

The Taxonomic Recognition of *Pterothamnion crispum* (Rhodophyta, Ceramiales), with a Survey of the Carposporophyte Position in Genera of the Antithamnieae

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The marine alga commonly referred to as *Antithamnion plumula* (Ell.) Thur. var. *crispum* (Ducl.) Hauck was cultured from the North Aegean Sea and the Channel Islands. The two strains interbred successfully, demonstrating a *Polysiphonia*-type life history. Chromosome counts in gametophytes and tetrasporophytes gave 24 ± 2 and 48 ± 4 , respectively. Crossing attempts with *Pterothamnion plumula* (Ell.) Näg. from the Swedish west coast, with the same approximate numbers of chromosomes, were unsuccessful. On the basis of the crossing results a specific status for this alga is recognized and features of its reproductive morphology are examined.

A lateral position of carposporophytes is described for the first time in that species and it is found to occur similarly in *P. plumula*. Number of procarps (1–6), late or early initiation and their fertilization, and continuation or suppression of fertile axes during carposporophyte development are found to be variable features, and consequently unreliable taxonomic criteria at the level of species. The relationship of the genera *Antithamnion*, *Pterothamnion* and *Platythamnion* is studied, and resurrection of the name *Pterothamnion crispum* (Ducl.) Näg. is recommended.

A survey of the position of the carposporophyte within six genera of the Antithamnieae, *Antithamnion*, *Antithamnionella*, *Balliella*, *Pterothamnion*, *Platythamnion*, and *Scagelia*, shows that three types occur: apical, lateral and intercalary.

The ceramiaceous alga commonly referred to in the literature as *Antithamnion plumula* (Ell.) Thur. var. *crispum* (Ducl.) Hauck was first described as *Ceramium crispum* Ducluzeau (1805, p. 47), from material collected at Sète on the Mediterranean coast of France. It has later been placed in *Callithamnion* Lyngbye (Agardh, 1851–52, 1876), *Antithamnion* Nägeli (Le Jolis, 1863; Hauck, 1885; Agardh, 1892; Feldmann, 1942; Feldmann-Mazoyer, 1941; L'Hardy-Halos, 1968; and others), *Pterothamnion* Nägeli (Nägeli, 1862) and in *Platythamnion* Agardh (Feldmann, 1937). Some of these authors have regarded it as an independent species while others placed it as a variety of *Antithamnion plumula*, a species recognized recently as *Pterothamnion plumula* (Ellis) Nägeli by Wollaston (1979) and Moe & Silva (1980).

Sundene (1975) and later Rueness (1978) presented evidence to support a specific status for it. Sundene (1975) demonstrated a *Polysiphonia*-type of life history and interfertility in two strains from the Channel Islands, and discovered a sterility barrier in crossing attempts with *Pterothamnion plumula*; Rueness reported intersterility in crossing attempts with *Platythamnion pectinatum* Kylin, a taxon regarded as closely related by some authors (Feldmann-Mazoyer, 1941; Dawson, 1962).

New observations on the position and development of procarps and carposporophytes of this alga and *Pterothamnion plumula* are presented here based upon culture and/or field material from several localities along the coasts of Europe. Chromosome counts and crossing experiments of the culture strains are also

undertaken, and the results are in good agreement with those reached by Sundene (1975). These morphological observations contribute to the taxonomic delimitation of the genera *Antithamnion*, *Pterothamnion* and *Platythamnion*, and support the recognition of the name *Pterothamnion crispum* (Ducluzeau) Nägeli (1862, p. 376).

MATERIALS AND METHODS

Pterothamnion crispum was collected in the sublittoral zone (2–10 m) in May 1981 at Sarti, Greece, 40°0'N, 26°6'E. The material gave rise to two culture strains; one female, the other remaining sterile.

J. Rueness kindly provided male, female and tetrasporic culture material of the same species, reared by Sundene (1975) from material collected in Guernsey, the Channel Islands, 49°25'N, 2°35'W. In addition, fertile material collected in the sublittoral zone (2–5 m) in July 1983 at Banyuls-sur-Mer, France, 42°29'N, 3°8'E, and preserved in 70% alcohol was studied.

