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New fossil Odonata from the Upper Jurassic of Bavaria with a new fossil calibration point for Zygoptera

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Abstract

Three new taxa of odonates are described from the Upper Jurassic Solnhofen limestone from Eichstätt and Painten in Bavaria (Germany), including the first two genuine Zygoptera (*Andrephlebia buergeri* **gen. et sp. nov.** in fam. inc. sed. and *Jurahemiphlebia haeckeli* **gen. et sp. nov.** in Hemiphlebiidae) and a new taxon of Stenophlebioptera (*Reschiostenophlebia koschnyi* **gen. et sp. nov.** in Stenophlebiidae). With an age of about 152 million years, the holotype of *Jurahemiphlebia* from the Painten locality represents the oldest fossil record and thus a new calibration point for crown group Zygoptera, Lestoidea, and Hemiphlebiidae, and the oldest record for any living odonate family. Furthermore, the first relatively complete specimen of the dragonfly *Prohemeroscopus kuehnapfeli* (Prohemeroscopidae) is described, which was previously known only from a pair of isolated hind wings. A revised diagnosis is provided for the species and genus.

Keywords: Zygoptera, Anisoptera, Hemiphlebiidae, Stenophlebiidae, Prohemeroscopidae, Solnhofen, Painten

Introduction

The famous Upper Jurassic Solnhofen limestones of Bavaria has yielded one of the most diverse palaeofaunas of fossil odonates, with 48 valid species in 21 families and 7 suborders (Bechly, 2015a, b). The first fossil dragonfly from this locality was described by Schmidel (1780), and the most recent descriptions were added by Nel & Martínez-Delclòs (1993), Nel *et al*. (1993, 1996, 1998, 2001), Bechly (1998b, c, 2000, 2001, 2003, 2005, 2015a), Bechly *et al*. (1998, 2001), Fleck & Nel (2003), and Fleck *et al*. (2001, 2003, 2004). I here describe three new odonate taxa from this locality and the first complete specimen of the dragonfly *Prohemeroscopus kuehnapfeli* (Prohemeroscopidae).

Material and methods

Observations and drawings were made using a Leica M80 (1.6 Plan Achromat lens) stereo microscope with camera lucida system. Macro photos were made with a Sony SLT A65 and Sigma 105mm/f2.8 macro lens with JJC LED macro ring light, except for Fig. 1C, which was photographed 1995 on colour negative film with a Canon T70 and Tokina 90mm/f2.5 macro lens, and Fig. 10A which was made with a CanoScan 4200F flatbed scanner. Micrographs were taken with a Leica DFC490 digital macro camera on a Leica Z16-Apo Macroscope, using Leica Application Suite 3.8.0 for focus stacking. All photos were polished with Adobe Photoshop CC 2018 imaging software on a MacBook Pro, but no parts of the fossil image were manipulated except for overall hue, brightness, and contrast. Figures 3A–B, 4A, 4C, 5A, 5C, and 7A were photographed with the fossil damselfly covered with ethanol alcohol for contrast enhancement.

The classification of odonates is based on Bechly (1996, 2007b) and Dijkstra *et al*. (2013). The terminology of odonate wing venation is based on Riek & Kukalová-Peck (1984), modified by Nel *et al*. (1993) and Bechly (1996). The abbreviations used are: AA = Anal vein, ax = primary antenodal crossvein, C = Costal vein, CuA = Cubitus anterior vein, IR = Interradius intercalary vein, MA = Media anterior vein, MP = Media posterior vein, O = lestine oblique vein, RA = Radius anterior vein, RP = Radius posterior vein, ScP = Subcostal vein.

Systematic palaeontology

Order Odonata Fabricius, 1793
Suborder Zygoptera Selys, 1854
Family incertae sedis
Genus *Andrephlebia* gen. nov.

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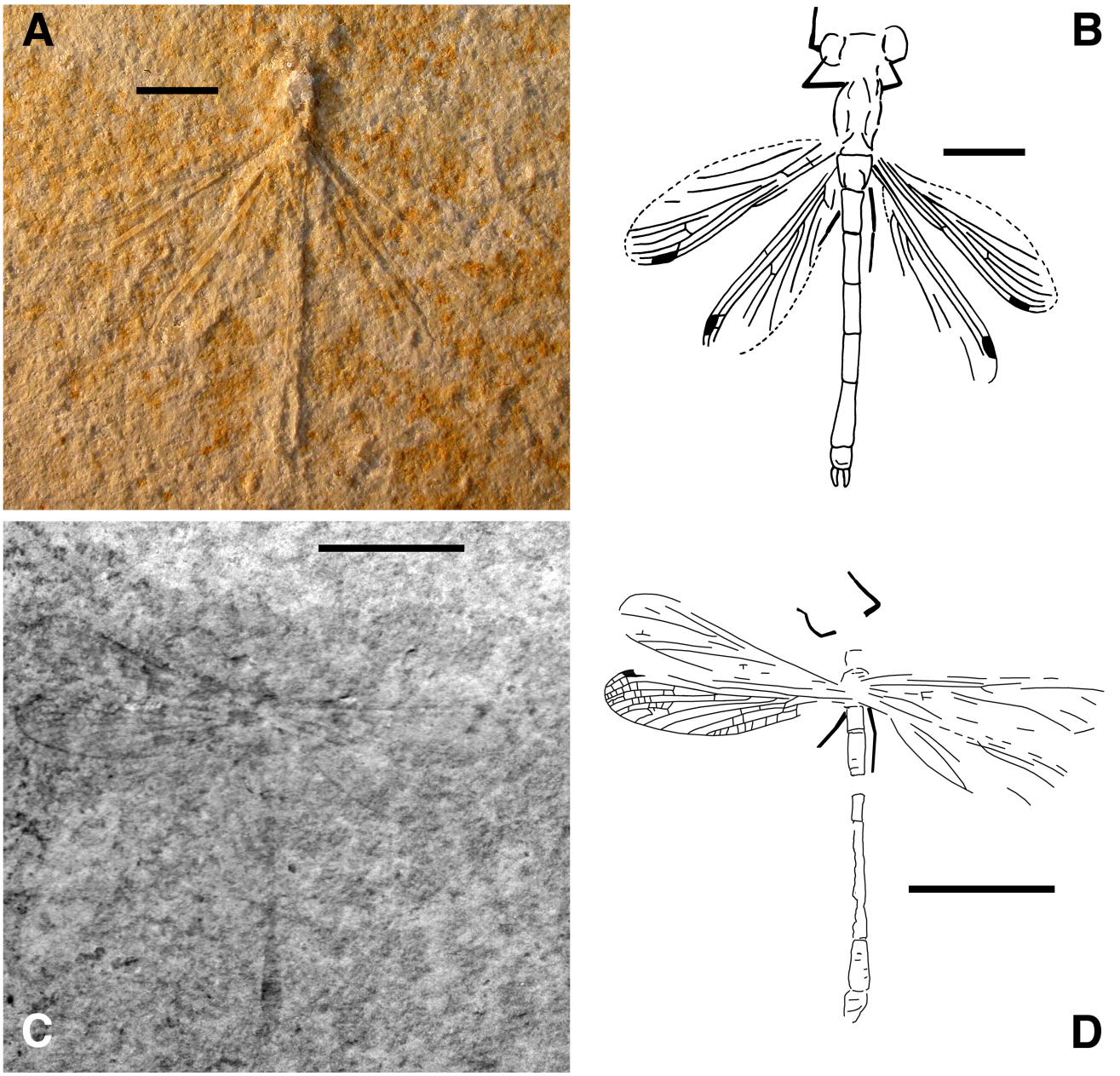

FIGURE 1. *Andrephlebia buergeri* **gen. et sp. nov. A**, Holotype, SMNS 67700, photograph (scale bar = 5 mm). **B**, Holotype, SMNS 67700, drawing (scale bar = 5 mm). **C**, Paratype JME 1938-2K, photograph (scale bar = 10 mm). **D**, Paratype JME 1938-2K, drawing (scale bar = 10 mm).

Type species. *Andrephlebia buergeri* **sp. nov.**

Etymology. Named in honour of Prof. Dr. André Nel (MNHN, Paris) for his outstanding contributions to palaeoentomology and after the Greek word φλέψ (phléps = vein).

Diagnosis. See type species since monotypic.

***Andrephlebia buergeri* sp. nov.**

(Figs 1–2)

Material. Holotype, a completely preserved damselfly SMNS 67700 at the state Museum of Natural History in Stuttgart (Germany) (SMNS) (Fig. 1A, B), acquired as donation from collection Peter Bürger. The counter plate initially remained in this private collection which, after the death of Mr. Bürger in 2013, was acquired by Bruce Lauer for the *Lauer Foundation for Paleontology, Science and Education* (https://www.lauerfoundationpse.org) and will be deposited in the Field Museum in Chicago.

Paratype: Almost complete specimen JME 1938-2K at the Jura-Museum in Eichstätt, Germany (Fig. 1C, D).

Further material: A complete specimen in the private collection Daniel Fauser (Fig. 2) might belong to this new taxon as well.

Etymology. Named after the late Mr. Peter Bürger (Bad Hersfeld, Germany), who generously donated the

holotype to SMNS. The dedicated fossil collector Peter Bürger died very unexpectedly on 12 March 2013 in young age of only 52 years.

Diagnosis. Wing length about 15–16 mm; pterostigma braced and elongate, covering 1.5 cells; RP1 not kinked at stigmal brace; IR1 long; midfork (origin of IR2 and RP3+4) halfway between RP2 and arculus; wing space between RP1 and RP2 narrow, but widened between IR2 and RP3+4 and between MA and MP respectively; discoidal cell open in hind wing but basally closed in forewing (this would be a unique autapomorphy within Odonata, but is still somewhat uncertain due to poor preservation, and in recent *Hemiphlebia* an open hind wing discoidal cell can occur as rare aberration according to Cordero-Rivera, 2017); wings only weakly stalked.

