SHORT COMMUNICATION

The earliest damselfly-like insect and the origin of modern dragonflies (Insecta: Odonatoptera: Protozygoptera)

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JARZEMBOWSKI, E. A. & NEL, A. 2002. The earliest damselfly-like insect and the origin of modern dragonflies (Insecta: Odonatoptera: Protozygoptera). *Proceedings of the Geologists' Association*, **113**, 165–169. The first Carboniferous protozygopteran is formally described from the late Westphalian Coal Measures of southern England. *Bechlya ericrobinsoni* gen. et sp. nov. (Bechlyidae fam. nov.) is the oldest representative of a lineage which includes all living dragonflies and damselflies. This discovery shows that small, damselfly-like forms co-existed with the giant dragonflies of the Euramerican coal swamps.

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1. INTRODUCTION

The insect order Odonatoptera (damselflies, dragonflies and their extinct relatives, i.e. dragonflies *sensu lato*) is an ancient one first appearing in the Upper Carboniferous (Upper Namurian B of Germany and Argentina: Brauckmann *et al.*, 1985; Gutiérrez *et al.*, 2000). The Carboniferous Odonatoptera include the celebrated giant dragonflies (Meganisoptera), some of which attained wingspans of *c.* 70 cm, exceeding that of any living insect (Carpenter, 1992). However, the discovery of a small odonatopteran with an estimated wingspan of under 6 cm in the Upper Carboniferous of southern England shows that small species also existed. Moreover, it is a significant find because this fossil is the earliest representative of the Protozygoptera, the sister group of the Panodonata – a clade which includes all living dragonflies and damselflies (Bechly, 1996). Triassic fossils show that Protozygoptera were slender, damselfly-like insects (Fig. 1).

2. GEOLOGY

The new find, a unique wing, represents eighteen years of collecting by amateur and professional geologists on the site of a former colliery tip, now a SSSI/RIGS, known as Writhlington Geological Nature Reserve at Lower Writhlington, near Radstock, (Bath & NE) Somerset [National Grid Reference ST 703 553]. Over 1000 insect fossils belonging to other groups have been recovered here over the same period. The reserve lies in the Radstock Syncline of the Westphalian Foreland Basin in southern England and the wing is preserved as an impression in grey roof shale from the Farrington Formation (Upper Westphalian D: *Dicksonites plueckenetii* Subzone; Thomas & Cleal, 1994), probably from above the No. 10 Coal Seam (Jarzembowski, 1989). The insect is associated with plant compression fossils interpreted as representing the litter of a lycopsid forest dominated by the arborescent clubmoss *Lepidodendron aculeatum* (Proctor & Jarzembowski, 1999) which was deposited on an upper delta floodplain (Assemblage 4 of Proctor, 1994). Odonatoptera are rare in this facies, as in other Euramerican coalfields, only a single meganisopteran having been described previously from the Foreland Basin (Bolton, 1914).

3. SYSTEMATIC PALAEONTOLOGY

We follow the wing venation nomenclature of Riek (1976), Riek & Kukalová-Peck (1984) and Kukalová-Peck (1991), emended by Nel *et al.* (1993) and Bechly (1996), and the phylogenetic classification of Odonatoptera proposed by Bechly (1996).

Order Odonatoptera Martynov, 1932
Clade Stigmoptera Bechly, 1996
Suborder Protozygoptera Tillyard, 1925
Superfamily Archizygopteroidea Handlirsch, 1906
Family Bechlyidae fam. nov.

