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Floral anatomy of *Saururus chinensis* (Saururaceae) and *Zippelia begoniaefolia* (Piperaceae)

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(With 6 text-figures and 2 plates)

ハンゲショウ（ドクダミ科）の花と *Zippelia*（コショウ科）の花の類似性

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コショウ科の一種で，中国南部及び東南アジアに分布する *Zippelia begoniaefolia* BL. の花の維管束走向を連続横断切片の観察から明らかにし，花の構造を詳しく調べた。あわせて，かつて類縁性を指摘されたことのあるドクダミ科ハンゲショウ属2種のうち，ハンゲショウ *Saururus chinensis* (LOUR.) BAILL. の花の維管束走向を観察し，これら2属の花の構造上の関連性について考察した。

その結果，*Zippelia* の花は，コショウ科の特徴の一つとされる子房1室で胚珠が1個という形質をもちながら，花の基本的な構造は *Saururus* の花とほぼ同じであることがわかった。すなわち，*Zippelia* の雌蕊では，4本の維管束が子房と4本の花柱に入り，その4本の維管束からの分枝が基生する胚珠に入るので，前者が心皮の背行維管束に，後者が心皮の腹行維管束に相当すると考えられ，*Zippelia* の雌蕊は *Saururus* 様の花の4心皮の癒合によって導くことができるからであり，さらに，*Zippelia* の花では，花序軸と苞を結ぶ線上にある2本の子房維管束の基部から各1本の雄蕊維管束が分岐し，それと直交する線上にある残りの2本の子房維管束の基部から各2本の雄蕊維管束が分岐するので，この維管束走向から推定される心皮の数及び心皮と雄蕊の位置関係が *Saururus* の花と同じであると考えられるからである。

Introduction

According to MELCHIOR (1964, pp. 147–151), the Piperaceae and the Saururaceae are included in the order Piperales with the Chloranthaceae and the Lactoridaceae, although the latter two families' inclusion in this order has been subject to controversy. The Piperales generally has the flower without perianth, and this has aroused the interest of many systematists in the affinity of Piperales. ENGLER and GILG (1924) considered that the Piperales is closely related to the Amentiferae and is one of the most primitive groups of dicotyledons. RENDLE (1925, pp. 88–93) regarded it to be allied to the Polygonales. Recently, some systematists asserted that the absence of perianth in the Piperales was assumed to be a secondary phenomenon and that the Piperales could be considered a group to be derived from Magnoliales (MELCHIOR, 1964; CRONQUIST, 1968, pp. 132–145;

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TAKHTAJAN, 1969, pp. 95–107). Another (BURGER, 1977) suggested that the Piperales was the order more closely related to monocotyledons. Such difference in views on its taxonomic position is mainly due to the lack of detailed analyses of the flowers.

The comparative morphology in some genera of this order was studied by RAJU (1961) in the Saururaceae and by MURTY (1958, 1959) in both the Saururaceae and the Piperaceae. However, the structure of the flower, especially of its vasculature, is not fully recognized, and only several have been investigated out of 3000 species of the Piperaceae. In such a simple flower as that of the Piperales, the investigation of vasculature is useful and necessary for understanding the structure of the flower and elucidating the affinity of taxa in this order. Thus I observed the vasculature of flower of *Saururus chinensis* in the Saururaceae and *Zippelia begoniaefolia* in the Piperaceae.

Saururus is regarded as the most primitive among four genera in the Saururaceae, because of its apocarpous gynoecium (TAKHTAJAN, 1969, pp. 137–163). *S. cernuus*, the American species, was investigated by MURTY (1959), RAJU (1961) and TUCKER (1975, 1976). However, the vasculature in pedicel was not fully observed. RAJU (1961) studied floral anatomy and regarded the carpel arrangement as spiral. But TUCKER (1975) observed floral development and showed the bilateral arrangement of floral organs. It is necessary to examine and confirm the arrangement of floral organs in *Saururus*.

Zippelia is a monotypic genus occurring in Southeast Asia, and is characterized by the flower having six stamens, four conspicuous styles and by the glochidiate fruit. Most species in other piperaceous genera share none of these features. Nevertheless, this genus has been included in the Piperaceae (ENGLER, 1894, pp. 1–11), or in the tribe Pipereae (BENTHAM and HOOKER, 1883, pp. 125–133), since *Zippelia* has one ovule in a single locule of the gynoecium, which is the common diagnostic feature in piperaceous genera. However, BLUME (1830) who first described this genus placed it in the tribe Saurureae. When it was first discovered in China, WU and WANG (1957, 1958) considered it as a new genus of the Saururaceae, *Circaeocarpus*. Both of them recognized the similarity of the flower of *Zippelia* to that of *Saururus* from the external morphology. No anatomical study of the flower has been made yet, therefore it is significant to consider the taxonomic position of *Zippelia*.

