

ONTOGENESIS AND POTENTIAL EVOLUTIONARY PATHWAYS OF FERN SORI

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ABSTRACT

In the light of the hypothesis that the superficial position of sporangia and sori is the primitive condition, different forms of sori are analysed using the methodical framework of the botanical construction morphology. Proceeding according to this method means to compare sori on the basis of their construction including their ontogenesis as well as their developmental potencies for further evolution. Different developmental potencies of the sori depend on the various positional relationships between the sori and the sporophyll, which are caused by differences in sporophyll development.

Concerning the construction of their sporangia, the megaphyllous ferns can be arranged in two main groups, one with delicate leptosporangia and one with massive leptosporangia. In each group, there are possible ways for the origin of marginal sori from superficial initial forms. In both main groups similar developmental processes characterize the step by step transition from superficial singly-arranged sporangia into marginal sori. These processes are: sorus formation, phase differentiation with subblastozonal or blastozonal receptacle formation, costa-relation, and development of special receptacular growing zones and of indusial envelopes. Since all these processes are suitable for demonstrating possible ways to an increase in complexity, marginal sori, especially highly complex constructions such as costa-related marginal sori, cannot be regarded as representing the initial forms of sorus evolution.

Based on the presented morphological results some unconventional systematic conclusions can be drawn.

Key words: Megaphyllous ferns, construction morphology, sporophyll development, sorus ontogenesis, developmental processes, sorus evolution.

Introduction

In the megaphyllous ferns (Filicatae, Kramer 1990) the sporangia are produced exclusively on the leaf. The sporangia occur either singly or in sori. The sori are different not only in their construction, but also in their position on the sporophyll. According to Zimmermann, the founder of the telome theory, and his supporters, the marginal position of the sporangia and sori is regarded as the primitive condition and the

superficial (abaxial) position as the derived state (e.g. Zimmermann 1959, Bierhorst 1971, Bold *et al.* 1980, Gifford and Foster 1989).

While, according to the telome concept, one can derive megaphylls with marginal sporangia or sori from the original telome system (Zimmermann 1959, Bold *et al.* 1980, Bresinsky 2008), the set of Zimmermann's elementary processes fails to give an explanation for the derivation of megaphylls with superficial sori. Therefore, Zimmermann (1959) and other proponents of the telome

theory (e.g. Bierhorst 1971, Gifford and Foster 1989, Stewart and Rothwell 1993) adopted the idea of a "phyletic slide" of the sorus from the leaf margin to the leaf underside as an additional evolutionary process. This hypothesis was developed by Prantl (1875, 1881, 1892) and Bower (1918, 1984) and possible evolutionary stages were illustrated by Goebel (1930) and Gifford and Foster (1989). According to Gifford and Foster (1989), in the course of evolution the upper indusial flap becomes modified as the new leaf margin and becomes vascularized, while the lower indusial flap becomes thinner and remains as the indusium. It is assumed that the "phyletic slide" can be observed in the ontogenesis of certain ferns (Bower 1918, Zimmermann 1959, Gifford and Foster 1989). But an ontogenetic slide in the sense of a migration of the marginal sorus onto the underside of the leaf is unconceivable in higher plants because of their rigid tissue construction (Thorspecken and Hagemann 1983).

In recent times, it has been criticized that also not all elementary processes of the telome theory are supported by known ontogenetic processes (Stein 1998, Sanders *et al.* 2007). Especially the processes of planation and webbing which are used by Zimmermann (1959) and other authors (e.g. Bold *et al.* 1980, Stewart and Rothwell 1993, Kenrick and Crane 1997, Bresinsky 2008, Taylor *et al.* 2009) to derive the megaphyll from the original telome truss are incompatible with the ontogenesis really taking place (Hagemann 1976, 1984a, see also Imaichi 2008). Moreover, Beerling and Fleming (2007) argue that if the fusion process (webbing) cannot be observed in leaf ontogenesis, then the requirement for planation is not obvious. According to

Hagemann (2005a), it is also not understandable that leaf laminae should arise from branched telome systems by planation and webbing, considering that the gametophytes of liverworts and ferns are already frondose thallose organisms.

Meanwhile, some authors have doubted the validity of the hypothesis that marginal sporangia or sori are primitive (Wagner 1964, 1974, Kramer *et al.* 1995). According to Hagemann (1984a, 1991, 1999) not the marginal, but the superficial position of the sporangia or sori is the primitive condition. On the basis of comparative morphological studies on recent plants, he holds the view that the *repens* type of plant construction is the archetype of land plant form (Hagemann 1999, 2005a, b).

According to Hagemann, primitive land plants are thallose frondose organisms growing by means of marginal blastozones which are the primary growing zones in contrast to the adult parts of the vegetation body (Hagemann 1999, 2005a, b). In frondose liverworts and fern gametophytes they produce ribbon-like thalli which grow continuously at their anterior part and die at their posterior part (Hagemann 2002, Strother, 2010). In the fern gametophytes the reproductive organs arise from single protodermal cells on the underside of the thallus (Hagemann 2000 Fig.51), where especially the archegonia are formed near the growing blastozone (Sheffield 2008 Fig.2.4).

Also in higher plants, the primary shaping of the vegetative shoot is always combined with growth originating in blastozones. As special terminal growth zones they are responsible for primary morphogenesis (Hagemann and Gleissberg 1996, Hagemann 1999, 2000, 2002, 2005a, b, see also Sanders, 2006). Their form is decisive

for the form of the resultant primary organs. Form growth is the primary developmental process affecting the organ primordia. Cell wall formation follows shaping of the vegetation body during its growth. The cell walls are integrated according to the preexisting form and thus, the growing form outlined by the blastozones becomes stabilized (Hagemann 1999, Hagemann *et al.* 2008).

The leaf marginal blastozone is produced by fractionation of the apical shoot blastozone on the flank of the shoot apex and, therefore, has from its beginning the form of a vegetation line which outlines the future dorsiventral flag-like form of the megaphyll (Hagemann and Gleissberg 1996, Hagemann 2002, Hagemann *et al.* 2008). In its flat construction with marginal growth the megaphyll is comparable to the construction of the fern gametophyte (Hagemann 2002, 2005a, b, see also Sattler 1998). In the simplest case the sporangia are produced singly on the underside of the sporophyll near the marginal blastozone and thus in a position homologous to that of the fern antheridia and archegonia (Hagemann 2000 Figs.63, 64).

In this study the relationships between submarginal and marginal sori are examined in the light of Hagemann's hypothesis. For this purpose different forms of sori are studied ontogenetically and analysed using the methodical framework of construction morphology of Hermann Weber (1958), which was developed into a botanical construction morphology by Hagemann (1999, 2000, see also Schölch 2000a).

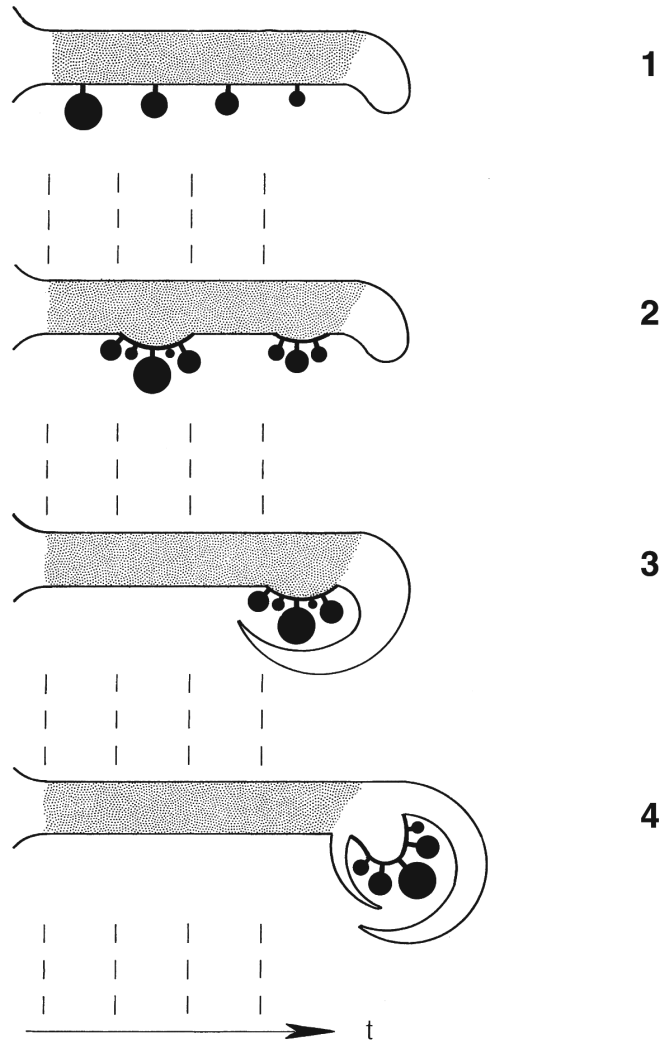
Proceeding according to this method means to compare organisms on the basis of their constructions and their developmental potencies for further evolution.

Because evolution tends to produce organisms of ever increasing complexity (e.g. Hagemann 1984b, Brooks and Wiley 1986), this increase in complexity serves as a criterion for reading the direction of possible constructional transformation. Surely, in certain cases, evolution may also lead to secondary simplicity, if it is of advantage to the organism. But a high level of complexity must always be considered derivative, even if the preceding simpler conditions are not known.

Sporophyll development

The analysis of the sori departs from the idea that the dorsiventral sporophyll is comparable with the construction of the fern gametophyte. In the simplest case singly-occurring sporangia are produced simultaneously with the development of the vegetative structures. The sporangia arise by integration of periclinal walls into single surface cells of the developing lower leaf surface (Schölch 2000a, Punetha and Mehta 2008). A receptacle is not formed (Schölch 2003). Thus the sporangia are scattered all over the leaf underside, a state which is called "superficial singly-arranged sporangia" (Fig.1).

