

- Takhtajan, A.L., Meyer N., Kosenko, R., Kosenko, V.N. 1985. Pollen morphology and classification in Rafflesiaceae s.l. Bot. Žurn. (Moscow and Leningrad) 70: 153–162.
- Vattimo, I. de. 1971. Contribuição ao conhecimento da tribo Apodanthea R. Br., Parte I. Conspecto das espécies (Rafflesiaceae). Rodriguésia 26: 37–62.
- Watanabe, K. 1936. Morphologisch-biologische Studien über die Gattung *Mitrastemon* IV. J. Jpn. Bot. 12: 848–858.
- Watanabe, K. 1937. Morphologisch-biologische Studien über die Gattung *Mitrastemon* VII. J. Jpn. Bot. 13: 154–162.
- Winkler, H. 1927. Über eine *Rafflesia* auf Zentral Borneo. Planta 4: 1–97.

Ranunculaceae

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Ranunculaceae Juss., Gen. Pl.: 231 (1789), incl. Helleboraceae Loisel. (1819), Hydrastidaceae Lemesle (1948) and Kingdoniaceae Airy Shaw (1965).

Perennial herbs, often with more or less developed rhizome, sometimes annual or biennial herbs, half-shrubs or lianae. Roots adventitious, sometimes tap root developed. Leaves simple or compound, usually petiolate, exstipulate, rarely stipulate; blades cordate, sometimes truncate or cuneate at the base, variously divided, sometimes undivided, incised, dentate, sometimes entire; petioles mostly sheathy at the base. Inflorescence usually definite, sometimes single-flowered, rarely infinite. Flowers mostly moderately large, bisexual, sometimes unisexual, actinomorphic, sometimes zygomorphic, exclusively hypogynous, principally entomophilous. Sepals 3–6, or more, free, petaloid, sometimes sepaloid, imbricate, sometimes valvate, deciduous, sometimes caducous or persistent. Petals 1–13, free, usually secreting nectar, or absent. Stamens several to numerous, free, centripetally initiated. Carpels numerous to single, free, sometimes connate to various degree. Ovules numerous to single, anatropous, sometimes hemitropous, bitegmic or unitegmic. Fruits aggregated, sometimes simple, follicular, achenial, rarely baccate, sometimes capsulate. Seeds numerous to one in a carpel; endosperm copious; embryo often undifferentiated when shed. Cotyledons usually two, their petioles usually fused downward to various degree, rarely single.

VEGETATIVE MORPHOLOGY AND ANATOMY. In many of the annual and biennial species, the primary root develops into a tap root. In *Ceratocephala*, *Myosurus* etc., the hypocotyl is persistent and adventitious roots are produced at the transition between the hypocotyl and the primary root. In many of the perennial species with a horizontal sympodial rhizome, the hypocotyl produces adventitious roots, which replace the primary root system sooner or later. A horizontal monopodial rhizome is found in *Hepatica*; this type is rare in the family. In many of the species with an erect rhizome, as in *Aquilegia*, the primary root and also often the hypocotyl develop into the root system. In *Ranunculus* and its allies, adventitious roots are produced from the cotyledonary node, and both primary root and hypocotyl wither sooner or later after germi-

nation, either in annual species or in perennial species.

The phyllotaxis changes from the seedling to the adult plant in various ways, but basically from distichy, through spiro-distichy, to dispersion with proper divergence and finally to opposite or whorled. In some cases, distichy continues further, and in the extreme case, as in *Ranunculus laterifolius*, all leaves are arranged in distichy. In other cases, the third leaf slips out of the opposite position of the second with a slight angle, and the fourth leaf is opposite to the third or slips out of the opposite position of it (Haccius 1950). Decussate phyllotaxis is one of the most important characteristics of *Clematis*, but it can be explained as a case in which any of the stages of the complete series of phyllotactic change is suppressed (Tamura 1963, 1980).

Although leaves are very diverse, they show uniformity in their ontogenetic development. Whether a blade is lobate or divided into petiolulate leaflets depends on the degree of the additional growth (Schrödinger 1914), and most leaves of the family are similar to each other in the early stage of development (Kürbs 1973). That is, a marginal meristem is at first divided into three portions except in undivided leaves, as in *Caltha*. In ternate leaves, the three fractions develop nearly simultaneously. When the ternation occurs twice or more, the leaves are ternate in higher order. If the middle fraction remains without any more division, whereas the lateral ones develop further in a basitonic way, a pedate type is formed as typically found in *Helleborus niger*. If the middle fraction after a further ternation remains stunted and the lateral fractions develop further, a ternate-pedate type, the commonest in the family, originates. If the middle fraction further divided in acropetal succession and lateral fractions are inhibited, a pinnate type as found in *Adonis*, *Clematis*, *Nigella* etc. is formed.

In the vascular bundles of the family, the xylem partly surrounds the phloem and presents a so-called V-shaped appearance. Sometimes the xylem is strongly concave with elongate arms and, in the extreme case, the bundle becomes concentric (Tamura 1962). In cross-section of the stem, the bundles are arranged not in a perfect circle but more or less irregularly. In the extreme case, the medullary bundles occur as typically found in *Anemone vitifolia* and its allies. The activity of cambium is generally weak and stems are prevalingly herbaceous. In *Clematis* the secondary xylems are produced in the fascicular regions. The secondary rays are narrow and do not appear from the beginning of secondary xylem formation but only in the lately produced parts accompanied with lateral expansion of the fascicular regions (Kumazawa 1935). The woody stem is considered as secondary at least in this family.

Based on the arrangement of vascular bundles in the proper part of petiole, Tamura (1962) classified the petioles of the family into four types. There are 3, 5 or more leaf traces. Except for reduced or scaly leaves, unilacunar leaves are found in *Kingdonia*. Its leaves have open dichotomous venation and 2 or 4 leaf traces; this may be the primitive condition. The leaves of *Coptis japonica* are mostly pentalacunar with 6 or 8 leaf traces, and in the petiole the middle bundle and also the lateral bundles are double. The leaves of *Coptis* are considered in the process of midrib formation from the open dichotomous venation (Tamura 1981).

INFLORESCENCE. The inflorescence is often not sharply delimited from the branch system with foliage leaves, and such a condition is considered to be in the initial stage. Inflorescences are fundamentally definite. When the number of flowers in the racemiform inflorescence increases, the opening of flowers changes from simultaneous to sequential and the inflorescence from definite to infinite, as found in *Aconitum* and *Cimicifuga*. In many species of *Clematis*, the axillary buds develop into shoots, and after the vegetative growth they produce axillary cymes. In *C.* sect. *Aragene*, the shoot sprouting from an axillary bud produces a terminal flower and one or a few pairs of leaves or bracts. In *C.* sects. *Bebaeanthera* and *Cheirosopsis*, flowers arise from axils of winter-bud scales or of a few lowermost leaves of a new shoot. The internodes of the lowermost part of the shoot are contracted, so that the flowers and the new leaves appear to be fasciculate at the leaf-axils of the old shoot.

FLORAL MORPHOLOGY AND ANATOMY. The flowers are monochlamydeous with sepals or dichlamydeous with sepals and petals. Prantl (1887) called the petals of the family honey-leaves ("Honigblätter"), because they usually secrete nectar, and those without nectar secretion staminodes, but it is convenient to call all organs between sepals and stamens petals, whether nectar secreting or not. Petals are considered to be derived from stamens, and monochlamydeous flowers are regarded as primitive (Tamura 1965). Schrödinger (1909) recognised two types of petals, cup-shaped ("becherig") and flat ("flächig"). In the former, the whole petal blade forms a nectary-cup, while in the latter the blade is flat, the covering of nectary never extends to the margins of the blade and distinct rims are present on both sides. Generally cup-shaped petals are peltate and flat petals are epeltate, though these features are not always combined with each other. The petals of *Ranunculus* have a scale-like or pocket-like structure covering the nectary and are classified in the flat type. Leinfellner (1958) showed various types in *R. pallasii* which can be arranged in a

continuous line from the peltate petal with tubular base to the flat petal with a free adaxial scale.

Peltate petals often become epeltate by the reduction of the adaxial wall as found in *Coptis*, *Dichocarpum*, *Aconitum* etc. (Schrödinger 1909, Tamura 1965; Kosuge and Tamura 1988; etc.). As Hiepko (1965) stated, peltation is combined with nectar secretion and it becomes obscure secondarily by the loss of the secretory function. Thus, the petals in this family are considered to be originally peltate; however their early development shows no sign of the peltate nature. They are initiated as hemispherical primordia like a stamen. A primordium becomes flat and depressed and then an adaxial ridge arises at the lower edge of the depression, except in the nectarless petal (Kosuge and Tamura 1989).

The multiovular carpel usually has one dorsal and two ventral bundles. The ovules are produced from both lateral margins of the carpel and supplied with branches of both ventral bundles. The uniovular carpel has a single trace. A single fertile ovule is ascending or pendulous from the adaxial ridge or wall of the carpel, and in many cases supplied with a middle division of a ventral bundle. The multiovular carpels usually become follicles and the uniovular carpels become achenes. In *Callianthemum* and *Adonis*, though the carpels become achenes, a fertile ovule is produced from the carpel margin and supplied with the ovular trace branched from one of the ventral bundles like multiovular carpels. The uniovular carpel is considered to be derived from the multiovular one by reduction of the number of ovules and the fusion of carpellar traces (Smith 1928; Eames 1931; Kumazawa 1938; etc.).

The ranunculaceous carpel has been interpreted as a peltate structure (Troll 1932; Rohweder 1967). Schaeppi and Frank (1962) tried to explain the carpel of the family from the standpoint of U-type placentation. Van Heel (1981, 1983) showed that in *Clematis*, *Ranunculus*, *Consolida* etc., a circular or convex meristem develops into an oblique cup-shaped primordium and the terminal mouth of a cup becomes the lateral cleft of the carpel by unequal growth. In *Aquilegia*, *Delphinium* etc., the inside region is not or only faintly demarcated from the floral apex, and the primordium develops into a horseshoe-shaped wall. The uniovular carpels tend to show a stronger cup-shaped development, while in the multiovular carpels, except a terminal carpel as in *Consolida*, by the extreme dominant growth of the outside margin later on, the actual cup-shaped development is no longer traceable.

EMBRYOLOGY. The anther is tetrasporangiate, the tapetum is usually single-layered and pollen grains are usually three-celled. The ovules are prevailingly

anatropous, but hemitropous in Ranunculaceae, except *Myosurus*, tenuinucellate or crassinucellate. They are bitegmic in the genera with multiovular carpels and in the primitive condition, except *Helleborus* and *Leptopyrum*, and unitegmic in the genera with uniovular carpels, except *Adonis*, *Callianthemum* and *Thalictrum* (Prantl 1887; Kumazawa 1938). The embryo sac follows mostly the monosporic, 8-nucleate Polygonum type. *Adonis* has the bisporic Allium type as far as examined (Bhandari 1966). Both Polygonum- and Allium types are found in *Callianthemum* (Bhandari and Vijayaraghavan 1970), *Ceratocephalus* (Bhandari and Asnani 1968) and *Trollius* (Bhandari and Kapil 1964). In *Thalictrum*, a tetrasporic Adoxa type was reported (Picci 1969) besides the Polygonum type. It is a well-known fact that in *Adonis*, *Anemone* and *Clematis*, sterile rudimentary ovules are present besides a fertile one. In the species of *Anemone* and *Clematis* which have a monosporic Polygonum type embryo sac in a fertile ovule, bi- or tetrasporic types are found in the sterile ones. In the sterile ovules of *Anemone vitifolia*, all mono-, bi- and tetrasporic types were observed (Bhandari 1965). In these cases, the bi- or tetrasporic types are considered to be derived from the original monosporic Polygonum type by reduction.

The embryo sac generally has well-developed antipoda. The antipodal cells are generally persistent and often have increased their volume (Huss 1906, etc.), except, e. g. *Kingdonia* (Mu 1984). The DNA volume is also increased; in *Aconitum* it reaches the level of 64–128-ploidy (Tschermak-Woess 1956). The antipodal nuclei and the antipodal cells are also divided, and in *Trautvetteria* the number of antipodal cells reach five to nine or more (Huss 1906).

Endosperm is copious and of the nuclear type, but helobial in *Kingdonia* (Mu 1984). Embryogenesis is mostly of the Onagrad type, but sometimes of the Solanad type, rarely of the Caryophyllad type.

Although in *Aquilegia*, *Consolida*, *Nigella*, some *Ranunculus* etc. the embryo in the seeds is well developed, in most species of the family the embryo develops slowly and often does not complete growth and differentiation by the time of shedding of the seeds. In the extreme case, as found in *Anemone flaccida*, the fertilised egg is not divided yet at the time of shedding (Tamura and Mizumoto 1972).

There is a remarkable tendency to form a cotyledonary tube, and in most species the cotyledonary petioles are fused at the base to various extent. Sometimes the fusion reaches up to the base of the blade as in *Adonis* sect. *Consiligo*, *Anemone* sect. *Omalocarpus*, *Eranthis* sect. *Eranthis* etc. In *Anemone flaccida*, *A. apennina*, *Eranthis pinnatifida*, *Ranunculus ficaria*, *R. glacialis* etc., there is a single cotyledon. In the embryo of *Eranthis pinnatifida*, the cotyledon oc-



cupies a terminal position and the growing point is situated in the lateral notch. In *Anemone flaccida*, the growing point is terminal and the single cotyledon lateral, and their relative position is not altered during later development (Tamura and Mizumoto 1974).

