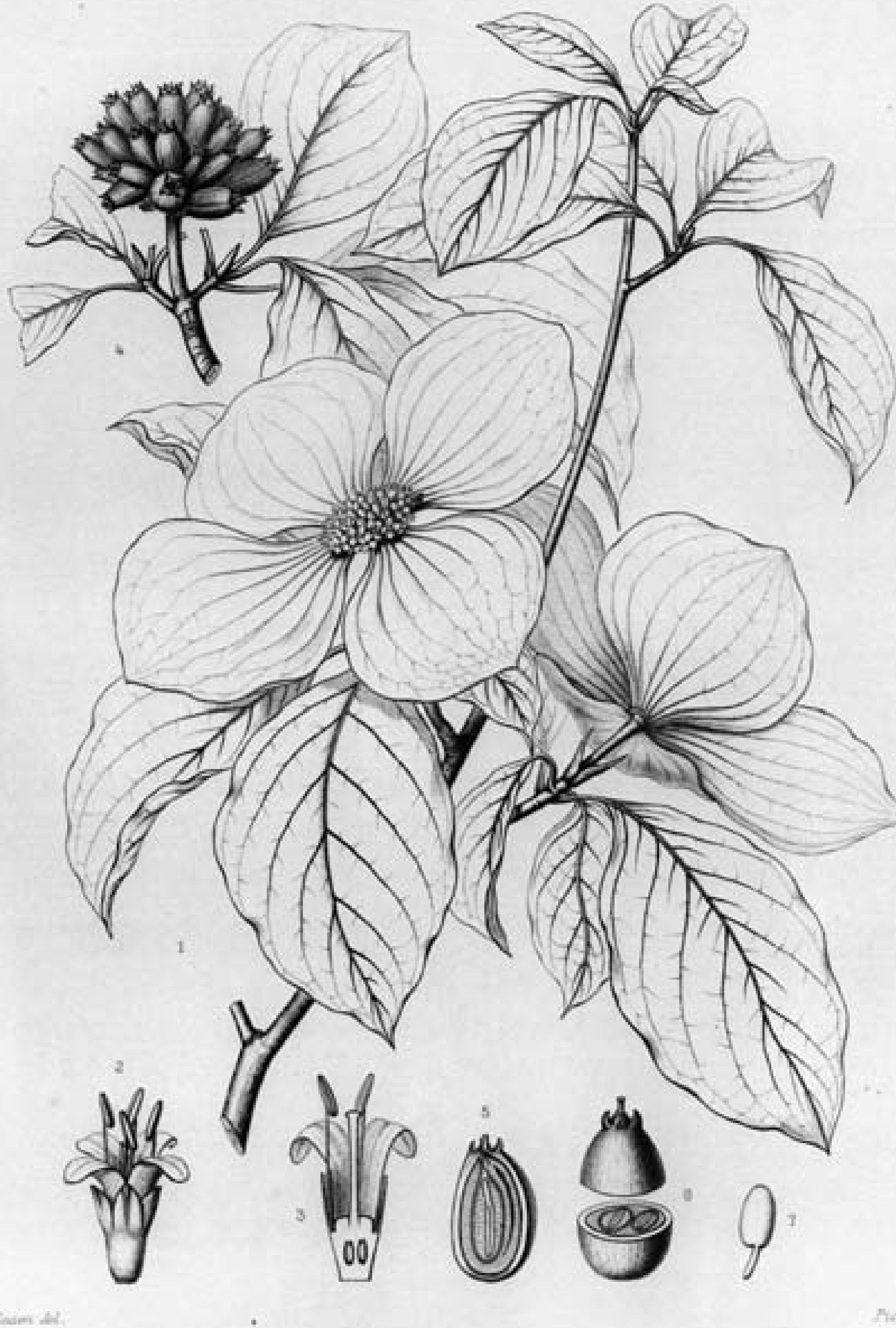


C.E. Faxon del. Picart sc.

CORNUS NUTTALLII, Aud.