In most sporophylls, however, the leaf surface is differentiated into vegetative and reproductive areas. The sporangia then appear in groups which are separated from one another by sporangia-free areas. Such a sporangial aggregation including the sporangia-producing site of the lamina is termed a "sorus" (Schölch 2000a). The confined site of the leaf surface bearing the sporangia is called "receptacle" (Gifford and Foster 1989, Schölch 2000a). The receptacle frequently develops indusia which display constant positional relationships



Figures 1-4 : Time of initiation of the reproductive organs: 1. Superficial singly-arranged sporangia. 2. Superficial sori. 3. Submarginal sorus. 4. Marginal sorus. Dotted: leaf blade; white: leaf margin or marginal sorus; *t*: time of initiation. (1-4 from Schölich 2000a).

to it. Indusia occur only in connection with the receptacle.

Based on the time of initiation in relation to leaf development, superficial, submarginal and marginal sori are distinguished. Comparable to the superficial singly-arranged sporangia, superficial sori are also formed simultaneously with the development of the vegetative structures (Fig.2).

In the simplest case, superficial sori arise as minute, island-like areas of the leaf underside which are specialized to produce sporangia (Figs.5-6). They are comparable to the archegonial sori of certain ribbon-shaped fern gametophytes. In these prothalli, instead of a continuous midrib intermittend archegonia-bearing cushions are produced (Fig.7) (Takahashi *et al.* 2009, additional literature in Schölch 2008).

The formation of submarginal and marginal sori, however, correlates with a phase differentiation in leaf development. This means that the development of the sporophyll is differentiated into two separate phases, an initial vegetative and a final reproductive phase. In contrast to the gametophytic thallus, the fern leaf is characterized by a normally limited marginal growth (closed development, Hagemann 1999, 2002) which implies a decline of the blastozone activity. As a result of this, the blastozone tissue is used up by histological differentiation. Therefore, the initiation of the reproductive organs as a protohistogenetical process, can also be delayed with respect to the development of the vegetative structures.

In the submarginal sori the tissue of the leaf underside last produced by the blastozone is used up for the receptacle formation. Phase differentiation concerns only the underside of the leaf surface

which becomes differentiated into an initial vegetative zone and a subblastozonal reproductive zone (Fig.3). The former leaf marginal blastozone itself is not used for differentiation of receptacular tissue. Submarginal sori are therefore regarded as a special case of superficial sori (Schölch 2000a).

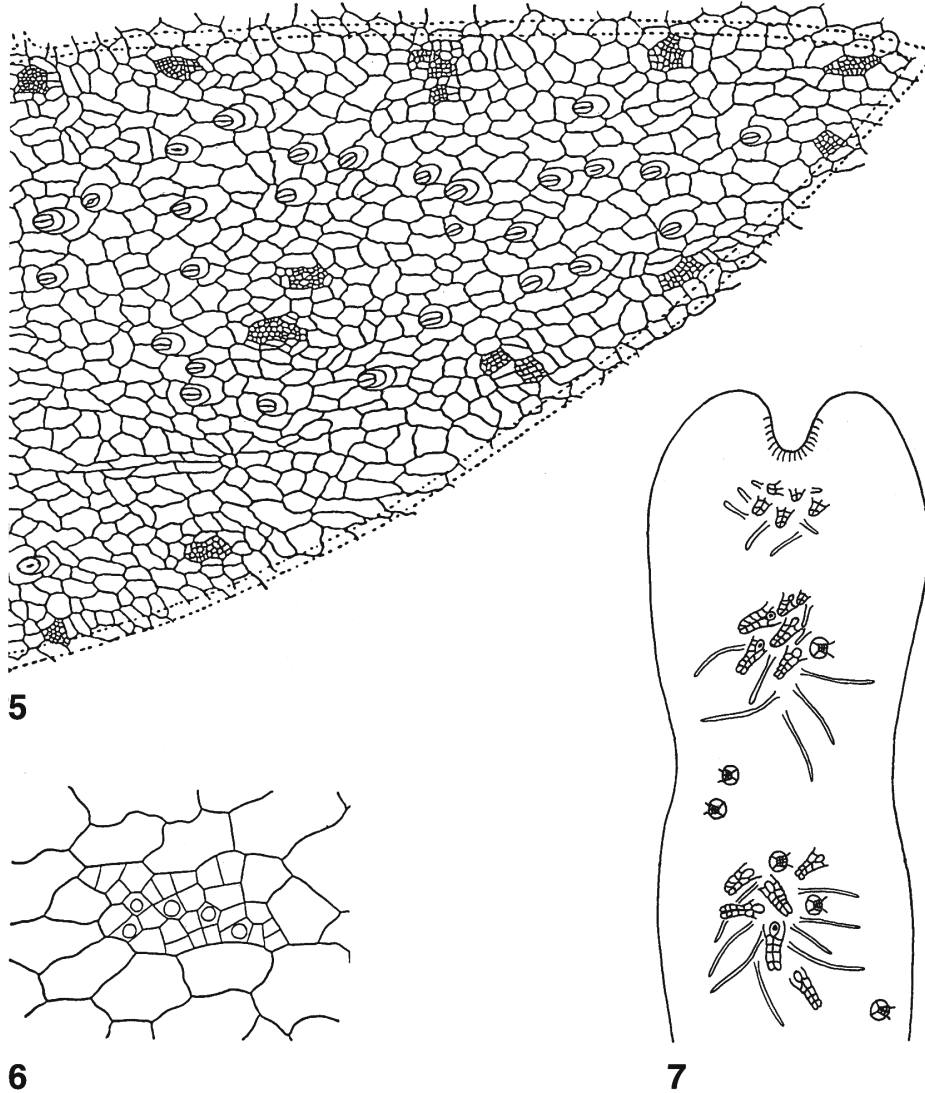
Marginal sori are the result of an extreme phase differentiation in leaf development. In this case the tissue of the declining blastozone itself is used up for the receptacle formation (Fig.4).

In the leaf areas bearing submarginal and marginal sori the leaf margin is usually bent revergently, which means bent towards the underside of the leaf. The revergence is a curvature opposed to the acrovergence. It is caused by the growth activity of a special tissue called bending meristem

Sorus ontogenesis (main group I)

On the basis of the construction of their sporangia the megaphyllous ferns can be arranged in two main groups, one with delicate leptosporangia and one with massive leptosporangia. The delicate sporangia have a transverse, oblique, or vertical annulus which are all connected by transitional forms, while the massive sporangia are characterized by an apical annulus or an annulus plate (Hagemann 1984b Fig.260). In each group there are possible ways for the origin of marginal sori in superficial singly-arranged sporangia.

In the first main group, superficial singly-arranged sporangia are provided by *Pityrogramma calomelanos* var. *austramericana* (Fig.8) and *Anogramma chaerophylla* (Fig.9). For the formation of delicate sporangia thickening tissue is not a prerequisite. The delicate sporangia



Figures 5-7 : Superficial sori. 5-6. *Anetium citrifolium* (Vittariaceae): 5. Portion of a sporophyll comprising half a mash. Groups of small cells representing the soral primordia. 6. Soral primordium with sporangial initials. 7. Ribbon-shaped fern gametophyte with archegonial sori. (5-6 from Schölich 2003; 7 from Goebel 1930, modified). Bar: 100 μ m (6), bar: 1mm (5).

may therefore arise on the costae as well as between the costae. This can be seen in the *Pityrogramma* state (Fig.33). Alternatively, they may also be restricted to the costae as in the *Anogramma* state (Fig.33). Since the delicate sporangia are long-stalked, younger sporangia can be initiated between the older ones, so that a mixed sequence of sporangial initiation results (Fig.9).

If a sporangial arrangement as in *Pityrogramma* is restricted to the subblastozonal region of the leaf, a submarginal sorus is formed. The receptacle of such a sorus runs across the ends of several costae and the tissue lying between the costae and produces sporangia in mixed sequence.

In *Pteris quadriaurita* the submarginal sori are linear and extend nearly to the apex of the pinna (Fig.10). Preceding sorus initiation, the former leaf marginal initials are displaced towards the underside of the leaf (Fig.11). As soon as sufficient vegetative leaf lamina is built up, sorus formation takes place subblastozonally in the arch of the revergence and the first sporangia become visible (Figs.12, 15). Further sporangia are formed between the older ones, and become covered as in *Pteris cretica* (Fig.13) by a continuous marginal membranous flap (Fig.15).

