

Epiphyte survival on skin-shedding macrophytes

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ABSTRACT: Skin-shedding in *Himanthalia elongata* (L.) S. F. Gray is more active on receptacles than on vegetative thalli. *Elachista scutulata* (Sm.) Aresch. and *Herponema velutinum* (Grev) J. Ag. are epiphytes specific to *Himanthalia* receptacles. Scanning electron microscope (SEM) studies indicate that their ability to by-pass the antifouling effects of skin-shedding may be due to successful exploitation of cryptostomata and other natural breaks in the host thallus surface. SEM investigation of spore settlement by *E. fucicola* (Vell.) Aresch. on *Fucus vesiculosus* L. also revealed dense spore aggregation in the vicinity of cryptostomata.

INTRODUCTION

Periodic abscission of epidermis by *Ascophyllum nodosum* (L.) Le Jol. has been reported by Filion-Myklebust and Norton (1981). Moss (1982, 1984) has since demonstrated the shedding of flakes of outer cell wall material from epidermis of *Halidrys* and other furoid genera, this process being accomplished without loss of, or damage to, the epidermal cells. Although the 2 accounts differ in detail, they agree that skin-shedding is a defence mechanism against fouling by algal epiphytes. The following observations suggest that a slightly modified interpretation of this process may be necessary, as reported briefly by Russell and Veltkamp (1982).

MATERIALS AND METHODS

Skin-shedding was studied in *Himanthalia elongata* (L.) S. F. Gray collected from Scarlett Point, Isle of Man, U.K. (53° 3' 25" N, 4° 39' 30" W) in late summer 1981. Portions of thallus were fixed in 5 % formalin-seawater for 24 h, washed in distilled water, then dehydrated in an acetone series of 2.5, 5, 7.5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100, 100 %. Two changes were made daily so that dehydration was accomplished in 8 d, slow dehydration having been found to minimise cell-wall distortion. Thallus pieces were critical-point dried, coated with 60 % gold-palladium and scanned using a Philips 501B Scanning Electron Microscope (SEM). Development of the epiphytes *Elachista scutulata* (Sm.) Aresch. and *Herponema velutinum*

(Grev) J. Ag. on *Himanthalia*, was also studied by SEM, using the same approach. Spore settlement by *E. fucicola* (Vell.) Aresch. was examined by pipetting a zoospore suspension obtained from fertile thalli into culture vessels containing clean thallus apices of *Fucus vesiculosus* L. The material was incubated for 24 h at 10 °C in an 8–16 h photoperiod of 11 Wm⁻². It was then fixed in 5 % formalin-seawater and prepared for SEM as described above. The choice of these species was determined by the fact that they are more readily obtainable and easier to manipulate experimentally than *E. scutulata* and its host.

RESULTS

Skin-shedding was most active and most extensive on reproductive tissue, Fig. 1. The skin always consisted of wall material only, Fig. 2, and, in agreement with Moss (1982), no cells were shed or damaged. The dorsal surface of the vegetative thallus sheds skin less frequently and more in the form of small flakes, while the ventral surfaces were the least active of all. On the ventral surface microbial fouling was evident and there appeared to be little skin-shedding. Transverse sections through developing *Elachista scutulata* thalli usually revealed the emergence of this epiphyte from conceptacles of *Himanthalia*, Fig. 3. Located between the expanding epiphyte and its host were 15 to 20 skin layers which the epiphyte had effectively imprisoned (Fig. 4). These layers had been trapped prior to fixation and treatment for SEM, thus dispelling any suspicion that skin-shedding might be an artifact. The rapid

