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research paper

Description of pereiopod setae of scyllarid lobsters, *Scyllarides aequinoctialis*, *Scyllarides latus*, and *Scyllarides nodifer*, with observations on the feeding during consumption of bivalves and gastropods

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ABSTRACT.—The morphological and behavioral aspects of slipper lobster (Scyllaridae) feeding have remained largely unexplored. Using scanning electron microscopy, the gross morphological structure of all segments of the pereiopods were described for three species of scyllarid lobsters. Five types of setae within three broad categories were found: simple (long and miniature), cuspidate (robust and conate), and teasel (a type of serrulate setae). Setae were arranged in a highly-organized, row-like pattern on the ventral and dorsal surfaces. Cuspidate setae were found on all surfaces of all segments. Simple setae were found only on the dactyl, whereas teazel setae were concentrated on the lateral-most edge of the alate carina on the merus in only one species [*Scyllarides aequinoctialis* (Lund, 1793)]; this species also differed from the other two [*Scyllarides nodifer* (Stimpson, 1866), *Scyllarides latus* (Latreille, 1803)] in setal patterning. All examined slipper lobsters differed in setal types and patterns from nephropid and palinurid lobsters, likely due to the more rigorous use of their pereiopods in accessing food. Feeding sequences of two of the slipper lobster species were videotaped and analyzed, and demonstrated a complex set of behaviors involving contact chemoreception by the antennules as part of an initial assessment of the food item, followed by extensive manipulation, probing, and eventual wedging behavior by the pereiopods as previously described for *Scyllarides*. Use of the antennules for food assessment and heavy reliance on the pereiopods, rather than the mouthparts, for food handling contrasts with nephropid and palinurid lobsters.

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Slipper lobsters (Scyllaridae) are fished in several localities and are exploited as byproduct of some shrimp fisheries, yet little is known about their basic biology, including functional morphology of their appendages and body sculpturing, their behavioral attributes, and their sensory capabilities (Holthuis 1991, Spanier and Lavalli 2007a). Numerous anatomical drawings exist in taxonomic descriptions of the approximately 88 species (Holthuis 1985, 1991, 1993a,b, 1991, 2002, Brown and Holthuis 1998), and these drawings provide information regarding the position of different types of hair-like structures (setae) on pereiopods and antennules, but there is little information on setal types, their functions, or the information they provide for the guidance of behavior. Even in studies directly examining scyllarid feeding appendages (Suthers and Anderson 1981, Ito and Lucas 1990, Mikami and Takashima 1994, Johnston and Alexander 1999, Weisbaum and Lavalli 2004), a detailed analysis of setal patterns is generally lacking. Few studies have provided information on the development of the setation pattern from larval to adult stages (Ito and Lucas 1990, Mikami et al. 1994). By contrast, in the well-studied nephropid lobster, *Homarus americanus* Milne-Edwards, 1837, setation developmental patterns, innervation, and responsiveness have been the focus of numerous studies on mouthparts, pereiopods, and antennules (Milne-Edwards 1837, Factor 1978, Derby and Atema 1982a, Derby et al. 1984, Moore et al. 1991a,b, Lavalli and Factor 1992, 1995, Gomez and Atema 1996, Guenther and Atema 1998, Kozlowski et al. 2001). The information gleaned from such studies shows that the setae and their sensory modalities are extremely important for many aspects of nephropid lobster biology including orientation to food sources, initial assessment of food (Derby 1982), final acceptance of food items for ingestion (Derby and Atema 1982b), initiation of grooming activities, and for facilitating mating activity (Cowan 1992). A similar scenario exists in the well-studied palinurid lobster, *Panulirus argus* (Latreille, 1804), where setal innervation and responsiveness has been a major focus of study (Derby and Ache 1984, Daniel and Derby 1988, Derby 1989, Steullet et al. 2000a,b, 2001, 2002, Cate and Derby 2001, Derby and Steullet 2001, Derby et al. 2001, Garm et al. 2004). Currently, only three *Scyllarides* species and *Ibacus ciliatus* (von Siebold, 1824) have been examined specifically for purported sensory structures on appendages typically used for feeding (pereiopods) (Mikami et al. 1994) and orientation (antennules) (Weisbaum and Lavalli 2004). The present study provides information on the setal pattern of the pereiopods for three *Scyllarides* species and integrates this knowledge with observations of the feeding sequence of two representatives of the genus.

Adult nephropid, palinurid, and scyllarid lobsters commonly consume mollusks and gastropods (Herrick 1909, Herrnkind et al. 1975, Lau 1987). However, techniques used to open mollusks vary due to morphological differences in pereiopod shape and mouthpart capabilities. Nephropids use their large dimorphic claws to apply a loading force to the valves until a structural failure occurs and cracks emerge to fracture the valves (Moody and Steneck 1993). In contrast, spiny lobsters bite small holes into the edges of the valves with their mandibles; once these holes are created, they use their pereiopods to further wedge open the bivalve (Carlberg and Ford 1977). Slipper lobsters simply use the sharp dactyls (often called “nails”) of their pereiopods to “shuck” open the shell (Lau 1987).

Although we understand the various techniques used to open such prey, we do not fully recognize what functions are served by setae on pereiopods. In both nephropids and palinurids, many setae are characterized as sensilla and serve as chemoreceptors and/or mechanoreceptors that are necessary to provide information about potential food sources prior to further handling and/or ingestion (Laverack 1968, Derby 1982, Derby and Atema 1982b). The loss of these sensory structures can result in deficits in feeding, such that appropriate food is rejected prior to sampling by the mouthparts or rejected by the pereiopods before food is even passed to the mouthparts (Derby and Atema 1982b). Thus, sensory setae of pereiopods may typically function in controlling grasping reflexes important for food manipulation (Derby and Atema 1982b).

Nephropid lobsters have been the focus of most of the studies on functional morphology of setae, although more studies are emerging for spiny lobsters that show that they seem to function as both contact chemoreceptors (i.e., taste organs) and mechanoreceptors (i.e., current and touch detectors) (Derby 1982, Derby and Atema 1982b, Cate and Derby 2001, Derby and Steullet 2001). These setae fall into one of two categories established by Watling (1989): Type I setae that bear small, scale-like setules; and Type II setae that lack such setules. No studies have yet focused on the setal morphology of adult slipper lobster pereiopods. Given the suggested sister group relationship between palinurids and scyllarids (Tam and Kornfield 1998, Ptacek et al. 2001) and the similarities in using the pereiopods to pry open molluscan valves, one might hypothesize that the pereiopods in these two families would bear similar types of setae with similar functions.

While the present study and a few others have focused on external feeding mechanisms using *Scyllarides* spp.—*Scyllarides aequinoctialis* (Lund, 1793), *Scyllarides haanii* (De Haan, 1841), *Scyllarides nodifer* (Stimpson, 1866), *Scyllarides latus* (Latreille, 1803), *Scyllarides squammosus* (Milne-Edwards, 1837), and *Scyllarides tridacnophaga* Holthuis, 1967—as representatives of the family (Holthuis 1968, Lau 1987, 1988, Malcom 2003), only four species have been examined for feeding sequences: two *Thenus* species (Jones 1988) [*Thenus indicus* Leach, 1816 and *Thenus orientalis* (Lund, 1793)], *Parribacus antarcticus* (Lund, 1793), and *Arctides regalis* Holthuis, 1963 (Lau 1988). Despite some similarities in methods used to open food items, care should be taken before overgeneralizing to other scyllarid species, especially since species within the four subfamilies differ greatly in body size and also in food preferences, with some appearing to be invertebrate generalists, while others are molluscan specialists (Lavalli et al. 2007). Furthermore, some fundamental differences exist in the structure of the mouthparts of genera among different subfamilies: the Arctidinae (*Arctides* and *Scyllarides*) and Ibacinae (*Evibacus*, *Ibacus*, and *Parribacus*) species possess multi-articulated flagella on their maxillipeds, whereas the Scyllarinae (*Acantharctus*, *Antarctus*, *Antipodarctus*, *Bathyarctus*, *Biarctus*, *Chelarctus*, *Crenarctus*, *Educartus*, *Galearctus*, *Gibbularctus*, *Petrarctus*, *Remiarctus*, *Scammarctus*, and *Scyllarus*) and Theninae (*Thenus*) species lack such a flagellum on their first and third maxillipeds, and bear only a single-segmented flagellum on their second maxilliped (Webber and Booth 2007). Ibacinae species have a mandibular palp of only two segments, but Arctidinae have a three-segmented mandibular palp (Webber and Booth 2007). There is also a fundamental difference that separates the Theninae from the other subfamilies—the fifth pereiopod of the female is achelate in *Thenus* sp., but is sub-chelate in genera within the other subfamilies (Jones 2007, Webber and Booth 2007). Thus, it is important to characterize the feeding behavior for specific genera within a subfamily and the present study spotlights the feeding sequence of *Scyllarides* (Arctidinae) species only.

The present study describes the morphology and distribution of setae on the pereiopods of the Spanish slipper lobster, *S. aequinoctialis*, the Mediterranean slipper lobster, *S. latus*, and the ridged slipper lobster, *S. nodifer*, to understand the functional basis for the differences in feeding behavior observed among lobster families. The objectives of our study were to use a combination of Watling's (1989) and Garm's (2004) classification systems to: (1) identify the setal structures on all five pairs of pereiopods of the three species of slipper lobsters, (2) determine and compare the distribution patterns of the setae on each segment of each leg for each species, (3) compare the setal distributional patterns of scyllarid lobsters with those of nephropid and palinurid lobsters, and (4) discuss the possible function of the setae of the pereiopods with regards to setal distribution on the segments comprising each perieopod. In addition, behavioral observations of the movements of these leg appendages, as well as the movements of antennules and mouthparts, during feeding sequences for both *S. aequinoctialis* and *S. latus* aim to provide additional empirical information of how specific setae on the pereiopods may be important for food analysis. Because chemical signals are a driving force in the marine environment where visual signals are often obscured, descriptions of both setal types on appendages used while feeding and movements of those appendages during feeding can be useful for suggesting the possible chemosensory or mechanosensory functions of the setae and can lead to a better understanding of how these species use and manipulate their environment (Atema 1985, 2018).

Methods

Specimen Collection

Scyllarides aequinoctialis and *S. nodifer* ranging from 48 to 75 mm in carapace length (CL, measured from back of eyestalk to end of carapace using calipers) were obtained from local fishers or collectors and purchased from the Keys Marine Laboratory in Long Key, Florida. These two species are sympatric throughout part of their ranges and are found in the western Atlantic Ocean from South Carolina, USA, through the Gulf of Mexico; *S. aequinoctialis* is also found in the Caribbean Sea and in the western Atlantic Ocean to southern Brazil (Holthuis 1991). *Scyllarides aequinoctialis* tends to have a greater depth distribution (1–180 m) and prefers to shelter in complex coral outcroppings, whereas *S. nodifer* occurs at depths of up to 42 m and is less specific about the substrates in which it is found, possibly even preferring soft sediments (Sharp et al. 2007). Both species were housed in a 200-L aquarium at room temperature (approximately 22.2 °C) that contained recirculating, filtered, artificial seawater (Instant Ocean®) at approximately 35 salinity.

Pereiopod (P) samples were obtained from dead specimens of *S. aequinoctialis* and *S. nodifer*. Twelve pereiopods (a right and left sample of P.1 through P.5, including male and female samples of the P.5) were removed with scissors at the proximal end of the ischial segment, rinsed with distilled water, and stored in 100% acetone in glass vials for later wet viewing. The specimens were sonicated six times at 30-s intervals for a total of 3 min to remove debris prior to viewing.

