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LIFE HISTORY OF *COLPOMENIA SINUOSA* (SCYTOSIPHONACEAE, PHAEOPHYCEAE) IN THE AZORES[1]

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Colpomenia sinuosa **(Mertens ex Roth) Derbès and Solier (Scytosiphonaceae, Phaeophyceae) is a common species on the rocky intertidal shores of the Azores, where reproductive gametophytes occur throughout the year. Life-history studies of this species were carried out in culture, and both sexual and asexual reproduction were observed. Anisogamous gametes fused to form zygotes. The zygotes gave rise to a filamentous prostrate sporophyte generation bearing unilocular sporangia, under both short-day and long-day conditions at 15 and 22° C, and to both unilocular and plurilocular sporangia, under the lower temperature condition. Unispores developed into gametophytes, and plurispores gave rise to filamentous sporophytes. Asexual reproduction was carried out by unfused female gametes and asexual plurispores produced from the same gametophyte. Unfused gametes developed into filamentous prostrate sporophytes producing unilocular sporangia in both culture conditions, and unispores released from the sporangia gave rise to gametophytes. Asexual plurispores from field gametophytes, under both culture conditions, developed directly into new gametophytes. The species exhibited three types of life history: a heteromorphic, diplohaplontic; a heteromorphic, monophasic (both with alternation between the erect and filamentous prostrate thalli); and a monomorphic, monophasic.**

Key index words: ***Colpomenia sinuosa*****; life history; morphology; Phaeophyceae; Scytosiphonaceae**

Two species of the brown algal genus *Colpomenia* are reported for the Azores (South and Tittley 1986), *C. sinuosa* (Mertens ex Roth) Derbès and Solier and *C. peregrina* Sauvageau, but only the former has been found on the Azorean shores, where it is a common species in the rocky intertidal shores, mainly in spring and summer (Neto 2000). Thalli of the two species are spherical and saccate and similar in appearance. The distinction between the two species, proposed by Clayton (1975) working with material from southern Australia, is based on a few morphological characters. *Colpomenia sinuosa* has plurilocular sporangial punctate sori with a cuticle and commonly four to six layers of medullary cells, whereas *C. peregrina* has extensive sori without a cuticle and a thinner thallus wall of three to four layers of colorless medullary cells (Clayton 1975). *Colpomenia sinuosa* is widely distributed in tropical to warm temperate seas throughout the world (Wynne and Norris 1976, Parsons 1982). It was first reported to the Azores by Agardh (1870), and there is an Azorean specimen in the Farlow Herbarium (Blackler 1967).

Sexual (Kunida and Suto 1938, Tatewaki 1966, Nakamura and Tatewaki 1975, Clayton 1980) and asexual (Nakamura and Tatewaki 1975, Clayton 1980, 1982, Fletcher 1987, Wynne 1969, Kogame 1997) reproduction have been reported in members of the Scytosiphonaceae, by means of both direct-type (Clayton 1982, Fletcher 1987, Wynne 1969) and heteromorphic life histories. Blackler (1981) and Clayton (1982) reported the occurrence of a direct-type life history for *C. sinuosa*, and Kogame (1997) reported a heteromorphic life history for this species with an alternation between erect and prostrate thalli. In this type of life history, erect gametophytes bearing plurilocular gametangia alternate with prostrate sporophytes bearing unilocular sporangia (Nakamura and Tatewaki 1975, Clayton 1979, 1980, Kogame 1996) or both unilocular and plurilocular sporangia (Kogame 1997, Kogame and Yamagishi 1997). Algae with heteromorphic life histories are known to have a great degree of independence and differentiation among the different stages as well as a tremendous plasticity in regard to their life history (Wynne and Loiseaux 1976, Lubchenco and Cubit 1980).

Despite the important structural role in many intertidal communities and widespread occurrence of *C. sinuosa*, only a few studies have been produced, and little is known about the biology and life history of this species in the Atlantic. The present investigation is a contribution to the knowledge of the strategies of reproduction, growth patterns, and the life history of *C. sinuosa* in this region.

