DESCRIPTION AND DISTRIBUTION OF ANTENNULAR SETAE OF SCYLLARID LOBSTERS (*SCYLLARIDES AEQUINOCTIALIS*, *S. LATUS*, AND *S. NODIFER*) WITH COMMENTS ON THEIR POSSIBLE FUNCTION

THESIS

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ABSTRACT

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This study describes the morphology and distribution of setae on the lateral flagella of the antennules of three species of scyllarid (slipper) lobsters. Setae were examined using Scanning Electron Microscopy and their distribution patterns were directly mapped for three regions of the antennule (base, tuft, and tip). The distribution pattern was then analyzed for differences between left and right antennules and males and females within a species, and then among species by comparing counts of setae per annulus in the ventral tuft region only. Parsimony analyses were conducted on setal distribution data compiled from the entire antennule for each individual of the three species to resolve the relationships among the species. Using a modified version of Watling s scheme for setal morphology, six types of antennular setae were identified based on their external morphology: aesthetascs, simple, modified simple, asymmetric, hemi-plumose, and toothbrush setae. These different types were found to be organized in a clear pattern over the ventral and dorsal surfaces of the lateral flagella of the antennule. Aesthetasc, asymmetric, modified simple and hemi-plumose setae were only found on annuli in the tuft region between the distal and proximal ends of the flagellum. Simple setae were found on all annuli of all regions of the antennule, and toothbrush setae were mainly concentrated on all annuli of the base region and on proximal annuli of the tuft region. All species of scyllarids had the same general pattern of setal distribution and there were no differences found between left and right, or male and female antennules. The parsimony analyses provided little resolution indicating that there was general overlap in the number and distribution of setae among the three species. Similar setae located on the lateral antennules of species from the families Nephrophidae and Palinuridae (clawed and spiny lobsters) are chemo- and/or mechanoreceptive and are used for distance chemoreception (olfaction). Given the similarity in structure to these previously described setae, it is almost certain that the aesthetascs on slipper lobsters have a chemoreceptive function and that the simple and toothbrush setae described most likely have a bimodal chemomechanoreceptive function.

INTRODUCTION

Chemical and mechanical stimuli present in the environment provide cues that allow animals to detect, identify and orient themselves relative to potential food items, shelter, predators, or conspecifics, and mates (Carr and Derby, 1986; Atema, 1995). Chemical stimuli are generally carried downstream from their source and, due to turbulence in the medium (either air or water), are variable in both time and space (Moore and Atema, 1991; Murlis et al., 1992; Ditmer et al., 1995; Zimmer-Faust et al., 1995; Finelli et al., 1999). Sensory abilities derived from chemo- and mechanoreceptors, enable an animal to track stimuli to its source by combining information on both intensity of the chemical signal and the direction of movement of the medium (Kennedy, 1986; Weissburg, 1994). Chemo- and mechanorectors can take many forms, depending on the integument of the organism.

For arthropods, the cuticular exoskeleton is a shared and unique structure that forms a protective interface limiting communication between the organism's internal organs and the external environment (Hallberg and Hansson, 1999). In order to regain communication with the environment, arthropods have developed cuticular hair organs (or setae) over their bodies to assist them in sensory reception. These cuticular hair organs can occur in a diversity of forms. Much of this diversity can be attributed to the type and number of setules present on the hair shaft. Setules are cuticular outgrowths and elaborations on the exterior of the setal shaft itself (Factor, 1977).

Although setae are ubiquitous in arthropods, early authors working on decapods provided few names or classifications of the setae found on their study organism (Watling, 1989). The first comprehensive system of classification was conducted by Thomas (1970) on the setae of the adult crayfish *Austropotamobius pallipes*. Thomas divided the setae of

the *A. pallipes* into two main groups: 1) setae having no basal septum, with relatively thick walls and inconspicuous ampulla; and 2) setae having a basal septum with relatively thin walls and a well-developed ampulla. These categories were further divided into several subdivisions based on denticulation. Group 1 contained smooth and denticulated setae, while Group 2 consisted of septate denticulate, plumed, and plumodenticulate setae.

Fish (1972) divided the setae on the isopod *Eurydice pulchea* into two groupings based on size: macrotrichs (0.025 to 0.4 mm in length), and microtrichs (2 to 10 μm in length). She separated the macrotrichs depending on whether the structures were simple, setulose, denticulated, or non-denticulated and non-setulose, and further subdivided these divisions by their degree of chitinization and thickening of the shaft wall to form a seta, a bristle, or a spine. Seta represented the least chitinized structure, while spines represented the most chitinized structure. Microtrichs were likewise divided into two divisions based on whether the setae arose from single sockets or crescentic rows.

Farmer (1974) studied the functional morphology of mouthparts and pereiopods of *Nephrops norvegicus* and classified the setae into 3 basic types: simple, plumose, and serrate. He identified twelve different setal structures, which were simple variations of one of his three basic types. Farmer gave the location of the various setal types and tried to interpret possible function according to the location. According to Watling (1989), Drach and Jaques (1977) proposed the most complex setal classification system at that time by considering all aspects of setal morphology, from internal to external structure, and formulated a set of descriptors for both smooth seta and seta with cuticular outgrowths.

By the late 1970's there was considerable confusion regarding discriminant names and their application; thus, Factor (1977) modified the groupings characterized by Thomas (1970) in the hopes of standardizing terminology. Factor established ten categories: plumose, pappose, plumodenticulate, serrate, triserrate, serrulate, triserrulate, cuspidate, simple, and hamate. Out of these categories pappose, plumodenticulate, serrate, serrulate, and cuspidate contained subsidiary classes.

Despite these many attempts at useful classification, the result of the differing descriptions of arthropod setae was confusion in the literature and inconsistency of research methodology. In an effort to improve this situation, Watling (1989) reviewed and evaluated the existing literature, and subsequently created a classification system based on the criteria of homology. This re-evaluation provided a framework allowing any seta, regardless of the taxon investigated, to be accurately named. Watling's system was based on Remane's (1971) account of the homology theorem criteria, which was refined by probability calculations first proposed by Riedl (1978) and modified for ultrastructural research by Rieger and Tyler (1979). First, similar structures may be considered homologues if they have similar positions with respect to other structures when compared to other species; likewise, their component parts will also have similar positions with respect to one another. Second, dissimilar structures can be determined to be homologues if a sequence can be resolved that illustrates the order of a series of transformations for that structure (i.e., a morphocline). Finally, similarities may be homologues if they coincide with other characters or are similar in their distribution within a group of organisms. Generally, homologues are likely to co-occur in the same genera of organisms so the identification of one may form a basis for recognizing another.

Before a structure can be considered a homologue, it must also be established that it is not an analogue (Rieger and Tyler, 1979). According to Rieger and Tyler (1979), similarities may be viewed as analogues if: 1) they are subject to common selective pressures; 2) their material composition is similar due to similar environmental conditions; 3) they are likely the result of being the only solution for a particular functional problem; 4) they are ontogenically derived from different tissues; or 5) they are influenced by similarity-dependent selective pressure. Finally, homoiologous structures may occur that contain both homologous and analogous substructures, or have an analogous form on a homologous base (Riedl, 1978; Watling, 1989).

Watling (1989) used these criteria to determine what morphological components on setae could be used to determine homology and developed the following guidelines. Structures that indicate a high probability of homology are referred to as primary structures: presence or absence of annulation, presence or absence of setules on the shaft, mode of articulation and, possibly, the presence of a chemoreceptive tip. Secondary structures are features that have no value for indicating homology and range from the presence or absence of denticulations to features of the basal septum (Watling, 1989). On the basis of these categories, Watling (1989) established four fundamental setal types (for illustrations and descriptions see Table 1): Type I--annulate, with setules; Type II--annulate, without setules; Type III--non-annulate, robust; and Type IV--non-annulate, small and non-robust. Within this framework, Watling retained the descriptive names used by previous investigators for several of the setal types, including such terms as "plumose", "acuminate", and "cuspidate."

Similar setal types occur on lobsters and, in particular, on their appendages. In lobsters, the principle organ involved in distance chemotaxis is the antennule (1st antenna). This structure includes three peduncle segments and a medial and lateral flagellum. The lateral flagellum possesses both chemo- and mechanoreceptors (Derby et al., 1982; Schmidt et al., 1992; Schmidt et al., 1996a; Schmidt et al., 1996b; Guenther and Atema, 1998; Cate and Derby, 2001). Studies show that lobsters use their lateral antennules in social behavior (Zimmer-Faust et al., 1985; Cowan, 1991; Karavanich and Atema, 1998) and in locating food (Derby and Atema, 1981; Zimmer-Faust 1987; Basil and Atema, 1994; Beglane et al., 1997; Derby et al., 2001). Both left and right antennules of nephropid lobsters are necessary for successful chemo-orientation to near- and far-field sources (Devine and Atema, 1982; Beglane et al., 1997). When an entire antennule was ablated (removal of both chemo- and mechanoreceptors), lobsters could not orient normally to a far-field source. However, the removal of only chemoreceptive abilities in one antennule still allowed for successful orientation, which suggests that a sense of flow on both antennules and

Table 1. Descriptions and illustrations for the setal types in Watling's (1989) classification listings complied from various authors.

Type I. Annulate, with setules

A. With infracuticular socket

1. Plumose°

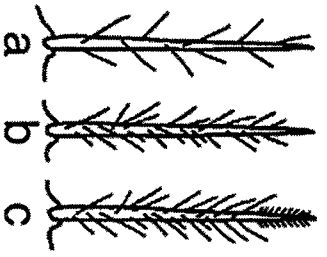
— Setae bear two distinct rows of long, fine, ribbonlike setules along most of the length of the shaft. The setules may be densely or sparsely arranged, but rows are always opposite each other, forming an angle of 180°. Annulations of the shaft may or may not be present (Lavalli and Factor, 1992).

2. Pappose°

— a) Pappose setae have long, fine setules, which are irregularly arranged about the shaft in a seemingly random manner. These setae may or may not have a terminal pore (Lavalli and Factor, 1992).

— b) Densely pappose setae are similar to (a), but bear more setules along the shaft (Lavalli and Factor, 1992).

— c) Setae are similar to (b), but have fine denticulations only at their tips (Lavalli and Factor, 1992).



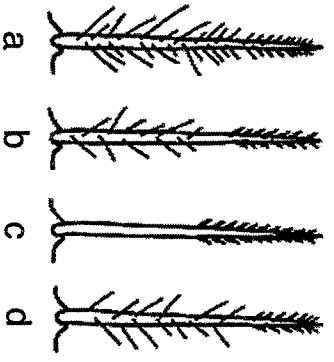
3. Plumodenticulate°

— a) Randomly and sparsely arranged setules of the proximal portion of the shaft gradually give way to finer and more densely arranged distal setules (Lavalli and Factor, 1992).

— b) The sparse setules of the proximal portion of the shaft are sharply separated from the finer, denser setules of the distal shaft. The two regions may be separated by a bulbous swelling of the setal shaft (Lavalli and Factor, 1992).

— c) Setae are nearly identical to (b), but no setules are present on the proximal portion of the shaft. The distal portion of the shaft bears fine, densely packed setules. A bulbous swelling may or may not be present midway along the shaft (Lavalli and Factor, 1992).

– d) Setae bear long, sparse setules proximally (identical to those in (a) and (b)), but have shorter, coarser setules distally (Lavalli and Factor, 1992).



4. Forked setae[§]

— These setae are well chitinized recurved spines with a sharply pointed apex that contain two accessory spines that arise distal to the annulation (Fish, 1972).

B. With supracuticular socket

1. Plumose[Σ]

Same description as A.1. plumose setae above except that they contain a supracuticular socket instead.

Type II. Annulate, without setules or with denticulae

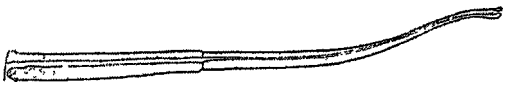
A. With smooth shaft

1. Acuminate[Σ]

— Setae have a smooth, thick cuticle with a tapering shape after the mid-length annulation (Guenther and Atema, 1998).

2. Rod[†]

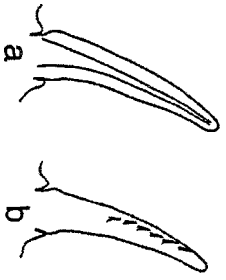
— Relatively long setae which taper gently from the annulation to the tip. These setae have a blunt apex and the preannular portion of the shaft is columnar (Thomas, 1970).



3. Cuspidate[Ω]

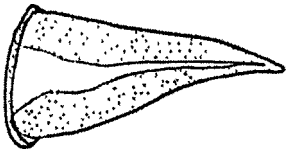
— a) Setae are long, conical, and toothlike. They are stout, with thick walls, relatively narrow lumens, and lack setules (Lavalli and Factor, 1992).

— b) Setae are similar to (a), but bear sparsely arranged, fine, short setules on the shaft (Lavalli and Factor, 1992).



4. Conate[†]

— Relatively short stout setae with a distinct annulation near the base. Conate setae are sharply conical and have pointed apices (Thomas, 1970).



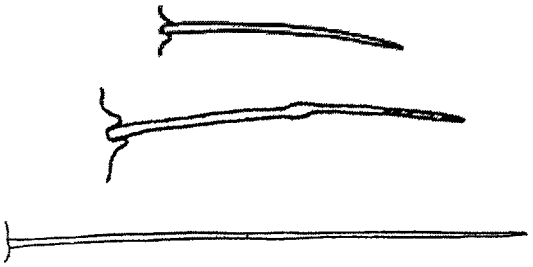
5. Papillate

— Fairly long setae, with the distal third of the shaft curved away from the vertical (Thomas, 1970).

IMAGE NOT AVALIABLE

6. Simple[°,†]

— Simple setae can be long or short and bear no setules. They are conical in shape and some gradually taper towards the tip, while others may have a blunt apex. Some simple setae may contain a bulb midway along the length of the shaft (Lavalli and Factor, 1992).



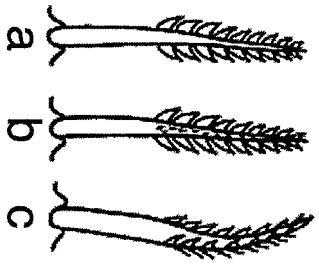
B. With denticulate shaft

1. Serrate[°]

— a) Serrate setae are characterized by large, distinct, toothlike denticles along the distal half of the shaft, arranged in two rows forming an angle of less than 180° (Lavalli and Factor, 1992).

— b) Along with the two rows of toothlike denticles, setae bears scales on the opposite side of the shaft. These scales may be arranged in several ways: sparsely (scales arise only occasionally along the distal half of the shaft); in rows of three (scales overlap each other); and densely packed in a random pattern (Lavalli and Factor, 1992).

— c) Setae contain a shorter, finer row of scales opposite the larger toothlike denticles (Lavalli and Factor, 1992).



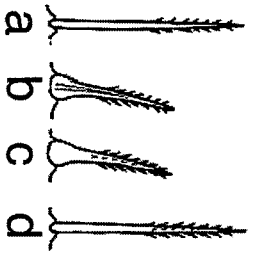
2. Serrulate[°]

— a) The distal half of the shaft appears to bear notches, which under high magnification are short, fine, peglike denticles, arranged in two rows forming an angle less than 180°. These setae are quite similar to typical serrate setae, but are smaller and thinner, and have shorter, finer denticles (Lavalli and Factor, 1992).

— b) Setae are distinguished from (a) by thicker walls, a narrower lumen, and a bulbous base. The subterminal pore is clearly visible (Lavalli and Factor, 1992).

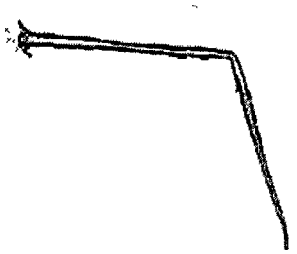
— c) Setae are similar to (b), but bear scales on the opposite side of the shaft (Lavalli and Factor, 1992).

— d) Setae are similar to (a) in that they bear short, fine, peglike denticles in two rows, but it also bears scales on the opposite side of the shaft (Lavalli and Factor, 1992).



3. Multidenticulate[†]

— Long, non-septate setae characterized by the presence of two or more rows of denticulations, which vary in size according to their locality (Thomas, 1970).



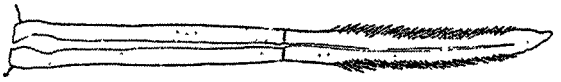
4. Setobranch[†]

— Elongate setae with a faint annulation at the base of the shaft. Setobranch setae resemble a whip bearing an extremely long lash. The distal portion of the shaft bears leaf-like projections. The tip is sharply but smoothly pointed with little diminution of size amongst the distal diminutions. The denticulations of the setobranchs are the only denticles that are themselves denticulate on their distal edges (Thomas, 1970).

FULL IMAGE OF SETAE IS NOT AVAILABLE.

5. Teazel[†]

— Teazel setae have a smooth rounded tip and denticulations on the shaft that are elongate and needle-like (Thomas, 1970).



