The first fossil representative of the dragonfly family Synthemistidae

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Gallosynthemis bechlyi gen. et sp. nov., described from the Paleocene maar of Menat (Puy-de-Dôme, France) is the first-ever fossil record of the dragonfly family Synthemistidae. It shows the main synapomorphies of the family, viz. hind wing with 3–5 costal braces (complete antenodal crossveins) alternating with non-aligned antenodals; presence of crossveins in median area and between CuP and PsA; absence of postsubnodal crossveins below first postnodal crossveins; in hind wing, a very large and elongate anal loop without a well-defined mid-rib; and CuAa without posterior branches. It belongs to the stem group of this family and is attributed to its own subfamily Gallosynthemistinae subfam. nov., characterized by a very long stem of hind wing cubitus anterior vein (autapomorphy), plus some symplesiomorphies such as sectors of arculus separated at their bases. While extant Synthemistidae sensu Bechly (2016) are Australasian, the present new taxon demonstrates that the family may have been much more widespread during the Paleocene. These dragonflies probably became extinct in the Northern Hemisphere in relation with the Cenozoic dramatic episodes of cooling.

Key words: Insecta, Odonata, Anisoptera, Libelluloidea, new taxa, Paleocene, Menat, France.

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Introduction

The Synthemistidae Tillyard, 1917 (sensu Bechly 1996, 2016) is an extant dragonfly family nowadays restricted to Australia, Tasmania, New Caledonia, Fiji, Solomon, and Papua New Guinea (Carle 1995; Theischinger and Richards 2013). Carle et al. (2015) proposed an expanded concept of the "GSI/Synthemistidae" to include the Gomphomacromiidae Tillyard & Fraser, 1940, Pseudocorduliidae Lohmann, 1996{a–c?}, and several other taxa considered in separate families by Bechly (2016). More precisely, Carle et al. (2015: 295) proposed a concept of a "further expanded Synthemistidae which includes all of Fraser's Corduliidae except Macromiinae and Corduliinae" (i.e., the GSI of Ware et al. 2007). GSI is an abbreviation proposed by Ware et al. (2007: 298) for the group "Gomphomacromiinae + Synthemistinae + Cordulephyinae + Idionychinae". Davis et al. (2011) recovered the Synthemistidae as the sister lineage to all other Libelluloidea. Carle et al. (2015) considered the "GSI/Synthemistidae" as a much wider set of taxa, sister group to the (Macromiidae + (Corduliidae + Libellulidae)), while Bechly (2016) considered the Synthemistidae sensu stricto as sister group to the Neolamellida Bechly, 1996 (a group that would comprise the same last families plus those included into the "GSI/Synthemistidae" sensu Carle et al. (2015) that do not fall in the Synthemistidae sensu Bechly (2016). Fleck and El Adouzi (2013) separated the Synthemistidae into Synthemistinae (= Synthemistidae sensu Bechly 1996, 2016) and Gomphomacromiinae. As the crown Cavilabiata (Libelluloidea sensu lato) are dated at at least 168 Ma, and the stem Libellulidae are dated at 93.9–89.8 Ma (Kohli et al. 2016), the most recent common ancestor of Synthemistidae sensu stricto is certainly Mesozoic too. To date, no fossil Synthemistidae sensu Bechly (2016) have ever been recorded.

The fact that the extant Synthemistidae sensu Bechly (1996, 2016) are Australasian does not imply that the family could not be found as fossils in other regions. The termite Mastotermitidae is a spectacular example of a strictly

Australasian family that is now known from fossils on all continents, except Antarctica (Jouault et al. 2022).

Here we describe the first-ever fossil representative of the Synthemistidae sensu Bechly (1996, 2016), which was collected from the Paleocene of Menat (France). This first occurrence may provide a time point for calibration in phylogenetic analyses.

