

## Morphology, anatomy and vegetative reproduction of *Fosliella paschalis* (Corallinaceae, Rhodophyta)

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The morphology, anatomy and vegetative reproduction have been examined in the holotype collection of *Fosliella paschalis* (Lemoine) Setchell & Gardner (Corallinaceae, Rhodophyta) and in new material of this species from the Canary Islands. All attributes characteristic of *Fosliella* Howe, with the exception of conspicuous spore germination discs, are present in the holotype. Morphologically, the type material is characterized by the coexistence of creeping filamentous thalli, minute suborbicular crustose thalli and larger crustose thalli. Loosely and closely coalescent hypothalial filaments occur in different thallus types. Sporangial conceptacles occur on minute orbicular thalli that develop on top of crustose thalli but are not in cellular connection with them. Vegetative propagules occur on some plants. In the Canary Islands plants, propagules arise from non-trichocytic, apparently unmodified hypothalial cells, and at maturity they form plano-convex discs that are attached by a unicellular stalk.

### INTRODUCTION

The circumscription of genera in the *Pneophyllum-Fosliella* complex (Corallinaceae, Rhodophyta) has been attended by uncertainties as indicated by Jones & Woelkerling (1984). Some authors have treated all taxa in the complex as a single genus using the name *Fosliella* Howe (e.g. Taylor 1957, 1960; Cabioch 1972; Bressan 1974; Dawes 1974), or *Heteroderma* Foslie (e.g. Adey 1970; Adey & MacIntyre 1973) or *Melobesia* Lamouroux (Hamel & Lemoine 1953; Kylin 1956; Ardré 1970); others have recognized two genera: *Fosliella* for taxa possessing trichocytes and *Heteroderma* for taxa which apparently lack trichocytes (e.g. Mason 1953; Dawson 1960; Masaki 1968; Johansen 1976, 1981).

Recently, Chamberlain (1983, 1984) recognized two genera: *Fosliella* for taxa possessing terminal hypothalial trichocytes and a four-celled central element in the spore germination disc; and *Pneophyllum* for taxa possessing intercalary hypothalial trichocytes and an eight-celled central element in the spore germination disc. Chamberlain's two genus scheme is supported by data obtained by Jones & Woelkerling (1984) and Harlin *et al* (1985). According to Harlin *et al* (1985), of the 40 species hitherto assigned to the *Pneophyllum-Fosliella* complex, at least 20

have been found to conform to Chamberlain's classification scheme. The present investigation was designed in part to evaluate the criteria of Chamberlain in *Fosliella paschalis* (Lemoine) Setchell & Gardner.

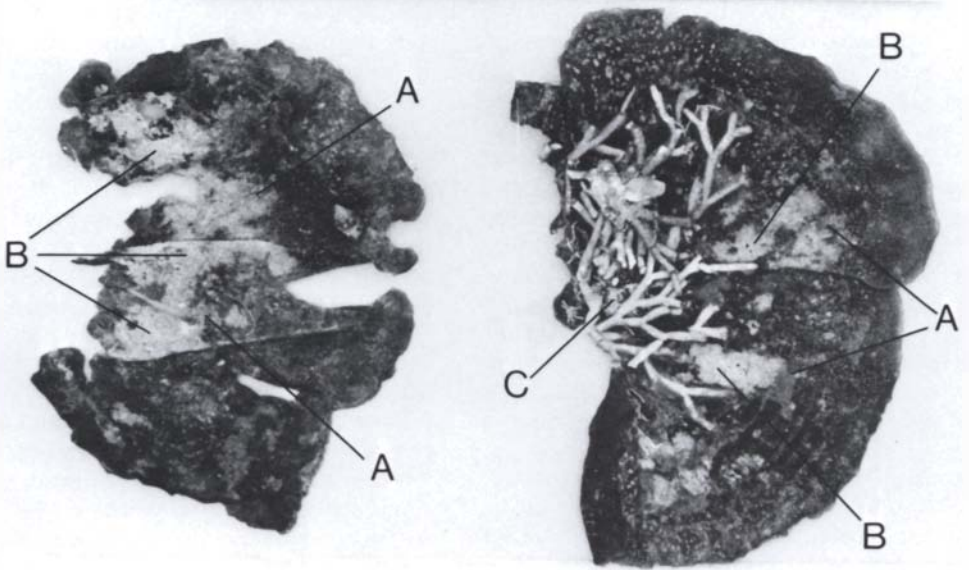
*Fosliella paschalis* was first described by Lemoine (1923, as *Melobesia paschalis*) from Easter Island. According to Lemoine, this taxon is characterized by: a) small, greyish plants in which the thalli are never superimposed; b) loosely coalescent hypothalial filaments; c) terminal hypothalial trichocytes; d) conceptacles smaller than in *Fosliella farinosa* (Lamouroux) Howe; and e) conceptacles in the middle of a mound of perithalial cells. *Melobesia paschalis* was later recorded from Guadalupe Island (and assigned to *Fosliella*) by Setchell & Gardner (1930); Idelfonso Island (Dawson 1960); Japan (Masaki 1968); and California (Hollenberg 1970; Johansen 1976). All these authors have noted the apparent absence of superimposition of thalli and the small conceptacle size in *F. paschalis*, but none has mentioned the presence of perithalial mounds. In addition, Hollenberg (1970) described discoid bodies (propagules) that are believed to function as a vegetative means of reproduction. Similar structures were reported by Solms-Laubach (1881) as occurring on *Fosliella farinosa* (Lamouroux) Howe f. *callithamnioides*

SVENSKA PACIFICEXPEDITIONEN 1916-17.

