

STUDIES IN *RANUNCULUS* SUBGENUS *BATRACHIUM* (DC.) A. GRAY  
II. GENERAL MORPHOLOGICAL CONSIDERATIONS IN THE TAXONOMY  
OF THE SUBGENUS

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ABSTRACT

An account is given of the characters that are taxonomically important in separating subgenus *Batrachium* from *Ranunculus*. The morphology of the stipules and achenes is discussed in some detail as they have been largely overlooked. Although of no direct taxonomic importance, embryology, teratology and chromosome size are described.

INTRODUCTION

*Batrachium* was first described by De Candolle (1818) as a section of *Ranunculus*. S. F. Gray (1821) gave it generic status and A. Gray (1886) designated it a subgenus of *Ranunculus*. Some recent authors such as Kreczetovicz in Komarov (1937), Janchen (1958), Rostrup (1958) and Löve (1961) have chosen to give *Batrachium* generic rank, while most other workers include it within *Ranunculus*; the infrageneric rank is frequently not designated, but Ascherson & Graebner (1935), Benson (1948) and Clapham (1952) have recognised it as a subgenus.

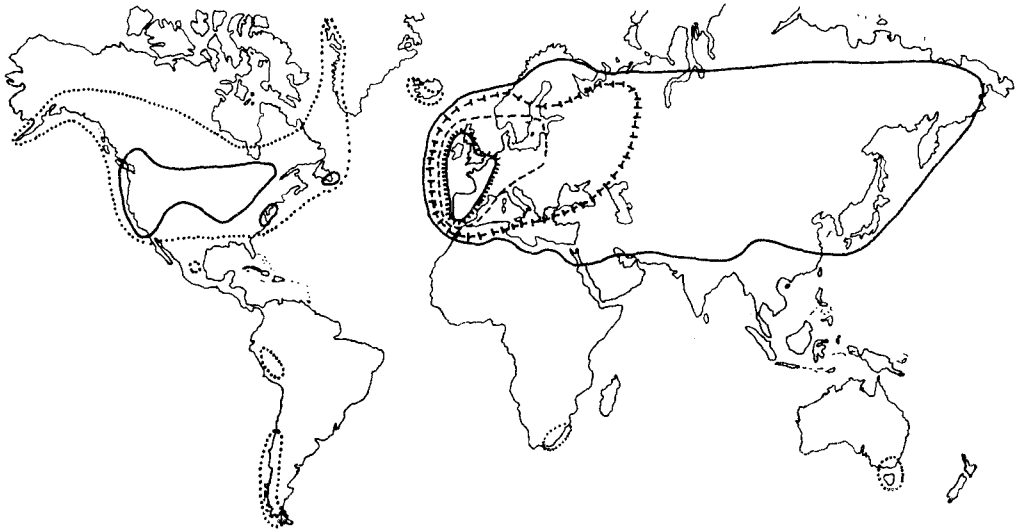
The full description of De Candolle's section *Batrachium* is as follows :

*Pericarpia ovata mutica rugulis transversis striata. Flores albi ungue flavo foveola ad basin nectarifera exsquatulata. Plantae aquaticae; folia glaberrima, emersa dentato-sublobata, immersa capillaceo-multifida; radices fibrosae; pedunculi uniflori oppositifolii.*

Clapham adds that the species are annual or perennial and that they have stipules. In most Floras it is a combination of these characters that is normally used to delimit this group. There are, however, some exceptional species which will be discussed later.

The batrachian group contains about eighteen morphologically recognisable species, found in climatically temperate regions throughout the Northern Hemisphere and in limited areas of South America, South Africa, Australia, Tasmania and New Zealand. Atlantic Europe is the region containing the greatest species density (Fig. 1a) and the greatest morphological diversity (Fig. 1b). The distributions shown on Figs. 1a and 1b are semi-diagrammatic and the species boundaries are not as smooth as illustrated. It is hoped to publish detailed distribution maps of each species later. Except in South America the species that are heterophyllous or entirely laminate-leaved are always found in areas also occupied by species that develop only capillary leaves.

