

**A re-examination of *Sanango racemosum*. 2. Vegetative and floral anatomy.**

**Taxon 43: 601-618.**

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## A re-examination of *Sanango racemosum*. 2. Vegetative and floral anatomy

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### Summary

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A study of floral and vegetative anatomy of the woody, monotypic Amazonian genus *Sanango* was undertaken in an attempt to help clarify the relationships of the genus. Detailed descriptions of leaf, stem, nodal, wood, and floral anatomy are presented. Wood is characterized by a combination of solitary and grouped vessels with elements having few-barred scalariform perforation plates, imperforate tracheary elements with very reduced pit borders, exceptionally tall and broad heterocellular rays, and vasicentric axial parenchyma. Of special interest is the presence in *Sanango* of a very uncommon multilacunar nodal structure having split-lateral traces. Stems possess cortical vascular bundles. Leaf stomata are anisocytic and distributed in clusters on the undersurface of the lamina. Anatomical evidences suggest that *Sanango* is most closely related to the *Scrophulariales*, sharing many important features with the *Gesneriaceae*.

### Introduction

In the first paper of this series, Norman (1994) outlined the systematic history of the monotypic amazonian genus *Sanango* G. S. Bunting & J. A. Duke (1961) and pointed out that the familial affinities of this rare taxon remain unsettled. Critical examination of the vegetative and floral anatomy of dicotyledons has long provided an extra measure of confidence for the independent resolution of systematic problems, particularly by helping place systematically difficult taxa and strengthening alliances not otherwise firmly established. This report includes the first account of the vegetative and floral anatomy of this woody genus and presents important evidence in determining its closest relationships.

### Materials and methods

Liquid preserved leaves, young stems and flowers of *Sanango racemosum* (Ruiz & Pav.) Barringer (*Neill 9458*) were available for study. After dehydration in tertiary butyl alcohol, floral buds, leaves, and stems were paraffin embedded, serially sectioned transversely and longitudinally, and stained with a combination of safranin and fast green. Entire flowers were also cleared in 5 % hot NaOH to reveal vascular patterns. Floral parts were critical-point dried, sputter-coated with gold-palladium, and viewed with the SEM.

Wood samples (*Ceran 2627*; *Woytkowski 5925*) were boiled in water and cut on a sledge microtome at a thickness of 15-20  $\mu\text{m}$ . Resulting sections were stained with safranin. Data relating to wood cell length were obtained from mature wood by making 50 measurements from macerations prepared using Jeffrey's fluid. Cell diameters were measured from transverse sections and included walls. Stomatal patterns were observed in prepared paradermal sections. All drawings were made from prepared and stained sections with a Wild Heerbrugg camera lucida. Unless indicated otherwise, comparative data were obtained from Metcalfe & Chalk (1950).

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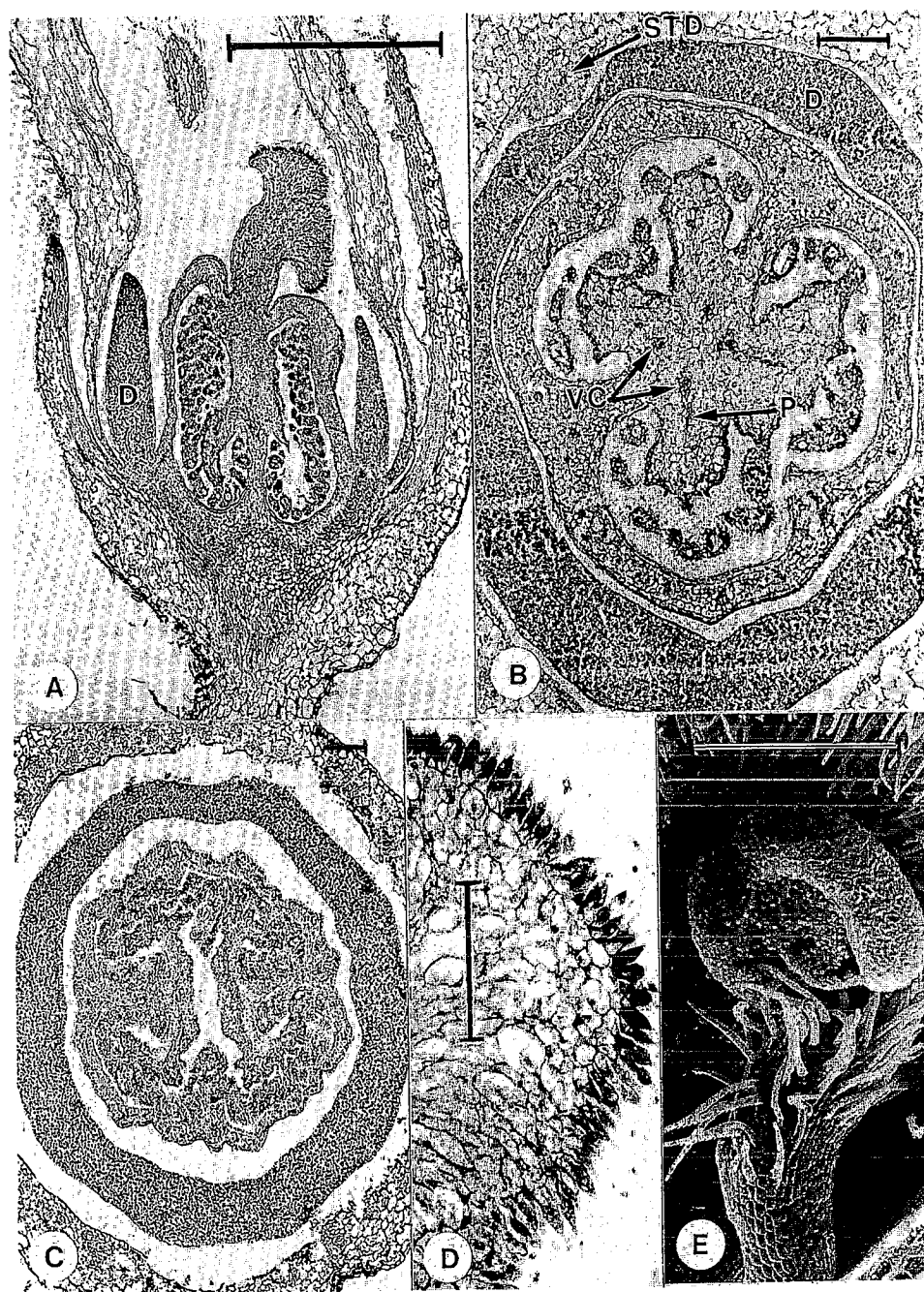


Fig. 1. Floral morphology and anatomy of *Sanango*. - A, longitudinal section of flower; B, transverse section of flower at the level of placentation; C, transverse section of flower with corolla removed; D, longitudinal section of stigma, showing specialized surface cells; E, SEM view of stamen following anthesis. - D = disk; P = placental bundle; STD = staminode; VC = ventral carpellary bundle. - Bar = 1 mm (A, E) or 0.1 mm (B-D).

## Results

*Floral morphology* an hypogynous, and zygom more commonly five me base of the ovary and s proximately the lower h the sympetalous corolla ( alternating with the sep anthesis. The tube wall is 10 cells) at more distal l corolla tube is reportedly is not always evident. Th the outer surface and fr (1961) reported petal ae lobes in bud is imbricate fifth with one margin cc of one of the exterior pet interior, and the remain rior. Four-parted corolla remaining two with half composed of thin-wallec tissues are devoid of idiot

Intermixed trichomes tacle, and both outer a Stamen filaments are als by numerous short hair mixture of long and shor

The epipetalous andr stamens. An additional a posterior position, just at flowers the staminode. Stamens are borne high sepal plane. Stamens are and narrowed at the ape base and united distally tinct epidermal layer an that extend into the cel between the two locules. The two thecae also bec (horseshoe-shaped) type

The bi-loculate gyno completely fused along superior for most of its l in the receptacle. The c lobed disk that is partia nectariferous tissue cor spicuous nuclei.

*Results*

*Floral morphology and anatomy.* - Flowers of *Sanango* are pedicellate, bisexual, hypogynous, and zygomorphic. The perianth is composed of two cycles of four or more commonly five members each. Both whorls of perianth parts are adnate to the base of the ovary and surrounding disk (Fig. 1A). The calyx is synsepalous in approximately the lower half, forming a tube around the other floral parts. At maturity the sympetalous corolla exceeds the calyx by several millimetres, with the petal lobes alternating with the sepals. The tube is curved and undergoes abscission following anthesis. The tube wall is thin at the base and becomes progressively thickened (up to 10 cells) at more distal levels where it extends beyond the calyx (Fig. 1A, 2A). The corolla tube is reportedly gibbose or ventricose above the base although this feature is not always evident. The inner epidermal cells of the corolla are larger than those of the outer surface and frequently become extended as trichomes. Bunting & Duke (1961) reported petal aestivation to be cochlear; however, aestivation of the corolla lobes in bud is imbricate or quincuncial, i.e., two petals exterior, two interior, and a fifth with one margin covering an interior petal and another margin covered by that of one of the exterior petals (Fig. 2B). Some flowers have one petal lobe exterior, one interior, and the remaining three petals with one margin interior and the other exterior. Four-parted corollas typically have one petal interior, one exterior, and the remaining two with half interior and half exterior (Fig. 2C). Perianth members are composed of thin-walled parenchymatous cells showing little differentiation. Floral tissues are devoid of idioblasts, crystals, tannins, or other diagnostic histologic features.

