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Feeding in myodocopid ostracods: functional morphology and laboratory observations from videos

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Abstract High-resolution videos, scanning electron microscopy and histology were used to study the feeding mechanism of myodocopid ostracods from the Pacific Coast of Japan, as exemplified by *Vargula hilgendorfii* (Müller, 1890) and a few other cypridinid species. Ostracods observed in the laboratory were attracted to a wide spectrum of natural food sources, behaving as predators of living prey (e.g. polychaete annelids), as opportunistic scavengers on dead animals (e.g. annelids, fishes, squid), and also consuming artificial food. Food sources may be detected by chemoreception. The fourth limb (endopodites with strong sclerotized setae) and the furcal lamellae (claws with teeth) act in coordination to abrade and eventually tear open the protective integument of living/dead prey such as annelids. The mandibular palps are used mainly to hold the food. Food sections and soft-body contents are transferred to the mouth by the fourth limb (endopodial "rake") and fifth limb (exopodite with pectinate setae) and are passed to the oesophagus by the endites (mandibles, fourth and fifth limbs). Food is subsequently pumped up to the stomach by peristaltic contractions of the oesophagus (ring muscles) and stored in the stomach pouch. The upper lip of bioluminescent (*V. hilgendorfii*) and non-bioluminescent species of Cypridinidae often contact food, suggesting that some of the glands housed in this organ may emit digestive enzymes prior to ingestion. Ostracods are able to ingest massive quantities of food within a few minutes and to survive starvation for several weeks. In *V. hilgendorfii*, the midgut is a huge sac-like organ with no partition and is lined with a single layer of columnar epithelial cells. No differentiated hepatopancreas is present. The cypridinid produces a single faecal pellet wrapped in a thin reticulated, peritrophic membrane. Myodocopid ostracods exhibit a wide range of feeding strategies (detritus-feeding, comb-feeding, scavenging, predation, ectoparasitism) in both benthic and pelagic niches, and constitute a substantial source of food for many zooplankters. Adaptation of cypridinids to scavenging/predation is reflected in the morphology of their furcae, mandibles, fourth and fifth limbs, and their digestive system. Palaeontological data suggest that early Triassic cypridinids and possible late Ordovician myodocopids may have been carnivorous scavengers feeding on carcasses of cephalopods (ammonoids or orthoconic nautiloids), thus playing the same role of "recyclers" as modern representatives of the group.

Introduction

Only sparse information is available on the feeding mode of the thousands of species of ostracods (Podocopa: Myodocopa: Cohen 1982; Maddocks 1992) which are known to inhabit almost the entire spectrum of marine environments from tidal pools to the deep-sea. This contrasts markedly with other microcrustaceans such as planktonic copepods, whose feeding mechanisms have been studied intensively using modern techniques (e.g. Koehl and Strickler 1981; Paffenhöfer et al. 1982; Nishida and Ohtsuka 1996). In all ostracod groups, the biomechanics of feeding have mainly been

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deduced from anatomical and histological studies of preserved material (e.g. Cannon 1931, 1933, 1940; Iles 1961), and rarely from direct observations of living specimens (Lochhead 1968; Cohen 1983). An exception is a recent study based on the analysis of video-recordings of living ostracods which describes in detail the role of the furcae in the feeding process of scavenging cypridinids (Parker 1997).

Materials and methods

Even in tiny crustaceans a few milimetres long, feeding is a complex cycle which begins with the detection of food and ends with the production of assimilable nutrients (Fig. 1). Our study concentrates on two major aspects of the feeding cycle: (1) the attraction of ostracods to food (food-acquiring behaviour and range of food eaten), and (2) the biomechanics of nutrition (appendages involved in the capture and breakdown of food, and the digestive system). We used a combination of high-resolution video-recordings of live specimens observed in the laboratory, scanning electron microscopy (SEM), and light microscopy of microtome paraffin-sections.

The transparent carapace of myodocopid ostracods facilitates direct observation of the functioning appendages and digestive tract whilst they feed. *Vargula hilgendorfii* (Müller, 1890) (see Fig. 4A, B) was used extensively for experiments, together with a few other associated bioluminescent and non-bioluminescent cypridinid species. Samples were collected from two localities along the Pacific Coast of Japan, south of Tokyo: Tateyama (Boso Peninsula; Longitude 139°51′E, Latitude 35°00′N; water depth, <5 m) and Shimoda (Longitude 138°56′E, Latitude 34°39′N; water depth <5 m), and included an undescribed pigmented cypridinid (see Fig. 4D, E) which differs from *Melavargula japonica* Poulsen, 1962 and probably belongs to *Paravargula* Poulsen, 1962 (Parker personal communication) a genus known from south-east Asia (e.g. Philippines, Indonesia; Hanai et al. 1980). The material was collected at night using baited traps (methods of Vannier and Abe 1993; Abe 1994; see also Natas 1979 for *Cypridina norvegica*), and maintained for several weeks (April to May 1996) at Shizuoka University in aquaria at a constant temperature of ≃12 °C). Living ostracods were transferred to shallow dishes or small Plexiglas containers (see Vannier and Abe 1993) with a pipette, and were viewed under a binocular microscope (Olympus SZH 10: DF PlanApo IX lenses for routine observations; Olympus BX 50 for higher magnification) set up either in a vertical or a horizontal position. Repeated video-recordings were made by means of a high-resolution video-camera (Ikegami MKC 385 with camera control unit) connected to a Panasonic NVW1 VHS video-recorder and Hitachi VY 170 colour video-printer. Transmitted and reflected cool-light sources were provided by fibre optics. Recent studies have detailed the biology of *V. hilgendorfii* (Vannier and Abe 1993; Abe and Vannier 1995; Abe et al. 1995, 1996; Ikeya and Abe 1996; Ikuta 1997). Underwater observations of this species in its natural environment (Abe unpublished data) have revealed that these ostracods behave similarly (e.g. swimming, burrowing, swarming on carcasses) in natural and laboratory conditions. The use of artificial light from fibre optics during our video-recordings induced no visible changes in the behaviour of ostracods (attraction to food sources, feeding mechanism, ingestion). The timing of emergence of ostracods from the sediment in possible relationship to feeding habits would require accurate field observations and further appropriate laboratory experiments, and was without the scope of the present paper.

Feeding experiments

Frozen larvae of *Chironomus* sp. (Diptera: Insecta) the "akamushi" commonly used by Japanese anglers, proved to be particularly suitable for the laboratory feeding-experiments. Besides their relatively small size (≃1 cm), simple morphology, and brightly-coloured body contents (which greatly facilitated our video observations under the microscope), these larvae have morphological characteristics (i.e. a segmented body lined with a thin cuticle, underlying muscular layers and locally sclerotized parts) comparable to those of many invertebrates on which myodocopid ostracods feed in their natural environment [for example smaller crustaceans, annelids, worms (sensu lato), etc]. Living (both intact and injured), dead and decaying polychaetes, dead bioluminescent squid (*Watasenia scintillans*, Theutoidea: Cephalopoda), and small dead fishes were also used as experimental food; these constitute, unlike insect larvae, possible natural food sources for *Vargula hilgendorfii*. Feeding of ostracods on detritus was tested by offering them small shreds of "surimi" (crab sticks). This human food, made of processed fish, attracts ostracods, has a relatively soft and uniform fabric, and does not produce clouds of suspended particles in the field of observation as is often the case with natural animal detritus such as decaying tissues.

Tests of feeding response to chemical stimulus

Other experiments conducted at the Aichi University of Education, Japan (Y. Toya and colleagues) were devised to determine which chemical substances in the food might trigger feeding activity in *Vargula hilgendorfii*. A petri dish was used, with two identical agar discs placed diametrically opposed to each other (Fig. 2). Agar is a neutral substance which is not consumed by ostracods. One disc (= sample disc SD; e.g. amino acids) was impregnated with the chemical substance to be assayed, the other disc (CD) was used as a control. Ten specimens of *V. hilgendorfii* were used for each experiment and observed during a period of 5 min (video-recordings). The response of the ostracods (e.g. biting SD, contacting SD) to the chemical substance and to the agar disc (contacting CD) was evaluated as indicated in Fig. 2. A wide range of chemical substances present in natural food such as amino acids and nucleic acids are currently being tested by this method (Y. Toya work in progress).

Scanning electron microscopy

The morphology of those appendages and mouth parts which were observed to contact or handle food particles was examined by scanning electron microscopy (SEM). The cypridinid material was fixed in 3% glutaraldehyde (TAAB) in 0.1 *M* cacodylate buffer, at a pH of 7.0 (Felgenhauer 1987). It was then dried with a Hitachi Freeze Dryer ES 2030, coated with platin–palladium or gold, and observed with Hitachi S-4500 and S-800 SEMs. Appendages were also dissected in 100% ethanol and then immersed for 5 min in hexamethyldisilazane (HMDS; Nation 1983) before being air-dried and mounted on stubs for SEM observations. Two specimens of *Vargula hilgendorfii* (a male and a female) were embedded in a styrene-metacrylate resin, cut sagittally with the glass knife of an ultramicrotome, de-embedded with acetone, and observed under the SEM; this method revealed some of the three-dimensional aspects of the digestive system.

Histology

Fresh specimens were fixed with Bouin's solution (2,4,6-trinitrophenol, formaldehyde and acetic acid), dehydrated in graded ethanol-*n*-butanol (=2-methyl-2-propanol) series, and imbedded in paraffin (Paraplast®; melting point 55 to 57 °C). They were then prepared for 5 µm microtome serial sections and stained with Mayer's hematoxylin-eosin or Heidenhain's azan (azocarmine-aniline blue-orange G). Optical observations and microphotography of histological sections were made with a Vanox and BX50 Olympus microscope.