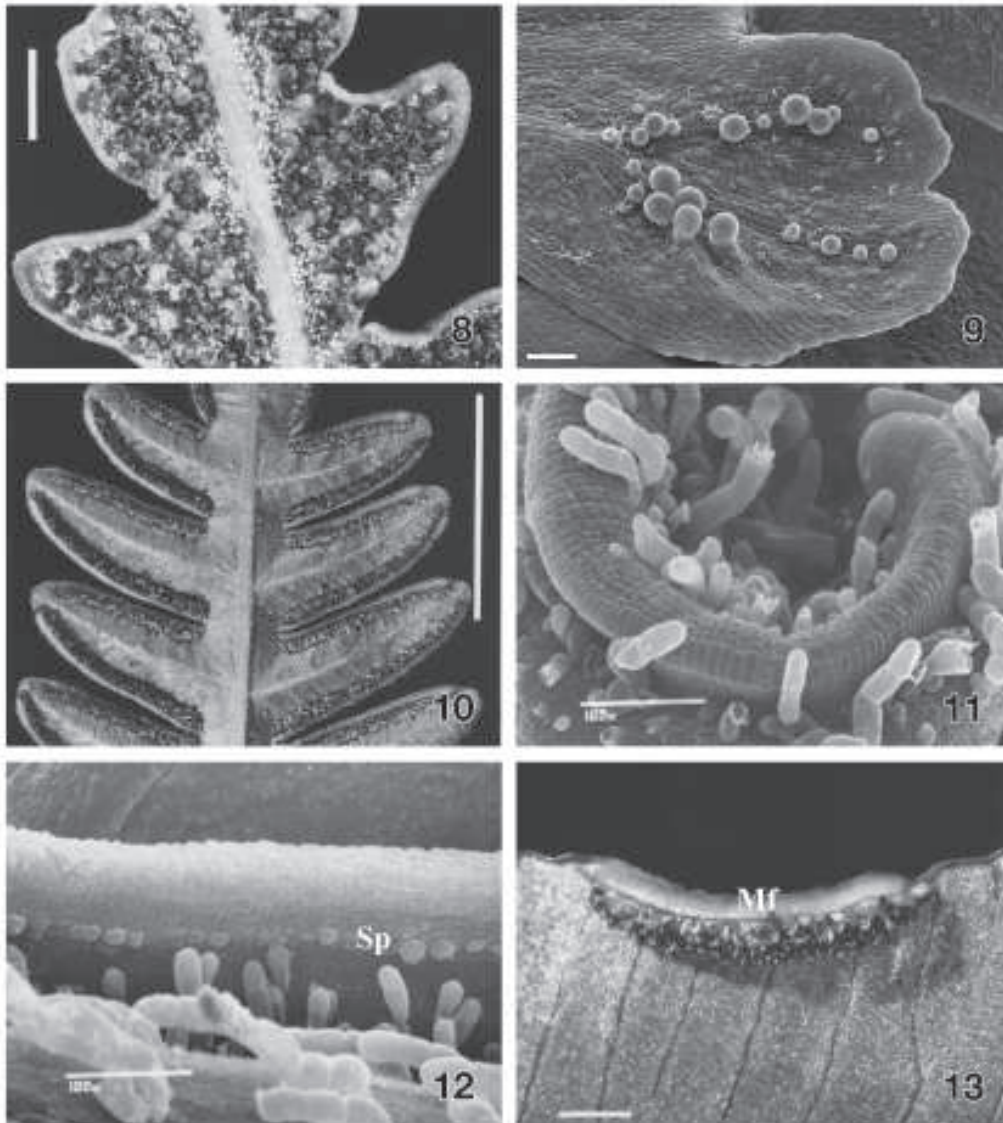
The term *Pteris* type (Figs.14, 15) is introduced for a sorus formation which is typical of *Pteris* and *Adiantum*. A sorus of this type may occupy different positions in relation to the revergent leaf margin. It is either located on the lower surface of the recurved leaf margin and the receptacle is flat as in *Adiantum* (Fig.14), or it lies exactly in the arch of the revergence and the receptacle is ridge-shaped as in *Pteris* (Fig.15). In both cases the former

leaf marginal blastozone is used up for the formation of a veinless membranous flap.

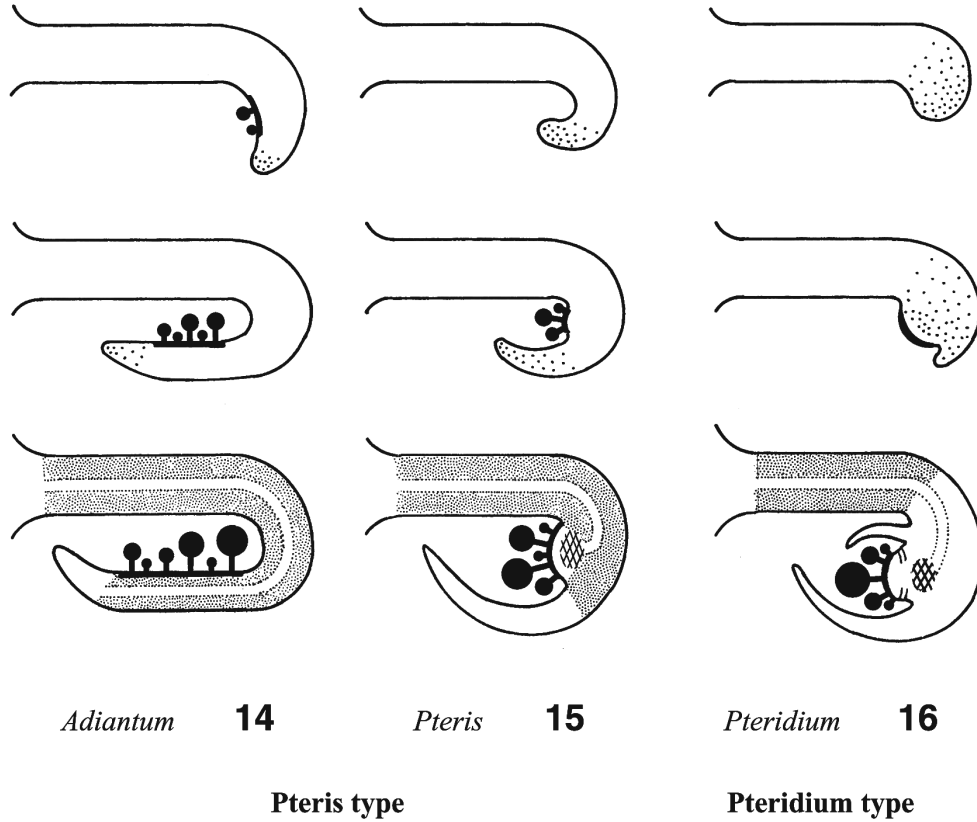
A ridge-shaped receptacle may also be formed by the declining leaf marginal blastozone itself. Then the sorus occupies a marginal position as seen in *Pteridium aquilinum*. The linear sorus runs round the apex of the pinna (Fig.17). Preceding sorus initiation, the former leaf marginal initials are displaced towards the underside of the leaf (Fig.18). The bending growth of the leaf margin is maintained until the sorus is oriented against the lower leaf surface, ultimately turning through 180° (Fig.16). The receptacle projects from the area of the former leaf marginal blastozone (Figs.19, 16). The upper indusium is formed on the upper side of the receptacle. The lower indusium appears later than the upper one (Fig.20). Its marginal cells grow out into hairs. After the formation of the two indusia the first sporangia arise from the apex of the receptacle (Fig.21). Later, further sporangia are initiated at the flanks of the receptacle in basipetal sequence (Fig.22).

Pteridium is representative of the *Pteridium* type (Fig.16), a non-costa-related basipetal marginal sorus. The former leaf marginal initials occupy the apex of the receptacle and produce the first sporangia. This provides the potency for basipetal sporangial initiation. Owing to the continuing growth activity of the tissue below the former marginal initials, the receptacle develops a basal intercalary growing zone on either side (Fig.16).

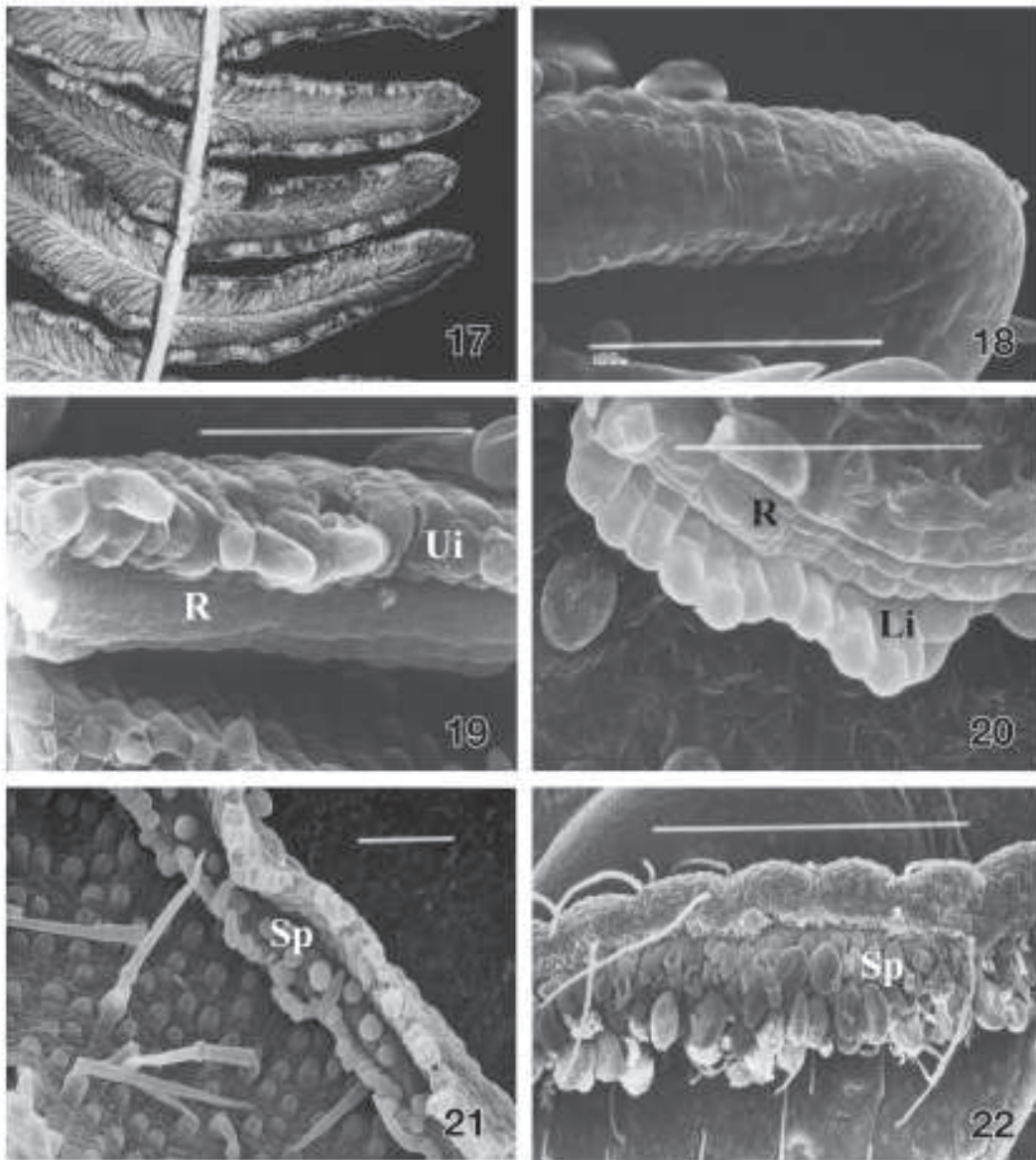
Concurrently with the growth activity of the subblastozonal bending meristem being now integrated into the receptacle, an upper indusium arises at the upper side of the receptacle. The lower indusium