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MATERIALS AND METHODS

Fertile specimens of *C. sinuosa* were collected monthly between September 1999 and September 2000 from the intertidal shores of two localities (Caloura and Mosteiros) on the coast of the island of São Miguel (Fig. 1). In the laboratory, the plants were examined and numbered, and a reference collection was prepared by storing samples in a 5% buffered formaldehyde–seawater solution. All collections are deposited in the Department of Biology at the University of the Azores. The code numbers of the more representative specimens are given in the text. The systematic organization and nomenclature synopsis used in this study generally follows that adopted by Silva et al. (1996). Whenever necessary, the entire thallus, portions, or sections of it were observed microscopically. Sections were obtained by using a freezing microtome. Measurements of cells and other structures were made using a micrometer eye piece. Camera lucida drawings were prepared, and a representative collection of color slides was made using a microphotography system (Olympus-PM 10-35 AD-1) (Olympus, Porte Delgada, Azores, Portugal).

Culture studies were carried out with a total of 153 erect plants collected from the intertidal shores. Segments of thalli bearing mature plurilocular organs were cut out and washed in sterile seawater. The isolation technique used was the same as that described by Wynne (1969), and the culture medium used was Grund (von Stosch 1963). Two culture regimes, reflecting the intertidal conditions of São Miguel during the winter and summer, 15° C, 8–16 h light-dark, and 22° C, 16–8 h light-dark, respectively, were used. For each cultured plant, four petri dishes were set up, two for each regime. Mixtures of gametes from different parental thalli were prepared and checked for mating reaction and zygote formation. When a subsequent generation was required, fertile material was subcultured by using the same hanging-drop method. Special attention was given to the different phases of development of the life cycle and the occurrence of the reproductive organs. To better follow development patterns or specific cells and/or structures, petri dishes were marked underneath. Cultures were examined every 4–5 days, and the medium was changed every week. Microphotography and drawings of the development stages were made.

RESULTS

Morphology. Plants studied were as follows: SMG-99-875; SMG-99-877; SMG-99-880; SMG-99-884; SMG-99-912; SMG-99-925; SMG-99-919; SMG-00-24; SMG-00-28; SMG-00-68; SMG-00-166; SMG-00-184; SMG-00-192; SMG-00-221; SMG-00-272. Erect gametophyte thalli were globular, spherical, or saccate to 7 cm across, hollow and convoluted, with a broad attachment by downwardly growing rhizoids (Fig. 2A). In surface view, cells were polygonal and irregularly placed, 10–18 × 9–13 µm, each one containing a single, parietal, plate-like plastid with one pyrenoid. In section (Fig. 2B), thalli comprised an outer cortex and an inner medulla. The cortex comprised a single layer of small pigmented cells, 10–13 µm across and 9–10 µm high. The medulla had four to five layers of irregularly shaped colorless cells, with thick walls, the outer cells measuring 12–20 × 8–12 µm and the inner ones measuring 79–134 × 63–134 µm. Hairs (7–10 µm in diameter) arose from the superficial cells in tufts, rarely single (Fig. 2C). Plurilocular organs, commonly uniseriate, sometimes biseriate, 18–32 µm long, 5–7 µm in diameter, had subquadrate to rectangular loculi. They originated from the cortical cells, were closely packed in vertical rows (Fig. 2D), and located in sori covered by a cuticle