Intermixed trichomes of various morphologies are found on the pedicel, receptacle, and both outer and inner surfaces of perianth members (Norman, 1994). Stamen filaments are also pubescent (Fig. 1E). The corolla tube is covered externally by numerous short hairs whereas the inner surface of the upper tube contains a mixture of long and short trichomes that fill the space of the tube.

The epipetalous androecium consists of three or typically four equal, included stamens. An additional antherless staminode is adnate to the lower corolla tube in a posterior position, just above the narrow basal segment of the tube (Fig. 1B). In some flowers the staminode is only a rudimentary protrusion or is essentially absent. Stamens are borne higher up on the corolla tube, with each stamen positioned in a sepal plane. Stamens are differentiated into a long cylindrical filament that is curved and narrowed at the apex, and a small versatile anther. Thecae are divergent at the base and united distally (Fig. 1E). The mature anther wall is composed of an indistinct epidermal layer and a conspicuous endothecium with thin fibrous thickenings that extend into the cells of the connective. Before pollen is shed, the partition between the two locules of the same theca breaks down, leaving a single chamber. The two thecae also become confluent distally to form an introrse, hippocrepiform (horseshoe-shaped) type of dehiscence (Fig. 1E).

The bi-loculate gynoecium is composed of a pair of glabrous carpels that are completely fused along their abaxial surfaces throughout their length. The ovary is superior for most of its length although at the base the locules are slightly embedded in the receptacle. The ovary is surrounded by a very prominent cup-like, distally lobed disk that is partially united at the base with the ovary (Fig. 1A, 2A). The nectariferous tissue consists of cells with densely staining cytoplasm and conspicuous nuclei.



itudinal section of flower; transverse section of flower; specialized surface cells; vascular bundle; STD = staminode (B-D).  
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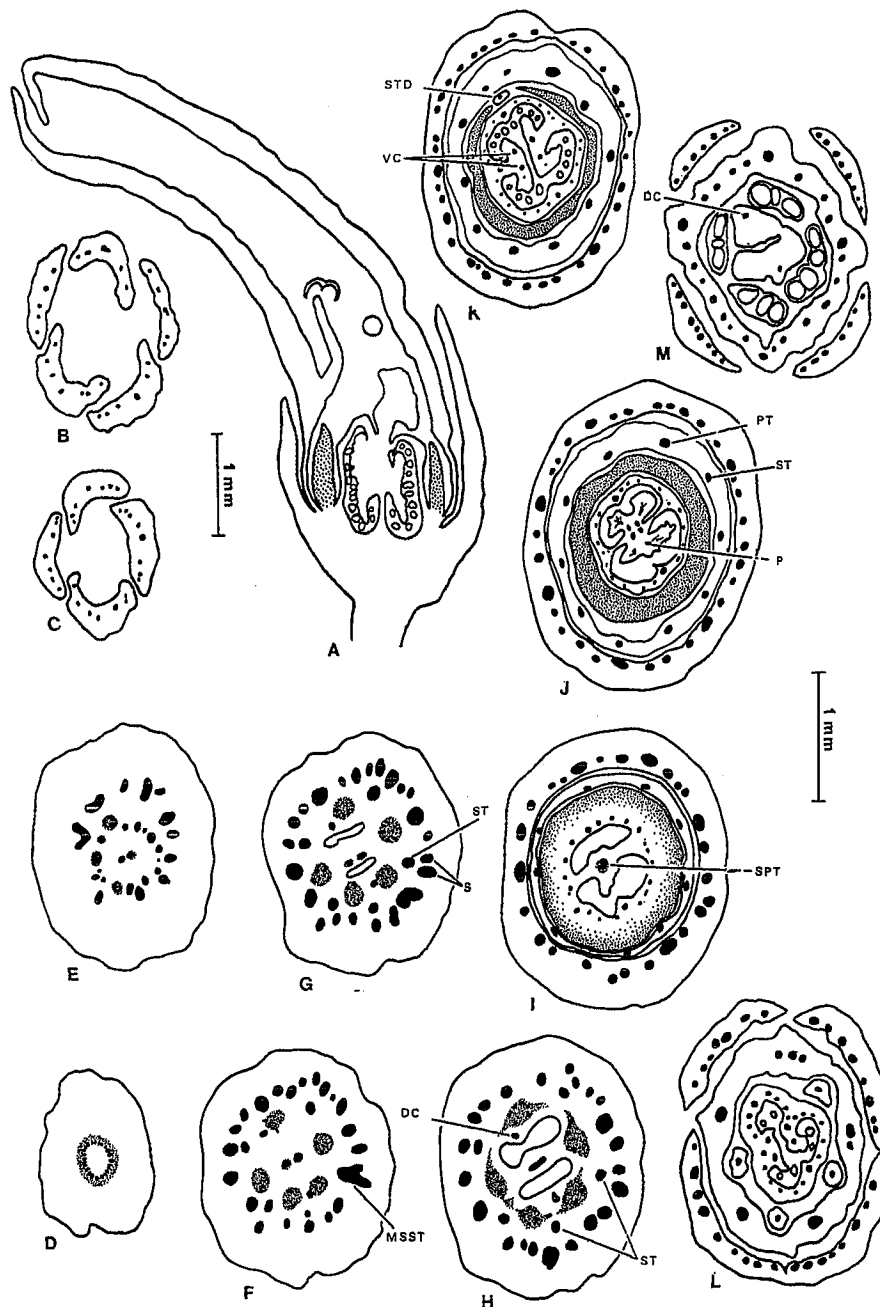


Fig. 2. Floral morphology and anatomy of *Sanango*, camera lucida drawings. - A, longitudinal section of flower; B, C, transverse sections through upper corolla tube showing aestivation patterns of distal lobes; D-M, serial transverse sections of the flower from pedicel (D) to level of stigma (M), showing major vascular patterns. - DC = dorsal carpellary bundle; MSST = median sepal stamen bundle; P = placental bundle; PT = petal bundle; SPT = septal bundle; ST = stamen bundle; STD = staminode; VC = ventral carpellary bundle; blackened areas = vascular tissue; stippled areas = nectariferous tissue. - Bar = 1 mm.

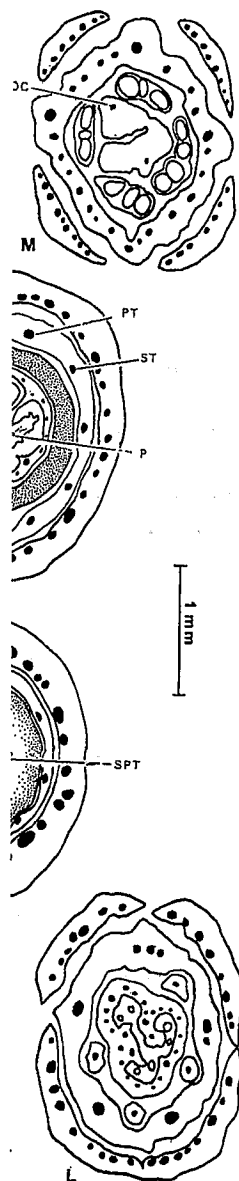
In the lower half of the bilocular condition (Fig. 2D-F) the unilocular ovarian cavity is complete. A small ridge on the dorsal wall of each locule at the level of the stigma shows that each locule is formed by the fusion of four or five layers of thickened epidermis, four or five or three layers of thickened lignified endocarp in the lower half of the ovary at the level of the stigma. In the mature flowers the style has a short canal but is not transmitting tissue. The stigma is stigmatic surface (Fig. 2M).

Placentation is axile, being at the middle portion of the septum. The placental bundle becomes large, irregular in outline, numerous small, unitegmic (Bunting & Duke (1961)).

Examination of serial sections of *Sanango* shows the arrangement of the floral parts to be arranged in a closed cylinder. Approximately between 12-15 degrees they diverge (Fig. 2D-F). Occasionally a trace of adjacent sepals associated with three stamens upon leaving the center of the ovary composed of a high number of calyx (Fig. 2G-I). Each stamen has an equal diameter that extends from the lower tube and into the upper part of the calyx tube and is associated by a prominent fibrous bundle.

Within a short distance the stamens diverge tangentially to give rise to a tube approximately the same diameter as the stamens to form an intercalary tube that continues as the sepal corolla tube to the level of the stigma. The divided bundle that extends from the staminodium receives its nutrients through the corolla tube and the staminal bundle typical of the stamens.

