

Floral anatomy and development of *Piper kadzura*
(CHOIS.) OHWI (Piperaceae)

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フウトウカズラ（コショウ科）の花の形態と発生

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コショウ科フウトウカズラ *Piper kadzura* (CHOIS.) OHWI の花の維管束走向と器官発生の観察から花の構造を解析し、他のコショウ属 (*Piper*) や *Zippelia* との比較を行った。その結果、従来雄花は3本の雄しべからなり、雌花は1個の雌しべからなるとされてきたが、雌花の子房基部には通常3本の退化雄しべが見られ、雄しべの中央にはまれに退化雌しべが見られた。そのほか、雄しべ1本または2本からなる雄花、雌しべと1本の雄しべをもつ両性花などが見られた。花序では通常の雄花序・雌花序のほか、上部が雄花序で下部が雌花序、あるいは上部と基部が雄花序で中間部が雌花序となる雌雄が混生する花序が観察された。基生する胚珠には心皮の腹行維管束と推定される維管束組織が集合して入ること、雌しべの初期発生の形態が三角形であることから、フウトウカズラの雌しべは合生心皮であり、3心皮に由来することが推定され、これまで研究されたコショウ属の雌しべの構造と一致した。雌花では3本の退化雄しべが子房の周囲にはほぼ輪生状に出るが、少なくとも花序に側生する花では、花の相称性はこれまでのコショウ属の例のように左右相称である。コショウ科 *Zippelia* やドクダミ科諸属に見られる雄しべと雌しべが対をなす構造は、他のコショウ属同様フウトウカズラでも見られない。その理由は、雄しべも雌しべも花序軸との癒合が進み、心皮とおしの癒合がより進んでいることによるためと推定される。

Introduction

The group of taxa having oligomerous stamens and carpels without perianth such as Piperales has been regarded as one of the most primitive angiosperms (ex. MELCHIOR, 1964), or to the contrary, as being advanced within the Magnoliidae (ex. STEBBINS, 1974). Recent paleobotanical studies (FRIIS *et al.*, 1986; TAYLOR and HICKEY, 1990) suggest that the smaller and simpler floral types are more primitive than the large Magnolia-like flow-

ers. For creating a better understanding the ancestral angiosperm, HICKEY and TAYLOR (1996) proposed the designation of "eoangiosperms" with mostly apocarpous gynoecia, and small, simple floral units, which consists of Chloranthaceae, Saururaceae, Piperaceae, Aristolochiaceae, Barclayaceae, Cabombaceae, Nymphaeaceae, and Ceratophyllaceae. BURGER (1977) put forward a hypothesis suggesting that Piperales is the taxa connecting the dicotyledons and the monocotyledons from a comparative overview of their flowers.

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Manuscript received August 31, 1997. Contribution from the Yokosuka City Museum, No. 505.

Key words: **floral anatomy, development, floral morphology, *Piper kadzura*, Piperaceae** キーワード: コショウ科, フウトウカズラ, 花部解剖, 花部形態, 花部発生

Piperaceae consist of eight genera and ca. 3000 species (MABBERLEY, 1996). Among them, *Piper* is the largest genus, whose number of species is estimated 2000 (MABBERLEY, 1996) or 1500 (BORNSTEIN, 1989). Key characters among the species of *Piper* are the veneration of leaf, the position of inflorescence, the number of stamens, and the presence of pedicel. The flowers of *Piper* are minute, apetalous and asepalous, which are produced in spikes or racemes. The taxonomy of this genus at species level is very difficult, because of large number of species and poor number of features in gross morphology. Although it is important to know the number of stamens and carpels for understanding basic flower structure, it is difficult practically to clarify them in dried specimens in Piperaceae (TUCKER, 1982a). Thus, for example, the carpel number has been estimated mainly by the number of lobes of stigma (ex. EICHLER, 1878). In some species having four or six stamens, the carpel number has been clearly confirmed by floral anatomy and ontogenetic studies (JOHNSON, 1902; TUCKER, 1982b). One of the remarkable features in flower construction of Saururaceae is that the module of their flowers is regarded as to be composed of a carpel with one or two stamens (RAJU, 1961; YAMAZAKI, 1978). The genus *Zippelia* which appears to be represent a transitional genus between Saururaceae and Piperaceae (TUCKER *et al.*, 1993) has also such a flower construction as interpreted as the module (OMORI, 1982).

The present paper describes anatomy and development of flower of *P. kadsura* (CHOIS.) OHWI, which has three stamens in male flowers and one gynoeceium in female flowers. The main aims of this work are an examination of the number of carpel, the floral symmetry and the presence of the module or the sympodium vascularizing the carpel and stamens.

Materials and methods

Inflorescences of *Piper kadsura* (CHOIS.) OHWI collected from Mabuni, Okinawa Pref. and from Awamatsu, Chiba Pref. were preserved in FAA solution

(formalin:glacial acetic acid: 95 % ethanol:water =10:5:50:35). Combinations of the flowers and the inflorescences were observed through an optical microscope. Floral vasculature was examined by serial sections counterstained in Heidenhain's hematoxylin, safranin and fastgreen FCF. The flowers were dehydrated in normal butyl alcohol series, embeded in Paraplast and cut 10 μ m thick with a rotary microtome. Ontogenetical observation of female flowers was conducted by a scanning electron microscope. The materials were dehydrated through an ethanol-isoamyl acetate series and critical point dried with carbon dioxide. The pieces were coated with gold in a sputter coater.

