



Phylogenetic Definitions for *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae*

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Abstract

Formal phylogenetic definitions are here provided for the angiosperm clades *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae*. After decades of progress in understanding the phylogeny of *Asteridae* and *Campanulidae*, the three clades here associated with those three names are better supported than ever, and the phylogenetic definitions presented here therefore differ little from the pre-*PhyloCode* phylogenetic definitions provided 25 years ago by Donoghue *et al.* (2001). It is abundantly clear that *Dipsacales* is a clade composed of two very well-supported and easily identified sister clades—here *Adoxaceae* and *Caprifoliaceae*—that were not recognized in pre-phylogenetic angiosperm classification systems. The impetus for solidifying these names now under the *PhyloCode* is that decisions made in the past decade by the Nomenclatural Committee for Vascular Plants of the *International Code of Nomenclature for algae, fungi, and plants (ICN)* have led to the mandatory replacement of the name *Adoxaceae* by *Viburnaceae* for a family that includes *Viburnum*, *Sambucus*, and *Adoxa*. This unfortunate decision to replace a widely accepted name, used many thousands of times in the literature, by a name that has rarely been used, can now be circumvented (by those who wish to do so) by correctly observing that *Adoxaceae* is the accepted name for this clade under the *PhyloCode*. This paper prepares the way for a comprehensive phylogenetic classification and nomenclature of both *Adoxaceae* and *Caprifoliaceae*.

Key words: classification, nomenclature, *PhyloCode*, taxonomy, *Viburnaceae*

Introduction

The history of the classification of the asterid angiosperm clade *Dipsacales*, with some 1,100 species, has been complex, with uncertainties about relationships and differences in taxonomic philosophy reflected in widely contrasting taxonomic circumscriptions and naming schemes. However, over the past four decades phylogenetic relationships have been clarified, and we now have great confidence in *Dipsacales* as a clade and in its major subclades. As phylogenetic studies have progressed, the application of names largely settled down—that is, until recently, when a set of decisions made by the Nomenclature Committee for Vascular Plants (NCVP) and the General Committee of the *International Code of Nomenclature for algae, fungi, and plants (ICN)* generated unnecessary confusion. The primary purpose of this paper is to describe how this came about and—in an attempt to solve this problem—to establish formal phylogenetic definitions for the three main clade names in question, *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae*.

Looking back at angiosperm taxonomic systems in use prior to the rise of phylogenetic systematics, the order *Dipsacales* was typically viewed as containing four or five families. The four families recognized by Arthur Cronquist (1981) are superimposed in Figure 1 onto a tree that represents currently well-supported phylogenetic relationships (references in the caption of Fig. 1). Cronquist's *Caprifoliaceae* is paraphyletic with respect to his *Adoxaceae*, but also with respect to *Valerianaceae* and at least the bulk of his *Dipsacaceae*. Furthermore, *Dipsacaceae* and *Valerianaceae*, as circumscribed by Cronquist, do not form clades, owing to the placements of *Triplostegia* and of *Morina* and its relatives. Armen Takhtajan's classification (e.g., Takhtajan 1980) was similar to Cronquist's, although he recognized a fifth family for *Morina*. Importantly, Cronquist's classification (Fig. 1), like others in that time period (e.g., Takhtajan 1980; Thorne 1983) did not recognize major clades that are now supported with great confidence. In particular, these systems provided no names for the two very distinctive major clades within *Dipsacales*—one including *Viburnum*, *Sambucus*, and *Adoxa* and its relatives, labeled A in Fig. 1, and the other including everything from *Diervilla* and its relatives through *Valeriana* and its relatives, labeled B.

Dipsacales taxonomy of Cronquist (1981)

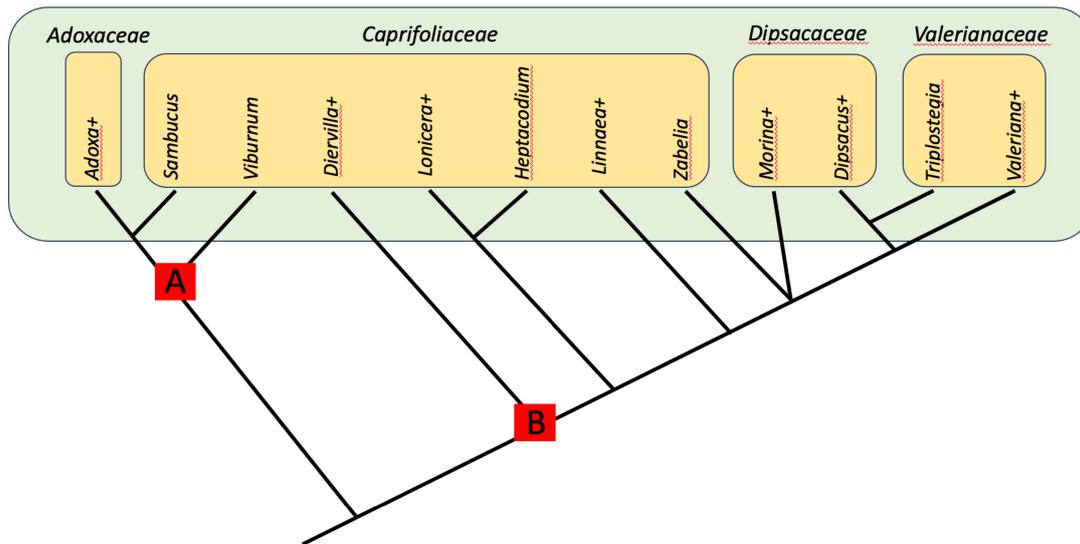


FIGURE 1. The four families of *Dipsacales* recognized by Cronquist (1981) shown on a tree that represents current knowledge of phylogenetic relationships (based on concordant results in, e.g., Donoghue *et al.* 2001; Bell *et al.* 2001; Winkworth *et al.* 2008a; Tank and Donoghue 2010; Jacobs *et al.* 2011; Soltis *et al.* 2011, Fan *et al.* 2018, Xiang *et al.* 2020; Wang *et al.* 2020; Lee *et al.* 2021; additional references in text). The long-disputed placement of *Heptacodium* (see Pyck and Smets 2000) has been resolved with reasonable confidence, but the position of *Zabelia* remains uncertain and hence is represented as a polytomy (e.g., contrast Jacobs *et al.* [2011] with Lee *et al.* [2021]). A and B mark two major clades that had not been named in pre-phylogenetic taxonomic systems. A “+” following a name indicates that the clade includes additional taxa traditionally recognized at the genus rank.

In recognition of these shortcomings, and with the advent at the time of phylogenetic nomenclature (de Queiroz and Gauthier 1990), phylogenetic definitions were put forward for these two major clades (Fig. 2). Judd *et al.* (1994) applied the name *Adoxaceae* to clade A in Figure 1 and provided the following pre-*PhyloCode* minimum-clade phylogenetic definition: “the most recent common ancestor of *Viburnum*, *Sambucus*, and *Adoxa*, and all of its descendants, whether recent or extinct” (p. 25). *Adoxaceae* was the name chosen because it had been conserved relative to other available names and had already been associated with this clade by Thorne (1983). Later, Donoghue *et al.* (2001) selected *Viburnum lantana* L., *Sambucus nigra* L., and *Adoxa moschatellina* L. as specifiers (Fig. 2). Judd *et al.* (1994) applied the name *Caprifoliaceae* to clade B in Fig. 1 and provided this phylogenetic definition: “the most recent common ancestor of plants previously considered to be *Caprifoliaceae s.s.* (or subfamily *Caprifolioideae* sensu Hara, 1983) as well as those assigned to *Valerianaceae* and *Dipsacaceae*, and all of the descendants of that ancestor” (p. 25). *Caprifoliaceae s.s.* here referred to all pre-phylogenetic *Caprifoliaceae* (e.g., sensu Cronquist 1981) except for *Viburnum* and *Sambucus* (see Fig. 1). The conserved names *Caprifoliaceae* and *Dipsacaceae* were published at the same time (Jussieu 1789); Judd *et al.* (1994) chose *Caprifoliaceae* for the combined family. Donoghue *et al.* (2001) later selected the following specifiers in their corresponding minimum-clade definition: *Lonicera caprifolium* L., *Diervilla lonicera* Miller, *Linnaea borealis* L., *Valeriana pyrenaica* L., and *Dipsacus fullonum* L. (Fig. 2). Donoghue *et al.* (2001) also provided a node-based definition for *Dipsacales* using these four specifiers: *Dipsacus fullonum* L., *Linnaea borealis* L., *Lonicera caprifolium* L., and *Viburnum lantana* L. (Fig. 2). Tank and Donoghue (2010) used the same definition for *Dipsacales* but substituted *Dipsacus sativus* (L.) Honck. (which was included in their phylogenetic analyses) for *D. fullonum*.