Just above the level of the stigma the tissue resolves itself into a defined, circular plexus



drawings. - A, longitudinal corolla tube showing of the flower from pedicel - DC = dorsal carpellary ; PT = petal bundle; SPT = ventral carpellary bundle; ue. - Bar = 1 mm.

In the lower half the ovary is divided by a complete septum that results in a bilocular condition (Fig. 2H, I). At mid-level the septum is incomplete, resulting in a unilocular ovarian cavity (Fig. 1C). At uppermost levels the septum may again be complete. A small ridge or incomplete septum projects internally from the median dorsal wall of each locule. Transverse sections of the ovary through extreme distal levels show that each locule may become subdivided as a result of a complete partition forming in the median carpel plane. The ovary wall is composed of an epidermis, four or five layers of parenchymatous mesophyll and an inner zone of two or three layers of thin-walled, transversely oriented cells that differentiate into a lignified endocarp in the fruit. A single short, thick style arises from a depression at the top of the ovary and widens into a large, grooved or bilobed, capitate stigma. In mature flowers the style typically appears curved to one side (Fig. 1A). Styles may have a short canal but are mostly solid with a central core of loosely arranged transmitting tissue. Large bottle-shaped papillae with elongate necks compose the stigmatic surface (Fig. 1D).

Placentation is axile at lower levels, with the intruding, bilobed placentas originating at the middle portion and on either side of the complete septum (Fig. 1B). When the septum becomes incomplete placentation is parietal. At maturity the placentas are large, irregular in outline, with ascending and descending portions (Fig. 2A). The numerous small, unitegmic ovules are anatropous, not orthotropous as reported by Bunting & Duke (1961), and are borne on all surfaces of the placenta.

Examination of serial transverse sections shows the vascular system in the pedicel of *Sanango* to be arranged as many closely spaced bundles that form an essentially closed cylinder. Approaching the torus the stele expands and numerous traces (between 12-15) diverge outward from the central cylinder to supply the calyx (Fig. 2D-F). Occasionally a pair of traces diverge together from a common gap. Lateral traces of adjacent sepals are united at a lower level. Although each sepal is initially associated with three traces, the frequent branching of these bundles immediately upon leaving the central cylinder results in the formation of a rich vascular system composed of a high number of bundles that progress acropetally into the synsepalous calyx (Fig. 2G-I). Each individual sepal contains about eight veins of approximately equal diameter that extend in parallel and with little interconnection through the lower tube and into the free distal lobe. Sepal bundles are positioned on the inner side of the calyx tube and are individually completely surrounded throughout their length by a prominent fibrous sheath.

Within a short distance after their departure, each median sepal trace divides tangentially to give rise to a stamen trace (Fig. 2F, G). All stamen traces form at approximately the same level. Compound stamen-sepal median bundles, therefore, divide to form an internally positioned stamen trace and one or two outer portions that continue as sepal traces. Stamen traces subsequently proceed upward into the corolla tube to the level of androecial insertion. Each stamen receives a single undivided bundle that extends into the connective between anther lobes (Fig. 2I-K). The staminodium receives a branch from one of the five staminal traces proceeding through the corolla tube (Fig. 1B). Following departure of the branch, the vertical staminal bundle typically divides in two and continues up the tube.

Just above the level of departure of the calyx vasculature, the remaining vascular tissue resolves itself into a few loosely organized pith bundles and five large, ill-defined, circular plexuses, each one located in a petal radius (Fig. 2F-H). An individ-

ual plexus is composed of a few clusters of dispersed tracheary elements, phloem, and procambium. Higher up, each plexus breaks up to furnish a single trace to a petal, several tenuous carpellary wall bundles, and a rich, entirely phloic vascular supply to the disk. Below the base of the carpel locules an undivided dorsal, or median, carpellary bundle arises from each of the two vascular plexuses lying approximately in the two median carpel planes (Fig. 2H). Occasionally a dorsal carpel-



Fig. 3. Leaf anatomy of *Sanango*. - A, transverse section of lamina showing conspicuous hypodermis and single-layered palisade mesophyll; B, paradermal section of abaxial epidermis showing cells with straight anticlinal walls and grouped stomata. - Bar = 0.1 mm.

lary bundle originates from the midrib and contains a single bundle sheath. The lateral bundles remain undivided until they separate into three and four (2L, M).

The gynoeceum is vascularized by numerous small, laterally positioned vascular bundles. In the midrib, discrete bundles are evident. A single median bundle separates into a pair of bundles soon after the midrib. Each bundle divides repeatedly at mid-places to form a series of ovules. The dorsal bundle is prolonged through the stem.

*Leaf anatomy.* - Leaf anatomy shows a distinct arrangement. The bases of the leaves are glabrous, cellular, unbranched trichomes. The mature leaves are glabrous on both surfaces. Adaxial and abaxial surfaces are covered by a layer of approximately equal thickness of curved, non-pitted anticlinal cells. The veins are curved. Stomata are located in groups of 2 or more. Guard cells are level with the surrounding cells. Guard cells are 18.5  $\mu$ m in length, base to base.

Lamina construction of the leaf shows a distinct arrangement of adaxial hypodermis, palisade mesophyll, and spongy mesophyll. The major vein is located in the midrib. The major vein shows a distinct extension to the level of the spongy mesophyll surface. The cortex of the leaf is composed of chlorenchyma and parenchyma. The cortex is parenchymatous element in the region on either side of the midrib. The dorsal bundles that are located in the midrib region contain small abaxially positioned bundles. All vascular tissue in the leaf is located in the midrib region. Small, clustered crystals are present in the petiole.

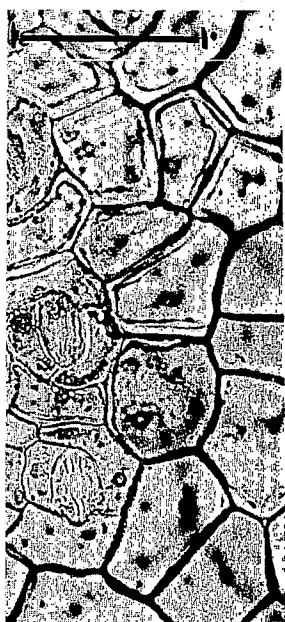
heavy elements, phloem, furnish a single trace to a, entirely phloic vascular an undivided dorsal, or vascular plexuses lying ap- occasionally a dorsal carpel-

lary bundle originates from the pith bundles. At its point of insertion, the corolla tube contains a single bundle per petal alternating with the individual stamen traces. Petal bundles remain undivided to a level below the base of the distal lobes; here each separates into three and subsequently more veins that continue to the petal tip (Fig. 2L, M).

The gynoecium is vascularized by a single unbranched dorsal bundle per carpel, numerous small, lateral ovarian wall bundles (10-12 per carpel), and a centrally positioned vascular column in the septum. At the level of locule initiation two discrete bundles are evident within the septum (Fig. 2G). These strands soon merge into a single median bundle (Fig. 2H, I). Near the middle of the septum the central strand separates into a pair of veins situated in the plane of the septum. Each of these bundles soon divides into two marginal or ventral bundles. A pair of placental bundles, one on either side, branches from each ventral strand, and then divides repeatedly at mid-placenta (Fig. 1B, 2J-L). No vascular tissue is detectable within the ovules. The dorsal bundle of each carpel recurves to the style base and is then prolonged through the style (Fig. 2M).

*Leaf anatomy.* - Leaves are simple, petiolate, exstipulate and decussate in arrangement. The bases of the opposite leaves are connate (Fig. 4M). Uniseriate, multicellular, unbranched trichomes are present on both surfaces of young leaves, but mature leaves are glabrous. A very thin cuticle covers both adaxial and abaxial surfaces. Adaxial and abaxial epidermal cells are small and moderately thick-walled, of approximately equal size, 4-7-sided in surface view, with straight or slightly curved, non-pitted anticlinal walls. Epidermal cells are larger and more elongate over the veins. Stomata are confined to the abaxial surface, with a tendency to be clustered into groups of 2 or more (Fig. 3B). Mature stomata conform to the anisocytic type. Guard cells are level with the unspecialized epidermal cells. Guard cell pairs average 18.5  $\mu\text{m}$  in length, based upon twenty measurements.

