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THE PLEATED SURFACE OF THE UNDISCHARGED THREAD OF A NEMATOCYST AND ITS SIMULATION BY MODELS

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The complex appearance in electron micrographs of sections, both transverse and longitudinal, of the undischarged thread of a nematocyst—the large holotrichous isorhiza of *Corynactis viridis* Allman—is compatible with the pleating of a tubular thread to form a triple-screw surface (Skaer & Picken, 1965). This interpretation of the sections was facilitated by a study of the properties of folded paper models, and by the construction of a three-dimensional wax model following, essentially, the method of His (1887), but with the difference that sections modelled in wax were serial electron micrographs of ultrathin transverse sections (Picken & Skaer, 1966). This wax model being fragile and opaque, it was subsequently cast in more robust and translucent Araldite resin by a *cire perdu* method.

The model was stood on a glass plate and surrounded by a Perspex cylinder. A fairly dilute aqueous suspension of plaster of Paris was poured in, so as to fill the cavities of the model and the space between model and cylinder. The plaster was allowed to dry for a week, and the whole then placed in a hot-air oven at *c.* 110° C. until the wax had melted and drained away. Rough surfaces on the inside of the resulting plaster mould were smoothed, and the internal surface was dressed with Araldite release-agent, QZ 19. This quickly dries, forming a skin over the surface. Standing the mould on a glass plate previously coated with release-agent, a small volume (*c.* 200 c.c.) of a mixture of Araldite resin, MY 753, with 8% of hardener, HY 992, was poured into the mould and allowed to polymerize for 2 days at room temperature. A further 200 c.c. of mixture was poured in every 2 days, until the total volume of 1700 c.c. was reached. This progressive filling of the mould is necessary because the setting of Araldite resin is highly exothermic. The mould and its contents were left undisturbed for a further week, and the plaster then chipped off.

The resulting Araldite cast is shown in Pl. 1, fig. 1. The helically pleated, triple-screw surface, the triadic symmetry of the core (in the thread itself occupied by barbs —see later), the origin of the three pleats from the core, the barb-pockets into which the bases of the barbs are inserted, and a slight longitudinal rifling of the surface due to longitudinal registration of gentle undulations in the pleats—these are all exhibited by the model.

A short length of the discharged thread, on the other hand, can be represented as a cylindrical tube (Pl. 1, fig. 2), with barbs disposed in whorls of three on three helical barb-rows. (The construction of this model will be described later.) Leaving aside for the present the question of the forces leading to transformation from the undischarged to the discharged condition, there remains the question whether a surface such as that in Pl. 1, fig. 1 can be converted to that in fig. 2 by a simple process of eversion (turning inside-out), associated with the smoothing of folds.

If the surface configuration of the undischarged thread were that of a carpenter's screw, it would be impossible to develop it to a cylinder without local dilatation or contraction of the surface. For this reason, it was suggested in a previous paper (Skaer & Picken, 1965) that 'portions of the membrane in the trough of the screw increase in area, or portions of the pleats decrease in area' during discharge. Calculation of the surface area of the undischarged thread, and comparison of the value so obtained with the surface area of an equivalent length of discharged thread, had shown (Skaer & Picken, 1965) that there is no significant change in surface area on discharge. This might mean either that local dilatation and contraction were exactly equal and opposite in their effects, or that the surface was not strictly comparable with that of a carpenter's screw and could in fact be developed to a cylinder without deformation. It seemed necessary, therefore, to examine the folding of the surface in more refined models.

Accurately longitudinal and transverse sections of the undischarged thread had revealed that the barbs form a relatively compact core, the barb-tips of a single whorl of three barbs being closely pressed together, while their broad triangular bases are relatively widely separated, owing to the taper of the tips and the curvature of the barb-shafts (Pl. 1, fig. 3). The bases are distributed in space in open hexagonal array over the surface of an imaginary cylinder—the cylinder of minimal volume enclosing the packed barbs. The real surface of the thread, to which the barbs are attached, is folded, so that deep helical folds invade the space between the whorls of barbs. The relationship between the barbs and this surface is not shown in the Araldite model, and if barbs were incorporated into such a model the interpretation of that relationship would be difficult, since the resin is incompletely transparent.

Accordingly, a further model was made, using Cellophane to imitate the wall of the thread. The procedure in making this model (Pl. 1, fig. 3), was as follows.

