

**CHAPTER 4: ANTARCTIC AMPHIPODS  
FEEDING HABITS INFERRED BY GUT  
CONTENTS AND MANDIBLE  
MORPHOLOGY**

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To be submitted

## ABSTRACT

In this work, we have investigated the possibility to infer amphipod feeding type from morphology of amphipod mandible combined to the gut content composition. Ten species mouthparts have been dissected and examined with scanning electron microscopy (SEM). From gut content composition, four main trophic categories were distinguished: (micro- and macro-) herbivores, opportunistic predator, specialist carnivore and opportunistic scavenger. Macro-herbivores (*Djerboa furcipes*, *Oradarea* n. sp., *Oradarea walkeri*) show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The suspension-feeder (*Ampelisca richardsoni*) shows few molar ridges and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae. The opportunistic predator (*Eusirus perdentatus*) shows mandible morphology close to the basic model excepted for the molar which is tall, narrow and topped by a reduced triturative area. This could facilitate a fast ingestion. The species revealed as specialised carnivores (*Epimeria similis* and *Iphimediella cyclogena*) have been compared with other Antarctic species which also feed exclusively on the same item and the mandible morphology presented numerous dissimilarities. Finally, the molar development of scavenger species (*Tryphosella murrayi* and *Parschisturella carinata*) suggests that these animals rely on a broader dietary regime than carrion only. In any case, the smooth and sharp incisor of these lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

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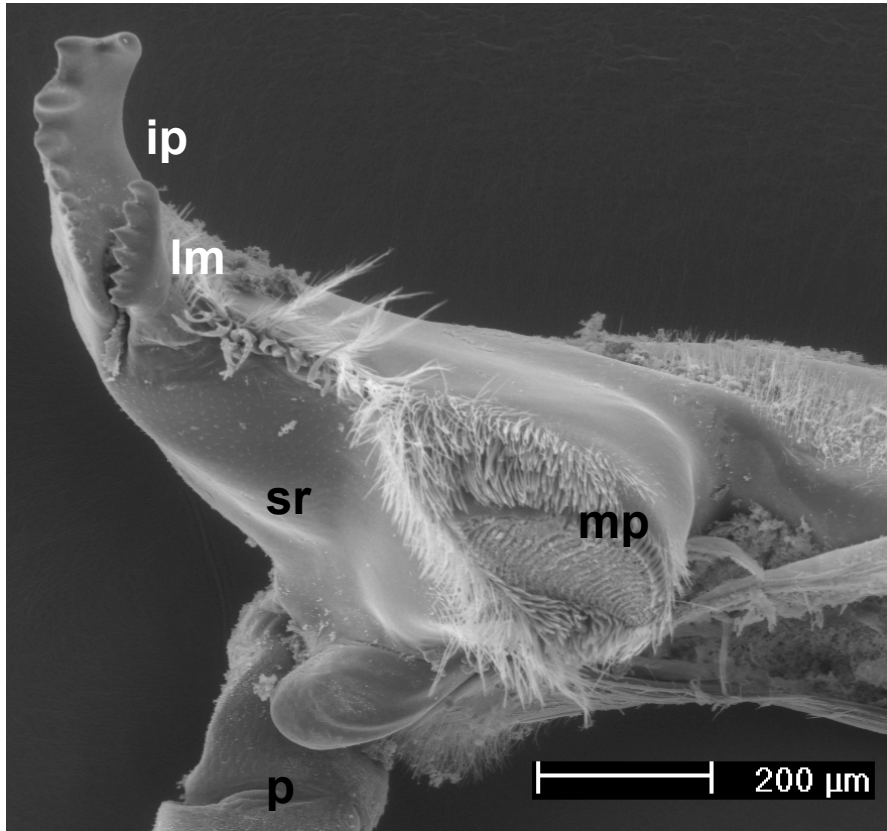
## 4.1. INTRODUCTION

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Despite a relatively low biomass Amphipoda constitute a significant group in terms of energy flux in the Antarctic shelf ecosystems (Jarre-Teichmann et al. 1997, Dauby et al. 2001b). Among Antarctic zoobenthos, these crustaceans represent one of the most speciose groups and probably the most diversified with respect to lifestyles, trophic types, habitats and size spectra (De Broyer & Jazdzewski 1996, Dauby et al. 2001a, Chapelle & Peck 1999, Nyssen et al. 2002). The ecofunctional and specifically the trophic role of those Antarctic amphipods is still poorly known. Constant and predictable environmental conditions as well as the high diversity (Knox and Lowry 1977) lead to an expectation of close niche adaptation and consequently the presence of many specialists to exploit the full spectrum of resources. The highly specialized mouthparts of many Antarctic amphipods widely illustrated by Coleman's work on Iphimediidae (1989a, b, c, 1990a, b) support the hypothesis of close niche adaptation to a preferred food source. The structure of the mandibles in particular has been sometimes interpreted as an adaptation to the presumed food source (Watling 1993).

The structure and function of crustacean mandibles have extensively been described by Manton in 1977. The basic gammaridean amphipod mandible is of the type observed in the genus *Gammarus* and most other gammaridean families (Barnard 1969). This basic morphology consists of a mandible body where four main structures are typically to be found, starting distally and going to the mouth opening: the **incisor process**, generally provided with cusps and teeth; the *lacinia mobilis*, inserted close to the incisor and generally in line with; the **spine-row**, filling the space between incisor and molar and probably involved in the transfer of the food to the mouth opening by forming a kind of bridge; and the **molar process**, a plane surface provided with diverse tritulative structures (Watling 1993).

Figure 4.1. mandible basic morphology (*Oradarea* n. sp. left mandible). ip: incisor process, mp: molar process, lm: *lacinia mobilis*, p: mandibular palp, sr: spine row.



A large panel of modifications to the basic pattern can be observed among peracarids. In his review of the functional morphology of the amphipod mandible, Watling (1993) divided the larger amphipod families into four groups in function of the degree of the modification of their mandible from the basic plan. As modifications, reduction of the incisor process, disappearance of the spine-row, reduction or complete loss of the molar process are observed in the different families. Most of those morphological changes appear as evolutionary patterns resulting from different feeding strategies as predation and/or scavenging feeding behavior. Several species of Iphimediidae and Lysianassoidea are good illustrations of some of those morphological adaptations (Dahl 1979, Sainte-Marie 1984, Coleman 1989b, c, 1990b, 1991, Watling 1993).

As a part of a multidisciplinary study of the amphipod ecological roles in Antarctic benthic systems (De Broyer et al. 2002), amphipod trophic patterns have been investigated (Dauby et al. 2001a, Graeve et al. 2001, Nyssen et al. 2002, De Broyer et al. 2004). The mandible morphology of ten species of Antarctic gammaridean amphipods has been studied and combined to gut contents analyses in an attempt to correlate mandible structure and feeding strategies.