Lamina construction is bifacial. The mesophyll is composed of one or two layers of adaxial hypodermis, generally a single layer of short palisade cells, and a prominent loosely arranged spongy region (Fig. 3A). The hypodermal cells are enlarged and thin-walled. The hypodermis is consistently two cells thick in the vicinity of the midrib. The major veins of the lamina are surrounded by a fibrous sheath of moderately thick-walled cells that extends above the vein as an adaxial vertical sheath extension to the level of the hypodermis. Minor veins are accompanied by a weakly developed parenchymatous sheath. The region of the midrib has a raised dorsal surface. The cortex of the midrib is composed of 3-4 layers of subdermal collenchyma and parenchyma near the vascular tissue. The pith consists of thicker walled parenchymatous elements. Palisade mesophyll protrudes into the adaxial cortical region on either side of the vascular system. The midrib is supplied by a more or less closed, dorsally flattened vascular cylinder and a pair of superimposed, median dorsal bundles that are accompanied on either side by additional lateral bundles. All of the dorsal bundles have an inverted arrangement of the xylem and phloem. Four small abaxially positioned cortical bundles extend the length of the midrib (Fig. 4L). All vascular tissue in the midrib is enclosed by a fibrous sheath. Parenchyma cells of the midrib region contain starch and crystals in the form of small needles and prisms. Small, clustered crystals are also occasionally present. A similar crystal composition is present in the petiole.



mina showing conspicuous abaxial epidermal section of abaxial epidermal cells. - Bar = 0.1 mm.



The vascular tissue in the petiole forms an inrolled arc proximally, that is accompanied by many scattered, inverted adaxial bundles (Fig. 4J). At more distal levels a closed cylinder is present and the dorsal bundles become organized into a pair of median bundles with, on either side, two or three major lateral bundles (Fig. 4K).

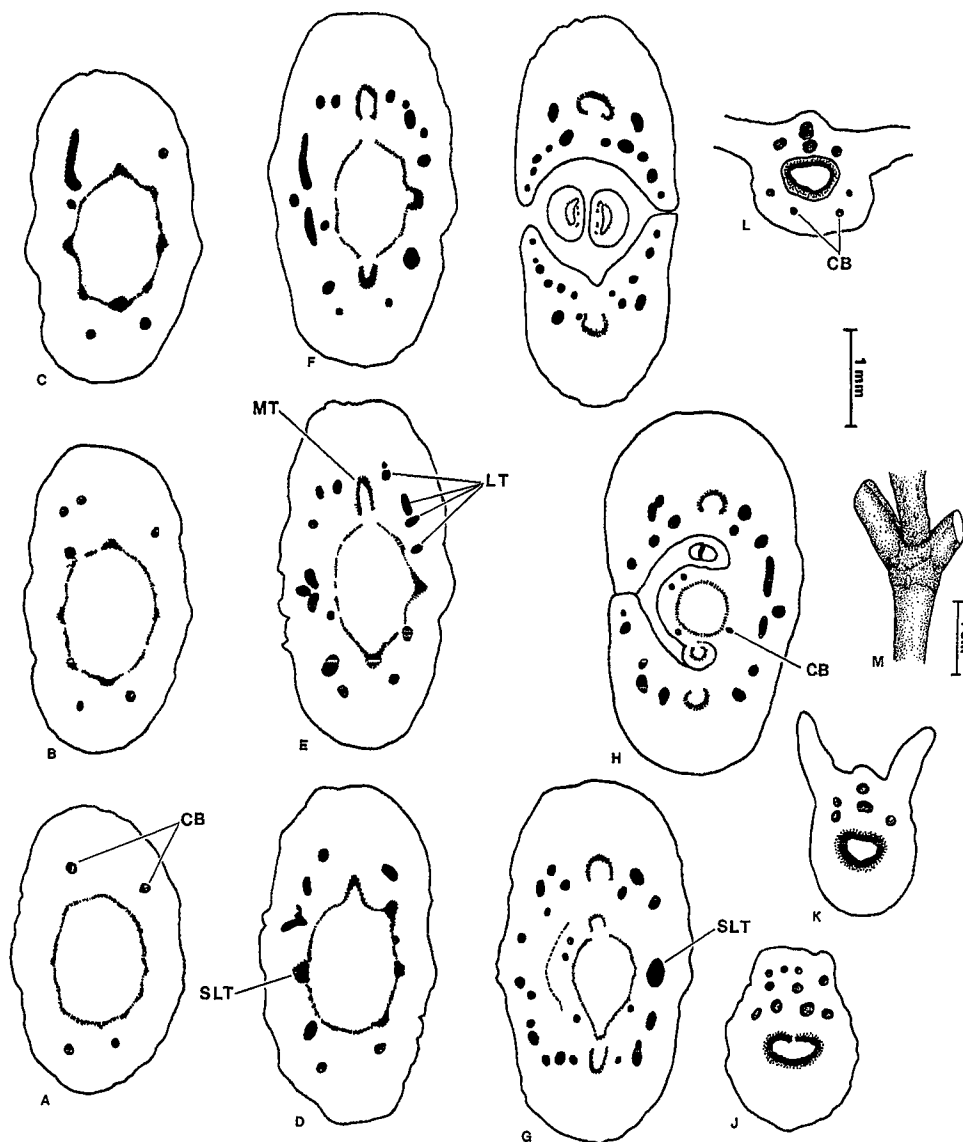


Fig. 4. Nodal and petiolar anatomy of *Sanango*, camera lucida drawings. - A-I, serial transverse sections of the node from a level below the node (A) to a level above the node (I); J, transverse section through the proximal region of the petiole. K, transverse section through the distal region of the petiole. L, transverse section through the midrib of the lamina. M, external morphology of node from young stem, showing connate leaf bases. - CB = cortical bundle; LT = lateral leaf trace; MT = median leaf trace; SLT = split-lateral trace. - Bar = 1 mm (A-L) or 1 cm (M).

Cortical bundles are accompanied by fibres.

*Young stem and nodal stems*, but older axes are thin cuticle. The cortex is thick walls and an inner material, scattered paren into brachysclereids in needles and prisms are essentially complete cylindrical continuous ring of per Small cortical vascular Bark is well-developed. are rectangular in transv without sclerenchyma in

Nodal anatomy is mu of split-lateral traces, i.e side of the node arise a midway between the two are each supplied by a traces, and a pair of lat traces. All traces are as traces supplying each le median trace and first p with one of the laterals distally, the second pair along with the split-lateral same level. Both pairs o As the lateral traces ext extended cortical stem l split-lateral traces trifur strands redivide and me shaped and eventually f nished by numerous dorsa shed lateral traces. At ea of the cauline stele (Fig continue upward through

*Wood anatomy.* - G some rounded, and occ multiples of 2-3 (14 %) square millimetre is 50 ( with an average of 70  $\mu$  elements have predomi although a very few ve perforations are compos of variable thickness, an vestigial bars that do no

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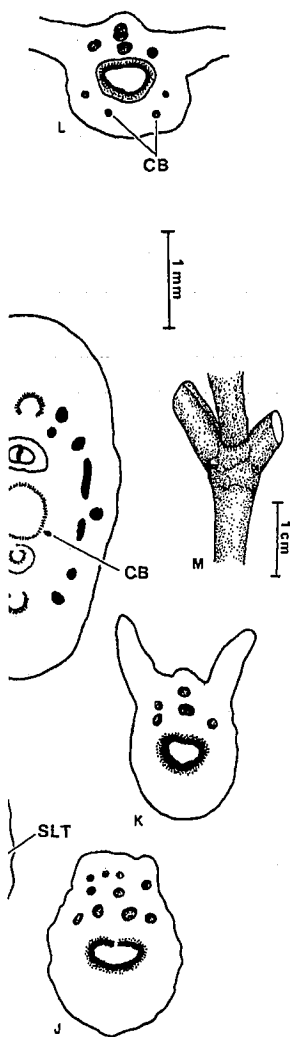


Fig. 4. – A-I, serial trans-  
verse sections of stem at  
level above the node (I);  
J, transverse section through  
midrib of the lamina. M,  
longitudinal section through  
leaf bases. – CB = cortical  
split-lateral trace. – Bar =

Cortical bundles are absent in the petiole. Petiolar vascular strands are not accompa-  
nied by fibres.

*Young stem and node.* – Multicellular unbranched hairs are abundant on young stems, but older axes are glabrous. Epidermal cells are rectangular and covered by a thin cuticle. The cortex is differentiated into an outer region of cells with moderately thick walls and an inner zone of cells with thinner walls. At the nodal region of older material, scattered parenchyma cells become thick-walled, lignified, and transformed into brachysclereids in the cortical region. Starch and crystals in the form of small needles and prisms are present in cortical parenchyma. The vascular tissue forms an essentially complete cylinder that in older stems is capped by a broad, more or less continuous ring of perivascular sclerenchyma in the form of fibres and sclereids. Small cortical vascular bundles extend the length of the internodal region (Fig. 4A). Bark is well-developed. The periderm is composed of thin-walled empty cells that are rectangular in transverse section. The secondary phloem is well-developed and is without sclerenchyma in the functional region.

