

**DESCRIPTION OF THE SETAE ON THE PEREIOPODS OF THE
MEDITERRANEAN SLIPPER LOBSTER *SCYLLARIDES LATUS*,
THE RIDGED SLIPPER LOBSTER, *S. NODIFER* AND THE
SPANISH SLIPPER LOBSTER *S. AEQUINOCTIALIS***

THESIS

**Presented to the Graduate Council of
Southwest Texas State University
in Partial Fulfillment of
the Requirements**

For the Degree

Master of SCIENCE

By

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**San Marcos, Texas
May 2003**

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ACKNOWLEDGMENTS

Foremost, thank you to God, through whom all things are possible. I would like to thank my mother and brother for supporting me throughout this entire ordeal called a thesis. Without your love and support none of this would have been accomplished. Thanks also to Dianna Marsh whose friendship kept me sane when insanity encroached. Thanks also to my grandfather who long ago sent me down this road for better or worse, and whom I am sure is watching over me now.

I wish to express my gratitude to Dr. Kari Lavalli, for her mentorship and guidance these past years. She opened a door for me into the world of marine research and she was there to offer help even when it was no longer technically her job. In my book this makes her a great professor willing to go the extra mile to help students. I also want to thank Dr. Samuel Tarsitano for his support and giving me the chance to teach comparative anatomy labs. Teaching labs for him has been a fun and enlightening experience. Thanks also to the rest of my committee, Dr. Horne and Dr. Gris , for stepping in to be on my committee and for all of their help.

Finally, thanks to Dr. Spanier for providing specimens. Many thanks go to Dr. Schmerling at the University of Texas in Austin, and the staff at Rice University in Houston, for allowing the use of their machinery. Thanks also to the Honors Department at Southwest Texas State University whose initial support and funding allowed this project to get off to a good start. Being part of the Honors program was a great experience and everyone involved with it works really hard to support the students.

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May 2003

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ABSTRACT

This study describes the morphology of setae on the five pairs of pereopods (walking legs) of three species of scyllarid lobsters. Setae were examined using scanning electron microscopy and environmental scanning electron microscopy, with their location being directly mapped for five segments of the endopod (dactyl, propus, carpus, merus and ischium) of each of the pereopods. Using Watling's (1989) scheme for setal morphology, five types of setae were found: cuspidate, simple, conate, miniature simple and teazel. Setae were found to have a highly organized row-like pattern on the ventral (aboral) and dorsal (oral) surfaces of the pereopods. Cuspidate setae were found on all surfaces and faces of the dactyl, propus, carpus, merus and ischium segments of each of the five pereopods examined. Simple setae were found only on the dactyl of each pereopod, and the teazel setae were concentrated on the rim, the lateral most edge of the merus shield, for *S. aequinoctialis* only. Comparisons of setal types between the species demonstrate that *S. nodifer* bears the exact same setae and setal pattern as *S. latus*, while *S. aequinoctialis* shows slight differences. Based on comparisons between the more intensely studied nephropid (clawed lobsters) and palinurid (spiny lobsters) species, scyllarids (slipper lobsters) have fewer setae on their pereopods, probably due to the abrasive manner in which they manipulate and open their preferred food (clams, oysters, mussels).

INTRODUCTION

Lobsters support important fisheries throughout the world and are intensely studied as a result. Most biological studies thus far have concentrated on the widely distributed spiny (or rock) lobsters and the less-widely distributed clawed lobsters. The slipper lobster, while also supporting fisheries, has been little studied compared to its more commercially popular cousins (Holthuis, 1991). Thus, we know little about its functional morphology, behavior, and ecology.

It has been long known that lobsters evolved from shrimp-like ancestors (George and Main, 1967), but it is unclear if scyllarid (slipper) lobsters evolved from the same ancestor as nephropid (clawed) lobsters or palinurid (spiny) lobsters. While there is limited knowledge available regarding the evolution of slipper lobsters (Phillips et al. 1980), morphological evidence strongly suggest that scyllarids are a sister group to the palinurids (Moe, 1991, Tam and Kornfield, 1998). Morphological and molecular evidence shows little similarity between nephropids and palinurids or between nephropids and scyllarids (Moe, 1991; Tam and Kornfield, 1998). Thus any morphological similarities between nephropids and scyllarids could indicate convergence of characters used for food and mate location (i.e., antennules), food acceptance (i.e., pereopods and mouthparts), and predator deterrence (i.e., carapace shape and sculpturing, spination patterns, antennal design). Dissimilarities in morphologies among these families may indicate divergence in ecological niches and/or behavior.

Nephropid lobsters possess three pairs of walking legs (pereiopods) that are chelate, with the first pair growing into large, dimorphic claws. The fourth and fifth legs are nonchelate in males; only the fourth legs are nonchelate in females (see Table 1 for a comparison of leg structure by family). All segments of all pereiopods bear setae, which are thought to be important in contact chemoreception (Derby, 1982). In contrast, palinurids possess nonchelate legs except for the subchela of the male's first pereiopods and the female's fifth pereiopods (Holthuis, 1991; Moe, 1991; Table 1). Similarly, the pereiopods of scyllarids are nonchelate except for the female's fifth pereiopod (Moe, 1991; Table 1).

Table 1: Differences in Pereiopod Morphology Among Three Lobster Families (Moe, 1991)

Morphology	Family Nephropidae	Family Palinuridae	Family Scyllaridae
1 st pair	Chelate (differentiated into large claws)	Nonchelate in most; subchelate in some genera (males only)	Nonchelate
2 nd pair	Subchelate	Nonchelate	Nonchelate
3 rd pair	Subchelate	Nonchelate	Nonchelate
4 th pair	Nonchelate	Nonchelate	Nonchelate
5 th pair	Chelate	Chelate	Chelate
Setae of pereiopods	Type I (with setules) and Type II (simple)	Type I (with setules) and Type II (simple)	Unknown

All three morphological "types" of lobsters are predators, preferentially consuming mollusks as adults (Herrick, 1909; Herrnkind, 1975; Lau, 1987). Techniques used to open mollusks vary due to morphological differences in pereiopod shape. Nephropids use their large claws to apply a loading force to the valves until a structural failure occurs and cracks run through 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 open the bivalve further (Carlberg and Ford, 1977). Slipper lobsters simply use the sharp dactyls (often called “nails”) of their pereiopods to “shuck” open the shell (Lau, 1987, Table 2).

Table 2: Different Feeding Strategies Among Three Lobster Families

Feeding Behavior	Family Nephropidae	Family Palinuridae	Family Scyllaridae
Crush Bivalve	Yes	No	No
Bite bivalve	No	Yes	No
Shuck Bivalve	No	No	Yes

While we understand the various techniques used to open such prey, we do not fully understand what functions the different types of hair-like structures, termed setae, serve that are found on lobster pereiopods. In both nephropids and palinurids, many setae are 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, 1982). 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, 1982). Thus, leg sensory structures typically function in controlling grasping reflexes (Derby and Atema, 1982).

Nephropid lobsters have been the focus of most of the studies on functional morphology of such setae, and such setae seem to function as contact chemoreceptors (i.e., taste) and mechanoreceptors (i.e., current detectors) (Derby, 1982; Derby and Atema, 1982; Cate and Derby, 2001). These setae fall into one of two categories established by Watling (1989)—Type I setae (Fig. 1) which bear small, scale-like setules, and Type II setae that lack such setules (Fig. 2). Fewer studies have focused on spiny

lobsters, but again the setae of the pereopods seem to be bimodal in function, acting as both chemo- and mechanoreceptors (Moe, 1991; Cate and Derby, 2001; Derby and Steullet, 2001) and are of Type I and II. No studies have, as yet, focused on the setal morphology of adult slipper lobster pereopods. Given the suggested sister group relationship between palinurids and scyllarids (Tam and Kornfield, 1989), one might hypothesize that the pereopods would bear similar types of setae with similar functions.

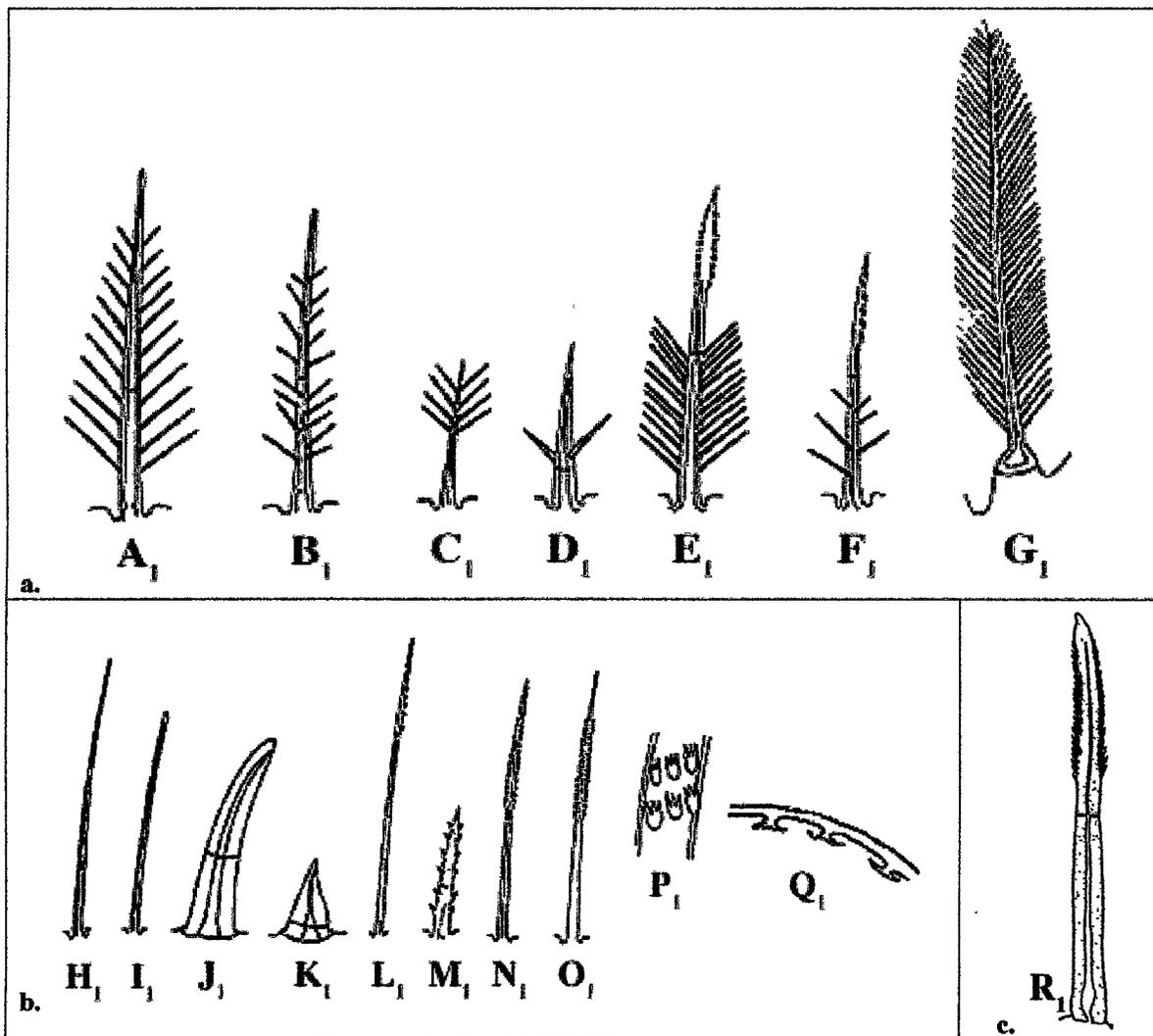


Fig. 1. Different setal types (a) Type I setae, annulate with setules: A₁ & C₁ - plumose, B₁ - pappose, D₁ - forked, E₁ & F₁ - plumodenticulate, G₁ - plumose with supracuticular pocket (b) Type II setae without setules: H₁ & I₁ - simple, J₁ - cuspidate, K₁ - conate, L₁ & M₁ & N₁ & O₁ - various types of serrate, P₁ - complex denticules of serrate seta, Q₁ - anvil shaped denticules of seta from branchial epipod of crab (c) Type 1 (new): R₁ - teazel (A₁ - Q₁ from Watling, 1989; R₁ from Thomas, 1970).

This study focuses on describing the morphology and distribution of setae on the pereopods of the Mediterranean slipper lobster, *Scyllarides latus* (Fig. 3a), the Spanish slipper lobster, *Scyllarides aequinoctialis* (Fig. 4a), and the ridged slipper lobster, *Scyllarides nodifer* (Fig. 5a), to understand the functional anatomical basis for the differences in feeding behavior observed between lobster families. The objectives of this study are to use Watling's (1989) classification system to: (1) identify the setal structures on all five pairs of pereopods 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 that of nephropid and palinurid lobsters. The inclusion of three related species, two of which are sympatric and one which is allopatric, will allow the determination of whether the setal morphologies and patterns are the same among species comprising the scyllarid family. As chemical signals are a driving force in the natural world, particularly in the marine environment where visual signals are often obscured, the description of setal types and the determination of their possible chemosensory or mechanosensory functions will lead to a better understanding of how these lobster pereopods are used in feeding the purpose of these lobsters' pereopods and thus, their biology, giving scientists a better grasp of how these lobsters function in and manipulate their environment (Atema, 1995).

MATERIALS AND METHODS

Animal Distribution, Collection, and Specimen Preparation

S. latus has a wide distribution, ranging from the eastern Atlantic (Portugal to Senegal, the Azores, and the Cape Verde Islands) and throughout the Mediterranean (Maigret, 1978; Fisher et. al., 1981; Martines, 1985; Holthuis, 1991; Fig. 2b). It is found in depths of 4 to 100 meters, usually on rocky or sandy bottoms (Holthuis, 1991). Scuba divers fishing off 20 m reefs in Haifa, Israel in 1999 obtained pereopods of *S. latus* (Fig. 2b).