NR. *Melobesia paschalis* Lemm.  
 (*Zonaria variegata*) *Typus.*  
 ISLA DE PASCUA: *Atord nam Hanga O'ke*  
 ; M. S. M. <sup>20</sup> 1917  
 DET. *M. Lemoine* CARL O. INGA SKOTTSBERG.  
 BR NA WEISS TR

2 cm

TYPUS.



*Ile de Pâques*

1

*Zonaria variegata*  
*Melobesia paschalis* nov. sp.

Fig. 1. Holotype collection of *Melobesia paschalis* Lemoine (GB). Note the distribution of different growth forms: unconsolidated thalli (A); subcircular, superimposed thalli (B); and consolidated thalli (C).

(Foslie) Y. Chamberlain (as *Melobesia callithamnioides*) from the Gulf of Naples, and by Sauvageau (1912, p. 50) from Tenerife (Canary Islands); and recently on *Fosliella farinosa* f. *farinosa* by Coppejans (1978, 1983) from Corsica and by Woelkerling (1988, p. 121, fig. 104) on *Fosliella* sp. from Australia. The occurrence of propagules in both the type and Canary Islands collections of *F. paschalis* has provided an opportunity to study their structure and development in greater detail as a second aim of the present study.

## MATERIALS AND METHODS

Data were obtained from the holotype specimen of *Melobesia paschalis* housed at GB (Botanical Museum, Göteborg, Sweden) and plants collected in the Canary Islands and deposited at TFC (Departamento de Botánica, Universidad de La Laguna, Canary Islands) with the numbers Phyc. 2596 and 5613.

Permanent slides for anatomical studies were prepared both from fresh specimens and dried herbarium specimens (after long rehydration), fixed in 4% formalin in seawater, decalcified in Pérényi's solution and embedded in paraffin. Sections, 8  $\mu\text{m}$  thick, were cut and stained in Ehrlich's haematoxylin-eosine (Bressan 1974). Observations in surface view were carried out on decalcified plants attached to portions of host material, stained with 5% aqueous aniline blue and mounted in 20% aqueous 'Karo' dextrose.

Scanning electron micrographs were obtained from herbarium specimens rehydrated in 4% formalin in seawater, dehydrated in an ethanol series, critical point dried, coated with gold and examined in a Hitachi S-450 Stereoscan Microscope.

