

The Comparative Floral Anatomy and Systematics of the Berberidaceae

I. Morphology

By

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Abstract. The floral vascular anatomy in the Berberidaceae is discussed, with special reference to the anatomical relationships of sepals, petals and stamens, the nature of the cortical bundles and the evolutionary trends in the floral receptacle and in the pistil. The followings are revealed in the Berberidaceae. Petals are more closely related to stamens than to sepals in the most genera of the Berberidaceae, but those of *Nandina* are more closely related to sepals than to stamens. There are three different types of cortical bundles in the floral receptacle. These three types of cortical bundles are related to the arrangement of vascular bundles in the stem or to the size of the floral receptacle. There is a tendency of the suppression of the floral receptacle. Different structure of the pistils in the Berberidaceae is considered to be derived through different evolutionary lines from the common ancestral form.

Introduction

The Berberidaceae s. l. are a family of perennial herbs and shrubs distributed mainly in temperate regions of the northern hemisphere and contain 16 genera; *Achlys* DC., *Berberis* L., *Bongardia* Mey., *Caulophyllum* Michx., *Diphylleia* Michx., *Dysosma* Woodson, *Epimedium* L., *Gymnospermium* Spach, *Jeffersonia* Bart., *Leontice* L., *Mahonia* Nutt., *Nandina* Thunb., *Plagiorhegma* Maxim., *Podophyllum* L., *Ranzania* T. Ito and *Vancouveria* Morr. et Decne. This family is placed in the order Ranunculales (or Berberidales) together with such families as Lardizabalaceae, Sargentodoxaceae, Menispermaceae and Ranunculaceae (Buchheim 1964, Thorne 1974, Takhtajan 1980).

Within the Berberidaceae s. l., four groups of genera; *Nandina*, *Berberis-Mahonia*, *Epimedium-Vancouveria-Plagiorhegma-Jeffersonia-Achlys-Caulophyllum-Leontice-Gymnospermium-Bongardia*, and *Diphylleia-Dysosma-Podophyllum*, have been recognized, although the systematic position of *Ranzania* is still uncertain and the taxonomic status of these groups have been variously treated (Janchen 1949, Buchheim 1964, Thorne 1974, Takhtajan 1980, Kosenko 1980, Meacham, 1980). There are large gaps in the characters of these groups, and it has been considered difficult to determine their true relationship. In connection with this, there also remains a problem in the delimitation of the family. Tischler (1902) split the Berberidaceae s. l. into Berberidaceae

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and Podophyllaceae. Hutchinson (1959) split it into three families, Nandinaceae, Berberidaceae and Podophyllaceae. In the system proposed by Airy Shaw (1966), the Berberidaceae s. l. are composed of Nandinaceae, Berberidaceae, Leonticaceae and Podophyllaceae. The classification of the Berberidaceae s. l. has been based on comparative morphological studies of various parts of the plant as well as karyological, pollen morphological, comparative serological and chemotaxonomical studies (Terabayashi 1982).

The flowers of this family are considered to be specialized in such features as a single terminal pistil with uni-locular ovary and anthers opening by valves, but to be primitive in having many perianth lobes. In this family, the comparative study of floral morphology provides aid in estimating the relationships of the groups of genera as well as in the delimitation of the family. Several contributions have been made for understanding the floral structure. Schmidt (1928) studied the floral construction and interpreted the trimerous flowers as being derived secondarily from a 2/5 spiral arrangement. Hiepko (1965) compared the morphology and ontogeny of the perianth, and pointed out the morphological gap between sepals and petals in this family, except in *Nandina*.

Despite Kumazawa's observation on the vasculature in the floral receptacle in *Diphylleia*, *Podophyllum*, *Ranzania* and *Achlys* (Kumazawa 1930, 1937a, 1937b), the comparative study of the vascular anatomy in the floral receptacle has remained insufficient. To get more information on the vasculature in the receptacle, I have studied the vascular anatomy in the receptacle throughout the family (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c). These studies have shown that there are various types of traces to the sepals, petals and stamens and that cortical vascular systems are observed in *Ranzania*, *Diphylleia*, *Dysosma*, *Podophyllum* and rarely in *Jeffersonia*. The pistillate structure of the Berberidaceae s.l. has been one of the most important subjects; it has been interpreted that the pistils are either truly monomerous (Eckardt 1937, Leinfellner 1956, Sastri 1969, Guédès 1977) or pseudomonomerous (Saunders 1925, 1928, Chapman 1936, Kaute 1963). In the studies of the vascular anatomy (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c), special attention was paid to critical comparisons of the pistils among the related genera. These studies have revealed that the pistils of the Berberidaceae s.l. are somewhat diverse, but retain fundamentally the same morphological plan.

In this article, I intend to deal with the anatomical relationships of the sepals, petals and stamens, the nature of the cortical vascular system in the receptacle, and evolutionary trends in the receptacle and in the pistil in the Berberidaceae s.l. Based on floral anatomy, the relationships of the genera will be reexamined throughout the family, and a new system will be proposed.

Morphology

1) Vasculature in the receptacle

Tepfer (1953) made it clear that the vasculature in the floral receptacle is constructed differently even in the same flower, based either on the observation of the whole vascular bundles, including secondary tissue, or on the observation of the lignified elements only; mainly xylem strands. Some works on the receptacular vasculature in the flower of Ranunculales or Berberidales were done in the former manner (Smith 1926, 1928, Eames 1931, Tobe 1980a).

In the vasculature reconstructed in the former manner, the receptacular stele is recognized as a vascular cylinder from which traces to the sepals, petals, stamens and carpels are given off leaving trace gaps. However, in the vasculature reconstructed in this way, it is impossible to distinguish case where two strands arising from two adjacent stelar bundles unite into a single trace just after their separation from the stele and lead to the trace, from the case where only one strand derived from a single bundle leads to the trace. In both cases, the traces are described as uni-lacunar single traced.

For a more exact understanding of the receptacular vasculature, Sporne (1958) paid special attention to the behaviour of the primary vascular system as was done in the analysis of the vasculature in the vegetative shoot (Dormer 1946, 1954, Balfour and Philipson 1962, Ezelarab and Dormer 1963, Slade 1971). Only by this analysis of the floral receptacular vasculature, is it possible to distinguish the two cases mentioned above; traces of the first case are described as being of a double nature, traces of the second case are described as being of a single nature. From the studies by Tepfer (1953) and Sporne (1958), it is clear that the vasculature in the receptacle reconstructed from the primary vascular bundles and that from the xylem strands are nearly identical.

