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The *Porphyra* species of Helgoland (Bangiales, Rhodophyta)

P. Kornmann & P.-H. Sahling

Biologische Anstalt Helgoland (Meeresstation); D-W-2192 Helgoland, Federal Republic of Germany

"In an investigation into the life-history of an alga the aim should be to obtain a series of observations of the development of the thallus from the germinating spore and then of the development of the reproductive organs on the mature thallus. In cases where both sexual and asexual spores are formed the germination of both types of spore should be followed, . . ." (Drew, 1954, p. 184)

ABSTRACT: This revision of seven *Porphyra* species of Helgoland was based on a study of the structure of their fertile thalli and the behaviour of their spores. Regarding the reproductive organization the species may be arranged in two groups. *P. leucosticta* and *P. purpureo-violacea* are obligate monoecious species. Asexual thalli have never been observed in the field. The other five species are generally dioecious. Isomorphic sexual thalli and asexually propagating ones are mixed in uniform populations. Carpospores originating from sexual fusion develop into the diploid Conchocelis phase. Sporangia of asexual plants, though homologous in formation, produce spores of different kinds: aplanospores that give rise to the vegetative thallus directly (in *P. umbilicalis*, *P. insolita* n. sp. and *P. ochotensis*) and spores that develop into haploid Conchocelis (in *P. laciniata* and in *P. linearis*). *P. laciniata* – formerly considered synonymous with *P. purpurea* – is an independent species.

INTRODUCTION

Differentiation of *Porphyra* species from Helgoland

The relatively small area around Helgoland harbours 7 monostromatic *Porphyra* species. Several of these species form large stocks, brought forth most certainly by the eutrophic waters that occur even in summer and display an extremely high content of inorganic dissolved nitrogen. Favoured habitats are the extensive harbour piers and the protective dams along the shore. The red sandstone rock of the coast is exposed to the sea at only few places, and is in any case not a suitable substrate for *Porphyra*. Even though the individual species lack definite and easily recognizable taxonomic features for identification, the ecological characteristics of their respective habitats suffice in practice for their determination. The species inhabit distinct tidal zones as uniform populations. *P. umbilicalis* and *P. linearis* grow in the supralittoral zone and in the upper eulittoral zone; they can be easily distinguished by their morphology. The mid-eulittoral zone harbours *P. insolita*, mainly long to oval in shape and up to 90 cm long, a new species which will be described in this paper. At the edge of the sublittoral zone, the fragile

P. laciniata and *P. ochotensis* are met with. The latter is presumably a Japanese species that settled around Helgoland about 30 years ago. Its thick, olive-brown to greenish thallus distinguishes it quite clearly from the other species. The remaining two species are fragile, monoecious inhabitants of the mid-eulittoral zone of the rocky intertidal region. *P. purpureo-violacea* is easily recognized by the separation of the thallus into a male and female zone. The spermatangia of the generally epiphytic *P. leucostica* are easily discerned as small, whitish areas on the thallus.

Photographs of the species and their habitats can be found in earlier publications (Kornmann, 1961b; Kornmann & Sahling, 1977).

Comments on the nomenclature

This chapter deals with necessary nomenclatural remarks on the studied species. In our previous papers (Kornmann, 1961b; Kornmann & Sahling, 1977), *Porphyra laciniata* Ag. was not mentioned. Obviously, this species, which is widespread along the European coasts, either did not occur in this area of investigation or was present in such small numbers that it escaped our notice. Meanwhile, the situation regarding the *Porphyra* vegetation has changed to a great extent. At present *P. insolita*, a species which has been observed since 1988 and which is described in this paper for the first time, dominates in quantity. *P. laciniata* was found in 1989 in several places of the investigated area; its presence could no longer be overlooked. On this basis, a regrettable error in the paper published in 1961 must be corrected: the supposed identity of *P. purpurea* (Roth) C. Ag. as *P. umbilicalis* var. *laciniata* (Lightf.) J. Ag. caused by their similar external morphology was wrong. The responsibility for this error must be borne by the first named author, who, with great relief, takes this opportunity to make the necessary correction.

This error has had a negative influence not only on the European literature (e.g. Conway, 1964a). Kurogi (1972, p. 170), comparing his material with herbarium material from Helgoland, named the species that had been designated in Japan as *P. umbilicalis* (L.) Kütz. *P. purpurea*. Kurogi's numerous illustrations of the morphology and his analysis of the structure of the carposporangium exclude its identity with *P. purpurea*. This conclusion was also reached by Wynne (1972), who in accordance with the Japanese authors compared *P. purpurea* (Roth) C. Ag. with *P. umbilicalis* (L.) Kütz. in the area of Amchitka (Aleutian Islands). In the same year, Krishnamurthy (1972) published his revision of the genus *Porphyra* from the Pacific coast of North America. In this paper he also checked material from Amchitka. He came to the conclusion that *P. purpurea* is conspecific with a species designated by Hus (1902) as *P. laciniata* f. *umbilicalis*. While Wynne (1972) points out that *P. purpurea* is monoecious, Krishnamurthy (1972) describes this species as dioecious: "occasionally intersex plants are met with, sporocarpic and spermatangial portion of the frond delimited by a sharp line" (p. 42). Krishnamurthy uses the older name of the supposed synonym, pointing out that Roth himself had described this alga as *P. purpureo-violacea* 9 years previously. This name will be used in the present paper.

The material on which Drew (1954) based her classical study was doubtlessly identical with *Porphyra laciniata* found recently at Helgoland. This conclusion can be derived from the description of the plants as well as from the details of their habitat. The Helgoland plants, which grow alongside the promenade on stones at low tide level, are

also sometimes covered with sand. Drew cautiously designated her material as *P. umbilicalis* (L.) Kütz. var. *laciniata* (Lightf.) J. Ag.; the question of whether this was identical with *Ulva laciniata* Lightf. (1777) or with *P. laciniata* C. Ag. (1824) was left open to discussion. Dixon (1959, 1983) was able to remove all doubt: the sample in the Lightfoot herbarium is *Polyneura laciniata* (Lightf) P. Dixon. So the use of the name *Porphyra laciniata* C. Ag. continues to be uncertain.

Porphyra umbilicalis is understood here as the species described by Conway (1964a, b). The three species named in this chapter so far belong, together with *P. linearis* and *P. leucosticta*, to the inventory of the European flora. The probably immigrant *Porphyra* sp. of our paper "Meeresalgen" (Kornmann & Sahling 1977) is similar to the Japanese *P. ochotensis* Nagai. The suspicion that *P. insolita* nov. sp., presently growing in abundance at Helgoland, may also be indigenous to the European coasts, will be considered later in the text.

The following will give individual and extensive reports on 6 species; an earlier paper on *P. leucosticta* (Kornmann 1961a) will be supplemented by a short comment only.

A systematic classification of the genus *Porphyra*

The revision of the *Porphyra* species from Helgoland provided fresh information on their properties which will form the basis for a new classification. The study of the formation and structure of *Porphyra* reproductive organs as well as culture experiments with spores have revealed these new facts.

Hus (1902) recognized the three-dimensional pattern of the mature reproductive organs as an important diagnostic character. The Japanese authors (Ueda. 1932a, b; Tanaka, 1952; Kurogi, 1972) basically used this character to identify their *Porphyra* species. In 21 monostromatic Japanese species, Kurogi distinguished between two groups: in surface view of the mature thallus, the "cystocarps" are packets of four or eight spores. In cross-section through the mature thallus the spores form two or four rows.

The morphological structure of the thalli and their reproductive organs does not suffice to distinguish the species further; it must be supplemented by the developmental pattern of the spores and their role in the life history. Spores germinate in culture experiments within a few days, giving rise either to Conchocelis filaments or to *Porphyra* blades. On this basis, the *Porphyra* species can be assigned to three groups.

Group 1: Surface view 4 spores, cross-section 2 rows.

Subgroup 1a: Genuine carposporangia, arising from a fertilized carpogonium. Life-cycle heteromorphous and bi-phasic. Example: *Porphyra gardneri* (Hawkes, 1977, 1978).

Subgroup 1b: A mother cell can be divided according to the pattern shown in Subgroup 1a for the carpogonium. However, no fertilization takes place; the spermatia are rudimentary. Life cycle heteromorphous and monophasic. Example: *Porphyra carolinensis* (Freshwater & Kapraun, 1986).

Group 2: Surface view 4 spores, cross-section 4 rows.

Subgroup 2a: Spores develop directly into *Porphyra* blades. Example: asexual form of *Porphyra umbilicalis* (Figure 1).

Subgroup 2b: Spores develop into Conchocelis. The spermatia are rudimentary. The life cycle is heteromorphous and monophasic. Example: asexual form of *Porphyra laciniata* (Krishnamurthy, 1959).

Group 3: Mature carposporangia appear to be divided into packets of 8 spores in surface view. They arise from fertilized carpogonia at some distance from the margin of the thallus. Carposporangia (lying detached) are spindle-shaped; sections through compact layers display four or more rows. Example: sexual form of *Porphyra laciniata*.

The sexual plants of Group 3 are always accompanied by an asexual thallus of Group 2. The isomorphic thalli occur in the same population. *Porphyra linearis* from Helgoland, however, is only known with plants of Subgroup 2b. The plants of Group 2 could easily be considered as individual species. The interrelationship of the group 2 and 3 components in the life cycle is not known.

MATERIAL AND METHODS

Material for the studies was taken from uniform populations. When spread out in a flat basin, suitable objects for culture experiments could easily be selected. In general, mature thalli released reproductive cells which lay on the bottom of the vessel. Small fragments were broken off from the edges of these thalli for cultivation and for microscopical examination. These samples received the same identification mark in the herbarium and in the cultures. For microscopical examinations, sections with a razor were sufficient. They were photographed either in a fresh state or after addition of a small amount of Formol. Cross-sections and pieces of the thalli were kept as permanent slides. The collection comprises several hundred slides.

The culture experiments were carried out according to proven methods. In general, culture medium after Provasoli with addition of soil extract was used. A fluorescent lamp (40 W) fixed 30 cm above a 50-cm wide table was a sufficient source of light. Two temperature regimes were used to accomplish the whole life cycle of the examined species. At 14–15 °C and 14 h light per day, conchosporangia were formed in all species and some also released their spores under these conditions. A few days after transfer to 5 °C, conchospores were released in all species except in *Porphyra linearis*. Daylength and irradiance were less important for our qualitative experiments; in one species, conchosporangia matured and released spores even in cultures kept in the dark.

RESULTS AND DISCUSSION

Porphyra umbilicalis (L.) J. Ag.

Porphyra umbilicalis occurs from the supralittoral zone to about the mid-eulittoral zone. Its morphology varies according to the exposure. This common Helgolandic alga and its Conchocelis phase has been the subject of extensive and illustrated reports (Kornmann, 1961b; Kornmann & Sahling, 1977). Detailed illustrated studies on the taxonomy, ecology and development of this species on the English coast have been supplied by Conway (1964a, b).

Originally, it had not been planned to include *Porphyra umbilicalis* in the revision of the *Porphyra* species of Helgoland, as essentially new facts were not expected. A chance observation, however, proved to be decisive for the further course of the investigation: a *P. umbilicalis* thallus, considered to be female, became fertile after a few days in the culture medium shedding spores which gave rise to *Porphyra* directly. After this unexpected observation, 22 individual plants were collected from the end of September to the beginning of October 1989 at 6 different localities. In seven cultures, Conchocelis was

observed to develop; in the other 15 cultures *Porphyra* blades developed. There was no doubt that the examined material belonged to *P. umbilicalis*; therefore, its spores must differ genetically. A morphological examination of the basic material confirmed that the reproductive organs were either aplanosporangia or carposporangia.

Direct development

The direct development of the spores of two thalli is shown in Figure 1. On the left hand side, a fertile thallus from the upper eulittoral zone is shown in surface view and cross-section, also the free spores and the 5- to 10-day old germlings. The plant on the right hand side of the figure was taken from the supralittoral zone. It took 12 days before the thallus, kept in the culture medium, released its spores. A comparison of the cross-sections reveals that the thallus of this plant was thinner than that of the upper littoral plant, and the spores were somewhat smaller. 15-day old Porphyra blades were about 300 µm in size.

Even though this discovery was surprising, it was not new. The surface view on the edge of a thallus of *Porphyra umbilicalis* in Conway (1964a, Figs 7, 8) shows without doubt asexual sporangia. The released "alpha-spores" developed directly into *Porphyra* (Conway 1964b, Figs 9–12).

Porphyra spores that develop directly from 4-row sporangia first became known through Krishnamurthy (1969). The unusual reproduction of this alga exclusively with aplanosporangia was reason enough to describe it as an individual species, *P. sanjuanensis*. It has a local distribution in British Columbia and Washington, where it occurs in winter and spring. After the findings in three *Porphyra* species from Helgoland, one question must again be posed – a question which is answered in the negative by Krishnamurthy: Could *P. sanjuanensis* be a seasonal asexual partner in the life cycle of a *Porphyra* species, which has, besides, a heteromorphous cycle? In his diagnosis published in 1972, Krishnamurthy does not mention aplanosporangia; Krishnamurthy considered *P. sanjuanensis* to be a probably dioecious species with unknown spermatangia. Conway (1974) identified one of the isolates of *P. perforata* J. Ag. in the herbarium in Lund as *P. sanjuanensis*.

Spores with direct development were not always aptly described. Relative to the manner of their origin, a distinction must be made between the monospores from single cells, and aplanospores from sporangia. Kapraun & Lemus (1987, p. 485) write, with reference to Conway (1964a, b): "*Porphyra umbilicalis* is characterized by a simple, cordiform blade with marginal monospores . . ." But here we are clearly dealing with aplanospores from sporocysts. In West & Hommersand (1981, p. 139), however, we are obviously dealing with monospores: "A few species, including the economically important *P. tenera* and *P. yezoensis*, release aplanospores from young dwarf thalli . . ." In their diagram of the life history of *Porphyra* (Fig. 4. 1), the spores from a few-celled germling as well as the spores from asexual sporangia of an adult thallus are described as aplanospores. The diagram is misleading for another reason: no heteromorphous life cycle is known, in which the foliose thallus is provided with aplanosporangia. Similarly, in a diagram by Cole & Conway (1980, Fig. 1) monospores from a young flat thallus are called aplanospores. Monospores are formed in the young stages of many foliose thalli. In *P. yezoensis* and *P. kuniedai*, large thalli of 6–7 cm length can reproduce by means of monospores (Kurogi, 1972, Table 4).

The female thallus

The mature carposporangia are not always so closely packed in the pink edges of the fertile thallus as shown in Figure 4G, but may lie singly or in groups between vegetative cells or between young sporangia (Fig. 2A). A cross-section of such a thallus shows the mature sporangia in spindle-shaped groups of cells; the younger ones are in pairs and narrow, separated by periclinal walls, elliptic in shape and acute at both ends (Fig. 4F, G). The surface of the thallus shows bumps above and below the sporangia and their initials. Thin appendices of the young sporangia extend into these protuberances almost reaching the surface. The surface view of the thallus confirms the evidence of the cross-sections. Figures 2B and 2C show the same piece of a thallus but at a different focus. It can be clearly seen that the delicate membrane of the bump encloses 2 or 4 young carposporangia whose trichogynes protrude into the delicate papillae (Fig. 2D). Sometimes, the network of a brown epiphyte adjusts to the structure of this surface by spreading its filaments in the 'valleys' between the 'hills' (Fig. 2E).

Figure 3, taken from a permanent slide, displays younger developmental stages of the plant shown in Figure 2. The young carpogonia consist of to or four small sister cells originating from one mother cell; they extend on both sides to form trichogynes, penetrating into the domes almost up to the surface. Fertilization takes place before the first transverse cell division. Whether all four carpogonia of a bundle are fertilized can be established only by further caryological investigations. Spores of former sister cells are united to form a spindle-shaped carposporangium. The morphological difference between this and a cylindrical aplanosporangium that has arisen from a regularly dividing mother cell is obvious: the spores in the spindle-shaped carposporangium are not arranged in rows of four.

Figure 4G illustrates the margin of a thallus with closely packed mature carposporangia. Surface view and cross-sections show stages of their development. The sporangia at the edge of the thallus are almost mature (Fig. 4G, H); eight spores can be seen in surface view. Further inwards, younger sporangia are still in division (Fig. 4E, F). In an even younger zone (Fig. 4C, D), the ends of some of the trichogynes are swollen; they can only be interpreted as stages of the fertilization process. The corresponding Figure 4B shows the primary divisions of the mother cells of the carpogonia in surface view.

These observations leave no doubt that the carposporangium of *Porphyra umbilicalis* produces diploid spores, in agreement with the results of caryological studies (Kito et al., 1971).

