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Cornus, Benthamidia, Dendrobenthamia, and *Swida*: Oh My – Making Taxonomy Less Taxing

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Summary

Different opinions among taxonomists lead to differences in classification schemes and result in frequent name changes and confusion in communication. New evidence from phylogenetic studies using genetic/genomic data have also led to the need for reclassification of many groups, leading to new names being given to many previously familiar plants. Frequent name changes not only lead to misunderstandings in communications but also cause problems in data storage and information retrieval. We need new plant classification systems that are resilient to name changes resulting from the splitting of large genera or families, lumping of small genera, or due to personal opinions on plant characteristics instead of new names being frequently proposed, accepted, and then rejected. Examining the highly controversial taxonomy and classification history of dogwoods demonstrates evident limitations of the traditional Linnaean System that organizes taxa hierarchically from the kingdom to the species level and gives each species a unique two-word Latin name. The limitations present the need for a classification system that is rank-free and aims to make taxonomy and names more stable. PhyloCode is an alternative to the traditional Linnaean system that names taxa/clades without assigning ranks and can

be used concurrently with the Linnaean system. The Fundamental ideas about PhyloCode will be introduced and a PhyloCode-based classification of dogwoods is proposed.

INTRODUCTION

Taxonomic Chaos in the Dogwood Genus *Cornus* L. and Major Limitations of the Traditional Linnaean Classification System

The dogwood genus *Cornus* was first published by Linnaeus (1753) who included five species *C. florida* L., *C. mas* L., *C. canadensis* L., *C. suecica* L., and *C. sanguinea* L. **(Fig. 1**). These plants are fundamentally similar in vegetative and reproductive morphology, such as in their simple, opposite leaves with entire margin, arched lateral veins, and appressed two-armed hairs, small 4-merous flowers with parts that are free, a hypanthium fused with a 2-carpellate ovary each with a single pendulous ovule, and a fleshy drupaceous fruit. Later, additional species sharing these common features were discovered and added to the genus, including two alternate-leaved species, *Cornus alternifolia* L. f. and *C. controversa* Hemsl. The genus now consists of approximately 55-60 species (Xiang and Boufford, 2005; Murrell and Poindexter, 2016; Xiang et al, 2006).

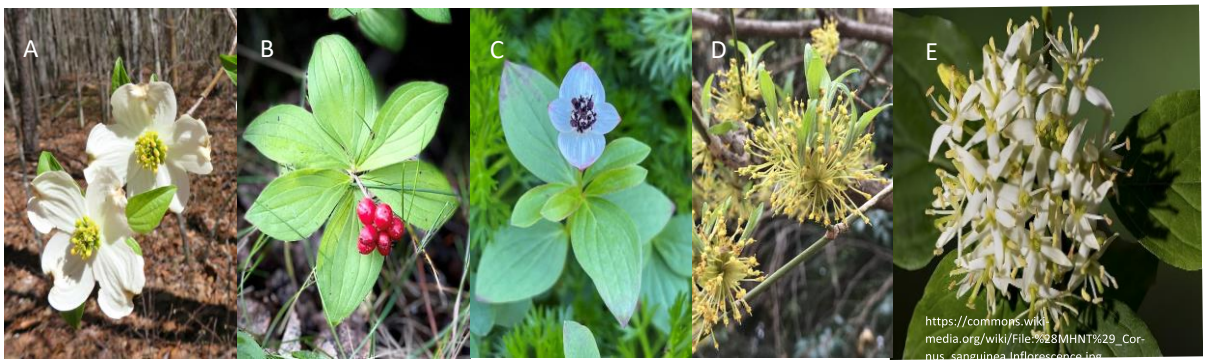

Figure 1. Species included by K. Linnaeus in *Cornus* in Sp. Pl. 1: 117, 1753. A-E: *C. florida* L., *C. canadensis* L., *C. suecica* L., *C. mas* L., and *C. sanguinea* L.

