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Floral anatomy of *Piper nigrum* (Piperaceae)

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コショウ（コショウ科）の花部解剖

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Key words: ***Piper nigrum*, Piperaceae, floral anatomy, morphology**

The floral vascular system of *Piper nigrum* was investigated, and the arrangement and construction of its floral organs were analyzed. Piperaceae have simple, entire leaves and achlamydeous flowers that consist of a single ovary with one locule and three- or four-lobed stigma and basically six stamens. This study was carried out as one of a series of the floral anatomy of Piperales, in which anatomical investigations were preceded in the species of *Saururus*, *Zippelia*, and three- and six-staminate *Piper*. *Piper nigrum* has some peculiar characters such as unisexual or hermaphrodite flowers, a sessile bract with two bracteole-like organs and two stamens. The results are as follows: 1) two bracteole-like organs are not simple ridges nor lobes of the inflorescence axis but are just the rims of the upper right- and left-hand bracts because vascular bundles run through them; 2) the symmetry of the flower is bilateral because two stamens are across the gynoecium from each other; 3) one of gynoecium bundles enters the ovule and the remaining about twelve bundles run through the ovary wall.

コショウ科コショウの花の維管束走向が明らかにされ，花の構造が解析された。コショウ科は，葉が単葉，全縁，常緑で，花は無花被花で，子房は1室からなり，3，4個の柱頭があり，おしべは6本が基本数とみなされている。その特異な形態から，コショウ科の認識は比較的容易にできるものの，花が小型で単純であることから，押し葉標本による花の比較は難しく，種レベルの分類はかなり難しい。コショウ科の花から有用な分類形質を引き出すには解剖学的な観察が有効である。筆者は，コショウ科の花の構造を解析するために，これまで *Zippelia begoniaefolia*，3雄ずい性のフウトウカズラ *Piper kadsura*，6雄ずい性のタイヨウフウトウカズラ *P. postelsianum* の花解剖を行ってきたが，これらの研究の一環として，本報告では2雄ずい性のコショウ *P. nigrum* を取り上げた。コショウの花のおもな特徴は，単性花と両性花があり，1枚の側着した苞葉とその内側左右に2枚の小苞葉類似器官があること，おしべが2本あることである。維管束走向の解析の結果，1）花の左右側方にある2枚小苞葉類似器官は，維管束があるので，花序軸の稜ではなく，上方左右にある苞葉の縁の一部とみなされる。2）2本の雄しべは維管束走向においても互いに独立し，子房の左右に向き合ってでき，左右相称性を示している。3）雌しべに基生する胚珠には1本の維管束が入り，子房には約12本の維管束が入る。それらはほぼ同じ平面で分枝し，同じ太さであり，心皮の腹行維管束または背行維管束に相当する維管束を識別することは難しい。したがって，コショウの苞葉は花序軸との合着が進み，雌しべは，4心皮による合生子房を持つ *Zippelia* の雌しべのように，各心皮から2本ずつの腹行維管束の分枝が胚珠に入って4心皮性が明瞭な構造とは異なり，癒合が進んだ構造を示し，さらに雄しべの減数と左右相称性が明瞭な構造である。

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A series of the anatomical studies of the flowers of Piperaceae - *Zippelia begoniaefolia* (Omori, 1982), and three- and six-staminate species of *Piper* - showed the floral diversity in the branching pattern of the stamen and ovular bundles and the number of ovary bundles.

The flowers of *Piper* species are characterized by a single gynoecium with one locule and three- to four-lobed stigma, usually six stamens, no perianth and a peltate bract. The floral structure of three-staminate *P. kadsura* (Omori, 1997), and six-staminate *P. geniculatum* (Eckardt, 1937) and *P. postelsianum* (Omori and Kobayashi, 2001) have been analyzed. The floral arrangement and symmetry have been discussed by the developmental studies in Piperaceae and Saururaceae (Tucker, 1982). The phylogeny in the genus *Piper* began to be discussed based on both molecular and morphological data (Jaramillo and Manos, 2001).

