

## Short communication

## A possible true Mesozoic Gomphidae s. str. from the mid-Cretaceous Burmese amber (Odonata: Anisoptera)

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## ABSTRACT

*Gunterbechlya pumilio* gen. et sp. nov., first putative Mesozoic Gomphidae sensu stricto, is described from the mid-Cretaceous Burmese amber. It is remarkable in its reduced venation with quadrangular discoidal triangles, only found in the extant gomphid genera *Lestinogomphus* and *Archaeogomphus*, the 'libelluloid' Cordulephyidae and the Libellulidae: 'Tetrathemistinae'. All these taxa are small dragonflies with reduced venation. Possibly the particular quadrangular discoidal triangles of these insects are related to their small sizes. The positions of some Mesozoic taxa currently attributed to the Gomphidae are discussed and none can be considered as genuine representatives of this family.

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## 1. Introduction

Burmese amber Gomphides Bechly et al., 1998 are rather diverse compared to the other Anisoptera, with four described species, viz. *Burmalindenia imperfecta* Schädel and Bechly, 2016 (Lindeniidae), *Paraburmagomphides zhaoi* Zheng et al., 2018 (Paraburmagomphidae), *Burmagomphides electronica* Zheng et al., 2018 (Burmagomphidae), and *Araripegomphus shai* Zheng et al., 2018 (Araripegomphidae) (Zhang et al., 2018a,b,c; Ross, 2018). Here we describe a new Gomphides that strongly differs from all the other Burmese amber representatives of this clade in its reduced wing venation and very particular quadrangular shapes of the discoidal triangles. Similar associations of quadrangular discoidal triangles and reduced venation can be found in few extant Gomphidae and in some Cavilabiata (Neophyinae, Cordulephyinae, and the Libellulidae 'Tetrathemistinae').

All the Mesozoic Gomphides currently described belong to gomphides families more inclusive than the Gomphidae (see below

for the attributions of the taxa currently included in the Gomphidae). The new fossil is the first accurate Mesozoic Gomphidae.

## 2. Material and methods

The amber containing the dragonfly was collected in the Hukawng Valley (26° 29' N, 96° 35' E) of Kachin Province, Myanmar (locality in Kania et al., 2015: fig. 1). The re-deposition age of Burmese amber was considered to be 98.79 ± 0.62 Ma (Shi et al., 2012), but palynology and an ammonite from the amber-bearing layers suggest a late Albian age (Cruickshank and Ko, 2003) which we adopt herein. The amber containing the dragonfly is yellow and transparent. The individual shows fragments of a forewing (basal and apical sections missing) and fragments of a hind wing. Photographs were taken using a Zeiss Discovery V20 microscope system. The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China. All taxonomic acts established in the present work have been registered in Zoo-Bank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:14D41825-4E33-4D12-BEED-313A43DC693A.

We follow the wing venation nomenclature of Riek and Kukulová-Peck (1984), amended by Nel et al. (1993) and Bechly

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(1996). The higher classification of fossil and extant Gomphides, as well as familial and generic characters followed in the present work are based on the phylogenetic system proposed by [Bechly \(1996, 2016\)](#), which mainly follows the work of [Carle \(1986\)](#). No extensive phylogeny of the extant (and fossil) Gomphides has been proposed since these works, except the molecular analysis devoted to the Nearctic Gomphidae by [Ware et al. \(2017\)](#). Abbreviations for wing venation are as follow: a.l. = anal loop; CuA = cubitus anterior; PsA = pseudo-anal vein; IR = intercalary radial vein; MA = media anterior; MP = media posterior; N = nodus; Cr = nodal crossing; PsA = pseudo-anal vein; Pt = pterostigma; RP = radius posterior; ScP = subcostal posterior; Sn = subnodus; t = discoidal triangle.

### 3. Systematic palaeontology

Order Odonata Fabricius, 1793

Clade Gomphides [Bechly et al., 1998](#)

Family Gomphidae [Rambur, 1842](#) (sensu [Bechly, 2016](#))

Subfamily undetermined

Genus *Gunterbechlya* gen. nov.

(urn:lsid:zoobank.org:act:C11E2A35-9C69-4968-B474-F7BFB853FCFA)

Type species: *Gunterbechlya pumilio* sp. nov.

*Etymology.* Named after our friend and colleague Günter Bechly, for his contribution in Odonatology.