Despite the similarities, the original five species of *Cornus* differ dramatically in some detailed morphology of the inflorescence and fruit (**Fig. 2**), as detailed below. *Cornus florida*, the flowering dogwood tree, bears four large, petaloid bracts subtending a capitulum/head inflorescence. Species like *C. florida* are often referred to as the Big-Bracted Dogwoods (BB dogwoods). The BB dogwoods now have 9 species and nine subspecies species disjunctly distributed in eastern Asia and North America, extending to Mexico and Central America. The three American species bear simple, red fruits in clusters. *Cornus florida* occurs in the eastern U.S. with subspecies disjunct in Mexico, *C. disciflora*, whose bracts fall

off before expansion, extends from Mexico to Costa Rica, while *C. nuttallii*, whose bracts vary from 4 to 6, is restricted to mountains of the Pacific Northwest. The eastern Asian BB dogwoods include the kousa dogwood, *C. kousa* H. Bürger ex Hance and the likes, which make compound red fruits. They occur in most parts of China, except in the northwest, and adjacent countries to the northeast and southwest (Du et al., 2023a, b). *Cornus canadensis* and *C. suecica*, the dwarf cornels or bunchberries, are rhizomatous perennial herbs that produce minute, condensed, dichasial inflorescences subtended by four, enlarged petaloid bracts and simple red fruits in clusters. They are often referred to as the Dwarf Dogwoods (DW group). They now include four disjunct species in circumboreal regions and in the high mountains of Myanmar (Burma) (Wahlsteen et al., 2020).

Figure 2. Examples of inflorescence and fruit variation in *Cornus* L. 1. Determinate head with petaloid bracts; 2. Determinate umbel with non-petaloid bracts; 3. Corymbose compound cymes without apparent bracts; 4. minute compound dichasia with petaloid bracts; 7. compound/multiple fruit. Remainders: simple fruits in clusters.

In contrast, *C. mas*, the European cornelian cherry, has flowers in umbels and distinct red elongate fruits in clusters, subtended by four small, non-petaloid bracts. The cornelian cherries (CC group) now include six medicinally valuable species in eastern Asia (*C. officinalis* Sieb. & Zucc., *C. chinensis* Wangerin, *C. eydeana* Q. Y, Xiang & Y. M. Shui, Europe (*C. mas*), western North America (*C. sessilis* Torr. ex Durand), and Africa (*C. volkensii* Harms) (Xiang et al., 2003; refs). *Cornus sanguinea*, the blood twig dogwood, represents a group of shrubs and trees that bear elongated compound, corymbose or paniculate cymes that have rudimentary and early deciduous bracts and simple, blue, white, or black fruits **(Figs. 1, 2**). This group, often referred to as the Blue- or White-fruited Dogwoods (BW Group), is the most diverse, containing the remaining species of the genus. Interestingly, the evident differences in inflorescences and fruits plus additional variation within the BB, CC, and BW groups were emphasized variously among subsequent taxonomists. As a result, the Linnaean concept of *Cornus* has been split

into multiple genera by some (e.g., Hutchison, 1942; Pojakova, 1950) whereas others recognized the morphological subgroups as subgenera or sections within *Cornus* (e.g., Wangerin, 1990; Xiang, 1987; Ferguson, 1966). Some better-known genera that have been segregated from *Cornus* include *Swida* Opiz (all BW dogwoods), *Bothrocaryum* (Koehne) Pojark. (the alternate-leaved BW dogwoods), *Thelycrania* (Dumort.) Fourr. (all opposite-leaved BW dogwoods), *Afrocrania* Hutch. (African Cornelian Cherry), and *Macrocarpium* Nakai (CC group; synonym of *Cornus* s. s.), *Chamaepericlymenum* Hill (the DW dogwoods), *Benthamidia* Spach. (all BB dogwoods), *Cynoxylon* Raf. (all BB dogwoods or American BB dogwoods), *Discocrania* (Mexican 'BB' dogwood) and *Dendrobenthamia* (Asian BB dogwoods). Each author differed in the circumscriptions and compositions of genera or infrageneric subgroups (subgenera or sections) in one way or another (see Hutchinson, 1942; Hara, 1948; Pojarkova, 1950; Ferguson, 1966; discussion in Eyde, 1987, 1988; Xiang et al., 1993, 1996).

