THE ORIGIN AND FORMATION OF HAIR ON EXTERNAL VALVE SURFACES OF THE TROPICAL MARINE MUSSEL *MODIOLUS TRAILLII* (REEVE, 1857)

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ABSTRACT

Direct observations using digital videography in an aquarium showed that hairs on the valve surfaces of *Modiolus traillii* are not periostracal in origin, as often assumed for similar features in other mussels, but are secreted and planted individually by the foot, so they are correctly termed 'byssal hairs'. Deposition of byssal hair occurred most frequently just after dark, and the time taken to form a strand of serrated hair varied between slightly more than 1 min to almost 10 min, with a mean time of 4.4 min. We observed one individual deposit a total of 11 hairs in 3.5 h. The formation of some 25 hairs were successfully observed on video for six individuals, and about 3,000 individual hairs from 12 mussels were measured in relation to their position, size and density. While hairs varied considerably in length and width, they are consistently flattened, with one edge bearing serrations and the other edge being smooth. Long hair required more time to form compared with shorter hair, and longer hair was deposited farther away from the byssal gape towards the posterior end of the valves. However, a higher density of short hair was laid around the byssal gape. Smaller mussels tended to have an overall higher density of hair compared with larger individuals. There was no discernible pattern in the order in which long and short hairs were secreted on the periostracal surfaces of either valve. Byssal hair microstructure was generally consistent with the distal region of byssal threads, having a tough but thin outer cortex surrounding a 'spongy' honeycomb matrix.

INTRODUCTION

The presence of hair-like protuberances on the external surfaces of molluscan shells is well known amongst members of a number of bivalve groups, including the Arcoida, Mytiloida, Unionoida and Veneroida (e.g. Soot-Ryen, 1955; Watabe, 1988; Kafanov, 2001; Agüera García & Oliver, 2008; Zieritz *et al.*, 2011). Such hairs may extend the range of tactile perception and/or provide protection against predators, fouling and mechanical wear in epifaunal bivalves (Bottjer & Carter, 1980; Wright & Francis, 1984; Dixon *et al.*, 1995). Their physical origins, however, appear to be less well understood. A common assumption is that these hairs are secreted by the mantle edge in association with the periostracum, and have thus been referred to variously as periostracal hairs (Tullberg, 1882; Bottjer & Carter, 1980), periostracal adventitious hairs (Dixon *et al.*, 1995), periostracal awns (Wright & Francis, 1984), periostracal shingles (Watabe, 1988) or periostracal bristles (Oliver, 1992). Their connection with the periostracum is widely accepted in the arcids (as periostracal shingles or bristles) but, in the case of some venerids, fine calcified hairs on the shell surface grow through channels in the periostracum to form a felt-like layer over the shell surface, as recently shown by Glover & Taylor (2010). In mytilids, however,

Ockelmann (1983) stated that hairs are produced by the byssal gland and are subsequently attached to the surface by the mussel's foot, although he did not provide supporting evidence. In the same year, Board (1983) observed and illustrated what he assumed were the remains of distal ends of byssus threads attached to the surfaces of postlarval shells of *Mytilus edulis* by other individuals but, again, no direct observations were made to ascertain their origin.

In order to determine the origin and formation of these hairs in mytilids, we observed living adult *Modiolus traillii* (Reeve, 1857) from Singapore in the aquarium by first removing all traces of hair from the shell surface and then recording the deposition of new hair on video. We also briefly characterized the physical structure and distribution of hairs in this mussel, as well as their size relationships.

MATERIAL AND METHODS

Animals

Living adult *Modiolus traillii* (Fig. 1; shell length [SL] range = 26–44 mm; *n* = 25) were obtained in April 2012 and July 2012 from a shallow subtidal fouling community occurring on two
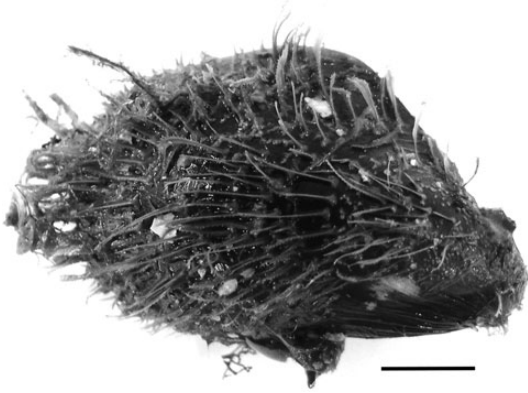
Figure 1. *Modiolus traillii*: right valve with hair (SL = 48 mm). Scale bar = 10 mm.
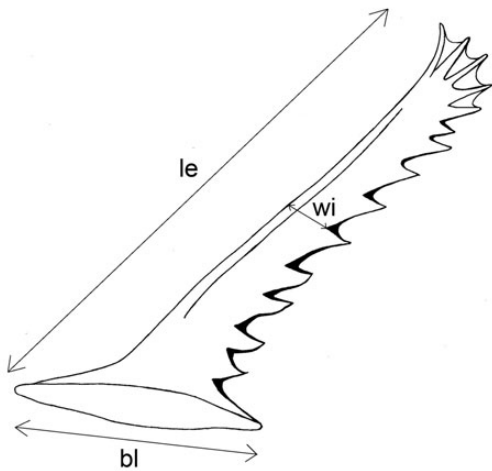

