

Floral anatomy of *Piper postelsianum* MAXIM. (Piperaceae)

OMORI Yuji * and KOBAYASHI Sumiko **

タイヨウフウトウカズラ *Piper postelsianum* MAXIM. の花部解剖学

大森雄治*・小林純子**

Key words: Bonin Islands, floral anatomy, vasculature, Piperaceae, *Piper postelsianum*
キーワード：花部解剖学，維管束走向，コショウ科，タイヨウフウトウカズラ，小笠原諸島

Floral vascular system of *Piper postelsianum* MAXIM. was observed for making clear the number and the arrangement of the floral leaves of both the male and female flowers. The male flowers usually have six stamens and a rudimentary gynoecium at the center, which are regarded to be arranged in two wholes with three each. The female flowers usually have an ovary with four stigmas at the top. They are regarded as four-carpellate gynoecium because they have four ovary bundles and stigmas. In a recent monographic study of the Micronesian *Macropiper*, *P. postelsianum* was included in *Macropiper* and considered to be a synonym of *M. guahamense* f. *glabrum* (YUNCKER) A.C.SM. because of the number of stamens, which was regarded as three on the basis of the original description. However the result of this anatomical study doesn't support such an opinion but reconfirms to be obviously a good species, *P. postelsianum*.

小笠原に固有のコショウ科植物、タイヨウフウトウカズラの雄花と雌花の維管束走向を観察し、各花葉の数と配列を明らかにした。雄花は多くは6本の雄しべを持ち、3本ずつが2輪生すると解釈され、中央には退化雌ずいが見られた。雌花は1個の雌しべからなり、多くは4個の柱頭をもち、子房に4本の維管束が入ることから、4心皮性の合心皮と推定した。ミクロネシアのマクロピペル属のモノグラフ(SMITH, 1975)では、原記載(MAXIMOWICZ, 1887)にしたがって、本種の雄しべの数は2、または3と判断され、花序が腋生することから、*Macropiper*属に分類され、*M. guahamense*の1種内分類群、*M. guahamense* f. *glabrum* (YUNCKER) A.C.SM. の異名同種とされた。しかし、今回の結果はこれを支持せず、独立種 *P. postelsianum* であることを再確認した。

*Yokosuka City Museum, 95 Fukadadai, Yokosuka 238-0016. 横須賀市自然・人文博物館

**4-2-23 Yukinoshita, Kamakura 248-0005. 鎌倉市雪ノ下 4-2-23

Manuscript received October 31, 2000. Contribution from the Yokosuka City Museum, No. 548

Introduction

Piperaceae consists of about ten genera, which are classified by the position of inflorescence, the presence of pedicel and the number of stamens, and 3000 species (ex. MABBERLEY, 1997). It is very difficult to examine the interrelationships among genera or among species because their flowers are very small, achlamydeous and simple. Piperaceae is one of the key families for studying early evolution of angiosperms because it is suggested that Piperaceae might be and an ancestor of monocotyledons (BURGER, 1977) and one of the most primitive families by recent DNA analysis (ex. SYTSMA and BAUM, 1996) and fossil information (ex. TAYLOR and HICKEY, 1990). However, there are little exact data even about floral morphology. The present study for clarifying the flower structure of *Piper postelsianum* (Fig. 1) follows *Zippelia begoniaefolia* (OMORI, 1982) and *P. kadsura* (OMORI, 1997).

Piper postelsianum is an endemic species of Bonin Islands in Japan (MAXIMOWICZ, 1887). It is one of only two species of *Piper* which grow wild in Japan. The erect stem, the large and round leaf, the axillary and umbellate spike are characteristics of this species. It is difficult even to examine the number of stamens because of small sessile flowers growing thick on the spadix. The original description about the number of stamens is ambiguous, 'stamens 2(3?)' (MAXIMOWICZ, 1887). This species is distributed in an extremely limited small area only in Hahajima of the Bonin Islands and the population is very small, so we have been very few opportunities to examine well preserved specimens at anthesis. Therefore the ambiguity of the stamen number, which is one of very important characters for classification of Piperaceae, have been accepted as it is. SMITH (1975) examined the relationships between *P. postelsianum* and Micronesian species of *Macropiper* and came to the conclusion that it was a synonym of *M. guahamense*

var. *glabra*. The classification of this species should be re-examined on the basis of exact description of the flower.