Materials and methods

Floral materials of *Saururus chinensis* (LOUR.) BAILL. used for this study were collected from the Botanical Gardens of University of Tokyo, and those of *Zippelia begoniaefolia* BL. were collected from Sandacan of Borneo by Dr. M. HOTTA, Kyoto University. These were fixed and preserved in 50% FAA

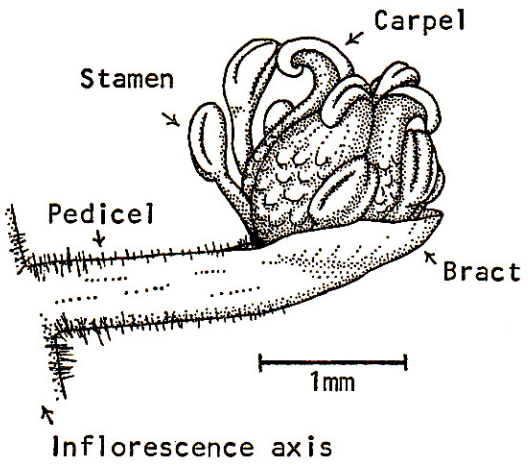

Fig. 1. Flower of *Saururus chinensis*.

(formalin-acetic acid-alcohol) solution. They were dehydrated through a normal butyl alcohol series, embedded in paraffin or in Paraplast, cut into serial sections of 10 μm in thickness and stained with Heidenhain's hematoxylin, safranin and fast green schedule.

Observations

Saururus chinensis (LOUR.) BAILL.

Many flowers are densely borne in the raceme inflorescence. The flower has a short pedicel, six stamens and four carpels but has no perianth, and a bract is adnate to the pedicel and surrounds the flower. The pedicel attaches nearly at right angles to the inflorescence axis. The stamens and the carpels are opposite to each other. The four carpels are arranged in a whorl, two of them are in the median sagittal plane, and the other two on the lateral plane bisecting the former plane. Two median carpels are attached by a single stamen dorsally while the other two lateral carpels possess two stamens each (Fig. 1).

The vasculature is observed in the serial transverse sections from the inflorescence axis to the flower and is shown in Figure 2. In the influorescence axis, the vascular bundles are arranged in a ring (Fig. 2·1), and are named the bundles of the inflorescence axis (AX). Two adjacent bundles, AX1 and AX2 (Figs. 2·1–2·4), give off two branches, AX1′ and AX2′ (Figs. 2·2–2·4), which form a united bundle in the pedicel (Figs. 2·4, 2·5), but in some cases only a single AX bundle bifurcates to form two traces leading into the pedicel.

The bundles in the pedicel, after dividing and fusing, finally produce four bundles arranged in a ring in its upper level (Fig. 2·6). Four bundles are independently recognized: adaxial bundle of pedicel (A), bundle of bract side in