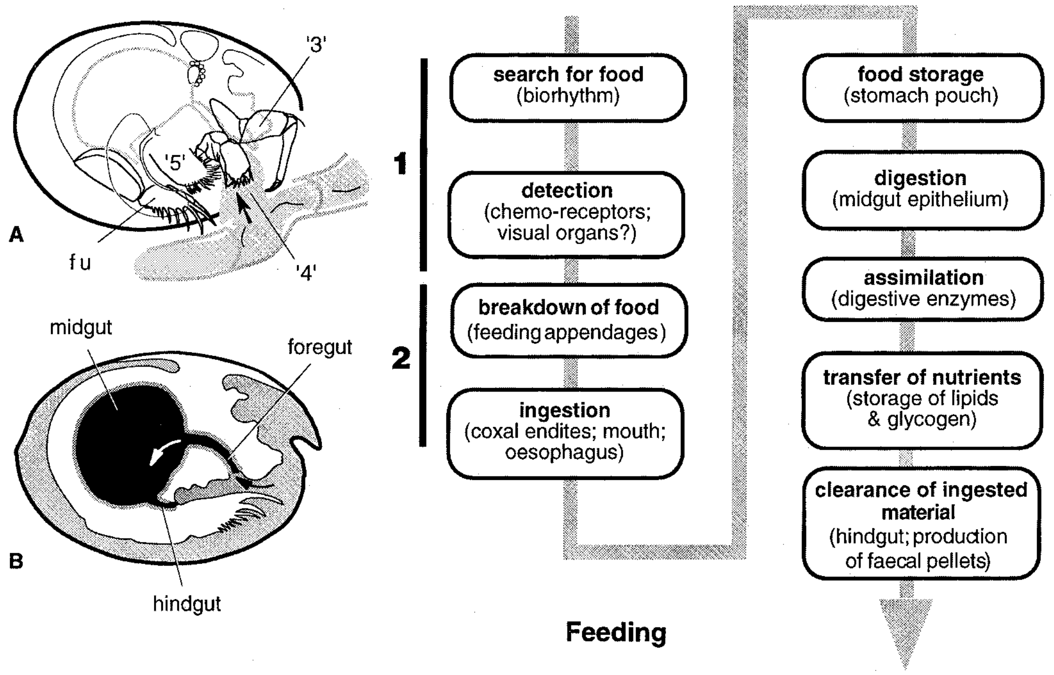


Fig. 1 Feeding cycle in myodocopid ostracods [*1* detection of food (living or dead prey, decaying tissues, detrital particles); *2* physical breakdown of food; *3* chemical breakdown; *4* synthesis of nutrients] and simplified sketches (**A**, **B**) of *Vargula hilgendorfii* (Müller, 1890) (Ostracoda: Myodocopida) showing location and overall morphology of feeding appendages and digestive system, respectively [*fu* furcae; '*3*' third limb (mandible); '*4*' 4th limb (maxillule); '*5*' 5th limb (maxilla)]

Results

Search for and attraction to food

During the day and in its natural habitat, *Vargula hilgendorfii* lives buried in the few top milimetres of sediment and becomes active in the water column after sunset and for ~10 h thereafter. Activity increases abruptly at dusk and, after a few hours, decreases gradually until dawn (Irie 1953; Nakamura 1954; Hiruta 1980; Abe et al. 1995; Abe unpublished observations from field collections using baited traps). A similar circadian rhythm of emergence from the sediment occurs in most cypridinid ostracods from coastal environments (Cohen and Morin 1986), and in many other crustaceans such as *Nebalia bipes* (Macquart-Moulin 1979) and isopods (e.g. *Excirolana* sp. which is often associated with *V. hilgendorfii*). The feeding activity of *V. hilgendorfii* appears to be controlled by the alternation of day and night and may be triggered by the onset of darkness. However, *V. hilgendorfii* kept in aquaria emerged from the sediment in which they were buried every time food was offered (e.g. small shreds of "surimi"), irrespective of light conditions, even during the day. Similarly, *Skogsbergia* sp. (Cypridinidae) from the Pacific Coast of south-east Australia became active at 16:00 h during daylight conditions when a fish carcass was placed on the sea floor (Parker 1995 and personal communication).

In laboratory conditions, *Vargula hilgendorfii* and other cypridinids (e.g. see Fig. 4D, E) were attracted to and fed on a wide range of items including living polychaete annelids and dead animals (annelids, fish, squids, gastropods). In the case of dead animals, the ostracods were even attracted to material in an advanced state of decay. Fresh fish muscle from tuna and vertebrate liver (e.g. pork liver which is routinely used in baited traps) proved powerful attractants, although generally absent in the natural environment of the ostracods. A strong feeding response was also obtained using processed fish products consumed by humans (e.g. "surimi").

Immediately after being dropped into an experimental container containing a living annelid (errant or sedentary polychaete), the ostracods would rush towards the food source and almost invariably begin biting either the mouth or anal opening of the prey (Fig. 3A, B). The presence of undigested food remains or body secretions most probably attracted the ostracods to these particular sites. Other preferential feeding sites included the gills and feeding tentacles of sedentary polychaetes. Ostracods preying on the body wall of annelids, especially in the ventral region, were also frequently observed (Fig. 3C–F). A few ostracods even caused visible damage to the prey, including circular wounds to the epidermis and musculature (Fig. 3F). Although relatively deep, most of these injuries were not lethal. Even the tiniest cuts along the body wall of the annelid (induced by an experimenter or by ostracod attacks) were detected by *Vargula hilgendorfii*, which immediately swam to and voraciously fed on the cut regions. Similarly, fragments of any dead animal (annelid, mollusc, fish) whose body contents were exposed triggered similar behaviour. As soon as one or several

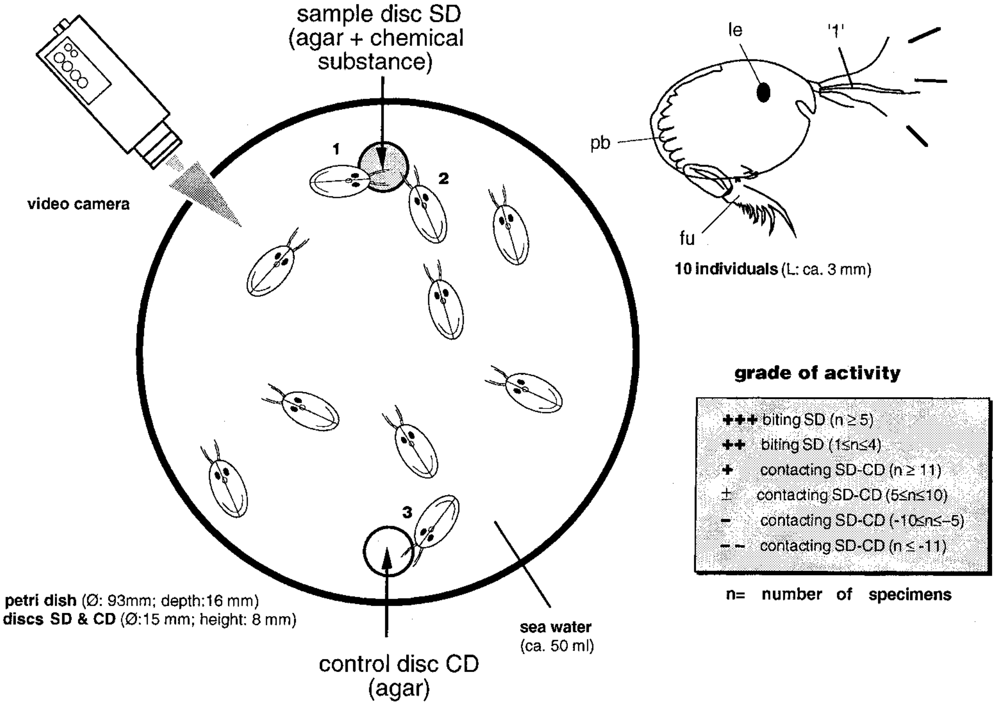


Fig. 2 Set-up of experiment to test attraction of *Vargula hilgendorfii* to chemical substances contained in natural food. Activity level of ostracod was evaluated by counting number of contacts (actual biting or simple contact) of 10 specimens with a sample disc (*SD*) impregnated with chemical substance and with a control disc (*CD*), over period of 5 min [*1* specimen biting SD; *2* contacting SD; *3* contacting CD; + + +, + + represent number of times SD was bitten during the experiment; +, ±, –, – – represent number of contacts with CD subtracted from number of contacts with SD (–, – – indicate number was negative); *fu* furca; *le* lateral eye; *pb* posterior of body; '*1*' 1st pair of antenna] (after Y. Toya personal communication)

ostracods began tearing at the body of a live or dead animal, thus releasing body fluids (e.g. blood) into the surrounding medium, many other individuals would rush to the food source within a few seconds. Swarms of ostracods feeding on live prey or scavenging on carcasses were commonly observed both in the laboratory and field (submarine observations of baited traps; Abe unpublished videos). The activity of several tens of ostracods sufficed for small live or dead annelids or food pieces (e.g. shreds of surimi 2 to 5 cm long, 2 to 3 mm thick) to be rapidly broken up and consumed within a few minutes. The escape movements of living annelids (even very active errant polychaetes) usually failed to dislodge their predators. When feeding on undecayed fish carcasses, ostracods entered the body cavity through the anus, the genital opening and the gill chamber, and generally clustered in places where mucus, skin or soft body contents were available (e.g. injured parts, eyes). Very similar laboratory and field observations have been made on other cypridinid ostracods from Australia (Parker unpublished data and personal communication). *V. hilgendorfii* was able to sever the membrane covering the eye of squid, invade the cavity eye and consume the liquid contents (Fig. 3H, I). The youngest juveniles (Fig. 4M) exhibited the same feeding behaviour as conspecific adults of both sexes.

Chemodetection of food

Although *Vargula hilgendorfii* has well-developed lateral coumpound eyes, it probably does not use its visual organs to locate food, as in its natural environment it feeds mainly after the onset of darkness. It is more likely to rely on chemical senses to detect food. Experiments (Fig. 2) using a wide array of substances (Y. Toya and colleagues), including amino-acids and nucleic acid compounds (e.g. ATP, ADP, AMP, NADH, FAD), studied the response of ostracods to chemical stimuli. The compounds containing an adenine nucleotide moiety were found to act at low concentrations as specific feeding stimulants for *V. hilgendorfii*, inducing feeding behaviour (e.g. biting the sample disc: see Fig. 2). ATP is widespread in living organisms and is usually converted to ADP, AMP, and finally inosine after their death. Such molecules when released from living and dead tissues or from bait (e.g. pork liver) into the surrounding medium may stimulate specific receptors triggering ostracod feeding-activities. Although no direct evidence from transmission electron microscopy studies is yet available, chemoreceptors may be located on the first pair of antennae, which always protrude beyond the frontal opening of the ostracod carapace prior to contact with food. Chemosensory organs such as halophores located on the first antennae of many myodocopids may play a major role in the detection of food sources (Parker personal communication).

