

## STUDIES ON MARINE ALGAE OF THE BRITISH ISLES. 10. THE GENUS *RHODYMENIA*

By MICHAEL D. GUIRY\*

Department of Biology and Geology, The Polytechnic of North London,  
Holloway Road, London N7 8DB

(Text-figs 1-62)

### CONTENTS

	Page
<b>THE GENUS <i>RHODYMENIA</i></b>	
Original description	386
Type species	386
Synonymy	386
Description of genus	387
Identification	389
Key to the British species	390
 <b><i>RHODYMENIA PSEUDOPALMATA</i> VAR. <i>PSEUDOPALMATA</i></b>	
Synonymy	390
Structure and development of the thallus	390
Structure and development of reproductive organs	394
Reproductive phenology	397
Habitat	397
Distribution	398
 <b><i>RHODYMENIA PSEUDOPALMATA</i> VAR. <i>ELLISIAE</i></b>	
Original description	401
Synonymy	403
Structure and development of the thallus	403
Structure and development of reproductive organs	406
Reproductive phenology	408
Habitat	408
Distribution	408
Comparison of <i>R. pseudopalmata</i> var. <i>pseudopalmata</i> and <i>R. pseudopalmata</i> var. <i>ellisiae</i>	410
 <b><i>RHODYMENIA DELICATULA</i></b>	
Original description	411
Synonymy	411
Structure and development of the thallus	414
Structure and development of reproductive organs	416
Reproductive phenology	418
Habitat	418
Distribution	419
Comparison of <i>R. delicatula</i> and <i>R. phylloides</i>	419
 Acknowledgements	423
References	423

\* Present address: The Marine Laboratory, Portsmouth Polytechnic, Ferry Road, Hayling Island, Hants., PO11 0DG, U.K.

## ORIGINAL DESCRIPTION

The genus *Rhodomenia* (sic) was proposed by Greville (1830, p. xlviii) to include 16 species. J. Agardh (1841) added many species, most of which are now referred to the Kallymeniaceae. In 1851 J. Agardh changed the concept of the genus and adopted Montagne's (1839, p. 44 footnote) suggestion that the orthography *Rhodymenia* be adopted. The latter spelling has been conserved over the original "*Rhodomenia*". J. Agardh (1851) divided the genus into two sections or subgenera, the *Palmatae* and the *Palmettae*, and characterized the *Palmatae* as bearing tetrasporangia sparsely scattered over the whole surface or in scattered sori while the *Palmettae* (as the type species of the genus was included in the *Palmettae* it should be referred to as the section or subgenus *Rhodymenia*) as having tetrasporangia collected in sori just below the apices. In 1876 J. Agardh created a further section or subgenus the *Clinophora*, which had tetrasporangia aggregated in small sori just below the apices but the cortical layers underwent modification to give a more or less nemathecoid structure. Dawson (1941) distinguished a new section the *Pertusae*, mainly on the basis that the species had tetrasporangia scattered over the surface of the frond in a relatively unmodified cortical layer and not in sori, and he placed the sections *Rhodymenia*, *Palmatae*, *Clinophora* and *Pertusae* in the subgenus *Eurhodymenia* (which, as it contains the type species of the genus, should be referred to as the subgenus *Rhodymenia*) and reduced the genus *Dendrymenia* Skottsberg to a subgenus of the genus *Rhodymenia*, with one section, the *Dendrymeniae*.

Guiry (1974a, b) has proposed that the genus *Palmaria* Stackhouse, over which the genus *Rhodymenia* had been conserved, should be reinstated for the species *Rhodymenia palmata*. The spelling "*Rhodymenia*" has been conserved over the original "*Rhodomenia*".

The genus *Rhodymenia* is represented in Britain only by species of the subgenus *Rhodymenia* and the section *Rhodymenia*.

## TYPE SPECIES

Greville (1830) did not indicate a type species of the genus *Rhodomenia* Greville; apparently the earliest lectotypification is that of Schmitz [1889, p. 444, as *Rhodymenia palmetta* (Esper) Greville]. *Rhodymenia palmetta* sensu Greville would seem to be the type species as it has been shown that *Fucus palmetta* Esper is a misinterpretation of *Fucus palmetta* S. G. Gmelin (a delesseriaceous alga; see Silva, 1952). In his treatment of *Rhodomenia palmetta*, Greville (1830, p. 88) cited, amongst others, the following synonyms:

"*Delesseria Palmetta*, Lamour. Essai p. 37.

*Fucus Palmetta*, Esp. Ic. Fuc. p. 84. t. 40. excluding all the synonyms. Stackh. Ner. Brit. p. 102. t. 16. Sm. Eng. Bot. t. 1120. Turn. Syn. Fuc. p. 21. Hist. Fuc. t. 76.

*Fucus bifidus*, Huds. Fl. Aug. p. 581."

It would appear that the confusion between *Fucus palmetta* Esper and *Fucus palmetta* S. G. Gmelin was appreciated by Stackhouse (1801, p. 102) and by Turner (1809, p. 5) both of whom refused to choose a new epithet, mainly as a consequence of the then current distaste for "... that constant and arbitrary changing of names affixed to plants ... ." (Turner 1809, p. 5). In effect, therefore, it would seem that there exists a *Fucus palmetta* Stackhouse, a later homonym of *Fucus palmetta* S. G. Gmelin. The earliest name for this entity seems to be *Delesseria palmetta* Lamouroux (1813, p. 125). As Greville (1830, p. 88) obviously recognized this confusion by his clear citation of these synonyms, the combination *Rhodymenia palmetta* can be attributed to "(Lamouroux) Greville", which is the type species of the genus. As the earliest taxonomically correct synonym cited by Greville (1830) is *Fucus palmetta* Stackhouse, a lectotype of this entity has been chosen by the present author from herb. Stackhouse (BM) and this should serve as the type specimen of the type species.

The earliest name for *Rhodomenia palmetta* (Lamouroux) Greville is, according to Greville (1830) and Papenfuss (1950, p. 190), *Fucus bifidus* Hudson (1778, p. 581), which name is a later homonym of *Fucus bifidus* S. G. Gmelin, a laminariaceous plant now known as *Arthrothamnus bifidus* (S. G. Gmelin) Ruprecht. Mrs L. M. Irvine (pers. comm.) has expressed the opinion that Hudson's description of *Fucus bifidus* does not suggest a species of *Rhodymenia* sensu stricto, particularly as the species is said to be diaphanous; genuine material of *Fucus bifidus* Hudson has not as yet been located.

Silva (1952) has pointed out that the correct name for *Rhodymenia palmetta* (Lamouroux) Greville is *Rhodymenia pseudopalmata* (Lamouroux) Silva.

## SYNONYMY

Dawson (1941, p. 124, 143) proposed that *Dendrymenia* Skottsberg (1923, p. 16) be reduced to a subgenus of the genus *Rhodymenia*. Sparling (1957) agreed with Dawson but Taylor (1945), Kylin (1956) and others have retained *Dendrymenia* as a genus distinct from *Rhodymenia*.

## DESCRIPTION OF GENUS

*Thallus* of multiaxial construction, erect or prostrate, 1–300 (1000) mm long, stipes terete or slightly flattened, monopodially or sympodially branched, blades flattened or flat 500  $\mu\text{m}$ –20 (200) mm broad, entire or dichotomously, pseudodichotomously, palmately or irregularly split or lobed; regeneration from stolons, apical or marginal meristems common; colour bright red, sometimes purplish red; substance soft cartilaginous to stiffly cartilaginous; cells differentiated into an assimilatory layer of small cortical filaments 2–5 cells in length and a medulla of (2) 4–13 (20) layers of large, hyaline, axially elongated cells which often have a small parietal iridescent body of unknown function.

*Tetrasporangia* with cruciately arranged spores, formed from the cells of assimilatory filaments, interspersed with sterile filaments 2–3 cells long, aggregated in relatively unmodified sori which may be confined to a specific part of the thallus or spread over the whole surface.

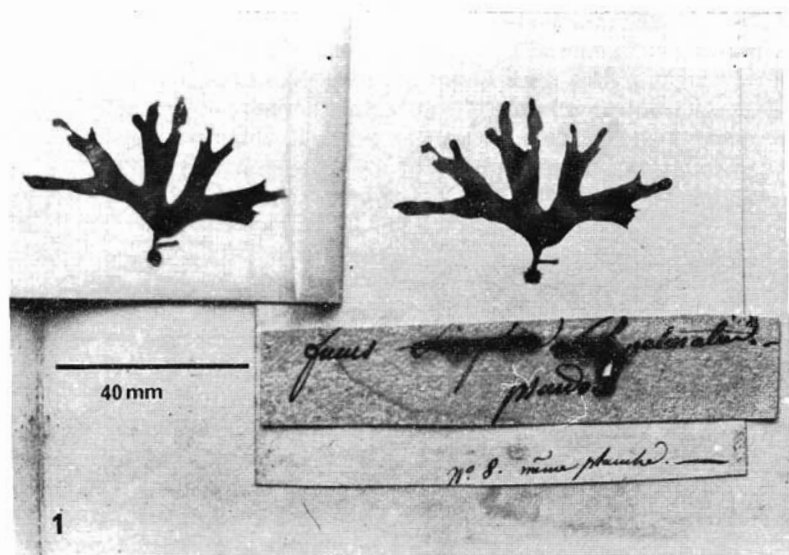


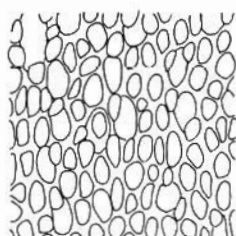
FIG. 1. *Rhodymenia pseudopalmata* (Lamouroux) Silva. Lectotype specimen of *Fucus pseudopalmatus* Lamouroux (CN). On the right the original drawing for Lamouroux's (1805, p. 23, Fig. 2) illustration and on the left the tetrasporangial specimen.

*Gametangial plants* apparently always dioecious and morphologically similar to the tetrasporophyte; spermatia hyaline, formed singly in spermatangia derived singly or in pairs from spermatangial mother cells formed from terminal assimilatory cells and aggregated either in small rounded subapical sori or spread in irregular patches over the whole surface of the flattened blade; procarps formed in the younger parts of the thallus, often in considerable quantities; carpogonial branches 3- or 4-celled, terminated by an elongated trichogyne and borne on a large supporting cell which also bears a 2-celled auxiliary cell branch; after fertilization the nucleus is transferred to the auxiliary cell (sometimes via a connecting cell); cystocarps hemispherical, large, not sunken, with a small centrally-placed ostiole which is sometimes necked, pericarp smooth without projections; carposporophyte usually entirely filling the cystocarpic cavity when mature, usually composed of three lobes or masses of carposporangia; gonimoblast entirely transformed to sporangia except for a few large, branched, centrally-placed, columnar cells which originate from the auxiliary cell; carposporophyte nourished by an irregular basal group of small nutritive cells; connecting filaments between the gonimoblast and the pericarp absent.

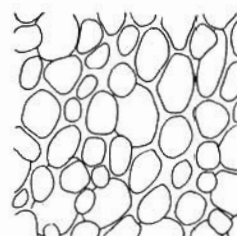
Species entirely marine and widely distributed in the tropical, subtropical, warm-temperate and cold-temperate waters of the world.



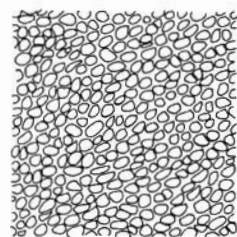
2



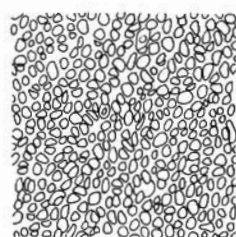
3



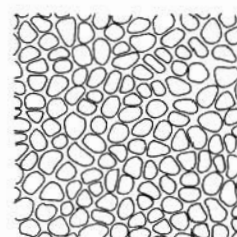
4



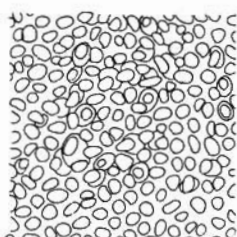
5



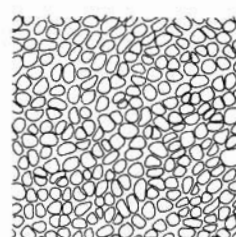
6



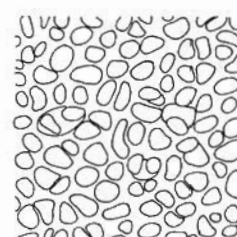
7



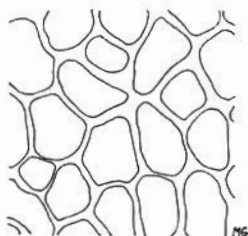
8



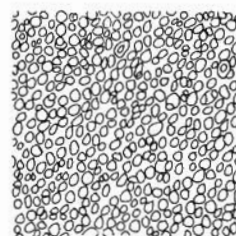
9



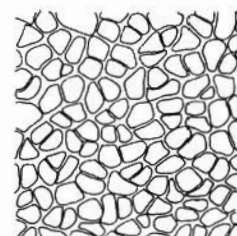
10



11



12



13

50  $\mu$ m

FIGS. 2-13. See captions opposite.

## IDENTIFICATION

The British species of *Rhodymenia* have been frequently confused with various other red algae, particularly species of *Phyllophora* and *Schottera* (Phylloporaceae; Gigartinales). This confusion has arisen largely as the result of a scarcity of fertile material of species of these genera. It seems desirable to attempt to provide some anatomical features upon which tentative determinations can be made. The British species of *Phyllophora*, *Schottera* and *Rhodymenia* are variable in form, not only within populations, but also seasonally.

The anatomical structure of representatives of the Phylloporaceae and species of the genus *Rhodymenia* are very similar, but specimens of *Rhodymenia* can be distinguished from specimens of *Phyllophora* on the basis of the arrangement and size of their cortical cells. Species of *Rhodymenia* have relatively loose cortex of irregularly sized cells. These cells should be viewed at a distance from the apex corresponding to one tenth the total length of the plant. The uppermost cortical cells of the thallus at this stage of development are rather loosely arranged and the less-pigmented cells of the next (subcortical) layer are visible (Figs 2-4). Species of *Phyllophora* (Figs 5-8), *Schottera* (Fig. 9) and *Stenogramme* (Fig. 10), on the other hand, have smaller, more regularly-sized cells which are usually closely packed and consequently the subcortical layers are rarely visible in surface view.

Species of *Rhodymenia* have often been confused with species of *Rhodophyllis* (particularly older, more cartilaginous specimens), species of *Callophyllis* (usually sterile, depauperate, intertidal specimens) and, on occasion, with very young specimens of *Palmaria*. *Rhodophyllis divaricata* (Stackhouse) Papenfuss is easily distinguished from species of *Rhodymenia* by means of its very large, angular cortical cells (Fig. 11). The surface cells of *Callophyllis laciniata* (Hudson) Kützing are, on the other hand, very small (Fig. 12) and this species should pose no problem. The surface cells of *Palmaria palmata* (Linnaeus) O. Kuntze are similar to those of species of *Phyllophora* in that they are closely packed (Fig. 13) but are larger and more obviously hexagonal.

---

FIGS 2-13. Surface view of the cortical cells of the British species of *Rhodymenia* and other species which may be confused with them. Scale line = 50  $\mu$ m. Fig. 2. *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva, Treaddur Bay, Anglesey, 19 August 1974, leg. M. D. Guiry, 10 mm from the apex. Fig. 3. *R. pseudopalmata* var. *ellisiae* (Duby) Guiry, Seaford Bay, Sussex, 1 July 1973, leg. M. D. Guiry, 10 mm from the apex. Fig. 4. *Rhodymenia delicatula* P. J. L. Dangeard, Cemlyn Bay, Anglesey, 5 April 1973, leg. M. D. Guiry, 3 mm from the apex. Fig. 5. *Phyllophora crista* (Hudson) Dixon, Shanklin, Isle of Wight, 9 April 1975, leg. N. A. Jephson, 10 mm from apex. Fig. 6. *P. traillii* Holmes ex Batters, Bembridge, Isle of Wight, 11 September 1975, leg. N. A. Jephson, 3 mm from apex. Fig. 7. *P. sicula* (Kützing) Guiry & L. M. Irvine, Lulworth Cove, Dorset, 17 February 1973, leg. M. D. Guiry, 10 mm from apex. Fig. 8. *P. truncata* forma *brodiaei* (Turner) Newroth & A. R. A. Taylor, Dale Voe, nr. Lerwick, Shetland Isles, 28 July 1973, subtidal, leg. divers, 10 mm from apex. Fig. 9. *Schottera nicaeensis* (Lamouroux ex Duby) Guiry & Hollenberg, Lulworth Cove, Dorset, 20 March 1973, leg. M. D. Guiry, 10 mm from apex. Fig. 10. *Stenogramme interrupta* (C. Agardh) Montagne, Sherkin Island, Co. Cork, August 1975, leg. N. A. Jephson, 10 mm from apex. Fig. 12. *Callophyllis laciniata* (Hudson) Kützing, Horse Sound Fort, Solent, Hampshire, subtidal: 2-5 m, 1 September 1974, leg. N. A. Jephson, 10 mm from apex. Fig. 13. *Palmaria palmata* (Linnaeus) O. Kuntze, Lulworth Cove, Dorset, 17 February 1973, leg. M. D. Guiry, 10 mm from apex.