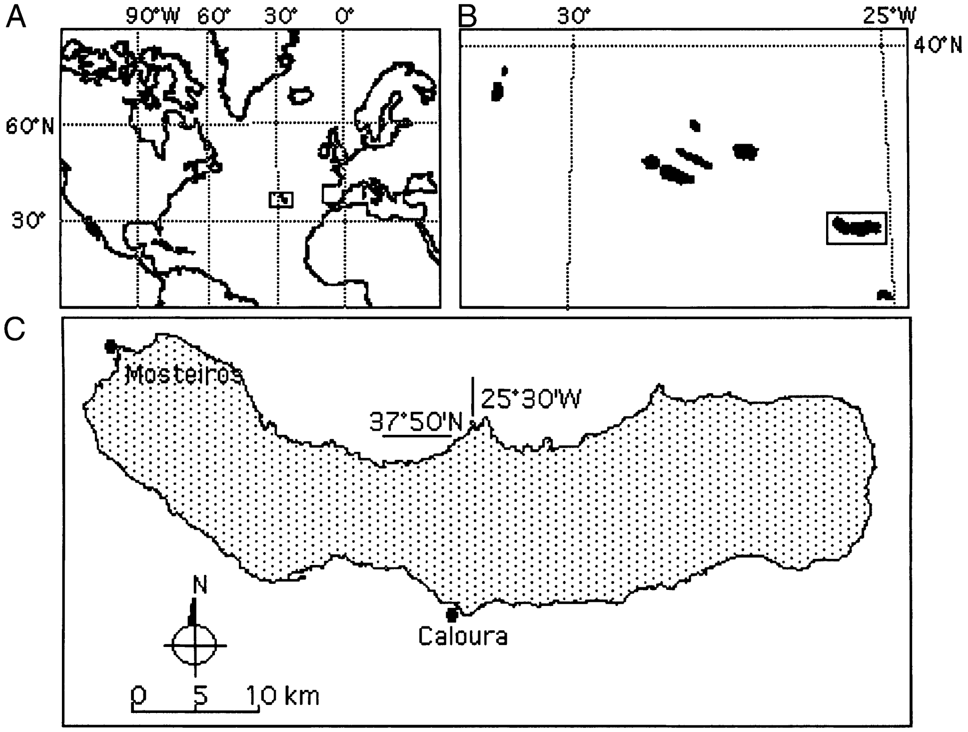

Fig. 1. Location of the archipelago of the Azores in the North Atlantic (A), position of the island of São Miguel on the archipelago (B), and the location of the study sites (C).

