Cretaceous Research 80 (2017) 13-26



Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes



Systematic revision of the fossil snakefly family Baissopteridae (Insecta: Raphidioptera) from the Lower Cretaceous of China, with description of a new genus and three new species



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ARTICLE INFO

Article history: Received 24 May 2017 Received in revised form 28 July 2017 Accepted in revised form 3 August 2017 Available online 5 August 2017

Keywords: Neuropterida Taxonomy Yixian formation Mesozoic

ABSTRACT

The fossil snakefly family Baissopteridae from the Lower Cretaceous (upper Barremian) of the Yixian Formation of Liaoning Province, China is reviewed. Two genera and five species of Baissopteridae are recorded, including a new genus, namely *Microbaissoptera* gen. nov., and three new species, i.e., *Baissoptera bicolor* sp. nov., *Baissoptera sinica* sp. nov., and *Microbaissoptera monosticha* sp. nov. Moreover, *Baissoptera euneura* Ren, 1997 is herein treated as a new junior synonymy of *Baissoptera grandis* Ren in Ren et al., 1995. *Baissoptera minima* Ponomarenko, 1993 is transferred to the presently described new genus *Microbaissoptera* gen. nov. based on the small body-size and the presence of a single gradate series of crossveins in radial and medial areas of posterior part of both fore- and hind wings. A key to genera of Baissopteridae is provided.

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1. Introduction

The extinct snakefly family Baissopteridae is the second predominant group among the Mesozoic Raphidioptera, characterized by the presence of numerous RP branches and crossveins in radial and medial areas of posterior part of both fore- and hind wings (Bechly & Wolf-Schwenninger, 2011; Liu et al., 2014). This family had been present in the Early Cretaceous of Eurasia and South America, and the late Eocene of North America, mostly restricted to three localities, i.e., the Zaza Formation of Russia (Martynova, 1961; Ponomarenko, 1993), the Crato Formation of Brazil (Nel et al., 1990; Oswald, 1990; Martins-Neto & Nel, 1992; Jepson et al., 2011), and the Yixian Formation of China (Ren, 1994, 1997; Ren et al., 1995) (Table 1), with 20 described species in six genera (Engel, 2002; Pérez-de la Fuente et al., 2012; Makarkin & Archibald, 2014). The existing evidence indicates that Baissopteridae appears to be the sister-group of the remaining four families (Mesoraphidiidae, Metaraphidiidae, Raphidiidae and Inocelliidae) of the suborder

http://dx.doi.org/10.1016/j.cretres.2017.08.004 0195-6671/© 2017 Elsevier Ltd. All rights reserved. Raphidiomorpha (Liu et al., 2014). However, the monophyly of Baissopteridae is still not confirmed.

The known palaeofauna of Baissopteridae from China consists of only three species of the genus *Baissoptera* Martynova (Ren, 1994, 1997; Ren et al., 1995; Engel, 2002). Besides the original descriptions, Ren (1997) provided a revisionary work on these species based on additional fossil materials. Nevertheless, the current knowledge of the Chinese baissopterids is from the studies on totally less than 10 pieces of fossils (Ren, 1994, 1997; Ren et al., 1995, 2010). The morphology and palaeodiversity of Baissopteridae from China await further exploration.

In this study, we examined more than 40 specimens of unidentified baissopterid fossils from the Lower Cretaceous of Yixian Formation of China. The materials include five species of Baissopteridae, i.e., two known species of *Baissoptera* [*B. grandis* Ren in Ren et al., 1995 (*B. euneura* Ren, 1997 is herein synonymized as *B. grandis*) and *B. liaoningensis* Ren, 1994], two new species of *Baissoptera*, and a new species of a new genus *Microbaissoptera* gen. nov. A review of these genera and species of Baissopteridae, with descriptions and detail illustrations, is herein presented. A checklist of the species of Baissopteridae (Table 1), as well as a key to the genera of this family, are also provided.

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Table	1
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	List	of	known	species	of	Baissopteridae.
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Age	Species	Locality	Reference
Early Cretaceous	Austroraphidia brasiliensis (Nel. Séméria and Vulcano, 1990)	Ceará, Pernambuco, Brazil	Willmann, 1994
Early Cretaceous	Baissoptera bicolor sp. nov.	Beipiao, Liaoning, China	
Early Cretaceous	Baissoptera brasiliensis Oswald, 1990	Ceará, Pernambuco, Brazil	Oswald, 1990
Early Cretaceous	Baissoptera cellulosa Ponomarenko, 1993	Baisa, Burvat, Russia	Ponomarenko, 1993
Early Cretaceous	Baissoptera elongata Ponomarenko, 1993	Baisa, Burvat, Russia	Ponomarenko, 1993
Early Cretaceous	Baissoptera grandis Ren in Ren et al., 1995	Beipiao, Liaoning, China	Ren et al., 1995
Early Cretaceous	Baissoptera kolosnitsynae Martynova, 1961	Baisa, Buryat, Russia	Martynova, 1961
Early Cretaceous	Baissoptera liaoningensis Ren, 1994	Beipiao, Liaoning, China	Ren, 1994
Early Cretaceous	Baissoptera lisae Jepson, Ansorge & Jarzembowski, 2011	Ceará, Pernambuco, Brazil	Jepson et al., 2011
Early Cretaceous	Baissoptera martinsoni Martynova, 1961	Baisa, Buryat, Russia	Martynova, 1961
Early Cretaceous	Baissoptera pulchra (Martins-Neto and Nel, 1992)	Ceará, Pernambuco, Brazil	Engel, 2002
Early Cretaceous	Baissoptera sibirica Ponomarenko, 1993	Baisa, Buryat, Russia	Ponomarenko, 1993
Early Cretaceous	Baissoptera sinica sp. nov.	Beipiao, Liaoning, China	1
Early Cretaceous	Baissoptera? Cretaceoelectra Pérez-de la Fuente, Peñalver,	Moraza, Burgos, Spain	Pérez-de la Fuente et al., 2012
-	Delclòs & Engel, 2012		
Early Cretaceous	Cretaraphidiopsis bontsaganensis (Ponomarenko, 1988)	Bon-Tsagan Nuur, Bayankhongor, Mongolia	Ponomarenko, 1988; Engel, 2002
Early Cretaceous	Cretoraphidia certa Ponomarenko, 1993	Romanovka, Transbaikalia, Russia	Ponomarenko, 1993
Early Cretaceous	Cretoraphidia macrocella Ponomarenko, 1993	Baisa, Buryat, Russia	Ponomarenko, 1993
Early Cretaceous	Cretoraphidia magna Ponomarenko, 1993	Baisa, Buryat, Russia	Ponomarenko 1993
Early Cretaceous	Cretoraphidia reticulata Ponomarenko, 1993	Baisa, Buryat, Russia	Ponomarenko, 1993
Early Cretaceous	Lugala longissima (Ponomarenko, 1988)	Bon-Tsagan Nuur, Bayankhongor, Mongolia	Willmann, 1994
Early Cretaceous	Microbaissoptera minima (Ponomarenko, 1993) comb. nov.	Baisa, Buryat, Russia	Ponomarenko, 1993
Early Cretaceous	Microbaissoptera monosticha gen. et sp. nov.	Beipiao, Liaoning, China	/
Late Eocene	Dictyoraphidia veterana (Scudder, 1890)	Florissant, Colorado, U.S.A.	Makarkin & Archibald, 2014

