EPIPHYTIC CORALLINE CRUSTS (CORALLINALES, RHODOPHYTA) FROM SOUTH NORWAY

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SARSIA

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Eight species of epiphytic crustose coralline algae (Corallinaceae, Rhodophyta) were identified from southern Norway. The species were studied by light microscopy and scanning electron microscopy (SEM), and were identified by vegetative and reproductive features and the morphology of the spore germination discs. The four genera *Titanoderma* Nägeli, *Hydrolithon* Foslie, *Pneophyllum* Kützing and *Melobesia* Lamouroux were represented. *Hydrolithon cruciatum* (Bressan) Y. Chamberlain and *Pneophyllum myriocarpum* (P. & H. Crouan) Y. Chamberlain were new records for Norway. *Titanoderma pustulatum* (Lamouroux) Nägeli was represented by the two varieties: var. *pustulatum* (Lamouroux) Nägeli and var. *confine* (P. & H. Crouan) Y. Chamberlain.

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Keywords: Red algae; coralline crusts; epiphytic.

INTRODUCTION

Coralline red algae have a global distribution and occupy a range of habitats in both warm and cold waters (Littler 1972, Johansen 1981, Woelkerling 1988). Their calcareous thalli make them resistant to grazing (Steneck 1986). Overgrazing by sea urchins of the kelp beds in North Norway has resulted in “barren grounds” where bleached corallines are the only macrophytes left (Hagen 1983). A similar situation is found on stipes of *Laminaria hyperborea* (Gunnerus) Foslie, where crustose corallines may be the only macroscopic epiphytes in areas with high densities of sea urchins (Fredriksen & al. 1995).

Although there have been many studies of algal communities along the Norwegian coast, few of them have dealt with corallines since Foslie’s numerous collections and publications (e.g. Foslie 1905, for bibliographies and type collections see Printz 1929 and Woelkerling 1993). Adey (1971) reported on geographical and depth distributions of epilithic crustose corallines on the Norwegian coast, but recent information on epiphytic species is scant. Recent taxonomic revisions of corallines from various parts of the world (see Woelkerling 1988) have resolved many taxonomic, nomenclatural and biological problems related to this group of algae. The thorough studies of epiphytic crustose corallines by Chamberlain e.g. 1983, 1991) and the published flora of coralline red algae of the British Isles by Irvine & Chamberlain (1994) have greatly facilitated and encouraged the present study of some Norwegian entities of epiphytic coralline crusts. This paper is part of a cand.scient. thesis (Kjøsterud 1995).

MATERIAL AND METHODS

Samples were collected by scuba diving and dredging at various localities between the Oslofjord and Bergen (Fig. 1) from February 1992 to October 1994 (Table 1).

Plants supporting epiphytic corallines were examined when fresh, air-dried or preserved in 4 % neutralized formaldehyde-sea water. Sections for light microscopy (thickness 20-30 µm) were made using a Leitz-Kryomat freezing microtome. Material was decalcified in Perenyi’s liquid, soaked in 70 % alcohol for 15 minutes and sectioned in Hamilton’s freezing solution (Chamberlain 1983) or in distilled water. The sections were transferred to a solution of Lactophenol-Wasserblau (Chroma) on microscopic slides.

For scanning electron microscopy (SEM), air-dried material was mounted on stubs using double-sided tape and coated with platinum/palladium in a Polaron E 5000 sputter coater at 1.2 kV for 2 × 2 minutes. Specimens were examined in a Jeol LSM-6400 scanning electron microscope at 10 kV.

Germination of carpospores and tetraspores from *Melobesia membranacea* (Esper) Lamouroux was studied in culture. Spores were released from crusts bearing uniporate and multiporate conceptacles and isolated into petri dishes, containing IMR 1/2 culture medium (Eppley & al. 1967) at a salinity of 30 ‰ and maintained at 12° C and 17° C.

Measurements of diagnostic features and descriptive terminology follow Irvine & Chamberlain (1994).

Voucher specimens of collected algae from this study have been deposited at the Section for Marine Botany, University of Oslo.

OBSERVATIONS

Eight species of epiphytic crustose coralline algae were identified (Table 2) in this study. A key to the species is given in Table 3. In the following account details of morphological and anatomical features are presented along with field data, substrata relations and information on earlier Norwegian records. Nomenclature and delimitation of coralline taxa follow Irvine & Chamberlain (1994).

Because taxonomic concepts have changed so much in recent years, older collections from Norway kept in herbaria are in need of critical re-examination. It has not been possible to confirm species identification for earlier records. Data on epiphytic crustose corallines from Norway in the literature should therefore be treated with caution.

Table 1. Sample sites, dates and depths.

Station number	Area	County	Date	Depth
1	Tisler	Østfold	June 1992	0-5 m
2	Akerøya	Østfold	August 1992	0-5 m
3	Vesleøy	Østfold	August 1993	8-12 m
4	Kalkgrunnen	Østfold	August 1992	2-7 m
5	Seikrakk	Østfold	August 1993	5-20 m
6	Rauer	Østfold	June 1992, July 1993	3-20 m
7	Engelsviken	Østfold	July 1993	3-20 m
8	Jeløya	Østfold	July 1993	0-4 m
9	Storskjær	Østfold	April 1992	5-35 m
10	Hallangspollen	Østfold	August 1993	0-4 m
11	Sandspollen	Østfold	April 1992	0-4 m
12	Vollen	Akershus	September 1992, July 1993	0-4 m
13	Gåsøya	Akershus	September 1993	0-2 m
14	Komersøya	Vestfold	August 1992	0-4 m
15	Fjærholmen	Vestfold	May 1992	0-2 m
16	Ørastranda	Vestfold	October 1992, August 1993	———
17	Hvasser	Vestfold	October 1992, August 1993	———
18	Verdens ende	Vestfold	October 1992, August 1993	0-3 m
19	Lyngholmen	Vestfold	June 1992	2-14 m
20	Rakke	Vestfold	May 1992	0-4 m
21	Oddaneskjær	Vestfold	June 1992	2-27 m
22	Vestre Rauane	Telemark	September 1993	2-25 m
23	Portør	Telemark	October 1992	5-10 m
24	Risør	Aust-Agder	October 1994	6 m
25	Lyngør	Aust-Agder	February 1992	2-15 m
26	Tromøy Nord	Aust-Agder	June 1992	2-20 m
27	Præstholmen	Aust-Agder	June 1992	2-21 m
28	Kverven	Aust-Agder	August 1992	0-3 m
29	Humleøy	Aust-Agder	June 1992	1-10 m
30	Stolen	Vest-Agder	June 1992	2-20 m
31	Rossøya	Rogaland	June 1992	1 m, 24 m
32	Orresanden	Rogaland	August 1993	5 m
33	Ylvesøy	Hordaland	June 1992	2-12 m
34	Risøy	Hordaland	September 1992	10-15 m
35	Eggholmen	Hordaland	September 1992	0-3 m

