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A REVIEW OF THE CLASSIFICATION OF THE GENUS
HYDRASTIS (RANUNCULACEAE)

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ABSTRACT

The genus *Hydrastis* has been variously classified as a monotypic taxon in the Ranunculaceae, the Berberidaceae, the Glaucidiaceae, or its own monogeneric family, the Hydrastidaceae. The objectives of this paper were 1) to review the previous classifications of *Hydrastis* and 2) to critique a recent paper by Tobe and Keating reevaluating the classification of the genus based on comparative morphological and anatomical studies. One conclusion of this review was that Tobe and Keating overlooked certain important papers which might have substantially altered their conclusions, viz., that *Hydrastis* is sufficiently distinct from the other genera of the Ranunculaceae to warrant a classification as a monogeneric family. Another conclusion was that, with the present information available, *Hydrastis* can be classified as a subfamily within the Ranunculaceae, but that molecular data might well alter this conclusion.

Key Words: Systematics, classification, Ranunculaceae, *Hydrastis*.

INTRODUCTION

Hydrastis is, undoubtedly, one of the most problematic genera within the Ranunculales (Berberidales), and this is certainly reflected by its interesting and checkered taxonomic history. In 1789, Jussieu classified *Hydrastis* in the Ranunculaceae where it remained until 1903 when Engler transferred it to the Berberidaceae. But in the 11th edition of the *Syllabus der Pflanzenfamilien*, Engler and Diels (1936) reclassified *Hydrastis* in the Ranunculaceae, a decision followed likewise in the manuals dealing with the flora of the eastern United States (e.g., Small 1933; Fernald 1950; Gleason and Cronquist 1963, 1991). (For a more thorough review of the taxonomic history of *Hydrastis* see Tobe and Keating 1985.) However, primarily based on the scalariform perforations of the vessel element plates, Lemesle (1948, 1950, 1955) was the first to propose that *Hydrastis* constituted a monogeneric family, the Hydrastidaceae. Despite this proposal, *Hydrastis* has since been classified either in its own segregate family, or in the Ranunculaceae, or even in the Berberidaceae (e.g., Nowicke and Skvarla 1979, 1981). At one time Tamura considered the differences between *Hydrastis* and the Ranunculaceae to be too great to warrant classifying *Hydrastis* within the Ranunculaceae, but he later reversed himself and included this genus as a subfamily within the Ranunculaceae (Tamura 1962, 1966, 1984, 1990, 1992). Likewise, Takhtajan reversed himself several times but currently he does accept the Hydrastidaceae as a monogeneric family within the Berberidales (Takhtajan 1969, 1980, 1987; see also Savitskii 1982). A similar shift has occurred with Dahlgren who at one time segregated *Hydrastis* as a monogeneric family, then later gave it a subfamily rank within the Ranunculaceae, but in a posthumously published paper by his wife apparently reverted to his initial position (R. Dahlgren 1975,

1983; G. Dahlgren 1989). And Thorne, who for many years classified *Hydrastis* in the Ranunculaceae (Thorne 1974, 1976, 1981, 1983), now classifies *Hydrastis* in its own monogeneric family (Thorne 1992a, b). On the other hand, Cronquist (1968, 1981, 1988) has always included *Hydrastis* within the Ranunculaceae (see also Gleason and Cronquist 1991). Nevertheless, in a thorough study of *Hydrastis*, Tobe and Keating (1985) proposed once more that *Hydrastis* be reestablished in its own family. By marshalling a broad array of facts they argued that *Hydrastis* is an exceptional genus with a marked divergence from the Berberidaceae, Glaucidiaceae, Circaeasteraceae, and Ranunculaceae. Moreover, their studies apparently have influenced some recent classifications of *Hydrastis* (e.g., Takhtajan 1987; Thorne, 1992a, b).

With respect to the classification of *Hydrastis*, at least the following arrangements appear possible, and, in fact, all were at one time recommended dispositions of *Hydrastis* (Cronquist 1981; Tobe and Keating 1985): 1) classify *Hydrastis* with *Glaucidium* to form a separate family transitional between the Ranunculaceae and Berberidaceae, 2) classify both *Hydrastis* and *Glaucidium* into separate, monogeneric families, 3) classify *Hydrastis* in the Berberidaceae, or 4) in the Ranunculaceae. These various possibilities will be elaborated in more detail in the following discussion.