## RESULTS

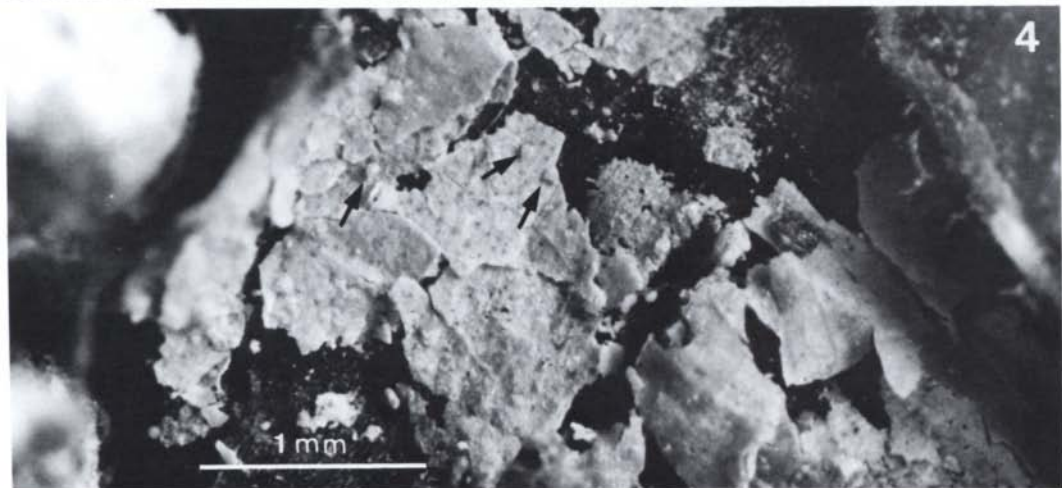
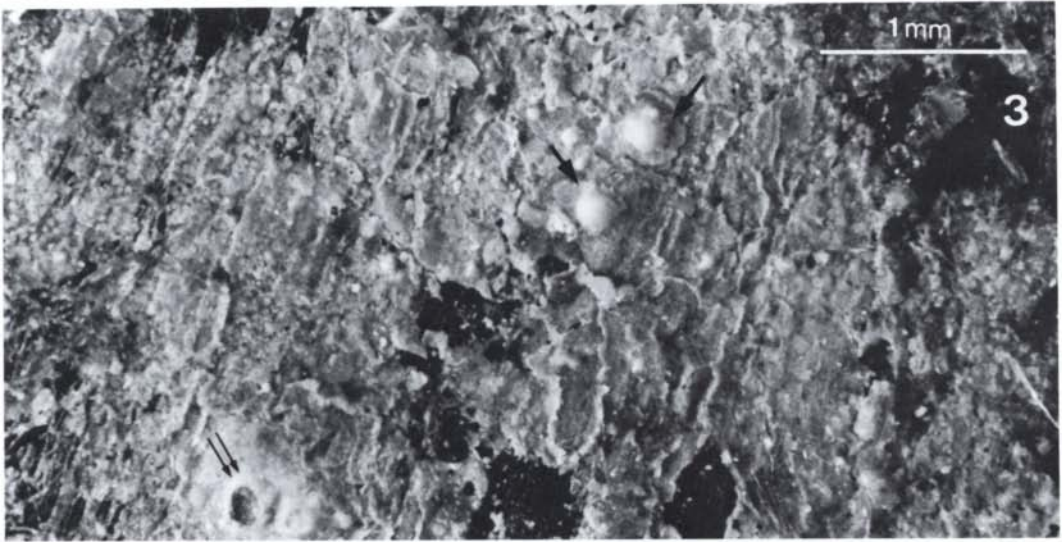
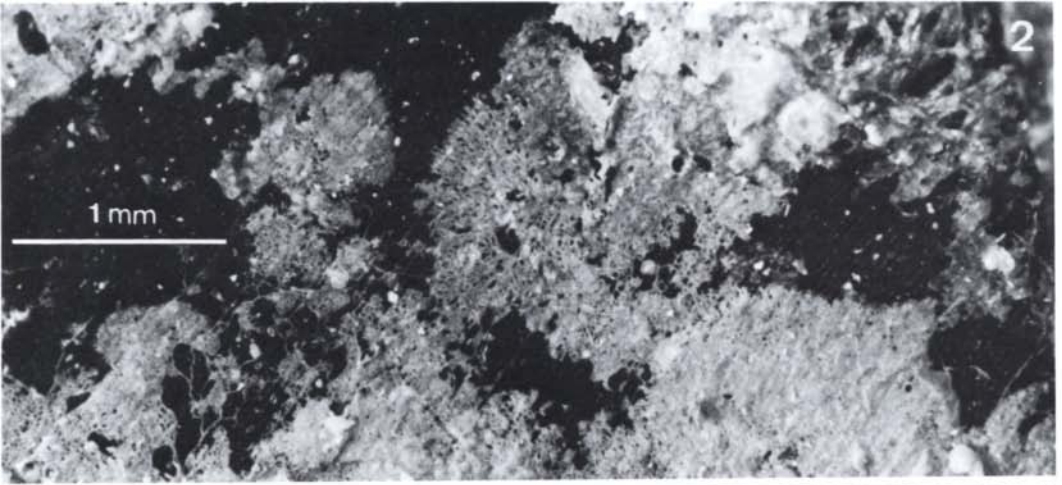
### Holotype collection

The original collection of *Melobesia paschalis* Lemoine consists of a number of small greyish plants of varying appearance growing on *Lobophora variegata* (Lamouroux) Womersley (Dictyotales) (Fig. 1). The irregularly shaped plants are attached to one surface of the host in an area of less than 3 cm diameter. One *Lobophora* plant also has *Galaxaura* sp. branches ad-

hering to the same surface. Three growth forms are present: a) a network of unconsolidated anastomosing filaments which do not superimpose and do not bear propagules and conceptacles (Fig. 2); b) minute, suborbicular, crustose thalli (up to 0.5 mm) occurring on the surface of unconsolidated filamentous thalli, either with a uniporate hemispheric-conical conceptacle (Fig. 3) that arises very abruptly or a small concavity formed by the collapse of the conceptacle; and c) fragments of consolidated crustose thalli (up to 3 mm) with only a uniporate hemispheric-conical conceptacle and discoid vegetative propagules (Fig. 4). No morphological differences are to be found between the conceptacles from the minute crustose thalli and the single conceptacle from consolidated crustose thalli. These different growth-forms are distributed on the dorsal thallus surface of *Lobophora* (Fig. 1). Fragments of consolidated thalli occur only on the more central area of host thallus, while unconsolidated thalli occur more marginally. Minute suborbicular thalli occur on the surface of the more centrally situated filamentous thalli.

