Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapods

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The crustacean cuticle has numerous projections and some of these projections, the setae, have important mechanical as well as sensory functions. The setae display a wide diversity in their external morphology, which has led to great problems separating setae from other projections in the cuticle and problems in making a consistent classification system. Here, the cuticular projections on the mouthparts of seven species of decapods are examined by scanning and transmission electron microscopy. A new definition is given: a seta is an elongate projection with a more or less circular base and a continuous lumen; the lumen has a semicircular arrangement of sheath cells basally. From the details of the external morphology the mouthpart setae are divided into seven types: pappose, plumose, serrulate, serrate, papposerrate, simple and cuspidate setae, which are suggested to reflect mechanical functions and not evolutionary history. This classification system is compared with earlier systems.   © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **142**, 233–252.

ADDITIONAL KEYWORDS: functional morphology – mechanical function – setal types.

INTRODUCTION

One defining adaptive character in arthropods is that they are clad in an exoskeleton, the cuticle, which offers both protection and mechanical support. One consequence of this body design is that all interactions between the living tissues and the external environment at all levels must take place through specialized cuticular structures. These structures are of all shapes and sizes, ranging from large teeth on chelipeds to minuscule ornaments. One large group of such structures consists of elongate, hair-like projections that normally have a distinct articulation at the base, making them flexible. There is a general consensus that these structures are homologous both within Crustacea and probably also with similar structures in other arthropods. There are many terms for these structures, including setae, sensilla, bristles or even 'hairs'. For crustaceans, which are the prime subject of this

paper, the most often used term is setae and it will therefore be used here.

Within Crustacea, different definitions have been proposed for setae (Thomas, 1970; Fish, 1972; Watling, 1989). The most widely accepted is the one proposed by Watling (1989), who stresses that the definition should be based on homologies and suggests that a basal articulation with the general cuticle is such a homology. Watling's definition is attractive because it enables us to categorize easily a large number of cuticular structures as setae, but it nevertheless falls short of the impressive variation in size and shape displayed by cuticular projections. There are indications that not all articulated projections are setae (Holmquist, 1989; Martin, 1989; Garm & Høeg, 2000) while on the other hand, some structures seem to resemble setae but lack the basal articulation (Høeg, Karnick & Frølander, 1994; Garm & Høeg, 2000; Garm, 2004).

The structural variation displayed by setae undoubtedly contains a large amount of information on the function of crustacean appendages and on the phylogeny of the group. Information at both of these levels is likely to be expressed in the morphology of setae, and this has led to numerous classificatory sys-

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tems to extract that information. Unfortunately, most studies have based their classifications on a single species only, and such an *ad hoc* approach impedes their use in comparative studies. This led Watling (1989) to suggest that not only setae but also their classification into types should be based on the homology concept. As homologies useful for classifying setae, Watling lists the type of articulation with the general cuticle, the presence of an annulus and the presence of articulated outgrowths on the setal shaft (setules).

Watling's approach is definitely a step in the right direction, but strict use of his system has been very limited. One reason could be that too few homologies can be pinpointed to adequately distinguish the morphological groupings amongst crustacean setae. On the other hand, it maybe counterproductive to use each and every morphological characteristic as a basis for new types of setae, since this will probably only lead to a profusion of setal types and to subtypes with little practical value.

In this paper I use both scanning electron microscopy (SEM) and transmission electron microscopy (TEM) to readdress the definition of a seta and its substructures and thereby, try to create a classificatory system that will encompass both a wide systematic range and still extract as much functional information as possible. TEM is used to answer some very specific problems concerned with classifying cuticular projections, such as whether all articulated projections represent a homologous type. I examine the setal armament of the mouthparts in seven species of decapods from a wide range of taxa, and covering a wide range of body size and ecology. Mouthparts are chosen because they not only have a very high density of setae but also, a high diversity.

MATERIAL AND METHODS

The seven species chosen for this study are: *Penaeus monodon* Fabricius, 1798, *Palaemon adspersus* Rathke, 1837, *Stenopus hispidus* Olivier, 1811, *Cherax quadricarinatus* von Martens, 1868, *Panulirus argus* Latreille, 1804, *Pagurus bernhardus* (L.) and *Carcinus maenas* (L.). These seven species cover a wide phylogenetic range within the Decapoda, ensuring that the results are not based on a specialized group of animals. They also cover a large size range, from the small shrimps (*Pal. adspersus* and *S. hispidus*) to large spiny lobsters (*Pan. argus*), and ecologically they cover a range from truly omnivorous (*Pag. bernhardus*) to specialists (*S. hispidus*).

Penaeus monodon was obtained from the Australian Institute of Marine Science (AIMS), Townsville, Australia. They were young adults of both sexes with a carapace length between 4.0 and 5.5 cm. *Palaemon adspersus* was caught in Øresund, north of Copenhagen, Denmark. The specimens were all large adults. Medium-sized adult *S. hispidus* were obtained from the public aquarium, Denmarks Akvarium, in Copenhagen, as were adult *Ch. quadricarinatus*. *Panulirus argus* were shipped from the Bermuda Biological Station of Research. They were of both sexes and had carapace lengths between 8 and 13 cm. Adult *Pag. bernhardus* and *Ca. maenas* were caught in Øresund, north of Copenhagen.

LIGHT MICROSCOPY

A specimen of *Ch. quadricarinatus* was fixed in 70% ethanol and dissected through the midline. For the line drawing in Figure 1, a standard dissection microscope equipped with a camera lucida was used.
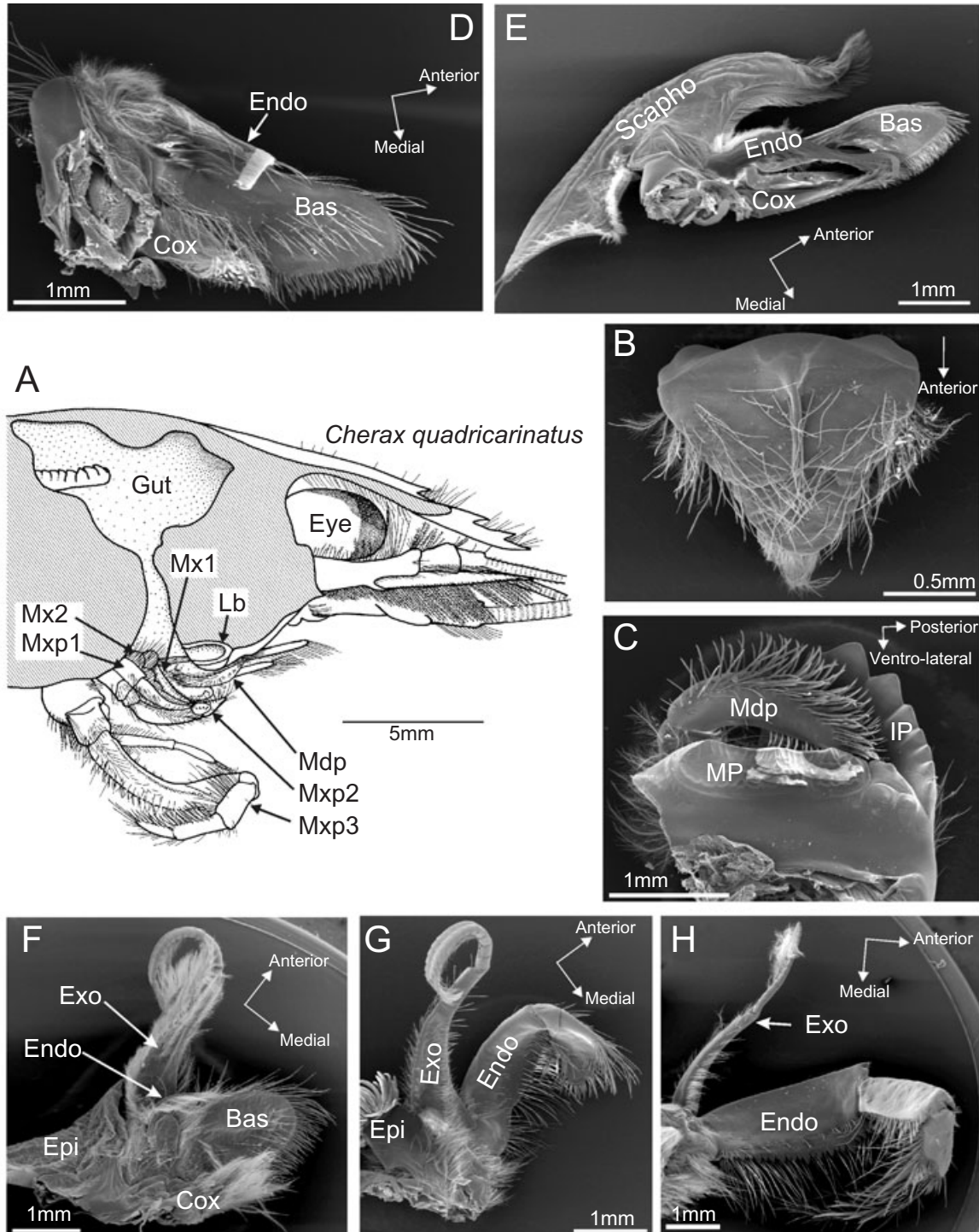
SCANNING ELECTRON MICROSCOPY

Both sides of the mouth apparatus from one or two specimens of each species were prepared for SEM. The specimens were anaesthetized in a freezer and dissected in sea or fresh water relative to the species. The individual mouthparts were cleaned with a beaver-hair brush and fixed in 2.0% formalin in either sea or fresh water. After at least 3 days of fixation, they were dehydrated in a series of ethanol concentrations,

