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# New homoiopterids from the Late Carboniferous of England (Insecta: Palaeodictyoptera)

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**Abstract**

A new palaeodictyopteran, *Anglopterum magnificum* gen. et sp. n., is described from concretions of Late Carboniferous (Langsettian) in the Lancashire County (UK). The new genus, based on the hind-wing venation, is attributed to Homoiopteridae and compared with other homoiopterid genera. A previously figured homoiopterid from Late Carboniferous (Upper Asturian) roof shales in Somerset (UK) is bearing venation pattern of anal area similar to *Mazonopterum wolfforum* Kukalová-Peck and Richardson, 1983. These are the first formally described species of Homoiopteridae from the British Isles. Furthermore, their similarity in venation pattern to *Mazonopterum wolfforum* Kukalová-Peck and Richardson, 1983 from Mazon Creek (USA) provides evidence for a Euramerican connection during the Late Carboniferous. ***To cite this article: J. Prokop et al., C. R. Palevol 5 (2006)***.


**Résumé**

**Nouveau Palaeodictyoptera du Carbonifère supérieur d'Angleterre.** Un nouveau Palaeodictyoptera, *Anglopterum magnificum* gen. et sp. n., est décrit de concrétions du Carbonifère supérieur (Langsettien) du Lancashire (Angleterre). Ce nouveau genre, basé sur la nervation de l'aile postérieure, est attribué aux Homoiopteridae et comparé avec d'autres genres de cette famille. Un Homoiopteridae figuré auparavant du Carbonifère supérieur (Asturien supérieur) du Somerset a un champ anal similaire à celui de *Mazonopterum wolfforum* Kukalová-Peck et Richardson, 1983. Ce sont les premières espèces décrites d'Homoiopteridae des îles Britanniques. De plus, leur nervation, similaire à celle de *Mazonopterum wolfforum* Kukalová-Peck et Richardson, 1983 du Mazon Creek (États-Unis), apporte des indices supplémentaires en faveur d'une connexion euro-américaine au Carbonifère supérieur. ***Pour citer cet article : J. Prokop et al., C. R. Palevol 5 (2006)***.


*Keywords:* Palaeodictyoptera; Homoiopteridae; Taxonomy; Palaeogeography; Late Carboniferous; Pennine and Radstock basins; UK

*Mots clés :* Palaeodictyoptera ; Homoiopteridae ; Taxonomie ; Paléogéographie ; Carbonifère supérieur ; Bassins de Pennine et Radstock ; Angleterre

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## 1. Introduction

The fossil insect order Palaeodictyoptera Goldenberg, 1877 within the superorder Dictyoneuridea Handlirsch, 1906 (Palaeodictyopteroida *sensu* Bechly [5]) represents a widely diverse group of Palaeozoic insects ranging from the Lower Carboniferous (Namurian A) through the Permian up to the Early Triassic (a single record of *Thuringopteryx gimmi* Kuhn, 1937 from the Middle 'Buntsandstein') with a peak of abundance in the Late Carboniferous [6,24]. Palaeodictyopteran insects have a distribution mainly restricted to the palaeotropical belt of the northern hemisphere and are most commonly found in Euramerican Late Palaeozoic deposits, observations that support their probable thermophily [24]. The taxon Palaeodictyoptera is considered to be paraphyletic after Bechly [5,6], and it is therefore necessary to revise the described species in the context of a future phylogenetic study of this group. Many species are, however, based only on more or less complete wings, so that such an analysis may be very difficult to achieve. Other orders of Palaeodictyopteroida, like Megasecoptera, Diaphanopterodea, and Permothemistida, differ clearly in wing venation patterns and are therefore likely to be monophyletic groups [13]. We follow the wing venation terminology of Kukalová-Peck [18], whilst the systematics of Palaeodictyoptera is based mainly on the work of Sinitshenkova [24], partly adapted from Riek [23]. These authors and the current position of Homoiopteridae were critically reviewed and discussed in a previous paper [22], describing a new genus from the Late Carboniferous of the northern Czech Republic (see also [17]).