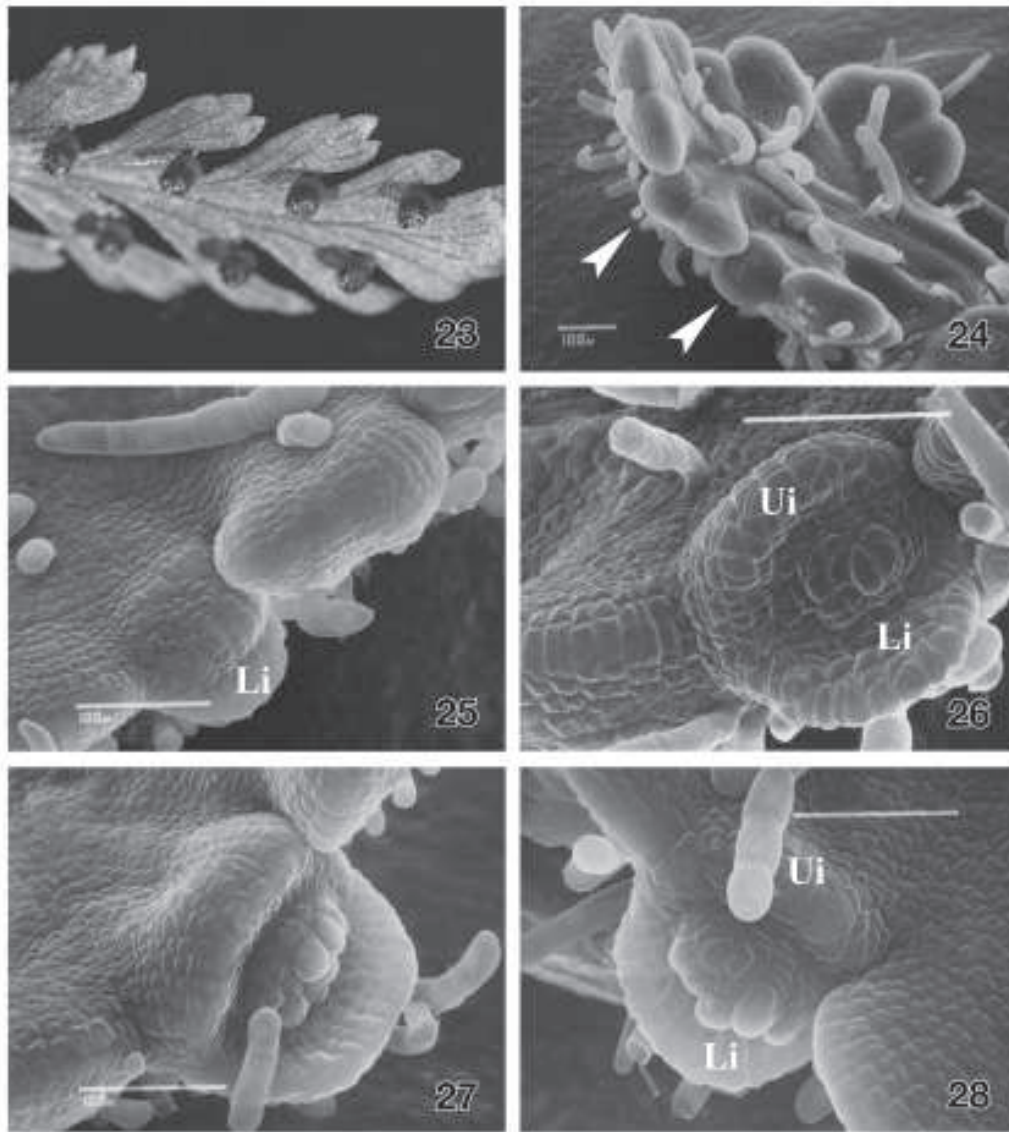
Figures 8-13 : 8-9. Superficial singly-arranged sporangia. 8. *Pityrogramma calomelanos* var. *austroamericana* (Pteridaceae): Pinna portion from the lower side, showing non-costa-related sporangia intermingled with glandular trichomes. 9. *Anogramma chaerophylla* (Pteridaceae): Pinna portion from the lower side, showing costa-related sporangia initiated in mixed sequence. 10-13. Submarginal sori. 10. *Pteris quadriaurita* (Pteridaceae): Portion of a pinnate leaf with mature sori. 11. *P. quadriaurita*: Displacement of the leaf marginal initials towards the lower side of the leaf. 12. *P. quadriaurita*: First sporangia, marking the position of the receptacle in the arch of the revergence. 13. *P. cretica* (Pteridaceae): Sorus, covered by the veinless membranous flap (**Mf**). (8, 10-13 from Schölch 2003). Bar: 100 μ (9, 11, 12), bar: 1mm (8, 13), bar: 1cm (10).



Figures 14-16 : Ontogenesis of the Pteris type and the Pteridium type in comparison. Schematic drawings of different stages of sori development. There are differences in the initiation of the sori in relation to the leaf marginal blastozone and their position in relation to the revergent leaf margin. 14. *Adiantum*: Sorus on the lower side of the revergent leaf margin. Subblastozonal flat receptacle with sporangia initiated in mixed sequence, narrow veinless membranous flap. 15. *Pteris*: Sorus in the arch of the revergence. Subblastozonal ridge-shaped receptacle, initiation of sporangia in mixed sequence, broadened veinless membranous flap covering the sorus. 16. *Pteridium*: Sorus arising from the edge of the revergent leaf margin. Blastozonal ridge-shaped receptacle, covered by an upper and a lower indusium, initiation of sporangia in basipetal sequence. As in *Hypolepis* (Fig.29), the revergence starts before the initiation of the upper indusium. Loosely dotted: blastozone region; white: marginal membranous flap (14-15) or marginal sorus (16); hatched: peripheral intercalary growing zone; diamond-hatching: sorus-specific vascular strand. (14-16 from Schölch 2003, modified).



Figures 17-22 : *Pteridium aquilinum* (Hypolepidaceae): 17. Pinnae from the lower side with mature sori. 18. Displacement of the leaf marginal initials towards the lower side of the leaf. 19. Initiation of the receptacle (**R**), upper indusium (**Ui**) already becoming apparent. 20. Early stage of the lower indusium (**Li**). 21. Initiation of sporangia (**Sp**), upper indusium removed. 22. Mature sorus, upper indusium removed to show the basipetally-initiated new sporangia. (17-20, 22 from Schölch 2000a; 21 from Schölch 2008). Bar: 100µm (18-22).



Figures 23-28 : *Dennstaedtia glauca* (Dennstaedtiaceae): 23. Pinna from the lower side with mature sori. 24. Pinna margin with sori initiation (arrows) at the lobes. 25. Younger pinna lobe in the upper half of the picture and older pinna lobe in its lower half, the latter showing a young sori with the lower indusium (**Li**) arising before the upper one. 26. Young sori with fusing ends of the upper (**Ui**) and lower indusium, at the tip of the receptacle the first sporangial initials. 27. Upward growth of the joined indusia and bending growth of the sori. 28. Intercalary growing zone at the base of the receptacle. (23-24, 26-28 from Schölch 2000a; 25 from Schölch 2008). Bar: 100µm (24-28).

can be traced back to trichomes (Schölch 2000a, 2008).

Basipetal marginal sori may also be confined to the end of a costa. Owing to fractionation of the leaf marginal blastozone, short blastozone portions are produced and transformed into soral primordia.

Costa-related basipetal marginal sori occur in *Dennstaedtia glauca*. The sori with their cup-shaped indusium are located at the acroscopic margins of the pinna lobes (Fig.23). Preceding sorus formation, the pinna lobe primordium is fractionated into an acroscopic and a basispic part (Fig.24). The young soral primordium is at first oriented in the plane of the lamina. The indusia arise as crescent-shaped outgrowths on both sides of the receptacle, at first the lower indusium and then the upper one (Fig.25). The ends of the indusial primordia facing one another are so close together that they incorporate the meristematic receptacular tissue lying between them, and thus fuse together to form a ring-like indusial structure (Fig.26). Simultaneously with the formation of the upper indusium, the receptacle undergoes revergent bending growth (Figs.27, 30), during the course of which the sorus turns through 90° (Figs.23, 30). At the apex of the receptacle the first sporangia become visible (Fig.26). Due to a basal intercalary growing zone, further sporangia are produced in basipetal sequence (Fig.28).

Together with *Hypolepis* and *Dicksonia*, also *Dennstaedtia* belongs to the Dicksonia type (Figs.29-31). The receptacle of this type is either cushion-shaped as in *Hypolepis*, or cone-shaped as in *Dennstaedtia* and *Dicksonia*. If the diameter of the receptacle becomes smaller, an annular peripheral intercalary growing zone may extend over the cross-section of the receptacular basis, finally traversing it (Fig.30). The indusial envelope is

a fusion product of an upper indusium originating from the bending meristem with a lower indusium derived from trichomes.

Evolutionary pathways (main group I)

Figure 33 shows possible pathways for the evolution of submarginal and marginal sori belonging to the main group with delicate leptosporangia.

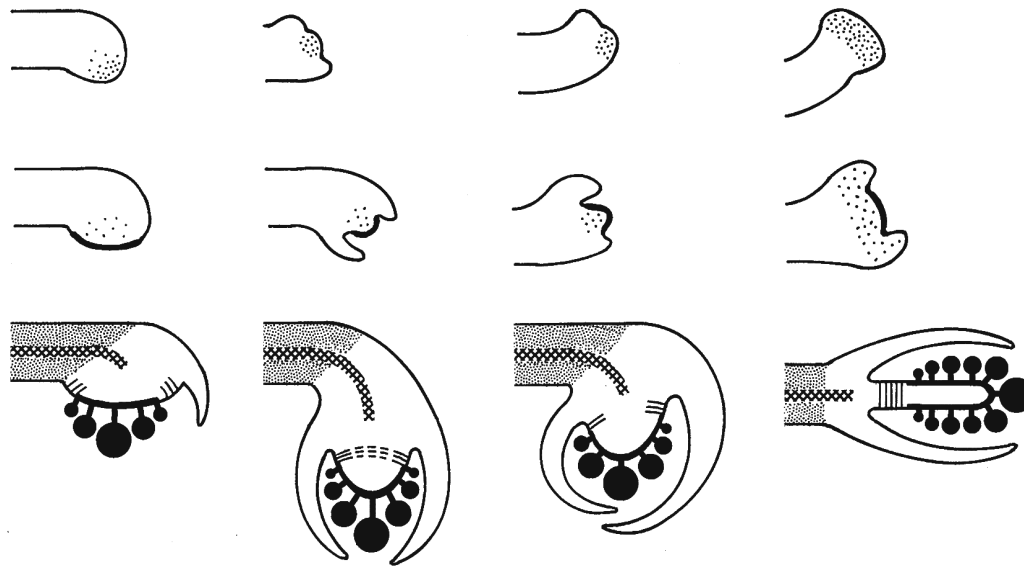
The Pteris type may evolve from the non-costa-related *Pityrogramma* state by phase differentiation in lamina development combined with subblastozonal receptacle formation.

