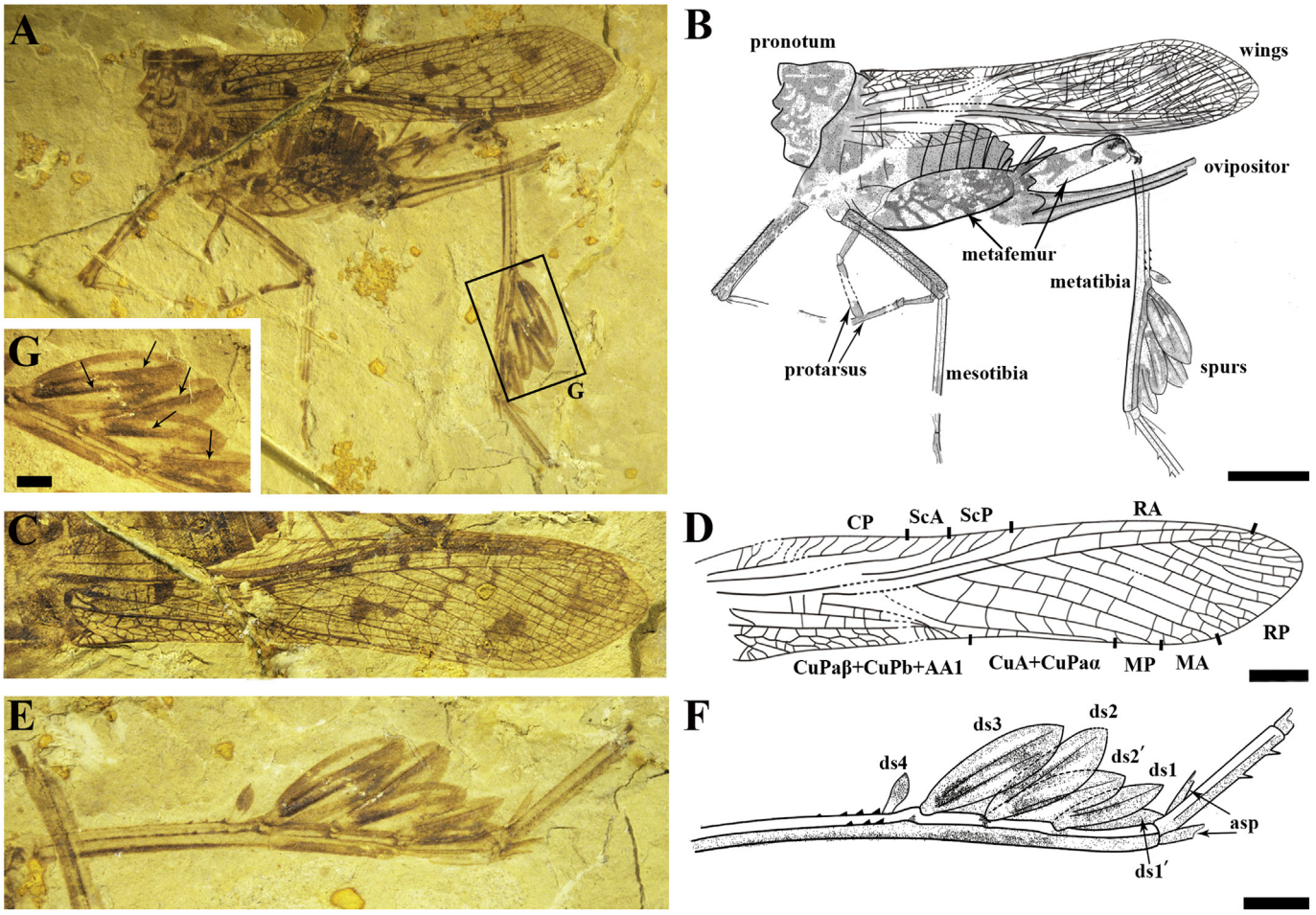

Fig. 2. Photo and drawings of the holotype, CNU-ORT-NL2011035. A and B. Photo and drawing of habitus, C and D. Photo of wings and interpretive drawing of forewing, E and F. Photo and drawing of metatibia, G. Photo of leaf-like spurs with rachises (arrows indicated) in middle part, ds3 and ds3′ strongly overlapped leading to one of them being all but invisible except for the rachis. Scale bar for A and B = 5 mm; C and D = 2 mm; E and F = 2 mm; G = 1 mm.