All plants in the holotype collection have a single basal layer (Fig. 9) of radiating hypothallial filaments with or without an epithallial cell on the upper distal surface of each cell. Perithallial cells are absent except in the vicinity of conceptacles. Germination discs do not occur. Unconsolidated thalli (Figs 5, 6) are characterized by anastomosing hypothallial filaments that have radially elongated, subcylindrical cells subtending rounded epithallial cells; terminal trichocytes are present and cell fusions are rare. Dimensions of vegetative structures are summarized in Table 1. Two different types of hypothallial filaments are present (Figs 5, 6). In one, the filaments are very long and sparingly branched, forming an irregular open, angular framework which becomes infilled by a second type of richly branched, secondary, lateral filaments. The significance of these apparently different types of filaments in thallus development is difficult to assess at present, and culture studies are needed to clarify this matter. Minute crustose thalli grow on the surface of filamentous thalli but there is no cellular connection between these and the filaments below.

No anatomical differences occur between the minute crustose thalli and fragments of consolidated thalli. Both are composed of closely coalescent hypothallial filaments (Fig. 7) with rare fusions between contiguous cells. The dimen-



sions of hypothallial cells, trichocytes and epithallial cells (Table 1) are similar to those described for anastomosing thalli. Vegetative propagules occur on some thalli; young propagules are unicellular and pear-shaped, whilst mature ones (Fig. 8) are multicellular, discoid, and are attached by a unicellular stalk to nontrichocytic hypothallial cells (Fig. 8). Vertical sections of anastomosing and consolidated thalli show hypothallial cells that are either subquadrate or slightly wider than high (Fig. 9). Epithallial cells are not evident in sections. Two-celled perithallial filaments are present on discoid thalli in the vicinity of conceptacles (Fig. 10). One conceptacle from a minute crustose thallus of the holotype material was examined anatomically (Fig. 10). This has a more or less ovoid chamber; the roof is 2–3 cells thick and thickens markedly round the ostiole to form a canal about 30  $\mu\text{m}$  long. A few tetrasporangia and bisporangia are present but sterile paraphyses are not apparent. Dimensions of the reproductive structures are summarized in Table 1.

### Canary Islands plants

Epiphytic consolidated thalli of *F. paschalis* were collected on *Sargassum vulgare* C. Agardh. Individual plants are up to 5 mm in diameter, greyish in colour and adhere strongly to the host (Fig. 11). Adjacent thalli do not superimpose, but small suborbicular crustose thalli develop superimposed on old consolidated thalli. Conceptacles are absent.

Thallus organization in surface view (Fig. 12) is similar to that of the consolidated thalli of the holotype (Fig. 7). Germination discs were not observed, but numerous propagules occur (Fig. 11). Scanning electron micrographs (Figs 13–15) obtained from herbarium specimens show slightly deformed discoid propagules attached by a small stalk to the thallus surface. The convex surface of each propagule shows some epithallial concavities (Fig. 14). At the margin, the terminal cells have collapsed (Fig. 15) because the outer wall is uncalcified; a similar structure occurs in

**Table 1.** Dimensions of vegetative and reproductive structures of the holotype of *Melobesia paschalis* Lemoine (in  $\mu\text{m}$  unless stated)

Vegetative structures (including all three growth forms)	
Thallus diameter	up to 3 mm
Thallus depth	c. 15
Thallus cell length	9–21
Surface width	5–12
Thallus cell height	5–9
Epithallial cell length	2.4–5
Surface view width	5–7
Trichocyte type	terminal
Trichocyte length	12–15
Surface view width	7–9
Propagules	discoid
Tetrasporangial and bisporangial conceptacle	
External diameter surface	144
VS internal diameter	113
VS height	96
Tetrasporangium length	24–36
Tetrasporangium width	14–20
Bisporangium length	21–34
Bisporangium width	9–17

the terminal meristematic cells of the hypothallial filaments.