Therefore, a species of dogwood often has more than one name and depending on personal preferences, it can be labelled or annotated with different names, which has resulted in confusion and obstacles in communication and information retrieval from herbaria and databases. For instance, in the herbaria of Smithsonian Institutions and Harvard University, specimens of the giant pagoda dogwood are filed under *Cornus controversa*, while in China and European countries, some herbaria may file the species under *C. controversa*, while others may file it under *Swida controversa*, still others may file it under *Bothrocaryum controversum*, or under all these names, based on annotations on the specimens. One may not be able to find all specimens of the species in an herbarium if he/she looks only for specimens under one name. Similarly, one may not find all information for the species in a database if only one name is used in searching. The flowering dogwood tree has been called *Cornus florida* L, *Benthamidia florida* (L.) Spach., or *Cynoxylon floridum* (L.) Raf. ex B.D. Jackson, and the kousa dogwood has been called *Cornus kousa* Hance, *Benthamia japonica* Sieb. & Zucc., *Benthamidia japonica* (Sieb. & Zucc.) Hara, *Cynoxylon japonica* (Sieb. & Zucc.) Nakai, or *Dendrobenthamia japonica* (Sieb. & Zucc.) Hutch. at different times in different places. In America, the flowering dogwood tree has long been called *C. florida* until recently (see Weakley et al., 2022). Due to the change of classification to recognize the four major clades of *Cornus* revealed in phylogenetic studies (Xiang et al., 2006; 2011; Fu et al., 2019; Thomas et al., 2021; Du et al., 2023) as four distinct genera by Weakley et al. (2022), the name of the flowering dogwood tree was changed to *Benthamidia florida* (L.) Spach.).

Clearly, the taxonomic controversy and species name variations in *Cornus* are results of differences in personal opinions and compliance to the rules of a rank-based nomenclature. Taxonomic ranks (Division, Class, Order, Family, Genus, Species and the ranks below them; names of higher ranks above the genus level need to have prescribed endings) are fundamentally arbitrary and assigned subjectively by authors. In a well-resolved phylogeny, two authors can derive contrasting classification schemes giving different ranks at a given node **(Fig. 3)**, resulting in changes of names due to the prescribed name endings of ranks or difference in assigning the genus rank.

Taxa of the same rank are often thought to be equivalent and comparable in some ways, but not in many ways (e.g., ages, diversity level, or ecological breadth). For example, the ages of flowering plant families and orders currently recognized varies widely (Stevens. 2001 onwards; Kumar et al, 2022; Santiago et al., 2020). Naively treating taxa at the same rank as equivalents can lead to flawed science or wrong actions in biodiversity conservation. Clearly, the need to maintain the hierarchy of the ranks leads to instability of names (names being changed without good reasons).