In a series of floral morphological studies in the Berberidaceae s.l., I described the floral vasculature in the receptacle and in the pistil, based on the primary vascular bundles and xylem strands (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c).

Trace pattern

As for the departure of the traces to the sepals, petals and stamens from the stele, the following types are observed; i). traces of a single nature, ii). traces of a double nature, iii). traces of a triple nature, iv). traces of a multiple nature. Traces of a single nature are formed by the trifurcation of one of the stelar bundles and the departure of the median branch (Fig. 1-A). Traces of a double nature are formed by the two bundles arising from two adjacent stelar bundles becoming the trace. In some cases, the two traces unite into a single trace while entering the floral element, and in the other cases the two traces enter the floral element without uniting (Fig. 1-C). There

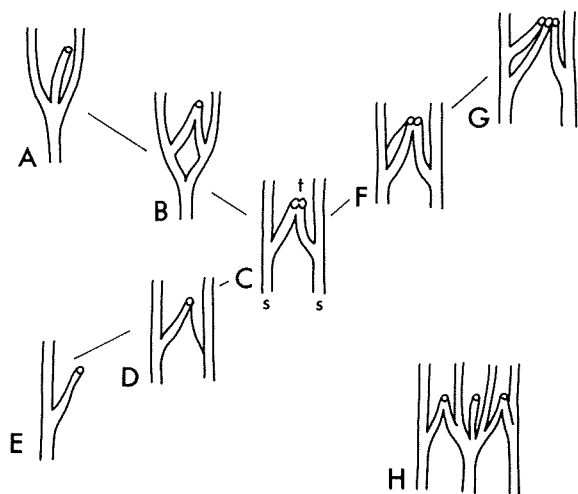


Fig. 1. Diagrammatic illustrations of trace pattern. A, Trace of a single nature; B-D, Trace of a double nature; E, Maybe trace of a double nature, one of the trace is lacking; F and G, Trace of a triple nature; H, Trace of a multiple nature. s=stelar bundle, t=trace bundle.

are intermediate conditions between the first and the second types as shown in Fig. 1. Cases are observed in which the phloem of the trace is of a double nature, but the xylem is of a single nature in origin from the stelar bundles. In the second type, one of the two traces is sometimes lacking (Fig. 1-E). In rare cases, observed in *Epimedium*, two of the traces arise from the same stelar bundle at different levels and another trace arise from an adjacent stelar bundle. This is a trace of a triple nature (Fig. 1-G). In the fourth type of trace more than three traces arise from separate stelar bundles and enter the floral elements. This type of trace is regarded as composed of traces of a single nature and a double nature (Fig. 1-H).

It is well known that there is correlation between the size of the floral elements and the trace pattern in the Angiospermae (Carlquist 1969). There is a tendency that floral elements with wide bases (usually sepals) receive a large number of traces and those with narrower bases (usually petals and stamens) receive a smaller number of traces. For example, in the Ranunculaceae sepals usually receive 3 traces from separate stelar bundles, while petals and stamens receive a single trace, usually of a double nature (Smith 1926, 1928, Tepfer 1953, Sporne 1958, Tobe 1980a, 1980b). A similar condition is observed in some genera of the Lardizabalaceae (Taylor 1967). The condition observed in the Berberidaceae s.l. are as follows (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c). In most genera, the outermost small sepals are traversed by traces of a single nature, while the inner sepals, petals and stamens are traversed by traces of a double nature (Table 1). The elements with more or less wide bases, sepals of *Plagiorhegma*, *Jeffersonia*, *Ranzania*, *Podophyllum*, *Dysosma* and *Diphylleia*, and petals of *Ranzania*, *Podophyllum*, *Dysosma* and *Diphylleia*, often receive more than 3 traces arising from separate stelar

Table 1. The vascular anatomy in the receptacle

	Se	Pe	St	Co
<i>Nandina</i>	1-2	2	2	—
<i>Berberis</i>	1-2	2	2	—
<i>Mahonia</i>	1-2	2	2	—
<i>Ranzania</i>	1-2*	2*	2	+, II, III
<i>Epimedium</i>	1-2(-3)	2(-3)	2	—
<i>Vancouveria</i>	1-2	2	2	—
<i>Plagiorhegma</i>	1-M	2	2	—
<i>Jeffersonia</i>	1-M	2	2	-, +, III
<i>Achlys</i>			1	—
<i>Caulophyllum</i>	1-2	2	2	—
<i>Leontice</i>	1-2	2	2	—
<i>Gymnospermium</i>	1-2	2	2	—
<i>Bongardia</i>	1-2	2	2	—
<i>Diphylleia</i>	1-M*	2*	2	+, I, III
<i>Dysosma</i>	1-M*	2(-M)*	2	+, I, III
<i>Podophyllum</i>	1-M*	2(-M)*	1-2	+, I, III

Se: sepal trace. Pe: petal trace. St: stamen trace. 1, trace of a single nature; 2, trace of a double nature; 3, trace of a triple nature; M, trace of a multiple nature.

* Cortical bundles supply traces.

Co: cortical vascular system in the receptacle. +, present; I, 1st type; II, 2nd type; III, 3rd type; —, absent.

bundles and/or cortical bundles. In the Berberidaceae s.l., a correlation between the size of the floral elements and the trace pattern is recognized.