Locality and horizon. Eichstätt, southern Franconian Jura, Bavaria, Germany; Solnhofen Limestone, Malm zeta 2b, *Hybonotum*-Zone, Upper Jurassic, Lower Tithonian, ca. 150 million years.

Description. Holotype (Fig. 1A, B): A complete damselfly with body and all four wings preserved as imprint. The strong abdominal forceps suggest that it is a male specimen. Body 27 mm long with a relatively large head; legs incompletely preserved but apparently rather short; wing length about 15 mm; nodus at 42% of wing length; pterostigma elongate, covering 1.5 cells, and with distinct stigmal brace; RP1 not kinked at stigmal brace; IR1 long, originating half way between pterostigma and origin of RP2; field between RP1 and RP2 relatively narrow; midfork recessed; IR2 and RP3+4 divergent with widened field between them; MA and MP distally diverging, thus post-discoidal field distally widened; distal discoidal vein oblique but short and not aligned with MA (distal angle of discoidal not very acute); discoidal cell elongate and basally closed in forewing, but apparently open in hind wing; arculus aligned with ax2; wing hardly petiolate. Apart from these characters and some faint traces of the main longitudinal veins, the wing venation is hardly preserved.

Paratype (Fig. 1C, D): Specimen JME 1938-2K at the Jura-Museum in Eichstätt, which was labelled in March 1995 with the unpublished manuscript name "*Litholestes*" (unavailable because already used for a genus of Acari) during a joint visit to the Jura-Museum by André Nel, Xavier Martínez-Delclòs and me. It has a body length of 24 mm (without the missing head), four preserved short legs, and a wing length of about 16 mm (all four wings are spread). Only the venation of the left hind wing is sufficiently preserved to provide some data: nodus in midwing position; pterostigma elongate, probably covering more than one cell; IR1 originates far basal of pterostigma; RP2 apparently aligned with subnodus; field between RP1 and RP2 relatively narrow; midfork recessed; IR2 and RP3+4 strongly divergent with a widened field between them (at least 2–4 cells wide); MA and MP distally diverging, thus post-discoidal field distally widened; discoidal cell basally open; subdiscoidal cell free; a single row of cells in cubito-anal area; hardly stalked with a very short petiole (2.2 mm long in right hind wing).

Another possible specimen of this new taxon was discovered about 1995 by Mr. Daniel Fauser in the Blumenberg quarry (Eichstätt). It is an almost completely preserved damselfly with a body length of 27.6 mm (apex of abdomen missing); head small (3.1 mm wide); pterothorax strongly skewed; legs not visible; wings obliquely spread but overlapping on both sides; wings hardly stalked, slender, and 16.7 mm long (Fig. 2). Unfortunately, the poorly preserved and superimposed wings make an interpretation of the wing venation very difficult. The visible pattern in the right pair of wings could even suggest a new species of Protomyrmeleontidae because of an apparent strange forking pattern of RP, but this could rather be an artefact of preservation of the superimposed wings. This specimen is here only very tentatively attributed to the new genus *Andrephlebia*, based on the shape and dimension of wings.

Remarks. The visible characters suggest that this fossil is a zygopteran, but an attribution to basal "anisozygopteres" cannot be totally excluded. Unfortunately, the poor preservation does not allow a safe attribution to a family, or even the description of a new family group taxon.

Family Hemiphlebiidae Tillyard, 1926
Genus *Jurahemiphlebia* gen. nov.

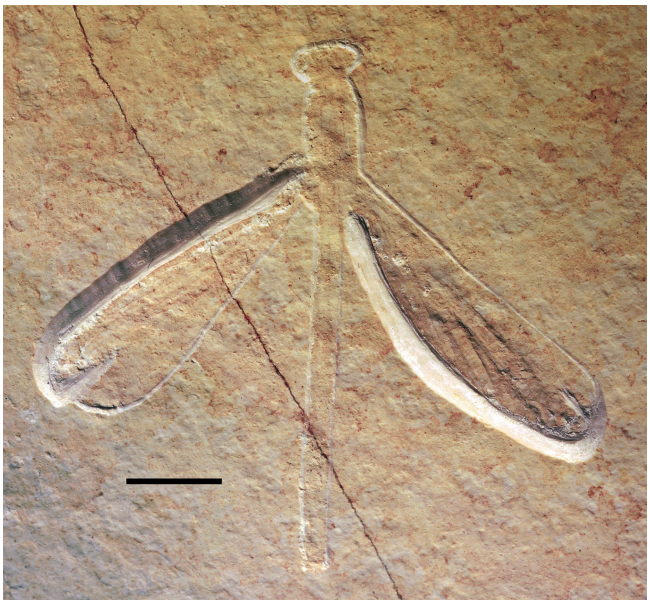

FIGURE 2. cf. *Andrephlebia buergeri* ? **gen. et sp. nov.**, coll. Fauser, photograph (scale bar = 5 mm).

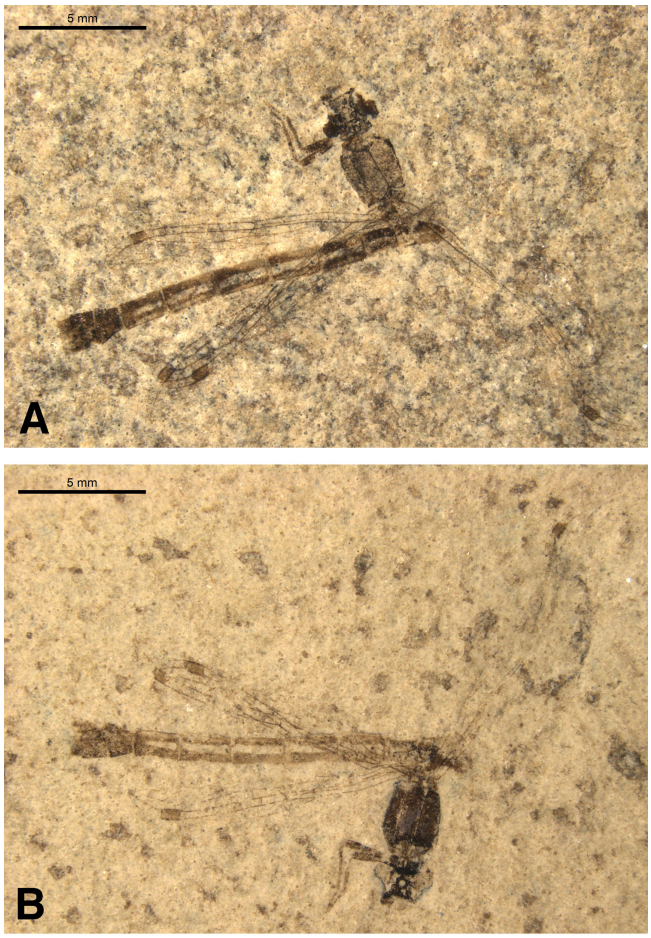

FIGURE 3. *Jurahemiphlebia haeckeli* **gen. et sp. nov.**. **A**, Holotype, SMNS 70154, photograph (scale bar = 5 mm). **B**, Counter plate of holotype, coll. Albersdörfer, photograph (scale bar = 5 mm).

Type species. *Jurahemiphlebia haeckeli* **sp. nov.**

Etymology. Named after the Jurassic age and the modern genus *Hemiphlebia*.

Diagnosis. See type species since monotypic.

Remarks. The new genus is distinguished from the recent genus *Hemiphlebia* Selys, 1868 by the shorter distance between ax1 and ax2, lower number of only 4 postnodals, more distinct stigmal brace, shorter IR1, only 2 cells between RP1 and RP2 basal of IR1 (instead 3), much larger cell between the bases of IR2 and RP3+4, distally divergent RP2 and IR2, and the very different shape of broader forewing discoidal cell.

It is distinguished from all other Mesozoic Hemiphlebiidae by the following diagnostic characters: From *Burmahemiphlebia* Zheng *et al*., 2016b by veins MP and CuA not shortened; from *Cretarchistigma* Jarzembowski *et al*., 1998 by the lower number of postnodals, shorter IR1, and the arculus not aligned with ax2 (also see Bechly 1998a, 2007a); from *Cretacoenagrion* Jarzembowski, 1990 by the shorter pterostigma, shorter IR1, lower number of 4 non-aligned postnodals (instead of 9 aligned ones), very different shape of the discoidal cell (less acute); from *Cretahemiphlebia* Jarzembowski *et al*., 1998 by the lower number of postnodals, shorter IR1, and distally divergent RP2 and IR2; from *Electrohemiphlebia* Lak *et al*., 2009 by the very different shape of the forewing