DISCUSSION

Classification of Hydrastis with Glaucidium

Although there are a number of similarities between *Hydrastis* and *Glaucidium* [e.g., creeping rhizomes with one terminal leaf, lack of radical leaves (bud scales only) at the base of the flowering stems, two foliage leaves in a 1/2 phyllotaxy, medullary bundles in the stem and petiole, tendency for fused cotyledons, lack of a V-shaped xylem in the vascular bundles, and the presence of scalariform and reticulate vessel element perforations], as Tobe and Keating (1985) point out, many of these features are shared also by *Podophyllum* and *Diphylleia* of the Berberidaceae (see also Kumazawa 1938b; Tamura 1972). On the other hand, Tobe and Keating (1985) highlight at least 17 differences between these two genera, including such aspects as carpel number, fusion and dehiscence, seed shape, floral vasculature, direction of stamen initiation, base chromosome number, pollen structure, and various embryological features such as the number of embryo sacs per nucellus. In their view, these differences "make it unlikely that *Hydrastis* has a [close] phyletic relationship with *Glaucidium*." It appears thus that the phyletic divergence between *Hydrastis* and *Glaucidium* is too great to classify these genera in a single bigeneric family, the Glaucidiaceae, a conclusion reached earlier by Tamura (1962, 1972).

Classification of Hydrastis in the Berberidaceae

Although *Hydrastis* does share a number of distinctive features with members of the Berberidaceae (e.g., a striate-reticulate pollen tectum plus those features in common between *Hydrastis* and *Glaucidium* mentioned above) there are a number of critical differences including an ascidiate carpel ontogeny, vascularized placental tissue, trimerous flowers, dual origin of vascular bundles to the stamens, chromosomal base numbers of 6, 7, 8, 10, and 14, differentiated leaf mesophyll,

V-shaped xylem tissue in vascular bundles—all present in the Berberidaceae, but lacking in *Hydrastis* (Tobe and Keating 1985). These differences led Tobe and Keating (1985) to conclude that “evidently there is as great a gap between *Hydrastis* and the Berberidaceae as between *Hydrastis* and the Ranunculaceae,” and therefore including *Hydrastis* with either of these families would entail “an unreasonable and artificial definition of the family containing *Hydrastis*.” This conclusion requires a closer examination of the reasons why Tobe and Keating (1985) believe that *Hydrastis* should be *excluded* from the Ranunculaceae.

Classification of Hydrastis in the Ranunculaceae

In recent classification schemes, *Hydrastis* is usually included within the Ranunculaceae (e.g., Tamura 1968; Thorne 1974, 1981, 1983; Cronquist 1981, 1988; R. Dahlgren 1983; Loconte and Estes 1989; Gleason and Cronquist 1991 [but cf. Takhtajan 1987, G. Dahlgren 1989, and Thorne 1992*a,b*, for a different view]), on the grounds of several shared reproductive characters, including the convex shape of the receptacle, centripetal initiation of the spirally arranged stamens, distinct conduplicate spirally arranged carpels, 1-celled archesporia, and persistent and dividing antipodal cells (Tobe and Keating 1985).

Tobe and Keating maintain, however, that there are a number of important key features (“family level distinctions”) separating *Hydrastis* from all other genera of the Ranunculaceae, including a base chromosome number of 13, a distinctive pollen tectum, formation of the micropyle (formed by *both* integuments), cross-sectional shape of the xylem in the vascular bundles (straight, not V-shaped), scalariform vessel element perforations, undifferentiated leaf mesophyll, distinct patterns of vascular supply to the stamens and carpels, a unique pattern of stem medullary bundles, and the presence of D-galactose. These putative differences are sufficient, in Tobe and Keating’s view, to recommend “the reestablishment of a monotypic family, Hydrastidaceae.” In any case, Tobe and Keating hold that “the inclusion of *Hydrastis* in the Ranunculaceae is unreasonable.”

