# Taxonomic studies of the *Ranunculaceae*: retrospect and prospect

# Michio Tamura

#### Abstract

It is the classifications of the *Ranunculaceae* of De Candolle, Prantl and Langlet, which strongly influenced my work, that were reviewed here. My system is well congruent with molecular phylogeny. In future studies, the collections of southern materials are necessary, and there still remain works on the anatomy of achenes, etc.

#### Key Words

Anatomy of achenes - Deficiency of southern materials - molecular phylogeny - Ranunculaceae

I have been occupied in the studies of the *Ranunculaceae* for more than forty years. In 1995, I published the *Ranunculaceae* for the second edition of 'Die natürlichen Pflanzenfamilien'. In this opportunity, I would like to retrospect the previous works which have influenced my work, and also about what studies should be done to complete the work in the future.

This article is based on my invitation paper read at the beginning of the session of the IV International Congress for Plant Taxonomy, on 19th Sept. 1996, modified and amplified.

# 1. Previous works

In the history of the studies of the *Ranunculaceae*, there were three monumental works. The first is that of Augustin Pyrame De Candolle. The *Ranunculaceae* were first classified by De Candolle. In 1817, he considered the *Ranunculaceae* to be consisting of two groups, *Ranunculaceae vernae* including four tribes, *Clematideae*, *Anemoneae*, *Ranunculaee* and *Helleboreae*, and *Ranunculaceae supriae* including *Actaea*, *Xanthorhiza* and *Paeonia*. In 1824, he regarded *Ranunculaceae supriae* as a tribe and classified the *Ranunculaceae* into five tribes, i.e., four previous tribes and *Paeoniaceae* (Fig. 1). The tribe *Paeoniaceae* has ending not of a tribe but of a family. I suppose De Candolle was wondering if the group should be placed in the rank of a tribe of the *Ranunculaceae* or an independent family. Anyway, the family delimited by De Candolle had been considered to be one of the typical natural families for a long time.

The second is Prantl. He wrote about the phylogeny of the *Ranunculaceae* for the journal (1887) and it was the essential part of the first edition of 'Die natürlichen Pflanzenfamilien' (Fig. 2, 1888). De Candolle had used the outer morphological characters, but Prantl took up the inner morphological characters positively, and tried to make a phylogenetic system. He classified the family Trib. Clematideae Clematis, Naravelia

Trib. Anemoneae Thalictrum, Tetractis, Anemone, Hepatica, Hydrastis, Knowltonia, Adonis, Hamadryas

Trib. Ranunculeae Myosurus, Ceratocephalus, Ranunculus, Ficaria

Trib. Helleboreae Caltha, Trollius, Eranthis, Helleborus, Coptis, Isopyrum, Enemion, Garidella, Nigella, Aquilegia, Delphinium, Aconitum

Trib. Paeoniaceae Actaea, Zanthorhiza, Paeonia

Fig. 1. System of Ranunculaceae proposed by A. P. De Candolle (1824).

into 3 tribes, Paeonieae, Helleboreae and Anemoneae.

His Paeonieae included 3 genera, Paeonia, Glaucidium and Hydrastis, which were thought improper as members of the Ranunculaceae by Prantl (1887). He considered that Paeonieae was the direct offspring of the ancestor from which Berberidaceae and Ranunculaceae were derived.

Prantl (1887, 1888) divided other genera into *Helleboreae* and *Anemoneae*. He considered in the family there are two ways in reduction of number of ovules. One is in *Helleboreae*, in which the carpel has three main bundles, that is, one dorsal bundle and two ventral bundles. Ovules are produced along both carpel margins and supplied with branches of both ventral bundles, and the carpel becomes follicle, as in *Caltha, Trollius, Helleborus, Eranthis, Nigella* and so on (Fig. 3:1). The final condition of this reduction way of carpel is in *Callianthemum*,

