

Modern View on the Taxonomy of the Genus *Anemone* L. Sensu Stricto (*Ranunculaceae*)

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As a result of the re-examination of the *Anemone* genus taxonomy, we accept this genus as including 15 subgenera, 23 sections, 4 subsections, 23 series and 118 species. Within *Anemone*, 6 subgenera, 2 sections and 16 series were proposed originally by us, and we re-examined the taxonomic state of ca. 50 species and intraspecific taxa. Besides, we elaborated the annotated conspectus of the genus *Anemone* and the key for determination of its species, series, subsections, sections and subgenera on the basis of the analysis of about 70 characters of the achenes, flowers, leaves, above-ground and underground shoots and roots. (Continued from J. Jpn. Bot. **81**: 193–224, 2006)

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Literature survey

The genus *Anemone* L. is one of the largest genera within the family *Ranunculaceae*. The status of this genus, the number of its species, its division into sections and other intergeneric taxa, as well as their taxonomic and evolutionary relationships are long-debated.

Beginning from Linnaeus (1753), who described the genus *Anemone*, there have been different opinions on its delimitation and size. One year after Linnaeus, Miller (1754) separated from *Anemone* the genera *Pulsatilla* Mill., *Hepatica* Mill. and *Anemonoides* Mill., and shortly afterwards Adanson (1763) described the allied genus *Oriba* Adans.

Jussieu (1789) recognized the genus *Anemone* in the Linnaean sense, while Candolle (1817, 1824) was the author of the

first systematic treatment of this genus. He regarded *Hepatica* as independent genus and proposed to place *Anemone* and *Hepatica* into the tribe *Anemoneae* DC., together with *Knowltonia* Salisb., *Thalictrum* L., *Hydrastis* L. and *Hamadryas* Comm. & H. Lév., etc. In his *Anemone* system, there were six groups, and only four of them included species of *Anemone* sensu proprio (*Anemonanthea* DC., *Anemonospermos* DC., *Omalocarpus* DC., and *Pulsatilloides* DC.), while two groups (*Pulsatilla* DC. and *Preonanthus* DC.) embraced species currently placed in *Pulsatilla*.

Gray (1821) elevated the section *Anemonanthea* to generic level (*Anemonanthea* S. F. Gray), although exactly this group of species was already described as the genus *Anemonoides* (Miller 1754). Rafinesque (1825) recognized the North American species (*A. caroliniana* and others)

as the genus *Hepatica* Raf., while Gay (1845) described the genus *Barneoudia* C. Gay from South America as close to *Anemone*. Meanwhile, Schur (1866) regarded *A. narcissiflora* and allied species as the genus *Homalocarpus* Schur, Schlechtendal (1856) segregated the South American species allied to *Pulsatilla* as the monotypic genus *Oreithales* Schlecht., and some forty years later the same taxon was erroneously described as the genus *Capethia* Britt. (Britton 1892).

Sprengel (1825) accepted generic state of *Anemone* and *Pulsatilla* only, Spach (1839) who described subtribe *Anemoninae* recognized both *Pulsatilla* and *Hepatica* as the genera, and Pritzell (1841) did not recognize *Pulsatilla*. Prantl (1887) regarded it as a genus, but included *Hepatica* in *Anemone* and did not recognize *Knowltonia* and *Barneoudia*. Finally, Janczewski (1892) accepted all the forementioned taxa (except *Knowltonia*) as groups within the delimitation of *Anemone*.

After Candolle, several new sections within *Anemone* were described: *Diplocalymnata* Spreng. (Sprengel 1825), *Sylvia* Gaudin (Gaudin 1828), *Oriba* (Adans.) Spach, *Anemonidium* Spach and *Phaeandra* Spach (Spach 1839), *Eriocephalus* Hook. f. & Thomson (Hooker and Thomson 1855) and some others.

The most detailed system of the genus *Anemone* s. l. was worked out by Ulbrich (1905, 1906). The author recognized genera *Pulsatilla*, *Knowltonia*, *Barneoudia* and *Capethia*, but he regarded *Hepatica* as the subgenus of *Anemone*. Within subgenus *Euanemone*, Ulbrich recognized six sections already proposed, viz., *Anemonanthea* DC., *Omalocarpus* DC., *Pulsatilloides* DC., *Anemonidium* Spach, *Eriocephalus* Hook. f. & Thomson, and *Rivularidium* Jancz. This author described four subsections (*Tuberosa* Ulbr., *Stolonifera* Ulbr., *Brevistylae* Ulbr. and *Longistylae* Ulbr.), and he also described

17 series (viz., *Himalayicae* Ulbr., *Begoniifolia* Ulbr., etc.). As a whole, Ulbrich revised in his monograph 76 species of *Anemone* distributed worldwide.

Ulbrich's *Anemone* system was generally accepted for many years, and its profound examination was absent, except for the particular proposals, mainly within the so called "local floras". Thus Juzepchuk (1937) gave several additions for species occurring within the borders of the former Soviet Union and he regarded all *Anemone* sections sensu Ulbrich as subgenera (viz., *Anemonanthea* DC., *Homalocarpus* DC., *Pulsatilloides* DC., *Anemonidium* Spach, *Eriocephalus* Hook. f. & Thomson, and *Rivularidium* Jancz.), besides, he elevated most of Ulbrich's subsections and series to section level. Juzepchuk also described several additional series (viz., *Nemorosae* Juz., *Flaccidae* Juz., *Baicalenses* Juz., *Sylvestres* Juz. and *Rupicolae* Juz.) but did not support them with Latin diagnoses, like other taxonomic novelties.

Nakai (1949) separated some species of the section *Anemonospermos* as the genus *Eriocapitella* Nakai, and Wang (1974) admitted the generic state of the monotypic series *Anemoclema* Franch. (Franchet 1886, 1888, 1890) as the genus *Anemoclema* (Franch.) W. T. Wang.

Sixty years after Ulbrich, Tamura (1967) re-shaped the *Anemone* system while the revising the system of *Ranunculaceae*. As a whole, this author accepted all six sections of *Anemone* sensu Ulbrich, however, he added three *Anemone* sections, and only one of them (the monotypic section *Keiskea* Tamura) was really new because sections *Begoniifolia* Tamura and *Anemoclema* Tamura were the former series *Begoniifolia* Ulbr. and *Anemoclema* Franch. Besides, Tamura re-examined section *Pulsatilloides*, and he ignored its subsections *Brevistylae* and *Longistylae* sensu Ulbrich but moved the series *Himalayicae* sensu Ulbrich from

Pulsatilloides to the section *Omalocarpus* as the subsection *Himalayicae*. This author described three series (*Nemorosae* Tamura, *Flaccidae* Tamura and *Rupicola* Tamura), although all of them were described in 1937 by Juzepchuk (1937). Despite the fact that the Juzepchuk series were invalid, Tamura's taxa were not supported by Latin diagnoses and were invalid too.

Beside the recognition of the genera *Pulsatilla*, *Hepatica*, *Knowltonia* and *Barneoudia*, Tamura accepted also three "narrow" or segregate genera *Capethia*, *Miyakea* and *Eriocapitella*. Like most of his predecessors, Tamura recognized the tribe *Anemoneae* and subtribe *Anemoninae*.

After Tamura, further splitting of the genus *Anemone* continued. So Löve and Löve (1975) separated from it the monotypic series *Richardsonia* Ulbr. as the genus *Jurtsevia*, Holub (1973) recalled the genus *Anemonoides* Mill. and described the genera *Anemonastrum* Holub (former sect. *Omalocarpus* DC. or genus *Homalocarpus* Schur) and *Anemonidium* (Spach) Holub (former sect. *Anemonidium*), and Wang (1980) separated the narrow genus *Metanemone* W. T. Wang. While working out his taxonomic scheme of the genus *Anemone* for the flora of China, this author mainly followed Ulbrich (1906) and Tamura (1967), but he included both *Eriocapitella* and *Anemoclema* in *Anemone*.

While discussing the phylogeny of the family, Ziman (1985) proposed several alterations for the system of *Anemone* and *Anemoninae*, viz., she recognized the genera *Pulsatilla*, *Hepatica*, *Knowltonia* and *Barneoudia* but did not except the genera *Eriocapitella*, *Anemoclema*, *Anemonidium*, *Anemonastrum*, and *Anemonoides* (recognizing them as parts of the genus *Anemone*), and *Capethia*, *Oreithales* and *Miyakea* (parts of the genus *Pulsatilla*). Beside, Ziman proposed to elevate the rank of four of Ulbrich's series to sections *Richardsonia*

(Ulbr.) Ziman, *Parviflora* (Ulbr.) Ziman, *Flaccida* (Ulbr.) Ziman, and *Himalayicae* (Ulbr.) Ziman. She also separated some species of the section *Rivularidium* into the section *Rivularis* (Ulbr.) Ziman, and some species of the section *Anemospermos* into the section *Vitifolia* Ziman. The first five sections were supported by Latin diagnoses, therefore, they may be considered as the valid ones.

The novations of Starodubtsev (1989, 1991) represented a new stage of the further complication of the genus *Anemone* and the system of the subtribe as a whole, and in fact he revised the huge forementioned taxonomic group. Beside admitting the genera *Pulsatilla*, *Hepatica* and *Barneoudia*, Starodubtsev followed Holub (1973) in confirming the generic independence of *Anemonoides*, *Anemonastrum* and *Anemonidium*. He moved several species from section *Rivularidium* to *Anemonidium*, and he elevated the rank of three sections to the generic level [viz., *Pulsatilloides* (DC.) Starod., *Arsenjevia* Starod. (former section *Flaccida* Juz.) and *Tamuria* Starod. (former sect. *Keiskea* Tamura)]. Within the genus *Anemone* sensu strictissimo, Starodubtsev recognized three sections (*Anemone*, *Eriocephalus* and *Diplocalymnata*) and ten subsections.

The results of the Starodubtsev study are very valuable but they were based on the peculiarities of the fruits only, and his new concept of the tribe *Anemoninae* was based mostly on material from the Russian Far East. Moreover, our re-examination of his herbarium materials in LE and VLA has shown that his data were mostly inadequately documented. In our opinion, some taxonomic proposals of Starodubtsev within the genus *Anemone* s. l. and the subtribe *Anemoninae* are debatable, especially his narrow generic concept, but all of them provide a serious base for the further examination of this taxon in detail.

About at the same time as Starodubtsev, Tamura (1991, 1995) proposed some improvements and alterations to the system of the family *Ranunculaceae*, subtribe *Anemoninae* and genus *Anemone*. This author confirmed the recognition of genera *Pulsatilla*, *Hepatica*, *Knowltonia*, *Barneoudia*, *Metanemone* and *Oreithales* (instead of *Capethia* in 1967), and, like earlier, he recognized all six subgenera of Juzepchuk (1937). Beside that, Tamura elevated the rank of section *Anemoclema* (Franch.) Tamura to subgenus *Anemoclema* (Franch.) Tamura, series *Hepaticifolia* Ulbr. to subgenus *Hepaticifolia* (Ulbr.) Tamura, and series *Rigida* Ulbr. to subgenus *Rigida* (Ulbr.) Tamura. He confirmed his own section *Keiskea* (within the subgenus *Anemonanthea*), and he elevated subsections *Tuberosae* Ulbr., and *Stoloniferae* Ulbr., and series *Richardsoniae* Ulbr., *Alchimillefolia* Ulbr., and *Kilimandscharica* Ulbr. to the level of sections.