6. Cincinnuli

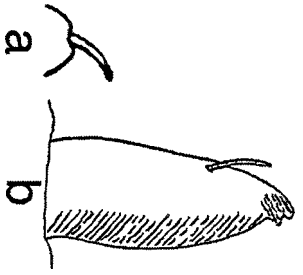
— Setae have a short rounded shaft, extending distally into a flattened hood with digitate margin oriented 90° to the shaft (Pohle and Telford, 1981).

Type III. Non-annulate, robust

1. Tooth seta (Hamate)[Ω,§]

—a) relatively short stout setae, oval in cross section that arise from well-developed sockets (Thomas 1970); they are shaped like hooks and lack setules (Lavalli and Factor, 1992).

— b) a heavily chitinized spine occurs off the seta (Fish 1972).

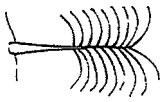


Type IV. Non-annulate, small, non-robust

A. Plumose[§]

1. Brush

— Small seta (~ 0.05mm in length) with a bulbous base; long recurved setules exist distal to the annulation and leave the shaft at all angles (Fish, 1972).



2. Scaled Microseta

DESCRIPTION NOT AVALIABLE

IMAGE NOT AVALIABLE

[°] Illustrations were taken from Lavalli and Factor (1992).
[§] Illustrations were taken from Fish (1972).
[Ω] Illustrations were taken from Factor (1978).
[Σ] Illustrations were taken from Guenther and Atema (1998).
[†] Illustrations were taken from Thomas (1970).

chemoreception on one is sufficient for orientation abilities (Beglane et al., 1997). Likewise, when aesthetascs and bimodal receptors are removed from antennules of spiny lobsters, the lobsters cannot successfully orient to food sources (Derby et al., 2001). This ability of lobsters to chemo-orient in odor plumes has mainly been studied in nephropid (clawed) and palinurid (spiny) lobsters (Zimmer-Faust, 1987; Moore and Atema, 1991; Moore et al., 1991a, 1991b; Nevitt et al., 2000; Derby et al., 2001), while little work has focused on the family Scyllaridae (slipper or shovel-nosed lobsters) (Cate and Derby, 2002a).

Current molecular evidence suggests that the scyllarids are a sister group to the palinurids (Ptacek et al., 2001), and classical taxonomists propose that they diverged from the palinurids approximately 230 million years ago (Moe, 1991; Tam and Kornfield, 1998). An examination of the antennules suggest that scyllarids may be more similar to the most primitive palinurids (i.e., *Jasus* sp.) in that their lateral flagellum (where the sensory hairs are located) is extremely short, and their 1st, 2nd, and 3rd antennular peduncle segments are short (Holthuis, 1991). This morphology provides a contrast to the well-studied palinurid, *Panulirus argus*, which has long antennular flagella and longer peduncle segments (Holthuis, 1991). While clawed lobsters have short peduncle segments, their antennular flagella are similar in length to many *Panulirus* species (Holthuis, 1991). Slipper lobsters, while sharing ancestry with palinurids, may differ in both their setal structures and chemo/mecho-orientation abilities from those described for *Panulirus argus*, the species that has been the focus of nearly all studies on palinurid chemoreception.

Panulirus argus, however, is not representative of the majority of species in the genus *Panulirus*. This is because the genus *Panulirus* is separated into four groups according to the degree of maxilliped modification, with Group I being the most primitive (includes *P. argus*). Since all the other palinurid genera possess fully formed exopods on the maxillipeds, those groups of *Panulirus* with the most reduced exopods are regarded as the most advanced (Group 4) (George and Main, 1967). Recently, nucleotide sequence data from the mitochondrial large subunit (16S) ribosomal RNA gene and the cytochrome *c*

oxidase subunit I (COI) gene was used to determine the molecular phylogeny of the *Panulirus* genus (Ptacek et al., 2001). The molecular phylogeny agreed with the morphological phylogeny presented by George and Main (1967) with only a few minor rearrangements, such as the placement of *Panulirus argus* as a sister group to the *Panulirus* species making up the primitive Group I (Ptacek et al., 2001). Due to this determination of the placement of *P. argus* outside of the group from which the ancestor to scyllarids was likely to have occurred, it is possible that scyllarids may possess structurally different antennules from *P. argus*, either via the presence or absence of certain setal types, or differences in distributions patterns on antennular annulus.

Because of the potential for structural differences in the antennules among species of different families, it is important to examine if there are any differences or similarities in setal types and their distributions on the antennule. The antennule seems to be a vital olfactory organ used in distance chemoreception to detect shelter (via conspecific odors) (Childress and Herrnkind, 2001), food, predators, and mates. Thus, it is necessary to advance our understanding of how the antennule functions, with the initial step being the identification and distribution of setae. While setal types and some of their distribution patterns have been identified for representatives of nephropid and palinurid lobsters, no data exist for the scyllarids.

The objectives of this study were to use a modified version of Walting's (1989) classification system to: 1) identify the setal structures on the lateral antennular flagellum of three scyllarid species: *Scyllarides latus, S. aequinoctialis, and S. nodifer*; 2) determine the distribution pattern of setae on the lateral antennular flagellum for all three species; 3) compare the distribution of the setae among the three scyllarid species; 4) compare the results obtained among the three species to existing nephropid and palinurid data; and 5) discuss the possible function of the setae of the antennule with regards to setal distribution.

METHODS AND MATERIALS

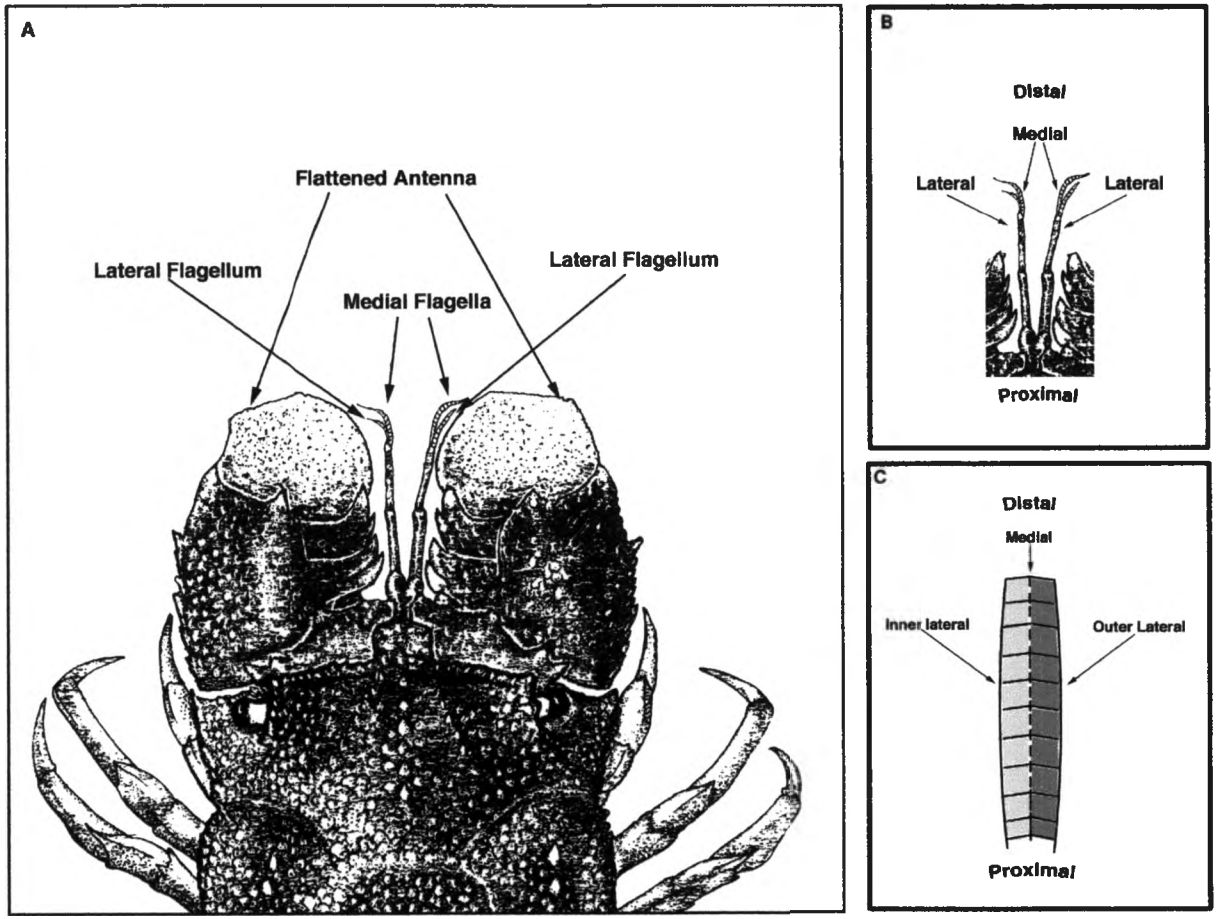
Specimen Collection

Scyllarides aequinoctialis and *Scyllarides nodifer* ranging in carapace length (CL, measured from back of eyestalk to end of carparace) from 48-75 mm were collected by local fisherman and purchased from the Keys Marine Laboratory in Long Key, Florida. Animals were housed in a 55-gal aquarium tank at room temperature (≈22.2°C) that contained recirculating, filtered artificial seawater (Instant Ocean) at approximately 3.5 ppm salinity.

Pairs of lateral antennules (Fig. 1A) from 5 specimens each of *S. aequinoctialis* and *S. nodifer* were removed at the base (to maintain left/right discrimination) and rinsed in deionized water. Antennules were then placed in fungicide/bactericide treatment as described in Felegenhauer (1987) for 2-3 days.

Scyllarides latus ranging in carapace length from 70-96 mm were caught off the coast of Haifa, Israel by local fishermen. Antennules were removed by local fisherman at the base to ensure that left/right discrimination was maintained, and placed in deionized water. The antennules were treated with fungicide/bactericide as described above. Antennules were then shipped to Southwest Texas State University in San Marcos, Texas by the University of Haifa in Mount Carmel, Haifa, Israel after being fixed and dehydrated to 70% ethanol as described below. The remainder of the preparation was

Figure 1. (A) Anterior aspect of a slipper lobster (*Scyllarides* sp.). The paired first antennae, or antennules, have four segments, the most distal of which branches into two flagella (lateral and medial). The lateral and medial flagella are composed of smaller segments, called annuli. Drawing was modified from Holthuis, 1991. (B) Location of setae on antennules when discussing hair location on both antennules. Medial and lateral on each antennule are in reference to the lobster's body, as are proximal and distal. (C) When discussing a location on a particular surface of a single antennule, medial refers to the midline and lateral refers to the two sides of the antennule. A face refers to the outer edge of each side, while proximal and distal are in reference to the body. For (B) and (C), all sides of the antennule also are in reference to the body: ventral, dorsal, lateral, medial.


A
Flattened Antenna
Lateral Flagellum
Medial Flagella
Lateral Flagellum
B
Distal
Medial
Lateral
Lateral
Proximal
C
Distal
Medial
Inner lateral
Outer Lateral
Proximal

conducted at Southwest Texas State University for pairs of lateral antennules (Fig. 1A) from 5 specimens.

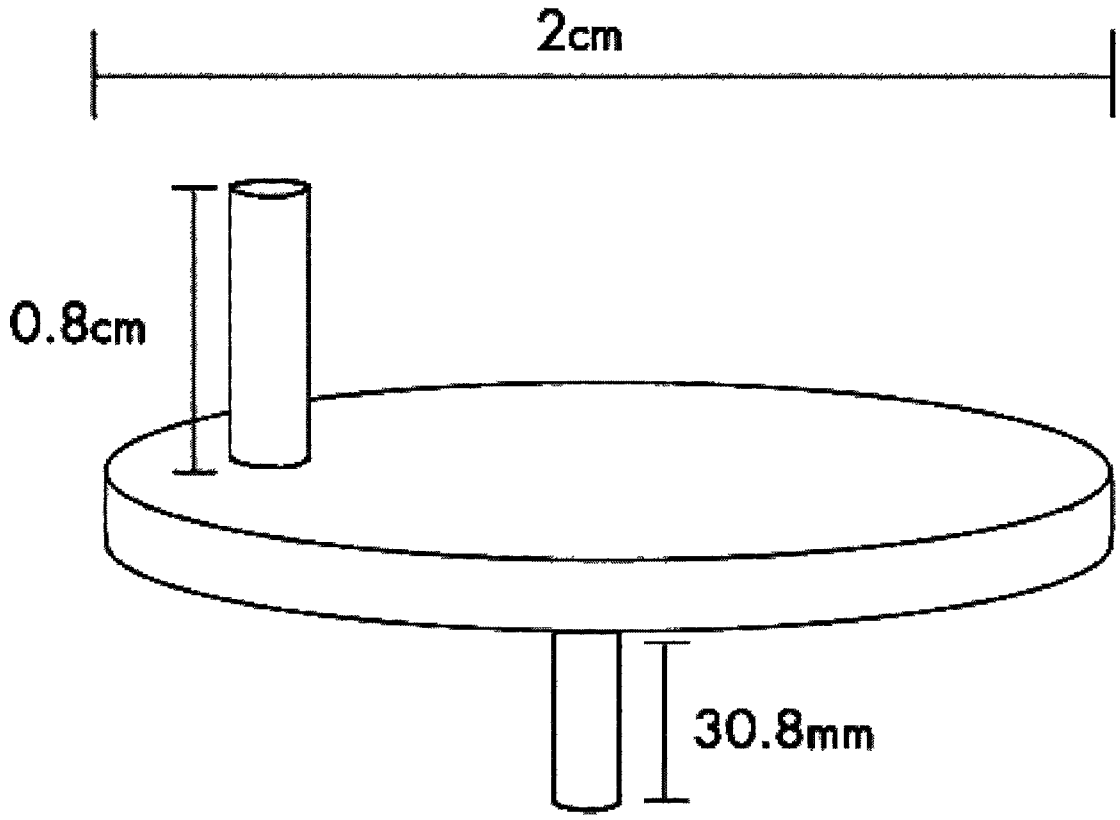
Scanning Electron Microscopy (SEM)

Antennules were fixed in 1% gluteraldehyde and 0.05M cacodylate acid (pH 7.2) for a minimum of 3 hours. After the fixation, the specimens were washed in 0.05M cacodylate acid for 15 min, 3 times. Samples were sonicated six times at 30 sec intervals for a total of 3 min and dehydrated in a sequential ethanol series of 10, 20, 30, 40, 50, 70, 85, and 95% concentrations, each for 15 min. At the end of this dehydration sequence, the antennule sections were placed in 100% ethanol 3 times, each for 15 min. The specimens were transferred into a series of three 100% acetone washes, each for 15 min, and critical point dried with CO_2 using a Denton Vacuum, Inc. DCP-1 Critical Point Drying Apparatus. Antennules were skewered on pins and sputter coated with silver using an Electron Microscopy Sciences 575 Sputter coater.

Samples were examined and directly mapped under a Hitachi S-4500 Field Emission SEM at The Texas Materials Institute at University of Texas in Austin, Texas. A special SEM mount (Fig. 2) was designed specifically for the Hitachi S-4500 Field Emission SEM to hold the samples and allow for the rotation of the antennular flagella for viewing of all surfaces. The mount was manufactured by the Machine Shop at the Marine Biological Laboratory in Woods Hole, Massachusetts.

All observable setal types on the antennule were described and representative images were recorded for each type. All sides of the antennule were examined for the presence of setae, and setal distributions were recorded for each antennule examined for

Figure 2. Construction schematic for scanning electron microscope mount specifically designed to hold the antennule skewed on a pin and allow for the rotation of the specimen for viewing of all surfaces. Pin was mounted on the upper portion of the top column and was turned in order to rotate the specimen. The mount was constructed of aluminum.


2cm
0.8cm
30.8mm

all species. The antennule was divided into four radial 90° quadrats: ventral, dorsal, medial and lateral. On each quadrat, both location and number of various setae were recorded. Due to the inability to count the aesthetasc setae on the ventral surface because of their density, all setae were removed from the ventral face after accounting for all other observable setae. The flagellum was again sputter coated, and the sockets of the aesthetascs were counted. This was not necessary for the remaining quadrats of the antennules because setal densities were not so high as to obscure setal counts.

Terminology

The terminology and categories of Watling (1989) were used to describe the basic morphological features of setal types. In addition, descriptive names and terminology established prior to and after Watling (1989) also were applied to classify the setae further (see Thomas, 1970; Fish, 1972; Farmer, 1974; Factor, 1977; Derby 1982; Lavalli and Factor, 1992; Guenther and Atema, 1998; Cate and Derby, 2001). Thus, the terminology used herein is a composite of Watling's (1989) type classifications (Table 1) and specific terms established for particular setal morphologies.

When describing locations of the setae on the antennules, in general, locations are given in reference to the body of the lobster (Fig. 1B). When referring to actual distributions of setae upon particular quadrats of the flagella, their location was described in reference to an individual flagellum (Fig.1C).

Data Analysis

Following the divisions of Guenther and Atema (1998), the length of the antennule was partitioned into three regions—base, tuft, and tip —with transition zones between each region based on the distribution of the aesthetasc setae. The "base" was defined as the proximal region of the antennule containing segments bearing few setae. The "base transition zone" contained one aesthetasc seta, but fewer than two full rows of aesthetasc per segment. The rows of the "base transition zone" contain a greater variety of setal types than the "base" region. The "tuft region" was defined by segments each consisting of at least two full rows of aesthetascs, while the "tuft transition zone" had poorly organized aesthetascs and other setae. The "tip region" lacked aesthetascs and most other setae. For each region, setae were counted per annulus while being examined by SEM, and the types and numbers of setae were recorded directly onto data sheets.

