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# Development of Sporangia in *Polypodium aureum* var. *undulatum*: Initial Scanning Electron Microscopical Observations

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## ABSTRACT

Preliminary SEM observations of developing sori of *P. aureum* revealed several potential areas for future ultrastructural (SEM and TEM) study, including ontogeny of sporangial initials, annulus differentiation, and spore wall development.

## INTRODUCTION

The basic organization and development of the sorus, sporangium and spore in ferns have been shown with light microscopy (Bierhorst, 1971; Foster and Gifford, 1974). The continuation of such studies at the ultrastructural level has not been extensive. Although Peterson and Kott (1974) included some scanning electron microscopical (SEM) observations in their light and transmission electron microscopical (TEM) study of the structure and development of paraphyses in the sori of *Polypodium virginianum*, a definitive SEM investigation of fern sorus, sporangium and spore development has not yet been attempted.

Wilson (1958), using light microscopical observations, demonstrated the ontogenetic development of the leptosporangium of *Polypodium (Phlebotium) aureum*. The present paper reports on an exploratory and preliminary SEM investigation on various aspects of sorus, sporangial and spore development of *Polypodium aureum* var. *undulatum* (*Polypodiaceae*).

## MATERIALS AND METHODS

Plants of *Polypodium aureum* var. *undulatum* grown in the greenhouse of the University of Arkansas at Little Rock were used in this study. Portions of fronds showing sori in various stages of development were removed during the fall and winter of 1976-77. Small pieces of fronds with one or more sori were fixed in 2% glutaraldehyde buffered with Sorensen's phosphate buffer (pH 7.2), dehydrated in ethanol and amyl acetate, critical point dried with CO<sub>2</sub>, and vacuum coated with carbon and gold-palladium (60/40). Some mature sori were coated without prior fixation. All specimens were examined with a Cambridge S-600 scanning electron microscope operating at 7.5 or 15 KV.

## RESULTS

Club-shaped trichomes were randomly distributed on the abaxial surface of the fronds of *P. aureum* (Fig. 1). These trichomes were not specifically associated with any of the numerous sori that were located submarginally along either side of the main vein of the pinnae. Round, exindusiate sori developed within a slightly depressed area or receptacle (Fig. 1-3).

Within each sorus, only one type of structure was seen to originate from the receptacle. Since they all subsequently developed into typical leptosporangia, these structures were sporangial initials. Sporangia originated, developed and matured at the same time in most sori (Fig. 2-3). The only exception was found in sori collected in January; these sori showed sporangia in at least two stages of development (Fig. 11). Our SEM observations did not reveal the presence of the paraphyses commonly associated with fern sori.

A sorus begins development when one or more epidermal cells enlarge, their outer walls pushing up from the surrounding epidermal surface; these were the sporangial initials. Additional sporangial initials rapidly emerge until the receptacle floor was virtually covered

with initials. Each sporangial initial underwent considerable growth, expanding in budlike fashion above surrounding epidermal cells, before any internal cell division was evident (Fig. 4). As divisions occurred within, the pattern of the new outer cells was apparent on the surface of the initial (Fig. 5-8). Each initial developed an apical ball-shaped structure atop a short sporangial stalk (Fig. 6-8). The annulus and lip cells were evident at this early stage of development. The apical portion then underwent a period of uniform growth and expansion. Further growth and differentiation produced a sporangium that was flattened in one plane with a vertical annulus and lip cells clearly defined (Fig. 9). Surface cells, including those of the annulus, appeared inflated; that is, the outer walls bulged out between the junctions of adjacent cells. Nonfixed mature sporangia, in which lip cells were separating to form a transverse stoma prior to spore release, did show the characteristic collapsing of the thin outer walls of the annulus (Fig. 10).