Earlier records on carposporangia and asexual sporangia

The described structure of the fertile female thalli has long been known, but not enough attention has been paid to this knowledge. Numerous illustrations by Ueda (1932a) and by Tanaka (1952) show carpogonia with trichogynes or young carposporangia with acute ends. There is a surprising similarity between our photographs and the cross-sections of *Porphyra crispata* by Ueda (1932a, Pl. III, 4 and 5). Miura (1967) illustrated the origin of the carposporangium of the same object, and this accords

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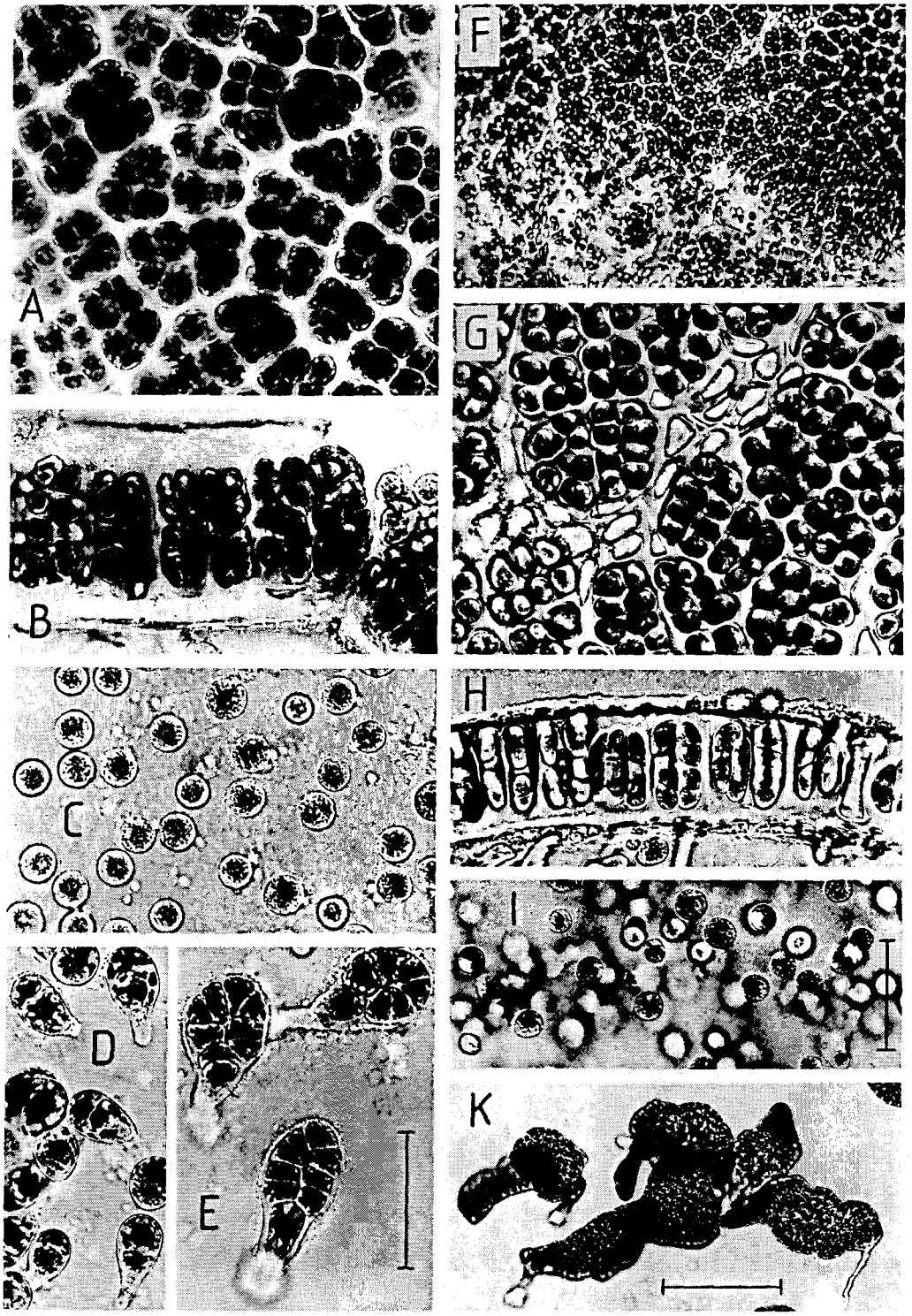
Fig. 1. *Porphyra umbilicalis* with aplanosporangia. A–E: Plant from the upper eulittoral zone. A: Surface view of the margin of the thallus with aplanosporangia. B: Cross-section. C–E: Aplanospores and 5- to 10-day old germlings. F–K: Material from the supralittoral zone. K: 18-day old thalli. Scale: A–E, G–I: 50 μm; F, K: 200 μm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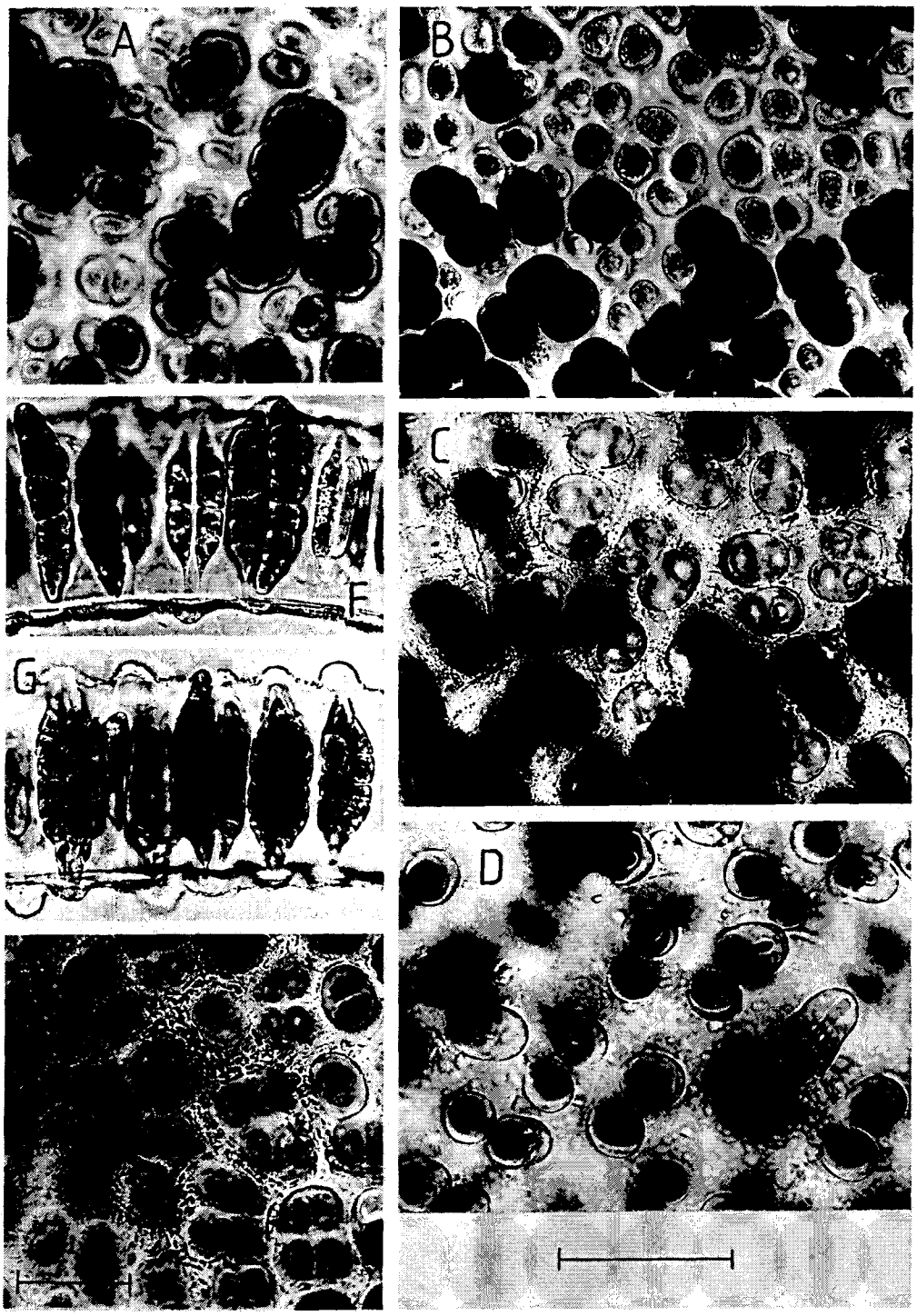
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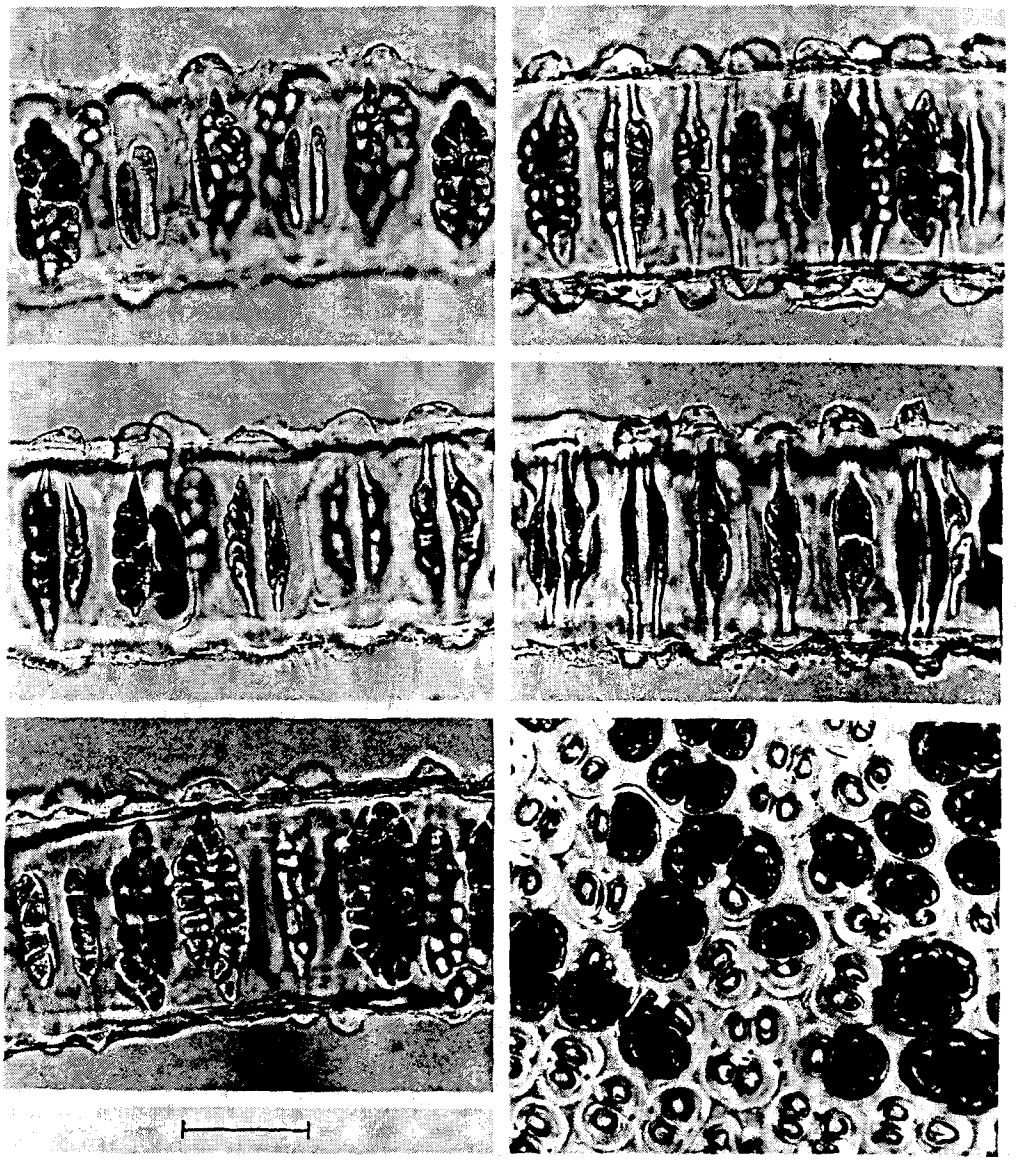
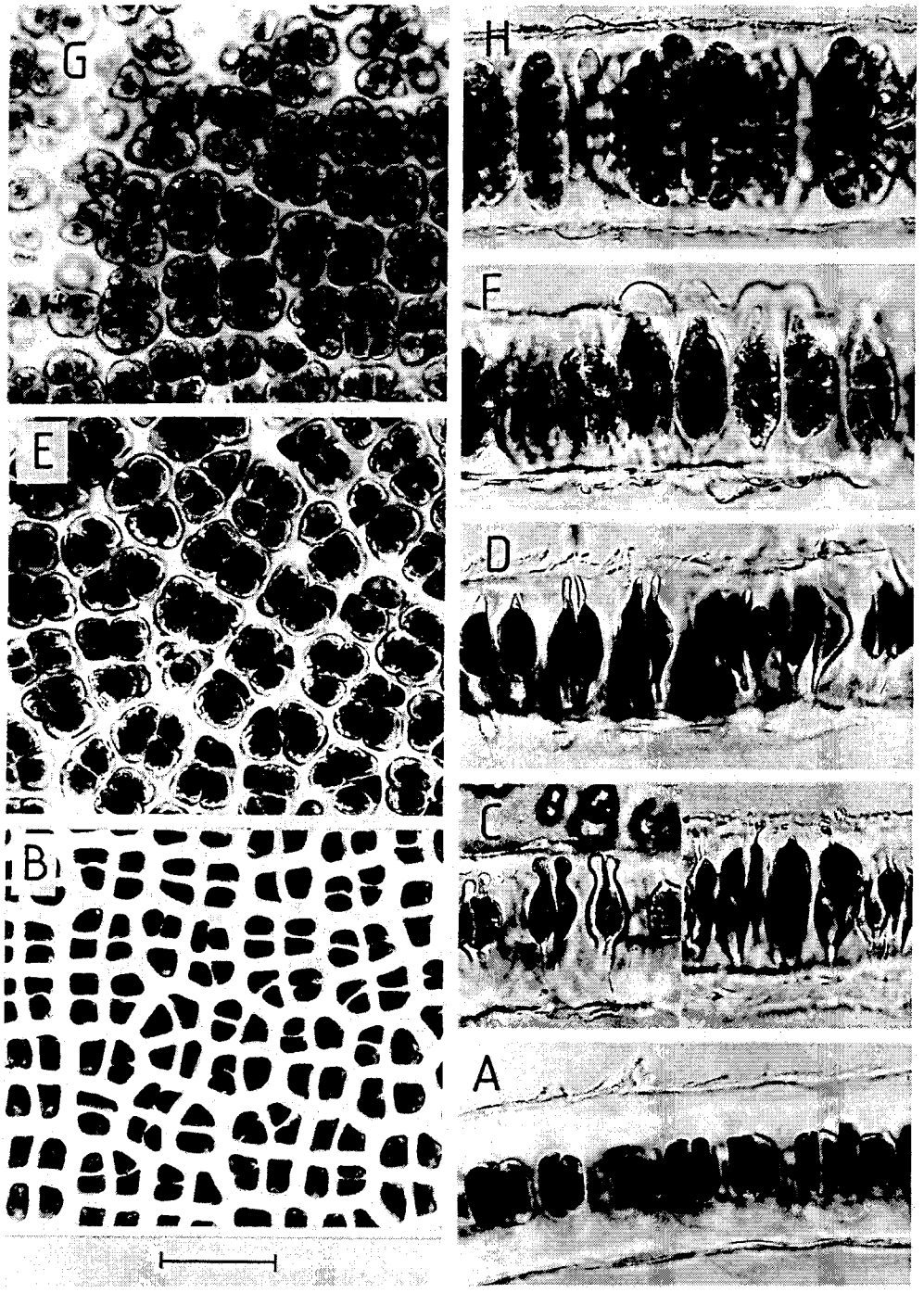


Fig. 3. *Porphyra umbilicalis*. Sections of the thallus shown in Figure 2 displaying carposporangia at all stages of development Scale: 50 μm

Fig. 2. *Porphyra umbilicalis*. A: Surface view of thallus margin with interspersed carposporangia. B, C: Same detail, but at different focus. D: Trichogynes protruding into vesicular bumps above the carpogonia. E: Brown epiphyte spreading in the "valleys" between the "hills". F, G: Cross-sections with carposporangia of different maturity. Scale: 50 μm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completely to our observations. Clear drawings on three plates show the cruciate anticlinal division of a cell into four carpogonia with two-sided trichogynes, which are also visible in surface view of the thallus. The carpogonia, packed in fours, are separated first by a periclinal cell wall. The further division is irregular, so 'that the produced carpospores are arranged very irregularly in both surface view and sectional view' (Miura, 1967, p. 70). For this reason, the attempt of the authors to find a formula for the division of the mature carposporangium of *P. crispata* was doomed to failure; it was interpreted in different ways by Ueda, Tanaka und Kurogi.

