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ORIGINAL ARTICLE

A new and diverse paleofauna of the extinct snakefly family Baissopteridae from the mid-Cretaceous of Myanmar (Raphidioptera)

Xiumei Lu[1,2] · Weiwei Zhang[3] · Bo Wang[4] · Michael S. Engel[5,6] · Xingyue Liu[1]

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Abstract
Raphidioptera (snakeflies) are the least diverse order among extant Holometabola, representing relicts of their rich Mesozoic paleofauna. Baissopteridae are one of the two major lineages from the Mesozoic, but with a poorly known evolutionary history. Here, we report the first fossil record of Baissopteridae from the mid-Cretaceous of Myanmar, represented by a diverse assemblage including 10 new species in six genera: *Allobaissoptera oligophlebia* gen. et sp. nov., *Baissoptera burmana* sp. nov., *B. maculata* sp. nov., *B. monopoda* sp. nov., *B. pankowskiorum* sp. nov., *B. wangi* sp. nov., *Burmobiassoptera jiaxiaoae* gen. et sp. nov., *Electrobaissoptera burmanica* gen. et sp. nov., *Rhynchobaissoptera hui* gen. et sp. nov., and *Stenobaissoptera xiai* gen. et sp. nov. The new Cretaceous baissopterids provide significant morphological evidence in favor of the monophyly of this family. The morphological diversity in these Cretaceous baissopterids, particularly with some specialized and unique characters, highlights the early radiation of snakeflies formed in the complex tropical forest ecosystem of the mid-Cretaceous.

Keywords New taxon · Paleodiversity · Morphological modification · Systematic position

Introduction

Raphidioptera (snakeflies) are the smallest holometabolous order, with only about 250 extant species (Engel et al. 2018). Adult snakeflies are characterized by a prognathous head, a slenderly elongate prothorax, the presence of a pigmented pterostigma, and a long ovipositor, while their larvae, with a terrestrial life-style, can be recognized by their elongate, flattened body, a prognathous head with chewing-mandibulate mouthparts, and a soft, 10-segmented abdomen. Both adults and larvae are entomophagous, preying on soft-bodied arthropods, but the adults have been found to feed on pollen as well (Aspöck and Aspöck 2009). Raphidioptera belong to the superorder Neuropterida, and has been recovered as the sister group of Megaloptera + Neuroptera in many recent phylogenetic studies based on both morphological and molecular evidence (Aspöck et al. 2001; Aspöck and Aspöck 2008; Wang et al. 2017; Winterton et al. 2018; Vasilikopoulos et al. 2020). Recent snakeflies are considered to be a relict group, comprising only two families, i.e., Raphidiidae and Inocelliidae (Neoraphidioptera), and their distributions are confined to the Northern Hemisphere, in particular to the Holarctic region (Aspöck and Aspöck 2009). Conversely, Raphidioptera were much more diverse in the Mesozoic, documented by abundant

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✉ Xingyue Liu
xingyue_liu@yahoo.com

[1] Department of Entomology, China Agricultural University, Beijing 100193, China

[2] Institute of Ecological and Environmental Protection, Shanghai Academy of Agricultural Sciences, Shanghai 201403, China

[3] Three Gorges Entomological Museum, P.O. Box 4680, Chongqing 400015, China

[4] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

[5] Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas, 1501 Crestline Drive – Suite 140, Lawrence, KS 66045, USA

[6] Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

fossil occurrences with around 90 species in six families (Liu et al. 2014, 2016a). Putative stem-group raphidiopterans have been recorded from deposits dating to the Permian (Shcherbakov 2013; Engel et al. 2018). However, the richest paleodiversity of snakeflies was present during the Cretaceous, comprising over 80 species described from various deposits throughout the Americas and Eurasia (Engel 2002; Liu et al. 2014, 2016a; Lyu et al. 2017a). By the end of the Cretaceous, Raphidioptera suffered considerable losses, and this was apparently already underway prior to the Cretaceous/Tertiary (K/T) event. Tropical snakeflies persisted into the Eocene (Engel 1995, 2002), as did at least one survivor of a Mesozoic family (*Dictyoraphidia* of the Baissopteridae), but seem to have been wiped out by the time of or during the Eocene-Oligocene transition, a period of rapid and dramatic cooling followed by considerable drying in many regions during the Neogene. By perhaps the Oligocene and certainly by the Neogene only cold-adapted snakeflies remained.

Despite the rich fossil record of snakeflies, the evolutionary history of the order and its major familial lineages are poorly understood, especially the early phases of their evolution, and this is due at least in part to the lack of a comprehensive phylogenetic estimation covering both extant and fossil taxa. Previous attempts have been based on limited sampling, and thus did not provide substantial resolution (Ren and Hong 1994; Willmann 1994; Bechly and Wolf-Schwenninger 2011; Liu et al. 2014). A major constraint for phylogenetic analyses combining extant and fossil groups is the incomplete morphological data available from the majority of the known fossil taxa. Actually, most of the described fossil snakeflies are preserved as compressions in sedimentary rock, with mostly wings and sometimes other fragmentary body parts preserved and therefore preserving merely a fraction of the phylogenetically informative characters needed to resolve their relationships. As a result, the generic and specific validity of some fossil snakeflies remains obscure due to poorly preserved material as well as incorrect and incomplete descriptions/drawings of characters. Thus, prior to any attempt at phylogenetic inference, taxonomic revisions of fossil snakeflies based on a critical re-examination of primary types and exploration of exquisitely preserved new materials are greatly needed.

Among the extinct families of Raphidioptera, Baissopteridae are the second largest family after Mesoraphidiidae, with 23 species in seven genera described from the Lower Cretaceous of Eurasia and South America, and the Upper Eocene of North America. Adult baissopterids in general are characterized by the profusely branched RP, MA, and MP veins and the enriched crossveins in both fore- and hind wings (Martynova 1961; Makarkin and Archibald 2014; Lyu et al. 2017a), which make the family easily recognizable from the sparse-veined mesoraphidiids. Remarkably, some species of Baissopteridae are among the largest snakeflies, with forewing spans around 60 mm (Lyu et al. 2017a) [the largest extant species in Raphidioptera is *Sininocellia gigantos* Yang, 1985 (Inocelliidae) with a forewing span of ~47 mm in the female (Liu et al. 2012)]. Most baissopterid species are found in Lower Cretaceous deposits; e.g., the Zaza Formation of Russia, the Yixian Formation of China, and the Crato Formation of Brazil (see Table 1); and they are preserved as compressions. Hitherto, there is only one amber species described in Baissopteridae, which is found in the Lower Cretaceous of Spain, but with only distal portions of the wings preserved (Pérez-de la Fuente et al. 2012). The monophyly of Baissopteridae has been questioned for a long time owing to a lack of convincing autapomorphies (Willmann 1994; Bechly and Wolf-Schwenninger 2011).

Here, we report the first record and a new assemblage of Baissopteridae from the mid-Cretaceous (lowermost Cenomanian) of northern Myanmar, including five new genera and 10 new species. Accordingly, these species constitute the most diverse paleofauna of Baissopteridae currently known. Importantly, these species are well preserved, with not only wings but also the other part of the body, and in particular the male genitalia. The present findings largely enrich the diversity of Mesozoic snakeflies and provide significant new morphological evidence for understanding the phylogeny and evolution of this family.

Material and methods

The amber specimens described herein are from the Hukawng Valley, Tanai Township, Myitkyina District, Kachin State, Myanmar (see Kania et al. 2015: Fig. 1). The age of this deposit is dated to be ~99 million years (the earliest Cenomanian) by U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi et al. 2012). The specimens are currently housed in the Entomological Museum of China Agricultural University (CAU), Beijing; the Century Amber Museum (CAM), Shenzhen; the Three Gorges Entomological Museum (EMTG), Choqing; the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing; and the Natural History Museum, University of Kansas, Lawrence, Kansas (SEMC).

Photographs and drawings were taken and made using a Zeiss SteREO Discovery V12 stereo microscope system or an Olympus SZX12 stereomicroscope. Terminology of wing venation generally follows Aspöck et al. (1980) and Kukalová-Peck and Lawrence (2004). Abbreviations used for wing veins are A, anal vein; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; ScA, subcosta anterior; ScP, subcosta posterior; pt, pterostigma; and pv, pterostigmal veinlet. Abbreviations used for wing cells are *r*, radial cell; *dc*, discal cell; *m*, medial cell; and *doi*, discoidal cell. Abbreviation used for legs is t, tarsomere. Terminology of genitalic sclerites follows Aspöck

Table 1 Fossil species of Baissopteridae

No.	Species	Age	Locality	Reference
1	*Austroraphidia brasiliensis* (Nel, Séméria & Vulcano, 1990)	Lower Cretaceous	Ceará, Pernambuco, Brazil	Nel et al. (1990); Willmann (1994)
2	*Baissoptera bicolor* Lyu, Ren & Liu, 2017	Lower Cretaceous	Beipiao, Liaoning, China	Lyu et al. (2017a)
3	*Baissoptera brasiliensis* Oswald, 1990	Lower Cretaceous	Ceará, Pernambuco, Brazil	Oswald (1990)
4	*Baissoptera cellulosa* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
5	*Baissoptera elongata* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
6	*Baissoptera grandis* Ren in Ren et al., 1995	Lower Cretaceous	Beipiao, Liaoning, China	Ren et al. (1995)
7	*Baissoptera kolosnitsynae* Martynova, 1961	Lower Cretaceous	Baisa, Buryat, Russia	Martynova (1961)
8	*Baissoptera liaoningensis* Ren, 1994	Lower Cretaceous	Beipiao, Liaoning, China	Ren (1994)
9	*Baissoptera lisae* Jepson, Ansorge & Jarzembowski, 2011	Lower Cretaceous	Ceará, Pernambuco, Brazil	Jepson et al. (2011)
10	*Baissoptera martinsoni* Martynova, 1961	Lower Cretaceous	Baisa, Buryat, Russia	Martynova (1961)
11	*Baissoptera pulchra* (Martins-Neto & Nel, 1992)	Lower Cretaceous	Ceará, Pernambuco, Brazil	Engel (2002)
12	*Baissoptera sibirica* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
13	*Baissoptera sinica* Lyu, Ren & Liu, 2017	Lower Cretaceous	Beipiao, Liaoning, China	Lyu et al. (2017a)
14	*Baissoptera? cretaceoelectra* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012	Lower Cretaceous	Moraza, Burgos, Spain	Pérez-de La Fuente et al. (2012)
15	*Cretoraphidiopsis bontsaganensis* (Ponomarenko, 1988)	Lower Cretaceous	Bon-Tsagan Nuur, Bayankhongor, Mongolia	Ponomarenko (1988); Engel (2002)
16	*Cretoraphidia certa* Ponomarenko, 1993	Lower Cretaceous	Romanovka, Transbaikalia, Russia	Ponomarenko (1993)
17	*Cretoraphidia macrocella* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
18	*Cretoraphidia magna* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
19	*Cretoraphidia reticulata* Ponomarenko, 1993	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
20	*Lugala longissima* (Ponomarenko, 1988)	Lower Cretaceous	Bon-Tsagan Nuur, Bayankhongor, Mongolia	Willmann (1994)
21	*Microbaissoptera minima* (Ponomarenko, 1993)	Lower Cretaceous	Baisa, Buryat, Russia	Ponomarenko (1993)
22	*Microbaissoptera monosticha* Lyu, Ren & Liu, 2017	Lower Cretaceous	Beipiao, Liaoning, China	Lyu et al. (2017a)
23	*Allobaissoptera oligophlebia* gen. et sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
24	*Baissoptera burmana* sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
25	*Baissoptera maculata* sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
26	*Baissoptera monopoda* sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
27	*Baissoptera pankowskiorum* sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
28	*Baissoptera wangi* sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
29	*Burmobiassoptera jiaxiaoae* gen. et sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
30	*Electrobaissoptera burmanica* gen. et sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
31	*Stenobaissoptera xiai* gen. et sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
32	*Rhynchobaissoptera hui* gen. et sp. nov.	Upper Cretaceous	Tanai, Kachin, Myanmar	Present paper
33	*Dictyoraphidia veterana* (Scudder, 1890)	Upper Eocene	Florissant, Colorado, USA	Makarkin and Archibald (2014)

and Aspöck (2008). Abbreviations used for terminalia are T, tergum; S, sternum; gx, gonocoxite; gst, gonostylus; op, ovipositor; and e, ectoproct.

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Systematic paleontology

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

Diagnosis: This family is characterized by the following characters: (1) ocelli present; (2) RA veinlet within pterostigma usually present; (3) forewing M with stem usually shorter than *doi*1; (4) forewing M and CuA diverging at angle of > 40°; (5) venation enriched, especially crossvenation, forming at least three radial cells in forewing and four radial cells in hind wing, at least two discal cells in both fore- and hind wings, usually four or more discoidal cells in both fore- and hind wings; (6) male gonocoxites IX paired and shell-like; (7) male gonapophyses IX reduced.

Remarks: The familial diagnostic characters were previously revised by Makarkin and Archibald (2014). This family is generally defined by the enriched venation, which was considered to be secondary and possibly a familial autapomorphy

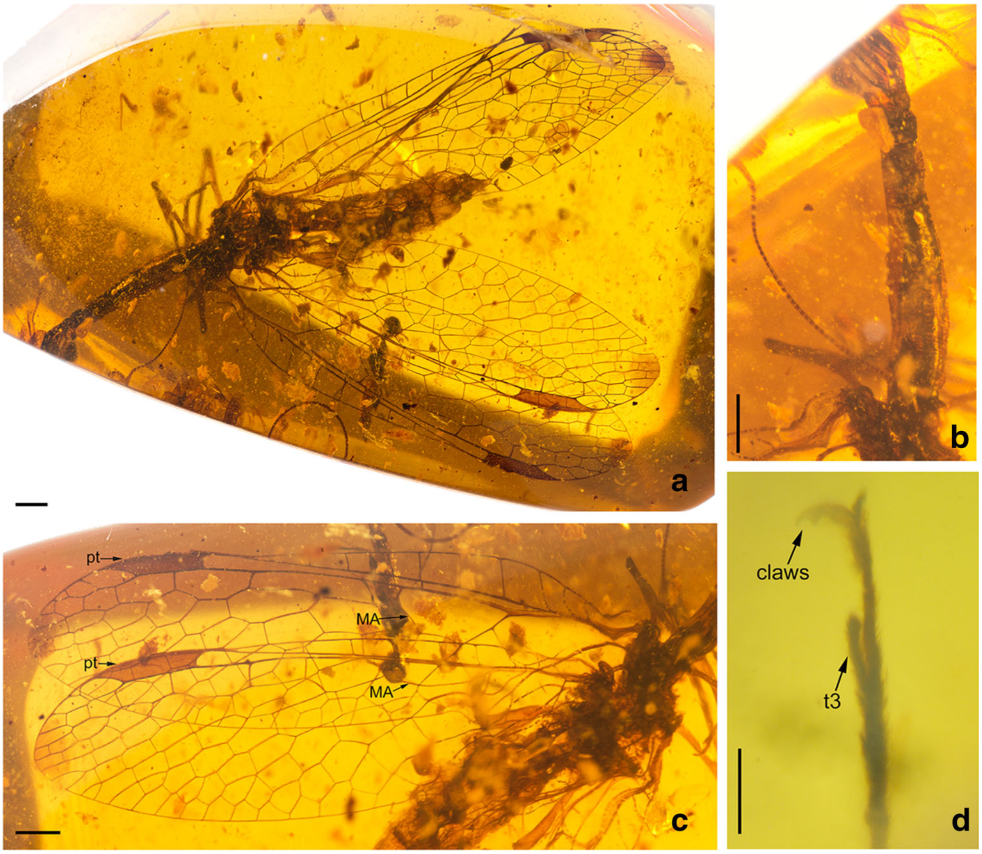


Fig. 1 *Baissoptera burmana* sp. nov., holotype: CAU-BA-XF-20001. **a** Habitus, dorsal view. **b** Head and prothorax, dorsal view. **c** Left wings. **d** Right hind leg. Scale bar = 1.0 mm (**a**–**c**); 0.1 mm (**d**)

by Makarkin and Archibald (2014). Exceptionally, in some small-sized baissopterids, as described herein (e.g., *Allobaissoptera oligophlebia* gen. et sp. nov.), the wing venation is much sparser than in species of *Baissoptera*, but similar in number to some mesoraphidiids, such as *Cretoinocellia cellulosa* Ponomarenko, 1988. However, we found two additional characters that are useful to distinguish baissopterids from such mesoraphidiids. First, the stem of forewing M is usually shorter than *doi*1 and diverged with CuA at an angle > 40° in Baissopteridae. The combination of these two characters is present in all Burmese amber baissopterids as well as most baissopterids from other deposits (see Willmann 1994; Lyu et al. 2017a). In Mesoraphidiidae, the forewing M has its stem usually as long as or longer than *doi*1 and diverged with CuA at an angle ~ 30°. Second, there are numerous forewing *doi* in medium- to large-sized baissopterids; otherwise, two or three forewing *doi* are present but not triangularly arranged, and two forewing *dc* and three forewing *m* are present in small-sized baissopterids. In Mesoraphidiidae, there are three forewing *doi* triangularly arranged, which is a typical feature of this family, while in some minute mesoraphidiids with one or two forewing *doi*, the number of forewing discal and medial cells are also decreased to one or two. Based on the revised familial diagnosis present above, the baissopterid affinity of *Cretoraphidiopsis bontsaganensis* (Ponomarenko 1988) from the Lower Cretaceous of Mongolia is suspect because the configuration of the proximal part of forewing M is identical to that in Mesoraphidiidae (see Ponomarenko 1988: Fig. 6). However, the number and arrangement of forewing *doi* are baissopterid-like in this species. If truly a baissopterid as other traits suggest, then the condition of the forewing M is either a secondary reversal to a putatively plesiomorphic condition or perhaps this species is sister to the remainder of the family. Only a future phylogenetic analysis will determine which scenario is accurate. It is also notable that the configuration of the forewing M stem is greatly differed among the species of *Cretoraphidia* Ponomarenko, 1993 from the Lower Cretaceous of Russia. In *Cretoraphidia certa* Ponomarenko, 1993 (the type species of the genus), the forewing M has an extremely long stem, while in *C. macrocella* Ponomarenko, 1993 and *C. reticulata* Ponomarenko, 1993, this vein is short or very short, respectively (see Ponomarenko 1993: Figs. 7, 8, 9, 10, and 11). The accuracy of the original drawings as well as the baissopterid affinity of these species needs further consideration once the primary types are re-examined. Besides the wing character, the shell-like male gonocoxite IX is present in all of the currently described species with male genitalia preserved. Interestingly, this feature is quite similar to that in the extant snakefly family Inocelliidae. The shell-like male gonocoxite IX is known to be a reliable character to distinguish Inocelliidae from the other extant family, Raphidiidae (Aspöck et al. 1991). However, whether this character can be used to distinguish Baissopteridae from Mesoraphidiidae is still unclear.