For an understanding of the floral structure, it has been considered to be helpful to elucidate the relationships of the sepals, petals, stamens and carpels. In the Berberidaceae s.l., the sepals, petals and stamens are lateral organs on the floral receptacle, but the pistils are terminal, and we can safely compare the vascular anatomy of sepals, petals and stamens. The vascular supply to the terminal pistil is much modified and difficult to compare directly with the vasculature of the lateral organs. In this chapter, the relationships of the sepals, petals and stamens are discussed. In the Ranunculaceae, the vascular supply from the stele to the petals is comparable with that to the stamens, and this fact has been used as evidence to suggest that petals are modified stamens (Neumayer 1924, Smith 1926). In the Berberidaceae s.l., there is no distinct gap in the trace pattern between the stamens and petals, except in *Podophyllum* which has secondarily modified stamen traces (Terabayashi 1983b), and *Achlys* which lacks petals. In general, the traces to the petals and stamens are of a double nature. In such genera as *Ranzania*, *Podophyllum*, *Dysosma* and *Diphylleia* having a cortical vascular system in the receptacle, the petals sometimes receive additional traces from the cortical vascular system but the stamens rarely do. However, in these genera the traces to the petals from the stele are apt to be of a double nature as in the stamen traces. The modified form of stamen traces in *Podophyllum* is considered to be derived from traces of a double nature (Terabayashi 1983b). The constantly single nature of the stamen traces in *Achlys* is considered to be derived by extreme reduction (Terabayashi 1981). The venation of the stamen is rather simple in this family; usually a single midvein only, but rarely a single midvein and two lateral veins in *Plagiorhegma*, *Jeffersonia* and *Diphylleia*. In contrast, the petals are covered with well developed venation composed of dichotomously branched veins.

In the Berberidaceae s.l., the petals are easily distinguished from sepals in having glands (*Berberis*, *Mahonia*, *Ranzania*), having spurs or nectariferous pockets (*Epimedium*, *Vancouveria*, *Bongardia*), being small glands (*Caulophyllum*, *Leontice*, *Gymnospermium*) or being membranous (*Plagiorhegma*, *Jeffersonia*, *Podophyllum*, *Dysosma*, *Diphylleia*). In connection with the different size and shape of the sepals and petals, the venation of the sepals and petals is also distinguishable, but the fundamental dichotomous branching pattern is in common (Hiepkö 1965), and the sepals and petals are not drastically distinct from each other in the vascular supply from the stele (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c). The innermost sepals receive traces of a double nature as in the petals, although the outer and middle sepals receive traces of a single nature or of a multiple nature. The petals of *Nandina* are similar to the sepals in shape; broadly elliptic, and the vascular anatomy of the petals and sepals is identical; the traces are of a double nature, and the venation is composed of a midvein and a few laterals branched dichotomously (Terabayashi 1983c).

Hiepkö (1965) indicated that in such genera as *Berberis*, *Mahonia*, *Caulophyllum*, *Epimedium*, *Plagiorhegma*, *Jeffersonia*, *Diphylleia* and *Podophyllum*, petals show retardation in development, being situated between the sepals and stamens. But the petals of *Nandina* show no retardation in development. Hiepkö (1965) also gave results that showed that the initiation of the sepals, petals and stamens is visualized in the periclinal division of the second layer of the tunica in the genera *Berberis* and *Mahonia*. In my preliminary observation, the same initiation pattern was observed in *Epimedium* and *Diphylleia*.

Teratological evidence is given in a few cases. Leinfellner (1955) showed various abnormal forms between petals and stamens in *Berberis*. I found such abnormal forms in *Jeffersonia* and *Diphylleia*.

The evidence from vascular anatomy (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c), of ontogeny (Hiepko 1965) and of teratology (Leinfellner 1955) suggests that petals are more closely related to stamens than to sepals in most genera, but that the petals of *Nandina* are more closely related to sepals than to stamens. To arrive at a final conclusion on this subject, detailed ontogenetic studies of sepals, petals and stamens should be made throughout the family.

Cortical vascular system

It is noteworthy that a cortical vascular system is present in the floral receptacle in the Berberidaceae s.l. since the presence of the cortical vascular system in the floral receptacle is unusual in the Ranunculales to which the Berberidaceae s.l. belongs. A cortical vascular system in the receptacle is observed in *Ranzania*, *Podophyllum*, *Dysosma* and *Diphylleia*, and rarely in *Jeffersonia* (Terabayashi 1977, 1981, 1983b).

It is possible to classify the manner of origin of the cortical vascular bundles into three types. The first type is observed in the genera *Podophyllum*, *Dysosma* and *Diphylleia* (Terabayashi 1983b). In these genera, the stele of the peduncle and pedicel is composed of two circles of vascular bundles; the inner medullary bundles and surrounding weak bundles. The surrounding bundles give rise to the cortical bundles in the floral receptacle (Fig. 2-A, D, H). The second type is observed in *Ranzania* (Terabayashi 1977). In this genus, a few of the cortical bundles arise from the bundles situated slightly outside of the main stelar bundles in the pedicel. The pedicellate stele doesn't have the medullary bundles that are observed in the above three general (Fig. 2-B, E, I). In the third type of cortical bundle the main stelar bundles give off bundles at the lowermost level of the receptacle and these bundles lead to the cortical bundles (Fig. 2-C, F, J). Most of the cortical bundles observed in *Ranzania*, and those rarely observed in *Jeffersonia*, originate in this way. Cortical bundles of the third type are also observed in *Podophyllum*, *Dysosma* and *Diphylleia*.

In *Podophyllum*, *Dysosma* and *Diphylleia*, the cortical bundles enter the outer sepals as main traces and enter the middle-inner sepals and petals as additional traces. In *Ranzania*, the cortical bundles enter the sepals and petals as additional traces or fuse with the main traces to the petals and stamens. In *Jeffersonia*, the cortical bundles enter the sepals as additional traces.