Spores in *P. aureum* apparently matured while they were still tightly clustered in tetrads. As a result, the various faces of the mature spore wall may or may not be sculptured depending on the spore's orientation within the tetrad. Those wall faces oriented to the inside of a tetrad were relatively smooth (Fig. 12). In contrast, the faces on the outside of a tetrad were distinctly sculptured (Fig. 12-13). In some instances, the cluster of cells comprising a tetrad apparently become separated during spore maturation; consequently, scattered wall sculpturing did occur on inner wall faces that were otherwise relatively smooth (Fig. 14). Wall sculpturing in *P. aureum* appeared to involve the deposition of a material that is not produced by the spore itself.

## DISCUSSION

In sori of many leptosporangiate species, the development of sporangia has been shown to be accompanied (before, during or after) by the development of various nonsporangial structures. In *P. virginianum*, Peterson and Kott (1974) demonstrated that sporangial initials can develop into either sporangia or vesiculate paraphyses; the latter were numerous and conspicuous in mature sori of this species. They also demonstrated that epidermal trichomes were conspicuously associated with young sori in this species. Wilson (1958) reported that very small paraphyses did occur in the sori of *P. aureum*, but that their development followed that of sporangia. Our SEM observations of *P. aureum* var. *undulatum* did not demonstrate the presence of either trichomes in direct association with the sori or any type of paraphyses. It is possible, however, that the presence of extremely small paraphyses escaped detection during the present exploratory SEM study. From a developmental point of view, the sorus of *P. aureum* proved to be an ideal model for future SEM and TEM studies on the ultrastructural differentiation of fern sporangia and spores. Such studies should provide insight into why some, but not all, receptacular cells in a sorus develop into sporangial initials, the ultrastructural transformations that provide for and accompany this morphogenetic event, and the differentiation of unique and highly specialized annulus, and so forth.