To determine setal distribution differences, only the ventral tuft region of the antennules were used to compare left and right antennules within a species, antennules among species, and, where possible, antennules between sexes. Only the ventral tuft region was used because it was the site of main chemoreceptor setae and it contained a spatial array including all setal types of the antennule. Differences and similarities in setal numbers and types between left and right antennules for each species separately were examined using chi-square contingency tables after testing each of the five individual specimens for homogeneity via a heterogeneity chi-square analysis. If heterogeneity was found among the five individuals within a species, the individual(s) causing the heterogeneity was determined by eliminating individuals one at a time from

the sample and repeating the analysis (Zar, 1999). Male/female differences within a species were determined by the heterogeneity testing, when possible. Chi-square contingency tables were used to determine differences in setal types and distribution among the three species, by using counts per ventral tuft annulus only from the left antennules.

Parsimony Analysis using Quartet Puzzling

As the chi-square contingency tables were constructed solely from data drawn solely from the ventral tuft surface of the antennules, a cladistic analysis using parsimony and quartet puzzling was performed to compare the entire antennule among the three species. In order to compare the entire antennule among the three species, a data matrix for all segments and faces of each individual's pair of antennules for all species was compiled (Appendix 1). Characters for the data matrix consisted of segments for each region and transition zone of the antennule. For all regions and transition zones except the tuft region, all setal counts for each face were pooled for each of the setal types. For the tuft region, each face was treated separately since the region contains the majority of receptors types including the main chemoreceptors. To align the regions of each antennule, the first segment of each region and zone was matched together for all antennules. Counts for each setal type on each segment were averaged for each individual's antennule pair. To assure equidistant character values in the data matrix, counts for each setal type per segment were assigned unique and equidistant character states (Table 2).

Table 2. State changes for all characters used in the phylogenetic data matrix.

Number of setae*	Simple	Toothbrush	Aesthetasc	Hemi-plumose	Modified simple	Asymmetric
1–5	A	B	C	D	E	F
6–10	G	H	I	J	K	L
11–15	M	N	O	P	Q	R
16–20	S	T	U	V	W	X

* If none of the setal types were present on a segment, Y was entered into the data matrix (Y = No setae present).

Relationships among the taxa were analyzed using PAUP Version 4.0b10 (Swofford, 2002). The number of constant, missing, and uninformative characters in the data matrix was determined. However, all characters were used in each analysis and they were weighted equally to avoid incorporating *a priori* assumptions regarding the relative significance of different characters in determining affinity. A distance matrix was constructed for the entire dataset. Cladistic analyses were performed using parsimony and iterative quartet puzzling (2500 puzzle steps). Quartet puzzling was performed for all taxa in a total analysis, then pairwise for *S. latus* and *S. aequinoctialis* only, *S. latus* and *S. nodifer* only, and *S. aequinoctialis* and *S. nodifer* only.

RESULTS

Description of Setal Types Found on the Lateral Flagellum of the Antennules

Hemi-plumose (Fig. 3) — Hemi-plumose setae bear a single distinct row of long, fine, thread-like setules along the majority of the hair shaft (A, D). The row becomes denser towards the tip (approximately 1/4 of upper distal shaft) (A, E). On the distal portion of the shaft, 180° from the row of setules, scaling occurs in two distinct rows (E, F). No annulations are present the setal shaft, and the shaft has an invaginated socket (A, D). Hemi-plumose setae are located on the ventral, lateral side adjacent to the modified simple setae (C) and on the ventral, medial side of the flagellum adjacent to the simple setae, which are next to the modified simple setae (B). Setae that are located in these positions are termed "companion" hairs by other authors (Laverack, 1964; Derby, 1982; Guenther and Atema, 1998; Cate and Derby, 2001). Hemi-plumose setae do not fall within one of Watling's (1989) setal classifications.

Toothbrush (Fig. 4) — Toothbrush setae have dense rows of elongated, flattened setules along only one face of the hair shaft, resembling an old, frayed toothbrush head (A, D, E, F). Scaling is present on the opposite face of the hair shaft, 180° from the setules (A, E). The hair shaft tapers sharply towards the tip, with a concomitant increase in setule density (A, D, E, F). Toothbrush setae sit in what resembles a ball joint with an invaginated socket with a raised lip (A, E). Directly above the socket is an annulation

Figure 3. Hemi-plumose setae on ventral surface of antennular flagella. (A) Structure of seta (Scale = 75 μm; X 400). (B) Location of setae within tuft region of ventral medial face that borders simple setae (Scale = 87.7 μm; X 342). (C) Pairs or triplets of setae within tuft region of ventral lateral face, adjacent to modified simple hairs (Scale = 120 μm; X 250). (D) Row on ventral lateral face, showing setules and invaginated socket (Scale = 49.9 μm; X 601). (E) Distal portion of shaft, illustrating scaling and increase in setule density (Scale = 14.9 μm; X 2010). (F) Distal portion of shaft with two distinct rows of scaling (Scale = 20μm; X 1500). Sc = Scaling; S= Setules; TSc = Texture scaling on antennule segments.

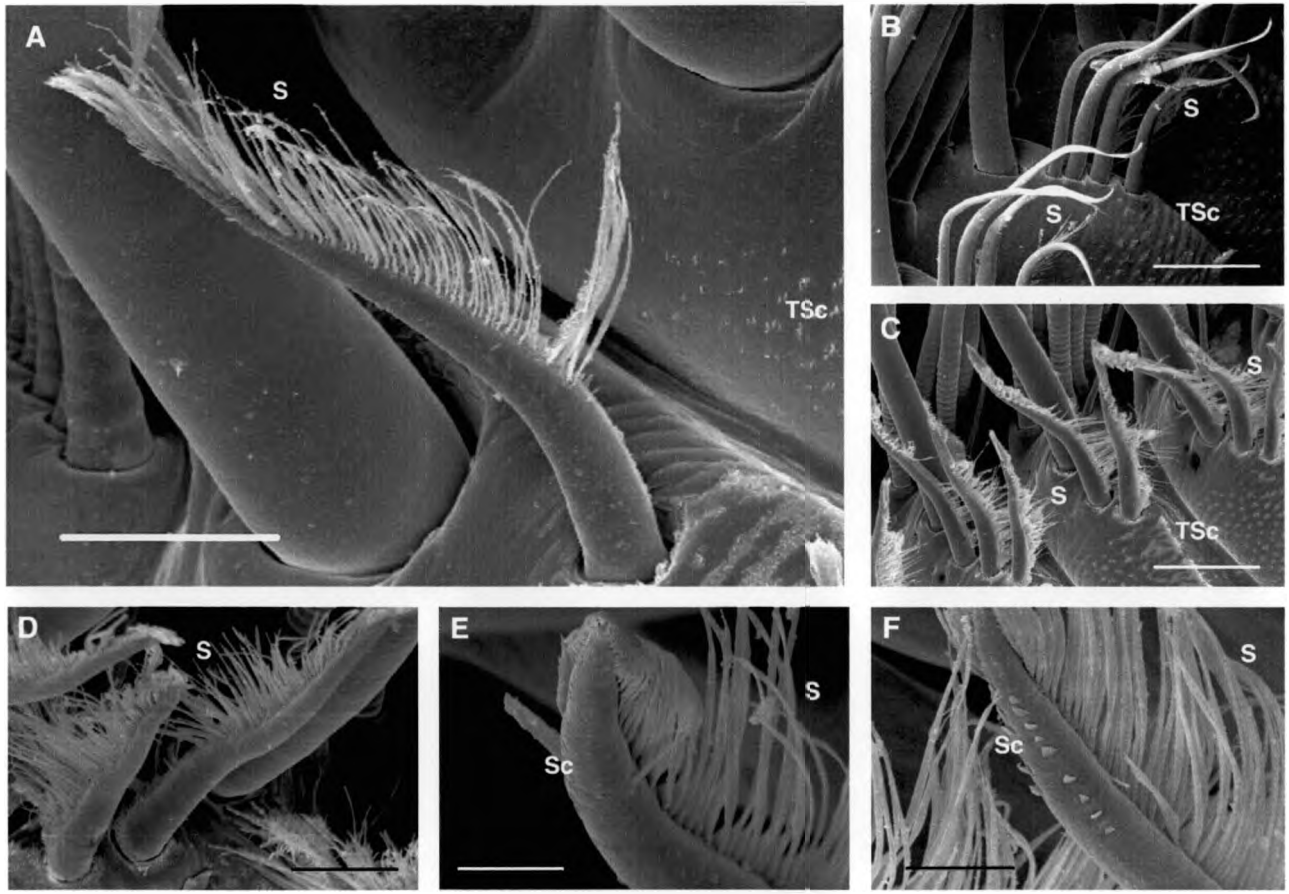
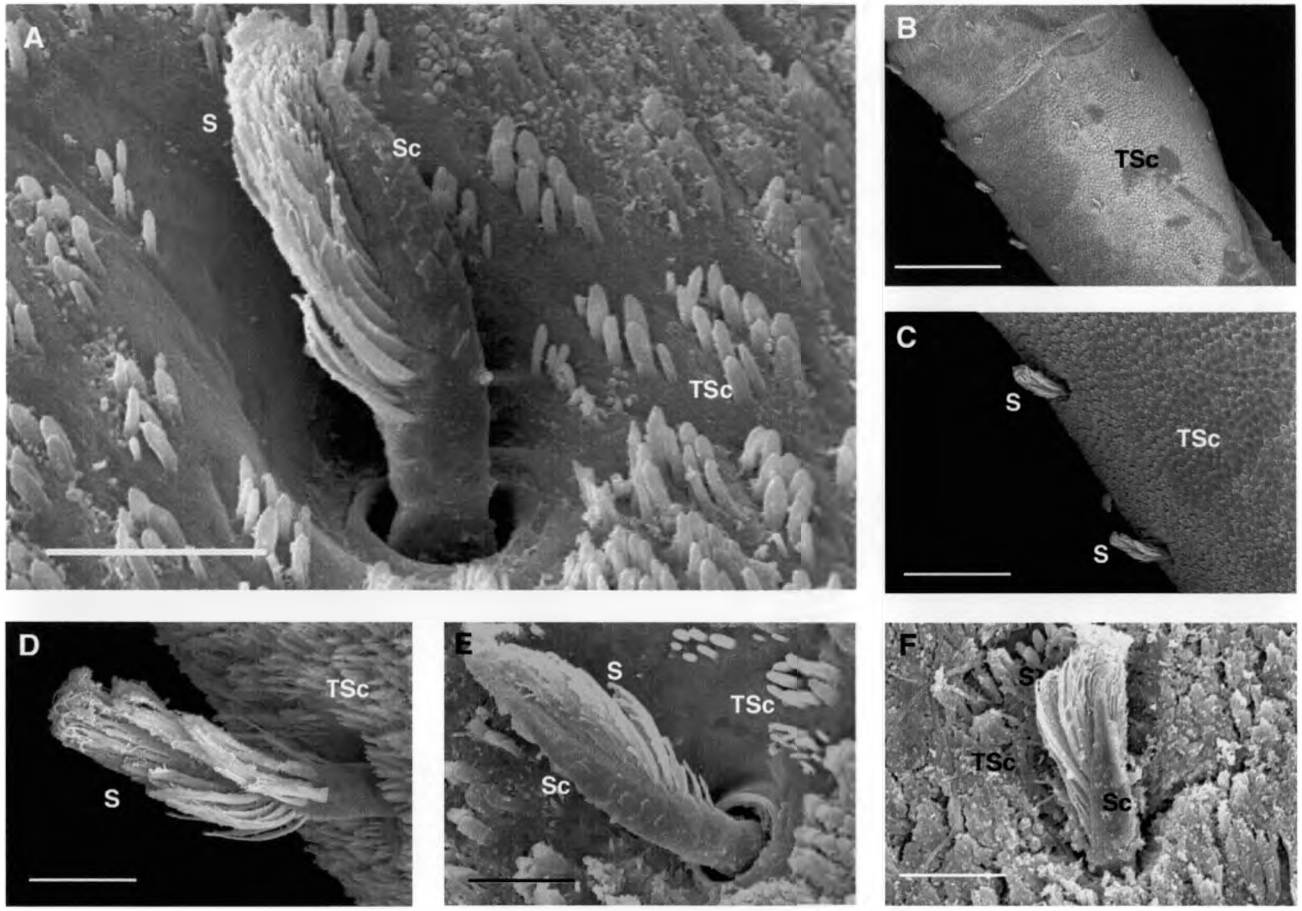

A
S
TSc
B
S
S
TSc
C
S
S
TSc
D
S
E
S
Sc
F
S
Sc

Figure 4. Toothbrush setae of dorsal surface of antennular flagella. (A) Structure of seta (Scale = 20 μm; X 1500). (B) Distribution upon first segment of dorsal surface (Scale 429 μm; X 70). (C) Distribution on dorsal medial face (Scale = 150 μm; X 200). (D) Elongated, flattened setules (Scale = 27.3 μm; X 1100). (E) Concomitant increase in setule density as hair shaft tapers with scaling on opposite face (Scale = 16.7 μm; X 1800). (F) Tapering of setal shaft (Scale = 23.4 μm; X 1280). Sc = Scaling; S= Setules; TSc = Texture scaling on antennule segments.


A
S
Sc
TSc
B
TSc
C
S
TSc
S
D
TSc
S
E
S
TSc
Sc
F
S
TSc
Sc

upon the hair shaft (A). Toothbrush setae can be found on all four surfaces towards the base of the flagellum (B, C). Toothbrush setae can be considered a homologue of hooded sensilla found on *P. argus* by Cate and Derby (2002a). Toothbrush setae fall within Watling's (1989) Type I classification.

Modified Simple (Fig. 5) — Modified simple setae are long, and taper gradually towards the tip (A). Scale-like setules are present along the distal portion of the shaft in a single row (E, F). The shaft sits within an invaginated socket (D). No annulations are present. Modified simple setae are located on the ventral surface of the flagellum, flanking the aesthetasc setae. Setae that reside in this position are referred to as "guard" hairs by various authors (Laverack, 1964; Derby, 1982; Guenther and Atema, 1998; Cate and Derby, 2001). Modified simple setae do not fall within any of Watling's (1989) classifications.

Aesthetasc (Fig. 6) — Aesthetasc setae have distinct annulations all along the hair shaft (C, F). Annulations towards the distal portion of the shaft may or may not be visible (C, D, E). The shaft tapers sharply towards a distinct tip (D, E). The aesthetasc setae sit within an invaginated pocket (F). Aesthetasc setae are located generally in two rows per segment on the medial, ventral surface of the flagellum (A, B). Aesthetascs belong within Watling's (1989) Type II classification.

Simple (Fig. 7) — Simple setae can be long or short and bear no setules (A–F). They are conical in shape and some gradually taper towards the tip, while others may have a blunt

Figure 5. Modified simple setae on ventral surface of antennular flagellum. (A) Structure of setae (Scale = 161 μm; X 186). (B) Location of setae adjacent to aesthetascs. Arrow points to a modified simple hair (Scale = 273 μm; X 110). (C) Modified simple setae flanking both sides of aesthetasc setae rows (Scale = 429 μm; X 70). (D) Invaginated socket (Scale = 33.3 μm; X 900). (E) Single row of scale-like setules located on distal portion (Scale = 16.7μm; X 1800). (F) Scale-like setules (Scale = 12 μm; X 2510). ScS = Scale-like setules.