Scyllarides latus ranging in size from 70 to 96 mm CL were caught off the coast of Haifa, Israel, by local fishers. This species is found mainly on hard, complex substrates at depths of 4–100 m in the Mediterranean Sea and eastern Atlantic Ocean from the coast of Portugal to Senegal, Madeira, the Azores, the Selvagens, and Cape Verde Islands (Holthuis 1991). Pereiopods of this species were removed by local fishers at the proximal end of the ischial segment and placed in filtered seawater. The pereiopods were then rinsed in deionized water and treated with fungicide/bactericide for 2–3 d. Pereiopods were fixed in 3% gluteraldehyde and 0.05-M cacodylate buffer (pH 7.2) for a minimum of 1 wk. After fixation, the specimens were washed three times in 0.5-M sodium cacodylate buffer for 15 min. Samples were sonicated six times at 30-s intervals for a total of 3 min and dehydrated in a sequential ethanol series of 10%, 20%, 30%, 40%, 50%, and 70% each for 15 min. Pereiopods were then shipped to Texas State University in San Marcos, Texas, by personnel at the University of Haifa in Mount Carmel, Haifa, Israel. The remainder of the dehydration sequence (to 85%, 95%, and 100% ethanol, followed by three washes of 100% acetone) was conducted at Texas State University.

Microscopy

Prior to SEM analysis, pereiopods (including a male and female sample of the P.5) of *S. latus* were drawn and photographed using a Sony MAVICA digital camera (Model MVCFD91) for mapping purposes. Pereiopod specimens of *S. latus* were critical point dried with CO_2 using a DCP-1 Critical Point Dryer (Denton Vacuum, Inc.) and then sputter-coated in a Denton Vacuum Sputter Coater at 30-s intervals for a total of 3 min of coating. Each pereiopod was then viewed using a Cambridge S90B Scanning Electron Microscope at an accelerating voltage of 15 kV. Scanning electron micrographs of setae were taken from each of the five major segments (dactyl, propus, carpus, merus, and ischium) of each pereiopod, and locations were marked on the previously made pereiopod maps. Two additional specimens were examined as wet mounts without critical point drying or sputter coating on an environmental scanning electron microscope (ESEM) (Enviroscan with Evex EDS) at an accelerating voltage of 15 kV.

Digital images were also taken of each of the five pairs of pereiopods of *S. aequinoctialis* and *S. nodifer* (including a male and female sample of the P.5) that were stored in 100% acetone without dehydration and rendered into maps using the Sony MAVICA digital camera (Model MVCFD91). Environmental scanning electron micrographs of setae were taken from each of the five major segments (dactyl, propus, carpus, merus and ischium) of each pereiopod, and locations were marked on the previously made pereiopod maps. Three samples of the pereiopods for each species were then viewed on a Philips XL30 ESEM with EDAX Detector at an accelerating voltage of 10 kV.

Behavioral Observations

Live lobsters of both sexes (*S. aequinoctialis*, 48–75 mm CL, *n* = 15; *S. nodifer*, 48–7 mm CL, *n* = 7) were purchased from Florida Keys Marine Laboratory, Layton, Long Key. A number, using nontoxic paint, or a colored rubber band code, was assigned to each lobster for easy identification and was placed on or around the modified, flattened second antennae. All lobsters were placed individually in a 200-L aquarium with a bare (glass) bottom to allow filming from below. Live specimens of *S. latus* (81–108 mm CL, *n* = 8) were obtained in one of two ways: (1) by divers from just outside the Achziv Marine Reserve in northern Israel at depths ranging from 5 to 10 m, or (2) purchased live at a nearby local fish market. All *S. latus* specimens were transported in coolers to the University of Haifa Marine Lab and kept in two large holding aquaria (100 L) that were equipped with filtration systems, aeration, and held at ambient water temperature and lighting regimes.

After acclimatization to the tank (a minimum of 24 hrs), *S. aequinoctialis* and *S. nodifer* lobsters were provided a choice of prey by setting bivalves (mussel, oysters, and clams) at the bottom of the tank. Feeding behaviors were recorded using a digital video recorder (SONY DCR TRV-9). Trials ended either when the lobster finished eating, or after 1 hr if no feeding behavior was observed. Because no *S. nodifer* lobsters actually completed a full feeding sequence, only data from *S. aequinoctialis* were used for analysis. Video footage was analyzed using the Noldus Observer program, v4.0 (Noldus Information Technology, Wageningen, The Netherlands). An ethogram was also generated describing the types of behaviors observed. The duration of behaviors within a behavioral category (investigative, manipulative, consumptive, grooming, rejection) was initially examined to determine if it followed a normal distribution; durations of behavioral categories were then compared by 2-tailed, paired *t*-tests via SPSS v13.0 (LEAD Technologies, Inc.). Transitional probabilities from one behavioral category to another were determined to examine the temporal structure of feeding sequences. The independence of the transitional probabilities of the behavioral categories was tested with a Chi-square contingency table (Zar 1999).

Feeding behavior on gastropods (limpets) was videotaped for *S. latus* in individual aquaria tanks (40 L) and recorded using an infrared CCD camera (Super Circuits model PC1771RHR08) digitized to a converter using video capture software (Gawker v0.8.4). A goodness-of-fit test (*G*-test) was used to assess manipulation and consumption of limpets over a 30-min timeframe. We also determined the maximum size limpet that lobsters of different sizes were capable of prying and opening. We made morphometric measurements of each limpet (length, width, and height) using digital calipers and calculated their total surface area for comparisons.

Results

Pereiopod Morphology

In all lobsters, seven separate segments comprise each pereiopod and are, from the distal to the proximal end, the dactyl, propus, carpus, merus, ischium, basis, and coxa. Each segment has a lateral and medial edge, and a dorsal and ventral surface. Because the pereiopods are rotated and clasped around bivalves when shucking and scraping food for consumption, the ventral surfaces face the mouth region during feeding and, with the lateral edges, are more likely to come in direct contact with the food than the dorsal surfaces and medial edges.

Some segments bear ridges and grooves, which are rounded crestings of the dorsal surface that vary in length and location. The merus segment of P.1 to P.4 also develops an alate carina, which is an extension of the lateral edge of the merus. This carina extends from the proximal to distal ends of the merus and is visible both ventrally and dorsally, but with a concavity toward the ventral view. There is no carina on the medial edge of the merus in any view.

Description of Setal Types Found on the Pereiopods

Following Thomas's (1974) terminology for decapod setae as modified by Factor (1981) and Factor and Lavalli (1992), only five types of setae were found on the pereiopods of *S. aequinoctialis, S. latus,* and *S. nodifer:* cuspidate (H_1), conate/hamate (J), simple (I), miniature simple (I_m), and teazel (T), which Garm and Watling (2013) would categorize as "composite." In several of these types, there are variants that are designated by a letter and a number (Fig. 1), and each type may also be considered a variant of a broad category in which it is placed per Watling (1989) and Garm (2004). Of these types, the greatest variation in length occurred in the cuspidate setae, whereas other setae tended to occur only within one length class (small, medium, or long) (Table 1). Setae were arranged in uneven rows over all surfaces of the

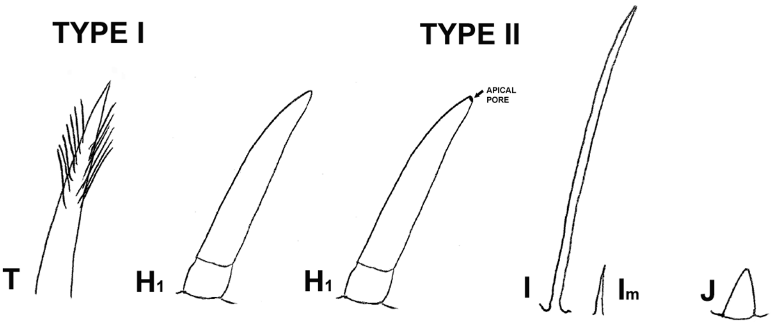


Figure 1. Different setal types. Type I setae, annulate with setules: (T) teasel or hooded, aka "composite" via Garm and Watling (2013). Type II setae without setules: (H_1) cuspidate setae; (I, I_m) simple setae, normal or miniature; (J) conate/hamate (or form of cuspidate as per Garm 2004 and Garm and Watling 2013). H_1, I, J redrawn from Watling 1989; T, I_m from present study.

pereiopods. Only the distal tip or "nail" of the dactyl, a dark brown colored area on both ventral and dorsal surfaces, was devoid of setae. Unless otherwise stated, all descriptions of setal types apply to all three species examined.

Table 1. Setal types found on the pereiopods of three scyllarid lobsters (*Scyllarides latus, Scyllarides nodifer, Scyllarides aequinoctialis*).

Setal type	Segment location	Found on	Size variation	Species found on
Cuspidate	All five segments	P.1–P.5 (both male and female P.5)	Short, medium, long	*S. latus, S. nodifer, S. aequinoctialis*
Simple	Dactyl	P.1–P.5 (both male and female P.5)	Long	*S. latus, S. nodifer, S. aequinoctialis*
Conate	Lateral edge of alate carina of merus	P.1–P.4	Short	*S. latus, S. nodifer*
Miniature	All five segments	P.1–P.5 (both male and female P.5)	Extremely microscopic, approximately 20 µm	*S. latus, S. nodifer, S. aequinoctialis*
Teazel	Lateral edge of alate carina of merus	P.1–P.4	Long	*S. aequinoctialis*
Hooded	Dorsal surface of alate carina of merus (rare)	P.1–P.4	Long	*S. aequinoctialis*

Cuspidate Setae (Figs. 1 H_1, 2, 3, 4, 5).—Cuspidate setae are robust and conical in shape (Figs. 1–3), and range in length from long (Fig. 2A, B) to short (Fig. 2C, H, J); some are of medium length (Fig. 2D, E, G). All cuspidate setae found were smooth and lacked setules and annulations, although some had an apical pore (Fig. 2C). Each seta lay within an invaginated socket (Fig. 2A–H). Therefore, they fell within Watling's (1989) Type II category. In all species, short cuspidate setae (<150 µm) occurred on the ventral surface and toward the medial edge of the dorsal surface of the propus, carpus, merus, and ischium of all pereiopods examined (e.g., *see* Fig. 4B). They also occurred on both ventral and dorsal surfaces of the alate carina of the merus of P.1 to P.4. Medium length cuspidate setae (150–300 µm; Fig. 2D, E, G) occurred between the medial and lateral edges of the dorsal surface of the propus, carpus, merus, and ischium of all pereiopods. Short, medium, and long cuspidate setae