Note that these definitions for *Adoxaceae* and *Caprifoliaceae* greatly broaden their circumscriptions relative to pre-phylogenetic systems. *Adoxaceae* now includes *Viburnum* and *Sambucus*, in addition to *Adoxa moschatellina* and its more recently discovered relatives, *Sinadoxa corydalifolia* C. Y. Wu, Z. L. Wu & R. F. Huang (Wu *et al.* 1981) and *Tetradoxa omeiensis* (H. Hara) C. Y. Wu (Hara 1981; Wu 1981). This raises the number of species of *Adoxaceae* from three to ~190 and adds shrubs and trees (some of them quite large and showy) to what pre-phyloge-

netically was a group of inconspicuous herbaceous plants. Likewise, *Caprifoliaceae*, pre-phylogenetically a group of ~185 mainly shrubby species, is expanded to include the pre-phylogenetic *Morinaceae*, *Dipsacaceae*, and *Valerianaceae*, thus adding nearly 700 species of mainly herbaceous plants. The clades variously subsumed under these broader circumscriptions could of course also be recognized, and several of these were in fact given phylogenetic definitions by Donoghue *et al.* (2001) (e.g., *Adoxoideae* for the smallest clade including *Sambucus* and *Adoxa*).

***Dipsacales* taxonomy of Judd *et al.* (1994) and Donoghue *et al.* (2001)**

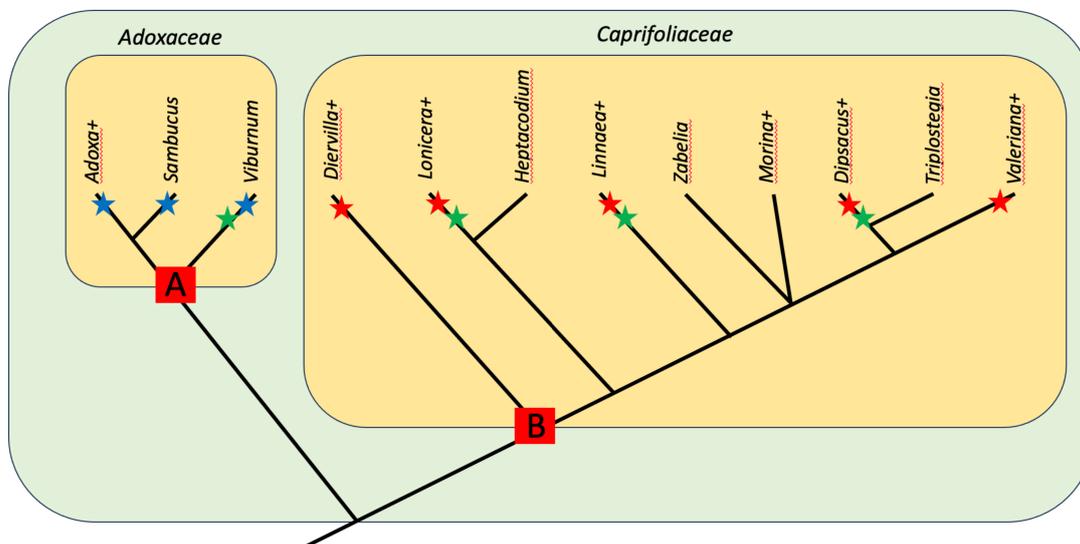


FIGURE 2. Judd *et al.* (1994) applied *Adoxaceae* and *Caprifoliaceae* to nodes A and B, respectively, in Fig. 1, and provided minimum-clade phylogenetic definitions that were later modified by Donoghue *et al.* (2001) who selected relevant specifiers from the clades marked with blue stars for *Adoxaceae* and with red stars for *Caprifoliaceae*. Donoghue *et al.* (2001) also provided a phylogenetic definition for *Dipsacales*, selecting specifiers from the clades marked with green stars. A “+” following a name indicates that the clade includes additional taxa traditionally recognized at the genus rank.

With respect to standard rank-based nomenclature, Backlund and Bremer (1996) favored the continued recognition of *Valerianaceae* and *Dipsacaceae* and argued in favor of also recognizing *Morinaceae*. Backlund and Pyck (1998; also see, e.g., Pyck and Smets 2004) proposed the recognition of six families as opposed to accepting the expanded *Caprifoliaceae* of Judd *et al.* (1994). This entailed the recognition of four previously named families (*Caprifoliaceae* Juss. [1789] nom. cons., *Dipsacaceae* Juss. [1789] nom. cons., *Morinaceae* Raf. [1820], and *Valerianaceae* Batsch [1802] nom. cons.) and the naming of two new families: *Diervillaceae* (Raf.) Pyck, and *Linnaeaceae* (Raf.) Backlund. Their classification is shown in Figure 3. Note especially that *Caprifoliaceae* is circumscribed much more narrowly than in either Figure 1 or Figure 2 and corresponds to the pre-phylogenetic *Caprifolieae* (*Leycesteria*, *Lonicera*, *Symphoricarpos*, and *Triosteum*) plus the enigmatic *Heptacodium*. As in pre-phylogenetic systems, this leaves major clade B (*Caprifoliaceae* of Judd *et al.* [1994] and Donoghue *et al.* [2001]) unnamed.

The influential Angiosperm Phylogeny Group (APG) classification system waived on this issue through its various versions. In the first APG treatment of 1998, *Adoxaceae* was not included in *Dipsacales*, but instead was placed as uncertain within the euasterids. In APG II (2003) *Adoxaceae* (now presumably in the broad sense of Judd *et al.* 1994, and Donoghue *et al.* 2001) was added to *Dipsacales*, and *Caprifoliaceae* (again presumably in the sense of Judd *et al.* 1994, and Donoghue *et al.* 2001) was tentatively recognized, but with an indication that the recognition of six families, as proposed by Backlund and Pyck (1998), would be an acceptable “option”. In APG III (2009) it was decided to recognize just the two families, *Adoxaceae* and *Caprifoliaceae*, as by this time the association of *Caprifoliaceae* with Clade B was “widely preferred” (p. 118). These two families were also recognized in APG IV (2016), but with an indication that the Nomenclatural Committee for Vascular Plants (NCVP) had approved the conservation of *Viburnaceae*, which would then replace *Adoxaceae* (see below). The authors of APG IV did not accept this decision by the NCVP in hopes that the ICN General Committee would not accept it.

