

Observations on *Ceramium tenuicorne* (Rhodophyta) and its reproduction¹

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Abstract — *Ceramium tenuicorne* (Kützinger) Wærn (including *C. gobii* Wærn) is a common red alga in the Skagerrak–Baltic Sea region. A *Polysiphonia*-type of life history and asexual reproduction by paraspores, previously demonstrated in cultures for this species, have been confirmed. In addition, a characteristic kind of reproductive structure ('Gobi's monosporangia') has been described in field-collected material from the Baltic Sea. This type of structure was used by Wærn (1992) to distinguish his new species *Ceramium gobii*. We studied the formation and function of 'Gobi's monosporangia' in culture and found them to be modified branch apices in which cells transformed directly into enlarged rounded bodies that detached and grew into a new generation of similar plants. They are referred to as vegetative propagules rather than sporangia. Tetrasporangia were occasionally found on the same individuals that bore either parasporangia or vegetative propagules. The tetraspores from these plants usually failed to develop, but in a few cases mature gametophytes developed, as well as plants with mixed spermatangia and parasporangia or spermatangia and vegetative propagules. Thus an interconnection between sexual and asexual modes of reproduction was demonstrated.

***Ceramium* / marine red algae / parasporangia / reproductive structures / vegetative propagules**

Résumé — **Observations sur *Ceramium tenuicorne* (Rhodophyta) et sa reproduction.** *Ceramium tenuicorne* (Kützinger) Wærn (incluant *C. gobii* Wærn) est une algue rouge commune des régions de Skagerrak et de la mer Baltique. Un cycle de reproduction de type *Polysiphonia* et une reproduction asexuée par paraspores, précédemment démontrés en cultures pour cette espèce, ont été confirmés. En complément, un type spécifique de structure reproductive (les 'monosporocystes de Gobi') a été décrit sur du matériel récolté en mer Baltique. Ce type de structure a été utilisé par Wærn (1992) pour distinguer sa nouvelle espèce : *Ceramium gobii*. Nous avons étudié la formation et la fonction des 'monosporocystes de Gobi' en culture ; ce sont des apex modifiés chez lesquels les cellules se transforment directement en gros éléments arrondis qui se détachent et se développent en une nouvelle génération de thalles identiques. Ces structures doivent donc être assimilées à des propagules végétatives plutôt que considérées comme des sporocystes. Des tétra-

1. Dedicated to M.-T. L'Hardy-Halos, on the occasion of her retirement.

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sporocystes ont occasionnellement été trouvés sur des individus portant des parasporocystes ou des propagules végétatives. Les tétraspores issues de ces individus ne se sont généralement pas développées mais, dans quelques cas, des gamétophytes matures ont été obtenus, de même que des thalles portant soit des spermatocystes et des parasporocystes, soit des spermatocystes et des propagules végétatives. Une interconnection entre des modes de reproduction sexuée et asexuée a donc été démontrée. (Traduit par la Rédaction)

algues rouges / *Ceramium* / parasporocyste / propagules végétatives / structures reproductives