Fig. 1. *Piper postelsianum*, cultivated at the Botanical Garden of University of Tokyo, Tokyo.

Materials and methods

Male inflorescences of *P. postelsianum* were collected at Mt. Sekimon, Isl. Hahajima, the Bonin Islands, on 17 March 1972 (MAK-126899, Makino Herbarium, Tokyo Metropolitan university) and preserved as dried specimens. Male flowers were softened in 1% ammonium solution for the anatomical study. Female flowers were collected at the same location on 20 June 1979 to be fixed and be preserved in FAA solution (formalin-acetic acid-ethyl alcohol). The flowers were dehydrated in normal butyl alcohol series and embed-

ded in Paraplast. They were cut into serial sections of 10 μ m in thickness with a rotary microtome and counterstained with haematoxylin, safranin and fastgreen FCF.

Results

Piper postelsianum is dioecious. Large number of flowers is produced in spikes or spadices. One to four axillary inflorescences occur in umbell (Fig. 1). Herbarium specimens in TI (Herbarium, University of Tokyo) and MAK (Makino Herbarium, Tokyo Metropolitan University) showed that the anthesis of male flowers occurred from March to the beginning of May and that of female ones from June to August.

1. Male flower

The male flower of *P. postelsianum*, which is subtended by a peltate bract (Fig. 2-1,3:B), consists of six stamens and one rudimentary gynoecium (Fig. 2-3, Fig. 3-7: RG) surrounded by the stamens. It usually has six stamens (Fig. 3), but five (Fig. 2-3) in some cases.

One vascular bundle from the stele of the inflorescence axis supplies a bract - flower bundle, *a* (Fig. 3-1). The bundle *a* supplies a bract bundle, *b* (Fig. 3-1,2). At the base of flower the vascular tissue of the bundle *a* spreads (Fig. 3-2,3) to divide into one stamen bundle in the adaxial side (Fig. 3-3: *s1*) and two ones in the abaxial side (Fig. 3-3: *s3*, *s5*). Then the bundle *a* supplies two adaxial (Fig. 3-4: *s2*, *s6*) and one abaxial bundles (Fig. 3-4: *s4*). Thus six stamen bundles (Fig. 3-5) are supplied by the bundle *a* and then the stamens of *P. postelsianum* are arranged in two whorls consisting of each three.

One ovular bundle (Fig. 3-5: *ov*) and four ovary bundles (Fig. 3-5: *o1-o4*) remain under the rudimentary gynoecium (Fig. 3-7: RG). Each of the stamen and ovary bundles branches off from the bundle *a* at almost the same level and the remaining bundle tissue becomes an ovular bundle *ov*, therefore the branch

system between the stamen bundles *s1-s6* and the ovary bundles *o1-o4* is not clear. Thus it is impossible to regard each of the stamen bundles as a branch of an ovary bundle. The stamen bundles *s1-s6* branch off in six directions at almost the same plane, but one central adaxial bundle and two lateral abaxial bundle branch off before other bundles; two lateral adaxial and one central abaxial bundles. Thus the former three stamens are regarded as outer whole of stamens (Fig. 3-8,9: *s1*, *s3*, *s5*) and the latter ones as inner whole of stamens (Fig. 3-8,9: *s2*, *s4*, *s6*).

An ovular bundle *ov* enters the basal part of ovule (Fig. 3-5: *ov*). Four ovary bundles *o1*, *o2*, *o3* and *o4* (Fig. 3-5) run through ovary wall (Fig. 3-5,6,7) and each of the stamen bundles *s1-s6* enter the stamens (Fig. 3-6,7: *s1-s6*) to the center of the anthers (Fig. 3-8: *s1-s6*). The bract bundle *b* runs through the stalk of the bract to branch off in the peltate blade (Fig. 3-9: *b*).

2. Female flower

The female flower of *P. postelsianum* is sessile (Fig. 2-4) and subtended by a peltate bract (Fig. 2-2,4: B). The stigma is divided in four and the ovary has one locule with one ovule. The ovule is attached to basal placenta and orthotropous (Fig. 4). The female flower of *P. postelsianum* does not have rudimentary stamens as that of *P. kadsura* has (OMORI, 1997).

