Setal Morphology of the Grooming Appendages of *Macrobrachium rosenbergii* (Crustacea: Decapoda: Caridea: Palaemonidae) and Review of Decapod Setal Classification

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ABSTRACT Setae are vital in grooming activities and aiding in the removal of epibionts and sedimentary fouling from the body surfaces of decapod crustaceans. Thus, the setal structures and their arrangement on the grooming appendages and sensory structures of the commercially important shrimp, *Macrobrachium rosenbergii*, were examined using scanning electron microscopy. *Macrobrachium rosenbergii* is extensively grown in aquaculture and exhibits unique male morphological forms, termed morphotypes. The three male morphotypes are termed blue-clawed males, orange-clawed males, and small-clawed or undifferentiated males and all three differ in their dominance, behavior, body morphology, and reproductive success. Seven setal types, two of which have never been described in the literature, are identified on the grooming appendages (third maxillipeds, first, second, and fifth pereopods) and antennae: simple, serrate, serrulate, spiniform, pappose, crinoid, and spinulate. The latter two setae are newly identified. Certain setal types, such as serrate and serrulate setae were located and associated with specific grooming appendages such as the first pereopods. The types of setae on the grooming appendages varied among females and male morphotypes and the novel setal types (crinoid and spinulate) were found only on two of the male morphotypes. A literature review of terminology related to the structure of setae and setal types in decapod crustaceans is offered as the usage of various terms is ambiguous and conflicting in the literature. The intention of this review is to provide future authors with a comprehensive collection of terms and images that can be used to describe various aspects of setal morphology in decapods. J. Morphol. 275:634–649, 2014. © 2014 Wiley Periodicals, Inc.

KEY WORDS: *Macrobrachium*; grooming; decapod crustacean morphology; SEM; setae

INTRODUCTION

Grooming is a common behavior seen among decapod crustaceans (Bauer, 1977, 1978, 1979, 1981, 1989, 1998, 1999, 2002, 2004; Felgenhauer and Schram, 1979; Felgenhauer, 1992); these behaviors remove fouling organisms and debris from the body and promote proper body functioning. Grooming has been described as an adaptive behavior and the structures associated with this activity help to prevent or remove fouling (Bauer, 1978). Fouling of the body surfaces is particularly intensive for aquatic animals with hard exoskeletons as they are constantly bathed in a medium that is laden with microorganisms, sediment and particulate matter that can settle on or clog the body (Bauer, 1989). Aquatic swimming decapods likely have increased levels of fouling, leading to higher selective pressures for the development of more grooming behaviors and structures to remove or prevent fouling (Bauer, 1977, 1978, 1979, 1981, 1989, 1999, 2004).

Although, the exoskeleton of decapods is periodically molted, removing fouling, severe fouling of the body can occur in the intermolt period, leading to impairment or death (Bauer, 2004). The jointed appendages of decapod crustaceans can clog with fouling organisms, sediment or particulate matter that may impede movement and locomotion. Thus, decapods have evolved specialized appendages with setae that are adapted for grooming the body surfaces and can prevent or remove fouling (Bauer, 1981). Setae are articulated outgrowths of the cuticle that come in a variety of forms with microstructures and can be arranged to form specialized combs and brushes (Bauer, 1981, 1989;

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Felgenhauer, 1992). Setal structure in decapods is important in overall mechanical, sensory (chemo- and mechano-sensory) reception, feeding, and morphological function including sensory mating and grooming (Bauer, 1989, 2004; Felgenhauer, 1992). In the past, there have been many classification schemes of decapod crustacean setae, leading to confusion and conflict among researchers about certain terminology (Bauer, 1989; Jacques, 1989; Watling, 1989; Felgenhauer, 1992; Garm, 2004; Short, 2004). A clear description of setal types, their associated microstructures and the terminology of these microstructures, is needed for researchers to consistently and accurately identify these anatomical structures.

Representatives of *Macrobrachium* Spence Bate, 1868 are known for having long and robust chelipeds (second pereopods, Fig. 1) and undergo aquatic migrations from freshwater to marine environments that may increase fouling pressure on these organisms (Bauer, 1989). The giant freshwater prawn, *Macrobrachium rosenbergii* (De Man, 1879), the study species, has been introduced to nearly every continent due to its aquacultural importance. The adults grow very large and are easily grown for human consumption (Bauer, 2004).

Macrobrachium rosenbergii males have three distinct morphological forms, termed morphotypes, that differ in body structure, physiology, and behavior (Ra'Anan and Sagi, 1985, Fig. 2). The largest males, blue-clawed males (BC), are dominant, found in the lowest proportion within the population and have the highest reproductive success with females compared with the moderately sized males, orange-clawed males (OC males), that are subdominant to BC males and have the lowest reproductive success. The smallest males, small-clawed males (SM males), are nonterritorial, subordinate, found in the largest proportion within the population and exhibit "sneak copulation" events with females, resulting in high reproductive success (Ra'Anan and Sagi, 1985; Kuris et al. 1987). Juvenile males develop into SM males, that molt into the intermediate OC males, that then molt into the terminus BC male morphotype; when a BC male is removed from the system, the other morphotypes will molt and fill the niche of the dominant position (Barki et al. 1991; Karplus et al. 1992). This social hierarchy results in behavioral differences among the morphotypes (Ra'Anan and Sagi, 1985). Blue-clawed males spend much time resting, grooming or courting/protecting females while SM males are highly mobile and active, spending time searching for food and females (Ra'Anan and Sagi, 1985). Because activity level is linked to increased fouling pressures (Bauer, 1989), SM males may have a greater need to groom compared to the other male morphotypes.

The objective of this study is to identify the appendages and microstructures of *M. rosenbergii*

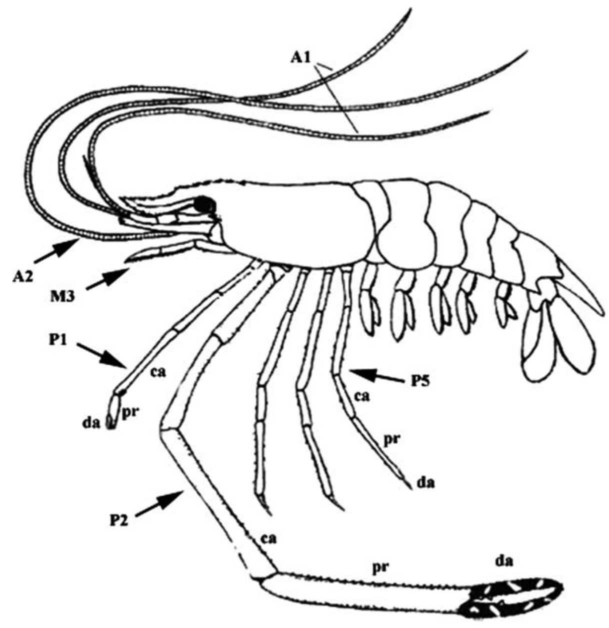

Fig. 1. *Macrobrachium rosenbergii* generalized morphology (Diagram modified from Short, 2004). A1 = antennae; A2 = antennules; ca = carpus; da = dactyl; M3 = third maxilliped; P1: first pereopod; P2 = second pereopod; P5 = fifth pereopod; pr = propodus.

that have been documented to be involved with grooming. Understanding the grooming appendages, sensory structures and associated setal structures of *M. rosenbergii* will help elucidate differences in grooming behaviors and morphologies of the male morphotypes and females. It is hypothesized that similar morphologies of the appendages will be present on all individuals within the species, but individuals of each male morphotype may have unique setal arrangements and types that correspond with their behavioral niches within the social hierarchy.

METHODS AND MATERIALS

Scanning Electron Microscopy (SEM)

Representative individuals of *M. rosenbergii* (Crustacea: Decapoda: Caridea: Palaemonidae; De Man, 1879) sexes and male morphotypes (females: $N = 2$; SM males: $N = 2$; OC males: $N = 2$; BC males: $N = 2$) were prepared for SEM and photography to evaluate the different morphological structures of the antennae and grooming appendages (third maxillipeds, first pereopods, second pereopods, and fifth pereopods; Fig. 1). These were the only appendages observed grooming the body structures in *M. rosenbergii* (VanMaurik and Wortham, 2011). Shrimps were preserved in 70% ethyl alcohol and taken through standard SEM technique (Felgenhauer, 1987). Grooming appendages were sputter coated in gold–palladium 2–6 times