KARYOLOGY. Langlet (1932) recognised two types of chromosomes in the Ranunculaceae, i.e. the R(anunculus) type with long chromosomes generally winding or curved several times, and the T(halictrum) type with small chromosomes generally simply curved. In the R-type group the chromosome size varies remarkably. Especially in *Ranunculus* the chromosome size of *R. nipponicus* and *R. sceleratus* are not so different from those of *Aquilegia*, *Coptis* and *Dichocarpum* in the T-type group. Apart from chromosome size, however, both karyological types can be distinguished by stainability and distribution pattern of chromatin in the interphase nuclei and prophase chromosomes (Kurita 1960; Okada and Tamura 1979). The only exception known at present is *Myosurus*, which has the combined features of R-type and T-type (Kurita 1963). Accordingly, both chromosome types still stand as the character by which the principal subdivision of the family is defined.

In the group with R-type chromosomes, the basic number is mostly 8. It is 7 in *Komaroffia*, some species of *Anemone*, of *Ranunculus*, 6 in *Garidella*, *Nigella*, 9 in *Kingdonia*, rarely in *Delphinium* and *Consolida*, and 10 rarely in *Delphinium*. Considering the distribution and frequency of these numbers, 8 seems to be the primary number. In the group with T-type chromosomes, the basic number is mostly 7, but it is 6 in *Dichocarpum*, 8 in *Asteropyrum*, 9 in *Coptis*, *Xanthorhiza*, and 13 in *Hydrastis*. The number 7 seems to be primary. The numerical variation does not follow a continuous line, because the genera with the basic number 8 and 13 are monotypic, and the number 10, 11 and 12 are skipped. The differentiation of the basic number in the T-type group may have been established in an earlier stage of the evolution of the family than in the R-type group.



Fig. 123 A–Y. Ranunculaceae. **A, B** *Caltha palustris*. **A** Flowering shoot. **B** Fruit. **C** *Helleborus viridis*, petal, adaxial view. **D** *Eranthis hyemalis*, petal, adaxial and side view. **E** *Trollius europaeus*, petal, adaxial view. **F** *Actaea spicata*, petal, adaxial view. **G–I** *Aconitum anglicum*. **G** Flower with the lateral and lower sepals removed and the upper petal in longitudinal section to show petals in position. **H** Upper hooded sepal. **I** Lateral sepal. **K, L** *Anemone nemorosa*. **K** Fruit. **L** Achene. **M, N** *Clematis vitalba*. **M** Fruit. **N** Achene. **O–S** *Ranunculus acris*. **O** Flowering plant. **P** Petal, adaxial view. **Q** Stamen. **R** Fruit. **S** Achene. **T–W** *Aquilegia vulgaris*. **T** Part of inflorescence. **U** Flower, showing a stamen, two staminodes and gynoecium. **V** Sepal. **W** Petal. **X, Y** *Thalictrum alpinum*. **X** Flowering plant. **Y** Fruit. (S. Ross-Craig, Drawings of British Plants, Vol. 1)

Some genera of the family are stable karyologically, but some other genera, such as *Anemone*, *Ranunculus* and *Thalictrum*, show remarkable polyploid changes. Aneuploid changes in the intraspecific level are found in *Caltha*, *Ranunculus* etc., and in many cases they are caused by the occurrence of B-chromosomes.

In the group with R-type chromosomes, the 5V + 3J karyotype with 5 large, median or submedian chromosomes and 3 small, subterminal ones is the commonest. Goepfert (1974) regarded the karyotype consisting of 4 median or submedian and 4 subterminal chromosomes to represent, at least in *Ranunculus*, the least derived, ancestral pattern. In *Anemone* and its allies Baumberger (1971) regarded as basic the karyotype with 4 long, median chromosomes, 1 medium-sized, submedian chromosomes and 3 short, terminal or subterminal chromosomes. Lewitsky (1931) postulated symmetric chromosomes represented a condition more primordial than the strongly asymmetrical ones.

Anemone and *Ranunculus* have the two polyploid series based upon the basic chromosome number, $x = 8$ and $x = 7$. In *Anemone* the basic karyotype in the $x = 7$ series consists of 6 large V-type chromosomes and 1 small J-type chromosome. That in the $x = 8$ series consists of 5 large V-type chromosomes and three small J-type ones. The basic karyotype of $x = 8$ series can be explained to be derived from that of $x = 7$ series by the fusion of two J-type to form one V-type (Moffett 1932; Kurita 1958; Heimburger 1959; Baumberger 1971). In many species of *Ranunculus*, the basic karyotype in the $x = 7$ series consists of 3 V-type chromosomes and 4 J-type ones, and that in the $x = 8$ series consists of 4 V-type chromosomes and 4 J-type ones. The karyotype of $x = 7$ series can be explained to be derived from that of $x = 8$ series by the loss of one V-type in the set (Kurita 1958). In *Nigella*, with $x = 6$, the basic karyotype consists of 5 long V-type chromosomes and 1 short J-type chromosome. In *Komaroffia*, with $x = 7$, the karyotype consists of 4 V-type and 3 J-type chromosomes, and this karyotype may be explained by the loss of 1 V-type chromosomes of the 5V + 3J karyotype commonly found in Helleboroideae. The karyotype of *Nigella* may be explained by the fusion of 2 J-type chromosomes of *Komaroffia* to form a long V-type chromosome.

POLLEN MORPHOLOGY. Pollen grains in Ranunculaceae are tricolpate, pantocolpate or pantoporate. While pollen is invariably tricolpate in genera such as *Helleborus*, *Adonis*, *Eranthis* and *Trollius*, most genera comprise more than one basic type. Thus tricolpate and pantocolpate grains co-occur in different species of *Clematis*, for example, whereas pantocolpate and pantoporate grains characterise different species of

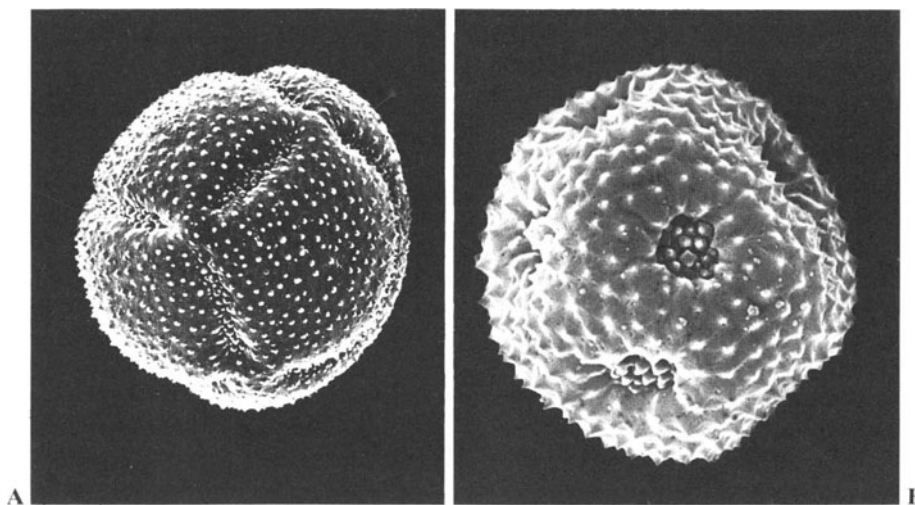


Fig. 124 A, B Ranunculaceae. Pollen. **A** *Pulsatilla alpina* subsp. *apiifolia*, $\times 1000$. **B** *Thalictrum kiusianum*, $\times 3200$. (Phot Palynological Laboratory, Swedish Museum of Natural History)

Ranunculus and *Anemone*; in *Coptis*, for example, all species have pantoporate grains (Erdtman 1952). The sculpture of the grains is remarkably uniform (Nowicke and Skvarla 1979): the only exceptions to a spinulose/perforate tectum are found in *Helleborus*, *Trollius*, *Hydrastis* and *Kingdonia*. The striate tectum of the two latter genera is particularly similar to that of *Circaea* and of various genera of the Berberidaceae, for example *Epimedium* and *Vancouveria* (Nowicke and Skvarla 1982). The exine is often underlain by an endexine of considerable thickness (main difference to Centrospermae), while the columellae are often large in size, sparsely distributed, or strongly reduced so that the tectum and the foot layer are scarcely separated. For a detailed palynological study of tribe Ranunculeae see Santisuk (1979).

POLLINATION SYSTEMS (by S. Vogel). Despite a rather primitive morphology, the Ranunculaceae exhibit an ample variety of pollination contrivances, experimenting with rearrangements and functional shifts of their floral phyllomes (Knuth 1898, 1904). Except for a number of habitually wind-pollinated species of *Thalictrum*, the family is zoophilic, usually provided with a coloured, showy perianth of up to 6 cm in diameter (species of *Clematis*, *Laccopetalum*, some *Ranunculus* etc.), often capable of thermonastic movements. In certain entomophilous species of *Thalictrum*, in *Actaea*, *Cimicifuga* and *Hydrastis* with caducous or poor perianths, coloured filaments take over the visual attraction. Prevailing floral colours are yellow (by carotinoid plasmochromes), bee-purple and white; blue, purple, and scarlet tints (by

anthocyanine chymochromes) are also frequent. In *Helleborus* the perigon is green, or may turn green postflorally. Natural polychromy occurs in *Ranunculus asiaticus* and, dependent on soil minerals, in *Anemone coronaria* (Horovitz 1976). UV-absorbing patterns have been found in the yellow corollas of *Caltha palustris* and *Ranunculus ficaria*, and there are nectar guides in *Nigella* and *Delphinium*. The petals of most yellow-flowered *Ranunculus* are unusually bright, due to a subepidermal light-reflecting tapeum (layer of starch-filled cells), which is also present in red-flowered *Adonis* species. Petals of *Ranunculus*, in addition, appear varnished ("butter cup") while *Adonis* has a silky brilliance.

Basically, the perianth is a perigon of corollinic sepals (tepals). In many genera of various subfamilies petals (of staminodial origin) contribute to attraction, being transformed either to nectariferous scales or to laminar petals proper with a basal nectary (so in *Ranunculus*, *Callianthemum*, *Garidella*, Hiepkö 1965; Daumann 1969), then replacing in their visual function the tepals, which are small and inconspicuous. In *Aquilegia* two corollinic pentamerous whorls of tepals and spurred petals alternate. In *Adonis*, some groups of *Ranunculus* (*R. asiaticus* and relatives in sect. *Ranunculastrum*; *R. sardous*) and *Actaea* the laminar petals lack a functional nectary. Usually the nectariferous petals are small, spatulate-ascioid, cup-shaped (so also in *Aphanostemma apiifolius*) or cucullate. The numerous small petals of *Pulsatilla* (Kratochwil 1988) and *Clematis* are epeltate and the filament bases of the fertile stamens may join in the secretory function. The nectaries, throughout foliar in Ranunculaceae, are epithelia with transcuticular secretion of sucrose-dominated nectar. *Laccopetalum* bears many nectar grooves on the distal part of each petal, and *Caltha* is exceptional in having trichomatic carpellary

nectaries, which form patches on either flank of each carpel. In *Eranthis* and *Cimicifuga* the nectar leaves are also responsible for scent production.

The polymeric androecium shows, with some exceptions, a centripetal sequence of anther dehiscence; the anthers are extrorse or introrse and longicidal, exposing the pollen on the reflexed thecal walls. By a consecutive outward movement the anthers just functional may be brought into nototribical (*Nigella*) or sternotribical contact with the visitors (*Pulsatilla*, *Aquilegia*). Styles, when receptive, move accordingly. Usually there are many styles (except *Actaea* and *Consolida* with only one). The stigmas are of the dry type, the compatibility system where known is gametophytic. Most Ranunculaceae are dichogamous; protogyny occurs in *Pulsatilla*, *Helleborus*, *Isopyrum* and some *Ranunculus*. *Nigella*, *Aquilegia*, *Delphinium*, parts of *Clematis* and *Anemone* are proterandric; *Clematis virginiana* and (Kaplan and Mulcahy 1971) many *Thalictrum* are dioecious, *Xanthorhiza* and others polygamic. Regular autogamy occurs in *Myosurus* and *Ranunculus* spp., apomixis in *Ranunculus auricomus* and *Thalictrum purpurascens*.

In the majority of genera, the perianth is regular, flat or bowl-shaped and thus also accessible for a variety of non-specialised insects (allophilic). In some genera, including *Nigella*, *Helleborus*, *Eranthis* and *Aquilegia*, the whorl of nectaries is arranged to form a perambulatory apparatus ("revolver blossom"). To probe them consecutively, the visitor moves around and thus intensifies anther and stigma contacts. Also all nectarless proper pollen flowers of Ranunculaceae are actinomorphic, shallow cups as in *Anemonopsis*, *Adonis*, *Knowltonia*, *Anemone* s. str., *Hepatica*, *Barneoudia*, some *Pulsatilla* and *Clematis*, or (finally) achlamydic staminal bunches as in *Cimicifuga* and *Thalictrum* spp., usually with yellow anthers, and "mess and soil-pollination" by bees. Mediterranean red-flowered *Ranunculus asiaticus* and *Anemone coronaria* having pollen flowers with black anthers, join in the "poppy guild", pollinated by beetles (*Amphicoma*, Dafni et al. 1990).

