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Article

Life cycle of *Punctaria latifolia* (Chordariaceae, Phaeophyceae) from the coast of Buenos Aires Province, South America

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With 19 figures

Abstract: The objective of this study was to describe the morphology of *Punctaria latifolia* individuals from the natural environment, their life cycle under culture conditions and the caryology of different phases. The life cycle of *Punctaria latifolia* was studied under culture conditions (140 µmol m^{-2} s^{-1}; 12 h/12 h; 21 ± 1 °C). Fertile sporophytes were collected in the intertidal zone of Bahía San Blas (Buenos Aires, Argentina, South America), in August and December 2003. These macroscopic laminar plants were found adhered to the rocky substrate and on *Spartina alterniflora* plants. Sporophytes from the natural environment presented both plurilocular and unilocular sporangia, which released plurispores and unispores, respectively. The asexual reproduction was evidenced by the germination of unispores by formation of a single - pole germination that formed microscopic filamentous gametophytes. Terminal and intercalar gametangia released isogametes. Zygotes reconstituted the macroscopic phase. Chromosome counts gave 16 and 8 for sporophytic and gametophytic phases, respectively. This species presented a haplodiplobiontic heteromorphic life cycle as well as a direct type, when plurispores produced plethysmothalli.

Key words: Argentina, chromosomic number, life cycle, Phaeophyceae, *Punctaria latifolia*

Introduction

Representatives of the genus *Punctaria* Greville 1830 (Phaeophyceae, Chordariaceae) are characterized by parenchymatous thalli, reproductive organs immersed in frond, as well as by epidermic and medullar cells of approximately equal size, arranged in regular layers (Asensi 1966). They present an alternance of

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heteromorphic generations. Unilocular and plurilocular sporangia or both are located on the entire surface of the sporophytic macrothallus, frequently associated to paraphyses. Iso - or anisogametes are released from microscopic gametophytes (HAMEL 1931–1939, ASENSI 1966).

The marine brown alga *Punctaria latifolia* GREVILLE was frequently registered for several parts of the world, under this name or different synonyms (*Punctaria hiemalis* KYLIN 1907, *Punctaria plantaginea* var. *crouanii* THURET). FETCHER (1987) and GUIRY & GUIRY (2010) treat *P. plantaginea* var. *crouanii* as conspecific with *P. latifolia*.

P. latifolia was mentioned for the European coasts (ADAMS 1907, GUIRY 1977, 1978, MUNDA 1979, IRVINE 1982, WHELAN & CULLINANE 1985, FLETCHER 1987, MORTON 1994, RUENESS 1997, NIELSEN & GUNNARSSON 2001), for those of North America (TAYLOR 1957, 1960, SCHNEIDER & SEARLES 1991), Asia (TSENG 1984, YOSHIDA et al. 1990), for Australia and New Zealand (WOMERSLEY 1987, ADAMS 1994, NELSON 1999). In Argentina, *Punctaria plantaginea* was reported in the Patagonia, Tierra del Fuego and Islas Malvinas and *Punctaria latifolia* in the Patagonia (JOLY 1967) and the province of Santa Cruz (ASENSI 1966, MENDOZA & NIZOVOY 2000).

The investigations of the life cycle of the Phaeophyceae continue being made and the accumulated data in the recent years have contributed for a better understanding of the existing variations between these seaweeds. Moreover, this information was reconsidered as the fundamental basis for the classification of the brown seaweeds, particularly at an order level (FLETCHER 1987).

Only a small number of studies have been published on the life cycle of the genus *Punctaria*. They suggest that it possesses a "direct type" cycle, as in *Punctaria latifolia* studied in France by DANGEARD (1963, 1966) and in Australia by CLAYTON & DUCKER (1970).

Refined cultural techniques such as clonal isolates and the culture of defined single cells combined with chromosome counts are necessary to confirm the occurrence of sexual phenomena in the isogamous microscopic gametophytes (MÜLLER 1984), which are characteristic of the families Chordariaceae and Dictyosiphonaceae.

