

Late Carboniferous scavenging ostracods: feeding strategies and taphonomy

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ABSTRACT: Direct fossil evidence of scavenging ostracods is rare. A convincing example, representing the earliest recorded occurrence of ostracods feeding on vertebrate carrion, is described from the Bowland Shale Formation (Kinderscoutian, Upper Carboniferous) of Derbyshire, UK. It consists of the anterior end of a shark (*Orodus* sp.) whose upper surface is crowded with adults and juveniles of the nektobenthic ostracod *Eocypridina carsingtonensis* Wilkinson, Williams, Siveter & Wilby, 2004 (Myodocopida: Cypridinidae). Extrapolation of their preserved density suggests that the entire carcass may have hosted over a thousand individuals. It presented a rare opportunity for benthic scavenging in the Widmerpool Gulf because it was sufficiently large to have protruded above the inhospitable, and probably soupy, substrate surface. Although not necessarily a necrophagous specialist, *E. carsingtonensis* appears to have been well adapted to rapidly locating and exploiting widely dispersed nekton food drops. Its absence from the background sediment suggests that it commuted to the shark over relatively large distances, probably from adjacent basin highs. This implies a well-developed chemosensory capability. The ostracods are interpreted as having been overwhelmed by sediment dislodged during the sudden collapse of the partially buried carcass.

KEY WORDS: Bowland Shale Formation, chemosensors, necrobenthic island, necrophagous myodocopids, *Orodus*



Scavenging is a common feeding strategy in many Recent marine invertebrate classes and plays a crucial role in the recycling of organic material (e.g. see Smith 1985). Ostracods are no exception: experimental studies have demonstrated that a number of different species are efficient scavengers and are rapidly attracted to a wide variety of carrion in various states of decay (Stepien & Brusca 1985; Keable 1995; Vannier & Abe 1993; Vannier *et al.* 1998). Indeed, in certain settings they can form an important and prolific part of the scavenging guild (e.g. see Keable 1995). Nevertheless, direct fossil evidence of their involvement in this activity, in the form of preserved associations with scavenged carcasses, is rare and limited to four putative cases:

1. Bate (1971, 1972) noted a close association between several hundred podocopid ostracods and a teleost fish from the Lower Cretaceous of Brazil which he believed represented evidence of scavenging behaviour. However, in a recent re-evaluation, Smith (1998, p. 28) proposed that the ostracods and the fish in such associations had actually died simultaneously in widespread mortality events.
2. Dzik (1978) documented the presence of several myodocopid ostracods in the gut region of an Upper Jurassic plesiosaur from Russia. These were originally assigned to *Cycloleberis*, but have subsequently been placed into *Eocypridina* (Kornicker & Sohn 2000). Dzik considered that they had been inadvertently ingested by the reptile, but Boucot (1990, p. 209) offered scavenging as a conceivable alternative explanation. The latter now seems unlikely following the description by Vannier & Siveter (1995) of appendages in one of the ostracods homologous to those of Recent filter-feeding (or 'comb-feeding') forms (see Cannon 1933).
3. Weitschat (1983) provided more compelling and widely accepted evidence of scavenging activity. He described examples of ammonoids from the Lower Triassic of Spitzbergen which are closely associated with large numbers (50–100 individuals) of myodocopids (*Triadocypris spitzbergensis* Weitschat 1983). Not only are the ostracods concen-

trated in the body chambers (where they would have had greatest access to the animals' soft tissues) but, crucially, they also retain anatomical features indicative of a predatory/scavenging mode of life (Vannier *et al.* 1998, p. 405–406).

4. Gabbott *et al.* (2003) have also reported associations between ostracods and cephalopod tests. They described the occurrence of small numbers (typically <10) of myodocopids (*Myodoprigenia fistuca* Gabbott, Siveter, Aldridge & Theron, 2003) mostly on, but apparently also sometimes within, the body chambers of orthoconic cephalopods from the Upper Ordovician Soom Shale of South Africa. As a consequence of the vagaries of preservation, including the apparent superposition of pseudoplanktic epibiont brachiopods on some of the ostracods, Gabbott *et al.* (2003) entertained a number of possible explanations for the associations, but favoured scavenging as the most likely relationship.

The paucity of unambiguous fossil examples of scavenging activity in ostracods presumably reflects their mobility, their effectiveness at dispatching carrion, and the unusual conditions necessary to preserve such transient relationships. This paper describes a high-density, monospecific congregation of myodocopid ostracods on a shark from the Upper Carboniferous (Kinderscoutian) Bowland Shale Formation (formerly the Edale Shales, Waters *et al.* 2005) of the UK (Wilby *et al.* 2001). The means by which the ostracods located the carcass are discussed and the circumstances leading to the fortuitous preservation of the association are examined. All of the material (GSM 105458–105522) is housed in the palaeontological collections of the British Geological Survey, Keyworth, Nottingham.