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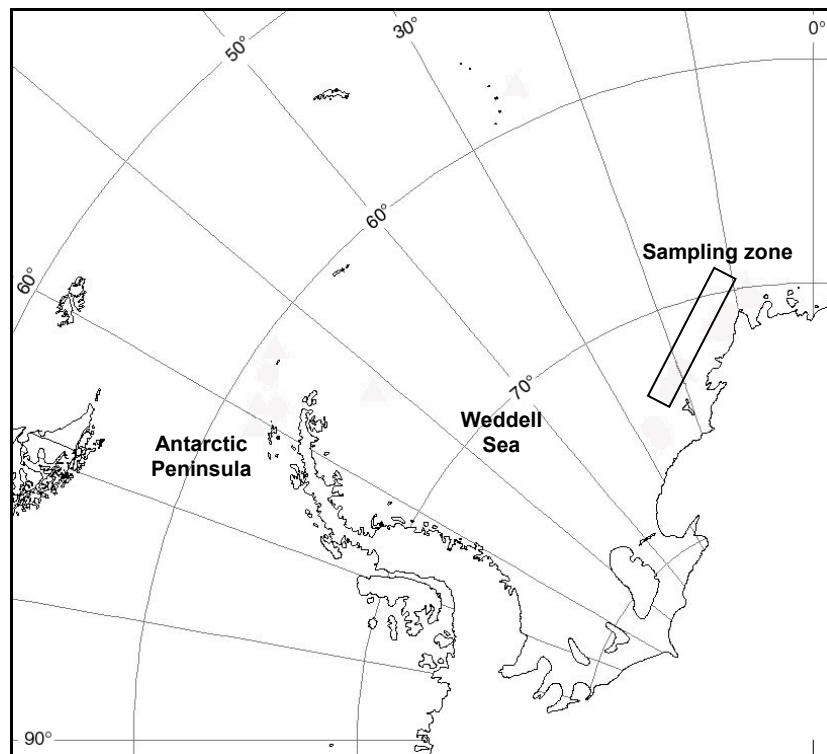
## 4.2. MATERIAL AND METHODS

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### 4.2.1. SAMPLING AND STORAGE

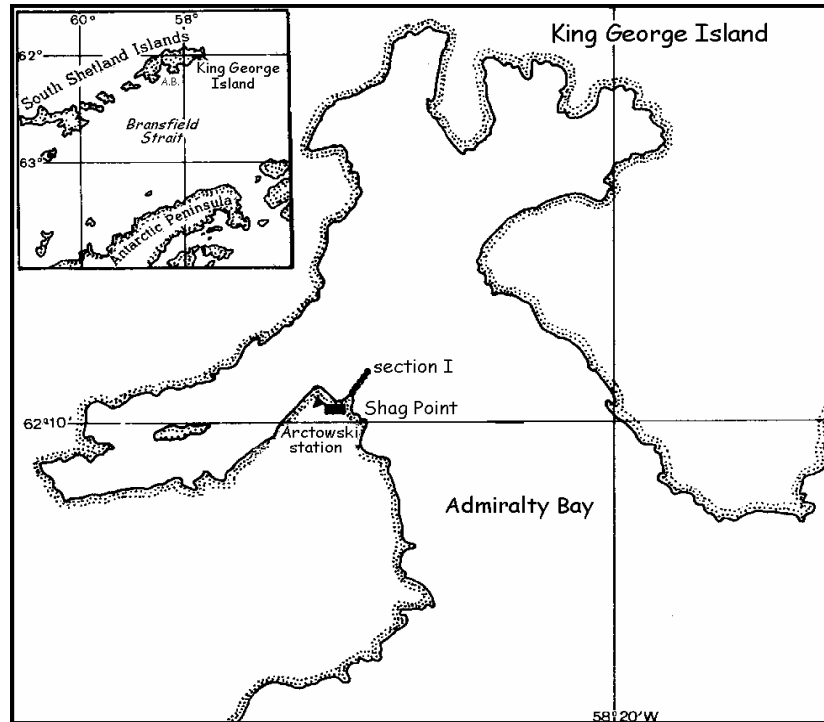
Amphipods (except three species) were collected from benthic and suprabenthic samples taken in the eastern Weddell Sea during three Antarctic summer cruises of RV “Polarstern”: EPOS leg 3 (1989; Arntz et al. 1990; De Broyer & Klages 1990), EASIZ I (1996; Arntz & Gutt 1997; De Broyer et al. 1997) and EASIZ II (1998; Arntz & Gutt 1999; De Broyer et al. 1999). Gears used included Agassiz, benthopelagic and bottom trawls, dredges and baited traps (Fig 4.2).

**Fig.4.2. Map displaying sampling zone (rectangle) in the Eastern Weddell Sea**



Catches of *Oradarea* n. sp., *Oradarea walkeri* and *Djerboa furcipes* were achieved in the upper part of the infralittoral of Admiralty Bay (King George Island, South Shetland Islands, Antarctic Peninsula) during spring tides and also by dredging in shallow water in the vicinity of the Polish base “Henryk Arctowski” during the summer season 1993 (Fig 4.3). All sampled species are listed in Table 4.1.

**Fig.4.3. Map of Admiralty Bay, King George Island, Antarctic Peninsula**



**Table 4.1. List of sampled species, sampling sites and years, sex, size and feeding types**

<b>Family</b>	<b>Species</b>	<b>sampling</b>	<b>Site</b>	<b>Sex / size</b>	<b>Feeding type</b>
Ampeliscidae	<i>Ampelisca richardsoni</i>	1998	E. Weddell Sea	Fem / 22mm	Suspension feeder
Eusiridae	<i>Oradarea</i> n. sp.	1994	S. Shetlands	Fem / 25mm	Herbivorous
Eusiridae	<i>Oradarea walkeri</i>	1993	S. Shetlands	Fem / 19mm	Herbivorous
Eusiridae	<i>Djerboa furcipes</i>	1993	S. Shetlands	Fem / 19mm	Herbivorous
Eusiridae	<i>Eurirus perdentatus</i>	1998	E. Weddell Sea	Fem / 38mm	Predator
Iphimediidae	<i>Iphimediella cyclogena</i>	1998	E. Weddell Sea	Fem / 35mm	Micro-predator
Epimeriidae	<i>Epimeria similis</i>	1996	E. Weddell Sea	Fem / 36mm	Micro-grazer
Epimeriidae	<i>Epimeria georgiana</i>	1998	E. Weddell Sea	Male / 26mm	Deposit feeder
Lysianassidae	<i>Parschisturella carinata</i>	1998	E. Weddell Sea	Fem / 20mm	Opport. scavenger
Lysianassidae	<i>Tryphosella murrayi</i>	1996	E. Weddell Sea	Fem / 25mm	Opport. scavenger



### **4.2.2. GUT CONTENT ANALYSIS**

Analyses of gut contents were performed on 20 specimens from each species preserved in 4% formalin solution. Macroscopic dissections were conducted under a binocular dissecting microscope (Leica MZ12), using forceps and scissors. The digestive tract was cut at the oesophagus level and removed together with the midgut glands. Afterwards, it was separated from the midgut glands, opened and the content was spread on a micro slide. All the surface of the slide has been examined under optical microscope Leica DMLB (equipped with reflection contrast system). Every item has been identified as precisely as possible. The optic system was equipped with a video camera (JVC KY-F50) connected to a computer and pictures of the different food items were taken.

