

## Branching and leaf initiation in the erect aerial system of *Stromatopteris moniliformis* (Gleicheniaceae)

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The erect, upright shoots of *Stromatopteris moniliformis* Met., a gleicheniaceous fern endemic to New-Caledonia, are studied morphologically and histologically. The shoots are produced by an underground branching system (not studied) and traverse the soil litter. They form dormant buds in their lowermost part and several leaves in the upper part, before the terminal meristem degenerates. Afterwards, the dormant lateral buds start to develop, successively and basipetally, toward the soil litter surface. These also produce dormant buds in their lowermost part and some leaves distally. This fern, therefore, has a bushlike form of dense branching axes, with leaves confined to the tip, unique in this group.

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La partie aérienne dressée du *Stromatopteris moniliformis* Met., une fougère Gleicheniacée endémique de la Nouvelle-Calédonie, a fait l'objet d'une étude histomorphogénique. Partant d'un système souterrain ramifié (non étudié), des axes aériens dressés traversent la litière. Ils portent des bourgeons latéraux dormants dans les parties profondes, puis plusieurs feuilles au sommet, avant que le méristème terminal ne dégénère. Les bourgeons latéraux se développent à leur tour successivement, dans le sens basipète, pour atteindre la surface de la litière; ils portent aussi des bourgeons latéraux et quelques feuilles de la même façon que l'axe principal, etc. On aboutit ainsi à un buissonnement très dense d'axes ramifiés prolongés par des feuilles, port original dans ce groupe.

### Introduction

*Stromatopteris*, a member of the primitive group (Nayar 1970), is a gleicheniaceous fern endemic to New-Caledonia (Mettenius 1861). Bierhorst (1971) raised this genus to the rank of family. It has unique form and ramification, with underground, branched, creeping axes and erect shoots bearing leaves at the tips (Thompson 1917; Bierhorst 1969). *Stromatopteris* is of particular interest as it is a fern which has been considered as representing a "living fossil" after comparisons with certain fossil ferns (Holmes 1977). A valid comparison between fossil and modern ferns requires an accurate ontogenic analysis of extant ferns. Such an approach represents the only method of understanding the possible relations between different organs of the mature plant.

Thompson (1917) studied the orthotropic part of *Stromatopteris*. He stated that, "the development of the leaf is accompanied by the arrest and displacement of the supporting axis, and the dominating leaf may appear to be an upward continuation of the axis." Thompson's interpretation is shown diagrammatically for the specimen of Fig. 4, in Fig. 1. The basal part of the shoot is monopodial and laterally branched, while the upper part is unbranched and leafy.

More recently, Bierhorst (1968, 1969, 1971, 1973, 1977) described the gametophyte and sporophyte in detail. His conclusions on the aerial orthotropic parts of the plant contradict the results of Thompson (1917). He concluded that the leaves result from the transformation of shoots, and bear epipetiolar buds. Branching is dichotomous. Neither of these interpretations satisfactorily explain the actual morphology of samples collected for this study.

Our study, based mainly on morphology and histology, pro-

vides additional information confirming the results of Thompson which were based on anatomical studies of only a few, incomplete specimens.

### Material and methods

Collection and study of *Stromatopteris* are difficult. Its stems form dense tufts of tangled branches that are rigid, thin (1.5–3 mm in diameter), and brittle. The rhizomes grow in deep compacted, ferruginous soil. Only a few fragile growing apices were found. The developmental stage of field samples is unknown. Dissection, embedding, and sectioning often destroy the very areas of interest.

More than 100 specimens were individually dissected and fixed in the field using Craf I (Sass 1958) after their positions on the plant had been recorded (Figs. 2–6, levels I, II, III, and IV indicate deeper levels within the soil litter where *Stromatopteris* branches extend vertically up to the soil surface). The number of usable apices per plant was often low. The developmental stage of apices affected their reaction to different fixing and embedding agents. Cortical cells normally are full of polyphenols except in the areas of meristematic activity. After meristem dormancy, these polyphenols may fill the immediate apical cell derivatives. The polyphenols cause poor fixation and poor embedding (N. Michaux-Ferrière, personal communication). Embedding was in "Paraplast" with long infiltration times (up to several weeks) under low heat and vacuum. The meristematic areas were difficult to section to 8–12  $\mu\text{m}$  because the surrounding cells were filled with polyphenols which shattered during sectioning. Histological preparations were stained using fast green (Sass 1958) and Groat hematoxyline (Gabe 1968). All serial sections were photographed and compared to reconstruct the meristematic structures including the apical cells and their segmentation.

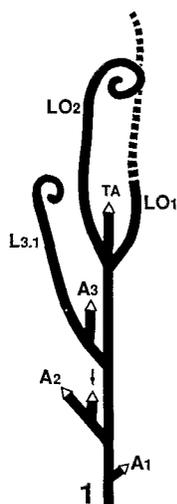
Some specimens were observed without embedding, in surface view (Bierhorst 1977). This technique gave considerably less information than embedded serial sections, but increased the observed

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ABBREVIATIONS: A, apex or apical cell of a shoot; CZ, cortical zone; IC, initial cell; L, leaf; LA, leaf apical cell; L0, leaf produced by the terminal apex TA; L1.1 etc., leaf produced by the lateral apex A1 etc.; OW, oblique wall separating a leaf or shoot apical cell from the initial cell; P, prismatic cell on the surface of the last segments produced by the shoot apical cell; PC, procambium; PW, periclinal wall separating the procambial zone and the deep cortical zone from the superficial zone, in the internal part of the segments produced by the shoot apical cell; R, root; S, segments of the shoot or leaf apical cell; TA, terminal apex of the erect main axis.