Figure 1. Mouth apparatus of *Cherax quadricarinatus*. A, line drawing of the head region giving a medial view of the left side of the mouth apparatus. Striated area indicates sectioned tissue. Position of mouthparts resembles the live animal when not eating. B, labrum seen ventrally. *Ch. quadricarinatus* is the only species with setae on the labrum. C, left mandible seen dorso-laterally. All species have a heavy setation on the mandibular palp with the major part on the distalmost segment. D, left maxilla 1 seen dorsally. Most setae are found on the medial rim. E, left maxilla 2 seen dorsally. The scaphognathite has a setal rim but most of the other setae are found on the medial edge of the basis and coxa. (F) left maxilliped 1 seen dorsally. Most setae are found on the exopod and the medial rim of the basis and coxa. (G) left maxilliped 2 seen dorsally. Most setae are on the medial side of the endopod and on the exopod. (H) left maxilliped 3 seen dorsollay. The medial side of the endopod has heavy setation. *Abbreviations* Bas, basis; Cox, coxa; Endo, endopod; Epi, epipod; Exo, exopod; IP, incisor process; Lb, labrum; Mdp, mandibular palp; MP, molar process; Mx1, maxilla 1; Mx2, maxilla 2; Mxp1, maxilliped 1; Mxp2, maxilliped 2; Mxp3, maxilliped 3; Scapho, scaphognathite.

transferred to 100% acetone and critical point dried. After drying they were sputter coated with gold and the specimens were viewed in a JEOL 840 microscope or a JEOL JSM 6335F field emission microscope. The resulting digital images were taken using the programs SEMafore 3.0 or PC-SEM, and manipulated in CorelDraw 10.0.

TRANSMISSION ELECTRON MICROSCOPY

Mouthparts were removed from one specimen of *Pal. adspersus* (female, CL = 22 mm), one specimen of *Pe. monodon* (male, CL = 40 mm) and one specimen of *Pan. argus* (female, CL = 45 mm), and fixed in cold 2.5% glutaraldehyde and 2.0% paraformaldehyde in

0.2 M sodium cacodylate buffer (pH 7.3). In that fixative they were dissected into single segments or less to allow the fixative to enter. They were kept in the fixative for at least 3 days before being washed in buffer and postfixed in 1.0% osmium tetroxide in buffer for 2 h at room temperature. After postfixation, the tissue was dehydrated in a series of ethanol concentrations, transferred to 100% acetone and embedded in Epon resin (TAAB 812 resin). Ultrathin sections were made with a diamond knife on a LKB Nova ultramicrotome and placed on single-slot grids. Sections were contrasted with uranyl acetate for 20 min at 60°C and observed in a JEOL 1240 transmission electron microscope. Digital micrographs were taken with a Gatan multiscan 791 camera.

RESULTS

The typical arrangement of the complex decapod mouth apparatus is shown in Figure 1A. All of the mouthparts are heavily armed with highly diverse cuticular projections, especially on their medial edges and distal ends (Fig. 1B–H).

TYPES OF PROJECTIONS

Based on the external morphology and the ultrastructure, all the examined projections in the general cuticle (the relatively flat and even cuticle covering the entire body surface) of the mouthparts could be assigned to one of four types.

I. Large (50 μm–2 mm) and circular (at least in the basal region) projections with a clear articulation with the general cuticle in a socket area (Fig. 2A). They have a continuous lumen, which holds semicircular sheath cells basally and normally also sensory cilia (Fig. 3A, B). They always have an annulus (Fig. 4C) and often display secondary outgrowths, and a terminal or subterminal pore (Fig. 4H–I). They were found in great numbers on all the mouthparts of all the species and will be considered as setae.

II. Large (50 μm–2 mm), circular, elongate, tapering projections, but with no articulation with the general cuticle (Fig. 2B). They have a continuous lumen containing semicircular sheath cells basally along with sensory cilia (Fig. 3C). They have an annulus, which may disappear during intermoult and may or may not have small teeth-like outgrowths (Fig. 2B), and a subterminal pore. They are found in two rows on the medial rim of the basis of maxilla 1 of *Pag. bernhardus* where type 1 projections are found on all the other six species (Fig. 11A) and on the endopod of maxilliped 2 of
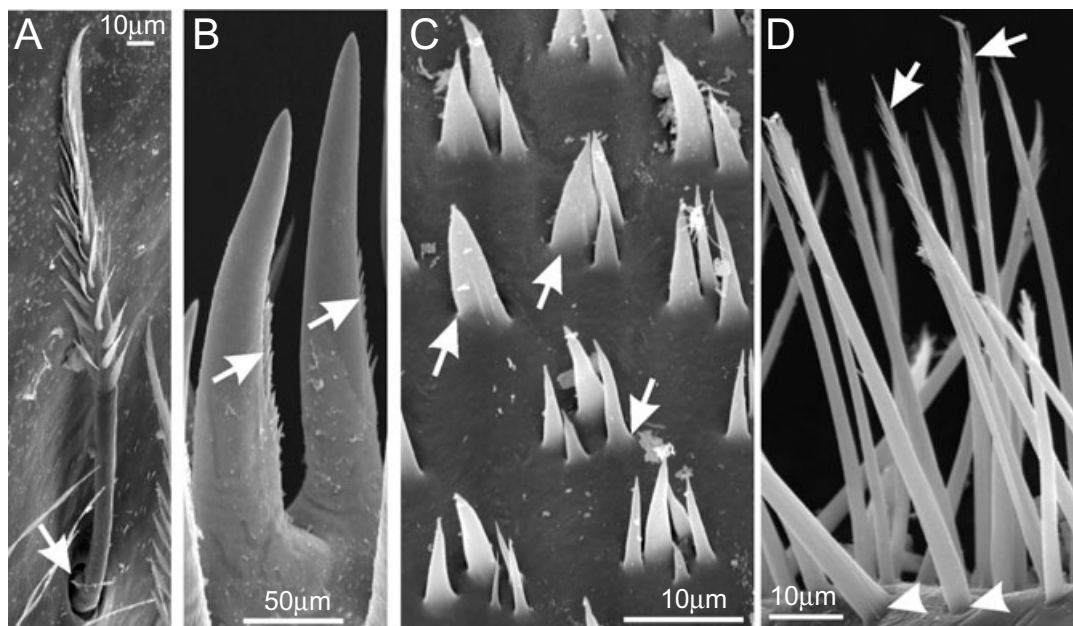

Figure 2. Types of projections found on the general cuticle. A, type I projection, a seta, is an elongate circular projection, which is articulated with the general cuticle (arrow). It is the most common type of projection. B, type II projection, a seta, from maxilla 1 of *Pagurus bernhardus* with a more or less direct transition into the general cuticle. In the other species articulated setae are situated in the same place (compare with Fig. 11A). They may have small outgrowths (arrows). C, type III projections, denticles, from maxilliped 1 of *Panulirus argus*. Arrows indicate direct transition into general cuticle without an articulation. D, type IV projections, setules, from the paragnath of *Stenopus hispidus*. Arrows indicate serration and arrowheads indicate articulation with the general cuticle. Note the flattened shape at the base.

Ca. maenas (Fig. 11D) and maxilliped 3 of *Pal. adspersus*. They will also be considered as setae.

III. Very small (1–30 µm long), smooth, flat and pointed projections with no articulated socket (Fig. 2C). They have no outgrowths, no pore and no lumen (Fig. 3G). This type of projection is particularly numerous on all the mouthparts of *Pan. argus*, but it was also found on the labrum of the other species. Additionally, they were found on some of the setae (Figs 3G, 4D). They will be referred to as denticles.

IV. Medium sized (2–150 µm), flat and elongate projections with an articulation in a socket area (Figs 2D, 3D, arrowheads). They are normally serrated along the distal edge (Fig. 2D, arrows) and they always lack a pore. They may have a lumen distally, but it never continues through the entire projection (Fig. 3D, E). They are made solely of cuticle and with no associated cells (Fig. 3D). Such projections are situated on the labrum and paragnaths of *Pe. monodon*, *S. hispidus* and *Pal. adspersus*, and on the paragnaths of *Ca. maenas* and *Pag. bernhardus*. Additionally, they were found on many of the setae (Fig. 3F, G). They will be referred to as setules.

SUBSTRUCTURES OF SETAE

When the two groups of setae just described are examined in detail, they are found to differ in the large variety of substructures they can possess.

Three types of attachments to the general cuticle are seen: I. The socket is drawn into the general cuticle and provides the seta with an infracuticular articulation (Fig. 4A). II. The socket is extended from the general cuticle, giving the seta a supracuticular articulation (Fig. 4B). III. The articulation is weak or absent and the general cuticle has a direct transition into the cuticle of the seta (Fig. 2B).

An annulus situated on the proximal half of the shaft is found on all of the setae (Fig. 4C). The annulus is a by-product of the ontogeny, where the setae develop in an invaginated state (see Watling, 1989 for more details). The annulus can be difficult to detect since it often diminishes as the cuticle thickens, stretches and wears down during the intermoult.

The main substructures accounting for the diversity of setae are the presence or absence of outgrowths on the setal shaft and, when present, their appearance and arrangement. The outgrowths are divided into two groups: denticles and setules. Denticles, as defined above, are rather small (< 30 µm long), flat and pointed outgrowths with smooth edges and no articulation with the setal shaft (Fig. 4D). They are solid cuticle, i.e. they lack a lumen (Fig. 3G). They occur on the setae in two parallel rows, they are always orien-

tated with their broad axis parallel to the setal shaft and they point distally (Fig. 4D). Denticles are always found distal to the annulus.

