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Setal morphology in cirripedes: a useful tool in phylogenetic studies?

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The morphology of the setae, on the mouthparts and the cirri of 33 barnacle species, was investigated by scanning electron microscopy. The species examined were selected from a range of pedunculate and balanomorph families living in a variety of habitats from the littoral zone to deep-sea vents. It was found that the setae could be divided into five groups: simple, denticulate, setulate, plumo-denticulate and aesthetascs. The categories were subdivided resulting in 43 setal types being recognized. Balanomorph cirripedes were found to have a greater variety of setae than pedunculates. Setulate setae on the cirri, and specialized setae on the mandibular palps and the first maxillae tended to be associated with the development of the balanomorph form. Setal type was correlated with taxonomy, whether based on shell structure and soft body morphology or DNA analysis, but with some anomalies which deserve further investigation. The problems of reconciling the proposed cirripede setal categories with those described in the Decapoda are discussed.

Keywords: cirripedes, setae, setal morphology, setal classification, phylogeny, aesthetascs

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INTRODUCTION

The setae which clothe the limbs and mouthparts of cirripedes have a number of important functions in feeding, sensory perception and reducing the fouling of the body surface and mantle lining by epizoites (Anderson & Anderson, 1985), but very little is known about their detailed morphology. Thomas (1970) defined decapod setae as 'hair-like cuticular outgrowths articulating with the cuticle by a well-defined basal socket' (see also Pohle & Telford, 1981). Garm (2004) refined this definition to '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 details of setal morphology are at or beyond the limits of light microscopy and few studies of cirripede structure have used scanning electron microscopy (SEM). Most studies on cirripede structure, functional morphology and classification have concentrated on shell morphology, structure of the cirri and mouthparts and the distribution of the setae on the appendages (Darwin, 1851, 1854; Pilsbry, 1916; Newman & Ross, 1976; Foster, 1978 and many other authors). Setal morphology has been used to a limited extent in cirripede taxonomy (Henry & McLaughlin, 1975; Southward, 1976; Foster, 1978; Chan, 2001; Pitombo, 2004; Chan *et al.*, 2007, 2008, 2009). Several studies on ecology and feeding have also figured some of the setae on the cirri (Anderson & Anderson, 1985; Hunt & Alexander, 1991; Chan *et al.*, 2008).

Høeg *et al.* (1994) were the first to use SEM to describe and classify the setae on the mouthparts of six barnacle species: three pedunculates and three balanomorphs. They recognized that there were inconsistencies in the terms used by previous authors to describe setae, the same terms being used by different authors to describe setae that are not the same. This problem was also highlighted by Chan *et al.* (2008). Høeg *et al.* (1994) suggested that setal morphology, as revealed by SEM, could make a useful contribution to elucidating cirripede phylogeny.

Similar inconsistencies in the terminology used to describe setae, particularly in the Decapoda, were noted by Watling (1989). Garm (2004) addressed this problem in his study of the structure and function of mouthpart setae in seven species of decapods. He described seven categories of setae. He concluded that his classification reflected mechanical function rather than evolutionary history. Using Garm's setal classification Chan *et al.* (2008) compared setal morphology and cirral setation in six species of pedunculate and sessile cirripedes and related their observations to differing feeding strategies. They concluded that the changes in feeding behaviour seen during cirripede evolution were accompanied by an increase in the variety of the setae and changes in the setation patterns.

The present paper extends the work of Høeg *et al.* (1994). The range of setal types seen in a wider variety of cirripedes is described. A three level classification is suggested that might be applied to setae throughout the Cirripedia, bringing consistency to setal descriptions, thus enabling setal characteristics to be used as part of the character sets used in future studies of cirripede phylogeny and taxonomy. The problems of reconciling the proposed setal categories with those defined by Garm (2004) for the Decapoda are discussed.

MATERIALS AND METHODS

The pedunculate and sessile cirripedes examined in this study included species collected from intertidal, sub-littoral and

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deep-sea vent locations. The 33 species studied are listed in Table 1.

For fixation of those species where living specimens were available, bodies were removed still attached to the opercular plates by cutting the opercular membrane with a fine scalpel. They were placed in filtered seawater and relaxed by the addition of MS 222 (3-amino benzoic acid ethyl ester methane sulphonate salt, SIGMA A 5040) powder to the seawater. Once relaxed, with the cirri unfurled, they were rinsed in three changes of filtered seawater before fixation in 2.5% glutaraldehyde in filtered seawater for 4 hours. Fixed material was rinsed in filtered seawater followed by three changes of tap water. Bodies were then separated from the opercular plates, before soaking in a dilute detergent (Decon) solution for 15 minutes followed by 15 seconds ultrasonication (Felgenhauer, 1987). Cleaned material was then rinsed with three changes of distilled water and, either dehydrated through a graded series of ethanol and finally into acetone before critical-point drying from liquid carbon dioxide, or stored in 70% ethanol. Dissection to yield individual limbs and mouthparts was usually carried out on material in 70% ethanol. Mouthparts for most but not all the species, cirri, the oral cone and in some cases whole bodies were then mounted on aluminium stubs using double-sided Sellotape before being gold-coated and examined in a Cambridge Stereoscan 120 scanning electron microscope (SEM) operated at 10 kV. Specimens already preserved in alcohol or formalin, were thoroughly rinsed in tap water before dissection, cleaning with detergent, ultrasonication, rinsing and dehydration as above.

To avoid losing very small items such as dissected mouthparts or very small limbs, they were dehydrated and dried inside small, custom-made, polythene tubes closed at both ends with fine plankton netting. To dissect very small specimens, fine stainless steel entomological pins, mounted on the end of cocktail sticks with Araldite, were used. To transfer

Table 1. Species examined with sources of specimens. Nomenclature based mainly on Southward (2008).

Species	Source
Order PEDUNCULATA	
Ibloidea	
Ibla quadrivalvis (Cuvier, 1817)	Australia, Dr G. Walker (G.W.)
Ibla cumingii Darwin, 1851	Australia, Dr D. Jones (D.J.)
Heteralepadoidea	
Heteralepas microstoma (Gruvel, 1901)	548 m off the Azores, the late Professor A.J. Southward (A.J.S.)
Anelasma squalicola Darwin, 1851	Source unknown (G.W.)
Lepadoidea	
Lepas anatifera Linnaeus, 1758	Anglesey, strandline, Dr J. Hamer
Lepas pectinata Spengler, 1789	Cornwall, strandline, Dr P. Tompsett
Dosima fascicularis (Ellis & Solander, 1786)	Source unknown (G.W.)
Conchoderma auritum (Linnaeus, 1758)	Anglesey, hull of tanker, Dr A.B. Yule (A.B.Y.)
Scalpelloidea	
Leucolepas longa Southward & Jones, 2003	Edison Seamount, off Papua New Guinea (A.J.S.)
Neolepas rapanuii Jones, 1993	2600 m on the East Pacific Rise (A.J.S.)
Vulcanolepas parensis Southward, 2005	Pacific Antarctic Ridge (A.J.S.)
Pollicipes pollicipes (Gmelin, 1789)	Atlantic coast, Portugal (G.W.)
Scalpellum scalpellum (Linnaeus, 1758)	North-west Irish Sea, E.I.S. Rees (E.I.S.R.)
Order BALANOMORPHA Pilsbry 1916	
Chthamaloidea	
Catomerus polymerus (Darwin, 1854)	Australia, (G.W.)
Eochionelasmus ohtai Yamaguchi, 1990	G.W. via D.J. and Dr M. Turkay
Octomeris angulosa Sowerby, 1825	Source unknown (G.W.)
Chthamalus stellatus (Poli, 1795)	North Wales author; English Channel (A.J.S.)
Chthamalus montagui Southward, 1976	Anglesey, author
Chthamalus antennatus Darwin, 1854	Australia (G.W.)
Tetraclita squamosa Darwin	Hong Kong (G.W.)
Tesseropora rosea (Krauss, 1848)	Australia (G.W.)
Tetraclitella purpurascens (Wood, 1815)	Australia (G.W.)
Balanoidea	
Chirona hameri (Ascanius, 1767)	Northern North Sea (E.I.S.R.)
Austrominius modestus Darwin, 1854	Anglesey, author
Semibalanus balanoides (Linnaeus, 1767)	Anglesey, author
Semibalanus cariosus (Pallas, 1788)	Friday Harbor, Washington, USA Dr R. Strathmann
Balanus balanus (Linnaeus, 1758)	Anglesey, author
Balanus crenatus Bruguière, 1789	Anglesey, author
Balanus improvisus Darwin, 1854	Laboratory reared (A.B.Y.)
Balanus nubilus Darwin, 1854	British Columbia, Professor V. Tunnicliffe
Perforatus perforatus Bruguière, 1789	South Wales, author
Megabalanus psittacus (Molina, 1788)	Chile, Professor C.A. Richardson
Megabalanus tintinnabulum (Linnaeus, 1758)	Taiwan, Dr B.K.K. Chan

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and mount these smaller specimens, eyelashes also fixed to cocktail sticks and moistened with saliva were used. Eyelashes are flexible and therefore do not damage dried delicate structures.

RESULTS

General setal morphology

Cirripedes conform to the basic crustacean setal morphology already described in numerous studies and Figure 1 illustrates the basic features of a denticulate seta.

The setal socket and setal shaft

Where the seta articulates with the cuticle surface, there is usually a raised circular area of thin, flexible cuticle from the centre of which the setal shaft arises (Figures 1 & 2A). This socket in most cases allows the seta to move relative to the surface from which it arises. This supra-cuticular articulation is the normal situation in the Cirripedia. However, in particularly robust and rigid setae, such as many of those on the rami of *Conchoderma auritum* it is difficult to see a socket (Figure 2B) and these setae might be thought to be large denticles. Their true nature may only be confirmed by observing the mode of formation during the moulting cycle (see below), or whether a lumen is present. In several species, setae on the anterior face of the rami of those cirri comprising the cirral net were found to have hinged sockets allowing them to fold flat against the face of the ramus facilitating withdrawal of the cirri into the mantle cavity (Figure 2C). Setae found on the lateral surfaces of the mandibles and some setae on the maxillae of all the cirripedes examined, have the base of the setal shaft sunk into a pit in the cuticle (Figure 2D). This arrangement is described as infra-cuticular articulation and is the normal situation in the Decapoda that have been studied so far (Watling, 1989; Garm, 2004).

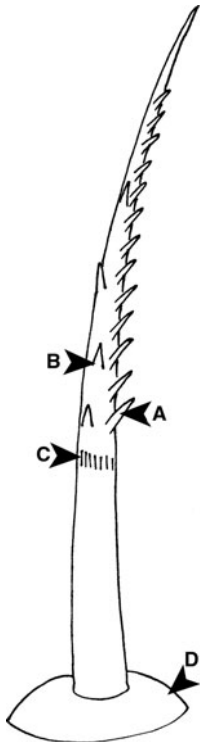


Fig. 1. Diagram illustrating the basic morphology of a denticulate seta. Only one row of denticles is shown: (A) denticle; (B) supplementary denticle; (C) annulus; (D) setal socket.

The setal shaft often exhibits a discontinuity approximately one-third to one-half of the distance along its length (Figures 1 & 2E), which is the point at which the characteristic pattern of denticulation begins, or, is the point of transition between two differing patterns of cuticular ornamentation. This feature is called the annulus and marks the position of the base of the epidermal invagination in which the new seta forms during the moulting cycle (Nilsson-Cantell, 1921; Drach, 1939; Reaka, 1975; Watling, 1989).

In fresh and fixed specimens setal shafts may be straight or more frequently slightly curved. They may be flexible or stiff. Stiff shafts are often strongly ridged (Figure 2F) or may be relatively massive (Figure 2B). Most setal shafts are circular in section but some on the mouthparts appear to be flattened (Figure 2D). An unusual feature of the eolepadines were setae with an angular cross-section and a spiral twist, most clearly seen in the robust setae on the distal edge of the first maxillae (Figure 2G) and in the distal regions of the long collecting setae of cirri 3–6 (Figure 2H).

Sub-terminal or terminal pores were found in several different types of setae in a number of different locations (Figure 2I, J). *Pollicipes pollicipes*, *Catomerus polymerus*, *Octomeris angulosa*, *Tetraclita squamosa*, *Tesseropora rosea*, *Tetraclitella purpurascens* and *Megabalanus tintinnabulum*, were found to have some setae with bifid tips and a very small terminal pore (Figure 4A).

Outgrowths from the setal shaft

Cuticular outgrowths from the setal shaft can broadly be divided into setules and denticles. In this study the term setule is applied to very long (up to 20 μm), slender, flexible, usually flattened outgrowths from the setal shaft. Setules do not taper: they are the same width throughout their length. They usually arise seamlessly from the shaft (Figure 3A) but may, in some cases arise from pits (Figure 3B).

Cuticular outgrowths that cannot be described as setules are here termed denticles. Denticles arise seamlessly from the surface of the setal shaft (Figure 3C) and may be rigid (Figure 3D, F) or flexible (Figure 3E), varying in length from 2–15 μm. Some are needle-shaped (Figures 2F, 3D & 3F) others taper to a point from a broader base (Figure 3C). Some are stout but blunt while others are conical (Figure 3G). Some are flattened and leaf-shaped (foliate; Figure 3H).

Distribution of setules and denticles on the setal shaft

In setulate setae the setules are usually distributed along the whole length of the setal shaft but sometimes they are confined to the distal region beyond the annulus. In the species studied they were found to be arranged either in two irregular rows on opposite sides of the shaft or irregularly over half the circumference of the shaft. In setulate setae the annulus is often not easy to see.