Genus *Baissoptera* Martynova, 1961 (Figs. 1, 2, 3, 4, 5, 6, and 7; Figs. S1–S2)

Synonyms: *Cratoraphidia* Martins-Neto and Nel, 1992: 426. Type species: *Cratoraphidia pulchra* Martins-Neto and Nel, 1992, by original designation. Synonymy by Engel (2002).

Rudiraphidia Ren, 1997: 175. Type species: *Baissoptera liaoningensis* Ren, 1994, by original designation. Synonymy by Engel (2002).

Type species: *Baissoptera martinsoni* Martynova, 1961.

Revised diagnosis: Medium- to large-sized (forewing length ~ 10.0–28.0 mm); head nearly rectangular, about twice as long as wide, with vertex slightly longer than compound eye (diameter of compound eye about one-half head length). Tarsomere III simple, symmetrically bilobed, or asymmetrically bilobed. Forewing long elliptical, ~ 3.0–4.0× as long as wide; ScP terminating into costal margin posteriad midpoint of wing; pterostigma ~ 3.5–8.0× as long as wide, closed by a crossvein proximally, mostly with one RA veinlet incorporated; MA originating at or close to initial branching point of MP; three or more radial cells, three or more discal cells, and five or more discoidal cells present; three cua-cup crossveins present. Hind wing with four or more radial cells, three or more discal cells, and five or more discoidal cells; stem of MA proximally fused with MP or R ("fusion with R" described mostly in compression fossils, in which the true fusing condition is actually hard to discern); three mp-cua crossveins, 1mp-cua connecting to stem of MP at or slightly proximad its midpoint, distinctly inclined or slightly vertical to MP; CuA simple or distally forked. Male gonocoxite IX shell-like, but varied in length and width.

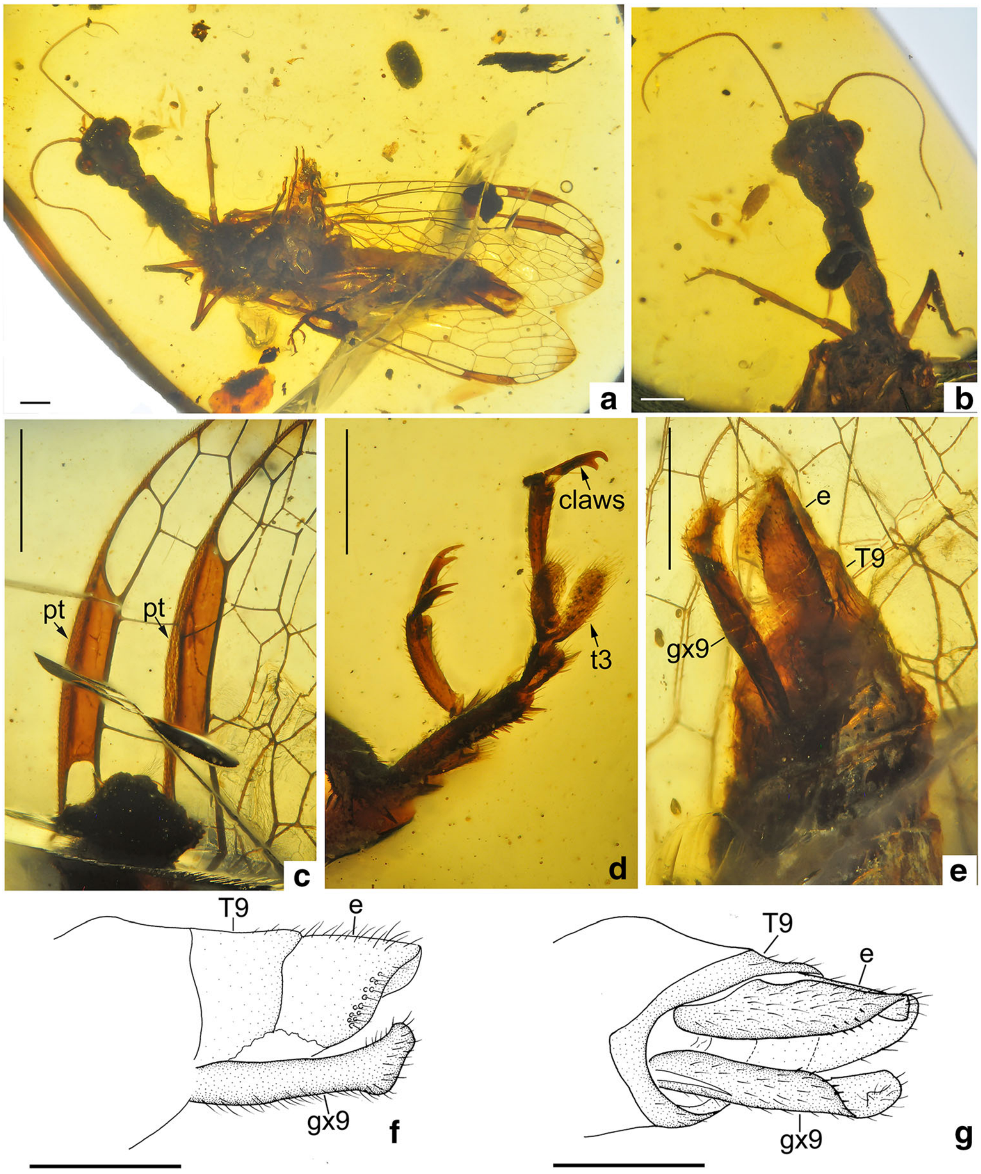


Fig. 2 *Baissoptera maculata* sp. nov., holotype: NIGP163570. **a** Habitus, ventral view. **b** Head and prothorax, dorsal view. **c** Pterostigma of left wings. **d** Tarsus and pretarsus of hind leg. **e** Male genitalia, ventral view. **f** Drawing of male genitalia, lateral view. **g** Drawing of male genitalia, ventral view. Scale bar = 1.0 mm (**a**, **b**, **e**–**g**); 2.0 mm (**c**); 0.25 mm (**d**)

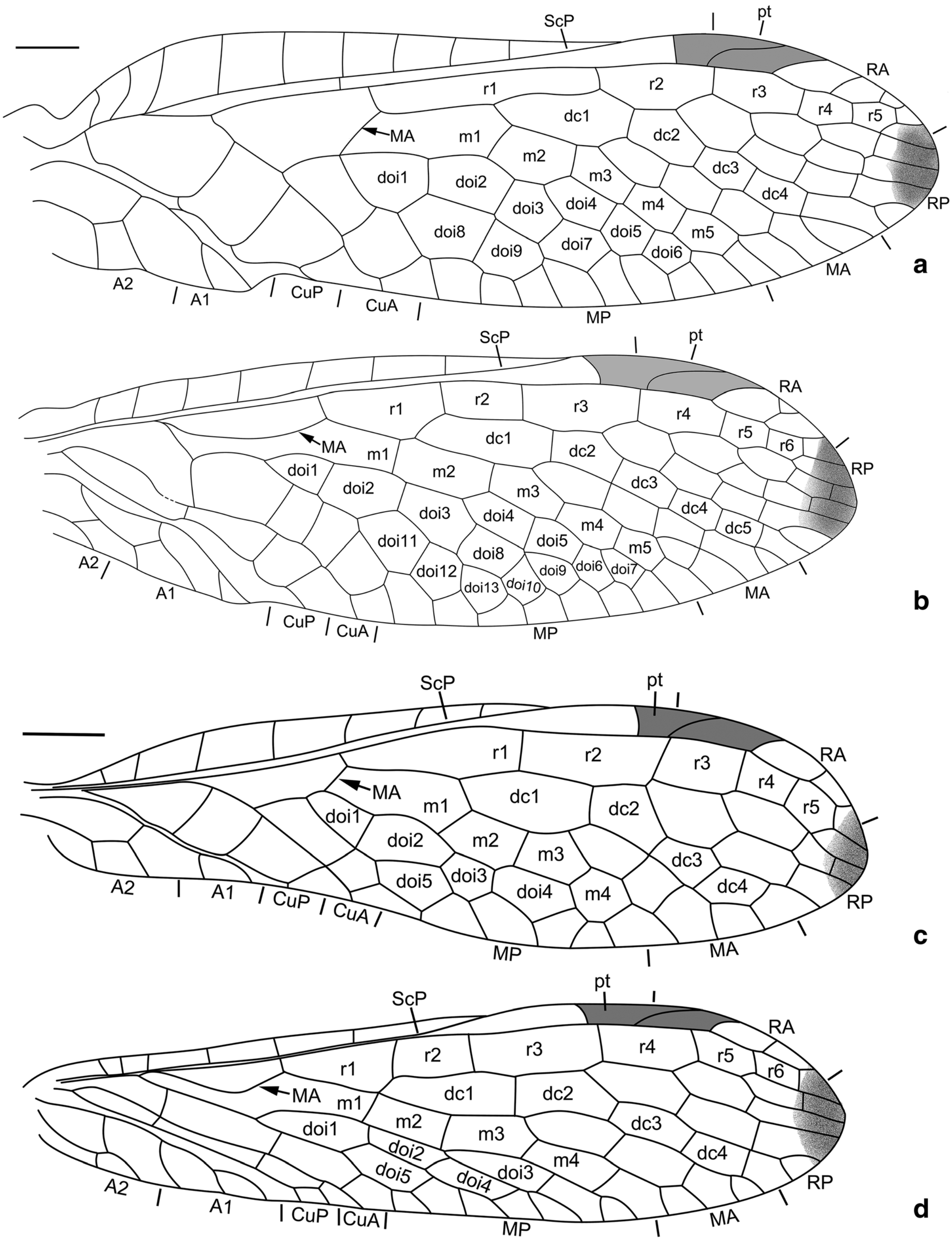


Fig. 3 Wing venations of Baissopteridae. **a**, **b** *Baissoptera burmana* sp. nov., holotype: CAU-BA-XF-20001. **a** Left forewing. **b** Left hind wing. **c**, **d** *Baissoptera maculata* sp. nov., holotype: NIGP163570. **c** Left forewing. **d** Left hind wing. Scale bar = 1.0 mm

Baissoptera burmana sp. nov. (Figs. 1 and 3a, b; Figs. S1–S2)

Diagnosis: Tarsomere III asymmetrically bilobed, with a long and a short lobe; a dark marking present on apex in both fore- and hind wings; forewing MA with stem separating at initial branching point of MP; nine forewing *doi* and 13 hind wing *doi* present.

Description: Holotype CAU-BA-XF-20001. Female. Body (head largely not preserved) length 15.4 mm; pronotum length 4.4 mm, width 0.9 mm; mesothorax length 1.4 mm,

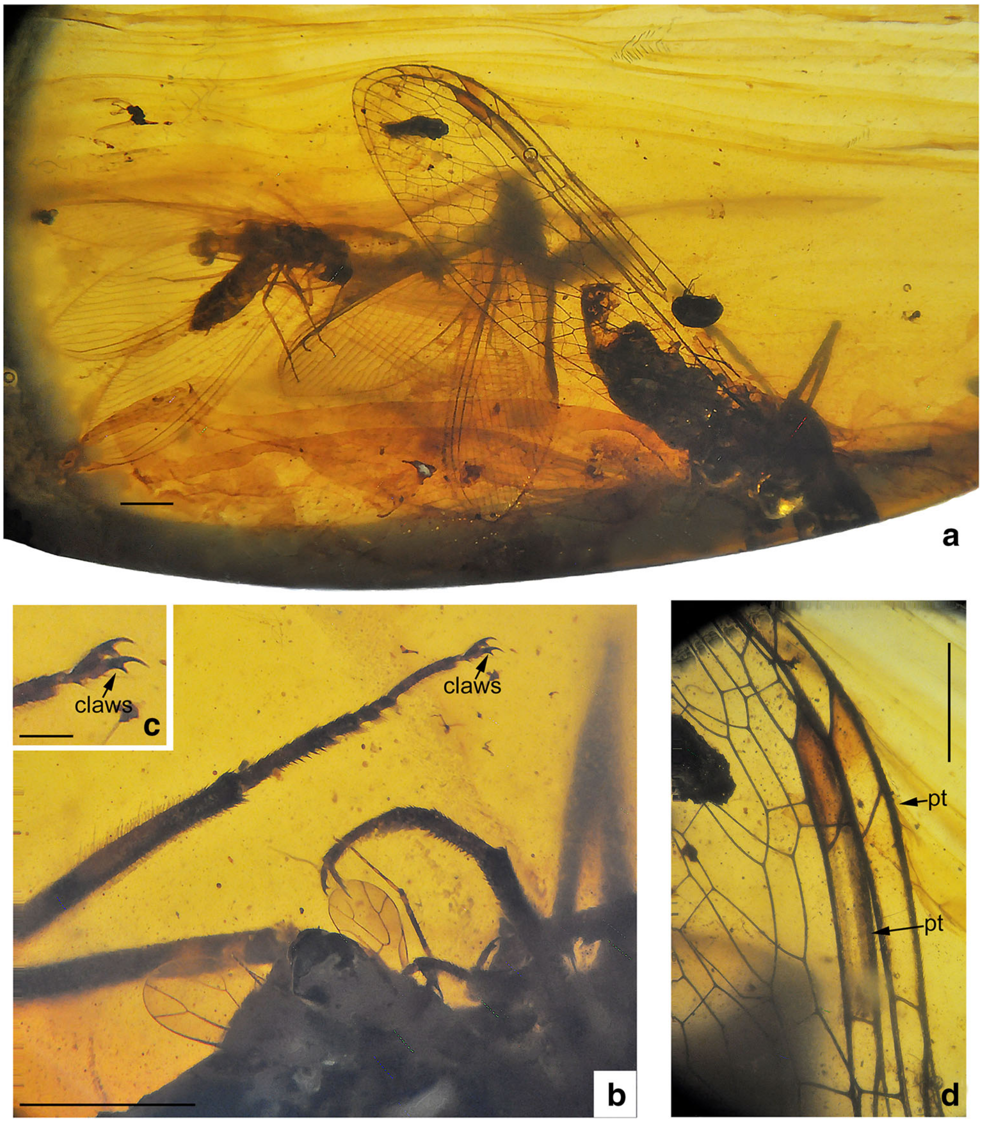


Fig. 4 *Baissoptera monopoda* sp. nov., holotype: NIGP163571. **a** Habitus, lateral view. **b** Foreleg. **c** Pretarsus of foreleg. **d** Pterostigma of fore- and hind wings. Scale bar = 1.0 mm (**a**, **b**, **d**); 0.25 mm (**c**)

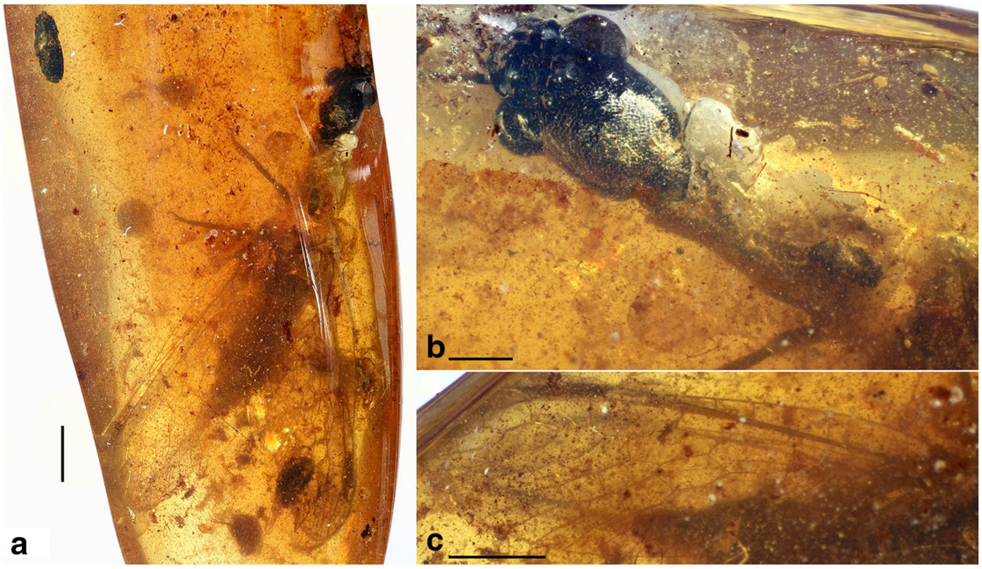


Fig. 5 *Baissoptera pankowskiorum* sp. nov., holotype: SEMC F000385 (Bu-131). **a** Habitus, dorsal view. **b** Head, dorsal view. **c** Left forewing. Scale bar = 2.0 mm (**a**, **c**); 1.0 mm (**b**)

