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Short communication

Contribution to the embryology of *Leiothrix fluitans* (Eriocaulaceae: Poales)

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Abstract

This paper presents a contribution to the understanding of the embryology, especially microsporogenesis, the antipodal cell behavior, and the early stages of the micropylar seed operculum, in *Leiothrix fluitans*, to elucidate these aspects both within the subgenus *Rheocaulon* and within the genus in Eriocaulaceae. Contrarily to previous descriptions of this same species, our results show the following: microsporogenesis is of the successive type and results in isobilateral microspore tetrads; the antipodal cells gradually fuse together to form a conspicuous cyst; and the inner integument, which does not develop into an endothelium, shows evidence of the initiation of the seed operculum in its micropylar end. Such features are common to the family as a whole. Evidenced for the first time in the family, the chalazal end of the ovule differentiates into a hypostase closely associated to the antipodal cyst. These overall features of *L. fluitans* point out previous misinterpretations on some of its embryological aspects, especially those concerning the only report of simultaneous microsporogenesis and proliferation of the antipodal cells. Furthermore, the results presented here allow us to reinforce the uniformity of the embryological aspects within the Eriocaulaceae, strengthening the cystic arrangement of the antipodal cells as a potential autapomorphy of the family within the other Poales (commelinids).
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Keywords: Antipodal cyst; Commelinids; Microsporogenesis; Pollen grain; Seed operculum

1. Introduction

Eriocaulaceae is a well-defined monocot family comprising eleven genera and circa 1200 species distributed throughout the tropics and subtropics (Giulietti et al., 1995; Sano, 2004) and distinguished by its characteristic inflorescence called capitulum. The greatest species diversity for the family is found in South America, especially in the Cadeia do Espinhaço Mountain Range, Brazil.

Leiothrix Ruhland includes about 37 species distributed exclusively in South America, mainly restricted to Brazil (Giulietti et al., 1995; Stützel, 1998). According to Giulietti and Pirani (1988), the State of Minas Gerais (Brazil) is the centre of diversity of the genus with 30 species, mostly endemic to small areas. Ruhland (1903) divided the genus *Leiothrix* into five subgenera: *Calycocephalus*, *Eleutherandra*, *Psilandra*, *Rheocaulon*, and *Stephanophyllum*. In their taxonomic studies on the genus, Giulietti (1984) and Giulietti et al. (1995) recognized four of those subgenera were valid, but merged *Psilandra* into a section of genus *Syngonanthus*.

Although taxonomically important, subgenus *Rheocaulon* only includes one species, *Leiothrix fluitans*. It was distinguished by Ruhland (1903) and Giulietti (1978) because of the elongate stem and of the free inner tepals of the staminate flower. *Leiothrix fluitans* is the only aquatic species in the whole genus and its occurrence is restricted to the State of Minas Gerais (Brazil). It grows on riverbeds and on the rocks of waterfalls (Giulietti, 1984). The species possesses many adaptations to the aquatic environment, mainly represented by the submerged and reduced leaves, with only one vascular bundle, the absence of trichomes and presence of air spaces, the low stomata number, and two root types, specialized in air storage and in substrate fixing (Monteiro et al., 1985; Coan et al., 2002).

The embryology of specimens of all the accepted subgenera of *Leiothrix* has been studied, from pollen morphology (Thanikaimoni, 1965), to embryogeny (Ramaswamy and Arekal, 1982a) and to seed structure and development (Giulietti et al., 1988). Monteiro-Scanavacca and Mazzoni (1978) described the embryology and seed development of *L. fluitans*, stressing the occurrence of tetrahedral microspore tetrads resulting from simultaneous microsporogenesis, the presence of a well-developed endothelium in the ovule, the proliferation of the antipodal cells in the megagametophyte, and the formation of a reduced caruncle in the seeds. When comparing

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these embryologic data of *L. fluitans* with those of a related species, *L. nubigena*, Ramaswamy and Arekal (1981a,b) first pointed out some misinterpretations in the study by Monteiro-Scanavacca and Mazzoni (1978). According to Ramaswamy and Arekal (1981a,b), the antipodal cells do not proliferate in *Leiothrix*, but develop into a conspicuous cyst, as is known for all the species from the other genera already studied.

Based on the description by Monteiro-Scanavacca and Mazzoni (1978), some embryological aspects of *L. fluitans* suggest different character states in the family, which are not consistent features when compared to the other species studied (Begum, 1968; Arekal and Ramaswamy, 1980; Ramaswamy and Arekal, 1981a,b,c, 1982b; Ramaswamy and Nagendran, 1996; Giulietti et al., 1988; Scatena and Bouman, 2001; Coan and Scatena, 2004; Coan et al., 2007), mainly those related to the type of microsporogenesis, the endothelium formation in the ovule, the antipodal behavior, and the origin of the caruncle in the seed.

