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Two new dragonflies (Odonata: Anisoptera) from the Miocene of Carinthia (Austria)

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Abstract

Two new species of fossil dragonflies from the Middle Miocene fossil site Schaßbach (Carinthia, Austria) are described. The presence of *Gomphaeschna carinthiae* **sp. nov.** and *Ictinogomphus hassleri* **sp. nov.** in the fossil record of Central Europe confirms the scenario of a more widespread distribution of the represented genera in the Miocene in contrast to their Recent distribution.

Key words: Badenian, Central Paratethys, Mühldorf Formation, Lake Lavant, fossil insect, Gomphaeschnidae, Gomphaeschninae, Gomphidae, Lindeniinae

Introduction

Fossil Lindeniinae

The earliest Lindeniinae fossils are known from the Cretaceous of Brazil (Bechly 2000) and Myanmar (Schädel & Bechly 2016).

List of all known fossil Lindeniinae

Cratolindenia knuepfae Bechly, 2000, from the Lower Cretaceous of Brazil;
Burmalindenia imperfecta Schädel & Bechly, 2016, from the Upper Cretaceous Burmese amber, Myanmar;
Gomphoides occultus Hagen, 1856, from the Upper Eocene Baltic amber (Pictet & Hagen 1856; Nel & Paicheler 1994);
Petalura acutipennis Hagen, 1859, from the Oligocene of Sieblos, Germany (Nel *et al.* 1998);
Miopetalura shanwangica Zhang, 1989, from the Miocene of China (Nel *et al.* 1998);
Gen. et sp. indet. Nel & Paicheler, 1994, from the Latest Oligocene of Turkey;
Gen. et sp. indet. Huang & Nel 2009, from the Miocene of China;
Ictinogomphus (*Ictinus*) *fur* Hagen, 1863, Oligocene Rott, Germany, currently considered as an Anisoptera of uncertain family (Nel & Paicheler 1994; Petrulevičius *et al.* 2011);
Ictinogomphus sp. Yasuno, 1990, Lower Miocene of Japan (Nel & Paicheler 1994);
Ictinogomphus sp. from Oligocene of Seifhennersdorf, Germany (Prokop & Fikacek 2007; Prokop *et al.* 2016).

Fossil Gomphaeschnidae

The systematics within the Aeshnida sensu Bechly 1996 is still under debate (Dijkstra *et al.* 2013) with two

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approaches being at issue. Von Ellenrieder (2002) used the taxon Aeshnidae Leach, 1815, for all extant species that could be found within the taxon Aeshnida Bechly, 1996, sensu Bechly (2001, 2003) that comprises multiple taxa on a family level. Von Ellenrieder's interpretation of the Aeshnidae is generally used, because it defines a group that is clearly a clade. Bechly's approach, however, bears the opportunity for a practical way of recognizing the divisions within the clade. This is very useful, especially in the field of paleoentomology. Hence we follow the nomenclature proposed by Bechly (2003).

A phylogenetic analysis based on morphological characters of larvae and adults of extant species showed strong evidence for a sister-group relationship between the genera *Gomphaeschna, Sarasaeschna*, *Oligoaeschna* and *Linaeschna* and the remaining species (=Aeshnodea Bechly, 1996) (von Ellenrieder 2002).

The family Gomphaeschnidae Tillyard & Fraser, 1940 (sensu Bechly 1996 and Bechly *et al.* 2001), is at least of Lower Cretaceous age (Bechly *et al.* 2001) and comprises the subfamilies Gomphaeschnaoidinae Bechly *et al.* 2001 and Gomphaeschninae Tillyard & Fraser, 1940 (sensu Bechly *et al.* 2001) as well as some taxa that were not assigned to a subfamily.

