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Microanatomy of the marsupium, juveniles, eggs and cuticle of cyamid ectoparasites (Crustacea, Amphipoda) of whales

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Abstract

Preliminary ultrastructural findings are presented for the first time on three species of amphipod whale lice, *Cyamus boopis*, *C. scammoni* and *C. erraticus* with particular reference to developmental structures, i.e. marsupium, eggs, juveniles and also the adult cuticle. The inner integumental surface of the marsupium presented a cobblestone appearance, with finger-like setae lining the edges of the marsupial oostegites. Unhatched eggs were spheroid with a microgranular surface. Juveniles of undetermined instar stage were elongated with well developed dactyli and a cluster of multiple sensilla at the tips of the antennae. Other small sensilla were observed elsewhere on the body. Numerous epicuticular pores, some releasing secretory material, were seen on the cyamid surfaces by scanning electron microscopy. Transmission electron microscopy of the cuticle of the adult amphipods demonstrated an architecture typical for crustaceans with multiple, microfibrillar lamellae of the exocuticle and endocuticle traversed by both pore canals and electron dense fibers. Large numbers of small pores opened through the epicuticle. These morphological findings illustrated both specialized adaptations of cyamids, as well as a general conformation to the Malacostracan configuration.

Introduction

The family, Cyamidae, consists of a group of ectoparasite crustaceans which live on whales, a habitat which has rendered them difficult to study. Consequently, very little is known about the biology of these amphipods, found primarily but not exclusively on the slower moving baleen whales. Early reports dating to the last century have described their macroscopic anatomy (Pouchet, 1892; Fage, 1932; Margolis, 1955; Agrawal, 1967) and in more recent years their musculature (Sawaya, 1938), ecology (Berzin & Vlasova, 1982; Brownell & Mead, 1985; Balbuena & Raga, 1991; Rowntree, 1996) and new species that have been found (Margolis, 1954; Leung, 1970*a*, 1970*b*; Waller, 1989). Cyamids, commonly called whale lice, live all of their life cycle upon whales and transfer between adult cetaceans, and between adults and calves. Although the reproductive behavior of other amphipod species, such as some caprellids (Harrison, 1940; Lim & Alexander, 1986) have been well characterized, very little is known about the life cycle, juvenile development, molting and early life within the marsupium of female cyamids. A single report by Leung (1976) discusses the life cycles of cyamids living on gray whales, and Rowntree (1996) has recently discussed gravidity of female cyamids in relation to season. Accordingly, the purpose of the present communication is to report the first data of some of the detailed structural findings of early cyamid life in the female brood pouch as well as a preliminary description of the cyamid cuticle.

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Methods

Healthy cyamids were collected from whale strandings. Specifically, *Cyamus boopis* Lütken 1870, specimens were collected from humpback whales (*Megaptera novaeangliae* Borowski 1781) stranded at Truro, MA. *Cyamus scammoni* Dall 1872 (Fig. 1) were collected from California gray whales (*Eschrichtius robustus* Lilljeborg 1861) stranded on the California coast, and *Cyamus erraticus* Roussel *de Vauzème 1834* were collected from a northern right whale (*Balaena glacialis* Müller 1776) stranded on the Florida coast. Multiple specimens of each species were fixed in the field either initially in 70% ethanol or in 10% formaldehyde and were post-fixed in 5% glutaraldehyde/4.4% formaldehyde/2.75% picric acid in 0.05 M sodium cacodylate buffer at pH 7.4, which we have used previously for marine invertebrates (Pfeiffer & Lowe, 1989). Fixed

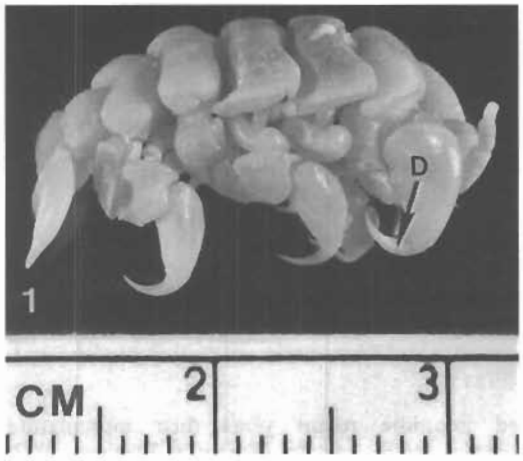

Figure 1. Lateral view of *C. scammoni*. Note segmented body and prominent dactyli (D). Anterior end of cyamid is on the right. Scale in cm.

cyamids were dissected with aid of a stereomicroscope, and samples were washed with 0.1 M cacodylate buffer (pH 7.4), post-fixed in 1% osmium tetroxide in 0.1 M cacodylate buffer for 1 h, washed in buffer again and dehydrated in a series of alcohols for transmission electron microscopy (T.E.M.). Semithin sections (1 μm) were cut from specimens embedded in Poly/Bed 812 (Polysciences), using standard methods we have employed for marine invertebrates (Pfeiffer & Lowe, 1989) and cetacean tissues (Pfeiffer & Rowntree, 1996), for purposes of orientation and preliminary study by light microscopy. Thin sections for T.E.M. were subsequently cut and doubly stained with lead citrate and uranyl acetate and studied with a JEOL 100 CX-II transmission electron microscope operating at 80 KV. Other specimens, fixed in a similar manner, were examined by scanning electron microscopy (S.E.M.). These specimens were critical point dried, mounted and coated with gold (approximately 1500Å) in a SPI sputter coater for 5 min and examined in a JEOL JSM 35C scanning electron microscope operating at 15 KV.