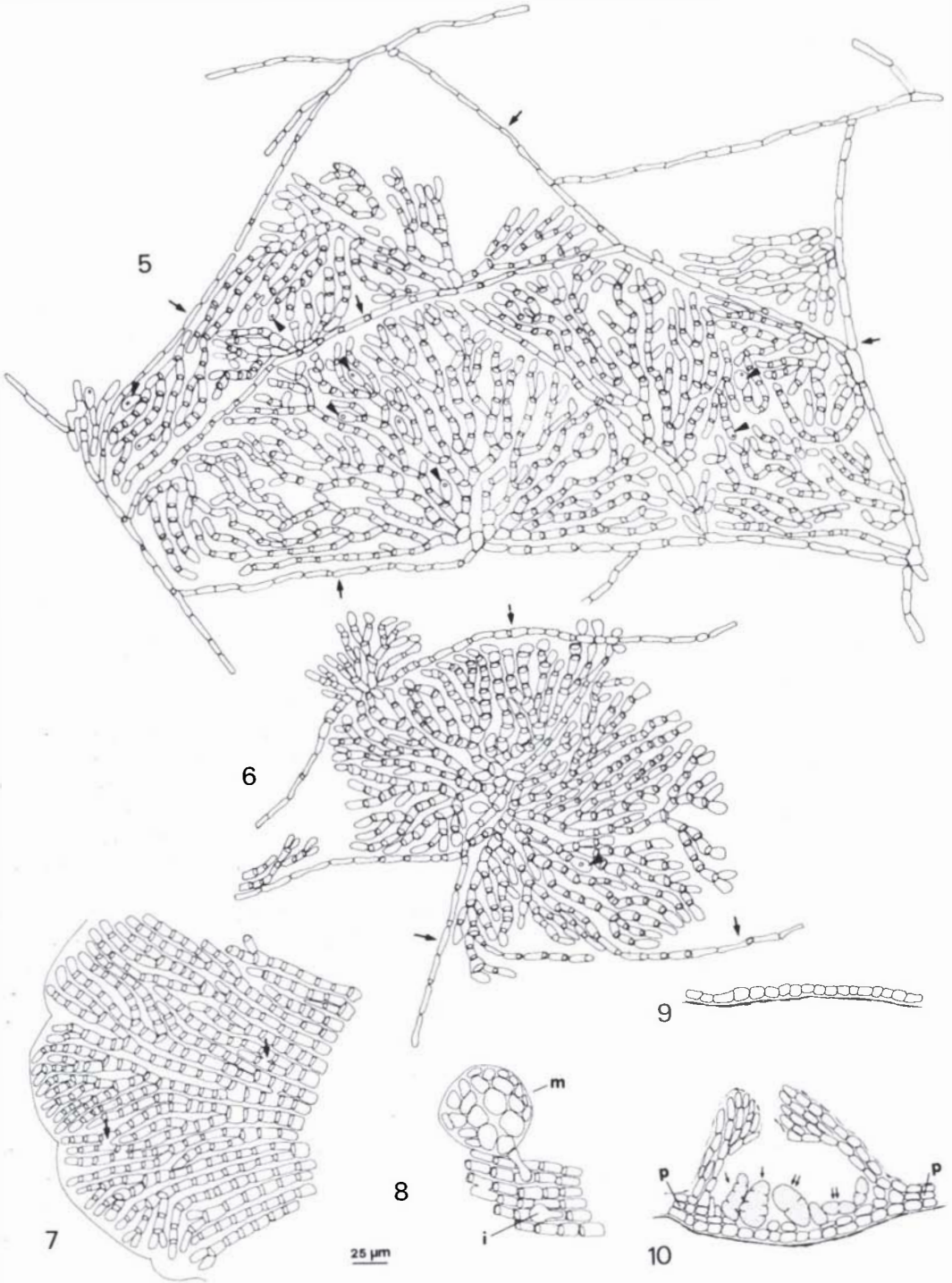
Propagules arise from nontrichocytic, apparently unmodified, hypothallial cells. In section, the first detectable sign of propagule development is a transverse cell division (Fig. 16). The new cell elongates and becomes pear-shaped (Fig. 17) and visible in surface view (Fig. 20). The pear-shaped cell divides transversely to produce a spherical terminal cell and an elongated basal cell (Fig. 18). The cellular disc (propagule) then develops from the spherical terminal cell (Fig. 19) whilst the basal cell becomes a stalk. Scission of the stalk results in detachment of the mature propagule. Different stages of propagule development, seen in surface view, are shown in Figs 20–27. At maturity, the racquet-shaped propagules are up to 80  $\mu\text{m}$  broad by 100  $\mu\text{m}$  long (Fig. 27) and slightly plano-convex in side view. Propagules are monostromatic except for small epithallial cells present only on the convex surface. This monostromatic organization is comparable with a hypothallium. It consists of two principal

**Figs 2–4.** Holotype of *Melobesia paschalis* Lemoine.

**Fig. 2.** Surface of the holotype showing anastomosing, unconsolidated filamentous thalli covering the substratum.

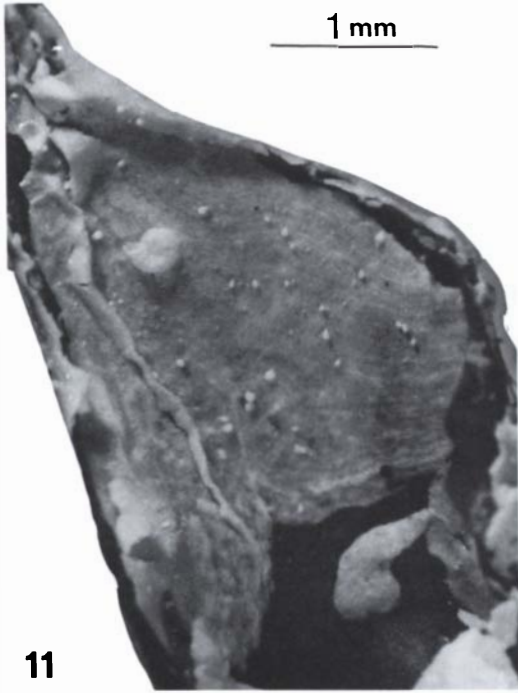
**Fig. 3.** Surface of the holotype showing minute suborbicular crustose thalli placed on the filamentous thalli, with uniporate conceptacles (arrow) or small concavity formed by the collapse of the conceptacle (arrows).