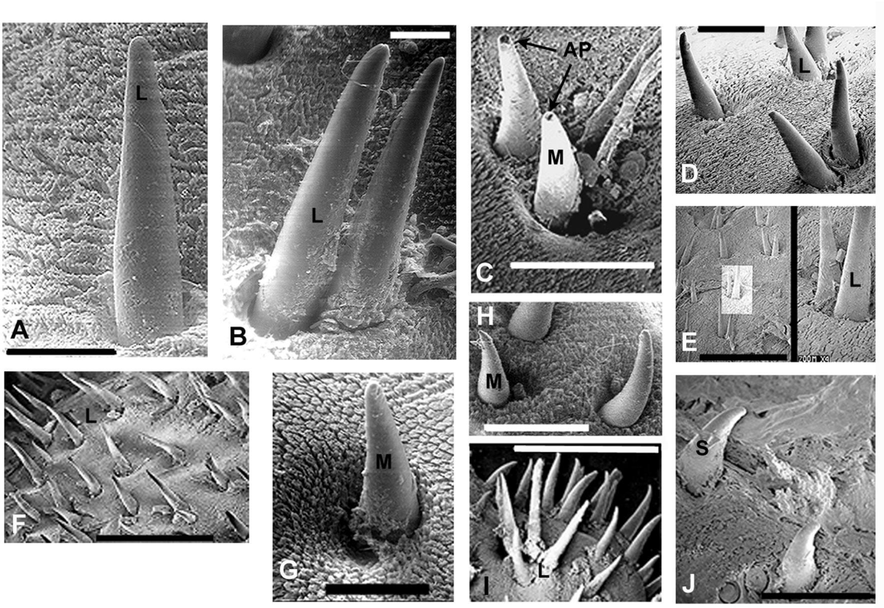


Figure 2. Long and medium cuspidate setae for all three species: (A) long setae on proximal end of left dactyl of P.2; (B) long paired setae on dorsal surface of merus of right P.1; (C) medium length setae with apical (terminal) pores (arrow) on ventral surface of merus of left P.1; (D) long setae of ventral surface of merus of female's left P.5; (E) paired long setae on dorsal surface of propus of left P.1; (F) long setae covering dorsal surface of right merus on female's P.5; (G) medium length setae on ventral surface of propus of right P.3; (H) medium length setae on dorsal surface of ischium of left P.4; (I) long setae on proximal end of dorsal surface of left merus of P.2; (J) short setae on alate carina of left P.1. Photos: B and G from *Scyllarides aequinoctialis*; C, D, E, F, I and J from *Scyllarides latus*; A and H from *Scyllarides nodifer*. Scale bars: A, B, C, D, H, J = 200 µm; E, F, I = 1 mm; G = 100 µm. Labels: L = long cuspidate setae; M = medium cuspidate setae; S = short cuspidate setae; AP = apical (terminal) pore.

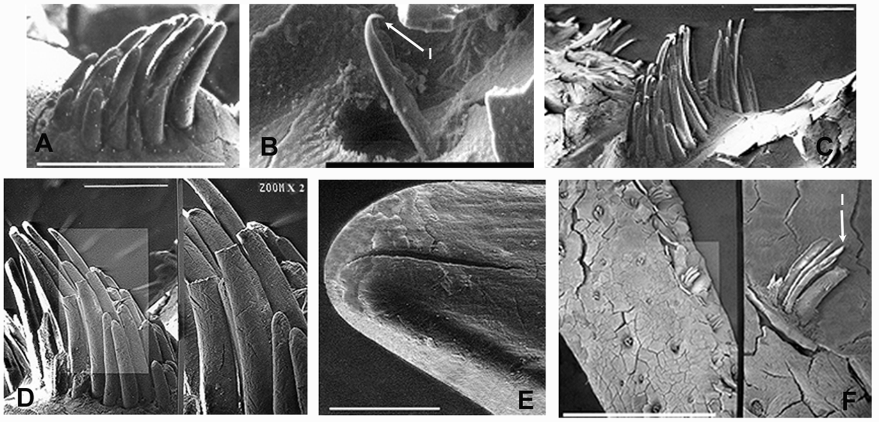


Figure 3. Dactyl tufts for all three species (A) Long cuspidate setal tuft on the dorsal surface of right P.3. (B) simple seta (H_1) on the ventral surface of left P.3. (C) two dactyl tufts of cuspidate setae on the ventral surface of right P.3. (D) large cuspidate tuft on the ventral surface of left P.3. (E) completely bare dactyl tip from ventral surface of left P.2. (F) Stripped dactyl pits and broken dactyl tufts of both cuspidate (H_1) and simple setae (I) on ventral surface of left P.2. Photos: E from *Scyllarides aequinoctialis*; B from *Scyllarides nodifer*; A, C, D, and F from *Scyllarides latus*. Scale bars: A, C = 1 mm; D = 100 µm; B, E = 200 µm; F = 2 mm.

were found within tufts on the dactyls of P.3 to P.5 (Fig. 3A, C, D, F). It is likely that they also occur in tufts on dactyls of P.1 to P.2, but in all specimens examined, the setae found within the invaginated pits of these tufts were broken and not identifiable. Long cuspidate setae (>300 µm; Fig. 2A, B, 3C, D) occurred in several locations: toward the lateral edge of the ventral and dorsal surface, and distally on the edge of the dorsal surface on the propus, merus, carpus, and ischium of all pereiopods (Fig. 4A–F); on the dorsal ridges of the propus, merus, carpus, and ischium on P.3 to P.5 (both male and female); and within the brush pad of the dactyl on P.5 of the female (Fig. 5A–D). In *S. aequinoctialis* only, they also occurred on the ventral and dorsal surface of the lateral rim of the alate carina of the merus of P.1 to P.4.

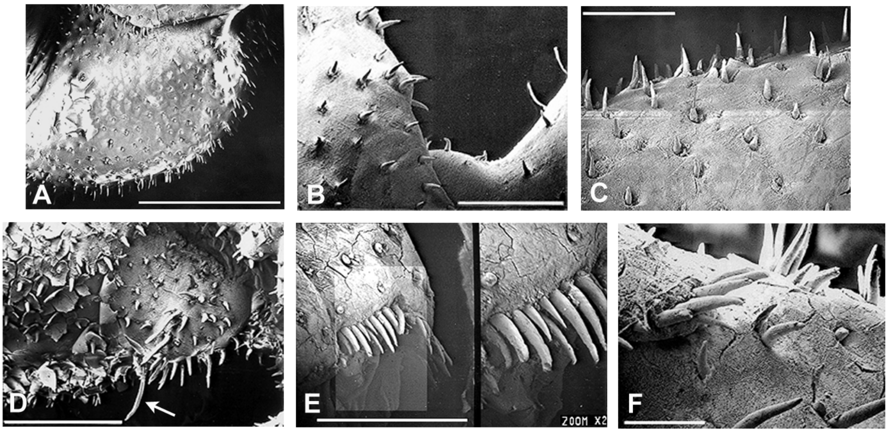


Figure 4. Cuspidate setal patterns on perieopod segmental surfaces: (A) ventral surface of carpus of left P.2 showing short setae on segmental surface and long setae on lateral edge; (B) long setae at distal end of dorsal surface of left carpus of male's P.5; (C) short setae on ventral surface of propus and long setae on lateral edge of left propus of P.2; (D) long setae on right lateral edge of dorsal surface of carpus with one extremely long (arrow) cuspidate seta (typical of this area) of P.2; (E) row of long setae at distal end of dorsal surface of right propus of P.1; (F) long setae at distal end of dorsal surface of left propus of P.3. Photos: A–F from *Scyllarides latus*. Scale bars: A = 5 mm; B, C = 1 mm; E, D = 2 mm; F = 500 µm.

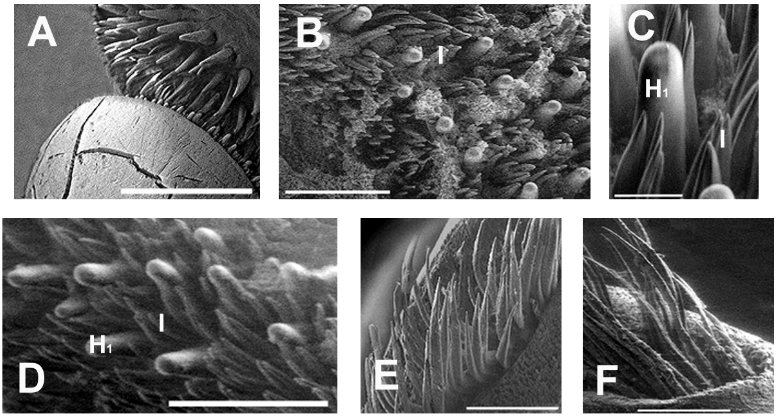


Figure 5. Brush pad of sub-chela of female's P.5: (A) brush pad of cuspidate (H_1) and simple (I) setae on ventral surfaces of articulating dactyl and propus; (B) long cuspidate (H_1) setae in rows with simple (I) setae interspersed on ventral surface of dactyl; (C) cuspidate (H_1) setae with simple (I) setae on ventral surface of dactyl; (D) magnified long cuspidate (H_1) and simple (I) setae of ventral surface of dactyl; (E) and (F) simple setae (I) set in a groove on ventral surface of propus that articulates with dactyl. Photos: A from *Scyllarides latus*; B, C and D from *Scyllarides aequinoctialis*; F and E from *Scyllarides nodifer*. Scale bars: A = 500 µm; B, D, E, F = 200 µm; C = 50 µm.

Conate (Hamate) Setae (Figs. 1 J, 6).—According to Garm (2004) and Garm and Watling (2013), conate setae are a category of cuspidate setae, but Watling (1989) distinguishes them from cuspidate setae because they are shorter and more robust, although they are still categorized as Type II setae. Using Watling's scheme here, conate setae are pyramidal in shape (Fig. 6A, C, D), bear no setules, and are very short in size (<125 µm). Each seta lies within an invagination (Fig. 6B–D) and occurs only as a single unit, not in pairs or tufts as do some cuspidate setae. Conate setae were found on ventral and dorsal surfaces of the lateral edge of the alate carina of the merus on P.1 to P.4 in *S. latus* (Fig. 6A–C) and *S. nodifer* (Fig. 6D) only. They were not found on any other segment, nor were they found on either the male or female P.5, which lacks the alate carina.

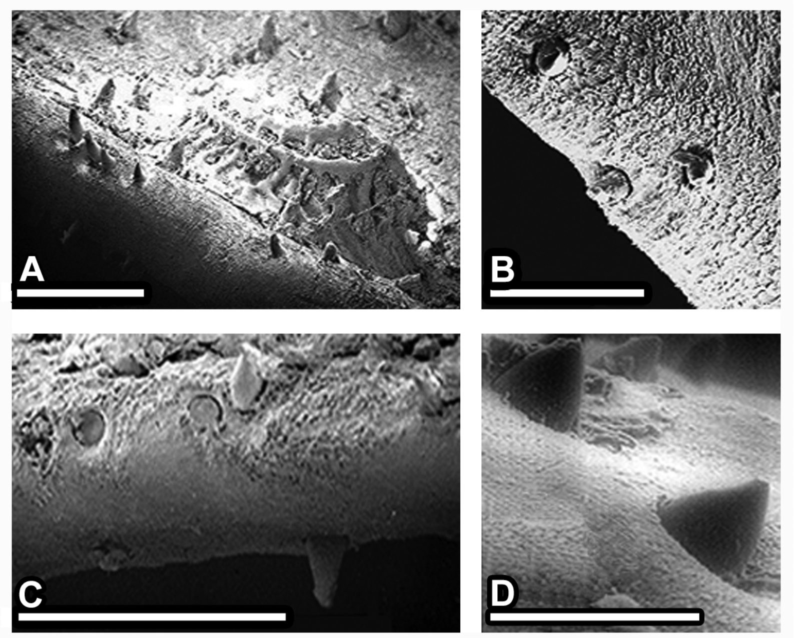


Figure 6. Conate setae (aka short cuspidate setae as per Garm (2004)) found on all three species: (A) dorsal alate carina of dorsal surface of right P.1 merus; (B) edge of alate carina of dorsal surface of right P.4 merus; (C) edge of alate carina of dorsal surface of left P.1 merus; (D) magnified conate setae of P.3. Photos: A, B, C from *Scyllarides latus*; D from *Scyllarides nodifer.* Scale bars: A, C = 500 µm; B = 200 µm; D = 250 µm.

