Development of the sorus in tree ferns: Dicksoniaceae

Hugh Churchill, Rolla Tryon, and David S. Barrington

Abstract: Studies of soral development in the tree-fern family Dicksoniaceae in comparison with the Cyatheaceae led to (1) recognition of two basic patterns in the Dicksoniaceae, (2) clarification of marginal versus superficial sori and their indusia in tree ferns, and (3) phylogenetic interpretations. In *Cibotium* the sorus originates directly from the marginal initial file. The outer and inner indusia arise simultaneously, early in development, on the adaxial and abaxial sides of the receptacle, respectively. The receptacle in *Dicksonia* originates from a shifted segment of the marginal initial file. The outer indusium is initiated first, approximately at the same time as the receptacle. The initial cells of the marginal meristem give rise to the soral receptacle in both groups of dicksoniaceous genera. Preliminary studies of soral morphogenesis in some cyatheaceous genera indicate that abaxial derivatives originate the sorus. The Cyatheaceae have a single, abaxial indusium proximal to the sorus at maturity, or none. Consideration of these morphogenetic data in light of recent molecular phylogenies suggests that fundamental changes in the meristematic origin of tree-fern sori have taken place since the origin of the lineage that includes both Dicksoniaceae and Cyatheaceae.

Key words: *Cibotium*, *Dicksonia*, Dicksoniaceae, sorus, tree ferns.

Résumé : Comparativement à celle des Cyatheaceae, les études conduites sur le développement des sores dans la famille de fougères arborescentes Dicksoniaceae ont conduit à (1) la reconnaissance de deux patrons de base chez les Dicksoniaceae, (2) la clarification des sores marginaux versus les sores superficiels ainsi que leurs indusies chez les fougères arborescentes, et (3) des interprétations phylogénétiques. Chez les *Cibotium*, le sore prend son origine directement à partir de la lignée cellulaire initiale marginale. Les indusies externes et internes se forment simultanément, tôt dans le développement, sur les côtés adaxiaux et abaxiaux du réceptacle, respectivement. Chez les *Dicksonia*, le réceptacle origine d'un segment déplacé de la lignée initiale marginale. L'indusie externe apparait en premier, approximativement au même moment que le réceptacle. Les cellules initiales du méristème marginal donnent naissance au réceptacle du sore chez les deux groupes des genres Dicksoniaceae. Des études préliminaires conduites sur la morphogénèse du sore, dans quelques genre de Cyatheaceae, indiquent que des dérivées abaxiales donnent naissance aux sores. À maturité, les Cyatheaceae ont une seule indusie abaxiale à proximité du sore, ou aucune. L'examen de ces données morphogénétiques, à la lumière des données moléculaires récentes, suggère que des changements fondamentaux dans l'origine méristématique des sores, chez les fougères arborescentes, ont eu lieu depuis l'origine du phylum qui inclut les Dicksoniaceae ainsi que les Cyatheaceae.

Mots clés : *Cibotium*, *Dicksonia*, Dicksoniaceae, sore, fougères arborescentes.

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Introduction

Tree ferns are prominent components of the wetter tropical forests in both hemispheres. The families Cyatheaceae and Dicksoniaceae are the most common and diverse of the tree-fern lineages. They include some 650 taxa, at least 95% of the living species of tree ferns. The families share sporangia with an oblique annulus, initiation of the sporangia in a gradate sequence, and four or more rows of cells in the sporangium stalk. These character states are generally taken to be relatively primitive. The two lineages differ in the position of the sorus, the structure and position of the mature indusia, and the nature of the indument that invests different parts of the plant.

Although the investigation reported here focuses on *Dicksonia* and *Cibotium* (Dicksoniaceae), our work is relevant to the broader question of the phylogenetic relationships of the Dicksoniaceae and Cyatheaceae. Arguments for or against recent common ancestry of these two major tree-fern families have centered on divergent interpretations of sorus position and indusium homology. Two major hypotheses have been proposed based on developmental material.

Bower (1899, 1926) argued that common ancestry was ancient (i.e., each is more closely related to other lineages) be-

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H. Churchill.[1] Office for Information Technology, Network & Systems Group, Jesup Hall, Williams College, Williamstown, MA 01267, U.S.A.
R. Tryon. Biology Department, University of South Florida, Tampa, FL 33620, U.S.A.
D.S. Barrington.[2] Department of Botany, University of Vermont, Burlington, VT 05405-0086, U.S.A.

