

June, 1984

Kor. Jour. Pl. Tax.

Vol. 14, No. 1, 33-42

Phylogenetical consideration on the Ranunculaceae

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The Ranunculaceae have been regarded as one of the primitive angiospermous families, and studied in various aspects mainly from the interest in phylogeny. The family was first divided into 4 tribes by De Candolle (1818), and since then the classification has been revised repeatedly. The present author also revised the family and divided it into 6 subfamilies (1966).

In this article, the author wants to discuss the important criteria of the Ranunculaceae and propose an amendment to the previous classification of the family.

1. Carpel Morphology

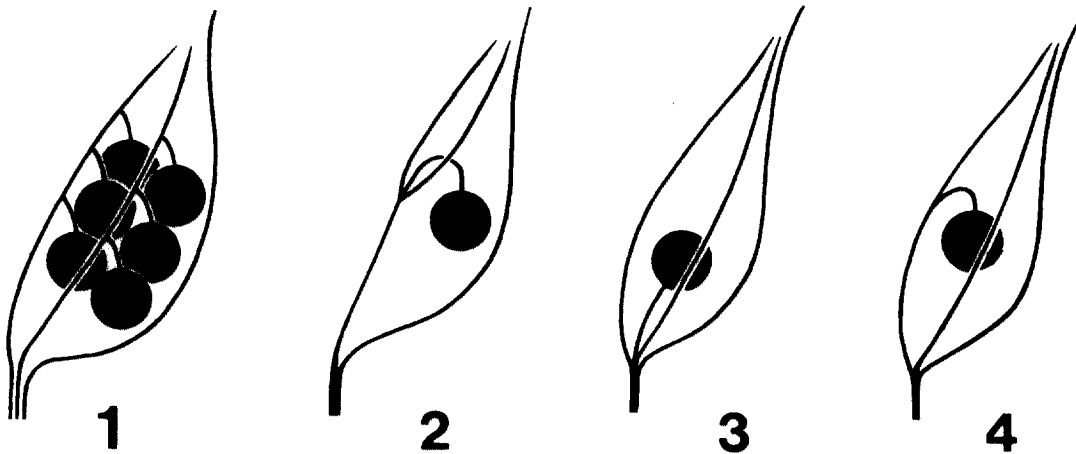
The Ranunculaceae have been often divided into the group with uniovular carpels or 1-seeded fruitlets such as achenes and the group with multiovular carpels or many-seeded fruitlets such as follicles, since Adanson (1763). Some authors, such as Spach (1839), Nakai (1949), etc, regarded the two groups as different families, Ranunculaceae with 1-seeded fruitlets and Helleboraceae with many-seeded ones.

Prantl (1887, 1888) divided the family into 3 tribes, Paeonieae, Helleboreae and Anemoneae. In Trib. Paeonieae, he included 3 genera, which were regarded as unusual or abnormal among the Ranunculaceae, namely, *Paeonia*, *Glaucidium* and *Hydrastis*. *Paeonia* is usually considered to have no close relationship to the Ranunculaceae, and treated as a different family, Paeoniaceae. For *Glaucidium*, Tamura (1972) created a monotypic family, Glaucidiaceae, and this family is generally accepted now. *Hydrastis* is sometimes treated as a different family, Hydrastidaceae, by some authors such as Eames (1961) and Takhtajan (1969). But this genus does not seem so different from usual members of the Ranunculaceae, and Tamura (1966) retained it in the family as a monotypic subfamily, Hydrastidoideae.

Prantl (1887, 1888) divided other genera than the above mentioned three into Trib. Helleboreae with multiovular carpels and Trib. Anemoneae with uniovular carpels. He characterized both tribes not only by the number of ovules but also by the vasculature of carpel, especially the origin of ovular trace. That is, in Trib. Helleboreae, a carpel is supplied with 3 traces, and the middle trace is a dorsal bundle and 2 lateral traces are ventrals. The ovules are arranged in 2 rows along the ventral suture and supplied with branches of both

ventral bundles. While in Trib. Anemoneae, a carpel is supplied with a single trace, and a single fertile ovule is ascending or pendulous from the middle of adaxial ridge. In *Anemone*, *Clematis*, and their allied genera, usually a carpel trace is divided into a dorsal bundle and a ventral trunk bundle. The latter is divided again into 3, and the middle branch is a ovular trace and 2 lateral branches are ventral bundles. In *Ranunculus* and its allied genera, a carpel trace is divided into 4 nearly at the same point, i.e., 1 dorsal, 2 ventral and 1 ovular trace bundles.

