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Secondary cortex formation in *Osmundaria prolifera* (Amansieae: Rhodomelaceae)

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KURZFASSUNG: **Entwicklung einer sekundären Rinde bei *Osmundaria prolifera* (Amansieae: Rhodomelaceae).** Die polysiphonen Sprosse der Rotalge *Osmundaria prolifera* tragen an jeder Gliederzelle 5 Perizentralzellen. Mit Ausnahme der ventral gelegenen bilden die jeweils benachbarten Perizentralen je eine Reihe von Flügelzellen. Der so entstehende zweischichtige Flügelsaum wird frühzeitig von einer dicht geschlossenen, kleinzelligen Rinde eingehüllt. An den älteren Teilen des Thallus gehen die Flügelsäume verloren, wahrscheinlich werden sie durch Sand abgerieben. Dadurch dürften die primären Rindenzellen zu erneuter meristematischer Tätigkeit angeregt werden, so daß eine sekundäre Rinde entsteht; diese kann bis zu 0,5 cm dick werden. So ergibt sich die rundliche und knorpelige Achse im unteren Teil des Thallus.

INTRODUCTION

In contrast to the largely rhizoidal cortication of many members of the Ceramiales (especially in the families Ceramiaceae and Dasyaceae), some tribes in the Rhodomelaceae show a pseudoparenchymatic cortication (FALKENBERG 1901). Included in the latter category is the tribe Amansieae, where pseudoparenchymatic cortication is particularly well developed (SAENGER 1970). Cortex formation in Amansieae occurs by periclinal and anticlinal divisions of the pericentral cells and their derivatives, resulting in a primary cortex of 3 to 4 cells in thickness. The only exception in this tribe is *Amansia* where the primary cortex develops only along the midrib (FALKENBERG 1901, KYLIN 1956).

During subsequent development, however, the primary cortex of some species of this tribe may assume a meristematic activity and produce a secondary cortex, often up to 0.5 cm in thickness. Formation of such a secondary cortex in *Osmundaria prolifera* LAMOUROUX is described.

MATERIAL AND METHODS

Material on which this investigation was based, was collected at Venus Bay, South Australia (tetrasporic and cystocarpic), November 23, 1967; at Eucla and Twilight Cove, Western Australia (sterile), December 7, 1967; D Estrees Bay, Kangaroo Island, South Australia (cystocarpic), 11 December, 1968.

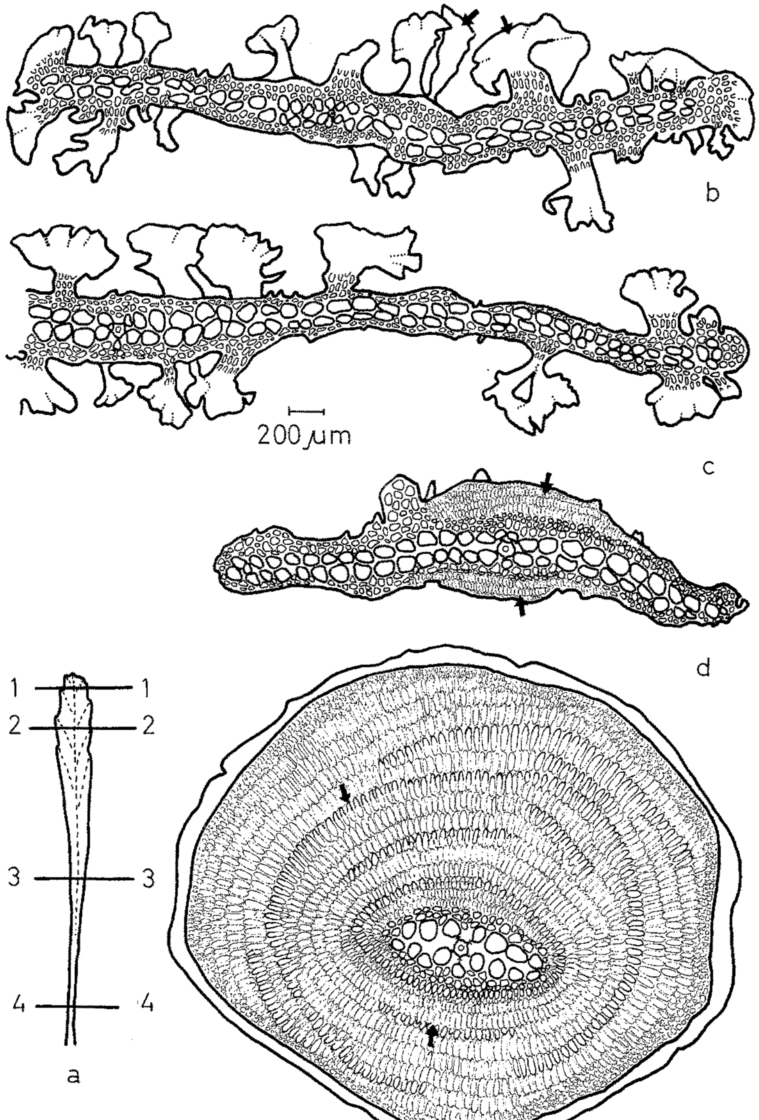

Fig. 1: *a* Blade of O. *prolifera* showing position of transverse sections illustrated in the subsequent figures (1:2). *b* Transverse section 1–1 with surface laterals (arrows), two-layered wing, and primary cortex. *c* Transverse section 2–2. Only half the section is shown but extended wing is complete. Note absence of secondary cortex. *d* Transverse section 3–3. Distal parts of wings have been lost and secondary cortex formation has commenced (arrows). Note loss of surface laterals. *e* Transverse section 4–4. Extensive secondary cortex has formed and growth zones are indicated (arrows)

All material was preserved in 4 % formalin-seawater, and sections were cut on a freezing microtome. The sections were dehydrated by means of an ethanol series and mounted in glycerine jelly with 0.5 % gentian violet.