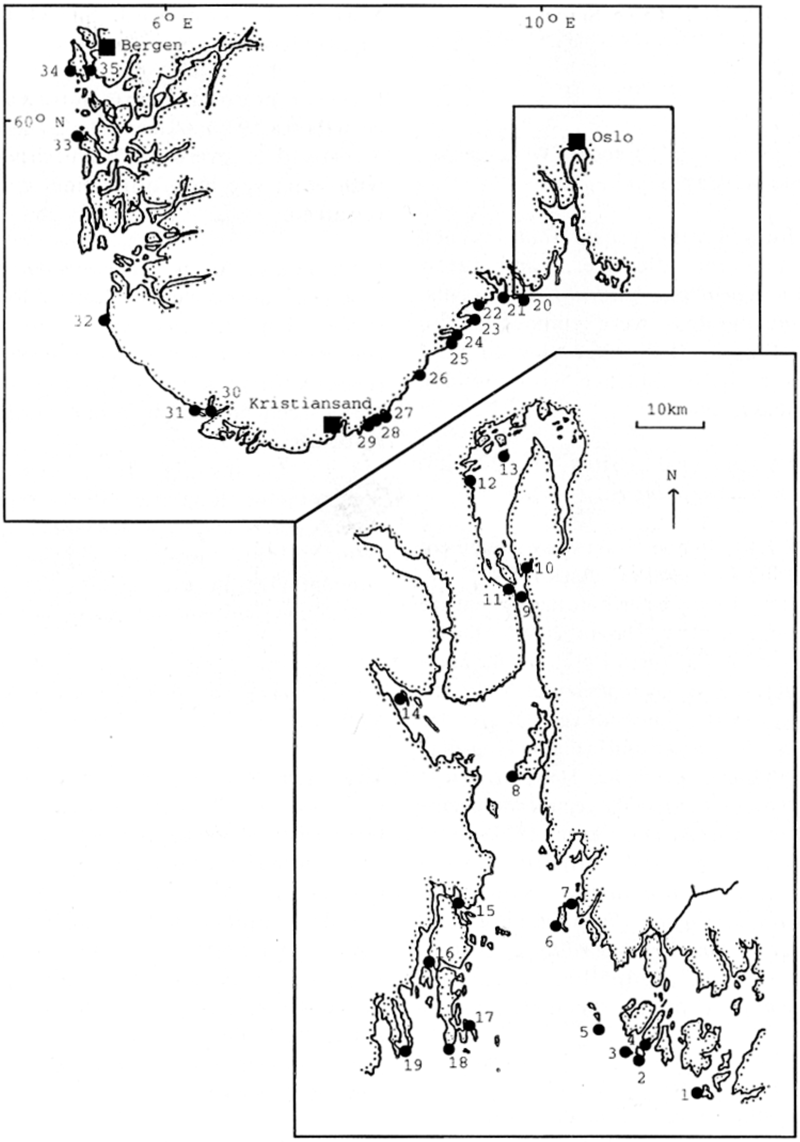

Fig. 1. Map of the southern part of Norway and the Oslofjord, showing the numbered sampling sites.

Table 2. Epiphytic calcareous algae from Norway, found in this study.

Subfamily Lithophylloideae	Subfamily Mastophoroideae
Titanoderma coralinae	*Hydrolithon cruciatum* (Bressan) Y. Chamberlain
(P. & H. Crouan) Woelkerling, Chamberlain, Silva	*Pneophyllum fragile* Kützing
Titanoderma laminariae	*Pneophyllum limitatum* (Foslie) Y. Chamberlain
(P. & H. Crouan) Y. Chamberlain	*Pneophyllum myriocarpum*
Titanoderma pustulatum var. confine	(P. & H. Crouan) Y. Chamberlain
(P. & H. Crouan) Y. Chamberlain	
Titanoderma pustulatum var. pustulatum	Subfamily Melobesioideae
(Lamouroux) Y. Chamberlain	*Melobesia membranacea* (Esper) Lamouroux

Subfamily Lithophylloideae SETCHELL

Titanoderma NÄGELI

Titanoderma corallinae (P. & H. CROUAN) WOELKERLING, CHAMBERLAIN & SILVA (1985 p. 333)

This species formed pink crusts that reached at least 4 mm in diameter, and grew epiphytically on *Corallina officinalis* LINNAEUS. Uniporate conceptacles were immersed to slightly raised (Figs 2, 3). Surface view in SEM showed a smooth thallus surface with rounded epithallial concavities.

Material examined: Sites 19, 22, 25. Epiphytic on *Corallina officinalis.*

Earlier records from Norway: Southern Norway (FOSLIE 1905, LEVRING 1937, ÅSEN 1978).
Remarks: Distinguishing features are the conceptacle floor that are situated at least 6 cell layers below the thallus surface (WOELKERLING & CAMPBELL 1992), and the internal diameter of the bisporangial conceptacle chamber (< 250 µm) (CHAMBERLAIN 1991). Since no vertical sections through conceptacles were successful in this investigation, these characters could not be ascertained. However, sinuate palisade cells, which are typical for the genus *Titanoderma* (CHAMBERLAIN 1991, CHAMBERLAIN et al. 1991), were seen. The immersed and slightly raised conceptacles exclude *Titanoderma pustulatum*, while the host *Corallina officinalis* is the most common basiphyte for *Titanoderma corallinae* (CHAMBERLAIN 1991). Rounded epithallial concavities are found to be typical of the species (GARBARY 1978).

Titanoderma laminariae (P. & H. CROUAN) Y. CHAMBERLAIN (1991 p. 69)

Crusts were up to 3 mm in diameter. Conceptacles were flat and immersed (Figs 4, 5) with the conceptacle floor 5-7 cells below the thallus surface. Old conceptacles were often buried in thallus. No gametangial conceptacles were seen. Tetrasporangial conceptacle (Fig. 6) was observed once. The conceptacle chamber was elliptical, 291 µm in diameter × 135 µm high and the roof was 103 µm thick. Bisporangial conceptacle chambers (Fig. 7) were elliptical, 168-344 µm in diameter × 31-100 µm high, roof 31-188 µm thick. Bisporangia were 34-70 µm in length × 16-40 µm in diameter.

Material examined: Site 34. Epiphytic on the stipes of *Laminaria hyperborea*.

Earlier records from Norway: The northern coast (FOSLIE 1905) and the west coast near Bergen (HYGEN & JORDE 1935, LEVRING 1937). Due to possible confusion with other species, verification of earlier finds is required.

Remarks: As in *Titanoderma corallinae* the conceptacle floor is situated at least 6 cells below the thallus surface, but *Titanoderma laminariae* has larger conceptacles (tetrasporangial conceptacles > 300 µm) (IRVINE & CHAMBERLAIN 1994). *Laminaria* LAMOUROUX is the most common basiphyte for *Titanoderma laminariae* (CHAMBERLAIN 1991).

The species is rare, and bisporangial conceptacles have not been reported in this species before (IRVINE & CHAMBERLAIN 1994). FOSLIE (1905) did however notice bisporangial conceptacles in the species (as *Lithophyllum pustulatum* f. *laminaria* (CROUAN) FOSLIE).

Titanoderma pustulatum (LAMOUROUX) NÄGELI (1858 p. 532)

This is a species aggregate separated into four varieties by CHAMBERLAIN (1991). Two of these were recorded in the present survey. Some specimens could not be referred to any of the infraspecific entities. WOELKERLING & CAMPBELL (1992) also found a similar variation in southern Australian populations of the species, but could not identify the same four varieties. This is probably because the British populations of *Titanoderma pustulatum* are bisporangial, while Australian ones are mostly tetrasporangial- and gametangial (WOELKERLING & CAMPBELL 1992, Chamberlain pers. commn).