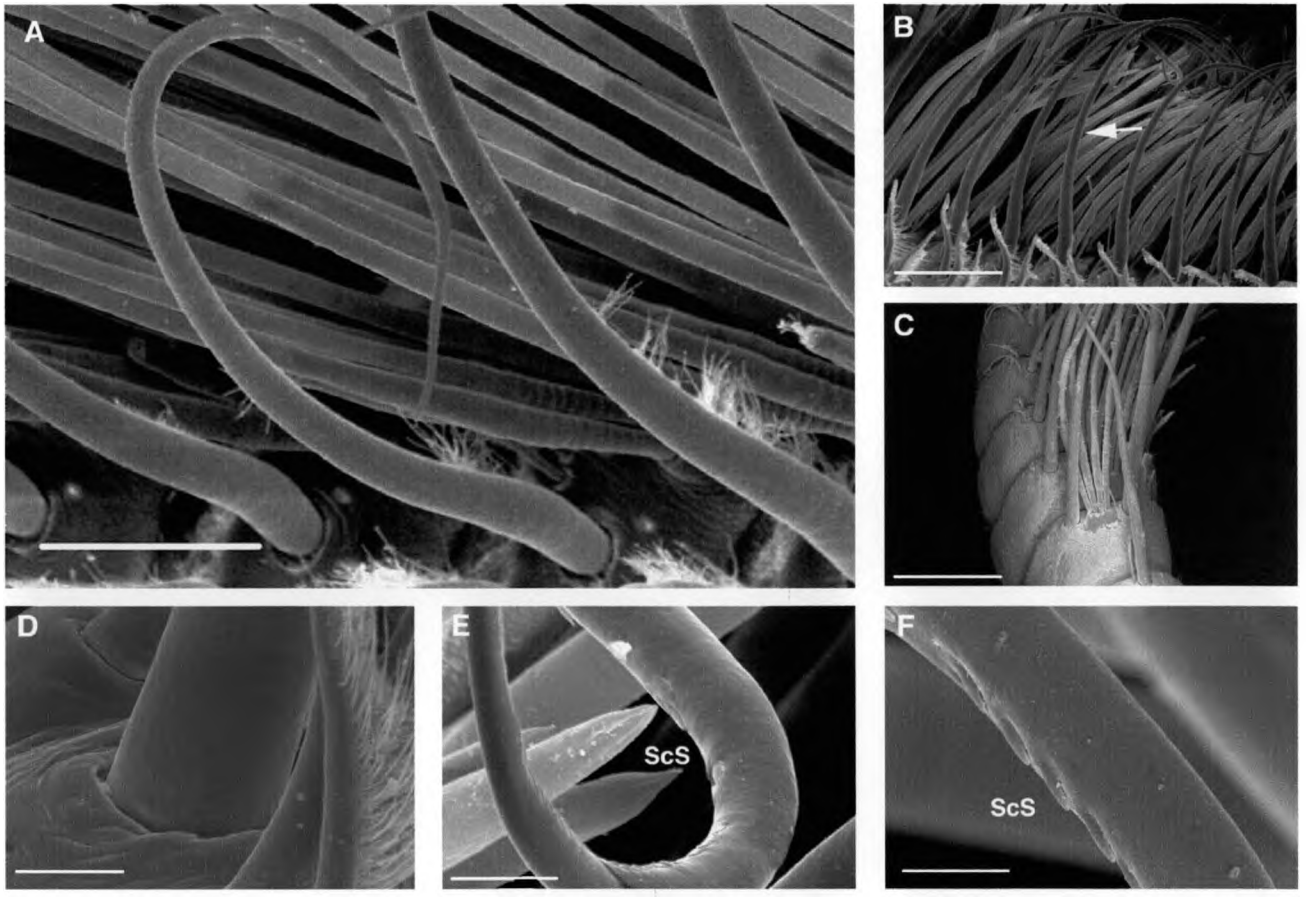

A
B
C
D
E
ScS
F
ScS

Figure 6. Aesthetasc setae on ventral surface of antennular flagella. (A) Full length of setae, annulations upon shaft, and general location on medial ventral surface within the tuft region. Arrow points towards aesthetascs. (Scale = 273 μm; X 110). (B) Bare sockets illustrating how aesthetasc setae form in proximal and distal rows on all tuft segments on ventral surface (Scale = 200 μm; X 150). (C) Cluster of aesthetasc setae (distal portion of setal shafts) (Scale = 136 μm; X 221). (D) Distinct tips (Scale = 43.6 μm; X 687). (F) Invaginated socket of setae (Scale = 31.1 μm; X 965). An = annulation; R1 = distal row; R2 = proximal row.

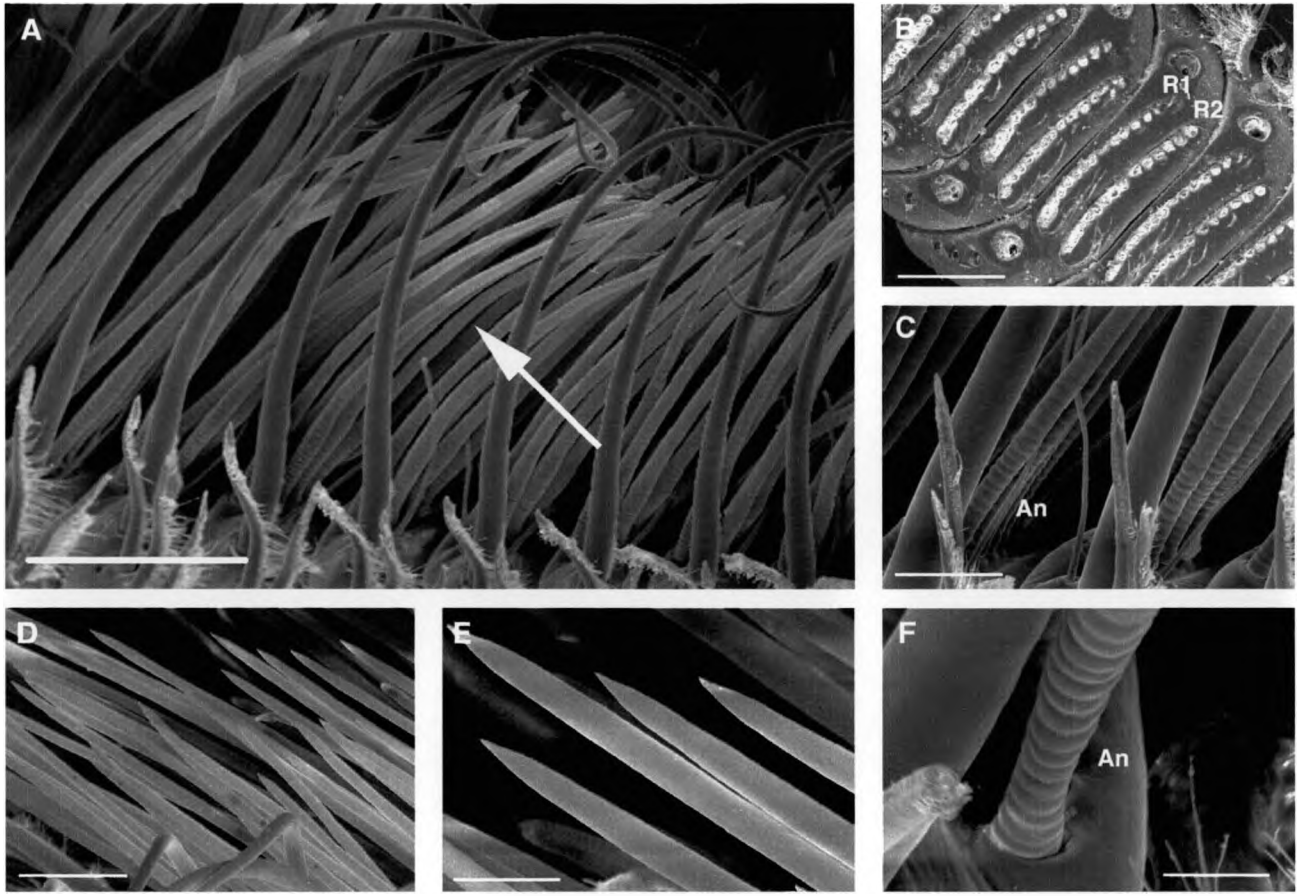
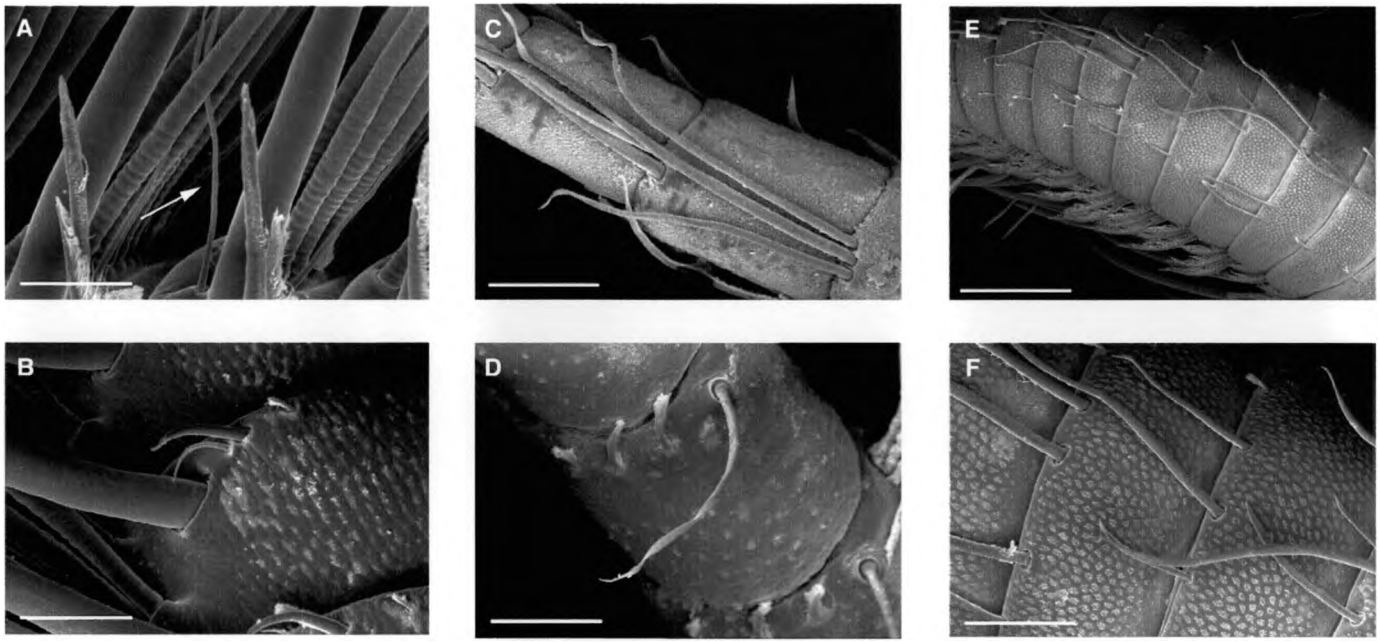

A
B
R1
R2
C
An
D
E
F
An

Figure 7. Various simple setae upon antennular flagellum. (A) Asymmetric setae indicated by arrow (Scale = 100μm; X 300). (B) Simple setae on tuft segments on ventral medial face adjacent to modified simple seta (Scale = 100μm; X 300). (C) Long simple setae on tip segments (Scale = 97.4μm; X 308). (D) Short and long simple setae on tip segments (Scale = 57.1; X 526). (E) Long and short simple setae occurring on tuft segments of dorsal face resembling a lateral-line formation (Scale = 429μm; X 70). (F) Simple setae on dorsal face (Scale = 150μm; X 200).


A
C
E
B
D
F

apex. Some simple setae may contain a bulb midway along the length of the shaft (Lavalli and Factor, 1992). Simple hairs that occur lateral to the rows of aesthetasc hairs (A) have been termed "asymmetric hairs" by Gleeson et al. (1993) and are described as wiry and sometimes twisted (Guenther and Atema, 1998). Short simple hairs occur either singly or in pairs alongside guard and hemi-plumose hairs on the ventral medial surface, and are referred to as "companion" hairs by various authors (Laverack, 1964; Derby, 1982; Guenther and Atema, 1998; Cate and Derby, 2001) (B). On the dorsal surface, one to two long simple hairs occur between one to two shorter simple hairs resembling a lateral-line formation (E, F). Simple hairs that occur on the tip segments are either long hairs that have a blunt apex or short hairs that gradually taper towards the tip (C, D). All simple setae belong in Watling's (1989) Type II classification.

Distribution of Setae on the Lateral Flagellum of the Antennule

The scheme developed by Guenther and Atema (1998) for separating the antennule into three sections and two zones was modified after the discovery of the modified simple setae. The base transition zone is defined here as having, at most, one modified simple hair on the medial ventral surface, containing a greater variety of setae, and possibly having at least one aesthetasc, but fewer than two full rows of aesthetasc per segment. All other definitions of sections and zones remain the same.

For *S. nodifer*, *S. aequinoctialis*, and *S. latus* the average base region contained 9.6 (± 3.16 standard error mean, or SEM), 10.5 (± 0.49 SEM), and 10.4 (± 0.48 SEM) segments, while the base transitions zone consisted of 2.1 (± 0.18 SEM), 1.8 (± 1.33 SEM), 2.2 (± 0.21 SEM) segments, respectively. The tuft region comprises 17 (± 0.53

SEM), 17.5 (± 0.97 SEM), and 21.4 (± 1.42 SEM) segments for *S. nodifer, S. aequinoctialis,* and *S. latus*, respectively. All species had a short tip transition zone with 0.9 (± 0.18 SEM) segments for both *S. nodifer* and *S. aequinoctialis*, and 0.9 (± 0.10 SEM) for *S. latus*. The tip region consisted of 7.9 (± 0.46 SEM), 6.3 (± 0.70 SEM), and 8 (± 0.39 SEM) segments for *S. nodifer*, *S. aequinoctialis*, and *S. latus*, respectively.

Abundance of setal types on specific regions and all faces of the lateral flagellum was determined by averaging counts from all samples for each species. Overall, for the three species, aesthetascs were the most common setae followed by simple setae; asymmetric setae were the least abundant. The tuft region was the only region to possess all types of setae and here aesthetascs were the most abundant, followed by simple setae, and hemi-plumose setae. The base transition and tuft transition zones possessed the next greatest variety of setal types. Toothbrush setae were most abundant in the base transition zone, and simple setae were most abundant in the tuft transition zone. Tip segments contained only simple setae, while base segments only possessed toothbrush setae and few simple setae for all species (Table 3). Because all setal types were present only in the ventral tuft region and were limited to one to two types in the other regions and surfaces, analyses for heterogeneity, as well as qualitative and quantitative differences between flagella and among species were conducted only on this region

All individual specimens within a species were tested for heterogeneity of setal types and counts separately for both left and right annuli comprising the tuft region. There were no significant differences found between the individual left or right tuft regions of the lateral antennules of *S. nodifer* ($\chi^2 = 48.180$ left; $\chi^2 = 69.124$ right; DF = 372, $P > 0.999$ for both), *S. aequinoctialis* ($\chi^2 = 105.628$, DF = 384 left and $\chi^2 = 37.829$,

Table 3. Average abundance for antennular setal types of *S. nodifer*, *S. aequinoctialis*, and *S. latus* on each region and zone of the lateral flagellum. Average total abundance and the percentage of total are also given.

Setal Types	Base*	Base Transition*	Tuft*	Tuft Transition*	Tip*	Average number on flagellum*	% on flagellum
a) *S. nodifer*							
Hemi-plumose	0	0.6±0.22	60.8±2.02	0.3±0.15	0	61.7±2.15	8.87
Toothbrush	25.4±5.86[δ]	4.1±1.18	11±1.78	0	0	40.5±7.49	5.82
Modified Simple	0	2.6±0.34	34.1±1.08	0.3±0.21	0	37±1.14	5.32
Aesthetasc	0	2.5±0.65	407.8±18.53	3.3±0.96	0	413.6±18.64	59.45
Asymmetric	0	0	16.4±0.56	0.1±0.10	0	16.5±0.62	2.37
Simple	5.6±1.56	2.1±0.57	80.1±4.67	2.2±0.55	36.4±3.11	126.4±3.11	18.17
b) *S. aequinoctialis*							
Hemi-plumose	0	0.8±0.29	54.3±9.52	0.2±0.13	0	55.3±3.13	7.45
Toothbrush	69±14.02	5.6±0.85	21.3±9.09	0.2±0.20	0	96.1±23.12	12.94
Modified Simple	0	2±0.15	34.5±1.86	0	0	36.5±1.89	4.91
Aesthetasc	0	0.6±0.43	419.4±29.90	3.1±0.97	0	423.1±30.13	56.96
Asymmetric	0	0	16.3±0.87	0	0	16.3±0.87	2.19
Simple	4.4±1.65	3.7±0.80	74.9±3.54	2.8±1.05	29.7±4.87	115.5±6.79	15.55
c) *S. latus*							
Hemi-plumose	0	0.9±0.23	86.1±6.56	0.1±0.10	0	87.1±6.58	8.74
Toothbrush	49.3±5.63	8.4±1.13	13±1.86	0	0	70.7±6.75	7.10
Modified Simple	0	2.9±0.23	42.6±2.89	0.4±0.22	0	45.9±3.04	4.61
Aesthetasc	0	3.4±0.69	596.3±51.15	3.4±0.82	0	603.1±51.07	60.55
Asymmetric	0	0.3±0.15	21.1±1.39	0	0	21.4±1.32	2.15
Simple	5.4±0.78	2.6±0.54	97.7±5.47	3.4±0.82	58±4.32	167.8±8.66	16.85

*Values are means ± SEM.

[δ] Some specimens were covered with fungus at the base and made distinction or observation of the toothbrush setae difficult, so these might have been classified as simple instead or were not counted at all.

DF = 348 right, $P > 0.999$ for both), or *S. latus* ($\chi^2 = 59.353$, DF = 444, left, and $\chi^2 = 100.388$, DF = 438, right, $P > 0.999$ for both). No significant differences between male and female antennules were determined for all species since all of these heterogeneity chi-squares proved that the antennules were homogeneous. After determining that all specimens were homogeneous, average setal counts were determined for each annulus for each species for subsequent analyses.