## KEY TO THE BRITISH SPECIES AND VARIETIES

1. Mature plant < 30 mm high and < 80  $\mu$ m thick 10 mm from the apex . . . . . *R. delicatula*  
Mature plant > 30 mm high and > 80  $\mu$ m thick 10 mm from the apex . . . . .
2. Plants not with extensive stoloniferous growth; blades > 5 mm wide 10 mm from the apices; cystocarps, if present, borne in a predominantly apical or subapical position on the flattened fronds . . . . . *R. pseudopalmata* var. *pseudopalmata*  
Plants with extensive stoloniferous growth; blades < 5 mm wide 10 mm from the apices; cystocarps, if present, borne in a median or basal position on the flattened fronds . . . . . *R. pseudopalmata* var. *ellisiae*

*RHODYMENIA PSEUDOPALMATA* VAR. *PSEUDOPALMATA*

## SYNONYMY

- Rhodymenia pseudopalmata* (Lamouroux) Silva, 1952, p. 265.  
Basionym: *Fucus pseudopalmatus* Lamouroux, 1805, p. 29, pl. 25, Fig. 2. [See Fig. 1 of the present study.]  
Synonyms: *Fucus bifidus* Hudson, 1778, p. 581 (?) [see p. 386] non *Fucus bifidus* S. G. Gmelin, 1768, p. 201, pl. 29, Fig. 2 [= *Arthrothamnus bifidus* (S. G. Gmelin) Ruprecht]. non *Fucus bifidus* sensu Goodenough & Woodward, 1797, p. 159, pl. 17, Fig. 1 [= *Rhodophyllis divaricata* (Stackhouse) Papenfuss].  
*Sphaerococcus bifidus* (Hudson) Stackhouse, 1797, p. xxiv (as to name only).  
*Rhodomenia bifida* (Hudson) Greville, 1830, p. xlvi, 85 (as to name only).  
*Rhodophyllis bifida* (Hudson) Kützing, 1847, p. 23 (as to name only).  
*Fucus palmetta* var.  $\beta$  *bifidus* (Hudson) Turner, 1809, p. 4, pl. 4, Fig. g.  
*Sphaerococcus palmetta* var.  $\beta$  *bifidus* (Hudson) C. Agardh, 1822, p. 246.  
*Delesseria palmetta* Lamouroux, 1813, p. 125.  
= *Fucus palmetta* sensu Turner, 1809, pp. 4–5, pl. 4, (pro parte, as to materials, Fig. a, b, c, d, e, f, g only).  
= *Fucus palmetta* sensu Stackhouse, 1801, p. 102, pl. 16 (as to materials).  
= *Fucus palmetta* sensu Esper, 1798, p. 84, pl. 40, pro parte, excl. syn. (as to materials, partly).  
non *Fucus palmetta* S. G. Gmelin, 1768, p. 183, pl. 22, Fig. 3, pl. 23, [= *Delesseria gmelini* Lamouroux, 1813, p. 124].  
*Delesseria pseudopalmata* (Lamouroux) Lamouroux, 1813, p. 125.  
*Sphaerococcus palmetta* (Lamouroux) C. Agardh, 1822, p. 245.  
*Halymenia palmetta* (Lamouroux) Gaillon, 1828, p. 361.  
*Rhodomenia palmetta* (Lamouroux) Greville, 1830, p. xlvi, 88.  
*Delesseria palmetta* Lamouroux, 1813, p. 125.  
= *Fucus palmetta* sensu Turner, 1809, pp. 4–5, pl. 4, (pro parte, as to materials, Fig. a, b, c, d, e, f, g only).  
= *Fucus palmetta* sensu Stackhouse, 1801, p. 102, pl. 16 (as to materials).  
= *Fucus palmetta* sensu Esper, 1798, p. 84, pl. 40, pro parte, excl. syn. (as to materials, partly).  
non *Fucus palmetta* S. G. Gmelin, 1768, p. 183, pl. 22, Fig. 3, pl. 23, [= *Delesseria gmelini* Lamouroux, 1813, p. 124].  
*Delesseria pseudopalmata* (Lamouroux) Lamouroux, 1813, p. 125.  
*Sphaerococcus palmetta* (Lamouroux) C. Agardh, 1822, p. 245.  
*Halymenia palmetta* (Lamouroux) Gaillon, 1828, p. 361.  
*Rhodomenia palmetta* (Lamouroux) Greville, 1830, p. xlvi, 88.

## STRUCTURE AND DEVELOPMENT OF THE THALLUS

## EXTERNAL MORPHOLOGY

Plants of *R. pseudopalmata* var. *pseudopalmata* formed erect, flattened, thick, cartilaginous fronds from a small disc (to 5 mm diam.) or, less commonly, from creeping stolons. The stolons were cylindrical or flattened, very stiff and cartilaginous, and were invariably found ramifying in sponges or creeping in cracks in rock. Stolons were lightly coloured when embedded and often formed irregularly shaped secondary attachment organs. Plants growing subtidally on the stipes of *Laminaria hyperborea* (Gunnerus) Foslie were usually found to have larger basal discs and never formed stolons. Erect fronds had a bright crimson colour when young, which tended to be deeper or purplish in older plants.

There was considerable morphological variation in the plants examined, particularly of the shape and mode of branching of the fronds (Fig. 14C, D). Plants collected intertidally from rock pools tended to have short stipes (Fig. 14F, G, H) which rapidly expanded to form the flattened portion of the fronds. Such intertidal plants were generally less than 50 mm tall at maturity. Younger

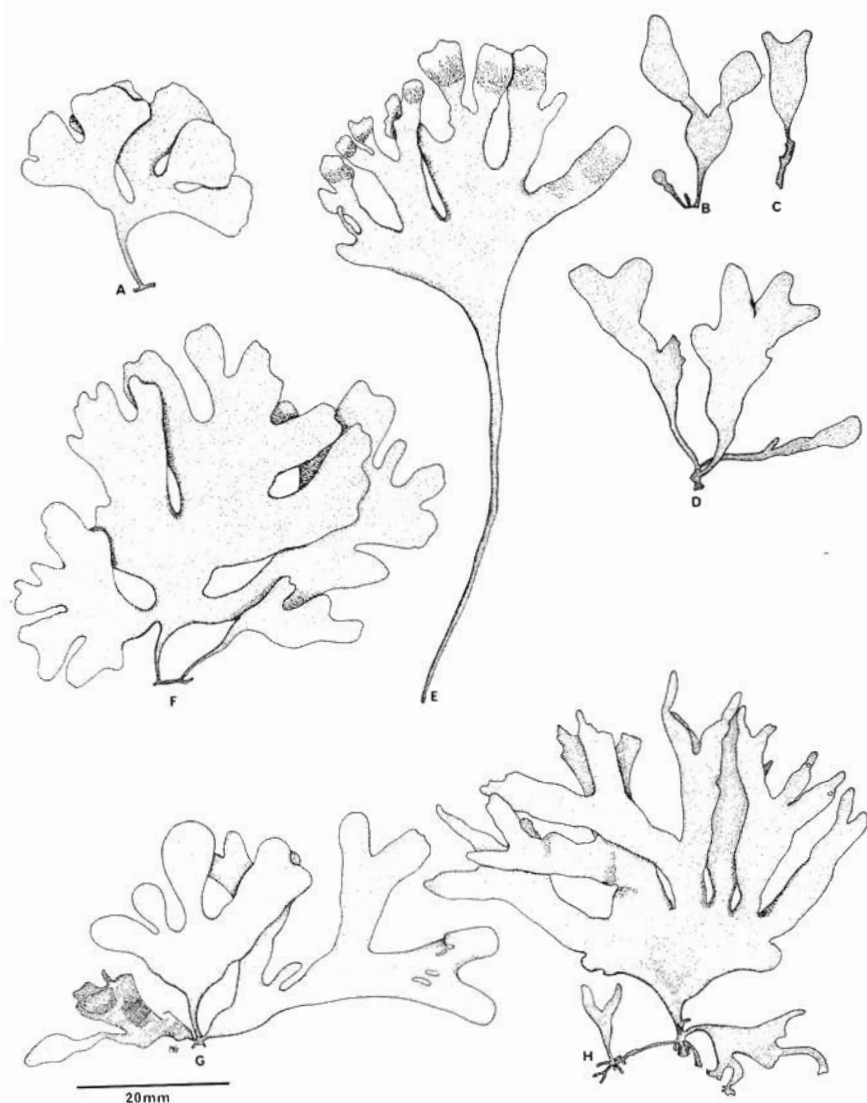


FIG. 14A-H. Range of variation in external morphology of British Isles material of *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva. Fig. 14A. Black Head, Co. Clare, 19 April 1972, subtidal: 5 m, leg. W. F. Farnham. Fig. 14B,C,D. Rhosneigr, Anglesey, 11 December 1973, pool: MLWS, leg. M. D. Guiry. Fig. 14E. Kilkee, Co. Clare, 29 June 1972, tetrasporangial plant, drift on the stipe of *Laminaria hyperborea* (Gunnerus) Foslie, leg. M. D. Guiry. Fig. 14F. Caherrush Point, Co. Clare, 30 June 1972, vertical walls: ELWS, leg. M. D. Guiry. Fig. 14G. Elberry Cove, S. Devon, 3 July 1973, leg. M. D. Guiry. Fig. 14H. Treaddur Bay, Anglesey, 19 August 1974, pool: MLWS, leg. M. D. Guiry.

intertidal plants had rounded apices (Fig. 14A, B, C, D), while older plants often tended to have bifid or irregular apices (Fig. 14H). The base of the flattened portion of the blade tended to be cuneate or rounded-cuneate. Branching of the fronds was usually dichotomous but the first divisions were often very close together, giving the plants a fan-shaped appearance (Fig. 14A). Later divisions, particularly of intertidal plants, were more irregular but usually maintained a more or less dichotomous pattern. Where there was a reasonable distance between the first and second dichotomies the intervening portion of the frond often had a strap-shaped appearance (Fig. 14G, H). Lateral proliferations of the blades were uncommon except in extremely old plants and even then were very small (to 5 mm) and were usually dichotomously divided. Proliferation from the basal disc or from stolons was much more common (Fig. 14B, F, H). Proliferation from the torn or truncated apices of older plants was also a common occurrence and a blade with a similar morphology to the parent plant was formed.

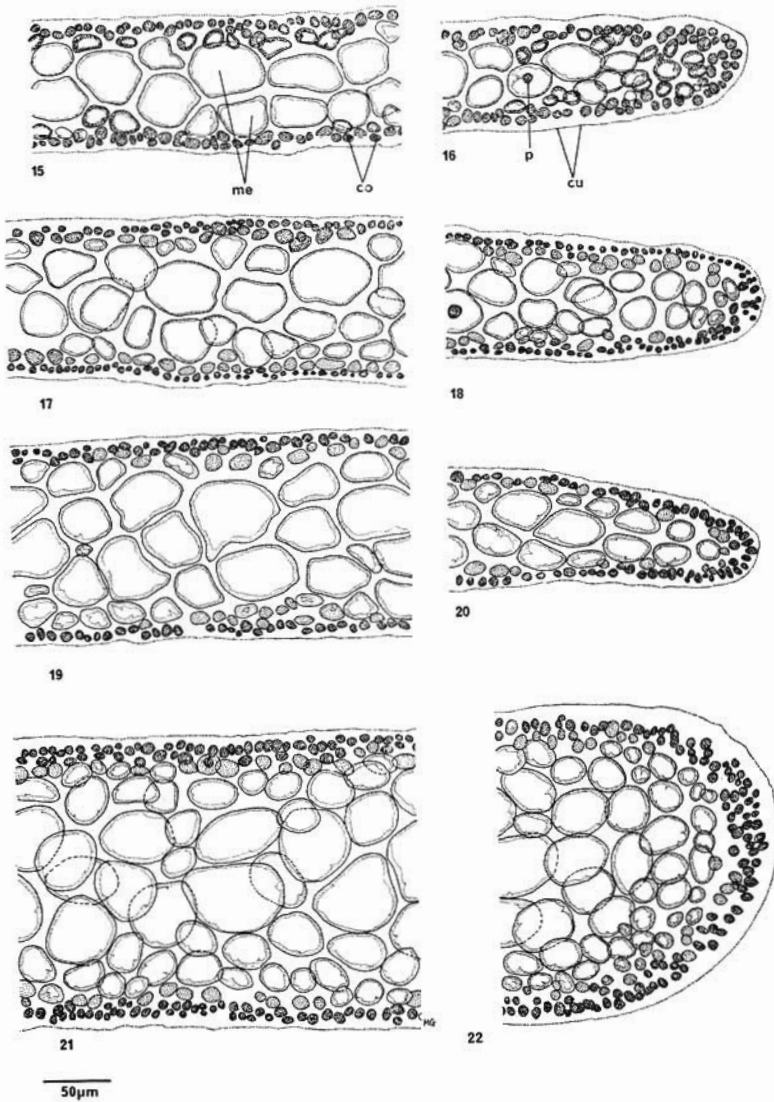
Subtidal plants growing on rocks or boulders had a morphology similar to that described for intertidal plants but tended to be slightly larger on average (to 60 mm) and occasionally had very long stipes (to 40 mm). In a few plants some linear elongation of the apices was observed but this was not found to be characteristic of the variety. Plants growing epiphytically on the stipes of *Laminaria hyperborea* in the subtidal were the largest specimens examined (to 120 mm) and also had the longest stipes (in length and proportionally) (Fig. 14E). The morphology of these specimens is otherwise more or less the same as that found in intertidal specimens.

#### ANATOMY

The thallus was composed of a cortex of 2–3 layers of chloroplast-bearing cells and a medulla of 2–8 layers of more or less colourless cells (Figs 15, 21). The thallus when first formed (within 2 mm of the apices), was usually quite thin and was composed of 2 layers of medullary cells. At 10 mm from the apices the thallus was quite thick (100–200  $\mu\text{m}$ ) and was composed of 2–3 layers of medullary cells (Figs 15, 16). At the base of the frond the thallus was 200–250  $\mu\text{m}$  thick and was composed of 6–8 layers of medullary cells (Fig. 21). The cortical cells appeared widely spaced in optical section 10 mm from the apices (Fig. 2) and were slightly axially elongated. These cells measured (in optical section) (3.8) 9.0–13.4 (23.2)  $\mu\text{m}$  long axially and (3.6) 8.7–11.6 (15.4)  $\mu\text{m}$  broad adaxially. Some difficulty was experienced in measuring these cells as the next layer of subcortical cells was usually visible between the cells of the uppermost layer (Fig. 2). The subcortical layer was usually composed of cells with a slightly lighter colour. The surface cortical cells, when first formed, had chloroplasts which filled the entire cell but as the cells aged (i.e. in the lower parts of the thallus) the chloroplasts tended to become more fragmented and parietally placed.

Medullary cells, in the younger parts of the thallus, occasionally had a small amount of very fragmented, parietally placed chloroplast, the colour of which was easily destroyed by most preserving fluids. Medullary cells were large and measured (26) 41–51 (61)  $\mu\text{m}$  periclinally in transverse section (TS) and





FIGS 15–22. Camera lucida drawings of transverse sections of *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva and *R. pseudopalmata* var. *ellisiae* (Duby) Guiry. Fig. 15. *R. pseudopalmata* var. *pseudopalmata*, Treaddur Bay, Anglesey, 18 August 1974, leg. M. D. Guiry, TS at centre of thallus 10 mm from apex. Fig. 16. Collection data as Fig. 15, TS at edge of thallus 10 mm from apex. Fig. 17. *R. pseudopalmata* var. *ellisiae*, Vierville-sur-Mer, Calvados, France, 21 July 1974, leg. M. D. Guiry, TS at centre of thallus 10 mm from apex. Fig. 18. Collection data as Fig. 17, TS at edge of thallus 10 mm from apex. Fig. 19. *R. pseudopalmata* var. *ellisiae*, Seaford, Sussex, 2 July 1973, leg. M. D. Guiry, TS at centre of thallus 15 mm from base. Fig. 20. Collection data as for Fig. 19, TS at edge of thallus 15 mm from base. Fig. 21. *R. pseudopalmata* var. *pseudopalmata*, Cap Fagnet, France, 9 September 1972, leg. J. H. Price & I. Tittley, TS at centre of thallus 15 mm from base. Fig. 22. Collection data as for Fig. 21, TS at edge of thallus 15 mm from base. *co*: cortical cells; *cu*: cuticle; *me*: medullary cells; *p*: proteinaceous (iridescent) body.

(65) 102–133 (153) axially in longitudinal section (LS). These cells were strongly coherent and even when soaked in 2N HCl or 2N HNO<sub>3</sub> for long periods (5 min to 1 h) would not separate even when squashed forcibly between microscope slides, the cell walls breaking rather than separate. In LS the medullary cells dovetailed into one another. In the older parts of the thallus (30–40 mm from the apices in mature plants) the thallus thickness was more or less the same at the edge of the thallus as at the centre (Figs 21, 22). The medullary area was also more extensive, having 7–8 layers of cells (Figs 21, 22) and seemed to have been added to by growth of the cortical cells which eventually formed new layers of medullary cells. The anatomy of the stipes and stolons was similar to that of the older parts of the fronds. Some of the medullary cells had a large iridescent body which stained deeply with acetocarmine. Such bodies were particularly common in the older cells of the attachment disc.