INTRODUCTION

Ceramium tenuicorne (Kützting) Wærn is one of the most common red algae in the Baltic Sea, where it is widely distributed (Nielsen *et al.*, 1995) and grows both epiphytically and epilithically. It can be found throughout the year to depths of 20–25 m, but is most common in the littoral and upper part of the sublittoral zone during late summer (Wallentinus, 1979), when plants become 3–8 cm high. Sexual reproductive structures have been found all the way into the islands of Åland (Bergström *et al.*, 2001) and Tvärminne (present study) where salinities are 5–6 psu. Sexual reproduction and no marked reduction in thallus size have been taken to support the view that *C. tenuicorne* is a genuine brackish-water species, perhaps endemic to the Baltic Sea (Wærn, 1952). More recently, Wærn (1992) split *C. tenuicorne* into two species: *C. gobii* Wærn and *C. tenuicorne s. str.* The main distinguishing feature was their type of asexual reproductive structures. *Ceramium gobii* was characterized by a kind of structures first depicted by Gobi (1877) for material from the Gulf of Finland. Wærn (1992) called these ‘Gobi’s monosporangia’. Nothing is known about their development and function from culture studies. *Ceramium tenuicorne s. str.* is known to bear parasporangia that develop in a lateral position from cortical bands and contain many spores. Similar sporangia are known in other *Ceramium* species as well as in other representatives of Ceramiaceae (L’Hardy-Halos, 1970; Guiry, 1990). In cultures of *C. tenuicorne* from Oslofjorden, Norway (as *C. strictum* Harvey *sensu* Kylin) successive generations of plants bearing parasporangia were recycled by paraspores (Rueness, 1973). The two species distinguished by Wærn (1992) were geographically separated in the Baltic Sea, with *C. gobii* mainly found in the Baltic proper and northwards, whereas the entity bearing lateral parasporangia was recorded at higher salinities in the southern and western Baltic Sea. The morphology of the two species was otherwise very similar. Tetrasporangia and gametangial reproductive structures are known in both taxa, but they are apparently of little value in species discrimination. We recently demonstrated that isolates from populations along the Skagerrak-Baltic Sea gradient had virtually identical DNA sequences (nrDNA ITS2 and cpDNA Rubisco spacer) and were interfertile (Gabrielsen *et al.*, 2002a), strongly suggesting that *C. tenuicorne* and *C. gobii* are conspecific. Culture experiments have demonstrated ecotypic differentiation in growth responses among isolates along the salinity gradient (Rueness & Kornfeldt, 1992; Düwel 2001). In this paper we report on the reproductive characteristics of *Ceramium tenuicorne* with particular emphasis on the structure and function of the so-called ‘Gobi’s monosporangia’.

MATERIAL AND METHODS

Material was derived from a total of 32 sites distributed along the gradient from the Norwegian coast to the inner Baltic Sea (Fig. 1, Tab. 1). Some of these isolates were the same as those used previously in salinity experiments (Düwel, 2001, sites 3, 4, 9, 12, 23) and in molecular genetic analyses and crosses (Gabrielsen *et al.* 2002a, b, sites 3-7; 8-10; 15, 23, 25, 28). In addition, type specimens of *Gongroceras tenuicorne* Kützing (1841, p. 736) housed in Rijksherbarium Leiden (L) and the holotype of *C. gobii* Wærn from Uppsala Universitet (UPS), were examined.

Cultures were established from most sites and often with several individuals from each site. Mode of reproduction was observed in all field-collected and cultured isolates. Most of the detailed observations of "Gobi's monosporangia" were made on an isolate from site 26 (Finland).

Unialgal cultures were obtained by repeated cuttings of growing apical portions or by isolation of sporelings. Culture medium was an enriched sea water-medium IMR/2 (Eppley *et al.*, 1967) adjusted to salinities from 5–30 psu by diluting with de-ionized water prior to nutrient enrichment. Most cultures were initially treated with $5 \text{ mg L}^{-1} \text{ GeO}_2$ to inhibit growth of diatoms. Cultures were maintained at 7°C and 12°C under a 16:8 light:dark regime at or below $30 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Permanent slide preparations of field-collected and cultured specimens were mounted in 30 % corn syrup colored with aniline blue after fixation in 4 % formalin-seawater.