Setules have a wide size range (2–150 µm long) but they share common features. They all have an articulation with the setal shaft although, especially in smaller setules, the articulation is often weak (Fig. 4E, F). They are all flat with their broad axis perpendicular to the setal shaft at the point of articulation. Setules taper distally and often have a serrate edge with most of the minute tooth-shaped extensions distally (Fig. 4F). Like denticles, setules are made of solid cuticle (Fig. 3F, G). Setules always point towards the tip of the seta but the angle changes with size. Long setules may be almost perpendicular with the setal shaft, whereas small setules lie almost flat against the shaft (often referred to as scales). Long setules can be found along the whole length of a seta, whereas small setules are only found distal to the annulus. They can be arranged in rows but are normally randomly placed on the shaft. Even though denticles and setules are often very distinct and easy to separate, there are intermediate forms. In some cases rows of outgrowths gradually changing from setules to denticles (from base to tip) can be found on the same seta (Fig. 4G).

Another feature that varies within setae is the L/W ratio of the shaft when the width is measured at the base of the seta. The vast majority of setae are slim with a L/W ratio of more than 15, but some of the setae are more stout and robust with a L/W ratio below 8.
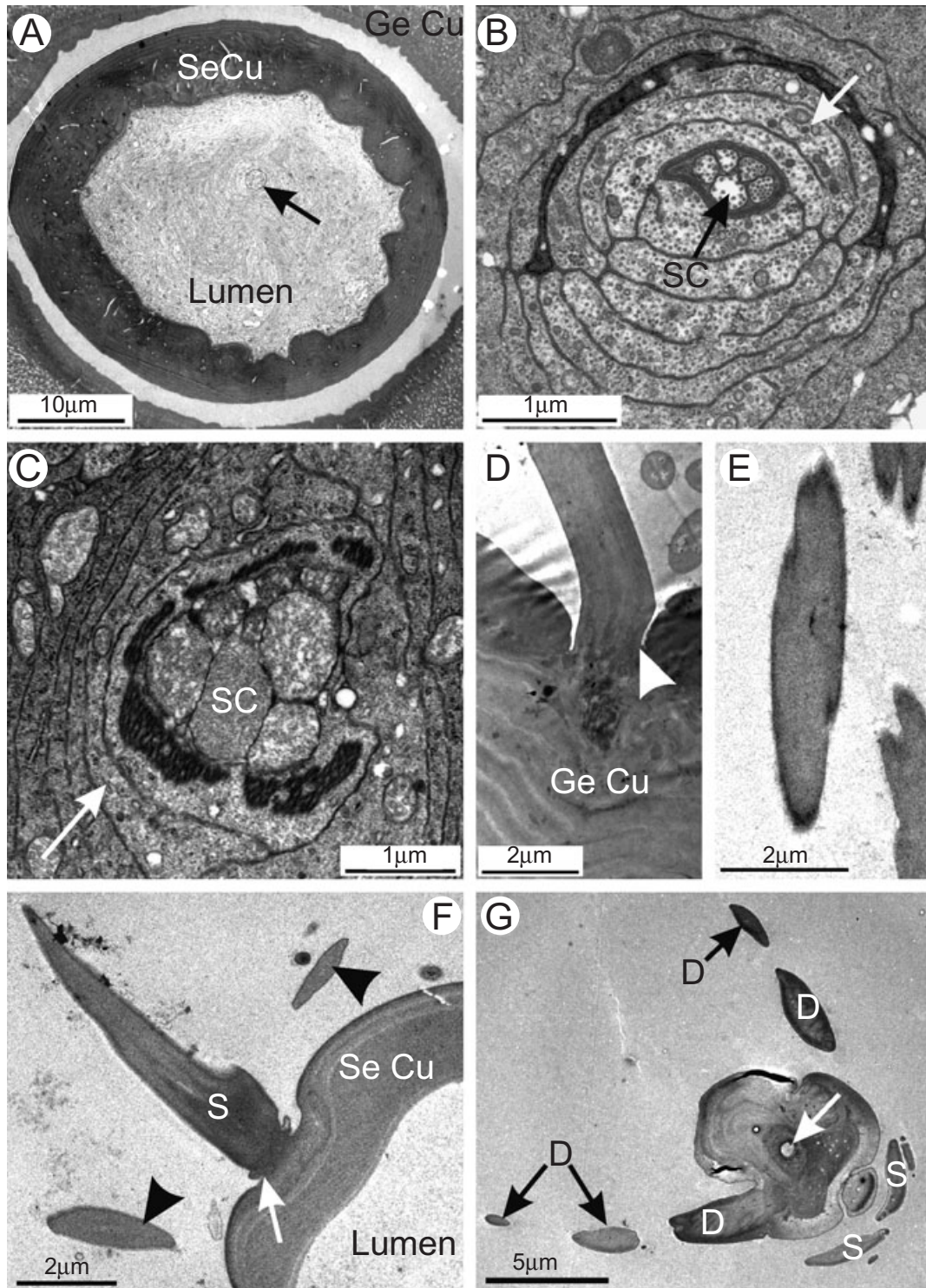
The pore-bearing setae may have the pore in two different positions: terminal and subterminal pores. Most common is a terminal pore situated at the very tip of the seta, often bending to make the pore point to the side of the seta (Fig. 4I). Less common is a subterminal pore situated on the side of the seta a little proximal to the tip (Fig. 4H).

TYPES OF SETAE

Seven types of setae can be distinguished by the way the substructures are combined: pappose, plumose, serrulate, serrate, papposerrate, simple and cuspidate setae. The characteristics of the seven classes are summarized in Table 1. For detailed setal maps, see Garm (2004). It should be noted here that this nomenclature is not invented by the author; all but papposerrate are used by several authors (e.g. Farmer, 1974; Factor, 1978; Derby, 1989; Watling, 1989) (see also Table 2).

Pappose setae

The shafts of pappose setae are often very long and slender and they never display a pore. They have long

(50–150 μm), well defined setules scattered randomly along the entire length of the shaft (Fig. 5A, B). The setules are clearly articulated with the shaft and have serrated edges with most teeth situated distally (Fig. 5C). The setules normally project at an angle between 45° and 90° to the setal shaft and they often get shorter towards the tip (Fig. 5B). The sockets of a pappose setae are infracuticular but a wide membranous area makes the seta flexible. In the material examined here, they are almost exclusively found lat-

Figure 3. Ultrastructure of the projections on the mouthparts. A, cross-section of the basal part of type I projection, which is circular in cross-sectional shape. The lumen is filled with semicircular sheath cells. Arrow indicates bundle of sensory cilia. B, close-up of semicircular sheath cells (arrow) in the basal part of a type I projection encircling the sensory cilia. C, cross-section of the basal part of a type II projection. Arrow indicates semicircular sheath cells. D, oblique section of a type IV projection, note no lumen or sheath cells. Arrowhead indicates articulation. E, cross-section of the basal part of a type IV projection showing flattened shape and no lumen. F, oblique and cross-section of setules from a pappose seta. Arrowheads indicate cross-sections, arrow indicates the articulation with the cuticle of the setal shaft. G, cross-section of setules and denticles from the distal part of a serrate seta. Arrow indicates lumen of seta. *Abbreviations:* D, denticle; Ge Cu, general cuticle; S, setule; Se Cu, cuticle of seta; SC, sensory cilium.
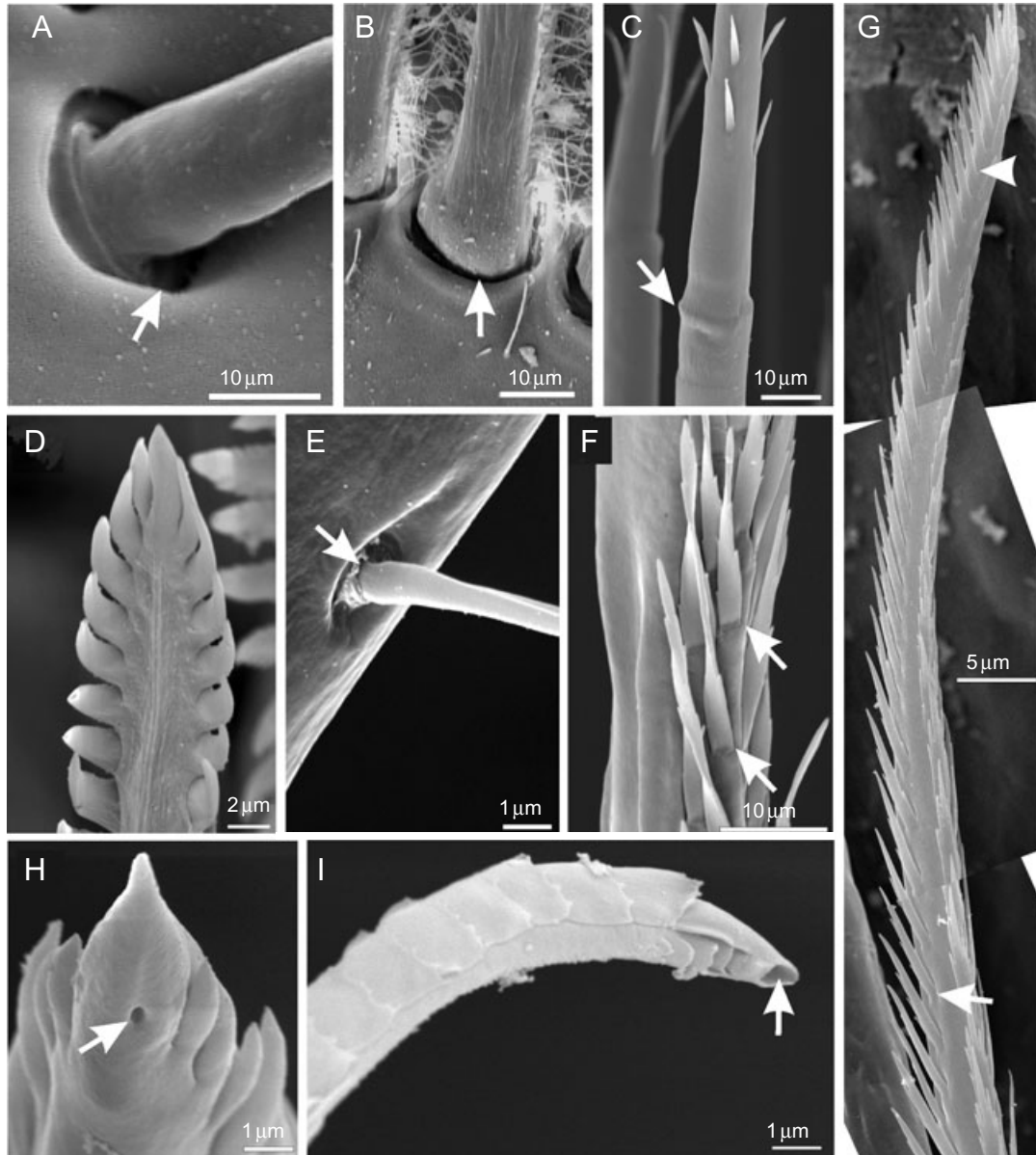