List of all known fossil Gomphaeschnidae (sensu Bechly 1996, Bechly *et al.* 2001)

Not assigned:

Cretalloaeschna cliffordae Jarzembowski & Nel, 1996, from the Lower Cretaceous of England (Bechly *et al.* 2001);

Anglogomphaeschna eocenica Nel & Fleck, 2014, from the Late Eocene of the Isle of Wight; *Sophoaeschna frigida* Zhang *et al.*, 2008, from Late Jurassic to Early Cretaceous of Inner Mongolia, China;

Falsisophoaeschna generalis Zhang *et al.*, 2008, from Late Jurassic to Early Cretaceous of Inner Mongolia, China;

Gomphaeschnaoidinae:

Anomalaeschna berndschusteri Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Cretagomphaeschnaoides jarzembowskae Zheng *et al.*, 2016, from the Cretaceous of Myanmar;

Sinojagoria imperfecta Bechly *et al.*, 2001, from the Lower Cretaceous of China (Liaoning);

Sinojagoria cancellosa Li *et al.*, 2012, from the Upper Jurassic or Lower Cretaceous of China (Liaoning);

Sinojagoria magna Li *et al.*, 2012, from the Upper Jurassic or Lower Cretaceous of China (Liaoning);

Paramorbaeschna araripensis Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Progomphaeschnaoides ursulae Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Progomphaeschnaoides staniczeki Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Plesigomphaeschnaoides mongolensis Bechly *et al.*, 2001, from the Lower Cretaceous of Mongolia;

Plesigomphaeschnaoides pindelskii Bechly *et al.*, 2001, from the Lower Cretaceous of England;

Gomphaeschnaoides obliquus (*Gomphaeschna obliqua*) Wighton, 1987, from the Lower Cretaceous of Brazil (Bechly *et al.* 2001);

Gomphaeschnaoides magnus Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Gomphaeschnaoides petersi Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Gomphaeschnaoides betoreti Bechly *et al.*, 2001, from the Lower Cretaceous of Brazil;

Gomphaeschninae:

?Oligoaeschna anglica Cockerell & Andrews, 1916, Upper Eocene, Isle of Wight (Nel & Fleck 2014; Nel *et al.* 2005);

Oligoaeschna needhami Cockerell, 1907, from the Lower Oligocene of Colorado (Nel *et al.* 1994b);

Oligoaeschna oligocenica Nel & Papazian, 1983, from the Lower Oligocene of France (Nel *et al.* 1994b);

Sarasaeschna (*Oligoaeschna*) *pryeri* Martin, 1909, from the Upper Pliocene of Japan (Esaki & Asahina 1957; Nel *et al.* 1994b);

Oligoaeschna conjuncta Martynov, 1929, from the Upper Oligocene of Kasakhstan (Nel *et al.* 1994b);

?Gomphaeschna inferna Pritykina, 1977, from the Lower Cretaceous of Russia (Buryatia);

?Gomphaeschna sibirica Bechly *et al.*, 2001, from the Lower Cretaceous of Russia (Siberia);

Gomphaeschna miocenica Prokop & Nel, 2002, from the Lower Miocene of the Czech Republic;

?Gomphaeschna danica Madsen and Nel, 1997, from the Paleocene/Eocene of Denmark;

Gomphaeschna paleocenica Madsen and Nel, 1997, from the Paleocene/Eocene of Denmark;

Gomphaeschna schrankii Lewis, 1988, from the Paleocene of North Dakota.

Geological Setting. The active clay pit Schaßbach (46°47'53.32"N, 14°48'23.77"E) is located in eastern Carinthia about 3.8 km northwest of the historical town center of St. Andrä (District Wolfsberg). The site lies within an intramontane basin that was formed during late Early (Karpatian) and early Middle Miocene (Badenian) pull-apart phases (Reischenbacher & Sachsenhöfer 2013). The Koralpe restricts the basin on its eastern side, whereas the Saualpe is the western boundary of the basin.

The fine laminated mudstones ('fish-shale') that alternate with siltstones are referred to the lacustrine lower part of the Lower Badenian Mühldorf Formation (Reischenbacher *et al.* 2007; Reischenbacher & Sachsenhöfer 2013). The overlying marine sediments were dated to an age of 14.91 Ma (Reischenbacher *et al.* 2007). Harzhauser *et al.* (2015) suggested the name 'Lake Lavant' for the fossil lake.