Results

1. Sex impression in inflorescence and flower

Although *Piper kadsura* is ordinarily dioecious, male and female flowers were often either produced in a male inflorescence and various combinations of both unisexual flowers were observed. For example, the male flowers were produced at the upper half of inflorescence and the female flowers at the basal half, or male flowers at both upper and basal, and female flowers at the intermediate part. In *P. kadsura*, the male flower consists of three stamens and the female flower has only one gynoeceium with three- or four-parted stigma. However, three rudimentary stamens were observed at basal part of ovary in most female flowers and a rudimentary

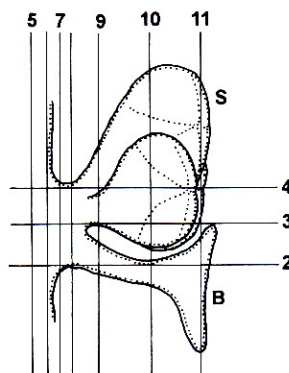


Fig. 1. Male flower with three stamens of *Piper kadsura*. The levels 2-11 with straight lines correspond to the respective sections in Figs. 2-11. B: bract, S: stamen

gynoecium was observed at the central part surrounded by three stamens in some male flowers; besides, seemingly bisexual flowers were observed, and some kinds of morphological intermediate forms from hermaphrodite to unisexual flowers were observed.

2. Vasculature of male flower (Fig. 1)

Each male flower consisting of three stamens is subtended by a peltate bract (Fig. 1: *B*) at nearly right angles to the inflorescence axis. A vascular tissue (Figs. 2, 5: *a*) extending from the inflorescence axis supplies at first a bract bundle (Figs. 2, 6: *b*) to divide into three stamen bundles (Figs. 3, 4, 7, 8: *s*) in the inflorescence axis. Each of the three bundles enters an anther (Fig. 10: *s*) through a short pedicel (Fig. 8) and filament (Fig. 9). The bract bundle is divided into three or more branches at the top of bract (Fig. 11: *b*).

3. Vasculature of female flower

As well as the male flower, a female flower is subtended by a peltate bract at almost right angles to the inflorescence axis. The female flower has one gynoecium with three staminodes at the basal part of ovary. The gynoecium has only one ovule at basal placenta. Two types of vasculature were observed in *Piper kadsura* corresponding to the position of the flower; lateral and terminal flowers.

1) Lateral female flower (Fig. 12)

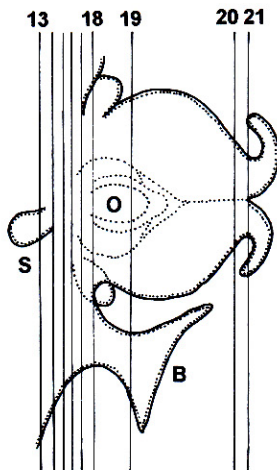


Fig. 12. Female flower with a gynoecium and three staminodes at the lateral of the spike in *P. kadsura*. Levels 13-21 correspond to the respective sections in Figs. 13-21. *B*: bract; *O*: ovule; *S*: staminode.

A vascular tissue (Fig. 13: *a*) extending from the inflorescence axis supplies bundles to one unit of bract and flower. In some cases, the vascular tissue bifurcates before supplying vascular bundles to the unit. It gives off a branch to supply a bract bundle (Fig. 15: *b*), and then supplies a bundle to a staminode at the anterior-median and two bundles to two staminodes at the posterior-lateral (Fig. 16: *s*). The anterior-median staminode (Fig. 18: *s*) is shifted somewhat on the right or the left from the median sagittal plane at anthesis. After giving off three branches to the staminodes, the vascular tissue supplies six or seven, usually six bundles, to the ovary (Figs. 18, 19: *or* and arrows) and the remaining bundle enters an ovule at the basal center of ovary (Figs. 20, 21). Six ovary bundles run through ovary wall to the upper top of ovary, however, do not enter the stigma.

2) Terminal female flower (Fig. 22)