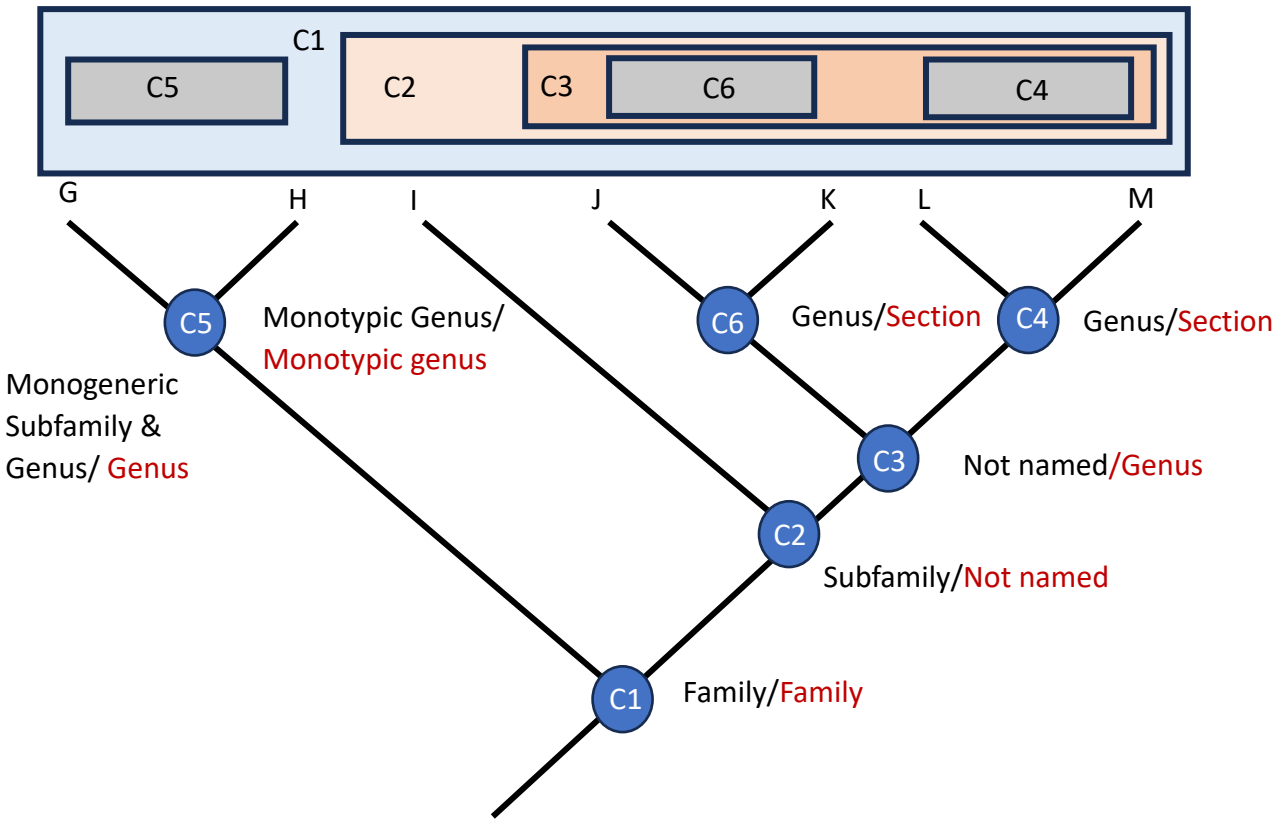

Figure 3. A hypothetical phylogeny showing clades C1 through C6 which are hierarchically nested within one another. Clade C1 consists of Clade C2 and C5; Clade C2 consists of species I and Clade C3 while Clade C5 consists of species G and H. Clade C3 consists of Clade C6 and Clade C4, each consists of two species, J and K in clade C6 and L and M in Clade C4. The classification with reference to this phylogeny using PhyloCode will give a name to each of these clades without assigning a rank. In traditional rank-based classification, authors may differ in the rank assignments of clades (black vs red illustrating one of the many ways of possible different classification schemes), leading to name changes.

In addition to these issues, the traditional Linnean nomenclature is limited by ranks to suffice in classifying the tree of flowering plants, not mentioning the tree of life that has millions of branches. Given these limitations and disadvantages, a rank-free nomenclature would be desirable to resolve the rank-associated problems.

PhyloCode for a Rank Free Classification and Stabilizing Names

An alternative method to the traditional Linnaean System is the PhyloCode (http://phylonames.org/code/), which eliminates the rank associated problems (de Queiroz and Cantino, 2020). The PhyloCode is a set of principles, rules, and recommendations governing phylogenetic nomenclature and a system for naming taxa by explicit reference to phylogeny (the evolutionary history of organisms drawn as a branching line pattern or called phylogenetic tree to show ancestor-descendent relationships, e.g., **Fig. 3**). In contrast to the Linnaean system, PhyloCode attaches names to clades (or branches of the tree) without assigning ranks, such as taxa C1, C2, and C3 in Figure 3, each representing a progressively less inclusive clade (i.e., a monophyletic group or an ancestor and all its descendants). It is a system of nomenclature developed to explicitly name taxa by reference to phylogeny, using 'phylogenetic definitions' to delineate the clade with 'specifiers.' The phylogenetic definitions of a named clade can be node-based, apomorphy (derived features)-based, or branch- or stem-based (**Fig. 4**). For example, in **Figure 4**, X is for the least inclusive clade containing specifiers B and C. It is node based, while Y is for the most inclusive clade exhibiting the red character synapomorphic (derived and shared) with that in B and/or C, which is apomorphy based, and Z is for the most inclusive clade containing C but NOT A, which is branch based.