The closed perigon of some actinomorphic Ranunculaceae forms a globular (*Trollius europaeus*) or campanulate corolla (*Pulsatilla*, *Clematis* p.p.), more or less absconding the sexual organs and excluding non-specialised visitors (euphily). In *Clematis heracleifolia* even postgenital pseudo-syntepaly occurs. A kind of separate paracorolla is shaped by nectariferous petals in certain *Clematis* and in *Komaroffia*.

In Delphinieae, the only tribe with zygomorphic flowers, the most elaborate euphily evolved. Surrounded by a corollinic perigon, only two adaxial petals are nectariferous and coadapted to the adjacent median tepal by jointly forming a gullet or a labiate apparatus. The sternotribic sexual organs are con-

cealed and only exposed by the visitor's movements. In *Aconitum*, slender petals are with their nectary hidden inside the hooded tepal (some Asian spp. of *Aconitum* including *A. gymnandrum* and *A. rotundifolium* still have free nectaries not coadapted to the rather flat tepal). In *Delphinium* the nectariferous spurs of the two petals (in *Consolida* united) are enveloped by the median sepal's spur, while their frontal entrance forms a "separate mask blossom" amidst the perigon.

Most of the euphily Ranunculaceae are bee-pollinated, many Delphinieae and *Aquilegia* spp. typically bumblebee-pollinated. In both groups also adaptive radiations occurred towards hawkmoth and bird pollination. *Delphinium* achieved sphingophily (*D. leroyi*) and ornithophily (*D. marcoplectron*) in tropical Africa, and independently developed the bird flower syndrome in North America (*D. nudicaule*, *D. cardinale*). Sphingophily probably also occurs in Asian and North American species of *Delphinium*. *Aquilegia* evolved sphingophilous (e.g. *A. fragrans*) and phalenophilous species (*A. viridiflora*) in Asia, and in North America (Grant 1976) sphingophilous (e.g. *A. pubescens*) and several ornithophilous species. The bird syndrome is also found in *Clematis texensis* (North America) and the Andean *Ranunculus gusmani*. The floral features of *Xanthorhiza* point to sapromyiophily (probably fungus gnats).

Certain flower insects depend obligately on ranunculacean flowers (though the reverse is not true), such as the primitive pollen-eating *Micropteryx calthella* (Microlepidoptera) from *Caltha palustris*, the fly *Chiastochaeta trollii* from *Trollius europaeus*, and the bumblebee *Bombus gersteckeri* from *Aconitum vulparia*.

Populational aspects of various Ranunculaceae are treated, for example, by Price and Waser (1979), Melampy and Hayworth (1980), Waddington (1981) and Lubbers (1982).

PHYTOCHEMISTRY. Many genera, especially those belonging to subfam. Isopyroideae, Thalictrioideae and Hydrastidoideae, i.e. the group with T-type chromosomes, richly accumulate isoquinoline alkaloids, such as magnoflorine, berberine etc. The genera belonging to subfam. Helleboroideae and Ranunculoideae, i.e. the group with R-type chromosomes, accumulate no or little isoquinoline alkaloids, but *Aconitum*, *Delphinium* and *Consolida*, which belong to Delphinieae, contain diterpene alkaloids like aconitine, and in *Cimicifuga*, N-methyl-cytisine, an alkaloid of quinolizine type, is found (Hegnauer 1966).

Ranunculin is a characteristic compound of the family, but the occurrence is generally restricted to subfam. Ranunculoideae. In *Helleborus*, which belongs to Helleboroideae, ranunculin is richly con-

tained. It may show, to some extent, the phyletic relationship between both subfamilies, which have R-type chromosomes (Ruijgrok 1966).

Cyanogenetic compounds are contained in some genera belonging to subfam. Isopyroideae, such as *Aquilegia*, *Enemion*, *Isopyrum* and *Leptopyrum*. In some species of *Clematis*, *Ranunculus* and *Thalictrum*, which belong to other subfamilies, also cyanogenetic compounds are present, but only very sporadically (Ruijgrok 1966).

DISTRIBUTION AND HABITATS. The Ranunculaceae are distributed nearly all over the world. The family comprises 59 genera and ca.2500 species. It has 19 monotypic genera, most of which have restricted distribution areas, such as *Anemonopsis*, *Hydrastis*, *Kingdonia*, *Laccopetalum*, *Megaleranthis*, *Souliea*, *Xanthorhiza* etc. Although the geographical distribution of the family seems to indicate an old age, some genera with advanced characteristics extended their distribution rather recently, e.g. *Ceratocephala*, *Consolida*, *Myosurus* and some sections of *Ranunculus*.

The family prefers the temperate or cool climate and is rare in the tropics. Most members prefer humid places, and *Ranunculus* subgen. *Batrachium*, some species of *Caltha*, etc. are water plants. Many of the species grow in forests, especially deciduous broad-leaved forests, and also in grasslands. The family includes many calciphilous species.

Many genera are restricted to the extratropical part of the northern hemisphere, while others, such as *Anemone*, *Caltha*, *Clematis*, *Myosurus*, *Ranunculus* and *Thalictrum*, are widely distributed in the northern and southern hemispheres. Purely southern genera are rather few: *Knowltonia* and *Peltocalathos* in southern Africa, and *Aphanostemma*, *Barneoudia*, *Callianthemoides* and *Hamadryas* in South America. There are no genera endemic to Oceania. In the tropical zone, 12 genera are known, including four endemics: *Naravelia* in tropical Asia, and *Krapfia*, *Laccopetalum* and *Oreithales* in tropical South America. Most species grow in the alpine or montane zone and purely tropical species growing under tropical climate are very few, including only *Naravelia*, some species of *Clematis* and of *Ranunculus*. Although the family has a cosmopolitan distribution, it may be regarded basically as a north extratropical family.

The family is abundantly represented in East Asia, where 44 genera occur, of which 13 including *Anemonopsis*, *Asteropyrum*, *Beesia*, *Calathodes*, *Dichocarpum*, *Kingdonia*, *Megaleranthis*, *Souliea* etc. are endemic. Temperate East Asia is the most important area for the development of genera and species of the family. In Europe 24 genera occur, but there are no endemics. In North America 24 genera occur, of which *Arcteranthis*, *Cyrtorhyncha*, *Hydrastis*, *Kum-*

lienia and *Xanthorhiza* are endemic. Temperate North America with extension to montane and temperate South America is also important area for generic development of the family.

SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY. Since Adanson (1763), the family has been often divided into a group with one-seeded fruits and another with many-seeded fruits. Prantl (1887) regarded *Paeonia*, *Glaucidium* and *Hydrastis* as members of tribe Paeonieae. The other genera he classified into the tribes Helleboreae and Anemoneae, mainly based on the position of ovules and vascular supply for them. Langlet (1932) recognized two chromosome types and proposed subdivision of the family into Ranunculoideae with R-type chromosomes and Thalictrioideae with T-type chromosomes. He emphasised that in both subfamilies the group with one-seeded fruits were independently derived from the group with many-seeded fruits. Tamura (1966) accepted the argument of Langlet in principle, and divided the family in six subfamilies, i.e. Helleboreoideae, Ranunculoideae, Isopyroideae, Thalictrioideae, Coptidoideae and Hydrastidoideae, but later (1988) Coptidoideae were reduced to Isopyroideae as a tribe.

In the R-type group the basic chromosome number seems to be originally eight, and Ranunculoideae with one-seeded fruits were derived from Helleboreoideae with many-seeded fruits. In Helleboreoideae, tribe Helleboreae seems to be ancestral. Tribe Cimicifugeae is specialised in the racemose inflorescence, Nigelleae in the annual habit and basic chromosome number $x = 6$ and $x = 7$, and Delphinieae in the zygomorphic flowers. In Ranunculoideae, tribe Adonideae with laterally produced bitegmic ovules are phylogenetically different from other tribes. Anemoneae, mostly without petals, do not seem to be the ancestral group of Ranunculaceae mostly with petals, because petals originated independently in both tribes.

In the T-type group, Isopyroideae have follicles and consist of tribes Isopyreae with the basic number $x = 7$, Dichocarpeae with $x = 6$ and Coptideae with $x = 9$ rarely $x = 8$. Thalictrioideae with $x = 7$ have achenes and seem to be derived from Isopyreae. Hydrastidoideae with $x = 13$ are an isolated subfamily within the Ranunculaceae.

AFFINITIES. *Paeonia*, *Glaucidium* and *Circaeaster* had been often classified in the Ranunculaceae, but they cannot be the members of the family (see Tamura 1962; also see Cronquist (1981) on *Paeonia*; Tamura (1972) on *Glaucidium*; Hutchinson (1959) on *Circaeaster*). The Ranunculaceae are classified in Ranunculales, a herbaceous polycarpicean order. Among them, the Lardizabalaceae are distinguished by their laminar placentation. The Nelumbonaceae differ

from the Ranunculaceae by the apical placenta, the receptacle embedding the carpels, exalbuminous seeds etc. The Berberidaceae have valvate anthers and carpels without any sutures and do not seem to have a close relationship to the Ranunculaceae. The Menispermaceae and *Sargentodoxa* (Lardizabalaceae) resemble the Ranunculaceae in many features, but the former is specialized by the the drupe and the latter by the fleshy receptacle. Trimerous and unisexual flowers prevailing in both families are also advanced characteristics. They are considered to be derived from the Ranunculaceae. The Ranunculaceae seem to be the most primitive member and with two derived families isolated within the order Ranunculales (but see p. 7).

ECONOMIC IMPORTANCE. Many genera of this family have beautiful flowers and include species with cultivars or garden hybrids, and are cultivated as ornamental plants, such as the species of *Aconitum*, *Adonis*, *Anemone*, *Aquilegia*, *Caltha*, *Cimicifuga*, *Clematis*, *Consolida*, *Delphinium*, *Eranthis*, *Helleborus*, *Hepatica*, *Nigella*, *Pulsatilla*, *Ranunculus*, *Thalictrum* and *Trollius*.

Many genera contain substances with pharmacological activities and some of them are used as medicinal plants, e.g. *Aconitum* with diterpene alkaloids, *Coptis*, *Thalictrum*, *Hydrastis* with isoquinoline alkaloids, *Helleborus*, *Adonis* with cardiotonic glycosides, *Cimicifuga* with triterpenes, *Clematis* with ranunculin and saponin.

CONSPECTUS OF SUBFAMILIES AND TRIBES

1. Fruitlets follicular, or baccate with many seeds, or fruits capsular 2
 - Fruitlets achenial, or baccate with 1 or 2 seeds 8
2. Flowers zygomorphic **Helleboroideae: Delphinieae** (p. 575) 3
 - Flowers actinomorphic, rarely slightly irregular 3
3. Annuals. Carpels connate to various degrees
 - Helleboroideae: Nigelleae** (p. 574) 4
 - Perennials; if annuals, carpels free 4
 - 4. Follicles 2, connate at the base, with a distinct longitudinal vein **Isopyroideae: Dichocarpeae** (p. 580) 5
 - Follicles 1 to many, usually free; if 2 and connate, without a longitudinal vein 5
 - 5. Follicles without distinct transverse veins **Isopyroideae: Coptideae** (p. 581) 6
 - Follicles with distinct transverse veins or reticulation, or fruits baccate 6
6. Inflorescence racemiform or racemose, several to many-flowered **Helleboroideae: Cimicifugeae** (p. 573) 7
 - Inflorescence not racemiform 7
7. Leaves ternately compound, follicles free **Isopyroideae: Isopyreae** (p. 579) 9
 - Leaves simple, palmate or pedate; if ternate, follicles connate downward **Helleboroideae: Helleboreae** (p. 572) 8
8. Fruitlets baccate. Sepals 3 **Hydrastioidae** (p. 582) 9
 - Fruitlets achenial; if baccate, sepals 5 or more 9
9. Petals lacking. Ovule pendulous. Achenes with distinct longitudinal veins **Thalictroideae** (p. 581) 9

- Petals present; if lacking, ovule ascendent, or achenes without longitudinal veins 10
- 10. Ovule produced from lateral margin of a carpel **Ranunculoideae: Adonideae** (p. 575) 11
 - Ovule produced at nearly the middle of ventral wall or ridge 11
- 11. Ovule pendulous. Sepals flat **Ranunculoideae: Anemoneae** (p. 575) 11
 - Ovule ascendent; if pendulous, sepals with basal projection **Ranunculoideae: Ranunculeae** (p. 577) 11