*Diagnosis.* Wing venation characters only. No Rspl; no Mspl; no trigonal planate; MAb straight; a very strong pterostigmal brace; unicellular anal loop; no 'libelluloid gap'; pseudo-anal vein PsA long sigmoidal; subdiscoidal triangle of hindwings pentagonal with an angular AA; free hypertriangles with a distinctly curved anterior margin; costal margin and RA thickened along pterostigmata; a 'cordulegastrid gap' in forewing but not in hind wing; free short discoidal triangles quadrangular, with veinlet between it and hypertriangle ending in MA before its fork into MAa and MAb; IR2 and MA without any secondary branch; only two antefurcal crossveins between sectors of arculus in forewing, and none in hind wing; no large elongated cell beneath submedian area of forewings; CuAa distinctly shortened, with a course distally converging with the wing margin; branching of RP at midfork symmetrical; lestone oblique vein one cell distal of subnodus in all wings.

#### *Gunterbechlya pumilio* sp. nov.

(urn:lsid:zoobank.org:act:9FB77E53-F936-4EA2-9E7C-2D208B03F775)

(Fig. 1)

*Etymology.* Named pumilio after its very small dimensions.

*Holotype.* One amber piece contents a forewing (NIGP168872) and a hind wing (NIGP168873), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

*Diagnosis.* Wings very short, hyaline; fore wing with six postnodals and four postsubnodals, both approximately equidistant.

*Locality and Horizon.* Hukawng Valley, Kachin Province, Myanmar; late Albian, late Lower Cretaceous.

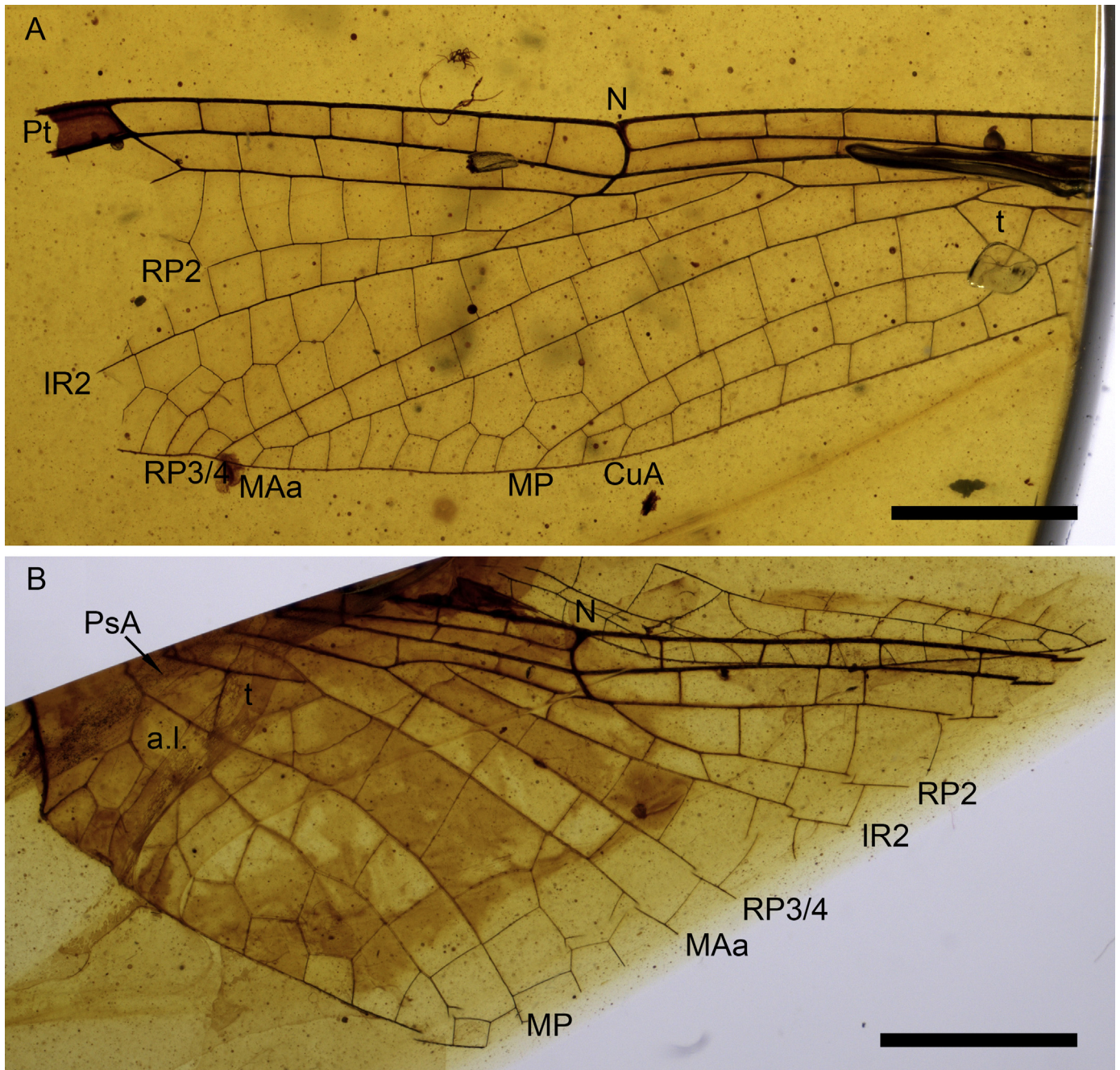
*Description.* Wings hyaline; forewing with base and apex missing, fragment 11.5 mm long, wing 3.8 mm wide; distance from arculus to nodus 4.8 mm, from nodus to pterostigma 5.4 mm; pterostigma 0.5 mm wide, elongate, covering one crossvein, with costal and posterior margins widened; pterostigmal brace distinctly oblique and strong, with RP1 making a distinct angle; six postnodals, not aligned with the four postsubnodals; base of RP2 slightly distal of subnodus; RP2 smoothly curved, one row of large cells between RP1 and RP2 basal of pterostigma; two rows distally; oblique vein