Various plant fossils are known from the Schaßbach clay pit including *Ginkgo adiantoides* (Meller *et al.* 2015). Most of the plant remains come from siltstones without a continuous lamination. Plant fossils from fine laminated mudstones are way less common but show a more optimal kind of preservation. Vertebrate fossils so far include the very abundant cyprinid and gobiid fishes as well as rare skeletal bird remains. Also small down feathers are not uncommon in the biolaminites. Only one freshwater snail species (Harzhauser *et al.* 2015) and one terrestrial pulmonate species (Harzhauser pers. communication) are known up to the present.

Fossil arthropods from Schaßbach and their preservation

Although there were some findings of fossil insects and spiders (Joanneum, State Museum Graz, Geological Collection, University of Tübingen & private collection of Dr. Andreas Hassler, Schönweg, St. Andrä), until now no published work has been done on the arthropod fauna of this site. In two field trips a considerable amount of new arthropod fossils (over 400 specimens) were sampled. Also the private collection of Dr. Andreas Hassler was inspected where one of our herein described specimens was noticed.

Most of the arthropod fossils are found in bituminous laminites (Dysodil). Nevertheless, there are exceptional findings in uncontinuous laminated siltstones.

The Dysodil sediments contain a substantial amount of water as well as hydrocarbons and are very flexible under moist conditions. When the sediment gets dry, the arising stresses can lead to a curling of individual layers and ruptures due to horizontal stresses. Also the formation of gypsum crystals was observed during transport and storage of the samples. This could be due to changes in the moisture and air conditions. These effects can damage or even destroy the fossils.

For analogous material from other sites (e.g. Randeck Maar), the fossils together with their matrix were dried under consistent pressure to avoid the curling effect.

For a better optical contrast we copied the technique used for the fossil insects of the Eocene Messel Maar (Gruber & Micklich 2011) and stored our material separately in boxes with pure glycerin.

Material and methods

The specimen from the private collection of Dr. Andreas Hassler (SHI-14) was photographed fully submerged in a water basin using a Sony Alpha 77 camera with a Minolta 50 mm close-up lens (Minolta AF 50/2.8 Macro). Afterwards it was transferred into a box with glycerin for long-term conservation.

The specimen from the Joanneum (UMJG&P 211472) was photographed under dry condition using a Nikon D7100 camera with a Sigma 150 mm close-up lens.

The TrakEM2 plugin for ImageJ™ from the image processing package Fiji was used for stitching together multiple images to create high-resolution images that cover a large area. Measurements for scale bars and measurements for the description were calculated with ImageJ™. If necessary, pictures were post processed in Photoshop™ CS5 but without local images. Both drawings were created in Inkscape™ volume 0.91.

In case of the specimen from the Joanneum, pictures of both halves of the fossil were used to produce a line drawing true to scale by mirroring and repositioning the drawing layer in Inkscape™.

The terminology of wing venation (Figs. 2 & 5) is based on Riek and Kukalová-Peck (1984) emended by Nel *et al.* (1993) and Bechly (1996b).

Entire areas between primary veins are defined as wing fields. Multicellular areas completed by longitudinal and or crossveins are defined as wing spaces. Wings that are convex from a dorsal view on the wing surface are marked with a '+'. Concave veins on the contrary are marked with a '-'.
Areas that are labeled as cells can also be multicellular due to the presence of secondary crossveins.

Abbreviations

A +	Analis	Veins
AA +	Analis anterior	
AP	Analis posterior	
CA +	Costa anterior	
CP –	Costa posterior	
Cu	Cubitus	
CuA +	Cubitus anterior	
CuP –	Cubitus posterior	
ddv	Distal discoidal vein MAb	
IR +	Intercalated vein Interradialsector	
M	Media	
MA +	Media anterior	
MP –	Media posterior	
PsA	Pseudo-analis	
RA +	Radius anterior	
RP –	Radius posterior	
Rspl -	Intercalated vein Radial-supplement	
ScA +	Subcosta anterior	
ScP –	Subcosta posterior	
sdv	Subdiscoidal vein	
tcv	Costal trigonal crossvein	
Tspl –	Intercalated vein Trigonal-supplement	
htc	Hypertriangular cell	Cells
sdc	Subdiscoidal cell	
stc	Subtriangular cell	
tc	Triangular cell	
ans	Antenodal space	Spaces
ars	Arcular space	
bs	Basal space	
cus	Cubital space	
pds	Postdiscoidal space	
rs	Radial space	
ACuf	Antecubital field	Fields
Af	Anal field	
IRf	Interradial field	
Mf	Medial field	
PRf	Postradial field	
PrAf	Preanal field	