Dipsacales taxonomy of Backlund and Pyck (1998)

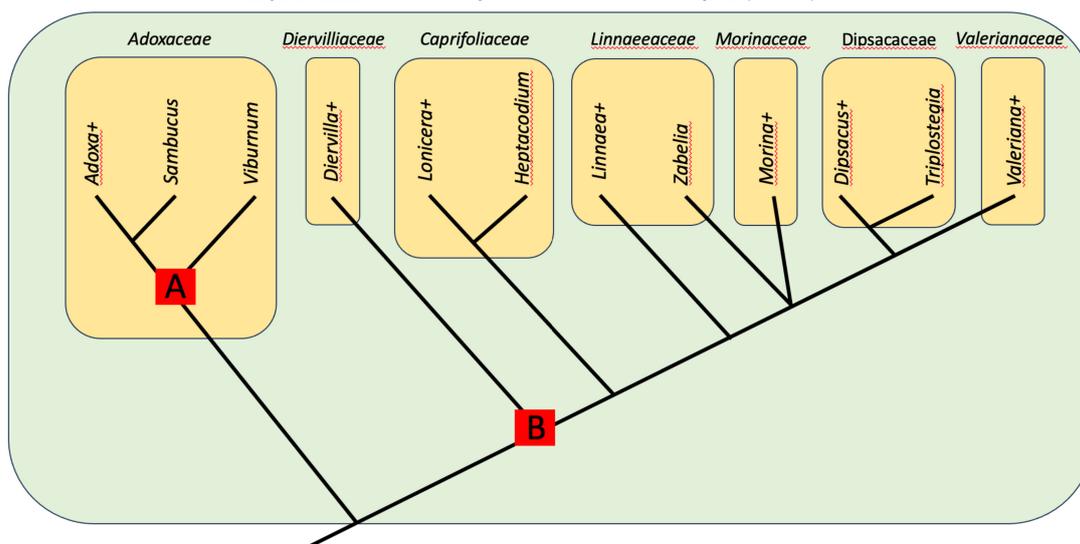


FIGURE 3. The classification of *Dipsacales* proposed by Backlund and Pyck (1998) and highlighted as an “option” in APG II (2003). In this scheme, *Adoxaceae* is applied to node A, but node B (*Caprifoliaceae* in Fig. 2) remains unnamed. A “+” following a name indicates that the clade includes additional taxa traditionally recognized at the genus rank.

Reveal (2008) put forward three proposals relevant to this discussion that were then considered by the NCVP. Proposal 1800 would conserve *Viburnaceae* Raf. (Oct.–Dec. 1820) against all competing names at the same rank, including the earlier names *Sambucaceae* Batsch ex Borkh. (1797) (unless it were also conserved—see below) and *Tinaceae* Martinov (Aug. 1820), as well as *Adoxaceae* E. Mey. (1839). Regardless of whether this proposal was approved, *Viburnaceae* (1820) would then have priority over *Adoxaceae* (1839) if the two families were combined. For this reason, Reveal crafted proposal 1801 to “super-conserve” *Adoxaceae*, thus allowing it to be used for the family level taxon including *Viburnum*, *Sambucus*, and *Adoxa*. Finally, proposal 1802 would conserve the name *Sambucaceae*, which would then have priority over *Adoxaceae* and *Viburnaceae* if it were decided not to super-conserve *Adoxaceae* under 1801. If 1800 were approved, and 1801 and 1802 were rejected, then *Viburnaceae* would need to be used for the family-level taxon including *Viburnum*, *Sambucus*, and *Adoxa*. This is eventually what happened, but the decisions unfolded in several steps over several years, as reported by Applequist (2013) and Wilson (2016a, b); see also the account by Waswa *et al.* (2022).

Applequist (2013), reporting on the activities of the Nomenclature Committee, first noted that the conservation of *Viburnaceae* (proposal 1800) had been recommended by a vote of 11 in favor, three opposed, and two abstaining. She summarized the state of affairs with respect to 1801 and 1802 as follows:

“The conservation of *Viburnaceae* by Prop. 1800, above, would protect the use of *Viburnaceae* when *Viburnum* is segregated into its own family, but it would also make that the correct name for the combined family that is now called *Adoxaceae*. The simultaneously published Props. 1801 and 1802 were intended to avoid that outcome either by superconserving *Adoxaceae* or, alternatively, by conserving *Sambucaceae*. All three proposals have been the subject of considerable disagreement among members of the Committee, though Prop. 1800 was ultimately recommended with the minimum required number of votes. The Committee has been unable to achieve any consensus for or against Prop. 1801. A final vote has not yet been taken on Prop. 1802 to conserve *Sambucaceae*, but as of this writing, it appears unlikely that it will gain 60% support. (Authors of future proposals might note that simultaneously offering competing proposals with opposite effects may make it less likely that any of the alternatives will be perceived as necessary by an adequate majority.) In the five years since these proposals were published, the Angiosperm Phylogeny Group’s preferred single-family classification has gained popularity, so that *Viburnum* is most often placed within *Adoxaceae*. Approving Prop. 1800 without Prop. 1801 would make *Viburnaceae* the correct name when a single family is recognized, an outcome that the proposer considers undesirable (Reveal, pers. comm.)”

Several things stand out here: first, the confusion surrounding the way that the three proposals were bundled by Reveal (2008); second, the lack of consensus in the committee; third, the recognition that *Adoxaceae*, in the sense of Judd *et al.* (1994) and Donoghue *et al.* (2001), had gained popularity; and, finally, and ironically, that the proposer himself did not want *Viburnaceae* to replace *Adoxaceae*.

Wilson (2016a), reporting on decisions of the General Committee, stated that proposal 1800 had been approved by a vote of 18 in favor, three against, none abstaining, and one desiring more discussion. Thus, *Viburnaceae* was conserved over *Tinaceae*. However, she also noted the following:

Two proposals – (1801) to “superconserve” *Adoxaceae* against *Viburnaceae* and (1802) to conserve *Sambucaceae* – were reported without recommendation by the NCVF after two rounds of inconclusive voting. The General Committee’s vote (9–11–1) on (1801) failed to reach a super-majority, so this proposal is still being discussed. The General Committee voted (1–19–1) not to conserve *Sambucaceae* (1802).

So, at this stage, *Viburnaceae* was conserved (proposal 1800), *Sambucaceae* was not conserved (proposal 1802), and the fate of *Adoxaceae* (proposal 1801) was in limbo. However, later that same year Wilson (2016b) reported that a supermajority had ultimately been reached on proposal 1801, with a vote of eight in favor, 15 against, and two abstaining. Thus, the super-conservation of *Adoxaceae* was rejected. Based on these three rulings, *Viburnaceae* would need to replace *Adoxaceae* for a family including *Viburnum*, *Sambucus*, and *Adoxa*.

Note that 22 members of the General Committee voted the first time around, and 25 the second time; one fewer person voted in favor of conservation of *Adoxaceae* the second time; and four more voted against. Initially 50% were against conservation of *Adoxaceae*, but this became 60% in the second round, putting it at the threshold for a supermajority. If one fewer person had voted against on proposal 1801, a super-majority would not have been reached. To summarize, over a period of eight years, and eventually decided by just a single vote, an outcome was achieved that no one working in the field had requested or felt was necessary, and that was not supported by the original proposer. Furthermore, this decision is directly at odds with the intention of *ICN* Article 14.2, which states the common-sense principle that “Conservation aims at retention of those names that best serve stability of nomenclature.” Even more generally, it is at odds with the Preamble of the *ICN*, which states: “This *Code* aims at the provision of a stable method of naming taxonomic groups, avoiding and rejecting the use of names that may cause error or ambiguity or throw science into confusion.” As shown in Figure 4, *Adoxaceae* was being widely used at the time that these decisions were taken, while *Viburnaceae* had hardly been used at all, with citations rising slowly only after the *ICN* General Committee ruling in 2016. Here it is relevant to cite a portion of *PhyloCode* in Art. 10.1:

“Clade names are generally to be selected in such a way as to minimize disruption of current and/or historical usage (with regard to composition, diagnostic characters, or both) and to maximize continuity with existing literature.”

The choice of *Adoxaceae* for the clade including *Viburnum*, *Sambucus*, and *Adoxa* clearly aligns with this Rule, whereas the choice of *Viburnaceae* creates confusion and an unnecessary disconnect with the relevant literature (Fig. 4).

Given the history described above, I maintain that it is a mistake to shift to *Viburnaceae*. Instead, it would be in the best interest of the scientific community to continue to use *Adoxaceae* in the sense of the pre-*PhyloCode* phylogenetic definitions of Judd *et al.* (1994) and Donoghue *et al.* (2001). For this reason, I am here providing a formal phylogenetic definition for the name *Adoxaceae*, as well as for *Caprifoliaceae* and *Dipsacales*, to establish these names under the *PhyloCode* (Cantino and de Queiroz 2020). This will allow the continued use of these names in publications, for those who wish to do so, despite the unfortunate decision with respect to *Adoxaceae*. If editors of relevant journals insist on the use of *Viburnaceae*, citing the *ICN*, it can now be pointed out that its use is mandated only if one adheres to that nomenclatural code. If, on the other hand, one adopts the *PhyloCode*, as I do, *Adoxaceae* is the correct name for the clade including *Viburnum*, *Sambucus*, and *Adoxa*.

