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The Vascular Pattern of a Rhizomatous Ginger (*Alpinia speciosa* L. Zingiberaceae). 1. The Aerial Axis and its Development

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ABSTRACT

Alpinia speciosa L. (Zingiberaceae) has a horizontal sympodially branching rhizome. The distal end of each sympodial unit develops vertically to form a determinate axis some three metres high bearing foliage leaves with sheathing bases, and terminating in an inflorescence. A transverse section of the aerial axis indicates that the vascular tissue of 'scattered' vascular bundles is arranged in two distinct zones – an *inner system* and an *outer system*, separated by a cylinder of undifferentiated tissue, the *intermediate zone*, retaining the features of a meristem. The multiplicity of terminology applied to this zone in the literature is clarified. The distribution and interconnection of the vascular system in the aerial stem are described together with a consideration of their development. The observations on which the descriptions are based were achieved by the 'optical shuttle' and 'surface' methods of serial cinematography. The presentation of such data in three-dimensional diagrammatic form is explained. The inner system of vascular bundles is found to have the simple basic design of that of a 'typical' palm stem – a system of upwardly branching leaf traces with interconnections. The outer system of functional vascular bundles in *Alpinia* anastomoses freely and is considered to be equivalent to the anastomosing cortical system of non-conducting fibrous bundles present at the periphery of many palm stems. Communication between the two systems in the aerial stem of *Alpinia* is by means of an extensive bridging to the outer system from departing inner system leaf traces.

Key words: *Alpinia speciosa* L., shell ginger vascular anatomy.

INTRODUCTION

The axial distribution of vascular bundles in monocotyledons has until recently received little attention largely because of its complexity in three dimensions. Most of the species studied have been relatively small and herbaceous with comparatively simple, and possibly reduced, vascular systems (Bell, 1976*a* and *loc. cit.*). Accurate details of the vascular pattern of large woody monocotyledons have been virtually non-existent; a survey is to be found in Zimmermann and Tomlinson (1965) and Tomlinson and Zimmermann (1966). However, these authors have pioneered a painstaking investigation of the underlying principles behind monocotyledon vascular anatomy, commencing with a small palm, *Rhapis*, and extending to many of the larger woody representatives of the group (Zimmermann and Tomlinson, 1972, 1974, and *loc. cit.*).

The success of these investigations depends upon the technique of photographing successive sections of a transverse series on successive frames of cine film. Individual bundles can then be followed during subsequent project and their origins and associations noted. This principle is quite old (Reicher, 1907) and has been modified in detail for a variety of purposes (Bell, 1975 and *loc. cit.*).

The vascular pattern of the Zingiberales has not been described in great detail before, accounts being largely of a histological nature (Falkenberg, 1876; Barthelat, 1893; Skutch,

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1932; Barker and Steward, 1962; Tomlinson, 1962, 1969 and *loc. cit.*; Kumar, 1973). However the presence of a cortical system in addition to the 'inner' system found in palms is commonly recognized. This additional feature of the vascular system results in a more complex vascular pattern than is found in many other monocotyledons. The complexity is also increased by the differing vascular patterns of rhizome and aerial stem. The present account is restricted to the aerial stem of *Alpinia speciosa*, which seems representative of many members of the family. A subsequent paper (Bell, 1980) deals specifically with the anatomy of the rhizome.

MATERIALS AND METHODS

Alpinia speciosa L. (shell ginger) is a horticultural plant widespread in cultivation in the tropics, but probably of old world origin. It forms an extensive underground sympodial rhizome system having a rather precise branching pattern. Each branch unit of the sympodium (i.e. each sympodial unit) turns erect at its distal end, developing into an aerial photosynthesizing shoot. Rhizome extension continues by means of one or two lateral buds. Each aerial shoot persists for three years and then dies, rotting back to an abscission layer at soil level.

A 35-year-old clump contains about 30 'individuals'. Each individual consists of a number of sympodial units, and is extending at the distal ends whilst rotting at the proximal end. The individuals themselves are not connected; each time the rotting reaches a branch junction, the single individual becomes two. Each sympodial unit lives for about ten years before it becomes the oldest and rots. The rhizome thus moves through the soil by addition at one end and loss at the other.

The morphological details of this branching pattern have been considered in detail in connexion with rhizome mobility, as its very precise nature has far reaching ecological significance (Bell, 1979).

