*Zootaxa* 4103 (6): 537–549
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://doi.org/10.11646/zootaxa.4103.6.4
http://zoobank.org/urn:lsid:zoobank.org:pub:09A664E2-4322-4ED9-B146-61EB64B7924C

# First Record of Anisoptera (Insecta: Odonata) from mid-Cretaceous Burmese Amber

MARIO SCHÄDEL[1] & GÜNTER BECHLY[2,3]

[1] *Department of Evolutionary Biology of Invertebrates, University of Tübingen, Auf der Morgenstelle 28E, 72076 Tübingen, Germany. E-mail: mario.schaedel@student.uni-tuebingen.de*

[2] *Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany. E-mail: guenter.bechly@smns-bw.de*

[3] *Corresponding author*

## Abstract

The fossil dragonfly *Burmalindenia imperfecta* **gen. et sp. nov.** is described from mid-Cretaceous Burmese amber as the first record of the odonate suborder Anisoptera for this locality and one of the few records from amber in general. The inclusion comprises two fragments of the two hind wings of a dragonfly. The fossil can be attributed to a new genus and species of the family Gomphidae, presumably in the subfamily Lindeniinae, and features a strange teratological phenomenon in its wing venation.

**Key words:** dragonfly, Gomphidae, Lindeniinae, fossil insect, Cenomanian

## Introduction

Modern representatives of the order Odonata are classified in the three suborders Zygoptera (damselflies), Anisoptera (dragonflies) and Anisozygoptera (Dijkstra *et al.* 2013). While the fossil history of the Odonatoptera goes back to the earliest Upper Carboniferous, the earliest known crown group Anisoptera (*Sinacymatophlebia mongolica* from Daohugou / China) stems from the Middle Jurassic (Kohli *et al.*, in press).

**Cretaceous odonates.** Numerous Cretaceous odonate species have been described from compression fossils from various fossil deposits. More than 16 families were discovered in the Early Cretaceous Crato-Formation in northeastern Brazil (Bechly 2007, 2010). Also fossil sites in Great Britain such as the Purbeck Beds and Weald Clay (Jarzembowski *et al.* 1998), Montsec and Las Hoyas in Spain (Martínez-Delclòs 1989, Martínez-Delclòs and Nel 1994, Whalley and Jarzembowski 1985), Israel (Vassilenko 2014), Abu Ras in Egypt (Schlüter and Hartung 1982), Koonwarra in Australia (Tillyard 1918), Baissa in Russia (Pritykina 1977), Bon Tsagan in Mongolia (Pritykina 1977), and Liaoning in China (Nel and Huang 2010) have yielded many Cretaceous odonate taxa from all three Recent suborders as well as from extinct Mesozoic suborders such as Archizygoptera, Tarsophlebioptera, Isophlebioptera, Stenophlebioptera, and Heterophlebioptera. The latter four fossil groups represent a grade of stem Epiprocta and stem Anisoptera that were formerly classified together with Recent Epiophlebiidae in a paraphyletic suborder "Anisozygoptera," while this suborder was recently defined as a monophyletic clade that includes only Epiophlebiidae (Dijkstra *et al.*, 2013).

**Fossil odonates in amber.** Odonates in amber are relatively rare even in the well-known Cenozoic Baltic and Dominican amber (Bechly 1996a, Bechly 1998). An unnamed libelluloid dragonfly from Eocene French Oise amber (Fleck *et al.* 2000) and *Gomphoides occulta* Hagen in Berendt, 1856, from Eocene Baltic amber are the only two records of dragonfly (Anisoptera) wing inclusions in amber yet published, but the latter has to be considered as a nomen nudum and the specimen seems to be lost (Bechly 1998). Still undescribed specimens of a Macromiidae and two Gomphaeschninae (Aeshnidae), all from Baltic amber, are present in the amber collection of the State Museum of Natural History Stuttgart in Germany.

Unsurprisingly, fossil odonates in Cretaceous amber are even more elusive and have only been described in

*Accepted by D. Paulson: 14 Mar. 2016; published: 18 Apr. 2016*

relatively recent publications. Dejax *et al.* (1996) first mentioned an undescribed wing fragment of a damselfly from Lebanon amber. Since then, three hemiphlebiid damselflies were described in amber from Jordan, France, Lebanon and South Dakota (Azar *et al.* 2010, Kaddumi 2007, Lak *et al.* 2009, Nel *et al.* 2010).

**Fossil odonates in Burmese amber.** Only two damselfly (Zygoptera) and one damsel-dragonfly (Epiophlebioptera, Anisozygoptera) species have yet been described from Burmese amber (Bechly and Poinar 2013, Huang *et al.* 2015, Poinar *et al.* 2010). However, numerous fossil damselflies are present in museum collections (e.g. SMNS) and include several new taxa of different families (Bechly, pers. comm. 2015).

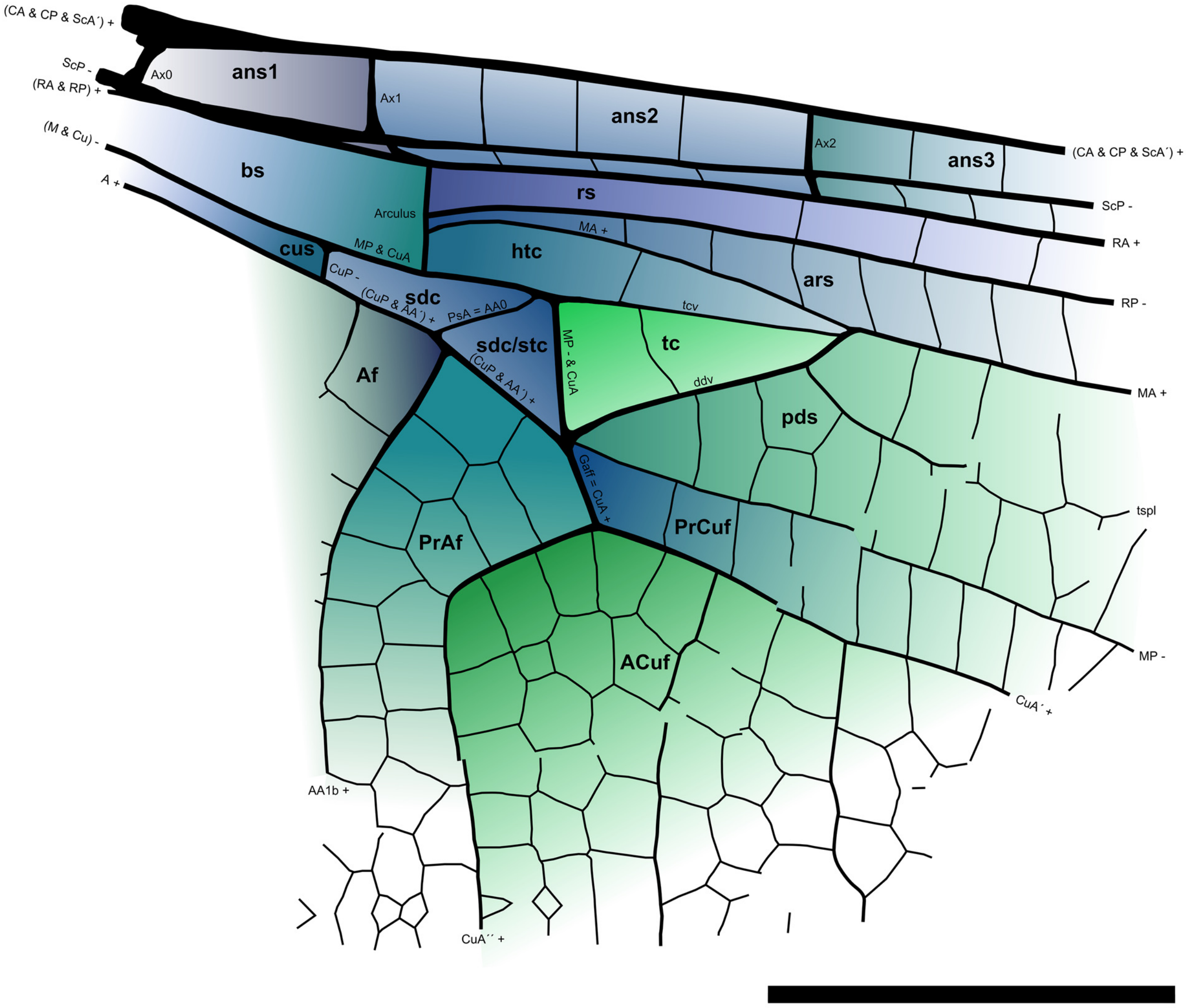

**FIGURE 1.** Drawing of left hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94, with terminology of wing venation. Scale bar = 5 mm.

