

# The first fossil representative of the extant clubtail dragonfly genus *Lindenia* from the mid-Miocene of Öhningen, Germany

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Clubtail dragonfly *Lindenia heeri* sp. nov., is described and figured as the first fossil representative of the extant lindeniiine genus *Lindenia*, based on a finely preserved forewing from the mid-Miocene lacustrine maar of Öhningen, Germany. The new species differs from the type and only species of *Lindenia tetrphylla* in the dark brown pterostigma covering ten cells vs. only five. Otherwise its forewing venation is identical to that of the modern species. The paleoclimatic data fit well with the climatic preferences of extant *Lindenia tetrphylla*, consistent with the generally warmer climate of that region during that period of time, allowing for more Mediterranean or even subtropical elements of the flora and fauna to persist.

**Key words:** Insecta, Odonata, Anisoptera, Gomphidae, Lindeniinae, fossil record, Miocene, Germany.

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## Introduction

The club-tailed dragonflies (Gomphidae) are a diverse and familiar lineage of Odonata throughout the world, with over 90 genera and nearly 1000 species. Among the many groups of Gomphidae, the subfamily Lindeniinae comprises nine extant genera, plus two recently described Cretaceous species in two genera (Bechly 2000; Schädel and Bechly 2017), while the several Cenozoic species have nearly all been attributed to the extant *Ictinogomphus* Cowley, 1934b, with the exception of the two species placed in the Miocene *Miopetalura* Zhang, 1989.

Here, we expand the fossil record of Lindeniinae from the Cenozoic with the first occurrence of the extant genus *Lindenia* De Haan, 1826. The fossil is from the mid-Miocene lacustrine deposits of Öhningen, southern Germany.

The discovery is based on a reinterpretation of various insect groups from the famous Öhningen Lagerstätte, following on prior reviews of Bibionidae and Hydrophilidae (Fikáček and Schmied 2013; Skartveit and Pika 2014).

**Institutional abbreviations.**—ETH, Zürich Eidgenössische Technische Hochschule, Switzerland.

**Other abbreviations.**—AA, anterior anal; Arc, arculus; Ax, primary antenodal crossvein; Bqs, crossveins in space between base of IR2, RP1/2; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; IR, intercalary radial vein; IR2a, anterior branch of IR2; IR2b, posterior branch of IR2; MAa, anterior branch of anterior media; MAb, posterior branch of anterior media; MP, posterior media; “O” oblique vein between IR2 and RP2 distal of subnodus; Pt, pterostigma; RA, anterior radius; RP, posterior radius; ScP, posterior subcostal; t, discoidal triangle; tspl, trigonal planate.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:46D124FC-1198-4125-B3DA-67CE214B7209

## Geological setting

The limnic sediments of the old Öhningen quarry were set down in a meromictic maar lake of approximately 1000 m in diameter and perhaps up to 100 m in depth (Lutz 1997). There was contribution from and discharge to connected riverine systems, and periodic episodes of high salinity in the littoral (Lutz et al. 2000). The climate at the time was moderately warm, with an estimated average annual temperature of 15.5–16.5°C, ranging from 8–11°C during the coldest parts of the year up to 24°C during the warmest month, and with rainfall of 1300–1500 mm/annum (Mai 1995; Lutz 1997; Lutz et al. 2000).

## Material and methods

The specimen belongs to the historical collection of Oswald Heer, and was collected during 19<sup>th</sup> century in the historical outcrop of old Öhningen quarry. It was photographed with a Canon EOS 90D and an attached Canon MP-E 65mm f/2.8 1–5× Macro Photo and a Canon EF 100mm f/2.8 Macro USM lens, while UV-light photography was done exclusively with the first lens. A UV light (365 nm) was used to find different visible fluorescence contrast with the sedimentary matrix, and to obtain a greater resolution of the wing venation. The application of UVA (365 nm rather than 390 nm) for the study of fossil insects is a new promising technique for enhancing observation with a simple, portable, and economical device (Nel et al. 2023, 2024). Photographs were exported in TIF format and final images were cropped and enhanced using Pixelmator Pro 3.3.6 Mosaic software. All measurements were obtained with ImageJ software and recorded in millimeters.

We follow the higher classification of fossil and extant Odonoptera Martynov, 1932 (total group of the extant Odonata Fabricius, 1793) based on the phylogenetic system of Bechly (1996, 2016), and employ the dragonfly wing venation nomenclature of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993), Bechly (1996), and Jacquelin et al. (2018).

