

Floral anatomy of *Sarcandra glabra* (Thunb.) Nakai (Chloranthaceae):
reevaluation of the hypothesis that the flower of
Sarcandra was derived from an inflorescence

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センリョウ(センリョウ科)の花解剖学：
センリョウの花が花序に由来する仮説の再評価

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It is well known that *Sarcandra* has the simplest hermaphrodite flower, which consists of a pistil and a stamen attached midway up on the dorsal side of the ovary. Some taxonomists have advocated a hypothesis that the simple flower was derived from an inflorescence. Therefore, the hypothesis will be reevaluated based on an analysis of floral anatomy, including some variations in the number of locules, stigmas and stamens, of *Sarcandra glabra* in the present paper. Four to six vascular bundles are arranged in a circle at the basal part of the flower. The vascular bundles are separated into two independent groups throughout the floral organs from the basal part of the flower: an adaxial group of the bundles runs into the pistil and an abaxial one mainly into the stamen. The adaxial group of bundles is composed of one ventral and two lateral bundles of pistil, which run through the ovary wall to join and enter the ovule drooping down at the top of the ovary. The abaxial group of bundles is composed of one or two stamen bundles and one of them sometimes supplies a slender bundle running through the dorsal side of ovary. These vascular systems suggest that the pistil of *Sarcandra* is composed of a single carpel. Comparing a simple inflorescence consisting of a female and a male flower in *Ascarina lucida* belonging to the same family, the inflorescence completely resembles the hermaphrodite flower of *Sarcandra*. The independence between pistil and stamen vascular systems and the similarity between the simple inflorescence of *Ascarina* and the flower of *Sarcandra* can support the hypothesis that the flower of *Sarcandra* was derived from an inflorescence.

センリョウ属は被子植物でもっとも単純な花—1個の雌しべと1個の雄しべからなる花—をもっている。それが花序に由来するとの考えがあり、センリョウの正常な花と子房室と雄しべの数に変異のある花の花部維管束走向の比較解析からその再評価を行った。センリョウの花の基部では4-6本の維管束が環状に配列し、これが互いに独立した2群の維管束に分かれ、向軸側の維管束が雌しべに、背軸側の維管束が雌しべの背面に合着した雄しべに入る。雌しべ維管束には、1本の腹管束と2本の側管束があり、背軸側には独立した維管束、または雄しべ維管束の分枝が背管束として見られる。子房上部から下垂する胚珠には1本の腹管束と2本の側管束の合わせて3本の維管束が胚珠に入る。これはセンリョウの雌しべが1心皮に由来することを示唆している。子房室や雄しべの数に変異のある花の場合も維管束走向のパターンの基本は同様であった。同じくセンリョウ科 *Ascarina* 属の1種、*A. lucida* の雌雄1対の単性花からなる退化した花序がセンリョウの両性花と外見上類似していることと、雌しべと雄しべの維管束が互いに独立した維管束走向を示すことは、センリョウの花が雌花と雄花の合着に由来する可能性を示唆している。

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The flower of *Sarcandra glabra* is small and consists of only a globular pistil and a fleshy obovoid stamen adnate on the abaxial side of the pistil, which shows the simplest constitution as a hermaphrodite flower in the angiosperms. From paleobotanical research found flower fossils resembling to the chloranthaceous flowers (Friis, Crane & Pedersen, 1986; Taylor & Hickey, 1990). Therefore Chloranthaceae is often regarded as one of the most primitive angiosperms such as Nymphaeaceae, Austrobaileyaceae and *Amborella*, and they are related to each other and sister to monocots, although their systematic placement is uncertain (Judd, Cambell, Kellogg, Stevens & Donoghue, 2002).

Swamy & Bailey (1950), Swamy (1953) and Endress (1987) have carried out morphological studies in the flowers of Chloranthaceae. The interpretation of the simple and enigmatic structure of the flower is still open to question. For getting the clue of resolving the basic floral structure of Chloranthaceae, comparative study between the external morphology of the flower and their vascular system was conducted in this study. Some variations in the number of the lobe of bract, the stamen and the stigma can be often observed in the flowers of *Sarcandra glabra*. In *Chloranthus japonicus* of which stamens are three in number and adnate to the abaxial side of pistil, Maekawa (1970, 1971) reported the variation - from one to three - in the number of stamens. In the present paper, the variations of the flowers with two lobed stamens, with two stamens and with two locules in *Sarcandra glabra* were anatomically analyzed in detail.

Materials and Methods

The flowers of *Sarcandra glabra* (Thunb.) Nakai, which were cultivated at the Botanical Gardens, University of Tokyo, in Hakusan, Bunkyo-ku, Tokyo and at a flower pot in Nokendai, Kanazawa-ku, Yokohama, and were naturalized at the Mabori Biological Garden attached to the Yokosuka City Museum in Mabori, Yokosuka, were collected and fixed by FAA (formalin, acetic acid and

ethanol) solution. They were dehydrated by n-butanol-ethanol series to be embedded in Paraplast or Histosec. Serial cross sections of the flowers were cut in 10 μ m in thickness by microtome and were counterstained by Heidenhain's hematoxylin, Fast Green and Safranin.