**Burmese amber and its inclusions.** Burmese Amber, also called Burmite, has been exploited and traded for almost two millennia (Zherikhin and Ross 2000). While at least four other locations in Burma historically yielded amber, only the amber from the Hukawng Valley in Kachin state, the northernmost state of Myanmar (Burma), retained its commercial exploitation (Grimaldi *et al.* 2002, Zherikhin and Ross 2000). Mainly overlaid by young sediments of the Chindwin River, the amber-bearing sediments in the syncline Hukawng basin outcrop at the largest anticline inside the basin (Zherikhin and Ross 2000).

The arthropod fauna in the resin was early suspected to be much older than the original (erroneous) dating of the fine clastic sediments as Miocene or Eocene (Cockerell 1917). Along with the weathered structure of the raw amber pieces, this suggested that they were allochthon to this sediment (Grimaldi *et al.* 2002). A Cretaceous age of the sediments was supported by relative lithostratigraphical dating based on paleontological data from palynomorphs and ammonites (Cruickshank and Ko 2003). An absolute age of 98.79±0.62 mya (earliest Cenomanian) was established with $^{206}$Pb/$^{238}$U isotopic values in Zircon crystals in the crust of unprocessed amber (Shi *et al.* 2012). As the only Southeast Asian site for Mesozoic amber, Burmese amber is one of the southernmost Cretaceous amber sites known yet (Grimaldi *et al.* 2002), apart from the recently discovered Ethiopian amber (Schmidt *et al.* 2010).

Anatomical as well as nuclear magnetic resonance (NMR) analyses suggested trees of the conifer family Araucariaceae—especially of the genus *Agathis*—as the botanical source for Burmite resin (Poinar *et al.* 2007), while some data rather suggested Pinaceae (Dutta *et al.* 2011) or the angiosperm family Dipterocarpaceae (Poinar *et al.* 2007) as the Burmese amber tree.

With 27 insect orders in 130 families and some 300 species, Burmese amber provides insight into a very diverse entomofauna at the beginning of the Late Cretaceous (Grimaldi and Engel 2005).

## Material and methods

Drawings were made with a Leica M80 (1.6 Plan Achromat lens) stereoscopic microscope by using a camera lucida system. The drawings were scanned by a flatbed scanner and digitized with Inkscape™ volume 0.91. Photographs were taken with a Leica DFC490 digital macroscopic photo system working on a Leica Z16-Apo macroscope. Images were processed by Leica Application Suite 3.8.0. Focus stacking was done either with Leica Application Suite 3.8.0 or with Adobe Photoshop™ CS5. All images are post processed with Adobe Photoshop™ CS5 but without local edits.

The terminology of wing venation (Fig. 1) is based on Riek and Kukalová-Peck (1984) emended by Nel *et al.* (1993) and Bechly (1996b).

**Abbreviations.** Wing fields are defined as the entire area between two primary veins, whereas wing spaces are defined as multicellular areas which are completed by longitudinal veins and/or crossveins. The spatial orientation of major veins creates a corrugation pattern of the wing surface. Veins that create a fold that is convex to the dorsal side of the wing are designated as convex or positive with “+”, while veins that create a fold that is convex to the ventral side of the wing are designated as concave or negative with “–”.

| | | |
|---|---|---|
| CA + | Costa anterior | Veins |
| CP – | Costa posterior | |
| ScA + | Subcosta anterior | |
| ScP – | Subcosta posterior | |
| Ax1 and Ax2 | Primary antenodal brackets | |
| RA + | Radius anterior | |
| RP – | Radius posterior | |
| M | Media | |
| MA + | Media anterior | |
| MP – | Media posterior | |
| tcv | Costal trigonal crossvein | |
| ddv | Distal discoidal vein MAb | |
| PsA | Pseudo-Analis | |
| Cu | Cubitus | |
| CuA + | Cubitus anterior | |
| CuP – | Cubitus posterior | |
| A + | Analis | |
| AA + | Analis anterior | |
| Tspl – | Intercalated vein Trigonal-Supplement | |

| | | |
|---|---|---|
| htc | Hypertriangular cell | Cells |
| tc | Triangular cell | |
| sdc | Subdiscoidal cell | |
| stc | Subtriangular cell | |
| ans | Antenodal space | Spaces |
| bs | Basal space | |
| rs | Radial space | |
| ars | Arcular space | |
| pds | Postdiscoidal space | |
| cus | Cubital space | |
| PrCuf | Precubital field | Fields |
| ACuf | Antecubital field | |
| PrAf | Preanal field | |
| Af | Anal field | |

## Systematic Paleontology

### Class Insecta Linné, 1758

### Order Odonata Fabricius, 1793

### Family Gomphidae Rambur, 1842

### Subfamily cf. Lindeniinae Jacobson & Bianchi, 1905

Following (Bechly, 1999) we consider the "légion *Lindenia*" Selys, 1854, not as a valid family-group taxon and therefore reject Selys' authorship for the subfamily Lindeniinae.

### *Burmalindenia* n. gen.

**Type species.** *Burmalindenia imperfecta* n. sp.

**Diagnosis.** Same as type species since monotypic.

**Etymology.** The genus name refers to the old name (Burma) of the country of origin and the presumably related Recent genus *Lindenia*.

### *Burmalindenia imperfecta* n. sp.

Figures 2–6, 8

**Holotype.** SMNS Bu-94, State Museum of Natural History Stuttgart, Germany.

**Diagnosis.** This species can be discriminated from all known Recent and fossil odonates by the following characters in the hindwing venation: bracket-like Ax1 and Ax2 with 3 secondary antenodals between them; straight arculus; basal radial area free; 7 or more antefurcal crossveins between RP and MA; distinctly curved hypertriangle with two cells; discoidal triangle elongated and with two cells; ddv/MAb not strongly sigmoid but with slight angle; distinct Tspl in the postdiscoidal space with 2 rows of cells; strong PsA (plesiomorphic compared to Recent Lindeniinae and Hageniinae); subdiscoidal triangle free; anal vein secondary branched; no anal loop; gaff not prolonged.

**Description.** The fossil-bearing piece of amber (SMNS Bu-94) is more or less oval shaped and measures 30.9 mm in length and 16.3 mm in width. It includes two completely hyaline fragments of the left and right hindwing of a dragonfly.

