

Morphology of the Gastric Mill of *Nyctiphanes australis* (Euphausiacea, Crustacea)

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SEM observation revealed that the gastric mill of *Nyctiphanes australis* consists of paired cluster spines and paired lateral teeth, while the filter-press is absent. The morphology of the gastric mill was extremely constant; the numbers of both setiform processes of cluster spines and serrated spines of lateral teeth increased with increasing body length. The cluster spines of *N. australis* consisted of a single row of stout setiform processes but the lateral teeth comprised a large projection with small serrated spines. The cluster spines are symmetrical in setiform process distribution, however, the lateral teeth are asymmetrical in number of serrated spines.

Introduction

Morphology of crustacean alimentary tracts has drawn the attention of biologists for more than a century (Huxley, 1880; Patwardhan, 1934; 1935a-b; Powell, 1974; Meiss and Norman, 1977; Felgenhauer and Abele, 1985; Abele and Felgenhauer, 1986). Although many of these investigations have been concentrated on decapod crustaceans (see review of Dall and Moriarty, 1983), little is yet known about euphausiid morphology. Nemoto (1966, 1967, 1977) provided descriptions of euphausiid foreguts of 25 species representing 8 genera. He showed that the cluster spines are located on the posterior parts of side plates of the foregut as the main structure of trituration throughout the alimentary tract. Using a scanning electron microscope (SEM), Ikeda et al (1984) confirmed the presence of the cluster spines in the foregut of Antarctic krill, *Euphausia superba*. Suh and Nemoto (1988) studied the foregut morphology of the following 10 species of euphausiids, except for *Nyctiphanes* species: *Bentheuphausia amblyops*, *Meganyctiphanes norvegica*, *Pseudeuphausia latifrons*, *Euphausia superba*, *Tessarabrachion oculatum*, *Thysanoessa longipes*,

Thysanopoda acutifrons, *Nematoscelis microps*, *Nematobrachion boopis*, and *Stylocheiron maximum*. On the basis of the foregut morphology, they suggested that there are three categories of gastric mill and filter-press within euphausiids. They also noticed that the gastric mill structure seems to be a conservative feature more related to the phylogeny of euphausiids than to its feeding patterns.

The foregut morphology of the genus *Nyctiphanes* is still unclear. Thus, the morphology of the gastric mill of *N. australis* was studied by SEM with a comment on the phylogeny of euphausiid genera.

Materials and Methods

There are four species in the genus of *Nyctiphanes* (Mauchline and Fisher, 1969). Of these *N. australis* was chosen for the present study. I examined 19 specimens that were captured by Dr. D. A. Ritz in Lodge Bay of Tasmania, Australia, on 23 July 1985. The body length, measured from the tip of the rostrum to the posterior margin of the telson, ranged from 13.4 to 17.2mm. All specimens examined were adults.

The detailed description of preparation for SEM observation was given in Suh and Nemoto (1988). The foreguts were observed with an Akashi Alpha 25A scanning electron microscope.

The foregut index (FGI) was calculated for the degree of swelling of the foregut using the following formula (after Suh and Nemoto, 1988): $FGI (\%) = LC \times 100 / LV$. The abbreviations are denoted in Fig. 1A.

Results

As shown in Fig. 1, it is clear that the cluster spines and lateral teeth are found in *N. australis*, but the filter-press is absent. The cluster spines consisted of a single row of stout setiform processes (Fig. 1B), while the lateral teeth comprised a large projection with small serrated spines (Fig. 1C). It is noteworthy that the morphology of the gastric mill was extremely constant; the numbers of both setiform processes of cluster spines and serrated spines of lateral teeth increased with increasing body length. In addition, the symmetrical feature is found in setiform processes distribution of the cluster spines. The lateral teeth, however, are asymmetrical in number of serrated spines.

The foregut index of *N. australis* attained a range of 89.5~104.5% with a mean of 96.6% (Table 1). This implies that the foregut is not well adapted for storage of foods, in contrast to the other raptorial feeders, such as *Nematobranchion*, *Nematoscelis*, and *Stylocheiron* (see Suh and Nemoto, 1988).