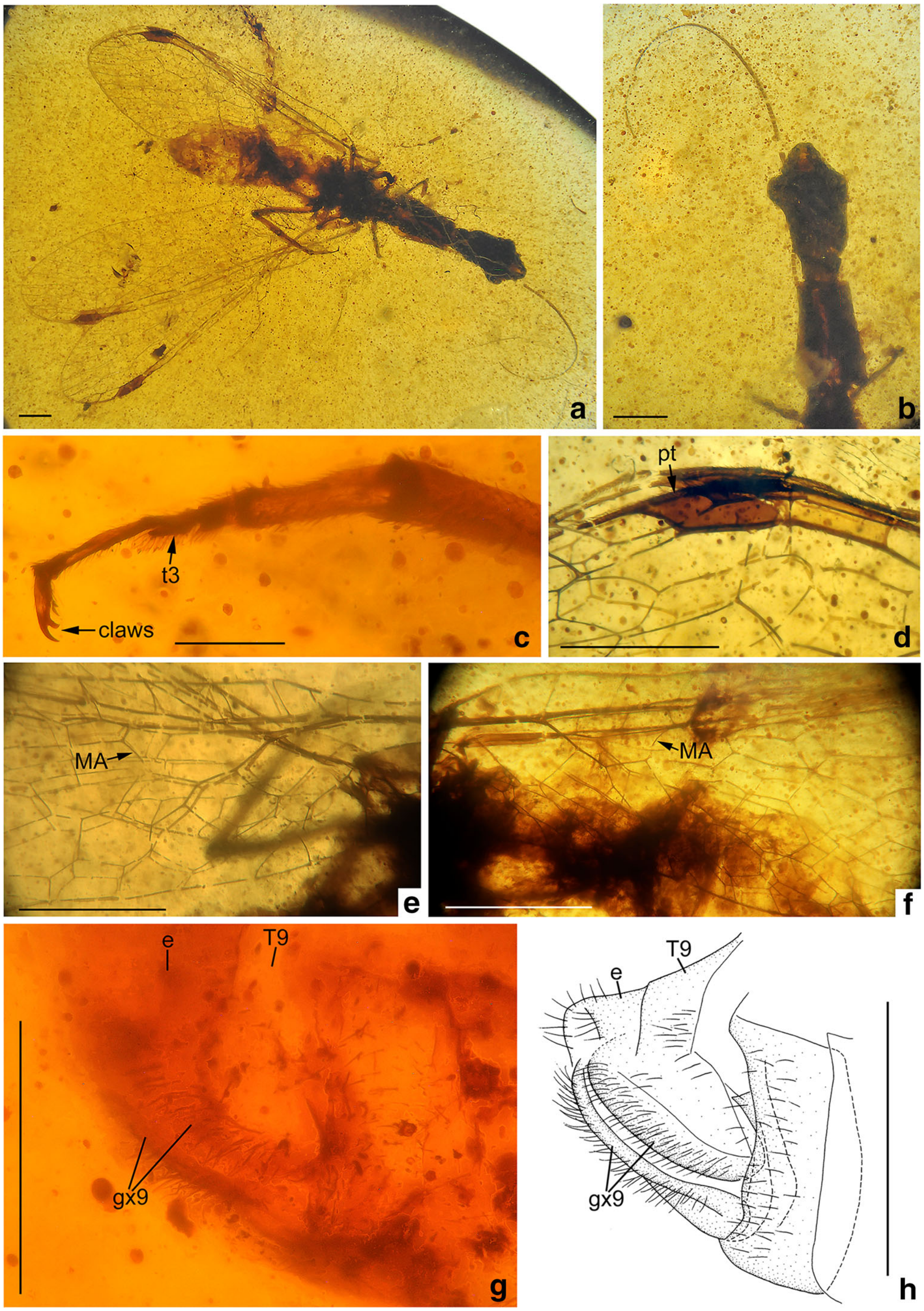


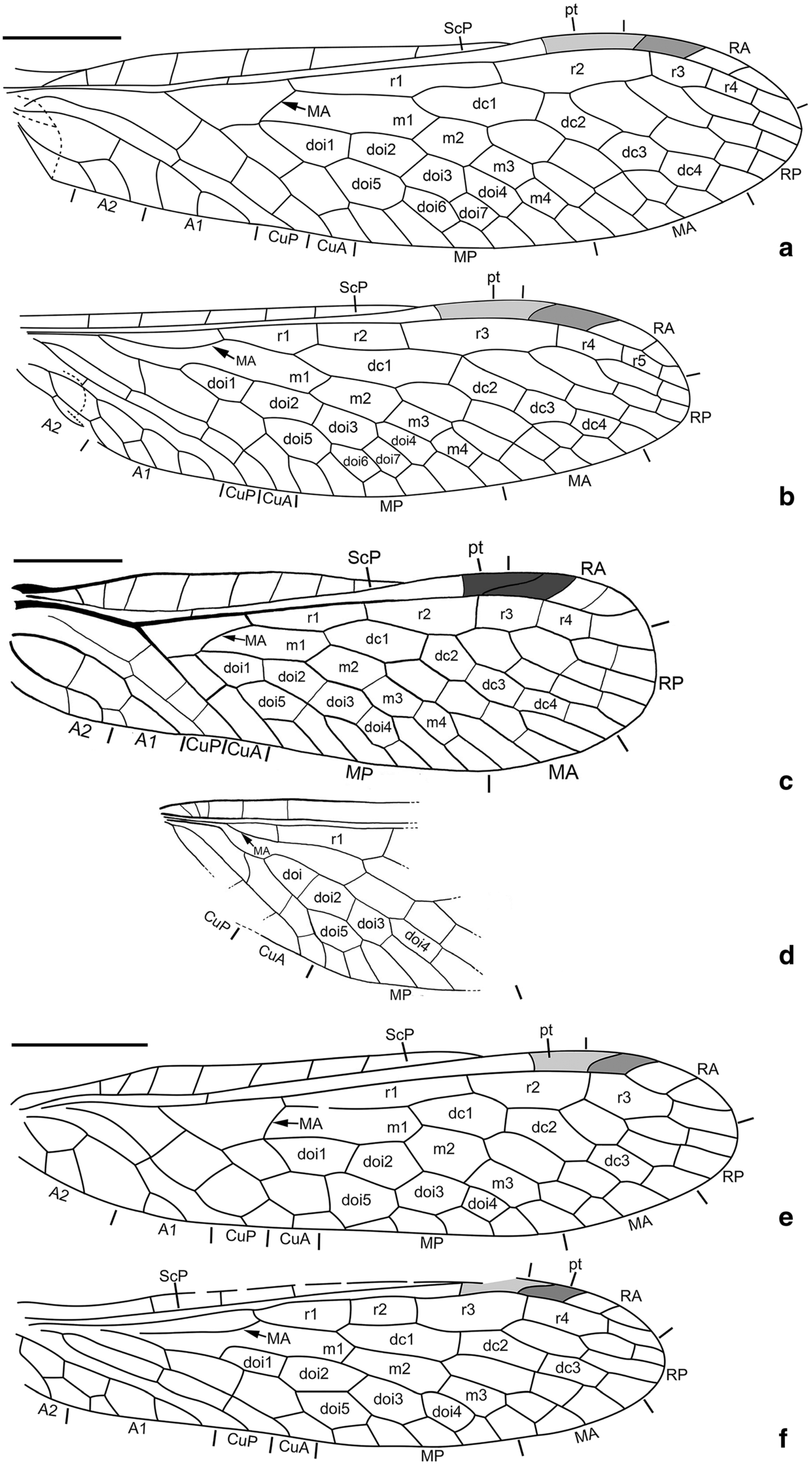
Fig. 6 *Baissoptera wangi* sp. nov., holotype: CAU-BA-WN-20001. **a** Habitus, ventral view. **b** Head and prothorax, ventral view. **c** Hind leg. **d** Pterostigma of right wings. **e** Left forewing. **f** Right forewing. **g** Male genitalia, lateral view. **h** Drawing of male genitalia, lateral view. Scale bar = 1.0 mm (**a**, **b**, **d**, **g**, **h**); 0.5 mm (**e**, **f**); 0.25 mm (**c**)

width 2.7 mm; metathorax length 1.3 mm, width 2.6 mm; forewing length 14.6 mm, width 4.1 mm; hind wing length 13.5 mm, width 4.0 mm; abdomen length 6.3 mm.

Body dark brown. Prothorax slender. Legs slender, densely setose; tarsomere III asymmetrically bilobed, with an elongate narrow lobe and a short narrow lobe; pretarsal claws with proximal half broad, distally forked into a subtriangular projection.

Forewing: Long elliptical, ~3.0× as long as wide; costal space broadened at proximal 1/3, with nine crossveins; ScP terminating into costal margin at distal 2/5 of wing; five simple RA veinlets present; pterostigma long, ~3.5× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at second veinlet of RA, with a slightly sinuate RA veinlet incorporated; five radial crossveins present, five radial cells gradually shortened, *r*1 strongly narrowed and elongate; RP forked slightly proximad its midpoint, with five pectinate branches, most of them simple except posterior-most one forked marginally; four rp-ma crossveins, forming four discal cells; MA with stem originating at branching point

Fig. 7 Wing venations of Baissopteridae. **a**, **b** *Baissoptera monopoda* sp. nov., holotype: NIGP163571. **a** Forewing. **b** Hind wing. **c**, **d** *Baissoptera pankowskiorum* sp. nov., holotype: SEMC F000385 (Bu-131). **c** Forewing. **d** Hind wing. **e**, **f** *Baissoptera wangi* sp. nov., holotype: CAU-BA-WN-20001. **e** Left forewing. **f** Left hind wing. Scale bar = 2.0 mm



between MP1 and MP2; MA deeply forked at its proximal 1/3, with two marginally forked branches; five ma-mp crossveins, forming five medial cells; MP deeply forked, with nine short terminal branches and nine discoidal cells arranged in three series; CuA and CuP simple; three cua-cup crossveins present; A1 and A2 forked.

Hind wing: Slightly shorter than but almost as wide as forewing; costal space narrow, with seven crossveins preserved; ScP terminating into costal margin at distal 1/3 of wing; four RA veinlets, with third one forked; pterostigma similar to that of forewing but slightly paler and starting closer to termination of ScP; a distinctly curved RA veinlet present within pterostigma; six radial crossveins present, *r*3 longest; RP forked slightly proximad its midpoint, with five pectinate branches, most of them simple except posterior-most one forked marginally; five rp-ma crossveins, forming five discal cells; MA with stem originating from base of MP stem, long and sinuate; MA initially branching at its proximal 1/3, with two marginally forked branches; five ma-mp crossveins, forming five medial cells; MP deeply forked, with eight short terminal branches and 13 discoidal cells arranged in three series; five mp-cua crossveins, with 1mp-cua slightly vertical to stem of MP; CuA and CuP simple; three cua-cup crossveins present; A1 with four pectinate branches; A2 simple.

Genitalia largely not preserved.

Paratype EMTG BU-002258 (Fig. S1A-C). Adult with sex unknown. Head and prothorax entirely lacking. Meso- and metathorax, and abdomen partially preserved. Tarsomere III in hind leg asymmetrically bilobed as in holotype. Wings partially preserved; right fore- and hind wings with distal markings partly preserved; venation largely similar to that in holotype.

Paratype EMTG BU-002190 (Fig. S1D-E). Adult with sex unknown. Only head, thorax, and basal parts of right fore- and hind wings preserved. Head nearly rectangular, length 3.0 mm, width 1.5 mm, with clypeus + labrum 0.5 mm long, vertex 1.0 mm long; compound eye length 1.1 mm, width 0.5 mm; ocelli present; antennae with more than 60 flagellomeres. Prothorax much narrower than head, but much wider on proximal half, 3.0 mm long, 1.0 mm wide; meso- plus metathorax 4.2 mm long. Tarsomere III in all preserved legs asymmetrically bilobed.

Paratype EMTG BU-002104 (Fig. S2). Male pupa. Exarate. Body length 14.0 mm; head nearly rectangular, length 3.2 mm, width 1.1 mm, with vertex 1.1 mm long; compound eye length 1.0 mm, width 0.5 mm; prothorax length 1.9 mm, width 0.8 mm; tarsomere 3 asymmetrically bilobed. Genitalia with a pair of gonocoxites IX and ectoproct discernible; gonocoxite IX subtriangular, slightly longer than wide, with a spinous apex.

Type material: Holotype: CAU-BA-XF-20001: Amber piece with a nearly complete adult female of *Baissoptera burmana* sp. nov., with apical part of head not preserved. Paratype: EMTG BU-002190: Amber piece with an adult of *B. burmana* sp. nov., with head and thorax preserved. Paratype: EMTG BU-002258: Amber piece with an incomplete adult of *B. burmana* sp. nov., with wings partly preserved. Paratype: EMTG BU-002104: Amber piece with a pupa of *B. burmana* sp. nov.

Etymology: The specific epithet "*burmana*" (meaning, "Burma") refers to the occurrence of the new species in Myanmar. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:D490D7F7-ECF7-4E42-884D-9635E2FCEA7D.

Remarks: The new species has a distinct dark marking on the apex of both fore- and hind wings, and this feature is only shared by another Burmese amber species of *Baissoptera*, i.e., *B. maculata* sp. nov. (see below). However, the new species differs from *B. maculata* sp. nov. by the asymmetrically bilobed tarsomere III, the broader wings, the stem of MA in forewing originating from the branching point between MP1 and MP2, and the presence of more discoidal cells in both fore- and hind wings. In *B. maculata* sp. nov., tarsomere III is symmetrically bilobed, the wings are apparently narrower than that of *B. burmana* sp. nov., the stem of forewing MA originates from MP1 (slightly distad branching point between MP1 and MP2), and there are only five discoidal cells in both fore- and hind wings.

Baissoptera maculata sp. nov. (Figs. 2 and 3c, d)

Diagnosis: Tarsomere III symmetrically bilobed, with a pair of ovoid lobes; a dark marking present on apex of both fore- and hind wings; forewing MA with stem originating slightly distad initial branching point of MP; five *doi* present in both fore- and hind wings.

Description: Holotype NIGP163570. Male. Body length 13.9 mm; head length 2.3 mm, width 1.3 mm, with clypeus + labrum 0.5 mm long, vertex 1.1 mm long; compound eye length 0.8 mm, width 0.5 mm; antenna (partly preserved) length 5.3 mm; occiput length 0.1 mm; pronotum length 2.6 mm, width 0.8 mm; meso- plus metathorax length 2.2 mm; forewing length 11.9 mm, width 3.1 mm; hind wing length 10.8 mm, width 2.9 mm; abdomen length 6.7 mm.

Body blackish brown; head nearly rectangular, with vertex nearly as long as compound eye; occiput short; clypeus anteriorly truncate; compound eyes ovoid; ocelli present; antennae with about 70 flagellomeres.

Prothorax slender, slightly longer than head; meso- plus metathorax almost as long as prothorax. Legs short, slender, densely setose; tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pretarsal claw forked at distal 1/3 into acutely tapering tooth.

Forewing: Long elliptical, ~3.5× as long as wide; costal space broadened at proximal 1/3, with seven crossveins; ScP terminating into costal margin slightly distad midpoint of wing; four simple RA veinlets present; pterostigma ~5.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally terminating at second veinlet of RA, with a slightly curved RA veinlet incorporated; five radial crossveins present, five radial cells gradually shortened, *r*1 elongate and broadened distad; RP forked proximad its midpoint, with four simple branches; four rp-ma crossveins, forming four discal cells; MA with stem originated at MP1, slightly distad initial branching point of MP; MA deeply forked at its proximal 2/5, with MA1 marginally forked and MA2 simple; four ma-mp crossveins, forming four medial cells; MP deeply forked, with five terminal branches and five discoidal cells arranged in two series; CuA and CuP simple; three cua-cup crossveins present; A1 and A2 bifurcate.

Hind wing: Slightly shorter and narrower than forewing; costal space narrow, with six crossveins preserved; ScP terminating into costal margin slightly distad midpoint of wing; four simple RA veinlets present; pterostigma similar to that of forewing but slightly narrower, a strongly inclined but slightly curved RA veinlet present within pterostigma; six radial crossveins present, *r*3 longest; RP forked slightly proximad its midpoint, with four branches, most of them simple except posterior-most one forked marginally; four rp-ma crossveins, forming four discal cells; MA with stem originating from base of MP stem, elongate and distinctly sinuate; MA initially branched slightly proximad its midpoint, with two marginally forked branches; four ma-mp crossveins, forming four medial cells; MP deeply forked, with eight terminal branches and five discoidal cells arranged in three series; three mp-cua crossveins, with 1mp-cua nearly vertical to stem of MP; CuA simple; CuP with a marginal fork; three cua-cup crossveins present; A1 with four pectinate simple branches; A2 simple.

Terminalia visible in lateral and ventral views; tergum IX broad, ventrally fused with sternum IX; gonocoxites IX paired, slenderly shell-like, nearly as long as tergum IX plus ectoproct, much longer than wide, with apex slightly curved dorsad in lateral view; ectoproct large, nearly as long as tergum IX, slightly protruding posterodorsad, with trichobothria present along posterior margin.

Type material: Holotype: NIGP163570: Amber piece with a complete adult male of *Baissoptera maculata* sp. nov.

Etymology: The specific epithet "*maculata*" refers to the presence of a distinct marking on apices of both fore- and hind wings in the new species. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:FA5F16F8-23A6-4B88-B70E-40818DF44576.

Baissoptera monopoda sp. nov. (Figs. 4 and 7a, b)

Diagnosis: Tarsomere III not bilobed; pterostigma bicolored in both fore- and hind wings; forewing MA with stem separating at initial branching point of MP; seven *doi* present in both fore- and hind wings.

Description: Holotype NIGP163571. Sex unknown. Meso- plus metathorax length 2.6 mm; forewing length 13.4 mm, width 3.4 mm; hind wing length 12.1 mm, width 3.3 mm; abdomen length 5.6 mm.

Body blackish brown. Head not preserved.

Pronotum partly preserved, slender. Meso- and metathorax robust. Legs slender, densely setose; tarsomere III not bilobed; pretarsal claws forked at distal 1/3 into an acutely tapering tooth.

Forewing: Narrowly elongate, ~4.0× as long as wide; costal space narrow, slightly broadened at proximal 1/3, with six crossveins; ScP terminating into costal margin at distal 2/5 of wing; pterostigma long, ~8.0× as long as wide, bicolored, with part distad incorporated RA veinlet much darker, closed by a crossvein proximally, distally ending at second veinlet of RA, with a straight but inclined RA veinlet incorporated; four radial crossveins, four radial cells gradually shortened, *r*1 longest, *r*2 broadest; RP forked proximad its midpoint, with four simple branches; four rp-ma crossveins, forming four discal cells; MA with stem originating at branching point of MP1 and MP2; MA deeply forked at its proximal 1/3, MP1 forked slightly distad its midpoint, MP2 deeply forked at its proximal 1/3, branching of MP1 much shorter than branching of MP2; four ma-mp crossveins, forming four medial cells; MP deeply forked, with six terminal branches and seven discoidal cells arranged in two series; CuA and CuP simple; three cua-cup crossveins present; A1 with three simple branches; A2 bifurcate.

Hind wing: Slightly shorter than but almost as wide as forewing; costal space narrow, with five crossveins preserved; ScP terminating into costal margin at distal 2/5 of wing; four simple RA veinlets present; pterostigma similar that of forewing, but with a short and slightly curved RA veinlet incorporated; five radial crossveins present, *r*3 longest; RP forked proximad its midpoint, with four simple branches; four rp-ma crossveins, forming four discal cells; MA with stem originated from base of MP stem, long and sinuated; branching condition of MA similar to that of forewing; four ma-mp crossveins, forming four medial cells; MP deeply forked, with six terminal branches and seven discoidal cells arranged in two series; three mp-cua crossveins, with 1mp-cua distinctly inclined to stem of MP; CuA and CuP simple; three cua-cup crossveins present; A1 with five pectinate simple branches; A2 simple.

Genitalia not preserved.

Type material: Holotype: NIGP163571: Amber piece with an incomplete adult of *Baissoptera monopoda* sp. nov., with head, apical parts of prothorax, and forewing not preserved.

Etymology: From the Greek "*mono-*" (single) and "-*podus*" (leg), in reference to the unpaired tarsomere III in the new species. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:65528BCB-6345-4523-858D-CC179EB14237.

Remarks: The new species mostly resembles *B. wangi* sp. nov. in having a similar wing shape, bicolored pterostigma, and forewing MA stem originating from the initial branching of MP. However, the new species can be distinguished from *B. wangi* sp. nov. and other species of *Baissoptera* by the unpaired tarsomere III. In addition, the venation of *B. wangi* sp. nov. is relatively reduced by comparison to that of the present new species, with only five *doi* in both fore- and hind wings (see below).

Baissoptera pankowskiorum sp. nov. (Figs. 5 and 7c, d)

Diagnosis: Tarsomere III symmetrically bilobed, with a pair of short lobes; forewing MA with stem originating slightly distad initial branching point of MP; hind wing MA with stem nearly half length of *r*1; five *doi* present in both fore- and hind wings.

Description: Holotype SEMC F000385 (Bu-131). Female. Body length 14.7 mm; head length 3.1 mm, width 1.8 mm; compound eye length 0.8 mm; pronotum length 3.2 mm, width 1.5 mm; forewing length 11.7 mm, width 3.6 mm; ovipositor length 4.7 mm (beyond abdominal apex).