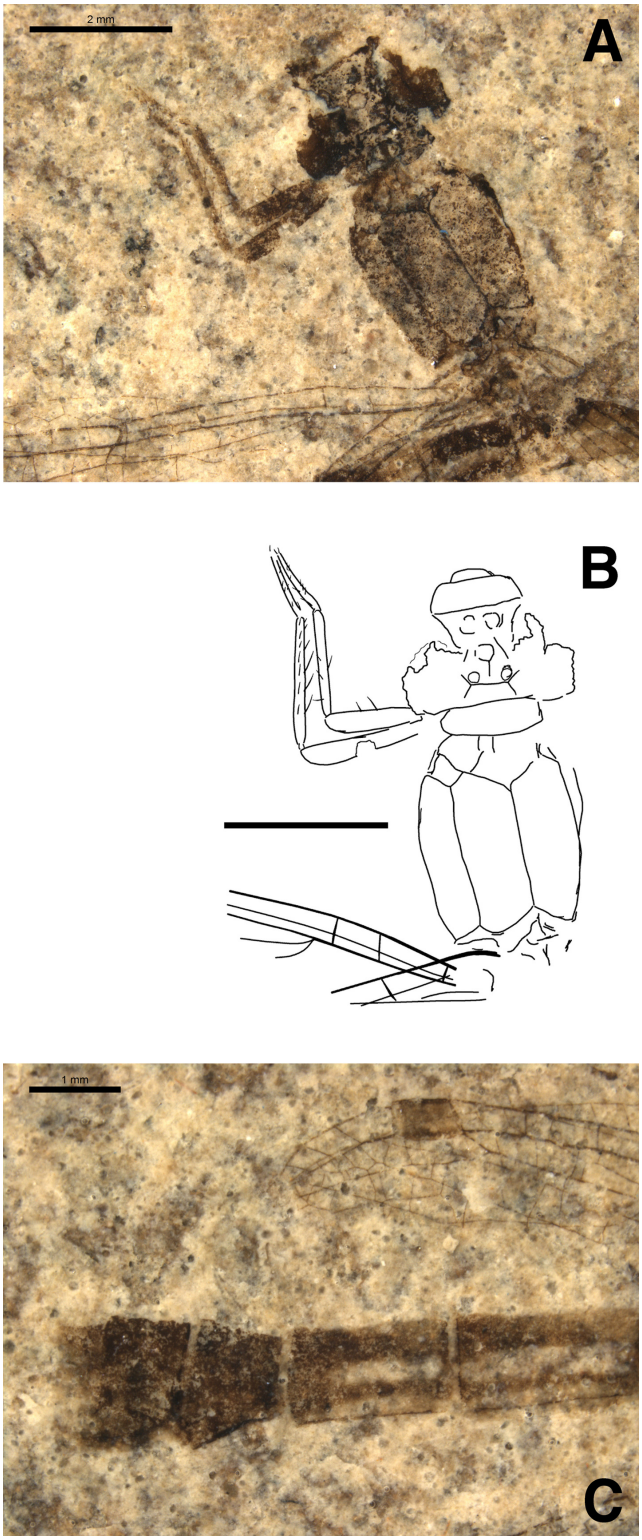

FIGURE 4. *Jurahemiphlebia haeckeli* **gen. et sp. nov.**, holotype, SMNS 70154. **A**, Photograph of head and thorax (scale bar = 2 mm). **B**, Drawing of head and thorax (scale bar = 2 mm). **C**, Photograph of ovipositor (scale bar = 1 mm).

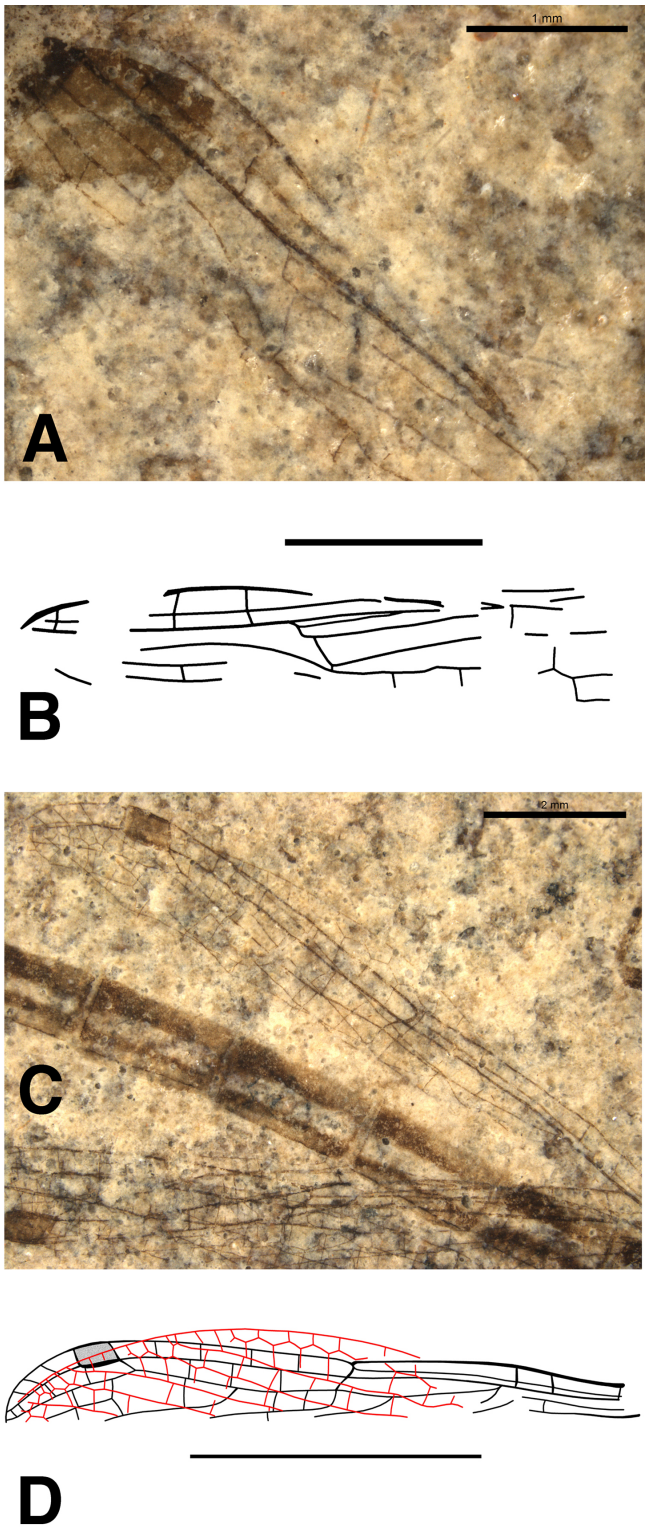

FIGURE 5. *Jurahemiphlebia haeckeli* **gen. et sp. nov.**, holotype, SMNS 70154. **A**, Photograph of right forewing base with discoidal cell (scale bar = 1 mm). **B**, Drawing of right forewing base with discoidal cell (scale bar = 2 mm). **C**, Photograph of left hind wing (scale bar = 2 mm). **D**, Drawing of left hind wing (scale bar = 5 mm).

discoidal and subdiscoidal cells; from *Enteropia* Pritykina & Vassilenko, 2014 by the lower number of postnodals (4 instead 6), and 2 (instead 3) cells between RP1 and RP2 basal of IR1; from *Jordanhemiphebia* Kaddumi, 2009 by only 2 (instead 4) cells between RP1 and RP2 basal of IR1; from *Mersituria* Vasilenko, 2005 by the lower number of postnodals (4 instead of 8), the much shorter IR1, and the very different shape of the discoidal cell; from *Pantelusa* Vassilenko, 2014 by vein MP straight (not upward slanted) at discoidal cell; from *Parahemiphlebia* Jarzembowski *et al*., 1998 (also see Bechly, 1998a, 2007a) by the absence of a mesothoracic interpleural suture, only 2 cells between RP1 and RP2 basal of IR1, bigger distance between arculus and ax2, distinct kink in arculus before the origin of the discoidal vein MAb, and very short vein MAb; and from *Thairia* Felker & Vasilenko, 2018 by a shorter IR1 and straight MP at discoidal cell. Finally, the new genus differs from an unnamed possible hemiphlebiid from the Late Cretaceous Hell Creek Formation of South Dakota (Nel *et al*., 2010) by the shorter IR1, and the distally divergent RP2 and IR2.

***Jurahemiphlebia haeckeli* sp. nov.**

(Figs 3–7)

Material. Holotype, a completely preserved specimen SMNS 70154 (Figs 3A and 4, 5) (counter plate in collection Raimund Albersdörfer; Fig. 3B).

Paratype, a completely preserved specimen SMNS 67699 (acquired 2004 from collection Stefan Schäfer) (Fig. 7A, B).

Further material: Plate and counter plate of a similar but very poorly preserved fossil damselfly (wing length 9 mm) from Eichstätt is in private collection Helmut Pochmann (Fig. 7C).

Etymology. Named after Dipl.-Geol. Wolfgang Häckel (Bayreuth), who has lead the fossil excavations in Painten since 2001.

Diagnosis. Wing length about 11 mm; only two antenodal crossveins ax1 and ax2; only four postnodal crossveins; postnodal- and postsubnodal crossveins not aligned; arculus distinctly distal of ax2; discoidal cell basally open in forewings, with distal discoidal vein MAb very short and originating at arculus distinctly distal of the RP-bent (unique shape of open discoidal cell); pterostigma short (only covering a single cell) and with stigmal brace vein; RP1 with kink at stigmal brace vein; only 2 cells between RP1 and RP2 basal of IR1; RP2 and IR2 distally divergent; IR2 originating at subnodus; MP straight at discoidal cell (not slanted upwards); thoracic interpleural suture reduced.

Locality and horizon. Painten limestone quarry, district Kehlheim, southern Franconian Jura, Bavaria, Germany; laminated limestones of the "Bunte Serie" in the lower part of the "Kieselkalkabfolge", Painten 1, Malm zeta 1, *Beckeri*-Zone, *Ulmense*-Subzone, *rebouletianum*-Horizon, Upper Jurassic, uppermost Kimmeridgian

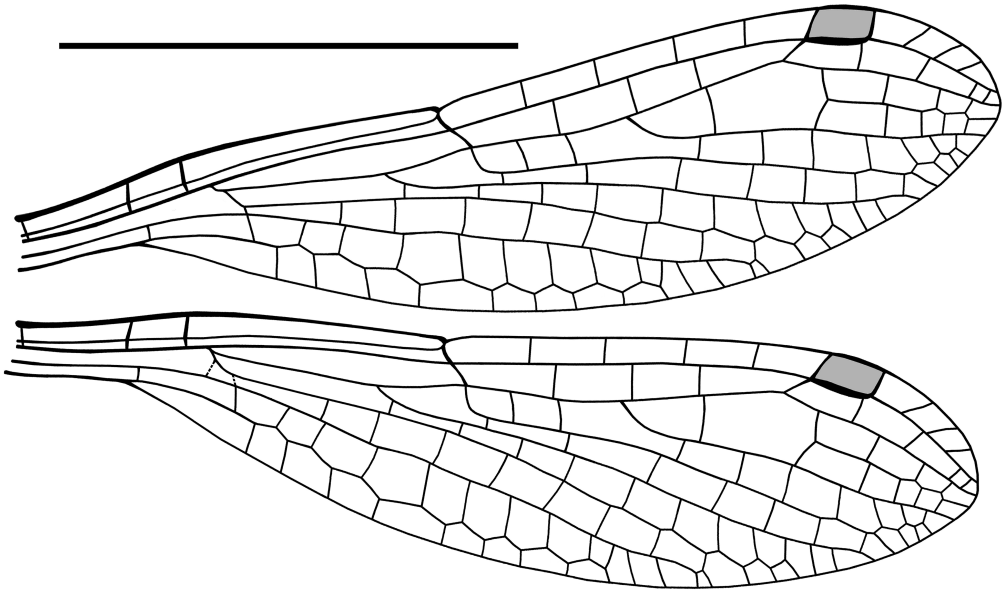

FIGURE 6. *Jurahemiphlebia haeckeli* **gen. et sp. nov.**, holotype, SMNS 70154, reconstruction of wing venation (scale bar = 5 mm).