For several species, the gut contents results have been completed by Dauby *et al.* (2001a) wherein the methodological details can be found.

### **4.2.3. MORPHOLOGICAL ANALYSIS**

Each species mouthparts were dissected (maxillipeds, maxillae 1 and 2, mandibles, upper and lower lips). Afterwards structures were dehydrated through an alcohol series, critical point dried and sputter-coated with carbon then gold to be observed with scanning electron microscopy (SEM). In this study, only the morphology of mandibles has been considered.

### 4.3. Results

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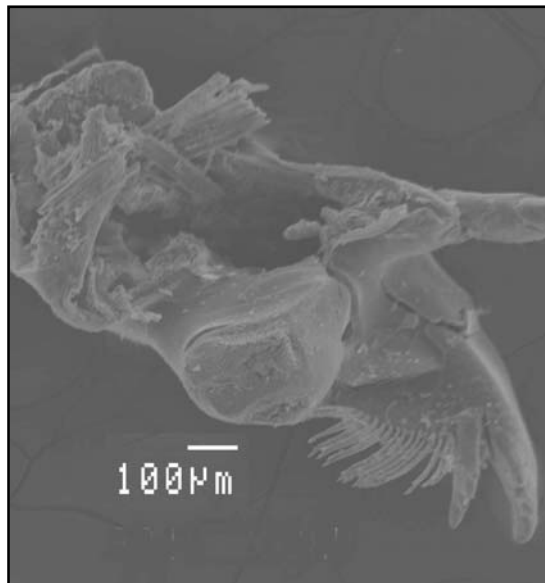
#### ***Ampelisca richardsoni* Karaman, 1975 (suspension feeder)**



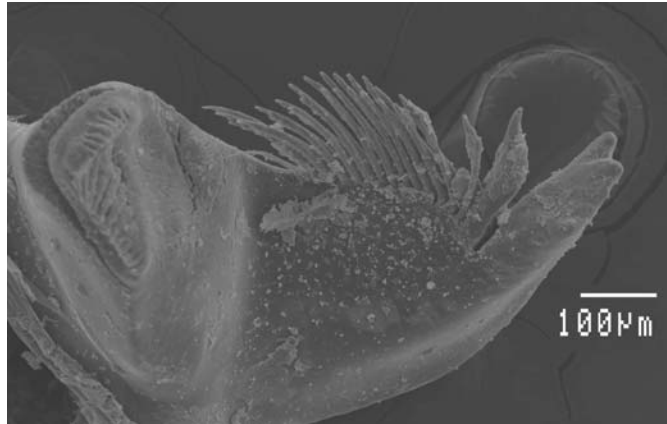
*Examination of foregut and gut contents* (see Dauby et al. 2001a). Food consists essentially of planktonic items (mainly diatoms) embedded in unidentified organic material (see picture on the left).

#### *Mandible morphology.*

Both mandibles bear well developed incisor and molar processes. Both incisors bear 5 rounded cusps but, whereas the left one (see picture on the right) is equipped by a strong 5-toothed *lacinia mobilis*.

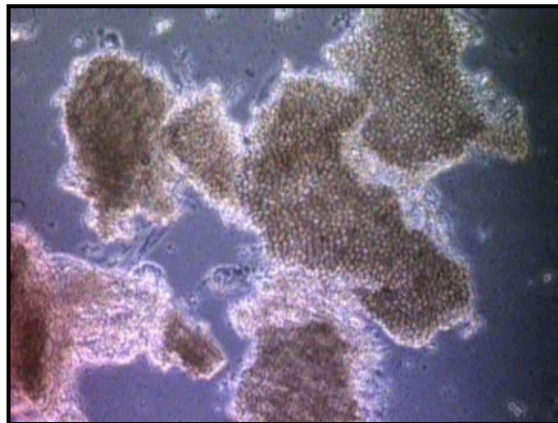


The right *lacinia mobilis* is smaller and more spine-like (see picture below). The molars are prominent and some smooth ridges are visible. The most striking feature of those mandibles is the development of the spine rows: on both side the row is composed of about 15 serrate spines nearly as long as the *lacinia mobilis* which could, by joining each other, form a kind of bridge between the tip of the mouthparts and the mouth itself.



**Oradarea n. sp. (macroherbivore)**

*Examination of foregut and gut contents.* The foregut and gut of 20 adult animals (female and ovigerous females) were examined. Those specimens were sampled by traps (400 meters depth) baited with different macroalgae (*Desmarestia menziesii* and *Iridea* sp.) and following the present algae species, gut composition



were totally different.

When baits consisted of pieces of the brown algae *D. menziesii*, 95% of the gut volume was filled with fragments of this algae

(see picture on the left, magnification X20).

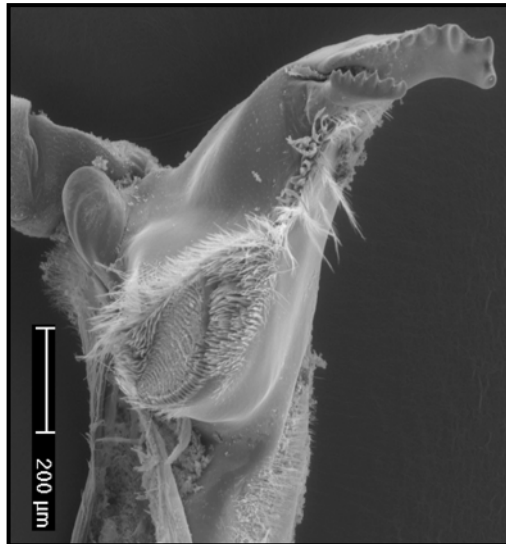


When baits consisted of pieces of algae belonging to the genus *Iridea*, (see picture on the left, magnification X80) the gut content was composed of:

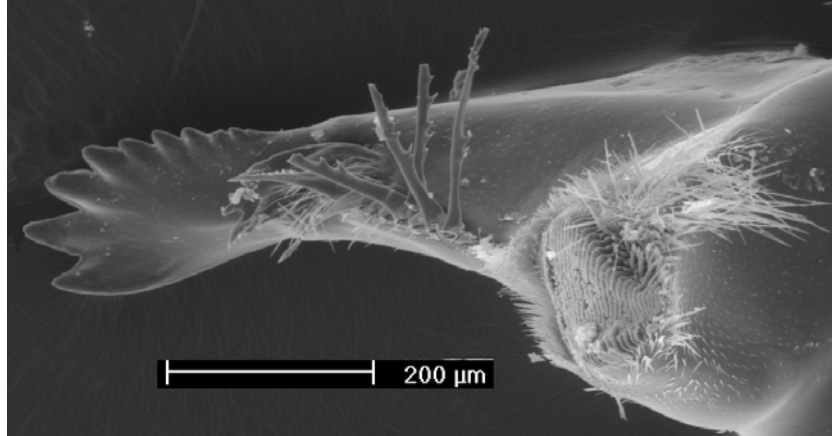
mineral particles, frustules of different kind of diatoms, chitinous structures and in some specimens, a very few amount of pieces of the macroalgae *Iridea* sp.

*Mandible morphology.*

The mandibles are asymmetrical, although differing only in morphology of the *lacinia mobilis*. Incisor bears 10 rounded cusps. The left *lacinia* (see picture on the right) is similar to incisor although reduced in size and with only 7 more acute cusps.

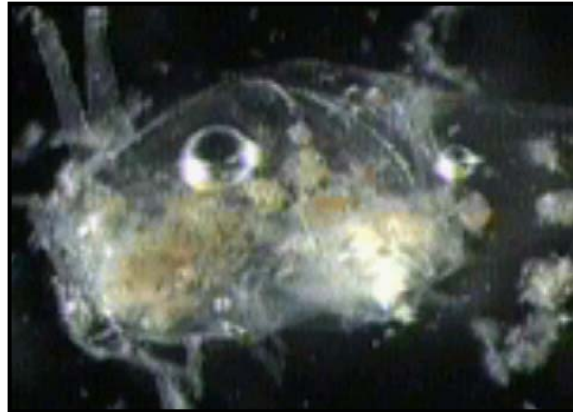


The right *lacinia* (see picture below) is slender. The spine row consists of stout serrate spines plus on the left mandible only a parallel row of plumose slender setae. The molar process is massive, sub columnar, and the trititative area is closely surrounded by short and thick setae and topped by a dense crown of setae. The grinding surface is provided with densely set short spinules and ridges with serrate distal margin.

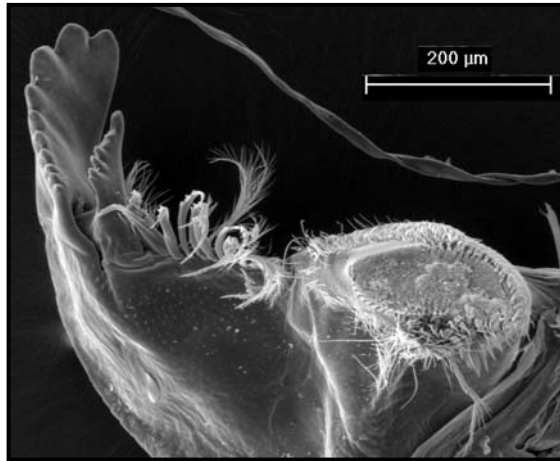


***Oradarea walkeri* Shoemaker, 1930 (macroherbivore)**

*Examination of foregut and gut contents.* 20 adult sampled by trawls (20-35m depth) were dissected. According to observation, 90% of gut contents were composed of pieces of macroalgae. The 10% left consisted of diatoms of



different types and inorganic material. The picture on the left represents the stomach of *O. walkeri* where pieces of macroalgae can be distinguished (green parts).



*Mandible morphology.*

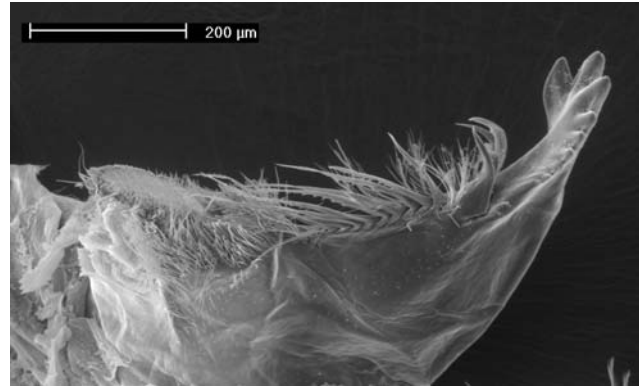
The morphology is nearly identical to that of *O. n.sp.* (see left mandible on the picture on the left). Both incisors are well developed and bear 10 strong teeth. The rather flat *corpus mandibulae*

is bordered ventrally by a double row of stout serrate setae and of slender plumose setae. The large and tall molars are topped by a dense fringe of setae and bear a large triturative area provided with ridges and other rasp-like structures. Both mandibles are flanked with a *lacinia mobilis*, strong and toothed (7 teeth) on the left mandible and weaker and spine-like on the right mandible.

***Djerboa furcipes* Chevreux, 1906 (macroherbivore)**

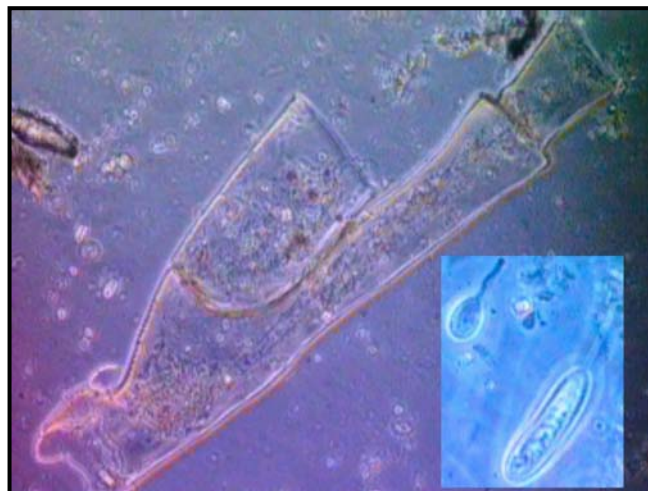
*Examination of foregut and gut contents.* Examination of the gut contents of 20 animals collected by trawls (20-35 m depth) allowed distinguishing – from the most to the less abundant item – : pieces of macroalgae thalli, pennate diatoms and a small amount of chitinous parts. All dissected specimens had also a significant amount of mineral particles in their gut.