Most of the species are annuals or short-lived perennials but *R. fluitans* Lam., *R. pseudofluitans* (Syme) Baker & Foggitt ex Newbould and *R. circinatus* Sibth. are long-lived perennials. Some species such as *R. tripartitus* DC., *R. peltatus* Schrank, *R. aquatilis* L. and *R. trichophyllus* Chaix may be annuals or perennials. They are often found in temporarily aquatic habitats; if the habitat dries out in summer they behave as annuals, but if the water remains throughout the year they may perennate. If cultivated in an aquatic habitat these species usually die in the third year, but this varies in different races of each species. For example, two morphologically distinguishable races of *R. peltatus*, one from Portugal and the other from southern France, are obligate annuals in cultivation in England.



(a)

- ..... 1 species
- 2 species
- - - - - 4 species
- - - - - 6 species
- ▬▬▬▬ 9 species

(b)

- ▬▬▬▬ plants with only laminate leaves
- plants with only capillary leaves
- - - - - plants with both laminate and capillary leaves



Fig. 1. Distribution of (a) species density, and (b) morphological diversity in *Ranunculus* subgen. *Batrachium*.

*R. hederaceus* L. and *R. omiophyllus* Ten. (*R. lenormandii* F. Schultz) are primarily terrestrial plants of wet places but all the other species are aquatic, completely or partly submerged in water. All the aquatic species cultivated (*R. tripartitus*, *R. ololeucos* Lloyd, *R. baudotii* Godr., *R. peltatus*, *R. aquatilis*, *R. trichophyllus*, *R. rionii* Lager, *R. sphaerospermus* Boiss. & Blanche, *R. pseudofluitans*, *R. fluitans* and *R. circinatus*) can be grown as terrestrial plants during the summer in water-logged soil.

#### DISCUSSION OF CHARACTERS

##### *Hairiness*

Almost all descriptions of *Batrachium* state that all the species are glabrous. This is not the case. All the specimens that I have seen bear unicellular hairs on the stem, leaves and stipules. Even the submerged capillary leaves have hairs surrounding the hydathodes.

##### *Heterophylly*

At all times of the year, in or out of water, *R. hederaceus* and *R. omiophyllus* produce only laminate leaves, while *R. trichophyllus*, *R. rionii*, *R. sphaerospermus*, *R. circinatus* and some races of *R. aquatilis*, *R. pseudofluitans* and *R. fluitans* bear only capillary leaves. The other species, *R. lobbii* (Hiern) A. Gray, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus* and some races of *R. aquatilis*, *R. pseudofluitans* and *R. fluitans* show heterophylly with capillary and laminate leaves. This type of heterophylly is not confined to *Batrachium* but is found in some other aquatic species of *Ranunculus* such as *R. polyphyllus* Waldst. & Kit. ex Willd., *R. gmelinii* DC. and *R. flabellaris* Raf.

In most aquatic plants that have both capillary and laminate leaves the change from one type to the other is gradual with the formation of sequential intermediates and is largely controlled by the presence or absence of water. In *R. lobbii*, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus* and *R. aquatilis* the change from one type of leaf to the other type is abrupt. In *R. peltatus* and *R. aquatilis* the initiation of the laminate leaf must take place underwater and if the apex is lifted above the water a capillary leaf of the terrestrial type develops. Intermediate types of leaves are occasionally found but they are not sequential intermediates but more of a mixture of the two types. The presence of these intermediate leaves can be correlated with pollen sterility, and they are found in high polyploids and hybrids. I have only just started studies on heterophylly but it appears that, in the presence of water, the form of the leaf is primarily controlled by temperature and day-length.

##### *Stipules*

In taxonomic accounts the Ranunculaceae are usually described as being exstipulate, but occasionally, for example Lawrence (1951), an exception is made in the case of *Thalictrum*, and Clapham (1952) describes both *Thalictrum* and *Batrachium* as stipulate. Hiern (1871), Freyn (1890), Glück (1919, 1924), Salisbury (1934) and Drew (1936) in monographic accounts have all described stipules in *Batrachium* and have used them as taxonomic characters within the subgenus. Morphologists, however, have been more reluctant to call them stipules and Goffart (1901) called them *auricules*, while Weberling (1956) called them *Scheidenlappen* or lobes of the leaf-sheath.