(Schweigert, 2007), ca. 152 million years (according to International Chronostratigraphic Chart v2019/05).

Description. Holotype (Figs 3–5): A perfectly preserved and complete fossil damselfly with very well visible wing venation. The left hind wing is half folded down, but allows for a graphic reconstruction of almost the complete wing (Fig. 6). Important details of the discoidal cell are visible in the right forewing. Very small size (body length 21.6 mm, wing span about 22 mm). Head 1.5 mm long and maximally 2.3 mm wide; compound eyes distinctly separated; three ocelli present. Thorax 3.2 mm long and maximally 2.1 mm wide; pterothorax apparently of uniform coloration; mesothorax without interpleural suture; legs rather short (tibia 1.7 mm) with medium-sized spurs. Abdomen 16.6 mm long, with faintly preserved colour pattern (broad medio-dorsal and more narrow ventro-lateral, longitudinal stripes); abdominal segments VIII and IX with strong ovipositor (thus it is a female specimen) (Fig. 4C). Hind wing length 10.6 mm; nodus at 44% of wing length; arculus 0.2 mm distal of second antenodal crossvein ax2; discoidal cell basally open in forewing (not visible in hind wing, but the different shape of MA suggests that it is closed and coenagrionid-like); very short distal discoidal vein MAb originates distinctly distal of RP-bent at arculus in forewing; four postnodal crossveins; postnodal- and postsubnodal crossveins not aligned; pterostigma short (0.7 mm), covering only a single cell; distinct and oblique stigmal brace vein; RP1 with strong kink at stigmal brace; just a single crossvein between RP1 and RP2 basal of stigmal brace, and only two cells basal of IR1; IR1 originates on level of first third of pterostigma; IR2 originates directly at subnodus; no lestine oblique vein 'O'; CuA zigzagged; only a single row of cells between all longitudinal veins; no intercalary veins apart from IR1 and IR2.

Paratype (Fig. 7A, B): A very small fossil damselfly from Eichstätt, which is relatively completely preserved and has the wing venation partly traced by iron oxide. The posterior parts of the wing membranes is folded down, which somewhat impedes the interpretation of the wing venation. Body length 18 mm; legs short; forewing 11.7 mm and hind wing 10.9 mm long; only two (primary) antenodal crossveins ax1 and ax2; nodus at 43% of wing length; 4–5 postnodal- and postsubnodal crossveins not aligned; pterostigma very short (0.5–0.6 mm), only covering a single cell; a distinct and oblique stigmal brace vein; RP1 with kink at stigmal brace; wing with only few crossveins and cells.

Remarks. The holotype was discovered during the fossil excavations in Painten in early November 2011 by excavation director Mr. Wolfgang Häckel. It was the first finding of a fossil insect from this locality after 11 years ([initial?] Albersdörfer, pers. comm. 6 Nov. 2011) and represents the first fossil odonate from this locality. The preservation is remarkable and ranks among the best of any fossil odonates from the Upper Jurassic of Germany. An attribution to the family Hemiphlebiidae is very well-supported based on the tiny size, reduced interpleural suture, basally open discoidal cell in forewing, position of the arculus distal of second antenodal crossvein ax2, non-aligned postnodal- and postsubnodal crossveins, short pterostigma, and kink of RP1 at the stigmal brace

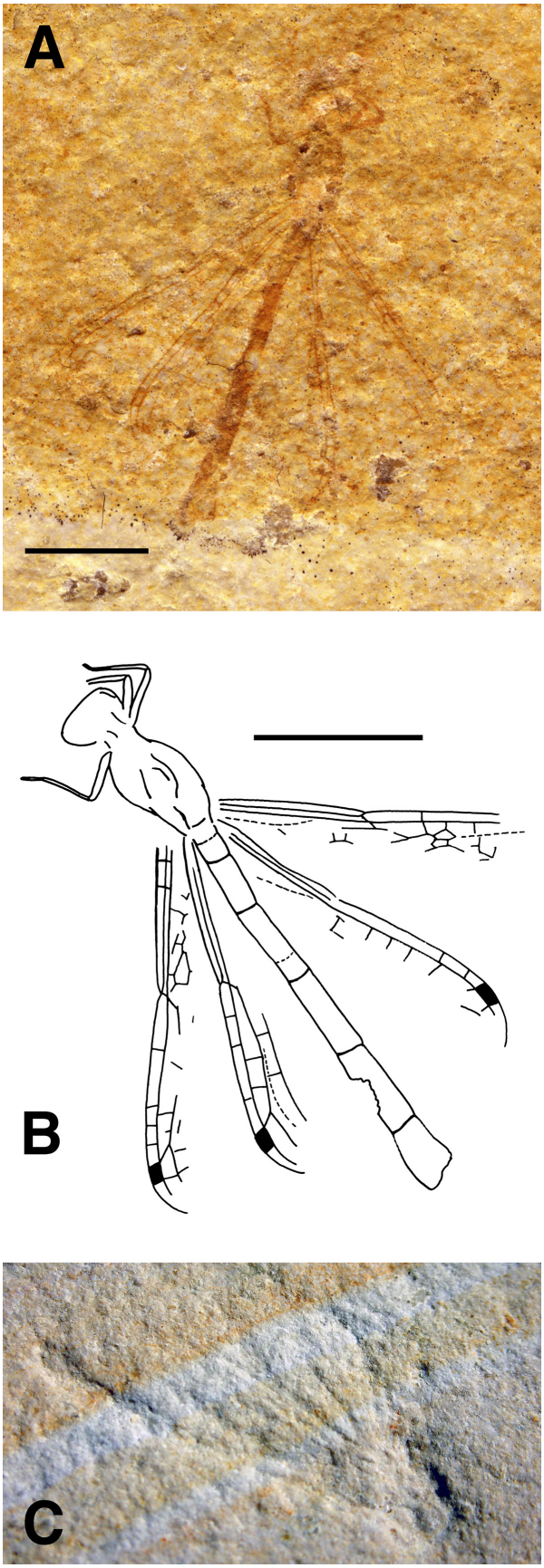

FIGURE 7. *Jurahemiphlebia haeckeli* **gen. et sp. nov. A**, Paratype, SMNS 67699, photograph (scale bar = 5 mm). **B**, Paratype, SMNS 67699, drawing (scale bar = 5 mm). **C**, Specimen in coll. Pochmann, photograph (wing length 9 mm).

vein as well as the general pattern of the wing venation with only few cells.

With this new genus the large diversity and worldwide distribution of Hemiphlebiidae in the Mesozoic era is further supported, as well as the status of the single recent species *Hemiphlebia mirabilis* as a relict of high conservational importance.

Suborder Stenophlebioptera Bechly, 1996
Family Stenophlebiidae Needham, 1903
Genus *Reschiostenophlebia* gen. nov.

Type species. *Reschiostenophlebia koschnyi* **sp. nov.**

Etymology. Named after the genus *Stenophlebia* and after Mr. Udo Resch (Eichstätt), who generously donated the holotype specimen to the State Museum of Natural History in Stuttgart.

Diagnosis. Typical stenophlebiid wing venation, but distinct from other genera by the following characters: wing length 44 mm; both wings with quadrilateral, free and not very transverse discoidal triangles; subdiscoidal cells not transverse and only divided by a single crossvein in hind wing; pterostigma very long and shifted basally; very oblique nodus and subnodus only covering a single cell; secondary basal prolongation of RP2 ('stenophlebiid oblique vein' between RP1 and RP2); two rows of cells in post-trigonal field; CuAa not shortened; arculus somewhat basal of ax2; no secondary antenodal crossveins between ax1 and ax2 and basal of ax1; no "heterophlebioid" anal loop; hind wing short petiolate.

Locality and horizon. Eichstätt, southern Franconian Jura, Bavaria, Germany; Solnhofen Limestone, Malm zeta 2b, *Hybonotum*-Zone, Upper Jurassic, Lower Tithonian, ca. 150 million years.

Remarks. *Reschiostenophlebia* **gen. nov.** shares with Stenophlebioptera (Liassostenophlebiidae and Stenophlebioidea) the following synapomorphies (Fleck *et al.*, 2003): nodus and subnodus very oblique; CuAa with broad area between two most distal posterior branches (absent in *Prostenophlebia*); presence of straight supplementary longitudinal veins in areas between IR2 and MP (dubious in *Liassostenophlebia*); and pterostigma not braced.

Unlike *Liassostenophlebia* Fleck *et al*., 2003 (Liassostenophlebiidae), *Reschiostenophlebia* **gen. nov.** shares with Stenophlebioidea (Prostenophlebiidae and Stenophlebiidae) the presence of a long convex intercalary parallel to MP, a long concave Mspl, the reduced lestine oblique vein 'O', and elongate slender wings.