Pterothamnion plumula was collected in the sublittoral zone (15–20 m) in June 1981 off Kristineberg Marine Biological Station, Sweden, 58°15'N, 11°27'E. Isolates produced tetrasporangia, and gametophytes were obtained from discharged tetraspores. In addition, the following fertile material preserved in 70% alcohol or in the dry state was studied. Several specimens collected in the sublittoral zone (5–12 m) in October 1983 at Tjärnö Marine Biological Station, Sweden, 58°53'N, 11°9'E; and a single herbarium specimen collected in June 1923 at Plymouth, England, 50°20'N, 4°10'W. A complete set of the above material is deposited at the Botanical Museum of Göteborg (GB).

Cultures were maintained in 32–33‰ seawater medium enriched according to von Stosch's (1964) basal medium and with GeO added to prevent contamination with diatoms, according to Chapman (1973). Illumination was at about 500 lux provided by cool-white fluorescent tubes, and with 14–10 h light–dark photoperiod at 10±1° and 15±2°C. For cytological studies, material was fixed in picric acid (Dammann, 1930) and stained in chrome–haematoxylin (Melander & Wingstrand, 1953).

OBSERVATIONS

Interbreeding capacity and chromosome counts

The female strain of *Pterothamnion crispum* from Sarti was cultivated for about

8 months before any crosses were attempted. Plants with procarps were then placed together with male isolates from the Guernsey strain carrying spermatangia, and after about 1 month mature carposporophytes developed. The crosses were achieved at 15±2°C in petri dishes. Liberated carpospores grew into fertile tetrasporophytes which bore both tetrasporangia and spermatangia on the same whorl-branches, and sometimes on the same branchlets (Fig. 1). The spermatangia were only few in number and in several experiments their spermatia did not fertilize haploid female gametophytes with procarps. The tetraspores grew into dioecious gametophytes. Mature male gametophytes were observed after only 2 weeks, while procarps developed later and fertilization occurred after about 3 months. The tetrasporophytes came to maturity again after 8 months, and at this time they produced only tetrasporangia on new whorl-branches. The fate of these tetraspores was followed through their development into mature gametophytes, which were also successfully crossed.

Attempted crosses between male isolates of *Pterothamnion plumula* from the Swedish west coast and female ones of *Pterothamnion crispum* from Sarti were unsuccessful, though the plants continued to grow vegetatively.

Cytological investigations were undertaken to clarify the phenomenon of mixed phases and confirm the alternation of ploidy in the triphasic life history. Chromosome counts in late prophase stages of mitosis gave 24±2 in gametophytes and 48±4 in tetrasporophytes in both strains of *P. crispum* as well as in *P. plumula*. A year later, the crossing experiment between the two geographically isolated strains of *P. crispum* was successfully repeated.

