THE ANATOMY OF PHENAKOSPERMUM (MUSACEAE)

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IN A RECENT ACCOUNT of the anatomy of the Musaceae (Tomlinson, 1959) the anatomy of *Ravenala* is described. Although this dealt with only one species, *R. madagascariensis*, it is there implied that *Phenakospermum* (*Ravenala*) *guianense* (L. C. Rich.) Miq. falls within the range of anatomical variation of *Ravenala*. The anatomy of *Phenakospermum* has, however, never been described in detail.

Recently, thanks to the kindness of Dr. P. Campos-Porto of the Botanic Gardens, Rio de Janeiro, I received pickled material of parts of a mature plant, together with material of a juvenile plant, of *Phenakospermum guianense*. On first examination of this material it was immediately evident that there were significant differences between *Phenakospermum* and *Ravenala*. More recently it has been possible to examine this material in detail, and the present account is based on these anatomical observations. From these results a comparison between *Phenakospermum* and other members of the Musaceae, particularly *Ravenala* and *Strelitzia*, has been made from the standpoint of systematic anatomy.

Reasons for accepting *Phenakospermum* Endl. ex Miq. as a valid genus distinct from *Ravenala* Adans., within which it was formerly included, are given by Lane (1955). He also discusses the nomenclatural problems of *Phenakospermum*, and, since they are there satisfactorily resolved, it is not necessary to repeat them in the present paper. The chief diagnostic features which are considered by Lane to be characteristic of *Phenakospermum* are the terminal inflorescence, five stamens in each flower, four or more rows of ovules in each loculus of the ovary, the bright red-orange, filamentous aril and straight embryo with the micropylar opening at the end of the seed. *Ravenala*, on the other hand, has a lateral inflorescence, six stamens in each flower, only two rows of ovules in each loculus of the ovary, while the aril is blue and membranaceous and the embryo is bent so that the micropylar opening is in the side of the seed. In addition, in the material of *Phenakospermum* which I received, there were short stolons covered by overlapping, distichous scales, evidently a means by which the plant could spread vegetatively. *Ravenala* also propagates itself by growth of basal suckers, but these are never at first stoloniferous.

Apparently there are two distinct forms of the plant, the most obvious difference being that one has an erect, ligneous stem, the other having only an underground stem; small differences in the reproductive parts have also been recorded. Nakai (1948) has separated the form with a distinct trunk into a new genus, *Musidendron*. Lane suggests that the differences are not sufficiently constant to warrant this change.

The same methods used in studying the anatomy of other members of the Musaceae were employed (Tomlinson, 1959). In sectioning the stem on the sliding microtome it was found necessary to soften the hard outer sclerotic layer by directing a jet of steam onto the cut surface during the sectioning process.

ANATOMY OF THE VEGETATIVE PARTS

Lamina dorsiventral. HAIRS absent. CUTICLE forming a thick, abaxial, waxy layer, cracking and eroding from mature leaves although persisting as irregular tabular masses, often forming annular ridges above stomata; outer cutinized layer of epidermal cells rather thin. EPIDERMIS with markedly sinuous anticlinal walls. Adaxial epidermis very uniform, outer wall thickened, made up of files of tabular cells; cells in surface view (*Fig. 1*) either square, or rectangular and longitudinally extended although end walls often rather oblique. Abaxial epidermis mostly with inner wall thicker than delicate, wholly cutinized outer wall; made up of narrow costal bands of shallow cells, costal cells more or less square in surface view (*Fig. 2*) and each often including a small silica body; alternating with wider intercostal bands of larger, usually longitudinally extended but rather irregular cells, those in the same file as stomata sometimes wider than cells elsewhere. STOMATA occasional adaxially; abaxially absent below both longitudinal and transverse veins and so restricted to short rectangular areas; not in regular files but 3–5 irregular series situated within each intercostal band. Terminal subsidiary cells usually short, wide but not otherwise different from other epidermal cells. Lateral subsidiary cells narrow, deep, uniformly thin-walled; other epidermal cells sometimes modified adjacent to stomata but not uniformly arranged. Guard cells (*Fig. 11*) not sunken, each with 2 cutinized ledges. HYPODERMIS (*Fig. 3*) 2–3-layered adaxially, often 4-layered above main veins, 1-layered abaxially. Outermost adaxial hypodermal layer rather thick-walled, cells hexagonal and slightly transversely extended in surface view; inner layers composed of larger and more cubical cells with thinner walls. Abaxial hypodermal layers often interrupted by vascular buttresses, cells always smaller than outermost adaxial layer, most irregular in intercostal regions; substomatal chambers each surrounded by an annulus of 2–4 small cells. CHLORENCHYMA including 2 or 3 adaxial layers of palisade cells, uppermost layer most anticlinally extended. Abaxial mesophyll divided into rectangular compartments between longitudinal and transverse veins, including rather loose, isodiametric but shortly lobed cells. VEINS (*Figs. 3, 5*) all attached to each hypodermis by well-developed fibrous buttresses; adaxial buttresses narrow except for massive buttresses above few main veins, composed of unlignified fibers with wide lumina; abaxial buttresses made up of narrow lignified fibers with narrow lumina. Outer parenchymatous bundle sheath 1-layered lateral to all veins, composed of cubical or slightly longitudinally extended cells. Extended protoxylem only present in larger

