***Podophyllum pleianthum* HANCE.**
A Morphological Study, with Supplementary
Notes on Allied Plants.

By

Masao Kumazawa.

With 4 Text-figures.

Received October 19, 1935.

Podophyllum pleianthum is an interesting species discovered by WATTERS in Formosa in 1881, and described by HANCE in 1883; and it was also introduced afterwards as the synonyms *P. versipelle* HANCE, *P. Onzoi* HAYATA, etc. The species, distributed from the Himalayan districts to Formosa through mountainous parts of China, is, contrary to *Podophyllum peltatum* L. and *P. Emodi* WALL., rarely cultivated in any of the European or American botanical gardens,¹⁾ so that the morphological and histological studies have been rather neglected by foreign authors, although some descriptions were briefly given by CITERNE (1892) and by the present writer in his previous paper (KUMAZAWA, 1930).

At present, sufficient materials have been cultivated in the writer's hand, and some morphological studies were made.

1. External Morphology of the Vegetative Organs.

The aerial stem is 20–30 cm. in height, 1.0–1.5 cm. in diameter at its base, provided usually with two foliar leaves at its top (fig. 1, the plant on the right hand). Each of the two foliar leaves has a long petiole and very large peltate lamina, the laminae of the two leaves being usually similar in shape to each other. The petioles are apparently quite opposite to each other, and are inserted nearly at the same level of the stem as in *P. peltatum*. A cymose inflorescence is attached at the basis of the two petioles.

The rhizome is horizontal, about 2 cm. in diameter, and is dorsiventral in appearance. Each monopodial axis of the rhizome terminates in an erect stem every year, and an axillary bud on the monopodium elongates and also terminates in an erect stem the next year. The sympodial axis,

1) In Kew Gardens, *P. pleianthum* came first to bloom in 1889 (a coloured icon of the plant in full: vid. CURTIS's Bot. Mag. Vol. CXVI, T. 7098, 1890); and *P. versipelle* first in 1906 (a coloured icon of the plant: vid. *ibid.* Vol. CXXXIII, T. 8154, 1907).

thus formed, develops horizontally in one direction, producing one scar of the erect stem every year. The scars are arranged very close to each other, so that the rhizome of this species are quite identical in appearance with that of *Diphylleia*.

The fertile winter bud also resembles that of *P. peltatum* in structure and habit. The bud consists of four to six scale leaves. The axillary bud, embraced by the third or fourth scale leaf from the centre, is largest in size, and terminates in an erect stem the next year. The arrangement of the scale leaves in the bud is quite similar to that of *P. peltatum*.

Fig. 1.

Podophyllum pleianthum
HANCE.

Cultivated plants in bloom. The stem on the right is provided with two foliar cauline leaves; that on the left with three, one of which, having leaf-sheaths, is inserted at a remarkably lower level of the stem. The laminae of three leaves, except the petioles, are not visible being shaded by the front lamina.

Photo. May 1934. ca. $\times 1/5$.

In a cross section of the winter bud, the scale leaves show a divergence of nearly $2/5$ or are arranged in two spirally-wounded rows. It is noticed that the two foliar cauline leaves, which are nearly opposite in the fully-developed condition, are arranged, being spirally wounded (fig. 2 A, F_1 – F_2) in their early stages of development in the same divergence as in the scale leaves of the winter buds.

Besides the usual type of the stem with two foliar cauline leaves, the writer often found the aerial stem provided with three foliar cauline leaves (fig. 1, the plant on the left hand), two of which are inserted nearly at the same level, and the inflorescence occurs at the basis of the petioles of these leaves, while the rest,¹⁾ at a level, more or less lower, of the stem. In this case, three foliar leaves are not arranged in exact $1/2$ divergence even in the

1) When the stem has three foliar cauline leaves, the petiole of the lowest foliar leaves is often provided with membranaceous leaf-sheaths, upper parts of which, 5 mm. or more in length, forming a ligular part as in the case of the foliar radical leaf.

fully-grown condition, and the two leaves, which should form an orthostichy in the case of $1/2$ divergence, are situated, in reality, somewhat twisted, forming a parastichy, and show the spiral arrangement, suggesting nearly the $2/5$ or allied divergences.