1. Locality and stratigraphy

The Lower Hays Farm borrow pit (now flooded) [SK 2478 5033 to 2496 5042] near Carsington, Derbyshire, formerly

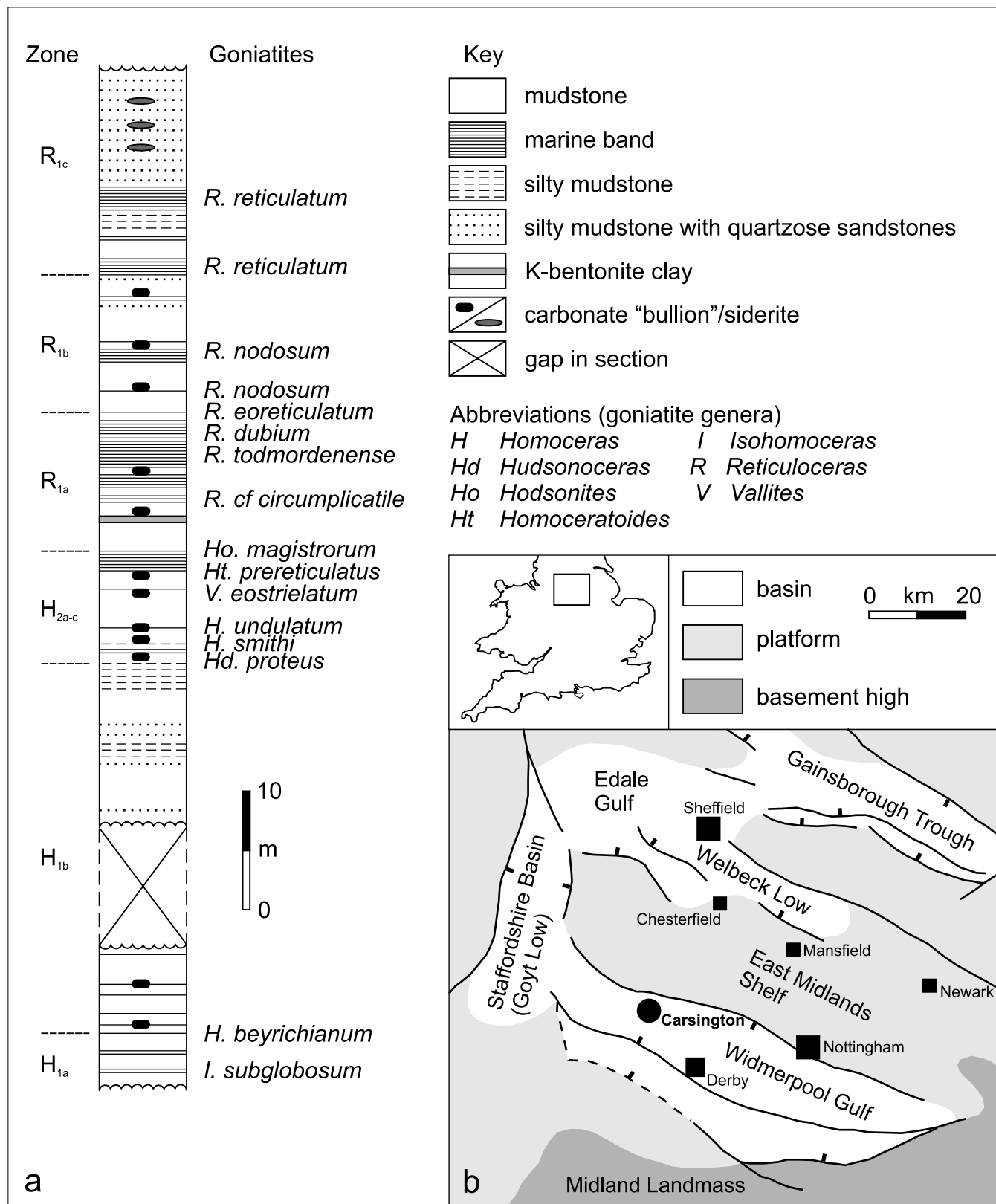


Figure 1 (a) Log of the Bowland Shale Formation sequence at Lower Hays Farm borrow pit showing the positions of biostratigraphically distinctive goniatite faunas; (b) palaeogeographical map of the English Midlands for the Namurian Stage, based on Ebdon *et al.* (1990).