Simple Setae (Figs. 1 I, 3, 5).—Simple setae lack setules, are slender but generally conical in shape, and taper towards the distal tip (Figs. 3B, 5C, E, F) or end bluntly (Fig. 3F) (Watling 1989). All simple setae observed on the pereiopods were long and of similar length to the long cuspidate setae (>300 µm). They appeared singly (Fig. 3B) or in association with cuspidate setae (Figs. 3F, 5B, C, D) on the dorsal and ventral surfaces of the dactyl of all pereiopods of all species examined, and as clumps (Fig. 5E, F) or interspersed among cuspidate setae (Fig. 5A–D) in the brush pads on the ventral surface of the dactyl and propus of P.5 of female *S. aequinoctialis* and *S. nodifer.* No simple setae were found in the brush pads of female *S. latus.* All simple setae fell into Watling's (1989) Type II classifications.

Miniature Simple Setae (Figs. 1 I_m, 7).—On all species examined, the cuticular surface of each pereiopod was covered with a layer of extremely short simple setae that, at a distance, provide a texturing look to the surface of these appendages (Fig. 7A, B, F–H). Each seta is a distinct unit (Fig. 7C, D), although in some cases, the seta appeared more similar in form to setules seen on the shaft of setal types of other decapods (e.g., compare Fig. 7E, F with figures in Garm 2004). Due to the extremely small size of these setae, they are referred to here as "miniature simple setae," and are probably a homologue to simple setae. These miniature setae may result in the fuzzy appearance of some species of slipper lobsters, often referred to as "pubescence" by many authors (e.g., *see* Holthuis 1991, 2002).

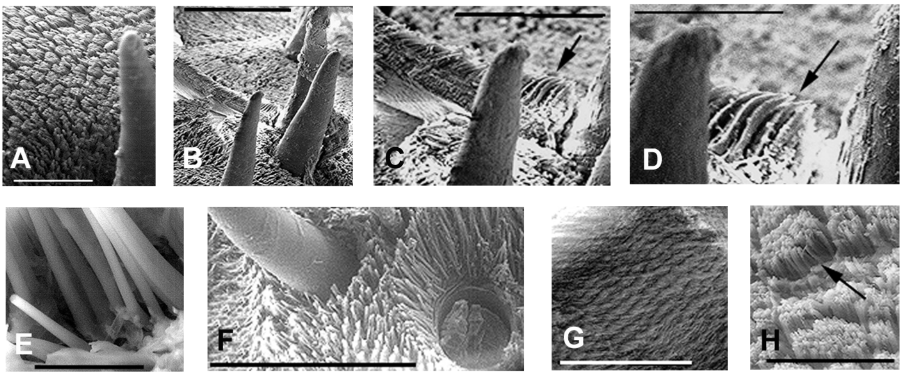


Figure 7. Miniature simple setae covering the entire surface of pereiopods of all three species: (A) surrounding cuspidate setae on ventral surface of left merus P.1; (B) rows on the dorsal surface of left propus of P.3; (C) close-up of dorsal surface of left propus of P.3 showing texturing; (D) magnification of individual setae on dorsal surface of left propus of P.3; (E) magnification of individual setae at distal end of dorsal surface of right carpus of P.1; (F) setae surrounding cuspidate setae at proximal edge of left propus of P.4; (G) setal patterning from proximal end of ventral surface of right dactyl of P.4, but found on entire ventral surface; (H) setal mat from ventral surface of left ischium of male's P.5. Photos: A, G, and H from *Scyllarides nodifer*; B, C and D from *S. latus*; E and F from *Scyllarides aequinoctialis*. Scale bars: D, E = 350 µm; C, G, H = 100 µm; A, B = 200 µm; F = 20 µm. Arrows indicate representative miniature setae.

Teazel Setae and Other, aka Composite, as per Garm and Watling (2013) (Figs. 1 T, 8A–D).—Teazel setae, described first by Thomas (1970), have a smooth rounded tip and denticulations or setules on the shaft that are elongate and needle-like. The setae found in the present study are probably a homologue to the teazel setae described by Thomas (1970), in that their tip is smooth and devoid of setules (Fig. 8A) and extends approximately 50 µm before elongate setules (about 50 µm in length) emerge from the shaft on all sides (Fig. 8A, B). The setules cover approximately one-quarter to one-third of the distal portion of the shaft. The rest of the shaft (about 500 µm in length) below the setules is bare (Fig. 8C). All teazel-like setae observed were set within invaginations and occurred singly, not in pairs. They did not fit into any of the schemes presented by Watling (1989) or Garm (2004), but do fit into the "composite" scheme presented by Garm and Watling (2013). They were arranged in rows on the dorsal and ventral surface of the lateral edge of the alate carina in *S. aequinoctialis*. These setae were not found on either *S. latus* or *S. nodifer*. Additionally, setae similar in form to hooded sensilla described by Cate and Derby (2002) were found on the dorsal right surface of the alate carina of *S. aequinoctialis* (Fig. 8D).

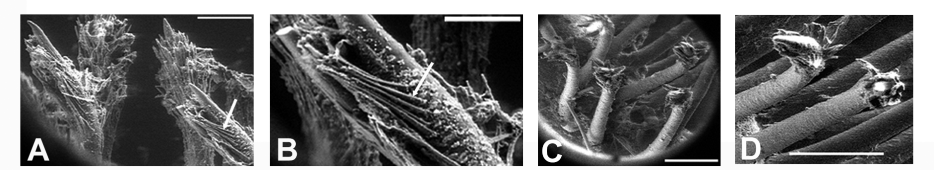


Figure 8. Setal types found on edge of the lateral alate carina of merus of P.1 - P.4 on *S. aequinoctialis* only. (A) teazel setae with setules (arrow) in rows on dorsal surface of left alate carina of P.1; (B) setules (arrow) of hooded-like setae; (C) top view of hooded-like setae on dorsal surface of right alate carina of P.3 showing distal tip without setules surrounded by setules proximally; (D) enlarged view of distal tip of hooded-like setae surrounded by more proximal setules on dorsal surface of right alate carina of P.3. Scale bars: A = 100 μm; B = 20 μm; C = 200 μm; D = 250 μm.

SETAL DISTRIBUTION PATTERNS ON THE PEREIOPOD SEGMENTS

Maps of the pereiopods were produced from photographs for all species; however, because there were no substantive differences in the overall shape and structure among species, the maps presented in Figures 9 and 11–15 represent an amalgamation of all three species (*S. aequinoctialis*, *S. latus*, and *S. nodifer*). The first four pereiopods of all scyllarids in the present study are non-chelate (Figs. 9, 11–13). In the male of all species, the fifth pereiopod is also non-chelate (Fig. 14); however, in the female, it is sub-chelate, with the distal ends of the dactyl and propus forming the claw (Fig. 15). In all species, right and left pereiopods are symmetrical with regards to shape and structure. Unless otherwise stated, descriptions of setal distribution are common to each of the three species studied.

First Pereiopod, P.1 (Fig. 9).—P.1 is the most prominent of the legs and bears no ridges along its lateral or medial edges. Its segments are both thick and wide, but are not particularly long. The dactyl is rather thick and wedge-like or blunt, with the distal tip or “nail” being darker in coloration. All three species exhibit the same setal distribution pattern for each segment of P.1, with the exception of the merus, which has a similar pattern in *S. latus* and *S. nodifer*, but differs in *S. aequinoctialis*. In all specimens examined, the dactyl had evidence of broken setae, in the form of both open invaginations and invaginations with shaft tissue. The invaginations were larger toward the proximal end of the dactyl on both ventral and dorsal surfaces, suggestive of larger setal bases. In Figure 9, these invaginations are represented by small black circles and are termed stripped “dactyl setal pits” (e.g, *see* Fig. 3F). The propus, carpus, and ischium bear single or paired cuspidate setae that are of medium length; these are arranged in rows on the segmental surfaces. The length of these cuspidate setae increases toward the lateral edge and distal end of the dorsal surface and decreases on the ventral surface and along the medial edge of the dorsal surface. The merus also has rows of single or paired medium-length cuspidate setae. These setae increase in length toward the lateral edge and distal end of the dorsal surface and decrease in length on the ventral surface and medial edge of the dorsal surface. The only exception to this setal distribution pattern is on the alate carina of the merus, which is a flattened, wing-like process along the lateral edge that curves slightly toward the dorsal surface. It is visible from both ventral and dorsal surfaces. The lateral edge of the alate carina of the merus of *S. aequinoctialis* can vary within a species and bears either rows of teazel (Fig. 10A) or long cuspidate setae (Fig. 10B), but not both types simultaneously in an individual, and these extend from the proximal to the distal end of the edge (Figs. 9, 10). In contrast, the alata carina of *S. nodifer* (Fig. 10C) and *S. latus* (Fig. 6A–C, 10C) bears only conate setae along the corresponding edge. All surfaces of the P.1 are covered with miniature simple setae that give the appendage a fine pubescence.

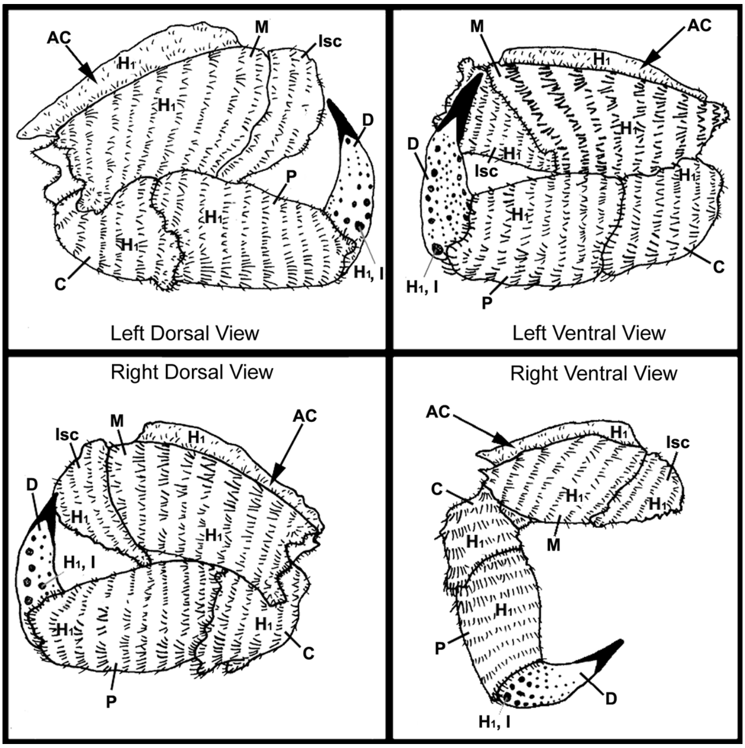


Figure 9. *Scyllarides* spp. P.1 showing left and right ventral and dorsal surfaces. D – dactyl, P – propus, C = carpus, M = merus, Isc = ischium, AC = alate carina, H_1 = cuspidate setae, and I = simple setae.

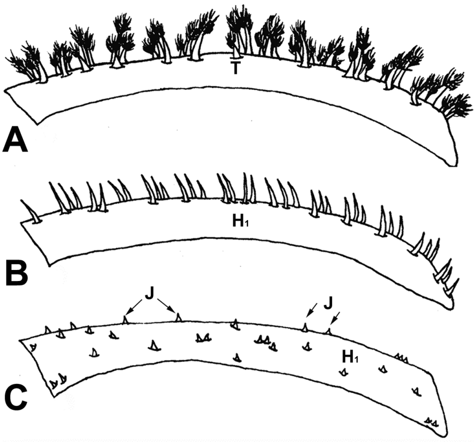


Figure 10. Alate carina of merus with setae on lateral edge; (A) T = teazel setae on *Scyllarides aequinoctialis*; (B) H_1 = long cuspidate setae on *S. aequinoctialis*; (C) H_1 = short cuspidate setae and J = conate setae on *Scyllarides latus* and *Scyllarides nodifer*.

