Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois

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ANDERSON, L. I. 1994. Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois. Proceedings of the Geologists' Association, 105, 265–275. Euproops kilmersdonensis Ambrose & Romano, 1972 is proposed as a synonym of Euproops danae (Meek & Worthen, 1865) from Mazon Creek, Illinois. Five other species attributed to Euproops Meek, 1867 and one species attributed to Prestwichianella nitida Dix & Pringle, 1929, from the Westphalian D of the South Wales Coalfield, described by Dix & Pringle (1929, 1930) are also synonymized with E. danae. In addition, six species described by Raymond (1944) from Mazon Creek are synonymized with E. danae. The taphonomic processes acting upon xiphosuran body fossils produce spurious morphological differences between specimens, which have been used in the past to define species. It is concluded that species diversity within the Carboniferous Xiphosura was low, contrary to previous reports (Fisher, 1984). The mode of life of E. danae is re-evaluated in the light of trace fossils recently described by Pollard & Hardy (1991) from Writhlington Geological Nature Reserve, and from palaeophysiological considerations.

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1. INTRODUCTION

Xiphosuran body fossils collected from the mine tip of the Kilmersdon Colliery near Radstock, Somerset by students of the Department of Geology, University of Sheffield were described as Euproops kilmersdonensis Ambrose & Romano, 1972. Previous to this, Greenwell (1867) had noted the occurrence of xiphosurans from the Radstock Basin. Recently, more material collected from the similar strata of the Writhlington Geological Nature Reserve rock store, was supplied to the author by Dr E. Jarzembowsi. Examination of this new material, now housed in the collections of Manchester Museum, together with re-examination of the original Kilmersdon fossils housed in the collections of the NHM, has prompted questioning of the validity of the species. This concern was hinted at by Fisher (1979) and Jarzembowski (1989). This paper suggests a number of reasons why excessive taxonomic splitting exists within the xiphosuran fossil record.

The xiphosurans of the Coal Measures, as a whole, are in need of taxonomic revision, with many synonyms apparent in the two most common genera Euproops Meek, 1867 and Bellinurus Pictet, 1846 (spelling following Morris, 1980), as a result of over forty years of splitting. In addition, the chance finds of rare xiphosuran body fossils has caused the literature to develop in a rather haphazard way, with many species and even genera being represented by single specimens (Siveter & Selden, 1987). Ambrose & Romano (1972) doubted the value of defining new species on length/ width ratios within deformed rock; an observation which

would have served previous workers well had they taken this into consideration. However, there is another factor which could potentially cause distortion of a fossil: dorso-ventral compressional approximation, and it was recognition of this that prompted re-examination of material.

Institutional abbreviations: NHM, British Museum (Natural History), London; BGS GSM, British Geological Survey, Geological Survey Museum, Keyworth, Nottingham; NMW, National Museums of Wales, Cardiff; MCZ, Museum of Comparative Zoology, Cambridge, USA; LL, Manchester Museum.

2. TAPHONOMY AND PRESERVATION

The recognition of E. kilmersdonensis as a synonym of E. danae is based on the unpublished work of Fisher (1975a), along with previously unrecognized features in the new material. Fisher (1975a), working on Euproops danae preserved in sideritic nodules from Mazon Creek, noted that compressional approximation, the process by which dorsal and ventral topographic features of the cuticle are combined on one surface, with the degree of deformation controlled by solid structures lying between the dorsal and ventral cuticular surfaces, had resulted in a spurious number of species. These could be anatomical structures such as the prosomal appendages, or sediment infill, or diagenetic mineral growth of kaolinite and pyrite within the shelter porosity, defined by the ventral surfaces of the prosoma and opisthosoma. The genus

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Fig. 1. (a) LL 11041, Manchester Museum, *Euproops danae* (part), WGNR (\times 2). (b) LL 11041, counterpart (\times 2). (c) BGS GSM 25424, British Geological Survey, Holotype of *E. graigolae* (\times 1.5). (d) LL 11049 Enrolled *Euproops danae*, WGNR. (e) BGS GSM 48529, British Geological Survey, Holotype of *E. meeki* (\times 2). (f) LL 11045 (\times 5) *E. danae* from Lower Writhlington, in enrolled posture. (g) BGS GSM 48524, holotype of *E. gwenti* (\times 2).