Piper has atactostele as monocotyledons, which consists of large bundles in the center and smaller bundles around them (Fig. 4-1,2). A bract - flower bundle *a* branch off from the outer small bundle of the stele (Fig. 4-1,2: *a*). The bundle *a* (Fig. 5-1,2,3: *a*) spreads to five directions just under the gynoecium (Fig. 5-3, 4: *a*) to supply a bract bundle *b* at the abaxial side (Fig. 5-3,4: *b*) and four ovary bundles to one abaxial (Fig. 5-4: *o3*) and adaxial (Fig. 5-4: *o1*) and two lateral sides (Fig. 5-4: *o2*, *o4*). The ovary bundles *o1-o4* run through ovary wall (Fig. 5-5,6,7,8) and enter the style (Fig. 5-9). The branches from the ovary bundles fuse each other to

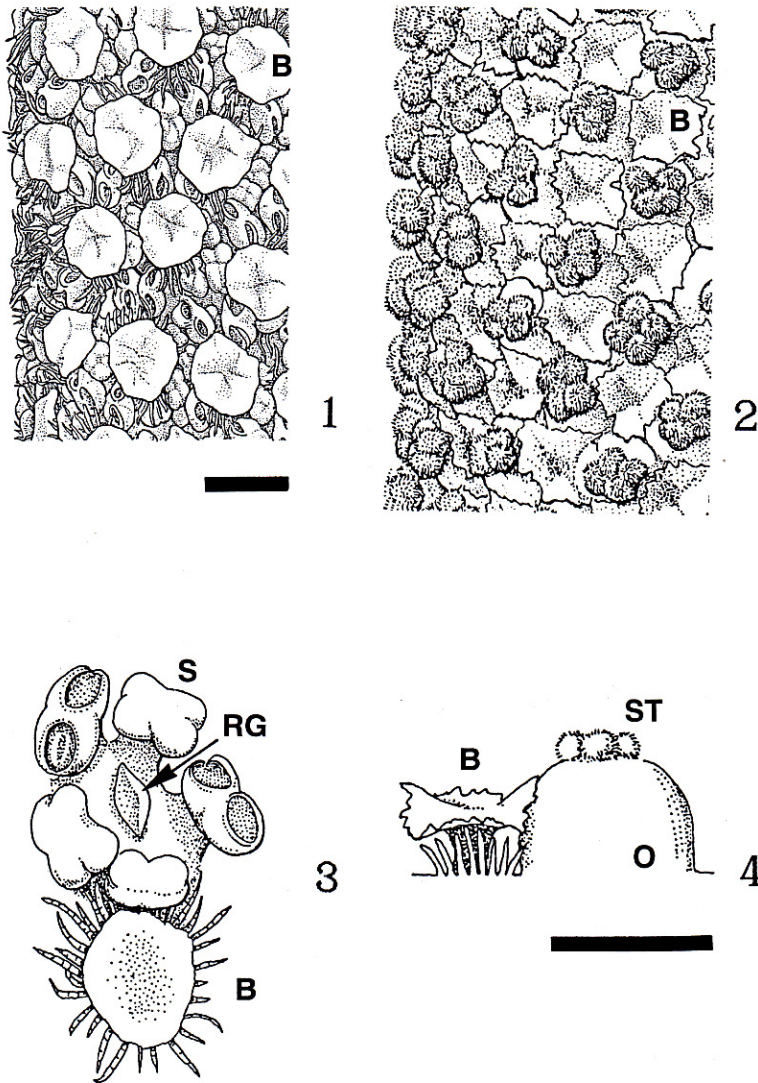
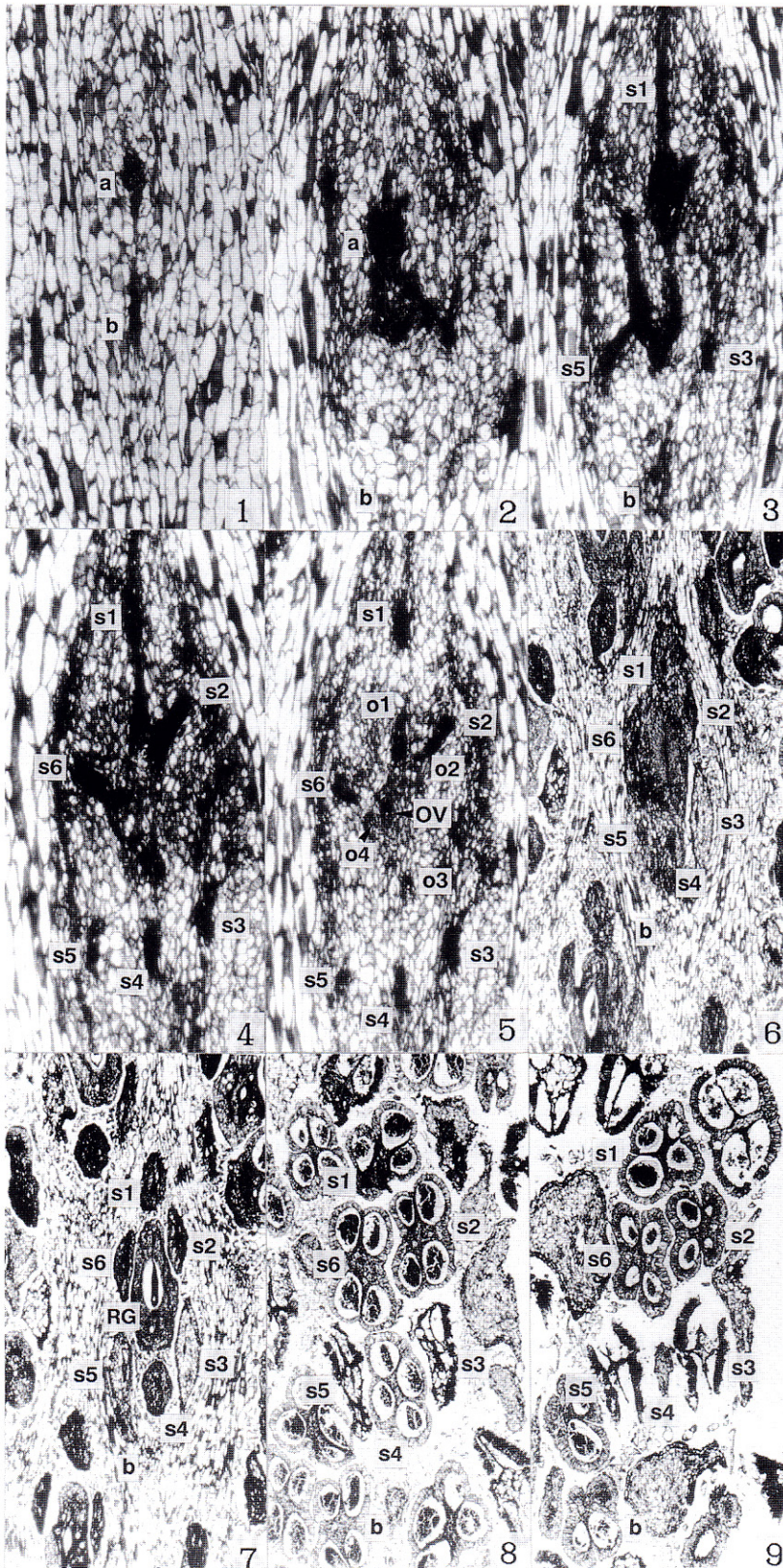


Fig. 2. Inflorescence and flowers of *Piper postelsianum*. 1: a part of male inflorescence, 2: a part of female inflorescence, 3: male flower with five stamens and a rudimentary gynoecium subtended by peltate bract, 4: female flower subtended by peltate bract. B: bract, O: ovary, RG: rudimentary gynoecium, S: stamen, ST: stigma. Scale bars = 1mm. [drawn by M. NAKAJIMA]

Fig. 3. Serial transverse sections from the basal to the upper part of male flower of *Piper postelsianum*. Six stamen bundles branch off from a branch of a stelar bundle at almost the same plane, three stamens are regarded as outer whole of stamens s1, s3, s5 and inner whole of stamens s2, s4, s6. Further explanations are in the text. a: bract - flower bundle, b: bract bundle, o1- o4: ovary bundle, ov: ovular bundle, RG: rudimentary gynoecium, s1-s6: stamen bundle. 1-5. $\times 71.6-9.$ $\times 29.$