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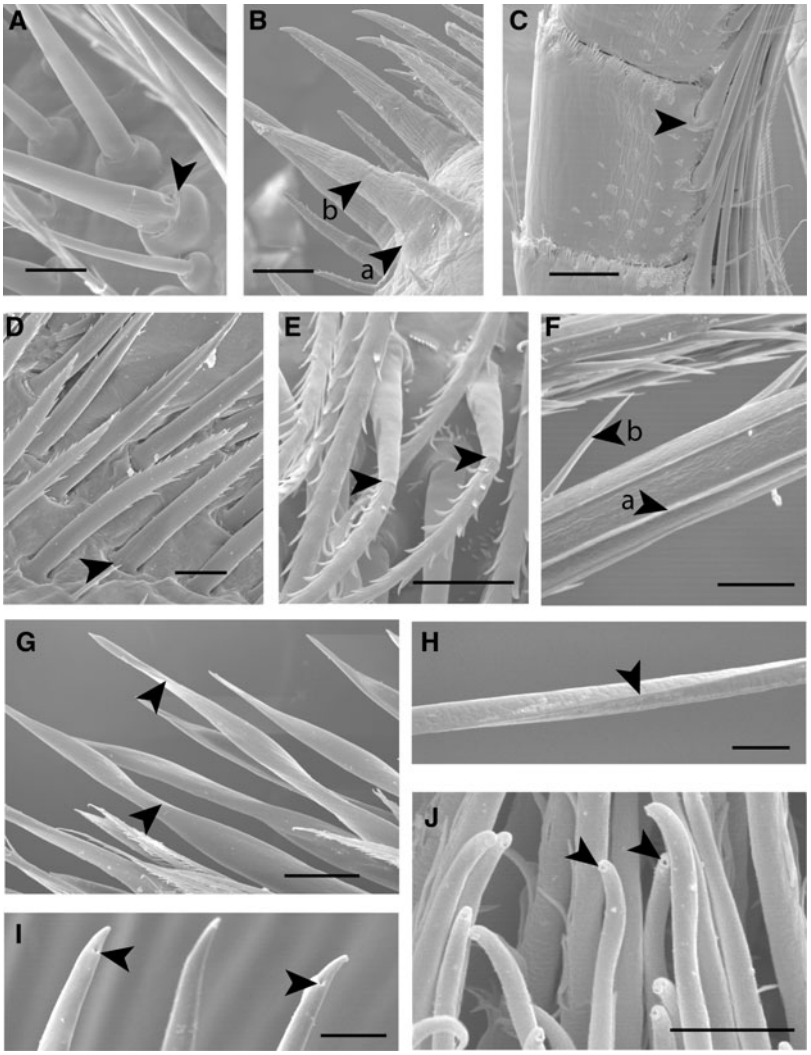


Fig. 2. The setal socket and the setal shaft. (A) *Balanus crenatus*, supra-cuticular articulation of setae on the exopodite of cirrus 2. Arrow indicates setal socket; (B) *Conchoderma auritum*, rigid seta, Type 1b1, on the distal region of a ramus of cirrus 1: (a) setal socket and (b) annulus; (C) *Ibla quadrivalvis*, hinged setae lying along the face of a ramus of cirrus 4. Arrow indicates the hinged socket; (D) *Heteralepas microstoma*, Type 2b1 setae on the lateral face of a mandible. Arrow indicates infra-cuticular socket; (E) *Balanus balanus*, shafts of setae on the exopodite of cirrus 1. Arrows indicate clearly marked annuli; (F) *Lepas anatifera*, part of the shaft of a stiff seta. Arrows indicate one of the surface ridges (a) and a needle-shaped denticle (b); (G) *Leucolepas longa*, Type 1b3 setae on the distal edge of maxilla 1. Arrows indicate the angular twisted setal shafts; (H) *Neolepas rapanui*, distal region of a Type 1a2 seta from the anterior faces of the rami of cirri 4–6. Arrow indicates the angular nature of the shaft; (I) *Tesseropora rosea*, tips of Type 1b2 setae on the distal edge of maxilla 1. Arrows indicate sub-terminal pores; (J) *Semibalanus balanoides*, tips of Type 1a4 setae on proximal region of the endopodite of cirrus 1. Arrows indicate the terminal pores. Scale bars: (A) 10 μm; (B) 50 μm; (C) 50 μm; (D) 10 μm; (E) 10 μm; (F) 10 μm; (G) 20 μm; (H) 5 μm; (I) 10 μm; (J) 5 μm.

In most denticulate setae the denticles arise distally, beyond the annulus, and are usually arranged in two rows. The denticular layout may be irregular immediately distal to the annulus, but further along the shaft the denticles take up the pattern characteristic of a particular setal type (see below). Most setae taper distally and the denticular layout may alter towards the tip of the setal shaft: in some denticles are present right to the tip, but in others the tip is free of ornamentation.

In denticulate setae with curved setal shafts (Figure 4B) the rows of denticles tend to be on the inner face of the curve. However, in *P. pollicipes*, *C. polymerus*, *O. angulosa*, *T. squamosa*, *T. rosea* and *T. purpurascens*, setae were found with denticles on the outer face of the curve (Figure 4B) while the inner face of the curve was without denticles.

In denticulate setae of a given type, some of the setae may have extra denticles on the opposite side of the setal shaft to the rows of denticles which define the type. These denticles can be scattered apparently at random (Figure 1) or arranged in highly ordered rows (Figure 4C, D). These 'supplementary' denticles can be recognized because the spacing and/or characteristics of the denticles differ from those in the rows which characterize the setal type. They are also seen on setulate setae.

Where setae are not crowded together it is relatively easy to work out the disposition of denticles or setules and hence assign a seta to a category or type. However, in dense, complex setal fields, such as those found on the inner/anterior faces of the maxillipeds in various balanomorph species it is often extremely difficult to work out the setal structure because the view of a particular seta may be obscured by other setae. It would be possible to isolate individual setae for study on the rami of the captorial cirri of the larger cirripedes, but it would be difficult in the complex setal fields on the maxillipeds. In such fields, setae are often found which are intermediate between defined setal types, as one setal

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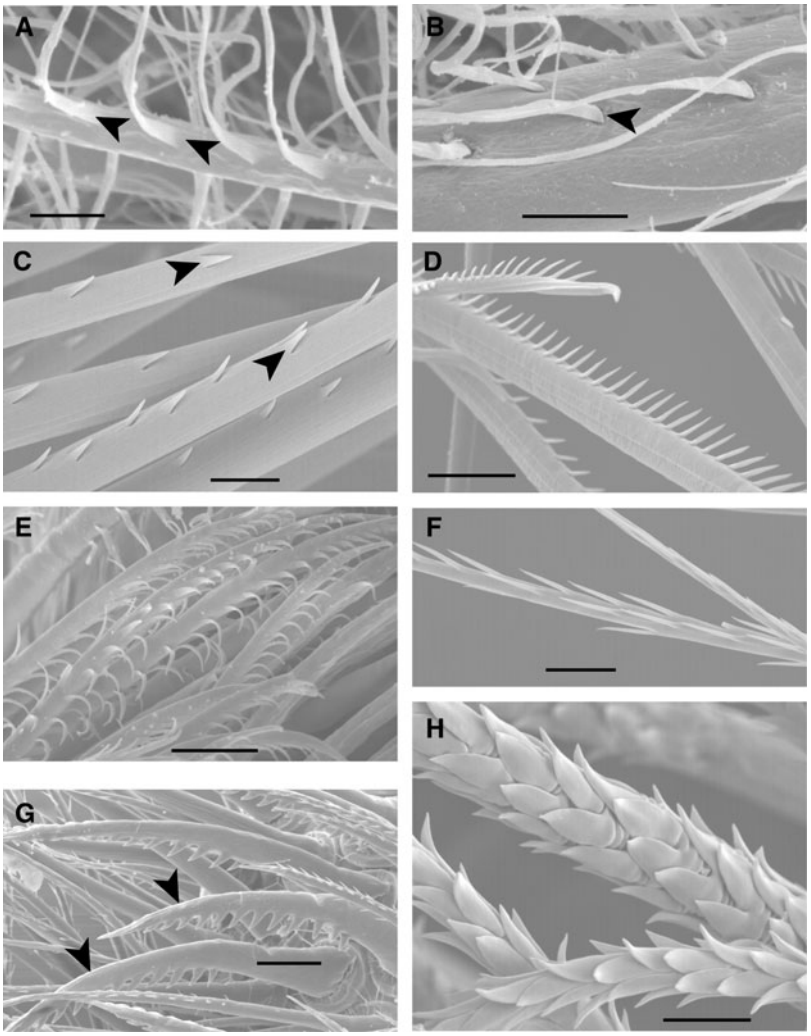


Fig. 3. The variety of setules and denticules arising from the setal shaft. (A) *Tesseropora rosea*, part of the shaft of a Type 3b, setulate seta on the posterior border of the coxopodite of cirrus 1. The arrows indicate the setules arising seamlessly from the shaft; (B) *Heteralepas microstoma*, part of the shaft of a Type 3a, setulate, seta found on the exopodite of cirrus 1. The arrow indicates a setule arising from a pit in the setal shaft; (C) *Pollicipes pollicipes*, part of the shaft of a seta from the ramus of cirrus 2. Arrows indicate the seamless origin of the denticles; (D) *Ibla quadrivalvis*, part of the shaft of a Type 2a3 seta on a ramus of cirrus 4, with rigid needle-shaped denticles; (E) *Balanus perforatus*, shafts of setae, on the exopodite of cirrus 1, with flexible denticles; (F) *Balanus balanus*, part of the shaft of a seta on the anterior face of a ramus of cirrus 4, with long, slender needle-shaped denticles; (G) *Chthamalus antennatus*, bidentate Type 2d3 setae (arrows), with large conical denticles, on the tip of the endopodite of cirrus 2; (H) *Balanus nubilus*, part of the shaft of a Type 2e3 seta from the median face of the mandibular palp, with broad, flattened (foliate) denticles. Scale bars: (A) 2 μm; (B) 5 μm; (C) 10 μm; (D) 10 μm; (E) 10 μm; (F) 10 μm; (G) 20 μm; (H) 5 μm.

type will grade into the adjacent type without a sharp boundary.

Description of setal types

In the 33 barnacle species examined 43 setal types have been described. These have been allocated to five Groups:

Group 1, simple: shaft without setules or denticles. A pore may be present at or close to the setal tip.

Table 2 summarizes the characteristics of the setal types comprising Group 1;

Group 2, denticulate: shaft with denticles usually in a row or rows distal to the annulus. A pore may be present at the setal tip.

Table 3 summarizes the characteristics of the setal types comprising Group 2.

In considering the features used to characterize the Group 2 setal types in Table 3 some qualifications must be made.

It is usually easy to determine from an SEM image whether or not a setal shaft is stiff or flexible but sometimes there may be an element of doubt. In most rows of denticles along the setal shaft the denticles are aligned in a single line but in Types 2a8 and 2a9 the denticles are in pairs. In Type 2a7 there is an irregular double row of denticles which may change to a single line towards the setal tip. The use of the term 'small' to describe a denticle is a relative not an absolute term: a small denticle has a length considerably less than the diameter of the setal shaft. Denticles defined as 'stout' would have a round or oval section at the base. In Type 2a6 (+* in Table 3) the denticles are relatively long and taper to a fine point. In Type 2b2 and Type 2c2 the denticle is much shorter and blunt. The Types 2d2, 2d3 and 2d4 setae all have quite distinct denticular shapes illustrated in Figure 10H. The morphology of Type 2d3 setae is an important characteristic in *Chthamalus* taxonomy and there are several sub-types. In *C. stellatus* (Figure 10E; +** in

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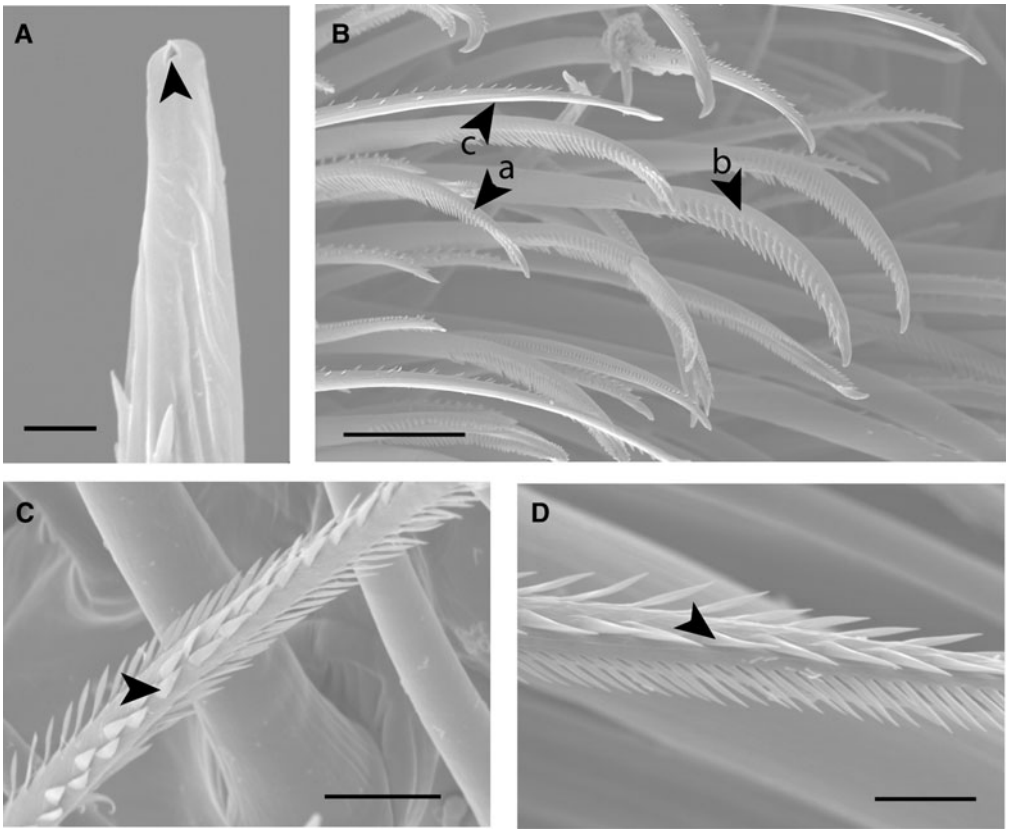


Fig. 4. (A) *Pollicipes pollicipes*, distalmost region of a Type 2f2 seta from the anterior face of a ramus of cirrus 4 showing the bifid tip and pore; (B) *Pollicipes pollicipes*, setae on the endopodite of cirrus 1: (a) Type 2d1 seta with denticles on the inner face of the curved shaft; (b) Type 2d2 seta; (c) Type 2a7 with denticles on the outer face of the curved shaft; (C) *Scalpellum scalpellum*, part of the shaft of a Type 2c1 seta on the exopodite of cirrus 1. Arrow indicates supplementary denticles; (D) *Lepas anatifera*, part of the shaft of a bipectinate seta, Type 2c1, on the exopodite of cirrus 2. Arrow indicates supplementary denticles. Scale bars: (A) 2 μm; (B) 50 μm; (C) 10 μm; (D) 10 μm.

Table 3) the distal region of the Type 2d3 setae resembles the Type 2d1 setae of *C. montagui* (Figure 10B). Type 2e2 (single*** in Table 3) has multiple single rows of small denticles around the setal shaft (Figure 11B).

Group 3, Setulate: shaft with setules.