The objective of this investigation was to describe the morphology of *Punctaria latifolia* individuals from the natural environment, their life cycle under culture conditions and the caryology of different morphological phases to reach a better understanding of its biology.

Materials and methods

Thalli of *Punctaria latifolia* were collected at the intertidal zone of Bahía San Blas (40º32'60''S, 62º15'W), Argentina on August 15th and December 8th 2003.

Bahía San Blas is situated in a cold temperate region, with average air temperature of 7.6 ºC in winter and 19.2 ºC in summer. The vertical profiles of seawa-

ter temperature show a homothermic state, presenting an annual average value of 12.2 ºC and its extreme values coincident with times of minima and maxima air temperatures, reaching a difference of 16 ºC (Alvarez & Ríos 1988). It presents rocky substrate, which allows the establishment of an algal vegetation.

The material was identified following the criteria proposed by Asensi (1966): morphology of the thalli, position and size of reproductive organs and disposition of cortical and medullar cells, and by Hamel (1931–1939): presence, forms and distribution of plurilocular sporangia. The identified material was deposited in the Herbarium of Universidad Nacional del Sur: BBB (Gauna 100), BBB (Gauna 101).

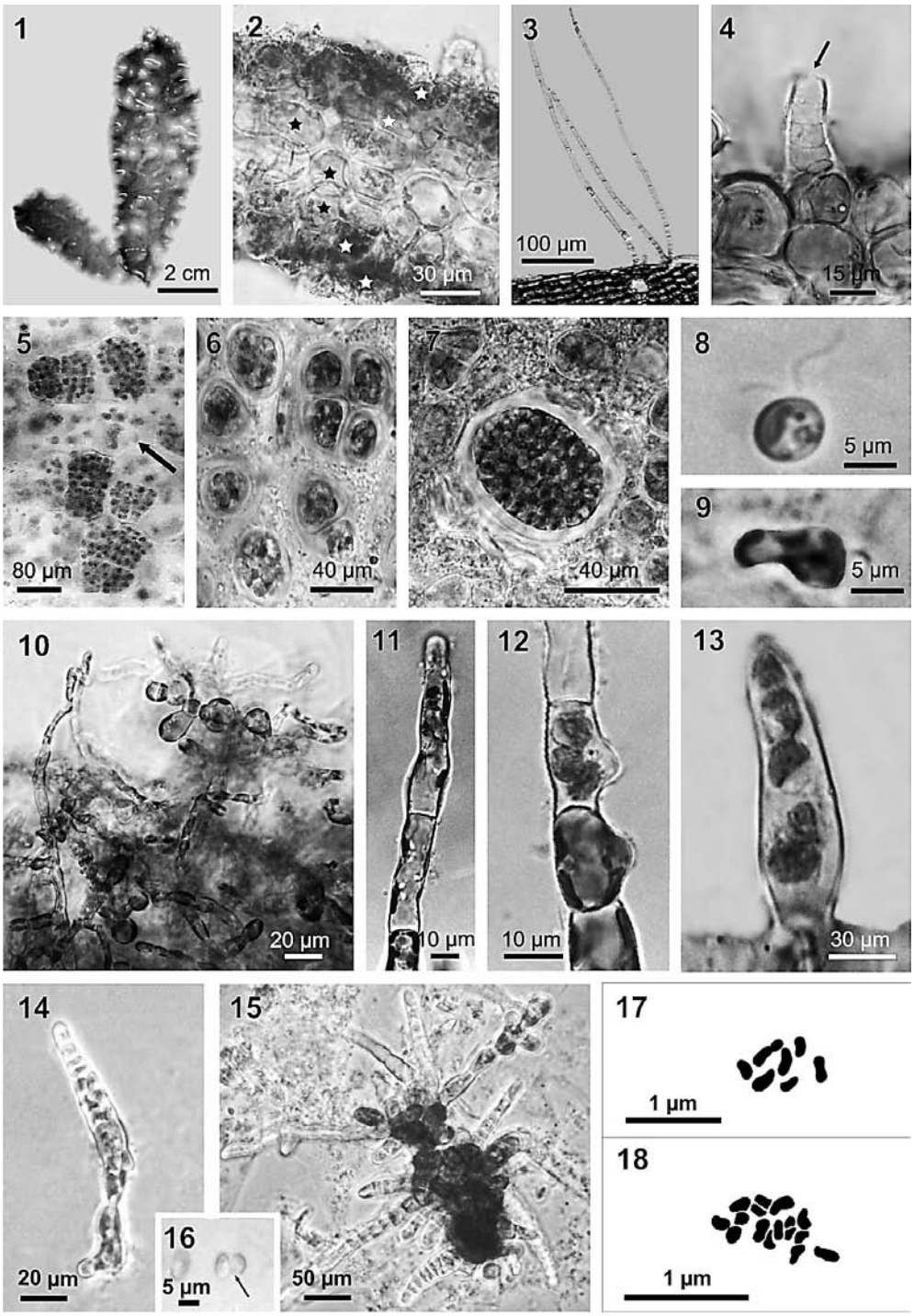
Fragments of *Punctaria latifolia* thalli with unilocular or plurilocular sporangia were individually inoculated into 20 Nalgene tubes containing 6 mL filtered (Millipore 5 µm) and sterilized (121 ºC and 1 atm, during 15 minutes) seawater which was enriched according to Provasoli (1968). Cultures were maintained at room temperature (21 ± 1 °C) and illuminated with 140 µmol m^{-2} s^{-1} from a daylight-type fluorescent lamp for 12 h/day during two months. The culture media were replaced weekly. In order to avoid the contamination by diatoms, one or two drop of 2.5 % germanium dioxide (GeO_2) solution was added to 10 mL of culture medium (Lewin 1966). Part of the material was fixed in formaldehyde 4 %.

