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Arthropod Body Fossils from the Union Chapel Mine

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ABSTRACT: Arthropod body fossils are rare in the Pottsville formation. The assemblage of fossil material from the Union Chapel Mine, while containing a number of trackways which were made by arthropods or their larvae, includes, thus far, only two wing impressions and a possible arachnid body fossil. The fossils from the Union Chapel site were preserved only 15 million years after the oldest known winged insect. Thus, they represent relatively early and important representatives of this large and interesting group of animals. I will here attempt to review, first, the significance of insect body fossils from the Pennsylvanian in the fossil record of insects, followed by a description of the actual specimens. This report is intended to be a relatively superficial description of the arthropod finds to date at Union Chapel Mine with the hope of stimulating further, and more rigorous, future studies of these specimens.

INTRODUCTION

The first insects developed some 415 to 390 million years ago in the Lower Devonian (Gradstein and Ogg, 1996). These earliest members of the group, such as the collembolan (springtail) *Rhyniella* precursor from Scotland (Ross and Jarzembowski, 1993), were wingless. Interestingly, recent information derived from the analysis of mitochondrial DNA suggests that the evolution of the primitive wingless collembolans may have taken place separately from that of later winged insects (Nardi et al., 2003). Unfortunately, fossil remains from the first 90 million years of insect evolution are very rare (Labandeira and Sepkoski, 1993), and because of this large gap, both the time and the manner in which wings first developed in insects are unclear. Also, the pace at which insect evolution proceeded following the development of wings is unknown. The earliest winged insect, *Delitzschala bitterfeldensis* (Palaeodictyoptera: Spilapteridae), dates from the end of the Lower Carboniferous of Germany (Brauckmann and Schneider, 1996). However, it is apparent that for some time preceding that point, approximately 325 million years ago, a period of radical diversification occurred in insect evolution coincident with the development of wings and no doubt due to the increase in the number of ecological niches that flight permitted. When they become well represented in the fossil record at the end of the Early Carboniferous, winged insects are already more diverse at the ordinal level than they are today (Shear and Kukalová-Peck, 1990; Dudley, 2000). The wing structure in more primitive orders is palaeopterous while that of more advanced insects is neopterous (palaeopterous = insects with wings not folded over abdomen, laterally outstretched with the exception of the Diaphanopterodea; neopterous = insects with wings folded over abdomen.).

The selective pressure that favored the development of wings likely involved escape from predators as well as the ability to gain access to new food sources. Two theories have been put forth regarding anatomic origins in the evolution of wings in insects: (1) modification of existing limb branches that probably were functioning as gills in the progenitor arthropod and (2) *de novo* outgrowths from the body wall. Recent genetic evidence supports the former hypothesis: crustacean genes homologous to two wing-specific insect genes are specifically expressed in distal epipodite cells, part of a dorsal limb branch with respiratory and osmoregulatory functions (Averof and Cohen, 1997). This genetic evidence agrees with a common pattern in evolution: modification of previous structures to serve new functions. The modified gills may first have functioned for swimming and then to permit short gliding movements prior to their further development for fully independent flight.

The Paleozoic peak of insect diversity was reached in the Late Carboniferous to Early Permian (Labandeira and Sepkowski, 1993); however, this diversity was present at the ordinal but not at the family level (Jarzembowski, 2001). Some of these insects were the largest that have ever lived. The giant Carboniferous dragonfly *Meganeura monyi* had a wingspan of 66 cm and a thoracic diameter of 2.8 cm, and some paleodictyopterans were not far behind with wingspans up to 56 cm (Graham et al., 1995). It has been speculated that the development of gigantism among insects during the latter half of the Carboniferous was permitted by increases in the atmospheric oxygen concentration, which by some estimates may have reached 35% (Berner, 2001; Dudley, 1998). The increase in the partial pressure of oxygen could have permitted an increase in the size of animals such as insects with diffusion-limited tracheal systems for gas exchange. In addition, the increased partial pressure of oxygen was likely accompanied by an increase in total atmospheric pressure, further augmenting diffusion rates as well as resulting in additional lift from aerodynamic forces produced by wing movements (Dudley, 2000). Another change in ambient gas concentrations that could have facilitated rapid rates of cellular respiration was the tenfold decline in CO_2 levels from the late Silurian to Early Permian, eventually reaching levels comparable to those of today during the Middle to Late Pennsylvanian (Mora et al., 1996).