Asexual sporangia have been known for a long time. However, they were not recognized as asexual sporangia but looked upon as carposporangia. Kylin (1956, Fig. 24) took over the illustrations of Thuret & Bornet (1878). The cross-section and the surface view of a fertile thallus of *Porphyra laciniata* (Lightf.) Ag. do not show carposporangia, but correspond to the asexual sporangia of this species as illustrated in Figure 14A, B. Excellent photos in a recent study on *Porphyra abottae* (Cannon, 1989) indicate that the investigated material was composed of sexual and asexual thalli. Cannon's Figure 6 shows a carpogonium with trichogynes on both sides and a young carpogonium. The cross-sections in Cannon's Figures 9 and 10 show slightly older carposporangia and the surface of the thallus with bumps on both sides. The distromatic stage, in contrast, shows the initiation of spore development in an asexual thallus (Cannon, 1989, Fig. 7). The mother cells are divided regularly by longitudinal and transverse walls, and no trichogynes were formed. A similar drawing of *P. abbottae* was given by Krishnamurthy (1972, Fig. 2c) which was interpreted by this author as a 'section through the sporocarpic portion of the frond showing division into two layers of cells'. The legend to Figure 7 of Cannon (1989) is similar. The existence of female thalli in Krishnamurthy's description of the species may only be deduced from his Figure 2d.

Porphyra insolita nov. sp.

It was astonishing to find in 1988 an unknown *Porphyra* species at Helgoland in view of the numerous biological stations established along the European coasts. Thalli up to a length of 90 cm were fairly densely attached in the mid-eulittoral zone of the northeastern harbour in front of the laboratory. As this place has not been regularly visited, the alga probably settled unnoticed in this and other neighbouring habitats. Neither this alga nor *Porphyra laciniata* were met with in the course of our extensive studies of the *Porphyra* vegetation in 1961.

It would have been easy to conclude that it was, like *P. ochotensi* (p. xxx) and *P. yezoensis* (Kornmann, 1986), an immigrant from East Asia; however, it could not be identified with any of the species listed by Kurogi (1972). While *P. ochotensis* and the new species have spread extensively at Helgoland, *P. yezoensis* was limited to the one find of small plants; the thalli attained their normal length only in culture.

However, *Porphyra insolita* may not be so strange as its specific epithet suggests. It is

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Fig. 4. *Porphyra umbilicalis*. Carposporangia form a compact layer at the margin of the thallus; surface view and cross-sections of samples taken from different zones. A: Vegetative thallus. B–D: Cells forming carpogonia after anticlinal cruciate division. E, F.: Immature carposporangia. G, H: Mature carposporangia at the margin of the thallus. Scale: A–H: 50 µm

quite possible that it occurs, unrecognized, on other European coasts. Rosenvinge (1909) published three excellent photographs of *P. umbilicalis* in Table 1 of his paper. However, only his Figure 2 portrays this species; his Figure 1 shows a monoecious specimen of *P. laciniata*. Rosenvinge's Figure 3 could be considered – with all due care – as an illustration of *P. insolita*.

In *P. insolita* as in *P. umbilicalis*, plants with direct and with heteromorphic development occur simultaneously.

Direct development

Thalli of *Porphyra insolita* with aplanosporangia were observed during the whole course of the vegetative period from January to August. In mid-January 1990, the plants were 5–6 cm long and not yet fertile. At the end of January, the plants in the same locality were 10 cm long on average, and released large amounts of aplanospores from the margins. The discharge could be observed directly under the microscope. It began at the edge of the thallus in several sharply limited areas (Fig. 5 C, D). The streaming spores issuing from the thallus edges can be clearly observed in the larger photograph. Within a few minutes, a 0.2- to 0.5-mm broad zone of the margin was emptied of spores, and a distinct empty net of cell walls remained (Fig. 5 E).

The origin and structure of the fertile, asexual thallus are clearly visible in surface view and in cross-section (Fig. 5A, B). Under the cruciately divided thallus cells, rows of 4 spores are arranged. Freshly discharged spores, 11–14 µm in diameter, developed quickly into small *Porphyra* plants (Fig. 5F–H). Thalli, collected every two weeks, reproduced only by aplanospores; by the beginning of April gametophytes were found.

In May and June, the population lacked unity with regard to the size of its individuals; the population obviously consisted of plants of different ages. The largest thalli were 90 cm long and 25 cm broad. Three of these large plants were supplied with aplanosporangia.

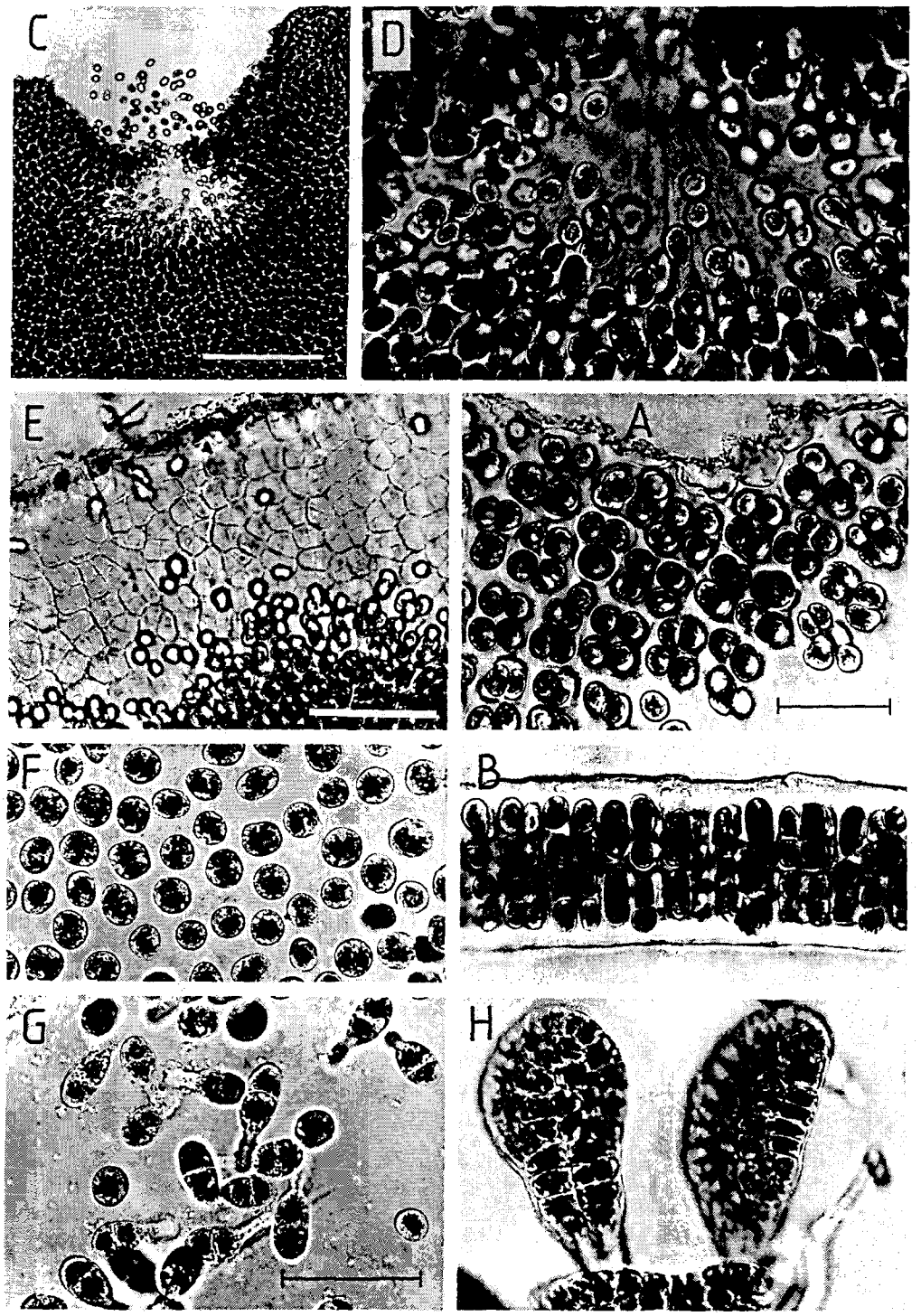
At the beginning of August 1989, *Porphyra insolita* was near the end of its vegetation period. For the most part, only 30-cm long senescent remnants of thalli of the formerly impressive plants remained. Their peripheral parts were perforated and often formed merely a wide-mesh net of thallus pieces. The age of these remmants could be exactly determined: up to a height of 20 cm above the basis, the barnacle *Elminius modestus* had settled. The 2- to 3-mm broad epizoa must have originated from a spawning event in early spring.

The net-work of the senescent, tough thalli contained numerous light coloured, or seemingly white, spots of dead cells that were clearly separated from the vegetative or fertile tissues (Fig. 6A, B). Some of the thalli were 80–90 µm thick. Even these old plants had numerous aplanosporangia at all developmental stages (Fig. 6D).

The female thallus

Just as in other species of the genus, the fertile margin of the female thalli of *Porphyra insolita* can vary in appearance. The margin may have a uniformly red colour, or may be more or less heavily spotted. Closer examination reveals the mature carpo-

Fig. 5. *Porphyra insolita* n. sp. Aplanosporangia. A, B: Fertile margin of thallus; surface view and cross-section. C, D: Initiation of spore release. E: Emptied sporangia. F: Aplanospores. G, H: Germlings 3–11 days old. Scale: A, B, D, F–H: 50 µm; C: 200 µm; E: 100 µm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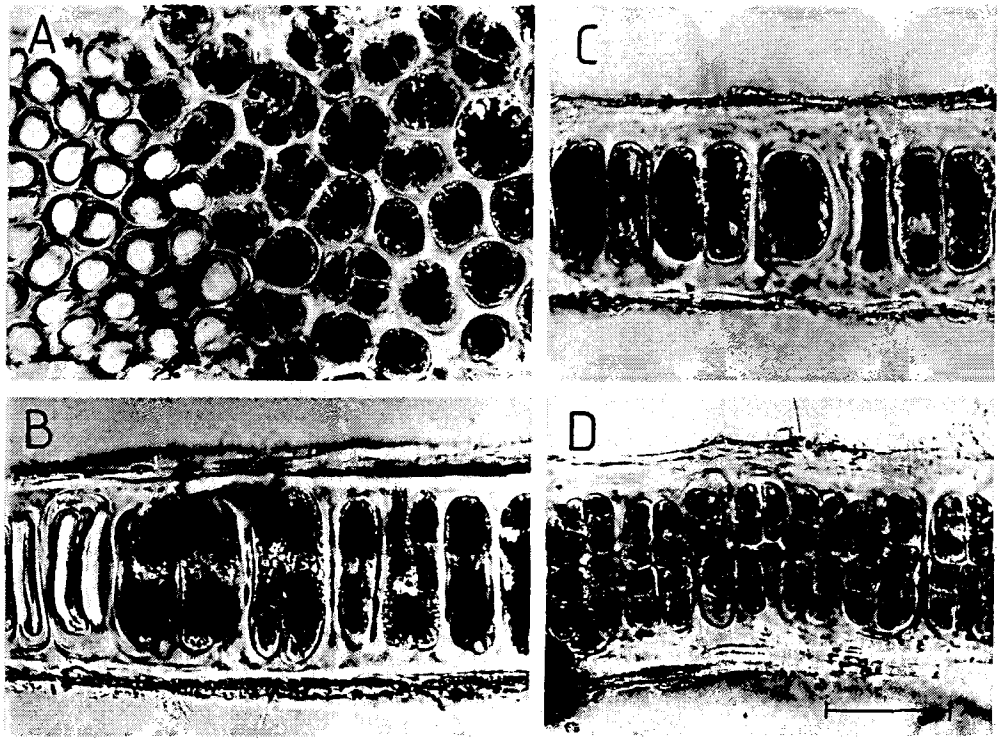
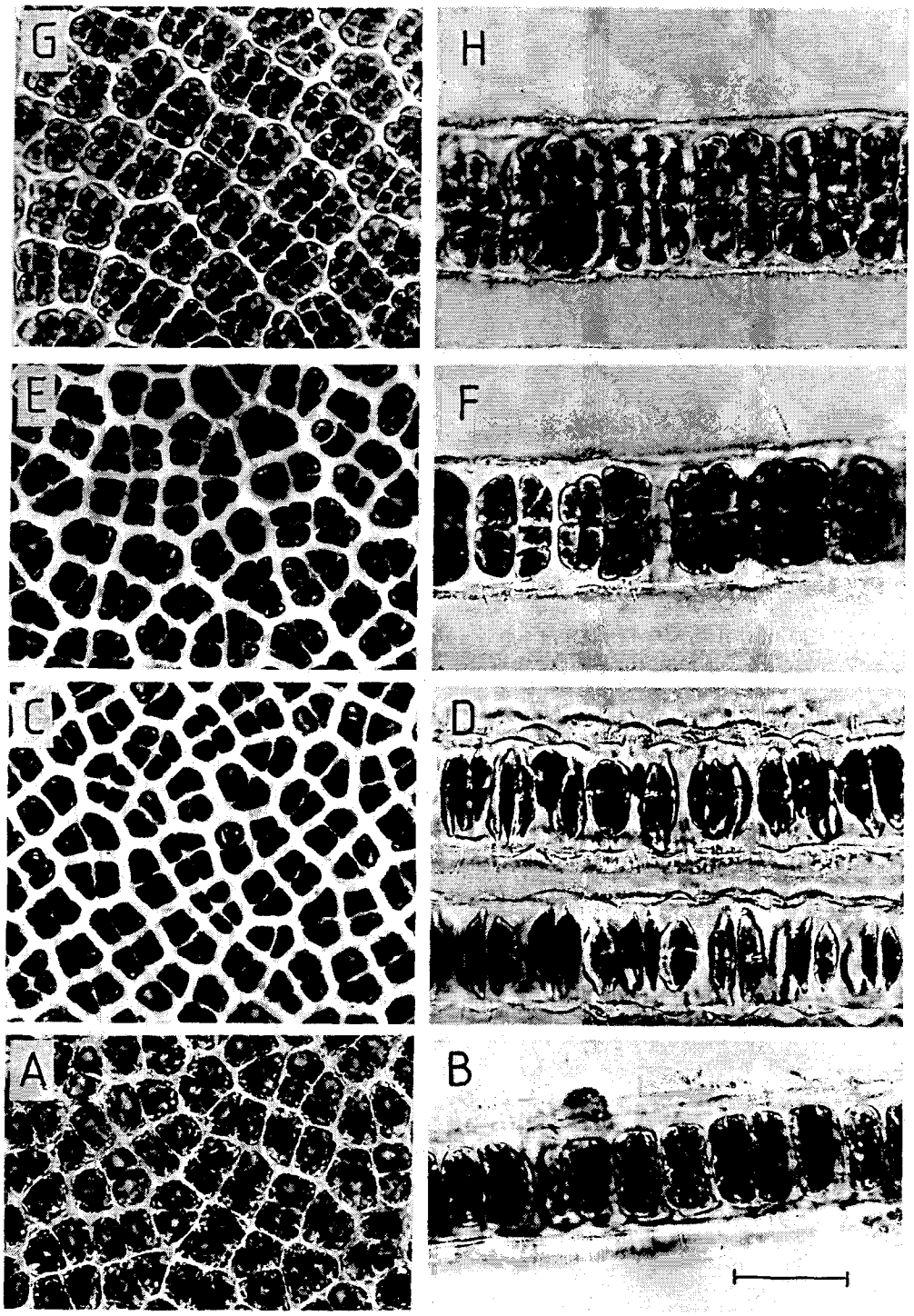


Fig. 6. *Porphyra insolita* n. sp. Senescent thallus, living cells bordering on dead tissue. A, B: Formation of aplanosporangia. C: Vegetative thallus. D: Thallus with aplanosporangia. Scale: 50 µm

sporangia to be either a compact layer (Fig. 7G) or to be in groups or singly placed between vegetative cells or young sporangia (Fig. 8A). These two variants will be described more closely in the following.