*Mandible morphology.* As both species of the genus *Oradarea*, *D. furcipes* displays basic amphipod mandibles (in the sense of Watling 1993); toothed incisor (10 teeth), left *lacinia mobilis* with 10 teeth, only three on the right one (next page on top, see right mandible); large molar (but smaller than in genus *Oradarea*), cylindrical and triturative, crowned by a dense fringe of small setae; spine-row composed of two sort of setae.

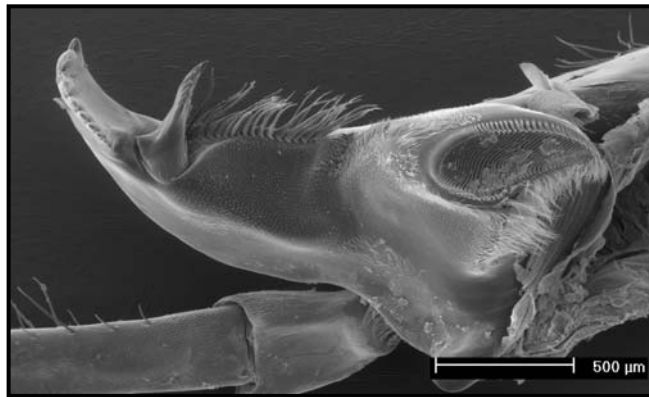


***Epimeria similis* Chevreux, 1912 (micropredator)**

*Examination of foregut and gut contents.* The gut content of *Epimeria similis* was dominated by hydroid perisarc fragments (see picture below) and cnidocysts of different shape and size (see small insert). The rest of the gut consisted of sponge spicules, microalgae (mainly centric diatoms and fragments of *Chaetoceros* sp.) and pieces of polychaetes.

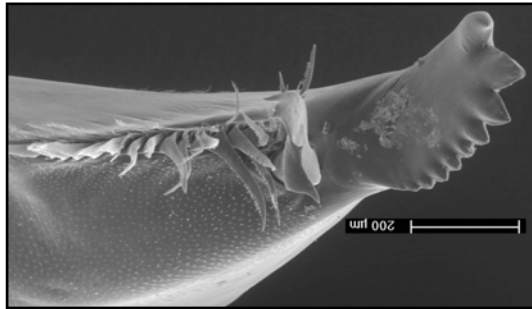


*Mandible morphology.* Both mandibles bear strong ten-toothed incisor and tall sub columnar molar provided with well-developed and smooth ridges.



The molar is surrounded by a row of stubby setae and fringed with bundles of hairs at dorsal margin.

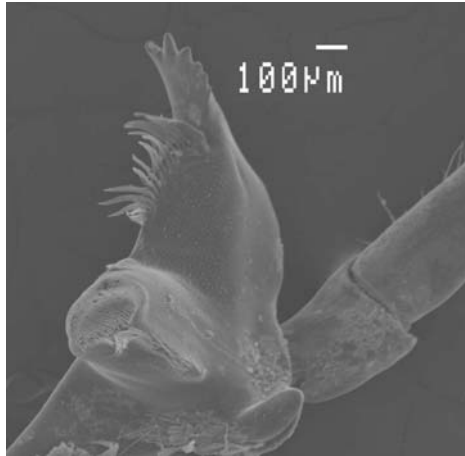
The left *lacinia mobilis* is armed with 7 cusps (see left mandible on the picture above) whereas the right one is smaller, bifurcated and spine-like (see the right mandible on the opposite picture). The spine-row is composed by stout denticulate setae, flanked on the ventral side by slender setae.



***Epimeria georgiana* Schellenberg, 1931 (deposit feeder)**

*Examination of foregut and gut contents.* The gut content of *E. georgiana* revealed a wide variety of food items: parts of crustaceans (mysids and amphipods), polychaetes, holothurian ossicles and hydrozoan perisares and planktonic items as diatoms, radiolarians and foraminifers. Sponge spicules and mineral particles complete the food (see Dauby et al. 2001).



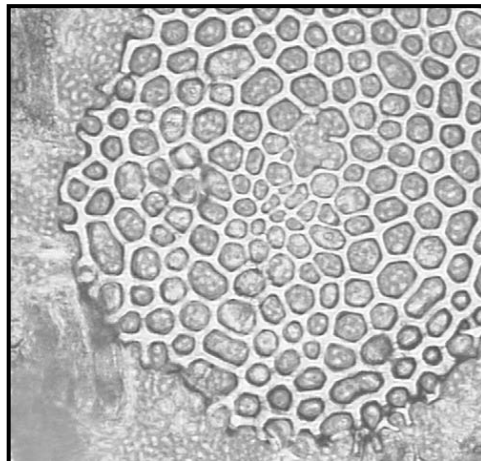


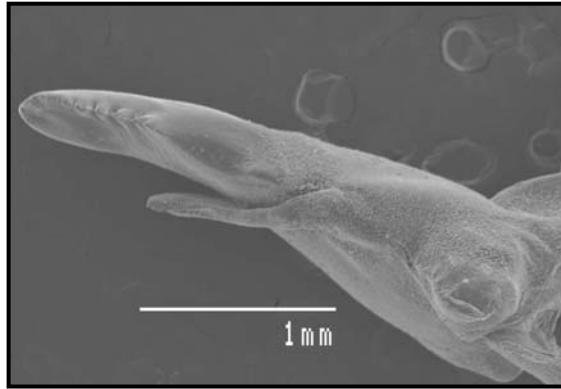
*Mandible morphology.* Both mandibles bear strong six-toothed incisor and as currently observed in this genus, the molars are prominent and provided with well developed ridges. The triturative area of molar is surrounded by a raw of stubby setae and topped backward by bundles of hairs.

The left *lacinia mobilis* is toothed (5 cusps) whereas the right one is smaller and narrower (see right mandible on the picture above). The spine-row is composed by thick denticulate setae.