Figure 4. Substructures of setae. A, infracuticular articulation with the general cuticle. Arrow indicates deep socket. B, supracuticular articulation (arrows) with the general cuticle. C, annulus seen as a ring in the cuticle (arrow). D, two rows of denticles arranged distally on a seta. E, large setule displaying articulation (arrow) with setal shaft. F, small setule with weak articulation (arrows). G, stitched picture showing gradual change from setule (arrow) to denticle (arrowhead) on the same seta. H, subterminal pore (arrow) from seta with denticles. I, terminal pore (arrow) from seta with denticles.

Table 1. Summary of the characteristics of the seven types of setae

Seta type	Annulus	Articulation	Long setules	Short setules	Denticles	Length/width ratio	Pore
Pappose	+	Infra	+	+/–	–	>15	–
Plumose	+	Supra	+	–	–	>15	–
Serrulate	+	Infra	–	+	–	>15	Ter/–
Serrate	+	Infra	–	+/–	+	>15	Ter/sub/–
Papposerrate	+	Infra	+	+/–	+	>15	Ter/–
Simple	+	Infra	–	–	–	>15	Ter/–
Cuspidate	+	Infra/absent	–	+/–	–	<8	Sub/–

Infra, infracuticular articulation; Supra, supracuticular articulation; Ter, terminal; Sub, subterminal; +, present; –, absent.
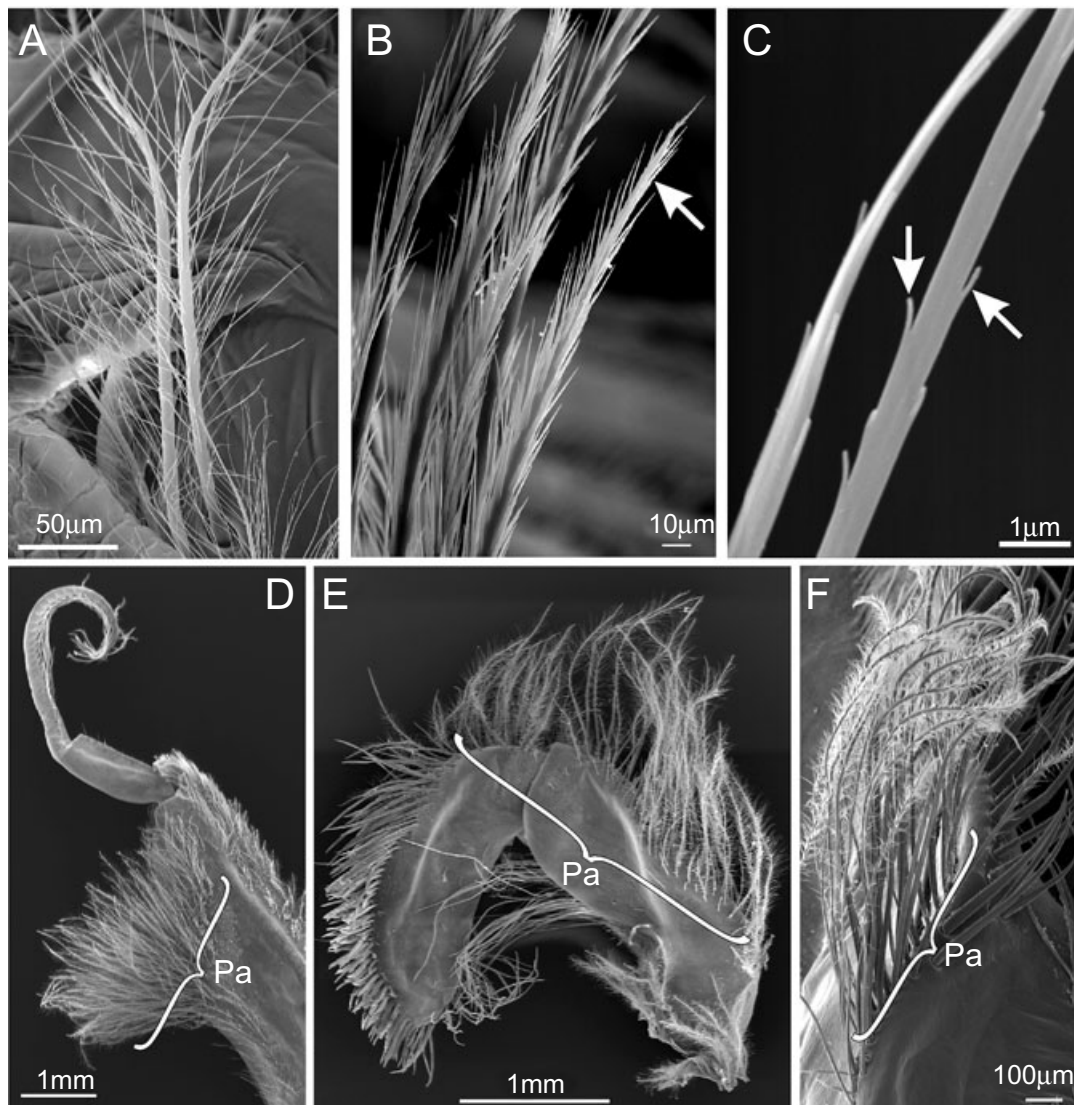

Figure 5. Pappose setae. A, overview of two typical pappose setae from *Cherax quadricarinatus*. Note random arrangement of setules. B, tips of pappose setae from *Stenopus hispidus*. Setules get smaller closer to the tip (arrow). C, serration on the setules (arrows) from pappose seta. D, pappose setae on the exopod of maxilliped 1 of *Carcinus maenas*. E, pappose setae on the mandibular palp of *Ca. maenas*. F, pappose setae on the coxa of maxilliped 1 of *Pagurus bernhardus*. *Abbreviation:* Pa, pappose setae.

Table 2. Comparison of setal classification systems

This study	Thomas, 1970	Fish, 1972	Pohle & Telford, 1981	Schembri, 1982	Lavalli & Factor, 1992	Loya-Javellana & Fielder, 1997	Coelho & Rodrigues, 2000
Pappose	Pappose, papillate?	brush spine	Pappose	Pappose	Pappose	Pappose, plumodenticulate 1	A 1–5, A 6–8?, C 16–19, C 1–16
Plumose	Plumose	Plumose	Plumose, plumose natatory	–	Plumose	Plumose	A 12–15
Serrulate	Teazel, setobranch, multidenticulate, serrulate, multiserrate	Serrate, plumose bristle	Serrate (type 11a), proboscate?	Serrulate, triserrulate, plumodenticulate	Plumodenticulate C3, triserrulate, serrulate, triserrate, multiscaled	Multidenticulate 1–4, rod 2, papillate 2	A 9–11, C 24–27
Serrate	Serrate	Comb seta, serrated bristle, serrated spine	Serrate	Serrate	Serrate, grooved, serrulate F4	Serrate, serrulate 2	B 1–7
Papposerrate	Papillate? plumodenticulate	Hooked bristle	Plumodenticulate	Serrulate?	Plumodenticulate	Plumodenticulate 2, 3, 4	C 17–21
Simple	Acuminate*, rod*, aesthetascs	Simple, seta with blunt apex, seta with nodules, aesthetascs	Simple, proboscate?	Simple?	Simple	Rod 1, papillate 1, acuminate	
Cuspidate	Tooth, cuspidate, conate	Forked spine, simple spine, blunt spine, toothed spine	Cuspidate	Cuspidate, simple?	Cuspidate	Cuspidate 1–2, conate, hamate, serrulate 1	B 8–10
Setules in GC	Digitate, proventricular pegs	–	Microtrichia	–	–	–	–
NA	Ooseta***, hamate**	Brush seta***					A 20***

GC, general cuticle; NA, not applicable; ?, not enough details are given to obtain certainty; –, not found in given study.
*They are not strict simple setae as they have very few setules near the tip.
** Probably not a seta.
***Type of seta not found in this study.

erally on the mouthparts and are most numerous on the exopods of the maxillipeds (Fig. 5D) where they have very little, if any, contact with food.

Plumose setae
Like pappose setae, plumose setae have long setules along the entire shaft, but they are arranged in two strict rows on opposite sites of the seta, giving them a feather-like appearance (Fig. 6A). The setules are never serrated, have a weak articulation with the setal shaft (Fig. 6B) and are often situated in a groove (Fig. 6C). Plumose setae are the only setae that have a supracuticular articulation with the general cuticle, and this makes them extremely flexible (Figs 4B, 6A, arrows). They fall into two groups: some of them have a normal smooth cuticle on the shaft, others have annulations (Fig. 6D) which provide extra flexibility. They never display a pore. Plumose setae are the only setae found on the flagella on the exopods of the maxillipeds (Fig. 6E) and on the scaphognathite.