Type 3a: setules arising from pits or sockets in the shaft (Figure 3B).

3a1: setules distributed over 180° of the shaft circumference.

3a2: setules arising in 2 irregular rows on opposite sides of the shaft (Figure 12A).

Type 3b: setules arise from the shaft without discontinuity (Figure 3A).

3b1: setules distributed over 180° of the shaft circumference (Figure 12B).

3b2: setules arising in 2 zones on opposite sides of the setal shaft.

The arrangement of the setules often changes as the setal shaft tapers towards the tip. Proximally the setules may be distributed over half the circumference or in two zones on opposite sides of the setal shaft (Figure 12A). Distally, as the shaft tapers, the setules are often arranged in single rows along

Table 2. Characteristics of setal types in Group 1: simple Setae.

		Stiff	Flexible	Prox. TS	Distal TS	Spiral twist	Curved	Pore	Figure
1a	Length/basal diameter >20								
	1a1	+	−	C	C	−	+/−	−	5A
	1a2	+	−	C	A	+*	−	−	2H
	1a3	−	+	C	C	−	−	−	5B
	1a4	−	+	C	C	−	−	Terminal	2J
1b	Length/basal diameter <20								
	1b1	+	−	C	C	−	−	−	2B
	1b2	+	−	C	C	−	−	Sub-terminal	2I, 5C
	1b3	+	−	A	A	+	−	Sub-terminal	2G
	1b4	+	−	C	C	−	+	−	5D
	1b5	+	−	C	C	−	−	Terminal**	5E, 5F

A, angular; C, circular; Prox., proximal; TS, transverse section; *, spiral twist distal to annulus; **, in *Chthamalus* spp. setal shaft projects beyond pore on one side.

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Table 3. Characteristics of setal types in Group 2: denticulate setae.

	Shaft	Denticle arrangement			Denticle characteristics						Figures
	Rigidity	Spacing	Prox/dist	Rows	Small	Stout	Needle	Fine taper	Foliate	Rigidity	
2a Denticles in a row along one side of the setal shaft (Figure 6A, B)											
2a1	Stiff	>	−/+	Single	+	−	−	−	−	Stiff	7A
2a2	Stiff	>	−/+	Single	−	−	+	−	−	Stiff	7B
2a3	Stiff	<	−/+	Single	−	−	+	−	−	Stiff	7C, 7D
2a4	Stiff	>	−/+	Single	−	−	+	−	−	Stiff	7E
2a5	Stiff	<	−/+	Single	−	−	−	+	−	Flexible	7F
2a6	Flexible	<	−/+	Single	−	+*	−	−	−	Flexible	7G
2a7	Stiff	>	−/+	Double	+	−	−	−	−	Stiff	8A
2a8	Stiff	<	−/+	Double	+	−	−	+	−	Either	8B, 8C
2a9	Stiff	>	+/+	Double	+	−	−	−	−	Stiff	8D
2b Denticles in two rows along setal shaft at 180° (Figure 6C)											
2b1	Stiff	>	−/+	Single	+	−	−	?	−	Stiff	2D
2b2	(Flexible)	>	−/+	Single	−	+	−	−	−	Stiff	8E
2b3	(Flexible)	<	−/+	Single	−	−	−	+	−	Stiff	8F
2b4	Stiff	>	−/+	Single	−	−	+	−	−	Stiff	8G
2b5	(Flexible)	<	−/+	Single	−	−	−	+	−	Flexible	8H
2c Denticles in two rows along setal shaft at 90° (Figure 6D, E)											
2c1	Stiff	<	−/+	Single	−	−	−	+	−	Stiff	9A
2c2	Stiff	<	−/+	Single	−	+	−	−	−	Stiff	9B
2c3	Prox. st/dist. fl.	<	−/+	Single	−	−	−	+	−	Flexible	9C
2c4	Stiff	>	−/+	Single	−	−	+	−	−	Stiff	9C, 9D
2d Denticles in two rows oriented parallel to median plane of setal shaft (Figure 6F)											
2d1	Stiff	<	−/+	Single	−	−	−	+	−	Stiff	10A, 10B, 10Ha
2d2	Stiff	<	−/+	Single	−	+	−	−	−	Stiff	10D, 10Hb
2d3	Stiff	<	−/+	Single	−	+**	−	−	−	Stiff	3G, 10E, 10Hc
2d4	Stiff	<	−/+	Single	−	+	−	−	−	Stiff	10F, 10G, 10Hd
2e Denticles arranged around the setal shaft											
2e1	Flexible	na	−/+	na	−	−	−	+	−	Either	11A
2e2	Flexible	>	−/+	Single***	+	−	−	−	−	Stiff	11B
2e3	Flexible	na	−	na	−	−	−	−	+	Stiff	3H, 11C
2f Denticles concentrated in the distalmost region of shaft. Terminal pores may be present. Bifid tip in 2f1 & 2f2											
2f1	Stiff	na	−/+	na	−	−	−	+	−	Stiff	11D
2f2	Stiff	na	−/+	na	+	−	−	−	−	Stiff	11E
2f3	Flexible	na	−/+	na	−	−	−	−	+	Flexible	11F

+, feature present; −, absent; (Flexible), flexibility uncertain; > spacing greater than denticle length; < spacing less than denticle length; na, not applicable; prox/dist, proximal or distal; +*, +**, single, ***, see text.

opposite sides of the shaft. The annulus is rarely observed. Some setulate setae have setules confined to the distal region of the shaft (Figure 12B), but usually setules extend proximally almost to the socket (Figure 12A).

Group 4, plumodenticulate: shaft with setules proximal to the annulus and denticles distal to the annulus.

Type 4: only one type was seen (Figure 12C).

Group 5, aesthetascs: slender shaft usually twisted distal to the annulus (Figures 12D & 12E).

Type 5: these slender setae appear flattened in cross-section distal to the annulus, having a thin shaft wall (Figure 12F) and often a terminal pore (Figure 12G). The twisted appearance is not a fixation artefact as the twisted shaft is clearly visible in fresh material.

Distribution of setae on the limbs and prosoma in the barnacles studied

With the exception of the two *Ibla* species, setae were found only on the mouthparts, cirri and penis. In *I. quadrivalvis* and *I. cumingii* denticulate setae (Type 2b3) were also found on the prosoma (Figure 13A) and on the ventral cone situated between the bases of the cirri just posterior to the oral cone (Figure 13B). Darwin (1851, p.187) described this structure as a 'conical prominence clothed with bristles' lying 'over the infra-oesophageal ganglion'. There are many gland pores on the lateral faces of this structure that are probably the pores of the sub-oesophageal 'salivary' glands seen in many cirripedes (Bocquet-Védrine & Ovechko, 1960; Walley, 1965). The eolepadines *Leucolepas longa*, *Vulcanolepas parensis* and *Neolepas rapanuii* also have gland pores on a protuberance in a similar position but without setae (Figures 13C & 13D). Darwin (1854) reported setae on the prosoma of *Chthamalus* species. There are processes arising from the prosoma cuticle in *C. montagui* but they do not seem to have a basal socket and are here interpreted as long flexible denticles up to 40 μm in length (Figure 13E). *Anelasma squalicola*, an ectoparasite on sharks, was the only species examined which was found to have no setae, confirming the observations of Johnstone & Frost (1927).

Occurrence of setal types in the barnacle species studied

The presence or absence of the different setal types in the species examined are summarized in Table 4. Some setal

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Table 4. Distribution of setal types across the taxa examined.

Setal type	1a				1b					2a									2b					2c				2d				2e			2f			3a		3b		4	5
	1	2	3	4	1	2	3	4	5	1	2	3	4	5	6	7	8	9	1	2	3	4	5	1	2	3	4	1	2	3	4	1	2	3	1	2	3	1	2		
PEDUNCULATA																																										
Ibla quadrivalvis	■					■			?	■	?	■		■					■	■	■							■				?											■
Ibla cumingii	■					■			?	■	■	■		■					■	?	■							■				?											?
Anelasma squalicola																																										
Heteralepas microstoma	■					■												■	■					■									■					■			■	■	■
Lepas anatifera	■					?		■			■						■		■					■				?					■										■
Lepas pectinata	?					■		■			■						■		■					■				■					■										■
Dosima fascicularis	■					■		■		■						■	■		■		■			■								■		?									■
Conchoderma auritum	?				■	■		■		?						■			■		■			■				■				■		?									■
Leucolepas longa	■	■					■								■		?		■		■			■	■	■						■		?									■
Neolepas rapanuii	?	■					■								■		?		■		?			■	■	■						?		?									■
Vulcanolepas parensis	?	■					■								■		■		■		■			■	?	■						?		?									■
Pollicipes pollicipes	?					■			■	■						■	■		■					■				■	■		■	■	?	?	■	■							■
Scalpellum scalpellum	?					■											■		■					■								■											■
BALANOMORPHA																																										
Eochionelasmus ohtai	■					■			■										■		■			■								■		?									■
Catomerus polymerus	■					?			?			■				■	■		?		■			?							■	■		■	■	?							■
Octomeris angulosa	?					?			?			■				■	?		?		?			■				■			■	?	?	?	■	■						?	■
Chthamalus stellatus	?					■			■	■							■		■	■	■		■	■						■		■	?			■	■	■			■	■
Chthamalus montagui	?					■			■	■							■		■	?	■		■	■				■				?	?			?	■	■			■	■
Chthamalus antennatus	?					■			■	■							■		?	?	■		■	■						■		■	?			?	■	?			■	■
Tetraclitella purpurascens	?					■			■	■		■							■		■			■				■	■			■	?	■		■					■	■
Tesseropora rosea	?					■			■	■		■				■	■		■		■			■				■			■	■	■		■				■			■
Tetraclita squamosa	■					■			■	■						■	?		■		■			■				■	■			■		■		■			■	■		■
Chirona hameri	?					■			■								■		■		?			?								■	?	■					■			■
Austrominius modestus	■		■	■		■			■			■	■						■		■	■		■			?					■		■					■	■	?	■
Semibalanus balanoides	■		■	■		■			■			?	■						■			?		■			■					■		■					?	■	■	■
Semibalanus cariosus	■		■	■		?			■			■		■					■			?		■			■					■		■					■	?		■
Balanus balanus	?		■			■			■										■					■			■					■		■					■	?		■
Balanus crenatus	■		■	■		■			■				■						■			■		■			■		■			■		■					?	■		■
Balanus nubilus	?		■			■			?			■	■						■		?			■			■					■		■					■	?		■
Balanus improvisus	?		■	?	?	■			■			?	?						■	■		■		■			■					■		■					■	?	?	■
Perforatus perforatus	■		■	?		■			■		?	?	?	?			?		■	?	?	?	?	■	?		■		■			■		■					■	?	?	■
Megabalanus psittacus	■		■	?		■			?			■							■		■			■			?	?				■		■					■	?	?	■
Megabalanus tintinnabulum	?				■	?			?	■									■		?			■	?			■	■			■		?					■	?	?	■

■ setal type recorded; ?, setal type not seen but may be present; no symbol, setal type thought to be absent.

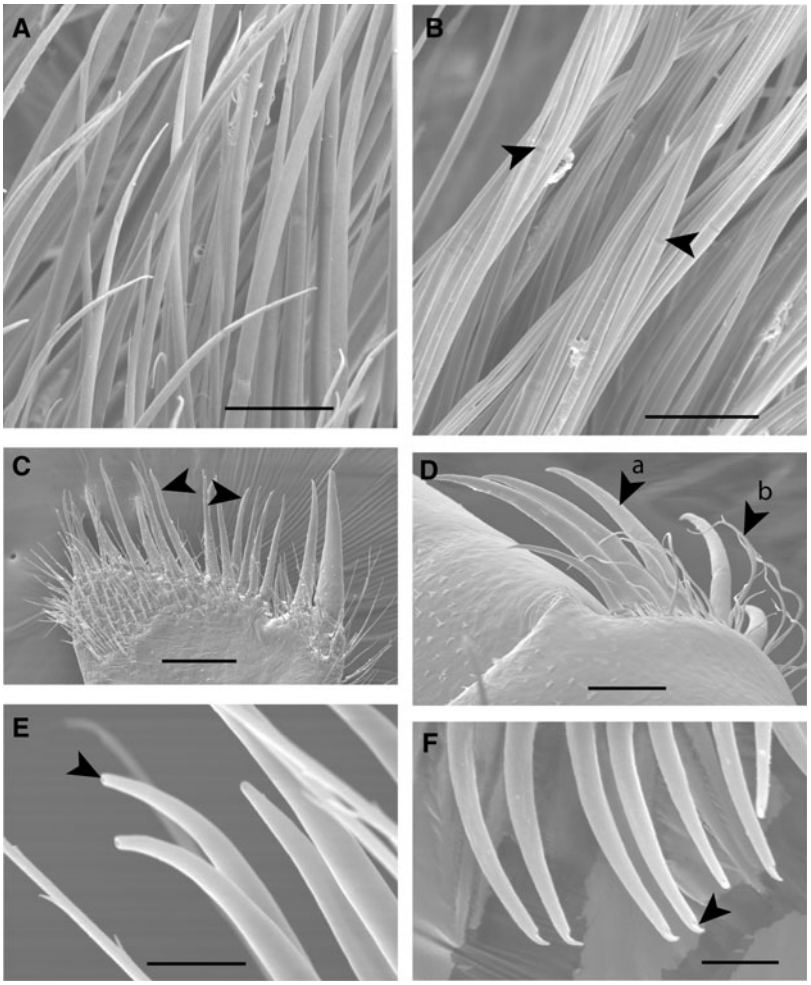


Fig. 5. Simple setae. (A) *Semibalanus balanoides*, Type 1a1 setae on the endopodite of cirrus 3; (B) *Balanus crenatus*, Type 1a3 setae on the distal face of maxilla 2. Arrows indicate annuli; (C) *Tesseropora rosea*, Type 1b2 setae on distal border of maxilla 1; (D) *Dosima fascicularis*, Type 1b4 setae (a) together with Type 5 setae (b) on the posterior distal border of a ramus segment of cirrus 4; (E) *Balanus balanus*, tips of Type 1b5 setae on the distal border of maxilla 1 showing terminal pores (arrow); (F) *Chthamalus stellatus*, tips of Type 1b5 setae on the distal border of maxilla 1 showing asymmetrical cuticular extension beyond terminal pores (arrow). Scale bars: (A) 20 μm; (B) 20 μm; (C) 100 μm; (D) 50 μm; (E) 5 μm; (F) 5 μm.

types are widespread but others seem to be restricted to particular species or taxonomic groups. Types that are recorded as common to different species fall into several distinct subtypes varying in the spacing, length or characteristics of the denticles. These finer variations could prove useful in differentiating genera or species.