KEY TO GENERA

1. Fruits baccate 2
 - Fruits follicular or achenial 4
2. Fruits single, many-seeded **11. Actaea** 3
 - Fruits aggregated, fruitlets 1–2-seeded 3
3. Sepals 3. Leaves simple, palmatifid **59. Hydrastis** 5
 - Sepals 5 or more. Basal leaves compound **26. Knowltonia** 5
4. Fruits follicular, single or aggregated 5
 - Fruits achenial, aggregated 31
5. Flowers zygomorphic 6
 - Flowers actinomorphic, or more or less irregular 8
6. Spurred petal single, sessile. Carpel single **17. Consolida** 7
 - Spurred petals 2. Carpels 3 or more 7
7. Spurred petals sessile **16. Delphinium** 8
 - Spurred petals stalked **15. Aconitum** 9
8. Petals absent 9
 - Petals present 12
9. Leaves simple, undivided 10
 - Leaves divided or compound 11
10. Carpels several. Inflorescence laxly corymbiform, or single-flowered **1. Caltha** 11
 - Carpel single. Inflorescence racemiform or subpaniculiform **5. Beesia** 12
11. Leaves palmati- or pedatisect **2. Calathodes** 13
 - Leaves ternately compound **47. Enemion** 13
12. Carpels connate. Annuals 15
 - Carpels free; if connate, perennials 15
13. Leaves palmate or undivided **12. Komaroffia** 14
 - Leaves pinnately compound 14
14. Petals shorter than sepals **13. Nigella** 15
 - Petals longer than sepals **14. Garidella** 16
15. Short shrubs with woody stem **57. Xanthorhiza** 17
 - Stem herbaceous, or slightly woody downward 16
16. Inflorescence racemiform. Stem without basal leaves **8. Souliea** 17
 - Inflorescence not racemiform, or single-flowered; if racemiform, stem with basal leaves 17
17. Inflorescence densely racemiform, with many flowers **10. Cimicifuga** 18
 - Inflorescence not or laxly racemiform, with at most several flowers, or single-flowered 18
18. Cauline leaves arranged nearly in a whorl to form an involucre **7. Eranthis** 19
 - Cauline leaves alternate or subopposite, not involucre 19
19. Follicles distinctly stalked 20
 - Follicles nearly sessile 21
20. Petals sessile. Seeds squamulose **9. Anemonopsis** 22
 - Petals stalked. Seeds smooth **56. Coptis** 22
21. Leaves shallowly lobate, distinctly peltate **55. Asteropyrum** 23
 - Leaves deeply divided or compound, not or slightly peltate 22
22. Leaves simple 23
 - Leaves compound 24

23. Cauline leaf single, approximate to flower **4. Megaleranthis**
 – Cauline leaves apart from flower, or absent **3. Trollius**
24. Sepals persistent **6. Helleborus**
 – Sepals deciduous 25
25. Scales between stamens and carpels present 26
 – Scales between stamens and carpels absent 28
26. Rhizome tuberous **51. Semiaquilegia**
 – Rhizome not tuberous 27
27. Petals shorter than a half of sepal length. Beaks nearly as long as follicle body **52. Urophysa**
 – Petals longer than a half of sepal length. Beaks at most a half length of follicle body **53. Aquilegia**
28. Follicles 2, with a distinct longitudinal vein. Petals long stalked **54. Dichocarpum**
 – Follicles without a longitudinal vein. Petals shortly stalked or nearly sessile 29
29. Petals nearly sessile. Stem simple **50. Paraquilegia**
 – Petals shortly stalked. Stem little branched 30
30. Annuals. Carpels usually more than 10 **49. Leptopyrum**
 – Perennials. Carpels usually less than 8 **48. Isopyrum**
31. Leaf venation open dichotomous **20. Kingdonia**
 – Leaf venation not open dichotomous 32
32. Achenes with a long, plumose tail 33
 – Achenes without a long, plumose tail 36
33. Cauline leaves arranged in a whorl to form an involucre **27. Pulsatilla**
 – Cauline leaves alternate or opposite 34
34. Cauline leaves alternate **28. Archiclematis**
 – Cauline leaves opposite at least on flowering shoot 35
35. Terminal leaflet transformed into a tendril. Petals narrow, longer than sepals **30. Naravelia**
 – Terminal leaflet not transformed into tendril. Petals absent; if present, shorter than sepals **29. Clematis**
36. Sepals valvate **29. Clematis**
 – Sepals imbricate 37
37. Petals absent 38
 – Petals present 44
38. Stem scapose, without cauline leaves 39
 – Stem with cauline leaves 40
39. Basal leaves lobate to partite, distinctly shorter than scape **25. Metanemone**
 – Basal leaves entire, as long as scape **24. Oreithales**
40. Ovule and seed ascending **31. Trautvetteria**
 – Ovule and seed pendulous 41
41. Achenes with longitudinal, often branched vein on lateral faces **58. Thalictrum**
 – Achenes without veins on lateral faces 42
42. Cauline leaves apart from flower **21. Anemone**
 – A whorl of cauline leaves approximate to flower 43
43. Leaves 3–5-partite. Achenes with long hairs **23. Barneoudia**
 – Leaves 3-lobed. Achenes shortly pubescent **22. Hepatica**
44. Flowers unisexual 45
 – Flowers bisexual 46
45. Sepals persistent, longer than or as long as petals **40. Paroxygraphis**
 – Sepals deciduous, shorter than petals **41. Hamadryas**
46. Sepals with a spur-like projection near the base **32. Myosurus**
 – Sepals without spur-like projection 47
47. Ovule and seed pendulous 48
 – Ovule and seed ascending 49
48. Petals with a nectary **18. Callianthemum**
 – Petals without a nectary **19. Adonis**
49. Androecium and gynoecium separated on receptacle by free, open zone 50
 – Androecium and gynoecium not separated on receptacle 51
50. Petals with 1–3 nectaries **45. Krapfia**
 – Petals with many nectaries **46. Laccopetalum**
51. Achenes with a bulging empty lateral chamber on each side **44. Ceratocephalus**
 – Achenes without lateral chambers 52
52. Achenes without distinct longitudinal veins on lateral faces, pericarp with well-developed sclerenchymatous layer 53
 – Achenes with a distinct longitudinal vein or veins on lateral faces, pericarp without well-developed sclerenchymatous layer 54
53. Petals shorter than a half of sepal length **42. Aphanostemma**
 – Petals longer than a half of sepal length **43. Ranunculus**
54. Achenes winged along a longitudinal vein on each lateral face **39. Callianthemoides**
 – Achenes not winged 55
55. Leaves simple, distinctly peltate **38. Peltocalathos**
 – Leaves or leaflets not peltate 56
56. Leaves ternate or biternate, Flowers several to many in a corymbiform or subpaniculiform cyme **36. Cyrtorhyncha**
 – Basal leaves simple, at most trisect. Flowers single, terminal to stems or branches 57
57. Sepals persistent **37. Oxygraphis**
 – Sepals deciduous 58
58. Sepals white. Petals shorter than a half of sepals **33. Kumlienia**
 – Sepals yellow. Petals longer to slightly shorter than sepals 59
59. Stolons present **35. Halerpestes**
 – Stolons not present **34. Arcteranthis**

I. Subfam. Helleboroideae Hutch. (1923)

Carpels multiovular. Ovules produced from lateral margins of the carpel. Fruitlets or fruits many seeded, follicular, sometimes capsular, with transverse veins, rarely baccate with many seeds. Chromosomes R-type.

1. Tribe Helleboreae DC. (1817)

Leaves simple, sometimes palmate or pedate. Flowers actinomorphic, bisexual, in loose corymbiform cyme, terminal to stem or branches, or fasciculate at nodes. Petals flat, cup-shaped with short stalks, or absent. Ovules bitegmic, sometimes unitegmic. Fruits aggregated, rarely single follicles, free, sometimes connate. $x = 8$.

1. *Caltha* L.

Fig. 123 A, B

Caltha L., Sp. Pl.: 558; Smit, Blumca 21: 119 (1973).

Perennials. Stem simple or sparsely branched in the upper part, with a few cauline leaves, or scapose. Basal leaves simple, cordate, undivided, rarely lobate, dentate, crenate, rarely nearly entire. Flowers

several in a lax corymbiform cyme, or single at the tip of stem. Sepals 5 or more. Petals 0. Follicles a few to numerous, free, sessile, rarely shortly stalked. Seeds smooth. $x = 8$. Two sections, about 12 spp. in the northern and southern hemispheres.

2. *Calathodes* Hook. f. & Thomson

Calathodes Hook. f. & Thomson, Fl. Ind. 1: 40 (1855).

Perennials. Stem simple or sparsely branched. Basal leaves pedatisect, segments incised-dentate. Flowers single at the tip of stem or branches. Sepals 5. Petals 0. Receptacle elongated between the insertion of sepals and that of carpels after flowering. Follicles 8–30, free, shortly stalked, with straight transverse veins running parallel to each other in the upper and middle parts of both faces. Seeds smooth. $x = 8$. Three spp. in montane and subalpine zones of E Himalayas, China and Taiwan.

3. *Trollius* L.

Fig. 123 E

Trollius L., Sp. Pl.: 556 (1753); Dorosz., Monogr. Bot. 41: 1 (1974).

Perennials. Stem sparsely branched or simple, leafy, sometimes scapose. Basal leaves palmatipartite to -sect, deeply cordate at the base, segments incised-dentate, mostly chartaceous. Flowers several in a lax corymbiform cyme, or single at the tip of stem or branches. Sepals 5 or more, often connivent. Petals 8–17, oblong to linear, flat or slightly concave near the base of the blade, unguiculate, sometimes longer than sepals. Follicles 3–50, free, sessile. Seeds smooth. $x = 8$. Two sections, about 31 spp. from temperate to cold zone of the northern hemisphere.

4. *Megaleranthis* Ohwi

Megaleranthis Ohwi, Acta Phytotaxon. Geobot. 4: 130 (1935).

Perennials. Stem simple, with a single cauline leaf and a single terminal flower. Basal leaves pedatisect, segments incised-dentate. Cauline leaf similar to the basal, close to the flower. Sepals 5. Petals 8, flat, obovate-oblong, unguiculate. Follicles several, free, sessile, with straight transverse veins running parallel to each other in the upper and middle parts of both faces. $x = 8$. One sp., temperate to subalpine zone of S Korea.

5. *Beesia* Balf. f. & W. Smith

Beesia Balf. f. & W. Smith, Notes R. Bot. Gard. Edinb. 9: 63 (1915).

Perennials. Rhizome horizontal, vigorous. Stem simple, subscapose. Basal leaves simple, undivided, cordate, regularly dentate. Inflorescence racemiform

in the upper part, with 1–3 flowers fasciculate at the nodes in the lower part, bracts subulate. Sepals 5. Petals 0. Follicle single, sessile. Seeds rugulose. $x = 8$. One sp., W and SW China and N Burma.

6. *Helleborus* L.

Fig. 123 C

Helleborus L., Sp. Pl.: 557 (1753); Schiffner, Bot. Jahrb. Syst. 11: 92 (1890).

Perennials sometimes halfshrubs. Basal or lower cauline leaves palmate, ternate, or pedately compound, leaflets cuneate at the base, minutely regularly dentate, mostly chartaceous or coriaceous. Flowers several in lax corymbiform cymes, sometimes solitary. Sepals 5, persistent, rarely deciduous. Petals 5–15, obliquely tubular or cup-shaped, stalked. Follicles 2–10, free or connate, or forming a capsule. Seeds usually more or less carinate. Six sections, about 21 spp., Europe and Asia.

7. *Eranthis* Salisb.

Fig. 123 D

Eranthis Salisb., Trans. Linn. Soc. London 8: 303 (1808).

Perennials with tubers or tuberous rhizome. Stem simple, subscapose. Basal leaves palmatisect, segments lacinate. Cauline leaves 3 or 2, arranged in a whorl to form an involucre. Flower single, terminal to stem. Sepals 5–8. Petals 5–10, bilobed upward, more or less tubular downward, stalked. Follicles 2–10, free, stalked. Seeds smooth or slightly wrinkled. Two sections, eight spp., Europe and Asia.

2. Tribe Cimicifugeae Torrey & A. Gray (1838)

Rhizome vigorous, creeping. Leaves ternately compound. Inflorescence many-flowered, definite, racemiform, or infinite, racemose or spicate. Flowers actinomorphic, sometimes more or less irregular, bisexual, rarely unisexual. Petals flat or concave, unguiculate. Ovules bitegmic. Fruits aggregated, free follicles, sometimes a single follicle or berry. $x = 8$.

8. *Souliea* Franchet

Souliea Franchet, J. Bot. (Morot) 12: 609 (1898).

Perennials. Stem simple, without basal leaves, with large membranaceous sheathy scales at the base. Cauline leaves bi- or triternate, leaflets incised-dentate. Inflorescence definite, racemiform, simple, several-flowered. Flowers actinomorphic, bisexual. Sepals 5, white. Petals 5, obovate-flabellate, concave, toward the base, dentate at the apex, shortly unguiculate. Follicles 1–3, stalked, reticulate-veined. Seeds

rough reticulate. One sp., temperate and subalpine zone of SW China.

9. *Anemonopsis* Sieb. & Zucc.

Anemonopsis Sieb. & Zucc., Abh. Math.- Phys. Cl. Königl. Bayer. Akad. Wiss. 4 (2): 181 (1846).

Perennials. Basal and lower cauline leaves 2–4-ternate, leaflets irregularly incised-dentate. Inflorescence definite, loosely racemiform, 3–8-flowered. Flowers nutant with slender pedicels. Sepals 7–10, reddish purple. Petals 10 or more, erect, concolorous with sepals, without a nectary. Fruits anchor-shaped with 2–4 follicles, fruiting pedicels bending down, follicles rising up with elongate stalks. Seeds squamate. $x = 8$. One sp., temperate zone of Japan: C Honshu.

10. *Cimicifuga* Wernisch.

Cimicifuga Wernisch., Gen. Pl.: 298, 321 (1763).

Perennials. Basal and lower cauline leaves 1–4-ternate, leaflets irregularly incised-dentate or dentate. Inflorescence densely racemose, sometimes spicate, many-flowered, simple or branched. Flowers rather small, actinomorphic sometimes slightly irregular, bisexual, sometimes unisexual. Sepals 4–5, white, often caducous. Petals 1–9, flat or concave, bilobed or forked, rarely entire, more or less unguiculate, with, sometimes without a nectary, often caducous, rarely absent. Follicles 1–8, stalked or sessile, free. Seeds squamate, rugose, rarely smooth. $x = 8$. Four sections, about 18 spp., temperate to cold zone of the northern hemisphere.