Diagosis

Three strong antenodal crossveins present between C and ScP corresponding to Ax0, Ax1 and Ax2; antenodal crossveins in second row (between ScP and RA) not well aligned with Ax1 and Ax2; Ax0 strongly curved; vein MAb strong but directed towards wing base and not aligned with free base of CuA; true nodus

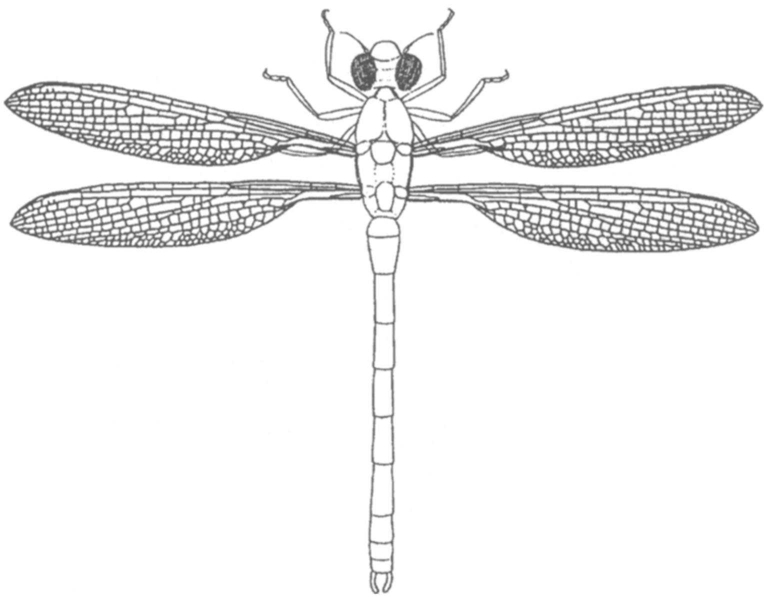

Fig. 1. General habitus of Protozygoptera by Carlo Pesarini, courtesy Prof. J.-C. Gall.

(N) present with nodal crossvein Cr and oblique subnodus (Sn); all main longitudinal veins with no secondary branches except CuA; petiole long and narrow with AA completely fused with AP (A); CuP reduced to a short crossvein between MP+CuA and anal margin; wing slender with few long cells.

Possible autapomorphies
Antenodal crossvein Ax0 incomplete, i.e. there is no corresponding subantenodal crossvein between ScP and R+MA; arculus lying midway between Ax1 and Ax2 (convergently acquired by Odonata: Epiproctophora).

Type genus

Bechlya gen. nov.

Genus *Bechlya* gen. nov.

Diagnosis
As for family.

Name
After Dr G. Bechly, odonatopterist.

Type species

Bechlya ericrobinsoni gen. et sp. nov.

Bechlya ericrobinsoni gen. et sp. nov.
(Fig. 2)

Diagnosis
As for genus.

Name
After Dr E. Robinson, a 'true spirit' of the Geologists' Association.

Description
Part and countpart of a basally complete wing with the wing tip missing; petiolate base and wing corrugation well preserved; no trace of colour pattern; length, 24.4 mm, width opposite nodus N, 4.5 mm; distance from base to N, 13.9 mm; exact position of N relative to wing apex and pterostigma unknown; some five antenodal crossveins between Costa C and ScP; basal antenodal crossvein Ax0 very strong and curved, 1.6 mm from wing base, without any corresponding antenodal crossvein in second row between ScP and R+MA; second antenodal crossvein Ax1 and third Ax2 stronger than two distal secondary antenodal crossveins; Ax1 4.1 mm distal of Ax0 and Ax2 2.5 mm distal of Ax1; five antenodal crossveins in second row between ScP and RA/R+MA; second row of antenodals distinctly weaker and not aligned with first row; two antesubnodal crossveins between RA and RP; very oblique arculus present, i.e. RP+MA separating from RA between Ax1 and Ax2; RP separating from MA 0.6 mm distal of base of arculus; no posterior part of arculus, only a strong oblique vein between MA and MP corresponding to MAb, 1.0 mm distal of base of RP; space between ScP and C in N sclerotized; strong nodal crossvein Cr forming posterior part of N; strong, oblique subnodus Sn, 1.1 mm distal of Cr; four postnodal crossveins preserved, curved/oblique but not aligned with three corresponding postsubnodal crossveins between RA and RP1; branches of RP poorly