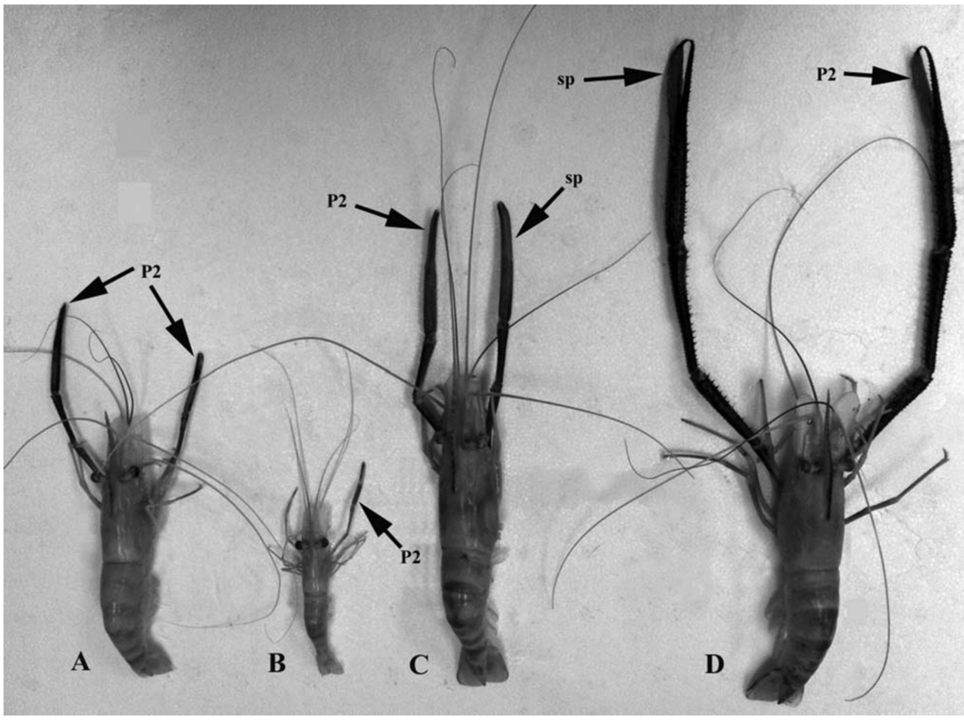

Fig. 2. *Macrobrachium rosenbergii* relative size of females and male morphotypes. **A**, Female (mean carapace length = 34.9 mm). **B**, Small-clawed (SM) male (mean carapace length = 22.1 mm). **C**, Orange-clawed (OC) male (mean carapace length = 38.7 mm), **D**. Blue-clawed (BC) male (mean carapace length = 46.3 mm). Note the difference in size and shades of grey on the chelipeds. Setal patch can be seen on OC and BC males, but not on female and SM male. P2 = second pereopod; sp = setal patch.

to ensure complete coverage (Pelco Model 2 Sputter Coater 91000). Scanning electron micrographs were captured using a JEOL JSM-6010A Analytical Scanning Electron Microscope from a magnification range of 14×–1300×. The SEM images were used to compare morphological differences between the sexes and morphotypes in setal type, pattern and structure. Live shrimp were shipped from Aquaculture of Texas overnight to the University of Tampa. Figures are arranged by structure/grooming appendage, not by sex or morphotype (i.e., the third maxilliped of females and male morphotypes are in one figure) and are from distal to proximal areas of the specified appendage. Orientation labels (i.e., dactyl, propodus, carpus) were put on as many images as possible so as not to cover appendage details. If labels could not fit on the image, then orientation information is located in the figure legend. Male morphotypes will be referred to as "morphotypes" for the remainder of the article.

Summary of Terms

A review of the classification and types of decapod crustacean setae was completed to ensure and evaluate the proper usage of terminology related to the setal structures of *M. rosenbergii*.

Seta. An articulated extension of the cuticle, typically of a different appearance than the surrounding integument (Supporting Information, appendix 1). Size may vary, ranging from micrometers to millimeters. Setae may have a pore (terminal or subterminal), annulus, or branches from the setal shaft and a socket of varying depth is visible (Jacques, 1989; Watling, 1989; Short, 2004). A seta grows distal end first; thus the distal end is the oldest portion (Jacques, 1989).

Spine. A pointed nonarticulated extension of the cuticle that is highly chitinized and does not have a pore or socket (Fish, 1972; Watling, 1989; Short, 2004; Supporting Information, appendix 1).

Tooth. A blunt nonarticulated extension of the cuticle that is highly chitinized and does not have a pore or socket. Commonly larger than a spine and seen on the inner dactyl of *M. rosenbergii* (Fig. 8A).

Denticule. A nonarticulated extension of the setal shaft that typically occurs in rows in a variety of patterns. Denticules are always located distal to the annulus and are typically flat with pointed outgrowths (Pohle and Telford, 1981; Watling, 1989; Garm, 2004; Supporting Information, appendix 1).

Scale. A type of denticule that has a variable number of projections or lobes at the distal edge. According to Watling (1989), this term is used to describe relatively large extensions of the setal shaft, similar to a denticule and should not be used to describe very small extensions. However, Jacques (1989) uses this term to describe thin, interlocking plates that usually lay flat against the setal shaft. The terminology of this structure is debated and will be discussed in the next section (Supporting Information, appendix 3).

Setule. An articulated extension of the setal shaft, although this articulation may be weak and difficult to see. Setules typically taper toward the distal tip and are oriented toward the end of the setal shaft (Pohle and Telford, 1981; Jacques, 1989; Watling, 1989; Garm, 2004) (Supporting Information, appendix 1).

Annulus. A ring that encompasses the circumference of the setal shaft; may be singular or multiple (Watling, 1989; Supporting Information, appendix 1).

Articulation. An area at which the cuticle is flexed outward or where there is a movable joint (Jacques, 1989; Watling, 1989; Garm, 2004; Supporting Information, appendix 1).

Nail. A nonarticulated rounded end of an appendage, often having an annulus (Tattersall and Tattersall, 1951; Tattersall, 1967; Fish, 1972; Fig. 4A).

Pore. Opening in a setal shaft that communicates with the setal lumen. It may be difficult to distinguish between a true pore and an invagination using SEM only (Jacques, 1989; Felgenhauer, 1992; Fig. 5E).

Setal patch. Aggregation of setae in a given area. The setae will each emerge from individual sockets (Fig. 4A), as opposed to a tuft of setae (compared to Fig. 5A).

Tuft. An aggregation of setae emerging from one large socket (Fig. 5A).

Simple setae. This most basic type of setae has a naked setal shaft with no branching (i.e., no setules or denticules). Simple setae taper to the distal tip, may or may not have a pore (terminal or subterminal) and may have an annulus (Farmer, 1974; Garm, 2004; Short, 2004; Supporting Information, appendix 2).

Spiniform setae. This type of seta is robust and spine-like in appearance, is smooth (i.e., no denticules or setules), but unlike spines, has a socket. These setae are usually found in low numbers, are short in length and are randomly arranged on the pereopods (Short, 2004; Supporting Information, appendix 2).

Pappose setae. These setae are very long, slender, and typically occur in dense aggregations or clumps. The long randomly arranged setules circumscribe the setal shaft (Farmer, 1974; Factor, 1978; Garm, 2004; Short, 2004; Supporting Information, appendix 2).

Serrate setae. This setal type has a naked proximal setal shaft and more distally with short denticules (or serrations, as termed by Farmer, 1974) branching from the shaft in two rows at an angle of 45°–120° from each other, creating a groove (Supporting Information, appendix 2). The denticules orient distally and typically begin above an annulus (Farmer, 1974; Garm, 2004; Short, 2004; Supporting Information, appendices 1 and 2).

Serrulate setae. This setal type has a naked proximal setal shaft and more distally with small scales circumscribing the shaft. The scales may appear articulated, but are not when viewed at high magnifications. Instead, there is a shadow due to the angle of the scale emerging from the shaft. The scales may be in rows or randomly arranged, are typically leaf-shaped and have a variable number of lobes along the distal edge (Garm, 2004; Supporting Information, appendix 2).

Clarification of Previous Terminology

When considering the extensions of the seta, the primary branch is the setal shaft, the secondary branching from the shaft includes denticules, scales or setules and the tertiary branch (termed lobe) is the outgrowth from the denticule or setule (Supporting Information, appendix 1; Pohle and Telford, 1981; Watling; 1989). It is important to note that although there are many descriptions of these terms in the literature, there is still much debate about their proper usage (Jacques, 1989; Watling; 1989; Garm, 2004; Short, 2004; Supporting Information, appendix 3). In particular, a structure may be described as a setule in one publication (Garm, 2004), but the same structure may be termed a denticule in another (Watling, 1989). For example, Garm (2004) describes three structures, which, based on our proposed definition, would be classified as denticules; one denticule is correctly termed, whereas the other two are identified as setules in Garm's paper, where there appears to be no visible articulation. Watling (1989) also describes denticules with serrations, but the illustration indicates the presence of articulations; therefore we apply the term setule following our definition of the term. This drawing is misleading because it appears as if denticules should have articulations, when in fact, they do not. The terms denticule and setule are often misunderstood and as a result, used incorrectly. The proper classification of these terms depends on the articulation at the setal shaft. Evidence of the presence or absence of this articulation should be very strong before terming the structure.

Jacques (1989) has described setae with serrations as "setae with scales" due to the appearance of the denticules as scale-like (Supporting Information, appendix 3). This terminology will be used in this study to describe any scale-like denticules. The scales of serrulate setae are not articulated with the setal shaft (so cannot be termed setules) and have serrations at the distal ends (termed lobes).

TABLE 1. Types of setae associated with each appendage evaluated in this study

Setal type/ appendage	Antennae (A2)	Third maxilliped (M3)	First pereiopod (P1)	Second pereiopod (P2)	Fifth pereiopod (P5)
Simple setae	×	×	×	×	×
Serrate setae		×	×		×
Serrulate setae			×		
Spiniform setae				×	×
Pappose setae				×	
Crinoid setae				×	
Spinulate setae				×	

RESULTS

Description of Setal Structures of Antennae, Third Maxillipeds, First Pereopods, Second Pereopods, and Fifth Pereopods

Five defined (identified on other decapods) setal types were identified on the pereopods [first (P1), second (P2), and fifth (P5)], third maxillipeds (M3), and antennae (A2) of *M. rosenbergii*: simple, spiniform, pappose, serrate, and serrulate. Simple setae were the most common setal type and were found on all appendages examined (Table 1). Spiniform and pappose setae were found only on the P2 of females and morphotypes. Serrate setae were found on the M3 and P1 of all individuals and serrulate setae were found only on the P1 of all individuals. Interestingly, two undefined and unknown types of setae were identified and occurred only on the P2 of the SM and OC males, termed crinoid and spinulate setae.