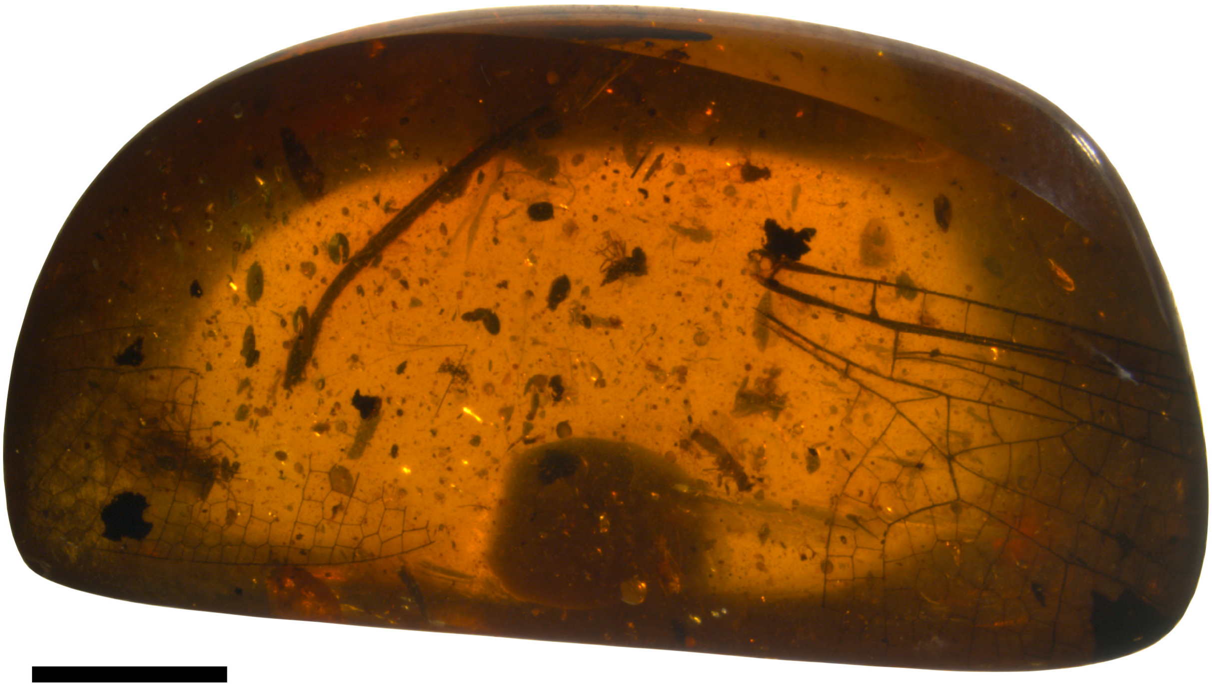

**FIGURE 2.** Photograph of complete Burmite amber piece SMNS Bu-94. Scale bar = 5 mm.

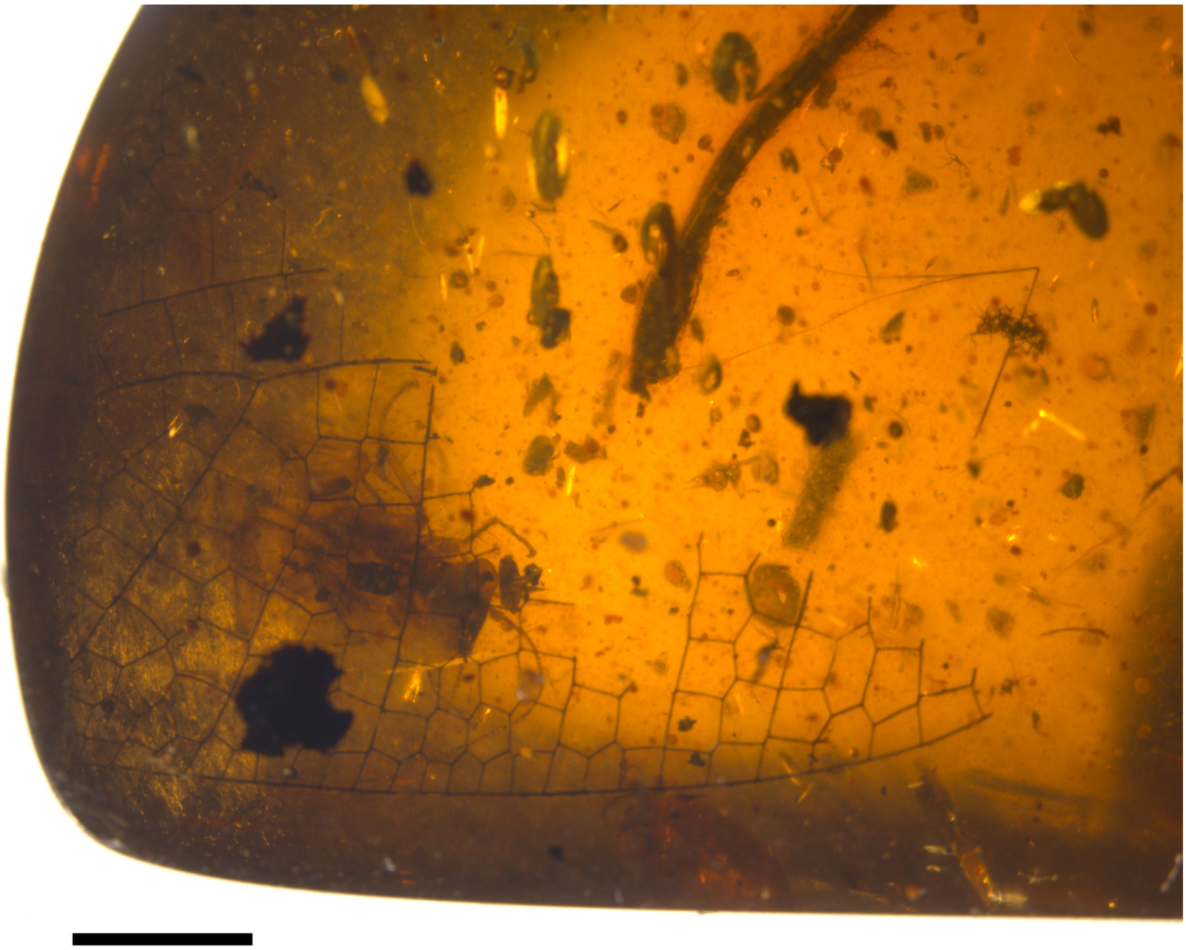

**FIGURE 3.** Photograph of right hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94. Scale bar = 2 mm.

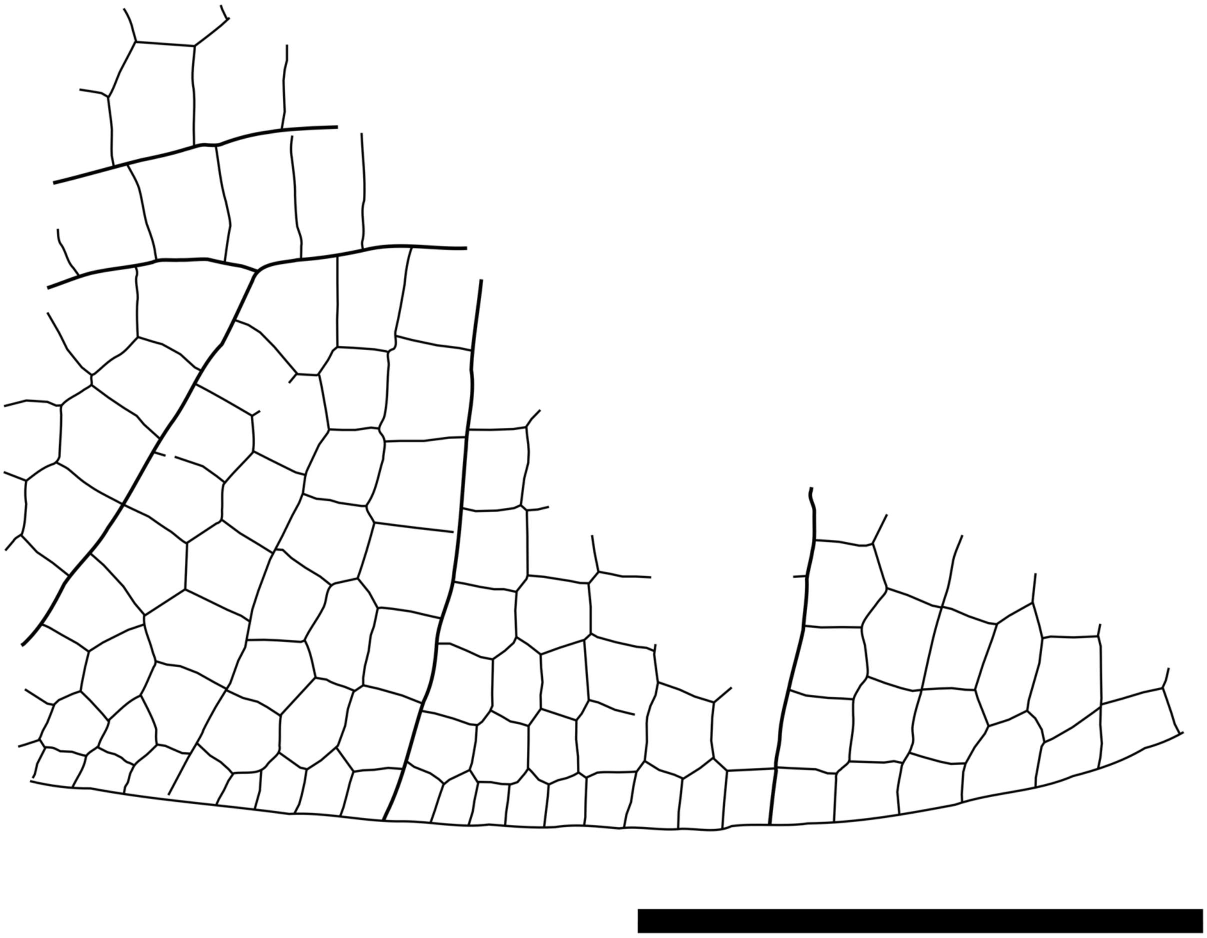

**FIGURE 4**. Drawing of right hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94. Scale bar = 5 mm.

**Right wing fragment.** The fragment of the right hindwing mainly consists of the cubital region. Posterior wing margin intact at full length of the fragment. Cubital region anteriorly completed with CuA'. In distal-proximal direction no such completion could be determined. In most anterior part of fragment MP and few cells (at least two rows) of postdiscoidal field preserved. Total dimensions 13.8 mm in horizontal direction and 9.0 mm in vertical direction (Costa as reference—estimated on the basis of the CuA'-Costa angle).

Two vertical branches of CuA' determined. A third vertical strong vein more basal could be either a CuA' branch or the CuA'' depending on the position of the fragment within the wing, but the visible terminal fork of CuA' rather suggests that the third vein also is a vertical branch of CuA', because CuA' would otherwise be unusually short. There are 7 rows of cells in the antecubital field.

MP and the CuA' run almost parallel, and only a single row of cells between them.

