New species of Protorthoptera and Protodonata (Insecta) from the Upper Carboniferous of Britain, with a comment on the origin of wings

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Synopsis

Narkeminopsis eddi gen. et sp. nov. (Protorthoptera) and *Erasipteron bolsoveri* sp. nov. (Protodonata) are described. The use of wings for functions other than flight in the earliest insects is discussed.

Origin of wings

New insect specimens from the Carboniferous of Britain are not common. The species of Protodonata from Derbyshire described here is one of the oldest Carboniferous fossil insects found in Britain, the only earlier British fossil insect being the wingless *Rhyniella* from the Devonian. The two new species described show the complex wing venation typical of these early winged insects. With such specialized forms flying, we have to look further back in time for the origins of wings. Even if *Rhyniella* is a genuine fossil insect, and this is still disputed (Crowson 1970), it is unlikely to have been ancestral to the flying forms since the proponents of its insect affinities suggest that it is a collembolan.

Fig. 1. *Narkeminopsis eddi* gen. et sp. nov. Upper Carboniferous (Westphalian D), Radstock, near Bristol. Wing, 25·5 mm × 9 mm.

There are no insect fossils yet known for the critical period in insect evolution from the Upper Carboniferous back into the Devonian, when the wingless *Rhyniella* occurs; thus we can still only speculate on the factors which stimulated the production of wings. However, I believe there is evidence available from Recent insects which has been overlooked and which can be used to support a multiple-factor theory for the origin of wings.

With the discovery of the circulation of the haemolymph in the wing veins of insects, first reported in 1934 by Yeager & Hendrickson, we can consider that wings may have evolved not

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only for flight, and perhaps gaseous exchange as suggested by Portier (1930), but also as heat-exchangers. Clench (1966) describes the use of wings in butterflies for heat exchange, and Gillett (1971) also suggests an alternative to their use in flight.

If these facts are applied to the earliest insect, it is possible to consider that outgrowths of the body wall, which would have been developed to help increase the surface-area/volume ratio, could have been used as a sort of aerial gill and heat-exchanger. They would need some musculature to move them for orientation, or even to allow more efficient heat or gaseous exchange. The outgrowths or 'proto wings' could then have been developed concurrently with flight, which became their most important function. It is not suggested that this is directly in line with the tracheal-gill theory (see Wigglesworth 1976) for which an aquatic stage is postulated, but merely that flight does not have to be considered as the only function of the early 'wing'.

Fig. 2. *Erasipteron bolsoveri* sp. nov. Upper Carboniferous (Westphalian A), Derbyshire. Wing, 87 mm × 12 mm.

Systematic descriptions

Order **PROTORTHOPTERA**
(including Protoblattoidea and Paraplecoptera)

Carpenter (1966) considered there were few essential differences between species formerly placed in the Protoblattoidea and Paraplecoptera, and those in the Protorthoptera; the latter name has priority. The species described below is placed in the Protorthoptera following Carpenter (1966), although the limits of the order still need to be defined.

Family **NARKEMIDAE** Handlirsch, 1911

Professor Carpenter (in litt.) suggests that *Narkeminopsis* gen. nov. and *Narkemina* Martynov are sufficiently distinct from the poorly-preserved *Narkema taeniatum* Handlirsch, the type of the family Narkemidae, to be placed in a new family. *N. taeniatum* does show bandings of light and dark across the wing as in *N. eddi* sp. nov., but the dark bands are much narrower and there are differences in the origin of the median veins. From *Narkemina angustatum* Martynov (the type-species of *Narkemina*) *N. eddi* differs in the narrower costal area and fewer cross-veins, and has a longer basal part to the median vein (Carpenter, in litt.). The basal part of the wing of *N. eddi* (Fig. 3) clearly shows the origin of CuA and CuP. Pending further research, no new family is proposed for the new genus *Narkeminopsis*, which is provisionally placed in the Narkemidae (Upper Carboniferous).

