Studies in the Morphology and Systematics of Berberidaceae (V) : Floral Anatomy of Caulophyllum MICHX., Leontice L., Gymnospermium SPACH and Bongardia MEY

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V. Floral Anatomy of *Caulophyllum* MICHX., *Leontice* L., *Gymnospermium* SPACH and *Bongardia* MEY.

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Abstract

The floral anatomy of *Caulophyllum*, *Leontice*, *Gymnospermium* and *Bongardia* are discussed with special reference given to vasculature. Comparisons of floral anatomy are made with the other genera of the tribe Epimedieae.

The vasculature in the receptacle of *Caulophyllum*, *Leontice* and *Gymnospermium* is similar, but that of *Bongardia* differs in the very thick xylem of the receptacular stele and in the independent origin of the traces to the sepals, petals and stamens from the stele. A tendency is recognized in that the outer floral elements receive traces of a single nature in origin from the stele while the inner elements receive traces of a double nature. The traces to the inner elements are often derived from common bundles in *Caulophyllum*, *Leontice* and *Gymnospermium*. A similar tendency is observed in the trace pattern in the other genera of Epimedieae, but the adnation of the traces is not as distinct as in the genera treated in this study.

The vasculature in the pistil, which is traversed by two ventral bundles (one in *Bongardia*) and several lateral veins, is similar in these four genera. No distinct dorsal bundle is observed. Only ventral bundles supply the stigma. The pistil anatomy of these four genera is different from that of other genera of Epimedieae where the pistillate vasculature consists of two independent systems, the presence of distinct dorsal bundles and ovular supplies from ventral bundles.

From anatomical evidence the tribe Epimedieae may be classified into two groups.

Introduction

In the course of comparative studies of the morphology of the flowers of Berberidaceae, *Caulophyllum*, *Leontice*, *Gymnospermium* and *Bongardia* are discussed in this article. These four genera along with *Epimedium*, *Vancouveria*, *Plagiorhegma*, *Jeffersonia* and *Achlys* constitute the tribe Epimedieae. Relationships between *Leontice*, *Gymnospermium* and *Bongardia* are suggested by the strong resemblance in the morphology and anatomy of the tuber-type rhizomes and in the seedlings with fused cotyledons (Tören, 1960; Terabayashi, in prep.). *Caulophyllum*, *Leontice* and *Gymno-*

spermium are closely related in seed coat anatomy (Takhtajan and Melikian, 1972), and basic number of chromosomes: $x=8$ in *Caulophyllum, Leontice* and *Gymnospermium*: $x=6$ or 7 in *Bongardia* (Langlet, 1928; Tören, 1950, 1954; Moore, 1963; Kawano and Ihara, 1967; Kosenko, 1977a, 1977b, 1978, 1979).

In order to discuss the relationships between these genera, it is necessary to examine their floral morphology. However, information available of the floral anatomy is insufficient at present. Vasculature in the receptacle has not been studied at all for these four genera. Although the vasculature in the pistil was described for *Caulophyllum, Leontice* and *Bongardia* by Saunders (1928), Chapman (1936) and Kaute (1963), they gave no critical comparisons of pistils between the related genera. The purpose of this study is to describe in detail the floral anatomy of *Caulophyllum, Leontice, Gymnospermium* and *Bongardia*, and to compare the results in order to elucidate the relationships between these four genera.

Materials and Methods

Most of the materials were fixed in formaldehyde-acetic acid-ethanol, dehydrated in an n-butyl-alcohol series and embedded in paraffin. Sections were cut at about 15 μm, and stained with safranin-fast green or hematoxylin-fast green. At the same time, some materials were cleared in NaOH, and stained with fuchsin to observe their vasculature directly. Several dried specimens were boiled and treated in the same way as described above.

Table 1. Sources of materials examined and voucher specimens.

Caulophyllum thalictroides (L.) Michx. ssp. *thalictroides*	Pennsylvania, Washington county, U.S.A.; *Boufford and Wood 21089* (CM, KYO)
ssp. *robustum* (Maxim.) Kitam.	Pref. Nagano, Miyanokoshi, Japan.; *Terabayashi and Yahara 41* (KYO)
	Pref. Yamagata, Mt. Kurobushi, Japan.; *Terabayashi 156* (KYO)
	Pref. Fukushima, Oze, Japan.; *Ueda and Ito 56* (KYO)
	Cultivated at Kyoto Univ. originated from Kifune, Pref. Kyoto and from Fukusada, Pref. Hyogo, Japan.
Leontice leontopetalum L. ssp. *leontopetalum*	Cultivated at Bot. Gard. of Leiden, Netherlands.
	Cultivated at Thebes, Greece.; *Pinatzi s. n.* (KYO)
ssp. *Ewersmannii* (Bunge) Coode*	Tyrkmen, Ashkhabadskij, USSR.; *Chapanov s. n.* (WIR, KYO)
Gymnospermium albertii (Regel) Takht.	Uzbekskaja, Taskentskaja, USSR.; *Kosenko s. n.* (KYO)
G. altaicum (Pall.) Spach*	Ukraineskaja, Odessa, USSR.; *Browikow s. n.* (KRA, KYO)
G. microrrhynchum (S. Moore) Takht.*	Kogen, Igawa-gun. Korea.; *Kin s. n.* (TI)
Bongardia chrysogonum (L.) Spach*	Tadzhikstan, Pushanbe, USSR.; *Lisheeva s. n.* (MHA, MAK)
	Azerbajdzhania, Baku, USSR.; *Karjagin s. n.* (LE, MAK)

* Dried herbarium specimens used in this study.

Observations

Caulophyllum thalictroides (L.) Michx. ssp. *robustum* (Maxim.) Kitam.

Observations were made for two subspecies of *Caulophyllum thalictroides*: *C. thalictroides* ssp. *thalictroides* and *C. thalictroides* ssp. *robustum*. There are no differences in floral morphology in the two subspecies, and the description will be given for *C. thalictroides* ssp. *robustum*.

The flowers are borne on a racemose cyme having a terminal flower. The floral elements are trimerous and arranged in whorls (Fig. 1-J). Floral elements of the

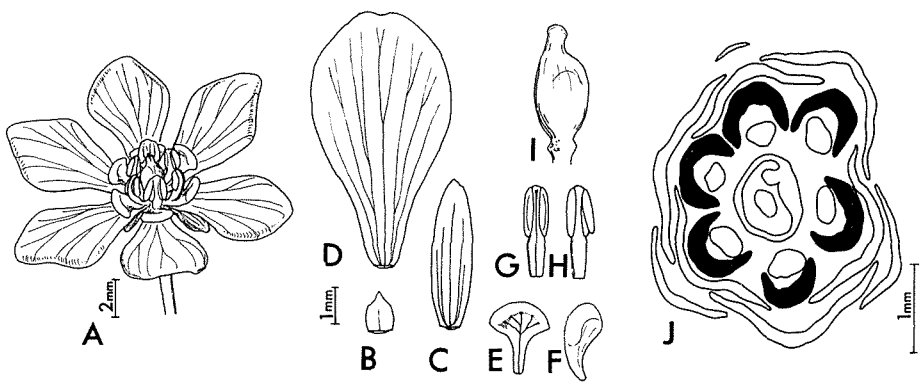

Fig. 1. *Caulophyllum thalictroides* ssp. *robustum*. A: Flower. B, C: Outer sepals. D: Inner petaloid sepal. E: Glandular petal, adaxial view. F: Petal, lateral view. G: Stamen, cleared, adaxial view. H: Stamen, abaxial view. I: Pistil. J: Transverse section of a floral bud. Petals are blacked out.