Results

Marsupium and eggs

The marsupium, or brood pouch, of *C. erraticus* is located on the ventral surface of the female cyamid and is formed by overlapping oostegites (cuticular plates) which provide the ventral wall of the brood pouch. The macroscopic character of the external perspective of the brood pouch has been described elsewhere (Fage, 1932; Leung, 1967) but the internal configuration has remained unreported. We observed that the entry of the oostegites to the lumen of the marsupium is lined by a single row of marginal setae approximately 250 μ in length and placed 30 μ apart (Figs 2 and 3). Presumably, this bioarchitectural arrangement will retain the eggs within the marsupium but would allow mobile juvenile cyamids to enter or depart through the marsupial gateway guarded by the finger-like projections. The inner surface of the marsupium, as revealed by scanning electron microscopy, is lined by a cuticle (Fig. 4) which shows in some regions distinct cellular boundaries, i.e., a cobblestone appearance due to convex apical cellular surfaces (Fig. 4). At high magnification the inner surface of the marsupium shows an undulating surface with evidence of minute (0.5 μ) surface projections (Fig. 5). Spheroid eggs were found within the marsupium. Some surface folding was observed (Fig. 6) on the eggs. At high magnification (13 000 ×) of the egg surface, a granulated appearance was evident (Fig. 7), a surface specialization which increased the surface area significantly.

Juvenile cyamids within marsupium

Minute (0.8 mm), immature cyamids of an unknown instar stage were also found within an adult cyamid (*C. erraticus*) brood pouch. Compared to the adult, these juveniles were elongated (Figs 8 and 9), had shorter legs, undeveloped, short antennae (Fig. 9) and club-shaped gills. Their dactyli, or claws, were nonetheless well-developed (Fig. 8). Sensilla were present, sparsely scattered on the antennular segments and elsewhere. A concentration of sensilla was found at the tips of the distal segments of the antennae (Figs 10 and 11). The latter sensory, finger-like projections were approximately 8–14 μ in length. They were tubular sensory structures, with a pore at the distal end (Fig. 11). At higher magnification by scanning electron microscopy, both small peg-type sensory microcuticular structures (Fig. 12) and small cuticular surface globular structures were discerned (Fig. 12). The latter were shown by high magnification (18 000 ×) to be secreted material, each globule associated with a pore on the cuticular surface (Fig. 13). Some pores were devoid of this material of unknown composition.

The cuticle of the cyamid was also studied by transmission electron microscopy. Adult cyamids of all three species were examined. The typical layers consisted of an outermost epicuticle overlying a prominent exocuticle, which overlaid a less distinct endocuticle which was placed upon an epithelium. The thin epicuticle of *C. scammoni* was electron dense and showed the presence of small branches of pore canals which had penetrated from the outer exocuticle (Fig. 14). Immediately subjacent to the dense epicuticle was a thin marginal zone

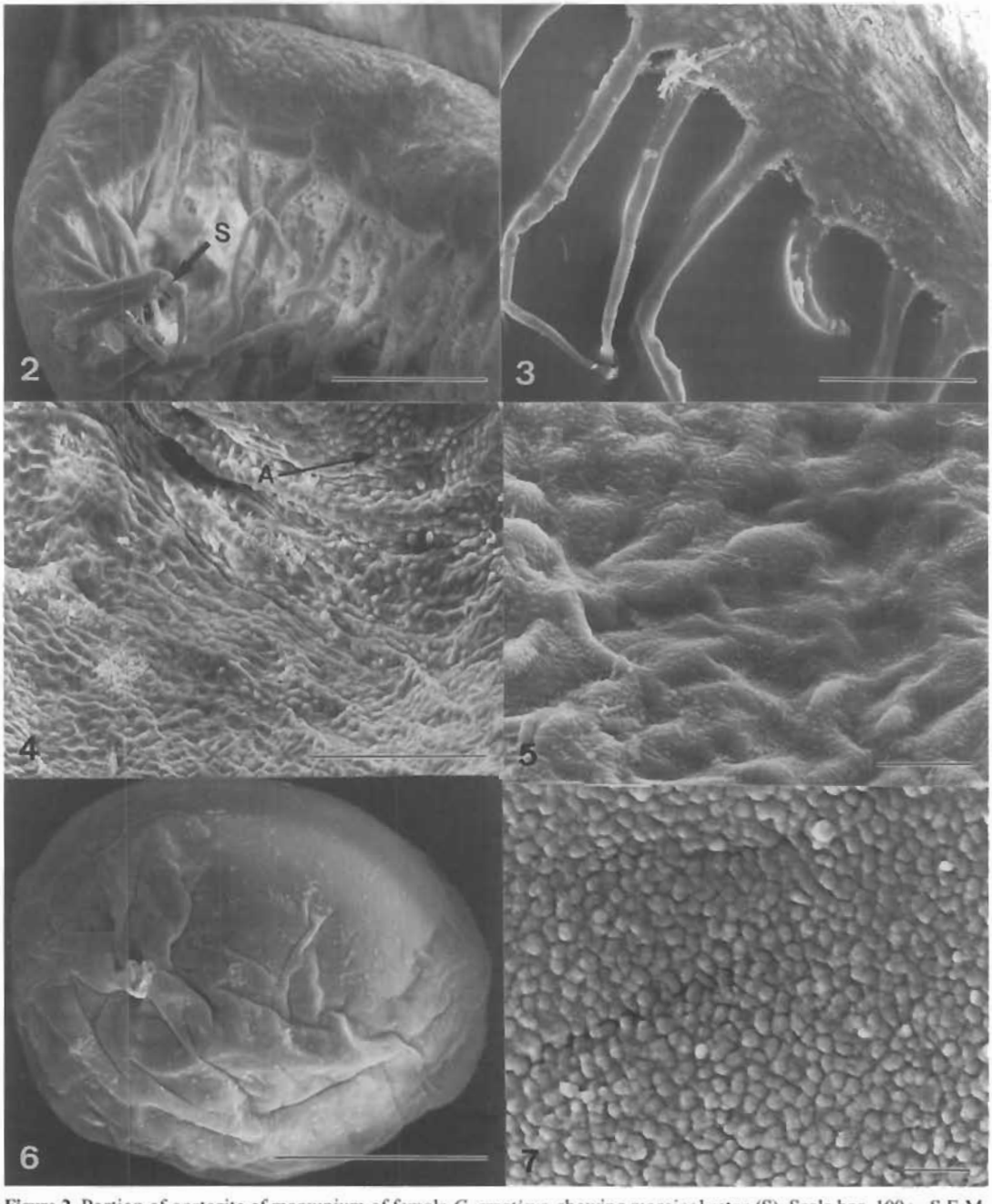

Figure 2. Portion of oostegite of marsupium of female *C. erraticus*, showing marginal setae (S). Scale bar, 100 μ. S.E.M.