Second Pereiopod, P.2 (Fig. 11).—P.2 is the longest and narrowest of the five pairs of legs. As with P.1, no segment bears any ridges. The dactyl of P.2 is longer and slimmer than that of any other pereiopod with the "nail" being darker in coloration and bare of setae (Figs. 3E, 11). As with P.1, the dactyl shows stripped pits (represented as black circles) where setae were once found. All three species exhibit the same setal distribution patterns for the segments of P.2 that were found for P.1.

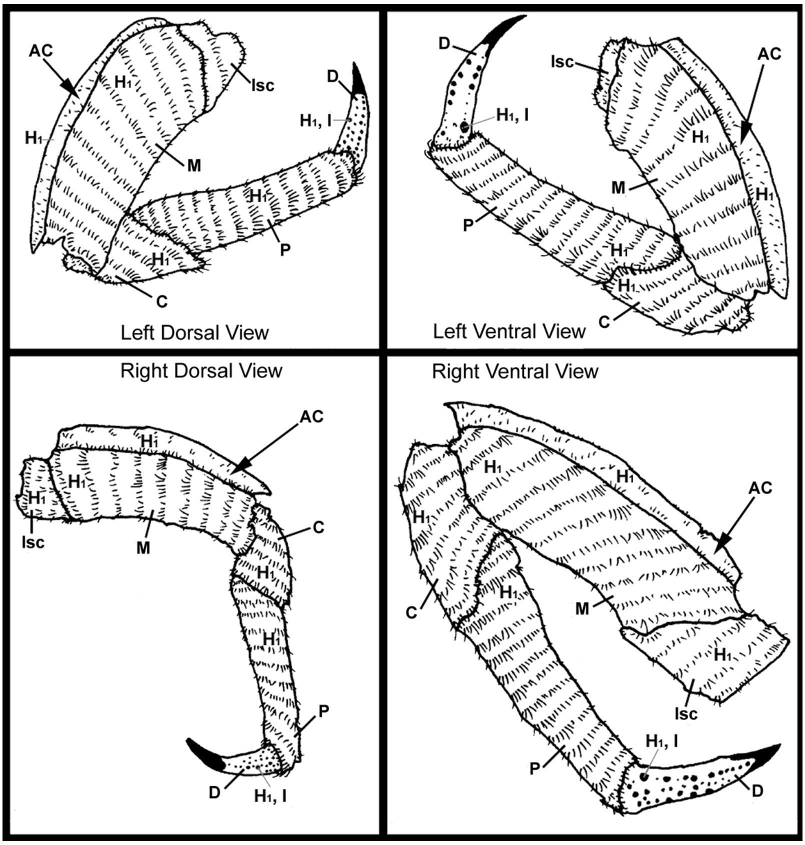


Figure 11. *Scyllarides* spp. P.2 showing left and right ventral and dorsal surfaces. D = dactyl, P = propus, C = carpus, M = merus, Isc = ischium, AC = alate carina, H_1 = cuspidate setae, and I = simple setae.

Third Pereiopod, P.3 (Fig. 12).—P.3 is shorter in length than P.2, but is greater in width. The dactyl is short and blunt, with a dark colored "nail." P.3 bears two grooves, each with an associated ridge on the longitudinal axis of the dorsal surface: (1) midsagittally on the propus, stretching from the distal end to most of the length of the segment; and (2) parasagittally from the proximal end to the midpoint of the carpus (Fig. 12 left and right dorsal views). All three species exhibit similar setal distribution patterns for P.3, but with several notable exceptions. The dactyl bears two large tufts ("dt" in Fig. 12 left and right ventral views) of long cuspidate and simple setae near the proximal end of the ventral surface (Fig. 3A, C, D). Toward the distal end of the dactyl are smaller tufts of long cuspidate and simple setae arranged in rows on both ventral and dorsal surfaces (Fig. 3C). The propus and carpus have single or paired cuspidate setae, arranged in rows, that are: (1) of medium length on the dorsal surface, becoming longer towards the lateral edge; (2) long on the dorsal ridges of both segments; (3) long at the distal end of the dorsal surface; and (4) short on the ventral surface and along the medial edge of the dorsal surface. The merus also bears single or paired cuspidate setae that are of medium length on the dorsal surface, short on the medial edge, but longer toward the lateral edge and distal end, and arranged in rows. On the ventral surface of the merus, the cuspidate setae are short. The only exception to this distribution pattern is found on the alate carina of the merus. The lateral edge of this carina in *S. aequinoctialis* bears either rows of teazel or long cuspidate setae (Fig. 10A, B) stretching from the proximal to the distal end, but in *S. nodifer* and *S. latus* (Fig. 10C), it bears only conate setae along its edge. The ischium bears rows of cuspidate setae of medium length on the dorsal surface of the segment (Fig. 12 left and right dorsal views). Within the rows, the setae are found singly or in pairs, and gradually increase in length toward the lateral edge and distal end of the ischium. Cuspidate setae are also present on the ventral surface and medial edge of the dorsal surface of the ischium (Fig. 12 left dorsal and right ventral views), but are shorter in length.

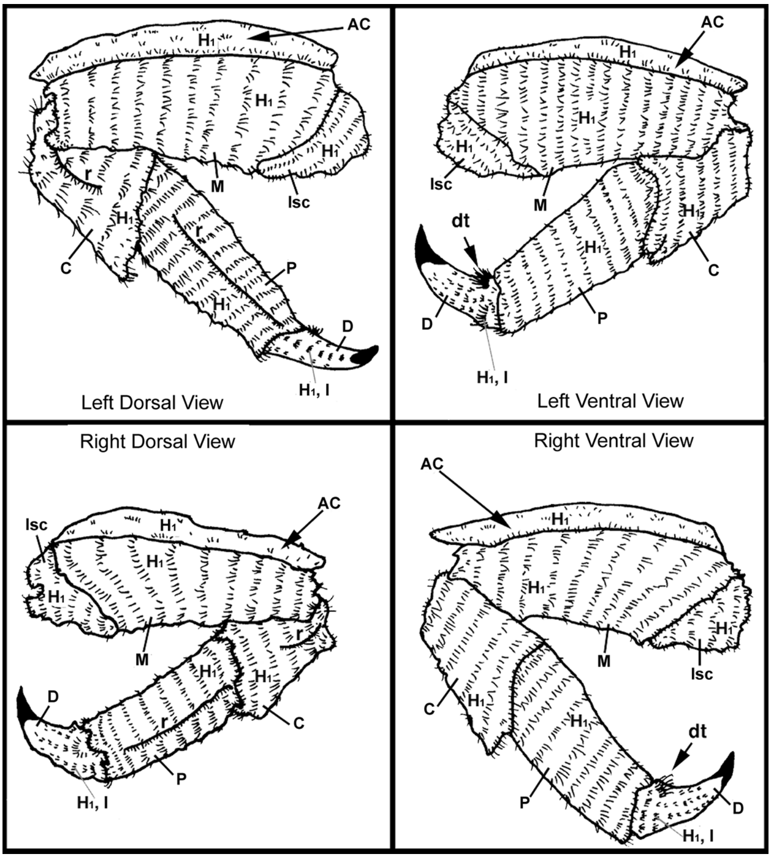
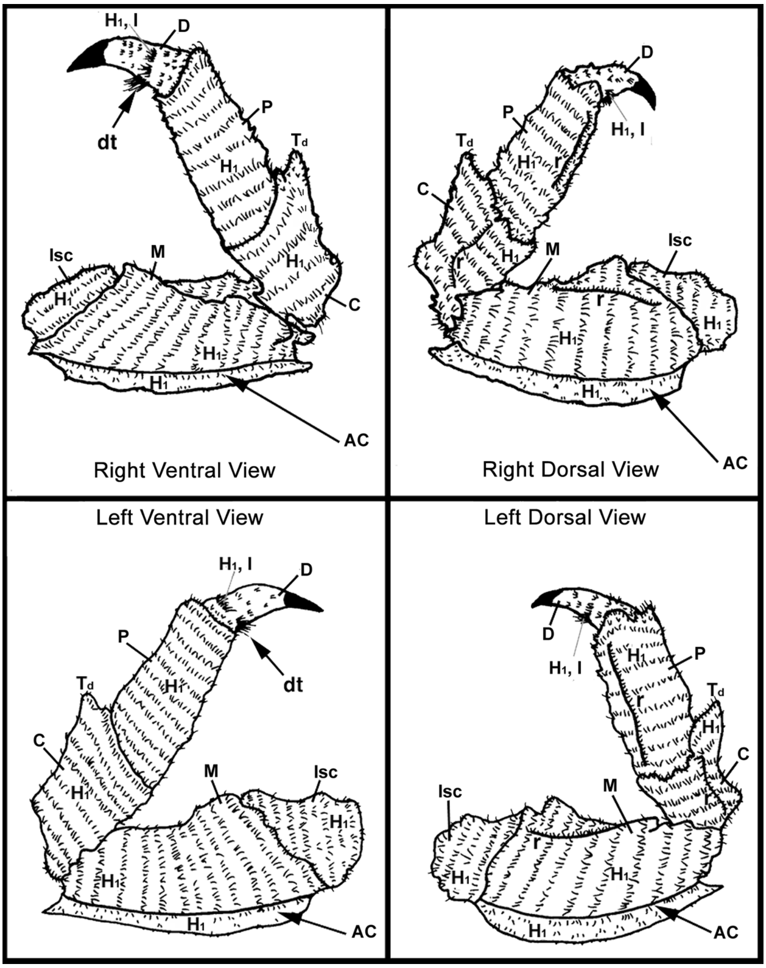


Figure 12. *Scyllarides* spp. P.3 showing left and right ventral and dorsal surfaces. D = dactyl, P = propus, C = carpus, M = merus, Isc = ischium, AC = alate carina, dt = dactyl tuft, r = ridge, H_1 = cuspidate setae, and I = simple setae.

Fourth Pereiopod, P.4 (Fig. 13).—P.4 is smaller in size than P.3. As with P.3, P.4 bears two grooves each with associated ridges on the longitudinal dorsal surface: (1) parasagittally near the medial edge of the propus that extends from the distal end to a point just past midway of the length of the segment, and (2) parasagittally towards the lateral edge of the carpus that extends from the distal end most of the length of the segment (Fig. 13 right and left dorsal views). In contrast to the same grooves and ridges found on P.3, these structures are more pronounced on P.4 and differ in their locations. A third groove and ridge is found on the medial edge of the dorsal surface of the merus, and extends about midway up the segment from the proximal end (Fig. 13 right and left dorsal views). Long cuspidate setae are found singly or in pairs, with a row like arrangement, on a third ridge formed on the medial edge of the dorsal surface of the merus (Fig. 13 right and left dorsal views). The carpus has a lateral extension that forms a tooth-like structure at the distal end (“T_d” in Fig. 13) such that it projects over the lateral edge of the proximal end of the propus. All three species exhibit the same setal distribution patterns on P.4 as those found on P.3.



Right Ventral View

Right Dorsal View

Left Ventral View

Left Dorsal View

Figure 13. *Scyllarides* spp. P.4 showing left and right ventral and dorsal surfaces. D = dactyl, P = propus, C = carpus, M = merus, Isc = ischium, AC = alate carina, r = ridge, T_d = distal tooth, H_1 = cuspidate setae, and I = simple setae.