[1]Deceased.

[2]Author to whom all correspondence should be addressed. e-mail: dbarring@zoo.uvm.edu

Table 1. Collection data.

Taxon	Collector	Original source	Where cultivated (accession number)
Cibotium Kaulfuss			
Cibotium glaucum (Sm.) Hook. & Arn.	Rock s.n.	Hawaiian Islands	Kew Gardens (197-57.19702)
Cibotium glaucum (Sm.) Hook. & Arn.	Unknown	Hawaiian Islands	San Francisco College
Cibotium glaucum (Sm.) Hook. & Arn.	Unknown	Hawaiian Islands	University of Massachusetts
Cibotium regale Versch. & Lem.	Unknown	Mexico?	University of Connecticut
Cibotium regale Versch. & Lem.	Unknown	?	Kew Gardens (00073.13402)
Cibotium schiedei Schlect. & Cham.	Unknown	Mexico	University of Massachusetts
Cnemidaria Presl			
Cnemidaria horrida (L.) Presl	Churchill 3056	Río Toro Negro, Puerto Rico	
Culcita Presl subgenus *Culcita*			
Culcita coniifolia (Hook.) Maxon	Churchill 3532, 3545	Puerto Cartago, Costa Rica	
Cyathea J.E. Smith			
Cyathea arborea (L.) Sm.	Churchill 3042, 3067	Monte Jayuya, Puerto Rico	
Cyathea caracasana (Kl.) Domin	Churchill 3060	Monte Jayuya, Puerto Rico	
Dicksonia L'Heritier			
Dicksonia antarctica Labill.	Churchill 3134, 3168, 3171, 3256	Australia	Golden Gate Park
Dicksonia sellowiana Hook.	Churchill 3271, 3319, 3338, 3618, 3649	Puerto Cartago, Costa Rica	
Thyrsopteris Kunze			
Thyrsopteris elegans Kze.	Stuessy et al. 5515	Juan Fernandez Islands	
Trichipteris Presl			
Trichipteris armata (Sw.) Tryon	Churchill 3068	Monte Jayuya, Puerto Rico	

Note: Voucher specimens are deposited at CR, GH, K, OS, and (or) VT.

cause in the Dicksoniaceae the sori are initiated and borne in close relation to the margin of the leaf segment, whereas in the Cyatheaceae they are initiated on the expanded, abaxial surface of the blade.

In contrast, Goebel (1901, 1915–1918, 1930) argued for a more recent common ancestry, postulating that a simple change in the timing of ontogenetic events could yield a soral position that appeared superficial instead of marginal.

The main difficulty in attempting to understand the hypotheses of Goebel and Bower lies in the different applications of the term marginal. Bower specifically used the term marginal to describe a sorus in which the receptacle develops directly from the initial cells of the marginal meristem of the leaf. In contrast, superficial was used for a receptacle that develops abaxially, distant from the marginal initials. Goebel used marginal similarly, but proposed that there was a physical shift in the position of the marginal initial cells in the origin of the abaxial (superficial) sorus. Goebel (1930) interpreted the ontogeny of *Dicksonia* as an example of an intermediate stage in this transformation.

In yet a different approach Holttum and Sen (1961) considered the origin of the receptacle in both the Cyatheaceae and Dicksoniaceae as near marginal. They stated that "Even in *Gleichenia*, where Bower indicates an entirely superficial origin of the sorus (1899, Fig. 10), some of Bower's own preparations indicate that at an early stage the receptacle-primordium is almost, if not quite, marginal" (Holttum and Sen 1961, p. 411). Since, to Holttum and Sen, the leaf margin survives soral development intact in all groups, they maintain that the outer indusium of the Dicksoniaceae is a false indusium homologous with the leaf margin.

We report here a series of developmental studies of the sorus in the Dicksoniaceae, especially of *Dicksonia* and *Cibotium*. We include preliminary observations on *Culcita* and *Thyrsopteris* (Dicksoniaceae), and on some genera in the Cyatheaceae. Based on these studies, we (1) describe two major patterns of soral morphogenesis in the Dicksoniaceae, (2) provide a morphogenetic demonstration that marginal and superficial sori are qualitatively different and address the homology of indusia in the Dicksoniaceae (with comments on the Cyatheaceae), and (3) assess phylogenetic implications in the light of recent molecular systematic work.