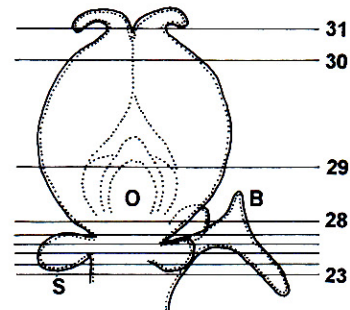
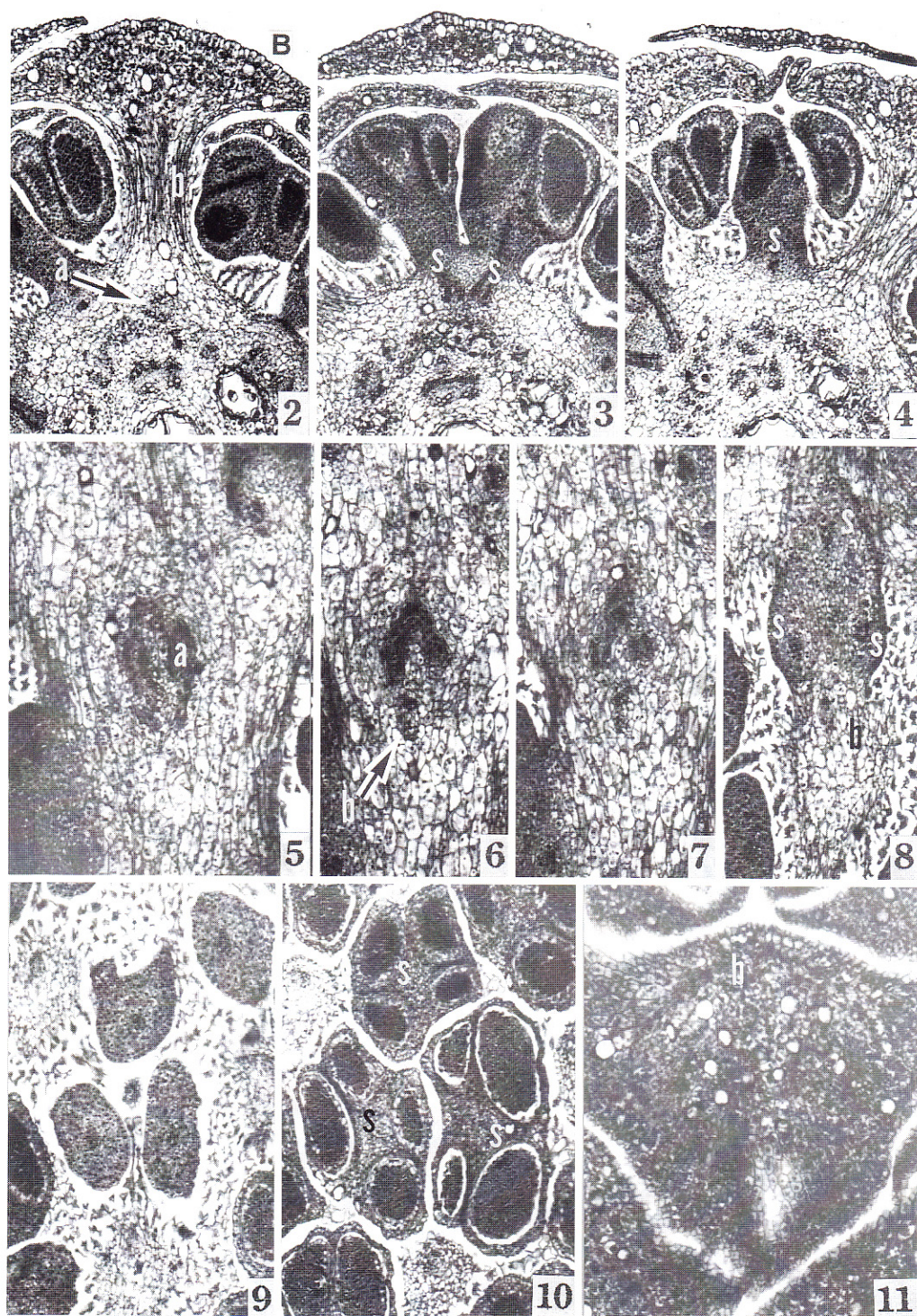


Fig. 22. Female flower with a gynoecium and three staminodes at the terminal of the spike in *P. kadsura*. Levels 23-31 correspond to the respective sections in Figs. 23-31. Abbreviations are the same as in Fig. 12

Four or five vascular bundles are remained under the terminal female flower of spike (Fig. 23). One of them becomes a bract bundle (Fig. 23: *b*), and then three staminode bundles are diverged radially from the remaining vascular tissue at 120° each other (Figs. 24-27: *s*). At the bottom of ovary, six bundles from the vascular tissue are supplied to the ovary (Figs. 28-30: *or* and arrows). The remaining vascular tissue at the center of ovary enter an ovule (Fig. 28: *o*). Six ovary bundles run through ovary wall to



the upper part of ovary and upwardly diminish under the stigma (Fig. 31).

Both in the lateral and the terminal female flowers, three staminode bundles and in succession six ovary ones are given off, and the remaining bundles fuse to enter an ovule. Since the staminode bundle is not paired any ovary bundles, sympodium structure of carpel and stamen was not recognized in *P. kadzura*.

4. Development of female flower

At the early stage of gynoecium development, the gynoecium rises in the form of a triangle (Fig. 32: G), which is surrounded by three staminodes; one is anterior and two are posterior (Figs. 32, 33: S). After that the gynoecium enlarges to become rhombic from triangle (Fig. 34), then the anterior staminode is shifted to the right or the left from the median sagittal plane. An older flower has a circular gynoecium primordium and central depression (Figs. 34-35). The gynoecium primordium rises much more and produces four to six lobes (Fig. 36). At the center of the bottom of locule, one ovular primordium rises in a cone shape (Fig. 37: O). The lobes become three or four distinct lobes, which remain separate distally (Fig. 38). At the same time, a nucellus is surrounded by an inner integument (Fig. 39). As the lobes enlarge much more (Fig. 40), the ovarian locule deepens and enlarges, and an outer integument appears outside the inner integument (Fig. 41). Enlargement of the lobes makes the

upper part of gynoecium cone shape (Figs. 42, 43), and the inner integument begins to cover the nucellus (Fig. 43). At maturity, the gynoecium lobes bend to the outsides to become stigmatic lobes, surfaces of which are covered with many small projections (Figs. 44, 45)