Genus *NARKEMINOPSIS* nov.

TYPE-SPECIES. *Narkeminopsis eddi* sp. nov.

DIAGNOSIS. Forewing. Costal margin smooth, gently curved. Sc with several unbranched oblique veins. Sc terminates on R_1. Rs forks from R roughly halfway to termen. Costal margin narrower, cross-veins less numerous and basal part of median vein shorter than in *Narkemina* Martynov.
Hindwing unknown.

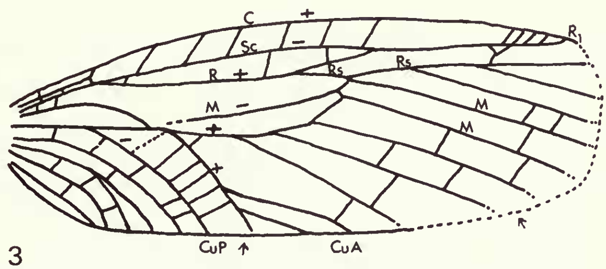

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Fig. 3. *Narkeminopsis eddi*, wing venation, diagram. +convex veins; — concave veins.

Narkeminopsis eddi sp. nov.
(Figs 1, 3)

DIAGNOSIS. Forewing. 25·5 mm × 9 mm. Wing impression (no counterpart) preserved upside down. Rs with several branches. Main wing cells distinctly spindle-shaped. MA and MP present, apical parts missing. CuA with several branches, CuP single to wing margin. Cross-veins prominent. Archedictyon present. Wing markings prominent as strong, dark, parallel cross-bands, each approximately 2 mm wide, at a slight angle across wing.

HOLOTYPE. BM(NH) In.64531. Upper Carboniferous (Westphalien D); Radstock, nr Bristol, Avon; collected by E. Jarzembowski.

DISCUSSION. The archedictyon on the wing is only faintly visible and can be seen between the branches of CuA and along part of the costal margin. The bands of darker colour are well defined and relatively smooth while the lighter areas are rougher, suggesting a more delicate (? less sclerotized) membrane which has virtually disappeared, leaving just the impressions of the wing veins. The transverse banding may well represent part of the original wing pattern.

Order PROTODONATA (Meganisoptera)

DIAGNOSIS. Dragonfly-like insects which lack the nodus, arculus and pterostigma of typical Odonata.

Family ERASIPTERIDAE Carpenter, 1939

DIAGNOSIS (modified after Carpenter, 1939). CuA present, reduced. Anal-crossing vein between CuP and 1A. MP absent. Archedictyon present. Basal part of costa of forewing toothed. One included genus.

Genus *ERASIPTERON* Pruvost, 1933

TYPE-SPECIES. *Erasipteron larischi* Pruvost 1933, by monotypy. Upper Carboniferous (Namurian C), Czechoslovakia.

DIAGNOSIS. Relatively few cross-veins. Sc roughly half length of forewing. Rs strongly branched in apical area of wing.

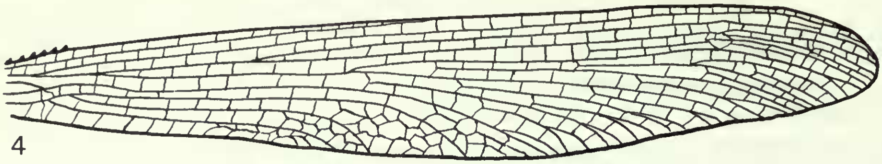

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Fig. 4. *Erasipteron bolsoveri*, reconstruction

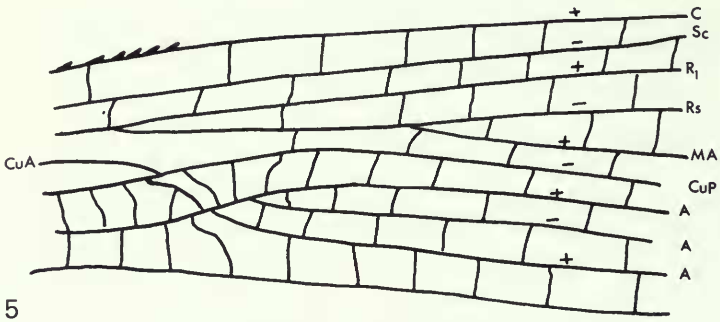

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Fig. 5. *E. bolsoveri*, basal third of wing, venation diagram. +convex veins; — concave veins.