provided one of the best sections in central England of the generally poorly exposed Bowland Shale Formation (Namurian, late Carboniferous). In 1986 the pit exposed *c.* 87 m of strata extending from near the base of the Chokierian (H_{1a}) stage to near the top of the Kinderscoutian (R_{1c}) stage. The sequence consists largely of unfossiliferous, grey, calcareous mudstones and silty mudstones, but includes numerous dis-

crete, organic-rich, dark grey to black, fissile mudstones, or so-called marine-bands (Fig. 1a). Many of these contain large carbonate concretions (locally known as bullions) and yield impoverished, but biostratigraphically distinctive, fully marine faunas dominated by goniatites (see Fig. 1a) and bivalves (e.g. *Dunbarella rhythmica*, *Coryella squamula*, *Posidonia minor* and *P. obliquata*). Conodont elements, the bivalve *Caneyella* sp.,

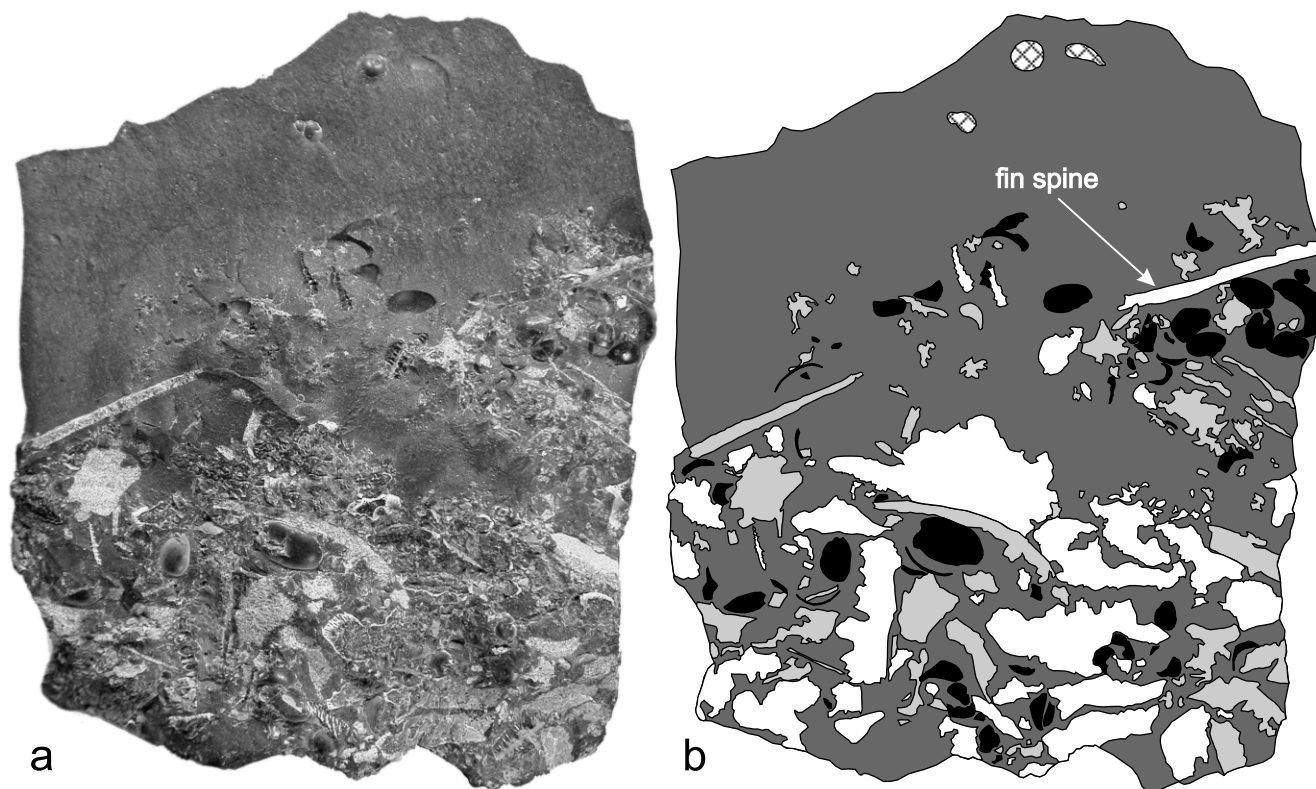


Figure 2 Representative portion of the shark:ostracod association. *E. carsingtonensis* occurs in large numbers amongst densely packed teeth and fragments of dermis within the main part of the specimen, and amongst displaced sections of dermis and a fin spine in the sediment above; GSM 105526, $\times 1$. (a) Photograph; (b) simplified camera-lucida drawing: teeth (white), dermis (light grey), ostracods (black), other shelly material (white, cross-hatched), concretion (dark grey).

radiolaria, sponge spicules and abundant bivalve and gastropod spat have also been reported from comparable parts of the sequence nearby (Holdsworth 1966; Frost & Smart 1979).

Except for a few thin (up to 60 mm thick), sharp-based sandstone beds, there are no arenaceous units in the section until immediately above the highest exposed marine band (*Reticuloceras reticulatum*). Here, 9.7 m of silty mudstone occur with interbeds of sandstone, siltstone and sideritic ironstone, each up to 0.1 m thick. These beds are inferred to lie below the highest R_{1c} marine band (*R. coreticulatum*) and have been interpreted as distal turbidites (Chisholm *et al.* 1988).