## 2. Geological setting

Workings for coal in the vicinity of Wigan and Manchester, Lancashire, UK yielded exceptional Late Carboniferous faunal material in the early part of the 20th century, in particular from the Sparth Bottoms locality [20]. A number of new sites were investigated and documented between 1995 and 2005 [2,3], in particular the Bickershaw Colliery spoil tips and opencast pits at Westhoughton, Cranberry Lea Farm, and Crock Hey (Fig. 1,2).

Anderson et al. [4] documented the stratigraphic succession exposed in the Westhoughton opencast pit, which was accessible from mid-1995 to early 1997. A 22-m interval here includes three main coals (Fig. 3). Above the thickest of the coals, the 'Wigan Four Foot', an 11-m coarsening-upward succession can be seen, recording delta progradation into a lake. Comparable

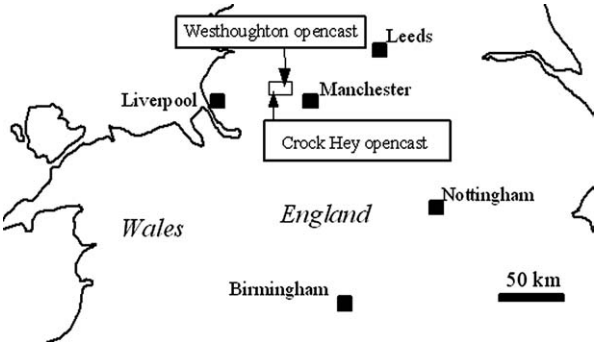


Fig. 1. General location map of Lancashire outcrops.
Fig. 1. Carte de répartition des gisements du Lancashire.

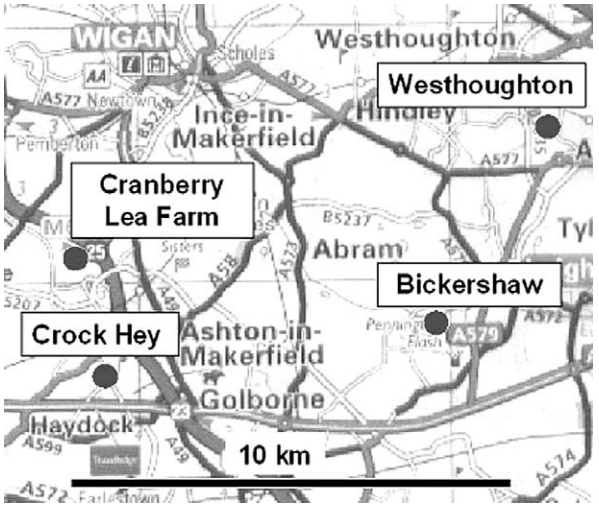


Fig. 2. Road map showing the location of sites mentioned in the text.
Fig. 2. Carte routière montrant la localisation des sites mentionnés dans le texte.

coarsening-upward patterns are commonly seen in other exposures in the area, including that of the more recently available Crock Hey opencast (Fig. 4,5), and above a coal at Crock Hey, with numerous siderite concretions present in the mudstones (Fig. 6).

The homoiopterid from the Somerset Coalfield was found over 24 years ago in Roof Shales (mudstones) near Radstock on the tip of the former Kilmersdon Colliery (National Grid Reference ST 682 536). Like the neighbouring Lower Writhlington Colliery, the pit worked the No. 10 coal in the lower part of the Upper Asturian Farrington Formation prior to closure in 1973 [15]. At Kilmersdon, however, the seam was worked longer (1951–1973, [1]). E.A. and J. Brigid have collected a small arthropod fauna from the old tip comprising Blattodea, Phalangiotarbida and Xiphosura, of which the insects are the most common. An archaeorthopteran and a trigonotarbid have also been de-