Discussion

Euphausiids display great diversity in the armament of the foregut. Suh and Nemoto (1988) showed that the gastric mill of euphausiids is composed of paired cluster spines, paired lateral teeth, and a filter-press (gland filter or ampulla). In the present study, the cluster spines and lateral teeth are found in *N. australis*, but the filter-press is absent (Fig. 1B and C). Suh and Nemoto (1988) suggested that the gastric mill structure of euphausiids could fall into three categories on the basis of the disappearance of the lateral teeth and filter-press in the foregut. In this sense, it is considered

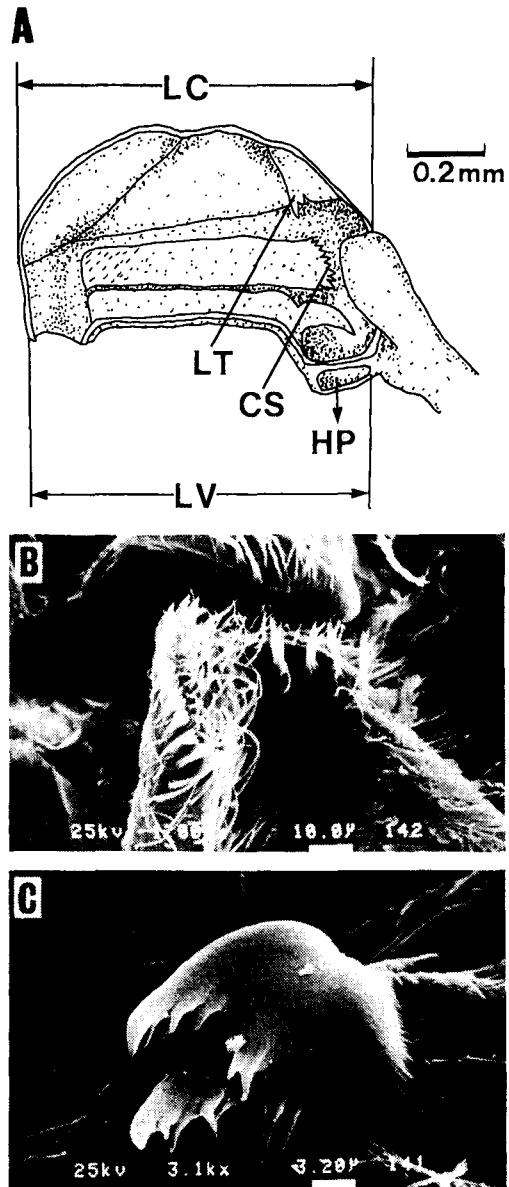


Fig. 1. Structure of gastric mill of *Nyctiphanes australis*. (A) Lateral dissected view of the external and internal structures of the foregut. LV-length of ventral plate; LC-length of the chamber; LT-lateral teeth; CS-cluster spines; HP-hepatopancreas. Note the absence of filter-press on entrance of the hepatopancreas. (B) Right cluster spines. (C) Right lateral teeth.

that *N. australis* is a member of Group II (Table 2).

Gurney(1942), Gordon(1955), and Brinton(1966) suggested that euphausiids and penaeid decapods are taxonomically coordinate. Suh and Nemoto(1988) found that the gastric mills of euphausiids closely resembles those of lower decapods (e.g., penaeid and caridean) (see Patwardhan, 1935c-e; Meiss and Norman, 1977; Felgenhauer and Abele, 1985). At present it is also known that the filter-press is present in all decapods examined (Kunze,

1981; Felgenhauer and Abele, 1985). The filter-press sorts food particles and transferring the finest particles in suspension to the hepatopancreas (Powell, 1974; Fryer, 1977; Gibson and Barker, 1979; Kunze and Anderson, 1979). In euphausiids, the filter-press is present only in the foregut of *Bentheuphausia amblyops*. Moreover, the filter-press of *B. amblyops* is morphologically similar with that of decapods. The presence of the filter-press appears to be of considerable importance in the phylogenetic relationships between euphausiids and

Table 1. Mean, SD and range of FGI in percentage of 11 species of euphausiids. N dentes the number of specimens examined.