Morphological aspects of different life cycle stages were observed with a stereoscopic microscope Wild Herbrugg and an inverted microscope Nikon Eclipse TE 300 with photo camera Nikon FDX 35. For caryology, material was fixed with ethanol – glacial acetic acid solution (3:1) or formaldehyde – ethanol – glacial acetic acid solution (6:3:1). In both cases, the samples were maintained at 5 ºC and conserved in ethanol 70 % until the moment of the coloration. A modified Schiff technique was used for staining (Núñez 1968). Hydrolysis was made at room temperature in hydrochloric acid 1N during 30 minutes. Then the material was washed with running water and stained with the reactive of Schiff (Johansen 1940) for 30 minutes. Distilled water was used to accentuate the colour. Previous to observation, a squash of the material was made between slides and cover slips in glacial acetic acid (45 %) and distilled water.

Results

Punctaria latifolia thalli were observed on *Spartina alterniflora* Loisel plants and on rocks. The sporophytes from natural environment showed olive brown unbranched laminar thalli, with irregular edges (Fig. 1). They reached 8 cm in height and 100 µm in thickness. Each lamina presented a very short and thin stipe. In cross sections, the thallus was differentiated into two distinct zones (Fig. 2): 1) medullar zone, constituted by 3 layers of roundish colourless cells; 2) cortical zone, constituted by mono- or bistromatic layers of roundish cells, with discoid plastids, at both sides of the fronds. The medullar cells were large, with roundish