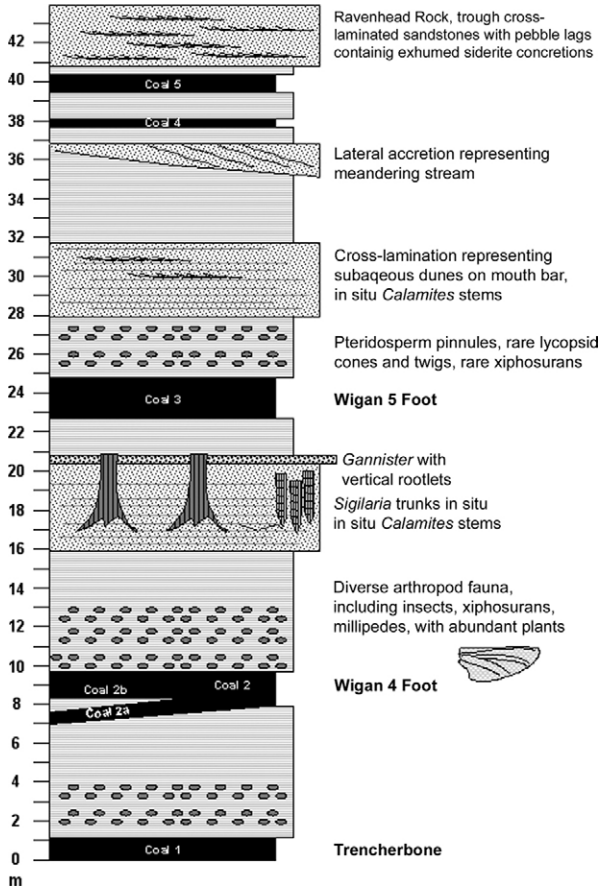


Fig. 3. Summarized stratigraphy at Westhoughton, based on [4]. The holotype of *Anglopterum magnificum* gen. n. et sp. n. comes from the mudstones overlying the Wigan Four Foot Seam.
Fig. 3. Stratigraphie résumée du site de Westhoughton, d'après Anderson et al. [4]. L'holotype d' *Anglopterum magnificum* gen. n. et sp. n. provient des argiles surmontant le niveau « Wigan Four Foot ».

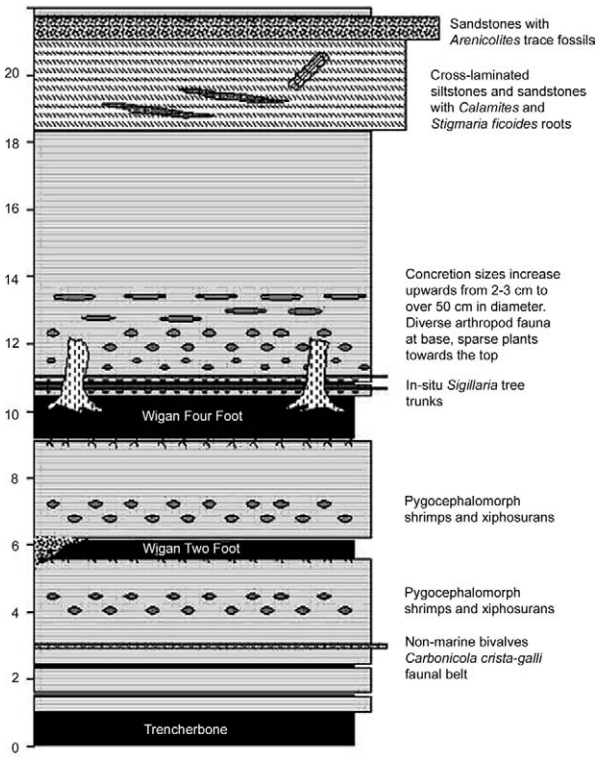


Fig. 4. Summarized stratigraphy at Crock Hey, as exposed in early 2005.
Fig. 4. Stratigraphie résumée du site de Crock Hey, tel qu'il se présentait au début 2005.