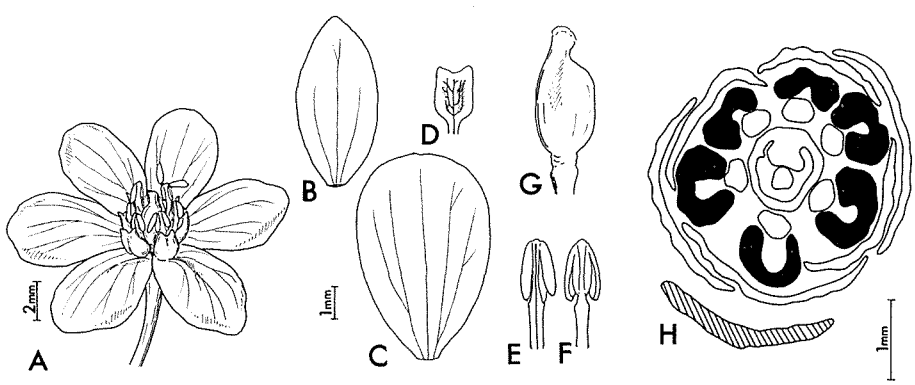

Fig. 2. *Leontice leontopetalum* ssp. *leontopetalum*. A: Flower. B, C: Sepals. D: Glandular petal. E: Stamen, cleared, abaxial view. F: Stamen, adaxial view. G: Pistil. H: Transverse section of a floral bud. A bract is shaded with oblique lines and petals are blacked out.

terminal flower are sometimes arranged in a spiral with a 2/5 phyllotaxy. Perianth lobes are classified into three groups, based on morphological features. The first group is composed of outer small sepals in one or two whorls. The outermost are very small and triangular in shape while the inner ones are narrowly elliptic in outline (Fig. 1-B, C). The second group consists of 6 petaloid sepals in two whorls. The venation of the petaloid sepals is well-developed (Fig. 1-D). The third group consists of 6 petals. The petals are rather small, glandular and fan-shaped (Fig. 1-E, F). The six stamens opposite the petals have anthers which open by valves (Fig. 1-G, H). The single terminal pistil is cylindrical and without a ventral suture. The ovoid ovary, short style and cristate stigma are distinct (Fig. 1-I). The stigma is parallel to a line combining the ventral and dorsal sides of the pistil. The ovary contains two bitegmic, anatropous ovules on the basal placenta.

In the pedicel 4–6 main, stout bundles and 1–4 weak bundles are observed (Pl. I-1). As they rise in the receptacle, each bundle expands laterally and some bundles fuse with each other. At the lowermost level of the receptacle, traces to the outer sepals are given off from the stele (Pl. I–2, 3, 4). Those to the 3 outer sepals originate from different levels of the stele. The trace is usually singular in the cortex. It is difficult to recognize the manner of origin of the trace from the stele from observations of transverse serial sections as the stelar bundles are arranged rather compactly. The behaviour of xylem strands of the stelar bundles helps to show the manner of origin from the stele. The following observations were made from cleared materials with only the xylem stained with fuchsin. The xylem strands leading to a sepal trace originate from a trifurcation or bifurcation of the xylem strand of the stelar bundle. In some cases, a xylem strand to a sepal trace originates at a lower level than the receptacle and passes through the pedicel and departs from the stele at the sepal level. Cases are also observed in which two xylem strands derived from two adjacent stelar bundles unite and lead to a strand of the sepal trace. Traces to the outer sepals are of either a single or double nature in their origin from the stele. The trace divides into three, one midvein and two laterals at the base of the sepal. Lateral veins give off a few branches. Several veins run in parallel and the vein endings are open (Fig. 1-B, C).

At the next level, traces to the 3 petaloid sepals of the outer whorl are given off (Pl. I-5). The traces are usually of a double nature in their origin from the stele. This is obvious in cleared materials: two xylem strands arising from two adjacent stelar bundles lead to the strand of the trace. Sometimes one of the two strands is lacking (Fig. 5-A, E).

The traces to the inner petaloid sepals, petals and sometimes stamens on the same radii usually originate as a common bundle from the stele (Pl. I–6, 7, 8). The common bundles divide into two or three in the cortex and the bundles give

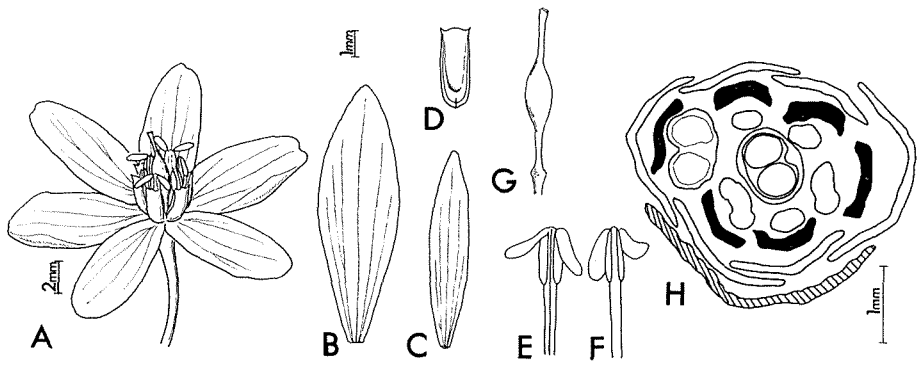

Fig. 3. *Gymnospermium albertii.* A: Flower. B, C: Sepals. D: Glandular petal. E: Stamen, cleared abaxial view. F: Stamen, adaxial view. G: Pistil. H: Transverse section of a floral bud. A bract is shaded with oblique lines and petals are blacked out.

rise to traces supplying the inner petaloid sepals, petals and sometimes also to the stamens. The behaviour of the xylem strands is as follows. Each of the two strands derived from two adjacent stelar bundles divides into two or three. The outer pair leads to the strand supplying the inner petaloid sepal trace, and the median pair to that suppying the petal trace and the inner pair of stamen traces. Cases are often observed in which one of the two strands of each pair is lacking (Figs. 5-A, E; 6).

The petals and stamens alternate with the inner petaloid sepals are traversed by a trace which departs from the stele as a common bundle (Fig. 6; Pl. I–7, 8). The common bundles divide into petal traces and stamen traces in the cortex. From observations on the xylem strands, the common bundles are regarded as being of a

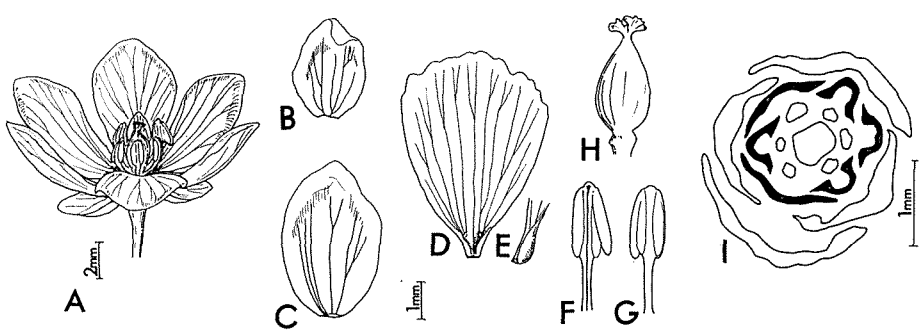

Fig. 4. *Bongardia chrysogonum.* A: Flower. B, C: Sepals. D: Petal. E: Petal, basal necteriferous pocket. F: Stamen, cleared, abaxial view. G: Stamen, adaxial view. H: Pistil. I: Transverse section of a floral bud. Petals are blacked out.

