Petra G. Smit: *Caltha*

a. Very small, creeping plants from 71° 14' N. Lat.
b. Plants intermediate between 3a and 3c from 70° 40' N. Lat.
c. Larger, more erect plants from 69° 50' N. Lat. (turn over please).

Fig. 3. Herbarium specimens of *C. palustris* var. *radicans* from the vicinity of Point Barrow, Alaska.

Very small, creeping plants from 71° 14' N. Lat.

Plants intermediate between 3a and 3c from 70° 40' N. Lat.

Larger, more erect plants from 69° 50' N. Lat. (turn over please).
A REVISION OF CALTHA (RANUNCULACEAE)

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INTRODUCTION

The family of the Ranunculaceae, although a large one (ca. 1200 species) occurring almost throughout the world, is generally regarded as a very natural one. The only genera with a recently more or less disputed position are Circaea, Glaucidium, Hydrastis, Kingdonia, and Patonia. The others may at present all be considered to be 'true' Ranunculaceae.

Various botanists have studied the delimitation of these genera, their affinity and phylogenetic links. Their ideas are often widely divergent. There is no need to go into the subject here, but some opinions on the place in the system of Caltha may be reviewed.

Hutchinson (1923) distinguished two subfamilies on the basis of morphological characters, the Helleboroidae with follicular fruits and the Ranunculoideae with achenes. All later authors working in the family maintained this primary subdivision on fruit characters. Langlet (1932) arrived at the conclusion that also the shape of the chromosomes and their basic number formed a good basis for subdividing the family. Gregory (1940/41), working on the same lines, by and large agreed with him but assigned some genera (Adonis, Nigella) a different place. Hammond (1952) did serological work and summed up his conclusions with regard to Caltha as follows: 'The position of Caltha is a central one; it is near to the main trunk of several lines of evolution'. Tamura (1966) also placed Caltha in the centre and called it one of the most primitive genera of the family, i.a. because of the absence of petals and of other derived characters. Ruygrok's chemotaxonomic work (1966) lead to the conclusion that chemotaxonomy largely supports Langlet's ideas. Jensen (1968) also applied chemotaxonomic methods and found himself in surprisingly close agreement with Gregory as regards his subdivision of the family; his conclusions were also a good match of those of Tamura. The ideas of four important authors about the place of Caltha in the Ranunculaceae are summed up in the following table.
The genus

*Caltha* is generally regarded as one of the most primitive genera of the *Ranunculaceae*. It lacks petals and also other derived characters. It occurs in moist to marshy places in Arctic and North- and South-temperate regions of both hemispheres.

The species of the Northern and those of the Southern Hemisphere distinctly fall into two different groups. A. de Candolle (1818) divided the genus into the sections *Populago* and *Psychrophila*. In the former the leaves are flat, undivided, cordate to reniform, in the latter the basal lobes of the foliar lamina form upturned erect auricles. His section *Populago* comprised all North-temperate, his section *Psychrophila* all South-temperate species. Though De Candolle knew only two species from section *Psychrophila*, the other South-temperate species, too, proved to find their natural place in it. Later authors, e.g. Engler & Prantl (1891), Tamura (1961), and the present one, maintained the subdivision as a natural one.

Species and their variation

Some species vary considerably in their morphological characters. Besides, there is much cytological variation between and also within some species. This has led to considerable differences in the number of species recognized and their delimitation.

Schott, Nyman and Kotschy (1854) divided the holarctic *Caltha palustris* into 6 species, *C. cornuta*, *C. latifolia*, *C. laeta*, *C. intermedia*, *C. vulgaris*, and *C. alpestris*. Beck (1886) also split up *Caltha palustris*, but not in the same way; he distinguished five species with a number of varieties. All these authors based their subdivision primarily on characters of the follicles.

Huth, in his *Monographie der Gattung Caltha* (1892), did not adopt these views. He recombined the segregate species, as their areas strongly overlap, as there are many transitional forms between them, and as the variation in one and the same population often exceeds the boundaries between the preceding authors’ ‘species’, but he still maintained 14 varieties. Reese (1954) and Tutin (in Heywood c.s., Flora Europaea I, 1964) also expressed as their opinion that a satisfactory classification of the different forms of *Caltha palustris* is very difficult to achieve.

The complex of *Caltha leptosepala* in western North America also poses many taxonomic problems. De Candolle (1818) described two species, *C. leptosepala* and *C. biflora*. Hooker (1833) copied his brief descriptions, adding to that of the latter: ‘I have seen no specimens which exactly accord with this, but it seems to me too nearly allied to *C. leptosepala*’. Torrey and Gray (1838—1840) followed Hooker. Lawson (1884) maintained only *C. leptosepala*, reducing *C. biflora* to a variety of it. Huth (1892) combined the two species completely. Greene (1899), on the other hand, distinguished 9 species, *C. biflora*, *C. malvacea*, *C. confinis*, *C. leptosepala*, *C. macounii*, *C. chelidonii*, *C. howellii*, *C. rotundifolia*, and *C. chionophila*, seven new species in addition to De Candolle's original two. Most modern authors like Hultén (1941), Abrams (1944), Anderson (1959), and Hitchcock (1964), recognize *C. leptosepala* and *C. biflora*, sometimes with subspecies or varieties.
Only *Caltha natans*, although widespread in the Northern Hemisphere, shows relatively little morphological variation.

Lourteig (1951) made a special study of the South American representatives and recognized three species. The present author, working only with herbarium material, completely accepts her results and conclusions.

![Map of the distribution of the two most common cytotypes of *C. palustris*: 2n = 32 and 56.](image)

The three species occurring in Australia and New Zealand are partly also quite variable but have more restricted areas than the North temperate ones; this may be the reason why they are less problematical.

The present author's cytotaxonomic work was restricted to European *Caltha palustris* (see fig. 1). As anticipated, its enormous infraspecific morphological variability was accompanied by great cytological variability. Cytotaxonomic study in other parts of its
area, and of the other species, may contribute to a better understanding of the genus as a whole.

It is hoped that the present study will help to solve some problems and also show were further study is most urgently needed.

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A. GENERAL DISCUSSION PART

I. Section Caltha

1. Caltha palustris L. sensu lato

The very large morphological variation of this species has led to various subdivisions at the level of the variety, subspecies, and even species. The very large circumboreal distribution of the species has also contributed to this. Perusal of the literature readily shows the great confusion prevailing. In the introduction the views of the principal older authors on the species have been reviewed. The same controversial opinions are found in the recent literature. In Flora Europaea 1 (Heywood, 1964) Tutin lists 5 taxa of dubious status under Caltha palustris, viz. C. cornuta Schott, Nyman & Kotschy, C. laeta S.N.K., C. longirostris Beck, C. minor Mill., and C. polygala Hochst. The principal differences are said to be in the follices. Soö and Kovács-Lang (1967) and Wcislo (1967) distinguished various subspecies for Hungary and Poland, respectively, also principally on the basis of follicular characters. In Davis's Flora of Turkey vol. 1 (1965) C. polygala is called 'doubtfully distinct from C. palustris'. Schipczinsky (in Komarov, Flora U.R.S.S. 7, 1937) listed 6 species as occurring in the Soviet Union: C. caespitosa Schipcz., C. arctica R. Br., C. palustris L., C. fistulosa Schipcz., C. membranacea (Turcz.) Schipcz., and C. polygala Hochst. In Olivi's Flora of Japan (1965) C. palustris is subdivided into 3 varieties, var. membranacea Turcz., var. pygmaea Makino, and var. barthei Hance. Hultén (1968) lists two subspecies from Alaska, ssp. arctica (R. Br.) Hultén and ssp. asarifolia (DC.) Hultén; in 1941 the same author treated ssp. arctica as a variety.

When one critically compares the treatments in these books, one is forced to conclude that the diagnoses of the taxa are often at variance with each other, and that even in one and the same work the descriptions are contradictory. Reliable determination of a given specimen becomes difficult, if not impossible. The conclusion is that the subdivision of C. palustris has been made solely on the basis of herbarium material, without the aid of biosystematic work. The characters employed are subject to great fluctuations, and their extremes can not rarely been found in plants from one and the same local population, or even in a single plant.

The present author, in her biosystematic work on C. palustris, therefore always studied several plants from one population. She investigated 35 populations from the Netherlands and 50 from elsewhere in Europe, namely, from Britain, Ireland, Iceland, Finland, Germany,
France, Austria, Spain, Portugal, and Yugoslavia. In the field phytosociological 'relevés' were made, some plants were collected for the herbarium, and others were dug up and transplanted to the experimental garden. The material was studied biometrically, morphologically, and cytotaxonomically. From these studies (Smit 1967, 1968), combined with work on herbarium material of *C. palustris* from its entire area, the following facts emerged:

1) The size of the plants fluctuates very strongly. In the lowlands very large, many-flowered plants with large flowers and foliage and thick stems are met with. In montane and arctic regions few-flowered dwarfed specimens are not uncommon. These extremes behaved differently in the experimental garden. The large lowland plants decreased in size from one year to the next, the dwarf specimens became larger. After 3 years there was a certain stabilization. The increase in size of the dwarf plants is the more striking when compared with a decrease of most plants from populations of 'average' dimensions; the latter became somewhat smaller in cultivation, until, after 3 years, they, too, showed stabilization. Extremely large plants showed a relatively much stronger reduction in size than plants of 'average' size (for measurements see Smit 1968, p. 288). In other words: Calthas from different populations with very different appearance, when grown under uniform conditions, become more and more similar.