Fig. 5. Photograph of the Crock Hey exposure.
Fig. 5. Photographie du gisement de Crock Hey.

scribed from here [7,12]. The arthropods are usually tectonically deformed due to the Variscan Orogeny and associated with a lycopsid-dominated flora representing a flood-basin forest as at Writhlington. The palaeodictyopteran found by Mr Cooper is unusual in that it is not only a new record, but it is also associated with a filicopsid (pinnule of *Lobatopteris vestita* (Lesquereux) Wagner det. C. Cleal, written communication, 2005). It is, however, unreddened, so is unlikely to have come from much earlier tipping of the Lower Cantabrian Radstock Formation.

## 3. Systematic palaeontology

Family Homoiopteridae Handlirsch, 1906

**List of genera after** [11] **supplemented in** [9* and 22+]: *Adolarryia* Kukalová-Peck & Richardson, 1983; *Ametretus* Handlirsch, 1911*; *Amousus* Handlirsch, 1911*; *Boltopruvostia* Strand, 1929; *Homoioptera* Brongniart, 1893; *Larryia* Kukalová-Peck & Richardson, 1983; *Mammia* Handlirsch, 1906*; *Mazonopterum* Kukalová-Peck & Richardson, 1983; *Mazothairos* Kukalová-Peck & Richardson, 1983; *Paraostrava* Prokop

Fig. 6. View of coal seam 2 splitting into two towards the East, Crock Hey opencast. The identification favoured here is that the combined seam at the right hand side of this photograph is a combination of the Wigan Four Foot (above) and Wigan Two Foot (below) coals. If this is correct then the coal seam exposed at the level of the water is the Trencherbone seam. The holotype of *Anglopterum magnificum* comes from the mudstones overlying Coal seam 2.
Fig. 6.Vue du gisement 2, divisée en deux parties vers l'est, Crock Hey. L'holotype d' *Anglopterum magnificum* provient du niveau surmontant le « Coal seam 2 ».

& Nel, 2004+, *Parathesoneura* Sinitshenkova, 1977; *Scepasma* Handlirsch, 1911*; *Thesoneura* Carpenter, 1944; *Turneropterum* Kukalová-Peck & Richardson, 1983.

Genus *Anglopterum* gen. n.

**Type species.** *Anglopterum magnificum* sp. n. by original designation.

**Etymology.** Compound name Anglo- after the name of the country (England) and *pterum* from Latin for wing; masculine in gender.

**Diagnosis.** Homoiopterid genus based on wing venation: *Anglopterum* gen. n. differs from all other homoiopterid genera by a combination of the following characters: convex ScA reaching anterior wing margin beyond midlength; broad area between ScP and ScA with numerous oblique sigmoidal veins, RA simple; RP dichotomously divided in distal part of wing with four main branches; first branch of RP a long distance from the base of RP; area between RA and RP area with numerous long sigmoidal cross-veins and small cells; MA simple; MP area very broad with more than five branches; CuA simple, without strong basal anterior curve; a broad area between Cu (CuA) and M basal of fork of M; CuP with more than four branches; AA divided into three branches; AP with about seven branches, forming a large anal area; anal brace in the form of a convex ridge [19].

*Anglopterum magnificum* sp. n. (Fig. 7,8)

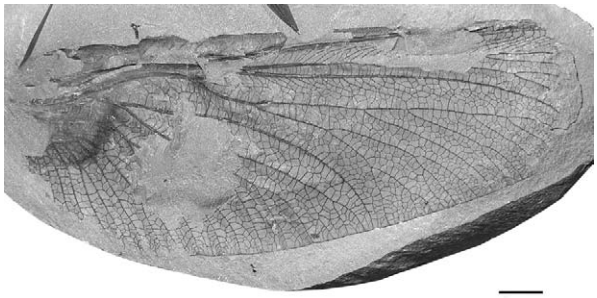

Fig. 7. *Anglopterum magnificum* gen. et sp. n., photograph of holotype (scale bar represents 10 mm).
Fig. 7. *Anglopterum magnificum* gen. et sp. n., photographie de l'holotype (échelle : 10 mm).

