

4 Ostracod carnivory through time

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4.1 Abstract

Carnivory in modern ostracods takes the form of predation, scavenging and parasitism. In the fossil record, carnivory is difficult to prove without the fossilisation of diagnostic functional morphological features or the preservation of the intimate association between the ostracods and the carrion or prey. Six examples of putative carnivory are known in geological deep time, the most persuasive being scavenging myodocopes of Ordovician, Carboniferous and Triassic ages (*Myodoprigenia*, *Eocypridina* and *Triadocypris*), where swarms of ostracods are found associated with carcasses, and the early Silurian *Colymbosathon* in which characteristic soft part anatomy is preserved. Other putative scavengers, such as late Jurassic *Juralebris*, are unlikely to be carnivorous.

Keywords: Ostracoda, carnivory, predation, scavenging, parasitism.

4.2 Introduction

Ostracods are small, bivalved crustaceans that occupy all aquatic niches from the deep sea to temporary ponds and in moist leaf-litter around tree-lined lakes. They are represented by an estimated 33,000 living and fossil species and form the most diverse and prolific class of arthropods. Their mineralised carapace is readily fossilised, so that their record is long, the

oldest known fossil carapaces of presumed Ostracoda being from the early Ordovician (about 490 million years old) (Hou et al. 1996). True ostracods (both Palaeocopa and Binodicopa) occur in the Tremadoc of Argentina (Salas, Vannier and Williams, in-press) and Estonia (Tinn and Meidla 2004).

Ostracods display a variety of feeding habits as filter-feeders, detritivores, herbivores and carnivores. Carnivory amongst modern ostracods is well established, having been observed in natural habitats and in aquarium experiments (e.g. Vannier et al. 1998). It takes three forms in ostracods: predation, scavenging and parasitism. Predation on larger animals is practiced by myodocopes such as *Gigantocypris* and *Macrocypridina* (Vannier et al. 1998; Moguilevsky and Gooday 1977). *Vargula* has been observed feeding on live polychaetes, but is also a scavenger (Vannier et al. 1998). Scavenging is the principle form of carnivory amongst ostracods, for example, in *Skogsbergia* (Cohen 1983) and in freshwater podocopes such as *Eucypris virens* and *Heterocypris incongruens*. Parasitism is poorly known, although the myodocope *Sheina orri* and, perhaps, *Vargula parasitica* have adopted this form of carnivory (Bennett et al. 1997).

Despite its widespread use as a feeding strategy amongst modern ostracods, carnivory is difficult to prove in the fossil record. It relies entirely on the exceptional preservation of distinctive, decay-prone, anatomical features and/or intimate association with food items. The importance and position of ostracods in ancient food webs is, therefore, difficult to assess. Six putative examples of fossilised scavengers are discussed herein. Although two of these are unlikely to be examples of carnivory, there is fossil evidence of scavenging ostracods in the Triassic, Carboniferous and Ordovician.

4.3 Carnivory in modern Ostracods

4.3.1 Predation

Predation by Recent myodocopes is normally restricted to small invertebrates such as worms, copepods and podocopid ostracods (Cohen 1982; Cohen and Kornicker 1987). One of the most voracious predators among ostracods is *Gigantocypris muelleri*, a large (up to 30mm long) and excellent swimmer that generally preys on fish fry, copepods and chaetognaths (Davenport 1990). Evidence for their diet being their gut

contents, which were examined by Vannier et al. (1998) and Moguilevsky and Gooday (1977).

The act of predation has not been widely observed *in vivo*, and the most detailed account remains that of Vannier et al. (1998) who carried out numerous laboratory-based experiments. The introduction of live annelid polychaetes into an aquarium containing *Vargula hilgendorfii*, caused rapid swarming of the ostracods, which began biting at the mouth, gills, feeding tentacles, anus or ventral region of the body wall of the polychaetes (Fig. 1a), perhaps attracted to undigested food particles or secretions. Circular wounds on the epidermis and musculature resulted (Fig. 1b), and although these were initially not deep enough to be fatal, the release of blood and body fluids attracted yet more ostracods, which fed on the wounded areas, tearing more flesh. It required only moderate numbers (a few dozen) of cypridinids to kill and rapidly consume such prey (Vannier et al. 1998).