The Pteridium type may be derived from the Pteris type or directly from the *Pityrogramma* state. For both pathways the decisive processes are the same: phase differentiation combined with blastozonal receptacle formation, formation of a basal intercalary growing zone, and development of an upper and a lower indusium. The upper indusium arises from the area of the bending meristem and corresponds in its orientation to the marginal membranous flap, as seen in *Pteris*.

The Dicksonia type may arise from the Pteridium type by linkage of sorus formation to the costae. Instead of a ridge-shaped receptacle cushion-shaped receptacles are formed. Owing to continued basal intercalary growth such a receptacle becomes conically elongated and develops a cup-like indusial envelope.

The Dicksonia type may also evolve directly from a superficial position. Initial forms are either the Anogramma state or the Cyathea type.

In the first case, costa-related superficial singly-arranged sporangia are confined to thickened blastozone tips. The former leaf marginal initials produce the first sporangia.

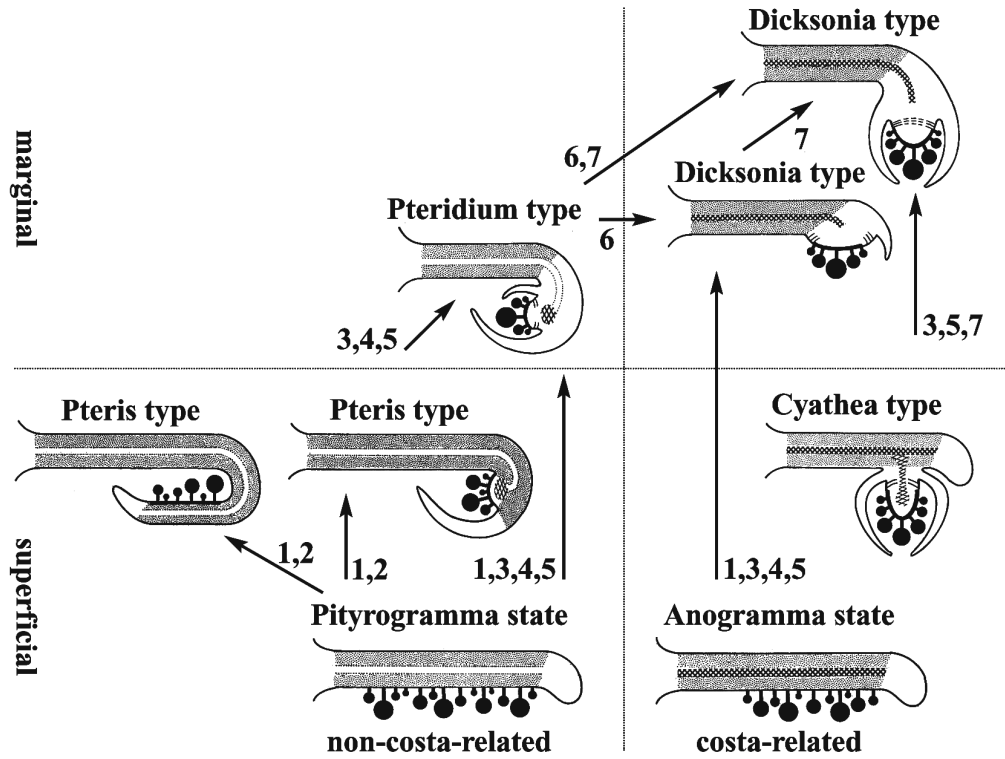


Hypolepis 29 *Dennstaedtia* 30 *Dicksonia* 31 *Hymenophyllum* 32

Dicksonia type

Hymenophyllum type

Figures 29-32 : Ontogenesis of the Dicksonia type and the Hymenophyllum type in comparison. Schematic drawings of different stages of sorus development. There are differences in the onset and extent of the revergent bending growth. 29. *Hypolepis*: Revergence starts before the initiation of the upper indusium, blastozonal cushion-shaped receptacle with initiation of sporangia in basipetal sequence. 30. *Dennstaedtia*: Revergence simultaneously with the initiation of the upper indusium, blastozonal cone-shaped receptacle with cup-like indusial envelope. 31. *Dicksonia*: Revergence after the initiation of the upper indusium, blastozonal cone-shaped receptacle with box-like indusial envelope. 32. *Hymenophyllum*: Revergence was not observed, receptacle subdivided into the basal socle bearing the cup-like indusium, the intercalary meristem, and the apical rod with basipetally-initiated sporangia. Loosely dotted: blastozone region; white: marginal sorus; hatched: peripheral intercalary growing zone or intercalary meristem. (29-32 from Schölch 2000b, modified).



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Figure 33 : Evolutionary pathways of submarginal and marginal sori (Main group I). Developmental processes: 1 Phase differentiation in lamina development. 2 Subblastozonal receptacle. 3 Blastozonal receptacle. 4 Basal intercalary growing zone. 5 Indusium by the bending meristem. 6 Costa-relation. 7 Cup-shaped indusial envelope.

This provides the potency for changing the mixed sporangial initiation into the basipetal one, as seen in the *Pteris-Pteridium* model.

In the second case, a costa-related sorus with a basal intercalary growing zone does not arise subblastozonally, but from the blastozone itself. Also along these two pathways the upper indusium originates from the bending meristem. Therefore, only the lower indusium corresponds to the indusium of the *Cyathea* type (Schölch 2003).

Apart from the *Dicksonia* type also the *Hymenophyllum* type (Fig.32) belongs to the costa-related basipetal marginal sorus. It is present in *Hymenophyllaceae*. The highly complex sorus is similar in its construction to the *Dicksonia* type, but differs from it essentially in its ontogenesis. The former leaf marginal initials are involved in the formation of a plateau-shaped thickening of the leaf margin (Figs.34, 32) preceding upward growth of the sporangia-producing part of the receptacle (Fig.35) and ring-like initiation of the indusium (Fig.34). The receptacle has a true intercalary meristem which allows it potentially indefinite growth (Figs. 36, 32). Until now the sorus of *Hymenophyllaceae* cannot yet be traced back to any superficial initial forms.

Sorus ontogenesis (main group II)

The second main group is characterized by massive leptosporangia. Comparable to the archegonia on the gametophytic midrib, they are formed in connection with the thickening growth of the costae which is preformed in the active blastozone. The superficial singly-arranged sporangia are therefore always restricted to the costae, as for example in *Todea barbara* (Fig.37). In the *Todea* state (Fig.55) neighbouring sporangia are almost of the same age, so that the

sequence of sporangial initiation is called simultaneous.

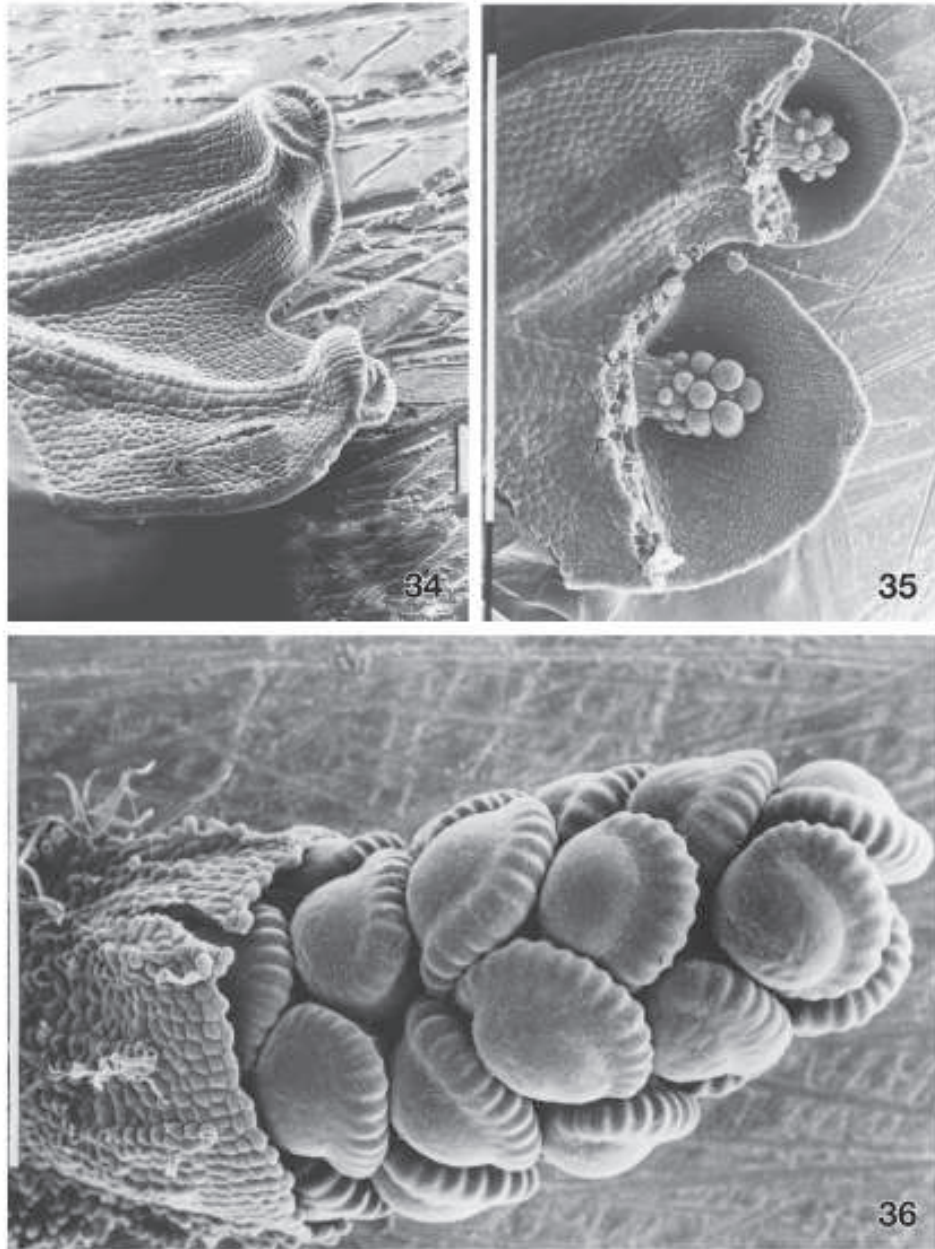
If, as a result of phase differentiation, in leaves like those of *Todea* the surface growth is completely reduced, the formation of sporangia is confined to the tip of short costae.