Adonis and *Callianthemum* have uniovular carpels which become achenes in maturing as usual members of Trib. Anemoneae, but 1 fertile ovule is produced not from the middle of



Pl. 1. Vasculature of carpel

1: multi-ovular carpel. 2: uniovular carpel of *Anemone* and its allied genera. 3: uniovular carpel of *Ranunculus* and its allied genera. 4: uniovular carpel of *Adonis* and *Callianthemum*.

adaxial ridge but from one of both lateral margins of a carpel and supplied with a branch of one of both ventral bundles. Considering these evidences, Prantl (1887, 1888) classified *Adonis* and *Callianthemum* not in Trib. Anemoneae but in Trib. Helleboreae. Schaeppi & Frank (1962) confirmed position and vascularization of the ovule.

Many authors, such as Smith (1926, 1928), Chute (1930), Eames (1931) and Kumazawa (1938), studied the anatomy and morphology of carpels of the Ranunculaceae, and emphasized that the uniovular carpels were derived from multi-ovular ones by the reduction of number of ovules and the fusion of carpel traces and dorsal and ventral bundles.

The present author agrees to their opinion principally. But the actual process from the multi-ovular carpel to the uniovular ones does not seem so simple, and ontogenetical studies show that the gap between both carpel types seems to be considerably deep and wide. Troll (1932) emphasized the universal occurrence of so-called Querzone in vascular plants from the standpoint of peltation theory. Van Heel (1981, 1983) showed that in *Consolida ajacis* and *Cimicifuga racemosa*, carpel primordia are bowl-shaped or asciform, but the adaxial part

of the margin does not develop further. Even if the multiovular carpels show the peltate nature in the primordial stage, they become different from the uniovular ones through the later development. In mature condition, the uniovular carpels has a distinct Querzone, while in the multiovular carpel, it is not distinct and only slightly recognizable or actually absent. The carpels of *Adonis* and *Callianthemum* have distinct Querzone as those of other genera forming achenes.

2. Karyology

Langlet (1932) recognized 2 types of chromosomes in the Ranunculaceae, namely R (anunculus)-type with "lange, im allgemeinen gewundene oder mehrfach gebogene, meist recht grosse" chromosomes and T (halictrum)-type with "im allgemain einfach gebogene, verhältnismässig kline" chromosomes. He proposed the subdivision of the family into Subfam. Ranunculoideae with R-type chromosomes and Subfam. Thalictrioideae with T-type chromosomes, and considered that in both subfamilies the groups with uniovular carpels or achenes were derived from the groups with multiovular carpels or follicles independently by the reduction of ovules. Both karyological types seem to have an important meaning in phylogeny of the Ranunculaceae. *Caltha* with follicles and some species of *Ranunculus* with achenes are very similar to each other in flowers and leaves, and both genera have R-type chromosomes. On the other hand, *Aquilegia* and *Isoyrum* with follicles resemble *Thalictrum* with achenes in leaves and stems, and these genera have T-type chromosomes.

The results from chemotaxonomical studies also support the distinction between both karyological groups (Ruijgrok 1966, Ichinohe & Tamura 1977). That is, all genera with T-type chromosomes accumulate isoquinoline alkaloids as far as examined, while genera with R-type chromosomes accumulate them rarely or only a little (Alston & Turner 1963). And also in the group with T-type chromosomes, a considerable number of genera, such as *Thalictrum*, *Isopyrum*, *Semiaquilegia* and *Aquilegia*, contain cyanogenetic compounds, while in the R-type group, cyanogenetic compounds are reported only in some species of *Ranunculus* and of *Clematis* (Ruijgrok 1966). On the contrary, distribution of ranunculin is restricted to the group with R-type chromosomes (Ruijgrok 1966).