The rhizomes bear scale leaves, adventitious roots, and rhizome buds; the aerial shoots bear only vegetative leaves and a terminal inflorescence. This difference is reflected in their vascular patterns as will be described.

The fresh plant specimens used in this investigation were obtained from the Fairchild Tropical Gardens, Miami, and from the United States Department of Agriculture, Subtropical Horticultural Research Station, 13601 Old Cutler Road, Miami. Investigation of the vascular system in mature aerial stems follows precisely the cinematographic methods of Zimmermann and Tomlinson, some material being cut and filmed by the 'surface method', and higher power details and development sequences of the apex being filmed from prepared serial sections by the 'shuttle method' (see, for example, Tomlinson, 1970).

Serial sections are obtained as follows.

Mature aerial axis (*middle portion of flowering stem*). Fresh sections are cut using a Reichert sliding microtome at an average thickness of 100 μm (nothing is to be gained by cutting thinner sections when following the longitudinal course of bundles over several cm). Each section ($\pm$ 1·5 cm diam.) is placed on a separate glass slide numbered in sequence, and stained in situ as follows:

(1) Flood section with an equal aqueous mixture of 0·1 per cent Crystal Violet reduced with 10 per cent sodium metabisulphite, and 0·1 per cent Safranin. The section can be left in this stain for any length of time over 1 min.
(2) Decant off.
(3) Flood with 50 per cent HCl for 2–3 min (or longer) to remove starch.
(4) Decant off.
(5) Flood with tap water – unlimited time.
(6) Decant off.
(7) Mount in warm liquid glycerine jelly.

This rapid method allows a series of several hundred sections to be cut, stained, and mounted in a few hours. Vascular tissue appears purple against an unstained background devoid of starch.

Shoot apex. Fresh young aerial apices are fixed, dehydrated, and embedded in Paraplast using a tertiarybutyl alcohol series in a conventional manner. This process cannot be hurried because of the size of the specimens ($\pm$ 1 cm cone). However perfectly adequate series of stained sections are rapidly prepared using a simplified version of the method proposed by Christensen (1973). Sections are individually cut at 15 μm on a Reichert sliding microtome and floated singly on to weak formaldehyde solution on numbered glass slides previously smeared with Haupt's adhesive.

After a period on the hot plate to flatten the wax, the formaldehyde is decanted off and the slide allowed to dry completely. The procedure is then as follows.

(1) Flood with a filtered equal mixture of 0·5 per cent Bismarck Brown and 50 per cent HCl. (0·1 per cent Safranin may be used instead.) Leave for at least 15 min.
(2) Wash in tap water.
(3) Allow to dry completely.
(4) Flood with xylene. Leave for 15 min or until wax is dissolved.
(5) Decant off.
(6) Mount with coverslip using a standard xylene soluble medium, e.g. Permount.

Recording the series of transverse sections on film follows the optical shuttle procedure described by Zimmermann and Tomlinson (1966).

Cinematographic analysis

A problem of three dimensional vascular studies is the difficulty of describing such complex structures in lucid terms and two dimensions. The system adopted to deal with the mature tissue is outlined below.

The film sequence is projected backwards and forwards many times and at varying speeds depending upon the intricacy of the 'events' being watched. This is achieved by means of an analytical film projector. As bundles are followed up and down and their associations and fates noted, the observer begins to visualize the three dimensional structures and any repetitive features are noted. Having gained a general understanding, a tracing is prepared of every 20th section by projecting the film images on to sheets of paper and outlining the bundles giving them temporary code numbers. A transparent overlay bearing a grid system is applied to each tracing in turn, the position of bundles being recorded as a pair of co-ordinates. The course of bundles can thus be detected down through the series of tracings.

A second overlay bearing a diamond-shaped perspective representation of the same grid system is now used to construct a three-dimensional diagram of the bundles by reproducing each tracing down through the perspective diagram in sequence. This results in somewhat crooked columns of circles, some standing behind the others, and showing their various interconnections. A second diagram is prepared straightening out these columns, maintaining their branching and fusions.

Considerable confusion can arise where many bundles occupy a small space and then it is necessary to display only representative bundles to show the repetitive features resulting from the previous film analysis. The three dimensional diagrams of the vascular system of *Alpinia* illustrating this and the subsequent paper were prepared in this way.