The fundamental principle here is that we, as individual systematists, have the agency to choose to operate under the rules and regulations of the *ICN* (as we have in the past for lack of an alternative), but we can also now choose to operate under the *PhyloCode*, which has formally been in existence since 2020 (Cantino and de Queiroz 2020). The *PhyloCode* is seen by many, including myself, as preferable to other codes by virtue of avoiding unnecessary name changes, such as the one described above. Laurin (2024) provides extended arguments for this and other reasons for favoring the *PhyloCode* over other nomenclatural codes. I will continue to use *Adoxaceae*

in my own work, and will encourage colleagues to do the same, referring now to the formal establishment of the name *Adoxaceae* under the *PhyloCode*. For those who favor the *ICN*, and who may also prefer the continued use of *Adoxaceae*, the confusion caused by substituting *Viburnaceae* could be rectified by revisiting proposal 1801 or by putting forward a new proposal that would undo the poor decisions made earlier. Mistakes of this sort are made from time to time, and there is no shame in recognizing them and making appropriate adjustments to uphold the fundamental principles underlying the *ICN*.

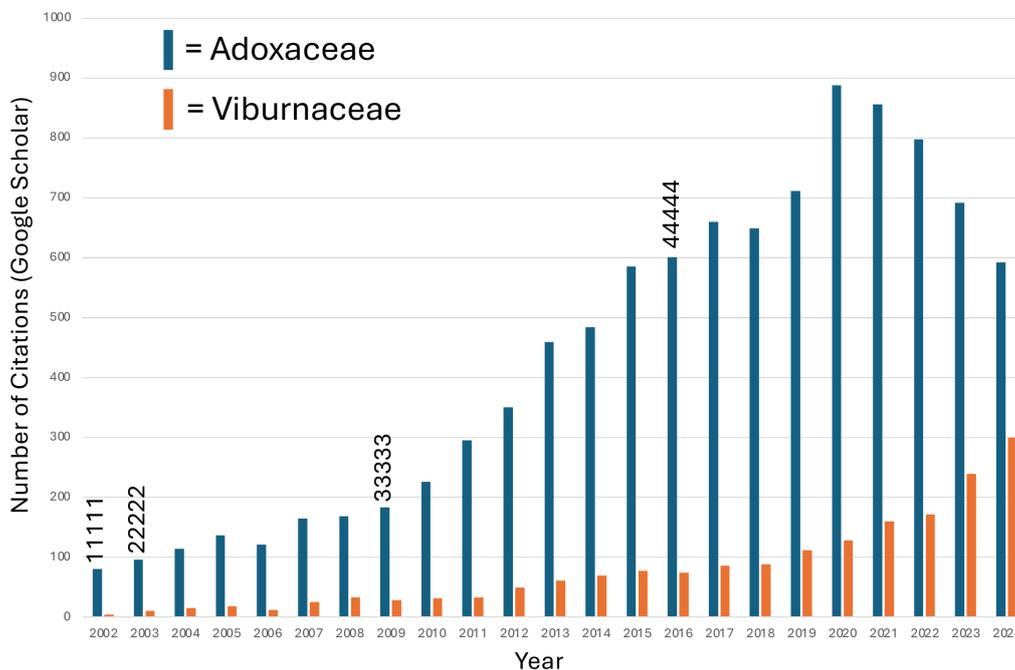


FIGURE 4. Approximate number of citations from 2002–2024 of *Adoxaceae* (blue; ~13,200 total) and *Viburnaceae* (orange; ~2190 total) obtained from Google Scholar on 09/15/2025. *Adoxaceae* was given a pre-*PhyloCode* phylogenetic definition by Donoghue *et al.* in 2001. 11111 = publication of the second edition of the Judd *et al.* *Plant Systematics* textbook; 22222 = publication of APG II; 33333 = publication of APG III; 44444 = *ICN* General Committee vote to mandate the use of *Viburnaceae* (see text).

Dipsacales A. L. Jussieu ex B. W. Berchtold and J. S. Presl, 1820 [M. J. Donoghue], converted clade name
Registration Number: 1199.

Definition: The smallest crown clade including *Dipsacus fullonum* Linnaeus 1753, *Linnaea borealis* Linnaeus 1753, *Lonicera xylosteum* Linnaeus 1753, and *Viburnum lantana* Linnaeus 1753 (see Figs. 2, 5). This is a minimum-crown-clade definition. These specifiers are the type species of their respective genera and were those used by Donoghue *et al.* (2001) and Tank and Donoghue (2010) in their pre-*PhyloCode* phylogenetic definitions of *Dipsacales*, with the one exception that *Lonicera caprifolium* L. is here replaced by *Lonicera xylosteum* L., which, despite earlier confusion (Britton and Brown 1913), is the lectotype for *Lonicera* (see Ferguson 1966; Hara 1983).

Etymology: *Dipsacales* is based on the genus name *Dipsacus*, derived from the Greek word “dipsa”, meaning thirst. This is said to refer to the cup-like perfoliate leaves produced in some species (e.g., *D. sativus*), which sometimes pool water.

Reference Phylogeny: Soltis *et al.* (2011), Figure 2G, is here selected as the reference phylogeny (see Fig. 5 of this article). This was a phylogenetic analysis based on 17 genes, from the chloroplast, nuclear, and mitochondrial genomes. Importantly, the broad analysis of angiosperms carried out by Soltis *et al.* (2011) found strong support for the monophyly of *Dipsacales* within *Asterideae* and *Campanulidae* (both defined in Cantino *et al.* 2007; de Queiroz *et al.* 2020). Soltis *et al.* (2011) included sufficient taxon sampling within and outside of *Dipsacales* and confidently resolved both *Adoxaceae* and *Caprifoliaceae* as clades. They also identified *Parcryphiaceae*, and in turn *Apiales*, as the closest living relatives of *Dipsacales*. Tank and Donoghue (2010), having inferred the same outgroup relationships, phylogenetically defined *Dipsidae* to include *Dipsacales* plus *Parachryphiaceae*, and *Dipsapiidae* to include *Dipsidae* plus *Apiales*.

More recent studies might have been chosen for the reference phylogeny, but these have mostly focused on resolving relationships *within Dipsacales* and have not simultaneously tested the monophyly of *Dipsacales* itself. Several earlier analyses of relationships within *Campanulidae* did test the monophyly and broader relationships of *Dipsacales* (Winkworth *et al.* 2008a, 2008b; Tank and Donoghue 2010), but these were based on a more limited sample of genes than analyzed by Soltis *et al.* (2011). Additionally, most of them were based exclusively on chloroplast genomes (Fan *et al.* 2018; Wang *et al.* 2020; Xiang *et al.* 2020). Lee *et al.* (2021) analyzed many nuclear genes for *Dipsacales* but did not test the monophyly of *Dipsacales* and did not include *Sinadoxa* or *Tetradoxa*.

Composition: *Dipsacales* is a clade of ~1,100 species belonging to the two major clades defined below, *Adoxaceae* (~190 species) and *Caprifoliaceae* (~900 species). *Adoxaceae* includes *Viburnum* and a clade comprising *Sambucus* plus *Sinadoxa*, *Tetradoxa*, and *Adoxa*. *Caprifoliaceae* here includes the woody genera assigned to the pre-phylogenetic *Caprifoliaceae*, minus *Viburnum* and *Sambucus* (e.g., see Cronquist, 1981), along with the pre-phylogenetically recognized, largely herbaceous *Morinaceae* (~14 species), *Dipsacaceae* (~300 species), and *Valerianaceae* (~375 species) (Figs. 1, 2). Additional details on the composition of *Adoxaceae* and *Caprifoliaceae* are given in their protologues below.