PrCuf	Precubital field
PrMf	Premedial field
PrRf	Preradial field
Rf	Radial field

Systematic paleontology

Class Insecta Linné, 1758

Order Odonata Fabricius, 1793

Family Gomphidae Rambur, 1842

Subfamily Lindeniinae Jacobson & Bianchi, 1905

Following Bechly (1999) the "légion Lindenia" Selys, 1854 is not considered as a valid family-group taxon. Therefore Selys' authorship is rejected for the subfamily Lindeniinae.

Genus cf. *Ictinogomphus* Cowley, 1934

***Ictinogomphus hassleri* sp. nov.**
Figures 1 & 2

Holotype. The holotype is stored in the private collection of Dr. Andreas Hassler. The deposition of the specimen is projected in the State Museum of Kärnten, Klagenfurt, Austria under collection number LMK-Pal-2016-5538 (Old working-title: SIH-14).

Diagnosis. This new fossil species is very similar to modern representatives of the genera *Ictinogomphus* and *Sinictinogomphus* Fraser, 1939. It differs from other Lindeniinae genera in the shape of the triangulum and the position of the Tspl-origin. The unique compilation of character states may not separate the fossil from all members of *Ictinogomphus* and *Sinictinogomphus*, but the remoteness in time and geographical range strongly suggests that the described specimen is not conspecific in the sense of a biological species concept.

The Lindeniinae fossil described by Huang & Nel (2009) from the Miocene of China has a distinctly larger hind wing than our specimen and 3 to 4 rows of cells between the origin of the secondary branch of IR2 and RP´´ instead of only two rows as in our specimen (which is probably due to the larger size). With a length of 40 mm, the hind wing is distinctly larger than the Chinese specimen.

Our specimen is very similar to the specimen described by Nel & Paicheler (1994) from the latest Oligocene sediments in Bes-Konak, Turkey. The Bes-Konak specimen differs only in the manifestation of intercalated veins and the oblique pterostigmal brace vein, based on the area of the fossil wings that is preserved in both specimens.

The *Ictinogomphus* specimen from Seifhennersdorf (Early Oligocene, Germany; Prokop & Fikacek 2007; Prokop *et al.* 2016) cannot be clearly differentiated from our herein-described specimen, because the Seifhennersdorf specimen is represented by a forewing in contrast to our specimen that is represented by a hind wing.

Description. An almost complete wing lacking only anal region and basalmost part of ACuf as well as area basal to discoidal triangle. Total length 32.5 mm and total width 11.1 mm. Preservation better towards wingtip than in more basal part.

Anterior wing margin from base to nodus (CA & CP & ScA´) with short spines; nodus 14.1 mm from wing base and 18.4 mm from tip (at 43% of the wing length); secondary antenodal crossveins at least in distal part of ans not aligned.

Pterostigma with parallel anterior and posterior margin; 5.7 mm in proximodistal dimension and maximum 0.9 mm in anteroposterior dimension; posterior margin of pterostigma broader than anterior margin; proximal margin orthogonal and distal margin oblique with an angle of 134° to posterior margin. Pterostigmal brace vein broad and pointing posterior at a right angle to RA +; Preradial and Interradial field both with one row of cells.

Distal part of antesubnodal space not free; at least one crossvein between RA and RP′ 2.4 mm proximal of subnodus; distance between RP′–RP′′ furca and subnodus 4.8 mm. Interradial sector with distinct secondary branch 7.8 mm distal from RP′–RP′′ furca; two intercalated veins between IR2 + and its secondary branch and between same secondary branch and RP′′ -.