Fig. 2. *Podophyllum pleianthum* HANCE.

Diagrams showing the arrangement of foliar cauline leaves and the branching system of the inflorescence observed in an early stage of development. F_1, F_2 in A and F_1, F_2, F_3 in B are foliar cauline leaves. The leaves in black are scaly bracts. F_1-F_4 are foliar or scaly leaves on the main axis T, and they are situated in a twisted manner which is a modification of the typical $1/2$ divergence. T_2-T_4 , the axes of axillary inflorescences on the main axis T. Compare with fig. 3.

Then we come to the conclusion that the original phyllotaxis of the present species is spirally wounded in arrangement; and that the appearance of the $1/2$ divergence of the foliar cauline leaves, observed in the fully-grown stem, is quite a secondary phenomenon accompanied by a decrease in the number of cauline leaves.

2. The Inflorescence.

A number of the nodding peduncles, forming a cymose inflorescence, occurs at the basis of the two petioles as if a pleiochasium or umbel (fig. 1). Peduncles forming the inflorescence are 10–17 in number, of which 5–8 peduncles are vigorous and are provided respectively with a flower, the rest of the peduncles being rudimentary and hardly recognizable in the adult condition of the stem.

The cymose nature of the inflorescence is not analyzed by any authors, so that the writer studied the ontogeny of the inflorescence. In the adult condition, it is not easy to ascertain on what system the inflorescence is constructed, because not only the bracts are extraordinarily reduced, being 1 mm. or less in length, but also the mutual arrangement of the peduncles is, more or less, secondarily changed.

Ontogenetically observed, the flowers forming the inflorescence may be divided always into three categories (fig. 3):

1) One terminal flower which is situated at the centre of the inflorescence (T in A and B).

2) One group of flowers which occur at the axillary part of one of the foliar cauline leaves (T_2 and the flowers on the peduncular axis of T_2 in A; T_3 and the flowers on the axis of T_3 in B). Although this foliar leaf seems to be opposite the other leaf, it is, in reality, inserted always at a slightly higher level of the stem than the other one or two which never embrace the peduncles at their axillary parts.

3) One or two groups of flowers which occur at the axillary parts of the bracts on the terminal peduncle (T_3 , T_4 and flowers on the axis of T_3 and of T_4 in A; T_4 and flowers on the axis of T_4 in B).

The first bract on the lateral axis, i.e. the prophyll, is laterally situated to the mother axis.

Fig. 3. *Podophyllum pleianthum* HANCE.

Diagrams analyzing the branching system of the inflorescence. A and B correspond respectively to fig. 2 A and fig. 2 B. T, T_1 – T_4 and rings without letters indicate the flowers. Other abbreviations as in fig. 2.

Now we know that the axillary inflorescence may be regarded usually as a cincinnus or scorpioid cyme (“*Wickel*”) as shown in fig. 2, although the internodes between bracts are extraordinarily reduced. Such a mode of the cincinnus-like branching is also observed in the rhizome of *Podophyllum*, *Diphylleia*, *Caulophyllum* and some Ranunculaceous genera (KUMAZAWA, 1932 a).

3. The Behaviour of Medullary Bundles.

Vascular bundles of the aerial stem are scattered in the fundamental tissue as in Monocotyledonous stem, usually 100–120 in number at the base of the stem. Peripheral bundles, half or more of the total number, are small and connected laterally to one another by the interfascicular mechanical sheath or tissue. The rest are large and situated at rather medullary parts (fig. 4). The peduncle, 2–3 mm. in diameter, has 15–20 bundles, 3–6 of which are large and medullary.

Fig. 4. *Podophyllum pleianthum* HANCE.