Serrulate setae
Serrulate setae are slim, with a naked proximal part but with small setules (< 15 µm long) distal to the annulus (Fig. 7A). The setules can be arranged in

rows, normally three (Fig. 7B), or can occur randomly along the shaft (Fig. 7C). The setules are smaller in size towards the tip, and the articulation with the shaft is often difficult to detect (Fig. 7C, D). They point towards the tip of the seta with an angle of less than 45°. The setules on serrulate setae vary somewhat in shape. The normal ones are leaf-shaped and have teeth along most of their edge (Fig. 7B–D), but some are almost square with teeth only on the distal edge (Fig. 7E). Serrulate setae can have two different types of tip. The most common type is very pointed, formed by the setules and has no pore; the other type is bent, has very small scale-like setules and a terminal pore (Fig. 7F). The socket of serrulate setae has an infracuticular articulation. Serrulate setae are the most common type on the mouthparts of the decapods examined here, and they are especially abundant on the distalmost segment of the mandibular palp, the medial rim of maxilla 2 and maxilliped 1 (Fig. 7G).

Serrate setae
Serrate setae have a naked proximal half but distal to the annulus, they have two rows of denticles with 120°–180° between them (Fig. 8A). The denticles are densely packed and become smaller towards the tip of
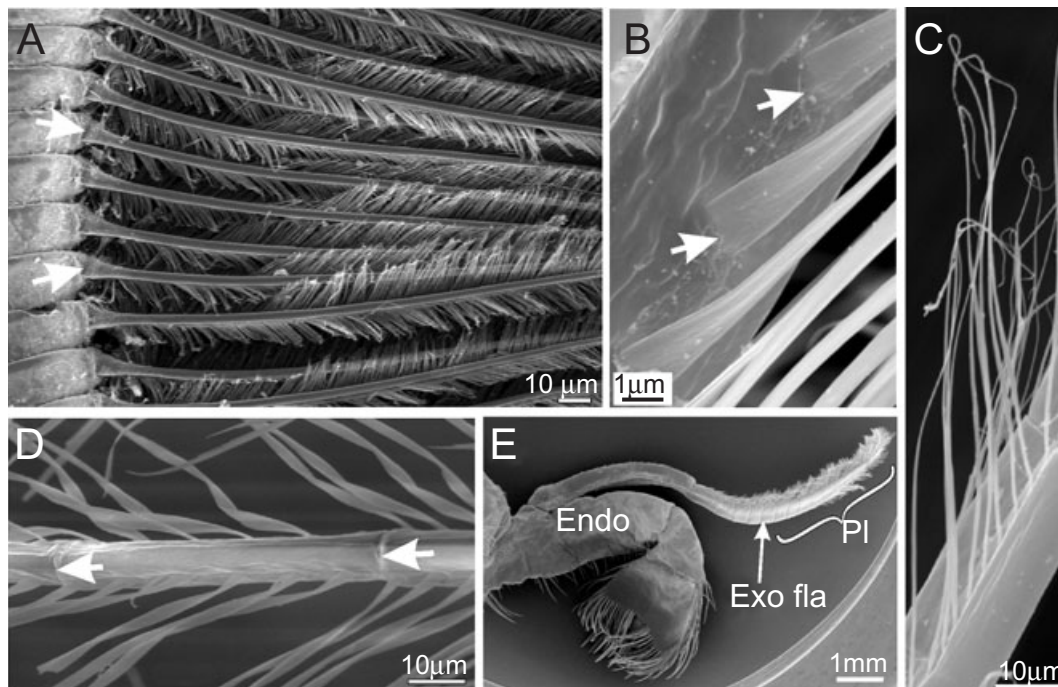

Figure 6. Plumose setae. A, Typical plumose setae from the exopod of maxilliped 2 of *Panulirus argus*. Arrows indicate supracuticular articulations. B, basal part of setule. No articulation is seen (arrows). C, setule (inserted in a groove) from plumose seta. Note absence of serration. D, plumose seta with pseudo articulations (arrows) from an exopod flagellum. E, plumose setae on the exopod flagellum of maxilliped 2 of *Pan. argus*. *Abbreviations:* Endo, endopod; Exo fla, flagellum of exopod; Pl, plumose setae.
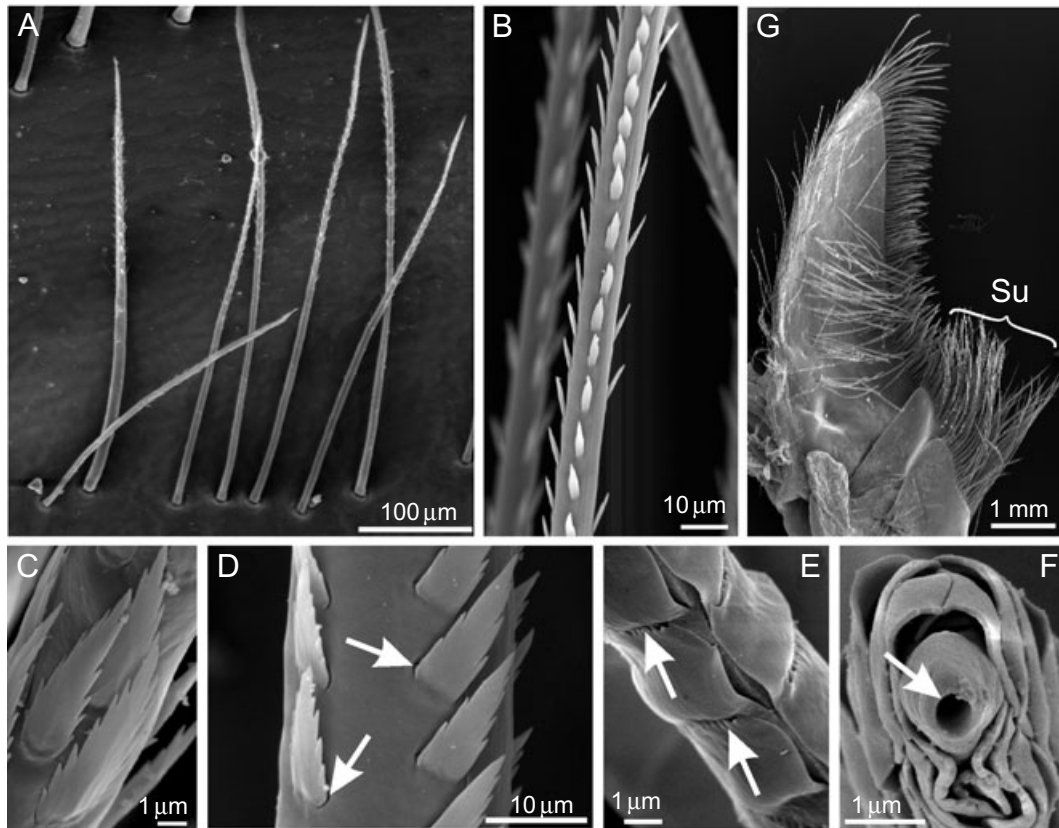
Figure 7. Serrulate setae. A, typical serrulate setae from maxilliped 1 of *Pagurus bernhardus*. Setules are small and only present on the distal half of the seta. B, middle part of serrulate seta with setules in three rows. C, setules from serrulate seta arranged randomly along the shaft. Note strong serration. D, small setules with weak articulations (arrows). E, scale-like setules from serrulate seta of *Palaemon adspersus*. Note serration on distal rim (arrows). F, terminal pore (arrow) from serrulate seta. G, serrulate setae on the coxa of maxilla 1 of *Penaeus monodon*. *Abbreviation:* Su, serrulate setae.

the seta. The distal half may also have setules on the opposite side of the shaft from the denticles, ranging in number from a few to a few hundred. When present, the setules are small, about the same size as the denticles, have teeth along their edge and lay almost flat against the shaft (Fig. 8B). Serrate setae have two different types of tip, similar to those described for the serrulate setae. In the more usual case, the denticles continue all the way to the tip, which they constitute, and there may be a subterminal pore (Fig. 4H). In other cases, the denticles stop a little before the tip, which is slender, has scale-like setules and is curved with the concave side between the two rows of denticles (Fig. 8C). The very tip then has a terminal pore. Serrate setae of the latter type are normally longer and more slender than of the former type. Modifications of the denticles occur in some setae in *Pe. monodon*. Here, the denticles partly or completely fuse to form two ridges along at least parts of the distal half (Fig. 8D). There is often a gradual change from fused to separated denticles on a single seta. The articulation of ser-

rate setae is infracuticular and the membranous area is often narrow. Serrate setae are amongst the most common setae and are found in all seven species on almost all mouthparts. They are found in the highest densities on the distalmost segments of the endopods of maxillipeds 2 and 3 (Fig. 8E, F).