To define stipules it is necessary to look at the development of the leaf. The first visible sign of leaf formation is a swelling below and to the side of the apical meristem. This swelling is usually called the leaf primordium and it may remain small and localised on one side of the stem apex or it may grow, occasionally forming a ring around the apex. The leaf proper (petiole and lamina) develops from a localised area of this primordium so the whole primordium contributes cells to the axis and the leaf proper. Eichler (1861)

proposed two terms : *Unterblatt* and *Oberblatt*. The *Oberblatt* is the area in the primordium that gives rise to the leaf proper and the *Unterblatt* is that which is left. He then defines stipules as being a product of the *Unterblatt*. Sinnott & Bailey (1914) carried out more detailed anatomical investigations of leaf development and found themselves in agreement with Eichler; they suggested 'leaf-base of the primordial leaf' as a translation of *Unterblatt*.

Colomb (1887) defined the stipule as 'an appendage inserted on the stem at the base of the leaf all the bundles of which are derived entirely from corresponding foliar bundles.' Sinnott & Bailey stated that this definition would fit Eichler's but they found that it was often hard to apply and could not be adopted as stipules occasionally lack bundles.

Sinnott & Bailey pointed out that leaf-sheaths, stipules, ligules and some other appendages at the base of the petiole arise from the *Unterblatt* and are morphologically homologous. Nobody has doubted that the leaf-sheaths found in the Ranunculaceae originate from the *Unterblatt*. It has been noted that these leaf-sheaths are occasionally lobed, so the problem is one of terminology. When should the lobe on a leaf-sheath be called a stipule? Weberling suggested that if the lobes show proleptic growth, that is, if they anticipate growth of the leaf proper (*Oberblatt*), then they should be called stipules. The lobes in *Batrachium* do anticipate growth of the leaf proper and therefore should be called stipules. It is perhaps worth mentioning that *Trollius* and *Caltha* also show well-developed stipules but the stipule ruptures as the next leaf develops.

#### *Petals*

Comparative studies on the floral parts of the Ranunculaceae (Eichler 1878, Prantl 1888) have shown that the so-called petals of *Ranunculus* are strictly speaking homologous to nectaries and are occasionally called *Nektarblätter* (usually translated into English as honey-leaves). It is proposed to call the *Nektarblätter* petals as this usage is generally accepted in *Ranunculus* and does not cause confusion.

The petals in *Batrachium* are usually described as being white with a yellow claw. This is true for the majority of species but in races of *R. ololeucos* they are entirely white and in *R. flavidus* (Hand.-Mazz.) C. D. K. Cook\* they are uniformly pale yellow. This species seems to be allied to *R. aquatilis* and is confined to the Himalayas.

The petals have a matt surface (Parkin 1928) and do not contain starch. This appears to be a good distinction between subgenus *Batrachium* and section *Hecatonia* of subgenus *Ranunculus* which contains the most batrachian-like species. This character is not of much practical use as it requires microscopical examination of living petals.

The nectary pit is highly reduced (Benson 1940). It may be lunate, circular or pyriform. Nectary characters are useful taxonomically within the subgenus but cannot be used to separate *Batrachium* from the rest of *Ranunculus*.

#### *Achenes*

The presence of transverse ridges on the achene is perhaps the most important diagnostic character of *Batrachium*, but it must be used with caution. *R. rivularis* Banks & Sol., *R. undosus* Melville, *R. papulentus* Melville and *R. inundatus* R. Br. ex DC., semi-aquatic species from Australasia, have transverse ridges on the achene. The ridges, however, are somewhat irregular and ill-defined. Anatomically the pericarp of *R. rivularis* consists of an inner layer of regular, almost symmetrical sclereids five to eight cells deep and an outer layer of loose parenchyma five to eight cells deep. The pattern is the same in longitudinal and transverse sections.

