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Guenther, Carla M. and Attema, Jelle, "Distribution of Setae on the Homarus americanus Lateral Antennular Flagellum October 1998" (1998). *Documents from Environmental Organizations*. 187. [https://digitalcommons.library.umaine.edu/maine\\_env\\_organizations/187](https://digitalcommons.library.umaine.edu/maine_env_organizations/187)

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We focus here on the potential of the lateral flagellum as a "passive" detector of water flow. The well-known flicking of the antennule, with maximum rates of 5 Hz, is thought to subserve chemosensory sampling. Moreover, the flow velocity of 10 cm/s during flicking far exceeds the maximum velocities used in this study. Flicking is rare during odor plume tracking.

We thank Drs. Richard Fay and Thomas Breithaupt for valu-

able advice and discussions. Special thanks to T. B. for loan of the shaker apparatus. Supported by NSF grant IBN# 9723542 and an REU supplement.

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Reference: *Biol. Bull.* **195**: 182–183. (October, 1998)

## Distribution of Setae on the *Homarus americanus* Lateral Antennular Flagellum

Carla M. Guenther and Jelle Atema (Boston University Marine Program, Woods Hole, Massachusetts 02543)

The lateral antennular flagellum of the lobster *Homarus americanus* is a well-studied chemoreceptor organ, but it may have an additional hydrodynamic receptor function. Its chemoreceptive function is linked to both social behavior and feeding behavior; reversible lesions of the chemoreceptor cells, but not mechanoreceptors, abolish individual recognition via urine-borne pheromones (1) and suppress chemotactic orientation and tracking of food odors (2). Most chemical stimuli are received by the 1000 or more aesthetasc sensilla located in a prominent "tuft" on the distal two-thirds of each bilateral flagellum. Each aesthetasc is innervated by some 300 chemoreceptor cells. Several other sensillar types are present that remain rather poorly known in all respects: morphology, physiology, and behavioral function. The most prominent among these sensilla are the "guard" and "companion" hairs, and more recently an "asymmetric" hair has been identified (3). Stimulation of these types of hairs causes clear mechanoreceptor responses in the flagellar nerve (C. Balint, pers. comm.). Other mechanoreceptive structures such as proprioceptors may be present.

We hypothesize that the antennules may function, not only as critical chemoreceptor organs, but also as essential hydrodynamic detectors of eddy features in odor plumes (4). Coincident detection of chemical and hydrodynamic features would allow the animal to track a plume of flavored eddies to the source of an odor. Here we present the first comprehensive study of the setal arrangement of the lateral flagellum. If we combine this work with studies of hydrodynamic coupling (5), we can begin to identify the receptor structures that are most likely involved in the analysis of water motion, especially motion in the range of eddy sizes and velocities common to odor plumes of interest to lobsters.

We examined 24 intact flagella, ranging in length between 32 mm and 53 mm from 21 animals that ranged in carapace length from 78 mm to 91 mm; most animals were ablated unilaterally. We used light and scanning electron microscopy to identify the different setal types and to map them onto the lateral flagellum (Fig. 1). Based on the distribution of the prominent aesthetasc sensilla, the flagellum can be divided into three regions with transition zones between them. The BASE is the

mechanically stiff (5) proximal region of 27 ( $\pm 4.5$  SEM) segments, each bearing few setae. A 5 ( $\pm 3.0$  SEM)-segment BASE TRANSITION zone has at least one aesthetasc sensillum, but fewer than two full rows of aesthetasc per segment; it contains a greater variety of setae. The TUFT region is defined by segments each of which bear at least two full rows of aesthetascs; the region comprises 57 ( $\pm 10.0$  SEM) segments, each supplied with a variety of different setae. A short, 2 ( $\pm 3.3$  SEM)-segment TIP TRANSITION zone with poorly organized aesthetascs and other setae leads to the 7 ( $\pm 5.2$  SEM)-segment TIP region, which lacks aesthetascs and most other setae. The number of segments within each region varies from one antennule to the next, even on the same animal. The tip can be missing entirely, and the transition zones can be very short as well.

