Mitsuko SUGIYAMA*: Comparative studies of vascular system of node-leaf continuum in the Ranalian complex (1)
*Clematis williamsii* and *Paeonia japonica*

杉山明子*: キンポウゲ目及びその類縁植物群の茎から葉への維管束系 (1)
シロバナハンショウズル及びヤマジャクヤクについて

Relatively little attention has been paid to the vascular system in the node-leaf continuum of angiosperms. On the other hand, the considerable attentions to the most phylogenetists have been devoted to the nodal anatomy which has been provided with the number of leaf traces and gaps at the node (Sinnott 1914, Ozenda 1949, Marsden & Bailey 1955, Canright 1955, Takhtajan 1956).

Yamazaki (1965) emphasized the significance of the vascular course from the node to the tip of lamina for the study of leaf phylogeny. Subsequently the present author elucidated the vascular system in the node-leaf continuum in the Magnoliales (sensu Takhtajan 1969) describing the seven types of vasculature in this group (Sugiyama 1972, 1974, 1976, 1979).

The present paper will attempt to show the vascular system of two Ranalian genera, *Clematis* and *Paeonia*, discussing the nature of the leaf in the Ranalian complex as the basic data in considering its phylogeny.

**Materials and methods**: *Clematis williamsii* was collected from Heta, Shizuoka Pref., and transplanted and cultivated in Tokyo. It was fixed in 50% FAA on April 20, 1971. *Paeonia japonica* was collected in Mt. Narukami, Tochigi Pref., and transplanted and cultivated at Botanical Gardens, University of Tokyo. This was also fixed in 50% FAA on March 21, 1972. Materials were treated in the same way as described elsewhere (Sugiyama 1979).

**Observations**

*Clematis williamsii* Climbing shoot possesses compound-ternate leaves in the opposite arrangement. Six large bundles and seven or more small

---

* Botanical Gardens, Faculty of Science, University of Tokyo, Hakusan, Bunkyo-ku, Tokyo 112.
東京大学理学部付属植物園．
bundles are running through the stem (Fig. I-1). Six large bundles bi- or trifurcate and one of segments of diverged bundles enters as the leaf traces (Fig. I-2). The nodal condition is trilacunar. The leaf traces are composed of a single median (M) and two lateral (L1) bundles.

At the petiolar base, M trace gives off small m bundle on its either side (Fig. I-2, 3). L1 trace bifurcates and one of the segments fuses with m bundle forming L1·m, while the other segment (L1) remains independent (Fig. I-3, 4). Thus the vascular system in the petiolar base composed of a single median bundle (M) and two pairs of lateral bundles (L1·m, L1) (Fig. I-5).

In the middle to upper level of the petiole, the marginal lateral bundle L1 gives off L1' which inverts in the xylem-phloem orientation forming the ventral bundle (V) (Fig. I-6, 7). The marginal lateral bundle (L1) further gives off small bundle between the adjacent inner lateral bundle L1·m. However, this last small bundle soon degenerates (Fig. I-8, 9).

In the upper petiole, bundle L1·m gives off bundle L1·m'; and V bundle bifurcates (Fig. I-9). Consequently three pairs of lateral bundle, L1·m, L1·m' and L1, are observed in this level.

At the base of the ternate-compound leaf, bundle L1·m gives off L1·m'' for an additional lateral pair in the petiolar vasculature. Finally four pairs of bundles (L1·m, L1·m', L1·m'' and L1) are located laterally at the leaf base (Fig. I-10). Above this level the petiole is diverged into three petiolules and each contains the main and lateral bundles. For example in the petiolule of the terminal pinna (T), bundle L1·m gives off L1·m'''' and thus the vasculature is composed of M bundle as the main vein and two pairs of L1·m and L1·m'''' as the lateral veins (Fig. I-11). Similarly in the petiolule for each basal pinna (B), the vascular system consists of L1·m' as the main vein, and two L1·m'' on the one side of main vein and L1 and V on the other side as lateral bundles (Fig. I-11, 12). The V bundle participates in the vasculature of the marginal lateral bundles which start for each petiolule of the basal pinna (B).

The individual pinna is trilobed in the middle lamina and a single terminal and two basal pinnules are recognized. In the terminal pinnule of the basal pinna, main vein (L1·m') and lateral veins (L1 and L1·m'') are situated but only V or L1·m'''' is located in the median of its basal pinnules
Fig. I. Node-leaf vascular system of *Clematis williamsii*. 1: stem, 2: at node, 3-10: successive levels in petiole, 11-14: successive levels of ternate lamina.