Cross sections of the base of the aerial stems, showing the vascular arrangement. Several medullary bundles shaded indicate the cauline bundles; bundles denoted by F_1 — F_3 are respectively the trace bundles of midribs of foliar cauline leaves. The stems of A and B correspond respectively to the plants shown in Fig. 3 A and B. ca. $\times 4.5$.

The course or behaviour of the medullary bundles is, as a whole, identical with *P. peltatum*, and may be included in Type IV in the previous paper (KUMAZAWA, 1932 b; pp. 260–261), but some features are different from the species. If the medullary bundles in the terminal peduncle are traced upwards, they are divided and bend outwards at the floral receptacle and enter into three outer perianths as in *P. peltatum*; tracing them downwards, we find them running downwards to the stem base, situated at the centre of the stem. Then these bundles may be regarded as the cauline bundles as in the case of *P. peltatum*. The cauline bundles of *P. peltatum* descend from the peduncle downwards quite independently without anastomosing with one another or with other peripheral or leaf trace bundles, although some of them may divide into two at the lower level. In the present species, the cauline bundles anastomose with themselves or are divided very frequently at the node in some individuals, or sometimes connect with a few peripheral bundles at the node in other individuals as in the case of *Diphylleia* (KUMAZAWA, 1930); in either case, they connect further with the trace bundles from the axillary peduncles or inflorescences. The axillary peduncle or inflorescence sends two large trace bundles into the mother axis at the node, and each of these trace bundles connects respectively to each of the two medullary cauline bundles which are rather closely arranged side by side in the mother axis, as usual in the case of the branch traces of most other herbaceous or arboreal plants. The medullary cauline bundles of the present species are, therefore, more complicated in their behaviour than those of *P. peltatum*, and are rather near those of *Diphylleia*.

Peripheral bundles of the terminal peduncle often anastomose with

those of the axillary inflorescence or peduncle and also with some trace bundles of the foliar cauline leaves. Trace bundles of the foliar leaves do not usually anastomose with cauline bundles, but some large ones enter into the medullary parts of the aerial stem, with or without anastomosing with the pre-existing peripheral bundles of the stem. In the stem base, therefore, some of the medullary bundles situated at the centre, are rather cauline, while some situated more or less peripherally are trace strands of the foliar cauline leaves (fig. 4, F₁–F₃). In this respect, the present species is quite similar to *P. peltatum* or *Diphyllia*.

4. Histological Structure.

The histological structure of the present species is mostly similar to that of *P. peltatum* except in a few respects, and was described by CITERNE (1892) to some extents, so that only a brief description is given below.

The xylem of the aerial stem is V-shaped as in *P. peltatum*, but the fascicular cambium is very evident and often produces small amounts of the secondary xylem elements. The interfascicular cambium is not found in the adult condition. The xylem of the peduncle and rhizome is not V-shaped. The fascicular cambium in the rhizome produces hardly any secondary elements in *P. peltatum*, while it is somewhat active in this species and produces small amounts of the secondary xylem elements, so that the xylem elongates somewhat radially.

Cortical bundles which are often found in the rhizome of *P. peltatum* are rarely observed in the rhizome of *P. pleianthum*.

In the rhizome, two or three cell-layers of the sclerenchymatous tissue are observed on the internal side of the very thin cork layer. Except such a sclerenchymatous tissue, the present species resembles *P. peltatum* concerning the histological structure of the rhizome.

Adventitious roots of the first order are 3–5 mm. in diameter, and the root itself or the central cylinder shows no thickening growth. The central cylinder is 5–10 arch, but is usually 6–7 arch. The pith is parenchymatous or sclerenchymatous. Endodermal cells are always thin-walled, and the epidermal ones do not peel off even in the later stage.

In the present species, the aggregate crystals of calcium oxalate are found in the fundamental tissue of the rhizome and root more abundantly than in the case of *P. peltatum*.