Pereopods were cut off from *S. latus* at the proximal end of each pereopod's ischial segment (Fig. 2a). These pereopods of *S. latus* were washed with filtered seawater and fixed in 3% gluteraldehyde and 0.05M cacodylic acid for a minimum of one week. After fixation, the pereopods were passed through a graded ethanol series to dehydrate the exoskeleton (15 min each in 10%, 20%, 30%, 40%, 50%, 60%, 70% ETOH). Specimens were then shipped to Southwest Texas State University in 70% ETOH in glass vials covered with parafilm to prevent evaporation and leakage. After arrival, specimens were passed through a graded ethanol series to 100% ETOH (15 min each in 80%, 90%, 100%) and then passed through a graded acetone series up to absolute (100%) acetone (15 min each in 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 100%). Specimens were then stored in 100% acetone in glass vials. Twelve pereopods

(a right and left sample of 1st through 5th pereopods, including male and female samples of the 5th pereopod) were selected for SEM work and dried in sealed plastic boxes.

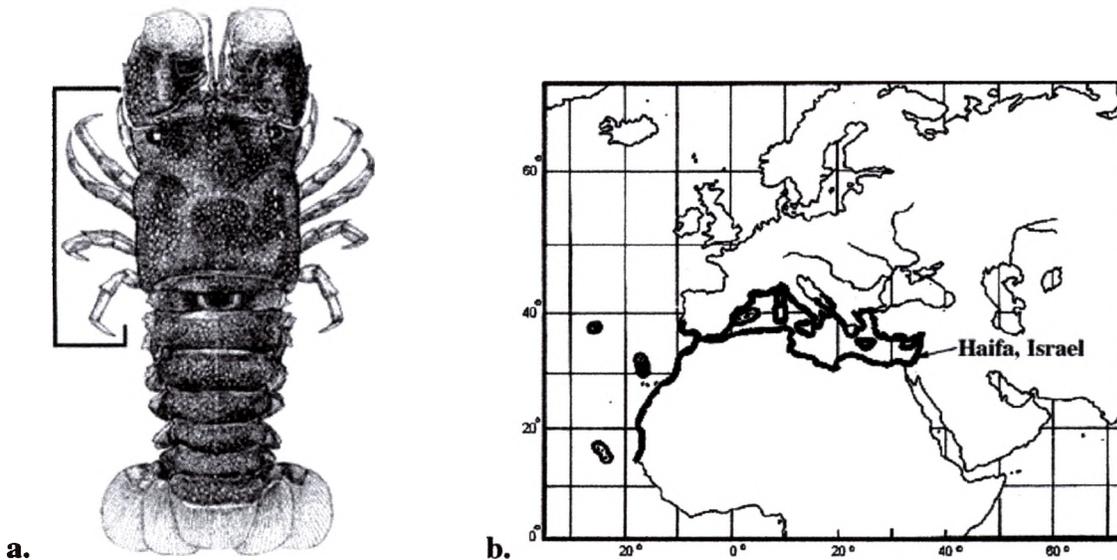
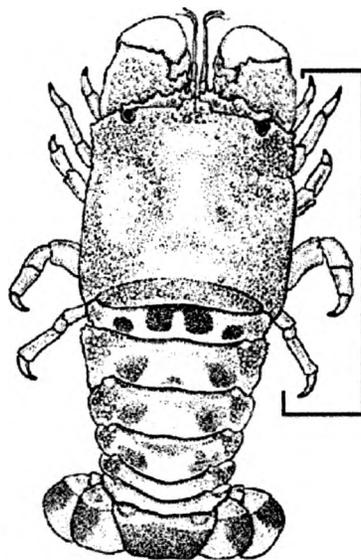
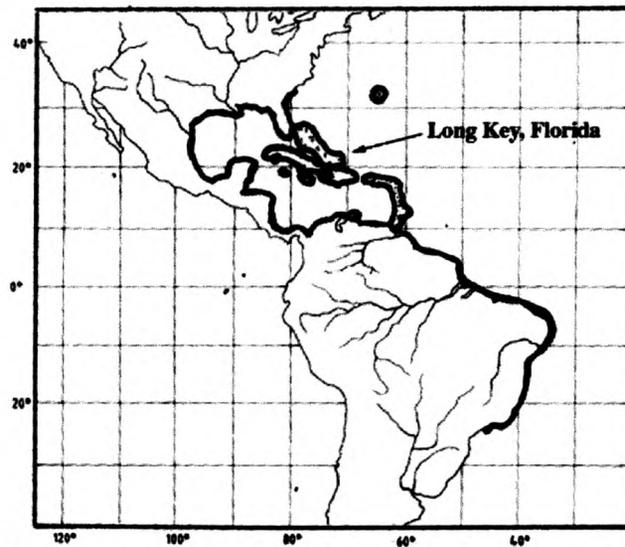


Fig. 2. *Scyllarides latus* (a) body structure showing the pereopods (bracket) examined; (b) distribution outlined in black with collection area shown by arrow (from Holthuis, 1991).

The Spanish lobster, *S. aequinoctialis*, also has a wide distribution, ranging from the western Atlantic (South Carolina, Bermuda and South Brazil) throughout the Gulf of Mexico (Holthuis, 1991; Fig. 3b). It is found in depths of 0.6 to 64 m, usually on rocky or sandy bottoms (Holthuis, 1991). The ridged lobster, *S. nodifer*, has a smaller distribution, ranging throughout the Gulf of Mexico, Florida Keys and Bermuda (Holthuis, 1991; Fig. 4b). It is found in depths of 2 to 91 m, usually on muddy or sandy bottoms (Holthuis, 1991). Live specimens of *S. aequinoctialis* and *S. nodifer* were obtained from local fisherman by the Keys Marine Laboratory, Long Key, Florida, and were subsequently shipped to Southwest Texas State University (Fig. 3b and 4b).

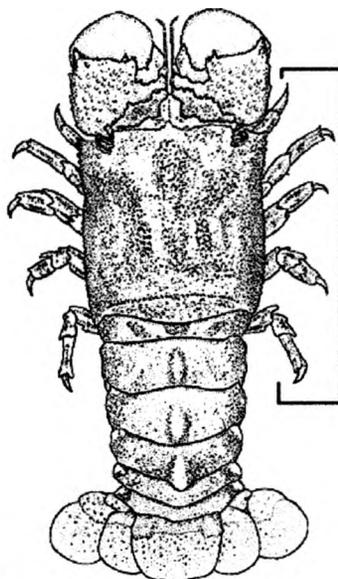


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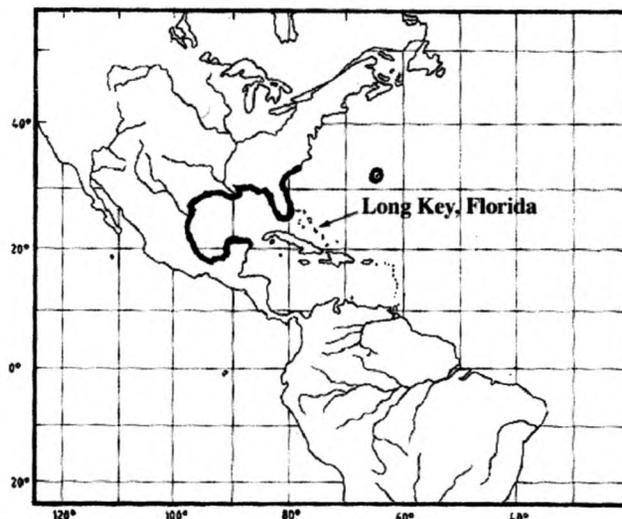


b.

Fig. 3. *Scyllarides aequinoctialis* (a) body structure showing pereopods (bracket) sampled; (b) distribution outlined in black with collection area shown by arrow (Holthuis, 1991).



a.



b.

Fig. 4. *Scyllarides nodifer* (a) body structure showing pereopods (bracket) sampled; (b) distribution outlined in black with collection area shown by arrow (Holthuis, 1991).

While specimens were being observed during a separate feeding behavior project, pereopod samples were obtained from molt shells or dead specimens. Twelve pereopods (a right and left sample of 1st through 5th pereopods, including male and female samples of the 5th pereopod) were removed with scissors at the proximal end of

the ischial segment and immediately stored in 100% acetone in glass vials (Fig. 3a and 4a). This procedure was possible as the ESEM allowed wet viewing of the pereopods of *S. aequinoctialis* and *S. nodifer* and no drying of the specimens was necessary.

Specimen Analysis

Before SEM work began, the pereopods of *S. latus* were drawn and photographed using a Sony MAVICA digital camera (Model MVCFD91) for mapping purposes.

Samples were sputter-coated in a Denton Vacuum Sputter Coater at 30-sec intervals for a total of 3 min of coating. Each pereopod was then viewed using a Cambridge S90B Scanning Electron Microscope at an accelerating voltage of 15 kV. SEM photographs of setae were taken from each of the five major segments (dactyl, propus, carpus, merus and ischium) of each pereopod, and locations were marked on the previously made pereopod maps. Two additional specimens were examined 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 again taken of each of the five pairs of pereopods of *S. aequinoctialis* and *S. nodifer* (including a male and female sample of the 5th pereopod) and rendered into maps using the Sony MAVICA digital camera (Model MVCFD91). ESEM photographs of setae were taken from each of the five major segments (dactyl, propus, carpus, merus and ischium) of each pereopod, and locations were marked on the previously made pereopod maps. Three samples of the pereopods for each species were then viewed on a Philips XL30 ESEM with EDAX Detector at an accelerating voltage of

10kV. Because samples were not pretreated with a fungicide/bactericide mixture prior to fixation, they were sonicated, as needed, to remove fungus or other debris.

RESULTS

Description of Setal Types Found on the Pereiopods

Five types of setae were found on the pereiopods of *S. latus*, *S. nodifer* and *S. aequinoctialis*: cuspidate (J_1), simple (H_1), conate (K_1), miniature, and teazel (R_1) (Figure 1). Of these types, the greatest variation in length occurred in the cuspidate setae, while other setae tended to occur only within one length class (small, medium, or long) (Table 3). Setae were arranged in uneven rows over all surfaces of the pereiopods. Only the distal tip or “nail” of the dactyl, a naturally, dark brown colored area on both oral and aboral surfaces, was devoid of setae.

Table 3: Setal Types found on the Pereiopods of Three Scyllarid Lobsters

Setal Type	Segment Location	Pereiopods Found On	Size Variation	Species Found On
Cuspidate	All 5 Segments	1 – 5	Short (>150 μm) Medium (150 – 300 μm) Long (<300 μm)	<i>S. latus</i> , <i>S. nodifer</i> , <i>S. aequinoctialis</i>
Simple	Only Dactyls	1 – 5	Long (<300 μm)	<i>S. latus</i> , <i>S. nodifer</i> , <i>S. aequinoctialis</i>
Conate	Rim of Merus shield	1 – 4	Short (>125 μm)	<i>S. latus</i> , <i>S. nodifer</i>
Miniature Simple-Like	All 5 Segments	1 – 5	Extremely Microscopic (>50 μm)	<i>S. latus</i> , <i>S. nodifer</i> , <i>S. aequinoctialis</i>
Teazel	Rim of Merus Shield	1 – 4	Long (500-800 μm)	<i>S. aequinoctialis</i>

Cuspidate Setae (Figures 1 (J₁), 5, 6, 7, 8)

Cuspidate setae are conical and tooth-like in shape (Fig. 5A-B), and range in length from short to long. All cuspidate setae found on the pereopods of slipper lobsters were smooth and lacked setules and annulations (Fig. 5A-D, G-H). Each seta lay within an invaginated socket (Fig. 5B-D, G-H). Therefore, they fell within Watling's (1989) Type II category. In all species, short cuspidate setae ($>150\ \mu\text{m}$, Figure 5J) occur on the oral surface and towards the medial edge of the aboral surface of the propus, carpus, merus, and ischium of all pereopods examined (Fig. 5J). They also occur on both oral and aboral surfaces of the merus shield of pereopods 1 – 4. Medium length cuspidate setae ($150 - 300\ \mu\text{m}$, Figure 5C, G, H) occur between the medial and lateral edges of the aboral surface of the propus, carpus, merus and ischium of all pereopods. Short, medium and long cuspidate are found within tufts of the dactyls of pereopods 3-5 (Fig. 6A, C-D, F). It is likely that they also occur in tufts on dactyls of pereopods 1-2, but in all specimens examined, the setae found within the invaginated pits of these tufts were broken and not identifiable. Long cuspidate setae ($<300\ \mu\text{m}$, Fig. 5A-B, D-F, I, and 7) occur in several locations. In all species, on the propus, merus, carpus, and ischium of all pereopods, they occur towards the lateral edge of the oral and aboral surface and on the distal edge of the aboral surface (Fig. 7A-F). In pereopods 3 –5 (both male and female), they are found on the aboral ridges of the propus, merus, carpus, and ischium, and on pereopod 5 of the female, they are borne in the brush pad of the dactyl (Fig. 8A-D). In *S. aequinoctialis* only, they also occur on the oral and aboral surface of the lateral rim of the merus shield of pereopods 1 –4.

Figure 5: Different sized cuspidate setae for all three species. (A) Long cuspidate setae on proximal dactyl end of the left, aboral surface of pereopod 2, from *S. nodifer*; (B) paired, long cuspidate setae of right pereopod 1, merus, aboral surface, from *S. aequinoctialis*; (C) medium length cuspidate setae with apical pores on the left, pereopod 1, merus, oral surface, from *S. latus*; (D) long cuspidate setae on left, female pereopod 5, merus, aboral surface, from *S. latus*; (E) paired, long cuspidate setae on left, pereopod 1, propus lateral edge, aboral surface, from *S. latus*; (F) long cuspidate setae covering the aboral surface of the female right pereopod 5 merus, from *S. latus*; (G) medium length cuspidate setae on right, pereopod 3, propus, oral surface, from *S. aequinoctialis*; (H) medium length cuspidate setae on left pereopod 4, ischium, aboral surface, from *S. nodifer*; (I) long cuspidate setae on the merus distal edge that articulate with the propus of the left pereopod 2, aboral surface, from *S. latus*; and (J) short cuspidate setae on merus shield of left pereopod 1, aboral surface, from *S. latus*. Scale bars: A, B, C, D, H and J = 200 μm ; E, F and I = 1 mm; G = 100 μm . L - long cuspidates, M - medium cuspidates, S - short cuspidates, AP - apical pore (arrow).