Swarms of ostracods on larger animals have also been recorded in freshwater lakes, although predation does not appear to have taken place. Seidel (1989) reported that swarms of the podocypid candonid *Cyclocypris serena* (which he erroneously called *C. ovum* – see Meisch 2000) were found clinging to toads (*Bombina variegata*) and newts (*Triturus vulgaris* and *T. cristatus*). In one case, 263 individuals were counted on a single toad and, in another instance, 65 observed on a newt. In these instances, there was neither evidence that the ostracod swarms were attacking their “hosts” (they may have been feeding on the amphibian secretions) nor that they caused their death.

Predation by freshwater ostracods has been recorded, although not commonly. Amongst the Cyprididae, *Cypridopsis hartwigi* attacks ciliates, rotifers and insect larvae, and a swarm of between 10 and 15 individuals have been observed killing molluscs such as *Bullinus contortus* and *Planorbis glabratus* (Deschiens et al. 1953; Deschiens 1954). *Eucypris virens* feeds on the terminal setae of the phyllopod *Tanymastix* and it is also cannibalistic (Kiefer 1936). *Heterocypris incongruens* often attacks small prey such as *Daphnia magna*, cyclops, copepods, other ostracods, oligochaeta, cladocera and insect larvae (Ganning 1971; Meisch 2000).

Amongst the Candonidae, *Cypria ophthalmica* has been observed attacking and killing the gastropod *Gyraulus crista* in aquarium experiments (Janz 1992). Normally, *C. ophthalmica* lays its eggs on the shell of the gastropod, immediately prior to it spawning and shortly before the snail's death. The newly hatched ostracods then feed on the snail carcass (Janz 1992).

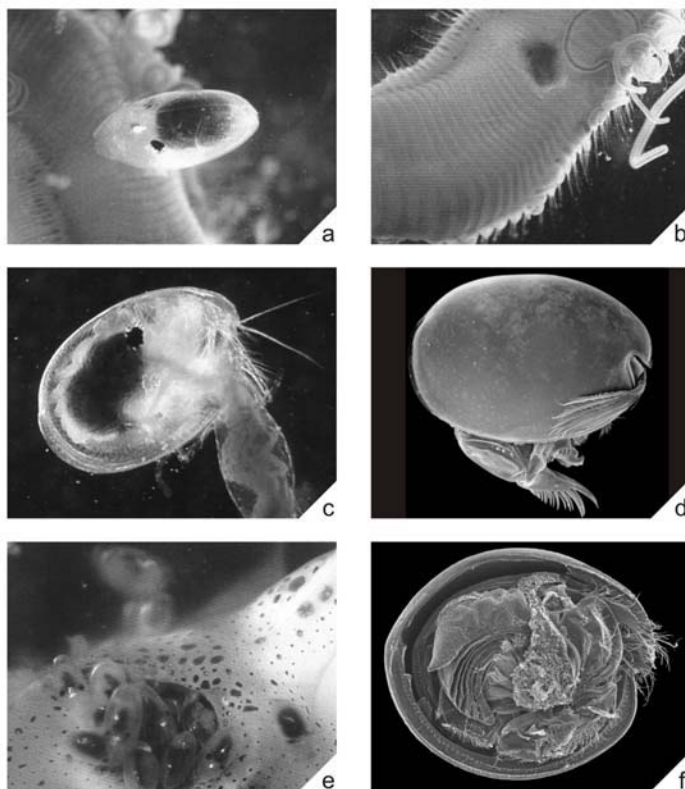


Fig. 1. A modern example of carnivory in ostracods: *Vargula hilgendorfii* (c. 3 mm long) predating on a live polychaete annelid. b. The wound on a live polychaete annelid after the attack of two specimens of *Vargula hilgendorfii*. c. *Vargula hilgendorfii* (c. 3 mm long) scavenging an insect larva, the a. food can be seen passing through the oesophagus and filling the stomach pouch. d. Lateral view of *Vargula hilgendorfii* (length carapace 2.5 mm) showing the furcae with claws and the second antennae for swimming. e. *Vargula hilgendorfii* (c. 3 mm long) scavenging on the carcass of a dead squid. The swarm attacked the eye first then penetrated into the body through the eye socket. f. *Leuroleberis surugaensis*, a typical cylindroleberidid, showing the soft parts (the gills and filtering setae are visible). (carapace c. 5 mm long)

