

Flagellar setae of the second antennae in decapod shrimps: sexual dimorphism and possible role in detection of contact sex pheromones

R.T. BAUER* and J.L. CASKEY

Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504-2451 USA
Tel. +1 (337) 482-6435; Fax: +1 (337) 482-5834; email: rtbauer@louisiana.edu

Received 12 October 2005; Accepted 4 April 2006

Summary

The antenna 2 (antennal) flagella of decapod shrimps are chemotactile, and their setae are proposed as sensilla involved in recognition of females by males via a contact sex pheromone on the surface of the female. Male recognition of females receptive to mating occurs in many caridean species upon contact of male antennal flagella with the surface of a newly molted parturial female. The hypothesis of sexual dimorphism in the number and kind of setae on the antennal flagella of four caridean and one penaeid shrimp species was tested with setal counts and observations on setal morphology. Unique male antennal setae (“male-specific sensilla”) were not identified in any of the species investigated. However, the abundance of antennal setae was significantly greater in males than in breeding females in the palaemonid carideans *Palaemonetes pugio* and *Macrobrachium ohione*. In the hippolytid caridean *Thor manningi* and alpheid caridean *Alpheus normanni*, no sexual dimorphism in setal abundance was demonstrated. In the penaeoid *Rimapenaeus similis*, males had a higher abundance of antennal setae than the larger breeding females but so did juvenile females, similar in size to males. The sexual dimorphism in antennal sensilla in the palaemonid species and its absence in *A. normanni* might be related to their different mating systems, but no such association is suggested for *T. manningi* and *R. similis*. Setal morphology suggestive of chemoreceptive function (a terminal pore) was observed in all species.

Key words: Caridean shrimps, contact chemoreception, sex pheromones, sensillae, setae

Introduction

The second antennae of decapod shrimps bear long flagella which, based on behavioral observations, are recognized as chemotactile, i.e., responsive to both mechanical and chemical stimuli (Bauer, 2004). The structure and physiology of specialized sensory setae (aesthetascs) on the first antennae (= antennules) have been shown to be olfactory in decapods (Ache, 1982;

Derby, 1989; Kamio et al., 2005). However, there is little information on the sensory setae of the flagella of the second antennae (= antennae). Aesthetascs do not occur on the second antennae of decapod crustaceans. Observational evidence indicates that presumptive sensory setae on the antennae must come into close contact a chemical stimulus to detect it (Bauer, 1979; Bauer, 2004; Caskey and Bauer, 2005). The antennal

*Corresponding author.

flagella thus serve in contact chemoreception (gustation or “taste”), responding to insoluble, surface bound, or very low solubility compounds at high concentration rather than to highly soluble compounds that can be perceived in very low concentrations at a distance from their source (olfaction or “smell”).

In addition to their important role in identification of food items, the long antennal flagella have been implicated in sex recognition in caridean shrimps (Burkenroad, 1947; Bauer, 2004; Diaz and Thiel, 2004; Caskey and Bauer, 2005). Parturial females mate and spawn soon after a molt. In the hippolytid carideans *Heptacarpus sitchensis* (Bauer, 1976), *H. paludicola* (Bauer, 1979), and the palaemonid caridean *Palaemonetes pugio* (Burkenroad, 1947; Berg and Sandifer, 1984; Caskey and Bauer, 2005), males strongly react to newly molted parturial females upon touching them with the antennal flagella by grasping and copulating with them. Behavioral experiments with *P. pugio* indicate that tactile stimuli (a soft cuticle) are not involved in recognition of a newly molted (receptive) parturial female by males. Rather, a possible sex pheromone perceived by the male through contact chemoreception was indicated. Contact sex pheromones, detected on the female by the antennae or mouthparts of males, are important in female sexual attractiveness and mating in a variety of insect species (e.g., Bray and Amrein, 2003; Ginzl et al., 2003; Howard and Bloomquist, 2005).

Sexual dimorphism in morphological structures is usually indicative of sexual differences in function, as exemplified by the antennal sensilla of many insects (e.g., Jourdan et al., 1995; Rani and Nakamura, 2001). Males of some isopod (Wagele, 1992) and copepod (Boxhall et al., 1997) species have a greater number of antennular (antenna 1) aesthetascs than females, suggestive of a role in olfactory detection of females. In some mysidan, cumacean, and amphipodan crustaceans, there are non-aesthetasc setae (“male-specific sensilla”) postulated to function in detection of females (Johansson et al., 1996; Hallberg et al., 1997). However, sexual dimorphism of setae on the second antennae of decapod shrimps has not been investigated.

Preliminary observations indicated to us that antennal flagellar setae are more numerous in males than in females in the caridean shrimp *Palaemonetes pugio*, whose sexual biology is well known (Berg and Sandifer, 1984; Bauer and Abdalla, 2000, 2001; Caskey and Bauer, 2005). We asked the question: is there sexual dimorphism in the number and type of setae on the antennal flagella that might indicate a role in mate recognition via contact chemoreception? We tested the null hypothesis of no difference in setal abundance and type (no sexual dimorphism) by comparing the number

of flagellar setae between males and females and by describing setal morphology in *P. pugio*. We similarly surveyed four other available shrimp species to determine if sexual dimorphism in possible antennal sensilla (setae) is widespread among decapod shrimps. We describe the microstructure of these setae as a first step in determination of their function.