11. *Actaea* L.

Fig. 123F

Actaea L., Sp. Pl.: 504 (1753).

Perennials. Stem simple, without basal leaves, with large sheathy scales at the base. Cauline leaves 2–3-ternate, leaflets incised-dentate. Inflorescence densely racemose, simple, many-flowered. Flowers actinomorphic, or slightly irregular, bisexual. Sepals 3–5, white, caducous. Petals 2–10, flat, clawed, cauducous, without a nectary. Fruit baccate, single, stigmas nearly sessile. Seeds flattened, smooth. $x = 8$. Eight spp., temperate to subcold zone of the northern hemisphere.

3. Tribe Nigelleae Langlet ex Tamura (1990)

Annuals or biennials with a tap root. Leaves pinnately compound, dissected into narrow lacinae, sometimes palmate or entire. Flowers terminal to stem and branches, actinomorphic, bisexual. Petals

bilabial, stalked. Ovules bitegmic. Fruits aggregated follicles, more or less connate, sometimes capsulate. $x = 6$, rarely $x = 7$.

12. *Komaroffia* Kuntze

Komaroffia Kuntze, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 144 (1887).

Nigella sect. *Komaroffia* (Kuntze) Brand (1895).

Annuals. Lower cauline leaves nearly sessile, entire, lanceolate or oblong. Upper cauline leaves 3–5-palmatipartite, segments or their partitions linear. Sepals 5. Petals mostly 8, stalked, shorter than sepals, bilabial, outer labium usually bifid, much longer than the inner. Follicles 2–5, sessile, connate to more than middle, dehiscent along both ventral and dorsal sutures. Seeds compresses, verrucose-rugulose. $x = 7$. Two spp., C Asia and Iran.

13. *Nigella* L.

Nigella L., Sp. Pl.: 534 (1753); M. Zohary, Pl. Syst. Evol. 142: 71–107 (1983) (rev.).

Annuals. Basal and lower cauline leaves usually 2–3-pinnate, leaflets divided into linear to ovate segments. Sepals 5(–8), unguiculate. Petals 5–10, smaller than sepals, stalked, bilabial, outer labium bilobed to -fid, longer than the inner. Follicles 2–10, partly to almost completely united to form a capsule. Seeds usually rugose or tuberculate. $x = 6$. Two subgenera, about 20 spp., in Europe, except the north, N Africa, SW Asia and C Asia.

14. *Garidella* L.

Garidella L., Sp. Pl.: 425 (1753).

Nigella sect. *Garidella* (L.) Prantl (1887).

Annuals. Basal and lower cauline leaves bipinnately compound, blades divided into linear segments. Flowers long pedicellate. Sepals 5, hardly petaloid. Petals 5, longer than sepals, long clawed, bilabial, outer labium bifid or -partite, much longer than the inner. Follicles 2–3, united downward, dehiscent along both ventral and dorsal sutures. Seeds ovoid, reticulate or striate. $x = 6$. Two spp., S Europe, SW Asia and C Asia.

4. Tribe Delphinieae Warm. (1884)

Inflorescence definite, sometimes infinite. Flowers zygomorphic, bisexual. Sepals 5, upper one unpaired, spurred or hollowed, lateral and lower ones paired, flat. Spurred petals 2 or 1, not-spurred petal 2 or 0.

Ovules bitegmic. Fruits aggregated, free follicles, or a single follicle. $x = 8$.

15. *Aconitum* L.

Fig. 123 G–I

Aconitum L., Sp. Pl.: 532 (1753); Stapf, Ann. R. Bot. Gard. Calcutta 10: 133 (1905).

Stem leafy, sometimes subscapose. Basal leaves palmati- or pedatifid to -sect, or ternate, segments coarsely dentate, incised or incised-laciniate. Inflorescence definite, many- to single-flowered, sometimes infinite. Upper sepal cucullate, galeate, navicular or tubular. Petals 2, long stalked, spurred. Follicles 3 to several, sessile. Seeds squamate or smooth. $x = 8$. Three subgenera, about 300 spp., Eurasia, N Africa and N America.

16. *Delphinium* L.

Delphinium L., Sp. Pl. 530 (1753).

D. subgen. *Eudelphinium* Huth, Bot. Jahrb. Syst. 20: 339 (1892).

Stem leafy, or subscapose. Basal leaves palmati- or pedatilobed to -sect, sometimes ternately or subpinnately compound, segments coarsely dentate, incised or laciniate. Inflorescence definite, many- to single-flowered, sometimes infinite. Upper sepal prolonged into a spur. Petals 4, arranged in 2 pairs; the upper pair sessile, elongate into a spur; the lower pair without spur, clawed. Follicles mostly 3 or 5, sessile. $x = 8$. Two subgenera, about 320 spp. in Eurasia, Africa and N America.

17. *Consolida* (DC.) S.F. Gray

Consolida (DC.) S.F. Gray, Nat. Arr. Brit. Pl. 2: 711 (1821).

Delphinium sect. *Consolida* DC. (1817).

Annuals. Basal and lower cauline leaves 1–3-ternate, palmate, sometimes palmatipartite, segments dissected into laciniae. Inflorescence racemiform or paniculiform. Upper sepal prolonged into a spur. Petal single, opposite to the upper sepal, spurred. Follicle single. Seeds squamulose. $x = 8$. Two sections, about 43 spp., Eurasia.

II. Subfam. Ranunculoideae Hutch. (1923)

Carpels uniovular, rarely biovular. Fruits a head of achenes, without sometimes with veins on lateral faces, rarely of 1-seeded berries. Flowers actinomorphic. Chromosomes R-type.

1. Tribe Adonideae Kunth (1838)

Flowers bisexual. Sepals petaloid or slightly sepaloid. Petals petaloid, longer than sepals. Carpels without well developed adaxial wall. Fertile ovule 1, bitegmic, produced from lateral margin of the carpel and supplied with a branch of the ventral bundle. $x = 8$.

18. *Callianthemum* C. Meyer

Callianthemum C. Meyer, in Ledeb. Fl. Alt. 2: 336 (1830).

Perennials. Stem simple or sparsely branched at the lower part, sometimes scapose. Basal leaves 1–3-ternate or -pinnate, segments usually subpinnatilobed to -sect, lobes entire, obtuse. Flowers at the tip of stems or branches. Sepals 5–10, slightly sepaloid, caducous. Petals 5–16, larger than sepals, clawed downward, with a nectary pit near the base. $x = 8$. About 14 spp., Eurasia, mostly isolated in small, restricted areas of alpine or subalpine zone.

19. *Adonis* L.

Adonis L., Sp. Pl.: 547 (1753).

Perennials or annuals. Stem leafy. Basal or lower cauline leaves often transformed into scales, or withered at anthesis. Cauline leaves alternate, 1–4-pinnate, segments multifid or -partite into narrow lobes. Flowers at the tip of stem or branches. Sepals 5–8, sepaloid or slightly petaloid. Petals 3–40, larger than sepals, without a nectary. $x = 8$. Two sections, about 26 spp., Eurasia.

2. Tribe Anemoneae DC. (1817)

Flowers usually bisexual. Sepals petaloid. Petals mostly lacking, or smaller than sepals. Fertile ovule single, unitegmic, pendulous at the middle of the upper margin of well developed adaxial wall, supplied with a ventral bundle or its middle division. $x = 8$, or 7, rarely 9.

20. *Kingdonia* Balf. f. & W. Smith

Kingdonia Balf. f. & W. Smith, Notes R. Bot. Gard. Edinb. 8: 191 (1914).

Perennials. Rhizome long, creeping, slender. Stem scapose. Basal leaves usually single, 5–7-palmatisect, segments lobate, irregularly dentate on the upper margin, with open dichotomous venation. Flower single, terminal to the scape. Sepals 5 or 6. Petals 9–12, small, stalked, limbs knob-like. Carpels 3–9, achenes 1–5, with thick stipe, beaks elongate, strongly bent outward. $x = 9$. One sp., subalpine zone of W China.

21. *Anemone* L.

Fig. 123 K, L

Anemone L., Sp. Pl.: 538 (1753); Tamura, Acta Phytotaxon Geobot. 42: 178 (1991).

Perennials, rarely short shrubs. Stem usually with 1–5 whorls of 3-, sometimes 2- or 4-leaved involucre. Basal leaves dispersed, sometimes absent at the base of stem, simple or compound. Inflorescence definite, trichasial, dichasial, umbelliform or single-flowered. Sepals 5, 6 or more. Petals 0. Achenes sessile or stalked, beaks straight, curved or indistinct. $x = 8$ or 7. Nine subgenera, about 144 spp., Eurasia, N America, extending to Chile, S and E Africa and Sumatra.

22. *Hepatica* Miller

Hepatica Miller, Gard. Dict. Abr. ed. 4: 28 (1754).

Perennials with monopodial, horizontal rhizome. Stem with a 3-leaved involucre, and a terminal flower. Basal leaves 3, sometimes 5–7-lobed, lobes entire. Involucral leaves sessile, entire, close to the flower. Sepals 5–10. Petals 0. Carpels 15–25, achenes several, pubescent, not compressed, pubescent, basal part projected like a short stalk, beaks short, stigmas capitate. $x = 7$. Seven spp. in temperate zone of Europe, E Asia and C and eastern N America.

23. *Barneoudia* C. Gay

Barneoudia C. Gay, Historia física y política de Chile. Botánica 1: 29 (1844).

Perennials with tuberous rhizome. Stem simple, with a 2-leaved involucre. Basal leaves 3-partite to ternate, segments entire or lobate. Flower usually single, close to the involucre and smaller than it. Sepals 8–18. Petals 0. Achenes cylindrical, slightly bent and reniform, with long, rigid hairs near the base, otherwise nearly glabrous, beaks straight or arcuate. Three spp. in Chile and Argentina.

24. *Oreithales* Schldl.

Oreithales Schldl., Linnaea 27: 559 (1856).

Perennials with thick, erect rhizome. Stem scapose, as long as or shorter than basal leaves, with a terminal flower. Basal leaves entire, elliptic to cordate. Sepals 8–18. Petals 0. Achenes villose, beaks long reflexed near the base, then straight. $2n = 48$ ($x = 8$). One sp., alpine zone of Andes from Ecuador to Bolivia.

25. *Metanemone* W.T. Wang

Metanemone W.T. Wang, Fl. Republ. Popul. Sin. 28: 72, 351 (1980).

Perennials. Rhizome short, erect. Stem scapose, longer than basal leaves, without cauline leaves, with a terminal flower. Basal leaves elliptic, obovate, ovate to subreniform, entire, 3-lobed or -partite. Sepals ca. 19. Petals 0. Carpels ca. 18, densely covered with long hairs, styles long, slightly curved, stigmas capitate. One sp., China: Yunnan.

26. *Knowltonia* Salisb.

Knowltonia Salisb., Prodr. stirp. in horto ad Chapel Allerton vident.: 372 (1796); Rasm., Opera Bot. 53: 14 (1979).

Perennials with erect or horizontal rhizome. Stem simple or sparsely branched, with whorled or congested cauline leaves forming involucre or involucl. Basal leaves 1–3-ternate rarely simple, leaflets mostly ovate, 3-lobed to -sect, or undivided, dentate. Inflorescence cymose, umbelliform, simple or irregularly compound. Sepals 8–22. Petals 0. Fruitlets baccate, pericarp consisting outer fleshy layer and inner fibrous layer, beaks short. $2n = 48$ ($x = 8$). Eight spp., S Africa and southern C Africa.

27. *Pulsatilla* Miller

Pulsatilla Miller, Gard. Dict. Abr. ed. 4: 28 (1754); Aichele and Schweg., Feddes Repert. Spec. Nov. Regni Veg. 60: 17 (1957).

Perennials covered with long soft hairs. Rhizome thick, erect. Stem subscapose, with a 3-leaved involucre and a terminal flower. Basal leaves rosulate, pinnately, ternately or subpalmately compound, rarely simple. Flower campanulate, sometimes widely opened and nearly flat. Sepals usually 6. Petals small, capitate with the stalk, club-shaped or spatulate, or lacking. Achenes sessile, with a plumose beak elongated like a tail. $x = 8$. Two subgenera, about 38 spp., Eurasia, N America.

28. *Archiclematis* (Tamura) Tamura

Archiclematis Tamura, Sci. Rep. Osaka Univ. 16–2: 31 (1967); Acta Phytotaxon. Geobot. 24: 151 (1970).

Scandent shrubs. Stem leafy, elongate with long internodes. Cauline leaves alternate, simple, cordate, 3–5-lobed, dentate. Inflorescences axillary, 1–3-flowered. Flowers campanulate, nutant. Sepals 4, valvate, erect. Petals 0. Stamens hairy. Carpels barbate, styles caudately elongate, plumose. One sp., temperate zone of Nepal and S Tibet.

29. *Clematis* L.

Fig. 123 M, N

Clematis L., Sp. Pl.: 543 (1753); Tamura, Acta Phytotaxon. Geobot. 38: 38 (1987).

Shrubs, half-shrubs, sometimes perennials with woody base. Stem scandent, sometimes erect, internodes elongate. Cauline leaves opposite, ternately or pinnately compound, with distinct rachises, rarely simple, petioles mostly twining. Inflorescences terminal or axillary, trichotomously compound principally, sometimes single-flowered. Flowers bisexual or unisexual. Sepals 4, sometimes 6 or 8. Petals absent, rarely present. Achenes nearly sessile, beaks elongate like a tail, plumose, rarely not tail-like, pubescent. $x = 8$. Four subgenera and about 295 spp., Eurasia, N America, S America, Africa, Madagascar and Oceania.