Erasipteron bolsoveri† sp. nov.
(Figs 2, 4, 5)

DIAGNOSIS. Forewing. 87 mm × 12 mm. No pattern visible. Concave and convex veins clear (Fig. 5). R_1 terminates near wing apex. Rs sharply curved down at apex. Rs and MA fork one-third from base. Anal veins curved in basal area. Anal cells simple, single row.

Hindwing unknown (but see Discussion).

HOLOTYPE. BM(NH) In.64532. Upper Carboniferous (Westphalien A); Derbyshire, Bolsover deep hard seam, at 586 m, approx. 15 cm above seam. Collected by M. Spencer.

DISCUSSION. This species can be separated from *E. larischi* by the presence of cells in the area formed by the anal-crossing vein, and by the simple arrangement of cells in the basal part of the anal area. An incipient nodus is supposed to be present in *E. larischi* (Carpenter 1939; Kukalová 1964); no trace of a nodus can be seen in *E. bolsoveri*, but there is some damage to this part and the presence of a nodus cannot be entirely ruled out.

The specimen from Derbyshire is the second species of the genus *Erasipteron* Pruvost, family Erasipteridae *sensu* Carpenter (1939). The type-species, *Erasipteron larischi* Pruvost, was described from a single hindwing from the Upper Carboniferous (Namurian C) of Czechoslovakia, and redescribed by Kukalová (1964); the new species is based on a forewing.

The type specimen of the new species probably consists of two wings, although only one is immediately visible. The two wings lie exactly one above the other, separated by a matrix of 0·5–1·0 mm. These wings were broken in the basal third, the two parts lying at right-angles to

† This name has already appeared a number of times in the popular press, but without formal diagnosis.

one another (Fig. 2). The double nature of the fossil can be seen one-third from the apex, where some of the overlying wing has been removed. The lower wing matches exactly the size and vein positions of the upper wing. There is a trace of the underlying wing near the base, but this is not as clear as the apex.

Two possibilities have to be considered. A single wing may have become separated into an upper and lower wing membrane and the space between filled up like a sac; the resulting 'double wing' would therefore be only the upper and lower membranes of one wing. Alternatively there are two wings which have been fossilized exactly together.

From an examination of the specimen the latter explanation seems more probable; for example, the thickness of the matrix between suggests two wings rather than an upper and lower surface of one wing.

It is difficult to tell from the amount of the lower wing revealed whether it is a fore or hind wing, but it is, in the apical part at least, an exact replica of the upper wing but with most of the convex–concave vein system flattened out. It is possible that the convex–concave system is identical with the upper wing. If this is correct then the lower wing is likely to be the hindwing from the same side as the upper wing (which I regard as a forewing), thus indicating that the insect was homoneurous, with a simpler anal area than in *E. larischi*. This would provide conclusive evidence of the two species being generically distinct. Unfortunately this hypothesis is based on the condition of the convex–concave state of the lower wing, which is not clearly visible.

With the information available I do not propose to describe a new genus but to redefine *Erasipteron* Pruvost. It is possible that there were differences between the forewings and hindwings in species of *Erasipteron*, which would explain some of the discrepancies between *E. larischi* (hindwing) and *E. bolsoveri* (forewing), but data are not available to support or contradict this. The new species may well be homoneurous but the facts are inconclusive.

E. bolsoveri is the most complete specimen of the larger, dragonfly-like Protodonata found in Britain, with an estimated wingspan of nearly 200 mm (8 inches), larger than any extant species.

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