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Short communication

A new species of Mesoraphidiidae (Raphidioptera) from mid-Cretaceous Kachin amber, with discussion on anal veins in Raphidiomorpha

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ABSTRACT

Dolichoraphidia groehni sp. nov. (Raphidioptera: Mesoraphidiidae: Nanoraphidiini) is described from mid-Cretaceous Kachin amber of northern Myanmar based on a well-preserved male specimen. The new species is most similar to *D. aspoecki* Liu et al., 2016, but differs from it by the distal location of crossvein 3ra-rp (distad pterostigma) and the short presumed gonocoxites 9 (or gonocoxites 9 + gonostyli 9). A comparative analysis of the anal veins in the fore- and hindwings of Raphidiomorpha is provided. The analysis shows that the apomorphic states of the anal veins, characteristic of extant taxa (Raphidiidae and Inocelliidae), may be derived from conditions occurring in both Cretaceous families of Raphidioptera, Mesoraphidiidae and Baissopteridae.

1. Introduction

Raphidiomorpha represents a taxon of higher snakeflies, which comprises five families of Raphidioptera: Metaraphidiidae (Early Jurassic), Mesoraphidiidae (Early Jurassic to mid-Cretaceous), Baissopteridae (Early Cretaceous to late Eocene), Raphidiidae (early Eocene to Recent), and Inocelliidae (early Eocene to Recent) (Liu et al., 2014). These are numerous and diverse in Kachin amber, despite its humid tropical climate, which is not characteristic for the habitats of modern species of the suborder. Five species of Mesoraphidiidae (Engel, 2002; Liu et al., 2016) and eleven species of Baissopteridae (Lu et al., 2020; Jouault et al., 2022) have been described to date, and a number of species are still awaiting description (Liu, 2019). Three larvae are also known (Engel, 2002; Perrichot and Engel, 2007; Haug et al., 2020).

Herein, a new species of the mesoraphidiid genus *Dolichoraphidia* Liu et al., 2016 is described based on a male specimen possessing well-preserved venation and genitalia. In particular, only two simple anal veins are present in its hind wing. In this regard, all available data has been analysed, with respect to the configuration and number of anal veins, in Raphidiomorpha.

2. Material and methods

The study is based on a specimen of snakefly embedded in a piece of Kachin amber originating from the Hukawng Valley, the state of Kachin in northern Myanmar; a map of this valley can be seen in Grimaldi et al. (2002, fig. 1). The age is currently considered to be earliest Cenomanian (Shi et al., 2012; Smith and Ross, 2018). The amber piece is deposited in Leibniz-Institut zur Analyse des Biodiversitätswandels (Humburg, Germany) and was legally obtained before June 2017 (see Museum Catalogue Entry in Supplementary material).

The photographs were taken by Carsten Gröhn using a Zeiss stereomicroscope (modified with variable objectives: NikonMPlan 5×, 10×, 20×, 40×; ZEISS Luminar 18 mm, 25 mm, 40 mm) and an attached Canon EOS 450D digital camera. Line drawings were prepared by VM using Adobe Photoshop CS3.

The venational terminology follows Breitkreuz et al. (2017). Terminology of wing spaces and details of venation (e.g., traces, veinlets) follows Oswald (1993). Terminology of genitalia follows Aspöck and Aspöck (2008).

Abbreviations: A1–A3, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; *doi*, discoidal cell; hv, humeral veinlet; M, media; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; RP2, branch of RP distad RP1; Sc, subcosta.