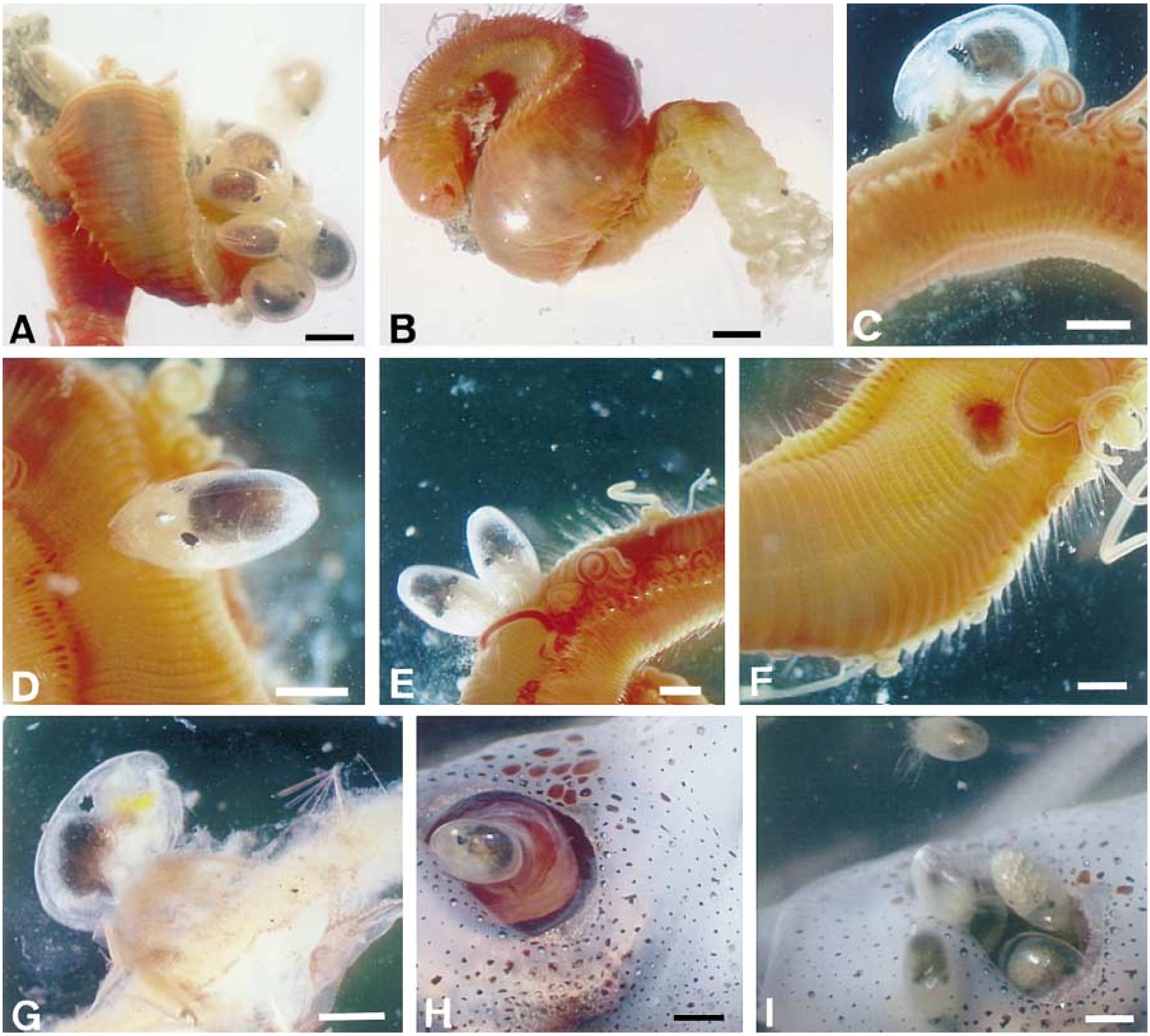


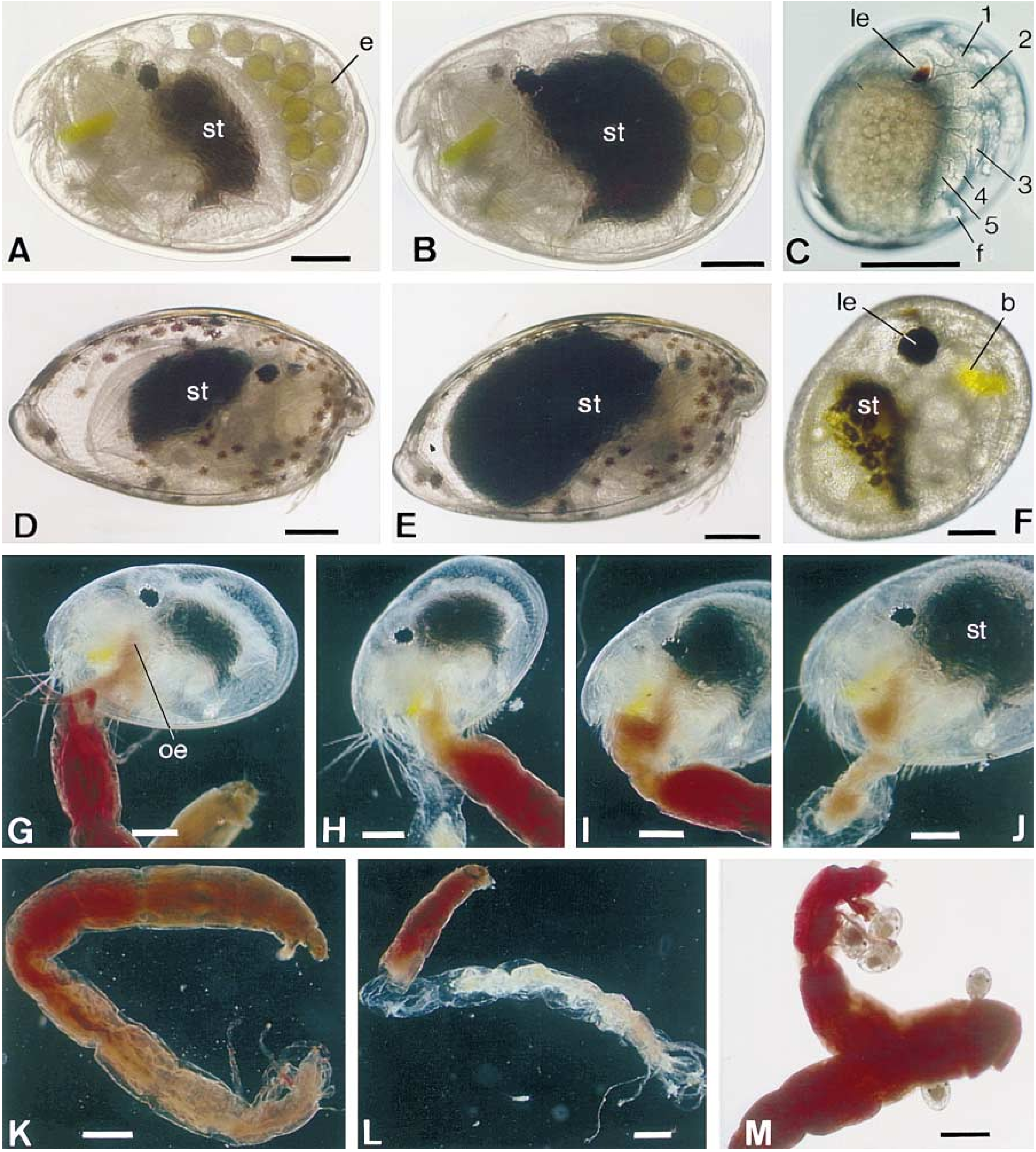
Fig. 3 *Vargula hilgendorfii*. Predatory and scavenging behaviour in ostracods from Japan. **A** ostracods gathering round and feeding on posterior part of living polychaete annelid; **B** same living annelid after a few minutes of ostracod feeding; **C–E** ostracods piercing cuticle and feeding on epidermis, muscles and body fluids of polychaete annelid (ventral part of body); **F** deep wound in body of prey (ventral part) after few minutes of ostracod predation; **G** scavenging on dead annelid in advanced stage of decay; **H**, **I** scavenging on eye of dead bioluminescent squid, one specimen can be seen cutting out external membrane of eye (**H**) before other specimens gather within eye cavity and consume the soft parts (**I**). All photographs are from video-recordings. Scale bars = 1000 μm in **C**–**G** and 1500 μm in **A**, **B**, **H** and **I**

Biomechanics of feeding

Feeding appendages

Three pairs of appendages are used by *Vargula hilgendorfii* in feeding, irrespective of the nature of the food. These are the mandibles, the 4th limbs (maxillules) and the 5th limbs (maxillae). The furcal lamellae, which are attached to the posterior end of the body, are also involved in feeding. The first antennae, the second antennae and the 7th limbs play no role either in the capture or the physical breakdown of food. No movement of the 6th limb (Fig. 5C) has been observed during feeding.

The mandibles are situated at either side of the mouth, and consist of a long endopodite palp terminated by sclerotized claws (Fig. 6A–C). The first endopodial article functions like a knee allowing the tip of the appendage to project forward as well as to flex back towards the mouth (Fig. 7A, B). Two prominent horn-like endites, entirely covered with spines, protrude from the inner side of the coxa and point symmetrically into the mouth cavity (= atrium oris; Fig. 6D–F). The main body of the 4th limb consists of a two-jointed endopo-



dite provided with a strong longitudinal musculature allowing the limb to flex up obliquely towards the mouth. The distal segment of the endopodite bears numerous strong setae of varying morphology (e.g. pectinate, claw-like), and is directed inwards so that the distal setae of the 4th limbs interlock ventrally to form a rake-like feature in a relaxed position (Fig. 6H). Sclerotized "cutting teeth" are present along the posterior edge of the first endopodial segment. The 4th limb has three coxal endites bearing bunches of mainly stout spiny setae which project inwards and towards the mouth (Fig. 6L). The large epipodial fans of the 5th limbs are used to ventilate the domiciliary cavity, thus creating and maintaining partial pressure gradients between the medium and the respiratory surfaces (Vannier and Abe 1995). Simultaneously, water is sucked in from