The most commonly occurring setal types were 1b2, 2b1, 2c1, 2e1 and 5. Type 1b2 (Figures 2I & 5C) is found only along the distal edge of the first maxilla. In some of the largest examples the basal socket and sub-terminal pore are difficult to see and in *Lepas anatifera* (Høeg *et al.*, 1994) and *P. pollicipes* the dorsalmost projections on the edge of the first maxilla seem to be large denticles rather than setae. (The Type 1b3 setae of the Eolepadidae also found on the distal edge of the first maxilla can be regarded as homologous with Type 1b2.) The sub-terminal pores in these setae suggest a chemo-sensory function (Høeg *et al.*, 1994).

Type 2b1 setae are found on the lateral faces of the mandibles (Figure 2D) and sometimes on the first maxillae. These were the only cirripede setae that were found to have infracuticular articulation. The size and spacing of the lateral denticles and the characteristics of the setal shaft vary between species. In order to compare Type 2b1 setae from different species it is important to look at setae from a similar location in the setal field. Towards the edge of the setal field the denticulation may become sparser or even disappear altogether, particularly where they grade into adjacent fields of slender denticles.

Type 2c1 setae (Figure 9A) are found on the rami of cirri 1–3, often as part of the complex fields of setae on the median faces of the rami. They were not found on the anterior faces of cirri 4–6 forming part of the cirral net.

Type 2e1 setae are found on both limbs and mouthparts but very commonly on maxilla 2 (Figure 11A).

Type 5 setae are usually found on the posterior distal borders of the ramus segments of cirri 4–6, in close association with whatever setal type is characteristic of this position in a given species (Figures 5D & 12D–G). They are also found along the length of the antenniform rami of cirri 1–3 and on the penis. The precise morphology varies from species to species. The external morphology suggests that these may be sensory setae and their possible function is discussed below.

Certain setal types occur in particular species or taxonomic groups (see Table 4). The two *Ibla* spp. are characterized by Type 2a setae (Table 3; Figure 6A). Those setae with two rows of denticles that are present are Type 2b3 (Table 3;

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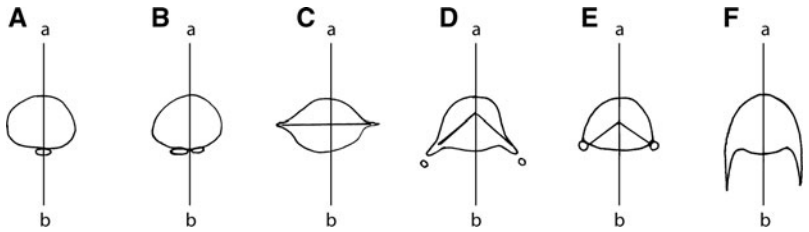


Fig. 6. Diagram illustrating the alignment of the rows of denticles on the setal shaft in Types 2a, 2b, 2c and 2d. The line (a)–(b) represents the median plane of the setal shaft. (A) Types 2a1–2a6; (B) Types 2a7–2a9; (C) Types 2b1–2b5; (D) Types 2c1–2c3; (E) Type 2c4; (F) Types 2d1–2d4.

Figures 6C & 8F) in contrast to other cirripedes where Type 2c1 (Table 3; Figures 6D & 9A) is the most common type. *Heteralepas microstoma* is unique in having Type 2a9 setae (Figure 8D), and among the pedunculates examined in having setulate, Type 3a, and plumodenticulate, Type 4, setae on the exopodite of cirrus 1. The three members of the Eolepadidae examined, *L. longa*, *N. rapanuii* and *V. parensis*, are characterized by 5 setal types: Types 1a2, 1b3, 2a6, 2c2

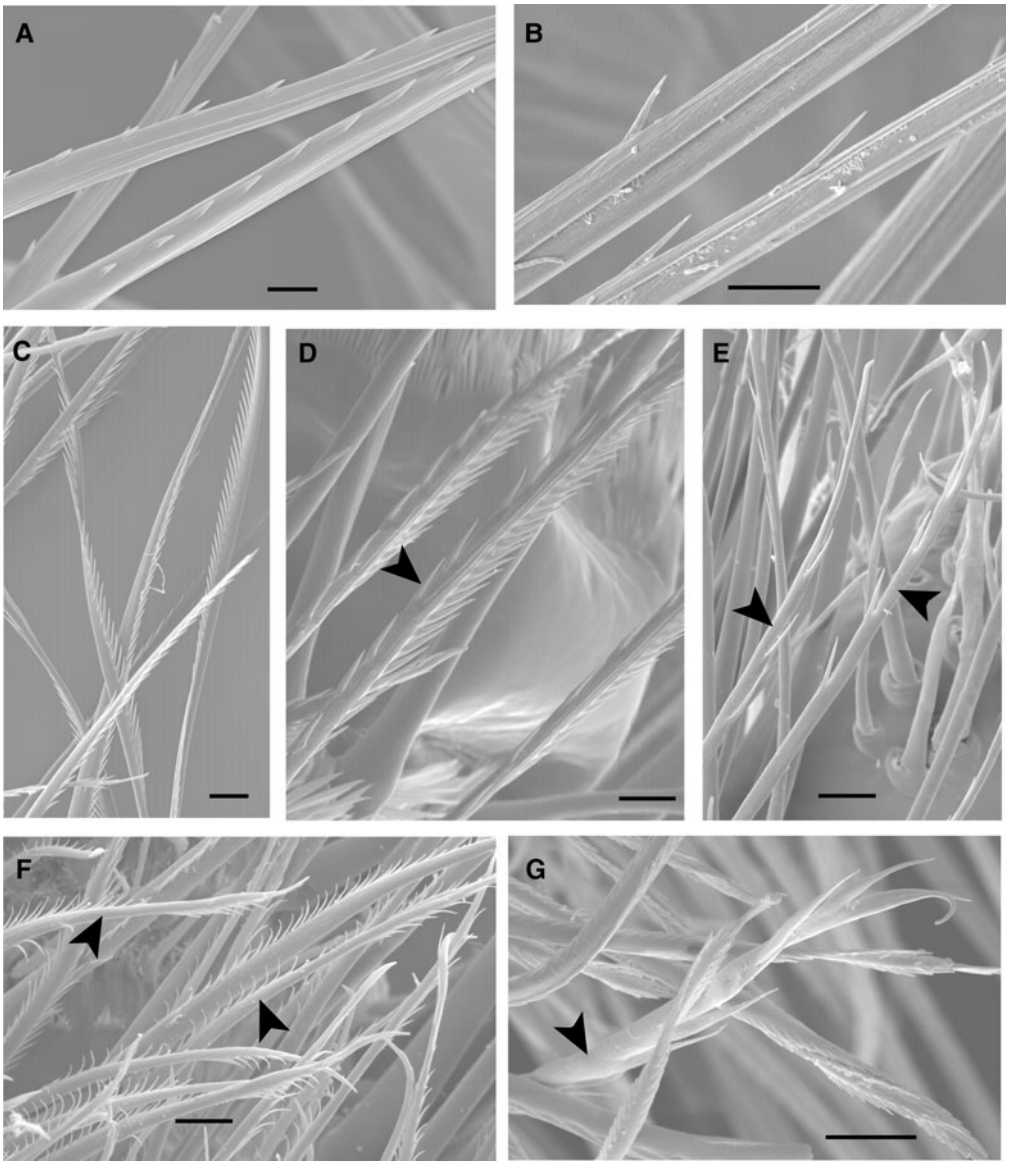


Fig. 7. Examples of Types 2a1–2a6 setae. (A) *Tetraclitella purpurascens*, part of the shaft of a Type 2a1 seta from the anterior face of a ramus of cirrus 5. Note the small denticles in a single row; (B) *Lepas anatifera*, part of the shaft of Type 2a2 setae on the anterior face of a ramus of cirrus 4. Note the long slender needle shaped denticles in a single row; (C) *Balanus nubilus*, Type 2a3 setae on the anterior face of the rami of cirrus 4. Note the single row of regularly arranged needle shaped denticles; (D) *Tetraclitella purpurascens*, Type 2a3 setae with supplementary denticles (arrow) on the exopodite of cirrus 1; (E) *Balanus crenatus*, Type 2a4 setae (arrows) on the anterior face of a ramus of cirrus 3. Note the well-spaced distally directed needle-shaped denticles; (F) *Ibla cumingii*, Type 2a5 setae (arrows) on the proximal region of the endopodite of cirrus 1; (G) *Neolepas rapanuii*, Type 2a6 setae (arrow) on the exopodite of cirrus 2. Scale bars: (A) 10 μm; (B) 20 μm; (C) 20 μm; (D) 10 μm; (E) 10 μm; (F) 10 μm; (G) 10 μm.

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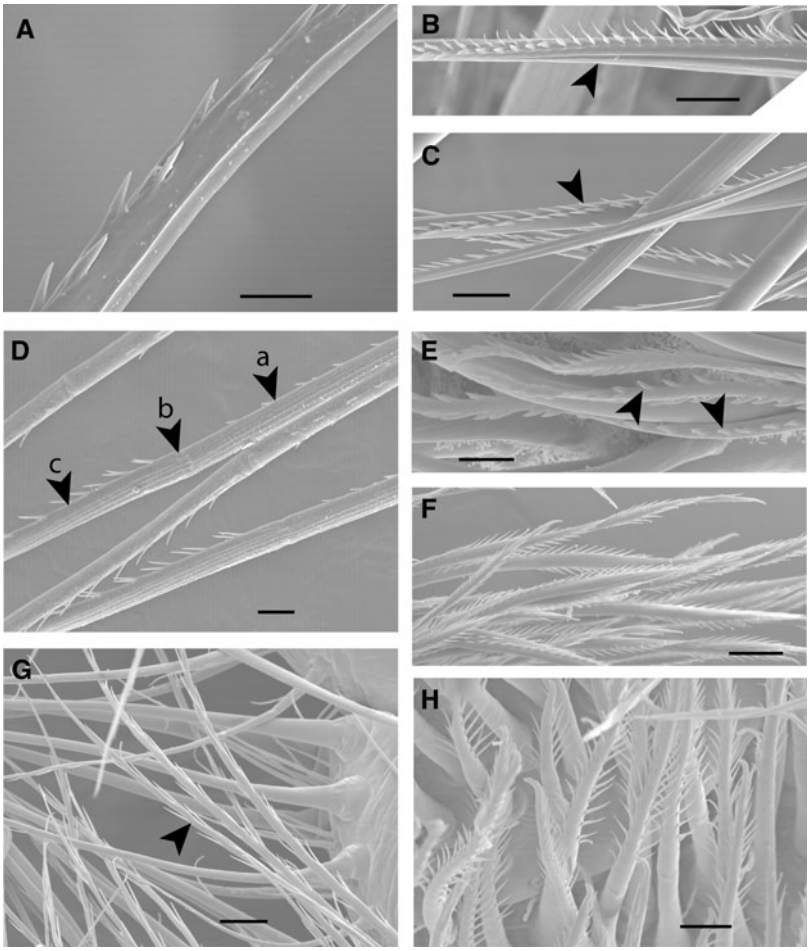


Fig. 8. Examples of Type 2a7, 2a8 and 2a9 setae, and Type 2b setae. (A) *Tesseropora rosea*, part of the shaft of a Type 2a7 seta on the anterior face of a ramus of cirrus 4. Note the irregular double row of denticles; (B) *Chirona hameri*, part of the shaft of a Type 2a8 seta (arrow) on the anterior face of a ramus of cirrus 4. Note the double row of slender denticles; (C) *Scalpellum scalpellum*, Type 2a8 setae (arrow) on the anterior face of a ramus of cirrus 4; (D) *Heteralepas microstoma*, Type 2a9 setae on the anterior face of a ramus of cirrus 5: (a) proximal region of seta, (b) annulus and (c) distal region of seta; (E) *Ibla quadrivalvis*, Type 2b2 setae on the exopodite of cirrus 1. Arrows indicate the stout denticles; (F) *Ibla cumingii*, Type 2b3 bipectinate setae on the exopodite of cirrus 1 with two rows of slender needle shaped denticles; (G) *Balanus crenatus*, Type 2b4 seta (arrow) on the anterior face of a ramus of cirrus 4. Note the long, slender, distally directed denticles; (H) *Chthamalus antennatus*, Type 2b5 setae on proximal segments of the exopodite of cirrus 1. Note the long flexible denticles. Scale bars: (A) 20 μm; (B) 10 μm; (C) 20 μm; (D) 20 μm; (E) 20 μm; (E) 10 μm; (F) 20 μm; (G) 20 μm; (H) 10 μm.

and 2c3 (Figures 2H, 2G, 7G, 9B & 9C). The Type 2c2 and 2c3 setae comprise the prominent field of anteriorly directed setae on the proximal podomeres of cirrus 1 and cirrus 2. The Type 2c3 setae are up to 1 mm long. These setae are overlain on the median face of the ramus by the Type 2c2 setae.

Pollicipes pollicipes, *C. polymerus*, *O. angulosa*, *T. rosea*, *T. squamosa* and *T. purpurascens* have a number of setal types in common. They all have Type 2a7 or 2a1 (Figures 8A & 7A) on cirri 3–6 comprising the cirral net (Type 2a1 may have arisen by simplification of Type 2a7). *P. pollicipes*, *C. polymerus* and *O. angulosa* all have Type 2f1 setae (Figure 11D) on the posterior distal borders of the podomeres of the rami of cirri 3–6. All six species have Type 2f2 setae (Figure 11E) comprising the setal tufts located on the anterior faces of the rami between the bases of the captorial setae. *P. pollicipes*, *C. polymerus*, *O. angulosa* and *T. rosea* all have the robust Type 2d4 setae (Figure 10F–H) in various locations on cirri 1–3. *P. pollicipes* also has Type 2d2 setae (Figure 10C, H) on the exopodite of cirrus 3. Type 2d2 setae are found on the endopodite of cirrus 3 in *T. purpurascens* (Figure 10D), *T. squamosa* and *M. tintinnabulum*.