Diagnostic Apomorphies: Character polarities near the base of *Dipsacales* have been difficult to assess owing to uncertainties concerning outgroups and the great ages of the relevant clades (see below). However, referring here primarily to *Paracryphiaceae* as likely relatives of *Dipsacales* (Tank and Donoghue 2010; Soltis *et al.* 2011), the following are potential apomorphies for *Dipsacales*: opposite leaves; sympetalous corollas; stamens adnate to the corolla tube; and unitegmic tenuinucellate ovules. With less certainty the following may also be apomorphic: loss of a nectar disc; cellular endosperm; a base chromosome number of 8–9 (versus 11), and the production of iridoid compounds.

Synonyms: None; however, *Caprifoliaceae* of several late 20th century authors (e.g., Takhtajan 1980, Cronquist 1981, and Thorne 1983) was used for a paraphyletic taxon originating in the same ancestor.

Comments: Despite the lack of unique morphological traits, *Dipsacales* has long been recognized as an angiosperm order within *Asteridae* and *Campanulidae* (e.g., Thorne 1976; Takhtajan 1980; Cronquist 1981). All members have opposite or (rarely) whorled leaves and half- to fully inferior ovaries, and almost all have flowers that are 5- or 4-merous, are sympetalous with adnate stamens, and have anatropous ovules. But these traits are all widespread in angiosperms, and in asterids in particular. Otherwise, *Dipsacales* members are extremely variable. They can be herbs, shrubs, trees, or vines, with simple or compound leaves, and with large or tiny, radial or bilaterally symmetrical flowers. Their fruits are especially diverse, ranging from fleshy berries and drupes to dry capsules and achenes. They also vary in a host of more obscure characters, including scalariform versus simple vessel-element perforations, *Polygonum*- versus *Adoxa*-type embryo-sac development, and pollen that can be large, round, and tectate (*Caprifoliaceae*) to small, prolate, and semi-ectate/reticulate (*Adoxaceae*). With a few notable exceptions (e.g., *Viburnum* and *Valeriana* in the Andes, *Scabiosa* in South Africa, *Sambucus* in Australia), most *Dipsacales* are native to the Northern Hemisphere, but they occupy a very wide range of biomes. Many are in temperate forests, but some occupy tropical rainforests, high alpine regions, and arid habitats from deserts to Mediterranean chaparral. A few have high latitude circumboreal distributions, such as *Adoxa moschatellina* and *Linnaea borealis*.

Given this enormous diversity, Donoghue (1983) evaluated evidence for and against the monophyly of *Dipsacales*, but the results were inconclusive. Using morphological characters and a limited sample of potential outgroups, Judd *et al.* (1994) supported *Dipsacales* as a clade, but a morphological analysis by Backlund and Donoghue (1996) included *Columellia* and *Desfontania* (now treated as *Collumeliaceae* within *Bruniales*) within *Dipsacales*. Chase *et al.* (1993) supported *Dipsacales* monophyly based on a parsimony analysis of large *rbcl* dataset. Other molecular studies published at around that time were less conclusive (e.g., Donoghue *et al.* 1992; Olmstead *et al.* 1993; Backlund and Bremer 1997). These early molecular analyses suffered from very limited taxon and gene sampling (generally only one or two chloroplast loci). Taxonomic sampling was expanded considerably by Donoghue *et al.* (2001) and Bell *et al.* (2001), who inferred *Dipsacales* monophyly with much greater confidence. Other molecular studies at that time also supported *Dipsacales* (e.g., Olmstead *et al.* 2000; Bremer *et al.* 2001, 2002), but two studies by Savolainen *et al.* (2000a, b) did not, and instead weakly supported the inclusion of *Desfontainia* (*Collumeliaceae*), *Paracryphia* and *Sphenostemon* (*Paracryphiaceae*), and *Polyosma* (*Escalloniaceae*) within *Dipsacales* (Savolainen *et al.* 2000b). However, from that time onward, every published study that I am aware of that has tested the monophyly of *Dipsacales* has strongly supported it (e.g., Zhang *et al.* 2003; Pyck and Smets 2004; Bell and Donoghue 2005a Winkworth *et al.* 2008a, b; Tank and Donoghue 2010; Soltis *et al.* 2011). Based on these analyses,

recent molecular studies have taken the monophyly of *Dipsacales* for granted and have concentrated on inferring relationships within the clade (e.g., Jacobs *et al.* 2010, 2011; Fan *et al.* 2018; Xiang *et al.* 2020; Wang *et al.* 2020; Lee *et al.* 2021).

Regarding broader relationships, pre-phylogenetic classification systems mostly allied *Dipsacales* with *Rubiaceae* (e.g., Hooker 1873; Engler 1898; Takhtajan 1980; Cronquist 1981), the main alternative being to place it, or parts of it, with *Cornales* and/or *Araliales* (e.g., Hutchinson 1973; Thorne 1976; Dahlgren 1980). Donoghue (1983) considered these conflicting interpretations from the perspective of phylogenetic systematics, trying to identify possible apomorphic traits that might unite these taxa. Again, these analyses proved inconclusive. Several of the molecular studies referenced above unequivocally ruled out *Rubiaceae* and *Cornaceae*. Instead, the evidence has pointed to a deep connection between *Dipsacales* and *Paracryphiaceae* (containing *Paracryphia*, *Quintinia*, and *Sphenostemon*), and in turn to *Apiales* (e.g., Winkworth *et al.* 2008b; Tank and Donoghue 2010; Soltis *et al.* 2011; Stull *et al.* 2018). As shown by Beaulieu *et al.* (2013), these relationships imply that the Northern Hemisphere *Dipsacales* originated within a radiation of mainly Old World, Southern Hemisphere plants.

Although phylogenetic relationships are now well established, the timing of the origin and radiation of *Dipsacales* remains somewhat uncertain owing to confusion surrounding the identity and placement of various fossils, but also to great heterogeneity in rates of evolution in the woody versus herbaceous subclades. Earlier efforts to date *Dipsacales* were based on a small number of plastid loci (Bell and Donoghue 2005a) or used whole plastid genomes but with limited taxon sampling (Fan *et al.* 2018; Wang *et al.* 2020). Bell and Donoghue (2005a) inferred a date of ~102 Ma for the *Dipsacales* crown, while Wang *et al.* (2020) estimated a date of ~112 Ma. These dates differ significantly from Fan *et al.* (2018), who inferred a date for crown *Dipsacales* of ~81 Ma. An analysis of nuclear genes by Lee *et al.* (2021) yielded an estimate for the crown of *Dipsacales* centered on 107 Ma, and *Adoxaceae* and *Caprifoliaceae* are inferred to have begun diversifying in the Late Cretaceous. Lee *et al.* (2021) estimated ~70 Ma for the *Adoxaceae* crown, and ~90 Ma for the *Caprifoliaceae* crown. Age estimates within *Dipsacales* are confounded by differences in rates of evolution within the largely woody *Adoxaceae* and the largely herbaceous *Caprifoliaceae* (also see Moore and Donoghue 2007). Finally, it should be noted that the dates obtained in studies that have focused on *Dipsacales* (cited above) are generally older than estimates in angiosperm-wide analyses (e.g., ~90 Ma for the *Dipsacales* crown in Ramírez-Barahona *et al.* 2020); this is likely due to the inclusion of fewer ingroup species and fossils in these broader studies.

As described in the introduction, pre-phylogenetic classification systems generally recognized four or five families within *Dipsacales* (see Fig. 1). In the phylogenetic era, based on the studies referenced above, and beginning with Judd *et al.* (1994) and Donoghue *et al.* (2001), the plant systematics community largely coalesced around the recognition of just two families, *Adoxaceae* and *Caprifoliaceae* (e.g., Judd *et al.* 2016; APG IV 2016; Stevens 2001 and onward). However, some authors have balked at greatly expanding the circumscription of these pre-phylogenetic families, which subsume several highly distinctive clades that have long been recognized as separate families (*Morinaceae*, *Valerianaceae*, and *Dipsacaceae*). An alternative classification system was proposed that recognized seven families within *Dipsacales*—*Adoxaceae* plus six corresponding to *Caprifoliaceae* as defined here (Backlund and Pyck 1998; Fig. 3; also see Reveal 2012). Several major subclades within both *Adoxaceae* and *Caprifoliaceae* were newly named and given pre-*PhyloCode* phylogenetic definitions by Donoghue *et al.* (2001), and my intention is to formally establish these (and other clade names) under the *PhyloCode*.