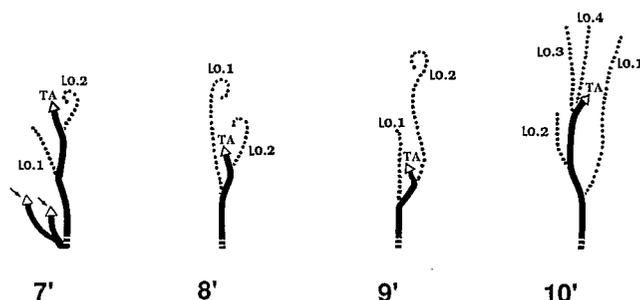
FIG. 1. Diagram illustrating the structural interpretation of the specimen shown in Fig. 4. Monopodial branching of the axis TA which produces three lateral shoots A1, A2, and A3, followed by leaves L0.1 and L0.2. A2 produces a lateral shoot (arrow) and A3 produces a leaf L3.1.

shoot number of each sample without any risk of destroying them during preparation. Grazing sections of apex surfaces, with scales removed, were placed in a fluorochrome solution (calcofluor white) for 1 or 2 h, and then examined in blue fluorescent light. The cell walls fluoresced sufficiently for photographs on very sensitive film.

## Results

### Morphology

Progressively more developed shoots were used to describe the development of *Stromatopteris*, taking into account the results of Thompson (1917), who regarded branches and



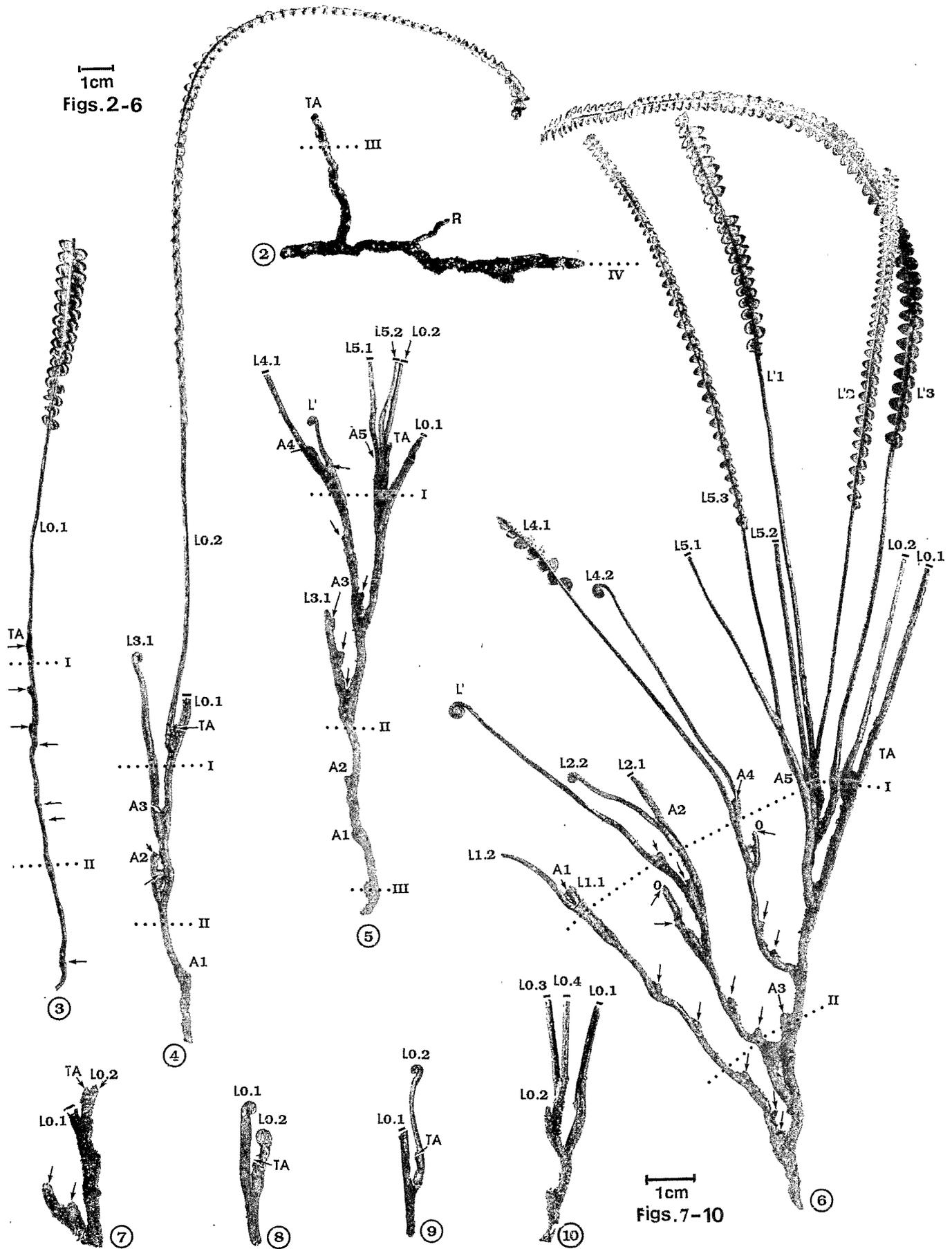
FIGS. 7'–10'. See figure caption for Figs. 2–10.