Figure 2. Diagram of a typical byssal hair of *Modiolus traillii* showing measurements made for hair length (le), and hair width (wi). Hair width was measured about halfway along its length as the distance between the smooth edge and base of serration. Plaque base length (bl) is the length of the hair plaque that is attached to the shell.

navigation buoys off the southwest and southeast coasts of Singapore (respectively, Kanan Buoy: 1°16′.90N, 103°40.25′E and Padang Buoy: 1°17.49′N, 103°58.98′E). These mussels generally occur singly, attached to hard substrates. After careful removal from buoy surfaces by cutting the byssal threads, the animals were maintained in running seawater at the aquarium facilities of the Tropical Marine Science Institute, National University of Singapore (St John's Island), and were fed a mixture of Aqua Pharm Pro Series Sea Plankton™ and live microalgae (*Chaetoceros* sp., *Skeletonema* sp., *Tetraselmis* sp., *Nanochloropsis* sp. and *Isochrysis* sp.).

Hair characteristics

We determined the position where each hair was laid on the valve surface by measuring the shortest distance along the surface of the valve between the base of the hair (attachment plaque, or adhesive disc) and the byssus gape, along the ventral edge of the valves. Hair length and width (Fig. 2) were measured in 12 individuals (SL range = 27.5–43.6 mm). The number of hairs in 14 grid squares each measuring 5 × 5 mm laid out over the surface of each valve were counted to determine the density and length of hair from different regions of each of
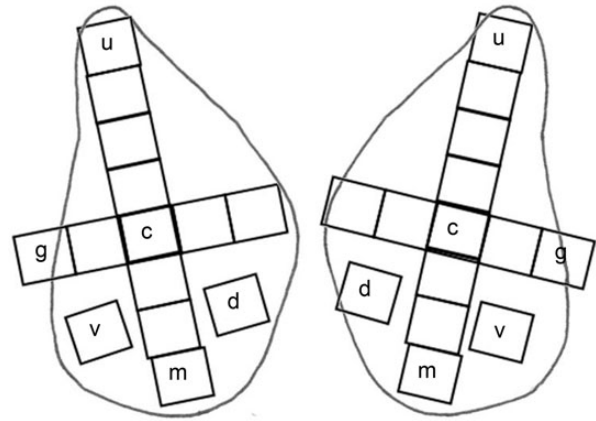

Figure 3. To determine and compare the positions of byssal hair laid by *Modiolus traillii* on its valve surfaces, grid squares each 5×5 mm^2 in size drawn on transparent film were laid over the valves of each individual. A single series of eight grid squares was laid along the SL, i.e. the greatest distance from the umbo (u) to the middle posterior margin of the shell (m). Another five grid squares were laid across the widest part of the shell perpendicular to the first grid from the ventral byssal gape (g) to the dorsal edge of the shell. The two series of grids meet at the centre (c) of the valve. The posterior region of each valve was further differentiated into posterior ventral (v) and dorsal (d) regions.

the two (left and right) valve surfaces (Fig. 3). In an additional five individuals (SL range = 26.0–44.5 mm) the length of hair and plaque base length (Fig. 2) were measured. Statistical analyses were performed using commercial software SPSS® and GraphPad Prism® 6.0d.

Histology

We sectioned seawater formalin-fixed foot tissue, byssus, byssal complex and hair at 8–10 µm using a microtome and stained the serial sections in haematoxylin and eosin, as well as Masson's Trichrome (modified from Kiernan, 2008).

Scanning electron microscopy

Intact periostracum and hair from ethanol-preserved specimens were removed from the shell, critical-point dried and coated with gold and palladium before observing them under the scanning electron microscope (SEM) (JEOL JSM-6510).