**Left wing fragment.** The fragment of the left hindwing consists of the proximal region of the wing. Anterior margin of wing is completed by Costa at full length of fragment. In distal direction the fragment ranges to the third antenodal region, in proximal direction to the ScA'' (= Ax0). The fragment lacks a posterior margin of the wing, although large parts of the cubital and anal region are preserved. Total dimensions 13.7 mm in horizontal direction and 10.1 mm in vertical direction (Costa as reference for direction).

First and the second antenodal crossveins (Ax1 and Ax2) aligned and stronger than others (bracket-like); three more or less aligned secondary antenodal crossveins between Ax1 and Ax2; distal of Ax2 there are two secondary antenodals of the first row, and three of the second row preserved and not aligned.

Arculus close to the Ax1 and straight. Bases of RA and MA on arculus and separated. Hypertriangle 5.3 mm long and maximum 0.8 mm wide; costal side (MA) distinctly curved; separated by one secondary crossvein at about half length. Basal space free.

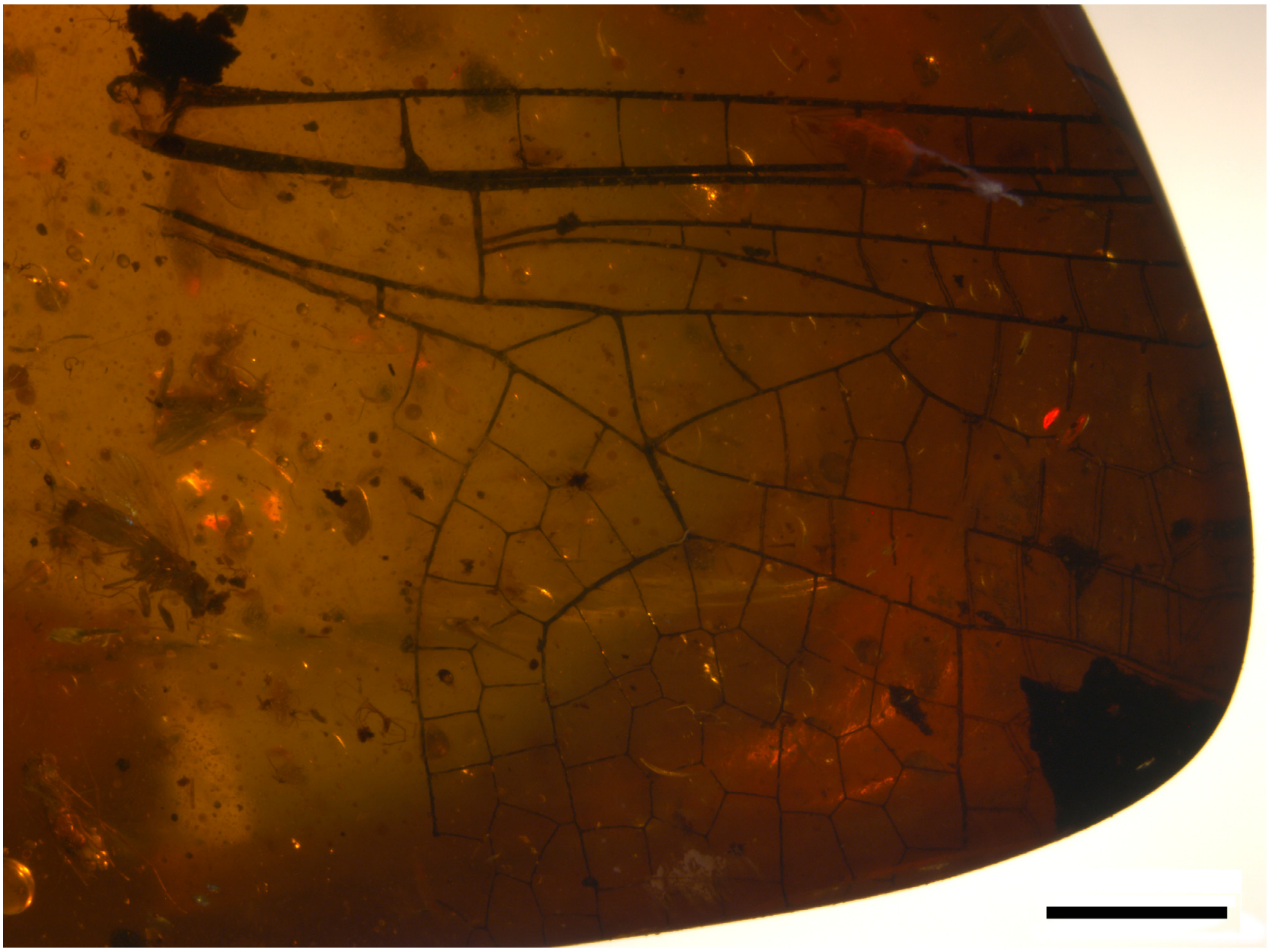

**FIGURE 5.** Photograph of left hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94. Scale bar = 2 mm.

Discoidal triangle longitudinally stretched with a slight kink (origin of trigonal supplement Tspl) in posterodistal side (MAb). Divided by an oblique secondary crossvein at one third length of anterior side. Basal side of discoidal triangle 1.7 mm long; costal side 3.6 mm; posterodistal side ddv/MAb 3.6 mm. Two rows of cells in basal postdiscoidal space.

CuP crossing 0.4 mm long and 1.2 mm proximal of arculus. Quadrangular subdiscoidal cell divided by a distinct and strong pseudo-anal vein (PsA=AA0) creating an almost equilateral subdiscoidal triangle. Subdiscoidal triangle free. Basal part of cubital cell free as well.