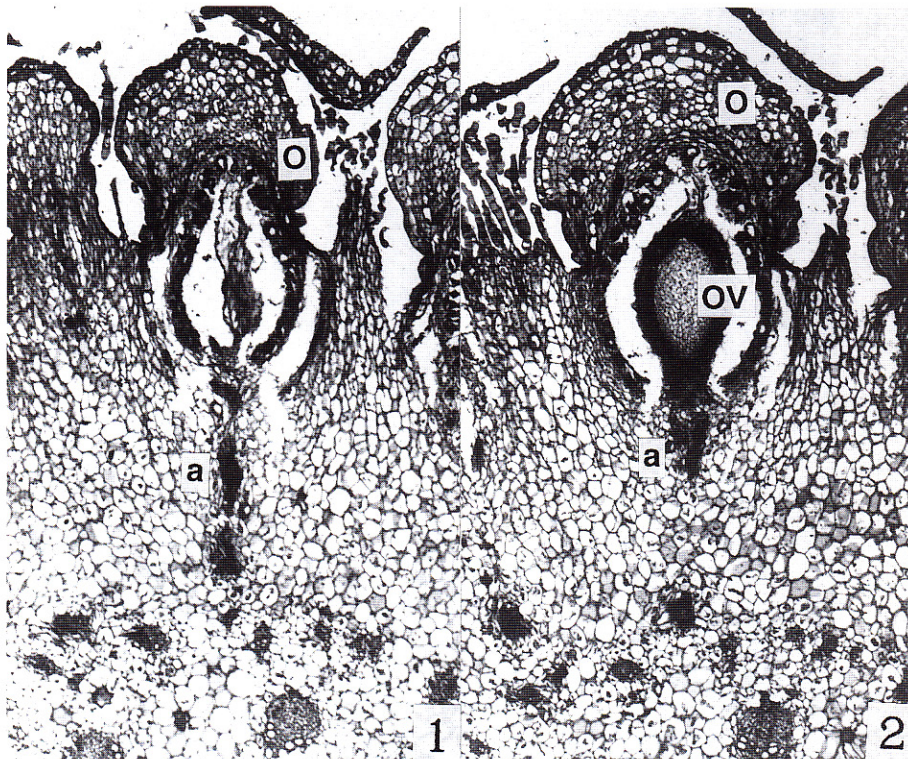


Fig. 4. Serial longitudinal sections of female flower of *Piper postelsianum*. A branch (a: bract and flower bundle) from the outer small bundle of the stele in the inflorescence axis run to the basal part of flower. O: ovary, OV: ovule, a: bract and flower bundle. $\times 50$.

become an ovular bundle *ov* (Fig. 5-5). The bract bundle *b* runs through the stalk of the bract to branch off in the peltate blade (Fig. 5-8,9: *b*). The ovary usually has four bundles, but sometimes has three or five bundles. The ovary bundles and the ovular bundle divide at the same plane, so it is impossible to judge whether the ovular bundle branch off from any particular ovary bundle.

Discussion

The male flower of *P. postelsianum* consists of six stamens, which arrange in two wholes with each three stamens from the standpoint of floral anatomy. MAXIMOWICZ (1887) described that the male flower had 2 or 3 stamens. The discussions about the relationships between this species and others of *Piper* due

to the original description because the stamen number has proved difficult to determine on dried specimens. Thus this species has been classified as *Macropiper* or *Piper sensu lato* section *Macropiper*, which has three stamens. Although the flower of *P. geniculatum* and that of genus *Enckea* have six stamens (ECKARDT, 1937; EICHLER, 1878) like *P. postelsianum*, it is hermaphrodite. Therefore it is impossible to classify *P. postelsianum* into *Macropiper* or *Enckea*. The classification of the genus *Piper* might be under review. At least the exact number and arrangement of stamens should be reexamined in much more species.