The drawings and photographs of the serial sections are placed their adaxial side at top and arranged in order from the basal part of flower to the stigma. Each vascular bundle is named as an abbreviation as follows. The vascular bundles at the basal part of flower are distinguished by numerical value such as 1,2,3, and the abbreviations of each organ are added to the numerical value just before entering the specific organs. The abbreviations of the organs are as follows; *b*: bract bundle, *d*: dorsal bundle of carpel, *l*: lateral bundle of carpel, *ov*: ovular bundle, *s*: stamen bundle, *v*: ventral bundle of carpel. Arrowheads in Figs. 5, 6 show the domain occupied by the main vascular bundles named after numerical value at the basal part of pistil. The abbreviations of each organ are as follows; *br*: bract, *in*: inflorescence, *pi*: pistil, *st*: stamen, *sg*: stigma.

Observations

The flowers of *Sarcandra glabra* (Fig. 1) are sessile, borne on the surface of the rachis of spike and subtended by bract. Normal flowers consist of a globular pistil (*pi* in Fig. 1) with one locule and an obovoid stamen (*st* in Fig. 1) adnate to the abaxial side of the pistil. Abnormal flowers having two lobed stamens, two stamens or two locules are often observed. Each vascular system is described here by comparison with that of normal flowers.

Flower consisting of a unilocular ovary and a stamen (Figs. 2, 3)

A vascular bundle (arrows in Figs. 2A, 3A), which was divided from the stelar bundles in the rachis, spreads into branches to be semicircular in cross section (Figs. 2A, 3A). A bract bundle (*b* in Figs. 2B, 3B) is divided from them to enter the bract. The remaining vascular bundles divide

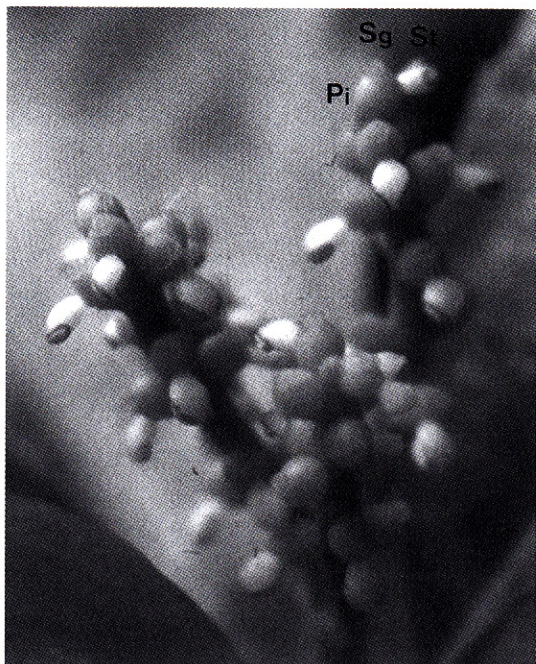


Fig. 1. Inflorescence of *Sarcandra glabra*, cultivated in Yokohama, Japan. *pi*: pistil, *sg*: stigma, *st*: stamen.

into four or five branches at the basal part of flower to be arranged in circle; four bundles in the case having one stamen bundle (1-4 in Fig. 2C), five in the case having two stamen bundles (1-5 in Fig. 3E). Although one of the bundles at the abaxial side (4 in Fig. 2E) occasionally supplies a small branch (4' in Fig. 2F), all or most of them enter the stamen (4s in Fig. 2F).

Another three bundles (1, 2, 3 in Fig. 2C) repeatedly divide and fuse each other, and over ten pistil bundles run through the ovary wall (Figs. 2D-G). Some pistil bundles disappear at the upper part of ovary and the other pistil bundles fuse into three bundles (1l, 2v, 3l in Fig. 2I) to enter the ovule (ov in Figs. 2H-I). These three ovular bundles originated in three bundles (1, 2, 3 in Fig. 2C) at the basal part of flower.

In the case of two stamen bundles, two bundles at the abaxial side (4, 5 in Fig. 3E) enter the stamen (4s, 5s in Fig. 3G). The lateral bundles divide several times into branches (1, 3 in Figs. 3E-G) and the ventral bundles has no branches

and runs through ovary wall to enter the ovule at the upper part of ovary (2v in Figs. 3I-L).

Flower consisting of a unilocular ovary and a bilobed stamen (Fig. 4)

Six vascular bundles (1-6 in clockwise in Fig. 4D) are arranged in circle. Two abaxial bundles (4, 6 in Fig. 4 F; 4s, 6s in Fig. 4G) enter the stamen without branching. The other abaxial bundle (5 in Fig. 4E) between 4s and 6s may be regarded as a dorsal bundle, but it disappears at the midway in the ovary wall. The central bundle (2 in Fig. 4D) of three adaxial bundles enters the ovule (2v in Fig. 4J) and the other two bundles on either side of the ventral bundle run through the lateral part of ovary (1, 1l, 3, 3l in Figs. 4E-J). Each lateral bundle divides into two at the lower part of ovary. At the upper part of ovary the ventral and lateral bundles fuse each other to enter the ovule (1, 1l, 2, 2v, 3, 3l in Figs. 4I-J).

Flower consisting of a bilocular ovary and two stamens (Fig. 5)

Six vascular bundles are arranged in circle at the basal part of flower (1-6 in Fig. 5B). The central bundle (2 in Fig. 5B) of three adaxial bundles enters the ovule at the top of ovary (Fig. 5H). The lateral bundle (1 in Fig. 5B) of the three becomes both a ventral bundle and a lateral bundle of pistil (Fig. 5H), and the other lateral one (3 in Fig. 5B) runs through the lateral side of ovary (Fig. 5H). These lateral bundles supply one or two branches. The central abaxial bundle (5 in Fig. 5B) is regarded as a dorsal or lateral bundle (5 in Figs. 5C-G) and the other abaxial bundles (4, 6 in Fig. 5B) enter the stamen without branching (4, 4s, 6, 6s in Figs. 5C-E).