Up to three rows of cells between AA1b and CuA”; no anal loop; basally of AA1b there is one row of small cells preserved which is basally completed by a thin and errant vein suggesting that there were at least two rows of small cells located basally of AA1b .

Gaff (CuA from posterior angle of discoidal triangle to CuA’/CuA”-branching) 1.1 mm long (not prolonged). CuA branches at an angle of 142° into CuA’ and CuA”. Two posterior branches of CuA’ are preserved.

One row of cells between CuA’ and MP at a width of 1.1 mm. Postdiscoidal area (basally 2.4 mm wide) with two rows of cells, divided by trigonal supplement tspl. Basal arcular area with one row of cells. Basal radial area free almost up to level of Ax2.

**Type locality and horizon.** Burmese amber (Hukawng Valley, Kachin State, Myanmar). Mid-Cretaceous: earliest Cenomanian.

**Etymology.** The species name *imperfecta* refers to the incomplete preservation of the holotype as well as its unique teratological wing venation.

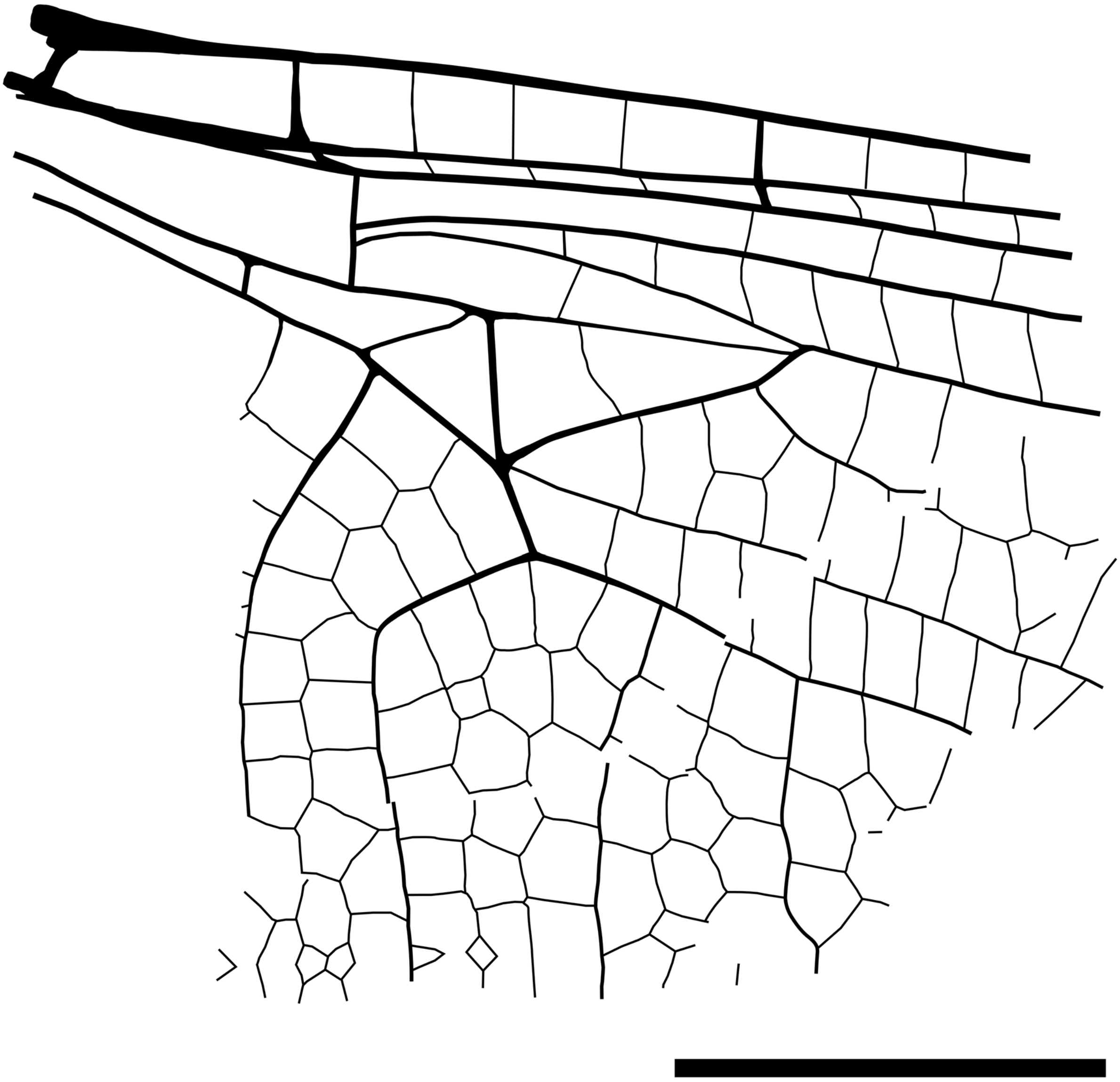

**FIGURE 6.** Drawing of left hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94. Scale bar = 5 mm.

**Syninclusions.** Apart from the dragonfly remains the amber piece contains several interesting botanical and hexapodan syninclusions (Figure 7), of which the oldest fossil record for the mayfly subfamily Cloeoninae (Ephemeroptera: Baetidae) is the most interesting (Hodunko, in prep.).

**Stellate hairs.** Plants produce trichomes for various reasons. They can help to reduce air fluctuation on the plant surfaces in order to regulate evaporation or protect leaves and buds from excessive sunlight and herbivores (Levin 1973, Werker 2000). Stellate hairs are a special morphotype of plant trichomes that occur in various amber sites.

Stellate hairs are characteristic of the Eocene Baltic Amber, where they have been determined as a product of oak trees (Fagaceae) (Weitschat *et al.* 2010). They also occur in Cretaceous ambers from Spain (Penalver *et al.* 2007), Lebanon (Koteja and Azar 2008), and Ethiopia (Schmidt *et al.* 2010). In the Cenomanian amber site in Ethiopia tree ferns and epiphytic ferns were determined as the source of the stellate trichomes (Schmidt *et al.* 2010). Ferns and conifers were suggested for the Early Cretaceous amber from Spain (Penalver *et al.* 2007). These two attempts of determination are based on comparison with Recent plant trichomes.

