MORPHOGENESIS OF APOGAMOUS SPOROPHYTE IN *CYRTOMIUM FALCATUM* (L. FIL.) C. PRESL (*Dryopteridaceae*)

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Formation of the apogamous sporophyte is initiated when the prothallus is two months old and cordate. The sporophyte is differentiated towards the apical, pitted region of the prothallus, in its median plane, on the inferior side. The apogamous tissue produces a kind of flattened crest with rounded margins, from which the first leaf of the sporophyte is differentiated. Later a second leaf is differentiated from the apogamous tissue, while between these two leaves the stem initial is differentiated. The stem apex is solely responsible for generating the growth axis of the postembryonic plant First stages of development of apogamous sporophytes in *Cyrtomium falcatum* don't possess roots. Their absence is compensated by numerous rhizoids, generated by the prothallus around the apogamous sporophyte and, sometimes, on cells at the basis of the sporophyte. The first root of the apogamous sporophyte begins to differentiate from a tetrahedral initial cell after development of two or three leaves. In some cases on a prothallus two apogamous meristematic zones are differentiated, on either side.

Key words: Cyrtomium falcatum, apogamous sporophyte, first leaf, stem, first root.

INTRODUCTION

Apogamy is known in numerous fern species, *e.g.* in *Actiniopteris* sp., *Asplenium resiliensis*, *Cheilanthes sp.*, *Notholaena incana*, *N. sinuata*, *Phegopteris connectilis*, *Pellaea atropurpurea*, *P. flavens*, *P. flexuosa*, *P. glabella*, *P. nivea*, *P. tenera*, *P. viridis*, *Pteris cretica*, etc. (Nayar, 1962, Nayar & Bajpai, 1964, Paniraghi, 1962, Stokey, 1938, Vladescu, 1934). In some species apogamy is ± frequent, while in others the sporophyte is always of apogamous origin. According to Wagner and Smith (1993) the apogamous life-cycle is common in leptosporangiate ferns growing in habitats of reduced humidity.

MATERIAL AND METHOD

The material of prothalli (gametophyte) bearing apogamous sporophytes in various stages of differentiation was obtained by cultivating *in vitro*, on 0.5 × Murashige Skoog substrate, green sporangia of *Cyrtomium falcatum*. For further processing we used inclusion in paraffin wax and sectioning by means of a microtome. Sections were stained by haematoxyline Heidenhain, mounted in Canada balsam and photographed at a Docuval light microscope. Drawings were made with the aid of a camera clara.

RESULTS AND DISCUSSION

Formation of the apogamous sporophyte is initiated when the prothallus is two months old and cordate, and also in species of *Pellaea* and *Notholaena* (Nayar & Bajpai, 1964). In some cases sporophytes are formed on small, ameristic prothalli, ribbon-like shaped.

The sporophyte is differentiated towards the apical, pitted region of the prothallus, in its median plane, on the inferior side, from a tissue shaped like a humps-back, which is differentiated from gametophytic tissue (Plate I, Figs. 1–7, Fig. 1). Within the apogamous tissue a procambium tissue is differentiated, consisting of prosenchymatous cells with sharp ends, dividing longitudinally. Procambium cells distinguish themselves by very long nuclei. The procambium tissue is arched like that differentiated in juvenile leaves of a sporophyte resulting from a zygotic embryo (Fig. 2). The procambium formed within the apogamous embryo extends into the prothallic tissue, which becomes plurilayered behind the hump-back (Nayar & Bajpai, 1964). Also in the prothallus, next to the procambium, differentiation of tracheids can be observed (Fig. 3). The presence of tracheids in the prothallus has been reported in *Pellaea viridis* by Nayar & Bajpai, 1964.