RP1 and RP2 parallel and with one row of cells in between just near to level of proximal margin of pterostigma; intercalated vein between RP1 and RP2 from mid-pterostigmal level to posterior wing margin dividing area between outer veins more or less centrally; numerous small cells anterior and posterior of this intercalated vein.

FIGURE 1. Photograph of the hind wing fragment of *Ictinogomphus hassleri* **sp. nov.**, holotype LMK-Pal-2016-5538.

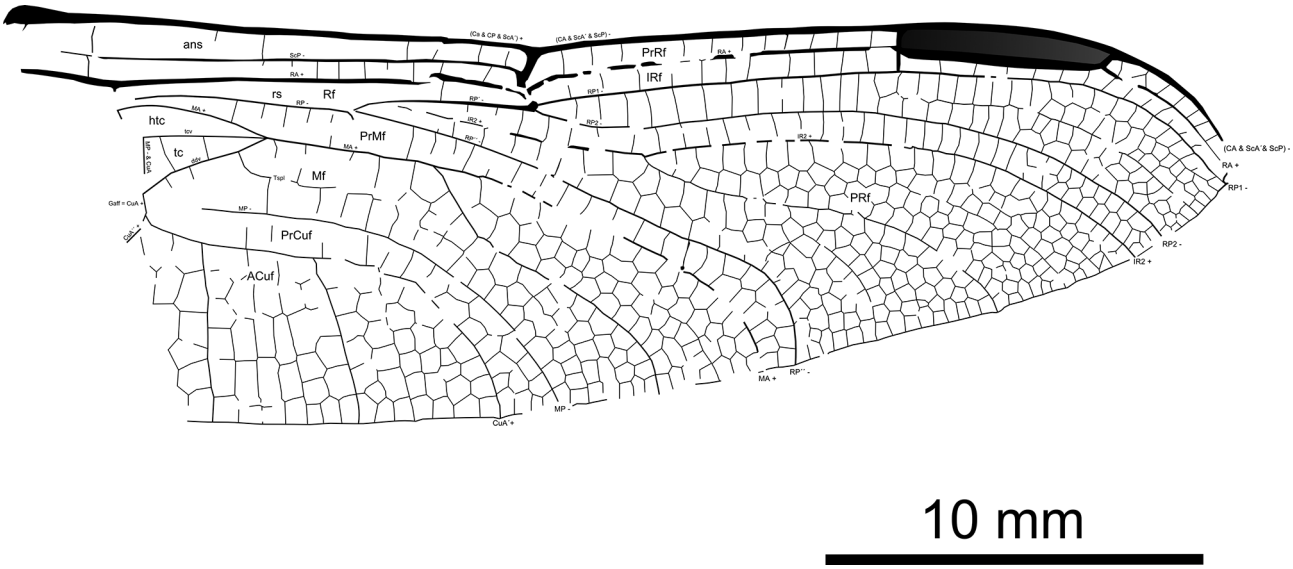

FIGURE 2. Drawing of the hind wing fragment of *Ictinogomphus hassleri* **sp. nov.**, holotype LMK-Pal-2016-5538, with terminology of wing venation.

Distance between arculus and RP furca (origin of RP´ & RP´´) 6.3 mm; premedial field with one row of cells and with more or less parallel boundaries except for the very posterodistal part; posterodistal part of premedial field with two rows of cells and broader than anteroproximal part.

At least five antefurcal crossveins between RP - and MA +.

Htc 3.9 mm long and 0.8 mm wide; anterior margin of htc (MA +) distinctly curved.

Discoidal triangle longitudinally stretched and divided by at least two secondary crossveins; basal side 1.5 mm long; costal side 3.2 mm; posterodistal side 3.6 mm; posterodistal side (ddv) almost straight with a slight kink at origin of the distinct Tspl. Two rows of cells in basal part of postdiscoidal space. Strong secondary branch of MA + 4.5 mm distal of distal angle of discoidal triangle.