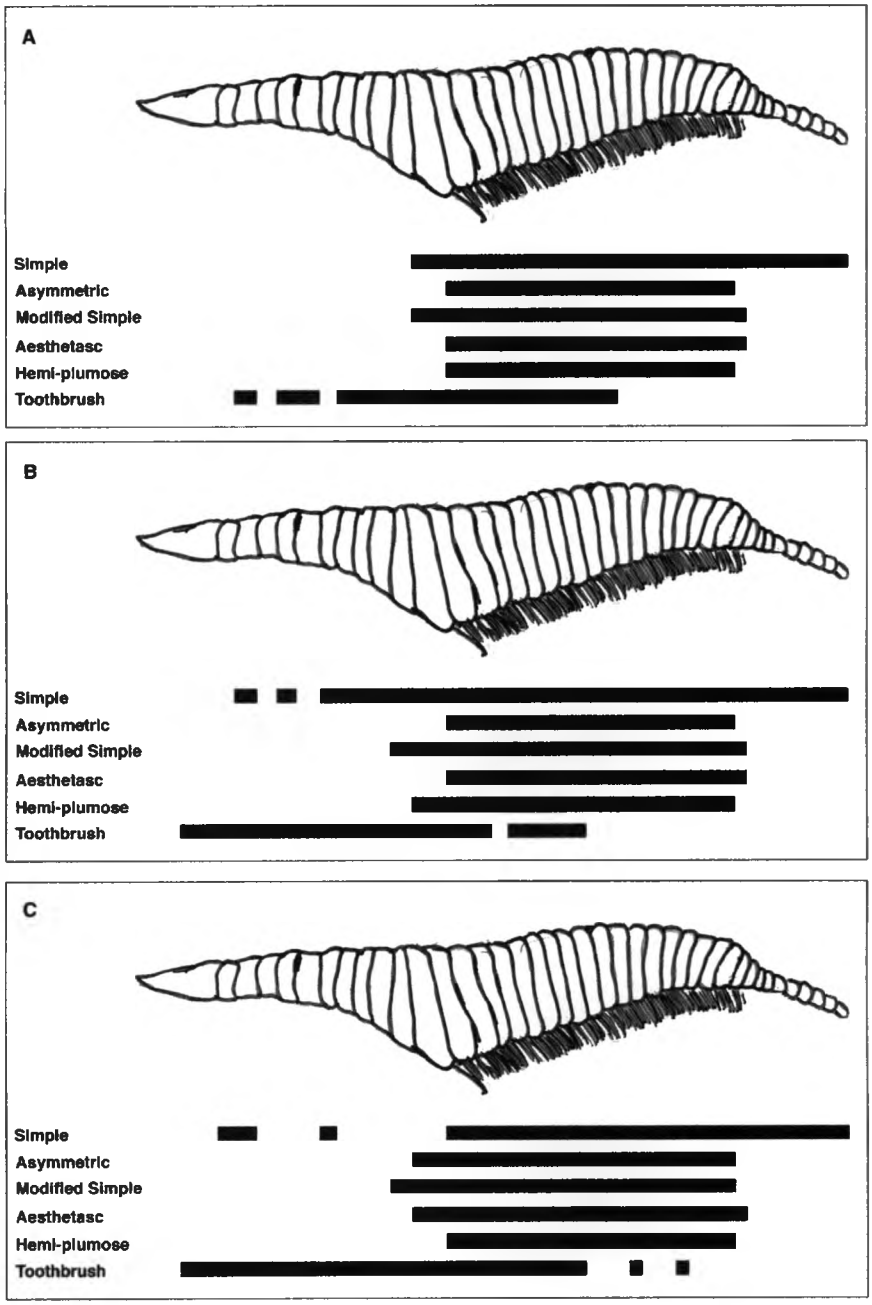
Three-dimensional chi-square contingency tables found no significant left-right differences between the representative annuli comprising the tuft region of the lateral antennules of *S. nodifer* ($\chi^2 = 22.545$, DF = 188, $P > 0.999$), *S. aequinoctialis* ($\chi^2 = 16.148$, DF = 188, $P > 0.999$), and *S. latus* ($\chi^2 = 25.497$, DF = 188, $P > 0.999$). Furthermore, no differences among the three species were found when comparing either left or right antennules ($\chi^2 = 30.945$, DF = 292, $P > 0.999$, and $\chi^2 = 32.150$, DF = 292, $P > 0.999$, respectively).

As neither left nor right, or male nor female lateral flagella had qualitative or quantitative differences in setal types or distributions, the lateral flagella containing the same number of annuli for each species was chosen to illustrate distribution of setal types (Fig. 8). The majority of variation in distribution occurred only in the positions of simple and toothbrush setae on the base and on a few tuft segments of all specimens for each species (Fig. 8); however, these differences were not compared statistically.

Parsimony analysis using Quartet Puzzling

A total of the 149 morphological characters were scored across all individuals for all species. Of those, 93 were constant, 28 contained ambiguous/missing information for 1 or more taxa, and 14 were parsimony uninformative. Thus, out of 149 morphological

Figure 8. Distribution of the setal types on a representative lateral flagellum of (A) *S. nodifer*, (B) *S. aequinoctialis*, and (C) *S. latus*. The solid bars indicate the distribution of the respective setal types on each of the 40 annuli along the length of the antennule. Minor differences between simple and toothbrush setae on the base segments occur among individuals, however this was not compared statistically.


A
Simple
Asymmetric
Modified Simple
Aesthetasc
Hemi-plumose
Toothbrush
B
Simple
Asymmetric
Modified Simple
Aesthetasc
Hemi-plumose
Toothbrush
C
Simple
Asymmetric
Modified Simple
Aesthetasc
Hemi-plumose
Toothbrush

characters 14 were informative across all individuals and all characters. Ambiguous characters in the data matrix often represent segments which are unshared among individuals due to variation in number of antennular segments. Thus if an individual failed to have a segment, all characters for that segment would be considered as ambiguous/missing data. However, all characters were used in all analyses to avoid incorporating assumptions regarding the relative significance of different characters in determining affinity. No penalty was assessed under parsimony for changes at unshared characters. Pair-wise distances (Table 4) for total character differences ranged from 0 to 47 while mean character differences ranged from 0 to 0.50538. *Scyllarides aequinoctialis* 3 was an outlier from the rest of the taxa having total distances ranging from 32 to 47, while the range for all other taxa was 0 to 22. Parsimony quartet puzzling generated an unrooted tree for each of the following analyses: all taxa (Fig. 9); *S. latus* and *S. aequinoctialis* (Fig. 10); *S. latus* and *S. nodifer* (Fig. 11); and *S. aequinoctialis* and *S. nodifer* (Fig. 12). In no analyses were any of the species found to resolve monophyletically. Paraphyletic results were most apparent in the analysis among all individuals from each species (Fig. 9). Similar results occurred in the subset analyses of individuals from *S. latus* and *S. aequinoctialis* (Fig. 10) and the *S. aequinoctialis* and *S. nodifer* (Fig. 12). In the analyses of *S. aequinoctialis* and *S. nodifer*, the two taxa were more distinguishable than the previous pair-wise parsimony analyses. Species level resolution was nearly achieved in the analysis of *S. latus* and *S. nodifer* (Fig. 11). This final analysis provides monophyletic species with the exception of a single individual of *S.nodifer* (*S. nodifer* 4) being placed in the clade of *S. latus*.

Table 4. Pairwise distances matrix using 149 morphological characters. Total character differences are below diagonal, while mean character differences (adjusted for missing data) are above diagonal. Note that *Sla*, *Sae*, and *Sno* are the abbreviations for *S. latus, S. aequinoctialis* and *S. nodifer*, respectively.

	Sla 1	*Sla* 2	*Sla* 3	*Sla* 4	*Sla* 5	*Sae* 3	*Sae* 4	*Sae* 5	*Sae* 6	*Sae* 7	*Sno* 1	*Sno* 3	*Sno* 4	*Sno* 5	*Sno* 6
Sla 1	—	0.04082	0.08081	0.13542	0.12371	0.45263	0.07368	0.03750	0.013402	0.05952	0.05556	0.6452	0.07527	0.06250	0.06250
Sla 2	4	—	0.08182	0.18557	0.14851	0.48936	0.10638	0.08750	0.14035	0.10714	0.07778	0.09574	0.12903	0.09091	0.08642
Sla 3	8	9	—	0.14583	0.16832	0.45263	0.17895	0.13750	0.11927	0.10714	0.16667	0.13978	0.10753	0.15625	0.15000
Sla 4	13	18	14	—	0.09375	0.34783	0.19565	0.20253	0.15625	0.12195	0.19318	0.19565	0.08602	0.22917	0.17284
Sla 5	12	15	17	9	—	0.37634	0.17204	0.20000	0.15842	0.13253	0.20225	0.17204	0.08602	0.20833	0.17500
Sae 3	43	46	43	32	35	—	0.49474	0.47500	0.37634	0.45238	0.46667	0.49462	0.40217	05.0538	0.44444
Sae 4	7	10	17	18	16	47	—	0.06250	0.19355	0.05952	0.04444	0.01075	0.09783	0.02151	0.05000
Sae 5	3	7	11	16	16	38	5	—	0.18750	0.10667	0.05000	0.03750	0.15190	0.05000	0.05063
Sae 6	13	16	13	15	16	35	18	15	—	0.15663	0.17678	0.18085	0.15054	0.17526	0.16250
Sae 7	5	9	9	10	11	38	5	8	13	—	0.10714	0.04819	0.03659	0.09639	0.09459
Sno 1	5	7	15	17	18	42	4	4	16	9	—	0.03371	0.14773	0.03371	0.03750
Sno 3	6	9	13	18	16	46	1	3	17	4	3	—	0.10870	0.0000	0.06250
Sno 4	7	12	10	8	8	37	9	12	14	3	13	10	—	0.13978	0.13750
Sno 5	6	9	15	22	20	47	2	4	17	8	3	0	13	—	0.06173
Sno 6	5	7	12	14	14	36	4	4	13	7	3	5	11	5	—

Figure 9. Unrooted parsimony network for *S. latus*, *S. aequinoctialis*, and *S. nodifer* individuals using 149 morphological characters assembled from antennule setal types. Numbers beside branches represent nodal support values from 2500 parsimony quartet puzzling steps.

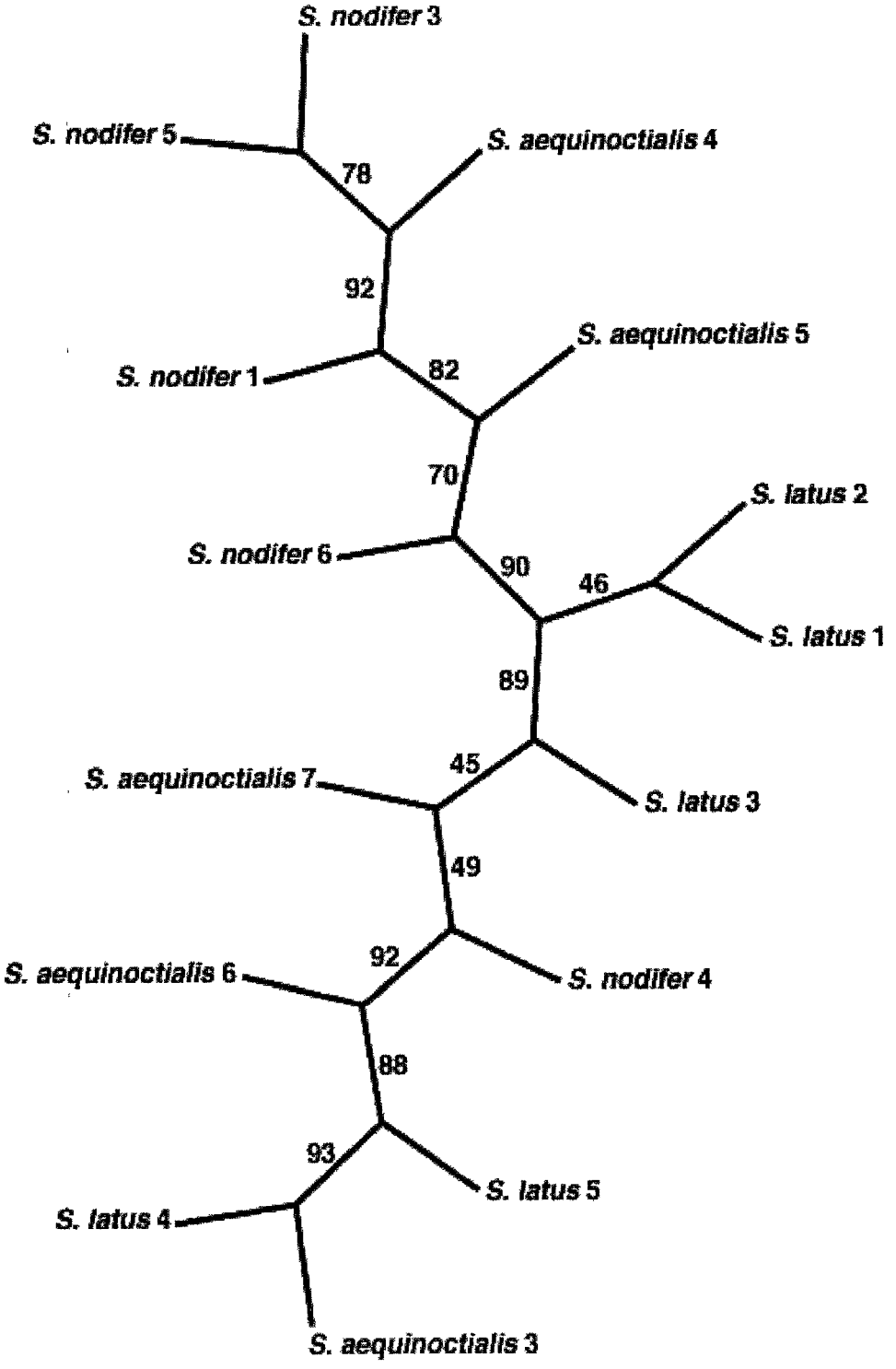

S. nodifer 3
S. nodifer 5
S. aequinoctialis 4
78
92
S. aequinoctialis 5
S. nodifer 1
82
70
S. latus 2
S. nodifer 6
90
46
S. latus 1
89
45
S. aequinoctialis 7
S. latus 3
49
92
S. aequinoctialis 6
S. nodifer 4
88
93
S. latus 5
S. latus 4
S. aequinoctialis 3

Figure 10. Unrooted parsimony network for *S. latus* and *S. aequinoctialis* individuals using 149 morphological characters assembled from antennule setal types. Numbers beside branches represent nodal support values from 2500 parsimony quartet puzzling steps.

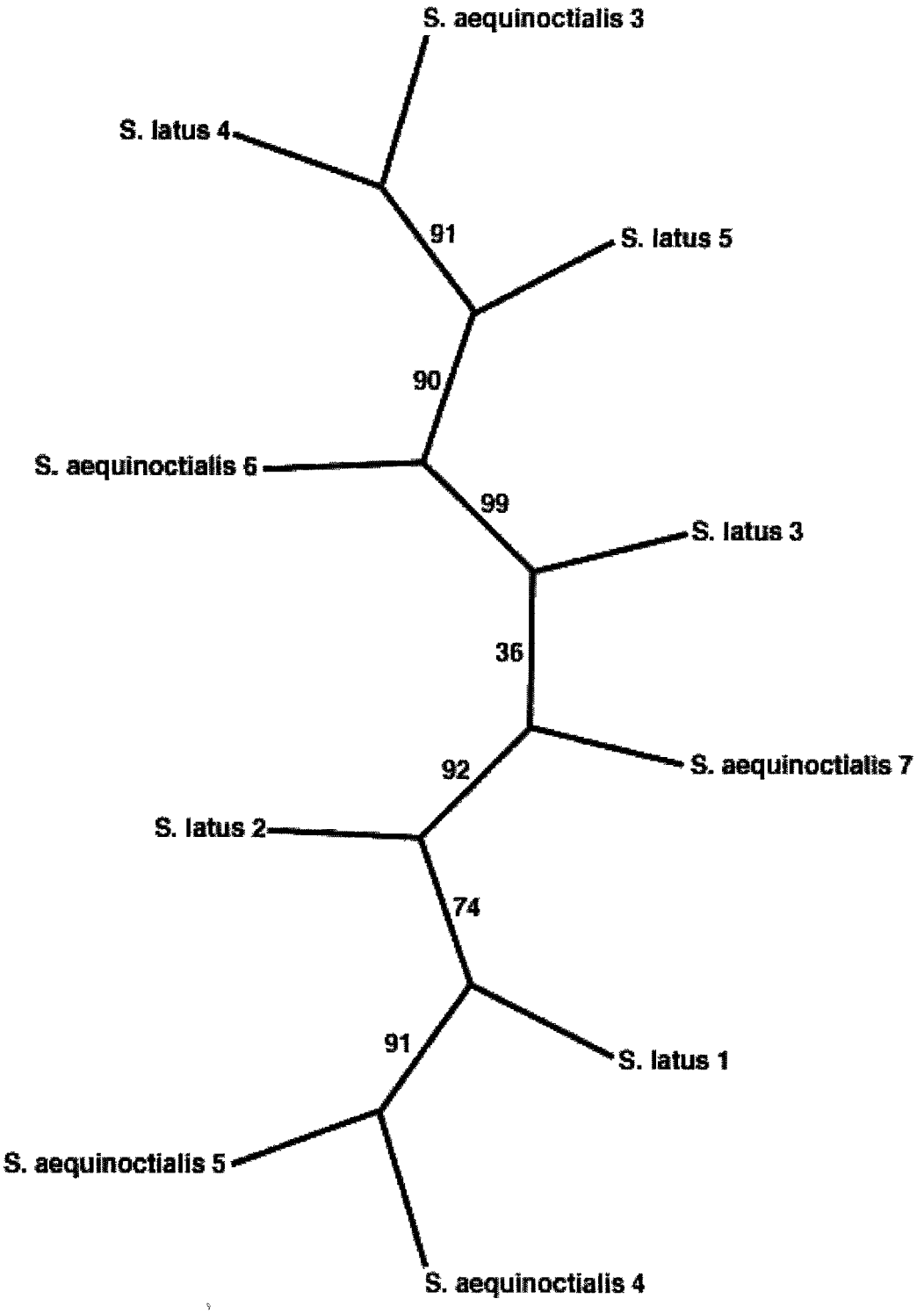

S. aequinoctialis 3
S. latus 4
91
S. latus 5
90
S. aequinoctialis 6
99
S. latus 3
36
92
S. aequinoctialis 7
S. latus 2
74
91
S. latus 1
S. aequinoctialis 5
S. aequinoctialis 4

Figure 11. Unrooted parsimony network for *S. latus* and *S. nodifer* individuals using 149 morphological characters assembled from antennule setal types. Numbers beside branches represent nodal support values from 2500 parsimony quartet puzzling steps.