leaves as lateral appendages of the stem. Figure 2 shows a fragment of an underground horizontal shoot bearing an upright axis TA. The upright shoot in Fig. 3 has grown through the soil litter and bears its first leaf L0.1 after producing several dormant buds (arrows). In Fig. 4 the main shoot bears two leaves (L0.1 and L0.2) whereas the underlying apex A3 bears only one young leaf L3.1; A3, therefore, started developing after TA. In Fig. 5 the terminal apex TA has produced two leaves L0.1 and L0.2; the apex A5 has produced two leaves L5.1 and L5.2 which are broken; the apex A4 has produced one leaf L4.1 and three lateral apices (arrows); the apex A3 has produced one leaf primordium L3.1 and two lateral buds; the apices A2 and A1 are still dormant. As illustrated by these three specimens (Figs. 3–5), the first leaves were produced by the terminal apex TA, and others, younger than these, formed below on the lateral axes inserted lower down on the main axis. The lateral axes are generally less developed proximally (Figs. 4–6). The development of buds, on the main shoot, occurs successively and basipetally. This organization is repeated on each lateral shoot (Fig. 6: A1, A2, and A4). The leaves, therefore, are all borne at about the same level on the shoots. The shoots become more elongated the lower down they are inserted on the main axis, and are thus at greater depths in the tufts. In Fig. 6 the leaves on axis A1 are aborted.

Generally, there is a great difference in degree of development between two successive leaves borne by the same axis (Fig. 6, A4: L4.1, L4.2; L'1, L'2, and L'3; Fig. 9, L0.1 and L0.2) and between those borne by two successive branches (Fig. 4, L0.2 and L3.1). In some very vigorous axes (Fig. 8), the two leaves L0.1 and L0.2 are always very young.

FIGS. 2–10. Morphological structure. Specimens showing the development of the erect shoots (Figs. 2–6) and leaves (Figs. 7–10). The Roman numbers I–IV and dotted lines indicate deeper levels within the soil litter where *Stromatopteris* branches horizontally, up to just below the soil surface. The branches of the axes were separated by pins for the photographs so that they could be seen clearly. Normally, the branches are vertical in dense tufts. Broken leaves are indicated by a line above the break. Fig. 2. Horizontal shoot bearing root (R) and vertical axis (TA) which is still unbranched. Fig. 3. Vertical axis bearing nondeveloped lateral buds (arrows), a first leaf (L0.1), and a terminal bud (TA). Fig. 4. Vertical axis bearing two leaves (L0.1 broken and L0.2) and lateral buds which are beginning to develop: A3 bears leaf L3.1; A2 bears a lateral bud (arrow). See Fig. 1. Fig. 5. Terminal apex (TA) has produced two broken leaves; the first one (L0.1) is aborted; the second (L0.2) overhangs apex TA. Axis A5 bears two broken leaves L5.1 and L5.2. Axis A4 has produced leaf L4.1 and several lateral apices (arrows) of which the last bears a young, hooked leaf L'. Axis A3 bears a leaf primordium L3.1 and two lateral apices (arrows). Axes A2 and A1 are still dormant. Fig. 6. The lateral shoots are all developed, except A3 (dead?). The most developed are those inserted high up on the main axis (except axis A4, whose buds are slightly less developed than those of A2). Axis A5 bears two older, broken leaves (L5.1 and L5.2) and a younger leaf L5.3 L'1 (oldest) and L'2 (youngest) are inserted on the same lateral apex produced from A5. L'3 is also inserted on a lower lateral apex produced from A5. FIGS. 7'–10'. Structural interpretation of specimens shown in Figs. 7–10. The single axis is a solid line and the leaves are broken lines. Figs. 7 and 7'. Vertical shoot top from between level I and II, with the left branch bearing a bud (arrows). Apex TA has produced an older leaf L0.1 followed by a younger leaf L0.2, which overhangs the apex. It also shows a leaf primordium in a distichous position in relation to L0.2 (not illustrated). Figs. 8 and 8'. Tip of one particularly vigorous shoot where there is no great age difference between L0.1 and L0.2. Apex TA has already produced a young leaf (illustrated in Fig. 21). The leaves are distichous. Figs. 9 and 9'. Tip of a vertical axis with two leaves and a residual apex TA with leaf initiation (illustrated in Fig. 20). Figs. 10 and 10'. The shoot produced four leaves (L0.1–L0.4) and at the base of the fourth leaf is a residual apex which cannot be seen.