RESULTS

Transverse sections (Fig. 1a) of the blades of *Osmundaria prolifera* show a central cell surrounded by 5 pericentral cells throughout their development. The first 2 pericentral cells are cut off in a dorsal position while the third and fourth pericentral cells are produced in a dorso-lateral position. The fifth, and last-formed, pericentral cell is cut off ventrally. Each of the 2 dorsal and 2 dorso-lateral pericentral cells give rise to a lateral row of wing cells, thereby producing a two-layered wing (Fig. 1b). The ventral pericentral cell does not form wing cells but divides to produce cortical cell initials. After wing formation, the 2 dorsal pericentral cells also give rise to cortical cell initials. Subsequently, cells of both wings also initiate cortical development by cutting off cortical cells towards outside of the blades (Fig. 1b and c). All

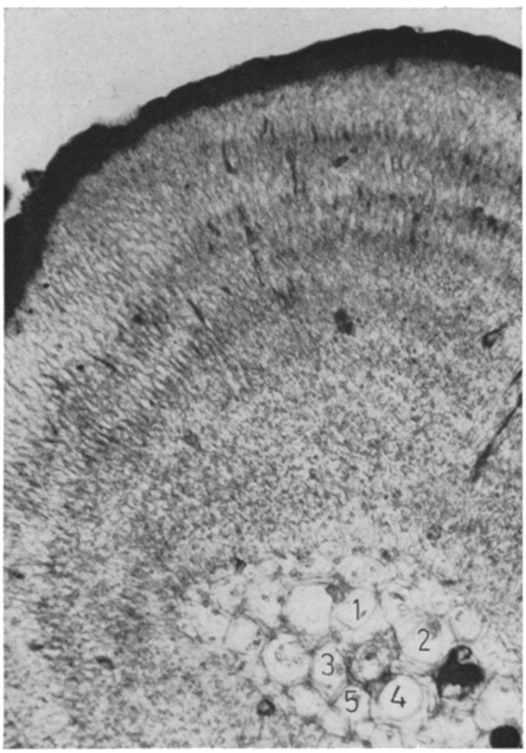

Fig. 2: Transverse section of thickened blade showing position of central and pericentral cells (numbered). Note outermost, dark pectic sheath (50:1)

cortical cell initials divide several times to produce a small-celled cortex, approximately 3–4 cells wide, which completely encloses the frond.

Small, exogenous, adventitious laterals arise from the cortex of this species (Fig. 1b and c) which give the frond its characteristically rough surface texture. These laterals are determinate, profusely branched, and do not develop beyond 8–10 segments.

As the fronds age, however, many of the surface laterals are lost together with some of the outer margins of the wings (Fig. 1d). The loss of these outer structures, presumably through sand abrasion, appears to stimulate the remaining cortical cells (especially those in the midrib region) into meristematic activity. Rapid division in this primary cortex produces a dense, compact, secondary cortex (Fig. 1d) which may reach a thickness of 0.5 cm. This rapid secondary cortex formation causes the blade to assume an almost terete cross-section (Fig. 1e). Cortical activity is more pronounced in the area adjacent to the original midrib than in those areas near the margins of the blade.

In the secondary cortex of the terete blades, concentric growth zones can be distinguished (Fig. 2). Although these growth zones undoubtedly reflect periods of high and low meristematic activity, the controlling factors of this activity are not known. It is interesting to note that the pectic sheath containing the pigment floridorubin (SAENGER 1970) is continuous around the outside of the enlarging blades (black zone in Fig. 2) at all stages of their development. This sheath and the massive cortical development combine to produce thick, tough stipes of a leathery texture.

DISCUSSION

Although several factors may be involved in stimulating the primary cortex into renewed meristematic activity, all transverse sections examined showed that this activity commenced only after the marginal ends of the lateral wings had been lost or damaged. While the lateral wings remain intact, the cortex of the blades consists of only 3–4 cell layers. The possibility that the bases of the exogenous determinate laterals on the surface of the blades may be involved in the formation of the secondary cortex, must be considered. In view of the uniformity of the secondary cortex in this species, and the fact that similar structures may be formed in related species lacking these surface laterals, this possibility is unlikely. For example, the process of secondary cortex formation as described for *Osmundaria prolifera* is similar to that in *Amansia glomerata* (FALKENBERG 1901) except that in the latter species, the primary cortex is restricted to the midrib only; consequently, the secondary cortex is initiated at the midrib only.

Development of terete stipes in *Lenormandia prolifera* (SAENGER 1970) occurs by a process almost identical with that in *Osmundaria prolifera*. In *L. prolifera*, however, the secondary cortex is not as massive as in *Osmundaria prolifera*, and it lacks the concentric growth zones. Whether the development of a secondary cortex in these plants is an adaptation towards their perennation is still to be determined.

SUMMARY

1. The development of the pericentral cells, lateral wings, and primary cortex is briefly described in the rhodophycean *Osmundaria prolifera* LAMOUROUX.
2. During subsequent development of the blades, a large part of the outer margins of the lateral wings is lost, presumably by sand abrasion.
3. The loss of the lateral wings appears to stimulate the primary cortex into meristematic activity, thereby producing a secondary cortex, attaining a thickness of up to 0.5 cm.
4. Secondary cortex formation in this species produces leathery, terete stipes which may be an adaptation towards perennation.

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