Flower consisting of a bilocular ovary and a bilobed stamen subtended by two-lobed bract (Fig. 6)

A vascular bundle, which was divided from

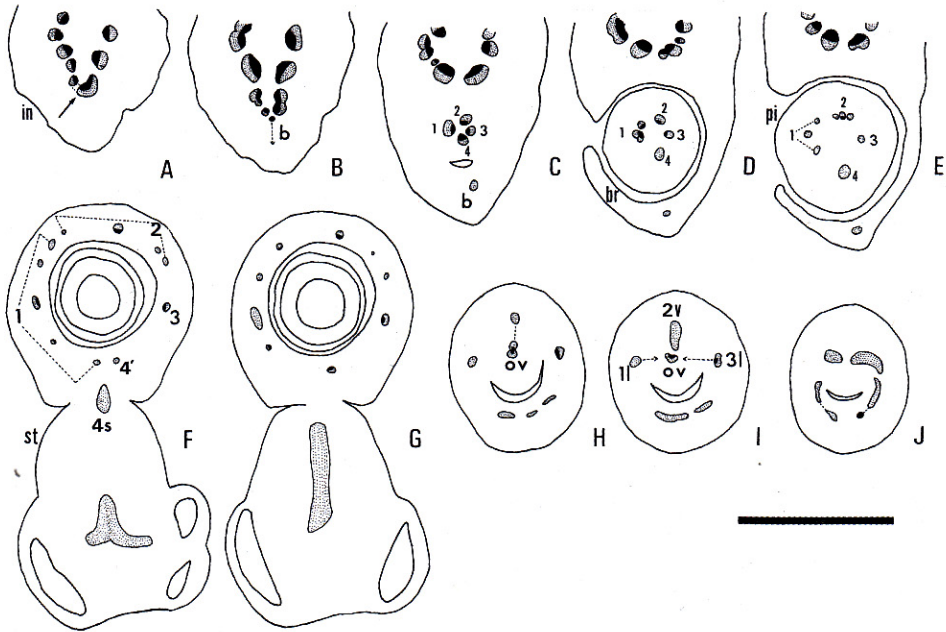


Fig. 2. Serial transverse sections of the flower with a single stamen bundle of *Sarcandra glabra*. A-C: inflorescence axis, D-E: a bract and basal part of pistil, F-G: middle part of pistil with stamen at its abaxial side, H-J: upper part of pistil. *b*: bract bundle, *d*: dorsal bundle, *l*: lateral bundle, *ov*: ovular bundle, *s*: stamen bundle, *v*: ventral bundle, *br*: bract, *in*: inflorescence axis, *ov*: ovule, *pi*: pistil, *sg*: stigma, *st*: stamen. Scale bar = 1 mm.

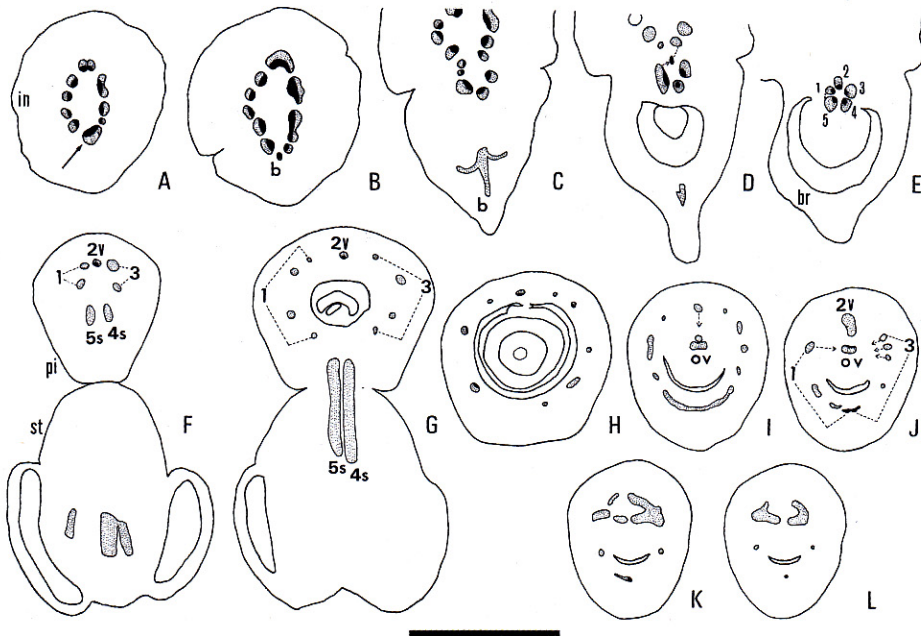


Fig. 3. Serial transverse sections of the flower with double stamen bundles of *Sarcandra glabra*. A-C: Inflorescence axis, D-E: a bract and basal part of pistil, F-G: middle part of pistil with stamens at its abaxial side, H-L: upper part of pistil. Abbreviations are the same as in Fig. 2. Scale bar = 1 mm.