Trib. Paeonieae Glaucidium, Hydrastis, Paeonia

Trib. Helleboreae

Caltha, Trollius, Callianthemum, Helleborus, Eranthis, Nigella, Leptopyrum, Isopyrum, Coptis, Xanthorrhiza, Anemonopsis, Actaea, Aquilegia, Delphinium, Aconitum

Trib. Anemoneae

Anemone, Clematis, Myosurus, Oxygraphis, Trautvetteria, Ranunculus, Hamadryas, Adonis, Thalictrum

Fig. 2. System of Ranunculaceae proposed by Prantl (1888).

in which an ovule is produced on one carpel margin and supplied with a branch of one ventral bundle (Fig. 3:4). Thus, Prantl classified *Callianthemum* with a single ovule and forming achene into *Helleboreae* with many ovules and forming follicle.

The other way is in Anemoneae, in which the carpel bundle is divided into three, that is, one is a dorsal and two are ventral bundles. A fertile ovule is produced on the ventral or the basal centre of the carpel and supplied with a central branch of a ventral bundle, and the carpel becomes achene, as in Anemone, Clematis, Myosurus, Oxygraphis, Trautvetteria, Ranunculus, and so on. In these carpels, the attaching point of a fertile ovule more or less rises. The difference of the group of Anemone and that of Ranunculus is where the ovules occur. In Anemone the ridge is long (Fig. 3:2), in Ranunculus it is very short (Fig. 3:3). A total view of a carpel looks like a slipper, sometimes some reduced ovules are produced on both carpel margins, and the placentation becomes U-type. This idea of a placentation is quite similar to the peltate carpel of Troll (cf. 1939), or to U-type placentation of Leinfellner (cf. 1951). I think the origin of the peltation theory goes back to Prantl.

The third is Langlet. His paper published in 1932 greatly exerted influence on phylogenetic consideration of the *Ranunculaceae*. His work is one of the most successful examples of cytotaxonomy. He moved *Paeonia*, *Glaucidium* and *Hydrastis* from the *Ranunculaceae* to the *Berberidaceae* (1928) according to Prantl's suggestion (1887), and recognized two types of chromosomes in the *Ranunculaceae*, that is, long, generally bent or repeatedly curved R (*anunculus*)-type chromosomes (Fig. 4 :C) and generally simply curved, smaller T (*halictrum*)-type chromosomes (Fig. 5 :C). And the *Ranunculaceae* were divided into two groups, *Ranunculoideae* with R-type chromosomes and *Thalictroideae* with T-type chromosomes. Also he regarded the basic number of chromosomes as important, that is, the basic number is mostly 8, rarely 6 or 7 in R-type group, while it is 7 or 9 in T-type group (Fig. 6).

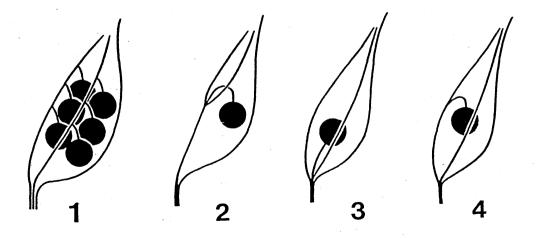


Fig. 3. Attachment and vascularization of ovules in carpel of Ranunculaceae.

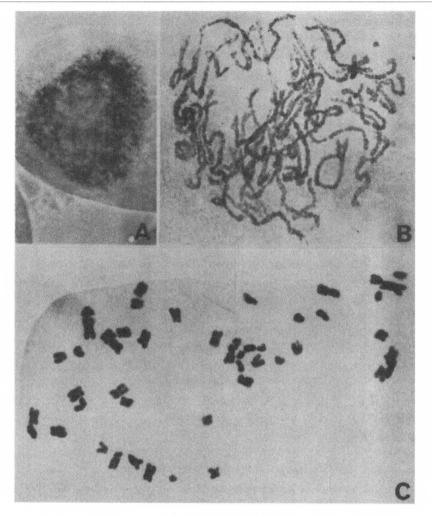


Fig. 4. Karyomorphology of *Ranunculus nipponicus* var. *major* (Okada & Tamura 1979).A. interphase nucleus. B. prophase chromosomes.C. metaphase chromosomes.