Materials and Methods

Specimens of *P. pugio* (Caridea: Palaemonidae) were collected in a salt marsh habitat at Cypremort Point, Vermilion Bay, Louisiana, USA (29°43'N, 91°51'W). *Macrobrachium ohione* (Palaemonidae) were taken in traps from the Atchafalaya River near Butte La Rose, Louisiana (30°16'N, 91°41'W) in June, 2004. Specimens of other species examined were taken from research collections of RTB. *Thor manningi* (Caridea, Hippolytidae) was collected from seagrass meadows at Twin Cays, Belize (16°48'N, 88°05'W) in May, 1986 and July, 1987. *Alpheus normanni* (Caridea, Alpheidae) was taken from seagrass meadows at Dorado, Puerto Rico (18°29'N, 66°15'W) in June, 1982. The penaeoidean shrimp *Rimapenaeus* (= *Trachypenaeus*) *similis* was collected by otter (shrimp) trawls near Horn Island, Mississippi (30°15'N, 88°45'W) in March–October, 1990. All specimens were initially preserved in 10% ambient water formalin and stored in to 70% ethanol.

The hypothesis of sexual dimorphism in antennal flagellar setae was tested by observations on the type and number of basic setal types. We examined the distal part of the antennal flagellum, that most likely to first touch another object in the environment (e.g., a possible mating partner). The distal third of a flagellum was mounted on a slide in the mountant CMC (Polysciences) with acid fuchsin stain for observation with light microscopy. The number and type of setae on 30 flagellar articles were recorded. For scanning electron microscopy, distal antennal flagella from a separate set of specimens were taken through an ethanol series to 100%, then critical-point dried in carbon dioxide and sputter-coated with gold at a thickness of 20–40 nm for examination with a Hitachi S-3000-N scanning electron microscope.

For all species, antennal flagella of 30 sexually mature males and females were examined. Sexual maturity in males was defined as the presence of an appendix masculina on the endopod of pleopod 2 in carideans and fused petasmata (endopods) of the first pleopods in the penaeoid *Rimapenaeus similis*. In caridean species, females incubating embryos on the abdomen (breeding) or within the size range of breeding

females were classified as sexually mature; in the penaeoid *R. similis*, females (thelycum present) in the size range at which inseminated females with mature ovaries are found (Bauer and Lin, 1994) were considered sexually mature. In addition, in two species with little overlap in size between mature males and females (*P. pugio* and *R. similis*), 30 juvenile females in the same size range as males were available and examined for comparisons with males. In *Thor manningi*, the sexual system is a form of protandry with three sexual morphs (Bauer, 1986), which were examined: primary (pure) males, male-phase hermaphrodites (equivalent to juvenile females), and female-phase hermaphrodites.

The median (Md) number of antennal setae from 30 articles is reported below together with the lower and upper 95% confidence limits. The hypothesis no difference in the number of antennal flagellar setae was tested by analysis of covariance (ANCOVA) where there was extensive overlap in body size (measured as carapace length, CL) between groups, the assumption of homogeneity of slopes was met (Sokal and Rohlf, 1981), and the coefficient for the covariate CL was statistically significant ($P \leq 0.05$). For comparisons among groups not meeting these criteria, the non-parametric Kruskal–Wallis (K–W) test was used. If the K–W test was significant, *post hoc* pairwise comparisons were made using a two-sample K–W test (Mann Whitney U test) with adjustment made for multiple testing by dividing the significance level of 0.05 by the number of comparisons.

Results

Palaemonetes pugio

Setae were more much more abundant on the antennal flagellum of males than in breeding and juvenile females (Fig. 1A). The hypothesis of no difference in number of antennal setae among groups was therefore tested and rejected (K–W test, $P < .001$). Pairwise comparisons using a two-sample K–W test showed that the median (Md) number of antennal setae of males (156; 95% confidence limits 146, 174) was significantly different from that of breeding females (99; 88, 102) and juvenile females (81; 86, 94) ($P < 0.001$ in both tests). Setal abundances were slightly but significantly different between breeding and juvenile females ($P = 0.011$).