Unlike *Prostenophlebia* Nel & Martínez-Delclòs, 1993 (Prostenophlebiidae), *Reschiostenophlebia* **gen. nov.** shares most of the characters of the revised diagnosis of Stenophlebiidae by Fleck *et al*. (2003), such

as: a long and straight convex intercalary vein in post-discoidal area, parallel to MP, originating at (or near) discoidal triangle; Cr long or very long, covering more than one or two cells between RA and RP; pterostigma shifted basally (not present in *Cretastenophlebia* and *Burmastenophlebia*); pterostigma very long (not present in *Burmastenophlebia*); all wings elongate and falcate; and numerous well-defined straight intercalary secondary longitudinal veins reaching posterior wing margin. It also shares with all Stenophlebiidae a very oblique subnodus. It shares with all Stenophlebiidae (except *Cretastenophlebia*, *Cratostenophlebia*, and *Burmastenophlebia*) the presence of a secondary basal prolongation of RP2 ('stenophlebiid oblique vein' between RP1 and RP2). These characters show that, within Stenophlebioptera, the new genus clearly belongs in Stenophlebiidae and not in Liassostenophlebiidae or Prostenophlebiidae.

However, *Reschiostenophlebia* **gen. nov.** differs from other Stenophlebiidae by the free and quadrilateral triangles in all wings, the forewing discoidal triangle being not long transverse, and the hind wing subdiscoidal space being not transverse (similar to *Hispanostenophlebia* and *Cratostenophlebia*) and not divided by two or more crossveins.

It can be distinguished from the other genera of Stenophlebiidae by the following characters: From *Burmastenophlebia* Huang *et al*., 2019 by the much larger size, denser venation, longer pterostigma, and secondarily prolonged RP2; from *Cratostenophlebia* Bechly, 2007a by the much smaller size, free triangles and hypertriangles, hind wing subdiscoidal cell only divided by a single crossvein, only two rows of cells in post-trigonal field, secondary vein parallel to MP is straight (not zigzagged), and secondarily prolonged RP2 (Bechly, 2010); from *Cretastenophlebia* Fleck *et al.*, 2003 by the free triangles, not transverse and less divided subdiscoidal cell in hind wing, secondarily prolonged RP2, and basally shifted pterostigma (Zheng *et al.*, 2017); from *Gallostenophlebia* Nel *et al*., 2015 by the larger size, free triangle and hypertriangle, only two rows of cells in post-trigonal field, and more prolonged RP2; from *Hispanostenophlebia* Fleck *et al*., 2003 by the free triangle and hypertriangle, only two rows of cells in post-trigonal field, arculus not aligned with ax2; from *Liaostenophlebia* Zheng *et al*., 2016a by the free triangle (also much less transverse) and hypertriangle, not transverse and less divided subdiscoidal cell in hind wing, only two rows of cells in post-trigonal field; from *Mesostenophlebia* Fleck *et al*., 2003 by vein CuAa not shortened; from *Stenophlebia* Hagen, 1866 in both wings by the quadrilateral, free and less transverse discoidal triangles, less divided and less transverse (not foot-shaped) subdiscoidal cells, CuAa less shortened, no "heterophlebioid" anal loop but only a single row of cells beneath subdiscoidal cell (Fleck *et al*., 2003); and from *Yixianstenophlebia* Nel & Huang, 2015 by the much smaller size, free and less transverse triangle, much less transverse and less divided subdiscoidal cell in hind wing, only two rows of cells in post-trigonal field. *Sinostenophlebia* Hong, 1984 was considered by Fleck *et al*. (2003) as an odonate of uncertain position, but a revision by Zheng *et al*. (2016) revealed it as an Aeschnidiidae. "*Stenophlebia*" *casta* (Hagen, 1862) was transferred by Bechly (2005) to a new genus *Parastenophlebia* (Parastenophlebiidae) in the unrelated Heterophlebioidea.

Consequently, the erection of a new genus of Stenophlebiidae is well justified. A relatively basal position could be suggested by the plesiomorphic quadrilateral and free discoidal triangles in all wings (similar to *Prostenophlebia* and *Mesostenophlebia*).

***Reschiostenophlebia koschnyi* sp. nov.**

(Figs 8–9C)

Material. Holotype, a very well and completely preserved specimen SMNS 70155 (acquired from collection Udo Resch) (Fig. 8A, B).

Paratype: A completely preserved specimen SMNS 67698 (counter plate remained in collection Günther Koschny) (Fig. 9A, B).

Further material: A complete specimen in the private collection Stefan Schäfer (Fig. 9C). Another stenophlebiid-like specimen of similar size is in private collection Dieter Kümpel (Fig. 9D) but rather belongs to a new large species of *Prostenophlebia*.

Etymology. Named after Mr. Günther Koschny (Bad Soden), who generously donated the paratype specimen to the State Museum of Natural History in Stuttgart (Germany).

Diagnosis. See genus since monotypic. Forewing length only 44–45 mm, contrary to all other Stenophlebiidae from the Upper Jurassic of Germany, *i.e*., *Stenophlebia latreillei* and *S. aequalis* (50–62 mm), *S. phryne* (55 mm), *S. lithographica* (55 mm), *S. eichstaettensis* (69 mm), *S. amphitrite* (82–84 mm), *S. rolfhuggeri* (76–80 mm).

Locality and horizon. Eichstätt, southern Franconian Jura, Bavaria, Germany; Solnhofen Limestone, Malm zeta 2b, *Hybonotum*-Zone, Lower Tithonian, Upper Jurassic, ca. 150 million years.

Description. Holotype (Fig. 8A, B): A completely preserved damsel-dragonfly with obliquely spread wings (the right pair of wings is overlapping). Body length 63 mm; head globular but with widely separated compound eyes; pterothorax obviously strongly skewed; legs short (only 2 prothoracic legs preserved); abdomen slender without clubbed apex. Forewing 44.7 mm and hind wing 43.5 mm long; wing shape (slender and falcate) and wing venation more or less identical in forewings and hind wings (the hind wings only have a slightly broader cubital area, a more transverse triangle, and a

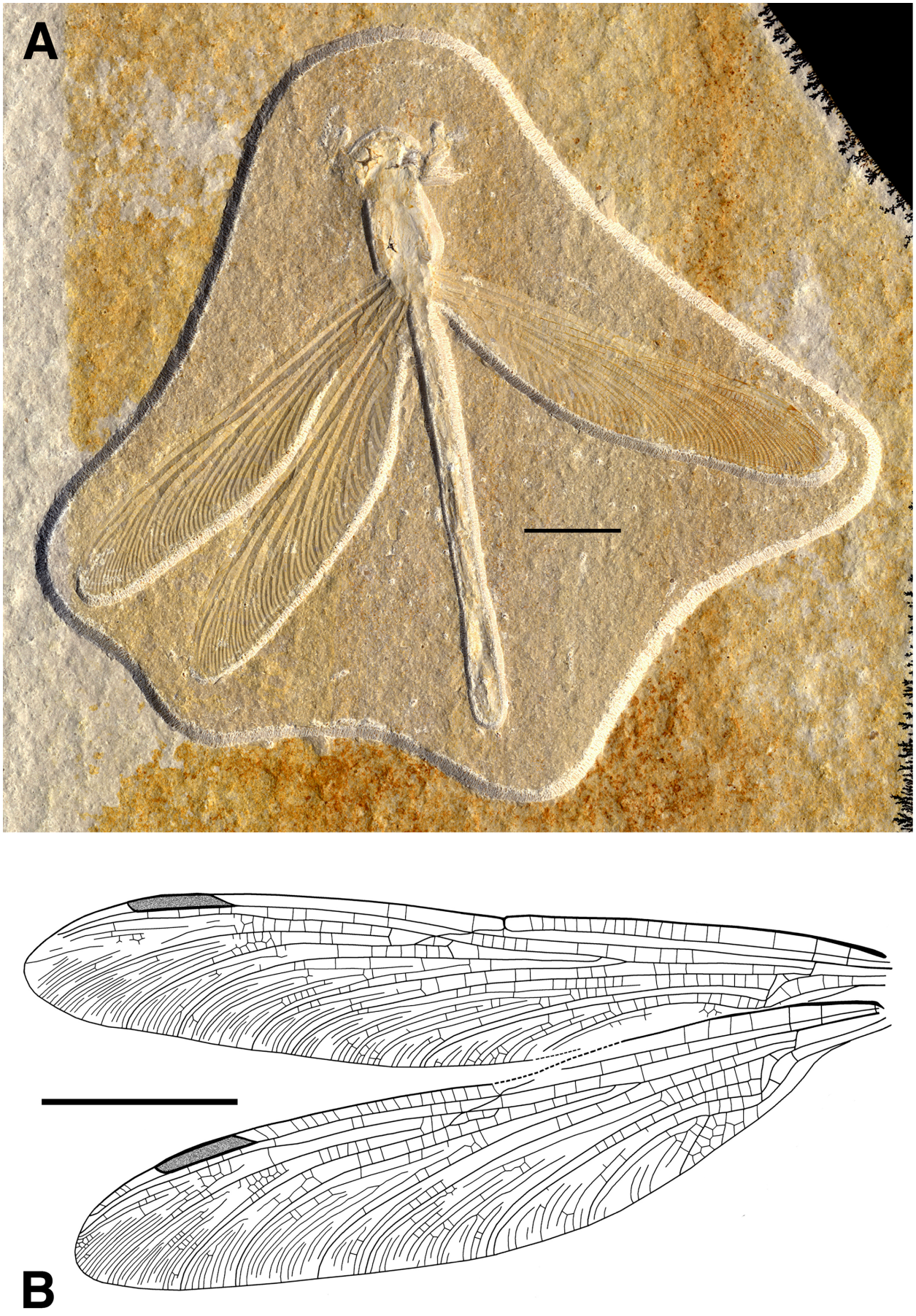

FIGURE 8. *Reschiostenophlebia koschnyi* **gen. et sp. nov.**, holotype, SMNS 70155. **A**, Photograph (scale bar = 10 mm). **B**, Drawing (scale bar = 10 mm).