Liutiaogou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Diagnosis. Forewing large size with relatively few branches of ScA, R branched into RA and RP at about mid-length of wing, RP with numerous comb-like branches, MP simple, anal area with irregularly reticulate veins.

General Description. Two well-preserved females, the body medium size, total estimated length at least 20 mm (from head to the end of abdomen without cercus).

Head. Head preserved poorly, hypognathous, visible part (probably vertex) with a light band.

Thorax. Pronotum saddle-shaped, not prolongated. Prothorax and mesothorax legs long and slender, femur with setulae preserved, protarsus with 3 tarsomeres, basitarsomere longest, second tarsomere very small, distalmost tarsomere long but shorter than basitarsomere; metacoxa subtriangular, metafemur much strong, outer surface of it with regular network stripes and inner surface with irregular dark spots; hind knee robust, longitudinally laminated semi-lunar processes on upper side; metatibia long and slender, dorsum with two rows of tiny spines in basal half and one small and three pairs of big leaf-like spurs in distal half; leaf-like spurs thickened and with a rachis in the middle part, then gradually thinned to the margin.

Abdomen. Abdomen short. Ovipositor elongated and sharply pointed, its length twice as long as pronotum; upper and lower vavulae almost of similar size, the surface of the upper vavulae smooth, base of the lower vavulae truncated. Cerci conical, slender and unsegmented.

Wings. Forewing size large, 20.5–22.5 mm long and 4.1–4.6 mm wide (the Maximum width). Costa area relatively broad; CP long, reaching anterior margin at 1/3rd of total wing length, with numerous branchlets; ScA with several short branches basally connecting with CP and 2 or 3 branches distally reaching anterior margin; area between ScA and CP narrower than that of anterior and CP; ScP ending in anterior margin close to the middle-length of forewing, giving off 4 or 5 distinct oblique branches reaching anterior margin; stem of R long and strong, forked into RA and RP near to the terminal point of ScP; area between R and ScP much narrow; RA ending in anterior margin close to apex and producing numerous oblique branches; RP with 10 or 11 comb-like branches, most of them reaching posterior margin, several distal terminals reaching anterior margin; most cross-veins between the branches of RP simple and straight, some cross-veins between distal terminals formed into network; area between RA and RP narrow; MA forking into MA1 and MA2 near to the ending point of ScA; MP simple, originates before ScA ending in anterior margin, MP reaching posterior margin at about 2/3 distal of forewing base; CuA+CuPaα simple, ending in posterior margin distal of the mid-length of wing; CuPaβ, CuPb and AA1 fused with each other at about 1/3rd of wing length; area between AA1 and posterior