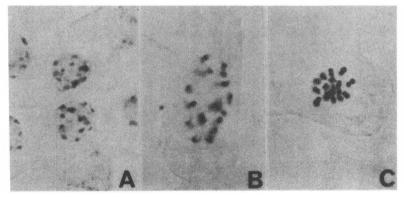


Fig. 5.
Karyomorphology of *Coptis ramosa*(Okada & Tamura 1979).
A. interphase nucleus.
B. prophase

chromosomes. C. metaphase

chromosomes.

Subfam. Thalictroideae Trib. Thalictreae Subtrib. Isopyrinae: Isopyrum, Leptopyrum, Aquilegia Subtrib. Thalictrinae: Thalictrum. Anemonella Trib. Coptideae: Coptis, Xanthorrhiza Subfam. Ranunculoideae Trib. Helleboreae Subtrib. Helleborinae: Helleborus. Eranthis Subtrib. Cimicifuginae: Anemonopsis, Cimicifuga, Actaea Trib. Ranunculeae: Myosurus, Trautvetteria, Ranunculus Trib. Anemoneae Subtrib. Anemoninae: Anemone, Knowltonia Subtrib. Clematidinae: Clematis Trib. Trollieae Subtrib. Trolliinae: Caltha, Trollius Subtrib. Delphiniinae: Delphinium, Aconitum Trib. Adonieae: Callianthemum, Adonis

Trib. Nigelleae: Nigella, Komaroffia

Fig. 6. System of Ranunculaceae proposed by Langlet (1932).

Langlet (1932) considered that, in both groups, *Ranunculoideae* and *Thalictroideae*, reduction of number of ovules took place, and the fruits became from follicle to achene. In *Thalictroideae*, *Thalictreae* with achene were derived from *Isopyrinae* with follicle, and *Xanthorhiza* from *Coptis*. In *Ranunculoideae*, *Adonieae* (must be *Adonideae*) with achene from *Trollieae* with follicle, and *Ranuunculeae* and *Anemoneae* with achene from *Helleboreae* with follicle. Prantl (1887) did not notice the close similarity between *Callianthemum* and *Adonis*. But Langlet (1932) noticed both genera quite resemble each other not only in carpel morphology, but also in a bitegmic ovule, different from other genera with achene which have an unitegumic ovule, except *Thalictrum*.

# 2. The systems proposed by me

To make the phylogenetic system of the *Ranunculaceae*, the treatment of *Paeonia*, *Glaucidium*, *Hydrastis*, *Circaeaster* and *Kingdonia* must be problematic. In my first preliminary system (1962, Fig. 7), I excluded *Paeonia* and included *Glaucidium* and *Hydrastis*, and left *Circaeaster* and *Kingdonia* out of consideration. And then (1966-1968, 1995), I excluded *Paeonia*, *Glaucidium* and *Circaeaster* from, and included *Kingdonia* and *Hydrastis* in the family.

Among them, *Paeonia* is decidedly not a member of the *Ranunculaceae*. It has no clear relationship not only to the *Ranunculaceae* but also to any other family of angiosperms. *Paeonia* has many particular features, and especially its embryogenesis is quite unique and it is unknown in any other angiosperms except *Paeonia* (Yakovlev & Yoffe 1957, Cave, & al. 1961, Carniel 1967).

Recently Chase & al. (1993) thought about relationship of *Paeonia* to *Saxifragaceae* in DNA arrangement. But the speciality of embryogenesis can not be explained in this case. In *Paeonia*, placentae have complicated vascular system, ovules have ariles, though they are not well developed in fruit, integuments are very thick, the outer integument is 14 to 20 and the inner about 4 cell layers thick, some of ovules do not mature to seeds, and disk is present around the ovule. In these features the ancient characters seem to remain. I think *Paeonia* is in quite isolated position in the angiosperms.