Figure 3. The finger-like setae of the marsupium of *C. erraticus* form a single row of widely-spaced projections. Scale bar, 100 μ. S.E.M.

Figure 4. Inner surface lining of marsupium of *C. erraticus*. Some cellular apices (A) are evident in the corner. Scale bar, 100 μ. S.E.M.

Figure 5. Higher magnification of inner surface of marsupium of *C. erraticus*. Small leaf-like microstructures are evident on the undulating surface. Scale bar, 10 μ. S.E.M.

Figure 6. Unhatched egg of *C. scammoni*, collected from marsupium. Scale bar, 100 μ. S.E.M.

Figure 7. High magnification (× 11 000) of outer surface of egg of *C. erraticus*, showing increase in surface area due to surface granulation. Scale bar, 1 μ. S.E.M.

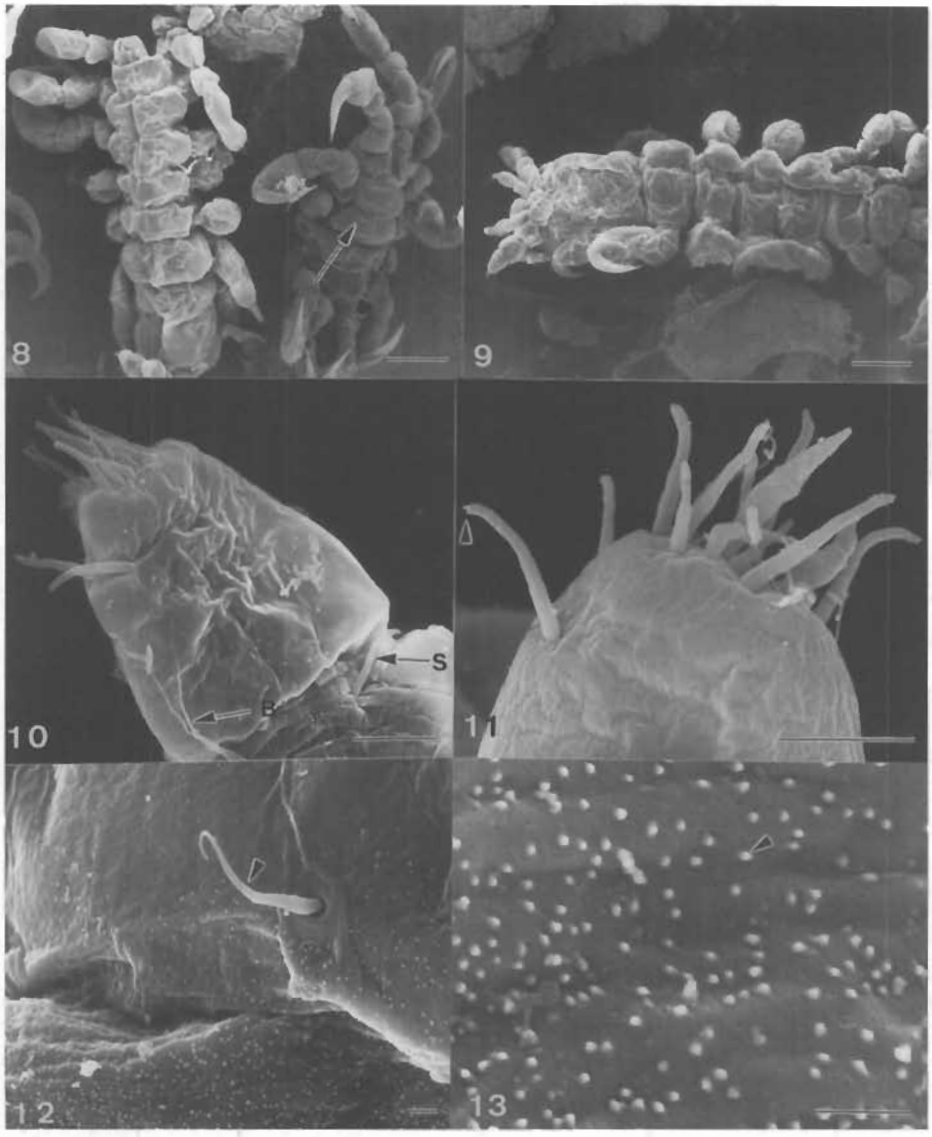

Figure 8. Juveniles of *C. erraticus* collected from adult marsupium. Dorsal aspect on left cyamid and ventral aspect on right cyamid. Note oostegites (arrow) on ventral surface of the female juvenile cyamid. Scale bar, 100 μ. S.E.M.

Figure 9. Juvenile *C. erraticus* collected from marsupium. Note increased linearity compared to typical adult of any cyamid species, and short antennae 1 and 2 at far left on head region. Scale bar, 100 μ. S.E.M.

Figure 10. Distal aspect of first antenna of juvenile *C. erraticus*, illustrating sensilla which, although concentrated at tip of antenna 1 or 2, are also present more proximally (S). Some sensilla are bifurcated (B) at the end. Scale bar, 10 μ. S.E.M.

Figure 11. The antennular tip sensilla can be seen in some cases to be segmented. Note the open pore (arrowhead) at the ends of some of the sensilla. Scale bar, 10 μ. S.E.M., $x=3000$.

Figure 12. At higher magnification, a small peg-like sensillum (arrowhead) protruding from an open pit can be observed on the antenule 1 or 2 of a juvenile *C. erraticus*. Also, small surface microstructures can be seen on the cuticle, especially in the lower one-third of the figure. Scale bar, 1 μ. S.E.M., $x=4800$.

Figure 13. At higher magnification, the surface microstructures (arrowhead) shown in Figure 12 can be resolved as secreted globular material, and their origin, i.e., small surface cuticle pores, are seen distributed across the surface. *C. erraticus* juvenile antenna. Scale bar, 1 μ. S.E.M., $x=18\,000$

Pacific and southwestern Atlantic have demonstrated that local killer whales learn how to take advantage of seasonally abundant prey within their home range, which may cover an area of many hundreds, or thousands, of square kilometers (Bigg, 1982, Iñiguez, *in press*). Heimlich-Boran (1988) suggests that, in the eastern North Pacific, killer whales use geographic features to maximize feeding efficiency, with transient pods feeding largely on harbor seals (*Phoca vitulina*) and resident pods preying mostly on salmon (*Onchorhynchus* spp.).