Discussion

1. Sex expression

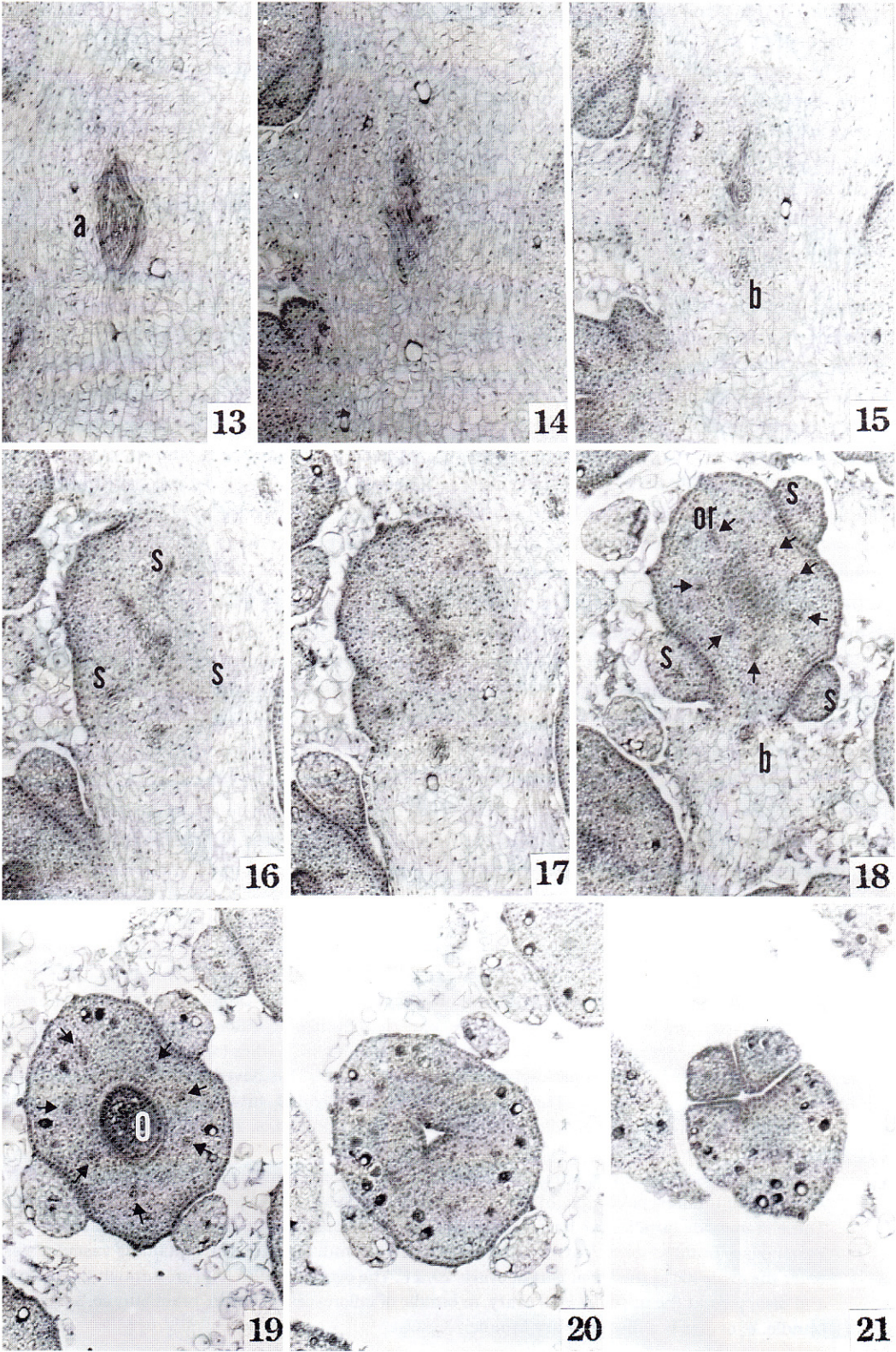
P. kadzura is ordinarily dioecious, although hermaphrodite flowers are widely seen in *Zippelia* and *Peperomia* of Piperaceae and in all genera of Saururaceae closely related Piperaceae. Dioecy in this species is not rigid but flexible, because not only unisexual flowers of both sexes but also hermaphrodite flowers are produced on the same inflorescence. Thus, the dioecy or the unisexuality of *P. kadzura* is supposed to be a derived character state from bisexuality.