A different procedure is necessary when investigating the course of procambial strands in the stem apex. The system adopted is that of Zimmermann and Tomlinson (1967) in which the distance in microns of a particular procambial strand from the centre of the section is plotted against the depth below the apex of that section. The location of the strand from section to section is thus recorded, continuity being afforded during the preparation of a film using the 'shuttle' method.

OBSERVATIONS

General anatomy of the aerial stem

The central cylinder is separated from the very broad cortex by a clear boundary of undifferentiated tissue. It is useful to refer to bundles of these contrasted regions as bundles of the 'inner' and 'outer' system respectively, for reasons which become clear later. The non-commital term *intermediate zone* (Petersen, 1892) is used to describe the undifferentiated region, as is explained later. There is no endodermis. Vascular bundles are collateral throughout, those of the cortex being wider with a well-developed fibrous sheath, but also most variable in diameter. Bundles closest to the surface may lack vascular tissue completely. Film analysis shows that many of the smaller cortical bundles are bridges which link the main axial bundles. Bundles of the inner system are seen to depart through discontinuities in the intermediate zone, and they are destined to link with a leaf as a leaf trace.

Course of bundles in mature stem

A great deal of information can be presented by means of a single diagrammatic reconstruction of the three dimensional associations in a sector of this aerial stem as shown in Fig. 1. The significant features indicated are as follows (1 to 8, and 10 in Fig. 1).

(1) The intermediate zone forms a continuous cylinder of undifferentiated tissue perforated only at the point of departure of inner system leaf traces.
(2) No axial bundle is given off from a departing inner system leaf trace.
(3) Inner system axial bundles occasionally split into two in an internode (when followed distally), but not often enough to replace all the departing inner system leaf traces. The number of inner system leaf traces thus decreases towards the apex. For example, the inner system bundle 'count' past two nodes was as follows:

Reduction in number of inner system bundles over two nodes:

The overall loss through these two nodes being 31. This is understandable as the aerial axis is a determinate tapering stem bearing a finite number of leaves and terminating in an inflorescence.

(4) There are no bridges or fine connexions between inner system bundles.
(5) Two types of outer system bundles depart into leaves – conspicuous major leaf traces (5a) which are associated with axial bundles, and much smaller peripheral bundles (5b) that arise as branches from the major traces at some point in the preceding internode (5c).
(6) Outer system bundles (except the small peripheral bundles) frequently split and rejoin to form many bridges, resulting in an elaborate anastomosing network.
(7) Numerous fine cross-connexions are formed in the outer system. These appear late in development ('tardy bundles') (and may well be analogous to the nodal plexus of many monocotyledons).
(8) Departing inner system leaf traces pass out almost horizontally into the leaf,

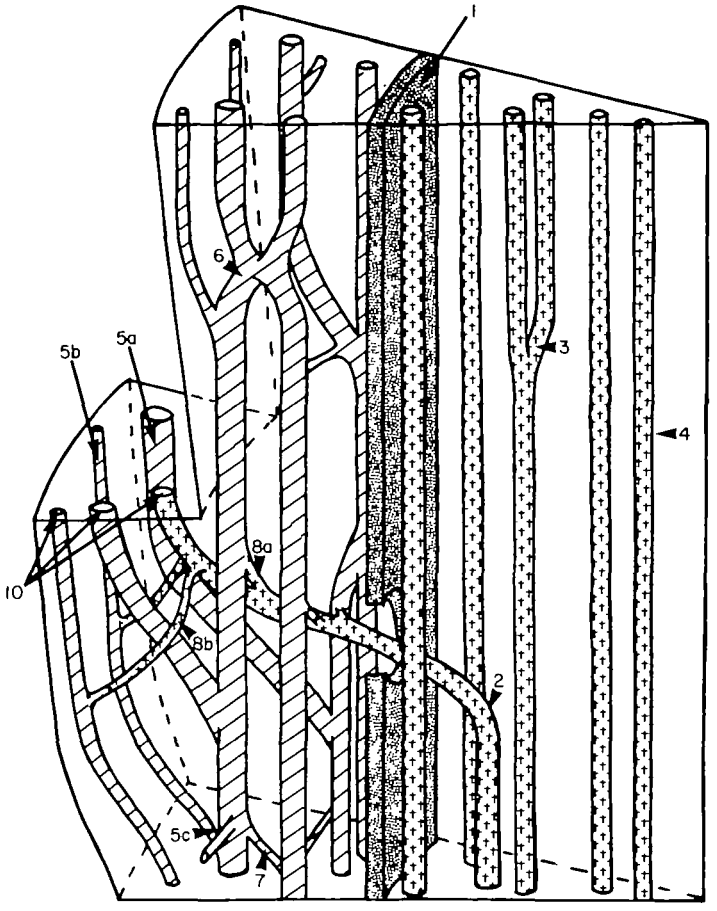
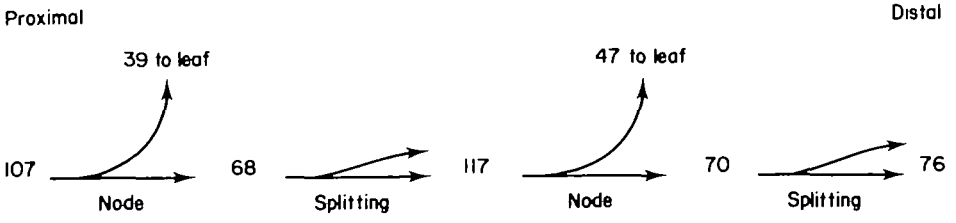