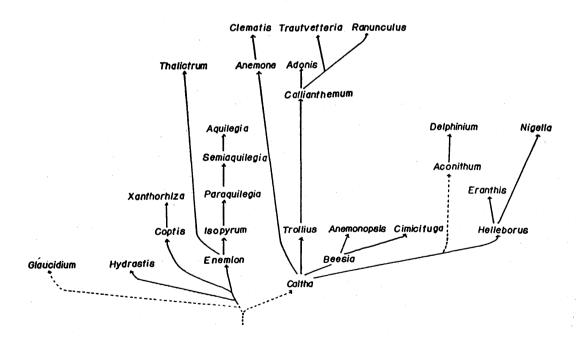


Fig. 7. Preliminary arrangement of genera of *Ranunculaceae* proposed by Tamura (1962).

I think *Glaucidium* is not a member of the *Ranunculaceae*, and created *Glaucidiaceae* for it (Tamura 1972). In *Glaucidium*, very many stamens initiated centrifugally, in contrast, in the *Ranunculaceae*, stamen initiation is centripetal. Integuments are also very thick, the outer integument is 6 to 15 and the inner about 5 cell layers thick, in the *Ranunculaceae* usually integuments are 6 to 8 cell layers thick, either single or double (Kumazawa 1938).

Tobe & Keating (1985) emphasized the peculiarity of *Hydrastis* and supported its separation as a monotypic family, *Hydrastidaceae*. Most of these features, however, are not unusual in the *Ranunculaceae*. According to them, in *Hydrastis*, micropyle is formed by both integuments. Kumazawa (1938) showed that in *Aquilegia* the outer integument is usually longer than the inner and this character is not stable. In *Hydrastis*, scalariform vessel perforations are found, but in the *Ranunculaceae*, they are sometimes observed as reported by Avita & Inamdar (1981). In *Asteropyrum*, all vessels are typically scalariform with over 30 bars (Chen & Li 1990), whereas in *Hydrastis*, they are at most three to 10 bars. Accordingly, although *Hydrastis* has some peculiar features, the genus does not necessarily need to be separated from the *Ranunculaceae*.

*Circaeaster* and *Kingdonia* have dichotomous venation, and their positions in *Ranunculaceae* were often discussed. But the embryological characters of the former are quite different from *Kingdonia* and also from genera of the *Ranunculaceae* (Junell 1931). In contrast, *Kingdonia* is not different from the family in many characters, except the helobial endosperm formation (Mu 1983). I think that *Circaeaster* is different from the *Ranunculaceae* in many characters, but *Kingdonia* can be retained in the family (Kosuge & al. 1989, Tamura & al. 1995).

Molecular phylogeny is referred to the relationships between *Glaucidium* and *Hydrastis* and between *Kingdonia* and *Circaeaster* (cf. Hoot & Crane 1995). For the moment, I don't feel like changing of these points according to molecular results.

The other genera are divided by chromosome size according to Langlet (1932). That is, Subfam. Helleboroideae and Ranunculoideae are in R-type group, and Subfam. Isopyroideae, Thalictroideae and Hydrastidoideae are in T-type group. But the distinction of both groups by chromosome size is sometimes obscure. For example, in Ranunculus nipponicus (Fig. 4:C), R. sceleratus, etc., chromosomes are short and ranging in T-type. But both chromosome types can be distinguished by the stainability of prophase chromosomes and interphase nuclei (Kurita 1960, Okada & Tamura 1979). In T-type genera, in the interphase nuclei, several deeply stained bodies can clearly be observed in a dilutely stained matrix (Fig. 5:A). The prophase chromosomes are stained deeply in the proximal part of the armes and the boundary between the stained and unstained parts is distinct (Fig. 5:B). In R-Type genera, in the interphase nuclei, only few dark stained bodies are obscurely observed in a well stained matrix (Fig. 4:A). The prophase chromosomes are stained throughout their length (Okada & Tamura 1979, Fig. 4.B). I think the distinction between R-type group and T-type group seems to be quite natural (Fig. 8).