2. Material

The material forming the subject of this paper is derived from a large, discoidal, dark grey, fine-grained concretion that was collected loose from the borrow pit in 1986. The precise marine band from which it came is not known but, based on the presence of the goniatite *Reticuloceras*, it has been assigned to the Kinderscoutian (R_{1a-c}) part of the sequence. Since all of the exposed R_{1c} marine bands appear to lack bullion concretions, it is assumed to have been derived from either an R_{1a} or R_{1b} marine band.

2.1. Shark:ostracod association

The concretion contains an unusual association between a moderately-sized shark and a large number of individuals of the myodocopid ostracod *Eocypridina carsingtonensis* Wilkinson, Williams, Siveter & Wilby, 2004. The shark, *Orodus* sp. (pers. comm. Peter Forey 2001), is noteworthy in that the genus was previously known in Britain only from isolated teeth. Only its anterior end is present, the rest presumably lay in the sediment beyond the margins of the concretion and

was not recovered. It is preserved parallel to the bedding and, based on its degree of articulation, does not appear to have become buoyant post-mortem or to have been excessively disturbed by macro-scavengers. Its teeth remain closely associated in the centre of the concretion and indicate that the specimen may have been originally approximately 2 m long. Posterior to the teeth are numerous fragments of intact dermis (up to 30×70 mm), some of which have become displaced to positions just above the majority of the rest of the fossil.

Myodocopids are rare elements of the British Carboniferous ostracod population (Wilkinson *et al.* 2004) and have not previously been recorded from bullion concretions. They not only crowd the upper surface of the shark and the displaced sections of its dermis (Figs 2, 3), but they also occur amongst the teeth and beneath flaps of dermis behind the head, although in lower numbers. None occur beneath the shark or at any other level within the concretion: all of them are associated directly with the upper surface of the carcass or with fragments derived from it. Although there are few entire carapaces preserved, the disarticulated left and right valves of numerous individuals lie in very close proximity.

At least 250 valves are associated with the preserved part of the shark's head alone (together with many more small fragments of presumed ostracod). They have an average preserved density of $1.1/\text{cm}^2$ and are randomly orientated. The majority of specimens are damaged (by sedimentary compaction) or are partly obscured by rock or dermal material so that they cannot be measured with accuracy. However, the valves of the remainder range from 3.2 to 8.6 mm in length (Fig. 4a). This indicates that, in addition to presumed adults, the population contains numerous immature instars. Sexual dimorphism cannot be categorically demonstrated, though the range of length to