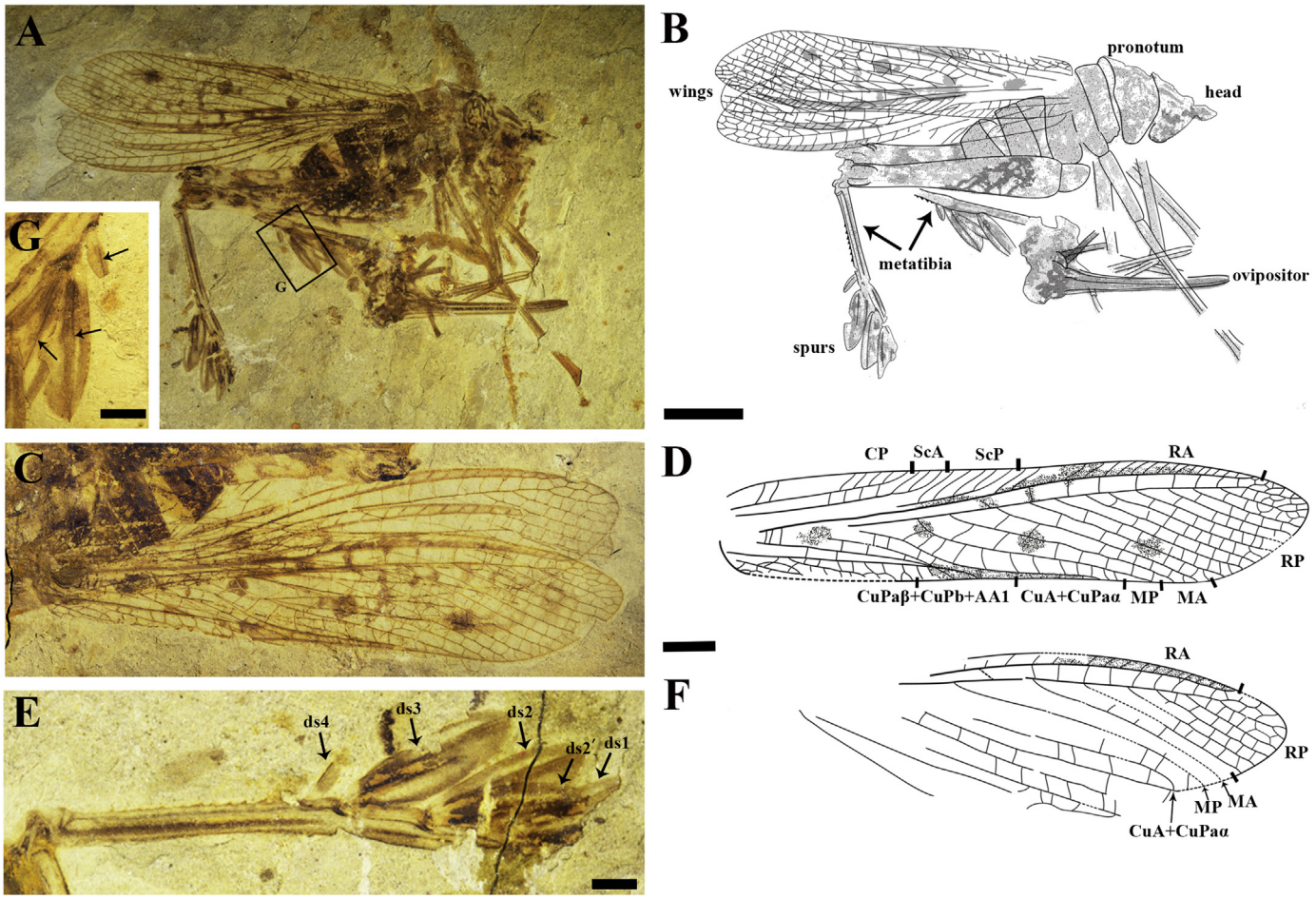

Fig. 3. *P. euryptera* sp. nov., paratype, CNU-ORT-NL2016048P. A and B. Photo and drawing of paratype, C and D. Photo of wings and interpretive drawing of forewing, E. Photo of metatibia, F. Interpretive drawing of hindwing, G. Photo of leaf-like spurs with rachises (arrows indicated). Scale bar for A and B = 5 mm; C, D and F = 2 mm; E and G = 1 mm.

margin filled with irregularly reticulate veins. Area between ScP and R and that of RA and anterior margin are colored, three round dark spots located at the area of RP branches and one spot located at the divergence point of CuP.