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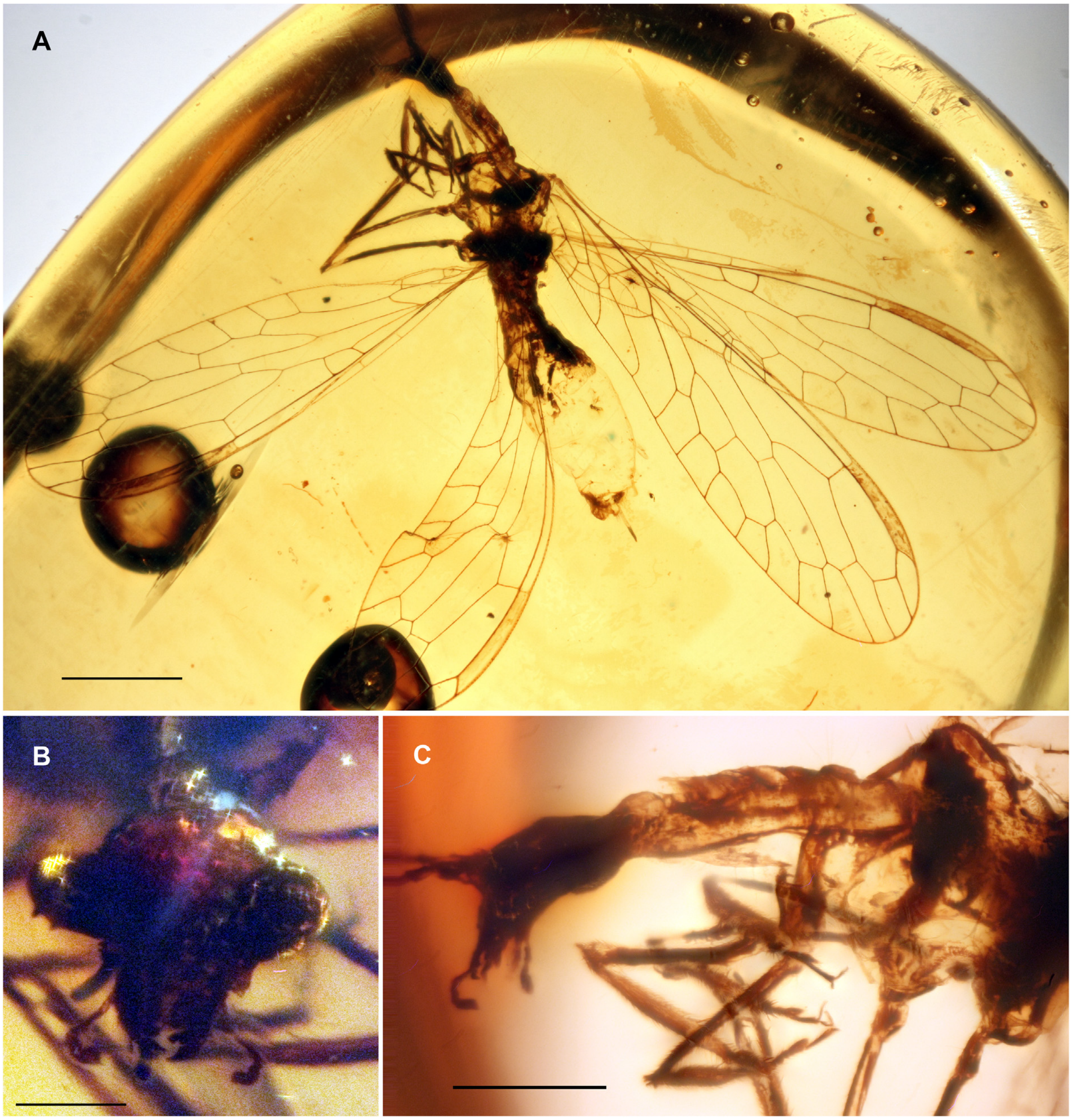

Fig. 1. *Dolichoraphidia groehni* sp. nov., holotype GPIH no. 5073, A, specimen as preserved; B, head (frontal view); C, anterior part of body (lateral view). Scale bars are 1 mm (A), 0.25 mm (B), 0.5 (C).

Institutional abbreviations: LIB, Leibniz Institute for the Analysis of Biodiversity Change [Leibniz-Institut zur Analyse des Bio diversitätswandels], Hamburg, Germany (formerly Geological-Paleontological Institute and Museum of the University of Hamburg [Geologisch-Paläaontologisches Institut und Museum der Universität Hamburg] and later Centrum of Natural History [Centrum für Naturkunde]); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.

All taxonomic acts established in the present work have been registered in ZooBankLSID (see below), together with the electronic publication urn:lsid:zoobank.org:pub:3C376E5E-C65D-49DB-8638-675DB3E1C66F.

3. Systematic paleontology

Order: Raphidioptera Navás, 1916
Family: Mesoraphidiidae Martynov, 1925a
Tribe: Nanoraphidiini Bechly and Wolf-Schwenninger, 2011