Figs 1–12. *Punctaria latifolia*. **1.** Sporophytic thallus from Bahía San Blas. **2.** Cross section of the middle part of a sporophytic thallus, showing a medullar zone with 3 layers of cells (🡻) and two cortical zones with 2 layers each one (☆). **3.** Hyaline hairs on the surface of a sporophytic thallus. **4.** Plurilocular sporangium with apical pore (arrow) projecting from the surface. **5.** Superficial view of plurilocular sporangia distributed in sori, surrounded by cortical cells. **6.** Superficial view of unilocular sporangia. **7.** Detail of superficial view of unilocular sporangium, showing the thickness of the cell wall. **8.** Biflagellated zoospore. **9.** Single-pole germination of the zoospore. **10.** Gametophytic thalli formed from unispores. **11.** Detail of gametophytic filament formed from unispores, note the plastids (arrows). **12.** Intercalate gametangia between empty and normal cells. **13.** Terminal gametangium. **14.** Fusion of gametes (arrow). **15.** Stage of protonema. **16.** Early stage of parenchymatous phase. Note the plurilocular sporangium (arrow). **17.** Schematic representation of a haploid metaphase plate with 8 chromosomes. **18.** Schematic representation of a diploid metaphase plate with 16 chromosomes.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to ovoid form (15 x 26 μm). The cortical pigmented cells were slightly smaller than medullar cells (10–11 μm) and exhibited a thicker wall. In surface view, the thalli showed long, straight, multicellular hyaline hairs of approximated 300–500 μm length (Fig. 3). Two types of sporangia were observed. The plurilocular sporangium was clearly projected from the surface of the sporophytic thallus (Figs 4 and 5). It was pear-shaped, 48 μm long and 20 μm wide, divided in small oval locules, where biflagellated plurispores originated. The plurispores were released through an apical pore (Fig. 4). These sporangia were surrounded by a thickened wall (Fig. 5). Immersed unilocular sporangia were distributed in sori, 74 to 83 μm in diameter. They were surrounded by small, rectangular cortical cells (Figs 6 and 7). The mature unispores were released by a terminal opening in the sporangia. Both unispores and plurispores were pear-shaped, with an approximated size of 5 x 3 μm, with basal chloroplast and stigma (Fig. 8).

In culture, it was possible to observe the adhesion of unispores to the substrate and their later germination (Fig. 9). During the initial steps, the fixed unispores lost the flagella and then they formed a hyaline germination tube (single – pole germination). Later, by cytogenesis, two portions were formed, one basal and colourless and the other apical and pigmented, which originated a young filamentous thallus through successive cell divisions. They developed microscopic, slightly heteromorphic filamentous gametophytes, in which gametangia were developed after five weeks.

Initially, gametophytic filaments presented cylindrical cells, with one or more discoid plastids. By the end of the development, two types of morphologically different gametophytes were observed: those formed by spherical cells (Fig. 10) and those formed by cylindrical cells; both with 1 or more discoid plastids (Figs 10 and 11). The cylindrical cells of gametophytes measured 31 μm in length and 8 μm in width (Fig. 11). Some of the first ones developed gametangia, 34 μm in length and 30 μm in width. Different types of gametangia were observed in them: intercalate, ovoid gametangia (Fig. 12) and terminal, pear-shaped or spherical gametangia (Fig. 13). Isogametes were ovoid and with stigma (Fig. 12). Syngamy took place, shortly (2 h) after liberation (Fig. 14).

On the other hand, plurispores formed in plurilocular sporangium, forming a protonema, primary stage of new macrocospic plants. It expanded constituting the plesthysmothallus, laminar stage in which basal and erect systems were observed (Fig. 15). Later, plurilocular sporangia developed in the apical region of the plesthymothallus (Fig. 16).

In the gametophyte, the haploid chromosomic number was n = 8 (Fig. 17), whereas in the sporophyte the diploid chromosomic number was 2n = 16 (Fig. 18).

The *Punctaria latifolia* haplodiplobiontic and heteromorphic life cycle is summarized in figure 19.

Discussion

Life cycle

The genus *Punctaria* is characterized by presenting a dimorphic life cycle, as all the representatives of the orders Chordariales and Dictyosiphonales (VAN DEN HOEK et al. 1995).

The populations of *Punctaria latifolia* studied in this work also presented a life cycle with alternance of sporophytic (2n) and gametophytic (n) generations but showed a "direct type" life cycle, similarly to other species (DANGEARD 1963, 1966, CLAYTON & DUCKER 1970). As was observed in our investigation, in a "direct type" life cycle, sporophytic generations appear to follow one another without the intervention of sexual processes. Successive generations of macrothalli from plurispores were formed, as it has been indicated for Australian populations of this species (CLAYTON & DUCKER 1970) and also for *P. orbiculata* JAO (JAO 1937, SOUTH 1980). Nevertheless, the formation of macrothalli from unispores, as CLAYTON & DUCKER (1970) described for *Punctaria latifolia,* has not been observed in the present paper.