But the distinction between R- and T-types are not always clear as far as the chromosome length or size is concerned. For example, *Ranunculus* is a typical genus with R-type chromosomes, but in some species, such as *R. scerelatus* and *R. nipponicus*, chromosomes are considerably small and not so different from those of *Coptis*, *Dichocarpum* and *Aquilegia* with T-type chromosomes, at least in size or length (Okada & Tamura 1979).

Besides chromosomes size, however, both karyological types are distinguishable by stainability or distribution pattern of chromatins in interphase nuclei and prophase chromosomes. In the interphase nuclei of R-type, a few dark stained condensed bodies are observed, but their boundaries are not clear, because the other part is also stained fairly well and unevenly. While in those of T-type, several condensed bodies are clearly observed, because the other part is stained only dilutely and evenly. In the prophase chromosomes of R-type, hetetochromatic segments are distributed through the length of chromosomes and

Table 1. Chromosome type, number and length of some species of the Ranunculaceae

Species	Type	Number 2n	Length (μ)	
			maximum	— minimum
<i>Ranunculus japonicus</i>	R	14	8	— 4
<i>R. cantoniensis</i>	R	32	7	— 4
<i>R. sieboldii</i>	R	48	6	— 3
<i>R. sceleratus</i>	R	32	3	— 1.5
<i>R. nipponicus</i>	R	48	3	— 1
<i>Coptis japonica</i>	T	18	2.5	— 2
<i>C. ramosa</i>	T	18	2	— 1.5
<i>Aquilegia flabellata</i>	T	14	2	— 1.5
<i>Hydrastis canadensis</i>	T	26	2	— 1
<i>Thalictrum filamentosum</i>	T	14	1.5	— 1
<i>Xanthorhiza apiifolia</i>	T	36	1	— 0.5

(Okada and Tamura 1979)

the boundaries between hetero- and eu-chromatic segments are indistinct. While in those of T-type, heterochromatic segments are in the proximal part of arms, and the boundaries between hetero- and eu-chromatic segments are distinct.

3. Subdivision of the Family

From the above mentioned, the karyology of the chromosome type can be still the first class important character in the phylogenetical consideration of the Ranunculaceae. But the carpel morphology also must not be undervalued. By way of the taxonomic treatment, it seems reasonable that the family, except for *Hydrastis* which is regarded as a monotypic subfamily Hydrastidoideae, is divided into 4 Subfamilies, i.e., Helleboroideae with R-type chromosomes and follicles, Ranunculoideae with R-type chromosomes and achenes, Isopyroideae with T-type chromosomes and follicles and Thalictrioideae with T-type chromosomes and achenes.

In Subfam. Helleboroideae, the basic chromosome number is mostly 8, but it is 7 in *Komaroffia*, and 6 in *Nigella* and *Garidella*. In Subfam. Ranunculoideae, also the basic chromosome number is mostly 8, but it is 7 in some species of *Ranunculus* and of *Anemone*. In the group with R-type chromosomes, the basic number seems to be originally 8, and 7 further 6 were derived by the phylogenetical reduction. On the other hand, in the group with T-type chromosomes, the basic number reported are 13 in *Hydrastis*, 9 in *Coptis* and *Xanthorhiza*, and 7 in all other genera examined. The numerical variation of chromosomes seemed to show a discontinuous line, in contrast to the aneuploidal series in R-type group. But recently Zhang (1982) reported that *Asteropyrum* had T-type chromosomes and the diploid number is 16. Its basic number is supposed to be 8. If this report is correct, Subfam.

Coptidoideae with the basic number 9 lose the most important base to be distinguished from Subfam. Isopyroideae with basic number 7 as a different subfamily, and is better to be reduced to Subfam. Isopyroideae.