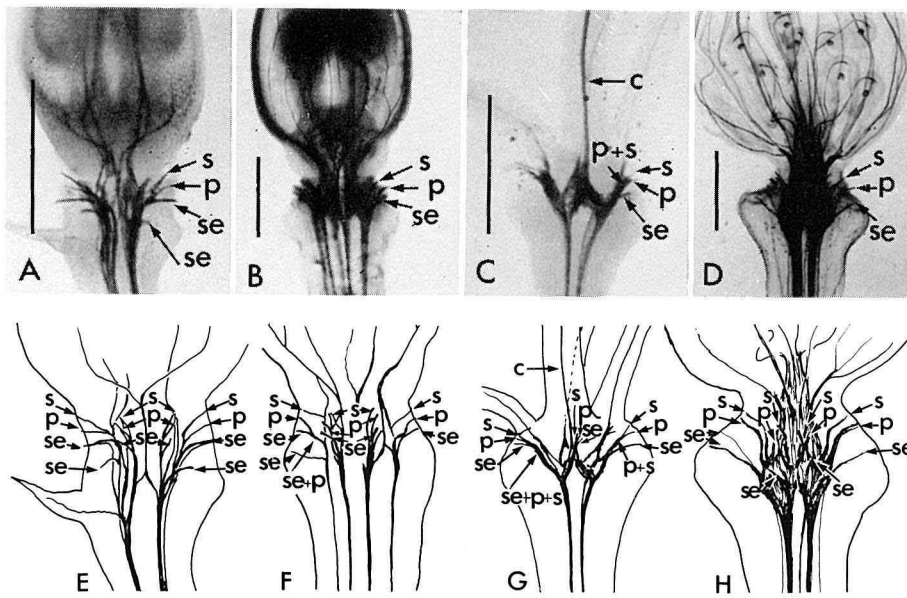

Fig. 5. Receptacular region. A, B, C, D: Cleared materials. E, F, G, H: Explanatory illustrations of A, B, C and D. A, E: *Caulophyllum thalictroides* ssp. *robustum*. B, F: *Leontice leontopetalum* ssp. *leontopetalum*. C, G: *Gymnospermium albertii*. D, H: *Bongardia chrysogonum*. Se, sepal trace; P, petal trace; S, stamen trace; Se+P, S+P, Se+P+S, common bundle; C, Concentric stipe bundle. The scales are all for the length of 1 mm.

either a double nature or a single nature in their origin from the stele. The frequency of fusion of the traces of the petaloid sepals, petals and stamens are shown in Fig. 7.

The traces to the petaloid sepals divide into three and lead to a midvein and two laterals at the transitional region between the receptacle and the sepal. The lateral veins usually divide into two at the base of the sepal. The veins each branch dichotomously a few times. The vein endings are open (Fig. 1-D). The traces to the petals are singular at a level lower than the fan-shaped lamina, where the trace branches dichotomously (Fig. 1-E). The traces to the stamens are signular throughout their course and dilate at the distal end of the connective (Fig. 1-G).

After the separation of the traces there are observed 6–9 stelar bundles which are intercalated by 6 gaps formed by the departure of the traces. The stelar bundles fuse with each other, resulting in an imperfect vascular ring entering the terminal pistil.

In the base of the pistil, several bundles are separated from the dorsal and lateral sides of the vascular ring (Pl. I–11, 12). The bundles given off become the

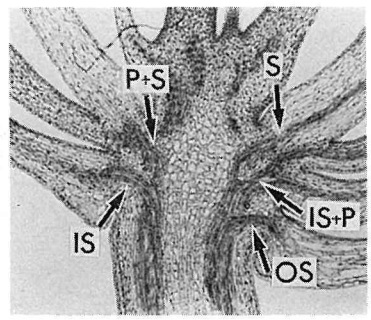

Fig. 6. A longitudinal section of a flower of *Caulophyllum thalictroides* ssp. *robustum* (×23). A common bundle to inner sepal trace and petal trace (IS+P), and that to petal trace and stamen trace (P+S) are observed. OS, outer sepal trace; IS, inner sepal trace; P, petal trace; S, stamen trace.

veins of the ovary wall and each extends to the top of the ovary, branching dichotomously. No distinct dorsal bundle* is observed. The remaining part of the vascular ring moves to the placental region. Two or rarely three ventral bundles* are separated from the ventral part of the vascular ring (Pl. I–13, 14). The ventral bundles pass through the ovary wall and style without giving off veins to the ovary wall, and dilate as they reach the stigmatic region (Fig. 8-A). In the base of the placenta two ovular bundles originate from the loculous side of the vascular ring at nearly the same level where the ventral bundles are given off (Pl. I–13). The ventral and ovular bundles are usually independent of each other. The ventral projection of the ovary wall containing ventral bundles is continuous with the basal placenta (Pl. I–13~16).

Leontice leontopetalum L. ssp. *leontopetalum*

The genus *Leontice* comprises three species. In this study two subspecies of one species *L. leontopetalum* L. ssp. *leontopetalum* and *L. leontopetalum* ssp. *Ewersmannii* (Bunge) Coode, were examined. The description of the floral anatomy will be given for *L. leontopetalum* ssp. *leontopetalum*, because no major differences between the two subspecies were found.

The flowers are borne on an indeterminate compound raceme and are subtended by large bracts. The sepals are 6(–7) in number, narrowly obovate to obovate in outline. Sepals equivalent to the outer sepals of *Caulophyllum* are not observed. The trimerous condition is not clear in the arrangement of the sepals. The case is most frequently observed in which two outer sepals are perpendicular to a bract and

* The terms "dorsal bundle" and "ventral bundle" are used tentatively in this series of the studies.

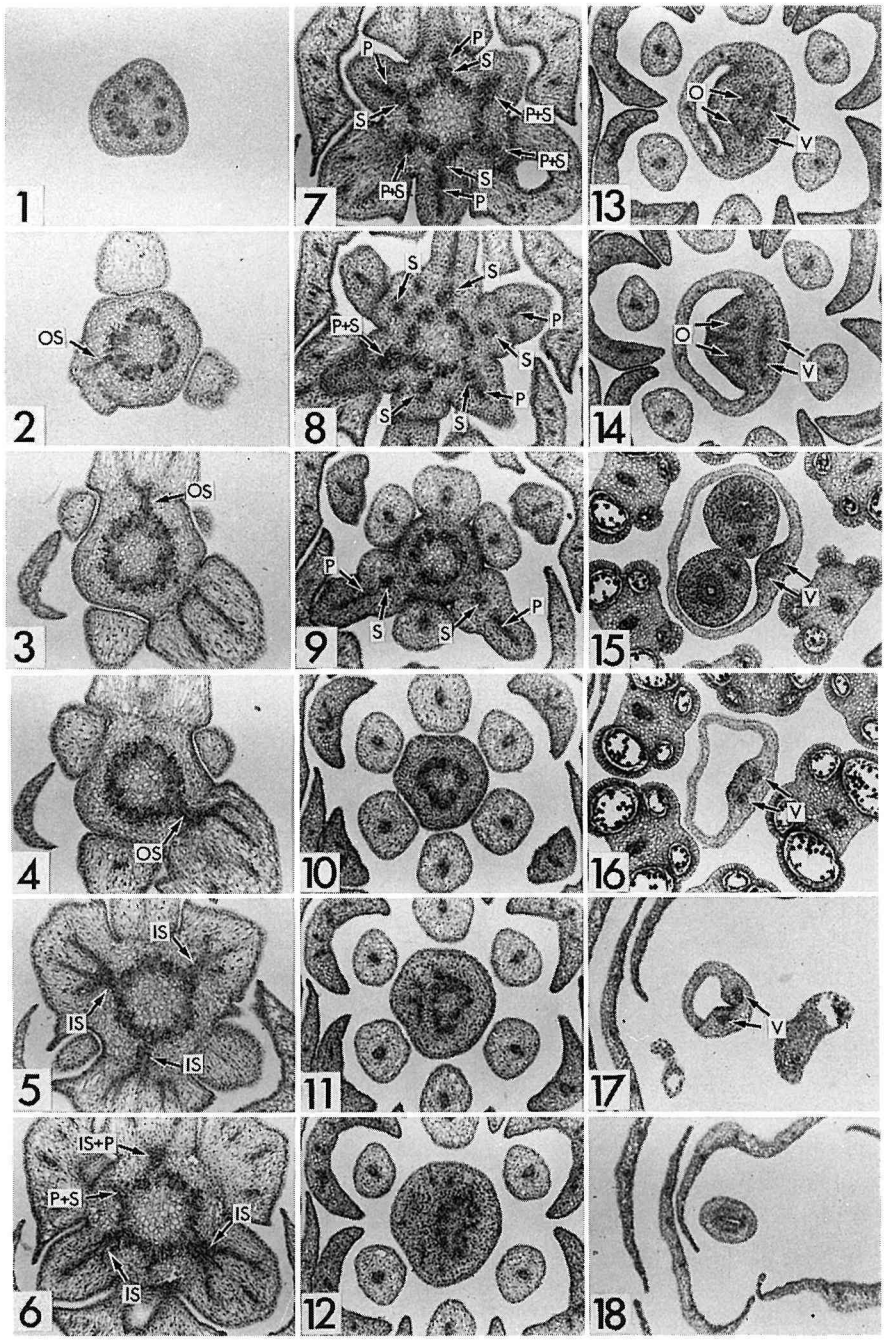
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Plate I.