***Iphimediella cyclogena* K.H. Barnard, 1930 (micropredator)**

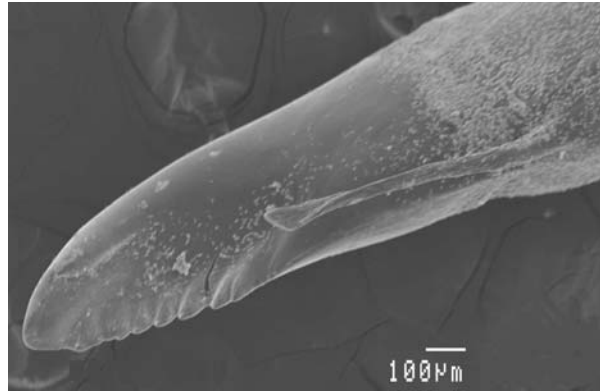
*Examination of foregut and gut contents.* The main food items observed in *I. cyclogena* gut were holothurian ossicles (see picture below) and polychaetes remains. In regard to the size of holothurians, it is more probable that this species scavenges instead of actually preying on it. *Iphimediella cyclogena* is considered as an opportunist consumer switching from predation to scavenging following the availability of food.





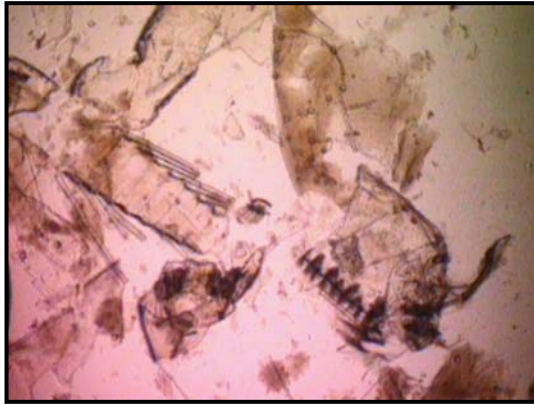
*Mandible morphology.*  
(see left mandible on picture on the left).  
The mandibular body is elongate tapering into the incisor that is much narrower than in all other species considered in this

work. Both incisor processes are toothed (10 cusps) and bear a long *lacinia mobilis* which is inserted near a molar process reduced to a small fleshy cone. The *lacinia mobilis* is thick and strongly chitinised on the left mandible and reduced to a thinner twiggy structure on the right mandible (see right mandible on picture below).



A major modification is the change in the orientation of the incisor, cutting in the vertical front plane. The position of the teeth along the incisor suggests a cutting in a scissor-like fashion.

***Eusirus perdentatus* Chevreux, 1912 (predator)**

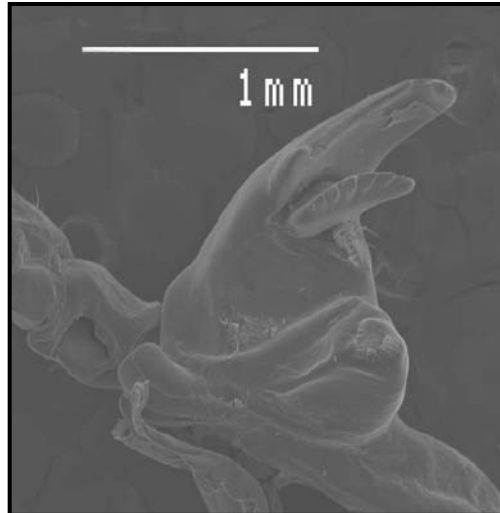


*Examination of foregut and gut contents. Crustacean hard parts and pieces of polychaetes form more than 50 percent of the gut contents (see picture on the left). Other food items consist of diatoms,*

*sponge spicules and inorganic material. These observations corroborated the conclusion of Klages & Gutt (1990) which said that *E. perdentatus* was a passive predator mainly feeding on crustaceans and polychaetes.*

*Mandible morphology.* Mandibles bear strong incisors and molar processes.

On the left mandible the large *pars incisiva* bears dorsal and ventral cusps and is flanked with a denticulated (7 teeth) *lacinia mobilis* (see picture on the right). The right *lacinia mobilis* is armed with two teeth. The short spine-row is composed of about 10 spines.





The apex of the tall sub columnar molar bears a small triturative area provided with rasp-like structures (see picture on the left). The reduced crushing area could explain the non-chewed state of some food items.

***Tryphosella murrayi* (Walker, 1903) (opportunistic necrophage)**

*Examination of foregut and gut contents.* Different items were observed in the digestive tract: pieces of crustaceans (antennae, buccal appendages, feathered setae, pleopods and ommatidia), pieces of polychaetes, very frequent fragments of flesh without any structure and some sponge spicules. The picture on the right presents a mid-gut full of fish flesh, parts of digestive caeca are also visible.





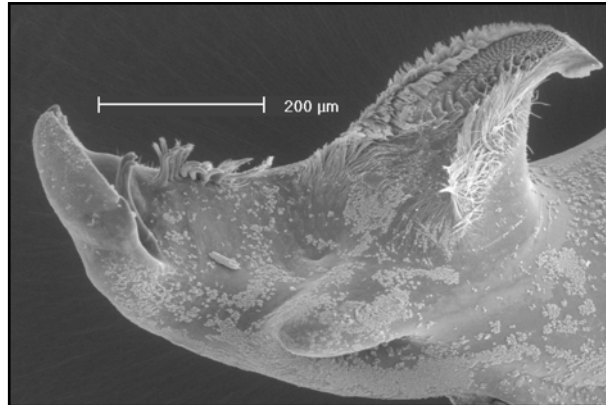
*Mandible morphology.* The proximal part of the incisors is narrow and the structure is broadening distally. The cutting edge is smooth and bears dorsal and ventral cusps. The *lacinia mobilis* is present on both mandibles. The spine-row is composed of 3 spines followed by a dense string of hairy setae which borders the corpus mandibulae. The molar is oval shaped and surrounded by a ventral fringe of setae that partly overlap the triturative area (see picture on the left).

***Parschisturella carinata* (Schellenberg, 1926) (opportunistic necrophage)**

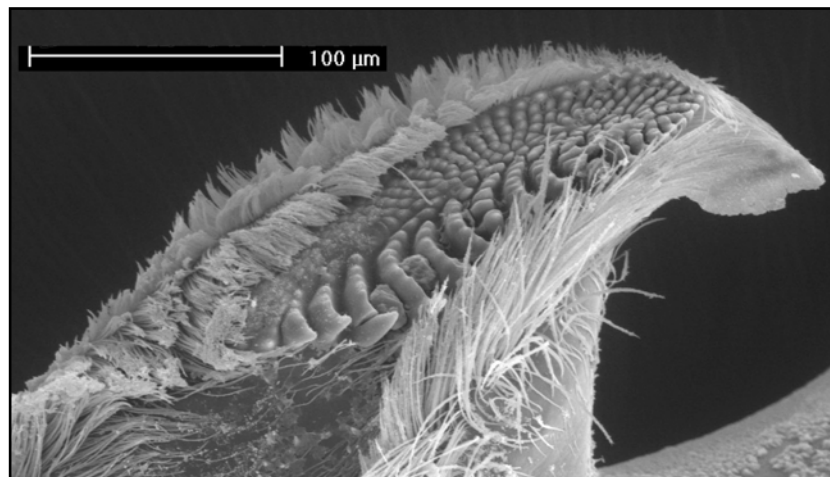
*Examination of foregut and gut contents.* Gut content observations revealed a diet composed mainly of crustaceans (see picture on the right). Nevertheless, this species is commonly observed in baited traps and in this case has the gut full of bait. This suggests a necrophage tendency, at least in an opportunistic way.