A rectangular sheet of Cellophane was marked out with equidistantly spaced horizontal lines, corresponding to the whorls of barbs, and with three equidistant lines crossing these at an angle of 65°, corresponding to the helical barb-rows. Models of the barbs were prepared by first modelling a single barb in dental wax, making a plaster mould of this, and subsequently casting a series of Araldite copies. These were stuck on to the Cellophane sheet with Sellotape (sticky on both sides) at positions determined by the points of intersection of the whorls and the helical rows. The sheet was then converted to a cylinder, with the barbs on the internal surface, by approximating the two sides and sticking with Sellotape. The barbs were then packed, whorl by whorl, drawing their tips together by means of an elastic band placed behind the posterior barbule (Skaer & Picken, 1965, fig. 5*b*). Each whorl in succession was inserted into the cavity of the preceding whorl with a left-handed twist of 30° between two whorls, and the slack of the Cellophane sheet was folded (thus forming the helical pleats) and smoothed into the space (between the barb-bases) thus forming the barb-pockets.

In the light of this model it is clear that, if the surface between the barb-bases is invaginated into the core, the excess surface of the Cellophane cylinder can easily be distributed over the model as three helical pleats and barb-pockets. Furthermore, unlike the folded paper models (Skaer & Picken, 1965, p. 150), these pleats do not lie flat against the core but stand out like screw-threads, the distal edges of which, however, do not lie in a plane normal to the axis of the core, but are reflected in the direction of the barb-bases and parallel to the axis of the core. This means that, were the thread wall infinitely thin, it would be unnecessary to suppose any non-homogeneous deformation of the surface to occur during discharge.

Though the Cellophane model shows that the surface of the undischarged thread is not strictly comparable with a screw-surface, it does not exactly reproduce the contours of the Araldite cast. This may be due in part to the rigidity of Cellophane and its consequent liability to kink and crease. It was found that a less rigid material such as velvet, which folds without kinking and creasing, gave a better result. The conspicuously smooth folds of velvet are due to racking of the weave (common to all woven fabrics), combined with accentuation of the folds by the absence of reflexion from the surface, owing to the pile, save at folds. Because of the possibility of racking (that is, of local, small-scale anisometric deformation) a woven fabric does not normally kink.

In making the velvet model (Pl. 1, fig. 4), the barbs were attached to the wrong side of the velvet, following the same procedure of marking the rectangular sheet of velvet as for the Cellophane model. The barbs were then gathered into the close-packed condition as before.

This model (Pl. 1, fig. 4), is evidently more like the Araldite cast than is the Cellophane model. In particular, the external portions of the barb-pockets are now clearly visible. The model does not, however, show the longitudinal fluting visible in the Araldite cast, and the edges of the pleats are less sharply folded. It is clearly unnecessary to suppose that any considerable local dilatation or contraction of the surface of the undischarged thread takes place during eversion, other than that which occurs in unfolding a folded surface of finite thickness. Transformation to the discharged condition would then be due exclusively to the smoothing of the folds in the thread-wall, and the 'extra' surface to be supplied during transformation would derive from the reflected pleats and from the barb-pockets.

Since the core of close-packed barbs was accepted as a determinant in the construction of both Cellophane and velvet models, it is necessary to consider whether the actual developmental sequence in fact resembles the stages followed in the construction of these models.

There is no evidence as yet that this is so. Indeed, the limited evidence available suggests that the barbs form comparatively late in development (Slautterback, 1963; Lentz, 1965). Furthermore, though barbs appear to be entirely absent in the spirocysts of *Corynactis* (Skaer & Picken, 1965), the undischarged thread of the spirocyst displays three helical pleats and some suggestion of pockets. It may be, therefore, that something in the structure and conditions of formation of the tubular thread itself predisposes it to form helical pleats and pockets when its volume is reduced—as it appears to be during the last stages of maturation of the nematocyst. The possible cause of the observed reduction in volume and change of shape of the undischarged thread during development was discussed by Skaer & Picken (1965).