The apogamous tissue produces a kind of flattened crest with rounded margins, from which the first leaf of the sporophyte is differentiated. Leaf primordia are covered by unicellular trichomes, identical with those prothallic, but also by uniseriate pluricellular trichomes. In some cases, as in *Pellaea viridis* (Nayar & Bajpai, 1964) on this apogamous tissue an obconic meristematic cell is early formed, from which the first leaf differentiates. Later a second leaf is differentiated from the apogamous tissue, while between these two leaves the stem initial is differentiated (Fig. 4). As indicated by Nayar & Bajpai (1964) for apogamous species of *Pellaea* and *Notholaena*, the successive juvenile leaves form from initials situated near the stem apex which is solely responsible for generating the growth axis of the postembryonic plant (Wardlaw, 1955).

The first stages of development of apogamous sporophytes in *Cyrtomium falcatum* do not possess roots. Their absence is compensated, as in apogamous species of *Pellaea* and *Notholaena*, by numerous rhizoids, generated by the prothallus around the apogamous sporophyte and, sometimes, on cells at the basis of the sporophyte. The first root of the apogamous sporophyte begins to differentiate from a tetrahedral initial cell after development of two or three leaves (Fig. 5). As Vladescu (1934) remarked this cell can be easily recognised by the segmental cells, formed by periclinal divisions, from which the root-cap will differentiate. After formation of the first root at the base of successive juvenile leaves will be differentiated for each root; but, as Vladescu observed (1934) in the case of zygotic origin, and Nayar & Bajpai (1964) in the case of the apogamous sporophyte in species of *Pellaea* and *Notholaena*, the regularity of this process is

lost. All postembryonic roots are also observed to originate near leaf bases and thus, fern roots are consistently lateral with respect to the longitudinal axis of the growing plant, which has been termed the homorhizic condition (Groff & Kaplan, 1988; Ehrendorfer, 1999).