4.3.2 Scavenging

Scavenging is a common feeding strategy in Recent cypridinid myodocopes which are able to ingest relatively large amounts of food

rapidly, between periods of fasting (Vannier et al. 1998). Morphological adaptation to scavenging includes the possession of a powerful furcal complex, which allows them to anchor firmly onto carrion and dismember it. Parker (1997) observed that the furca has several major functions in the feeding process of scavenging cypridinids such as *Azygocypridina lowryi*, including cutting and holding small food sections from an animal carcass and removing small fish scales. In baited trap experiments (Cohen 1983 1989; Collins et al. 1984; Stepien and Brusca 1985; Vannier and Abe 1993; Keable 1995; Parker 1997) swarms of cypridinids (sometimes in their thousands) were attracted to various food sources and in various states of decay. Swarms of several hundred individuals of *Vargula tsujii* gained access to internal tissues of dead or dying fish through natural openings (e.g. anus, gill chamber, genitalia) or lesions (Stepien and Brusca 1985; Vannier et al. 1998), although they alone did not cause the injury to the fish. They congregated along the base of their fins and around the operculae and anal openings, where they fed exclusively on mucus and skin, and it was only where isopods had caused serious injury that they fed on internal organs.

Vargula hilgendorfii behaves both as a predator, attacking for example, polychaete annelids, and as an opportunistic scavenger on carcasses of larger animals such as fish and squid. It is well adapted to this lifestyle morphologically; the fourth limb has strongly sclerotised setae on the endopodite and the furcal lamellae possess claws (Fig. 1d). These limbs are used to abrade and eventually tear open the integument of living prey and carcasses. Vannier et al. (1998) observed *V. hilgendorfii* clustering around injured areas of fish and penetrating the membrane covering the eye of a dead squid in order to consume the liquid contents (Fig. 1e).

Scavenging in the freshwater realm is exemplified by a number of members of the Cyprididae (Podocopa). Swarms of *Heterocypris incongruens* feed on dead gastropods (Meisch 2000) and carcasses of water birds (Reichholf 1983), and *Eucypris virens* has also been observed feeding on dead animals (Kiefer 1936).

4.3.3 Parasitism

Parasitism of fish by cypridinid myodocopes has been reported in several cases (Wilson 1913; Monod 1923; Harding 1966). The myodocope *Vargula parasitica* was said to congregate within the gills of hammerhead sharks (*Sphyrna zygaena*), sea bass (*Epinephelus adscensionis*) and jack fish (*Caranx crysos*) (Wilson 1913). It was argued that the ostracods had remained in the gills for some time, which was evidence of parasitism. The

myodocope, *Skogsbergia squamosa*, was considered to be a parasite (Monod 1923), having been found on dead fish and securely attached to the head, mouth and back of live scorpion fish (*Scorpaena scrofa*) where, it was said, they probably fed off the blood of the host. Harding (1966) recorded the cypridinid *Sheina orri* firmly attached to the gills of fantail rays (*Taeniura lymna*) and an epaulette shark (*Hemiscyllium ocellatum*) and assumed they were parasitic. The parasitic lifestyle of these species was questioned by Cohen (1983), who suggested that attacks were carried out on dead or dying fish that had been injured as a result of trapping. Although this is probably the case for some records, Bennett et al. (1997) showed that parasitic ostracods exist; the gills of healthy specimens of *Hemiscyllium ocellatum*, offshore eastern Australia, were infested with *Sheina orri*. Evidence that *Sheina orri* led a parasitic lifestyle, attached to fish gills are: puncture marks and grooves in the gill epithelium; the ostracods always occurred between gill filaments and had been positioned there for some time, such that gill filaments were distorted around the carapace to form 'pockets'; all of the ostracods were consistently orientated with respect to the gill septum and arch, and generally in the lower part of the hemibranch; the preferred orientation of the ostracods within the 'pockets' precludes the notion that they were feeding on water-borne food particles moving through the gills; and the fact that the ostracods were attached to the host by means of hook-like claws on the mandible and fourth limb.