Several setal types are absent from pedunculates but are found in balanomorphs. With the exception of *H. microstoma* setulate setae were not found in pedunculates but were found in most balanomorphs, the exceptions being *Eochionelasmus ohtai*, *C. polymerus*, *O. angulosa* and *T. purpurascens*. However, whereas the tetraclitids and the balanids have Type 3b setae (Figure 3A), the *Chthamalus* spp. have Type 3a (Figures 3B & 12A). In those balanomorphs that have setulate setae they are universally found fringing the posterior border of the coxopodite of cirrus 1. In the following balanids, *Balanus* spp., *Semibalanus* spp., *Perforatus perforatus* and *Austrominius modestus* there is a field of very long, flexible setulate setae arising from the base of cirrus 3 (Figure 14A) which in the living animal would hang down into the mantle cavity. This setal field is not present in *Chirona hameri*. *Megabalanus psittacus* has a flange with setulate setae at the base of cirrus 3 but it is not such an elaborate shape as the crescentic structure seen in *M. tintinnabulum* (Figure 14B) (see Darwin 1854, plate XXV, figure 1). Type 1b5 setae (Figure 5E) were also absent from the pedunculates with the exception of *P. pollicipes*. They were found in all the balanomorphs examined with the exception of *Balanus nubilus* (but see Høeg *et al.*, 1994), *M. psittacus* and *M. tintinnabulum*. Another setal type, Type 2e3 (Figures 3H & 11C),

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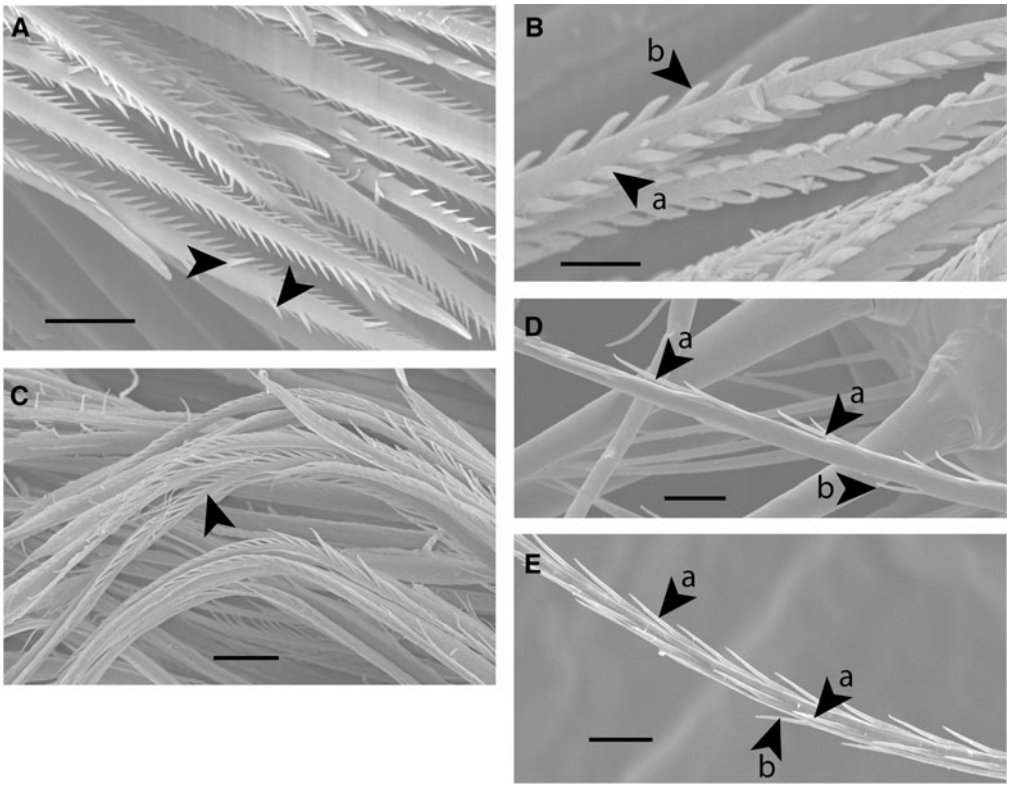


Fig. 9. Examples of Type 2c setae. (A) *Pollicipes pollicipes*, Type 2c1 setae on the exopodite of cirrus 1. Arrows indicate randomly arranged supplementary denticles; (B) *Leucolepas longa*, part of the shaft of a Type 2c2 seta from a ramus of cirrus 2. Note the 2 rows of stout denticles (a) and the regularly arranged supplementary denticles (b); (C) *Neolepas rapanuii*, distal regions of Type 2c3 setae on proximal podomeres of the endopodite of cirrus 1. The arrow indicates the flexible shaft with flexible denticles; (D) *Balanus crenatus*, Type 2c4 seta on the anterior face of a ramus of cirrus 4: (a) long, slender, distally directed denticles on either side of the face of the seta and (b) supplementary denticle on the opposite face of the seta; (E) *Perforatus perforatus*, part of the shaft of a Type 2c4 seta on the anterior face of a ramus of cirrus 6: (a & b) as for (D). Scale bars: (A) 20 μm; (B) 5 μm; (C) 10 μm; (D) 10 μm; (E) 10 μm.

was found on the median face of each mandibular palp in the balanoids and coronuloids but observations on the pedunculates were not adequate to determine whether or not this setal type was present. However Høeg *et al.* (1994) found this type in *Pollicipes cornucopia* (= *P. pollicipes*) but not in *L. anatifera*. In the same location in *Chthamalus stellatus* there is a field of specialized setae but of a different type, Type 2f3 (Figure 11F).

DISCUSSION

The classification proposed here, provides a framework for describing setal structure in cirripedes. Assignment to a type, within a three level scheme, is based on the presence or absence of denticles and setules on the setal shaft, their disposition on the setal shaft and their characteristics. A difficulty with the scheme is in finding sufficient names to describe the great variety of setal types observed. For this reason code numbers and letters are used which, though not directly descriptive, can be related to photographic or diagrammatic images. The system put forward here can be expanded and modified to accommodate more types as revealed by the study of further species.

Comparison with previous descriptions of setal morphology in cirripedes

Most of the species studied by Anderson & Anderson (1985), Hunt & Alexander (1991) and Høeg *et al.* (1994) were examined in the present study. Thus, it is possible to compare the setal types described by these authors with those described in the present study (see Tables, pp. 19, 20).

Anderson & Anderson (1985) compared the functional morphology of *Tesseropora rosea* and *Tetraclitella purpurascens*. Using optical microscopy they described five types of setae on the limbs and mouthparts. They divided their Type 2 serrulate setae into five sub-types but 9 setal types were seen in those setal fields described as serrulate. Table 5 equates the setal types described in various locations with the setal types seen in the same locations in this study.

Hunt & Alexander (1991) studying feeding in *Tetraclita squamosa* described 10 setal categories based on those of Anderson & Anderson (1985). It was not possible to equate all their types to those described here but where comparisons were possible they are set out in Table 6. Høeg *et al.* (1994) used SEM to describe the major denticles and setae on the mouthparts of three pedunculate species and three balanomorph species. They devised a classification scheme with six categories. Category 1, denticles, are not setae as defined here or by previous authors but some of their 'denticles' probably are setae. Category 6, stub setae, are not setae either but the ducts of labial glands opening on the second maxillae (Walley, unpublished data). The types and sub-types observed by Høeg *et al.* (1994) are compared with those described here in Table 7.

Chan *et al.* (2008) followed Garm (2004) and used 8 broad categories to describe the setae that they observed in *Ibla cumingii*, *Octolasmis warwickii*, *Capitulum mitella*, *Pollicipes*

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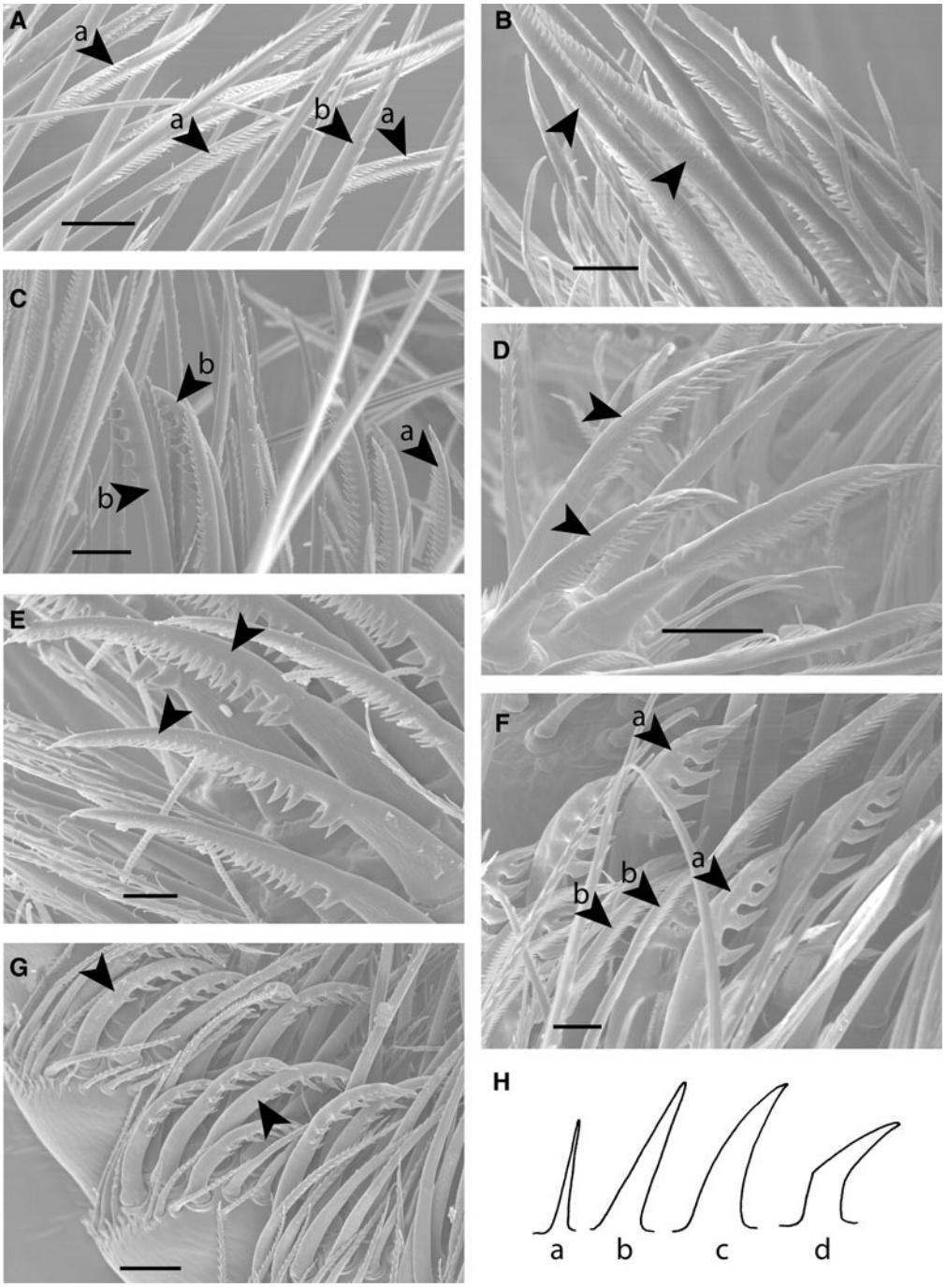


Fig. 10. Examples of Type 2d setae. (A) *Ibla cumingii*, (a) Type 2d1 setae on the exopodite of cirrus 2 and (b) Type 2a2 seta; (B) *Chthamalus montagui*, Type 2d1 setae on distal podomeres of the exopodite of cirrus 2; (C) *Pollicipes pollicipes*, setae on the exopodite of cirrus 3: (a) Type 2d2 and (b) Type 2d4; (D) *Tetraclitella purpurascens*, Type 2d2 setae (arrows) on the rami of cirrus 3; (E) *Chthamalus stellatus*, Type 2d3 setae on the terminal podomere of the exopodite of cirrus 2; (F) *Octomeris angulosa*, setae on the distal podomeres of the exopodite of cirrus 2: (a) Type 2d4 and (b) Type 2d1; (G) *Tesseropora rosea*, Type 2d4 setae (arrows) on the endopodite of cirrus 3; (H) diagram illustrating the morphology of the denticles of Type 2d setae: (a) Type 2d1, (b) Type 2d2, (c) Type 2d3 and (d) Type 2d4. Scale bars: (A) 20 μm; (B) 10 μm; (C) 50 μm; (D) 50 μm; (E) 10 μm; (F) 20 μm; (G) 50 μm.

polymerus, *Tetraclita japonica japonica* and *Megabalanus volcano*. *Ibla cumingii* was examined in the current study. With the exception of *O. warwickii* and *C. mitella*, species closely related to the remaining three species were also studied. Thus it is possible to suggest how their categories equate to those described here (see Table 8). They concluded that the development of the balanomorph form was accompanied by a greater variety of setae and more complex setation patterns, associated with changes in feeding strategy. The observations made in the current study broadly support this conclusion. They assumed that setal functions seen in decapods hold true for cirripedes, for example 'Pappose setae can be used for water current generation and filter-feeding purposes' and they speculated that the plumose setae on the coxopodite of cirrus 1 and cirrus 2 in *Tetraclita* and *Megabalanus* could serve in microfiltration. It seems unlikely that either of these suggestions is correct. The setulate (= plumose) setae are usually positioned where they could not be reached by