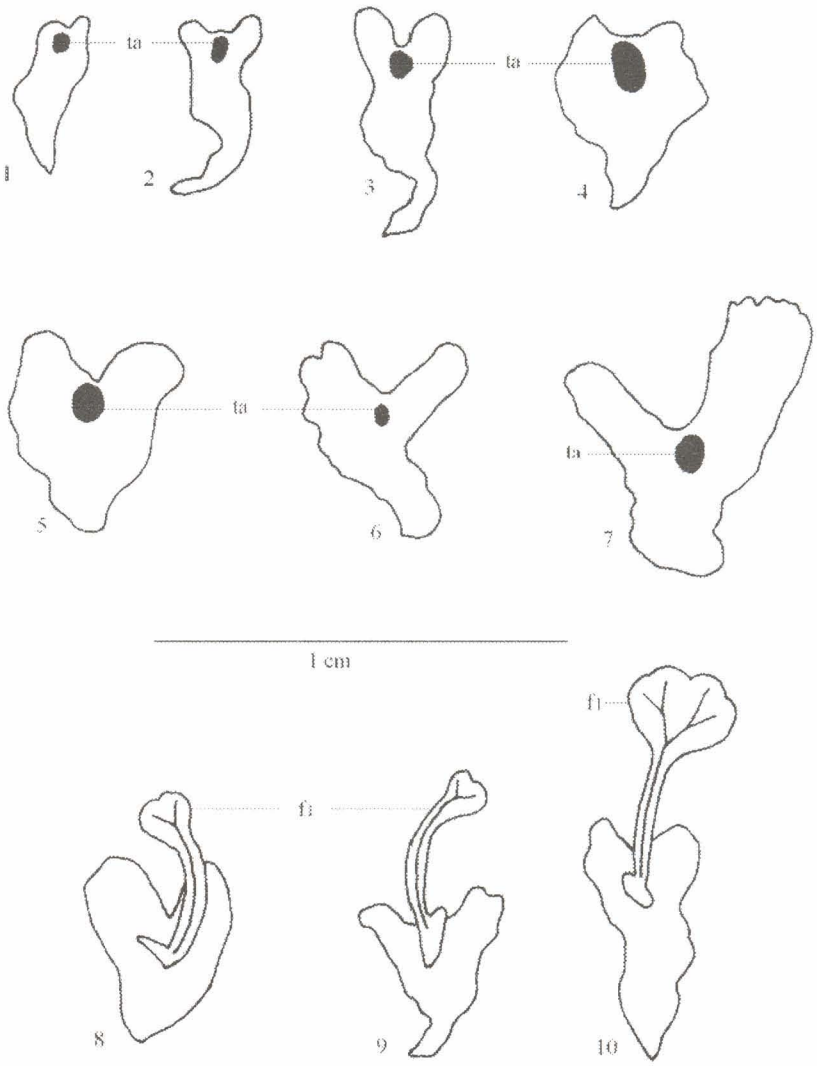

PLATE I

Figs. 1–7 *Cyrtomium falcatum* (L. Fil.) C. Presl – prothalli of various shape and dimension, on which apogamous embryo was differentiated (orig.).

Figs. 8–10 *Cyrtomium falcatum* (L. Fil.) C. Presl – prothalli with apogamous sporophyte with a single leaf (orig.) f_1-first sporophyte leaf, differentiated from apogamous tissue (ta).

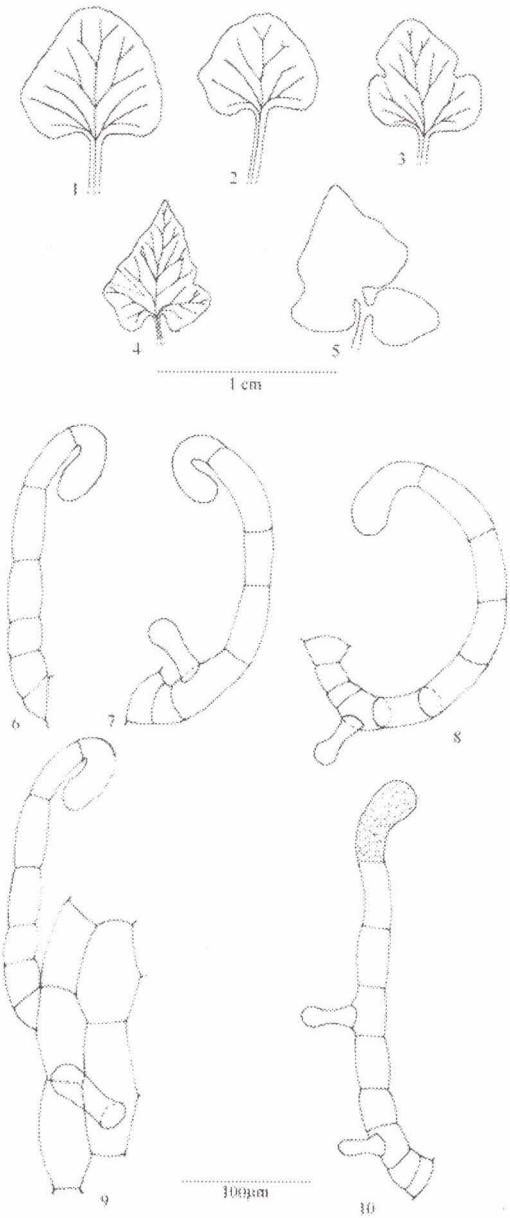

PLATE II

Figs. 1–5 *Cyrtomium falcatum* (L. Fil.) C. Presl – juvenile leaves of the apogamous sporophyte. In Fig. 4 the arrow indicates the transition from dichotomic nervation to reticulate nervation by way of uniting nerves (orig.).

Figs. 6–10 *Cyrtomium falcatum* (L. Fil.) C.resl – uniseriate pluricellular trichomes (6, 9) and pluricellular trichomes with branchings, resembling unicellular prothallic trichomes (7, 8, 10) from the petiole and blade of the leaves of apogamous sporophyte (orig.).