The odonatan fauna from Menat is rather diverse (Garrouste et al. 2017; Nel and Jouault 2022; Doriath-Döhler et al. 2023), with at least representatives of the families Epigomphidae Fraser, 1934, Dysagrionidae Cockerell, 1908 and superfamilies Lestinoidea Calvert, 1901, and Amphipterygoidea Selys-Longshamps, 1853. Several undescribed species of Odonata are also recorded by very fragmentary wings.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank:urn:lsid:zoobank.org:pub: urn:lsid:zoobank.org:pub:5A082E47-B4FF-47CB-9EFD-81281ED5F92F.

Institutional abbreviations.—MNT, Musée de Paléontologie de Menat¸ Menat, Puy-de-Dôme, France.

Other abbreviations.—AA/P, anal anterior/posterior; a.l., anal loop; Arc, arculus; Ax, primary antenodal crossvein; C, costa; CuA/P, cubitus anterior/posterior; CuAa/b anterior/posterior branch of CuA; GSI, Gomphomacromiinae + Synthemistinae + Cordulephyinae + Idionychinae; h, hypertriangle; IR, intercalary longitudinal veins between main branches of RP; m, median space; MA/P, median anterior/posterior; N, nodus; O, oblique crossvein; PsA, Pseudo-Anal vein; RA/P radius anterior/posterior; ScP, subcostal posterior; sm, submedian space; Sn, subnodus; t, discoidal triangle.

Material and methods

The lacustrine Lagerstätte of Menat (Puy-de-Dôme, France) is a rather small maar (about 1 km diameter), filled with spongodiatomites. It is among the oldest Paleocene outcrops providing insect fossils. According to palynology, mammalian biostratigraphy, and radiometric K/Ar analyses its age was estimated to ca. 56 Ma (Kedves and Russel 1982) vs macrofloral datings indicating the age of 60–61 Ma (Wappler et al. 2009), corresponding to the Selandian–Thanetian (Uhl et al. 2024). It is well known for its very rich and diverse floras (e.g., Laurent 1912; Piton 1940) and faunas (vertebrates and insects). Piton (1940) was the first to extensively study this Lagerstätte. Since then, several works have been done on the entomofauna, mainly during the last twenty years by the group from MNHN (see list in Nel 2022). The insect fauna is abundant and diverse, mainly comprising beetles, cockroaches, and bugs.

The composition of faunal and floral remains suggests that this lake was surrounded by a forest and that the palaeoenvironment was warm and humid (Wedmann et al. 2018).

The new discovery made during field works in 2019 was possible thanks to a careful examination of all the rock fragments during field and laboratory research. Insects are notoriously hard to detect on the dark brown rocks from this locality. The fossil studied herein is a dragonfly specimen that may have been regurgitated by a vertebrate predator as suggested by folded and crumpled wing remains and two abdominal segments. Nevertheless, a reconstruction of the basal half of the hind wing was possible.

The fossil was studied using stereomicroscopes (Olympus SCX9 and a Nikon SMZ1500), drawn with a camera lucida under a Nikon SMZ1500. It was photographed with a Canon MP-E 65 mm f/2.8 1–5× macro photo lens attached to a Canon EOS 6D camera, mounted on a semi-automatic Cognises Rail macro Stack Shot controlled by Helicon Remote software. The reconstruction was created through drawings of both part and counterpart. Photographs were focus-merged using Helicon Focus 6.7 software and were exported in TIF format. Final images, and drawings were realized using Pixelmator Pro 3.6.13 Archipelago software.

We follow the wing venation nomenclature of Riek and Kukalová-Peck (1984), modified by Nel et al. (1993), Bechly (1996), and Jacquelin et al. (2018). We follow Bechly (2016)'s classification of the Synthemistidae (= Synthemistinae sensu Fleck and El Adouzi 2013).

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Odonata Fabricius, 1793

Suborder Anisoptera Selys in Selys-Longschamps & Hagen, 1854

Family Synthemistidae Tillyard, 1917 (sensu Bechly 1996, 2016)

Subfamily Gallosynthemistinae nov.