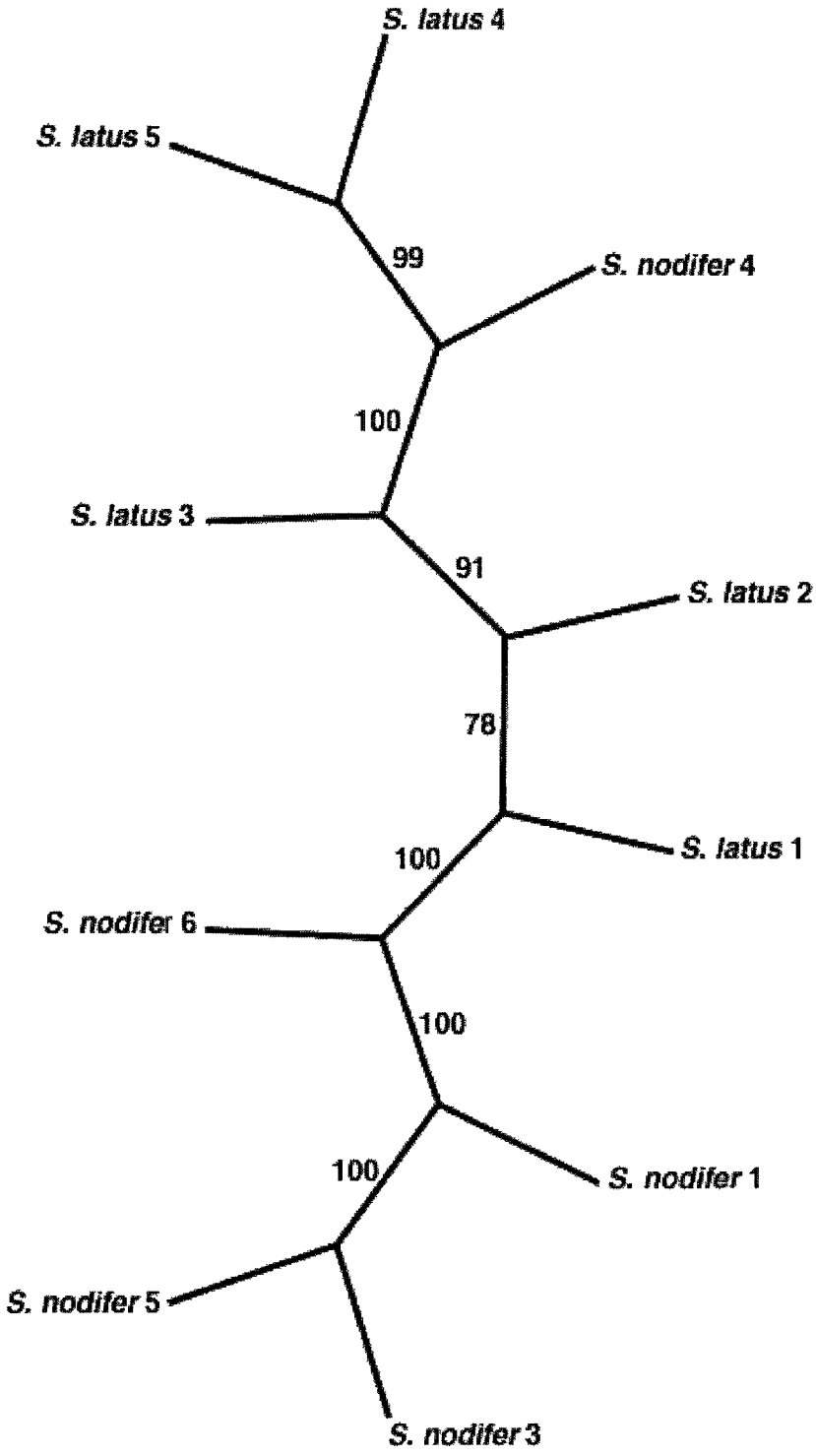
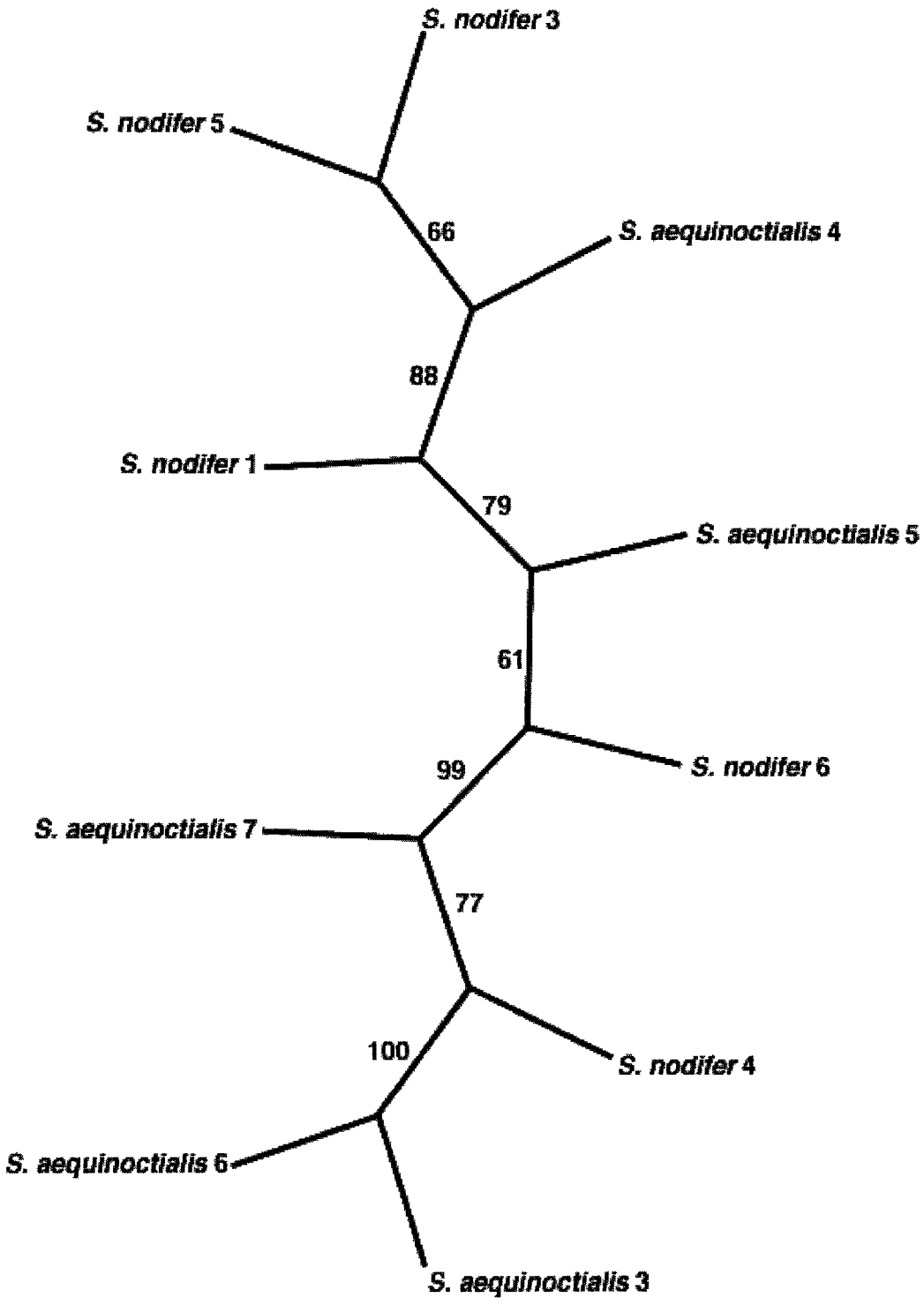

S. latus 4
S. latus 5
99
S. nodifer 4
100
S. latus 3
91
S. latus 2
78
100
S. latus 1
S. nodifer 6
100
100
S. nodifer 1
S. nodifer 5
S. nodifer 3

Figure 12. Unrooted parsimony network for *S. aequinoctialis* and *S. nodifer* individuals using 149 morphological characters assembled from antennule setal types. Numbers beside branches represent nodal support values from parsimony 2500 quartet puzzling steps.


S. nodifer 3
S. nodifer 5
66
S. aequinoctialis 4
88
S. nodifer 1
79
S. aequinoctialis 5
61
S. nodifer 6
99
S. aequinoctialis 7
77
100
S. nodifer 4
S. aequinoctialis 6
S. aequinoctialis 3

DISCUSSION

Patterns of setal distribution

The distribution pattern for setae was highly ordered on each of the three longitudinal regions (base, tuft, tip) of the lateral antennular flagellum in all three species. While small variations in distribution occurred between left and right lateral flagella of an individual, as well as between individuals of a given species and amongst species, these differences were not found to be significant ($P > 0.999$ for all analyses) for the ventral tuft region of the lateral flagellum, which is the site of the major olfactory organ of the antennule. Spatial patterning of setal types across the body surface is common in arthropods and has been described for olfactory organs, as well as individual annuli comprising these organs (Schafer, 1973; Schaller, 1978; Tominaga and Yokihari, 1982; Chapman and Greenwood, 1986; Lee and Strausfeld, 1990; Ray and Rodrigues, 1995; Rogers and Simpson, 1997; Grant et al., 1998; Guenther and Atema, 1998; Shanbhag et al., 1999; Cate and Derby, 2001); thus, it is not surprising to see it here in the olfactory organ of the slipper lobster.

For the three species of scyllarids studied, the base region consisted of toothbrush setae on all faces of the lateral flagellum, with a few simple setae that were generally located on the ventral face. All setal types (aesthetascs, hemi-plumose, simple, asymmetric, modified simple, and toothbrush) occurred only on annuli within the tuft region. On the ventral face of the tuft region, the aesthetascs were arranged medially in

two distinct rows on each annulus (Fig. 6A, B). The distal row of aesthetascs was flanked by a modified simple hair ("guard" hair) on each side of the annulus (Fig. 5B, C); these "guard" hairs were, in turn, flanked by a row of three or more "companion" hairs consisting of either simple or hemi-plumose setae. On the medial side of the annulus, the "companion" hairs consisted of 1-2 simple hairs adjacent to the modified simple setae and 2-3 hemi-plumose hairs adjacent to the simple setae (Fig. 3B). On the lateral side of each annulus, the companion setae generally consisted of 2-3 hemi-plumose setae (Fig. 3C). Occasionally on the proximal part of the tuft region, a toothbrush seta was positioned adjacent to companion setae. Asymmetric setae were generally present on every annulus of the ventral tuft region between the distal row of aesthetascs and the modified simple setae located on the lateral side of the annulus (Fig. 7A).

Toothbrush and simple setae occurred on the dorsal face of the annuli comprising the tuft region. Toothbrush setae were typically found on the proximal annuli of the tuft region (Fig. 4B, C), while the simple setae generally occurred on every annulus. A long simple seta was positioned on the medial portion of the dorsal face and was flanked by 1-2 smaller simple setae (Fig. 7E, F). In the proximal portion of the dorsal tuft region, toothbrush setae generally replaced a few of the smaller simple setae and occasionally the long simple setae.

The tip region of the lateral flagellum contained only long and short simple setae (Fig. 7C, D). The distribution pattern was generally similar between flagella, but was slightly more variable with regards to the number positioned on each of the faces. The cause of this difference between the tip and tuft region may be a result of the tip region being a terminal developmental stage (Steullet et al., 2000a; Harrison et al., 2001;

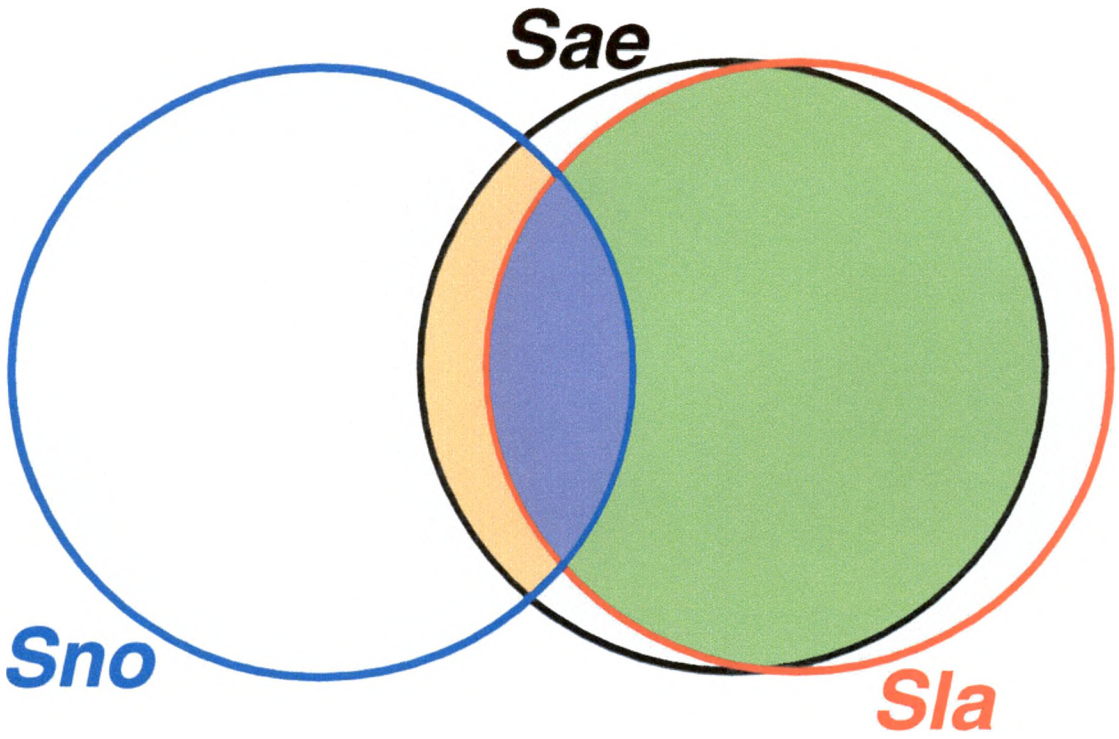
Sandeman and Sandeman, 1996). The annuli of this region typically break off after an adult lobster molts (Steullet et al., 2000a), which results in shedding of setae. Setal shedding also occurs in the tip transition zone. New setae are added to the proximal section of the tuft region, as well as to the base transition zone (Steullet et al., 2000a), and this is thought to cause variation in the setal distribution between individuals of the same species and among species of the same genus.

Comparison of the antennular lateral flagella of Scyllarides latus, S. nodifer, *and* S. aequinoctialis *using parsimony analysis.*

Parsimony analysis was conducted to compare the antennules among the individuals of the three species. This type of analysis differs from the chi-square analysis conducted in two ways. First, it took into account the entire antennule, where chi-square contingency tables were only used to analyze the setal counts from the ventral tuft region of the antennule. Secondly, parsimony analysis used raw character data to evaluate the relationships among the individuals of the three species, where chi-square analysis calculated its results based on the differences between observed and expected numbers of setae. It is possible that the inclusion of data from the entire antennule and the use of character-based comparisons may result in better resolution among the taxa.

The parsimony analyses provided little resolution indicating that there was general overlap in the number and distribution of setae among the three species. However, since two of the subset pairwise analysis showed slight resolution, it was possible to make an attempt to illustrate how the species overlapped paraphyletically (Fig. 13). It appears that *S. latus* and *S. aequinoctialis* almost completely overlap, while

Figure 13. This schematic illustrates how the three species overlap paraphyletically based on subset pairwise parsimony analyses conducted on the setal distribution of the lateral antennules. Note that *Sla*, *Sae*, and *Sno* are the abbreviations for *S. latus, S. aequinoctialis* and *S. nodifer*, respectively. Green shading represent the overlap between *S. latus* and *S. aequinoctialis*, while orange shading illustrates overlap between *S. aequinoctialis* and *S. nodifer*. Purple shading represents overlap among all three species.