Fifth Pereiopod, Male, P.5M (Fig. 14).—P.5M is the smallest of all the pereiopods and non-chelate. It bears three ridges on the longitudinal axis of its dorsal surface: (1) parasagittally near the lateral edge of the propus extending most of the length of the segment; (2) toward the lateral edge of the carpus extending proximally towards the distal end; and (3) parasagittally near the medial edge of the merus (Fig. 14 right and left dorsal views). These ridges are more pronounced than in P.4 and differ in their locations. Two new ridges appear on the dorsal surface: (1) a parasagittal ridge on the lateral edge of the merus, extending from the proximal to distal end; and (2) a parasagittal ridge on the medial edge of the ischium near its distal end (Fig. 14 right and left dorsal views). All three species exhibit the same setal distribution patterns for P.5M. The dactyl bears two large tufts of long cuspidate and simple setae on its ventral surface, near the proximal end (Fig. 14 right and left ventral views). Smaller tufts of long cuspidate and simple setae, arranged in rows from the proximal to distal

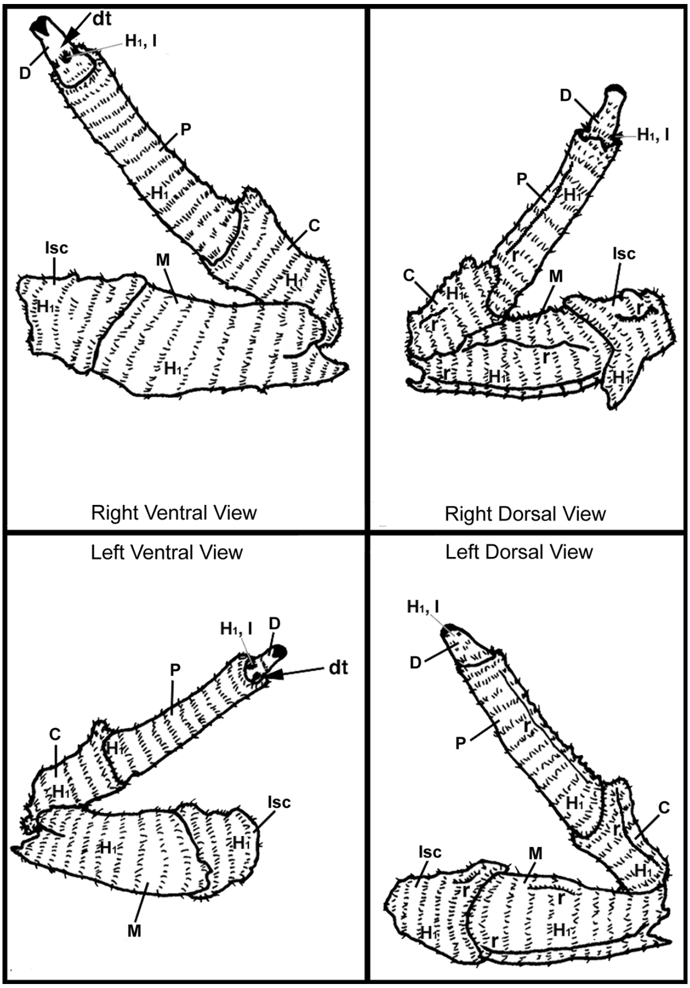


Figure 14. *Scyllarides* spp. P.5 of male showing left and right ventral and dorsal views. D = dactyl, P = propus, C = carpus, M = merus, Isc = ischium, r = ridge, H_1 = cuspidate setae, and I = simple setae.

end, are present on both ventral and dorsal surfaces. The propus and carpus bear single or paired units of cuspidate setae arranged in rows that are: (1) of medium length on the segmental surfaces, but longer toward the lateral edge of the dorsal surface only; (2) long on the dorsal ridges of both the propus and carpus; (3) long at the distal ends of the dorsal surface of the segments (Fig. 5B); and (4) short on the ventral surface and along the medial edge of the dorsal surface. The merus also bears single or paired medium length cuspidate setae in rows on the segmental surfaces. These setae become longer toward the lateral edge and distal end of the dorsal surface and shorter on the ventral surface and medial edge of the dorsal surface. In all species, the prominent alate carina of the merus of the P.1 to P.4 is reduced to a slight ridge that bears, from the proximal to distal end of the segment, only medium length cuspidate setae (Fig. 14 right and left dorsal views). The ischium also bears single or paired medium length cuspidate setae arranged in rows on the segmental surfaces. These setae become longer toward the lateral edge and distal end of the dorsal surface and shorter on the ventral surface and medial edge.

Fifth Pereiopod, Female, P.5F (Fig. 15).—P.5 in the female is slightly larger than that of the male. The distal tip of the dactyl articulates with the distal tip of the propus forming a sub-chela (Figs. 5A, 15 left and right ventral views). The ridges of the dorsal surface are identical to those of P.5M, and, as in the male, the right and left pereiopods are symmetrical with regard to shape and structure. However, the dactyl

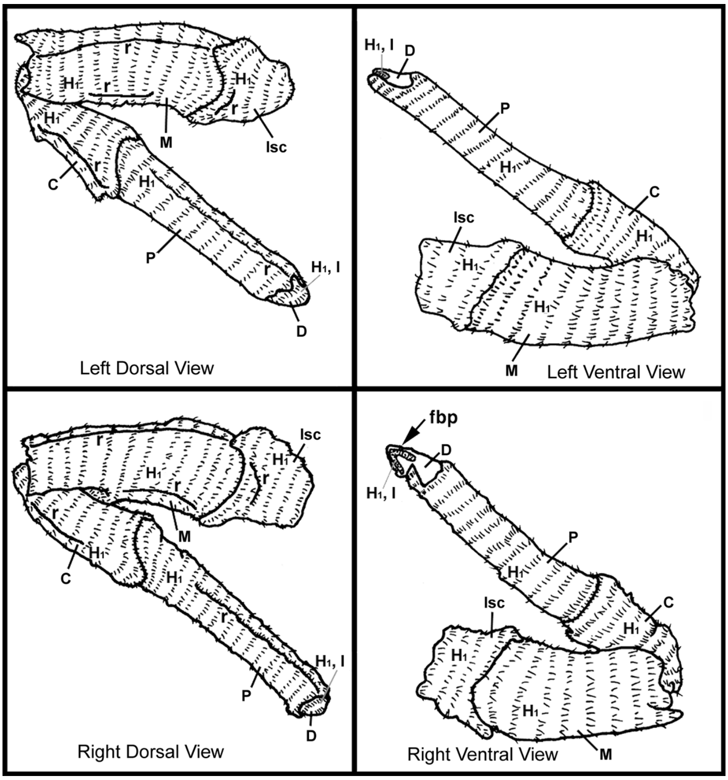


Figure 15. *Scyllarides* spp. P.5 of female showing left and right ventral and dorsal surfaces. D = dactyl, P = propus, C = carpus, M = merus, Isc = ischium, r = ridge, fbp = female brush, H_1 = cuspidate setae, and I = simple setae.

no longer bears large tufts of setae as seen in P.3, P.4, and P.5M (Fig. 15 left and right dorsal views). The ventral surface of the distal tips of the dactyl and propus bears a brush pad, set in a groove (labeled "fbp" in Fig. 15 left and right ventral views). This "brush pad" is composed of rows of long cuspidate and simple setae for *S. nodifer* and *S. aequinoctialis* (Fig. 5B–D), but only long cuspidate setae in *S. latus* (Fig. 5A). Towards the proximal end of the groove in which this pad lies, only simple setae are present in *S. nodifer* and *S. aequinoctialis* (Fig. 5E, F). The setal distribution pattern for the propus, carpus, merus, and ischium are the same as in P.5M.

BEHAVIORAL OBSERVATIONS

In *S. aequinoctialis*, the behavioral sequence involved in manipulating, prying open, and consuming bivalves and gastropods is quite complex and can be divided into several broad categories (investigative, manipulative, consumptive, grooming, and ingestion or rejection), each of which can be further divided into more precise movements; these categories and their subdivisions are described in Table 2. Behaviors occurred in bouts and rarely lasted >60 s in duration (Fig. 16) with the exception of probing bivalves with mouthparts, cutting of the adductor muscles to open the valves, and exopodite fanning (Fig. 17). The duration of each behavioral

Table 2. Description of the individual behaviors making up behavioral categories. *See* Figure 17 for durations.

Behavior	Display code	Description
Investigative		
Walking	WLK	Approaching the food while locomoting
Flicking	FL	A rapid up-down movement of the antennular flagellum
Leg wave	LW	Waving of the legs back and forth in the water column
Ant probe	AP	Touching and/or inserting the antennules into various locations of the aperture of the bivalve
Manipulative		
Leg spread	LS	Spreading and flattening of the pereiopods to maintain balance
Body tilt	BT	Tilting the body away from the bivalve to brace the body
Leg grasp	LG	Holding the bivalve with multiple pereiopods
Turning	TN	Flipping and turning the bivalve to reposition it
Leg probe	LPB	Probing by inserting the dactyl "nails" into the aperture of the bivalve
MP probe	MPB	Inserting the 3rd or 2nd maxillipeds into the aperture of the bivalve
Shield	SH	Using the flattened antennae to cover the bivalve
Consumptive		
Wedging	WD	Using P.1 and P.2 dactyls to create an opening in the aperture of the bivalve
Cutting	CT	Cutting adductor muscles with the pereiopods
Scooping	SC	Using the pereiopods to place the bivalve viscera into the oral region
Scraping	SCR	Moving the dactyls of the pereiopods over the inner surface of the bivalve to clean the flesh from it
Eating	ET	Passing food from the pereiopods to the mouthparts and to the mouth and ingesting it
Grooming		
Grooming	MG	Using the mouthparts to scrape debris off other appendages by passing those appendages into the mouthpart region
Exopodite fan	EF	Fanning of the exopodites of the first three pairs of mouthparts to create water currents and to help remove debris
Rejection		
Rejection	REJ	Refusing to eat the food after manipulation; dropping the food item; walking away from the food item after investigating it

category followed a normal distribution. Mean duration of broad categories of behavior differed: investigative behavior was significantly shorter in duration than either manipulative (2-tailed *t*-test: $t = -6.606$, df = 312, $P < 0.001$) or grooming behavior ($t = -4.049$, df = 55, $P < 0.001$), but did not differ in duration from consumptive behavior ($t = -1.756$, df = 19, $P = 0.095$) or rejection behavior ($t = 0.285$, df = 11, $P = 0.781$). Manipulative behavior was significantly shorter in duration than either consumptive ($t = -3.493$, df = 19, $P = 0.002$) or grooming behavior ($t = -4.507$, df = 55, $P < 0.001$), but longer in duration than rejection behavior ($t = -3.451$, df = 11, $P = 0.005$). Consumptive behavior was shorter in duration than grooming behavior ($t = 2.738$, df = 19, $P = 0.013$), but did not differ in duration from rejection behavior ($t = 1.764$, df = 11, $P = 0.105$). Grooming behavior did not differ in duration from rejection behavior ($t = -1.247$, df = 11, $P = 0.238$). Rejection of bivalves was rapid and averaged about 20s (Fig. 16). Only in two cases did lobsters reject bivalves in feeding trials.