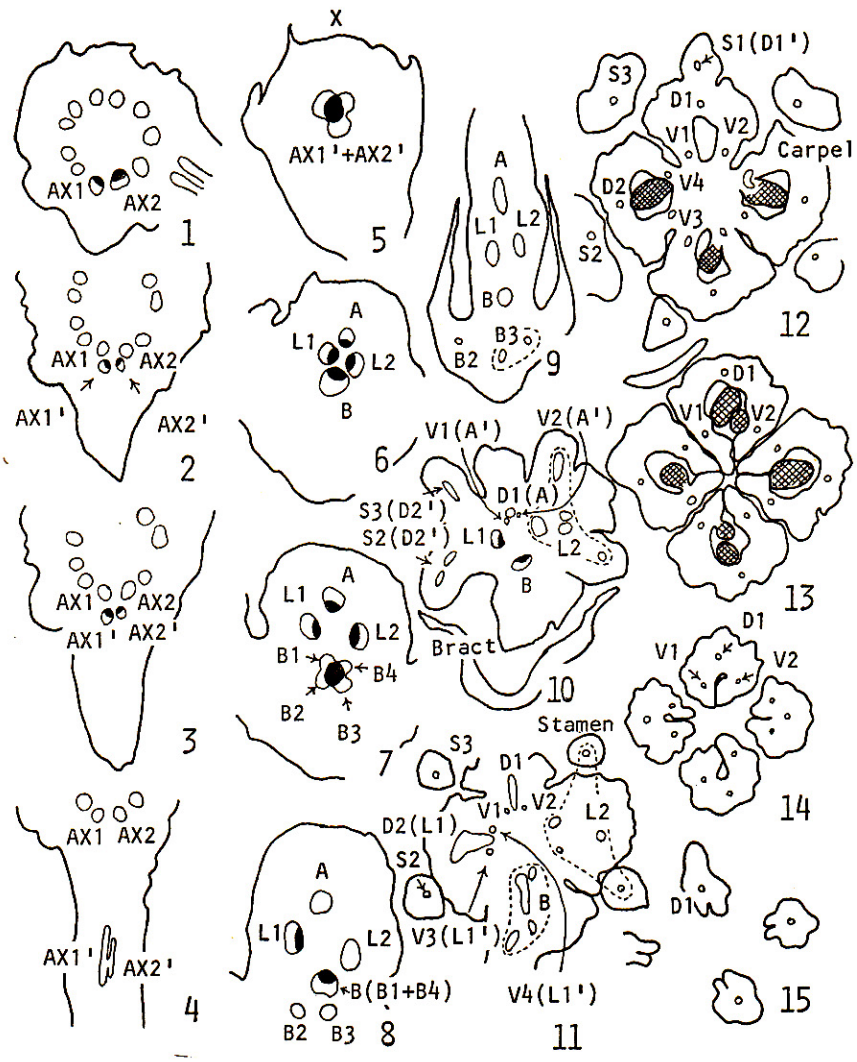

Fig. 2. Serial transverse sections illustrating vasculature of the flower of *Saururus chinensis*. 1–3: Inflorescence axis. 4–7: Pedicel. 8–10: Receptacle. 11: Receptacle and stamen. 12, 13: Ovary and stamen. 14, 15: Style. Abbreviations: AX1 and AX2, bundles of inflorescence axis; A, adaxial bundle of pedicel, B (B1, B2, B3 and B4), bundles of bract side in pedicel; L1 and L2, lateral bundles of pedicel; D1 and D2, dorsal bundles of carpel; V1, V2, V3 and V4, ventral bundles of carpel; S1, S2 and S3, stamen bundles. X in Figure 2·5 indicates the adaxial side and dark areas in Figures 2·12 and 2·13 indicate ovules. Figures 2·1–2·4 and 2·9–2·15 were drawn from a single specimen and Figures 2·5–2·8 were described from different one. 1–4 and 9–15 (×27); 5–8 (×50).

pedicel (B) and lateral bundles of pedicel (L1 and L2). Bundle B bifurcates twice to give rise to four small bundles, B1, B2, B3 and B4 (Fig. 2·7). They form a ring, orienting xylem inside and phloem outside. Two bundles B2 and B3 in the abaxial side pass into the bract (Fig. 2·8) and are further divided to give rise to the vascular supply for the bract (Fig. 2·9). The remaining two bundles B1 and B4, inversing xylem phloem orientation, fuse to form a single bundle which becomes one of the bundles of the pedicel vascular ring (Fig. 2·8). Thus pedicel vascular ring consists of bundles A, B, L1 and L2 in the upper level.

In the basal part of the carpel, each pedicel bundle trifurcates and gives rise to carpel bundles, a single dorsal (D) and two ventral (V) (Fig. 2·10). Each of the bundles D of median carpels gives off one stamen trace (Figs. 2·11, 2·12) but of lateral carpels gives off two stamen traces (Figs. 2·10, 2·11), respectively. The two vascular bundles in the medianly located stamens are given off at a slightly higher level than the remaining four bundles in laterally located stamens. In the lower level of the carpel, each bundle V gives off a branch as the vascular supply to the ovule which is borne on the margin of the carpel (Fig. 2·12). Two central (V) and one dorsal (D) bundles of each carpel extend to the upper part of the style (Fig. 2·14).

Zippelia begoniaefolia BL.

Flowers are sparsely borne in raceme inflorescence, and are subtended by boat-shaped bracts. The flower has a pedicel, no perianth, six stamens and a gynoecium. The stamens are arranged in a whorl and surround the gynoecium. The gynoecium consists of a one-celled ovary with four styles (Fig. 3).

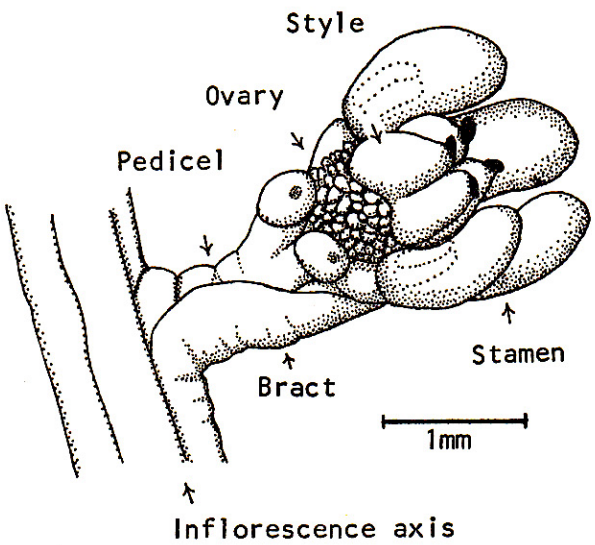

Fig. 3. Flower of *Zippelia begoniaefolia*. Two stamens are removed.