Materials and methods

Entire shoot apices and young leaves at various stages of development were collected in the field or from horticultural sources (Table 1). Fixation was in either Craf V (Sass 1958) or formalin – acetic acid – 50% ethanol (FAA) (Johansen 1940). Both fixatives gave comparable results. Some materials were partially dissected for more effective penetration of preserving fluids. All material was subsequently stored in 70% ethanol prior to examination.

Material for light microscopy was dehydrated in an alcohol series, embedded in glycol methacrylate (Feder and O'Brien 1968), and sectioned serially at 2–6 μm with a Sorvall MT-1 ultramicrotome. The sections were stained with 0.5% toluidine blue and examined with bright-field light microscopy. Photomicrographs were taken with Kodak Plus-X film.

Material for scanning electron micrography was dehydrated in an ethanol series, transferred to an acetone series, and critical-point dried with CO_2 (Cohen 1974). Specimens were coated with gold–palladium and viewed with a JEOL model JS 35 scanning electron microscope at 15 kV. Hand-sectioned material was processed in the same manner. Photographs of the raster images were taken on Polaroid Type 665 Positive/Negative Land film.

Results

Both the vegetative and reproductive leaf meristems in tree ferns are primarily organized around a single, conspicuous marginal file of surficial, anticlinally elongate, actively dividing initial cells (Churchill 1983). Soral initiation and morphogenesis follow from transformations of the marginal file. These are superimposed on a form or framework that is determined early in leaf development and hence identical in trophophylls and sporophylls.

Cibotium

At the inception of soral development, the file of marginal initials is continuous across the apex of each fertile lobe of the developing lamina (Fig. 1). Initiation of the sorus (the receptacle) in *Cibotium* is first evident as a conspicuous bulging of a central portion of the marginal initial file in a fertile lobe of the developing lamina (Fig. 2). Soon after the soral receptacle is initiated, the adjacent nonreceptacular initials undergo transverse divisions to become more or less isodiametric, leading to the disorganization of this portion of the marginal initial file.

In *Cibotium* the outer and inner indusia characteristic of the Dicksoniaceae become apparent early in soral development as elongate swellings that are parallel to the receptacle on the abaxial and adaxial sides of the lobe. Although at first the two indusia are separate from one another (Fig. 3), indusial growth gradually extends out to the sides of the sorus, and the indusia become fused at their base, forming a shallow collar around the receptacle base (Fig. 4).

Subsequent to the fusion of the two indusia, the entire soriferous lobe undergoes a 90° shift in orientation to a position at right angles to the plane of the lamina and the sorus becomes deflexed. The outer and inner indusia remain about equal in shape and size throughout development. The leading edge of each indusium is more or less rounded (Fig. 5).

The first row of sporangial initials forms at the apex of the receptacle directly from the former cells of the marginal initial file. Subsequent sporangial rows are initiated in an irregular basipetal sequence, between the first row and the base of each indusium, on both the abaxial and adaxial sides of the elongating receptacle. With continued growth the two indusia will eventually enclose the sporangiferous receptacle. Although the outer indusium often appears slightly exserted past the inner indusium, the margins do not overlap as they do in *Dicksonia* and *Culcita*, but simply come to be tightly appressed to one another (Fig. 6).

Dicksonia

The first visible indication of a switch from vegetative to sporogenous development in *Dicksonia* is the adaxial displacement of a short segment of the marginal file of a lobe away from the remainder of the cells in the file (Figs. 7, 9). The shift results from the enlargement or division of abaxial marginal derivatives and the development of a shallow notch, not from periclinal divisions of the marginal initials. The marginal initial file in the nonsoral portion of the segment remains intact throughout development (Fig. 8). At the same time the outer indusium begins to develop as a swelling, on the adaxial side, a few cells removed from the displaced portion of the marginal initial file (Fig. 9). The outer indusium meristem lacks a distinct file of initials. Churchill (1983) illustrates the histology of receptacle and outer-indusium origin in *Dicksonia* (his Figs. 30*a*–30*d*, p.103).