Body dark brown; head nearly rectangular, with vertex slightly longer than compound eye; occiput short; compound eyes ovoid; ocelli present; antenna with at least 75 flagellomeres.

Prothorax elongate, slightly longer than head; meso- plus metathorax slightly shorter than pronotum. Legs short, slender, densely setose; tarsomere III symmetrically bilobed, with a pair of short lobes.

Forewing: Long elliptical, ~ 3.0× as long as wide; costal space slightly broadened at proximal 1/3, with eight crossveins; ScP terminating into costal margin slightly distad midpoint of wing; four simple RA veinlets present; pterostigma ~ 4.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ended at second veinlet of RA, with a long, strongly inclined and slightly sinuate RA veinlet incorporated; four radial crossveins present, *r*2 nearly as long as *r*1 but much broader than *r*1, *r*3 and *r*4 much shorter; RP forked slightly proximad its midpoint, with four simple branches; four rp-ma crossveins, forming four discal cells; MA with stem originating at MP1, slightly distad initial branching point of MP; MA deeply forked at its proximal 1/3, MP1 forked at its distal 1/3; MP2 deeply forked at its midpoint, branching of MP1 slightly shorter than branching of MP2; four ma-mp crossveins, forming four medial cells; MP deeply forked, with six terminal branches and five discoidal cells arranged in two series; CuA and CuP simple; three cua-cup crossveins present; A1 and A2 respectively bifurcate.

Hind wing: Distal part not preserved; costal space narrow, proximally with five costal crossveins; MA with stem originated from R, short and nearly straight, nearly half length of *r*1; MP deeply forked, with six terminal branches and five discoidal cells arranged in two series; three mp-cua crossveins, with 1mp-cua distinctly sinuated and inclined to stem of MP.

Genitalia visible in dorsal view; ovipositor (incomplete as preserved) robust, straight, length beyond abdominal apex (as preserved), with numerous, minute setae.

Type material: Holotype: SEMC F000385 (Bu-131): Amber piece with a complete adult female of *Baissoptera pankowskiorum* sp. nov.

Etymology: The new species is named in honor of the Mark Pankowski family for their commendatory support of paleoentomological research. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:3745890B-3CA4-40E2-BC17-12AFFE7B50BD.

Remarks: The new species can be distinguished from the other species of *Baissoptera* by having the combination of three gradate series of crossveins in the RP and MA field and five *doi* in the forewing. These two characters do not co-exist in the other species of *Baissoptera*. Moreover, the stem of hind wing MA is very short, nearly one-half length of *r*1 in the new species, while it is as long as or slightly longer than hind wing *r*1 in the other species of *Baissoptera* in which the hind wing is preserved.

Baissoptera wangi sp. nov. (Figs. 6 and 7e, f)

Diagnosis: Tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pterostigma bicolored in both fore- and hind wings; forewing MA with stem originating at initial branching point of MP; five *doi* present in both fore- and hind wings; gonocoxites IX much wider than long.

Description: Holotype CAU-BA-WN-20001. Male. Body length 12.1 mm; head length 2.4 mm, width 1.1 mm, with clypeus + labrum 0.8 mm long, vertex 0.9 mm long; compound eye length 0.8 mm, width 0.3 mm; antenna length 5.9 mm; occiput length 0.3 mm; pronotum length 2.0 mm, width 1.1 mm; meso- plus metathorax length 2.3 mm; forewing length 11.0 mm, width 2.9 mm; hind wing length 10.7 mm, width 2.6 mm; abdomen length 5.0 mm.

Body blackish brown; head nearly rectangular, with vertex slightly longer than compound eye; occiput short; compound eyes ovoid; antenna with about 70 flagellomeres.

Prothorax stout, as long as head; meso- plus metathorax almost as long as prothorax. Legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pretarsal claws forked at distal 1/3 into an acutely tapering tooth.

Forewing: Narrowly elongate, ~ 4.0× as long as wide; costal space narrow, slightly broadened at proximal 2/5, with seven crossveins; ScP terminating into costal margin at distal 2/5 of wing; pterostigma ~ 5.0× as long as wide, bicolored (area distad incorporated RA veinlet much darker), closed by a crossvein proximally, distally ending at second veinlet of RA, with a sinuate RA veinlet incorporated; three radial crossveins present, three radial cells gradually shortened, *r*1 slenderly elongate; RP forked at its midpoint, with three simple branches; three rp-ma crossveins, forming three discal cells; MA with stem originated at initial branching point of

MP; MA deeply forked at its proximal 1/3, MA1 simple, MA2 deeply forked at its midpoint; three ma-mp crossveins, forming three medial cells; MP deeply forked, with five terminal branches and five discoidal cells; CuA and CuP simple; three cua-cup crossveins present; A1 and A2 bifurcate.

Hind wing: Slightly shorter and narrower than forewing; costal space quite narrow, with three crossveins preserved; ScP terminating into costal margin at distal 2/5 of wing; pterostigma similar to that of forewing, but starting closer to termination of ScP, a sinuate RA veinlet present within pterostigma; four radial crossveins present, *r*3 longest; RP forked at its midpoint, with three simple branches; three rp-ma crossveins, forming three discal cells; MA with stem basally damaged, elongate and slightly sinuate; MA initially branching proximad its midpoint, MA1 simple, MA2 deeply forked at its midpoint; three ma-mp crossveins, forming three medial cells; MP deeply forked, with five terminal branches and five discoidal cells; three mp-cua crossveins, with 1mp-cua distinctly inclined to stem of MP; CuA and CuP simple; two cua-cup crossveins present; A1 with four pectinate simple branches; A2 simple.

Terminalia visible in lateral view: Tergum IX short; gonocoxites IX paired, shell-like, much wider than long; ectoproct nearly as long as tergum IX.

Type material: Holotype: CAU-BA-WN-20001: Amber piece with a complete adult male of *Baissoptera wangi* sp. nov.

Etymology: The specific epithet honors Mr. Ning Wang, who kindly provided the specimen of the new species for our research. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:86156883-AE84-4F2F-9CAE-B303FF1F65C1.

Genus *Burmobaissoptera* gen. nov. (Figs. 8 and 9)

Type species: *Burmobaissoptera jiaxiaoae* sp. nov.

Diagnosis: Medium-sized (female forewing length ~ 12.0 mm); head rectangular, with vertex almost as long as compound eye (diameter of compound eye about one-half head length). Tarsomere III symmetrically bilobed. Forewing long elliptical, ~3.0× as long as wide, with distal half distinctly broadened; ScP terminating into costal margin slightly proximad wing midpoint; pterostigma extremely long and distinctly broadened distad, ~15.0× as long as wide; starting slightly distad termination of ScP, diffuse proximally, no RA veinlet incorporated; MA with stem originating at initial branching point of MP; four radial cells, three discal cells, and three discoidal cells present; two cua-cup crossveins present. Hind wing with five radial cells, three discal cells, and three discoidal cells; stem of MA originating at diverging point between R and M; two mp-cua crossveins, 1mp-cua connecting to stem of MP at its base, strongly inclined to MP and slightly sinuate; CuA distally bifurcate.

Etymology: From "*Burma*" (meaning "Myanmar") and *Baissoptera* (the type genus of Baissopteridae), in reference to the occurrence of the new genus from the mid-Cretaceous amber of Myanmar. Gender: Feminine. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:E560CDB1-F254-4F8B-92A5-9C28EE01CBCB.

Remarks: The baissopterid affiliation of the new genus is based on the presence of a short M stem, which is diverged with CuA stem at angle of > 40° in the forewing, and the moderately rich venation. However, it differs from the other genera of Baissopteridae by the ScP terminating into costal margin proximad wing midpoint, the presence of a greatly elongate pterostigma with diffuse base, and the lack of a pterostigmal RA veinlet. In the other genera of Baissopteridae, the ScP terminates into the costal margin at or distad wing midpoint; the pterostigma is relatively short, closed by a crossvein proximally; and a pterostigmal RA veinlet is present in most genera.

Burmobaissoptera jiaxiaoae sp. nov. (Figs. 8 and 9)

Diagnosis: Same as for the genus (see above).

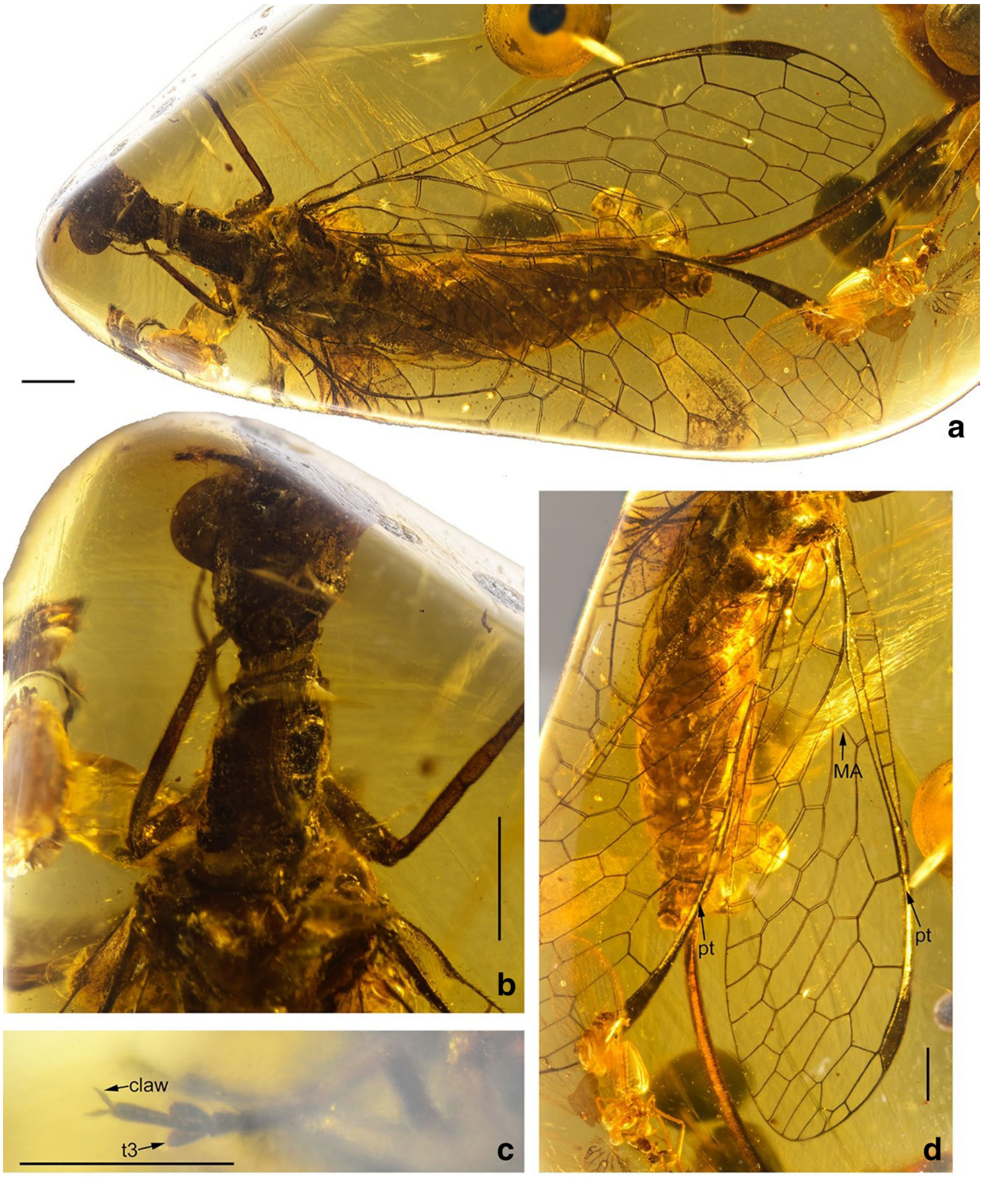
Description: Holotype CAM BA-0016. Female. Body length 13.3 mm; head length 2.6 mm, width 1.2 mm, with clypeus + labrum 0.5 mm, vertex length 1.0 mm; compound eye length 1.0 mm, width 0.5 mm; pronotum length 1.6 mm, width 0.7 mm; meso- plus metathorax length 2.6 mm; forewing length 11.8 mm, width 3.5 mm; hind wing length 11.4 mm, width 3.4 mm; abdomen length 6.4 mm; ovipositor length 6.3 mm, width 0.2 mm.

Body dark brown; head rectangular, with vertex almost as long as compound eye; occiput short; compound eyes ovoid; ocelli present.

Prothorax almost as long as head; meso- plus metathorax slightly longer than prothorax. Legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pretarsal claws forked at distal 1/3 into an acutely tapering tooth.

Forewing: Long elliptical, ~3.0× as long as wide, with distal half distinctly broadened; costal space narrow, with seven crossveins; ScP terminating into costal margin slightly proximad wing midpoint; three simple RA veinlets present; pterostigma greatly elongate and distinctly broadened distad, ~15.0× as long as wide, uniformly colored, proximally diffuse, starting slightly distad termination of ScP, distally ending at first veinlet of RA, no RA veinlet incorporated; four radial crossveins present, *r*1 longest, *r*2 broadest and as long as *r*3, *r*4 shortest and narrowest; RP forked at its proximal 1/3, with four simple branches; three rp-ma crossveins, forming three discal cells; MA with stem originating at initial branching point of MP; MA deeply forked at its proximal 1/3, with two simple branches; three ma-mp crossveins, forming three medial cells; MP deeply forked, with four terminal branches and a series of three discoidal cells; CuA bifurcate, CuP simple; two cua-cup crossveins present; A1 bifurcate; A2 simple.

Fig. 8 *Burmobaissoptera jiaxiaoae* gen. et sp. nov., holotype: CAM BA-0016. **a** Habitus, dorsal view. **b** Head and prothorax, dorsal view. **c** Tarsus and pretarsus of hind leg. **d** Right wings. Scale bar = 1.0 mm



Hind wing: Slightly shorter than forewing, proximal half much narrower than forewing, but distal half distinctly broadened; costal space quite narrow, with five crossveins preserved; ScP terminating into costal margin proximad wing midpoint; three simple RA veinlets; pterostigma similar to that of forewing; five radial crossveins present, *r*1 shortest, *r*3 longest and broadest, *r*4 almost as long as *r*3; RP forked slightly distad its proximal 1/3, with three simple branches; three rp-ma crossveins, forming three discal cells; MA with stem originating at diverging point between R and M, slightly longer than *r*1; MA initially branching at its proximal 1/3, with two simple branches; three ma-mp crossveins, forming three medial cells; MP deeply forked, with five terminal branches and a series of three discoidal cells; two mp-cua crossveins, with 1mp-cua connecting to base of MP, distinctly inclined to MP stem, and slightly sinuate; CuA distally bifurcate; CuP simple; one cua-cup crossvein present; A1 bifurcate; A2 simple.

Terminalia visible in ventral and lateral views; tergum VII almost as long as combined length of terga VIII+IX and ectoproct; sternum VII broad, slightly longer than tergum VII, with posterior margin convex; no sclerotized subgenitale discernible; tergum IX nearly one-half length of tergum VIII, distinctly narrowed ventrad; ectoproct slightly shorter than tergum IX; ovipositor long and stout; a pair of ovoid gonostyli IX present at tip of ovipositor.

Type material: Holotype: CAM BA-0016: Amber piece preserved with a nearly complete adult female of *Burmobaissoptera jiaxiaoae* gen. et sp. nov., with left wings largely not preserved.

Etymology: The specific epithet honors Mrs. Xiao Jia, who kindly provided the specimen of the new species for our

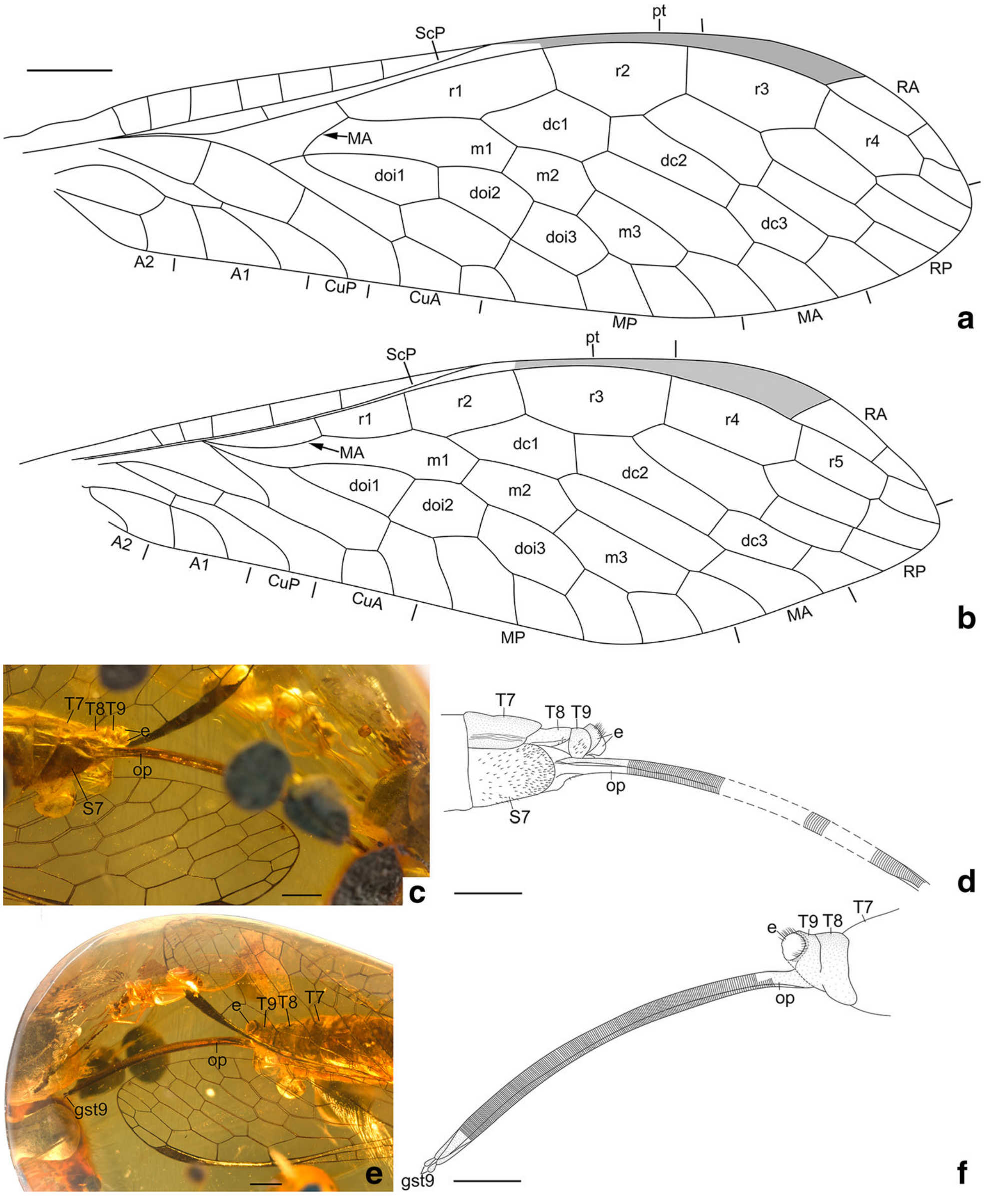


Fig. 9 *Burmobaissoptera jiaxiaoae* gen. et sp. nov., holotype: CAM BA-0016. **a** Right forewing. **b** Right hind wing. **c** Female genitalia, ventrolateral view. **d** Drawing of female genitalia, ventrolateral view. **e** Female genitalia, dorsolateral view. **f** Drawing of female genitalia, dorsolateral view. Scale bar = 1.0 mm

research. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:EDAFE551-EB59-4075-A75F-946C099E5D23.