Hair deposition

All animals used (*n* = 6; SL range = 31.8–47.4 mm) were kept for 24 h in running seawater before starting observations. Hairs on each adult mussel were first removed completely at their bases using a razor blade. The mussels were then placed singly in small tanks supplied with running seawater. A digital video camera (Panasonic HDC-HS900) was positioned over each such that either the surface of the left or right valve was wholly visible. As individuals were all unattached at the start of the experiment, they invariably first laid byssal threads to attach themselves to the inner surfaces of the tank before hair deposition began. Preliminary observations in nontidal aquarium conditions showed that hair deposition occurred mostly during the night. Recordings were therefore made overnight using a 60 W incandescent lamp placed about 0.5 m away from the tank to provide sufficient illumination. The length of time it took for the mussel to plant the hair was then noted and compared with the length of the hair, to test for correlation between the two variables. The time taken to lay byssal threads was also recorded
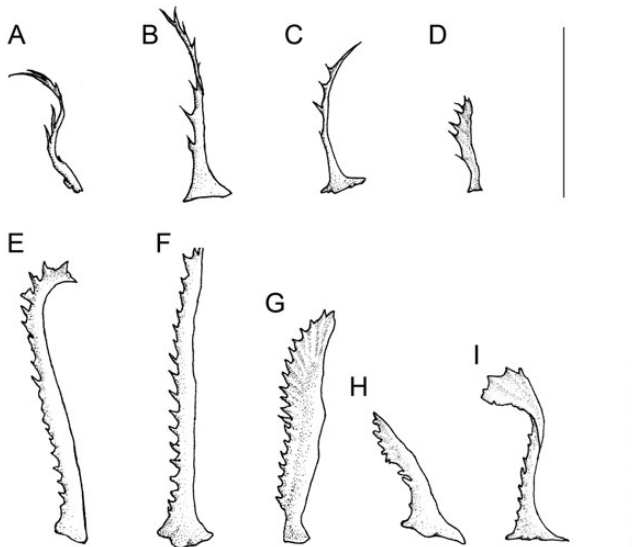
Figure 4. Morphological variation in byssal hair laid by *Modiolus traillii* on external valve surfaces. The hairs **A, E, F** and **G** are from the same individual, while **B–D, H** and **I** are from another individual. The hairs **A** and **B** were laid near the umbo, whereas **C** and **D** were from the ventral region near the byssal gape; **E** was from the central region of the shell, and **F–I** were from the posterior valve edge of the shell. Scale bar = 4.0 mm.

Figure 5. Relationship between shell size and number of byssal hairs present on the shell surface of *Modiolus traillii* ($n = 12$; Pearson's $r = -0.615$, $P < 0.05$).

Figure 6. Box-and-whisker plots of byssal hair lengths found in different sized individuals of *Modiolus traillii*.

Figure 7. Section of byssal hair of *Modiolus traillii* stained with Masson's Trichrome showing a dense, amorphous external cortex enclosing a diffuse core with a honeycomb structure. Scale bar = 100 μm.

for comparison with the time taken to lay byssal hairs. Information regarding the time when the hair was planted and the location of the shell where this occurred was also recorded for six individuals. The hairs laid after the pre-existing hairs were removed were also visually compared with hair present on the mussels before manipulation, using a dissecting stereomicroscope.

Another set of mussels ($n = 5$; SL range = 30–45 mm) was shaved, placed in a basket and left undisturbed off a pontoon in the sea (2.5 m depth) for 1 week. The position and length of the hairs laid down during this period were studied by measuring the shortest distance along the surface of the valve between the base of the hair and the byssal gape.

RESULTS

Hair morphology

Hairs deposited by *Modiolus traillii* were generally flattened and serrated along one edge (Fig. 4) and their overall shape was consistent, although their sizes varied greatly. Hair length varied from <1 mm to >8 mm in length, and hair width (at mid-region) was between 0.05 and 0.8 mm. Hair length was significantly and positively correlated with hair width ($n = 3,002$, $r = 0.387$, $P < 0.001$). The base length (= plaque length) of the hairs varied from 0.325 to 2.125 mm, which also had a positive and significant correlation with hair length ($n = 80$, $r = 0.398$, $P < 0.001$). The number of hairs on each individual varied between 127 and 686 ($n = 12$; SL range = 26.3–44.0 mm). A significant negative correlation ($n = 12$, $r = -0.615$, $P < 0.05$) was observed between shell size and number of hairs deposited (Fig. 5). However, there was no significant relationship between SL and mean hair length. The range of hair lengths found in different sized individuals was generally similar (Fig. 6).