5. Systematic Remarks.

WOODSON (1928) compared the floral and vegetative features of *P. pleianthum* with those of other species of *Podophyllum* by herbarium materials, and indicated some features which are quite different from the corres-

ponding features of the latter species. From this point of view, he expressed his opinion that *P. pleianthum* was the representative of one new genus *Dysosma* separated from other species of *Podophyllum*. He described and figured the reflexed pedicels, characteristic shape of pistils, introrse stamens, spherical and relatively small pollens in *P. pleianthum*, contrary to *P. peltatum* and *P. Emodi*.

The present writer also compared *P. pleianthum* with *P. peltatum* by using fresh plants cultivated in our garden to ascertain the statement of WOODSON. According to the own observations of the writer, the peduncles are, in fact, deeply nodding in *P. pleianthum*, but can not be stated as reflexed. In *P. pleianthum* the anthers are quite laterally situated on the connective and the dehiscence is extrorse. In *P. peltatum*, the connective, especially at its top, has a ridge on the ventral side; therefore, the anthers seem to attach somewhat on the dorsal side at the top of the connective, and nearly on the lateral side at the middle part of the connective, but the dehiscence is also extrorse as in *P. pleianthum*. The pollen grains of both species are ellipsoidal in shrunken state, spherical in swollen state, provided with three parallel folds (KUMAZAWA, 1936), and WOODSON's statement is not sufficient. The size of the pollen grain is larger in *P. pleianthum* than in *P. peltatum*, and this is quite contrary to his description.

Among other floral and vegetative features of *P. pleianthum* mentioned by WOODSON as characteristic, some do not seem to confirm his statements, some are not considered by the present writer to be important or sufficiently distinctive for the generic characters. But the cymose nature of the inflorescence, the dull violet petals which are drooping, not spreading, the pistil with a definite style and globose stigma, and the stamen with the sterile top of the connective are also considered by the writer as important characters which differ from *P. peltatum* or *P. Emodi*, and these characteristics may provide some grounds for the opinion that *P. pleianthum* may be treated as a separate genus *Dysosma*.

6. Supplementary Notes on Allied Plants.

It is hitherto believed that the phyllotaxis of the foliar cauline leaves are usually $1/2$ in *Podophyllum* and in its allied genera *Diphylla*, *Glaucidium* and *Hydrastis*; and the writer (1930) also described them as such in the adult stem. After that, observing the aerial stem of all these genera in its early stage of development, the writer found that the divergence of the cauline leaves is not $1/2$ in the strict sense, but the leaves are arranged somewhat in two spirally-wounded rows or often in nearly $2/5$ divergence; and that the leaves, thus arranged, turn into the exact $1/2$ divergence in the fully-grown condition. The writer described and figured previously

that the phyllotaxis of the scale leaves in the winter bud was $1/2$ in *Glaucidium* and *Hydrastis*, but later studies show that the arrangement of those scales are also a slight modification of the typical $1/2$ divergence, and the scales are situated somewhat in two spirally-wounded rows in the strict sense.

The writer, therefore, comes to the conclusion in considering all these genera, that the scale leaves in the winter bud and the foliar cauline leaves in the early developmental stage of the aerial stem do not show the $1/2$ divergence in the strict sense, but show the divergence which is a modification of $1/2$, or often the divergence somewhat near $2/5$, and further that the apparent $1/2$ divergence of the cauline leaves, found in the fully-grown condition, are quite secondarily derived from the original divergence.

SCHMIDT (1928) is of the opinion that the $1/2$ divergence is an original type from which nearly $2/5$ or allied divergences are derived among Berberidaceous plants. If his view is supported, the $1/2$ divergence, found in the adult aerial stem of the present genera, may be interpreted as tertiary from the phylogenetic point of view.

In his previous paper (1930, p. 374), the writer described the prophyll of the axillary bud as invertedly situated in *Podophyllum* and *Hydrastis*. This description needs a correction. Although the prophyll on the axillary bud of the rhizome seems to be inverted in its early stage of development, it is evidently lateral in the later stage.