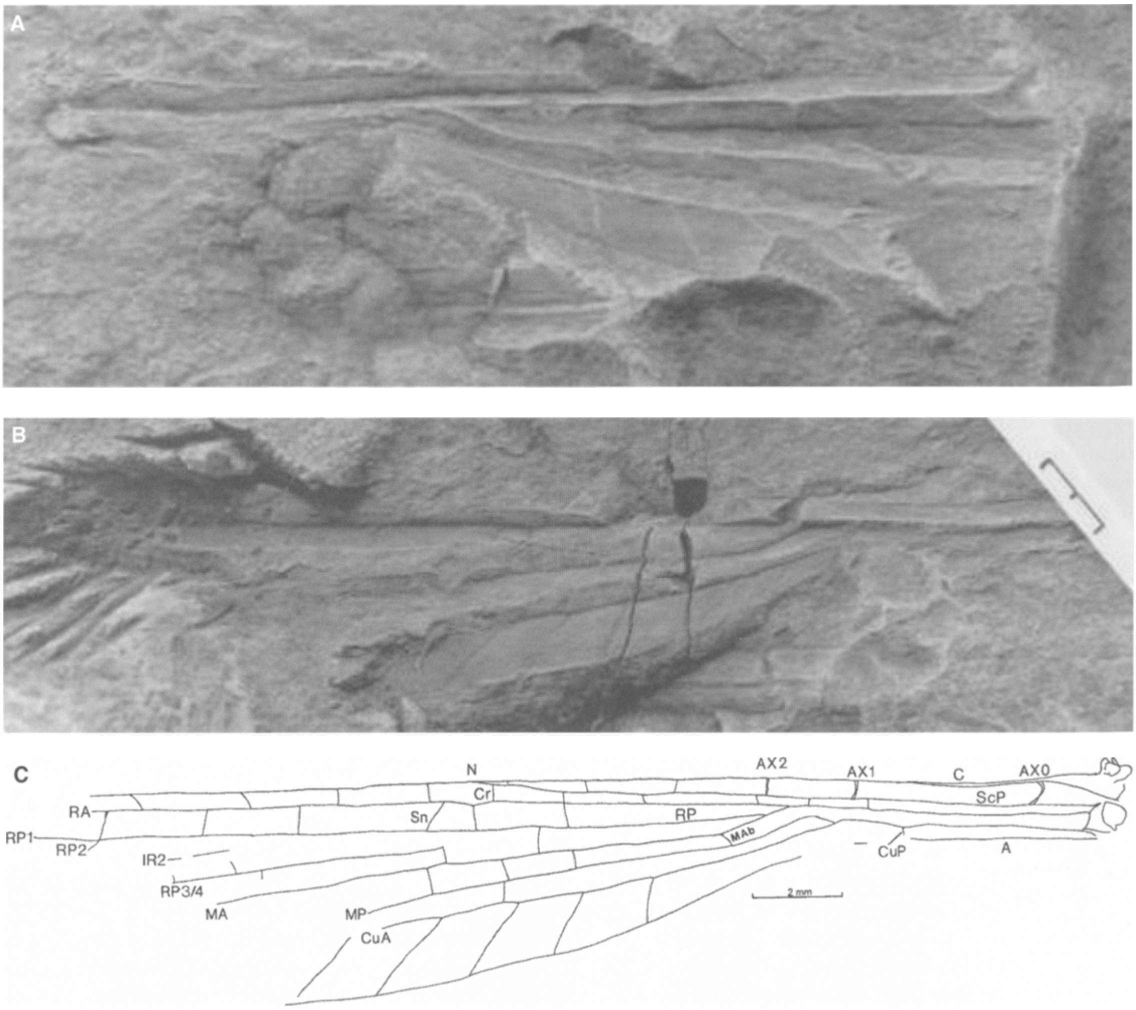

Fig. 2. *Bechlya ericrobinsoni*: gen. et sp. nov.: **(a)** part, BMB 018498; **(b)** counterpart, BMB 018499 (scale line 2 mm), photographed by R. Stutely; **(c)** venation diagram