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Fig. 4 *Vargula hilgendorfii* (**A**, **B**, **C**, **F–J**) and cypridinid sp. (**D**, **E**, **M**). **A–F** Stomach (midgut) of two cypridinids (Ostracoda: Myodocopida from Japan. **A**, **B** female with embryos before feeding (stomach empty) and after 2 min of feeding on annelids; **C**, **F** unhatched embryonic stages with yolk cells (**C**) and rudiments of stomach pouch with large pigmented amoeboid cells (**F**); rudiments of appendages are visible in **C**; **D**, **E** male pigmented cypridind sp. before feeding (stomach empty) and after 2 min of feeding; **G–J** *V. hilgendorfii* sucking out body contents of a dead insect larva (*Chironomus* sp.; see "Materials and methods – Feeding experiments") – note presence of red food masses in mouth cavity (atrium oris), in oesophagus, and in contact with upper lip. **G**, **H** is male and **I**, **J** female, at times $t = 0$ (**G**, **I**) and $t = 2$ min (**1 J**), respectively; **K**, **L** insect larva before and after being eaten by ostracods; **M** insect larva being eaten by young juveniles (first instars, 1 d after release from marsupium) of a cypridinid sp. [*b* bioluminescent organ; *e* embryos; *f* furca; *le* lateral eye; *oe* oesophagus; *st* stomach; *1* first antenna; *2* second antenna; *3* 3rd limb (mandible); *4* 4th limb (maxillule); *5* 5th limb (maxilla)] All photographs are from video-recordings. Scale bars = 50 μm in **F**; 100 μm in **C**; and 500 μm in **A**, **B**, **D**, **E** and **G–M**

the frontal opening of the carapace and channelled beneath the upper lip. The rhythmic ventilation of the epipodites stops as soon as the ostracod contacts food. Thus, the exopodites (Fig. 6M, N) and the endites are the only parts of the limb involved in feeding. The most important features of the exopodites are strongly sclerotized, densily packed setae, and a double row of teeth present on the inner side of the first and second segments (Fig. 6O). The three endites point inwards, the most proximal one (precoxal endite) projecting upwards into the atrium. From their external morphology and musculature, the endopodites of the 4th limbs and the exopodite of the 5th limbs were identified as the two major biting apparatus of the ostracod. The furcal lamellae bear a series of diverging powerful claws which decrease in size from the front to the rear, all of them being fringed with spines. The first pair of claws are jointed and armed with strong sclerotized "teeth" (Fig. 6S, U). The furcae have strong muscles (see present Fig. 9I; and Parker 1997 for other *Vargula* species) connected to the posterior of the body and, besides their role in feeding, act as powerful tools for digging into and penetrating the sediment (Vannier and Abe 1995). The morphology of the appendages is quite uniform among myodocopids (e.g. Cohen and Morin 1989), except in the case of *Cypridinodes* Brady, 1902 which has an unusually elongate 4th limb (Cypridinidae: Parker personal communication) and in comb-feeders (see Cannon 1933).

Feeding mechanism

The mechanics of feeding was reconstructed from repeated video-recordings of *Vargula hilgendorfii* feeding on experimental food (insect larvae "akamushi"; Fig. 4G–L). The ostracod uses both its mandibular palps and the tips of its furcae to hold the food tightly, thus anchoring itself to the cuticle of the larva (Figs. 7A; 8 A, B). Strong water currents induced by a pipette were unable to dislodge the ostracods from the food. The back and forth movements of the furcal claws rotating in a vertical plane combined with the clasping movement of the 4th limbs are able to abrade and eventually tear open the cuticle. This action involves different types of sclerotized features on the furcae (rows of teeth and spines) and the 4th limbs ("cutting teeth", claw-like setae). The mandibular claws play a role in passing food sections to the 4th limbs. Thereafter, the endopodites of the 4th limbs are flexed up towards the atrium, tearing off lumps of soft body contents from the larva and bringing them into position below the mouth (Figs. 7B; 8C). At this stage, the tips of the 4th limbs clearly function as biting jaws. Afterwards, the partly triturated food is transferred to the 5th limbs, whose exopodial setae extend forwards and inwards (Figs. 7C; 8D, E). The exopodite clearly has the dual role of physically breaking down food with its double row of inner teeth, and passing it further up into the atrium (Figs. 6F; 7C). The movements of the mandibles suggested that the mandibular

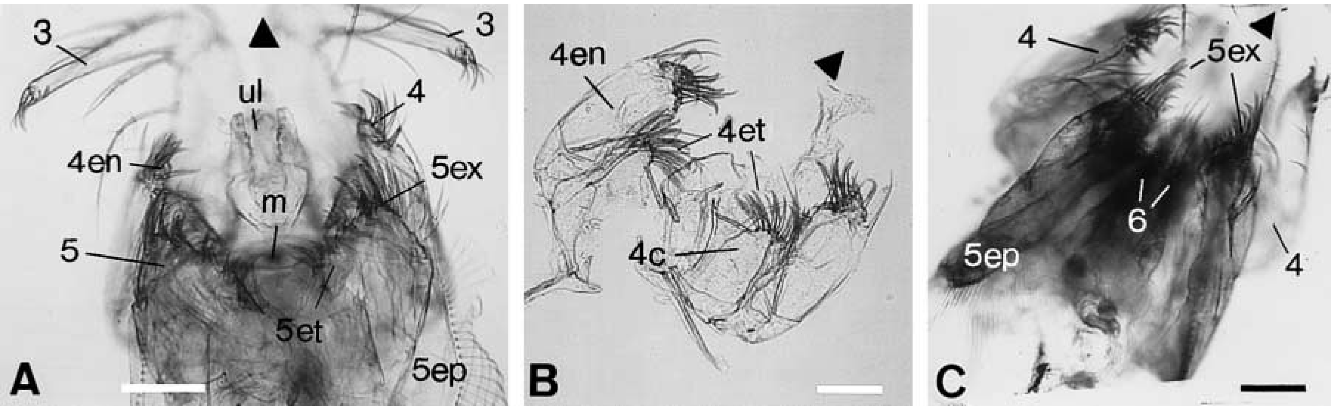

Fig. 5 *Vargula hilgendorfii*. Feeding appendages in transmitted light. **A** Ventral view showing mouth region and 3rd to 5th limbs, specimen immersed in alcohol; **B** dissected pair of 4th limbs (maxillules) mounted on slide; **C** ventral view showing 4th to 6th limbs; specimen immersed in alcohol [*Arrow heads* indicate anterior part; *m* mouth; *ul* upper lip with glands; *3* 3rd limb (mandible); *4* 4th limb (maxillule); *4c* coxa of 4th limb; *4en* endopodite of 5th limb; *4et* coxal endites of 4th limb; *5* 5th limb; *5et* endites on protopodite of 5th limb; *5ep* epipodite of 5th limb; *5ex* exopodite of 5th limb; *6* 6th limb] All photographs are from video-recordings. All scale bars = 200 μm

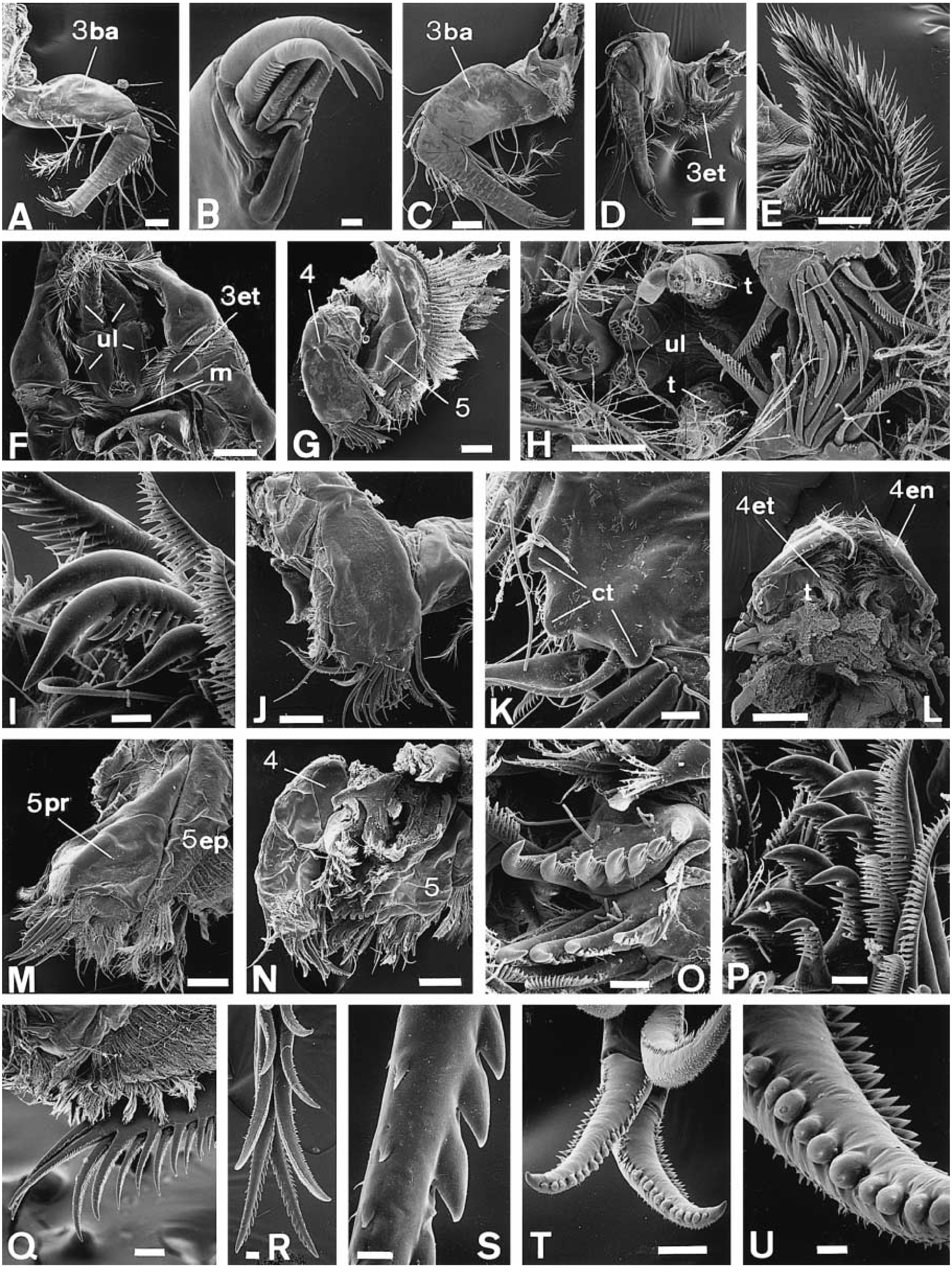
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Fig. 6 *Vargula hilgendorfii*. Scanning electron microscopy of feeding appendages. **A**–**F** Third limb (mandible): right limb in lateral external view (**A**), distal part of endopod (**B**), right limb in medial view (**C**) and in frontal view (**D**), detail of coxal endite (**E**), ventral view including mouth and coxal endites (**F**). **G**–**L** Fourth limb (maxillule): left limb in external lateral view (**G**), ventral view of endopodial setae and upper lip (**H**), detail of some endopodial setae (**I**), right limb in lateral view (**J**), "cutting teeth" on 1st article of endopodite (**K**), ventral view showing coxal endites (**L**). **M**–**P** Fifth limb (maxilla): left limb in lateral view (**M**), right limb in lateral view (**N**), detail of exopodial teeth and some setae (**O**, **P**). **Q**–**U** Furca: lateral view (**Q**), ventral view (**R**), teeth on 1st pair of claws (**S**), 1st pair of claws (**T**), detail of teeth on 1st pair of claws (**U**) [*ct* cutting teeth; *m* mouth opening; *t* tusk of upper lip; *ul* upper lip; *3ba* 3rd limb (basipodite); *3et* 3rd limb (coxal endite); *4* 4th limb; *4en* 4th limb (endopodite); *4et* 4th limb (endite); *5* 5th limb; *5ep* 5th limb (epipodite); *5pr* 5th limb (protopodite] Scale bars = 10 μm in **B**, **S**, **U**, 20 μm in **I** and **P**; 25 μm in **K**; 30 μm in **O** and **R**; 50 μm in **E** and **T**; 100 μm in **A**, **C**, **D**, **F**, **H**, **J**, **L**, **M**, **N** and **Q**; and 150 μm in **G**

coxal endites force the triturated food into the oesophagus. However, the action of the other endites (4th, 5th and 6th limbs) could not be observed on our videos. Their probable role is to trap food particles as efficiently as possible and to direct them into the atrium (Fig. 5A, B). Food accumulated within the funnel-shaped atrium and sometimes as far up as the area below the upper lip (Fig. 4G–J), was then sucked up by the peristaltic contractions of the oesophagus (Fig. 7D). The expansion of the stomach pouch while the ostracod was eating indicated the steady pumping action of the oesophagus and the movement of the food through the gut.