2) In the field as well as in the experimental garden plants with an erect and plants with a prostrate habit can be observed. These are often observed together in one and the same
population, and intermediates occur. However, in some populations erect plants prevail, in others prostrate ones, and some populations consist mainly of intermediates.

3) Some authors, e.g. Wcislo (1967), in subdividing the species make use of the size of the angle between the two basal parts of the margin of the radicular leaves. This fluctuates from 0° (touching or overlapping lobes) to 90°. However, this character proves to fluctuate very strongly in a single population, and there is much variation even among the leaves of one plant.

4) The leaf margin is also quite variable; it may be coarsely dentate, dentate-crenate, or even quite entire. Here again, considerable fluctuations can be observed in a single specimen. Some populations showed a definite tendency towards subentire, dentate, or dentate-crenate, respectively, but others showed all kinds of variation and transitions. Examination of the radicular leaves after the flowering period shows the external (oldest) leaves to be much more nearly entire than leaves having developed later in the season. It goes without saying that use of this character only increases the confusion.

5) The colour of the tepals of Caltha palustris varies from light yellow via golden yellow to orange yellow. A single population is fairly uniform to the eye in this respect, but distinct differences can be observed between one population and another. Field studies showed plants from shaded stations to be rather pale-flowered and plants from exposed stations bright and shining golden-yellow. After two years' cultivation in the experimental garden such differences could no longer be made out with the naked eye. A number of plants from Yugoslavia in their natural environment had strikingly orange-yellow flowers, but after cultivation for two years they had assumed the same shade of yellow as most populations in the experimental garden.

The number of tepals is also subject to fluctuation, even in one inflorescence. Gertz (1913) described this phenomenon in Swedish plants. Like various other authors, he found 5 as the most common number of tepals. In his studies out of a total 2260 flowers ca. 90% had 5 tepals, the remainder 4—9. In Dutch populations the present author only once observed a flower with 4 tepals, but flowers with 9 occurred very regularly. On the other hand, Gertz (l.c.) reported 17 flowers with 4 and only one with 9 tepals. Counts of 1000 flowers from Dutch plants yielded: ca. 66% with 5 tepals, 28% with 6, 10% with 7, 1% with 8, and >½% with 9.

6) The number of carpels per flower is by no means constant. Some populations have larger (11—16), others smaller (6—11) numbers of carpels, but the fluctuation within one population tends to be more or less consistently 5. Within one population or even one inflorescence differences of 5 carpels are not uncommonly found. In cultivation the number of carpels proved to increase (Smit, 1968); the same was observed by Woodell & Kootin-Sanwu (1971). Burkill (1895—97) already studied flowers of Caltha palustris biometrically; his conclusion was: 'It shows, then, that the oldest branches, i.e. those which produce most flowers, have in these flowers more stamens and carpels than the flowers in corresponding positions on weaker stems'.

7) In a considerable part of the literature the shape of the mature follicle is considered as one of the principal characters for taxonomic subdivision. Again, study of living populations as well as of herbarium material showed this to be a variable and unreliable character. The present author concurs with the opinion of Woodell & Kootin-Sanwu (1971) that it cannot be used either.

8) The seeds of European and American plants of Caltha palustris are asymmetric, dark brown with a light brown persistent raphe and chalaza serving as a floating organ. The seeds of most Asiatic herbarium specimens, however, proved to be symmetric and almost black and indistinguishable from those of C. leptosepala (see Smit & Punt, 1969). Un-
Fortunately, the herbarium material available to the author was insufficient for establishing the borderline between the two seed types, or the presence of transitional types, if any.

9) Another character used for subdividing *Caltha palustris* is the time of flowering of a given population. Hultén’s Atlas (1950) indicates a clear connection between the altitude and latitude at which a population occurs and its flowering period. Observations in the experimental garden showed unequivocally that an early spring (1967) made the plants flower earlier than in a year with a backward season (1966) (see Smit, 1968, fig. 1, p. 285). Populations from the Alps, after a year’s cultivation in the experimental garden, flowered approximately simultaneously with plants from the lowlands, whereas at the time they were collected they were still flowering and their lowland counterparts were long past flowering. The native populations in the Netherlands flower with an interval of about one month. Observations in three consecutive years confirmed that this remained fairly constant (see also Smit, 1968). The environment proved to influence this feature quite strongly.

This influence of the environment was clearly demonstrated by all experiments described above. The variation within a given population is smaller than the difference between different populations, but is nevertheless demonstrable. The extreme plasticity of *Caltha palustris* casts serious doubt on the tenability of the characters used for a taxonomic subdivision of the species. According to Davis and Heywood (1963) 'the subspecies, as a considerable segment of a species with a distinct area and more or less distinct morphology, often showing some intergradation, clearly fulfils a useful purpose'. It is at a higher taxonomic level than the distinct types observed within our material of *Caltha palustris*.

*Caltha palustris* var. *radicans*

Rooting at the nodes is a character often used for establishing a subordinate taxon of *Caltha palustris*. Forster (1804) described plants from Scotland showing this character as *Caltha radicans*. Likewise Hultén (1968) described ssp. *arctica* from North America as having roots on the nodes. In the present author’s experiments the character remained constant in the experimental garden, after transplantation from nature. Woodell and Kootin-Sanwu (1971) produced a cross between a plant rooting at the nodes and one that did not show this character; 6 out of 20 F1 descendants also rooted at the nodes. Their conclusion was that this feature is genetically controlled and therefore potentially useful for taxonomic subdivision. The Dutch material contained two interesting populations rooting at the nodes and reproducing vegetatively in this way. These plants were firstly from a population from Ulvenhout agreeing perfectly with the description of the type of *Caltha radicans* Forster. They had long-creeping few-flowered stems, rather small mother plants and, later in season, young daughter plants on the stem nodes. The other population was from the Biesbosch; these plants, too, rooted at the nodes of the flowering stems, but were large, erect, and many-flowered. Van Steenis (1971) regarded them as a distinct variety, *C. palustris* var. *araneosa* Van Steenis. He confined his studies to the phenomenon in populations from a limited area. The present author assigns the populations from Ulvenhout as well as those from the Biesbosch to *C. palustris* var. *radicans*. Comparison and juxtaposition of all specimens from the Northern Hemisphere showing this character proves the existence of a continuous series of transitions between on the one hand one- or few-flowered plants with prostrate stems to, on the other hand, large, erect, many-flowered plants. The two Dutch populations fit well in this series. A good illustration of this series of transitions was provided by material from the U.S. National Herbarium, chiefly from Alaska and the Yukon Territory. It contained numerous plants with rooting nodes as a common feature, but otherwise most diverse habit; see fig. 3a, b, c
The northernmost plants, in our case from Point Barrow, were strikingly dwarfed, few-flowered, and had prostrate stems. Specimens from southern Alaska, on the other hand, had more or less erect, much more robust, many-flowered stems. From North to South there was a complete series of intermediates, i.e. a gradual increase in size (leaves, flowers, height of the plants) and all transitions from prostrate to erect. As shown by fig. 4, this was quite evident between 69° and 71°30' N. Lat. When these results are considered together with other data about the plasticity of *C. palustris*, it seems safe to conclude that the variability of this character, too, is governed by the milieu of various populations. Comparison of the milieus harbouring these vegetatively reproducing populations brings to the light a common feature: they occur in places where the possibilities for seed germination are poorer (or perhaps quite absent) than in the biotopes were the 'normal' form occurs. E.g., in Ireland var. *radicans* often grows on abrading lake shores; at Ulvenhout the plants occur in shallow, swiftly flowing watercourses; in the Biesbosch on periodically emerging mud flats in a freshwater tidal area with great fluctuations between high- and low-water level; lastly, in Alaska and northern Europe climatic conditions are extreme, with short vegetation periods and poor chances for seed maturation (see also Smit, 1968: pp. 290—291). The author's views on what a variety is agree very well with Salisbury's, 'Categories in which the morphological distinctions are of a minor character but which are genetically different'. This seems to fit the case of the populations described above which are therefore regarded here as a variety, *C. palustris* L. var. *radicans* (Forst.) Beck (1886).
C. palustris var. alba and var. purpurea

Plants from the Himalayas diverge in the colour of their tepals from the normal, yellow hue of C. palustris; theirs are white or magenta. The white-flowered plants were originally described as a species, C. alba Cambessedes (1844), regarded as a variety of C. palustris by Hooker f. and Thompson. The present author shares their opinion. Initially it seemed as if the white-flowered plants also diverge in their pollen structure. Outside the Himalayas the pollen of C. palustris is tricolpate, but in the Himalayas, including the area harbouring C. alba, a number of flowers proved to possess pantoporate pollen-grains, which also

proved to be the case for nearly all plants of C. palustris var. alba (see fig. 5). As regards their other characters, the white-flowered plants fell well within the variation of C. palustris.