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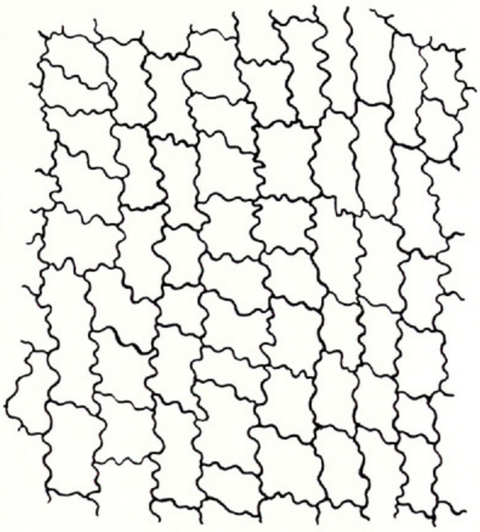

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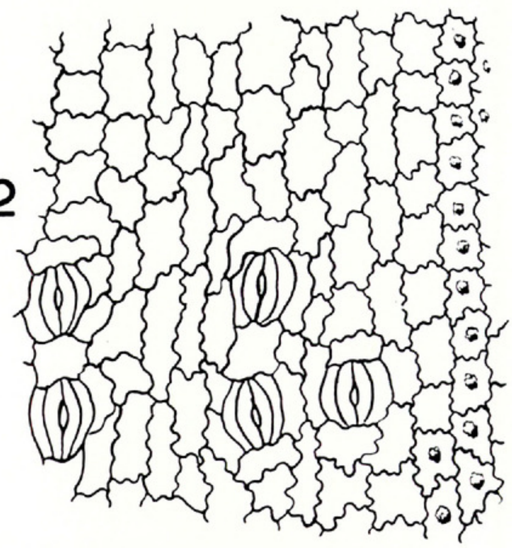

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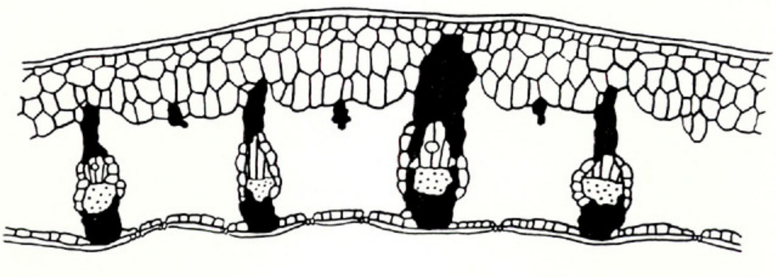

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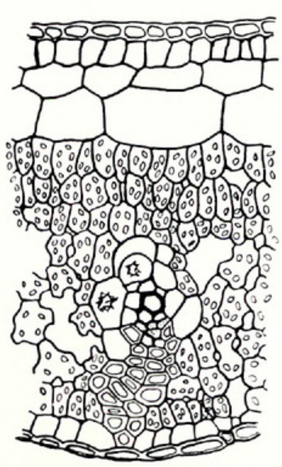