Antennae. Only simple setae are found on the antennae of females, SM males, OC males, and BC males (Fig. 3). The antennae are articulated (Fig. 3B) and simple setae are present in a setal crown (Fig. 3A,C) near the distal end of each article. The setal crown is present at every other articulation point in the females and SM males (Fig. 3A,B) and at every articulation point in the OC and BC males with one to two setae emerging from each deep socket (Fig. 3C,D).

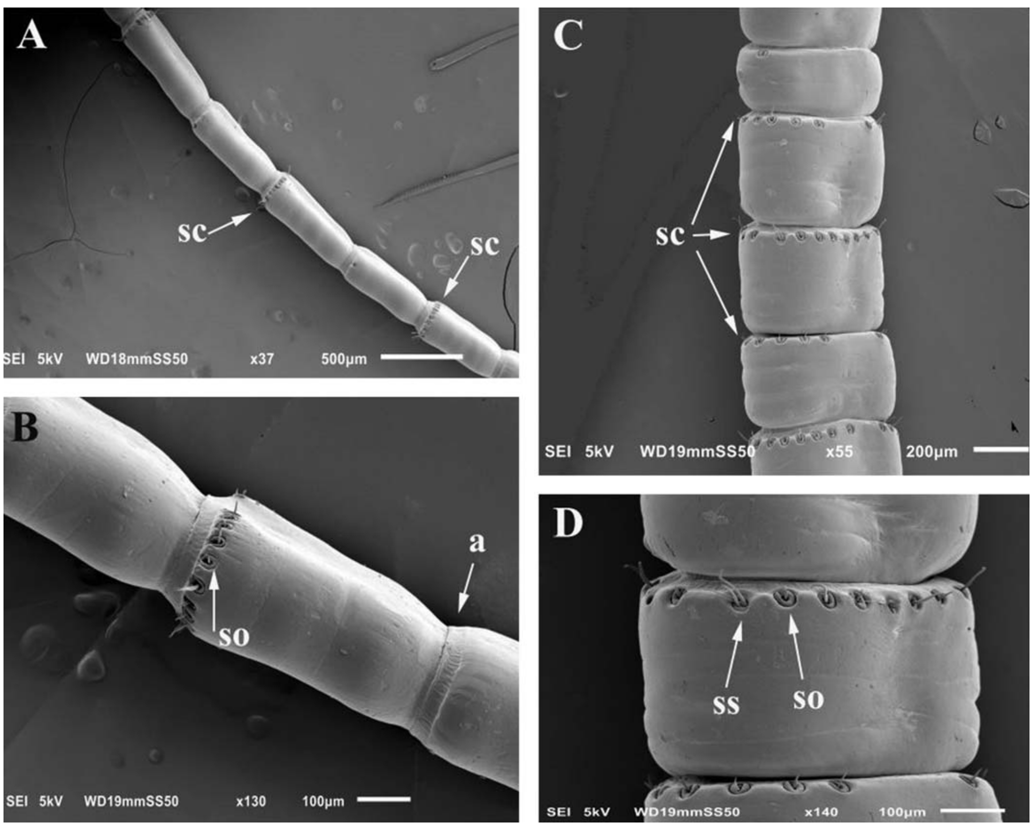

Fig. 3. *Macrobrachium rosenbergii* antennae (A2) of females and morphotypes. **A**, Female setal crown (arrows) at every other article. **B**, Female socket (arrow) and article articulation (arrow). **C**, OC male setal crown at every article (arrows). **D**, OC male setal crown (close-up) with simple setae (arrow) emerging from socket (arrow). a = articulation; so = socket; sc = setal crown; ss = simple setae.

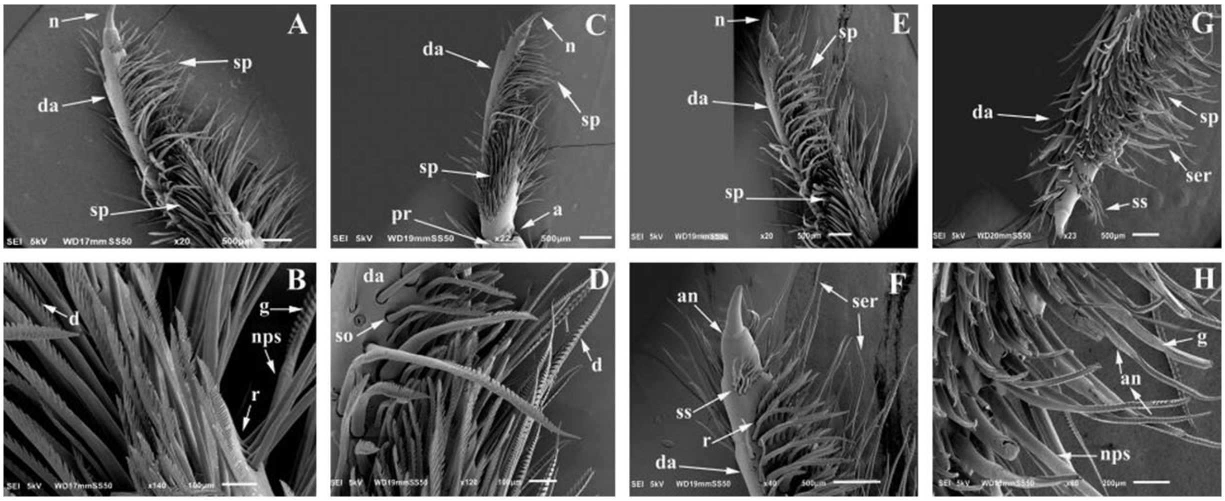

Fig. 4. *Macrobrachium rosenbergii* third maxilliped (M3) of females and morphotypes. **A**, Female setal patch (arrow) and nail (arrow) at distal tip of dactyl. **B**, Rows of serrate setae (arrow) of female setal patch, showing denticules (arrow, left), groove (arrow, right) and naked proximal shaft (arrow, right). **C**, SM male, showing nail (arrow) at distal tip of dactyl, setal patch (arrow) and the articulation (arrow, more proximal). **D**, SM male, showing close-up of serrate setae, denticules (arrow) and deep socket (arrow). **E**, OC male with nail (arrow) at distal tip of dactyl and setal patch (arrow) of serrate setae. **F**, OC male with annulus (arrow) toward distal tip of dactyl near the nail and setal patch of serrate setae (arrow). There is a small patch of simple setae (arrow) and rows of serrate setae (arrow). **G**, BC male with setal patch (arrow) of serrate setae (arrow). Small patch of simple setae (arrow) located near distal end of dactyl. **H**, BC male serrate setae, showing the groove (arrow, top) and naked proximal shaft (arrow, bottom) on dactyl. Denticules of serrate setae begin distal to annulus (arrow, middle). a = articulation; an = annulus; d = denticule; da = dactyl; g = groove; n = nail; nps = naked proximal shaft; pr = propodus; r = row; ser = serrate setae; so = socket; sp = setal patch; ss = simple setae.

Third Maxillipeds. For females and all morphotypes, the M3 is distally telescoping and two types of setae are found on the dactyl: simple and serrate (Fig. 4A,C,E,F). The exoskeleton appears to have rings, or annuli, that decrease in size (telescoping) toward the distal nail (Fig. 4A,C,E,F). At the distal tip of the dactyl, there are simple setae with deep sockets (Fig. 4F,G) and a setal patch of serrate setae of varying lengths that typically occur in rows (Fig. 4F). Each serrate seta has a deep socket (Fig. 4D), an annulus at the setal shaft (Fig. 4H) and a naked proximal shaft with two rows of denticules that occur in rows at an angle of 45°–120° to each other, creating a groove, (Fig. 4B,D,H). The denticules are generally blunt and become shorter near the distal tip (Fig. 4B,D).

First Pereopod. Three types of setae are found on the P1 of females and all morphotypes: simple, serrate, and serrulate (Fig. 5 and Supporting Information, appendices 4–6).

Females. Simple setae are found on both the dactyl and propodus in long interlocking tufts (Fig. 5A). The distal ends of the dactyl and propodus have curved pincers with an articulation and tufts of serrulate setae (Fig. 5A). On the propodus, there is a setal patch of serrate setae (Fig. 5D) with denticules that are thinner and more pointed than the serrate setae found on the third maxilliped (Fig. 4D). The serrulate setae are hollow (Fig. 5B), found in tufts (Fig. 5A), have multilobed scales (Fig. 5A,C) that are flattened, vary in number (Fig. 5C), are larger at the proximal end of the setal shaft and tend to get smaller toward the distal tip (Fig. 5B). Cuticular pores are present along the entire length of the propodus (Fig. 5E). At the articulation of the carpus and propodus, are setal patches of serrate setae and randomly dispersed simple setae (Fig. 5E).

Small-clawed Males. Tufts of simple setae with a subterminal pore (not pictured at this magnification) are present on the distal tip of the dactyl and propodus along with articulated curved pincers (Supporting Information, appendix 4A). More proximal on the propodus, there are tufts of serrulate setae that have naked proximal shafts, lobed scales, and an annulus toward the proximal end of each setal shaft (Supporting Information, appendix 4B). Also on the propodus is a setal patch with rows of serrate setae of varying lengths (Supporting Information, appendix 4C) and randomly spaced simple setae (Supporting Information, appendix 4D). Cuticular pores are present along the entire length of the propodus (Supporting Information, appendix 4D). At the carpus–propodus articulation (Supporting Information, appendix 4E), there is a setal patch with rows of serrate setae (Supporting Information, appendix 4E).