Diagnostic characters of *P. nigrum* consist in having hermaphrodite flowers with two stamens subtended by a bract and two bracteole-like lobes (Baillon, 1874); on the other hand, most of Asian species of *Piper* have the unisexual flower subtended by a single bract and six stamens (Jaramillo and Manos, 2001). Developmental studies of both the flowers of the genus *Piper* with four and six stamens revealed the arrangement of the stamens as to be zygomorphic (Tucker, 1982).

In this study I described and analyzed the vasculature of the hermaphrodite flower of two-staminate *P. nigrum*. The purpose of this study is to reexamine the following morphological problems: (1) to interpret two bracteole-like organs subtending a flower with a bract more reasonably, (2) to estimate the number of carples consisting a gynoecium, (3) to make clear the degree of fusion of stamen and carpel, (4) to estimate the basic structure of the flower of the genus *Piper*.

Materials and methods

The materials of *Piper nigrum* cultivated at the greenhouse in Shinjuku Gyoen National Park, Tokyo, were collected on Dec. 7, 1978. The inflorescences were fixed in FAA (formalin-acetic acid-alcohol) solution. They were washed by water and dehydrated in n-butanol-ethanol series and then were embedded in Palaplast. They were sectioned serially cut at 10 μm by rotary microtome, mounted and counterstained in hematoxylin-fast green-safranin.

Results

Inflorescence and flower morphology: The inflorescence of *P. nigrum* is solitary and opposite to leaves. The flowers sparsely bear on the inflorescence, and are subtended by an adnate bract and

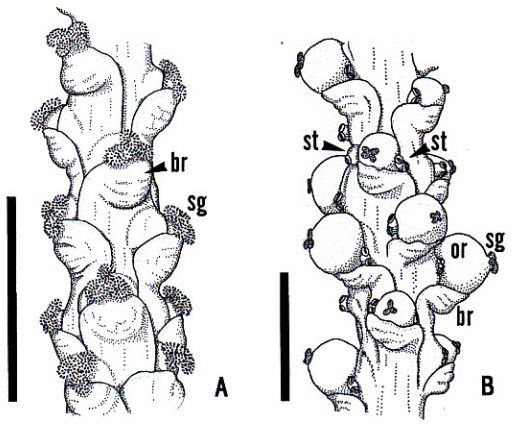


Fig. 1 Inflorescence and flowers of *Piper nigrum*. A: flowers, B: young fruits and stamens. br: bract, or: ovary, sg: stigma. st: stamen. Each scale bar indicates 5 mm.