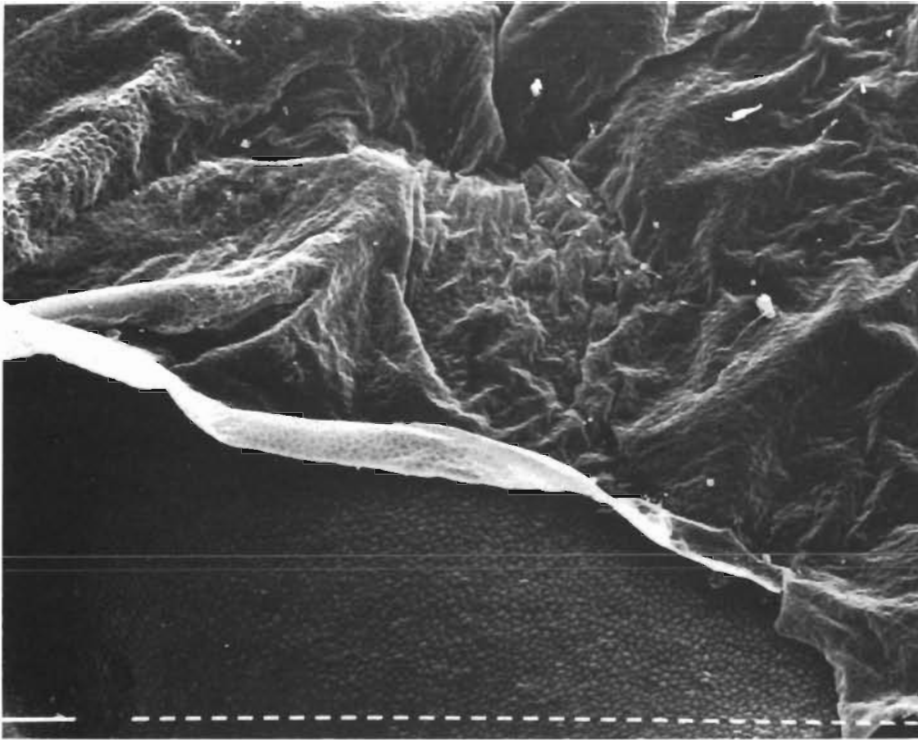


Fig. 1. *Himanthalia elongata*.
Portion of receptacle showing
abscission of extensive skin
layer. Scale bars = 10 μ m

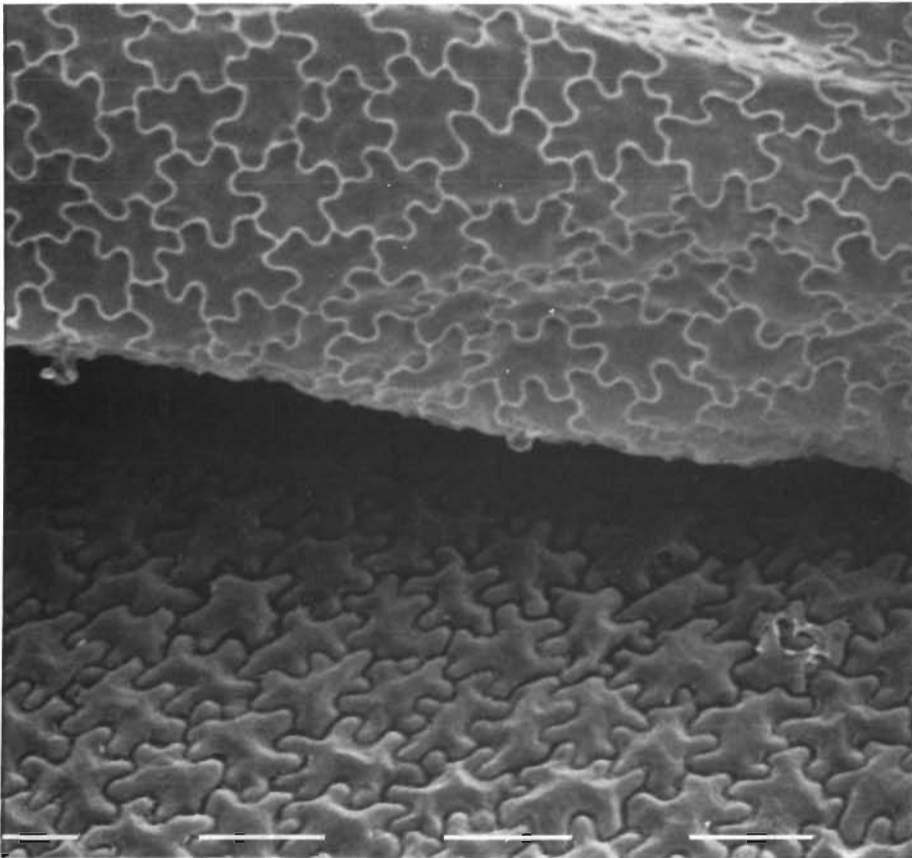


Fig. 2. *Himanthalia elongata*.
Detail of skin abscission from
receptacle. Skin consists of
outer wall layers of epidermis
plus a small portion of inner
wall material. Scale bars =
10 μ m