In my view, Tobe and Keating (1985) and Tamura (1962, 1972) have argued persuasively with sufficient evidence that *Hydrastis* and *Glaucidium* are too distinct to warrant inclusion in a bigeneric family, the Glaucidiaceae. Moreover, *Hydrastis* unquestionably shows affinities for both the Berberidaceae and the Ranunculaceae. Tobe and Keating (1985) are surely correct when they claim that the features *Hydrastis* shares in common with both the Ranunculaceae and Berberidaceae “seem to be a heritage from their common ancestor.” The overall phylogeny is not in question. What is at issue is whether *Hydrastis* is sufficiently distinct from either the Ranunculaceae or the Berberidaceae to justify classifying it in its own monogeneric family positioned somewhere among the Circaeasteraceae, Kingdoniaceae, and Glaucidiaceae. The crucial question is, therefore, if one recognizes the Hydrastidaceae, what features serve as convincing indicators of the family level for this rather exceptional genus?

In assessing the relationship between *Hydrastis* vis-à-vis *Glaucidium*, Ranunculaceae, and Berberidaceae, Tobe and Keating (1985) analyzed 64 characters. Based on their thorough comparative analysis, *Hydrastis* has more features in common with the Ranunculaceae s.s. than with either *Glaucidium* or the Berberidaceae. In the ensuing discussion, therefore, I shall aim to highlight several

of those features presumably distinguishing *Hydrastis* from the other genera of the Ranunculaceae.

Chromosome number.—The base number of $x = 13$ in *Hydrastis* is hard to explain. This number is unlike that of any other genus within the Ranunculaceae and, in this respect, *Hydrastis* is indeed distinctive. But there is no base number for the Ranunculaceae as a whole. Whereas $x = 7$ or 8 are the most common base numbers, $x = 6$ and 9 also occur. As such, *Hydrastis* may well be a hypotetraploid (i.e., $4n - 2$, $n = 7$), similar to the European *Anemone nemorosa* L. with its $2n = 30$ (i.e., $4n - 2$, $n = 8$) (Shirreffs 1986). Only additional cytological work can establish the phylogenetic base number for *Hydrastis*, and whether or not it represents an ancient aneuploid tetraploid lineage.

Morphology of the pollen tectum.—The ornamentation of the pollen tectum in the Ranunculaceae is remarkably uniform, consisting chiefly of pantoporate or tricolpate pollen grains with a spinulose and punctate/perforate tectum (Nowicke and Skvarla 1979). In fact, this type of pollen is in many cases indistinguishable from “various representatives of centrospermous families, particularly Amaranthaceae, Caryophyllaceae, and Chenopodiaceae” (Nowicke and Skvarla 1979), although the structure of the endexine differs between these two groups. Nevertheless, within the Ranunculaceae s.l. there are three notable exceptions: *Trollius*, *Helleborus*, and *Hydrastis*. The external features of the pollen of *Hydrastis* (i.e., tricolpate, striate) are remarkably like that of *Jeffersonia* in the Berberidaceae, and both resemble the pollen of *Trollius* (Nowicke and Skvarla 1979, Fig. 142 and 162; Nowicke and Skvarla 1981, Fig. 47–48, and 52–54). Thus, with respect to the Ranunculaceae s.l. the distinctive pollen of *Hydrastis* does not appear any more exceptional than the equally distinctive pollen of *Trollius* and *Helleborus*, the latter genus notable for other exceptional features within the Ranunculaceae.

Vascular anatomy of the flower.—In both *Hydrastis* and the Ranunculaceae, the origin of the vascular supply to the stamens issues from the vascular bundles of the central cylinder. In *Hydrastis*, however, the manner of the organization of the vascular supply to the stamens is more or less fascicled, but remains distinct in other genera of the Ranunculaceae. Moreover, there are four vascular bundle traces to each carpel in *Hydrastis*, but only one or three in the other genera of the Ranunculaceae investigated so far. In these aspects *Hydrastis* is different from the other genera of the Ranunculaceae (Tobe and Keating 1985).