The surface views and cross-sections shown in Figure 7 are taken of an approximately 3.5-cm broad piece of the marginal area. Following the vegetative thallus (Fig. 7A, B), there is a zone in which the cells show cruciate division in surface view (Fig. 7C). Sections of these parts reveal bundles of four young carpogonia at different stages of development (Fig. 7D): some are still small, undivided and elongated to trichogynes; others have formed a periclinal cell wall – certainly after having been fertilized. The surface of the thallus is bumpy as in other species. The young carposporangia run through all stages of their maturation until they are discharged at the margin of the thallus. The frond becomes thicker and the developing carpospores fill up the available space in the sporangia, until on maturity they look cylindrical in section (Fig. 7H). In

Fig. 7. *Porphyra insolita* n. sp. Ontogeny of carposporangia. A, B: Vegetative thallus. C, D: Formation of carpogonia, showing the first cruciate periclinal cell walls. E, F: Immature carposporangia. G, H: Mature carposporangia in a compact layer at the margin of the thallus. Scale: 50 µm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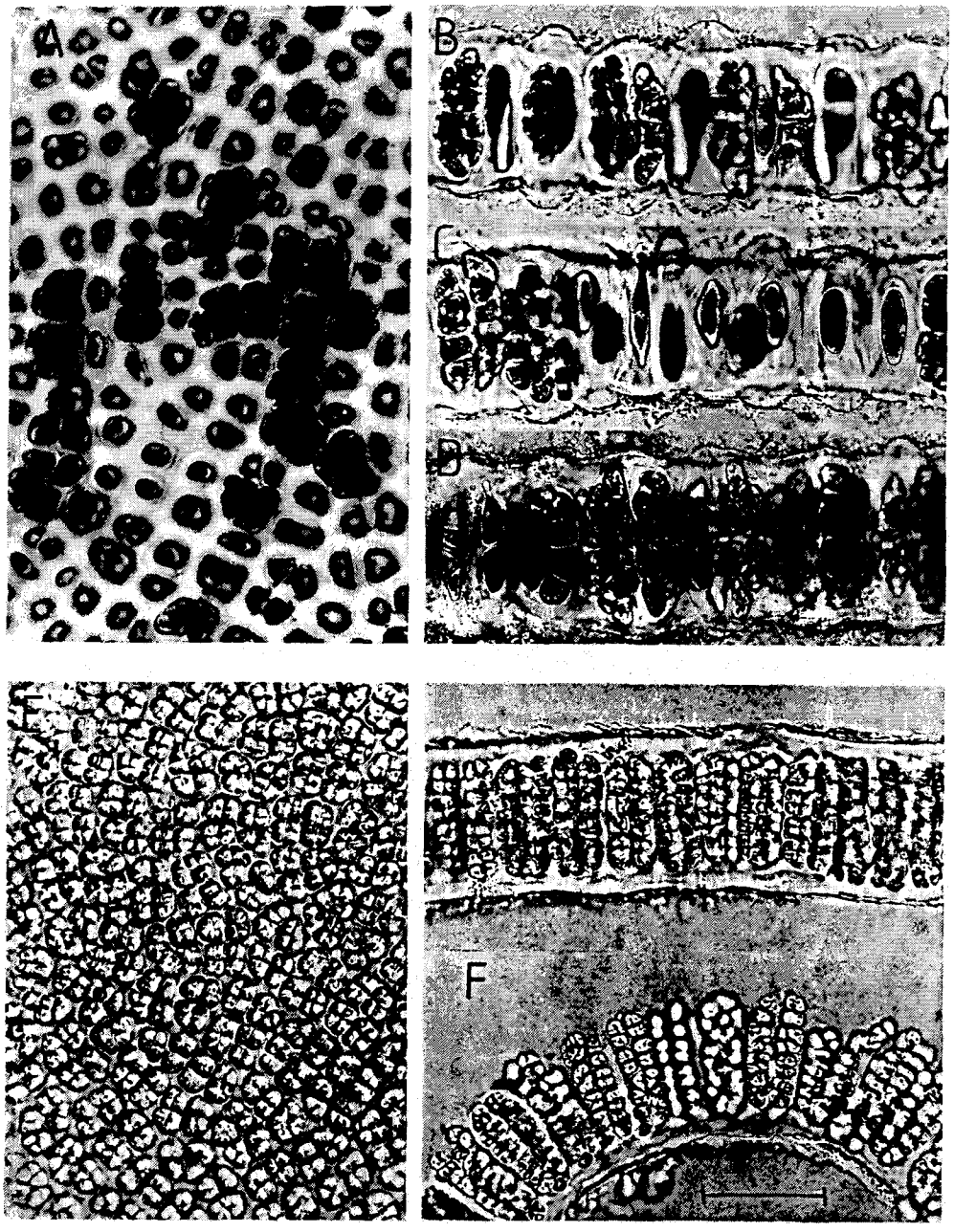


Fig. 8. *Porphyra insolita* n. sp. A: Surface view of thallus margin with interspersed carposporangia. B–D: Cross-sections through such a margin with undivided cells, carpogonia and carposporangia at all developmental stages. E–F: Thallus with spermatangia; surface view and cross-section. Scale: 50 μm

surface view they make their appearance as packets of eight spores (Fig. 7G). Without knowledge of the manner of their origin, one could regard the mature carposporangia as the result of a mother cell divided into 4 × 2 rows of spores. This was the interpretation used to characterize the carposporangium of Group 3 species.

In Figure 8A the carposporangia are not closely packed; to the naked eye, the fertile margin appears to be dotted or spotted. In these areas, deeply pigmented carposporangia or groups of carposporangia are intermingled with vegetative cells, carpogonia and carposporangia at all stages of development (Fig. 8B–D). The released contents of such thallus fragments are very heterogeneous: carpospores of normal size are mingled with round cells up to 18 µm in diameter, obviously the protoplasts of vegetative cells or immature carpospores (Fig. 9A). Similar observations were made in other species, e.g. in *P. laciniata* (Fig. 14H). Only the carpospores are able to germinate.

The male thallus of *Porphyra insolita* shows no special features. The spermatangia contain rows of 8 spermatia (Fig. 8E, F).

Life history

The carpospores are 5–7 µm in diameter; they are often mixed together with larger spheres that lack contents. These spheres originating from vegetative cells or immature sporangia perish (Fig. 9A). Nine-day old germlings are thin, coiled threads; they grow quickly to form densely curled tufts (Fig. 9B, C). After 24 days, they may already bear, in single cases, conchosporangial filaments, and after 45 days the tufts are covered with numerous dense clusters of conchosporangia. In 9- to 11-week old cultures, conchospores and germlings are found below these tufts on the bottom of the dish (Fig. 9E, F). The conchospores are only slightly larger than the carpospores. They germinate in high numbers, developing quickly into *Porphyra* plants (Fig. 9G).

The complete life cycle of *Porphyra insolita* can take place at 15 °C; this fact must be expressly indicated. The 14-h light period favours growth and fertilization of the Conchocelis thalli, but it obviously hinders the maturing process. Conchospores were found only below thick tufts on the bottom of the dish. The transfer of fertile cultures to 5 °C soon leads, after very few days, to the liberation of conchospores. Daylength is insignificant for their maturity; they also developed in darkness. The above mentioned observations motivated us to carry out such experiments.

In the two temperature regimes, the conchospores germinated readily. They broaden only slowly from their basal fixation, thus determining the primary form of the thalli in the natural habitat.

The following generations

This is a brief paragraph on observations made more by chance than according to plan on old, not regularly renewed, cultures. At a temperature of 15 °C, the thalli grew very slowly; after some months, however, they extended up to 7 cm in length and finally became fertile. Thalli arising from aplanospores abundantly reproduced in the same way. Some thalli that had grown from conchospores produced spermatangia at first, but some time later single tufts of Conchocelis grew on the frizzly margins. They originated presumably from the few scattered groups of dark red cells in the male thallus. Apparently, gametophytes are linked by means of the heteromorphus life cycle. The relationship between the isomorphic asexual and sexual Group 3 plants remains an open question.

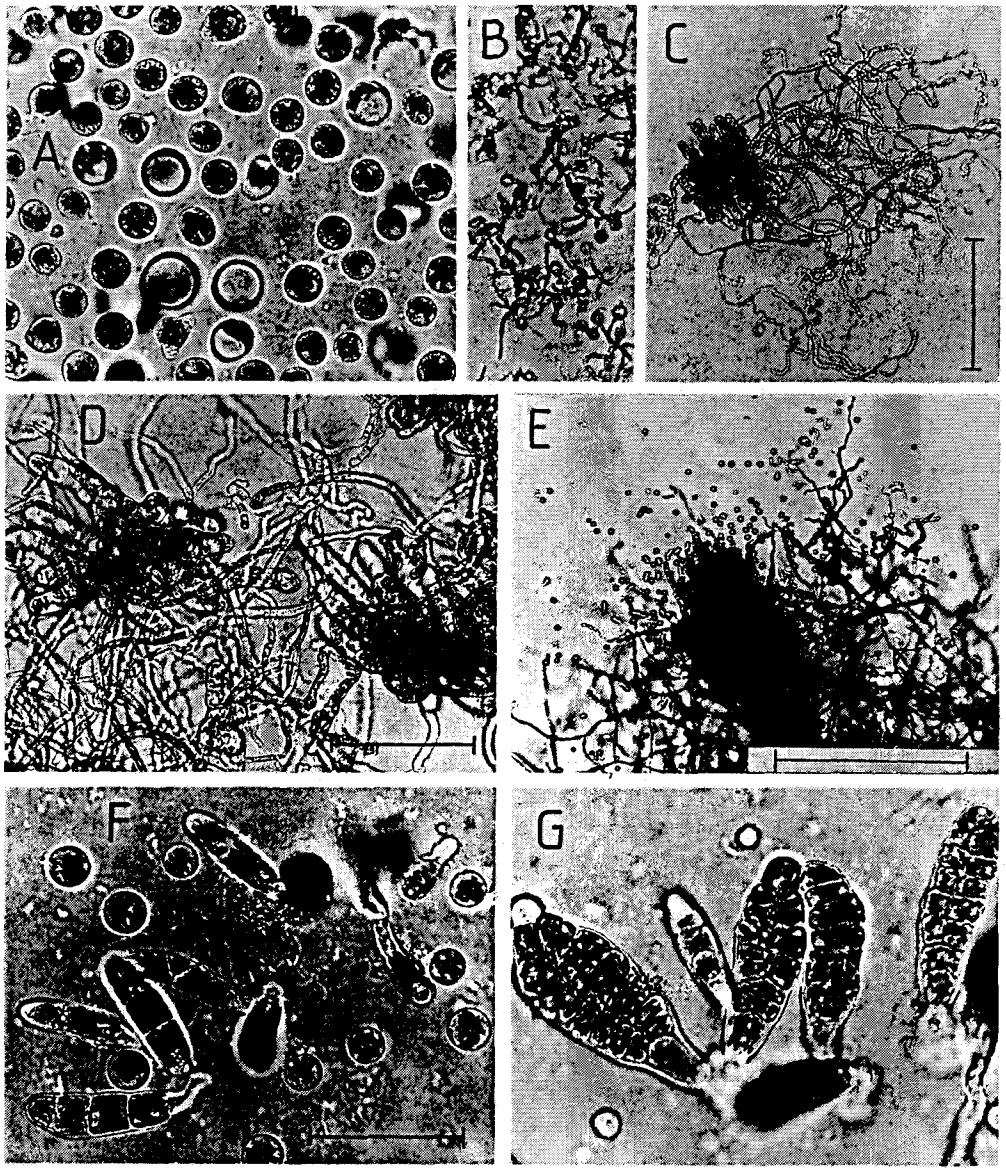


Fig. 9. *Porphyra insolita* n. sp. Ontogeny. A: Carpospores together with larger cell balls composed of immature sporangia or vegetative cells; cf. Figure 8 A–D. B: Germlings, 9 days old. C, D: Thin, filamentous, somewhat curly Conchocelis with clusters of conchosporangia, 7 weeks old. E: 11-week old culture with conchosporangia matured at 15 °C. F: Conchospores and germlings. G: Germlings from Figure 9F (bottom, left-hand corner) 4 days later. Scale: A, F, G: 50 μm; B, C: 200 μm; D: 100 μm; E: 500 μm

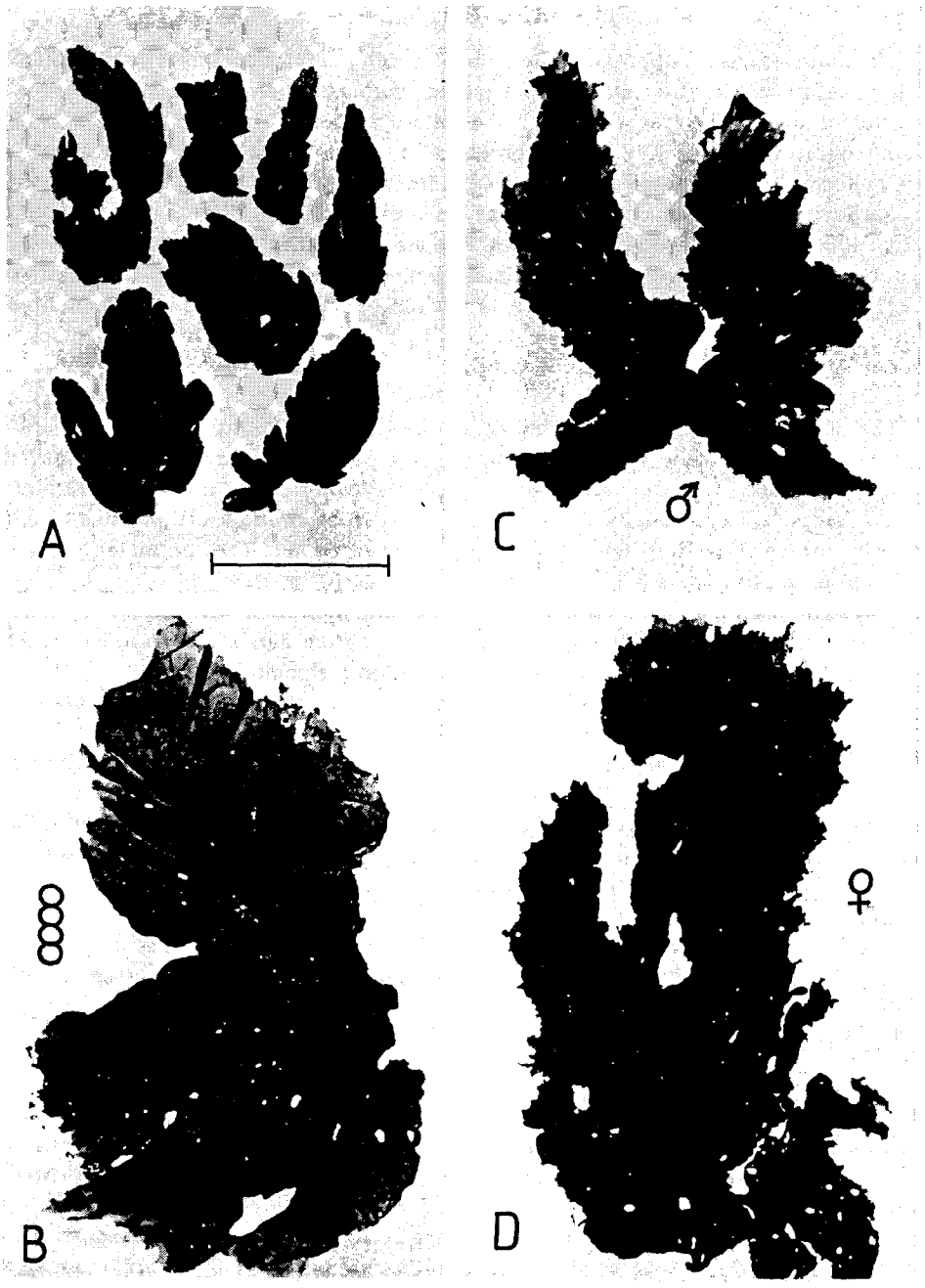


Fig. 10. *Porphyra insolita* n. sp. Exsiccates selected for species description. A: Young plants with aplanosporangia; collected 6th March 1989. B: Asexual plant and C, D: Sexual plants; outer landing-stage of the NO-harbour, 3rd June 1988. Scale: 10 cm

Description of species: *Porphyra insolita* nov. sp.

The monostromatic, approximately 50 to 65 (−80) µm thick thallus is deep brownish red to violet in colour. The cells contain a stellate chromatophore. The irregular shape of the adult thalli can be traced back to the long-oval, hardly split or slightly laciniate juvenile plants (Fig. 10A). The base is cordate. All herbarium samples shown in Figure 10 were collected in a sheltered habitat near the former landing-stage of the northeastern harbour facing the Biologische Anstalt. The small plants (Fig. 10A) were collected on 6th March, 1989; they produced aplanospores. The asexual plant (Fig. 10B) was collected on 3rd June, 1988 together with male and female gametophytes (Fig. 10C, D). Thalli from the opposite side of this harbour basin were, at this time, up to 90 cm long and 25 cm broad. In the same locality, senescent thalli colonized by the barnacle *Elminius modestus* were found in August 1989. In a very exposed locality, on the protective wall on the southwestern coast of the island, plants collected on 2nd June, 1990 were only about 15–20 cm long.

The species comprises isomorphic sexual and asexual thalli; their genetic link is unknown. In surface view, the aplanosporangia are packets of four spores, in transverse section arranged in four tiers. The aplanospores develop directly into *Porphyra* plants. The gametophytes are usually dioecious. Mature carposporangia are packets of eight spores in surface view; they develop from fertilized carpogonia. The spermatangia divide according to the formula $4 \times 4 \times 8$.

