X-ray micro-tomography of Carboniferous stem-Dictyoptera: new insights into early insects

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Computer reconstructions of Archimylacris eggintoni, a Carboniferous stem-group dictyopteran (‘roachoid’), are presented. A siderite-hosted specimen was scanned using high-resolution X-ray microtomography (μCT), and a ‘virtual fossil’ was created with a resolution of 17.7 μm. This has revealed the morphology in great detail, including adhesive limb structures indicative of climbing and specializations for rapid movement. The antennae are filiform, and the mandibles are comparable to those of certain extant cockroaches, suggesting a similar generalist, saprophagous diet. The reconstruction reveals a high degree of specialization, and provides insights into the mode of life of these common Palaeozoic insects. Further μCT study of insect fossils has the potential to supplement wing venation with new characters, and hence improve fossil insect phylogenies.

Keywords: carboniferous; computer tomography; roachoid; Dictyoptera; siderite; Blattoptera

1. INTRODUCTION

Prior to the Upper Carboniferous, the insect fossil record is limited to a small number of incomplete specimens. Insects are relatively common in Coal Measures Lagerstätten, by which time the crown groups of many clades (e.g. Odonatoptera, Palaeodictyoptera) are present, together with the ‘roachoid’ Blattoptera, a diverse paraphyletic assemblage of stem-group Dictyoptera (cockroaches, termites and mantises). Such fossils are commonly voids within siderite (FeCO₃) nodules, preserving three-dimensional representations of the organisms. Nodules typically split along the animal’s dorsal surface; structures enclosed within part or counterpart (e.g. limbs) are normally visually inaccessible. Accordingly, taxonomic and phylogenetic work on Carboniferous insects relies heavily upon wing venation. Many fossils comprise only wings, and thus venation remains vital, but is unfortunately not an ideal character. It can prove problematic taxonomically at species level owing to intraspecific variation in both fossil (Brauckmann 1991) and living (Jarzembowski 2008) insects. Further, in some groups (e.g. cockroaches), asymmetry—which results in variation on a single individual—is common (Bell et al. 2007). Venation is less problematic for family level taxonomy, but proves phylogenetically less useful at this level, being frequently convergent (Kristensen 1998), with vein translocation (rapid fusion) common (Béthoux & Wieland 2009). Additionally, different paradigms provide significantly different phylogenetic implications (Béthoux 2008). Limited venation data for extant insects compounds these problems (Béthoux & Wieland 2009). Perhaps unsurprisingly, the phylogeny of these taxa is poorly resolved. Appendage details could provide new characters for phylogeny and greatly improve our knowledge of the palaeoecology of Carboniferous insects, but relatively few have hitherto been described (e.g. Béthoux 2009). Garwood et al. (2009) demonstrated that a microtomography (μCT)-based ‘virtual palaeontology’ approach can extract appendage data from siderite nodule fossils; we apply this method here to a blattopteran fossil.

2. MATERIAL AND METHODS

The studied specimen is the holotype of Archimylacris eggintoni (Bolton 1921; =Aphthonoblatella eggintoni, see Schneider 1983), from the Natural History Museum (NHM), London (In 31273, figure 1); Middle Coal Measures (between the Brooch and Thock coals, Bolton 1921), of the Clay croft open-cast works, Coseley Lagerstätte, Staffordshire, UK; Duckmantian in age (ca 311 Ma; Garwood et al. 2009). The fossil is void within a siderite nodule; it was scanned twice at the NHM on a Metris X-Tek HMX-ST. An unfiltered tungsten reflection target, and 3142 projections were used for both scans, one of the entire fossil (200 μA/225 kV), the 2000 × 2000 detector providing a resolution of 25.5 μm, and one of just the anterior to increase limb resolution (180 μA/225 kV, 17.7 μm). Computer models were created using the custom software (SPIERS) written by one of us (M.D.S.; e.g. Garwood et al. 2009). Each slice was manually cleaned digitally; distinct structures were assigned to masks and rendered as individual isosurfaces. Images in figure 2 were ray-traced with BLENDER (blender.org).

3. RESULTS

The wings of A. eggintoni are fully resolved (figure 2b,c) see also animation, electronic supplementary material; broad tegminous forewings are absent in one area (figure 2d) where the underlying hindwing is revealed. Venation is resolved, and is as described by Bolton (1921).

The models show antennae (figure 2a,b) with two basal segments—the scape and pedicel—and a minimum of 10 anuli in the flagellum. Ventral and posterior to their attachment are the mandibles (figure 2c), which are dicondylic (i.e. possessing two pivotal points with motion roughly confined to a single plane) with a ventral serrated ridge bearing four denticles. Dorsal to this is a more robust grinding (molar) surface. The head is poorly preserved, with only lateral margins resolved. The antennae and mandibles attach anterior to the pronotum (head shield), suggesting that the head protruded, an interpretation supported by localized discoloration (figure 1). The models’ cephalic boundaries (figure 2) were approximated on the basis of the preserved lateral margins.

Limbs are fully resolved. The coxae appear flattened (as in extant cockroaches)—best shown in the left midleg (figure 2e), which also displays the trochanter. The femur—typically the second longest article—is well resolved in all limbs. Distal to this is the tibia. Both tibia and femur are dorso-ventrally flattened and bear longitudinal ridges. The tarsus is split into
The antennae preserve a scape, pedicel and flagellum. They are filiform, and while probably incomplete, long annuli suggest the flagellum could comprise significantly fewer pseudosegments than found in crown-group cockroaches, which can possess in excess of 150. One is preserved parallel to the long axis of the organism, with the other at 70° to this. This flexibility suggests that *A. eggintoni* had well-developed sensory abilities, using its antennae to sweep a broad sensory arc as it moved, in a manner analogous to extant cockroaches.