Zoobank LSID: urn:lsid:zoobank.org:act:158E1DA8D0E3-4692-808B-2B4BB0BC118D.

Type genus: *Gallosynthemis* gen. nov.; see below.

Diagnosis.—As for the type species of the type genus, by monotypy.

Genus *Gallosynthemis* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:2261A631-35B1-4329-9AAE-DFBBBD4CD9AA.

Type species: *Gallosynthemis bechlyi* sp. nov., see below; monotypic.

Etymology: Named after Gallia, Latin name for France and the genus name *Synthemis*. Gender feminine.

Diagnosis.—As for the type species, by monotypy.

Gallosynthemis bechlyi sp. nov.

Fig. 1.

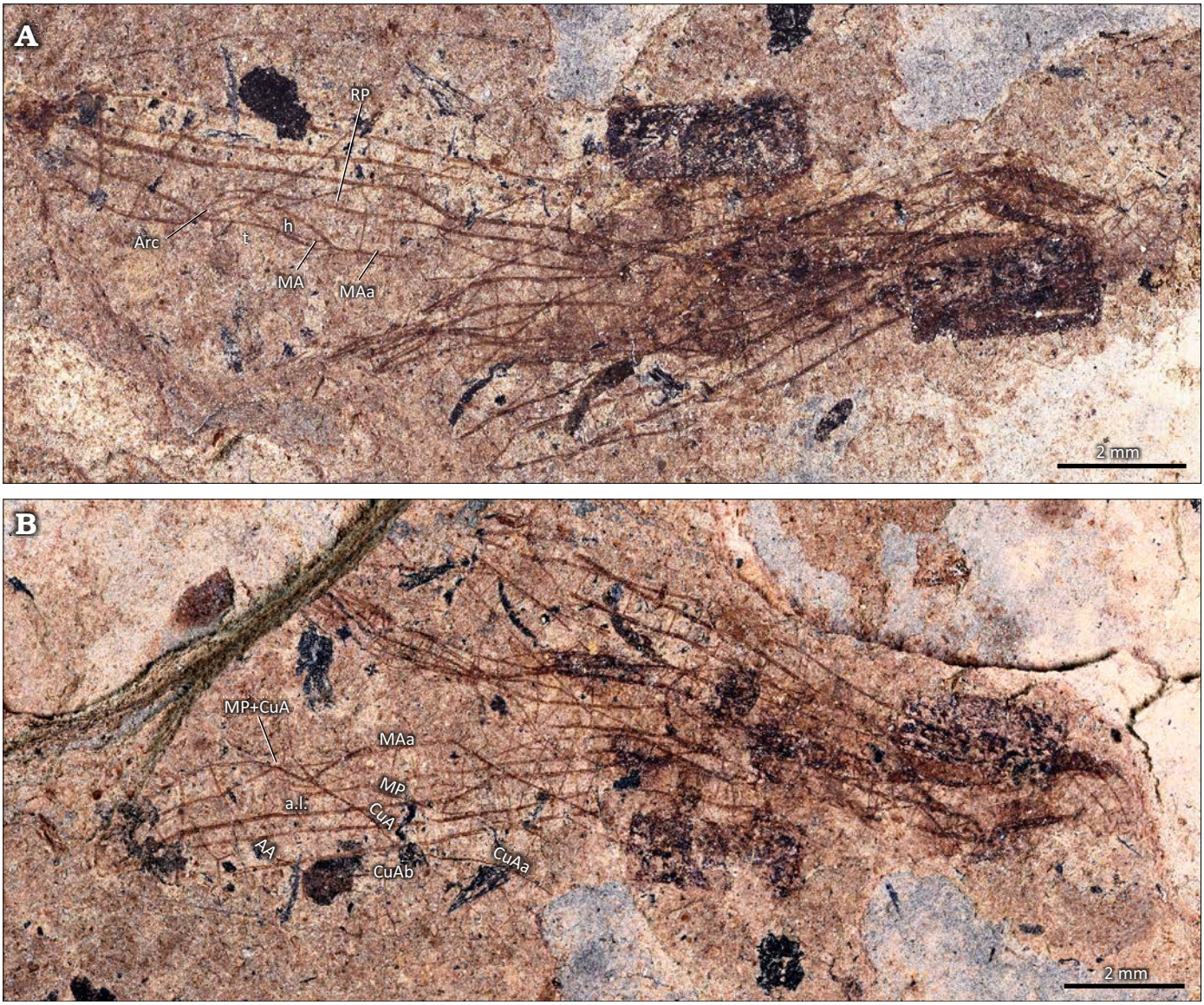

Fig. 1. Synthemistid dragonfly *Gallosynthemis bechlyi* gen. et sp. nov, holotype MNT Nel 2013 from Selandian–Thanetian, Paleocene, Menat, Puy-de-Dôme, France. Photograph of part (**A**) and counterpart (**B**). Abbreviations: AA, anal anterior; a.l., anal loop; Arc, arculus; CuA, cubitus anterior; CuAa/b, anterior/posterior branch of CuA; h, hypertriangle; MA/P, median anterior/posterior; RP radius posterior; t, discoidal triangle.

Zoobank LSID: urn:lsid:zoobank.org:act:BAC7293E-5A46-4C6C-954E-084393E9749F.

Etymology: After our friend and colleague Günter Bechly (1963–2025), who passed away in a dramatic accident at the beginning of January 2025, in recognition to his impressive and crucial contribution to palaeoentomology, especially on dragonflies.