The first type of cortical bundles is related to double circles of vascular bundles in the peduncle or pedicel, and these double circles of vascular bundles are continuous with the scattered arrangement of vascular bundles in the stem (Kumazawa 1930). A similar condition is observed in the Liliaceae: *Tricyrtis* (Takahashi 1980), *Erythronium* (Utech and Kawano 1975) and *Paris* (Utech and Kawano 1980). In these genera, the pedunculate or pedicellate stele is composed of two circles of vascular bundles and the stem stele consists of scattered bundles. The double circles of vascular bundles in the peduncle or pedicel are continuous with the scattered arrangement of vascular bundles in the stem. In *Nelumbo* (Ito, in prep.) and in *Calycanthus* (Smith 1928), the cortical bundles in the stem give rise directly to the cortical bundles in the floral receptacle. The cortical bundles of the second type are also related to the vascular arrangement in the stem. In *Ranzania*, the stele of the pedicel is composed of main bundles with weak bundles situated

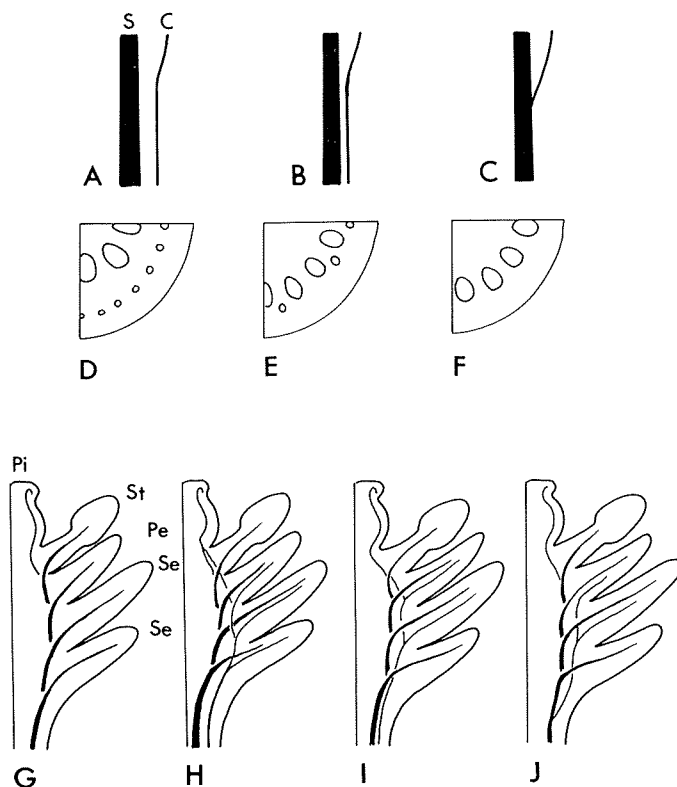


Fig. 2. Explanatory illustrations of cortical vascular system in the floral receptacle. A-F, Three types of cortical bundles; A-C, Longitudinal view; D-F, Trans sections of pedicel or peduncle; A and D, 1st type; B and E, 2nd type; C and F, 3rd type. s=stelar bundle, c=cortical bundle. G-J, Vascular anatomy of the receptacular region; G, Receptacle without cortical bundles; H, Receptacle with the cortical bundles of the 1st type (*Diphylleia*, *Dysosma* and *Podophyllum*); I, Receptacle with the cortical bundles of the 2nd type (*Ranzania*); J, Receptacle with the cortical bundles of the 3rd type (*Ranzania*, *Jeffersonia*, *Diphylleia*, *Dysosma* and *Podophyllum*). Pi=pistil, St=stamen, Pe=petal, Se=sepal.

slightly outside of the main bundles and is continuous with the stem stele consisting of nearly two circles of vascular bundles (Kumazawa 1937b, Terabayashi 1977). It can be said that the cortical bundles of the first and the second types are related to the two different kinds of stele in the stem.

The second and the third types of cortical bundles are partly due to the size of the floral receptacle. For example, *Jeffersonia*, which is considered to be a genus derived from *Epimedium* and *Vancouveria*, has larger flowers than those of the above two genera and rarely has cortical bundles in the floral receptacle: *Epimedium* and *Vancouveria* have no cortical bundles in the receptacle. In *Jeffersonia*, the cortical vascular system in the receptacle is speculated to have originated secondarily in parallel with an increase in flower size. In *Ranzania*, the larger terminal flower of the cyme has more cortical bundles than lateral smaller flowers. The condition observed in *Anemone japonica* (Ranunculaceae) is comparable with the second type. The flower of this species is relatively large in this family and the pedunculate stele is composed of nearly two circles of vascular bundles. The outer bundles lead to the cortical bundles and enter the sepals,

or fuse with the inner main bundles (Sporne 1958).

The cortical vascular system in the receptacle is sometimes observed in the taxa of woody Polycarpicae: Magnoliaceae, Annonaceae, Winteraceae, Himanthandraceae and Calycanthaceae, which are considered to be the most primitive taxa in the Angiospermae. And, therefore, the cortical vascular system in the receptacle has often been considered to be one of the primitive characteristics. However, the cortical vascular system of these taxa is so complicated and must be analyzed accurately before any discussion on the primitiveness of this feature is made. In the Berberidaceae s.l., it should be noted that the three types of cortical bundles each show a different nature. Namely, the cortical vascular system is related to the scattered arrangement of vascular bundles in the stem, to nearly two circles of vascular bundles in the stem or to the large size of the floral receptacle. To elucidate whether this characteristic is primitive or not, vascular anatomical studies of the stem will be needed.

Evolutionary trend in the floral receptacle

In the Berberidaceae s.l., a suppression is recognized in the upper portion of the receptacle. In other words, the floral elements of the inner whorls tend to become adnate. The stamens and petals on the same radii tend to fuse at their bases. Anatomically, the traces to the stamens and petals on the same radii separate from the stele more closely than those to the sepals in *Ranzania*, *Berberis*, *Mahonia*, *Epimedium*, *Vancouveria*, *Plagiorhegma*, *Jeffersonia*, *Bongardia*, *Diphylleia*, *Dysosma* and *Podophyllum* (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b). In *Gymnospermium*, *Leontice*, *Caulophyllum* and *Podophyllum peltatum*, common bundles giving rise to stamen traces and petal traces, or common bundles giving rise to petal traces and inner sepal traces are observed (Terabayashi 1983a, 1983b). In *Gymnospermium albertii*, the most specialized condition is observed: common bundles supply the stamen traces, petal traces and inner sepal traces. It can be said that the suppression of the receptacle proceeds from the upper portion downward in this family.

In the Berberidaceae s.l., cohesion is very rare. The stamens, petals and sepals are all free organs. The only exception is in *Vancouveria hexandra* which has six stamens fused at their bases into a staminal tube. In the related families, Lardizabalaceae and Menispermaceae, the staminate flowers usually have stamens that are variously fused. For example, *Dioscoreophyllum* (Menispermaceae) has a massive androecium formed by the complete fusion of six stamens (Shaeppi 1976).