Specimen CNU-ORT-NL2011035 (Figs. 1 and 2)

The holotype, nearly complete but without head, four wings strongly overlapped, sterna overlapped by metafemur. Pronotum about 4.8 mm long, reaching distally first abdominal segment. Prothoracic leg: profemur 7.9 mm long and 0.9 mm wide, protibial fragmental and >6.3 mm long, both protarsus preserved, relative length of segments about 10:1:6.7. Mesothoracic leg: mesofemur 7.5 mm long and 0.9 mm wide, mesotibia ≥8.2 mm long and 0.6 mm wide. Metathoracic leg: left metafemur >7.9 mm long and 3.1 mm wide at thickest section, right metafemur preserved distal half part, 7.0 mm long, right metatibia 15.6 mm long and 0.8 mm wide, ds1 3.5 mm long and 0.9 mm wide, ds2 4.1 mm long and 1.6 mm wide, ds3 4.2 mm long and 1.6 mm wide, ds4 1.4 mm long and 0.5 mm wide, two apical spur saved, the left one >1.3 mm long and right one >1.7 mm, metabasitarsus saved 4.9 mm long, with two distal spines. Abdomen preserved 7.1 mm long (not including cerci); seven terga of abdomen visible; cerci ca. 2.8 mm long. Ovipositor 11.1 mm long and nearly straight in profile. Forewing 20.5 mm long and 4.1 mm wide (the Maximum width), CP, ScA and ScP separately preserved 10, 2 and 4 branches, RA with 6 short and oblique branches visible, RP with 10 pectinate branches, distal branches of RP are dichotomous, CuP forking into CuPa and CuPb basally, and almost at same level that CuPa forking into CuPaα and CuPaβ, then the short CuPaα fused with M+CuA immediately.

Specimen CNU-ORT-NL2016048 (Fig. 3)

The paratype, very well preserved. Head incomplete, preserved portion 3.6 mm long. Pronotum >4.8 mm long. Prothoracic leg: both fragmented, left profemur >5.8 mm long and 0.8 mm wide, right profemur >6.6 mm long, left protibial >5.5 mm long and right protibial preserved 2.2 mm long. Mesothoracic leg: left mesofemur >6.0 mm long and 0.8 mm wide, right mesofemur 6.6 mm long and 1.0 mm wide, mesotibia ≥8.2 mm long and 0.6 mm wide. Metathoracic leg: left metafemur >9.0 mm long, right metafemur 13.1 mm long and 2.5 mm wide at the maximum width, left metatibia saved 7.6 mm long, ds2 3.6 mm long and 1.2 mm wide, ds2' 3.5 mm long and 1.1 mm wide, ds4 1.3 mm long and 0.5 mm wide, the right metatibia >11.5 mm long, ds1 incomplete, 3.3 mm long, ds2 3.8 mm long and 1.0 mm wide, ds3 4.2 mm long and 1.2 mm wide, ds4 1.1 mm long and 0.5 mm wide. Ovipositor broken, 10.3 mm long. Cerci >2.6 mm long. Forewing 22.5 mm long and 4.6 mm wide (the Maximum width), CP with 7 branches visible, ScA with 4 short branches ending in CP and 3 branches ending in anterior margin, ScP with 5 branches ending in anterior margin. RA with 17 short and oblique branches visible, RP with 11 pectinate branches. Color spots present between RA and anterior margin, and between CuA+CuPaα and posterior margin, also four small dark

spots along crossveins between branches of RP, M and CuPa. Hindwing incomplete and strongly overlapped, basal part obscure, recognizable part preserved 18.6 mm long and 6.3 mm wide; venation similar to that of forewing, RA with at least 17 branches ending in anterior margin; RP with 6 comb-like branches; MA and MP simple and long; CuA+CuPaα straight, curved backward to the posterior at its terminal; other branches of CuP and anal veins are confounded because of fold and overlapped.

4. Discussion

This new species can be assigned to Elcaninae by its relatively narrow area between RA and RP, and CuPaβ, CuPb, and AA1 fused with each other. It falls in *Probaisselcana* Gorochov, 1989 because of the following characters: few branched ScA; two longitudinal branches between basal part of RP and CuA+CuPaα; area between MP and posterior wing margin narrow and short, which divided by short crossveins (potential synapomorphy) and CuPaβ, CuPb, and AA1 fused with each other distally (Figs. 2D, 3D). It differs from *P. karatavica* (Sharov, 1968) in its greater number of branches of RP, wider area between CuPb and AA1 and anal region. It can be distinguished from *P. cretacea* Gorochov, Jarzembowski and Coram, 2006 in its larger size, narrower area between RP and RA, more branches of RP, simple MP and different coloration of forewing (four small dark spots along crossveins between branches of RP, M and CuPa).

