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Arthropod cuticles in coal

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Abstract: An abundance of scorpion cuticles from Westphalian (Upper Carboniferous) coals of Yorkshire is described, and other records of arthropod cuticles in coals are reviewed. The absence of cuticles assignable to arthropod groups other than scorpions is thought to be due to preferential preservation of the unique exocuticle of scorpions; it alone is preserved and appears to retain an organic nature. The cuticle is recovered from all the lithotypes of humic bituminous coals although it is most common in coals rich in inertinite macerals. From the present study it is uncertain whether the scorpions were aquatic or terrestrial. The recognition of arthropod cuticle as a coal maceral could aid environmental interpretations. The abundance of arthropod cuticle in the coals studied indicates its potential use in correlation and in determining the thermal maturity of sediments.

In recent years increasing numbers of arthropods and arthropod fragments have been isolated from rocks by acid treatment. There is now an increasing awareness of the value of such rock digestion to the study of fossil arthropods. The earliest terrestrial arthropods from America were discovered unexpectedly whilst etching Middle Devonian mudstones of Gilboa, New York for plant fossils (Shear *et al.* 1984). Preserved as minute, opaque, black flakes, the arthropods are indistinguishable from plant remains in incident light, but using transmitted light microscopy a wealth of morphological detail is revealed. In other instances too, lithologies apparently barren of arthropods at the macroscopic level have yielded beautifully preserved arthropod fragments and microarthropods on digestion. These have included insects, crustaceans and spiders from concretions of Miocene age from the Mojave desert, California (Palmer 1957), an exciting new scorpion from late Devonian Onteora beds of New York (Kjellesvig-Waering 1986, p. 126) and remarkable phosphatized trilobites and crustaceans from Cambrian 'Orsten' (calcareous nodules) of Sweden (Müller 1979, 1985; Müller & Walossek 1985). Recovery of mineralized parts of the exoskeleton of trilobites and crustaceans by acid digestion is well known (Cooper & Whittington 1965) and rare replacement of ostracode soft parts has enabled detailed observations of their cuticle and appendages (Bate 1972; Bate & East 1972).

Coal would seem to be a promising facies in which to search for arthropod remains using etching techniques because palaeobotanists recover well-preserved plant cuticles and spores from coals and they have already recovered some arthropod cuticles in the process. Additionally, coal is considered generally to be an autochthonous terrestrial deposit; terrestrial arthropods are uncommon, and to find new forms in their natural habitat would further knowledge of arthropod evolution and palaeoecology. Following recovery of abundant arthropod fragments in Yorkshire coals by one of us (KMB) during palaeobotanical investigations, further work is now being carried out (AJJ and PAS) on the arthropods. We present here a preliminary description of the material from Yorkshire, a review of other reports of arthropod material in coal, and a discussion of results and possible directions for future research.

The Yorkshire material

The cuticles were obtained from preparations of coals and associated sediments from three exposures of the Barnsley Seam (Westphalian B): Wistow Mine (NGR SE 59 36), St Aidans Extension Opencast Mine (NGR SE 40 28) and Lowther North Opencast Mine (NGR SE 39 28), and also from the Lidgett Seam and a series of thin coals exposed at Swillington Brickpits (NGR SE 38 31). Stratigraphically, the Swillington section (Westphalian B) lies below the Barnsley Seam.

The material was collected by bulk sampling, by interval sampling using 1 cm thicknesses of coal, and by incremental division of core material. The coals were macerated by oxidation in fuming nitric acid followed by distilled water and 10% ammonia solution. Initially the shales were digested in hydrofluoric acid, but it was found that arthropod cuticles could be recovered from weathered shales by gentle disaggregation in water, or if carbonaceous, in 100% volume hydrogen peroxide. The residues retained, after maceration on a 180-μm mesh sieve were examined, the arthropod cuticle picked from the wet residue and mounted in glycerine jelly for study using transmitted light microscopy.

The cuticles are translucent, pale yellow to orange-brown in colour, and they range in size from 0.2 to 10 mm. Detailed preservation is good, retaining such details as setae, sense organs and cuticular ultrastructure. Most of the cuticles (about 70%) occur as small fragments, although disarticulated organs such as chelae, podomeres and tergites are recovered. Occasionally, articulated pieces are found in connection, typically podomeres. They may form the basis for whole arthropod reconstructions. Almost all the material is readily assignable to the Scorpionida, and nearly all parts of the body have been found, including characteristic organs such as pedipalp chelae, pectines and stings (Fig. 1). The cuticle fragments are identified as being of scorpion origin by comparing their ornamentation with that of the recognizable scorpion organs. Numerous scorpion taxa are present, but their description awaits further material.

