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Author(s): Liang Han-Xing and Shirley C. Tucker
Reviewed work(s):
Published by: Botanical Society of America
Stable URL: http://www.jstor.org/stable/2445425
Accessed: 12/10/2012 07:59

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FLORAL ONTOGENY OF ZIPPELIA BEGONIAEFOLIA AND ITS FAMILIAL AFFINITY: SAURURACEAE OR PIPERACEAE?¹

LIANG HAN-XING AND SHIRLEY C. TUCKER²

Kunming Institute of Botany, Academy of Sciences of China, Kunming, Yunnan, China; and Department of Botany, Louisiana State University, Baton Rouge, Louisiana 70803

ZIPPELIA BEGONIAEFOLIA Bl., a monotypic species having characteristics of both Piperaceae and Saururaceae, has racemes of about 20 small flowers lacking a perianth, each with six free stamens and a four-carpellate syncarpous gynoecium. The inflorescence apical meristem initiates bracts acropetally and helically, each of which subvents a later initiated single floral apex; there are no "common" primordia. The six stamens are initiated as two lateral pairs and two solitary successive primordia, the latter two opposite in median sagittal positions. Four carpel primordia are initiated as a lateral pair and two successively initiated in the median sagittal plane. This order of organ inception is unique among Piperaceae and Saururaceae. Intercalary growth below carpellary attachment raises them up on a common cylindrical base that becomes the syncarpous ovary, covered with unique gladiolate hairs and containing a single basal ovule. The free portions of the carpels become the reflexed papillate stigmas. The floral vascular system has a single bundle at base that branches to supply the bract and flower traces. The floral vasculature is similar but not identical to that of Saururus (Saururaceae) and some Piper species (Piperaceae). Plesiomorphic character states of Zippelia that are shared with Saururus include hypogyny, free stamens, cleft stigma, and a similar floral groundplan. Synapomorphies, derived shared character states that unite Zippelia with Piperaceae, include syncarp, solitary ovule, basal placentaion, fused ventral carpellary bundles, and a double vascular cylinder in the stem. Cladistic analysis aligns Zippelia with Piperaceae because they share apomorphies, and because Zippelia shares only plesiomorphies with Saururus.

ZIPPELIA Blume (1830), a monotypic southeast Asian genus, has at various times been placed in two different families: Saururaceae (Blume, 1830; Wu and Wang, 1957, as Circaeocarpus saururoides Wu; Heywood, 1993), or Piperaceae (Engler 1893; Willis, 1957; Wu and Wang, 1958). The transitional nature of Zippelia has been suggested by similarities to Saururus (Omori, 1982) in Saururaceae. We have recently completed a cladistic analysis of the two families (Tucker, Douglas, and Liang, 1993) that is useful for comparisons. The present developmental study was undertaken to provide data for comparison with other taxa and to better determine the affinities of Zippelia. In particular, we wished to determine whether flowers and their subtending bracts are initiated separately as in Piperaceae (Tucker 1980, 1982a, b), or together from a common primordium as in some Saururaceae (Tucker 1975, 1981). Information on order of organ initiation also will be useful in determining affinities of Zippelia.

MATERIALS AND METHODS

Plants of ZIPPELIA BEGONIAEFOLIA were collected 9–20 May 1987 by Liang in Yunnan, China. Inflorescences and flowers of all stages were collected and preserved in FAA (5 ml formalin–5 ml acetic acid–90 ml 50% ethanol) fixative. Voucher specimens were deposited in the herbarium (KUN) of Kunming Institute of Botany, Kunming. Fixed inflorescences were dissected in 95% alcohol, and further dehydrated in an ethanol–acetone series. The dissected pieces were critical-point-dried with CO₂ in a Denton DCP-1 apparatus, mounted on aluminum stubs using colloidal graphite as adhesive, coated with gold-palladium in an Edwards S–150 sputter coater, and micrographs taken with an Hitachi S–500 scanning electron microscope (SEM) at 25 kV.

Fixed material was prepared for paraffin sectioning by dehydration in a tertiary butanol series, embedment in "Paraplast," sectioned at 7 μm thickness, and stained with aniline blue. Selected sections were drawn with a camera lucida attachment on a Leitz Ortholux microscope.

Some flowers were dissected and cleared by bleaching in 5% sodium hydroxide, clearing in saturated aqueous chloral hydrate, and staining with safranin. They were dehydrated and mounted permanently. The clearings were drawn with a camera lucida.

