

Life history of *Pseudobryopsis* sp.* (Codiales, Chlorophyta)**

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OKUDA, K., ENOMOTO, S. and TATEWAKI, M. 1979. Life history of *Pseudobryopsis* sp. (Codiales, Chlorophyta). Jap. J. Phycol. 27: 7-16.

Pseudobryopsis sp. from Amami Oshima, Japan, was found to have a heteromorphic biphasic life history in culture. Macrothallic gametophytes are monoecious and generally male and female gametangia on different ramelli. Sexual reproduction is anisogamous. Zygotes germinate into creeping filamentous microthalli with irregular and constricted branches. The microthalli mature holocarpically and produce many stephanokont zooids, but these zooids are morphologically different from those of *Bryopsis* and *Derbesia*. The zooids develop into macrothalli. Both macrothalli and microthalli grow well and mature at 18-26°C under either long or short day conditions. The macrothallic plant is multinucleate and coenocytic, and the nuclei are small and appear to distribute at the same level as the chloroplasts. The vegetative microthallus is uninucleate, and this single nucleus becomes gigantic. In both phases, cell walls appear to lack cellulose.

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The Bryopsidaceae includes two genera: *Bryopsis* and *Pseudobryopsis*. Recent life history studies on several species of *Bryopsis* have reported different life history patterns in different species: heteromorphic biphasic life history in *B. plumosa* (RIETEMA 1969, 1970, 1975; TATEWAKI 1973), in *B. monoica* and *B. hypnoides* (RIETEMA 1971, 1975), in *B. maxima* and *B. ryukyensis* (TATEWAKI 1973, 1977), and in *B. lyngbyei* (KORNMANN und SAHLING 1976); heteromorphic monophasic in *B. hypnoides* (BARTLETT and SOUTH 1973); monophasic in *B. hypnoides* (NEUMANN 1969; RIETEMA 1971,

1975) and in *B. plumosa* (RIETEMA 1969, 1970, 1975); and heteromorphic biphasic (diplohaplontic) but with no diminutive microthallic phase in *Bryopsisidella neglecta* (formerly *Bryopsis halymeniae*, HUSTEDE 1960, 1964; RIETEMA 1972, 1975). From these investigations, two plants of the same species, *B. plumosa* and *B. hypnoides*, were found to have different types of the life histories depending on their different habitats.

In contrast, in the genus *Pseudobryopsis*, only BERTHOLD (1880, in OLTMANN 1922) observed conjugation of biflagellate aniso-

* TAYLOR (1962) pointed out that the genus *Trichosolen* MONTAGNE (1860) has priority over *Pseudobryopsis* BERTHOLD (1904) and proposed that the alternative to conservation is to transfer the hitherto described species of *Pseudobryopsis* to *Trichosolen*. In this paper, however, *Pseudobryopsis* is used as the genus name because it is well-known and currently in use.

** Dedicated to Dr. L. PROVASOLI on the occasion of his official academic retirement with sincere wishes for continued scholarly productivity.

gametes in *P. myura* from Naples in the Mediterranean region and NEUMANN (1970) reported in the same species that germlings develop into uninucleate protonemata, although he observed neither sexual nor asexual reproduction. According to NEUMANN, the protonema is lobed and irregularly branched, and may produce upright pinnate thalli directly in the same way as *Bryopsis hypnoides* from Helgoland.

We have observed the lifehistory of *Pseudobryopsis* sp. from Amami Oshima, Japan in laboratory culture, and report for the first time the complete life history of a species of *Pseudobryopsis*.

Material and Methods

Thalli of *Pseudobryopsis* were collected at Ayamaru Point near Ushuku (28° 28'N; 129° 43'E), Amami Oshima, Japan on June 2, 1977 (by ENOMOTO). Only one tuft of plants was found in a water-filled depression in the rocks near low tide level.