The data on serology (Jansen 1968, Chupov 1975, etc.), biochemistry (Hantula et al. 1989, Hoot 1995, Hoot et al. 1994, etc.), geographical patterns (Ziman 1985, Ziman and Keener 1989, etc.) were also important for clarification of some problems of *Anemone* s. l. and they have added a wealth of new information concerning the overall relationships within all taxa of the subtribe *Anemoninae*.

However, many questions of the taxonomy of the genus *Anemone* s. l. are still open. Thus, one very important task is the revision of the generally accepted characters, and more accurate definition of their diagnostic and evolutionary significance, but also the selection and examination of approaches and diagnostic characters of *Anemone* taxa.

Morphologic characters essential for taxonomy of *Anemone*

Beginning from Candolle (1817), the majority of the systems of the genus

Anemone have been based on distinctions of fruits and perianth, and most authors paid the great attention to the shape, size and pubescence of these organs. Some authors (e.g., Tamura 1995) have also taken into consideration additional characters of leaves and shoots, especially while distinguishing sections and series.

The anatomical studies of fruits of *Anemone* taxa began with Janczewski (1890, 1892) and Smith (1926), and according to Starodubtsev (1991) and Tamura (1963, 1995), the structure peculiarities of *Anemone* achenes are very important for their taxonomy. However, the literature data on *Anemone* achenes (Ponomarenko and Berestetskaya 1981, Chaudhari and Trifonova 1988, etc.) encompasses approximately 60 species. Therefore, we tried to include in our study the fruit morphology (and partly anatomy) of as many *Anemone* species as possible. We examined ca. 110 *Anemone* species in detail (including data on cross section and microsculpture of a surface). Initially we published our results on study of achenes (and other organs) of *A. narcissiflora* and *A. biflora* aggregates (Ziman et al. 1997, 1998) but afterwards we published results for subgenera *Anemonanthea*, *Stoloniferae* and *Omalocarpus* (Ziman et al. 2004a, 2004b, 2004c, 2005, 2006a, 2006b), and section *Himalayicae* (Ziman et al. 2007). We realized the value of comparative study of *Anemone* carpels and achenes because most of their morphological characters are in common, and their distinctions help us to understand possible evolutionary trends.

Most authors used five to eight achene characters (mainly of external morphology) to distinguish *Anemone* species and their groups. According to Hoot et al. (1994), it is expedient to use around 10 achene characters, and they proposed to add to the known characters shape of fruitlets and number of achenes in them. Considering our recent

studies, we believe it possible to extend the number of the fruit characters of *Anemone* species to 25.

It is well known that *Anemone* fruits are apocarpic one-seeded achenes forming heads (fruitlets). We paid the attention to the common carpel and achene shape (viz., ovoid, globose or ellipsoid) but also the peculiarities of their basal (sessile, stalked or at least narrowed) and apical (rounded or narrowed) parts. We concluded that Starodubtsev has exaggerated the taxonomic significance of the stalked *Anemone* achenes when he separated several species (viz., *A. keiskeana* and *A. deltoide*) into genus *Tamuraia* because *Eriocapitella* and *Kilimandscharica* species also have the distinctly stalked carpels and achenes, moreover, several other *Anemone* species (viz., *A. antucensis*, etc.) are characterized by carpels and achenes basally narrowed into stalks.

Sometimes *Anemone* carpels and achenes are laterally compressed and ribbed or even winged, and *Anemone* species having the winged reproductive organs are separated into the *Omalocarpus* group. However, species characterized by compressed carpels and achenes (with more or less distinct lateral ribs) are also found within *Anemone* s. str., *Rivularidium*, *Begoniifolia*, *Anemonidium* and some other groups.

In *Anemone* species the ovoid shape of carpels and achenes predominates but there are also globose, cylindroid and spindle-like carpels and achenes. The length of carpels and achenes of *Anemone* species is frequently 2–10 mm, but there are taxa with large (4–8 mm long, viz., in *Omalocarpus* and *Rivularidium*) and small (1–2 mm long, viz., in *Anemone*, *Eriocephalus* and others) carpels and achenes.

The length and shape of carpel and achene styles are various, and they are typically persistent at maturity. Styles differ in *Anemone* species by their length being sometimes long (5–10 mm long and tail-like, viz., in

Pulsatilloides) or short (ca. 1 mm long, viz., in *Anemonanthea*, etc.) or sometimes hardly visible (viz., in *Eriocapitella* and *Stolonifera*). Carpels and achene styles are mainly straight or hooked (basally or apically) but sometimes uncinata, and they are narrow-conic (viz., in *Rivularidium*), sharply narrowed (viz., in *Omalocarpus*) or sometimes funnel-like (viz., in *Eriocapitella*).

Carpel and achene stigmas are mainly linear but sometimes capitate or subcapitate (viz., in *Eriocapitella*, *Kilimandscharica* and *Stolonifera*) or dilated, and the latter correlate with very short styles (sessile or subsessile stigmas).

Carpels and achenes are covered with hairs but sometimes they are glabrous or nearly so. The hairs are long (2–2.5 times longer than an achene diameter) or short (shorter than an achene diameter). Besides, carpel and achene villosity may be dense (lanate) or sparse. The carpel and achene hairs are typically monomorphic but sometimes they are dimorphic, especially in their basal and apical parts. In most taxa hairs cover achene bodies only but sometimes styles too (viz., in *A. baissunensis*, *A. capensis*, etc.).

In cross section *Anemone* achenes are suborbicular or elliptic to elongate, with narrow excrescences in which the vascular bundles are settled. Pericarp is well-developed and differentiated into exocarp, mesocarp and endocarp. A cross section of seeds resembles that of fruits; the seed coat consists of several layers, the latter usually being very compressed. Besides, *Anemone* taxa differ by the peculiarities of the microsculpture of achene surface (smooth, plicated, tuberculated, waved, folded, etc.).

At present about ten flower morphological characters are used for distinguishing *Anemone* species, and they pertain mainly to the tepal number, color and size, and sometimes to the stamens and receptacle shape

but the recent detailed study of the micro-morphology of perianth (Tamura 1962, Slavikova 1968, 1976, Gulanja 1974, etc.) has added important data to the understanding of the taxonomy and phylogeny of *Anemone*.

As a result of the critical examination of flowers within the genus *Anemone*, we distinguished the most essential ones, and we published these results (Ziman and Bulakh 2002a, 2002b, 2003, 2004, Ziman et al. 2004a, 2004b, 2004c, 2005, 2006a, 2006b, 2007, Ehrendorfer et al. 2007).

For distinguishing *Anemone* taxa (sections, subsections and series), beside the forementioned characters of carpels (ovary, style and stigma shape and villosity), we used also size, number and venation, but also peculiarities of filaments, connectives and anthers. The diagnostic characters of species are mainly tepal colour, size and hairiness, and tepal, but also ovary and style shape peculiarities, and they were used in our key for distinguishing species (Ziman et al. 2002).

The number of tepals is 5 to 8, rarely 4 or 9, however, there are 10 or even more tepals in several groups (viz., *Carolinianae*, *Pulsatilloides*, *Alchimillifolia*, *Altaicae*, *Tuberosa*, *Hepaticifolia*, *Tuberosae*). In these groups the tepals are usually sublinear, they occur in two whorls and differ in shape, size, colour and venation (dimorphic perianth). However, most *Anemone* species have ovate to obovate tepals with obtuse or acute bases and tips.

We obtained data on the peculiarities of tepal venation (including anastomosing veins), initially in the *Anemone narcissiflora* (Ziman et al. 1997) and *A. biflora* aggregates (Ziman et al. 1998) tepals but afterwards we studied the flower peculiarities in all *Anemone* species and our results confirmed the diagnostic significance of the forementioned characters.

As happened, most species are characterized by 3–7 anastomosing veins on tepals but

some of them have more than 10 anastomoses (viz., *A. coronaria*, *A. virginiana*, *A. hepaticifolia*, etc.) or their tepals lack anastomosing veins (viz., in sections *Himalayicae*, *Parviflora*, *Caroliniana*, etc.).

However, the tepal size and colour and sometimes shape of many *Anemone* taxa frequently vary, therefore, they could be regarded as characters of a specific level not of a higher taxonomic value.

Stamens are inconstant in number (40 to 100), and the shape of their filaments (linear or dilated) is already used to distinguish some *Anemone* species. After the examination of the shape and size of all parts of stamens including their filaments, connectives and anthers, we came to the conclusion to use the former two characters in the *Anemone* taxonomy.

Within the subtribe *Anemoninae*, staminodes were regarded as a diagnostic character for several *Pulsatilla* groups, and had not been noted in flowers of *Anemone* taxa. However, as a result of the precise examination of *Anemone* flowers, we found staminodes of various shapes in several *Anemone* species (viz., in the sections *Himalayicae* and *Rosulantes*).

The data on the pollen grains of *Anemone* species are sufficient. According to existing literature on pollen structure (Kumazawa 1936, Mittra and Sharma 1963, Si and Chjan [Xi and Zhan] 1964, Huynh 1970a, 1970b, Savitski 1982, etc.), their pollen grains are radial-symmetric, isopolar, globose, sometimes ellipsoid or ovoid, mainly of a middle size, with equatorial diameter 19–45 μm . There are colpi or pores on the surface of pollen grains. Colpi are meridional or not meridional, narrow or wide, long or short, with pointed, rounded or blunt tips. Their number is 3 to many (up to 10), and germinated pores are mostly 18 to 26, and they are irregularly arranged. Exine is 1.0–3.0 (–4.0) μm thick, sexine is thicker than nexine, or

equal to it; and triline is thin. Surface of pollen grains differs in peculiarities of their sculpture, tuberculate, granulate, wavy, spined, plicated, etc. The foregoing authors recognized five types of pollen grains within the genus *Anemone*: tricolpate (majority of species), polycolpate (three groups), pantocolpate or rugose (nine groups), pantoporate (five groups), and spiroaperturate (two groups).

Many authors regard the foregoing pollen grain characters as very important for taxonomy and phylogeny of many taxa within the vascular plants including the genus *Anemone*. But as long ago as in 1936, Kumazawa noted that in *Anemone* the various types of pollen grains did not seem to be coincident with the differentiation of traditional diagnostic characters generally supported by taxonomists. According to the modern data, there are several groups of *Anemone* species (viz., *Stoloniferae*, *Multifidae*, *Rivulares*, etc.) within which three main types of pollen grains (tricolpate, rugose and pantoporate) are present including intermediate types. Besides, a large variability of pollen grains is observed within some groups of species or even within the same species or population.

The majority of taxonomists used several morphological characters of leaves and partly of shoots to distinguish *Anemone* species and groups of species. They used mainly size and shape of basal and involucral leaves, number and size of stems, some peculiarities of underground shoots, and pubescence of the vegetative organs. Moreover, Starodubtsev (1991) proposed to take into consideration several additional characters of seedlings (number of cotyledons, their size and position, and size of hypocotyl). Besides, this author paid attention to the number of involucral leaves and to structure of shoots (rosetteous or unrosetteous, monopodial or sympodial). Unfortunately, Starodubtsev revised all fore-

going characters based on the literature data only, and in other manuscripts on *Anemone* taxa the data on leaves, shoots and roots are fragmented.