The pistil number and number of whorls of stamens and petals are constant, except in *Achlys* which has (7–)9(–12) stamens. *Podophyllum peltatum* has 12–18 stamens, but these stamens are in two whorls; $3 + 3^3(-4)$. In contrast, the number of whorls of sepals is variable (Table 2). In the case of *Epimedium*, *Vancouveria* and *Nandina*, the number of whorls of sepals varies in the same inflorescence. The genus *Nandina* has the largest number of whorls of sepals in this family. In connection with this, the receptacle of this genus is longer than broad (Terabayashi 1983c).

There is an argument as to whether the condition where many sepals are borne on a long receptacle is original or such a condition is derived secondarily through an increase in the number of sepals, accompanied by an elongation of the floral receptacle. For reasons mentioned below, it is most probable to consider that the condition where the longer receptacle bearing sepals in many whorls is original in the Berberidaceae s.l. 1). In a group of closely related genera, the

Table 2. The number of whorls of floral elements

	A	B	C	D	E
<i>Nandina</i>	3	7-10	2	2	1
<i>Berberis</i>	3	1-4	2	2	1
<i>Mahonia</i>	3	1-3	2	2	1
<i>Ranzania</i>	3	3(-4)	2	2	1
<i>Epimedium</i>	2	4-5	2	2	1
<i>Vancouveria</i>	3	5-6	2	2	1
<i>Plagiorhegma</i>	3	2-3	2	2	1
<i>Jeffersonia</i>	4*	5-7*	8*	8*	1
<i>Achlys</i>				(7-)9(-12)**	1
<i>Caulophyllum</i>	3	3-4	2	2	1
<i>Leontice</i>	3	2	2	2	1
<i>Gymnospermium</i>	3	2	2	2	1
<i>Bongardia</i>	3	2	2	2	1
<i>Diphylleia</i>	3	2-3	2	2	1
<i>Dysosma</i>	3	2-3	2	2	1
<i>Podophyllum</i>	3	2(-3)	2	2	1

A: Type of flower. 3 = trimerous, 2 = dimerous. B: Number of whorls of sepals.

C: Number of whorls of petals. D: Number of whorls of stamens. E: Number of pistil.

* The flowers of *Jeffersonia* look tetramerous, but floral elements are arranged in a spiral with a fraction of 2/5-3/8. In this genus, the number of floral elements are indicated.

** No clear whorled arrangement is recognized.

number of sepals tends to decrease. *Epimedium-Vancouveria* are closely related to *Plagiorhegma-Jeffersonia*, which are allied to *Achlys*. Based on a comparison of several characteristics, such as inflorescence, pistils and leaves, *Plagiorhegma-Jeffersonia* are considered to be derived genera from *Epimedium-Vancouveria* and *Achlys* is considered to be a derived genus from *Plagiorhegma-Jeffersonia*. The number of whorls of sepals is 4-5 (8-10 sepals) in *Epimedium* and is 5-6 (15-18 sepals) in *Vancouveria*, while the number of whorls of sepals is 2-3 (6-9 sepals) in *Plagiorhegma* and the sepals arranged in a spiral are 5-7 in number in *Jeffersonia*. *Achlys* has no sepals (Table 2). A similar case is observed in *Podophyllum* and *Dysosma*. In such characteristics as inflorescences, pollen and floral vasculature, *Podophyllum* shows derived features. The number of whorls of sepals is usually 3 (9 sepals) in *Dysosma* and usually 2 (6 sepals) in *Podophyllum*. 2). An increase in the number of whorls is not recognized in the petals and stamens in this family. The increase in number of petals observed in *Plagiorhegma*, *Podophyllum* and *Dysosma* is due to the dedoublement of a single petal (Schmidt 1928, Terabayashi 1983b). In *Podophyllum peltatum*, many stamens are arranged in $3+3^3(-4)$. Namely, trifurcation or tetrafurcation occurs in the inner whorl (Terabayashi 1983b). The stamens of *Achlys* are (7-)9(-12) in number and are not arranged in clear whorls. The manner of increase in stamens is not clear in this genus at present. 3). In addition, examples of an increase in sepal whorls are infrequently reported in other families of the Angiospermae.

In conclusion, I give the following interpretation. In the Berberidaceae s.l., the original structure of the floral receptacle is considered to be the condition where a long receptacle bears

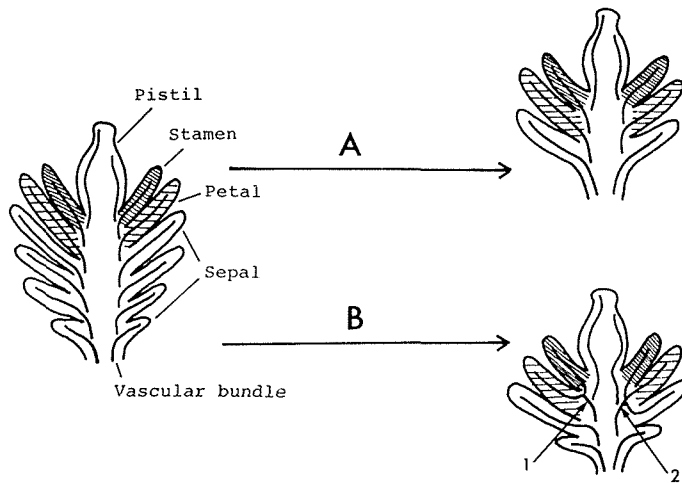


Fig. 3. Evolutionary trends in receptacular region. A, Suppression by a lack of whorls of sepals; B, Suppression by the occurrence of common bundles. Arrow 1, Common bundle giving rise to stamen trace and petal trace; Arrow 2, Common bundle giving rise to stamen trace, petal trace and sepal trace.

a single terminal pistil, stamens in two whorls, petals in two whorls and sepals in many whorls. From this condition, some types of receptacle may be derived by the suppression of the upper portion and/or the loss of whorls of sepals in the lower portion, but retaining the pistil and a constant number of whorls of stamens and petals (Fig. 3).

2) Vasculature in the pistil

The pistil of the Berberidaceae s.l. have a unique structure among other closely related families where the gynoecea are apocarpous. Without exception, the pistils are singular in each flower and have ovaries with a single locule and no ventral suture. In some genera, the placenta is of a parietal-type, and in the other genera the placenta is of a basal-type (Table 3).