'O' one cell distal of subnodus; one row of cells between RP2 and IR2; two Bq-crossveins; fork of RP into RP1/2 and RP3/4 symmetrical; base of IR2 rather distant from that of RP3/4; five visible secondary antenodal crossveins of first row not aligned with those of second row (less numerous); three antesubnodal crossveins, a 'cordulegastrid' gap; two antefurcal crossveins (= postmedian) between sectors of arculus; hypertriangle free with MA strongly curved; free discoidal triangle quadrangular with veinlet between it and hypertriangle ending in MA before its fork into MAa and MAb; postdiscoidal area with one row of cells and two rows very distally; subdiscoidal triangle unicellular, well defined, triangular; a well-defined elongate PsA; area between RP3/4 and MAa with one row of cells; no Mspl, no Rspl but a rudimentary zigzagged longitudinal vein apparently emerging from IR2 and two main rows of cells in distal part of area between IR2 and RP3/4; one row of cells between MP and CuAa; one row of cells in cubito-anal area; CuAa without posterior branches, reaching level of nodus.

Hind wing incomplete with base and distal third missing; fragment 10.8 mm long; wing 4.3 mm wide; pterostigma not preserved; five postnodal crossveins and four postsubnodals visible, no 'libelluloid' gap; base of RP2 slightly distal of subnodus; area between RP1 and RP2 rather broad but with one row of cells; oblique vein 'O' two cells distal of subnodus; only one Bq-crossvein; three antesubnodal crossveins, two of them being distal of base of RP3/4; two secondary antenodal crossveins of first row distal of Ax2 and only one of second row; Ax2 opposite apex of hypertriangle; fork of RP into RP1/2 and RP3/4 symmetrical; base of IR2 rather distant from that of RP3/4; no antefurcal (= postmedian) crossvein retained between sectors of arculus; hypertriangle free, with anterior side (MA) strongly curved; free discoidal triangle quadrangular with veinlet between it and hypertriangle ending in MA before its fork into MAa and MAb; postdiscoidal area with one row of cells and two rows very distally; subdiscoidal triangle unicellular, well defined, pentagonal with an angular AA; a well-defined PsA; anal loop unicellular and posteriorly close; CuAa without defined posterior branches and two rows of cells in cubito-anal area; one row of cells in area between CuAa and MP; a distinct anal angle (male specimen).