We began to study the vegetative organs (life forms) of *Anemone* species about 30 years ago (Ziman 1978, Ziman and Savitski 1980, Ziman 1985, 1986, etc.). Initially we studied about 25 *Anemone* species in detail in the natural populations, and also examined the life forms of nearly all species of this genus (ca. 150 species) from herbarium material. As a result, we came to the conclusion that the diagnostic value and evolutionary significance of many characters of leaves, shoots and roots of *Anemone* taxa is essential indeed. Therefore, we enlarged the number of the discussed characters of the vegetative organs of *Anemone* s. str. to about 40.

All *Anemone* plants are perennial herbs, erect and mainly scapose. *Anemone capensis* from the *Pulsatilloides* group is the only exception because it is a subshrub with lignified stem bases.

The plants with semirosetteous shoots predominate but within some groups (viz., *Anemonanthea*, *Richardsonia*, *Anemondium*, *Stolonifera* and *Keiskea*) the adult plants have solitary basal leaves with distinct blades, and other leaves are scale-like.

Most *Anemone* species are characterized by sympodial renewal of shoots, however, the main shoot is monopodial in plants of some *Eriocephalus* and all *Omalocarpus*, *Himalayicae* and *Parviflorae* groups, and their flowering scapes develop from axils of basal leaves every year.

The adult plants of all *Eriocapitella*, *Himalayicae*, *Anemoclema*, *Pulsatilloides*, and also of several species of *Rupicolae* and *Rivularis* groups have tap-roots; all other groups are characterized by adventitious roots only. The underground shoots of the tap-rooted plants are represented by branches of the caudex, and in plants having adventitious roots the underground shoots are

rhizomes, stolons or tubers but sometimes root-runners.

Anemone species differ in number of stems and their size, as well as peculiarities of inflorescences. Racemose inflorescences predominate, but *Anemonidium* species are characterized by a dichotomous inflorescence in which the main axis is extremely reduced. In the *Rivularis* group the dichasium is observed in which the axillary branches overtop the main axis. The umbelliferous cymes are characteristic for most *Omalocarpus* species. Finally, some *Anemone* groups (viz., *Himalayicae*, *Rupicolae*, *Richardsonia*, *Parviflora*, *Crassifolia*, etc.) have solitary flowers, due to reduction of various types of inflorescences.

All the forementioned characters of shoots and roots of *Anemone* taxa are constant and may be regarded as having high taxonomic value.

The basal leaves of *Anemone* species are usually long-petiolate with a broad blade. However, in a few species (viz., *A. trullifolia*, etc.) leaf blades are narrow, and petioles are indistinct. The leaves with cordate base are predominate. The basal leaf blades are deeply palmately or ternately sected or parted, and sometimes ternately compound, but several groups have pinnate leaf blades (viz., *Anemoclema*). Biternate or triternate, as well as bipinnate or tripinnate leaves, are known in *Anemone* species. The palmately lobed basal leaf blades occur rather seldomly (viz., in *A. hepaticifolia*, *A. palmata*); the leaves with entire blades are also rare (viz., in several *Himalayicae* and *Alchimillifolia* species).

The basal leaf blade petioles are usually narrow and sometimes basally vaginate. However, we found in several sections (viz., *Anemone* s. str., *Himalayicae*, *Hepaticifolia*, etc.) the sharply dilated (auriculate) basal parts of basal leaf petioles. These characters are always constant, therefore, have a diagnostic value.

The involucral leaves are petiolate or sessile and they are mainly similar to basal ones and smaller but sometimes larger (viz., in most *Anemonanthea* species). However, in some taxa the involucral leaves differ from the basal ones by their shape and size. The number of involucral leaves is often regarded as diagnostic but our detailed study (Ziman et al. 1997) has demonstrated the variability of this character within section *Omalocarpus*.

Some peculiarities of ontogeny in *Anemone* could be used as additional characters for distinguishing species and higher taxonomic groups (Ziman 1985, Ziman et al. 1997, 1998, etc.). Epigeal germination within *Anemone* species predominates but sometimes seedlings with underground small cotyledons occur (viz., in the *Anemonanthea* and *Stolonifera* groups). The majority of *Anemone* seedlings is characterized by the short tube (result of the partial fusion of petioles of the cotyledonary leaves), but within some groups (viz., *Omalocarpus*, *Anemone* s. str., etc.) these petioles are fused completely. Long hypocotyl is observed in most *Anemone* groups, and in some of them (viz., *Flaccidae*, *Rivularis*, *Omalocarpus*, etc.) the short hypocotyl is combined with the long cotyledonary petioles. The position of the cotyledonary petioles during germination (erect or bent) is also a diagnostic character. The size and shape of cotyledones, and juvenile, immature and virginile leaves are also the rather important additional diagnostic characters.

The genus *Anemone* is the most diversified in petiolar anatomy within the family *Ranunculaceae* (Tamura 1962, 1964, Trifonova and Zubkova 1990), and it is unique within the family in having all four types of the vascular bundle arrangement (dorsiventral, dorsiventral scattered, radial and radial scattered). Moreover, the dorsiventral scattered type was found in *Anemone* only (*A. rivularis*). Our study of

more than 30 populations of the *Anemone narcissiflora*-aggregate (Ziman et al. 1997) confirmed the taxonomic significance of a detailed anatomical investigation of this genus.

The analysis of the data on karyology of *Anemone* taxa (Zhukova 1961, 1965a, 1965b, Madahar 1967, Baumberger 1970, Starodubtsev 1987, 1991, etc.) has shown the presence of two basic types of chromosome sets, $x = 8$ and $x = 7$. Baumberger (1970) considered the former as the initial one (three acrocentric, one submetacentric and four metacentric chromosomes), with $x = 7$ being derivative. There were several attempts to group 8-chromosome (*Anemone* s. str., *Carolinianae*, *Eriocapitella*, *Virginianae*, *Rupicolae*, *Tuberosae*, etc.) and 7-chromosome (*Crassifoliae*, *Richardsonia*, *Anemonidium*, *Himalayicae*, *Omalocarpus*, etc.) *Anemone* species into two large associations. But in fact, in this genus plants with $x = 7$ were found within species normally having $x = 8$ (viz., in *Anemone* s. str., *Eriocapitella*, *Baldenses*, *Tuberosae*, *Anemonanthea*, etc.) and vice versa (viz., in *Anemonidium*, *Himalayicae*, *Omalocarpus*, etc.). Therefore, it seems to be more realistic not to exaggerate the taxonomic significance of the above chromosome sets, but to pay peculiar attention to size and arrangement of chromosomes and to the occurrence of polyploidy in various groups.

The recent cytological investigations (Marks and Schweizer 1974, Cullis and Schweizer 1974, Hagemann et al. 1993, etc.) have shown the significance of the evolutionary dynamics of chromosome banding patterns and accumulation of highly repetitive DNA in *Anemone* species. The rather important results of study of the taxonomic relationships in some *Anemone* groups were obtained recently on cpDNA analysis by restriction endonucleases and cpDNA analysis and restriction endonucleases and cpDNA probes (Hantula et al. 1989, Hoot 1995, Hoot

et al. 1994, Ehrendorfer 1995, Ehrendorfer and Samuel 2000, 2001, Schuettpelz and Hoot 2000, Schuettpelz et al. 2001, etc.). Ehrendorfer (1995) and Ehrendorfer and Samuel (2000, 2001) have realized the very important aim to compare and synthesize the data on morphology and DNA analysis. Their strict consensus trees resulting from survey of about 30 selected morphological characters of more than 40 *Anemone* species, and the cladograms from cpDNA restriction site data differed substantially, especially in the basal branching patterns. Therefore, proposals on taxonomy of *Anemone* by these authors differ much from the systems of their predecessors.

The foregoing patterns in the study of *Anemone* are very important but very complicated. Since sufficient data for discussion of the comparison and synthesis of molecular data are absent, it seemed to us to realise the detailed comparative morphological study of *Anemone* for clarification of relationships of their groups of species.

Diagnostic significance of the morphologic characters in genus *Anemone*

Here we present the grouping of essential morphological characters of *Anemone* taxa into sets for distinguishing the main groups of species (sections) on the basis of the results of our comparative analysis of the *Anemone* species.

Taking into consideration the essential carpel and fruit characters, we divided all *Anemone* taxa into two large groups. The first group includes 12 sections (82 species) characterized by a densely pubescent carpel and achenes, symmetrical, mainly ovoid and sharply narrowed into substraight styles, meanwhile, the second group includes 9 sections (36 species) having glabrous (sometimes subglabrous) carpels and achenes, mainly asymmetrical, oblong-ovoid and gradually narrowed into curved or hooked styles. These groups are artificial because

they embrace diverse taxa, for instance, both of them include plants having sessile or stalked, compressed or not compressed carpels and achenes, with linear or dilated stigmas. Nevertheless, we believe this division is useful to produce a key for determination of *Anemone* plants at any taxonomic level.

We accept the sections as the main taxonomic groups within the genus *Anemone* and for their more precise distinction we used the essential characters of flowers, achenes and vegetative organs. Below we present the brief characteristics of the *Anemone* sections which differ from ones worked out by Tamura (1995).

1. Sect. **Anemone**

Carpels and achenes sessile, ovoid or subglobose, mainly compressed, densely pubescent (hairs 2–5 mm long); styles narrow, 0.5–3 mm long; carpel stigmas linear. Tepals 5–18, typically having anastomosing veins. Plants with tuberous rhizomes and sympodial scapes.

Within this section we recognize four series (*Anemone*, *Somaliense*, *Biflora* and *Caroliniana*) which differ by ovoid or subglobose, compressed or not compressed carpels and achenes, length of their hairs, deciduous or persistent tepals, with solitary or numerous anastomosing veins (sometimes absent), length of styles and hairs, and basally narrow or sharply dilated basal leaf petioles.

2. Sect. **Eriocapitella**

Carpels and achenes basally distinctly stalked, inversely-ovoid, apically dilated, lanate (hairs 3–7 mm long), styles funnel-like, shorter than 1 mm, stigmas capitate. Tepals 5–20, anastomosing veins more than 10. Plants with caudices and monopodial scapes.

3. Sect. **Eriocephalus**

Carpels and achenes sessile, ovoid or spindle-like, apically narrowed, not compressed, densely pubescent (hairs 1–7 mm long), styles narrow, 1–3 mm long; carpel stigmas linear or dilated. Tepals 5–9, anastomosing veins from solitary to more than 10. Plants with caudices or non-tuberous rhizomes and sympodial or monopodial scapes.

Within this section we recognize four series (*Rupicolae*, *Sylvestres*, *Virginianae* and *Multifidae*) which differ by compressed or not compressed carpels and achenes, length of their hairs, linear or dilated carpel stigmas, sympodial or monopodial scapes, many or solitary flowers, basal and involucre leaf shape, and types of underground shoots (caudices, rhizomes or runners).

4. Sect. **Parviflora**

Carpels and achenes sessile, ovoid, not compressed (with hairs 0.1–0.3 mm long), styles narrow, ca. 1 mm long, carpel stigmas linear. Tepals 5, monomorphic, without anastomosing veins. Plants with long creeping rhizomes and monopodial scapes.

5. Sect. **Anemoclema**

Carpels and achenes sessile, spindle-like, slightly compressed (hairs 3–5 mm long); styles narrow, 5–10 mm long, stigmas linear. Tepals 5, monomorphic, with more than 10 anastomosing veins. Herbaceous semi-rosetteous plants with caudices and monopodial scapes.

6. Sect. **Pulsatilloides**

Carpels and achenes sessile, spindle-like, not compressed (hairs 2–5 mm long); styles narrow, 4–5 mm long, stigmas linear. Tepals 15–25, dimorphic, with 5–9 anastomosing veins. Non-rosetteous semi-shrubs with caudices and sympodial scapes.