The distinction is supported by the phytochemical studies. That is, in T-type genera, benzylisoquinoline-type alkaloids are present, and in R-type genera, they

are little or not present.

An exception to this is *Myosurus*, which usually is considered to be closely related to *Ranunculus*. According to Kurita (1963), *Myosurus minimus* has comparatively small metaphase chromosomes, interphase nuclei of T-type, and prophase chromosomes of R-type. It is necessary to confirm these observations in other species of *Myosurus*.

Asteropyrum has considerably large chromosomes and the basic number is 8. According to Yang & al. (1993) chromosomes of Asteropyrum belong to R-type, but according to Zhang (1982), they are of T-type. This genus contains benzylisoquinoline alkaloids (Hsiao 1980, Zhu & Hsiao 1991). Thus, Asteropyrum may be said to belong to T-type group from a phytochemical point of view.

The examples of *Myosurus* and *Asteropyrum* lead to doubt about the subdivision of the family into R-typ group and T-type group. I believe, however, that this karyological character is still of prime importance in the classification of the *Ranunculaceae*.

#### 3. Anatomy of achenes

Trib. Ranunculeae contains 16 genera, and in this tribe, Subtrib. Ranunculinae contains 14 genera. It is desirable that this subtribe is subdivided, though I didn't do it in my system (1955). I think in this case, the good idea is in Prantl. Prantl (1887) distinguished his Ranunculus with the hard layer in the pericarp from his Oxygraphis, Myosurus and Trautvetteria without the hard layer.

That is, in his *Ranunculus*, the pericarp has several layers of thickly walled, sclerenchymatous cells. If achenes are cut horizontally, sclerenchymatous cells are in cross-section, and inner epidermal cells are long or oblique (Fig. 9 :A,B,C). While, in his *Oxygraphis*, the pericarp has not sclerenchymatous cell layers, but an inner epidermis is distinct and often has more or less thickly walled cells. If achenes are cut horizontally, inner epidermal cells are in cross-section (Fig. 9:D).

The group of *Ranunculus* contains *Aphanostemma*, *Ceratocephala* and *Laccopetalum*. In *Ranunculus*, pericarps are diverse. Usual members have sclerenchymatous cell layers and a fibrous inner epidermis in pericarp. But in *Ranunculus pallasii*, there are no sclerenchymatous cell layers in pericarp. It may be due to the water life of this species. In *Ranunculus ficaria* (Fig. 10:B), the pericarp has sclerenchymatous cell layers, but no fibrous inner epidermis, as already Prantl (1887) wrote. In *Hamadryas argentea*, there are sclerenchymatous cells, but no fibrous inner epidermal cells (Fig. 10:D), similar to *Ranunculus ficaria*.

Subfam. I. Helleboroideae Trib. 1. Helleboreae Subtrib. a. Calthinae: Caltha, Calathodes, Trollius, Megaleranthis Subtrib. b. Beesiinae: Beesia Subtrib. c. Helleborinae: Helleborus, Eranthis Trib. 2. Cimicifugeae: Anemonopsis, Souliea, Cimicifuga, Actaea Trib. 3. Nigelleae: Komaroffia, Nigella, Garidella Trib. 4. Delphinieae: Aconitum, Delphinium, Consolida Subfam. II. Ranunculoideae Trib. 5. Adonideae: Callianthemum, Adonis Trib. 6. Anemoneae Subtrib. a. Kingdoniinae: Kingdonia Subtrib. b. Anemoninae: Anemone, Hepatica, Metanemone, Barneoudia, Oreithales, Knowltonia, Pulsatilla Subtrib. c. Clematidinae: Archiclematis, Clematis, Naravelia Trib. 7. Ranunculeae Subtrib. a. Trautvetteriinae: Trautvetteria Subtrib. b. Myosurinae: Myosurus Subtrib. c. Ranunculinae: Kumlienia, Arcteranthis, Halerpestes, Oxygraphis, Peltocalathos, Callianthemoides, Cyrtorhyncha, Paroxygraphis, Hamadryas, Aphanostemma, Ranunculus, Ceratocephala, Krapfia, Laccopetalum Subfam. III. Isopyroideae Trib. 8. Coptideae Subtrib. a. Asteropyrinae: Asteropyrum Subtrib. b. Coptidinae: Coptis, Xanthorhiza Trib. 9. Isopyreae Subtrib. a. Isopyrinae: Enemion, Isopyrum, Leptopyrum, Paraquilegia Subtrib. b. Aquilegiinae: Semiaquilegia, Urophysa, Aquilegia Subtrib. c. Dichocarpinae: Dichocarpum Subfam. IV. Thalictroideae Trib. 10. Thalictreae: Thalictrum Subfam. V. Hydrastidoideae Trib. 11. Hydrastideae: Hydrastis