### 4. Discussion

This fossil cannot be related to the Libellulidae: 'Tetrathemistinae' because of the complete absence of Rspl, presence of a hind wing subdiscoidal space, presence of a male anal angle, and very strong pterostigmal brace. Also it differs from *Cordulephya de Selys-Longchamps, 1870* in the strong pterostigmal brace. It differs from *Neophya Selys, 1881* (Eocene and extant) in the unicellular anal loop, the absence of 'libelluloid gap' and the pattern of cells in area between IR2 and RP2 ([Nel and Fleck, 2014](#)). It differs from the Cretaceous *Palaeophya Petrulevičius and Nel, 2009* in the absence of a Mspl and the reduced anal loop ([Petrulevičius and Nel, 2009](#)). An attribution to the Gomphides [Bechly et al., 1998](#) is supported by few synapomorphies: pseudo-anal vein PsA and subdiscoidal triangle of hindwings well defined, pentagonal with an angular AA (unlike in the Tetrathemistinae and Cordulephyidae, [Tillyard, 1911; Fraser, 1947](#)); hypertriangles with a distinctly curved anterior margin; costal margin and RA thickened along pterostigmata. Unfortunately the structure of the arculus, an important character of this clade, is not preserved. It would share with the Araripegomphidae [Bechly, 1996](#) the discoidal triangles unicellular (convergent to Proterogomphidae and Gomphida); and presence of a distinct 'cordulegastrid gap' (lack of crossveins in the distal antesubnodal space), but unlike in this family, this 'gap' is only present in the forewing of *Gunterbechlya* gen. nov., not in the hind wing. Also the



**Fig. 1.** *Gunterbechlya pumilio* gen. et sp. nov. from the mid-Cretaceous Burmese amber. A. Fore wing (NIGP168872), with general view; B. Hind wing (NIGP168873), with general view immersed in mineral oil. Scale bars represent 2 mm.

anal loop of *Gunterbechlya* is not obsolete, not reduced and posteriorly open as in this family. The Progomphidae Carle, 1986 are excluded for the anal loop not obsolete and the hind wing discoidal triangle unicellular. The Lindeniidae Jacobson and Bianchi, 1905 are excluded for the free hypertriangle, not elongate discoidal triangles, and IR2 and MA without any secondary branch. It falls in the Oligophlebiata Bechly, 2003 because of the presence of only two antefurcal crossveins between the sectors of arculus in forewing. The complete absence of a trigonal planate and MAb straight exclude affinities with the Mesozoic Proterogomphidae Bechly et al., 1998 and with the Hageniidae. The absence of a large elongated cell beneath the submedian area of forewings also excludes affinities with the Proterogomphidae. In the Hageniidae, the

discoidal triangles are distinctly longitudinally elongate in both pairs of wings, and the distal sides (MAB) of triangles are strongly sigmoidal. *Gunterbechlya* can be attributed to the Brevicubitalia Bechly, 2003 because of the CuAa distinctly shortened, with a course distally converging with the wing margin, instead of running parallel to it, and with a reduced pectinate branching. The Zonophoridae Belle, 1983 are excluded because the hindwing discoidal triangle of *Gunterbechlya* is not elongate. *Gunterbechlya* fits in the Gomphida Bechly, 1996 because the discoidal triangles are unicellular in both pairs of wings; and the anal loop is reduced to one cell (putative synapomorphies, but also present in Araripogomphidae and Proterogomphidae, excluded above). The Epi-gomphidae Fraser, 1934 are excluded because the pterostigmal

brace of *Gunterbechlya* is not reduced. *Gunterbechlya* falls well in the Gomphidae Rambur, 1842 because the branching of RP at midfork is symmetrical (but convergent to Hagenioidea, excluded above); lestine oblique vein is one cell distal of the subnodus in all wings (but convergent to Proterogomphidae, excluded above); in forewings only two antefurcal (= postmedian) crossveins retained between the sectors of arculus, and none in hind wings (but convergent to Proterogomphidae: Cordulagomphinae, excluded above). Of course, because the lack of information on some characters (viz. structure of pseudo-IR1, number of cells beneath the pterostigmata), and because the wing venation characters can be homoplastic in dragonflies, this attribution to Gomphidae sensu stricto is tentative. The discovery of new specimens with complete wings and body structures will help to precise its affinities.

Within the Gomphidae, Austrogomphini Carle, 1986, Cyanogomphini Carle, 1986, and Phyllogomphinae Carle, 1986 have well-defined branches of CuA in forewing and much more intercalary rows of cells between main veins than in *Gunterbechlya*. The Onychogomphinae Chao, 1984, Octogomphinae Carle and Cook, 1984, and Gomphinae Rambur, 1842 have also much more intercalary rows of cells between main veins than in *Gunterbechlya*.