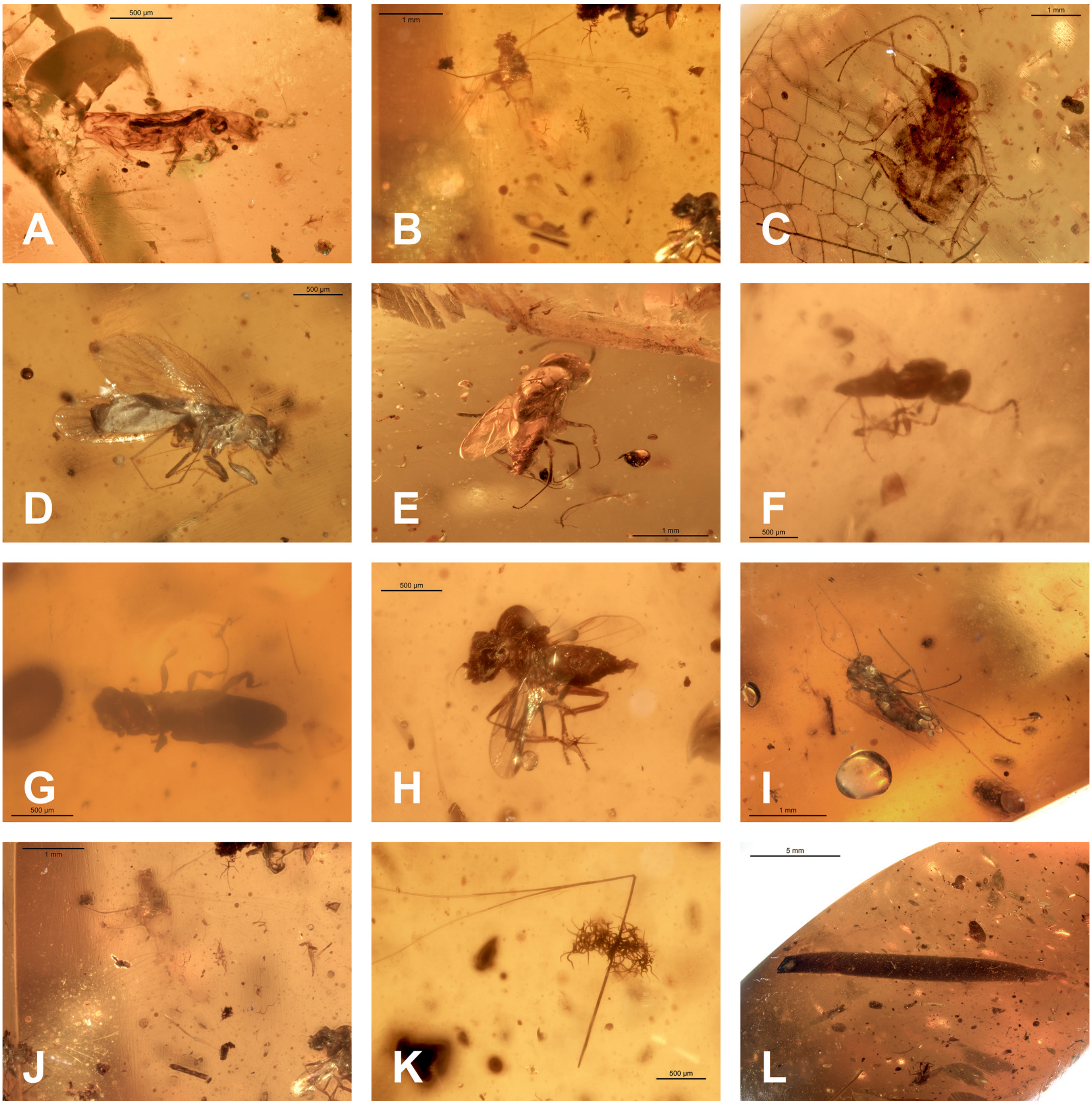

**FIGURE 7.** Syninclusions in Burmite amber piece SMNS Bu-94: A: springtail (Collembola, Entomobryomorpha); B: female mayfly (Ephemeroptera, Baetidae, oldest record of Cloeoninae); C: cockroach nymph (Blattodea); D: Psocoptera; E: male parasitoid wasp (Hymenoptera, Megalyridae); F: parasitoid wasp (Hymenoptera, Scelionidae); G: beetle (Coleoptera); H: fly (Diptera, Brachycera); I: fly (Diptera, “Nematocera”); J: fly (Diptera, “Nematocera”); K: stellate plant hair; L: pinaceous leaf.

Stellate hairs have also already been mentioned as syninclusions in Burmese Amber (Koteja 2004). In the studied amber piece there are numerous stellate hairs embedded as syninclusions, but their botanical origin is still undetermined.

## Discussion

**Taphonomy.** The fact that the two fragments are both embedded in almost the same plane, with their bases opposed to each other and separated by about the width of a dragonfly thorax, suggests that the animal got stuck to the gluey resin with the dorsal surfaces of the wings. The body and the rest of the wings could have been eroded or eaten by an insectivorous animal before the resin could cover it. It is also possible that the animal had freed itself, rupturing the hindwings.

**Double-lined veins.** In the distal regions of the left wing fragment minor veins appear double lined (Fig. 5) due to a taphonomic artefact. A dragonfly wing consists of two superimposed membranes, which are fused in the interspaces between wing veins, but each forming a semicircular tube along the wing veins. Due to plastic deformations in the resin these membranes can separate and slightly shift, so that the detached two half-tubes of the wing veins create the impression of a duplicated venation.

**Sex determination.** Most Anisoptera (except Anactini and Libelluloidea) show a strong sexual dimorphism in the shape and venation of the anal hindwing area. Typically males have a distinct anal triangle and an acute anal angle, whereas females have no anal triangle and a rounded anal region. Unfortunately, in the fossil specimen the anal area is not sufficiently preserved to allow a determination of the sex.

**Deformities.** Proximal and distal of the CuA" in the posteriormost part of the left hindwing fragment there are cells differing from all surrounding cells in their shape and size. They are about a quarter of the size of the contiguous cells. One cell shows a quadrangular outline, where only the anterior and the posterior angles are joined by veins creating two big irregular-shaped cells on the proximal and distal sides. All of these abnormal cells have in common that they have at least one angle ending free on the wing membrane without a joining vein. This is very unusual even for a teratological wing in dragonflies.

This pattern probably had no significant impact on the flight capacity of the animal. Thus it is most likely an individual deformity that occurred during the ontogeny or was caused by a genetic defect.

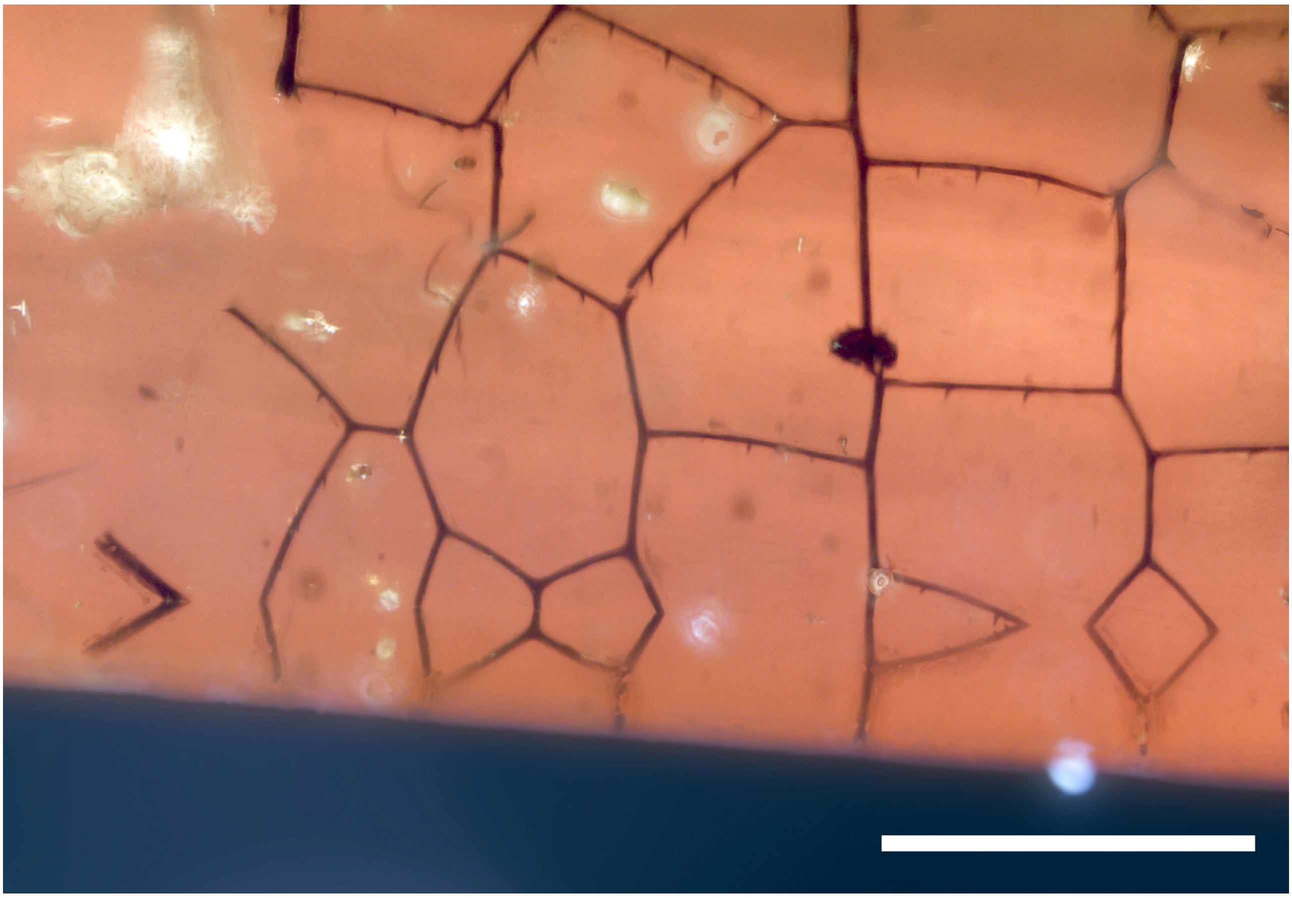

**FIGURE 8.** Aberrant cells in the left hindwing fragment of *Burmalindenia imperfecta* **gen. et sp. nov.**, holotype SMNS Bu-94. Scale bar = 1 mm.