**Fig. 4.** Surface of the holotype showing fragments of large, consolidated crustose thalli with discoid vegetative propagules (arrow).



**Figs 5–10.** Holotype of *Melobesia paschalis* Lemoine.

**Figs 5, 6.** Surface view of anastomosing filamentous thalli with large, sparingly branched hypothalial filaments forming an irregular framework (arrows) in-filled with richly branched hypothalial filaments. Note terminal trichocytes (arrowheads).



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Fig. 11. Large crustose thallus of *Fosliella paschalis* from the Canary Islands showing numerous propagules (TFC Phyc. 2596).



Fig. 12. Surface view of thallus of *Fosliella paschalis* from the Canary Islands showing coalescent hypothalial filaments (TFC Phyc. 2596).

filaments of rounded cells, 8–14  $\mu\text{m}$  in diameter (Fig. 27), surmounted by epithalial cells. The cells of the principal filaments form very short, lateral filaments of smaller cells. The diameters of cells decrease from the centre to the margin resulting in a convex surface.

Detached propagules settle on the thalli of both *Fosliella paschalis* itself and *Sargassum vulgare*. Propagule germination occurs by centrifugal growth of the disc margin (Figs 28, 29).

## DISCUSSION

Five of the six characters (Chamberlain 1983) used to circumscribe *Fosliella* Howe are present in the holotype of *Melobesia paschalis*. These are:

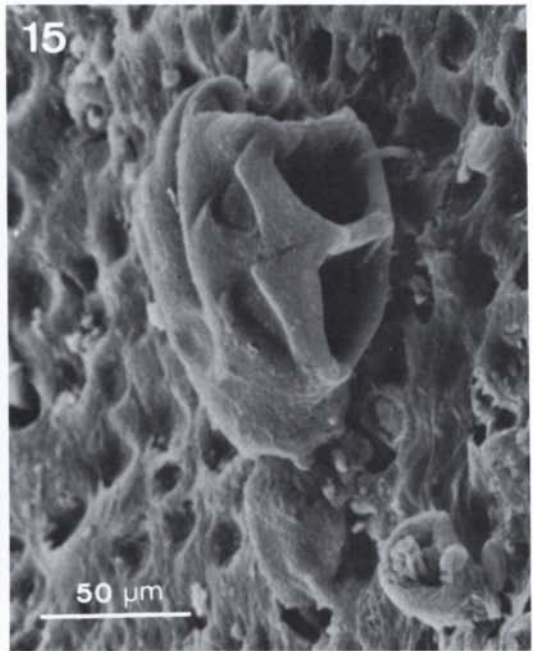
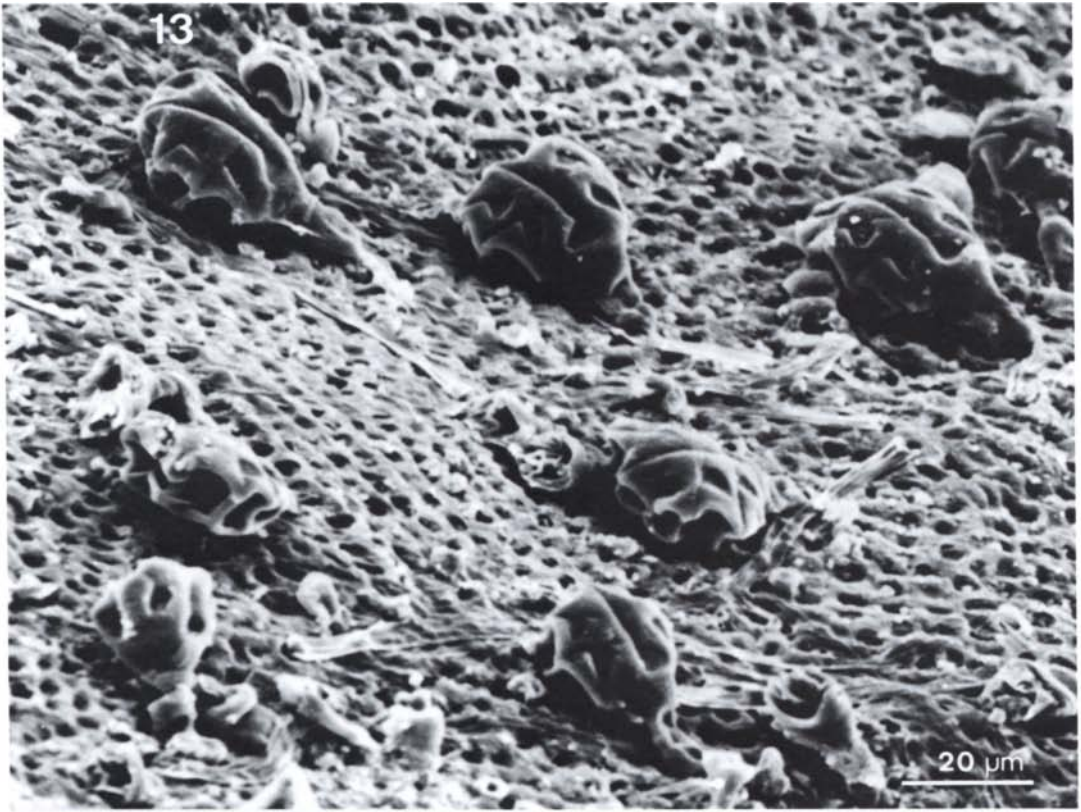
a) thallus nongeniculate; b) tetrasporangial conceptacles uniporate; c) crustose vegetative thallus composed of rectangular-celled hypothalial filaments and rounded epithalial cells; d) cells of contiguous filaments interconnected by cell fusions; and e) terminal hypothalial trichocytes. A spore germination disc with a central element of four cells is the only character not recognizable in the holotype. According to Chamberlain (1983) and Jones & Woelkerling (1984), the cellular arrangement in the germination disc is the most significant character for delineating *Fosliella* from *Pneophyllum*, although this character is correlated with the trichocyte position. The presence of terminal trichocytes in the holotype of *Melobesia paschalis* confirm the assignment of this taxon by Setchell & Gardner (1930) to *Fosliella*.