RESULTS

Organography—Zippelia begoniaefolia is an herbaceous perennial with upright aerial stems 40–60 cm high, with alternate, simple, ovate leaves 8–14 cm long and 5–8 cm wide, with cordate bases. The leaf blade is often asymmetric. There are five to seven basal veins per leaf and a petiole 2–5 cm long with a basal sheath. Adventitious roots form at the basal nodes.

The inflorescences are terminal racemes; the plant has a sympodial arrangement of inflorescences. A single acutely tipped bract subvents the inflorescence (Figs. 1, 2), which includes about 20 flowers. Each flower (Fig. 3) is subtended by a green bract that is narrow, acutely tipped, and about one-quarter the length of the flower (Fig. 14).

Individual flowers (Figs. 3, 14) are short-pedicellate and hypogynous, lack a perianth, and have six free stamens with basifixt tetrasporangiate anthers. The filaments of the six stamens are cylindrical. Anthers commonly abscise at a basal constriction (Figs. 3, 14). The gynoecium has

¹ Manuscript received 31 May 1994; revision accepted 2 November 1994.
² This research was supported by NSF grants BSR87-22514 and DEB-9207671 to SCT. Figure 17 A–F was used by permission of Systematic Botany (Tucker, Douglas, and Liang, 1993).
³ Author for correspondence.
Figs. 1–6. Inflorescence, flower, and early stages in floral ontogeny (SEM micrographs). Bracts removed in 4–6. Bars = 450 μm in 2; =300 μm in 3; =100 μm in 1, 4; =50 μm in 5, 6. 1. Tip of inflorescence. Apical meristem (at arrow) has produced bracts (B) that subend floral meristems (F). 2. Young inflorescence and subtending inflorescence bract (IB, at left). The inflorescence apex has produced floral bracts (B) in acropetal, helical succession. A floral meristem (F) forms in the axil of each floral bract. 3. Flower with syncarpous ovary (O) and free stigmas (St). Stamens (two of which have been removed) have anthers (A) and cylindrical filaments (F). B, floral bract; P, pedicel. 4. Bare floral apex before organogenesis. 5, 6. Polar and oblique views of floral meristem during initiation of the first stamen pair ("1") followed by the median adaxial stamen. 5. The first stamen pair ("1") includes a solitary stamen at right, and what appears to be a common primordium at left. 6. The third stamen ("2") has been initiated in median adaxial position.
Figs. 7–10. Organogeny of stamens and carpels (SEM micrographs). Subtending bracts have been removed in all. Bars = 50 μm. 7. Two lateral stamen primordia ("3") have been initiated toward the abaxial side, while earlier initiated stamens ("1," "2") have enlarged somewhat. 8. Initiation of last stamen ("4") in the median abaxial position, opposite stamen 2. 9. The first two carpel primordia (C) are being initiated on the sides of the concave floral apex. One of the first pair of stamens has been removed. 10. All six stamens have enlarged including the last-initiated ("4"), although size differences persist. A third carpel primordium has been initiated in the median adaxial position; the two lateral carpel primordia have enlarged slightly. One of the latter is nearly obscured by stamen "3" at left.

four stigmas, a single locule, and a single basal ovule. The ovary surface is verrucose (warty) and becomes glochidiate in fruit, unlike any other fruits in either Saururaceae or Piperaceae.

**Inflorescence and flower ontogeny**—The inflorescence apex (Fig. 1) produces bracts in acropetal, helical succession. The inflorescence shown in Fig. 2 has ceased bract initiation; it is probably near the end of its activity. No indication of a terminal flower, similar to that in some Saururaceae, was seen in any inflorescences of *Zippelia*.

Each floral apex is initiated in the axil of a bract (Figs. 1, 2) when the bract is about 50 μm in height. The floral meristem is wide tangentially and narrow radially, and
reaches a width of about 150 μm (Fig. 4) before organogeny begins. The subtending bract rapidly arches over the developing floral apex (Fig. 2).

Two lateral primordia (Figs. 5, 6) are initiated first on either side of the broad floral apex. These either produce individual adaxial lateral stamens (as at right in Fig. 5) or common primordia, as in the left-hand primordium in Fig. 5, which appears abnormally wide for a single stamen primordium. Later, however, there is little or no indication that the lateral stamen primordia share common origin; no zonal growth below each pair, for example, was seen (Fig. 2). More flowers need to be examined (when more material can be obtained) to determine the frequency of these large, possibly “common” lateral stamen primordia.

After the adaxial lateral pair of stamens primordia is formed, the floral apex is flat and remains so during stamen initiation. The next primordium to appear is the median adaxial stamen (“2” in Figs. 6, 7). Next, the two abaxial lateral stamens become evident (“3” in Figs. 7, 8). The last stamen primordium to appear is the median abaxial one (“4” in Figs. 8, 9). Stamens of the median sagittal pair are sequential in time of initiation, while the members of each lateral pair are initiated synchronously.