Gaff (CuA from posterior angle of discoidal triangle to CuA'/CuA''-branching) 0.6 mm long (not prolonged); CuA´ + with 2 distinct secondary branches.

Type locality and horizon. Claypit Schaßbach (46°47'53.32"N, 14°48'23.77"E), St. Andrä, Wolfsberg (district), Carinthia, Austria. Fine laminated mudstone of the lacustrine lower part of the Mühldorf Formation. Age late Early Miocene.

Etymology. The species name *hassleri* refers to the finder of the specimen and local specialist for the field site Dr. Andreas Hassler, St. Andrä, Wolfsberg, Austria.

Wingspan estimation. The wingspan for the whole animal is estimated as about 70 mm, taking into account that the forewing is a bit longer than the hind wing in recent *Ictinogomphus* species.

Sex determination. The sex determination is not possible lacking the basal part of the wing.

Phylogenetic affinities. Anisoptera Selys, 1854: strong expansion of the cubito-anal field, presence of a discoidal triangle and a hypertriangle (Bechly 2007).

Gomphidae Rambur, 1842: posterodistal side of the triangulum with a slight angle; presence of a trigonal supplement; distinctly curved anterior side of hypertriangle (Bechly 1996, 2003).

Lindeniinae Jacobson & Bianchi, 1905: IR2 and MA both with a distinct secondary branch; hind wing discoidal triangle elongated in distal direction; distal side of triangulum sigmoidal shaped with a slight kink at origin of Tspl; triangulum with more than two cells (Bechly 2003).

According to the slight differences in wing morphology and the large distance between the two fossil sites it seems not very likely that *Ictinogomphus hassleri* is truly conspecific but is closely related to the undetermined Lindeniinae fossil from Turkey (Nel & Paicheler 1994).

Although our specimen resembles modern species of both *Ictinogomphus* and *Sinictinogomphus*, we suggest *Ictinogomphus* as the most suitable genus name due to the older age of the name.

Family Gomphaeschnidae Tillyard & Fraser, 1940 (sensu Bechly 1996 and Bechly *et al.* 2001)

Subfamily Gomphaeschninae Tillyard & Fraser, 1940

Genus *Gomphaeschna* Selys, 1871

Gomphaeschna carinthiae sp. nov.

Figures 3–5

Holotype. UMJG&P 211472, collection of the Universalmuseum Joanneum, Graz, Austria.

Diagnosis. The specimen differs from all Recent and fossil gomphaeschnid species in the broad space between Rspl and IR2 and the distinct oblique crossvein that connects these two veins.

Description Graz. The fossil was split during its excavation and is now present in two halves. Both halves show mostly the same but mirrored parts of the venation. Almost the complete wing is preserved and visible. The preservation lacks only the proximal posterior part of the wing. The tip of the wing dips into the sediment of plate A whereas the proximal anterior edge of the wing dips in plate B.

Total length 28.4 mm; total width 9.6 mm. Secondary antenodal crossveins not aligned. Pterostigma roughly parallel sided; 3.1 mm in proximodistal dimension and maximum 0.9 mm in anteroposterior dimension; proximal and distal margin oblique with an angle of 134° between RA and proximal margin and 135° between posterior margin and distal margin. Pterostigmal brace vein oblique in extension of proximal margin of pterostigma.

FIGURE 3. Photograph of the hind wing fragment of *Gomphaeschna carinthiae* **sp. nov.**, holotype UMJG&P 211472, plate A. The wingtip is covered with sediment.

FIGURE 4. Photograph of the hind wing fragment of *Gomphaeschna carinthiae* **sp. nov.**, holotype UMJG&P 211472, plate B. The posterobasal area of the wing is covered with sediment.

Preradial and interradial fields both with one row of cells.

Distalmost crossvein in antesubnodal space at level of junction between RP′ and IR2.

Distance between RP′–RP′′ furca and subnodus 4.0 mm. Distinct 1.3 mm long oblique crossvein at distance of 9.8 mm from RP′–RP′′ furca between IR2 and Rspl with an angle of 127° to proximal side of IR2. The part of Rspl proximal to the distinct IR2-Rspl crossvein is not preserved. At least five straight veins running from Rspl towards posterior wing margin.