The pericarp of *Batrachium* has a much more complicated structure and consists of three well defined layers. The innermost consists of a single layer of fibres forming a continuous sheath arranged tangentially around the achene at right angles to the longitu-

\**Ranunculus flavidus* (Hand.-Mazz.) C. D. K. Cook, *comb. nov.* *Batrachium flavidum* Hand.-Mazz., *Acta Hort. Gotob.* 13, 168 (1939)

dinal axis. The fibres are as much as twenty times as long as broad and have thick walls with numerous simple pits. The next layer consists of a layer of elongated sclereids, three to four cells deep and from five to ten times as long as broad with thick walls and many simple pits. The sclereids lie at right angles to the fibres, parallel to the longitudinal axis. Each cell lies directly on top of the one below. The ends are slightly swollen and tend to turn away from the longitudinal axis. As these cells are in simple ranks the upturned ends form quite large ridges between 0.4 and 0.1 mm apart. The ridges lie at right angles to the longitudinal axis and are found on the lateral walls of the achene.

The outer layer consists of between four and eight layers of loose parenchymatous cells which wither and die as the achene matures. The outermost layer may or may not bear unicellular hair cells. Fig. 2a shows a median transverse section and Fig. 2b a median longitudinal section. The ends of the sclereids swell and turn outwards before fertilization and, to a large extent, subsequent development is not dependent on fertilization. Normally, the walls of the sclereids start to lignify just as the endosperm starts laying down cell walls. Lignin is first laid down at the ends of each cell while the middle is still elongating. The fibres of the inner layer do not become lignified until the embryo is almost mature.

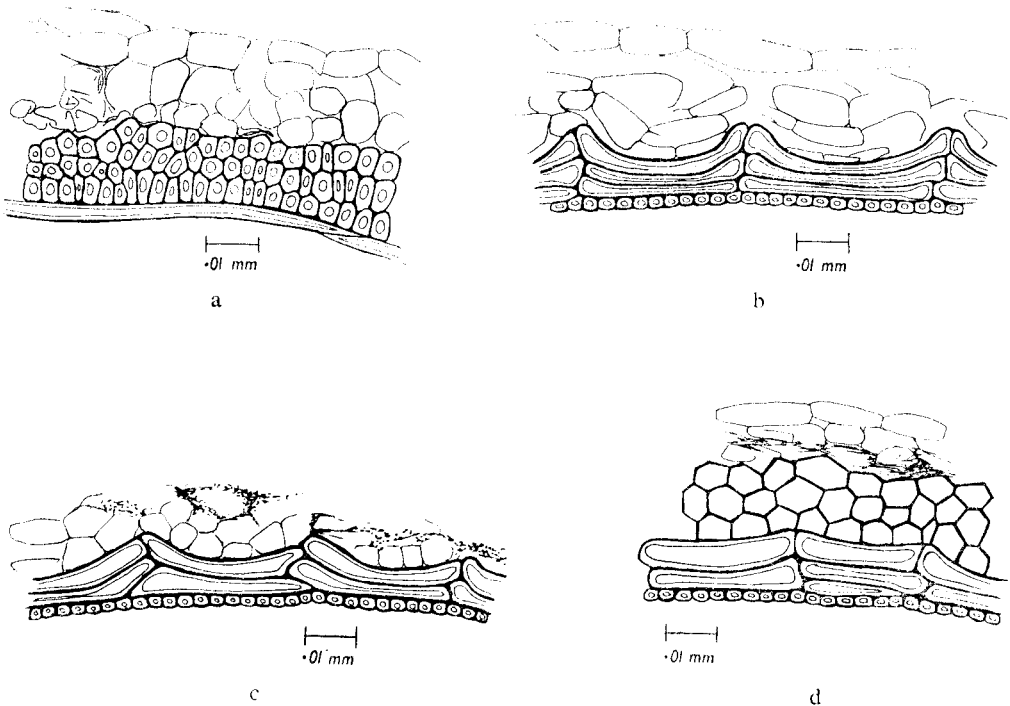


Fig. 2. Sections of the lateral wall of achenes of *Ranunculus* spp., c. half-way from base to apex. (a) *R. tripartitus* 175/57, T.S.; (b) *ibid.*, L.S.; (c) *R. sceleratus*, Bács-Bodrog, nr. Zombor, Hungary, J. Proden May 1912 (achenes ridged), L.S.; (d) *R. sceleratus* (achenes non-ridged), L.S.