Genus *Dolichoraphidia* Liu et al., 2016

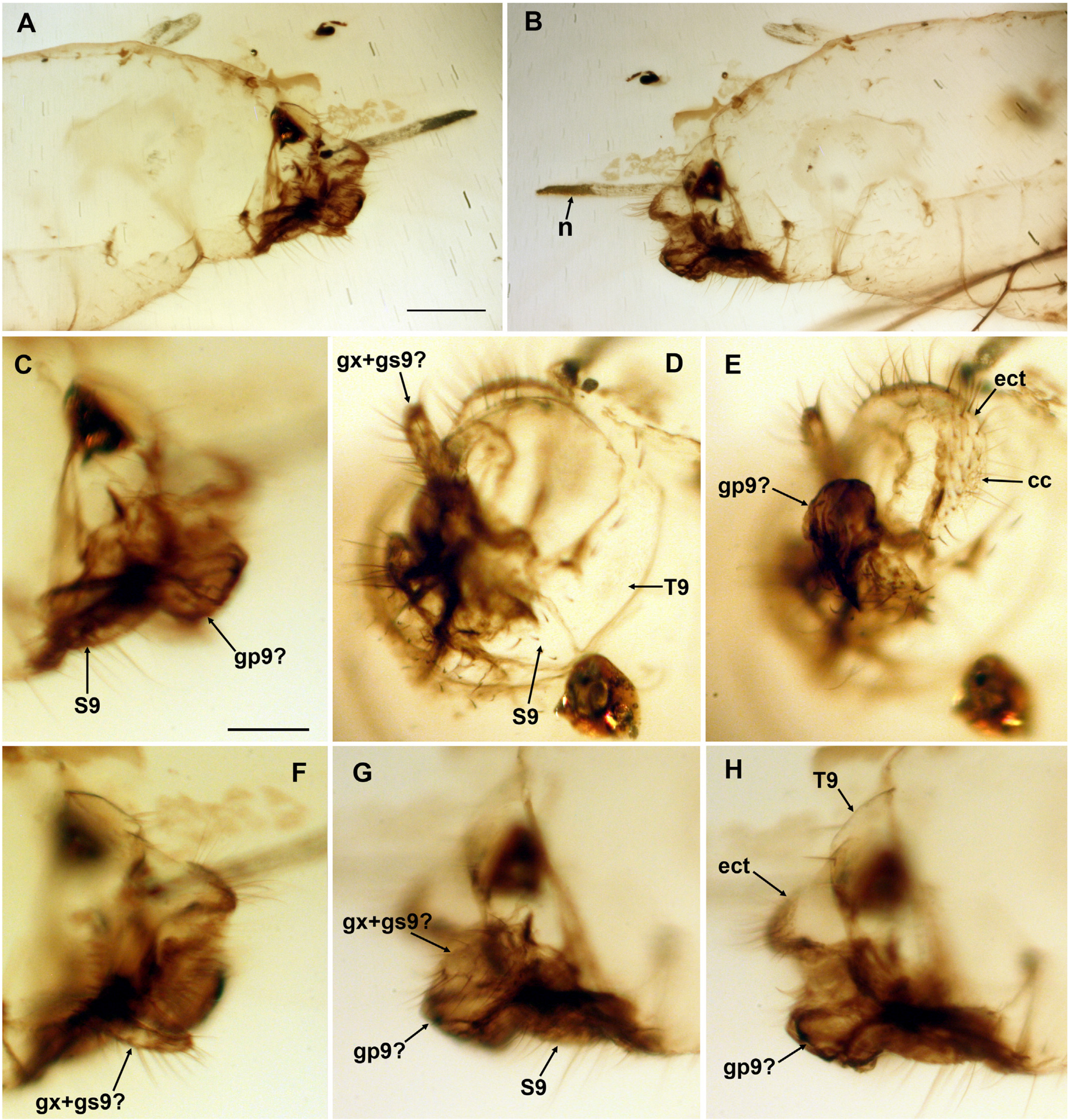

Fig. 2. *Dolichoraphidia groehni* sp. nov., holotype GPIH no. 5073, end of abdomen and genital segments. A, left side of abdomen; B, right side of abdomen; C, F, genital segments, left latero-ventral view; D, E, same, caudal view; G, H, same, right lateral view. cc, callus cerci; ect, ectopropt; gp9, gonapophyses 9; gs9, gonostyli 9; gx9, gonocoxites 9; n, unknown structure not belonging to the specimen; S9, 9th sternite; T9, 9th tergite. Scale bars are 0.2 mm (A, B, both to same scale), 0.1 (C–H, all to same scale).

Dolichoraphidia groehni sp. nov.
(urn:lsid:zoobank.org:act:BCB126C1-FFE5-47E6-9A1A-295DDB3DD7BE)
Figs. 1–3

Derivation of name. The specific epithet is formed from the family name of Carsten Gröhn, Glinde (Germany), in recognition of his efforts in collecting and promoting the study of Kachin amber inclusions.

Type material. Holotype GPIH no. 5073 (CCGG no. 11655), deposited in LIB (the collection of Mr. Carsten Gröhn is separately deposited with the abbreviation CCGG). A complete male specimen.