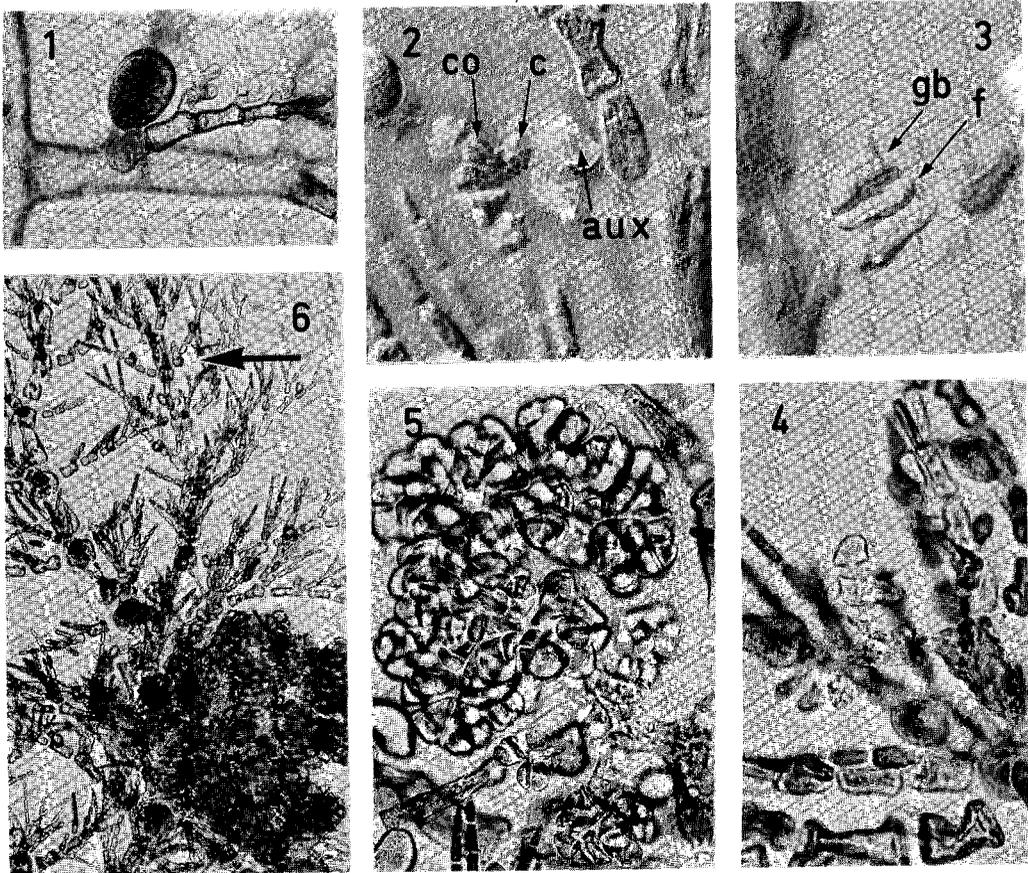
Thallus structure

The morphology of the vegetative thallus of *P. crispum* and *P. plumula*, as well as their spermatangial and tetrasporangial structures are well known. Attention was thus concen-

trated on possibly distinctive features dealing with the development and position of procarp and carposporophytes.

***Pterothamnion crispum*.** Female gametophytes of the two culture strains from Sarti and Guernsey developed one or two (occasionally three) procarps on lateral axes, but in the plants from Banyuls-sur-Mer up to six were observed. Procarp were occasionally initiated and fertilized early, one or two cells below the apices only. They were usually borne on secondary or tertiary axes and developed from basal cells of externally borne major whorl-branches.

After fertilization the zygote was transferred from the carpogonial cell to the auxiliary cell via a connecting cell (Fig. 2). The auxiliary cell was then divided to form a foot cell and a gonimoblast cell (Fig. 3). During the initiation or the development of gonimolobes, fusions occurred between the axial cell, supporting cell, foot cell and the gonimoblast cell (Figs 4, 5). Fertile axes developed only one carposporophyte which sometimes suppressed further growth of its axis. Procarp were occasionally borne on unsuppressed axes (Fig. 6), but no further carposporophytes were formed. Each carposporophyte developed several gonimolobes,



Figs 1–6. *Pterothamnion crispum*. Fig. 1. Development of spermatangia and tetrasporangia on a tetrasporophyte ($\times 300$). Fig. 2. Early stages in the fertilization of procarp. Carpogonium cell (co), auxiliary cell (aux), and connecting cell (c) ($\times 580$). Fig. 3. Division of auxiliary cell into a foot cell (f) and a gonimoblast cell (gb) ($\times 560$). Fig. 4. Formation of fusion cell from an axial cell, supporting cell and a foot cell ($\times 430$). Fig. 5. Mature carposporophyte ($\times 300$). Fig. 6. Continuation of axial growth during carposporophyte development and formation of one additional procarp (arrow) ($\times 100$).

usually four to six, the largest being up to 250 μm in diam., with carposporangia of about 25 μm in diam. The carposporophytes were surrounded by a loose involucre formed by subtending whorl-branches.

