For Alcheringa

A new Early Jurassic damselfly from the Grand-duchy of Luxembourg

(Odonata: Campterothlebiidae)

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Gallodorsettia kronzi gen. et sp. nov., the first representative of the damselfly family Campterothlebiidae from the Toarcian of Grand-duchy of Luxembourg is described herein. Its closest relative is the genus *Dorsettia* Whalley, 1985, known from the early Lower Jurassic of UK and China. The Campterothlebiidae seem to be rare in the Early Jurassic of Western Europe, despite being one of the most diverse odonatan families at that time, especially in Asia.

Key words: Odonata, Isophlebioptera, Campterothlebiidae, gen. et sp. nov., Toarcian, Luxembourg.

THE LOWER Jurassic of Western Europe is characterized by several marine outcrops with thousands of fossil insects, especially in England, Germany, northern France, Belgium, and

Luxembourg (Whalley 1985; Ansorge 1996, 2003). Among them, the entomofauna of the Bascharage area (Grand-duchy of Luxembourg) is exceptionally rich and diverse, although the outcrops opened by road and factory construction works are no longer accessible for study. This fauna comprises Dictyoptera, Phasmatodea, Orthoptera, Amphiesmenoptera, Hemiptera, Neuroptera, Hymenoptera, Diptera, Coleoptera, and Odonata. This last order is especially interesting for the quality and diversity of the collected material, with fossils of the families Protomyrmeleontidae Handlirsch, 1906, Sphenophlebiidae Bechly, 1997, Liassophlebiidae Tillyard, 1925, Heterophlebiidae Handlirsch, 1908, Myopophlebiidae Bode, 1953, Henrotayiidae Fleck *et al.* 2003, and Liassogomphidae Tillyard, 1935 (Nel *et al.* 1993; Henrotay *et al.* 1997; Fleck *et al.* 2003). Surprisingly, the clade Isophlebioidea Handlirsch, 1906, very diverse during the Jurassic and early Cretaceous, was not recorded in this entomofauna, while it is known from the lower Lower Jurassic of UK and the upper Lower Jurassic of Germany. We describe here the first representative of this group from the upper Lower Jurassic of the Grand-duchy of Luxembourg.

Geological setting and location

The lower Toarcian (Lower Jurassic) sediments outcropping in the southern part of the Grand-duchy of Luxembourg (Fig. 1) are long renowned for their rich fossil content and excellent preservation (Godefroit 1994), justifying their designation as Konservat-Lagerstätte. Preserved in a similar setting to the coeval Posidonienschiefer Formation of South-West Germany, these outcrops consist of bituminous black shales with intercalated nodular limestone beds that formed at an early diagenetic stage and thus permitted the preservation of delicate fossilized remains (Hanzo 1978; Henrotay *et al.* 1998). Rare insect remains have been known from the marine formations of the north-eastern Paris Basin since the 19th century. Maubeuge (1973) first illustrated an odonatan forewing (a Heterophlebioidea erroneously

attributed to the Protomyrmeleontidae) from the Grand-duchy of Luxembourg (Schouweiler site), followed by a report of Delsate *et al.* (1992) from the nearby Belgian Province of Luxembourg (Aubange site). Since then, several insects have been reported from different localities, with the best-known site Bascharage, where finds have been made M. Henrotay, P. Godefroit and D. Delsate during temporary construction works in the ‘Bommelscheier’ and ‘Op Zaemer’ industrial areas over the last 30 years. A few other specimens, now preserved in the Palaeontological collection of Musée national d’histoire naturelle de Luxembourg (MNHNL), originate from temporary construction works south of Sanem and from the construction of the motorway A13 “Collectrice du Sud”, near Foetz. The specimen described herein originates from the latter site, discovered in March 1993 by Guy Kronz, a volunteer scientific collaborator of the MNHNL, and later donated to the Palaeontological collections of the MNHNL. The ‘Couches à *Harpoceras falciferum*’ formation (lo₁ of the Geological map edited by the Geological Survey, Luxembourg; Dittrich 1993) outcrops at the Foetz site, consisting at this locality of bituminous black shales containing several nodular limestone beds attributed to the *Harpoceras serpentinum* Ammonite Zone (Lucius 1948, Delsate *et al.* 1999, Guérin-Franiatte *et al.* 2010, Hermoso *et al.* 2014). The specimen described herein was found in situ in a laminated limestone bed about 1.5 m above a nodular bed bearing numerous ammonite fossils (*Cleviceras elegantulum* (Sowerby, 1825), *Ovaticeras ovatum* Young & Bird, 1822), and *Dactylioceras* spp.). In all mentioned sites, the insect fossils were found in flat, laminated lenticular limestone (named LENT in Henrotay *et al.* 1998, fig. 2; named ‘laminated limestone bed’ in Hermoso *et al.* 2014, fig. 2). Apart from insect remains, the lenticular limestone also yielded marine organisms such as rare cephalopods, arthropods, small fishes (*Leptolepis* a.o.), occasional marine reptile remains and rare land plants (Henrotay *et al.* 1998; Delsate *et al.* 1999). Insect-bearing limestone beds can be found throughout the entire south-western part of the Grand-duchy of Luxembourg and the adjacent