Fig. 8. System of Ranunculaceae proposed by Tamura (1995).

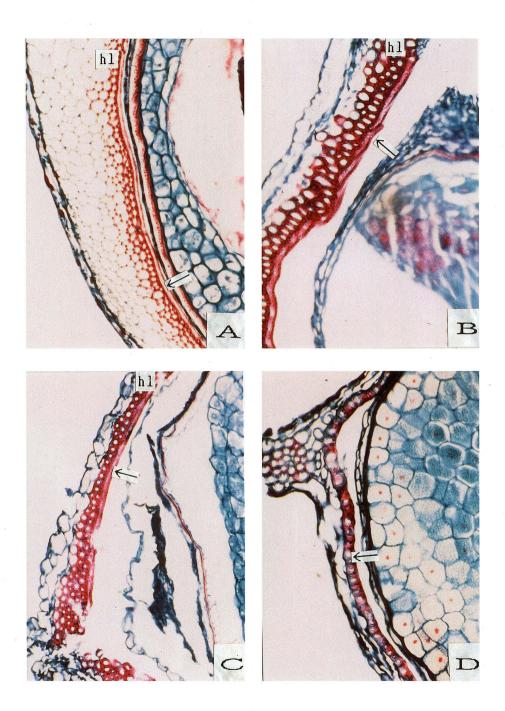


Fig. 9. Anatomy of Achenes (I).
A. Ranunculus silerifolius. Preserved in KYO. B. Ranunculus pulchellus. Preserved in KYO. C. Ranunculus glacialis. Preserved in KYO. D. Oxygraphis glacialis. Preserved in KYO. hl: layer of sclerenchymatous cells. Arrows: inner epidermis.