Paraffin sections of hair stained in Masson's Trichrome (Fig. 7), as well as SEMs of sectioned hair, showed that each hair comprised a thin, dense outer cortex enclosing a thick, but diffuse, porous core. This is consistent throughout the length of
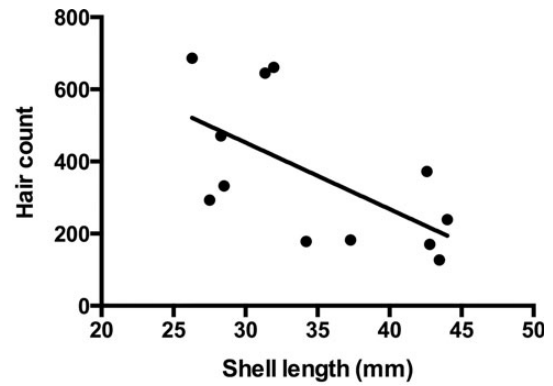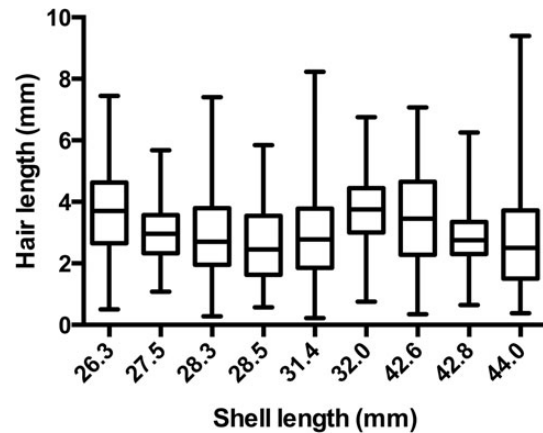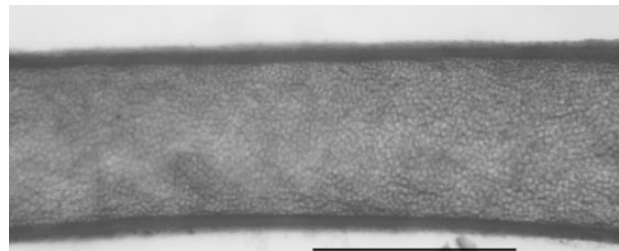
the hair and appears to be equivalent to the distal region of a byssus thread secreted by the same animal, with both structures staining red in Masson's Trichrome. However, they differ from the proximal region of the length of the byssus thread, which stained blue. Attachment of hair to the periostracum is made directly with the inner honeycomb-like core (Fig. 8). Comparisons of the byssal gland in the foot of *M. traillii* with those of nonhirsute mussel species (unpublished observations) showed that the overall distribution and size of these glands were comparable, and no additional structures were discernible in the foot of *M. traillii*.
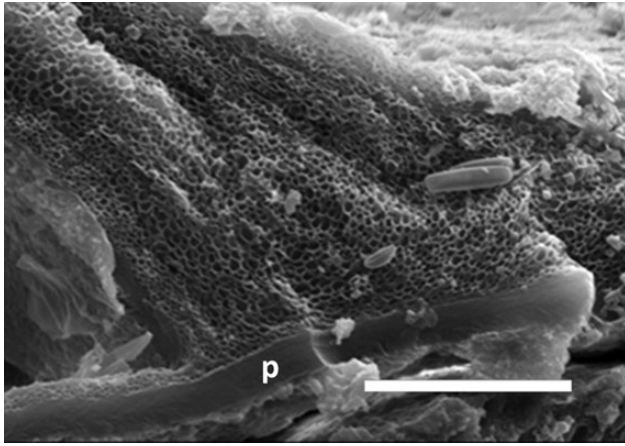
Figure 8. Section of byssal hair plaque of *Modiolus traillii* showing direct contact of honeycomb matrix with the shell periostracum (p). Scale bar = 50 μm.

Table 1. Mean number of byssal hairs, their mean lengths and widths with standard errors (SEs) recorded from different regions of the 24 left and right valve surfaces of 12 individuals of *Modiolus traillii*.

Region of shell	Mean number ± SE of byssal hairs on shell	Mean length ± SE of byssal hairs (mm)	Mean width ± SE of byssal hairs (mm)
c	16.0 ± 2.3	2.35 ± 0.07	0.129 ± 0.004
d	15.2 ± 1.6	3.93 ± 0.09	0.289 ± 0.007
g	31.5 ± 5.5	3.02 ± 0.04	0.146 ± 0.004
m	19.0 ± 1.4	3.08 ± 0.09	0.216 ± 0.006
u	19.9 ± 5.7	3.96 ± 0.06	0.244 ± 0.005
v	20.1 ± 2.9	3.88 ± 0.09	0.316 ± 0.009

c, centre, or midregion of shell; d, near the dorsal posterior edge of the shell; g, byssal gape; m, middle posterior valve edge; u, umbo; v, posterior ventral region of the shell (see also Figs 2 and 3).