FIG. 1. Diagrammatic reconstruction of a sector of the aerial stem of *Alpinia speciosa* at the point of insertion of a foliage leaf. Diagonal hatch: outer system of vascular bundles. Stipple: intermediate zone. Crosses: inner system of vascular bundles. Features labelled 1–10 are described in the text.

forming numerous bridges (8a) with adjacent outer system axial bundles. They may also form one or two very fine and often long connexions (8b) with the departing peripheral leaf traces of the outer system. These connexions are made obliquely downwards as shown.

(9) The number of cortical bundles also decreases distally and is partially maintained by splitting as in the inner system:

Reduction in number of outer system bundles over two nodes:



Thus a total of 252 bundles entering these two successive nodes from below is reduced to 190, having 'gained' 80 by splitting and 'lost' 142 to leaves.

(10) In the Zingiberaceae, leaf traces occur in up to four distinct arcs in the leaves. Three arcs are typical at the base of the leaf sheath in *Alpinia* – abaxial bundles, main bundles, and adaxial bundles (Tomlinson, 1969). These three arcs represent the three types of leaf trace reported here – peripheral outer system bundles, main outer system bundles, and inner system bundles, respectively.

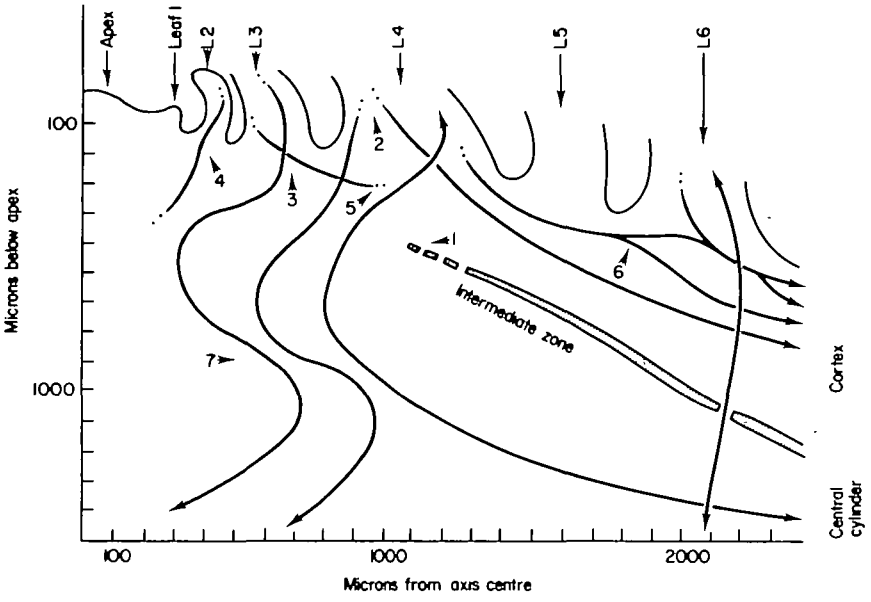


FIG. 2. Diagrammatic radial longitudinal section through the apex of the aerial vegetative axis of *Alpinia speciosa*. The vertical axis indicates estimated centre of each section. All leaf bases (L1–L6) are rotated into a single radial plane. The solid lines represent procambial strands. The outer system is differentiating in the cortex; the inner system in the central cylinder. Features 1–7 are described in the text.