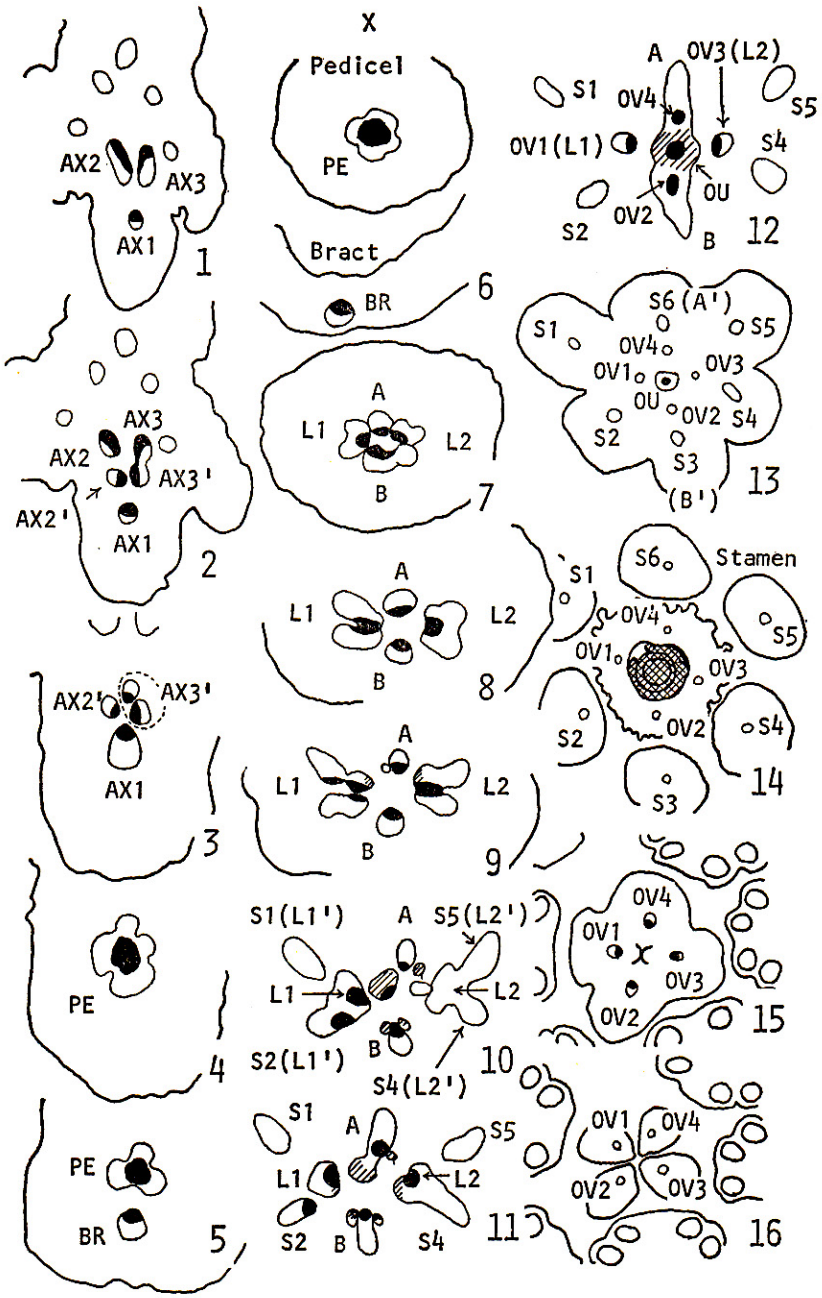

Fig. 4. Serial transverse sections illustrating vasculature of the flower of *Zippelia begoniaefolia*. 1–3: Inflorescence axis. 4, 5: Basal part of pedicel. 6: Pedicel. 7–13: Receptacle. 14: Ovary and stamen. 15, 16: Style. Abbreviations: AX1, AX2 and AX3, bundles of inflorescence axis; PE, pedicel bundle; BR, bract bundle; OU, ovule bundle. For other abbreviations see Figure 2. Oblique lines in Figures 4·9–4·12 show the vascular bundles leading into ovule and the dark area in Figure 4·14 indicates an ovule. X in Figure 4·6 indicates the adaxial side. 1, 2 (×40); 3–12 (×60); 13–16 (×35).