The plants were taken to the Iwaya Marine Biological Station, Kobe University, on June 5 and maintained in a diluted PES medium at 25–30°C. Original stock cultures were started from excised apices of main axes 5–10 mm in length and grown in screw-cap test tubes (18 mm×135 mm) containing 10 ml medium. Sterile apical parts were employed as the inoculum. Clone-culture plants were taken to the laboratory at Muroran on November 10. Small branched apices 2–3 mm in length were excised and rinsed several times inside a sterile 0.5–1.0% seawater-agar plate to establish unialgal cultures. The apices were first cultured in screw-cap test tubes containing 10 ml medium. Some of the cultures grown unialgally were transferred into petri-dishes (65 mm×80 mm) containing

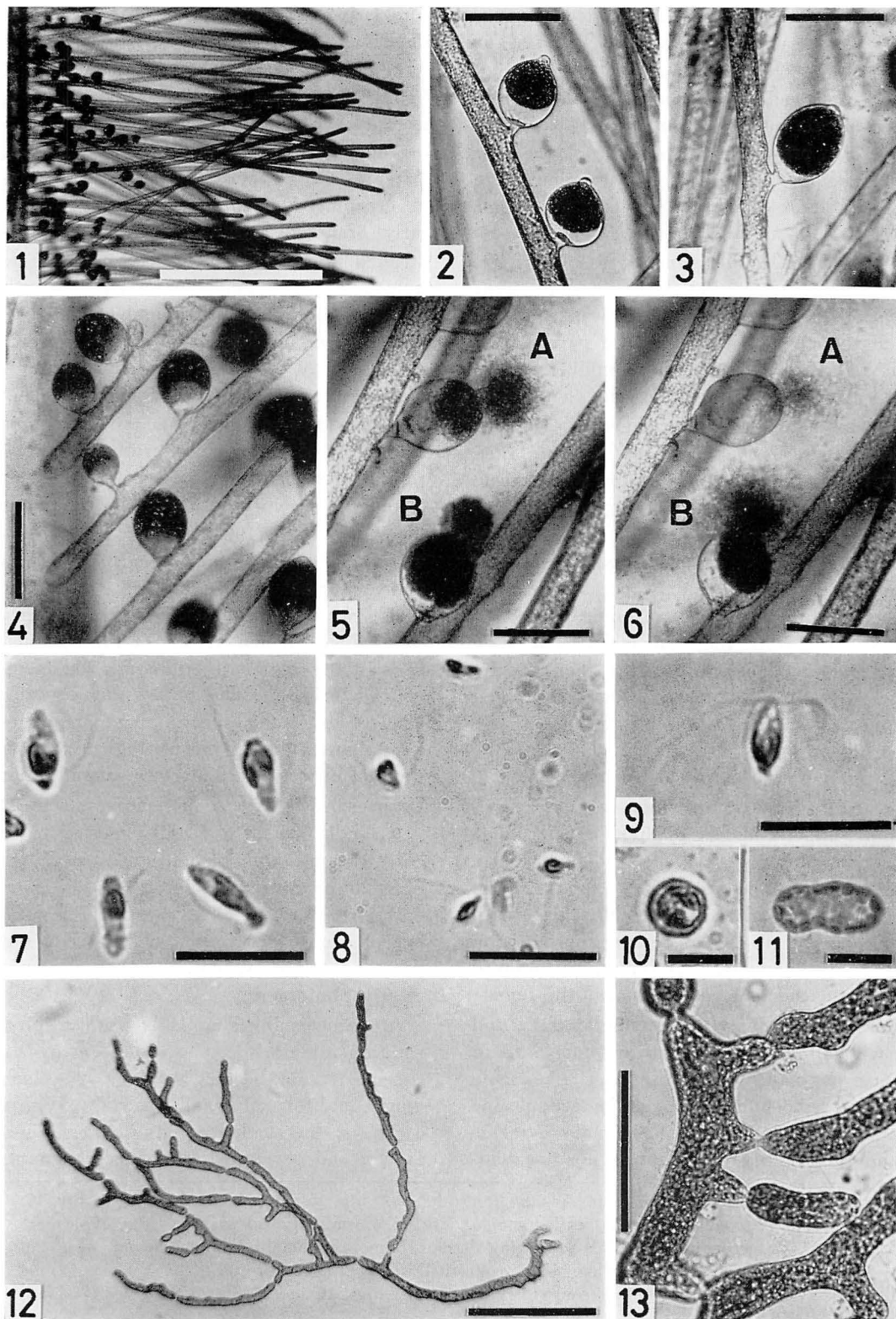
about 180 ml medium. PES culture medium (PROVASOLI 1968) was used, and it was changed every 15–20 days. In this experiment, nine incubators equipped with cool white 40 W fluorescent lamps (*ca.* 2000–3000 lux) were employed under the following temperature-photoperiod regimes: 10°C–14 hr (No. 1), 10°C–10 hr (No. 2), 14°C–14 hr (No. 3), 14°C–10 hr (No. 4), 18°C–14 hr (No. 5), 18°C–10 hr (No. 6), 22°C–14 hr (No. 7), 22°C–10 hr (No. 8), and 26°C–14 hr (No. 9).