## Systematic palaeontology

Class Insecta Linnaeus, 1758

Superorder Odonoptera Martynov, 1932

Order Odonata Fabricius, 1793

Family Gomphidae Rambur, 1842

Subfamily Lindeniinae Jacobson & Bianchi, 1905

Genus *Lindenia* De Haan, 1826

*Type species:* *Aeshna tetraphylla* Vander Linden, 1825; Recent; Lago d’Averno, Italy.

*Lindenia heeri* sp. nov.

Fig. 1.

*ZooBank LSID:* urn:lsid:zoobank.org:act:17FD46AF-8346-43D1-8212-D2F9E70DC592

*Etymology:* The specific epithet honors Oswald Heer (1809–1883), one of the founders of palaeoentomology and who discovered and published numerous insects from the Öhningen outcrop (e.g., Heer 1847).

*Holotype:* ETH S.N. 228 (labelled “*Aeshna tyche* Hr.”), a complete forewing.

*Type locality:* Area around Lake Constance (Bodensee) north of the cities of Öhningen and Wangen, southern Germany.

*Type horizon:* Upper Öhningen beds Member, Upper Freshwater-Molasse Formation, Sarmatian, 12.7–11.6 Ma, mid-Miocene (Selmeier 1990; Lutz 1997).

*Material.*—Type material only.

*Diagnosis.*—Forewing with 10 cells directly adjacent on posterior side of pterostigma; posterior branch of IR2 at level of vein “O”; 12 small cells between C and RA distad to pterostigma; elongate discoidal triangle, with a distinctly curved MAb; base of IR1 situated below basal side of pterostigma; presence of a secondary curved vein apparently emerging from posterior branch of IR2.

*Description.*—A complete forewing, 44.6 mm long, 9.6 mm wide; distance from base to arculus 6.2 mm, from arculus to nodus 18.0 mm, from wing base to Ax1 4.5 mm, from Ax1 to Ax2 6.2 mm; Ax2 slightly basal to distal angle of discoidal triangle; three antenodal crossveins of first row between Ax1 and Ax2, 16 secondary antenodal crossveins of first row distal of Ax2; 13 preserved postnodals; 12 crossveins between RP and MAa basad RP3/4; eight Bqs veins; oblique vein “O” four cells distal of subnodus; hypertriangle with two crossveins; discoidal triangle elongate, subdivided into five cells, with costal side 3.6 mm long, basal side 2.3 mm long, distal side MAb 4.1 mm long, MAb curved, with a slight angle at base of tspl; RP3/4 and MAa weakly curved and parallel, with one row of cells between and two rows near posterior margin of wing; three rows of cells in basal part of postdiscoidal area, broadened distally; a distinct distal posterior branch of MAa, with four rows of cells between it and MAa; median area free; submedian area crossed by CuP and two other veins; PsA strong and oblique; subtriangle divided into three smaller cells; distance between nodus and pterostigma 0.9 mm; pterostigma dark brown, 6.9 mm long, 1.0 mm wide, with costal and posterior margin widened, with 10 cells directly adjacent on posterior side of pterostigma; pterostigmal brace slightly oblique, aligned with basal side of pterostigma; 12 small cells between C and RA distad to pterostigma; base of IR1 below basal side of pterostigma, basally zigzagged, and curved distally; base of RP2 aligned with subnodus, RP2 regularly curved; main