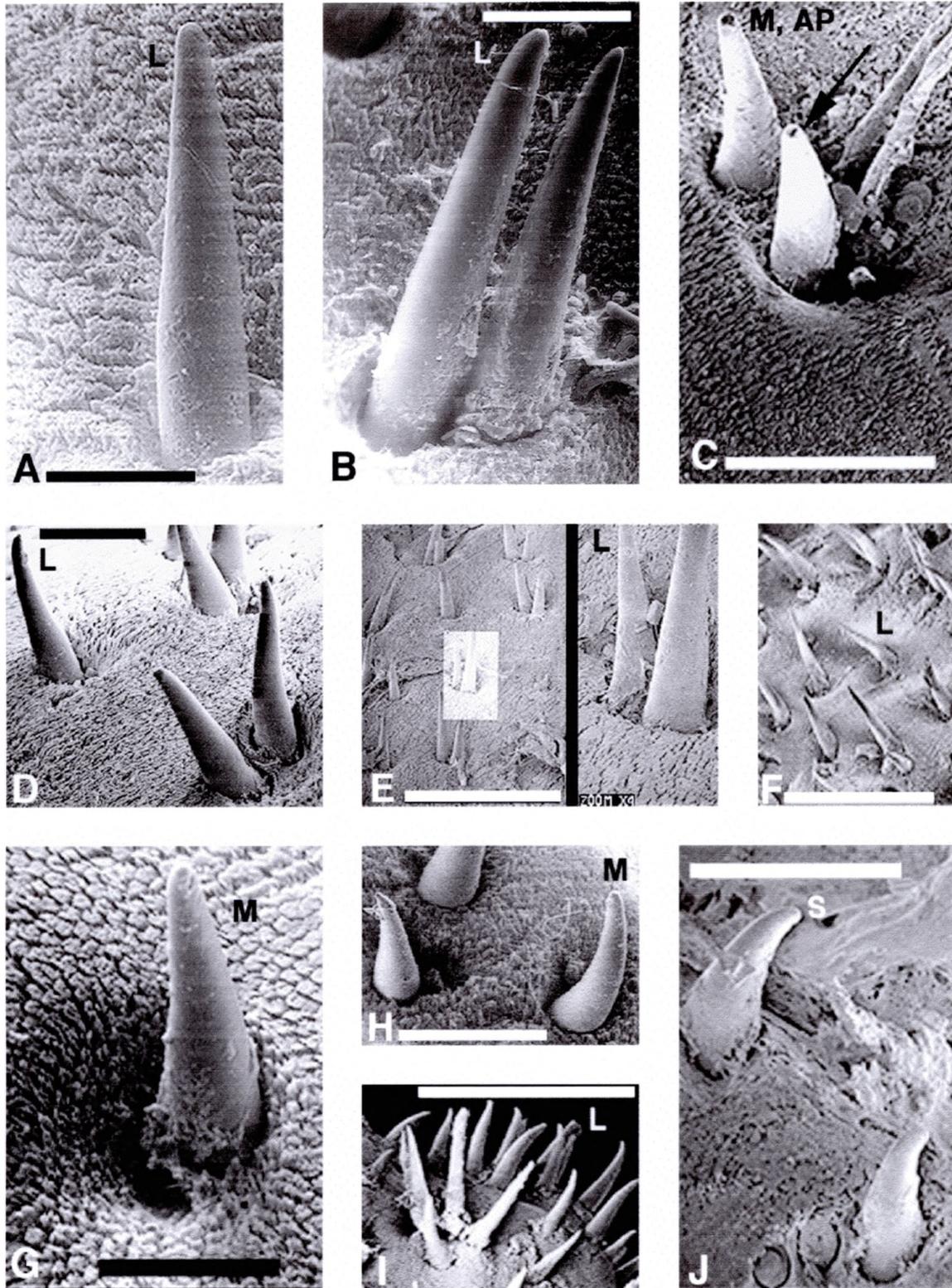


Figure 6: Dactyl tufts for all three scyllarid species. (A) Long cuspidate comprising setal tuft at proximal end of right pereopod 3, oral surface, from *S. latus*; (B) simple seta at lateral edge of left pereopod 3, aboral surface, from *S. nodifer*; (C) two dactyl tufts located at proximal end of right pereopod 3, oral surface, from *S. latus*; (D) long cuspidate setal tuft located at proximal end of left pereopod 3, oral surface, from *S. latus*; (E) distal dactyl tip (“nail”) on oral surface of left pereopod 2, from *S. aequinoctialis*; and (F) empty invaginations and broken tufts between proximal and distal ends of left pereopod 2, oral surface, from *S. latus*. Scale bars: A and C = 1 mm; D = 100 μm ; B and E = 200 μm , F = 2 mm. H₁ – simple setae (arrow).

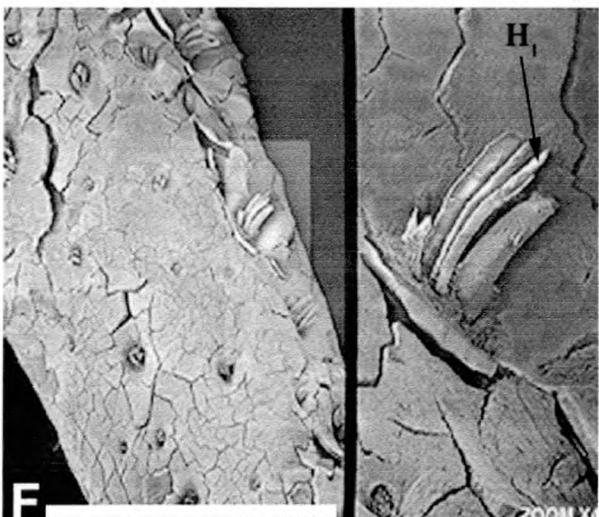
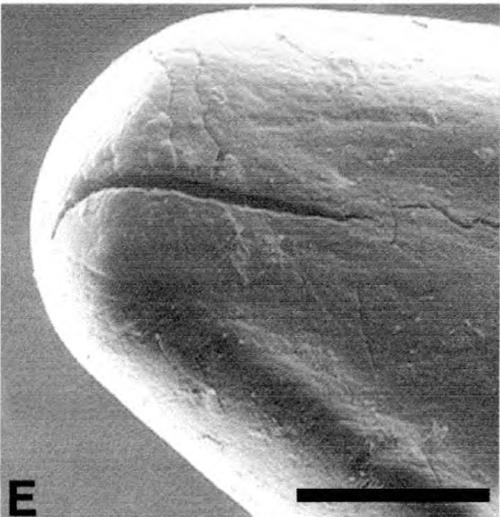
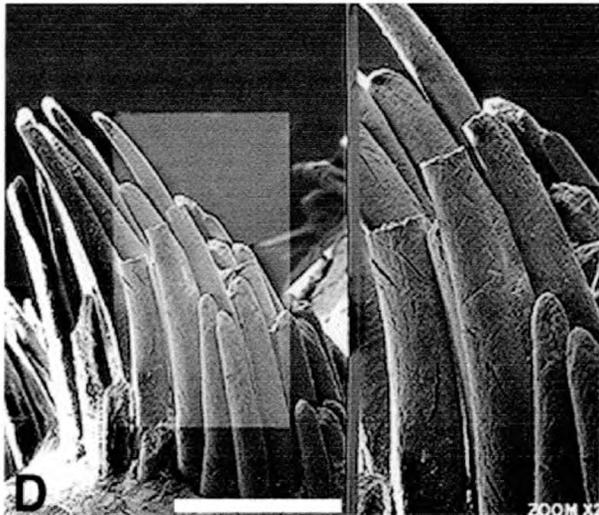
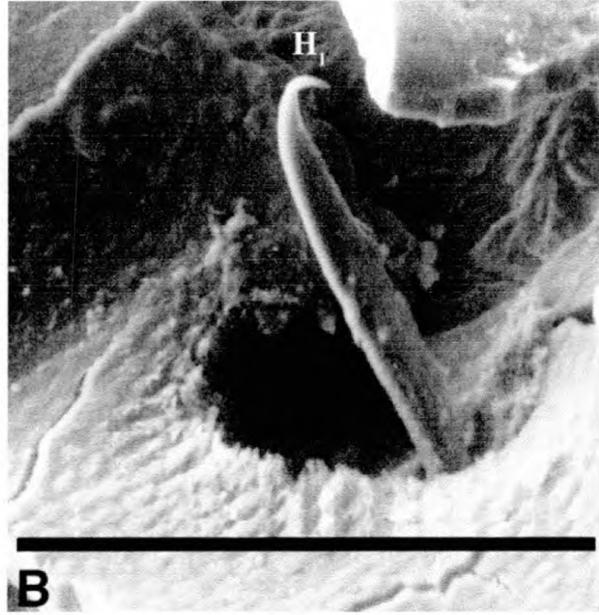
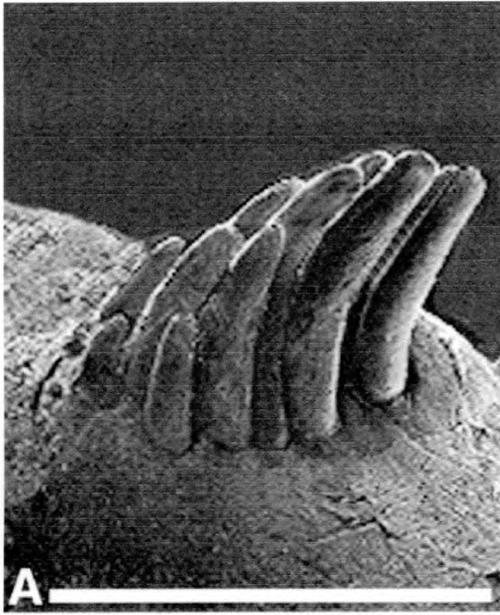


Figure 7: Setal distribution patterns along segmental edges. (A) Oral surface of carpus of left pereopod 2, showing short cuspidate setae on surface and medium length cuspidate setae along lateral edge; (B) long cuspidate setae at distal bend of carpus, articulating with proximal end of merus of the male, left pereopod 5, aboral surface; (C) short, medium and long cuspidate setae of left 2nd pereopod 2, oral surface; (D) long cuspidate setae along lateral bend of carpus of right pereopod 2, aboral surface – arrow points to one extremely long cuspidate setae typically found in this area; (E) row of long cuspidate setae on distal propus that overhangs proximal dactyl of right pereopod 1, aboral surface; and (F) row of long cuspidate setae on distal propus that overhangs dactyl of left pereopod 3, aboral surface. All photos are from *S. latus*. Scale bars: A = 5 mm; B and C = 1 mm; D and E = 2 mm; F = 500 μ m.