This can be seen in *Osmunda*. In *Osmunda regalis* the fertile pinnae lack expanded laminar parts (Fig.38). Only short costae are formed. Their former blastozones are transformed into receptacles due to continued thickening growth. The sporangia are tightly arranged on the receptacle, so that the sorus attains the shape of a globose cluster (Fig.39).

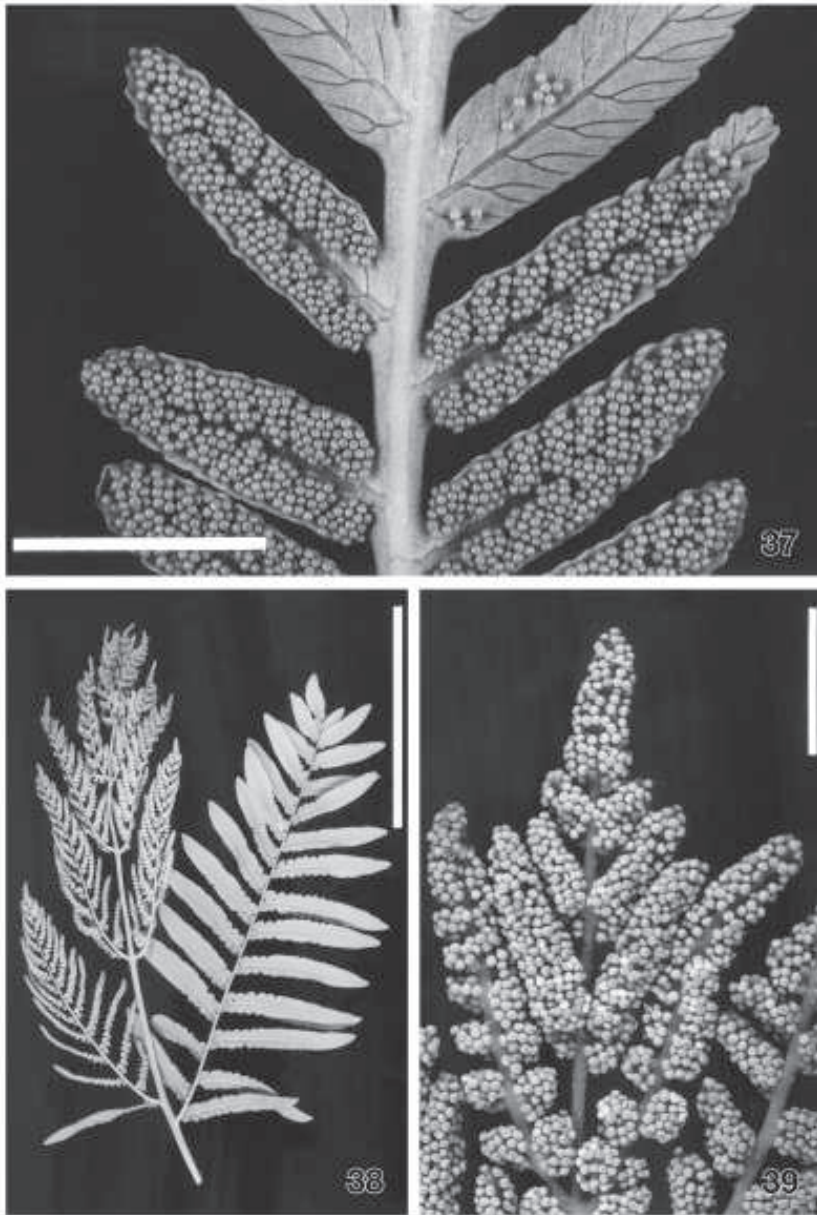
The *Osmunda* type (Fig.55) represents a thickened costa tip, and is characterized by an indusia-free knob-like receptacle which produces the sporangia simultaneously all over its surface.

If a state as in *Todea* is confined to the tips of the declining blastozone maintaining their apical growth, a costa-related marginal sorus with a bifacial receptacle and acropetal sporangial initiation results.

In *Mohria* the receptacle is minute because of an only briefly persisting apical growth. The pinna lobes of *Mohria vestita* bear up to three sori (Fig.40). The reproductive phase of a pinna lobe begins with displacement of the marginal initials towards its underside and transformation of short blastozone portions into receptacular meristems. At each end of such a meristem one sporangium is initiated by enlargement of a single marginal cell (Fig.41). The sporangium is separated from the row of the initials by a specific narrow marginal cell. When the receptacular margin increases somewhat in length, a third sporangium arises between those previously formed (Fig.42). Owing to the growth activity of the bending meristem,



Figures 34-36 : 34-35. *Mecodium rarum* (Hymenophyllaceae): 34. Part of a leaf with blastozonal soral primordia of various ages. 35. Sori of different ages, one indusial flap removed. 36. *Sphaerocionium applanata* (Hymenophyllaceae): Mature sporangia pushed out of the cup-shaped indusium. (34-36 from Schölch 2000b). Bar: 100 μ m (34), bar: 1mm (35-36).



Figures 37-39 : 37. *Todea barbara* (Osmundaceae): Underside of the leaf with superficial singly-arranged sporangia along the costae of the second-order pinnae. 38-39. *Osmunda regalis* (Osmundaceae): 38. Tip of a fertile leaf. Vegetative second-order pinnae with well developed laminae, fertile second-order pinnae with completely reduced laminae. 39. Fertile pinnae with globose sori. The sori become smaller towards the pinna tip and their outlines indistinct due to their tight arrangement. (37-39 from Schölch 2007). Bar: 1cm (37, 39), bar: 10cm (38).

an upper indusium is initiated during the early development of the sporangia (Fig.43). As sporangial development continues, the indusium grows upwards over the receptacular margin (Fig.44). Later it covers the receptacular tip (Fig.45).

In the Mohria type (Fig.55) the former leaf marginal initials are conserved as soral initials in the tip of the receptacle and function as an apical meristem. The receptacular margin remains short and produces only up to four sporangia.

If the apical growth persists for a while, the bifacial receptacle becomes elongated as in *Schizaea*. *Schizaea fistulosa* has rush-like sporophylls which run out into a sorophore, an elongated costa-like leaf part which bears on either side a row of sori (Fig.46). While the sorophore primordium is still coiled acrovergetly, its marginal blastozone is displaced towards the underside (Fig.47). Continued fractionation of the sorophore blastozone produces short blastozone portions which are transformed into sorus primordia in acropetal sequence (Fig.48). The sorus primordia grow into auriculate receptacles (Fig.49). Since the receptacular primordia and their margins are turned towards the underside, also the sporangia are oriented towards the underside of the receptacle. At the two ends of the receptacular meristem every second marginal cell becomes a sporangial initial in acropetal sequence (Fig.50). At the receptacular tips no sporangia are formed. The upper indusium arises from the outer side of the revergent curvature (Fig.50) and surrounds the receptacular tip (Fig.51).

Schizaea is a member of the *Anemia* type (Figs.52-54). The sori of this type arise either from the end of a costa as in *Anemia elegans* (Fig.52) or from the margin of a sorophore as in *Schizaea*

and *Anemia phyllitidis* (Figs.53, 54). Owing to persisting apical growth, numerous sporangia are formed in the considerably elongated receptacular margin.

Evolutionary pathways (main group II)

Figure 55 illustrates possible ways for the evolution of marginal sori in the main group with massive leptosporangia.