4.4 Carnivory in the fossil record

Despite the fact that carnivory in ostracods is widespread in modern oceans, examples in the fossil record are sparse and sometimes equivocal. Evidence of predation in deep time is unknown, although it is reasonable to suppose that it existed given the long history of nekto-benthonic myodocopes, at least back to the Silurian (Siveter 1984), and the known feeding habits of myodocopes such as *Gigantocypris*, *Macrocypridina* and *Vargula*. Parasitism is likewise unknown in the fossil record as, without the intimate ostracod-host relationship, parasitism cannot be directly proved. Scavenging is a feeding strategy adopted by many Recent marine invertebrates and ostracods are no exception (isopods for example which are sometimes found together with ostracods on the same carcass). Indeed, in certain settings ostracods form an important and prolific part of the scavenging guild (e.g. Keable 1995). In order to demonstrate more positively the occurrence of this lifestyle in ancient communities, the

preservation of the scavenger in association with the scavenged carcass. It might be supposed that fossil evidence of scavenging by ostracods should be easily demonstrated, but it is in fact rare. There are six putative examples in the geological record that have been considered to demonstrate carnivory by scavenging, although two of these can no longer be sustained.

4.4.1 Early Cretaceous *Pattersonocypris micopapillosa* from Brazil

Bate (1971 1972) described an association between several hundred podocopid ostracods, *Pattersonocypris micopapillosa* (Figure 2a) and a teleost fish, *Cladocyclus gardneri*, from nodules within the Lower Cretaceous Santana Formation (Romauldo Member) on the flanks of the Chapada do Araripe, west of Recife, north-eastern Brazil. Bate considered *Pattersonocypris* to belong to Cyprididae/Cypridinae, but Smith (2000) pointed out its similarity with the modern species *Eucypris virens* and concluded that it should probably be placed into Cyprinotinae.

Bate drew attention to the powerful ‘toothed’ mandibles and the apparently close taphonomic relationship between the ostracods and the fish, concluding that “the animal was a scavenger, feeding on decaying plant and animal debris ...” He argued that the *Pattersonocypris* specimens “were suddenly buried and rapidly asphyxiated, dying with their valves slightly agape.” Considering the feeding habits of certain modern cyprids, this appears to be a reasonable argument, but there are several reasons why this conclusion cannot be supported. Ostracods occur in large numbers throughout the succession, in some cases forming coquina or thin ostracodal limestones, even when fish carcasses are absent. Therefore, the large numbers of carapaces associated with the fish cannot be unequivocally interpreted as swarming on carrion. The taphonomic relationship between the ostracods and the fish has not been fully resolved; none were found in an intimate relationship with the fish carcass, as is the case of other examples of scavenging discussed herein, and there is still a question whether they died at different times, or during the same widespread mortality event. In addition, Smith (1998 2000) demonstrated that the soft part anatomy of *P. micopapillosa* (Fig. 2b) showed close similarities with modern *E. virens* and concluded that not only can it be inferred that their limb functions were similar, but they also shared similar lifestyles. *Pattersonocypris*, he argued, would have been morphologically better suited to a nekto-benthonic, detritus feeding lifestyle rather than to a specialised scavenging one (Smith 2000, p. 95).

4.4.2 Jurassic *Juraleberis jubata* from Russia

Dzik (1978) documented the presence of several myodocope ostracods in the gut region of an Upper Jurassic pliosaur reptile from the early Volgian (Tithonian) of Pugatchov, Saratov District of Russia, which he considered had been inadvertently ingested by the reptile. Boucot (1990, p. 209) acknowledged this possibility but, in addition, suggested that scavenging was a conceivable alternative explanation for the association.

Following a detailed examination of the holotype by Vannier and Siveter (1995), a scavenging relationship now seems unlikely. Although its soft part anatomy is imperfectly known, *Juraleberis jubata* (Fig. 2c) shows affinities with *Leuroleberis* (Fig. 1f) and *Cycloleberis* and is assigned to Cylindroleberididae and questionably to Cyclasteropinae. In modern cylindroleberidids, the maxillae and fifth limb create water currents and food particles are collected by the maxillar setae and directed to the mouth by spatulate-like exopodites (Cannon 1933; Vannier and Siveter 1995). However, Cannon (1933) interpreted structures on the 4th, 5th (exopodite) and 6th limbs in Recent myodocopes, such as *Cyclasterope*, as filtering devices, although he made no *in vivo* observations. It now seems possible that these large ostracods were opportunistic filter feeders, able to grasp and tear open carcasses by using their furca, releasing food particles (especially if decay is advanced) so that the synchronized filtering device formed by the 3 pairs of appendages, can be used by the ostracod to gather the small food particles. This situation has been observed in association with truly scavenging *Vargula*; clouds of minute food particles are sometimes created when it feeds (Vannier, unpublished information). The presence of similar structures on the appendages of *Juraleberis* (Figure 2d) suggests that it belongs to this category of filter feeders.