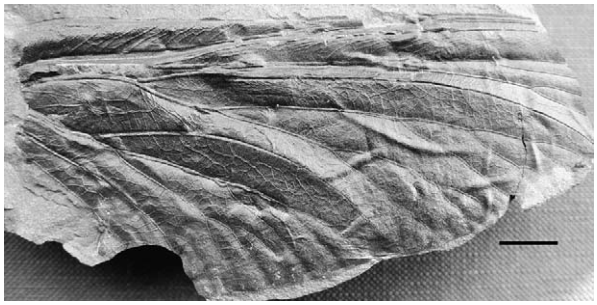

Fig. 8. *Anglopterum magnificum* gen. et sp. n., photograph of paratype (scale bar represents 10 mm).
Fig. 8. *Anglopterum magnificum* gen. et sp. n., photographie du paratype (échelle : 10 mm).

**Description.** Wing membrane probably originally hyaline; wing covered with a dense irregular venational network ('archaedictyon'); convex ScA only partly preserved; concave ScP straight, running close to radius (R), and partly preserved, reaching anterior wing margin very distally, close to wing apex; area between ScP and ScA broad and with numerous oblique cross-veins; distal part of same area with several short cross-veins; RA and RP fused basally, separating at about 1/3 wing length from base; RA simple and straight, ending on anterior margin probably in wing apex; RA and RP area with numerous long sigmoidal cross-veins and small cells; RP dichotomically divided ending on posterior margin near wing apex with four main branches; first branch of RP a long distance (60 mm) from base of RP; stem of M basally curved, divided into MA and MP at about the same level as separation of RA and RP; MA simple, strongly curved basally, ending on posterior wing margin about 30 mm from wing apex; base of MP about 45 mm from wing base; first fork of MP 15 mm distal to its base; anterior branch of MP dichotomously divided four times, and reaching posterior

wing margin with five main branches; posterior branch of MP divided into four main branches, second and third terminally twigged; MP area very broad and reaching posterior wing margin from 35 to 85 mm from wing apex; M and R very close for a short distance near their bases, opposite first fork of MP; stem of Cu divided into CuA and CuP about 30 mm from wing base; forks of Cu and of M rather distant, 17 mm apart; CuA simple, slightly curved, and ending on posterior wing margin about 95 mm from wing base; CuP slightly curved, more or less parallel to CuA and forked into two main branches; anterior branch of CuP terminally twigged, posterior branch dichotomously forked into three branches; stem of AA distinct and divided into three branches; AP area partly preserved, AP ending on posterior wing margin with about seven branches, forming a large anal area (hind wing); anal brace in the form of a convex ridge.

**Dimensions**. Holotype: length of fragment about 130 mm, probable total length about 145 mm (wingspan more than 300 mm). Paratype: length of fragment 103 mm.

**Material**. Holotype specimen in A. Tenny private collection, Lancashire, UK, a nearly complete hind wing in a half concretion; paratype specimen RS. UC.93 in RDA. Smith private collection, The Netherlands, median part of a wing in a concretion.

**Type locality.** Holotype: Crock Hey opencast pit (accessible from 2001 until 2005), paratype: Westhoughton opencast pit (accessible from 1995 to 1997, described in [3], Lancashire, UK.

**Type strata.** Holotype: concretion in mudstone above Crock Hey Coal 2 (tentatively identified as the Wigan Four Foot seam); Paratype: concretion in mudstone above the Wigan Four Foot Coal (described in [4]). Langsettian (Westphalian A), Late Carboniferous.

**Etymology.** After the wonderful state of preservation of one of the specimens.

**Discussion**. These fossil wings appear very similar to the hind wing of the homoiopterid *Mazonopterum wolfforum* Kukalová-Peck and Richardson, 1983 [19 (Fig. 8,9)]. The few differences are as follows: presence of long sigmoidal veins in area between ScA and ScP, instead of short simple cross-veins; first branch of RP very far from its base, distal of midway between base of RP and second branch of RP in *Anglopterum magnificum* gen. et sp. n. instead of being before midway in *M. wolfforum*; forks of Cu and M well apart instead of being rather close; 2/3 rows of cells between CuA and MP in the narrowest part of area between them, instead of only one; CuA less curved basally; area between RA and RP broad and with network of long sigmoidal veins instead of being narrow with only simple cross-veins or reticulate with irregular small cells; RP with only four main branches instead of seven; wing shorter and broader.