Sae
Sno
Sla

S. nodifer has slight overlap with *S. aequinoctialis*, and nearly no overlap with *S. latus*. *Scyllarides nodifer* 4 was the individual responsible for the minor overlap with *S. latus*; otherwise, this pair-wise analysis would have separated the species into two monophyletic groupings. However, it is unknown whether *S. nodifer* 4 was an outlier from the other *S. nodifer* individuals because of intraspecific variation in the lateral flagellum or because of some other as yet unknown factor. The determination is complicated as several of the species which were monophyletically separable contained fungus on the base region resulting in lower setal counts. This may have artifactually led to their grouping rather than actual synapomorphic changes.

Comparison of the antennular lateral flagella of Scyllarides latus, S. nodifer, *and* S. aequinoctialis *to* Homarus americanus *and* Panulirus argus

Although, there are methodological and unresolved terminological differences in the literature, there is enough information to make a comparison among *H. americanus*, *P. argus*, and the scyllarid lobsters used in this study. The majority of setal types and their basic distribution patterns have been described to differing degrees of detail for each of the above species. The following is a compilation of comparable information from the literature that disregards the differences in methodology and terminology in order to discuss similarities and differences (Table 5).

Six to eight distinct setal types were found on the lateral flagella of the antennules of the three scyllarid species, *H. americanus*, and *P. argus*. For the scyllarids these types were: aesthetasc, hemi-plumose, simple, asymmetric, modified simple, and toothbrush setae. For *H. americanus*, the setal types consisted of campaniform (Derby, 1982),

Table 5. Comparison of setal types and their distribution on the lateral antennular flagella among *S. latus*, *S. nodifer*, *S. aequinoctialis*, *H. americanus* and *P. argus*.

Position	*S. nodifer*	*S. aequinoctialis*	*S. latus*	*H. americanus*	*P. argus*
— Main chemoreceptive setae forms in 2 rows per segment located medial on ventral surface in the tuft region	Aesthetascs	Aesthetascs	Aesthetascs	Aesthetascs	Aesthetascs
— One seta flanks each side of the aesthetascs per segment ("guard" hair)	Modified simple	Modified simple	Modified simple	Slim acuminate	Simple
— Setae are adjacent to "guard" hairs and are positioned on the side 180° from the aesthetascs ("companion" hair)	Simple Hemi-plumose	Simple Hemi-plumose	Simple Hemi-plumose	Slim acuminate	Simple
— Seta positioned between the aesthetascs and the "guard" hair on the lateral ventral face in the tuft region	Asymmetric	Asymmetric	Asymmetric	Asymmetric	Asymmetric
— Seta positioned between the aesthetascs and the "guard" hair on the medial ventral face in the tuft region	None Present	None Present	None Present	Supracuticular plumose	None Present
— Bimodal homologues located on dorsal and lateral surfaces and annuli of proximal regions (based on Cate and Derby, 2002a).	Toothbrush	Toothbrush	Toothbrush	Serrulate Cupped serrulate	Hooded
— Spatial lateral-line-like distribution pattern	Present; located on dorsal surface of tuft region	Present; located on dorsal surface of tuft region	Present; located on dorsal surface of tuft region	Present; located on medial and lateral faces of the antennule	None Present

supracuticular plumose, serrulate, cupped serrulate, aesthetasc, slim acuminate ("guard' and "companion"), and asymmetric setae (Guenther and Atema, 1998). *Panulirus argus* has aesthetasc, simple ("guard", "companion", short, medium, and long), asymmetric, hooded, plumose, and short setuled setae (Cate and Derby, 2001).

The ventral surface of the tuft region for the three scyllarid species, as well as that for *H. americanus* and *P. argus*, have the same basic distribution of aesthetascs positioned medially, flanked by "guard" hairs, which are in turn flanked by "companion" hairs. However, the setal types which reside in the "guard" and "companion" positions differ among the three scyllarid species, *H. americanus* and *P. argus*. In all three scyllarids, "guard" hairs are modified simple setae, while "companion" hairs are simple and hemi-plumose setae. Both the "guard" and the "companion" hairs of *H. americanus* are slim acuminate setae (Guenther and Atema, 1998), while the "guard" and "companion" hairs of *P. argus* are simple setae (Cate and Derby, 2001). The three scyllarid species, *H. americanus*, and *P. argus* all have an asymmetric seta located on the lateral side of the ventral surface of the flagellum for the majority of the annuli of the tuft region; this seta is located in between the aesthetascs and the "guard" hair (Gleeson et al., 1993; Guenther and Atema, 1998; Steullet et al. 2000a; Cate and Derby, 2001). However, only in *H. americanus* is a supracuticular plumose seta located in the same position on the medial ventral surface of the flagellum (Guenther and Atema, 1998).

Toothbrush setae on the three scyllarids, serrulate and cupped serrulate setae of *H. americanus* (Guenther and Atema, 1998), and hooded sensilla of *P. argus* (Cate and Derby, 2001) appear to be homologues based on their similar structures and locations upon the lateral flagellum of the antennule (Cate and Derby, 2002a). In all species, these

setae are found on dorsal and lateral surfaces and proximal annuli of the entire flagellum. In all three scyllarids and *H. americanus* they are also located on the medial surface.

A spatial lateral-line-like structure has been described for *H. americanus* (Guenther and Atema, 1998) and also is present on all three scyllarid species. On *H. americanus*, the regular spacing of serrulate setae along the medial and lateral faces of the lateral flagellum resemble a lateral-line distribution (Guenther and Atema, 1998), while on the three scyllarid species simple setae form this spatial lateral-line pattern along the dorsal face. No lateral-line like pattern has been described for *P. argus*. The presence of a spatial lateral-line-like system has ramifications for detection of mechanical stimuli.

Differences and similarities of the types and distributions of setae may reflect differences and similarities in the life histories of these species. Behavior, food choice and environment may require a few of the variations found among the lateral flagella. Differences in the structure of the second antenna between the three scyllarids, *H. americanus*, and *P. argus* also might influence variation on the first antenna, or antennule. The scyllarids have a lateral flagellum that is extremely short, with the 1st, 2nd, and 3rd antennular peduncle segments being short as well. *Panulirus argus* has a long lateral flagellum and longer peduncular segments, while *H. americanus* has a long lateral flagellum (similar in length to many *Panulirus* species) and short peduncular segments (Holthuis, 1991). The differences in length among the lateral flagella, as well as the movement of the peduncular segments, may be responsible for differences in setal types, density, and distribution, in order to allow for maximum perception of their surrounding environment.

Possible functional morphology of the setae

Scanning electron microscopy provides information about external structure, not ultrastructure. As such, one cannot infer function of setal types from external structure alone. Instead, transmission electron microscopy along with electrophysiological studies are needed to determine if all setae are sensory structures. Nonetheless, one can use the extensive work on antennular flagella in nephropid and palinurid lobsters to predict the function of specific setal types found on scyllarids.

Aesthetascs are the only unimodal chemoreceptor characterized both functionally and anatomically (ultrastructure: Laverack and Ardill, 1965; Spencer and Lindberg, 1986; Grünert and Ache, 1988; Hallberg et al., 1992; physiology: Spencer, 1986; Michel et al., 1991; Ache and Zhainazarov, 1995; behavior: Reeder and Ache, 1980; Devine and Atema 1982; Gleeson, 1991). Aesthetasc sensilla are located exclusively on the tuft region of the antennular lateral flagellum and are the prominent type of olfactory sensilla in decapod crustaceans (Hallberg et al., 1992). Each aesthetasc has no fixed number of olfactory receptor neurons (ORNs), but in *P. argus* has been found to contain, on average, three hundred ORNs (Steullet et al., 2000a). Aesthetasc ORNs respond to food related odors such as amino acids, ammonium compounds, nucleotides, and/or organic acids (Derby and Atema, 1988). Aesthetascs ORNs also respond to some pheromones in blue crabs (Gleeson, 1982; Cate et al., 1999). Within an individual flagellum, aesthetascs are generally identical in function, with limited diversity in odor sensitivity being partly related to the aesthetasc age, and possibly condition of the sensilla (Steullet et al., 2000a).

Simple setae are typically both chemo- and mechanosensory (bimodal); however, these sensilla were previously only characterized on body parts other than the antennular flagellum (Derby 1982; Hatt 1986). Recently, Cate and Derby (2001) examined long and medium simple setae on the antennules of *P. argus* and showed them to be bimodal, responding to both chemical and mechanical stimuli. The regular spacing of the simple setae along the dorsal face of the tuft region (Fig. 7E, F) suggests a possible function analogous to the lateral-line system. The lateral-line in fish serves to detect and localize objects and to measure water flow (Pough et. al., 1999). A crustacean analog has been suggested by a spatial lateral-line-like system found on the second antennae of several penaeid shrimp (Denton and Gray, 1985). The ratio of displacement of the mechanoreceptors on the antenna due to frequency changes is similar to that found on lateral-lines of some fish. Denton and Gray (1985) suggest that while fish lateral-lines are better positioned to relay information on forces generated by the animal's own motion through water, the lateral-line-like structures of penaeids are positioned to relay only some information on the forward momentum of the animal and mainly focus on the location of external sources of sound. Hence, the spatial lateral-line-like system in the three scyllarid species might be used in detecting small-scale, near-field mechanical stimuli.

Asymmetric setae are positioned lateral to the distal row of aesthetascs for the majority of annuli of the ventral tuft region. Extracellular recordings from cells innervating the asymmetric setae revealed mechanosensory function in blue crabs (Gleeson, 1982). Gleeson (1982) also suggested that asymmetric hairs might serve to

monitor water flow through the tuft region because of the above physiological data combined with the orientation of the setae on the antennule.

Toothbrush setae appear to be homologues of the hooded sensilla described by Cate and Derby (2002a). The toothbrush setae have minor structural differences that set them apart from hooded setae. In place of small setules, scales are located 180° from longer setules on the shaft. The longer setules do not form a hood over the setal shaft and the setal shaft possesses a knob above its socket. Hooded sensilla are bimodal chemo-mechanosensilla, and their receptor pathway parallels that described for aesthetascs (Cate and Derby, 2002b). Given their similar location on the antennular flagellum and their similar structure, the toothbrush setae of scyllarids may also be bimodal receptors.

Modified simple setae occur in the same positions in scyllarids as do other simple-like setae, termed "guard" hairs, in nephropid and spiny lobsters (Laverack, 1964; Derby, 1982; Guenther and Atema, 1998; Cate and Derby 2001). The modified simple setae of scyllarids, like the "guard" hairs of *P. argus*, project laterally along the edge of the aesthetascs and "interdigitate" at the margins of those sensilla (as per Laverack, 1964). This positioning of the modified simple setae ("guard" hairs) encloses the aesthetasc and asymmetric setae, and forms a channel open to water flow along and across the tuft region surface (Laverack, 1964). A general model of water flow between neighboring hairs in an array on olfactory antennae showed that when hairs are moved rapidly, the volume of flow rate increased and velocity gradients along the hair surfaces became steeper, thereby causing higher molecule encounter rates and increased sensitivity to changes in odor concentrations. However, the more closely spaced the setae, the less sensitive they are to effects of speed (Koehl, 1996). Modified simple setae

also may act as mechanoreceptors as has been speculated through structural observations for other described "guard" hairs (Laverack, 1964; Guenther and Atema, 1998).

Hemi-plumose setae are macrosetae, which possess long, feather-like and flexible setules. The seeming flexibility of the setules would allow the seta to follow the movements of the appendages that bear them (Jacques, 1989). Thus, like long plumose setae, hemi-plumose setae may function to increase the surface area of the appendage (Jacques, 1989; Factor, 1978), may strongly deflect in response to water currents, and may even create water currents that alter the environment surrounding chemoreceptors. All of these hypothesized functions may allow for increased ability to detect chemical signals by serving to enhance the contrast of chemical detection through control of water flow over receptors and control of stimulus access (Atema, 1985). As in plumose setae, the ability to create currents might be related to both the spacing of the setules on the setal shaft and the distance between adjacent setae (Lavalli and Factor, 1992). Hemi-plumose setae also may act as mechanoreceptors, since they reside in positions of "companion" setae that have been speculated through structural observations to possess this function (Laverack, 1964; Guenther and Atema, 1998).

Possible functional morphology of the antennule in relation to setal distribution

The specific distributions, structure, and innervations of these distinct types of chemo- and mechanoreceptors aid in environmental sampling, as well as functional specificities (odor differentiation), which allow for maximal stimulation of the sensory organ. The first antenna of lobsters and its position at the anterior end of the body is an example of a sensory organ with a highly ordered arrangement of sensory hairs designed

to provide both chemical and mechanical information of odor plumes. Location of the aesthetasc sensilla on the distal portion of the lateral flagellum of the antennule places them in a position where stimuli carried by currents can reach them first. In crayfish, these chemoreceptors also occur in the region where water currents can be altered by fan organs, which enhance chemical information flow by directing odors toward or away from receptors (Breithaupt, 2001). It is speculated that this may also be the case for American lobsters (Atema 1985).

Aesthetasc sensilla also are in a position to be maximally affected by periodic intense downward motions of the antennule, known as flicking (Schmitt and Ache, 1979; Mellon, 1997). Flicking may occur independently between the left and right antennule (Leonard et al., 1994), and flick frequency increases when an odor or an odor plume is encountered (Prince and Ache 1977; Leonard et al., 1994, Daniel and Derby 1988, 1991). Flicking increases the water flow within the boundary layer surrounding the densely packed aesthetasc sensilla (Snow, 1973), thereby allowing for increased exposure to the surrounding environment and allowing stimuli to enter the tuft's interior space (Schmitt and Ache, 1979). Antennule flicking in *P. argus* revealed that water flows through the aesthetasc array during a rapid downstroke, but not during the slower upstroke. Hence, the antennules can take samples of the plume structure that are discrete in both time and space (Goldman and Koehl, 2001; Koehl et al., 2001).

If flicking represents a mechanism to compensate for the inherent temporal weakness of olfactory stimuli (Schmitt and Ache, 1979), then a diversity of sensory hairs may enhance the ability to discriminate specific attributes of chemical stimuli and aid in identifying their spatial location. In addition to aesthetascs, non-aesthetasc

chemoreceptors exist on the antennule; their existence was first predicted by electrophysiology (Fuzessery, 1978; Thompson and Ache, 1980; Derby, 1982; Derby and Ache, 1984; Derby et al., 1985), and behavioral studies (Horner et al., 2000; Steullet et al. 2000b). However, their identity was unknown until Cate and Derby (2001) described the bimodal capabilities of hooded and long and medium simple setae.

On the antennules of the three scyllarid species, the non-aesthetasc chemoreceptors are most likely the simple and toothbrush setae. These two setal types can be considered, on the basis of position and morphology, to be homologues of the simple and hooded setae (Cate and Derby, 2002a) described for *P. argus*. Both simple and toothbrush setae occur in greater numbers on the faces and regions of the antennule where aesthetascs do not occur. The positioning of these setae along the entire length of the flagellum increases the spatial resolution of detection (Cate and Derby, 2001; Derby and Steullet, 2001). Multiple types of sensors on a sensory appendage can have a variety of neuron types that differ in their sensitivities, thereby increasing the range of detectable stimuli and extracting different stimulus features from the external environment. This function creates a better representation of chemical and mechanical features of any odor signal (Derby and Steullet, 2001).

Finally, multiple sensors in a sensory system allow for compensation for both localized damage and nonfunctioning developmental stages of sensors (Derby and Steullet, 2001). Multiple sensors increase the probability that some sensors are undamaged and functional (Daniel et al., 2000), thereby maintaining the chemoreceptive ability of the organ.

Conclusions

Over evolutionary time, chemoreceptor systems may have optimized their properties to detect and differentiate between the changing aspects of an odor plume. The spatial array of the setal types on the lateral antennular flagellum of various lobsters may be part of such a chemoreceptive system. Since the antennules function to provide environmental cues essential for detection of food, shelter, predators, mates and conspecifics and receive this information by similar benthic turbulent flow patterns (which carry odors from their sources to the olfactory organ), the antennules of all lobsters may be under similar selective pressures.

The first step in filtering the spatial and temporal patterns of odor concentrations in the environment is the physical interaction of the lateral flagellum with the surrounding medium (Koehl et al., 2001). The diversity of the receptor types (whatever they may be) and the setae positioning, particularly along the ventral tuft region of the lateral flagellum, seem to be conserved across spiny, slipper, and clawed lobsters, even though the length of the lateral flagellum and movement of the peduncle segments differ among these types of lobster. The setae of the various lobsters differ either in setal type or structure from their homologues; however, this may be due to slight adjustments to compensate for differences in length and movement of the flagellum. Overall, the spatial array of setae on the lateral flagellum, as well as the sampling behavior (i.e. flicking) of the animals, is similar. Thus, the arrangement of antennular setae may be the most efficient design for lobsters to physically sample and gather the most information from an odor plume.

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APPENDIX 1

Data matrix for parsimony analysis.