### STRUCTURE AND DEVELOPMENT OF REPRODUCTIVE ORGANS

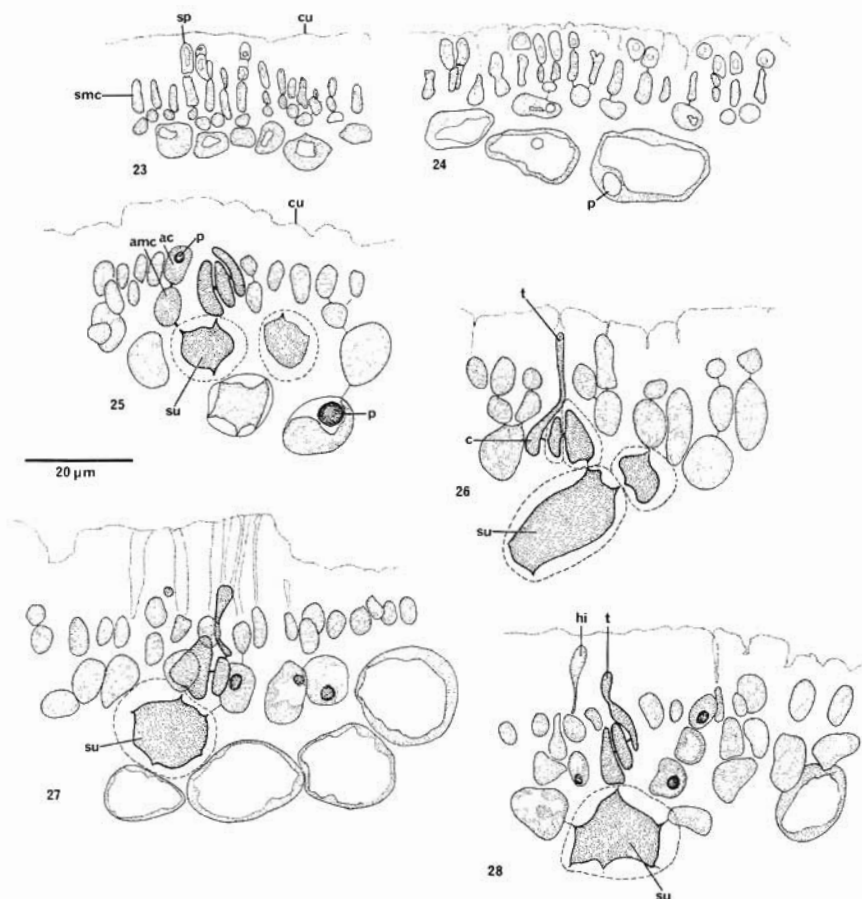
Plants of *Rhodymenia pseudopalmeta* var. *pseudopalmeta* bearing carposporophytes and tetrasporangia have frequently been recorded in the literature (e.g. Harvey, 1847, pl. 134; Newton, 1931, Fig. 260; Sparling, 1957, pl. 55a; Fig. 12h, i, k), but spermatangia and carpogonial branches have been much more rarely recorded (Sparling, 1957, p. 357, Fig. 11a–g; for South African specimens). Reproductive organs were not common on the intertidal plants examined from the British Isles and northern France by the present author but were occasionally found on large plants at ELWS (extreme low water of spring tides). Subtidal plants, to judge from the preserved material examined, are much more commonly fertile. The following description of reproductive organs is largely based on a collection made at Finnavara, Co. Clare, Republic of Ireland (30 August 1973, leg. M. D. Guiry) at ELWS on boulders.

#### GAMETANGIAL PLANTS

In this variety spermatangia and carpogonia were borne on separate plants. Spermatangia were formed in a small, rounded sorus 2–5 (8) mm diam. at the apices of male plants. The sori were conspicuous as areas of whitish tissue. In all the plants examined the spermatangia were fully mature and consequently little can be said of their development. Mature spermatia were formed singly in spermatangia borne singly or in pairs on spermatangial mother cells which were probably developed from surface cortical cells (Figs 23, 24) (Guiry, 1974b, pl. II, Fig. c). Mature spermatangia were rounded or elongate-oval and measured (3.6) 4.5–7.2 (9.0)  $\mu\text{m}$  in diameter and (3.6) 5.4–7.2 (10.8)  $\mu\text{m}$  in length. Spermatangia were shed through the cuticle which became very thickened during spermatangial development (Figs 23, 24). In older sori the cuticle tended to be rather irregular with anticlinally orientated striations which were probably a result of spermatial discharge (Fig. 24). Spermatial discharge was not observed in fresh material. Spermatangial plants were, in general, rather rare.

Carpogonial plants were difficult to find and carpogonial branches were only observed in plants from the Finnavara collection. The most satisfactory stain for carpogonial branches in this species was iron–alum/acetocarmine (Austin,

1959). Carpogonial branches were only found in the first few mm of thallus. These structures were most easily located in TS by means of the deeply-staining supporting cell (Figs 25–28). The latter was a modified subcortical cell which bore a 3-celled carpogonial branch. The supporting cell measured 15–25  $\mu\text{m}$  in diameter and was usually rounded (Figs 25, 27, 28) but was occasionally elliptical or oval (Fig. 26). In the proximity of carpogonial branches (particularly those with well developed trichogynes) the cuticle was very much thickened (Figs 25–28), often to 20–25  $\mu\text{m}$ . In all specimens examined the carpogonial branch was composed of 3 cells which were joined by large pit connections. The



FIGS 23–28. *Camera lucida* drawings of transverse sections of the male and female reproductive organs of *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva. Material was collected at Finnavara, Co. Clare, 30 August 1974, boulders: ELWS, leg. M. D. Guiry. Fig. 23. Mature spermatangial sorus. Fig. 24. Older spermatangial sorus. Figs 25–28. Carpogonial branches at various stages of development. Abbreviations as in Figs 15–22 except: *ac*: auxiliary cell; *amc*: auxiliary mother cell; *hi*: hair cell; *smc*: spermatangial mother cell; *sp*: spermatangium; *su*: supporting cell; *c*: carpogonium; *t*: trichogyne.

carpogonium was always uninucleate but the second cell of the carpogonial branch was always binucleate. Contrary to the observation of Sparling (1957, p. 325) that the auxiliary cell was easily distinguished after its formation by the presence of a proteinaceous body (= iridescent body), in the material examined it was rather difficult to decide which cells with such bodies represented the auxiliary cell branch. In some cases (Fig. 25), a proteinaceous body was observed in the terminal cell of a filament but in others (Fig. 27) it was observed in a subterminal cell. Occasionally an apparently 3-celled filament was observed on the supporting cell (Fig. 26). In this particular case the terminal cell did not seem to have any proteinaceous body. Cells other than those involved in reproduction may also have proteinaceous bodies (Fig. 28) and, as remarked previously, these seem frequent in medullary cells of this species. Sjöstedt (1926, p. 32), Kylin (1931, p. 33) and Sparling (1957, p. 325) observed that the auxiliary cell was suffused with "food-material" and consequently stained deeply. This would seem also to be a difficult distinguishing feature as it has been observed that many of the cells surrounding the carpogonial branch are nutritive in function and consequently are also full of "food-material". It is however possible that the stain used in the present study did not differentiate between cells with a moderate amount of "food-material" and those with a large amount. In conclusion therefore it seems that the only auxiliary cell branch observed in this variety during the present study which corresponds with the classical concept is that illustrated as Fig. 25.

Another feature of carpogonial branch development in this variety deserving special mention was the disruption of the surrounding cortical cells, many of which became anticleinally elongated (Fig. 28) forming what may have been the beginnings of hair cells. These cells may possibly have been disrupted by the process of sectioning, as Sparling (1957) observed that hair cell formation frequently occurred in the proximity of carpogonial branches. Fertilization was not observed in any of the many procarps of this variety observed during the present study. Sparling (1957) reported that a connecting cell was cut off from the fertilized carpogonium which coalesced with the auxiliary cell.

#### CYSTOCARP

Three groups of carposporangia at different stages of development were invariably present in the mature cystocarp which corresponded to the 3 largest lobes of the gonimoblast. The most mature gonimolobe was always the largest and occupied two-thirds or more of the total volume of the cystocarp. The carposporangia of this lobe were the largest and the most mature. Each contained a single carpospore and measured (5.4) 7.2–21.6 (32.4)  $\mu\text{m}$  maximum diameter and (5.4) 7.2–14.4 (21.6)  $\mu\text{m}$  minimum diameter. Mature carposporangia were usually hexagonal in shape (probably due to crowding) and immature carposporangia were rounded or angular-rounded. Presumably when the oldest carposporangia have been discharged, the second and third lobes expand and fill the resulting space, the carposporangia maturing prior to release.

Externally cystocarps appeared as irregularly-placed hemispherical protuberances (532–909  $\mu\text{m}$  in diameter; 500–965  $\mu\text{m}$  maximum height) irregularly scattered at the apices of the ultimate branches of the fronds (cf. Harvey, 1847,

pl. 134, Figs 2, 7). Cystocarps were observed half-way down the fronds but this was rare. Cystocarps had a small, centrally-placed ostiole which was slightly raised.

#### TETRASPORANGIAL PLANTS

Tetrasporangia were formed in small rounded sori 2–5 (9) mm in diameter at the apices of the fronds. The sori were usually concave, apparently due to developmental stresses and tetrasporangia were formed on both sides of the thallus. In the formation of tetrasporangia cortical cells enlarged (Guiry, 1974b, Fig. 1A, B) and were densely staining. The accompanying cortical cells underwent a slight elongation and division at this stage. The tetrasporangial mother cells expanded in size and eventually divided forming a sporangium with 4 cruciately-arranged spores. The cleavages were successive, a median cleavage preceding the longitudinal cleavages. Mature tetrasporangia were distinctly elongate-oval and measured 25–30  $\mu\text{m}$  periclinally and 15–22  $\mu\text{m}$  anticlinally. Sparling (1957) gave dimensions of 23–28  $\mu\text{m}$  by 13–15  $\mu\text{m}$  for South African material she considered to represent this variety. When tetrasporangial sori were examined in TS, sporangia appearing to have two spores were frequently observed (Guiry, 1974b, Fig. 1C–G). From a surface examination of such sori, it was concluded that these sporangia had four spores but the longitudinal divisions were in a plane parallel to the plane of view in TS. Occasionally (Guiry, 1974b, Fig. 1E) tetrasporangia were observed with the periclinal divisions in two different planes which gave the appearance of a sporangium with three spores.

Sporangia in mature sori were very crowded (Guiry, 1974b, Fig. 1G) and were interspersed with elongate, sterile filaments two cells long. In this variety cleavage of the tetrasporangia did not occur synchronously and developing tetrasporangial mother cells were always observed in mature sori. Secondary tetrasporangia and further divisions of tetrasporangia in situ were not observed. Tetraspores, when shed, measured 19.8–28.6  $\mu\text{m}$  diameter (78 spores measured). Boney (1975, Table 2) reported tetraspore diameters of (7.5) 9.0–12.0  $\mu\text{m}$  from specimens dredged at Plymouth; this would seem unusual, particularly as such diameters are more typical of spores of species belonging to the Phylloporaceae.

#### REPRODUCTIVE PHENOLOGY

Of the 145 collections of *R. pseudopalmata* var. *pseudopalmata* examined only 102 were clearly dated and 58 bore discernible reproductive organs. Most plants were collected in June, July, August and September with a scarcity of collections in October through to March, which may reflect difficulties in locating plants of this variety during the winter months. Spermatangial, carposporangial and tetrasporangial plants were commonest in July, August and September, indicating that this variety is "summer fertile" in the British Isles.

#### HABITAT

This variety was found to grow in both intertidal and subtidal habitats. In the intertidal, populations were not common and were invariably confined to the subtidal fringe. Populations were commonest in deep pools at MLWS

(mean low water of spring tides) but, in exposed areas, tended to be found in narrow, shallow pools at MLWN (mean low water of neap tides). Such pools were invariably well-shaded and populations were usually confined to vertical or near vertical walls well below the water surface. Under certain conditions of shade and humidity populations were capable of surviving emersion. Such populations were common on the west coast of Ireland (Kilkee, Co. Clare), but were invariably associated with habitats which were not well colonized by other algae. At one of the sites examined in Britain (Elberry Cove, Torbay, South Devon) this variety grew in considerable quantity on vertical open rock at ELWS together with *Schottera nicaeensis* (Lamouroux ex Duby) Guiry & Hollenberg. In the subtidal, plants of this variety were commonest on stones, boulders and ledges and epiphytically on the stipes of *Laminaria hyperborea* to 20 m.

## DISTRIBUTION

### BRITISH ISLES

The distribution records of *Rhodymenia pseudopalmata* as reported in the literature under various synonyms are summarized in Fig. 29; some of the literature records cited possibly refer to *R. pseudopalmata* var. *ellisiae* and *Schottera nicaeensis*. The records of "*Rhodymenia palmata*" from the Orkney Isles, all refer, as far as can be ascertained, to *R. delicatula* (see p. 419). Fig. 30 illustrates the distribution of *R. pseudopalmata* var. *pseudopalmata* according to specimens examined by the author. The data used to compile Figs 29 and 30 may be found in Guiry (1976). A comparison of Figs 29 and 30 shows that a considerable number of earlier records may represent misidentifications and that the variety seems to be confined to southern and western coasts of the British Isles. The Scottish records are in need of confirmation as they represent, if correct, the northernmost extension of *Rhodymenia pseudopalmata* in the Atlantic.

### WORLD

*Rhodymenia pseudopalmata* seems to be confined to the north and south Atlantic. There have been a few records from the Pacific (e.g. Setchell & Gardner, 1903; Taylor, 1945) but these probably represent other species of *Rhodymenia* belonging to the section *Rhodymenia*. Moreover, in the Atlantic, many records of *Rhodymenia pseudopalmata* (often as *R. palmata*) possibly are not the type variety but are included here because of uncertainty as to the correct names which should be applied to these specimens.

In the eastern north Atlantic the species has been recorded from the British Isles south to Morocco, the Canary Islands and the Azores. In the south Atlantic Sparling (1957) tentatively recorded *Rhodymenia pseudopalmata* from South Africa but her material had a four-celled carpogonial branch whereas the material described above has a three-celled carpogonial branch. Further investigation of material of this species from the south Atlantic is needed. Records of this species from the Mediterranean (e.g. Giaccone, 1969; Gerloff & Geissler, 1971) are probably incorrect. The records may refer to *Rhodymenia ardissoni* J. Feldmann or *R. ligulata* Zanardini, both of which species are apparently common in the Mediterranean.

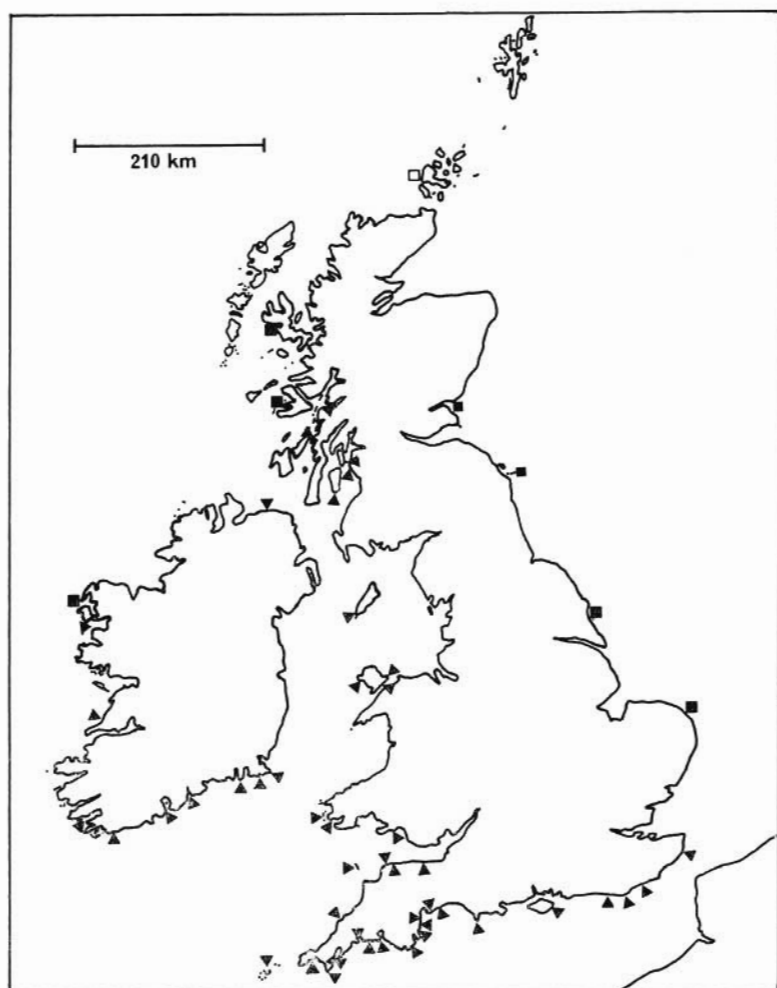


FIG. 29. Distribution in the British Isles of *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva as recorded in the literature searched. ▲ = Records which are probably correct; ■ = doubtful records; □ = incorrect records.

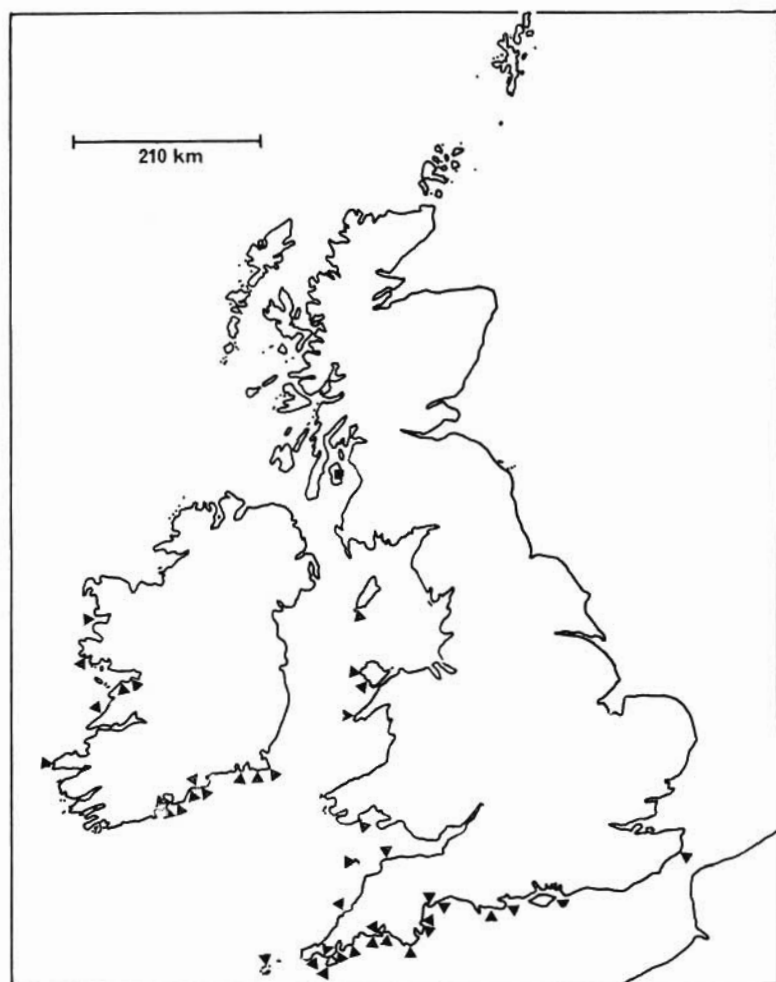


FIG. 30. Distribution in the British Isles of *Rhodymenia pseudopalmata* var. *pseudopalmata* (Lamouroux) Silva according to specimens examined during the present study. ▲ = Specimens with clear locality citations; ■ = specimen with doubtful locality citation.