2. Material and methods

All fossil specimens examined herein are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), Beijing. They are derived from the upper Barremian (126.1 ± 1.7 to 124.6 ± 0.1 Ma), Lower Cretaceous of Jianshangou Member (Bed), Yixian Formation (Wang and Zhou, 2008; Walker et al., 2013), the Huangbanjigou locality ($41^{\circ}36'44''N$, $120^{\circ}49'48''E$) (see Wang et al., 2015: fig. 1), Sihetun area, Beipiao City, Liaoning Province, China. The Yixian Formation has a lithology of gray, greenish and purplish tinged, fine-grained sandstones and volcanic tuffs. The Jianshangou Member (Bed) ranges from 50 to 80 m in thickness and yields abundant fossil insects (Ren, 1998; Gao et al., 2013; Yang et al., 2014; Yao et al., 2014).

All specimens were examined using a Zeiss Discovery V12 stereo microscope, photographed with a Nikon D800 digital camera, and illustrations compiled in Adobe Photoshop CC. The terminology of wing venation generally follows Aspöck et al. (1991) and Kukalová-Peck & Lawrence (2004).

Abbreviations used for wing veins and spaces are: A, anal; *ac*, anal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; *dc*, discal cell; *doi*, discoidal cell; M, media; MA, media anterior; MP, media posterior; *m*, medial cell; pt, pterostigma; R, radius; RA, radius anterior; RP, radius posterior; *r*, radial cell; ScP, subcosta posterior; *sr*, subradial cell.

All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication under urn:lsid:zoobank.org:pub:D37B79AE-3328-4B84-B93C-01A1574BD8AB.

3. Systematic palaeontology

Order Raphidioptera Navás, 1916 Suborder Raphidiomorpha Engel, 2002 Family Baissopteridae Martynova, 1961

Genus Baissoptera Martynova, 1961 Type species: Baissoptera martinsoni Martynova, 1961 Revised diagnosis. Body medium- to large-sized for the family (body length 14.6-38.6 mm, forewing length 8.7-27.7 mm) (Table 2). Head elongate, twice as long as wide, tapering caudad or not. Ocelli present (sometimes invisible, but probably due to poor preservation as two states of presence/absence of ocelli in a same snakefly genus are unlikely). Pronotum rectangular, slightly shorter than head length. Legs slender. Wings broad, approximately three to four times as long as wide; ScP terminating into costal margin posteriad wing midpoint; a single scp-ra crossvein present; pterostigma proximally approximating ending point of ScP and distally ended at an anterior RA veinlet, usually with one or two pterostigmal crossveins (occasionally absent) (Martynova, 1961: figs. 6, 7; Oswald, 1990: figs. 1–4); rich numbers of crossveins in radial and medial areas forming three or more closed radial cells, two or more medial cells and more than seven discoidal cells. Forewing: More than four pectinate RP branches present; MA originating close to first MP branching point; diverging point between CuA and M obviously distad separation between R and M + CuA. Hind wing: MA stem originating from R and coalescent with RP for a short distance.

Baissoptera grandis Ren in Ren *et al.*, 1995 Fig. 1

Baissoptera grandis Ren in Ren et al., 1995: 97 Baissoptera euneura Ren, 1997: 173. syn. nov.

Revised diagnosis. Body large-sized (body length 18.4–38.6 mm, forewing length 15.6–27.7 mm) (Table 2). Head rectangular. Ocelli present. Pronotum elongate, rectangular. Legs slender, dark-colored throughout. Wings broad, approximately three to four times as long as wide; uniformly colored pterostigma long, *ca* one-fifth to one-fourth of wing length, with a single pterostigmal crossvein at distal 1/3; crossveins in radial and medial areas forming three gradate series in posterior part of wing. Forewing: Five pectinate RP branches present, each simple or forked.

Materials examined. Holotype: LB93001 & LB93002 (c/p), a well preserved specimen (sex unknown) compressed laterally with thorax, legs and a piece of forewing. Additional materials: LB95101 [holotype of *B. euneura* syn. nov.], a well preserved almost complete female compressed dorsoventrally; CNU-RAP-LB-2017020c/p, a well preserved almost complete female compressed laterally; CNU-

Table 2

Summary of forewing length of species of Baissopteridae.