Since the embryologic data on Eriocaulaceae have proved uniform in specimens of the different genera already studied, and even in other *Leiothrix* species, but contrast with those previously presented by Monteiro-Scanavacca and Mazzoni (1978) for *L. fluitans*, the aim of the present study was to elucidate its embryology, with an emphasis on the microsporogenesis, the ovule integument development, and the antipodal cell behavior.

2. Material and methods

Inflorescences of *L. fluitans* (Mart.) Ruhland at different developmental stages were collected in the Serra do Cipó, district of Santana do Riacho, along the highway MG-010 (Minas Gerais, Brazil), and fixed in FAA 50 (1 formalin:1 glacial acetic acid:18 ethanol, v/v) (Johansen, 1940). The material was then transferred and stored in 70% ethanol with a few drops of glycerin. Vouchers of *L. fluitans* were deposited at the Herbarium of the Department of Botany, Universidade Estadual Paulista (HRCB 33562, HRCB 39172) and at the Herbarium of the Department of Botany, Universidade de São Paulo (SPF 146328).

For light microscope (LM) examination, the material was dehydrated through a normal-butyl alcohol series under vacuum (Feder and O'Brien, 1968, with modifications in dehydration times), embedded in (2-hydroxyethyl)-methacrylate, and sectioned at 4–8 μm on a Reichert-Jung Model 2040 Microtome using glass knives. The sections were then stained with periodic acid–Schiff's reagent (PAS reaction) and toluidine blue (Feder and O'Brien, 1968).

For scanning electron microscopy (SEM), fixed mature anthers were dehydrated through an absolute ethanol series, critical point dried, coated with gold, and examined using a JEOL JSM-P15 scanning electron microscope.

3. Results

The present study confirms most of the embryological characters Monteiro-Scanavacca and Mazzoni (1978) described for *L. fluitans*. To avoid data duplication, we only present the characters differing from this previous work here.

In *L. fluitans*, the cells of the sporogenous tissue differentiate into microsporocytes that undergo meiotic divisions and form dyads (Fig. 1A and B) and isobilateral microspore tetrads (Fig. 1C and D) enclosed in a callose coat. Microsporogenesis is of the successive type. At the tetrad stage (Fig. 1D), the longitudinal sections show two microspores in each tetrad, which forms a row and fills completely the anther locule.

The fairly thick callose coat deposited around each microspore (Fig. 1D) dissolves soon after meiosis and releases the four microspores into the anther locule (Fig. 1E). The microspores enlarge, separate, acquire a spherical shape, and accumulate starch in their cytoplasm (Fig. 1E and F). At anthesis stage, pollen grains are shed at the binucleate stage (Fig. 1G). Pollen is spiraperturate (Fig. 1H).

The anther wall develops according to the "monocotyledonous" type and comprises epidermis, endothecium, middle layer and tapetum (Fig. 1B). As the anther develops, the epidermal cells shrink, except at the stomium (Fig. 1E and F). The endothecial cells increase in size and develop regular band-like thickenings on their anticlinal and outer periclinal walls, while the inner periclinal one constitutes the complete and non-perforated baseplate (Fig. 1E and F). The endothecial thickening is of the baseplate type (Fig. 1E and F), following the terminology proposed by Manning (1996).

In the ovular primordium, the inner integument forms before the outer one (Fig. 2A) and both are initially dermal and possess two cell layers. The one-layered nucellar epidermis (Fig. 2A and B) is gradually compressed as the ovule develops (Fig. 2C) and leaves remains in the micropylar region (Fig. 2F and G).

The inner cell layer of the inner integument of the ovule does not differentiate into an endothelium and shows no cell differentiation or amyloplast accumulation (Fig. 2F and H).

The meiosis of the megasporocyte (Fig. 2A) produces a T-shaped tetrad of megaspores in which only the chalazal one is functional (Fig. 2B). During megagametogenesis, the functional chalazal megaspore divides to form a megagametophyte of the Polygonum type (Fig. 2C).

The three-celled egg apparatus lies in the micropylar region of the megagametophyte (Fig. 2F). Soon after organization, the antipodal walls dissolve and the three uninucleate protoplasts gradually fuse together resulting in a conspicuous antipodal cyst (Fig. 2D). This cyst acquires a dense cytoplasm and its three nuclei increase in size (Fig. 2E). The three enlarged nuclei of the cyst then fuse together to form a single large nucleus (Fig. 2F). After fertilization and megagametophyte nutrition, the antipodal cyst becomes less conspicuous and recedes (Fig. 2G).

Concomitantly with the antipodal cyst formation, some chalazal cells become cutinized to form the hypostase (Fig. 2D and F). As for the antipodal cyst, the hypostase also becomes less conspicuous after fertilization (Fig. 2G).

As the megagametophyte develops, the cells of the inner integument that constitute the micropyle divide anticlinally (Fig. 2H, arrow). These cells become cutinized after fertilization (Fig. 2I, arrow) and point out the initiation of the

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