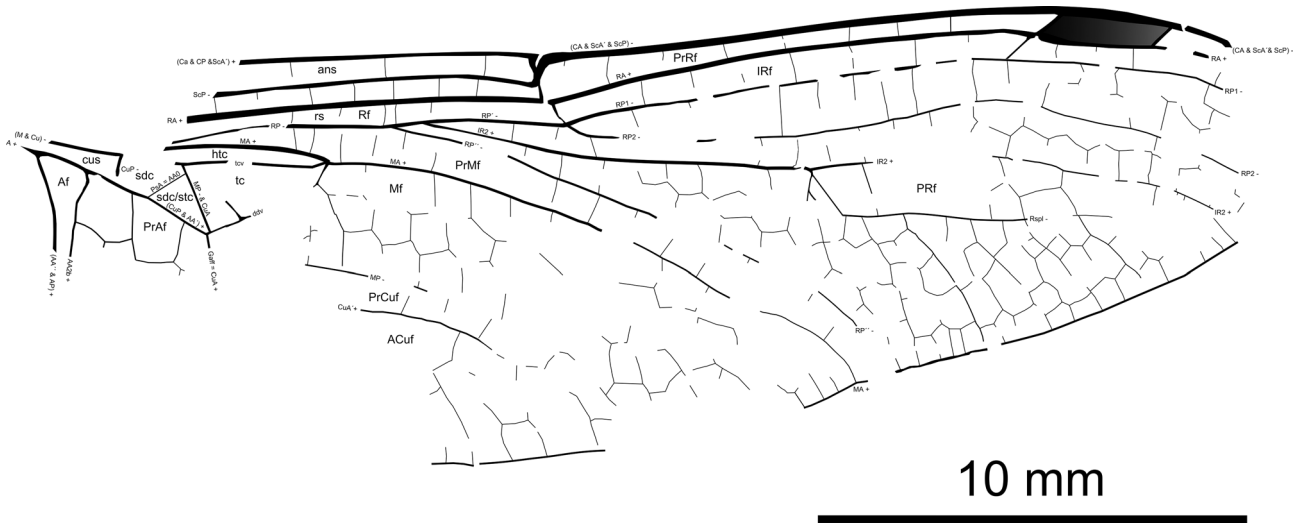

FIGURE 5. Drawing of the hind wing fragment of *Gomphaeschna carinthiae* **sp. nov.**, holotype UMJG&P 211472. The drawing involves features of both plates.

RP2 slightly undulating with least distance to RP1 at level of the pterostigmal brace vein. One row of cells between RP1 and RP2 in proximal part; two rows of cells from 13.5 mm distance to RP´-RP´´ furca to distalmost preserved part.

Premedial field with one row of cells and with parallel boundaries; posterodistal part of premedial field not distinctly broader than rest.

At least four antefurcal crossveins between RP - and MA+.

Htc at least 3.8 mm long and 0.4 mm wide at half length of tcv; MA almost parallel to tcv and only curved in its distal part.

Discoidal triangle longitudinally stretched and divided by at least one secondary crossvein; basal side 1.7 mm; costal side 3.3 mm; posterodistal side 3.2 mm; posterodistal side (ddv) almost straight with a slight kink at the origin of the distinct Tspl. Tspl meets MP almost orthogonally.

Three rows of cells in basal part of postdiscoidal space. One intercalated vein in medial field. At least one intercalated vein or secondary branch of CuA´ in antecubital field.

Preanal field with 3 cells on anterior side; anterior side width 3.1 mm. Anal field 1.2 mm wide and unicellular on anterior side, narrowing towards posterior wing margin. (AA´´ & AP) concave on proximal side and approaching AA2b posteriorly.

CuP crossing 0.7 mm long and 1.4 mm proximal to anteroproximal angle of triangulum. Anterior side of subdiscoidal cell 1.4 mm long. PsA joins proximal side of triangulum 0.2 mm posterior to anteroproximal angle of triangulum.