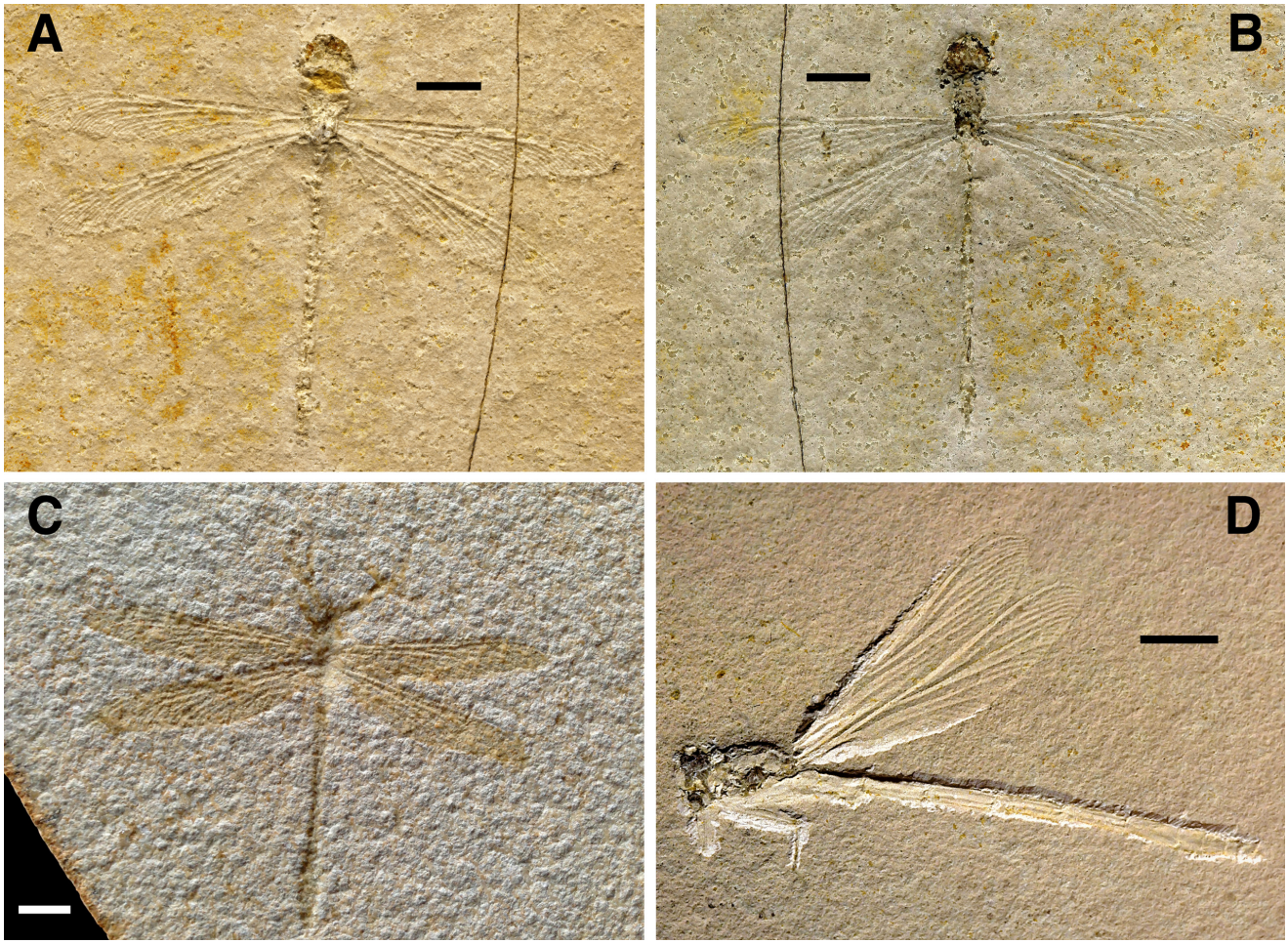

FIGURE 9. *Reschiostenophlebia koschnyi* **gen. et sp. nov. A**, Paratype, SMNS 67698, photograph (scale bar = 10 mm). **B**, Counter plate of paratype, coll. Koschny, photograph (scale bar = 10 mm). **C**, Specimen in coll. Schäfer, photograph (scale bar = 10 mm). **D**, *Prostenophlebia* spec., coll. Kümpel, photograph (scale bar = 10 mm).

longer petiole); no secondary antenodals basal of ax1 and no secondary antenodal between ax1 and ax2; ax2 is only slightly distal of arculus; numerous non-aligned secondary antenodals distal of ax2; nodus at 44% of wing length; nodus and subnodus very oblique and long, but only covering a single cell; RP2 originating at subnodus with 'stenophlebiid oblique vein', posteriorly prolonged for 2 (forewing) or 3 (hind wing) cells; IR2 originating on RP1+2 near midfork; no lestine oblique vein 'O' between RP2 and IR2; pterostigmata very long (covering 4–5 cells), unbraced, and somewhat shifted basally; numerous very long and straight secondary longitudinal veins; distinct Mspl; post-discoidal secondary vein parallel to MP, originating at triangle; discoidal cell divided by a single crossvein, which does not precisely end at distal angle, into a quadrilateral hypertriangle and triangle, both free; triangle not very transverse in both pairs of wings, especially in forewing; subdiscoidal cell not transverse, divided by 2 crossveins in forewing but free in hind wing; only 2 rows of cells directly distal of triangle for about 9 cells length; RP originating at arculus midway between origin of MA and fusion with RA; basal space free; no 'heterophlebioid' anal loop; hind wing with short but distinct petiole. The absence of an anal angle and the slender apex of the abdomen both suggest that it is a female specimen.

Paratype (Fig. 9A, B): Imprint of a complete damsel-dragonfly with spread wings. Body length 63.2 mm, forewing length 44 mm and hind wing length 43 mm. Hind wing shortly petiolate. Visible wing venation very similar to holotype.

Specimen in collection Schäfer (Fig. 9C): Imprint of a complete damsel-dragonfly in dorsal aspect. Body length about 56 mm, wing length about 43 mm. The apex of the abdomen is somewhat expanded ('clubbed'). The wing venation is only poorly preserved, but the pattern of longitudinal main veins and intercalary veins is clearly of stenophlebiid type.

Specimen in collection Kümpel (Fig. 9D): Imprint of a complete damsel-dragonfly in lateral position. Body length 76.8 mm, wing length 42.7 mm. Even though the size would agree with *Reschiostenophlebia koschnyi*

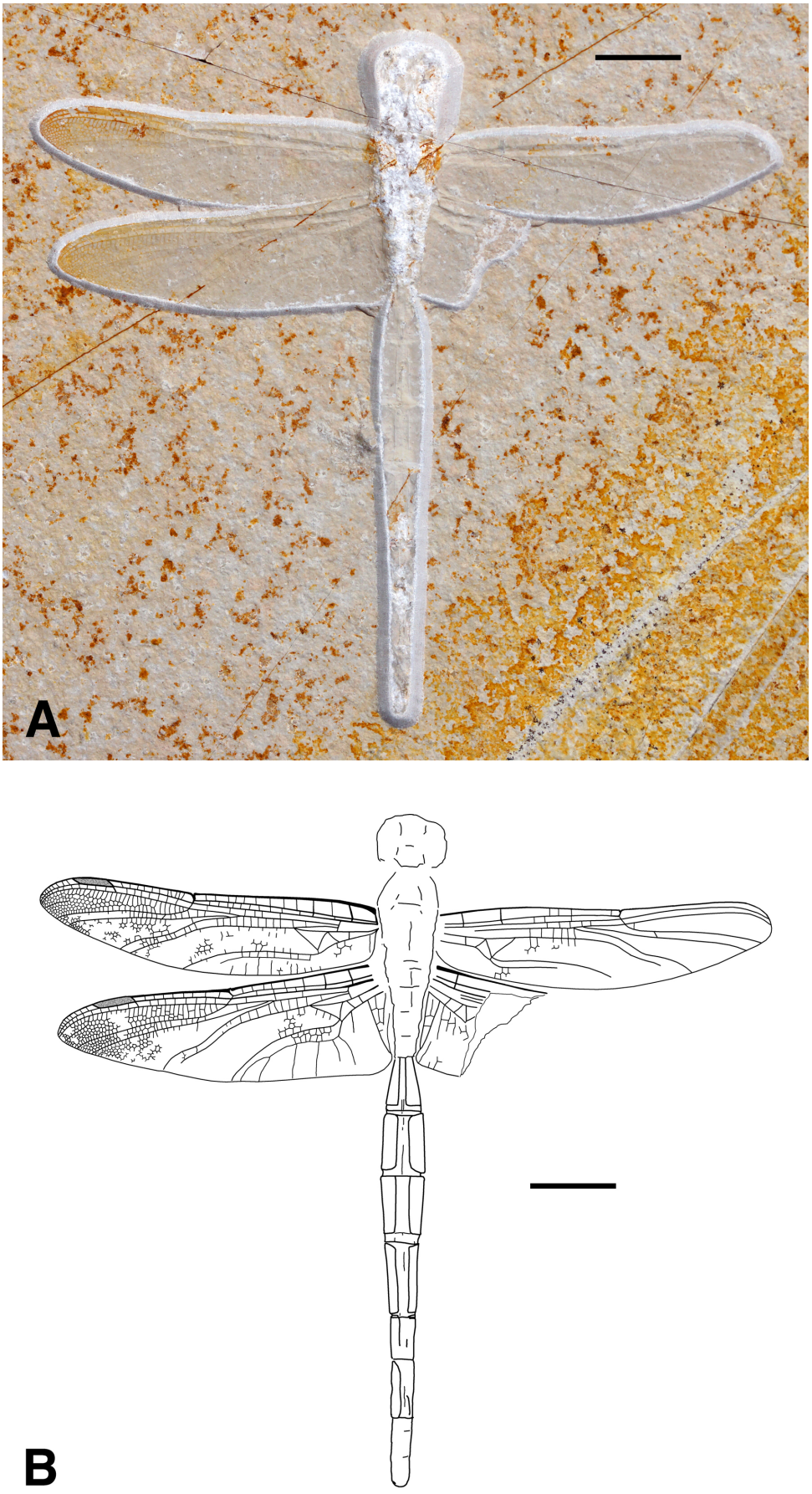

FIGURE 10. *Prohemeroscopus kuehnapfeli*, SMNS 70293. **A**, Photograph (scale bar = 10 mm). **B**, *Prohemeroscopus kuehnapfeli*, SMNS 70293, drawing (scale bar = 10 mm).

gen. et sp. nov., the distinctly longer petiolation of the wings and the visible wing venation strongly suggest an attribution of this specimen to the genus *Prostenophlebia*. However, the significant size difference of 22% (wing length of about 43 mm instead of about 35 mm) could suggest a new large species of *Prostenophlebia*.