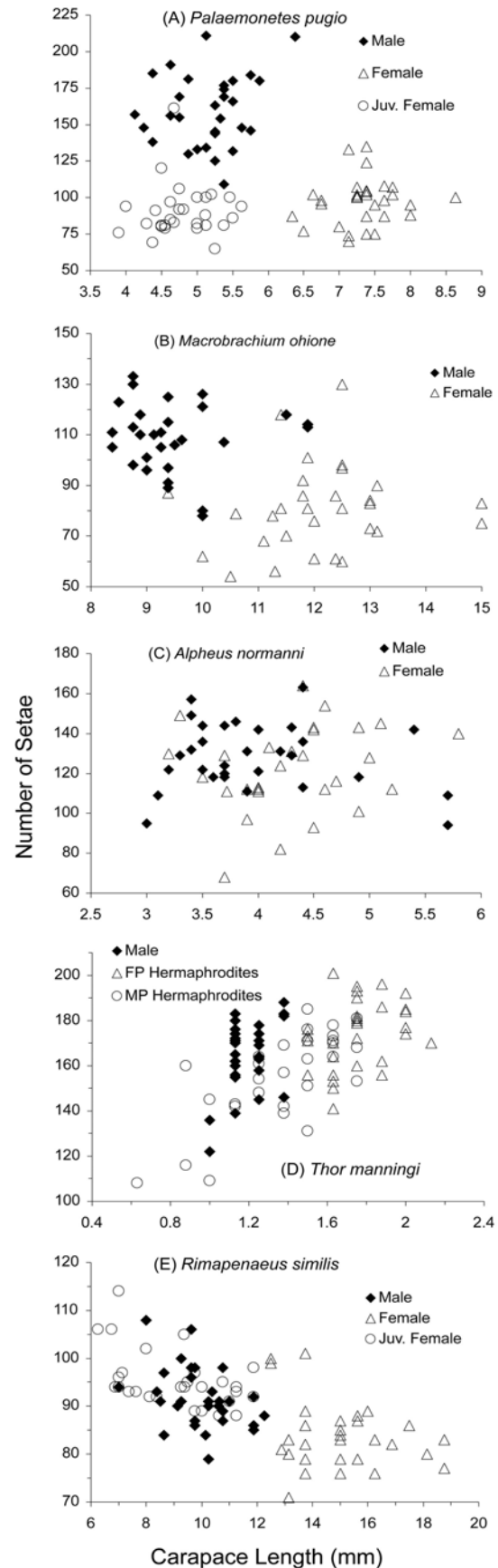


Fig. 1 (right). Variation in setal abundance on distal antennal flagella of sexual morphs of five decapod shrimps. (A) *Palaemonetes pugio*; (B) *Macrobrachium ohione*; (C) *Alpheus normanni*; (D) *Thor manningi*; (E) *Rimapenaeus similis*.

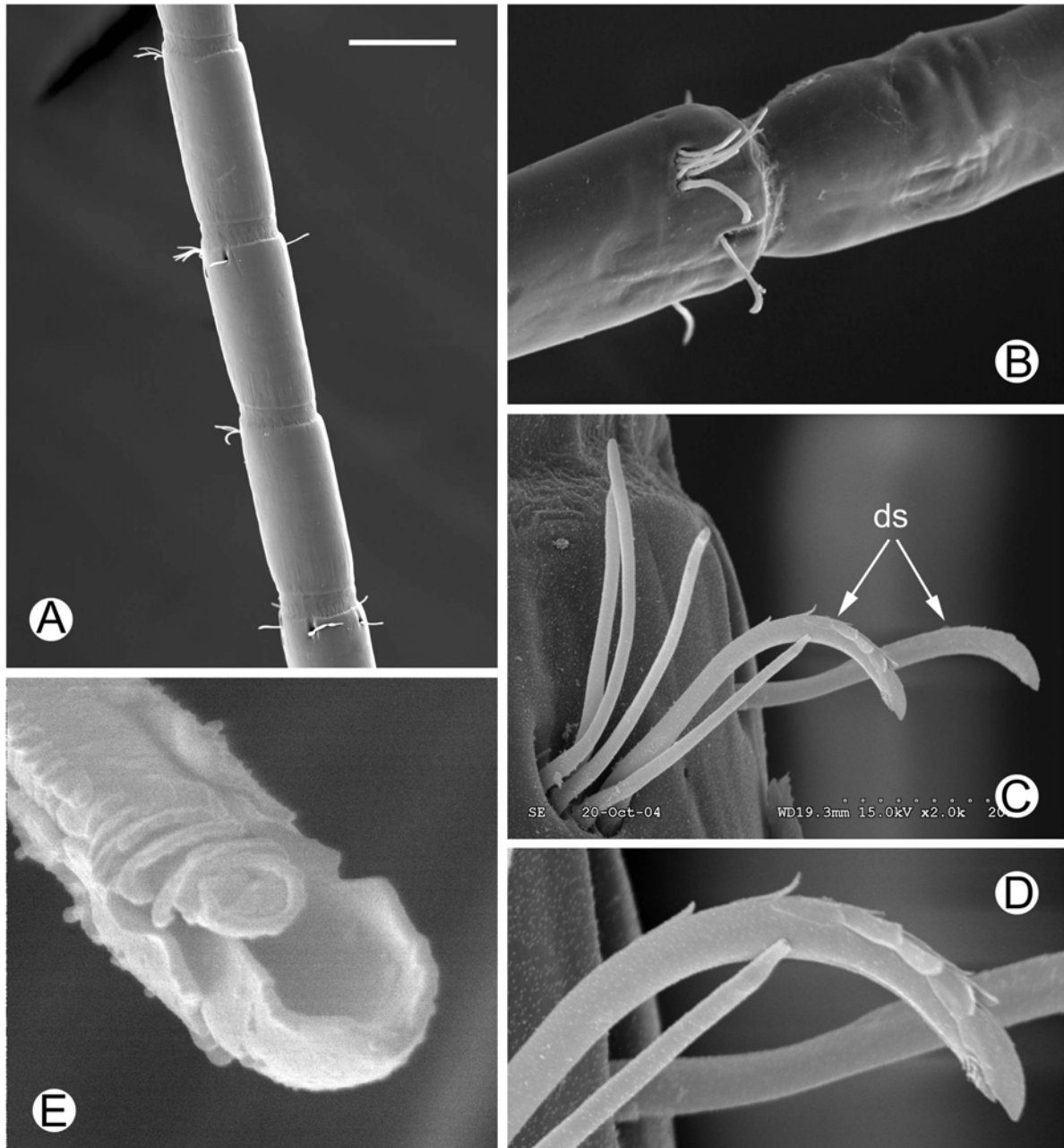


Fig. 2. Antennal flagellar setae of *Palaemonetes pugio*. A: Portion of antennal flagellum with individual articles. B: Setae at the distal end of a flagellar article. C: Mixed group of simple and denticulate setae. D: Distal portions of a denticulate and a simple seta. E: Terminal end of a denticulate seta, showing complex ornamentation. ds, denticulate seta. Scale bar in A is 120 μm in A, 38 μm in B, 13 μm in C, 5 μm in D, and 1 μm in E.