Plants with magenta-pink flowers were described in 1929 as C. palustris L. var. purpurea Spare & Fischer. More recently (1965) Burtt & Lauener described the species C. rubriflora,
said to be closely related to C. scaposa but differing in magenta-pink flowers. The stations of these two taxa are not far apart: Spare & Fischer's type is from the Deli Valley in Assam (28°14' N. Lat., 96°20' E. Long.), Burtt & Launer's from Doshong La in southern Tibet (29°29' N., 94°59' E.). Both localities are at an altitude of ca. 4000 m. In contrast to C. palustris var. alba the form with magenta-pink flowers is known by only little material, which renders a decision about its taxonomic status quite difficult. In the herbarium material at the author's disposal there was only a single other specimen with this unusual flower colour, *Farrer 1764* from the Mokuji Pass, frontier area Tibet-Assam, alt. ca. 4000 m (E); this is about 560 km SE of the type locality of *C. rubriflora*. In other characters the plant is not unusual. The same was reported by Spare & Fischer who, therefore, did not assign their plant more than variety status.

It is true that at first sight *C. rubriflora* does not conform with the usual appearance of *C. palustris* but more with that of *C. scaposa* which occurs in the same area. However, the best diagnostic feature of *C. scaposa*, stipitate follicles, is lacking in *C. rubriflora*. Moreover, the leaves of *C. scaposa* are ovate, those of *C. rubriflora* reniform, like those of *C. palustris*. In general appearance the type material of *C. rubriflora* is much like the montane dwarf forms of *C. palustris*.

In spite of the scarcity of material of the magenta-pink-flowered form it seems best to treat it for the present as a variety of *C. palustris*, which must then be called *C. palustris* L. var. *purpurea* Spare & Fischer.

2. *Caltha leptosepala* coll.

In comparison with *C. palustris*, the complex species *C. leptosepala* is less bewildering, presumably at least in part because of its considerably smaller area. This comprises a number of states of the northwestern United States, the west coast of Canada, and parts of southwestern Alaska (see fig. 6).

In the introduction the views of the most important authors on this complex have been surveyed briefly. The present author, with Punt (1969), arrived at the conclusion that the complex is best regarded as a single species* with two subspecies, *C. leptosepala* DC. ssp. *leptosepala* with rosulate ovate-cordate leaves, a single flower, approximately linear tepals, and tricolpate pollen grains; and *C. leptosepala* DC. ssp. *howellii* (Huth) Smit (see below) with rosulate mostly reniform leaves, a one- or two-flowered stem, tepals more tending towards an oblong shape, and pantoporate (or occasionally pantocolpate) pollen grains. In the last-cited paper instead of ssp. *howellii* the name *C. leptosepala* DC. ssp. *bisflora* (DC.) Smit was used, but later bibliographic work showed that the name *howellii* is the oldest name applied in the rank of a subspecies and therefore takes precedence.

Virtually all specimens from northern Washington, Idaho, western Canada, and Alaska show characters of both subspecies (see fig. 6); these intermediates vindicate treatment as two subspecies rather than as full species of the two extreme forms. For more data see Smit & Punt (1969). These plants cannot be named more precisely than *C. leptosepala* DC.

Hitchcock (1964) described a var. *sulfurea* of *C. leptosepala* ssp. *leptosepala*. This variety seems to be tenable, analogous to *C. palustris* var. *alba* and var. *purpurea*.

* This conclusion was confirmed by Morris, A biosystematic analysis of the *C. leptosepala* complex in the Rocky Mountains, Brittonia 24 (1972) 177—188, who analysed the *C. leptosepala* complex chromatographically.
Fig. 6. Map of the herbarium specimens studied of *C. leptosepala s. lat.* in W. North America, showing their variability and the intergradation of the various forms.
Fig. 7. Map of the herbarium specimens studied of the three South American Caltha species.
II. Section Psychrophila

This section is confined to South Temperate areas. The species belonging to it occur in the high mountains, descending to lower levels only in subantarctic regions, e.g., Tierra del Fuego.

On the basis of the attachment of the foliar appendages Troll (1932) subdivided the section into three groups:

1) *Sagittata* Group: appendages attached at the leaf base, appearing like inflexed or replicate leaf-sauricles;

2) *Dionaeifolia* Group: the appendages have the appearance of being independent excrescences of the leaf bases;

3) *Appendiculata* Group: the appendages spring from the upper side of the lamina on both sides of the costa.

Morphologically this subdivision is sound, but the species assigned by Troll to these three groups are in part untenable. As treated in the present revision, almost all species of section *Psychrophila* (*C. obtusa*, *C. novae-zelandiae*, *C. introloba*, and of course *C. sagittata*) would belong to the first group; the second would comprise only *C. dionaeifolia*, the third only *C. appendiculata*. The three species after which Troll's groups were named all occur in South America. Their areas are not identical (see fig. 7), but they all overlap in one region.

Apart from some taxonomic details, the present author agrees completely with the conclusions of A. Loureteig's taxonomic revision (1951) of the South American species. This is partly due to the good morphological distinctions based on the basal leaf appendages.

The Australian and New Zealand species of this section (see fig. 8), on the other hand, had been neglected in the literature and had to be studied more closely. Thanks to large series of material from the herbaria of Christchurch, Melbourne, and Wellington, the taxonomic problems could be satisfactorily solved by means of comparison and quantitative approach.

The present author examined, measured, and compared the length and width of the foliar lamina and its appendages, the leaf margin, length and structure of the leaf sheath and the petiole, length of the peduncle during and after anthesis, the number and dimensions of the tepals and, where possible, their colour, number and shape of the stamens and carpels, and the shape of the stigma and the seeds. The pollen grains all proved to be tricolpate.

The greatest fluctuation in characters was observed in *C. novae-zelandiae* (see fig. 9b). Two sheets of material collected by *Townson*, s.n., from SW. Nelson and Buckland Peak (WELT), contained only plants without appendages. A collection by Petrie from Kellip Hill, Otira River (WELT) and one by Hay from the Whanaluia Range (CHR) provided a solution. Some leaves were without appendages, but most had short ones. This was the only instance encountered of a species of section *Psychrophila* that was occasionally without leaf-appendages.

In 1890 Colenso described *C. marginata* and noted: 'A species evidently closely allied to *C. novae-zelandiae* Hook. (discovered by me on the same range, but much higher up); but this is a smaller plant...'. Series of herbarium specimens with indication of altitude show that at higher elevation the plants tend to be smaller. Cultivation experiments in *C. palustris* showed that such dwarf forms are nothing but modifications caused by the environment. It may safely be concluded that the same is true for *C. novae-zelandiae* and that *C. marginata* is untenable as a species.
C. obtusa (fig. 9a) showed less variation and posed few problems, perhaps also because it has a more restricted range (see fig. 8).

Compared with these species from New Zealand the Australian C. introloba is as a rule more robust (fig. 9c). Besides this species the literature often refers to another Australian species, C. phylloptera Hill. The holotype of C. phylloptera, seen by the author, in no way differs from C. introloba. It is from Tasmania; only two other sheets from that island were examined, which also fell well within the variation of C. introloba. Curtis in his 'Students flora of Tasmania' (1956) reported only C. phylloptera. In spite of the scarcity of material from Tasmania his opinion seems untenable, and the Tasmanian specimens should be assigned to C. introloba, which is also phytogeographically plausible. As there are hardly any illustrations of the three species from Australia and New Zealand extant, it seemed worthwhile to include drawings of them in the present revision (fig. 9a—c).

Map of the herbarium specimens studied of the three Australian Caltha species.

B. TAXONOMIC PART

Materials

The taxonomic part of the present paper is based on the study of about 3000 herbarium sheets. For reasons of space only a number of specimens per species are cited; these were either geographically selected, in order to give an impression of the range of the species, or whenever they seemed taxonomically important. The distribution maps, given for every species, are based on all available herbarium material. The following herbaria (cited by the standard abbreviations in 'Index Herbariorum') made material available to the author:

**BA** Buenos Aires, Argentina: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' e Instituto Nacional de Investigaciones de las Ciencias Naturales.

**BAB** Buenos Aires, Argentina: Instituto de Botanica Agricola del I.N.T.A.

**BM** London, Great Britain: British Museum (Natural History).

**CAL** Calcutta, India: Central National Herbarium.

**CHR** Christchurch, New Zealand: Botany Division, Dept. of Scientific and Industrial Research.

**DD** Dehra Dun, India: Forest Research Institute and Colleges.

**E** Edinburgh, Great Britain: Royal Botanic Garden.

**GRO** Groningen, Netherlands: Dept. for Systematic Botany of the Botanical Laboratory.

**K** Kew, Great Britain: The Herbarium, Royal Botanic Gardens.

**KYO** Kyoto, Japan: Dept. of Botany, Faculty of Science, Kyoto University.
Glabrous perennial herbs. Leaves alternate, simple, lamina sometimes with basal appendages; venation palmate; margin entire, dentate, or crenate. Flowers single or in few-flowered corymbiform inflorescences, actinomorphic; perianth in a single whorl, (4- or) 5-pleiomerous, corolla-like, yellow or white or rarely magenta-pink; nectaries wanting; stamens and carpels numerous, inserted on a flat torus; carpels at least 3, free, with numerous ovules inserted along the ventral suture. Fruits several to many, free, sessile or shortly stipitate, follicular; seeds oblong to subglobose, not winged.

