*Zootaxa* 4450 (1): 108–114
http://www.mapress.com/j/zt/


**Article**

ISSN 1175-5326 (print edition)
**ZOOTAXA**
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4450.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:1F034BB7-919B-4AC8-9682-09F64D73A94F

# First record and a new species of the fossil dragonfly genus *Proinogomphus* (Odonata: Liassogomphidae) from the Early Jurassic of Bascharage in the Grand Duchy of Luxembourg

GÜNTER BECHLY
*Biologic Institute, Redmond, WA, USA. E-mail: gbechly@biologicinstitute.org*

## Abstract

A new species of fossil dragonfly, *Proinogomphus kreuzerorum* **sp. nov.** (Liassogomphidae), is described from the Early Jurassic black shale of Bascharage in the Grand Duchy of Luxembourg, based on a very well-preserved isolated female hind wing. This genus was previously only known from the Liassic of Braunschweig region in Germany, and is here recorded for the first time for this fossil locality. The classification of the family Liassogomphidae Tillyard, 1935 and the genus *Proinogomphus* Cowley, 1942 is briefly discussed and the diagnosis of the latter is emended.

**Key words:** fossil insect, upper Liassic, lower Toarcian, Anisoptera

## Introduction

The fossiliferous Liassic black shales of the 'schistes carton' Formation from Bascharage (Grand Duchy of Luxembourg) represent a bituminous offshore mudstone deposited in the Lower Toarcian about 183 million years ago in the Tethys Ocean (Henrotay *et al.* 1998, Delsate *et al.* 1999, Hermoso *et al.* 2014, Nel & Weis 2017). They are lithostratigraphically equivalent to the famous Posidonia shale from SW Germany. Fossil insects of this "Konservat-Lagerstätte" are relatively rare allochthonous elements of this taphocoenosis, and are preserved in calcareous lenses of intercalated nodular limestone beds (Fig. 1), usually as isolated wings or wing fragments. This paleoentomofauna comprises Odonata, Dictyoptera, Phasmatodea, Orthoptera, Hemiptera, Hymenoptera, Neuroptera, Coleoptera, Amphiesmenoptera, and Diptera. Odonates are represented at Bascharage with fossils of the families Protomyrmeleontidae, Sphenophlebiidae, Liassophlebiidae, Campterophlebiidae, Heterophlebiidae, Myopophlebiidae, Henrotayiidae, and Liassogomphidae (Nel *et al.* 1993, Henrotay *et al.* 1997, Fleck *et al.* 2003, Nel & Weis 2017).

The Liassic dragonfly family Liassogomphidae Tillyard, 1935 (= Gomphitidae Tillyard, 1925) currently includes the following 4 monotypic genera:

***Elattogomphus* Bode, 1953.**
*Heterothemis* Handlirsch, 1906 (= *Gomphites* Handlirsch, 1920, *Liassogomphus* Cowley, 1934, *Palaeogomphus* Handlirsch, 1939) with the single type species *H. brodiei* (Buckman, 1843).
Comment: The synonymy of *Liassogomphus* with *Heterothemis* Handlirsch, 1906 was established by Ansorge (2004).
*Phthitogomphus* Cowley, 1942 (= *Paragomphus* Handlirsch, 1939).
*Proinogomphus* Cowley, 1942 (= *Proinogomphus* Handlirsch, 1939 numen nudum).

A key was provided by Cowley (1942), and the family was first revised by Nel *et al.* (1993), who removed the genera *Strongylogomphus* Bode, 1953 and *Necygomphus* Cowley, 1942 (= *Necrogomphus* Handlirsch, 1939) from Liassogomphidae and transferred them to Myopophlebiidae within Heterophlebioidea. A second revision by Etter & Kuhn (2000) retained these remaining four genera, but reduced the number of species from 9 to 4 based on

 *Accepted by M. Marinov: 31 May 2018; published: 23 Jul. 2018*

assumed wing venational variability similar to extant Aeshnidae. An additional genus *Chrysogomphus* Ren, 1994 was described from the Early Cretaceous of China, but later identified as a basal Aeshnoptera (Huang *et al.* 2003). According to the cladistic analysis by Fleck *et al.* (2003), Liassogomphidae represents the sister group of crown group Anisoptera.