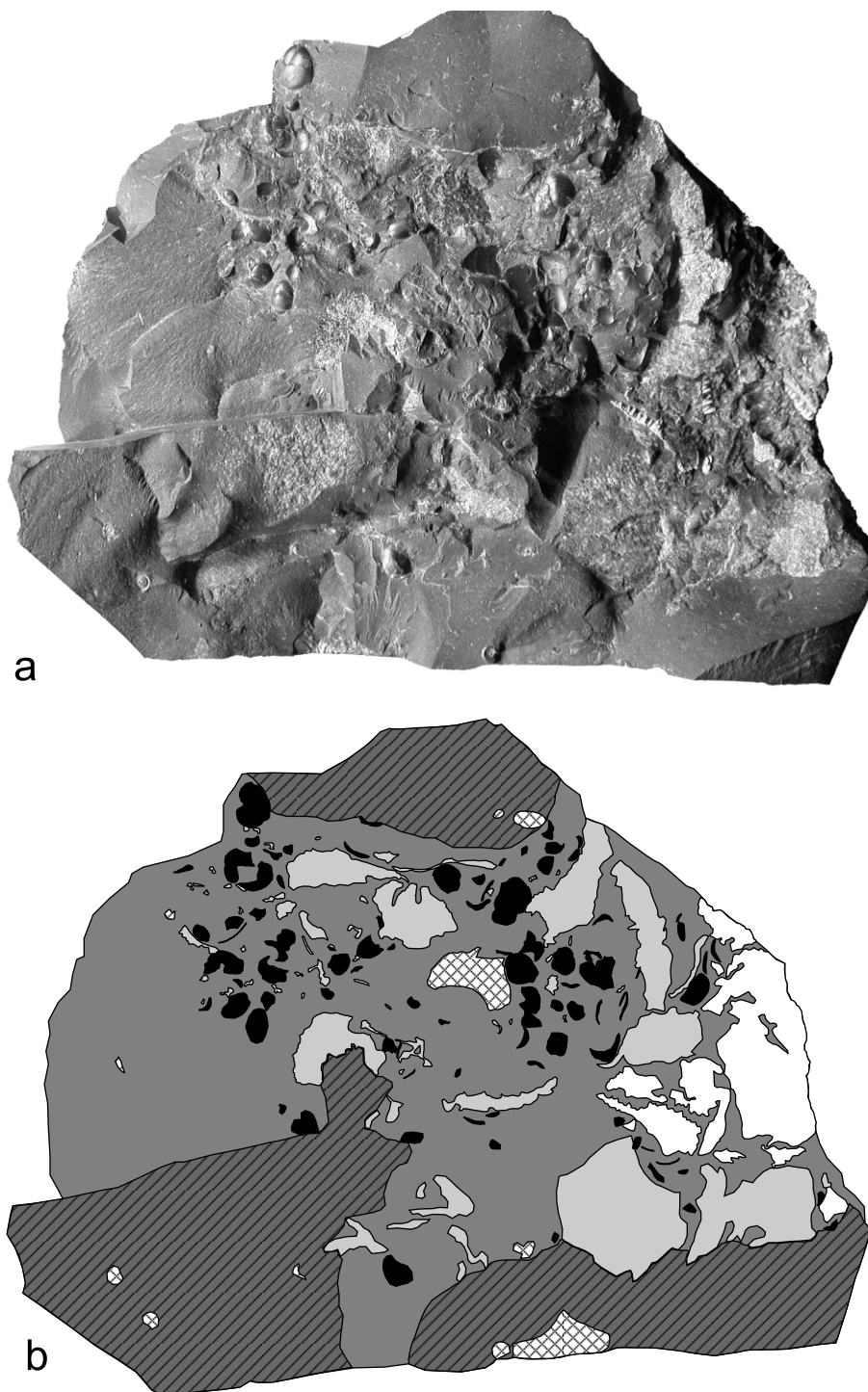


Figure 3 Representative portion of the shark:ostracod association showing the density of *E. carsingtonensis* valves on the upper surface of the carcass; GSM 105524, $\times 0.85$. (a) Photograph; (b) simplified camera-lucida drawing; key as for Figure 2 with, in addition, areas of sediment overlying the carcass shown as a diagonal fill.

height ratios of the largest specimens suggests that it may be present.

E. carsingtonensis has been described in detail by Wilkinson *et al.* (2004). It has a large, ovate carapace with a well-developed, hook-like rostrum and a broad rostral sinus (Fig. 4b, c). Internal moulds preserve strong 'fan-like' adductor muscle scars and an integumental circulatory system represented by anatomising sinuses (Wilkinson *et al.* 2004, pl. 1). These morphological features suggest that it was capable of active swimming. However, unlike Recent pelagic mydocopids (e.g. *Gigantocypris*), which typically have weakly calcified valves, those of *E. carsingtonensis* are well mineralised. Consequently, a nektobenthic ecology comparable to

that of many extant, morphologically similar species, including *Vargula hilgendorfi* (Müller, 1890), is considered most likely.

2.2. Associated fauna

In addition to the shark and the ostracods, the concretion contains a moderately abundant, low diversity, shelly fauna. This consists of small (<4 mm high), holostomatous turbate gastropods (uncommon); bivalve spat (rare); small (2–4 mm long) orthoconic nautiloids (moderately common); and goniatites (moderately abundant). Juvenile goniatites (generally <1 mm high) are relatively common and occur both individually and in small (12–15 mm diameter), ovoid to discoid