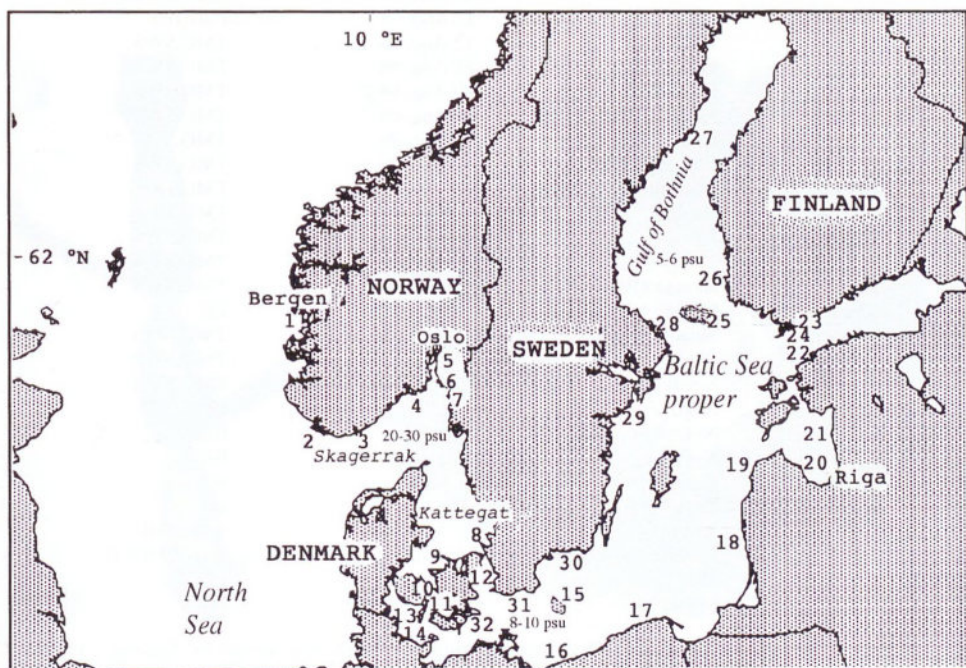


Fig. 1. Map of collecting sites along the Skagerrak – Baltic Sea salinity gradient, from where samples of *Ceramium tenuicorne* were examined.

Tab. 1. List of sites from which *Ceramium tenuicorne* (including *C. gobii*) samples were studied. Dates of collection and initial letters of collector's names are given. Full names are mentioned below.