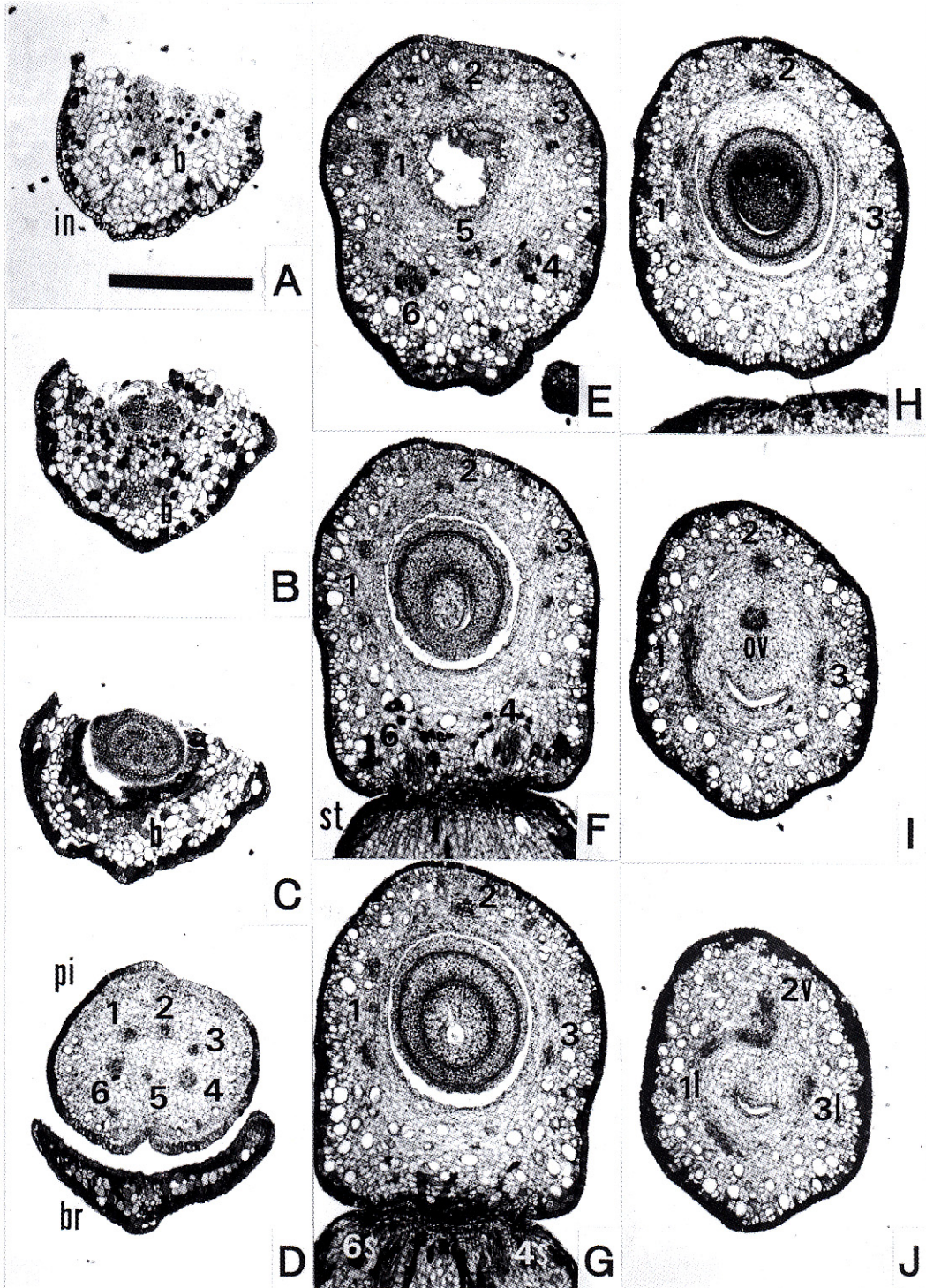


Fig. 4. Serial transverse sections of the flower with a bifurcated stamen of *Sarcandra glabra*. A-B: inflorescence axis, C-D: a bract and basal part of pistil, E-H: middle part of pistil with stamen at its abaxial side, I-J: upper part of pistil. Abbreviations are the same as in Fig. 2. Scale bar = 0.5 mm.