**Type:** *Caltha palustris* L.

**KEY TO THE SECTIONS**

Lamina flat; peduncles mostly leafy, usually several-flowered; **North-temperate**

Lamina with inflexed basal appendages*); flowers solitary on leafless peduncles; **South-temperate**


**Section I. Caltha.**

1a. Flowers yellow, 2—5 cm in diam.; follicles (8—)10—20(—25) .......................... 2
   b. Flowers white or magenta-pink .................................................. 5

2a. Follicles sessile; lamina reniform or cordate ........................................ 3
   b. Follicles stipitate; lamina ovate-cordate; flowers solitary or 2 per peduncle; **Eastern Himalayas** .................................................. 4. *C. scaposa*

3a. Stems leafy; flowers saturated yellow ................................................. 4
   b. Stems scapose or one-leaved; flowers sulphureous. 2a*. *C. leptosepala* var. *sulfurea*

4a. Nodes producing roots and shoots after anthesis ............................. 1d. *C. palustris* var. *radicans*
   b. Nodes without roots and shoots after anthesis ................................ 1a. *C. palustris* var. *palustris*

5a. Flowers 1—1.2 cm in diam.; follicles 20—40 in a globular capitule; stems either floating in the water, or prostrate and rooting at the nodes. ................. 3. *C. natans*
   b. Flowers 2—5 cm in diam.; follicles 3—20 .......................................... 6

6a. Flowers white ................................................................. 7
   b. Flowers magenta-pink, mostly only one per peduncle; **Assam and East Tibet**

1c. *C. palustris* var. *purpurea*

*) These very rarely wanting in *C.novae-zelandiae.*
The three Australian species of *Caltha*, showing a plant, a single leaf, and one tepal.

7a. Flowers one or two per peduncle; stem with one leaf or leafless; *Western North America* ........................................ 8
b. Flowers several per peduncle; *Pakistan and Kashmir* .................. 1b. *C. palustris* var. *alba*

8a. Lamina orbicular-reniform or orbicular-ovate, to 15 cm long, as wide as long or wider; flowers white, 2 (i) per peduncle; cauline leaves one or none; pollen pantocolpate ........................................ 2b. *C. leptosepala* ssp. *howellii*
b. Lamina cordate, oblong-ovate, to 7 cm long, $\frac{1}{2}-\frac{4}{5}$ as wide; pollen tricolpate.

2a’. *C. leptosepala* var. *leptosepala*
Section II. Psychrophila

1a. Flowers bright yellow; southern South America .......................... 2
b. Flowers pale yellow or white; *Australia and New Zealand* ............. 4

2a. Plants to 25 cm tall. Lamina ovate or subtriangular; laminar appendages obliquely reflexed, half as long as the lamina. Stamens 35–75 per flower; follicles 50–85, in a globular capitule ......................................................... 7. *C. sagittata*
b. Plants small, to 8 cm tall; not over 12 stamens and 8 follicles per flower .... 3

3a. Lamina obovate-oblong with retuse apex; mostly 2 (sometimes 3 or 4) laminar appendages, inserted on the upper surface, on both sides of the costa

5. *C. appendiculata*
b. Lamina ovate or suborbicular, bilobate, concave and embracing the two basally inserted, semi-ovate appendages ........................................ 6. *C. dionaeifolia*

4a. Lamina ovate-lanceolate, with hastate base, apically acute or emarginate; appendages lanceolate; flowers white; *Australia* ................................. 10. *C. introloba*
b. Lamina ovate-oblong or suborbicular with subcordate, bilobed base, apically emarginate; appendages semi-ovate-oblong; *New Zealand* ............................... 5

5a. Lamina ovate-oblong to oblong, margin entire to sinuate; laminar appendages to \( \frac{1}{2} \) as long as the lamina (very rarely wanting). Tepals pale yellow, lanceolate, acute. 8. *C. novae-zelandiae*
b. Lamina broadly oblong to suborbicular, mostly wider than long; margin crenate or crenate-dentate; laminar appendages more than 1/2 as long as the lamina. Tepals white, obovate, obtuse to subacute ........................................ 9. *C. obtusa*

I. Section Caltha


1. *Caltha palustris* L.

*C. palustris* Linnaeus, Spec. Pl. 1 (1753) 558. — Type: *Linnaeus herb. no. 719*, s. loc. (LINN, not seen, microfiche in U).

a. var. *palustris*

C. major Miller, Gard. Dict. ed. 8 (1768). — *C. palustris* var. major De Candolle, Syst. Nat. 1 (1818) 308. — Type: a specimen without data, presumably from Great Britain (BM).

C. minor Miller, Gard. Dict. ed. 8 (1768). — *C. palustris* var. minor De Candolle, Syst. Nat. 1 (1818) 309. — *C. palustris* f. minor Hetho, Helios 9 (1892) 73. — *C. palustris* ssp. minor Clapham, Fl. British Isles (1952) 9. — Type: (not cited, not seen; *ex char. et loc.)*.


C. *ficarioides* Pursh, Fl. Am. Sept. 2 (1814) 389. — Type: N. America (not cited, not seen; *ex char.)*.


C. *rippling* G. Don, Gen. Hist. Dichtl. Pl. 1 (1831) 44. — Type: (not cited, not seen; *ex char. et loc.)*


C. polyptela Hochstetter ex Lorent, Wanderungen (1845) 339. — C. palustris var. polyptela Huth, Helios 9 (1892) 71. — Type: presumably from Armenia (not cited, not seen; ex char.).


C. alpestris Schott, Nyman & Kotschy, Analecta Bot. 54 (1834) 33. — C. palustris var. alpestris Rouy & Foucaud, Fl. de France 1 (1893) 114. — Type: Hanny s.n., Austria subalpina (presumably W?, not seen; ex char. et loc.).


C. intermedia Schott, Nyman & Kotschy, Analecta Bot. 54 (1834) 32. — Type: Kotsky s.n., Transylvania (presumably W, ?; ex char. et loc.).

C. laeta Schott, Nyman & Kotschy, Analecta Bot. 54 (1834) 32. — C. palustris var. laeta Huth, Helios 9 (1892) 74. — Type: Kotsky s.n., Transylvania (W, ?; ex char. et loc.).

C. latifolia Schott, Nyman & Kotschy, Analecta Bot. 54 (1834) 32. — C. palustris var. latifolia Rouy & Foucaud, Fl. de France 1 (1893) 114. — Type: Kotsky s.n., Transylvania (W, ?; ex char. et loc.).

C. vulgari Schott, Nyman & Kotschy, Analecta Bot. 54 (1834) 33. — C. palustris var. vulgarius Rouy & Foucaud, Fl. de France 1 (1893) 114. — Type: Kotsky s.n., Austria inferior (W, ?; ex char. et loc.).


C. palustris var. minima Regel in Regel et al., Bull. Soc. Imp. Nat. Moscou 32 (1859) 227. — Type: Pauwesky & Stbersdorf s.n., ad ripas lacus Tomobaical (LE, not seen; ex char.).


C. poliiliflora Martin-Donos, Bull. Soc. Bot. Fr. 9 (1862) 130. — Type: Martin-Donos s.n., Dept. du Tarn, Mts. Noirs (L, not seen; ex char. et loc.).

C. pumila Schur, Enum. Pl. Transs. (1866) 26. — Type: Schur s.n., Transylvania, Reussen (W, ?; ex char.).

C. ranunculoides Schur, Enum. Pl. Transs. (1866) 26. — Type: Schur s.n., Transylvania, Hermannstadt (W, ?; ex char.).


The following 6 taxa were not treated explicitly as varieties by Schur, but the accompanying text points to such an intention:

C. palustris var. crenata Schur, Verh. N.V. Brünn 15, 2 (1877) 59. — Type: Schur s.n., Niederösterreich, Moosbrunn (herb; ex char. et loc.).

C. palustris var. cuneata Schur, Verh. N.V. Brünn 15, 2 (1877) 57. — Type: Schur s.n., Transylvania, Kronstadt (herb; ex char. et loc.).

C. palustris var. ficariaeformis Schur, Verh. N.V. Brünn 15, 2 (1877) 58. — Type: Schur s.n., Czeckslovakia, near Brün (Brno) (herb; ex char. et loc.).

C. palustris var. holubyi Schur, Verh. N.V. Brünn 15, 2 (1877) 58. — Type: Holuby s.n., Hungaria, Nemes Podhrad (herb; ex char. et loc.).

C. palustris var. ranunculiflora Schur, Verh. N.V. Brünn 15, 2 (1877) 58. — Type: Schur s.n., Czeckoslovakia, near Brünn (herb; ex char. et loc.).

C. palustris var. recurvirostris Schur, Verh. N.V. Brünn 15, 2 (1877) 58. — Type: Schur s.n., Transylvania, Hermannstadt (herb; ex char. et loc.).