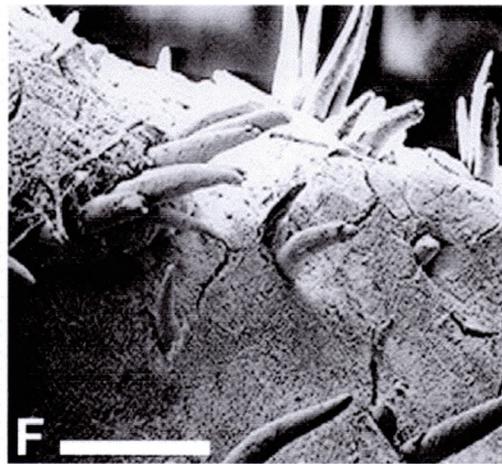
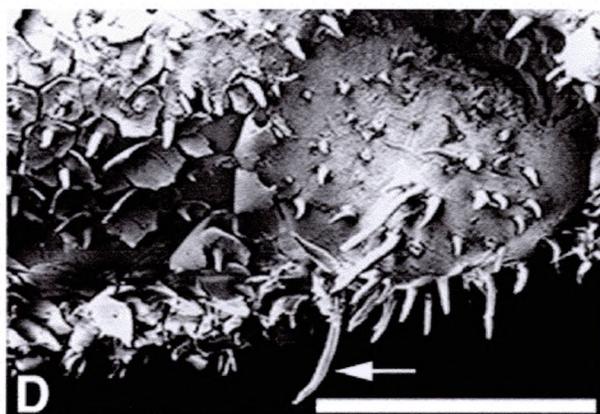
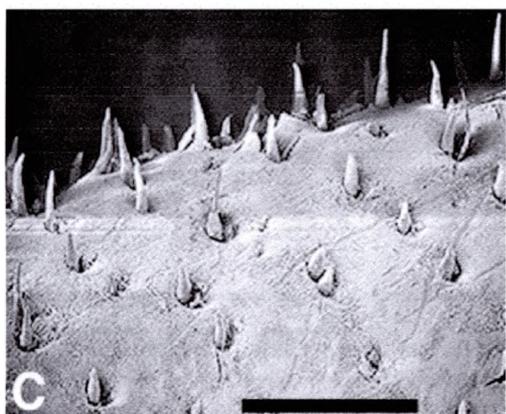
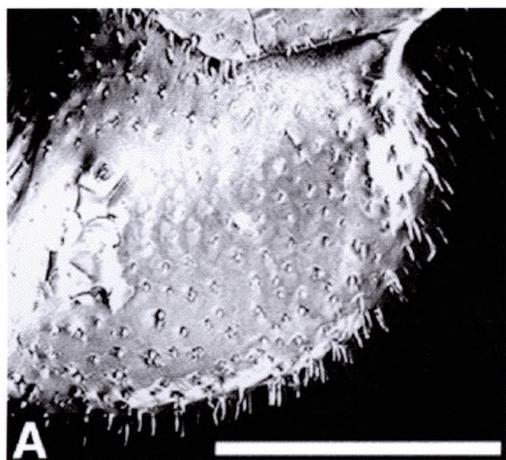
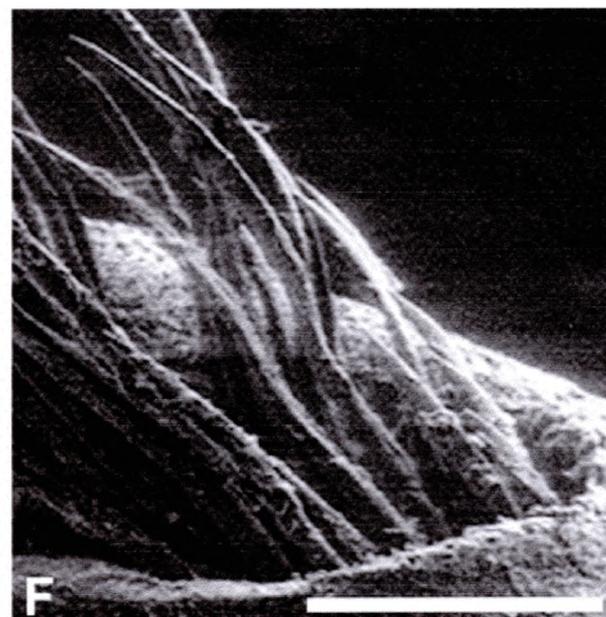
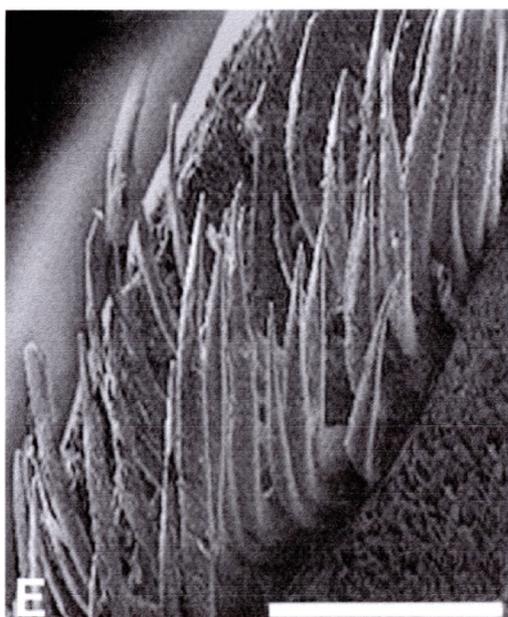
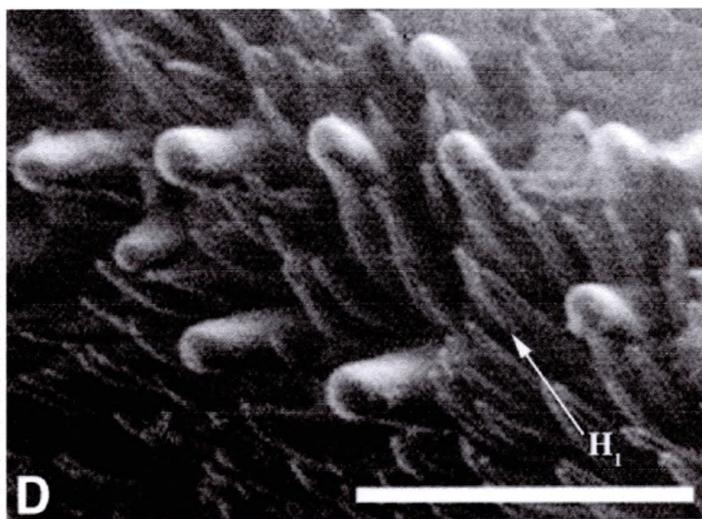
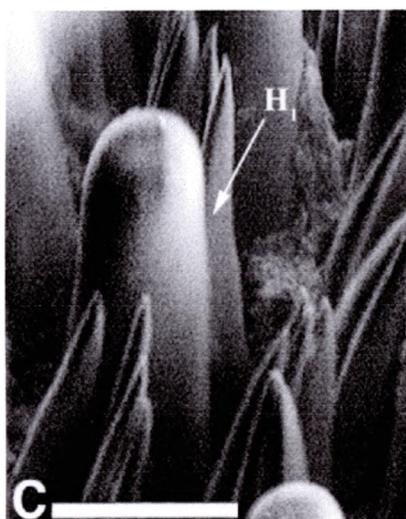
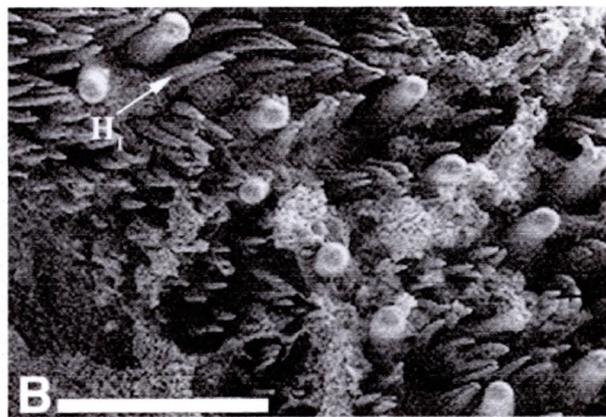
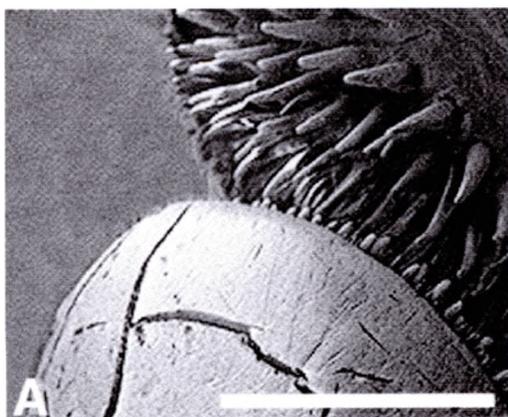


Figure 8: Brush pad setae of chela on pereopod 5 for female of all three scyllarid species. (A) Pad on oral surface of distal dactyl tip and on oral surface of articulating distal propus tip, from *S. latus*; (B) rows of long cuspidate and simple setae on dactyl of right pereopod 5, oral surface, from *S. aequinoctialis*; (C) cuspidate and simple setae of right pereopod 5, dactyl, oral surface, from *S. aequinoctialis*; (D) long cuspidate and simple setae on right pereopod 5, dactyl, oral surface, from *S. aequinoctialis*; (E) simple setae set in groove on oral surface of propus that articulate with dactyl of left pereopod 5, from *S. nodifer*; and (F) simple setae set in groove on oral surface of propus that articulate with dactyl of left pereopod 5, from *S. nodifer*. Scale bars: A = 500 μm ; B, D, F and E = 200 μm ; C = 50 μm . H₁ – simple setae (arrow).



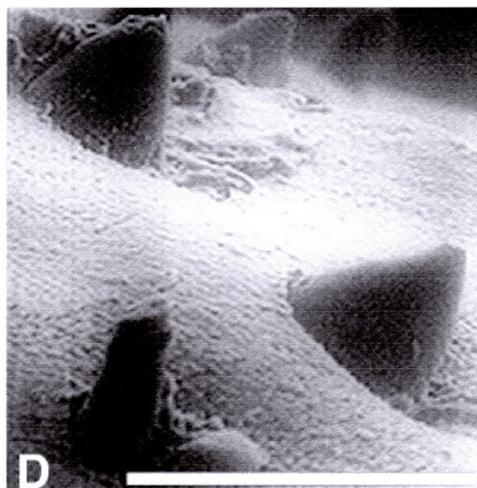
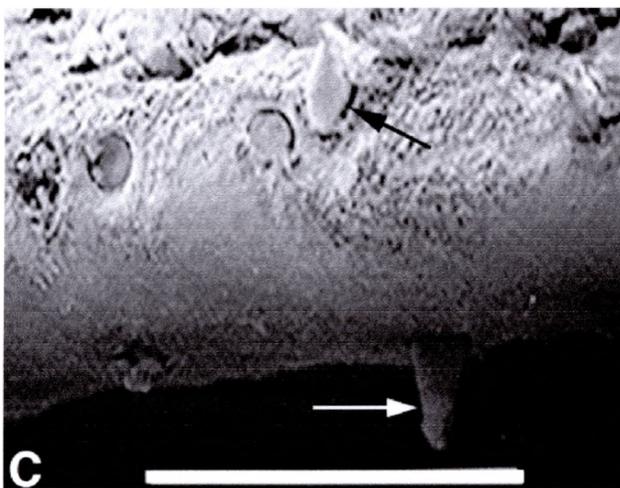
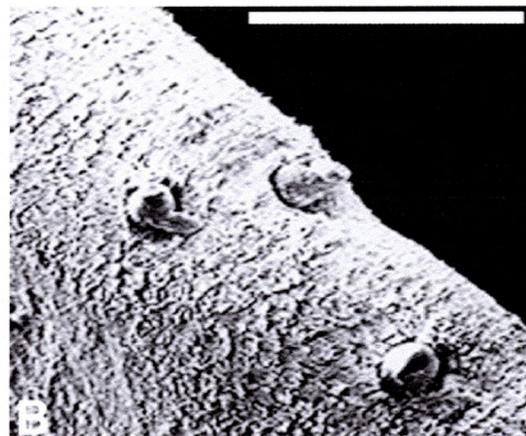
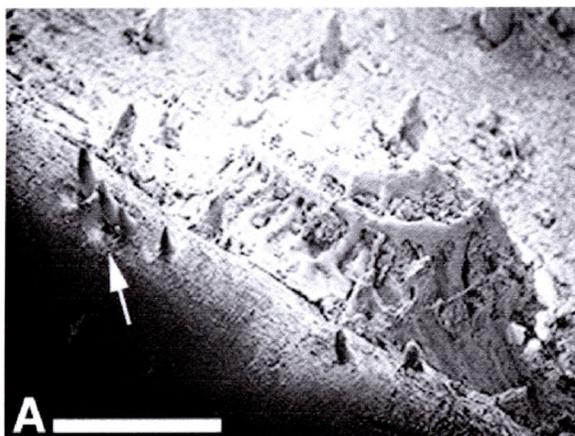
Simple Setae (Figures 1 (H₁), 6, 8)

Simple setae lack setules, are generally conical in shape, and range in length from short to very long, tapering towards the distal tip or ending bluntly (Fig. 6B, 8E-F; Watling, 1989). Long simple setae lie within invaginations or pits (Fig. 6B). All simple setae observed on the pereopods were long and of the same length as the long cuspidate setae (<300 μm). They appear singly or in association with cuspidate setae on the aboral and oral surface of the dactyl of all pereopods of all scyllarid species (Fig. 6B, F), and in the brush pads on the oral surface of the dactyl of the 5th pereopod of female *S. aequinoctialis* and *S. nodifer* (Fig. 8A-F). No simple setae are found in the brush pads of female *S. latus*. All simple setae fall into Watling's (1989) Type II classifications.

Conate Setae (Figures 1 (K₁), 9)

Conate setae are pyramidal in shape (Fig. 9A, D), bear no setules, and are very short in size (>125 μm) (Watling, 1989). As such, they are shorter than short cuspidate setae. Each seta lies within an invagination (Fig. 9B, D) and occur only as single units, not in pairs. Conate setae were found on oral and aboral surfaces of the lateral rim of the merus shield on pereopods 1 - 4 in *S. latus* (Fig. 9A-C) and *S. nodifer* (Fig. 9D) only. They were not found on any other segment, nor were they found on either the male or female version of the 5th pereopods since these lacked the merus shield.

Figure 9: Conate setae on rim of merus shield of *S. latus* and *S. nodifer*. (A) Setae (arrow) on right pereopod, aboral surface, from *S. latus*; (B) setae on right pereopod 4, aboral surface, from *S. latus*; (C) setae (arrow) of left pereopod 1, aboral surface, from *S. latus*; and (D) setae on right pereopod 3, oral surface, from *S. nodifer*. Scale bars: A and C = 500 μm ; B = 200 μm ; D = 250 μm .



Teazel Setae (Figures 1 (R₁), 10 C-E)

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 this study are probably a homologue to the teazel setae described by Thomas (1970), in that their tip is smooth and devoid of setules (Fig. 10C), and extends approximately 50 μm , before elongate setules ($\sim 50 \mu\text{m}$ in length) emerge from the shaft on all sides (Fig. 10D, E). The setules continue proximally for one third of the distal portion of the shaft. The rest of the shaft ($\sim 500 \mu\text{m}$ in length) below the setules is bare. All teazel-like setae observed were set within invaginations and occurred singly, not in pairs. They were arranged in rows on the aboral and oral surface of the rim of the merus shield for *S. aequinoctialis*. These setae were not found on either *S. latus* or *S. nodifer*.

Miniature Simple-Like Setae (Figure 11)

The cuticular surface of all five pereopods is covered with a layer of simple-like setae that, at a distance, provide a texturing look to the surface of these appendages (Fig. 11 A-B, G-H). Each seta is set into its own invagination (Fig. 11 E-F) and seems to be a distinct unit, rather than an extension of the cuticular surface (Fig. 11 C-F, I). These short, simple-like setae were found on all surfaces of all five segments of all pereopods of all three species. Due to the extremely small size of these setae, they have been termed as “miniature simple-like setae,” but are probably a homologue to the simple setae (H₁).

Figure 10: Setal types found on rim of merus shield of pereopods 1-4 on *S. aequinoctialis* only. (A) Rows of long cuspidate setae on left pereopod 2, aboral surface; (B) pairs of long cuspidate setae on right pereopod 1, aboral surface, (C) rows of teazel-like setae with long setules (arrow) on left pereopod 1, aboral surface; (D) setules (arrow) on teazel-like setae on left pereopod 1, aboral surface; (E) high magnification of setules on teazel-like setae on left pereopod 1, aboral surface; and (F) possible hooded homologue setae or frayed setae on right pereopod 3, aboral surface. Scale bars: A, B and F = 200 μm ; C = 100 μm ; D = 20 μm ; E = 10 μm .