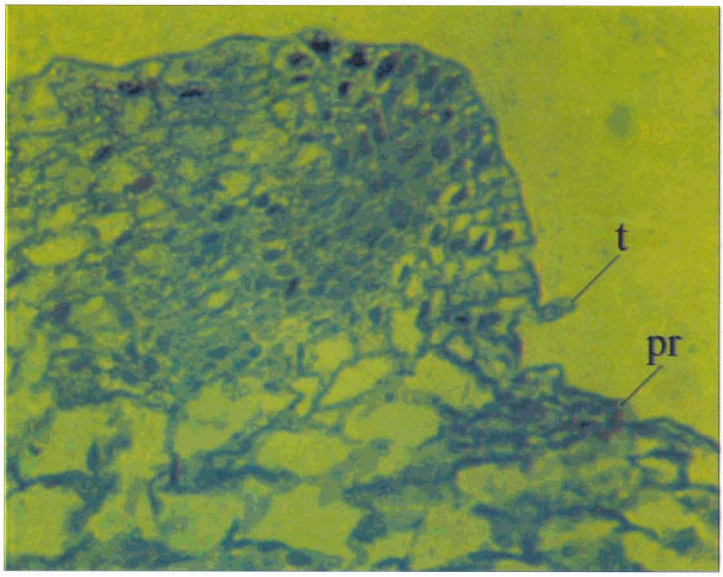

Fig. 1. *Cyrtomium falcatum* (L. Fil.) C. Presl longitudinal section through apogamous tissue (apogamous embryo) differentiated from the prothallus (**p**); on this tissue a unicellular trichome (**t**) can be seen (oc. 10×, obj. 20) (orig.).

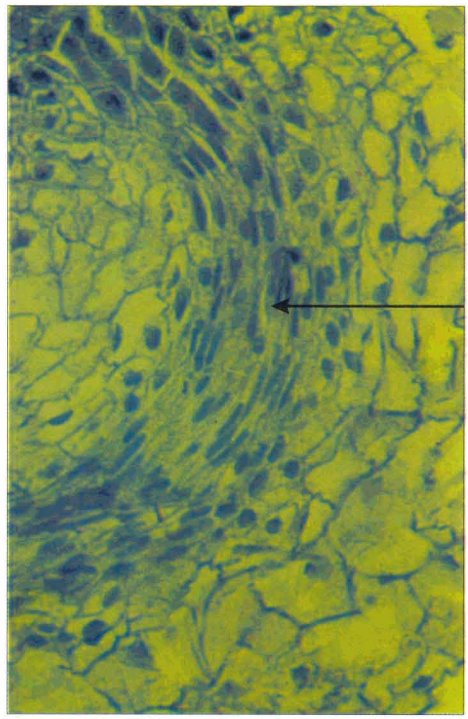

Fig. 2. *Cyrtomium falcatum* (L. Fil.) C. Presl procambium (arrow) differentiated in the apogamous tissue and in the prothallic tissue (oc. 10×, obj. 40)(orig.).

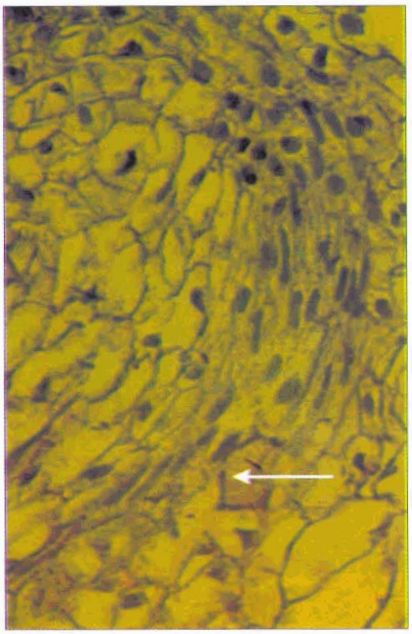

Fig. 3. *Cyrtomium falcatum* (L. Fil.) C. Presl procambium differentiated in the apogamous tissue and the prothallic one, and a tracheid (arrow) differentiated in prothallic tissue (oc. 10×, obj. 40)(orig.).