Fig. 7. Surface view of closely coalescent hypothalial filaments of minute suborbicular crustose thalli. Cell fusions (arrows) are uncommon.

Fig. 8. Surface view of initial (i) and mature propagule (m) on a large consolidated thallus.

Fig. 9. Vertical section of vegetative thallus showing hypothalial cells.

Fig. 10. Vertical section of conceptacle from minute thallus with tetrasporangia (arrow), bisporangia (arrows) and perithalial cells (p).



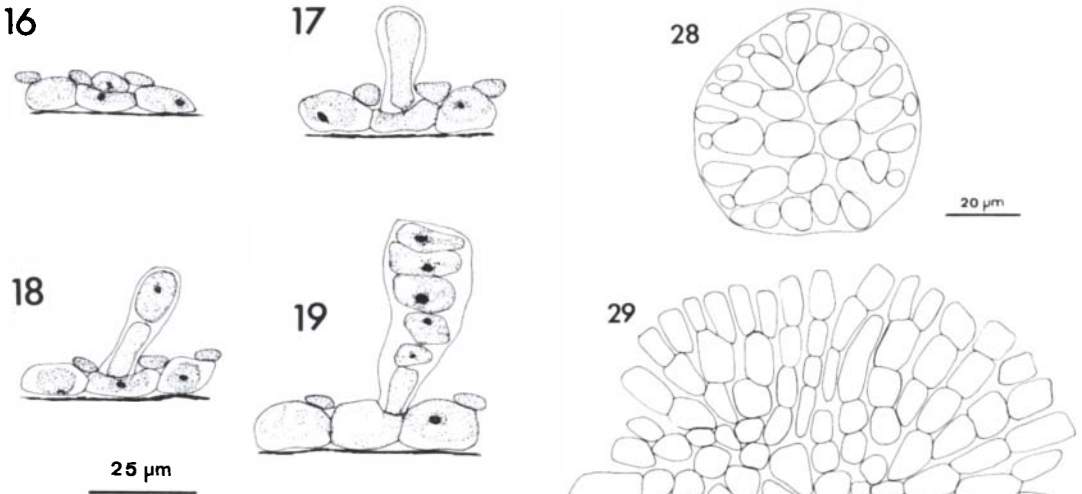
**Figs 13–15.** Scanning electron micrographs of propagules of *Fosiella paschalis* from the Canary Islands (TFC Phyc. 2596).

**Fig. 13.** Surface of the thallus with propagules.

**Fig. 14.** Surface view of a propagule showing some epithallial concavities (arrows) on the convex surface.

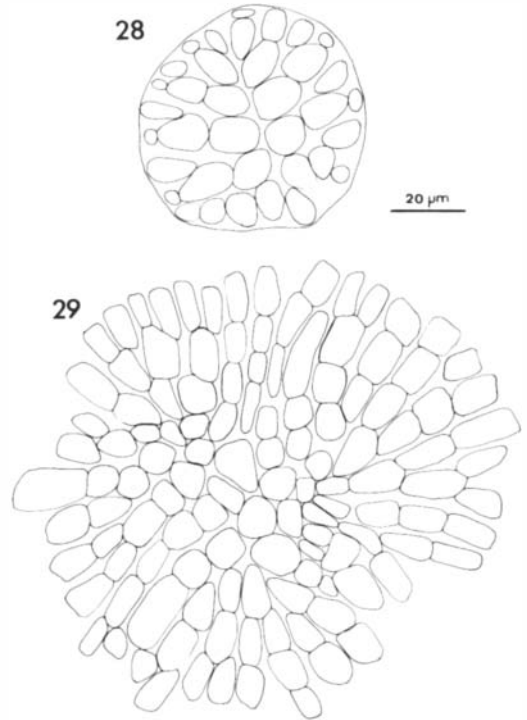
**Fig. 15.** Marginal view of a propagule showing the spaces formerly occupied by terminal cells.