The present study describes a new species of the liassogomphid genus *Proinogomphus*. Its type species *P. brodei* was described by Handlirsch (1939), based on a figure of Bode (1907), but his introduction of the genus *Proinogomphus* was considered a nomen nudum by Cowley (1942) because "Handlirsch has not complied with Art. 25c 1–3 of the International Code, so that Cowley redescribed this genus. Cowley's view was ignored by Carpenter (1992) and the revision of Nel *et al.* (1993) (adopted in the Paleobiology Database PaleoDB taxon number 180639), but accepted in the latest revision by Etter & Kuhn (2000). Bode (1953) described two further species *P. aequalicellatus* and *P. bicellatus*, which have been synonymized with the type species by Etter & Kuhn (2000), because they shall not differ in any major character from the type species, which appears to be at least a bit dubious concerning *P. aequalicellatus* because this species differs from *P. brodei* in the fact that the triangle and subtriangle seem to be free in as in the new species described here. Nevertheless, I herein tentatively retain this synonymy, as there are sufficient other diagnostic characters to distinguish the new species.

## Methods

Observations and drawings were made using a Leica M80 (1.6 Plan Achromat lens) stereoscopic 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. Drawings and photos were subsequently edited and polished using Photoshop CC2018® imaging software on a MacBook Pro, but no parts of the fossil were manipulated except for overall hue, brightness, and contrast, except for Fig. 2, which is a manual focus-stacking composited with Photoshop from 5 original macro photos.

The used classification of odonates is mainly based on Bechly (1996, 2002). The terminology of odonate wing venation is based on Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996).

Abbreviations:

C = Costal vein
ScP = Subcostal vein (Subcosta posterior)
RA = Radius anterior vein
RP = Radius posterior vein
IR = Interradius vein
MA = Media anterior vein
MP = Media posterior vein
CuA = Cubitus anterior vein
CuP = cubital crossing (= anal crossing)
arc = arculus
ax1 and ax2 = primary antenodal brackets
br = pterostigmal brace vein
bs = basal space
ddv = distal discoidal vein Mab
ht = hypertriangle
m = midfork
n = nodus
o = lestine oblique vein
pt = pterostigma
st = subtriangle
sn = subnodus
tr = triangle

## Systematic Paleontology

### Class Insecta Linné, 1758

### Order Odonata Fabricius, 1793

### Suborder Anisoptera Selys, 1854

### Family Liassogomphidae Tillyard, 1935

### Genus *Proinogomphus* Cowley, 1942

**Included species:** *Proinogomphus bodei* (Handlirsch, 1939) (type species; synonyms: *P. aequalicellatus* Bode, 1953 and *P. bicellatus* Bode, 1953); *P. kreuzerorum* n. sp.

**Revised Diagnosis.** The genus *Proinogomphus* is distinguished from the other genera within Liassogomphidae by the presence of mostly only 2 rows of cells between MA and MP at least to 8 cells distal of the triangle (max. 3 triplets of cells in this area).

### *Proinogomphus kreuzerorum* n. sp.

Figures 1–4

**Holotype.** Isolated complete hind wing of a female dragonfly with collection no. SMNS 67854, deposited in the paleontological department at the State Museum of Natural History in Stuttgart (Germany). The counter plate remains in private collection Kreuzer, but does not show any further details.

**Type locality and horizon.** Bascharage (49.6° N, 5.9° E: paleocoordinates 38.2° N, 14.8° E), south-west of the Grand Duchy of Luxembourg. "Calcareous nodules" of the Schistes carton Formation (Hermoso *et al.* 2014); Early Jurassic, Early Toarcian, Upper Liassic (Lias epsilon), ca. 183 million years.

**Etymology.** A noun in the genitive case, named after Claudia and Frances Kreuzer (Trier, Germany), in appreciation of their kind donation of the holotype to the State Museum of Natural History Stuttgart.