In addition to the obvious scorpion cuticle, a few tergites and podomeres exhibit a distinctive eurypterid-like ornamentation. In all other aspects these pieces are scorpion-like and it is interesting to note that Kjellesvig-Waering (1986 p. 21) remarked on the eurypterid-like ornamentation of the Lower Carboniferous scorpion *Archaeoctonus glaber* (Peach).

The cuticles were sectioned for examination using transmission electron microscopy, and were torn and sputter-coated with gold for scanning electron microscopy. These techniques revealed that the cuticle possessed a layered, finely banded ultrastructure. The total cuticle thickness ranged from 1.2 μm to 4.3 μm.

Cuticle preservation

The virtual absence of cuticles of arthropods other than scorpions in the Yorkshire material is surprising, as macrofossil evidence suggests diverse arthropod faunas (e.g. Rolfe 1980). A possible explanation of this apparent enigma is that the cuticle of modern scorpions is unique amongst extant arthropods in containing a hyaline layer in the exocuticle (Kennaugh 1959) (although it may be present in *Limulus*). The fossil scorpions may also have had this layer which contributed to their preferential preservation.

Scorpion macrofosils, although rare, yield a far better record than any other arthropod group with a non-mineralized exoskeleton. The vast majority of scorpion fossils has been recovered from the Upper Carboniferous Coal Measures of Europe and North America (Kjellesvig-Waering 1986) where they are most commonly preserved in ironstone nodules. Most others are compression fossils, but in both kinds of preservation cuticle frequently adheres to the fossil (e.g. Wills 1959, 1961). In comparison, fossilized cuticle of other arthropods is much less frequently found, even in cases of exceptional preservation such as that of the Mazon Creek biotas.

The arthropod cuticle is one of nature's most complex tissues and cannot be characterized simply by reference to one of its components, e.g. the common polysaccharide chitin. Possession of an exoskeleton is characteristic of all arthropods and is a contributing factor in their great success, for arthropods account for around 85% of extant animal species. Not surprisingly therefore, the structure of arthropod cuticle varies greatly in different types of arthropods, and on different parts of the same individual. Nevertheless, there are fundamental similarities in the cuticle structure of all arthropods, details of which can be found in numerous texts (see Barrington 1979 for a general account, and also Neville 1975). Arthropod cuticle consists of a basal layer of epidermal cells, a thick procuticle with an architecture of chitin protein fibrils, and a thin epicuticle, devoid of chitin, consisting predominantly of waterproofing lipids. The procuticle, the part most likely to be preserved, consists of a thick inner zone, the endocuticle, which is