Taxon	base1	base2	base3	base4	base5	base6	base7	base8	base9	base10	base11	base12	base13	basetrans1	basetrans2	basetrans3	tufttrans1
latus 1	AB	AB	B	B	B	AB	AB	AB	AB	AB	AB	AB	?	ABE	ABCDE	?	ACD
latus 2	AB	AB	B	AB	AB	B	B	B	AB	AB	B	?	?	ABE	ABCDE	ACDE	AEI
latus 3	AN	H	H	H	B	H	AH	B	H	AH	H	B	B	ABE	ABCDEF	?	CEG
latus 4	AH	H	AB	H	AB	AH	AH	AH	AB	?	?	?	?	AEH	ABCEF	ACDE	AC
latus 5	H	B	AB	AB	AH	AH	AH	AB	AH	B	?	?	?	EH	ACEFH	?	CG
aeq 3	T	T	N	H	N	N	N	AN	N	N	H	AN	?	AEH	ADEH	?	ABCDF
aeq 4	H	AB	AB	AB	AB	AB	AB	AH	AB	AB	AB	AB	?	ABDE	ABDE	?	A
aeq 5	B	AB	B	B	B	B	AH	B	B	B	?	?	?	ABCE	BE	?	AC
aeq 6	T	H	H	H	H	B	B	B	B	AB	?	?	?	ABE	ABCDE	?	AC
aeq 7	B	H	B	H	AH	AH	AH	AH	AH	B	AB	?	?	ABE	ABDE	?	AC
nodıfer 1	B	B	B	B	B	B	B	AB	AB	AB	AB	?	?	ADE	ACDE	?	ACE
nodıfer 3	AB	B	AB	AB	AB	AB	AB	AB	AB	AB	?	?	?	ABE	ACDE	?	ACD
nodıfer 4	H	H	B	AH	AB	AB	AH	AH	AH	?	?	?	?	ABE	ABCDE	?	AC
nodıfer 5	B	AB	B	AB	B	AB	B	B	B	AB	?	?	?	ABE	ABE	ACDE	ACD
nodıfer 6	H	B	AB	B	H	AB	AB	AB	B	?	?	?	?	ABE	ABCE	ACDE	ADEFI

Taxon	tufttrans2	tıp1	tıp2	tıp3	tıp4	tıp5	tıp6	tıp7	tip8	tıp9	tıp10	tıp11	tuftlat1	tuftlat2	tuftlat3	tuftlat4	tuftlat5
latus 1	?	A	G	G	G	G	G	A	A	?	?	?	Y	Y	Y	Y	Y
latus 2	?	G	G	G	G	G	G	G	G	G	A	A	Y	Y	Y	Y	Y
latus 3	?	G	G	G	G	G	G	A	G	?	?	?	Y	Y	Y	Y	Y
latus 4	?	G	G	G	G	G	G	A	A	?	?	?	B	Y	Y	Y	Y
latus 5	?	G	G	G	G	G	G	G	A	?	?	?	B	Y	B	Y	B
aeq 3	AD	G	G	G	G	A	G	A	A	?	?	?	B	B	B	B	B
aeq 4	?	A	A	A	A	A	A	A	A	?	?	?	Y	Y	Y	Y	Y
aeq 5	?	A	G	A	G	A	A	A	?	?	?	?	Y	Y	Y	Y	Y
aeq 6	?	G	G	G	G	G	A	A	A	A	?	?	Y	Y	Y	Y	Y
aeq 7	?	A	A	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y
nodıfer 1	?	A	G	G	A	A	A	A	A	?	?	?	Y	Y	Y	Y	Y
nodıfer 3	?	A	A	A	A	A	A	A	A	A	?	?	Y	Y	Y	Y	Y
nodıfer 4	?	A	A	G	G	G	G	A	A	?	?	?	B	Y	Y	Y	Y
nodıfer 5	?	A	A	A	A	A	A	A	A	A	A	?	Y	Y	Y	Y	Y
nodıfer 6	ACDF	A	G	G	G	A	A	A	A	?	?	?	Y	Y	Y	Y	Y

Taxon	tuftlat6	tuftlat7	tuftlat8	tuftlat9	tuftlat10	tuftlat11	tuftlat12	tuftlat13	tuftlat14	tuftlat15	tuftlat16	tuftlat17	tuftlat18	tuftlat19	tuftlat20
latus 1	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?
latus 2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	A	A	A	?
latus 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	A	A
aeq 3	B	Y	Y	B	B	B	B	B	B	Y	B	B	B	?	?
aeq 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?
aeq 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?	?	?	?
aeq 6	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
aeq 7	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?	?
nodıfer 1	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	A	?	?	?
nodıfer 3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?
nodıfer 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?
nodıfer 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?
nodıfer 6	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?	?	?	?

Taxon	tuftlat21	tuftlat22	tuftlat23	tuftlat24	tuftlat25	tuftlat26	tuftlat27	tuftlat28	tuftlat29	tuftlat30	tuftmed1	tuftmed2	tuftmed3	tuftmed4	tuftmed5
latus 1	?	?	?	?	?	?	?	?	?	?	B	Y	Y	Y	Y
latus 2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 3	Y	Y	?	?	?	?	?	?	?	?	B	Y	Y	Y	Y
latus 4	?	?	?	?	?	?	?	?	?	?	B	B	B	B	B
latus 5	?	?	?	?	?	?	?	?	?	?	B	B	B	B	B
aeq 3	?	?	?	?	?	?	?	?	?	?	B	B	B	B	B
aeq 4	?	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y
aeq 5	?	?	?	?	?	?	?	?	?	?	B	Y	Y	Y	Y
aeq 6	Y	Y	Y	?	?	?	?	?	?	?	B	B	B	B	B
aeq 7	?	?	?	?	?	?	?	?	?	?	B	B	Y	Y	Y
nodıfer 1	?	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y
nodıfer 3	?	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y
nodıfer 4	?	?	?	?	?	?	?	?	?	?	B	B	Y	B	Y
nodifer 5	?	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y
nodifer 6	?	?	?	?	?	?	?	?	?	?	Y	Y	Y	Y	Y

Taxon	tuftmed6	tuftmed7	tuftmed8	tuftmed9	tuftmed10	tuftmed11	tuftmed12	tuftmed13	tuftmed14	tuftmed15	tuftmed16	tuftmed17	tuftmed18
latus 1	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 4	B	B	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
latus 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
aeq 3	B	B	B	B	B	B	B	B	B	Y	B	Y	B
aeq 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
aeq 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?	?
aeq 6	Y	Y	Y	Y	Y	Y	Y	B	B	Y	Y	Y	Y
aeq 7	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?
nodıfer 1	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?
nodıfer 3	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
nodıfer 4	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
nodıfer 5	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
nodıfer 6	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	?	?	?

Taxon	tuftmed19	tuftmed20	tuftmed21	tuftmed22	tuftmed23	tuftmed24	tuftmed25	tuftmed26	tuftmed27	tuftmed28	tuftmed29	tuftmed30	tuftdorsal1
latus 1	Y	?	?	?	?	?	?	?	?	?	?	?	AB
latus 2	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	AB
latus 3	Y	Y	Y	Y	?	?	?	?	?	?	?	?	AB
latus 4	Y	?	?	?	?	?	?	?	?	?	?	?	AB
latus 5	Y	Y	?	?	?	?	?	?	?	?	?	?	AB
aeq 3	?	?	?	?	?	?	?	?	?	?	?	?	AB
aeq 4	?	?	?	?	?	?	?	?	?	?	?	?	A
aeq 5	?	?	?	?	?	?	?	?	?	?	?	?	AB
aeq 6	Y	Y	Y	Y	Y	?	?	?	?	?	?	?	AB
aeq 7	?	?	?	?	?	?	?	?	?	?	?	?	AB
nodıfer 1	?	?	?	?	?	?	?	?	?	?	?	?	A
nodıfer 3	?	?	?	?	?	?	?	?	?	?	?	?	AB
nodıfer 4	?	?	?	?	?	?	?	?	?	?	?	?	AB
nodıfer 5	Y	?	?	?	?	?	?	?	?	?	?	?	AB
nodıfer 6	?	?	?	?	?	?	?	?	?	?	?	?	AB

Taxon	tuftdorsal2	tuftdorsal3	tuftdorsal4	tuftdorsal5	tuftdorsal6	tuftdorsal7	tuftdorsal8	tuftdorsal9	tuftdorsal10	tuftdorsal11	tuftdorsal12
latus 1	AB	AB	AB	AB	AB	AB	AB	A	A	A	A
latus 2	AB	AB	AB	AB	AB	A	AB	AB	AB	A	A
latus 3	AB	AB	AB	A	A	A	AB	A	A	A	A
latus 4	AB	AB	AB	AB	AB	A	A	A	A	AB	A
latus 5	AB	AB	AB	AB	AB	AB	AB	A	AB	AB	AB
aeq 3	AB	AB	AB	AB	AB	AB	AB	AB	AB	AB	AB
aeq 4	AB	AB	AB	AB	A	A	A	A	A	A	A
aeq 5	AB	AB	AB	AB	AB	A	A	A	A	A	AB
aeq 6	AB	AB	AB	AB	A	A	A	A	AB	AB	AB
aeq 7	A	A	A	AB	AB	A	A	A	A	A	A
nodıfer 1	AB	A	A	A	A	A	A	A	A	A	A
nodıfer 3	AB	A	A	A	A	A	A	AB	A	A	A
nodıfer 4	AB	AB	AB	AB	AB	AB	AB	AB	AB	AB	AB
nodıfer 5	AB	AB	AB	AB	A	AB	AB	A	AB	A	A
nodifer 6	AB	AB	AB	AB	AB	AB	AB	A	A	A	A

Taxon	tuftdorsal13	tuftdorsal14	tuftdorsal15	tuftdorsal16	tuftdorsal17	tuftdorsal18	tuftdorsal19	tuftdorsal20	tuftdorsal21	tuftdorsal22	tuftdorsal23
latus 1	A	A	A	A	A	A	A	?	?	?	?
latus 2	A	A	A	A	A	A	A	A	A	A	A
latus 3	A	A	A	A	A	A	A	A	A	A	?
latus 4	A	A	A	A	A	A	A	?	?	?	?
latus 5	A	AB	A	A	A	A	A	A	?	?	?
aeq 3	A	A	A	A	AB	B	?	?	?	?	?
aeq 4	A	A	A	A	A	A	?	?	?	?	?
aeq 5	A	A	A	?	?	?	?	?	?	?	?
aeq 6	A	AB	A	A	A	A	A	A	A	A	A
aeq 7	A	A	A	A	A	?	?	?	?	?	?
nodıfer 1	A	A	A	A	A	?	?	?	?	?	?
nodifer 3	A	A	A	A	A	A	?	?	?	?	?
nodıfer 4	AB	AB	AB	AB	AB	AB	?	?	?	?	?
nodıfer 5	A	A	A	A	A	A	?	?	?	?	?
nodifer 6	A	A	A	?	?	?	?	?	?	?	?

Taxon	tuftdorsal24	tuftdorsal25	tuftdorsal26	tuftdorsal27	tuftdorsal28	tuftdorsal29	tuftdorsal30	tuftventral1	tuftventral2	tuftventral3
latus 1	?	?	?	?	?	?	?	ADEFI	ABDEFO	ABDEFO
latus 2	A	A	A	A	A	A	A	ABDEFI	ADEFO	ADEFO
latus 3	?	?	?	?	?	?	?	ABDEFI	ABDEFI	ABDEFO
latus 4	?	?	?	?	?	?	?	ABDEFI	ADEFI	ADEFO
latus 5	?	?	?	?	?	?	?	ABCDEF	ABDEFO	ABDEFO
aeq 3	?	?	?	?	?	?	?	ABDEFI	ABDEFI	ABDEFO
aeq 4	?	?	?	?	?	?	?	ABDEFI	ADEFI	ADEFI
aeq 5	?	?	?	?	?	?	?	ADEFI	ADEFI	ADEFO
aeq 6	?	?	?	?	?	?	?	ABDEFI	ABDEFI	ABDEFO
aeq 7	?	?	?	?	?	?	?	ADEFI	ADEFI	ABDEFO
nodıfer 1	?	?	?	?	?	?	?	ADEFI	ADEFI	ADEFO
nodıfer 3	?	?	?	?	?	?	?	ABDEFI	ADEFI	ADEFO
nodıfer 4	?	?	?	?	?	?	?	ABDEFI	ABDEFI	ABDEFO
nodıfer 5	?	?	?	?	?	?	?	ABDEFI	ABDEFO	ABDEFO
nodıfer 6	?	?	?	?	?	?	?	ABDEFI	ABDEFI	ADEFI

Taxon	tuftventral4	tuftventral5	tuftventral6	tuftventral7	tuftventral8	tuftventral9	tuftventral10	tuftventral11	tuftventral12	tuftventral13
latus 1	ADEFO	ADEFO	AEFJO	ADEFO	ADEFO	ABDEFO	ADEFO	ADEFO	ADEFO	ADEFO
latus 2	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU
latus 3	ADEFO	ADEFO	ADEFO	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	AEFJU
latus 4	ADEFO	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFO	ADEFU
latus 5	ADEFO	AEFJO	ADEFO	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU
aeq 3	ABDEFO	ABDEFO	ADEFO	ABDEFU	ABEFJO	ABDEFO	ABEFJO	ABDEFO	ABDEFO	ABDEFO
aeq 4	ADEFI	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO
aeq 5	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFI
aeq 6	ABDEFO	ABDEFU	ABDEFO	ABDEFO	ADEFU	ADEFU	ADEFU	ADEFU	ABDEFU	ABDEFU
aeq 7	ABDEFO	ADEFO	ABDEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO
nodifer 1	ADEFI	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO
nodıfer 3	ABDEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFU	ADEFO	ADEFO	ADEFO
nodıfer 4	ABDEFO	ADEFO	ADEFO	ADEFU	ADEFU	ADEFO	ADEFO	ADEFU	ADEFU	ADEFO
nodifer 5	ABDEFO	ABDEFO	ABDEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO
nodıfer 6	ADEFO	AEFJO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO

Taxon	tuftventral14	tuftventral15	tuftventral16	tuftventral17	tuftventral18	tuftventral19	tuftventral20	tuftventral21	tuftventral22	tuftventral23
latus 1	ADEFO	ADEFO	ADEFO	ADEFO	ADEF	ADEFI	?	?	?	?
latus 2	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU	ADEFU
latus 3	ADEFU	ADEFU	ADEFU	ADEFU	ADEFO	ADEFO	ADEFO	ADEFI	ACDEF	?
latus 4	ADEFO	ADEFO	ADEFO	ADEFO	ADEFI	ADEFI	?	?	?	?
latus 5	ADEFU	ADEFO	ADEFO	ADEFO	ADEFO	ADEFI	DEFI	?	?	?
aeq 3	ABDEFO	ABDEFO	ABDEFO	ADEO	ADEFI	?	?	?	?	?
aeq 4	ADEFO	ADEFO	ADEFO	ADEFI	ACDE	?	?	?	?	?
aeq 5	ADEFI	ADEFI	?	?	?	?	?	?	?	?
aeq 6	ADEFU	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	ADEFO	BDEFI	ADEI	BCDE
aeq 7	ADEFO	ADEFO	ADEFI	ADEFI	?	?	?	?	?	?
nodifer 1	ADEFO	ADEFI	ADEFI	ADEFI	?	?	?	?	?	?
nodifer 3	ADEFO	ADEFO	ADEFO	ADEFO	ADEI	?	?	?	?	?
nodifer 4	ADEFO	ADEFO	ADEFO	ADEFO	ADEFI	ADEFI	?	?	?	?
nodifer 5	ADEFO	ADEFO	ADEFI	ADEFI	ADEFI	CD	?	?	?	?
nodifer 6	ADEFO	ADEFI	?	?	?	?	?	?	?	?

Taxon	tuftventral24	tuftventral25	tuftventral26	tuftventral27	tuftventral28	tuftventral29	tuftventral30
latus 1	?	?	?	?	?	?	?
latus 2	ADEFU	ADEFU	ADEFU	ADEFO	ADEFO	ADEFO	ADEI
latus 3	?	?	?	?	?	?	?
latus 4	?	?	?	?	?	?	?
latus 5	?	?	?	?	?	?	?
aeq 3	?	?	?	?	?	?	?
aeq 4	?	?	?	?	?	?	?
aeq 5	?	?	?	?	?	?	?
aeq 6	?	?	?	?	?	?	?
aeq 7	?	?	?	?	?	?	?
nodifer 1	?	?	?	?	?	?	?
nodifer 3	?	?	?	?	?	?	?
nodifer 4	?	?	?	?	?	?	?
nodifer 5	?	?	?	?	?	?	?
nodifer 6	?	?	?	?	?	?	?

VITA

Dolores Maria Weisbaum was born in New Rochelle, New York on May 6, 1977. She is the daughter of Howard and Maria Weisbaum. After graduating from Herbert H. Lehman High School in May 1995, she entered Boston University in Boston, Massachusetts. She earned the degree of Bachelor of Arts in Biology with a specialization in Marine Sciences in May 1999. After graduation she went to Woods Hole, Massachusetts, to consult for various members of the Marine Biological Laboratories and Woods Hole Oceanographic Institute. In 2000, she entered the graduate program in Biology at Southwest Texas State University in San Marcos, Texas. While at Southwest Texas State University she worked as an instructional assistant for Functional Biology, Oceans and Estuaries, and Genetics.

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