The first row of sporangial initials arises directly from the adaxially displaced segment of the marginal initial file (Fig. 10). A second row of sporangia is initiated from the row of cells adjacent (proximal) to the first row (the former marginal initial file), and so on, in a basipetal, gradate sequence. Sporangial initiation is largely suppressed on the abaxial side of the former marginal file so that the sorus develops mostly from the adaxial derivatives of the former margin. Eventually new rows of sporangial initials are intercalated between the last row and the base of the outer indusium, forming a broad but still essentially adaxial receptacle on the inner indusium. After several rows of sporangia have been initiated, the inner indusium will start to develop, abaxially adjacent to the oldest row. At first the inner indusium appears as a narrow group of cells extending from one end of the sporangial row to the other; distinct marginal initial cells are missing (Fig. 11). The distal side of these cells (the outer surface of the indusium) is smoothly continuous with the cells of the apical sector of the lobe. The proximal side of the cells (the inner surface) ends at the base of the first sporangial row. By the time the inner indusium has reached the level of the distal sporangia, the outer indusium has arched over and enclosed the entire receptacle (Fig. 12). The outer indusium continues to grow much more rapidly, eventually arching over the inner indusium. Late in ontogeny, pronounced apical growth of the inner indusium forces its leading edge between the outer indusium and the sporangial files.

Culcita and *Thyrsopteris*

Our preliminary studies of other dicksoniaceous genera show patterns of soral morphogenesis that parallel those in *Cibotium* and *Dicksonia*. In *Culcita coniifolia* (Hook.) Maxon the entire receptacle develops on the adaxial surface of a lobe and gradually becomes broadened and flattened as new sporangial rows are initiated in a basipetal sequence. Thus the later developmental stages in *Culcita coniifolia* are strikingly similar to comparable stages in *Dicksonia*. Early indusial morphogenesis in *Thyrsopteris* resembles that in *Cibotium*, although the two genera are strikingly different at sporangial dehiscence. Differences in the indusia of *Cibotium* and *Thyrsopteris* appear to be in the degree of fusion between the outer and inner indusia at the sides of the receptacle. The earliest stages of receptacular development were not studied in *Culcita* or *Thyrsopteris*.

Cyatheaceae

Preliminary observations of soral morphogenesis in selected cyatheaceous taxa (*Cyathea arborea* (L.) Sm., *Cyathea caracasana* (Kl.) Domin, *Cnemidaria horrida* (L.) Presl, and *Trichipteris armata* (Sw.) Tryon) suggest that the file of marginal initials is not involved in either receptacular origin or subsequent receptacular development. The receptacle appears to arise abaxially removed from the marginal

Figs. 1–6. Stages of soral development in *Cibotium regale* Versch. & Lem., adaxial surface at the top, except in 3 to the upper right and in 4 to the left. (1) Leaf margin prior to receptacular origin. Top view of the marginal initial file (M) extending across the lobe apex. Scale bar = 50 µm. (2) Marginal view of the elevated group of receptacle cells (R) that has differentiated directly from the file of marginal initials. Scale bar = 50 µm. (3) Initiation of indusia; apical view of a fertile lobe. The newly initiated outer indusium (O) and inner indusium (I) appear as swellings adjacent to the receptacle (R). Scale bar = 100 µm. (4) The inner and outer indusia joined in a shallow cup surrounding the receptacle. Scale bar = 100 µm. (5) Section of the sorus showing a number of sporangial initials on the raised receptacle. The outer indusium (lower left) appears continuous with the lamina segment. The leading edges of the indusia are rounded. Scale bar = 150 µm. (6) Margins of the indusia touching and completely enclosing the sorus. Scale bar = 150 µm.

Figs. 7–12. Stages of soral development in *Dicksonia antarctica*, adaxial surface at the top. (7) Edge view of a marginal lobe, showing the meristem file (arrow) shifted adaxially, characterizing the switch to soral development. Scale bar = 100 µm. (8) Apex of fertile segment showing an intact marginal initial file (M). Scale bar = 50 µm. (9) Soral lobe with outer indusium (O) initiated, appearing as a steplike swelling above the marginal initial file (M). Scale bar = 50 µm. (10) Receptacle (R) differentiated from the shifted file of marginal initials. O, outer indusium. Scale bar = 100 µm. (11) Soral lobe with the inner indusium (I) appearing as a thin structure distal to developing sporangia; three anomalous sporangial initials below. O, outer indusium. Scale bar = 50 µm. (12) Section through sorus with sporangia developing on the receptacle. The outer indusium is above, the inner below. Scale bar = 50 µm.

Table 2. Comparative summary of developmental events in *Cibotium* and *Dicksonia*.