*RHODYMENIA PSEUDOPALMATA* VAR. *ELLISIAE*

## ORIGINAL DESCRIPTION

*Rhodymenia pseudopalmeta* var. *ellisiae* (Duby) Guiry in Guiry & Hollenberg (1975) has long been confused with a number of other algae, particularly *Schottera nicaeensis*. This confusion arose largely as a result of J. Agardh's (1842, p. 153-154) reduction of *Halymenia nicaeensis* Lamouroux ex Duby [= *Schottera nicaeensis* (Lamouroux ex Duby) Guiry & Hollenberg] to a variety of *Rhodymenia palmetta* and Montagne's (1846, p. 68-69) transfer of *Halymenia nicaeensis* to the genus *Rhodymenia* as *Rhodymenia nicaeensis*. The materials of both J. Agardh and Montagne (BM; PC) undoubtedly represent the alga presently known as *Schottera nicaeensis* (Phylloporaceae; see Guiry & Hollenberg, 1975, for a more complete synonymy). Confusion of the Phylloporacean alga with *Rhodymenia palmetta* was largely a result of a scarcity of fertile material.

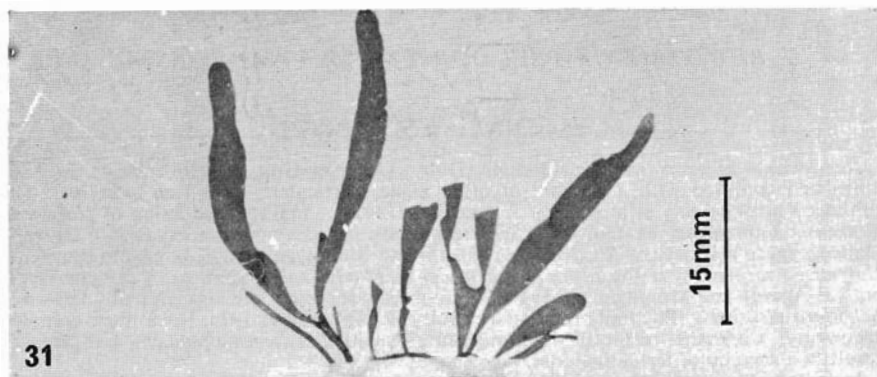
In Britain, Harvey (1847, p. 134, Fig. 3) described plants collected by Mrs Griffiths and Miss Cutler at Sidmouth as "*Rhodymenia palmetta* var. *nicaeensis* J. Agardh". It is clear from duplicate specimens collected at Sidmouth by Griffiths (BM) that Harvey (1847) confused specimens of *Schottera nicaeensis* from the Mediterranean (then known as *Rhodymenia palmetta* var. *nicaeensis* J. Agardh) with British specimens of a species of *Rhodymenia* sensu stricto. Holmes (1883) seemed primarily concerned with the confusion between *Rhodymenia palmetta* var. *nicaeensis* and *Phyllophora palmettoides* J. Agardh stating that:

"Owing to the great similarity in the shape and structure of the frond to that of *Phyllophora palmettoides*, the two plants often pass the one for the other when the terminal cirrhi are absent and the fronds are collected without the root, which in the latter is a spreading disc and in the former [= *Rhodymenia palmetta* var. *nicaeensis*] is a creeping stoloniferous prostrate stem."

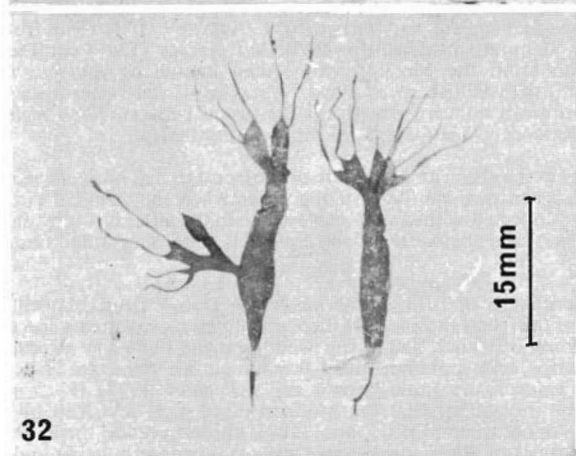
Holmes examined cystocarpic specimens of "*Halymenia nicaeensis* Duby" from Marseilles and concluded that the structure of the frond showed that these specimens represented a species of *Phyllophora*, and cited the opinion of Hauck that in the Mediterranean there was a species of *Phyllophora* which bore cystocarps, tetrasporangia and spermatangia which he (see Hauck, 1885) thought was *Phyllophora palmettoides* [now known as *Phyllophora sicula* (Kützinger) Guiry & L. Irvine]. Despite these indications that the Mediterranean alga described by J. Agardh (1842) represented a Phylloporacean alga, Holmes (1883) chose to retain the epithet "*nicaeensis*" for his material (a species of *Rhodymenia* sensu stricto), apparently being under the mistaken impression that he was making a new combination. *Rhodymenia nicaeensis* sensu Holmes was invalidated by *Rhodymenia nicaeensis* (Lamouroux ex Duby) Montagne (Montagne, 1846, pp. 68-69).

The earliest valid name which can be applied to Holmes's specimens would seem (as appreciated by Batters, 1902) to be *Halymenia palmetta* var. *ellisiae*\* Duby (Duby, 1830, p. 934). Duby cited Chauvin's specimen no. 16 of the exsiccata *Algues de Normandie* (Chauvin, 1827) as the basis for his description, although Chauvin did not provide a description and credited Lamouroux with the name. Duby's (1830) description would seem to constitute the earliest valid account of this entity. Nine specimens labelled "*Sphaerococcus palmetta* var. *ellisiae*" were found by the present author in Duby's herbarium at the Institut de Botanique, Université de Strasbourg (STR); one of these, inscribed "M. Chauvin 1827" in Duby's handwriting (Fig. 34; the centre specimen) is selected as lectotype specimen of *Halymenia palmetta* var. *ellisiae* Duby. All specimens labelled *Sphaerococcus palmetta* var. *ellisiae* [sic] in Duby's herbarium are representative of a species of *Rhodymenia* similar to that described by Harvey (1847, pl. 134, Fig. 3; as *Rhodymenia palmetta* var. *nicaeensis*) and that described by Holmes (1883, pl. 240: as *R. nicaeensis* sensu Holmes) and all Duby's and Lamouroux's specimens originated in the Calvados region of northern France (see Fig. 41). Holmes's (1883) specimens from Hastings, Sussex are preserved in the British Museum (Natural History) (BM) (Figs 31, 32).

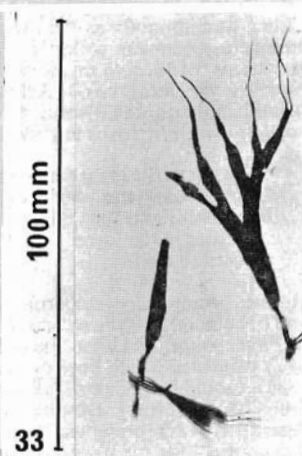
\* Two orthographic variants of the varietal epithet have been used by various authors: "*ellisiae*" and "*elisiae*". The former was used in the original description (Duby, 1830) and (in accordance with recent practice) is here retained (see Guiry & Hollenberg, 1975, p. 149 footnote).



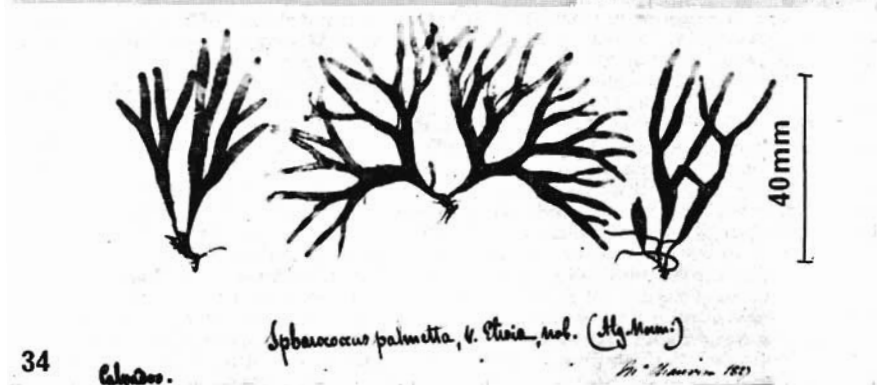
31



32



33



34

*Calodes.*

*Sphaerococcus palmata*, v. *Ellisia*, n. sp. (H. Guiry)

M. Chauvin 1966

FIGS 31-34. Herbarium material of *Rhodymenia pseudopalmata* var. *ellisiae* (Duby) Guiry. Figs 31, 32, Type material of *Rhodymenia nicaensis* sensu Holmes (BM); illustrated as tab. 240c and 240a, respectively, in Holmes (1883). The cystocarpic specimen in Fig. 31 is selected as the lectotype. Fig. 33. Material with long apical proliferations, Baie de Morlaix, Brittany, France, 10 August 1966, leg. M.-Th. L'Hardy-Halos (MDG). Fig. 34. Material of *Halymenia palmata* var. *ellisiae* Duby from Duby's herbarium (STR), annotated "M. Chauvin" in Duby's handwriting (lower right). The centre specimen is chosen as the lectotype.

## SYNONYMY

*Rhodymenia pseudopalmetta* var. *ellisiae* (Duby) Guiry, in Guiry & Hollenberg, 1975, p. 149.

Basionym: *Halymenia palmetta* var.  $\beta$  *ellisiae* Duby, 1830, p. 943.

Synonyms: *Sphaerococcus palmetta* var. *ellisiae* (Duby) Kützinger, 1868, p. 34, tab. 99 Fig. a.

*Rhodymenia palmetta* var. *ellisiae* [sic] (Duby) Bornet, 1892, p. 286.

*Rhodymenia nicaeensis* sensu Holmes, 1883, p. 289, pl. 240, Fig. a, b, c, d.

non *Rhodymenia nicaeensis* (Lamouroux ex Duby) Montagne, 1846, pp. 68–69.

[= *Schottera nicaeensis* (Lamouroux ex Duby) Guiry & Hollenberg, 1975, p. 153].

*Rhodymenia* (?) *holmesii* Ardissonne, 1893, p. 682.

As the name *Sphaerococcus palmetta* var. *ellisiae* was not validly published by Chauvin (1827, no. 16), its usage by Kützinger (1868, p. 34, Table 99, Fig. a) constituted a new combination. The combination of *Rhodymenia palmetta* var. *ellisiae* was probably first made by Bornet (1892, p. 285). Ardissonne (1893) recognizing the confusion between Holmes's *Rhodymenia nicaeensis* and the Mediterranean phylloporacean alga then known as *Phyllophora nicaeensis*, proposed the new name *Rhodymenia holmesii* Ardissonne for *Rhodymenia nicaeensis* sensu Holmes.

As the earliest valid and legitimate name for *Rhodymenia palmetta* (Lamouroux) Greville is *R. pseudopalmetta* (Lamouroux) Silva the new combination *Rhodymenia pseudopalmetta* var. *ellisiae* (Duby) Guiry, in Guiry & Hollenberg has been proposed (Guiry, in Guiry & Hollenberg, 1975).

## STRUCTURE AND DEVELOPMENT OF THE THALLUS

## EXTERNAL MORPHOLOGY

Plants of *Rhodymenia pseudopalmetta* var. *ellisiae* formed erect, flattened fronds from stolons which were usually terete and were found to ramify extensively in soft rock or sponges. Stolons were colourless or lightly coloured when completely embedded and were branched irregularly, often resulting in large clumps of erect blades (Fig. 35C). Erect fronds had a dark crimson or purplish-red colour and were often spirally twisted (Fig. 35A). Some slight changes in the appearance of the erect blades were observed to take place throughout the growing season. Epiphytic specimens were not observed.

In the intertidal plants tended to grow gregariously. In March at Seaford, Sussex (27 March 1974) stolons of this variety were found ramifying in soft rock and forming short, upright, slightly flattened fronds. Plants collected in April, 1883 by E. M. Holmes at Hastings, Sussex (Holmes, 1883, pl. 240, Fig. c, d; **BM**) were 10–35 mm in height with elongated linear blades arising from narrow stolons. These plants had, at most, one dichotomy. Several of the erect blades had probably regenerated from the bases of the previous year's fronds (Holmes, 1883, pl. 240, Fig. c [left]). Plants collected in July at Seaford (2 July 1973) were to 35 mm in height and often had weakly spirally twisted fronds with two or three narrow dichotomies (Fig. 35E, F). A characteristic feature of such fronds was the slightly mottled appearance of the thallus which was found to be caused by the accumulation of large quantities of floridean starch in the medullary cells in localized areas. Plants collected at Vierville-sur-Mer, Calvados, France near the type locality (21–23 July 1974) were to 80 mm in height (average 50 mm) with long, narrow fronds (to 5 mm broad) and 2–4 dichotomies (Fig. 35B). These plants had short cylindrical stipes to 10 mm long, gradually expanding to form a linear frond which maintained more or less the same width (less than 5 mm) for most of its length. Such specimens grew on

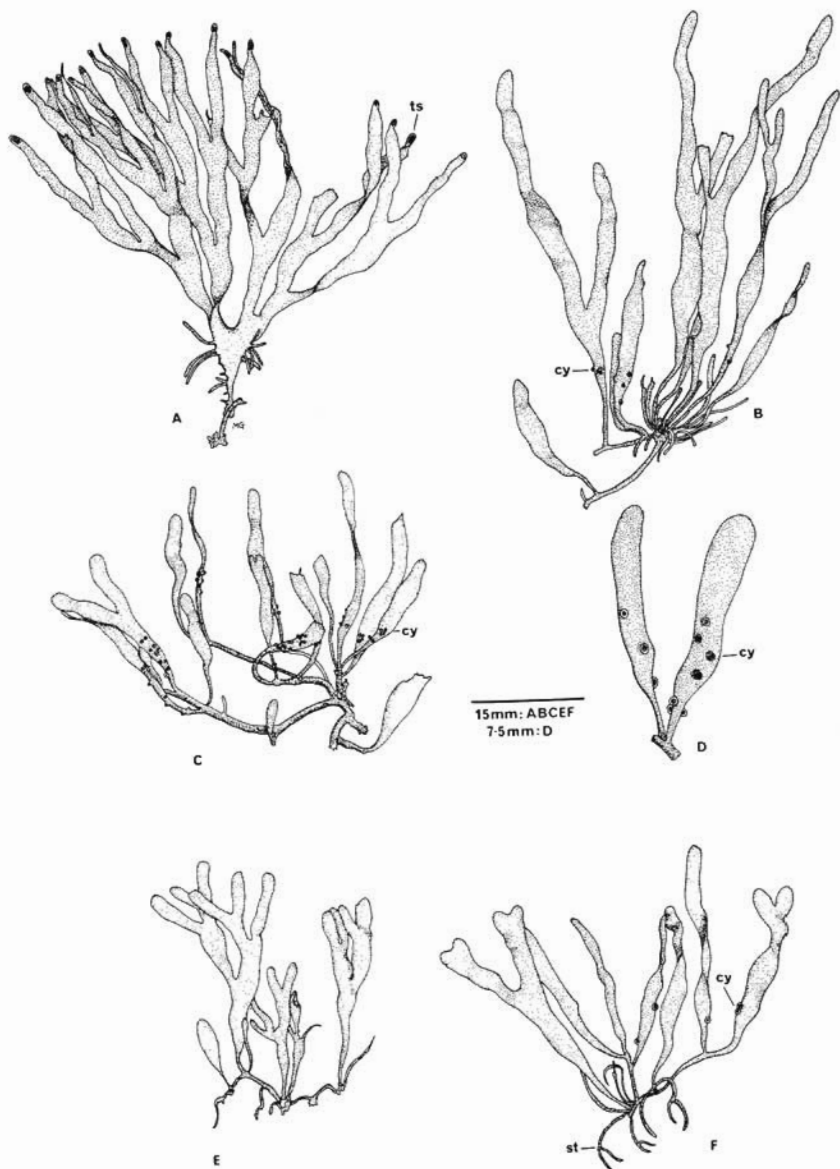


FIG. 35A-F. Range of variation in external morphology and appearance of tetrasporangial and carposporangial plants of north Atlantic material of *Rhodymenia pseudopalmata* var. *ellisiae* (Duby) Guiry. Fig. 35A. Cap Fagnet, France, 9 September 1972, leg. J. H. Price & I. Tittley; tetrasporangial plant, note the apical sorus (*ts*). Fig. 35B. Vierville-sur-Mer, Calvados, France, 21 July 1974, vertical walls; MLWN, leg. M. D. Guiry, cystocarpic plant (*cy*). Fig. 35C. Collection data as for Fig. 35B, but growing on sandy ledges at MLWS, note the shorter fronds. Fig. 35D as Fig. 35C, showing the basal position of the cystocarps. Fig. 35E. Seaford, Sussex, U.K., 2 July 1973, rocks: MLWS, leg. M. D. Guiry, sterile plant, showing the development of stoloniferous growth. Fig. 35F as Fig. 35E, but collected as drift, note the basal and median position of the cystocarps (*cy*) and stoloniferous growth (*st*).

the vertical walls of soft rocks at MLWN-ELWS. At the same locality, growing on the protruding tips of flat sandy rocks at ELWS, small plants were found growing erect with short, sometimes simple, fronds (Fig. 35C, D). This type of plant seemed to be confined to such wave-washed plateaux. However, the larger plants described above were occasionally found to have such short simple blades borne on short lateral stolons (Fig. 35B). Some plants collected at this locality were found to have small apical proliferations, particularly where the frond apex had become eroded (Fig. 35C) but these rarely exceeded a few mm in length. Holmes (1883, pl. 240, Fig. a; Fig. 32 of the present work) illustrated a specimen from Hastings with cirrose apical proliferations to 10 mm long. Specimens from Brittany (Baie de Morlaix, 10 August 1966, leg. M.-Th. L'Hardy-Halos) with long apical proliferations to 20 mm bore an extraordinary resemblance to some plants of *Schottera nicaeensis* (cf. Fig. 33 and Guiry & Hollenberg, 1975, Fig. 14c, d, e). Such plants were common in collections made in August and September and have occasionally been found in April.