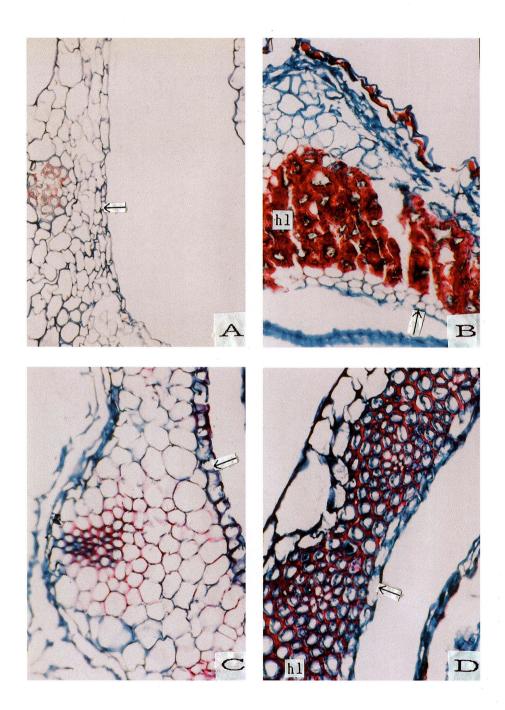


Fig. 10. Anatomy of achenes (II).
A. Peltocalathos baurii. Preserved in B. B. Ranunculus uniflorus. Preserved in P. C. Ranunculus ficaria. Preserved in KYO.
D. Hamadryas argentea. Preserved in P.
hl: layer of sclerenchymatous cells. Arrows: inner epidermis. The group of Oxygraphis contains Oxygraphis, Arcteranthis, Halerpestes and perhaps Paroxygraphis. I described two genera of this subtribe, Pelthocalathos and Callianthemoides. They have one inner epidermis, cells of which are sometimes thickly walled, and belong to the group of Oxygraphis (Fig. 10:A). Ranunculus lancisepalus and R. uniflorus (Fig. 10:B) are shown to be in Oxygraphis-type. I think achenes of this tribe must be more studied anatomically.

The pericarps of the family were studied by Wiegand (1894), and his paper must be studied in details under present eyes. Emura (1970) studied on the achenes of *Thalictrum* anatomically and made the new system, but her studies were restricted to mostly Eastern Asiatic species. Anatomical studies are necessary for the phylogenetical classification not only of *Thalictrum* and *Ranunculeae* but also of the whole family.

#### 4. Deficiency of southern materials

The Ranunculaceae are generally well studied and there are many informations on many species. But our knowledge of the family is mostly on the northern taxa. I have felt the deficiency of our knowledge on the southern taxa. But genera or infrageneric taxa are not so rare in the southern hemisphere, for example, Barneoudia, Oreithales, Knowltonia, Pelthocalathos, Callianthemoides, Hamadrya s, Aphanostemma, Krapfia, Laccopetalum, Caltha sect. Psychlophila, Anemone subgen. Rigida, A. subgen. Hepaticifolia, A. subgen. Pulsatilloides, Clematis sect. Pseudanemone, Ranunculus sect. Casalea, R. sect. Pseudadonis, etc. are all southern taxa. Except some taxa, species of these taxa are distributed in rather narrow, restricted areas. This fact shows that the outlines of distribution of these taxa in the southern hemisphere are established in rather old age.

For the moment, in materials of the molecular phylogeny, the southern materials are still very few, but Hoot (I995b) published her molecular studies of Anemone and the related genera including three southern species, that is, Anemone crassifolia in Tasmania, A. caffra and Knowltonia vesicatoria in South Africa. Accordiing to her result, the group with basic chromosome number b=8 and the group with basic chromosome number b=7 are separated clearly from each other, and the southern species including Knowltonia are subsumed within Anemone with b=8.

The materials of southern species must be collected and studied more accurately. The phylogenetic system of the *Ranunculaceae* will be finally established by reorganization of present system with enough data of southern materials.

# 5. Congruity with molecular phylogeny

Recently, molecular phylogeny becomes more popular and common, and reports on the *Ranunculaceae* have already been published. The molecular results are highly congruent with the distinction between the group of R-type genera and that of T-type genera. For example, Hoot (1995a) analyzed the chloroplast genes *atpB* and *rbcL*, and nuclear ribosomal 18Snr DNA for 23 genera and two outgroup taxa, *Glaucidium* and *Hydrasts*. The combination of these three data sets showed that R-type chromosome groups monophyletic with 87% bootstrap support, and T-type chromosome group is paraphyletic. That is, *Coptis* and *Xanthorhiza* form a monophyletic group with 100% bootstrap support, and *Thalictrum, Isopyrum, Aquilegia* and *Semiaquilegia* form another monophyletic group with 100% bootstrap support. The close relationship between *Adonis* and *Trollius* was also strongly supported by her results.