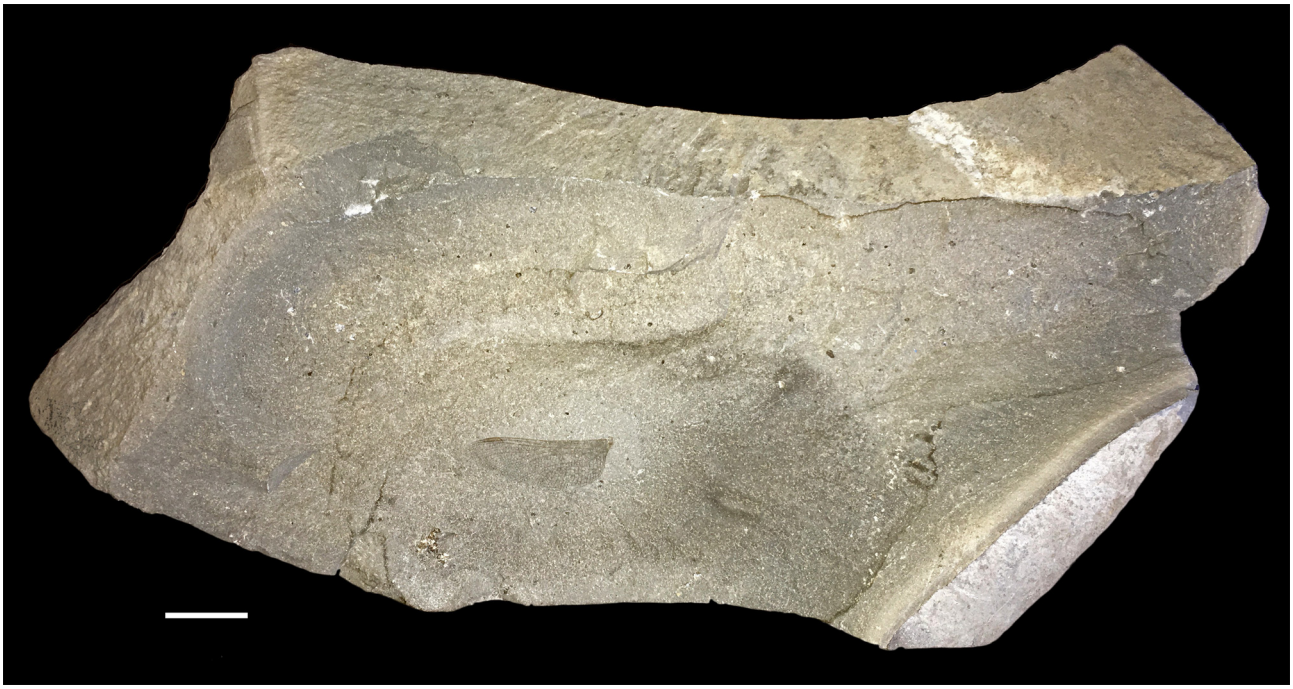

**FIGURE 1.** Photograph of the calcareous lens with the holotype SMNS 67854 of *Proinogomphus kreuzerorum* **sp. nov.** Scale bar = 20 mm.

**FIGURE 2.** Photograph of holotype SMNS 67854 of *Proinogomphus kreuzerorum* **sp. nov.** Scale bar = 5 mm.

**Diagnosis.** This species can be distinguished from the type species *P. bodei* by the following combination of characters: hind wing length only 35 mm (instead 45 mm), thus about 25% smaller; triangle and subtriangle free (instead of both crossed, with possible exception of the type specimen of *P. aequalicellatus*); posttrigonal field with 2-3 rows of cells (instead strictly two rows until 8 cells distal of triangle); 8 branches of CuA (instead only about 5-6); lestine oblique vein 'o' is 7 cells distal of subnodus (instead only about 5).