The important property of these ridges on the batrachian achene is that they are areas of weakness. When the achenes are roughly handled they break along the ridges. During germination the pericarp ruptures along the ad- and abaxial crests which are areas of upturned sclereids. Although there is no direct evidence it is tempting to regard the ridges as possible passages of water through the periderm when the seeds are wetted after being dried.

Some races of *R. sceleratus* L. have transverse ridges on the lateral walls of the achene that look similar to those found in *Batrachium*. Plants with ridged achenes are sympatric with non-ridged ones.

Anatomically the periderm of *R. sceleratus* is similar to that found in *Batrachium* (Fig. 2c). The ends of the sclereids, however, are not markedly swollen and it appears that the ridges are largely formed by a collapse of the central part of the cell. The unridged race has a layer of symmetrical sclerenchyma cells, three deep, between the sclereids and the outer parenchyma (Fig. 2d). When the sclerenchyma is present the sclereids do not collapse and no ridges are formed. Lonay (1901, 1907) examined the structure of the achenes of many species of *Ranunculus* and it would appear that these elongated, ranked, sclereids may well be confined to *Batrachium* and *R. sceleratus*.

Chute (1930) stated that the achene of *Batrachium* represented the most reduced type of any known. She said 'so complete is this reduction that the ventrals, as distinct bundles, have completely disappeared: hence the ovule trace appears to come from the dorsals.' The vascular anatomy of so few species of *Ranunculus* has been studied that it is not known if it is possible to use the lack of ventral bundles as a diagnostic character.

#### *Embryology*

Each achene contains a single anatropous ovule. The nucellus is monosporic, 8-nucleate, of the *Polygonum*-type with early fusion of the endosperm nuclei. Most pollen tubes reach the nucellus by travelling down the funicle, none have been seen ascending the micropyle. After fertilization the endosperm nucleus divides rapidly and cell walls are not laid down until the embryo has reached a sixteen- or thirty-two-celled stage. The embryo of *R. tripartitus* has the same development as the *Myosurus* variation of the Onograd type (terminology after Johansen 1950). A limited number of embryological stages have been seen in *R. hederaceus*, *R. omiophyllus* and *R. aquatilis*; they all appear similar to *R. tripartitus*.

No self-incompatibility, pseudogamy or agamosperous processes have been discovered.

The synergid cells disappear before or just after fertilization; their disappearance does not appear to be correlated with pollination. The antipodal cells do not disappear until late in embryo development. They become enlarged and show considerable activity and are often borne on a short well-differentiated stalk. Enlargement of the antipodal cells has been seen in several species within the Ranunculaceae, Fumariaceae and Papaveraceae (Coulter 1898, Osterwalder 1898, Grafl 1941, Tschermak-Woess 1956). Not only do the antipodal cells become enlarged, they show giant chromosomes which continually divide forming highly polyploid cells; Hasitschka-Jenschke (1959) estimated cells up to 64-ploid for *Eranthis hyemalis* (L.) Salisb. An interesting feature that has not, I believe, been noted before is that the activity and growth of these cells is increased if pollination is withheld. Conversely, if pollination is carried out as soon as the nucellus is mature, there is very little development of the antipodal cells. In *Batrachium* the antipodal cells have never been seen to divide.

#### *Teratological variants*

Although teratological variants can hardly be used in taxonomy, it is, perhaps, worth mentioning the commonest types found. Occasionally one sepal is partly petaloid; sometimes it is laterally asymmetrical with one half petaloid and sometimes it is the distal end that is petaloid. Petaloid sepals are without nectary pits. Intermediates between petals and stamens are more common; one extreme is an almost perfect stamen with a flattened filament and the other extreme is an almost perfect petal bearing one or two functional anther loculi. In the latter case the anther may occur laterally or centrally on the petal

but if it is central it usually replaces the nectary pit; sometimes this type of anther is so reduced that it looks like a pollen-producing nectary.

Supernumerary petals (more than five) are quite common in *R. fluitans*, *R. pseudo-fluitans*, *R. peltatus* and *R. aquatilis*. They appear to be formed at the expense of stamens and in one population of *R. pseudo-fluitans* in the River Wye in Derbyshire plants have up to fifteen petals and no stamens. The plants examined in this population were sterile pentaploids. This 'double-flowered' character has been seen to breed true in cultivation in plants of *R. peltatus* collected from Slayley in Derbyshire.