The mandibles of *A. eggintoni* are closely comparable to the mouthparts of crown-group cockroaches, which are generalists, with great dietary versatility. The asymmetry preserved (left mandible larger) is often seen in extant cockroaches (*Zhuzhikov 2007*), the left overlapping the right, allowing the teeth to interdigitate (figure 2c). *Archimylacris eggintoni* has four sizeable denticles in the incisor region, an arrangement also seen in *Blaberus atropos* (*Zhuzhikov 2007, fig. 4d*), but simpler to that in pest species such as *Periplaneta americana*, which has several additional denticles (*Zhuzhikov 2007, fig. 4c*). *Blaberus atropos* is often found in decaying litter, epiphytes, hollows of trees and inside rotting logs (*Bell et al. 2007*). This—coupled with the Coal Measures environments in which the Blattoptera are typically found—suggests that *A. eggintoni* and other Carboniferous forest-dwelling stem-group Dictyoptera were saprophagous/detritivorous.

The limbs display adaptations that are indicative of rapid movement in extant cockroaches (i.e. a cursorial habit), including flattened, thin podomeres (*Full & Tu 1990*), a long femora and tibiae in all limbs (*Gullan & Cranston 2005*) and a low angle between the limbs and the body (*Kram et al. 1997*). Motion studies (*Frazier et al. 1999*) have shown that the five tarsomere arrangement is highly advantageous for rapid traversing of irregular terrain. The proportionally longer hind limbs of *A. eggintoni* are also present in pest species such as *P. americana*. This species takes a bipedal stance when running, overcoming limitations imposed upon stride length by shorter anterior limbs (*Full & Tu 1990*); *P. americana* is one of the fastest invertebrates known, relative to mass (*Bell et al. 2007*). The specializations towards cursorial habit seen in *A. eggintoni* suggest that it too was capable of very rapid movement.

Pretarsal claws are used in crown-group cockroaches only for climbing rough surfaces (*Bell et al. 2007*), suggesting that *A. eggintoni* was capable of venturing beyond the relative safety of the leaf litter. This is supported by the presence of euplantulae (figure 2f–i), used in modern forms for climbing smooth vertical surfaces such as those of plants (*Bell et al. 2007*). These structures tend to be lost by pure leaf-litter dwelling cockroaches, but retained by those which perch, forage or oviposit in leaves and on plants (e.g. *Deans & Roth 2003*).

The posterior of a flattened body is preserved (figure 2c). This, in conjunction with the low-angle limbs, creates a flat insect that could fit easily into crevices, suggesting a cryptic habit similar to that of crown roaches. Cerci (paired tail appendages) are known in all crown-group cockroaches, and their presence in primitive winged insects, e.g. the Palaeoptera, and Polyneoptera, suggests they are plesiomorphic to the Dictyoptera. Their absence here could result from decay. *Duncan et al. (2003)* present a series of cockroach decay experiments in which the disarticulation of cerci precedes that of the limbs, which themselves precede the loss of the ovipositor. The left
Figure 2. Computer reconstructions of *A. eggintoni*. (a) Dorsal view of anterior. (b) Ventral view of anterior. (c) Ventral view, showing all limbs and body. (d) Dorsal view showing wings, pronotum and head. (e) Mandibles. Looking posteriorly, labelling after Zhuzhikov (2007). (f) Right foreleg in the lateral view. (g) Right ventral foreleg. (h) Right midleg in the lateral view. (i) Right ventral midleg. Scale bars, (a,b) 1 mm; (c,d) 5 mm; (e–i) 0.5 mm. All images from the higher resolution model except (c,d). AA, anterior acetabulum; AN, antennae; CA, coxa; D.ap, apical tooth; D.m1 – D.m3, marginal teeth; EU, euplantulae; FE, femur; FL, flagellum; FW, forewing; HE, head; HW, hindwing; IN, incisor; L1, foreleg; L2, midleg; L3, hindleg; LC, lateral claw; MA, mandibles; ML, left mandible; MR, right mandible; MS, molar surface; PC, posterior condyle; PE, pedicel; PN, pronotum; SC, scape; T1–5, tarsomeres 1–5; TA, tarsus; TI, tibia.
hindleg in this fossil is missing, suggesting that partial limb decay is recorded, and hence that decay has progressed beyond the loss of the cerci. The remaining limbs appear well preserved, suggesting that the absence of an ovipositor is not taphonomic. A more plausible explanation for its absence is that the specimen is a male.

This study demonstrates the use of μ-CT-based approaches in the study of siderite-hosted fossils; otherwise unobtainable characters are resolved that—in insects—provide additional characters to wing venation for building phylogenies. The resolution of appendage morphology can provide new insights into the mode of life of Carboniferous organisms. Archimylacris eggintoni shows a high degree of specialization early in the evolution of insects. It was likely to have been a fast runner in life, but also had the ability to climb plant surfaces. Its diet was probably comparable to that of modern forest cockroaches. Its anatomical—and by inference functional and ecological—similarity to crown-group cockroaches (e.g. Bell et al. 2007, figs 1.4, 2.7A, 2.8 and 3.7) is apparent; this emphasizes the cockroach-like nature of the dictyopteran stem group, highlighting in contrast the derived and specialized nature of the mantids.

We thank Claire Mellish (NHM) and Andy Ross (NMS) for the loan of material. Thanks also to Andy Ross, and two anonymous referees for valuable comments on the manuscript. R.G. thanks Richard Abel for CT training and Olivier Béthoux for valuable discussion and advice. R.G.’s work is funded by an NERC PhD studentship.