Our results are similar to the observations by HAMEL (1931–1939) and CLAYTON (1982) in *Punctaria latifolia*. HAMEL (1931–1939) reported that the early spring zoospores, released from plurilocular sporangia, germinated producing protonemata of rapid development that in turn generated germlings. Before the formation of these plantules, plesthymothalli with sessile and siliquiformes plurilocular sporangia formed. CLAYTON (1982) showed that zooids released by macrothalli did not behave as gametes and most of them developed directly into similar macrothalli in culture.

RUSSELL (1970), when studying *Desmotrichum undulatum* (AGARDH) REINKE, currently a synonym of *Punctaria tenuissima* (C. AGARDH) GREVILLE, reported that plurispores released from plurilocular sporangia never generated microthalli. In our study, the plesthymothalli were always originating from plurispores. Moreover, RUSSELL (1970) did not report sexual reproduction and presence of unilocular sporangia as we described in this work. Also, these populations of *P. latifolia* fom San Blas presented the same pattern of isogamy described by CLAYTON & DUCKER (1970).

As CLAYTON & DUCKER (1970), we observe that the early stages of growth of *P. latifolia* resemble *Streblonema* spp. having entirely postrate filaments from which arise upright, colourless hairs with a basal meristem and plurilocular sporangia. These are the plethysmothalli which initiate the parenchymatic fronds. The unispores and plurispores both produce plants resembling the unilocular sporangium. These types of life cycle are not uncommon in the Phaeophyceae and have been discussed several years ago by CARAM (1965), MATHIESON (1967) and WYNNE (1969).

Caryology

To date, the chromosomic number had been determined for *P. plantaginea* (n = 8 and 2n = 16) (KNIGHT 1929). The same results obtained in *Punctaria latifolia* indicate a haploid chromosomic number, included in the basic haploids complements of the Phaeophyceae, which range from 8 to 13 (COLE 1967, 1968, MÜLLER & STACHE 1989).

Taxonomy

In the present paper, we show that individuals of Argentine populations of *Punctaria latifolia* were different from those of Australia (CLAYTON & DUCKER 1970) by presenting small, solitary, plurilocular pear-shaped sporangia, located among cortical cells of the fronds. This trait is also coincident with those observed by KYLIN (1933) in *Desmotrichum undulatum*.

The differences between *Punctaria latifolia* and the other species of the genus are mainly associated with the presence/absence and the morphology of the sporangia.

In this sense, *P. latifolia* differs from *P. plantaginea* var. *crouani* THURET by the forms of their plurilocular sporangia, because *P. plantaginea* var. *crouani* has siliquiform sporangia. In both species, moreover, plurilocular sporangia are observed like projections on the thallus, but in *P. plantaginea* var. *crouani* they are longer, exceeding a third of the cells height (HAMEL 1931–1939). On the other hand, *P. latifolia* also differs from *Punctaria crispata* (KÜTZING) BATTERS and the lectotype of the genus *Punctaria, Punctaria plantaginea,* because both lack plurilocular sporangia. HAMEL (1931–1939) reported for *P. crispata* another difference like the greater size and thickness of the fronds, the absence of hairs and the same number of cell layers in cross section for *P. plantaginea* and *P. latifolia*, but the hair and zoospore dimensions were smaller in the latter.

We adhere to the criterion of SOUTH & TITTLEY (1986) in judging both species, i.e. *Punctaria latifolia* and *P. plantaginea* as synonymous since we consider that environmental conditions influence morphology and the reproductive stages, as was indicated by RUSSELL (1970) and LÜNING (1990), thus reducing the weight of morphological differences between them as variations in the size of the sporophyte, zoospores and hairs. Moreover, both species present an equal chromosomal complement in their haploid and diploid phases. Consequently, we consider that the previous reports of *P. plantaginea* for Argentina correspond to *Punctaria latifolia*, extending thus the distribution of the latter from parallel 47°S to parallel 40°S.