#### STOLONS

Stolon production in *Rhodymenia pseudopalmata* var. *ellisiae* is remarkable in its intensity, whole stands of plants often having a common origin. In more mature plants the bases of the flattened portion of the fronds were often observed forming lateral proliferations (Fig. 35A) which, on occasion, seemed positively geotrophic (or perhaps negatively phototropic) curving towards the substratum and presumably forming stolons.

#### ANATOMY

The thallus was composed of a cortex of 2-3 layers of chloroplast-bearing cells and a medulla of 2-6 layers of colourless cells. Within 2 mm of the apex of the thallus the fronds were usually thin (to 38  $\mu\text{m}$  thick in TS) and were composed of two layers of medullary cells. The cortical cells appeared fairly widely spaced in optical section (Fig. 3) and were slightly axially elongated. Surface cortical cells measured (5.4) 9.0-14.4 (19.8)  $\mu\text{m}$  long axially and (3.6) 4.5-7.2 (10.8)  $\mu\text{m}$  wide adaxially. A characteristic feature of this variety was that the subcortical cells appeared very regularly arranged when viewed from the surface. The chloroplasts had a similar morphology and developmental pattern to that described for the type variety. Medullary cells, when mature, were large and measured (24) 41-53 (57)  $\mu\text{m}$  periclinally in TS and (98) 102-133 (137)  $\mu\text{m}$  axially in LS. These cells were very strongly coherent in the manner described for the type variety. In the lower parts of the thallus the medulla was to six layers in extent but the cortex remained quite thin (Fig. 19). The margin of the thallus was very much narrower than the centre (Figs 19, 20) which contrasts well with *R. pseudopalmata* var. *pseudopalmata*, where the thallus edge had more or less the same thickness as the centre (Figs 21, 22). In *R. pseudopalmata* var. *ellisiae* the thallus was 116-145  $\mu\text{m}$  thick in the flattened fronds at 10 mm or more from the apex, increasing to 188  $\mu\text{m}$  thick at the extreme base of the flattened portion.

## STRUCTURE AND DEVELOPMENT OF REPRODUCTIVE ORGANS

As far as can be ascertained, the description and illustrations given by Holmes (1883, pl. 240; as *R. nicaeensis* sensu Holmes) are the only published records of reproductive organs in this variety. He illustrated tetrasporangia occurring in a small apical sorus on terminal filiform proliferations and cystocarps occurring at the apices of short, erect, terete fronds, but stated that cystocarps were also found near the base of the fronds, which is more typical.

## GAMETANGIAL PLANTS

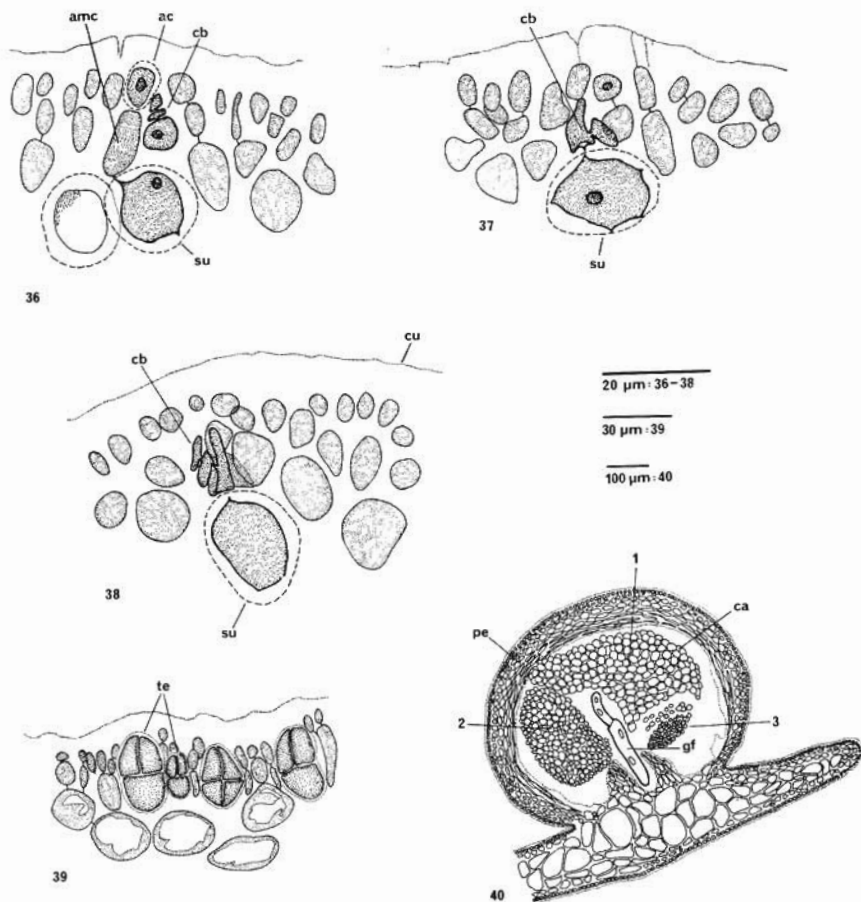
Spermatangia were not found on any of the plants collected. The description of Buffham (1894, pp. 294–295, pl. 13: Figs 15–17) of the spermatangia of a specimen of "*Rhodymenia palmetta*" collected by J. T. Neeve at Deal, Kent in August, 1892 may in fact represent the spermatangia of this variety. There is a specimen in the Ulster Museum (BEL) labelled "*Rhodymenia nicaeensis*" by E. M. Holmes which was collected at Deal by Neeve which bears spermatangia. This specimen was however collected in November 1898. I have not been able to locate the material cited by Buffham (1894).

Carpogonial branches were found in one collection (Vierville-sur-Mer, 21 July 1974) at the apices of small plants which had simple blades (Figs 35C, D) and which also bore basal cystocarps. Most of these carpogonia were in an advanced state of post-fertilization development and all carpogonial branches observed (Fig. 38) were without trichogynes but seemed to be composed of three cells. The supporting cells were large and stained deeply with Acetocarmine and Harris's Haematoxylin. Figs 36 and 37 show some post-fertilization stages which were not observed in the type variety. Fig. 36 shows what seemed to be a very young fertilized auxiliary cell with the carpogonial branch deteriorating. As observed by Sjöstedt [1926; for *Rhodymenia pertusa* (Postels & Ruprecht) J. Agardh], the auxiliary cell stained very deeply and the proteinaceous body was very large and obvious, however, as in the type variety a number of nearby cells also stained deeply. A connecting cell between the carpogonium and the auxiliary cell was not observed. Fig. 37 shows a similar stage but in this case the second cell of the carpogonial branch seemed to have fused. Several further stages in the development of the gonimoblast were observed but a satisfactory account of these cannot be given. The procarps and young gonimoblasts of species of the Rhodymeniales sensu stricto can only be observed after sectioning. All the genera studied by the present author show a remarkable resistance to any form of squash preparation (such as that used by Norris, 1957 on members of the Kallymeniaceae; see Sparling, 1957, pp. 321–322).

## CYSTOCARP

Mature cystocarps were found to be commonest on the smaller plants (Fig. 35C, D) and were usually present only at the bases of the blades. On the larger plants cystocarps were rarer but when present were usually confined to the bases of the flattened fronds (Fig. 35B, F). Holmes (1883, pl. 240, Fig. c [left]) illustrated a plant of this variety from Hastings which bore cystocarps at the apices of a seemingly terete, erect frond. This does not seem uncharacteristic,

as such a frond would probably have grown on and formed a flattened blade, in which case the cystocarps would have eventually been basally placed. In a single case, in a specimen collected at Bulverhythe, (near St Leonard's, Sussex, 23 August 1889, collector unknown, **BM**) the cystocarps were borne at the apices. Otherwise the cystocarps had more or less the same dimensions and structure as that described for the type variety and, when mature, had three generations of carposporangia (Fig. 40).



FIGS 36–40. *Camera lucida* drawings of transverse sections of some reproductive organs of *Rhodymenia pseudopalmata* var. *ellisiae* (Duby) Guiry. Figs 36, 37, 38. Carpopogonial branches at various stages of development, probably all post-fertilization, Vierville-sur-Mer, Calvados, France, 21 July 1974, sandy ledges: MLWS, leg. M. D. Guiry. Fig. 39. Transverse section of mature tetrasporangial sorus; only a portion of the sorus is shown, Cap Fagnet, France, 9 September 1972, leg. J. H. Price & I. Tittley, Fig. 40. Transverse section of a mature cystocarp showing three generations of carposporangia, note the large, central, sterile, gonimoblast filaments, Seaford, Sussex, U.K., drift, 2 July 1973, leg. M. D. Guiry. Abbreviations as in Figs 15–28, except for: *ca*: carposporangium; *cb*: carpopogonial branch; *gf*: gonimoblast filament; *pe*: pericarp; *te*: tetrasporangium.

## TETRASPORANGIAL PLANTS

Only a few tetrasporangial plants have been examined. Plants collected at Cap Fagnet, France (9 September 1972, leg. J. H. Price & I. Tittley) bore tetrasporangia in a small apical sorus (2–3 mm diam., Fig. 35A). These sori were concave in a similar fashion to that described for the type variety. Other tetrasporangial plants examined had slightly elongate sori (to 5–6 mm long). Tetrasporangia were borne on both sides of the thallus and mature sori measured 100–140  $\mu\text{m}$  in thickness. The spores were cruciately arranged and the sporangia measured (14) 23–25 (29)  $\mu\text{m}$  long and (11) 14–18 (20)  $\mu\text{m}$  broad (Fig. 39). The development of tetrasporangia was exactly as described for the type variety. Holmes (1883) illustrated tetrasporangia as occurring in terminal filiform proliferations but a similar specimen from the Baie de Morlaix, France (Fig. 33) did not have tetrasporangia in the apical proliferations.

## REPRODUCTIVE PHENOLOGY

The scanty phenological data available suggested that *Rhodymenia pseudopalmata* var. *ellisiae* bears reproductive organs in April, June–September, which is more or less the same period of fertility as the type variety.

## HABITAT

Plants of *R. pseudopalmata* var. *ellisiae* seemed to be commonest on shores where soft rocks such as chalk and limestone predominated. Most of the British records are from Sussex and Kent, where such rock dominates the shore formations. At Vierville-sur-Mer, Calvados, France (which is near the type locality) zones of this variety were present on soft chalky limestones at MLWS–ELWS. The enormous capacity for stolon production seemed to give the plants a competitive advantage on such soft rocks. In Britain the species was less common on the shores examined but was frequent at ELWS in similar situations at Seaford, Sussex. Many of the specimens examined were collected as drift (particularly in Kent, Sussex and Norfolk) but the frequent occurrence of such fresh drift material suggests that there are considerable populations in sublittoral habitats.

## DISTRIBUTION

## BRITISH ISLES

Specimens have been recorded for most of the counties bordering the English Channel (Fig. 41). Records outside this area are rare (Lundy, North Devon and Saundersfoot, Pembrokeshire). N. A. Jephson & S. Hainsworth (pers. comm.) found this variety growing subtidally at Sherkin Island, Co. Cork, south-west Ireland in August 1975. The specimens were sterile and were growing on open rock below the kelp forest (c. 15 m) in a stand of typical *R. pseudopalmata* var. *pseudopalmata*. This record constitutes the first for the Irish coastline and considerably extends the known range of this variety (Fig. 41).



## WORLD

Most specimens examined from the northern coast of France originated in the Caen-Calvados area where the type material of this variety was collected by Chauvin (Fig. 41). As on the southern coast of England populations of this variety seemed commonest on the eastern shores.

Specimens have been examined from the following localities from where the variety does not seem to have been recorded previously: Biarritz, Côte Basque, Atlantic France (28 August 1854, herb. Thuret no. 869, **PC**); Gijon, northern Atlantic Spain (16 September to 15 November 1895, leg. Sauvageau, **PC**).

The material cited by Bornet (1892, p. 285) from Tangiers under the name *Rhodymenia palmetta* var. *ellisiae* are probably not representative of this variety to judge from specimens (**BM**). Dangeard (1949) recorded specimens of this variety from Atlantic Morocco but his material has not been examined.

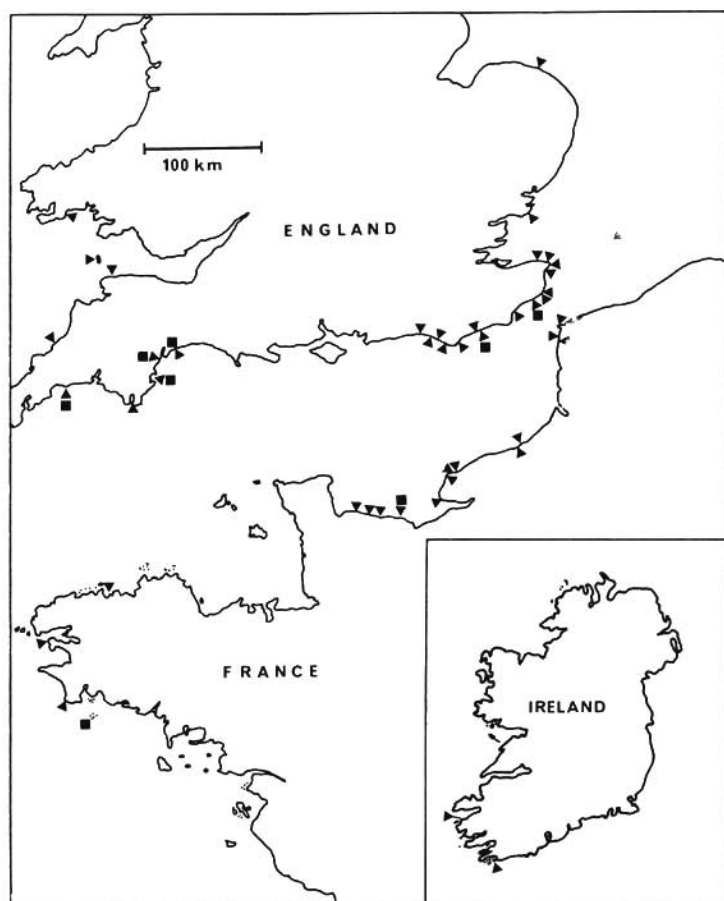


Fig. 41. Distribution of *Rhodymenia pseudopalmata* var. *ellisiae* (Duby) Guiry in Britain and north France as known to date. ▲ = Specimens examined during the present study; ■ = literature records.

COMPARISON OF *RHODYMENIA PSEUDOPALMATA* VAR. *PSEUDOPALMATA* AND *R. PSEUDOPALMATA* VAR. *ELLISIAE*

*Rhodymenia pseudopalmata* var. *ellisiae* (hereafter referred to as "var. *ellisiae*") and *R. pseudopalmata* var. *pseudopalmata* (hereafter referred to as "var. *pseudopalmata*") differ in several morphological and reproductive characters. The gross morphology of the thallus is probably the most distinctive feature. The regularly dichotomous, elongated-linear fronds of var. *ellisiae* contrast strongly with the broad, irregular fronds of var. *pseudopalmata*. Spiral twisting of the fronds, which is common in the larger specimens of var. *ellisiae*, has not been observed in var. *pseudopalmata*. The frequency of stolon formation in specimens of var. *ellisiae* also distinguishes this variety from var. *pseudopalmata* where, although stolons are formed, the intensity of production observed in var. *ellisiae* is never matched. The apical cirrose proliferations of var. *ellisiae* seem also to characterize the variety; such proliferations are extremely uncommon in var. *pseudopalmata* and when they occur in the latter they always seem to be merely flattened extensions of the apex whereas those of var. *ellisiae* are invariably terete.

TABLE I. A comparison of the principal morphological features of *Rhodymenia pseudopalmata* var. *pseudopalmata* and *R. pseudopalmata* var. *ellisiae*

	<i>Rhodymenia pseudopalmata</i> var. <i>pseudopalmata</i>	<i>Rhodymenia pseudopalmata</i> var. <i>ellisiae</i>
Height	To 120 mm	To 80 mm
Width of fronds	To 10 mm	To 5 mm
Thickness of fronds	(60) 100-200 (250) $\mu\text{m}$	(58) 116-145 (188) $\mu\text{m}$
Stolons	Sometimes formed	Commonly formed
Cortical cells (axially at 10 mm from apex)	(3.8) 9.0-13.4 (23.2) $\mu\text{m}$	(5.4) 9.0-14.4 (19.8) $\mu\text{m}$
Cortical cells (adaxially at 10 mm from apex)	(3.6) 8.7-11.6 (15.4) $\mu\text{m}$	(3.6) 4.5-7.2 (10.8) $\mu\text{m}$
Medullary cells periclinally in transverse section	(20) 41-51 (61) $\mu\text{m}$	(24) 41-53 (63) $\mu\text{m}$
Medullary cells axially in longitudinal section	(65) 102-133 (153) $\mu\text{m}$	(98) 102-133 (137) $\mu\text{m}$
Position of cystocarps	Apical, rarely median	Basal, occasionally median
Position of tetrasporangia	Small apical sorus	Small apical sorus
Size of tetrasporangia (length by breadth)	25-30 $\times$ 15-22 $\mu\text{m}$	23-25 $\times$ 14-18 $\mu\text{m}$

Table I shows a comparison of some of the morphological parameters of these two varieties of *R. pseudopalmata*. In var. *ellisiae* specimens were rarely found to exceed 80 mm in height while var. *pseudopalmata* attained heights of 120 mm. As already noted, however, var. *pseudopalmata* only reached its maximum potential height in subtidal habitats and most intertidal plants were less than 60 mm in height, so that in more or less equivalent habitats, var. *ellisiae* may be longer. The width of the fronds is also an important feature: var. *ellisiae* is never more than 5 mm broad at the centre of the blade while var. *pseudopalmata* frequently attains 10 mm, even in intertidal habitats. The fronds of var. *ellisiae*

tend to be thinner in TS but there is considerable overlap (see Table I). When first formed (at 10 mm from the apices) the thalli of these two varieties are very similar in appearance in TS (Figs 15–18). At this stage of development the edge of the thallus has more or less the same thickness as the centre of the blade in var. *ellisiae*. At the base of the fronds, however, the two varieties are quite different in TS (Figs 19–22). In var. *pseudopalmata* (Figs 21, 22) the thallus is very thick (200–250  $\mu\text{m}$ ) with 7–8 layers of medullary cells and the edge of the thallus has more or less the same thickness as the centre (Fig. 22). In contrast the thallus of var. *ellisiae* (at the same level) is relatively thin (130–145  $\mu\text{m}$ ), with 4–5 layers of medullary cells, but the edge of the thallus is only 80–100  $\mu\text{m}$  thick, appears to taper gradually to a point in TS (Fig. 20) and has 2–4 layers of medullary cells. This character is remarkably consistent and may account for the seemingly more delicate thallus of var. *ellisiae*. The dimensions of the cortical and medullary cells of both varieties are, however, remarkably similar (Table I).