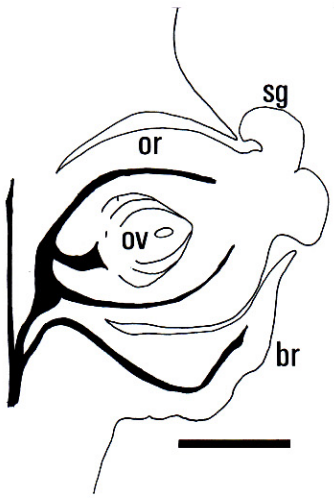
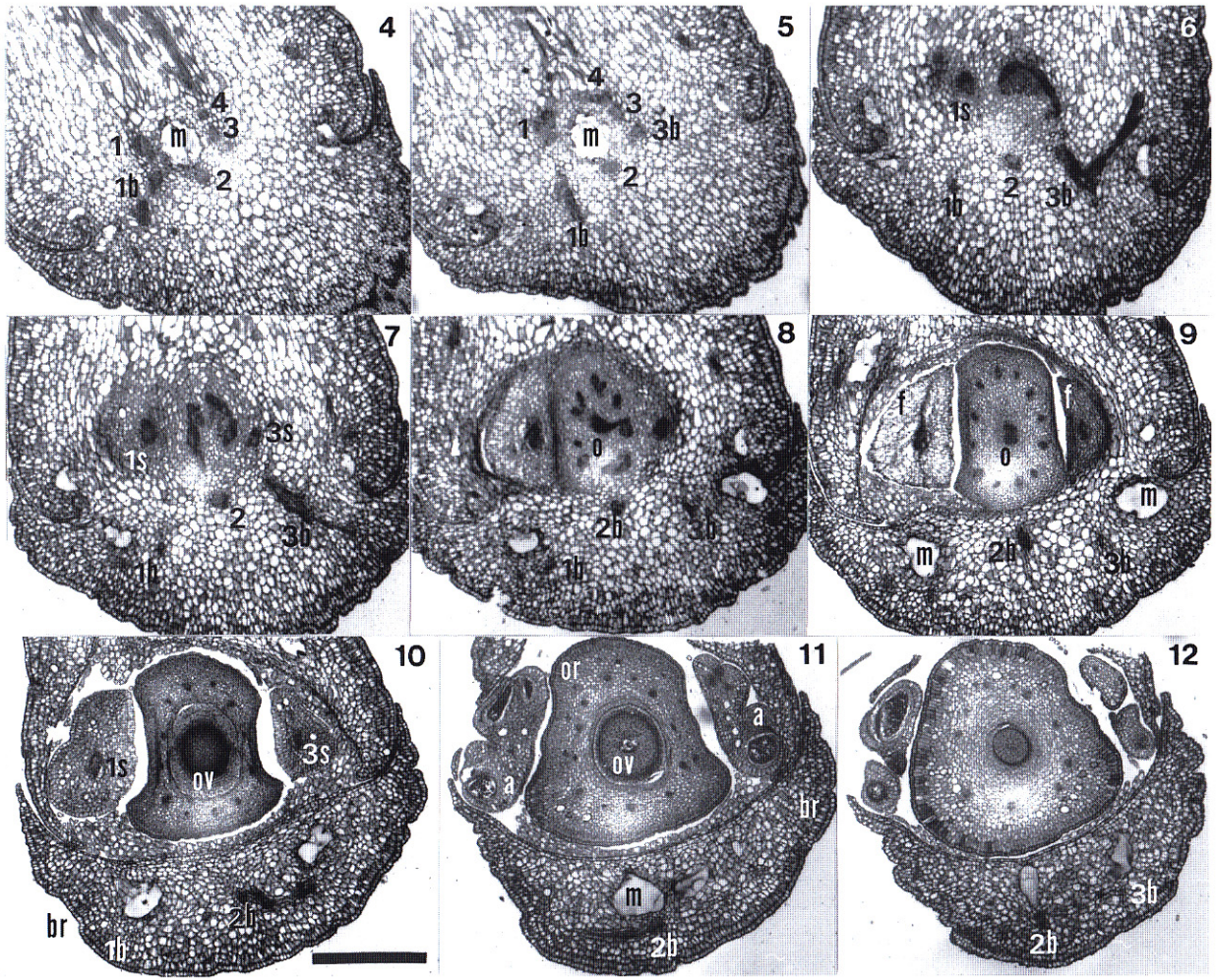


Fig. 2 Longitudinal section of the flower of *Piper nigrum*. ov: ovule. Other abbreviations are the same as in Fig. 2. A scale bar indicates 0.5 mm.

Fig. 3 Serial transverse sections illustrating floral vascular system of *Piper nigrum*. A- I: The transitional part from inflorescence axis to flower, I-J: The basal part of flower, K: The middle part of flower. A. A single vascular bundle that diverges from the axial vascular cylinder splits to produce four bract-flower bundles (1, 2, 3 and 4). B, C. The bundle 1 produces a bract bundle 1b. D. The bundle 1 produces a stamen bundle 1s. The bundle 3 joins the bundle 4 and the bundle 3 produces a bract bundle 3b. The bundles 1, 3 and 4 fuse each other to become a flower bundle (1+3+4). E. The flower bundle supplies a stamen bundles 3s, and the bundle 3b into bract bundles 3b1 and 3b2. F. The bundle 3b1 enters the bract, and the bundle 3b2 joins the vascular bundle of the upper right-hand bract. G, H. The gynoecium bundle (1+3+4) begins to split. H. The bundle 2 branches bract bundle 2b and the remaining bundle joins to the fused bundle 1+3+4. The gynoecium bundle supplies an ovular bundle o. I. The gynoecium bundle splits into twelve ovary bundles at the same level, and the bundle 2b enters the bract. J, K. The ovary bundles run through the ovary wall. 1, 2, 3, 4: bract-flower bundles, 1b, 2b, 3b1, 3b2: bract bundles, 1s, 3s: stamen bundles, o: ovular bundle, +: junction of vascular bundles. a: anther, br: bract, f: filament, m: mucilage canal, or: ovary, ov: ovule. A scale bar indicates 1 mm.