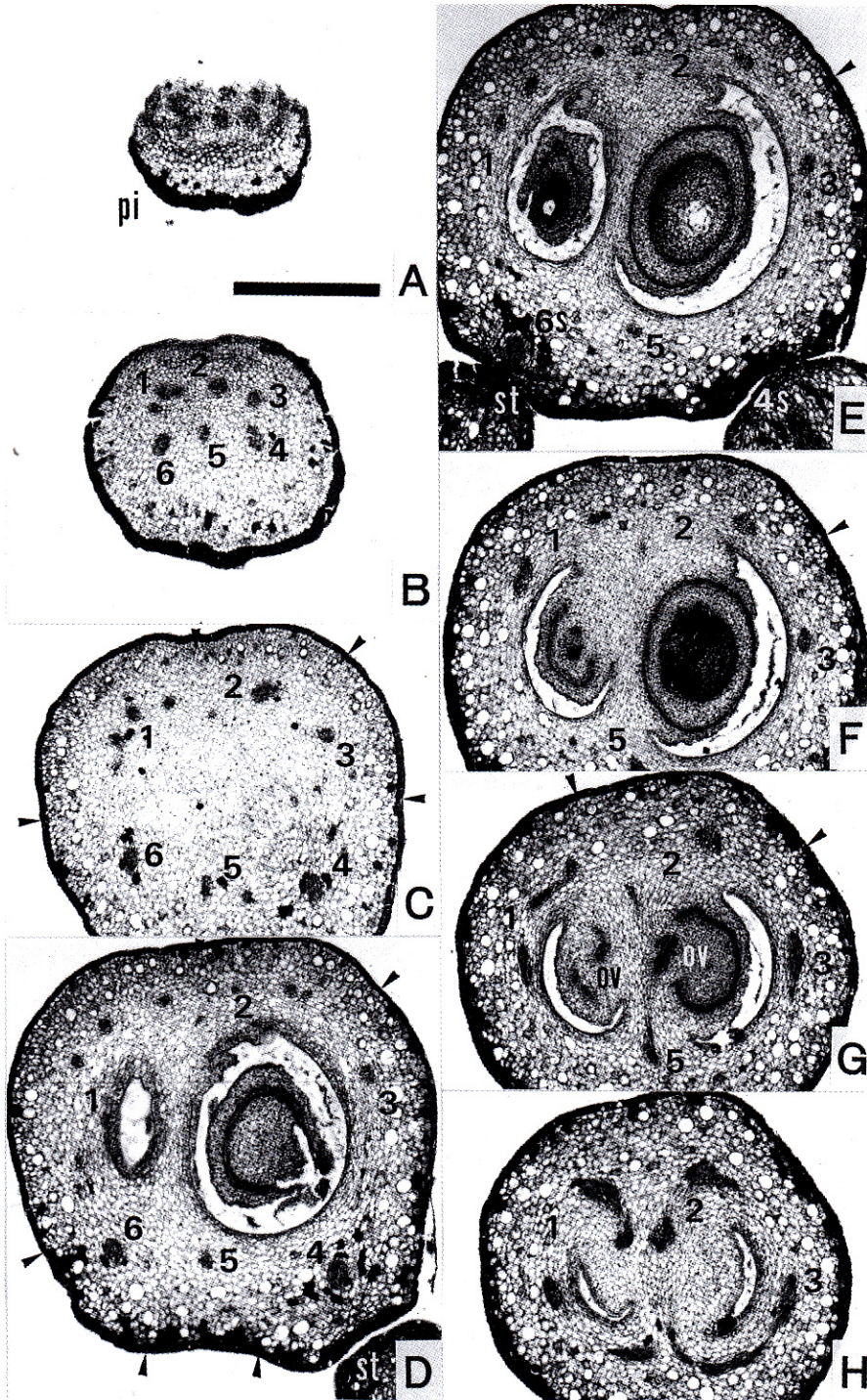


Fig. 5. Serial transverse sections of the flower with two locules and two stamens of *Sarcandra glabra*. A-C: basal part of pistil, D-F: middle part of pistil with two stamens at its abaxial side, G-H: upper part of pistil. Arrowheads show the domain occupied by the main vascular bundles at the basal part of pistil. Abbreviations are the same as in Fig. 2. Scale bar = 0.5 mm.