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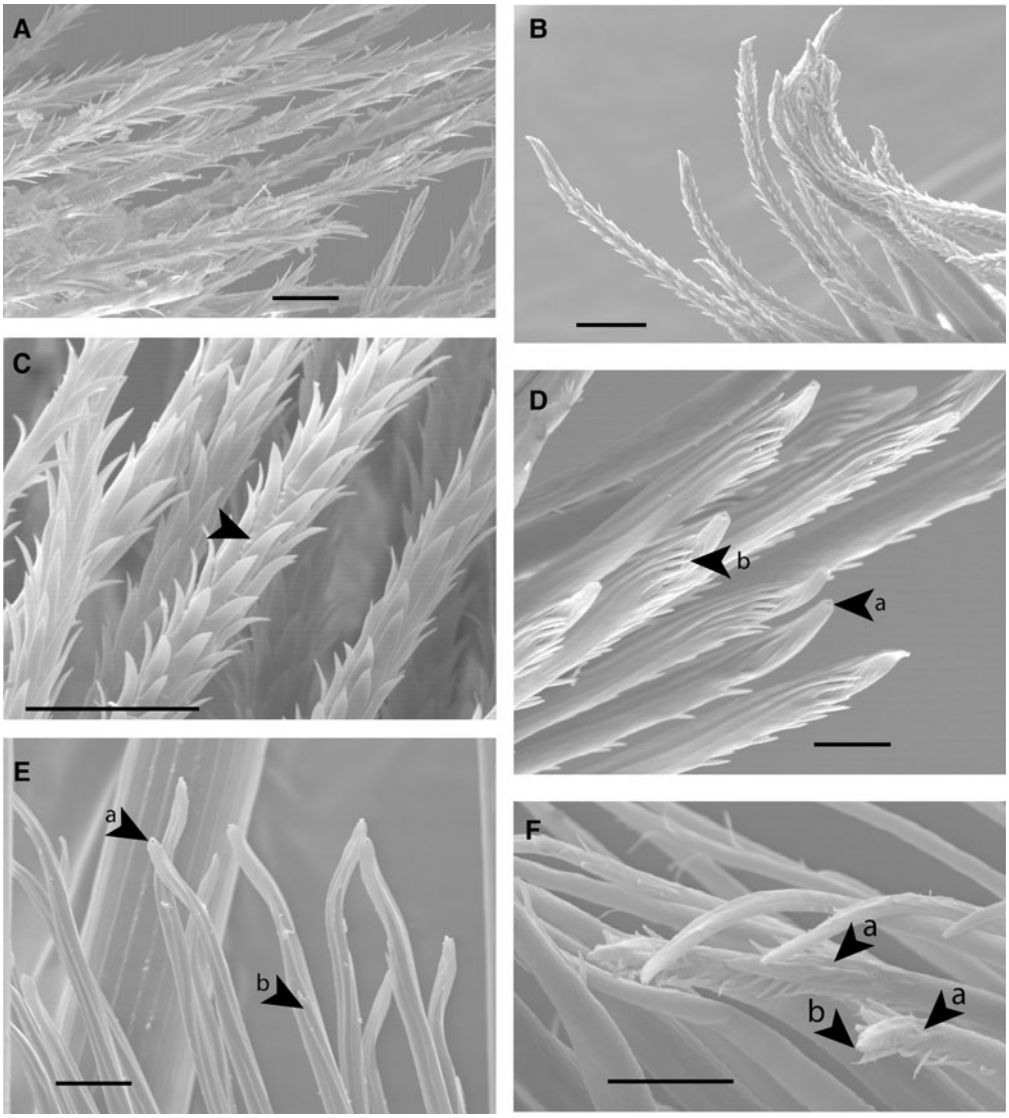


Fig. 11. Examples of Type 2e and Type 2f setae. (A) *Conchoderma auritum*, Type 2e1 setae fringing maxilla 2; (B) *Heteralepas microstoma*, Type 2e2 setae on maxilla 2; (C) *Semibalanus cariosus*, part of the distal region of a Type 2e3 seta from the median face of the mandibular palp. Note the wrinkled setal shaft (arrow); (D) *Pollicipes pollicipes*, Type 2f1 setae on the posterior distal border of a ramus segment of cirrus 2: (a) bifid setal tip with pore and (b) 'collar' of denticles; (E) *Tesseropora rosea*, Type 2f2 setae between the bases of the captorial setae on the anterior face of the rami of cirrus 4: (a) bifid setal tip with pore and (b) sparse denticles on setal shaft; (F) *Chthamalus stellatus*, (a) Type 2f3 seta on the median border of the mandibular palp and (b) pore in setal tip. Scale bars: (A) 20 μm; (B) 20 μm; (C) 10 μm; (D)10 μm; (E) 10 μm; (F)10 μm.

the maxillipeds to transfer food particles to the mouthparts. The generation of water currents seems to result from movements of the whole body and limbs (Crisp & Southward, 1961). It is much more likely that the plumose/pappose (=setulate) setae in the balanomorphs are involved in the direction of the currents within the mantle cavity.

Comparison of cirripede and decapod setal classifications

Garm (2004) is the most recent of a series of authors (Thomas, 1970; Drach & Jacques, 1977; Factor, 1978; Pohle & Telford, 1981; Watling, 1989; Lavalli & Factor, 1992) to tackle the problem of devising a system for the classification of crustacean and more particularly decapod setae. From SEM studies of setae on the mouthparts of seven decapod species, covering a range of families, Garm (2004) defined seven types which he considered to provide an adequate framework for describing the setae that he observed.

There are many points of agreement between the setal groups defined by Garm (2004) and those described in the present study. In both cases the groups are defined with reference to the nature and arrangement of the outgrowths from the setal shaft. The main point of disagreement is in defining when an outgrowth is a denticle and not a setule. Thomas (1970) restricted the use of the term 'setule' to the very long slender outgrowths seen in plumose, pappose and plumodenticulate setae. Thomas described setules as arising from indentations in the setal shaft but does not use this feature—basal articulation—as defining a setule. He uses the term 'denticle' for the other types of cuticular outgrowths referring to setae with such structures as denticulate. Pohle & Telford (1981)

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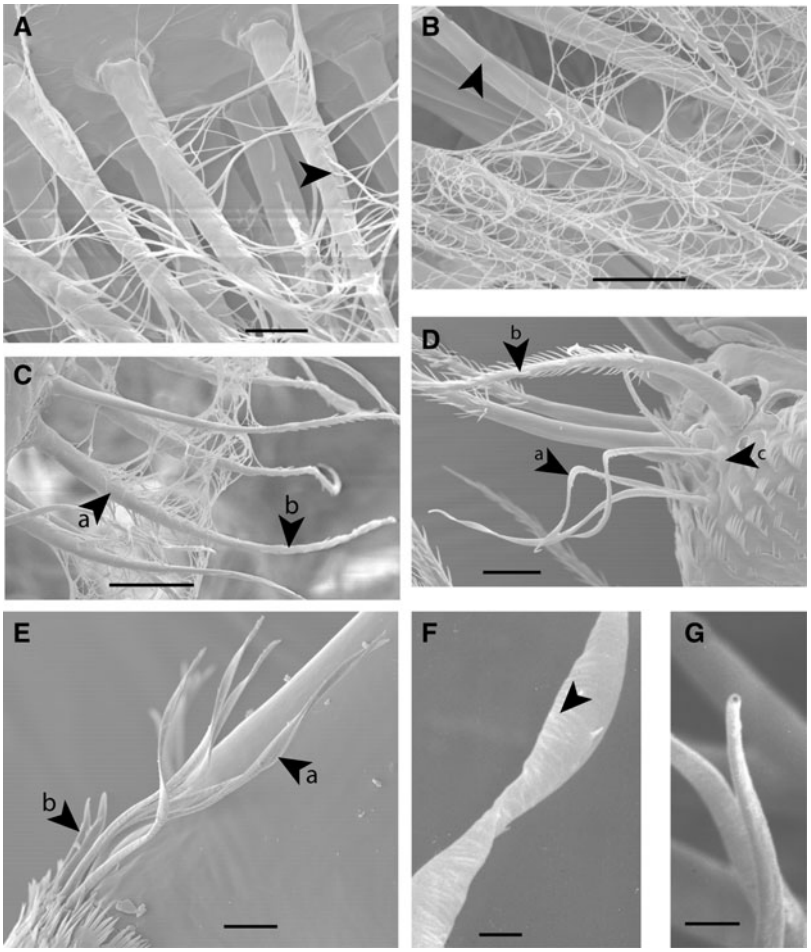


Fig. 12. Examples of Type 3 setulate setae (A & B), Type 4 plumodenticulate setae (C) and Type 5 setae, aesthetascs (D–G). (A) *Chthamalus montagui*, Type 3a2 setae (arrows) on posterior border of the coxopodite of cirrus 2; (B) *Balanus nubilus*, Type 3b1 setae arising from the posterior border of the coxopodite of cirrus 1, showing the origin of the setules distal to the annulus (arrow). The setules are located on one side of the shaft; (C) *Chthamalus montagui*, Type 4, setae along the posterior border of the coxopodite of cirrus I: (a) setulate section of shaft and (b) denticulate section of shaft; (D) *Tetraclitella purpurascens*, Type 5 setae (a) arising from the posterior surface of the endopodite of cirrus 2, together with Type 2c1 setae with supplementary denticles (b). (c) Socket of Type 5 seta; (E) *Tesseropora rosea*, Type 5 setae (a) arising from the posterior distal border of a podomere of a ramus of cirrus 4: (b) associated Type 1b1 setae; (F) *Dosima fascicularis*, part of distal setal shaft. Note the delicate wrinkled cuticle of the shaft wall (arrow); (G) *D. fascicularis*, tip of Type 5 seta showing the terminal pore. Scale bars: (A) 10 μm; (B) 20 μm; (C) 20 μm; (D) 20 μm; (E) 20 μm; (F) 2 μm; (G) 2 μm.

used the terms setule and denticule to describe the two most common cuticular outgrowths from the setal shaft. They clearly differentiated between the long, slender, setules and the shorter tooth or needle-shaped denticules. They state 'While denticule-like structures are direct and continuous extensions from the shaft wall, setules are articulated at their bases'. Examining their images it appears that the 'articulation' takes the form of an indentation in the shaft surface from which the setule arises. As successive authors described setal morphology in decapods, basal articulation became the defining characteristic of a setule rather than its long, slender shape. Watling (1989, figure 1b) shows setules as slender outgrowths from the setal shaft 'of uniform width from base to tip, and forming an articulated or flexible junction with the shaft'. However, he did not figure or describe what he understood by the term 'flexible junction'. Garm (2004) accepted Watling's definition and his figure 4G shows a seta bearing two rows of needle-shaped processes which is said to show a transition from setules to denticles between annulus and setal tip although the structures and their origin from the setal shaft appear the same throughout. Figure 8B in Garm (2004) shows part of a setal shaft with tapering denticles on one side and 'setules' with serrated borders on the opposite side. But the 'setules' show no evidence of articulation—either a socket (as illustrated in Figure 4E) or a 'flexible junction'. Chan *et al.* (2008) adopted Garm's definition of a setule and used his setal categories in their study of setal morphology and cirral setation in cirripedes. They used the term 'setule' for 'any ornament on a seta that has an articulated base irrespective of its morphology'. However, the current study has shown that very few setae in cirripedes have cuticular outgrowths that are articulated at the base. The only setae that were found to have articulated outgrowths were setulate setae in the *Chthamalus* species and *Heteralepas microstoma*. There seems no logical reason for using basal articulation as an overriding defining feature and so the original definition of the term setule as a very long and very slender outgrowth from the setal shaft is used here.

The 'serrulate' category defined by Chan *et al.* (2008), is described as 'slim with a naked proximal part but with small setules distally which can be arranged in rows (normally three) or scattered randomly along the shaft'. Observations in

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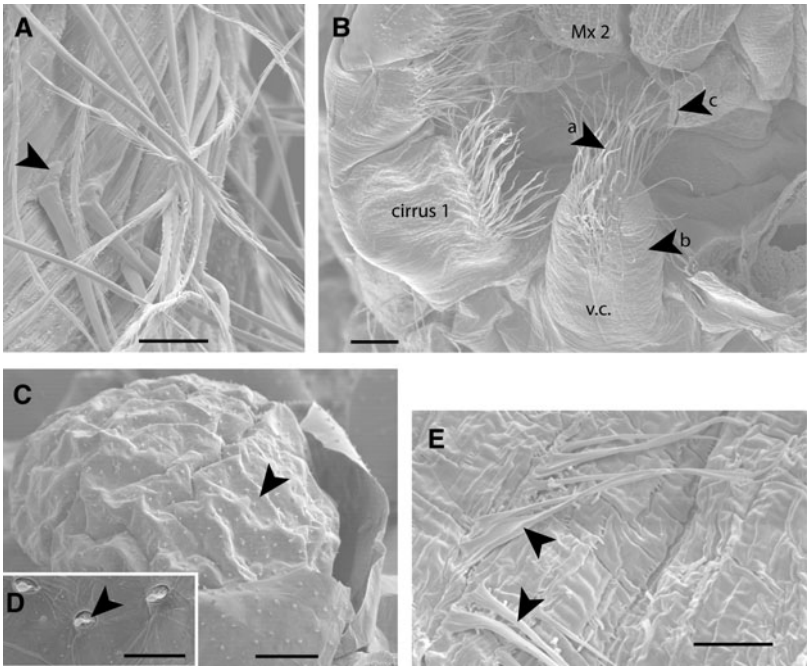


Fig. 13. (A) *Ibla quadrivalvis*, Type 2b3 setae arising from the prosoma cuticle. Note the setal socket (arrow); (B) *Ibla quadrivalvis*, ventral cone (v.c.) between cirri 1 and 2 behind the oral cone: (a) setae on ventral cone, (b) location of gland pores on the lateral face of the ventral cone and (c) opening of the maxillary gland at the base of maxilla 2 (Mx 2); (C) *Leucolepas longa*, ventral cone with pores of sub-oesophageal glands; (D) *Leucolepas longa*, pores of the sub-oesophageal glands (arrow) on the ventral cone; (E) *Chthamalus montagui*, long cuticular processes (arrows) arising from the prosoma cuticle. Scale bars: (A) 20 μm; (B) 100 μm; (C) 100 μm; (D) 20 μm; (E) 10 μm.

the current study do not support this interpretation. Most of the cuticular outgrowths arising from the setal shafts in those setal types encompassed by the 'serrulate' category arise seamlessly from the setal shaft without any discontinuity and are described as denticles in this paper. Furthermore, in cirripedes two rows of denticles rather than three are the norm.

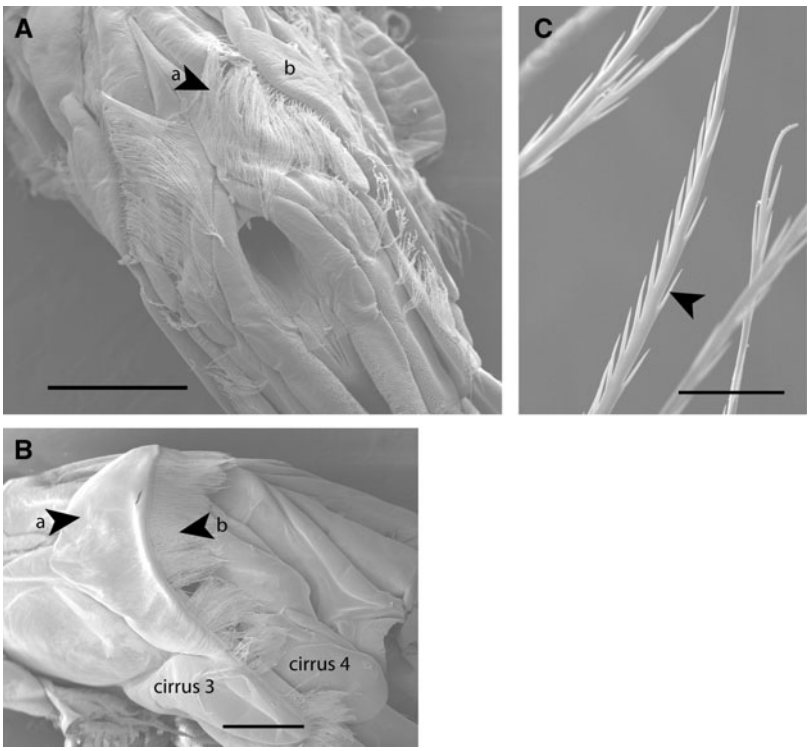


Fig. 14. (A) *Balanus crenatus*, posterior view of thorax. The arrows (a) indicate the very long setulate setae extending from the base of cirrus 3 (b); (B) *Megabalanus tintinnabulum*, dorso-lateral view of thorax showing extension (a) from base of cirrus 3 bearing a fringe of setulate setae (b); (C) *Balanus balanus*, unidenticulate distal region of a Type 2c4 seta on the anterior face of the ramus of cirrus 4. Arrow indicates supplementary denticle. Scale bars: (A) 500 μm; (B) 1 mm; (C) 20 μm.