Holotype: MNT Nel 2013 (part and counterpart).

Type locality: Menat, Puy-de-Dôme, France.

Type horizon: Selandian–Thanetian, Paleocene.

Material.—Holotype only.

Diagnosis.—Hind wing characters only. A very long stem of CuA, covering five large cells between CuA and MP (autapomorphy); discoidal cell elongate, not equilateral; sectors of arculus not stalked; anal loop transversely elongate with a strongly zigzagged midrib.

Description.—Only basal half of hind wing can be described. Distance from base to nodus 10.4 mm, from base to arculus 3.2 mm, wing 6.4 mm wide; two primary antenodal crossveins visible, Ax1 situated 0.9 mm basal to arculus, Ax2 1.1 mm distal to it, a third secondary antenodal complete, other secondary antenodals of first row not aligned with those of second row; median area with two distal crossveins; submedian area with one or two crossveins between CuP and PsA (pseudo anal vein); sectors of arculus touching only at their bases; hypertriangle free; discoidal triangle free, elongate, not equilateral; two crossveins between MAa and RP basal of RP3/4; antesubnodal crossveins not discernable; base of RP2 aligned with subnodus; oblique vein O close to base of RP2; two postnodal crossveins discernable but no corresponding postsubnodals; postdiscoidal area with one row of cells just distal to discoidal triangle and