Euproops occurs both in sideritic nodules (Ambrose & Romano, 1972), and in non-nodular preservational settings. The latter generally takes two forms: roof shales to coal seams; and laminar sideritic claystone beds, also overlying coals (van der Heide, 1951). Preservation in roof shales shows the most extreme effects of compression, with little surface detail preserved and, in some cases, the fossil is reduced to little more than a graphitic film. Sideritic claystones exhibit intermediate levels of preservation between these two extremes.

Compression of the prosoma, in the first instance, causes distortion of the otherwise curved anterior prosomal margin. Flattening of the anterior prosomal arch results in a relatively straight anterior border (see Fig. 2). This was one of the features by which E. kilmersdonensis was diagnosed different from E. danae (Ambrose & Romano, 1972). Further compression results in the collapse and wrinkling of the cuticle in the vicinity of the cardiophthalmic region, splaying out of the genal spines, and an increase in the angle defined by these genal spines and the posterior margin of the prosoma. Pickett (1984) stated that in compression experiments performed on juveniles of the extant xiphosuran Limulus polyphemus, the length of the prosoma was reduced by around 10%. This seems to have been accommodated in the wrinkling and creasing of the cuticle. Obviously, this has marked implications for any xiphosuran fossil species defined purely on length/width ratios of the prosoma and the magnitude of the genal angles.

The way in which the fossil matrix splits has a bearing on the final appearance of the fossil. In dorso-ventrally flattened xiphosurans, splitting occurs along a line of weakness which approximates to the dorsal surface of the animal. Any structure projecting out from, or above this line will be snapped off on splitting, and left embedded in the counterpart of the nodule. This is the case where spines project up from the axial nodes of the opisthosoma, a character of both Euproops and Bellinurus. The same process affects the ophthalmic spines, the posteriorly directed continuations of the ophthalmic ridges which bear the lateral compound eyes of the xiphosuran. Ophthalmic spines are present in both Euproops and Bellinurus (see Fig. 2). It is always the case that in sideritic nodule preservation, the ophthalmic spines are separated from the plane of the dorsal surface of the opisthosoma by intervening matrix. On splitting open the nodule, the spines are left hidden in the counterpart. However, the same process operates in the laminar sideritic claystones of Writhlington and the South Wales occurrences. Without preparation of the specimens, such spines may be interpreted as being absent. Under instances of more extreme compression, the spines may be forced down onto, and imprint the surface of, the opisthosoma through the intervening body of sediment (see Ambrose & Romano, 1972, pl. 113, fig. 1).



Fig. 2. NHM IA 1. $(\times 2)$ Isolated prosoma showing the extent of the ophthalmic spines.

Ambrose & Romano (1972) stated that original cuticular material was preserved on the Kilmersdon xiphosurans. This appears not to be the case, with preservation in the form of carbonaceous compressions or even as a graphitic film (Fig. 1(f)). It may be that comparisons were drawn with eurypterid fossils, which commonly retain original cuticle. Much more unusual conditions may be required to preserve xiphosuran cuticle, such as those encountered in the Lower Carboniferous (Dinantian) 'Shrimp Beds' of Scotland (Briggs & Clarkson, 1989; Briggs & Kear, 1993).

3. MODE OF LIFE

(a) Subaerial excursions?