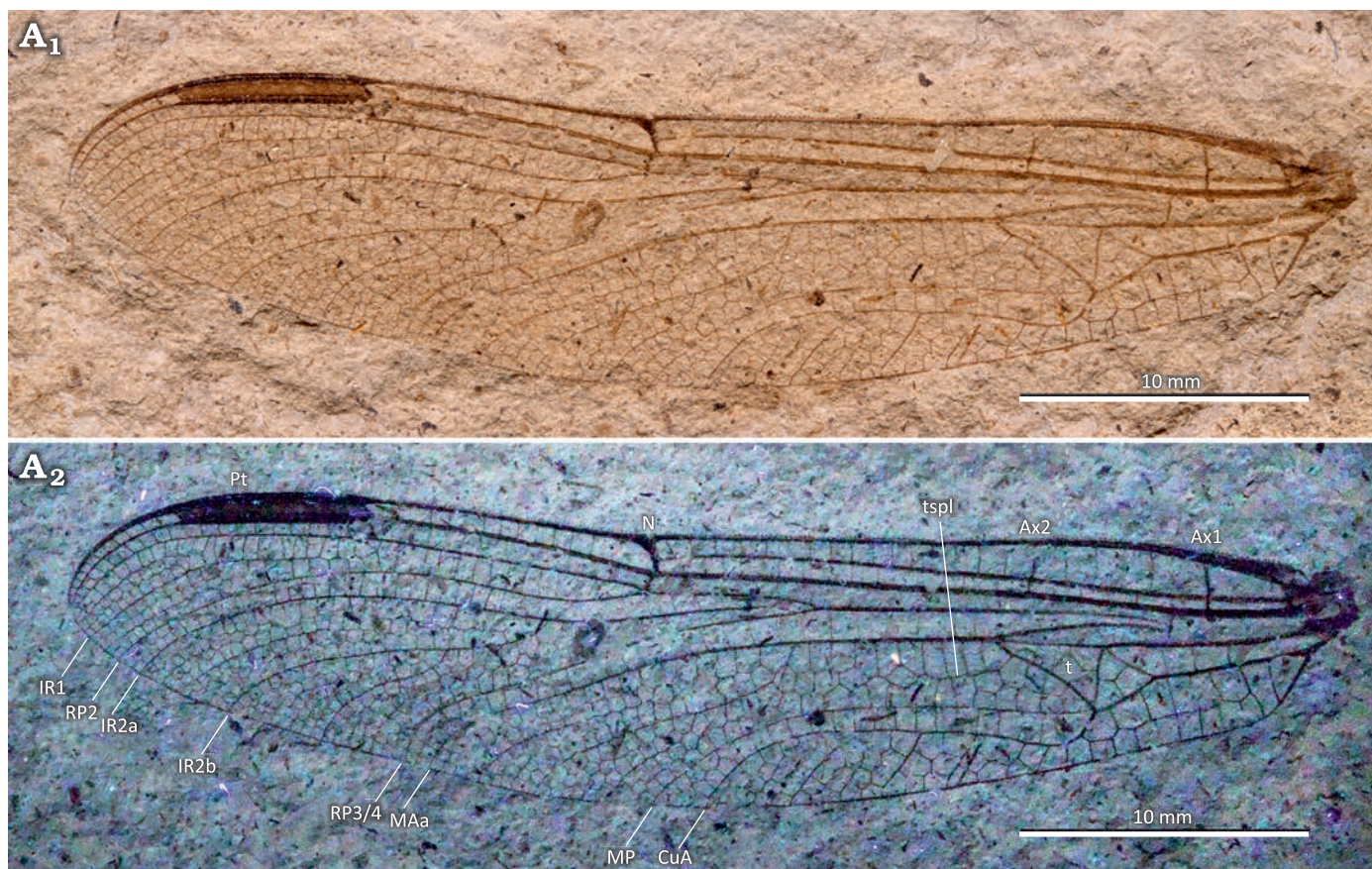


Fig. 1. Clubtail dragonfly *Lindenina heeri* sp. nov., holotype, ETH S.N. 228 from Upper Öhningen beds Member, mid-Miocene. Forewing photographed under standard light (A<sub>1</sub>) and UV light (A<sub>2</sub>).

branch of IR2 parallel to RP2; posterior branch of IR2 at level of vein “O”, well-defined with four to seven rows of cells and a well-defined secondary longitudinal vein between it and main branch; three rows of cells between posterior branch of IR2 and RP3/4 in narrower part; a secondary curved vein apparently emerging from posterior branch of IR2; cubito-anal area broad with four rows of cells between CuA and posterior margin of wing.

**Remarks.**—Attribution of the wing to the family Gomphidae is supported 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 curved; straight arculus (Bechly 1996, 2003). The new fossil has an elongate discoidal triangle with a distinct tspl, which is a feature found among Gomphidae only in the subfamilies Hageniinae Davies & Tobin, 1985, and Lindeniinae. The Hageniinae have the IR1 vein secondarily elongate, originating well basad the pterostigma. Also, the costal margin and RA are not widened along the pterostigmata. These characters are not present in the new fossil thereby excluding a placement in Hageniinae. Alternatively, Lindeniinae are characterized by the following synapomorphies: secondary branch of IR2 very distinct, therefore IR2 appears to be dichotomously forked distal of the lestine oblique vein; discoidal triangles divided into more than two

cells; in the forewing the basal part of the subdiscoidal cell (between CuP-crossing and pseudo-anal vein PsA) is traversed by supplementary cubito-anal-crossveins; hypertriangle divided by at least two or more crossveins. All of these characters are present in the current fossil wing.

Among extant lindenine genera, *Diastatomma* Burmeister, 1839, from Africa has strongly curved distal halves of the main longitudinal veins, and many more cells (ca. 20) cells directly adjacent on the posterior side of the pterostigma, unlike the new fossil. *Gomphidia* Selys, 1854 (Africa and south-east Asia) and *Gomphidictinus* Fraser, 1942 (Thailand, Viêt Nam, Laos) have a forewing discoidal triangle more equilateral than in the new fossil (Fraser 1942; Garrison et al. 2015). Neotropical *Cacoides* Cowley, 1934a, and *Melanocacus* Belle, 1986, and *Ictinogomphus* from Africa and south-east Asia, and its closely related genera *Austrictinogomphus* Fraser, 1940 (Papua), *Sinictinogomphus* Fraser, 1939 (East and south-east Asia), and *Indictinogomphus* Fraser, 1939 (Oriental, Australo-Papua), also differ from the new fossil in the forewing discoidal triangle not elongate, nearly equilateral (Fraser 1957; Belle 1986).