Scanning electron microscopy (SEM) revealed two setal types in both males and females that could not be reliably distinguished with the light microscopy used to make setal counts. Denticulate and simple setae, 20–40 μm in length, were scattered along the antennal flagellum, singly or in groups (Fig. 2A–C). Denticulate setae are adorned with flattened scale-like denticles (Fig. 2D). Ornamentation is more complex distally, with

the seta terminating in a hood which extends a subterminal layer of denticles, possibly ending in a pore (Fig. 2E). Simple setae lack any ornamentation except for an apparent terminal pore, which may be at least partially plugged with material (Fig. 3A, B).

To determine if one or the other of these two setal types might be more abundant in males than in females, accounting for the greater total number of male antennal

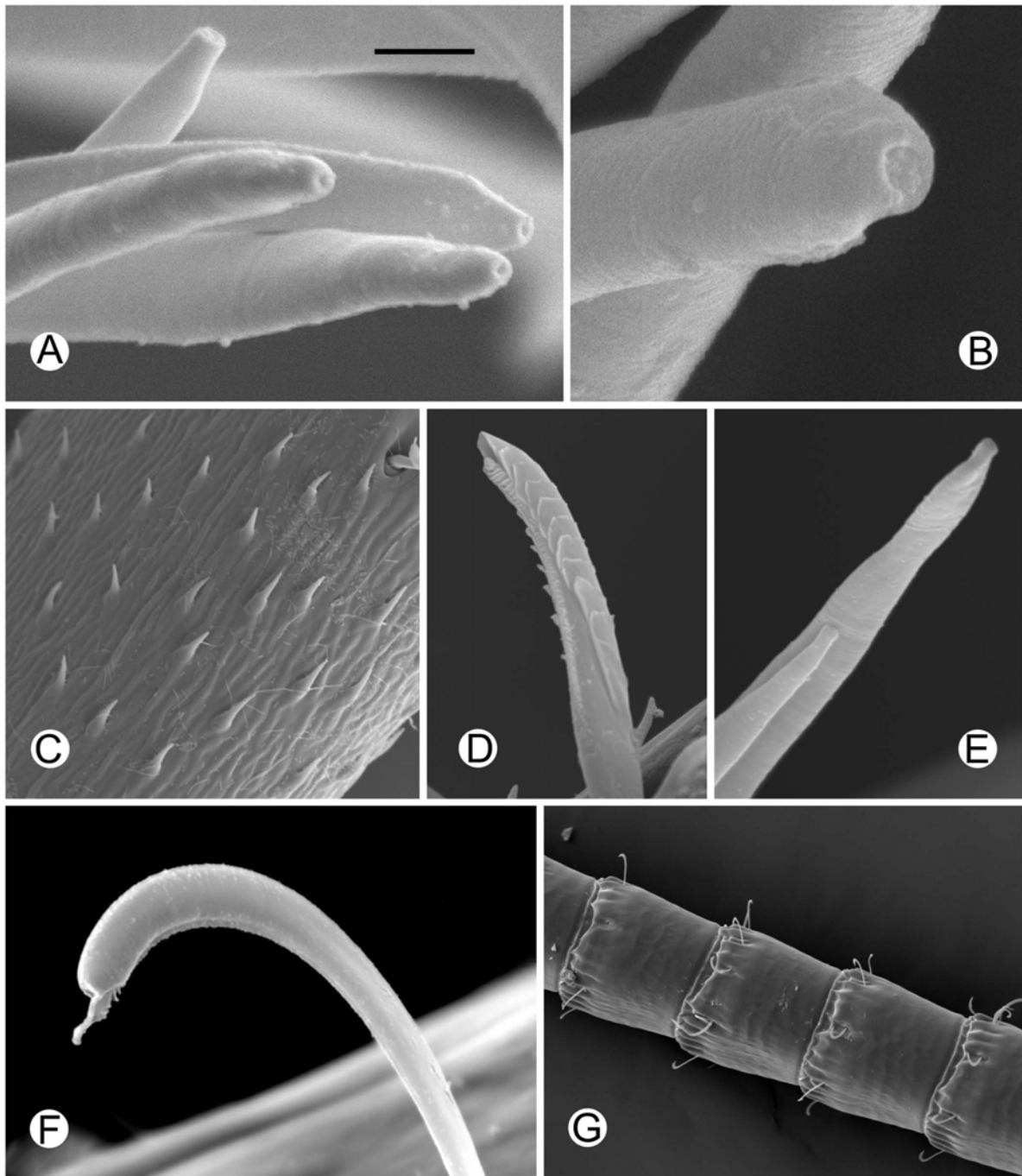


Fig. 3. Antennal flagellar setae of *Palaemonetes pugio*, *Macrobrachium ohione*, and *Alpheus normanni*. A: Distal ends of simple setae of *P. pugio* with pores at the tip. B: Terminal pore, apparently plugged, of a simple seta of *P. pugio*. C: Denticulated surface of a flagellar article, *M. ohione*. D: Denticulated seta, *M. ohione*. E: Simple setae, *M. ohione*. F: Antennal flagellar seta, *A. normanni*, showing terminal spur and apparent pore. G: Flagellar articles, *A. normanni*. Scale bar in A is 2 μm in A, 1 μm in B, 59 μm in C, 8 μm in D, 4 μm in E and F, 100 μm in G.

setae, SEM was used to make counts of each type of seta on 10 articles from 10 males and 10 females. Simple setae were more abundant than denticulate setae in both sexes. However, the median ratio of the number of

simple to denticulate setae (2.6 in males, 2.8 respectively in females) was not significantly different between the sexes (K–W test, $P = 0.68$).