The importance of higher oxygen levels in the development of gigantism in Carboniferous arthropods has been questioned by some authorities. Bechly et al. (2001) suggest that gigantism and its disappearance correlates with the prior absence and later evolution of flying vertebrates. True giants make up only 1% of the fossil insects in the Coal Measures of southern England (E. Jarzembowski, written commun.); obviously, the level of preservation of insect fossils affects the ability to recognize smaller forms, for example, no blattoids (roach-like insects) have been recovered from the Union Chapel site to date, although they were likely very abundant. Other factors, such as drastically different predator-prey relationships than those of today, may have also played a role in the development of giant forms (Jarzembowski and Ross, 1996). It is interesting that by the close of the Permian, 5 of 32 orders of insects had become extinct, including two orders of the superorder Paleodictyopteroidea: Megasecoptera and Diaphanopterodea (Ross and Jarzembowski, 1993; Jarzembowski and Ross, 1996). The Paleodictyoptera became much less abundant as well; Bechly (1997) demonstrated a surviving member of the Palaeodictyoptera from the Lower Triassic, but this is the only member of that order which is known beyond the Permian. The disappearance of these orders, including nearly all of the gigantic forms, coincided, probably not coincidentally, with a drop in atmospheric oxygen levels, which eventually reached about 15% at the end of the Permian (Graham et al., 1995).

As Shear and Kukalová-Peck (1990) point out in their review of Paleozoic arthropods, wings are by far the most frequently preserved insect fossils, being relatively inedible and decay-resistant. The presence of large wing impressions as the sole representative of Insecta thus far from the Union Chapel site suggests, first, that conditions for preservation of insect body fossils favored relatively large insects, presumably at least partly because of the tidal ebb and flow through the marshes, and, second, that among large insects in this locality, palaeopterans were among the more abundant (since the only three known insect body fossils from the Pottsville of Walker County are of that group). However, as noted above, although it has been estimated that the four orders of the Palaeodictyopteroidea together make up almost half of the late Paleozoic entomofauna preserved in coal swamp deposits (Shear and Kukalová-Peck, 1990), some bias of ascertainment is likely present, in other collections as well as this, since large insect parts are more likely to be preserved and more likely to be recognizable, especially to amateurs, than small ones.

The Union Chapel site is a surface coal mine in Walker County, Alabama. The fossil-bearing slabs were all recovered from spoil piles adjacent to the highwall, which represents the point at which, some two years prior to the first collections from the site, excavation by the company had been halted due to the rising height of the overburden above the coal seams. The rocks at the site are characteristic of the Pottsville formation with cycles of coal-bearing shales alternating with sandstones and marine layers containing siderite nodules and brachiopods. Clear evidence of rapid tidal deposition of sediments can be found in the shales (Pashin, 2005). The track-bearing slabs appear to have derived from layers of shale adjacent to the coal seams. This is in accord with the previous observations in an underground mine in Walker County by Aldrich and Jones (1930); in that instance the tracks were found in shales within 76-107 cm (30-42 inches) above the Jagger coal seam. At the Union Chapel site the most detailed vertebrate tracks were found on slabs with a very fine particle size and surfaces bearing an almost polished appearance, suggesting that deposition of sediments occurred following the gentle withdrawal of the water, perhaps on a tidal mud flat relatively far from the coast. The particle composition of the shale bearing the wing impressions, while still quite fine as to permit considerable detail, is of a somewhat coarser grade, indicating a different local environment with higher depositional energy.

THE UNION CHAPEL INSECT WINGS

The first set of wing impressions found at the Union Chapel Mine are illustrated in Figures 1 and 2. They consist of fore and hind wings from a palaeopterous insect (8.1×3.7 cm and 9.1×4.1 cm respectively) in a reasonably life-like orientation suggesting that at least some portion of the thorax may have been present in the original specimen. All major veins are present, but neither archedictyon nor crossveins can be discerned (see below). No other invertebrates were evident in the small slabs of shale that contained the impressions, but lycopod and seed fern leaves are present in the layers of shale immediately adjacent to the impressions. They were found in July 2000, surprisingly enough in the middle of a rough dirt access road that led down to the base of the highwall of the mine, having presumably tumbled down one side of the adjacent embankment. The edge bearing the proximal part of the impressions appeared freshly broken, but a careful search of the roadbed and the embankment over several visits to the site failed to yield the remainder of the fossil. The impression corresponding to the obverse (dorsal) view of the wings was intact, but the reverse impression corresponding to the ventral view was fractured into five pieces that were still, however, associated with one another in a more or less undisturbed fashion. The image of this pair of fragile impressions, lying open like a book in the middle of a roadbed, up and down which heavy machinery had moved, still stand vividly in the author's memory as a breathtaking example of how the unlikeliest of chance events may still come to pass.