4.4.3 Triassic *Triadocypris spitzbergensis* from Spitzbergen

One of the most compelling and widely accepted examples of scavenging in the fossil record has been documented by Weitschat (1983), who recovered exceptionally well-preserved myodocopes in close association with ammonoids from the Lower Triassic of Spitzbergen. The association is so well preserved that even the ciliate ectoparasites were present (Weitschat and Guhl 1994), and the ostracods retain anatomical features (Fig. 3a), including the first and second antennae, the epipodial fan of the fifth limb and the seventh limb. Similarities can be seen between the preserved soft parts of *Triadocypris spitzbergensis* and the modern nekto-benthonic *Vargula hilgendorfi*, although the feeding appendages are

missing or poorly preserved (questionable setae of the ‘biting apparatus’ on the fourth limb are present) (Vannier et al. 1998). Unfortunately, a complete furca with furcal lamella (with claws) is absent, although a sclerotised plate (or sclerosome) is present (Weitschat 1983; Parker 1997). However, their close association with the ammonoids suggests a predatory or scavenging mode of life (Vannier et al. 1998, p. 405-406).

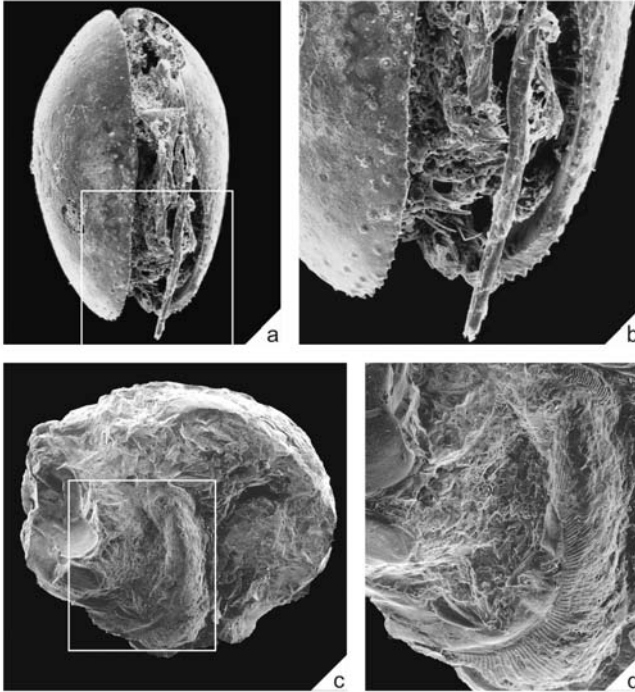


Fig. 2. Filter-feeding ostracods that were originally believed to be carnivorous: a. *Pattersonocypris micopapillosa*. A gaping carapace with preserved soft tissue from the Lower Cretaceous Santana Formation, Brazil, and originally considered to be scavenging teleost fish carcasses. Length: 1 mm (MPK13401). b. Details of the same specimen preserved soft tissue. c. *Juraleberis jubata*, an opportunistic filter-feeder.. Carapace (3.3 mm long) left lateral view with left valve removed to show the soft anatomy (holotype PIN 3775/1). Collected from the late Jurassic of Russia, and found in association with a pliosaur. d. Lateral detail of the epipodite of left 5th limb of the same specimen. (Taken from plate 22, 91, figs 1 and 2 of Vannier, J. and Siveter, D. J. 1995. *Stereo-Atlas of Ostracod Shells* 22, 86-95)

Swarming is one of the characteristics of scavenging ostracods and large numbers (50-100 individuals) of *Triadocypris spitzbergensis* were found

restricted to the body chambers of the ammonoid *Keyserlingites*, where they apparently fed on soft tissues.