Event no.	*Cibotium*	*Dicksonia*
1	No shift of marginal initial file	Adaxial shift of segment of marginal initial file yields receptacle
2	Nonreceptacle cells in lobe undergo periclinal divisions, become isodiametric	File of initials maintains distinctive morphology continuous around entire segment including distal (apical) sterile portion
3	Initiation of outer and inner indusium simultaneous	Outer indusium initiated first and early, soon after sporangial initiation; inner after several rows have been initiated
4	Indusial collar formed by extension of indusial growth to sides and fusion at ends	No indusial collar
5	Sorus shifts 90° abaxially preceding sporangial initiation	No early shift in sorus attitude
6	First sporangia initiated from unshifted marginal initial file cells	First sporangia initiated from shifted marginal initial cells
7	Later sporangia initiated basipetally between first row and base of each indusium	Later sporangia initiated adaxially adjacent to first row, abaxial sporangia repressed
8	Leading edge of each indusium rounded, never wedge shaped	Inner indusium initiated by wedge-shaped group of cells
9	Indusium margins come to rest against one another, never overlap	Apical growth of inner indusium forces its leading edge between the outer indusium and the sporangia files

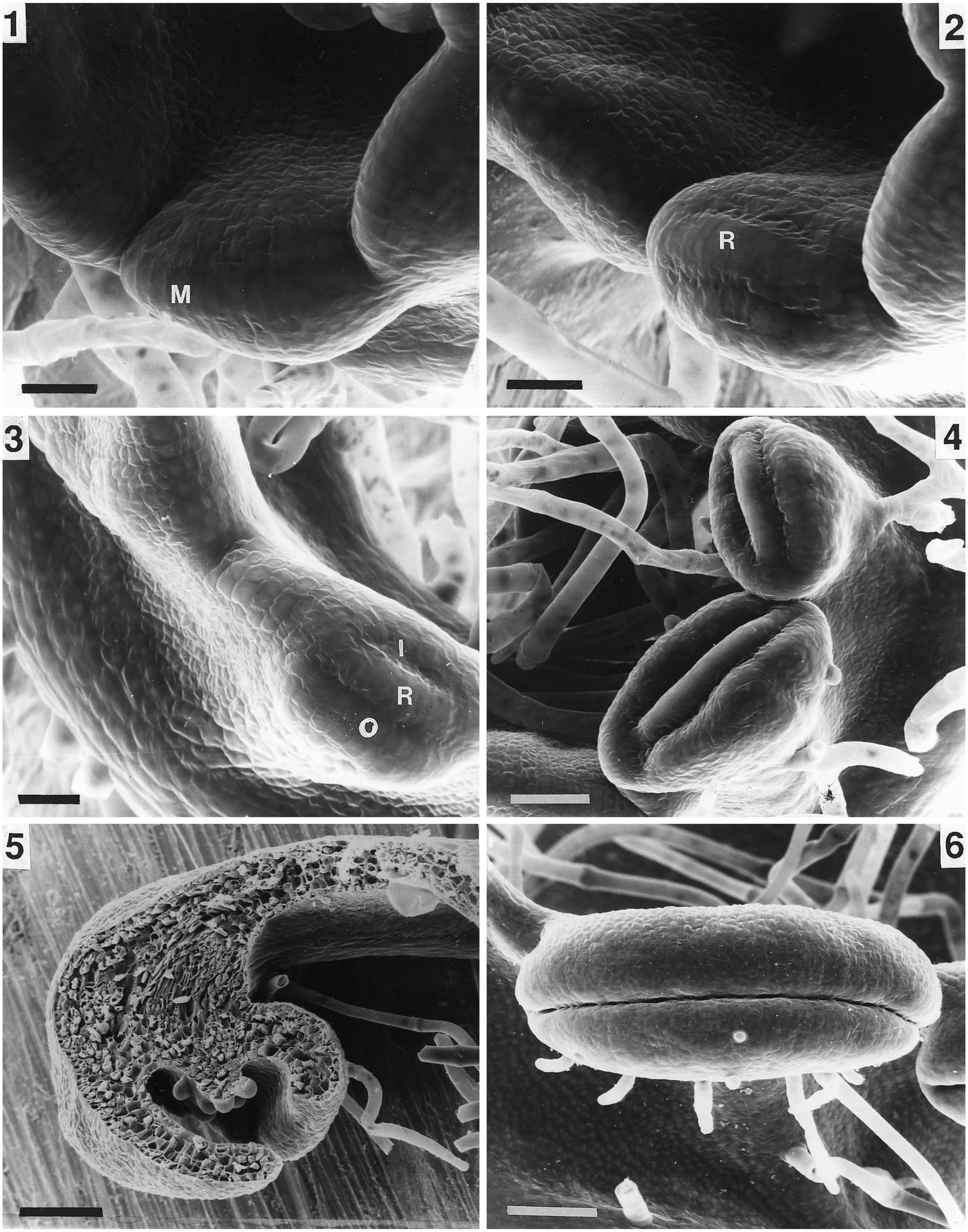
file, although close to the margin. Thus, derivatives of the marginal meristem, not the initials themselves, yield the soral receptacle (Churchill 1983).