7. Sect. **Alchimillifolia**

Carpels and achenes sessile, oblong-ovoid, not compressed (hairs 2–4 mm long); styles narrow, 5–10 mm long. Tepals 10–12, monomorphic or dimorphic, with more than 10 anastomosing veins. Herbaceous semi-rossetteous plants with caudices and sympodial scapes.

8. Sect. **Kilimandscharica**

Carpels and achenes shortly stalked, cylindroid, not compressed (hairs 3–4 mm long); styles narrow, ca. 1 mm long; stigmas capitate. Tepals 10–15, dimorphic, with solitary anastomosing veins. Herbaceous semirosetteous plants with short ascending rhizomes and sympodial scapes.

9. Sect. **Anemonanthea**

Carpels and achenes sessile, ovoid (hairs shorter than 1 mm long); styles narrow, 1–1.5 mm long; stigmas mainly linear. Tepals typically monomorphic (in some taxa dimorphic). Plants with long or short rhizomes and sympodial scapes.

Within this section we recognize five series (*Anemonanthea*, *Altaicae*, *Nikoenses*, *Reflexae* and *Quinquifoliae*) which differ by number and venation of tepals, width of involucre leaf petioles, and shape of rhizomes (monomorphic or dimorphic, long or short).

10. Sect. **Rosulantes**

Carpels and achenes sessile, ovoid, mainly subglabrous (hairs ca 0.1 mm long), styles narrow, 1–2 mm long, stigmas linear or slightly dilated. Tepals 5, monomorphic, anastomoses mainly absent. Plants with non-tuberous rhizomes and sympodial scapes.

Within this section we recognize two series (*Rosulantes* and *Exiguae*) which differ by achene shape (compressed or not compressed, with ribs or without them), villosity of tepals, presence or absence of staminodes, the number of scapes and flowers, and length

of involucre leaf petioles.

11. Sect. **Tuberosa**

Carpels and achenes sessile, slightly compressed, ellipsoid, sparsely puberulent (hairs ca. 1 mm long); styles 0.2–1.2 mm long, stigmas linear or subcapitate. Tepals 8–12, dimorphic, with 1–9 anastomoses. Plants with tuberous rhizomes and sympodial rhizomes.

Within this section we recognize two series (*Tuberosae* and *Caucasicae*) which differ by width of achene ribs, length of achene styles, shape of carpel stigmas (linear or subcapitate), tepal length and number, length of involucre leaf petioles and shape of rhizomes.

12. Sect. **Stolonifera**

Carpels and achenes sessile, ovoid (hairs ca. 1 mm long), styles hardly recognizable; carpel stigmas dilated or subcapitate. Tepals 5–7, anastomoses 3–9 or absent. Plants with dimorphic rhizomes and sympodial scapes.

Within this section we recognize two series (*Baicalenses* and *Flaccidae*) which differ by presence or absence of scale-like basal leaves, basal leaves with distinct blades developing after or before anthesis, and presence or absence of stolons.

13. Sect. **Keiskea**

Carpels and achenes stalked, ovoid (hairs 0.1–0.3 mm long), styles distinct, stigmas linear. Tepals 5–22, anastomoses 5–13. Plants with long rhizomes and sympodial rhizomes.

Within this section we recognize two series (*Keiskea* and *Deltoidea*) which differ by length of achene stalks, achene shape and villosity, number of tepals, their shape and venation, and shape of rhizomes.

14. Sect. **Omalocarpus**

Carpels and achenes sessile, subglobose-obovate, compressed, with lateral wings 1–

2 mm wide, subglabrous, styles mainly bent or hooked, 1–2 mm long, carpel stigmas linear. Tepals 5–10, having 1–7 anastomosing veins. Plants with short vertical rhizomes and monopodial scapes.

Within this section we distinguish three series (*Involucratae*, *Involucellatae* and *Fuscopurpurea*) which differ by shape of achene styles, tepal length, filament shape, types of inflorescences and shape of basal leaf blades.

15. Sect. **Imbricata**

Carpels and achenes sessile, broadly ellipsoid, compressed, with lateral wings ca. 2 mm wide, glabrous, styles bent, ca. 1 mm long, carpel stigmas linear. Tepals 5–9, without anastomosing veins. Plants with short rhizomes and monopodial scapes.

16. Sect. **Himalayicae**

Carpels and achenes sessile, ovoid, typically not compressed, densely pubescent (hairs ca. 1 mm long) or subglabrous, styles narrow, 1–2.5 mm long, carpel stigmas linear. Tepals 5–8, without anastomosing veins. Plants with short vertical rhizomes and monopodial scapes.

Within this section we recognize three series (*Obtusilobae*, *Trullifoliae* and *Rupestres*) which differ by compressed or not compressed carpels and achenes, densely pubescent or subglabrous, filaments shape, and shape of basal leaf blades and petioles.

17. Sect. **Rigida**

Carpels and achenes sessile, ovoid, not compressed, glabrous but with minute spinous projections, styles 1–2 mm long, stigmas linear. Tepals 5–7, vein anastomoses more than 10. Plants with short rhizomes and sympodial scapes.

18. Sect. **Rivularidium**

Carpels and achenes sessile, oblong-ovoid, subglabrous, styles conic, apically hooked,

2–10 mm long, stigmas linear. Tepals (4–) 6–10, with anastomosing veins or without them. Plants with caudices or short rhizomes and sympodial scapes.

Within this section we recognize four series (*Rivularidium*, *Angustilobae*, *Mexicanae* and *Jamesonii*) which differ by the length of achenes and their styles, tepal number and venation, the length of involucral leaf petioles and underground shoots (caudices or rhizomes).

19. Sect. **Begoniifolia**

Carpels and achenes sessile, rhombic-ovoid, compressed, with solitary lateral ribs, subglabrous, styles ca. 1 mm long, stigmas linear. Tepals 5, having anastomosing veins. Plants with short rhizomes and sympodial scapes.

20. Sect. **Richardsonia**

Carpels and achenes sessile, spindle-like, not compressed, glabrous, styles narrow, 5–6 mm long, carpel stigmas linear. Tepals 5–6(–8), with solitary anastomosing veins. Plants with long horizontal rhizomes and sympodial scapes.

21. Sect. **Crassifolia**

Carpels and achenes sessile, ellipsoid, compressed, with paired lateral ribs, basally sparsely pubescent (hairs 1–2 mm long), styles narrow, ca. 1 mm long, carpel stigmas linear. Tepals 6–7, having anastomosing veins. Plants with tuberous and stolon-like rhizomes and sympodial scapes.

22. Sect. **Hepaticifolia**

Carpels and achenes sessile, cylindroid, slightly compressed, smooth, subglabrous, styles narrow, 1–2 mm long, carpel stigmas linear. Tepals 5, without anastomosing veins. Anther connectives with large subglobose projections. Plants with short rhizomes and sympodial scapes.

23. Sect. *Anemonidium*

Carpels and achenes sessile, ellipsoid, compressed, with lateral wings 0.5–1.5 mm wide, styles narrow, 2–6 mm long, carpel stigmas linear. Tepals 4–5, anastomosing veins more than 10. Non-rosetteous plants with short rhizomes, stolon-like runners and sympodial scapes.

Key to subgenera, sections, subsections, series and species of *Anemone*

Our Key for determination of *Anemone* sections, subsections, series and species was elaborated on the basis of the analysis of the about 70 characters of the achenes, flowers, leaves, above-ground and underground shoots and roots.

The most complicated step of our work with the key of *Anemone* taxa was the attempt to follow Tamura (1995) in recognition of subgenera. Unfortunately, most of them were described by a few achene characters only, viz., for subgen. *Rivularidium* this author noted glabrous achenes with hooked beaks, despite these characters occurring in other *Anemone* subgenera. For several subgenera Tamura used few other characters, viz., in his opinion subgen. *Anemonanthea* is characterized by horizontal or tuberous rhizomes and subgen. *Omalocarpus* by erect, not tuberous rhizomes. Meanwhile, these peculiarities are also found in other subgenera. Therefore, while examining the forementioned characteristics of subgenera sensu Tamura, we added to them also the most essential peculiarities of shoots and roots (life forms) and took into consideration the basic chromosome numbers ($x = 8$ and $x = 7$).

As a result, we accepted within genus *Anemone* 15 subgenera because we divided subgen. *Anemone* on three ones: subgen. *Anemone* sensu Adanson (1763), subgen. *Eriocapitella* (= genus *Eriocapitella* Nakai) and subgen. *Eriocephalus* sensu Juzepchuk (1937). Besides, we separated sect. *Kiliman-*

dscharica from subgen. *Pulsatilloides* as the monotypic subgen. *Kilimandscharica*, sect. *Stolonifera* as subgen. *Stolonifera* and sect. *Keiskea* as subgen. *Keiskea* from subgen. *Anemonanthea*. Moreover, we moved sect. *Begoniifolia* from subgen. *Omalocarpus* in subgen. *Rivularidium*. We recognized the subgenera *Pulsatilloides*, *Anemoclema* and *Rigida* sensu Tamura (1991) but in fact sensu Juzepchuk (1937). At last, we accepted monotypic sections *Hepaticifolia*, *Crassifolia* and *Richardsonia* as the subgenera *Hepaticifolia*, *Crassifolia* and *Richardsonia*.

- 1a. Carpels and achenes more or less densely pubescent, symmetrical, mainly ovoid, sharply narrowed into sub-straight styles 2
- 1b. Carpels and achenes glabrous or subglabrous, typically assymetrical, oblong-ovoid, mainly gradually narrowed into curved or hooked styles 83
- 2a. Carpels and achenes embedded into dense hairs, mainly longer than their bodies; tepals densely pubescent 3
- 2b. Carpels and achenes covered with hairs shorter than their bodies; tepals scarcely pubescent or glabrous 34
- 3a. Plants with tuberous rhizomes; scapes sympodial; carpels and achenes mainly compressed, 2–5 mm long; tepals typically having anastomosing veins, mainly densely pubescent (subgen. 1. *Anemone* sect. 1. *Anemone*) 4
- 3b. Plants with caudices or non-tuberous rhizomes; scapes sympodial or monopodial; carpels and achenes not compressed; tepals having or nor having anastomosing veins, mainly glabrous 19
- 4a. Carpels and achenes ovoid, not compressed, with styles 1.5–3 mm long and hairs 2–4.5 mm long; tepals mainly elliptic-obovate, with 3–13 basal veins and 0–30 anastomosing veins; basal leaf blades 3-sected or 3-parted (rarely 3–5-