**Description of holotype (Figures 1-4).** Well-preserved and complete isolated hind wing of a female dragonfly. Total length 35.2 mm, max. width 12.0 mm. Wing articulation with costal and radio-anal plates preserved. Only the primary antenodal crossvein ax1 is very distinct and 2.5 mm distal of basal brace ax0 (wing base), while ax2 is not clearly discernible in the fossil (either the fourth or rather the sixth antenodal distal of ax1); about 11 secondary antenodal crossveins in both rows, incl. several ones between ax1 and ax2. Space between RA and RP basal of subnodus regularly crossed by 11 antesubnodal crossveins (no cordulegastrid gap of antesubnodals near subnodus). Nodus at 44% of wing length; nodal veinlet n short and perpendicular; subnodal veinlet sn oblique. Nine postnodal crossveins non-aligned with the 9 postsubnodal crossveins beneath them; no libellulid gap of postsubnodal crossveins near subnodus. Pterostigma 4.3 mm long and max. 1.0 mm wide, elongate, with oblique sides and broadened margins; stigmal brace aligned with anterior margin of pterostigma, but not very oblique and strong; only 2 crossveins (3 cells) beneath pterostigma; 4 crossveins between C and RA distal of pterostigma. Primary IR1not developed; secondary IR2 originating 2 cells distal of pterostigma with a single row of cells between it and RP1; RP1 and RP2 distally divergent with 2-4 rows of cells between them; RP2 originates at subnodus; a single lestine oblique vein 'o' between RP2 and IR2 7 cells (4.9 mm) distal of subnodus. IR2 originating on RP3/4 (rather that RP1/2) a single cell distal of origin of RP3/4. No Rspl, but there is a single stronger intercalary vein distally branching from IR2. Midfork 7.7 mm distal of arculus; 10 antefurcal crossveins between RP and MA. RP3/4 and MA undulate and distally divergent with 2-4 rows of cells between them. Posttrigonal area between MA and MP with 2-3 rows of cells (in the area within 8 cells distal of triangle there are only 3 cell triplets, but 5 duplets); no Mspl, but there is a single stronger intercalary vein distally branching from MA. Between MP and CuA there is basally a short gap of crossveins; MP and CuA distally very divergent, with MP reaching far beyond level of nodus. CuA reaching to level of nodus with 8 posterior branches and 7 rows of cells in the cubital field. Anal vein with 4 posterior branches and 6 rows of cells in the anal field; anal margin rounded without anal angle or anal triangle. Arculus complete (closed) and broken (kinked), situated between ax1 and ax2, only 0.6 mm distal of ax1; hypertriangle very wide (2.7 mm long, max. width 0.7 mm), undivided, and quadrangular because trigonal vein ends distinctly below its distal angle; discoidal triangle transverse and undivided (length of basal side 1.5 mm, upper side 1.9 mm, distal side 2.1 mm); subdiscoidal vein parallel to CuP-crossing (= "anal crossing") and delimiting a subdiscoidal cell, which is hardly developed as subtriangle. Basal space free. Wing hyaline without trace of color pattern, except for the dark pterostigma.

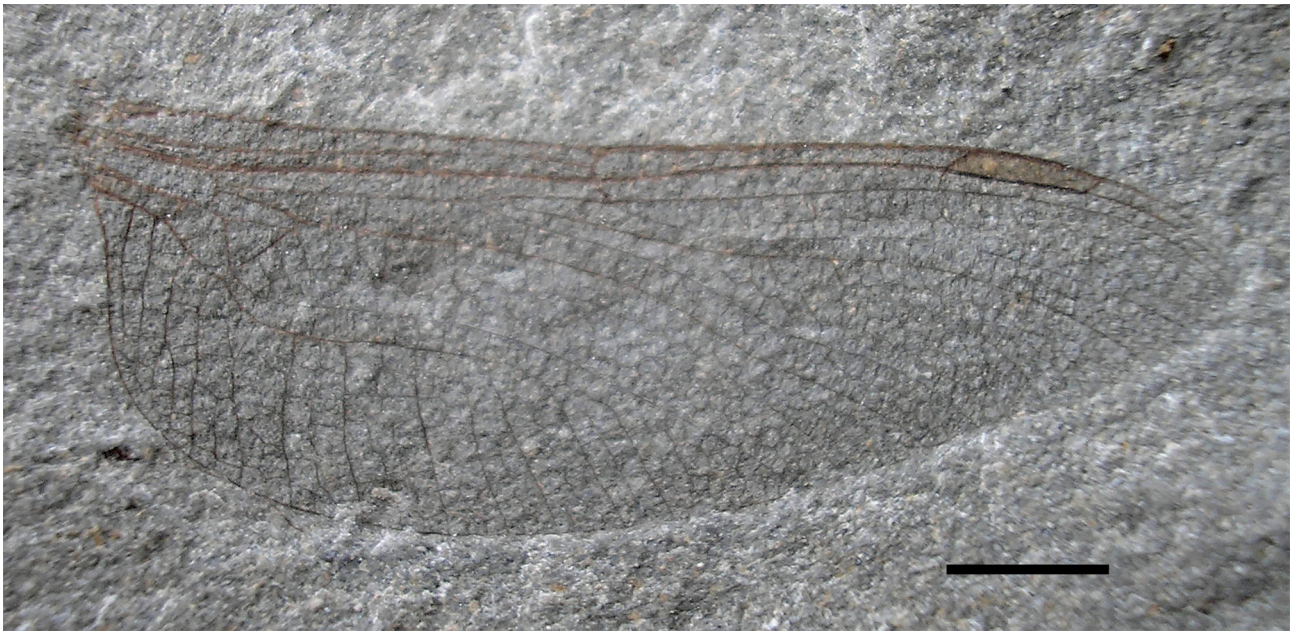

**FIGURE 3.** Photograph of counter plate of the holotype of *Proinogomphus kreuzerorum* **sp. nov.**, in private collection Kreuzer. Scale bar = 5 mm.