For cytological observations whole plants or fragments in various stages of development were fixed in acetic alcohol (1:3), and were stained with acetocarmine or iron-haematoxylin. Also chlor-zinc-iodine and Congo red were used for staining the cell walls of the culture material to determine whether or not the cell walls contained cellulose.

Result

Cultures started from 2–3 mm long apical fragments grew rapidly in incubator No. 7 and in a month attained heights of 3–10 cm and 150–280 μm in diameter in the middle part of the main axis. Such plants reached reproductive maturity within a few days after transfer into fresh medium in incubators No. 7–9. Formation of gametangia occurred on older ramelli on the lower part of the plant and spread gradually upward. Gametangia were initiated only adaxially on the proximal part of each ramellus (Fig. 1), and they gradually swelled and developed into mature gametangia (Fig. 4). The mature gametangia were often asymmetrical, ovate or obovate, and measured 88–(120)–136 μm long and 80–(91)–112 μm wide. Each gametangium was pedicellate with a plug separating it from the ramellus. A papilla was produced at the distal end of the game-

Fig. 1. Gametangia borne near the proximal end of each ramellus. Fig. 2. Male gametangia. Fig. 3. Female gametangium. Fig. 4. Adaxial initiation of gametangia. Figs. 5–6. Liberation of gametes, male (A) and female (B). Fig. 7. Female gametes. Fig. 8. Male gametes. Fig. 9. Planozygote. Fig. 10. Settled zygote. Fig. 11. Germination of a zygote in 3-day-old culture. Fig. 12. Microthallus in 1-month-old culture. Fig. 13. A part of a microthallus showing constrictions. Scale: (Fig. 1)=1 mm, (Figs. 2–6)=100 μm, (Figs. 7–9)=20 μm, (Figs. 10–11)=10 μm, (Figs. 12)=200 μm, (Fig. 13)=50 μm.



tangium, and the gametes tended to mass toward the papilla (Fig. 2). The mass of male gametes (male gametangium, Fig. 2) appeared yellowish brown in color, while the female gametangium (Fig. 3) was dark green or brownish green. The plants were monoecious, and each fertile ramellus bore 1-3 or more gametangia, generally either all male or all female.