**Phylogenetic affinities.** An attribution to Anisoptera is clearly proved by the following synapomorphic characters: Strong expansion of the cubitoanal field; presence of a discoidal triangle, a hypertriangle, and a subtriangle (Bechly 2007). Although there is no anal loop in the hindwing the specimen shows a secondary branch of the anal vein (AA1b). In many anisopteran dragonflies this vein is the basal completion of the anal loop. The anal loop is a character that has been only observed within the Anisoptera. The anal loop emerged or was reduced many times within the Anisoptera (Bechly 2007).

An attribution to the family Gomphidae is suggested by the following synapomorphies: Distinct PsA; slight angle in the posterodistal side of the discoidal triangle caused by the presence of the tspl; anterior side of the hypertriangle distinctly curved; straight arculus (Bechly 1996b, 2003).

The following diagnostic characters suggest an attribution to either the subfamily Hageniinae or more likely Lindeniinae: The specimen shows an elongated discoidal triangle with a distinct tspl, which is a feature only known within Gomphidae from the Hageniinae and Lindeniinae. Due to the incompleteness of the wing fragments no secure position within the two subfamilies could be determined. Also, unlike in Recent species of Hageniinae or Lindeniinae, the distal side of the discoidal cell is not strongly sigmoid but slightly kinked at the origin of the tspl. Recent Hageniinae or Lindeniinae further show a secondary less distinct PsA, which is linked to a very elongate discoidal triangle.

The presence of numerous (7 preserved) antefurcal crossveins between the RP and the MA in the left wing fragment represents a plesiomorphic character and excludes a position within the Oligophlebiata (Bechly 1996b, 2003), which could refute a position in the Hageniinae. Recent Hageniinae, the Brevicubitalia (including most Recent gomphids) and the Proterogomphinae (Bechly 2007) as the sister group of the Hageniinae show less than 5 antefurcal crossveins between RP and MA in the hindwing. The divided hypertriangle is another feature rather suggesting an attribution to Lindeniinae.

However, within the Lindeniinae several plesiomorphic character states in the amber fossil would suggest a very basal position in the stem group of this subfamily: Discoidal triangle and hypertriangle with only 2 cells each; distinct PsA; ddv/MAb not strongly sigmoidal.

The specimen is sufficiently distinct from all known fossil and Recent Anisoptera to warrant the description of a new genus and species.

**Paleoecological significance.** Most extant gomphids are confined to riverine habitats with rheophilic larvae (Corbet 1962). The phylogenetic position of the specimen within the crown group of the family Gomphidae suggests that the Burmese amber forest included such habitats. The presence of mayflies (Ephemeroptera) in Burmite (McCafferty and Santiago-Blay 2008, Sinitshenkova 2000) also supports this conclusion, as the larvae of the vast majority of mayfly species live in flowing freshwater.

## Conclusions

The specimen represents a new taxon from the mid-Cretaceous Burmese amber from the Hukawng Valley in northern Myanmar. The venation of the hind wing fragments allows an attribution to the Recent dragonfly family Gomphidae (Anisoptera) and tentatively suggests a position within the subfamily Lindeniinae.

Strangely deformed cells near the hind margin of one wing fragment document a rare teratological phenomenon.

This fossil is the first record for Anisoptera in the Burmese amber fauna and only the second record for Anisoptera in amber at all. The ecological preferences of modern relatives of the fossil dragonfly as well as those of the mayfly syninclusion indicate the presence of riverine habitats in the Burmese amber forest.

## Acknowledgements

The first author is indebted to Oliver Betz (Univ. Tübingen) for accepting and supervising this research as his bachelor thesis (scientifically supervised by the second author) and for providing a working place. We are very grateful to Karin Wolf-Schwenninger (SMNS) for help with the microphotography. We thank Roman Hodunko (State Museum of Natural History, Lviv, Ukraine), André Nel (MNHN, Paris), Lars Krogmann (SMNS), and Arnold Staniczek (SMNS) for their help with determination of the syninclusions.

## References cited

Azar, D., Prokop, J. & Nel, A. (2010) The first damselfly from the Early Cretaceous Lebanese amber (Odonata, Zygoptera, Lestomorpha). *Alavesia*, 3, 73–79.

Bechly, G. (1996a) Fossil odonates in Tertiary amber. *Petalura*, 2, 1–15.

Bechly, G. (1996b) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata) unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der *Odonata. *Petalura*, special Volume 2, 1–402.

Bechly, G. (1998) New fossil damselflies from Baltic amber, with description of a new species, a redescription of *Litheuphaea carpenteri* Fraser, and a discussion on the phylogeny of Epallagidae (Zygoptera: Caloptera). *International Journal of Odonatology*, 1, 33–63.
http://dx.doi.org/10.1080/13887890.1998.9748092

Bechly, G. (1999) Epallagidae versus Euphaeidae revisited. *International Journal of Odonatology*, 2, 137–139.
http://dx.doi.org/10.1080/13887890.1999.9748124

Bechly, G. (2003) Phylogenetic systematics of Odonata. *In:* Schorr, M. & Lindeboom, M. (Eds.), *Dragonfly Research, Volume 1.* Zerf-Tübingen (CD-ROM).

Bechly, G. (2007) Chapter 11.5 Odonata: damselflies and dragonflies. *In:* Martill, D.M., Bechly, G. & Loveridge, R.F. (Eds.), *The Crato fossil beds of Brazil: window into an ancient world.* Cambridge University Press, Cambridge, pp. 184–222.

Bechly, G. (2010) Additions to the fossil dragonfly fauna from the Lower Cretaceous Crato Formation of Brazil (Insecta: Odonata). *Palaeodiversity*, 3, 11–77.

Bechly, G. & Poinar Jr., G. (2013) *Burmaphlebia reifi* gen. et sp. nov., the first anisozygopteran damsel-dragonfly (Odonata: Epiophlebioptera: Burmaphlebiidae fam. nov.) from Early Cretaceous Burmese amber. *Historical Biology*, 25, 233–237.
http://dx.doi.org/10.1080/08912963.2012.753884

Cockerell, T. (1917) Arthropods in Burmese amber. *American Journal of Science*, 263, 360–368.
http://dx.doi.org/10.2475/ajs.s4-44.263.360

Corbet, P.S. (1962) *A Biology of Dragonflies*: Witherby, London, 247 pp.

Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455.
http://dx.doi.org/10.1016/S1367-9120(02)00044-5

Dejax, J., Masure, E. & Azar, D. (1996) Analyse palynologique d'un échantillon de sédiment du Crétacé inférieur du Liban. *Strata*, 1, 66–67.

Dijkstra, K.-D.B., Bechly, G., Bybee, S.M., Dow, R.A., Dumont, H.J., Fleck, G., Garrison, R.W., Hämäläinen, M, Kalkman, V.J., Karube H., May, M.L., Orr, A.G., Paulson, D.R., Rehn, A.C., Theischinger G., Trueman, J.W.H., van Tol, J., von Ellenrieder, N. & Ware, J.L. (2013) The classification and diversity of dragonflies and damselflies (Odonata). *In:* Zhang, Z.-Q. (Ed.), Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013). *Zootaxa*, 3703, 36–45.