Orange-clawed Males. The distal tips of the dactyl and propodus have tufts of simple setae (Supporting Information, appendix 5A). More proximally on the propodus are large tufts of long serrulate setae (Supporting Information, appendix

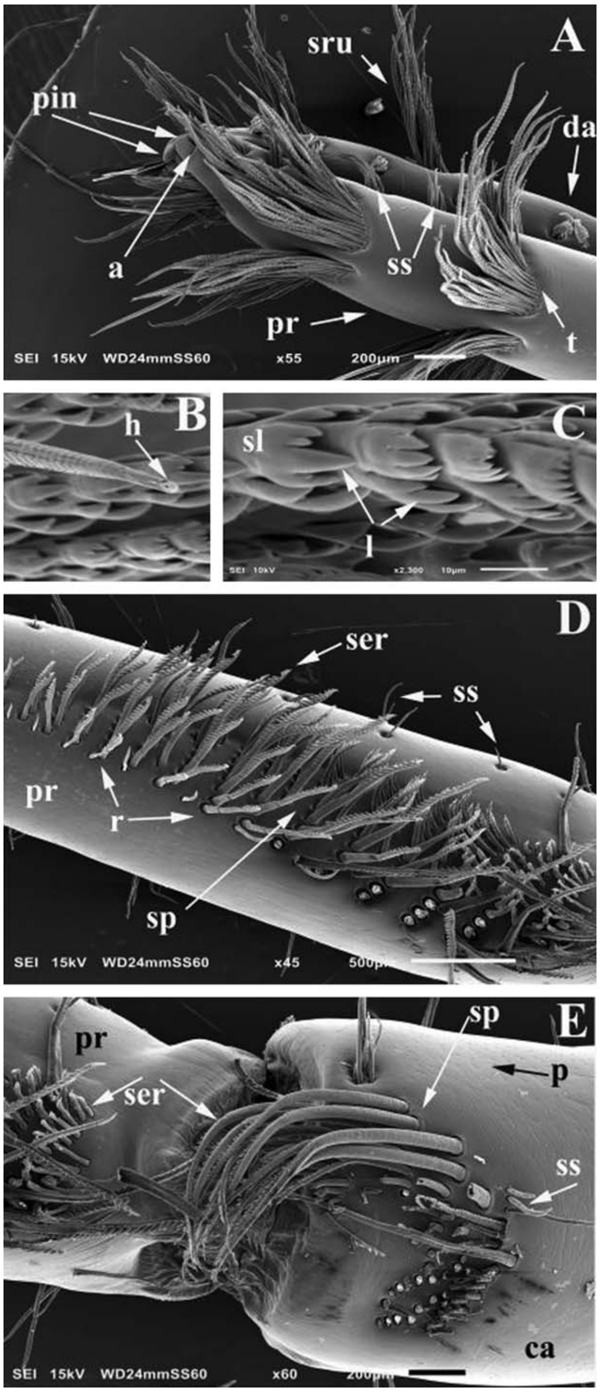

Fig. 5. *Macrobrachium rosenbergii* first pereopod (P1) of females. **A**, Distal tip of propodus with tufts (arrow) of long serrulate setae (arrow) and interlocking simple setae (arrow) between dactyl and propodus. Pincer (arrow) of propodus at distal tip. **B**, Hollow serrulate setae with scales (close-up of image C). **C**, Lobes on serrulate setae scales are variable in number and shape (×850 magnification, scale bar = 20 μm). **D**, Rows (arrow) of serrate setae (arrow) in setal patch of propodus with random spacing of simple setae (arrow). **E**, Propodus-carpus articulation with simple setae (arrow) and setal patch of serrate setae (arrow) of varying lengths. Pores (arrow) on exoskeleton. a = articulation; ca = carpus; da = dactyl; h = hollow; l = lobe; p = pores; pin = pincer; pr = propodus; r = row; ser = serrate setae; sl = scale; sp = setal patch; sru = serrulate setae; ss = simple setae; t = tuft.

5B) with scales that have lobes that vary in their number of projections (Supporting Information, appendix 5C). On the inner dactyl and propodus are small tufts of interlocking simple setae (Supporting Information, appendix 5B). There is a setal patch on the propodus distal to the carpus–propodus articulation that has rows of serrate setae and randomly arranged simple setae (Supporting Information, appendix 5D) with deep sockets, grooves, and annuli near the proximal portion (Fig. 10C).

Blue-clawed Males. At the distal end of both the dactyl and propodus are tufts of simple and serrulate setae, an articulation and a pincer (Supporting Information, appendix 6A). The tufts have multiple simple setae emerging from a single socket and have terminal pores, visible at the distal tip (Supporting Information, appendix 6B). More proximal on the dactyl, are interlocking rows of simple setae (Supporting Information, appendix 6A) and dense tufts of long serrulate setae (Supporting Information, appendix 6C,D). Visible pores are present along the entire length of the propodus (Supporting Information, appendix 6D). There are two setal patches with rows of long serrate setae with denticules (Supporting Information, appendix 6E,F) occurring on the propodus (Supporting Information, appendix 6F) just proximal to the carpus–propodus articulation (Supporting Information, appendix 6E). The serrate setae emerge from a deep socket (Supporting Information, appendix 6G). One of the serrate setae at the carpus–propodus articulation is broken, revealing a hollow shaft (Supporting Information, appendix 6E). At the carpus–propodus articulation, are tufts of simple setae (Supporting Information, appendix 6E,F) and a setal patch consisting of rows of serrate setae of varying lengths (Supporting Information, appendix 6E–H). A close-up examination of the serrate setae shows two different denticule morphologies. Some denticules are short and blunt and do not extend to the tip whereas others have longer denticules extending to the distal tip (Supporting Information, appendix 6G,H).

Second Pereopods. Three types of setae are common among females and male morphotypes: simple, spiniform, and pappose. The SM and OC males also have novel setae types: crinoid and spinulate (Figs. 6–9).

Females. Three types of setae are found on the second pereopods of females: simple, spiniform, and pappose. These setae are found on the distal portion of the appendage. On the dactyl and propodus there is a curved nail, random spiniform setae (Fig. 6A), circular tufts of simple setae with terminal pores, (Fig. 6B,D,E) and setal patches of long thick simple setae (Fig. 6 C). Between the dactyl and propodus, are interlocking simple setae (Fig. 6A). Dense tufts of long pappose setae that taper toward the distal tip are present on the