Abbreviations. M: median leaf trace; L1: lateral leaf trace; m: derivative bundle from M; L1+m: lateral bundles in the petiolar vascular system; L1+m', L1+m'', L1+m''', L1+m''''': vascular system in the petiolule; V: ventral bundle; ¶F: terminal pinna; ¶G: basal pinna.

1-2: ca. x9, 3-4: ca x8, 5-7: ca x13, 8-12: x20, 13-14: ca x8.
In the vascular system of the median pinnule of the terminal pinna (T), M bundle is situated in the median and L1•m in the lateral position whereas L1•m''' forms the main vein in that of basal pinnules (Fig. I-14).

*Paeonia japonica* This perennial herb possesses biternate-compound leaves. The trilacunar nodal condition is observed and three leaf traces, a single M and two L1, enter the petiolar base (Fig. II-1). The lateral trace L1 in the petiolar base diverges to give rise to three bundles (L1a, L1b, L1c) on either side of M (Fig. II-2). The small bundle (L1e) is derived from L1c and is located marginally in the petiolar base, but soon diminishes in the upper level (Fig. II-3).

In the lower petiole, the marginal lateral bundle (L1c) gives off L1c' which inverts in the xylem-phloem orientation and fuses to form the ventral bundle (V) (Fig. II-4, 5).

In the middle level of the petiole, two L1a bundles fuse first with M bundle, and later with L1b forming the compound large bundle L1a•b on either side of M (Fig. II-5, 6).

In the upper petiole the lateral bundle (L1a•b) gives off L1a•b' to the additional lateral bundle; and the ventral bundle (V) bifurcates in the adaxial region (Fig. II-7). Thus three pairs of lateral bundles (L1a•b, L1a•b' L1c), two ventral bundles (V) and a single median bundle (M) are formed.

In the base of the biternate compound leaf, bundle L1a•b bifurcates and one of the segments (L1a•b'') supplies the petiolute of the basal pinnae (B) and the others form the lateral bundles (L1a•b') of the terminal pinna (T). Subsequently, individual petiolute contains a single main vein and a few lateral veins (Fig. II-9, 10). In the terminal pinna (T), the vascular system of the petiolute consists of a main vein (M) and two lateral veins (L1a•b') (Fig. II-10). In each basal pinna (B), the vascular system of the petiolute is composed of main vein (L1a•b) as well as lateral veins of L1a•b'' on one side and L1c and V on the other side (Fig. II-9, 10).

In the lamina of this compound leaf each pinna is deeply trilobed forming three pinnules, one terminal and the other two basal; and individual pinna as well as pinnule possesses the obvious main and lateral veins (Fig. II-11). In the basal pinna (B), each of three pinnules contains the main vein of either L1a•b, L1a•b'' or L1c bundle (Fig. II-11), and their lateral veins are com-
Fig. II. Node-leaf vascular system of *Paeonia japonica*. 1: at node, 2-7: successive levels in petiole, 8-14: successive levels in binate lamina.

Abbreviations. L1a, L1b, L1c: derivative bundles from L1; L1e: branch from L1c; L1a·b, L1a·b', L1a·b'', L1a·b''': vascular system in the petiolule. Other symbols see Fig. I.
posed of either a combination of L1a•b" and its derivative vein or L1c and V. At this level, V bundle takes part in one of the lateral bundle in the pinnule.

In the lower level of terminal pinna (T), L1a•b' bundle is located in the lateral position and M bundle in the median (Fig. II-12). In the middle level of the terminal pinna (T), M bundle trifurcates and gives rise to M' bundle on either flank of M (Fig. II-13). M' bundle further gives off segments to give rise to M" bundles which become lateral veins of each pinna (Fig. II-14). Individual pinnule of the terminal pinna (T) possesses such combination of main and lateral veins as either M and two M" or M, M" and L1a•b' (Fig. II-14).

Discussion

In the previous paper the present author has described the seven types of the vascular system in the node-leaf continuum of the Magnoliales and discussed the phylogeny of the nodal anatomy (Sugiyama 1979). Since Marsden & Bailey (1955), unilacunar, two-trace node (2:1 type) was generally accepted as the most primitive nodal structure in the angiosperms. In the Magnoliales (sensu Takhtajan 1969), however, none of such 2:1 type of nodal condition has been investigated nor reported but either the multilacunar or trilacunar node was found (Ozenda 1949, Canright 1955, Sugiyama 1972, 1974, 1976, 1979). In the detailed studies of the vascular behavior in the node-leaf continuum, the present author found that the significance of the nodal structure lied in the behavior of the ventral bundle rather than in the number of leaf gaps and traces at the node.