4.4.4 Carboniferous *Eocypridina carsingtonensis* from Central England

The Lower Hays Farm borrow pit near Carsington, Derbyshire, formerly exposed the Namurian Bowland Shale Formation. It yielded a large carbonate concretion containing marine faunas dominated by goniatites and bivalves, together with an association between a shark (*Orodus* sp.) and a large number of individuals of the myodocope ostracod *Eocypridina carsingtonensis* (Fig. 3b) (Wilkinson et al. 2004; Wilby et al. in press). At least 250 individuals of *E. carsingtonensis* crowd the upper surface of the shark and the displaced sections of its dermis, and also occur in smaller numbers amongst the teeth and beneath flaps of dermis behind the head (Fig. 3c-d). None occur beneath the shark or at any other level within the concretion.

The association was located near the northern edge of the WNW-ESE orientated Namurian Widmerpool Gulf where soupy mud-rich substrates accumulated in poorly oxygenated water, locally at depths of at least 100m (Holdsworth 1966; Trewin and Holdsworth 1973; Church and Gawthorpe 1994). As *E. carsingtonensis* has a well-developed, hook-like rostrum and a broad rostral sinus, it was probably capable of active swimming. However, unlike Recent pelagic non-mineralized halocypridids such as *Conchoecia* and, for example *Gigantocypris*, which typically have weakly calcified valves, those of *E. carsingtonensis* are moderately well mineralised suggesting a nekto-benthonic ecology, comparable to that of the extant, morphologically similar species *Vargula hilgendorfii* (Wilkinson et al. 2004). The association suggests that *E. carsingtonensis* was feeding on the shark, the relationship being predatory, scavenging or parasitic.

Although there are numerous examples of Recent myodocopes attacking small invertebrates (such as worms, copepods and fish fry), they alone could not cause serious injury to larger fish. Indeed, unrestrained fish would have simply evaded the ostracods or shaken them off. Consequently, a predatory relationship is unlikely. The only known examples of parasitism in myodocopes show intimate association with fish gills. This is inconsistent with the fossil association from Carsington, and the number and the size of the ostracods involved are very different, making a conclusion involving parasitism, unlikely.

Eocypridina carsingtonensis is interpreted as having been preserved whilst scavenging the carcass (Wilby et al. in press). Scavenging is a common feeding strategy and cypridinids are rapidly attracted, often in thousands, to a variety of food sources (including fish) in various states of decay. Certainly, it can be that the relatively large *Orodus* carcass would have exerted a powerful attraction on any opportunistic scavenging ostracods. Although it is unlikely that they would have been able to inflict serious damage to large fish such as *Orodus*, they may have gained access to internal tissues through natural openings (e.g. anus, gill chamber, genitalia) or lesions of a dead or dying fish to achieve their observed distribution. Recent carnivorous myodocopes have well-developed eyes (Vannier and Abe 1992) and some predatory mesopelagic species (e.g. *Gigantocypris* and *Macrocypridina*) show adaptations to low light levels (Land and Nilsson 1990). Opportunistic, scavenging myodocopes, however, do not appear to rely on vision to locate carrion (Stepien and Brusca 1985; Vannier et al. 1998), but chemoreceptors detect leaking body fluids and other organic constituents (Anderson 1977; Parker 1998; Stepien and Brusca 1985; Vannier et al. 1998). This appears to have been the case in *Eocypridina carsingtonensis* was clearly capable of locating the *Orodus* carcass and was prepared to travel relatively large distances into the basinal parts of the Widmerpool Gulf, in order to reach the shark (its absence from the background sediment indicates that it did not generally inhabit this part of the Gulf). Light levels would have been greatly reduced at depths in excess of 100m, but this was clearly not a problem; it may have behaved in a similar way to modern scavenging myodocopes, which are most active at night.

4.4.5 Early Silurian *Colymbosathon epecticos* from Herefordshire, England

The Lower Silurian Wenlock Series of Herefordshire, west Central England, includes volcanic ash with nodules (Briggs *et al* 1996; Orr et al. 2000). A number of animals, including soft part anatomy, are preserved in 3-dimensions within the nodules, including *Colymbosathon* (Fig. 3c), a cylindroleberidid myodocope that lacks the setose comb on the fifth appendage characteristic of modern forms (Siveter et al. 2003). It led a nekto-benthonic lifestyle at water depth of 150-200 m and is believed to have been a micro-predator and scavenger. As in modern scavengers, its furca is well developed, perhaps to hold and cut prey or carrion. Abe et al. (1996) showed that enzymes were present in the upper lip of Recent *Vargula* to aid digestion, and Siveter et al. (2003) speculated that processes

on the labrum of *Colymosathon* may have been similar enzyme-secreting organs.