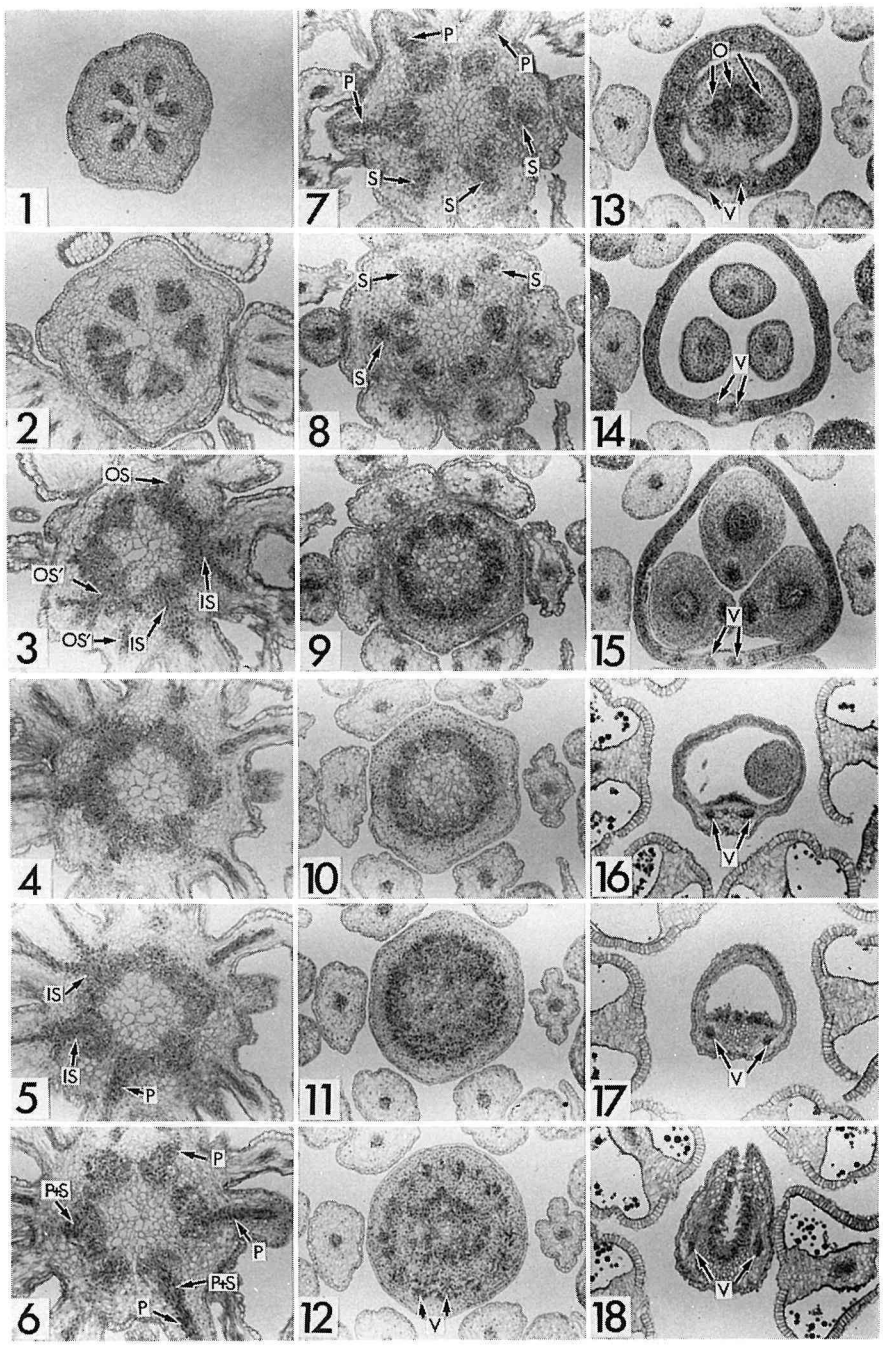
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Plate II.

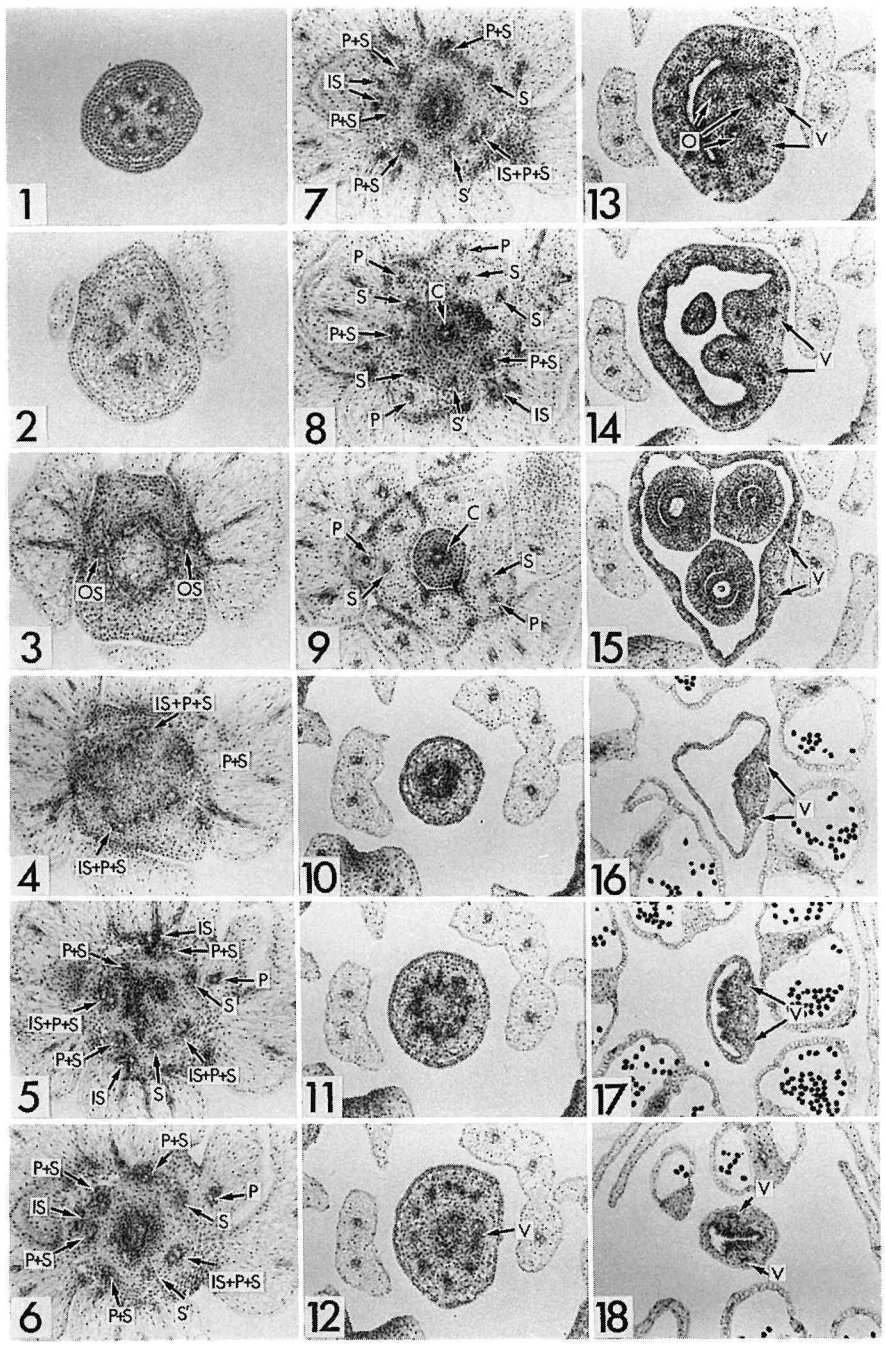
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Plate III.