Adonis and *Callianthemum* seem better to be classified in Subfam. Ranunculoideae than in Subfam. Helleboroideae, because a type of fruitlet, either follicle or achene, is much easier to be distinguished than vascular supply of carpels, and also each carpel of these genera has a distinct Querzone as usual members of Subfam. Ranunculoideae have. But *Adonis* and *Callianthemum* are different from other members of the Ranunculoideae, not only by the vascularization of carpels and position of ovules but also by the number of integument. That is, in both genera, ovules are bitegmic, though in other genera of the Ranunculoideae, ovules are unitegmic. Accordingly, both genera do not seem to have a close relationship to other members of Subfam. Ranunculoideae. Prantl's idea, that *Adonis* and *Callianthemum* are directly connected to the Helleboroideae, may be correct phylogenetically.

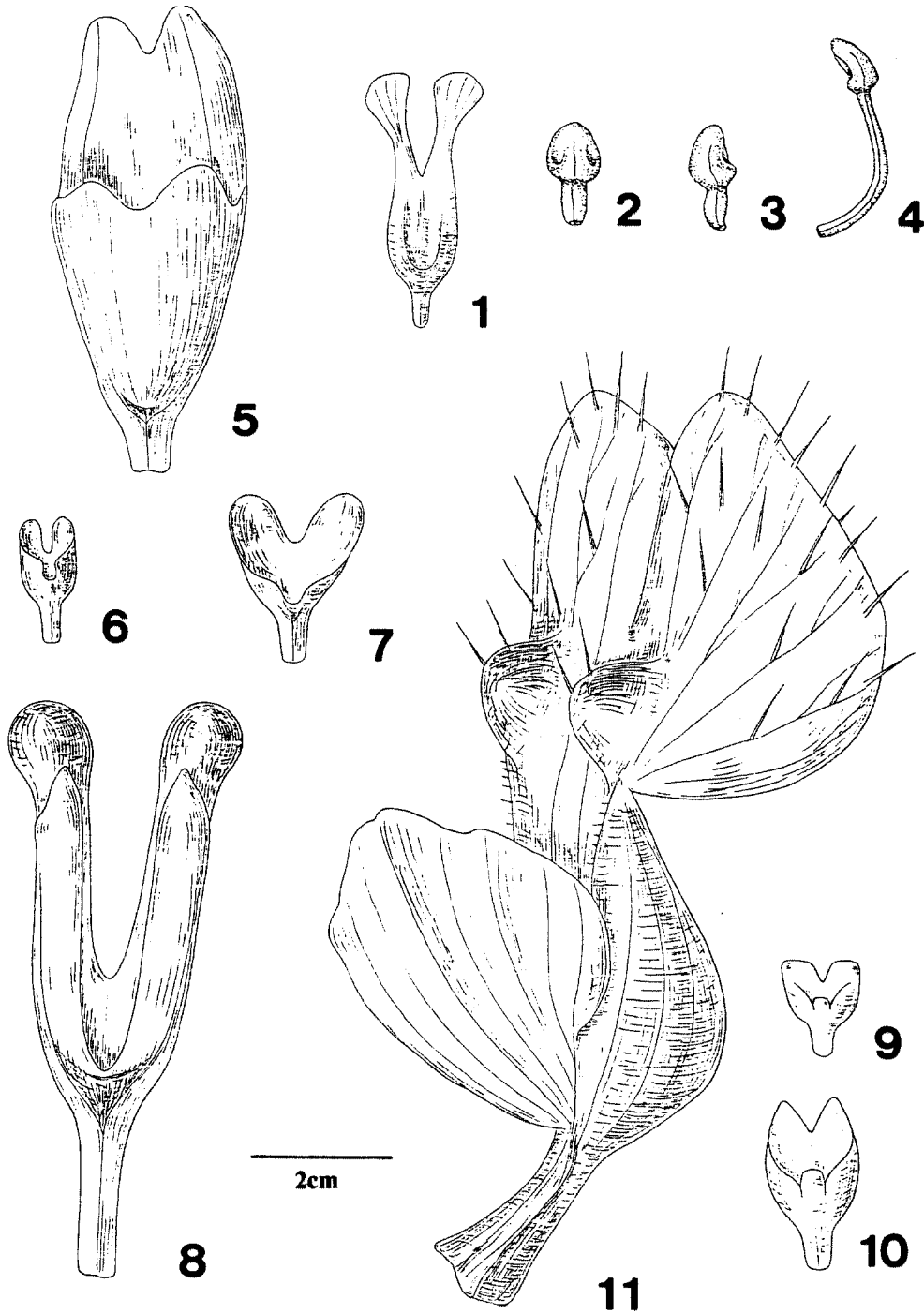
4. Petal and its Evolution

In the Ranunculaceae, the petal is considered to be derived from the stamen. The reasons are: (1) petals and stamens are arranged on the same parastichy, and a petal is the first member of a staminal parastichy. (2) petals resemble stamens in primordial stage, and initiate as the outermost members of stamens in time or in size. (3) a petal is a unilacunar organ supplied with 1 trace bundle as a stamen, while a sepal is trilacunar or unilacunar and supplied with 3 trace bundles. (4) Petals sometimes quite resemble stamens in appearance, and also there are sometimes intermediate structures between stamens and petals (Tamura 1965). The petal of this family usually secretes honey, and Prantl (1887, 1888) called it Honigblatt.

In the Ranunculaceae, petals appeared sporadically and independently in various groups. Within the family, subfamilies Hydrastidoideae and Thalictroideae have no petals. In other subfamilies, petals in various stages of evolution are observed, and genera without petals are considered to be principally primitive.