4.4.6 Late Ordovician *Myodoprimigenia fistuca* from South Africa

Gabbott et al. (2003) reported associations between ostracods and orthoconic cephalopods in the Upper Ordovician (upper Asgill) Cedarberg Formation of South Africa. An argillaceous unit at Keurbos, the Soom Shale Member, comprises finely laminated mudstones believed to have accumulated in a shallow water milieu in a sheltered embayment. Small numbers (typically <10) of the benthonic or nekto-benthonic myodocope ostracod, *Myodoprimigenia* (Fig. 3f), are preserved on the upper surface or within the body chambers of the orthocones (Fig. 3g-h) and, in one case, associated with the radula. Several explanations for the associations can be envisaged due to indifferent preservation (Gabbott et al. 2003). For example, a purely fortuitous taphonomic causation for the ostracod/cephalopod association might be argued, although this can be discounted as the delicate myodocopes show no signs of transportation and the sediment preserves evidence of neither current activity or bioturbation. The intimate association of ostracods with the orthocones and their rarity in adjacent sediment and elsewhere in the Soom Shale Member, suggests that the ostracods were scavenging cephalopod carrion. The association, therefore, represents the oldest known evidence of ostracod carnivory.

4.4.7 Cambrian bradoriids and the origin of carnivory

The origins of carnivory amongst Ostracoda are difficult to identify, as evidence in the Cambrian is wanting, although this trophic position may have been attained very early in the evolution of the group. Ostracods may have been represented in the Cambrian by some Bradoriida (Fig. 4a-b), although this probably polyphyletic taxon includes definite non-ostracod genera such as *Kunmingella* (Fig 4c) (Hou et al. 1996; Shu et al. 1999; Hou et al. 2004). Bradoriids such as *Kunmingella douvillei* are different from ostracods morphologically, but they may have occupied similar ecological niches (Shu et al. 1999; Vannier and Chen 2005). Carapace morphology amongst bradoriid arthropods varies considerably, perhaps reflecting, in some way, their preferred environmental niches and trophic position.

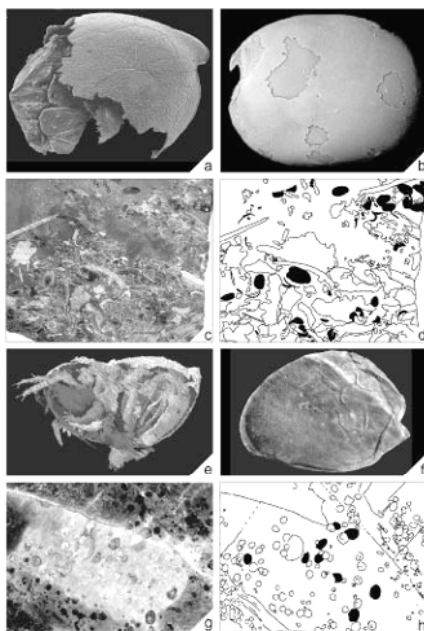


Fig. 3. Ancient scavenging myodocope ostracods. a. *Triadocypris spitzbergensis*, from the early Triassic of Flowerdalen, Spitzbergen, was found associated with ammonoids, and considered to be scavenging. Right valve, lateral view showing gill-like structures, epipodite of 5th limb and 7th limb (holotype, GPIHM 2558, 2.9 mm long). (taken from Wietschat, W. 1983. Stereo-Atlas of Ostracod Shells 10, 127 –138, late 10, 130, fig 1). b. *Eocypridina carsingtonensis* from the Carboniferous of Derbyshire, Central England, scavenged the shark *Orodus*. Left valve, lateral view (8 mm long) (GSM105459) (taken from plate 1 fig. 2 of Wilkinson et al. 2004, *Revista Española de Microplaeontología*). c. swarm of *E. carsingtonensis* in association with dermis from *Orodus*. d. diagrammatic representation showing the ostracods (black) and dermal tissue (white). e. *Colymbosathon ecplecticos* from the Early Silurian of Herefordshire, England. Left lateral view of the male holotype (OUM C.295670) (taken from Siveter et al. 2003, fig. A, Science, 300). f. *Myodoprigenia fistuca*, from the Late Ordovician of South Africa, fed on the carcasses of orthoconic cephalopods. Right lateral view of a carapace (holotype) (on slab C409). g. Swarm of *Myodoprigenia fistuca* on a cephalopod (slab C1002). Soom Shale, S. Africa.. h. Diagrammatic representation of swarming *Myodoprigenia fistuca* (black) on cephalopod remains (white) (taken from Gabbott et al. 2003, figs 2c-d, 4c *Lethaia*)