- lobed) 5
- 4b. Carpels and achenes subglobose, distinctly compressed, with styles 0.5–1.2 mm long and hairs 4–5.7 mm long; tepals linear-oblong or lanceolate, with 5 basal veins and without vein anastomose; basal leaf blades 1–2-ternate (subsect. 4. *Carolinianae*) ... 13
- 5a. Tepals deciduous, 20–50 mm long, with 3–9 basal veins and 1–17 anastomosing veins; basal leaf petioles basally sharply dilated (“ear-like”); basal and involucre leaf blades pubescent (subsect. 1. *Anemone*) 6
- 5b. Tepals persistent, 10–30 mm long, with 5–13 basal veins and 0–30 anastomosing veins; basal leaf petioles without “ear-like” basal parts; basal and involucre leaf blades glabrous 8
- 6a. Tepals with 10 or more anastomosing veins, mainly red; basal and involucre leaves multi-divided; stolon-like rhizomes present 1. *A. coronaria*
- 6b. Tepals with 1–3 anastomosing veins, usually not red; basal and involucre leaves little divided; stolon-like rhizomes absent 7
- 7a. Achene hairs 3.5–5 mm long and styles 3.5–4 mm long; flowers solitary; basal leaves dimorphic, 3-sected 2. *A. hortensis*
- 7b. Achene hairs 3–3.5 mm long and styles 4.5–5 mm long; scapes few-flowered; basal leaves monomorphic, 3-lobed 3. *A. palmata*
- 8a (5b). Achene hairs 3–3.5 mm long; fruiting heads elongated; tepals blue or mauve, glabrous; basal leaf blades palmately 3-parted (subsect. 2. *Somaliense*) 4. *A. somaliensis*
- 8b. Achene hairs 2–5 (–6) mm long; fruiting heads globose; tepals yellow, red or whitish, pubescent; basal leaf blades 3-parted to 3-sected (subsect. 3. *Biflorae*) 9
- 9a. Basal leaves more than 2, many-sected; involucre leaves with petiole-like bases; tuberous rhizomes irregular ... 10
- 9b. Basal leaves 1–2, little divided; involucre leaves subsessile; tuberous rhizomes subglobose 12
- 10a. Tepals yellow, 10–15 mm long, with 1–3 anastomosing veins; filaments linear; basal leaf petiolules equal 5. *A. biflora*
- 10b. Tepals red or yellow, 15–30 mm long, with 7–30 anastomosing veins; filaments dilated; basal leaf petiolules unequal (central petiolule distinctly longer than lateral ones) 11
- 11a. Tepals red or reddish; filaments slightly dilated; achenes 2.5–3 mm long, with hairs 2.5–3.5 mm long and glabrous styles 6. *A. bucharica*
- 11b. Tepals yellow; filaments sublanceolate; achenes 3.5–5 mm long, with hairs 4–5.5 mm long and apically pubescent styles 7. *A. baissunensis*
- 12a. Achenes 3–3.5 mm long, with hairs 5–6 mm long and styles 1.7–2.5 mm long; tepals 15–30 mm long, white or bluish, with 7–15 anastomosing veins, pilose outside; basal and involucre leaf blades 3-parted 8. *A. tschernjaewi*
- 12b. Achenes 1.7–2.3 mm long, with hairs 1.7–2.3 mm long and styles 0.5–1.2 mm long; tepals 5–8 mm long, yellowish-green, without anastomosing veins, glabrous; basal and involucre leaf blades 3-sected ... 9. *A. serawschanica*
- 13a (4b). Achenes with ribs ca. 0.2 mm wide; scapes 1-flowered; leaf blades glabrous; tubers suborbicular; stolon-like rhizomes present 10. *A. caroliniana*
- 13b. Achenes with ribs 0.2–0.5 mm wide; scapes 1–few-flowered; leaf blades pubescent or glabrous; tubers elongate; stolon-like rhizomes absent 14
- 14a. Achenes with ribs 0.3–0.5 mm wide; tepals sparsely pubescent; basal leaves 1–2-ternate, with petiolate scale-like

- “ears” 15
- 14b. Achenes with ribs 0.2 mm wide or indistinct; tepals densely pubescent; basal leaves typically 2-ternate, without “ears” 16
- 15a. Achenes 2.7–3.5 mm long; tepals 8–12, 12–20 mm long, reddish-white; scapes 1-flowered; basal leaves sparsely pubescent; involucre leaves basally connate.. 11. *A. berlandieri*
- 15b. Achenes 1.3–2.2 mm long; tepals 6–8, 10–12 mm long, white or blue; scapes mostly 2–3-flowered; basal leaves glabrous; involucre leaves basally distinct 12. *A. edwardsiana*
- 16a. Achene hairs 2–3.5 mm long; tepals 6–10 17
- 16b. Achene hairs 4–6 mm long; tepals more than 10 18
- 17a. Tepals 10–20 mm long, pink or white; basal leaves glabrous; basal and involucre leaves similar 13. *A. tuberosa*
- 17b. Tepals 6–12 mm long, greenish-white; basal leaves pubescent; basal and involucre leaves dissimilar 14. *A. okennonii*
- 18a. Tepals 8–20, 2–5 mm, with 5–7 basal veins and 1–2 anastomosing veins; filaments linear; inflorescences few-flowered; basal and involucre leaves dissimilar, basal leaves dimorphic 15. *A. decapetala*
- 18b. Tepals 10–15, 2–3 mm, with 3 basal veins and without anastomosing veins; filaments filiform; flowers solitary; basal and involucre leaves similar, basal leaves monomorphic 16. *A. triternata*
- 19a (3a). Plants with caudices; scapes monopodial, inflorescences compound, 2–3-branched; carpels and achenes basally distinctly stalked, apically dilated, lanate, with funnel-like styles shorter than 1 mm and capitate stigmas (subgen. 2. *Eriocapitella* sect. 2. *Eriocapitella*) 20
- 19b. Plants with caudices or rhizomes; scapes monopodial or sympodial, inflorescences typically few-flowered; carpels and achenes sessile or subsessile, apically narrowed, densely pubescent, with narrow styles longer than 1 mm and linear stigmas (rarely in carpels dilated (subgen. 3. *Eriocephalus*) 22
- 20a. Carpels and achenes covered with hairs 2–3 mm long; basal leaf blades 3–7-lobed 18. *A. vitifolia*
- 20b. Carpels and achenes covered with hairs 3–7 mm long; leaf blades ternate 21
- 21a. Ovaries 1.5–2 mm long, on stalks ca. 1 mm long, covered with hairs 2–4 mm long; tepals 20–30 mm long, anastomosing veins 5–7; leaf blades abaxially strigose 17. *A. hupehensis*
- 21b. Ovaries 0.5–0.7 mm long, on stalks ca. 0.3 mm long, covered with hairs 4–6 mm long; tepals 15–20 mm long, anastomosing veins more than 30; leaf blades abaxially tomentose 19. *A. tomentosa*
- 22a. Plants with caudices or short rhizomes; scapes sympodial or monopodial, inflorescences 1- to several-flowered; carpels and achenes ovoid or spindle-like, compressed or not compressed; tepals 5–9, anastomosing veins from solitary to more than 10 (sect. 3. *Eriocephalus*) 23
- 22b. Plants with long creeping rhizomes; scapes monopodial, flowers solitary; carpels and achenes ovoid, not compressed; tepals 5, without anastomosing veins (sect. 4. *Parviflora*) 20. *A. parviflora*
- 23a. Carpels and achenes ovoid, basally dilated, with styles 2–3(–6) mm long, carpel stigmas linear; tepals with few anastomosing veins; scapes monopodial; involucre leaves subsessile; plants with caudices (ser. 4. *Multifidae*)

- 30
- 23b. Carpels and achenes obovoid or spindle-like, with styles 0.5–1.5 mm long; carpel stigmas linear or globose; tepals with many anastomosing veins; scapes sympodial or monopodial; involucre leaves petiolate; plants with rhizomes 24
- 24a. Carpel stigmas mostly linear; tepals 5–9; scapes few-flowered 25
- 24b. Carpel stigmas globose; tepals 5(–6); scapes 1-flowered (ser. 3. *Sylvestres*) 29
- 25a. Achenes not compressed, 2–3 mm long, with hairs 4–7 mm long; basal and involucre leaf blades 3-sected or 3-parted; involucre leaf petioles 5–10 mm long (ser. 1. *Rupicolae*) 26
- 25b. Achenes compressed, 2–4 mm long, with hairs 2–3 mm long; basal and involucre leaf blades ternate; involucre leaf petioles 1–5 cm long (ser. 2. *Virginianae*) 28
- 26a. Tepals 5–9, purplish or yellowish; carpel stigmas globose; basal and involucre leaf blades 3-sected; involucre leaf petioles ca. 1 cm long; stolon-like root-runners present 21. *A. rupicola*
- 26b. Tepals 5, white or greenish; carpel stigmas linear; basal and involucre leaf blades 3–5-parted; involucre leaf petioles less 1 cm long; root-runners absent 27
- 27a. Tepals white, 20–25 mm long; anther connectives without projections; basal leaf blades densely puberulent 22. *A. laceratoincisa*
- 27b. Tepals greenish, 15–20 mm long; anther connectives with slight projections; basal leaf blades subglabrous 23. *A. tibetica*
- 28a (25b). Achene styles 1–1.5 mm long; fruiting heads oblong-ellipsoid; tepals 10–20 mm long, with more than 10 anastomosing veins; involucre leaves 3–5, with petioles 3–7(–12) cm long 24. *A. virginiana*
- 28b. Achene styles 0.5–1 mm long; fruiting heads cylindroid; tepals 7–15 mm long, with less than 10 anastomosing veins; involucre leaves 5–9, with petioles 1–3 cm long 25. *A. cylindrica*
- 29a (24b). Achenes basally distinctly narrowed, with styles ca. 1 mm long; tepals 5–25 mm long, with wide bases and apices; involucre leaf petioles 1–2 cm long 26. *A. sylvestris*
- 29b. Achenes basally not narrowed, with styles ca. 0.5 mm long; tepals 10–15 mm long, with narrow bases and wide apices; involucre leaf petioles 4–10 cm long 27. *A. ochotensis*
- 30a (23a). Achene styles 1.5–2 mm long; tepals 5–6, with narrow bases and apices, anastomosing veins present; scapes few-flowered, 10–40 cm long; basal leaf blades 2–3-ternate; involucre leaves similar to basal ones 31
- 30b. Achene styles 3–6 mm long; tepals 5–15, with wide bases and apices, anastomosing veins absent; scapes 1-flowered, 5–25 cm long; basal leaf blades ternate-palmatifid or pinnatifid; involucre leaves reduced 33
- 31a. Achenes subellipsoid, 3–4 mm long, with hairs 3–6 mm long; tepals 6–10, 8–15 mm long, blue to reddish, with 0–1 anastomosing veins; scapes typically 2–7-flowered; basal leaf blades 2-ternate; involucre leaves 3-parted to 3-lobed 28. *A. multifida*
- 31b. Achenes subglobose, 2–3 mm long, with hairs 2–3 mm long; tepals 5–8, 10–20 mm long, white, with 1–3 anastomosing veins; scapes 1–2-flowered; basal leaf blades 3-ternate; involucre leaves ternate 32
- 32a. Fruiting heads oblong-ovoid; tepals 12–20 mm long, elliptic-ovate; filaments sublanceolate; scapes 10–15 cm long 29. *A. baldensis*