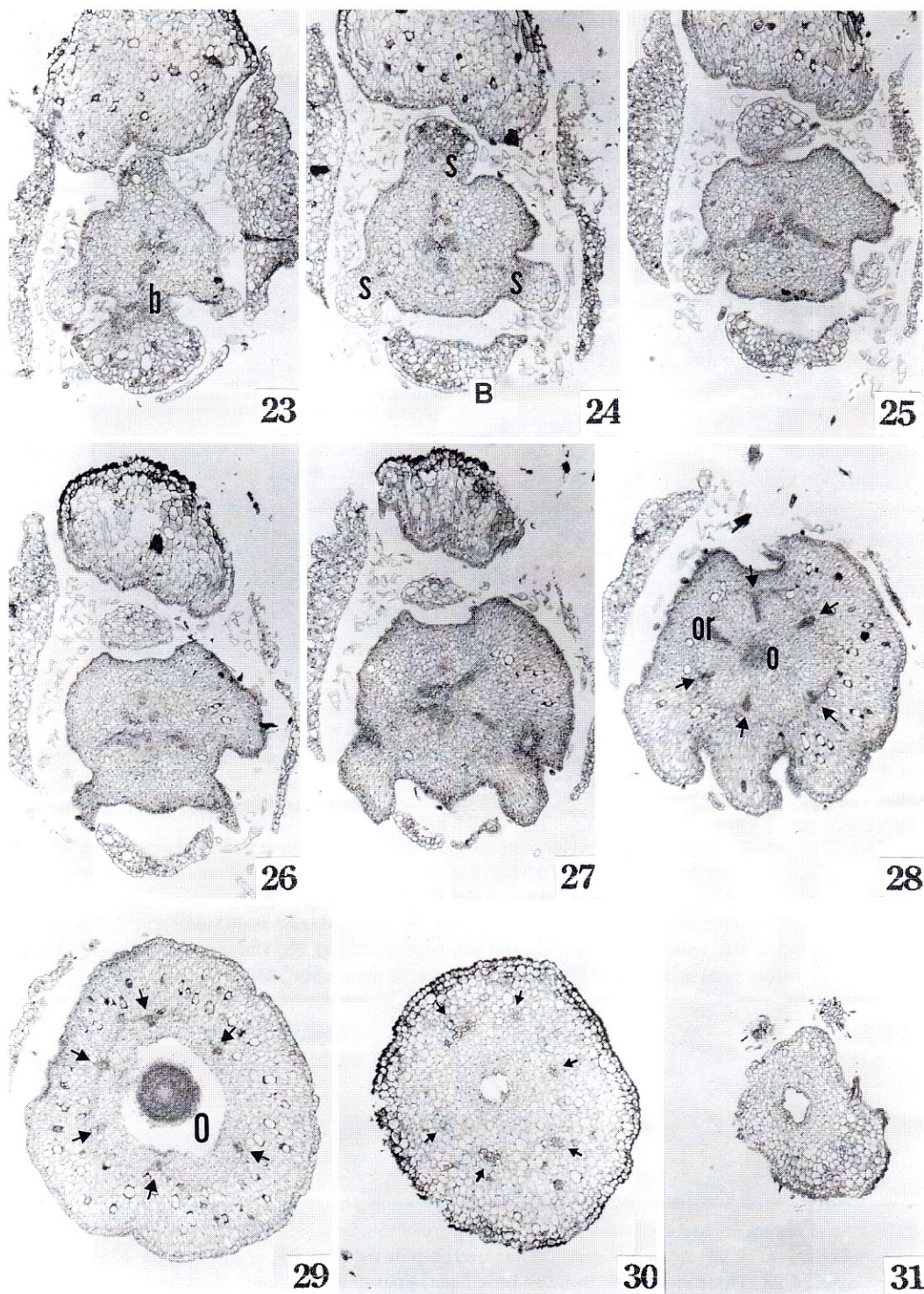
2. Stamen arrangement

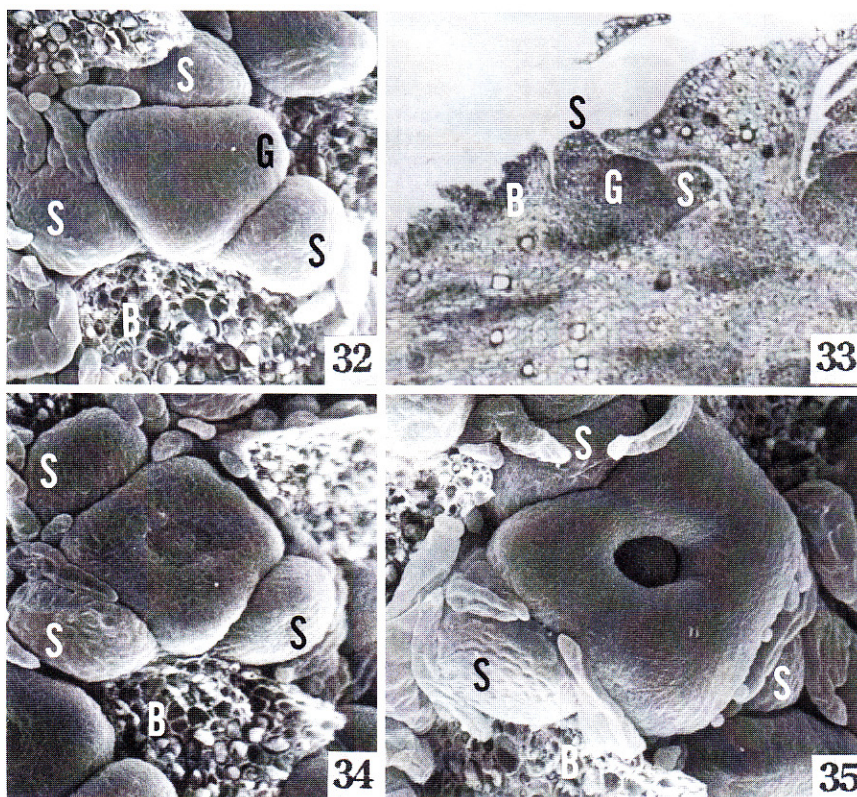
The male flower of *P. kadzura* consists of three stamens. Each stamen receives one bundle which is given off by simple tri-furcation of a branch of the bundles of inflorescence axis. Almost the same branching pattern occurs also in the case of staminodes of the female flower. In lateral flowers, an anterior staminode is not situated just on the medial sagittal plane but located in somewhat left or right side apart from the plane. This deviation is interpreted as the movement accompanied by