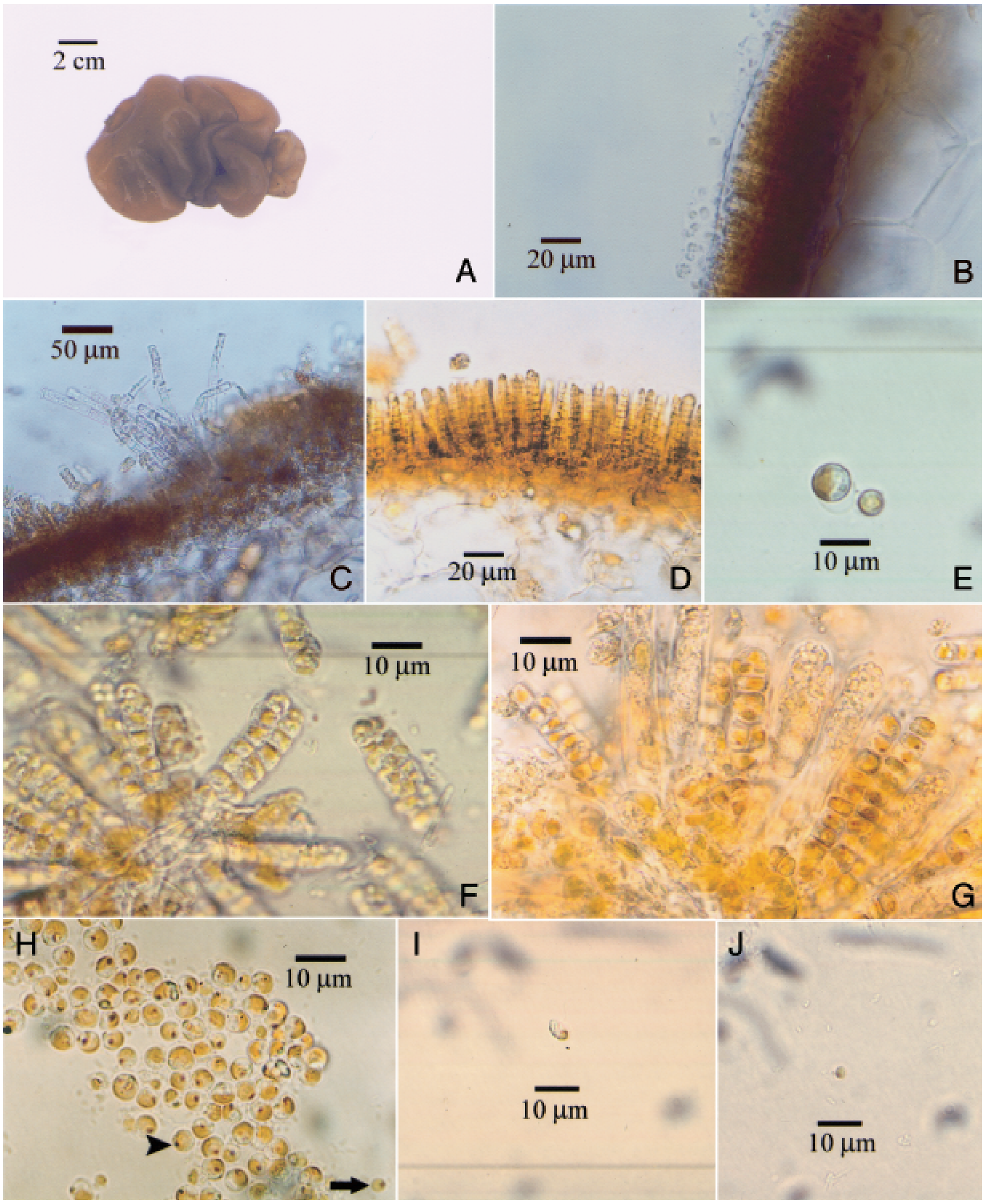

FIG. 2. Habit and anatomy of *Colpomenia sinuosa* collected in the field and its development in culture. (A) Habit of plant. (B) Cross-section of mature thallus showing a punctate sorus with a cuticle. (C) Cross-section of a mature thallus showing tufts of hairs emerging from superficial cells. (D) Plurilocular organs closely packed in vertical rows. (E) Settled male and female gametes. (F) Female gametangia/zooidangia. (G) Male gametangia (mg), zooidangia (pz), and ascocyst like cell (ac). (H) Settled male gametes (arrow) and asexual plurispores (arrow head). (I) Female gamete/asexual plurispore with one eyespot and two flagella laterally inserted. (J) Settled male gamete with one eyespot.

(Fig. 2B) forming extensive or discrete dark patches on thallus surface. Ascocyst-like cells, elongate to pyriform in shape (20–36 × 9–13 µm), were present. Unilocular sporangia are unknown on the erect thalli.

Habitat and phenology. Reproductive gametophytes with plurilocular sporangia were found all year round. This species was common in the mid- to lower tidal region, both exposed and in pools, and was found both epilithic and epiphytic mainly on *Corallina elongata* Ellis et Sol., *Jania rubens* (L.) J. V. Lamour., and *Chondracanthus acicularis* (Roth) Fredericq, mainly.

Cultures established from field gametophytes. Colpomenia sinuosa comprised sexual dioecious thalli, which produced female and male gametes (Fig. 2E) differing in size, color, mobility, and future progeny (anisogamy). Female gametophytes produced both gametes and asexual plurispores. These two cell types and the reproductive organs that produced them were morphologically indistinguishable (Fig. 2F), measured up to 33.9 µm long and comprised five to eight tiers of loculi. The only way to distinguish them was to observe the future progeny. Gametes always produced a prostrate microthallus, whereas asexual plurispores produced exclusively erect plants. Male gametophytes also produced gametes and asexual plurispores in separate organs, but in this case, both reproductive organs (Fig. 2G) and their cells (Fig. 2H) were morphologically distinct. The male gametangia measured up to 32 μm in length and consisted of 9–13 loculi. The female gametes and asexual plurispores were dark yellow, pear shaped, measured 5–8.5 μm when settled, possessed a large, yellow, plate-like chloroplast, one pyrenoid, one eyespot, two flagella laterally inserted (Fig. 2I), and maintained mobility for up to 5 h. Male gametes (Fig. 2J) were smaller (2.5–4 μm in diameter when settled), possessed one eyespot, were lighter in color, and usually settled 1–2 h after the female gametes.