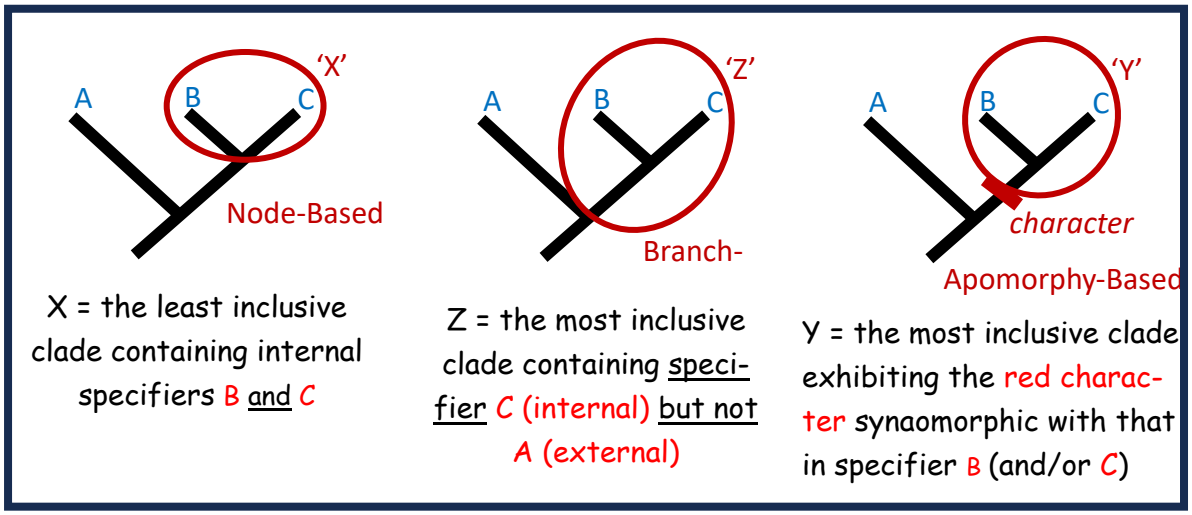

Figure 4. Three forms of phylogenetic definitions and specifiers. Taxa 'X', 'Y', and 'Z' are clades defined using the node-based, branch-based, and apomorphy-based definitions, respectively. Apomorphy: derived feature; Synapomorphy: shared, derived features.

These different definitions allow precision and enable differentiating a crown clade from a stem clade that contain the exact same species-membership. Application of the definitions with care can avoid future name changes if specifiers are carefully chosen in the phylogenetic definitions. In this system, future name changes may occur, but they will be due to changes in our understanding of phylogeny or relationships, rather than arbitrary decisions on taxonomic rank. Here are three examples illustrating the naming of angiosperm clades based on different phylogenetic definitions

with PhyloCode in reference to the phylogeny (APG IV, 2016). The *Asteridae* A. Takhtajian 1967 [R. G. Olmstead & W. S. Judd 2020] clade is 'least inclusive clade containing *Lamium purpureum* Linnaeus 1753 (Lamiidae/Lamiales), *Cornus mas* Linnaeus 1753 (Cornales), *Aster amellus* Linnaeus 1753 (Campanulidae/Asterales), and *Arbutus unedo* Linnaeus 1753 (Ericales)'. It is a node-based definition or a minimum/smallest-crown clade definition. The *Superrosidae* D.E. Soltis, S. Smith & N. Cellinese 2011 [W. S. Judd, D. E. Soltis & P. S. Soltis 2020] clade is the 'maximum clade containing *Rosa cinnamomea* L. 1753 (Rosidae/Rosales) but not *Aster amellus* L. 1753 (Asteridae/Asterales)'. Here one internal and one external specifier were used in the definition. It is a branch-based definition, or a maximum/largest-crown clade definition. The *Tricolpatae* P. D. Cantino, J. A. Doyle, S. W. Graham, W. S. Judd and R. G. Olmstead 2007 [Donoghue, M.J., J.A. Doyle, and P.D. Cantino 2020] clade is defined as 'The most inclusive clade exhibiting tricolpate (or derivative) pollen grains synapomorphic with those found in *Platanus occidentalis* Linnaeus 1753 (Eudicotyledoneae). A tricolpate pollen grain is one having three elongate, furrow-like apertures (colpi) located at and oriented perpendicular to the equator.' (RegNum, https://phyloregnum.org/?). It is an apomorphy-based definition with one internal specifier and an apomorphy.