In the Magnoliales, the phylogenetically basic vascular structure in the node-leaf continuum was found in the ventral bundle that consists of the innermost pair of lateral trace (A) and of branches (m) from the median trace (M). This composition of the ventral bundle with A and m bundles was derived from median group of bundles and was designated to belong in Type I (Sugiyama 1972, 1979). As a result of serial reductions, both A and m or either A or m bundle may be reduced. With advancement, the ventral bundle appeared from the branches (L1') of the marginal lateral bundles (L1). This type of the ventral bundle was derived from the lateral group of bundles and was represented as Type VI (Sugiyama 1979). Except for
Type VII, the adaxially located vascular bundle was found in all the genera of the Magnoliales and their ventral bundle was extended at least in the lower level of the lamina remaining in the adaxial side of the midrib.

In the present observation, both *Clematis williamsii* and *Paeonia japonica* show Type VI with trilacunar node (Fig. I-2, II-1). In the Magnoliales, *Eupomatia laurina* showing 7:7 type in nodal condition was the only plant possessing Type VI (Sugiyama 1976).

Dr. H. Tobe, Chiba University, studied 14 species of the *Clematis* and observed that most species showed Type VI except for *Clematis japonica* of Type V. Such type V is a transitional state of the ventral bundle consisting of derived bundles (m and L1') both from the median and lateral group. Considering other diagnostic characters altogether, he concluded that *Clematis japonica* possessed basic character in the genus (personal communication in 1978).

The vascular behavior in the node-leaf continuum was carefully followed, and the similarities in the present two genera was observed. In *Clematis williamsii* the inner pair of lateral petiolar bundles (L1•m) covers most part of the ternate-compound lamina, but both marginal lateral (L1) and ventral (V) bundles of the petiole supply only lateral veins for the basal pinnae (B) (Fig. I-12). In *Paeonia japonica* the lateral trace (L1) trifurcates to give rise to three lateral bundles (L1a, L1b, L1c) on either side of M in the petiolar base (Fig. II-2). The bundle L1a anastomose with L1b to give rise to a compound bundle L1a•b which participates in the vascular system of most part of binate-compound lamina (Fig. II-9). The ventral bundle (V) and the marginal lateral bundle (L1c) supply only lateral veins of one of the basal pinnae (B) (Fig. II-11).

The behavior of the ventral bundle (V) in the present two genera is characteristic. Their ventral bundle (V) is derived from the marginally located lateral bundles (L1 or L1c), remaining adaxially in the petiole but in the lamina they are translocated in the lateral position supplying the lateral veins for basal pinnules (Fig. I-13, II-11).

The behavior of the ventral bundle (V) in the node-leaf continuum in the two genera of Ranalian complex differs from that of the Magnoliales. In the Magnolean genera, if it occurs, the ventral bundle remains in the adaxial possession of the midrib at least up to the level of the laminar base.
This is true in all the genera of Magnoliales whose ventral bundle (V) is derived from median and/or lateral bundles (Sugiyama 1979). In the present two genera of Ranalian complex the ventral bundle occurs adaxially in the petiole arising from either median and/or lateral group of bundles. However, the ventral bundle becomes situated laterally in the lamina and behaves as one of the lateral bundle (Fig. I-12, II-11).

Above difference in the behavior of the ventral bundle may depend on either simple leaves vs. compound or phylogeny of Magnoliales vs. Ranalian complex. Only further accumulation of knowledges will be able to lead us to the correct answer.

I wish to express my cordial thanks to Prof. T. Yamazaki, University of Tokyo for his critical reading of the manuscript.

References

キョーロッパに於けるイチョウの老樹など (小林義雄) Yosio Kobayasi:
The maidenhair trees (Ginkgo biloba) planted in several botanical gardens in Europe

本誌のカットにイチョウが載っている。 高等学校時代の旧友星野昌一君がデザインしたこの模様が今も東大のシンボルマークになっていることも懐く、これに関連してヨーロッパの植物園に植えられているイチョウの老樹を改めて見直す気分になった。