30. *Naravelia* DC.

Naravelia DC., Syst. Nat. 167 (1817); H. Eichler, Bibl. Bot. 124: 53 (1958); Tamura, Acta Phytotaxon. Geobot. 37: 106 (1986).

Scandent shrubs or half-shrubs. Stem woody at least in the lower part, internodes elongate. Leaves opposite, pinnate with 3-paired pinnae, lower and middle pinnae foliar, upper and terminal pinnae converted into tendrils. Inflorescences terminal or axillary, trichotomously compound principally, sometimes single-flowered. Sepals 4, spreading, often reflexed. Petals 6–12, glabrous, longer than sepals, claviform or spoon-shaped. Stamens glabrous. Achenes with a long, plumose tail, or with a pubescent beak. $x = 8$. Seven spp., tropical Asia: from India to S China and Malesia.

3. Tribe Ranunculeae DC. (1817)

Flowers bisexual, sometimes unisexual. Sepals petaloid or sepaloid. Petals present, rarely lacking. Carpels without well developed adaxial wall, rarely with it. Ovule single, unitegmic, ascendent, rarely pendulous, supplied with a middle ventral division of a carpel bundle, sometimes with a ventral bundle or its middle division. $x = 8$ or 7.

31. *Trautvetteria* Fischer & C. Meyer

Trautvetteria Fischer & C. Meyer, Ind. Sem. Hort. Bot. Petrop. 1: 22 (1835).

Perennials with horizontal rhizome, producing stolons. Stem simple, or branched upward. Basal leaves 1 to 3, palmatifid to -partite, coarsely dentate. Cauline leaves 2 or 3, resembling the basal. Inflorescence corymbiform or subpaniculiform, many-flowered. Flowers bisexual. Sepals 3 to 5, caducous. Petals 0.

Achenes inflated, pericarp without sclerenchymatous layer, with a longitudinal vein on each lateral face, beaks distinct. $x = 8$. One sp., with three local varieties separated in eastern N America, western N America and NE Asia, from temperate to subcold, often to alpine zones.

32. *Myosurus* L.

Myosurus L., Sp. Pl. 284 (1753); G. Campbell, Aliso: 390 (1952).

Small, scapose annuals with a persistent, elongate hypocotyl. Leaves linear to linear-oblong. Flower terminal, bisexual. Sepals 5, sepaloid, with spur-like projection at the base. Petals mostly 5, as long as or slightly shorter than sepals, with a nectary-pocket, long-clawed. Carpels numerous, with well-developed adaxial wall, hanging an ovule. Receptacle greatly elongate like a tail in fruit. Achenes small, with a distinct dorsal ridge, with poorly developed sclerenchymatous layer, beaks large. $x = 8$. About 15 spp., all continents, lacking in tropical zone and E Asia, and most richly represented in western N America.

33. *Kumlienia* E. Greene

Kumlienia E. Greene, Bull. Calif. Acad. Sci. 1: 337 (1886).

Perennials. Stem simple, sometimes once branched. Basal leaves 3–5-lobed or -fid, lobes lobulate. Cauline leaves 1 or 2, bract-like, or none. Flower terminal, bisexual. Sepals 5, petaloid, white. Petals 8–12, much shorter than sepals, long-clawed, sup-shaped with a fissure at the adaxial wall. Achenes with longitudinal veins on each lateral face, pericarp without sclerenchymatous layer, beaks elongate, hooked. $x = 8$. One sp., western N America.

34. *Arcteranthis* E. Greene

Arcteranthis E. Greene, Pittonia 3: 190 (1897).

Perennials. Stem simple, subscapose. Basal leaves 3–5-fid to -parted, segments cleft to lobate-crenate. Cauline leaf usually single, resembling the basal, sometimes scaly or none. Flower terminal, bisexual. Sepals 5, petaloid, yellow. Petals 7–16, slightly shorter than sepals, long clawed, nectary scale forming a pocket, or forked with a deep fissure. Achenes with longitudinal veins on each lateral face, without sclerenchymatous layer, beaks elongate. $x = 8$. One sp., northwestern N America.

35. *Halerpestes* E. Greene

Halerpestes E. Greene, Pittonia 4: 207 (1900).

Perennials producing runners. Stem scapose, subsca-
pse or sparingly branched, with bracts. Basal leaves
crenate, lobate, tri- or pedatifid to -parted, sometimes
entire or trisect, segments entire, lobate-crenate, or
trisect into linear lobes. Flowers terminal, bisexual.
Sepals 5, usually sepaloid. Petals 5–12, longer than or
as long as sepals, clawed, yellow, a nectary with thic-
kening or pocket, sometimes with elongate margin.
Achenes with a longitudinal vein or veins, often
branched, pericarp without sclerenchymatous layer,
beaks short. $x = 8$. About ten spp., Asia, N America
and S America.

36. *Cyrtorhyncha* Nutt. ex Torrey & A. Gray

Cyrtorhyncha Nutt. ex Torrey & A. Gray, Fl. N. Amer. 1: 26
(1838); E. Greene, Pittonia 3: 193 (1897).

Perennials. Stem erect, branched, leafy. Basal leaves
ternate or biternate, blades distinctly petiolulate, 3-
lobed to -sect, segments lanceolate to elliptic. Cauline
leaves similar to the basal. Flowers in many-flowered
corymbiform or subpaniculiform cyme, bisexual. Sep-
als 5, sepaloid. Petals 5–9, longer than sepals, long
clawed, yellow, nectary with a transverse thickening.
Achenes with prominent longitudinal veins on lateral
faces, pericarp without sclerenchymatous layer,
beaks long, hanging down inside. $2n = 32$. One vari-
able sp., western N America.

37. *Oxygraphis* Bunge

Oxygraphis Bunge, Verz. Suppl. Fl. Alt. 46 (1836); Freyn, Flora
70: 140 (1887), ex. p.

Perennials. Stem simple, scapose. Basal leaves entire,
crenate, or lobate at the apex, coriaceous. Flower ter-
minal, bisexual. Sepals 5, sepaloid, coriaceous, per-
sistent, not marcescent. Petals 7–16, longer than se-
pals, clawed, yellow, nectary with a transverse ridge
or shallow slit. Achenes with a longitudinal vein or
veins on each lateral face, without sclerenchymatous
layer, beaks short. Five spp., C Asia, Himalayas, W
China, Siberia to Alaska.

38. *Peltocalathos* Tamura

Peltocalathos Tamura, Acta Phytotaxon. Geobot. 43: 139 (1992).

Perennials. Stem branched, bracteate. Basal leaves
simple, distinctly peltate, undivided, minutely den-
tate. Flowers 1–several in a corymbiform cyme.
Sepals caducous. Petals 11–17, longer than sepals,
yellow, nectary with a thick burse. Achenes with lon-

gitudinal veins on lateral faces, without sclerenchy-
matous layer. One sp., S Africa.

39. *Callianthemoides* Tamura

Callianthemoides Tamura, Acta Phytotaxon. Geobot 43: 140
(1992).

Perennials. Stem subsca-
pse. Leaves semibasal, 3–7-
times pinnately ternate, segments linear-oblong.
Flowers 1–2, terminal. Sepals 5. Petals 10–20, slightly
longer than sepals, white, nectary thick, broad, upper
margin undulate. Achenes winged along a longitudi-
nal vein on each lateral face without sclerenchyma-
tous layer. One sp., southern S America.

40. *Paroxygraphis* W. Smith

Paroxygraphis W. Smith, Rec. Bot. Surv. India 4: 344 (1913).

Small dioecious perennials. Stem scapose. Basal
leaves coriaceous, in male plants: elliptic to ovate, en-
tire, in female plants: orbicular or broadly ovate, cre-
nate or entire. Flower terminal, unisexual. Sepals 5,
persistent. Petals 5, shorter than or as long as sepals,
with a nectary pit or thickening. Achenes with a lon-
gitudinal, unbranched, costate vein on each lateral
face, pericarp thin, beaks short, triangular. One sp.,
alpine zone of E Himalayas.

41. *Hamadryas* Comm. ex Juss.

Hamadryas Comm. ex Juss., Gen. Pl.: 232 (1789).

Dioecious perennials with thick rhizome. Stem sca-
pse, or sparsely branched with bracts. Basal leaves
3–7-fid to -parted, or ternately or pinnately com-
pound, segments incised or dentate. Flowers termi-
nal, unisexual. Sepals 5–8, ovate, obovate to oblong,
Petals 7–20, longer to slightly shorter than sepals,
clawed, yellow, with a nectary pocket or slit. Achenes
longitudinally striate on each lateral face, beaks
short. About six spp., southern S America.

42. *Aphanostemma* A. St.-Hil.

Aphanostemma A. St.-Hil., Fl. Brasil. MÉR. ed. fol. 1: 9 (1825).

Annuals. Stem leafy, branched. Basal leaves 5–7-par-
tite, segments 3-lobed to -fid, lobes crenate-dentate.
Cauline leaves 3-fid to -sect. Flowers bisexual, in
loose cyme, often oppositifolius. Sepals 5. Petals 5,
white or pinkish, much smaller than sepals, bilabial,
outer-wall larger than the inner, stalked. Achenes
smooth on faces, beaks short. One sp. from S Brazil
to C Argentina.

43. *Ranunculus* L.

Fig. 123 O–S

Ranunculus L., Sp. Pl.: 584 (1753), ex. p.; L. Benson, Amer. Midl. Naturalist 40: 23 (1948), ex. p.

Perennials or annuals, usually without a tap-root. Stem branched or simple, leafy, sometimes scapose. Basal leaves lobate to cut, or ternately or pinnately compound, sometimes undivided. Cauline leaves similar to the basal, or bract-like, sometimes none. Flowers in corymbiform or subpaniculiform cyme, or terminal to stem, bisexual. Sepals usually 5 or 3, deciduous, rarely persistent and marcescent, petaloid or sepaloid. Petals 5 or more, sometimes 3, usually longer than sepals, with a nectary, rarely nectaries. Achenes without distinct longitudinal veins, rarely faintly veined on lateral faces, pericarp with sclerenchymatous layer. Cotyledons 2, sometimes strongly fused, rarely single. $x = 8$ or 7. Seven subgenera. Subgen. *Coptidium* (Prantl) L. Benson (1940): perennials, basal leaves 3–5-parted to -sect, margin dentate, sepals 3, petals 5–8, yellow, achenes turgid, differentiated into lower seed-bearing part and upper spongy part. One sp. in arctic and subarctic zone of the northern hemisphere. Subgen. *Pallasiantha* L. Benson (1940): perennials, basal leaves 3-lobed to -parted, or undivided, margin entire, sepals 3, petals 5–12. One sp., arctic zone of the northern hemisphere. Subgen. *Ficaria* (Hudson) L. Benson (1940): perennials, basal leaves cordate, entire or slightly dentate, sepals 3, petals 6–14. Five spp., Europe, N Africa, W Asia and C Asia. Subgen. *Crymodes* A. Gray (1886): perennials, basal leaves ternate, blades 3-parted to -sect, sepals 5, persistent, marcescent, petals 5–8. Four spp., arctic and alpine zone of Europe, Siberia, western N America and Greenland. Subgen. *Batrachium* (DC.) Peterm. (1849): perennials sometimes annuals, aquatic or semi-terrestrial, submerged leaves ternate, blades finely divided into capillary segments, aerial leaves flabellate, lobate to partite, flowers mostly leaf-opposite. About 30 spp., all continents, except tropical zone. Subgen. *Ranunculus*: perennials or annuals, basal leaves lobate to cut, or ternately or pinnately compound, sometimes undivided. About 550 spp., all continents, but scanty in tropical zone. Subgen. *Gampsoceras* (Steven) Tamura (1991): annuals with persistent hypocotyl, basal leaves usually trifid, segments crenate. One sp., W Asia.

44. *Ceratocephala* Moench

Ceratocephala Moench, Meth.: 218 (1794).

Annuals with a persistent hypocotyl. Stem scapose. Basal leaves 3- or 5-sect, segments partite to cut into linear to lanceolate lobes. Sepals 5, sepaloid, persistent. Petals 5, yellow, longer than sepals, nectary

single, with a flap. Achenes not disjointed when mature, with an empty-chambered lateral bulge on each lateral face, pericarp thick, beaks large, lanceolate. Receptacle elongate in fruit. $x = 7$. Three spp., Europe, N Africa, W Asia to NW China, and New Zealand. Naturalised in N America.

45. *Krapfia* DC.

Krapfia DC., Syst. Nat. 228 (1817).

Perennials with short, thick rhizome. Stem simple or branched, sometimes subscapose. Basal leaves 3–5-lobed to -parted, or undivided, dentate, incised or entire. Flowers terminal, bisexual, subglobose. Sepals 5–9, persistent, concave, fleshy. Petals 5–7, slightly longer to shorter than sepals, concave, red, orange, purplish or greenish, nectaries single, often laterally enlarged, sometimes to several. Achenes small, without longitudinal veins on faces, beaks usually long, filiform. Receptacle clavate, fleshy, enlarged in fruit, a free zone sometimes present between the part producing stamens and that producing carpels. Three sections, about eight spp., alpine zone of Andean S America.

46. *Laccopetalum* Ulbr.