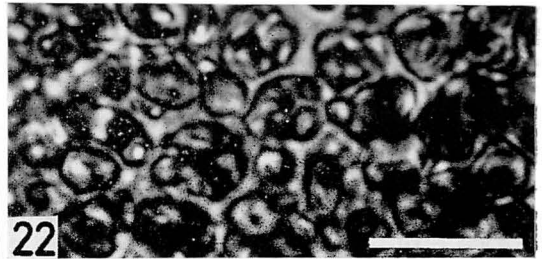
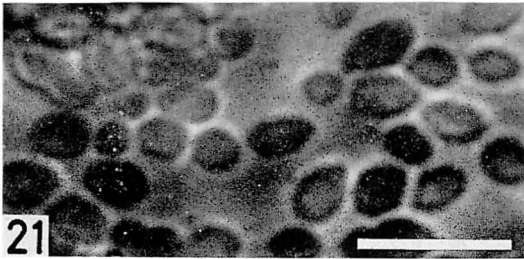
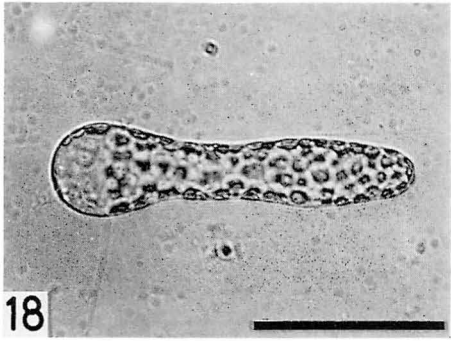
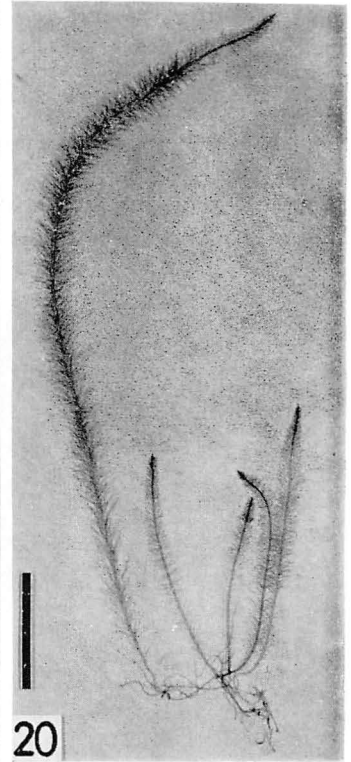
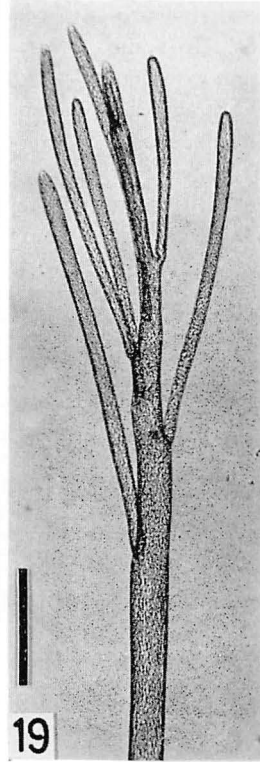
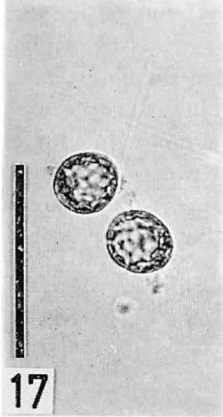
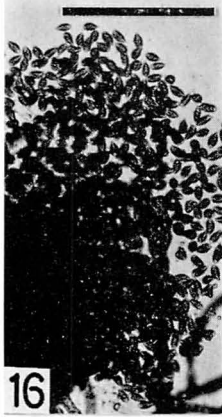
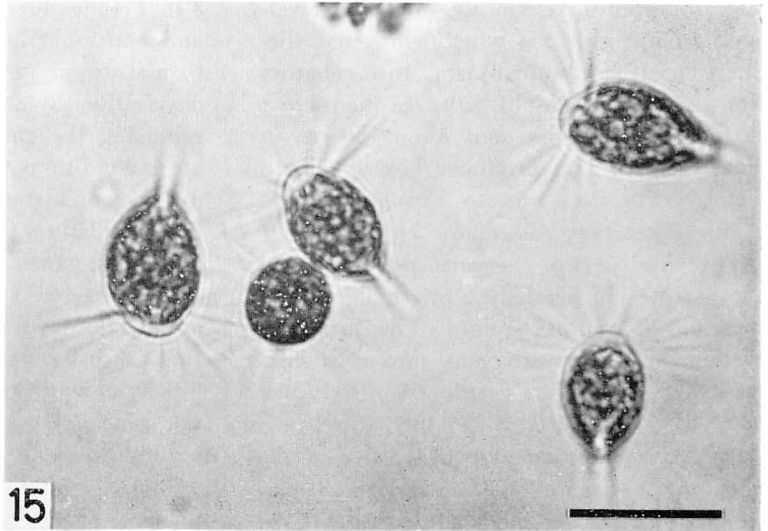
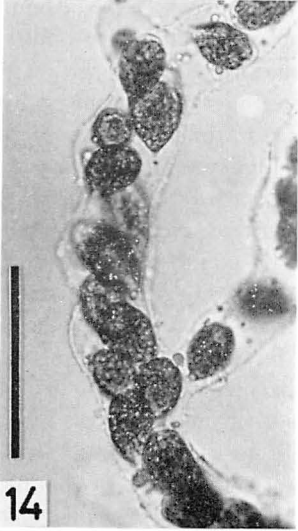
Discharge of the gametes was light-triggered and occurred at the onset of the light period. A mass of gametes was squeezed out through an ostiole in the papilla (Fig. 5). This discharge ceased completely when the plant was moved to a dark place. The male gametes usually remained massed near the papilla for about 1 minute and then swam away (Fig. 6 A), while the female gametes remained densely aggregated and wriggled around the tip of the gametangium (Fig. 6 B). The male gametes swam vigorously for 5-10 min., whereas the female swam slowly but had a longer period of motility (2-4 hr) than the male. The male gametes were much smaller than the female, $4-(4.8)-6 \times 1.2-(2.1)-3.2 \mu\text{m}$ as compared to $10.5-(12.1)-14 \times 4-(4.2)-4.6 \mu\text{m}$. The male gametes were biflagellate (*ca.* $14.2 \mu\text{m}$ long), elongated pear-shaped or fusiform and had a degenerated chloroplast, or sometimes none, and lacked an eyespot (Fig. 8). The female gametes were also biflagellate (*ca.* $19.5 \mu\text{m}$ long), pear-shaped or elongate pear-shaped but had a distinct chloroplast with an eyespot (Fig. 7). Sexual reproduction was anisogamous. Conjugation followed between the male gametes and the female ones around the female gametangium, and each pair freely swam away and fused to form a planozygote (Fig. 9). The male gametes did not have a clearly recognizable phototaxis, but both the female gametes and the planozygotes showed positive pho-