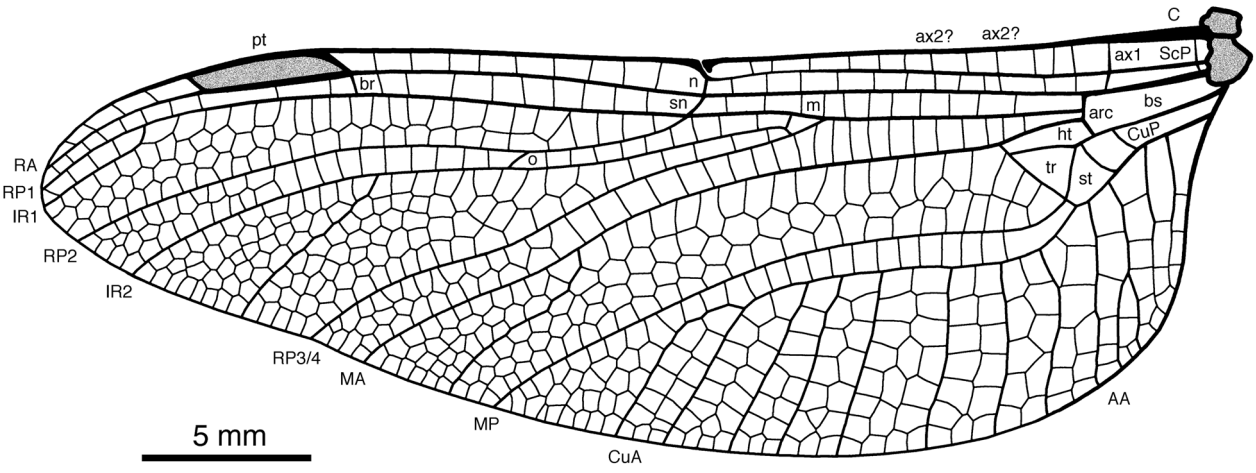


**FIGURE 4.** Drawing of *Proinogomphus kreuzerorum* **sp. nov.**, holotype SMNS 67854, female hind wing. Scale bar = 5 mm.

## Discussion

**Systematic attribution.** The following combination of hind wing characters prove that this anisopteran fossil belongs within the extinct family Liassogomphidae (Nel *et al.* 1993, Etter & Kuhn 2000): hypertriangle quadrilateral because its ventral margin does not end at its distal angle (the photo in text-fig. 1 of Etter & Kuhn 2000 clearly shows that this is also the case at least in the left hind wing of their articulated specimen, contrary to the drawing in text-fig. 3); discoidal triangle not longitudinal elongate, but rather transverse; no true subtriangle present, but just a primitive subquadrilateral cell; field between RP2 and IR2 distally expanded, likewise the fields between RP3/4 and MA and between MP and CuA; a single lestine oblique vein 'o' between RP2 and IR2 far distal of subnodus; IR1 originates beneath distal side of pterostigma or distal of it; pterostigma elongate but with only 2-3 cells beneath it; pterostigma braced with a thickened but only weakly oblique brace vein.

Within Liassogomphidae the genus *Proinogomphus* can be distinguished from other genera by the presence of only 2 rows of cells between MA and MP adjacent to the triangle for a length of about 8 cells distal to it (Cowley 1942, Etter & Kuhn 2000). All other genera have 3-4 rows of cells in this area. The new fossil species has mostly 2 rows of cells in this area (5 duplets and 3 triplets) and is therefore here considered as most basal representative of the genus *Proinogomphus*.

**Sex determination.** The lack of an anal angle and anal triangle clearly demonstrates that it is a female specimen.

## Conclusions

This fossil dragonfly represents a new species of the previously monotypic liassogomphid genus *Proinogomphus*, and the first record of this genus for the Bascharage fossil locality. It adds to our knowledge of the Liassic odonate fauna of Middle Europe in general and the Grand Duchy of Luxembourg in particular.

## Acknowledgments

I thank Claudia and Frances Kreuzer (Trier, Germany) for the donation of the holotype to SMNS. I am grateful to an anonymous reviewer for helpful comments.

## References

Ansorge, A. (2004) Insekten aus Liasgeoden der Ahrensburger Geschiebesippe – mit einem Ausblick auf lokale Anreicherungen von Liasgeoden in Mecklenburg-Vorpommern. *Archiv für Geschiebekunde*, 3, 779–784.