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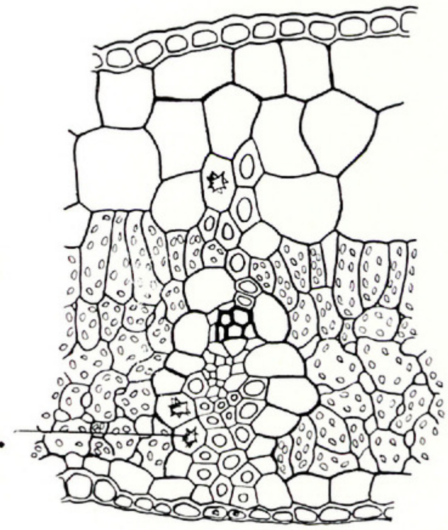
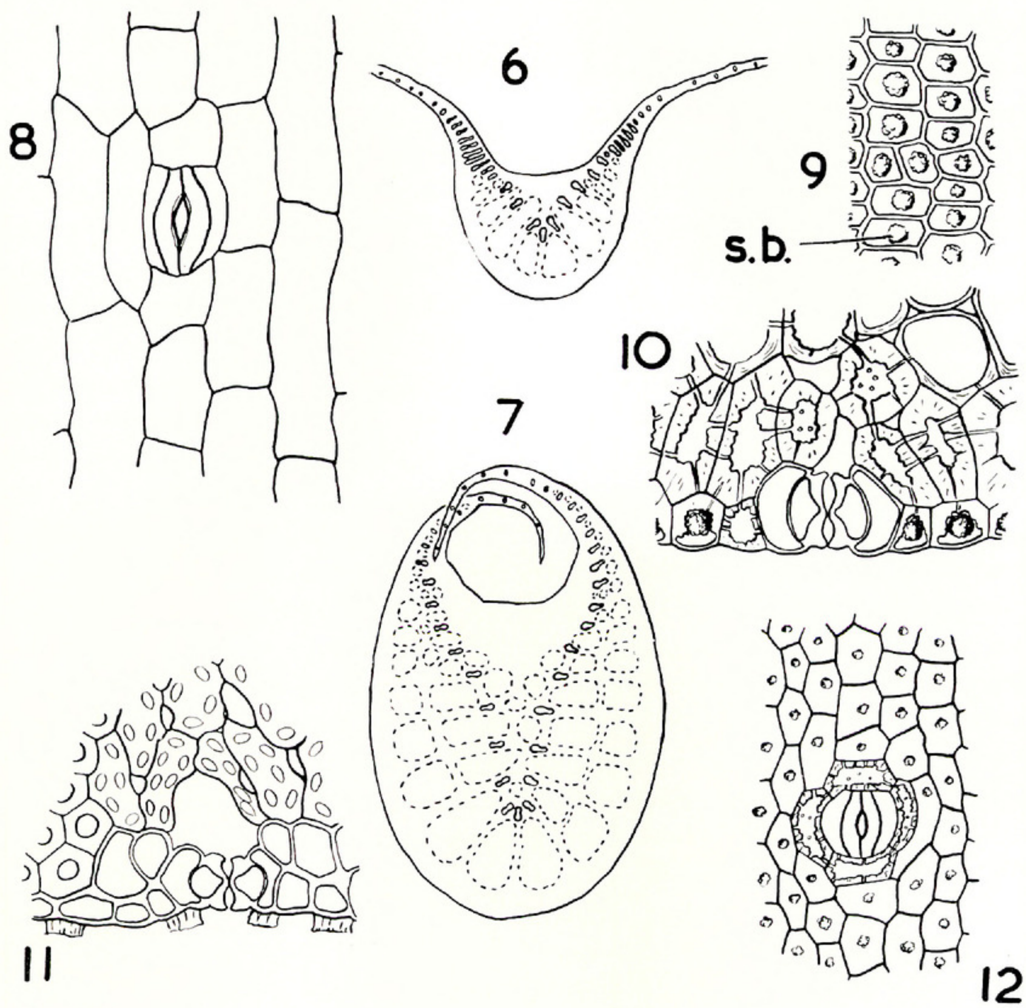


FIGS. 1–5. ANATOMICAL DETAILS OF THE LEAF OF PHENAKOSPERMUM. 1, Adaxial epidermis of lamina, surface view, × 300. 2, Abaxial epidermis of lamina, surface view, including part of a costal band, × 300. 3, Transverse section of lamina, including a main vein, × 54; sclerenchyma solid black, phloem stippled, xylem lined. 4, Longitudinal section of lamina including a transverse vein in transverse section, × 125. 5, Transverse section of lamina, including a small longitudinal vein, × 145; s.b. = silica bodies.