Creation	Ferry view longth (mm)	Deferrer et
species		Reference
Austroraphidia brasiliensis (Nel, Séméria and Vulcano, 1990)	10.2	Nel et al., 1990
Baissoptera bicolor sp. nov.	11.3-15.1	/
Baissoptera brasiliensis Oswald, 1990	14.5	Oswald, 1990
Baissoptera cellulosa Ponomarenko, 1993	15.0	Ponomarenko, 1993
Baissoptera elongata Ponomarenko, 1993	13.5	Ponomarenko, 1993
Baissoptera grandis Ren in Ren et al., 1995	15.6-27.7	Ren et al., 1995; Ren, 1997
Baissoptera kolosnitsynae Martynova, 1961	12.5	Martynova, 1961
Baissoptera liaoningensis Ren, 1994	14.7-16.9	/
Baissoptera lisae Jepson, Ansorge & Jarzembowski, 2011	12.0	Jepson et al., 2011
Baissoptera martinsoni Martynova, 1961	10.5-14.5	Martynova, 1961; Ponomarenko, 1993
Baissoptera pulchra (Martins-Neto and Nel,1992)	14.6	Martins-Neto and Nel, 1992
Baissoptera sibirica Ponomarenko, 1993	16.0-17.0	Ponomarenko, 1993
Baissoptera sinica sp. nov.	21.5	/
Baissoptera? cretaceoelectra Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012	Partly preserved	Pérez-de la Fuente et al., 2012
Cretaraphidiopsis bontsaganensis (Ponomarenko, 1988)	12.0	Ponomarenko, 1988
Cretoraphidia certa Ponomarenko, 1993	14.0	Ponomarenko, 1993
Cretoraphidia macrocella Ponomarenko, 1993	15.0	Ponomarenko, 1993
Cretoraphidia magna Ponomarenko, 1993	More than 18.5 (hind wing length)	Ponomarenko, 1993
Cretoraphidia reticulata Ponomarenko, 1993	14.0	Ponomarenko, 1993
Dictyoraphidia veterana (Scudder, 1890)	At least 9.0	Makarkin & Archibald, 2014; Scudder, 1890
Lugala longissima (Ponomarenko, 1988)	17.5	Ponomarenko, 1988
Microbaissoptera minima (Ponomarenko, 1993) comb. nov.	9.0-10.0	Ponomarenko, 1993
Microbaissoptera monosticha gen.et sp. nov.	8.7-10.8	/

RAP-LB-2016023, a complete forewing; CNU-RAP-LB-2017025, a well preserved almost complete female compressed dorsoventrally; CNU-RAP-LB-2017027c/p, a well preserved almost complete female compressed laterally; CNU-RAP-LB-2017048, an incomplete female compressed laterally; CNU-RAP-LB-2017049c/p, a poorly preserved male compressed laterally; CNU-RAP-LB-2017069c/p, a vell preserved almost complete forewing; CNU-RAP-LB-2017062c/p, a well preserved almost complete male compressed dorsoventrally; CNU-RAP-LB-2017064, a well preserved almost complete female compressed dorsoventrally; CNU-RAP-LB-2017065, an incomplete specimen with abdomen not preserved almost complete female compressed laterally; CNU-RAP-LB-2017066, a well preserved almost complete female compressed dorsoventrally; CNU-RAP-LB-2017066, a well preserved almost complete female compressed laterally; CNU-RAP-LB-2017066, a well preserved almost complete female compressed dorsoventrally; CNU-RAP-LB-2017070, an poorly preserved specimen compressed dorsoventrally.

Remarks. Ren et al. (1995) considered this species is most similar to *B. liaoningensis* in wing venation, but it can be distinguished from *B. liaoningensis* by the presence of more costal crossveins, six RP branches, two MA branches, 11 MP branches, and three cua-cup crossveins. However, the number of RP, MA and MP branches as well as the number of cua-cup crossveins varies within the same species. So, here we propose additional characters to distinguish this species from *B. liaoningensis* by the larger body-size (forewing 14.7–16.9 mm long in *B. liaoningensis*) (Tables 2–3), the rectangular head (Figs. 2A–D) [head ovoid in *B. liaoningensis* (Fig. 2E)], the uniformly colored femora and tibiae (Fig. 3A) [femora pale-colored but tibiae dark-colored in *B. liaoningensis* (Figs. 3B–E)], and the presence of three gradate series of crossveins in radial and medial areas (two gradate series of crossveins present in *B. liaoningensis*).

Ren (1997) described another large-sized baissopterid species from Lower Cretaceous of Yixian Formation of China, namely *Baissoptera euneura* Ren, 1997. This species was considered to be distinguished from *B. grandis* by the presence of marginal fork of RA and RP branches, three A1 branches and elongate A2. In this study, we examined 16 large-sized baissopterid specimens, morphological variations mentioned above between the two species are considered to be unstable and changed gradually, such as the RA possessing two or three veinlets, the RP branches marginally simple or bifurcated, and the A1 possessing three to five branches. Moreover, we did not find stable differences distinguishing them effectively. In the original description (Ren et al., 1995; Ren, 1997), head shape of them seems to be different, while the elongate, slender head versus the rectangular head are caused due to preservation conditions (Figs. 2A–D). So, here we treat *B. euneura* to be a junior synonym of *B. grandis*.

Baissoptera liaoningensis Ren, 1994

Fig. 4

Baissoptera liaoningensis Ren, 1994: 132

Revised diagnosis. Body medium-sized (body length 15.5–21.0 mm, forewing length 14.7–16.9 mm) (Table 2). Head ovoid, tapering caudad. Ocelli probably present, but invisible so far. Pronotum elongate, rectangular. Legs slender, with pale-colored femora but dark-colored tibiae. Wings broad, approximately four times as long as wide; uniformly colored pterostigma long, *ca* one-fifth of wing length, with a single pterostigmal crossvein at distal 1/3; crossveins in radial and medial areas forming two gradate series in posterior part of both fore- and hind wings.

Materials examined. Holotype: Sh001 & Sh002 (c/p), a well preserved almost complete specimen (sex unknown) compressed dorsoventrally. Additional materials: CNU-RAP-LB-2017018, a well preserved specimen (sex unknown) compressed dorsoventrally, with meso- and metathorax, wings and legs partly preserved; CNU-RAP-LB-2017022, a poorly preserved female compressed dorsoventrally; CNU-RAP-LB-2017026, a well preserved specimen (sex unknown), with only meso- and metathorax, wings and legs partly preserved; CNU-RAP-LB-2017029, a well preserved almost complete female specimen compressed laterally; CNU-RAP-LB-2017034, a poorly preserved male compressed dorsoventrally; CNU-RAP-LB-2017035, a well preserved female compressed dorsoventrally, with head not preserved; CNU-RAP-LB-2017050, a well preserved specimen (sex unknown), with meso- and metathorax, wings and legs partly preserved; CNU-RAP-LB-2017053, a poorly preserved male compressed dorsoventrally.

Remarks. In the original description (Ren, 1994), this species was mentioned to be characterized by the following combination of forewing characters: a single scp-ra crossvein, five closed radial cells, RP originating from R proximad midpoint of wing, rich numbers of radial and medial cells, and two cua-cup crossveins.