1cm  
Figs. 2-6



Leaves rapidly overarch the apex from which they are produced (Figs. 7–9 and 7'–9', TA and L0.2). This apex becomes dormant, after initiation of the next primordium and takes up a lateral position (arrow) in relation to the underlying shoot. The petiole of the previous leaf, however, continues growing in the same direction as the underlying shoot. After the development of this leaf, the apex may recommence growth simultaneously with its last initiated primordium. Figures 20 and 21 are of the apical meristems of specimens illustrated in Figs. 9 and 8, respectively, and show the next leaf already in position. Such a feature is typical of meristems from this level, whether the visible leaf is large or small (Fig. 7, leaf L0.2 is very short and apex TA also shows a foliar initiation). Rapid growth of each leaf leads to shoot displacement (Figs. 10 and 10').

No precise phyllotaxy was determined from external morphology. The next leaf initiation on some apices is positioned opposite the immediately preceding leaf (Figs. 8 and 21, 9 and 20). Leaves on other specimens (Figs. 7–10) are more or less distichous.

#### Anatomy

Hand-cut sections of even the most morphologically ambiguous samples strongly support the observations of Thompson (1917). We therefore have nothing to add to the very informative illustrations of his article as most of the results described here (based on over 20 specimens) correspond exactly to his findings. The protostele is always axially symmetrical along the shoots until the separation of the upward continuing cauline meristem (shoot tip) and petiole base. At each fork, the petiole base (seen in Figs. 7–10 and indicated by dotted lines in Figs. 7'–10') is more or less asymmetrical as shown at least in tracheid arrangement (Thompson 1917, plates I and II; Bierhorst 1971, Figs. 13–4, D–F). Thus, the main shoot does not dichotomise at the level of leaf trace divergence. The leaves are lateral and are differentiated from the shoots at the level of each fork.

#### Histology

##### Cauline meristems

These resemble all other small protostelic ferns already studied, for example *Trichomanes* (Héban-Mauri 1973 and 1984). In longitudinal section (Fig. 11) the same zones described previously are observed. There is a tetrahedral apical cell surrounded by prismatic cells. These cells are above the procambium which in turn is separated from the cortical zone by periclinal walls. In transverse section (Figs. 14 and 14') or in surface view (Figs. 18 and 18', 19 and 19'), in the best specimens, apical segmentation can be followed. In non-functioning apices (poor climatic periods, very dry and compact soil, or other unfavourable conditions), anomalies are

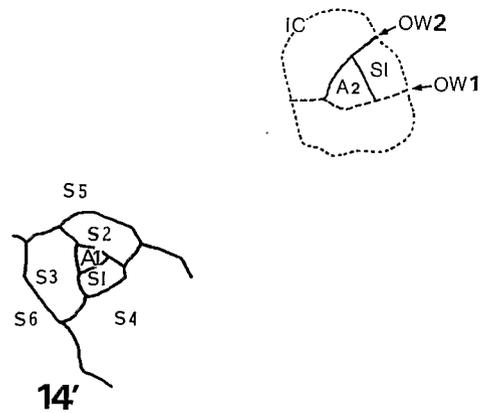


FIG. 14'. See figure caption for Figs. 11–17.

often observed. In place of a tetrahedral apical cell surrounded by typical segments there are extremely large cells or very redivided cells without any characteristic patterns (Fig. 22, arrow).