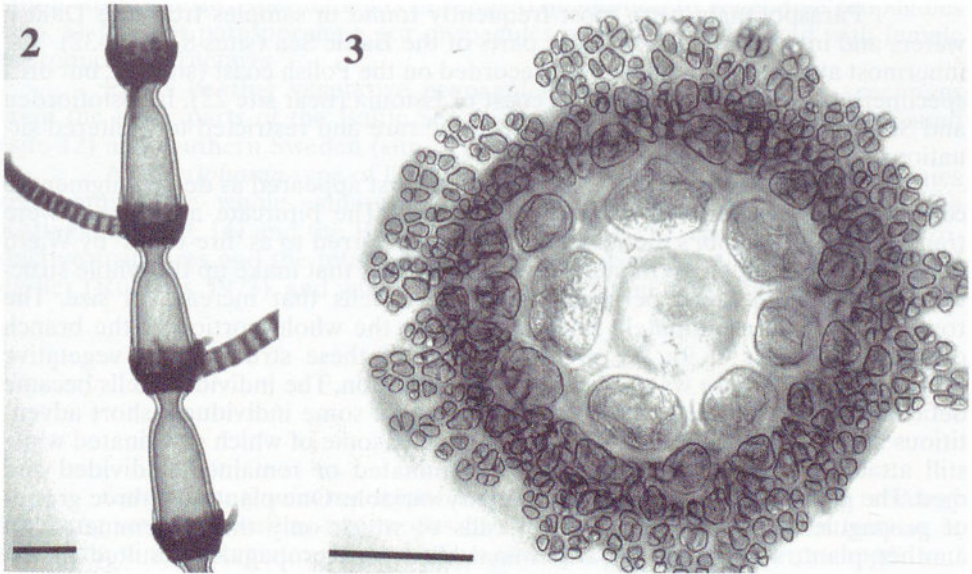
Site no.	Country	Locality	Date collected	Collector
1	Norway	Hardangerfjord ^a	21 Jul.-55	IJ
2	Norway	Farsund	03 Apr.-99	TMG
3	Norway	Høvåg	20 Jun.-98;	JR
			18 May-2000	JR
4	Norway	Sandefjord	11 Aug.-99	TMG,SWS
5	Norway	Inner Oslofjord	Aug.- Nov.-98	TMG
			14 Jun.-99;	TMG
			May-Jun.-94	SE
			Jun.-Sep.-95	SE
6	Norway	Oslofjord, Drøbak	07 Oct.-99	TMG,JR
			21 Jul.-95	SE
7	Norway	Iddefjord	2 Nov.-98	JR
8	Sweden	Båstad	04 Aug.-99	TMG,SWS
			10 Jun.-98	PMP,AK,LD
9	Denmark	Hundested	05 Aug.-99	TMG,SWS
10	Denmark	Risinge Hoved	05 Aug.-99	TMG,SWS
11	Denmark	Klinteby Klint	05 Aug.-99	TMG,SWS
12	Denmark	Dragør	07 Jun.-98	LD
			16 Jul.-2000	LD,BH
	Sweden	Limhamn; Lernacken	Aug.-Sep.-98	JC,LH
13	Germany	Geltlinger fjord ^b	28 Apr.-98	TMG,JR
14	Germany	Kielerfjord, Bülk	30 Apr.-98	TMG,JR
15	Denmark	Bornholm	22 Jul.-98	SF
			26 May.-99	PMP,AK,LD
16	Poland	Dziwnow	10 May.-98	PMP,JRe
17	Poland	Wladyslawowo	12 Aug.-98	TMG,SWS
18	Lithuania	Klaipeda	12 Aug.-98	TMG,SWS
19	Latvia	Pavilosta	09 Aug.-98	TMG,SWS
20	Latvia	Jurmala (Riga Bay)	08 Aug.-98	TMG,SWS
21	Estonia	Kabli (Riga Bay)	07 Aug.-98	TMG,SWS
22	Estonia	Iohusalu	07 Aug.-98	TMG,SWS
23	Finland	Tvärminne	20 Jun.-99	TMG,JR
24	Finland	Hangö	22 Jun.-99	TMG,JR
25	Finland	Åland	05 Aug.-98	TMG,SWS
			16 Aug.-99	TMG,SWS
26	Finland	Rauma (Rihtniemi)	06 Aug.-98	TMG,SWS
27	Sweden	Umeå	13 Aug.-98	LB
28	Sweden	Singö; Öregrund ^c	04 Aug.-98	TMG,SWS
		Fogdö	17 Aug.-99	TMG,SWS
		Nordkapp	17 Aug.-99	TMG,SWS
29	Sweden	Askö	Oct.-74	IW
		Nyköping	Sep.-90	BE
		Nyköping - Trosa	Aug.-98	BE
30	Sweden	Karlshamn	Aug.-98	JC
31	Sweden	Trelleborg	Aug.-98	JC
		Smygehamn; Kåseberga	25 May.-99	AaK,PMP
32	Denmark	Sjælland	02 Jun.-98	AaK,PMP,LD
		Møn	19 Aug.-98	LD
		Falster	12 Jun.-98	LD

^a Location No. 31 in Jorde & Klavestad (1963); ^b type locality for *Gongroceras tenuicorne* Kützing; ^c near type locality for *Ceramium gobii*; LB = Lena Bergström; JC = Jim Coyer; LD = Lene Düwel; SE = Sissel Eikvar; BE = Britta Eklund; SF = Stein Fredriksen; TMG = Tove M. Gabrielsen; LH = Lars Haumann; BH = B.Hansen; IJ = Ingrid Jorde; AaK = Aase Kristiansen; PMP = Poul Møller Pedersen; JRe = Johnny Reker; JR = Jan Rueness; SWS = Snorre W. Steen; IW = Inger Wallentinus.