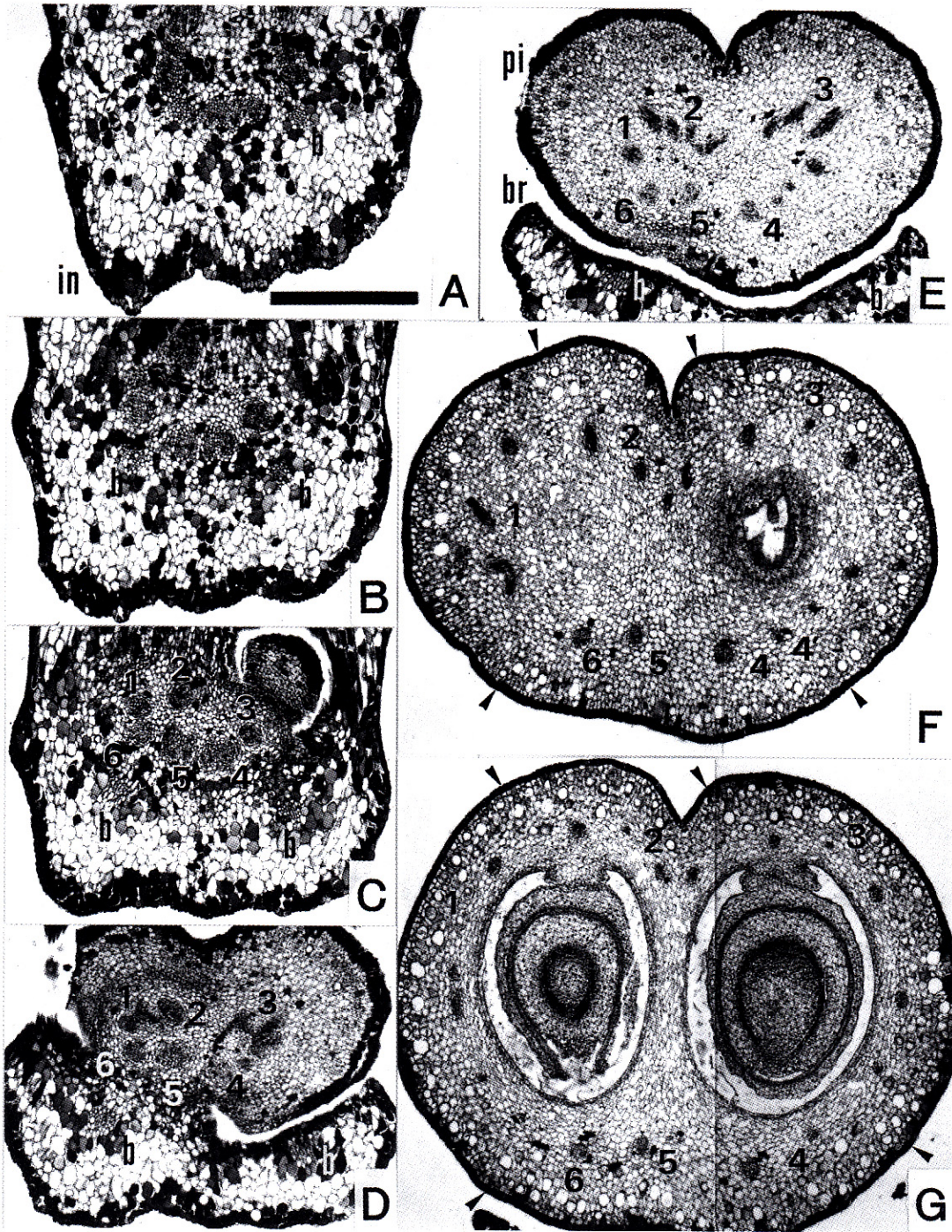


Fig. 6. Serial transverse sections of the flower with two locules and a bifurcate stamen of *Sarcandra glabra*. A-C: inflorescence axis, D-F: a bract and basal part of pistil, G-I: middle part of pistil, J-M: upper part of pistil with stamen at its abaxial side. Arrowheads show the domain occupied by the main vascular bundles at the basal part of pistil. Abbreviations are the same as in Fig. 2. Scale bar = 0.5 mm.

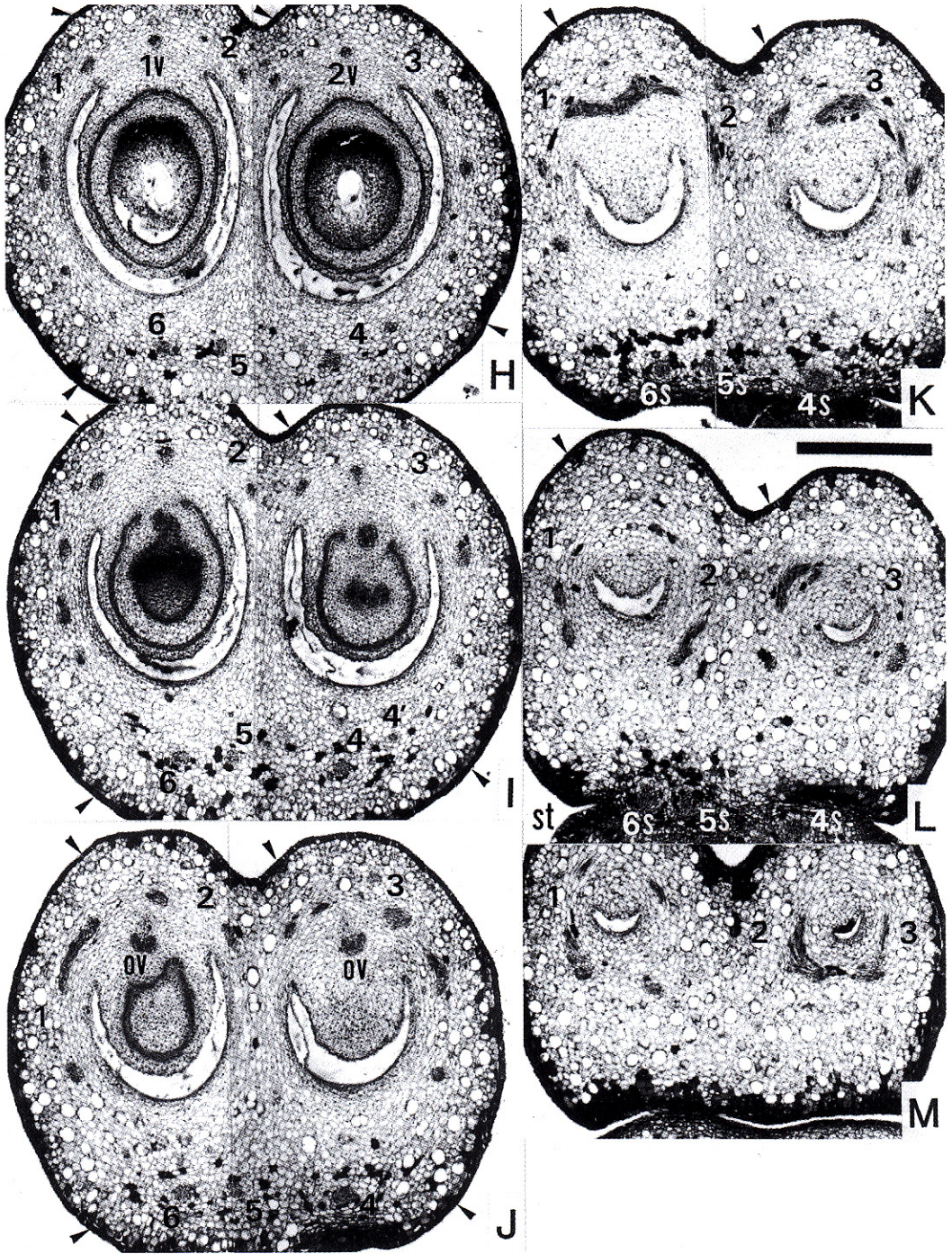


Fig. 6. (Continued)