The possibility that Euproops danae was partially subaerial in its habits was suggested by Fisher (1975a, b, 1979). This particular idea has subsequently been perpetuated by a number of authors, e.g. Brauckmann (1982), Todd (1991). The hypothesis of a subaerial component to the mode of life of Euproops was based on three lines of evidence. First, the more frequent occurrence of Euproops with terrestrial rather than aquatic elements of the flora and fauna. This, however, is explainable by invoking a rather shallow-water habitat for the animal, where the relative input of land-derived material would be greater than that expected in the deeper lacustrine setting. Second, the resemblance between the genal and ophthalmic spines of Euproops and lycopod foliage, in particular Lepidophyllum, was interpreted by Fisher (1979) as being indicative of a mimetic relationship. This does not explain why the other common Carboniferous genus, Bellinurus, recorded from the Westphalian A and B of the Coal Measures, possesses somewhat similar ophthalmic spine morphology, a feature which Fisher (1979) did not recognize. No claims have been made for subaerial activities for this genus, widely held to be an inhabitant of the deep lacustrine (van der Heide, 1951) or deltaic environment (Hardy, 1970a, b). Third, the association of Euproops with millipedes and scorpions in one type of coprolitic concretion, whilst bivalves and aquatic crustaceans occur exclusively in another type was cited as possible evidence for the presence of Euproops in the subaerial context, where it could be predated on by animals feeding on these other undeniably terrestrial elements of the fauna. However, I suggest that this is due to a preservational or taphonomic bias, with the chitinous exoskeletons of millipedes, scorpions and xiphosurans requiring different diagenetic conditions for the preservation to the calcium carbonate of the bivalves and crustaceans.

As to the extent and duration of subaerial activity, Fisher (1979) hypothesized that periods of several hours to several days may have been involved. This invokes a more amphibious existence than is proposed here for *Euproops*. It is accepted that from what is known of extant xiphosurans' high tolerance to adverse environmental conditions, *Euproops* could feasibly have emerged from the shallow water environments which it inhabited, for short periods of time. The reasons as to why it should indulge in such behaviour were not made clear, although the most obvious one is for reproduction.

An aspect of the palaeophysiology of *Euproops* which should be taken into consideration in the viability of subaerial activity, is the increased demands on the respiratory system on emergence from the aqueous environment. The respiratory organs of Limulus, the 'book-gills', collapse (Reisinger, Tutter & Welsch, 1991) when out of water due to a lack of support. Although still functioning, they operate at a much reduced efficiency, and supply insufficient oxygen to allow sustained locomotory activity (Rudloe, 1978). In order to work efficiently, the gills must be fully submerged in flowing oxygenated water, or at least kept moist in the subaerial environment. The closely related eurypterids are interpreted as having both lamellate gills and a kiemenplatten, an accessory aerial respiratory organ (Manning & Dunlop, in press). Without similar accessory respiratory organs, Euproops may have had great difficulty in obtaining sufficient oxygen in the subaerial environment, let alone embarking on sustained subaerial activity. Accessory respiratory structures have not been recorded in Limulus.

One reason as to why *Euproops* may have ventured forth into the subaerial environment, that of exploiting alternative food sources, also presents difficulties, when one considers the problems associated with xiphosuran feeding mechanisms in relation to the subaerial environment. *Limulus* feeds by grinding up food in the gnathobases before passing it, in aqueous suspension, to the mouth. This process is only effective in the subaqueous environment. Subaerial feeding requires the development of different mechanisms, such as external digestion in a pre-oral cavity, a method utilized by some terrestrial chelicerates (Selden & Jeram, 1989). The possibility that *Euproops* moved between adjacent pools in the search for food cannot be ruled out.

(b) Locomotion

Limulus polyphemus has been the subject of a number of studies in relation to its burrowing and swimming capabilities (Eldredge, 1970; Vosatka, 1970; Fisher, 1975a, b). Larval Limulus is an active swimmer (Rudloe, 1978) but, at first moult, it becomes a predominantly benthic animal. During subaqueous walking, Limulus walks in-phase. This is effectively an adaptation of the swimming movement, which is sufficient for walking on a subaqueous substrate, due to the bouyant support lent to the animal by the surrounding water. However, on emergence, such a mode of locomotion is clumsy. The overall effect of in-phase locomotion subaerially is to make the animal flop forward, perhaps producing a similar trace fossil to that described by Briggs, Dalingwater & Selden (1991), which clearly shows the repeated imprint of the coxal region of a eurypterid. All trace fossils attributed to the walking activity of xiphosurans exhibit an in-phase mode of locomotion, and were formed in the sub-aqueous environment (Goldring & Seilacher, 1971).