Behavioral sequences involved in locating, manipulating, opening, and consuming a bivalve were investigated in *S. aequinoctialis* with Markovian chains (Fig. 18). Transitional probabilities of behavioral categories were not independent of each other ($\chi^2 = 206$, df = 16, $P < 0.001$); thus, behavioral sequences were the result of behaviors that previously occurred. With the exception of grooming and rejection behaviors, all behaviors fed back onto themselves—i.e., a specific investigative behavior (walking, flicking, leg waving, antennule probing) will lead to another investigative behavior 37.56% of the time; manipulative behavior (leg spread, body tilt, leg grasp, turning, probing with legs or mouthparts, and shielding) will lead to another manipulative behavior 46.15% of the time; consumptive behavior (wedging, cutting, scooping, scraping, eating) will lead to another consumptive behavior 29.17% of the

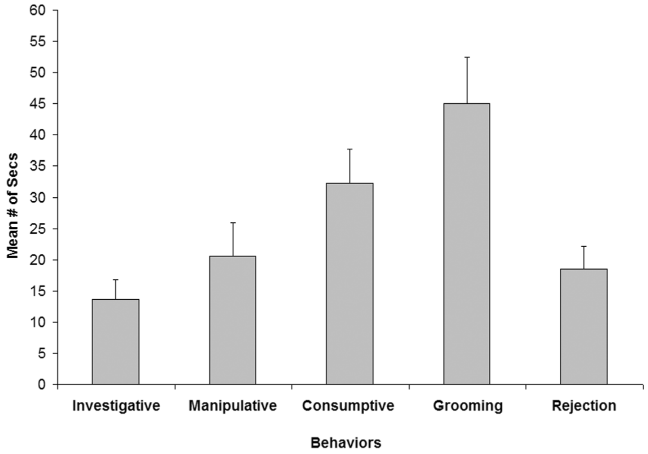


Figure 16. Behavioral categories (mean with SD) in seconds comprising the feeding sequence of *Scyllarides aequnioctialis*. Investigative behaviors include those needed to locate and make an initial assessment of the food; manipulative behaviors include those needed to position the food item for opening and to assess the food during the process of exposing the flesh; consumptive behaviors include those necessary for removal of flesh and passing to mouthparts for ingestion; grooming behaviors include those needed to clean appendages and to keep the mouth region clear of debris; and rejection behaviors include those involved in dropping, moving away from, or refusing to eat food. Statistical differences were seen between durations of investigative and manipulative or grooming behaviors (*t*-test: $P < 0.001$); manipulative and consumptive behaviors ($P < 0.002$); manipulative and grooming behavior ($P < 0.001$); manipulative and rejection behavior ($P < 0.005$); and consumptive and grooming behavior ($P < 0.013$).

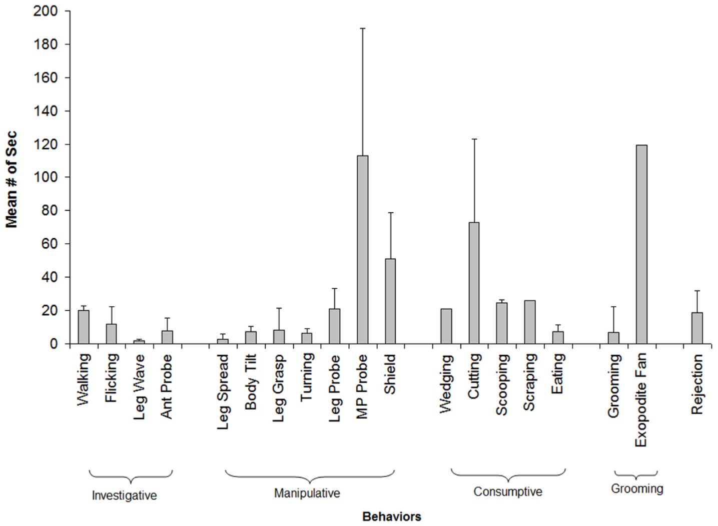


Figure 17. Duration (mean with SD) of specific individual behaviors making up the larger categories of investigative, manipulative, consumptive, and grooming behaviors of *Scyllarides aequinoctialis* illustrated in Figure 16. Most behaviors are under 60 s in duration, with only probing by mouthparts, exopodite fanning, and cutting typically lasting close to 120 s. *See* Table 2 for more detailed definitions of individual behaviors.

time; and grooming behavior will lead to further grooming behavior 16% of the time. Because investigative behaviors include those actions that allow for sampling of both the environment (via antennule flicking, leg waving, and walking) and of the food item (via antennule probing), most other behaviors fed back to them a large percent of the time (16.67%–60%). Likewise, manipulative behaviors allow direct assessment of the food item (via leg grasping, turning, leg, and mouthpart probing) and maintenance of body and food position (via leg spreading, body tilting, shielding) and, as a result, all behaviors fed back to them a moderate percent of the time (16% to about 46%). Consumptive behaviors fed back primarily (25% to about 30% of the time) to additional consumptive behaviors (e.g., scooping leads to eating; eating leads to more scooping and then scraping the shells clean) and to manipulative behaviors needed to reposition the food during consumption, but can also result in the need to groom appendages (legs and antennules) that may be needed for food assessment, reassessment of the food via flicking and antennule probing (investigative behavior), and dropping of the shell when the lobster completes the feeding sequence (rejection behavior). In contrast, grooming behaviors (grooming by mouthparts and exopodite fanning) lead primarily to investigative behavior (60%), only a moderate amount of the time to additional grooming and manipulative behaviors (16% of the time), and infrequently to rejection behaviors (8%). Rejection behaviors led primarily to a re-investigation of the food or the area in which the food was found, and a moderate amount of the time to manipulative or grooming behaviors (25%).

During the feeding sequence, *Scyllarides* spp. (*S. aequinoctialis* and *S. nodifer*) typically approached a bivalve with antennules flicking. Upon encountering a bivalve, the lobster gathered the shell with paired P.1, P.2, and/or P.3 and repetitively probed the outer valves with its antennules, as though tasting and assessing the shell for its possible value. After the initial assessment of the shell by the antennules, lobsters

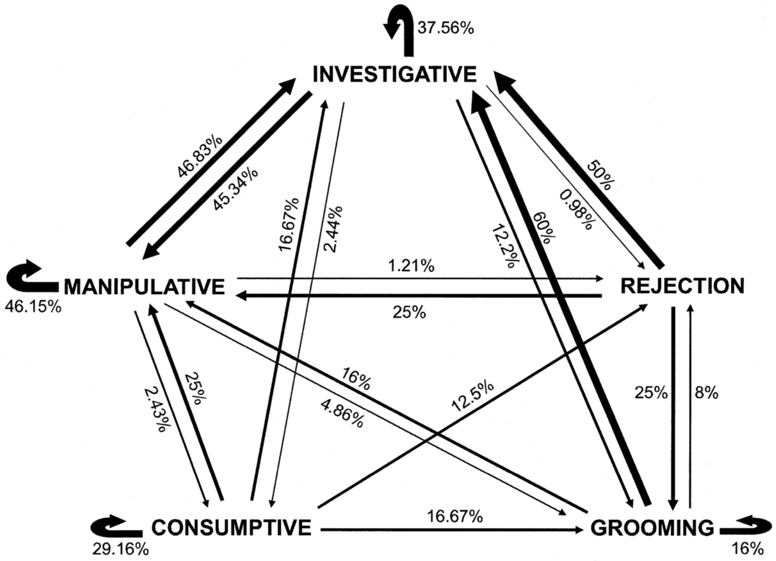


Figure 18. Transitional probabilities of behaviors comprising a feeding sequence of *Scyllarides aequinoctialis*. Several specific chains were more common than others: (A) investigative → manipulative → consumptive and then either investigative or grooming or rejection followed by investigative, and (B) investigative → manipulative → grooming and then either investigative or rejection followed by investigative. These chains are similar to those seen in clawed lobsters by Derby and Atema (1982b).

then held the shell firmly with either paired P.1, P.3, and P.4, or paired P.2, P.3, and P.4, and used the dactyl tips of either P.1 or P.2 to repetitively probe the edges of the valves. By such repetitive probing, dactyl tips were wedged into the shell edge and inserted further and further, a process known as "wedging" (Lau 1987). Once one pair of pereiopod dactyls was inserted, another pair—usually those of P.2 and/or P.3—was used to cut the mantle tissue along the pallial line. Then the lobster used a "scissoring" motion of P.1 and P.2 to increase the opening angle and to provide access to the adductor muscles. The adductor muscles were cut by P.2 so that the valves opened freely. The meat was then repetitively scraped out of the valves, scooped up in opposing pereieopods, and passed directly to the third maxillipeds. The maxillipeds stretched the flesh and passed strands back to the subsequent five pairs of mouthparts for ingestion. Until the flesh was passed to the third maxillipeds, the antennules made repeated downward motions to probe inside the valves, to touch the flesh, and to touch the shell as the pereiopods scraped the flesh from it. Feeding bouts ranged in duration from 22.92 s to 26.6 min, averaging 7.68 (SD 7.33) min.

Feeding behavior by *S. latus* entailed methodical prying and opening of each limpet by the dactyls of P.1, before flipping the limpet from the dorsal to ventral side (aided by the dactyls of P.3) for consumption. The average time for all *S. latus* lobsters to pry, flip, and open limpets was 10.6 (SD 1.4) min. The time that animals spent opening limpets was significantly longer than the time to pry, flip, and position the limpet for consumption [5.1 (SD 0.94) vs 3.3 (SD 0.82) min, $P < 0.05$]. Lobster carapace length was significantly related to the maximum limpet size that a lobster could handle and consume ($r^2 = 0.85$, $F_{1,7} = 43.9$, $P < 0.001$; Fig. 19).

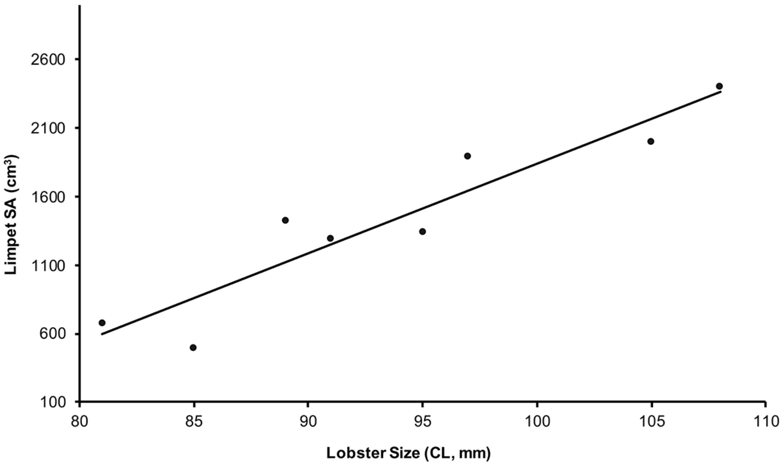


Figure 19. Relationship between the maximum limpet size that could be opened (measured in surface area) with lobster size (measured in carapace length) for *Scyllarides latus*. There was a significant relationship between lobster carapace length ($n = 8$ tested) and the maximum limpet size that was handled.