Genus *Allobaissoptera* gen. nov. (Figs. 10 and 12a–c)

Type species: *Allobaissoptera oligophlebia* sp. nov.

Diagnosis: Small-sized (male forewing length ~ 6.0 mm); head narrowly rectangular, with vertex slightly longer than compound eye (diameter of compound eye about one-half head length). Tarsomere III symmetrically bilobed, with a pair of narrow lobes. Forewing narrow, ~ 3.5× as long as wide; ScP terminating into costal margin at midpoint of wing; pterostigma long, ~ 6.0× as long as wide, closed by a crossvein proximally, without RA veinlet incorporated; RA distally bifurcate; RP and MA each with two branches, branching of RP half-length of branching of MA; MA with stem separating from MP distinctly distad branching point between MP1 and MP2; three radial cells, two discal cells, and two discoidal cells present. Hind wing with four radial cells, two discal cells, and two discoidal cells; stem of MA proximally fused with MP, medially with a short crossvein connecting to MP1; CuA distally bifurcate. Male gonocoxite IX slightly longer than wide, strongly produced posteriad.

Etymology: From the Greek "*allos*" (meaning "different") and *Baissoptera* (the type genus of Baissopteridae), in reference to the unusual reduction of wing venation in the new genus compared with other baissopterids. Gender: Feminine. The name is registered with ZooBank LSID: LSID urn:lsid:zoobank.org:act:E1D1AD4F-EE92-4E1A-8D2A-3C3EF92F095E.

Remarks: The new genus is placed in Baissopteridae based on the presence of a short M stem, which is diverged with CuA stem at angle of > 40° in the forewing. However, it

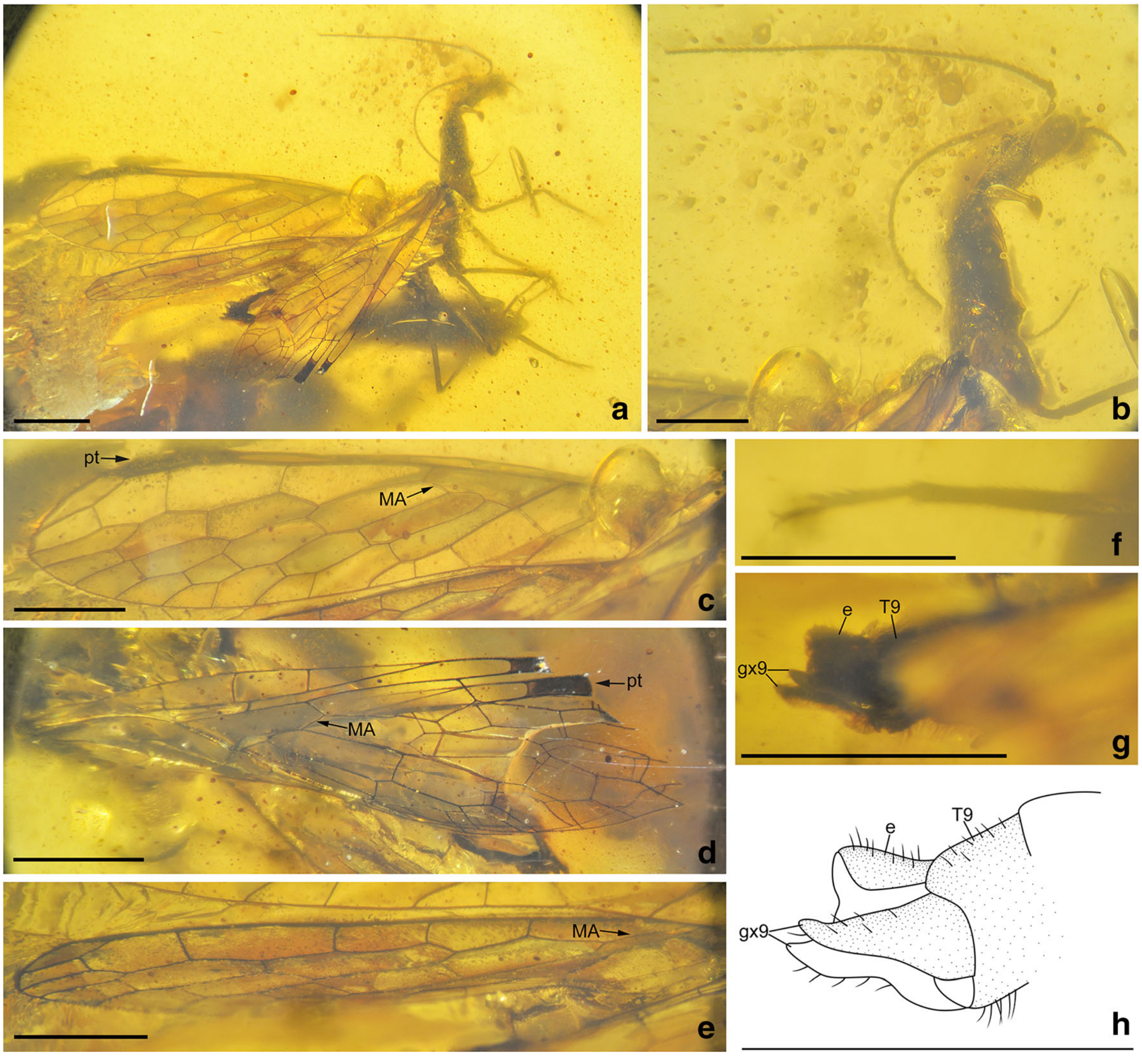


Fig. 10 *Allobaissoptera oligophlebia* gen. et sp. nov., holotype: NIGP163572. **a** Habitus, dorsolateral view. **b** Head and prothorax, dorsolateral view. **c** Left forewing. **d** Right forewing. **e** Right hind wing. **f** Mid leg. **g** Male genitalia, lateral view. **h** Drawing of male genitalia, lateral view. Scale bar = 1.0 mm

differs from the other genera of Baissopteridae by the presence of only two *doi* and the RP branching nearly one-half length of the MA branching in both fore- and hind wings. This new genus mostly resembles *Electrobaissoptera* gen. nov. in having similar relatively smaller body size, and the generally reduced wing venation, but can be distinguished from the latter genus by the termination of ScP at the wing midlength, the absence of a RA veinlet within the pterostigma, and the aforementioned unique generic features.

Allobaissoptera oligophlebia sp. nov. (Figs. 10 and 12a–c)

Diagnosis: Same as for the genus (see above).

Description: Holotype NIGP 163572. Male. Body length 6.6 mm; head length 1.0 mm, with clypeus + labrum 0.1 mm long, vertex 0.5 mm long; compound eye length 0.5 mm; antenna length 3.3 mm; pronotum length 1.6 mm; meso- plus metathorax length 1.5 mm; forewing length 5.9 mm, width 1.6 mm; hind wing (proximal part not preserved) length 5.4 mm; abdomen length 3.0 mm.

Body dark brown; head narrowly rectangular, with vertex slightly longer than compound eye; occiput short; compound eyes ovoid; ocelli present; antenna with ca. 50 flagellomeres.

Prothorax slightly longer than head; legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of narrow lobes; pretarsal claw tiny, distally forked.

Wings transparent. Forewing: Narrow, ~3.7× as long as wide; costal space narrow, with five crossveins; ScP terminating into costal margin at midpoint of wing; two simple RA veinlets present; pterostigma long, ~6.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at anterior veinlet of RA, RA veinlet within pterostigma absent; three radial crossveins present, three radial cells gradually shortened; RP forked distad its midpoint, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating from MP1, distinctly distad branching point between MP1 and MP2, MA forked slightly proximad its midpoint, with two simple branches, length of branching of MA nearly twice as long as branching of RP; three ma-mp crossveins, forming three medial cells; MP deeply forked, with four short terminal branches and two discoidal cells; CuA distally forked, with two simple branches; CuP simple; two cua-cup crossveins present; A1 and A2 simple.

Hind wing: Much narrower than forewing; costal space with four crossveins preserved; ScP terminating into costal margin at midpoint of wing; two simple RA veinlets present; pterostigma similar to that of forewing but slightly paler and starting more distad termination of ScP, RA veinlet within pterostigma absent; four radial crossveins present, *r*3 longest; RP forked at its distal 1/4, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating from base of MP stem, long, sinuate; MA forked at its midpoint, with two simple branches, branching of MA twice as long as branching of RP; four ma-mp crossveins, with 1ma-mp crossvein connecting MA stem and MP1, four medial cells present; MP deeply forked, with four short terminal branches and two discoidal cells; two mp-cua crossveins, with 1mp-cua nearly vertical to stem of MP; CuA distally bifurcate; incomplete CuP simple; one cua-cup crossvein; anal region not preserved.

Terminalia visible in lateral view; tergum IX broad; gonocoxites IX paired, shell-like, much longer than wide, distinctly produced posteriad, with apex slightly bent dorsad; ectoproct slightly shorter than tergum IX.

Type material: Holotype: NIGP163572: Amber piece with a nearly complete adult male of *Allobaissoptera oligophlebia* gen. et sp. nov.

Etymology: From the Greek "*oligos*" (few) and "*phlebos*" (vein), in reference to the reduced venation of the new species. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:C047362A-B3C8-47C5-8B39-73735801A15E.

Genus *Electrobaissoptera* gen. nov. (Figs. 11 and 12d, e)

Type species: *Electrobaissoptera burmanica* sp. nov.

Diagnosis: Small-sized (female forewing length ~ 7.0 mm); head narrowly rectangular, about twice as long as wide, with vertex almost as long as compound eye (diameter of compound eye about one-fourth head length). Tarsomere III symmetrically bilobed, with a pair of slender lobes. Forewing long elliptical, ~ 3.5× as long as wide; ScP terminating into costal margin slightly distad wing midpoint; pterostigma ~ 5.0× as long as wide, closed by a crossvein proximally, with one RA veinlet incorporated; MA with stem originating at MP1, distinctly distad initial branching point of MP; three radial cells, two discal cells, and three discoidal cells present; two cua-cup crossveins present. Hind wing with five radial cell, two discal cells, and three discoidal cells; stem of MA proximally fused with MP; *doi*1 with a short veinlet (an incomplete ma-mp crossvein) directed toward stem of MA; three mp-cua crossveins, 1mp-cua short and straight, almost vertical to MP; CuA distally bifurcate.

Etymology: From the Greek "*elektron*" (meaning "amber") and *Baissoptera* (the type genus of Baissopteridae), in reference to the discovery of the new genus from amber. Gender: Feminine. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:E92040C0-F05C-41D2-B97A-1749FFC440B6.

Remarks: The new genus is similar to *Allobaissoptera* gen. nov. as both are small-sized baissopterids. It is also notable that there is a crossvein between the stem of hind wing MA and the MP1 (or *doi*1) in these two genera, although it is incomplete in both hind wings in the holotype of the type species of *Electrobaissoptera* gen. nov. Whether it is an aberrant development needs to be clarified when more specimens of *Electrobaissoptera* gen. nov. are available. Refer to the comparison between these two genera in the Remarks of *Allobaissoptera* gen. nov. (see above).

Electrobaissoptera burmanica sp. nov. (Figs. 11 and 12d, e)

Diagnosis: Same as for the genus (see above).

Description: Holotype CAM BA-0017. Female. Body length 11.6 mm; head length 1.2 mm, width 0.5 mm, with clypeus + labrum 0.3 mm long, vertex 0.7 mm long; compound eye length 0.3 mm, width 0.1 mm; antenna length 1.1 mm; pronotum length 1.7 mm, width 0.2 mm; meso- plus metathorax length 1.3 mm; forewing length 6.7 mm, width 1.9 mm; hind wing length 6.3 mm, width 1.8 mm; abdomen length 3.2 mm; ovipositor length 4.4 mm, width 0.1 mm.

Body dark brown; head narrowly rectangular, with vertex slightly longer than compound eye; occiput short; compound eyes ovoid; ocelli present.

Prothorax slenderly elongate, slightly longer than head; meso- plus metathorax as long as prothorax. Legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of slender lobes; pretarsal claws forked at distal 1/3 into an acutely tapering tooth.

Forewing: Long elliptical, ~ 3.5 times as long as wide; costal space broadened at proximal 1/3, with five simple crossveins; ScP terminating into costal margin slightly distad wing midpoint; four simple RA veinlets present; pterostigma ~ 5.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at second veinlet of RA, with a straight but distinctly inclined RA veinlet incorporated; three radial crossveins present, three radial cells gradually shortened, *r*1 longest, *r*2 broadest; RP forked proximad its midpoint, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating at MP1, distinctly distad initial branching point of MP; MA deeply forked proximad its midpoint, with two simple branches, length of branching of MA as long as branching of RP; three ma-mp crossveins, forming three medial cells; MP deeply forked, with three terminal branches and a series of three discoidal cells; CuA marginally forked; CuP simple; two cua-cup crossveins present; A1 and A2 simple.

Hind wing: Slightly shorter and narrower than forewing; costal space narrow, with five crossveins; ScP terminating into costal margin slightly proximad wing midpoint; four simple RA veinlets present; pterostigma similar to that of forewing; five radial crossveins present, *r*3 longest and broadest, remaining radial cells almost in equal length; RP forked proximad its midpoint, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating from base of MP stem, long and sinuate; MA forked at its midpoint, with two simple branches, branching of MA as long as branching of RP; four ma-mp crossveins, forming three medial cells; MP deeply forked, with four terminal branches and a series of three discoidal cells; *doi*1 with a short veinlet (an incomplete ma-mp crossvein) directing toward stem of MA; three mp-cua crossveins, with 1mp-cua almost vertical to stem of MP; CuA distally forked; CuP simple; two cua-cup crossveins present; A1 and A2 simple.

Terminalia visible in lateral view, with distal part not preserved; sternum VII broad, with arcuate posterior margin in lateral view; tergum VIII slightly shorter than tergum VII; ovipositor long and stout; a pair of gonostylus IX present at tip of ovipositor.

Type material: Holotype: CAM BA-0017: Amber piece with a nearly complete adult female of *Electrobaissoptera burmanica* gen. et sp. nov.

Etymology: The specific epithet "*burmanica*" (meaning, "of Myanmar"), in reference to the discovery of the new species from Myanmar. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:665BEF10-AB8B-4019-BE52-9971D094D7BE.

Genus *Rhynchobaissoptera* gen. nov. (Figs. 13 and 15a, b)

Type species: *Rhynchobaissoptera hui* sp. nov.

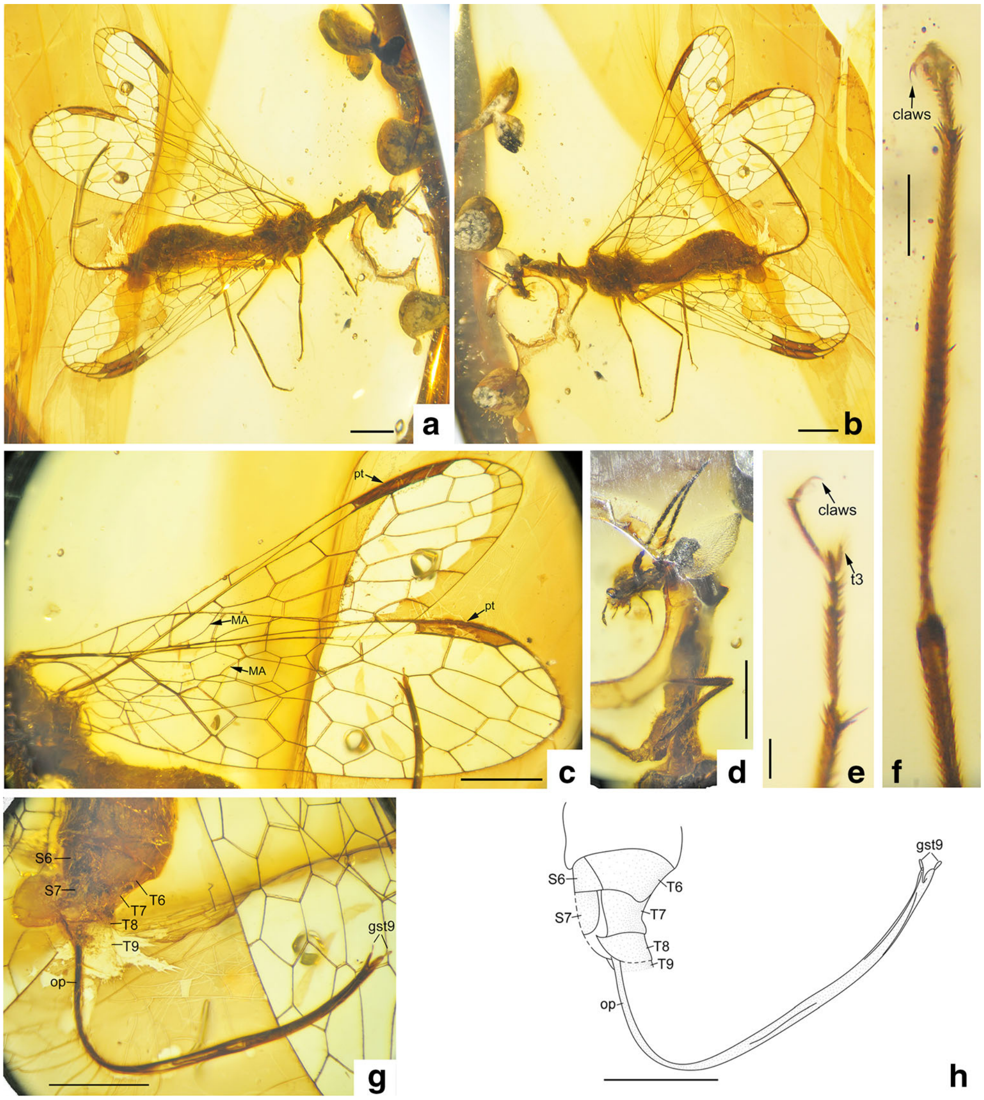


Fig. 11 *Electrobaissoptera burmanica* gen. et sp. nov., holotype: CAM BA-0017. **a** Habitus, right lateral view. **b** Habitus, left lateral view. **c** Right wings. **d** Head and prothorax, lateral view. **e** Tarsus and pretarsus of hind leg. **f** Mid leg. **g** Female genitalia, lateral view. **h** Drawing of female genitalia, lateral view. Scale bar = 1.0 mm (**a**–**d**, **g**–**h**); 0.1 mm (**e**); 0.2 mm (**f**)