The Lestinogomphini Carle, 1986 and the Archaeogomphini Carle, 1986 remain the sole extant Gomphidae that share with *Gunterbechlya* this drastic reduction of the number of intercalary rows of cells and supplementary longitudinal veins. *Lestinogomphus* differs from *Gunterbechlya* in the shape of hind wing discoidal triangle and the more numerous antefurcals (three in forewing instead of two in *Gunterbechlya*). *Archaeogomphus* shares with *Gunterbechlya* very similar discoidal triangles and hypertriangles, anal loop, CuAa and MP, one row of cells in postdiscoidal areas, but they differ in crucial structures, viz. *Gunterbechlya* has much less antenodal crossveins than *Archaeogomphus*, the fork between RP1/2 and RP3/4 is more symmetrical in *Gunterbechlya* than in *Archaeogomphus*, *Gunterbechlya* has only two forewing antefurcals, instead of 3–4 in *Archaeogomphus*, the pterostigmal brace of *Gunterbechlya* is much more oblique than in *Archaeogomphus*, *Gunterbechlya* has a distinct 'cordulegastrid gap' in forewing, unlike *Archaeogomphus* (in fact *Gunterbechlya* has only four antesubnodal crossveins instead of seven in *Archaeogomphus*).

#### 4.1. Remarks on the Mesozoic taxa currently attributed to the Gomphidae

The internet Gateway to the Paleobiology Database Fossilworks (site <http://fossilworks.org>) gives a list of the fossil dragonflies currently included in the family Gomphidae. The lower Cretaceous Spanish genus *Ilerdaegomphus* Martínez-Delclos, 1989 is currently in the family Gomphidae sensu lato (Martínez-Delclòs and Nel, 1994). Its discoidal triangles unicellular are also present in the Araripegomphidae, the Proterogomphidae and the Gomphida. Affinities with the Araripegomphidae are excluded because its sectors of arculus are well-separated at bases. Affinities with the Cretaceous Proterogomphidae are also excluded because its forewings is without a large elongated cell beneath the submedian area. But it does not fall in the Gomphida because its anal loop is four-celled instead of being max. two-celled, and its CuAa have well-defined 4–5 posterior branches. It does not fall in the Gomphidae themselves because its branchings of RP at midfork are asymmetrical. Thus this taxon does not fall in any of the defined families of Gomphides. A restudy of the type material would be necessary at the light of the recent progresses in the 'gomphid' systematics. The Lower Cretaceous nymphs *Dissurus quinquanensis* Hong, 1982, *Yixiangomphus labius* (Lin, 1976), and the abdomen *Cercus clavus* Hong, 1982 are Anisoptera incertae sedis (Nel and Paicheler, 1994). The nymph *Pseudosamarura largina* Lin, 1976 is not an Anisoptera.

The nymph *Neimeugomphus dougwugaieusis* Hong, 1985 is a Gomphides. Nel and Paicheler (1994) indicated that the original description of *Huaxiangomphus taushanensis* (Hong, 1982) is not very precise. Nevertheless, the lestine oblique vein drawn very far from the subnodus would exclude any affinities with the Gomphidae, and the large posteriorly opened anal loop excludes affinities with the Gomphida (Hong, 1982: text-fig. 23, 1984), if this taxon can be attributed to the Gomphides. *Jibeigomphus xinboensis* Hong, 1984 is even more poorly described, nevertheless its forewing discoidal triangle divided into three cells excludes affinities with the Gomphidae, if it is a Gomphides (Hong, 1984). The Lower Jurassic *Pheugothemis westwoodi* (Phillips, 1866) is certainly not a Gomphidae, and probably not a Gomphides (Phillips, 1866). None of these taxa can be accurately attributed to the Gomphidae, or even the Gomphida.

Kohli et al. (2016) considered the Jurassic Proteromphidae as oldest 'crown Gomphidae', together with some Lower Cretaceous Hageniidae, but these taxa are not representatives of the Gomphidae sensu Bechly (2016).

## 5. Conclusion

If the clade Gomphides was very diverse during the Mesozoic, and especially the Cretaceous, the fossil record of the extant family Gomphidae sensu stricto is reduced to Cenozoic taxa. Here we describe the first putative Cretaceous representative of this family, of interest for future calibrations in phylogenetic analyses of the Gomphides. Its wing venation is reduced with highly specialized quadrangular discoidal triangles. Unfortunately, its exact affinities within the Gomphidae remain obscure because of the lack of the body characters.

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