Papposerrate setae

Like pappose and plumose setae, papposerrate setae are long and slender (Fig. 9A). On their proximal half to two thirds they have long, randomly arranged setules like pappose setae, but on the distal part they have two rows of denticles like serrate setae (Fig. 9B). In the area with the denticles there may be additional small setules on the opposite side of the denticles (Fig. 9B). The most proximal denticles often appear as small setules, as indicated by a weak articulation and a serrate edge. The articulation of papposerrate setae with the general cuticle is infracuticular with a well developed membranous area. Papposerrate setae are not very
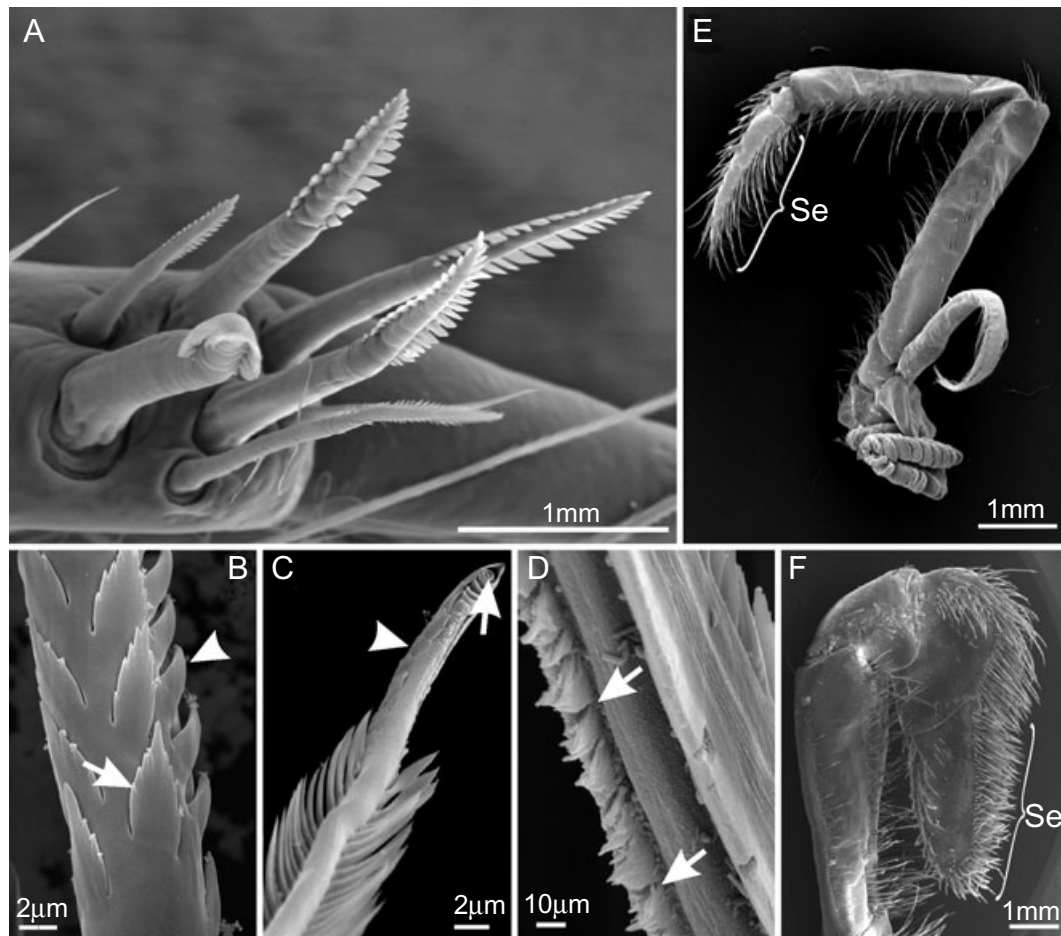
Figure 8. Serrate setae. A, typical serrate setae from the endopod of maxilla 1 of *Cherax quadricarinatus*. Denticles in two strict rows on the distal half. B, serrate seta with setules (arrow). Arrowhead indicates denticles. C, tip of serrate seta with terminal pore (arrow). No denticles, only scale-like setules near the tip (arrowhead). D, partial (arrows) and complete fusion of denticles on serrate seta from *Penaeus monodon*. E, serrate setae on the dactylus of maxilliped 3 of *Palaemon adspersus*. F, serrate setae on the dactylus of maxilliped 2 of *Pe. monodon*. *Abbreviation:* Se, serrate setae.

common. They only occur in large numbers on the labrum and paragnath of *Ch. quadricarinatus* (Fig. 1B), but they are also seen on the lateral part of some of the mouthparts in *Ca. maenas*, *S. hispidus* and *Pe. monodon*.

Simple setae
Simple setae are long and slender and, as the name implies, they completely lack outgrowths on the setal shaft (Fig. 10A). They have a pointed tip, which may or may not have a terminal pore (Fig. 10B). They have an infracuticular articulation. This type of seta is found on almost all of the mouthparts of *Pan. argus* and in this species, they are the more abundant setal type. Simple setae are also found in large numbers on the medial rim of the basis of maxilla 2 of *Ch. quadricarinatus*, *Pag. bernhardus* and *Ca. maenas* (Fig. 10C).

Cuspidate setae
Cuspidate setae are very robust with a L/W ratio below 8 when width is measured at the base of the seta (Fig. 11A). They have a broad base and taper gradually towards the somewhat rounded tip. They may or may not have a subterminal pore (Fig. 11C) and in most cases, they have no outgrowths. They can have two rows of small outgrowths in the mid-region that look like denticles but their bases are orientated perpendicular to the shaft (Fig. 11B). This is often combined with a weak curvature of the setal shaft with the outgrowths on the concave side. The distal third is always naked. In most cases they have an infracuticular articulation with a very weak membranous area but sometimes, the articulation is completely lacking (Figs 2B, 11D). In both cases the seta is in a fixed position. Most cuspidate setae are found on
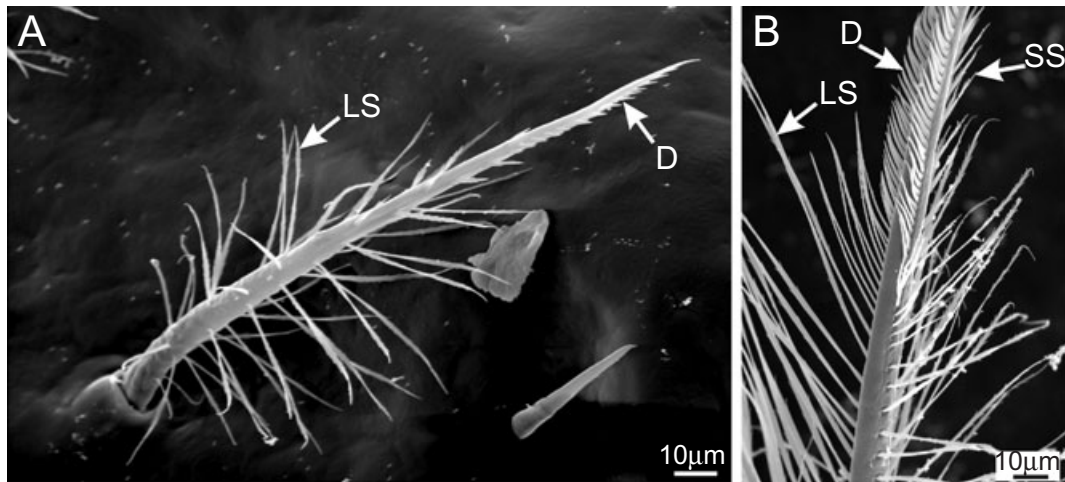
Figure 9. Papposerrate setae. A, typical papposerrate seta from maxilliped 1 of *Cherax quadricarinatus*, with long, randomly arranged setules on proximal part and denticles in two rows on distal part. B, transition region between long setules and denticles. *Abbreviations:* D, denticles; LS, long setules; SS, short setules.
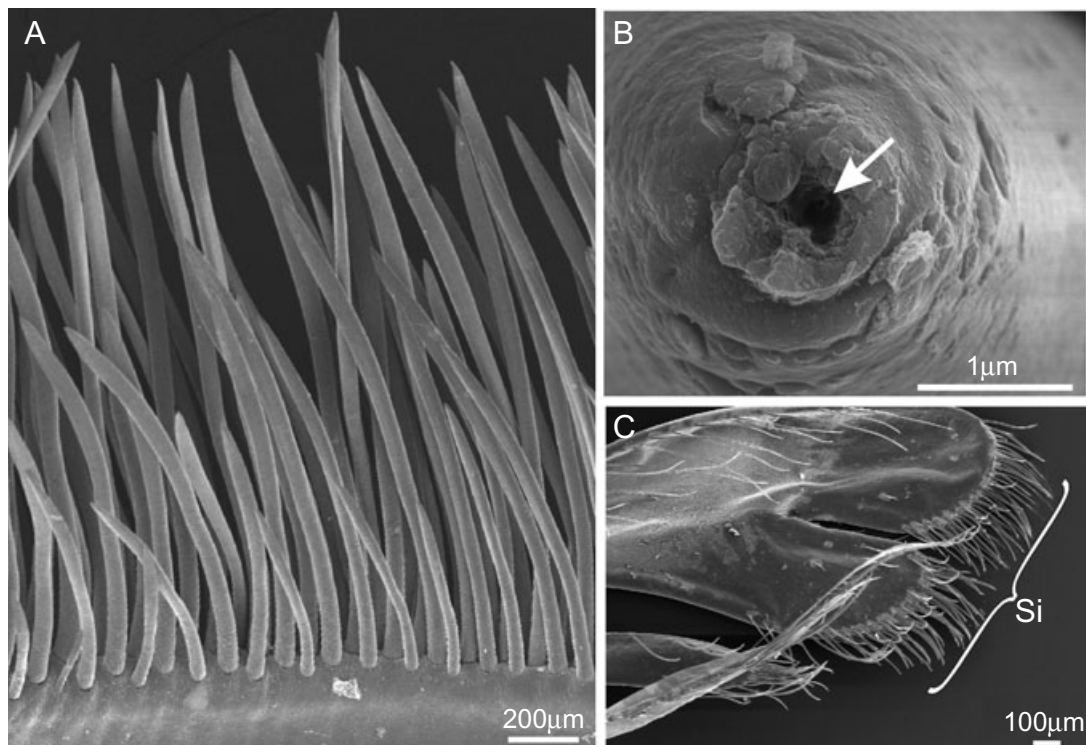

Figure 10. Simple setae. A, typical simple setae from the mandibular palp of *Panulirus argus*. No outgrowths are seen. B, terminal pore (arrow) from simple seta. C, simple setae situated on the basis of maxilla 2 of *Carcinus maenas*. *Abbreviation:* Si, simple setae.

the medial rim of the basis of maxilla 1 and on the distal segments of maxilliped 2 (Figs 2B, 11A, D), but they can be found in low numbers in a few other places (Fig. 11E).