Nodal anatomy is multilacunar, multi-trace, and is characterized by the presence of split-lateral traces, i.e., the outermost lateral traces of adjacent leaves on the same side of the node arise as a united bundle from a single common gap at a position midway between the two leaf bases (Fig. 4A-I). The opposite leaves at the same node are each supplied by a median bundle, two pairs of independently derived lateral traces, and a pair of lateral traces derived from the subdivision of the split-lateral traces. All traces are associated with a well-defined gap in the cauline stele. The traces supplying each leaf arise at different levels and are quite variable in size. The median trace and first pair of lateral traces arise below the level of leaf attachment, with one of the laterals typically forming at a higher level than the other. Somewhat distally, the second pair of independently derived and rather small lateral traces arises along with the split-laterals. The two split-lateral traces usually do not originate at the same level. Both pairs of lateral traces subdivide immediately upon leaving the stele. As the lateral traces extend to the leaf base, branch bundles join with the vertically extended cortical stem bundles that originated at the node immediately below. The split-lateral traces trifurcate soon after entering the cortical region. The resulting strands redivide and move to opposite leaves. The median leaf trace becomes C-shaped and eventually forms a closed cylinder in the leaf base where it is accompanied by numerous dorsally positioned bundles that are derived from the highly branched lateral traces. At each nodal level two pairs of small bundles arise on either side of the cauline stele (Fig. 4G, H). These bundles may subsequently branch as they continue upward through the internode as stem cortical bundles.

*Wood anatomy.* – Growth rings are absent. Pores are angular in outline, with some rounded, and occur mostly in a solitary position (80 %) as well as radial multiples of 2-3 (14 %) or small clusters of 3-5 (6 %); average number of vessels per square millimetre is 50 (Fig. 5A). Tangential pore diameter ranges from 39 to 80  $\mu$ m, with an average of 70  $\mu$ m. Vessel walls are thin, with a diameter of c. 2  $\mu$ m. Vessel elements have predominantly scalariform perforations in highly inclined end walls, although a very few vessel elements only possess simple perforations. Scalariform perforations are composed of up to 20 bars, usually 3-10. Bars are unevenly spaced, of variable thickness, and typically show bizarre branching patterns or are reduced to vestigial bars that do not extend across the perforation (Fig. 5D). Ligules are promi-

ment on the vessel elements. Intervascular pitting is alternate and composed of pits that are rounded in outline, with a diameter of 2.5-3.0  $\mu\text{m}$ . Vessel elements range in length from 216 to 887  $\mu\text{m}$ , with a mean of 577  $\mu\text{m}$ .

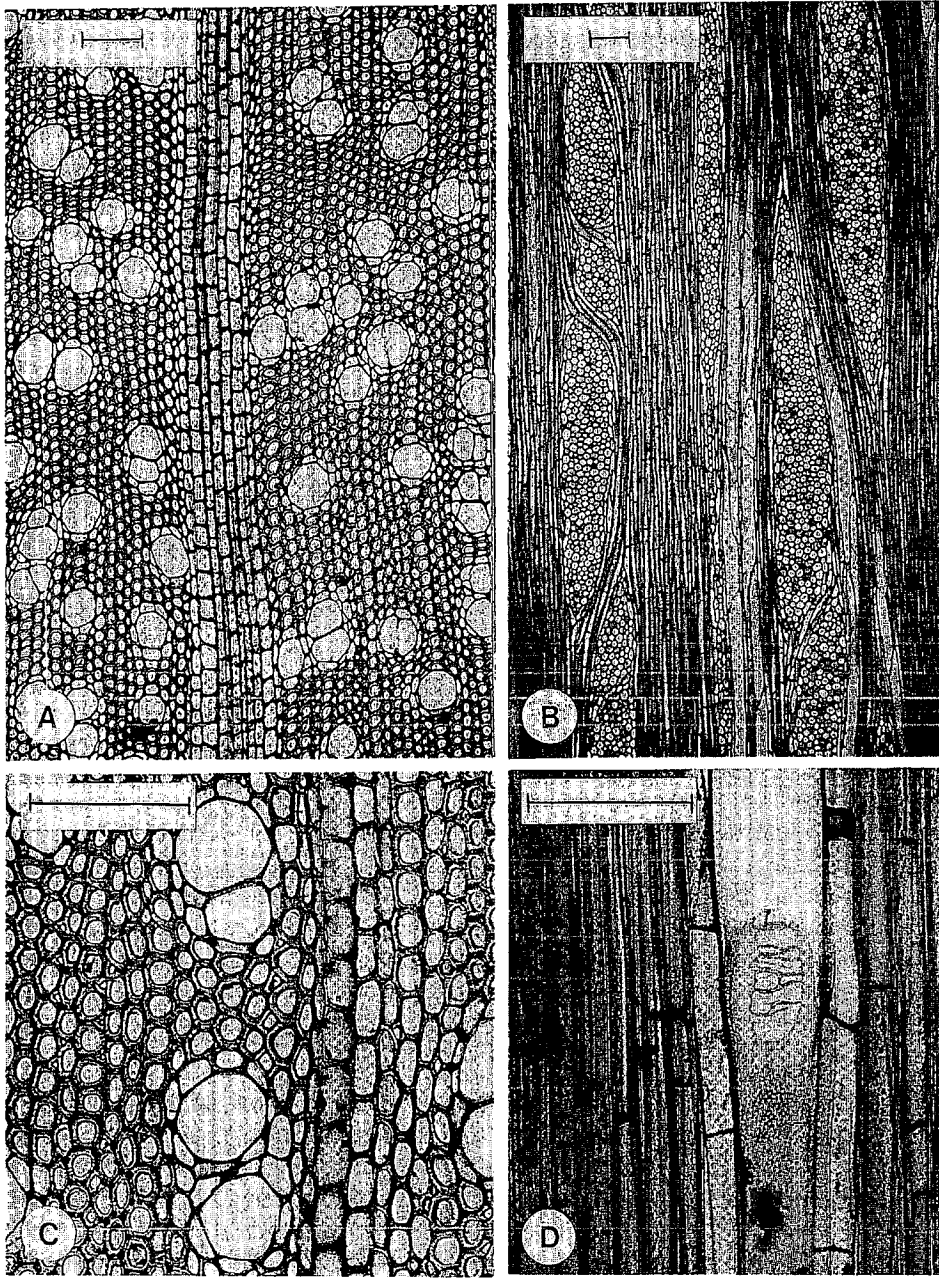


Fig. 5. Wood anatomy of *Sanango*. - A, transverse section, showing solitary pores and radial multiples and small clusters; B, tangential section, showing exclusively large multi-seriate rays; C, transverse section, showing vasicentric distribution of axial parenchyma; D, longitudinal section, illustrating malformed scalariform perforation plate. - Bar = 0.1 mm.

The ground tissue is pits having very reduce three rows. Elements c element length ranges fr

Rays are nearly excl and 10 cells and incom are narrower, with some body ray cells procumb extensions. Ray cells h by very tall multiseriate evident.

Axial parenchyma is sheaths around vessels a No mineral deposits v

#### Discussion

*Evidence from floral clusions from floral ana and detailed observatio parisons, therefore, are provides no conclusive though there is no unus clearly serves to relate t ment close links with th*

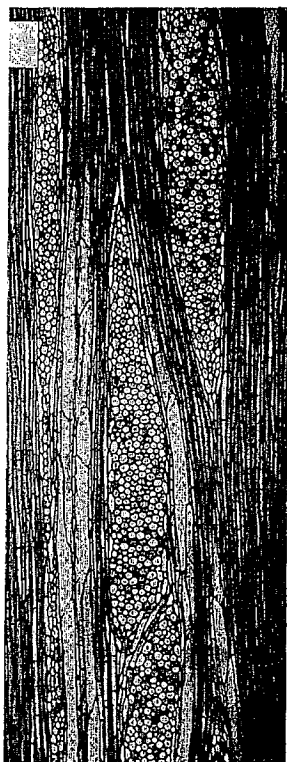
Features common to morphology, a nectariferou functional stamens equ: staminodium.

Vascular patterns of anatomically show few venation are: numerous each bundle surround median sepal traces for single petal trace, sever: disk vasculature; a gyn many independently de derived from a single c strands at the level of th vascularized by dorsal b

In the hypogynous l various floral cycles ar: *Mitreola* L., on the oth stamens, and carpels ar the upper part of the ov (1972).

The many gross flor *phulariaceae* include: a

ite and composed of pits  
Vessel elements range in



showing solitary pores and  
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tion plate. – Bar = 0.1 mm.

The ground tissue is composed of thin-walled, septate imperforate elements with pits having very reduced borders. Pits are numerous and often distributed in two or three rows. Elements contain multiple septations (Fig. 5D). Imperforate tracheary element length ranges from 557 to 1498  $\mu\text{m}$ , with an average of 908  $\mu\text{m}$ .

Rays are nearly exclusively multiseriate, very wide, ranging in width between 4 and 10 cells and incompletely surrounded by sheath cells (Fig. 5B). A very few rays are narrower, with some only one cell wide. Rays are weakly heterocellular, with the body ray cells procumbent or square, and erect cells that may form short terminal ray extensions. Ray cells have extensively pitted walls. Young stems are characterized by very tall multiseriate rays. In mature wood the breakup of the large primary rays is evident.