Porphyra insolita grows on firm substrate, forming a girdle in the mid-eulittoral zone below *P. umbilicalis*. Numerous exsiccates collected from January to August are preserved in the herbarium of the Biologische Anstalt on Helgoland.

Latin diagnosis: Frons membranacea, monostromatica, plantae iuvenes ovali-oblongae, adultae irregulariter expansae rotundatae-laceratae, ad basin cordatae, colore obscuro brunneorubra-violaceo. Thallus 50–65(−80) µm crassus, cellula singuliter praedita chromatophoro stellato. Plantae habitudinis isomorphae aut asexualiter aut sexualiter propagantur, quarum incognitus est modus coniunctionis. Sporae in aplanosporangio 16, modis divisionis 2:2:4. Gametophytae fere dioeciae. Carposporangiae maturae a viso superficiali octopartitae. Spermatangia 128 spermatia formantia, modus divisionis secundum formulam 4:4:8.

Habitat: In substrato firmo in parte media zonae litoralis Januario ad Sextilem.

Type locality: Helgoland, inner walls of the NO-harbour in front of the Biologische Anstalt Helgoland, coll. 3.VI.1988. P.-H. Sahling.

Type: Deposited at the Herbarium of the Biologische Anstalt Helgoland.

Porphyra ochotensis Nagai

This *Porphyra* species which was first observed in 1959 at Helgoland and was still unnamed in our „Algenflora" (Kornmann & Sahling 1977, p. 270), has in the meantime become completely familiar at the island. As it could not be identified with any of the species known from the European shores, it was compared with species reported from Japan. An indication in this direction was also the finding of small *Porphyra* plants that were recognized as *P. yezoensis* after laboratory cultivation (Kornmann, 1986).

Porphyra ochotensis was described by Nagai (1941) as being an independent species, after Ueda (1932a) had erroneously considered it to be *P. perforata* J. Ag. Wynne (1972) was able to compare the two species at Amchitka Island. This Aleutian island is

situated within two distribution areas: *P. ochotensis* has spread eastwards from Sachalin and the Kuril islands. The North American *P. perforata* has spread westwards, but has not reached the Asian coast. It is remarkable that both *P. ochotensis* and *P. purpureo-violacea* occur at Amchitka Island as well as at Helgoland.

In the thorough description by Nagai (1941), the thalli of *Porphyra ochotensis* are reported to be usually 20–70 cm long and 10–40 cm wide. The largest specimen was 115 cm long and 50 cm wide. The thallus thickness is 60–100 µm. The colour is reddish purple; older samples may be olive-brown. Plants are generally dioecious, and become fertile at the margins.

Actually, an identification of the alga was only possible by referring to the systematic study of the 21 monostromatic *Porphyra* species by Kurogi (1972). In this review, external morphological features are combined with the structure of the fertile thallus. *Porphyra ochotensis* is one of the few species whose carposporangia display packets of 8 spores in surface view. This was decisive for the identification of our Helgoland species with the Japanese plant.

Neither Nagai's illustrations (1941, Pl. IV, Figs 3–8) nor those of Tanaka (1952, Fig. 22) contribute much to the characterizing of this alga. The essential feature described in the text, the division of the carposporangia in 2×4 spores in surface view, is not clearly expressed in the drawings by the two authors. With regard to the pattern of their division and the vertical four-rows, the drawings of the sporangia could be interpreted as representing aplanosporangia. A statement in Nagai's paper could also be interpreted as confirming this (Nagai, 1941, p. 146): "In the Kurile specimens, it is not rare that carpospores are found which have not yet completed the final parallel (to each other) and perpendicular divisions. In this case, the carpospores count 16 in number." A critical evaluation of the incorporation of our Helgoland alga to *Porphyra ochotensis* should be made by Japanese colleagues carrying out comparisons on the basis of authentic material.

Since the 'double nature' of 3 other Group 3 species was well known to us, photographs of earlier collections of *P. ochotensis* were easily identified as asexual or female thalli. Fresh material was collected on 26th June, 1990 forming the basis for further experimental tests. This material contained one asexual thallus among many dioecious plants.

Direct development

The photographs of Figure 11 need hardly be commented on. The aplanospores are discharged from the edge of the thallus. The transverse sections illustrate Nagai's observations on the plants from the Kuril islands, whose sporangia he considered to be incompletely split (see above quotation). At a very early stage, the germlings became roundish. 10-week old thalli were 2–3 mm large and were similar to adult plants in their broad form and cordate basis.

The female thallus

The carposporangia develop in a similar manner to that observed in comparable species of Group 3; this is illustrated in Figure 12 by a series of surface views and transverse sections. At some distance from the margin, the mother cells of the carpogonia undergo cruciate division by forming anticlinal cell walls. The units of 4 carpogonia with trichogynes at both ends that have developed in this way (Fig. 12A, B) are vaulted by bumps. The surface view of mature carposporangia presents the appearance of 2×4

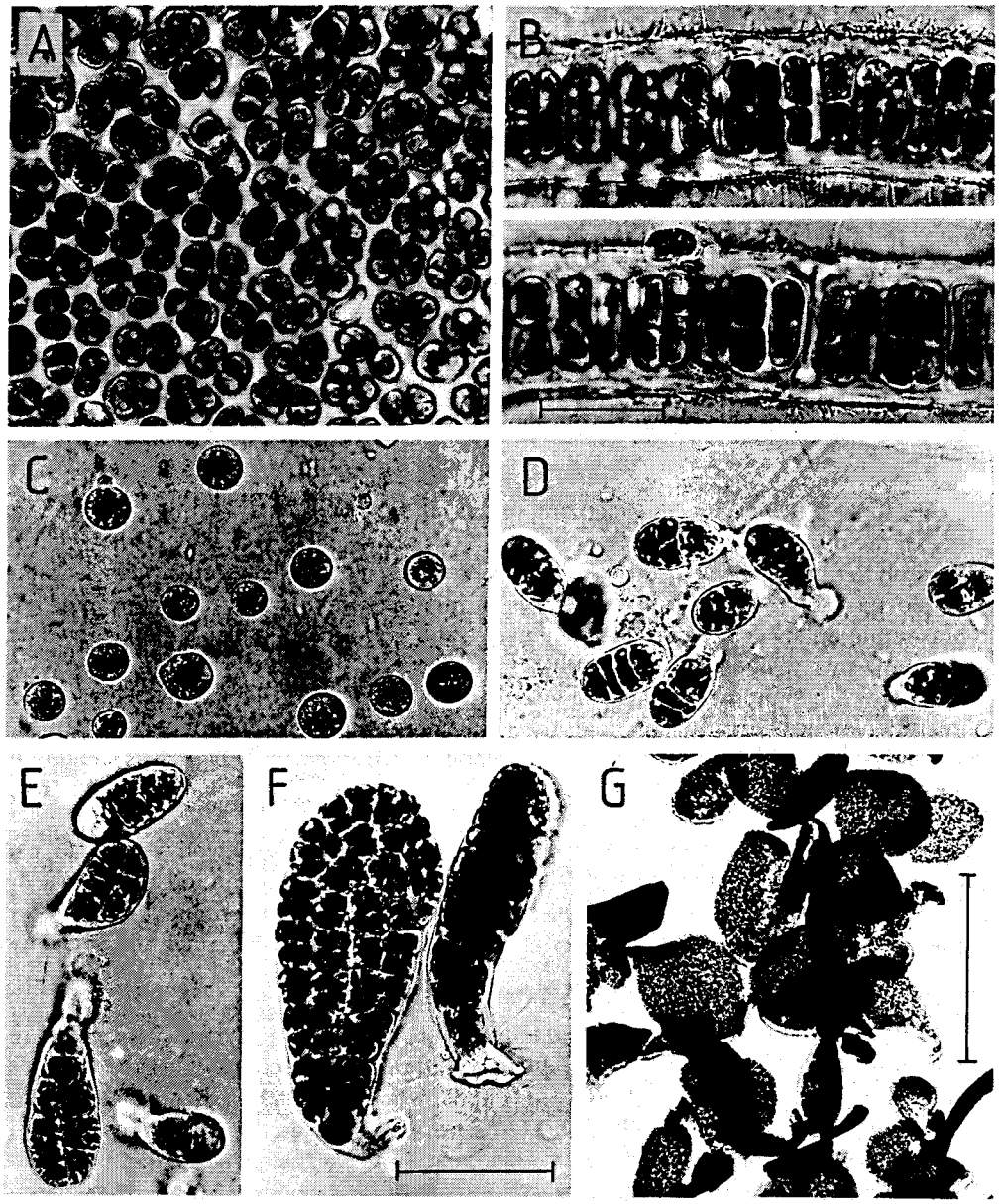
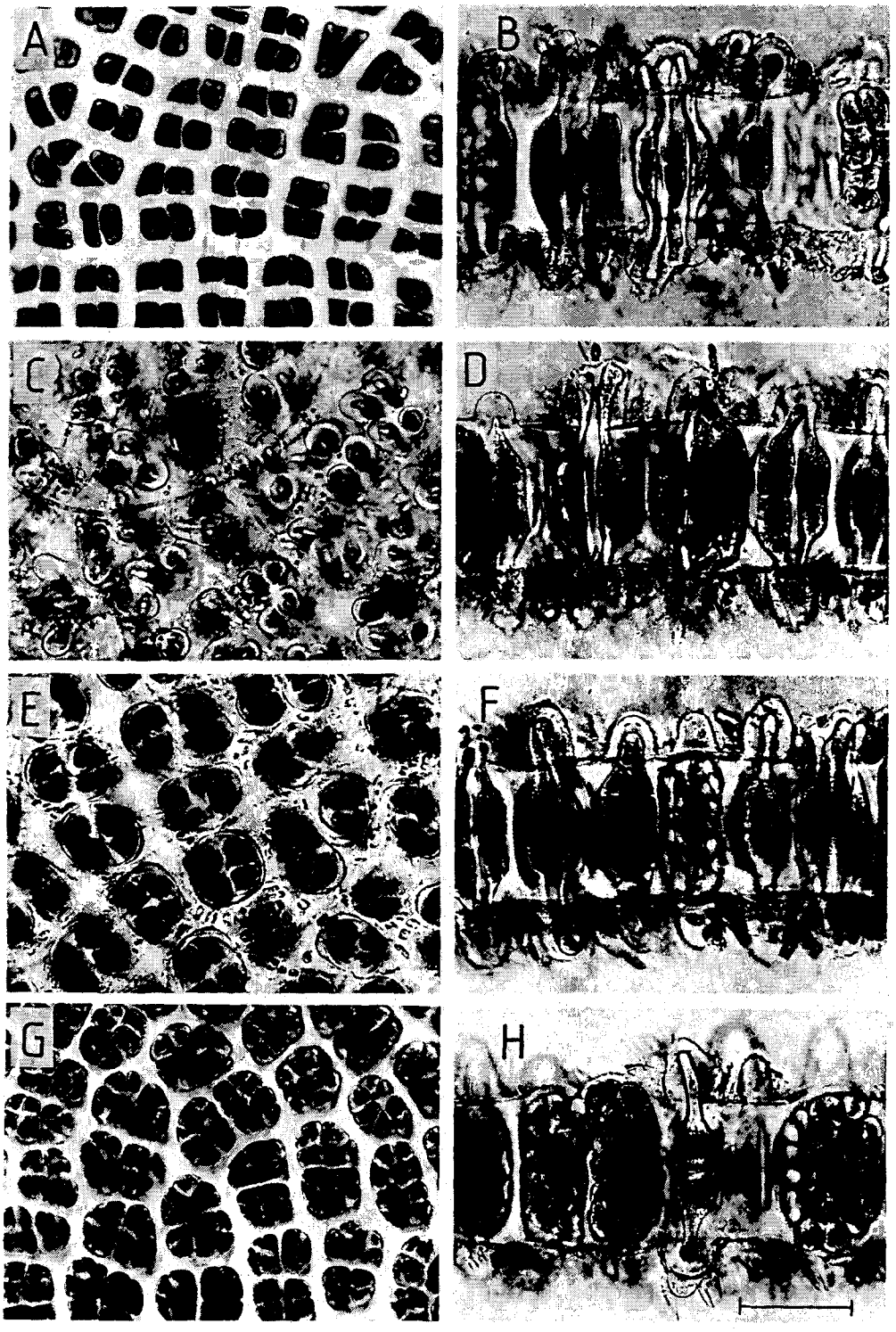


Fig. 11. *Porphyra ochotensis.* A, B: Thallus with aplanosporangia. C: Aplanospores. D–F: Germlings, 5, 7 and 10 days old. G: 24-day old thalli. Scale: A–F: 50 μm; G: 500 μm

Fig. 12. *Porphyra ochotensis.* Female thallus; formation of carposporangia. A, B: Mother cells of carpogonia divided by anticlinal cell walls. C: Ends of trichogynes clearly visible at high focus. D: carpogonia and young carposporangia. E, F: Immature carposporangia. G: Surface view of thallus margin with mature carposporangia in a compact layer. H: Mature carposporangia with interspersed younger developmental stages. Scale: 50 μm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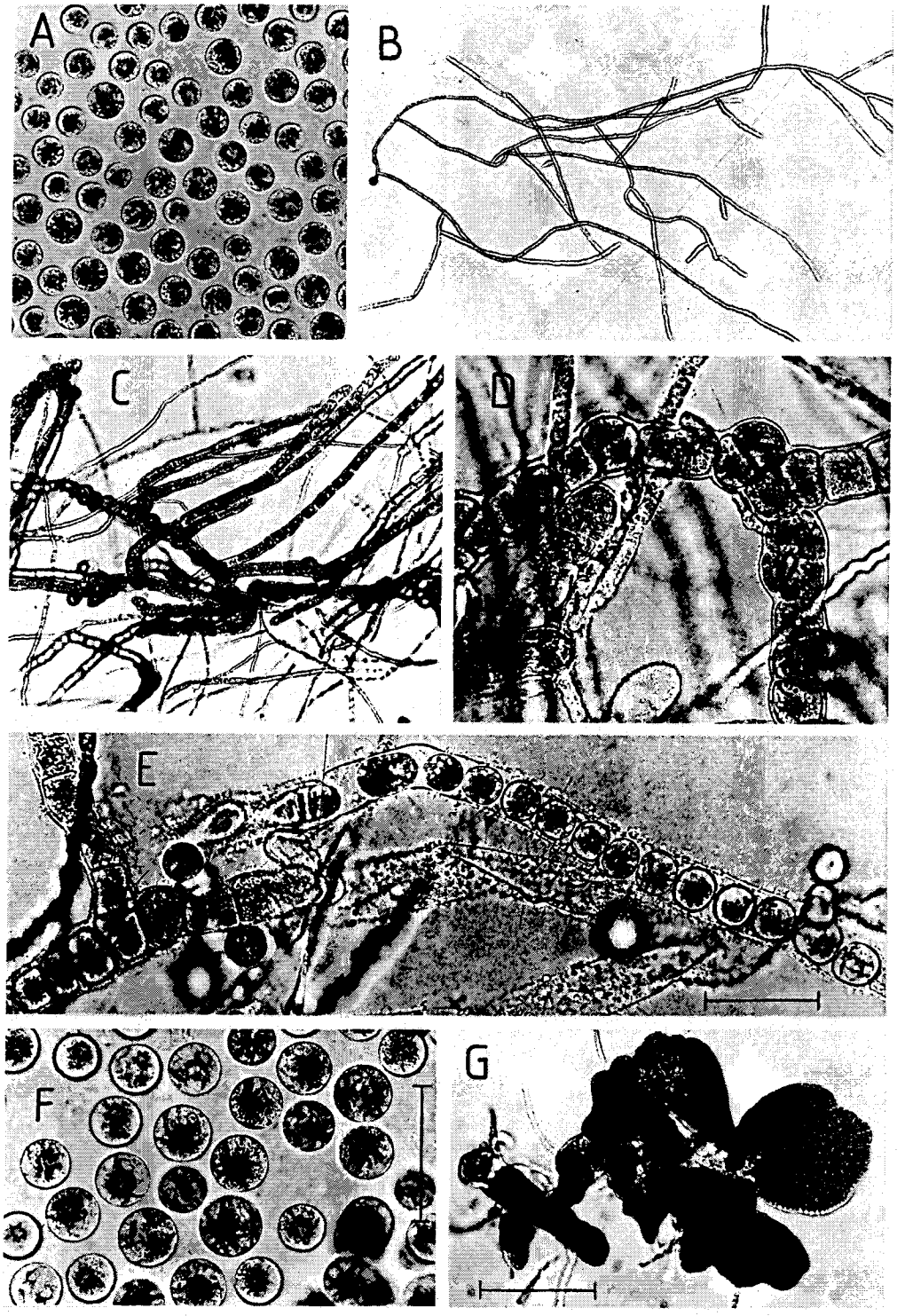
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spores (Fig. 12 G). The carposporangia are filled to capacity with carpospores. This becomes clear, especially when vegetative cells or young carpogonia are scattered among the mature sporangia (Fig. 12H). The difference between carpasporangia and aplanosporangia is evident.