Laccopetalum Ulbr., Bot. Jahrb. Syst. 37: 404 (1906).

Perennials with short, thick rhizome. Stem simple. Basal leaves spatulate or oblanceolate, dentate upward. Flower terminal, large, bisexual, subglobose. Sepals usually 5, persistent, concave, fleshy. Petals 5 or 6, persistent, smaller than sepals, concave, fleshy, nectaries up to more than 30, arranged in an arch, in pits or pockets. Achenes numerous, small, without longitudinal veins on faces, pericarp with sclerenchymatous layer, beaks distinct. Receptacle clavate, fleshy, enlarged in fruit, a broad, free zone present between staminate and carpellate zones. One sp., alpine zone of Andean Peru.

III. Subfam. Isopyroideae Tamura (1968)

Carpels multiovular to biovular. Ovules produced from lateral margins of the carpel. Fruitlets or fruits follicular, with or without transverse veins. Flowers actinomorphic. Chromosomes T-type.

1. Tribe Isopyreae Schrödinger (1909)

Leaves ternately compound. Flowers terminal to stem or branches, or in a loose corymbiform or subpaniculiform, sometimes subumbelliform cyme, bisexual. Petals shortly stalked or sessile, sometimes

spurred or succate near the base, shorter than sepals, sometimes petals absent. Ovules several to 2 in a carpel, bitegmic, rarely unitegmic. Follicles 1 to many in a fruit, free, sometimes slightly connate, without longitudinal veins, with branched transverse veins on lateral faces, beaks distinct. $x = 7$.

47. *Enemion* Raf.

Enemion Raf., Jour. Phys. 41: 70 (1820).

Perennials with or without creeping rhizome. Roots fibrous, sometimes tuberous. Basal leaves biternate, blades usually 3-lobed to -fid, lobes obtuse or emarginate, pointed at apex. Cauline leaves alternate, sessile. Sepals 5. Petals 0. Follicles 3–6, attenuate to the base, or stalked. $x = 7$. Two sections. Sect. *Enemion*: flowers solitary at the tip of stem or branches, four spp., temperate to subcold zone of N America. Sect. *Umbellata* Drumm. & Hutch. (1920): flowers in an umbellate cyme; two spp., temperate to subcold zone of NE Asia and western N America.

48. *Isopyrum* L.

Isopyrum L., Sp. Pl.: 557 (1753), ex. p.; Tamura and Lauener, Notes R. Bot. Gard. Edinb. 37: 272 (1968).

Perennials with creeping rhizome. Roots fibrous, sometimes tuberous. Basal leaves 2–4-ternate, blades 3–5-lobed to -sect, emarginate, pointed at apex. Cauline leaves alternate to subopposite, shortly petiolate to sessile, 1–3-ternate. Flowers in loose racemiform or corymbiform cyme. Sepals 5. Petals 5, slightly concave at the base, or tubulose, shortly stalked. Follicles 1–5, shortly stalked or sessile. $x = 7$. Four spp., Eurasia.

49. *Leptopyrum* Reichb.

Leptopyrum Reichb., Consp. Regni Veg.: 192 (1828).

Annuals with a tap root. Basal leaves subbiternate, blades often 3-lobate to partite, lobes obtuse. Cauline leaves alternate or subopposite, resembling the basal, upper ones often whorled. Flowers usually in more or less modified trichasial cyme, broadly campanulate. Sepals 5. Petals 5, tubulose, inner wall shorter than the outer, shortly stalked. Follicles 6–20, nearly sessile. $x = 7$. One sp., from Siberia to N Korea. Naturalised in Europe.

50. *Paraquilegia* Drumm. & Hutch.

Paraquilegia Drumm. & Hutch., Kew Bull. 1920: 156 (1920).

Perennials with thick, erect rhizome, densely covered with remains of old leaf-bases. Basal leaves ternately

compound, blades 3-lobed to -sect, thick, glaucous beneath. Stem simple, with 2 bracts. Flower single, broadly campanulate. Sepals 5. Petals 5, nearly sessile, obovate, bilobed, concave at the base. Follicles 3–10, sessile or shortly stalked. $x = 7$. Five spp., alpine zone of Himalayas, west to Iran, C Asia and W China.

51. *Semiaquilegia* Makino

Semiaquilegia Makino, Bot. Mag. Tokyo 16: 119 (1902).

Perennials with tuberous rhizome. Basal leaves ternate, blades 3 or 2-fid to -sect, segments lobate to partite, lobes obtuse. Cauline leaves alternate, similar to the basal, upper ones nearly sessile. Flowers at the tip of stems and branches, nutant, broadly campanulate. Sepals 5. Petals 5, sessile, with short, saccate spur at the base. Intrastaminal scales membranaceous, 1–4. Follicles 2–5, diverged, sessile, beaks short. $x = 7$. One sp., China, S Korea and W Japan.

52. *Urophysa* Ulbr.

Urophysa Ulbr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 868 (1929).

Perennials with thick, erect rhizome. Basal leaves 3-sect or ternate, blades obovate, lobate to partite, lobes lobulate, obtuse. Cauline leaves bract-like, 3-lobed to entire. Flowers 1–3 in corymbiform cyme, opening nearly flat. Sepals 5. Petals 5, navicular, shorter than a half of sepals. Intrastaminal scales membranaceous, ca. 7. Follicles 5, sometimes to 8, nearly erect, sessile, beaks about twice as long as the follicle body. Two spp., China.

53. *Aquilegia* L.

Fig. 123T–W

Aquilegia L., Sp. Pl.: 533 (1753); Munz, Gentes Herb. 7: 3 (1946).

Perennials with thick, erect rhizome. Basal leaves 1–3-ternate, blades 3-lobed to -partite, lobes lobulate, obtuse. Cauline leaves similar to the basal, upper ones bract-like. Flowers terminal to stem and branches, usually pentamerous. Sepals 5, spreading. Petals 5, nearly erect, usually spurred or saccate at the base. Intrastaminal scales membranaceous, 10. Follicles 5, sometimes to 15, or to 3, nearly erect, slightly connate downward. $x = 7$. About 80 spp., widely distributed in the northern hemisphere.

2. Tribe Dichocarpeae (Tamura & Kosuge)

W. T. Wang & D. Z. Fu (1990)

Leaves mostly pedately compound. Flowers in a dichasium, bisexual. Petals long stalked, not saccate at the base, shorter than sepals. Ovules several in a carpel, bitegmic. Follicles 2, connate at the base, with a distinct longitudinal vein and faint transverse veins on each lateral face. $x = 6$.

54. *Dichocarpum* W. T. Wang & Hsiao

Dichocarpum W. T. Wang & Hsiao, Acta Phytotaxon Sin. 9: 323 (1964); Tamura and Lauener, Notes R. Bot. Gard. Edinb. 28: 270 (1968).

Perennials with creeping or short rhizome, sometimes annuals. Basal leaves pedately 5–13-, rarely 3-foliolate, middle leaflet without further division, blades 3–5-lobed, crenate-dentate, teeth emarginate, pointed at apex. Flowers 3 to more than 50, in a dichasium or its modification, sometimes cleistogamous flowers produced. Sepals 5. Petals usually 5, blades cup-shaped, bilabial or unilabial, stalks longer than blades. Follicles 2, divaricate, connate at the base, beaks distinct. $2n = 24$ or 36. Three sections, about 20 spp., from Himalayas to Japan.

3. Tribe Coptideae Langlet ex Tamura & Kosuge (1989)

Leaves ternately or pinnately compound, pedate, rarely simple. Flowers terminal to stem, or in a racemiform cyme or cymes, bisexual, sometimes unisexual. Petals stalked, shorter than sepals, blades basically thick. Ovules several to 2 in a carpel, bitegmic. Follicles several, free, without, rarely with a longitudinal vein, without distinct transverse veins on lateral faces. $x = 8$, or 9.

55. *Asteropyrum* Drumm. & Hutch.

Asteropyrum Drumm. & Hutch., Kew Bull. 1920: 155 (1920).

Perennials. Basal leaves simple, distinctly peltate, blade round, shallowly 5–7-lobed to nearly entire. Stem simple, with 2 or 3 bracts. Flower single, terminal, opening nearly flat. Sepals 5. Petals 5–8, stalks longer than thick, cup-shaped blades. Follicles 5–10, spreading, without longitudinal veins on lateral faces, beaks straight. $x = 8$. Two spp., China.

56. *Coptis* Salisb.

Coptis Salisb., Trans. Linn. Soc. London 8: 305 (1807); Satake, J. Jpn. Bot. 24: 73 (1949).

Perennials with creeping rhizome, or producing stolons. Basal leaves 1–4 times ternate or subpinnate, sometimes pedately 5-foliolate, blades chartaceous, coarsely dentate. Stem simple, with linear to partite bracts. Flowers 1 to several, terminal to stem, or in a loose racemiform cyme, hermaphrodite or polygamous. Sepals 5–8. Petals 5 to more than 10, blades cup-shaped, hollowed, or ovate to lanceolate, usually thick with nectary tissue on upper surface. Follicles 5–15, stalked, arranged in a whorl, spreading. $x = 9$. Two subgenera, 15 spp., from warm to subalpine zone of E Asia and western N America.

57. *Xanthorhiza* Marshall

Xanthorhiza Marshall, Arb. Amer. 167 (1785), "*Xanthorrhiza*".

Deciduous, rhizomatous shrub, producing suckers. Leaves aggregate near the top of stem, pinnate or bipinnate, blades usually 5, often 3-fid to -parted, incised-serrate. Inflorescences simple or compound racemiform, drooping, many-flowered. Flowers polygamous. Sepals 5. Petals 5, more or less spreading, blades thick, dilated upward, slightly bilobed, with nectary tissue on upper surface, narrowed downward to stalk. Follicles 5 or 10, without veins on lateral faces, ventral side more developed than the dorsal, beaks turning outside, short, containing 1 hanging seed. One sp., temperate eastern N America.

IV. Subfam. Thalictrioideae Heintze (1927)

Flowers a few to many, actinomorphic or more or less irregular, without petals. Ovule single, produced from the middle of the upper margin of well-developed adaxial wall of the carpel, supplied with the middle division of a ventral bundle, bitegmic. Fruits a head of achenes with longitudinal, often branched veins on lateral faces. Chromosome T-type. $x = 7$.

58. *Thalictrum* L.

Fig. 123 X, Y

Thalictrum L., Sp. Pl.: 545 (1753); Lecoyer, Bull. Soc. R. Bot. Belg. 24: 78 (1885); Boivin, Rhodora 46: 346 (1944).

Perennials usually with sympodial rhizome, sometimes stoloniferous. Roots sometimes tuberous. Basal leaves ternately to pinnately compound, rarely simple, blades 3–7-lobed to -parted, sometimes undivided, lobes entire, lobulate, crenate, sometimes dentate. Cauline leaves alternate, sometimes subopposite or whorled, similar to the basal. Inflorescence

usually definite corymbiform, paniculiform, racemiform, umbelliform, or their modification. Flowers bisexual or unisexual. Sepals 3–10. Petals 0. Achenes sessile or stipitate, with 1–3, often branched or reticulate veins on each lateral face. $x = 7$. Two subgenera. Subgen. *Thalictrum*: flowers hermaphrodite, stigmas usually not exceeding sepals in flower time; about 250 spp., Eurasia, south to Aethiopia and New Guinea, and N America. Subgen. *Lecoyerium* Boivin (1944): flowers monoecious, dioecious or polygamous, sometimes hermaphrodite, stigmas elongate, exceeding sepals in flower time; about 80 spp., N and S America, Africa, S Europe and W China.

V. Subfam. Hydrastidoideae Engler & Gilg (1924)

Flower terminal to stem, actinomorphic, without petals. Ovules 2–4 in a carpel, produced from both lateral margins of the carpel supplied with branches of both ventral bundles. bitegmic. Fruits a head of berries. Chromosome T-type. $x = 13$.

59. *Hydrastis* L.

Hydrastis L., Syst. Nat. ed. 10: 1088 (1759).

Perennials with thick horizontal rhizome. Basal leaves usually not at the base of stem, 5–7-lobed to -fid, incised-serrate. Cauline leaves 2–3, similar to the basal, upper one almost sessile. Flower single, terminal to stem, bisexual. Sepals 3, caducous. Petals none. Berries 5–15 in a head, red, containing 1–2 seeds. One sp., temperate C and eastern N America.

Selected Bibliography

- Adanson, M. 1763. Familles des plantes. 2 Vols. Paris: Vincent.
 Aichele, D., Schwegler, H. W. 1957. Die Taxonomie der Gattung *Pulsatilla*. Feddes Repert. Spec. Nov. Regni Veg. 60: 1–230.
 Baumberger, H. 1971. Chromosomenzahlbestimmungen und Karyotypanalysen bei den Gattungen *Anemone*, *Hepatica* und *Pulsatilla*. Ber. Schweiz. Bot. Ges. 80: 17–95.
 Benson, L. 1948. A treatise on the North American Ranunculi. Amer. Midl. Nat. 40: 1–264.
 Bhandari, N.N. 1965. Studies in the family Ranunculaceae VIII. Variations in the development of the embryo sac of *Anemone vitifolia*. Phytomorphology 15: 285–291.
 Bhandari, N.N. 1966. Id. IX. Embryology of *Adonis*. Phytomorphology 16: 578–587.
 Bhandari, N.N., Asnani, S. 1966. Studies in the family Ranunculaceae. XI. Morphology and embryology of *Ceratocephalus falcatus* Per. Beitr. Biol. Pflanz. 45: 271–290.
 Bhandari, N.N., Vijayaraghavan, M.R. 1970. Id. XII. Embryology of *Aquilegia vulgaris*. Beitr. Biol. Pflanz. 46: 337–354.
 Blanché, C. 1990. *Delphinium* L. Subgen. *Delphinium*: origin and evolutionary trends. Collect. Bot. (Barcelona) 19: 75–95.
 Boivin, J.R.B. 1944. American *Thalictra* and their Old World allies. Rhodora 46: 337–377, 391–445, 453–487.