Earlier reports of depredation by killer whales on longline fisheries have been made in the Indian Ocean (Sivasubramanian, 1965). Nemoto (1968) and Nakamura (1985) noted similar fishery interactions in the North Atlantic. Studies on killer whale/fishery interactions have also been carried out in the North Pacific (Matkin, 1986; Matkin *et al.*, 1987*a,b*; Dahlheim, 1988; Matkin, 1988; Leatherwood *et al.*, 1990).

In contrast, very little is known of the ecology and feeding habits of killer whales in Brazilian waters (Castello, 1977; Bittencourt, 1983; Geise & Borobia, 1988). In southern Brazil, they are commonly found near longliners where their attacks on tuna and tuna-like fish are extensive, particularly on swordfish. To date, no assessments have been made on the magnitude of such depredation and its impact on the economy of the Brazilian fisheries. In this study we address the problem by focusing on the interactions between killer whales and the tuna longline fishery and also report sightings of these whales in the region.

Materials and methods

Observations on the interactions were made during nine cruises, between August 1987 and August 1991, on board national longline tuna boats from the ports of Rio Grande and Santos, southern and southeastern Brazil respectively. Each fishing cruise lasted 15–20 days, in the area 26°S–34°S, beyond the Brazilian continental slope (Fig. 1), where depth ranged from 250–3500 m. There were no summertime cruises, due to the fact that during this season the longliners change their fishing grounds to lower latitudes.

Losses of swordfish were estimated by counting the number of damaged fish hauled out per day. Attacks of killer whales were distinguished from those of sharks by the shape and size of bites. Killer whale bites leave torn borders on the fish, while sharks leave clear-cut bites which are smaller than those made by orcas. Despite longline length, which may vary from 40–120 km, sightings occurred in an incidental manner, whenever the killer whales were passing close to the vessel. Additional data were obtained by interviewing fishermen both on board vessels and nearby boats, the latter via VHF radio.

Results

The fisheries

During our cruises on Brazilian boats, the daily average fishing effort was about 1500 hooks per day per vessel. The hooks were set in depths of 50–150 m. The longlines ranged from 35–90 km long and were released early in the dawn. After four to five hours hauling of the gear was started. The catch per unit effort rates for swordfish ranged from 0.8–10.5 fish/1000 hooks per cruise, with an average of approximately 3.5 fish/1000 hooks.

Killer whale/longline fishery interactions

In the southern region, mainly during winter, more than 50% of the daily swordfish catch may be lost to killer whale depredation. According to fishermen this loss may occasionally reach almost 100%. Skippers sometimes change the fishing areas, advance the longline casting time and even shoot at the whales, but these procedures did not stop depredation. Often killer whales would continue following the boats and attacking the catch. Carcharhinid sharks (*Carcharhinus* spp.), blue sharks (*Prionace glauca*), shortfin makos (*Isurus oxyrinchus*) and hammerhead sharks (*Sphyrna* spp.) commonly prey on fish taken by longlines, leaving clear-cut bites which are relatively small (Fig. 2a). On the other hand, killer whale bites leave torn borders, largely ripping the body of the fish, avoiding the head and sometimes the vertebral column and fins (Fig. 2b). Generally, when killer whales attack during fishing, the percentage of fish damages is higher than that caused by sharks. The fish damaged by sharks seem to be found at random along the whole longline, while attacks by killer whales may be in an orderly manner, as was observed in the Indian Ocean (Sivasubramanian, 1965).

Cumulative sightings of killer whales in southern Brazil are shown in Fig. 1. No pairs of whales were seen; they occurred in herds of 3–10 animals or sometimes alone (Fig. 3). These single animals were always adult males. If swordfish are caught in great numbers, killer whales may appear more frequently, waiting for the longline sometimes as close as 50 m from the vessel. The sightings reported here occurred only during the afternoon and evening hours, but it is difficult to assume that killer whales feed on fish only at this time of the day, while the longline has been out since day-break.