We recognized 7 setal types grouped into 2 classes according to Watling (6):

Type I annulate, with setules

*Supracuticular plumose*: ball socket, setules emerge along shaft in two opposite rows; 170  $\mu\text{m}$  long  $\times$  10  $\mu\text{m}$  diameter

*Serrulate*: woven setules on one side only; 80–120  $\mu\text{m}$  long  $\times$  20  $\mu\text{m}$  diameter

*Cupped serrulate*: cuticular lip, woven setules over  $\frac{3}{4}$  of surface; 90  $\mu\text{m}$  long  $\times$  25  $\mu\text{m}$  diameter

Type II annulate, without setules

*Aesthetasc*: cylindrical shaft, multiannulate, thin cuticle; 600  $\mu\text{m}$  long  $\times$  20  $\mu\text{m}$  diameter

*Guard (slim acuminate)*: smooth, thick cuticle, tapering shape after mid-length annulation; 900  $\mu\text{m}$  long  $\times$  40  $\mu\text{m}$  diameter

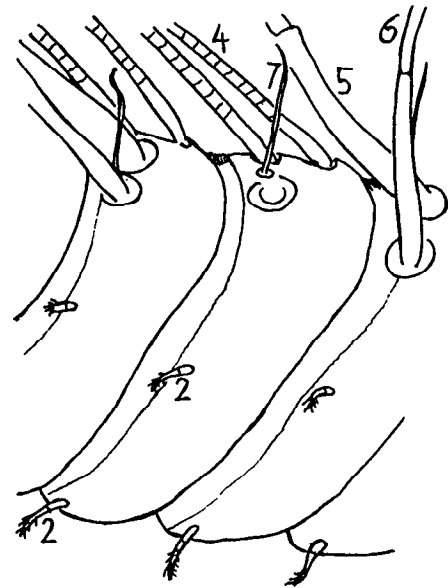
*Companion (slim acuminate)*: similar to guard; 580  $\mu\text{m}$  long  $\times$  30  $\mu\text{m}$  diameter

*Asymmetric (simple)*: smooth, wiry, twisted, tapering; 180  $\mu\text{m}$  long  $\times$  12  $\mu\text{m}$  diameter

A typical tuft segment contains all seven setal types arranged as follows. Two straight rows of 10–12 aesthetasc sensilla perpendicular to the long axis of the antennule occur on the ventral side. The distal row is flanked on either side by a guard hair; these are flanked in turn by one or two companion hairs; an asymmetric hair is irregularly found between aesthetasc and guard hairs on the lateral side; and a plumose hair can be found

Sheet1

| Setae          | Regions                    | Location  |            |            |            |           |
|----------------|----------------------------|-----------|------------|------------|------------|-----------|
|                |                            | Base      | Transition | Tuft       | Transition | Tip       |
| Segment Number | [no./region]               | 1-27 [27] | 28-32 [5]  | 33-89 [57] | 90-91[2]   | 92-98 [7] |
| <b>Type I</b>  |                            |           |            |            |            |           |
| 1              | supracuticular plumose     |           | x          | x          |            |           |
| 2              | serrulate                  |           | x          | x          | x          | x         |
| 3              | cupped serrulate           |           | x          | x          | x          |           |
| <b>Type II</b> |                            |           |            |            |            |           |
| 4              | aesthetasc                 |           | x          | x          | x          |           |
| 5              | guard (slim acuminate)     |           | x          | x          | x          |           |
| 6              | companion (slim acuminate) |           | x          | x          | x          |           |
| 7              | asymmetric (simple)        |           |            | x          |            |           |



**Figure 1.** Table: Location of 7 setal types along the 5 regions of the lateral flagellum of the lobster antennule. The regions are defined by the presence and arrangement of aesthetasc sensilla (see text). Segments are numbered sequentially from the base to the tip; the number of segments per region [in brackets] is an average derived from a study of 15 antennules. All scale bars: 100  $\mu\text{m}$ ; the smaller scale bar applies to the Type II setae, excluding the asymmetric form. Two forms of asymmetric hairs are shown.

Diagram: Setal arrangement on tuft segments. Three segments of medial flank of left flagellum shown in ventro-lateral view (ventral: up; distal: left). Setae numbered as in the table. Plumose setae (typical of lateral flank) and cupped serrulate setae (mostly dorsal) are not shown.

in the same position on the medial side. Serrulate setae are located distally on the flanks, with one larger one (120  $\mu\text{m}$ ) on the lateral flank and one smaller one (80  $\mu\text{m}$ ) on the medial flank; other serrulates, including the cupped serrulate setae, are found along the dorsal edge of the segment bordering the distal intersegmental joint.

Inferring function from external morphology has often proved misleading. But we know from preliminary electrophysiological experiments (C. Balint, pers. comm.) that the guard, companion, and asymmetric hairs are mechanoreceptive, responding to tactile and hydrodynamic stimuli. The mechanical filter properties of these hairs remain unknown, and the sensory function of the remaining setae has not been studied. The size and drag-producing morphology of the plumose setae suggests that they could respond to water flow in the antennular boundary layer. The regular spacing of the

serrulate setae along the medial and lateral flanks of the antennule give the appearance of a "lateral line," as seen in fish. The variety of setal types could provide specific filters for hydrodynamic as well as tactile stimuli.

We thank Louie Kerr and Jamin DeProto for their help with microscopy and Dr. Kari Lavalli for discussions on setal morphology. Supported by NSF.IBN 9723542.

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