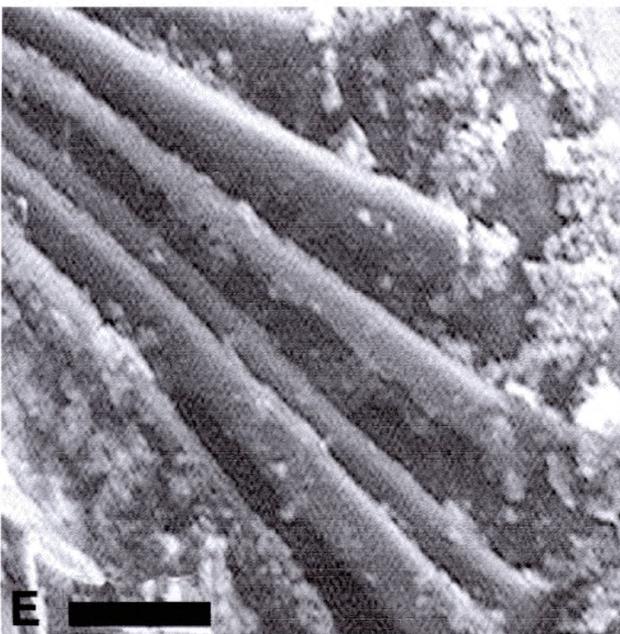
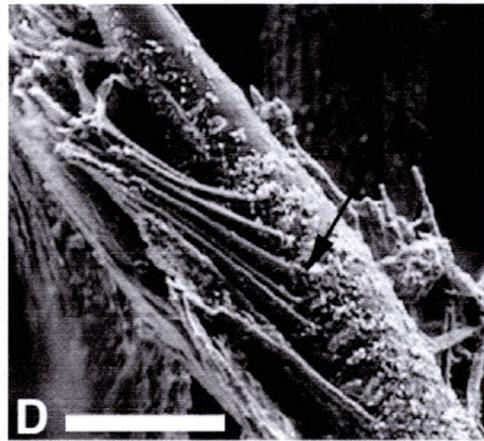
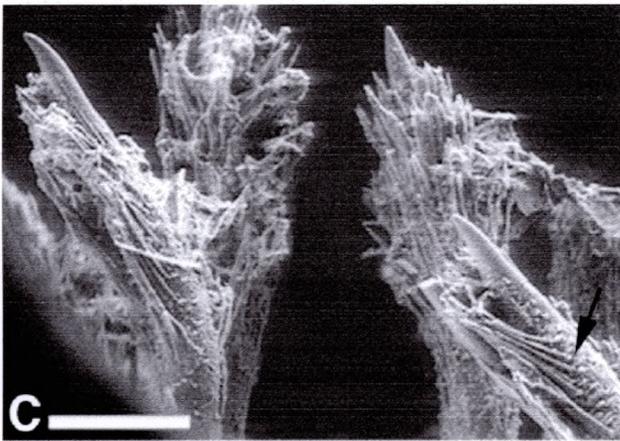
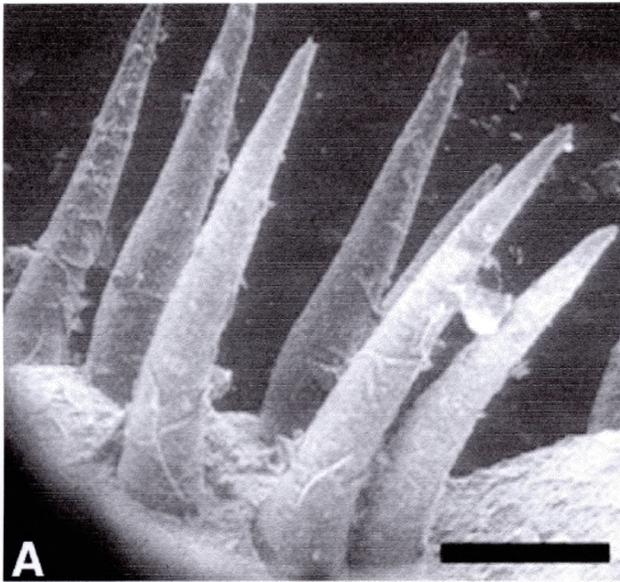
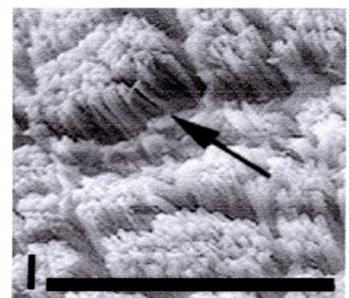
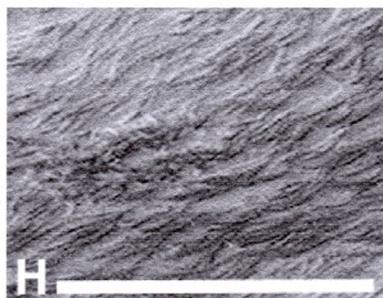
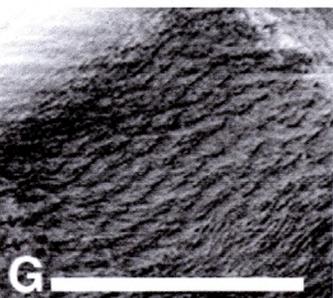
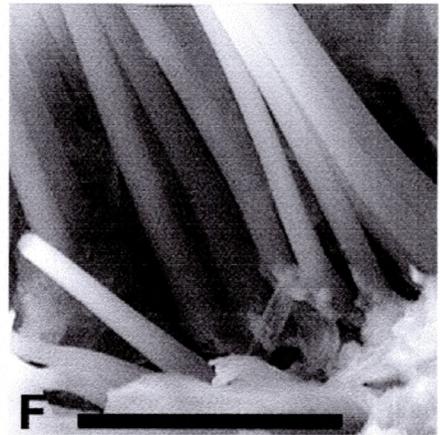
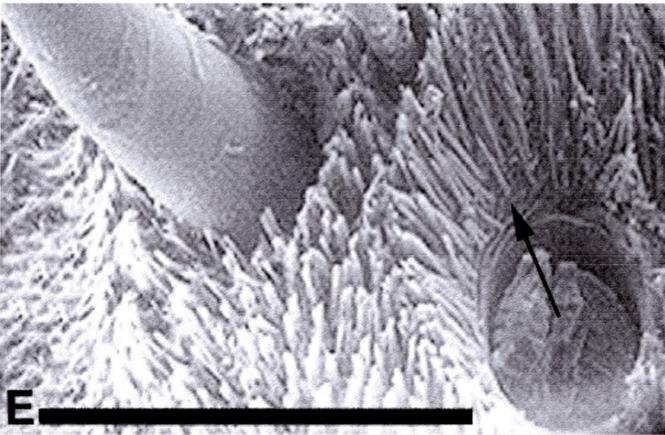
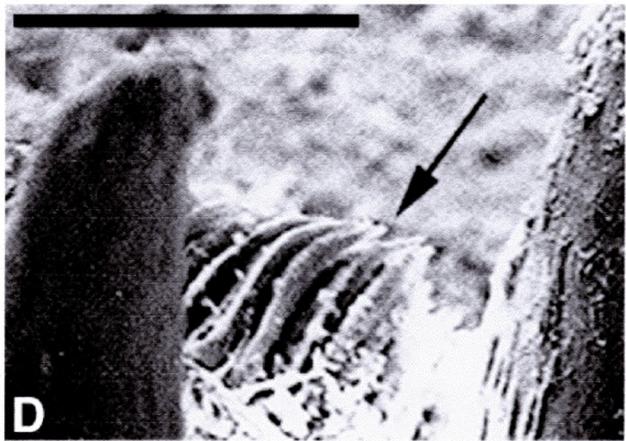
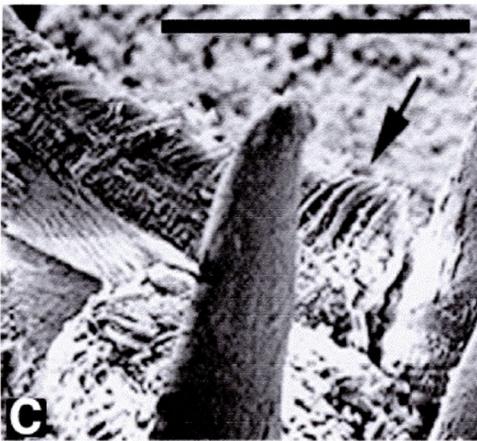
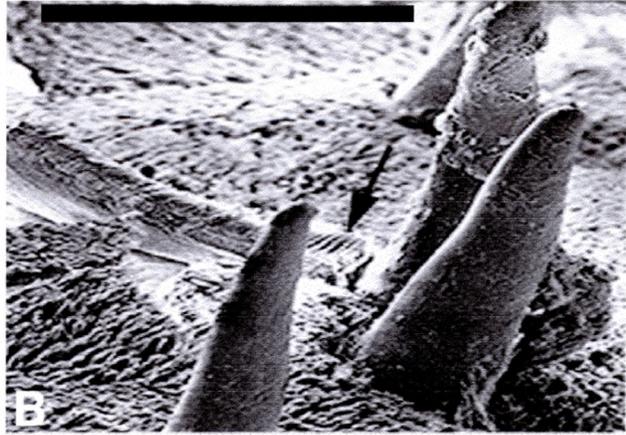
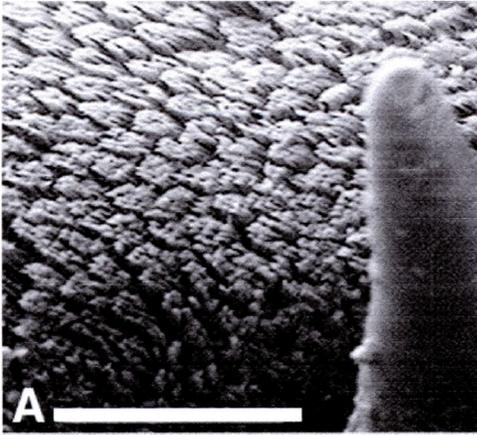


Figure 11: Miniature simple-like setae covering the cuticular surface of pereopods 1-5 for all three scyllarid species. (A) Small, simple-like setae surrounding cuspidate setae on left pereopod 1, merus, oral surface, from *S. nodifer*; (B) rows of small setae (arrow) at break in carapace on left pereopod 3, propus, aboral surface, from *S. latus*; (C) high magnification view of setae (arrow) on left pereopod 3, propus, aboral surface, from *S. latus*; (D) high magnification view of setae (arrow) on left pereopod 3, aboral surface, from *S. latus*; (E) setae (arrow) surrounding empty cuspidate setal invagination on left pereopod 4, proximal propus, aboral surface, from *S. aequinoctialis*; (F) high magnification view of individual setae on right pereopod 1, distal carpus, aboral surface, from *S. aequinoctialis*; (G) patterning caused by presence of miniature setae on right pereopod 4, proximal dactyl, oral surface, from *S. nodifer*; (H) patterning caused by presence of miniature setae on right pereopod 4, proximal dactyl, aboral surface, from *S. nodifer*; and (I) small setal mat (arrow) on male left pereopod 5, ischium, oral surface, from *S. nodifer*. Scale bars: A and B = 200 μm ; C, G, and I = 100 μm ; D and H = 50 μm ; E = 350 μm ; F = 20 μm .



Setal Distribution on the Pereiopods and Their Segments

The first four pereiopods of slipper lobsters are nonchelate. In the male of all species, the fifth pereiopod is also nonchelate; however, in the female, it is chelate, with the dactyl and propus forming the claw (Table 1). Because of the rotation of these appendages with respect to the mouth, it is easier to refer to the surface facing inwards toward the mouth as the oral surface, and that facing outwards toward the substrate on which the lobster walks, as the aboral surface (Figure 12). Thus, the oral and aboral surfaces correspond to the ventral and dorsal surfaces, respectively. Seven 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. Some segments bear ridges, which are rounded crestings of the aboral surface that vary in length and location. The merus segment of pereiopods 1 - 4 also develops a shield, which is an extension of the lateral edge of the merus. This shield extends from proximal to distal ends of the merus and is visible both orally and aborally, but with a concavity towards the aboral view. There is no version of this shield on the medial edge of the merus in any view.

First Pereiopod (Figure 13)

The 1st pereiopod is the most prominent of the legs and bears no ridges along its lateral or medial edges (Fig. 13A-D). Its segments are both thick and wide, but are not particularly long. The dactyl of this pereiopod is rather thick and wedge-like or blunt, with the distal tip or “nail” being darker in coloration (Fig. 13A-D). Right and left pereiopods are symmetrical with regard to shape and structure.

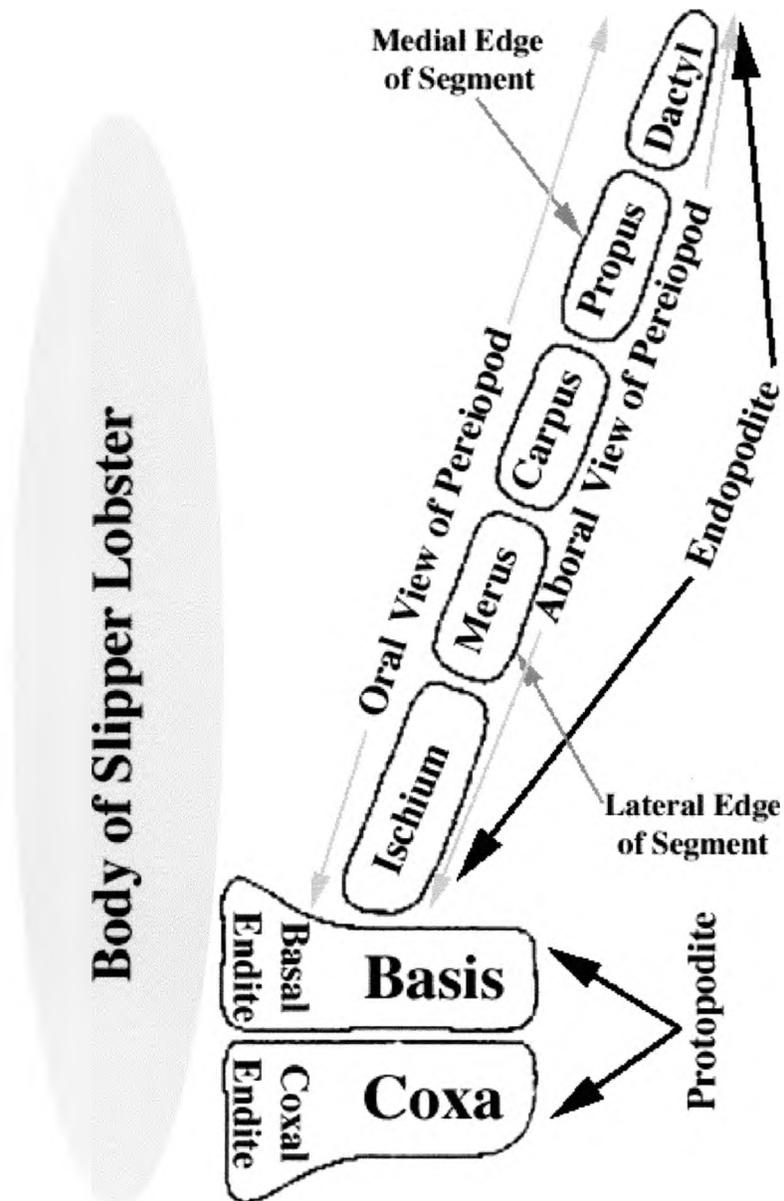


Figure 12. Basic leg diagram (adapted from Lavalli and Factor, 1995) with positional information shown along the endopodite. Exopodites on legs are lost after the larval stages. The epipodite is not shown here. While the basis and coxa are part of each pereopod, they were not examined in this study.