Hair distribution on valves

A total of 144 measurements from six different regions of the shell were taken from 12 individuals. The number of hairs and their sizes as measured in grid squares each of area 0.025 cm^2 from various regions on the shell surface is shown in Table 1.

The density of hair differed on the six different regions of the shell (one-way ANOVA: $F_{(5, 138)} = 2.253$, $P < 0.05$). Post hoc analyses using Tukey's HSD test indicated that the density of hairs in the byssal gape area (region g; mean ± SD = 41.9 ± 23.0 hairs per 0.025 cm^2) was significantly ($P < 0.05$) higher than at the dorsal margin (region d; 19.0 ± 6.70 hairs per 0.025 cm^2). Hair density was similar on other areas of the valve surface.

The mean length of hair deposited near the umbo (region u) was significantly shorter ($F_{(5, 138)} = 87.746$, $P < 0.001$; Tukey's HSD post hoc test) than those deposited elsewhere on the valve surfaces. Hair deposited on the mid-region (regions c and g) were in turn shorter than those at the posterior end of the mussel (regions m, v and d). Hence, hair length increased from the anterior to the posterior region of the valves.

Hair deposition

Video observations (see Supplementary Material) of 25 occurrences of hair secretion in six mussels (SL = 31.8, 34.2, 37.3, 43.0, 44.0 and 47.4 mm) showed that the foot of the mussel was invariably used to plant the adventitious hairs onto the surface
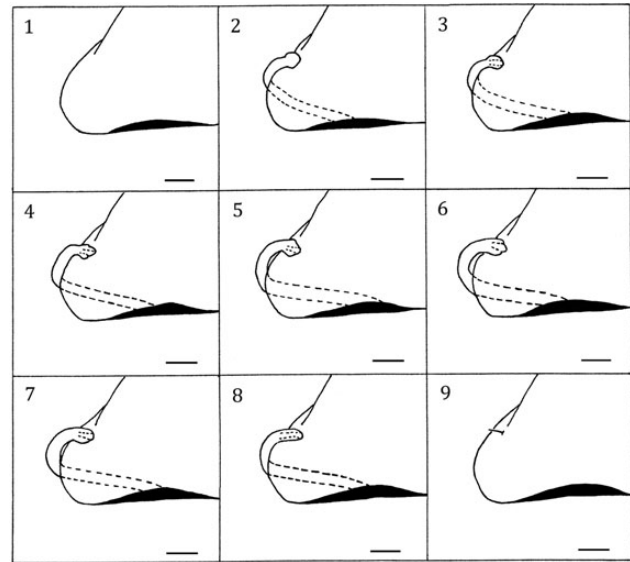

Figure 9. Byssal hair deposition in *Modiolus traillii*. The series of drawings 1–9 show the changes in the shape of the foot tip during the process of hair formation and deposition at the anterior region of the left valve. The dotted region at the tip of the foot denotes temporary folds visible from the surface. The ventral byssus gape is shaded black. Scale bar = 5 mm.

of the periostracum already present on the shell. The mantle edge was never involved in hair formation or deposition.

The process of formation of a single hair on the valve surface (Fig. 9) was as follows. The foot was first extended out of the ventral byssal gape towards the shell surface as if to feel the surface of the periostracum in the region of the shell where the hair was to be laid (Fig. 9.1, 2), a few days before or on the day of formation of the hair. The foot was subsequently extended and remained motionless on the surface of the periostracum (Fig. 9.3). The tip of the foot at this time was in close contact with the shell surface, with sides flattened against the shell surface, giving the tip a triangular shape (Fig. 9.4). The tip of the foot was then gradually inflated while the foot extended lengthwise. As the hair was being planted, an increase in curvature of the foot was observed (Fig. 9.5, 6), so that only the tip of the foot was in contact with the valve surface. During this period, regular contractions along the foot towards the tip were seen as the hair was formed in the byssal groove of the foot. Just before the hair was completely formed, the foot slackened and the tip deflated (Fig. 9.7, 8), afterwhich the foot was very rapidly withdrawn within a second or less. The elongated plaque of the hair was generally laid parallel to the direction of the tip of the foot as positioned during the deposition of the hair on the shell surface, and the serrations on the hair were formed along the inner wall of the byssal groove in the foot (Fig. 10). The entire process of hair laying took *c.* 4 min (mean ± SD = 265 ± 103 s; min: 89 s; max: 551 s; $n = 25$) and generally occurred just after dark between 20.00 and 21.00 h. The time taken to deposit a hair on the shell was significantly shorter ($t = 4.01$, $P < 0.001$) than the time taken to lay a typical strand of byssal thread (mean ± SD = 507 ± 292 s; min: 82 s; max: 1395 s; $n = 55$) (Fig. 11). Not unexpectedly, long hair took more time to produce than short hair (Fig. 12).