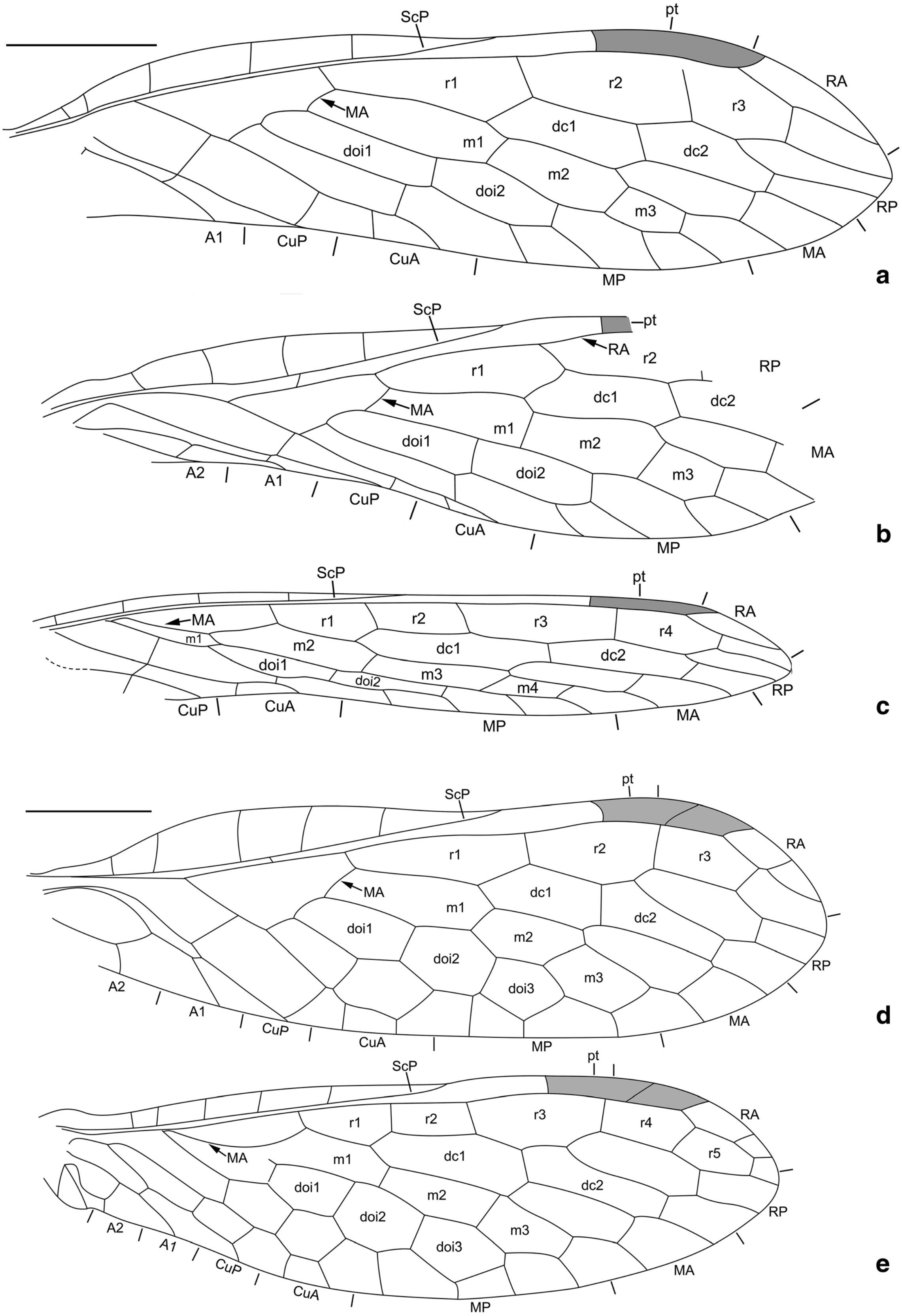


Fig. 12 Wing venations of Baissopteridae. **a**–**c** *Allobaissoptera oligophlebia* gen. et sp. nov., holotype: NIGP163572. **a** Left forewing. **b** Right forewing. **c** Right hind wing. **d**, **e** *Electrobaissoptera burmanica* gen. et sp. nov., holotype: CAM BA-0017. **d** Right forewing. **e** Right hind wing. Scale bar = 1.0 mm

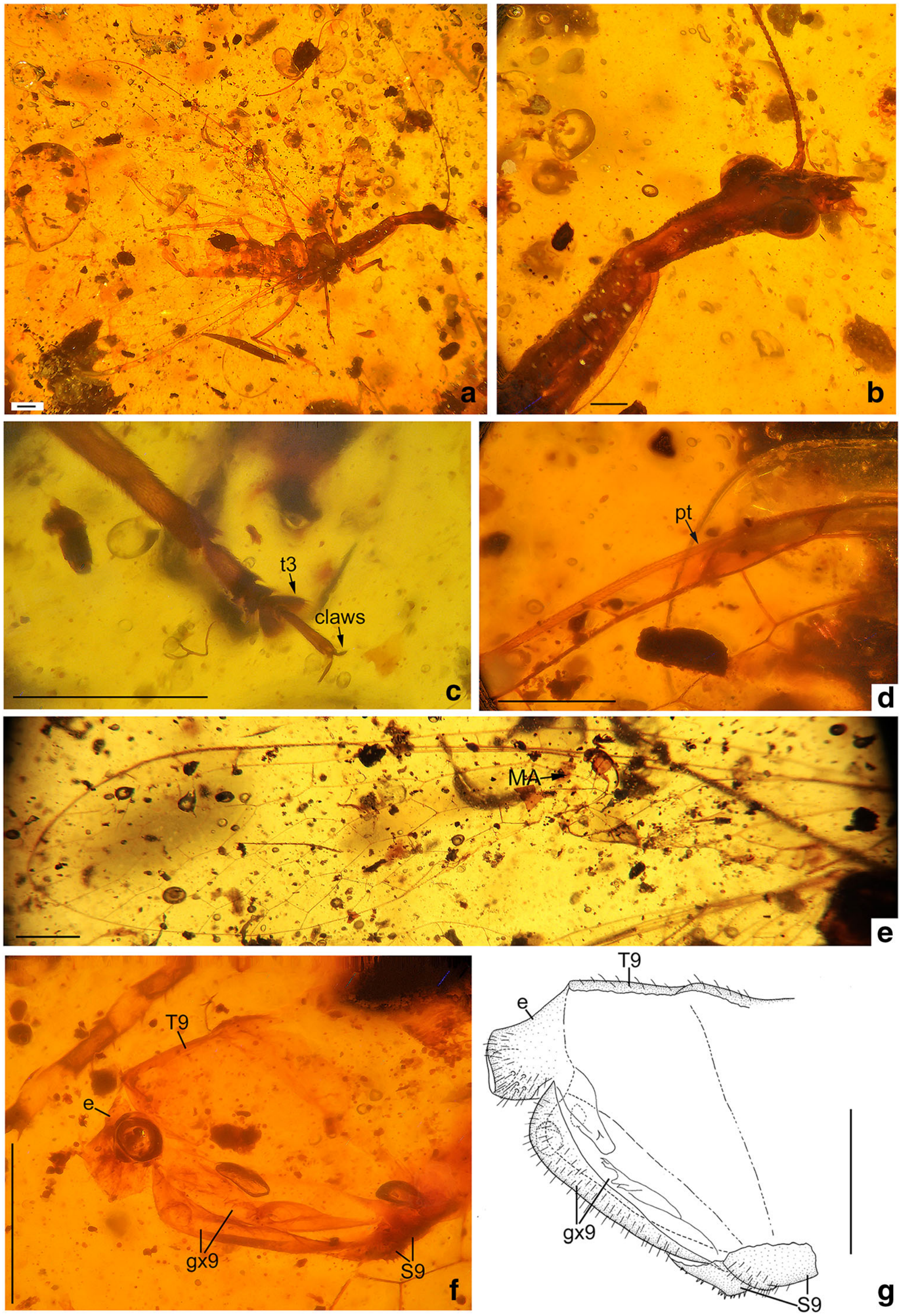


Fig. 13 *Rhynchobaissoptera hui* sp. nov., holotype: CAU-BA-HZ-20001. **a** Habitus, dorsolateral view. **b** Head and prothorax, dorsolateral view. **c** Tarsus and pretarsus of foreleg. **d** Pterostigma of right hind wing. **e** Left forewing. **f** Male genitalia, lateral view. **g** Drawing of male genitalia, lateral view. Scale bar = 1.0 mm

Diagnosis: Medium-sized (male forewing length ~ 15.0 mm); clypeus distinctly elongate; vertex greatly elongate, together with occiput about twice as long as compound eye (diameter of compound eye about one-third head length). Tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pretarsal claws simple. Wing long elliptical, ~ 5.0× as long as wide; ScP terminating into costal margin slightly distad wing midpoint; 1scp-ra crossvein absent; pterostigma ~ 4.0× as long as wide, closed by a crossvein proximally, with one RA veinlet incorporated; MA with stem originated at MP1, slightly distad initial branching point of MP; three radial cells, three discal cells, and at least five discoidal cells present. Hind wing with three radial cells, two discal cells, and six discoidal cells present; stem of MA proximally fused with MP; three mp-cua crossveins, 1mp-cua straight and inclined to MP. Male gonocoxites IX shell-like, much wider than long.

Etymology: From the Greek "*rhynchos*" (meaning "snout") and *Baissoptera* (the type genus of Baissopteridae), in reference to the presence of elongate rostrum in the new genus. Gender: Feminine. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:F0F5536A-8306-4E91-A362-C10A17E20740.

Remarks: The new genus differs from the other genera of Baissopteridae by the distinctly elongate vertex, the simple pretarsal claws, and the absence of forewing 1scp-ra crossvein. In the other baissopterid genera, the vertex is nearly as long as or much shorter than the compound eye, the pretarsal claws are forked subdistally, and the forewing 1scp-ra crossvein is present.

Rhynchobaissoptera hui sp. nov. (Figs. 13 and 15a, b)

Diagnosis: Same as for the genus (see above).

Description: Holotype CAU-BA-HZ-20001. Male. Body length 16.0 mm; head length 2.7 mm, width 0.6 mm, with clypeus + labrum 0.9 mm, vertex 1.4 mm long; compound eye length 1.0 mm, width 0.4 mm; antenna length 9.5 mm; occiput length 0.6 mm; pronotum length 3.3 mm, width 0.8 mm; meso- plus metathorax length 3.0 mm; forewing length 15.2 mm, width 3.2 mm (posteriorly damaged, probably wider if complete); hind wing length 13.4 mm, width 3.2 mm; abdomen length 6.0 mm.

Body blackish brown; head slenderly elongate, slightly thinner than prothorax, with vertex plus occiput about twice as long as compound eye; occiput short; clypeus elongate, slightly shorter than compound eye; compound eyes ovoid; ocelli present; antenna with at least 60 flagellomeres.

Prothorax slenderly elongate, slightly longer than head; meso- plus metathorax slightly shorter than prothorax. Legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of ovoid lobes; pretarsal claws slender and simple.

Forewing: Long elliptical, ~5.0× as long as wide; costal space narrow, with eight crossveins; ScP terminating into costal margin slightly distad wing midpoint; 1scp-ra absent; three simple RA veinlets present; pterostigma short, ~4.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at second veinlet of RA, with a straight but distinctly inclined RA veinlet incorporated; three radial crossveins present, three radial cells gradually shortened, *r*1 longest; RP forked proximad its midpoint, with five simple branches; three rp-ma crossveins, forming three discal cells; MA with stem originating at MP1, slightly distad initial

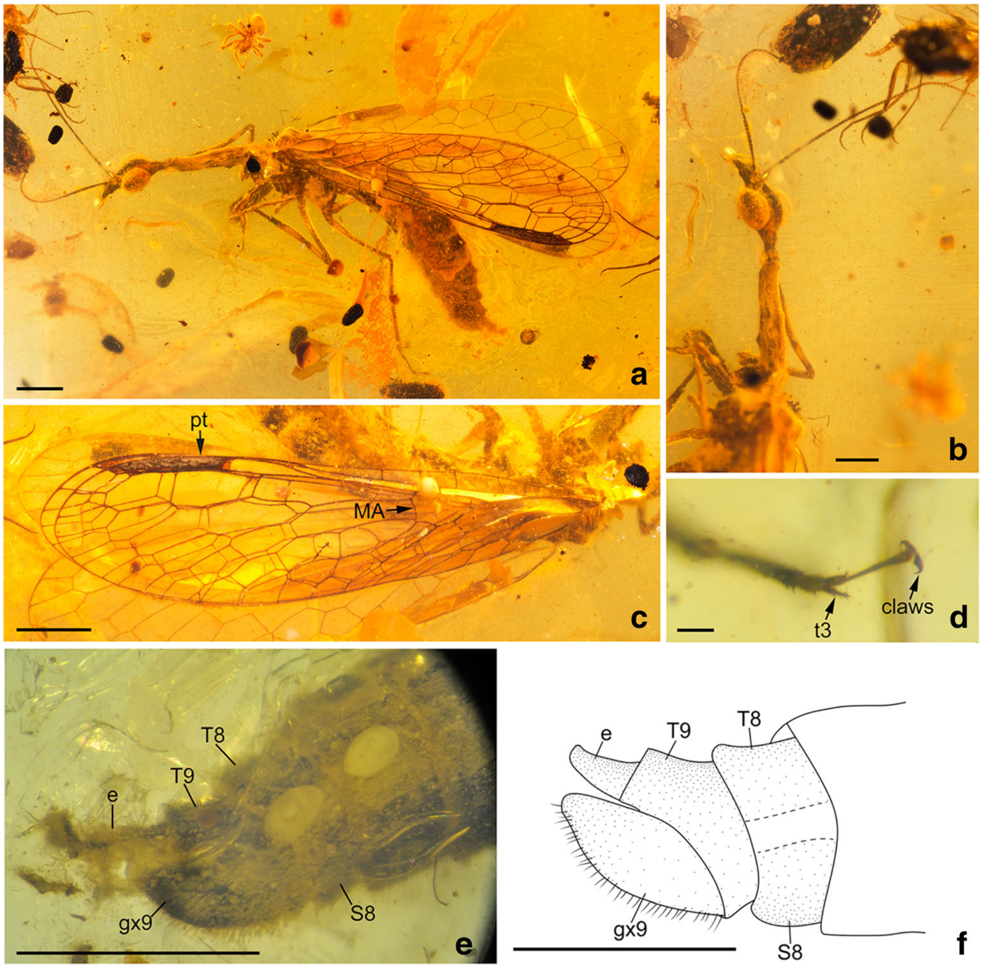
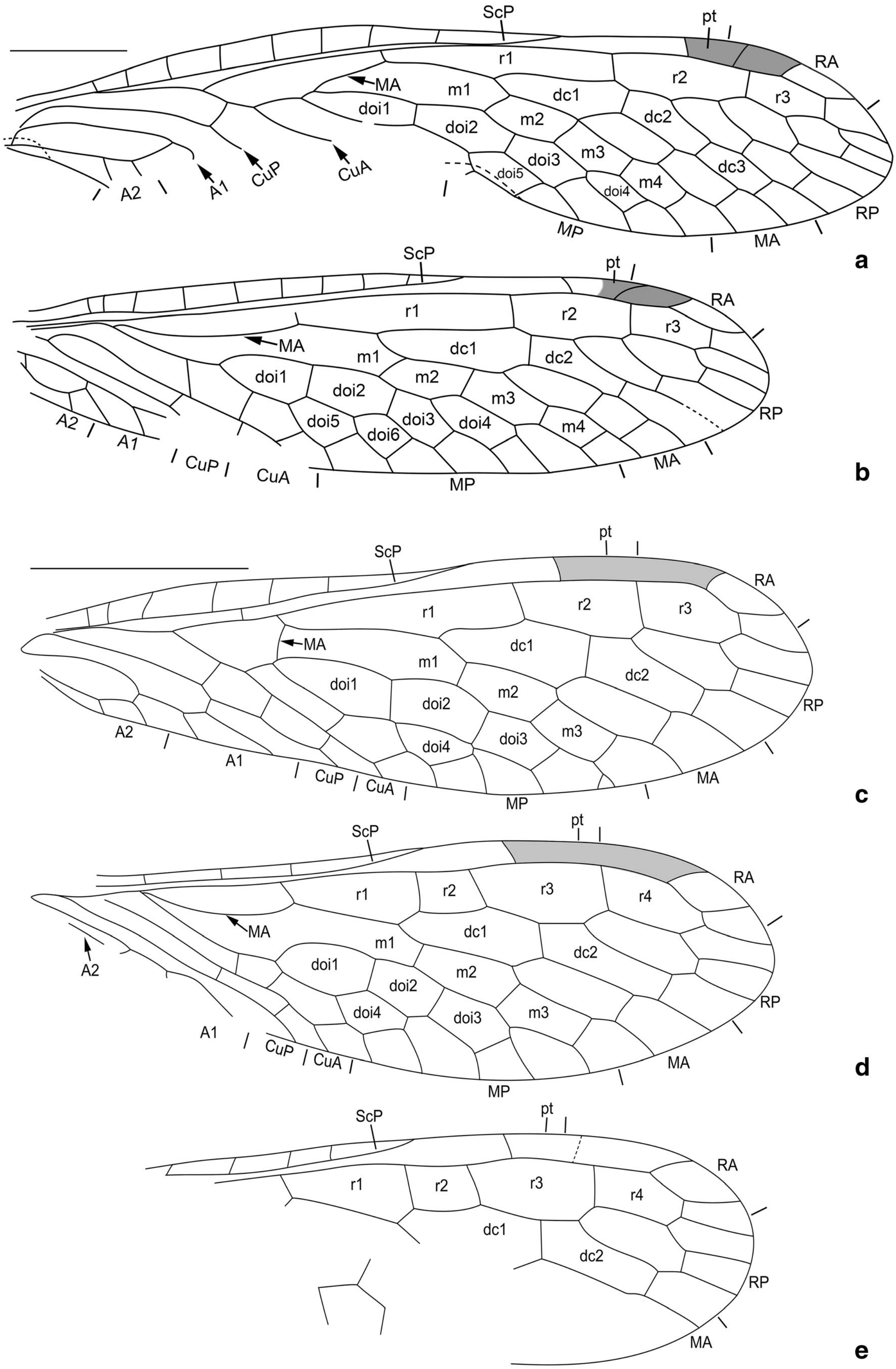


Fig. 14 *Stenobaissoptera xiai* gen. et sp. nov., holotype: LPAM BA-17004. **a** Habitus, lateral view. **b** Head and prothorax, dorsolateral view. **c** Left wings. **d** Tarsus and pretarsus of foreleg. **e** Male genitalia, lateral view. **f** Drawing of male genitalia, lateral view. Scale bar = 1.0 mm (**a**–**c**, **e**–**f**); 0.1 mm (**d**)


ScP
pt
RA
r1
r2
r3
MA
m1
dc1
doi1
doi2
m2
dc2
doi3
m3
dc3
doi5
doi4
m4
RP
A2
A1
CuP
CuA
MP
MA
a
ScP
pt
RA
r1
r2
r3
MA
m1
dc1
dc2
doi1
doi2
m2
m3
doi5
doi6
doi3
doi4
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RP
A2
A1
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CuA
MP
MA
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ScP
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r1
r2
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MA
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m1
dc2
doi1
doi2
m2
RP
doi4
doi3
m3
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CuP
CuA
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MA
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doi1
doi2
m2
A2
doi4
doi3
m3
RP
A1
CuP
CuA
MP
MA
d
ScP
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RA
r1
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r3
r4
dc1
dc2
RP
MA
e

◀ **Fig. 15** Wing venations of Baissopteridae. **a**, **b** *Rhynchobaissoptera hui* sp. nov., holotype: CAU-BA-HZ-20001. **a** Left forewing. **b** Right hind wing. **c–e** *Stenobaissoptera xiai* gen. et sp. nov., holotype: CAU-BA-XF-20002. **c** Left forewing. **d** Left hind wing. **e** Right hind wing. Scale bar = 2.0 mm

branching point of MP; MA deeply forked at its proximal 1/3, with two simple branches; four ma-mp crossveins, forming four medial cells; incomplete MP with two terminal branches and five discoidal cells.