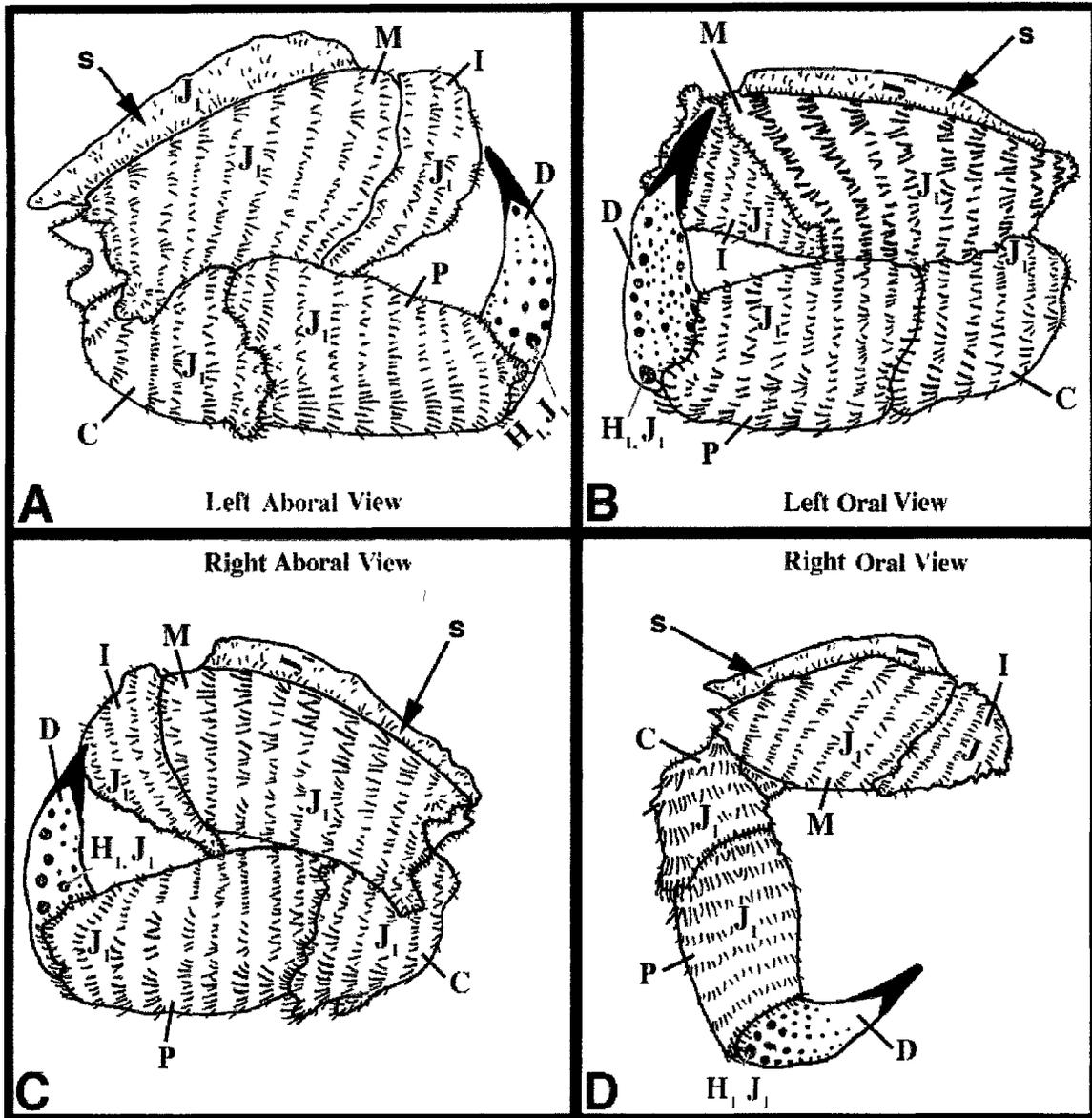


Figure 13: 1st pereiopod showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, s – shield, J₁ – cuspidate setae, H₁ – simple setae, • – stripped dactyl setal pit.

All three species exhibit the same setal distribution pattern for each segment, 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 towards the proximal end of the dactyl on both oral and aboral surfaces, suggestive of larger setal bases. In Figure 13, these invaginations are represented by small black circles and are termed stripped “dactyl setal pits.” 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 aboral surface and decreases on the oral surface and along the medial edge of the aboral surface. The merus also has rows of cuspidate setae, with the setae found singly or in pairs, which are medium in length. These setae increase in length towards the lateral edge and distal end of the aboral surface and decrease in length on the oral surface and medial edge of the aboral surface. The only exception to this setal distribution pattern is on the shield of the merus, which is a flattened process along the lateral edge that curves slightly toward the aboral surface. It is visible from both oral and aboral surfaces (Fig. 13A-D). The lateral edge of the merus shield of *S. aequinoctialis* bears either rows of teazel or long cuspidate setae, but not both types, that extend from the proximal to the distal end of the edge (Fig. 10B, 14A-B). In contrast, the shield of *S. nodifer* (Fig. 9D, 14C) and *S. latus* (Figure 9A-C, 14C) bears only conate setae along the corresponding edge. All surfaces of the first pereopod are covered with miniature simple-like setae.

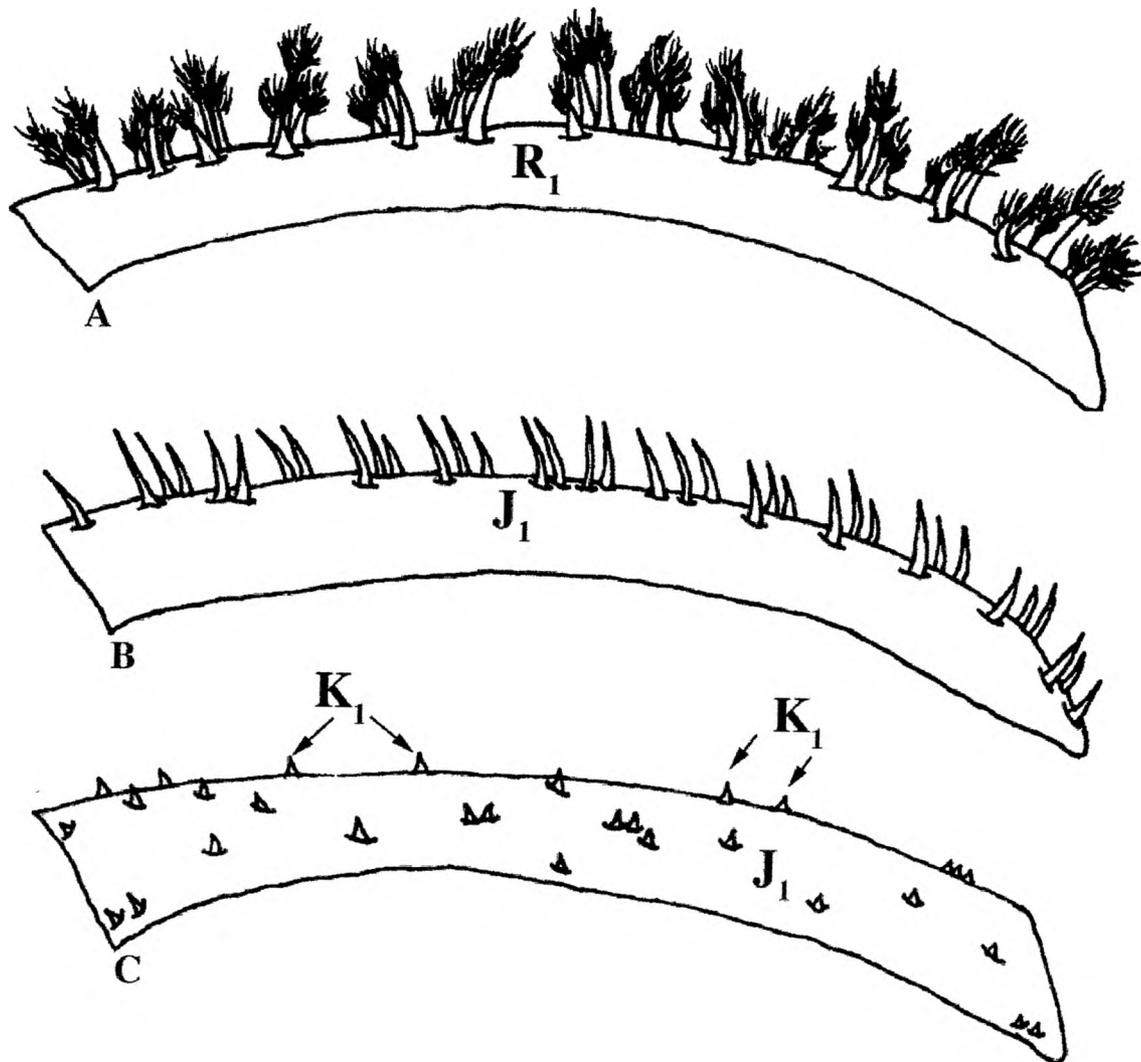


Figure 14: Merus "Shield" with Setae on Rim (lateral most edge). (A) Teazel-like setae (R_1) on *S. aequinoctialis*; (B) long cuspidate setae (J_1) on *S. aequinoctialis*; (C) short cuspidate (J_1) and conate (K_1) setae on *S. latus* and *S. nodifer*.

Second Pereiopod (Figure 15)

The 2nd pereiopod is the longest and narrowest of the five pairs of legs. As with the 1st pereiopod, no segment bears any ridges. Segments are not as thick or as wide as those of the 1st pereiopod. The dactyl of this pereiopod is very long and slim with the “nail” being darker in coloration and bare of setae (Fig. 6E). Right and left pereiopods are symmetrical with regard to shape and structure. All three species exhibit the same setal distribution patterns for the segments of the 2nd pereiopod that were found for the 1st pereiopod.

Third Pereiopod (Figure 16)

The 3rd pereiopod is shorter in length than the 2nd pereiopod, but is greater in width. The dactyl of this pereiopod is short and blunt, with a dark colored “nail.” The 3rd pereiopod bears two ridges on the longitudinal axis of the aboral surface (Fig. 16A-B): (1) mid-sagittally on the propus, stretching from the proximal to distal end, and (2) parasagittally near the proximal end of the carpus towards lateral edge. Right and left pereiopods are symmetrical with regards to shape and structure.

All three species exhibit the same setal distribution patterns for the 3rd pereiopod, with several exceptions. The dactyl bears two large tufts (Fig. 16B, D) of long cuspidate and simple setae near the proximal end of the oral surface (Fig. 6A, C-D). Toward the distal end of the dactyl are smaller tufts of long cuspidate and simple setae arranged in rows on both oral and aboral surfaces (Fig. 6B). The propus and carpus have single or paired cuspidate setae, arranged in rows, that are: (1) of medium length on the aboral surface, becoming longer towards the lateral edge and (2) long on the aboral ridges of

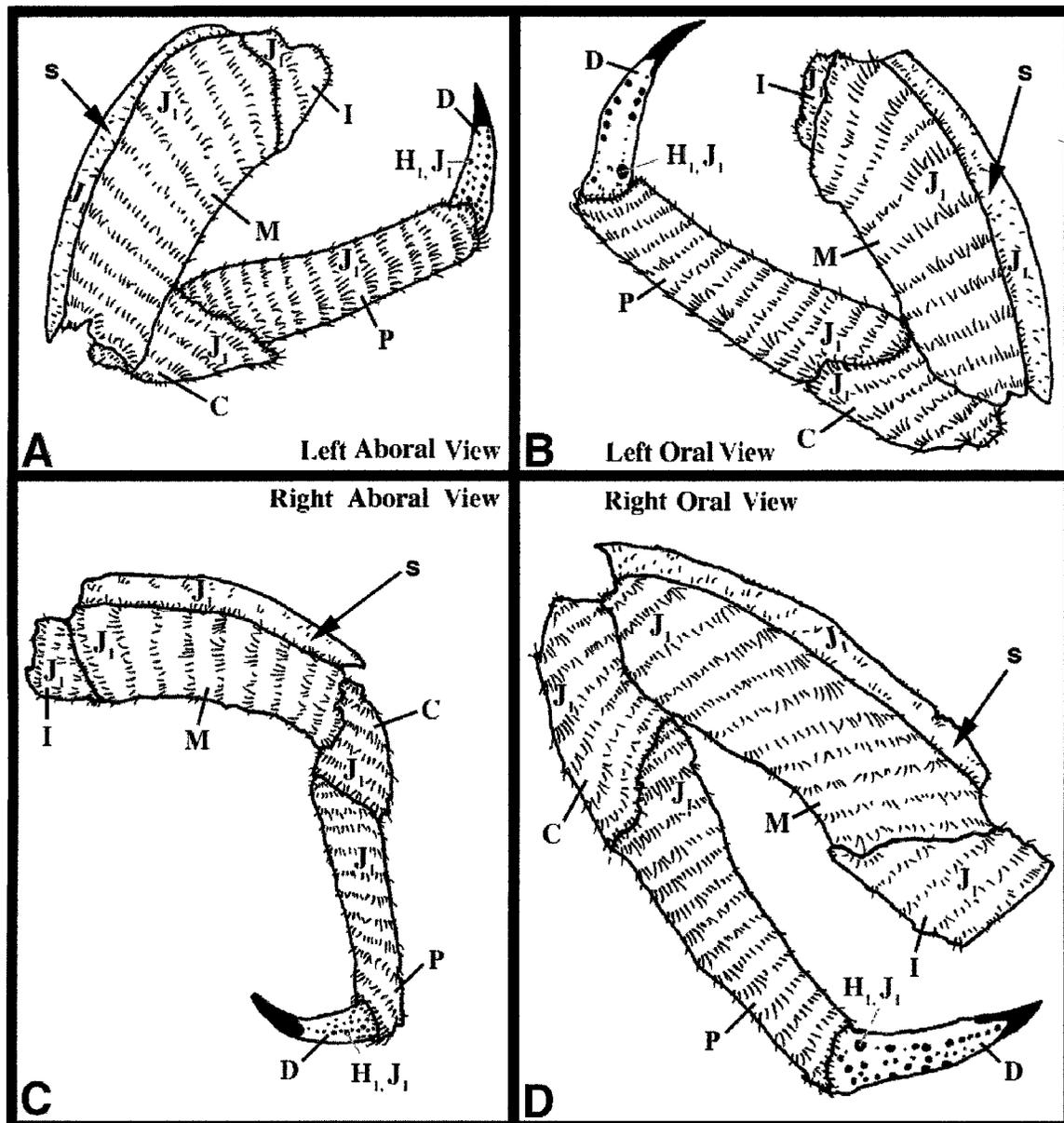


Figure 15: 2nd pereopod showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, s – shield, J₁ – cuspidate setae and H₁ – simple setae, • – stripped dactyl setal pit.