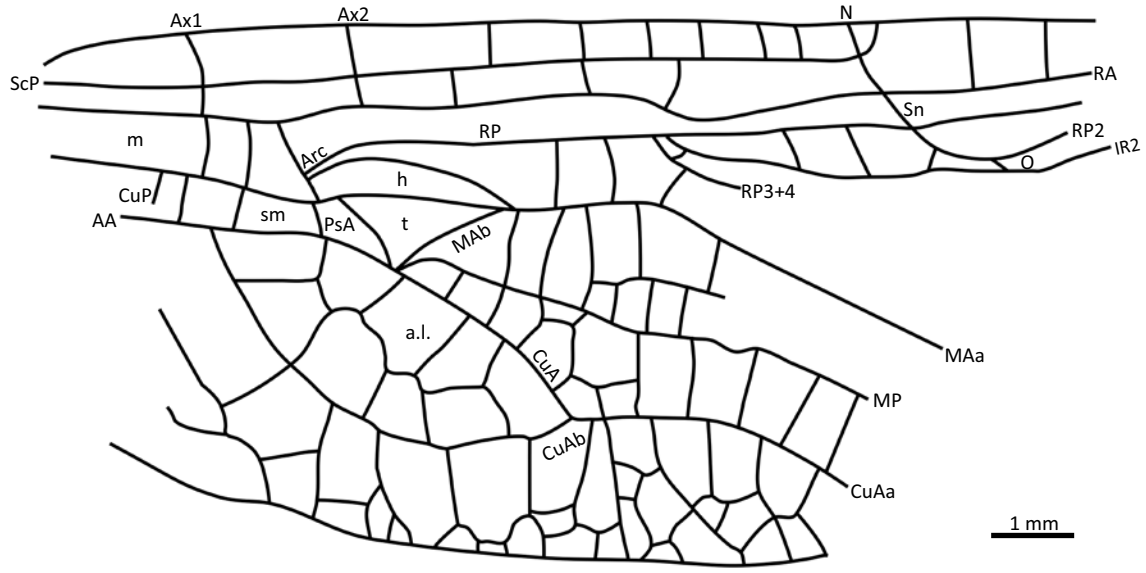

Fig. 2. Synthemistid dragonfly *Gallosynthemis bechlyi* gen. et sp. nov, holotype MNT Nel 2013 from Selandian–Thanetian, Paleocene, Menat, Puy-de-Dôme, France. Hind wing venation reconstruction. Arrow indicates an oblique vein. Abbreviations: AA, anal anterior; a.l., anal loop; Arc, arculus; Ax, primary antenodal crossvein; CuA/P, cubitus anterior/posterior; CuAa/b anterior/posterior branch of CuA; h, hypertriangle; IR, intercalary longitudinal veins between main branches of RP; m, median space; MA/P, median anterior/posterior; N, nodus; O, oblique crossvein; PsA, pseudo-anal vein; RA/P, radius anterior/posterior; ScP, subcostal posterior; sm, submedian space; Sn, subnodus; t, discoidal triangle.

two rows more distally; area between MP and CuA/CuAa with one row of cells basally, two rows distally and more distally only one row; stem of CuA very long; CuAb short fused with AA and closing posteriorly anal loop; CuAa smoothly curved and parallel to MP, without well-defined posterior branch; cubito-anal area rather narrow, with three rows of cells between CuAa and posterior margin of wing; anal loop obliquely elongate, with a poorly defined zig-zagged midrib; at most two rows of cells between anal loop and posterior margin of wing.

Stratigraphic and geographic range.—Selandian–Thanetian, Paleocene, Menat, Puy-de-Dôme, France.

Discussion

In the hind wing, the very large and elongate anal loop without a well-defined mid-rib, the CuAa without posterior branches, the presence of crossveins in the median area and between CuP and PsA (putative synapomorphies), and the absence of postsubnodal crossveins below the first postnodal crossveins are characters of the family Synthemistidae sensu Bechly (2016). Chlorogomphidae also displays crossveins in the median and submedian spaces and a rather similar anal loop, but these strongly differ from the new fossil by the presence of a strong posterior branch of CuAa (Fraser 1957; Bechly and Ueda 2002). Extant Chlorogomphidae also have postsubnodal crossveins just distad of the subnodus, absent in the Cretaceous Araripechlorogomphidae Bechly & Ueda, 2002. The Araripechlorogomphidae have no median and submedian supplementary crossveins.

Carle (1995: 408) proposed the character state "hind-wing with 3–5 costal braces [antenodal crossveins] alternating with non-aligned antenodals" as synapomorphy of the Synthemistidae, which is present in *Gallosynthemis bechlyi* gen. et sp. nov.. But he also proposed the character "sectors of arculus stalked" as apomorphy, which is not the case for *Gallosynthemis bechlyi*. Nevertheless, the character state "unstalked sectors of arculus" is likely plesiomorphic, and does not exclude a position of the new fossil *G. bechlyi* in the stem group Synthemistidae sensu Bechly (2016).