Fig. 1. Baissoptera grandis Ren in Ren et al., 1995. A. Habitus photograph of CNU-RAP-LB-2017025, female, dorsal view; B. Drawings of wing venation of CNU-RAP-LB-2017025; C. Habitus photograph of CNU-RAP-LB-2017066, female, dorsal view; D. Drawings of wing venation of CNU-RAP-LB-2017066; E. Habitus photograph of CNU-RAP-LB-2017023, sex unknown, single forewing; F. Drawings of wing venation of CNU-RAP-LB-2017023. Colored cells include radial cells (purple), discal cells (yellow), medial cells (green), discoidal cells (blue). Scale bar = 5.0 mm (A, C, E), 2.0 mm (B, D, F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Measurements of species of Baissopteridae from the Lower Cretaceous of China.

Species/sex	Body length (mm)	Head length (mm)	Prothorax length (mm)	Meso- plus metathorax length (mm)	Forewing length (mm)	Forewing maximum width (mm)	Hind wing length (mm)	Hind wing maximum width (mm)	Ovipositor length (mm)
B. bicolor sp. nov./male	13.5-15.3	3.1-3.2	2.0-2.8	2.5-3.1	12.1-13.4	3.3-3.6	10.1-11.4	3.2-3.6	1
B. bicolor sp. nov./female	16.0-20.0	3.7-3.9	2.4-3.1	3.0-4.1	14.5-15.1	3.8-4.3	12.5-13.2	3.4-4.3	8.3-9.5
B. grandis/male	18.4-22.7	4.6-5.7	3.1-3.6	3.3-3.6	16.0-18.3	4.1-4.5	15.0	3.9-4.8	/
B. grandis/female	21.3-38.6	4.4-5.8	3.7-5.8	3.0-6.7	15.6-17.7	3.9-5.9	13.9-23.8	3.8-5.5	8.5-15.3
B. liaoningensis/male	15.5-21.0	3.9-4.0	2.0-3.3	3.1	14.7	3.9-4.2	12.4-13.3	3.3-3.9	/
B. liaoningensis/female	17.8-19.7	3.4-4.2	2.5-3.0	3.1-4.0	16.1-18.9	4.3-4.8	11.6-13.8	/	9.3-9.4
B. sinica sp. nov./female	26.6-32.1	5.2 - 6.7	4.7-5.2	5.0 - 5.4	21.5	5.3-6.7	20.3	5.6-6.0	13.1
M. monosticha gen.et sp. nov./female	14.3	2.9	1.9	2.7	10.8	3.2	9.3	2.7	6.2

However, the forewing of all genera of Baissopteridae has the RP originating from R proximad midpoint of wing. The presence of three or more closed radial cells and two to four cua-cup crossveins can be found as intraspecific morphological variations in

B. liaoningensis and a number of other *Baissoptera* species. Based on our examination of 10 medium-sized baissopterid specimens, we consider this species to be distinguishable from other species of *Baissoptera* by the pale-colored femora but dark-colored tibiae



Fig. 2. Photographs of head of the Baissoptera species. A. Baissoptera grandis Ren in Ren et al. 1995, CNU-RAP-LB-2017049; B. B. grandis, CNU-RAP-LB-2017062; C. B. grandis, CNU-RAP-LB-2017064; D. B. grandis, CNU-RAP-LB-2017070; E. B. liaoningensis Ren 1994, CNU-RAP-LB-2017053; F. B. bicolor sp. nov., holotype CNU-RAP-LB-2017028; G. B. sinica sp. nov., paratype CNU-RAP-LB-2017032; H. Microbaissoptera monosticha gen. et sp. nov., holotype CNU-RAP-LB-2017061. Arrow points to ocelli. Scale bar = 1.0 mm.

(Fig. 3), the uniformly colored pterostigma with a single pterostigmal crossvein at distal 1/3 (Fig. 5), and the crossveins in radial and medial areas forming two gradate series.

Baissoptera bicolor sp. nov.

Fig. 6

urn:lsid:zoobank.org:act:B470FD77-E03B-4325-A031-8357F8C1D534

Diagnosis. Body medium-sized (body length 15.3–20.0 mm, forewing length 11.3–15.1 mm) (Table 2). Head ovoid, tapering caudad. Ocelli probably present. Legs slender, uniformly colored. Pronotum slightly longer than wide. Wings broad, approximately three to four times as long as wide; pterostigma pale-colored proximally and dark-colored distally, ca one-fifth of wing length, and a pterostigmal crossvein present; crossveins in radial and medial areas forming two gradate series in posterior part of fore- and hind wings.

Description of holotype male. Head ovoid, tapering caudad, 3.1 mm long. Antennae partially preserved. Ocelli invisible. Prothorax obviously shorter than head, 2.0 mm long. Meso- and metathorax well preserved, combined length 3.0 mm. Legs slender, uniformly colored. Abdomen length 6.0 mm.

Forewing: 13.4 mm long, 3.6 mm wide. Costal space with nine crossveins preserved; ScP terminating into costal margin posteriad wing midpoint; three simple RA veinlets present; pterostigma palecolored proximally and dark-colored distally, ca one-fifth of wing length, proximally approximating ending point of ScP, with one oblique pterostigmal crossvein present at distal 1/2, and distally closed by an anterior veinlet of RA; three closed radial cells present: 1r longer than 2r, and 2r longer than 3r; RP poorly preserved, probably with four or five pectinate branches (Figs. 6D, F); three crossveins between RP and MA forming three discal cells; MA originating from first branching point of MP, coalescent with stem of RP for a short distance, separating near midpoint of wing into anterior simple and posterior bifurcate branches distally and two crossveins present between these branches; four crossveins present between MA and MP forming one long and three short medial cells; MP deeply forked, with eight terminal branches and seven discoidal cells present; CuA and CuP simple; three cua-cup crossveins perpendicular to CuA and CuP; A1 bifurcate; A2 trifurcate.