Adoxaceae E. Meyer, 1839 [M. J. Donoghue], converted clade name

Registration Number: 1200.

Definition: The smallest crown clade including *Viburnum lantana* Linnaeus 1753, *Sambucus nigra* Linnaeus 1753, and *Adoxa moschatellina* Linnaeus 1753 (see Figs. 2, 5). This is a minimum-crown-clade definition that corresponds to the pre-*PhyloCode* phylogenetic definitions of Judd *et al.* (1994) and Donoghue *et al.* (2001). The specifiers are the type species of their respective genera and were those used by Donoghue *et al.* (2001).

Etymology: *Adoxaceae* is based on the name of the included taxon *Adoxa*, which was named by Linnaeus in 1753. *Adoxa* is from the ancient Greek “adoxos” and translates to “without glory” or “without stature”, evidently a reference to the small inconspicuous plants of *Adoxa moschatellina*.

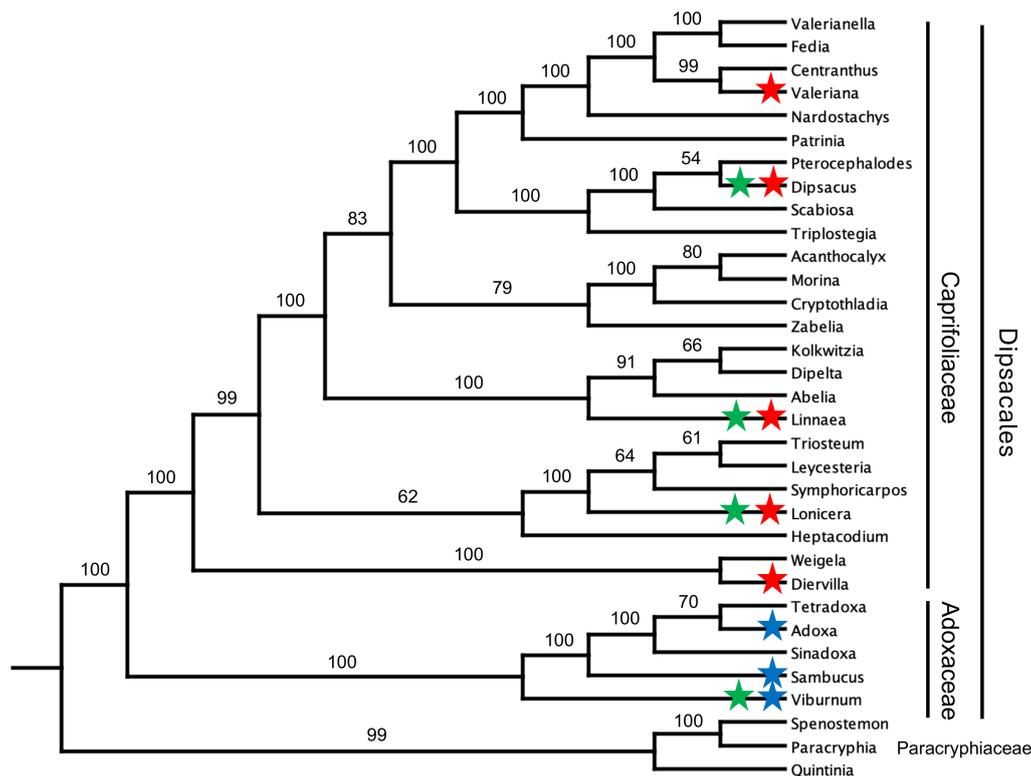


FIGURE 5. Relevant portion of the reference phylogeny for the minimum-crown-clade definitions of *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae* used herein (redrawn from Soltis *et al.*, 2011, Fig. 2G). Bootstrap values from Soltis *et al.* (2011) are shown on branches. Stars mark branches that include the specifiers for *Dipsacales* (green), *Adoxaceae* (blue), and *Caprifoliaceae* (red).

Reference Phylogeny: Soltis *et al.* (2011), Figure 2G, is here selected as the reference phylogeny (see Fig. 5 of this article). This is used as the reference phylogeny in the definitions of *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae*, and is justified for all three in the protologue of *Dipsacales* above. Specifically in reference to *Adoxaceae*, Soltis *et al.* (2011) included representatives of all five subclades: *Viburnum*, *Sambucus*, *Adoxa*, *Tetradoxa*, and *Sinadoxa*. *Adoxaceae* as defined here was strongly supported, as was the subclade including *Sambucus*, *Adoxa*, *Tetradoxa*, and *Sinadoxa* (the *Adoxoideae* as phylogenetically defined in Donoghue *et al.* 2001; also see Thorne 1983), and the subclade including *Adoxa*, *Tetradoxa*, and *Sinadoxa* (*Adoxina* as phylogenetically defined in Donoghue *et al.* 2001). As far as I am aware, these relationships, and particularly the monophyly of *Adoxaceae*, have been inferred in all molecular phylogenetic analyses published over the past several decades (Bell *et al.* 2001; Donoghue *et al.* 2001; Zhang *et al.* 2003; Pyck and Smets 2004; Bell and Donoghue 2005; Winkworth *et al.* 2008a, b; Tank and Donoghue 2010; Jacobs *et al.* 2011; Fan *et al.* 2018; Wang *et al.* 2020; Xiang *et al.* 2020; Lee *et al.* 2021).

Composition: *Adoxaceae*, as here defined, includes ~190 species in *Viburnum* (~165 species), *Sambucus* (~20 species), *Adoxa* (1 species), *Tetradoxa* (1 species), and *Sinadoxa* (1 species). Virtually all phylogenetic analyses show that these taxa are related as follows: (*Viburnum* (*Sambucus* (*Sinadoxa*, (*Tetradoxa*, *Adoxa*))))). Most species occupy forests in the temperate zones of the Northern Hemisphere, with eastern Asia (China in particular) being the center of modern species diversity. However, *Viburnum* is present in the Southern Hemisphere in tropical forests of south-east Asia and in cloud forests in the mountains of South America as far south as northern Argentina. *Sambucus* is exceptionally widespread and even includes several species in Australia. *Adoxa moschatellina* has a circumboreal distribution, while *Sinadoxa corydalifolia* and *Tetradoxa omeiensis* are narrowly endemic within China.

Diagnostic Apomorphies: Character polarities near the base of *Dipsacales* have been difficult to assess owing to uncertainties concerning outgroups and the great ages of the relevant clades (see Comments for *Dipsacales*). However, referring here primarily to *Paracryphiaceae* as likely relatives of *Dipsacales* (Tank and Donoghue 2010; Soltis *et al.* 2011), and *Caprifoliaceae* as sister to *Adoxaceae*, the following are probable apomorphies for *Adoxaceae*:

indehiscent, fleshy fruits, containing a small number of seeds (reduced to just one in *Viburnum*), each surrounded by endocarp tissue; reduced calyx lobes, with one vascular trace each; and glandular tapetum in the anthers. With less certainty, additional apomorphies may be the production of flat-topped, umbel-like inflorescences, with many small flowers. Benko-Iseppon and Morowetz (2000) highlighted several cytological/karyological differences between *Adoxaceae* and *Caprifoliaceae*; these are likely apomorphic, but their broader phylogenetic distribution is uncertain. Although the following are likely not apomorphic, they serve to readily distinguish *Adoxaceae* from *Caprifoliaceae*: small radially symmetrical, rotate corollas; small, prolate pollen grains with semitectate-reticulate exine; short styles with separated stigmatic lobes; and an extensive vascular system in the gynoecium.