INTERMEDIATE TYPES OF SETAE

Most of the setae found on decapod mouthparts can easily be placed in one of the seven described categories, but there is morphological variation within the
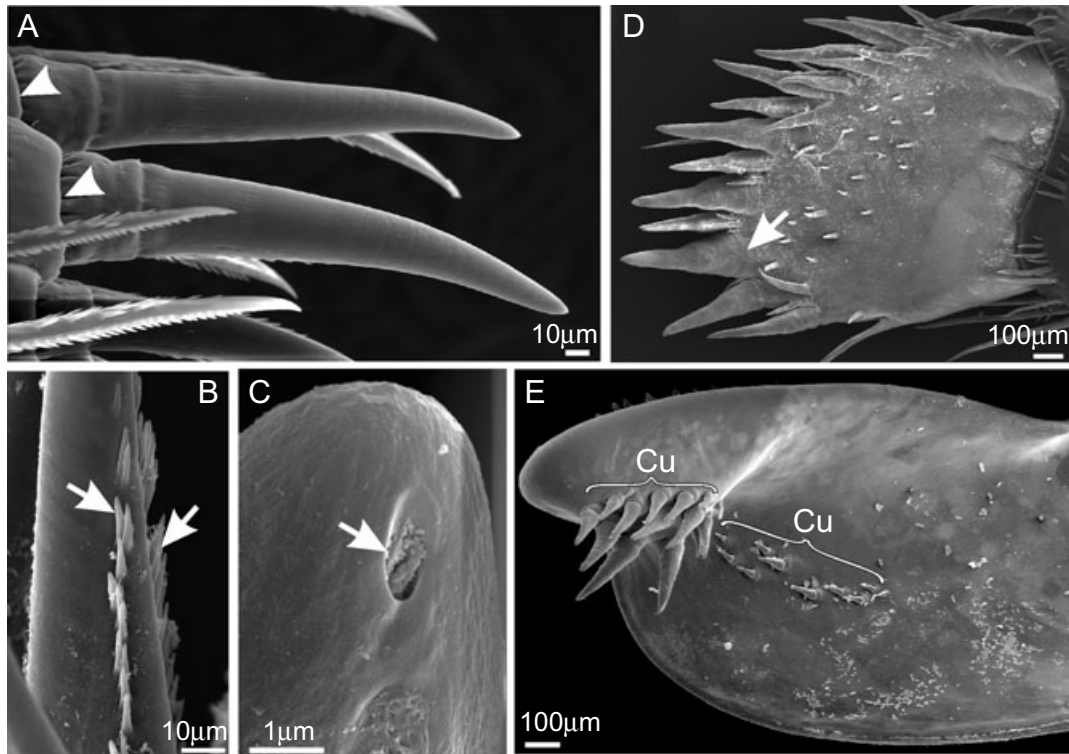
Figure 11. Cuspidate setae. A, Typical cuspidate setae from the basis of maxilla 1 of *Cherax quadricarinatus*. Note clear articulation with general cuticle (arrowheads) and compare with Figure 2B. B, cuspidate seta with teeth-like outgrowths in two rows (arrows). C, subterminal pore (arrow) from cuspidate seta with debris in pore. D, cuspidate setae on the dactylus of maxilliped 2 of *Carcinus maenas*. One is lacking articulation (arrow). E, cuspidate setae on the endopod of maxilla 2 of *Penaeus monodon*. *Abbreviation:* Cu, cuspidate setae.

groups and this results in intermediate types of setae. One reason for this is the not always clear distinction between setules and denticles.

Intermediate forms are found between the following types.
1. Pappose and plumose, where the proximal part has two distinct rows of setules but on the distal part they are randomly spaced. This is only seen for some setae on the mandibular palp of *Pe. monodon*.
2. Pappose and papposerrate, where the proximal part has long, randomly arranged setules but the distal part has short setules arranged in rows. This intermediate form is found in small numbers on all the species.
3. Pappose and serrulate, where the proximal part has few long setules and the distal part has small or medium sized setules.
4. Serrulate and serrate, where the proximalmost outgrowths are setules but they change gradually into denticles, as shown in Figure 4G. They are found in all the species and are seen especially on the medial edge of the basis of maxilliped 1.

5. Serrulate and simple, where the seta has a few small setules on the distal part. This type is seen on the medial edge of the basis of maxilla 2.
6. Serrate and cuspidate, where the outgrowths are denticle-like but the distal part is naked and the seta has a L/W ratio between 10 and 15. They are mostly found on the medial edge of the coxa of maxilla 1.
7. Cuspidate and simple, where the seta has no outgrowths and a L/W ratio between 8 and 15. They are found in small numbers on most of the species but are most common on the mouthparts of *Pan. argus*.

DISCUSSION

The mouth apparatus of the seven species of decapods from this study hold literally thousands of setae in total, which provides good grounds for assessing what their common features are and proposing a setal classification system. The setae on the mouthparts of decapods display a high diversity probably due to the wide range of functions they have to serve (Schembri, 1982a; Hunt, Winsor & Alexander, 1992;

Stemhuis, Dauwe & Videler, 1998; Johnston, 1999; Garm & Høeg, 2001; Garm, Hallberg & Høeg, 2003). I provide a new definition for the term 'seta', showing that the presence of an articulation is an insufficient criterion (Watling, 1989). From the details of the external morphology of the setae, I suggest a classification system with seven major types: pappose, plumose, serrulate, serrate, papposerrate, simple and cuspidate. This terminology, except for papposerrate, has been widely used in the literature (e.g. Factor, 1978; Pohle & Telford, 1981; Schembri, 1982a; Lavalli & Factor, 1992; Loya-Javellana & Fielder, 1997; Garm & Høeg, 2000) although often with divergences in the definitions. I have found no basis for any further subdivision of these types. The seven types are compared with the literature to test whether they apply to nonmouthpart setae, and to setae from taxa other than decapods.

DEFINITION OF A SETA – EXISTING DEFINITIONS

The many elongate projections of the cuticle of crustaceans have been the subject of numerous studies since they play a major role in many aspects of their biology and since they are useful tools in crustacean taxonomy and phylogeny (i.e. Huys & Boxshall, 1991; Newman & Ross, 2001). This has led to a sometimes very confusing terminology, although most authors are agreed on using the term seta. However, it is not obvious which projections should be included in this term. Thomas (1970) proposed that all elongate outgrowths with pores distally were setae, but this has since been shown with SEM to be a far too narrow definition. Fish (1972) considered elongate outgrowths filled with 'cytoplasm' to be setae, but this would include many spines and teeth and exclude setae with no cells in the lumen. Watling (1989) stressed the need for a definition based on homologies and suggested that the articulation with the general cuticle is such a homology. This definition seems to hold true for the vast majority of setae, as is seen here. It is probably also true for the ground plan of setae, but there are some problems.

Some of the cuticular outgrowths with clear articulations cannot be considered setae. These are the type IV projections, which do not have a continuous lumen, are not innervated and do not contain semicircular sheath cells basally. Their external and internal morphology is so similar to the long setules found on some of the setae that there are no structural arguments to consider them as being different (compare Fig. 2D with Fig. 9B and Fig. 3D, E with Fig. 3F, G). Setules are therefore a general feature of the crustacean cuticle and are not restricted to setae. Another argument for this is that denticles are also found both on setae and on the general cuticle (type III projections), indicating that the cuticle of the setae has the same features as the general cuticle.

There is also little doubt that some of the nonarticulated projections of the cuticle should be considered as setae. The spine-like projection found on the dactylus of maxilliped 3 of *Pal. adspersus* is innervated, has a continuous lumen and has a cellular arrangement very similar to other setae (Fig. 3C). Furthermore, such projections on the basis of maxilla 1 of *Pag. bernhardus* are situated in the same place and arranged in the same way (two parallel rows) as articulated projections in the other species that are clearly setae. The same pattern is seen for the squat lobster *Munida sarsi* (Garm & Høeg, 2000); the articulation is probably lost so as to encompass mechanical functions requiring a very robust and steady seta (Garm & Høeg, 2001). Such a reduction has probably occurred many times during the evolution of setae.

DEFINITION OF A SETA – NEW DEFINITION

As can be seen from the discussion above, there is a need for a new definition of a seta. From this study the following is suggested:

A seta is an elongate projection with a more or less circular base and a continuous lumen; the lumen has a semicircular arrangement of sheath cells basally.

The literature on the ultrastructure of setae provides good support for the internal characteristics – the continuous lumen and the semicircular sheath cells (Alexander, Hindley & Jones, 1980; Guse, 1980; Altner, Hatt & Altner, 1983; Crouau, 1989; Hallberg, Johansson & Elofsson, 1992; Crouau, 1997; Paffenhöfer & Loyd, 2000; Garm *et al.*, 2003). One of the very important functions of sheath cells is to make the cuticular parts of a seta during its development and after each moult cycle (Guse, 1980). This indicates that understanding the seta as a unit requires a careful study of ontogeny, and that such a study probably will provide an even better definition of a seta. In insects, the development and ontogeny of the seta is very strict and the seta has a very strict cellular arrangement (Keil, 1997).

Another function of at least the innermost sheath cells is to support and protect the dendrites of the associated sensory cells. The innervation might actually be found to be an additional and very strong character combining all setae, but insufficient data are available at present to verify this. For many setae, the sensory functions are closely connected to the presence of a continuous lumen, since many of the sensory cells send their cilia out to the tip of the setae. The cuticular arrangement forming the lumen probably

also serves mechanical purposes, and setae with no sensory cilia in the lumen are common.