Belgian Province of Luxembourg. Note that the Foetz site is currently the easternmost occurrence of insect-bearing limestone in the Luxembourg Toarcian outcrop area, as the specimen mentioned by Delsate *et al.* (1999: 20) as an Odonata from Bettembourg was revealed to have originated from Bascharage instead (collection data researched by RW in 2016).

Materials and methods

The specimen was examined dry using a Zeiss stereomicroscope. Photographs were taken under alcohol, using a Ricoh CX1 digital camera with a Maginon 2.8/90 Will-Wetzlar lens. The of the dragonfly venation nomenclature used in this paper is based on the interpretations of Riek and Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). Vein abbreviations are as follows: AA anterior anal; AP posterior anal; Arc arculus; CuAa distal branch of anterior cubitus; CuAb proximal branch of anterior cubitus; CuP posterior cubitus; d. cell discoidal cell; MAa anterior branch of anterior median; MAb posterior branch of anterior median; MP posterior median; RP posterior radius. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016). All measurements are given in mm.

Systematic paleontology

Class INSECTA Linnaeus, 1758

Order ODONATA Fabricius, 1793

Clade ISOPHLEBIOPTERA Bechly, 1996

Subclade ISOPHLEBIIDA Bechly, 1996

Superfamily ISOPHLEBIOIDEA Handlirsch, 1906

Family CAMPTEROPHLEBIIDAE Handlirsch, 1920

Genus *Gallodorsettia* gen. nov.

Type species. Gallodorsettia kronzi gen. et sp. nov.

Etymology. After Gallia, Latin name for the area that now comprises France, Belgium, and Luxembourg.

Diagnosis. Hindwing characters only. Subdiscoidal space posteriorly open; absence of a hook-like anal angle in male hindwing; distinct posterior branches of AA in anal triangle; anal triangle longer than broad; presence of three rows of cells in area between MP and CuAa; distal part of subdiscoidal space crossed by a strong secondary vein separating it into two rows of cells; absence of a secondary long straight branch of AA parallel to posterior wing margin; a very broad sub-elliptical brown membrane along anal triangle, not reaching anal angle.

Gallodorsettia kronzi sp. nov. (Figs 2-4)

Holotype. Specimen TU847, stored at the Musée national d'Histoire naturelle, Luxembourg (MNHNL).

Etymology. Named after our colleague, volunteer research associate of the MNHNL Guy Kronz (Soleuvre, Luxembourg) who collected and donated the type specimen.

Formation, age and locality. “Couches à *Harpoceras falciferum* (I₀₁)”, Lower Jurassic, lower Toarcian, Serpentinum (Falciferum) Chronozone (ca. 182.7 Ma), outcrop temporarily accessible (in 1993) during the construction works of the motorway A13 south of Foetz (49°31'8.46"N; 6° 0'13.74"E), Grand Duché du Luxembourg.

Diagnosis. As for the genus.

Description. Hindwings apparently infusate, darker in the anal triangle. Preserved length 21.5 mm, preserved width 15.9 mm; distance from wing base to Arc about 7.1 mm; wing not petiolate, anal area broad, triangular in shape, longer than broad, with 3-4 rows of irregular

cells between AA and AP, some cells being very small and others very large; a very broad subelliptical brown membrane along anal triangle; AA with four parallel posterior branches in anal triangle, anal angle pronounced but not hook-like (male specimen); AA nearly parallel with MP + CuA basally; main branch of AA distally strongly bent towards posterior wing margin; median area probably free of crossveins; submedian area with one crossvein; submedian and subdiscoidal areas separated by curved vein CuP; subdiscoidal space transverse, posteriorly open, with two rows of cells separated by a secondary zigzagged vein; DC closed basally, free of crossveins, with anterior side 3.2 mm, basal side 0.9 mm, and distal side MAb 2.5 mm long. RP separated from MA in Arc; MA basally very strong, divided into MAa and MAb distally; MAb short, well aligned with basal part of 'gaff'; MAa nearly straight in preserved part, somewhat parallel with MP basally with one row of large cells in between; CuA separating from MP 10.7 mm from wing base, distally dividing into CuAa and CuAb; stem of CuA 4.6 mm long, CuAb long, directed towards wing base, not meeting main branch of AA, leaving subdiscoidal space posteriorly open; CuAa basally somewhat parallel to posterior wing margin with 4-5 rows of cells in between, distally strongly curved towards MP, short; area between CuAa and MP with three rows of cells, smaller distally; MP curved; RP3/4 poorly preserved but clearly undulate in its preserved part.