veins, vascular tissues rather inconspicuous in smaller veins. Probable free vein extensions, pectinating with longitudinal veins, visible as occasional fibrous strands below adaxial hypodermis near main veins. TRANSVERSE COMMISSURES (*Fig. 4*) frequent, all buttressed to either abaxial hypodermis or epidermis by short, unlignified, thick-walled prosenchymatous elements or short fibers with wide lumina; adaxial sheath usually consisting of a single layer of colorless parenchyma in contact with the palisade; vascular tissues reduced, xylem often consisting of a single file of tracheal elements, phloem incompletely sheathed by lignified elements. EXPANSION CELLS represented by well-developed hypodermal layers above main veins (*Fig. 3*). Indistinct "pulvinar band" also present at junction of midrib and lamina, veins in this region with very tall and well-developed adaxial buttresses.

Leaf axis (lamina midrib [*Fig. 6*], petiole [*Fig. 7*], leaf sheath). EPIDERMIS varying in structure in different parts: (i) Adaxial epidermis of midrib and upper part of leaf sheath: cells cubical or slightly longitudinally extended, outer walls distinctly thickened, anticlinal walls often slightly sinuous in midrib; rarely containing silica bodies. (ii) Adaxial epidermis of leaf base (*Fig. 8*): cells thin-walled, rectangular and considerably longitudinally extended, anticlinal walls not sinuous. (iii) Abaxial epidermis of midrib and leaf sheath together with whole of epidermis of terete part of petiole (*Fig 12*): cells more or less cubical, inner wall becoming markedly thickened and often enveloping a spherical silica body, especially in leaf sheath (*Fig. 9*). Sometimes slight differentiation between costal and intercostal regions. STOMATA occasional on both surfaces, guard cells and lateral subsidiary cells like those in stomata of lamina, arrangement of other subsidiary cells varying in different parts of leaf axis: (i) Adaxial epidermis of midrib and upper part of leaf sheath: arrangement more or less as in lamina. (ii) Adaxial epidermis of leaf base (*Fig. 8*): terminal subsidiary cells short, thin-walled. (iii) Abaxial epidermis of leaf sheath and whole of epidermis of terete part of petiole: terminal subsidiary cells with uniformly thickened and conspicuously pitted walls, similar cells also usually adjacent to lateral subsidiary cells (*Figs. 10, 12*). HYPODERMIS usually conspicuously different from ground parenchyma cells of leaf axis: (i) Abaxial hypodermis in all parts consisting of 2 to many layers of small, short cells with massively thickened, pitted lignified walls, interrupted by small, loose, lobed cells below stomata but these cells also becoming sclerotic in old leaves (*Fig. 10*). (ii) Adaxial hypodermis in midrib and upper part of leaf sheath including at least 1 regular layer of stone cells either immediately below epidermis (leaf sheath) or separated from epidermis by a thin-walled layer (midrib). (iii) Adaxial hypodermis of leaf base always with thin-walled, markedly tangentially extended cells. CHLORENCHYMA present as an inconspicuous abaxial band. AIR LACUNAE in one to many series extending from leaf insertion to distal part of midrib (*Fig. 6*). Most conspicuous in petiole

(*Fig. 7*) as several arcs of lacunae abaxial to main vascular arc, separated from each other by vertical partitions; represented by a single arc of air canals in leaf sheath; small system of air canals also adaxial to main vascular arc in petiole. Air lacunae segmented at regular intervals by thick TRANSVERSE SEPTA, each septum consisting of 2–3 layers of large, fairly compact, colorless parenchyma cells on either side of a central plate of 2 or 3 layers of small, stellate cells, the arms of which include wide intercellular spaces. Air lacunae in the midrib often containing a loose network of algiform cells. Abaxial FIBROUS STRANDS abundant in all parts of leaf axis, together with the sclerotic abaxial hypodermis forming a peripheral rigid mechanical zone. Fibrous bundles pectinating with abaxial vascular bundles, usually separated from epidermis by a sclerotic hypo-



FIGS. 6–12. ANATOMICAL DETAILS OF THE LEAF OF PHENAKOSPERMUM. 6, Transverse section of midrib, with only main arc of vascular bundles shown, × 2. 7, Transverse section of base of petiole, with only main arc of vascular bundles shown, × 2. 8, Adaxial epidermis of sheathing leaf base in surface view, × 300. 9, Abaxial epidermis of leaf base in surface view, × 300; s.b. = silica bodies. 10, Transverse section of abaxial epidermis of leaf base including a stoma, × 430. 11, Transverse section of stoma from abaxial epidermis of lamina, × 430. 12, Epidermis of petiole in surface view, × 300.