Titanoderma pustulatum var. *confine* (P. & H. CROUAN) Y. CHAMBERLAIN (1991 p. 50)

Crusts at least 2 mm in diameter. Conceptacles were flat to slightly raised. Conceptacle floor was situated 2-3 cells below the thallus surface. The conceptacle roof was thicker near the pore, to four cells thick, and roof cells irregularly sized. There were small papillae around the pore opening. Bisporangial conceptacle (Fig. 8) chambers were hemispherical to elliptical, 130-188 µm in diameter × 25-63 µm high, roof 33-53 µm thick. Bisporangia were 23-65 µm in length × 13-30 µm in diameter. Some of the vertical sections apparently showed trichocyte like structures in the conceptacle chamber (Fig. 8).

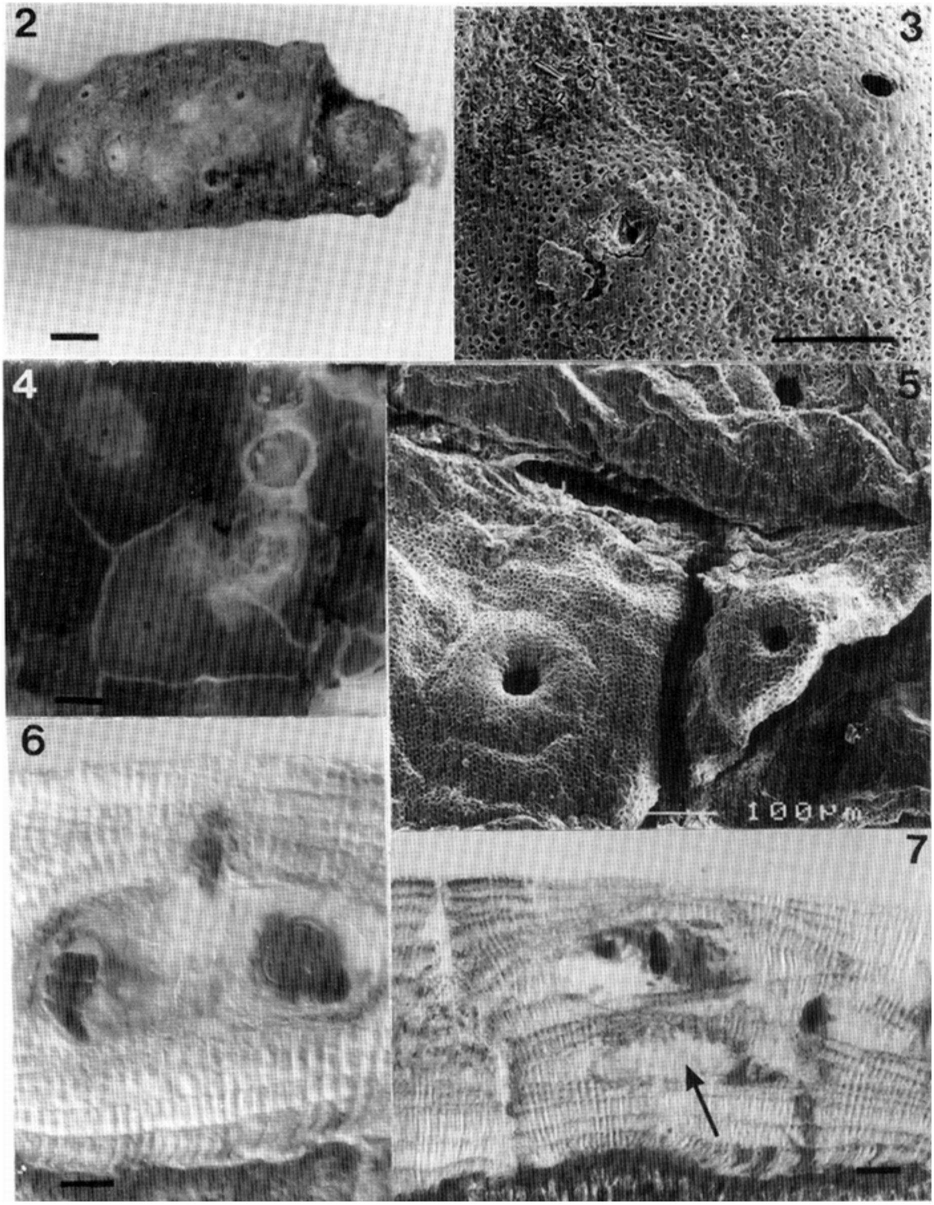

Fig. 2. *Titanoderma corallinae* growing on *Corallina officinalis*, immersed conceptacles, bar = 200 µm. Fig. 3. *Titanoderma corallinae*, SEM showing slightly raised conceptacles. Rounded epithallial concavities, bar = 100 µm. Fig. 4. *Titanoderma laminariae*, slightly immersed conceptacles, bar = 200 µm. Fig. 5. *Titanoderma laminariae*, SEM showing flat conceptacles, bar = 100 µm. Fig. 6. *Titanoderma laminariae*, cross section of tetrasporangial conceptacle. Basal palisade layer, bar = 20 µm. Fig. 7. *Titanoderma laminariae*, cross section of bisporangial conceptacle. Old conceptacles (arrow) buried in thallus, bar = 80 µm.

Material examined: Site 32. Epiphytic on *Furcellaria lumbricalis* (HUDSON) LAMOUROUX, overgrowing *Melobesia membranacea*.

Earlier records from Norway: Only reported by SUNDENE (1953) from the outer Oslofjord (as *Lithophyllum litorale* SUNESON).