Development of asexual plurispores from gametophytes. Asexual plurispores, 5–8 μm in diameter after settling, gave rise, under both culture regimes, to germlings that more or less directly developed into new erect plants. Two types of germination pattern were observed:

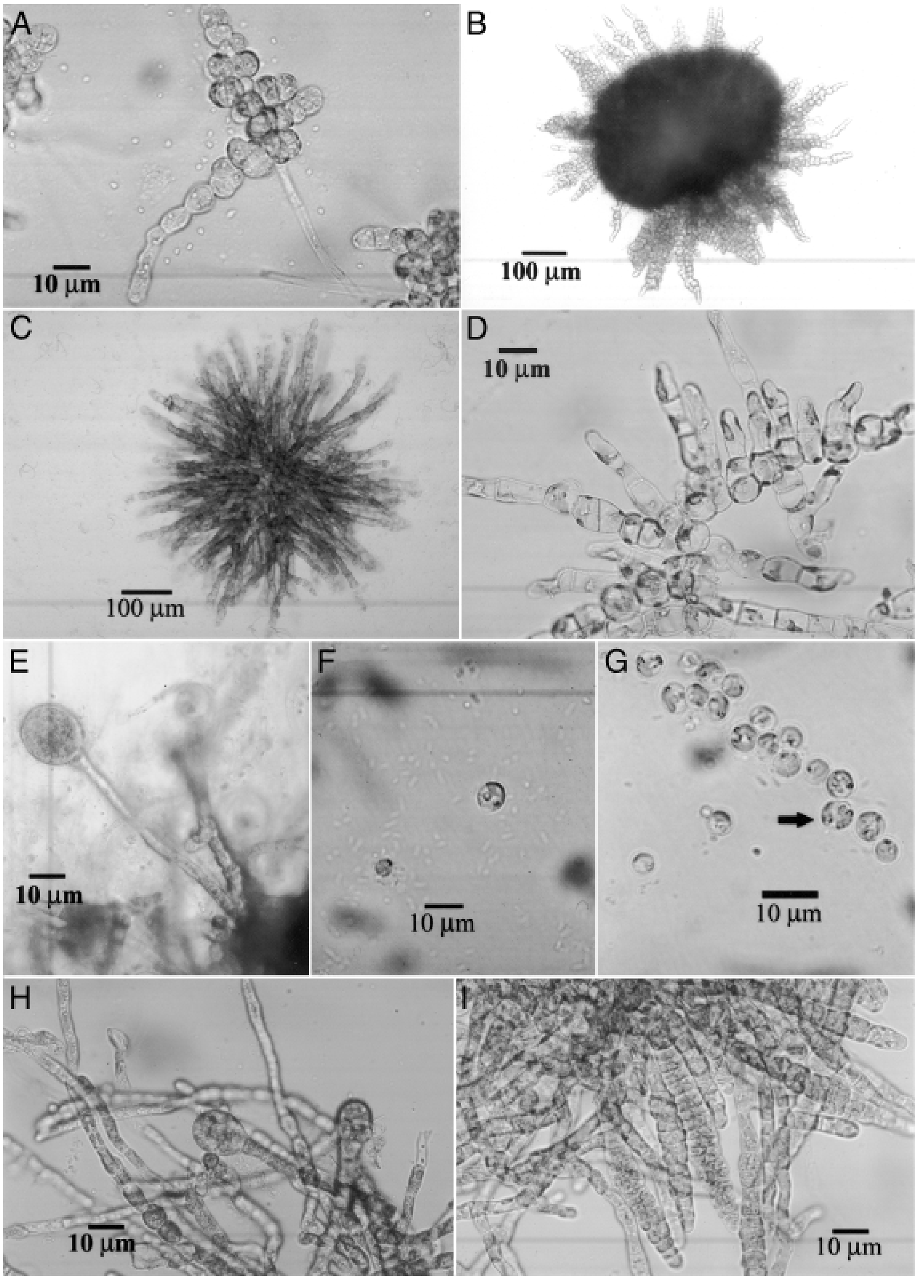

FIG. 3. Development of *Colpomenia sinuosa* in culture. (A and B) Progeny derived from asexual plurispores. (A) Pearl necklace. (B) "Blossom." (C–E) Parthenogenetic pathway. (C) Filamentous prostrate tuft; (D) 1- to 2-week-old filamentous germling; (E) unilocular sporangium on prostrate thallus. (F–I) Sexual fusion, progeny derived from zygotes. (F) Smaller male gametes (mgt) surrounding larger female gametes (fgt); (G) zygote, with two eyespots (arrow); (H) obovoid unilocular sporangia on prostrate thallus; (I) ectocarpoid plurilocular sporangia on prostrate thallus.

one resembling a pearl necklace (Fig. 3A) and another involving a prostrate system that was given the name "blossom" (Fig. 3B). In the first pattern, asexual plurispores germinated into small spherical balls of cells, which gave rise to a saccate thallus. The second pattern of development gave rise to small pseudodisks with a concentration of central cells that rapidly became swollen, also developing into a saccate thallus. These new saccate plants produced in the laboratory gave rise to a new generation of erect plants.