Figs. 2-11. Serial longitudinal (2-4) and transverse (5-11) sections showing the vasculature of the male flower of *P. kadzura*. 2-4: $\times 58$, 5-11: $\times 52$. 2. A bract bundle (b) has diverged from a bundle of inflorescence axis (a). 3. Two posterior stamen bundles (s) have separated from the bundle a. 4. An anterior stamen bundle (s) from the bundle of inflorescence axis. 5. A bundle of inflorescence axis (a). 6. A bract bundle (b) has separated from the bundle a. 7. Three stamen bundles (s) have been divided. 8. The stamen bundles have been separated each other. 9. Three stamens have been divided. 10. Each three anthers has four locules. 11. The bract bundle (b) has divided into some small bundles at the terminal of bract. a: bundle of inflorescence axis, b: bract bundle, s: stamen bundle.

Figs. 13-21. Serial transverse sections showing the vasculature of the lateral female flower of *P. kadzura*. $\times 70$. 13. A bundle of inflorescence axis (a), 14, 15. A bract bundle (b) has separated from the bundle a. 16. Three staminode bundles (s) have separated from the remaining bundles at 120° each other. 17, 18. Seven ovary bundles (or and arrows) have been divided radially. 19. The remaining vascular tissue enter the ovule (O) at the basal part of ovary. 20, 21. The ovary bundles (or) run through the ovary wall and disappear at the upper part of ovary. a: bundle of inflorescence axis, b: bract bundle, s: staminode bundle, o: ovular bundle, or: ovary bundle.