In subfam. Helleboroideae, *Caltha* and *Calathodes* have no petals. In *Cimicifuga*, petals are epeltate, flat and concave downwards, and often with vestigial anthers as in *C. dahurica*, and seem to be in a primitive condition. In such a type of petal, the main part is a dilated staminal filament. *Trollius* and *Megaleranthis* have also flat petals. In *Delphinium*, *Consolida* and *Aconitum*, petals are intricate, but the epeltate nature can be detected in them. In *Nigella* and its allied genera, petals are bilabial, and in *Helleborus* and *Eranthis*, they are cup-shaped at least in the early stage of development. These petals are peltate, and the limbs correspond to staminal anthers and the stalks to filaments.

In Subfam. Ranunculoideae, most members belonging to Trib. Anemoneae have no petals, except for *Naravelia*, *Clematis* sect. *Atragene* and some species of *Pulsatilla*. In *Clematis* sect. *Atragene*, petals are spatulate, flat and epeltate, and connected to stamens by the transitional structures with reducing anthers and dilating filaments in various degrees. In *Clematis*, many species have more or less dilated filaments, and the case of Sect. *Atragene* is

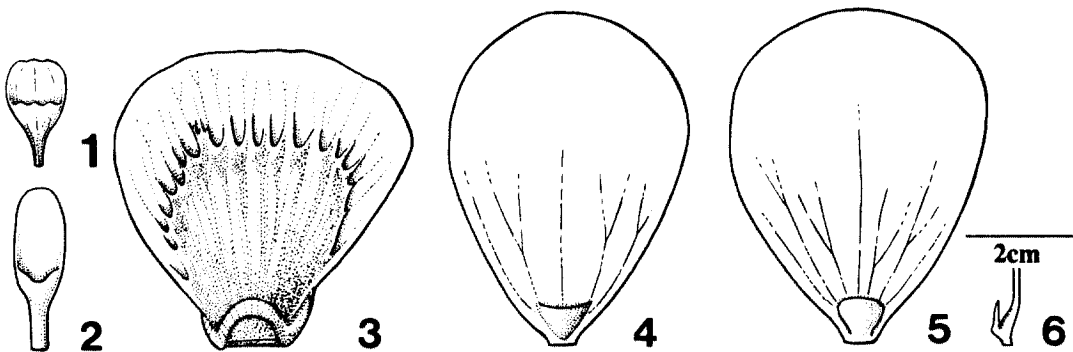


Pl. 2. Petals of the Ranunculaceae I

1: *Cimicifuga dahurica*, x15, 2, 3: *Pulsatilla vulgaris* (3: side view), x20. 4: *Pulsatilla pratensis* (side view), x20. 5: *Eranthis hyemalis*, x20. 6, 7, 8: *Eranthis pinnatifida* (6, 7: early stages of development), x20. 9, 10, 11: *Nigella damascena* (9, 10: early stages of development), x35.

an extreme condition of the tendency. In *Naravelia*, petals are generally long spatulate or club-shaped, but sometimes they are spoon-shaped and the limbs and the stalks are distinguishable in them, as found in *N. pilulifera*. Some species of *Pulsatilla* have small capitulate and stalked structures secreting honey. The structure is a modified stamen and regarded as a kind of petal.