The vasculature from the inflorescence axis to the flower is shown in Figure 4. The vascular bundles in the inflorescence axis run along the grooves and ridges of the axis. They are named the bundles of the inflorescence axis (AX). Two bundles AX2 and AX3, running along the grooves of the inflorescence axis, give off branches to give rise to bundles AX2′ and AX3′ (Figs. 4·1, 4·2). The bundle AX1, running along the ridge of the peduncle, gives rise to the vascular supply for a single flower together with bundles AX2′ and AX3′ (Fig. 4·3). These bundles form the vascular supply for the pedicel (bundle PE). The bundles PE are either divided or anastomosed in the transitional level of the pedicel and peduncle (Fig. 4·4). Although the pedicel bundles (PE) become independent from the vascular ring of the inflorescence axis, external recognition of bundles PE is not possible at this level. Above the level of Figure 4·4, the bract bundle is given off abaxially from the cluster of bundles PE (Fig. 4·5). The remaining cluster of bundles PE forms the vascular ring again (Fig. 4·6).

At the upper level of the pedicel, the cluster of bundles PE is divided into four bundles. They are depicted as bundles A, B, L1 and L2, respectively (Fig. 4·7). Bundle A is located adaxially and gives off a stamen bundle S6, while bundle B is situated abaxially and gives off another stamen bundle S3. In the laterally located bundles L1 and L2, each gives off two stamen bundles, thus four lateral stamen bundles S1, S2, S4 and S5 are formed (Figs. 4·10–4·12). The bundles of these lateral four stamens are derived at a lower level than the bundles of the other two stamens (Figs. 4·10–4·13).

Bundles, A, B, L1 and L2 give off one or two small branches toward the center of the receptacle and these branches become united in the upper level to give rise to a single ovular bundle (OU) which supplies the basal part of the ovule (Figs. 4·9–4·13). Thus every pedicelar bundle gives off the branch leading into the ovule and these branches are illustrated as the area of oblique lines in Figures 4·9–4·12. The remaining four pedicelar bundles A, B, L1 and L2 become four independent ovary bundles OV4, OV2, OV1 and OV3 in the upper level (Figs. 4·13, 4·14) and each bundle passes into the respective styles (Figs. 4·15, 4·16).

Results and discussion

In this investigation, I observed the floral vasculature of *Zippelia* and *Saururus* and studied the floral structure of the former in comparison with that of the latter and those of other genera in the Piperaceae for elucidating the taxonomic position of *Zippelia*. As a result of the examination, the flowers of *Zippelia* in the Piperaceae and *Saururus* in the Saururaceae are similar both in the gross morphology and vascular anatomy. The characteristics of the floral vascular system in *Zippelia* and *Saururus* and the similarity in the structure

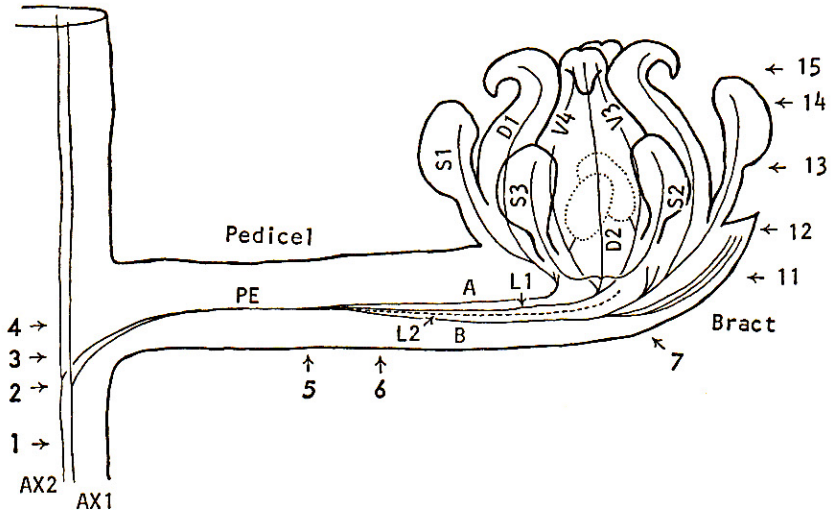

Fig. 5. Reconstruction illustrating vasculature in the flower of *Saururus chinensis*. The numbers 1 to 15 with arrows correspond to the respective levels illustrated in Figure 2. PE, pedicel bundle. For other abbreviations see Figure 2. Two dotted lines in the figure represent two ovules in a single carpel.

of their flowers are discussed as follows. The reconstructions of the floral vasculature of *Saururus* and *Zippelia* are shown in Figures 5 and 6, respectively.