Discussion

Cibotium and *Dicksonia*

These two genera share two key developmental steps. First, the receptacle is initiated by direct transformation of the marginal meristem initials. The first sporangia differentiate directly from these transformed initials, so soral development is fundamentally determinate. Second, two indusial primordia, one abaxial and one adaxial, are formed as new outgrowths from derivatives of the marginal meristem. These early events lead to the shared features in mature stages that have contributed to inclusion of the genera in a single family, the Dicksoniaceae. Our recognition of these events as critical supports Sachs's (1982) contention that early morphogenetic events are the most difficult to alter and the most influential on the form of the mature plant.

Later stages diverge substantially, leading to remarkably different morphologies (Table 2). At receptacle inception the marginal-meristem initials in *Dicksonia* go through an adaxial shift that has no parallel in *Cibotium*. The receptacle in *Cibotium* is discrete at its inception. The remainder of the marginal-meristem initials in the soriferous lobe undergo periclinal divisions, become isodiametric, and cease to show the marginal initial morphology. These periclinal divisions are absent in *Dicksonia*, and indusium initiation is timed differently. In *Cibotium* the two indusia originate simultaneously, whereas in *Dicksonia* the outer indusium is initiated first and early in soral development. The inner one develops only after several rows of sporangia have been initiated. The two indusial primordia have rounded leading edges in *Cibotium*, but the inner indusium of *Dicksonia* is initiated by a group of cells with a narrower leading edge. The indusial collar in *Cibotium*, which is the product of fused meristems of the abaxial and adaxial indusial primordia, has no parallel in *Dicksonia*. The initiation of later sporangia in *Dicksonia* is primarily from derivatives to the adaxial side of the first row. However, both abaxial and adaxial portions of the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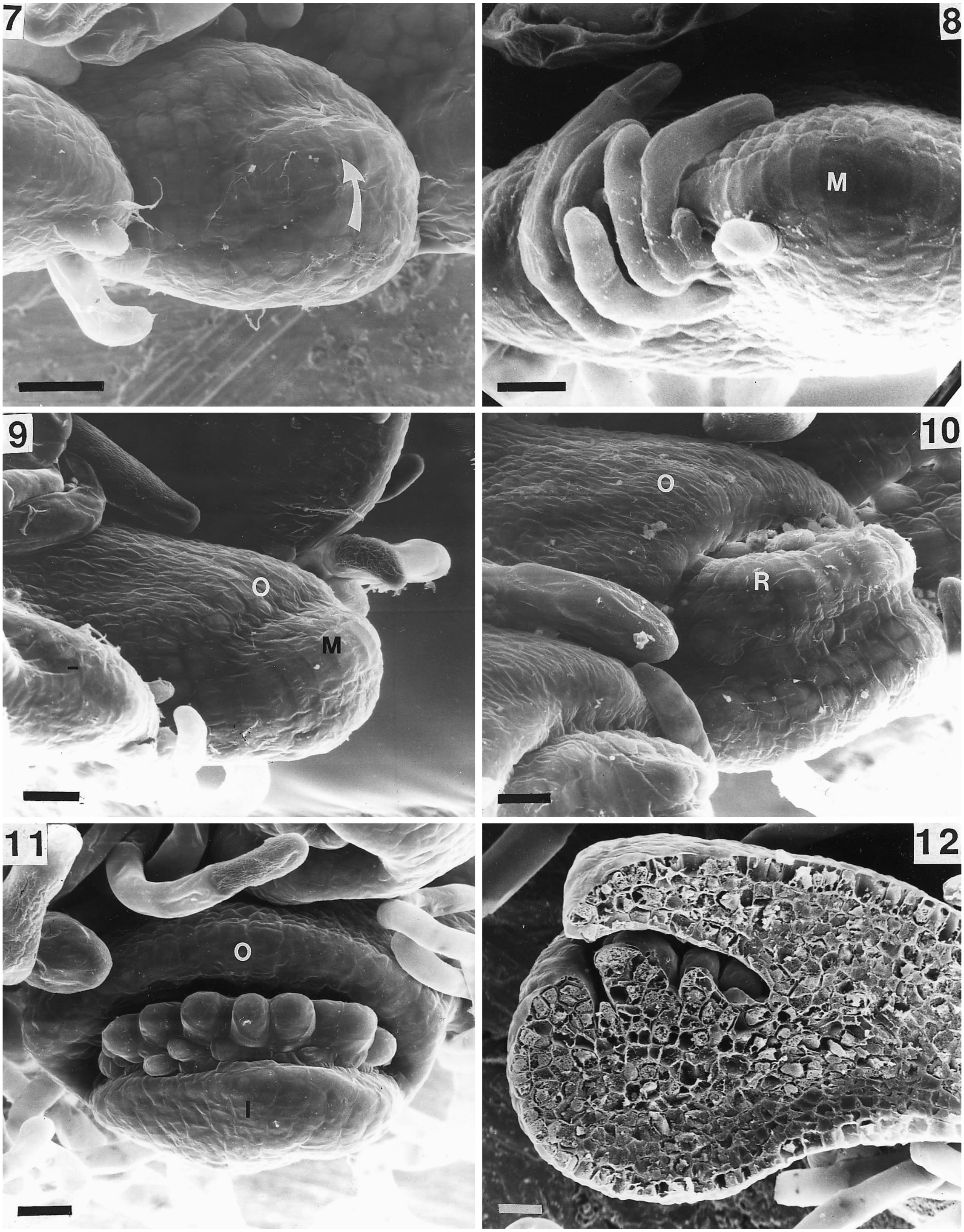
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receptacular meristem yield sporangia in *Cibotium*. At later stages of development, the leading edges of the two indusia come to rest against one another in *Cibotium*. In *Dicksonia* apical growth of the inner indusium forces its leading edge between the outer indusium and the sporangial files.