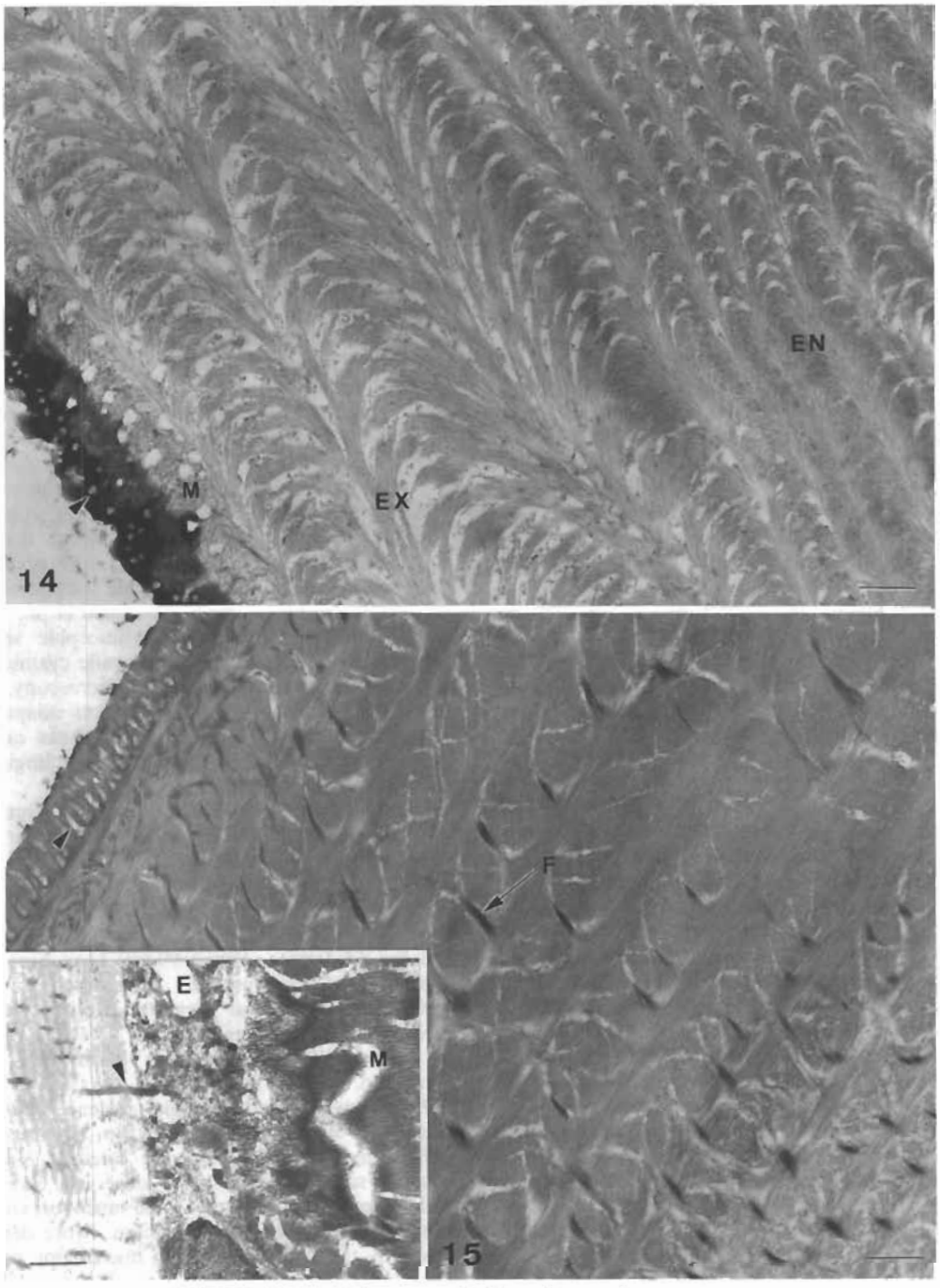

Figure 14. The cuticle of *C. scammoni* is composed of an electron dense epicuticle traversed by pores (arrowhead), a subjacent marginal zone (M), an exocuticle (EX) of wide lamellae and an endocuticle (EN) of narrow lamellae. Clear area are pore canals within the exocuticle and endocuticle, shown in this oblique section. Scale bar, 680 nm. T.E.M.

Figure 15. The cuticle of *C. erraticus* shows prominent tubular pores traversing the epicuticle (arrowhead) and numerous electron dense fibers (F) crossing the exocuticle and endocuticle. Scale bar, 662 nm. T.E.M. Insert: at the base of the endocuticle, pore canals can be seen penetrating (arrowhead) from the epithelial cell zone (E), and striated muscle (M) of the subepithelial region is also evident. Scale bar, 809 nm. T.E.M.

containing few microfibrillar lamellae but many pore canals (Fig. 14). The exocuticle and endocuticle were differentiated in *C. scammoni* mainly by the width of chitin-protein, prismatic lamellae, with smaller lamellae comprising the latter zone (Fig. 14). Pore canals were observed between the microfibrils of the lamellae (Fig. 14). In the cuticle of adult *C. erraticus* the exocuticle and endocuticle were similar to that of *C. scammoni* except that electron dense intracuticular fibers, scarce in *C. scammoni*, were observed running perpendicular to the cuticular surface (Fig. 15). Further, the thin (0.70 μm) epicuticle contained a more tubular-shaped array of canals traversing the width of the epicuticle. The intermediate zone between the epicuticle and the exocuticle contained numerous arrays of electron dense fibers (Fig. 15). The epithelium beneath the endocuticle was poorly developed, with muscle fibers from the sub-epithelial region extending almost to the base of the endocuticle. Tubular canals were observed traversing this endocuticle-epithelial junction (Fig. 15 insert). The cuticle of *C. boopis* also illustrated a thick exocuticle which was traversed by a greater concentration of regularly-spaced electron dense fibers (Fig. 16). At higher magnification of oblique sections through the chitin-protein prisms, the electron dense fibers had a stellate configuration when cut in cross section (Fig. 17).

Discussion

Although most of the 23 known species of cyamids have long been identified structurally, their inaccessible habitat on whales has meant that there are not many collections of these amphipods. Indeed, whale lice have not previously been described at the ultrastructural level, and little is known about their reproductive behavior, number of juvenile instar stages of development, frequency of molting in juveniles and adults, and life within the brood pouch. Therefore, the present data are provided as a preliminary overview of some of the cyamid reproductive and integumentary features.

At the present time we do not know about the age and frequency of transit of most species of juvenile cyamids in and out of the adult female's brood pouch. Juveniles of other amphipod species, such as an Atlantic haustoriid, have been observed moving in and out of the marsupium (Croker, 1968). Leung (1976) has provided data on *C. scammoni* juveniles. He reported an ovigerous female with a clutch of 980–1078 eggs in the marsupium, and stated that the young remained in the marsupium two to three months. In the caprellid amphipod, *Caprella scaura typica*, juveniles hatch from four day old eggs, remain in the brood pouch for only 12 hours, and permanently depart from the brood pouch at an age of one week (Lim & Alexander, 1986). Newly hatched juveniles of *Caprella unica* remain in the brood pouch for 35–50 hours (Berrill, 1971). Juvenile and adult cyamids have a poorly developed or non-existent visual ability, and because their food source is primarily the skin upon which they rest, sight is not an essential sense for this crustacean as it is for some other crustaceans. It has been established that in some aquatic crustacean species pheromones serve as major chemical attractants particularly with respect to mating behavior (Dunham, 1978). It can be speculated that pheromones may likely play a role in cyamid interactions, sexual behavior, and perhaps maternal–juvenile identification. Indeed, other amphipod species have exhibited important pheromone-directed behavior (Dahl *et al.*, 1970), including mediation by water-borne chemical attractants (Borowsky, 1984). The morphologic evidence we observed ultrastructurally of apparent secreted material on the epicuticle of whale lice may be pheromone material, but this has not been proven. The receptor for the female sex pheromone in the gammaridean amphipod (Dahl *et al.*, 1970) was located in the sexually dimorphic second antennae of the male. In the juvenile cyamids we observed by scanning electron microscopy, two structural features showed significant adaptation at an early age; well-developed sensilla on the antennae, and well-developed claws for clinging to the substratum.