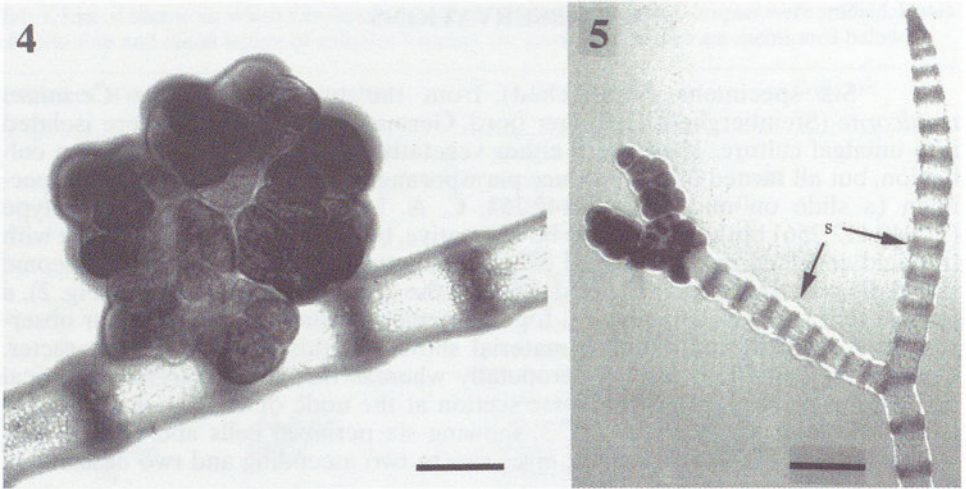
OBSERVATIONS

Six specimens (unattached) from the type locality for *Ceramium tenuicorne* (Steinberghaff, Geltinger fjord, Germany, site 13, Fig. 1) were isolated into unialgal culture. These were either vegetative or bore parasporangia on collection, but all turned out to produce parasporangia in culture. The lectotype specimen (a slide on mica, L. 940.142.254, C. A. Maggs 04.12.92) and a syntype (L. 940.112.256) both appeared to be vegetative, but were in good accordance with the field collected material. Axial cells in the lower part of thallus often become markedly constricted near the nodes giving the cells an urceolate shape (Fig. 2), a feature that is regarded as typical for the species (including *C. gobii*). Our observations from field and cultured material show that this is a variable character. Cortical filaments may stretch acropetally whereas the lower margin of cortical bands remains straight. A transverse section at the node of an axis of a field-collected specimen is shown in Fig. 3, showing six periaxial cells and cortical filaments. Usually each periaxial cell gives rise to two ascending and two descending filaments.

A parasporangium is shown in Fig. 4. Usually only one parasporangial cluster developed per cortical band, but occasionally 2-3 sporangial heaps were formed, each with 10 to 30 paraspores, 35-90 μm in diameter. A high percentage of paraspores (ca 90 %) germinated and formed new plants that again produced parasporangia within 3-4 weeks in culture. After discharge of paraspores the same individuals occasionally produced tetrasporangia. These tetrasporangia usually failed to develop beyond a few cell divisions, but on a few occasions grew into males



Figs 2-3. *Ceramium tenuicorne*. Fig. 2. Cultured isolate from the type locality (site 13) showing urceolate axial cells and cortical bands near the base of the thallus. Fig. 3. Trans-section of axis at the node, showing 6 periaxial cells and cortical filaments. Field-collected material from the type locality. Scale bars = 100 μm .