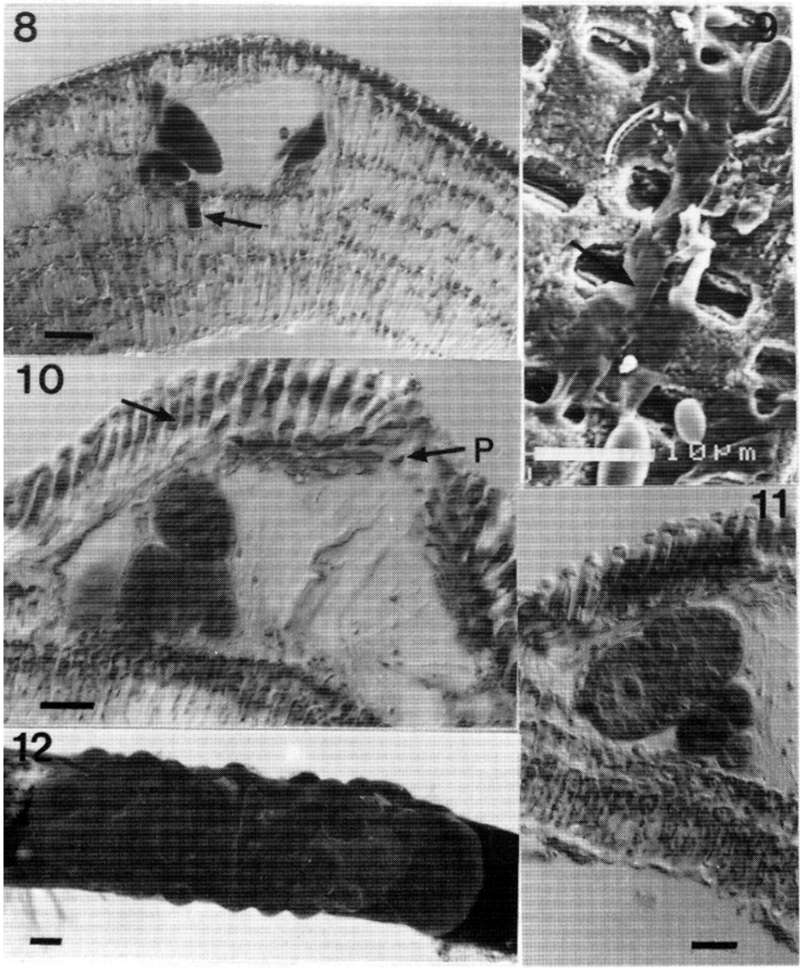

Fig. 8. *Titanoderma pustulatum* var. *confine*, cross section of bisporangial conceptacle. Trichocyte-like structure (arrow), bar = 40 µm. Fig. 9. *Titanoderma pustulatum* var. *pustulatum*, SEM showing two trichocyte hairs (arrow), bar = 10 µm. Fig. 10. *Titanoderma pustulatum* var. *pustulatum*, cross section of bisporangial conceptacle. Conceptacle floor is situated three cell layers below the thallus surface. Conceptacle roof is three cells thick, with tall central cells (arrow). Small papillae at the pore opening (P), bar = 20 µm. Fig. 11. *Titanoderma pustulatum* var. *pustulatum*, cross section showing an uninucleate bisporangium, bar = 40 µm. Fig. 12. *Titanoderma pustulatum* var. *pustulatum*, raised and domed conceptacles, bar = 400 µm.

Remarks: It seems rather unusual that trichocytes are produced in conceptacle chambers. In earlier observations of this variety, hair cells have been seen in palisade and perithallial filaments (CHAMBERLAIN 1991). SUNESON (1943, fig. 20 A-C) recognized trichocytes quite frequently in var. *confine* (as *Lithophyllum litorale* SUNESON).

Titanoderma pustulatum (LAMOUROUX) NÄGELI (1858 p. 532) var. *pustulatum*

Crusts were up to 6 mm in diameter. Trichocytes were seen in surface view in SEM (Fig. 9). Conceptacles were raised and domed (Fig. 12). The conceptacle floor was situated 2-3 cells below the thallus surface. Only bisporangial conceptacles were seen, with elliptical chambers 161-248 µm in diameter × 59-140 µm high. Roof was 3 cells thick (28-70 µm), with small epithallial and inner cells and tall, thin middle cell (Fig. 10). There were small papillae around the pore opening. Bispores were uninucleate (Fig. 11), and sporangia 22-81 µm in length × 9-68 µm in diameter.

Material examined: Site 18, growing on *Furcellaria lumbricalis*; site 22, on *Chondrus crispus*

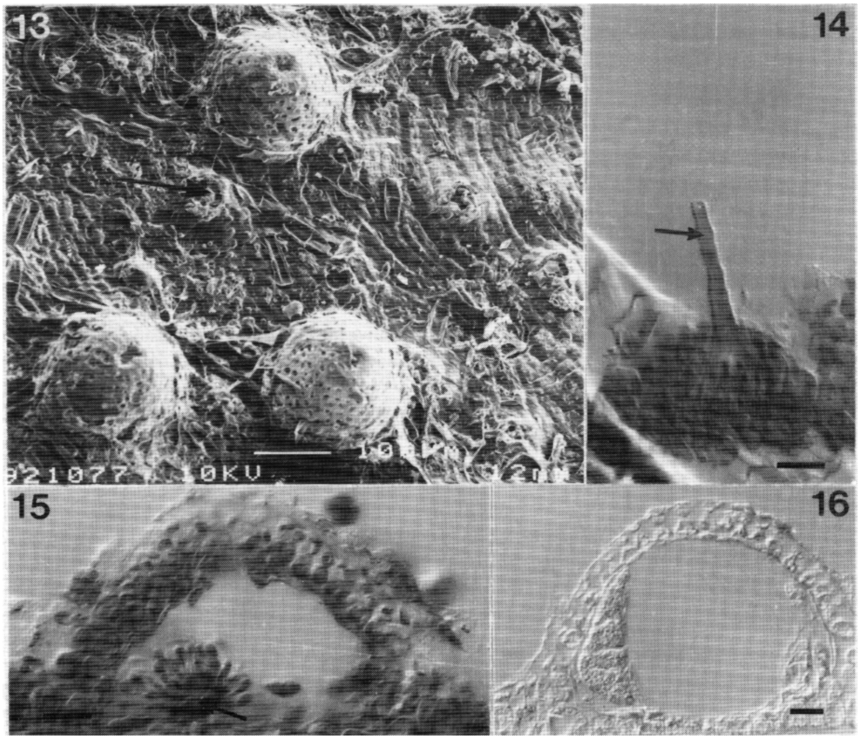

Fig. 13. *Hydrolithon cruciatum*, SEM showing domed conceptacles and trichocyte fields (arrow), bar = 100 µm.
Fig. 14. *Hydrolithon cruciatum*, cross section of spermatangial conceptacle with a spout (arrow), bar = 20 µm.
Fig. 15. *Hydrolithon cruciatum*, cross section of a carposporangial conceptacle. Fusion cell (arrow) with three-celled gonimoblast filaments, bar = 20 µm.
Fig. 16. *Hydrolithon cruciatum*, cross section of a tetrasporangial conceptacle, bar = 20 µm.

STACKHOUSE and lamina of *Laminaria hyperborea*; site 23, on lamina of *Laminaria* sp.; site 29, on holdfasts of *Laminaria hyperborea*; site 32, on *Furcellaria lumbricalis*. The species was often found overgrowing other corallines such as *Melobesia membranacea, Pneophyllum fragile, Pneophyllum limitatum* and *Pneophyllum myriocarpum*.

Earlier records from Norway: Geographical distribution is uncertain because of confusion with other species. Some finds from the west coast of Norway have been published by FREDRIKSEN & al. (1995).

Subfamily Mastophoroideae SETCHELL

Hydrolithon FOSLIE

Hydrolithon cruciatum (BRESSAN) Y. CHAMBERLAIN in IRVINE & CHAMBERLAIN (1994 p. 120)

Crusts were up to 2 mm in diameter, and orbital rings were seen on the surface. Spore germination discs consisted of a four-celled central element and eight surrounding cells (Fig. 17). A field of terminal trichocytes was evident in surface view (Figs 13, 18). Conceptacles were raised and domed. Sporangial conceptacles with pore cells oriented vertically to the conceptacle roof. Bisporangial plants were not seen.