Dutta, S., Mallick, M., Kumar, K., Mann, U. & Greenwood, P.F. (2011) Terpenoid composition and botanical affinity of Cretaceous resins from India and Myanmar. *International Journal of Coal Geology*, 85, 49–55.
http://dx.doi.org/10.1016/j.coal.2010.09.006

Fleck, G., Nel, A., de Plöeg, G. & Masselot, G. (2000) A fossil dragonfly from the Paris Basin amber of France (Lowermost Eocene) (Insecta, Odonata, Anisoptera). *Acta Geologica Hispanica*, 35, 131–134.

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*: Cambridge University Press, New York, 755 pp.

Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361, 1–71.
http://dx.doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2

Huang, D., Azar, D., Cai, C. & Nel, A. (2015) New damselfly genera in the Cretaceous Burmese amber attributable to the Platystictidae and Platycnemididae Disparoneurinae (Odonata: Zygoptera). *Cretaceous Research*, 56, 237–243.
http://dx.doi.org/10.1016/j.cretres.2015.05.004

Jarzembowski, E., Martí, X., Bechly, G., Nel, A., Coram, R. & Escuillié, F. (1998) The Mesozoic non-calopterygoid Zygoptera: description of new genera and species from the Lower Cretaceous of England and Brazil and their phylogenetic significance (Odonata, Zygoptera, Coenagrionoidea, Hemiphlebioidea, Lestoidea). *Cretaceous Research*, 19, 403–444.
http://dx.doi.org/10.1006/cres.1997.0113

Kaddumi, H.F. (2007) *Amber of Jordan The oldest prehistoric insects in fossilized resin*. Eternal River Museum of Natural History, Jordan.

Kohli, M.K., Ware, J.L. & Bechly, G. (in press) How to date a dragonfly - Fossil calibrations for odonates. *Palaeontologia Electronica*.

Koteja, J. (2004) scale insects (Hemiptera: Coccinea) from Cretaceous Myanmar (burmese) amber. *Journal of systematic Palaeontology*, 2, 109–114.
http://dx.doi.org/10.1017/S1477201904001166

Koteja, J. & Azar, D. (2008) Scale insects from lower cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea). *Alavesia*, 2, 133–167.

Lak, M., Fleck, G., Azar, D., Engel, M.S., Kaddumi, H.F., Neraudeau, D., Tafforeau, P. & Nel, A. (2009) Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae). *Zoological Journal of the Linnean Society*, 156, 913–923.
http://dx.doi.org/10.1111/j.1096-3642.2008.00497.x

Levin, D.A. (1973) The role of trichomes in plant defense. *Quarterly Review of Biology*, 48, 3–15.
http://dx.doi.org/10.1086/407484

Martínez-Delclòs, X. (1989) Insectos del Cretácico inferior de Las Hoyas (Cuenca). *In:* Sanz, J.L. (Ed.), *Actas del I Curso de Paleontología. La fauna del pasado en Cuenca.* Instituto Juan de Valdés, Cuenca, pp. 51–82.

Martínez-Delclòs, X. & Nel, A. (1994) Los Gomphidae (Insecta, Odonata, Anisoptera) del Cretacico Inferior de España. *Revista española de paleontología*, 9, 176–184.

McCafferty, W. & Santiago-Blay, J.A. (2008) A new Cretaceous mayfly from Burmese amber (Ephemeroptera: Australiphemeridae). *Entomological News*, 119, 492–496.
http://dx.doi.org/10.3157/0013-872X-119.5.492

Nel, A., Martinez-Delclos, X., Paicheler, J. & Henrotay, M. (1993) Les "Anisozygoptera" fossiles: phylogénie et classification: Odonata. *Martinia*, 3, 1–311.

Nel, A., DePalma, R.A. & Engel, M.S. (2010) A possible hemiphlebiid damselfly in Late Cretaceous amber from South Dakota (Odonata: Zygoptera). *Transactions of the Kansas Academy of Science*, 113, 231–234.
http://dx.doi.org/10.1660/062.113.0312

Nel, A. & Huang, D. (2010) A new Mesozoic Chinese genus of aeshnopteran dragonflies (Odonata: Anisoptera: Progobiaeshnidae). *Comptes Rendus Palevol*, 9, 141–145.
http://dx.doi.org/10.1016/j.crpv.2010.05.005

Penalver, E., Delclos, X. & Soriano, C. (2007) A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretaceous Research*, 28, 791–802.
http://dx.doi.org/10.1016/j.cretres.2006.12.004

Poinar Jr., G., Bechly, G. & Buckley, R. (2010) First record of Odonata and a new subfamily of damselflies from Early Cretaceous Burmese amber. *Palaeodiversity*, 3, 15–22.

Poinar Jr., G., Lambert, J.B. & Wu, Y. (2007) Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. *Journal of the Botanical Research Institute of Texas*, 1 (1), 449–455.

Pritykina, L.N. (1977) New dragonflies from Lower Cretaceous deposits of Transbaikalia and Mongolia. *Trudy SovmestnayaSovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya*, 4, 81–96.

Riek, E.F. & Kukalová-Peck, J. (1984) A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62, 1150–1166.
http://dx.doi.org/10.1139/z84-166

Schlüter, T. & Hartung, M. (1982) *Aegyptidium aburasiensis* gen. nov., spec. nov. (Aeschnidiidae) und *Gondvanogomphus bartheli* gen. nov., spec. nov. (Gomphidae) aus mutmasslicher Unterkreide Südwest Ägyptens. *Odonatologica*, 11, 297–307.

Schmidt, A.R., Perrichot, V., Svojtka, M., Anderson, K.B., Belete, K.H., Bussert, R., Dörfelt, H., Jancke, S., Mohr, B., Mohrmann, E., Nascimbene, P.C., Nel, A. Nel, P., Ragazzi, E., Roghi, G., Saupe, E.E., Schmidt, K., Schneider, H., Selden, P.A. & Vavra, N. (2010) Cretaceous African life captured in amber. *Proceedings of the National Academy of Sciences*, 107, 7329–7334.
http://dx.doi.org/10.1073/pnas.1000948107

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, 37, 155–163.
http://dx.doi.org/10.1016/j.cretres.2012.03.014

Sinitshenkova, N. (2000) The first fossil prosopistomatid mayfly from Burmese amber (Ephemeroptera; Prosopistomatidae). *Bulletin of the Natural History Museum, Geology Series*, 56, 29–37.

Tillyard, R.J. (1918) Mesozoic insects of Queensland No. 2. The fossil dragonfly *Aeschnidiopsis* (Aeschna) *flindersiensis* Woodward, from the Rolling Downs (Cretaceous) series. *Proceedings of the Linnean Society of New South Wales*, 42, 676–692.
http://dx.doi.org/10.5962/bhl.part.4866

Vassilenko, D.V. (2014) The first damselfly (Insecta: Odonata, Hemiphlebiidae) recorded from the Turonian of Israel. *Far Eastern Entomologist*, 278, 1–7

Weitschat, W. & Wichard, W. (2010) Baltic amber. *In:* Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 80–115.

Werker, E. (2000) II. D. Functions of Trichomes. *In:* Hallahan, D.L., Callow, J.A. & Callow, J.A. (Eds.), *Advances in Botanical Research Incorporating Advances in Plant Pathology. Vol. 31. Plant Trichomes.* Academic Press, London, pp. 13–19.

Whalley, P. & Jarzembowski, E. (1985) Fossil insects from the lithographic limestone of Montsech (late Jurassic-early Cretaceous), Lerida Province, Spain. *Bulletin of the British Museum, Natural History. Geology*, 38, 381–412.

Zherikhin, V. & Ross, A. (2000) A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum. Geology series,* 56, 3–10.