*Mandible morphology.* Incisor process is smooth and its edge is rather sharp and flanked by a single cusp at each end. The slightly concave *corpus mandibulae* is bordered by a row of (7-8) thick spines. The left mandible bears a weak digitiform apically bidentated *lacinia mobilis* (see picture on the right).



Tall molars are highly provided with setae and the oval tritritative area displays impressive series of deep toothed ridges and rasp-like structures (see picture below).



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## 4.4. Discussion

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The feeding type of any organism can be assessed in different ways, according to the chosen approach. Regarding the gut composition, distinction can be made among herbivory, detritivory and carnivory. Regarding the size of the ingested food, it is possible to distinguish between microphagy and macrophagy. The third way to assess the trophic category depends on the feeding behaviour of the organisms and, it is possible, for example, to discriminate between predation and necrophagy among carnivores.

### **Herbivorous species**

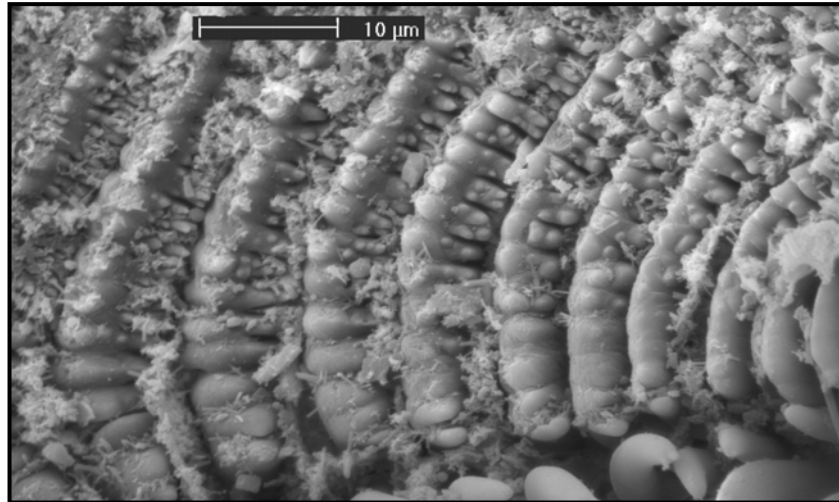
Among the species considered in this work, four of them can be classified in the herbivores: *A. richardsoni*, *O. n.sp.*, *O. walkeri* and *D. furcipes*.

The first species is a microphage feeding mainly on phytoplankton items whereas the three other species consuming essentially macroalgae tissues are categorized as macrophages. These macroherbivores show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The left mandible of the three species is also provided with a strong denticulate *lacinia mobilis* which probably works as an additional cutting edge.

Recently, the origin, function and phylogenetics implication of *lacinia mobilis* have been reconsidered. In 1982, Dahl & Hessler reaffirmed Boas' (1883) hypothesis of a spine-row origin for Peracarida *lacinia mobilis*. In 2002, Richter et al. approved it for the right mandible but for the left mandible, a separation from the incisor process could be more probable - although an origin from the spine row could not be totally excluded. In typical peracaridan biting, the right incisor process enters the gap between the left incisor and the left lacinia, which glides into the gap left between the right incisor and the right lacinia, where the latter is present. The function of

the lacinia in biting appears to be three- or possibly fourfold. It contributes to cutting, it helps guide the incisor processes into the right planes and to lock them into their final closing position. Probably a toothed or spiny lacinia also helps to hold food particles in place during the bite (Dahl & Hessler 1982, Watling 1993).

In macroherbivores, the molar area is provided with strongly denticulate ridges, necessary to triturate the tough macroalgal tissue. The picture below shows *Oradarea* n. sp. molar details.



The diatom consumer, *A. richardsoni*, has a less incurved and elongated incisor process which is also stouter. The molar ridges are few and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae.

Following their diet composition, the new species of the genus *Oradarea* seems to feed preferentially on brown macroalgae. Indeed, a clearly different diet composition has been observed following the offered baits in the traps. When the bait consisted of pieces of algae of the genus *Desmarestia*, the gut was completely filled with plant fragments. Meanwhile, when pieces of the



red algae (*Iridea* sp.) were offered, the gut content was only composed of mineral particles and diatoms. This preferential consumption of *Desmarestia* is not surprising as Amsler et al. (1998) have demonstrated the development of chemical defenses against herbivory for the species *Iridea cordata*. Furthermore, as the repartition area of Desmarestiales (down to 90-100 meters depth, the limit of the phytal zone) is deeper than the one of the genus *Iridea* (from 0 to 10 meters depth), the probability to find those brown algae at 400 meters depth (the sampling depth) is higher. So, the presence of herbivore species in rather deep zones (400 meters depth) is not surprising as the contribution of drifted macroalgae to the organic matter in the deep basins of Admiralty bay is rather high (Fischer & Wiencke, 1992).

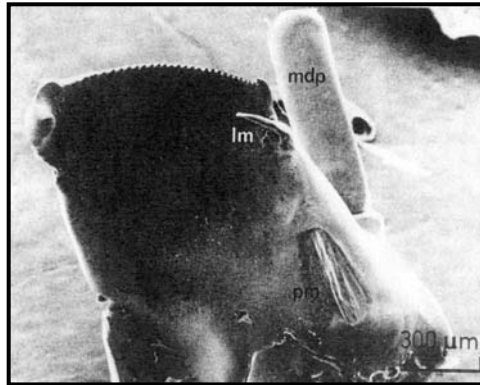
#### **Specialist carnivore species**

According to their gut contents, *Epimeria similis* and *Iphimediella cyclogena* are both specialist consumers. The first is considered as a cnidarian-feeder (gut contents essentially composed of cnidocysts and hydroid perisarc fragments), and the second consumes mainly holothurians (high amount of ossicles in gut). However, if each species mandibles are compared with those of other Antarctic species which also feed exclusively on cnidarians or holothurians, as respectively, the iphimeriid *Maxilliphimedia longipes* and the stilipedid *Bathypanoploea schellenbergi* (Coleman 1989a, 1990b), totally different morphologies are observed. These different morphologies are summarized in the following Table as well as *M. longipes* and *B. schellenbergi* mandibles are illustrated in pictures provided by Coleman (1989a, 1990b).