Hind wing: 11.1 mm long, 3.4 mm wide. Costal space with seven crossveins preserved; ScP terminating into costal margin posteriad wing midpoint; three simple RA veinlets present; pterostigma proximally approximating ending point of ScP, pale-



Fig. 3. Photographs of leg of the *Baissoptera* species, showing difference in color among species. A. *B. grandis* Ren in Ren et al. 1995, CNU-RAP-LB-2017048; B. *B. liaoningensis*, CNU-RAP-LB-2017022; C. *B. liaoningensis*, CNU-RAP-LB-2017023; E. *B. liaoningensis*, CNU-RAP-LB-2017026; F. *B. bicolor* sp. nov., paratype CNU-RAP-LB-2017051. G. *B. sinica* sp. nov., paratype CNU-RAP-LB-2017032; H. *Microbaissoptera monosticha* gen. et sp. nov., paratype CNU-RAP-LB-2017060. Arrow points to femur and triangle points to tibia. Scale bar = 1.0 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

colored proximally and dark-colored distally, *ca* one-fifth of wing length, with one inclined pterostigmal crossvein at distal 1/2, ended at an anterior veinlet of RA; RP with four simple pectinate branches; five closed radial cells present: *3r* longer than the other radial cells; three crossveins between RP and MA, forming three long discal cells; MA originating from R approximate to MP separating point from R and coalescent with stem of RP for a short distance, then deeply forked, ended with simple anterior branch, bifurcate posterior branch, and two crossveins between MA branches; two crossveins visible, probably four crossveins between MA and MP (Fig. 6F); incomplete preserved MP deeply forked, probably with seven terminal branches (Fig. 6F); posterior

portion of left and right hind wing incomplete preserved; CuP probably simple (Fig. 6F); at least three A1 branches present.

Description of paratype female. CNU-RAP-LB-2017055c/p (Figs. 6C, D). Body laterally preserved, 17.9 mm long (excluding ovipositor). Ovipositor 9.5 mm long, Head *ca* 3.7 mm long, slightly longer than prothorax. Ocelli present. Prothorax *ca* 2.7 mm long. Meso- and metathorax 3.0 mm long. Legs not preserved. Forewing 14.9 mm long, nearly 3.8 mm wide. Hind wing 12.5 mm long, nearly 3.4 mm wide. Wing venation almost identical to that in holotype. Other morphological characters differ from holotype present as follows. Forewing: Five simple pectinate RP branches, with four crossveins



Fig. 4. *Baissoptera liaoningensis* **Ren**, **1994**. A. Habitus photograph of CNU-RAP-LB-2017029, female, lateral view; B. Drawings of wing venation of CNU-RAP-LB-2017029; C. Habitus photograph of CNU-RAP-LB-2017026, sex unknown, dorsal view; D. Drawings of wing venation of CNU-RAP-LB-2017026; Colored cells include radial cells (purple), discal cells (yellow), medial cells (green), discoidal cells (blue). Scale bar = 5.0 mm (A, C), 2.0 mm (B, D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

among them; seven MP branches and eight discoidal cells present; CuA bifurcate; A1 trifurcate and A2 bifurcate. Hind wing: Two simple RA veinlets present; four radial cells present between RA and RP; five pectinate RP branches, with one bifurcate, others simple; MA deeply forked, and each branch bifurcate.

Type materials. Holotype: CNU-RAP-LB-2017028, a well preserved almost complete male compressed dorsoventrally. Paratypes: CNU-RAP-LB-2017021, a poorly preserved female compressed dorsoventrally with head and wings incomplete; CNU-RAP-LB-2017041, a poorly preserved male compressed dorsoventrally with head and prothorax not preserved; CNU-RAP-LB-2017042, a well preserved specimen (sex unknown) compressed dorsoventrally with mesoand metathorax, wings and mid- and hind legs; CNU-RAP-LB-2017043, a poorly preserved male compressed laterally; CNU-RAP-LB-2017044, a poorly preserved female compressed dorsoventrally; CNU-RAP-LB-2017045, a well preserved specimen (sex unknown) compressed dorsoventrally with anterior portion of head and abdomen not preserved; CNU-RAP-LB-2017047, a poorly preserved specimen (sex unknown) compressed dorsoventrally with abdomen not preserved; CNU-RAP-LB-2017051, a poorly preserved female compressed dorsoventrally; CNU-RAP-LB-2017055, a well preserved almost complete female compressed laterally.

Locality and horizon. The Yixian Formation (upper Barremian, Lower Cretaceous), Huangbanjigou locality (41°36′44″N, 120°49′48″E), Beipiao City, Liaoning Province, northeastern China.

Etymology. The name derives from the Latin adjective *bicolor*, referring to the pterostigma that is pale-colored proximally and dark-colored distally.

Remarks. The new species appears to be most similar to *B. liaoningensis*, however, it differs from the latter species based on the bicolored pterostigma (Fig. 5C) [pterostigma uniformly colored in *B. liaoningensis* (Fig. 5B)], and the uniformly colored femora and tibiae (Fig. 3F) [femora pale-colored but tibiae dark-colored in *B. liaoningensis* (Figs. 3B–E)].

Baissoptera sinica sp. nov.

Fig. 7

urn:lsid:zoobank.org:act:47FFD70D-421E-410A-BAFE-FB30148A008C

Diagnosis. Body large-sized (body length 26.6–32.1 mm, forewing length 21.5 mm) (Table 2). Head rectangular. Ocelli probably present, but not preserved. Legs slender, uniformly colored throughout. Both fore- and hind wings broad, approximately three to four times as long as wide; pterostigma pale-colored proximally and dark-colored distally, without pterostigmal crossvein; crossveins in radial and medial areas forming three gradate series in posterior part of wing.

Description of holotype female. Head partly preserved, rectangular, preserved portion 4.3 mm. Prothorax elongate, 5.1 mm long. Mesoand metathorax combined length 5.3 mm. Legs invisible, probably



Fig. 5. Photographs of pterostigma of the *Baissoptera* species, showing difference in color among species. A. *B. grandis* Ren in Ren et al. 1995, CNU-RAP-LB-2017064; B. *B. liaoningensis* Ren 1994, CNU-RAP-LB-2017050; C. *B. bicolor* sp. nov., holotype CNU-RAP-LB-2017028; D. *B. sinica* sp. nov., paratype CNU-RAP-LB-2017032; E. *Microbaissoptera monosticha* gen. et sp. nov., holotype CNU-RAP-LB-2017061. Arrow

slender, uniformly colored (Fig. 7C). Abdomen 13.7 mm long (excluding ovipositor). Ovipositor with only anterior portion preserved.