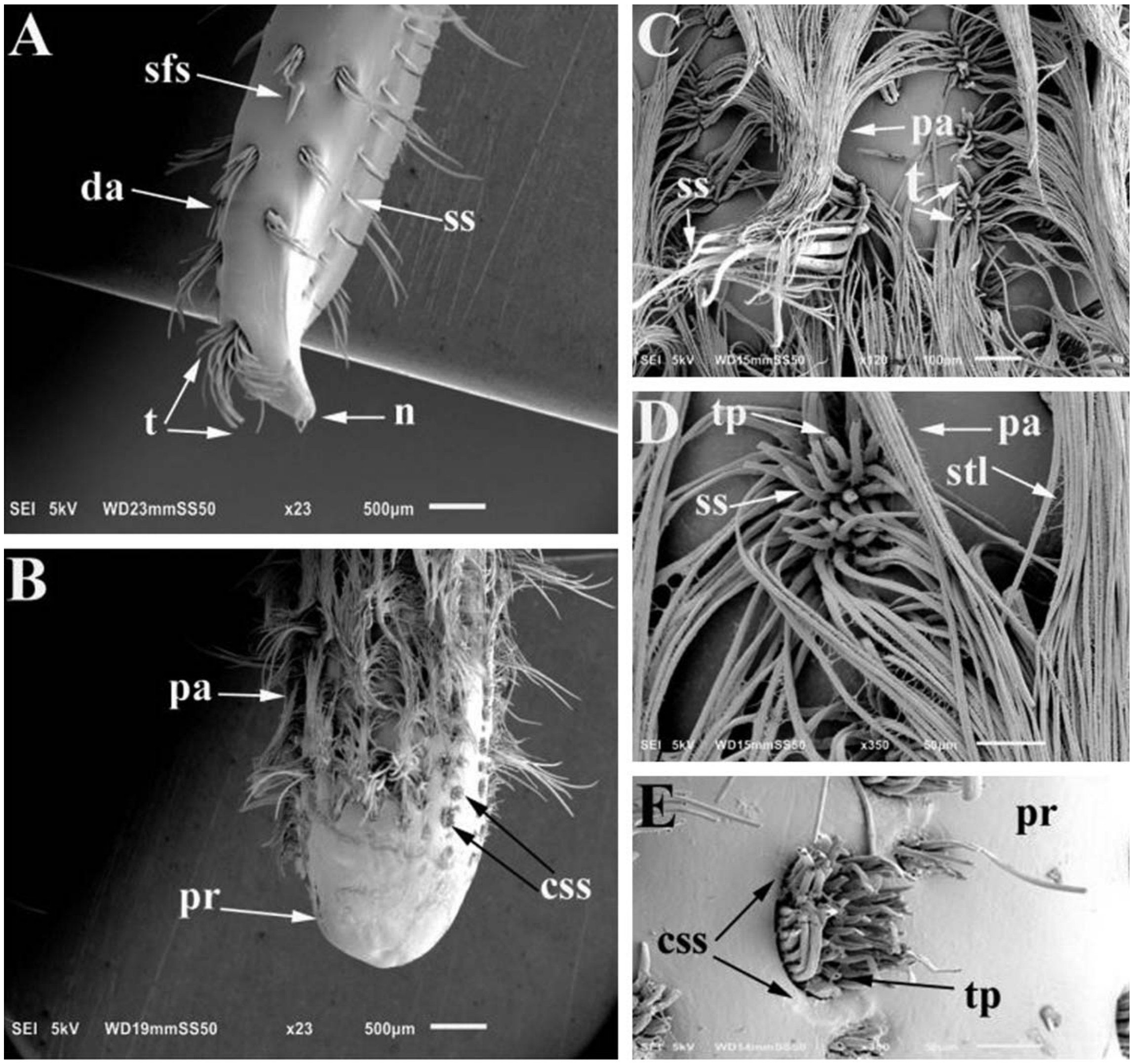

Fig. 6. *Macrobrachium rosenbergii* second pereopod (P2) of females. **A**, Propodus and dactyl with spiniform setae (arrow) and tufts (arrow) of simple setae (arrow). Interlocking simple setae (arrow) between dactyl and propodus. A nail is present at distal tip (arrow). **B**, Distal tip of propodus with pappose setae (arrow) and tufts of circular simple setae (arrow). **C**, Close-up of dense pappose setae (arrow) on propodus. Long thick, simple setae (arrow) and closely spaced tufts (arrow) are present on the propodus. **D**, Close-up of setae on propodus shows short simple setae (arrow) with terminal pore (arrow). Pappose setae (arrow) with setules (arrow) branching off the setal shaft. **E**, Close-up of circular simple setae in tufts (arrow) with terminal pore (arrow). css = circular simple setae tuft; da = dactyl; n = nail; pa = pappose setae; pr = propodus; sfs = spiniform setae; ss = simple setae; stl = setule; t = tuft; tp = terminal pore.

dactyl and propodus with thread-like setules circumscribing the setal shaft (Fig. 6B,C,D).

Small-clawed Males. Four types of setae are found on the P2 of the SM males: simple, spiniform, pappose, and spinulate setae. Unlike females, SM males have a novel setal type, spinulate setae. This second type of unique setae was found only on the P2 of the SM (Fig. 7A,B) and OC males (Fig. 8D–F,H) of *M. rosenbergii*. These setae were named for the very short, spine-like extensions (1–3 μm), termed denticules, that branch off the setal shaft (see inset Fig. 8H). They do not appear to be articulated, but seem to be extensions of the shaft. The main shaft is similar in shape to that of simple setae, except for the presence of denticules. In fact, these spinulate setae appear almost identical to simple setae, but at high magnifications, there is a clear distinction between these two types.

The distal tips of the dactyl and propodus have curved nails (Fig. 7A), randomly dispersed spiniform, simple setae (Fig. 7C) and tufts of spinulate setae (Fig. 7A,B) that appear very similar to simple setae, but have spine-like denticules circumscribing the setal shaft (Fig. 7A inset). On the propodus, are tufts of long pappose setae with long thread-like setules (Fig. 7C,D). Among the pappose setae are random long, simple setae (Fig. 7D).

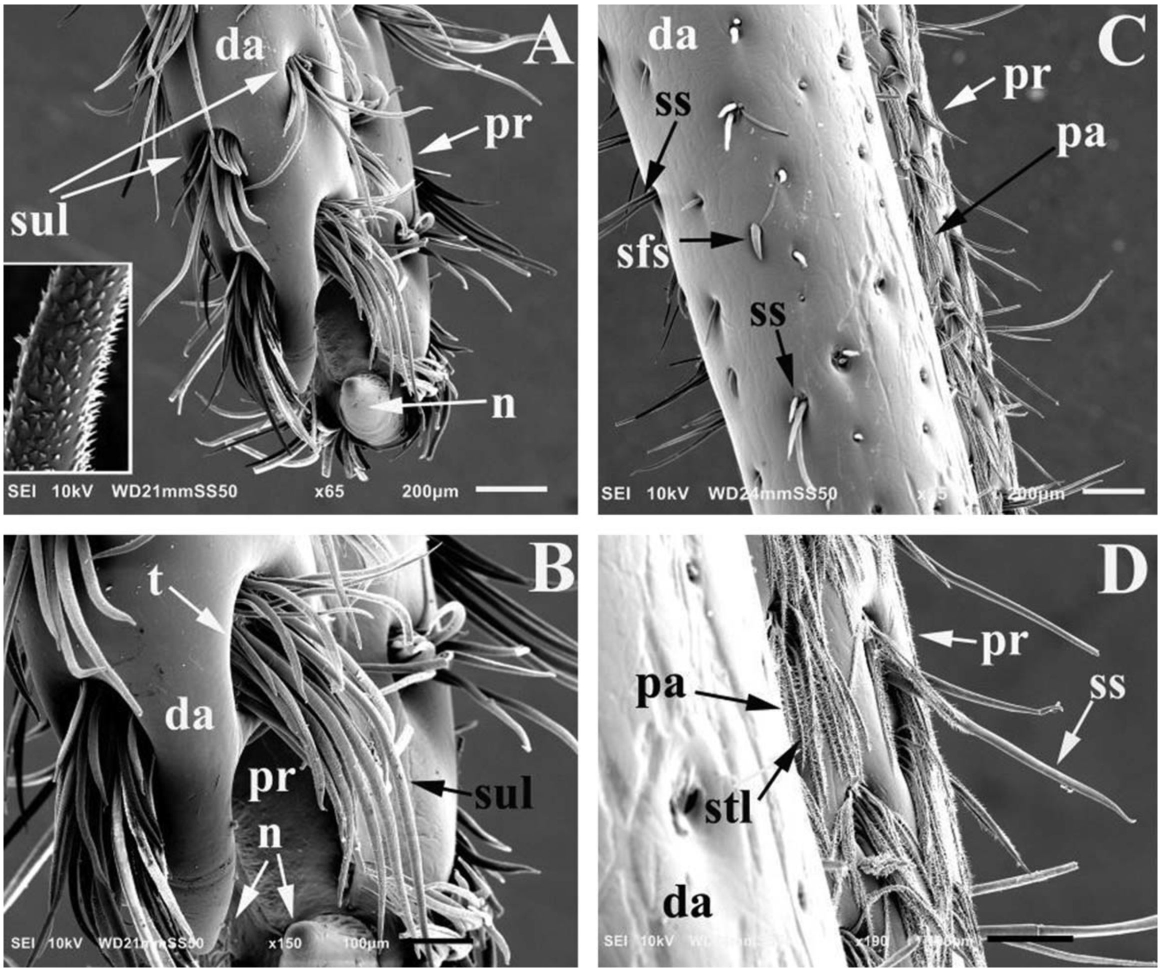

Fig. 7. *Macrobrachium rosenbergii* second pereopod (P2) of SM males. **A**, Distal tip of propodus with tufts of spinulate setae (arrow) that resemble simple setae. Spinulate setae has spine-like denticules (inset—×1, ×400 magnification). A nail (arrow) is at distal tip of propodus. **B**, Close-up of distal tip of propodus with tufts (arrow) of spinulate setae (arrow). A closer view of nail (arrow) at the distal tip is visible. **C**, More proximal view of propodus showing random spiniform setae (arrow), simple setae (arrow) and dense pappose setae (arrow). **D**, Close-up of the proximal view of propodus. Random long simple setae (arrow) are visible along with dense pappose setae (arrow) and setules (arrow). da = dactyl; n = nail; pa = pappose setae; pr = propodus; sfs = spiniform setae; ss = simple setae; stl = setule; sul = spinulate setae; t = tuft.

Orange-clawed Males. Five types of setae are found on the P2 of OC males: simple, spiniform, pappose, spinulate, and crinoid. The OC males, similar to the SM males, have newly identified spinulate setae, but also have a second novel setae type, crinoid setae. This unique type of setae was found, typically in tufts, only on the P2 of OC males of *M. rosenbergii* (Fig. 8E,F,G). The name "crinoid" was given to these setae due to their resemblance to a group of echinoderms known as crinoids. The setal shaft is naked only at its base. Short denticules (8–12 μm) (see inset Fig. 8G) arise from the setal shaft in a circumscribed pattern and continue to the distal tip. They may appear unbranched and spine-like, but are in fact not articulated with the setal shaft.

Large robust teeth are present on the inner dactyl and propodus (Fig. 8A) along with tufts of spinulate setae (Fig. 8B,C), randomly spaced spiniform setae (Fig. 8B) and a nail at the distal tip (Fig. 8C). The propodus has tufts of long pappose setae (Fig. 8A) that form a dense patch toward the distal tip (Fig. 8A). The pappose setae have long thread-like setules that often clump and tangle together, forming a mat (Fig. 8A). Toward the proximal propodus are tufts of intermixed spinulate and crinoid setae (Fig. 8E,F), but there is a clear difference in the lengths of the denticules of these setae (Fig. 8G,H inset). The denticules of crinoid setae (8–12 μm) are four times longer than those of spinulate setae (1–3 μm) (see inset, Fig. 8G,H), whereas the denticules of the spinulate setae are more pointed, resembling spines (see inset, Fig. 8H).