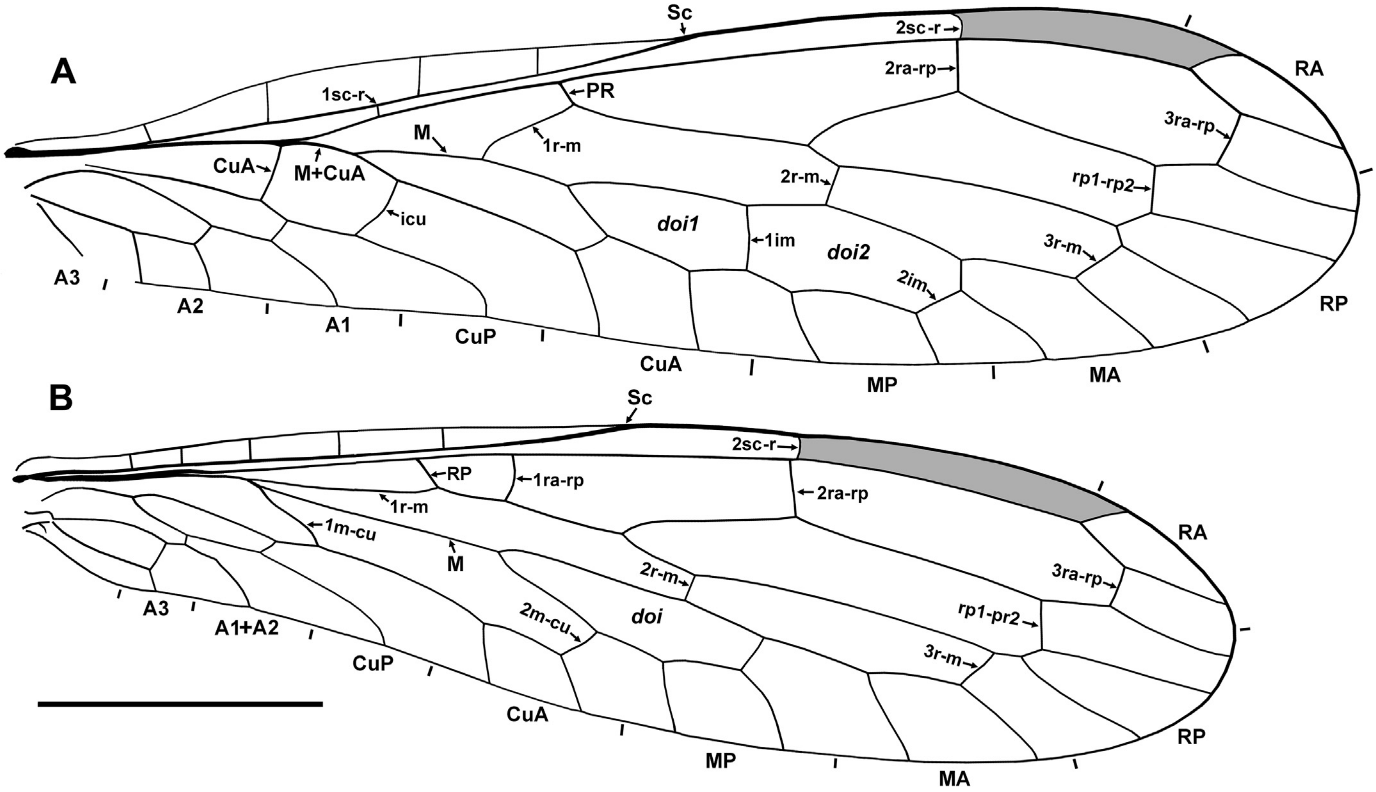

Fig. 3. Wing venation of *Dolichoraphidia groehni* sp. nov., holotype GPIH no. 5073. A, forewing; B, hind wing. Scale bar is 1 mm (both to same scale).

Type locality and horizon. Kachin amber (Northern Myanmar: Kachin State: Myitkyina District: Tanai Township: Hukawng Valley). Upper Cretaceous: lowest Cenomanian.

Diagnosis. May be easily distinguished from other species of the genus by short presumed gonocoxites 9 (or gonocoxites 9 + gonostyli 9) [long in *D. aspoecki*], distal location of crossvein 3ra-rp (distad pterostigma) [3ra-rp within pterostigma in *D. aspoecki* Liu et al., 2016, *D. engeli* Liu et al., 2016], two *doi* in the forewing [one *doi* in *D. engeli*], branch of RP within pterostigma absent [one weak branch present in *D. engeli*].

Description. Male. Body 4.2 mm long. Head elongate in lateral view, with large compound eyes. Ocelli not detected. Antennae not complete; scapus large, slightly conical; pedicellus elongate. Mandibles strong, with at least two nearly symmetrical and equal in length teeth. Maxillary palpi longer than mandibles, conspicuously enlarged distad, with last segment apically blunt. Labial palpi 3-segmented, with two proximal segment slender and apical segment broadly fusiform.

Thorax. Prothorax rather narrow in lateral view, nearly twice longer than head, ca. 0.84 mm. Meso- and metathorax together ca. 0.9 mm long; their details not clearly discernible.

Legs. Forelegs relatively short; coxa long; femur relatively short; tibia slightly swollen, nearly as long as femur, with several long strong distal setae at inner side, covered with very dense short setae; tarsus with slender, elongated claws. Mid- and hind legs relatively long; coxa short; femur relatively long, slender; tibia only slightly swollen, elongated, with several long strong distal setae at inner side, covered with very dense short setae.

Forewing 4.8 mm long, 1.14 mm wide (length/width: 4.21). Costal space narrow, widest at approximately half of length; four simple subcostal veinlets (right forewing), all widely spaced. Sc short, terminating on costal margin very proximad 2ra-rp; length from termination of Sc to pterostigma approximately equal to length of pterostigma. Subcostal space moderately broad, with basal crossvein located at proximal third between origin of RP, divergence of M, CuA; distal crossvein 2sc-r (enclosed pterostigma proximally) curved. Pterostigma long, evenly, rather weakly, pigmented. One RA branch forming distal margin of pterostigma; no branches incorporated in pterostigma. RA entering margin near apex. RA space with two crossveins forming two radial cells: 2ra-rp long, located nearly opposite 2scp-r; 3ra-rp long, located much distad pterostigma. RP originating far from wing base (0.45 wing length), with one deeply forked branch (RP1). One long intraradial crossvein rp1-rp2 between stem of RP, anterior branch of RP1. Three crossveins between RP, M/MA: 1r-m very long, oblique, slightly sinuate, connecting stem of RP near its origin, M; 2r-m connects stem of RP1 near its origin, MA; 3r-m connects posterior branch of RP1, anterior branch of MA. M fused with CuA for rather long distance; forked far proximad origin of RP. MA deeply forked once. MP with one simple branch. Two intramedian crossveins form two *doi*; 2im connects posterior branch of MA, stem MP; *doi1* somewhat shorter than *doi2*. Anterior trace of CuA strongly zigzagged, simple terminally, fused with MP for long distance forming most part of posterior margin of *doi1*; posterior trace of CuA simple. CuP simple. Crossvein icu between CuA, CuP long. Crossvein between CuP, A1 closer to origin of CuA than to icu. A1 simple; A2 with one simple branch; A3 short, simple. Between anal veins one relatively long crossvein connecting A1, A2.