Forewing: 21.5 mm long, 6.5 mm wide. Costal space with nine costal crossveins; ScP terminating into costal margin posteriad wing midpoint; four simple RA veinlets present; pterostigma palecolored proximally and dark-colored distally, 3.0 mm long, ca onefifth of forewing length, without pterostigmal crossvein, distally closed by an anterior veinlet of RA; four closed radial cells present between RA and RP: 1r longer than other radial cells; RP with six pectinate branches: three forked, three simple; four crossveins present between RP and MA, forming one long and three short discal cells; MA originating slightly distad first branching point of MP and coalescent with stem of RP for a short distance, then deeply forked, both bifurcate marginally; five crossveins present between MA and MP, forming one long and four short medial cells; MP deeply forked, with 12 terminal branches marginally and 17 discoidal cells posteriad MP; CuA and CuP simple; three cua-cup crossveins perpendicular to CuA and CuP; five simple pectinate A1 branches present; three pectinate A2 branches present, one bifurcate and two simple.

Hind wing: 20.3 mm long, 5.6 mm wide. Costal space with seven crossveins; ScP terminating into costal margin posteriad wing midpoint; three simple RA veinlets present; pterostigma originating distad termination of ScP, without pterostigmal crossvein, and distally closed by anterior veinlet of RA; five crossveins present between RA and RP, forming five closed radial cell, 3r longer than others; RP with six pectinate branches, three forked, three simple; four crossveins present between RP and MA, forming one long and three short discal cells; MA proximally incomplete, probably originating from R posteriad branching point of MP from R (Fig. 7D) and coalescent with RP for a short distance, then deeply forked, ended with five terminal branches; three crossveins present between MA and MP, forming three medial cells; MP deeply forked, with 11 terminal branches and 13 discoidal cells present; CuA trifurcate and CuP simple; two cua-cup perpendicular to CuA and CuP; five simple pectinate A1 branches present; A2 bifurcate.

Description of paratype female. CNU-RAP-LB-2017032. Head well preserved, rectangular, 6.7 mm long. Antennae well preserved, 8.8 mm long. Ocelli invisible. Prothorax elongate, 5.2 mm long. Meso- and metathorax combined length 5.4 mm. Legs slender, uniformly colored. Abdomen 15.7 mm long (excluding ovipositor), ovipositor with only anterior portion preserved. Fore- and hind wings apex incomplete. Wing venation almost identical to that in holotype. Other morphological characters different from holotype present as follows. Forewing: Costal space with 10 crossveins; probably only three closed radial cells present between RA and RP present; MP with 14 terminal branches and 16 discoidal cells; A1 and A2 both with four pectinate branches. Hind wing: Costal space with eight crossveins.

CNU-RAP-LB-2017039. Ovipositor preserved completely, measured length 13.1 mm. Forewing: Four pectinate A1 branches present; three simple pectinate A2 branches present.

Type materials. Holotype: CNU-RAP-LB-2017038, a well preserved nearly complete female compressed dorsoventrally. Paratypes: CNU-RAP-LB-2017032, a well preserved nearly complete female compressed dorsoventrally; CNU-RAP-LB-2017039, a poorly preserved female compressed dorsoventrally.

indicates bicolored pterostigma. Scale bar = 1.0 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 6. *Baissoptera bicolor* sp. nov. A. Habitus photograph of holotype CNU-RAP-LB-2017028, male, dorsal view; B. Drawings of wing venation of CNU-RAP-LB-2017028; C. Habitus photograph of paratype CNU-RAP-LB-2017055; E. Habitus photograph of paratype CNU-RAP-LB-2017025; E. Habitus photograph of paratype CNU-RAP-LB-2017021, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017021, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017021, female, dorsal view; S. Drawings of wing venation of paratype CNU-RAP-LB-2017021, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017021. Colored cells include radial cell (purple), discal cells (yellow), medial cells (green), discoidal cells (blue). Scale bar = 5.0 mm (A, C, E), 2.0 mm (B, D, F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



Fig. 7. *Baissoptera sinica* sp. nov. A. Habitus photograph of holotype CNU-RAP-LB-2017038, female, dorsal view; B. Drawings of wing venation of holotype CNU-RAP-LB-2017038; C. Habitus photograph of paratype CNU-RAP-LB-2017032, female, dorsal view; D. Drawings of wing venation of paratype CNU-RAP-LB-2017032; E. Habitus photograph of paratype CNU-RAP-LB-2017039, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017039, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017039, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017039, female, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017039. Colored cells include radial cells (purple), discal cells (yellow), medial cells (green), discoidal cells (blue). Scale bar = 5.0 mm (A, C, E), 2.0 mm (B, D, F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Locality and horizon. The Yixian Formation (upper Barremian, Lower Cretaceous), Huangbanjigou locality (41°36′44″N, 120°49′48″E), Beipiao City, Liaoning Province, northeastern China.

Etymology. The specific epithet *sinica* refers to the occurrence of the new species in China.

Remarks. The new species appears to be most similar to *B. grandis*, however, it differs from *B. grandis* based on the bicolored pterostigma (Fig. 5D) [pterostigma uniformly colored in *B. grandis* (Fig. 5A)], and the absence of pterostigmal crossvein (a single pterostigmal crossvein present at distal 1/3 in *B. grandis*).

Microbaissoptera gen. nov.

urn:lsid:zoobank.org:act:8FC0E5D7-1861-4070-8023-DD58C20AB89A

Type species: Microbaissoptera monosticha sp. nov.

Diagnosis. Body small-sized (body length probably less than 14.3 mm, forewing length 8.7–10.8 mm) (Table 2). Head ovoid. Ocelli present. Prothorax elongate. Legs slender, uniformly colored. Fore- and hind wings broad, approximately three times as long as wide; ScP terminating into costal margin posteriad wing midpoint; a single scp-ra present; pterostigma proximally approximating ending point of ScP and distally ended at an anterior RA veinlet, with one pterostigmal crossveins; crossveins in radial and medial areas forming only one gradate series in posterior portion and only a single crossvein present between RP branches. Forewing: MA originating from first MP branching point, then deeply forked. Hind wing: MA separated from R distad MP separating point from R.