Axial parenchyma is vasicentric, with complete or incomplete, one cell wide sheaths around vessels and vessel groups (Fig. 5C).

No mineral deposits were observed in the secondary xylem.

#### Discussion

*Evidence from floral anatomy.* – In discussing the relationships of *Sanango*, conclusions from floral anatomy are preliminary since comparative data are incomplete and detailed observations on critically important genera are largely lacking. Comparisons, therefore, are necessarily made between only a few taxa. Floral anatomy provides no conclusive information to clarify the nearest relatives of *Sanango*. Although there is no unusual or diagnostic floral anatomical feature, or features, that clearly serves to relate the genus with a particular taxon, present observations document close links with the *Scrophulariales*.

Features common to flowers of *Loganiaceae* but not *Sanango* include: actinomorphy, a nectariferous disk that is poorly developed or more typically absent, functional stamens equal in number to corolla lobes, and the absence of a reduced staminodium.

Vascular patterns of the few species of *Loganiaceae* that have been examined anatomically show few similarities to *Sanango*. Major aspects of *Sanango* floral venation are: numerous calyx tube bundles of approximately equal diameter, with each bundle surrounded by a fibrous sheath; stamen vascular traces united with median sepal traces for a short distance; an association at their point of origin of a single petal trace, several carpellary wall bundles, and a portion of the entirely phloic disk vasculature; a gynoeceum supplied by one median or dorsal bundle per carpel, many independently derived lateral wall bundles, and a placental vascular supply derived from a single centrally positioned septal bundle; distinct marginal or ventral strands at the level of the placenta; an absence of ovular vascular tissue; and the style vascularized by dorsal bundles only.

In the hypogynous loganiaceous taxon *Strychnos nux-vomica* L., traces to the various floral cycles arise essentially independently. In the partially epigynous genus *Mitreola* L., on the other hand, the floral vascular traces supplying sepals, petals, stamens, and carpels are all united to a level about half the height of the ovary, and the upper part of the ovary and style is devoid of vasculature (Tiagi & Kshetrapal, 1972).

The many gross floral morphological resemblances between *Sanango* and *Scrophulariaceae* include: a four or five-lobed, sympetalous corolla; zygomorphy; a bi-

carpellate gynoecium with axile to parietal placentation and a single terminal style with a capitate, two-lobed stigma; nectariferous tissue at the base of or surrounding the ovary; multicellular hairs including glandular forms with sculptured walls; and, significantly, an epipetalous androecium of generally four or fewer stamens often accompanied by a single adaxial rudimentary staminodium.

Most *Scrophulariaceae* differ from *Sanango* by having a more strongly zygomorphic, often two-lipped corolla and an androecium that is sometimes didynamous. Schrock & Palser (1967) interpreted the *Scrophulariaceae* as showing a reduction series in the androecium, from a condition of five fertile stamens, to four stamens with a fifth well-developed staminode, to four and finally two fertile stamens with the staminode, when it still occurs, represented by a rudimentary non-vascularized protrusion. Flowers of *Sanango* represent an intermediate level of specialization in this regard. No members of the *Scrophulariaceae* have a nectary that is comparable to the one in *Sanango*.

Buddlejaceous flowers diverge from *Sanango* by being mostly actinomorphic; frequently having a combination of stellate and glandular hairs; a mostly tetramerous corolla; and stamens equal in number to the corolla lobes and all fertile. Bunting & Duke (1961) were of the opinion that although *Sanango* has no close relatives, it most closely approximates the genera *Buddleja* L., *Nuxia* Lam., and *Peltanthera* Benth. Particular emphasis was placed upon the distal confluence of anther lobes (*Nuxia*, *Peltanthera*) prior to dehiscence. The corolla of *Peltanthera* is valvate. Examination of histological preparations of *Buddleja* flowers reveal no evidence of nectariferous tissue. *Peltanthera* and *Nuxia* differ from *Sanango* in the following characters: presence of branched and stellate hairs, respectively; long, exserted stamens; long, exserted styles; and the absence of a well-developed disk, although *Peltanthera* appears to have a small disk around the ovary. Nothing is known of the floral anatomy of the latter two genera.

The floral vascularization of only a few *Scrophulariaceae* and *Buddlejaceae* has been described in detail. Armstrong (1985) noted that the calyx vascularization of *Scrophulariaceae* tends to be composed of a large number of similar-sized bundles, such that no larger median calyx lobe bundles are identifiable. A somewhat similar condition is present in *Sanango*, with the median sepal bundle only slightly wider than the laterals. Among *Scrophulariaceae* stamen traces either arise independently from sepal traces, or, as in *Sanango*, androecial traces form by the radial bifurcation of common calyx-androecial bundles (Armstrong, 1985).

Examination of serial transverse sections of flowers of cultivated *Buddleja davidii* Franch., prepared especially for this study, showed that the floral vascular pattern agrees with that of *Sanango* in that the median sepal traces arise conjointly with the staminal traces. Two or three small marginal sepal traces may also be fused with median petal traces. The observations confirm the report of Tiagi & Kshetrapal (1972). Unlike *Sanango*, the calyx tube of *Buddleja* is supplied by four major median sepal bundles and only a few weak laterals. It is of interest that in some *Gesneriaceae* vascular traces to the stamens are also united with sepal traces for part of their passage (Stern & al., 1969; Wilson, 1974). This is noteworthy in view of the fact that some gesneriads have a well-developed disk and a rudimentary staminode accompanying four functional stamens. However, those *Gesneriaceae* with superior ovaries often have a reduced, bi-staminate androecium. In *Sanango* the staminode receives a branch from one of the five staminal bundles in the corolla tube. The presence of a

vascular bundle associated with the stamens is a distinctive feature of members of *Scrophulariaceae*. The floral anatomy of *Sanango* differs from that of *Scrophulariaceae* in that the style appears bilocular with axile placentation in the locules. The styles in *Sanango*, a feature of interest that in the style is longer than the accompanying stamens, are specialized, enlarged cells at the base of the locules. This condition is not typical in the *Scrophulariaceae*. Furthermore, the condition in *Sanango*, is not typical in the single undivided placental apex of the ovary (Armstrong, 1985). This is more usual condition in the *Scrophulariaceae*.

Tiagi & Kshetrapal (1972) noted that members of the *Scrophulariaceae* and *Buddlejaceae* possess two lateral bundles of vascular tissue (the median bundle is always associated with the style). The carpels in the *Scrophulariaceae* always contain two median bundles (the lateral bundles are always associated with the style). Furthermore, the bicarpellary ovary containing two median bundles and a pair of bundles and a pair of bundles and a pair of bundles (ventral) bundle of the dorsals and are associated with the *Scrophulariaceae* ovaries possess four median bundles (a pair of bundles opposing the wall bundles of *Buddleja* at the base of the ovary). This is apparently specialized, a pair of bundles and a pair of bundles. Among *Scrophulariaceae* the ventral carpellary bundle is associated with the lateral bundles (Hartl, 1956; Schrock & Palser, 1967). *Scrophulariaceae* show agreement in the lateral bundles, and in vascular bundles, and in vascular bundles, and in vascular bundles.

*Evidence from vegetative characters* among the species of *Sanango* from the standpoint of vegetative characters is of interest. Some *Gesneriaceae*. The vascular traces, coupled with the distinctive features of the Multilacunar nodes that are associated with the vascular bundles among dicotyledons, especially the split-lateral traces (How

and a single terminal style at the base of or surrounding the base of or surrounding with sculptured walls; and, four or fewer stamens often present.

*Sanango* is more strongly zygomorphic than *Buddleja* and sometimes didynamous. *Sanango* is similar to *Buddleja* as showing a reduction of stamens, to four stamens in *Sanango* and only two fertile stamens with lignified non-vascularized filaments in *Buddleja*. The level of specialization in *Sanango* in the nectary that is comparable

to *Buddleja* is mostly actinomorphic; *Sanango* has long, unilobed hairs; a mostly tetra-lobed corolla lobes and all fertile. *Sanango* has no close relatives like *Buddleja*, *Nuxia* Lam., and *Peltanthera* in the distal confluence of the corolla of *Peltanthera* is similar to *Buddleja* flowers reveal no evidence to differ from *Sanango* in the hairs, respectively; long, of a well-developed disk, and the ovary. Nothing is

known about the vascularization of the calyx in *Buddleja* and *Sanango*. A somewhat similar bundle only slightly wider than the radial bifurcation

in *Buddleja davidii* the floral vascular pattern arises conjointly with the stamens as may also be fused with the style. The pattern of *Sanango* is similar to that of *Buddleja* and *Gesneriaceae* in some *Gesneriaceae* in the presence of radial traces for part of their length in view of the fact that the primary staminode accompanies the ovary in *Gesneriaceae* with superior ovaries and the staminode receives a single tube. The presence of a

vascular bundle associated with the staminodium is found in many, but not all, members of *Scrophulariaceae* (Armstrong, 1985). Gynoecial morphology and vascular anatomy of *Sanango* generally conform to the basic plan in *Loganiaceae*, *Buddlejaceae*, *Scrophulariaceae* and *Gesneriaceae* (Tiagi & Kshetrapal, 1972). The ovary appears bilocular with axile placentation in the lower half, and unilocular with parietal placentation in the middle position. Of potential significance is the curvature of styles in *Sanango*, a feature that occurs in at least some *Scrophulariaceae*. It is of interest that in the style of *Sanango* the dorsal bundle on the elongated side is longer than the accompanying bundle. In both groups the stigmatic surface is composed of specialized, enlarged cells. However, the ovary in *Sanango* is partially inferior, with the base of the locules slightly sunken in the receptacle. Such a situation is unknown in the *Scrophulariaceae*. It is known, however, in *Mitreola* L. of the *Loganiaceae*. Furthermore, the condition of two placental ridges per locule at mid-level, as occurs in *Sanango*, is not typical for *Scrophulariaceae*. Most *Scrophulariaceae* have a single undivided placental lobe per locule that simply divides by a slit toward the apex of the ovary (Armstrong, pers. comm.). Two placental ridges per locule are a more usual condition in members of the *Gesneriaceae* (and *Bignoniaceae*).