The absence of critical features from the base of the wing and any other anatomical features make it less likely that any definite identification can be made in more thorough studies. After review of photographs, one authority has identified the impressions as most likely repre-

FIGURE 1A. Palaeopterous wings from the Union Chapel Mine: Reverse (ventral) impression. Scale in inches (left) and centimeters (right).

senting a member of the large extinct order Palaeodictyoptera, whose members have been reported from the Upper Carboniferous to the Upper Permian (Günter Bechly, written commun.). None of three other authorities in the field who reviewed this report took issue with this tentative assignment. The wing structure of the order Palaeodictyoptera is defined as follows: "Wings containing all main veins, including MA, MP, CUA, and CUP, with alternation of convexities and concavities; main veins usually without coalescence and always arising independently; area between veins with a delicate, irregular network (archedictyon) or with true crossveins, or with a combination of both; intercalary veins present in a very few families (e.g., Syntonopteridae); fore and hind wings similar in form and venation in some families (e.g., Dictyoneuridae); in others (e.g., Spilapteridae) hind wings much broader than the fore pair with basic venational pattern remaining the same; in some others (e.g., Eugereonidae and Megaptilidae) hind wings only about half as long as fore wings; in one family (Diathemidae) hind wings minute, in a related family (Permothemistidae) hind wings com-

FIGURE 1B. Palaeopteran wings from the Union Chapel Mine: Obverse (dorsal) impression.

pletely absent; front margin of wing commonly serrate, costa with or without setae; wings in some families with prominent pigment markings" (Carpenter, 1992). After review of the photographs Jarmila Kukalová-Peck disagreed with the identification as a member of the Palaeodictyoptera, preferring instead to assign the specimen to the Ephemeroptera (mayflies). The Paleozoic representatives of this latter order are mainly from the Permian, including nymphs and adults from five extinct families, although some members are known from the Upper Carboniferous. Further definitive assignment will have to await the day when the actual specimen can be studied by authorities on the subject.

Since no members of the Palaeodictyoptera are extant, a few words on what is known or surmised about the biology of these insects are appropriate. The development of wings in palaeodictyopterans occurred gradually as the animal passed through a series of nymphal stages, so evidently these insects were hemimetabolous, i.e., they underwent gradual or "incomplete" metamorphosis. When fully developed, the wings were permanently outstretched as seen in mayflies or dragonflies, an adaptation which facilitates gliding movements, useful in conserving energy while searching for food but making flight difficult in dense foliage and presenting difficulties in high winds (Figure 3). The mouthparts of palaeodictyopterans were adapted for piercing and sucking, forming a formidable beak up to 32 mm long (Shear and Kukalová-Peck, 1990). Depending on the species, those with more robust mouthparts likely fed on the vascular tissue of tree fern fronds and seed fern pollen organs and ovules of *Cordaites* (Labandeira, 1998; Labandeira and Phillips, 1996), the latter two plant types both found in abundance among the plant material from the Union Chapel Mine tailings (Dilcher et al., 2005). Fossil nymph specimens have been described with spores or pollen filling the gut (Kukalová-Peck, 1985). Some species may have been able to bore holes in seeds or megaspores and extract the contents. The nymphs of paleodictyopterans were strictly terrestrial and fed on