В

D

F

Etymology. From *micro*- (small) and *Baissoptera* (a common genusgroup name of Baissopteridae) in reference to the relatively small body-size of the new genus in comparison to the other baissopterids. Gender: Feminine.

Remarks. Microbaissoptera gen. nov. appears to be closely related to *Baissoptera* and *Lugala* Willmann, 1994, but can be distinguished from the latter two genera by the small body-size, and the presence of a single gradate series of crossveins in radial and medial areas of posterior portion of wings. *Microbaissoptera* gen. nov. can be distinguished from *Austroraphidia* Willmann, 1994 and *Cretoraphidia* Ponomarenko, 1993 by the forewing MA originating from first branching point of MP (forewing MA originating distad first

branching point of MP in the latter two genera). *Microbaissoptera* gen. nov. differs from *Cretoraphidiopsis* Engel, 2002 by the presence of a single crossvein among RP branches (crossveins among RP branches absent in *Cretoraphidiopsis*). Lastly, *Microbaissoptera* gen. nov. can be distinguished from *Dictyoraphidia* Handlirsch, 1910, by the presence of a single scp-ra crossvein, while two scp-ra crossveins are present in *Dictyoraphidia*.

Based on our examination of materials of the new genus, we found *Baissoptera minima* Ponomarenko, 1993, shares all characters of *Microbaissoptera* gen. nov., i.e., the small body-size and the presence of a single gradate series of crossveins in radial and medial



Fig. 8. *Microbaissoptera monosticha* gen. et sp. nov. A. Habitus photograph of holotype CNU-RAP-LB-2017061, female, dorsal view; B. Drawings of wing venation of holotype CNU-RAP-LB-2017061; C. Habitus photograph of paratype CNU-RAP-LB-2017037, sex unknown, lateral view; D. Drawings of wing venation of paratype CNU-RAP-LB-2017037; E. Habitus photograph of paratype CNU-RAP-LB-2017036, sex unknown, dorsal view; F. Drawings of wing venation of paratype CNU-RAP-LB-2017036. Colored cells include radial cells (purple), discal cells (yellow), medial cells (green), discoidal cells (blue). Scale bar = 5.0 mm (A, C, E), 2.0 mm (B, D, F). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

areas of both fore- and hind wings. Therefore, *B. minima* is herein transferred from the genus *Baissoptera* to *Microbaissoptera* gen. nov. as *Microbaissoptera minima* (Ponomarenko) comb. nov.

Microbaissoptera monosticha sp. nov.

Fig. 8 urn:lsid:zoobank.org:act:2039F399-8C48-4904-9DF2-1658A887B0D2

Diagnosis. Mostly same as the generic diagnosis. Head ovoid. Flagellum with more than 40 flagellomeres. Both fore- and hind wings uniformly colored pterostigma with an oblique pterostigmal crossvein.

Description of holotype female. Body 14.3 mm long. Head ovoid, 2.9 mm long. Antennae 4.4 mm long; flagellum with more than 40 flagellomeres, each flagellomere nearly half as long as wide. Ocelli present. Prothorax elongate, rectangular, 1.9 mm long. Meso- and metathorax combined length 2.7 mm. Legs slender, uniformly colored. Abdomen 6.2 mm long. Ovipositor 6.2 mm long.

Forewing: 10.8 mm long, 3.2 mm wide. Costal space preserved with seven crossveins; ScP terminating into costal margin posteriad wing midpoint; two simple RA veinlets present; pterostigma uniformly colored, 2.1 mm long, proximally approximating ending point of ScP, ended at anterior veinlet of RA, probably with one oblique crossvein (Figs. 8D, F); three radial crossveins present between RA and RP, 1r longer than 2r+3rcombined length; RP branches probably with three pectinate RP branches (Fig. 8F); a single crossvein present between RP branches; two crossveins present between RP and MA, forming two discal cells, 1dc longer than 2dc; MA originating from first branching point of MP and coalescent with stem of RP for a short distance, then deeply forked, marginally with one simple and one bifurcate branches; three crossveins present between MA and MP, forming one long and two short medial cells; MP deeply forked, with five terminal branches and five discoidal cells; CuA and CuP simple; three cua-cup crossveins present; A1 simple, A2 trifurcate.

Hind wing: 9.3 mm long and 2.7 mm wide. Costal space with six crossveins visible; ScP terminating into costal margin posteriad wing midpoint; two simple RA veinlets present; pterostigma proximally approximating ending point of ScP and ended at anterior veinlet of RA, pterostigmal crossvein invisible (probably present but not preserved) (Fig. 8F); proximal portion of RP and MA unclear, only with distal two closed radial cells visible (probably four present) (Fig. 8D); four simple pectinate RP branches present; MA deeply forked, one simple, one bifurcate, with two crossveins between these branches; two crossveins visible between MA and MP (probably three present) (Fig. 8D); MP deeply forked, with eight terminal branches and probably five discoidal cells present; CuA bifurcate; posterior portion incomplete.

Description of paratype. CNU-RAP-LB-2017037c/p. Sex unknown. Head poorly preserved, 2.9 mm long. Prothorax elongate, 2.2 mm long. Meso- and metathorax combined length 2.7 mm. Legs slender, uniformly colored throughout. Abdomen not preserved. Preserved part of forewing 8.6 mm long, nearly 2.7 mm wide. Hind wing 8.1 mm long, nearly 2.6 mm wide. Wing venation almost identical to that in holotype. Other morphological characters different from holotype present as follows. Forewing: Seven MP branches and six discoidal cells present; three simple pectinate A1 branches and five discoidal cells present, Hind wing: Seven MP branches and five discoidal cells present; CuA bifurcate, CuP simple; three simple pectinate A1 branches and two simple A2 branches present. *Type materials.* Holotype: CNU-RAP-LB-2017061, a well preserved almost complete female compressed dorsoventrally. Paratypes: CNU-RAP-LB-2017036, a well preserved specimen (sex unknown) compressed dorsoventrally with legs and wings; CNU-RAP-LB-2017037c/p, a well preserved specimen (sex unknown) compressed dorsoventrally with abdomen not preserved; CNU-RAP-LB-2017060, a well preserved specimen (sex unknown) compressed laterally with thorax, legs and wings.

Locality and horizon. The Yixian Formation (upper Barremian, Lower Cretaceous), Huangbanjigou locality (41°36′44″N, 120°49′48″E), Beipiao city, Liaoning Province, northeastern China.