preserved, base of proximal concave branch RP3/4 nearly opposite N; base of convex IR2 about 5.3 mm distally; base of RP2 visible 3.0 mm distally; branches of RP, MA, MP and CuA nearly straight and more or less parallel; one crossvein between MA and RP basal of base of RP3/4; comparatively few, non-aligned crossveins between main longitudinal veins; MP+Cu straight in its proximal part; CuP a short crossvein near distal end of petiole, very similar to that of Recent Odonata, 0.3 mm long; distance from wing base to CuP, 4.2 mm; MP+CuA with a distinct curve distal of CuP, MP and CuA separating 1.5 mm distally, 1.0 mm basal of arculus; AA and AP not separated; petiole very long, 5.5 mm long and 1.2 mm wide; cubital area broad, 1.4 mm wide, broader than all other areas between main veins; one row of cells in cubital area; CuA with 5 preserved simple posterior branches, directed obliquely towards posterior wing margin.

Horizon and locality
Upper Westphalian D, Writhlington Geological Nature Reserve.

Holotype
BMB 018498,-9 [W477 a,b], coll. E. A. Jarzembowski, Booth Museum Brighton, UK.

Discussion
The unique type has been examined under alcohol and coated with ammonium chloride. It is impossible to determine whether the type is a fore- or hindwing. *Bechlya ericrobinsoni* gen. et sp. nov. can be attributed to the Odonatoptera on the basis of the following synapomorphies: presence of antenodal crossvein Ax0; MP unbranched; CuP joining A; ScP fused with C distinctly basal of wing apex. The basal fusions of MA with R and of MP with Cu are synapomorphies of

Neodonatoptera (*sensu* Bechly, 1996). The small size of the wing, the presence of a true odonatan N with an oblique Sn, a strong nodal Cr crossvein, and a sclerotized space between ScP and C, together with the unbranched MA, exclude the new species from Meganisoptera and are synapomorphies of the more advanced clade Panodialata Nel *et al.*, 1999 (=Lapeyriidae+Nodialata Bechly, 1996=Protanisoptera+Triadophlebioptera+Protozygoptera+Recent Odonata). The presence of a typical odonatoid discoidal cell closed distally by a strong, oblique vein MAb between MA and MP is a synapomorphy of the Discoidalia *sensu* Bechly (1996=Triadophlebioptera+Protozygoptera+Recent Odonata) that excludes any relationships with the Permian Lapeyriidae and Protanisoptera. Within the Discoidalia, the reduced 'reticulation', the non-basally recessed N, the low density of postnodal crossveins, the absence of branches of RP3/4 and MP are symplesiomorphies that would exclude it from Triadophlebioptera *sensu* Bechly (1996= Triadotypidae + Piroutetiidae + Triadophlebiomorpha *sensu* Pritykina, 1981). Furthermore, the fusion of the distal part of CuP with A, giving the former a crossvein-like appearance, and CuA not resembling a crossvein basally parallel with CuP are synapomorphies of the Stigmoptera *sensu* Bechly (1996= Protozygoptera + Panodonata, = Archizygoptera + Odonata). The pterostigma is unknown. *B. ericrobinsoni* gen. et sp. nov. lacks an alignment of MAb with the free base of CuA which is a synapomorphy of the Panodonata. The long, petiolated wing with AA completely fused with AP are synapomorphies of the Protozygoptera *sensu* Bechly (1996, including Archizygoptera, = Kennedyomorpha Pritykina, 1980), but these characters have been convergently acquired by Triadophlebiomorpha and many Recent Zygoptera demonstrating that they are of little value for placing the new species in the Protozygoptera. *B. ericrobinsoni* gen. et sp. nov. shares with Protozygoptera the following characters that Bechly (1996) proposed as potential synapomorphies of this clade: nodal crossvein Cr not aligned with Sn; antenodal crossveins of first and second rows not aligned. This last character is not shared by all Protozygoptera (A. Nel, pers. obs.). These characters are, however, also present in the more basal Lapeyriidae and Protanisoptera. Thus their polarity is questionable. According to Bechly, 'CuP shifted in a very basal position' would also be a synapomorphy of the Protozygoptera. This structure is not preserved in many Protozygoptera but has nearly the same position in the new species and several definite species of this suborder. Thus this character is the best potential synapomorphy linking *B. ericrobinsoni* gen. et sp. nov. with the Protozygoptera. Finally, it may be noted that it does not share any synapomorphies with Odonata. Consequently it is the oldest stigmopteran, implying that not only this clade, but also the Protanisoptera and Lapeyriidae existed by the Upper Carboniferous. They have not yet been recorded, showing that our current knowledge of fossil Odonatoptera is patchy.