The observation of detailed vascular system on *Saururus chinensis* agrees mostly with the results of MURTY (1959) and RAJU (1961) on *S. cernuus*, though there are the following differences. In *S. chinensis*, two bundles (AX1 and AX2) from the peduncle vascular ring enter the pedicel base to form a united bundle (PE) and it is divided into four bundles (A, B, L1 and L2) in the upper part of the pedicel, and the bract supply is derived from the branch from one of the four pedicelar bundles (B), but, in *S. cernuus* MURTY (1959) observed that a single bundle from the peduncle vascular ring enters the pedicel to split up into five bundles and one of them in the pedicel directly enter the bract.

There are two different interpretations on the arrangement of floral organs of *Saururus*. Namely, in *S. cernuus* RAJU (1961) discussed the spiral arrangement of stamens and carpels on the basis of the study of the external morphology and vascular anatomy, whereas TUCKER (1975, 1976) studied the ontogeny of the floral parts and concluded that the arrangement of floral organs is bilateral. In the present study on *S. chinensis*, the vascular anatomy supports the TUCKER's view in this respect.

In *Zippelia*, four vascular bundles of the receptacle (A, B, L1 and L2) become ovary bundles (OV) to pass into the ovary and the respective styles, and each of them gives off one or two branches toward the center of the flower

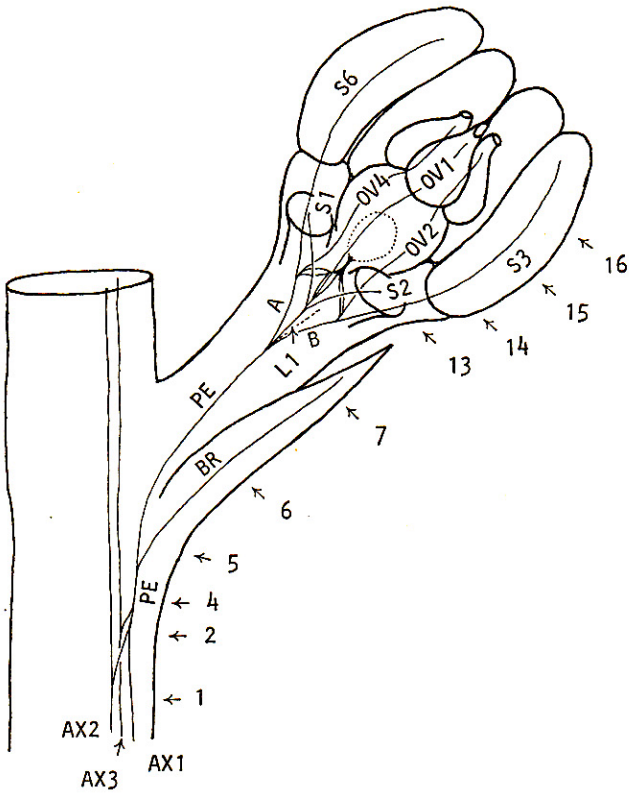

Fig. 6. Reconstructed vasculature in the flower of *Zippelia begoniaefolia*. The numbers 1 to 16 with arrows correspond to the respective levels illustrated in Figure 4. For abbreviations see Figures 2 and 4. A dotted line in the figure represents an ovule.

which fuse together to form an ovule bundle (OU). This vascular anatomy suggests the ovary bundle and the ovule bundle of *Zippelia* respectively correspond to the dorsal bundle and the ventral bundle in such a carpel as *Saururus*. Thus a single locule of the gynoecium of *Zippelia* is regarded to have been derived from the connation of original four carpels. Besides, each of two median ovary bundles (OV2 and OV4) is opposite to a single stamen bundle while of two lateral ovary bundles (OV1 and OV3) is opposite to two stamen bundles, and two median stamen bundles (S3 and S6) are branched earlier than four lateral stamen bundles (S1, S2, S4 and S5). Therefore, the carpel is considered to be placed opposite to the stamen: the two carpels in the median plane opposite to one each stamen and other two carpels in the lateral plane are opposite to two each stamens. The number and arrangement of stamens and carpels of *Zippelia* is the same as in *Saururus*, though the former differs from the latter in the number of the locules and ovules.

On the other hand, JOHNSON (1902) observed, in the flower of *Piper medium*, that its six stamens were arranged in two whorls having three each and the wall of its ovary appeared as a usually three-lobed ring on its development. This floral structure of *P. medium* is similar to that of *Enckea amalago* which EICHLER (1878, pp. 3–6) regarded as the basic type of piperaceous flowers with six stamens in two whorls having three each and with three carpels. The flowers of the above two species are different from that of *Zippelia* in the arrangement of stamens and in the number of carpels composing a syncarpous gynoecium.