Development of the aerial stem vascular system. Figure 2 is a plot of some of the procambial strands occurring within a distance of 1·5 mm below the apex of an aerial shoot of *Alpinia* prior to its conversion into an inflorescence. The vertical axis represents the estimated centre of each section. For convenience leaf positions in the distichous arrangement are rotated so that they all occupy the same orthostichy. In the actual stem, of course, successive leaves occupy opposite sides of the axis.

The following points are to be noted from the figure (labelled 1–7).

(1) At about plastochrone 4, i.e. 500 μm below the apical meristem, the cells of the ground tissue become vacuolated. The intermediate zone remains undifferentiated and is therefore recognizable below this level.

(2) Both inner and outer system traces of leaf four are well developed proximally – descending several millimetres down in the stem. Distally their differentiation continues in the leaf primordium.

(3) An inner system trace of leaf three is at a similar stage of development, but an outer system trace is only just differentiating (both basipetally and basifugally).

(4) Inner system bundles of leaf two are only just differentiating; outer system bundles of leaf two have not yet appeared.

(5) Procambial strands may be distinguished as potentially inner or outer by their

orientation in the apex before the intermediate zone is visible as a junction between these two systems at the same level.

(6) There are no bridges between differentiating inner system procambial strands, even after about 16 plastochrones. Connexion occur between outer system strands after only four plastochrones.

(7) The apparent erratic plotting of some bundles is probably due to their spiral path in the apex.

The distinction between inner and outer system bundles can be recognized topographically, even above the level at which the intermediate zone is clearly demarcated, by their relative position in the leaf primordia, since inner system bundles are always adaxial. This shows that the two types of bundle can differentiate simultaneously. It also allows the number of procambial strands belonging to each system to be counted in successive leaves thus indicating their rate and time of formation. These data are summarized in Fig. 3, which shows that inner system bundles appear first, but the total number which differentiate is almost complete by the fourth plastochrone; outer system bundles first begin to differentiate in about the third plastochrone and new ones continue to be differentiated in the fifth plastochrone. During the third and fourth plastochrone, bundles of the two systems are differentiated simultaneously.

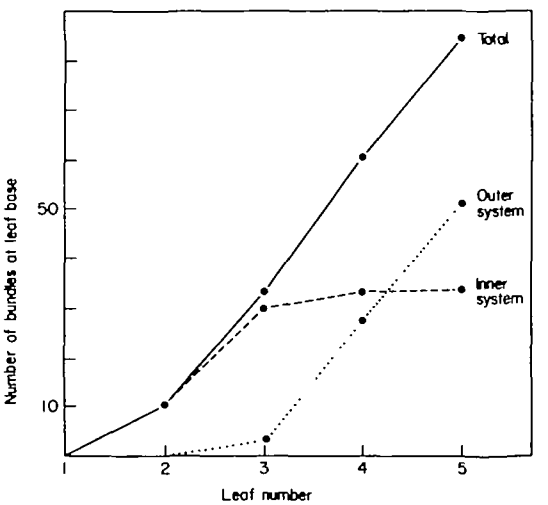


FIG. 3. The number of vascular bundles present in the base of leaf 1 (the youngest) to leaf 5. Solid line: total number of bundles. Dash line: inner system bundles. Dot line: outer system bundles.

DISCUSSION

The tissue at the interface between the cortex and the central cylinder is of particular interest and in many different monocotyledons it is potentially meristematic. This is apparent in the rhizome, the intermediate zone becoming a functional vascular cylinder. Here it has been referred to as 'undifferentiated' although it retains some features of a meristem, i.e. its cells remain thin-walled and little vacuolated. In the mature aerial stem, however, cells of this region eventually differentiate as thin-walled fibres (Tomlinson, 1969). The versatility of this tissue and the differing ways in which it may differentiate has resulted in the multiplicity of names given to it by different authors. Many terms

intimate a function which may be true of one species, but not another. A selection of terms is included in Table 1, but to avoid any confusing implications the interface has here been referred to as the 'intermediate zone'. (Petersen, 1892).