C. grosse-serrata Pantoćek, Verb. V.N. Heilk. Fressb. 2 (1871/72) 86. — Type: Pantoćek s.n., presumably from Hercogorina (herb; ex char. et loc.).

C. palustris var. dentata Čelakovský, Prod. Fl. Böhmen (1874) 419. — C. palustris f. dentata Huth, Helios 9 (1892) 73. — Type: presumably from Bohemia (not cited, not seen; ex char. et loc.).
C. palustris var. bosnica Huth, Helios 9 (1892) 72. — Lectotype: Beck s.n., Yugoslavia, Treškavica Ms. (PRC).
C. palustris var. acetoserrata Huth, Helios 9 (1892) 72. — Type: Hayne s.n., Austria, Dornbach (W, †; ex char. et loc.).
C. palustris f. pratensis Huth, Helios 9 (1892) 73. — Type: Winkler s.n., Schönberg near Berlin (W, †; ex char. et loc.).
C. palustris var. stagnalis Rouy & Foucaud, Fl. de France 1 (1893) 114. — Type: (not cited, not seen; ex char.).
C. procumbens Huth in Baenitz, Prosp. Herb. Eur. (1894) 13. — Type: Baenitz s.n., Austria, Reinerz (WRS, not seen; ex char. et loc.).
C. confinis Greene, Pittonia 4 (1899) 76. — Type: White s.n., Alaska, Port Clarence (US).
C. elata Duthie, Gard. Chron. 1 (1909) 178. — Type: Duthie’s collector s.n., Himalayas, Hazara (K).
C. palustris f. erecta Makino, Tokyo Bot. Mag. 22 (1908) 176. — Type: Japan (not cited, not seen; ex char. et loc.).
C. palustris f. gigas Léveillé, Fedde Rep. 7 (1909) 102. — Type: Korsakof 455, Sakhalin (P, not seen; ex char. et loc.).
C. palustris var. umbrosa Diels, Notes R.B.G. Edinburgh 25 (1900) 264. — Type: Forrest 2479, China, Yunnan, Lichiang (E).
C. palustris subvar. palmata Takeda, Kew Bull. (1912) 218. — Syntype: Hancock 164, China, Yunnan, Menglü (K).
C. palustris var. nipponica Hara, J. Fac. Sc. Un. Tokyo III, 6 (1952) 50. — Type: Hara s.n., Honshu, Ozenuma (TI, not seen; ex char.).

D i s t r i b u t i o n: temperate and Arctic Europe, Asia, and North America.

E c o l o g y: in marshes, fens, ditches, and wet woods, up to 4300 m alt. in the Himalayas.

I.c.: Muller, Fl. Danica 4 (1777) t. 668.

Plants 10—80 cm tall, with numerous principal roots 2—3 mm thick and strongly branched; peduncles erect or ± decumbent. Young radical leaves surrounded by a membranous sheath, this in fully developed plants ca. 3 cm long; lamina of radical leaves reniform, 3—25 cm long, 3—20 cm wide, petiole about 4× as long as lamina; lamina of cauline leaves reniform-deltoid, subsessile. Leaf apex obtuse; margin basally mostly dentate or crenate-dentate, apically crenate or entire. Peduncle up to 80 cm tall, bearing (1—)3—6—(25) flowers. Flowers ca. 40 (20—55) mm in diam.; tepals (4)5(—9), yellow, broadly obovate, ca. 19 (10—25) mm long, ca. 13 (8—18) mm wide, obtuse or occasionally acute. Stamens 50—120; pollen grains tricolpate. Ovaries ca. 10 (5—25), linear-oblong, with numerous ovules; style basally not sharply delimitated, apically with an obliquely inserted bilobed stigma. Follicles sessile, patent, 8—20 mm long, 2½—5 mm wide, flattened,
asymmetrically oblong, gradually or abruptly passing into a short or occasionally longer, straight or curved beak (stemming from style and stigma), with 7—20 seeds. Seeds of European populations obliquely ovoid, ca. $2\frac{1}{2} \times 1\frac{1}{2}$ mm, dark brown with swollen, light brown, persistent raphe; of Asiatic populations black, lustrous, evenly ovoid. Flowering time April to July.

The Japanese literature makes mention of *C. palustris* var. *pygmea* Makino, Tokyo Bot. Mag. 16 (1902) 146 = *C. pygmea* Makino, J. Jap. Bot. 5 (1928) 17. The specimens seen by the author, all from MAK, were all cultivated. This seems to be nothing but another Japanese miniature cultivar.

Selected citations:


SWEDEN. Östmanland, Haglund and Källström s.n. (GRO); Göteborg, Belfrage s.n. (MEL).


GREAT BRITAIN. Godalming, Melderis 565 (BM); New Forest, *Smit D1081—1086* (U); Carlton, Phillips 32 (BM).


GERMANY. Bentheim, *Smit D141—150* (U); Chiemsee, id. *D921—925* (U).

FRANCE. Île de Saintonge, Culteed s.n. (MEL); Cévennes, *Smit D409* (U); Lac Mt. Cenis, id. *D410—445* (U); Hospice de France, id. *D906—997* (U).


SPAIN. El Ferrol, *Smit D325—333* (U); Mirador de la Reina, id. *D334—340* (U); Sierra de Covadonga, id. *D343—347* (U); Val d’Aran, id. *D1006—1007* (U).

ANDORRA. West of Soldeu, *Smit D985—993* (U).

AUSTRIA. Dürrenstein, Beck s.n. (PRC, 4 sheets); Weitra, id. s.n. (PRC, 3 sheets); Drüssing, id. s.n. (PRC, 3 sheets); Neusiedl am See, *Smit D926—330* (U); Deutschlandsberg, Hebalpe, id. *D936—960* (U); Wolfangsee, id. *D468—457* (U).

CZECHOSLOVAKIA. Bohemia, Beck s.n. (PRC, 2 sheets).

YUGOSLAVIA. Treskavica in Bosnia, Beck s.n. (PRC, 8 sheets); Montenegro, Szyszylowicz, id. s.n. (PRC); Croatia, Gospic, id. s.n. (PRC); Slovenia, Podkoren, *Smit D1105—1107* (U); Macedonia, Tetovo, id. *D190—1905* (U).

ROMANIA. Transylvanian Alps, Beck s.n. (PRC).

U.S.S.R. Turgai, Korotky 15 (LE); Uralsk, Larin 1 (LE); Petropawlowski, Spiridonow 1928 (LE); Semi-palatinsk, Kossinsky 510 (LE); Perm, Augusteweg s.n. (MEL); Tomsk, Sergievskaja s.n. (CHR); Blagowjetschensk, col? (MEL).

TURKEY. Bingöl, Kotschy s.n. (L); Erzincan, iter Leydense 1666 (L, U).

ARMENIA. l.s., *Aucher-Eley 400A* (LE).

IRAN. Amirabad, Zargari s.n. (U).

PAKISTAN. Swat, Otto, Zeffer Ali 4009 (RAW); Gilgit, Seddighi & Nasir 2788 (RAW).

INDIA. NW. India, Royle s.n. (K); Pangi, Simla Dist., Mohindar Nath 2835 (RAW); Kalimpur, Srivastava & single 6299 (WGO); Kashmir, Duthe s.n. (DD); Tehri Garhwal, Awasthi 5250 (DD).

TIBET. Sülle to Padum, Herb. Schlauptwein s.n. (MEL).

NEPAL. W. Nepal, Bir Ram 439 (MEL).

SRI LANKA. s. loc., Bar & Kirat Ram 1933 (DD); s. loc., *King 4212* (CAL).

CHINA. Szechwan, Tachenlu, Pratt 30, 753 (DD); Yünnan, Li-Kiang Hsien, Wang 71594 (TAI); Yünnan, Wei-si Hsien, *Wang 64630* (TAI).

SAKHALIN. Korsakov, Miyake s.n. (SAP).

KOR.A. Kyonson, Ohui 117 (KYO); Mt. Hakutozan, Ishidoya s.n. (KYO).

JAPAN. Sapporo, CLASS s.n. (Daisetsu, Tamura s.n. (KYO); Shokambetsu, Hotta 1719 (KYO); Ishihawa, id. 5910 (KYO); Koyasan, Murata 7090 (KYO); Tochigi, Suzuki 2590 (TAI, 4 sheets).


U.S.A. N. DAKOTA: Eddy Co., Lunell s.n. (US); Pleasant Lake, id. s.n. (US); Richland Co., Stevens 1359 (US). — MINNESOTA: Minnesota Point, Lakela 1359 (US); Ford Smelling, Meurs s.n. (US); Clearwater
b. var. alba (Cambess.) Hook. f. & Thomson


*C. palustris* f. *alpina* Gilli, Fedde Rep. 69 (1964) 138. — Type: Gilli?, Kamdesch (herb?, not seen; *ex* char.).

*C. palustris* f. *silvatica* Gilli, Fedde Rep. 69 (1964) 138. — Type: Gilli?, Kamdesch (herb?, not seen; *ex* char.).

**Distribution:** Mountains of N. India, Pakistan, and Afghanistan; chiefly Kashmir.

Ecology: Damp places, along rivulets; 2200–3500 m alt.


Flowers white; pollen pantoporate, sometimes tricolpate.