Parthenogenetic pathway. Most settled unfused female gametes, under both culture conditions, gave rise to filamentous prostrate tufts (Fig. 3C) bearing unilocular sporangia. In about 1–2 weeks, the female gametes developed into filamentous germlings (Fig. 3D), and in about 4–5 weeks these gave rise to prostrate tufts reaching 2–3 mm in diameter. These became fertile in 2 months. The unilocular sporangia (Fig. 3E) measured $20–25 \times 30–35\,\mu m$, were ovoid and terminal on the erect filaments. Most unfused male gametes did not geminate. A few developed into small germlings but died a short time later. The unispores ($5–8\,\mu m$) released from the unilocular sporangia, under both culture regimes, developed into small germlings which gave rise to saccate thalli.

Plasmogamy. When female and male gametes where mixed, the large female gametes settled first and were surrounded by several smaller male gametes (Fig. 3F). On each occasion, only one male gamete fused with a female gamete to form a zygote, with two eyespots (Fig. 3G).

Development of zygotes. The zygotes gave rise to filamentous prostrate tufts bearing obovoid unilocular sporangia (Fig. 3H) under both culture regimes and to both obovoid unilocular and ectocarpoid plurilocular sporangia (Fig. 3I) under low temperature/short-day condition. Unispores from zygotic thalli and those produced from parthenogenetic thalli were morphologically very similar, and both produced saccate plants under any of the culture conditions. Plurispores from zygotic prostrate tufts germinated into filamentous germlings that developed into filamentous prostrate tufts, similar to those produced by the development of zygotes and unfused female gametes.

The culture conditions did not seem to affect the morphological expression or the development of the reproductive cells. Erect and prostrate thalli, unispores, asexual plurispores, and gametes were developed in both culture regimes, the only exception being the plurispores from the plurilocular sporangia on the prostrate thalli that were only produced in 15° C short-day conditions. Three types of life history (Fig. 4) were observed on Azorean material. In the heteromorphic diplohaplontic life history, the zygotes gave rise to filamentous prostrate tufts (diploid sporophytes) bearing unilocular and plurilocular sporangia. The development of unispores from zygotic prostrate thalli allowed the passage of the sporophyte phase to the gametophyte phase and the plurispores developed into new sporophytes.

DISCUSSION

Studied gametophytes collected in the field were in agreement with the descriptions of Sauvageau (1927), Fritsch (1945), Blackler (1964), Clayton (1975), Wynne and Norris (1976), and Parsons (1982), and the studied material was confirmed to be *C. sinuosa.* The present work was the first attempt to study the life history of this species in the Azores and revealed the occurrence of three types of life history. Sexual reproduction, and consequently the formation of zygotes, was also reported by Kunieda and Suto (1938) for *C. sinuosa* from Japan, but no sporophyte generation with sporangia was observed from the development of the zygotes.

The morphology and motility of female and male gametes produced by Azorean *C. sinuosa* were similar to those previously reported by Clayton (1979) and Kogame and Yamagishi (1997) in *C. peregrina* from Australia and Japan, respectively. In the present study, and for the first time, female and male gametophytes simultaneously produced gametes and asexual plurispores. Male gametes and asexual plurispores from the same erect plant were easily distinguished by their size and appearance. On the other hand, female gametes and asexual plurispores could only be distinguished based on their progeny. Similar findings were reported by Toste et al. (2003) for the Azorean *Hydroclathrus clathratus* (Bory ex C. Agardh) M. Howe. Clayton (1981), working with *Scytosiphon* from Australia, also reported the occurrence of both reproductive organs on the same plant, but the liberation of reproductive cells was not simultaneous, depending instead on the sexual maturity of the plant. Gametophytes 8–10 weeks old produced asexual plurispores. The same plants after 22–24 weeks produced functional gametes.