Blue-clawed Males. Three types of setae are found on the P2 of BC males, similar to females:

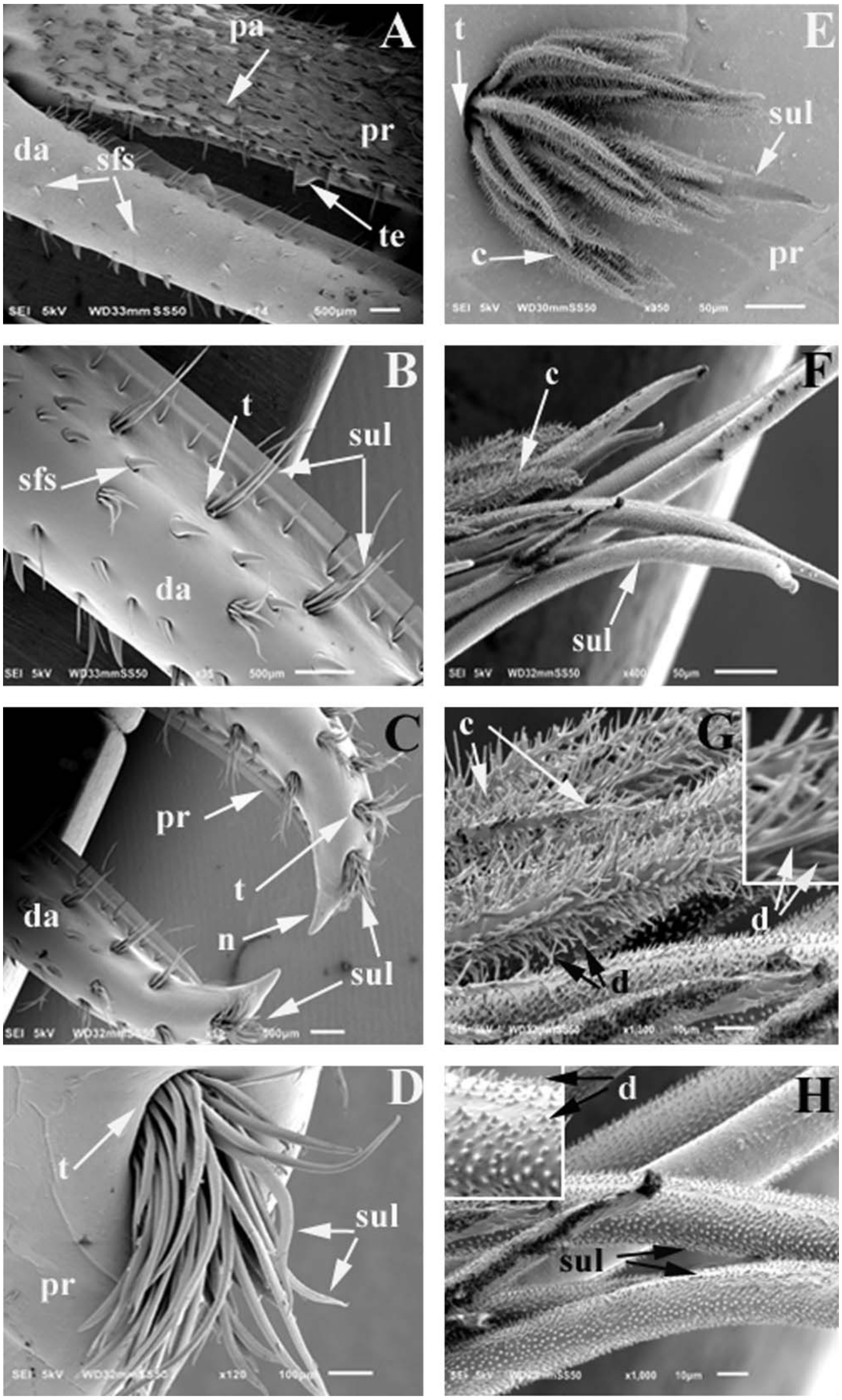

Fig. 8. *Macrobrachium rosenbergii* second pereopod (P2) of OC males. **A**, Dense pappose setae (arrow) on the propodus, spiniform setae (arrow) and robust teeth (arrow) on inner portions of dactyl and propodus. **B**, Close-up of dactyl showing tufts (arrow) of spinulate setae (arrow) and randomly dispersed spiniform setae (arrow). **C**, Nail at distal tip of propodus with tufts (arrow) of spinulate setae (arrow). **D**, Tuft (arrow) of spinulate setae (arrow) on propodus. **E**, Tuft of intermixed crinoid (arrow) and spinulate setae (arrow) on propodus. **F**, Intermixed crinoid (arrow) and spinulate setae (arrow) on propodus. **G**, Close-up of the denticules (arrow) on crinoid setae (arrow) on propodus. Inset shows close up of nonarticulated denticules (arrow) of the crinoid setae. **H**, Close-up of spinulate setae (arrow) on propodus showing nonarticulated denticules (arrow) on setal shaft of spinulate setae (inset). c = crinoid setae; d = denticule; da = dactyl; n = nail; pa = pappose setae; pr = propodus; sfs = spiniform setae; sul = spinulate setae; t = tuft; te = teeth.

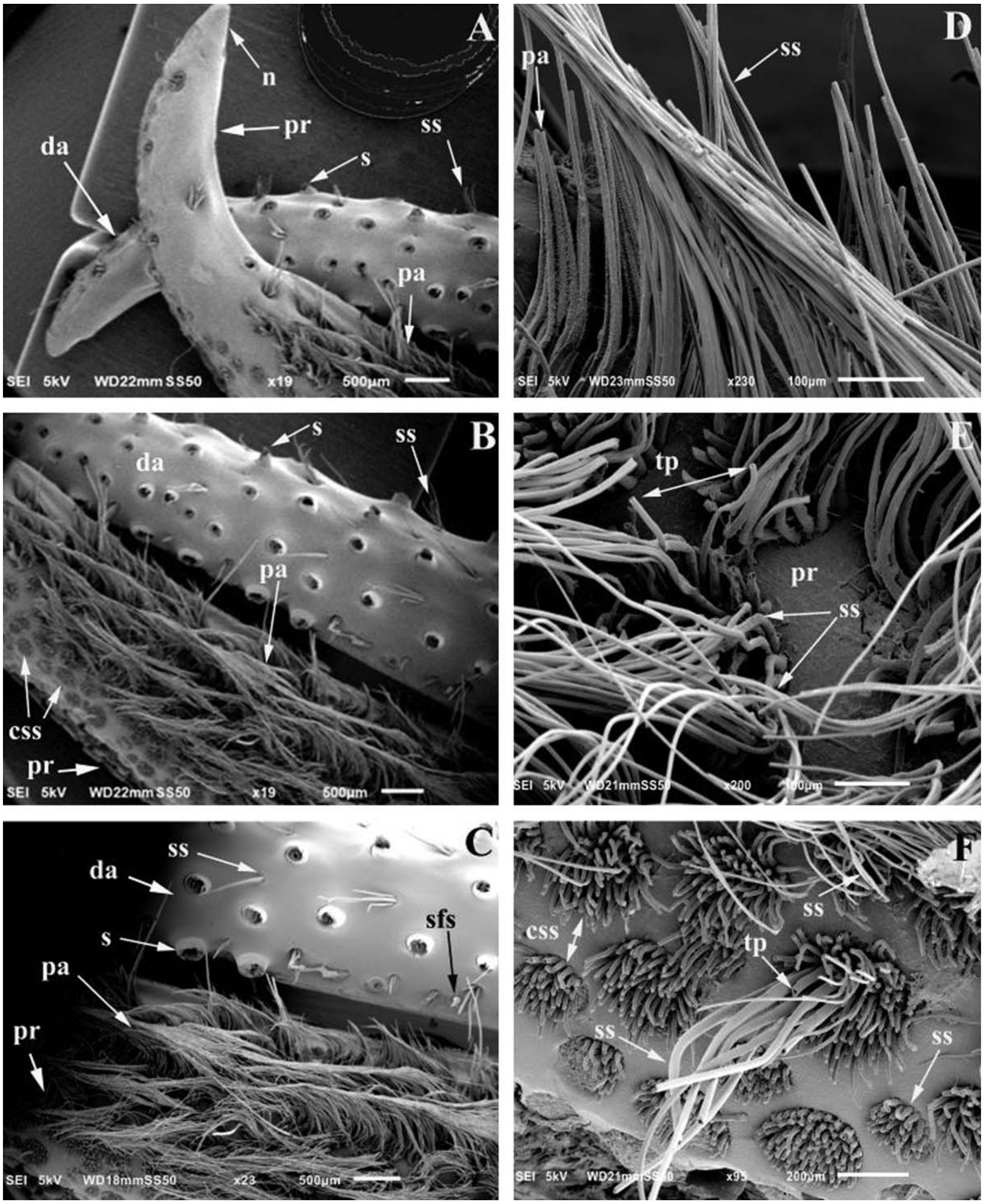

Fig. 9. *Macrobrachium rosenbergii* second pereopod (P2) of BC males. **A**, Distal propodus showing the nail (arrow) at the distal tip. Random simple setae (arrow) and spines (arrow) are dispersed along propodus along with pappose setae (arrow). **B**, Propodus (more proximal) showing dense pappose setae (arrow) and tufts of short circular simple setae (arrow). Spines (arrow) and random simple setae (arrow) on propodus. **C**, Close-up of propodus (more proximal) with dense pappose setae (arrow). Dactyl with random spiniform (arrow), simple setae (arrow) and large robust spines (arrow) are visible (some are broken off). **D**, Close-up of dense setae on propodus with both long pappose (arrow) and simple setae (arrow). **E**, Close-up of long simple setae (arrow) with terminal pore (arrow). **F**, Short circular simple setal tufts (arrow) on propodus with terminal pore (arrow). Long simple setae (arrow) are randomly spaced among the circular simple setal tufts. css = circular simple setae tuft; da = dactyl; n = nail; pa = pappose setae; pr = propodus; s = spine; sfs = spiniform setae; ss = simple setae; tp = terminal pore.

simple, spiniform, and pappose. On the dactyl, are robust spines, most of which appear broken off (Fig. 9A–C) along with randomly dispersed simple and spiniform setae (Fig. 9A–C). On the dactyl and propodus there is a nail at the distal tip (Fig. 9A); a very dense setal patch of long pappose setae with thread-like setules and a small setal patch of simple setae consisting of both short and long setae with terminal pores is present on the propodus (Fig. 9A–F).