Fig. 9. *Mazonopterum* cf. *wolfforum* Kukalová-Peck and Richardson, 1983, photograph of specimen In. 64687 (coated in ammonium chloride): (**a**) print, (**b**) counterpart.
Fig. 9. *Mazonopterum* cf. *wolfforum* Kukalová-Peck and Richardson, 1983, photographies de l'empreinte (**a**) et de la contre-empreinte (**b**), In. 64687.

Among the Homoiopteridae with CuA simple or with weak terminal branches, *Ostrava* Kukalová, 1960 shares with *Anglopterum* gen. n. the absence of a strongly curved CuA, but differs from *Anglopterum* and *Mazonopterum* in the absence of a broader area between M and Cu (CuA) basal of the fork of M. *Parathesoneura* Sinitshenkova, 1977 and *Scepasma* Handlirsch, 1911 have an MP with few branches (less than four) instead of nine main branches as in *Anglopterum*. Lastly, *Paraostrava* Prokop and Nel, 2004 differs from *Anglopterum* in the presence of a terminal twig of CuA, seven main branches of MP (nine in *Anglopterum*), absence of a broad area between M and Cu basal of M fork, and probably more basal ending of ScA in costal margin.

**Remarks**. The other material is very similar to the holotype, differing from the latter in the forks of Cu and M being closer. This character alone is not sufficient for specific separation, as a similar difference occurs in *Homoioptera vorhallensis* Brauckmann and Koch, 1982 [8 (Figures 11b and 12b),10]. The two wings were probably of about the same length.

Genus *Mazonopterum* Kukalová-Peck and Richardson, 1983

**Type species.** *Mazonopterum wolfforum* Kukalová-Peck and Richardson, 1983

*Mazonopterum* cf. *wolfforum* Kukalová-Peck and Richardson, 1983 (Fig. 9,10)

**Description.** Posterior-basal part of hind wing (large, broad anal fan present); wing membrane with well-developed archaedictyon [16 (pl. 1, fig. 11)]; Sc and R areas poorly preserved except for tubercles in ScA; stem of M basally curved, dividing (asymmetrically) into MA and MP; M branching distal of Cu but MP dividing opposite the posterior branch of CuP; basal portion of CuA simple, strongly curved; CuP slightly curved, more or less parallel to CuA and dividing into two main branches; posterior branch of CuP dichotomously forked into three branches; AA double corrugated and evidently dividing into two paired branches; AP ending on posterior wing margin with eight main branches (one end-twigged), forming a large anal area; anal brace (b) gently curved and in the form of a convex fold.

**Dimensions.** Length of fragment: 48 mm.

**Material.** Specimen In. 64687, Natural History Museum, London, coll. R. Cooper of Tewkesbury, Gloucestershire, UK; part and counterpart of hind wing base (partly obscured by fern pinnule) in mudstone.

**Type locality.** Kilmersdon Colliery tip, near Radstock, Somerset, UK.

**Type strata.** Roof Shale probably above the No. 10 coal, Farrington Formation, Upper Asturian (late 'Westphalian D'), Late Carboniferous (Middle Pennsylvanian).

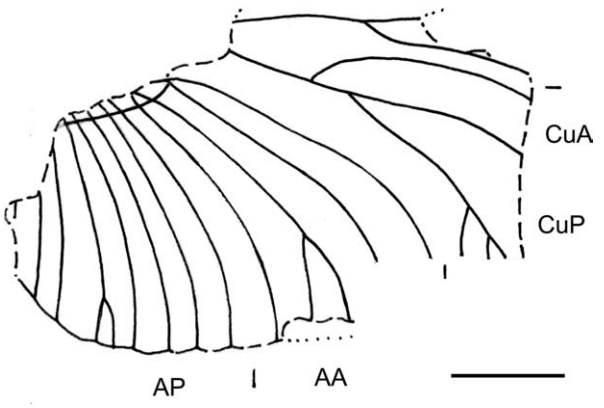


Fig. 10. *Mazonopterum* cf. *wolfforum* Kukalová-Peck and Richardson, 1983, longitudinal venation.
Fig. 10. *Mazonopterum* cf. *wolfforum* Kukalová-Peck and Richardson, 1983, nervation longitudinale.