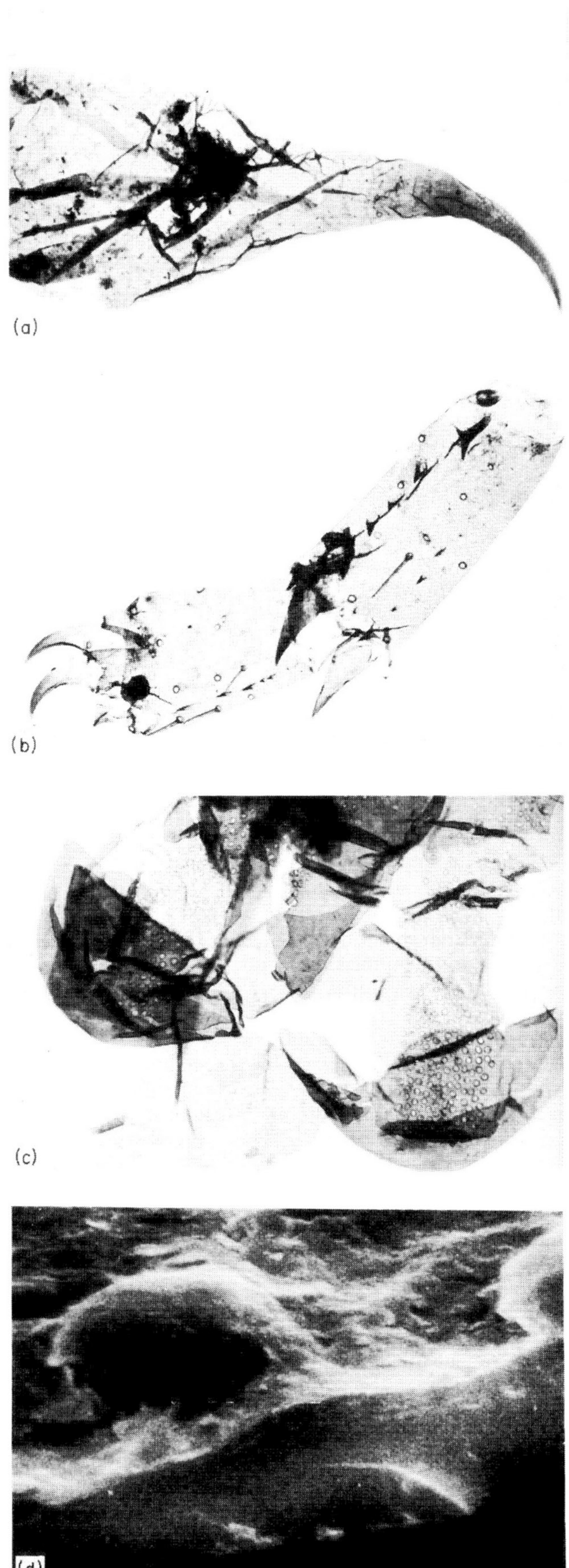

Fig. 1. Scorpion cuticles macerated from coal. (**a**) Sting organ; ×40; (**b**) Tarsi and metatarsi showing tarsal claws and spurs, setae and cuticular ornament; ×50; (**c**) Two pectine teeth with peg organs; ×80; (**d**) SEM photomicrograph of a torn edge of cuticle showing surface texture and non-laminate, but finely banded structure; ×6000.

partly calcified in most Crustacea and Trilobita, and a thinner exocuticle which may be sclerotized (hardened and darkened by impregnation and quinone-tanning of the protein) and pigmented. The chitin–protein microfibrils of the procuticle commonly occur in sheets (lamellae); where the microfibrils in successive, closely packed lamellae are parallel the cuticle is termed non-laminate (they may appear finely banded in section). In laminate cuticle, on the other hand, darker bands represent lamellae in which the microfibrils are parallel to the plane of section, and are separated by broader, paler bands in which the microfibrils have different orientations.

Preservation of arthropod cuticle relies partly on the extent of hardening of the original cuticle, so that heavily calcified (e.g. trilobite) or sclerotized (e.g. beetle elytron) cuticles are less likely to suffer bacterial or chemical decay, and to fragment. The chemistry of natural degradation of arthropod chitin and protein in sediments is undoubtedly complex and is little studied. Degradation of chitin *in vivo* by moulting arthropods involves the action of enzymes. The manner of preservation of sclerotized arthropod cuticles found in the fossil record is generally unknown, although in some instances chemical replacement at a fine ultrastructural level has been observed (Rolfe 1962; Dalingwater 1973, 1975; Müller 1985; Conway Morris 1985).

Preservation of the Yorkshire material

The cuticle of scorpions has been more extensively studied than that of any other chelicerate group (see Dalingwater 1986 for review). Filshie & Hadley (1979) recorded a total thickness of about 10 μm for *Hadrurus*, consisting of a 0.3 μm epicuticle, a finely laminate outer hyaline exocuticle about 2 μm thick, a non-laminate inner hyaline exocuticle, 5.5 μm thick, an innerlaminate exocuticle, 5 μm thick, and an endocuticle 65–85 μm thick with broad inter laminae and vertically orientated elements. The cuticles of the scorpions *Pandinus* and *Scorpiops* studied by Kennaugh (1959) were 120 μm and 45 μm in total thickness with exocuticles 25 μm and not more than 17 μm respectively. Kennaugh's staining techniques revealed that the inner exocuticle is quinone-tanned, and the cuticle immediately below the inner exocuticle stained red with Mallory's triple stain. This layer Kennaugh termed colourless exocuticle but on structural grounds is undoubtably part of the endocuticle as described by Filshie & Hadley 1979. The staining reaction classifies it as mesocuticle (Neville 1975, p. 24), a layer which has been impregnated with proteins and lipids but not quinone-tanned.