Hind wing: Slightly shorter than forewing; costal space narrow, with nine crossveins; ScP terminating into costal margin slightly distad midpoint of wing; three simple RA veinlets present; pterostigma shorter than that of forewing, and starting distad 2scp-ra crossvein; a short but slightly curved RA veinlet present within pterostigma; three radial crossveins present, *r*1 longest; RP branched at its midpoint, with four simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating from base of MP stem, long and slightly sinuate; MA forked slightly proximad its midpoint, with two simple branches; four ma-mp crossveins, forming four medial cells; MP deeply forked, with six terminal branches and six discoidal cells arranged in two series; three mp-cua crossveins, with 1mp-cua distinctly inclined; A2 simple.

Terminalia visible in lateral view; tergum IX and sternum IX partly preserved; gonocoxites IX paired, shell-like, much wider than long, probably with some modifications on inner side (not clearly discernible); ectoproct slightly shorter than tergum IX, posteriorly exceeding apex of gonocoxites IX.

Type material: Holotype: CAU-BA-HZ-20001: Amber piece with a complete adult male of *Rhynchoraphidia hui* gen. et sp. nov.

Etymology: The specific epithet honors Mr. Zhengkun Hu, who kindly provided the specimen of the new species for our research. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:2BEF5735-A931-492F-8FDD-A552364C67C1.

Genus *Stenobaissoptera* gen. nov. (Figs. 14 and 15c–e; Fig. S3)

Type species: *Stenobaissoptera xiai* sp. nov.

Diagnosis: Small-sized (male forewing length ~ 7.5 mm); head ovoid, with vertex nearly one-half length compound eye; compound eyes enlarged, greatly exophthalmic. Tarsomere III symmetrically bilobed, with a pair of slender lobes. Forewing long elliptical, ~ 4.0× as long as wide; ScP terminating into costal margin slightly distad wing midpoint; pterostigma ~ 6.0× as long as wide, closed by a crossvein proximally, with one RA veinlet incorporated; MA with stem originating at MP1, slightly distad initial branching point of MP, and nearly vertical to RP + MA; three radial cells, two discal cells, and four discoidal cells present; two cua-cup crossveins present. Hind wing with four radial cells, two discal cells, and four discoidal cells; stem of MA fused with MP; three mp-cua crossveins, 1mp-cua short and straight, almost vertical to MP; CuA simple. Male gonocoxites IX shell-like, slightly longer than wide.

Etymology: From the Greek "*stenos*" (meaning, "slender") and *Baissoptera* (the type genus of Baissopteridae), in reference to the slender body shape of the new genus. Gender: Feminine. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:91A3F959-7660-4BFB-A8EA-C1FACE6AA9E1.

Remarks: The new genus together with *Allobaissoptera* gen. nov. and *Electrobaissoptera* gen. nov. are among the small-sized baissopterids, with slightly reduced wing venations and tarsomere III with a pair of slender lobes. However, the new genus is distinguished from the other closely related genera by the greatly enlarged compound eyes in association with the distinctly shortened vertex, the forewing MA stem close to the initial branching point of MP, the presence of four *doi* in both fore- and hind wings, and the hind wing *doi*1 without a crossvein connecting to stem of MA. In *Allobaissoptera* gen. nov. and *Electrobaissoptera* gen. nov., the vertex is nearly as long as compound eye, the forewing MA stem is far distad the initial branching point of MP, the fore- and hind wings both have two or three *doi*, and there is a crossvein connecting *doi*1 and stem of hind wing MA.

Stenobaissoptera xiai sp. nov. (Figs. 14 and 15c–e; Fig. S3)

Diagnosis: Same as for the genus (see above).

Description: Holotype CAU-BA-XF-20002. Male. Body length 11.6 mm; head length 1.2 mm, with clypeus + labrum 0.4 mm long, vertex 0.2 mm long; compound eye length 0.5 mm; antenna length 4.0 mm; pronotum length 2.6 mm; meso- plus metathorax length 1.6 mm; forewing length 7.4 mm, width 1.9 mm; hind wing length 7.0 mm, width 1.8 mm; abdomen length 5.2 mm.

Body dark brown; head ovoid, with vertex slightly shorter than compound eye; occiput short; clypeus distinctly elongate; compound eyes ovoid, extremely enlarged; ocelli present; antenna with at least 60 flagellomeres.

Prothorax elongate, longer than head; meso- plus metathorax shorter than prothorax. Legs slender, densely setose; tarsomere III symmetrically bilobed, with a pair of slender lobes; pretarsal claws forked at proximal 1/3 into an acutely tapering tooth.

Forewing: Long elliptical, ~ 4.0× as long as wide; costal space narrow, with eight simple crossveins; ScP terminating into costal margin at midpoint of wing; at least two simple RA veinlets present; pterostigma ~ 6.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at a veinlet of RA, incorporated RA veinlet not visible; three radial crossveins, three radial cells gradually shortened, *r*1 longest, *r*2 broadest; RP forked at its midpoint, with three simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating at MP1, slightly distad initial branching point of MP; MA deeply forked proximad its midpoint, with two simple branches; three ma-mp crossveins, forming three medial cells; MP deeply forked, with five terminal branches and four discoidal cells; CuA and CuP simple; three cua-cup crossveins present; A1 and A2 bifurcate.

Hind wing: Slightly shorter and narrower than forewing; costal space quite narrow, preserved part with three crossveins; ScP terminating into costal margin at wing midpoint; at least two simple RA veinlets present; pterostigma similar to that of forewing, except paler and longer; RA veinlet within pterostigma not visible; four radial crossveins present, *r*1 longest, as long as *r*3, *r*2 shortest, *r*3 broadest; RP similar to that of forewing; two rp-ma crossveins, forming two discal cells; MA with stem originating from base of MP, long and sinuate; MA similar to that of forewing; three ma-mp crossveins, forming three medial cells; MP deeply forked, with five terminal branches and four discoidal cells arranged in two series; three mp-cua crossveins, with 1mp-cua short and straight, almost vertical to MP stem; CuA and CuP simple.

Terminalia visible in lateral view: tergum VIII as long as sternum VIII; tergum IX as long as tergum VIII, greatly extended and narrowed ventrad; gonocoxites IX paired, shell-like, much longer than wide, obliquely directed dorsad; ectoproct slightly shorter than tergum IX, in lateral view slightly narrowed posteriad.

Paratype CAU-BA-WN-20002. Male. Body length 8.4 mm; head length 1.1 mm, width 0.3 mm, with clypeus + labrum 0.4 mm long, vertex 0.1 mm long; compound eye length 0.6 mm, width 0.3 mm; pronotum length 1.8 mm, width 0.3 mm; meso- plus metathorax length 1.6 mm; forewing length 5.9 mm, width 2.0 mm; abdomen length 3.7 mm. Pterostigma with a straight but distinctly inclined RA veinlet incorporated in both fore- and hind wings. Genitalia visible in abdominal view, with a pair of shell-like gonocoxites IX.

Type material: Holotype: CAU-BA-XF-20002: Amber piece with a complete adult male of *Stenobaissoptera xiai* gen. et sp. nov. Paratype: CAU-BA-WN-20002: Amber piece with an almost complete adult male of *S. xiai* gen. et sp. nov.

Etymology: The specific epithet honors Mr. Fangyuan Xia, who kindly provided the specimen (the holotype designated herein) of this new species for our research. The name is registered with ZooBank LSID: urn:lsid:zoobank.org:act:0028E777-5576-4AF7-87F2-52AB4F92593D.

Key to genera of Baissopteridae

1 Hind wing with stem of MA short, crossvein-like (Makarkin and Archibald 2014: Fig. 4); recorded from Late Eocene…………….........*Dictyoraphidia* Handlirsch

– Hind wing with stem of MA long, slightly sinuate; recorded from Cretaceous…......…………………...............2

2. Head with enlarged compound eyes and greatly shortened vertex (Fig. 14a, b)…………......*Stenobaissoptera* gen. nov.

– Head with normal-sized compound eyes and well-developed vertex…………………………..……...............3

3. Hind wing *doi*1 with a crossvein directed toward or connecting to stem of MA………………..….................4

– Hind wing *doi*1 without any crossvein directed toward or connecting to stem of MA………….….........................6

4. Large body size, with forewing 17.5 mm long; forewing RP with five branches; forewing MA separating from MP at initial branching point of MP (Willmann 1994: Fig. 6d)……………………………….*Lugala* Willmann

– Small body size, with forewing 5.5–7.0 mm long; forewing RP with only two branches; forewing MA separating from MP obviously distad initial branching point of MP…………..…………..…………..…………..…….5

5. RP branches nearly one-half length of MA branches in both fore- and hind wings (Fig. 12a, b).......*Allobaissoptera* gen. nov.

– RP branches almost as long as MA branches in both fore- and hind wings (Fig. 12c–e).....*Electrobaissoptera* gen. nov.

6. Forewing MP with stem longer than *doi*1 and diverging with CuA at angle ~ 30° (Willmann 1994: Fig. 6l)...........7

– Forewing MP with stem shorter than *doi*1 and diverging with CuA at angle ~ 40–60° (Fig. 3)…..…......................8

7. Forewing RP and MA with fewer branches and crossveins (Ponomarenko 1988: Fig. 6)…...*Cretoraphidiopsis* Engel

– Forewing RP and MA with rich branches and crossveins (Ponomarenko 1993: Fig. 7).........*Cretoraphidia* Ponomarenko

8. Pterostigma apparently elongate and proximally diffuse (Figs. 8a, d and 9a, b); origin of hind wing 1mp-cua close to diverging point between R and M (Fig. 9b)....…………....*Burmobaissoptera* gen. nov.

9 Pterostigma relatively short, proximally closed by a crossvein; origin of hind wing 1mp-cua distinctly shifted distad.……………………………...........................10

10 Large body size, with forewing 10.5–27.7 mm.……....12

– Small body size, with forewing 8.7–10.8 mm…...........11

11. Forewing MA separating from MP obviously distad initial branching point of MP (Willmann 1994: Fig. 6e)...………………….......*Austroraphidia* Willmann

– Forewing MA separating from MP at initial branching point of MP (Lyu et al. 2017a: Fig. 8)................*Microbaissoptera* Lyu, Ren & Liu

12\. Head about 3.0× as long as wide (Fig. 13a, b)............................*Rhynchobaissoptera* gen. nov.

– Head about 1.5–2.0× as long as wide (Fig. 2a, b)………….……….........*Baissoptera* Martynova

Discussion

Familial characters of Baissopteridae

The exquisitely preserved baissopterids in amber from the mid-Cretaceous of Myanmar reported herein provide valuable new information on some familial characters. The diagnostic characters of Baissopteridae listed in this paper (refer to Systematic Palaeontology, above) comprise seven characters. Among them, characters (2) and (5) were previously considered as diagnostic wing characters of Baissopteridae by Makarkin and Archibald (2014). The discussion in this section mainly focuses on these characters.

(1) The presence of ocelli. Lyu et al. (2017a) noted in their revision of Baissopteridae from the Lower Cretaceous of China that the ocelli in some well-preserved baissopterid fossils could not be observed. However, in all of the present amber baissopterids, the ocelli are clearly present. So far, there has been no baissopterid species reported that undoubtedly lacks ocelli. The putative absence of ocelli in compression fossils of Baissopteridae is most likely owing to preservation; i.e., absence of preservation (not visible as preserved) rather than absence of the character state. Although the presence/absence of ocelli is an important character to distinguish Raphidiidae and Inocelliidae, both character states have been found within Mesoraphidiidae (Liu et al. 2016a). Thus, the presence/absence of ocelli should at least be approached with caution when attempting to distinguish families in fossil Raphidioptera. It may be that the character performs well in parts of the raphidiopteran tree (e.g., distinguishing families of Neoraphidioptera), but not universally (e.g., diagnosing Mesoraphidiidae).

(2) The presence of pterostigmal RA veinlet. The presence/absence of pterostigmal RA veinlet is also an important character to distinguish Raphidiidae and Inocelliidae, while it is highly variable among the genera of Mesoraphidiidae in terms of the presence/absence, number, and position (Pérez-de la Fuente et al. 2012; Liu et al. 2016a; Lyu et al. 2017b). Among the Burmese amber baissopterids, only *Burmobaissoptera* gen. nov. probably lacks the pterostigmal RA veinlet. We could not confirm whether the pterostigmal RA veinlet is absent in *Allobaissoptera* gen. nov. because the pterostigma in both fore- and hind wings of the holotype of the type species is too dark to be clearly observed in detail with a transmitted light source. A similar preservation is also present in the holotype of *S. xiai* gen. et sp. nov., which makes the pterostigmal RA veinlet indiscernible. However, in the paratype of the same species with a paler pterostigma, the pterostigmal RA veinlet can be found. Among the baissopterid genera from other deposits (all preserved are compressions), the pterostigmal RA veinlet is absent or indiscernible in *Cretoraphidia* and *Lugala* (Ponomarenko 1988, 1993). In addition, the absence of a pterostigmal RA veinlet was previously reported in a few species of *Baissoptera* (Oswald 1990; Lyu et al. 2017a). Nonetheless, the Burmese amber baissopterids show less variation among genera and species concerning the presence/absence of a pterostigmal RA veinlet in comparison to their highly disparate traits on the other body parts.

(3) Forewing M with stem shorter than *doi*1. We define the stem of forewing M to be the part from the branching point between M and CuA to the initial branching point of MP. The stem of forewing M was incorrectly termed as a basal m-cu crossvein, and its elongation was considered to be a synapomorphy of Raphidiomorpha by Willmann (1994). The length of forewing *doi*1 is measured as the straight-line distance from the initial branching point of MP to the connecting point of the first crossvein between main MP branches to the posterior branch of MP. In the Burmese amber baissopterids, the ratio in length of the forewing M stem: *doi*1 ranges from 0.20 to 0.74. As noted in the Remarks of Baissopteridae (see above), there are two genera (i.e., *Cretoraphidia* and *Cretoraphidiopsis*) having the opposite character state (i.e., the forewing M stem longer than *doi*1), which, however, needs to be corroborated after the type specimens can be re-examined. If confirmed, then this character state in *Cretoraphidiopsis* and *Cretoraphidia* would likely be plesiomorphic and might suggest they are sister to other baissopterids, pending a cladistic analysis. In most genera of Mesoraphidiidae, the forewing M stem is as long as or longer than *doi*1, with the exception of *Siboptera* and some genera of the tribe Nanoraphidiini that have a relatively short stem of MP (Ren 1994; Liu et al. 2016a). All genera of Raphidiidae also have the elongate forewing M stem, but in Inocelliidae, both long and short conditions of the forewing M stem are present (Aspöck et al. 1991).

(4) Forewing MP and CuA diverging at angle of > 40°. This character seems to be more or less related to character (3)

as the snakefly species that have relatively short forewing M stem often have this character state. In the Burmese amber baissopterids, the diverging angle between forewing MP and CuA is nearly 60°. In the other baissopterids, the diverging angle between forewing MP and CuA is not less than 40° except in *Cretoraphidia* and *Cretoraphidiopsis* that have the long stem of forewing MP. Besides Baissopteridae, the other snakeflies that have this character include only *Siboptera* and some inocelliids (see Ren 1997: Fig. 4; Aspöck et al. 1991: Figs. 467, 469, 479). In the genera of Nanoraphidiini having a relatively short stem of the forewing MP, the diverging angle between MP and CuA is much less than 40° (see Liu et al. 2016a: Figs. 4 and 6).

(5) Enriched venation. This character is present in all species of Baissopteridae. In a few mesoraphidiids, the number of RP and M branches as well as crossveins is slightly increased (see Ponomarenko 1988: Fig. 5; Ren 1997: Fig. 5), but these species have the triangular arrangement of three forewing *doi* (a typical feature of Mesoraphidiidae) and lack characters (3) and (4).

(6) Shell-like male gonocoxite IX. The gonocoxites IX are a pair of large, external sclerites in the male genitalia of Raphidiomorpha. In extant Raphidioptera, the shell-like male gonocoxite IX is a reliable character to distinguish Inocelliidae from Raphidiidae (Aspöck et al. 1991). The shell-like feature of this genital sclerite is actually formed by the lack of external modifications (e.g., projections, well-developed exposed gonostylus IX, *&c.*), although there are diverse modifications on the inner side of gonocoxites IX in Inocelliidae. In Raphidiidae, the male gonocoxite IX has highly diversified morphological modifications, with various projections posteriorly and an exposed gonostylus IX on the posterodorsal portion of gonocoxite IX (Aspöck et al. 1991). The present finding indicates that the shell-like male gonocoxite IX has been present at least since the mid-Cretaceous. The shell-like male gonocoxite IX in the Burmese amber baissopterids is different in shape among some genera and species. In *Allobaissoptera* gen. nov. and *Stenobaissoptera* gen. nov., the male gonocoxite IX is broad and distinctly produced posteriad, similar to that in some species of *Inocellia* (Liu et al. 2010, Liu et al. 2013). In *Baissoptera* and *Rynchobaissoptera* gen. nov., the male gonocoxite IX is quite short, and this form is not present among Inocelliidae.

(7) Reduction of male gonapophyses IX. The male gonapophyses IX are a pair or fused sclerites, which form a distinct ventral structure termed the hypovalva in Raphidiidae (Aspöck et al. 1991; Aspöck and Aspöck 2008). However, the male gonapophyses IX are not conspicuous and usually present as a pair of small internal sclerites termed as pseudostyli in Inocelliidae (Aspöck et al. 1991; Aspöck and Aspöck 2008). The Burmese amber baissopterids apparently have similarly reduced male gonapophyses IX, as in Inocelliidae.