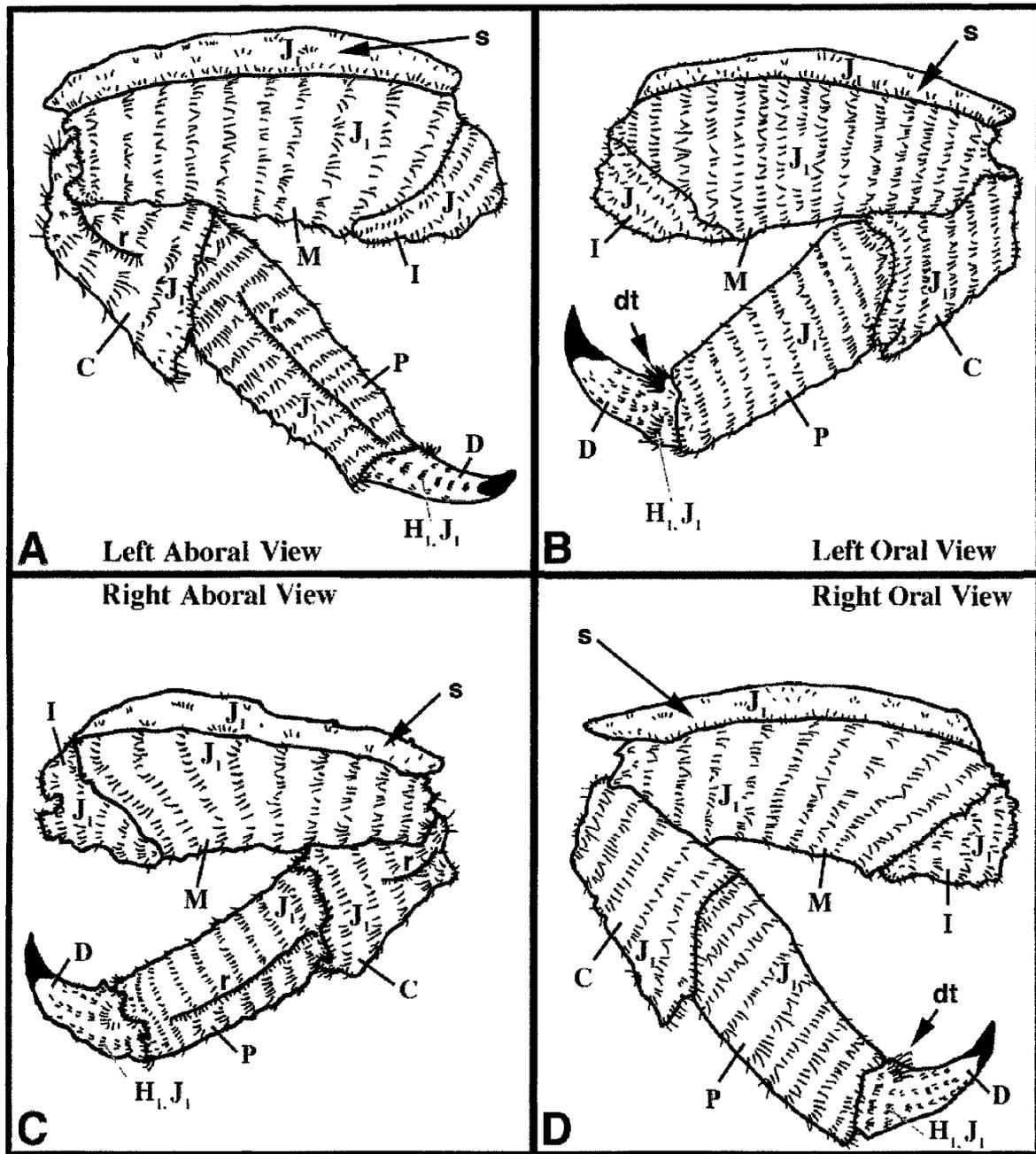


Figure 16: 3rd pereopod showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, s – shield, r – ridge, dt – dactyl tuft, J₁ – cuspidate setae and H₁ – simple setae.

both segments; (3) long at the distal end of the aboral surface (Fig. 7F); and (4) short on the oral surface and along the medial edge of the aboral surface. The merus also bears single or paired cuspidate setae, arranged in rows, that are of medium length on the aboral surface, short on the medial edge, but longer towards the lateral edge and distal end. On the oral surface of the merus, the cuspidate setae are short. The only exception to this distribution pattern is found on the flattened process of the merus that curves slightly toward the aboral surface and arises along the lateral edge. This process is shield-like and visible from both the oral and aboral surfaces. The lateral rim of this shield in *S. aequinoctialis* bears either rows of teazel or long cuspidate setae, stretching from the proximal to the distal end, while in *S. nodifer* (Fig. 9D) and *S. latus* (Fig. 9A-C) it bears only conate setae along its rim. The ischium also bears rows of cuspidate setae of medium length on the aboral surface of the segment (Fig. 16A, C). Within the rows, the setae are found singly or in pairs, and gradually increase in length towards the lateral edge and distal end of the ischium. Cuspidate setae are also present on the oral surface and medial edge of the aboral surface of the ischium, but are shorter in length (Fig. 16A-D).

Fourth Pereiopod (Figure 17)

The 4th pereiopod is smaller in size than the 3rd pereiopod. As with the 3rd pereiopod, the 4th pereiopod bears two ridges on the longitudinal aboral surface (Fig. 17B, D): (1) parasagittally near the medial edge of the propus from proximal to distal end, and (2) parasagittally towards the lateral edge of the carpus from proximal to distal end. Compared with those same ridges found on the 3rd pereiopod, these ridges are more

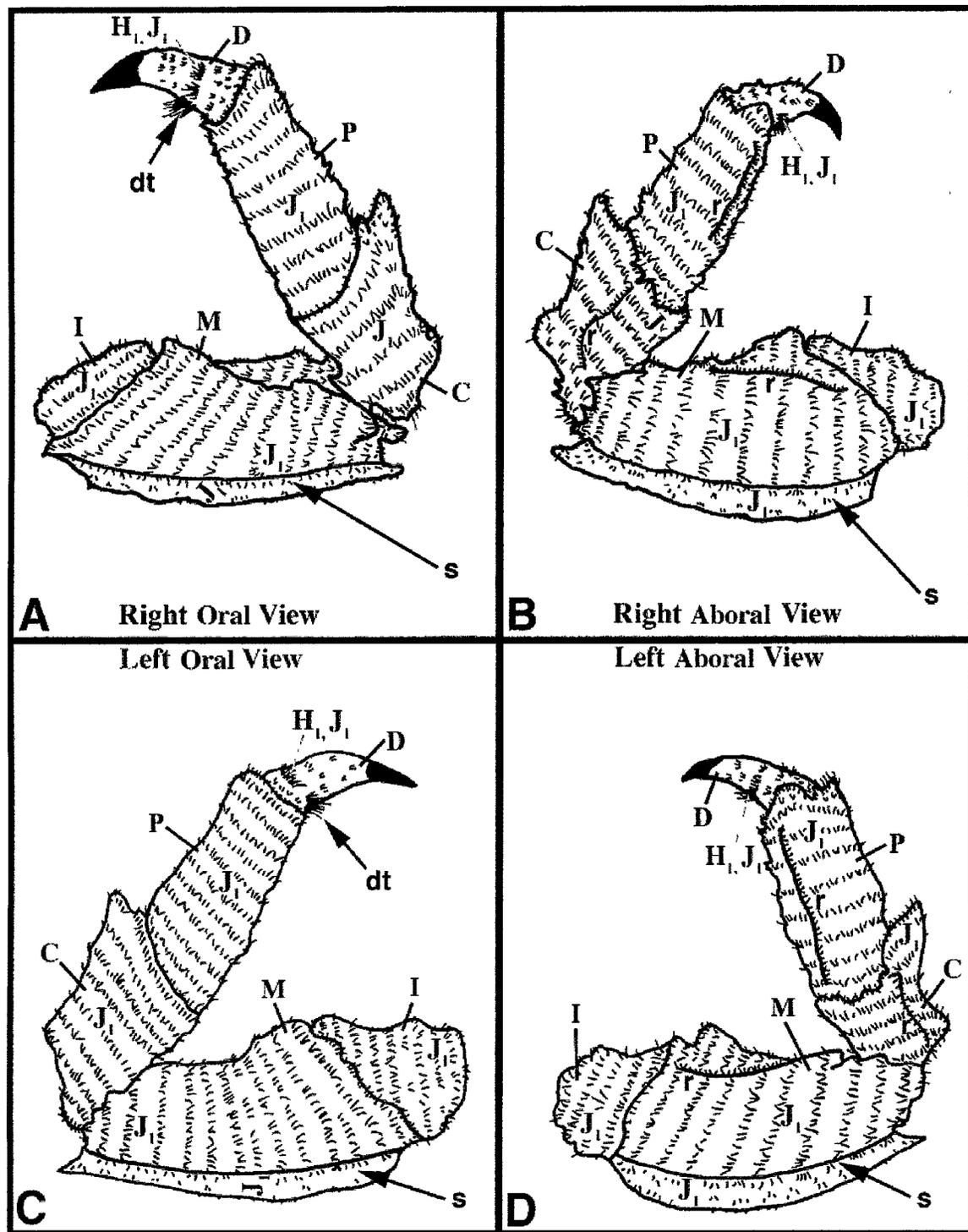


Figure 17: 4th pereiopod showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, s – shield, r – ridge, dt – dactyl tuft, J₁ – cuspidate setae and H₁ – simple setae.

pronounced on the 4th pereiopod and differ in their locations. A third ridge is found on the medial edge of the aboral surface of the merus, and extends from the proximal to distal end (Fig. 17B, D). Right and left pereiopods are symmetrical with regard to shape and structure.

All three species exhibit the same setal distribution patterns for the 4th pereiopod and all of its segments as that found for the 3rd pereiopod. Long cuspidate setae are found singly or in pairs, with a row like arrangement, on the new ridge formed on the medial edge of the aboral surface of the merus (Fig. 17B, D).

Fifth Pereiopod – Male (Figure 18)

The 5th pereiopod is the smallest of all the pereiopods and nonchelate in the male. It bears three ridges on the longitudinal axis of its aboral surface (Fig. 18B, D): (1) parasagittally near the lateral edge of the propus extending from the proximal to distal end; (2) towards the lateral edge of the carpus extending from the proximal to distal end; and (3) parasagittally near the medial edge of the merus extending from the proximal to distal end. These ridges are more pronounced than in the 4th pereiopod and are changed in their locations. Two new ridges appear on the aboral surface (Fig. 18B, D): (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. Right and left pereiopods are symmetrical with regard to shape and structure.

All three species exhibit the same setal distribution patterns for the 5th pereiopod. The dactyl bears two large tufts of long cuspidate and simple setae on its oral surface, near the proximal end (Fig. 18A, C). Smaller tufts of long cuspidate and simple setae,

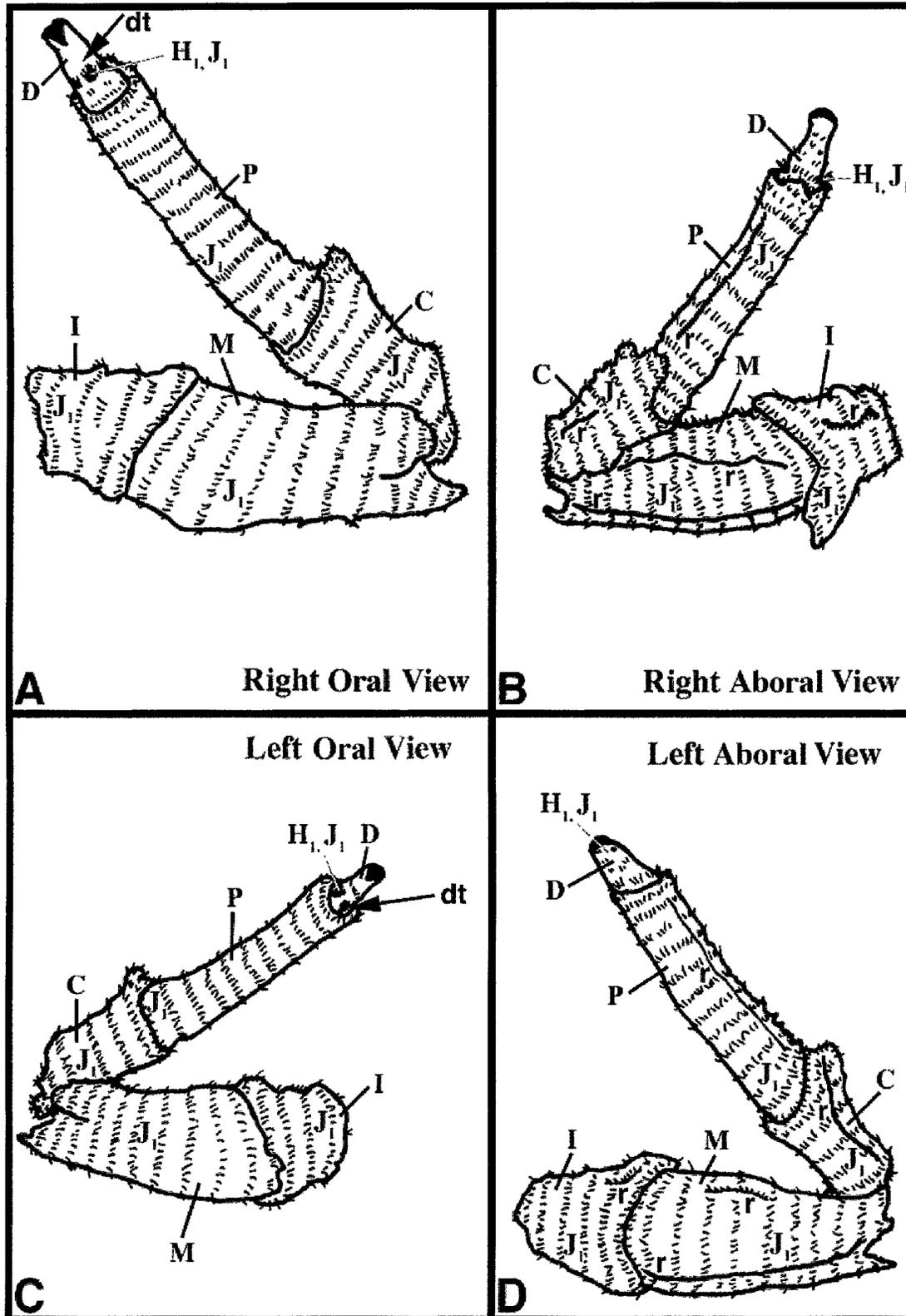


Figure 18: 5th pereiopod (male version) showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, r – ridge, dt – dactyl tuft, J₁ – cuspidate setae and H₁ – simple setae