The ultrastructure of the cyamid marsupium has not previously been described and its physiologic regulation of secretion or absorption has not been clarified. The morphologic organization and physiology of the male brood pouch of the other types of marine forms such as seahorses and pipefish (*Teleostea, Syngnathidae*) have been well characterized and provide an environment for swimming, nutritional transfer of amino acids, feeding and osmoregulating of juveniles (Quast & Howe, 1980; Haresign & Shumway, 1981; Azzarello, 1991; Carcupino *et al.*, 1997). Fage (1932) provided morphologic evidence that the oostegites of cyamids develop from antennae-like projections which are located laterally. In the present study we have not observed elaborate cellular surface structures on the inner surface epithelium of the cyamid marsupium. More detailed study by transmission electron microscopy will be required to determine if diverse cell types such as mitochondrial rich 'chloride' cells, pavement cells, etc. are present, as have been found lining the male Syngnathidian brood pouch (Carcupino *et al.*, 1997). Although we have observed eggs within the cyamid marsupium, as described above, we have not observed eggs in the process of hatching. We cannot conclude whether hatching is by mechanical

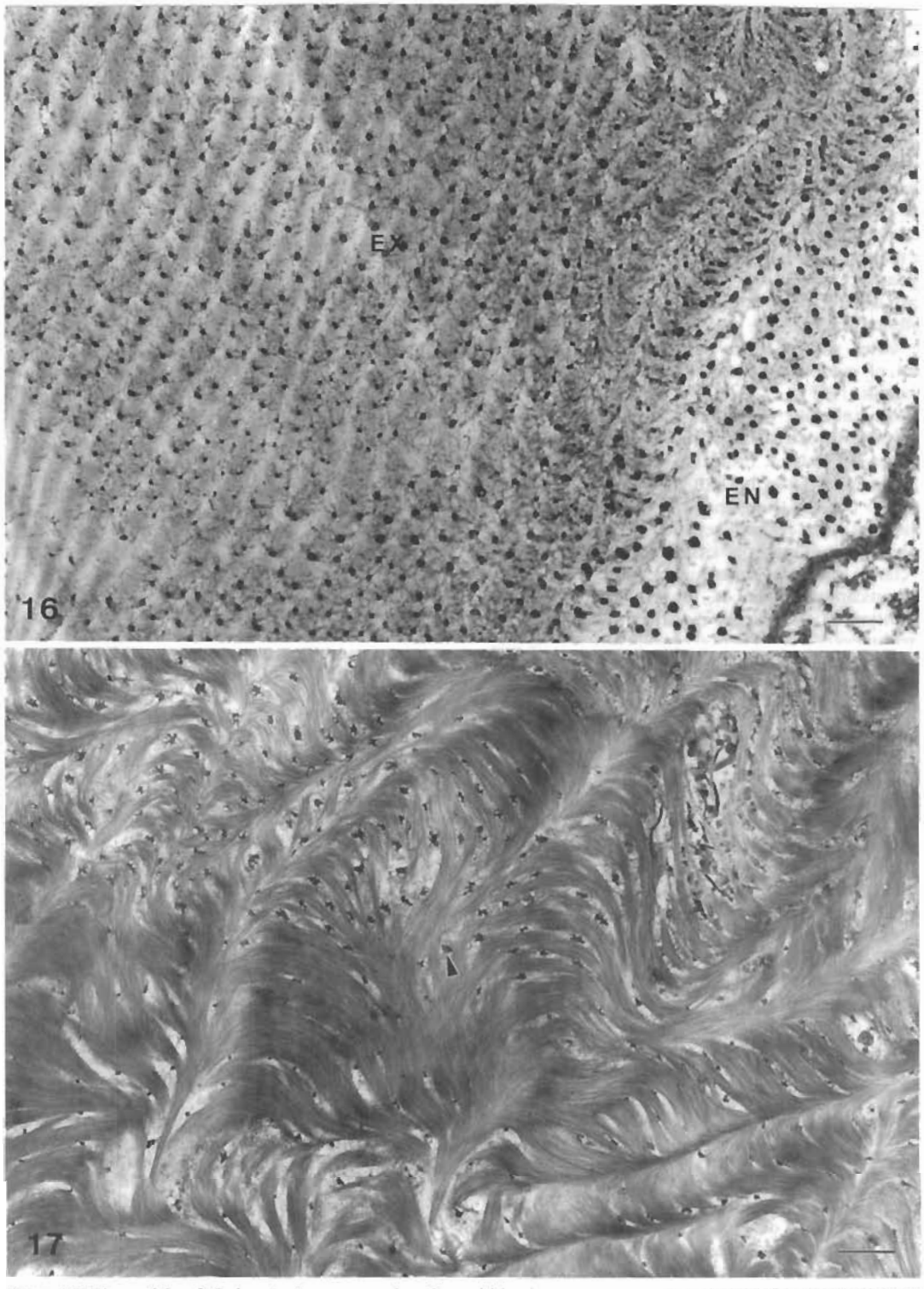

Figure 16. The cuticle of *C. boopis* shows many lamellae within the exocuticle (EX) and a considerably less dense endocuticle (EN). Scale bar, 740 nm. T.E.M.

Figure 17. Oblique section through exocuticle of *C. boopis*, illustrating the microfilaments of the lamellae and cross sections of small fibers (arrowhead), illustrating a stellate shape. Scale bar, 690 nm. T.E.M.

means, as in the amphipod *Gammarus*, or the gastropod *Amnicola limosa*, or by osmotic changes within the marsupium as with some copepod eggs (Davis, 1959). Hatching spines have also been observed on the embryonic telson cuticle in some species of amphipods (Fish, 1975). It has also been observed by others (Dunham, 1986) that the presence of juveniles or eggs within the brood pouch of the amphipod, *Gammarus lawrencianus*, influences the male guarding behavior. The granulated surface appearance of the egg, which increased its surface area, was distinct from the egg surface of the dipteran invertebrate, such as *Ceratitis capitata*, as the latter showed even more extensive development of cytoplasmic microprojections (Callaini & Fanciulli, 1987).