The problem of the first primary antenodal crossvein Ax0.

Bechly (1996) included in his list of synapomorphies of the Odonatoptera the following structure: 'a basal cross-vein between ScP and R+MA aligned with an oblique branch of ScA between costal margin and ScP ('basal brace')...' (p. 355). There is a strong oblique crossvein corresponding to the 'basal brace' (originally named Ax0 by Chao, 1951) in all Recent Odonata, but it is also present in the Lower Permian meganeurid *Megatypus schucherti* Tillyard, 1925 and the Carboniferous *Eugeropterum lunatum* Riek, 1984 (based on the reconstructions of Riek & Kukalová-Peck, 1984). Nevertheless, this 'basal brace' is not figured in nearly all available reconstructions of described Carboniferous and Permian Odonatoptera. It is not visible in the wings of the various species of *Meganeura* in the collections of the Laboratory of Palaeontology, National Museum of Natural History, Paris, because of their poor preservation. Furthermore, the basal crossvein between ScP and R+MA is absent in *Bechlya ericrobinsoni* gen. et sp. nov. Thus, it is not always present in Odonatoptera. We provisionally interpret this absence of a crossvein between ScP and R+MA as an autapomorphic reversal in *Bechlya* gen. nov., but the presence of Ax0 needs to be investigated in all the known Carboniferous and Permian Odonatoptera. For example, Bechly (1995, 1996) considered that Ax0 (= basal brace ScA) in the Protanisoptera is in a very distal position, more or less exactly in the position of Ax1 in Recent Odonata (and that there is actually no distal, strong antenodal crossvein homologous with Ax1 or Ax2). An examination of *Polytaxineura stanleyi* Tillyard, 1935 (Protanisoptera; Upper Permian, Australia) shows that two strong antenodal crossveins are clearly visible, exactly in the position of Ax1 and Ax2 of Recent Odonata. A basal brace is also present between C and ScP, prolonged between ScP and R+MA, in well-preserved specimens of Protanisoptera (Huguet *et al.*, in press). It probably corresponds to basal vein Ax0.

4. CONCLUSION

Prior to the Writhlington find, the earliest Stigmoptera (Protozygoptera+Panodonata) were reported from the Permian. The new find shows that the stigmopteran lineage leading to modern dragonflies and damselflies had differentiated earlier, dating back to the earliest-known radiation of the winged insects, that of the non-Holometabola in the mid–late Carboniferous (Jarzembowski & Ross, 1996). The damselfly-like habitus of *Bechlya ericrobinsoni* gen. et sp. nov. (small size, petiolate wing base) is an ancient adaptation, showing that narrow-winged Odonatoptera co-existed with broad-winged Meganisoptera by the Upper

Carboniferous. Interestingly, *Campyloptera eatoni* Brongniart, 1893 from the Stephanian of Commentry is also an odonatopteran with a systematic position more basal than the Panodialata and rather large, sub-petolated wings (Nel & Huguet, under review). Finally, this discovery implies that Lapeyriidae, Protanisoptera and Triadophlebioptera, as well as Protozygoptera, had appeared by the Upper Carboniferous, and their discovery may be anticipated in the Coal Measures of Euramerica.

ACKNOWLEDGEMENTS

This study is PRIS contribution no. 832 and was partly supported by Royal Society research grant no. 18525 (EAJ).

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Manuscript received 8 September 2000; revised typescript accepted 1 February 2002