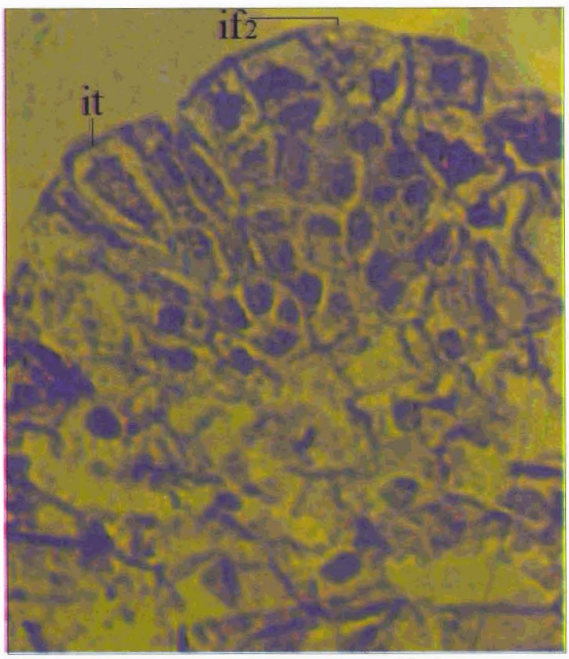

Fig. 4. *Cyrtomium falcatum* (L. Fil.) C. Presl longitudinal section through apogamous embryo, where leaf initial (**if$_2$**) and stem initial are shown (**it**) (oc. 10×, obj. 40)(orig.).

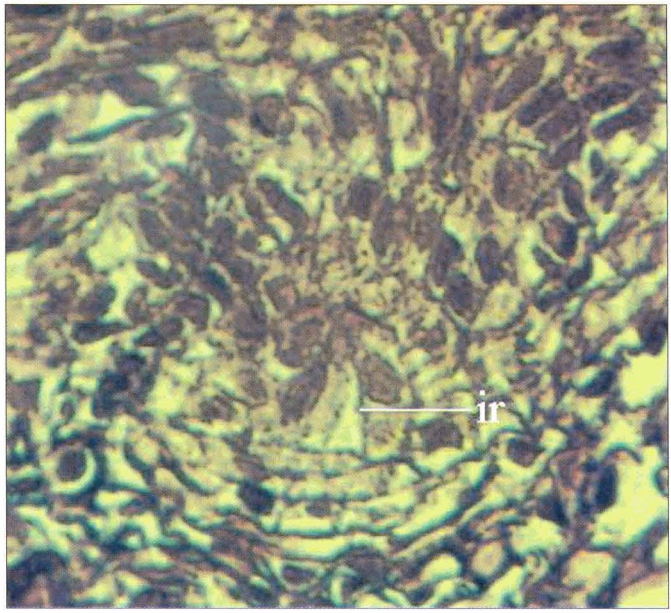

Fig. 5. *Cyrtomium falcatum* (L. Fil.) C. Presl longitudinal section through apogamous embryo bearing three leaves; the initial cell (**ir**) of the first root is to be seen (oc. 10×, obj. 40)(orig.).