dermis but in petiole often immediately adjacent to epidermis. VEINS arranged in 3 distinct systems: (i) Main V- or U-shaped arc of large vascular bundles mostly adaxial to main system of air lacunae (*Figs. 6, 7*). (ii) A very feeble system either of narrow adaxial bundles with reduced, often obliquely or inversely orientated vascular tissues or of purely fibrous strands, most conspicuous in petiole. (iii) Abaxial system of numerous, mostly medium-sized vascular bundles below main arc, bundles uniformly scattered and not arranged in obvious arcs, frequent in longitudinal partitions between air lacunae, bundles in this position in midrib often inversely orientated. Large vascular bundles with normal Scitaminean construction (cf. Solereder and Meyer, 1930; Tomlinson, 1956); phloem parenchyma often thick-walled and lignified. TRANSVERSE COMMISSURES connecting longitudinal veins at irregular intervals, sometimes extending across transverse partitions of air lacunae. GROUND PARENCHYMA uniform, often including tannin cells.

Stem. Narrow cortex abruptly delimited from central cylinder by a dense sclerotic zone of congested vascular bundles. EPIDERMIS as in abaxial part of leaf sheath with files of cubical cells, each with inner wall thickened and enclosing a spherical silica body. STOMATA occasional, each surrounded by sclerotic subsidiary cells as in the leaf sheath. HYPODERMIS usually including 2 or 3 (locally many more) markedly sclerotic layers. CORTEX including 3 or 4 innermost irregular series of large vascular bundles together with smaller bundles in outer cortex. Each bundle with a well-developed fibrous sheath external to the phloem; xylem sheathed by parenchyma, usually including only one wide metaxylem vessel and without extended protoxylem. CENTRAL CYLINDER with a peripheral zone of congested vascular bundles separated from each other by narrow bands of sclerotic parenchyma. Vascular tissues of peripheral bundles reduced to a single xylem element and a narrow phloem strand and completely sheathed by a wide fibrous cylinder. Inner limit of peripheral sclerotic zone showing a sharp transition to central region of central cylinder with its irregularly scattered bundles. Largest vascular bundles (apparently recently entered leaf traces), each including many wide metaxylem vessels, conspicuously extended protoxylem and a small phloem strand; fibrous sheath narrow and inconspicuous. Other vascular bundles (traces well below their insertion into a leaf), each with a single wide metaxylem vessel, no extended protoxylem and a complete, fibrous sheath. GROUND PARENCHYMA of inner part of central cylinder spongy and enclosing large intercellular spaces, individual cells rounded but not lobed, including abundant starch.

Stolons. Notable features include a wide cortex containing many scattered vascular bundles, the largest of which are either bicollateral or amphivasal, each surrounded by a complete fibrous sheath; a narrow central cylinder delimited from the cortex by a discontinuous endodermis of cells with U-shaped thickenings; peripheral tissues of central cylinder immediately within endodermis consisting of a congested region of irregular vascular bundles. Central vascular bundles less congested, usually collateral.

Root. (Structure described possibly not typical since only underground roots from juvenile plants and aerial roots from base of mature stems available.) (i) Underground roots: piliferous layer sometimes persistent, but usually shrivelled in old roots. EXODERMIS of narrow compact thick-walled cells with truncate ends, often separated from piliferous layer by 2 or 3 thin-walled layers. Cells of inner CORTEX very uniform; air lacunae absent. ENDODERMIS of mature roots with U-shaped wall thickenings; pericycle thin-walled, mostly 1-layered. STELE as in *Ravenala* and *Strelitzia* with wide vessels scattered throughout the central tissues together with scattered phloem strands each containing a wide sieve tube. (ii) Aerial roots: normal polyarch monocotyledonous root structure.