Our preliminary observations on the Yorkshire cuticles indicate that is is only the exocuticle that is preserved, assuming Carboniferous scorpions had a similar cuticle to that of extant forms. The cuticle is too thin to include endocuticle and the characteristic broad interlaminae and vertical elements have not been observed. Any preserved epicuticle would be extremely thin and difficult to detect. In addition, Filshie & Hadley (1979) recorded that hyaline exocuticle is absent from intersegmental membranes, and such membranes have not been observed in the Yorkshire material.

Energy dispersive electron microprobe analyses of cuticle fragments showed that more than 80% by weight of the material was composed of elements of atomic number less than 11. Such elements are the major constituents of organic materials. Of the heavier elements detected only Cl, S, Ca, and Si accounted for greater than 1% by weight in each analysis. Of these, chlorine was most abundant (7%), followed by sulphur (3%). Whereas it is likely that the high chlorine content is a product of cuticle storage in dilute hydrochloric acid, sulphur has been recognized in the hyaline exocuticle of scorpions (Kennaugh 1959). The insolubility of the cuticle in hydrofluoric and hydrochloric acids supports the conclusions that the cuticle is organic and that it has not suffered any mineral replacement.

The scorpion hyaline exocuticle is characterized by the structure and packing of the microfibrils (Filshie & Hadley 1979) and staining reactions (Kennaugh 1959). It is this unique structure which we suggest has allowed recovery of cuticles of scorpions, but not those of other arthropods, from coals and associated shales. Normal arthropod cuticle would be removed by the oxidation treatment of fuming nitric acid on coal. However, the absence of arthropod cuticles other than those of scorpions in shales treated only by disaggregation in water or hydrogen peroxide suggests that other arthropods were not preserved in the shales.

Taphonomy

Macerations of coal rarely produce arthropod fragments which can be fitted together again to produce an entire organ let alone a complete animal. This suggests that the animal (or moult) was disarticulated and in some cases fragmented prior to burial. The cuticle of modern scorpions is brittle, yet the coal cuticles commonly exhibit folding. It is possible that the thick endocuticle had already suffered organic decay prior to the incorporation of the material within the peat, and indeed signs of decomposition of the outer layers of the thicker cuticles may commonly be seen.

Preliminary observations indicate that the arthropod cuticles occur in all coal lithotypes but do not occur in all seams. Where relatively abundant arthropod material is found the coal is commonly poor and dirty. Scott (1978, p. 486) recorded that within the poor coal seam 20 f at Swillington, the arthropod cuticle is particularly abundant in a grey shale layer within the seam, associated with fusained and coalified plants, megaspores, plant cuticles and coprolites containing plant material.

Smith (1962), in a study of Yorkshire coals, recognized an incursion phase during which the peat was flooded by a rise in the water-table and variable amounts of sediments and miospores were introduced into the swamp. This caused inertinite macerals to be concentrated by flotation. The increase in abundance of arthropod cuticles in poor or dirty coals may similarly reflect the effect of a rise in water-table concentrating comminuted and partially degraded arthropod cuticle by flotation.

Modern scorpions are terrestrial but Siluro-Devonian forms were aquatic. In a recent monograph on fossil scorpions (Kjellesvig-Waering 1986) gilled scorpions were considered to have persisted into the Triassic (though on the same evidence Wills (1947) concluded that the Triassic forms had book lungs) whilst air-breathing scorpions were already present in the Carboniferous. The inference of the mode of life from morphology is still equivocal, however, some gilled scorpions in the Carboniferous could have been amphibious like their eurypterid relatives (Selden 1985). Thus whilst the coal layers containing the scorpion pieces show evidence of land plants, it is impossible to ascertain whether the scorpions themselves were aquatic or terrestrial. As more material accumulates sufficient pieces should eventually be recovered to show positive evidence of gills and/or lungs.