Carposporophytes were borne on lateral axes (usually as procarps), while the main axes continued their development and cut off new laterals.

***Pterothamnion plumula*.** Female gametophytes of the culture strain from Kristineberg occasionally developed three to five procarps (Fig. 7), frequently also in the plants from Tjärnö. Early initiation and fertilization of procarps occurred, as in *P. crispum*. In one case, an axis bearing two fertilized procarps in sequence was seen (Fig. 8). Carposporophytes developed on lateral axes while main axes continued their vegetative growth and cut off new laterals, as in *P. crispum*. The growth of fertile axes was generally inhibited by the development of carposporophytes, but in the single herbarium specimen from Plymouth, further growth was occasionally observed.

DISCUSSION

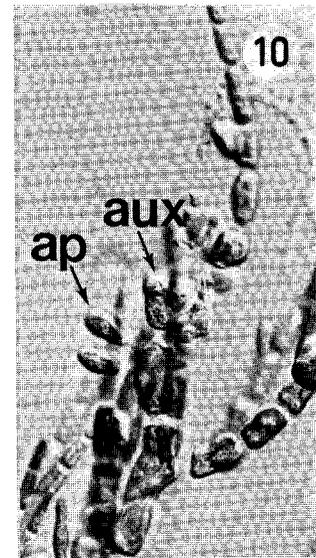
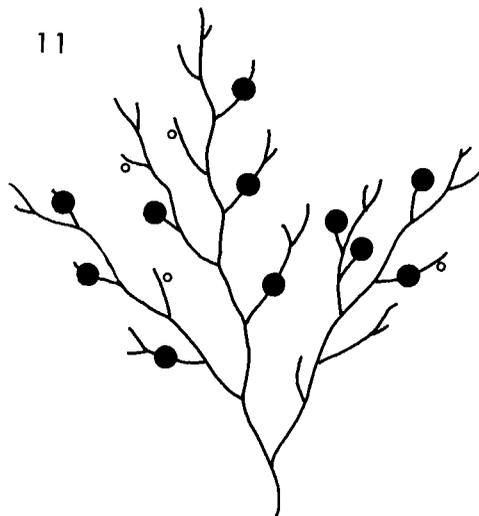
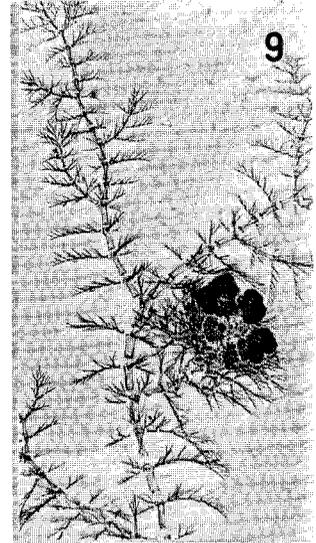
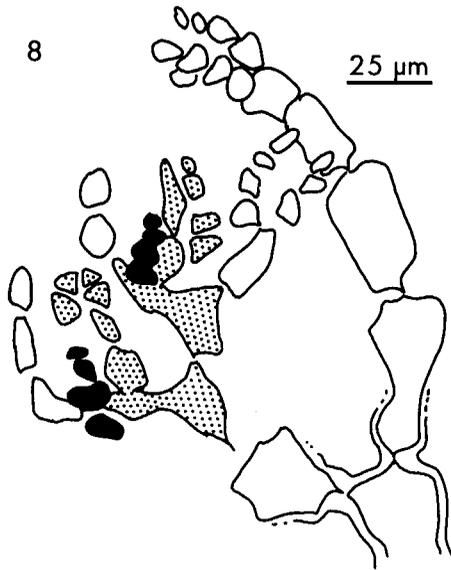
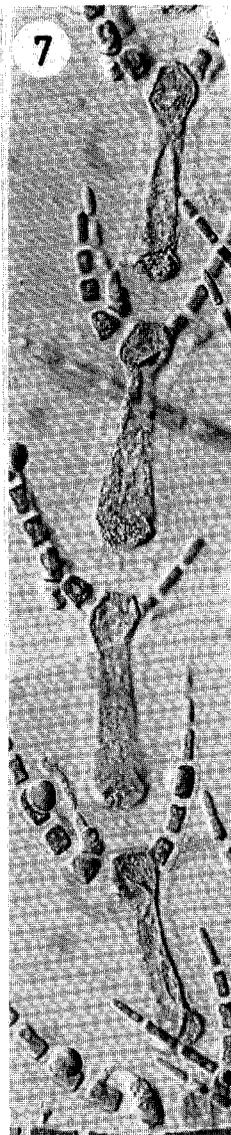
The results of the crossing experiments confirm those reached by Sundene (1975) and justify the recognition of *P. crispum* as a species distinct from *P. plumula*. The sexual compatibility between the two strains, one from the Channel Islands and the other from the North Aegean Sea, suggests that a single species is involved with a warm-temperate distribution along the coasts of Europe, as referred to in the literature.