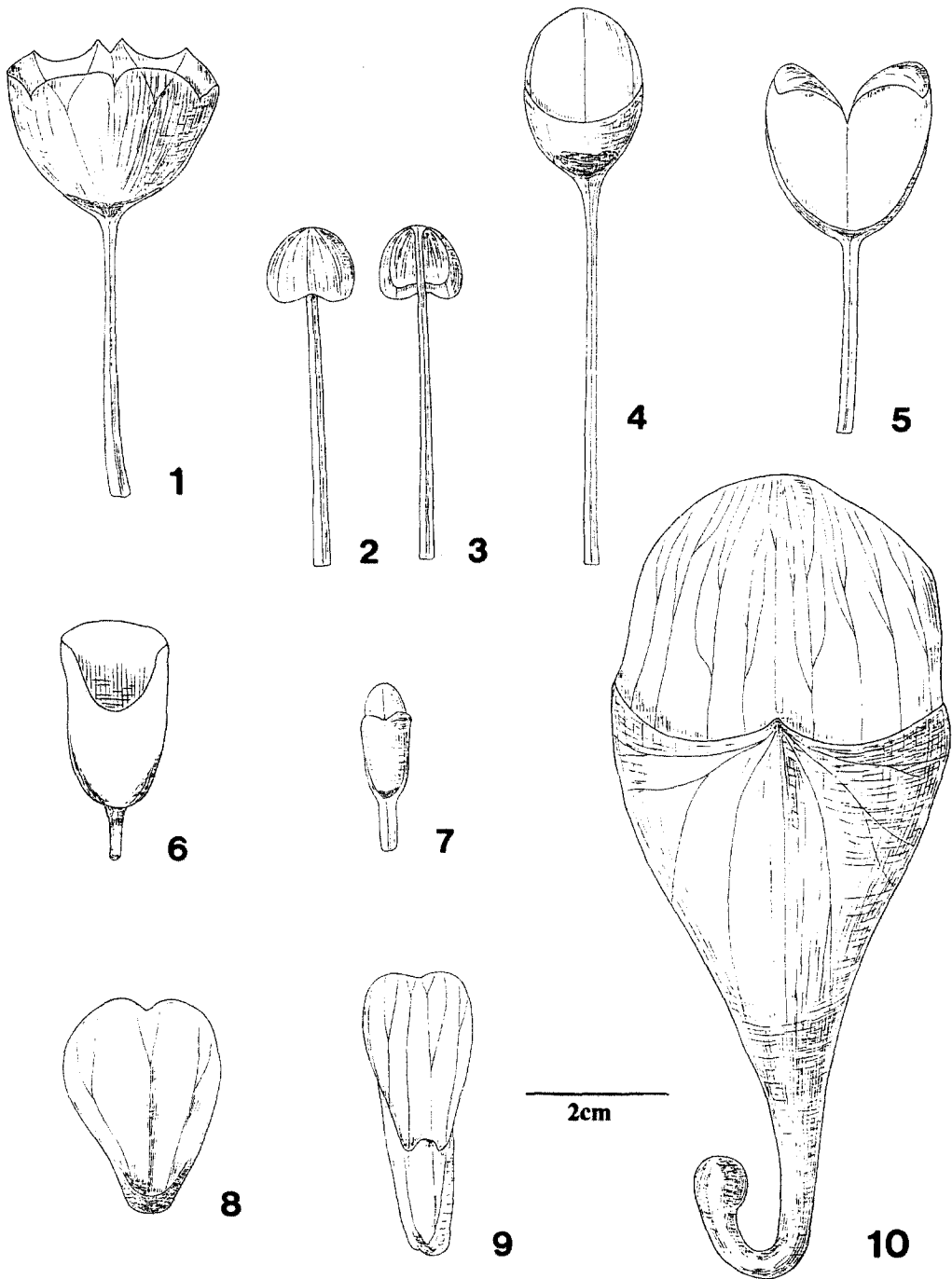
In Trib. Ranunculeae, *Trautvetteria* has no petals. *Aphanostemma* has small cup-shaped stalked peltate petals, distinctly shorter than petaloid sepals. *Kumlienia* and *Arcteranthis* have also similar petals, but they become larger, though still distinctly smaller than the sepals. In *Krapfia*, *Laccopetalum* and some species of *Ranunculus*, especially those belonging to Sect. *Casalea*, petals are smaller than the sepals, and both sepals and petals are petaloid. The petal of *Ranunculus* is flat, but it usually has a nectary near the base, which covered with a flap, or in a pocket or in a hollow. These structures suggest that petals of these genera are peltate originally. In *Krapfia* and *Laccopetalum*, flowers are large, petals have many nectaries and seem to be specialized by amplification. In most species of *Ranunculus*, petals are larger than sepals. The sepal is sepaloid and a protective organ, and the petal is petaloid and an attractive organ. Thus, the flower becomes heterochlamydeous.