Etymology. The name derives from the Greek adjective *monostichus*, which means a single row, referring to the presence of a single gradate series of crossveins in radial and medial areas.

Remarks. The new species can be distinguished from *M. minima* by the pterostigma [the elongate pterostigma originating slightly distad ending point of ScP, with one pterostigmal crossvein, in the new species, while in *M. minima*, the short pterostigma originating strongly distad ending point of ScP, and pterostigmal crossvein absent].

Key to genera of Baissopteridae

- Small body size (body length less than 14.3 mm, forewing length 8.7–10.8 mm) and crossveins in radial and medial areas forming a single gradate series (Fig. 8); Lower Cretaceous (Barremian)
 Microbaissoptera gen. nov.
- Wing length less than 4.0 times as long as wide; Lower Cretaceous (Berriasian – Albian)...... Baissoptera Martynova

Key to species of Baissopteridae from China

- Pterostigma uniformly colored (Fig. 5A); a single inclined pterostigmal crossvein present.... Baissoptera grandis Ren in Ren et al.

4. Discussion

The family Baissopteridae is a remarkable fossil snakefly group considering relatively large body-size, dense wing venations and the long period of recorded existence from at least Early Cretaceous to late Eocene. Most Mesozoic raphidiopteran fauna became extinct at the end of Cretaceous (Aspöck, 1998), yet it is surprising that a baissopterid survived during Paleogene, besides the two extant families Raphidiidae and Inocelliidae. As noted in some previous studies (Willmann, 1994; Bechly & Wolf-Schwenninger, 2011), the monophyly of this family still lacks conclusive supports because no autapomorphies have been found through comprehensive phylogenetic analysis. Nevertheless, the high degree of similarities in the wing venation of Baissopteridae from various localities and periods may support the assumption of a monophyly. So far, there are six genera and 22 species known in Baissopteridae, with more than half described as the species of Baissoptera. Most of these species in Baissoptera only differs from each other in minute morphological characters, such as the proportion of head length/prothorax length (Ponomarenko, 1993) and the branching number of longitudinal veins (Ren, 1994; Ren et al., 1995). Comprehensive systematic revision of Baissopteridae, particularly of the genus Baissoptera, is necessary and will be important for future work on the phylogeny of this family.

The abundant fossil materials of Baissopteridae from the Lower Cretaceous of China provide plenty information on the morphology and palaeodiversity of Baissopteridae. Based on the materials we examined here, some morphological features as well as their variations should be noted.

First, the relatively large body-size is a general feature of many baissopterid species. Among the present specimens examined, there is a female of *Baissoptera grandis* (CNU-RAP-LB-2017066), with forewing length nearly 27 mm (wing span ~60 mm), being the largest snakefly hitherto reported (see summary of forewing length of all known baissopterid species in Table 2). Whereas, we also found a specimen of *M. monosticha* sp. nov. (CNU-RAP-LB-2017037) probably represents the smallest species of Baissopteridae with forewing length about 9 mm.

Second, it is notable that among all baissopterid fossils we examined the ocelli in some specimens could not be observed although the fossils seem to be well preserved (see Figs. 4A, 6A, 7C). Among other described species of Baissopteridae, four species of *Baissoptera*, i.e. *B. euneura* (herein synonymized as *B. grandis*), *B. lisae* Jepson, Ansorge & Jarzembowski, 2011, *B. martinsoni* and *B. sibirica* Ponomarenko, 1993, were described as having three ocelli in the original descriptions (Ponomarenko, 1993: figs. 1, 4; Ren, 1997: fig. 1; Jepson et al., 2011: fig. 6). The presence/absence of ocelli is an important character to distinguish extant Raphidiidae and Inocellidae. However, the both states of ocelli have been found within Mesoraphidiidae (Liu et al., 2016) although those

mesoraphidiids with or without ocelli belong to different genera. But, it is surprising if the ocelli are present or absent in a same snakefly genus, which is very unlikely indeed. Thus, development of ocelli in Baissopteridae and Mesoraphidiidae as well should be carefully examined in further studies based on more materials.

Third, the feature of pterostigma conforms to the previous description that it is proximally closed by a crossvein and distally incorporated at least one veinlet of RA (Makarkin & Archibald, 2014) although this feature is shared by many snakefly species of other families, such as Mesoraphidiidae and Raphidiidae. Mostly, the pterostigmal crossvein (alternatively interpreted as one of the RA veinlets) is present in the Chinese species of Baissopteridae, while it is confirmed to be absent in *B. sinica* sp. nov. The presence/ absence of pterostigmal crossvein is an important character to distinguish the two extant snakefly families, i.e. Raphidiidae and Inocelliidae. However, this feature is apparently variable within family or even within genus in Raphidioptera, which was previously reported in Mesoraphidiidae (Liu et al., 2016; Lyu et al., 2017) and herein also found in Baissopteridae. Nevertheless, it should be cautious when determining the presence/absence of pterostigmal crossvein because it could be not preserved in fossils (see Figs. 1E, 4C). The bicolored pterostigma is first taken into account for distinguishing baissopterid species. Besides, based on the figures in the originate description, we consider bicolored pterostigma probably also present in B. kolosnitsynae Martynova, 1961 and L. longissima (Ponomarenko, 1988) (Martynova, 1961: fig. 7; Ponomarenko, 1988: fig. 3). In order to confirm the pterostigmal character, future revision of the described species of Baissopteridae is demanded.

5. Concluding remarks

The present taxonomic revision of Baissopteridae from the Early Cretaceous of China improves the knowledge on the palaeodiversity and morphological variations of the family. Further understanding on the phylogeny and evolution of Baissopteridae needs exploration of more non-wing characters with phylogenetic relevance, particularly the genital characters, which is however hard to be preserved in compression fossils. Morphometric study could be another approach for further distinguishing baissopterid genera and species with similar wing venations and for evaluating the phylogenetic status of the family.

Acknowledgements

This research was supported by the National Natural Science Foundation of China (Nos. 31672322, 31322501 and 41688103), the Beijing Natural Science Foundation (No. 5162016), and the Chinese Universities Scientific Fund (No. 2017TC031). We thank Dr. Ulrike Aspöck and an anonymous reviewer for their valuable comments to improve the manuscript.

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