totaxis for a while. Unfused gametes never developed parthenogenetically.

The planozygotes swam for a few hours before settling on the substratum. Settled zygotes became spherical (Fig. 10), and in 3-6 days they began to germinate (Fig. 11). After about 3 weeks, germlings appeared as creeping filaments which were irregularly branched, swollen, curved and constricted in places (Figs. 12 and 13). These unicellular microthalli increased in length but not much in diameter and by about 50 days had attained a length of 3-5 mm but were only 20-50 μm in diameter. Chloroplasts were irregularly shaped measuring 2-6 μm wide and did not contain pyrenoids (Fig. 22). The 50-day-old microthalli reached reproductive maturity within 5 days after changing the medium, even in the same incubators (No. 7-9). Some microthalli divided their contents holocarpically into many tear-shaped zooids (Fig. 14). The zooids were usually discharged through a rent which opened at one of the terminal ends of the filament, but some zooids remained inside the filament as aplanospores. The zooids of this species were stephanokont, but differed morphologically from those of other species of *Bryopsis* and other Derbesiaceae. The zooids measured $16-22 \times 10-15 \mu\text{m}$, with a long tail posteriorly (*ca.* 7-10 μm long) and a small constricted ring of 8-20 or more flagella (10-15 μm long) anteriorly (Fig. 15). The zooids had a number of evenly distributed chloroplasts but no recognizable eyespot, and they were not clearly phototactic.

After swarming sluggishly with a spiral rotation for a while, the zooids settled on the substratum, became spherical (20-30 μm diam.), and formed a wall (Fig. 17). Within 4-5 days, the settled zooids began to germinate and developed into erect filaments

Fig. 14. Formation of zooids in the microthallus. Fig. 15. Stephanokont zooids. Fig. 16. Liberation of zooids. Fig. 17. Settled zooids. Fig. 18. Germination of a zooid. Fig. 19. Apical part of the erect macrothallus producing lateral branches (ramelli), one-week old. Fig. 20. Macrothalli. Fig. 21. Chloroplasts of a macrothallus. Fig. 22. Chloroplasts of a microthallus. Scale: (Figs. 14, 17 and 18)=50 μm , (Fig. 15)=20 μm , (Figs. 16 and 19)=200 μm , (Fig. 20)=1 cm, (Figs. 21-22)=10 μm .



(Fig. 18). These germlings rapidly developed an upright axis which showed a distinctly positive phototropism. In incubators No. 7-9, one-week-old cultures had erect axes 2.5-3 mm high and about 50 μm in diam. These axes produced lateral ramelli distally (Fig. 19), thereby developing into a new *Pseudobryopsis* plant (Fig. 20).

The basal part of the germlings produced a prostrate rhizoidal system which was an irregularly ramified stolon. The prostrate system later sent out many new erect filaments, each of which developed into a *Pseudobryopsis* plant (Fig. 20). Thus 20-50 *Pseudobryopsis* thalli developed from a single germling. After about one month incubation, the plants attained heights of 3-10 cm and reached reproductive maturity producing biflagellate anisogametes. In some macrothalli the erect axes became ramified. Chloroplasts were flat discs or spindle-shaped discs without pyrenoids, measuring $1.5 \times 1-3 \mu\text{m}$ (Fig. 21).

Both macrothalli and microthalli grew better in incubators No. 5-9 than in No.