Discussion. The specimen, although incomplete, can be attributed to the family Campterophlebiidae, following the diagnosis provided by Nel *et al.* (2009), emended by Li *et al.* (2012), based on the longitudinal veins of the hindwing (especially RP3/4) being more or less undulate (apomorphy). Affinities with the family Isophlebiidae (see diagnosis in Nel *et al.* 2009) are excluded because the distal side (MAb) of DC and the 'gaff' are not orientated in one transverse plane; and the male hindwing angle is not rounded. Few Campterophlebiidae have their hindwing subdiscoidal spaces posteriorly open, viz. *Campterophlebia* Bode, 1905, *Pritykinia* Nel *et al.*, 2009, *Pternopteron* Pritykina, 1970,

Oreophlebia Pritykina, 1985, *Amnifleckia* Zhang *et al.*, 2006, *Qibinlina* Nel *et al.*, 2009, and *Dorsettia* Whalley, 1985 (Nel *et al.* 1993, 2009; Zheng *et al.* 2016). *Campterothlebia* is only known from a female hindwing, difficult to compare with this male hindwing. Nevertheless, our fossil differs from *Campterothlebia* in the presence of only one row of cell in the subdiscoidal space, only two rows of transversely elongate cells instead of four rows of small cells in the postdiscoidal area, and in the basal part of the area between MP and CuAa (Nel *et al.* 2009). Our fossil differs from all these taxa except *Dorsettia*, *Qibinlina*, and *Pritykinia* in the absence of a hook-like anal angle in the male hindwing. *Qibinlina* has no clear posterior branches of AA in the anal triangle, unlike *Dorsettia* and *Gallodorsettia* gen. nov. *Gallodorsettia* shares with *Pritykinia* the anal triangle longer than broad, unlike *Dorsettia* in which it is broader than long. *Gallodorsettia* also differs from *Dorsettia* in the presence of three rows of cells in the area between MP and CuAa, instead of a series of long transverse cells. *Gallodorsettia* shares with *Dorsettia* the presence of a strong secondary vein separating the distal part of subdiscoidal space into two rows of cells, and the absence of a long straight secondary branch of AA parallel to posterior wing margin, as seen in *Pritykinia*. *Gallodorsettia* has a very strange subelliptical brown membrane along the anal triangle, similar to a structure present in *Dorsettia*, which Whalley (1985) and Zheng *et al.* (2016) considered to be a hairy AP vein. The present discovery suggests that it is more likely a weakly sclerotized membrane analogous to those found in modern Aeshnidae. The membrane in *Gallodorsettia* is simple while it is divided into two parts by a vein in *Dorsettia*; also this membrane does not reach the anal angle in *Gallodorsettia*, unlike *Dorsettia*. A similar structure is probably also present in *Angaroneura* Pritykina, 1985, *Pteronopteron* Pritykina, 1970, and *Amnifleckia* Zhang, Ren, et Cheng, 2006 (Zhang *et al.*, 2006).

Conclusion. The description of *Gallodorsettia* gen. nov. increases the odonatan diversity of Toarcian outcrops in southwestern Luxembourg (Bascharage area) and more generally in the Lower Jurassic of Western Europe. Besides *Campterothlebia*, the new genus is the only representative of the Campterothlebiidae in the lower Toarcian of continental Europe. It is possible that campterothlebiid larvae did not live close to the sea, but rather in more elevated or mountainous regions. As a result, the adults only occasionally entered the fossil record within the marine taphocoenoses common in continental Europe at this time; in contrast, campterothlebiids from Asia were preserved in freshwater environments. It shows that our knowledge on the entomofauna remains fragmentary for Europe in the Early Jurassic.

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Fig. 1. A. Geographic map of the Grand-duchy of Luxembourg (L) with indication of the study area; B. Close-up of the study area (region of Bascharage), with indication of the insect-bearing sites; C. Simplified stratigraphic log of the Bascharage section (adapted from Hermoso et al. 2014) with indication of the insect-bearing limestone bed.

Fig. 2. Gallodorsettia kronzi gen. et sp. nov., holotype TU847, photograph of wing.

Fig. 3. Gallodorsettia kronzi gen. et sp. nov., holotype TU847, photograph of anal triangle.

Fig. 4. Gallodorsettia kronzi gen. et sp. nov., holotype TU847, photograph of anal angle.

d.cell

RP3/4

MAa

MP

AA

CuAb

CuAa

10mm

5 mm

MAa

d. cell

MAb

MP

CuA

AP

membrane

membrane

anal angle

CuAb

5 mm