From these observations, one could conclude that to classify an animal as a cnidarian feeder is not restrictive enough, this phylum being composed by organisms with very different structures. In this case, *E. similis* and *M. longipes* must be classified respectively as consumers of hydrozoans and anthozoans respectively. In the latter, gut contents are characterised by the

presence of nematocysts: spirocysts - typical of Hexacorallia, and mastigophores which can frequently be found in Anthozoa and Hydrozoa (Coleman 1989a) whereas *E. similis* gut is essentially composed of perisarc fragments and nematocysts of hydrozoans. The discrepancies in mandible morphology could be explained by the consumption of these different organisms.

In *M. longipes* (see picture on the right from Coleman, 1989a), the remarkable absence of hair-like setae and the smooth aspect of the setae present could be an adaptation to the food source. Setose mouthparts and feather-like setae would



easily be embedded together by the mucus of anthozoans. Furthermore the long cutting edge of their incisor processes can cut larger pieces of prey and the rudimentary molars are not able to triturate food. This could point to very soft food (Coleman 1989a). On the other hand, *E. similis* well-toothed incisors and tall and strongly ridged molars are more adapted to harder kind of food as hydrozoans perisarc.

The dissimilarities in mandible morphology of both holothurian feeders considered in this work: *B. schellenbergi* and *I. cyclogena* is also surprising. Holothurians are a quite uncommon food source for invertebrates. Their integument is leathery with embedded ossicles. On the other hand, their reduced motility makes them a rather ideal prey for other slow predators. Some seastars and among the gastropods, some genera of the prosobranch

family Eulimidae have been observed feeding on holothurians (see references in Coleman 1990b).

*B. schellenbergi* appeared to be the first “food specialist” feeding on holothurians in the Antarctic. Its mouthparts are interpreted to be highly adapted to cope with the tough tissues of these echinoderms (Coleman 1990b). Its mandibles are remarkably stout. The incisors are strongly serrate, both bearing a *lacinia mobilis*; the left one, also well-toothed, might act as a third cutting edge. This highly integrated cutting mechanism would enable *Bathypanoptea* to cut such firm tissue as the body wall of holothurians. In this species, the molar is reduced so that the reduction of the food in little



pieces relies solely on the actions of the incisors and their laciniae. The picture on the left displays the left incisor process and its *lacinia mobilis*.

Although they seem to rely mainly on the same food source, *Iphimediella* mandible morphology is completely different. As summarized in Table 3.2., the mandibular body is elongated and the incisors are much narrower. Both incisor processes are toothed (10 cusps) and bear a *lacinia mobilis*. But, with such a smooth structure, none of the *lacinia mobilis* could help in cutting tissue as tough as holothurian body wall is. Furthermore, in view of the reduced molar process, the food reduction can not rely only on them. The question is: how do they feed on holothurians? One hypothesis could be that they actually scavenge on rotting holothurians and that the process of decomposition make the tissues softer and easier to cut.

Table 4.2. Summary of the mandible morphological differences between specialist consumers

	CNIDARIAN CONSUMERS		HOLOTHURIAN CONSUMERS	
	<i>E. similis</i>	<i>M. longipes</i>	<i>I. cyclogena</i>	<i>B. schellenbergi</i>
<b>Mandible</b>	- stout	- stout	- elongated	- stout
<b>Incisor &amp; lacinia mobilis (I.m)</b>	- normal - strong teeth - strong and toothed left <i>I. m</i> - weak right <i>I. m</i> - seta row	- broadened - weak teeth  - both <i>I.m.</i> are vestigial - no seta row	- very narrow - longitudinally toothed  - strong and smooth left <i>I.m</i> - weak right <i>I. m.</i> - no seta row	- normal - strongly serrate - strong and toothed left <i>I. m</i> - weak right <i>I. m.</i> - seta row
<b>Molar</b>	- strong - smooth ridges - fringe of setae	- vestigial	- small fleshy lobe without any ridges and setae	- reduced

**Opportunistic predator**

According to its gut contents and feeding behaviour observations, *Eusirus perdentatus* is a true predator which seems to be able to switch its diet following the food availability (crustaceans, polychaetes). The most characteristic feature of *E. perdentatus* mandibles is their tall molar bearing a high and small triturative area provided with rasplike structures. The reduced crushing area could explain the rather large food items observed in the gut contents. This ability to ingest big parts of prey could facilitate a fast predation.

**Opportunistic necrophages**

Besides all other food sources, there is strong evidence that large food falls play a significant role in the vertical flux to the sea bottom, too. On the one hand, there are reports of the encounter of such large food items on the sea floor such as big marine mammal carcasses, fishes, large pelagic invertebrates or their remains (Smith *et al.* 1989, Jones *et al.* 1998, Klages *et al.* 2001). On the other hand, well developed associations of highly mobile scavengers (mainly lysianassoid amphipods) are present on shelf and deep sea bottoms throughout the world oceans. In this context lysianassoids have evolved morphological, physiological and behavioral traits which seem to enable them to rely on this food source. According to Dahl (1979), three adaptations are necessary for efficient carrion feeding. The first adaptation is the development of efficient chemoreceptors to detect and locate carrion. Secondly the ability to feed on large, muscular food items, such as squid, fish or marine mammals by the use of adapted mandibles characterised, briefly, by a wide and sharp incisor edge, a bowl-shape *corpus mandibulae* and a non-tritulative molar (Dahl 1979, Sainte-Marie 1984). Lastly, necrophage lysianassoids seem to solve the starvation problem due to the rarity of their food sources by storing large quantities of carrion in capacious guts.

The scavenging lysianassoids have evolved along two divergent lines represented by the genera *Hirondellea-Eurythenes-Paralicella* and *Orchomene* (Dahl 1979). The former group appears to be the strict (obligate?) necrophage group, the latter being more opportunistic in their feeding. Regarding their mandible morphology, although the basic plan is similar, their mandible features are quite different, and their gut contents analysis, the lysianassoid species considered in this work, *T. murrayi* and *P. carinata*, would belong more probably to the second group. Although it has been classified as a true necrophage by Dauby et al. (2001), our new gut content analyses of *P. carinata* (several individuals were full of crustaceans' remains) and furthermore the extreme development of its molar (tall and strongly ridged) obviously enabling this species to feed on other items than carrion, suggest a more opportunistic feeding behaviour. Besides its necrophagous behaviour, *T. murrayi* is also a predator and has already been observed killing and eating others crustaceans and even fishes (Dauby et al. 2001).

So, for both species the molar development suggests that these animals rely on a broader dietary regime. In any case, the smooth and sharp incisor of lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

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