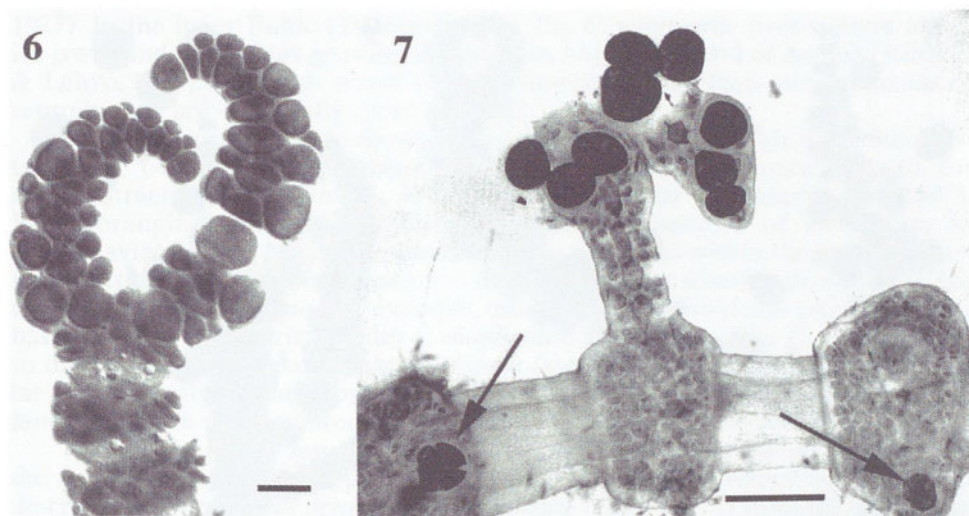


Figs 4-5. *Ceramium tenuicorne* in culture. Fig. 4. Mature parasporangium developed from cortical band. Isolate from site 14. Scale bar=100 μ m. Fig. 5. Isolate from site 26 with vegetative propagules developing in branch tips ('fire-tongs'), and also producing spermatangia, s. Scale bar = 50 μ m.

(dwarfish), or more rarely females. In addition, a mixture of spermatangia and parasporangia was also observed in culture.

Parasporangia were most frequently found in samples from the Danish waters and in southern and western parts of the Baltic Sea (sites 8-19, 31-32). The innermost attached specimens were recorded on the Polish coast (site 17), but drift specimens were found on the north coast of Estonia (near site 22). In Oslofjorden and Skagerrak, parasporangia appeared to be rare and restricted to sheltered situations with reduced salinity (sites 3-6).

The so-called 'Gobi's monosporangia' first appeared as deeply pigmented cells in apical portions of branches (Figs. 5, 6). The bifurcate apices that were transformed into 'Gobi's monosporangia' were referred to as 'fire-tongs' by Wærn (1992) and were visible to the unaided eye. The cells that make up the whole structure include both axial, periaxial and cortical cells that increase in size. The rounded cells were ultimately released because the whole portion of the branch disintegrated (Figs 8, 9). We prefer to refer to these structures as vegetative propagules, since there was no sporangium formation. The individual cells became detached at maturity and were of variable size. In some individuals, short adventitious branches transformed into a series of cells, some of which germinated while still attached (Fig. 11). Detached cells germinated or remained undivided and died. The germination percentage was highly variable. One plant with three groups of propagules released a total of 59 cells of which only three germinated. In another plant, a branch with a terminal cluster of propagules resulted in the release of 24 cells, of which 19 germinated (Fig. 10). The germination pattern was similar to that of spores. When germlings reached beyond a certain size in culture (ca. 1 cm high), propagules were again formed. Several generations were followed in culture. In addition to the clonal propagation by vegetative propagules, plants were occasionally seen bearing simultaneously vegetative propagules and



Figs 6-7. *Ceramium tenuicorne* from site 26. Fig. 6. Apices with initial development of vegetative propagules showing some enlarged cells with dense cell contents. Scale bar = 25 μ m. Fig. 7. Field-collected specimen with a short adventitious branch transformed into propagules, and with tetrasporangia seen in cortical bands of the main axis (arrows). Scale bar = 100 μ m.