Hind wing 4.32 mm long, 1.02 mm wide (length/width: 4.24). Costal space narrow; five widely spaced, simple subcostal veinlets. Sc relatively short; length from termination of Sc to pterostigma much shorter than length of pterostigma. In subcostal space, one crossvein detected (2sc-r, forming proximal margin of pterostigma), slightly curved. Pterostigma elongate, markedly longer than in forewing, evenly, rather weakly, pigmented. RA with one branch forming distal margin of pterostigma. RA entering margin near apex. Three crossveins between RA, RP: 1ra-rp much proximad 2r-m; 2ra-rp much distad termination of Sc; 3ra-rp distad pterostigma. RP originates at 0.35 wing length. Anterior trace of RP simple apically, with one branch (RP1) which is rather deeply forked, both branches simple. One intraradial crossvein (rp1-rp2), between stem of RP, anterior branch of RP1. Three crossveins between R, M: 1r-m long, running subparallel to R; 2r-m connects RP1, MA; 3r-m connects RP1, anterior branch of MA. M forked much distad origin of RP. MA, MA rather deeply forked once; all their branches simple. One intramedian crossveins forming one elongate *doi*. Two crossveins between M, Cu: 1m-cu very long, slightly sinuous; 2m-cu connects MP, CuA. Anterior trace of CuA simple distally, with one simple branch. CuP simple, not fused with A1. Between CuA, CuP short crossvein located proximad 1m-cu. Between CuP, presumed A1 + A2 short crossvein. Presumed A1 + A2, 3A simple; between them long crossvein; basally short vein-like appendix (possibly incomplete jugal vein).

Abdomen swollen in caudal half; 5th to 9th tergites and 5th to 9th sternites very light, nearly transparent, covered with scarce setae. 9th tergite relatively short, far extended laterally; 9th sternite relatively short, slightly extended laterally; its left side appears more heavily pigmented (Figs. 2C, D); these segments closely approach, but not fused (Fig. 2D). Tenth tergite (ectoproct) triangle in lateral view, entire, covered with relatively dense, long setae; callus cerci with several trichobothria (difficult to count precisely) (Fig. 2E). Presumed gonocoxites 9 + gonostyli 9 digitiform, relatively short, directed caudally, covered relatively dense, long setae (Figs. 2F, G). Presumed gonapophyses 9 (judged from its location) rather small, heavy pigmented, pear-shaped in ventral view (Figs. 2E, H).

4. Discussion

4.1. Comparative characters of the new species

The venation of the new species is very similar to that of *Dolichoraphidia aspoecki*, but can be distinguished from it mainly by the distal location of crossvein 3ra-rp in both wings. The position of crossvein 3ra-rp distad the pterostigma as found in *D. groehni* sp. nov. is an apomorphic condition (see Makarkin and Archibald, 2014). In two other species of the genus, this crossvein is plesiomorphically located within the pterostigma. The apomorphic position of 3ra-rp is also present in two other species of the Kachin amber Nanoraphidiini (*Burmoraphidia reni* and *Nanoraphidia electroburmica* Engel, 2002) and the majority of other species of that tribe from other Cretaceous localities (see Grimaldi, 2000, fig. 1; Pérez-de la Fuente et al., 2010, fig. 2; 2012, fig. 8; Jepson et al., 2011, fig. 4; Liu et al., 2016, figs. 9, 12B). This apomorphic condition occurs extremely rarely in other Mesoraphidiidae, but it is present in all extant Inocelliidae and many Raphidiidae.

The male genitalia of *D. aspoecki* and *D. groehni* sp. nov. are also similar, but differ in details, e.g., by the length of the presumed gonocoxites 9 (or gonocoxites 9 + gonostyli 9) (long in *D. aspoecki*, short in *D. groehni* sp. nov.) (Fig. 2; Liu et al., 2016, fig. 2E).

In general, the male genitalia of Mesoraphidiidae are difficult to interpret, even in *D. groehni* sp. nov., in which these can be clearly discernible. The ninth tergite and ninth sternite are plesiomorphically not fused in two species of *Dolichoraphidia*, including the new species. A pair of elongate extending sclerites are probably the gonocoxites (or the fused gonocoxites 9 and gonostyli 9), as assumed by Liu et al. (2016) (Figs. 2D, F). The fused gonapophyses 9 are determined by their ventral location in the place where they are present in the extant Raphidiidae (Figs. 2E, H). It is interesting that the gonapophyses 9 are not detected in *D. aspoecki* by Liu et al. (2016). The genital sclerites of the 10th abdominal segment cannot be determined for sure in any Mesoraphidiidae, except for ectoproct.