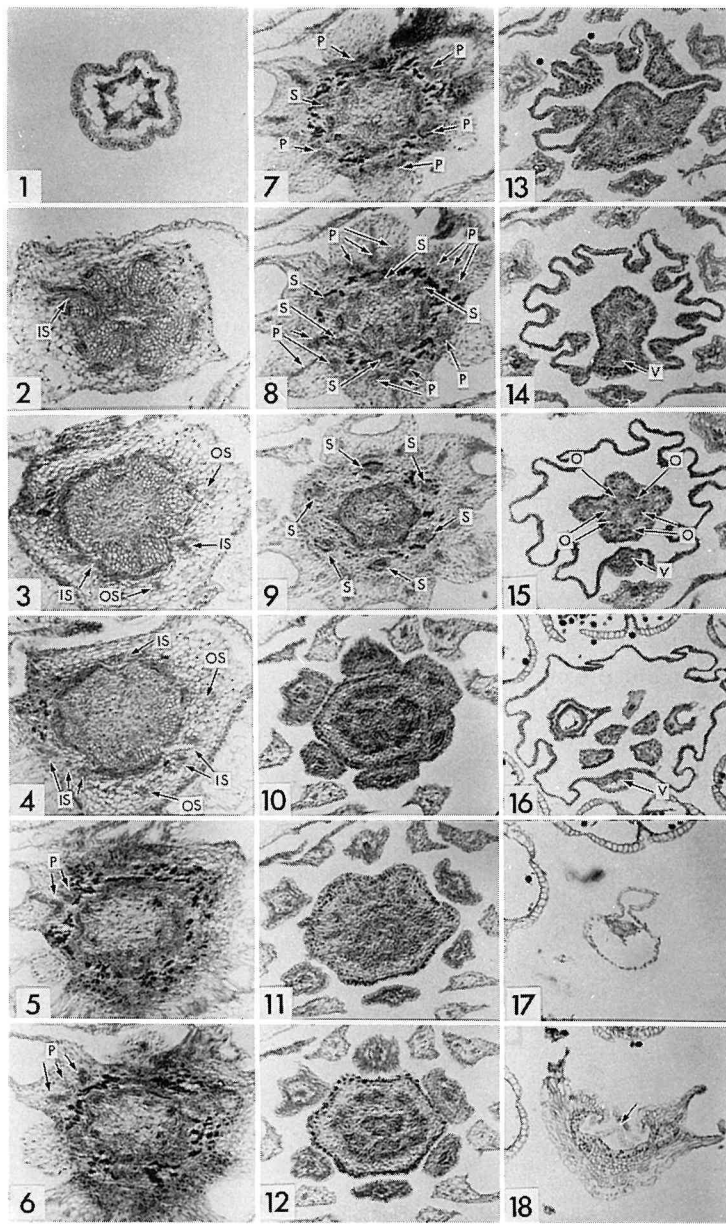
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Plate IV.

the four inner sepals are in two pairs which tend to be alternate with the outer sepals (Fig. 2-H). The two adjacent inner sepals are sometimes fused with each other partially at their bases or entirely. The six petals are small and glandular as in *Caulophyllum* and truncate and biaristate at the apex (Fig. 2-D). The six stamens are opposite the petals and have anthers which open by valves (Fig. 2-E, F). The single terminal pistil consists of an ovoid ovary, short style and cristate stigma (Fig. 2-I). The ovary contains 3–4 bitegmic, anatropous and basal ovules.

In the pedicel 4–6 main, stout bundles and 0–2 weak bundles are observed (Pl. II–1). Each bundle expands laterally as it rises in the receptacle. At the lowermost level of the receptacle, the traces to two outer sepals, which are each perpendicular to a bract, are given off from the stele (Pl. II–3). The traces are usually of a single nature. One of the stelar bundles divides into three, the median of which leads to the trace, or one stelar bundle directly gives off the trace. Cases in which one of the stelar bundles divides into four, the median two of which become the traces to single element, are rarely observed.

At the next level the traces to the four inner sepals are given off (Pl. II–3, 4, 5). The traces to the inner sepals and petals, and rarely the stamens, on the same radii are sometimes separated from the stele as a common bundle as in *Caulophyllum*. In cases with common bundles, two xylem strands arising from two adjacent stelar bundles divide and the outer pair leads to the sepal trace and the inner pair to the petal trace. Sometimes one strand of each pair is lacking. The petals and stamens on the same radii as that of the outer sepals sometimes receive traces from common bundles in the same manner as described above (Fig. 5-B, F; Pl. II-6, 7). In the cases in which traces to the sepals, petals and stamens are given off independently, the traces are either of a single or a double nature in their origin from the stele.

The traces to the sepals are divided into three and lead to a midvein and the two lateral veins of the sepal. The lateral veins divide at the lower level of the sepal (Fig. 2-B, C). The traces to the petals give rise to a single midvein which branches pinnately in the first order. Several anastomoses are observed in the second or third order of venation (Fig. 2-D). The traces to the stamens are singular through their course. The vein is dilated at the distal end of the connective (Fig. 2-E).

Regular division and fusion are not observed in the receptacular stele. After the separation of stamen traces, there are observed 6–9 vascular bundles which soon fuse with each other into a vascular ring entering the terminal pistil (Pl. II–9, 10).

In the base of the pistil, the veins of the ovary wall are given off from the lateral and dorsal sides of the vascular ring (Pl. II–11, 12). No distinct dorsal bundle was observed, with the exception of one example where a distinct dorsal bundle extending to the stigmatic region was seen. The veins of the ovary wall end at a level lower

than the style. The branching pattern is one of open dichotomies, but the networks of procambial strands are observed between lignified veins. The remaining part of the vascular ring moves to the placental region. From the ventral part of the vascular ring ventral bundles are given off (Pl. II–12). The number of ventral bundles is usually two. After the separation of the veins of the ovary wall and ventral bundles, the vascular ring divides into 3–4 parts, each leading to 3–4 ovular bundles (Pl. II –12, 13). The ventral bundles and ovular bundles tend to originate independently. The ventral bundles give off a few branches laterally during their course and extend to the stigmatic region (Fig. 8-B). Fan shaped mechanical tissue, which stains well with fuchsin, is observed between the two ventral bundles at the uppermost level of the ovary, style and stigmatic regions. The basal placenta is continuous with the ventral projection of the ovary wall containing two ventral bundles.