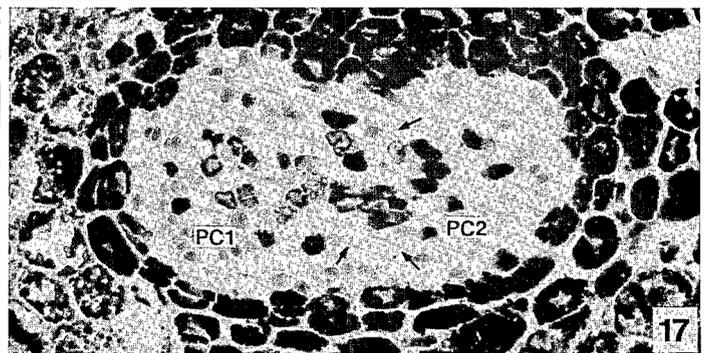
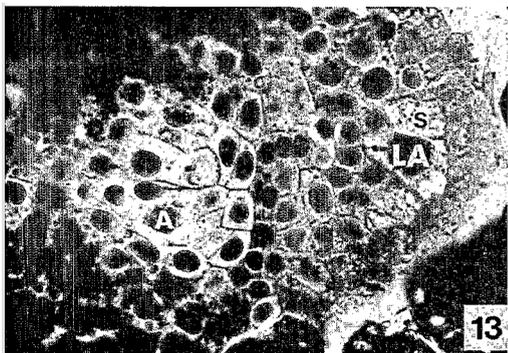
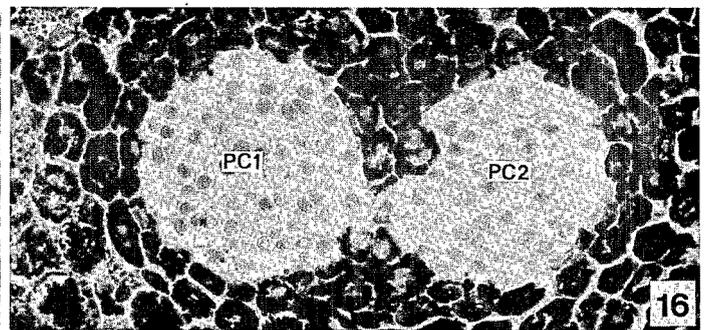
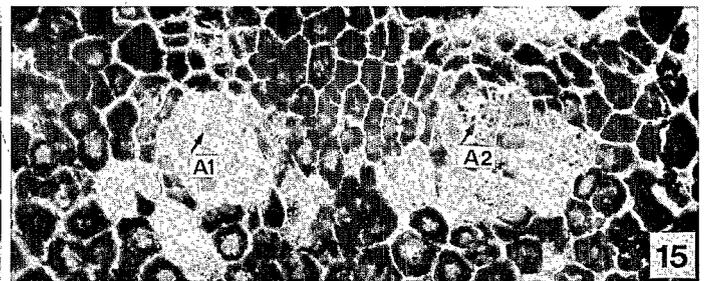
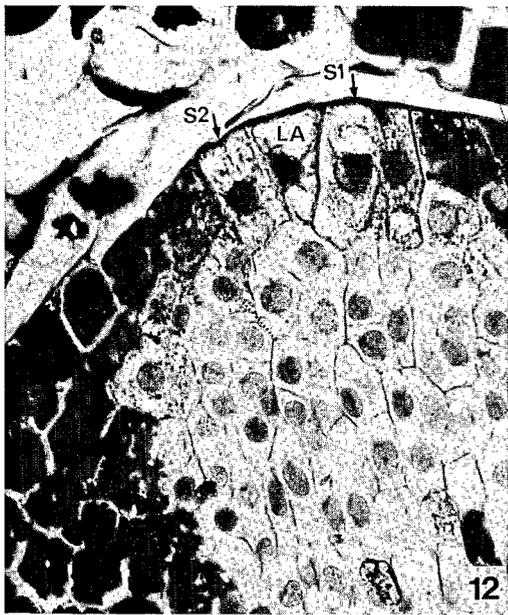
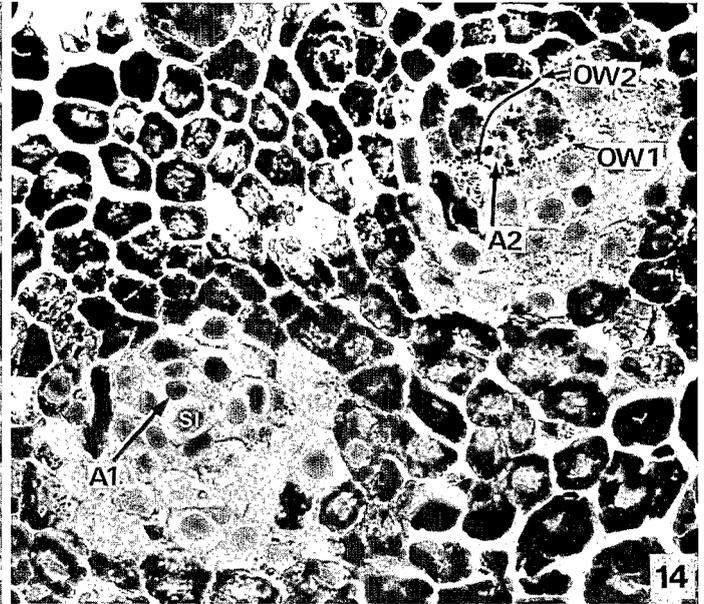
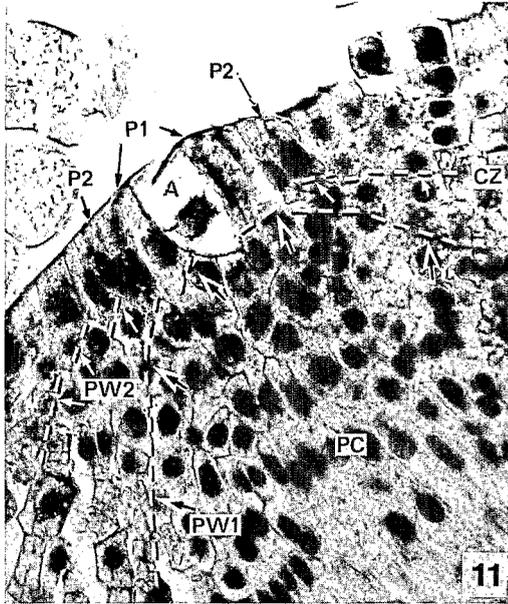
##### Branching