Remarks. This new taxon represents the second genus of Stenophlebiidae from the Upper Jurassic of Germany and demonstrates the great diversity of this family in this era and region.

Suborder Anisoptera Selys in Selys & Hagen, 1854
Family Prohemeroscopidae Bechly & Ueda, 2002
Genus *Prohemeroscopus* Bechly *et al.*, 1998

Diagnosis (revised after Bechly *et al*., 1998)**.** *Prohemeroscopus* differs from the *Hemeroscopus* in the following characters: smaller size (wing length 30–40 mm, instead of about 52 mm); pterostigmata more distinctly braced; Rspl absent; hind wing CuA longer and more smoothly curved; hind wing anal loop smaller; male abdomen very long and anteriorly inflated behind a narrow "waist".

Prohemeroscopus kuehnapfeli Bechly *et al.*, 1998
(Fig. 10)

Material. Holotype, specimen SOS 1673 at the Jura-Museum in Eichstätt (Germany), which only featured an isolated pair of hind wings.

New material: Complete specimen SMNS 70293 at the State Museum of Natural History in Stuttgart (Germany), acquired from collection Udo Resch (Fig. 10).

Diagnosis (revised after Bechly *et al*., 1998)**.** *Prohemeroscopus kuehnapfeli* differs from the type species *P. jurassicus* by a distinctly larger size (wing length 39–40 mm instead of 30 mm), more undulate veins RP3+4 and MA, forewing MP ending on level of nodus (instead of far distal of nodus), more distinct and more numerous (5–6 instead of 2–3) branches of CuAa in hind wing, undivided triangles in both pairs of wings, and less oblique and more crossvein-like subdiscoidal vein.

Locality and horizon. Eichstätt, southern Franconian Jura, Bavaria, Germany; Solnhofen Limestone, Malm zeta 2b, *Hybonotum*-Zone, Lower Tithonian, Upper Jurassic, ca. 150 million years.

Description (revised after Bechly *et al*., 1998)**.** Body length about 80 mm; head with separated compound eyes; abdomen very long (much longer than wings) and (after a narrow "waist") anteriorly strongly inflated in a very unique way, unlike most known fossil and living dragonflies (except for *P. jurassicus*).

Forewing 40.0 mm long and max. 9.4 mm wide; basal space free; between ax1 and ax2 there is a single non-aligned secondary antenodal in both rows; ax1 somewhat basal of arculus, and ax2 on level of mid of triangle; 9 secondary antenodals distal of ax2 in first row, non-aligned with 10 antenodals in second row; short 'cordulegastrid gap' of antesubnodal crossveins (maybe divided by a single crossvein); 11 postnodal crossveins, non-aligned with 7 postsubnodal crossveins; no distinct 'libelluloid gap' of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma braced and elongate, with 4 cells beneath it; pseudo-IR1 weakly developed, without obvious origin beneath pterostigma; RP2 and IR2 distally somewhat divergent, with 3 rows of cells between them; a single lestine oblique vein 'O' between RP2 and IR2 4 cells distal of subnodus; at least 6 bridge crossveins basal of oblique vein; two rows of cells between distal parts of RP3+4 and MA that are strongly undulate; no Rspl and no Mspl; 7–8 antefurcal crossveins; arculus straight with separate origins of RP and MA (not stalked); post-trigonal space probably with 3–4 rows of cells; hypertriangle long, narrow, and free; triangle elongate and free; distal side MAb straight; subtriangle free; pseudo-analis (subdiscoidal vein) only slightly hypertrophied; MP reaches till level of nodus; CuA with several posterior branches; anal area with 3–4 rows of cells.

Hind wing 38.8 mm long and max. 12.4 mm wide; basal space free; no secondary antenodals visible between ax1 and ax2; ax1 somewhat basal of arculus, and ax2 on level of the mid of triangle; 5–6 secondary antenodals distal of ax2, not aligned except for the first pair on the level of the distal angle of triangle (easy to be confused with ax2); short 'cordulegastrid gap' of antesubnodal crossveins (maybe divided by a single crossvein); 8 postnodal crossveins, non-aligned with the 8 postsubnodal crossveins; no distinct 'libelluloid gap' of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma braced and elongate with 4 cells beneath it; pseudo-IR1 originates beneath distal side of pterostigma; RP2 and IR2 distally divergent, with a 3–5 rows of cell between them; a single lestine oblique vein 'O' between RP2 and IR2 far distal of subnodus; two rows of cells between the distal parts of RP3+4 and MA that are strongly undulate; no Rspl and no Mspl, but a single intercalary vein between IR2 and RP3+4; 5–6 antefurcal crossveins; arculus angular with separate origins for RP and MA (not stalked); post-trigonal space with 4 rows of cells; hypertriangle free; triangle strongly elongate and free; distal side MAb somewhat concavely curved; subtriangle small and undivided; pseudo-analis (subdiscoidal vein) not hypertrophied, like an oblique crossvein, ending slightly basal of basal angle of triangle; space between MP and CuA basally widened with 2 rows of cells between them; CuAa with 5 posterior branches; elongated 'gaff' of CuA present; anal loop transvers but

posteriorly not distinctly closed, at least 4-celled; anal triangle present, narrow, and divided into 4–6 cells; distinct anal angle, thus it is a male specimen.

Remarks. Bechly *et al*. (1998) mentioned the following nine diagnostic differences of *Prohemeroscopus kuehnapfeli* from the type species *P. jurassicus*: 1) wing length 40 instead of 30 mm; 2) one cell row between MP and CuA instead of two; 3) RP3+4 and MA more undulate; 4) CuAa with 5–6 branches instead 2–3; 5) three intercalary veins between IR2 and RP3+4 instead of only one; 6) triangles free instead of divided in both pairs of wings: 7) several secondary antenodal crossveins between ax1 and ax2 instead of only one; 8) ax2 on level of distal angle of triangle instead of mid of triangle; 9) anal loop more distinctly closed posteriorly. Of these characters the new specimen shares 1, 3, 4, 6 with the holotype of *P. kuehnapfeli* and 2, 5, 7–9 with the holotype of *P. jurassicus*. Two further diagnostic differences between the two holotypes were not mentioned by Bechly *et al*. (1998): subdiscoidal vein shorter, less oblique and more crossvein-like (shared by holotype of *P. kuehnapfeli* and the new specimen); 2–3 rows of cells in post-trigonal field instead of 3–4 rows (only in holotype of *P. kuehnapfeli*, while the new specimen agrees with *P. jurassicus*). The mixture of characters in the new specimen thus blurs the distinction between the two species and might suggest a synonymy. However, the 25% larger size, the free triangles in both wings, and the very different subdiscoidal vein are clearly characters that would not be expected as intraspecific variability and thus still justify the retention of *P. kuehnapfeli* as distinct species. The very unusual, anteriorly widened abdomen in the new specimen is also visible in the male holotype SOS 1716 of *Prohemeroscopus jurassicus* (compare Bechly *et al*., 1998: fig. 2) and thus seems to be an autapomorphy of the genus. The attribution of *P. kuehnapfeli* to the genus *Prohemeroscopus*, which was still indicated as preliminary with a question mark by Bechly *et al*. (1998), is definitely confirmed by the new specimen with its more intermediary character pattern.

Conclusion

The here described specimens demonstrate that even after 239 years of palaeo-odonatological research at this famous fossil locality, still new odonate taxa can be discovered and further remain to be described (Bechly, 2015a). The new genera and species supplement our knowledge about the large diversity of damselflies and dragonflies from the Upper Jurassic Solnhofen limestones of Bavaria. This diversity is congruent with a subtropical to tropical palaeoclimate and strongly suggests a variety of different freshwater habitats in the vicinity of the Solnhofen lagoon.

The new genus and species *Jurahemiphlebia haeckeli* replaces *Mersituria ludmilae* from the Upper Jurassic (Tithonian) or Lower Cretaceous (Valanginian) of Transbaikalia as the oldest known fossil record of the primitive damselfly family Hemiphlebiidae. With an estimated age of 152 million years the holotype from the Painten locality is the oldest fossil record of any living odonate family, and becomes the new fossil calibration point (Kaur Kohli *et al*., 2016) for crown group suborder Zygoptera, the superfamily Lestoidea, and the family Hemiphlebiidae.

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References

Bechly, G. (1996) 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. https://www.bechly.at/science/publications/

Bechly, G. (1998a) New fossil dragonflies from the Lower Cretaceous Crato Formation of north-east Brazil (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde Serie B*, 264, 1–66.

Bechly, G. (1998b) A revision of the fossil dragonfly genus *Urogomphus*, with description of a new species (Insecta: Odonata: Pananisoptera: Aeschnidiidae). *Stuttgarter Beiträge zur Naturkunde Serie B*, 270, 1–47.

Bechly, G. (1998c) *Juracordulia schiemenzi* gen. et. sp. nov., Eine

neue Libelle aus den Solnhofener Plattenkalken (Insecta: Odonata: Anisoptera). *Archaeopteryx*, 16, 29–36.

Bechly, G. (2000) Two new fossil dragonfly species (Insecta: Odonata: Pananisoptera: Aeschnidiidae and Aktassiidae) from the Solnhofen Lithographic Limestones (Upper Jurassic of Germany). *Stuttgarter Beiträge zur Naturkunde Serie B*, 288, 1–9.

Bechly, G. (2001) A new species of *Cymatophlebia* (Insecta: Odonata: Anisoptera: Cymatophlebiidae) from the Solnhofen Lithographic Limestone (Upper Jurassic, Germany). *Stuttgarter Beiträge zur Naturkunde Serie B*, 301, 1–5.