Macrobrachium ohione

There is little overlap in body size between males and breeding females of *M. ohione*; juvenile females were not available for the analysis. In spite of their smaller size, males had significantly more antennal setae (Md = 110; 105, 115) than breeding females (Md = 86; 73, 81) (Fig. 1B). The hypothesis of no difference in number of antennal setae was tested and rejected (K–W test, $P < 0.001$).

Unlike *P. pugio*, the general cuticle of the antennal flagellum was studded with numerous denticles in both males and females (Fig. 3C). As in *P. pugio*, SEM of the antennal flagellum revealed two setal types, denticulate and simple, (30–50 μm in length), both with probable terminal pores (Fig. 3D, E). These setal types could not be reliably distinguished in setal counts made with light microscopy, and SEM was used to count the two kinds of setae on 10 articles from 10 males and 10 females. The median ratio of simple to denticulate setae was similar in males (1.4) and females (1.6) ($P = 0.14$), indicating that the greater total number of antennal setae in males was not due to one setal type or another, but rather a greater abundance of both types.

Alpheus normanni

Scanning electron microscopy revealed a single setal type (20–40 μm in length) in both males and females on the antennal flagellum, a curved simple seta terminating in a flattened spur below a terminal pore (Fig. 3F). Few to several of these setae occur singly at the distal end of flagellar articles (Fig. 3G). Males (Md = 129; 120, 136) and females (Md = 121; 112, 131) of this species had similar numbers of antennal setae. The hypothesis of no difference in number of antennal setae of males and females was tested and accepted (K–W test, $P = 0.22$).

Thor manningi

The single setal type found in the three sexual morphs was very similar to that found in *Alpheus normanni* in size, structure, and placement on the antennal flagellum. Primary males (PMs) had a greater number of antennal setae (Md = 170; 160, 173) than male-phase hermaphrodites (MPs) (Md = 160; 148, 168) (Fig. 1D). The hypothesis of no difference in adjusted mean number of antennal setae was tested using ANCOVA and was rejected ($P < 0.001$). The hypothesis of no difference in median number of antennal setae between PMs and female-phase hermaphrodites (FPs), and MPs and FPs, groups not meeting ANCOVA assumptions, was tested with two-sample K–W tests. Female-phase hermaphrodites had a significantly higher median number of antennal setae (175; 170, 182) than

MPs ($P < 0.001$) but not PMs ($P = 0.04$) when the significance level was adjusted for multiple testing ($P = 0.025$).

Rimapenaeus similis

Setal diversity was much greater on the antennal flagella of the penaeid shrimp *Rimapenaeus similis* than in caridean species. Along one side of the flagellum on each article are usually two long plumose setae (200–250 μm), arising from the distal end of one article, arching and extending over the distal two articles (Fig. 4A, B, D). Less abundant is a short pappose seta (20–30 μm length) (Fig. 4C), often beneath and covered by the arched plumose setae but clearly visible using light microscopy. Scattered along the flagellar articles outside of the area covered by the plumose setae are two types of relatively smooth, simple setae distinguished by their length. The long simple seta (100–150 μm in length) is as long or slightly longer than a flagellar article (Fig. 4D) while the short simple seta (30–70 μm) is distinctly shorter than an article (Fig. 4F). Although described here for convenience as “simple” because they lack setules or well-defined denticles, these simple setae are usually ornamented distally by irregularities in the setal cuticle or poorly formed scale-like denticles (Fig. 4E–G). Ornamentation is often more complex at the tip, surrounding a possible pore (Fig. 4G).

The total number of antennal setae was greater in males (Md = 91; 89, 93) and juvenile females (Md = 94; 93, 97) than in breeding females (Md = 83, 86) (Fig. 1E). The ANCOVA test for difference in adjusted mean number of setae of juvenile females and males was not significant ($P = 0.12$). Comparisons of breeding females with the other groups, using two-sample K–W tests because ANCOVA assumptions were not met, showed that breeding females had significantly fewer total setae than both juvenile females ($P = 0.005$) and males ($P < 0.001$).

In this penaeid species, several setal types could be distinguished with light microscopy: plumose, pappose, short simple and long simple. Plumose setae were the most abundant of the setal types, making up 72%, 66%, and 64% of the total setae in females, males, and juvenile females, respectively (based on medians of plumose and total setae). To determine if any one of these setal types was more abundant in males than in females, the hypothesis of no difference in the median of each setal type was tested (two-sample K–W tests). Males consistently had more setae of each type than females, although the absolute numbers were quite small, and these differences were statistically significant except for large simple setae (Table 1). Likewise, juvenile females had more setae of each type than