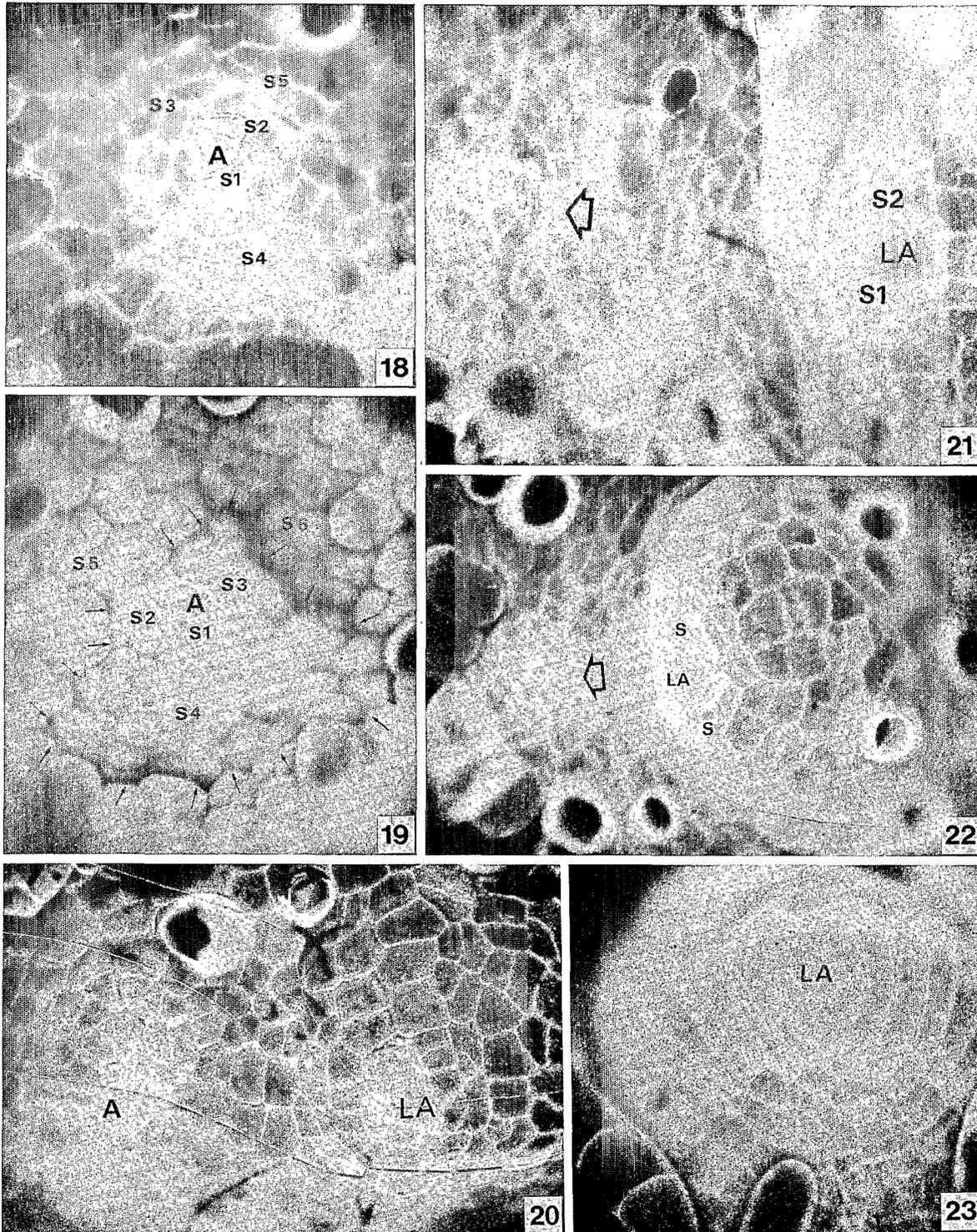
Branching was examined only in the erect, branched aerial systems. On a single shoot, lateral bud position is highly variable. Buds may be in the same phyllotactic line and at regular intervals (Fig. 5) or positioned irregularly along the shoot (Figs. 3 and 6).

Active meristems in growing stems at level II, III, and IV of the soil litter (Figs. 2–6) were the only ones useful to study branching (meristems from level I always produce leaves). Figures 14 and 14' show branching pathways in *Stromatopteris*. There are two cauline apical cells, A1 and A2. The cell division patterns are very different around each of them. A1 is surrounded by typical delineation of its segments (segments 1–6 can be seen). A1 is the apical cell of this meristem. A2 is isolated by two oblique walls inside a family group of cells (IC) (dotted line Fig. 14'). IC was previously a cell at some distance from the apical cell (A1) and one of its derivatives. A2 is the lateral apical cell isolated within the meristem around A1 (A2 had produced only one segment). There is no equal division of the apical cell A1 (= true dichotomy, Troll 1937) nor equal division of its surrounding meristem (= terminal branching, Steeves and Sussex 1972). Figures 15–17 corroborate this result. Figure 15 shows the offset position of A2, in Fig. 16 the procambium under A2 is reduced, and Fig. 17 shows that the junction of the two protosteles is oblique (arrows at level of the smaller procambium, PC2).