The heteromorphous cycle

The Conchocelis filaments of *P. ochotensis* which develop from carpospores are thicker than in all the other Helgoland species (Fig. 13A, B). When cultivated at a temperature of 15 °C, the sporogenous filaments grow very long (Fig. 13C, D). Conchospores did not develop until cultures were transferred to 5 °C. Figure 13E illustrates the sucessful development 25 days later on. The mature conchospores lie like a string of pearls in the fertile filaments; some of the tubes had already been discharged. Conchospores, 18–20 µm in diameter, are essentially thicker than carpospores (Fig. 13F). Only occasionally could *Porphyra* thalli – usually roundish in shape – be cultivated from conchospores (Fig. 13G).

Porphyra laciniata C. Ag.

Preliminary remarks

For practical purposes, the results taken from the literature already published on *Porphyra laciniata* C. Ag. will be discussed here first before our own observations are described. Krishnamurthy (1959), using cytological methods, investigated similar material to that on which Drew (1954) based her classical studies. The 'spores' – at that time only spores and spermatia were discriminated – developed by regular divisions of one cell of the thallus. A fertilization of free spores was neither observed in the experiment nor in the caryological investigations. The spores developed into Conchocelis. Krishnamurthy found 5 chromosomes in the vegetative cells, in the spores and in the Conchocelis cells.

Giraud & Magne (1968) investigated *Porphyra umbilicalis* (L.) J. Ag. var. *laciniata* (Lightf.) Thuret from Roscoff. They determined 4 chromosomes in the vegetative cells and in the spermatia, but 8 chromosomes in the developing carposporangium and in the Conchocelis cells. Meiosis occurred in the formation of conchospores. Kito et al. (1971) achieved the same results with *P. umbilicalis* (L.) J. Ag. from Nova Scotia.

The heteromorphous life cycle of *Porphyra* species may thus be monophasic or biphasic. Our investigations of *P. laciniata* show however that both cycles may be met with in one species. These seemingly contradictory results are explained by the fact that *P. laciniata* and *P. umbilicalis* include asexual as well as sexual thalli. However, the asexual spores of *P. laciniata* do not develop into *Porphyra*, but give rise to a haploid Conchocelis generation. Neither Drew nor Krishnamurthy recognized the asexual nature of their investigated material. Female thalli perhaps were rare (compare the following paragraph).

Fig. 13. *Porphyra ochotensis*. Ontogeny. A: Carpospores. B: Conchocelis, 26 days old. C, D: Fertile Conchocelis at 15 °C, 130 days old. E: Same culture but transferred to 5 °C on day 105; mature and released conchosporangia. F: Conchospores. G: Young thalli derived from conchospores, 43 days old. Scale: A, D–F: 50 µm; B, C, G: 200 µm

Drew (1955, p. 6) missed the chance to clarify the relations: 'On one occasion I found cells with protrusions of considerable size and in many instances from both sides of the cell, and with genuine spermatia adhering to them. Observation of these cells over some hours produced no evidence of the establishment of any open connection between these cells and the spermatia, however.' This important observation remained unnoticed not only by Krishnamurthy and, thus, nearly 40 years passed until the life cycle of *Porphyra laciniata* was clarified.

The asexual cycle

Porphyra laciniata thalli were collected from a uniform population in the lower eulittoral zone on 29th March, 1990, after many investigations conducted during the course of 1989. Most of the plants were male. The others were different with regard to their fertility: some thalli released large quantities of brown-red spores. Only a few plants with reddish thallus margins were female. Cultures of both spore types were set up.

The structure of the thalli which released numerous brown-red spores is shown in Figure 14. The surface view mostly shows groups of four, more seldom of two cells, in quite regular arrangement (Fig. 14A). They are the products of simple or cruciate division of the mother cells. The transverse section shows two rows with four spores (Fig. 14B). The cylindrical mature sporangia generally contain $2 \times 2 \times 4 = 16$ spores, which is in accordance with the observations of Krishnamurthy (1959, Figs 45–60). The illustrations of Thuret & Bornet (Kylin, 1956, Fig. B–D) also clearly describe the asexual form of *Porphyra laciniata*.

A skeleton of the vertical walls of the sporangia remains after spontaneous spore release (Fig. 14C). The spores are obviously released by disintegration of the surface cuticle. A corresponding observation was described for *Porphyra insolita* where a transparent 'skin' remains after discharge of the aplanosporangia. After discharge of carposporangia, however, there are generally no recognizable remnants of the cell skeleton left.

The asexual spores developed into a Conchocelis generation as described by Krishnamurthy (Fig. 14E, F). Fertile branches developed at 15 °C within 7 weeks, but like Krishnamurthy's cultures they did not release conchospores. Transferred to 5 °C, the conchosporangia released numerous thick conchospores (Fig. 14G, H). Only a few spores germinated at this low temperature, but they did not develop further.

The sexual cycle

Plants with a distinct red margin were female and thereby easily distinguished from asexual thalli. The surface view of mature carposporangia shows packets of 2×4 spores (Fig. 15A). In younger stages, 2 or 4 sister cells are vaulted by bumps as can be seen at high focus. The trichogynes protrude to just below the surface of the bumps (Fig. 15C, D). The corresponding transverse sections complete the picture of the structure of the fertile thallus. Four sisters cells are bundled together in one developing carposporangium (Fig. 15E–G). Further development is analogous to that of *Porphyra insolita*. The investi-

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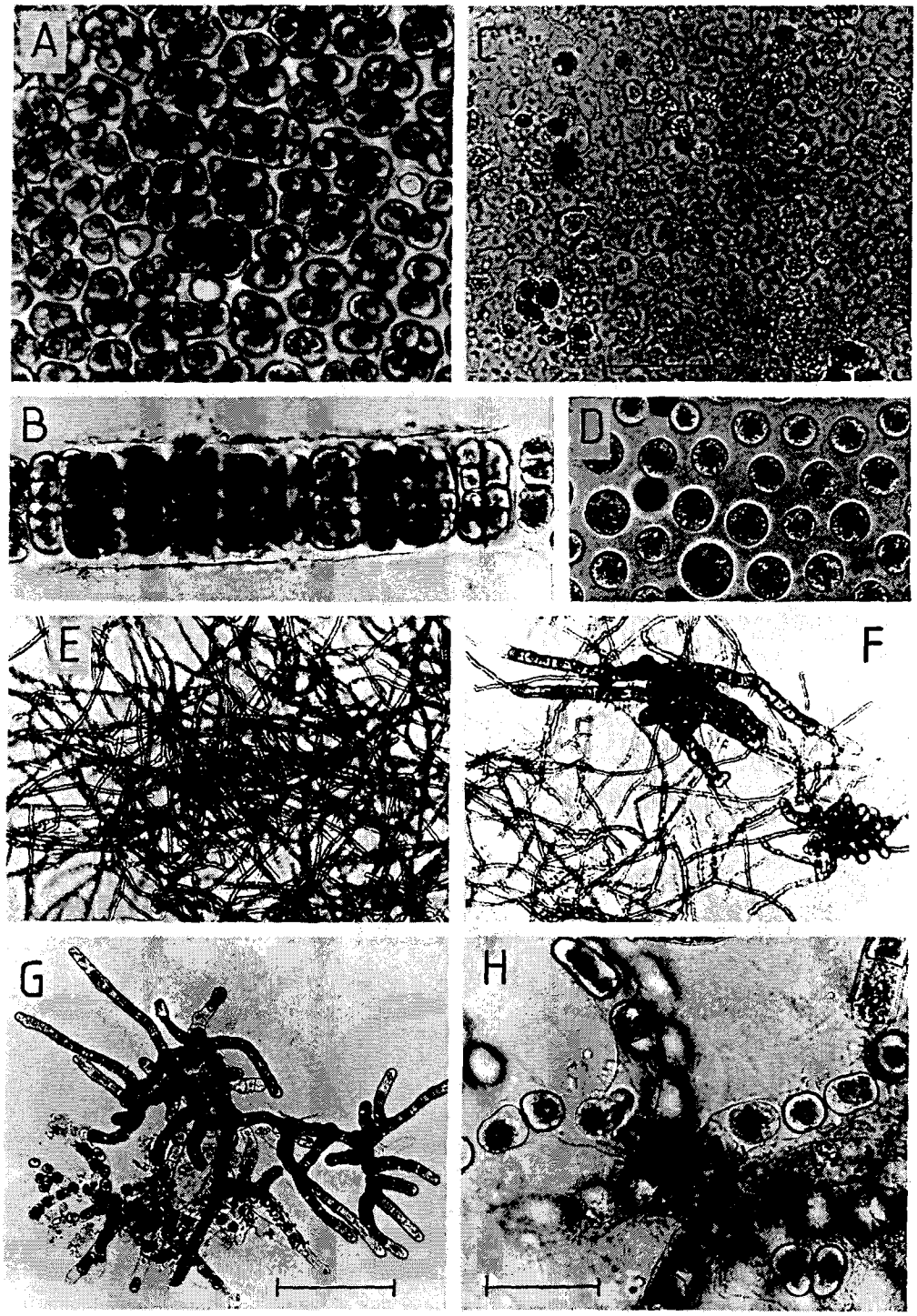
Fig. 14. *Porphyra laciniata*. Monophasic development. A, B: Mature thallus with asexual sporangia. C: Membrane left over after release of spores. D–F: Asexual spores that develop into fertile Conchocelis after 8 weeks at 15 °C. G, H: Mature conchosporangia after transfer of culture to 5 °C. Scale: A, B, D, H: 50 μm; C: 100 μm; E–G: 200 μm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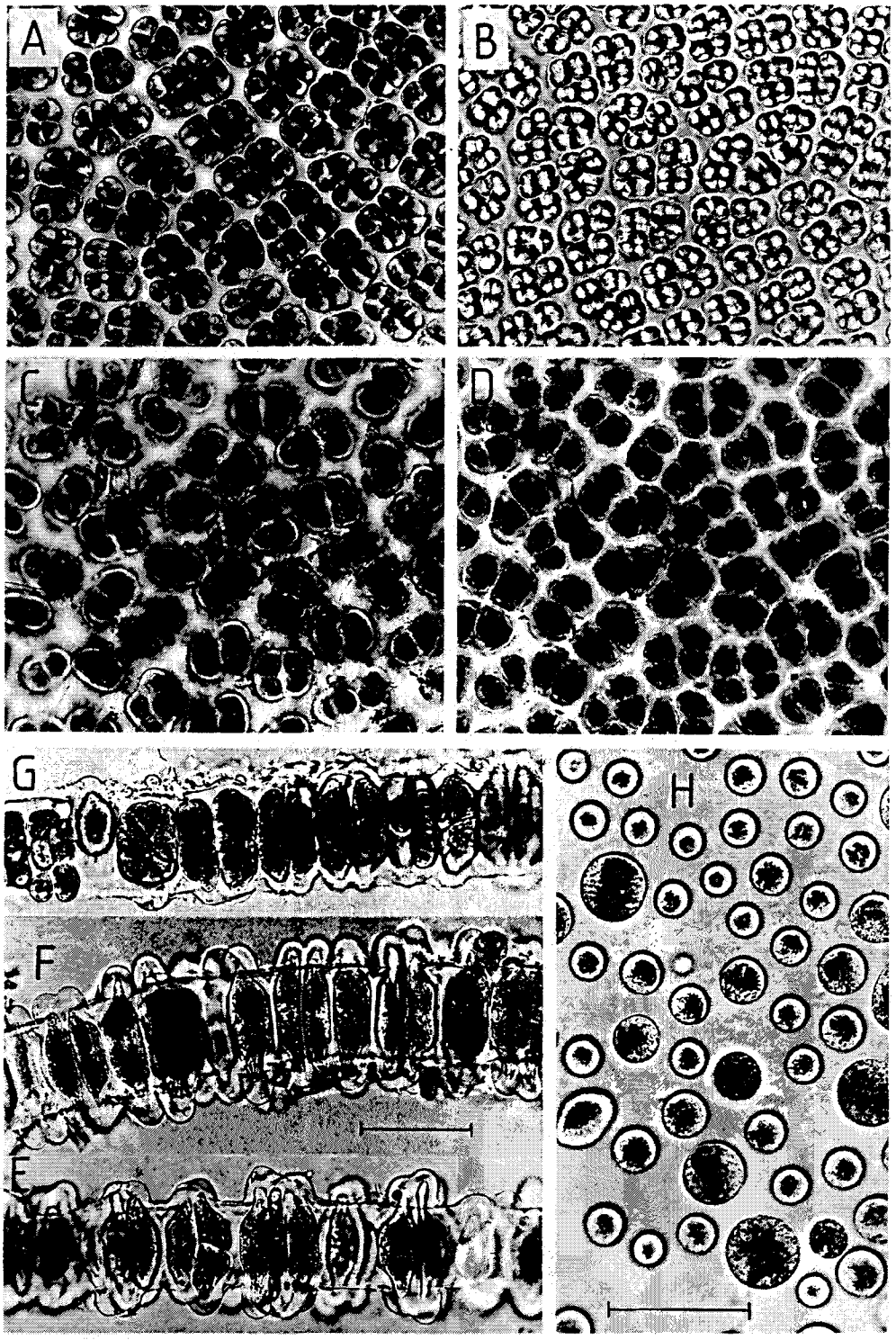

Fig. 15. *Porphyra laciniata*. Sexual plants. A, B: Surface view of mature female and male thallus. C, D: Immature carposporangia at different focus; ends of trichogynes visible in C. E–G: Cross-sections showing carposporangia of different ages; mature carposporangia in Fig. 15G on left hand side. H: Carpospores together with cell balls composed of vegetative cells or immature carposporangia. Scale: 50 μm

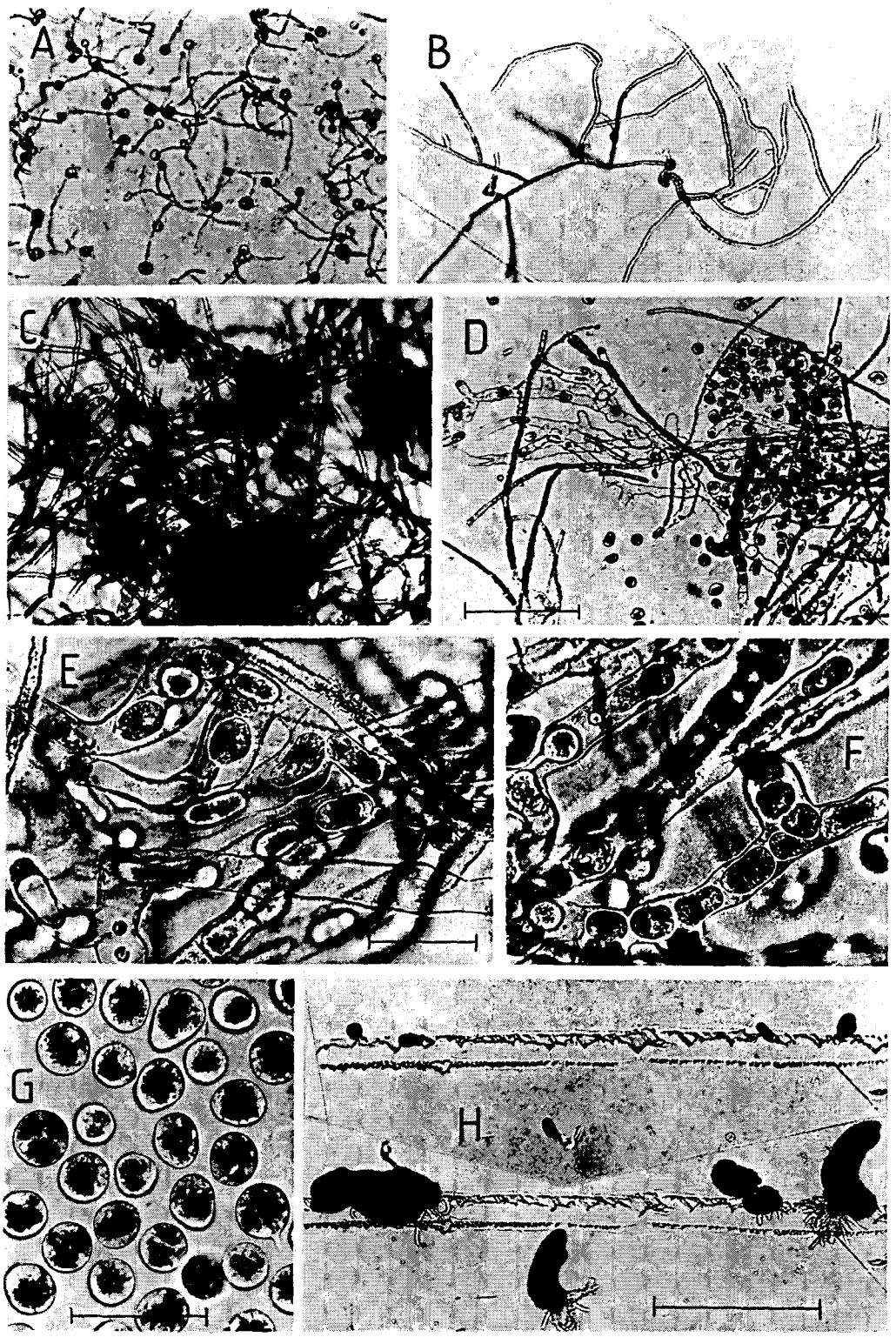

Fig. 16. *Porphyra laciniata*. Biphasic development. A, B: Conchocelis derived from carpospores, 12 and 21 days old. C: Fertile Conchocelis at 15 °C, 59 days old. D–F: Conchosporangia releasing conchospores, 84 days old of which 9 days were at 5 °C. G: Conchospores. H: Conchospores that germinated on scratches on bottom of Petri dish; plantlets in the upper and lower part of the photograph are 8 and 19 days old, respectively. Scale: A–D: 200 µm; E–G: 50 µm; H: 500 µm

gated thallus measured only 40 µm in thickness and, thus, the carporangia contained only a small number of spores.