- 32b. Fruiting heads subglobose; tepals 10–12 mm long, elliptic-oblong; filaments linear; scapes 25–40 cm long 30. *A. pavoniana*
- 33a (30b). Tepals 7–15, 8–20 mm long, whitish-blue, sometimes dimorphic; filaments filiform; scapes 10–25 cm long; basal leaves palmatifid, villous 31. *A. drummondii*
- 33b. Tepals 5–6, 10–12 mm long, dark blue to reddish, monomorphic; filaments dilated; scapes 5–15 cm long; basal leaves pinnatifid, subglabrous 32. *A. multiceps*
- 34a (2b). Plants with caudices or rhizomes; scapes sympodial, flowers solitary; carpels and achenes compressed or not compressed, covered by hairs 4–10 mm long, styles densely pubescent 35
- 34b. Plants with rhizomes; scapes sympodial or monopodial, inflorescences 1–several-flowered; carpels and achenes typically not compressed, covered with hairs 1–3 mm long, styles glabrous 39
- 35a. Plants with caudices; carpels and achenes sessile, oblong-ovoid or spindle-like, 5–10 mm long; styles densely pubescent, stigmas linear; tepals with more than 5 anastomosing veins, densely pubescent 36
- 35b. Plants with tuberous rhizomes; carpels and achenes shortly stalked, cylindroid, 3–5 mm long; styles 1–2 mm long; stigmas capitate; tepals with solitary anastomosing veins, sparsely pubescent (subgen. 6. *Kilimandscharica* sect. 10. *Kilimandscharica*) 37. *A. thomsonii*
- 36a. Carpels and achenes slightly compressed; styles straight; tepals 5, anastomosing veins ca. 30; basal leaf blades pinnatipartite and obtusely dentate (subgen. 4. *Anemoclema* sect. 5. *Anemoclema*) 33. *A. glaucifolia*
- 36b. Carpels and achenes not compressed; styles apically curved; tepals 10–25, anastomosing veins 5 to more than 10; basal leaf blades 3-ternate or palmately lobed and acutely dentate 37
- 37a. Non-rosulate semishrubs; carpels and achenes spindle-like; tepals 15–25, linear-lanceolate, anastomosing veins 3–9, densely pubescent; leaf blades 3-ternate, subglabrous (subgen. 5. *Pulsatilloides* 6. sect. *Pulsatilloides*) 34. *A. capensis*
- 37b. Semi-rosulate herbaceous plants; carpels and achenes oblong-ovoid; tepals 10–12, wide-lanceolate, anastomosing veins more than 10, sparsely pubescent; leaf blades palmately-lobed, villous (sect. 7. *Alchimillifolia*) 38
- 38a. Carpels and achenes 4–5 mm long, covered with dimorphic hairs 1–5 mm long; tepals monomorphic; filaments distinctly dilated; basal leaf blades 5–7 cm wide 35. *A. caffra*
- 38b. Carpels and achenes 5–10 mm long, covered with monomorphic hairs 3–6 mm long; tepals dimorphic; filaments slightly dilated; basal leaf blades 12–20 cm wide 36. *A. fanninii*
- 39a (34b). Plants with ascending or horizontal rhizomes; scapes sympodial or monopodial; involucre leaves petiolate, similar to basal leaves and frequently of a larger size; carpels and achenes covered with hairs shorter than 1 mm (usually 0.1–0.2 mm) 40
- 39b. Plants with short vertical rhizomes; scapes monopodial; involucre leaves sessile, reduced (much smaller than basal leaves); carpels and achenes covered with hairs longer than 1 mm (subgen. 9. *Omalocarpus* sect. 15. *Himalayicae*) 73
- 40a. Plants with short or long, sometimes tuberous rhizomes; involucre leaves petiolate, carpels and achenes sessile, with distinct styles and mainly linear stigmas; basic chromosome number $x = 8$ (subgen. 6. *Anemonanthea*) 41

- 40b. Plants with short or long but non-tuberous rhizomes; involucreal leaves sessile, carpels and achenes sessile or stalked, with distinct or hardly recognizable styles and mainly capitate stigmas; basic chromosome number $x = 7$..
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- 41a. Achene styles mainly 1–1.5 mm long; basal leaves several, scale-like, persistent; solitary leaves with distinct blades and long petioles developing on rhizomes after anthesis (sect. 8. *Anemonanthea*) 42
- 41b. Achene styles mainly 0.5–0.7 mm long; basal leaves several, with distinct blades and long petioles developing on reproductive shoots before anthesis 61
- 42a. Tepals 5–8 (rarely 9–10); rhizomes monomorphic, long and 1–3 mm in diameter, branched, mainly horizontal (ser. 1. *Anemonanthea*) 43
- 42b. Tepals 5–12; rhizomes dimorphic, short, thick (nodulose) or long, thin 52
- 43a. Carpel styles ca. 1 mm long; stigmas subcapitate or slightly dilated; involucreal leaf petioles 3–5 mm wide
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- 43b. Carpel styles longer than 1 mm; stigmas linear; involucreal leaf petioles 1–2 mm wide 47
- 44a. Achenes (2–) 3–5 mm long; tepals 5–8, glabrous; cymes 1-flowered; involucreal leaf petioles 1–3 cm long; involucreal leaf blades similar to the basal leaf blades 45
- 44b. Achenes 1–2 mm long; tepals 5, pubescent; cymes 1–2-flowered; involucreal leaf petioles 3–5 mm long; involucreal leaf blades larger than the basal leaf blades 46
- 45a. Achene stigmas slightly dilated; tepals 6–10, mainly dimorphic, basally rounded, having 3–5 anastomosing veins; central leaflets of basal leaf blades 3-lobed, ellipsoid-oblong, with wedge-like bases 38. *A. nemorosa*
- 45b. Achene stigmas sublinear; tepals 5–8, monomorphic, basally narrowed, lacking anastomosing veins; central leaflets of basal leaf blades 3-sected or 3-parted, rhombic, with semicordate bases 39. *A. amurensis*
- 46a. Tepals basally narrowed, mainly blue or whitish, densely puberulent; filaments basally dilated 40. *A. caerulea*
- 46b. Tepals basally rounded, mainly rose or red, sparsely puberulent; filaments apically dilated 41. *A. uralensis*
- 47a (43b). Cymes 1–few-flowered; tepals pubescent, usually with anastomosing veins; achenes slightly compressed, with lateral ribs 48
- 47b. Cymes 1-flowered; tepals glabrous or subglabrous, lacking anastomosing veins; achenes compressed or not compressed 50
- 48a. Basal and involucreal leaflets 2–3-lobed (sometimes parted); involucreal leaf petioles 3–5 cm long; tepals dimorphic, basally narrowed; achene styles 0.8–1.5 mm long 42. *A. ranunculoides*
- 48b. Basal and involucreal leaflets undivided; involucreal leaf petioles 1–3 cm long; tepals monomorphic, basally rounded; achene styles 1.5–2.5 mm long 49
- 49a. Cyme 1-flowered; tepals 5, mainly pilose, having 5–9 anastomosing veins 43. *A. udensis*
- 49b. Cymes few-flowered; tepals 5–8, glabrous, having solitary anastomosing veins 44. *A. trifolia*
- 50a (47b). Central segments of basal leaf blades 3-lobed; tepals 5; achene hairs 0.2–0.3 mm long 45. *A. umbrosa*
- 50b. Central segments of basal leaf blades serrate or coarsely toothed; tepals 5–7; achene hairs ca. 0.01 mm long 51
- 51a. Tepals 10–15 mm long, basally not narrowed, white; achenes not compressed, without ribs, 4–5 mm long, sparsely puberulent 46. *A. soyensis*

- 51b. Tepals 4–8 mm long, basally narrowed, white-greenish; achenes slightly compressed, with narrow ribs, 2–4 mm long, densely puberulent 47. *A. debilis*
- 52a (42b). Tepals 8–15, glabrous, spreading; cymes 1-flowered (ser. 2. *Altaicae*) 53
- 52b. Tepals 5–8, glabrous or pubescent, spreading or bent; cymes 1–few-flowered 55
- 53a. Ovaries and achenes basally narrowed, with narrow lateral ribs; achene hairs 0.1–0.3 mm long; achene styles puberulent; carpel stigmas subcapitate; achene stigmas slightly dilated; basal leaf petiolules 5–10 mm long; tepals dimorphic 48. *A. altaica*
- 53b. Ovaries and achenes basally narrowed or rounded, with ribs or lacking them; achene hairs 0.2–0.5 mm long; achene styles glabrous; carpel and achene stigmas linear or sublinear; basal leaf petiolules 2–5 mm long; tepals monomorphic 54
- 54a. Achenes basally rounded, not compressed, styles 0.5–1 mm long; tepals 8–12, having 3–5 anastomosing veins; basal and involucre leaflets deeply 3-lobed; involucre leaf petioles 10–20 × 3–5 mm, distinctly dilated 49. *A. pseudoaltaica*
- 54b. Achenes basally narrowed, slightly compressed, styles 1–1.5 mm long; tepals 9–15, having 1–3 anastomosing veins; basal and involucre leaflets medially 3-lobed or toothed; involucre leaf petioles 5–12 × 1–2 mm, basally slightly dilated 50. *A. raddeana*
- 55a (52b). Achenes densely puberulent; tepals 5 (–6), spreading, with narrow bases and apices, 15–30 mm long, having 5–9 anastomosing veins, sparsely puberulent; involucre leaf petioles 3–5 mm wide (ser. 3. *Nikoenses*) 51. *A. nikoensis*
- 55b. Achenes sparsely puberulent; tepals 5–7, spreading or bent, with rounded bases and apices, 5–20 mm long, mainly without anastomosing veins, subglabrous; involucre leaf petioles 1–2 mm wide 56
- 56a. Achene hairs less than 0.1 mm long; tepals 5–7 × 1–2 mm, bent, sparsely puberulent; cymes few-flowered; bracteoles present (ser. 2. *Reflexae*) 52. *A. reflexa*
- 56b. Achene hairs 0.1–2 mm long; tepals 10–25 × 4–10 mm, spreading, glabrous; cymes 1-flowered; bracteoles absent (ser. 4. *Quinquefoliae*) 57
- 57a. Achene styles sparsely puberulent; tepals 5, having solitary anastomosing veins; involucre leaf petioles 0.5–2 cm long 58
- 57b. Achene styles glabrous; tepals 5–7, lacking anastomosing veins; involucre leaf petioles 1–3 cm long 59
- 58a. Carpels and achenes covered with hairs 0.5–1 mm long; lateral leaflets often deeply two-lobed; basal leaf blades puberulent; involucre leaf blades and stems puberulent or subglabrous 53. *A. quinquefolia*
- 58b. Carpels and achenes covered with hairs 0.1–0.2 mm long; lateral leaflets all lanceolate, undivided; leaves and stems glabrous 54. *A. lancifolia*
- 59a. Carpels and achenes densely covered with hairs 1–2 mm long; scapes few, puberulent; rhizomes mainly vertical 55. *A. piperi*
- 59b. Carpels and achenes covered with hairs 0.1–0.2 mm long; scapes solitary, glabrous; rhizomes horizontal or ascending 60
- 60a. Achenes basally narrowed, slightly compressed, with narrow lateral ribs; tepals 7–10 × 4–6 mm, mainly white or blue 56. *A. grayi*
- 60b. Achenes basally rounded, non-compressed, without ribs; tepals 10–20