The structure of the pistil in the Berberidaceae s.l. has been studied morphologically and/or anatomically by several authors. Some authors gave the interpretation that the pistils of the Berberidaceae s.l. are composed of a single carpel (Eckardt 1937, Leinfellner 1956, Sastri 1969, Guédès 1977), but others considered that it is most probable that the pistils may be derived from syncarpous pistils through reduction and that the pistils are pseudomonomerous (Saunders 1925, 1928, Chapman 1936, Kaute 1963). The interpretation of pseudomonomerous pistils is various, depending on the author. Saunders (1925, 1928) considered that the pistils of the Berberidaceae s.l. consist of three types of carpels; valve carpels (V), solid carpels (S) and semi-solid carpels (SS), and the following combinations of carpels are possible; V+SS, V+S, V+V, V+V+V. Chapman's (1936) conclusion was that the pistils of the Berberidaceae s.l. are heterogenous in structure and that they may be biphyletic in origin, namely, those derived from syncarpous pistils, in which three carpels are involved, through a reduction of two of the three carpels, while the others are derived from bicarpellate pistils through a reduction of one of the two. The pseudomonomerous theory of Kaute (1963) is based on evidence that the abnormally dimerous pistils, which are uni-locular but with two placentas, are widely observed in the Berberidaceae s.l.

Table 3. The pistillate character of the Berberidaceae

	A	B	C	D
<i>Nandina</i>	Parietal	2-3	Berry	-
<i>Berberis</i>	Basal	1-15	Berry	-
<i>Mahonia</i>	Basal	1-18	Berry	-
<i>Ranzania</i>	Parietal	20-30	Berry	-
<i>Epimedium</i>	Parietal	6-15	Capsule	+
<i>Vancouveria</i>	Parietal	4-7	Capsule	+
<i>Plagiorhegma</i>	Parietal	20-30	Capsule	+
<i>Jeffersonia</i>	Parietal	30-40	Capsule	+
<i>Achlys</i>	Basal	1	Achene	+
<i>Caulophyllum</i>	Basal	2	*	-
<i>Leontice</i>	Basal	3-4	Capsule	-
<i>Gymnospermium</i>	Basal	2-4	Capsule	-
<i>Bongardia</i>	Basal	6-9	Capsule	-
<i>Diphylleia</i>	Parietal	10-15	Berry	-
<i>Dysosma</i>	Parietal	30-50	Berry	-
<i>Podophyllum</i>	Parietal	30-50	Berry	-

A: Type of placentation. B: Number of ovules. C: Type of fruit.

D: Elaboration on the ovary. +, present; -, absent.

* Pericarp ruptures before maturation of seeds.

From careful and critical observations and comparisons of the vasculature in the pistils in the Berberidaceae s.l. (Terabayashi 1977, 1978, 1979, 1981, 1983a, 1983b, 1983c), it is indicated that the pistils of this family are based on the same morphological plan, rather than that they are heterogenous in structure. Each pistil is traversed by (1-)2-3(-4) ventral bundles*, a dorsal bundle* and some lateral bundles. Although in such genera as *Caulophyllum*, *Leontice*, *Gymnospermium* and *Bongardia*, in some species of *Berberis* and *Mahonia* and some examples of *Ranzania*, a distinct dorsal bundle is not observed; this is due to the secondary lack of the dorsal bundle. In the genera having parietal-type placentas, there are two kinds of vascular bundles in the placental region. The bundles at the loculous side, sometimes having xylem oriented inversely, give off the ovular traces to ovule occupying mainly the lower to middle portion of the locule. The other bundles in the placental region are ventral bundles and they give off the traces to ovules occupying the middle to upper portion of the locule. In the genera having basal-type placentas, two kinds of vascular bundles are also observed in the placental region. But in most cases in the basal-type placentas, the ovular traces arise from bundles other than the ventral bundles. The ventral bundles rarely supply ovules with traces.

As for the derivation of the pistillate structure in the Berberidaceae s.l., this study does not give any conclusion. Abnormal pistils with a single locule and two placentas found widely in this family (Kaute 1963), and intermediate forms between normal pistils and such abnormally dimerous pistils found in *Berberis* and *Diphylleia* (Leinfellner 1956, Kaute 1963), seem to suggest that the pistils of the Berberidaceae s.l. may be derived through reduction from dimerous pistils bearing two placentas. However, at the same time, the interpretation is possible that such

* The terms "ventral bundle" and "dorsal bundle" are used here tentatively.

dimerous pistils are derived through multiplication from normally monomerous pistils. In addition, syncarpous pistils are unnatural in the order Ranunculales where pistils are apocarpous. The ontogenetic studies will be needed in order to make it clear whether abnormally dimerous pistils in the Berberidaceae s.l. are comparable with normally dimerous pistils with one locule and two placentas observed in the families of Papaveraceae and Capparidaceae, or not.

There is some diversification in the pistillate morphology in the Berberidaceae s.l., and the relationships of pistillate morphology within this family will be discussed below.

Placentation

There are two types of placentas in the Berberidaceae s.l.: a parietal-type in *Diphylleia*, *Dysosma*, *Podophyllum*, *Nandina*, *Ranzania*, *Epimedium*, *Vancouveria*, *Plagiorhegma*, *Jeffersonia* and a basal-type in *Berberis*, *Mahonia*, *Achlys*, *Caulophyllum*, *Leontice*, *Gymnospermium*, *Bongardia*. The basal placentation in this family is not truly basal but the placentas are situated towards the ventral side and continuous with the ventral projection on the ovary wall (Terabayashi 1978, 1981, 1983a). As mentioned above, there is no fundamental difference in the vasculature of the placental region between the parietal-type and basal-type placentas. From the vascular anatomy, it is not unnatural to consider that basal placentation is secondarily derived from parietal placentation in this family. According to Kumazawa's observation (Kumazawa 1938), ovular primordia appear on the lateral wall of the pistil at an early stage of development in all genera of the Berberidaceae s.l. The basal placentation is formed by the enormous elongation of the upper part of the pistil, and he interpreted that the parietal placentation is original in this family.