Spermatangial conceptacles (Fig. 14) were slightly raised, 34-50 µm in diameter × 30-32 µm high, spout up to 40 µm long and simple spermatangial system. Carposporangial conceptacle chambers (Fig. 15) were domed, 60-96 µm in diameter × 30-70 µm high, roof 4-28 µm thick. Carpospores were 4-40 µm in length × 4-22 µm in diameter. One fusion cell with gonimoblast filaments born from the periphery. Tetrasporangial conceptacle chambers (Fig. 16) were domed, 80-110 µm in diameter × 68-124 µm high. Tetrasporangia were 32-82 µm in length × 8-52 µm in

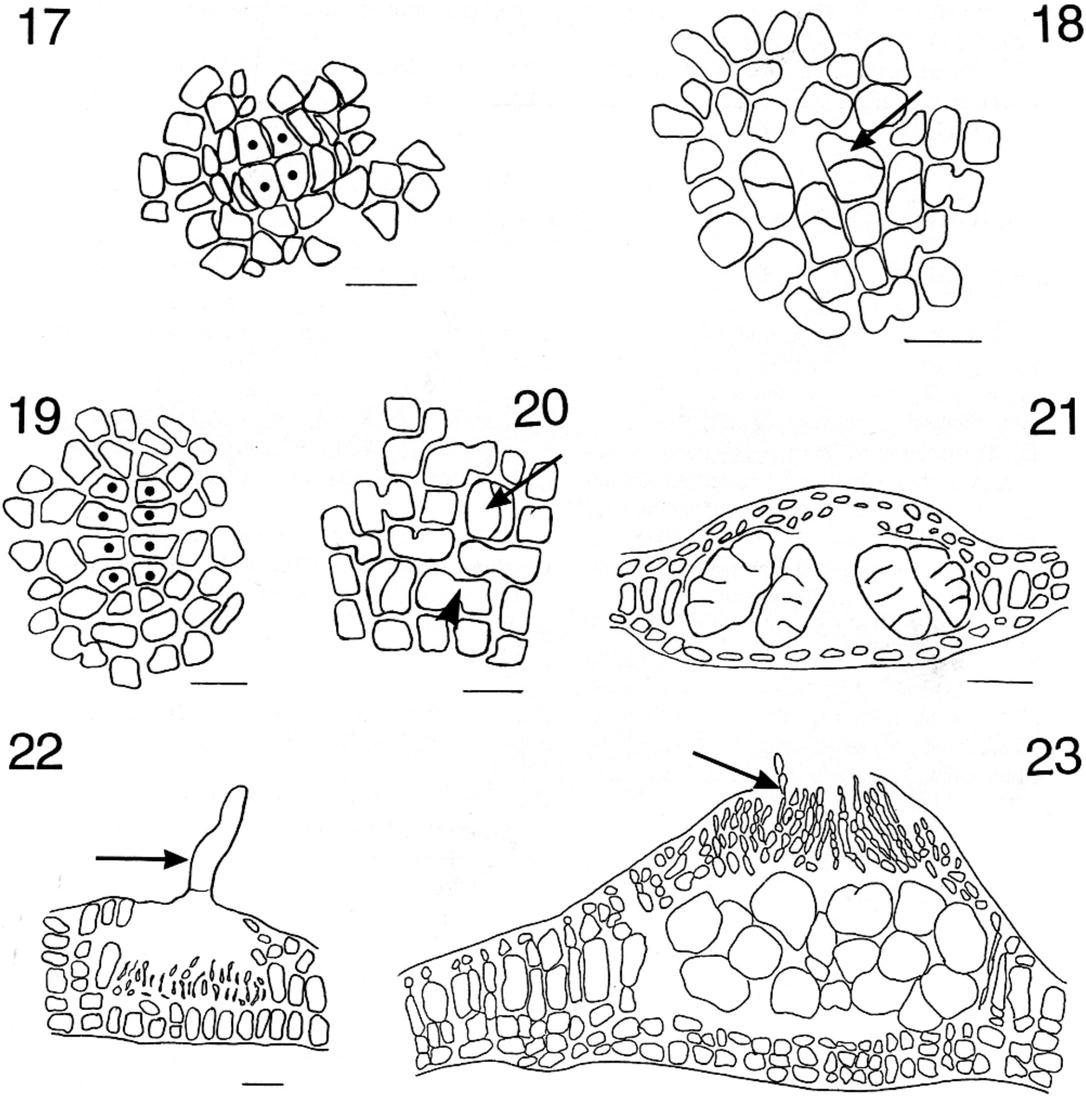

Fig. 17. *Hydrolithon cruciatum*, spore germination disc with four central cells (•) and eight surrounding cells, bar = 20 µm. Fig. 18. *Hydrolithon cruciatum*, trichocyte field consisting of four terminal trichocytes (arrow), bar = 20 µm. Fig. 19. *Pneophyllum fragile*, spore germination disc with eight central cells (•), bar = 20 µm. Fig. 20. *Pneophyllum fragile*, intercalary trichocytes (arrow) and cell fusions (arrow head), bar = 20 µm. Fig. 21. *Pneophyllum fragile*, cross section showing tetrasporangial conceptacle, bar = 20 µm. Fig. 22. *Pneophyllum limitatum*, cross section of spermatangial conceptacle with spout (arrow) and simple spermatangial system, bar = 20 µm. Fig. 23. *Pneophyllum limitatum*, cross section of carposporangial conceptacle with multicellular free pore filaments (arrow), bar = 20 µm.

diameter. All conceptacle types had one layer of triangular cells in the conceptacle roof.

Material examined: Site 28, growing on *Zostera marina* LINNAEUS, as the only crustose calcareous algae. The material was collected by Professor J. Rueness, and the locality is situated in a warm water bay where summer temperatures are high.

Remarks: This is the first find of *Hydrolithon cruciatum* in Norway, and there are only a few records of this species from northern Europe. Kylin recorded it from Sweden, where he observed it epiphytically on *Zostera* (as *Melobesia lejolisii* ROSANOFF) in 1905 and 1933 (Chamberlain pers. commn). From the British Isles there are only three records of *Hydrolithon cruciatum* (IRVINE & CHAMBERLAIN 1994). In the Adriatic Sea the species has been noted as rather common, growing on seagrasses and algae (BRESSAN & al. 1977).

Pneophyllum KÜTZING

Pneophyllum fragile KÜTZING (1843 p. 385)

Crusts up to 700 µm in diameter. Epithallial concavities were broader than long seen in SEM (Fig. 24). The spore germination disc had eight-celled central element (Fig. 19). Intercalary trichocytes occurred (Fig. 20). Uniporate sporangial conceptacles were flat or slightly raised. Vertical sections showed the typical tall, thin erect filament beside the conceptacles. The conceptacle roof is thin, with one cell layer plus epithallial cells. Small pore cells around the pore canal were not specialized. Carposporangial and tetrasporangial conceptacles were observed.

Carposporangial conceptacle chambers were elliptical, 50-105 µm in diameter × 18-33 µm high, roof 8-13 µm thick. Carpospores were 20-40 µm in length × 3-28 µm in diameter. Tetrasporangial conceptacle chambers (Fig. 21) were elliptical, 58-138 µm in diameter × 18-55 µm high, roof 10-18 µm thick. Tetrasporangia were 22-58 µm in length × 8-46 µm in diameter.

Material examined: Site 2, growing on *Furcellaria lumbricalis*; sites 13, 16, on *Zostera marina*; sites 17, 18, 23, 24, on laminae of *Laminaria* and *Zostera marina*.

Earlier records from Norway: The Oslofjord and Tønsbergfjord (GRAN 1893, 1897), southwestern coast of Norway (FOSLIE 1905, HYGEN & JORDE 1935, ARWIDSSON 1936) and Trondheimsfjorden (PRINTZ 1926).

Remarks: *Pneophyllum fragile* was observed from the inner Oslofjord to the coast of the Skagerrak. The species has not been registered in this area since GRAN's (1897) record from the outer Oslofjord.