The rate of hair deposition by the mussels varied greatly. One individual planted 11 hairs in about 3.5 h, whereas another individual managed only a single hair in 9 d. It was also observed that that rate of deposition of hair in the aquarium decreased over the period of captivity. The first individual mentioned was obtained from the sea less than a day before the video was taken,
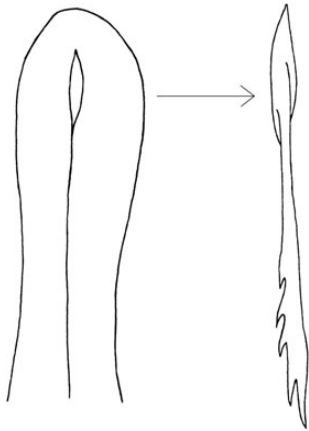
Figure 10. *Modiolus traillii*: orientation of byssal hair formed by foot in relation to the byssal groove. The serrations on the hair are formed and directed towards the inside of the byssal groove.
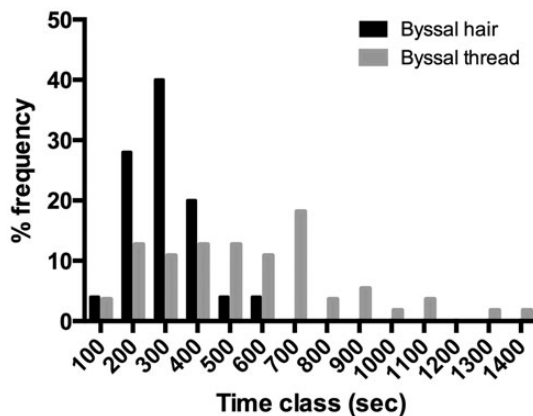

Figure 11. Frequency distribution of time taken (as 100 s interval classes) to complete byssal hair and byssal thread formation in *Modiolus traillii* in the aquarium. Secretion and deposition of byssal hair on the shell surface (black bars; $n = 25$) was generally faster than byssal threads (grey bars; $n = 55$) in the six individuals observed.
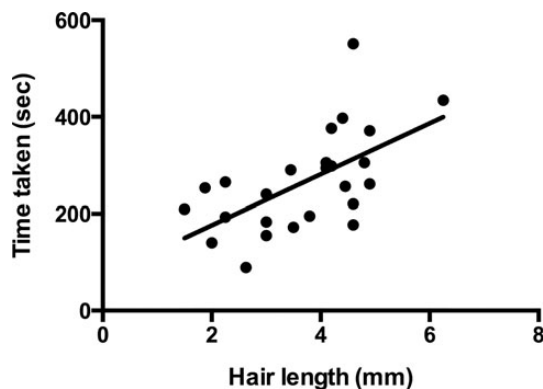

Figure 12. Relationship between the length of byssal hair and time taken for each hair to be completely formed and attached to the shell surface in *Modiolus traillii* (Pearson's $r = 0.597$, $P < 0.01$). Observations were based on 25 hairs laid by six individuals.

while the second individual had been in the aquarium for more than a month before observations began.

Based on observations of mussels ($n = 5$) that were shaved and left in the sea for one week, newly laid hairs occurred on both
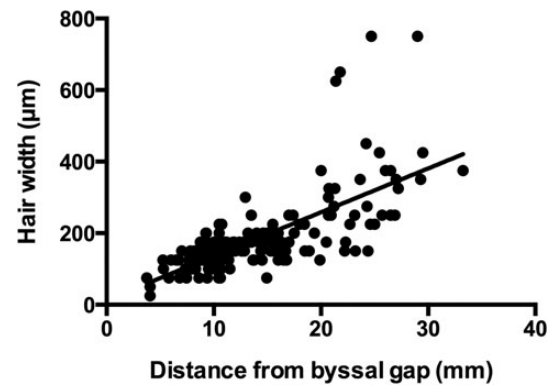

Figure 13. Relationship between byssal hair thickness (wi in Fig. 2) and position of hair on shell surface, as determined by the distance of hair plaque from ventral byssal gape in *Modiolus traillii* (Pearson's $r = 0.70$, $P < 0.01$). Observations were based on 175 hairs laid by five individuals.

valves of the mussel. The distribution of newly planted hairs on the valve did not appear to follow any discernible pattern in terms of their position, and hairs were deposited over the entire external surface of the shell. However, thicker hairs (i.e. of greater width) were generally laid further away from the byssal gape (Fig. 13).