The ingestion of food was almost invariably accomplished by repeating the sequence reconstructed in Figs. 7 and 8. However, the coordinated movements of the 4th and 5th limbs varied in pace according to the nature of the food (e.g. soft or hard). A series of fast strokes of the furcae rotating in the vertical plane often resulted in tearing open cuticular parts of the food with greater efficiency. Similar anterodorsal to posterodorsal furcal movements (up to 10 per second cutting/recovery strokes) have been observed in other myodocopids feeding on fishes under laboratory conditions (Parker 1997). Hard cuticular material was not ingested by the ostracods and was expelled from their mouth opening with the help of their furcal claws.

Digestive system

The oesophagus is a curved tube, slightly compressed dorsally and lined with a cuticle of ectodermal origin. In *Vargula hilgendorfii*, ≃20 ring muscles are present along the oesophagus. Their peristaltic contractions combined with those of dilator muscles inserted on the inner wall of the oesophagus convey food up to the stomach pouch. As clearly observed in transverse sections (Fig. 9J), the oesophagus wall has many longitudinal infoldings which accommodate the expansion of the lumen when food is transferred from mouth to stomach. A very similar structure is known in other maxillopod crustaceans such as *Argulus maculosus* (Overstreet et al. 1992; their Fig. 49).

The midgut consists of a huge sac-like organ with no partition, as is often the case in ostracods (e.g. podocopids and cladocopines: Hartmann 1967) and the vast majority of larger crustaceans (e.g. decapods). The whole pouch is lined with a single layer of columnar epithelial cells. Only one cell-type occurs, with a large nucleus located toward the basal region and a cytoplasm containing granules or numerous vacuoles. A basement membrane and intersecting muscle fibres separate the epithelium from large pigmented cells. The surrounding parenchyma is filled with stored material (e.g. lipids, glycogen) and bathed by the hemolymph. The folded basement membrane most probably accommodates the massive increase in stomach volume observed during feeding experiments (Fig. 4A, B, D, E). Within a few minutes of feeding, the stomach volume was increased by two or even three times (Fig. 4D, E), reducing the parenchyma to a thin layer.

No differentiated hepatopancreas is present in *Vargula hilgendorfii* or in the other Japanese cypridinid species we examined (e.g. pigmented species: Fig. 4 D,E). This contrasts with other myodocopid ostracods such as planktonic halocyprids and cylindroleberidids (see: Müller 1894; Hartmann 1967, his Fig. 226), and with benthic podocopid ostracods (Müller 1894; Hartmann 1967, his Fig. 237). Transverse microtome-sections made through *Conchoecia* sp. (Halocyprididae) from Japan (Vannier unpublished observations) revealed the presence of a sac-like hepatopancreas on both sides of the midgut, these organs being absent from *V. hilgendorfii*. In *V. hilgendorfii*, a thick "ring" of closely packed, elongated cells, heavily stained purple by hematoxylin, was found (present study) at the junction between the oesophagus and stomach. The function of these cells, which are a continuation of the columnar epithelium, is unknown. Since no associated muscles are present, they are unlikely to actively regulate food transfer from the oesophagus to the stomach. The absence of ducts and open tubules also excludes their function as hepatopancreatic cells. Conspicious round-shaped cells (up to 80 μm diam; Fig. 9I) containing fine granules were often observed within the stomach lumen among food masses; they were usually found close to the columnar epithelium and sometimes deeply embedded within the epithelial cells. Whether these large cells originate from the epithelium and contain and release digestive enzymes [? = "Fermentzelle" (sensu Claus 1895) or "Sekretzelle" (sensu Müller 1894; see Hartmann 1967)] in the stomach cavity remains unclear. The hindgut is a very narrow tube, flattened dorso-ventrally and provided with ring muscles. The anus opens above the furcal lamellae (Fig. 9I).

Specimens fed with surimi and then kept in a petri dish without food produced a single large faecal pellet (see Fig. 9N) wrapped in a thin reticulated membrane similar to the peritrophic membrane of numerous crustaceans, including copepods (Yoshikoshi and Ko 1988).

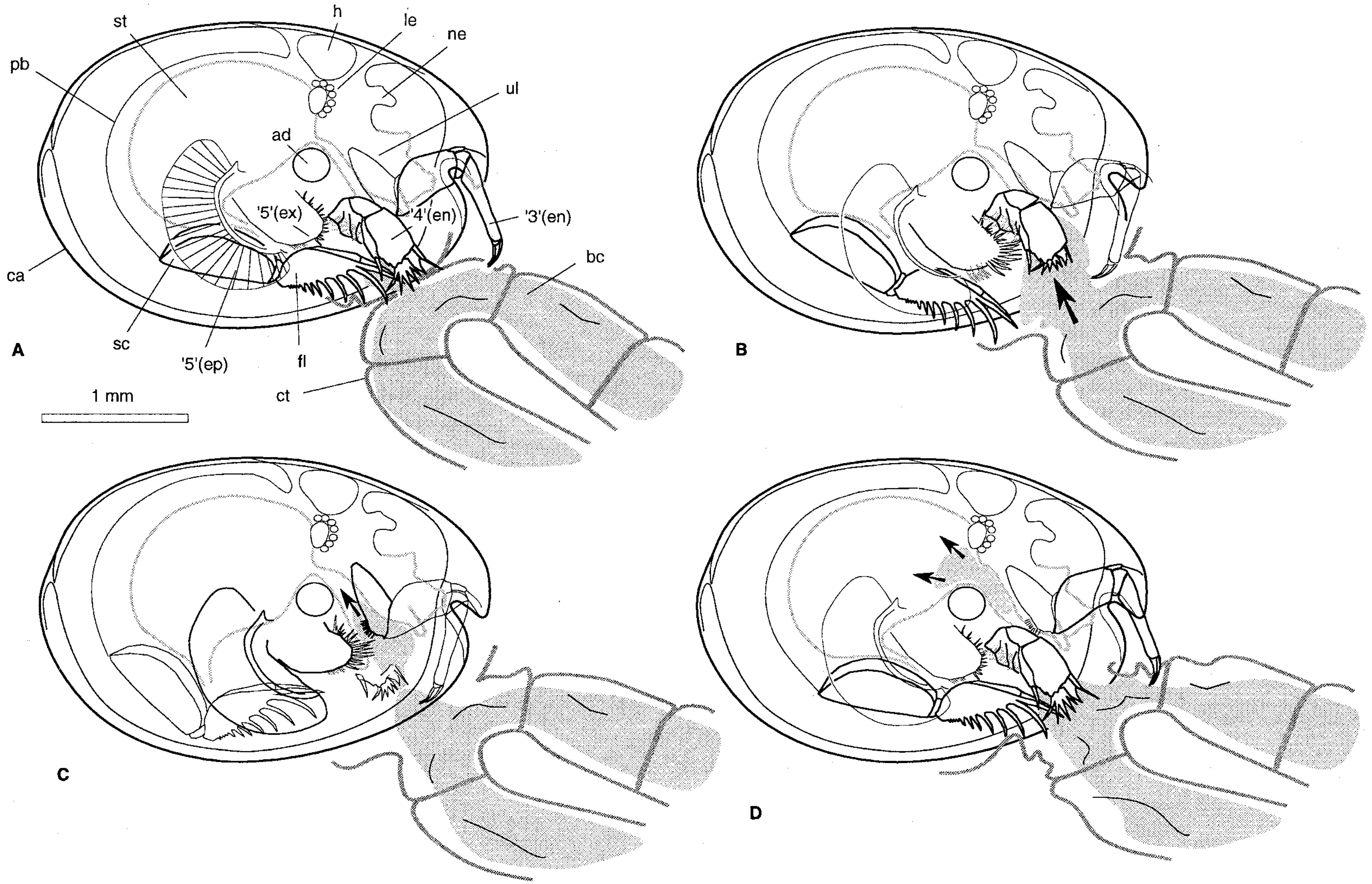

Fig. 7 *Vargula hilgendorfii*. Lateral reconstruction of feeding cycle from video-recordings. Right lateral view of specimen feeding on experimental food (insect larva, body contents represented in grey). 3rd, 4th and 5th limbs correspond to mandible, maxillule and maxilla, respectively, in standard terminology of crustacean limbs; not all appendages are represented [*ad* attachment of adductor muscles; *bc* body contents of insect larva; *ca* carapace; *ct* cuticle of insect larva; *fl* furcal lamella; *h* heart; *le* lateral eye; *ne* nauplius eye; *pb* posterior of body; *sc* sclerosome; *st* stomach; *ul* upper lip; '*3*'(*en*) 3rd limb (endopodite); '*4*'(en) 4th limb (endopodite); '*5*' (*ep*) 5th limb (epipodite); '*5*'(*ex*) 5th limb (exopodite)]