The female flower of *P. postelsianum* is estimated to be four-carpellate gynoeceium because four stigmas and four ovary bundles in many cases. The ovule bundle is regarded to be not a fused bundle consisted of the branches of all ovary bundles as in *Zippelia*

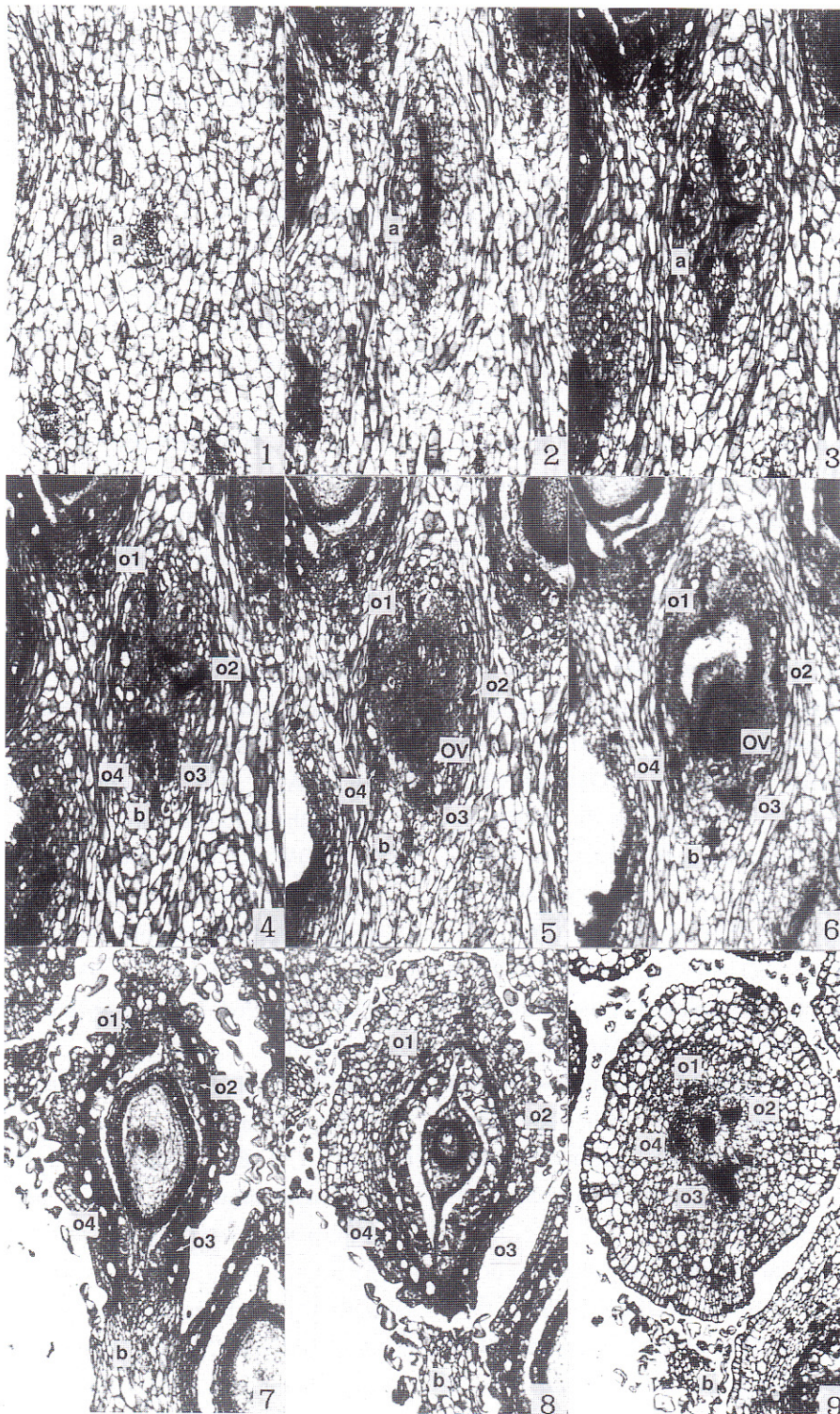


Fig. 5. Serial transverse sections from the basal to the upper part of female flower of *Piper postelsianum*. A bract-flower bundle *a* is a branched from a stellar bundle. Further explanations are in the text. Abbreviations as per Fig. 3. $\times 54$.

begoniaefolia (OMORI, 1982), but a branch of an ovary bundle or fused bundles from two or three ovary bundles.