Fifth Pereopod. Three types of setae are found on the P5 of females and all morphotypes: simple, serrate, and spiniform (Figs. 10, 11, and Supporting Information, appendices 7 and 8).

Females. On the dactyl, a setal patch of serrate setae with small, fine denticules is present (Fig. 10A–C). At the dactyl-propodus articulation, is a setal patch with serrate setae of varying lengths (Fig. 10A,E). On both the dactyl and propodus, there are randomly arranged simple setae that typically occur in small aggregations of three to six setae emerging from the same area (Fig. 10A,D). The serrate setae emerge from deep sockets and the denticules begin distal to the annulus (Fig. 10C). Spiniform setae occur along the propodus (Fig. 10A).

Small-clawed Males. On the dactyl and propodus, there are randomly arranged simple setae (Fig. 11B,G). A setal patch of serrate setae (Fig. 11A,B) with very small denticules is present on the dactyl (Fig. 11C–E). Similar to females, the denticules are very thin (Fig. 11D,E) and different from the denticules found on M3 and P1, which appear to be more robust (Fig. 11; Supporting Information, appendices 4 and 6). The groove of the serrate setae is wider (Fig. 11C) and not as deep as seen on M3 (Fig. 4C). On the propodus, individual spiniform setae are located in close proximity to simple setae where both types occur in a row (Fig. 11F–H). At the dactyl-propodus articulation, there is a setal patch of varying lengths of serrate setae, similar to the female setal patch at the dactyl-propodus articulation (Fig. 11G).

Orange-clawed Males. On the dactyl are randomly arranged simple setae (Supporting Information, appendix 7A) and a setal patch of serrate setae with fine and short denticules (Supporting Information, appendix 7A,B), similar to that of females and SM males. Proximal to the dactyl-propodus articulation are spiniform setae that are

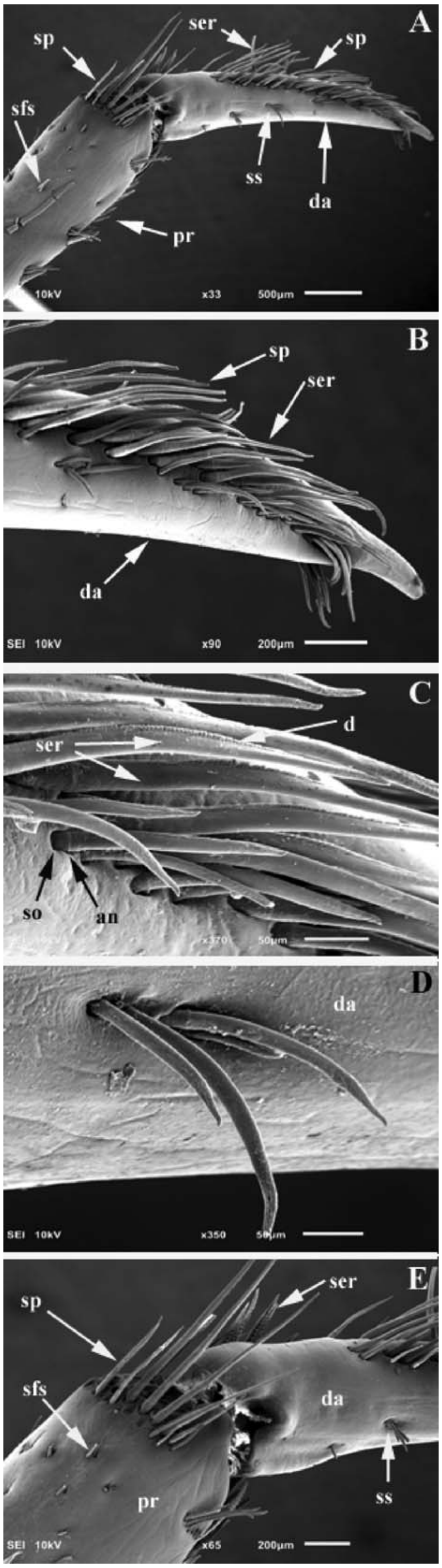

Fig. 10. *Macrobrachium rosenbergii* fifth pereopod (P5) of females. **A**, Setal patch of serrate setae at distal end of dactyl and at articulation between dactyl and propodus. Random simple setae and spiniform setae are located on dactyl and propodus. **B**, Close-up of setal patch of serrate setae on dactyl. **C**, Close-up of serrate setae in setal patch of the dactyl. **D**, Simple setae randomly arranged on dactyl. **E**, Dactyl-propodus articulation with serrate setae setal patch, spiniform setae on the propodus and random simple setae on dactyl. an = annulus; d = denticule; da = dactyl; pr = propodus; ser = serrate setae; sfs = spiniform setae; so = socket; sp = setal patch; ss = simple setae.

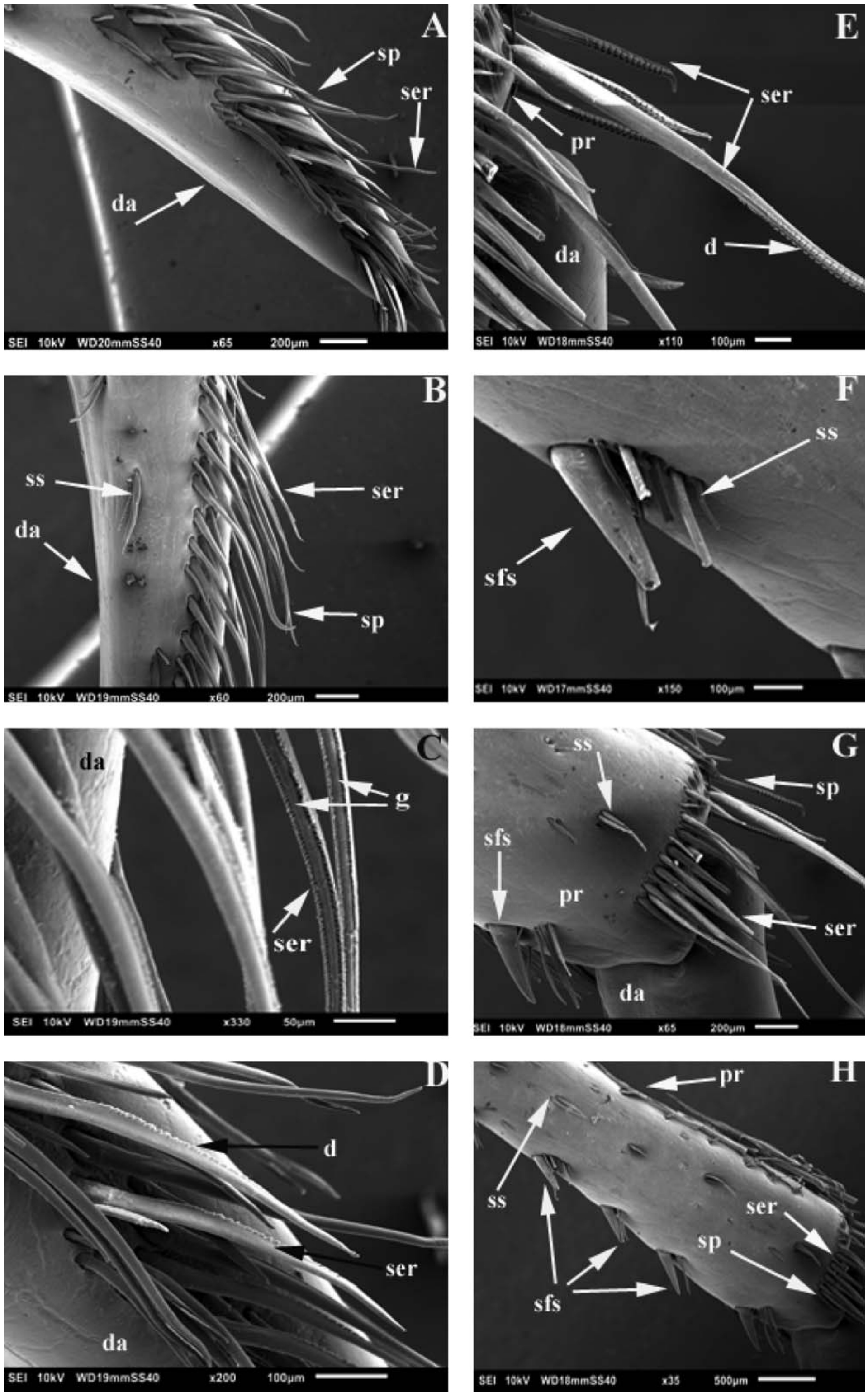

Fig. 11. *Macrobrachium rosenbergii* fifth pereopods (P5) of SM males. **A**, Distal tip of dactyl with setal patch of serrate setae. **B**, Serrate setae of setal patch on dactyl with random simple setae. **C**, Groove on the serrate setae of the dactyl. **D**, Close-up of serrate setae in setal patch showing the small and thin denticules. **E**, Serrate setae at dactyl-propodus articulation setal patch. **F**, Spiniform setae intermixed with simple setae. **G**, Setal patch at the dactyl-propodus articulation with varying lengths of serrate setae. There are random simple setae and large, robust spiniform setae intermixed with simple setae. **H**, Proximal portion of propodus showing setal patch at dactyl-propodus articulation with large spiniform setae intermixed with randomly arranged simple setae. d = denticule; da = dactyl; g = groove; pr = propodus; ser = serrate setae; sfs = spiniform setae; sp = setal patch; ss = simple setae.

not intermixed with simple setae (Supporting Information, appendix 7C) as seen in SM males (Fig. 11C). At the dactyl-propodus articulation, there is a setal patch with varying lengths of serrate setae (Supporting Information, appendix 7C,D) that are more dense than the corresponding setal patches of females and SM males (Figs. 10 and 11). The propodus has randomly spaced simple setae and spiniform setae (Supporting Information, appendix 7E).