One can agree with Liu et al. (2016) that the male genitalia of Mesoraphidiidae (in fact mainly Nanoraphidiini) are clearly more similar to those of Raphidiidae than of Inocelliidae. For comparison, male genitalia in the early Eocene *Archiinocellia protomaculata* (Engel, 2011) (the oldest known Raphidiidae which has relatively well discernible genitalia) are simpler than those in *D. groehni* sp. nov. Genital sclerites of the ninth segment in *A. protomaculata* are not detected or poorly preserved; at least gonocoxites 9 and gonostyli 9 are certainly lost (see Archibald and Makarkin, 2021, figs. 13A, B).

4.2. Anal veins in Raphidiomorpha

The homology of the anal veins in insects is probably the most difficult problem in the interpretation of wing venation. Comstock (1918) was absolutely right when writing that “the determination of the probable primitive number and form of the anal veins in the wings of insects is a more difficult matter than the determination of the probable number and forms of the other principal veins” (p. 107).

The hypothetical primitive (archetype) insect wing venation was considered to have two dichotomously branching anal veins (AA and AP) according to the hypothesis of Kukalová-Peck (1983, fig. 15), three after Comstock and Needham (1898), and five according to Snodgrass (1935, fig. 121). Snodgrass (1935) distinguished between the poscubitus (first anal vein) and vannal veins (other anal veins). Recently, Schubnel et al. (2020) revived this hypothesis, i.e., the presence of an independent postcubital vein (PCu vein = A1 of authors) located between the cubital and anal veins.

Regardless of the number of anal veins in insect archetype venation, the anal system in Raphidiomorpha is obviously apomorphic: all extant Raphidioptera (Raphidiidae and Inocelliidae) possess two apparent anal veins (at most once forked) in both fore- and hind wings.

Although imprints of fossil Raphidiomorpha are numerous (known mainly from the Mesozoic), specimens with the well-preserved anal region are very rare. Therefore, the study of the Kachin amber Raphidiomorpha is very important for understanding their venation in general, and the configuration of the anal veins in particular. *Dolichoraphidia groehni* sp. nov. possesses well-preserved anal veins in both fore- and hindwings, which has prompted a summary of all available data on anal veins of Raphidiomorpha.

4.2.1. Forewing

The configuration of anal veins in the forewing in extant Raphidiidae and Inocelliidae is similarly apomorphic: A1 is simple or shallowly forked, A2 and A3 are fused for a considerable distance (almost entirely fused basally in Raphidiidae, while A2 and A3 are basally free for some distance before their fusion in Inocelliidae) (Makarkin and Archibald, 2014, figs. 2A, C). In some extant Raphidioptera, two simple anal veins are present: A1 is simple and A2 and A3 are fused for their entire length, often in Inocelliidae and extremely rarely in Raphidiidae (see e.g., Monserrat and Papenberg, 2006, fig. 2; Aspöck et al., 2011, figs 1, 10, 19, 20, 23–25, 27, 28).

The anal veins of the Cenozoic Raphidiidae and Inocelliidae (including the early Eocene, oldest taxa) are probably similarly configured, see e.g. the raphidiid *Megaraphidia klondika* Archibald and Makarkin, 2021 (fig. 5A) in which the basal part of the forewing is relatively well preserved, and the inocellid ‘*Fibla*’ *erigena* (Menge in Pictet-Baraban and Hagen, 1856), in which the basal free A2 and A3 are well discernible in MCZ 5120 and MCZ 5121 (pers.

data), and *Paraksenocellia borealis* Makarkin et al., 2019 (fig. 2), in which anal veins are similar to that of *Sininocellia gigantos* Yang, 1985 (Liu et al., 2012, figs. 1, 3). However, no specimens of the Cenozoic Raphidioptera are known with two simple anal veins.

The maximum number of anal veins in the forewing of known Mesozoic Raphidiomorpha are three, considered here as being a plesiomorphic state at the level of Raphidiomorpha: A1 and A3 are simple, A2 is forked. This condition is clearly discernible in only a few species, e.g., the Early Jurassic *Metaraphidia vahldieki* Willmann, 1994 (fig. 3c) (Metaraphidiidae), the Early Cretaceous mesoraphidiid *Mesoraphidia sinica* Ren, 1997 (fig. 7), and at least two species of the mid-Cretaceous *Dolichoraphidia*, including the new species (Fig. 3). This configuration may be characteristic of many other species of Mesoraphidiidae, in which the basal-most part of the forewing is not preserved or obscured and A3 is not preserved, e.g., the Middle Jurassic *Ororaphidia megalocephala* Engel and Ren, 2008; the Early Cretaceous *Mesoraphidia durlstonensis* Jepson et al., 2009; *M. purbeckensis* Jepson et al., 2009; *M. websteri* Jepson et al., 2009; *Lebanoraphidia nana* Bechly and Wolf-Schwenninger, 2011; *Amarantoraphidia ventolina* Pérez-de la Fuente et al., 2012; the mid-Cretaceous *Nanoraphidia electroburmica* (Jepson et al., 2009, figs. 1, 4, 5; Pérez-de la Fuente et al., 2012, fig. 9A; Bechly and Wolf-Schwenninger, 2011, fig. 16; Liu et al., 2016, fig. 12B; Lyu et al., 2017a, fig. 3B).