The lateral position and development of procarps and carposporophytes in this species is similar to that in *P. plumula*, as observed in this study and previously partly described or illustrated by Kylin (1923, fig. 41), Kornmann & Sahling (1977, fig. 130F, G, H), Halos (1966, fig. I), and L'Hardy-Halos (1970, fig. 18). It is also identical to that described for species of *Platythamnion* by Wollaston (1972b). On the other hand, the number (one to six) and

initiation (early or late) of procarps and the development of fertile axes (whether suppressed or not) showed considerable variation. As a result these characters cannot be used as reliable taxonomic criteria to separate this species from *P. plumula*. The early initiation and fertilization of procarps could be related to the suppression of fertile axes (Figs 9, 10), whereas the late fertilization could be related to the continuation of growth. Such correlation remains to be investigated by further studies however.

Since the morphology of reproductive organs shows no distinctive characters in this species, its vegetative features remain the chief specific criteria in separating it from *P. plumula*. These are the regular development of four whorl-branches (two major ones borne at the plane of laterals and two minor ones secondarily developed), and the production of pairs of first-order branchlets (Ducluzeau, 1805; Agardh, 1851–52; Hauck, 1885; Feldmann, 1942; L'Hardy-Halos, 1968; and others). The same features are found, however, in at least two species of *Platythamnion*, *P. pectinatum*, Kylin (1925), and *P. recurvatum*, Wollaston (1972b), which are distinguished morphologically on the basis of other vegetative features, such as pectinate and complanate thallus (found in *Platythamnion pectinatum*) and abaxial development of branchlets (found in *Platythamnion recurvatum*) (Wollaston, 1972b).

The development of carposporophytes on lateral axes in *Pterothamnion crispum* (Fig. 11) as well as in *P. plumula* is a striking feature and has high diagnostic value in the taxonomy of these species. In *Pterothamnion plumula*, this feature is shown clearly in the illustrations of Kornmann & Sahling (1977, fig. 130G, H). Agardh (1892) first used the position of carposporophytes in the taxonomy of antithamnioid algae. He observed that the carposporophytes of *Antithamnion cruciatum* (C. Agardh) Nägeli were borne near the apices of axes (Agardh, 1879, p. 103, "*Hos Callithamnion cruciatum*, . . ., är favellan terminal, . . ."), and included this feature in distinguishing *Antithamnion* Nägeli (Agardh, 1892, p. 18, "*Favellae ad*



FIGS 7, 8. *Pterothamnion plumula*. Fig. 7 Development of five procarps in sequence ($\times 300$). Fig. 8. Early stages in the development of two carposporophytes on the same axis (mature carposporophytes were not observed in this case). Camera lucida drawing.