**Discussion.** The pattern of the preserved veins is similar to that of *Mazonopterum* and *Anglopterum*, especially the cubital and median veins, and notably in the presence of a broad area between Cu and M basal of the fork of M (into MA and MP).

This specimen shares with *M. wolfforum* the basal fork of AA being in a very basal position; CuA having a strong anterior curve at its base; and one row of cells between CuA and MP in the narrowest part of the area between them. Thus it could belong to the same genus, but the lack of information on the subcostal and radial areas precludes a more definite conclusion as to its taxonomic position. It is about the same size (circa 4-cm wide) as *M. wolfforum*, but exact comparison with the latter is impossible because of the lack of important structures (costal, radial, and median areas) and tectonic deformation (oblique anterior-posterior extension).

This specimen differs from *M. wolfforum* in the following: AA is narrower with fewer distal branches; CuP is distinctly broader (more branched); the archaedictyon in AA has more rows of cells – commonly up to five [14 (Fig. 7)], compared with three or four in the latter species [19 (Fig. 8)].

Finally, due to the fragmentary state of preservation we prefer to leave this specimen attributed as *Mazonopterum* cf. *wolfforum* rather than establishing a new species.

## 4. Comments on palaeogeography

*Anglopterum magnificum* gen. et sp. n. and *M.* cf. *wolfforum* are the first described homoiopterid species from the British Isles. They show a similar structure of the wing venation to *Mazonopterum wolfforum* (Westphalian D/ Cantabrian, Mazon Creek, Illinois, USA). The close affinities of these taxa support the well-known Euramerican connection during the Late Carboniferous. Other non-marine arthropod species such as the chelicerates *Euproops danae* (Meek & Worthen, 1865), *Pleophrynus verrucosa* (Pocock, 1911) and *Adelophthalmus imhofi* Jordan & Meyer, 1856 are known both from Radstock and Mazon Creek [2,12,21].

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## References

[1] K.C. Allen, Fossil plants from the Somerset coalfield, in: R.J.G. Savage (Ed.), Geological excursions in the Bristol district, University of Bristol, UK, 1977, pp. 73–78.

[2] L.I. Anderson, Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, in: E.A. Jarzembowski (Ed.), Writhlington Special Issue, Proc. Geol. Assoc. 105, the South Wales Coalfield and Mazon Creek, Illinois, 1994, pp. 265–275.

[3] L.I. Anderson, J.A. Dunlop, C.A. Horrocks, H.M. Winkelmann, R.M.C. Eagar, Exceptionally preserved fossils from Bickershaw, Lancashire, UK (Upper Carboniferous, Westphalian A (Langsettian)), Geol. J. 32 (1997) 197–210.

[4] L.I. Anderson, J.A. Dunlop, R.M.C. Eagar, C.A. Horrocks, H.M. Wilson, Soft-bodied fossils from the roof shales of the Wigan Four Foot coal seam, Westhoughton, Lancashire, UK, Geol. Mag. 135 (1999) 321–329.

[5] G. Bechly, 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 2 (1996) 1–402 (special volume).

[6] G. Bechly, New fossil odonates from the Upper Triassic of Italy, with a redescription of *Italophlebia gervasuttii*, and a reclassification of Triassic dragonflies (Insecta: Odonata), Riv. Mus. Civ. Sc. Nat., 'E. Caffi' 19 (1997) 31–70.