The two visible anal veins in those Mesoraphidiidae which have more branches are more difficult to interpret, but its structure is likely to be the same as in extant taxa. In the well-preserved Late Jurassic *Mesoraphidia inaequalis* Martynov, 1925b, A1 is simple and the next anal vein is pectinate with three branches which are confidently interpreted as being the fused A2 and A3 (see Makarkin and Archibald, 2014, fig. 1A). The basal fusion of A2 and A3 for a considerable distance is detected in the mid-Cretaceous *Burmoraphidia reni* Liu et al., 2016, fig. 9. In some Mesoraphidiidae, the presumed A1 is deeply forked (rarely pectinate) and the presumed A2 + A3 is pectinate, e.g., the Cretaceous *Alloraphidia* Carpenter, 1968 and *Siboptera eurydictyon* Ponomarenko, 1993 (Carpenter, 1968, fig. 2; Ponomarenko, 1993, fig. 12g; Makarkin and Khramov, 2015, fig. 3A).

The two visible anal veins of many of the multi-veined Early Cretaceous Baissopteridae are concordant with this interpretation: A1 is simple or forked and the presumed A2 + A3 is pectinate (e.g., *Baissoptera minimai* Ponomarenko, 1993; *B. liaoningensis* (Ren, 1994); *Cretoraphidia macrocella* (Ponomarenko, 1993) (Ponomarenko, 1993, figs. 2g, 8; Lyu et al., 2017b, fig. 4B). In some Baissopteridae, both preserved anal veins are pectinate with up to four branches, e.g., *Baissoptera martinsoni* Martynova, 1961; *B. sinica* Lyu et al., 2017b (Ponomarenko, 1993, fig. 1a; Lyu et al., 2017b, fig. 7B), allowing different interpretations.

The anal veins in the mid-Cretaceous Baissopteridae from Kachin amber became slightly more simplified; both the presumed A1 and the presumed A2 + A3 are forked in most species (Lu et al., 2020, figs. 3a, c, 7c, e, 15c). Only one species (*Burmobaissoptera jiaxiaoae* Lu et al., 2020) has a different configuration of anal veins: the anterior anal vein is deeply forked (A1 of the authors), and the posterior is simple (A2 of authors) (Lu et al., 2020, fig. 9a), but it is possible to interpret this similarly other Kachin amber species: A1 is simple but fused for a short distance with A2, which is basally fused with A3. In *Electrobaissoptera burmanica* Lu et al. (2020), two simple veins are present, which the authors named A1 and A2 (Lu et al., 2020, fig. 12d), however this designation may be incorrect. Since A2 and A3 in the majority of Kachin amber species may be interpreted as basally fused, it is highly likely that A2 of the authors is the entirely fused A2 + A3.

Therefore, the most apomorphic condition of the anal veins (i.e., two simple veins) in the forewing is present in three families of Raphidiomorpha (Inocelliidae, Raphidiidae and Baissopteridae), in all probably consisting of A1 and A2 + A3.

4.2.2. Hind wing

The two simple anal veins in the hind wing of *Dolichoraphidia groehni* sp. nov. are superficially similar to those of some extant Inocelliidae (e.g., Aspöck et al., 1991, fig. 46). This configuration is probably characteristic of the genus *Dolichoraphidia* Liu et al., 2016 as a whole (see Liu et al., 2016, figs. 2A, 4).

Makarkin et al. (2019) suggested that the configuration of anal veins in the hind wings of extant Inocelliidae and Raphidiidae strongly differ: in Inocelliidae, A1 is a simple separate vein for its entire length, A2 and A3 are often free basally and then fused completely (e.g., Aspöck et al., 1991, fig. 44) or for most of their distance but distally free, for example, *Sininocellia* (Liu et al., 2012, figs. 1–3). In contrast, in Raphidiidae, A1 and A2 are fused with each other and often with CuP for some distance but distally free, and A3 is a simple entirely separate vein (see Aspöck et al., 1991, fig. 23).

The configuration of anal veins in most fossil Inocelliidae is similar to that of extant taxa, e.g., *'Fibla' exusta* (Cockerell and Custer, 1925) (Makarkin and Archibald, 2014, fig. 23); *'F.' erigena*, judging from the photograph of specimen MCZ 5120 (pers. obs.); *Electrinocellia peculiaris* (Carpenter, 1957), judging from the photograph of the holotype (per. obs.); and *Paraksenocellia* sp., but its A1 is deeply forked, and A2 shallowly forked (Makarkin et al., 2019, fig. 3.). A1 is simple and A2 + A3 are forked in these species (i.e., A2 and A3 are free distally).

However, the anal vein configuration of the Baltic amber *Saccinofibla aperta* Aspöck and Aspöck, 2004 is unusual, A1 is deeply forked, and A2 is simple (Aspöck and Aspöck, 2004, fig. 8). This may be alternatively interpreted as A1 + A2 being forked and A3 is simple, similar to that of some raphidiids with plesiomorphic venation, e.g., the Rovno amber *Succinoraphidia radioni* Perkovsky and Makarkin, 2019 (fig. 4D). If so, this is the only known species of Inocelliidae, which has a configuration of anal veins as in Raphidiidae.