the stelar bundles in rachis, spreads into branches to be arranged in semicircular in cross section (Fig. 6A). Two bract bundles (*b* in Figs. 6A-B) are divided from them to enter the bract (*b* in Figs. 6D-E). Six vascular bundles (1-6 in Figs. 6C-D) are arranged in circle at the basal part of flower. One of three adaxial bundles becomes a lateral bundle (1 in Figs. 6C-K); the other two of them turn to ventral and lateral bundles (2,3 in Figs. 6C-K). Each pistil bundle divides two or three times into branches (1, 2, 3 in Figs. 6F-I). Three abaxial bundles (4, 5, 6 in Figs. 6F-J) run through ovary wall to enter the stamens (4s, 5s, 6s in Figs. 6K-L) and one of them branches a slender bundle (4' in Figs. 6E-I).

Discussion

Basic plan of the flower of *Sarcandra glabra*

Comparing the floral vascular system among the normal flower and the flowers having two stamens or bilocular ovary, any important difference could not be found, that is, an independent vascular bundle at the basal part of flower usually enters the stamen. Three or four pistil bundles run at the basal part of pistil in normal flowers; one ventral and two lateral bundles. They enter the ovule at the top of ovary. Even in the case of the bilocular ovary, independent two ventral bundles are supplied and each of them accompanies two lateral bundles as in the unilocular ovary.

Swamy & Bailey (1950) reported that abaxial pistil bundles in the flowers of *Sarcandra glabra* supply two stamen bundles, therefore the stamen bundles are not independent from the pistil bundles. The difference between their observations and the present ones may reflect the differences of the materials because they may have analyzed the flowers of *Sarcandra chloranthoides* instead of *S. glabra* (Verdcourt, 1984).

In *Sarcandra*, if we stick to the position of the diversification of vascular bundles, we may not be able to draw a reasonable conclusion because

some variations in vascular system are observed even in the case of no morphological difference in appearance.

Basic vascular system in the flower of *S. glabra* is summarized as follows. 1) Four to five bundles are arranged in circle at the basal part of flower. 2) One or two abaxial bundles enter the stamen without branching. 3) Three adaxial bundles become one ventral two lateral bundles to enter the ovule together at the upper part of ovary. Therefore, the pistil of *Sarcandra* is not interpreted to be pseudomonomerous one such as the ulmaceous flowers (Omori & Terabayashi, 1993) but to be derived from one carpel as the same as in *Hedyosmum* (Endress, 1971). The vascular system to the stamen shows that the stamen bundle is a very independent of the pistil bundles as in *Chloranthus* (Swamy & Bailey, 1950, Hickey & Taylor, 1996), which suggests that the hermaphrodite flowers of *Sarcandra* may be derived from the fusion of male and female flowers. It is known that the flowers of *Triglochin*, *Scheuchzeria* and *Potamogeton* are interpreted as inflorescences composed of several staminate and pistillate flowers (Uhl, 1947).

Based on observing the variation of stamen number of *Chloranthus japonicus*, Maekawa (1970, 1971) reasoned that the single stamen of *Sarcandra* is derived from both the loss of the central stamen and the fusion of two lateral stamens, or the loss of lateral stamens. The fact that the number of the stamen bundles in *Sarcandra* is one or two and that the flowers of *Sarcandra* have two-lobed stamen or two stamens suggests supporting the former hypothesis. Although comparing the flowers of *Sarcandra* and *Chloranthus* leads to exclusively such an alternative hypothesis among hermaphrodite flowers, counting the flower of *Ascarina* in them can broaden our horizons.