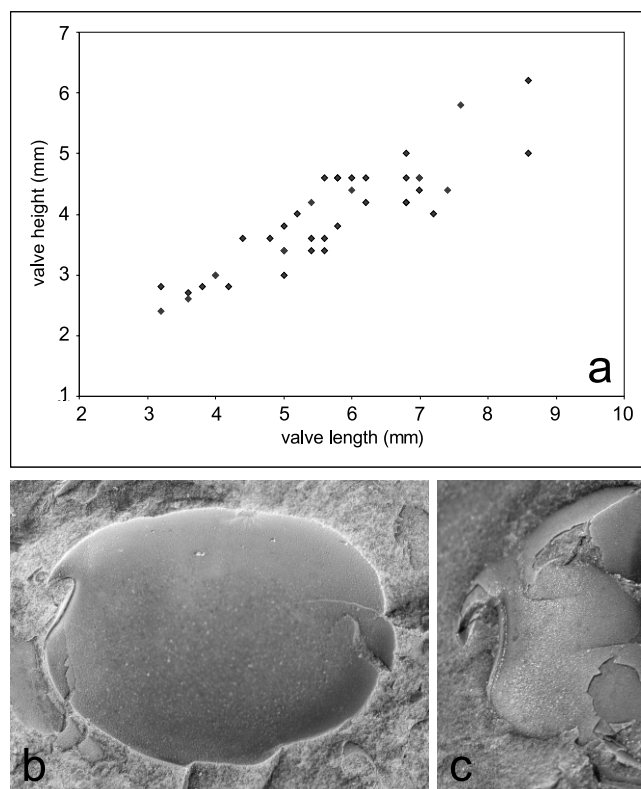


Figure 4 *E. carsingtonensis* Wilkinson, Williams, Siveter & Wilby 2004. (a) Size distribution of valves ($n=48$) on the *Orodus* carcass. Note that there is an increase in the range of lengths among those valves that are greater than 4 mm in height. Although unproved, this is probably the result of sexual dimorphism within the adult population. (b) External mould of right valve (lateral view), showing diagnostic ovate form, well-developed hook-like rostrum and broad rostral sinus; GSM 105464 (paratype), $\times 6$. (c) Left valve (lateral view), detail of rostrum and rostral sinus; GSM 105523 (paratype), $\times 9$.

concentrations. Some of the goniatites in the latter are fragmentary and the concentrations are interpreted to be disgorgements or faecal pellets. In addition to the shelly fauna, the concretion also contains relatively common coalified plant fragments up to 110 mm long. Over a dozen specimens of the epibiont bivalve *Caneyella* sp. are associated with one such fragment.

Bedding is difficult to discern in the concretion, presumably because of the low contrast in grain size, but some darker, finer-grained units (each up to 15 mm thick) are present. Most of the fossil material is preserved parallel to the bedding, but a few of the goniatites lie at low angles to it. There is no apparent bioturbation. The concretion's correct stratigraphical orientation (or 'way-up') has been determined from taphonomic and geopetal evidence.

3. Depositional environment

The Bowland Shale Formation was deposited on a highly irregular bathymetric surface consisting of a series of structurally controlled platforms and troughs (Fraser & Gawthorpe 1990). The Lower Hays Farm borrow pit is located near the northern edge of the WNW–ESE orientated Widmerpool Gulf (Fig. 1b), one of three interlinked troughs at the southern margin of the principle Namurian depo-centre in England (Ebdon *et al.* 1990). Deposition took place under a regime of repeated glacio-eustatic changes in sea level (Maynard & Leeder 1992; Church & Gawthorpe 1994). Periods of low-stand prompted delta progradation, a desalination of the waters (Collinson 1988) and the deposition of the unfossilifer-

ous mudstones. Periods of high-stand caused sediment starvation and the deposition of the thin, condensed, regionally widespread marine bands (Trewin & Holdsworth 1973).

The marine bands are widely believed to have been deposited from suspension as soupy substrates in poorly oxygenated water, locally probably more than 100 m deep, under conditions of low environmental stability (Holdsworth 1966; Trewin & Holdsworth 1973; Church & Gawthorpe 1994). The occurrence of rare benthic elements, such as the gastropods and *Dunbarella*, indicate that the sediment surface was at least intermittently colonised by species tolerant of low oxygen levels (Wignall 1987). However, the low diversity of the fauna and the predominance of nekton (e.g. goniatites, nautiloids, fish) and pseudoplankton (e.g. sponges, Holdsworth 1966; *Caneyella*, Wignall & Simms 1990) suggests that the sediment surface was, for much of the time, inhospitable. The relative importance of substrate consistency versus oxygen deficiency (or other factors) in limiting colonisation of the sediment surface is uncertain but, based on the orientation of some goniatites (see section 2.2.) and on crude porosity calculations (Holdsworth 1966, p. 319–320), the case for soupiness is relatively strong. Whatever the cause, the abundance of spat in some sections suggests that unfavourable conditions were maintained over a sufficient period, or occurred in close enough succession, to inhibit repeated attempts at colonisation by planktic larvae. Moreover, the absence of burrowing indicates that the sediment itself was permanently inhospitable and probably anoxic.

4. Interpretation

4.1. Nature of the association

The characteristics of the association described above suggest that *E. carsingtonensis* was preserved whilst actively feeding on the shark. Recent mydocopids employ a variety of feeding strategies (for a summary see Vannier *et al.* 1998 and references therein) and the association most likely records either predatory, parasitic or scavenging behaviour.

4.1.1. Predatory behaviour. This has been recorded in numerous Recent mydocopids and is normally restricted to attacks on small invertebrates such as worms, copepods and podocopid ostracods (Cohen 1982; Cohen & Kornicker 1987). Laboratory observations have shown that it requires only moderate numbers (several tens) of cypridinids, such as *V. hilgendorffii*, to consume such prey items (Vannier *et al.* 1998). In contrast, fish are much less susceptible to predation by mydocopids, except when they are fry (Davenport 1990). Collins *et al.* (1984) and Stepien & Brusca (1985) showed that although swarms of *V. tsujii* (consisting of several hundred individuals) were rapidly attracted to fish caged off the southern coast of California, they alone did not cause serious injury. Instead, they congregated in large numbers along the base of the fishes' fins and around their operculae and anal openings where they fed exclusively on mucus and skin. Only where isopods accompanied the ostracods was serious injury inflicted and the fish eventually killed. Indeed, unrestrained fish were able to simply evade the ostracods or to shake them off. Consequently, a predatory relationship is considered unlikely for the Carboniferous association described here.