Now, some results of miscellaneous observations, which were made after publication of the paper of 1930, must be added.

The seeds of *Glaucidium* and *Diphylla* germinate in the next spring after sowing. It was later known that there were some individual variations in the cotyledonary features of *Glaucidium*, besides such a type as previously described in which two cotyledonary petioles and the bases of the cotyledonary laminae are respectively fused. In some seedlings, both of the bases of cotyledonary laminae and the tops of petioles—a few millimeters in length—are respectively free, while in others the cotyledonary laminae are quite free and the petioles are perfectly fused with each other. The last type seems to be most usual in *Glaucidium*. These variations of the cotyledonary features were already reported in Japanese (1931, p. 537).

7. Summary.

1. A morphological study of *Podophyllum pleianthum* HANCE was made, particularly in respects to the leaf arrangement, the branching system of the inflorescence and the behaviour of the medullary bundles.

2. The foliar cauline leaves are not arranged in the $1/2$ divergence in the strict sense, if observed in the early developmental stage of the stem.

3. The inflorescence which is apparently a pleiochasium or umbel, belongs to a modified type of the cincinnus or scorpioid cyme.

4. The medullary bundles are similar to those of *P. peltatum* in their course and origin, but the medullary cauline bundles are more complicated in behaviour.

5. Some remarks were given regarding the opinion of WOODSON that *P. pleianthum* belongs to the monotypic genus *Dysosma* separated from other species of *Podophyllum*.

6. The cauline leaves of *Podophyllum*, *Diphylleia*, *Glaucidium* and *Hydrastis* are arranged as slight modifications of the typical $1/2$ divergence in the early stage of their development. The scale leaves of the winter bud are also arranged in two slightly-wounded rows and do not show the exact $1/2$ divergence in *Glaucidium* and *Hydrastis*. Therefore, the apparent $1/2$ divergence of the cauline leaves, observed in these four genera, may be derived from the spirally-wounded or nearly $2/5$ divergence accompanied by the decrease in the number of leaves.

7. Some supplementary notes and corrections were given to the previous paper of the writer regarding the morphology of these genera.

The writer wishes to express his thanks to Prof. Y. OGURA of the Tokyo Imperial University for his criticism and encouragement throughout the course of this study.

Biological Laboratory,
Daisi-Kôtô-Gakkô, Kanazawa,

Literature.

(Literatures listed in the first paper of the writer
are omitted here.)

- KUMAZAWA, M. (1930) Morphology and biology of *Glaucidium palmatum* SIEB. et ZUCC. with notes on affinities to the allied genera *Hydrastis*, *Podophyllum* and *Diphylleia*. Journ. Fac. Sci. Imp. Univ. Tokyo. Sec. 3, Bot. Vol. 2, Part 4.
- (1931) Supplementary notes on the cotyledons of *Glaucidium palmatum*. (in Japanese). Bot. Mag. Tokyo. Vol. 45, p. 537.
- (1932 a) Morphological studies of *Anemonopsis*, *Actaea* and *Cimicifuga*. Journ. Fac. Sci. Imp. Univ. Tokyo. Sec. 3, Bot. Vol. 2, Part 6.
- (1932 b) The medullary bundle system in the Ranunculaceae and allied plants. Bot. Mag. Tokyo, Vol. 46.
- (1936) Pollen grain morphology in Ranunculaceae, Lardizabalaceae and Berberidaceae. Jap. Journ. Bot. Vol. 8.
- SCHMIDT, E. (1928) Untersuchungen über Berberidaceen. Beih. Bot. Zentralbl. Bd. 45.
- WOODSON, R. E. (1928) *Dysosma*: a new genus of Berberidaceae. Ann. Missouri Bot. Garden. Vol. 15.
- ZIMMERMANN, W. (1935) Die Phylogenie der Angiospermen-Blütenstände. Untersuchungen zur Gesamtphylogenie der Angiospermen. 1. Beih. Bot. Zentralbl. Bd. 53. Abt. A.