The carpospores are 11–14 µm in diameter but the released mass of spores often contains to a major extent balls of up to 28 µm in diameter (Fig. 15H). These obviously originate from vegetative cells or from immature sporangia that may lie interspersed in fertile areas. Like the asexual spores, the carpospores developed from relatively thick, slightly interlaced filaments (Fig. 16A, B) into tufts of Conchocelis. The first sporogenous branches were formed after about 5 weeks; two-month old filaments bore numerous small clusters of fertile branches (Fig. 16C). Cultures transferred to 5 °C became mature surprisingly fast; 9 days later, many conchospores were found on the bottom of the culture dish. The discharge of the conchospores was observed by chance under the microscope in a slide preparation (Fig. 16D–F). Within a few minutes, the spores streamed out of the tubes; when they passed through narrow parts they became slightly elongate. The conchospores left the mouth of the tube at intervals of approximately one second. The conchospores, 14–20 µm in diameter, were much thicker than the carpospores.

Even though numerous conchospores were released, they did not germinate at 5 °C and only a few germinated at 15 °C. These few spores had obviously found a suitable substrate for their development on scratches on the bottom of the culture dish (Fig. 16H). Young *Porphyra* thalli initially grew quite fast, but then remained small under the culture conditions provided.

Conclusion

The main result of our developmental study on *Porphyra laciniata* may be summarized in one sentence: Spores of asexual thalli and carpospores develop into Conchocelis generations which cannot be distinguished morphologically. Krishnamurthy (1959) stated the monophasic cycle with five chromosomes for the asexual thallus. Perhaps a caryological result is also known for the biphasic cycle. Kito et al. (1971) investigated *P. purpurea* (Roth) C. Ag. from western Ireland, synonymously specified as *P. umbilicalis* var. *laciniata*. They found 5 chromosomes at the formation of spermatia and 10 in the developing carposporangium. This result could complement the study of Krishnamurthy (1959). The identity of the investigated material is, however, not completely certain. A confusion with the erroneously synonymized *P. purpureo-violacea* cannot be excluded.

Porphyra linearis Grev.

Our observations on *Porphyra linearis* can be combined with observations by Bird et al. (1972) on material from Nova Scotia. The results of their culture experiments were not uniform. In most experiments the complete life cycle could be followed five times while other cultures only formed Conchocelis whose sporangia did not release conchospores.

A critical assessment of these different results is not possible without knowledge of the structure of the studied material. The supposition is that the basis material was not uniform, but contained thalli with carposporangia and thalli with asexual sporangia. This supposition is not unfounded: on the one hand, Magne (1952) observed fertilization in *Porphyra linearis* and determined diploidy in carpospores; on the other hand, plants from Helgoland formed only asexual sporangia. Their spores develop into Conchocelis, similar to some of the above mentioned Nova Scotia strains.

Porphyra linearis from Helgoland appears to be dioecious judging by the colour of

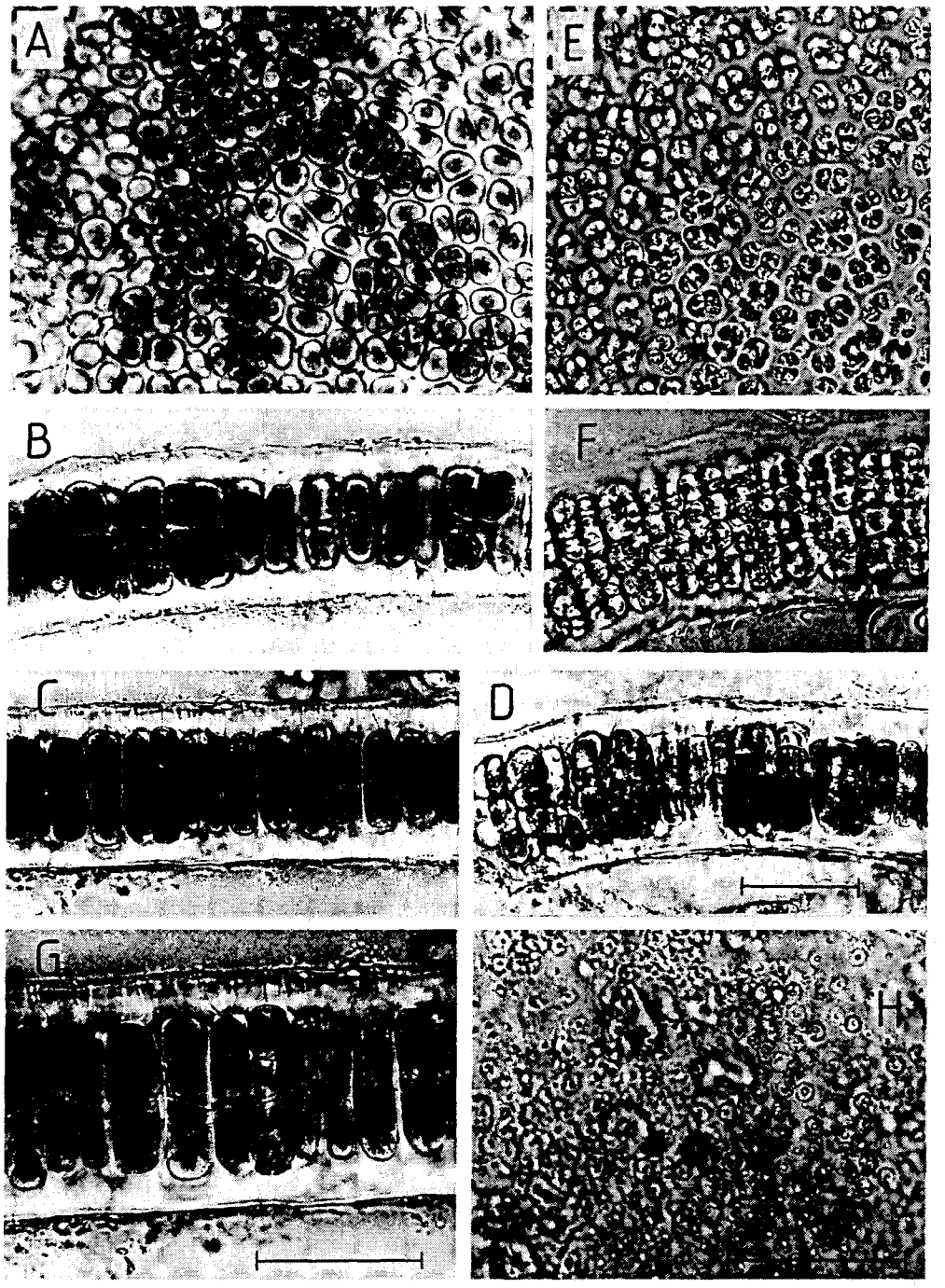

Fig. 17. *Porphyra linearis*. A–D: Thallus with asexual sporangia. E, F: Spermatangia. G, H: Thallus with distinct "fertilization tubes" ("Befruchtungskanäle"). Scale: 50 μm

the margin of fertile thalli, few individuals also being monoecious. The sporangia of a 'female' thallus are imbedded as irregular spots in vegetative tissue and are divided by anticlinal cell walls (Fig. 17A). Transverse sections show tiers of 4 spores in mature sporangia, similar to those in *P. laciniata* (Fig. 17B–D). Nothing indicates a sexual formation.

In many transverse sections, delicate stripes can be clearly distinguished that infiltrate the membrane perpendicularly to the surface. They originate from a bright nodule and in surface view look like haloed spots (Fig. 17G, H). These stripes were also observed in other species and were already known to Hus (1902). He argued that they were bacteria adhering to the surface of the thalli. They are also present in vegetative and male thalli, even if they remind one of the fertilization-tubes that were described by Berthold (1882). Rosenvinge, too, (1909, Fig. 5A–C) interpreted and illustrated them as fertilization-tubes sensu Berthold. The real nature of these stripes is unknown.

The spores of *P. linearis* quickly develop into Conchocelis with characteristics that easily distinguish it from other species. The branches grow vertically from the axis, and their short thick basal cells elongate into thin filaments (Fig. 18A). Conchosporangia

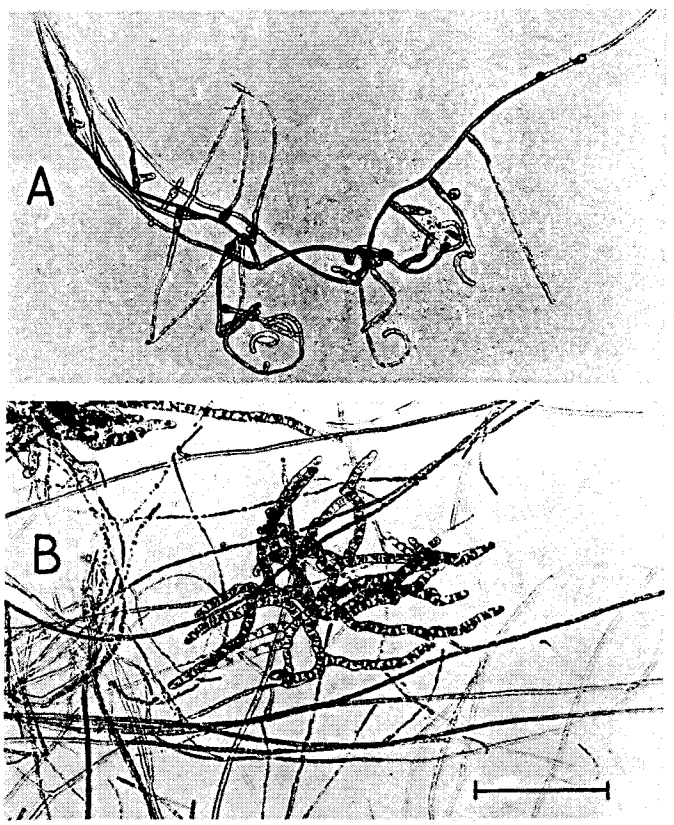

Fig. 18. *Porphyra linearis*. A: Conchocelis, 24 days old. B: Fertile Conchocelis, cultivated at 15 °C. Scale: 200 µm

formed after 4–5 weeks on the slightly entwined filaments, but spore discharge never occurred, not even at 5 °C. *Porphyra linearis* from Helgoland thus corresponds to the asexual from of *P. laciniata* in the manner of sporangia formation and in the development of its spores.

Porphyra purpureo-violacea and *P. leucosticta*

Introductory remarks

Only these two *Porphyra* species of Group 1 of our above described scheme occur at Helgoland. Their monoecious thalli are much thinner than those of the other species. It is hence not surprising that the fertile female thallus consists of only two cell layers.

Only few of all the *Porphyra* species investigated so far belong to Subgroup 1a with a biphasic cycle, for example *P. gardneri* (Hawkes, 1978). It seems sufficiently safe to place *P. leucosticta* in Subgroup 1b (see page 3). With regard to *P. purpureo-violacea* we have no observations to assign it to one of the two Subgroups.

Porphyra purpureo-violacea (Roth) Krishnamurthy

The fertile thallus is divided by a clear line into a male and a female half. Surface views of the mature female thallus reveal groups of four spores. In transverse sections, they are arranged in two layers (Fig. 19D, E). Each carposporangium therefore contains 8 carpospores, 11–14 µm in diameter. The spermatangia contain 64 spermatia in 8 tiers (Fig. 19I, K).

The carposporangia are emptied after swelling and disintegration of the cell walls near the thallus edge. The numerous released spores trace the outline of the thallus on the bottom of the dish. Very often the carpospores accumulate at the bottom of the dish forming round spots. These derive from thallus spots which look like 'eyes' and can hardly be overlooked in the fertile thalli (Fig. 19F, G). In transverse section, these look like flat lenses in the thallus (Fig. 19H). Only the extremely delicate cuticle prevents the spores from flowing out; this can occasionally be observed unter the microscope. Similar 'eyes' have been observed in other species; some can be clearly recognized, for example, in the asexual plant shown in Figure 10B.

Like the foliose thallus, the Conchocelis phase shows distinct characteristics. The relatively thick filaments are considerably coiled and only slightly branched. At the age of 4–5 weeks, the ends of the filaments grow thicker and branch profusely (Fig. 20B–D). In 9- to 10-week old cultures, the thin vegetative filaments decrease in number in comparison to the thick, sporogenous filaments with often longitudinally divided cells (Fig. 20D).

Large amounts of spores are discharged from the conchosporangia. Only few, however, germinate; the majority disappear, leaving no visible signs of their disintegration. The young thalli develop very slowly at first, until they attain a size of 8–10 mm. Transferred singly to fresh culture medium, the small plants grow in 3–4 weeks into the typical long thalli. When the culture medium is renewed often, they may reach a size of 30 cm in undisturbed culture dishes.

The thalli become fertile during this rapid increase in size; large apical parts of the thallus are transformed into spermatangia. This process takes place on one side of the

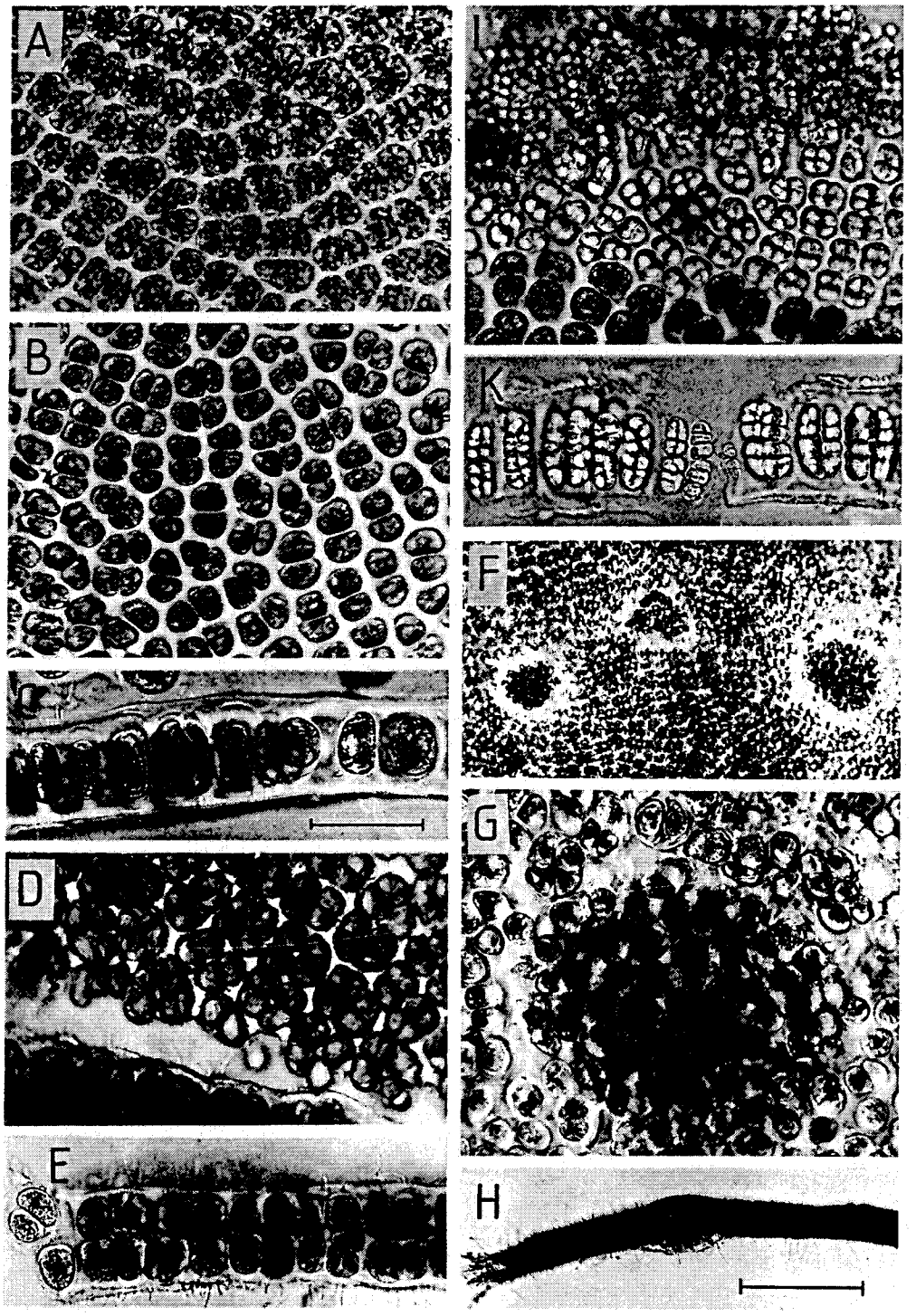

Fig. 19. *Porphyra purpureo-violacea*. A–H: Female part of thallus. A–C: Vegetative thallus; in B: cells in division. D, E: Surface view and cross-section of fertile thallus. F, G: Local release of mature carpospores. H: Cross-section through cluster of carposporangia with raised cuticula. I: Spermatangia bordering on vegetative cells. K: Spermatangia in cross-section. Scale: A–E, G, I, K: 50 μm; F, H: 200 μm