3-4. None survived in No. 1-2. About one-month-old macrothalli had the ability to mature in incubators No. 5-9 within 5 days either by changing the medium or by removing the cultures from lower temperature conditions to higher temperature conditions, for instance, as from incubator No. 5 to incubators No. 7 or No. 9. The initiation of gametangia could be induced in incubators No. 3-4, but the gametangia did not attain reproductive maturity. Microthalli also became fertile in incubators No. 5-9 by changing the medium, but they did not reach reproductive maturity in incubators No. 3-4.

The vegetative macrothallus was a multinucleate cell, or coenocyte. Interphase (resting) nuclei in the vegetative macrothallus were all of about the same size (2-3 μm in diameter) and contained a single nucleolus. They were more easily visible at the apices of ramelli (Fig. 23). These nuclei were distributed rather evenly at the same level as the chloroplasts and were sometimes observed adhering closely to the

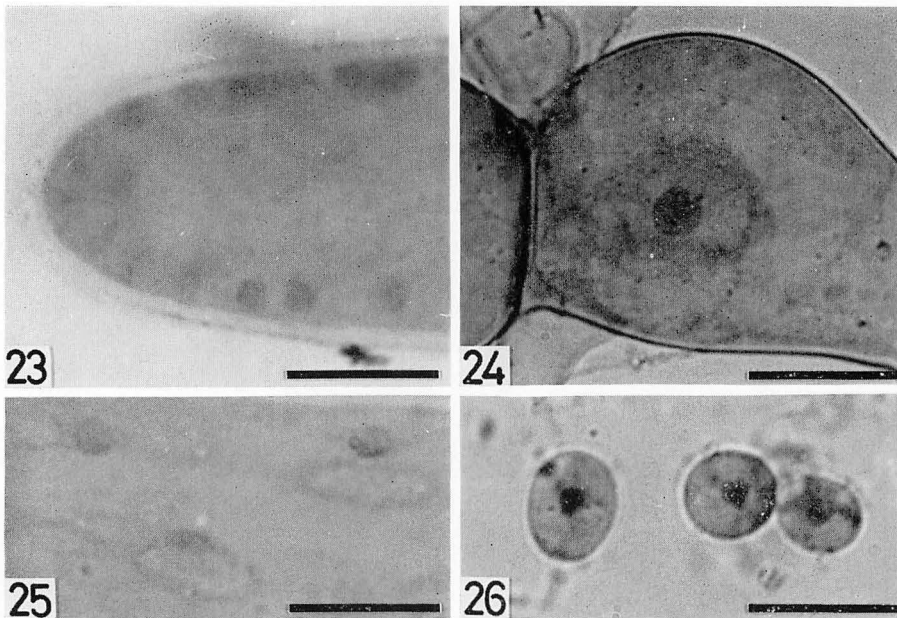


Fig. 23. Nuclei at an apical part of a ramellus. Fig. 24. Giant nucleus in about 2-month-old microthallus. Fig. 25. Nuclei in the main axis of a macrothallus, showing occurrence at the same level as the chloroplasts. Fig. 26. Nucleus in each zygote, a day after liberation. Scale: (Figs. 23, 25 and 26)=10 μm , (Fig. 24)=20 μm .

chloroplasts (Fig. 25). On the other hand, the germlings derived from zygotes developed into mononucleate microthalli. The nuclear diameter increased and in a 50-day-old microthallus it had attained a diameter of about 16–20 μm . Such a giant nucleus was usually spherical or somewhat elongated and contained a big nucleolus (7–9 μm in diam.) which stained deeply with iron-haematoxylin (Fig. 24).

Staining reaction of the cell walls was examined in both macrothallic and microthallic plants. Cell walls stained negatively with chlor-zinc-iodine and Congo red, indicating a lack of cellulose.

Discussion

As noted in the introduction, the life history of the genus *Bryopsis* has been investigated by several authors in different localities. Heteromorphic biphasic, heteromorphic monophasic and monophasic life history patterns were found, and in the widely distributed species *B. plumosa* and *B. hypnoides* different types of the life history patterns were found according to different habitats

In contrast, in the genus *Pseudobryopsis*, only NEUMANN (1970) has reported on cytological observations in the life history of *P. myura* from Naples. According to him, the formation of specialized gametangia is induced by refreshment of the medium, and germlings, probably derived from zygotes, develop into uninucleate branched protonemata, each of which directly produces erect pinnate thalli after transition to the multinucleate stage. His results are quite similar to that of *Bryopsis hypnoides* from Helgoland.