SMITH(1975) included *P. postelsianum* in *Macropiper* because of axillary spikes, three stamens and round leaf and classified it to be a synonym of *M. guahamense* var. *glabra*. However the flower of *M. guahamense* is hermaphrodite with three stamens and the spike attaches separately on the axil. Thus it is a question to include *P. postelsianum* in the genus *Macropiper*, although it is impossible to discuss the adequate position of this species because of no anatomical data of the flowers of other species with six stamens. *P. postelsianum* is obviously a good species and it is not clear whether this species might be related to the species of *Macropiper* which are distributed in the Micronesia in and south of Guam Islands. It might be included in *Pothomorphe* Miq. if the axillary umbellate spikes would be regarded as important.

It is suggested that the flower of *Zippelia* is similar to that of *Saururus* of Saururaceae (OMORI, 1982) and is the most primitive in Piperaceae. The basic number of stamens of piperaceous flowers has been supposed to be six, which consists of two wholes with three stamens, and that of carpels three (ex. MELCHIOR, 1964; YUNCKER, 1958). TUCKER (1982) examined the development of the hermaphrodite flowers of three species with four and six stamens, which are distributed in the America. In these flowers the stamens develop independently or in a pair, therefore she decided that the symmetry of stamen arrangement of *Piper* was not radial but bilateral or dorsiventral (TUCKER, 1982).

Although rudimentary stamens were observed in the female flowers of *P. kadsura* (OMORI, 1997), they were not observed in those of *P. postelsianum*, but on the contrary rudimentary gynoecia were observed in the male flowers of this species. These suggest that both the male and the female flowers could be derived from the hermaphrodite flowers in Piperaceae. *P.*

postelsianum is considered to be a key species for examining more adequate classification of *Piper* because of axillary umbellate spikes and six-staminate flowers.

Acknowledgement

The authors thank Ms. NAKAJIMA Mutsuko for drawing the inflorescence and flowers of *P. postelsianum* (in Fig. 2) and TI and MAK for examining the specimens.

References cited

- BURGER W.C. 1977. The Piperales and the monocots, alternate hypotheses for the origin of monocotyledonous flowers. *Bot. Rev.*, **43**: 345-393.
- ECKARDT T. 1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudimonomeren Gynoeceums. *Nova Acta Leopoldina (N.F. 5)*, **26**: 1-112.
- EICHLER A.W. 1878. Bluthendiagramme II. Verlag von Wilhelm Engelmann, Leipzig.
- MAXIMOWICZ C.J. 1887. *Piper*. (Diagnoses plantarum novarum asiaticarum. VI. - Insunt stripesquaedam nuper in Japonica detectae.) *Bull. Acad. Sci. St. Petersb.*, **31**: 93-95.
- MELCHIOR 1964. Engler's Syllabus der Pflanzen Familien.
- MABBERLEY D.J. 1997. The plant-book, 2nd ed. 858 pp. Cambridge.
- OMORI Y. 1982. Floral anatomy of *Saururus chinensis* (Saururaceae) and *Zippelia begoniaefolia* (Piperaceae). *Sci. Rept. Yokosuka City Mus.*, (29): 51-61, pls. 3-4.
- OMORI Y. 1997. Floral anatomy and development of *Piper kadsura* (CHOIS.) OHWI (Piperaceae). *Sci. Rept. Yokosuka City Mus.*, (45): 11-22.
- SMITH A.C. 1975. The genus *Macropiper* (Piperaceae). *Bot. Journ. Linn. Soc.*, **71**: 1-38, 11 pls.
- SYTSMA K.J. and BAUM D.A. 1996. Molecular

- phylogenies and the diversification of the angiosperms. In TAYLOR D.W. and HICKEY L.J. ed., *Flowering plant origin, evolution & phylogeny*: 314-340. Chapman & Hall.
- TAYLOR D.W. and HICKEY L.J. 1990. An Aptian plant with attached leaves and flowers: implications for angiosperm origin. *Science*, **247**: 702-704.
- TUCKER S.C. 1982. Inflorescence and flower development in the Piperaceae III. Floral ontogeny of *Piper*. *Amer. J. Bot.* **69**(9): 1389-1401.
- YUNCKER T.G. 1958. The piperaceae - a family profile. *Brittonia*, **10**: 1-7.