**Pakistan.** Kalam Swat, *Stewart 24631* (RAW); Bunda Chitral, *Harris* s.n. (DD); Kurram, *Har Sukh* s.n. (DD).

**Kashmir.** Gulmarg, *Ihalayal* 26459 (DD); s. loc, *Keshwanand* 302 (DD); Banihal, s. leg. s.n. (LWG).

Deosai, *Nair* & *Webster* 6382 (RAW).

**Himalaya Occ.** Hook. f. & Thomson s.n. (CAL, MEL, 3 sheets).

c. var. *purpurea* Spare & Fischer


**Distribution:** Himalayas in Assam and S. Tibet.

Ecology: In alpine meadows and on moist slopes amongst scrub or tall herbage; 4000–5000 m alt.

Flowers magenta-pink.

d. var. *radicans* (Forst.) Beck


*C. palustris* var. *zeltlandica* Beeby, Scott. Naturalist 3 (1887/88) 31. — *C. zeltlandica* Dörfler, Herb. Norm. (1911) 60. — Type: Beeby s.n., Shetland (herb?, not seen; *ex* char. et loc.).

C. caespitosa Schipczinsky, Not. Syst. Herb. Hort. Petrop. 2 (1921) 165. — Type: Pohle s.n., Novaya Zemlya (LE, not seen; ex char. et loc.).
C. palustris var. araneosa Van Steenis, Gorteria 5 (1971) 218. — Type: Van Steenis 3546, Biesbosch, Netherlands (L, not seen; seen many plants of the same population).

**Distribution:** Locally distributed in the area of *C. palustris*, most Arctic specimens belonging to this variety.

**Ecology:** Places with often more extreme environmental conditions than *C. palustris var. palustris*, like abraded shores, tidal fresh water areas, and swift running rivers; tundra climate.

I.c.: Forster, Trans. Linn. Soc. 8 (1807) t. 17.
Plants after anthesis rooting at the nodes of the flowering stems.

**Norway.** Hamarstift, Trøndfjeld, Kjøllstrøm s.n. (GRO).
**Sweden.** Jämtland, Smith s.n. (MEL).
**Great Britain.** Between Perth and Forfar, Linton s.n. (BM); Loch Alvie, Marshall 2136 (BM); Shetland, Alston 12069 (BM).
**Ireland.** Camlin River, Smit D976—979 (U); Lough Ree, id. D980—984 (U).
**Netherlands.** Ulvenhout, Smit D301—310 (U); Biesbosch, id. D386—397 (U).
**U.S.S.R.** Cape Serdtze, White s.n. (US).
**Sakhalin.** Aba Shisuka, Imai & Otomi s.n. (SAP); Pilriver, Kudo & Ishida 7062 (TAI).
**Japan.** Honshu, Kawaguchi-mura, Furuse s.n. (KYO).
**Alaska.** Point Barrow, Spetzman 335, 1316, 1802, 2353, 2575, 2698 (US); St. Lawrence I., Coville ex. 1985 (US); Nome, Fleet 1668 (US); Bering Sea, Hall L, Macoun s.n. (US); Kodiak I., Rutter 4951 (US); Unalaska, Piper 4467 (US); Skagway, Cowles s.n. (US).
**Canada.** Yukon Territory: Between Yukon and Nation R., Merrie 29 (US). — NW. Territories: Coppermine, Findley 45 (US); Cape Dalhouse, Forsild 2752 (US).

2. Caltha leptosepala DC.

*C. chelidonii* Greene, Pittonia 4 (1899) 78. — Type: Spreadborough s.n., Alberta, Yellow Head Pass (Can. Survey Herb., not seen; ex char. et loc.).
*C. uniflora* Rydberg, Mem. N.Y. Bot. Gard. 1 (1900) 474. — Type: Koch s.n., Montana, Haystack Peak (herb., not seen; Rydberg, Fl. Rocky Mts., 1934, 304, equalled *C. uniflora* with *C. chelidonii*).


**Ecology:** Wet alpine and subalpine herb fields, 1500—4000 m alt.
I.c.: Hooker, Fl. Boreal-Am. 1 (1833) t. 10.
Plants 10—40 cm tall; main roots long (15—20 cm), 2 mm diam., branched. Lamina oblong-ovate with cordate base, or orbicular-reniform to ovate, 4—15 cm long, 2—15 cm wide, obtuse to subacuminate, entire, crenate, or crenate-dentate; petiole slightly shorter than to 2 or even 3 x as long as the lamina; sheath membranous, to 3 cm long. Scape without or with one cauline leaf, bearing 1 or 2 flowers; peduncle attaining 30 cm, lengthening after anthesis. Tepals (5)—7—10—13, white, linear-oblong or oblong-ovobate, ca. 15 (10—18) mm long, 6 mm wide, obtuse. Stamens ca. 60, with rather broadly flattened filaments; pollen grains tricolpate, pantocolpate, or pantoporate. Ovaries ca. 8 (5—16), flattened, linear-oblong; style and stigma as in the preceding species.
Follicles short-stipitate or sessile, patent, 12—20 mm long, 3 mm wide, flattened, ellipsoid-oblong, many-seeded. Seeds symmetrically ovoid, ca. 2.3×1.1 mm, black, lustrous. Flowering time June to August.

**Alaska.** Deer Mt., Went 92 (U); Yes Bay, Gorman 34 (US); Kodiak, Piper 4472 (US); Windham Bay, Culbertson 498 (US, 2 sheets); Skagway, Eastwood 308 (US); Haines, Scheuber s.n. (US).

**Canada.** Yukon: Summit and Middle Lakes, Bolton s.n. (US, 4 sheets). — **British Columbia:** Selkirk, Heatock 382 (US); Vancouver I, Forbidden Plateau, Calder & Mackay 32278 (US); North Fork Moose R., Hollister 49 (US); Banff Nat. Park, Hermann 13219 (US).

**U.S.A.** Washington: Seattle, Mosier s.n. (US); Mt. Rainier, Piper 2001 (US); Okanogan Co., Elmer 731 (US); Goat Mts., Allan 147 (US). — Idaho: Boise Co., Hitchcock & Muhlick 3727 (US); Grangeville, Jones 232 (US).

a. ssp. leptosepala


C. leptosepala DC. var. rotundifolia Hutch, Helios 9 (1892) 68. — C. rotundifolia Greene, Pittonia 4 (1899) 80. — C. biflora DC. var. rotundifolia Hitchcock, Vasc. Pls. Pac. N.W. 2 (1934) 335. — Type: Asa Gray s.n., Rocky Mts. (W, † ex char. et loc.).


**Ecology:** Open marshy subalpine and alpine places, 1500—4000 m alt.

**Lamina** oblong-ovate, to 7 cm long and half (but up to 4½) as wide, basally cordate with open sinus, apically obtuse to subacuminate. Flowers solitary or exceptionally paired; tepals linear; pollen grains tricolpate.

**Alaska.** Prince William Sound, Menzies s.n. (K); Boreal America, Hooker s.n. (MEL).


a'. var. *sulfurea* Hitchcock


**Distribution:** Rocky Mts. of Idaho and Montana.

**Ecology:** Wet subalpine and alpine places.

**Tepals** canary-yellow.

b. ssp. *howellii* (Huth) Smit, *comb. nova*


Ecology: Open marshy vegetation, 1500–2300 m alt.

Rosulate leaves reniform, up to 15 cm long, usually broader than long, sinus closed or the rounded lobes overlapping, apex obtuse. Stem with one or two flowers, tepals tending to be more oblong than inssp. leptosepala, pollen grains pantoporate (sometimes panto-colpate).


3. Caltha natans Pallas

C. natans Pallas, Reise 3 (1776) 284. — Type: Pallas s.n., Siberia maxime orientalis (BM).

Distribution: N. America: N. Wisconsin to Alaska, and northern Asia.

Ecology: Floating aquatic plant or creeping on moist mud.

I c.: Gmelin, Fl. Siberica 3 (1768) t. 82.

Aquatic plant; stems floating or creeping, 15–50 cm long, rooting at the nodes; main roots 1–2 mm diam., branched. Lamina reniform, 2–5 cm long and as wide, obtuse, basally cordate, entire or crenate; petiole about 4 × as long as the lamina; sheath membranous, inconspicuous. Flowers (1) 2–6, at the end of branches of the creeping main stem, ca. 10 (8–13) mm in diam. Tepals 5, white or pinkish, ovate, 6–8 mm long, 5 mm wide, obtuse. Stamens ca. 17 (12–25), with broadly flattened filaments; pollen grains tricolpate. Ovaries 20–40, linear-oblong, stigma ± sessile. Follicles forming a dense globose head, sessile, asymmetrically oblong, ca. 4 mm long, with short beak. Seeds dark brown, less than 1 mm long. Flowering time June to August.

U.S.S.R. Irkutsk, Turchaninoff s.n. (MEL); ibid., Tunz s.n. (MEL); Nertochnik, Kuro 224 (GRO, L).

Alaska. Central Alaska, Scammon 4800 (US); American Creek, Calhame 801 (US); Fairbanks, Anderson 1245 (US); King Salmon, Schonfels 2710 (US).