Elaboration of the ovary wall

Elaboration for dehiscence is observed in the ovary in the genera *Epimedium*, *Vancouveria*, *Plagiorhegma* and *Jeffersonia*, whose fruits are capsule-types that dehisce along the line of this elaboration. It is indicated that the deep groove observed on the ovary of *Achlys*, whose fruits are achene-type, is homologous to the elaboration observed in the above four genera (Terabayashi 1979, 1981). The elaboration is not so distinct at anthesis in *Epimedium* and *Vancouveria*, but appears as a groove at anthesis in *Plagiorhegma* and *Jeffersonia*. In *Achlys*, the groove is very deep and differences in maturation are recognized in the parts divided by the groove. The groove appears at an earlier stage of development of the ovary in *Achlys* than in *Plagiorhegma* and *Jeffersonia*, where the grooves are recognized earlier than those in *Epimedium* and *Vancouveria* (Terabayashi 1979, 1981). This evidence suggests that the elaboration of the ovary may originate secondarily on the cylindrical ovary and that the elaboration may become specialized as a more noticeable groove. In the Berberidaceae s.l., the pistils without mechanisms for dehiscence are considered to be original.

Evolutionary trend in the pistil

The pistils of *Podophyllum*, *Dysosma* and *Diphylleia* have parietal-type placentas bearing rather many ovules (Table 3), and have no elaboration for dehiscence on the ovary. The pistils are traversed by a few ventral bundles, some lateral bundles and a dorsal bundle, and these bundles pass through the ovary wall and style and supply the stigma. The venation of the ovary is

Table 4. The vascular anatomy in the pistil

	A	B	C	D
<i>Nandina</i>	1-2	+(++)	-	-
<i>Berberis</i>	1-4(-5)	++, -	-	-
<i>Mahonia</i>	1-4(-5)	++, -	-	-
<i>Ranzania</i>	2-3	++, -	-	-
<i>Epimedium</i>	2-3(-4)	+	-	-
<i>Vancouveria</i>	1-2	+	-	-
<i>Plagiorhegma</i>	3-5	+	-	-
<i>Jeffersonia</i>	3-5	+	-	-
<i>Achlys</i>	2-3	+	-	-
<i>Caulophyllum</i>	2	-	-	-
<i>Leontice</i>	2	-	-	-
<i>Gymnospermium</i>	2	-	-	-
<i>Bongardia</i>	1	-	-	-
<i>Diphylleia</i>	2-3	++	+	-
<i>Dysosma</i>	1-2	++	+	+
<i>Podophyllum</i>	2-4	++	+	+

A: Number of ventral bundles.

B: Dorsal bundle. ++, extending to stigmatic region; +, ending at the ovary level; -, absent.

C: Venation of ovary. +, network present; -, network absent.

D: Placental vascular network system. +, present; - absent.

composed of dichotomously branched veins. The anastomoses are observed in the second-third order venation and large networks are observed. In the genera *Podophyllum* and *Dysosma*, the placenta is swollen and supplied with a well-developed placental vascular network which gives off many ovular traces. The vascular network is considered to be related to the swollen placenta and large number of ovules and this condition may be specialized from the normal condition in which the ovular traces are given off directly from ventral or other bundles in the placental region, as in *Diphylleia* (Terabayashi 1983b).

The pistils of *Ranzania* have parietal-type placentas with many ovules but have no elaboration for dehiscence on the ovary. The pistils are traversed by a few ventral bundles, some lateral bundles and a dorsal bundle. The ventral and dorsal bundles only pass through the ovary wall and style and supply the stigma. In some examples, a dorsal bundle is lacking. The venation of the ovary wall consists of veins once or twice dichotomously branched. Differing from *Podophyllum*, *Dysosma* and *Diphylleia*, no anastomoses are observed in the venation of the ovary wall in this genus (Terabayashi 1977).

The pistils of *Nandina* also have parietal-type placentas bearing 2-3 ovules. The pistils are traversed by 1-2 ventral bundles, a few lateral bundles and a dorsal bundle. In this genus, the dorsal bundle becomes blind at the middle level of the ovary and only the branches from the ventral bundles pass through the style and supply the stigma (Terabayashi 1983c). The examples in which a dorsal bundle extends to the stigmatic region are also reported (Kaute 1963). The branching pattern of the venation of the ovary is openly dichotomous as in the case of *Ranzania*.

The ancestral form of the pistils of these three groups may have had a parietal-type placenta bearing rather many ovules with no elaboration for dehiscence on the ovary. Such ancestral pistils may have been traversed by a few ventral bundles, some lateral bundles and a dorsal bundle. These bundles may all have passed through the ovary and style and supplied the stigma. The branching pattern of the venation of the ovary may have been openly dichotomous. From this type of pistil, the pistil of the above three groups may have been derived through three different trends. In one course of evolutionary trend in the pistil, a decrease in ovule number and a retreat of the dorsal bundle from the stigmatic region to the ovary might have occurred and the *Nandina*-type of pistil may have been formed. In the course of evolution of the pistil in *Ranzania*, a retreat of the lateral bundles from the stigmatic region to the ovary might have occurred sometimes accompanying a loss of dorsal bundles. In the course of evolution of the pistil in *Podophyllum*, *Dysosma* and *Diphylleia*, anastomoses of veins might have occurred in the venation of the ovary wall and networks may have been formed. Moreover, in *Podophyllum* and *Dysosma* a placental vascular network system might have been formed, accompanied by an increase in ovule number (Fig. 4).