In our *Pseudobryopsis* sp. from Amami Oshima, a gametophytic phase is a multinucleate macrothallus and a sporophytic phase is a much reduced uninucleate microthallus which has a single gigantic nucleus. This cytological evidence quite agrees with that of *P. myura* described by NEUMANN. Our species, however, has heteromorphic

biphasic life history in which the macrothallus producing biflagellate anisogametes alternates with a microthallus producing stephanokont zooids, but it never develops directly into a macrothallic gametophyte.

From this, it suggests that some species of this genus may, like *Bryopsis*, have several different types of life history patterns.

The *Pseudobryopsis* sp. examined here differs in several important characteristics from the *Bryopsis* species.

In macrothallic gametophytes, gametogenesis in *Pseudobryopsis* occurs in specialized gametangia on pinnae (ramelli) rather than in direct transformation of vegetative pinnae as in *Bryopsis*. The presence of this specialized gametangium is one of reasons for the separation of *Pseudobryopsis* from the genus *Bryopsis*. The microthallic sporophytes are prostrate and irregularly branched, resembling those of *Bryopsis*, but the branched filaments are more slender and are considerably constricted in places. Furthermore, the stephanokont zooids are tear-shaped or ovoid provided with a long tail posteriorly, in contrast to those of *Bryopsis* and other Derbesiaceae (*Derbesia* or *Bryopsisidella*) hitherto known.

RIETEMA pointed out an important difference in the cell wall constituents between the gametophytic phase and the sporophytic phase in all species of *Bryopsis* and the Derbesiaceae investigated by him: the cell wall of the gametophyte stains positively with Congo red and chlor-zinc-iodine because it contains cellulose, whereas the cell wall of the sporophyte does not stain and apparently lacks cellulose. In *Pseudobryopsis myura*, however, the cell walls of both macro- and microthallic phases are obtained negative reaction with these two stains (RIETEMA, unpublished data). Furthermore, HUIZING and RIETEMA (1975) clearly confirm the above mentioned results by an infrared spectrum analysis and thin layer chromatography. According to them, the cell walls of gametophytic phases of *Bryopsis* and *Derbesia* contain a xylan and cellulose as the main constituents and those

of their sporophytic phases contain mainly mannan, but in *Pseudobryopsis myura* the cell walls of the both macro- and microthallic phases contain mainly mannan. In fact, in all our species of *Bryopsis* investigated previously (*B. plumosa*, *B. maxima* and *B. ryukyuensis*), the cell wall of the gametophytic phase (macrothallus) stains a deep violet with chlor-zinc-iodine and red with Congo red, but the cell wall of the sporophytic phase (microthallus) does not, while in *Pseudobryopsis* sp. the cell walls of the both phases do not and apparently lack cellulose. The present results quite agree with RIETEMA's opinion.

According to BURR and WEST (1970) working on *Bryopsis hypnoides* with the electron microscope, in mature parts of the macrothallus the cytoplasm is divided into two layers: the outer layer adjacent to the cell wall contains most of the organelles including the nuclei, whereas the inner layer next to the vacuole contains only chloroplasts with polypyramidal pyrenoids. RIETEMA (1975) also reported this fact in all his species investigated except for the sporophyte of *Bryosidella neglecta*. In the present species the cytoplasm of the macrothallus is apparently not divided into two layers between the cell wall and the vacuole, and the nuclei intermingle in the same level as the chloroplasts or actually attach to the chloroplasts. Pyrenoids are not observed in the chloroplasts at any stage. These features differ from those of *Bryopsis* and rather resemble those of the sporophytes of *Bryosidella neglecta* as described by RIETEMA (1975).

The influences of temperatures and day-length on growth and reproduction in both phases of the present species were investigated and compared with *Bryopsis ryukyuensis*. In *B. ryukyuensis* from Ushuku, Amami Oshima, which is an almost identical habitat to the one where the present species was collected, the macrothalli grow well under 18–26°C in long-day conditions but not under short-day conditions, whereas the microthalli experience a dormancy

under long-day conditions and sporogenesis occurs only during short days at 22–23°C or more (TATEWAKI 1977).