FIGS 9–11. *Pterothamnion crispum*. Fig. 9. Suppression of axial growth by the development of carposporophyte ($\times 20$). Fig. 10. Early initiation and fertilization of procarp borne just two cells below the apex of an axis. Auxiliary cell (aux), apical cell (ap) ($\times 410$). Fig. 11. Lateral position of carposporophytes (black circles) and procarps (white circles). Schematic illustration.

apices ramulorum ..." from *Platythamnion* J. Agardh, where he observed subapical position of carposporophytes borne on lateral axes (J. Agardh, 1892, p. 22, "*Favellae ... , a ramulo quasi heterogeneo,*

juxta axillam infimam plumulae emergente, ...").

Studies by Wollaston (1968, 1971, 1972a, b, 1978, 1979) and Moe & Silva (1980) on Ceramiaceae, have contributed

considerably to the taxonomy of Antithamnieceae. Wollaston (1968, 1971, 1972a) limited the circumscription of *Antithamnion* in conformity with Nägeli's (1847) criteria of the genus and Agardh's observation on the position of carposporophytes, and she added features such as development of one carposporophyte only at each fertile axis, small isodiametric periaxial cells with limited functions, gland cells on specialized short branchlets, and absence of cortication, which are features so far recognized for the type of the genus, *Antithamnion cruciatum* (cf. Moe & Silva, 1980).

For those plants with a distichous branching of sub-equal whorl-branches and laterals in one plane, Wollaston (1979) and Moe & Silva (1980) recognized the genus *Pterothamnion* Nägeli (in Nägeli & Cramer, 1855), as typified by *Pterothamnion plumula* (Ellis) Nägeli (1862). Additional features that separate the type species of this genus from *A. cruciatum* are the development of carposporophytes on lateral axes which may continue their growth, gland cells on ordinary cells of whorl-branches and branchlets, sinusoidal apices, and facultative development of three or four whorl-branches (cf. Moe & Silva, 1980).

Moreover, Kylin (1925, 1956) and Wollaston (1968, 1972b, 1978, 1979) maintained *Platythamnion*, as typified by *P. heteromorphum* (J. Agardh) J. Agardh (1892), to include species differing from *Pterothamnion plumula* and *A. cruciatum* by a regular development of four whorl-branches, and monostichous, distichous (opposite or not) or tristichous first-order branchlets.

Agardh's concept of the genus is based upon only two taxa, *Platythamnion heteromorphum* and *Platythamnion orbignianum* (Mont.), J. Ag. and includes some features in addition to those adopted by Kylin and Wollaston. However, these features either occur also in other genera, or characterize few species of *Platythamnion* as recognized by Kylin and Wollaston. The lateral and subapical position of carposporophytes also occurs in *Pterothamnion plumula* and thus has to be recognized as a feature of

Pterothamnion too. The absence of cortication is a common feature of many antithamnioid species and genera, although not of *Platythamnion nodiferum* (J. Agardh) Wollaston (1968). The abaxial development of tetrasporangia is known to occur only in *Platythamnion heteromorphum* and in *P. reversum* (Setchell et Gardner) Kylin (1925), whereas naked carposporophytes (not surrounded by subtending whorl-branches) have so far only been reported from *P. heteromorphum* and *Pterothamnion antarcticum* (Kylin) Moe & Silva (1980).

These observations suggest that *Platythamnion* has to be limited according to Wollaston's criteria, if not included within an amended *Pterothamnion*. Reasons that support the latter possibility are that the polymorphous arrangement of branchlets in *Platythamnion* is a specific character, as used currently to distinguish species of this genus from each other (see Wollaston, 1972b). Conversely, development of opposite first-order branchlets occurs in several other species currently placed within other genera, e.g. *Antithamnion callocladus* (Itono, 1971) and species of *Balliella* (Itono & Tanaka, 1973); whereas development of monostichous first-order branchlets as occurs in *Platythamnion cuspidatum* (Wollaston, 1978), occurs in species of *Pterothamnion*, too.

The regular presence of four whorl-branches in species of *Platythamnion* seems to be the only uniform feature that distinguishes them from *Pterothamnion*; but this feature is not sufficient to support generic segregation especially since vigorous plants of *Pterothamnion plumula* occasionally develop four whorl-branches too (Rueness & Rueness, 1975; Rueness, 1978).