The position of the reproductive organs, particularly the cystocarps, also provides a means of distinguishing these two entities. In var. *ellisiae* cystocarps have been observed to occur on small simple blades (Fig. 35C, D) and in a basal or median position on the mature fronds (Fig. 35B, C, D, F).

Cystocarps have never been found to occur in such positions in var. *pseudopalmata*. However, in one specimen which was thought to be representative of var. *ellisiae* (Bulverhythe, Sussex, 23 March 1889, BM) cystocarps were scattered from just below the apices to approximately half-way down the thallus. This has only been observed on one occasion. Tetrasporangia occur in small subapical sori in both varieties but in var. *ellisiae* they have been reported to occur also on apical proliferations. Tetrasporangia tended to be smaller in var. *ellisiae* (Table I) but the differences are slight.

As many of the characters distinguishing these two varieties are not quite clearcut in some specimens and as the anatomy and basic structure of the thallus is very similar in both, it has seemed best to retain *R. pseudopalmata* var. *ellisiae* as a variety. There would seem to be insufficient evidence to consider recognizing the entity as a species distinct from *Rhodymenia pseudopalmata*.

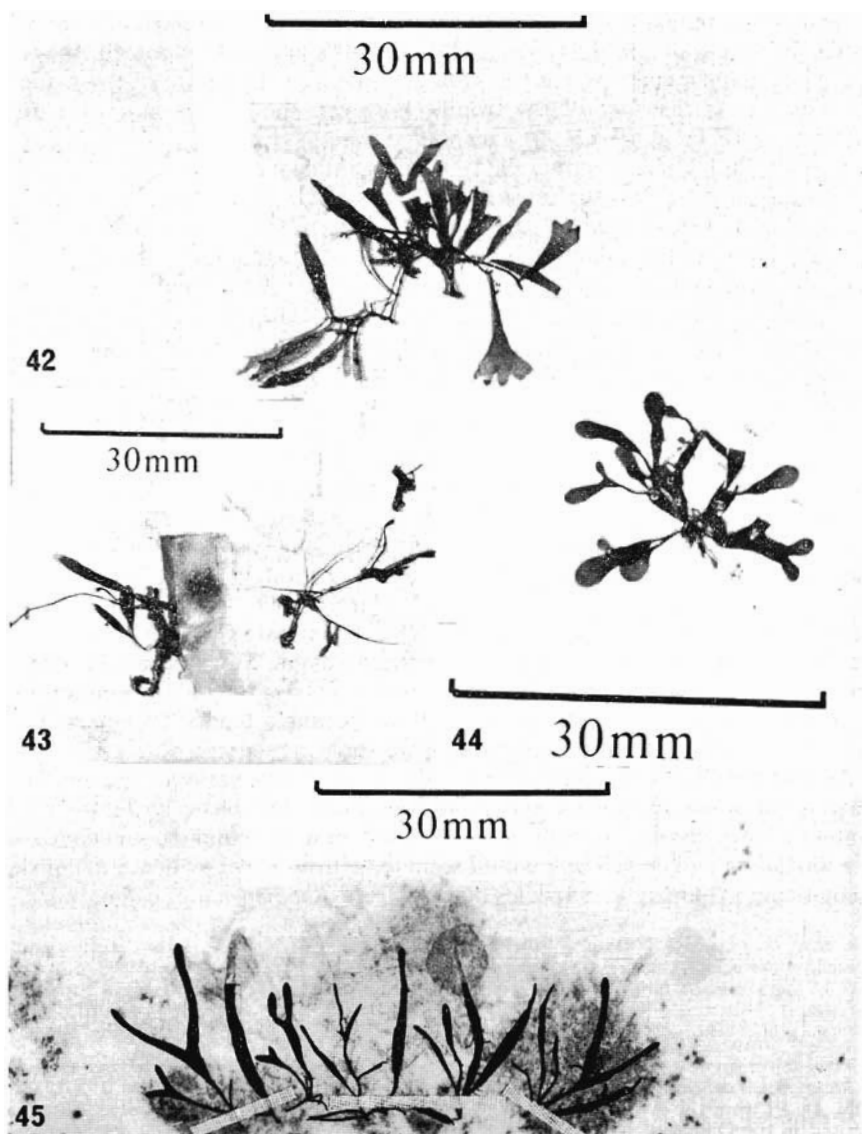
## RHODYMENIA DELICATULA

### ORIGINAL DESCRIPTION

*Rhodymenia delicatula* P. J. L. Dangeard was described by Dangeard (1949, pp. 172–173, Fig. 10N, O, P) from the Atlantic coast of Morocco. Two specimens of this species have been located in the Dangeard herbarium at the Laboratoire de Botanique, Faculté des Sciences de Bordeaux at Talence. One specimen is that illustrated by Dangeard (1949, Fig. 10 N) and was collected by P. J. L. Dangeard at Agadir, Morocco on 28 June 1938 (Dangeard 1177 bis). The second specimen was collected at the same locality on 5 July 1948 (Dangeard 5543 bis). Both specimens are sterile (Figs 42, 43). As Dangeard 1177 bis is the specimen illustrated in the original description, this plant (Fig. 42) has been selected as the lectotype of the species.

### SYNONYMY

It is possible, as will be discussed later, that *Rhodymenia phylloides* L'Hardy-Halos (1970) should be included in the synonymy of *R. delicatula*.



FIGS 42–45. Herbarium material of *Rhodymenia delicatula* P. J. L. Dangeard. Fig. 42. Lectotype specimen of *R. delicatula*, Agadir, Morocco, 21 June 1938 (Dangeard 1177 bis), leg. P. Dangeard. Fig. 43. Agadir, Morocco, 5 July 1943 (Dangeard 5543 bis), leg. P. Dangeard. Fig. 44. Kirkwall Bay, Orkney Islands, 1837, dredged, ex herb. J. H. Pollexfen, (BM). Fig. 45. Probably collected at Beaumaris, Anglesey, North Wales, 30 August 1882, leg. J. E. Griffith, (BM).

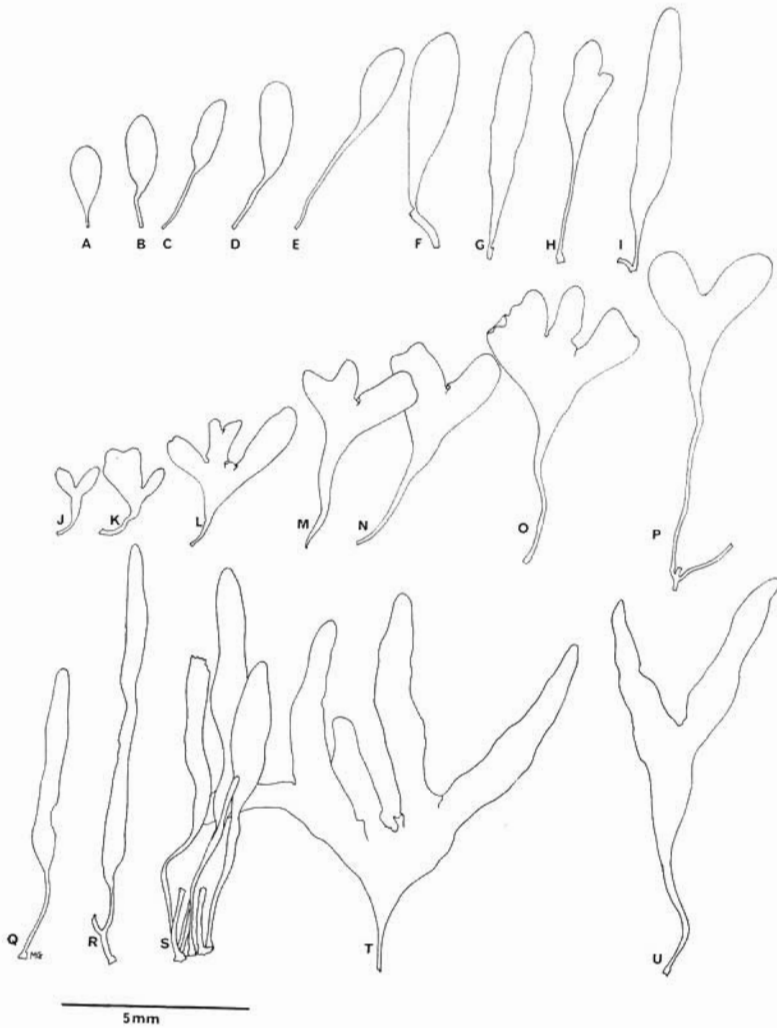


FIG. 46A-U. Range of morphological variation in sterile specimens of British Isles material of *Rhodymenia delicatula* P. J. L. Dangeard. Fig. 46A-I. Variation of spring specimens with simple fronds, Penmon, Anglesey, North Wales, 3 April 1973, pools: MLWS, leg. M. D. Guiry. Fig. 46J-P. Variation of spring specimens with branched fronds, note the differing length of the stipes, collection data as for A-I. Fig. 46Q-S. Variation of summer specimens with simple fronds, note the peg-like attachment organ, Penmon, Anglesey, North Wales, pools: MLWS-ELWS, 19 August 1974, leg. M. D. Guiry. Fig. 46T-U. Variation in summer specimens with branched fronds, note the long stipes and the elongation of the ultimate dichotomies, collection data as for Q-S.

## STRUCTURE AND DEVELOPMENT OF THE THALLUS

### EXTERNAL MORPHOLOGY

Plants were delicate or flaccid to slightly cartilaginous and had a light rose-red colour which was often obscured by epibionts. There was considerable form variation within the populations examined. The maximum length of plants collected was 22 mm (Fig. 45) but most plants were considerably smaller (Fig. 46) and the average height was about 15 mm. In December (Penmon, Anglesey 12 December 1973) plants were little more than simple oval bladelets not more than 5 mm in height borne on short stipes. In April (Penmon 3 April 1973; Porth Trecastell, 2 April 1973) small oval bladelets were still to be found (Fig. 46A-D) but elongated, elliptical blades on both short and long stipes were also present (Fig. 46F-I). In addition fronds with one or occasionally two dichotomies were also found, usually with long thin terete stipes (to 330  $\mu$ m diam.) most of which gradually expanded to form a flattened frond with a basally cuneate appearance (Fig. 46J-P). Some of these fronds arose from short stolons, presumably of a previous year's growth. The apices of the fronds were occasionally curled in one direction (Fig. 46O). Plants collected in July and August (Vierville-sur-Mer, Normandy, 21 July 1974; Penmon, 19 August 1974) were either simple elongated blades arising from peg-like discs (Fig. 46Q-S) or stolons (Fig. 47F), or irregularly dichotomously divided plants with long or short stipes (Fig. 46T, U). At this stage of development the dichotomous fronds were often elongated and strap-shaped with rounded apices.

Some regeneration was apparent amongst the plants examined but seemed to be largely from the stipes of the previous year's growth or from the apices of truncated, flattened fronds. Plants with torn apices were also common amongst the populations examined (Fig. 60C).

In one population examined (Penmon, 19 August 1974) lightly coloured protuberances were found on the surface of the fronds of some of the plants (Fig. 60A). These structures were a much lighter whitish-red colour than the nearby frond and usually had the appearance of a collapsed balloon when mature. These measured to 3 mm long and 0.77 mm broad and often had one or two dichotomies. When preserved material was examined with a binocular microscope these structures were often brownish, greenish or yellow-brown. Other irregularities were also observed in the frond shape (Fig. 60B) which may have been developmental stages in the formation of these protuberances or may have been galls. L'Hardy-Halos (1970) found such structures on the surface of the fronds of *Rhodymenia phylloides* and suggested that these might represent vegetative reproductive organs.

Stolons, as already discussed, were rarely found, but were well developed in a few collections. Fig. 47F shows such a specimen from Vierville-sur-Mer, Normandy (21 July 1974) (from a sandy pool) where a stolon was formed high up on the primary stipe of the plant. This stolon formed several irregular attachment organs along its length which often had grains of sand firmly embedded in them. Flattened fronds were usually formed terminally and subterminally on such stolons. Stoloniferous plants were mainly found in silty or soft sand areas.

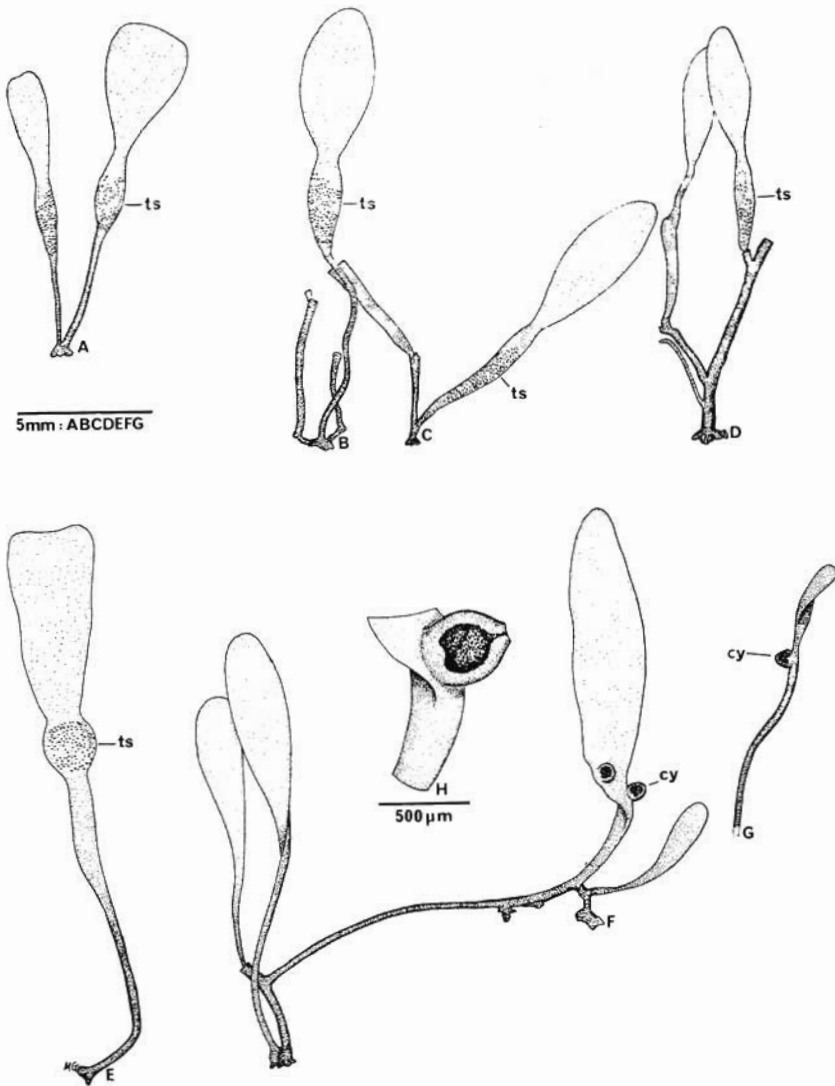


FIG. 47A–H. Plants of *Rhodymenia delicatula* P. J. L. Dangeard bearing reproductive organs. Fig. 47A–D. Tetrasporangial plants with tetrasporangia in median, elongated sori, Porth Trecastell, Anglesey, U.K., 2 April 1973, pools: MLWN, leg. M. D. Guiry. Fig. 47E. Tetrasporangial plant with tetrasporangia in a median, rounded sorus, Cemlyn Bay, Anglesey, U.K., 5 April 1973, pools: MLWN, leg. M. D. Guiry. Fig. 47F. Carposporangial plants with basal cystocarps, note the stolon with terminal, erect blades, Vierville-sur-Mer, Calvados, France, 21 July 1974, sandy pools: MLWS, leg. M. D. Guiry. Fig. 47G. Carposporangial plant with a cystocarp at the base of a short, flattened frond, Penmon, Anglesey, North Wales, U.K., 3 April 1973, pools: MLWS, leg. M. D. Guiry. Fig. 47H. Enlargement of the basal cystocarp in Fig. 47F. Abbreviations as in Figs 15–28 and 36–40, except for: *o*: ostiole; *ts*: tetrasporangial sorus.

## ANATOMY

Plants were multiaxial, growth and differentiation taking place over a broad area at the apices. Cortical cells of the uppermost part of the fronds were widely spaced (Figs 4, 55) with the cells of the subcortex showing through the "gaps". The cortical cells at 10 mm from the apex measured (4.0) 8.0–14.2 (20.5)  $\mu\text{m}$  long axially and (4.0) 7.2–10.8 (21.6)  $\mu\text{m}$  broad adaxially and had many discoid chloroplasts which seemed parietally concentrated in preserved material. In TS the cortical cells were slightly elongated anticlinally and only the first two layers of cells had distinct chloroplasts. The medulla was composed of 2–3 layers of strongly coherent, axially elongated cells which appeared entirely colourless in preserved material but have parietally-placed chloroplasts which are easily destroyed by preserving fluids.

Medullary cells measured (15) 25–58 (73)  $\mu\text{m}$  periclinally in TS and (48) 67–100 (108)  $\mu\text{m}$  axially in LS. An iridescent body (probably proteinaceous) was present in some of these cells. The thallus was (30) 58–87 (102)  $\mu\text{m}$  in thickness.