Hitherto, the Elcaninae included 14 species in 5 genera, with most of these species documented only by forewings (Sharov, 1968; Gorochov, 1986; Martins-Neto, 1991; Gorochov et al., 2006; Fang et al., 2015). But, finely preserved adult fossil records are very rare. The materials of *P. euryptera* sp. nov. provide a suite of new information on the morphology (Figs 1 and 2A, 3A). The fore-legs have three-segment protarsus with longer basi- and disti-tarsomeres and much smaller second tarsomere as well as simple claws without an arolium. It resembles a nymph in amber (Peñalver and Grimaldi, 2010) and some adults in compression fossils (Martins-Neto, 1991; Fang et al., 2015). Meanwhile, the strong sword-shaped ovipositor resembles that of *Cratoelcana zessini* (Martins-Neto, 1991) and some members of Archelcaninae (Zessin, 1987). This kind of elongated and sharply pointed ovipositor can be found in many extant ensiferans, which indicates that *P. euryptera* might have laid their eggs in the moist soil or loose barks.

The metatibial spurs of elcanids can be readily distinguished from all other orthopterans. From the fossil record of the Jurassic and the Cretaceous, 46 species in 12 genera of Elcanidae has been discovered from Asia, Europe and South America. The spurs are varied, with leaf-like, spine-like or paddle-like shapes, indicating a rapid morphological differentiation of this structure. Handlirsch (1925) considered these flattened (leaf-like and paddle-like) spurs as an adaptation to function as oars. Zeuner (1939) considered the spurs related to swimming or preventing the insects from sinking in dry sand. Logically, we can exclude the possibility of the latter conjecture because of the humid environment of Jehol Biota, and other localities which yielded plenty of elcanids (Ansorge, 2003; Zhou et al., 2003; Dera et al., 2011; Tramoy et al., 2016). Moreover, the ensiferans which live in sandy environments avoid sinking in sand with their specially modified tarsi, like schizodactyloid species (Aydin and Khomutov, 2008; Dawwrueng et al., 2018). Even some orthopteran species without modified structures on their legs can swim when they escape from danger or enemies (Robert Franklin and Karen, 1977; Lockwood and Schell, 1994; Gardiner, 2009). It is reasonable to assume that the spurs of elcanids are related to swimming because of their flattened shape. Their flattened spurs are morphologically similar to some extant tridactylids, which have moveably natatory lamellae on distal part of tibia (Chopard and Callan 1956; Günther, 1972; 1978; 1994; 1995; Cao, 2017). These lamellaes can be floated the insects for swimming and aided them jump off the water surface (Chopard and Callan, 1956; Wickler, 1966; Burrows and Sutton, 2012). In addition, the leaf-like spurs of elcanids have a rachis in its middle part which is analogous to the blade of oar (figs. 2G and 3G; figs. 2 and 4 in Fang et al., 2018a). Undoubtedly, this kind of spur would improve the swimming capacity when the locomotion happened on the surface of the water. Furthermore, as to the palaeoenvironment of the fossil locality, we can infer that these insects were likely living close to the lake or stream and adapted to aquatic or semi-aquatic niches. This functional hypothesis requires further future discoveries of finer structures, e.g. the tibio-femoral joints etc., to more robustly support it.

5. Conclusions

A new fossil species of Elcaninae, *Probaisselcana euryptera* sp. nov., was documented by two well-preserved female specimens from Yixian Formation. It is the first record with sword-shaped ovipositor of Elcanidae from northeast of China, showing a preference of laying eggs in the earth or loose barks. In addition, the delicately preserved leaf-like metatibial spurs of the new species morphologically resembles as oar, indicates a function related to swimming.

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