U.S.A. Minnesota: St. Louis Co., Deep Lake, Sandberg s.n. (US); Hibbing, Labela 5177, 17892 (US). — Wisconsin: s. loc., Labela 5110 (US).

4. Caltha scaposa Hook. f. & Thomson

C. scaposa Hooker f. & Thomson, Fl. Indica 1 (1855) 40. — Type: Hooker f. & Thomson, Sikkim (K; authentic specimen, isotype?, in i.a., U).

C. scaposa H. f. & Th. var. pusilla Huth, Helios 9 (1892) 101. — Type: Przewalsky s.n., inter fl. Hoangho et Yangzte, 'Tibet borealis' (LE, not seen; ex char.).

C. scaposa H. f. & Th. var. parnassoides Ulbrich, Not. Bot. Gart. Mus. Berlin 10 (1939) 865. — Type: several collections (no material seen; ex char.).


**Distribution:** Sikkim, S. Tibet, and China (Yunnan and Kansu).

**Ecology:** Marshy alpine vegetation, 4000—6000 m alt.

Plants ca. 11 (8—20) cm tall, with thick, branched main roots. Lamina ovate, 2.2 (1.5—4) cm long, 1.6 (1—3) cm wide, obtuse, basally deeply cordate, entire or dentate; petiole about 3× as long as the lamina; sheath narrow, membranous, 2—3 cm long. Flowers single or two together; 2.5 (1.5—4) cm diam. Tepals 5—9, yellow, obovate, 13 (7—19) mm long, 8 (5—9) mm wide, obtuse. Stamens ca. 30 (20—40), with broadly flattened filaments; pollen grains tricolpate. Ovaries 12 (8—25), asymmetric, linear-oblong, apically gradually passing into the style, this bearing the oblique, oblong, apically curved stigma. Follicles stipitate (14—3 mm), patent, flattened, oblong, 10×3 mm, shortly beaked; seeds 3—6, evenly ovoid, ca. 1.8×1 mm, black. Flowering time July.

**China.** Yunnan, Shi-gi-tung, Wang 67417 (TAI).

Tibet. Hills S. of Lhasa, Ludlow & Sherriff 8793 (E); Thieppa, King s.n. (CAL).

Nipal. Mouma, Nishihoka 760 (KYO).

Sikkim. Hooker f. & Thomson s.n. (CAL, L, LE, MEL, U, syntypes); King 4472 (CAL, 3 sheets); Donkia, Gammie 810 (CAL).

**II. Section Psychrophila DC.**


C. paradoxa Solander ex Forster, Trans. Linn. Soc. 8 (1807) 344. — Type: Banks & Solander s.n., Terra del Fuego (3M, not seen; ex char.).

C. limbata Schlechtendal, Linnaea 11 (1834) 556. — C. appendiculata Pers. var. chilenis Huth, Helios 9 (1892) 67. — Type: Lechner 3041, in summis Cordillearum parcuis terrae Pehuenchorum (W, †).

_Psychrophila_ holophylia Leybold, Ann. U. Chile 16 (1859) 678. — Type: Leybold s.n., Chile, Prov. del Maule (herb.?; not seen; ex char.).

**Distribution:** S. Andes of Chile and Argentina 35° S. Lat., to the subantarctic islands, 56° S. Lat.

**Ecology:** Wet open places, ‘Regenpolstermoore’ (turberas pluviales almohadas), Roivainen, 1954). In the Andes up to 2000 m alt.

I c.: Lourteig, Darwiniana 9, no. 3—4 (1951) fig. 6.

Plants to ca. 8 cm tall; rhizome to 10 cm long, bearing scars and remnants of leaves and ca. 20 cm long branched roots. Lamina bearing 2 (sometimes 3) well-developed obovate-oblong appendages inserted on its upper side at both sides of the costa; sheath very well developed, amplexicaul, free in its upper 1/3; lamina elliptico-oblong, 8—30 mm long, 2—10 mm wide, mostly retuse at apex, irregularly crenate or sinuate, undivided or 3-lobed, sessile or passing into an up to 10 mm long petiole. Flowers solitary; peduncle short, ca. 3½ mm long, strongly lengthening after anthesis; tepals 5, yellow, lanceolate to oblong, 8—15 mm long, 1.5—4 mm wide, acuminate. Stamens 8—10(—12), with broad

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filaments and distinct connective; pollen grains tricolpate. Ovaries 3—5(—8), with short style and thickened, flattened, oblique stigma. Follicles sessile, flattened, obliquely semi-ovoid, 5—7×2—3 mm, slightly beaked. Mature fruits and seeds not seen. Flowering time December.

ARGENTINA. Neuquén, Copahué, O'Donnell 2110 (LIL); Nahuel-Huapi, Dim 910, 1761, 1914 (LIL); Río Negro, Cerro López (BAB); Chubut, Manantial, Hogberg s.n. (SI); Lago Argentino, Brazo Onelli, Vervoort 4594 (LIL); Isla de los Estados, Castellanos s.n. (BA); ibid., Rodríguez 12932 (SI); Ushuaia, Skottsberg 107 (BA).

FALKLAND ISLANDS. Port Stanley, Skottsberg 3 (BA).

CHILE. Linares, Castellanos s.n. (BA); Peulla, Casa Pangue, Andreas 321 (GRO, U); Wellington I., Puerto Eden, Godley 609A (CHR); Penins. Brunswick, Donat 301 (BA, LIL SI); Hermite I., Hooker s.n. (MEL, 2 sheets, and U).


Distribution: S. Chile and Argentina, 50° S. Lat., to the Subantarctic Is., 56° S. Lat.

Ecology: Open marshy places, 'Regenpolstermoore' (turberas pluviales alomhadadas).

I. c. Darwiniana, no. 3—4 (1951) fig. 8.

Plants cushion-shaped, to ca. 3 cm tall; rhizome to 7 cm long and 5 mm in diam., regularly branched and covered with leaves; roots fibrous, to 15 cm long. Lamina thick, ovate or suborbicular, 2.5—4 mm long and as wide, bilobed, concave, enclosing the two basally inserted semi-ovate-oblong appendages; margin hyaline, fimbriate; petiole 6—9 mm long; sheath membranous, amplexical, almost equaling the petiole. Flowers solitary; peduncle 4 mm long; tepals 5—7, yellow, thick, oblong or linear-subspathulate, 3.5—6 mm long, 1.5—2 mm wide, obtuse, sometimes apically membranous. Stamens 6—9; pollen grains tricolpate. Ovaries 2—5, flattened-ovoid, with short style and orbicular stigma. No mature fruits or seeds seen. Flowering time December.

ARGENTINA. Lago Argentino, Brazo Onelli, Vervoort 4594 (LIL); Río Grande, Alhoff 17265 (SI); Isla de los Estados, Castellanos s.n. (BA); Canal de Beagle, Rodríguez 12931 (BAB, SI); Puerto Cook, Skottsberg 262 (BA); Isla Lennox, Hicken 17265 (SI).

CHILE. Wellington I., Puerto Eden, Godley 616 a (CHR); Cape Horn, Hermite I., Hooker s.n. (MEL, U).

7. Caltha sagittata Cav.

C. sagittata Cavanilles, Icon. 5 (1799) 8, t. 414. — Psychrophila sagittata Gay, Hist. Chile Bot. 1 (1845) 50. — Type: s. coll. s.n., Islas Malvinas, Puerto Egmont (Herb. Cavanilles, not seen).

C. multicapsularis Solander ex Forster, Trans. Linn. Soc. 8 (1807) 324. — Type: Solander s.n., Am. mer., ad rivulos in Success Bay (BM, not seen).


C. de Ranca [sic.] Steudel, Flora 39 (1850) 407. — Type: Lehmann 2981, Chile, Cordillera de Ranco (K).

C. sagittata var. latifolia Hueh, Helios 9 (1892) 66. — Type: Philippi s.n., Fretum Magellanicum (W, †; ex char.).


C. involuta Hill, Ann. Bot. 32 (1918) 427. — Type: several localities cited (no material seen; ex char.).

Distribution: This is the most widely distributed South American species, occurring in the Andes of Ecuador, Peru, Bolivia, Argentina, and in Chile south to 56° S. Lat.
Ecology: moist open places, 'Wiesenmoore' (Roivainen, 1954), 'turberas pradeñas de gramináis', in the Andes to an altitude of 3000 m.

I.: Cavanilles, loc. 5 (1799) pl. 414; Curtis, Bot. Mag. (1844) pl. 4036.

Plants to 30 cm tall; rhizome of mature plant to 40 cm long and to 2 cm diam., covered by remnants of leaves and sheaths; roots to 25 cm long, branched. Sheath very well developed, amplexicaul, membranous, 6—9 cm long, 1.5—3 cm wide; petiole 7—30 cm long, 7 mm diam.; lamina with two semi-ovate-oblong obliquely inflexed appendages reaching half its size; lamina subtriangular or ovate, 0.5—6.5 cm long, 0.7—6 cm wide, obtuse or retuse, irregularly crenate. Flowers solitary; peduncle short at anthesis (ca. 1.5 cm long and 2 mm diam.), accrescent after anthesis (to 10 cm long and 8 mm in diam.),tepals 5—7, yellow, somewhat unequal, ovate-oblong, 5—16 mm long, 2—8 mm wide, obtuse or exceptionally retuse. Stamens 35—75, with broad filaments and connectives; pollen grains tricolpate. Ovaries (30—)50—85, asymmetrically ovoid, apically passing into a lateral oblique stigma. Follicles sessile in a globose capsule to 3 cm in diam., 10—13 mm long, 3.5 mm diam., flattened asymmetrically oblong, with short beak, ca. 10-seeded. Seeds subglobose, with conspicuous raphe. Flowering time December.