Pneophyllum limitatum (FOSLIE) Y. CHAMBERLAIN (1983 p. 376)

Crusts at least 4 mm in diameter. Intercalary trichocytes were observed (Fig. 27). Conceptacles were slightly raised to conical with pore filaments appearing as a pale central ring. The pore filaments were united below and free above, forming a corona of long, multicellular fused filaments in an outer ring and an inner ring of shorter filaments (Figs 25,26). Tetrasporangial conceptacles were uniporate, bisporangial conceptacles not seen.

Spermatangial conceptacle chambers (Fig. 22) were domed, 53-78 µm in diameter × 38-55 µm high, spout up to 58 µm long, with a simple spermatangial system. Carposporangial conceptacle chambers (Fig. 23) were elliptical, 85-188 µm in diameter × 40-98 µm high, and the roof was 20-33 µm thick. Carposporangia were 8-40 µm in length × 10-30 µm in diameter. Tetrasporangial conceptacle chambers were elliptical, 60-180 µm in inner diameter × 45-65 µm high, roof 12-25 µm thick. Tetrasporangia were 20-50 µm in length × 10-38 µm in diameter.

Material examined: Sites 22, 24, growing on laminae of *Laminaria hyperborea*; site 23, on laminae of *Laminaria* and *Chondrus crispus*.

Earlier records from Norway: Outer Oslofjord (SUNDENE 1953), Sandefjordsfjord (IVERSEN 1981) and southwestern coast of Norway (FOSLIE 1905, LEVRING 1937).

Pneophyllum myriocarpum (P. & H. CROUAN) Y. CHAMBERLAIN (1983 p. 410)

Crusts up to 3 mm in diameter. Intercalary trichocytes were seen. Conceptacles were prominent and domed (Fig. 28). Pore filaments fused into a hyaline collar surrounding the ostiole (Figs 29, 30). Tetrasporangial conceptacles were uniporate, bisporangial conceptacles not seen.

Spermatangial conceptacle (Fig. 29) observed once. This was 51 µm in diameter × 37 µm high, spout 31 µm long, and was situated next to a tetrasporangial conceptacle. Carposporangial conceptacle chambers were domed (Fig. 30), 116-150 µm in diameter × 42-66 µm high. Carposporangia were 12-28 µm in length × 6-22 µm in diameter. Tetrasporangial conceptacle chambers were domed (Fig. 29), 104-204 µm in inner diameter × 66-133 µm high. Tetrasporangia were 24-64 µm in length × 10-31 µm in diameter.

Material examined: Site 21, growing on *Chondrus crispus*, *Phyllophora truncata* (PALLAS) NEWROTH et A.R.A. TAYLOR and *Phyllophora pseudoceranoides* (GMELIN) NEWROTH et A. TAYLOR; site 22, on *Chondrus crispus*; sites 27, 29, on holdfasts of *Laminaria hyperborea*.

Remarks: This is the first find of *Pneophyllum myriocarpum* in Norway. There were only a few obser-

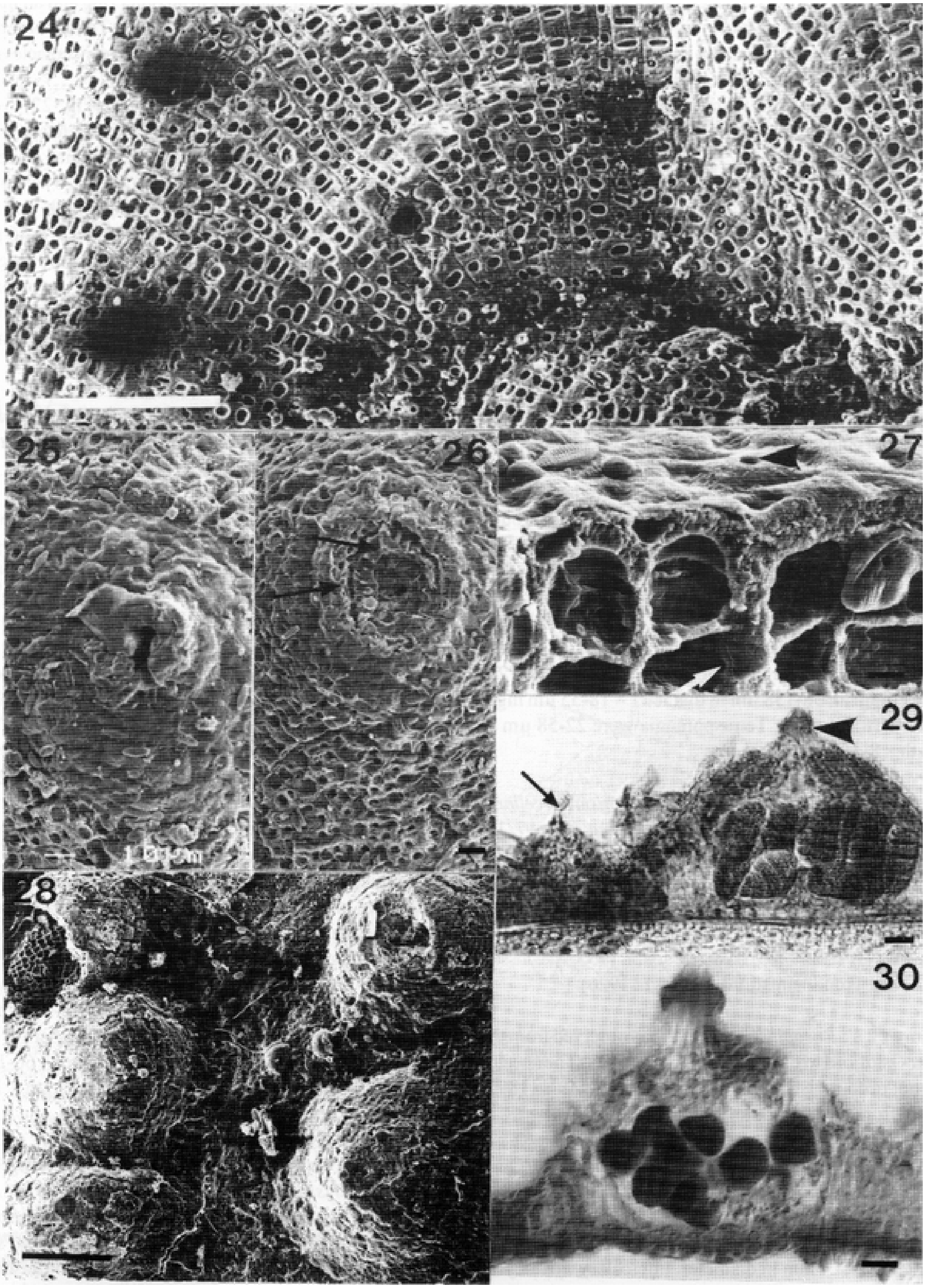

Fig. 24. *Pneophyllum fragile*, SEM showing flat conceptacles. Epithallial concavities are broader than long, bar = 100 µm. Fig. 25. *Pneophyllum limitatum*, SEM showing a corona of fused pore filaments, bar = 10 µm. Fig. 26. *Pneophyllum limitatum*, SEM showing an inner and outer ring of pore filaments (arrows), bar = 10 µm. Fig. 27. *Pneophyllum limitatum*, SEM showing intercalary trichocyte (arrow head), bar = 100 µm.