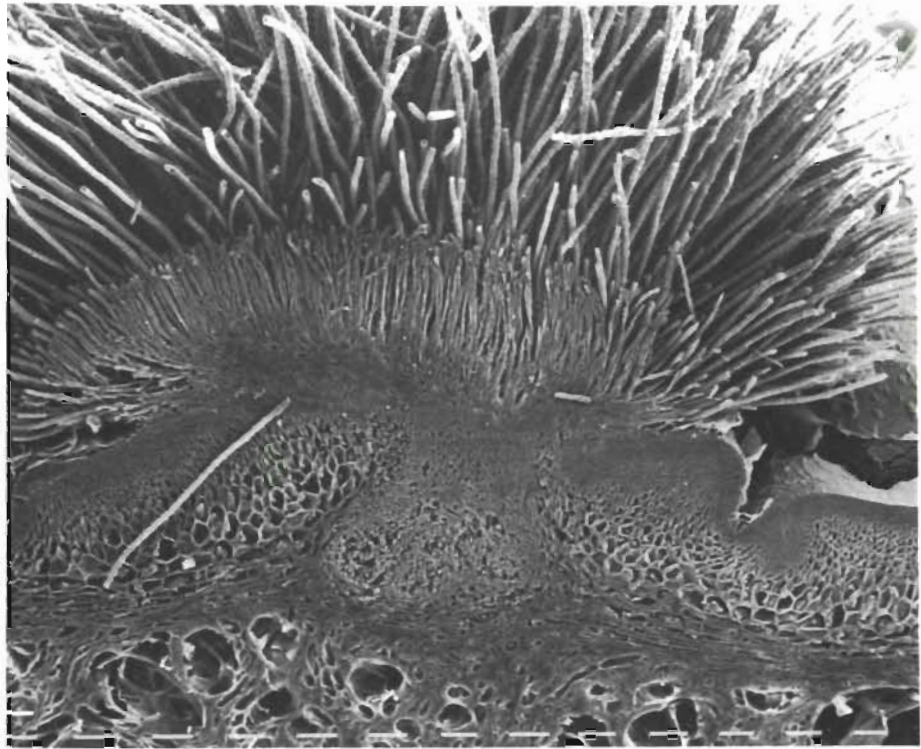


Fig. 3. *Himanthalia elongata*. Transverse section of receptacle showing emergence of *Elachista scutulata* from a host conceptacle. Scale bars = 100 μ m