Limulus is able to drag itself across sandy substrates, but it would seem reasonable to suspect that slightly more uneven substrates would present a sizeable obstacle to such subaerial locomotion. Where movement was attempted by *Euproops* through a rather dense and cluttered cover of forest floor litter, the conditions implied by Todd (1991), then overturning, an everpresent danger whilst not walking on a flat, horizontal surface, would result in vulnerability to predation. The righting mechanism employed by *Euproops*, upon overturning, requires further investigation. Due to its posteriorly-directed ophthalmic spines, it would perhaps be unable to use the same strategy as *Limulus*, flexing the opisthosoma and prosoma dorsally whilst gaining leverage from the tail spine.

Although *Euproops* possesses the anterior prosomal arch, used by *Limulus* as an adaptation to burrowing activities, burrowing may not have been common behaviour of *Euproops*. Ichnological evidence presented by Pollard & Hardy (1991) from Writhlington appears to back this hypothesis, consisting solely of walking trackways, *Kouphichnium* Nopsca, 1923, with no evidence of burrowing activity, such as *Selenichnites* Romano & Whyte, 1990, traces attributed to xiphosuran activity by Wang (1993). This would suggest a predominantly benthic lifestyle, possibly the result of low oxygen conditions infaunally.

(c) Functional significance of spines

In the defensive role, spines may be used to make the organism appear larger than it really is, provide an uncomfortable mouthful or increase the ratio of indigestible to nutritional material, making a less attractive meal option to the predator. Fisher (1977) suggested that the spine morphology of Euproops danae may have been used in defensive enrollment and subsequent settling to the substrate through the water column on attack by a predator. I agree with this suggestion. Enrollment of the prosoma and opisthosoma is facilitated by a microtergite positioned between the prosoma and opisthosoma. Two examples of enrolled Euproops were observed in the material studied, LL 11045 (Fig. 1(d)) and LL 11043 (Fig. 1(f)). Coaptive structures, such as those found in some trilobites, have not been identified in xiphosurans. As Fig. 4 shows, enrollment would not inhibit the respiratory demands of the animal as complete closure of the prosoma onto the opisthosoma still leaves both the anterior prosomal arch and the posterior opisthosomal arch open. This would allow oxygenated water to circulate around the book gills whilst still in a spiky ball posture, detering further

attack. Enrollment would be of little use, and potentially difficult to achieve infaunally, but would be highly effective on the sediment surface as a defensive measure.

Additionally, the pleural flange and the elongated pleural spines of *Euproops* could have increased the effective surface area of the opisthosoma, providing a 'snowshoe' to prevent sinking into soft substrates. This use of the pleural spines has been suggested for the Lower Carboniferous *Rolfeia fouldenensis* (Waterston, 1985) and may explain the morphology of the bizarrelooking Middle Triassic form, *Austrolimulus fletcheri* Riek, 1955 from Australia. Soft, black, anoxic muds which may have floored the Writhlington lake would have provided the habitat for *Euproops* to utilize these adaptations.

(d) Freshwater dwellers

Higgs (1988) suggested that the presence of trails attributable to both fish and xiphosurans on the same bedding plane of lacustrine sediments indicated a possible predator-prey relationship. He suggested that the palaeoniscid fish, *Cornuboniscus budensis* White 1939, endemic to the Westphalian A-C 'Lake Bude' (Higgs, 1988), would have been ideally adapted to picking off benthic xiphosurans from the sediment substrate with its belly-skimming mode of life, and I agree with this view. Fish body fossils are yet to be confirmed from the Writhlington Geological Nature Reserve. However, the ridged fish egg capsule, *Palaeoxyris*, has been recorded from Writhlington (Jarzembowski, 1989).