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The seven setal categories described by Garm (2004) were: pappose, plumose, serrulate, serrate, papposerrate, simple and cuspidate. With regard to basic setal morphology Garm's study confirms that setal articulation in the Decapoda is usually infra-cuticular, only the plumose setae have supra-cuticular articulation. In the Cirripedia, however, setal articulation is usually supra-cuticular. In both groups there are robust, rigid, setae notably on the first maxilla, where the basal attachment does not allow movement relative to the surrounding cuticle. A clearly marked annulus was observed on setal shafts in both groups. Although decapod setae tend to be much more elaborate than cirripede setae, presumably because of the more complex mechanical functions involved in feeding and grooming, it is possible to compare Garm's setal types with the groups described in the present study. The pappose and plumose setae equate to the setulate Group 3. The serrulate setae are said to have three rows of small setules distal to the annulus but Garm (2004) also states 'the articulation with the shaft is often difficult to detect' so perhaps the serrulate setae should be regarded as denticulate in which case the serrulate and serrate setae equate to the denticulate Group 2. The papposerrate equate to the plumodenticulate Group 4. The term 'plumodenticulate' is used in the current study because it is a long established and well understood term as shown in Table 2 of Garm (2004). Both the simple and cuspidate setae equate to the Group 1 simple setae. There is no equivalent to the cirripede Group 5. In cirripedes there are no functional antennae or antennules in the adults which in other Crustacea carry the aesthetascs. However, it seems highly likely that sensory setae fulfilling the same functions as aesthetascs will be found. The setae comprising Group 5 have features in common with those described for aesthetascs in other crustaceans (Derby, 1989), for example, a thin wall to the setal shaft and in some cases a terminal pore. The Group 5/Type 5 setae are located in positions on the limbs where they could pick up chemical signals during feeding (see Results above) or those on the penis could detect pheromones during the search for receptive individuals prior to insemination. It is suggested that these unusual setae are the functional equivalent of aesthetascs.

Some of the serrulate and serrate setae described by Garm (2004) as having three rows of 'setules' or as having 'setules' on the opposite side of the setal shaft from the two rows of denticles (see figure 8B in his paper) could be interpreted as being equivalent to the setae with supplementary denticles seen in cirripedes. It would be possible to use the scheme put forward here to describe decapod setae, for example, the serrate seta (figure 8A in his paper) could be placed in Type 2c1 in the current study. Garm also makes the point that some types, such as the simple setae, are based on shared morphological characteristics that have been convergently acquired through the loss of setules/denticles which also seems to be the case in cirripedes.

Setal morphology, cirripede phylogeny and taxonomy

One of the most important developments in cirripede phylogeny was the adoption of the balanomorph form. There are several aspects of setal morphology that are associated with this change.

RETENTION OF SETAL TYPES

Darwin (1854) suggested that the change from the pedunculate to the sessile barnacles could be envisaged by comparing the anatomy, shell structure, and mode of shell growth of *Pollicipes* and *Catophragmus* (=*Catomerus*). This was further explored by Anderson (1983) who compared the anatomy and functional morphology of *Catomerus polymerus* and the pollicipoid scalpellid *Calantica villosa*. Anderson (1983) stated 'Functional studies of *C. polymerus* and *C. villosa* have now shown that an evolution of catophragmid balanomorphs from calanticine scalpellids is functionally feasible, upholding Darwin's proposal. *C. polymerus* retains the scalpellid mode of planktivorous extension feeding. . .. . .The basic adaptive significance of the foreshortened form and flattened operculum of *C. polymerus* lies in allowing a species with this mode of feeding to inhabit a high energy intertidal environment.' Both authors emphasized the essential similarities between the soft body anatomy of *Catomerus* and *Pollicipes/Calantica*. They both drew attention to the characteristic setation of the posterior four pairs of cirri in *Catomerus* where each podomere carries several pairs of long antero-lateral setae and has a bunch of short forwardly projecting setae between them on the anterior face of the podomere, a feature also seen in *Calantica* (and *Pollicipes*). Darwin (1854) also pointed out that the anatomy and morphology of *Octomeris* could be derived from that of *Catophragmus* which also exhibits this setal arrangement on cirri 3–6. The current study has shown that the similarity extends beyond the disposition of the setae to the setal types (see Table 5): the long antero-lateral setae on the anterior face of the podomeres of cirri 4–6 in *Pollicipes pollicipes*, *C. polymerus* and also *Octomeris angulosa* are Type 2a7 and the setae comprising the dense bunch of shorter setae between the bases of the Type 2a7 setae are Type 2f2. All three species have type 2f1 setae (Figure 11D) on the posterior distal borders of the podomeres of the rami of cirri 3–6. Both setal types have bifid tips (Figures 4A & 11D, E) which are also seen on some of the other setal types found in these species and which were observed in *T. japonica* and *M. volcano* by Chan *et al.* (2008). There is further setal similarity between these three species in that Type 2d4, bidentate setae are found on the rami of the first three cirri. So in the transition from the pedunculate to the sessile form, setal type, as well as setal disposition on the cirri, is retained.

THE DEVELOPMENT OF SETULATE SETAE IN BALANOMORPH CIRRIPEDES

The development of setulate setae appears to be correlated with the adoption of the balanomorph form. In the balanids, chthamalids and tetraclitids (except for *Tetraclitella*) examined in this study the posterior border of the coxopodite of cirrus 1 is fringed with setulate setae: Type 3a in the chthamalids and Type 3b in the tetraclitids and balanids (Table 4). It has been suggested that setulate setae are involved in microfeeding; however, they are usually (but not always) positioned where they could not be reached by the maxillipeds to transfer food particles to the mouthparts. It seems much more probable that these linear fields of flexible setulate setae are involved in keeping the body surface free of epizoites and in

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the direction of water currents through the mantle cavity for respiration and the oxygenation of developing embryos. Such currents could then be exploited for micro-feeding by those species showing a 'strong pumping beat' (Anderson, 1981; Anderson & Southward, 1987).

SETAL TYPES ON THE MOUTHPARTS OF BALANOMORPH CIRRIPEDES

If we consider the mouthparts there are several morphological and setal characteristics that seem to be associated with the evolution of the balanomorph form. Type 2e3 setae were found on the mandibular palps of all the balanoids and tetraclitids but were absent from the pedunculates with the exception of *P. pollicipes*. In *Chthamalus stellatus* these setae are replaced by a field of another specialized setal type, Type 2f3. Type 1b5 setae were found on maxilla 1 in all the balanomorphs examined, except for *Balanus nubilus*, *Megabalanus psittacus* and *Megabalanus tintinnabulum*. However Høeg *et al.* (1994) reported, what appear to be setae of this type from *B. nubilus*, arranged in small groups on the distal margin of the first maxilla. Usually they are simple setae with a terminal pore (Figure 5E) but the Type 1b5 setae in the *Chthamalus* species have an asymmetrical cuticular extension beyond the terminal pore (Figure 5F). These setae are probably chemosensory.

The second maxillae of most lepadomorphs are simple structures bearing setae and the pores of the labial glands. *Pollicipes* has a dorsal notch and a second maxilla of almost identical structure is seen in *Catomerus*. This dorsal notch is probably the forerunner of the development of a distal mobile maxillary palp as described in *Tetraclita squamosa* by Hunt & Alexander (1991) and which is particularly well developed in the balanids, *P. perforatus* (Anderson, 1981), *B. nubilus* and *M. psittacus*. In the balanids examined in this study the distal surface of the maxillary palps were clothed with simple, often flexible, type 1a3 setae. The two exceptions were *Chirona hameri* and *M. tintinnabulum*, both of which have denticulate, Type 2e1, setae in this position as seen in the tetraclitids.

SETAL MORPHOLOGY AND CIRRIPEDE TAXONOMY

Classical cirripede taxonomy was based on shell morphology and to a lesser extent body morphology including mouthparts and the characteristic distribution patterns of setae on the limbs, but not much attention was paid to setal morphology. The emphasis on shell morphology enables comparisons to be made with palaeontological evidence allowing deductions to be made about the evolutionary history of modern species and groups. However, Darwin (1854) expressed the opinion that there were dangers in relying too much on shell structure in working out relationships and said that more attention should be paid to soft body morphology. The setal morphologies revealed in this study in most cases reflect the accepted taxonomic groups but there are anomalies in the Balanoidea (see below).

Cases of convergent evolution are also apparent for example in the Group 1 simple setae (see above) and in Group 2, denticulate setae where robust, Type 2d3 and Type 2d4, setae are found in a number of cirripede species inhabiting locations exposed to severe wave action but the morphology of the denticles in different genera is distinct. Another example of convergent or perhaps parallel evolution is provided by the setulate setae fringing the posterior border of the coxopodite of cirrus 1 in balanomorphs: in the chthamalids these fringing setae are Type 3a whereas in the balanids and tetraclitids they are Type 3b. This structural difference suggests the possibility of two independent lines of evolution for these setae.

If we consider the balanoid spp. examined in this study and compare the setae comprising the cirral net, on the anterior face of the rami of cirri 4–6, *C. hameri* with Type 2a8 setae and *M. tintinnabulum* with Type 2a1 setae (also seen in *M. volcano* Chan *et al.*, 2008) are clearly distinct from the other balanoid species. *Megabalanus psittacus*, however, has Type 2a3 setae as seen in *B. nubilus* (Figure 7C). The *Balanus* species (with the exception of *B. nubilus*), the *Semibalanus* species and *Perforatus perforatus*, all have Type 2c4 with characteristic long, slender, distally directed denticles. *Austrominius (Elminius) modestus* has Type 2a4 setae with a single row of the same long slender denticles as Type 2c4 setae, which could be interpreted as being derived from the Type 2c4 by simplification. Indeed in *A. modestus* further simplification is observed in that some of the setae of the cirral net have no denticles and are Type 1a1. *Balanus balanus* is particularly interesting in that the distalmost region of the longest setae on the rami of cirri 4–6 has a single row of closely set denticles along the anterior face of the shaft with more widely spaced supplementary denticles on the posterior face of the shaft (Figure 14C), suggesting how the denticular layout seen in the Type 2a3 setae of *B. nubilus* (Figure 7C) and *M. psittacus* might have arisen. The marked difference between the setae of the captorial cirri in *B. nubilus* and the other *Balanus* spp. and their resemblance to those of *M. psittacus* suggests that perhaps *B. nubilus* should not be included in the genus *Balanus*. However *M. tintinnabulum* has setae on cirri 4–6 which clearly resemble those seen in *Tetraclita squamosa* and are of the same type as those of *M. volcano* (Chan *et al.*, 2008). The morphology of cirri 1–3 and the oral cone in *M. tintinnabulum* also bear a striking resemblance to *T. squamosa*. The setae on the distal region of the maxillary palps are denticulate (see above)—not a balanid feature but typical of the tetraclitids. Perhaps it might be more appropriate to include *M. tintinnabulum* and *M. volcano* with the tetraclitids?

Recent studies have tested the accepted orthodoxies of cirripede classical taxonomy by applying the techniques of molecular biology. Pérez-Losada *et al.* (2008) reviewed previous attempts at elucidating barnacle phylogeny and then applied cladistic techniques to both molecular and morphological data from a very wide range of cirripedes. They used DNA sequences from three nuclear genes and 44 morphological characters collected from 76 thoracican and 15 rhizocephalan species, but setal morphology was not used in the range of morphological characters subjected to cladistic analysis. Of the 76 thoracican species studied 24 were examined in the current study. Analysis of the data led them to conclude that the Iblomorpha were a monophyletic group which diverged very early in cirripede evolution. The current study has also revealed a number of characteristics that set the two *Ibla* spp. apart from the rest of the cirripedes studied, for example the preponderance of unidenticulate setal types

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(2a1, 2a2 and 2a3) and the presence of setae on the prosoma and thorax. Those bidenticulate setae that are present are Type 2b3 in contrast to the other cirripedes examined where Type 2c1 is predominant.

Pérez-Losada *et al.* (2008) concluded that the plateless condition of the Heteralepadomorpha was not a primitive feature but had probably arisen at least twice within the Lepadomorpha. In the current study *H. microstoma* was shown to differ from all the other species examined in having Type 2a9 denticulate setae and was unique among the pedunculates in having setulate setae, Type 3a1, and plumodenticulate setae, Type 4. It would be interesting to see whether it shares these characteristics with other *Heteralepas* species and with *Paralepas*.

Analyses using the DNA data, the morphological characters and a combination of the two data sets, all resulted in the deep-sea vent scalpellomorphs *Neolepas*, *Leucolepas* and *Vulcanolepas* being clustered together. This is certainly reflected in their setal morphology. *Neolepas rapanuii*, *Leucolepas longa* and *Vulcanolepas parensis* are characterized by 5 setal types: 1a2, 1b3, 2a6, 2c2 and 2c3 not seen in any other species examined.