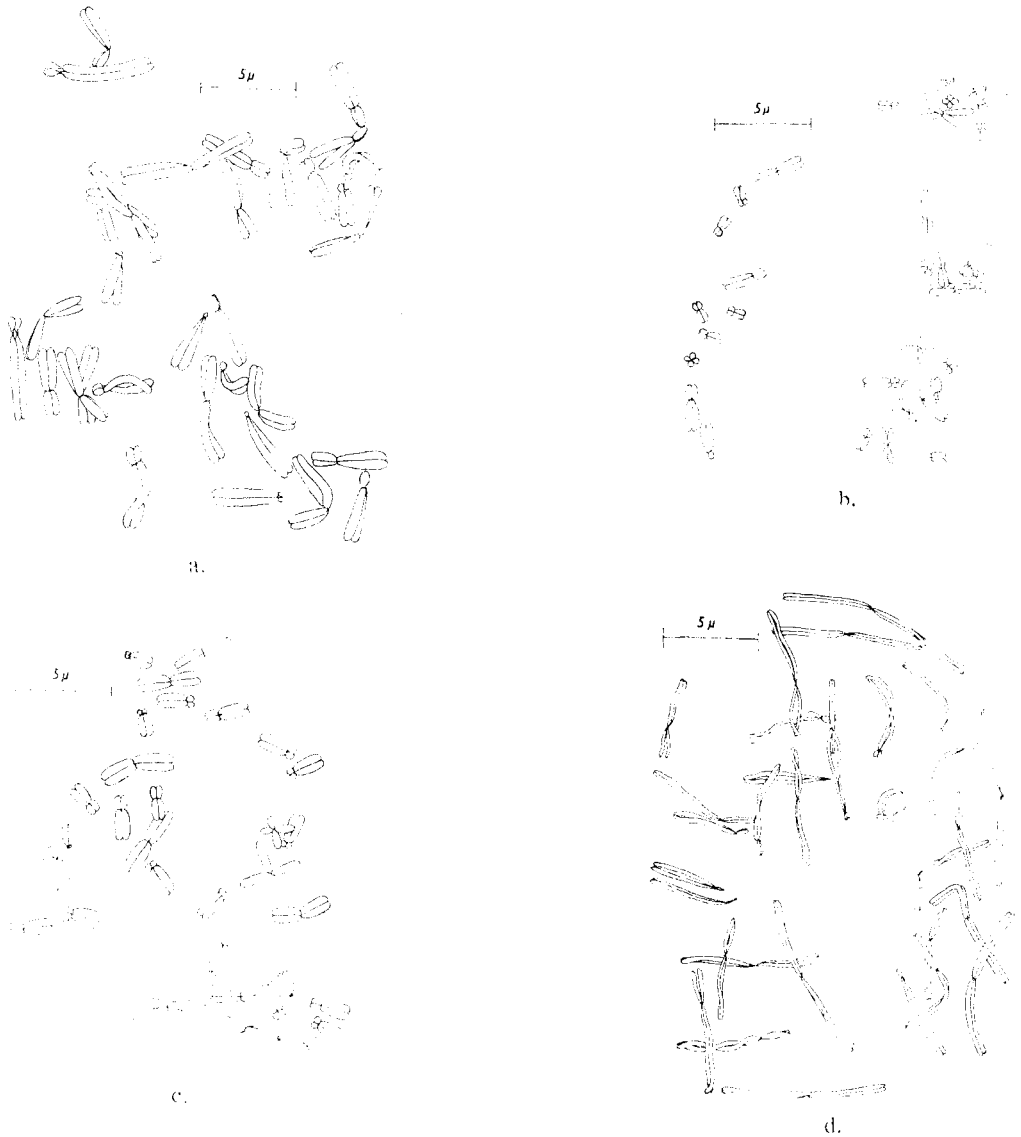


Fig. 3. Chromosomes of *Ranunculus* spp. from root-tip squashes,  $\times 2500$ ; Feulgen staining, all except (d) pre-treated for 3 hrs with  $\alpha$ -bromonaphthalene. (a) *R. ficaria*, under *Hippophae rhamnoides* by pond, Botanic Garden, Munich, Germany,  $2n = 32$ ; (b) *R. sceleratus*, from collection of aquatic plants, Botanic Garden, Munich,  $2n = 32$ ; (c) and (d) *R. trichophyllus*, collected wild from pool by R. Stillach, S of Möserbrücke, 1.5 km SW of Oberstdorf, S Germany (specimens deposited in M).