For comparison with these models of the undischarged thread, a further model was constructed, showing the result of transformation during discharge. In making this model (Pl. 1, fig. 2), a marked sheet, prepared as for the Cellophane model (p. 174) was placed in position inside a glass cylinder of appropriate diameter, and barbs were stuck to the external surface of the cylinder (with Araldite glue) at positions marked on the internal sheet. In Pl. 1, fig. 3, the Cellophane model is equivalent to the discharged model in fig. 2, but the barbs are not maximally close-packed, so that the pleats may show more clearly. The transformation from the maximally close-packed to the expanded condition amounts to an increase in length of 3·08 times. This figure may be compared with the value obtained by measurement of median longitudinal sections of partially discharged nematocyst threads, namely, 2·93 times (Skaer & Picken, 1965).

SUMMARY

1. Both Cellophane and velvet models have shown that packing barbs, attached to the inside of a fabric cylinder, in alternating whorls of three, generates a configuration of the fabric surface closely similar to that observed in the undischarged thread of the large holotrichous isorhizas of *Corynactis viridis* Allman.

2. When this assembly is caused to transform to the discharged configuration (*a*) there is no change in surface area and (*b*) there is no significant distortion of the fabric.

3. The model increases 3·08 times in length on transformation to the discharged configuration, as compared with an increase of 2·93 times measured on electron micrographs of median longitudinal sections.

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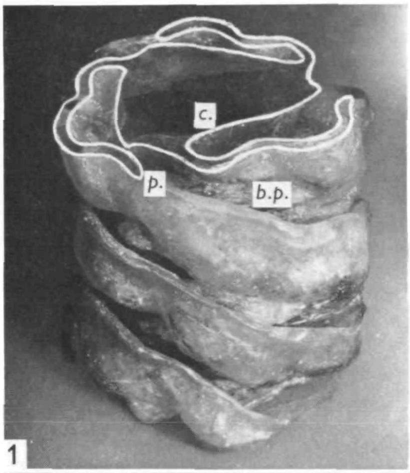
EXPLANATION OF PLATE

Fig. 1. Araldite cast of a wax model of a short length of the undischarged nematocyst thread of a large holotrichous isorhiza of *Corynactis viridis* Allman. The model was prepared by serial reconstruction from electron micrographs of transverse ultrathin sections, and the edge of the topmost section is outlined in white. The barbs, not shown, would occupy the central triangular core (*c.*), and their tips would point towards the bottom of the page. Because of the method of construction, this is a solid model, and the pleats (*p.*) in the thread surface are translated into helical flanges. Note portions of barb-pockets (*b.p.*), and longitudinal rifling of the surface. The approximate diameter of the sectioned thread was 4·5 μ.

Fig. 2. Glass and Araldite model of a short length of discharged nematocyst thread. A short length can be represented as a cylinder, although the entire thread exhibits a very gradual taper. The diameter of the tubular thread is about 5 μ. The barbs are disposed in whorls of three and on three helical barb-rows. A model of an equivalent length of undischarged thread is shown in fig. 3.

Fig. 3. Cellophane and Araldite model of a short length of undischarged nematocyst thread. The barbs are not maximally close-packed (p. 174), in order that the helical pleating may be seen more clearly. Fig. 2 is the equivalent of this model after discharge.

Fig. 4. Velvet and Araldite model of a short length of undischarged nematocyst thread, showing a pleated surface resembling that of the Araldite cast in fig. 1. Note also the external portions of the barb-pockets. The barb tips point towards the bottom of the page.



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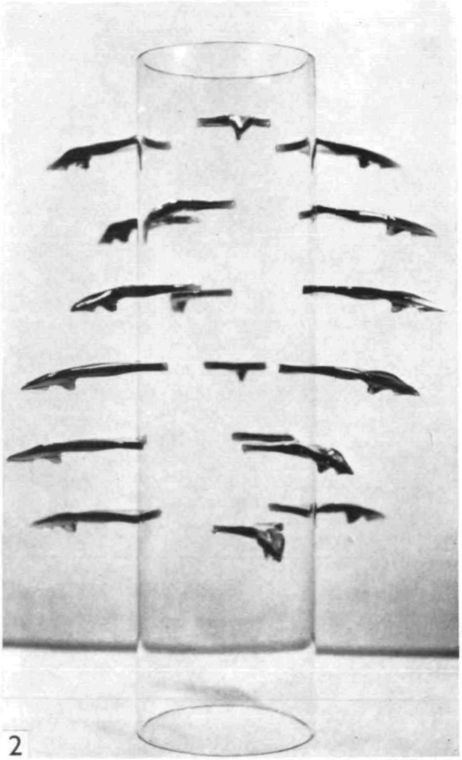

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