The PhyloCode focuses squarely on reflecting phylogenetic relationships and eliminates the reliance of taxonomic ranks. It is designed to allow concurrent uses with the rank-based code to provide an alternative system for governing the application of both existing and newly proposed names. The code currently only governs the names of clades; species names are still governed by traditional codes. However, in PhyloCode, 'the first part of the species binomen is not interpreted as a genus name but simply as the name of a taxon that includes that species' (Chapter X, Article 21.2, PhyloCode http://phylonames.org/code/articles/21/). There have been proposals for a completely rank-free PhyloCode without the species rank, which is also considered arbitrary. The proposal suggested using SNaRC (Smallest Named Registered Clade) in the place of species. In such a system, all taxon names are uninominal (Gellinese et al., 2012; Mishler and Wilkins 2018; Mishler, 2022) with the smallest named clade treated like other levels and given a formal (uninominal) name registered in a database. However, it is still controversial within the PhyloCode community whether the rank of species should be removed. Mishler (2022) argued that a complete rank-free system better serves today's research in ecology, evolution and systematics as well as conservation management.

The ideas of PhyloCode initially developed in several key papers in the 1990s (de Queiroz and Gauthier, 1990, 1992, 1994; For more literature, see: http://phylonames.org/literature/). It has gone through some hot debates (for Critiques, see http://phylonames.org/literature/#critiques, and Replies to Critiques, see http://phylonames.org/literature/#replies). PhyloCode (http://phylonames.org/code/articles/20/; de Queiroz and Cantino 2020) is a product of 30 years of thought by Kevin de Queiroz and Philip Cantino. The publication of the *PhyloCode* was accompanied by the volume *Phylonyms* (de Queiroz et al., 2020), an implementation of PhyloCode thatdocuments the real-world uses of PhyloCode. An online registration database

'*RegNum'* for names created using the rules of the PhyloCode, including those in '*Phylonyms*,' has been created. Taxonomists do not have to name all clades on the phylogeny of their study organisms, but only name clades that are well supported by evidence. Clades with uncertainty can be assessed by future phylogenetic studies and can be named when new evidence is available.

In summary, the following quotes speak well of the need of adopting PhyloCode in taxonomy in the genomic era when phylogeny can be robustly determined using genomic data.

"The traditional codes of nomenclature were first developed long before there was any knowledge of evolution and phylogeny. In this context, unfortunately, emphasis was placed on taxonomic ranks. The PhyloCode was developed specifically to connect nomenclature to evolution and phylogeny, and it works better (e.g., eliminating name changes based on arbitrary rank changes) in the current era where biologists of all types are focused on evolution and phylogenetic relationships. This is especially important as systematists have more important work to do as biodiversity is being lost. We should not be wasting our time on changing names based on outdated nomenclatural procedures that are tied to the wrong metric — that is, they are tied to ranks instead of to phylogenetic relationships." (Michael Donoghue, Yale University).

"Why do we keep trying to put what we know about evolution in a system that wasn't built to reflect it?" (Pamela Soltis, University of Florida).

Dogwood Phylogeny and PhyloCode-Based Classification

Several phylogenetic studies have been conducted in the past to elucidate species relationships and dating the divergence of clades, each varied in the scale of taxon and data sampling (Xiang et al., 1996, 1998, 2006, 2011; Fan et al., 2003; Fu et al, 2019; Thomas et al., 2020; Du et al., 2023). The most recent comprehensive phylogenetic study of the *Cornus* used three genomic datasets with the most complete species sampling and derived a robust phylogenetic tree of the dogwoods with estimates of the age of clades (Du et al., 2023). In the intention of stabilizing the naming of groups of dogwoods, names were proposed for clades with strong support using preexisting names without assigning a rank, following PhyloCode (**Fig. 5**). Minimum clades of the BB, CC, DW, and BW groups were named *Benthamidia, Macrocarpium, Arctocrania* and *Swida*, respectively. Within *Benthamidia*, the American clade and the Asian clade were named *Cynoxylon* and *Syncarpea*, respectively; within the *Swida* clade, the three subclades previously treated as genera were named *Yinquania, Mesomora* and *Kraniopsis*; all are preexisting names. Formal registration of these names and the phylogenetic definitions of the clades is in preparation (Du et al., in revision). In a practical way, all species of dogwoods can keep their names under *Cornus*. In nurseries and botanical gardens, the species can be labelled with reference to their respective clades withing *Cornus*. For example, one can label *Cornus florida* as *Cornus florida* L. (*Benthamidia/Cynoxylon*; Cornaceae) and *Cornus controversa* Hemsl. (*Swida/Mesomora*, Cornaceae) to indicate the clade to which they belong.