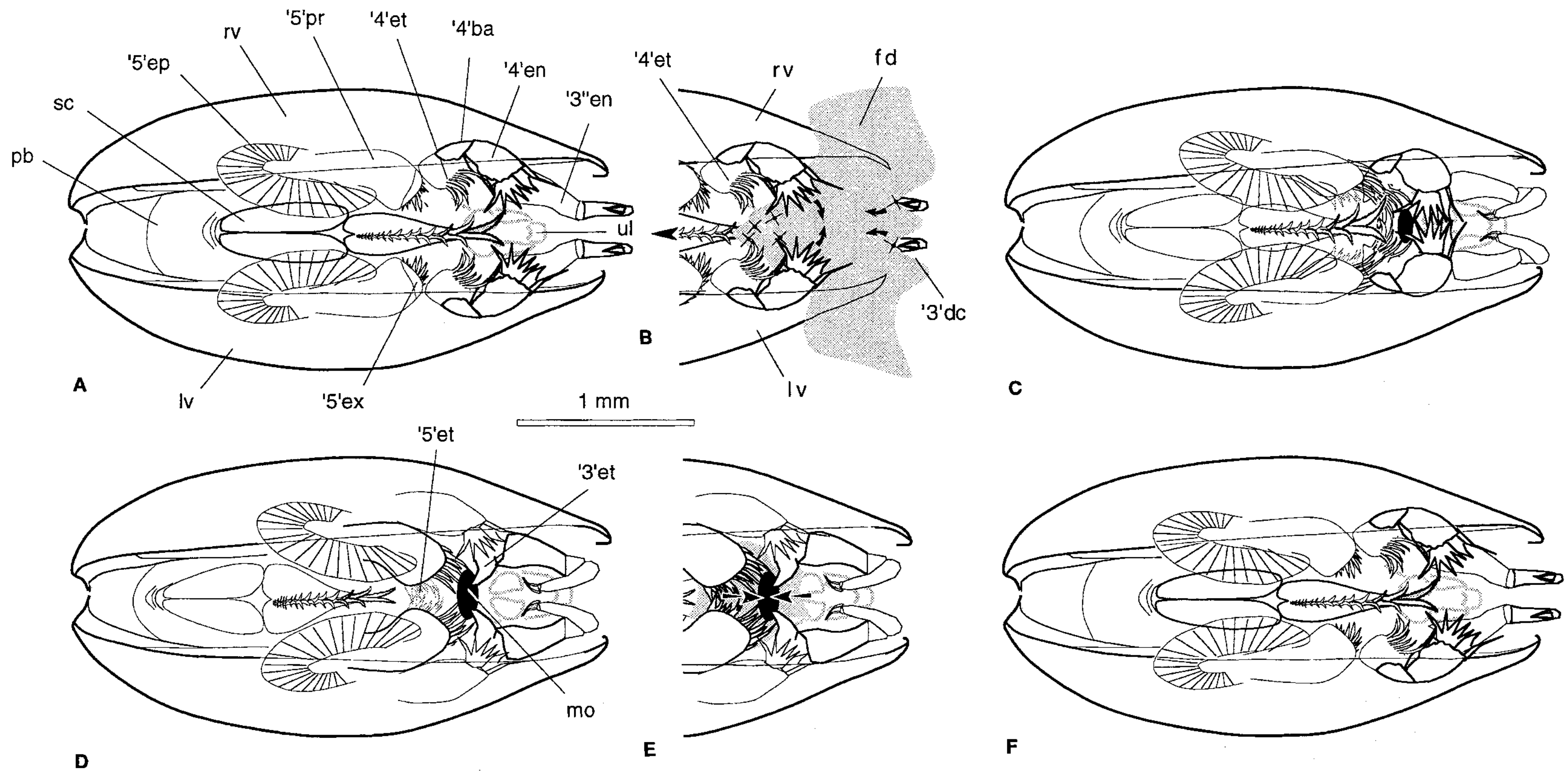

Fig. 8 *Vargula hilgendorfii*. Ventral reconstruction of feeding cycle from video-recordings. Ventral view of specimen feeding on experimental food (insect larva, body contents in grey). Terminology of limbs as in Fig. 7 [*fd* food (insect larva); *lv* left valve; *mo* mouth; *pb* posterior of body; *rv* right valve; *sc* sclerosome; *ul* upper lip; '*3*'(*dc*) 3rd limb (distal endopodial claw); '*3*'(*en*) 3rd limb (endopodite); '*3*'(*et*) coxal endite; '*4*'(*ba*) 4th limb (basipodite); '*4*'(*en*) 4th limb (endopodite); '*4*'(*et*) 4th limb (coxal endite); '*5*'(*ep*) 5th limb (epipodite); '*5*'(*et*) 5th limb (endites); '*5*'(*ex*) 5th limb (exopodite); '*5*'(*pr*) 5th limb (protopodite)]

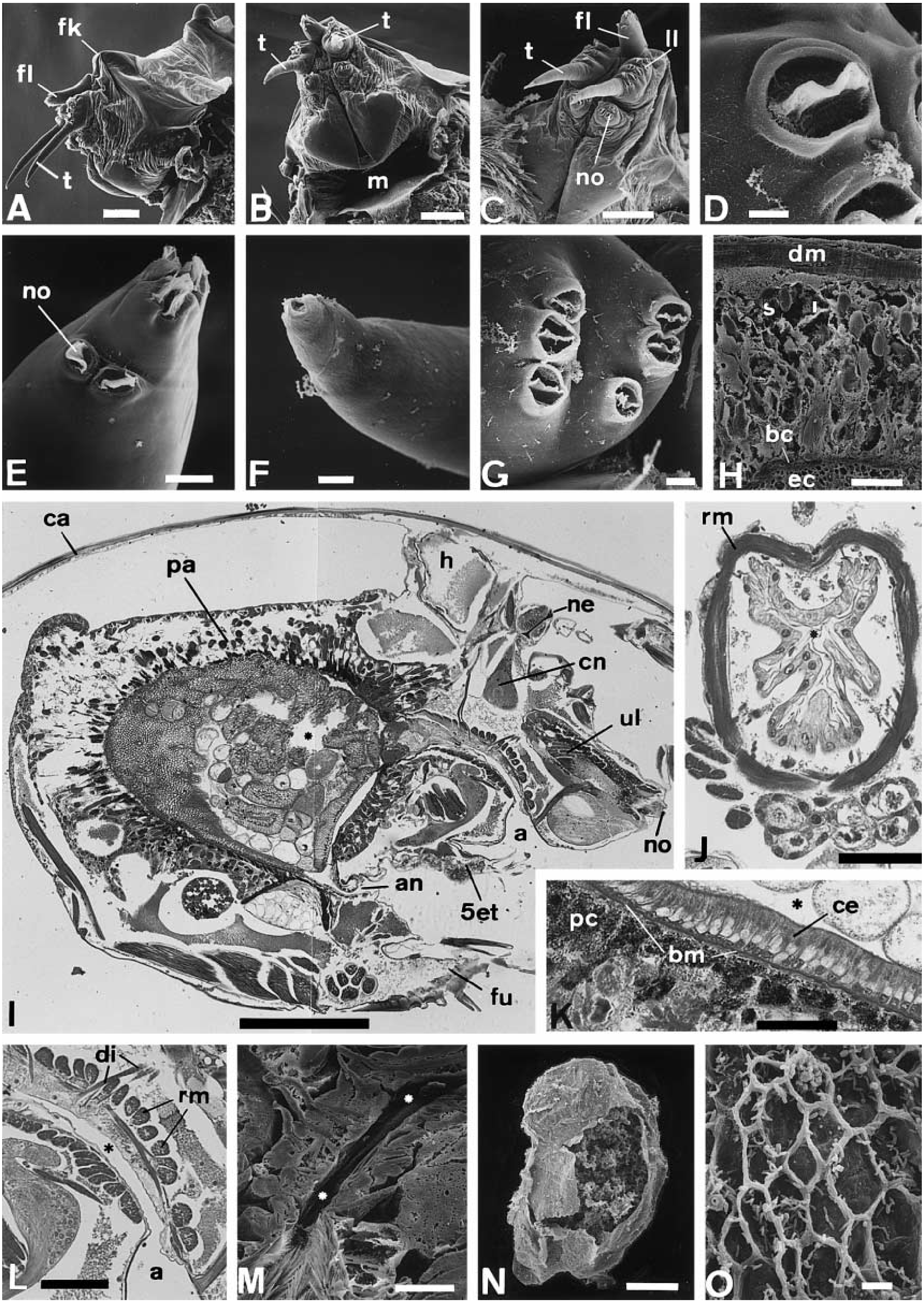
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Fig. 9 *Vargula hilgendorfii* (**G–O**) and cypridinid sp. (**A–F**). Mouth, upper lip, digestive tract and faecal pellets. **A–C** Lateral (**A**), ventral (**B**) and intermediate ventral (**C**) view of upper lip and mouth region; **D–F** nozzles on left posterior lobe of upper lip (**D**), frontal lobe (**E**), and tip of tusk (**F**) of same specimen as in **A–C**; **G** clustered nozzles raised on pegs; **H** sagittal section through dorsal part of body (specimen removed from metacrylate resin); **I–L** histological sections through body (sagittal, **I**), oesophagus (transverse, **J**), midgut columnar epithelium (**K**), and oesophagus (sagittal, **L**); **M** sagittal section through oesophagus (specimen removed from metacrylate resin); **N, O** faecal pellet in lateral view (**N**) and close-up showing external reticulation (**O**) [*a* atrium oris (mouth opening); *an* anus; *bc* basal complex (basement membrane + muscles); *bm* basement membrane; *ca* carapace; *ce* columnar epithelium; *cn* central nervous system; *di* dilator muscles; *dm* dorsal musculature; *ec* epithelial cells; *fk* frontal knob; *fl* frontal lobe; *h* heart; *ll* lateral lobes; *m* mouth; *ne* nauplius eye; *no* nozzle; *pa* parenchyma; *pc* pigmented cells; *rm* ring muscles; *t* tusk; *ul* upper lip; *5et* endite of 5th limb (maxilla); * gut lumen] All SEM micrographs except **I–L** (light photographs of histological sections). Scale bars = 5 μm in **D**, **F** and **O**; 10 μm in **E** and **G**; 50 μm in **J** and **K**; 100 μm in **A**, **B**, **C**, **H**, **L** and **M**; 200 μm in **N**; and 500 μm in **I**

The reticulation (Fig. 9O) observed on the surface of the faecal pellets is likely to represent the imprint of the junctions of the stomach cells (columnar epithelium). The peritrophic membrane stained with aniline blue, indicating the presence of chitinous material (sections through the stomach). The shape of the faecal pellets varied according to the shape of the stomach, being more elongated in the cypridinid sp. (Fig. 4D, E) than in *Vargula hilgendorfii* (Fig. 4A, B). In all species, the clearance of ingested material was usually completed within 24 h.