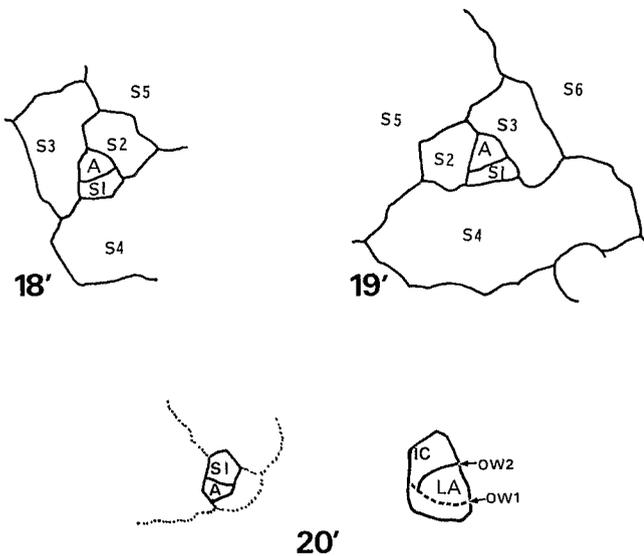
After development, the dominance of one apex over another depends on the development of the newly initiated apex. If the

Figs. 11–17. Histological sections. Fig. 11. Shoot apex in longitudinal section. Apical cell (A) is surrounded by prismatic cells (P1 and P2). The inner part of the segments cut off from the apical cell shows two sets of successive periclinal walls (PW1 and PW2). The periclinal walls (PW1) isolate the procambium (PC) from the cortical zone (CZ).  $\times 300$ . Fig. 12. Young leaf apex in longitudinal section. The leaf apical cell (LA), sectioned in face view, is surrounded by its last segments (S1 and S2). This young leaf is at the same stage of development as that in Fig. 20.  $\times 300$ . Fig. 13. Leaf primordium 100  $\mu\text{m}$  from the shoot apical cell (A), in oblique transverse section. The leaf apical cell (LA) has produced at least one segment (S).  $\times 300$ . Figs. 14 and 14'. Apex in transverse section showing two shoot apical cells 180  $\mu\text{m}$  apart (see labels Fig. 14'). The apical cell (A2) is included within a mass of cells where it was isolated in the initial cell (IC) by two oblique walls (OW1 and OW2). This apical cell has produced its first segment (S1).  $\times 300$ . Figs. 15–17. Serial sections within the same apex illustrated in Fig. 14, at lower magnifications ( $\times 200$ ). Fig. 15 is a section from above that shown in Fig. 14, and the position of apical cell A2 is excentric in relation to apical cell A1. Fig. 16 is a section from below that shown in Fig. 14 showing the procambium of the two apices before they fuse. Procambium PC2 corresponds to apical cell A2 and is more reduced than that of the procambium PC1 corresponding to apical cell A1. Fig. 17 shows the junction of two protosteles. PC2 has oblique cells where it meets PC1 (arrows).  $\times 200$ .





FIGS. 18–23. Surface observations in reflected fluorescent light. Figs. 18 and 18'. Shoot apex with apical cell (A) and discernable last segments.  $\times 300$ . Figs. 19 and 19'. Dormant apex. The cells are characteristically round. The segmentation remains visible, underlined by disjunctions of the middle lamella (arrows). This is exceptional, and was caused by manipulation of the apex during excision.  $\times 300$ . Figs. 20 and 20'. Most of labelling is on Fig. 20'. Leaf initiation  $100 \mu\text{m}$  above a residual apex of an axis with two previous leaves (cf. Fig. 9). The leaf apical cell (LA) is isolated by two oblique walls (OW1 and OW2) in the initial cell (IC). The sharp angle of the leaf apical cell is directed towards the apex. A dome is present but the leaf apical cell has not begun functioning.  $\times 300$ . Fig. 21. Terminal apex (TA) from Fig. 8. Leaf primordium,  $200 \mu\text{m}$  from a dormant apex (arrow) with indistinct apical cell. The leaf apical cell (LA) not yet bifacial, bulges in relief, above the dome, which has begun its asymmetric growth. At least two segments have been produced (S1 and S2).  $\times 300$ . Fig. 22. The young primordium overhangs and curves towards the shoot apex. The leaf apical cell LA now has two cutting faces. The arrow indicates very redivided cells frequently seen in nonfunctioning meristems.  $\times 300$ . Fig. 23. Young leaf  $250 \mu\text{m}$  high shown in surface view. Start of circinate growth, during petiole development.  $\times 300$ .



Figs. 18'–20'. See figure caption for Figs. 18–23.

new apex, such as A2, remains undeveloped, it is then displaced laterally by the continued growth of the main shoot. If, however, the two apices grow simultaneously, an apparently dichotomous fork develops rapidly and it becomes impossible to state which of the two apices gave rise to the other.

#### Leaves

Leaves are initiated only at the shoot tops, around level I, at the soil litter surface (Figs. 2–6). Meristems from this level show different stages of leaf initiation.

All apices (dormant or active) inserted at the leaf base (Figs. 3–10, TA) have leaf initiation or leaf primordia close to their cauline meristems. Likewise, apices at the top of not yet leafy shoots above level II (Fig. 4, A2; Fig. 6, arrow O) also have leaf initiation or primordia in their cauline meristems.