arranged in rows from the proximal to distal end, are present on both oral and aboral 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 towards the lateral edge of the aboral surface only; (2) long on the aboral ridges of both the propus and carpus; (3) long at the distal ends of the aboral surface of the segments (Fig. 7B); and (4) short on the oral surface and along the medial edge of the aboral surface. The merus also bears single or paired cuspidate setae in rows that are of medium length on the segmental surfaces. These become longer towards the lateral edge and distal end of the aboral surface and shorter on the oral surface and medial edge of the aboral surface. The ridge that formed a prominent shield on the merus of the 1st through 4th pereopod is reduced here in all species to a slight ridge that bears, from the proximal to distal end of the segment, only cuspidate setae of medium length (Fig. 18B, D). The ischium also bears single or paired cuspidate setae arranged in rows that are of medium length on the segmental surfaces. These setae become longer towards the lateral edge and distal end of the aboral surface and shorter on the oral surface and medial edge of the aboral surface.

Fifth Pereopod – Female (Figure 19)

The female's 5th pereopod is slightly larger than the male's. The distal tip of the dactyl articulates with the distal tip of the propus in order to form a chela (Fig. 8A, 18B, D). The ridges of the aboral surface are identical to the male's 5th pereopod, and, as in the male, the right and left pereopods are symmetrical with regard to shape and structure.

The dactyl no longer bears large tufts of setae as seen in the 3rd, 4th and 5th (male) pereopods (Fig. 18A, C). The oral surface of the distal tips of the dactyl and propus bears a brush pad, set in a groove. This "brush pad" is composed of rows of long

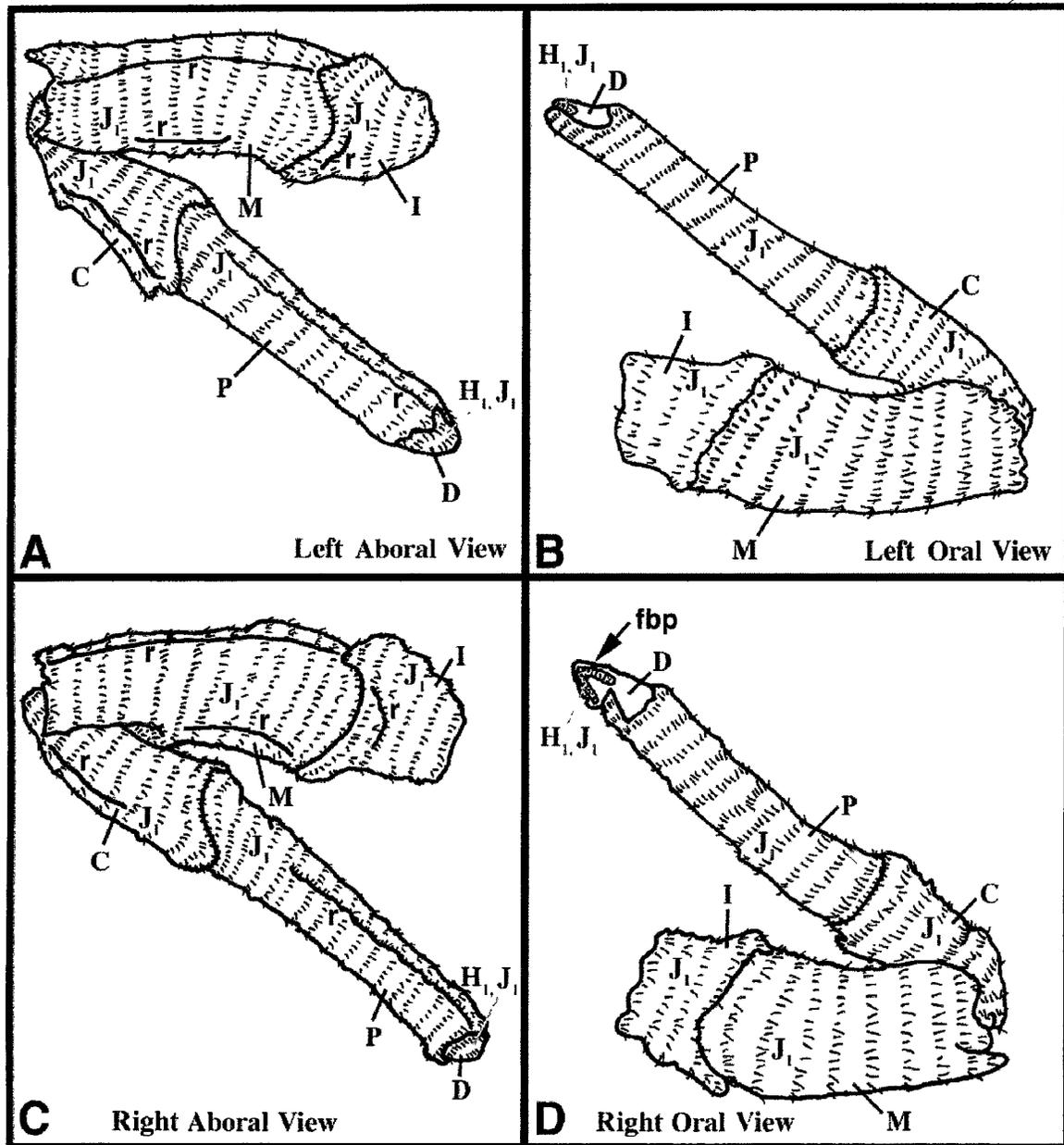


Figure 19: 5th pereiopod (female version) showing left and right legs with oral and aboral views. D – dactyl, P – propus, C – carpus, M – merus, I – ischium, r – ridge, fbp – female brush pad, J₁ – cuspitate setae pad and H₁ – simple setae.

cuspidate and simple setae for *S. nodifer* and *S. aequinoctialis* (Fig. 8B-D), but only long cuspidate setae are found in all sections of the brush pad for *S. latus* (Fig. 8A). Towards the proximal end of the groove in which this pad lies, only simple setae are present in *S. nodifer* and *S. aequinoctialis* (Fig. 8E-F). The setal distribution pattern for the propus, carpus, merus, and ischium are the same as in the 5th pereopod of the male.

DISCUSSION

In contrast to the slipper lobsters of this study, nephropid and palinurid lobsters have highly setose pereiopods, with a great diversity of setal types, some of which have been identified as contact chemoreceptors (taste) (Derby, 1982). Lobsters in those families insert their pereiopods into the substrate to locate potential prey by taste. They also use the pereiopods to scrape flesh from bivalves that have been opened via the chelae (nephropids) or mandibles (palinurids). The lack of both diversity of setal types and numerous setae on the pereiopods of scyllarids suggests that their pereiopods may be functionally different from those of nephropids and palinurids. As in nephropids and palinurids, scyllarids insert their pereiopods into substrate, presumably to locate potential prey (bivalves). However, they then use the pereiopods to open the located bivalves. The “nails” on the dactyl tips are sharp and cut through the adductor muscles of bivalves in a “shucking” process (Lau, 1987; Spanier, 1987). All pereiopods are then used to wedge open the bivalve and scrape the flesh towards the mouthparts (Lau, 1987). This harsh use of the pereiopods may necessitate fewer setae, particularly on dactyl segments, due to the likely loss or damage of setae while wedging and prying open the lobster’s prey. Even though the distal most portion of the dactyl is bare of setae, the remaining surfaces of the dactyl (particularly those of the 1st and 2nd pereiopods) appear to bear damaged setae in all specimens examined. The dactyl tufts seen on the 3rd and 4th pereiopods may compensate for the loss of the setae on the dactyls of the first two pereiopods. In addition,

scyllarids insert their antennule tips into the mantle tissue of the valves of mollusks both during the shucking process and while scraping the flesh from the valve inner surfaces (Malcom, personal observation). Nephropids do not use their antennules in such a manner, and while 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). In scyllarids, antennules may play a dual role in both distant and contact chemoreception, and may compensate for fewer setae on the pereopods.

As mentioned above, there was found to be less diversity of setal types and fewer setae for the three species examined than what is seen on the pereopods of the other two families of lobsters, the nephropids and palinurids. Only five types of setae were observed on the pereopods of slipper lobsters: simple, cuspidate, teazel-like, miniature simple-like, and connate. 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. Derby (1982) demonstrated that simple setae can serve both functions in nephropid lobsters, and Cate and Derby (2001) have shown that simple setae are bimodal in function for spiny lobsters. The presences of apical or terminal pores (Fig. 5C) that are seen on some of the cuspidate setae strongly suggest a chemosensory function (Watling, 1989; Jacques, 1989). Farmer (1974) suggested that cuspidate setae might serve to capture particles or food pieces; thus, they may also function to “taste” the food prior to passing it to mouthparts for further assessment and ingestion.

Teazel-like setae could possibly be chemosensory setae that are developed during a later growth stage. Farmer (1974) has suggested that some setae may serve as beginning

stages in the development of other setae. Chemosensory setae are often designed to perform different behavioral tasks (Atema, 1985) and, since some setae can change structure after molting (Cate and Derby, 2002), it is possible that the cuspidate setae found on some *S. aequinoctialis* specimens are replaced by the teazel-like Type I setae seen on other *S. aequinoctialis* specimens in order to fulfill a new behavioral objective. Since samples were gathered from molts and dead specimens, it would explain seeing both the long cuspidate and teazel-like setae on the lateral rims of the merus shield. More extensive studies need to be done observing specimens over a period of several molts to determine when and how these changes occur (Cate and Derby, 2002). Also it was unclear as to whether some setae, which were found in rows below the teazel-like setae, were a homologue to the hooded setae described by Cate and Derby (2002), or were simply broken/frayed setae (Fig. 10F). Since the teazel-like setae above were undamaged, it is less likely that these setae were frayed. Use of fungicides and bactericides prior to dehydration sequences, as well as higher magnification views, may help better determine the type of setae seen around the teazel-like setae.

The miniature simple-like setae observed may serve as a protective surface above the epicuticle against bacteria, protozoans, or fungi (Fig. 11A-I). 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 debris upon all examinations (Fig. 11F). Such setae are absent in nephropid and palinurid lobsters, which frequently have bacterial and fungal fouling on the epicuticle of their carapace and appendages. These miniature setae are probably a homologue to the Type II simple setae because while they

provide a sculptured look to the carapace, they are actually smooth and devoid of setules themselves.

Some trends were observed while documenting the setal morphology of *S. latus*, *S. nodifer* and *S. aequinoctialis*. Pereiopods become progressively smaller towards the posterior end of the lobster's body, with the 5th pereiopods of male lobsters being the smallest. The propus, carpus, merus and ischium segments bear additional longitudinal ridges along their lateral and medial edges, starting with the 3rd pereiopods. The oral surfaces of the pereiopods tend to have shorter cuspidate setae, often much shorter than those found on the aboral surfaces. Lateral edges of the aboral surface tend to have longer cuspidate setae. Medial edges of the aboral surfaces have cuspidate setae of medium length. The distal edges of segments, where articulation with the next segment occurs, also have long cuspidate setae (for the propus, carpus, merus and ischium only) (Fig. 7A-F). The large shield arising from the lateral edge of both oral and aboral surfaces of the merus is the first instance where a divergence from the typical cuspidate and simple setal types is found. The rim of this shield bears conate setae in *S. latus* and *S. nodifer* (Fig. 9A-D), but in *S. aequinoctialis* it has either teazel-like (Fig. 10C-E) or long cuspidate setae (Fig. 10A-B), but not both. The difference between male and female 5th pereiopods—the presence of a brush pad on the chela of the female (Fig. 8A-F)—can be explained by the need for female lobsters to be able to groom eggs extruded and cemented upon their abdominal pleopods. The first four pereiopods are anteriorly oriented, while the 5th pereiopod is rotated back towards the posterior end of the lobster. This orientation and the presence of the brush pad allow females to reach their eggs and remove parasites and fouling agents from them. Finally, the setal distribution pattern is very consistent

among the pereopods. The setae are arranged in uneven transverse rows on each segment, with tufts appearing on dactyl segments only. Cuspidate setae are the predominant type found on all segments. *S. latus*, *S. nodifer* and *S. aequinoctialis* were found to have almost exactly the same setal distribution pattern and their segment morphology was the same.

Future studies should include an examination of the mouthparts and antennules, which are other organs that have a sensory function for food location and identification. Transmission electron microscopy work on all setal types found on the pereopods needs to be done to confirm the presence of neurons necessary for sensory functions. Finally, studies of feeding behavior need to be conducted in order to correlate setal types and locations with the movement patterns of the pereopods to determine function during feeding.

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