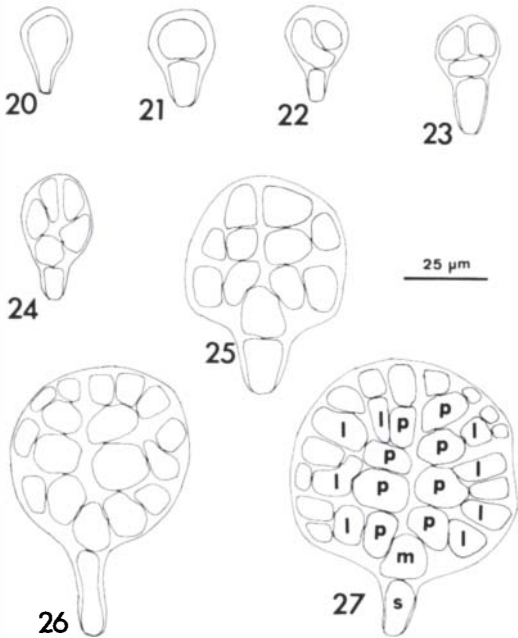


**Figs 16–19.** Vertical sections of plants of *Fosliella paschalis* from the Canary Islands showing different stages of propagule development (TFC Phyc. 2596).

- Fig. 16.** Transverse cell division of an apparently unmodified hypothalial cell.
- Fig. 17.** Elongation and differentiation of the pear-shaped cell.
- Fig. 18.** Transverse division of the pear-shaped cell forming the stalk and the mother cell of the cellular disc of the propagule.
- Fig. 19.** Mature propagule.



**Figs 28, 29.** Surface view of different stages of propagule germination (epithalial cells not represented). TFC Phyc. 2596.



**Figs 20–27.** Surface view of different stages of the propagule development on thalli of *F. paschalis* from the Canary Islands (epithalial cells not represented); (l, lateral filament; m, mother cell; p, principal filament cells; s, stalk). TFC Phyc. 2596.

The absence of germination discs can be correlated with the vegetative reproduction. In other species of the *Pneophyllum-Fosliella* complex, Harlin *et al* (1985) found that individuals without germination discs result from vegetative thalli fragmentation. Nevertheless, evidences of vegetative thalli fragmentation were not observed in the material examined and probably the absence of germination discs in the type material indicates the importance of propagules as a means of reproduction.

The holotype of *Melobesia paschalis* exhibits three morphologically diverse types of growth-form developing unconsolidated and consolidated thalli. A similar morphological plasticity has been reported in other species of the *Pneophyllum-Fosliella* complex. Chamberlain (1983, p. 352) reported the occurrence of consolidated and unconsolidated thalli in *Fosliella farinosa*; she suggested that the two forms were not genetically distinct, but nevertheless retained *f. calithamnioides* to designate the unconsolidated form until more accurate data were available to establish the relationship between the thallus types.

In *F. paschalis* the margins of adjacent thalli do not superimpose. Nevertheless, minute sub-orbicular crustose thalli grow on the surface of old filamentous thalli. These minute thalli lack a germination disc and consequently could have arisen from propagules. Frequently a conceptacle arises from the central portion of these thalli. The perithallial mounds described by Lemoine (1923) surrounding the conceptacles are really hypothallial cells of these minute thalli.

Propagules of *F. paschalis* show different features from those reported by Solms-Laubach (1881) and Coppejans (1978, 1983) in *F. farinosa*. Propagules of *F. farinosa* are triangular in morphology, have principal filaments marginally placed, cells without outer wall calcified restricted at the distal margin, and propagule germination occurring only by growth of the cells placed at the corners. The diagnostic value of these differences may be useful in absence of other characters. Propagule development is similar to that described by Hollenberg (1970) in *F. paschalis* from California, except that propagules arise from nontrichocytic, apparently unmodified, hypothallial cells. Hollenberg (1970) observed propagules as outgrowths of megacells (trichocytes), but this needs to be confirmed.

The discovery of *F. paschalis* in the Canary Islands represents the first record of this species from the coast of the Atlantic Ocean. This taxon may be widely distributed, and records of similar species should be checked for possible misidentification.

## ACKNOWLEDGMENTS

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