There are at least four instar moult stages of Euproops danae present within the population from Writhlington. Although transportational sorting of fossils could introduce artificial size classes, this is not considered to be a significant factor here. Todd (1991) noted that there were significant animal-sublithology associations within the fauna, and considered arachnids with attached legs and insects with attached wings to represent minimally transported material (The Writhlington trigonotarbids lack legs in many cases, although the prosoma and opisthosoma are still articulated indicating minimal transportation, J. Dunlop pers. comm.). Euproops was found occurring in the same sublithology, and presumably subject to similar, if not less energetic transport conditions. This suggests that Euproops was actually a freshwater dweller, and its presence in the fauna is due to a breeding population and not just to lost individuals, which may have wandered upstream from the delta front (Tyler, 1988). This fits in with its occurrence at other sites associated with freshwater and terrestrial floral and faunal elements (Beall, 1991). This seven exoskeletons preserved on the one slab described by Ambrose & Romano (1972) may represent a moulting assemblage, analogous to the trilobite moulting assemblages described by Speyer (1985). They are all of the same instar, and this may be of significance, as it has been noted that *Limulus* moults in large numbers, synchronously, in order to effectively flood the prey market (Rudloe, 1978). Dalingwater (1985) considers it unlikely that even a relatively small *Limulus* could moult on land, due to the mechanical stresses placed on the limbs whilst crawling out of the ecdysial suture and this may also be true of *Euproops*.

4. SYSTEMATIC PALAEONTOLOGY

Class XIPHOSURA Latreille, 1802 Order XIPHOSURIDA Latreille, 1802 Suborder LIMULINA Richter & Richter, 1929 Infraorder LIMULICINA Richter & Richter, 1929 Superfamily EUPROOPIDEA Eller, 1938 Family EUPROOPIDAE Eller, 1938 Genus EUPROOPS Meek, 1867

Type species Euproops danae (Meek & Worthen, 1865).

Emended diagnosis

Opisthosomal axis comprised of nine segments, of which the first segment is reduced to a microtergite, lacking adjacent pleural fields. Second and fourth segments possess a spine-bearing tubercle. Terminal fused segments 7–9 give rise to a single, large tubercle from which a sharp, posteriorly-directed spine projects.

Remarks

The recognition of the presence of nine segments forming the opisthosomal axis, instead of the previously recorded eight, is in agreement with the primitive number proposed by Pickett (1993) for the Upper Devonian form *Kasibelinurus* Pickett, 1993. Study of available specimens of the genus *Bellinurus* Pictet, 1846, also confirms the presence of nine segments in the axial column. This initial segment manifests itself as a microtergite in *Euproops* and *Bellinurus* and is clearly seen in specimens which are in an enrolled posture. It is commonly obscured by the posterior margin of the prosoma.

The genus *Prestwichianella* was synonymized with *Euproops* by Stubblefield (1947) (Størmer, 1955). The genus *Prestwichia* Woodward 1867, was shown to be preoccupied by Lubbock in 1863 (Cockerell, 1905), and subsequently renamed *Prestwichianella*. It was differentiated from *Euproops*, on the basis of the form and markings of the glabella, referring to the interophthalmic ridges, which show variable surface relief depending on the amount of compressional deformation suffered. In the synonymy list below, 'v' indicates that the specimen described in the paper has been seen by the author, whilst the date in italics indicates that the specimen was mentioned in the publication, but without

the addition of any new information. For a full treatment of synonymy listings, the reader is referred to Matthews (1973).

Euproops danae (Meek & Worthen, 1865)