The valvulidan families Gomphomacromiidae and Pseudocorduliidae have an anal loop rather similar to that of the new fossil, but they differ in having a more posteriorly curved CuAa, with a rudimentary secondary branch (vs. more longitudinal and with no branch at all), and the antenodal crossveins all complete, which may be a putative apomorphy of all the Valvulida Bechly, 1996 (Ellenrieder and Garrison 2005; Bechly 2016). The Pseudocorduliidae also have no crossvein in the median area.

All extant genera of Synthemistidae sensu Bechly (2016) (*Palaeosynthemis* Förster, 1903, *Eusynthemis* Förster, 1903, *Choristhemis* Tillyard, 1910, *Austrosynthemis* Carle, 1995, *Tonyosynthemis* Theischinger, 1998, *Synthemis* Selys, 1870, *Parasynthemis* Carle, 1995, *Calesynthemis* Carle, 1995), except *Synthemiopsis gomphomacromioides* Tillyard, 1910, differ from the new fossil genus *Gallosynthemis* in having the hind wing stem of CuA much shorter, and the discoidal cell nearly equilateral (Förster 1903; Tillyard 1910; Fraser 1957; Moulds 1985; Carle 1995; Theischinger 1998; Theischinger and Richards 2013, 2016; Fleck 2024).

In *Synthemiopsis* Tillyard, 1910 (unique representative of the Synthemiopsinae sensu Carle 1995), the stem of CuA

is distinctly longer than in the other Synthemistidae sensu Bechly (2016), even if shorter than in the new fossil genus *Gallosynthemis*, the anal loop is obliquely elongate as in *Gallosynthemis*, with a rudimentary strongly zigzagged mid-rib as in *Gallosynthemis*, and the hind wing discoidal cell is elongate, not equilateral as in *Gallosynthemis*. Nevertheless, it differs from the new fossil in the sectors of arculus with a long stalk, vs. separated at base.

Gallosynthemis bechlyi gen. et sp. nov. is thus attributed to the stem group of the Synthemistidae sensu Bechly (2016). It can be separated from the crown group in the very long stem of CuA (autapomorphy), discoidal cell elongate and sectors of arculus not stalked (putative symplesiomorphies).

Conclusions

Gallosynthemis bechlyi gen. et sp. nov., first fossil record of the dragonfly family Synthemistidae, is described from the Paleocene maar of Menat (Puy-de-Dôme, France). It belongs to the stem group Synthemistidae and is attributed to its own subfamily Gallosynthemistinae subfam. nov., characterized by a very long stem of hind wing cubitus anterior vein (autapomorphy). This finding is the first occurrence of a stem group Synthemistidae sensu Bechly (2016) (= Synthemistinae sensu Fleck & El Adouzi, 2013), and provides a key calibration point for the family Synthemistidae sensu Carle et al. (2015), because it belongs to the crown group of this clade.

While the extant Synthemistidae sensu stricto are Australasian, the description of the new species demonstrates that this family may have been much more widespread during the Paleocene. The fact that the Gomphomacromiidae (a part of the Synthemistidae sensu lato) are distributed in South America and Australia also supports a wider distribution of the Synthemistidae in the deep past compared to the present. This situation can be likened to that of the past distribution of the Mastotermitidae (Isoptera), nowadays strictly Australasian, and that were globally distributed during the Cretaceous–Paleogene. The extant Synthemistidae larvae are known to occur in lotic environments (Fleck 2005), permanent small streams (Fleck and El Adouzi 2013), river springs, or on seepages (Theischinger and Hawking 2000; Theischinger 2003). The presence of fishes in the paleolake of Menat indicates that it could have been linked to at least a river and likely springs.

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