Tiagi & Kshetrapal (1972) emphasized that bicarpellate gynoecia of the *Loganiaceae* and *Buddlejaceae* (treated by them as subfamilies: *Loganioideae* and *Buddleioideae*) possess two laterally positioned carpels whereas the gynoecium of the *Scrophulariaceae* always consists of two median carpels (assuming tetracarpellate ancestry). The carpels in *Sanango* are median, thus resembling the *Scrophulariaceae*. Furthermore, the bicarpellate scrophulariaceous gynoecium resembles *Sanango* by containing two median (dorsal) bundles, variously fused and centrally positioned marginal (ventral) bundles, and a number of smaller strands that arise independently of the dorsals and are located around the ovary wall. This pattern clearly distinguishes the *Scrophulariaceae* (and *Sanango*) from the related *Bignoniaceae*, whose ovaries possess four major outer wall bundles, two median or dorsal strands and a pair of bundles opposing the septum (Armstrong, 1985). The tenuous lateral ovarian wall bundles of *Buddleja* diverge independently from the central vascular cylinder at the base of the ovary. The placental vascular supply in *Sanango* is derived from an apparently specialized, centrally positioned vascular column that enters the septum as a pair of bundles and separates into distinct ventral strands at the placental level. Among *Scrophulariaceae* there is considerable variation in the degree of union of the ventral carpellary bundles within the septum even at the generic and specific level (Hartl, 1956; Schrock & Palser, 1967). *Sanango*, *Buddleja* and some *Scrophulariaceae* show agreement in their styles being supplied exclusively from dorsal carpellary bundles, and in vascular tissue not entering the ovules.

*Evidence from vegetative anatomy.* - The distribution of selected vegetative character states among the suggested allies of *Sanango* is presented in Table 1. From the standpoint of vegetative anatomy, *Sanango* shows the best structural agreement with some *Gesneriaceae*. The presence of a multilacunar nodal anatomy with split-lateral traces, coupled with the occurrence of cortical vascular bundles in the stem, are distinctive features of *Sanango* that assume particular phylogenetic importance. Multilacunar nodes that are associated with decussate phyllotaxy are very uncommon among dicotyledons, especially when the vascular pattern includes the presence of split-lateral traces (Howard, 1970). In *Sanango* these features are correlated with the

Table 1. Comparison of selected vegetative character states of *Sanango* and related families. - Character states are given as: - = absent, + = present in most representatives, (+) = or present in a few representatives only. - Log = *Loganiaceae*, Bud = *Buddlejaceae*, Scr = *Scrophulariaceae*, Ges = *Gesneriaceae*.

<i>Sanango</i>	Log	Bud	Scr	Ges
Leaves simple	+	+	+	+
Leaves opposite	+	+	(+)	+
Connate leaf bases	-	+	+	+
Unbranched hairs	+	-	(+)	+
Anisocytic stomata	+	-	(+)	+
Stomata in groups	-	-	-	+
Cortical bundles in stem	(+)	-	-	(+)
Multilacunar nodes	(+)	-	-	+
Split-lateral traces	-	-	-	+
Vascular trace of petiole forms ring with adaxial bundles	-	-	-	(+)
Vessels solitary, radial multiples, clusters	(+)	+	(+)	(+)
Perforations predominantly scalariform (few-barred)	(+)	-	-	(+)
Alternate intervacular pitting	+	+	+	+
Septate fibers	(+)	+	(+)	+
Rays multiseriate with very few uniseriates	-	-	(+)	(+)
Rays broad, weakly heterogeneous	(+)	-	(+)	+
Ray sheath cells	(+)	-	-	(+)
Axial parenchyma vasicentric	(+)	+	(+)	(+)
Crystals small needles, prisms, clusters	(+)	(+)	(+)	(+)

presence of connate leaf bases. Among the putative close relatives of *Sanango*, this specialized combination of anatomical features is known to occur in the *Gesneriaceae*. Trilacunar, three-trace nodes with split-lateral traces are the typical condition in the gesneriaceous tribe *Episcieae* (Wiehler, 1983) and are also seen among members of the subfamily *Cyrtandroideae* (Howard, 1970; Wiehler, 1983). Furthermore, the very uncommon, specialized pattern of multilacunar nodes with split-lateral bundles occasionally occurs in the gesneriaceous *Columnnea repens* Hanst. from Jamaica (Wiehler, 1983). In addition, cortical stem bundles are reported within the *Gesneriaceae* for a few neotropical species of *Rhynchoglossum* Blume (Metcalf & Chalk, 1950; Wiehler, 1983). Like other *Tubiflorae*, most *Gesneriaceae* and *Scrophulariaceae* have unilacunar nodes.

Multilacunar nodes (cortical stem bundles, & *graea* Thunb. (Hasselb.) is exceptional in the very different, unilacunar *cleista* R. Br. and *Potala* characters that are remarkable isolated position within family status (Mennega,

Foliar features that are a conspicuous adaxial bundle of short cells, and anisocytic stomata into stomatal clusters or glandular and non-glandular positioned on multicellular around the laminar venation within the neotrop *Sanango*, the petiole bundle vascular cylinder along petiole vascularization is

A comparison of the species of *Loganiaceae*, possession of scalariform few-barred perforations, however, as the tially absent, imperforate septate, and vessel elongating. It seems more likely frequent occurrence of juvenile feature. This character (Carlquist, 1969), *Asteraceae* (Carlquist & Hoekstra

Among *Loganiaceae* form intervacular pitting to the opinion that the scalariform perforations occasionally in the loganiaceae Forst., *Labordia* Gaudich. these genera is always a all have simple vessel elongating in the gesneriaceous species *Kohleria elegans* (Hemsl.) Fritsch, *K. schiedeana* (C. Wiehler (Wiehler, pers. com.)

The secondary xylem shows considerable diversity of distribution and the occa

les of *Sanango* and related  
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Log = *Loganiaceae*, Bud =  
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Multilacunar nodes (but not split-lateral traces), along with the tendency to form cortical stem bundles, are also encountered in the putative loganiaceous genus *Fagraea* Thunb. (Hasselberg, 1931). It must be emphasized, however, that this condition is exceptional in the *Loganiaceae*, since all other genera of this family possess a very different, unilacunar nodal structure with one to several traces. *Fagraea*, *Anthocleista* R. Br. and *Potalia* Aubl. (tribe *Potalieae*) also share several wood anatomical characters that are remarkable for the *Loganiaceae* and that would support their very isolated position within the family, even to the extent of elevating the *Potalieae* to family status (Mennega, 1980).

Foliar features that are common to many or all *Gesneriaceae* and *Sanango* include a conspicuous adaxial hypodermal layer, a uniseriate palisade mesophyll composed of short cells, and anisocytic mature stomata that show a tendency to be aggregated into stomatal clusters or island-like groups. Gesneriaceous leaves possess both glandular and non-glandular hairs and, like *Sanango*, the multicellular hairs are often positioned on multicellular pedestals. The usual absence of sheathing sclerenchyma around the laminar venation of *Gesneriaceae* contrasts with the condition in *Sanango*. Wiehler (1983) pointed out that the most distinctive pattern of petiole venation within the neotropical *Gesneriaceae* is found in the tribe *Gesnerieae*. As in *Sanango*, the petiole bundles of members of this tribe coalesce to form a closed vascular cylinder along with additional adaxially placed bundles. In both groups the petiole vascularization is without associated "pericyclic" sclerenchyma.