- × 5–10 mm, red to blue 57. *A. oregana*
- 61a (41b). Plants with non-tuberous rhizomes, 1–few-flowered cymes and gradually dilated basal leaf petioles; achenes ovoid, subglabrous or glabrous; tepals 5 (sect. 9. *Rosulantes*) 62
- 61b. Plants with tuberous rhizomes, solitary flowers and basally sharply dilated basal leaf petioles; achenes ellipsoid, sparsely puberulent; tepals 8–12 (sect. 10. *Tuberosa*) 66
- 62a. Achenes not compressed, without ribs; tepals puberulent, with or without anastomosing veins; staminodes present; scapes 2–3, few-flowered; involucreal leaf petioles 1–3 cm long; bracteoles present, small (ser. 1. *Rosulantes*) 63
- 62b. Achenes slightly compressed, with narrow ribs; tepals subglabrous, lacking anastomosing veins; staminodes absent; scapes solitary, 1-flowered; involucreal leaf petioles 0.5–1.5 cm long; bracteoles absent (ser. 2. *Exiguae*) 64
- 63a. Stigmas linear; tepals 5–10 mm long, lacking anastomosing veins; staminodes between tepals and stamens 58. *A. stolonifera*
- 63b. Stigmas subcapitate; tepals 15–20 mm long, having 5–15 anastomosing veins; staminodes between stamens and carpels 59. *A. davidii*
- 64a. Carpels and achenes sparsely puberulent; involucreal leaf petioles 3–5 mm wide, basally connate 60. *A. exigua*
- 64b. Carpels and achenes glabrous; involucreal leaf petioles 1–2 mm wide, free 65
- 65a. Carpel and achene styles nearly absent; stigmas subglobose; involucreal leaf blades ternate, larger than those in basal leaves 61. *A. griffithii*
- 65b. Styles distinct; stigmas linear; involucreal leaf blades 3-sected, smaller than those in basal leaves 62. *A. scabriuscula*
- 66a (61b). Carpels and achenes 3.2–3.6 mm long, with ribs ca. 0.2 mm (or absent) and curved styles 1–1.2 mm long; stigmas linear; tepals 12–15, 15–20 mm long; basal leaf petioles 10–20 cm long; involucreal leaf petioles 1.5–3 cm long; rhizomes cylindroid (ser. 1. *Tuberosae*) 67
- 66b. Carpels and achenes 2–2.2 mm long, with ribs ca. 0.5 mm and slightly curved styles 0.2–0.3 mm long; stigmas in carpels subcapitate, in achenes distinctly dilated; tepals 8–10, 8–10 mm long; basal leaf petioles 5–8 cm long; involucreal leaf petioles 0.5–1.5 cm long; rhizomes subspherical (ser. 2. *Caucasicae*) 65. *A. caucasica*
- 67a. Carpels and achenes without lateral ribs, scarcely pubescent; tepals of outer whorl with 1–3 anastomosing veins; basal leaf blades ternate, with petiolules 3–5 mm long 63. *A. apennina*
- 67b. Carpels and achenes with lateral ribs and pubescent only at the base; tepals of outer circle with 5–9 anastomosing veins; basal leaf blades 3-sected, with petiolules 1–2 mm long (frequently absent) 64. *A. blanda*
- 68a (40b). Plants with dimorphic rhizomes (short and stolon-like); involucreal leaves 3–5, partly reduced; cymes 1–3-flowered; tepals 5–7; carpels and achenes sessile (hairs ca. 1 mm long); styles hardly recognizable; stigmas dilated or subcapitate (subgen. 7. *Stolonifera* sect. 11. *Stolonifera*) 69
- 68b. Plants with long rhizomes; involucreal leaves 3, all reduced; flowers solitary; tepals 5–13; carpels and achenes stalked (hairs 0.1–0.3 mm long), styles distinct, stigmas linear (subgen. 8. *Keiskea* sect. 12. *Keiskea*) 72
- 69a. Scale-like basal leaves absent; basal

- leaves with distinct blades and basally vaginate petioles developing before anthesis; carpel stigmas subcapitate, achene stigmas slightly dilated (ser. 1. *Stolonifera*) 70
- 69b. Scale-like basal leaves present; basal leaves with distinct blades and narrow petioles developing after anthesis; carpel stigmas capitate or subcapitate, achene stigmas subcapitate or dilated (ser. 2. *Flaccida*) 71
- 70a. Rhizomes short, 8–10 mm in diameter, with long underground stolons; tepals 10–15 mm long, with 3–5 anastomosing veins; achene bodies basally narrowed, slightly compressed, with narrow ribs 66. *A. baicalensis*
- 70b. Rhizomes short, 5–7 mm in diameter, with long above-ground stolons; tepals 8–10 mm long, without anastomosing veins; achene bodies basally rounded, not compressed, without ribs 67. *A. prattii*
- 71a. Basal leaves having 2–4 blades; scapes 1–3, cymes few-flowered; bracteoles present; tepals 5–10 mm long, with 7–9 anastomosing veins; achenes sparsely puberulent or glabrate, hairs 0.1 mm long 68. *A. flaccida*
- 71b. Basal leaves having solitary blades; scapes solitary, cymes 1-flowered; bracteoles absent; tepals 7–15 mm long, lacking anastomosing veins; achenes densely puberulent, hairs ca. 0.5 mm long 69. *A. delavayi*
- 72a (68b). Rhizomes 1–2 mm in diameter; tepals 10–22, linear-lanceolate, having few anastomosing veins, basally sparsely puberulent; achene stalks 1.5–2 mm long, achene bodies long-obovate, sparsely puberulent, stigmas linear-lanceolate (ser. 1. *Keiskea*) 70. *A. keiskeana*
- 72b. Rhizomes 2–5 mm in diameter; tepals 5, elliptic, without anastomosing veins, glabrous; achene stalks 0.5–0.7 mm long, achene bodies subglobose, hispid proximally, stigmas triangular-subulate (ser. 2. *Deltoidea*) 71. *A. deltoidea*
- 73a (39b). Carpels and achenes ovoid, not compressed, densely pubescent; leaf blades once 3-sected to 3-lobed or sometimes undivided 74
- 73b. Carpels and achenes ellipsoid, distinctly compressed, sparsely pubescent or subglabrous; leaf blades twice 3-sected (ser. 3. *Rupestres*) 82
- 74a. Filaments lanceolate (basally dilated, apically narrowed); leaf blades typically wider than long, with bases cordate or rounded (Ser. 1. *Obtusilobae*) 75
- 74b. Filaments ovate (basally and apically narrowed); leaf blades typically longer than wide, with bases attenuate or truncate (Ser. 2. *Trullifoliae*) 79
- 75a. Tepals pilose; staminodes absent; cymes mainly few-flowered; basal leaf petioles 1–2 mm wide; involucre leaf blades 3-lobed to 3-parted 105. *A. obtusiloba*
- 75b. Tepals mainly subglabrous; staminodes sometimes present; flowers solitary; basal leaf petioles more than 2 mm wide; involucre leaf blades undivided or sometimes 3-lobed 76
- 76a. Tepals 5, 5–8 mm long; filaments linear; basal leaf blade central segments 3-sected or 3-parted, leaf blades appearing pinnatifid, petioles 2–5 cm long 106. *A. subpinnata*
- 76b. Tepals 5–8, 10–20 mm long; filaments mostly lanceolate or ovate; basal leaf blade central segments 3-lobed or undivided, petioles 5–20 cm long 77
- 77a. Ovaries ellipsoid; staminodes absent; filaments ovate; basal leaf blades orbicular-ovate, all segments sessile 107. *A. patula*
- 77b. Ovaries narrow-ovoid; staminodes present; filaments linear-lanceolate; basal leaf blades ovate, central segments distinctly petiolulate 78

- 78a. Tepals 10–20 mm long, dimorphic; filaments linear, 0.3–0.5 mm wide; basal leaf blade central segment petiolules 1–2 mm long 108. *A. rockii*
- 78b. Tepals 5–10 mm long, monomorphic; filaments lanceolate, 0.5–1.0 mm wide; basal leaf blade central segment petiolules 5–10 mm long 109. *A. geum*
- 79a (74b). Tepal anastomosing veins sometimes present; cymes 1–3-flowered; basal leaf blades basally attenuate 80
- 79b. Tepal anastomosing veins absent; flowers solitary; basal leaf blades basally truncate 81
- 80a. Filaments elliptic; cymes 1–3-flowered; basal leaf blades 3-parted, 3-cleft, or 3-lobed, broadly lanceolate or ovate; involucre leaf blades 3-lobed or 3-dentate 110. *A. trullifolia*
- 80b. Filaments linear; flowers solitary; basal leaf blades usually undivided, oblong-linear to oblanceolate; involucre leaf blades undivided 111. *A. coelestina*
- 81a. Tepals 8–15 mm long; basal leaf blades 3-parted to 3-lobed; involucre leaf blades 3-lobed 112. *A. yulongshanica*
- 81b. Tepals 5–10 mm long; basal leaf blades undivided or obscurely 3-lobed; involucre leaf blades entire or 3-dentate 113. *A. subindivisa*
- 82a (73b). Carpel and achene styles substraight and apically thin; tepals 5–10 mm long, glabrous or sparsely puberulent; filaments lanceolate; staminodes absent; leaves subglabrous 114. *A. rupestris*
- 82b. Carpel and achene styles uncinat and apically thickened; tepals 7–15 mm long, puberulent; filaments linear; staminodes present; leaves sparsely puberulent 115. *A. polycarpa*
- 83a (1b). Plants with caudices or short rhizomes; scapes sympodial; carpels and achenes mainly slightly compressed (without wings or ribs), elongate; styles up to 9 mm long; basic chromosome number $x = 8$ 84
- 83b. Plants without caudices; scapes sympodial or monopodial; carpels and achenes distinctly compressed (having wide lateral wings), cylindroid or suborbicular; styles up to 5 mm long; basic chromosome number $x = 7$ 102
- 84a. Plants with rhizomes; basal leaf blades 3-parted; tepals up to 7, with more than 10 anastomosing veins, glabrous; achenes with minute spinous projections, basally sparsely pubescent; styles 1–2 mm long (subgen. 10. *Rigida* sect. 16. *Rigida*) 72. *A. rigida*
- 84b. Plants with caudices or rhizomes; basal leaf blades from entire to ternate; tepals up to 15, mainly without anastomosing veins, sparsely pubescent (sometimes glabrous); achenes without projections, glabrous or subglabrous; styles 1–9 mm long (subgen. 11. *Rivularidium*) 85
- 85a. Plants with caudices or short rhizomes; basal and involucre leaf blades mainly ternate; tepals 5 to 15, mainly without anastomosing veins; carpels and achenes oblong-ovoid, compressed (with paired ribs) or not compressed, typically glabrous; styles 2–9 mm long (sect. 17. *Rivularidium*) 86
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- 86a. Tepals 4–5 (–7), with 5–10 anastomosing veins; scapes compound, 2–3-branched, many-flowered; involucre leaves more than 3 (bracts and bracteoles) 87
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- 87b. Achenes 2.5–4 mm long; tepals subglabrous or glabrous; basal and primary involucre leaves dissimilar (primary reduced and smaller); plants with caudices or rhizomes 90
- 88a. Achenes 5–8 mm long, with styles 2–3 mm long; tepals 7–15 mm long, bluish or reddish; basal leaf blades 5–10 × 5–15 cm, pubescent; involucre leaves 3-parted 73. *A. rivularis*
- 88b. Achenes 3–6 mm long, with styles 1–2 mm long; tepals 4–7 mm long, white; basal leaf blades 4–7 × 10–12 mm, subglabrous; involucre leaves palmately dissected or 3-lobed 89
- 89a. Achenes narrowly ovoid, 5–6 mm long; tepals 5–7 mm long, puberulent throughout; basal leaf blades 4–5 × 5–6 cm long; involucre leaves on petioles 6–7 mm long 74. *A. filisecta*
- 89b. Achenes ovoid, 3–4 mm long; tepals 4–5 mm long, puberulent only along central vein; basal leaf blades 5–7 × 10–12 mm; involucre leaves sessile 75. *A. orthocarpa*
- 90a (87b). Achenes 3–4 mm long, with styles 0.3–0.5 mm long; tepals 5–7, white, with 3–9 anastomosing veins; involucre leaves 3, on petioles 10–15 mm long; plants with caudices (ser. 2. *Angustilobae*) 91
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- 91a. Achenes with spirally uncinat styles ca. 1 mm long; tepals 5–7, anastomosing veins 3–5; basal leaf petioles basally
- vaginate 76. *A. angustiloba*
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- 92a. Tepals 12–15 mm long, red or whitish-pink, sparsely pubescent; connectives with projections; basal leaf petioles shortly vaginate, blades ternate to biternate, puberulent; involucre leaves sessile 78. *A. mexicana*
- 92b. Tepals 6–12 mm long, white or yellowish, glabrous; connectives without projections; basal leaf petioles basally sharply dilated, blades palmately parted, glabrous; involucre leaves petiolate 79. *A. helleborifolia*
- 93a (86b). Tepals 15–35 mm long; basal leaf petioles basally sharply dilated (auriculate) 94
- 93b. Tepals smaller; basal leaf petioles basally vaginate or narrow 97
- 94a. Achenes 1–2 mm long, with styles 1–2 mm long; filaments dilated; involucre leaves more than 3, on petioles 1–5 mm long, 3-parted or 3–5-lobed 95
- 94b. Achenes 4–9 mm long, with styles 2–5 mm long; filaments filiform; involucre leaves 3, sessile, entire 96
- 95a. Tepals with narrow bases and wide apices; scapes few-flowered; basal leaf blades 2- or 3-ternate, sparsely pubescent; involucre leaves 2-ternate 80. *A. jamesonii*
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- 96a. Carpel and achenes with substraight styles 4–6 mm long; tepals dimorphic, glabrous; basal leaflets 3-parted or 3-lobed 82. *A. sellowii*
- 96b. Carpels and achenes with hooked styles 2–3 mm long; tepals monomorphic, sparsely pubescent; basal leaflets entire