Soral morphogenesis in the Dicksoniaceae

In Bower's (1926) comprehensive review of the ferns, the chapter on the Dicksoniaceae includes a line drawing of a longitudinal section through a young sorus of *Cibotium schiedei* Schlect. & Cham. Although the drawing shows a late stage in which indusial growth had already begun, Bower (1926, Fig. 534) correctly interpreted the receptacle as marginal in origin, based on his interpretation of the segmentation patterns in the lobe apex. A later developmental stage is also correctly illustrated and was figured in his earlier work (Bower 1899). The results of the present study are in complete agreement with Bower's interpretation of *Cibotium*. However, his inclusion of *Culcita* (as *Balantium*) and *Dicksonia* as examples of two other genera with the same developmental pattern is at odds with our observations.

In studies of *Dicksonia antarctica* Labill., Goebel (1901, 1915–1918, 1930) illustrated the early positional shift of the cells of the marginal initial file that characterizes the switch to soral development, but made a cardinal error: two of his sections are upside down (Goebel 1930, Fig. 1392, I and II, and earlier editions)! Although he correctly concluded that the receptacle develops directly from the marginal initials, he mistakenly described them as being displaced toward the abaxial surface of the lobe.

Since, as we demonstrate, the receptacle originates from the true leaf margin and the outer (upper) and inner (lower) indusia, respectively, originate as outgrowths of the adaxial and abaxial lobe surfaces, the outer indusium cannot be a false indusium, as argued by Holttum and Sen (1961).

Holttum and Sen (1961) described the inner indusium in *Dicksonia*, *Cibotium*, and *Culcita* as fused with the base of the receptacle, so only the acroscopic side of the receptacle is free (see also Holttum 1963; Sen 1964). However, we found no evidence of such fusion in *Cibotium*. The mature receptacle in *Cibotium* is quite separate from the tissues of the inner indusium. We believe that the apparent fusion of the mature receptacle to the inner indusium in *Dicksonia* and *Culcita* is due to (1) the late development of the indusium at the distal end of the receptacle, and (2) the abaxial bending during leaf maturation of the entire lobe tip that bears the receptacle and inner indusium. However, the morphogenetic events we saw are also consistent with the interpretation of Holttum and Sen that the receptacle and inner indusium in *Dicksonia* and *Culcita* are fused. This interpretation was suggested more recently for *Dicksonia* and *Culcita* (sensu stricto) by White and Turner (1988). According to their view the inner indusium is initiated later because only the differentiation of the free, distal part of the indusium from a common indusium plus receptacle primordium is visible. (Note that, in any case, the fusion of the two indusia in *Cibotium* and *Thyrsopteris* is different from the fusion of indusium to receptacle postulated by Holttum and Sen (1961) and White and Turner (1988) for *Dicksonia* and *Culcita*.)