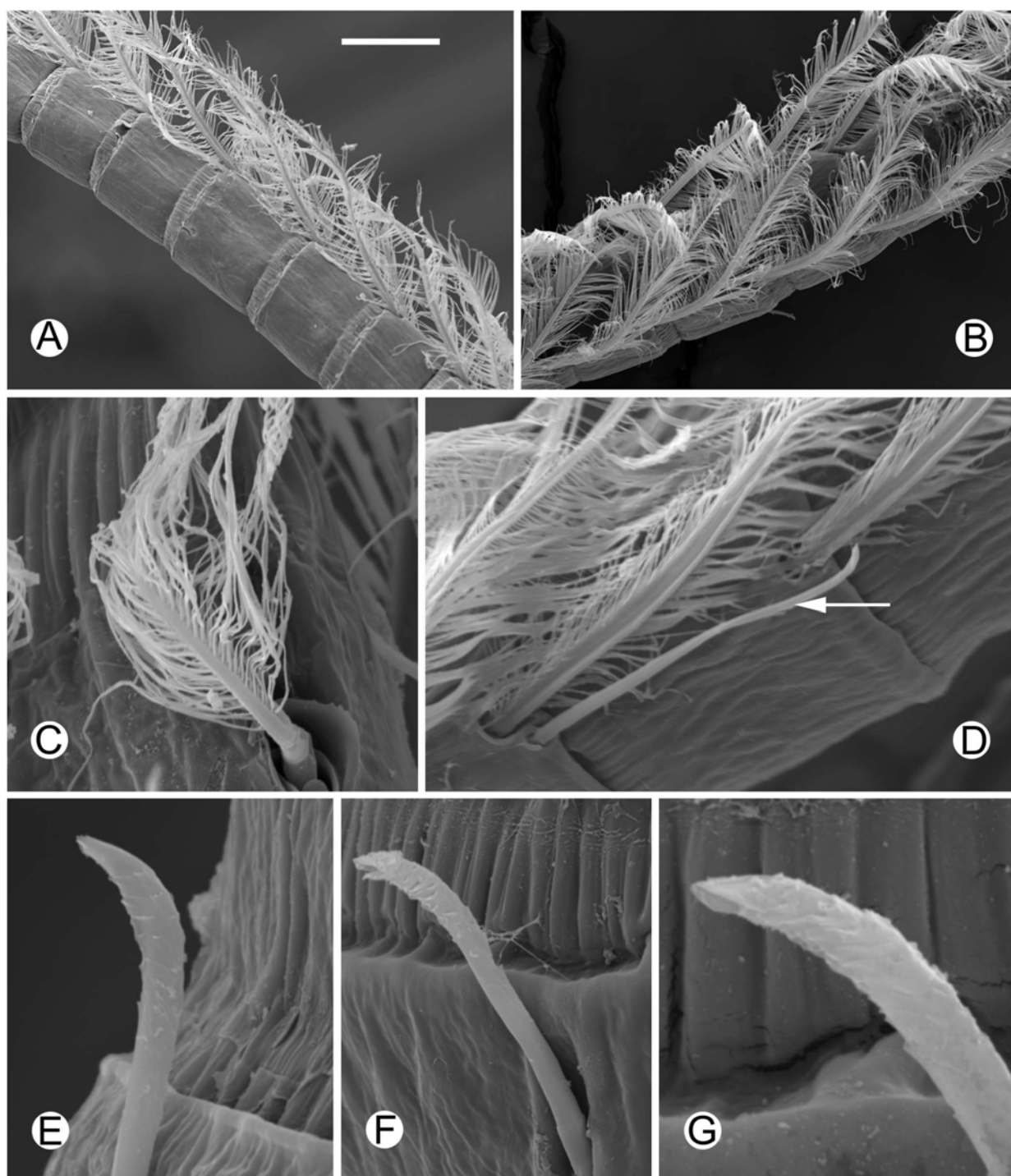


Fig. 4. Antennal flagellar setae of *Rimapenaes similis*. A, B: Arrangement of arched plumose setae on the antennal articles. C: Pappose seta. D: Long simple seta (arrow) along side of plumose setae. E: Distal end of long simple seta. F: Short simple seta. G: Distal end of short simple seta. Scale bar in A is 110 μm in A and B, 11 μm in C, 25 μm in D, 7 μm in E, 11 μm in F, and 4 μm in G.

breeding females (Table 1). Thus, breeding females of *R. similis*, in spite of a larger body size, had fewer antennal setae of all types than the similarly-sized males and juvenile females.

Discussion

In the species examined, males do not have unique setal types on the second antennae (antennal) flagella, i.e., no “male-specific” sensilla such as those found on

Table 1. Comparison of abundance (medians with 95% confidence limits in parentheses) of different setal types among males, breeding females, and juvenile females in *Rimapenaeus similis*. The probability of no difference in medians between males and breeding females is given with the male data, and between breeding females and juvenile females with the juvenile female data (significant difference indicated with an asterisk). Level of significance (comparison of breeding female data with two groups) is adjusted to 0.025 to account for multiple testing

	Setal type			
	Plumose	Pappose	Long simple	Short simple
Male	60 (60, 60) ($P < 0.001$)*	10 (9, 11) ($P = 0.005$)*	8 (7, 9) ($P = 0.027$)	13 (11, 15) ($P = 0.001$)*
Breeding female	60 (59, 60)	7 (7, 9)	7 (6, 8)	10 (8, 11)
Juvenile female	60 (60, 60) ($P = 0.022$)*	10 (9, 11) ($P = 0.002$)*	10 (9, 12) ($P < 0.001$)*	14 (13, 15) ($P < 0.001$)*

the first antennae (antennules) of some peracarids (Johansson et al., 1996; Hallberg et al., 1997). However, in the palaemonid carideans *P. pugio* and *M. ohione*, there is a fairly strong sexual dimorphism in the number of antennal flagellar setae. Antennal setae were significantly more numerous in males. At least in *P. pugio*, this was simply not an inverse size effect of smaller individuals (males) having more setae than larger individuals (breeding females). Like the breeding females, juvenile females, with similar body size as males, had significantly fewer flagellar setae than males. Both *P. pugio* and *M. ohione* had similar types of setae, simple and denticulate, both of which apparently terminate with a pore open to the outside environment.