The new fossil has a wing venation extremely similar to that of *Lindenina tetraphylla* (Van der Linden, 1825), especially in the elongate discoidal triangle, with a distinctly curved MAB; the base of IR1 situated below the basal side of the pterostigma; the same shape of veins RP2, IR2, RP3/4,

and MAa; and the same pattern of veins in the postdiscoidal area and the area between IR2 and RP3/4, especially in the presence of a secondary curved vein apparently emerging from the posterior branch of IR2. The only discernable difference is the number of cells directly adjacent on the posterior side of the pterostigma, viz. 10 in the new fossil vs. five to eight in the sole extant species of *Lindenia*, i.e., *L. tetraphylla* (Van der Linden, 1825).

Among fossil Lindeniinae, the oldest representative, *Cratolindenia knuepfae* Bechly, 2000, is from the Lower Cretaceous of Brazil. It differs greatly from the new fossil in a more distal position of the posterior branch of IR2, in a strongly oblique pterostigmal brace, and in having a quite broad area between RP2 and RP1 below the pterostigma (Bechly 2000). The second oldest lindeniiine is *Burmalingenia imperfecta* Schädel & Bechly, 2016, based on the basal parts of hind wings from “mid”-Cretaceous Kachin amber. It is not possible to compare the species from Myanmar with the new fossil forewing as the former is based on a hind wing (Schädel and Bechly 2016). Several Cenozoic fossils have been attributed to the *Ictinogomphus*, namely *I. hassleri* Schädel & Lechner, 2017, based on a hind wing which differs from the new fossil in only six cells directly adjacent on the posterior side of the pterostigma (Schädel and Lechner 2017); *Ictinogomphus engelorum* Nel et al., 2020, that has a significantly different forewing discoidal triangle (Nel et al. 2020); and “*?Ictinogomphus* species indet.” described by Prokop et al. (2016), known from only the apical two-thirds of a forewing, differs from the new fossil in the lower number of cells distal to the pterostigma, and only six cells directly adjacent on the posterior side of the pterostigma. Lastly, the Miocene Chinese *Miopetalura* would share with the new fossil the presence of ten cells directly adjacent on the posterior side of the pterostigma, but it differs from the new fossil in the forewing discoidal triangle nearly equilateral and the presence of much more secondary antenodal crossveins (Zhang 1989: text-fig. 10).

Lastly Huang and Nel (2009) described a “Lindeniiinae, genus undetermined” from the Miocene Shanwang Formation of China. If it shares with the new fossil the presence of numerous cells covered by the pterostigma, its posterior branch of IR2 is two cells distad to the oblique vein and its forewing is ca. 42.0 mm long vs. 44.6 mm in the new fossil. *Stratigraphic and geographic range.*—Upper Öhningen beds Member, Upper Freshwater-Molasse Formation, Sarmatian, 12.7–11.6 Ma, mid-Miocene.

## Concluding remarks

After Schorr et al. (1998: 65), *Lindenia tetraphylla* “reaches from Sardinia (Italy; in the past also Spain) in the West, along the northern coasts of the Mediterranean, the Caspian region and the Middle East, to Kazakhstan, Kirgizia, Afgha-

nistan, and Pakistan in the East”. It also has been cited from Corsica, Bulgaria, and Algeria (Tellez and Dommanget 2009; Gashtarov and Beshkov 2010; Khelifar and Zebza 2018). According to Boudot (2014), the female throws its eggs among submerged hydrophytes in standing water. The paleoclimate of the Öhningen maar fits quite well with the climates of these regions.

The discovery of *Lindenia* in the mid-Miocene Öhningen maar lake sediments is consistent with the generally warm climate of that region during that period of time, allowing for more Mediterranean or even subtropical elements of the flora and fauna to persist. While the extant *L. tetraphylla* could not live today in the area of southern Germany where Öhningen is located, with the impact of human-driven climatic change we may see organisms that once preferred warmer climates migrating gradually northward through Europe, with some lineages perhaps returning to areas from which their distant ancestors were exterminated by past climatic cooling. *Lindenia heeri* sp. nov. also reveals the first fossil for the hitherto monotypic genus, pushing this lineage back to at least 12.7 Ma.

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