Subtriangular cell with posterior side 1.6 mm; anterior side (PsA) 1.0 mm ; distal side 1.5 mm. Posterior side of subtriangulum not joining posterior angle of triangulum; sdv distinct but short (> 0.1 mm).

Type locality and horizon. Claypit Schaßbach (46°47'53.32"N, 14°48'23.77"E), St. Andrä, Wolfsberg (district), Carinthia, Austria. Laminated siltstone of the lacustrine lower part of the Mühldorf Formation. Age late Early Miocene.

Etymology. The species name refers to the state of Carinthia (Kärnten) in Austria where the fossil was found.

Sex determination. The holotype is presumably the hind wing of a male specimen. The anal field is relatively narrow and unicellular in the basal part. Also (AA´´ & AP) is concave on its proximal side and approaching the straight AA2b posteriorly. This could indicate an anal angle characteristic for male anisopterans that is not preserved in this fossil.

Phylogenetic affinities. The specimen can be clearly attributed to the suborder Anisoptera Selys, 1854, by the strong expansion of the cubito-anal field and the presence of a discoidal triangle as well as a hypertriangle and a subtriangle (Bechly 2007).

Aeshnoptera Bechly, 1996: space between RP1 and RP2 narrowed with only one row of cells to pterostigma; Rspl present (Bechly 2003).

Aeshnomorpha Bechly, 2001: RP2 slightly undulating (Bechly 2003).

Euaeshnida Bechly, 1996: RP2 and IR2 distinctly non-parallel (Bechly 2003).

Gomphaeschnidae Tillyard & Fraser, 1940: 'cordulegastrid gap' (distalmost part of the antesubnodal area without crossveins); no accessory crossveins between CuP-crossing and PsA in subdiscoidal cell; triangulum divided by one crossvein; hypertriangle unicellular (Bechly *et al.* 2001; Bechly 2003).

Gomphaeschna Selys, 1871: IR2 and Rspl more or less parallel; RP2 undulating; hind wing triangle with basal side longer than 1/2 costal side; cubito-anal space with 1 crossvein (CuP-crossing); Rspl with no distinct connection to wing margin (Garrison *et al.* 2006).

No elongated paranal cell basal to anal loop in hind wing as in Gomphaeschnaoidini Bechly, 2001 (Bechly *et al.* 2001).

Discussion

Biogeographical significance. There is no record of extant Lindeniinae species in Europe but for fossil specimens (Pictet & Hagen 1856; Hagen 1859; Hagen 1863; Nel & Paicheler 1994; Prokop *et al.* 2016; this study). Modern representatives of the genera *Ictinogomphus*, *Gomphidia* and *Sinictinogophus* occur in warmer temperate regions of Africa, Asia & Australia (Steinmann 1997). This specimen testifies that till the middle Miocene dragonflies of the subfamily Lindeniinae were present in Europe. Subsequently the niches of the Lindeniinae were presumably replaced by other taxa at a later time.

The recent distribution of *Gomphaeschna* covers the east coast of the US and Canada (Garrison *et al.* 2006; Steinmann 1997). Modern *Oligoaeschna* and *Linaeschna* species can be found in Southeast Asia (Steinmann 1997), while *Sarasaeschna* is indigenous to Southeast Asia and East Asia (Yeh *et al.* 2015).

Prokop & Nel, (2002) assumed a wide Holarctic distribution of Gomphaeschninae during the Paleogene and Neogene, in contrast to the Recent North American and Southeast Asian distribution of this group. The absence of Gomphaeschninae in Europe despite climatic conditions similar to those in eastern US and Canada could be explained by the impact of the massive glaciation events during the Quaternary and the lack of suitable areas of refuge.

Paleoecological significance. The occurrence of modern relatives of *Ictinogomphus hassleri* in warmer regions raises the question of whether the presence of Lindeniinae in the fossil record of Europe during the Oligocene and Miocene is correlated with higher temperatures in those time periods. It is possible that the Lindeniinae were less able than other anisopteran groups to tolerate low temperatures and frost.

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