The hippolytid caridean *T. manningi* has a complex sexual system with primary (pure) males (PMs) and protandric sex-changers which first go through a male phase (MP) before changing to females (female-phase hermaphrodites = FP, Bauer, 1986). Sexual dimorphism does occur in the third pereopods (first walking legs), which are prehensile in PMs but not in MPs and FPs. In addition, PMs have significantly larger male pleopod appendices than MPs. However, there was no sexual dimorphism in antennal setae between PMs and FPs. Antennal setae counts were slightly but significantly higher in FPs compared to those of MPs, contrary to a hypothesis that higher numbers of antennal setae are a male sensory adaptation for detection of females by contact chemoreception. In the alpheid caridean *A. normanni*, antennal setal counts were not different between males and females. In *T. manningi* and *A. normanni*, which are from closely related families (Bauer, 2004), the antennal flagellum had a single morphological type of seta, a simple seta with a terminal spur and pore.

The distribution of setae on the second antennae of the benthic penaeid (dendrobranchiate) *R. similis* is similar to those described in some pelagic dendrobranchiate shrimps (Foxton, 1969; Ball and Cowan, 1977). In the dendrobranchiates, a greater diversity of

setae occurs than in the carideans examined in this study, and numerically the setation is dominated by plumose setae not observed in the caridean species. These setae, usually two per article, arch distally, forming a space (tunnel) in which the pappose setae occurs. The structure and position of the plumose and pappose seta indicate that they are similar (homologous) to the “type 1” and “type 2” setae described in Foxton (1969) and Ball and Cowan (1977) for pelagic dendrobranchiate shrimps. In those species, the arched plumose setae, which are not innervated (Ball and Cowan, 1977), form a tunnel into which type 2 mechanoreceptors extend. This is a sensory system is sensitive to waterborne vibrations in species studied (Denton and Gray, 1985) and may serve a similar function in *R. similis*. The short and long simple setae appear to bear pores at their tip. Similar setae (“type 3”) in the sergestid *Acetes sibogae* show innervation indicative of a chemoreceptive function (Ball and Cowan, 1977).

In *R. similis*, the smaller-sized males did have a significantly greater total number of setae than the larger breeding females. However, juvenile females, similar in size as males, also had a greater number of setae than breeding females. This may simply indicate a general inverse relationship between antennal setae and size in this species and not a sexually dimorphic feature associated with male recognition of breeding females.

In *P. pugio*, males perceive postmolt parturial (receptive) females only upon contact with the antennal flagella, which is facilitated by the high mobility of individuals of this species and their high density in aggregations (Bauer and Abdalla, 2001). Males do not guard females before their parturial molt. This mating system, with a scramble competition among males for postmolt parturial females, is termed “pure searching” (Wickler and Seibt, 1981). The related *M. ohione*, with similar socioecological characteristics and sexual dimorphism in body size (small males, larger females), appears to have a similar mating system. A greater

number of possible chemoreceptive sensilla on the male antennal flagella might facilitate perception of a contact pheromone on the surface of postmolt parturial females. In contrast, males and females of snapping shrimps such as *A. normanni* live in pairs (extended mate guarding, Bauer, 2004). Males might not need chemoreceptive capabilities enhanced by greater numbers of antennal sensilla to detect the female living right next to it.

However, although the male mating tactics of the other species investigated in this report, *T. manningi* and *R. similis*, have not been described, their sexual dimorphism in size and occurrence in high density aggregations appears similar to that of *P. pugio* and *M. ohione*. It is quite likely that male morphs of *T. manningi* and males of *R. similis* have pure searching mating systems. However, they show no sexual dimorphism in antennal setae number.

In all species examined, there were antennal flagellar setae whose microstructure suggests a contact chemoreceptive (taste) function. These are the setae (sensilla) with terminal or subterminal pores, a characteristic often associated with chemoreceptive capacity in crustaceans (Derby, 1989). In the absence of a thin-walled, spongy (= permeable) cuticle, such as that of the olfactory aesthetascs of the antennules (Hallberg et al., 1997), a terminal pore may allow potentially stimulating molecules to enter inside the setal shaft where chemosensory neurons may occur. Innervation of setae indicates a sensory function, and ultrastructure of innervating neurons can distinguish between chemoreceptive and mechanoreceptive function (e.g., Ball and Cowan, 1977; Derby, 1989). Such ultrastructural studies need to be done on the antennal setae of the species studied. However, the contact chemoreceptive function of possible sensilla must be verified by electrophysiological studies. The lack of clear sexual dimorphism in antennal flagellar setae across species studied indicates that male capabilities to detect female contact pheromones in decapod shrimps will be found in the ultrastructure and physiology of setal neurons or at higher neurological levels.

Acknowledgements

This study was supported with funds to RTB from the National Oceanographic and Atmospheric Administration's Louisiana Sea Grant Program (R/SA-03). This is Laboratory of Crustacean Research Contribution No. 107.

References

Ache, B.W., Chemoreception and thermoreception. In: The Biology of Crustacea. Vol. 3, H.L. Atwood and D.C.