- Cronquist, A. 1981. See general references.
 Dafni, A., Bernhardt, P., Shmida, A., Ivry, Y., Greenbaum, S., O'Toole, Ch., Losito, L. 1990. Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. Isr. J. Bot. 39: 81–92.
 Daumann, E. 1969. Zur Blütenmorphologie und Bestäubungsökologie einiger Ranunculaceen (*Cimicifuga* L., *Actaea* L., *Thalictrum* L.). Preslia (Praha) 41: 213–219.
 Doroszevska, A. 1974. The genus *Trollius* L. A taxonomical study. Monogr. Bot. 41: 1–167.
 Drummond, J.R., Hutchinson, J. 1920. A revision of *Isopyrum* (Ranunculaceae) and its nearer allies. Kew Bull. 1920: 145–169.
 Eames, A.J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Amer. J. Bot. 18: 147–188.
 Eichler, H. 1958. Revision der Ranunculaceen Malesiens. Bibl. Bot. 124: 1–110.
 Emura, K. 1972. Cytotaxonomic studies on the genus *Thalictrum* in Eurasia with special reference to Japanese species. J. Fac. Univ. Tokyo, Sect. 3, Bot. 9: 93–135.
 Erdtman, G. 1952. See general references.
 Fu, D.-Z. 1990. Phylogenetic consideration on the subfamily Thalictrioideae (Ranunculaceae). Cathaya 2: 181–190.
 Goepfert, D. 1974. Karyotypes and DNA content in species of *Ranunculus* L. and related genera. Bot. Not. 127: 464–489.
 Grant, V. 1976. Isolation between *Aquilegia formosa* and *A. pubescens*: A reply and reconsideration. Evolution 30: 625–628.
 Gregory, W.C. 1941. Phylogenetic and cytological studies in the Ranunculaceae Juss. Trans. Amer. Philos. Soc. n.s. 31: 443–521.
 Haccius, B. 1950. Weitere Untersuchungen zum Verständnis der zerstreuten Blattstellung bei den Dikotylen. Sitzungsber. Heidelberger Akad. Wiss. Math.-Naturw. Kl. Jahrg. 1950, 6 Abh.: 289–337.
 Hegnauer, R. 1966. Comparative phytochemistry of alkaloids. In: Swain, T. (Ed.) Comparative Phytochemistry. London: Academic Press, pp. 211–230.
 Heimburger, M. 1959. Cytotaxonomic studies in the genus *Anemone*. Can. J. Bot. 37: 587–612.
 Hiepkö, P. 1965. Vergleichend-morphologische und entwicklungsgeschichtliche Untersuchungen über das Perianth bei Polycarpiceae. Bot. Jahrb. Syst. 84: 359–508.
 Horovitz, A. 1976. Edaphic factors and flower-colour distribution in the Anemoneae (Ranunc.) Pl. Syst. Evol. 126: 239–242.
 Huss, H.A. 1906. Beiträge zur Morphologie und Physiologie der Antipoden. Zürich: Doct. Diss.
 Hutchinson, J. 1923. Contribution towards a phylogenetic classification of flowering plants 1. Kew Bull. 1920: 65–89.
 Hutchinson, J. 1969. Evolution and phylogeny of flowering plants. Dicotyledons: facts and theory. London: Academic Press.
 Janchen, E. 1949. Die systematische Gliederung der Ranunculaceen und Berberidaceen. Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 108, 4. Abh.: 1–82.
 Kaplan, S.M., Mulcahy, D.L. 1971. Mode of pollination and floral sexuality in *Thalictrum*. Evolution 25: 659–668.
 Knuth, P. 1898. Handbuch der Blütenbiologie II, 1. Leipzig, W. Engelmann, pp. 1–55.
 Knuth, P. 1904. id. III, 1: 192–301.
 Kosuge, K., Tamura, M. 1988. Morphology of the petal in *Aconitum*. Bot. Mag. (Tokyo) 101: 223–237.
 Kosuge, K., Tamura, M. 1989. Ontogenetic studies on petals of the Ranunculaceae. J. Jpn. Bot. 64: 65–67.
 Kratochwil, A. 1988. Zur Bestäubungsstrategie von *Pulsatilla vulgaris*. Flora 181: 262–324.
 Kürbs, S. 1973. Vergleichend-entwicklungsgeschichtliche Stu-

- dien an Ranunculaceen-Fiederblättern. Bot. Jahrb. Syst. 93: 130–167.
- Kumazawa, 1935. The structure and affinities of *Paeonia*. Bot. Mag. (Tokyo) 49: 306–315.
- Kumazawa, M. 1938. On the ovular structure in the Ranunculaceae and Berberidaceae. J. Jpn. Bot. 14: 10–25.
- Kurita, M. 1958. Chromosome studies in Ranunculaceae IX. Comparison of chromosome volume between a 14- and a 16-chromosome species in *Anemone* and in *Ranunculus*. Rep. Biol. Inst., Ehime Univ. 6: 1–7.
- Kurita, M. 1960. Id. XVI. Comparison of an aspect of nucleus and chromosome between several genera. Mem. Ehime Univ., Sect. 2, Ser. B, 4: 53–58.
- Kurita, M. 1963. Id. XXI. Karyotypes of *Myosurus* and *Adonis*. Mem. Ehime Univ., Sect. 2, Ser. B, 4: 487–492.
- Langlet, O. 1932. Über Chromosomenverhältnisse und Systematik der Ranunculaceae. Sven. Bot. Tidskr. 26: 381–400.
- Leinfellner, W. 1958. Beiträge zur Kronblattmorphologie VIII. Der peltate Bau der Nektarblätter von *Ranunculus*, dargestellt an Hand jener von *Ranunculus pallasii* Schlecht. Österr. Bot. Z. 105: 184–192.
- Lewitsky, G. A. 1931. The karyotype in systematics, on the base of karyology of the subfamily Helleboreae. Tr. Prikl. Bot. 27: 187–240.
- Lourteig, A. 1952. Ranunculáceas de Sudamerica templada. Darwiniana 9: 397–608.
- Lourteig, A. 1956. Ranunculáceas de Sudamerica tropical. Mem. Soc. Cienc. Nat. La Salle 16: 19–228.
- Lubbers, A. E. 1982. Spatial and temporal variation in the reproductive characteristics of *Thalictrum thalictroides* (L.) Eames and Bivin, a forest herbaceous perennial. Ph. Thesis, Duke University.
- Malyutin, N. I. 1987. The system of the genus *Delphinium* L. based on the morphological features of seeds. Bot. Zhurn. (Leningrad): 683–693.
- Mathew, B. 1989. Helleborus. Woking: Alpine Garden Society.
- Melampy, M. N., Hayworth, A. M. 1980. Seed production and pollen vectors in several nectarless plants. Evolution 34: 1144–1154.
- Moffet, A. A. 1932. Chromosome studies in *Anemone*. I. A new type of chiasma behaviour. Cytologia 4: 26–37.
- Mu, X.-J. 1984. Early development of the endosperm in *Kingdonia uniflora*. Acta Bot. Sin. 26: 668–671.
- Nowicke, J. W., Skvarla, J. J. 1979. Pollen morphology: The potential influence in high order systematics. Ann. Mo. Bot. Gard. 66: 633–700.
- Nowicke, J. W., Skvarla, J. J. 1982. Pollen morphology and the relationships of *Circaea*, of *Kingdonia*, and of *Sargentodoxa* to the Ranunculales. Amer. J. Bot. 69: 990–998.
- Okada, H., Tamura, M. 1979. Karyomorphology and relationship on the Ranunculaceae, J. Jpn. Bot. 54: 65–77.
- Picci, V. 1969. Embryological research on the genus *Thalictrum*. II. G. Bot. Ital. 103: 475–483.
- Prantl, K. 1887. Beiträge zur Morphologie und Systematik der Ranunculaceen. Bot. Jahrb. Syst. 9: 225–273.
- Price, M., Waser, N. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. Nature 277: 294–296.
- Rasmussen, H. 1979. The genus *Knowltonia* (Ranunculaceae). Opera Bot. 53: 3–44.
- Rohweder, O. 1967. Karpellbau und Synkarpie bei Ranunculaceen. Ber. Schweiz. Bot. Ges. 77: 376–432.
- Ruijgrok, H. W. L. 1966. The distribution of ranunculin and cyanogenetic compounds in the Ranunculaceae. In: Swain, T. (Ed.) Comparative phytochemistry London: Academic Press, pp. 175–186.
- Santisuk, T. 1979. A palynological study of the tribe Ranunculaceae. Opera Bot. 48: 1–76.
- Satake, Y. 1949. A note on *Coptis* of Japan. J. Jpn. Bot. 24: 69–74.
- Schaeppi, H., Frank, K. 1962. Vergleichend-morphologische Untersuchungen über die Karpellgestaltung, insbesondere die Plazentation bei Anemoneen. Bot. Jahrb. Syst. 81: 337–357.
- Schrödinger, R. 1909. Der Blütenbau der zygomorphen Ranunculaceen und seine Bedeutung für die Stammesgeschichte der Helleboreen. Abh. K. K. Zool.-Bot. Ges. Wien 4–5: 1–63.
- Schrödinger, R. 1914. Das Laubblatt der Ranunculaceen. Eine organogeschichtliche Studie. Abh. K. K. Zool.-Bot. Ges. Wien 8–2: 1–71.
- Smit, P. G. 1973. A revision of *Caltha* (Ranunculaceae). Blumea 21: 119–130.
- Smith, G. H. 1926. Vascular anatomy of Ranalian flowers. I. Ranunculaceae. Bot. Gaz. 82: 1–29.
- Tamura, M. 1962. Petiolar anatomy in the Ranunculaceae. Sci. Rep. Osaka Univ. 11: 19–47.
- Tamura, M. 1963. Morphology, ecology and phylogeny of the Ranunculaceae I. Sci. Rep. Osaka Univ. 11: 115–126.
- Tamura, M. 1965. Id. IV. Sci. Rep. Osaka Univ. 14–1: 53–71.
- Tamura, M. 1966. Id. VI. Sci. Rep. Osaka Univ. 15: 13–35.
- Tamura, M. 1967. Id. VII. Sci. Rep. Osaka Univ. 16–2: 21–43.
- Tamura, M. 1968a. Id. VIII. Sci. Rep. Osaka Univ. 17: 41–56.
- Tamura, M. 1968a. A revision of genus *Naravelia*. Acta Phytotaxon Geobot. 37: 106–110.
- Tamura, M. 1972. Morphology and phyletic relationships of the Glauciaceae. Bot. Mag. (Tokyo) 85: 29–41.
- Tamura, M. 1980. Change of phyllotaxis in *Clematis lasiantha* Maxim. J. Jpn. Bot. 55: 257–265.
- Tamura, M. 1981. Morphology of *Coptis japonica* and its meaning in phylogeny. Bot. Mag. (Tokyo) 94: 165–174.
- Tamura, M. 1987. A classification of genus *Clematis*. Acta Phytotaxon Geobot. 38: 33–44.
- Tamura, M., Kosuge, K. 1989. Classification of the Isopyroideae. Acta Phytotaxon Geobot. 40: 31–35.
- Tamura, M., Lauener, A. L. 1968. A revision of *Isopyrum*, *Dichocarpum* and their allies. Notes R. Bot. Gard. Edinb. 37: 431–466.
- Tamura, M., Mizumoto, Y. 1972. Stages of embryo development in ripe seeds or achenes of the Ranunculaceae. J. Jpn. Bot. 47: 225–237.
- Tamura, M., Mizumoto, Y. 1974. The cotyledon and growing point in the monocotyledonous embryos of *Shibateranthus pinnatifida* and *Anemone flaccida*. J. Jpn. Bot. 49: 123–128.
- Tobe, H., Keating, R. C. 1985. The morphology and anatomy of *Hydrastis* (Ranunculaceae): systematic evaluation of the genus. Bot. Mag. (Tokyo) 98: 291–316.
- Troll, W. 1932. Morphologie der schildförmigen Blätter. Planta 17: 153–314.
- Tschermak-Woess, E. 1956. Notizen über die Riesenkerne und “Riesenchromosomen” in den Antipoden von *Aconitum*. Chromosoma 8: 114–134.
- Van Heel, W. A. 1981. A S. E. M.-investigation on the development of free carpels. Blumea 27: 499–522.
- Van Heel, W. A. 1983. The ascidiform early development of free carpels, a S. E. M. investigation. Blumea 28: 231–270.
- Waddington, K. D. 1981. Factors influencing pollen flow in bumblebee-pollinated *Delphinium virescens*. Oikos 37: 152–159.
- Wang, W.-T. 1974. Notulae de Ranunculaceis sinensibus III. Acta Phytotaxon Sin. 12: 155–180.
- Wang, W.-T., Hsiao, P.-K. 1965. Id. II. Acta Phytotaxon. Sin. Addit. 1: 49–103.