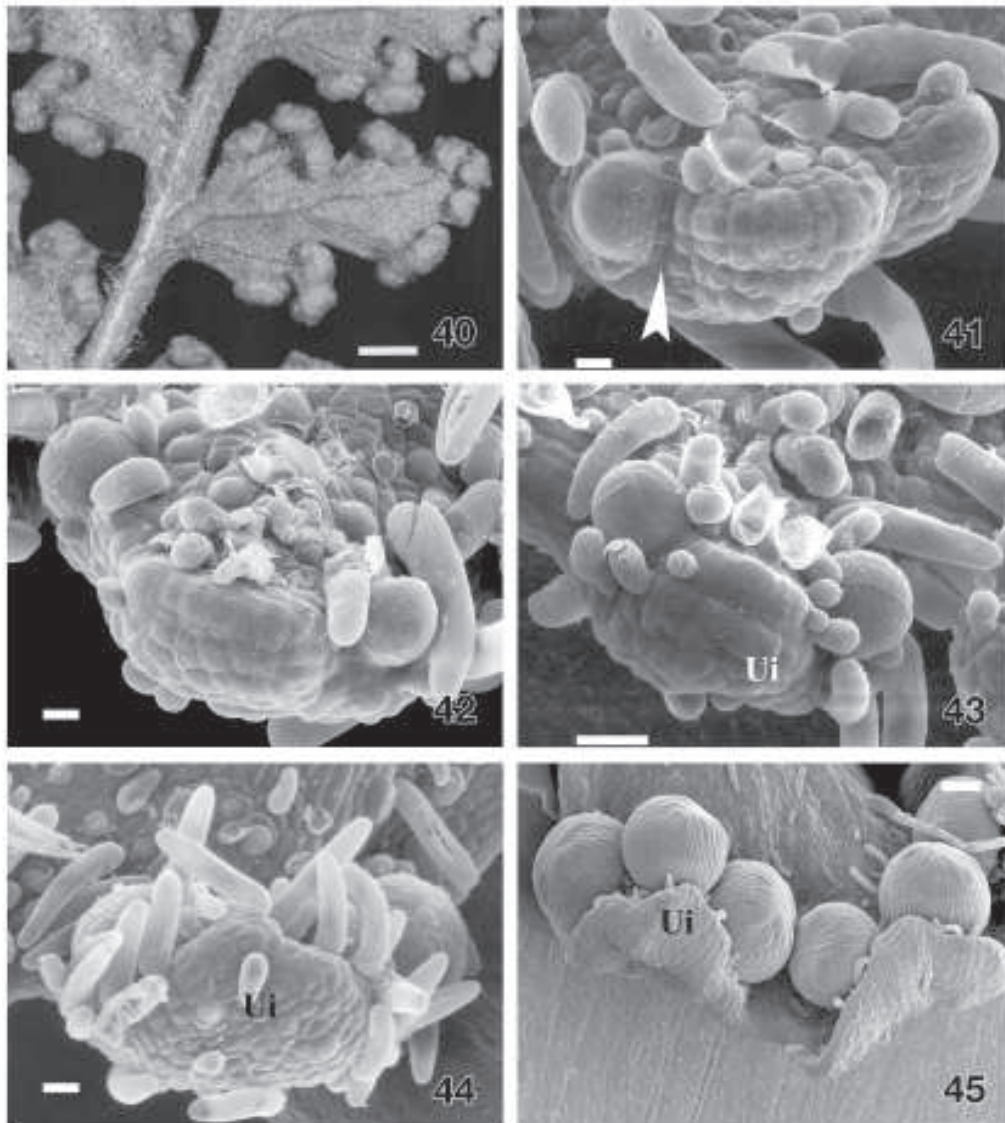
A state as in *Todea* may give rise to the *Osmunda* type as well as to the *Schizaeaceae* types. The *Osmunda* type arises due to phase differentiation with complete lamina reduction and thickening growth of the resultant short costae which is preformed in the active blastozone and continues during the reproductive phase.

For the evolution of the *Schizaeaceae* types the following processes are decisive: phase differentiation in lamina development combined with blastozonal receptacle formation, development of an apical growing zone in the receptacle, and formation of upper indusia by the bending meristem.

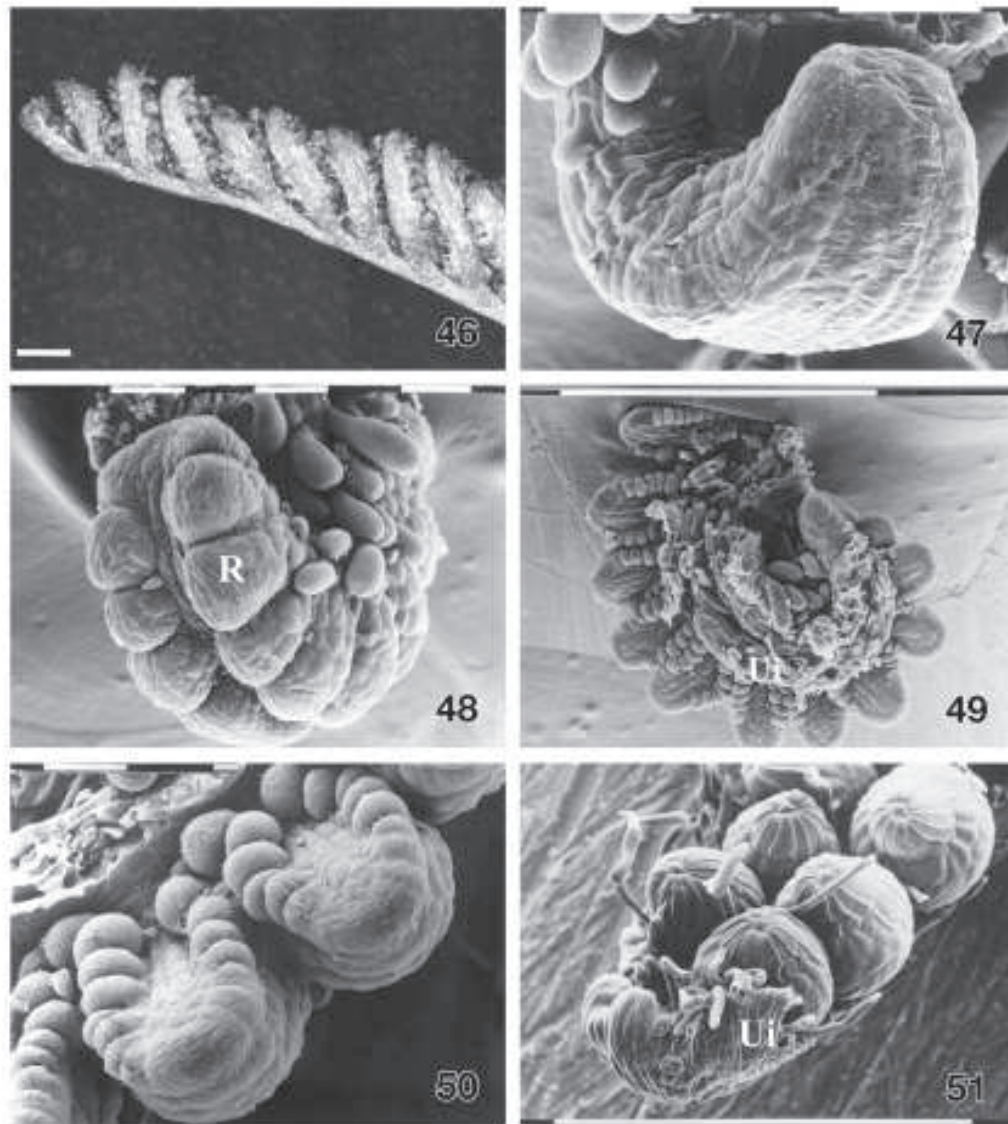
In the *Anemia* type the indusium is long-extended, while in the *Lygodium* type several separate indusia are formed, each confined to a single sporangium (Schölch 2008).

General conclusions

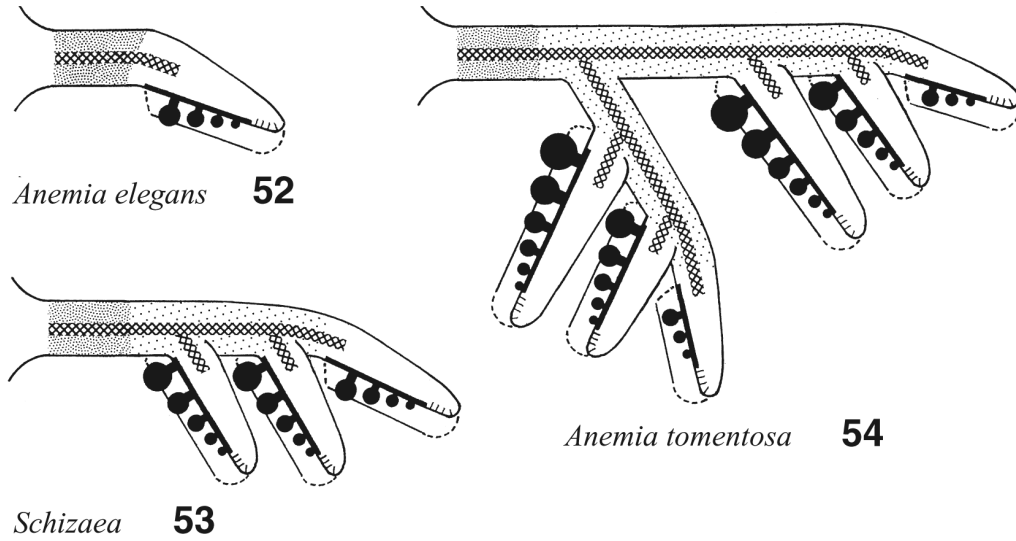
In summary, in both main groups similar developmental processes characterize the step by step transition from superficial singly-arranged sporangia into marginal sori. Submarginal sori, basipetal marginal sori, and acropetal marginal sori correlate with a phase differentiation in lamina development. Simultaneous marginal sori, however, are produced by a phase differentiation