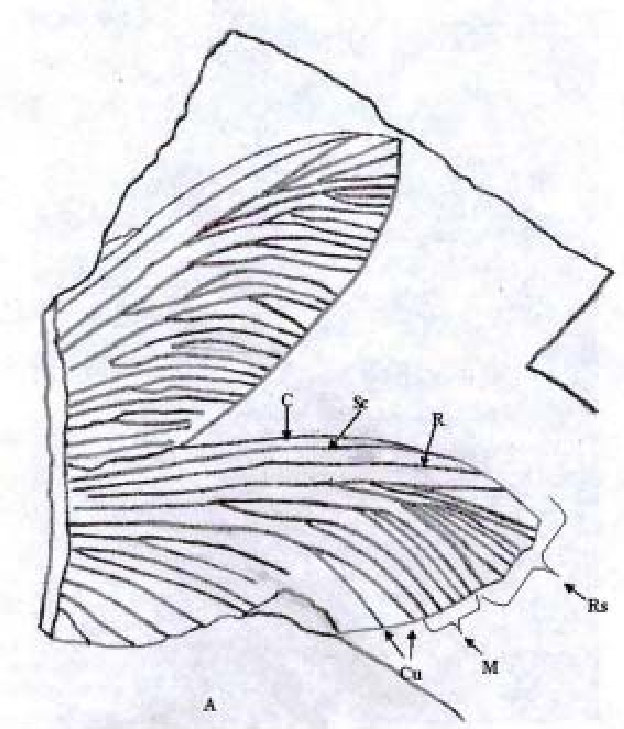

FIGURE 2. Line drawing detailing the venation of the wings. No archedictyon or crossvenation is evident. The venation is designated according to Tasch (1980). The costa is a heavy, unbranched vein forming the anterior margin of the wing. The subcosta is the next and is concave when viewed from the obverse (dorsal) aspect. The radius is commonly the heaviest vein in the wing and is convex in the obverse aspect. R branches into R1 and the Radial Sector which is then subdivided into four branches. Media is next, then cubitus, which branches to Cu1 (convex, often branched) and Cu2 (concave, unbranched). Anal veins (frequently unbranched) form a fan, generally set apart from Cu2 by the cubital furrow, along which the wing folds. C: Costa, Sc: Subcosta, R: Radius, Rs: Radial Sector, M: Media, Cu: Cubitus, A: Anal.

FIGURE 3. Restoration showing a paleodictyopteran insect (*Homaloneura* sp.) feeding on a *Cordaites* cone (Shear and Kukalová-Peck, 1990, with permission).

similar fructifications and probably vascular tissue. They were "peculiar, highly derived creatures ..... flattened, well-armored, and shaped like trilobites" (Shear and Kukalová-Peck, 1990), all obvious adaptations to escape predation. While these insects remained earthbound nymphs, such predators would have likely included a variety of insects and other arthropods, e.g. arachnids, as well as vertebrates, particularly land-dwelling amphibians and reptiles. Once the nymphs matured and became airworthy, they likely fell prey to the top predators of the Paleozoic skies: ancestral dragonflies similar to *Meganeura monyi* (although *M. monyi* is only described from the Late Pennsylvanian of Europe).

The abundance and diversity of invertebrate and vertebrate trace fossils and plant fossils in the Pottsville Formation (Westphalian A) at the Union Chapel site suggest that insects were probably well-represented in this ancient ecosystem. Insect trace fossils are abundant at the site (Rindsberg and Kopaska-Merkel, 2005). Arthropod body fossils are rare in the Pottsville Formation. A large insect wing impression, discovered by James A. Lacefield in tailings from another Walker County surface coal mine, is included for comparison; the specimen now resides in the collection of the Alabama Museum of Natural History (Figure 4; Lacefield, 2000). This specimen has been identified by Dr. Kukalová-Peck (written commun.), again from a photograph, as Palaeodictyoptera, family Breyeriidae, genus *Breyeria*.

One definite arachnid body fossil has been recovered from the Pottsville of Alabama (J. C. Pashin, personal commun., 2003). A possible trigonotarbid arachnid was found in May 2003 at the Union Chapel site by the author. The specimen has been tentatively identified by C. Labandeira from photographs (Figure 5). Further work is needed to establish the authenticity of this specimen as well as its assignment to a more specific group. Their inclusion in this report is permitted in the hope that it will stimulate further scholarly work.

Finally, a second large insect wing impression was found during the final stages of preparation of this report (Figure 6). From a photograph Kukalová-Peck felt that it was most likely a petiolate wing from a member of the Megasecoptera. As with the other specimens, a more definitive description will require careful study of the actual specimen by authorities in paleoentomology.

SUMMARY

Arthropod body fossils are present in the Union Chapel mine tailings and already comprise a considerable proportion of the scant total of such fossils recov-

FIGURE 4. Palaeodictyopteran wing impression from another surface coal mine on Alabama Highway 13 near its intersection with U.S. Highway 78, near Eldridge in Walker County, Alabama, collected in March 1993 by Jim Lacefield (Lacefield, 2000). Unlike the specimen from the Union Chapel site, in this impression a well-preserved archedictyon is present. This specimen was identified from photographs as a hind wing, order Palaeodictyoptera, family Breyeriidae, genus *Breyeria* (J. Kukalová-Peck, written commun.).

ered from the Pottsville of Alabama. One possible arachnid body fossil has been added to the UCM collection and awaits further study. The insect body fossils recovered to date consist of a pair of palaeopterous wings, likely representing either Palaeodictyoptera or possibly Ephemeroptera and another, more slender single wing, possibly from the Megasecoptera.

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FIGURE 5. Probable trigonotarbid arachnid (tentative identification by C. Labandeira, written commun.) collected by P. Atkinson, May 2003, Union Chapel Mine.

FIGURE 6. Single wing impression, probably from a member of the Megasecoptera (J. Kukalová-Peck, written commun.).

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