[7] O. Béthoux, A. Nel, Some Palaeozoic 'Protorthoptera' are 'ancestral' orthopteroids: major wing braces as clues to a new split among the 'Protorthoptera' (Insecta), J. Syst. Palaeontol. 2 (2005) 285–309.

[8] C. Brauckmann, Morphologie und Variabilität von *Homoioptera vorhallensis* (Insecta, Palaeodictyoptera, Ober-Karbon), Geol. Palaeontol. 25 (1991) 193–213.

[9] C. Brauckmann, R. Becker, Ein neues Riesen-Insekt aus dem Ober-Karbon des Saarlandes (Palaeodictyoptera: Homoiopteridae), Geol. Palaeontol. 26 (1992) 135–141.

[10] C. Brauckmann, L. Koch, Neue Insekten aus den Vorhalle-Schichten (Ober Namurium B) von Hagen-Vorhalle, Dortm. Beitr. Landeskde Naturwiss. Mitt. 16 (1982) 15–26.

[11] F.M. Carpenter, Superclass Hexapoda, R.C. Moore, R.L. Kaesler (Eds.), Treatise on Invertebrate Paleontology, The Geological Society of America and the University of Kansas, Boulder, Colorado, Arthropoda 4 (3/4) (1992) 1–655.

[12] J.A. Dunlop, The palaeobiology of the Writhlington trigonotarbid arachnid, in: E.A. Jarzembowski (Ed.), Writhlington Special Issue, Proc. Geol. Assoc. 105, 1994, pp. 287–296.

[13] D. Grimaldi, Insect evolutionary history from Handlirsch to Hennig, and beyond, J. Paleontol. 75 (2001) 1152–1160.

[14] E.A. Jarzembowski, Prospecting for early insects, Open Univ. Geol. Soc. J. 9 (1988) 34–40.

[15] E.A. Jarzembowski, Writhlington Geological Nature Reserve, Proc. Geol. Assoc. 100 (1989) 219–234.

[16] E.A. Jarzembowski, Atlas of animals from the Late Westphalian of Writhlington, United Kingdom, Geol. Balc. 34, 2004 (47–50).

[17] J. Kukalová, New Paleodictyoptera of the Carboniferous and Permian of Czechoslovakia, Sb. Ústř. Úst, Geol. 25 (1960) 239–251.

[18] J. Kukalová-Peck, Fossil history and evolution of hexapod structures, in: I.D. Naumann, P.B. Crane, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, R.W. Taylor, M.J. Whitten, M.J. Littlejohn (Eds.), The insects of Australia, A textbook for students and research workers, 2nd ed., Vol. 1, Melbourne University Press, Melbourne, Australia, 1991, pp. 141–179.

[19] J. Kukalová-Peck, E.S. (Jr.) Richardson, New Homoiopteridae (Insecta: Paleodictyoptera) with wing articulation from Upper Carboniferous strata of Mazon Creek, Illinois, Can. J. Zool. 61 (1983) 1670–1687.

[20] R.I. Pocock, A Monograph of the Terrestrial Carboniferous Arachnida of Great Britain, Palaeontographical Society, London, 1911 (84 p.)

[21] C.J. Proctor, An Upper Carboniferous eurypterid from the Writhlington Geological Nature Reserve, Proc. Geol. Assoc. 110 (1999) 263–265.

[22] J. Prokop, A. Nel, A new genus and species of Homoiopteridae from the Upper Carboniferous of the Intra-Sudetic Basin, Czech Republic (Insecta: Palaeodictyoptera), Eur. J. Entomol. 101 (2004) 583–589.

[23] E.F. Riek, Neosecoptera, a new insect suborder based on a specimen discovered in the Late Carboniferous of Tasmania, Alcheringa 1 (1976) 227–234.

[24] N.D. Sinitshenkova, Chapter 2.2.1.2.3. Superorder Dictyoneuridea Handlirsch, 1906 (Palaeodictyopteroidea), in: A.P. Rasnitsyn, D.L.J. Quicke (Eds.), History of insects, Kluwer Academic Publishers, Dordrecht, Boston, London, 2002, pp. 115–124.