TABLE 1. *Intermediate zone – some synonyms*

Holzcylinder	Karsten (1847)
Cambium ring	Schacht (1852)
Scheidegewebe, Assenscheide	Sanio (1864)
Zone génératice	van Tieghem (1866)
Stammeigene Platten dem Skelett der Beiwurzeln entstammend	Falkenberg (1876)
Cambium	de Bary (1877)
Zone intermédiaire	Guillard (1878)
Réseau radicifère	Mangin (1882)
Intermediate zone	Petersen (1892)
Pericycle	Barthelet (1893)
Root plate	Sargent and Arber (1915)
Root girdle	Arber (1934)
Fibrous cylinder (aerial stem), 'Cylinder of vascular tissue' (rhizome)	Tomlinson (1956)
Cambium band	Coetzee (1967)
'Boundary between cortex and central cylinder'	Zimmermann and Tomlinson (1967)
'Meristematic cambium-like zone separating the outer and inner system'	Kumar (1973)
Peripheral plexus	Bell (1976b)

The fundamental feature underlying monocotyledon vasculature appears to be the 'upwardly branching leaf trace' (Zimmermann and Tomlinson, 1972). If an axial bundle is followed distally it eventually 'departs' into a leaf. Almost invariably at some point near its departure a branch is given off which proceeds on up the stem acting in its turn as an axial bundle and then departing as a leaf trace. In this manner the stem does not 'run out' of bundles. In addition, axial bundles are interconnected by 'bridges'. Developmental studies (e.g. Zimmermann and Tomlinson, 1967) have shown that it is correct to consider the axial bundle/leaf trace as the basic constructional unit in this vascular pattern and not to think in terms of a continuous axial bundle from which leaf traces are given off at intervals. In *Rhapis*, bundles are initiated in a meristematic 'cap' situated just below the stem apex. They differentiate both out into the leaf primordium and basipetally in the stem axis to meet basifugal branches from older departing leaf traces. Bundles differentiating late at any particular level will fail to make contact with a leaf trace below and will peter out in the cortex, perhaps anastomosing to some extent with each other in the process (Zimmermann and Tomlinson, 1967). In some monocotyledons, typically in the Zingiberales, this cortical system is extensive and functional and constitutes an 'outer' vascular system in addition to the 'inner' system of upwardly branching leaf traces described above.

Discussion of the functional implications of the cortical system in *Alpinia* and the possible significance of the intermediate zone is best delayed until the rhizome vasculature has been described. However a number of points are worthy of note at this stage.

In the *Rhapis* stem, the outer system is merely represented by a non-functional anastomosing network of insignificant fibrous bundles with no connexions at their proximal ends. Cortical bundles in *Rhapis* and *Prionium* represent potential inner system bundles that have failed to make contact with departing leaf traces during their late basipetal differentiation outside the cap and thus fail to establish axial continuity (Zimmermann and Tomlinson, 1967, 1968).

The presence of an extensive and functional outer system in the aerial stem (and rhizome) of *Alpinia* suggests that here the development of the two systems is simultaneous or at least overlaps. The survey of procambial strands in the apex shows the latter to be the case. Zimmermann and Tomlinson state that in *Prionium* the cortical bundles do not anastomose amongst themselves as there are too few (about 50 per leaf), unlike *Rhapis* where the large number of cortical traces per leaf ($\pm$ 1000) allows contact between them to be made.

The lack of axial continuity in the inner system is curious. Each inner system trace of a foliage leaf makes contact with a departing leaf trace several nodes below. The number of aerial nodes is very limited and inevitably therefore most of the foliage leaf traces contact the leaf traces of scale leaves, within the rhizome. The only functional contact between inner system bundles in the aerial stem is by means of the extensive bridging to the cortical system from departing inner system leaf traces. This dependence of the inner system on the outer, together with the large size of the cortical bundles both in the stem and in the leaf sheath, and their elaborate interconnexions suggests that the outer system is functionally the most important in *Alpinia*. This condition may well be related to the determinate sympodial rhizome units of which the plant is constructed, and will be discussed further in the next paper.

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