Discussion

Some trends were observed while documenting the setal morphology of *S. aequinoctialis*, *S. latus*, and *S. nodifer*. Pereiopods become progressively smaller toward the posterior end of the lobster's body, with P.5 of male lobsters being the smallest. The propus, carpus, merus, and ischium segments bore additional longitudinal ridges and grooves along their lateral and medial edges, starting with P.3. The setal distribution pattern was very consistent among the pereiopods of a particular species and even among the three species examined, with setae being arranged in uneven transverse rows on each segment. Cuspidate setae were the predominant setal type found on all segments. The ventral surfaces of the pereiopods tended to have shorter cuspidate setae, often much shorter than those found on the dorsal surfaces. Lateral edges of the dorsal surface tended to have longer cuspidate setae whereas medial edges of the dorsal surfaces had cuspidate setae of medium length. The distal edges of segments, where articulation with the next segment occurs, also had long cuspidate setae (for the propus, carpus, merus and ischium only) (Fig. 4A, C, D). The alate carina arising from the lateral edge of both ventral and dorsal surfaces of the merus of P.1 to P.4 was the first instance where the species diverged. The lateral edge of this carina bore conate setae in *S. latus* and *S. nodifer* (Fig. 10C), but in *S. aequinoctialis* it bore either teazel (Fig. 10A) or long cuspidate setae (Fig. 10B), but not both simultaneously on individuals. Pereiopods 1 to 4 were anteriorly oriented, but P.5 was rotated back toward the posterior end of the lobster. This orientation and the presence of the sub-chelate brush pad in females, but not in males, allowed females to reach their eggs and remove parasites and fouling agents from them.

The three scyllarid species examined exhibited lower diversity of setal types and fewer setae than have been found on the mouthparts or pereiopods of nephropids

(Factor 1978, Lavalli and Factor 1992, 1995) and palinurids (Nishida et al. 1990, Wolfe and Felgenhauer 1991, Johnston and Ritar 2001). Only six types of setae were observed on the pereiopods of slipper lobsters: cuspidate, conate, simple, miniature simple, teasel, and more rarely hooded. Although function cannot be inferred from external morphology, it is likely that several of these types of setae may function as chemo- and/or mechanoreceptors due to their locations on the pereiopods and their ability to contact food during a feeding sequence. The presence of apical or terminal pores (Fig. 2C) that are seen on some of the cuspidate setae strongly suggest a chemosensory function (Jacques 1989, Watling 1989). However, Farmer (1974) suggested that cuspidate setae might serve to capture particles or food pieces and Garm (2004) suggested that these robust setae probably aid in shredding, tearing, and repositioning/manipulating food—functions that are more mechanical in nature. Nevertheless, while acting in a mechanical fashion, cuspidate setae with apical pores may also function to taste the food via contact chemoreception prior to passing it to mouthparts for further assessment and ingestion. Given the pattern of appendage usage seen during feeding, it is likely that these latter cuspidate setae are chemosensors.

Derby (1982) demonstrated that simple setae can serve both chemo- and mechanoreceptive functions in nephropid lobsters, and Cate and Derby (2001) showed that simple setae are bimodal sensors in spiny lobsters. Given their location on the dactyls and the brush pads of P.5 of the females, and the fact that they are interspersed among cuspidate setae, it is likely that they serve at least a chemosensory and possibly a mechanosensory function. Miniature simple setae observed on the surface of the pereiopods may serve to protect the epicuticle against fouling by bacteria, protozoans, or fungi. These densely packed setae are likely to present a thick boundary layer, preventing water from reaching the epicuticle, and were found to be very clean and free of fouling agents compared to other, larger setae (compare Fig. 7 with Figs. 2, 6, 8). Such setae are absent in nephropid and palinurid lobsters, which frequently have bacterial and fungal fouling on the epicuticle of their carapace and appendages. Miniature setae are probably a homologue to Type II simple setae (Watling 1989) because while they provide a sculptured look to the carapace, they are actually smooth and devoid of setules themselves.

Teazel setae could possibly be chemosensory setae that are developed during a later growth stage. Farmer (1974) suggested that some setae may serve as beginning stages in the development of other setae during the life history of an individual, and Cate and Derby (2002) noted that setae can change structure after molting. Teazel setae were only found on the alate carinae of the merus segments of P.1 to P.4 of *S. aequinoctialis*, a location that is unlikely to come in contact with food directly. Furthermore, not all individuals of *S. aequinoctialis* bore teasel setae in this location and instead bore cuspidate setae. In contrast, all *S. latus* and *S. nodifer* specimens bore conate setae on the alate carina. Although the function of these setae is uncertain in these three species, it is likely that they do not function as chemoreceptors considering their location. However, slipper lobsters can pull in their legs to form a barrier to their ventral surface, and these setae might act as sealants for that barrier. Cuspidate setae in the same location may serve a similar sealant function (Garm 2004).

Compared to the slipper lobsters in the present study, nephropid and palinurid lobsters possess highly setose pereiopods, with a great diversity of setal types, some of which have been identified as contact chemoreceptors (taste) (Derby 1982, 1989, Derby and Atema 1982a,b, Derby et al. 1984, 2001, Garm et al. 2004), and others of which have been identified as distance chemoreceptors (smell) (Devine and Atema 1982, Daniel and Derby 1988, Moore et al. 1991a,b, Gomez and Atema 1996, Guenther and Atema 1998, Cate and Derby 2001, Kozlowski et al. 2001, Steullet et al. 2000a,b, 2001, 2002). Lobsters in those families insert their pereiopods into the substrate to locate potential prey by taste (Derby 1982). They also use their pereiopods to scrape flesh from bivalves that have been opened via the chelae (nephropids) or mandibles (palinurids). The pereiopods in these species act as initial filters locating and providing a first assessment of the food prior to passing it to the mouthparts that act as a second filter before ingestion. The lack of both diversity of setal types and numbers of setae on the pereiopods of the scyllarids examined in this study (*Scyllarides* spp.) suggests that their pereiopods differ in sensory function from those of nephropids and palinurids. Similar to nephropids and palinurids, these scyllarids inserted their pereiopods into substrate, presumably to locate potential prey, and engaged in leg waving that should serve to change or clear the chemical environment surrounding the setae of the pereiopods. In contrast to nephropids and palinurids, these scyllarids then used their pereiopods to open the located bivalves and expose the flesh within. The "nails" on the dactyl tips are sharp and cut through the adductor muscles of bivalves in a "shucking" process (Lau 1987, Spanier 1987). These pereiopods are then used to help wedge open the bivalve and scrape the flesh towards the mouthparts (Lau 1987, the present study). This harsh use of the pereiopods may necessitate fewer setae, particularly on dactyl segments, due to the likely loss or damage of such setae during wedging and prying open of prey. Even though the distal-most portion of the dactyl is bare of setae, the remaining surfaces of the dactyl (particularly those on P.1 and P.2) appeared to bear damaged setae in all specimens examined. The dactyl tufts seen on P.3 and P.4 may compensate for the loss of setae on the dactyls of P.1 and P.2, but sensory function may be reduced over time for these "shucking" appendages. As a result, scyllarids, such as those in the present study, may shift sensory function normally associated with pereiopods to their antennules to taste (via contact chemoreception) the surface of the bivalve prey and later the mantle tissue during shucking process and scraping. Thus, we postulate that in these scyllarids, both pereiopods and antennules seem to act as the initial filters, finding food, and assessing its value prior to a secondary assessment by mouthparts before ingestion. Nephropids do not use their antennules in such a manner, and although palinurid antennule segments would allow for a similar bending action, they keep their antennules fairly stiff and forward bending. Thus, the antennules of nephropids and palinurids have been considered organs for distant chemoreception (smell) (Atema 1985, 2018). In scyllarids, however, antennules may play a dual role in both distant and contact chemoreception, compensating for fewer setae and the loss of setae with use. Once the flesh of the prey is exposed and passed to the third maxillipeds, assessment by mouthparts seems to become more important (*see* Fig. 17 where such activity occupies more time than antennule probing).

Scyllarides aequinoctialis used in the present study engaged in one of several sequences to process food (Fig. 18). All sequences involved an initial investigatory phase that was used to find a food source and determine its quality. Lobsters then shifted to manipulation of the food object to position it for "shucking" and, during this time, reinvestigated the food with antennule and leg probing. Consumption or rejection followed such a manipulation phase, and when surfaces became fouled, grooming ensued. Although it is likely that the overall sequences comprising feeding (investigative, manipulative, consumptive, grooming) is similar for many scyllarids, it is important to not overgeneralize to all scyllarids because some species have food preferences that are not as well suited to wedging behaviors (for example, *Arctides, Parribacus,* and *Thenus* spp.) (Jones 1988, Lau 1988, Kabli 1989). It is also not clear if all scyllarids would use their antennules to probe food objects in the manner seen here.

In nephropids, the feeding sequence for bivalves typically consists of an alert (what we here call investigative behavior) that involves antennule flicking, antennal waving, exopodite fanning, waving of the maxillipeds and dactyls of the pereiopods, and grooming of all of these organs (Derby and Atema 1982b). This alert behavior leads to searching where lobsters probe the substrate for food with their pereiopods and, when food is located, it is touched and manipulated by the pereiopods, the third maxilliped, and the antenna. The pereiopods and mouthparts eventually grab the bivalve, rotate it, and pass it to the crusher claw where a repeated loading force is applied to crush it. Often the bivalve is dropped and the sequence repeats itself where the lobster searches for, finds, touches, and eventually picks up and manipulates the bivalve back to the crusher claw (*see* fig. 2 in Derby and Atema 1982b). Once the shell is cracked, the mandibles will hold the valve while the third maxillipeds and first two pereiopods will pull on the valve and the other four pairs of mouthparts will tear away pieces of the shell and flesh. In contrast, because scyllarids lack crushing claws, they use their pereiopod dactyls to pick up, hold, shuck, and then wedge open the bivalve, while the mouthparts taste and/or shred the exposed flesh; there is less dropping of the food item unless it is outright rejected. The entire sequence in scyllarids is more streamlined; however, this does not necessarily translate into shorter feeding bouts as Lau (1987) reported that *S. squammosus* feeding bouts ranged in time from 10 to 40 min. However, in the present study, *S. aequinoctialis* feeding bouts were relatively short and took from 1.39 s to 26.6 min. Spiny lobsters also lack crushing claws, and their pereiopod dactyls are blunt and do not form “nails” as seen in scyllarids. Thus, spiny lobsters often chip bivalve shells at the posterior margin or at the umbo with their molariform mandibles and then insert opposing perieopod dactyls into the holes created and pry apart the hinge (Robles et al. 1990). Attempts at chipping often result in dropping and then grabbing again and manipulating for another attempt at chipping, and chipping success is dependent on shell thickness of the bivalve. Handling times from manipulation to ingestion can range widely from 5 s to 1.6 hr for spiny lobsters (Robles et al. 1990). Spiny lobsters also display size preferences for bivalve prey and their success in consumption scales with their body size such that smaller spiny lobsters kill and consume smaller bivalves, and larger lobsters prefer and consume larger bivalves (Griffiths and Seiderer 1980, Robles et al. 1990). In this way, spiny lobsters are similar to scyllarids feeding on gastropods.

Differences in preferred prey and/or methods of consumption may allow for niche separation where multiple scyllarid species within a subfamily or multiple genera among the subfamilies overlap in distribution. They may also allow for niche separation in cases where slipper lobster species are sympatric with palinurids or nephropids (Hearn et al. 2007). It is clear from what already is known of scyllarids that certain species may be generalists that maximize their intake of a variety of invertebrates (and some vertebrates), whereas others may be highly specialized to feed on a few molluscan species or echinoderm taxa (Lavalli et al. 2007). A better understanding of diet, feeding mechanics, and behaviors involved in a feeding sequence in the genera comprising the family Scyllaridae would improve our ability to manage this commercially important group and the habitats and ecosystems they occupy, especially in cases where multiple taxa are targeted for fisheries exploitation and where there is an important trophic relationship among the targeted species (Hearn et al. 2007, Spanier and Lavalli 2007b).

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