Number and relative length of the integuments.—The number of integuments within the Ranunculaceae varies from one to two with both types found in approximately equal numbers (Kumazawa 1938a). Within the bitegmic genera generally the inner integument is longer than the outer. Although in *Hydrastis* the outer integument is longer than the inner, and thus differs from most genera of the Ranunculaceae with two integuments, *Hydrastis* does share this integumentary pattern with *Aquilegia* (Kumazawa 1938a), a genus phylogenetically closely related to *Hydrastis* (Keener, unpublished research). By itself, integument number and orientation do not appear to be critical characters in segregating *Hydrastis* from the Ranunculaceae, and, in fact, we agree with Kumazawa (1938a) in concluding “. . . that the length of the integument is not to be regarded as one of the distinguishing characters of the tribes of the Ranunculaceae.”

Leaf anatomy and morphology.—*Hydrastis* does appear distinct from the other genera of the Ranunculaceae by its alternate, 1/2 (vs. 2/5) divergent phyllotaxy, medullary bundles in the petioles (present also in *Actaea*), undifferentiated (vs. differentiated) mesophyll, and plaited or palm type of vernation (vs. supervolute, involute, or conduplicated types found in other Ranunculaceae) (Tobe and Keating 1985). Additional research should be undertaken to establish the degree of correlation of each of these features with the type of habitat (rich moist mesic hardwoods) occupied by *Hydrastis*.

Stem anatomy.—Although *Hydrastis* has medullary bundles present in the lowest internode (a feature which occurs also in *Actaea* and *Anemonopsis*), the type of the course of the medullary bundles appears different from those in *Glaucidium*, the Ranunculaceae s.s., and the Berberidaceae (Tobe and Keating 1985). According to Kumazawa (1932) there are five such types within these four taxa (see Tobe and Keating, 1985, p. 309 for a condensed review of these types). In *Hydrastis*, which alone represents "Type III," "the medullary bundles, which are present only in the lowest internode of the aerial stem, do not directly enter the petiole at the upper node but shift their positions outward and into the central vascular cylinder. After passing upwardly through one internode, they depart from the central cylinder as traces to a small sessile leaf" (Tobe and Keating 1985, p. 309). Moreover, within the vascular bundles of both *Hydrastis* and *Glaucidium*, the cross-sectional orientation of the xylem is *straight* and not V-shaped as in the rest of the Ranunculaceae and the Berberidaceae (Tobe and Keating 1985, Fig. 26).

Furthermore, the perforation plate of the vessel elements is scalariform/reticulate to simple in *Hydrastis*, a feature found also in *Paeonia* and in some of the Berberidaceae (Kumazawa 1935, 1938b; Tobe and Keating 1985). In citing several references, Tobe and Keating (1985) claim that in the Ranunculaceae the perforations are *always simple* (see also Eames 1961, p. 414, for a similar claim). But this is not correct. In a thorough and superbly illustrated study of the primary xylem elements within the "Ranales," Zamora (1966, a paper not cited by Tobe and Keating 1985) recognized "5 arbitrary categories in terms of their [i.e., the genera of the Ranunculaceae] protoxylem-metaxylem intervacular overlap area transitions" (p. 502). These range from those with exclusive scalariform plates (e.g., *Paeonia*, classified by Zamora in the Ranunculaceae) to *Hydrastis* with "scalariform plates throughout the early protoxylem to the late metaxylem with imperforate intervacular contact areas throughout the protoxylem and some transitional and simple plates in the late metaxylem" (Zamora 1966, p. 502) to those genera with entirely simple plates [e.g., *Ranunculus* spp. and *Anemonella* (= *Thalictrum*)]. For our purposes here, however, Zamora's "category c" is of considerable interest. Under 'category c' Zamora lists and illustrates 12 genera (*Trollius*, *Aquilegia*, *Aconitum*, *Actaea*, *Caltha*, *Xanthorhiza*, *Coptis*, *Helleborus*, *Delphinium*, *Cimicifuga*, *Hepatica*, *Anemone*) in which there are "... 2 of the following kinds of perforation plates throughout the protoxylem-metaxylem transition: scalariform, transitional, simple" (p. 502). In short, within the Ranunculaceae possession of scalariform perforations is not restricted to *Hydrastis*, and hence cannot be used as a character demarking this genus from the rest of the Ranunculaceae (for similar studies see also Avita and Inamdar 1981, and Chen and Li 1990, 1991).