Some bradoriids may have been motile epibenthic dwellers of the sediment-water interface in a similar fashion to modern ostracods (Vannier et al. 2005), but the suggestion that bradoriids may have been micro-scavengers or micro-predators of unknown meiofaunal organisms (Vannier et al. 1998), is conjectural. The protruding antennae of *Kunmingella* appear powerful and might have been used for feeding. Their high abundance supports the notion that bradoriids were important recyclers on the Early Cambrian seabed (Shu et al. 1999), and coprolite evidence within the Chengjiang (Vannier and Chen 2005) and Burgess Shale Lagerstätten (Williams and Siveter unpublished data) indicates they were themselves, an important food source for larger animals.

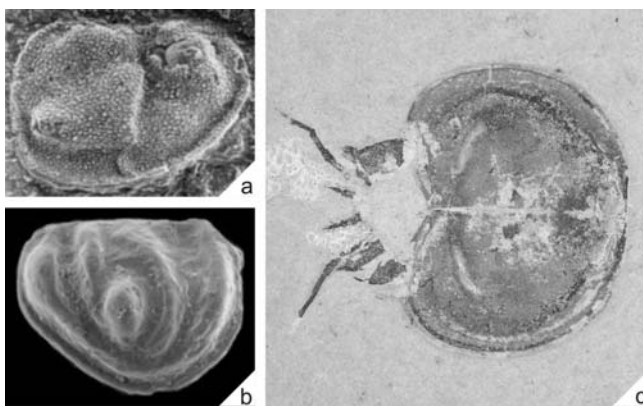


Fig. 4. Figure 4. Bradoriids may have been micro-scavengers or micro-predators and some may have been motile epibenthic species that occupied the same niches that ostracods were later to adopt. Some bradoriids may have been ostracods e.g. Fig. 4a. *Altajanella costulata* Melnikova (1.19mm long) from the Tandoshka Formation, Gorny Altay, Upper Cambrian, and Fig. 4b. *Vojbokalina magnifica* Melnikova (1.37mm long) from the Sablinka Formation, Leningrad Region, Russia, Middle Cambrian. However, *Kunmingella douvillei* (Fig. 4c, length of whole specimen including appendages is 7mm) is a bradoriid from the Chengjiang Lagerstaette, Lower Cambrian, Yunnan, China, that is no longer placed within the Ostracoda on the basis of the preserved soft part anatomy (Photograph by Derek Siveter; taken from Hou et al., 2004, *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*, Blackwell Science Ltd, Oxford)

There is no evidence of carnivory in bradoriids or in Ordovician palaeocopes. Myodocopes are, therefore, the oldest known carnivorous taxa amongst the Ostracoda. Carnivory may have been one mechanism that enabled ostracods successfully to colonise the water column and search for

food, and, once pelagic, to enter environments from which the palaeocopes were excluded.

4.5 Conclusions

The origins of carnivory amongst Ostracoda are difficult to identify, but this trophic position appears to have been attained very early in the evolution of the group. Predation may have begun amongst the benthonic and nekto-benthonic species of bradoriids and this lifestyle was adopted by early myodocopids.

Although there are numerous species of carnivorous ostracods in Recent marine and freshwater milieux, there are few convincing examples in the fossil record. Without soft part anatomy, functional morphology of carnivorous taxa cannot be identified and we are forced to rely on secondary evidence. There are, however, several cases of carnivory by scavenging, all by myodocope ostracods. These are the *Myodoprimgenia*/orthocone association in the Soom Shale Member, South Africa, the *Eocpridina*/shark association in the Bowland Formation, Central England, and the *Triadocypris*/ammonoid association in the Lower Triassic of Spitzbergen. Although not recovered in association with carrion or prey, the soft part anatomy of *Colymbosathon*, from the Lower Silurian of Herefordshire, England, suggests it was probably a predator or scavenger.

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