Synonyms: *Viburnaceae* as *Viburnidia* Raf., Ann. Gén. Sci. Phys. 6: 87 (1820) *sensu*, e.g., Waswa *et al.* (2022). This is an approximate synonym because a distinction was not made between different clade categories (minimum, maximum, or apomorphy).

Benko-Iseppon and Morowetz (2000), citing primarily cytological evidence, proposed the recognition of *Viburnales* for what is here named *Adoxaceae*, but they did not formally publish this name.

Comments: In pre-phylogenetic classifications, *Viburnum* and *Sambucus* were most often placed in *Caprifoliaceae*, and *Adoxa* in a separate family *Adoxaceae* (e.g., Cronquist 1981; Takhtajan 1980), both within *Dipsacales*. However, Dahlgren (1980) placed *Adoxaceae*, along with his *Sambucaceae*, in his *Cornales*. Donoghue (1983) made the case that *Viburnum* is most closely related to *Sambucus* plus *Adoxa*. This had been hypothesized previously (e.g., Hooker 1873) but had never been properly tested. Morphological phylogenetic analyses by Judd *et al.* (1994) and Backlund and Donoghue (1996) supported these relationships. In the early parsimony analyses of chloroplast *rbcL* data (Chase *et al.* 1993; Olmstead *et al.* 1993) the relationship of *Viburnum* to *Sambucus* plus *Adoxa* was equivocal, but a series of more focused molecular analyses during that time period strongly supported *Viburnum* as sister to *Sambucus* plus *Adoxa* (Donoghue *et al.* 1992; Donoghue *et al.* 2001, Bell *et al.* 2001; Zhang *et al.* 2003). A close relationship between *Sambucus* and *Adoxa*, which also had been hypothesized previously (e.g., Eichler 1875), is strongly supported by morphological apomorphies, especially compound leaves, extrorse anthers, vessel elements with simple perforations, and *Adoxa*-type embryo sac development (Donoghue 1983; Judd *et al.* 1994; Backlund and Donoghue 1996). Many subsequent analyses—of chloroplast, mitochondrial, and nuclear DNA datasets—have reached the same conclusion. They have also shown, as expected based on morphological apomorphies (e.g., herbaceous habit, nectaries of multicellular hairs, bifid stamens from a single primordium; Donoghue *et al.* 2001, 2003) that *Tetradoxa* and *Sinadoxa* are closely related to *Adoxa*, with *Sinadoxa* sister to *Tetradoxa* plus *Adoxa* (Winkworth *et al.* 2008a; Tank and Donoghue 2010; Soltis *et al.* 2011; Fan *et al.* 2018; Wang *et al.* 2020; Xiang *et al.* 2020; Lee *et al.* 2021). To my knowledge, no contradictory phylogenetic results have been published over the past several decades.

As noted in the introductory section of this paper, Judd *et al.* (1994) provided the first pre-*PhyloCode* minimum-clade phylogenetic definition for *Adoxaceae*, and this was followed-up by Donoghue *et al.* (2001), who added species specifiers. The formal definition provided here completely aligns with these early definitions. Importantly, *Adoxaceae* as defined here differs from most usage in the pre-phylogenetic era. Cronquist (1981) and Takhtajan (1980), for example, included only *Adoxa moschatellina* in their *Adoxaceae* (Fig. 1). Of the major authors of angiosperm classification systems at that time, Thorne (1983) was the only one to expand *Adoxaceae* to include *Sambucus* and *Viburnum*, based in part on personal communications with me at that time, and on the findings reported in Donoghue (1983). Thorne (1983) further recognized *Adoxoideae* for *Sambucus* plus *Adoxa*, and *Viburnoideae* for *Viburnum*.

In the first APG classification of angiosperms (APG, 1998), *Adoxaceae* was not placed in *Dipsacales*; its relationships were considered uncertain within the *Euasteridae*. It is unclear whether the authors at that time viewed *Viburnum* and *Sambucus* as part of *Adoxaceae* or as part of *Caprifoliaceae* (where both had been placed in the systems of Cronquist, Takhtajan, and others). In APG II (2003) and onward (APG III in 2009, and APG IV in 2016), *Adoxaceae*, presumably now including *Viburnum* and *Sambucus*, was placed in *Dipsacales*. However, in APG IV (2016) it was noted that *Viburnaceae* was under consideration for conservation under the *International Code of Botanical Nomenclature* (ICBN).

In the meantime, *Adoxaceae*, as circumscribed here, was adopted in major plant systematics textbooks (e.g., Judd *et al.* 2002 and subsequent editions; Simpson 2006), in the widely used Angiosperm Phylogeny Website taxonomy (Stevens 2001 and onward), and in the APG classifications, and this use spread in the taxonomic literature (e.g., Backlund and Bittrich 2016). It also spread in papers on a wide range of topics, including anatomy, paleobotany,

physiology, dispersal and pollination biology, ecology, and genomics (papers with *Adoxaceae* in their title include: Jacobs *et al.* 2010; Huang *et al.* 2012; Schmerler *et al.* 2012; Weber *et al.* 2012; Chatelet *et al.* 2013; Clement *et al.* 2014; Lens *et al.* 2016; Park *et al.* 2019; Chen *et al.* 2021; Zhong *et al.* 2021; Sinnott-Armstrong *et al.* 2023). This rise in use is shown in Fig. 4. It is against this backdrop of what has become traditional use that the unfortunate decision was taken by the ICN General Committee to mandate the use of the very rarely used *Viburnaceae* in place of the very widely used *Adoxaceae*. In contrast, the name *Adoxaceae* is applied here to this clade based on frequency of use, as recommended by the *PhyloCode* (Rec. 10.1A).

Caprifoliaceae A. L. Jussieu, 1789 [M. J. Donoghue], converted clade name

Registration Number: 1201.

Definition: The smallest crown clade including *Lonicera xylosteum* Linnaeus 1753, *Diervilla lonicera* Miller 1768, *Linnaea borealis* Linnaeus 1753, *Valeriana pyrenaica* Linnaeus 1753, and *Dipsacus fullonum* Linnaeus 1753 (see Figs. 2, 5). This is a minimum-crown-clade definition. These specifiers are the type species of their respective genera and were those used by Donoghue *et al.* (2001) in their pre-*PhyloCode* phylogenetic definition of *Caprifoliaceae*, with the one exception that *Lonicera caprifolium* L. is here replaced by *Lonicera xylosteum* L., which, despite earlier confusion (Britton and Brown 1913), is the type species for *Lonicera* (see Ferguson 1966; Hara 1983).

Etymology: The name *Caprifoliaceae* is based on *Caprifolium*, a synonym of the modern genus name *Lonicera* (for the honeysuckles). *Caprifolium* is derived from the Latin words “caper,” meaning goat, and “folium”, meaning leaf. It is unclear what “goat leaf” refers to, although it has been noted that goats favor *Lonicera* leaves.

Reference Phylogeny: Soltis *et al.* (2011), Figure 2G, is here selected as the reference phylogeny (see Fig. 5 of this article). This is used as the reference phylogeny in the definitions of *Dipsacales*, *Adoxaceae*, and *Caprifoliaceae*, and it is justified for all three in the protologue of *Dipsacales* above. Specifically in reference to *Caprifoliaceae*, Soltis *et al.* (2011) included multiple representatives of all major subclades of *Dipsacales* shown in Figure 3 and found very strong support for *Caprifoliaceae* as defined here. Monophyly of *Caprifoliaceae* has been confirmed in all other phylogenetic analyses published over the past several decades (Bell *et al.* 2001; Donoghue *et al.* 2001; Zhang *et al.* 2003; Winkworth *et al.* 2008a, b; Tank and Donoghue 2010; Jacobs *et al.* 2011; Fan *et al.* 2018; Wang *et al.* 2020; Xiang *et al.* 2020; Lee *et al.* 2021).