Gymnospermium albertii (Regel) Takht.

The genus *Gymnospermium* comprises eight species. In this study three species; *G. albertii*, *G. altaicum* and *G. microrrhynchum*, were examined. A description of the floral anatomy will be given for *G. albertii*. Morphological differences between the three species examined will be noted in the latter part of this chapter.

The flowers are borne on an indeterminate simple raceme and are subtended by large bracts. The flowers are composed of 6(-7) sepals, 6 petals, 6 stamens and a single terminal pistil. As in *Leontice*, the trimerous condition is not clear in the arrangement of sepals. The outer two sepals perpendicular to a bract are elliptic in outline and larger than the inner four sepals which are narrowly elliptic (Fig. 3-B, C). Sepals equivalent to the outer small sepals of *Caulophyllum* were not observed. The six petals are glandular and truncate apically (Fig. 3-D). The six stamens, opposite the petals, have anthers which open by valves (Fig. 3-E, F). The single terminal pistil is cylindrical and without a ventral suture. The long stipe, ovoid ovary, long, slender style and cylindrical stigma are distinct (Fig. 3-G). The ovary contains three bitegmic, anatropous and basal ovules.

In the pedicel 4–6 main, stout bundles and 0–2 weak bundles are observed (Pl. III–1). At the lowermost level of the receptacle, the traces to the two outer sepals are given off from the stele (Pl. III–3). The trace is derived from the medium bundle formed by the trifurcation of the stelar bundle. The trace is of a single nature in its origin from the stele. The trace divides into three at the transitional region or at the base of the sepal. The two laterals branch dichotomously once or twice (Fig. 3-B).

At the next higher level, two adjacent stelar bundles fuse and depart from the stele, or one stelar bundle is directly separated from the stele (Fig. 5-C, G). These

bundles are usually 6 in number, and are equivalent to the common bundles observed in *Caulophyllum* and *Leontice*. These bundles divide into three in the cortex. The outer bundle gives rise to the inner sepal trace, the median to the petal trace and the inner to the stamen trace. Or, the bundles divide into two traces to the petals and stamens on the same radii as the outer sepals, whose traces have already been given off (Fig. 5-C, G; Pl. III–5, 6, 7, 8). The stele rarely gives off a single trace directly to an additional stamen.

The traces to the inner sepals divide into three leading to a midvein and two laterals. The two laterals branch dichotomously at the base of the sepal (Fig. 3-C). The traces to the petals divide into three at the base of the petal. The midvein abruptly ends blindly, but the two laterals pass through the marginal region and reach the distal end of the petal (Fig. 3-D). The traces to the stamens are singular throughout their course (Fig. 3-E).

After the separation of the common bundles, the remaining stelar bundles move inwardly and fuse into a concentric vascular bundle which enters the terminal pistil (Pl. III–8), and passes through the long stipe of the pistil (Pl. III–9; Fig. 8–C). In the base of the ovary parenchyma begins to appear in the center of the concentric vascular bundle and the bundles change to a vascular ring which soon divides into several bundles (Pl. III–10, 11). From this circle of vascular bundles several bundles are separated and these bundles become the veins of ovary wall (Pl. III–11, 12). No distinct dorsal bundle is observed. Two ventral bundles are given off from the ventral side of the circle of vascular bundles (Pl. III–12). The veins of the ovary wall are unbranched or branch once and end at a level lower than the style. Only the two ventral bundles pass through the ventral side of the ovary wall and style and supply the stigma (Fig. 8-C).

The remaining vascular tissue in the base of the placenta is divided into three parts, one at the dorsal side and two at the ventral side, leading to three ovular bundles (Pl. III–12, 13). Sometimes vascular connection between the two ventral bundles and two ovular bundles at the ventral side is observed. The basal placenta is continuous with the ventral projection of the ovary wall which contains two ventral bundles (Pl. III–14, 15).

Gymnospermium altaicum and *G. microrrhynchum* are only slightly different from *G. albertii* in floral anatomy. The tendency of adnation of the traces to the sepals, petals and stamens is seen also in *G. altaicum* and *G. microrrhynchum*, but not so distinctly as in *G. albertii*. In *G. altaicum* and *G. microrrhynchum*, the pistils do not have a long stipe at their base. In connection with this, the pistils of *G. altaicum* and *G. microrrhynchum* receive vascular rings from the floral receptacle in a manner similar to *Leontice* and *Caulophyllum*. In these two species of *Gymnospermium*, concentric vascular bundles are not observed at the base of the pistil (Fig. 8-D).

Bongardia chrysogonum (L.) Spach

The flowers are borne on a panicle having a terminal flower. The flower is composed of 4–6 sepals, 6 petals, 6 stamens and a single terminal pistil (Fig. 4-I). The sepals are usually arranged in a decussate phyllotaxis. Morphological differences are not observed in the sepals. The sepals are suborbicular and the outer are smaller than the inner (Fig. 4-B, C). The petals and stamens are trimerous and are arranged in whorls. The petals are obovate, cuneate at the base, crenate at apex and membranous in texture (Fig. 4-D). A nectariferous pocket is observed at the base (Fig. 4-E). The six stamens, opposite the petals, have anthers which open by valves (Fig. 4-F, G). The single pistil consists of the ovoid ovary, short style and undulate, fan-shaped stigma (Fig. 4-H). The ovary contains 6–9 bitegmic, anatropous and basal ovules.

In the upper part of the pedicel, 4 main stout bundles and 4 weak bundles are observed (Pl. IV–1). These two types of vascular bundles are arranged alternately. Weak bundles end blindly or fuse with neighbourring main bundles as they rise in the receptacle. The main bundles increase in size, especially xylem, and fuse with adjacent bundles (Pl. IV–2). In the lowermost level of the receptacle, the receptacular stele consists of very thick xylem surrounded by the thin phloem and with a small amount of pith in the center (Pl. IV–2, 3). From this stele are separated traces to the sepals. Usually the traces to the sepals are of a single nature in their origin from the stele. The trace gap is rarely observed as the remaining vascular tissue fuses just after the separation of the traces (Fig. 5-D, H; Pl. IV–2, 3, 4). In the outermost small sepals the trace is unbranched throughout its course, while in the inner larger sepals the trace is divided into two or three on entering the sepal (Pl. IV–2, 3, 4). The branching pattern of the venation of the sepal is dichotomous (Fig. 4-B, C).

The xylem of the receptacular stele decreases in thickness as it rises in the receptacle. At the next level the traces to the 6 petals are given off from the stele (Pl. IV–6, 7, 8). The traces are often of a double nature in their origin from the stele (Fig. 5-D, H). The trace divides into three, one midvein and two laterals. The lateral veins repeatedly branch dichotomously. The veins cover the entire surface of the petal (Fig. 4-D). Successively, the traces to the stamens are given off (Pl. IV–8, 9). In this genus traces to the petals and stamens are given off from the stele at different levels, and no common bundle is observed (Fig. 5-D, H). The stamen traces are usually singular in their origin and through their course. Six gaps are formed by the separation of the stamen traces. The remaining stelar bundles fuse with each other resulting in a vascular ring entering the terminal pistil (Pl. VI–9, 10).