A comparison of the secondary xylem shows that *Sanango* differs from nearly all species of *Loganiaceae*, *Buddlejaceae*, *Scrophulariaceae*, and *Gesneriaceae* in the possession of scalariform perforation plates in the majority of vessel elements. The few-barred perforations of *Sanango* do not appear to represent indicators of primitiveness, however, as the wood is specialized in other respects. Tracheids are essentially absent, imperforate tracheary elements are medium to short in length and all septate, and vessel elements are of medium length with alternate intervascular pitting. It seems more likely that the scalariform perforation plates of *Sanango*, with the frequent occurrence of malformed or vestigial bars, result from the retention of a juvenile feature. This condition is also seen in the wood of some *Campanulaceae* (Carlquist, 1969), *Asteraceae* (Carlquist, 1960), and a very few species of *Gesneriaceae* (Carlquist & Hoekman, 1986).

Among *Loganiaceae* long, many-barred scalariform perforation plates and scalariform intervascular pitting occur only in *Desfontainia* Ruiz and Pav., lending support to the opinion that the latter genus should not be treated as member of that family. Scalariform perforations also occur regularly in *Retzia* Thunb. (*Retziaceae*) and occasionally in the loganiaceous genera *Spigelia* L. and *Geniostoma* J. R. Forst. & G. Forst., *Labordia* Gaudich., and *Mostuea* Didr., although the intervascular pitting in these genera is always alternate. *Buddlejaceae*, *Scrophulariaceae*, and *Gesneriaceae* all have simple vessel element perforations, although vestigial bars have been noted in the gesneriaceous species *Solenophora calycosa* Donn. Sm. (Stern & al., 1969), *Kohleria elegans* (Hemsl.) Loes. (Carlquist & Hoekman, 1986), *K. digitaliflora* Fritsch, *K. schiedeana* (Hemsl.) Hanst. and *Moussonia hirsutissima* (C. V. Morton) Wiehler (Wiehler, pers. comm.).

The secondary xylem of the fundamentally woody family *Loganiaceae* displays a considerable diversity of structure. Some genera are comparable to *Sanango* in vessel distribution and the occasional presence of septate fibres. Axial parenchyma distribu-



tion is variable but includes vasicentric patterns. In addition to the difference in perforation plate type, the *Loganiaceae* differ noticeably from *Sanango* in ray histology. Rays of the loganiaceous genera *Anthocleista* R. Br., *Antonia* Pohl, *Desfontainia*, *Fagraea* Thunb., *Logania* R. Br., *Neuburgia* Blume, *Norrisia* Gardner, *Potalia*, and *Spigelia* are homocellular and exclusively uniseriate or with a locally biseriate portion. In other genera both multiseriate and uniseriate heterogeneous rays are present. Sheath cells may be present along the body of multiseriate rays. In *Peltanthera*, a genus sometimes linked with *Sanango*, both the uniseriate and multiseriate rays are composed entirely or mostly of upright or square cells. In *Sanango* the rays are constructed predominantly of procumbent cells. The widespread, although not universal, possession of included phloem and vested intervacular pits in the *Loganiaceae* is not matched in *Sanango*.

In agreement with *Scrophulariales*, vessels in *Sanango* and *Buddleja* are grouped to various degrees, and axial parenchyma is scanty and vasicentric. Some important anatomical xylem differences between *Sanango* and *Buddleja* are: intervacular pits small in *Sanango*, pits often large in *Buddleja*; tracheids essentially absent in *Sanango*, vasicentric tracheids present in *Buddleja*; imperforate tracheary elements all septate and with reduced pit borders in *Sanango* but generally non-septate and of the libriform fibre type in *Buddleja* (a few septate fibres do occur in some species); rays essentially all multiseriate in *Sanango*, both uniseriate and multiseriate and uniformly heterogeneous in *Buddleja* (type IIA or IIB of Carlquist, 1992). As in *Sanango*, procumbent cells predominate in the rays of *Buddleja*. Crystals are common in the ray parenchyma of most species of *Buddleja*. Spiral thickenings are usually present on the vessel walls of some species of *Buddleja*, but are absent in some species, this is probably an ecologically conditioned feature.

Woody *Scrophulariaceae* have a varied xylem anatomy, with some taxa showing similarity to *Sanango*. Pore distribution is comparable and fibres are septate in a few taxa. Vascular rays are primarily or exclusively multiseriate and heterocellular in selected members of the family (Michener, 1981). The occurrence of vascular tracheids in the wood of some *Scrophulariaceae* and their absence in *Sanango* is an apparent reflection of the degree of xeromorphy in the woods.

Like other aspects of vegetative anatomy, the wood structure of *Sanango* compares favourably with that of various species of *Gesneriaceae*. As reviewed by Carlquist & Hoekman (1986), wood of *Gesneriaceae* is characterized by the following features: the vessels are circular in outline and grouped to a limited extent; perforations are simple; lateral wall pitting is composed of alternate circular or polygonal, elliptic bordered pits; helical sculpturing is present in the form of grooves interconnecting two or more pit apertures in a helix; imperforate tracheary elements are libriform fibres or, less commonly, fibre-tracheids with vestigial pit borders; imperforate tracheary elements are all septate, or septate only near the vessels; the axial parenchyma is vasicentric, scanty or infrequent or absent; vascular rays are multiseriate plus uniseriate, multiseriate only, or the wood is rayless. Like *Sanango*, the ray histology of a few *Gesneriaceae* is characterized by the almost exclusive presence of conspicuously broad, weakly heterocellular rays. However, in no species of *Gesneriaceae* are procumbent cells more abundant than erect cells in the ray tissue as they are in *Sanango*. *Besleria* L., a genus containing species that appear similar to *Sanango* in flower size and shape, has entirely rayless and thus structurally quite divergent wood.

## Conclusions

Investigation of the *Sanango* has yielded information related to the scrophulariacean construction of vegetative and floral parts and can be used to link *Sanango* to certain fundamental structural features, such as the presence of discrete groups, also known as certain fundamental structural features. *Sanango* possesses an anatomical structure that is fundamentally similar to that of the *Buddlejaceae*, *Scrophulariaceae*, and *Scrophulariales*. The combination of ray features, such as the presence of procumbent cells, is an exclusive presence of the *Scrophulariales* in general. The combination of ray features in *Sanango* would appear to be a unique feature of the order. Although *Sanango* remains to be determined.

## Acknowledgements

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### Conclusions

Investigation of the comparative vegetative and floral morphology and anatomy of *Sanango* has yielded results that reinforce the view that *Sanango* is more closely related to the scrophularialean complex than to *Loganiaceae*. The basic floral and vegetative construction of *Sanango* falls within the range of diversity of scrophularialean plants and can be used to establish affinities between the two groups. More specifically, the production of an anatomically complex and very uncommon multilacunar nodal anatomy with split-lateral traces, along with the presence of cortical vascular bundles in the stem, are features of considerable phylogenetic significance that can be used to link *Sanango* with the *Gesneriaceae*. Wood and leaf anatomical features, such as the shared possession of anisocytic stomata that are distributed in discrete groups, also confirm the putative relationship of these two taxa. Despite certain fundamental structural similarities to members of *Scrophulariales*, *Sanango* possesses an anatomically distinct combination of features. It differs from nearly all *Buddlejaceae*, *Scrophulariaceae*, and *Gesneriaceae* in the possession of predominantly scalariform perforation plates on the vessel element end walls and the nearly exclusive presence of tall, broad multiseriate xylem rays composed predominantly of procumbent cells. Evidence provided by Carlquist (1992) indicates that the *Buddlejaceae* most likely belong in *Scrophulariales*, and that the *Scrophulariaceae*, and *Scrophulariales* in general, are more structurally diverse than previously envisioned. The combination of reproductive and vegetative anatomical characters exhibited by *Sanango* would appear to be readily accommodated in most interpretations of the order. Although *Sanango* appears undoubtedly closely related to the *Gesneriaceae*, it remains to be determined what the most satisfactory assignment of the genus should be.

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## A re-examination of *S*

Søren Rosendal Jensen

### Summary

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A chemical investigation of *S* has been present by high microscopy of the crude extract, calceolarin named sanangosides, suggested *Loganiaceae* (Ge

### Introduction

Recently, it has been shown that *S* has systematic value since the biosynthesis of iridoid compounds in which including the complex compounds *Cornanae*, *Loasanae* and *Loasane*, decarboxylated iridoids in the pathway ("Group 2"), differences in the *Cornanae*

Another group of *S* has value since the biosynthesis of iridoid compounds in which including the complex compounds *Cornanae*, *Loasanae* and *Loasane*, decarboxylated iridoids in the pathway ("Group 2"), differences in the *Cornanae*

In an investigation (Jensen 1980), a representative *S* was screened for iridoids and the six tribes (*Spigeliaceae*, *Loasaceae*, *Loasaceae*, *Loasaceae*, *Loasaceae*, *Loasaceae*) that contained C<sub>11</sub> iridoids. In *S*, representatives of the tribe *Plocospermateae* only *S. premum procumbens*. In *S*, representatives had iridoids C<sub>11</sub>

When comparing the *S* taxa that appeared that taxa that had cellular endosperm taxa with Group 1 iridoid

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