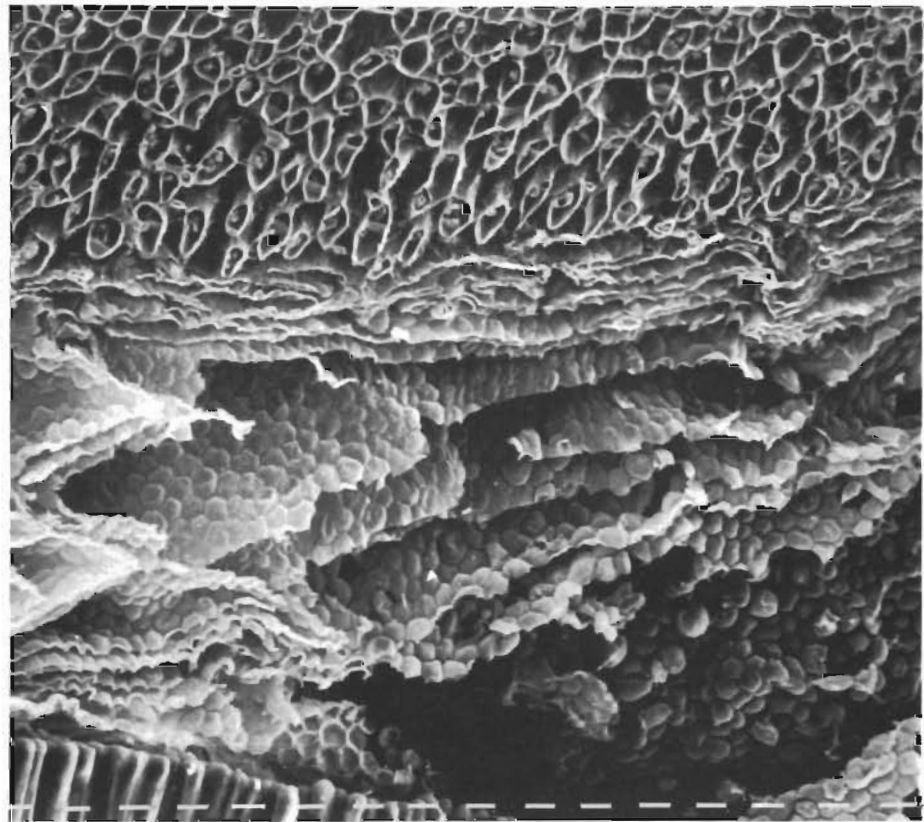


Fig. 4. Tangential section of *Elachista scutulata* filaments (top), and radial section of *Himanthalia elongata* (bottom), with accumulation of skin layers trapped between. Scale bars = 10 μ m

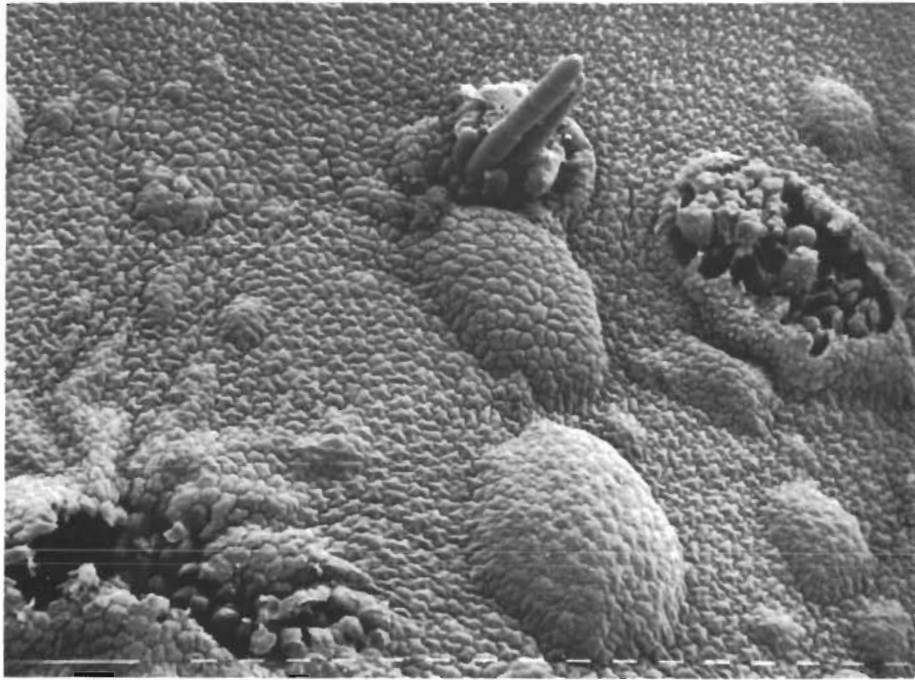


Fig. 5. *Herponema velutinum* filaments emerging from surface of *Himanthalia* receptacle which is shedding its skin. Scale bars = 10 μ m

expansion of emergent *Elachista* thalli in nature suggests an abscission frequency which may be measured in days rather than weeks. *Herponema* filaments were observed to emerge from many parts of the host receptacle and less frequently from conceptacle mouths than *E. scutulata*; they also grew from host tissue which was

actively shedding skin (Fig. 5). However, skin-shedding seemed to slow down with the rapid maturation of this epiphyte, and without the trapping of cell wall layers as in the case of *E. scutulata*.