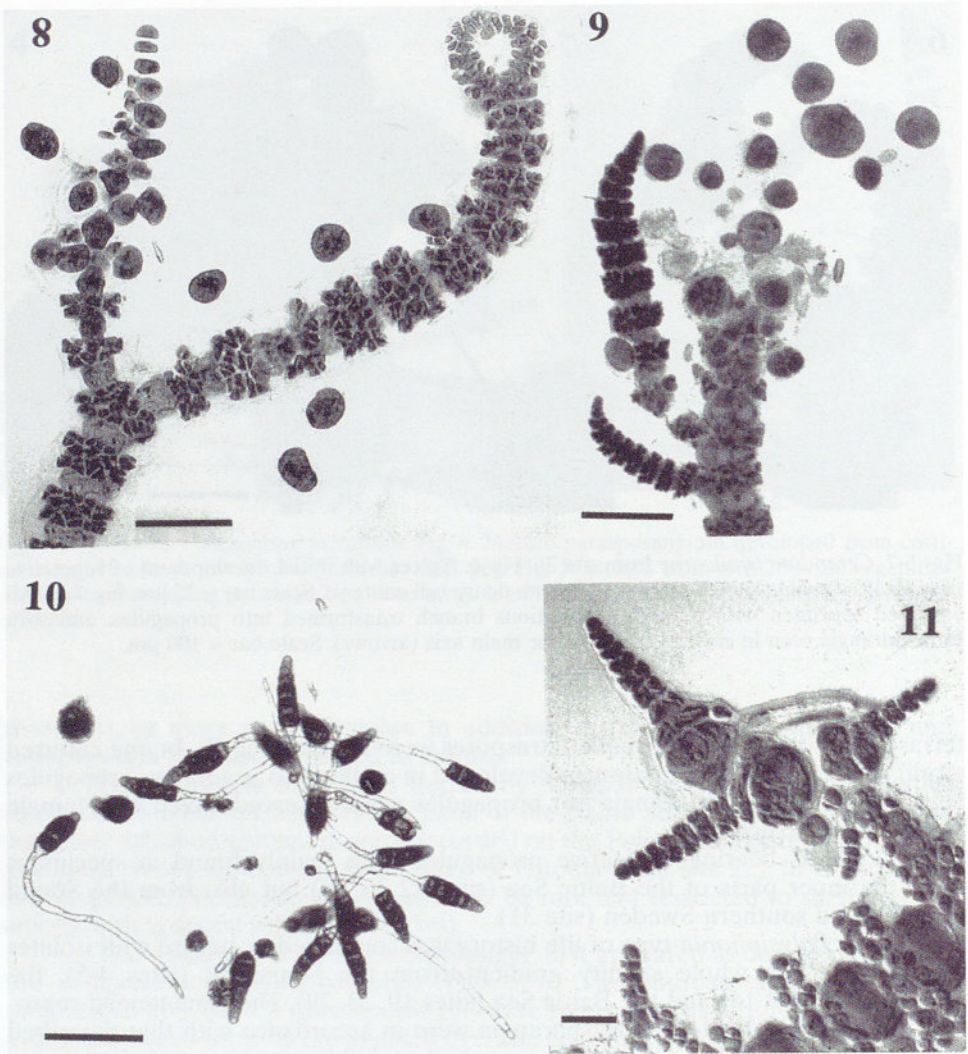
tetrasporangia from which viable tetraspores were formed (Fig. 7). In one cultured strain (from site 26), spermatangia developed in addition to vegetative propagules (Fig. 5). Neither parasporangia nor propagules were observed mixed with female reproductive structures.

Plants bearing vegetative propagules were mainly found in specimens from the inner parts of the Baltic Sea (sites 22-26, 28) but also from the Sound (site 12) and southern Sweden (site 31).

A *Polysiphonia*-type of life history was completed in culture with isolates representing the whole salinity gradient from the Skagerrak (sites 4-5), the Kattegat (sites 9, 14) and the Baltic Sea (sites 19, 23, 29). The gametangial reproductive structures and the tetrasporangia were in accordance with that described earlier (Rueness, 1973), and with no apparent variation among populations.