Pl. 3. Petals of the Ranunculaceae II

1: *Aphanostemma apiifolia*, x20. After Lourteig (1952). 2: *Kumlienia hystricula*, x10. 3: *Laccopetalum giganteum*, xl. After Hiepko (1965). 4: *Ranunculus auricomus*, x5. 5, 6: *Ranunculus japonicus* (6: longissection of the part with nectary flap), x5.

In Subfam. Isopyroideae, *Enemion* has no petals and is regarded as the first member of evolutionary series in this subfamily. *Dichocarpum* has peltate petals similar to stamens and is in the most primitive stage. Especially in *D. pterigionocaudatum*, the cup-shaped limb and the long stalk are clearly comparable with staminal anther and filament, respectively. In *D. hakonense* and *D. stoloniferum*, the inner wall of the limb becomes distinctly shorter than the outer wall, and in *D. nipponicum* and *D. trachyspermum*, the inner wall is perfectly reduced and the petal becomes epeltate. In *D. dicarpon*, petals are peltate, and the limb is bilabial periclinally and both outer and inner labia are hanging inside together. In *D. univalve*, the inner labium is considered to be lost from the comparison with the bilabial



Pl. 4. Petals of the Ranunculaceae III

1: *Dichocarpum pterigionocaudatum*, x30. 2, 3: *Dichocarpum dicarpon* (3: outside view), x30. 4: *Dichocarpum stoloniferum*, x40. 5: *Dichocarpum trachyspermum*, x40. 6: *Isopyrum tuberosum*, x25. 7: *Leptopyrum fumarioides*, x20. 8: *Paraquilegia grandiflora*, x20. 9: *Semiaquilegia adoxoides*, x20. 10: *Aquilegia flabellata*, x20.

petal of very similar species, *D. dicarpon*. Thus, the petal also becomes epeltate.

In *Isopyrum* and *Leptopyrum*, petals are peltate, and the limb becomes larger and tubular, and the stalk shorter, comparing with those of *Dichocarpum*. Lotsy (1911) showed that the petals of *Isopyrum anemonoidea* and of *Aquilegia* were intermediated by those of *Isopyrum grandiflorum* (= *Paraquilegia grandiflorum*) and *I. adoxoides* (= *Semiaquilegia adoxoides*).

In *Paraquilegia*, petals become epeltate, flat and more or less concave or swollen near the base, and nearly sessile. Further in *Semiaquilegia* and *Aquilegia*, petals become larger, though still slightly shorter than sepals, saccate or spurred at the base, and sessile. The spur is extremely long in *Aquilegia longissima*, and it seems to be an adaptation for pollination by moth.

It is also notable that in both genera, the innermost members of stamens are transformed into scaly structures. In *Semiaquilegia*, the transitional forms from stamens to the structures are usually observed.

In Trib. Ranunculeae and Subfam. Isopyroideae, the petal is an important character to trace the course of the evolution.

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