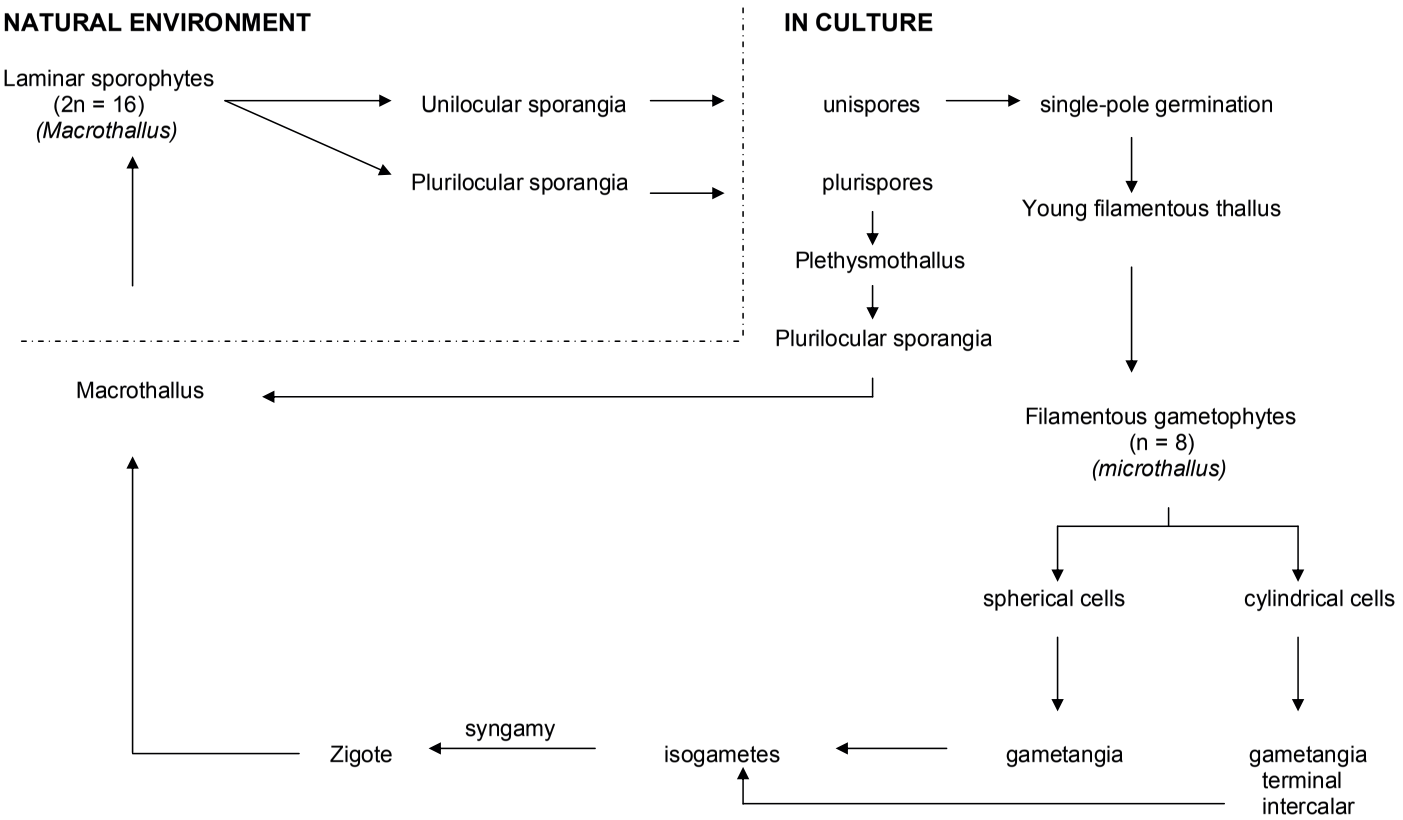

Fig. 19. *Punctaria latifolia*: Outline of the life cycle.

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