- Sandeman (eds.), Academic Press, New York, 1982, pp. 369–398.
- Ball, E.E. and Cowan, A.N., Ultrastructure of the antennal sensilla of *Acetes* (Crustacea, Decapoda, Natantia, Sergestidae). *Phil. Trans. R. Soc. Lond. B*, 277 (1977) 429–456.
- Bauer, R.T., Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *J. Nat. Hist.*, 10 (1976) 315–440.
- Bauer, R.T., Sex attraction and recognition in the caridean shrimp *Heptacarpus paludicola* Holmes (Decapoda: Hippolytidae). *Mar. Behav. Physiol.*, 6 (1979) 157–174.
- Bauer, R.T., Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea). A novel case of protandric hermaphroditism. *Biol. Bull.*, 170 (1986) 11–31.
- Bauer, R. T., Remarkable Shrimps: Adaptations and Natural History of the Carideans, Oklahoma University Press, Norman, OK, 2004.
- Bauer, R.T. and Abdalla, J.A., Patterns of brood production in the grass shrimp *Palaemonetes pugio* (Decapoda: Caridea). *Invert. Reprod. Develop.*, 38 (2000) 107–113.
- Bauer, R.T. and Abdalla, J.A., Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology*, 1107 (2001) 185–199.
- Bauer, R.T. and Lin, J., Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the northcentral Gulf of Mexico. *J. Exp. Mar. Biol. Ecol.*, 182 (1994) 205–222.
- Berg, A.B. and Sandifer, P.A., Mating behavior of the grass shrimp *Palaemonetes pugio* Holthuis (Decapod: Caridea). *J. Crust. Biol.*, 4 (1984) 417–424.
- Boxhall, G.A., Yen, J. and Strickler, J.R., Functional significance of the sexual dimorphism in the cephalic appendages of *Euchaeta rimana* Bradford. *Bull. Mar. Sci.*, 61 (1997) 387–398.
- Bray, S. and Amrein, H., A putative *Drosophila* pheromone receptor expressed in male-specific taste neurons is required for efficient courtship. *Neuron*, 39 (2003) 1019–1029.
- Burkenroad, M.D., Reproductive activities of decapod Crustacea. *Am. Nat.*, 81 (1947) 392–398.
- Caskey, J.L. and Bauer, R.T., Behavioral tests for a possible contact sex pheromone in the caridean shrimp *Palaemonetes pugio*. *J. Crust. Biol.*, 25 (2005) 571–576.
- Denton, E.J. and Gray, J., Lateral-line-like antennae of the Penaeidea (Crustacea, Decapoda, Natantia). *Proc. R. Soc. Lond. B*, 226 (1985) 249–261.
- Derby, C.D., Physiology of sensory neurons in morphologically identified cuticular sensilla of crustaceans. In: *Functional Morphology of Feeding and Grooming Appendages*, B.E. Felgenhauer, L. Watling and A.B. Thistle (eds.), A.A. Balkema, Rotterdam, 1989, pp. 27–47.
- Díaz, E. and Thiel, M., Chemical and visual communication during mate searching in rock shrimp. *Biol. Bull.*, 206 (2004) 134–143.

- Foxton, P., The morphology of the antennal flagellum of certain of the Penaeidea (Decapoda, Natantia). *Crustaceana*, 16 (1969) 33–42.
- Ginzel, M.D., Blomquist, G.J., Millar, J.G. and Hanks, M.L., Role of contact pheromones in mate recognition in *Xylotrechus colonus*. *J. Chem. Ecol.*, 29 (2003) 533–545.
- Hallberg, E., Johansson, K. and Wallén, R., Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. *Int. J. Insect Morphol. Embryol.*, 26 (1997) 173–180.
- Howard, R.W. and Bloomquist, G.J., Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Ann. Rev. Entomol.*, 50 (2005) 371–393.
- Kamio, M., Araki, M., Nagayama, T., Matsunaga, S. and Fusetani, N., Behavioral and electrophysiological experiments suggest that the antennular outer flagellum is the site of pheromone reception in the male helmet crab *Telmessus cheiragonus*. *Biol. Bull.*, 208 (2005) 12–19.
- Johansson, K.U.I., Gefors, L., Wallén, R. and Hallberg, E., Structure and distribution patterns of aesthetascs and male-specific sensilla in *Lophogaster typicus* (Mysidacea). *J. Crust. Biol.*, 16 (1996) 45–53.
- Jourdan, H., Barbier, R., Bernard, J. and Ferran, A., Antennal sensilla and sexual dimorphism of the adult ladybird beetle *Semiadalia undecimnotata* sch. (Coleoptera: Coccinellidae). *Int. J. Insect Morphol. Embryol.*, 24 (1995) 307–322.
- Rani, P.U. and Nakamura, K., Morphology of antennal sensilla, distribution, and sexual dimorphism in *Trogossita japonica* (Coleoptera: Trogossitidae). *Ann. Entomol. Soc. Am.*, 94 (2001) 917–927.
- Sokal, R.R. and Rohlf, F.J., *Biometry*, 2nd ed., W.H. Freeman, New York, 1981.
- Wägele, J.-W., Isopoda. In: *Microscopic Anatomy of Invertebrates*, Vol. 9, F.W. Harrison and A.G. Humes (eds.), Wiley-Liss, New York, 1992, pp. 529–617.
- Wickler, W. and Seibt, U., Monogamy in Crustacea and Man. *Z. Tierpsychol.*, 57 (1981) 215–234.