*Chromosome size*

It has been suggested that *Batrachium* could be delimited from the rest of *Ranunculus* on chromosome size, but no really significant difference has been found. Larter (1932) reported that the chromosomes of *R. peltatus* were less than one sixth the bulk of those of *R. acris* L. and considerably smaller than those of the other species illustrated in his paper. (*R. constantinopolitanus* (DC.) d'Urv., *R. trilobus* Desf., *R. serbicus* Vis., *R. parviflorus* L., *R. arvensis* L., *R. repens* L., *R. ficaria* L., *R. chius* DC., *R. nelsonii* A. Gray, *R. sprunerianus* Boiss., *R. oxyspermus* Bieb., and *R. ophioglossifolius* Vill.). From the work of Skalińska *et al.* (1959) it can be seen that the chromosomes of *R. circinatus* are approximately the same size as those of *R. flammula* but smaller than those of *R. montanus* and much larger than those of *Isopyrum thalictroides* L. and *Thalictrum aquilegifolium* L.

Langlet (1927) doubted that *Batrachium* was a distinct genus on the basis of chromosome size and number and in his later work (1932) on the relationships within the Ranunculaceae he included *Batrachium* within the same category as *Ranunculus*. Other workers on cytological variation in the Ranunculaceae (Coonen 1939, Gregory 1941, Kurita 1958) have also included *Batrachium* within *Ranunculus*.

It is difficult to compare chromosome sizes from data given by different publications as there are either variations in size within a single species or inaccuracies in the scales quoted. Fig. 3a shows chromosome preparations from root-tip squashes, with Feulgen staining (12 min. hydrolysis in normal hydrochloric acid at 60°C), all prepared within a week and all drawn with the same microscope and camera lucida. Except for Fig. 3b, the roots were given a three hour pre-treatment in saturated  $\alpha$ -bromo-naphthalene solution. This pre-treatment is necessary as the chromosomes of *Ranunculus* are rather long and somewhat sticky at metaphase and it is seldom that one gets a late prophase preparation with a good chromosome spread such as that shown in Fig. 3d.

It can be seen that the chromosomes of *R. ficaria* illustrated are larger than those of *R. trichophyllus* while those of *R. sceleratus* are smaller. In *Batrachium* there is a certain amount of variation in chromosome size; none has chromosomes as large as those of *R. ficaria* but in *R. tripartitus* they are as small as those of *R. sceleratus*. In many genera there are species with different chromosome sizes; *Anemone*, also within the Ranunculaceae, is a good example (Langlet 1932, fig. 2; Gregory 1941, plate 2.)

## CONCLUSION

In the introduction it was pointed out that the status of *Batrachium* has varied from section to genus. The group shows most affinities to *Ranunculus* and it cannot be confused with any other genera in the Ranunculaceae. However, it can only be separated from *Ranunculus* by the combination of the minimum of two characters (transversely-ridged achenes and matt-surfaced petals). Sectional status is inappropriate so the choice lies between genus and subgenus, but it is felt that the level of differentiation is insufficient to merit generic status so *Batrachium* is given subgeneric rank.

A suggested description of *Ranunculus* subgenus *Batrachium* is as follows :

Aquatic or semi-terrestrial annuals or perennials. Leaves mostly cauline, laminate or finely dissected; stipules membranous, partly fused to the petiole. Sepals usually five, not petaloid, caducous. Petals five or more, with matt surface; nectary-pit lunate, circular or pyriform. Achenes not strongly compressed, with regular transverse ridges from 0.4 to 1 mm apart on the lateral walls.

The lectotype of subgenus *Batrachium* is *Ranunculus hederaceus*, sheet number 74 (Savage 1945) in the Linnaean Herbarium, Linnean Society, London (LINN), selected by Britton and Brown, 1913, *Ill. Fl. N.U.S.*, ed. 2, 2, 115.

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