Bechly, G. (2003) Description of a new species of *Nannogomphus* (Insecta: Odonata: Nannogomphidae) from the Upper Jurassic Solnhofen Limestone in Germany. *Stuttgarter Beiträge zur Naturkunde Serie B*, 339, 1–6.

Bechly, G. (2005) A re-description of "*Stenophlebia*" *casta* (Insecta: Odonata: Parastenophlebiidae n. fam) from the Upper Jurassic Solnhofen Limestone in Germany. *Stuttgarter Beiträge zur Naturkunde Serie B*, 359, 1–12.

Bechly, G. (2007a) 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, UK, pp. 184–222.

Bechly, G. (2007b) *Phylogenetic Systematics of Odonata*. Available from: https://bechly.lima-city.de/system.htm (Accessed 27 Sept. 2019).

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

Bechly, G. (2015a) Insekten (Hexapoda). *In:* Arratia, G., Schultze, H.P., Tischlinger, H. & Viohl, G. (Eds.), *Solnhofen - Ein Fenster in die Jurazeit*. Vol. 1. Pfeil Verlag, Munich, pp. 239–270.

Bechly, G. (2015b) Fossile Libellennachweise aus Deutschland (Odonatoptera). *In:* Brockhaus, T. *et al.* (Eds.), Atlas der Libellen Deutschlands (Odonata). *Libellula Supplement*, 14, 423–464.

Bechly, G. & Ueda, K. (2002) The first fossil record and first New World record for the dragonfly clade Chlorogomphida (Insecta: Odonata: Anisoptera: Araripechlorogomphidae n. fam.) from the Crato Limestone (Lower Cretaceous, Brazil). *Stuttgarter Beiträge zur Naturkunde Serie B*, 328, 1–12.

Bechly, G., Nel, A., Martínez-Delclòs, X. & Fleck, G. (1998) Four new dragonfly species from the Upper Jurassic of Germany and the Lower Cretaceous of Mongolia (Anisoptera: Hemeroscopidae, Sonidae, and Proterogomphidae fam. nov.). *Odonatologica*, 27 (2), 149–187.

Bechly, G., Nel, A., Martínez-Delclòs, X., Jarzembowski, E.A., Coram, R., Martill, D., Fleck, G., Escuillié, F., Wisshak, M.M. & Maisch, M. (2001) A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). *Neue paläontologische Abhandlungen*, 4, 1–219, 48 pls.

Bechly, G., Dietl, G. & Schweigert, G. (2003) A new species of *Stenophlebia* (Insecta: Odonata: Stenophlebiidae) from the Nusplingen Lithographic Limestone (Upper Jurassic, SW Germany). *Stuttgarter Beiträge zur Naturkunde Serie B*, 338, 1–10.

Cordero-Rivera, A. (2017) Phenotypic variability in *Hemiphlebia mirabilis* (Odonata: Hemiphlebiidae): insights into the origin of the discoidal cell in odonates. *Austral Entomology*, 56 (4), 433–438.
https://doi.org/10.1111/aen.12262

Dijkstra, K.-D.B., Bechly, G. Bybee, S.N., 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., Rehn, A.C., Theischinger, G., Trueman, J.W.H., Tol, J. van, Ellenrieder, N. von & Ware, J. (2013) The classification and diversity of dragonflies and damselflies (Odonata). *Zootaxa*, 3703 (1), 036–045.
https://doi.org/10.11646/zootaxa.3703.1.9

Felker, A.S. & Vasilenko, D.V. (2018) A new genus and species of the damselfly family Hemiphlebiidae from the Lower Cretaceous Chernovskie Kopi locality (Eastern Transbaikalia). *Paleontological Journal*, 52 (2), 142–145.
https://doi.org/10.1134/S0031030118020041

Fleck, G. & Nel, A. (2003) Revision of the Mesozoic family Aeschnidiidae (Odonata: Anisoptera). *Zoologica*, 153, 1–172.

Fleck, G., Nel, A., Bechly, G. & Martínez-Delclòs, X. (2001) Revision and phylogenetic affinities of the Jurassic Steleopteridae Handlirsch, 1906 (Odonata: Zygoptera). *Insect Systematics & Evolution*, 32, 285–305.
https://doi.org/10.1163/187631201X00227

Fleck, G., Bechly, G., Martínez-Delclòs, X., Jarzembowski, E.A., Coram, R. & Nel, A. (2003) Phylogeny and classification of the Stenophlebioptera (Odonata: Epiproctophora). *Annales de la Société Entomologique de France*, n.s. 39 (1), 55–93.
https://doi.org/10.1080/00379271.2003.10697363

Fleck, G., Bechly, G., Martínez-Delclòs, X., Jarzembowski, E. & Nel, A. (2004) A revision of the Upper Jurassic-Lower Cretaceous dragonfly family Tarsophlebiidae, with a discussion on the phylogenetic positions of the Tarsophlebiidae and Sieblosiidae (Insecta, Odonatoptera, Panodonata). *Geodiversitas*, 26 (1), 33–60.

Huang, D., Fu, Y. & Nel, A. (2019) The first amber stenophlebiid damsel-dragonfly (Odonata, Epiproctophora, Stenophlebiidae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 94, 40–44.
https://doi.org/10.1016/j.cretres.2018.10.008

Jarzembowski, E.A. (1990) Early Cretaceous zygopteroids of southern England, with the description of *Cretacoenagrion alleni* gen. nov., spec. nov. (Zygoptera: Coenagrionidae; "Anisozygoptera": Tarsophlebiidae, Euthemistidae). *Odonatologica*, 19 (1), 27–37.

Jarzembowski, E.A., Martínez-Delclòs, X., Bechly, G., Nel, A., Coram, R. & Escuillé, F. (1998) The Mesozoic non-

calopterygoid Zygoptera: descriptions 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.
https://doi.org/10.1006/cres.1997.0113

Kaur Kohli, M., Ware, J.L. & Bechly, G. (2016) How to date a dragonfly: Fossil calibrations for odonates. *Palaeontologia Electronica*, 19.1.1FC, 1–14.
https://doi.org/10.26879/576

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.
https://doi.org/10.1111/j.1096-3642.2008.00497.x

Nel, A. & Huang, D. (2015) A new genus and species of damsel-dragonfly (Odonata: Stenophlebiidae) from the Lower Cretaceous of Inner Mongolia, China. *Cretaceous Research*, 56, 421–425.
https://doi.org/10.1016/j.cretres.2015.06.008

Nel, A. & Martínez-Delclòs, X. (1993) Essai de révision des Aeschnidioidea (Insecta, Odonata, Anisoptera). *Cahiers de Paléontologie* 1993, 13–99.

Nel, A., Martínez-Delclòs, X., Paicheler, J.C. & Henrotay, M. (1993) Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia Numéro hors série*, 3, 1–311.

Nel, A., Bechly, G. & Martínez-Delclòs, X. (1996) A new genus and species of Aeschnidiidae (Insecta: Odonata: Anisoptera) from the Solnhofen Limestone, Upper Jurassic, Germany. *Senckenbergiana lethaea*, 76 (1/2), 175–179.
https://doi.org/10.1007/BF03042848

Nel, A., Bechly, G., Jarzembowski, E. & Martínez-Delclòs, X. (1998) A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida). *Paleontologia Lombarda*, Nuova Serie, 10, 1–68.

Nel, A., Bechly, G. & Martínez-Delclòs, X. (2001) A new fossil dragonfly from the Upper Jurassic in Germany (Odonata: Anisoptera: Protolindeniidae). *Revue française d'Entomologie*, 23 (4), 257–261.

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 (3–4), 231–234.
https://doi.org/10.1660/062.113.0312

Nel, A., Fleck, G., Garcia, G., Gomez, B., Ferchaud, P. & Valentin, X. (2015) New dragonflies from the lower Cenomanian of France enlighten the timing of the odonatan turnover at the Early-Late Cretaceous boundary. *Cretaceous Research*, 52, 108–117.
https://doi.org/10.1016/j.cretres.2014.08.005

Pritykina, L.N. & Vassilenko, D.V. (2014) Odonata. *In:* Ponomarenko, A.G., Aristov, D.S., Bashkuev, A.S., Gubin, Y.M., Khramov, A.V., Lukashevich, E.D., Popov, Y.A., Pritykina, L.N., Sinitsa, S.M., Sinitshenkova, N.D., Sukatsheva, I.D., Vassilenko, D.V. & Yan, E.V. (2014) Upper Jurassic Lagerstätte Shar Teg, Southwestern Mongolia. *Paleontological Journal*, 48 (14), 1573–1682.
https://doi.org/10.1134/S0031030114140160

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

Schmidel, C.C. (1780) *Vorstellung einiger merkwürdigen Versteinerungen mit kurzen Anmerkungen versehen von Casimir Christoph Schmidel*. V. Bischoff, Nürnberg, 25 pp., 7 pls.

Schweigert, G. (2007) Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 245 (1), 117–125.
https://doi.org/10.1127/0077-7749/2007/0245-0117

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

Zheng, D., Wang, H., Jarzembowski, E.A., Wang, B., Chang, S.C. & Zhang, H. (2016a) New data on Early Cretaceous odonatans (Stenophlebiidae, Aeschnidiidae) from northern China. *Cretaceous Research*, 67, 59–65.
https://doi.org/10.1016/j.cretres.2016.07.005

Zheng, D., Zhang, Q., Nel, A., Jarzembowski, E.A., Zhou, Z., Chang, S.C. & Wang, B. (2016b) New damselflies (Odonata: Zygoptera: Hemiphlebiidae, Dysagrionidae) from mid-Cretaceous Burmese amber. *Alcheringa*, 41 (1), 12–21.
https://doi.org/10.1080/03115518.2016.1164402

Zheng, D., Zhang, H., Wang, B. & Chang, S.C. (2017) A new species of damsel-dragonfly (Odonata: Stenophlebiidae: *Cretastenophlebia*) from the Lower Cretaceous of the Jiuquan Basin, northwestern China. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107, 185–189.
https://doi.org/10.1017/S1755691017000093