Both tube-like thick antennular sensilla and smaller, bifurcated sensilla were observed on the juvenile cyamids. A thorough study of the sensilla must be undertaken, both of adults and juveniles, in order to classify these and other types, and distribution of the cyamid sensilla. Further, T.E.M. analysis in combination with S.E.M. will be needed to clarify cuticular mechanoreceptor hairs from chemoreceptor types of sensilla. Mauchline & Ballantyne (1975) earlier reported the patterns of distribution of integumental sensilla of hyperiid and gammaridean amphipods at a light microscopic level. Surface microtrich hair-like sensory structures, mostly on gammaridean amphipods, have been characterized by Cuadras (1982), Halcrow & Bousfield (1987) and Steele & Oshel (1987). All surface amphipod microstructures are not sensory (Klepal & Kastner, 1980; Halcrow & Bousfield, 1987), and some may be combined for chemo-, mechano- and vibroreception, and the complexity of their structure and function has been reviewed by Derby (1982) and Read & Williams (1991). The present data showing clusters of tubular setae on the antennae show evidence of an open pore at the tip suggesting a chemoreceptor. These characteristically contain dendrites of bipolar neurons, and have been noted on other amphipods, isopods, decapods, as well as terrestrial arthropods (Mauchline, 1977; Altner *et al.*, 1983; Heimann, 1984). Our finding of morphologic evidence of cuticular surface secretion confirms in amphipods the reports of dermal gland function in decapods (Gnatzy, 1984) and copepods (Hipeau-Jacquotte, 1987). Since various types of tegmental glands are present in crustaceans (Talbot & Demers, 1993), further studies are needed to characterize the surface glands we observed on cyamids.

The microstructural organization plan of the cuticle of amphipods closely resembled the general plan found in other crustaceans (Giraud-Guille, 1984; Compere, 1995). A great diversity of pore canal systems exists for various amphipods, as have been reviewed elsewhere by Halcrow (1978, 1993) and Halcrow & Powell (1992). Our ultrastructural perspectives of this system, as well as of the exocuticle and endocuticle protein-chitin microfilaments and integumentary fibers in cyamids were similar to the patterns observed in numerous other reports on arthropod cuticle.

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References

Agrawal, V. P. (1967) The feeding appendages and the alimentary canal of *Cyamus ovalis* (L.) In: Proc. Sympos. Crust. Jan 12–15, 1965, Ernakulam, India. Part II. *Mar. Biol. Assoc. India* 549–552.

Altner, I., Hatt, H. & Altner, H. (1983) Structural properties of bimodal chemo- and mechanosensitive setae on the pereiopod chelae of the crayfish, *Austropotamobius torrentium*. *Cell Tissue Res.* **228,** 357–374.

Azzarello, M. Y. (1991) Some questions concerning the Syngnathidae brood pouch. *Bull. Mar. Sci.* **49,** 741–747.

Balbuena, J. A. & Raga, J. A. (1991) Ecology and host relationships of the whale-louse *Isocyamus delphini* (Amphipoda: Cyamidae) parasitizing long-finned pilot whales (*Globicephala melas*) off the Faroe Islands (northeast Atlantic). *Can. J. Zool.* **69,** 141–145.

Berrill, M. (1971) The embryonic behavior of *Caprella unica* (Crustacea: Amphipoda). *Can. J. Zool.* **49,** 499–504.

Berzin, A. A. & Vlasova, L. P. (1982) Fauna of the cetacea Cyamidae (Amphipoda) of the world ocean. *Invest. Cetacea* **13,** 149–164.

Borowsky, B. (1984) Effects of receptive females' secretions on some male reproductive behaviors in the amphipod crustacean *Microdeutopus gryllotalpa*. *Mar. Biol.* **84,** 183–187.

Brownell, R. L. Jr. & Mead, J. G. (1985) Cyamid populations on Baird's beaked whales, *Beradius bairdii*, in Japanese waters. In: Abstracts from the Sixth Biennial Conference on the Biology of Marine Mammals. Vancouver, B.C., Nov. 22–26 (abstr).

Callaini, G. & Fanciulli, P. O. (1987) Surface changes during blastoderm formation in the embryo of *Ceratitis capitata* Wied. (Diptera). Scanning electron microscope studies. *J. Submicrosc. Cytol.* **19,** 627–637.

Carcupino, M., Baldacci, A., Mazzini, M. & Franzoi, P. (1997) Morphological organization of the male brood pouch epithelium of *Syngnathus abaster*, Risso (*Teleostea, Syngnathidae*) before, during, and after egg incubation. *Tissue and Cell* **29,** 21–30.

Compere, P. (1995) Fine structure and morphogenesis of the sclerite epicuticle in the Atlantic shore crab *Carcinus maenas*. *Tissue and Cell* **27,** 525–538.

Croker, R. A. (1968) Return of juveniles to the marsupium in the amphipod *Neohaustorius schmitze* Bousfield. *Crustaceana* **14,** 215.

Cuadras, J. (1982) Microtrichs of amphipod crustacea. Morphology and distribution. *Mar. Behav. Physiol.* **8,** 333–343.

Dahl, E., Emanuelsson, H. & Von Mecklenburg, C. (1970) Pheromone transport and reception in an amphipod. *Science* **170,** 739–740.

Davis, C. C. (1959) Osmotic hatching in eggs of some fresh-water copepods. *Biol. Bull.* **116,** 15–29.

Derby, C. D. (1982) Structure and function of cuticular sensilla of the lobster *Homarus americanus*. *J. Crust. Biol.* **2,** 1–21.

Dunham, P. J. (1978) Sex pheromones in crustacea. *Biol. Rev.* **53,** 555–583.

Dunham, P. J. (1986) Mate guarding in amphipods: a role for brood pouch stimuli. *Biol. Bull.* **170,** 526–531.

Fage, L. (1932) Les branchies accessoires, les oostegites et la sexualitie des Cyames (Amphipodes parasites des cetaces). *Soc. Ent. Fr.* Livre da Centenaire. 15 Juin, 127–138.

Fish, J. D. (1975) Development, hatching and brood size in *Bathyporeia pilosa* and *B. pelagica* (Crustacea: Amphipoda). *J. Mar. Biol. Assoc. U.K.* **55,** 357–368.