Thus the structure of the flower of *Zippelia* is more similar to that of *Saururus* than those of other genera of the Piperaceae. It is necessary to elucidate in detail the structure of the flowers in different genera and consider the derivation of the gynoecium with a single locule for the taxonomy of the Piperaceae and Piperales more precisely.

Concluding remarks

1) A single locule in the gynoecium of *Zippelia* is derived from the connation of four carpels, since all of the explanatory ventral bundles of the carpels fuse to form an ovule bundle which leads to the basal part of ovule.
2) In *Zippelia*, each of two medianly located carpels is opposite to a single stamen and each of two laterally located carpels is opposite to two stamens.
3) Judging from the vascular system of the androecium and gynoecium, the flower of *Zippelia* of the Piperaceae is more similar to that of *Saururus* of the Saururaceae than those of other genera of the Piperaceae.

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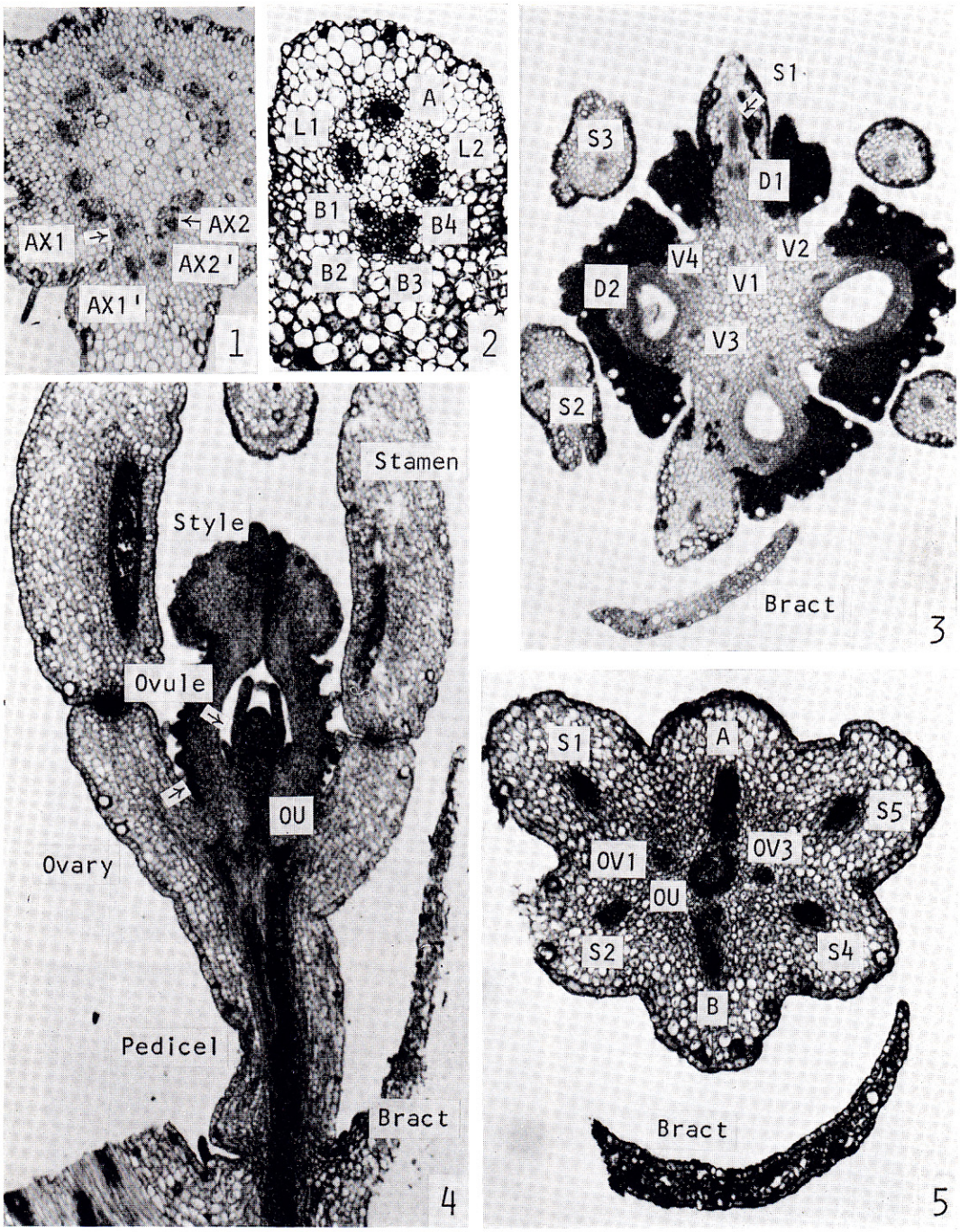

Plate 3. 1–3: *Saururus chinensis*. 4, 5: *Zippelia begoniaefolia*.
1: Transverse section of inflorescence axis. (×50).
2: Transverse section of the upper part of pedicel. (×84).
3: Transverse section of the lower part of ovary. (×50).
4: Longitudinal section. (×49). 5: Transverse section of receptacle. (×64).
For abbreviations see Figures 2 and 4.