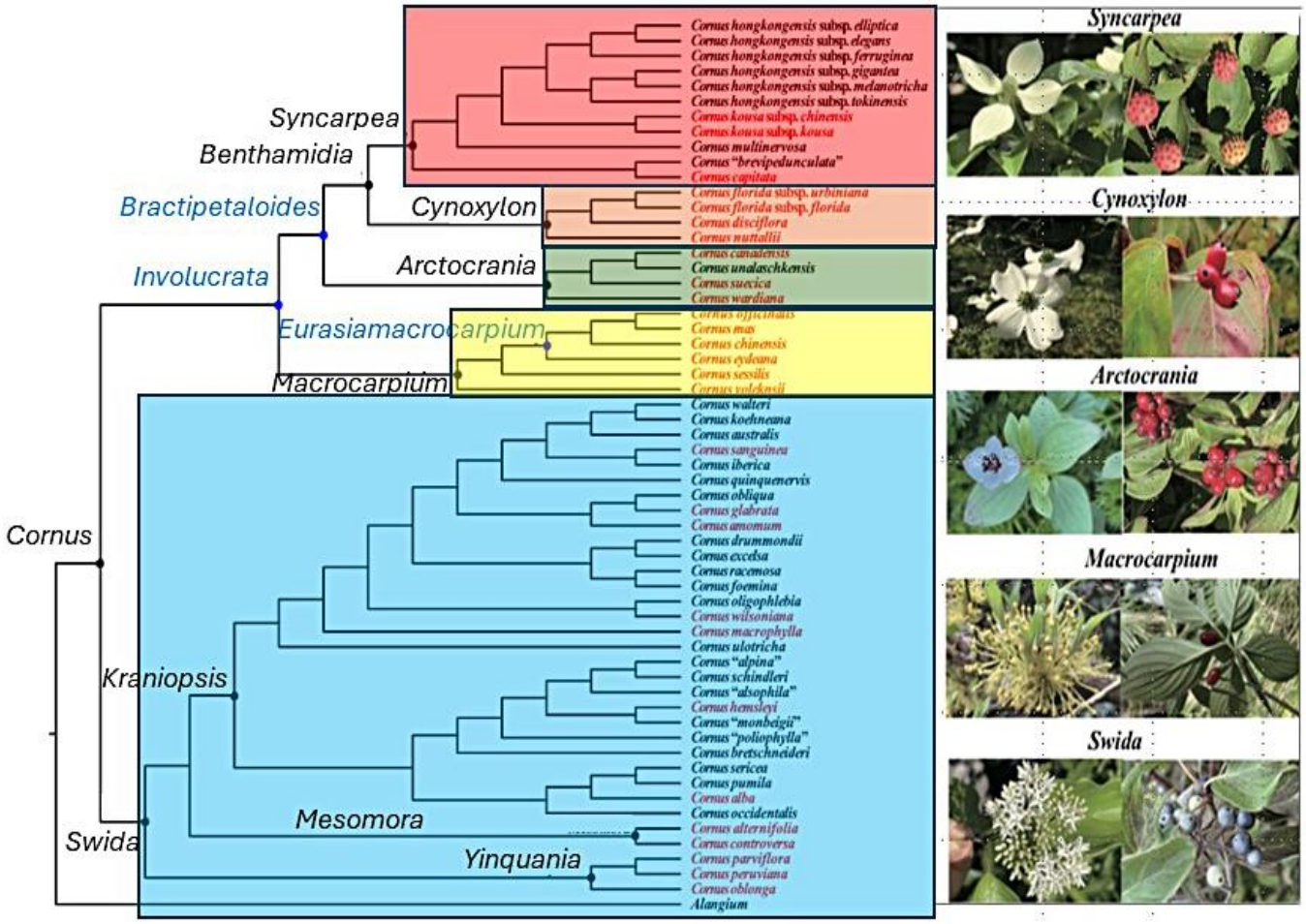

Figure 5. Phylogeny of *Cornus* L. based on three sets of genomic data from Du et al., (2023). PhyloCode-based hierarchical classification of the *Cornus* clade in reference to the phylogeny is shown. Clades marked with small dots are named using preexisting names except those in blue. Shaded clades are those shown with images at the right of the tree. Figure is modified from Du et al., 2023 in American Journal of Botany **https://doi.org/10.1002/ajb2.16116**

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