In the lower part of the flattened fronds and in the stipes the cortical cells were arranged much more closely together (Fig. 57). Such a pattern was also observed in older or more mature fronds (Fig. 58). In the protuberances described above the surface cells were also more regularly-sized than those of the frond and measured 6.3–10.3  $\mu\text{m}$  in diameter.

## STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS

### GAMETANGIAL PLANTS

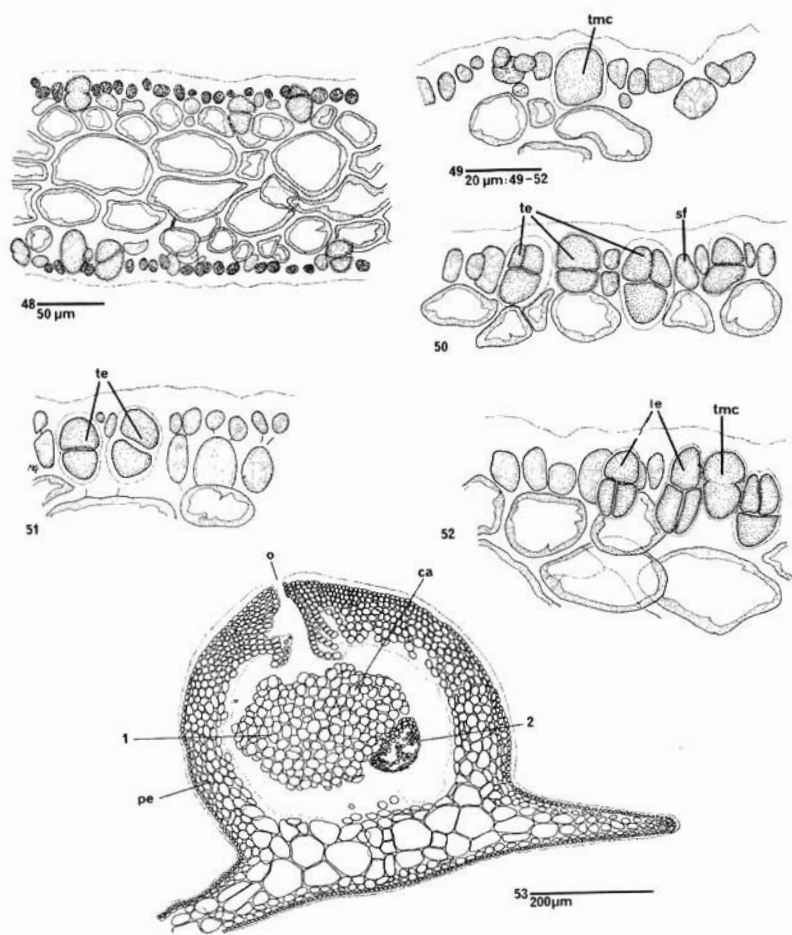
Plants bearing spermatangia or carpogonial branches were not observed. Two collections examined contained plants bearing cystocarps; these were formed only at the base of the flattened portion of the thallus (Fig. 47F, G) and were rounded, hemispherical and slightly flask-shaped (Fig. 47H) with a small centrally-placed ostiole and with a relatively thick pericarp. Mature cystocarps measured 400–500  $\mu\text{m}$  broad when mature and the gonimoblast was rounded and 300–400  $\mu\text{m}$  broad. The gonimoblast was composed of two lobes (Fig. 53) in the material examined, one of which was always considerably smaller than the other. The gonimoblast was nourished by a basal placenta of deeply-staining cells with many secondary pit connections from which arose large sterile cells which were irregularly branched with very large pit connections. The sterile gonimoblast cells formed large clusters of hexagonal-rounded carposporangia each of which formed a single carpospore. Carposporangia, when mature, measured 16.4–20.5  $\mu\text{m}$  in maximum diameter, but the carposporangia of the second lobe were considerably smaller (Fig. 53). Release of carpospores was not observed.

### TETRASPORANGIAL PLANTS

All tetrasporangial plants examined were collected in April. Tetrasporangia were formed in a small sorus at the base of the flattened portion of the frond (Fig. 47A–E). The sori were rounded, elliptical or elliptical-elongate and were 1.0–1.5 mm broad and 1.0–3.5 mm long. Tetrasporangia were small, rounded



and measured  $16.4\text{--}22.5\ \mu\text{m}$  broad and  $24.6\text{--}34.8\ \mu\text{m}$  long. The sporangia were not crowded and were interspersed with short, blunt, sterile filaments 1–2 cells long, derived from surface cortical cells (Figs 48–52). Tetrasporangia were formed from surface cortical cells (Fig. 49) which enlarged and divided successively forming sporangia which always had four cruciately arranged spores. These tetrasporangia often had the appearance of having only two or three spores but, as in *R. pseudopalmata*, this would seem to be a result of one or two of the



FIGS 48–53. *Camera lucida* drawings of transverse sections of some reproductive organs of *Rhodymenia delicatula* P. J. L. Dangeard. Fig. 48. Development of tetrasporangia on both sides of the thallus. Port Treacastell, Anglesey, North Wales, U.K., 2 April 1973, pools: MLWN, leg. M. D. Guiry. Figs 49–52. Various stages in the development of tetrasporangia. Collection data as for Fig. 48. Fig. 53. Cystocarp; note the relatively thick pericarp and the two generations of carposporangia. Collection data as for Fig. 48. Abbreviations as in Figs 15–28, 36–40 and 47 except for: *tmc*: tetrasporangial mother cell; *sf*: sterile filament.

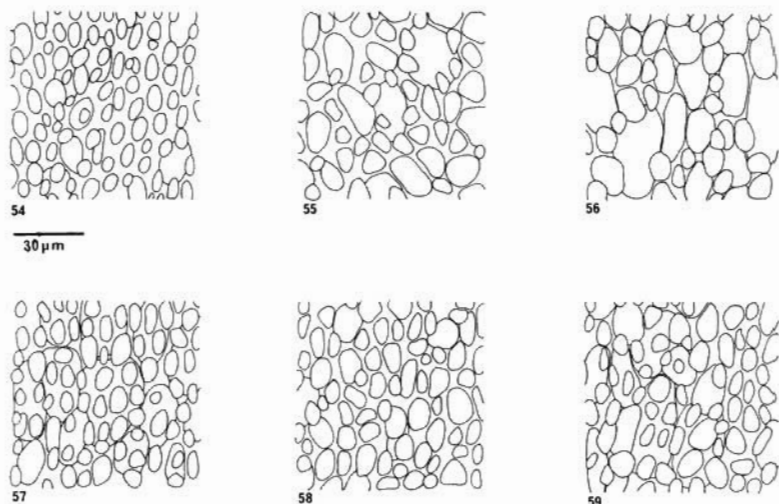
cleavages being in the plane of sectioning (Figs 50–52). Further divisions of the sporangia in situ were not observed and release of spores in culture was not achieved.

## REPRODUCTIVE PHENOLOGY

In the British Isles plants of this species form reproductive organs in early spring; the period of reproduction seems to be from December to April or May.

## HABITAT

In Britain *R. delicatula* has been collected from intertidal and subtidal habitats. The intertidal populations were found mainly in the sublittoral fringe: in pools at MLWN–ELWS and on open rock in sandy areas at ELWS. Pool populations were typically present on vertical or near-vertical walls in very deep, shaded pools in exposed situations. Plants were invariably well below the water surface and seemed particularly common (at least on Anglesey, North Wales) in the type of pool which is encrusted with very fine silt and where few other algae grow. At Penmon, Anglesey, plants were repeatedly found on gently sloping rocks at MLWS–ELWS, scattered amongst stands of *Plocamium cartilagineum*



FIGS 54–59. *Camera lucida* drawings of the surface cell morphology of specimens of *Rhodymenia delicatula* P. J. L. Dangeard and *R. phylloides* L'Hardy-Halos preserved in different ways and from different parts of the thallus. Fig. 54. Portion of the thallus of the lectotype specimen of *R. delicatula* taken 10 mm from the apex of dried material. Fig. 55. Portion of the thallus of a young plant of *R. delicatula* (Porth Trecastell, Anglesey, U.K., 2 April 1973), 5 mm from the apex of a liquid-preserved specimen. Fig. 56. Portion of the thallus of an isotype specimen of *R. phylloides*, 5 mm from the apex of a liquid-preserved specimen. Fig. 57. Portion of the thallus of a mature plant of *R. delicatula* (Penmon, Anglesey, U.K., 19 August 1974), 7.5 mm from the apex of a liquid-preserved specimen. Fig. 58. Portion of the thallus of *R. delicatula* (Kirkwall Bay, Orkney Islands, 1837, dredged, **BM**) 10 mm from the apex of a dried specimen. Fig. 59. Portion of the thallus of the lectotype specimen of *R. delicatula*, 5 mm from the apex of dried, mature material.

(Linnaeus) Dixon and *Cordylecladia erecta* (Greville) J. Agardh. At this locality *R. delicatula* became more luxuriant and common towards ELWS. Plants have occasionally been found in long guillies at MLWN but seemed rare in such situations and were generally associated with *R. pseudopalmata* var. *pseudopalmata*, various Delesseriaceous algae and *Cladophora pellucida* (Hudson) Kützing.

In subtidal situations in Britain this species has been collected down to 5 m, usually on the upperside of stones and boulders embedded in sand or silt.

## DISTRIBUTION

### BRITISH ISLES

There are no literature records of this species from the British Isles prior to that in Parke & Dixon (1976) but specimens of the entity were collected from various localities during the past century but misidentified.

There are many early literature references to specimens of *Rhodymenia pseudopalmata* (as *R. palmetta*) dredged at Kirkwall, Orkney Isles (W.H.C., 1838; Harvey, 1847, pl. 134; Traill, 1890, p. 327 etc.). The only specimens with a *Rhodymenia*-like thallus dredged at Kirkwall that have been found in the major British herbaria are those shown in Fig. 44 which are from herb. J. H. Pollexfen (BM) and are annotated "Kirkwall Bay, 1837". These specimens are also sterile but probably represent small plants of *Rhodymenia delicatula*. Fig. 58 shows the surface cortical cells of a soaked portion of the thallus of these specimens and there can be little doubt that these are very similar to those of the type specimen (Fig. 59). The thinness of the thallus and the small size of the specimens also suggest *R. delicatula* and not *R. pseudopalmata*. Fig. 62 shows the distribution of *R. delicatula* in the British Isles from specimens examined.

### WORLD

*Rhodymenia delicatula* was originally described by Dangeard (1949) from Cape Agadir, Atlantic Morocco. Specimens in the herbarium of Bory de Saint-Vincent (PC) collected at Cadiz, Spain show the size, morphology and structure of *Rhodymenia delicatula*. Ardré (1969, pp. 132–133 footnote) listed specimens from Portugal as resembling *Rhodymenia phylloïdes* L'Hardy-Halos. These have been examined (PC) and seemed to be referable to *R. delicatula*.

### COMPARISON OF *RHODYMENIA DELICATULA* AND *R. PHYLLOÏDES*

*Rhodymenia phylloïdes* was described from the Baie de Morlaix, Brittany growing in the sublittoral to 20 m; this species was very similar to *R. delicatula* in that plants were less than 20 mm in height, with fronds 0.1–0.3 mm wide and 50–90  $\mu\text{m}$  in thickness (L'Hardy-Halos, 1970, Figs 1, 2). Plants of this species had a thin cortex and 2–3 (4) layers of medullary cells. Specimens often had long, thin stipes 500  $\mu\text{m}$  to 3 mm long which expanded gradually, forming rounded-lanceolate blades which were simple or had one dichotomy. This species displayed a considerable capacity for regenerating new blades from eroded stipes or fronds (L'Hardy-Halos, 1970, Fig. 1A, B, D, F, H, K). Plants were attached to the substratum by a fleshy peg-like disc which was irregular in shape. The

reproductive organs were reported to be formed in winter and spring (L'Hardy-Halos, 1970, pp. 26–27) and were borne at the apices of the fronds on very small plants (300–700  $\mu\text{m}$  long: L'Hardy-Halos, 1970: Fig. 1D, F, G, H, I, J). Lightly-coloured protuberances were also reported to occur on some fronds with a frequency which led L'Hardy-Halos (1970, p. 23) to consider them characteristic of *R. phylloides*.

There are several points of close similarity between the collections examined and L'Hardy-Halos's description. A comparison of these specimens with *R. phylloides* and *R. delicatula* is given in Table II. The main points of difference are the position of the reproductive organs, the shape and mode of branching of the blades and the reported absence of stolons in *R. phylloides*.

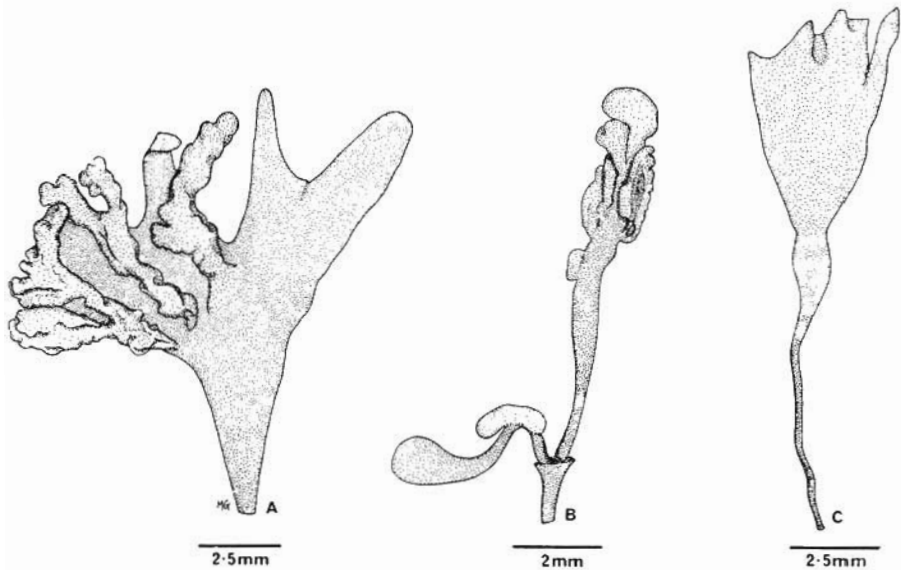
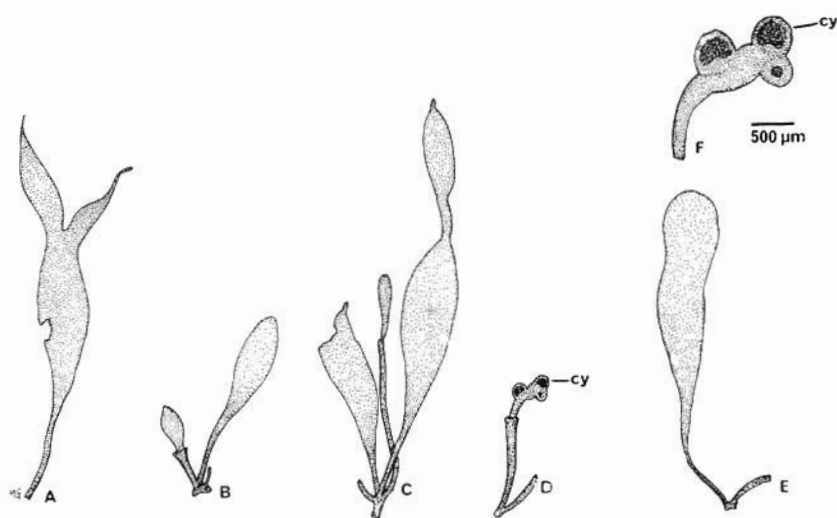


FIG. 60A–C. Unusual morphological features of British specimens of *Rhodymenia delicatula* P. Dangeard. Fig. 60A. Specimen with mature, dichotomously-branched, lightly-coloured protuberances on the surface of the thallus, note the collapsed appearance of these, Penmon, Anglesey, U.K., 19 August 1974, sandy ledges: MLWS, leg. M. D. Guiry. Fig. 60B. Specimens with irregular protuberances, Penmon, Anglesey, U.K., pools: MLWS, 3 April 1973, leg. M. D. Guiry. Fig. 60C. Specimen with truncated frond and subsequent (?) irregular development; collection data as for Fig. 60B.

Although tetrasporangial sori and cystocarps of *Rhodymenia phylloides* were described as occurring at the apices of the fronds and the material described above under the name *R. delicatula* had tetrasporangia in sori in the middle of the frond and cystocarps at the base of the frond, it seems probable that the precise location of these is variable in a winter/spring fertile entity where most of the growth of the frond takes place after the formation of reproductive organs. For example, in *Schottera nicaeensis* where tetrasporangial sori are also formed in winter and early spring (Schotter, 1952; Guiry & Hollenberg, 1975) on very small plants, the thallus continues to grow and what were initially more or less apical sori in January (Guiry & Hollenberg, 1975, Fig. 11A, F) may, by

TABLE II. Comparison of *Rhodymenia phylloides* and *R. delicatula* with British and French material examined. Details from L'Hardy-Halos (1970) and Dangeard (1949) and from an examination of the type material of the species described by these authors

	<i>Rhodymenia phylloides</i>	<i>Rhodymenia delicatula</i>	<i>Rhodymenia</i> specimens from the British Isles and Northern France
Height (mm)	To 20	To 12	To 22
Width of fronds (mm)	0.1-3	0.5-3	0.5-3
Thickness of fronds ( $\mu\text{m}$ )	50-90	40-70	(30) 58-87 (102)
Stolons	Not reported	Present	Present
Callosities	Present	Not reported	Present
Stipes	Often long and thin	Often long and thin	Often long and thin
Fronds	Simple or dichotomously branched	Simple or dichotomously branched	Simple or dichotomously branched
Peg-like attachment disc	Present	Not reported	Present
Tetrasporangia	In apical sorus	Unknown	In waisted sorus at centre of the frond
Size of tetrasporangia ( $\mu\text{m}$ )	16-18 $\times$ 28-30	Unknown	16-22 $\times$ 25-35
Cystocarps	At apices of plants	Unknown	At base of flattened portion of plants
Size of cortical cells ( $\mu\text{m}$ )	10-12 long, 3-6 broad	(4) 9-16 long	(4) 8-14 (20.5) long
Medullary cells	2-3 (4) layers	2-3 layers	(4) 7-11 (21.6) broad
			2-3 layers



5 mm: A-E

FIG. 61A-F. Morphology of fertile and sterile specimens of isotype material of *Rhodymenia phylloides* L'Hardy-Halos. Baie de Morlaix, Brittany, France, 19 December 1967, leg. M.-Th. L'Hardy-Halos no. R 2233. Fig. 61A-C. Range of variation in sterile thalli, note the long stipes and the beginnings of regeneration of flattened blades from truncated stipes. Fig. 60D,F. Cystocarpic plant, note the apical position of the cystocarps on an unflattened stipe. Fig. 61E, as Fig. 60A-C.