In the base of the pistil, several bundles are given off from the dorsal and lateral

sides of the vascular ring (Pl. IV–10, 11). These bundles become the veins of the ovary wall and dichotomously branch a few times. The veins end at a level lower than the style. No distinct dorsal bundle is observed. The remainder of the vascular ring moves toward the ventral side and enters the base of the placenta (Pl. IV–11, 12, 13). At the next level, the locule begins to appear and a single ventral bundle is given off from the ventral side of the vasculra ring (Pl. IV–13, 14). Within the protuberence of the basal placenta, vascular bundles are arranged in a single circle. These bundles are all exhausted as 6–9 ovular bundles (Pl. IV–15). The ventral bundle passes through the ventral projection of the ovary wall and short style, and supplys the fan-shaped stigma which is continuous with the ventral part of the ovary wall (Pl. IV–17; Fig. 8–E).

Discussion

Perianth

In *Caulophyllum*, the perianth is classified into three groups; small outer sepals, petaloid sepals and glandular petals. Based on outline, texture and venation they are as in *Epimedium* and *Vancouveria* (Terabayashi, 1979). The petaloid sepals of *Caulophyllum* do not show the retardation in development which is observed in *Epimedium* and *Vancouveria*. In *Leontice, Gymnospermium* and *Bongardia*, the sepals are more or less variable in size, and no distinct morphological gap is recognized. The sepals are trimerously arranged in *Caulophyllum*, while in *Leontice* and *Gymnospermium* the inner sepals, in two pairs, tend to be alternate with the outer two sepals. In *Bongardia* a decussate arrangement is observed.

In petal morphology *Caulophyllum* resemble *Leontice* and *Gymnospermium*. The petals are small and glandular in all three. The venation of the petals of *Caulophyllum* is more similar to that of *Leontice* than to that of *Gymnospermium*, where only three veins, one midvein, which soon becomes blind, and two lateral veins are observed. In contrast, the venation of *Caulophyllum* and *Leontice* is more developed and is dichotomous. Some anastomoses are observed. The petals of *Bongardia* are much larger than those of the above genera and differ in being membranous in texture and with well-developed venation. The venation is dichotomous and without anastomoses.

Vasculature in the receptacle

The vasculature in the receptacle of *Caulophyllum, Leontice* and *Gymnospermium* is similar. Traces to the sepals, petals and stamens usually leave a single gap, but the gap is not as distinct in the outer sepals because of the closure of the vascular tissue of the stele just after the separation of the traces. A tendency for the outer

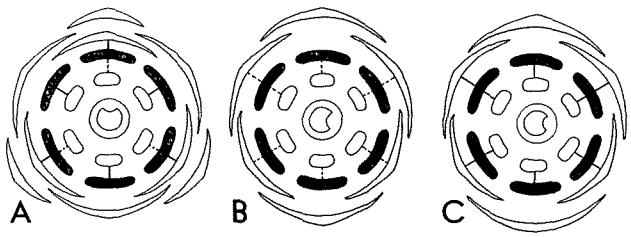

Fig. 7. Floral diagrams, showing the frequency of common bundles. A: *Caulophyllum thalictroides* ssp. *robustum*. B: *Leontice leontopetalum* ssp. *leontopetalum*. C: *Gymnospermium albertii*. Petals are blacked out. Solid line; Common bundles are often observed. Broken line; Common bundles are sometimes observed.

floral elements to receive traces of a single nature in origin from the stele and for the inner elements to receive traces of a double nature is recognized. As described above, traces to the inner elements are given off from the stele as common bundles. In *Caulophyllum* and *Leontice*, common bundles usually divide into traces to the inner sepals, to the petals and sometimes to the stamens or traces to the petals and to the stamens on the same radii. In *Gymnospermium albertii* common bundles almost always contain traces to the inner sepals, petals and stamens and a double nature of the traces is not clear. An intermediate condition in the frequency of common bundles is observed in *G. altaicum* and *G. microrrhynchum*.

As traces to sepals, petals and stamens are generally separated independently from the stele, the presence of common bundles is regarded as a derived condition. In connection with this, *Gymnospermium albertii* shows the most advanced or specialized condition in the receptacular vasculature.

The vasculature in the receptacle of *Bongardia* is different from that of *Caulophyllum*, *Leontice* and *Gymnospermium* in some respects. The very thick xylem of the stele at the lower level of the receptacle is observed only in this genus. Traces to the sepals, petals and stamens are given off independently from the receptacular stele, and no common bundles are observed.

The receptacular vasculature of *Caulophyllum*, *Leontice*, *Gymnospermium* and *Bongardia* is similar to that of *Epimedium* and *Vancouveria* in the following respects. In *Epimedium* and *Vancouveria*, traces to the outer elements tend to be of a single nature and traces to the inner elements tend to be of a double nature. Differences in vascular supply are not obvious between sepals and petals in common, in spite of the difference in outer morphology. Differences in vascular supply are observed between sepals and petals in *Plagiorhegma* and *Jeffersonia* where the sepals are often traversed by three traces leaving 2 or 3 gaps and the petals and stamens receive two traces leaving 1 gap. The frequency of common bundles is not as high in *Epimedium*, *Vancouveria*, *Plagiorhegma Jeffersonia* and *Achlys*.

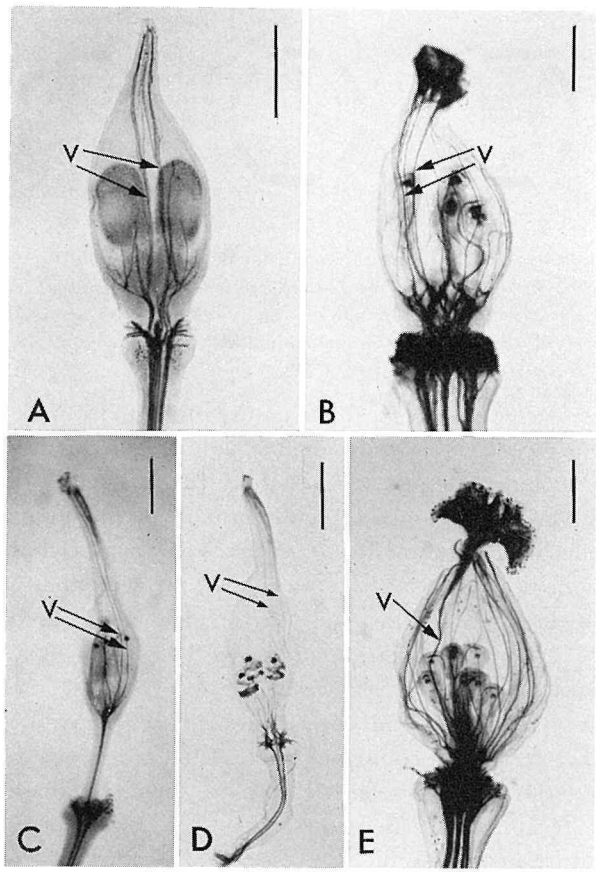

Fig. 8. Cleared pistils, showing the vasculature in the pistil. A: *Caulophyllum thalictroides* ssp. *robustum*. B: *Leontice leontopetalum* ssp. *leontopetalum*. C: *Gymnospermium albertii*. D: *Gymnospermium altaicum*. E: *Bongardia chrysogonum*. V, ventral bundle. The scales are all for the length of 1 mm.

Vasculature in the pistil

Pistils of *Caulophyllum, Leontice, Gymnospermium* and *Bongardia* all have basal placenta, although the number of ovules varies in the different genera: 2 in *Caulophyllum*, 3–4 in *Leontice*, 2–3 in *Gymnospermium* and 6–9 in *Bongardia*. Vasculature in the pistil is similar in these four genera. The pistils are traversed by two ventral bundles, (only one in *Bongardia*) and several lateral veins which branch dichotomously a few times. No distinct dorsal bundle is observed. Only the ventral bundles extend to the stigmatic region, passing through the short style. Lateral veins end at a level lower than the style. In spite of differences in the shape (cristate in

Caulophyllum, Leontice and *Gymnospermium*, undulate fan-shaped in *Bongardia*) the stigma is supplied only by branches from ventral bundles.