Upper lip

The upper lip of *Vargula hilgendorfii* is a very prominent organ overhanging the mouth and housing a glandular complex responsible for the production of bioluminescence (Fig. 9I). This results from the interaction of luciferin and luciferase secreted from the upper lip and oxygen present in the sea water (Tsuji 1978). Several types of vesicles (for cell terminology see: Saito et al. 1986; Huvard 1993) terminate at nozzles located in clusters on the anterior field of the upper lip and on two lateral tusks. Each nozzle is provided with a slit-like valve (Fig. 9D). Similar nozzles with associated exocrine cells were also found in the Japanese non-bioluminescent cypridinid ostracods studied by us (e.g. the cypridinid sp.; Fig. 4D, E), and are known to occur in all other cypridinid ostracods (see Cohen and Morin 1993, their Fig. 23; Parker 1997, his Fig. 10E). Only half the cypridinid genera are probably bioluminescent (Parker personal communication), indicating that the glandular complex of the upper lip has a function other than the generation of bioluminescence.

In the present study, the upper lip was often observed in close contact with food. In one non-luminescent *Vargula* species from Japan (not featured in this paper), the tusks acted in the manner of tactile finger-like organs, rubbing the food before its ingestion. The position of the downward and obliquely projecting tusks and the situation of the nozzles at the front of the mouth suggest that the upper lip might produce a secretion containing digestive enzymes or a medium for the entanglement of smaller food particles. This hypothesis is supported by recent work indicating the presence of hydrolytic enzymes (e.g. trypsin, chymotrypsin, protease, Dnase, Rnase, amylase) within the substances excreted from the upper lip of *Vargula hilgendorfii* (Abe et al. 1996), and of acidic mucosubstances in the tusks of *V. graminicola* (Huvard 1993).

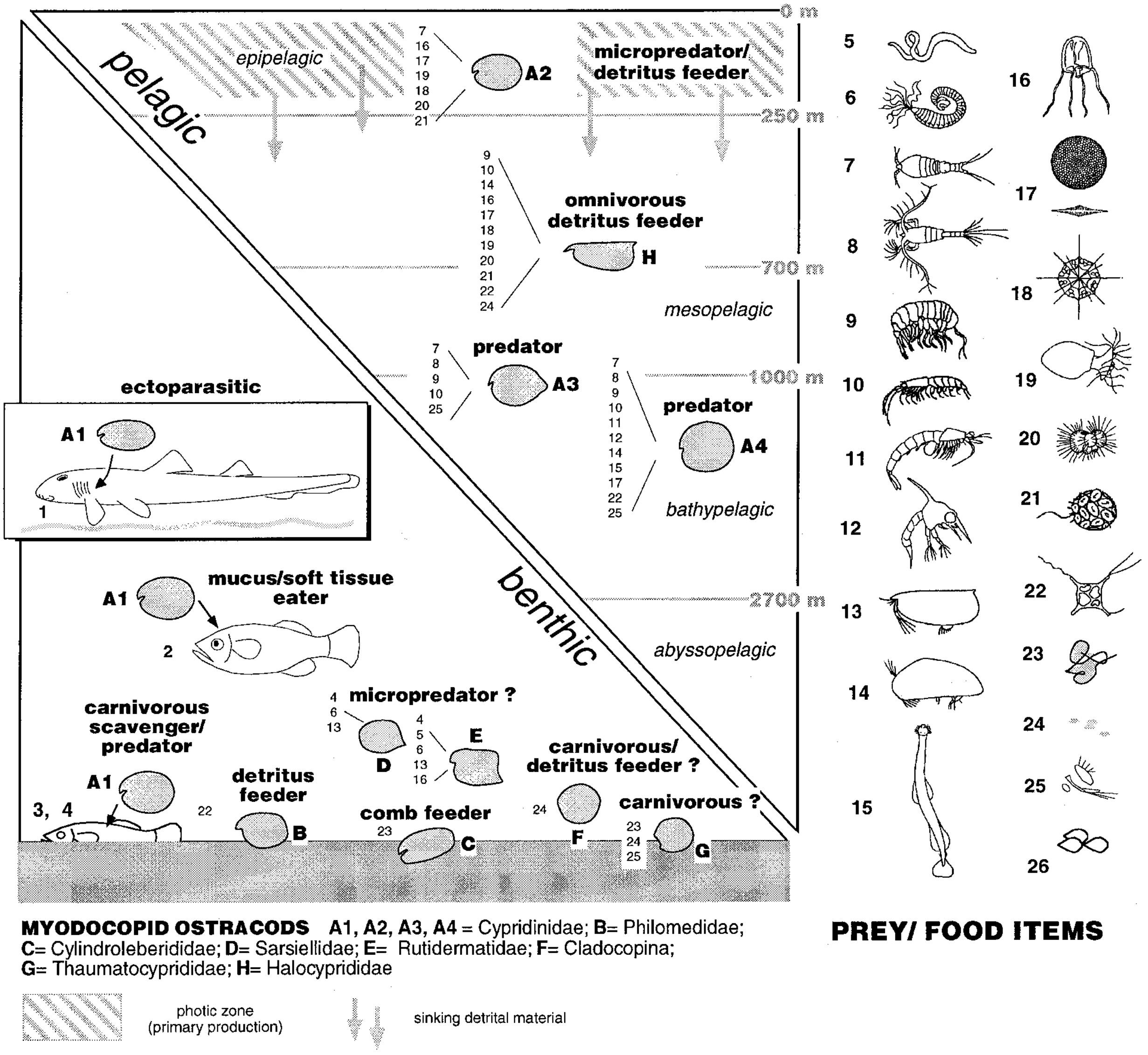
Discussion

Myodocopids in marine food webs: consumers and prey

Little is known of the exact role played by ostracods in marine food webs (Figs. 10, 11). Because of their small body weight, they represent only a small proportion of the total biomass in both benthic and mid-water communities, a factor which minimizes their ecological importance. However, in many coastal (e.g. eastern Australian continental shelf: Parker 1997) or planktonic environments, they appear as dominant or abundant taxa. For example, the halocyprid *Conchoecia pseudodiscophora* is the second most numerous group after copepods in the total zooplankton sampled in the Japan Sea (Ikeda 1990). More generally, the cosmopolitan halocyprid ostracods constitute a substantial source of food for many zooplankters, being the second most abundant prey (after copepods) in the stomach contents of mesopelagic gonastomatid fishes (Angel 1993). Halocyprids also enter the diet of many planktivorous invertebrates such as siphonophore hydrozoans, decapod crustaceans, heteropod molluscs (Aravindashan 1973; Angels 1983), and even the giant ostracod *Gigantocypris muelleri* (Moguilevsky and Gooday 1977). Evidence from field observations and the analysis of stomach contents indicates that nektobenthic myodocopids also undergo predation by fishes, at least in coastal waters (e.g. Hayashi and Goto 1979; Morin 1986 for the Caribbean Sea; Abe et al. 1995 for the Pacific Ocean).

Parasitic isopods and choniostomatid copepods frequently inhabit the shell of myodocopid ostracods (Shiino 1942; Bowman and Kornicker 1967; Bradford 1980), and use their host as part of their reproductive strategy. For instance, the parasitic isopod *Onisocryptus ovalis* (see Vannier and Abe 1993) feeds on the brooded eggs of the ostracod *Vargula hilgendorfii*.

Our knowledge of the diet of the myodocopids themselves is fragmentary and relies almost exclusively on the analysis of the stomach content of a few tens of planktonic and nektobenthic species (Fig. 11). Identifiable remains of a variety of animals (copepods, chaeotognaths, fishes, coelenterates, etc.) found in the stomach of two mesopelagic species, *Gigantocypris muelleri* (Moguilevsky and Gooday 1977) and *Macro-*



cypridina castanea (Kornicker et al. 1976), suggest that large planktonic ostracods are active predators, although it is still unknown whether they actually catch living prey or/and feed on dead food items (e.g. sinking bodies). Halocyprids are likely to be opportunistic microphagous feeders, with diatoms, silicoflagellates, coccolithophorids, foraminifers, detrital aggregates and various damaged organisms (e.g. crustaceans: Ikeda and Inamura 1992) constituting the most frequent components of their gut contents (Angel 1970, 1972). They appear to be important recyclers of the organic material (dead organisms, faecal pellets, marine snow) that sinks from the photic zone (Angel 1972, 1983). However, qualitative analyses of gut contents may not always be a reliable indicator of the actual diet of halocyprids, which continue to feed actively on almost all damaged organisms present in the plankton net (Angel 1970, 1993). All other myodocopids [which are mainly benthic/epibenthic dwellers, some with swimming activities related to a circadian rhythm of emergence (e.g. cypridinids: Vannier and Abe 1993)], are either filter-feeders (more accurately termed comb-feeders), i.e. cylindroleberidids (Cannon 1933), carnivorous scavengers (e.g. cypridinids: Cohen 1983; Vannier and Abe 1993; Abe et al. 1995; present paper), detritus feeders (e.g. philomedids: Hartmann 1975) or possibly predators on small invertebrates such as copepods, podocopid ostracods, polychaetes and nematodes (e.g. rutidermatids: Cohen 1982; Cohen and Kornicker 1987). No comprehensive study of the gut content of these ostracods has been made to date. Nocturnal attacks by swarms of bioluminescent myodocopids on fishes is a spectacular case of ostracod predation on vertebrates reported to occur in the coastal waters of California (Collins et al. 1984; Stepien and Brusca 1985). In the latter case, the ostracods mainly attacked fishes restrained in large cages for use in underwater experiments, but also clustered around unrestrained fishes (Stepien and Brusca 1985). A rare case of a parasitic mode of existence is that of *Sheina orri* (Bennett et al. 1997), a cypridind ostracod which an-

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Fig. 10 Myodocopid ostracods as consumers in Recent marine food chains. Main prey and food items features are based on field observations and analysis of gut contents [*1* living epaulette shark (bottom- dweller *Hemiscyllium ocellatum*) with ectoparasitic ostracods attached to gills; *2* living nearshore fish (ostracods feeding on gills, nostril, body cavity, skin and mucus); *3*, *4* fish-carcasses; *5* free-living nematodes; *6* annelids (e.g. polychaetes); *7* benthic copepods; *8* planktonic copepods; *9* amphipods; *10* euphausiaceans; *11* mysids; *12* decapod larval stages (e.g. brachyuran zoea); *13* halocyprid ostracods; *14* podocopid ostracods; *15* chaetognaths; *16* cnidarians; *17* pennate and centric diatoms; *18* radiolarians; *19* tintinnids; *20* foraminiferans; *21* coccolithophorids; *22* silicoflagellates; *23* detrital aggregates (e.g. marine snow); *24* deposited or suspended detrital particles from substratum (e.g. sediment, spicules, setae, etc.); *25* crustacean remains (fragments of appendages, bristles, setae, eye parts, etc. found in gut contents); *26* teleost fish scales. *A1* nektobenthic cypridinids from coastal environments; *A2* epipelagic cypridinids; *A3*, *A4* deep-sea cypridinids, *Macrocypridina castanea* and *Gigantocypris muelleri*, respectively]. Not to scale. Figure compiled from data in the following studies: Müller 1894; Brian 1909, 1931; Wilson 1913; Skogsberg 1920; Monod 1923; Cannon 1933, 1940; Elofson 1941; Iles 1961; Harding 1966; Lochhead 1968; Angel 1970, 1972, 1983, 1993; Hartmann 1975; Kornicker 1975; Kornicker et al. 1976; Arashkevich 1977; Moguilevsky and Gooday 1977; Cohen 1982, 1983, 1989; Collins et al. 1984; Stepien and Brusca 1985; Cohen and Kornicker 1987; Ikeda 1990, 1992; Ikeda and Inamura 1992; Abe et al. 1995; Monod and Laubier 1996; Bennett et al. 1997

chors itself by means of its mandibular and maxillar claws to the gill tissues of a species of epaulette shark.