4.1.2. Parasitic behaviour. Several authors have reported parasitism in ostracods including that of cypridinids on sharks (Wilson 1913; Harding 1966) and on other fish (Monod 1923). Whilst Cohen (1983) has suggested that these cases may actually represent attacks on dead or dying fish that were injured as a result of trapping, Bennett *et al.* (1997) have provided convincing histological evidence in support of at least

one example. They demonstrated that the gills of a large percentage (60%, $n=28$) of healthy specimens of the epaulette shark *Hemiscyllium ocellatum* from the Great Barrier Reef are infested with the cypridinid *Sheina orri*. The sharks had a mean length of 0.685 m and each hosted a maximum of 67 firmly attached ostracods (mean 11.9), the largest of which was 2.3 mm long and 1.4 mm high. With the exception of 13 ostracods (which may have become dislodged during processing), all of the 203 individuals recovered in their investigation were intimately associated with the sharks' gills. Clearly, this very specific distribution is inconsistent with that in the fossil association described here, and the number and the size of the ostracods involved are very different in the two cases. It is suggested, therefore, that the relationship was not a parasitic one.

4.1.3. Scavenging behaviour. *E. carsingtonensis* is interpreted as having been preserved whilst scavenging the *Orodus* carcass. Scavenging is a common feeding strategy in Recent cypridinids, for which they show several morphological adaptations (Vannier *et al.* 1998). These include the ability to ingest relatively large amounts of food rapidly between extended periods of fasting, and the possession of a powerful furcal complex, which allows them to anchor firmly onto carrion and dismember it. In baited trap experiments (Cohen 1983, 1989; Stepien & Brusca 1985; Vannier & Abe 1993; Keable 1995) cypridinids are rapidly attracted, often in their thousands, to a variety of food sources (including fish) in various states of decay. They feed for short periods before retiring from the carrion: none reside on it (pers. comm. Jean Vannier 2004) where they may themselves be susceptible to predation. Although they are not able to inflict serious damage to large fish on their own, they may gain access to internal tissues through natural openings (e.g. anus, gill chamber, genitalia) or lesions (Stepien & Brusca 1985; Vannier *et al.* 1998) and may achieve a distribution comparable to that observed in the fossil association. The absence of ostracods on the underside of the *Orodus* specimen indicates that scavenging was delayed until after the carcass had reached the sea floor.

4.2. Carcass detection

Carnivorous scavengers depend on being able to locate carrion rapidly. Recent carnivorous myodocopids have well-developed eyes (Vannier & Abe 1992) and some predatory mesopelagic species (e.g. *Gigantocypris* and *Macrocypridina*) show adaptations to low light levels (e.g. see Land & Nilsson 1990). Nevertheless, anecdotal evidence and the results of laboratory maze experiments suggest that many opportunistic scavenging myodocopids don't rely solely on vision to detect carrion (Stepien & Brusca 1985; Vannier *et al.* 1998). Indeed, many extant species (e.g. *Vargula*) feed at dusk when light intensity is very low. Instead, they use sensitive, anteriorly located, chemosensors (Andersson 1977; Parker 1998) to follow specific chemical cues, and in particular leaking body fluids (Stepien & Brusca 1985) and other organic constituents (Vannier *et al.* 1998), 'up-stream' to their source.

E. carsingtonensis occurs only in association with the *Orodus* specimen: it has not been recorded from elsewhere within the Bowland Shale Formation. This suggests that it was not a permanent inhabitant of the Widmerpool Gulf, and that it presumably resided on the nearby East Midlands Shelf; a location well beyond visual range of the deeply submerged shark. Consequently, it is argued that the ostracods most likely located the carcass with the aid of chemosensors. Certainly, it may be conjectured that the relatively large *Orodus* carcass would have exerted a powerful draw on opportunistic scavenging ostracods equipped with such organs. It represented a rare opportunity for benthic scavenging in the Widmerpool Gulf

because other potential 'nekton food drops' (e.g. goniates, nautiloids, faeces) would probably have been too small to have protruded above the soupy substrate, and would thus have been inaccessible. Based on the average preserved density of ostracods at the anterior of the shark, over a thousand individuals may well have been attracted to the carcass at any one time. Like *Vargula*, *E. carsingtonensis* probably commuted diurnally to carrion, perhaps spending just a few minutes feeding, before returning to its preferred habitat on the shelf.