Serology.—According to Jensen (1968), *Hydrastis* is, serologically, closer to at least five genera within the Ranunculaceae than either *Eranthis* or *Nigella* is to any of the 20 genera included in Jensen's study. *Eranthis* appears closest to *Coptis* and *Cimicifuga* (correlation number: 0.6), whereas *Nigella* is closest serologically to *Helleborus* (0.8) and *Delphinium* (0.7), thus reinforcing the rather anomalous position of that genus (Jensen 1968, Tab. 11, p. 270). *Hydrastis*, on the other hand, serologically is closest to *Aquilegia* (1.1), *Adonis* (1.0), *Helleborus* (0.9), *Trollius* (0.9), *Ranunculus* (0.9), and *Actaea* (0.8), and least close to *Nigella* (0.2). As such, however, *Hydrastis* is, on the average (average: 0.66), serologically closer to the set of 19 genera included in Jensen's study of the Ranunculaceae than is *Anemone* (average: 0.58), a genus nobody proposes removing from the Ranunculaceae (Jensen 1968, Tab. 11, p. 270). But to what extent serology should be utilized in determining phylogenetic relationships is, however, another question.

CONCLUSION

In concluding their useful study, Tobe and Keating (1985) claim that "the inclusion of *Hydrastis* in the Ranunculaceae is unreasonable." The key features ("family level distinctions") leading Tobe and Keating to this conclusion appear to be chiefly four (p. 310), all of which are stated to occur in *Hydrastis* but not in the rest of the Ranunculaceae. These are listed below.

- 1) Bitegumentary ovules having longer outer integuments than the inner.
- 2) Tricolpate pollen with a striate-reticulate tectum.
- 3) Presence of straight (rather than V-shaped) xylem.
- 4) Presence of scalariform vessel perforations.

It appears, thus, that of the four major characters purportedly separating *Hydrastis* from the rest of the Ranunculaceae, only the straight xylem is distinctive. Moreover, *Aquilegia* has both scalariform perforation plates as well as longer outer integuments, characters claimed by Tobe and Keating to be distinctive for *Hydrastis*. Furthermore, according to Jensen's (1968) serological results, *Hydrastis* is related closest to *Aquilegia*, but also is relatively close to *Helleborus*, *Actaea*, *Trollius*, *Adonis*, and *Ranunculus*. It is least similar serologically to *Nigella*, *Anemone*, and *Eranthis*. But the relative serological similarity of *Hydrastis* to *Aquilegia*, together with the perforation plate, integumentary, and chromosomal size features in common, point to a possible phylogenetic linkage that should not be overlooked.

Hydrastis is a distinctive genus, but whether it should be classified in its own monotypic family or be included within the Ranunculaceae remains an issue. If the Ranunculaceae are understood in a broad sense, *Hydrastis* can be classified within the family (Duncan and Keener 1991; Tamura 1992). But if the Ranunculaceae are more narrowly circumscribed, *Hydrastis* very reasonably can be recognized as a monotypic family, the Hydrastidaceae (Takhtajan 1987). Arguments can be advanced for either point of view. In any case, we must await current research into molecular systematic patterns involving *Hydrastis*, the Berberidaceae, the Ranunculaceae, and related families for additional clarification of the systematic position of *Hydrastis*.

As an aid to understanding some of the key differences between *Hydrastis* and the Ranunculaceae s.s., the following key is given.

1. Sepals 3; petals absent; flower 1; leaves simple with plaited (palm) venation and undifferentiated mesophyll; carpels numerous, each 2-ovuled, becoming baccate; carpellary traces 4; vascular bundle xylem straight in cross-section; integuments 2, the outer longer than the inner; pollen tricolpate, tectum striate; $x = 13$ *Hydrastis*
1. Sepals 4 or more; petals present or absent; flowers numerous to few or 1; leaves simple or compound with nonplaited venation and a differentiated mesophyll; carpels 1 to many, rarely 2-ovuled, becoming typically achenes or follicles (rarely capsular or baccate); carpellary traces 1 or 3, rarely 4; vascular xylem V-shaped in cross-section; integuments 1 or 2, the inner usually longer than the outer; pollen tricolpate or pantoporate, tectum typically spinulose-punctate/perforate; $x = 6, 7, 8, 9$ Ranunculaceae s.s.

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