Two asexual life history pathways were observed in the Azorean *C. sinuosa*: a monomorphic, monophasic life history in which the development of asexual plurispores from both female and male gametophytes gave rise to new erect plants, and a parthenogenetic pathway, carried out by unfused female gametes (a heteromorphic, monophasic cycle), in which new prostrate thalli, bearing unilocular sporangia, were produced. Blackler (1981), working with Atlantic *C. sinuosa*, and Clayton (1982), working with *C. sinuosa* from Australia, reported the occurrence of a direct-type life cycle by means of plurispores but did not observe a pathway corresponding to the parthenogenetic one of the Azorean *C. sinuosa*. On the other hand, Kogame (1997), working with Japanese *C. sinuosa*, reported that spores from plurilocular sporangia on erect thalli produced a prostrate system that became fertile with unilocular and plurilocular sporangia, without sexual reproduction. Similar findings were obtained by Wynne (1972), working with *C. sinuosa* f. *deformans* Setchell et Gardner from California, but in this case the prostrate thalli bore only plurilocular sporangia. In the Azorean material, only the zygotic prostrate thalli, assumed to be the sporophytes, developed both unilocular and

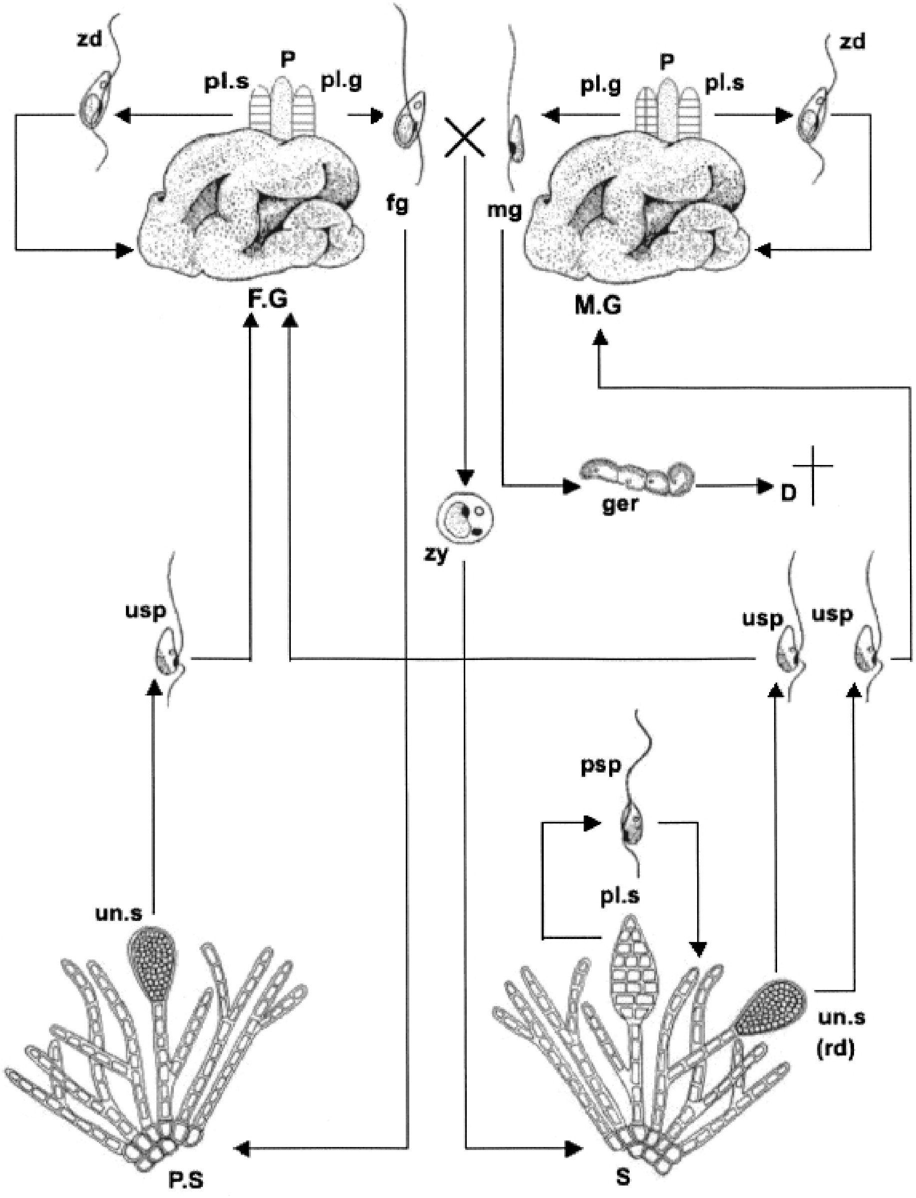

FIG. 4. Diagrammatic illustrations of the life history of Azorean *Colpomenia sinuosa* in culture. F.G, female gametophyte; M.G, male gametophyte; fg, female gamete; mg, male gamete; zy, zygote; S, sporophyte; pl.s, plurilocular sporangium; psp, plurispore; un.s, unilocular sporangium; rd, reduction division (based on Kogame and Yamagishi 1997 for *C. peregrina*); usp, unispore; P.S, parthenosporophyte; ger, germling; D, death; P, paraphysis; pl.g, plurilocular gametangium; ap, asexual plurispore.

plurilocular sporangia. Reproductive cells from the plurilocular sporangia of the Azorean pro-strate sporophytes developed directly into new prostrate thalli. The same was reported by Kogame (1997). Conversely, Wynne (1972) observed that spores liberated from plurilocular sporangia of prostrate microthalli developed into erect plants. In the studied material, the spores from the unilocular sporangia gave rise exclusively to new erect macrothalli. Similar findings have been reported for *C. sinuosa* (Kogame 1997), *C. peregrina* (Clayton 1979, Kogame and Yamagishi 1997), and *C. bullosa* (Saunders) Yamada (Nakamura and Tatewaki 1975).