April, due to growth of the frond, be placed at the base of the frond (Guiry & Hollenberg, 1975, Fig. 12B, D, E). Species of *Rhodymenia* seem to have similarly persistent reproductive organs and it is conceivable that what was an apical sorus or apical cystocarp on very small plants in December (L'Hardy-Halos, 1970, as *R. phylloides*) may become a basal sorus or cystocarp by April (cf. Fig. 61D, F and Fig. 47A-E). The type material of *Rhodymenia phylloides* (Baie de Morlaix, Brittany, 19 December 1967, PC, and liquid-preserved material from the same collection, courtesy of Mme L'Hardy-Halos: Fig. 61A-F) has been examined. The long stipes and the gradual expansion of these to form a flattened, thin blade are very similar to what has been described above. The surface cortical cells of a representative specimen of *R. phylloides* 5 mm from the apex are very

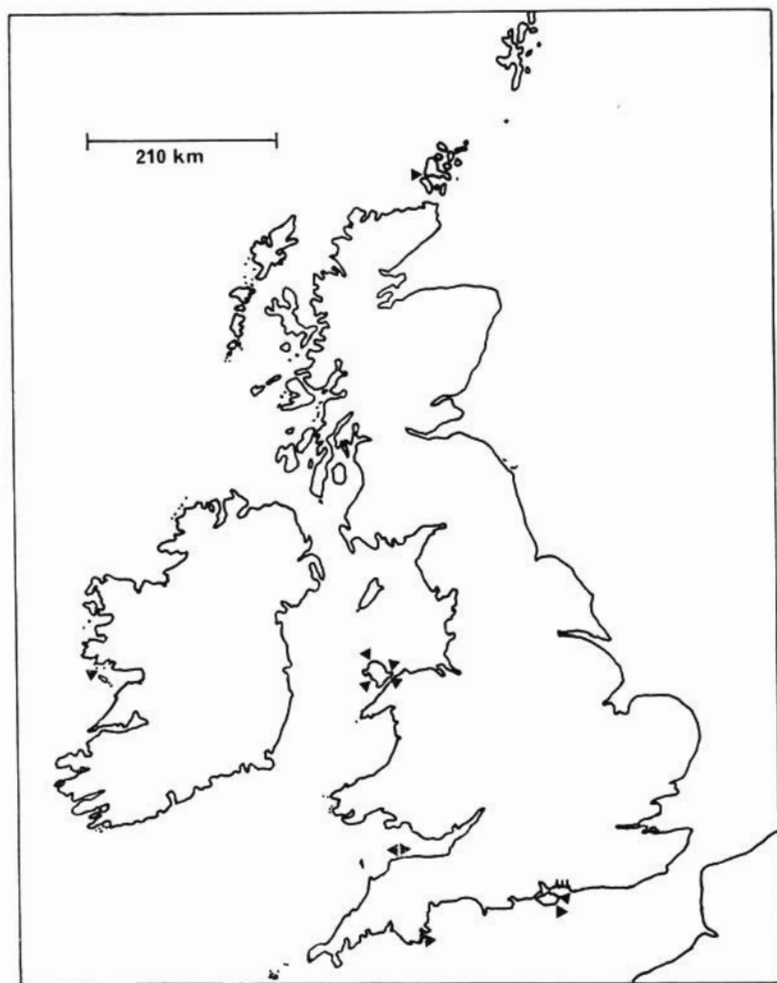


FIG. 62. Distribution in the British Isles of *Rhodymenia delicatula* P. J. L. Dangeard as known to date.

similar to those of young British specimens (cf. Figs 55 and 56). The surface cortical cells of an older British specimen are also illustrated (Fig. 57: 7.5 mm from the apex) and these show a close similarity to the type material of *R. delicatula* (which was also collected in summer: Fig. 54, 10 mm from the apex). In the latter illustration, however, the large subcortical cells seen in Figs 55 and 56 are not clearly visible. A similar portion of the thallus of the type specimen of *R. delicatula* taken at 5 mm from the apex (Fig. 59) shows a greater similarity with the *R. phylloides* material and the British specimens (Figs 56, 57). In pressed specimens such as the type material of *R. delicatula* it is often difficult to get the thallus cells to regain their former dimensions, particularly the subcortical layers; Fig. 58, which illustrates a portion of the thallus of a pressed specimen from the Orkney Isles also shows a similar lack of clarity of the subcortical layers.

The chief points of similarity between specimens from Britain and northern France and the Moroccan material of *R. delicatula* are the shape and mode of branching of the fronds (cf. Figs 42, 43 and 46, 47, 60), the formation of stolons in both, the thinness of the thallus and the small size of the fronds. Other morphological parameters seem also to correspond well (Table II).

It would thus appear that further investigation of the French populations of *R. phylloides*, as described by L'Hardy-Halos (1970) is required to determine the position and occurrence of the reproductive organs in spring and summer, and the gross morphology of intertidal specimens at the peak of vegetative growth. The occurrence of specimens of a species of *Rhodymenia* with thin fronds, small size and a lack of reproductive organs during the summer months on the shores of Atlantic Morocco, Atlantic Spain, Portugal, Brittany and the British Isles suggests that but one widely-distributed species may be in question.

#### ACKNOWLEDGEMENTS

I am indebted to Dr D. E. G. Irvine, Mrs L. M. Irvine and Dr P. C. Silva for their encouragement and critical observations; to Professor P. S. Dixon for his advice and reflections on the manuscript; to Mme M.-Th. L'Hardy-Halos and Dr P. R. Newroth for valuable discussion and herbarium material; and to Dr G. T. Boalch, W. F. Farnham, S. Hainsworth, Mrs L. M. Irvine, N. A. Jephson, J. H. Price and I. Tittley for permission to use some unpublished observations.

I would like to thank the Governors of the Polytechnic of North London and Mr D. Etherington for making financial support available during the tenure of a Research Assistantship. Grateful acknowledgement is made to the Directors and Curators of the herbaria mentioned in the text and to Professor Eyme, Laboratoire de Botanique, Faculté des Sciences de Bordeaux at Talence for permission to examine specimens from the herbarium of P. J. L. Dangeard. The completion of the manuscript was facilitated by N.A.T.O. grant no. 1130 to John West and the author.

#### REFERENCES

- AGARDH, C. A., 1822. *Species Algarum rite cognitae, cum synonymis, differentiis specificis et descriptionibus succintis*. Vol. 2(1), 169-531. E. Mauritis, Griefswald.
- AGARDH, J. G., 1841. In *historiam algarum symbolae*. *Linnaea*, **15**: 1-50, 443-457.
- AGARDH, J. G., 1842. *Algae maris mediterranei et adriatici, observationes in diagnosis specierum et dispositionem generum*. Pp. (2) + x + 164. Fortin, Masson et Cie, Paris.
- AGARDH, J. G., 1851. *Species genera et ordines Algarum*. Vol. 2(2): 505-720. Typis Berlingianus, Lund.
- AGARDH, J. G., 1876. *Species genera et ordines Algarum seu descriptiones succintae specierum, generum et ordinum, quibus algarum regnum constituitur*. Vol. 3(1). *Epicrisis systematis Floridearum*. Pp. viii + 724. T. O. Weigel, Leipzig.

- ARDISSONE, F., 1893. Note alla phycologia Mediterranea. *Re. Ist. lomb. Sci. Lett.*, ser. 2, 26: 674-690.
- ARDRE, F., 1969. Contribution à l'étude des algues marines du Portugal I. La flore. *Port. Acta biol.*, sér. B, 10: 137-555.
- AUSTIN, A. P., 1959. Iron-alum aceto-carmine staining for chromosomes and other anatomical features of Rhodophyceae. *Stain Tech.*, 34: 69-75.
- BATTERS, E. A. L., 1902. A catalogue of the British marine algae, being a list of all the species of seaweeds known to occur on the shores of the British Islands, with the localities where they are found. *J. Bot., Lond.*, 40 (Suppl.): 1-107.
- BONEY, A. D., 1975. Mucilage sheaths of spores of red algae. *J. mar. biol. Ass. U.K.*, 55: 511-518.
- BORNET, E., 1892. Les algues de P.-K.-A. Schousboe. *Mem. Soc. natn. Sci. nat. Cherbourg*, 28: 165-376.
- BUFFHAM, T. H., 1894. On the antheridia, etc., of some Florideae. *J. Quekett microsc. Club.*, ser. 2, 5: 291-305.
- C., W. H., 1838. Intelligence. *Miscellaneous. Mag. Zool. Bot.*, 2: 562-566.
- CHAUVIN, J., 1827. *Algues de la Normandie*, fasc. 1, 25 specimens. T. Chalopin, imprimeur de la Société Linnéenne de Normandie, Caen.
- DANGEARD, P. J. L., 1949. Les algues marines de la côte occidentale du Maroc. *Botaniste*, sér. 34: 89-189.
- DAWSON, E. Y., 1941. A review of the genus *Rhodymenia*, with descriptions of new species. *Allan Hancock Pacif. Exped.*, 3: 123-180.
- DUBY, J. E., 1830. *Aug. Pyrami de Candolle Botanicon Gallicum seu synopsis plantarum in flora gallica descriptorum*. ed. 2, part II, *Plantae cellulares continens*. Pp. 545-1068 + lviii. Desray, Paris.
- ESPER, E. J. C., 1798. *Icones fucorum cum characteribus systematicis, synonymis auctorum et descriptionibus novarum specierum*. Tome I, heft 2, pp. 55-126, pls. 25-29, 29a, 30-63. In der Raspeschen Buchandlung, Nürnberg.
- GAILLON, B., 1828. Thalassiphytes. *Dict. Sci. nat. (Lévraut)*, 53: 350-406.
- GERLOFF, J. & GEISSLER, M., 1971. Eine revidierte Liste der Meeresalgen Griechenlands. *Nova Hedwigia*, 22: 721-793.
- GIACCONE, G., 1969. Raccolte di fitobenthos sulla banchina continentale Italiana. *G. Bot. ital.*, 103: 485-514.
- GMELIN, S. G., 1768. *Historia fucorum*. Pp. 239+6. Ex typographia Academiae Scientiarum, Leningrad.
- GOODENOUGH, S. & WOODWARD, T. J., 1977. Observations on the British Fuci, with particular descriptions of each species. *Trans. Linn. Soc. Lond.*, 3: 84-235.
- GREVILLE, R. K., 1830. *Algae Britannicae, or Descriptions of the Marine and other Inarticulated Plants of the British Isles belonging to the order Algae; with Plates Illustrative of the Genera*. Pp. 4+lxviii+218. McLachlan & Steward, Baldwin & Cradock, London and Edinburgh.
- GUIRY, M. D., 1974a. A reappraisal of the genus *Palmaria* Stackhouse. *Br. phycol. J.*, 9: 219.
- GUIRY, M. D., 1974b. A preliminary consideration of the taxonomic position of *Palmaria palmata* (Linnaeus) Stackhouse = *Rhodymenia palmata* (Linnaeus) Greville. *J. mar. biol. Ass. U.K.*, 54: 509-528.
- GUIRY, M. D., 1976. Taxonomy, structure and reproduction of some members of the *Rhodymeniales* sensu Kylin. Ph.D. Thesis, Univ. of London.
- GUIRY, M. D. & HOLLENBERG, G. J., 1975. *Schottera* gen. nov. and *Schottera nicaeensis* (Lamour. ex Duby) comb. nov. (= *Petroglossum nicaeense* (Lamour. ex Duby) Schotter) in the British Isles. *Br. phycol. J.*, 10: 149-164.
- HARVEY, W. H., 1847. *Phycologia Britannica: or a History of British Sea-weeds containing coloured Figures, Generic and Specific Characters, Synonymes and Descriptions of all the Species Inhabiting the Shores of the British Islands*. Pls. [with text] 73-144. Reeve & Benham, London.
- HAUCK, F., 1885. Die Meeresalgen Deutschlands und Österreichs, In: *Kryptogamen Flora von Deutschland, Österreich und der Schweiz* (Rabenhorst, L., editor), Vol. 2: pp. xxiii+(1)+575. Kummer, Leipzig.
- HOLMES, E. M., 1883. *Rhodymenia palmetta*, var. *nicaeensis*. *J. Bot., Lond.*, 21: 289-290.
- HUDSON, W., 1778. *Flora anglica; exhibens plantas per regnum angliae sponte crescentes, distributas secundum systema sexuale: cum differentiis specierum, synonymis auctorum, nominibus incolarum, solo locorum, tempore florendi, officinalibus pharmacopaeorum*. ed. 2, vol. 2, pp. 397-690. J. Nourse, London.
- KÜTZING, F. T., 1847. Diagnosen und Bemerkungen zu neuen oder kritischen Algen. *Bot. Ztg.*, 5: 1-5, 22-25, 33-55, 164-167, 177-180, 193-198, 219-223.
- KÜTZING, F. T., 1868. *Tabulae phycologiae oder Abbildungen der Tange*. Vol. XVIII. Pp. (4)+35+100 tabs. Kosten der Verfassers, Nordhausen.



- KYLIN, H., 1931. Die Florideenordnung Rhodymeniales. *Acta Univ. lund.*, N.F., avd. 2, 26(11): 1-48.
- KYLIN, H., 1956. *Die Gattungen der Rhodophyceen*. Pp. xv+673. C. W. K. Gleerups, Lund.
- LAMOUREUX, M. J. V. F., *Dissertations sur plusieurs espèces de Fucus: avec leur description en Latin et en Français*. Pp. xviv+83+(2)+36 pls. Agen, Paris.
- LAMOUREUX, M. J. V. F., 1813. Essai sur le genres de la famille des Thalassiophytes non articulées. *Annls Mus. Hist. nat. Paris*, 20: 21-47, 115-139, 267-293.
- L'HARDY-HALOS, M.-Th., 1970. *Rhodymenia phylloides* nov. sp. (Rhodophycées, Rhodyméniale) nouvelle espèce des côtes Bretagne. *Bull. Soc. phycol. Fr.*, 15: 23-30.
- MONTAGNE, C., 1839. Cryptogamae brasilienses seu Plantae cellulares quas in itinere per Brasiliam à celeb. Auguste de Sainte-Hilaire collectas recensuit observationibusque nonnullis illustravit. *Annls Sci. nat.*, sér. 2, 12: 42-55.
- MONTAGNE, C., 1846-49. [Algae, pp. 1-240, publ. 1846]. In, *Flore d'Algérie . . . , sciences naturelles Botanique* (Durieu de Maisonneuve, M. C., editor). Imprimerie Impériale, Paris.
- NEWTON, L., 1931. *A Handbook of the British Seaweeds*. Pp. xiii+478. British Museum (Nat. Hist.), London.
- NORRIS, R. E., 1957. Morphological studies on the Kallymeniaceae. *Univ. Calif. Publs Bot.*, 28: 251-333.
- PAPENFUSS, G. F., 1950. Review of the genera described by Stackhouse. *Hydrobiologia*, 2: 181-208.
- PARKE, M. & DIXON, P. S., 1976. Check-list of British marine algae—third revision. *J. mar. biol. Ass. U.K.*, 56: 527-594.
- SCHMITZ, F., 1889. Systematische Übersicht der bisher bekannten Gattungen der Florideen. *Flora, Jena*, 72: 435-456.
- SCHOTTER, G., 1952. Note sur le *Gymnogongrus nicaeensis* (Dub.) Ardiss. et Straff. *Bull. Soc. Hist. nat. Afr. N.*, 43: 203-210.
- SETCHELL, W. A. & GARDNER, N. L., 1903. Algae of northwestern America. *Univ. Calif. Publs Bot.*, 1: 165-418.
- SILVA, P. C., 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. *Univ. Calif. Publs Bot.*, 25: 241-323.
- SJÖSTEDT, L. G., 1926. Floridean studies. *Acta Univ. lund.*, N.F., avd. 2, 22(4): 1-94.
- SKOTTSBERG, C., 1923. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907-1909. IX. Marine Algae. 2. Rhodophyceae. *K. svenska Vetensk Akad. Handl.*, 63(8): 1-70.
- SPARLING, S. R., 1957. The structure and reproduction of some members of the Rhodymeniaceae. *Univ. Calif. Publs Bot.*, 29: 319-396.
- STACKHOUSE, J., 1797. *Nereis Britannica containing all the Species of Fuci, natives of the British Coasts: with a Description in English and Latin and Plants Coloured from Nature*. fasc. 2, pp. ix-xxiv, 31-70. Hazard, Bath and London.
- STACKHOUSE, J., 1801. *Nereis britannica . . .*, fasc. 3, pp. xxv-xl, 71-112. Hazard, Bath and London.
- TAYLOR, W. R., 1945. Pacific marine algae of the Allan Hancock expedition to the Galapagos Islands. *Allan Hancock Pacif. Exped.*, 12: 1-528.
- TRAILL, G. W., 1890. The marine algae of the Orkney Islands. *Trans. bot. Soc. Edinb.*, 18: 302-342.
- TURNER, D., 1809. *Fuci sive plantarum fucorum generi a botanicis ascriptarum icones descriptiones et historia. Fuci, or colored figures and descriptions of the plants referred by botanists to the genus Fucus*. Vol. 2, pp. 162. J. & A. Arch, London.