Composition: *Caprifoliaceae*, as here defined, includes ~900 species assigned to the major subclades listed below. In Figure 3 these are recognized at the family level (following Backlund and Pyck 1998), but here I adopt the corresponding subfamily names used in Stevens *et al.* (2001 and onward): *Diervillioideae* (~16 species), including *Diervilla* and *Weigela*; *Caprifolioideae* (~170 species), including a core clade of *Leycesteria*, *Lonicera*, *Symphoricarpos*, and *Triosteum*, and the more distantly related *Heptacodium* (1 species); *Linnaeoideae* (~20 species), including *Abelia*, *Diabelia*, *Dipelta*, *Kolkwitzia*, *Linnaea*, and *Vesalea*; *Morinoideae* (~14 species), including *Acanthocalyx*, *Cryptothladia*, and *Morina*; *Valerianoideae* (~375 species), including *Centranthus*, *Fedia*, *Nardosstachys*, *Patrinia*, *Plectritis*, *Valerianella*, and *Valeriana s.l.* (i.e., including South American segregates *Astrephia*, *Belonanthus*, *Phylactis*, *Porteria*, and *Stangea*; Bell and Donoghue 2005b), and *Dipsacoideae* (~300 species), including *Bassecoia*, *Cephalaria*, *Dipsacus*, *Knautia*, *Lomelosia*, *Pseudoscabiosa*, *Pterocephalus*, *Pterocephalidium*, *Pterocephalodes*, *Pterothamnus*, *Pycnocomon*, *Scabiosa*, *Sixalix*, and *Succisa*, and the more distantly related *Triplostegia* (1 species) (Figs 1–3). The position of *Zabelia* (~8 species), which was initially considered a section within *Abelia* (Rehder 1911; Makino 1948), remains uncertain. In Soltis *et al.* (2011), and in several other studies (e.g., Jacobs *et al.* 2011; Wang *et al.* 2020; Xiang *et al.* 2020), it is linked directly with *Morinoideae*, but other relationships have been inferred, including as sister to the clade including *Morinoideae*, *Valerianoideae*, and *Dipsacoideae* (e.g., Lee *et al.* 2021).

Compared to pre-phylogenetic circumscriptions (e.g., Cronquist 1981; Takhtajan 1980), *Caprifoliaceae* here excludes *Sambucus* and *Viburnum* (now in *Adoxaceae*, see above), and otherwise greatly expands *Caprifoliaceae s.s.* to include the former families *Morinaceae*, *Valerianaceae*, and *Dipsacaceae*. Whereas members of pre-phylogenetic *Caprifoliaceae* were shrubs and small trees (except for the herbaceous *Triosteum*), the new circumscription includes a large, nested clade (the *Valerina* clade of Donoghue *et al.* 2001) of largely herbaceous plants (including the former *Morinaceae*, *Valerianaceae*, and *Dipsacaceae*). With this expansion, *Caprifoliaceae* now includes plants with a host of other derived traits, including compound leaves, pappus-like calyces in *Valerianoideae*, and the epicalyx of *Dipsacoideae*. In addition, a much wider range of biomes is occupied. Under pre-phylogenetic taxonomies,

species of *Caprifoliaceae* were viewed as largely occupying temperate forests around the Northern Hemisphere, initially in the Old World, but extending multiple times into the New World. Many *Valerianoideae* species occupy alpine habitats, with *Valeriana*, for example, having radiated extensively in the high Andes of South America (Bell and Donoghue 2005b). Species of *Morinoideae* are mainly also in high elevation and alpine habitats in Asia and extending into southeastern Europe (Bell and Donoghue 2003). Many *Dipsacoideae* species, which are native only to the Old World, have entered arid biomes in Asia, Europe, and Africa (Carlson *et al.* 2009).

Diagnostic Apomorphies: Character polarities near the base of *Dipsacales* have been difficult to assess owing to uncertainties concerning outgroups and the great ages of the relevant clades (see Comments for *Dipsacales*). However, referring here primarily to *Paracryphiaceae* as the most likely relatives of *Dipsacales* (Tank and Donoghue, 2010; Soltis *et al.* 2011), and *Adoxaceae* as sister to *Caprifoliaceae* within *Dipsacales*, the following are probable apomorphies for *Caprifoliaceae*: bilaterally symmetrical flowers; relatively long tubular corollas; a long style with a capitate stigma; a fully inferior ovary, constricted beneath the calyx; nectar production by unicellular hairs on the inside of the corolla tube; large spherical pollen grains; and pollen exine with a complete and typically echinate tectum. With less certainty, additional apomorphies may include lateral connections between the main petal veins (Backlund and Donoghue 1996), reduced carpel vasculature, pericyclic phellogen, a truncated polytelic inflorescence, sagittate anthers, generally smaller chromosomes, and biparental plastid inheritance (Hu *et al.* 2008). Of these, the traits that most readily distinguish *Caprifoliaceae* from *Adoxaceae* are overall flower size and symmetry (although small, radial flowers have evolved several times independently within *Caprifoliaceae*), relatively long styles, and capitate stigmas.

Synonyms: None.

Comments: Donoghue (1983) questioned the monophyly of *Caprifoliaceae* in the broad sense, suggesting that *Viburnum* and *Sambucus* were more closely related to *Adoxa* (the sole member of the pre-phylogenetic *Adoxaceae*), and that *Caprifoliaceae* in the narrower sense (i.e., excluding *Viburnum* and *Sambucus*) may be more closely related to *Dipsacaceae* and *Valerianaceae*. These hypotheses were supported by Bell *et al.* (2001) and Donoghue *et al.* (2001). Based on these findings, Donoghue *et al.* (2001) phylogenetically defined *Linnina* for the smallest clade including *Linnaea* and its relatives (the pre-phylogenetic *Linnaeae* Dumortier; see Hara 1983) plus the pre-phylogenetic *Morinaceae*, *Dipsacaceae*, and *Valerianaceae* (Fig 3). Notably, *Linnina*, as so defined, includes some of the pre-phylogenetic *Caprifoliaceae*, which are woody plants, and three major clades of predominantly herbaceous species. *Linnina* is supported by several strong morphological apomorphies (Judd *et al.* 1994; Backlund and Donoghue 1996; Donoghue *et al.* 2003): supernumerary inflorescence bracts, a reduction from five to four stamens, a reduction to just one nectary in the corolla tube, the abortion of two of the three carpels, leaving one fertile carpel containing one seed at maturity, and production of an achene fruit. Within *Linnina*, Donoghue *et al.* (2001) phylogenetically defined a strongly supported *Valerina* clade including the pre-phylogenetic *Morinaceae*, *Dipsacaceae*, and *Valerianaceae* (Fig 3). These are united by several morphological apomorphies, including simple vessel perforations, the production of monoterpenoids, reduced endosperm, and usually highly modified calyx lobes (Judd *et al.* 1994; Backlund and Donoghue 1996; Donoghue *et al.* 2003).

The phylogenetic definition provided here attaches *Caprifoliaceae* to node B in Fig. 1 (see Fig. 2). This is arguably the most strongly supported and most distinctive clade within *Dipsacales* based on morphological and molecular data but, ironically, was never recognized in pre-phylogenetic classification systems. This broad circumscription of *Caprifoliaceae* now appears to have become widely accepted and thus traditional. In part, this is a function of having been adopted in a popular textbook (Judd *et al.* 2002, and subsequent editions), in the APG system, and in the Angiosperm Phylogeny Website taxonomy (Stevens *et al.* 2001 and onward). APG II (2003) adopted this circumscription of *Caprifoliaceae* but also made note of an alternative that recognizes six families, following Backlund and Pyck (1998; see Fig. 3). APG III (2009) simply adopted the broad circumscription of *Caprifoliaceae* noting that it was by then widely used, and this was retained in APG IV (2016). It should be noted that the classification of Backlund and Pyck (1998) is similar to pre-phylogenetic systems in leaving unnamed the clade that is here named *Caprifoliaceae* (Fig. 3). My intention is to provide, in a separate paper, phylogenetic definitions for the major clades within *Caprifoliaceae*, including the *Morinoideae*, *Valerianoideae*, and *Dipsacoideae*, as well as the *Linnina* and *Valerina* clades of Donoghue *et al.* (2001, 2003).

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