Spore settlement by *Elachista fucicola* proved to be extremely uneven, being very sparse on the open sur-

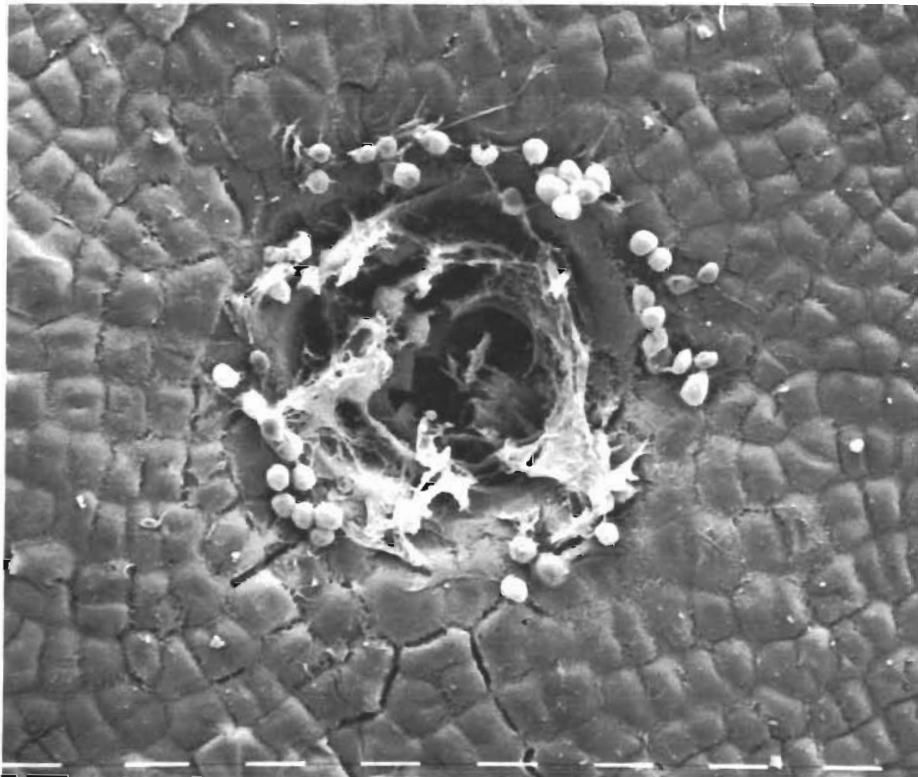


Fig. 6. *Fucus vesiculosus*. Mouth of developing conceptacle on thallus showing dense aggregate of 40 to 50 settled zoospores of *Elachista fucicola*. Scale bars = 10 μ m

face of the *Fucus* thallus, but dense in the concavities which marked the positions of developing cryptostomata (Fig. 6).

DISCUSSION

Elachista scutulata and *Herponema velutinum* are epiphytes strongly specific to *Himanthalia*. Their specificity is even more narrow, being restricted to the reproductive parts of the host (Hamel, 1931–39; Levring, 1937). The reproductive thallus at full size is a much larger structure than the vegetative 'button' and its greater surface area would therefore make it more likely to intercept randomly-moving zoospores. On the other hand, the greater longevity of the button might be expected to redress that imbalance a little, and occasional incidences of these epiphytes on vegetative thalli should occur. No such cases have been found either in the course of this investigation or in the literature, however. The absence of these epiphytes from *Himanthalia* buttons cannot be explained in terms of greater skin-shedding activity on vegetative thalli, since vegetative thalli are less active. It may be deduced, therefore, that the epiphytes possess means of by-passing the antifouling functions of the host receptacle. Preferential spore settlement by *E. fucicola* in the mouths of cryptostomata, where skin-shedding does not occur, offers a possible explanation. This settlement pattern need not involve cryptostomatal recognition, as spore aggregates were also observed in scratches formed naturally on the *Fucus* thallus surface. The vegetative thallus of *Himanthalia* lacks cryptostomata, as do those of *Ascophyllum* and *Halidrys*. The occurrence of a sparse epiflora on *Ascophyllum* (Filion-Myklebust and Norton, 1981) and the noted presence of epiphytes on spent receptacles of the latter (Moss, 1982) are therefore consistent with the view that

epiphytes may effect entry into host tissue via apertures in the thallus surface. The frequent associations of *E. scutulata* with *Himanthalia* conceptacles also led Hamel (1931–39) to this conclusion.

Skin shedding may serve as a defence mechanism against epiphytes in general, but it may also operate selectively in favour of those epiphytic species that have evolved the means to evade its effects. Skin shedding would appear to be most active in young, rapidly-growing tissue and hence it may also promote gradients in epiphyte distribution as occurs, for example, in *Laminaria* species (Russell, 1983a, b). It is thus possible for particular host-epiphyte associations to arise in nature through interactive effects such as these.

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