In many cases the developmental and ultrastructural characteristics have little impact because categorization is normally based on light or scanning electron microscopy. The round shape of the basal part of a seta is therefore an important character and seems to be very consistent, not only for the mouthpart setae of decapods but also for setae found on all body parts and for many groups of crustaceans. This is true for Remipedia (Schram & Lewis, 1989; Elofsson & Hessler, 1991; Elofsson & Hessler, 1994), Cirripedia (Høeg *et al.*, 1994; Lagersson, Garm & Høeg, 2003), Copepoda (Paffenhöfer & Loyd, 1999; Matsuura & Nishida, 2000; Paffenhöfer & Loyd, 2000), Ostracoda (Vannier, Abe & Ikuta, 1998), Conchostraca (Rieder, 1980; Martin, 1989), Amphipoda (Berge, 2001), Isopoda (Fish, 1972; Kaïm-Malka *et al.*, 1999), Mysidacea (Crouau, 1989; Hallberg *et al.*, 1992), Stomatopoda (Reaka, 1974; Jacques, 1981) and Decapoda (Shelton & Laverack, 1970; Thomas, 1970; Vedel & Clarac, 1976; Altner, Hatt & Altner, 1983; Altner *et al.* 1986; Derby, 1989). The finding that the setae of the earliest fossils of crustaceans and other arthropods also have a circular base is strong support for this character (Müller & Walossek, 1987; Walossek, 1993). The circular shape can, in a few cases, be difficult to recognize because it is only present at the very base (Derby, 1982; Altner *et al.*, 1983; Pohle, 1989). Articulated, but noncircular projections are also reported by other authors (Halcrow & Bousfield, 1987; Holmquist, 1989; Martin, 1989) and should be considered as setules and not setae.

From my data, it also seems as if an annulus could be a strong character in defining a seta, and the developmental system creating the annulus is, with little doubt, a homology (see Watling, 1989 for detailed description). Again, this points towards the presence of very strong characters in the developmental data. Some amphipod setae-like structures have a different developmental system (no invagination) and therefore no annulus (Watling, 1989). This of course begs the question as to whether these structures are true setae and this should be addressed using TEM.

SETAL TYPES

The results of this study show that the setae examined here fall into seven groups separated by the presence or absence of various structures. These seven types encompass the vast majority of setae, even though there are setae of intermediate types.

The morphological characters by which I have grouped the setae are not put forward as suggestions of homologies, and the seven types of setae are not to be considered as separate evolutionary lines. It is, in fact, very likely that some of the types (such as the simple setae) are based on shared morphological characteristics that have been convergently derived. Watling (1989) stressed that setal categories should be defined by homologies and presented three setal characters which he considered as separate homologies: an annulus, a supracuticular articulation and the presence of setules. This idea has been widely accepted but in my opinion, it is problematic to use a homology criterion to define types of crustacean setae for several reasons.

There is little doubt that strong selection pressures have acted on the external morphology of setae, deriving from the many mechanical functions that they serve. The outgrowths of setae directly involved in food handling, for example, should be closely correlated with the nature of the food items, and such a system is bound to create many convergences. To a large extent, this will probably impede homology-based groupings of setal types.

If the three suggested characters are good homologies, they still will not resolve much of the setal diversity as they will, at best, only create the basis for three types of setae, and when used on the setae described here, such a classification will result in plumose setae as the only valid type. An annulus is found for all of the setae and will therefore not define any specific types. Using the presence of setules is also problematic. As shown above, setules are not a strict setal character but a general character of cuticle. This means that setules are probably not closely linked, if at all, to the evolutionary history of setae but rather, to the evolutionary history of the cuticle. If so, it makes no sense to use them in a homology-based setal classification system.

Even if the setules from the two locations are to be considered convergences, the setules on the setae will have little resolution power. The fact that there are all kinds of intermediate stages between the long setules and denticles suggests that denticles, at least on the setae, are to be considered modified setules or vice versa. The gradual change from setule to denticle, sometimes on a single seta, may display the actual evolutionary history of these outgrowths. The presence of setules would therefore group pappose, plumose, serrulate, serrate, papposerrate and some of the cuspidate setae together and, furthermore, would leave the simple and the rest of the cuspidate setae to be defined by the absence of setules; this would not constitute an evolutionarily uniquely-derived grouping. The plumose setae would be a valid ingroup within these 'setulate setae', defined by the supracuticular articulation. However, this again leaves the rest of the setae with setules to be defined by the absence of such an articulation.

One solution to this resolution problem, of course, would be to search for more homologies within the setal characteristics but at the present state of knowledge, this is not feasible, as Watling (1989) also demonstrates.

FUNCTIONS AS A BASIS FOR CLASSIFICATION

At the moment, I find it more fruitful to create a setal classification system, as I have done here, following the general appearance of the setae without considering whether or not they are evolutionary units. Such a classification system will therefore not directly reflect the large-scale evolution of setae but rather, their mechanical functions, which are probably the major determining factors for their external morphology. Behavioural studies of setal functions support this connection (Schembri, 1982a; Hunt *et al.*, 1992; Stemhuis *et al.*, 1998; Vannier *et al.*, 1998; Johnston, 1999; Garm & Høeg, 2001; Garm, 2004). Many, if not most, authors classifying setae have used subdivisions of the major setal types, but it is my impression that this has little practical use. In effect, these elaborate classificatory systems cannot be used for species other than the one studied or its closest relatives. There is at least far from good support for these subgroups having separate functions. A system containing few, but well-defined major types, as suggested here, has a better chance of being used and probably also of conveying useful information on the functions of the setae.

Taking sensory function into consideration may lead to the construction of a more robust system, but more detailed studies are needed before any firm conclusions can be drawn. Ultimately, it is hoped that evolutionary and functional considerations can be united to form a single classification system.

VALIDITY OF SETAL TYPES AND TERMINOLOGY

It is, of course, of major concern how broadly the classification system applies. There are two obvious levels to test in this case: decapods in general, and crustaceans in general. A summary of comparisons with other detailed accounts of setae is given in Table 2.

By far the most detailed descriptions of setae come from decapods and here, there seems to be good support for all seven types (Thomas, 1970; Pohle & Telford, 1981; Schembri, 1982b; Lavalli & Factor, 1992; Loya-Javellana & Fielder, 1997; Coelho, Williams, & Rodrigues, 2000; Garm & Høeg, 2000), even though there is at times a poor match in terminology (see Table 2). Most of this mismatch comes from subdivisions of the seven types, which is especially true for serrulate setae. Such subdivisions often have very limited use, as discussed above.

Considering the terminology, there seems to be a broad consensus for the use of the terms plumose, pappose, serrulate, serrate, cuspidate and simple setae (Thomas, 1970; Fish, 1972; Farmer, 1974; Jacques, 1981; Pohle & Telford, 1981; Lavalli & Factor, 1992; Loya-Javellana & Fielder, 1997; Nickell, Atkinson & Pinn, 1998; Stemhuis *et al.*, 1998; Johnston, 1999; Pinn *et al.*, 1999; Coelho *et al.*, 2000; Garm & Høeg, 2000). The term 'papposerrate' is not used by other authors and similar setae are often referred to as 'plumodenticulate'. 'Plumodenticulate' indicates that the characteristics are a combination of plumose and having denticles (serrate), but since it actually is a combination of a pappose and a serrate seta, I find 'papposerrate' much more suitable.

One type of setae which has been dealt with in extreme detail compared with others is the so called aesthetascs, which are putative unimodal chemoreceptors found on antenna 1 of most crustacean taxa including: Decapods (Ghiradella, Case & Cronshaw, 1968a, b; Snow, 1973; Thompson & Ache, 1980; Fontaine, Passelecq-gerin & Bauchau, 1984; Spencer, 1986; Tierny, Thompson & Dunham, 1986; Hallberg *et al.*, 1992; Steullet *et al.*, 2000), Pericarida (Nielsen & Strömberg, 1973; Risler, 1977; Johansson *et al.*, 1996), Ostracoda (Anderson, 1975), Conchostraca (Rieder (1980), Branchiopoda (Rieder, 1978). So far they are the only assumed unimodal chemoreceptory setae found in crustaceans and they seem to be restricted to antenna 1. They are believed to be the primary site for olfaction (Voigt & Atema, 1992; Derby, 2000; Steullet *et al.*, 2000; Derby *et al.*, 2001; Harrison *et al.*, 2001). Even though they possess these special features, I still consider them normal simple setae (see also Table 2) since it is their external structure and not their sensory modality that is used for the classification.

I find the seven setal types I have put forward suitable for a general classification system when dealing with decapod crustaceans, but there is too little detailed information from other groups to finally conclude whether or not it will apply beyond decapods. Work done on pericarideans (Fish, 1972; Risler, 1977; Kaufmann, 1994; Kaïm-Malka *et al.*, 1999) suggests that most of their setae will fit into the seven categories, but there are also strong indications that additional types have to be included, like the 'sensory spines' from *Sphaeroma hookeri* (Brandt, 1988). They are somewhat similar to cuspidate setae but have a special bifid tip. Another setal type which probably has to be added is designated as 'ooseta' (Thomas, 1970), 'brush seta' (Fish, 1972), seta type A 20 (Coelho *et al.*, 2000) and Seta type U (Cals & Cals-Usciati, 1986). These represent the same type of seta, which is naked proximal to the annulus and has long setules distally. It was not found in my study but

seems to be a consistent type which will need further verification.

CONCLUSIONS

In this paper, I have investigated a wide range of cuticular projections to arrive at a more consistent definition of a seta and to show how these structures can be most constructively divided into types. The definition of a seta suggested here is meant to be homology-based, and it ultimately points towards the ways in which these all important cuticular structures may have first evolved in the crustacean or arthropod stem lineage. In contrast, my subdivision of setae into types is not based on homologies but rather, on their mechanical functions as we still lack most of the information needed to trace their actual evolutionary pathways.

ACKNOWLEDGEMENTS

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