(8) Hind wing MA stem fused with MP. Besides the above familial diagnostic characters, it is also worth mentioning the configuration of the hind wing MA stem. The stem of hind wing MA (or termed as 1r-m in Breitkreuz et al. 2017) is long and slightly sinuate in the Cretaceous baissopterids. The only Tertiary baissopterid, i.e., *Dictyoraphidia veterana* (Scudder, 1890), has a short stem to hind wing MA (Makarkin and Archibald 2014: Fig. 4b). In most Burmese amber baissopterids, the stem of hind wing MA is proximally separated from M but not R, although the point of separation is quite close to R (see Figs. 3, 7b, 12, and 15). However, the stem of the hind wing MA was described as separated from R in many baissopterids preserved as compressions (Ponomarenko 1988; Lyu et al. 2017a), except *Austroraphidia brasiliensis* Nel, Séméria & Martins-Neto, 1990 from the Lower Cretaceous of Brazil (see Nel et al. 1990: Fig. 3), which has the hind wing MA proximally separated from M based on the original drawing. We re-examined some baissopterid fossils (CNU-RAP-LB-2017029, CNU-RAP-LB-2017028, CNU-RAP-LB-2017055, CNU-RAP-LB-2017032, CNU-RAP-LB-2017037) described by Lyu et al. (2017a), but in none of them could the stem of hind wing MA be confirmed as separate from R. Actually, even if the hind wing MA proximally separates from M, because of the close position between R and M, we assume that the complete configuration could not be preserved clearly in most compressions of Baissopteridae.

(9) Pretarsal claw distally forked. In all Burmese amber baissopterids described herein, the pretarsal claws of all legs are forked, with a distinct tooth distally. This could be an apomorphic state for the family. Unfortunately, this character is hardly discernible in baissopterids preserved as compressions. In Mesoraphidiidae, the pretarsal claws are simple, although this character could be seen only in some amber species (Liu et al. 2016a). In Raphidiidae and Inocelliidae, the pretarsal claws are also simple (see Aspöck et al. 1991: Figs. 15 and 39).

Systematic position of Baissopteridae

The systematic position of Baissopteridae was first critically investigated under a phylogenetic framework by Willmann (1994), in which this family was recovered as a paraphyletic grade of stem-group representatives of Raphidiomorpha. Bechly and Wolf-Schwenninger (2011) also considered Baissopteridae to be paraphyletic, but noted that the characters used for phylogenetic inference in Willmann (1994) were poor and homoplastic. Particularly, the characters supporting the sister-group relationships between some baissopterid genera and the clades including other raphidiomorph families (Willmann 1994: characters 13–16) are numerical and poorly defined. The number of hind wing cua-cup crossveins (Willmann 1994: character 13) varies within *Baissoptera* [e.g., two cua-cup in *B. grandis* and *B. sinica* (Lyu et al. 2017a), but three cua-cup in *B. burmana* sp. nov., *B. maculata* sp. nov., and *B. monopoda* sp. nov.]. Moreover, the presence/absence of a particular crossvein may not be homologous (e.g., to arrive at two cua-cup rather than one could involve any of three crossveins and simple coding the number would confound a loss of 1cua-cup with a loss of 3cua-cup). The presence of three forewing medial cells (Willmann 1994: character 14) can be found in all baissopterid genera except *Lugala*. The relatively small number of hind wing ra-rp crossveins (Willmann 1994: character 16) is also present in Baissopteridae, e.g., *R. hui* gen. et sp. nov. The proximal shift of the forewing stem of M (Willmann 1994: character 15), which was considered to be present in *Austroraphidia*, is not the same as the configuration in Mesoraphidiidae. However, the relative length of the forewing M stem and the diverging angle between M and CuA are of the typical baissopterid state. Thus, those characters outlined by Willmann (1994) as supporting baissopterid paraphyly are confounded and do not constitute sufficient evidence. Therefore, there has been no convincing evidence that Baissopteridae are paraphyletic.

The evolutionary polarization of many wing characters is challenging to determine unambiguously in Raphidiomorpha as the wing venation in their Mesozoic relatives (i.e., Priscaenigmatomorpha and Juroraphidiidae) differ greatly from each other and determining the plesiomorphic state of such wing characters remains unclear. Moreover, the raphidiopteran affinity of Priscaenigmatomorpha and Juroraphidiidae remains to be confirmed in a cladistic framework (Aspöck and Aspöck 2004; Liu et al. 2014, 2017), although such a placement appears solid. Interestingly, there is a putative stem-group raphidiopteran family, i.e., Nanosialidae from the Permian of Russia (Shcherbakov 2013), which has not yet been used as outgroup for evaluating character evolution of wing venation traits in Raphidioptera. By having the fusion between forewing MP and CuA, the wing venation of Nanosialidae appears to be more similar and comparable to Raphidiomorpha than Priscaenigmatomorpha and Juroraphidiidae, which could imply monophyly of the latter two as a group relative to the former. Notably, the wing venation of Nanosialidae is not as rich as that in Baissopteridae, but in general similar to that in Mesoraphidiidae with fewer RP and M branches as well as fewer crossveins (see Shcherbakov 2013: Figs. 3 and 4). More importantly, the forewing M stem is also similarly configured between Nanosialidae and Mesoraphidiidae, being relatively long and separated from CuA at an angle of nearly 30°. Thus, assuming for the moment that the above wing characters shared by Nanosialidae and Mesoraphidiidae to be plesiomorphic, characters (3), (4), and (5) in Baissopteridae could potentially serve as apomorphic character traits to support the monophyly of the family, at least of most Cretaceous baissopterids except *Cretoraphidia* and *Cretoraphidiopsis*. The configuration of the forewing M stem in the Late Eocene genus *Dictyoraphidia* is unknown, and its baissopterid affinity remains to be further clarified.

Concerning characters of the male genitalia, the shell-like gonocoxite IX and reduction of gonapophyses IX are also potentially apomorphic. So far, the male genitalia of Mesoraphidiidae, albeit known only in some Burmese amber species (see Liu et al. 2016a: Figs. 2, 10, and 13), obviously differs from that of Baissopteridae by the shape of gonocoxites IX and the distinct gonapophyses IX, which, however, are similar to that in Raphidiidae. Interestingly, the similarly configured male genitalia between Baissopteridae and Inocelliidae may further suggest a closer relationship between these two families rather than the sister-group relationship between Inocelliidae and Raphidiidae, which is also contradicted by the similarity of the male genitalia between Mesoraphidiidae and Raphidiidae (Liu et al. 2016a). Under such a scenario, baissopterids would be allied to Inocelliidae and mesoraphidiids to Raphidiidae. If true, this would imply that the specializations for cold temperate climates evolved independently and in parallel in these two extant families, a pattern perhaps supported by the presence of subtropical inocelliids and raphidiids in the mid-Eocene (Engel 1995; Aspöck and Aspöck 2004). However, this hypothesis needs further testing once male genitalic characters are known for a far greater number of species of Mesoraphidiidae.

Regardless the morphological characters, it is noteworthy that Baissopteridae are known only from the Cretaceous and Paleogene (Eocene). All earlier records of Raphidiomorpha are of Mesoraphidiidae and Metaraphidiidae from several Jurassic deposits (Willmann 1994; Engel 2002; Lyu et al. 2017b). The discrepancy of the snakefly paleofaunas between the Jurassic and Cretaceous is probably not due to incomplete exploration. For example, the rich paleofauna of Neuropterida from the Middle Jurassic of China has been intensively studied for over 20 years, but Baissopteridae have never been found from these deposits (Ren et al. 2010). In light of the temporal occurrence along with the geological history, Baissopteridae seem to be a derived lineage among Raphidiomorpha, and probably descendants of certain ancestral species otherwise similar to Mesoraphidiidae or Metaraphidiidae.

Morphological diversity among Burmese amber baissopterids

The mid-Cretaceous baissopterids reported herein represent the youngest fossil record of Baissopteridae during the Mesozoic. Remarkably, the Burmese amber baissopterids possess some morphological modifications that have not been found in their precursors from the Lower Cretaceous. First, there are three Burmese amber baissopterid species with forewing lengths of approximately 6.0–7.5 mm, being among the smallest species in the family. The other seven Burmese amber baissopterids are similar to over half of the Lower Cretaceous species (12 of 22 species) in body size with forewing lengths 11.0–15.0 mm (see Table S1 for summary of forewing lengths among baissopterids; Fig. 16). The remaining Lower Cretaceous baissopterids are either large-sized (forewing lengths 15.0–28.0 mm) or relatively small-sized (forewing lengths 8.5–11.0 mm). Second, there are two species that have a head shape apparently differing from all other baissopterids. In most baissopterids, the head is ovoid or

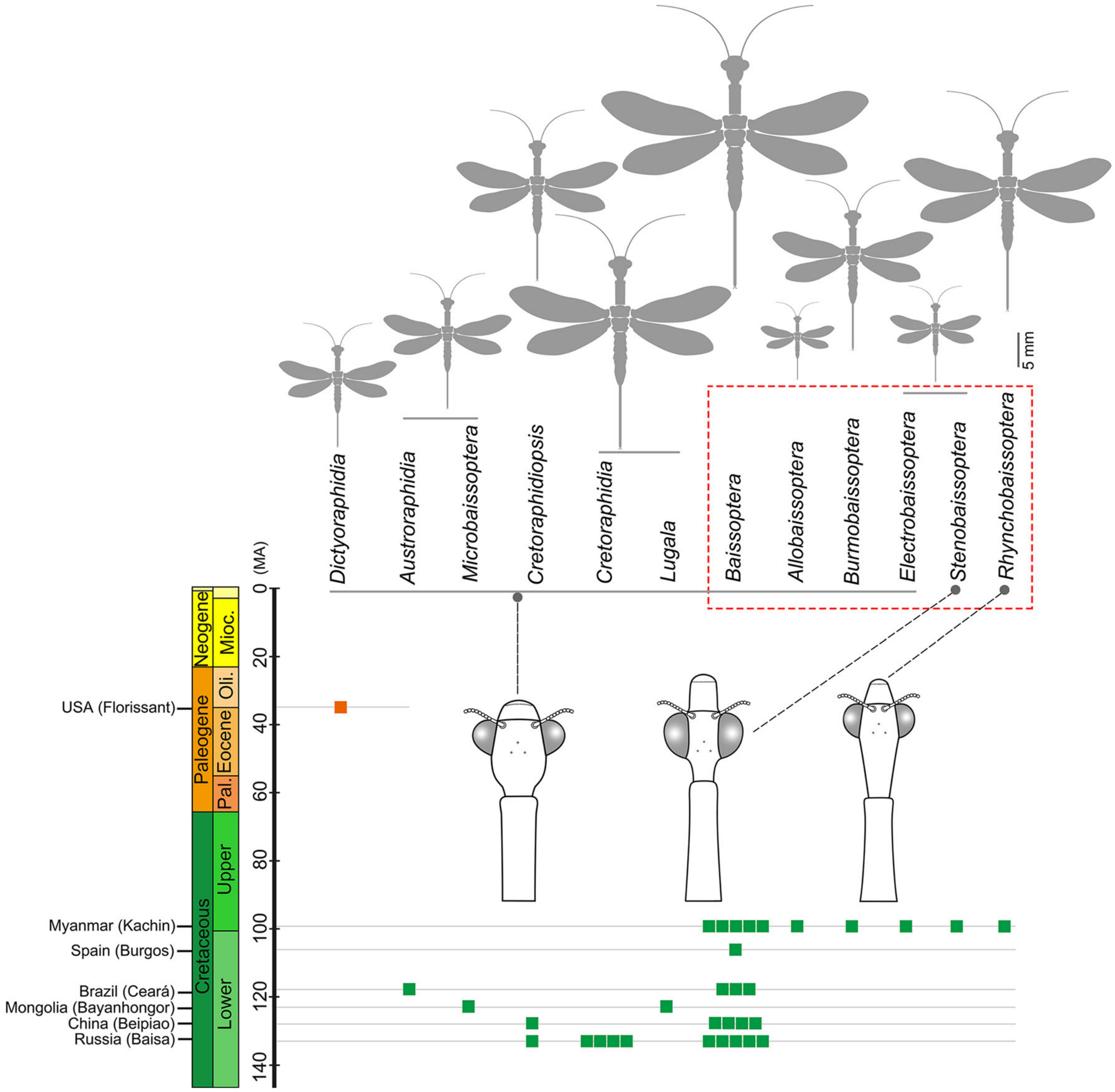

Fig. 16 Diversity of Baissopteridae through its evolutionary history. Number of squares represents the species number of each genus from each fossil locality. Green square indicates the Cretaceous records, while orange square indicates the sole Tertiary record. Habitus outlines reflect the differences in body size among genera (see Table S1 for the detailed data of measurements), with ovipositor directed toward corresponding genera. Schematic diagram of different types of head in Baissopteridae shown below corresponding genera from left to right: common type (ovoid or subrectangular head, ~1.5–2.0× head width, vertex ~0.5× head length); specialized type I (slender head with enlarged compound eyes, prolonged clypeus, and shortened vertex, ~4.0× head width, vertex 1/10–1/6× head length); specialized type II (elongate head, slightly narrower than pronotum, ~3.0× head width, vertex ~0.5× head length). Red dotted box highlights the genera recorded herein from the mid-Cretaceous of Myanmar

nearly rectangular, approximately 1.5–2.0× as long as wide, and slightly wider than the pronotum, with the vertex around one-half head length. However, *R. hui* gen. et sp. nov. has a distinctive head, which is slenderly elongate (approximately 3.0× as long as wide, and slightly narrower than the pronotum). *Stenobaissoptera xiai* gen. et sp. nov. also has a slender head (approximately 4.0× as long as wide), but with greatly enlarged compound eyes and a distinctly shortened vertex (only about 1/10–1/6× head length) (Fig. 16). Third, there are two species of *Baissoptera* having tarsomere III greatly modified relative to that of other baissopterids. Tarsomere III of Raphidiomorpha is symmetrically bilobed and medially connected with a reduced tarsomere IV (see Aspöck et al. 1991: Figs. 16 and 41; Pérez-de la Fuente et al. 2012: Fig. 7b; Figs. 2d and 6c). Strikingly, *B. burmana* sp. nov. has an asymmetrically bilobed tarsomere III on all pairs of legs, while *B. monopoda* sp. nov. has tarsomeres III simple (not bilobed) and nearly as long as tarsomere IV. These two kinds of tarsal specializations are certainly absent among extant Raphidioptera, and so far have yet to be found in other known fossil species of Raphidiomorpha. Lastly, spotted wings are present in two Burmese amber species of *Baissoptera*, i.e., *B. burmana* sp. nov. and *B. maculata* sp. nov. Unlike the other two neuropterid orders (Megaloptera and Neuroptera), in which there are many species with variously spotted wings, Raphidioptera have entirely transparent and immaculate wings in most species. Besides the above two spotted-wing baissopterids, the other snakefly species known with wing markings are three extant species of Inocelliidae (Liu et al. 2009, 2012).

In light of the above remarkable characters, the morphological diversity of these Burmese amber baissopterids appears to be greater than that of any earlier baissopterid paleofauna. The head and legs, on which the morphological specializations developed in some Burmese amber baissopterids, have significant functions in relation to certain behaviors of snakeflies. Extant snakeflies inhabit various woodland habitats (coniferous forests, deciduous forests, shrubs, *&c.*), and they mainly feed on soft-bodied arthropods as both larvae and adults (Aspöck 2002). However, snakefly adults (in particular those of Raphidiidae) prey preferably on aphids and other Sternorrhyncha, while they have been occasionally found to consume pollen (Aspöck 2002; Aspöck and Aspöck 2009). The head of adult snakeflies is extremely flexible (Aspöck and Aspöck 2009) and functions to search and manipulate prey during predation (Aspöck et al. 1991: Figs. 2933–2936). Furthermore, the head also acts together with the legs and abdomen in courtship and copulation (Aspöck 2002; Aspöck and Aspöck 2009), including a pre-mating cleaning behavior with the legs and antennae (Aspöck et al. 1991: Fig. 2930), and a fixed connection between the male head and female abdomen during copulation in Inocelliidae (Aspöck et al. 1994).

Because the adult morphologies (e.g., slender body shape, elongate prognathous head and prothorax, bilobed tarsomere III, and long female ovipositor) as well as the larval characters (Engel 2002; Perrichot and Engel 2007) are largely similar between Mesozoic snakeflies and their modern counterparts, the basic biological traits in Mesozoic snakeflies might not differ significantly from those in living snakeflies, such as a preference for arboreal habitats, predatory habits, *&c.* However, the distribution of Mesozoic and Paleogene snakeflies were tropical or subtropical, while modern snakeflies mainly occur in temperate regions or at high elevations (i.e., cooler environments) in otherwise more tropical regions (Aspöck 1998). The mid-Cretaceous of Myanmar harbored an extraordinarily diverse tropical forest biota (Grimaldi et al. 2002; Grimaldi and Ross 2017), with rich and highly partitioned niches, reflected by a wide range of morphologically varied but closely related species, some of which displayed morphological and behavioral specializations unknown in their modern counterparts. In Neuropterida, there have been various reports of spectacular morphological modifications associated with predation, mimesis, and camouflage in both adults and larvae of Burmese amber Neuroptera (Liu et al. 2016b, Liu et al. 2018a, b; Wang et al. 2016; Badano et al. 2018; Haug et al. 2018, 2019). Likewise, the diversified morphological characters among these Cretaceous baissopterid snakeflies might have evolved along with behavioral and microhabitat partitioning. For example, as active predators, the enlarged compound eyes in *S. xiai* gen. et sp. nov. might have enhanced the visual acuity when searching for prey. The asymmetrically bilobed tarsomere III in *B. burmana* sp. nov. might be a morphological specialization for crawling on certain plant surfaces where adults of this species lived or perhaps functioned during pre-mating cleaning. Admittedly, it is hardly possible to corroborate the above hypotheses by lack of direct evidence from the fossils, but may nonetheless serve as starting points for continued exploration into the paleobiology of these remarkable snakeflies.

Conclusions

The youngest but highly diverse paleofauna of the Mesozoic snakefly family Baissopteridae is documented from the mid-Cretaceous of Myanmar. Our findings provide significant new morphological evidence for understanding the phylogenetic status and diversity of Baissopteridae. The considerable morphological diversity observed in these baissopterids might result from behavioral or microhabitat partitioning in the complex tropical forest ecosystem of the mid-Cretaceous. Our results also highlight the Cretaceous radiation and early phases of evolution of Neuropterida.

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Authors' contributions Xingyue Liu and Xiumei Lu designed the project; Xiumei Lu, Bo Wang, Michael S. Engel, and Xingyue Liu prepared figures and wrote the manuscript; Xiumei Lu and Xingyue Liu performed the comparative and analytical work; Xiumei Lu, Bo Wang, Weiwei Zhang, Michael S. Engel, and Xingyue Liu collected data; all authors contributed to the discussion.

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Availability of data and material All data needed to evaluate the conclusions in the paper are present in the main text and/or Electronic Supplementary Material. Information of specimen depositions can be found in the Material and Methods. Specimens are available for study by contacting XL.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethics approval Not applicable.

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