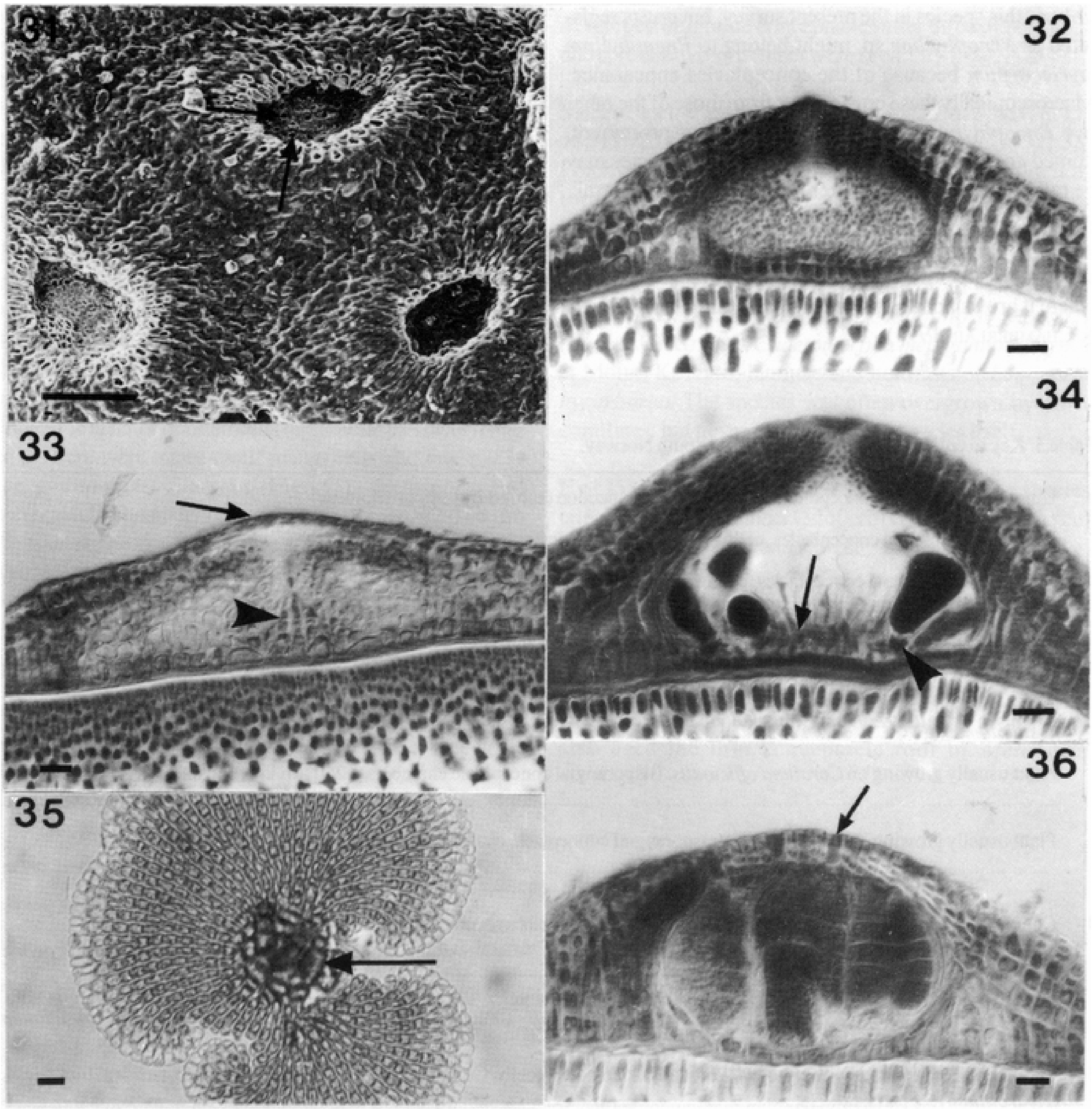

Fig. 31. *Melobesia membranacea*, SEM showing multiporate tetrasporangial conceptacles. Arrows denote pores, bar = 100 µm. Fig. 32. *Melobesia membranacea*, cross section of spermatangial conceptacle. Simple spermatangial system, bar = 20 µm. Fig. 33. *Melobesia membranacea*, cross section of newly developed carpogonial conceptacle with one layer of uplifted cells (arrow). Carpogonial branches (arrow head), bar = 20 µm. Fig. 34. *Melobesia membranacea*, cross section of carposporangial conceptacle. Many small fusion cells (arrow) and one cell in the gonimoblast filament (arrow head), bar = 20 µm. Fig. 35. *Melobesia membranacea*, from culture studies. Many-celled germination disc (arrow), bar = 100 µm. Fig. 36. *Melobesia membranacea*, cross section of multiporate tetrasporangial conceptacle. Arrow denotes pore plug, bar = 20 µm.

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Fig. 28. *Pneophyllum myriocarpum*, SEM showing domed conceptacles, bar = 100 µm. Fig. 29. *Pneophyllum myriocarpum*, cross section of spermatangial conceptacle with a spout (arrow) situated next to a tetrasporangial conceptacle. Pore filaments fused into a hyaline collar surrounding the pore canal (arrow head), bar = 20 µm. Fig. 30. *Pneophyllum myriocarpum*, cross section of carposporangial conceptacle. Note collar of pore filaments, bar = 20 µm.

vations of this species in the present survey, but crusts registered as *Pneophyllum* sp. might belong to *Pneophyllum myriocarpum* because of the conceptacles appearance. Macroscopically these crusts differ from those of the other two *Pneophyllum* species recorded, in their prominent, domed conceptacles. This indicates that the species is rather common in the outer Oslofjord and Skagerrak, where *Pneophyllum* crusts often were observed together with *Melobesia membranacea*. It is reported to be a common species in the British Isles, France and Italy where it grows both epiphytically and epilithically (Irvine & Chamberlain 1994).

Subfamily Melobesioideae Bizzozero

Melobesia Lamouroux

Melobesia membranacea (Esper) Lamouroux (1812 p. 186)

Crusts at least up to 2 mm in diameter. When dry they became wrinkled and remained attached to the substratum. Cell fusions were seen between adjacent filaments.

Table 3. Key to epiphytic coralline crusts from south Norway.