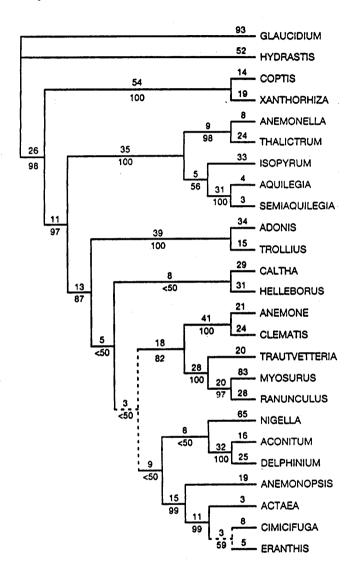


Fig. 11. Phylogeny of the Ranunculaceae based on a combination of the chloroplast genes atpB and rbcL, and nuclear ribosomal 18S nr DNA sequance data for 23 genera (Hoot 1995a). One of the four most parsimonious trees. Dotted lines indicate branches which collapsed in the strict consensus tree. Tree length = 824 steps, CI excluding autapomorphies = 0.55, RI = 0.62. Numerals above branches indicate the number of nucleotide changes. Numerals below indicate the percentage of times that the branches was recovered in 1000 bootstrap replications. Han (1955) also studied the molecular phylogeny of tha *Ranunculaceae*, and analized 26Sr DNA. She recognized R-type group as a monophyletic, and T-type group not as monophyletic, just like Hoot (1995a), and the *Ranunculaceae* is suggested as subfamilial classification, that is, *Hydrastidoideae* including *Hydrastis, Coptidoideae* including *Xanthorhiza* and *Coptis, Thalictroideae* including all other genera with T-type chromosomes, and *Ranunculoideae* including all Rtype genera. Her results also supported that *Trollius* and *Adonis* are also very near to each other. Even if other genes are analized or to other DNA methods are used, the results were almost the same (cf. Kosuge & al. 1995). Thus, molecular phylogeny is highly congruent with karyological characters, but they are not with the orthodox morphological characters, just as fruits are folliclar or achenial, carpels are multiovular or uniovular, etc. The results from Langlet (1932) and those of molecular phylogeny suggest that karyological characters are the first class important and carpel and fruit characters are less.

#### 6. Conclusion

I think that, in order to clear the phylogenetic relationship of the family, enough materials from the southern hemisphere must be necessary.

Further, I would emphasize that the results of the molecular phylogeny show only relationship of the taxa, but the results of taxonomic studies include everything on taxa. The results of molecular phylogeny are important, but at the same time, accumulations of taxonomic studies on morphology, embryogeny, cytology, phytochemistry, phytogeography, and so on, are also necessary.

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The materials of achenes were preserved in the herbarium of Kyoto University (KYO), Muséum Nationale d'Histoire Naturelle (P) and Botanischer Garten u. Botanisches Museum Berlin-Dahlem (B).

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#### 摘 要

私はこれまで50年にわたってキンポウゲ科の分類研究にたずさわってきた。1995年に植物 分科提要のキンポウゲ科を出版したが、この機会に、キンポウゲ科の諸分類のうち、私の分 類にもっとも強く影響した人の業績を振り返り、また、将来、どのように展開されるべきか を議論したい。

キンポウゲ科の分類において、初めてこの科を分類した De Candolle, 系統学的発想に 基ずいて分類した Prantl, 核型を重要な形質として取り入れた Langlet の3名の業績は歴 史的である。私は余り着目されていなかった Langlet の業績に着目し、種々の核型を共同 研究者と発表し、多くの矛盾点を解明した。その間を通じて、南半球の材料に乏しく、また、 多くの古いと思われる形質が南半球の植物にあり、これからの分類学は南半球の種をいかに 集めるかが中心になると思った。とくに、痩果の解剖のような古典的な事実すらも南半球の 種ではがよく知られていないことも、際だって強く受けた印象である。

最近、DNA の塩基配列の研究により植物種間の類縁が議論されるようになったが、この 分子分類学的結果は染色体の分類とよく一致する。今後、この方面の研究は進歩するであろ うが、DNA の研究は種間の系統的関係のみを問題とするが、分類学的研究は分類群の全て の情報を網羅する。DNA 分類学が如何に発達しても、それについても種々と問題点もあり、 分類学にとって代れるものでは決してありえない。