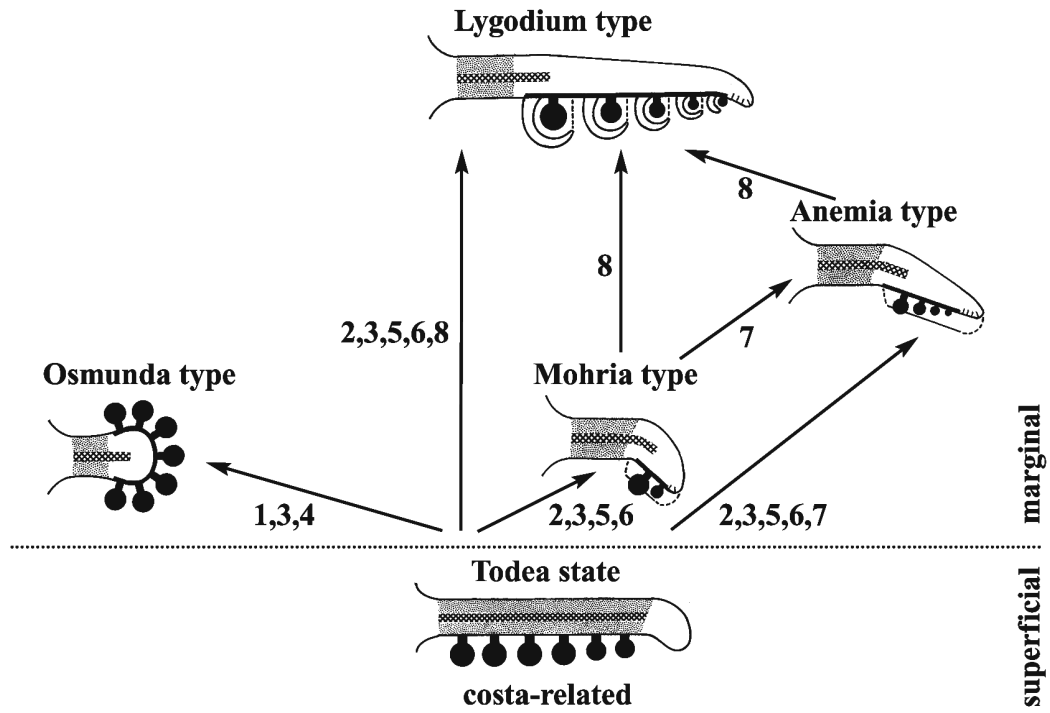
Figures 40-45 : *Mohria vestita* (Schizaeaceae): 40. Second-order pinnae with lobes bearing almost mature sori. 41. Sorus primordium. Two sporangia arising from the former leaf marginal initials, displaced towards the underside. On the left-hand side, hemispherical sporangial initial, next to it a narrow vegetative initial (arrow). 42. Sorus primordium with three sporangia in acropetal sequence, the oldest one on the left-hand side. 43. Sorus primordium with initiation of the upper indusium (**Ui**). 44. Upper indusium curving over the receptacle, partially covering the sporangia. 45. Sori with two resp. three sporangia. (40-45 from Schölch 2007). Bar: 20 μ m (41, 42), bar: 40 μ m (43, 44), bar: 100 μ m (40), bar: 200 μ m (45).



Figures 46-51 : *Schizaea fistulosa* (Schizaeaceae): 46. Sorophore with pinnately-arranged mature sori. 47. Sorophore apex with marginal blastozone displaced towards the underside of the leaf. 48. Sorophore with young receptacles (**R**) arising in acropetal sequence from the former marginal blastozone. 49. Sorophore cut longitudinally to show one row of receptacular primordia with incipient formation of sporangia. 50. Two receptacles, showing acropetal initiation of the sporangia. 51. The upper indusium (**Ui**) covers the sporangia-free tip of the receptacle. (46-51 from Schölch 2007). Bar: 100µm (46-48, 50), bar: 1mm (49, 51).



Figures 52-54 : *Anemia* type: Sorus with elongated bifacial receptacle, massive marginal sporangia initiated in acropetal sequence and long-extended upper indusium. 52. Sorophore lacking. 53. Sorophore unbranched. 54. Sorophore branched.



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Figure 55 : Evolutionary pathways of marginal sori (Main group II). Developmental processes: 1 Phase differentiation with laminar reduction. 2 Phase differentiation in lamina development. 3 Blastozonal receptacle. 4 Thickening growth. 5 Apical growing zone. 6 Indusium by the bending meristem. 7 Long-extended indusium. 8 Separate indusia.

which concerns whole pinnae and which is combined with complete lamina reduction. The development of submarginal sori involves subblastozonal receptacle formation, whereas for the development of marginal sori blastozonal receptacle formation is decisive. The formation of highly developed sori includes additional processes: Linkage of sorus formation to the leaf costae, formation of special receptacular growing zones and development of indusia.

As shown above, these developmental processes take place in different combinations yielding several potential pathways for the evolution of submarginal and marginal sori. Moreover, the processes of sorus formation by non-extreme and extreme phase differentiation, costa-relation and formation of a highly elaborate sorus apparatus are all suitable for demonstrating possible ways to an increase in complexity, as outlined by Schölch (2008).

Therefore, most of the common ideas about the phylogenetic direction in sorus evolution based on the fossil record are untenable. Assuming, that the concept of phase differentiation in the developing megaphyll proves to be accurate, the common view that marginal sporangia or sori are primitive cannot be maintained. Unlike e.g. Holttum (1973), costa-related basipetal marginal sori such as those of Hymenophyllaceae and Dicksoniaceae which are highly complex constructions cannot be regarded as initial forms in sorus evolution. In this regard it is interesting, that sori of the *Cyathea* type, i.e. basipetal superficial sori, which are thought by some authors (Goebel 1913, 1930, Churchill 1998) to be the result of a "shifting" of a basipetal marginal sorus to the superficial position are already present in the Carboniferous *Kaplanopteris clavata* (Tomescu *et al.* 2006).

Furthermore, it seems hardly likely that, according to the common hypothesis of a "phyletic slide" of the marginal sorus to the leaf underside, highly complex basipetal marginal sori develop into the simple state of superficial singly-arranged sporangia. Such a view fails to give a concept about the evolution of the highly elaborate marginal sori, which would be much more important than merely their phylogenetic dissolution as implied by the hypothesis of a "phyletic slide".

Moreover, indusia are formations of the receptacle of the sorus (Schölch 2000a). Like scales (Hagemann 1999) they are produced as appendages having no blastozones. In that respect, indusia, also the upper one, differ essentially from the leaf which grows at its margin with a blastozone from the very beginning anticipating and circumscribing the primary contours of the leaf (Hagemann 1999). This means that an upper indusium never develops into a new leaf margin.

In addition, it is questionable practice to base ideas about the phylogenetic direction of organismal development on fossil records alone. Fossils are the better conserved the more resistant and more durable their structures are (Sudhaus and Rehfeld 1992, Wiesemüller *et al.* 2003). Small and delicate organisms are disadvantaged in the fossilisation process (Strother 2010). For example, fern gametophytes are not known from the fossil record (Gifford and Foster 1989, Hagemann 1999, 2005a,b).

Therefore, fossil plants must be regarded critically on the basis of their construction with regard to their primitiveness. In this context construction morphology plays an important part (Hagemann 1999). Construction morphology can assess which state may be

primitive in view of its construction, and which may be not. Primitive organisms, extant or extinct, must have a simple organisation. Therefore, according to the above argumentation as a model for a megaphyll with a primitive sporangial condition one must search for forms, both recent and fossil, which during prolonged activity of the marginal blastozone develop singly-arranged sporangia simultaneously with the vegetative structures of the leaf (Schölch 2003).

The possible morphological relationships between the different forms of sori in conjunction with morphological data obtained from the vegetative parts of the sporophyte, from the gametophyte, and from fossils allow the following conclusions concerning a phylogenetic systematic arrangement of the treated families (see also Schölch 2008). The delimitation of the investigated families is concordant with Tryon and Tryon (1982), except their Dennstaedtiaceae, for which, according to Pichi-Sermolli (1970), the separation into the two families Hypolepidaceae and Dennstaedtiaceae is adopted (Schölch 2000a).

1) As confirmed by recent cladistic studies for Hymenophyllaceae (Smith 1995 Fig.4, Schuettpelez and Pryer 2006, Hennequin *et al.* 2008), for Dicksoniaceae (Smith 1995 Fig.4, Pryer *et al.* 2004, Wikström and Pryer 2005, Schuettpelez *et al.* 2006, Rothwell and Nixon 2006 Fig.4-6, Fischer 2009), and for Dennstaedtiaceae (Smith 1995 Fig.4, Hasebe *et al.* 1995 Fig.1, Stevenson and Loconte 1996, Pryer *et al.* 2004, Schuettpelez *et al.* 2006, Schuettpelez and Pryer 2006, Hennequin *et al.* 2008, Pryer and Schuettpelez 2009, Fischer 2009), these families cannot be regarded as basal groups.

2) As supported by molecular analyses (Hasebe *et al.* 1995 Fig.1, Pryer *et al.* 1995, 2001, 2004, Smith *et al.* 2006, Korall *et al.* 2006, Schuettpelez and Pryer 2007, 2008, Pryer and Schuettpelez 2009, Fischer 2009), Hymenophyllaceae cannot be regarded as closely related to Dicksoniaceae or to Dennstaedtiaceae.

3) Although molecular data (Wolf *et al.* 1994, Wolf 1995, Hasebe *et al.* 1994, 1995, Pryer *et al.* 1995, 2004, Schneider *et al.* 2004, Knoop 2005, Smith *et al.* 2006, Schuettpelez and Pryer 2007, Pryer and Schuettpelez 2009, Schneider *et al.* 2009) support a close relationship between Dicksoniaceae and Cyatheaceae, it can be questioned whether the two families are related at all, since a relationship of Dicksoniaceae to Dennstaedtiaceae cannot be excluded (e.g. Kramer *et al.* 1995, see also Schölch 2000b).

4) In accordance with molecular data (Hasebe *et al.* 1995 Figs.5-6, Pryer *et al.* 1995 Fig.5, 2004, Wolf 1997 Figs.3-4, Schuettpelez *et al.* 2006, Schuettpelez and Pryer 2006, Korall *et al.* 2006, Prado *et al.* 2007 Fig.6, Hennequin *et al.* 2008, Fischer 2009) Hypolepidaceae should be placed before Dennstaedtiaceae. A placement of Pteridaceae basal to Hypolepidaceae is also congruent with molecular studies (Wolf 1995, Hasebe *et al.* 1995, Pryer *et al.* 1995 Figs.3, 5, 10, Qiu *et al.* 2006, Qiu *et al.* 2007).

5) Concordant with cladistic approaches (Qiu *et al.* 1998, Rothwell 1999 Figs.3-4, 5F, Rothwell and Nixon 2006 Fig.3) Osmundaceae and Schizaeaceae may be regarded as related and may have a common ancestor in Botryopteridaceae (Rothwell 1994 Fig.2, see Schölch 2008).

Concluding remarks

Costa-related marginal sori, no matter whether they are basipetal or acropetal, arise along highly diversified evolutionary lines and attain the highest degree in complexity. Therefore, such sori cannot be regarded as representing the initial forms of sorus evolution. It seems much more probable that sorus evolution began with superficial singly-arranged leptosporangia comparable to the singly-arranged antheridia and archegonia

on the frondose gametophyte as a model for a primitive land plant. From them the amazing diversity of the sorus forms must have developed along distinct evolutionary pathways.

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