Giraud-Guille, M.-M. (1984) Fine structures of the chitin-protein system in the crab cuticle. *Tissue and Cell* **16,** 75–92.

Gnatzy, W. (1984) "Campaniform" structures on lobster antennae are dermal glands. *Cell Tissue Res.* **236,** 729–731.

Halcrow, K. (1978) Modified pore canals in the cuticle of *Gammarus* (Crustacea: Amphipoda); a study by scanning and transmission electron microscopy. *Tissue and Cell* **10,** 659–670.

Halcrow, K. & Bousfield, E. L. (1987) Scanning electron microscopy of surface microstructure of some gammaridean amphipod crustaceans. *J. Crust. Biol.* **7,** 274–287.

Halcrow, K. & Powell, C. V. L. (1992) Ultrastructural diversity in the pore canal systems of amphipod crustaceans. *Tissue and Cell* **24,** 417–436.

Halcrow, K. (1993) Pore canal systems and associated cuticular microstructures in amphipod crustaceans. Chapter 2. In: M. N. Horst & J. A. Freeman (eds) *The Crustacean Integument*. pp. 39–77. CRC Press, Boca Raton.

Haresign, T. W. & Shumway, S. E. (1981) Permeability of the marsupium of the pipefish *Syngnathus fuscus* to [^{14}C]-alpha amino isobutyric acid. *Comp. Biochem. Physiol.* **69A,** 603–604.

Harrison, R. J. (1940) On the biology of the Caprellidae. Growth and moulting of *Pseudoprotella phasma* Montagu. *J. Mar. Biol. Assoc. U.K.* **24,** 483–493.

Heimann, P. (1984) Fine structure and molting of aesthetasc sense organs on the antennules of the isopod, *Asellus aquaticus* (Crustacea) *Cell Tissue Res.* **235,** 117–128.

Hipeau-Jacquotte, R. (1987) Ultrastructure and presumed function of the pleural dermal glands in the atypical male of the parasitic copepod *Pachypygus gibber* (Crustacea: Notodelphydae). *J. Crust. Biol.* **7,** 60–70.

Klepal, W. & Kastner, R. J. (1980) Morphology and differentiation of non-sensory cuticular structures in Mysidacea, Cumacea and Tanaidacea (Crustacea, Peracarida). *Zool. Sci.* **9,** 271–281.

Leung, Y. M. (1967) An illustrated key to the species of whale-lice (Amphipoda, Cyamidae), ectoparasites of Cetacea, with a guide to the literature. *Crustaceana* **12,** 279–291.

Leung, Y. M. (1970*a*) *Cyamus orcini*, a new species of whale-louse (Cyamidae, Amphipoda) from a killer whale. *Bull. Inst. Fondam. Afr. Noire Ser A Sci. Nat.* **32,** 669–675.

Leung, Y. M. (1970*b*) First record of the whale-louse Genus *Syncyamus* (Cyamidae: Amphipoda) from the western Mediterranean, with notes on the biolgy of odontocete cyamids. *Invest. Cetacea* **2,** 243–247.

Leung, Y. M. (1976) Life cycle of *Cyamus scammoni* (Amphipoda: Cyamidae), ectoparasite of gray whale, with a remark on the associated species. *Sci. Rep. Whales Res. Inst.* **28,** 153–160.

Lim, S. T. A. & Alexander, C. G. (1986) Reproductive behavior of the caprellid amphipod, *Caprella scaura typica*, Mayer 1890. *Mar. Behav. Physiol.* **12,** 217–230.

Margolis, L. (1954) Three kinds of whale-lice (Cyamidae: Amphipoda) from the Pacific coast of Canada, including a new species. *J. Fish. Res. Bd. Canada* **11,** 319–325.

Margolis, L. (1955) Notes on the morphology, taxonomy and synonymy of several species of whale-lice (Cyamidae: Amphipoda). *J. Fish. Res. Bd. Canada* **12,** 121–133.

Mauchline, J. (1977) The integumental sensilla and glands of pelagic crustacea. *J. Mar. Biol. Ass. U.K.* **57,** 973–994.

Mauchline, J. & Ballantyne, A. R. S. (1975) The integumental organs of amphipods. *J. Mar. Biol. Ass. U.K.* **55,** 345–355.

Pfeiffer, C. J. & Lowe, K. J. (1989) Cirral structure of the pedunculated marine barnacle *Lepas anatifera* L. (Crustacea, Cirripedia) I. Ultrastructure of the neuromuscular apparatus. *Acta Zool.* **70,** 243–252.

Pfeiffer, C. J. & Rowntree, V. (1996) Epidermal ultrastructure of the southern right whale calf (*Eubalaena australis*). *J. Submicrosc. Cytol. Pathol.* **28,** 277–286.

Pouchet, G. (1892) Contribution à l'histoire des Cyames. *J. Anat. Physiol. (Paris)* **28,** 99–108.

Quast, W. D. & Howe, N. R. (1980) The osmotic role of the brood pouch in the pipefish *Syngnathus scovelli*. *Comp. Biochem. Physiol.* **67A,** 675–678.

Read, A. T. & Williams, D. D. (1991) The distribution, external morphology, and presumptive function of the surface microstructures of *Gammarus pseudolimnaeus* (Crustacea: Amphipoda), with emphasis on the calceolus. *Can. J. Zool.* **69,** 853–865.

Rowntree, V. J. (1996) Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. *Can. J. Zool.* **74,** 103–109.

Sawaya, P. (1938) Sobre o "piolho da baleia". *Zoologia* **2,** 227–247.

Steele, V. J. & Oshel, P. E. (1987) The ultrastructure of an integumental microtrich sensillum in *Gammarus setosus* (Amphipoda). *J. Crust. Biol.* **7,** 45–59.

Talbot, P. & Demers, D. (1993) Tegumental glands of crustacea. In: M. N. Horst & J. A. Freeman (eds) *The crustacean integument. Morphology and biochemistry*. Chapter 5, pp. 151–191. CRC Press, Boca Raton.

Waller, G. N. H. (1989) Two new species of whale lice (Cyamidae) from the ziphioid whale *Berardius bairdii*. *Invest. Cetacea* **22,** 292–297.