Although not supported by cytogenetic investigations (Nakamura and Tatewaki 1975), the results of the present study indicate a partial independence between the phenotypic expression and the ploidy level of Azorean *Colpomenia* plants in which erect haploid gametophytes alternate with prostrate diploid sporophytes in the heteromorphic diplohaplontic life history and with haploid prostrate microthalli in the heteromorphic monophasic cycle.

In the same dish with material from the same plant, two development pathways were observed, one giving rise to erect thalli and the other producing a filamentous prostrate thalli. This has not been described before for *Colpomenia*, although Wynne (1969) reported similar findings for *Petalonia fascia* (O. F. Müller) Kuntze and *Scytosiphon lomentaria* (Lyngbye) Link.

In the present study, the culture conditions did not affect the morphological expression. This is in agreement with the observations of Clayton (1979) and Kogame and Yamagishi (1997) for *C. peregrina*. However, Nakamura and Tatewaki (1975) reported the effect of the temperature on the type of thalli produced by several Scytosiphonaceae species. In *Colpomenia bullosa*, *Endarachne binghamiae* J. Agardh, *Petalonia zosterifolia* (Reinke) O. Kuntze, and *Scytosiphon lomentaria*, erect thalli were produced at lower temperatures and prostrate thalli were developed at higher temperatures. A similar situation was reported by Fletcher (1974) for *Petalonia fascia*, *P. filiformis* (Batters) O. Kuntze, *Scytosiphon lomentaria*, and *Ralfsia clavata* (Harvey) Crovan.

The only effect of the culture conditions on the development of reproductive organs or cells observed in the present study was the production of plurispores from the plurilocular sporangia on the prostrate thalli only in winter conditions. Other studies have documented more pronounced effects. In *C. sinuosa*, Kogame (1997) observed that the formation of reproductive organs on prostrate thalli was directly related to photoperiod and temperature, plurilocular zooidangia being formed in long-day conditions and unilocular zooidangia in short-day conditions. Peters (1987), working with *Spermatochnus paradoxus* (Roth) Kützing, reported that gametophytes produced gametes at lower temperatures and asexual plurizooids similar to gametes morphologically at higher temperatures in culture.

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