Marginal and superficial sori and indusia

Soral development in *Cibotium* and *Dicksonia* is marginal, whereas that in the Cyatheaceae is nonmarginal (abaxial or superficial). Qiu et al. (1995) show abaxial soral initiation distant from the margin in *Metaxya*, a tree fern with mature sori abaxial and distant from the margin. A study of *Cyathea fulva* (Mart. & Gal.) Fée by Tryon and Feldman (1975) concluded that the sorus originated on the abaxial surface of a segment near a midvein. In the cyatheaceous species they examined, they found a single indusium that develops into a sheathlike structure, although in section it may appear two-lobed. Indusial growth first becomes evident on the proximal side of the receptacle, away from the segment margin, and gradually extends out and completely encircles the receptacle. At no stage is there any evidence of separate outer and inner indusia such as we observed in the Dicksoniaceae. The portion of the lamina distal to the sori in the *Metaxya* and Cyatheaceae is thus not homologous with the adaxial indusium in the Dicksoniaceae, as proposed by Holttum and Sen (1961).

In contrast, all Dicksoniaceae have two indusia. The present studies have shown that in *Cibotium* and *Dicksonia* the outer and inner indusia originate adaxially and abaxially separated from the marginal initial file. The outer indusium is a true, adaxial indusium and not a false indusium. However, the inner indusium in the Dicksoniaceae may be homologous with the sole indusium of the Cyatheaceae, as Goebel (1901, 1915–1918, 1930) suggested.

Contrary to Holttum and Sen (1961), two types of soral differentiation occur in the tree ferns, marginal and abaxial. The marginal sorus results, as Bower (1926) proposed, from direct transformation of the marginal meristem initials, with the loss of the marginal meristem in the fertile region. In contrast, initiation of the sorus from derivatives of the marginal meristem gives rise to the abaxial (superficial) sorus, leaving the marginal meristem intact. From this perspective, a fundamental early event in sorus development distinguishes *Metaxya* (and probably the Cyatheaceae) from the Dicksoniaceae. The marginal meristem may be transformed into a marginal sorus as in the Dicksoniaceae or it may leave derivatives behind to initiate an abaxial sorus as in *Metaxya* (as demonstrated by Qiu et al. 1995). This latter sorus type would better be termed abaxial to identify which face of the leaf is the site of the sorus.

Phylogenetic assessment

Hasebe et al. (1995), Pryer et al. (1995), and Wolf (1995) provide molecular phylogenies of ferns based on data for the *rbc*L gene; Pryer et al. (1995) also report morphological data and incorporate them into a combined phylogeny. These papers provide a context for a phylogenetic interpretation of our developmental patterns.

Bower (1926) argues that the two major tree-fern families belong to different evolutionary lineages of ferns. The Dicksoniaceae he assigns to his *marginales* and the Cyatheaceae to his *superficiales*, distinguished on the basis of soral initiation. In agreement with Bower, we argue that fundamentally different cells (initials versus derivatives) initiate the sorus in the Dicksoniaceae and Cyatheaceae, respectively. However, all three *rbc*L studies conclude that the surveyed cyatheaceous and dicksoniaceous tree ferns are closely allied members of a single evolutionary lineage. *Metaxya*, with abaxial sori, is placed with the marginal *Dicksonia* and *Calochlaena* by Hasebe et al. (1995) and also by Pryer et al. (1995). If the molecular data are trustworthy, then the remote alliance of the two tree-fern families implied in Bower's argument for ancient divergence of the *marginales* and *superficiales* is to be rejected. Goebel then appears to have been correct in suggesting that the abaxial sorus in the Cyatheaceae and the marginal sorus in the Dicksoniaceae are separated by a simple transformation. The shift from soral origin among initials rather than among derivatives (or vice versa) appears to be much less significant than in Bower's perception.

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