The initiation of a leaf is illustrated in Figs. 20 and 20' approximately 100  $\mu\text{m}$  from the apical cell of the main shoot. The two oblique walls (OW<sub>1</sub> and OW<sub>2</sub>) separate the leaf apical cell (LA) from the initial cell (IC). IC was previous a cell at some distance from the shoot apical cell A, and one of its derivatives. Thus the leaves of *Stromatopteris* are lateral appendages of the stem. The leaf apical cell at this stage has three faces in transverse section. The sharp angle of the leaf apical cell, at the junction of the two oblique walls, may be either directed towards the apex (frequently the case as in Figs. 20 and 21) or directed laterally. These two orientations are also found in *Trichomanes* (Héban-Mauri 1984). The leaf apical cell, thus isolated, will grow and produce its first segments (Fig. 12, S1 and S2; Fig. 13, S; Fig. 21, S1 and S2). In Fig. 21, the outline of the young leaf already has the form of an asymmetrical dome and the apical cell is not yet bifacial. The oldest leaf, Fig. 22, is slightly asymmetrical, reflecting its future circinate coil and has produced a lenticular apical cell. Thus, leaf primordium elevation begins at the same time as the production of a number of segments by the primordium apical cell, but before this cell becomes bifacial. From this stage and during subsequent growth (including petiole development as shown in Figs. 22 and 23), this young leaf will keep its lenticular apical cell. All the young, growing leaves observed were circinate coiled with the characteristic fern leaf segmentation even in the absence of lamina (cf. Mueller 1982).

#### Discussion

The cauline apex structure of this fern is typical of leptosporangiate ferns with massive protosteles. The histological aspects of branching are very similar to those in *Trichomanes* and *Cardiomanes* (Héban-Mauri 1973, 1984). The lateral apical cell is isolated in a prismatic cell of the cauline meristem, at some distance from the main tetrahedral apical cell. None of these genera show an equal division of the tetrahedral apical cell (= dichotomy; Troll 1937) nor of the cauline meristem (= terminal division; Steeves and Sussex 1972) as described by Bierhorst (1968, 1969, 1971, 1973, 1977).

Several general features differentiate leaf and cauline initiations. This is a particular problem in *Stromatopteris* when the apices reach the surface of the soil litter; lateral outgrowths may be cauline or foliar. Only detailed histological studies enable recognition of the nature of the initiation. Leaf initiation occurs in a prismatic cell that is enlarged in relation to the surrounding cells. The first oblique walls (OW<sub>1</sub> and OW<sub>2</sub>, Fig. 20') isolate a wide cell on the surface. These walls generally terminate, after splitting, on different walls of the initial cell IC (this is not the case though in Fig. 20). The new leaf becomes a particularly obvious swelling on the cauline apex in *Stromatopteris* during the formation of the two oblique walls. In contrast, a cauline initiation occurs within a nonenlarged prismatic cell, where the two oblique walls isolate an elongate, deep cell. These walls generally terminate on the same wall of the mother cell (Fig. 14) depending on its form. Even after the formation of the third oblique wall (perpendicular to the first two and isolating the first segment), the cauline meristem does not project, or projects very little, from the surface of the apex from which it was initiated. These features do not always occur, and some are relative. *Stromatopteris* has the same type of meristems and initiations as *Trichomanes* (Héban-Mauri 1973, 1984). The cauline initiations, though rare, were sufficiently advanced to leave no doubt as to their nature.

This histological study shows that initiation and early development of *Stromatopteris* leaves are typical of ferns. The apical cell initiation and the production of the first segments, giving the apical cell a lenticular form, correspond to the classic scheme proposed by numerous authors (Bartoo 1930; Bierhorst 1977; Dasanayake 1960; Héban-Mauri 1975, 1984; Imaichi 1974, 1980, 1982; Mueller 1982). At the time of initiation, the leaf is a distinct organ within the cauline meristem, and is not produced by the transformation of this apex as described by Bierhorst (1968, 1969, 1971, 1973, 1977). The leaf vascularization, after separation from the cauline stele, becomes bilaterally symmetrical. The erect, upright shoots of *Stromatopteris* branch laterally at their base and produce leaves on their nonbranching apices.

#### Conclusion

Several conclusions arise concerning the mode of growth of *Stromatopteris*.

(i) Leaf production on shoots occurs only in the upper part of the soil litter, and branching or branch expansion terminates with the onset of leaf production. Leaf development displaces the cauline meristems from their terminal positions, and leads to their exhaustion after the production of two to four leaves.

(ii) The shoot apical meristem bearing a leaf terminates growth temporarily very early during the development of that leaf.

(iii) The terminal apex of an axis inhibits, in some way, the earlier formed apices below it on the same axis. These lower apices develop successively after the upper meristems have terminated their growth. The bushy growth habit thus produced resembles a phanerogamic remnant whose lateral buds grow successively downward after the end of growth of the top most bud.

(iv) This protostelic fern, otherwise similar in organization to other ferns, differs in that its axial growth terminates in leaf production. This is similar to cessation of axial growth by flowering in a remnant rose. In both *Stromatopteris* and in a remnant rose the end of axial growth is related to the reproductive function (some fertile leaves for the fern, flowers for the rose).

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