Species	Mean	SD	Range	N
* <i>Bentheuphausia amblyops</i>	91.7	4.6	83.3~97.8	15
* <i>Euphausia superba</i>	91.2	5.0	81.1~100.0	20
* <i>Meganyctiphanes norvegica</i>	103.4	3.9	95.2~108.8	10
* <i>Nematobranchion boopis</i>	153.8	11.0	139.0~169.6	11
* <i>Nematoscelis microps</i>	134.1	11.4	112.8~148.4	10
<i>Nyctiphanes australis</i>	96.6	4.2	89.5~105.9	19
* <i>Pseudeuphausia latifrons</i>	97.9	3.1	95.5~104.8	10
* <i>Stylocheiron maximum</i>	146.4	6.2	135.0~154.3	8
* <i>Tessarabranchion oculatum</i>	103.4	3.0	98.3~107.2	7
* <i>Thysanoessa longipes</i>	100.6	2.6	95.5~103.3	12
* <i>Thysanopoda acutifrons</i>	105.3	3.4	101.5~113.0	13

*: Modified from Suh and Nemoto(1988).

Table 2. The gastric mill structure of 11 species of euphausiids.

Group	Species	Cluster spines	Lateral teeth	Filter press
I	* <i>Bentheuphausia amblyops</i>	+	+	+
II	* <i>Euphausia superba</i>	+	+	-
	* <i>Meganyctiphanes norvegica</i>	+	+	-
	<i>Nyctiphanes australis</i>	+	+	-
	* <i>Pseudeuphausia latifrons</i>	+	+	-
	* <i>Tessarabranchion oculatum</i>	+	+	-
	* <i>Thysanoessa longipes</i>	+	+	-
III	* <i>Nematobranchion boopis</i>	+	-	-
	* <i>Nematoscelis microps</i>	+	-	-
	* <i>Stylocheiron maximum</i>	+	-	-
	* <i>Thysanopoda acutifrons</i>	+	-	-

+: Present; -: Absent; *: From Suh and Nemoto (1988).

decapods (Suh and Nemoto, 1988).

According to the early life history, Brinton (1966) reported that the deep-living genera *Bentheuphausia* and *Thysanopoda* seem to be the primitive genera in euphausiids. Casanova (1984) considered *Bentheuphausia* as the most primitive genus. She proposed a phylogenetic scheme of euphausiids based on 13 morphological characters. But she overlooked the importance of the morphology of the foregut. The present study supports the view of Brinton (1966), Casanova (1984), and Suh and Nemoto (1988); there is the genus *Bentheuphausia* at the base of the euphausiid phylogenetic tree (Fig. 2). On the basis of the foregut morphology, all euphausiids examined were distinguished into three categories (Table 2). Since the foregut morphology seems to be useful to understand phylogenetic relationship within euphausiids (Suh and Nemoto, 1988), it is probable that there are two radiations from *Bentheuphausia* in euphausiid phylogeny (Fig. 2). One is the group having well-developed gastric mill (*Meganyctiphanes*, *Pseudeuphausia*, *Euphausia*, *Tessarabrachion*, *Thysanoessa*, and *Nyctiphanes*); and the other is the group having gastric mill without lateral teeth (*Nematoscelis*, *Nematobrachion*, *Stylocheiron*, and *Thysanopoda*).

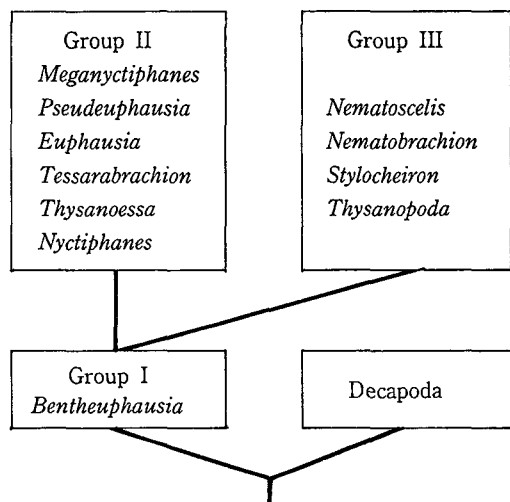


Fig. 2. Phylogenetic relationships within euphausiids on the basis of variation of the gastric mill structure.

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