On the basis of molecular evidence Pérez-Losada *et al.* (2008) separated *Calantica* from *Pollicipes*. Representatives of both genera have been used as models when considering the transition from the pedunculate to the sessile form (Darwin, 1854; Anderson, 1983). There can be little doubt that the ancestor of the balanomorph cirripedes was closely related to a pedunculate scalpellid ancestor closely resembling these genera. Both *Calantica* and *Pollicipes* have a similar arrangement of setae on the anterior faces of the rami of cirri 4–6: a dense tuft of slender setae between paired long, lateral setae. This arrangement is also seen in *Catomerus*. However the paired long lateral setae, in *Calantica spinosa* (plate 1C in Foster, 1978) appear to be Type 2a1 with a single row of well-spaced small denticules whereas *P. pollicipes* has Type 2a7 with a more closely spaced irregular double row of small denticules, a characteristic it shares with *C. polymerus*. Both *P. pollicipes* and *C. polymerus* have slender Type 2f2 setae comprising the anterior setal tuft. The nature of the setae in the setal tuft in *Calantica* is not known. If we consider the stout dentate setae seen on cirri 1, 2 and 3 in *Pollicipes*, and on cirrus 2 in *Calantica* and *Catomerus*, *P. pollicipes* has both Type 2d2 and 2d4 on the rami of cirrus 3. *Catomerus* has Type 2d4 on the terminal podomeres of the rami of cirrus 2. It is not clear from the images in Foster (1978) to which Type the stout dentate setae seen in *C. spinosa* belong. Thus in its setal morphology *C. polymerus* may have a greater affinity with *Pollicipes* than with *Calantica*.

Within the Balanomorpha the data presented by Pérez-Losada *et al.* (2008) seems to suggest a split, grouping *Catomerus* with the chthamalids and grouping the tetraclitids together with the balanids. This split is mirrored in the current study by some but not all features of setal morphology. For example, the chthamalids have Type 3a setulate setae, whereas the tetraclitids and the balanids have Type 3b setulate setae. Similarly all the balanomorphs studied have specialized setae along the median face of the mandibular palps, but while the tetraclitids and the balanids have Type 2e3 (as does *Catomerus*), *C. stellatus* has Type 2f3. When we consider the setae of cirri 4–6 comprising the 'cirral net' the situation is different. *Catomerus*, the chthamalids and the tetraclitids all have setae with relatively small denticles along one side of the setal shaft (Type 2a) (a characteristic also possessed by *M. tintinnabulum* and *M. volcano* see above), whereas the majority of the balanids (as currently defined) examined have setae with very characteristic long slender needle-shaped denticules directed distally along the setal shaft. The separation of *A. modestus* and *Elminius kingii* from the rest of the balanids is surprising: both species exhibit typical balanid features in particular the field of very long setulate setae arising from the base of cirrus 3 and the morphology of the setae on cirri 4–6.

To conclude, the five Groups of setal types described here are possibly functional groupings as suggested by Garm (2004). Study of the more detailed setal morphology reveals characteristics that are useful in elucidating relationships within crustacean groups such as the Decapoda or the Cirripedia rather than between groups. The demonstration in the current study that setal type can be correlated to some extent with taxonomic position within the Cirripedia supports the conclusion of Høeg *et al.* (1994) that setal structure and distribution of different setal types 'offer a new character set with likely phylogenetic significance at both lower and higher taxonomic levels'. However, the setal morphology described here would be of limited use in field taxonomy as most of the features described are beyond the limits of good resolution for optical microscopy.

Table 5. Setal types in *Tesseropora rosea* and *Tetraclitella purpurascens* described by Anderson & Anderson (1985) compared with the current study

T. rosea	*T. purp*	Setal types	C.S. types
Maxilla 1	Maxilla 1	1:Smooth	Simple, 1b2, 1b5
C5 rami	C5, rami	1:Smooth	Denticulate 2f2
C1		2: Serrulate	Denticulate
exopod.			2e1, 2a7, 2b3
endopod.			2c1, 2b3
	C1,	2:Serrulate	Denticulate
	coxopod.		2c1
	exopod.		2b5, 2c1, 2a3
	endopod.		2d2
C2		2:Serrulate	Denticulate
exopod.			2a1, 2a7, 2b4, 2e1
endopod,			2a1, 2a7
	C2, exopod. & endopod.	2:Serrulate	Denticulate 2c1
C3		2:Serrulate	Denticulate
rami prox.			2a1, 2a7
anten. rami			2e1, Type 5
	C3 exopod. & endopod.	2:Serrulate	Denticulate 2a1, 2d1
C5 rami		2:Serrulate	Denticulate 2a7, 2f2
	C5 rami	2:Serrulate	Denticulate 2a1
Maxilla 2		2:Serrulate	Denticulate 2e1
Md.palp	Md. palp	2:Serrulate	Denticulate 2e1
Md.palp	Md.palp	2a:Jointed	Denticulate 2e3
	C2 rami	3:Serrate	Denticulate 2d2
	C3 rami	3:Serrate	Denticulate 2d2
C3		4:Pectinate	Denticulate 2d4
rami prox.			
pods.			
C1, C2, C3		5:Pappose	Setulate, 3b1
cox. bas.			

anten., antenniform; bas., basipodite; C1, cirrus 1; cox., coxopodite; C.S., current study; Md., mandibular; pods., podomeres; prox., proximal.

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Table 6. Setal types in *Tetraclita squamosa* described by Hunt & Alexander (1991) compared with the current study.

T. squamosa	Setal types	CS types
C4–C6 rami	1: long serrulate	Denticulate 2a7
C4–C6 rami	2: short smooth	Denticulate 2f2
Rami all cirri	3: short smooth tufts	Combs of denticles
	4: stout serrulate	Denticulate 2a1, 2a2
C1, C2, C3	5: pappose	Setulate 3b1 Denticulate 2c1
C3 endopod.	6: pectinate	Denticulate 2d1
Md. palp & Maxilla 2	7: posterior/ant. serrulate	Denticulate 2e1
Md. palp	8: jointed	Denticulate 2e3
	9: small flattened	?
Maxilla 1	10: smooth comb	Simple 1b2

ant., anterior; C., cirrus; CS, current study; Md., mandibular.

Table 7. Setal types described by Høeg *et al.* (1994) compared with the current study.

	Setal types	CS types
Mouthparts	1a: small fan	Comb of denticles
	1b: variable	?
Maxilla 1	1b: denticle with terminal pore	Simple, 1b5
Maxilla 1,	1d: cuspidate denticle	
P. pollicipes		Large denticle
L. anatifera		Large denticle
B. nubilus		Simple: 1b2
Maxilla 1	2a: cuspidate seta	Simple: 1b2
Maxilla 2	2b: rod seta	?
P. pollicipes		
Maxilla 2	2c: acuminate seta	Simple 1a3
Balanids		
Maxilla 2	2d: small fan setae	?
B. nubilus		
B. balanus		
Mandible	2e: small tooth seta	Denticulate 2b1
Lateral face		
	3a: sparse omniserrate	?
Mandible,	3b: biserrate	Denticulate 2b1
Maxilla 1		
Md. palps,	3c,3d: long omniserrate	Denticulate 2e1
Maxilla 2		
Md. palps, Mx 2	4a: smooth tipped foliate	Denticulate 2e1
Balanids	foliate	
Md. palps	4b1: unjointed foliate	Denticulate 2e1
Balanids		
Md. palps	4b2: jointed foliate	Denticulate 2e3
Balanids		
Maxilla 2	Stub setae	Labial gland ducts
all species		

CS, current study; Md., mandibular.

Table 8. Comparison of setal types described by Chan *et al.* (2008) with the current study.

Setal types	CS types
Simple	Simple
Serrulate	Denticulate
Serrate	Denticulate 2c & 2d
Pappose	?
Plumose	Setulate
Pappo-serrate	Plumo-denticulate
Cuspidate	Simple
Multi-cuspidate	Denticulate 2d4

CS, current study.

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REFERENCES

Anderson D.T. (1981) Cirral activity and feeding in the barnacle *Balanus perforatus* Bruguière (Balanidae) with comments on the evolution of feeding mechanisms in thoracican cirripedes. *Philosophical Transactions of the Royal Society B* 291, 411–449.

Anderson D.T. (1983) *Catomerus polymerus* and the evolution of the balanomorph form in barnacles (Cirripedia). *Memoirs of the Australian Museum* 18, 7–20.

Anderson D.T and Anderson J.T. (1985) Functional morphology of the balanomorph barnacles *Tesseropora rosea* (Krauss) and *Tetraclitella purpurascens* (Wood) Tetraclitidae. *Australian Journal of Marine and Freshwater Research* 36, 87–113.

Anderson D.T. and Southward A.J. (1987) Cirral activity of barnacles. In Southward A.J. (ed.) *Barnacle biology*. Rotterdam: A.A. Balkema, pp. 135–174 [Crustacean Issues 5].

Bocquet-Védrine J. and Ovechko N. (1960) Contribution a l'étude des 'glandes salivaires' de *Chthamalus stellatus* (Poli). *Bulletin de la Société Linnéenne de Normandie* 10, 106–118.

Chan B.K.K. (2001) Studies on *Tetraclita squamosa* and *Tetraclita japonica* (Cirripedia: Thoracica). 1: adult morphology. *Journal of Crustacean Biology* 21, 616–630.

Chan B.K.K., Tsang L.M., Ma K.Y., Hsu C.H. and Chu K.H. (2007) Taxonomic revision of the acorn barnacles *Tetraclita japonica* and *Tetraclita formosana* (Crustacea: Cirripedia) in East Asia based on molecular and morphological analyses. *Bulletin of Marine Science* 81, 101–113.

Chan B.K.K., Garm A. and Høeg J.T. (2008) Setal morphology and cirral setation of thoracican barnacle cirri: adaptations and implications for thoracican evolution. *Journal of Zoology* 275, 294–306.

Chan B.K.K., Hsu C.H. and Tsai P.C. (2009) Morphology and distribution of the acorn barnacle *Tetraclita reni* nom. nov. (Crustacea: Cirripedia) in Madagascar and adjacent waters. *Zootaxa* 2019, 57–68.

Crisp D.J. and Southward A.J. (1961) Different types of cirral activity of barnacles. *Philosophical Transactions of the Royal Society B* 243, 271–308.

Darwin C. (1851) *A monograph on the sub-class Cirripedia, with figures of all the species. The Lepadidae or pedunculated cirripedes*. London, The Ray Society.

https://doi.org/10.1017/S0025315411001524 Published online by Cambridge University Press

Darwin C. (1854) *A monograph on the sub-class Cirripedia, with figures of all the species: the Balanidae (or sessile cirripedes), the Verrucidae, etc.* London, The Ray Society.

Derby C.D. (1989) Physiology of sensory neurons in morphologically identified cuticular sensilla of crustaceans. In Felgenhauer B.E., Watling L. and Thistle A.B. (eds) *The functional morphology of feeding and grooming in Crustacea*. Rotterdam: A.A. Balkema, pp. 27–47 [Crustacean Issues 6].

Drach P. (1939) Mue et cycle d'intermue chez les Crustacés Décapodes. *Annales de l'Institut Océanographique* 19, 103–391.

Drach P. and Jacques F. (1977) Système sétifère des Crustacés Décapodes. Principes d'une classification générale. *Comptes Rendus Académie des Sciences, Paris* Série D, 1–284.

Factor J.R. (1978) Morphology of the mouthparts of larval lobsters, *Homarus americanus* (Decapoda: Nephropidae), with special emphasis on their setae. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 154, 383–408.

Felgenhauer B.E. (1987) Techniques for preparing crustaceans for scanning electron microscopy. *Journal of Crustacean Biology* 7, 71–76.

Foster B.A. (1978) The marine fauna of New Zealand: barnacles (Cirripedia: Thoracica). *Memoir of the New Zealand Oceanographic Institute* 69, 1–160.

Garm A. (2004) Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapods. *Zoological Journal of the Linnean Society* 142, 233–252.

Henry D.P. and Mclaughlin P.A. (1975) The barnacles of the *Balanus amphitrite* complex (Cirripedia, Thoracica). *Zoologische Verhandelingen (Leiden)* 141, 1–254.

Høeg J.T., Karnick E.S. and Frølander A. (1994) Scanning electron microscopy of mouth appendages in six species of barnacles (Crustacea Cirripedia Thoracica) *Acta Zoologica (Stockholm)* 75, 337–357.

Hunt M.J. and Alexander C.G. (1991) Feeding mechanisms in the barnacle *Tetraclita squamosa* (Bruguière). *Journal of Experimental Marine Biology and Ecology* 154, 1–28.

Johnstone J. and Frost W.E. (1927) *Anelasma squalicola* (Loven): its general morphology. *Proceedings and Transactions of the Liverpool Biological Society* 41, 29–91.

Lavalli K.L. and Factor J.R. (1992) Functional morphology of the mouthparts of juvenile lobsters, *Homarus americanus* (Decapoda: Nephropidae), and comparison with the larval stages. *Journal of Crustacean Biology* 12, 467–510.

Newman W.A. and Ross A. (1976) Revision of the balanomorph barnacles: including a catalog of the species. *Memoirs of the San Diego Society of Natural History* 9, 1–108.

Nilsson-Cantell C.A. (1921) Cirripedien-Studien. Zur Kenntnis der Biologie, Anatomie und Systematik dieser Gruppe. *Zoologiska Bidrag fran Uppsala* 7, 75–395.

Perez-Losada M., Harp M., Høeg J.T., Achituv Y., Jones D., Watanabe H. and Crandall K.A. (2008) The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution* 46, 328–346.

Pilsbry H.A. (1916) The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. *Bulletin of the United States National Museum* 93, 1–366, + 76 plates.

Pitombo F.B. (2004) Phylogenetic analysis of the Balanidae (Cirripedia, Balanomorpha). *Zoologica Scripta* 33, 261–276.

Pohle G. and Telford M. (1981) Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). *Bulletin of Marine Science* 31, 736–752.

Reaka M.J. (1975) Molting in stomatopod crustaceans. 1. Stages of the molt cycle, setagenesis and morphology. *Journal of Morphology* 146, 55–80.

Southward A.J. (1976) On the taxonomic status and distribution of *Chthamalus stellatus* (Cirripedia) in the north-east Atlantic region: with a key to the common intertidal barnacles of Britain. *Journal of the Marine Biological Association of the United Kingdom* 56, 1007–1028.

Southward A.J. (2008) Barnacles. In Crothers J.H. and Hayward P.J. (eds) *Synopses of the British fauna (New Series). No. 57*. London: Linnean Society of London, pp. 1–140, + 4 plates.

Thomas W.J. (1970) The setae of *Austropotamobius pallipes* (Crustacea: Astacidae). *Journal of Zoology, London* 160, 91–142.

Walley L.J. (1965) *Histological and histochemical studies in cirripedes*. PhD thesis. University of Wales.

and

Watling L. (1989) A classification system for crustacean setae based on the homology concept. In Felgenhauer B.E., Watling L. and Thistle A.B. (eds) *The functional morphology of feeding and grooming in Crustacea*. Rotterdam: A.A. Balkema, pp. 15–26 [Crustacean Issues 6].

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