The configuration of anal veins in most Eocene species of Raphidiidae is the same as in extant species. The best preserved hind wings are the early Eocene *Megaraphidia klondika* Archibald and Makarkin, 2021 and the late Eocene *Megaraphidia* sp. (Makarkin and Archibald, 2014, fig. 8; Archibald and Makarkin, 2021, fig. 5D). Also, anal veins of the late Eocene *Succinoraphidia radioni* and *S. baltica* (Carpenter, 1957) is configured as in extant species, but in this genus CuP and A1 + A2 are not fused. However, A3 is deeply forked in *S. exhibins* Aspöck and Aspöck, 2004 (fig. 5), a unique condition in the family.

In some Mesoraphidiidae, the anal vein configuration is the same as extant Raphidiidae with plesiomorphic venation, e.g., the Middle Jurassic *Ororaphidia megalocephala* Engel and Ren, 2008; the Late Jurassic *Proraphidia turkestanica* Martynova, 1947; the Early Cretaceous *Mesoraphidia sinica* Ren, 1997; mid-Cretaceous *Nanoraphidia electroburmica* and probably *Rynchoraphidia burmana* Liu et al., 2016 (Martynova, 1947, fig. on p. 637; Ren, 1997, fig. 7; Liu et al., 2016, figs. 6A, 12B; Lyu et al., 2017a, fig. 4G). Raphidiid-like configuration of anal veins in Mesoraphidiidae from Kachin is evidenced by the fusion of A1 and A2 which is observed in *Burmoraphidia reni* Liu et al., 2016: A1 and A2 are fused for a relatively short distance far from their bases, and A3 is long and simple (Liu et al., 2016, fig. 9). Therefore, anal veins of *Dolichoraphidia* may be similarly interpreted as the genus belongs to the same tribe, i.e., the anterior vein is the fused A1 and A2, and the posterior is the simple A3.

Anal veins of other Mesoraphidiidae may be interpreted as in extant Inocelliidae, i.e., A1 is simple or forked, and A2 + A3 is deeply forked or pectinate. It is most clearly preserved in the Late Jurassic *Mesoraphidia inaequalis* Martynov, 1925b, and the Cretaceous *Stenoraphidia obliquivenatica* (Ren, 1994); *Alloraphidia* Carpenter, 1968; *Siboptera fornicata* (Ren, 1994); *Styporaphidia willmanni* Lyu et al., 2020 (Carpenter, 1968, fig. 1; Makarkin and Archibald, 2014, fig. 1B; Makarkin and Khramov, 2015, fig. 3B, D; Lyu et al., 2018, fig. 1I; Lyu et al., 2020, figs. 11B, D, 12).

The anal veins in Baissopteridae, which have the richest venation among Raphidiomorpha, may be reduced. A most extreme case is the Kachin amber *Electrobaissoptera burmanica* Lu et al. (2020), where two simple anal veins are present, which the authors named A1 and A2 (Lu et al., 2020, fig. 12e); the two other short veins in their figure located basad (not named by these authors) are the jugal fold and the jugal vein judging from their photograph (Lu et al., 2020, fig. 11c). This photograph shows that A1 appears to be basally duplicate so that it may be represented here by a very short free A1 and A2 which then fused (like in the extant Raphidiidae), and then this makes the A2 of the authors actually A3. This interpretation may be applied to other species of Baissopteridae: A1 + A2 is pectinate or at least deeply forked, and A3 is mostly simple, rarely forked, e.g., the Early Cretaceous *Baissoptera kolosnitsynae* Martynova, 1961, *Rudiraphidia liaoningensis* (Ren, 1994), *Siboptera fornicata* (Ren, 1994) (Martynova, 1961, fig. 7; Ponomarenko, 1993, fig. 1n; Ren, 1997, figs. 3b, 4).

Therefore, the most apomorphic condition of anal veins (i.e., two simple veins) in the hind wing is present in three families of Raphidiomorpha: Inocelliidae, Mesoraphidiidae and Baissopteridae. However, these differ by their origin: the presumed A1 + A2 and A3 in Mesoraphidiidae and Baissopteridae, and A1 and A2 + A3 in Inocelliidae.

5. Conclusions

The study of *Dolichoraphidia groehni* sp. nov., possessing a well-preserved abdomen, allows a better understanding of the structure of the male genitalia in Mesoraphidiidae. In particular, the clearly discernible presumed gonapophyses 9 is first detected in this family. This species possesses also well preserved anal veins, plesiomorphic in the forewing (i.e., simple A1 and A3, and forked A2), and strongly apomorphic in the hind wing (i.e., two simple veins). The analysis shows that the apomorphic condition of the anal veins in the fore- and hindwings which is characteristic of extant taxa (Raphidiidae and Inocelliidae) may be derived from conditions occurring in both families of Cretaceous Raphidioptera: Mesoraphidiidae and Baissopteridae.

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Appendix A. Supplementary data

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