1. Uniporate sporangial conceptacles, secondary pit connection (subfamily Lithophylloideae) 2
   Uniporate sporangial conceptacles, cellfusions (subfamily Mastophoroideae) 5
   Multiporate sporangial conceptacles, cellfusions (subfamily Melobesioideae) 9

2. Thallus with basal palisade layer. Conceptacles immersed in thallus, conceptacle floor at least 6 cell layers below thallus surface 3
   Thallus with basal palisade layer. Conceptacles raised, conceptacle floor 2-3 cell layers below thallus surface (*Titanoder pustulatum* agg.) 4
   Plant usually growing on *Corallina officinalis*. Bisporangial conceptacle chambers < 250 µm internal diameter .... *Titanoderma corallinae*
   Plant usually growing on *Laminaria*. Tetrasporangial conceptacle chambers > 300 µm internal diamete .... *Titanoderma laminariae*

4. Conceptacle roof thicker near pore, up to 4 cells thick. Roof cells irregulary sized .... *Titanoderma pustulatum* var. *confine*
   Bisporangial conceptacle roof 3 cells thick, with small epithallial and inner cells and tall,thin middle cell .... *Titanoderma pustulatum* var. *pustulatum*

5. Sporangial conceptacles with enlarged, vertically oriented porecells. Germination disc with 4-celled centre, terminal trichocytes (*Hydrolithon*) 6
   Sporangial conceptacles with porecells oriented horizontally at least initally. Germination disc with 8-celled centre, intercalary trichocytes (*Pneophyllum*) 7

6. Germination disc centre surrounded by 8 cells .... *Hydrolithon cruciatum*

7. Sporangial conceptacle flat to slightly raised. Porecells not specialized .... *Pneophyllum fragile*
   Sporangial conceptacle prominent 8

8. Conceptacles conical. Pore canal surrounded by corona of long, multicellular fused filaments in an outer ring and an inner ring of shorter filaments .... *Pneophyllum limitatum*
   Conceptacles domed. Pore canal surrounded by hyalin collar of fused pore filaments .... *Pneophyllum myriocarpum*

9. Conceptacles with dark coloured pore plate. Roof cells squarish, subepithallial and upper perithallial cells triangular. Many-celled germination disc .... *Melobesia membranacea*

Conceptacles were hemispherical, having a typical dark coloured pore plate and multiporate tetrasporangial conceptacles (Fig. 31) with an apical pore plug. Spermatangial, carposporangial and tetrasporangial conceptacles were observed, and both monoecious and dioecious crusts were seen.

Spermatangial conceptacle chambers (Fig. 32) were domed, 70-146 µm in diameter × 54-72 µm high, roof 22-34 µm thick. Simple spermatangial system with spermatangia scattered all around the conceptacle chamber surface. Carposporangial conceptacle chambers were domed, 80-150 µm in diameter × 48-76 µm high, roof 28-38 µm thick. Carpospores were 22-44 µm in length × 16-30 µm in diameter. Carpogonial branches developed under one layer of uplifted cells (epithallial cell layer) (Fig. 33). There were many small fusion cells and one cell in the gonimoblast filament (Fig. 34). Tetrasporangial conceptacle chambers (Fig. 36) were domed, 42-160 µm in diameter × 34-84 µm high, roof 14-52 µm thick. Tetrasporangia were 26-93 µm in length × 6-56 µm in diameter. All conceptacle types had squarish roof cells. Subepithallial and upper perithallial cells were often triangular.

In culture, *Melobesia membranacea* developed into a germination disc with up to 34 cells (Fig. 35). New crusts were observed 1-2 weeks after spore release. One crust developed uniporate conceptacles after three months, but no reproductive structures were seen.

Material examined: Sites 1, 2, 3, 4, 5, 6, 7, 8, 17, 18, 19, 20, 21, 22, 23, 25, 26, 27, 29, 30, 31, 32, 33. Epiphytic on various host species: *Furcellaria lumbricalis, Chondrus crispus, Phyllophora truncata, Phyllophora pseudoceranoides, Odonthalia dentata* (Linnaeus) Lyngbye, *Polysiphonia elongata* (Hudson) Sprengel, *Palmaria palmata* (Linnaeus) O. Kuntze, *Phycodrys rubens* (Linnaeus) Batters, *Cladophora rupestris* (Linnaeus) Kützing, *Chaetomorpha melagonium* (Weber et Mohr) Kützing, laminae and holdfasts of *Laminaria hyperborea*. The species was often overgrown by other corallines, but never overgrew other species itself.

Earlier records from Norway: The species is registered from the inner Oslofjord (Gran 1897, Klavestad 1978) to Vega, Nordland (Sørlie, 1994).

Remarks: *Melobesia membranacea* had squarish cells in the conceptacle roofs, and when new carposporangial conceptacles develop there was only one uplifted cell layer. Wilks & Woelkerling (1991) were the first to use these characters for species delimitation within the genus. They also used the thin conceptacle roof in *Melobesia*

Table 4. Earlier records of species of epiphytic calcareous algae from Norway not found in this study.

Species	Recorded as	Recorded by
Lithophyllum crouanii Foslie	*Lithophyllum crouanii* Foslie	Foslie 1905:115 Sørlie 1994:36 Frediksen et al. 1995
Titanoderma pustulatum var. *macrocarpum* (Rosanoff) Y. Chamberlain	*Melobesia macrocarpa* Rosanoff	Kleen 1874:11
	Lithophyllum macrocarpum (Rosanoff) Foslie	Printz 1926:134
Pneophyllum caulerpae (Foslie) P. Jones & Woelkerling	*Fosliella tenuis* Adey & Adey	Adey & Adey 1973:398
Pneophyllum confervicola (Kützing) Y. Chamberlain	*Melobesia fosliei* Rosenvinge	Levring 1937:99 Sundene 1953:193
	Melobesia minutula Foslie	Levring 1937:99 Jorde 1966:50 Sundene 1953:193
	Melobesia minutula (Foslie) Ganesa	Sivertsen 1981:78

membranacea as a species character (male conceptacle roofs < 20 µm thick and carposporangial conceptacle roofs < 25 µm thick). In this study the conceptacle roofs were thicker (male conceptacle roofs 22-34 µm thick and female conceptacle roofs 28-38 µm thick). IRVINE & CHAMBERLAIN (1994) also measured thicker conceptacle roofs than observed in south Australian material of *Melobesia membranacea*. Culture studies and field observations of other coralline crusts indicate that the dimensions depend on the environment (CHAMBERLAIN 1983), which may explain geographical differences.

Melobesia membranacea was the commonest species in this study, observed at several localities. It was also the most frequently recorded species in earlier studies, probably because *Melobesia membranacea* is readily recognized by the darker conceptacle surface (FOSLIE 1905, CHAMBERLAIN 1983).

DISCUSSION

A total of eleven different epiphytic calcareous crusts have now been recorded from Norwegian waters. The previously recorded *Pneophyllum confervicola, Pneophyllum caulerpae, Lithophyllum crouanii* and *Titanoderma pustulatum* var. *macrocarpum* (Table 4) were not observed in this study. In the outer Oslofjord, *Pneophyllum confervicola* was noted as a common species (SUNDENE 1953), whereas *Pneophyllum caulerpae* has been recorded only once (ADEY & ADEY 1973). *Lithophyllum crouanii* and *Titanoderma pustulatum* var. *macrocarpum* have been observed from the western and northern coast of Norway (PRINTZ 1926, FREDRIKSEN & al. 1995).

Epiphytic calcareous algae were found growing on many different host species, but some coralline algae were more common on specific host species than others. Substrata can therefore give useful information in species delimitation (CHAMBERLAIN 1978, CHAMBERLAIN 1983). *Melobesia membranacea* was usually observed on *Furcellaria lumbricalis*, growing on the lower, older parts of the host. It was also growing together with *Pneophyllum* species on *Chondrus crispus, Phyllophora* and holdfasts of *Laminaria. Pneophyllum fragile* was common on *Zostera marina*, but occasionally grew on lamina of *Laminaria hyperborea* and once on *Furcellaria lumbricalis*.

Most of the host species in this study were perennial. However, crustose calcareous algae were also observed on *Zostera* leaves, and laminae of *Laminaria hyperborea*. Newly developed parts of *Furcellaria lumbricalis* were often covered with young, vegetative crusts of *Melobesia membranacea*.

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