Blue-clawed Males. The dactyl has a setal patch of hollow serrate setae with fine, short denticules (Supporting Information, appendices 8A–C), similar to the denticules on the fifth pereopods of the other male morphotypes and females. On the dactyl and propodus are random simple setae (Supporting Information, appendix 8A,D). Spiniform setae and randomly arranged simple setae are present on the propodus (Supporting Information, appendix 8D). At the articulation of the dactyl and propodus, there is a dense setal patch of long serrate setae with two types of denticules (Supporting Information, appendices 8D–F). One type is more pointed and robust (Supporting Information, appendix 8C) whereas the second type is very fine, appearing to not have denticules like simple setae (Supporting Information, appendix 8F). The serrate setae with the fine denticules (Supporting Information, appendix 8F) have shallow grooves that are not as pronounced as the grooves found on other appendages [Fig. 4C (3M); Supporting Information, appendix 6 (P1)].

DISCUSSION

Setal Types of *M. rosenbergii* Morphotypes

Examination of the grooming appendages and antennae of *M. rosenbergii* revealed seven different types of setae, including two types not previously described in the crustacean literature (crinoid and spinulate setae). These setae types include simple, serrate, serrulate, spiniform, pappose, crinoid, and spinulate (Table 1).

The antennae are important sensory structures responsible for chemosensory reception (Bauer, 1977, 1978, 1981, 1989, 2002, 2004) and are frequently groomed structures in decapod crustaceans in general (Bauer, 1977, 1978, 1989, 2004) and in *Macrobrachium* (*Macrobrachium grandimanus*: VanMaurik and Wortham, 2014) in particular. Only simple setae were found on the antennae of *M. rosenbergii* (females and the male morphotypes). Simple setae do not have microstructures such as denticules, setules or scales, suggesting that the function of the antennular setae is related to chemosensory, not grooming activities. These setae are important structures to keep free of fouling, allowing them to function in chemosensory reception more efficiently. There appears to be conservation of behavior (high levels of grooming) and setal morphology (only simple setae) among the females and morphotypes in *M. rosenbergii*, with respect to the antennae.

TABLE 2. Setal type associated with each group or morphotype

Setal type/ morphotype	Females	SM males	OC males	BC males
Simple setae	×	×	×	×
Serrate setae	×	×	×	×
Serrulate setae	×	×	×	×
Spiniform setae	×	×	×	×
Pappose setae	×	×	×	×
Crinoid setae			×	
Spinulate setae		×	×	

Consistent patterns of setal types were found on the grooming appendages of the females and morphotypes, indicating a conservation of setal morphology within *M. rosenbergii*, even though the various morphotypes have different body structures and behaviors. The third maxillipeds exhibited two types of setae on all individuals: simple and serrate setae, whereas the first pereopods had three types: simple, serrate, and serrulate setae. The fifth pereopods exhibited the same three types of setae across all groups and morphotypes: simple, serrate, and spiniform setae (Table 2).

The second pereopods of all individuals (females and male morphotypes) exhibited three types of setae: simple, spiniform, and pappose setae indicating similarities among individuals regardless of sex or morphotype. In addition, crinoid and spinulate were identified on the SM (spinulate) and OC males (spinulate and crinoid). The newly described crinoid and spinulate setae have unique microstructures that resemble spines. These "spines" are denticules (no articulation with the setal shaft) and the denticules of crinoid setae are slightly longer than those of the spinulate setae. Small-clawed males have a very high activity level and therefore are likely to experience greater fouling pressures than other morphotypes and thus may need to groom more frequently than other males (Ra'Anan and Sagi, 1985; Bauer, 1989). The denticules on the spinulate setae may function like miniature combs and be robust enough to remove harder structures such as calcified organisms or deposits from the body surfaces. Orange-clawed males are typically immobile and will not likely experience the same fouling pressures as SM males, even though they possess both novel setae types (Ra'Anan and Sagi, 1985). It can be concluded that these unique setae types are found only on the SM and OC males and are lost during molting to BC males.

Proposed Setal Functions

Structures of the different setal types and their associated microstructures may elucidate functions

TABLE 3. Proposed functions of setal types

	Feeding	Grooming	Displays/ Protection	Sensory
Simple setae	×			×
Serrate setae	×	×		
Serrulate setae		×		
Spiniform setae			×	×
Pappose setae	×	×		
Crinoid setae		×		
Spinulate setae		×		

related to grooming efficiency (Table 3). Cuticular extensions can remove fouling debris, similar to combs on a human hair brush (Supporting Information, appendix 9). Unlike serrate and serrulate setae that normally occur in a setal patches or tufts, simple setae are most often randomly arranged on the grooming appendages and do not have extensions from the setal shaft, indicating a function related to chemosensory reception rather than grooming.

The serrate setae on *M. rosenbergii* often occur in rows on the third maxillipeds and first pereopods (Fig. 4B and Supporting Information, appendix 4), resembling the arrangement of combs found on a human hair brush (Supporting Information, appendix 9A–C). Rows of setae may thoroughly penetrate and detangle the surfaces groomed by the appendages (VanMaurik and Wortham, 2014). This is supported by Bauer (1989) who reported that these rows of serrate setae function like brushes and remove material from the body of decapods. The denticules and grooves on the serrate setal shaft trap particles as it scrapes along a body surface. In *M. rosenbergii* the denticules vary in morphology; some are longer and more robust (such as on the first pereopods), whereas others are very fine and small (such as on the fifth pereopods). The differences in denticule shapes and sizes may reveal differences in their functionality. A more robust, sturdy denticule may remove bulky or hard debris whereas a very fine and thin denticule may remove more delicate material from the body surfaces.

Serrulate setae are similar to serrate setae and possess lobed denticules (or a type of denticule, i.e., scales) along the setal shaft. These setae are only found on the first pereopods (VanMaurik and Wortham, 2014). These denticular lobes may function similar to the denticules of serrate setae and trap fouling material as the setae are scraped or brushed along the body surfaces. Spiniform setae resemble spines but emerge from a pore on the exoskeleton. These setae are robust and may function in chemosensory reception (via the pore) or protection (Felgenhauer and Schram, 1979; Bauer, 1981, 1989).

Pappose setae are found only on the second pereopods of *M. rosenbergii* and are often seen in dense aggregations. The setules extending from the setal shaft are very long and slender, resembling fine hair. These setae are similar to the bristles on some hair brushes that function in the removal of material from the hair shaft (Supporting Information, appendix 9D). As with the other hair brush type, the bristles occur in rows, but the function is different. These bristles have extensions from the distal shaft that will remove debris, but not as much as the denticules of serrate setae (Fig. 4D). The bristle extensions resemble the setules on the pappose setal shaft. These setules, due to their dense aggregation may function in grooming to trap and remove fouling material.

Crinoid and spinulate setae were found only on the SM and OC males. These setae have unique denticules resembling spines that may function similarly to those in serrate and serrulate setae; the denticules may scrape the body surfaces during grooming behaviors and remove fouling debris. This morphology of crinoid setae is similar to a hair brush bristles of pappose setae. The crinoid setae, for example, have extensions radiating from the setal shaft that may function in removal and trapping of debris (Supporting Information, appendix 9F). It does not appear the denticules of spinulate setae can trap the fouling material, only scrape and remove it from the body.

CONCLUSIONS

The different setal patterns and types found on the antennae and grooming appendages support the different morphologies and behaviors of females and the male morphotypes of *M. rosenbergii*. The social hierarchy of the male morphotypes dictates their behaviors (Ra'Anan and Sagi, 1985). Small clawed males are very active and likely experience higher fouling pressures than OC and BC males. They may need to groom more to remove the fouling material and need a suite of setal types to accommodate this need. Conversely, BC males spend a majority of their time resting, grooming and protecting their mates (Ra'Anan and Sagi, 1985). They do not have specialized setae like the SM and OC males, and as a result, need to be efficient when they are able to groom due to the lack of specialized structures.

It appears as if general setal patterns and types are mostly conserved within the species, *M. rosenbergii*, as most setal types are common among the appendages of females and male morphotypes. The same number of setal types are found on the same appendages of some morphotypes and setal arrangements often occur in the same pattern such as rows, patches or tufts. It is likely that similar setae are found on all individuals for grooming behaviors such as antennular preening, gill cleaning and general body grooming, exhibited among other caridean shrimp (Bauer, 1977, 1978, 1979).

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