Other records of coal arthropods

Previously published records of arthropod fragments in bituminous coals are few and have never been of great interest to those authors who have reported them. Wilson & Hoffmeister (1956, figs 1,2) figured arthropod material recovered from spore preparations of the Croweburg Coal (Desmoinesian age). The figured material is fragmentary but comparable to the Yorkshire scorpion cuticles. This type of material was reported to represent up to 30% of all cuticles recovered from the coal. Winslow (1959, figs 10 and 11) figured two pieces of arthropod cuticle from upper Mississippian and Pennsylvanian coals of Illinois. The cuticles were not identified but look very similar to the Yorkshire scorpion cuticles. Winslow reported that such cuticles occurred in several of the coals she macerated for megaspores. Scott made the initial discovery of scorpion fragments in the coals at Swillington Brickpit, and has reported some of them (Scott 1977, fig. 14; 1984, fig. 1). Like Winslow, Scott also reported that arthropod cuticles were common in spore preparations. Coal ball samples have yielded arthropod cuticles (T. N. Taylor & S. P. Stubblefield pers. comm.) the material, which comes from Ohio and is of Pennsylvanian age, is comparable in diversity and preservation to the Yorkshire material.

Arthropods have been recorded from post-Palaeozoic, lower rank coals. The Geiseltal lignite (Eocene, Germany) has produced excellently preserved insects, including larvae, pupae and imagines of several orders (Francis 1961, p. 30) and Australian Tertiary lignites have yielded arthropod cuticles (Blackburn in Goodarzi 1984). Goodarzi (1984) described material from sub-bituminous coals of Canada and attempted to characterize the optical properties of the cuticle. Unfortunately, in this paper it was assumed that the cuticles were composed entirely of chitin, a mat of setae was described as a fibrous structure in the cuticle, and it is not possible to identify arthropod type from the photographs. Nevertheless, this was the first attempt to describe arthropod cuticle as a coal maceral, and it drew the attention of coal petrologists to their importance.

Arthropod cuticle as a coal maceral

The recognition of arthropod cuticles from macerations of bituminous coals is significant in that their occurrence has not been recognized petrographically. A summary of the occurrence of recognizable arthropod organs from 20 g samples of coals taken from the Barnsley Seam is given below (Table 1).

Table 1. *The occurrence of arthropod cuticle in 20 g samples of coals from the Barnsley Seam according to lithotype*

Lithotype	Fusain	Clarain	Vitrain	Durain
No. of samples	7	155	25	19
No. of samples with arthropod cuticles	5	73	9	4

The distribution of arthropod cuticles is not restricted to single lithotypes, although it was most frequently recovered from fusain and clarain. It should therefore be expected to be encountered petrographically in association with various microlithotypes. Stopes (1935) introduced the maceral term cutinite for a coal constituent formed from cuticles. Cutinite has since then been asssumed to be of botanical origin and derived mainly from the outer resistant cutin layer of plants (Stach 1982, p. 107). Whilst cutinite normally occurs as a rare accessory maceral in Palaeozoic bituminous coals, in those instances where it occurs in sufficient quantities to form cuticle-clarites, some authors interpret it as environmentally significant (Teichmüller 1962; Hacquebard *et al.* 1967).

Both plant and arthropod cuticle are morphologically similar when viewed in section, perpendicular to stratification. The presence of significant quantities of arthropod cuticles within the Barnsley and other coals suggests that not all cutinite should be interpreted as being of plant origin. Goodarzi (1984) suggests that arthropod cuticles differ optically from plant cuticles in having a higher reflectance, placing arthropod cuticles in the inertinite rather than liptinite maceral group. It may be that further studies could identify a new maceral, Arthropodinite.

Conclusions

The identification of arthropod cuticle as a coal maceral would be of benefit to coal petrologists in the preparation and correlation of coal seam profiles, and could assist microenvironmental interpretations. Further studies using reflected and fluorescence light microscopy are needed to identify the petrographic signature of arthropod cuticle. The more volatile parts of the cuticle, for example the epicuticle, may provide lipids for the production of resinites.

For arthropod workers, coal-preserved cuticle is of interest for the information it may provide about both preservation and further applications of cuticle studies. For example, the presence of a hyaline exocuticle in Palaeozoic scorpions (and possibly eurypterids) could be of ecological and evolutionary significance. Investigations of coals throughout the geological periods could provide useful stepping stones across the wide gulfs which currently separate records of many terrestrial arthropod groups. Records from the Mesozoic are especially poor in this respect.

Comparisons of terrestrial arthropod taxa from different palaeocontinents may provide a means of timing continental collisions or splits, as shown by Rolfe (1982). A further application of arthropod cuticle studies to general geology, which has yet to be investigated, is in determining the thermal maturity of sediments. Recently, graptolites have been shown to be useful as temperature indicators particularly at high levels of conodont alteration indices (Goodarzi & Norford 1985); it may be that arthropod cuticle has a similar potential.

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