Argentine: Quilén, Pérez Moreau s.n. (LIL); Mendoza, Ruiz Leal 3617 (LIL, 2 sheets); Copahüe, O’Donnell 2213 (LIL); Nahuel-Huapi, De Barba 2818 (LIL); Valle Hermoso, Castellanos s.n. (LIL); Lago Blanco, Bette- freund 14257 (SI); Islas de los Estados, Castellanos s.n. (BA); Ushuaia, Vervoort 40 (LIL).

Chile: Baños de Chillán, Werdermann 1317 (LIL, SI); Lonquimay, Burkart 9324 (SI); Punta Arenas, Hicken 17265 (SI); Rio Minas, Donat 390 (BA, LIL, SI); Puerto Ibáñez, id. 488 (BA, LIL, SI); Cape Horn, Hermite I, Hooker s.n. (MEL, U), Navarino I, Puerto Williams, Godley 1131 (CHR, 2 sheets).


C. marginata Colenso, Trans. N.Z. Inst. 13 (1891) 382. — Type: Olson s.n., Co. of Waipawa, Ruahine Mts. (WELT?, not seen; ex char. et loc.; authentic specimen of Colenso seen in K).


Plants to 10 cm tall, rarely taller. Rhizome 2 (very short—6) cm long, with scars and remnants of leaves and with up to ca. 20 cm long branched roots. Sheath well-developed, amplexicaul, membranous to scariosus, 2 (0.8—3) cm; laminar appendages 2, inflexed, semi-ovate-oblong, 4 (2—10) mm long, 2.5 (2—5) mm wide, very rarely wanting, lamina ovate-oblong to oblong, 11 (6—19) mm long, 9 (4—11) mm wide, basally bilobed and subcordate, apically emarginate; entire to coarsely crenate or sinuate; petiole ca. 45 (20—80) mm long. Flowers solitary, peduncle at anthesis short, ca. 1.3 (1—3.5) mm long, lengthening after anthesis to ca. 3 (1.5—6) cm; tepals light yellow, 5—8, lanceolate, ca. 11.5 (9—15) mm long, ca. 2 (1—3) mm wide, acute, outside not rarely ± suffused with purple. Stamens ca. 15 (10—20), with broad filaments; pollen grains tricolpate. Ovaries ca. 8 (5—13), asymmetrically oblong-ovoid, apically tapering into the style and the oblong, oblique, curved stigma. Follicles sessile, 4—5 mm long, 4 mm diam., subglobose, unilaterally flattened, with short beak and (2)3(—6) oblong, brown seeds. Flowering time September to November.

New Zealand. North i.: Ruahine Range, Olson 1537 (WELT, 4 sheets); Mt. Hector, Petrie s.n. (WELT); Ruahine Range, id. 263 (WELT); Mt. Holdsworth, Cockayne s.n. (WELT); Mohai-Patea, Moor 688 (CHR); Mt. Kariharinga, Druce s.n. (CHR). — Southern I.: Mt. Arthur, Cheeseeman 260 (WELT); Mt. Kinnon Pass, Petrie s.n. (WELT); Mt. Barrow, Cockayne 1498 (WELT); Mt. Anglem, Melville 534 (CHR); Arthurs Pass, Scott s.n. (CHR); Mt. Cook, Petrie s.n. (CHR).
9. Caltha obtusa Cheeseman


**Distribution:** New Zealand, South Island.

**Ecology:** Subalpine herb fields, 1500–2200 m alt.

Plants to 3 cm tall; rhizome ca. 3 (0.5–7) cm long, with scars and remnants of leaves and with up to ca. 20 cm long branched roots. **Sheaths** well developed, membranous to scarious, ca. 10 (8–15) mm long; petiole ca. 22 (10–30) mm long. Laminar appendages 2, semi-ovate, ca. 4.5 (2–7) mm long, ca. 2.2 (2–4) mm wide, inflexed on the lamina. **Lamina** broadly oblong to suborbicular, ca. 6.5 (3–11) mm long and wide, subcordate at the bilobed base, apically emarginate, crenate to crenate-dentate. **Flowers** solitary; peduncle short at anthesis, ca. 4 (3–5) mm long, lengthening after anthesis to 18 (10–30) mm; tepals 5–8, white, obovate, ca. 13 (8–15) mm long, ca. 4 (3–6) mm wide, obtuse to subacute. **Stamens ca. 9** (7–12), filaments broad, especially at the base; pollen grains tricolpate. **Ovaries ca. 6** (4–9), asymmetrically oblong-ovoid, apically tapering into the style and the oblique, oblong, incurved stigma. **Follicles** subconical, sessile, unilaterally flattened, 4–5 mm long, 4 mm diam., with short beak and (1)2(3) ellipsoid brown seeds. Flowering time January.

**New Zealand.** Mts. of Broken R., Cheeseman s.n. (K, authentic specimen); Dunstan Mts., Petrie s.n. (WELT, syntype, 2 sheets); Blimut, Oliver s.n. (WELT, 2 sheets); Clutha R., Petrie s.n. (WELT); Avalanche Peak, Given s.n. (CHR); Ben Lomond, Connor s.n. (CHR); Travers Range, Figit Basin, Simpson 5097 (CHR).

10. Caltha introloba F. v. M.


**Distribution:** SE. Australia (Australian Alps) and Tasmania.

**Ecology:** Subalpine belt, in gravelly places irrigated during the summer by melting snow, 1500–2200 m alt.

Plants to 12 (–19) cm tall; rhizome 2 (very short –8) cm long, bearing scars and remnants of leaves and to 25 cm long, branched roots. **Sheaths** well-developed, amplexicaul, membranous to scarious, ca. 2.5 (1–6) cm long. **Petiole ca. 5** (1.5–12) cm long. Laminar appendages 2, lanceolate, ca. 14 (6–25) mm long, ca. 2.5 (1.5–5) mm wide, inflexed on the lamina; **lamina** obvate-lanceolate, ca. 22 (9–35) mm long, ca. 10 (4–16) mm wide, basally bilobed and hastate, apically acute, obtuse, or emarginate, entire or faintly crenate. **Flowers** solitary, peduncle at anthesis ca. 2 (1–4) cm, lengthening after anthesis to ca. 9.5 (3–19) cm; tepals 5–8, white, lanceolate, ca. 18 (10–33) mm long, 3.5 (3–7) mm wide, acute. **Stamens ca. 17** (14–25), filaments especially basally broadened; pollen grains tricolpate. **Ovaries ca. 11** (5–18), asymmetrically ovoid, apically tapering into the style with flattened suborbicular stigma. **Follicles** conical, unilaterally flattened, sessile, 5–7 mm long, 4 mm diam., with short beak, 1–5-seeded. **Seeds** ellipsoid, brown. Flowering time December.

**Australia.** **Australian Alps:** Mt. Latrobe, Mueller s.n. (K); Munyang Mts., *id.* s.n. (MEL, syntypes, 3 sheets); Bogong Range, *id.* s.n. (MEL, syntype); Australian Alps, *id.* s.n. (MEL, syntype); Mt. Buffalo, *Melville 2617* (MEL); Cradde Mt. Reserve, Curtis s.n. (CHR).

**Tasmania.** Mt. Field East, Mueller s.n. (MEL).
NOT VALIDLY PUBLISHED NAMES APPEARING IN THE LITERATURE

Caltha natans:

Caltha palustris:
*Caltha croatica* Schur ex Huth, Helios 9 (1892) 72, *nom. inval.* in synon.
*Caltha dentata* Muhlenberg, Cat. i (1813) 55, *nom. nud.*
*Caltha govaniana* Wallich, Cat. (1831) no. 4710, *nom. nud.*
*Caltha gracilis* Nakai in Mori, Enum. Pl. Cor. (1922) 153, *nom. nud.*
*Caltha paniculata* Wallich, Cat. (1831) no. 4711, *nom. nud.*

EXCLUDED SPECIES

*Caltha camschalica* Sprengel, Syst. 2 (1825) 660 = *Oxygraphis glacialis*; teste Ind. Kew.
*Caltha glacialis* Sprengel, Syst. 2 (1825) 660 = *Oxygraphis glacialis*; teste Ind. Kew.

REFERENCES

ABRAMS, L. 1944. Flora of the Pacific States 2.
CANDOLLE, A. P. DE, 1818. Systema naturae 1.
CURTIS, W. M. 1936. The Student's Flora of Tasmania 1.
DAVIS, P. H. 1965. Flora of Turkey and the East Aegean Islands.
Sparr, G. H., & C. E. C. Fischer, 1929. Plants new to Assam I. Kew Bull. 8: 248.