DISCUSSION

The results clearly show that hairs on the shell surface of *Modiolus traillii* (and likely in other mytilid mussels) are secreted by the foot of the animal, and not by other types of epithelium in the mussel such as the middle mantle fold, which forms the periostracum, as had earlier been suggested by Bottjer & Carter (1980). Our observations corroborate those of Ockelmann (1983), who stated that such hairs are formed separately by the byssal gland of the foot and are not contiguous with the periostracum. SEMs of the hairs attached to the shell obtained in the present study also showed that the hairs are deposited separately from the periostracum. These hairs are therefore correctly termed 'byssal hairs'.

The secretion and deposition of byssal hair and byssus (the latter consisting of byssal threads) are both carried out by the foot. Hair and byssus emerge from the depression at the foot tip and through the ventral byssal groove of the foot (Fig. 8; see also Waite, 1983). Before attachment of either hair or byssus onto their respective surfaces, the foot appeared to 'feel' the surrounding surfaces. The planting of either hair or byssus involves a stretching motion of the foot and a pumping movement before completion of attachment. However, after a strand of hair is laid, the foot retracts from the surface extremely quickly, whereas in laying of byssal thread there is no such rapid withdrawal of the foot. Instead, the foot either withdraws slowly back in the shell, or moves a short distance away to 'feel' a nearby area and then secretes another thread. Indeed, this study shows that the time taken for a strand of hair to be laid is generally shorter than the time taken to lay a byssal thread, i.e. in the process of hair laying the foot is exposed outside the shell for a shorter period of time as compared with byssal thread laying. This contrasting behaviour may be related to the relative locations where hair and byssus are laid. Hair occurs over the entire external surface of both valves, and the process of planting hair on the valves renders the foot vulnerable to predation by crabs and fish, since the pale-coloured foot is stretched over the dark surface of the shell during hair formation. In the case of byssal threads, these are usually laid near the ventral region of the

shell, so the foot is less exposed than when laying hairs, perhaps dispensing with the need of the foot to withdraw quickly.

Despite our observation that the same foot glands are likely to be involved in the secretion and formation of byssal threads and hairs, byssal threads differ considerably from hairs in terms of their structure, formation and function. Byssal threads have a smooth external surface and are cylindrical in cross section (Price, 1983; Waite, 1992), whereas hairs are typically asymmetrical with serrations along its length on one side and are flattened in cross section. Also, byssal hairs and byssal threads generally differ in length. The maximum length of hair recorded for *M. traillii* was 9.4 mm, whereas its byssal threads frequently reached lengths of 20 mm or more. When laying byssal threads, the foot is usually stretched out to reach the surface on which it is laying its byssal threads. However, in laying hairs, the foot is sharply bent to maintain a section of the foot that is nearly perpendicular to the surface of the shell, so that the tip of the hair is orientated away from the valve surfaces. Hairs feel stiff but are also flexible, properties likely imparted by their structure of a dense but thin cortex wrapped around a spongy, honeycomb-like matrix. Such a structure appears to be similar to the region nearer the distal end of a byssus thread of *Mytilus edulis*, as described by Benedict & Waite (1986).

From the measurements of hair length and thickness, there appears to be an increase in hair thickness as the length of hair increases. This could be due to the way the hair is produced by the foot. As the distance of the hair from the byssal gape decreases, the length of the upright foot in the process of laying the hairs on the shell is observed to decrease, and the decrease in the length of the ventral groove in a less stretched foot results in the smaller volume of the hair formed. Hence, the hairs near the byssal gape are usually shorter and thinner. The difference in volume of the ventral groove may likewise account for the formation of other variants of hair.

In addition, the slight increase in thickness together with length, as well as the correlation of plaque length with hair length, may point to the need for the hair to maintain its stiffness and stability on the shell as its length increases. Given the presence of serrations on the hairs and the stiffness of the hairs, it is possible that such byssal setae are involved in transmitting mechanical vibrations from the external environment (Wright & Francis, 1984; Iyengar, Sitvarin & Cataldo, 2008) to the mantle under the shell. This could help to explain the importance of planting multiple hairs on the shell surface, and of having long, stiff hairs to increase the sensory volume around the animal. The presence of long byssal setae at the posterior region of the shell could serve to discourage predatory fish and crabs from nipping off pieces of mantle tissue when the mussel is actively filter-feeding. The density of short hairs in the ventral byssal gape area was slightly higher than elsewhere on the valve surfaces, perhaps to provide a barrier against intrusion into the body cavity by small invertebrates through the byssal gape.