Figs. 4-12. Transverse sections of inflorescence and flower of *Piper nigrum*. Fig. 4 corresponds to Fig. 3B, Fig. 5 to Fig. 3C, Fig. 6 to Fig. 3D, Fig. 7 to the section between Fig. 3F and 3G, Fig. 8 to the section between Fig. 3H and 3I, Fig. 9 to the section between Fig. 3I and 3J, Fig. 10 to the section between Fig. 3J and 3K, Fig. 11 to Fig. 3K. and Fig. 12 is the upper part of ovary. Abbreviations are the same as in Fig.3. A scale bar indicates 0.5 mm.

surrounded by the rim of the upper right- and left-hand bracts (Fig. 1A). The flowers are simple, sessile and lacking perianth. All the flowers investigated in this study were hermaphrodite, although this species is described as having unisexual or bisexual flowers. The gynoecium with three- or four-lobed stigma and a pair of stamens are sunken in the axis of the inflorescence. The gynoecium and the stamens do not mature at the same time in the hermaphrodite flowers. When the gynoecium matures, the bracts (Fig. 1A) cover the immature stamens. After the maturity of the gynoecium, the stamens protrude out of the bract (Fig. 1B). A single ovule bears at the basal placenta (Fig. 2).

Bract and flower vascular system (Figs. 3A-K. Figs. 4-12): A single vascular bundle that diverges from the axial vascular cylinder splits to produce four bundles around a mucilage canal, which are here named the bract-flower bundles 1, 2, 3 and 4 counterclockwise (Fig. 3A). Bract bundles are derived from three bract-flower bundles 1, 2, 3 except the bundle 4. The bundle 1 produces a bract bundle 1b (Figs. 3B-C, Figs. 4-5), which further splits into the bract (Fig. 3E). The bundle 3 produces a bract bundle 3b (Fig. 3D, Fig. 6), that splits into bract bundles 3b1 and 3b2 (Fig. 3E, Fig. 7). The bundle 2 splits into a bract bundle 2b (Fig. 3H, Fig. 8), and then enters the bract (Figs. 3I-J, Figs. 8-9). The stamen bundles are derived from the bundles 1 and 3. The bundle 1 produces a stamen bundle 1s (Fig. 3D, Fig. 6). The bundle 3 joins the bundle 4 (Fig. 3D, Fig. 6), and then the joined bundle splits, one of which becomes a stamen bundle 3s (Figs. 3E-F, Fig. 7). The gynoecium bundles are derived from the fusion of the bundles 1, 3, 4 (Fig. 3E) and a branch of the bundle 2 (Figs. 3F-G, Fig. 6). At the basal part of ovary the gynoecium bundles are arranged in a circle (Fig. 3H-I, Figs. 8-9). These bundles split into about twelve bundles on the same plane (Fig. 3I, Fig. 9). One of them enters the ovule at the basal placenta (Figs. 3H-I, Fig. 8). The remaining bundles are arranged on a circumference in ovary wall (Figs. 3J-K, Figs. 10-12) and run through the ovary toward the basal part of stigma.

Discussion

Most of the species of *Piper* have peltate bracts, but *P. nigrum* has elliptical and sessile bracts with rim around. Baillon (1874) regarded a pair of lobes inside the bract in *P. nigrum* as a crest of the inflorescence axis. Eichler (1875, 1878) did not regard them as bracteoles either. On the other hand, Kanta (1963) reported that four bracts subtended each flower. This study proves that each flower is subtended by a bract, and in moreover is surrounded by the rims of two bracts, the upper right- and left-hand bracts, around the flower.