Origin of the flower of *Sarcandra glabra*

The flowers of *Ascarina*, which consists of one-

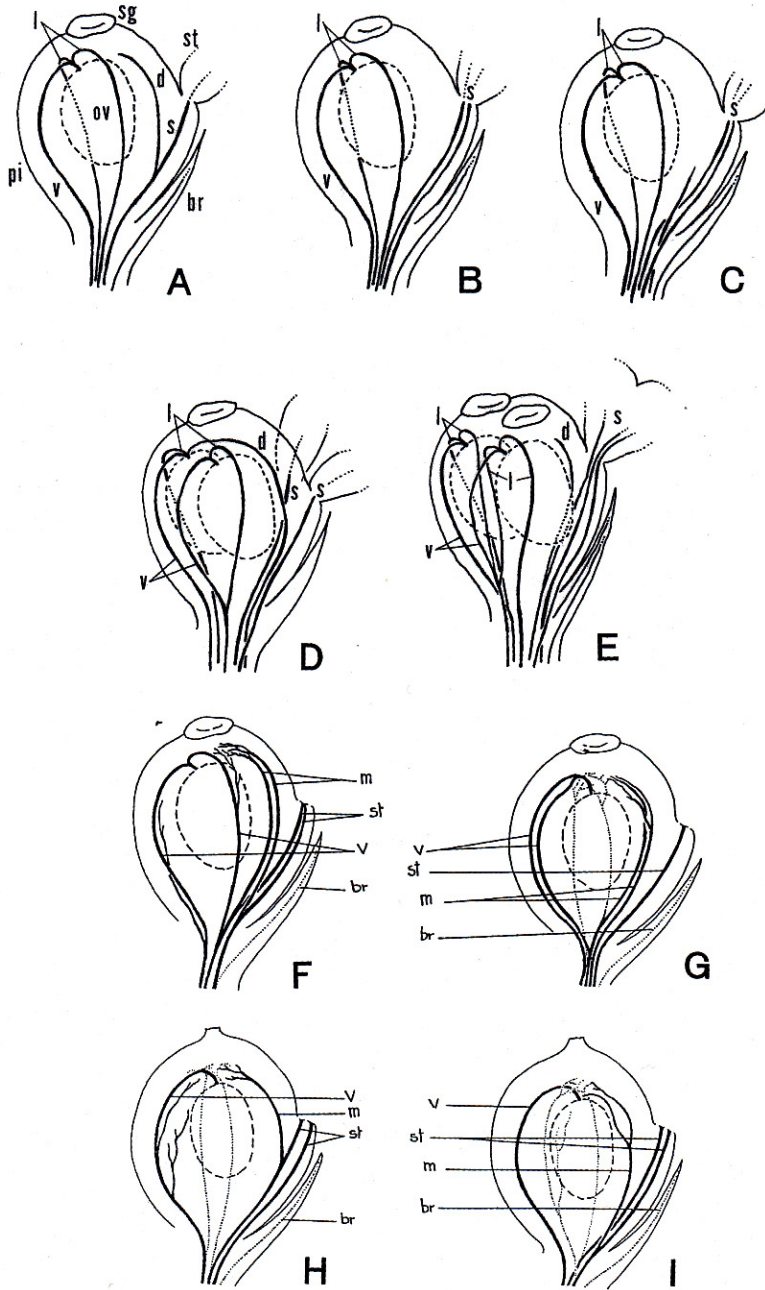


Fig. 7 Reconstructions illustrating vasculature of the flower of *Sarcandra*. A-E: *Sarcandra glabra*, F, G: *S. glabra* or *S. chloranthoides* and H, I: *S. hainanensis* (F-I from Swamy & Bailey, 1950). *br*: bract or bract bundle, *m*: median bundle, *ov*: ovule, *st*: stamen or stamen bundle, other abbreviations are the same as in Fig. 2.

stamen male flower and one-pistil female flower, are much simpler than the flowers of *Sarcandra*. The inflorescence constitution of *A. lucida* that consists of sessile male and female flowers was investigated in detail (Moore, 1977). One of several variations of the inflorescence in *A. lucida* gives the appearance of hermaphrodite flower, which is a much reduced cyme consisting of a single stamen (a male flower) and a single accompanying female flower mature almost simultaneously. This 'pseudo-bisexual flower' (Fig. 8A, in Moore, 1977) resembles a bisexual flower of *Sarcandra* (Fig. 8B). Considering that the stamen is adnate to the pistil in *Sarcandra*, however, the vascular bundles of the stamen is independent of those of the pistil, the vascular bundles arranged in circle at the basal part of flower may be interpreted as a stele of the cyme rachis consisting of a male and a female flowers. Thus, the enigmatic structure of flower of *Sarcandra*, whose stamen is adnate to the abaxial side of ovary can be regarded by the derivation from the fusion of one stamen and one-pistil flowers. Although the flower of *Sarcandra* is usually regarded as a hermaphrodite (Endress, 1994), this study supports the inference (Verdcourt, 1986) that it is derived from the cymule consisting of male and female flowers in *Ascarina*. And it

can reevaluate the hypothesis, the flowers of *Chloranthus* are not hermaphrodite flowers but are homologous to a modified cyme accompanied by the decrease of the number of the flowers (Cordemoy, 1863 in Swamy 1953).

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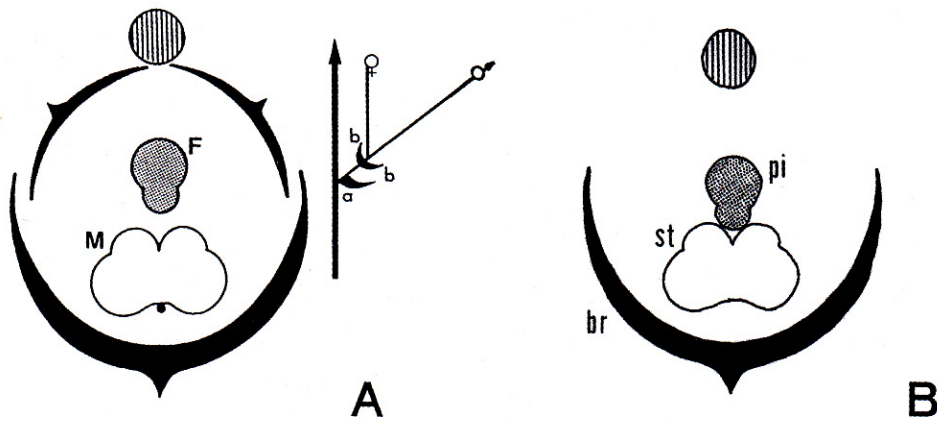


Fig. 8. Floral diagrams of *Ascarina* and *Sarcandra*. A: *Ascarina lucida* (redrawn from Moore, 1977) and B: *Sarcandra glabra*. F & ♀: female flower, M & ♂: male flower, a & br: bract, b: bracteole, pi: pistil, st: stamen.

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