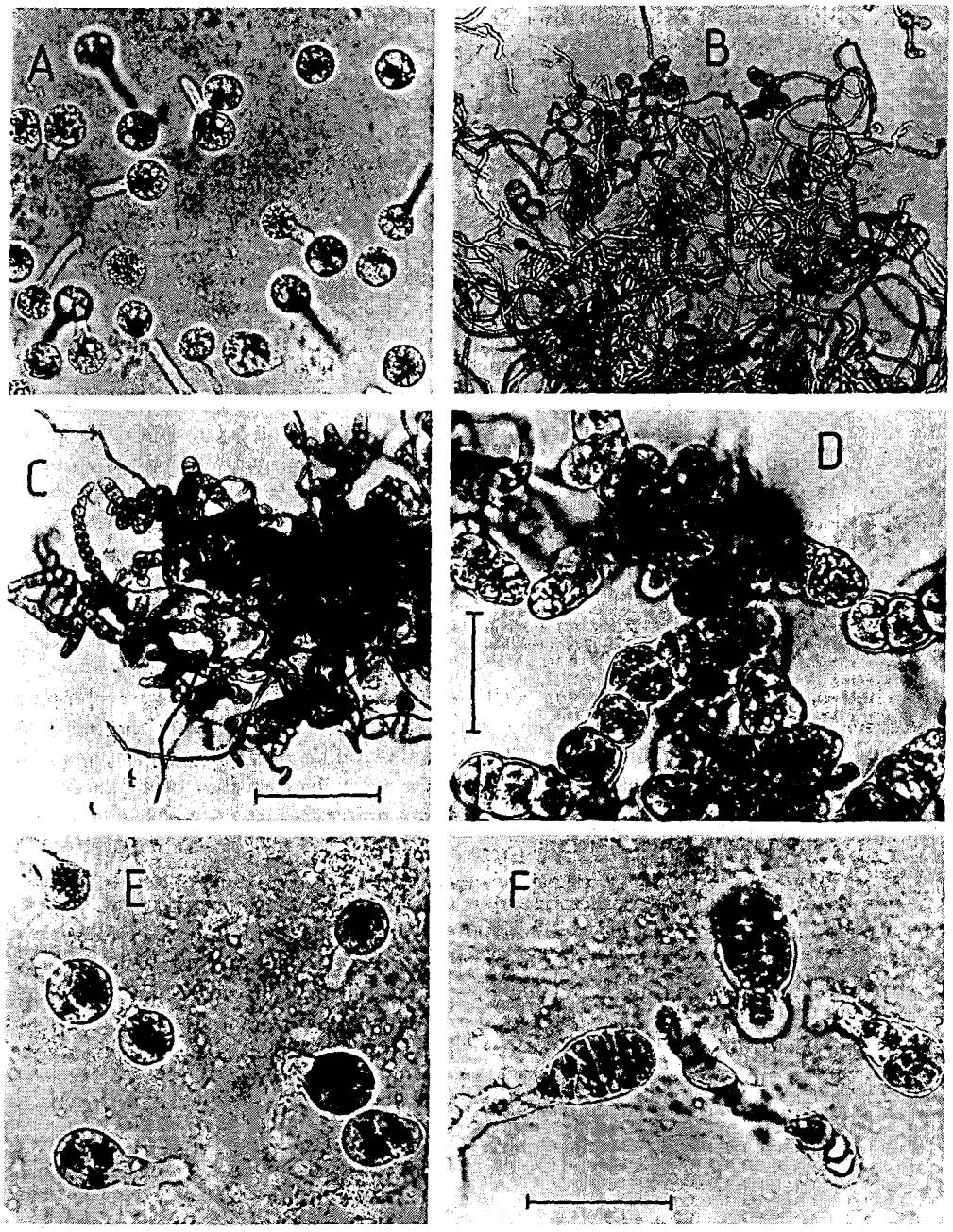

Fig. 20. *Porphyra purpureo-violacea*. Ontogeny. A: Germinating carpospores, 1-day old. B: 5-week old Conchocelis with conchosporangial branches. C, D: Mature conchosporangia. E, F: Germinating conchospores and young thalli. Scale: A, D–F: 50 µm; B, C: 200 µm

thallus only, up to a sharply delineated line marking approximately the middle of the thallus. Just as in nature proterandry takes place also in culture.

A comparable, massive formation of a female zone did not occur. Only a slight reddening near the margin of the thallus was to be seen. Single cells or smaller groups of cells were transformed into carposporangia. Carpospores were released in relatively small amounts. On the surface of the thallus, both Conchocelis filaments as well as *Porphyra* blades developed, the latter growing fast into larger thalli.

Porphyra leucosticta Thur. in Le Jol.

A detailed report exists on previous culture experiments with *Porphyra leucosticta* (Kornmann 1961a). The life history was interpreted in a scheme of development (Kornmann 1961a, Fig. 4) characterized by a foliose *Porphyra* thallus and a Conchocelis stage with the same ploidy level. This empirical result still holds true; the interpretation has in the meantime been confirmed by caryological examinations (Coll & Oliveira Filho 1977; Kapraun & Freshwater 1987). They confirmed four chromosomes in both heteromorphous generations. A similar type of development has been proved for *P. carolinensis*, where the spermatia have been recognized as rudimentary (Freshwater & Kapraun 1986).

Up till now, drawings in Berthold (1882) and Rosenvinge (1909) have been considered to illustrate stages of fertilization in *Porphyra leucosticta*, but convincing proof is lacking.

CONCLUSIONS AND FUTURE PROSPECTS

The results of the present study in combination with the evaluation of the mentioned literature have led to a completely new picture of the genus *Porphyra*. The methods described here may motivate scientists to examine other *Porphyra* populations. An essential basis for the identification of *Porphyra* species is the formation of the sporangia and the development of their spores in culture experiments.

Our observations on the Helgoland *Porphyra* species may readily be compared to the statements of Kurogi (1972, Table 1) on 21 monostromatic Japanese species. In 10 species, the 'cystocarps' are characterized by the formula 4/4; they correspond to Group 2 of our scheme. Nothing is known about the development of the spores of these 'cystocarps'. In five species, the formula 8/4 has been reported by Kurogi (1972). In these five species, genuine carposporangia may be expected, as in our Group 3. Possibly, there exists an asexual partner belonging to these gametophytes that has not yet been recognized as such. It may, perhaps, not be pure chance that the two groups are represented in the four species with dentated margins.

The literature on North Pacific *Porphyra* species contains several observations which accord well with our results on Helgoland species. Asexual thalli occur together with gametophytes in *P. abbottae*, which can be deduced from the figures in Cannon (1989).

Porphyra brumalis is very similar to *P. linearis* with regard to its outer morphology, its occurrence during the winter months and the morphology of the sporangia. Its spores develop into haploid Conchocelis just like the spores of the Helgoland isolate (Mumford & Cole, 1977).

Caryological results have also promoted the differentiation between and the identification of the *Porphyra* species. Lindstrom & Cole (1990b) separated *P. fallax* as a new

species from *P. perforata*, which for a long time had not been distinguished from one another. *P. fallax* has 2 chromosomes and *P. perforata* 3 chromosomes in the haploid phase.

Finally, the dual existence' discovered in several Helgoland species has also its parallel in two North Pacific species. Electrophoretic investigations carried out by Lindstrom & Cole (1990a) revealed that the asexual *Porphyra sanjuanensis* is a synonymous component of *P. perforata*. The genetic relationship between the sexual and asexual partner is an open question also for Lindstrom & Cole (l.c.).

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LITERATURE CITED

Berthold, G., 1882. Die Bangiaceen des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. – Fauna Flora Golf. Neapel *8*, 1–28.

Bird, C. J., Chen, L. C. & McLachlan, J., 1972. The culture of *Porphyra linearis* (Bangiales, Rhodophyceae). – Can. J. Bot. *50*, 1859–1863.

Cannon, M. J., 1989. Cell division patterns and diurnal cycle of *Porphyra abbottae* (Rhodophyta, Bangiales) carpogonial and carpospore development. – J. Phycol. *25*, 612–615.

Cole, K. & Conway, E., 1980. Studies in the Bangiaceae: Reproductive modes. – Bot. mar. *23*, 345–553.

Coll, J. & Oliveira Filho, E. C. de, 1977. The nuclear state of "reproductive" cells of *Porphyra leucosticta* Thuret in Le Jolis (Rhodophyta, Bangiales). – Phycologia *16*, 227–229.

Conway, E., 1964a. Autecological studies of the genus *Porphyra*: I. The species found in Britain. – Br. phycol. Bull. *2*, 342–348.

Conway, E., 1964b. Autecological studies of the genus *Porphyra*: II: *Porphyra umbilicalis* (L.) J. Ag. – Br. phycol. Bull. *2*, 349–363.

Conway, E., 1974. An examination of the original specimens of *Porphyra perforata* J. Ag. (Rhodophyceae, Bangiales). – Phycologia *13*, 173–177.

Dixon, P. S., 1959. Notes on two important algal herbaria. – British phycol. Bull. *1* (7), 35–42.

Dixon, P. S., 1983. The algae of Lightfoot's Flora scotica. – Bull. Br. Mus. nat. Hist. (Bot.) *11* (1), 1–15.

Drew, K. M., 1954. Studies in the Bangioideae. III: Life-history of *Porphyra umbilicalis* (L.) Kütz. var. *laciniata* (Lightf.) J. Ag. – Ann. Bot. *18*, 183–211.

Drew, K. M., 1955. Phycology and the British Phycological Society. – Phycol. Bull. *1* (3), 1–10.

Freshwater, D. W. & Kapraun, D. F., 1986. Field, culture and cytological studies of *Porphyra carolinensis* Coll et Cox (Bangiales, Rhodophyta) from North Carolina. – Jap. J. Phycol. *34*, 251–262.

Giraud, A. & Magne, F., 1968. La place de la méiose dans le cycle de développement de *Porphyra umbilicalis*. – C. r. hebd. Séanc. Acad. Sci., Paris (Ser. D) *267*, 586–588.

Hawkes, M. W., 1977. A field, culture and cytological study of *Porphyra gardneri* (Smith & Hollenberg), comb. nov., (= *Porphyrella gardneri* Smith & Hollenberg), (Bangiales, Rhodophyta). – Phycologia *16*, 457–469.

Hawkes, M. W., 1978. Sexual reproduction in *Porphyra gardneri* (Smith & Hollenberg) Hawkes (Bangiales, Rhodophyta). – Phycologia *17*, 329–353.

Hus, H. T. A., 1902. An account of the species of *Porphyra* found on the Pacific coast of North America. – Proc. Calif. Acad. Sci. (Ser. 3: Bot.) *2*, 173–241.

Kapraun, D. F. & Freshwater, D. W., 1987. Karyological studies of five species of *Porphyra* (Bangiales, Rhodophyta) from the North Atlantic and Mediterranean. – Phycologia *26*, 82–87.

Kapraun, D. F. & Lemus, A. J., 1987. Field and culture studies of *Porphyra spiralis* var. *amplifolia* Oliveira Filho et Coll (Bangiales, Rhodophyta) from Isla de Margarita, Venezuela. – Bot. mar. *30*, 483–490.

Kito, H., Ogata, E. & McLachlan, J., 1971. Cytological observations on three species of *Porphyra* from the Atlantic. – Bot. Mag., Tokyo *84*, 141–148.

Kornmann, P., 1961a. Die Entwicklung von *Porphyra leucosticta* im Kulturversuch. – Helgoländer wiss. Meeresunters. *8*, 167–175.

Kornmann, P., 1961b. Zur Kenntnis der *Porphyra*-Arten von Helgoland. – Helgoländer wiss. Meeresunters. *8*, 176–192.

Kornmann, P., 1986. *Porphyra yezoensis* bei Helgoland – eine entwicklungsgeschichtliche Studie. – Helgoländer Meeresunters. *40*, 327–342.

Kornmann, P. & Sahling, P.-H., 1977. Meeresalgen von Helgoland. Benthische Grün-, Braun- und Rotalgen. – Helgoländer wiss. Meeresunters. *29*, 1–289.

Krishnamurthy, V., 1959. Cytological investigations of *Porphyra umbilicalis* (L.) Kütz. var. *laciniata* (Lightf.) J. Ag. – Ann. Bot. *23*, 147–176.

Krishnamurthy, V., 1969. On two species of *Porphyra* from San Juan Island, Washington. – Proc. int. Seaweed Symp. *6*, 225–234.

Krishnamurthy, V., 1972. A revision of the species of the algal genus *Porphyra* occurring on the Pacific coast of North America. – Pacif. Sci. *26*, 24–49.

Kurogi, M., 1972. Systematics of *Porphyra* in Japan. In: Contributions to the systematics of benthic marine algae of the North Pacific. Ed. by I. A. Abbott & M. Kurogi. Jap. Soc. Phycol., Kobe, 167–191.

Kylin, H., 1956. Die Gattung der Rhodophyceen. Gleerup, Lund, 673 pp.

Lindstrom, S. C. & Cole, K. M., 1990a. An evaluation of species relationships in the *Porphyra perforata* complex (Bangiales, Rhodophyta) using starch gel electrophoresis. – Proc. int. Seaweed Symp. *13*, 179–183.

Lindstrom, S. C. & Cole, K. M., 1990b. *Porphyra fallax* a new species of Rhodophyta from British Columbia and northern Washington. – Jap. J. Phycol. *38*, 371–376.

Magne, F., 1952. La structure du noyau et le cycle nucléaire chez le *Porphyra linearis* Greville. – C. r. hebd. Séanc. Acad. Sci., Paris *234*, 986–988.

Miura, A., 1967. Two new species and a new record of *Porphyra* from Enoshima, Sagami Bay. – J. Tokyo Univ. Fish. *53*, 65–71.

Mumford, T. F. & Cole, K., 1977. Chromosome numbers for fifteen species in the genus *Porphyra* (Bangiales, Rhodophyta) from the west coast of North America. – Phycologia *16*, 373–377.

Nagai, M., 1941. Marine algae of the Kurile Islands II. – J. Fac. Agric. Hokkaido (imp.) Univ. *46*, 139–310.

Rosenvinge, L. K., 1909. The marine algae of Denmark. I. Rhodophyceae. I. – K. danske Vidensk. Selsk. Skr. *7*, 1–151.

Tanaka, T., 1952. The systematic study of the Japanese Protoflorideae. – Mem. Fac. Fish. Kagoshima Univ. *2*, 1–92.

Ueda, S., 1932a. Systematic study of the genus *Porphyra* in Japan. – Bull. Jap. Soc. Sci. Fish. *28*, 1–45.

Ueda, S., 1932b. A systematic study of the genus *Porphyra* found on the Japanese coasts. – J. imp. Fish. Inst., Tokyo *28*, 1–2 (Abstracted from the original report in Japanese).

West, J. A. & Hommersand, M. H., 1981. Rhodophyta: Life histories. In: The biology of seaweeds. Ed. by C. S. Lobban & M. J. Wynne. Blackwell, Oxford, 133–193.

Wynne, M. J., 1972. The genus *Porphyra* at Amchitka Island, Aleutians. – Proc. int. Seaweed Symp. *7*, 100–104.