When comparisons are made in the pistillate morphology between the genera of the tribe Epimedieae, the following can be said. The placentas of *Caulophyllum, Leontice, Gymnospermium* and *Bongardia* are basal and have fewer ovules, while those of *Epimedium, Vancouveria Plagiorhegma* and *Jeffersonia* are parietal and have many ovules. The simple pistil with a basal placenta bearing a single ovule in *Achlys* is considered to be derived from such pistils with parietal placentas as observed in *Plagiorhegma* and *Jeffersonia* (Terabayashi, 1981). The ovular bundles are often independent of the ventral bundles in *Caulophyllum, Leontice, Gymnospermium* and *Bongardia*, but the ovular bundles are given off from both the ventral bundles and the other bundles in the placenta in *Epimedium, Vancouveria, Plagiorhegma, Jeffersonia* and *Achlys*. In the former genera there is no groove or mechanism for dehiscence dividing the venation of the ovary into two groups. In contrast, ovaries have a groove or a mechanism for dehiscence in the latter genera. The venation of the pistil is divided into two groups by the line of the groove or the mechanism for dehiscence (Terabayashi, 1979, 1981). From this evidence it can be said that the pistils of *Caulophyllum, Leontice, Gymnospermium* and *Bongardia* are different in the type of the placenta, ovary wall and vasculature from that of *Epimedium, Vancouveria, Plagiorhegma, Jeffersonia* and *Achlys*.

From the viewpoint of pistillate anatomy, the tribe Epimedieae may be classified into two major groups, one group consisting of *Epimedium, Vancouveria, Plagiorhegma, Jeffersonia* and *Achlys* and the other of *Caulophyllum, Leontice, Gymnospermium* and *Bongardia*. This grouping agrees with the results of studies of comparative pollen morphology given by Nowicke and Skvarla (1979). In the latter group, *Bongardia* is placed more or less remotely from the other genera on the basis of differences in floral anatomy as described above. This idea is also supported by the seed coat anatomy (Takhtajan and Melikian, 1972) and karyological studies (Kosenko, 1977a, 1977 b, 1978, 1979).

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Explanation of Pates I~IV

Plate I. *Caulophyllum thalictroides* ssp. *robustum*. Transverse sections of the flower at successively higher levels (×28). 1: Pedicel. 2–9: Receptacular region. 2, 3, 4: Traces to 3 outer sepals are given off at different levels (OS). 5: Traces to 3 petaloid sepals of outer whorl are given off (IS). The traces are of a double nature in the origin from the stele. 6: Traces to 3 petaloid sepals of inner whorl are given off. Sometimes traces to inner sepals and petals on the same radii are derived from the common bundles departing from the stele (IS+P). 7, 8, 9: Traces to petals and stamens are given off. In some cases traces to petals and stamens are originated as common bundles (P+S), and in other cases these traces are given off successively (P, S). 10–18: Pistil. 10, 11, 12: Base of the pistil. Several bundles are separated from the dorsal

and lateral sides of the vascular ring. The remaining vascular ring moves toward placental region. 13, 14: The vasculr ring divides into four parts, 2 ventral bundles (V) and 2 ovular bundles (O). 15, 16: Middle to upper level of the ovary. A ventral projection containing 2 ventral bundles are continuous with basal placenta. 17, 18: Stylar and stigmatic region. Ventral bundles only pass through the style and supply the stigma. OS, outer sepal trace; IS, petaloid sepal trace; P, petal trace; S, stamen trace; V, ventral bundle; O, ovular bundle.

Plate II. *Leontice leontopetalum* ssp. *leontpetalum*. Transverse sections of the flower at successively higher levels (×28). 1: Pedicel. 2–8: Receptacular region. 2: Lowermost level of the receptacle. Each bundle expands laterally and begins to divide. 3, 4, 5: Traces to outer and inner sepals are given off (OS, IS). In this example one of the outer sepals receives traces leaving two independent gaps (OS'). Traces to outer sepals are singular and those to inner sepals tend to be of a double nature in the origin from the stele. 6, 7, 8: Upper level of the receptacle. Traces to petals and stamens are given off. Traces to petals and stamens on the same radii tend to be derived from the common bundles (P+S). 9: Transitional region from the receptacle to the pistil. Neighbourring bundles fuse with each other resulting in a vascular ring entering the terminal pistil. 10–18: Pistil. 10, 11, 12: Veins of ovary wall are given off from the vascular ring. No distinct dorsal bundle is observed. 12, 13: Two ventral bundles and three ovular bundles are originated independently (V, O). 14, 15: Lower to middle level of the ovary. Ventral projection containing two ventral bundles is observed. Two ovules are at the ventral side and one ovule is at the dorsal side. 16, 17, 18: Uppermost level of the ovary, stylar level and stigmatic region. Two ventral bundles only supply these region. OS, outer sepal trace; IS, inner sepal trace; P, petal trace; S, stamen trace; V, ventral bundle; O, ovular bundle.

Plate III. *Gymnospermium albertii*. Transverse sections of the flower at successively higher levels (×28). 1: Pedicel. 2–8: Receptacular region. 2: Lowermost level of the receptacle. Each bundle expands laterally. 3: Traces to two outer sepals are given off (OS). 4–8: Common bundles (IS+P+S, P+S) are given off from the stele and those divide into traces to inner sepals, petals and stamens or petals and stamens in the cortex. Remaining stelar bundles fuse with each other resulting in a concentric vascular bundle (C). An abnormally additional stamen trace (S') is given off directly from the stele. 9–18: Pistil. 9: A concentric vascular bundle runs through the long stipe. 10, 11: A concentric bundle changes into a circle of vascular bundles through expansion and division. 12: Veins of ovary wall are separated. Ventral bundles appear from the remaining vascular ring (V). 13: The vascular tissue in the placental region divides into three ovular bundles (O). 14, 15: Lower to middle level of the ovary. Two ventral bundles pass through the ventral projection of the ovary wall. 16, 17, 18: Uppermost level of the ovary, stylar level and stigmatic region. Two ventral bundles only supply these region. OS, outer sepal trace; IS, inner sepal trace; P, petal trace; S, stamen trace; C, concentric vascular bundle; V, ventral bundle; O, ovular bundle.

Plate IV. *Bongardia chrysogonum*. Transverse sections of the flower at successively higher levels (×30). 1: Pedicel. Four main bundles and four weak bundles are alternate with each other. 2–9: Receptacular region. 2, 3, 4: Lowermost level of the receptacle. The receptacular stele is composed of thick xylem and thin phloem. Traces to outer sepals (OS) and inner sepals (IS) are given off. The traces are of a single nature in the origin from the stele. Traces to outer sepals are singular through the course, while those to inner sepals are divided into three in the cortex. 5–9: Xylem of stelar bundles decreases in thickness. Traces to petals and stamens are given off successively (P, S). Petal traces are of a double nature and divide into three in the cortex. Stamen traces are usually singular both in the origin and through the course. 10–18: Pistil. 10, 11, 12: Base of the ovary. Venis of ovary wall are separated from the vascular ring, and remaining vascular ring moves toward placental region. 13, 14, 15: A single ventral bundle (V) is given off from the vascular ring and remaining part divides into 6 ovular bundles (O). 16: Middle level of the ovary. Ventral projection contains a single ventral bundle. 17, 18: Stylar and stigmatic levels. An arrow indicates ovary wall of dorsal side which is discontinuous with stigma. OS, outer sepal trace; IS, inner sepal trace; P, petal trace; S, stamen trace; V, ventral bundle; O, ovular bundle.