Adaptation of cypridinids to scavenging and predation

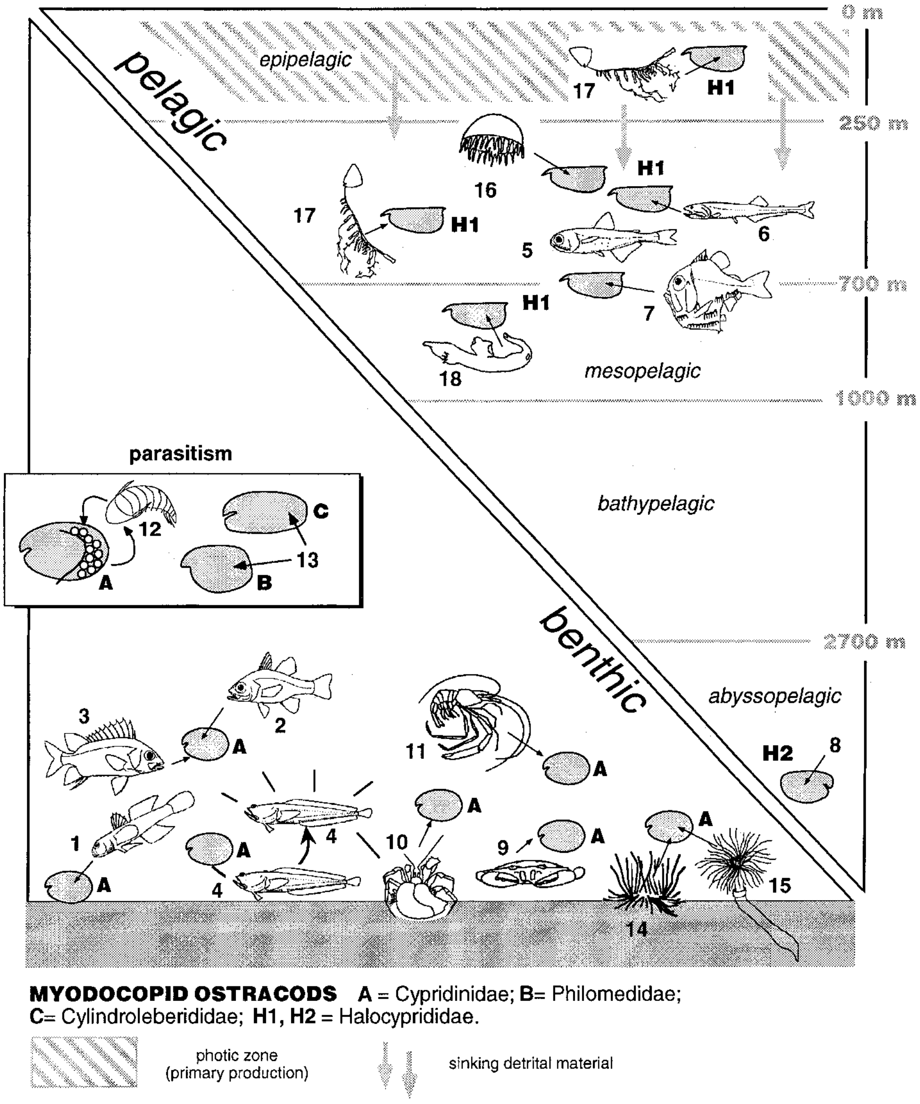
Cypridinid ostracods, exemplified by *Vargula hilgendorfii*, display numerous morphological adaptations for scavenging and predation. The furcal complex (Parker 1997) acts both as a powerful gripping tool to hold moving prey (e.g. annelids) and to anchor firmly on dead animals or other food items. Among myodocopids, all active scavengers and predators are provided with such powerful furcae, including the deep planktonic forms which are presumed to feed on live prey (e.g. *Gigantocypris muelleri*). In comparison, planktonic halocyprids, which probably feed essentially on sinking dead material, have a reduced furca that is used for the selective rejection of material from within the carapace (Lochhead 1968) and possibly for rotating food particles or for levering the halocyprid out of the grip of a predator (Angel 1993). Armed with heavily sclerotized claws and a strong musculature, the furcal complex of cypridinids is also a very efficient tool with which to slice food, to remove unedible parts (e.g. scales of fishes; Parker 1997) or to pierce the cuticular coverings of living or dead prey (Fig. 3). The 4th and 5th limbs are appendages well-designed to scrape off (distal setae) and triturate (endites) relatively large particles of food; these specialized features have no analogy in the comb-feeding cylindroleberidids (*Cyclasterope hendersoni*; Cannon 1933) nor in detritus-feeders such as podocopid ostracods (Hartmann 1966; Hartmann and Guillaume 1996). A sensory ability to locate carrion or living prey seems to characterize scavengers/predators such as *V. hilgendorfii*. In comparison, neither comb-feeders (cylindroleberidids) nor detritus feeders (philomedids) observed in laboratory conditions (Vannier and Abe unpublished data) react to food stimuli. The whole digestive system of *V. hilgendorfii* and other cypridinids seems to be well-adapted for both scavenging and predation. The foregut muscles and the shape and size of the stomach enable them to ingest and store massive quantities of food in a very short time; this feeding mode is clearly advantageous in environments where food supply is intermittent. The stomachs of planktonic halocyprids also consist of a broad pouch; this may indicate similar feeding stategies, for example occasional scavenging on sinking dead animals. In cylindroleberidids, the stomach is much smaller relative to the size of the body. The oesophagus has a distinctive T-shape, numerous setae along its inner wall, and has poorly developed ring muscles (Vannier personal observations). These features seem to be related to a mode of feeding based on the regular intake of small particles "filtered" by comb-like appendages.

Ancestry of scavenging in myodocopid ostracods

The origin of myodocopid ostracods can be traced back to the early Palaeozoic (Siveter and Vannier 1990). Detailed comparisons with the distribution, morphology and lifestyles of Recent myodocopids supports the hypothesis that Silurian representatives of the group may have been active swimmers and possibly the early colonizers of pelagic niches (Siveter et al. 1991; Vannier and Abe 1992); however, in the absence of fossilized soft parts, nothing is known about their feeding mode. Triassic and Jurassic specimens with sufficient preserved soft anatomy allow more accurate comparisons with the Recent fauna.

The 4th and 5th limbs of Recent cylindroleberidids (see Vannier et al. 1996) play an important role in creating water currents (epipodial fan), and collecting (setal comb on 4th limb) and eventually directing (spatulate exopodite of 5th limb) suspended particles to the mouth. Similar features found in *Juraleberis jubata* from the Upper Jurassic of Russia (Vannier and Siveter 1995) indicate that comb-feeders most probably existed among Mesozoic myodocopids. In many aspects, *Triadocypris spitzbergensis* from the Lower Triassic of Spitzberg (Weitschat 1983) is remarkably similar to modern benthic or nektobenthic cypridinids such as *Vargula hilgendorfii*. Although appendages (1st and 2nd antennae, epipodial fan of 5th limb, 7th limb), adductor muscles (Vannier and Weitschat in preparation), eggs, and even cilliate ectoparasites (Weitschat and Guhl 1994) are well-preserved, most feeding appendages are missing, except for the strong setae identified as the possible remains of the "biting apparatus" of the 4th limb (Recent; Fig. 6H, J). These ostracods have been found in large numbers (between 50 and 100) exclusively in the living chambers of

Fig. 11 Myodocopid ostracods as prey in Recent marine food chains. Main predators identified from field observations and gut content [*1* gobiid fish; *2* apogonid fish (cardinal fish); *3* holocentrine fish (squirrel fish); *4 Porichthys notatus* (possible dietary uptake of luciferin from ostracods to induce fish bioluminescence); *5* myctophid fish; *6* gonostomatid fish; *7* sternoptychid fish (hatchet fish); *8* deep-sea benthic fish; *9* Portunid swimming crab; *10* pagurid decapods; *11* free-swimming decapods; *12* epicarid isopods feeding on ostracod eggs; *13* choniostomatid copepods; *14*, *15* anthozoans (actinarian and cerianthid anemones, respectively); *16* scyphozoans; *17* free-floating hydrozoans (e.g. siphonophorans); *18* planktonic heteropod gastropods]. Figure compiled from data in the following studies: Bowman and Kornicker 1967; Angel 1972, 1983, 1993; Aravindashan 1973; Merett and Roe 1974; Tyler and Pearcy 1975; Ozawa et al. 1977; Robertson and Howard 1978; Hayashi and Goto 1979; Bradford 1980; Gorelova 1980; Hopkins and Baird 1981; Purcell 1981; Kirkpatrick and Pugh 1984; Sano et al. 1984; Morin 1986; Thompson et al. 1988a, b; Thompson and Tsuji 1989; Vannier and Abe 1993; Abe et al. 1995



ammonoids (*Keyserlingites* spp.). This occurrence strongly suggests that *T. spitzbergensis* was a scavenger which may have fed on decaying ammonites lying on the sea bottom, just as do swarms of modern cypridinids on the carcasses of fishes or squid (Fig. 3H, I). A sclerotized plate (sclerosome) was also present in *T. spitzbergensis* (Weitschat 1983; Parker 1997; Vannier and Weitschat in preparation), but no other parts of the furcal complex such as claws, which usually protrude from the ventral gape of the valves are fossilized. Apart from its protective role, the sclerosome and its associated musculature is of major importance in the cutting and/or digging action of the furcae. The recent find in the late Ordovician Soom Shale Lagerstätte of South Africa of possible myodocopid ostracods associated with orthoconic nautiloids indicates that ostracods may have fed on cephalopod carrion even in the Palaeozoic (Siveter personal communication). Myodocopids may have occupied very similar scavenging niches for at least the last 440 million yr, thus actively recycling organic matter on the sea bottom.

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