- 1865 *Bellinurus danae* Meek & Worthen: 44, figs 4–7, pls 9–13(f)
- 1867 Euproops danae Meek: 320
- 1892 Prestwichia (Euproops) scheeleana Ebert: 218-20
- 1918 Prestwichianella Woodward: 469
- 1918 Euproops amiae Woodward: 465, figs 2-4
- v1929 Euproops graigolae Dix & Pringle: 104–5, fig. 10; 114, fig. 16
- v1929 Euproops gwenti Dix & Pringle: 105–7, fig. 11; 114, fig. 16
- 1929 Euproops islwyni Dix & Pringle: 107, fig. 12; 114, fig. 16
- v1929 Euproops meeki Dix & Pringle: 108–9, fig. 13; 114, fig. 16
- v1929 Euproops scheeleana Ebert; Dix & Pringle: 111
- 1929 Prestwichianella nitida Dix & Pringle: 101, fig. 9
- v1930 Euproops graigolae Dix & Pringle: 144, table 1
- v1930 Euproops gwenti Dix & Pringle: 144, table 1 1930 Euproops islwyni Dix & Pringle: 144, table 1
- v1930 Euproops scheeleana Dix & Pringle: 144, table 1
- 1935 Euproops packardi Willard & Jones: 127, figs 1-2
- 1944 Euproops amiae Woodward; Raymond: 493
- 1944 Euproops danae Raymond: 484
- 1944 Euproops darrahi Raymond: 489
- 1944 Euproops laevicula Raymond: 490, fig. 3
- 1944 Euproops laticephalus Raymond: 491, fig. 4
- 1944 Euproops longispina Packard; Raymond: 491
- 1944 Euproops packardi Willard & Jones; Raymond: 493
- 1944 Euproops thompsoni Raymond: 486, fig. 1
- 1945 Euproops thompsoni Raymond; Raymond: 7
- 1945 Euproops laevicula Raymond; Raymond: 7
- 1957 Euproops amiae Raymond; Copeland: 49, pl. 17, figs 1–8
- 1957 *Euproops danae* Raymond; Copeland: 49, pl. 17, fig. 9, pl. 21, fig. 1
- v1972 Euproops kilmersdonensis Ambrose & Romano, text-fig. 2, pl. 112, figs 1–3, pl. 113, fig. 1
- v1979 Euproops kilmersdonensis Fisher: 431
- v1982 Euproops kilmersdonensis Brauckmann: 22
- v1989 Euproops kilmersdonensis Jarzembowski: 223
- v1991 Euproops kilmersdonensis Pollard & Hardy: 170; 176

Type material

Extensive literature research failed to reveal the repository of the holotype of *Euproops danae*. However, Raymond (1944) described the species with reference to two specimens in the collection of the Museum of Comparative Zoology, Harvard, Cambridge, USA

MCZ 4673 (refd. Raymond, 1944, p. 486), MCZ 4686 (refd. Raymond, 1944, p. 486). These should be considered as neotypes.

Material examined

NHM It. 61012 (holotype of *E. kilmersdonensis*), It. 61013 (paratype), 61014–61018 (figd.); BGS GSM 25424 (holotype of *E. graigolae*), BGS 48523–4 (holotype of *E. gwenti*), BGS GSM 48528–9 (holotype of *E. meeki*); NMW 70.17G.11, LL 11049 (Kilmersdon tip), LL 11041–LL 11048, LL 11050–LL 11054 (Writhlington rock store), NHM IA 1.

Emended diagnosis

Posterior of cardiac lobe constricted and bears a median tubercle. Genal spines long and narrow. Opisthosomal rim moderately narrow with long pleural spines. Interpleural ridges smooth, without tuberculation.

Description

Prosoma semicircular in outline, with the anterior margin formed into an arch (see Fig. 3). Genal spines narrow and parallel with long axis of the body; spines exhibit allometric growth. Cardiac lobe small, reduced



Fig. 3. Reconstruction of *Euproops danae* (scale bar = 1 cm). (a) Dorsal view; (b) lateral view (prosomal appendages not shown); *(c) anterior view.*

5. SIGNIFICANCE OF THE WRITHLINGTON XIPHOSURANS

The recognition of these synonymies raises the question of xiphosuran species and indeed, arthropod diversity within the Coal Measures sequence as a whole. The differences used to identify species in the past have been based on taphonomically introduced ones rather than biological ones. Dunlop (1994) reports a similar case of excessive taxonomic splitting in the arachnid Pleophrynus verrucosa (Pocock, 1911) from Mazon Creek, Writhlington and the South Wales Coalfield. Indeed, diversity within the Xiphosura as a whole appears to be based more on generic-level characters rather than specific characters. This is what one would intuitively expect from variable salinity tolerant organisms such as xiphosurans in the relatively stable, long-ranging Coal Measures environment. A similar situation is suspected to exist in the genus Bellinurus.

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