The floral apical meristem becomes slightly concave (Figs. 8, 9). A pair of carpel primordia arise simultaneously (Figs. 8, 9) in lateral positions on the margins of the concavity. The third carpel to form is the median adaxial one (Figs. 10–13), and the last is the median abaxial carpel (site at arrow in Fig. 12; the fourth carpel primordium is shown in Fig. 13). Zonal growth raises the free carpel primordia (which will become the four stigmas) upward on a common base (Figs. 13, 14) that will become the ovary; hair formation has begun on the ovary (Fig. 13).

**Organ differentiation** — Although the stamens form successively, they become equalized in size later. The anthers at first appear cylindrical, but by maturity their tangential diameter exceeds the radial diameter. Oil cells in depressions pock the surface of the anthers (Figs. 3, 14). The filaments remain cylindrical.

The carpel primordia also become equalized in size during development, despite their successively paired initiation. The hairs beginning to form on the ovary in Fig. 13 later become glochidiate hairs (Figs. 3, 14). The free carpel tips become arched inward (Fig. 3) at first, but later become reflexed papillate stigmas (Fig. 14).

**Vascular structure of the flower** — A single vascular bundle supplies the flower and the subtending bract (Figs. 15B, 16), although it splits at the base of the pedicel (Fig. 15C–E), where the bract is attached (Figs. 15A, 16). The bract midvein branches pinnately, producing several lateral bundles (Fig. 15A, F). The strand to the flower becomes a cylinder of bundles in the pedicel (Fig. 15G). Each such bundle is termed a sympodial bundle because it supplies more than one organ (stamen plus carpel) at higher levels in the flower. Four sympodial bundles produce branches to six stamens (Fig. 15A, H, I); each median carpel is associated with a single stamen bundle, while each lateral carpel is associated with two lateral stamen strands (Fig. 15F, J).

Each of the four sympodial bundles branches into three strands: a dorsal and two smaller ventral bundles that converge inward (Fig. 15J) and supply the single basal ovule (Figs. 15A, 16). The four dorsal carpellary bundles continue upward, some of them branching in the ovary wall (Fig. 15L, M), and then the four continuing into the stigmas (Fig. 15A) where each produces a tuft of tracheary elements (Fig. 15A). The glochidiate hairs do not receive vascular tissue.

Although only a few immature stages in vascular development were available for study, Fig. 16 illustrates some observed features. Procambial strands form acropetally, but xylem differentiates discontinuously in some areas such as the stigma. Differentiated xylem forms in the ovular bundle (“O” in Fig. 16) before it connects at base to the pairs of ventral carpellary bundles (not yet differentiated in Fig. 16).

**DISCUSSION**

**Common flower/bract primordia** — The affiliation with Piperaceae is supported by the fact that **Zippelia** floral meristems are initiated separately from their subtending bract initials, as in other Piperaceae that have been investigated (Tucker, 1980, 1982a, b). The unusual type of initiation of flower and bract from a common primordium occurs in some Saururaceae (Tucker, 1975, 1981) but not others (Tucker, 1985; Liang and Tucker, 1989). Common primordia appear to be a specialization (synapomorphy) in Saururaceae (Tucker, Douglas, and Liang, 1993; Tucker and Douglas, in press.)

**Comparison of floral characters** — Significant character states of **Zippelia** and taxa of Saururaceae and Piperaceae are compared in Table 1. **Zippelia begoniaefolia** has the same number of stamens and carpels as **Saururus**, **Gymnotheca**, and certain species of **Piper**. The multicarpellate syncarpous ovary of **Zippelia** is shared by **Gymnotheca** and Piper, but not **Saururus**. The free stamens of **Zippelia** differ from **Gymnotheca**, where the filaments are fused to the ovary wall. The order of initiation among stamens and carpels in **Zippelia** differs from that of any other taxa in either Piperaceae or Saururaceae that have been investigated (Fig. 17). All the flowers of saururaceous and piperaceous taxa have zygomorphic (dorsiventral) symmetry, with organs positioned either in the median sagittal plane or in mirror-image pairs on either side of that plane. Figure 17 makes clear that organs differ in number, position, and order of initiation among these taxa. The arrangement of organs and their order in **Gymnotheca** most closely approaches that of **Zippelia**, but the two differ significantly in that a lateral pair of stamens initiates first in **Zippelia**, while the median sagittal pair of stamens initiates first in **Gymnotheca** (Liang and Tucker, 1989; Tucker and Douglas, in press).