The pattern of sporangial maturation within a sorus has been given

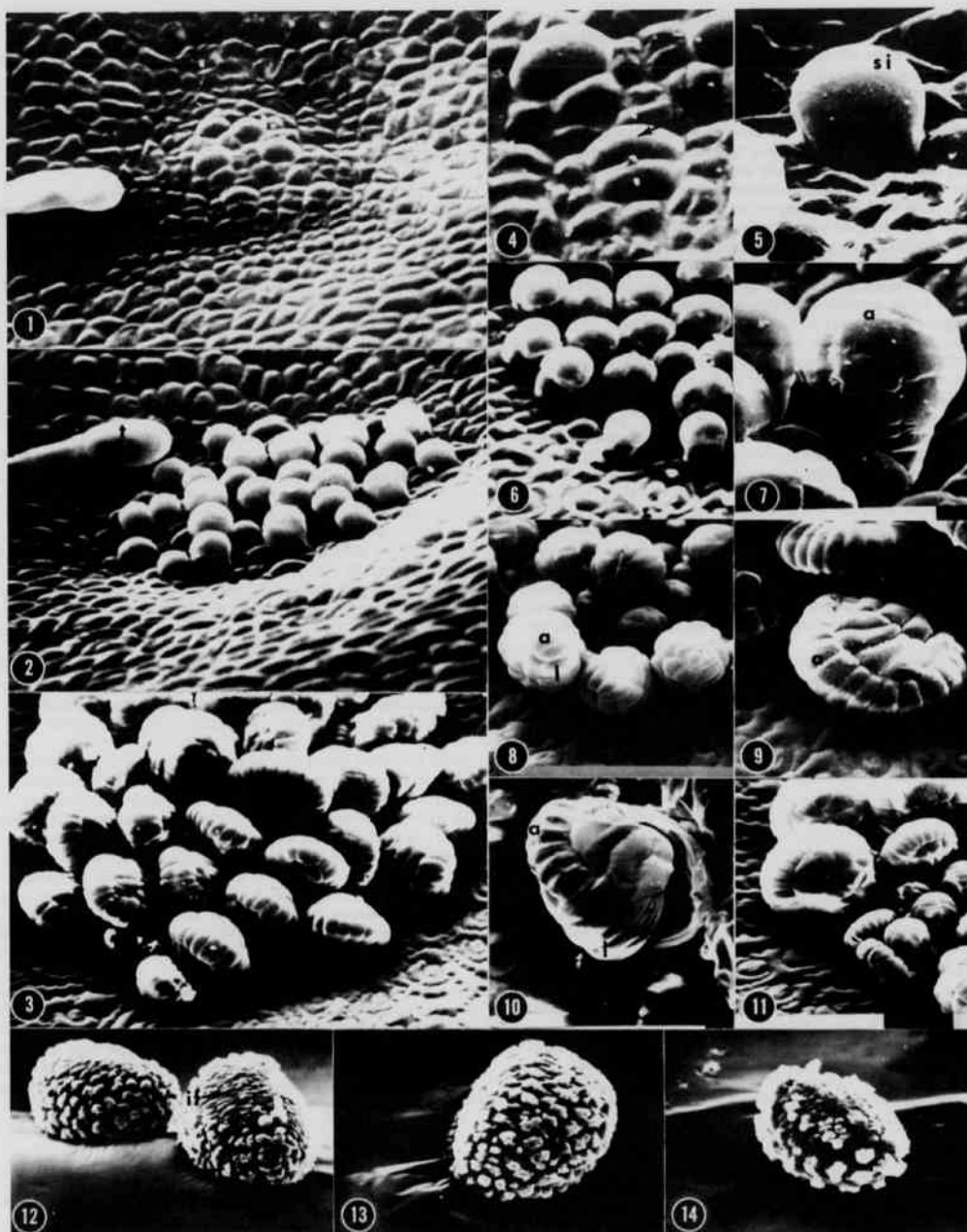


Fig. 1-3. Sorus development. Fig. 1. Sorus receptacle with emerging sporangial initials (X380). Fig. 2. Sorus with enlarged sporangial initials and a trichome (t) (X325). Fig. 3. Sorus with nearly mature sporangia (X100). Fig. 4-10. Sporangium development. Fig. 4. Sporangial initial (arrow) emerging (X940). Fig. 5. Sporangial initial (Si) fully emerged (X1250). Fig. 6. Sporangial initial beginning internal division (X325). Fig. 7. Young sporangium showing annulus (a) (X450). Fig. 8. Sporangium with annulus (a) and lip cells (l) (X180). Fig. 9. Fully enlarged sporangium showing vertical annulus (a) (X200). Fig. 10. Air-dried mature sporangium showing differentiated annulus (a), lip cells (l) and stomium (X175). Fig. 11. Mixed sorus with two stages of sporangial development evident (X125). Fig. 12-14. Spore development. Fig. 12. Spores showing smooth inner face (if) or wall and sculptured outer walls of spore tetrads (X730). Fig. 13. Sculptured spore wall (X860). Fig. 14. Sculpturing on inner face or wall (X770).

Development of Sporangia in *Polypodium*

evolutionary significance (Foster and Gifford, 1974); that is, a mixed sorus with sporangia in various stages of development represents a condition that is more advanced evolutionarily than a simple sorus in which all sporangia originate, grow and mature at the same time. The presence of both simple and mixed sori in *P. aureum* var. *undulatum* suggests that this conclusion may be inappropriate and inaccurate. The possibility certainly exists that environmental factors may be involved in the determination of soral types and that development of young sori could be experimentally manipulated through control of such environmental factors as photoperiod and temperature.

The nature of wall sculpturing of mature spores suggested that it involved the deposition of some foreign material. This origin of spore wall ornamentation in *P. aureum* is substantiated by the presence of sculpturing primarily on the exposed outer walls of spore tetrads. Where sculpturing did occasionally occur on the inner faces of spore walls within these tetrads, such deposition could occur if the cells comprising the tetrads were to become slightly separated. Disintegration of the tapetum (Foster and Gifford, 1974) could provide the material that eventually participates in the sculpturing of spore walls in *P. aureum* var. *undulatum*. Spore wall sculpturing that has been derived from the tapetum has been termed the perispore (Bower, 1923; Wagner, 1952). Since Bower (1923) states that a perispore is absent in spores from species of the Polypodiaceae, further ultrastructural studies (SEM and TEM) into the nature of spore wall development in *P. aureum* var. *undulatum* are justified.

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