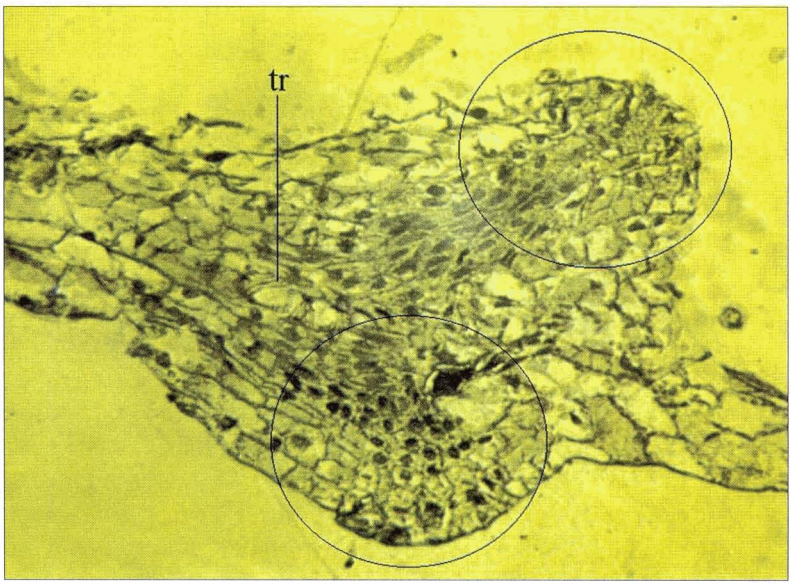

Fig. 6. *Cyrtomium falcatum* (L. Fil.) C. Presl prothallus on both sides of which ones of apogamous tissue have differentiated; **tr**-tracheid (oc.10×, obj. 20)(orig.).

In some cases on a prothallus two apogamous meristematic zones are differentiated on either side; in the prothallus between these two zones, tracheids are being differentiated (Fig. 6). The presence of two apogamous zones on the same prothallus has been observed by Nayar & Bajpai (1964) in *Notholaena sinuata*, but these were situated on the same side of the prothallus, on two large lobes of it, and not on both sides.

The first juvenile leaves of the sporophyte have a round blade, entire or weakly lobed (Plate I, Fig. 8, 9). The blade is crossed by a single, dichotomously branches again as the leaves are growing (Plate I, Fig. 10), so that nervation becomes similar to that in juvenile leaves of apogampous sporophytes in species of *Pellaea* and *Notholaena* (Nayar & Bajpai, 1964), but also of juvenile leaves produced by the sporophyte having as origin the zygotic embryo of *Gymnogramme sulphurea* (Vladescu, 1934). The leaf blade of succesive juvenile leaves enlarges dimensional and beginning with the 3rd or 4th leaf a midrib can be observed. Equally leaves become clearly lobed (Plate II, Fig. 3). By union of nerve branches occurs the transition from dichotomous nervation (Tutin *et al.*, 1993), characteristic for the nomophylls of the genus (Plate II, Fig. 4). The transition to a pinnate-sectate shape of the leaf results from the deepening of sines between leaf lobes, until reaching the midrib (Plate II, Fig. 5). The first juvenile leaves of the apogamous sporophyte in *Cyrtomium falcatum* present on blade and petiole unicellular trichomes similar to prothallic ones, but also pluricellular uniseriate trichomes (Plate II, Fig. 6, 9). Pluricellular trichomes are of 7–10 cells. Those at the base of the trichome are shorter, those terminal are longer. The apical cell of the trichome is curved, usually at un angle of about 180°, being oriented toward the base. This same cell is slightly swollen and has a dense content, which becomes brown. Besides these uniseriate pluricellular trichomes on leaves occur also similar trichomes, but presenting one or two unicellular branchings (Plate II, Fig. 7, 8, 10). Such trichomes were not signalled on juvenille leaves of apogamous sporophytes in species of *Pellaea* and *Notholaena* by Nayar & Bajpai, 1964.

CONCLUSIONS

– In the apogamous and prothallic tissues procambium and tracheids are being formed.

– From the apogamous tissue the first sporophyte leaf first differentiates.

– The stem initial differentiates between the first two leaves of the apogamous sporophyte.

– Successive leaves form from initials next to the stem apex, which is responsible for generating the growth axis of the postembryonic plant.

– The first root is formed when the sporophyte bears two or three leaves, from a tetrahedral initial cell; the absence of root is compensated by rhizoids generated by cells from the base of apogamous sporophyte.

– In some cases on the prothallus two apogamous meristematic zones are being differentiated, one on each side.

– The first juvenile leaves of the sporophyte have blades either entire or slightly lobed, crossed by a single, dichotomously branched nerve.

– By branching of the nerves and the union of these branchings is brought about the transition from dichotomous nervation, specific of sporophyte protophylles, to anastomosed nerves, characteristic for nomophylles of this genus.

– The first juvenile leaves present on the blade and petiole unicellular trichomes similar to those prothallic, but also pluricellular trichomes.

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