There are some features found in common among **Zippelia** and taxa of both families. For example, all lateral floral organs arise as members of simultaneous pairs. Organs in the median sagittal plane (which appear opposite) may arise successively (as in **Zippelia** and **Piper** species) or simultaneously (as in **Saururus** and **Gymnotheca**). Stamens and carpels in **Zippelia** are clearly in pairs, not in trimerous whorls as indicated by Eichler (1875–1878) and
Figs. 11–14. Carpel initiation and organ enlargement (SEM micrographs). Bracts have been removed in 11–13, and some or all stamen primordia or anthers also have been removed in 11, 13, and 14. Bars in 11–13 = 50 \( \mu \)m; in 14 = 70 \( \mu \)m. 11, 12. Stages in initiation and early growth of three of the four carpel primordia (C); site of the fourth is at arrow. 13. Initiation of the fourth carpel primordium in median abaxial position, at arrow. Hairs are forming on the ovary, which is enlarging by zonal growth below the free portions of the carpels (C). S, stamen scar. 14. Flower at anthesis, with anthers removed to show abscission scars on filaments (F). Note glochidiate hairs covering the ovary (Ova), and the recurved free stigmas (St). Ax, inflorescence axis; B, subtending floral bract; P, pedicel.

Burger (1977). Symmetry is dorsiventral, not radial as presumed by earlier authors.

**Vascularure**—As Omori (1982) reported for material from Borneo, the floral vascular pattern in *Zippelia* closely resembles that found in *Saururus chinensis*. We studied material from south China, but found only minor differences from the material used by Omori. *Zippelia* resembles *S. chinensis* (shown in Liang and Tucker, 1990, Fig. 17A) except all six ventral carpellary bundles converge
Fig. 15. Vasculature of flower of *Zippelia begoniaefolia*. The abaxial side of the flower is at the top in transverse sections B–O. Bar = 1.7 mm.

A. Whole cleared flower and subtending floral bract, showing the entire vasculature. At left, the levels are indicated for the transverse sections B–O. B–O. Transverse sections of a flower from the base upwards. B. A single bundle departs from the inflorescence axis to supply both flower and its subtending bract. C–E. Splitting (and occasional anastomosing) of the single bundle into two or three at the base of the pedicel where bract is
centripetally and fuse to supply the single basal ovule in *Zippelia*, while the two carpellary ventral bundles remain discrete in taxa of Saururaceae. *Piper* is similar to *Zippelia* in having a single basal ovule and several dorsal bundles in the ovary wall, but differs in that there is a single ovular bundle (Murty, 1959). In the more specialized taxa of Saururaceae (*Anemopsis, Gymnotheca, Houytuynia; Liang and Tucker, 1990*) pairs of carpellary ventral bundles converge and fuse into a single ventral bundle per carpel.

**Affinities**—*Zippelia*, with floral structure resembling that of *Saururus* in number and arrangement of floral organs and in floral vasculature (Omor, 1982), has been placed either in Saururaceae (Blume, 1830; Wu and Wang, 1957; Heywood, 1993) or Piperaeae (Engler, 1893; Willis, 1957; Wu and Wang, 1958). Based on the present work, *Zippelia* and *Saururus* differ in order of organ initiation, in whether common primordia are involved, and in apocarpy in *Saururus* vs. syncarpy in *Zippelia*.

Recent literature on Saururaceae and Piperaeae is reviewed in Tucker (1975 et seq.) and in Tucker, Douglas, and Liang (1993). Some papers not included in these sources include those on the differing chromosome numbers in saururaceous genera (Liang, 1991) and on saururaceous pollen (Liang, 1992). Liang has a Chinese-language synopsis of the floral organogenetic work in Saururaceae in press (Liang, in press).