4.3. Taphonomy

Despite the numerical abundance and probable wide distribution of Recent scavenging ostracods, fossil evidence of such activity is scant and has previously been recorded only from exceptionally well preserved biotas. Clearly, it requires the ostracods to be killed and preserved *in situ* with sufficient speed to prevent them from escaping the carrion and from being subject to scavenging themselves. This, it is suggested, was achieved in the Bowland Shale Formation via the following sequence of events:

1. Soon after death, the *Orodus* carcass arrived at the bottom of the Widmerpool Gulf and sank part-way into the soupy, inhospitable substrate.
2. Because of its large size, the shark's upper surface protruded above the sediment and formed a short-lived, necrobenthic island, to which *E. carsingtonensis* commuted to feed (Fig. 5a). Although there is no direct evidence of any of the associated fauna (e.g. *Reticuloceras*, orthoconic cephalopods) having scavenged the carcass, they may also have been visitors.
3. A catastrophic, decay-induced collapse of the carcass resulted in anoxic sediment caving-in from the walls of the shark and large numbers of the firmly anchored (furcal claws) ostracods being smothered and asphyxiated (Fig. 5b). Many other individuals presumably escaped being overwhelmed.
4. Further releases of putrefaction gases led to the partial disassociation of many of the ostracod valves and the displacement of others, together with fragments of dermis, to positions above the bulk of the carcass (Fig. 5c).
5. Minor sedimentary compaction caused the breakage of numerous valves and was halted by the development of the concretion centred on the shark.

5. Conclusions

Although there are several examples in the fossil record of ostracods apparently having been preserved whilst scavenging, that discussed herein is amongst the most persuasive. It represents the earliest recorded occurrence of ostracods feeding on vertebrate carrion and suggests that late Carboniferous myodocopids such as *E. carsingtonensis*, although not necessarily necrophagous specialists, had well-developed chemosensory capabilities and were capable of locating widely dispersed carrion. They were preserved *in situ* whilst feeding on the partially buried shark carcass due to its catastrophic, decay-induced collapse. This triggered anoxic sediment, that had previously been supported by the carcass, to cave in and smother a large number of the firmly attached individuals.

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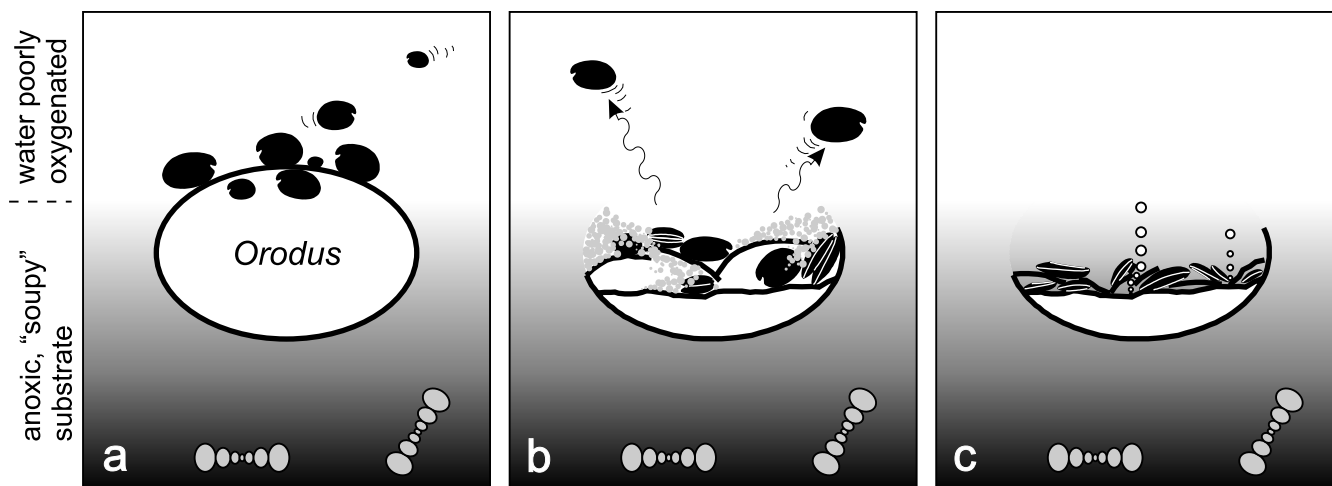


Figure 5 Schematic taphonomic model for the shark:ostracod association illustrating the key stages in its development. (a) Arrival of *E. carsingtonensis* on the *Orodus* carcass by chemosensory detection and feeding on those parts of the shark which lay above the inhospitable sediment surface. Some ostracods invade the body through the gill slits, eye socket and mouth. (b) Catastrophic decay-induced collapse of the shark, resulting in some of the ostracods being smothered by anoxic sediment caving in from the now unsupported sides of the carcass. Other ostracods not firmly attached by their furcal claws escape. (c) Further release of putrefaction gases causing displacement of the shark's tissues and the disassociation of most of the ostracod valves.

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