In the present species, the macrothalli grow well at 18–26°C under both long-day and short-day conditions, and gametogenesis occurs under the same conditions. The microthalli also grow well and sporogenesis occurs at 18–26°C under both long-day and short-day conditions. The dormancy period is shorter and it is broken more easily than that of *B. ryukyuensis*. In this experiment refreshment of the medium or transfer from lower to higher temperatures can induce gametogenesis and sporogenesis, and it seems that these treatments are one of the important factors causing the change from the sterile to fertile stage. Therefore, *Pseudobryopsis* sp. is expected to grow abundantly in the vicinity of Amami Oshima throughout the year because the water temperature of this area ranges between 18°C and 28°C and the day-length appears not to be an important factor for the growth or reproduction of either phase. Furthermore, since fragments of macrothalli develop into new macrothalli so easily in laboratory culture, and its stolon is able to issue so many plants, one would expect to find many *Pseudobryopsis* plants in the field. However, the plants are found only rarely at Amami Oshima, while *B. ryukyuensis* grows abundantly during its favorable season (May–July)!

Under our culture conditions, the plants appear morphologically similar to the original plants from nature. Unfortunately, however, we did not have the preserved collections from nature, so the species could not be clearly compared.

In general, the species of *Pseudobryopsis* have been classified on the basis of dimensions of gametangia; location of gametangia; morphology of gametangia; whether pedicellate or sessile; size, shape and ramification of main axis and lateral ramelli; whether the base of the ramellus is swollen; shape, size and dimension of chloroplasts; and presence or absence of pyre-

noids in the chloroplasts. Results from the present culture experiments from generation to generation under various conditions show that ovate to obovate pedicellate gametangia are produced on the lower half of each ramellus. The dimensions of the gametangia are within a constant range, and chloroplasts never have pyrenoids. However, length and diameter of axes and ramelli, shape of ramelli, shape of the base of the ramelli, number of gametangia on a ramellus, and pattern of ramification vary depending on culture conditions. According to the constant characters obtained in culture, the present species from Amami Oshima fits most closely that of *Pseudobryopsis oahuensis* described by EGEROD (1952). OGATA (1956) reported *P. hainanensis* TSENG, 1936, from Takarazima of Tokara Islands in southern Japan, but it is quite different from the present species.

Acknowledgements

We wish to express our gratitude to Prof. Y. SAKAI, Institute of Algological Research, Hokkaido University, for critical reading of the manuscript and to Miss S. LINDSTROM, Department of Botany, Faculty of Science, Hokkaido University, for correcting the English text.

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奥田一雄*・榎本幸人**・館脇正和*: ニセハネモ属 (*Pseudobryopsis*)

の 一 種 の 生 活 史 の 研 究

奄美大島産のニセハネモ属の一種は、異型二相性の生活史をもつ。ニセハネモ属特有の配偶子嚢をつくる大型の配偶体は、雌雄同株であり、配偶子は異型接合である。接合子は不規則に分枝し、所々にくびれのある匍匐糸状性の小型の胞子体に発達する。胞子体は全実的に成熟して遊走子を放出するが、この遊走子の形態は *Derbesia* 属及び *Bryopsis* 属で知られるものと異なる。遊走子は発芽し、再び配偶体となる。配偶体と胞子体は共に長日及び短日条件に関係なく、18~26°Cで良く生長し成熟する。配偶体は多核嚢状体で、核は葉緑体と同レベルに分布する。胞子体は生長に伴って巨大化する単核を有する。両世代の細胞壁は共にセルロースを欠くと思われる。(*051 室蘭市母恋南町1-13, 北海道大学理学部海藻研究施設; **656-24 兵庫県津名郡淡路町岩屋, 神戸大学理学部臨海実験所)

Addendum

KOBARA and CHIHARA (1978 a, b) have quite recently reported on the taxonomy and life history of *Pseudobryopsis hainanensis* TSENG. Their results and our results were both first reported at the 43rd Annual Meeting of the Botanical Society of Japan, Chiba, Sept. 1978.

KOBARA, T. and CHIHARA, M. 1978 a. On the taxonomy and sexual reproduction of the siphonous green alga *Pseudobryopsis hainanensis* TSENG. *J. Jap. Bot.* 53: 341-352.

KOBARA, T. and CHIHARA, M. 1978 b. On the life history of *Pseudobryopsis hainanensis* (Chlorophyceae). *J. Jap. Bot.* 53: 353-360.