In a cladistic analysis of taxa in Saururaceae and Piperaeae (Tucker, Douglas, and Liang, 1993), the similarities between *Zippelia* and *Saururus* are identified as plesiomorphies (shared unspecialized states): e.g., hypogyny, free stamens, cleft stigma, and a similar groundplan with six stamens and four carpels (Tucker, Douglas, and Liang, 1993; Tucker and Douglas, in press). The rationale for calling these character states plesiomorphies is based on both outgroup and (in some characters) ontogenic comparison. For example, floral primordia of *Zippelia begoniaefolia, Saururus cernuus* (Tucker, 1976), and *Anemopsis californica* (Tucker, 1985) all are hypogynous at one stage of development; flowers of the first two taxa do not change from the hypogynous condition during enlargement and differentiation. But in *A. californica* (Tucker, 1985), the floral meristem undergoes further growth changes to become epigynous; hence hypogyny is considered the plesiomorphic state based on developmental comparison. The free stamen state in *Zippelia* is considered plesiomorphic, compared to the fused state, also based on ontogenetic evidence; development in flowers produces initially-free organs that may undergo further ontogenic change to become fused (connation in *Anemopsis*, for example). The cleft stigma state in *Zippelia* and all four saururaceous genera is termed plesiomorphic because it is an intermediate stage followed by later development to either a capitate state (in *Piper* spp.; Tucker, 1982b) or a branched state (in *Peperomia* spp.; Tucker, 1980). In cladistic terms, plesiomorphic similarities are viewed as unreliable indicators of relationship. Tucker, Douglas, and Liang (1993) should be consulted for more extensive discussion of outgroup vs. ontogenetic-based comparisons in Saururaceae and Piperaeae.

While *Zippelia* shares certain unspecialized character states with *Saururus*, it shares several synapomorphies (specialized states) with Piperaeae: a double vascular cylinder in the stem, lack of discrete style, single ovule, basal placentation and fusion of two ventral bundles into

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Fig. 16. Vasculature of cleared young flower (longitudinal view) of *Z. begoniaefolia* before stamens and gynoecium have differentiated completely. Ovular bundle supplying the single ovule appears discontinuous, although a procambial connection (unstained) is probably present below. Xylem later differentiates in the ventral bundles, which then connect to the base of the ovular bundle. The dorsal carpellary bundles (two shown) are differentiated in the base of the carpel wall and in the stigmas. Subsequent differentiation would have produced continuous dorsal bundles. Stamen bundles are continuous below to the point of divergence from sympod. O = ovule; OB = ovular bundle; S = stamen; St = stigma.

attached. F. One bundle supplies the floral pedicel. The bract base, below its level of attachment, has traces of the midvein and lateral bundles. G. The flower bundle has split into a cylinder of bundles in the pedicel. H. I. Four sympodial bundles have produced branches to six stamens, leaving four carpel bundles at center. J. Level of attachment of stamen bases. Each carpel bundle has split in three, a dorsal (d) and two ventral bundles; the ventrals are the smallest bundles, most centrally located. They fuse at a slightly higher level to form the ovular bundle. K~M. The four dorsal carpellary bundles are present in the syncarpous ovary wall, and terminate in tufts of tracheary elements supplying the four stigmas. L and M show the four dorsal bundles branching terminally. O = ovule. N. The four dorsal carpellary bundles continue into the stigmas. At center is the space surrounded by the stigmas. Terminals of the four dorsal bundles are present.
Table 1. Character comparisons for Zippelia, four saururaceous taxa, and two of Piperaceae.

<table>
<thead>
<tr>
<th>Character</th>
<th>Zippelia</th>
<th>Saururus</th>
<th>Gymnotheca</th>
<th>Houttuynia</th>
<th>Anemopsis</th>
<th>Piper amalago</th>
<th>Peperomia</th>
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<td>Stem vasc. cylinder</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
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<tr>
<td>Perforation plate</td>
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<td>2</td>
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<td>1</td>
<td>1</td>
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<td>2</td>
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<td>Inflo. bracts: 1, one type; 2, two types</td>
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<td>1</td>
<td>2</td>
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<td>2</td>
<td>1</td>
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<tr>
<td>Flower/bract init.: 1, separate; 2, common</td>
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<td>2</td>
<td>1</td>
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<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
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<td>2</td>
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<tr>
<td>Stamens: 1, free; 2, fused</td>
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<td>1</td>
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<td>1</td>
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<td>1</td>
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<td>Carpel number: 1, four; 2, less than four</td>
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<td>2</td>
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<tr>
<td>Carpels: 1, free; 2, fused</td>
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<td>2</td>
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<td>Stigma shape: 1, cleft; 2, capitulate or branched</td>
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<td>Ovule number per flower</td>
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<td>Carpel vasc.: no. ventral bundles/carpet</td>
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one in each carpel. It also shares syncarpy with most Piperaceae except *Peperomia*. Reasons for considering these states as derived are based on both outgroup and ontogenetic comparisons (see Tucker, Douglas, and Liang, 1993). These synapomorphies are considered to indicate close phylogenetic relationship between *Zippealia* and other taxa of Piperaceae. Tucker, Douglas, and Liang (1993) place *Zippealia* as the basal taxon in Piperaceae. In that analysis, Piperaceae and Saururaceae are sister clades; *Saururus* is the basal taxon in the Saururaceae clade.

**LITERATURE CITED**