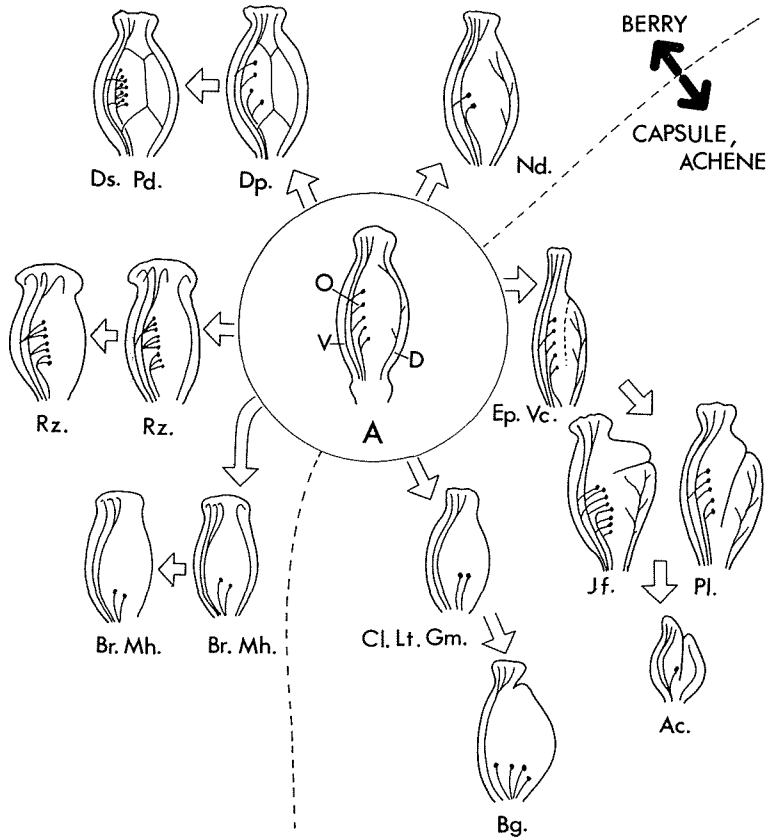


Fig. 4. Probable evolutionary trends in the pistils of the Berberidaceae. A, Ancestral form; Ac, *Achlys*; Bg, *Bongardia*; Br, *Berberis*; Cl, *Caulophyllum*; Dp, *Diphylleia*; Ds, *Dysosma*; Ep, *Epimedium*; Gm, *Cymnospermium*. Jf, *Jeffersonia*; Lt, *Leontice*; Mh, *Mahonia*; Nd, *Nandina*; Pd, *Podophyllum*; Pl, *Plagiorhegma*; Rz, *Ranzania*; Vc, *Vancouveria*. V=ventral bundle, D=dorsal bundle, O=ovular trace. \Rightarrow , possible line; \Rightarrow , highly possible line.

The pistils of *Berberis* and *Mahonia* ripen into berry-type fruits, as those of the above mentioned genera do. In these two genera the placentas are basal-type and the number of ovules is much smaller: less than 5 in most species (Ahrendt 1961). The pistils of these two genera are traversed by a few ventral bundles and a dorsal bundles in some species but no dorsal bundle in other species. In these two genera, the presence of lateral bundles is rare. Ovular traces usually arise from bundles other than the ventral bundles in the placental region, but the ventral bundles rarely give off ovular traces. It is noteworthy that in these two genera there are placental bundles, which arise in a manner similar to ovular traces and are situated in the placental region and in the ventral projection of the ovary wall, giving off no ovular traces. The placental bundle originally might have been the bundles giving off ovular traces in the parietal-type placenta (Terabayashi 1978). The branching pattern of the venation of ovary wall is openly dichotomous. The pistils of *Berberis* and *Mahonia* may be derived from those with a parietal-type placenta, and ventral, dorsal and lateral bundles extending to the stigmatic region, and with openly dichotomous venation. The pistils of these two genera are more comparable to those of *Ranzania* than to those of *Podophyllum*, *Dysosma*, *Diphylleia* and *Nandina* (Fig. 4).

The pistils of *Epimedium*, *Vancouveria*, *Plagiorhegma*, *Jeffersonia* and *Achlys* constitute a single group (Terabayashi 1981). The pistils of these five genera are traversed by two groups of vasculature. One is composed of the ventral bundles and their branches, and the other of the dorsal bundles and some other bundles. The two groups of vasculature are separated by the elaboration for dehiscence in *Epimedium*, *Vancouveria*, *Plagiorhegma* and *Jeffersonia*, and are divided by the deep groove in *Achlys*, whose fruits do not dehisce. The two groups of vasculature are not interlocked with each other. Only the ventral bundles pass through the style and supply the stigma. The distinct dorsal bundle ends at a level below the line of dehiscence or below the groove and does not reach the stigmatic region. In the evolutionary trend in the pistils of these five genera, the elaboration for dehiscence may be specialized into a deeper groove. The pistils of *Epimedium* and *Vancouveria* are the most unspecialized among these five genera and may be derived from pistils with parietal-type placentas, but without elaboration for dehiscence.

The pistils of *Caulophyllum*, *Leontice*, *Gymnospermium* and *Bongardia* constitute another group (Terabayashi 1983a). The pistils ripen into capsule-type fruits, as in the above genera, except in *Caulophyllum* where the pericarp ruptures before maturation of the seeds. The placentas of this group are basal-type, but they are situated towards the ventral side and continuous with the ventral projection of the ovary wall. In regard to the restriction of the placentas to the basal portion of the ovary, the placentas of these four genera show the most advanced condition among the genera having basal-type placentas. In *Bongardia* especially, the basal-type placenta is swollen and indicates an inclination towards free central placentation (Terabayashi 1983a). The number of ovules is small in these genera (Table 3). The pistils are traversed by two ventral bundles, but only one in *Bongardia*, and some weak bundles. No distinct dorsal bundle is observed. Only the ventral bundles pass through the style and supply the stigma. The branching pattern of the venation of the ovary wall is openly dichotomous. There is no elaboration for dehiscence on the ovary wall. When the pistils of these four genera are compared with those of *Berberis* and *Mahonia*, the placentas of which are also basal-type, important differences are recognized. The pistils of these four genera have no placental bundle in the placental region and no distinct dorsal bundle extending to the stigmatic region. In addition, the pistils of *Berberis*

and *Mahonia* ripen into berry-type fruits.

It may be possible to speculate that the pistils of this group are derived from forms of the pistil with parietal-type placentas bearing many ovules and no elaboration for dehiscence on the ovary wall. The fruits of this group show evolutionary trends similar to those in *Epimedium*, *Vancouveria*, *Plagiorhegma Jeffersonia* and *Achlys*: that is, dried fruits, capsules or achenes. However, the pistils of *Caulophyllum-Leontice-Gymnospermium-Bongardia* and those of *Epimedium-Vancouveria-Plagiorhegma-Jeffersonia-Achlys* are the result of two different lines of evolution from a common ancestral form (Fig. 4).

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