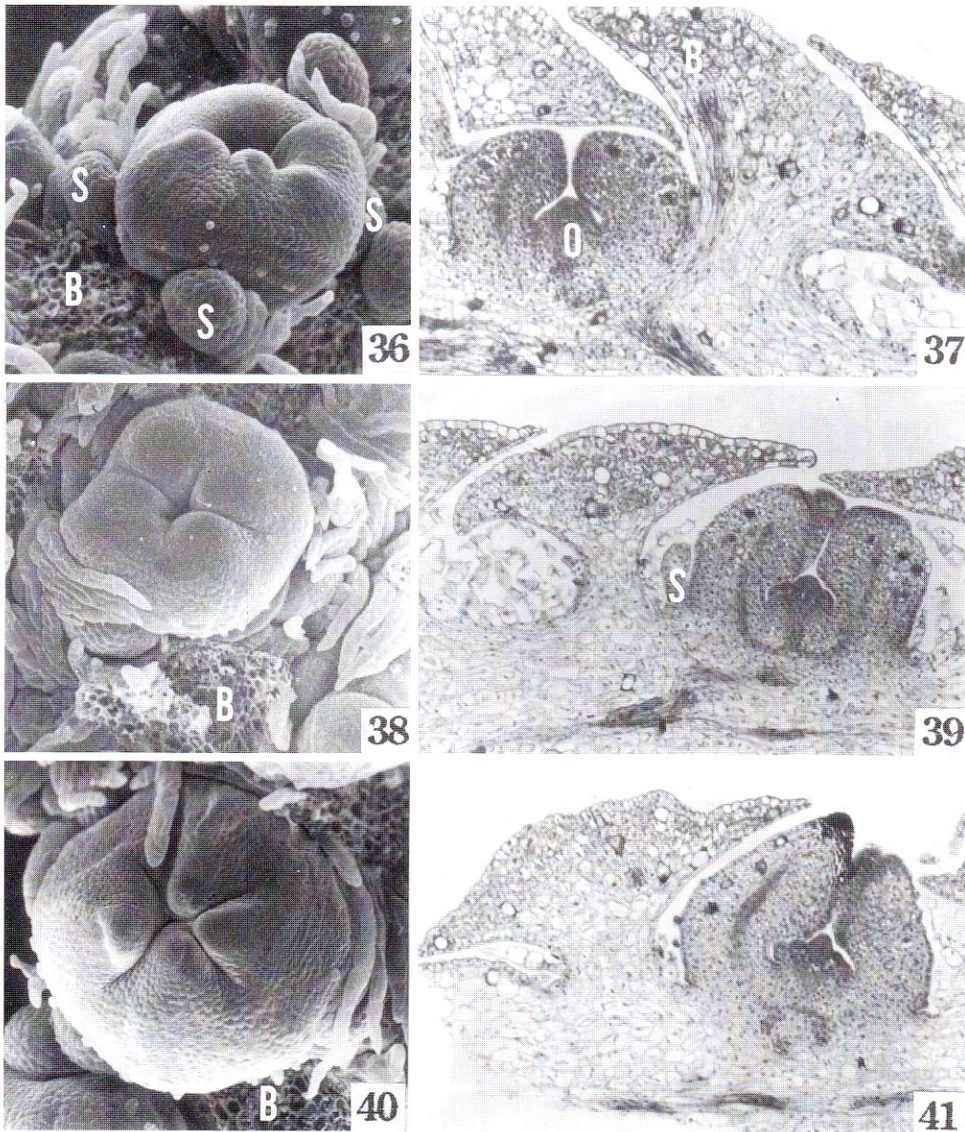




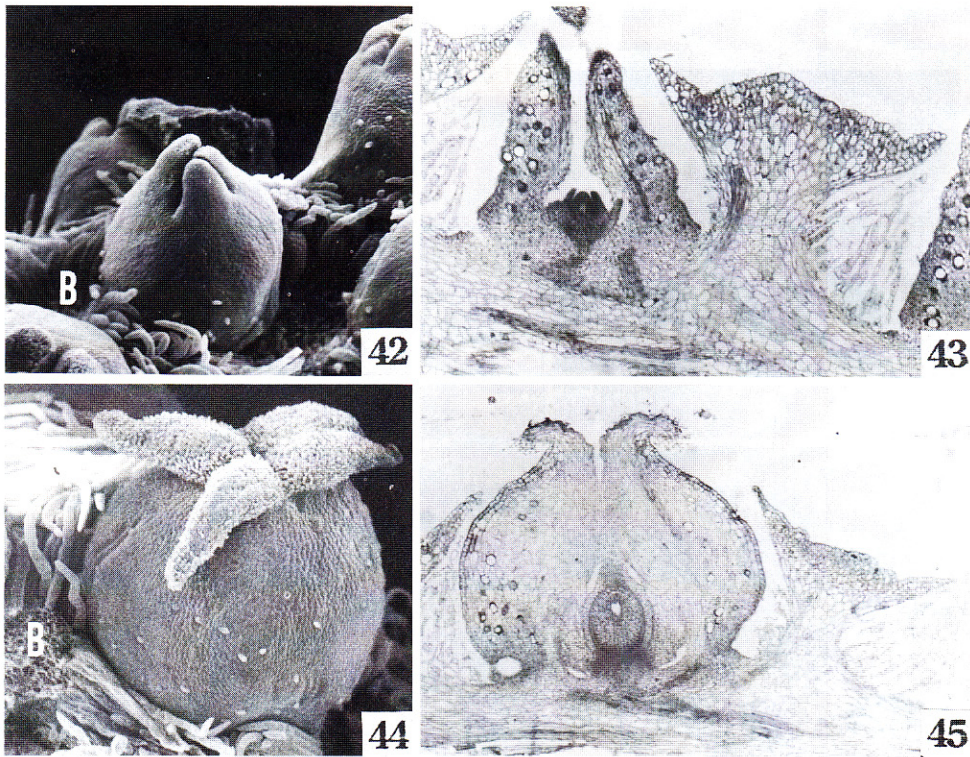


Figs. 32-35. Early female flower development of *P. kadzura*. The bracts have been removed. 32. Triangle-shaped gynoeceum (G) surrounded by one anterior-median and two posterior lateral staminodes (S) (SEM). $\times 200$. 33. Median longitudinal section of gynoeceum (G), staminodes (S) and bract (B). $\times 69$. 34. The anterior staminode has shifted to the left from the median sagittal plane (SEM). $\times 200$. 35. The gynoeceal primordium has risen in a ring (SEM). $\times 200$. B: bract, G: gynoeceum, S: staminode.

Figs. 23-31. Serial transverse sections showing the vasculature of the female flower of *P. kadzura* at the terminal of spike. $\times 42$. 23. A bract bundle (b) has been separated from one of the bundles of inflorescence axis. 24, 25. Three staminode bundles have been separated from another bundles of inflorescence axis. 26-28. The remaining vascular tissue has been divided into six ovary bundles (or and arrows) and one ovular bundle (o). 29, 30. The ovary bundles (arrows) run through the ovary wall. 31. The bundle or disappear gradually at the upper part of ovary. Abbreviations are the same as in Figs. 13-21.



Figs. 36-41. Middle developmental stage of the female flower of *P. kadzura*. The bracts have been removed. 36. The gynoecial primordium has four to six lobes (SEM). $\times 100$. 37. Gynoecium with ovule primordium at center (median longitudinal section). $\times 73$. 38. Three or four lobes have clearly separated (SEM). $\times 100$. 39. Basal ovule with nucellus and inner integument forming (median longitudinal section). $\times 51$. 40. The lobes enlarge and the staminodes are not visible (SEM). $\times 100$. 41. Ovule with two integuments surrounding the nucellus (median longitudinal section). $\times 54$. B: bract, O: ovule, S: staminode.