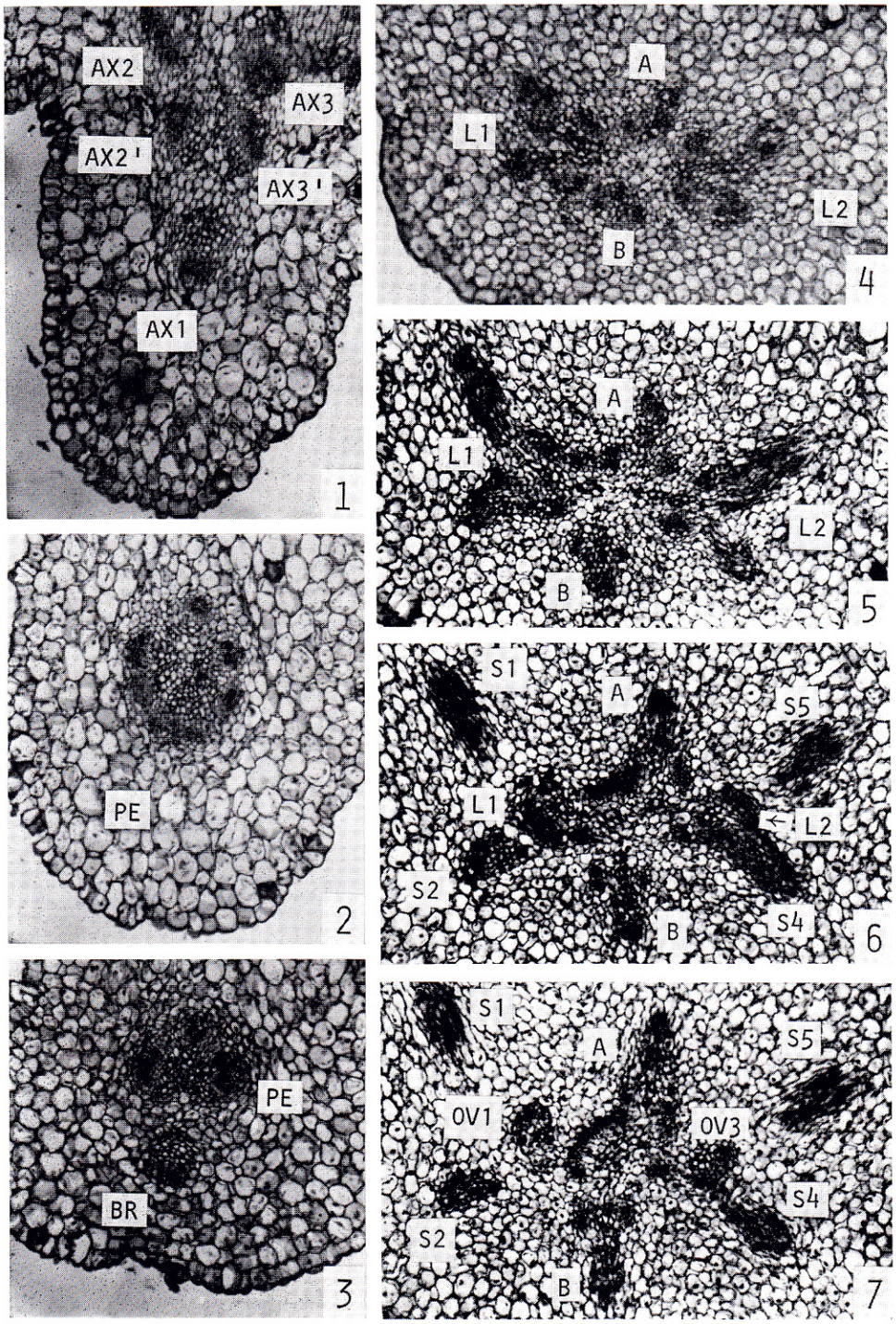

Plate 4. Transverse sections of *Zippelia begoniaefolia*.
1: Inflorescence axis. 2, 3: Basal part of pedicel. 4–7: Receptacle. (all ×112).
For abbreviations see Figures 2 and 4.