- 83. *A. assibrasiliana*
- 97a (93b). Carpels and achenes not compressed, basally sparsely pubescent, with substraight styles; tepals 20–35 mm long, anastomosing veins 5–7, sparsely puberulent along central vein; basal leaf blades 15–35 cm long, glabrous 84. *A. moorei*
- 97b. Carpels and achenes compressed, glabrous, with hooked styles; tepals 5–15 mm long, without anastomosing veins, subglabrous; basal leaf blades 3–8 (–10) cm long, sparsely pubescent 98
- 98a. Achenes basally shortly stalked, with styles 3–5 mm long; tepals 7–15 mm long, elliptic; scapes 2–3-flowered; basal leaf blades 3-parted or 3-lobed; plants with short rhizomes 85. *A. antucensis*
- 98b. Achenes sessile, with styles 1–2 mm long; tepals 4–6 mm long, linear-lanceolate; flowers solitary; basal leaf blades ternate or biternate; plants with short nodulose and long stolon-like rhizomes 86. *A. tenuicaulis*
- 99a (85b). Achenes 2–4 mm long, 1-ribbed; tepals basally pubescent; basal leaf blades 8–13 × 10–13 cm 100
- 99b. Achenes 4–5 mm long, without distinct ribs; tepals subglabrous; basal leaf blades 4–8 × 4–7 cm 101
- 100a. Achenes rhombic-ovoid, sparsely pubescent; tepals white, anastomosing veins 3–5; staminodes absent 87. *A. begoniifolia*
- 100b. Achenes globose-ovoid, glabrous; tepals purple, anastomosing veins more than 10; staminodes between stamens and carpels present 88. *A. hokouensis*
- 101a. Tepals 10–15 mm long, white, anastomosing veins more than 10; basal leaf blades 3–5 × 3–5 cm 89. *A. chapaensis*
- 101b. Tepals 8–10 mm long, reddish-white, without anastomosing veins; basal leaf blades 4–8 × 4–7 mm .. 90. *A. howellii*
- 102a (83b). Plants with dichotomic non-rosulate stems and stolon-like runners; carpels and achenes ellipsoid, wings 0.5–1.5 mm wide; styles substraight, 2–3 mm long; tepals 4–5 (subgen. 12. *Anemonidium* 19. sect. *Anemonidium*) 103
- 102b. Semi-rosulate plants with rhizomes; carpels and achenes oblong-ellipsoid or cylindroid; without wings; styles mainly curved or bent; tepals 5 or more ... 104
- 103a. Achenes with styles 1–2 mm long; tepals 4, 7–15 mm long; stems many-flowered; basal leaves scale-like only; all leaves opposite, with distinct blades 91. *A. dichotoma*
- 103b. Achenes with styles 3–6 mm long; tepals 5, 10–20 mm long; stems 1–2-flowered; basal leaves 2–3, scale-like and 1–2 leaves with distinct blades; involuclal leaves 3, with 3-cleft blades 92. *A. canadensis*
- 104a. Plants with short vertical rhizomes and monopodial scapes; carpels and achenes oblong-ellipsoid, with wings 1–3 mm wide (subgen. 9. *Omalocarpus*) 105
- 104b. Plants with short ascending or long horizontal rhizomes and sympodial scapes; carpels and achenes cylindroid, without wings 116
- 105a. Basal leaf blades 3-lobed to 3-sected, with subequal lobes or segments; basal and involuclal leaves similar; inflorescences typically umbelliferous; tepals mainly elliptic, having 1–7 anastomosing (sect. 3. *Omalocarpus*) 106
- 105b. Basal leaf blades pinnatifid, with large central segment and smaller imbricate lateral segments; involuclal leaves reduced; flowers solitary; tepals linear-lanceolate, without anastomosing veins (sect. 14. *Imbricata*) 104. *A. imbricata*

- 106a. Tepals linear-lanceolate, 6–10 mm long; basal leaf blades rhombic, glabrous, 2–3 × 2–4 cm (ser. 3. *Fuscopurpurea*) 103. *A. fuscopurpurea*
- 106b. Tepals wider, 10–25 mm long; basal leaf blades of various shape, pubescent (rarely subglabrous), much larger ... 107
- 107a. Achenes with styles pressed to their bodies; tepals mainly 6–15 mm long, filaments linear; inflorescences mainly umbelliferous; basal leaf blades 3-sected (ser. 1. *Involucratae*) 108
- 107b. Achenes with straight or bent styles; tepals 10–25 mm long, filaments dilated; inflorescences branched; basal leaf blades 3-parted or 3-lobed (ser. 2. *Involucellatae*) 113
- 108a. Tepals 15–20 mm long, glabrous; scapes 70–120 cm long; basal leaf blades orbicular-ovate, subglabrous 94. *A. robusta*
- 108b. Tepals smaller, pubescent; scapes lower; basal leaf blades of various shape, pubescent 109
- 109a. Basal leaf blades orbicular; involucreal leaves larger than basal leaves; tepals 6–10 95. *A. cathayensis*
- 109b. Basal leaf blades non-orbicular; involucreal leaves smaller than basal leaves; tepals 5–7 110
- 110a. Carpels and achenes ovate to obovate; tepals 5–7, subglabrous 111
- 110b. Carpels and achenes broadly ovate to suborbicular; tepals 4–5, pubescent 112
- 111a. Tepals monomorphic, white or yellowish; scapes mainly solitary, erect; basal leaf blades wider than long 93. *A. narcissiflora*
- 111b. Tepals sometimes dimorphic, mainly blue or pink; scapes 3–5, ascending; basal leaf blades longer than wide 96. *A. demissa*
- 112a. Tepals white, 7–10 mm long, with 3–5 anastomosing veins; basal leaf blades ovate 97. *A. taipaisensis*
- 112b. Tepals red or pink, 15–20 mm long, with 1–3 anastomosing veins; basal leaf blades pentagonal or rhombic 98. *A. smithiana*
- 113a (107b). Achenes 8–12 mm long, with styles 1.5–2 mm long; tepals 4; basal leaf blades 3-lobed, coriaceous, glabrous 99. *A. tetrasepala*
- 113b. Achenes and styles smaller; tepals 5–10; basal leaf blades 3-parted, herbaceous, pubescent 114
- 114a. Achenes orbicular-ovate, sparsely puberulent, with curved styles; tepals 5–10, reflexed, with 7–9 anastomosing veins, sparsely puberulent 100. *A. polyanthes*
- 114b. Achenes ovate-ellipsoid, glabrous, with substraight styles; tepals 5, straight, without anastomosing veins, subglabrous 115
- 115a. Achenes 6–8 mm long, with wings 1.2–1.3 mm wide and styles 1–1.5 mm long; tepals 12–20 mm long, with cuneate base and rounded apex 101. *A. elongata*
- 115b. Achenes 5–6 mm long, with wings 0.5–0.6 mm wide and styles 0.6–1 mm long; tepals 7–12 mm long, with rounded base and acute apex 102. *A. shikokiana*
- 116a (104b). Carpels and achenes cylindroid; tepals 5, without anastomosing veins; anther connectives with large subglobose projections; inflorescences many-flowered; basal leaf petioles basally sharply dilated; plants with short non-tuberous rhizomes (subgen. 13. *Hepaticifolia* sect. 19. *Hepaticifolia*) 116. *A. hepaticifolia*
- 116b. Carpels and achenes spindle-like or ellipsoid; tepals 5–8, having anastomosing veins; anther connectives without projections; flowers solitary; basal leaf petioles basally not sharply dilated; plants with long horizontal or

- short tuberous rhizomes 117
- 117a. Carpels and achenes spindle-like, not compressed, glabrous; styles 4–5 mm long; tepals 5–6, pubescent; plants with long horizontal rhizomes (subgen. 14. *Richardsonia* sect. 15. *Richardsonia*) 117. *A. richardsonii*
- 117b. Carpels and achenes ellipsoid, compressed, basally sparsely pubescent; styles ca. 1 mm long; tepals 6–7, glabrous; plants with short tuberous and long stolon-like rhizomes (subgen. 15. *Crassifolia* 18. sect. *Crassifolia*) 118. *A. crassifolia*

As a result of the above study, we accept a structure of the genus *Anemone* s. str. differing essentially from those of Ulbrich (1906), Juzepchuk (1937), Starodubtsev (1989, 1991) and Tamura (1991, 1995). Recently we published the results of the taxonomic revision of *Anemone* sensu proprio (viz., Ziman 1985, Ziman et al. 1997, 1998, 2004, 2005, 2006, 2007, Wang et al. 2001), but in this paper we concentrate all our proposals and conclusions on taxonomy of this genus. In our opinion, the genus *Anemone* includes 118 species, 20 subspecies and 27 varieties belonging to 23 series, four subsections, 23 sections and 15 subgenera. In the genus *Anemone* we propose the new understanding of three subgenera (*Stolonifera*, *Keiskea* and *Kilimandsharica*), series *Fuscopurpurea*, *Altaicae* and *Mexicanae*. In addition we published earlier sect. *Parviflora* (Ziman 1985) and *Rosulantes* (Ziman et al. 2005), subsection *Somalienses* (Ziman 2006) and 12 series (viz., *Obtusilobae*, *Trullifolia*, *Nikoenses*, *Caucasicae* and others - Ziman et al. 2006–2007).

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S. N. ジーマン, E. V. ブラーク, 門田裕一, C. S. キーナー: イチリンソウ属 [狭義] (キンポウゲ科) の分類

瘦果, 花, 葉, 地上部, 地下部など約70の形態的形質の解析の結果, キンポウゲ科イチリンソウ属 [狭義] に15亜属23節4 亜節23列118種が認識された. このうち6 亜属2 節16列は新しく報告されたものである. 本稿では, 各種内分類群の形態

的特徴を述べるとともに, 118種全種の検索表を提示した.

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