DISCUSSION

Ceramium tenuicorne apparently has a flexible reproductive strategy involving sexual as well as two modes of asexual reproduction. Plants bearing at the same time spermatangia and vegetative propagules or spermatangia and parasporangia were isolated in culture. The spermatia produced were demonstrated to be functional in crosses reported by Gabrielsen *et al.* (2002a). A clear differentiation in the frequency of sexual versus asexual reproduction in *C. tenuicorne* was documented (Gabrielsen *et al.*, 2002b) with dominance of gametophytes and tetrasporophytes in populations from Oslofjorden. Parasporangia were



Figs 8-11. *Ceramium tenuicorne* from site 26. Figs 8-9. Disintegration of branch tips with vegetative propagules showing the release of cells of various sizes. Scale bar = 100 μm . Fig. 10. Population of 24 propagules released from one reproductive apices, 18 of which germinated. Fig. 11. *In situ* germination from the tip of a short lateral branch. Scale bar = 25 μm .

most frequent in Kattegat and vegetative propagules were only observed in the populations from the Baltic proper.

In many red algae, asexual means of reproduction may be essential for maintaining marginal populations. This suggestion is consistent with the geographical distribution of *Plumaria plumosa* (Hudson) Kuntze, where triploid plants with parasporangia occur further north on both sides of the North Atlantic than gametophytes and tetrasporophytes (Drew, 1939; Rueness, 1968; Whittick,

1977). In the inner Baltic (Tvärminne, site 23), *C. tenuicorne* over-winters under ice cover and has a short growing season from May to the end of August (Kiirikki & Lehvo, 1997). Although sexual reproduction may take place, asexual means of reproduction are apparently more frequent.

Parasporangia were shown already by Kützing (1862, Tab. 82) in his illustration of *Gongroceras tenuicorne*. The first to use the term parasporangia for similar structures (in *Plumaria plumosa*) were Schmitz & Hauptfleisch (1897). Parasporangia have been described for various species of *Ceramium* in Scandinavian waters, but due to the taxonomic problems within the group of partially corticated *Ceramium* species it is difficult to assess whether or not these are the same as *C. tenuicorne*. For example, the epithet *arachnoideum* (Agardh, 1824) has been used for a variety under *C. diaphanum* (by others under *C. tenuissimum*) to distinguish plants bearing parasporangia (see Kylin 1907). Our recent molecular genetic analyses and crossing experiments (Gabrielsen *et al.*, 2002a) suggest, however, that a single, reproductively variable species is involved.

Schiller (1913) described a kind of parasporangia in *Ceramium strictum* from the Adriatic Sea that developed in the tips of the branches, resembling those first described in *Hormoceras acrocarpum* by Kützing (1863, Tab. 1) from the same area, and considered by him to be modified tetrasporangia. Similar structures were later reported from the western Mediterranean Sea by Feldmann-Mazoyer (1941) in an alga that she classified as *C. diaphanum* var. *zostericola* Thuret f. *acrocarpum* Feldmann-Mazoyer. An isolate of this taxon from Banyuls was used by Feldmann & L'Hardy-Halos (1977) to describe stages in the development, release and early germination of paraspores. Coppejans (1977) described a similar kind of terminal parasporangia in *Ceramium* sp. from Port-Cros (Var, France). This type of parasporangia in *Ceramium* shows some resemblance with the vegetative propagules we studied in *C. tenuicorne*. The main difference is that in parasporangia, whether lateral or terminal, many spores are formed within definite sporangia. It remains to be established whether vegetative propagules and terminal parasporangia have any homology. For this and for taxonomic reasons it would be interesting to examine the relationship between *C. tenuicorne* and the parasporangium-bearing entity from the Mediterranean Sea as well as material classified as *C. strictum* var. *zostericola* Thuret (type locality Cherbourg, Normandy). According to L'Hardy-Halos (1970) and Maggs & Hommersand (1993), parasporangia have not been recorded in *Ceramium* species from the Atlantic coast of France or in the British Isles. The occasional formation of gall-like proliferations from cortical bands in the genus *Ceramium* may however have led to confusion between such structures and lateral parasporangia (Dixon, 1960).

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