As to the possible inclusion of *Platythamnion* in *Pterothamnion*, caution is justified in the absence of a full description of the gametophytes of *Platythamnion heteromorphum* (cf. Wollaston, 1972b).

The recognition of *Pterothamnion crispum* here is recommended. Morphologically, this species may closely approach vigorous

plants of *Pterothamnion plumula* with four whorl-branches, differing from these only in the development of pairs of first-order branchlets. Approximate chromosome numbers were found the same in strains of these two species, and are in a good agreement with previous reports in *P. plumula* ($n = 23$, $2n = 46$; Magne, 1964). In *Antithamnion*, the lowest number reported is $n \approx 32$ (Rueness & Rueness, 1973), and that provides an additional criterion for separation of the two genera.

With regard to the position of carposporophytes within six genera of Antithamnieae where such information is available, three types of development are distinguished. In one type, carposporophytes are borne singly near the apices of main and lateral axes which usually suppress their vegetative growth. This is observed in species of *Antithamnion* (Agardh, 1879; Wollaston, 1968, 1972a; Athanasiadis, 1983), and according to Wollaston (1971) and Whittick (1980) also in *Antithamnionella* Lyle.

In a second type, the carposporophytes are also borne singly but develop near or below the apices of lateral axes, so that the main axes continue their growth and cut off new laterals. Occasionally, the axes with the carposporophytes also continue their growth and cut off laterals that may develop procarps, but no further carposporophytes are formed. This is observed in species of *Pterothamnion* (Fig. 11) and *Platythamnion* (Agardh, 1892; Wollaston, 1972b).

A third type occurs in *Scagelia* Wollaston (Wollaston, 1971; Hansen & Scagel, 1981) and in *Balliella* (Itono & Tanaka, 1973), where several carposporophytes are borne along the same fertile axis which continues its growth (cf. Moe & Silva, 1980).

The fertilization of two procarps in sequence, observed once in *Pterothamnion plumula* (Fig. 8), probably demonstrates a relationship between the second and third type of development.

With regard to the typification of *Antithamnion* by *A. cruciatum* (Nägeli, 1847, p. 200, table VI, figs 1-6), it should be

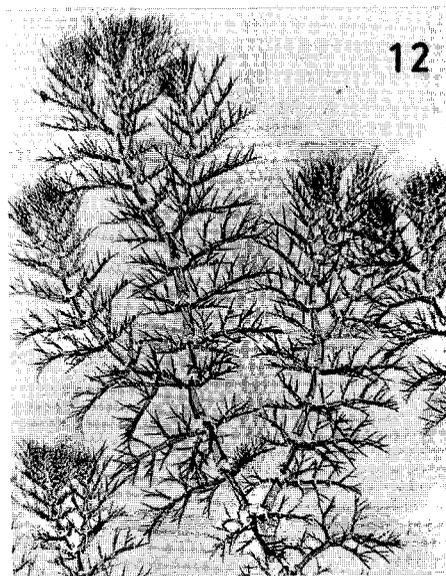


FIG. 12. *Pterothamnion crispum*. Neotype, IG110783 GB ($\times 40$).

mentioned that Nægeli's description which is based upon material collected at Sorrento (Italy) includes features not ascribed to this taxon (e.g. the alternate-distichous development of first-order branchlets in one plane, and the production of gland cells on second-order branchlets). These features characterize another species, later described as *Antithamnion antillanum* (Børgesen, 1915-20, 1930) and under that name recorded for the Mediterranean first by Schiffner (1931) and later by Boudouresque & Verlaque (1976). The mistake by Nægeli does not affect the typification, however, since the type of a genus is expressly said to be a name of a species (Voss *et al.*, 1983).

According to Stafleu & Cowan (1976) and W. F. Prud'homme van Reine (Rijks-herbarium Leiden; pers. comm.), Ducluzeau's herbarium and types are unknown. A neotype, IG110783 GB (Fig. 12) has been thus selected from the material collected at Banyuls-sur-Mer.

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