However, the advantage of having shorter hair around the umbonal region is unknown. Other possible functions of these hairs include the provision of stability to the shell in soft substrata (Tebble in Dixon *et al.*, 1995), camouflage and protection against borers and fouling (Bottjer & Carter, 1980; Wright & Francis, 1984).

SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies*.

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REFERENCES

AGÜERA GARCÍA, A. & OLIVER, G. 2008. Species discrimination in seven species of *Barbatia* (Bivalvia: Arcoidea) from Thailand with a redescription of *B. grayana* (Dunker, 1858). *Raffles Bulletin of Zoology Supplement*, **18**: 7–23.

BENEDICT, C.V. & WAITE, J.H. 1986. Composition and ultrastructure of the byssus of *Mytilus edulis*. *Journal of Morphology*, **189**: 261–270.

BOARD, P. 1983. The settlement of post larval *Mytilus edulis* (settlement of post larval mussels). *Journal of Molluscan Studies*, **49**: 53–60.

BOTTJER, D.J. & CARTER, J.G. 1980. Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). *Journal of Paleontology*, **54**: 200–216.

DIXON, D.R., SOLE-CAVA, A.M., PASCOE, P.L. & HOLLAND, P.W.H. 1995. Periostracal adventitious hairs on spat of the edible mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom*, **75**: 363–372.

GLOVER, E.A. & TAYLOR, J.D. 2010. Needles and pins: acicular crystalline periostracal calcification in venerid bivalves (Bivalvia). *Journal of Molluscan Studies*, **76**: 157–179.

IYENGAR, E.V., SITVARIN, M.I. & CATALDO, M. 2008. Functional morphology of flexible periostracal hairs in *Trichotropis cancellata* (Mollusca, Gastropoda). *Invertebrate Biology*, **127**: 299–313.

KAFANOV, A.I. 2001. Recent and fossil Clinocardiinae (Bivalvia, Cardiidae) of the world. V. Genus *Ciliatocardium* Kafanov, 1974 (part 1). *Bulletin of the Mizunami Fossil Museum*, **28**: 139–171.

KIERNAN, J.A. 2008. *Histological and histochemical methods: theory and practice*. Edn 4. Scion Publishing, UK.

OCKELMANN, K.W. 1983. Descriptions of mytilid species and definition of the Dacrydiinae (n. subfam.) (Mytilacea-Bivalvia). *Ophelia*, **22**: 81–123.

OLIVER, P.G. 1992. *Bivalved seashells of the Red Sea*. Verlag Christa Hemmen and National Museum of Wales, Cardiff.

PRICE, H.A. 1983. Structure and formation of the byssus complex in *Mytilus* (Mollusca, Bivalvia). *Journal of Molluscan Studies*, **49**: 9–17.

REEVE, L.A. 1857. *Conchologia iconica. Illustrations of the shells of molluscous animals*. *Vol. 10*. Genus *Modiola*. L.A. Reeve, London.

SOOT-RYEN, T. 1955. *A report on the family Mytilidae (Pelecypoda)*. University of Southern California Press, California.

TULLBERG, T. 1882. Studien über den bau und das wachsthum des hummerpanzers und der molluskenschalen. *Kungliga Svenska Vetenskaps Akademien Handlingar*, **19**: 1–57.

WAITE, J.H. 1983. Adhesion in byssally attached bivalves. *Biological Reviews*, **58**: 209–231.

WAITE, J.H. 1992. The formation of mussel byssus: anatomy of a natural manufacturing process. *Results and Problems in Cell Differentiation*, **19**: 27–54.

WATABE, N. 1988. Shell structure. In *The Mollusca: form and function*. Vol. 11 (E.R. Trueman & M.R. Clarke, eds), pp. 69–104. Academic Press, London.

WRIGHT, M.M. & FRANCIS, L. 1984. Predator deterrence by flexible shell extensions of the mussel *Modiolus modiolus*. *Veliger*, **27**: 140–142.

ZIERITZ, A., CHECA, A.G., ALDRIDGE, D.C. & HARPER, E.M. 2011. Variability, function and phylogenetic significance of periostracal microprojections in unionoid bivalves (Mollusca). *Journal of Zoological Systematics and Evolutionary Research*, **49**: 6–15.