Silica, crystals, tannin, starch. SILICA CELLS. (i) "False stegmata" with thin walls present in discontinuous files, each cell including a stellate, druselike silica body (*Fig. 5, s.b.*); common in leaf and stem adjacent to vascular bundles; in lamina common adjacent to fibrous vascular buttresses and in cells of outer parenchymatous sheath; also common adjacent to transverse commissures. In leaf axis common adjacent to vascular bundles but absent from vicinity of abaxial fibrous strands; also frequent adjacent to transverse veins. (ii) Epidermal cells of stem, abaxial epidermis of leaf axis (*Figs. 9, 10*) and sometimes costal abaxial epidermal cells of lamina (*Fig. 2, s.b.*) developed as "true" stegmata, each with a spherical, spinulose silica body becoming enveloped by thickenings of inner tangential wall of cell; most obvious in leaf base. CRYSTALS. Calcium oxalate abundant as small rhombohedral crystals usually in clusters in ground parenchyma, common in assimilating cells of leaf, especially abundant in cells of transverse diaphragms of air lacunae. Raphide-sacs frequent in all parts but especially abundant in ground parenchyma of stem, common on surface of transverse diaphragms in air lacunae. TANNIN. Abundant in all parts of ground parenchyma in unmodified cells. STARCH. Abundant in ground parenchyma of stem as large, more or less ellipsoidal but not flattened or markedly eccentric grains; small grains often common in cells adjacent to vascular bundles of leaf axis.

Vascular tissues. VESSELS present only in root and stem; elements in underground roots (see root above) of the order of 1500 μ but up to 5000 μ long, 160–200 μ wide with either simple or scalariform perforation plates with few thickening bars on slightly oblique end walls. Elements of aerial roots shorter, narrower, never with simple perforation plates. Elements in stem 2000–2500 μ (or as short as 1250 μ) long, 125–160 μ wide, with oblique or very oblique scalariform perforation plates with many thickening bars. Vessels absent from stolons and leaf. SIEVE TUBES apparently with simple sieve plates in stem and leaf.

DISCUSSION

THE ANATOMY OF PHENAKOSPERMUM IN RELATION TO ITS SYSTEMATIC POSITION

Phenakospermum in relation to the Musaceae as a whole. From the information recorded here and in the previous publication (Tomlinson, 1959) it is evident that *Phenakospermum* shares most of the features by which *Strelitzia* and *Ravenala* can be distinguished from other members of the Musaceae. The following combination of anatomical features is common to these three genera:

Terminal subsidiary cells short and distinct from other epidermal cells; other cells adjacent to stomata sometimes different from remaining epidermal cells; adaxial hypodermis multiseriate (up to six layers deep); abaxial hypodermal cells arranged concentrically around substomatal chambers; longitudinal veins of lamina all buttressed to each hypodermis; all transverse septa of lamina including vascular tissues; petiole including several arcs of air canals; transverse diaphragms of air canals each several cells thick; chlorenchyma of leaf axis situated in an abaxial band; stem often an erect woody trunk without an endodermis; subterranean roots with an anomalous stele including uniformly scattered metaxylem vessels and phloem strands, the latter each including a single, wide sieve tube; internal silica cells thin-walled, each including a stellate, druselike silica body; silica cells often situated adjacent to transverse as well as longitudinal veins.

On the basis of this close anatomical similarity it is evident that these three genera form a very distinct and natural subunit within the Musaceae. This unit corresponds to the Strelitziaceae of Nakai (1948) but not that of Hutchinson (1959) which also includes *Heliconia*.

Phenakospermum, however, is of peculiar interest because it possesses a number of features which are not found in *Ravenala* and *Strelitzia* but which may be present in other members of the Musaceae. These features are indicated below together with the names of other genera of the Musaceae, in parentheses, which also possess them:

Stomata not sunken (*Heliconia, Musa, Orchidantha*); anticlinal epidermal walls of lamina markedly sinuous (*Heliconia*); inner wall of abaxial epidermal cells of lamina thicker than outer; transverse septa of lamina attached to abaxial hypodermis by well-developed, mostly sclerotic buttresses (the corresponding buttresses in *Ravenala* and *Strelitzia* are never markedly sclerotic; in *Musa* the transverse septa only occasionally include sclerotic elements); lateral parenchyma of veins of lamina always one-layered (*Orchidantha*); leaf axis including fibrous and vascular bundles adaxial to main vascular arc (*Heliconia, Musa, Orchidantha*); starch grains neither as flattened as in *Ravenala* nor as spherical as in *Strelitzia*; stegmata, i.e. silica cells with unequally thickened walls, common in abaxial epidermis of leaf (such cells have been recorded and illustrated for *Ravenala* by Solereder and Meyer but they have never been observed by me in either *Strelitzia* or *Ravenala*); vessels in the root sometimes bearing simple perforation plates (*Musa*).