This study revealed that in *P. nigrum* a single vascular bundle from the vascular ring at the basal part of gynoecium enters the ovule and the remaining about twelve bundles run through the ovary wall (Fig. 13). This pattern of vasculature shows that the syncarpous gynoecium of *P. nigrum* is more closely fused structure than those of *Zippelia*, in which each two ventral bundles from four carpels enter an ovule (Fig. 13 from Omori, 1982). In *Piper* species, the ovary bundles vary in number (ex. three in *P. augustum*: Igersheim and Endress, 1998, four in *P. postelsianum*, six in *P.*

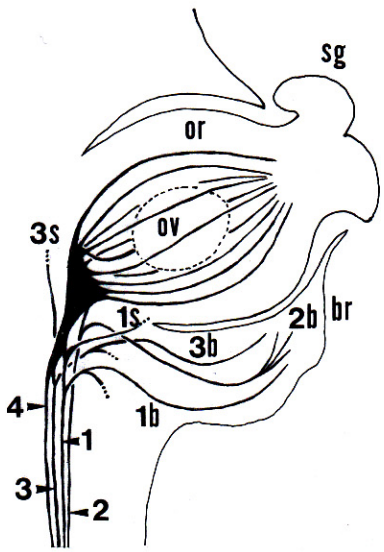


Fig. 13 Reconstruction of the floral vascular system of *Piper nigrum*. Abbreviations are the same as in Figs. 1 and 2.

kadsura), although the number of the stigma is usually three or four. The number of ovary bundles does not show a correlation with the number of carpels and the degree of fusion of the carpels.

Eichler (1875, 1878) pointed out that the arrangement of six stamens of *P. (Enckea) amalago* is spiral. Johnson (1902) asserted that *P. medium* has two trimerous whorls of stamens and the outer whorl initiates earlier than the inner one. Eckardt (1937) investigated the vasculature of six-staminate species (*P. genicuratum*) and interpreted the arrangement of the stamens as two whorls. These botanists regarded the arrangement of floral organs of *Piper* as radial symmetry.

On the other hand, Tucker (1982) analyzed the floral development of four-staminate *P. aduncum* and *P. marginatum* and six-staminate *P. amalago* to conclude that the developmental pattern shows bilateral or dorsiventral symmetry, which is common in Saururaceae.

Three-staminate species (*Piper kadsura*: Omori, 1997) and six-staminate one (*P. postelsianum*: Omori and Kobayashi, 2001) have the trimerous flower like many other species of *Piper*. Two-staminate *P. nigrum* is thought to be specialized by reduction of a pair of lateral stamens and a pair of median stamens. Because a single vascular bundle enters the ovule and all the remaining bundles run through the ovary toward the stigma, the gynoecium of *P. nigrum* shows more closely fused structure than other species of *Piper* and *Zippelia* (Fig. 14). *P. kadsura* and *P. postelsianum* have unisexual and radial symmetric flowers, on the other hand, *P. nigrum* has bisexual and zygomorphic flowers.

It is very difficult to verify even the number of the stamens and their arrangement in dried specimens in *Piper* species, which has many small flowers growing densely on spike or raceme.

Recent molecular analysis of sequences of the internal transcribed spacers of nuclear ribosomal DNA revealed three main clades: Asian, the South Pacific, and the Neotropic clade (Jaramillos and Manos, 2001). For laying the foundation of the classification of a huge genus like *Piper*, much more morphological data are indispensable. Anatomical and developmental analyses, in particular, in the floral vasculature and the arrangement of the floral organs, will let us reinvestigate the external morphology and give us much more new information.

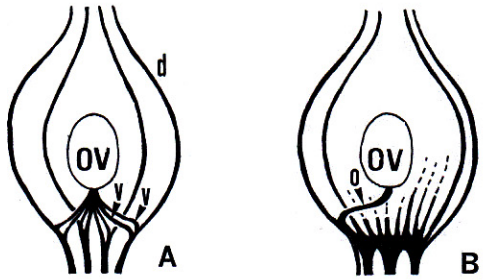


Fig. 14 Diagrams illustrating the number of vascular bundles into a single ovule. A: Eight bundles derived from each two ventral bundles of four carpels enter an ovule in *Zippelia begoniaefolia*. B: A single ovular bundle branched from the gynoecium bundle enters an ovule in *Piper nigrum*. d: dorsal bundle, v: ventral bundle, o: ovular bundle, ov: ovule.

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