Bechly, G. (1996) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertretern (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundbauplans der *Odonata. *Petalura*, 2(Special Volume), 1–402.

Bechly, G. (2002) Phylogenetic Systematics of Odonata. *In*: Schorr, M. & Lindeboom, M. (Eds.), *Dragonfly Research 1.2003*. Zerf-Tübingen. [CD-ROM, ISSN 1438-034x]

Bode, A. (1907) Orthoptera und Neuroptera aus dem oberen Lias von Braunschweig. *Jahrbuch der Preußischen geologischen Landesanstalt*, 25, 218–245, pls. 6–7.

Bode, A. (1953) Die Insektenfauna des Ostniedersächsischen Oberen Lias. *Palaeontographica*, Abteilung A, 103, 1–375, 15 pls.

Carpenter F.M. (1992) Superclass Hexapoda. *In*: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4. Vol. 3*. The Geological Society of America, Boulder, CO and The University of Kansas, Lawrence, KS, pp. 80–81.

Cowley, J. (1942) Descriptions of some genera of fossil Odonata. *Proceedings of the Royal Entomological Society of London (B)*, 11 (5), 63–78.
https://doi.org/10.1111/j.1365-3113.1942.tb00725.x

Delsate, D., Godefroit, P., Stomp, N., Faber, A., Massard, J.A., Maubeuge, P.L., Boulvain, F. & Roche, M. (1999) Remarks about the article of Henrotay, Margques, Paicheler, Gall & Nell (1998): «Le Toarcien inférieur des régions de Bascharage et de Bettembourg (grand-duché du Luxembourg): évidences paléontologiques et sédimentologiques d'environnements restreints proches de l'émersion». *Bulletin des Académies et Sociétés Lorraines des Sciences*, 38 (1–4), 15–27.

Etter, W. & Kuhn, O. (2000) An articulated dragonfly (Insecta, Odonata) from the Upper Liassic Posidonia Shale of northern Switzerland. *Palaeontology*, 43 (5), 967–977.
https://doi.org/10.1111/1475-4983.00157

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

Handlirsch, A. (1939) Neue Untersuchungen über die fossilen Insekten. II. Teil. *Annalen des Naturhistorischen Museums in Wien*, 49 (1938), 1–240, 16 pls.

Henrotay, M., Nel, A. & Jarzembowski, E.A. (1997) New Protomyrmeleontidae damselflies from the Triassic of Australia and the Liassic of Luxembourg. *Odonatologica*, 26, 395–404.

Henrotay, M., Marques, D., Paicheler, J.-C., Gall, J.-C. & Nel, A. (1998) Le Toarcien inférieur des régions de Bascharage et de

Bettembourg (grand-duché du Luxembourg): évidences paléontologiques et sédimentologiques d'environnements restreints proches de l'émersion. *Geodiversitas*, 20 (2), 263–284.

Hermoso, M., Delsate, D., Baudin, F., Le Callonnec, L., Minoletti, F., Renard, M. & Faber, A. (2014) Record of Early Toarcian carbon cycle perturbations in a nearshore environment: the Bascharage section (easternmost Paris Basin). *Solid Earth*, 5, 793–804.
https://doi.org/10.5194/se-5-793-2014

Huang, D.-Y., Nel, A. & Lin, Q.-B. (2003) A new genus and species of aeshnopteran dragonfly from the Lower Cretaceous of China. *Cretaceous Research*, 24, 141–147.
https://doi.org/10.1016/S0195-6671(03)00027-2

Nel, A. & Weis, R. (2017) A new Early Jurassic damselfly from the Grand Duchy of Luxembourg (Odonata: Campterophlebiidae). *Alcheringia*
https://doi.org/10.1080/03115518.2017.1289417

Nel, A., Martínez-Delclòs, X., Paichler, J.C. & Henrotay, M. (1993) Les 'Anisozygptera' fossiles. Phylogénie et classification (Odonata). *Martinia*, Numéro Hors Série 3, 1–311.

Ren, D. (1994) A new genus and species of Liassogomphidae (Insecta, Odonata) from Late Jurassic of Liaoning province. *Geoscience*, 8 (3), 254–258.

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

Tillyard, R.J. (1925) The British Liassic dragonflies (Odonata). *Fossil Insects*, 1, 1–40.

Tillyard, R.J. (1935) Upper Permian insects of New South Wales. IV. The order Odonata. *Proceedings of the Linnean Society of New South Wales*, 60, 374–384.