Lane (1955) has emphasized that *Phenakospermum* is sufficiently distinct from *Ravenala* to make its acceptance as a separate genus very desirable. The above information supports this contention, since the anatomical differences between *Strelitzia* and *Ravenala*, both of which are accepted as good genera, are not greater than the structural differences between *Phenakospermum* on the one hand and *Strelitzia* and *Ravenala* on the other. Indeed, it is anatomically easier to recognize *Phenakospermum* than it is to distinguish *Ravenala* from *Strelitzia*. On the whole *Phenakospermum* seems to be something of a connecting link between *Ravenala* and *Strelitzia* and the rest of the Musaceae.

The relation between Phenakospermum, Strelitzia, and Ravenala. Lane has suggested that *Phenakospermum* has more affinity with *Strelitzia* than with *Ravenala* even though it was originally thought to be congeneric with *Ravenala*. Anatomical information which might throw light on the interrelationships between these three genera is presented below.

Phenakospermum and *Ravenala* share the following features which are not found in *Strelitzia*: Wax on abaxial surface of the lamina tabular; abaxial hypodermis of leaf axis markedly sclerotic in most regions; subsidiary cells adjacent to stomata of abaxial surface of the leaf axis sclerotic, especially in *Phenakospermum* (occasionally so in *Strelitzia* according to Solereder and Meyer); periderm apparently never developed. In *Strelitzia* the wax on the abaxial surface of the lamina is rodlike, the abaxial hypodermis of the leaf axis is apparently never sclerotic, and root and stem frequently develop a specialized periderm.

Phenakospermum and *Strelitzia* share the following features which are not developed by *Ravenala*: Abaxial hypodermis mostly one-layered; only two arcs of air canals in the petiole; air lacunae apparently absent from the underground roots; vessels present in the aerial stems.

Ravenala on the other hand has a consistently two-layered abaxial hypodermis, several arcs of air canals in the petiole which may be a result of its great size, air lacunae in the cortex of the root and no vessels in the stem. The last observation, however, is open to doubt and needs confirmation.

Even if these differences are constant, they are not sufficiently large to be of taxonomic significance, although it should be noted that the anatomical resemblances between *Phenakospermum* and *Ravenala* are to be found in features which are likely to be plastic and influenced considerably by environmental conditions and so may not be a reliable indication of phylogenetic affinity. On the basis of this assumption it could be said that

Phenakospermum shows more qualitative anatomical resemblance to *Strelitzia* than to *Ravenala*.

Possible Phylogenetic Implications from the Anatomical Observations

In some respects *Phenakospermum* forms a connecting link between *Strelitzia* and *Ravenala* on the one hand and the rest of the Musaceae on the other, since, as has been shown above, many of the features in which it differs from *Strelitzia* and *Ravenala* are to be found in the remaining members of the Musaceae. In this respect it is particularly noteworthy that sinuous epidermal walls have previously only been recorded in *Heliconia*. This is of significance as it makes it easy to speculate on the possible evolution of the whole of the Musaceae from some ancestor with a *Phenakospermum*-like habit. *Ravenala* and *Strelitzia* would be least modified descendants, *Heliconia* and particularly *Orchidantha* would be most modified. It may also be significant that the anatomy of the stolons of *Phenakospermum* closely resembles that of the rhizomes of these herbaceous types. Thus by elimination of the erect woody trunk and persistence of the stolons it would be possible to produce rhizomatous plants of the *Heliconia* type. The fleshy corm of *Musa* and *Ensete* could have evolved from a woody trunk by telescoping of its internodes. The derivation of the Musaceae from an ancestor with a caulescent habit is implied by Lane in his paper, and he also suggests how the inflorescences of members of the family may be various modifications of the type shown by *Ravenala*. Thus it is possible to envisage the ancestral type from which the Musaceae have evolved as possessing the growth habit of *Phenakospermum* with the lateral inflorescence of *Ravenala*.

SUMMARY

The anatomy of the vegetative parts of *Phenakospermum guianense* is described for the first time. The systematic implications of these observations are that: (a) *Phenakospermum* is a valid genus; (b) together with *Ravenala* and *Strelitzia* it forms a natural unit within the Musaceae; (c) it may possibly be more closely allied to *Strelitzia* than to *Ravenala*. It is suggested that the Musaceae have evolved from an ancestor with the vegetative habit of *Phenakospermum* and the inflorescence of *Ravenala*.

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