Figs. 42-45. Late female flower development of *P. kadzura*. The bracts (*B*) have been removed. 42. Lobes elongate and gynoecium becomes cone-shaped (SEM). $\times 50$. 43. Median longitudinal section at almost the same stage of Fig. 42. $\times 45$. 44. Flower at anthesis with four stigmatic lobes (SEM). $\times 50$. 45. Median longitudinal section at anthesis. $\times 34$. *B*: bract.

growth of ovary from ontogenetical study and observation of the terminal flower having no such deviation.

3. Carpel number

The flower of *Zippelia begoniaefolia*, which is regarded as the basal taxon in Piperaceae (TUCKER *et al.*, 1993), has six stamens and one ovary. The ovule is supplied by one bundle which is made by the fusion of eight ventral bundles of four carpels (OMORI, 1982). In this study, the floral vasculature of *P. kadzura* reveals the ovule is supplied by one fused bundle of more than one carpel as well as in *Zippelia* (Figs. 46-48). Thus, *P. kadzura* shares almost the same basic structure plan of gynoecium with *Zippelia*.

The anatomical and ontogenetic studies in a few

species of *Piper* (JOHNSON, 1902; TUCKER, 1982b) suggested that their flowers had three-carpellate gynoecium instead of one or two. In *P. kadzura*, the ovary ordinarily has six vascular bundles and it is impossible to distinguish the dorsal and ventral bundles of the ovary. In early development of gynoecium, it rises in triangle alternate to staminode arrangement, and the gynoecium of *P. kadzura* is supposed to be derived from three-carpellate gynoecium as well as other species of *Piper* reported by TUCKER (1982b).

If the ovary bundles of *P. kadzura* are regarded as dorsal bundles of carpels as well as in *Zippelia*, *P. kadzura* is supposed to have six-carpellate gynoecium. Although a pair of stamen and carpel is a basic unit of the flowers of *Zippelia* and *Saururus* and other saururaceous genera (RAJU, 1961;

YAMAZAKI, 1978), in *P. kadmura*, the fusion of floral organs are progressed so much that the sympodium of carpel and stamen is not appreciable by vasculature.

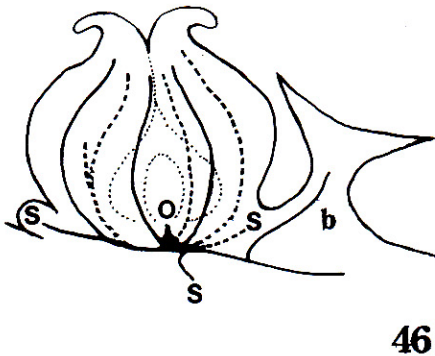
4. Comparison of the flower in Piperaceae

EICHLER (1878) interpreted that the basic structure of the flower of *Piper* consisted of three-carpellate gynoecium and six stamens (subgenus *Enkea*) and that other subgenera which have two to four stamens had been derived from *Enkea* by reduction of stamen number and thought that the flower of *Piper* was trimery and actinomorphic. JOHNSON (1902) described that the outer three stamens were produced earlier than the inner ones in *Piper* with six stamens and that the gynoecium developed from three lobes in some species of *Piper*. On the other

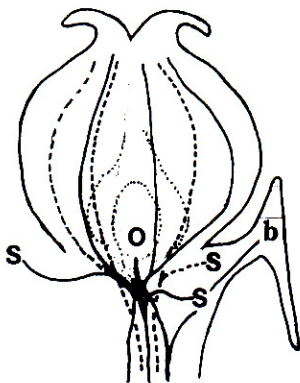
hand, TUCKER (1975, 1976, 1981, 1982b, 1985), LIANG and TUCKER (1989, 1990), TUCKER *et al.* (1993) and TUCKER and DOUGLAS (1996) investigated in detail the floral development of Piperaceae and Saururaceae, and made clear that the developmental pattern of stamens and carpels was not trimery but bilateral and/or dorsiventral symmetry. In female flowers of *P. kadmura*, the arrangement of three staminodes and early floral development supports the results of TUCKER (1982b) and TUCKER *et al.* (1993).

Acknowledgements

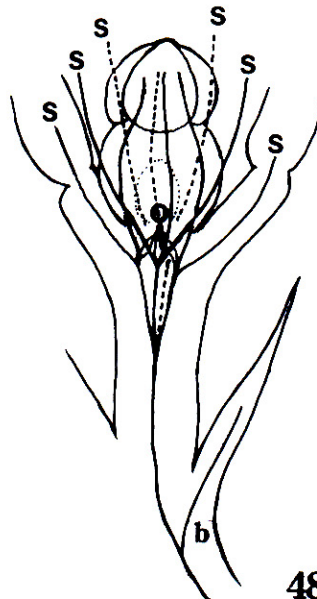
My sincere thanks are due to Drs. YAMAZAKI T. and ONO M. for their helpful support and encouragement. I thank also Dr. SUGIYAMA M. (Saitama Women's Junior College) for worthwhile advice and Dr. WAKABAYASHI M. (Tokyo Metropolitan University) for comments on an earlier draft of the manuscript



46



47



48

Figs. 46-48. Reconstruction of floral vasculature. 46-47. *P. kadmura*. 46. Female flower at the lateral of spike. 47. Female flower at the terminal of spike. 48. *Zippelia begoniaefolia* (modified after OMORI, 1982). b: bract bundle, o: ovular bundle, s: stamen or staminode bundle.

and encouragement during the course of this study.

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