A. Riocreux direx. Imp. R. Taneur, Paris

RESEARCH REPORT

The Case for Monkey-Mediated Evolution in Big-Bracted Dogwoods

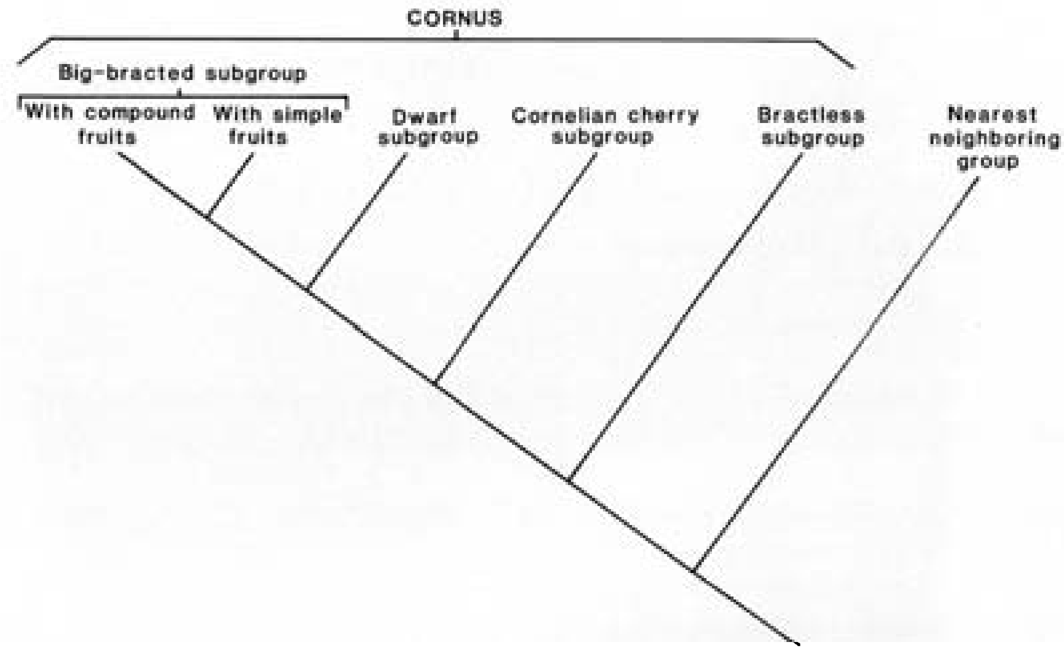
Richard H. Eyde

Because New World monkeys are blind to red and live only in warm regions, American big-bracted dogwoods produce only simple fruits

Say "dogwood" to anyone from eastern North America and the plant that comes to mind is *Cornus florida*, called flowering dogwood because four petal-like bracts beneath each tight flower cluster make a cluster look like one big showy flower. Dogwoods with such blossoms are a minority. Most of the 50-plus species in the dogwood genus—*Cornus* in the wide Linnaean sense—bear broadly branching flower clusters in which bracts are rudimentary or lacking. Dwarf cornels—*C. canadensis* and two similar species—have showy-bracted blossoms and tight clusters, but the bracts, like the plants themselves, are small. Besides *C. florida*, the subgroup with big-bracted clusters includes *C. nuttallii* of western North America and *C. disciflora*, a mountain tree of Mexico and Central America. (The bracts of *C. disciflora* are like those of *C. florida* and *C. nuttallii* only in the bud; they wither and fall off when buds turn into blossoms.) There are big-bracted dogwoods in Asia, too. Of the 19 species recognized in recent treatments (Poyarkova, 1950; Fang, 1953; Hu, 1980; Hu and Soong, 1981), only *C. kousa* is widely known and grown in North America.

Big-bracted dogwoods, American and Asian, had a common evolutionary origin: their chemistry attests to that (Bate-Smith *et al.*, 1975), as do serological experiments (Brunner and Fairbrothers, 1978) and cases of cross-breeding (Orton, 1969; Bean, 1970; Bond, 1984; Santamour and McArdle, 1985). The ease with which they hybridize weighs heavily against the taxonomic splitting of big-bracted dogwoods into two genera, *Dendrobenthamia* and *Cynoxylon*, a practice met with often enough to need condemning.

Though most species of *Cornus* have white, blue, or blue–black fruits, the fruits of showy-bracted species (dwarf cornels included) are red. Fruits of Old World members of the big-bracted subgroup differ from their New World counterparts, however, in that they are compound. [See the cover of this issue of *Arnoldia*.] Our flowering dogwood bears bunched fruits, the individuals parting readily from the bunch: in *C. kousa* and other Asian members of the subgroup, flowers can be separated, but the separability is lost as flowers change to fruits. Ripe compound fruits look enough like fat strawberries that one species, *C. capitata*, is called strawberry dogwood,



The evolutionary relationships among the subgroups of Cornus.

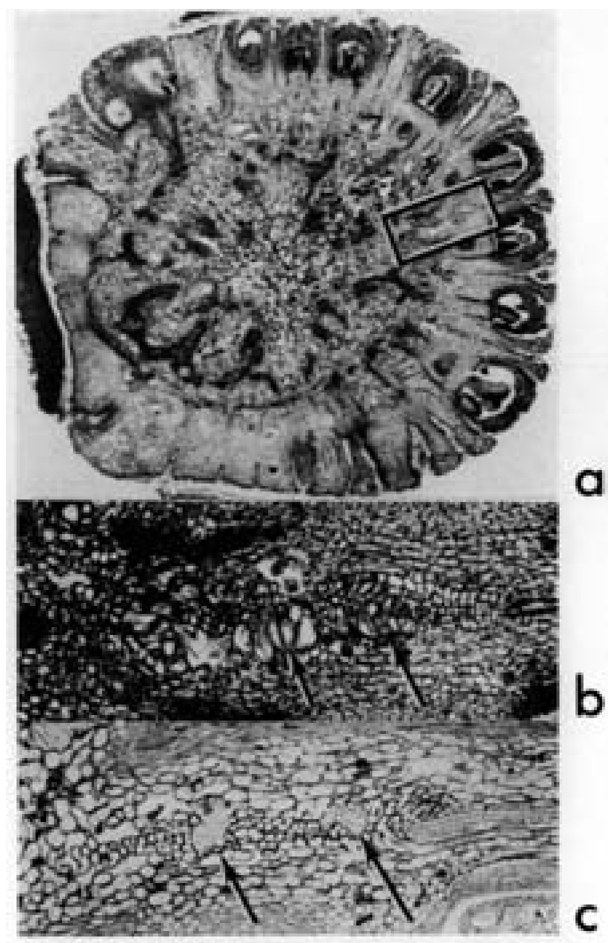
Because compound fruits occur in no genus of the dogwood family but *Cornus*, and there only in the Old World members of one subgroup, students of dogwood evolution can infer with confidence that they are derived This diagram makes the cornelian cherry subgroup (*Cornus mas* and allied species) more advanced than bractless dogwoods, yet switching these two branches of the diagram would not affect the derived status of compound fruits, and no matter which relative of *Cornus* is chosen as its nearest evolutionary neighbor, the conclusion remains that the change from simple fruits to compound fruits occurred just once, as big-bracted dogwoods separated into today's American and Asian forms

and the flesh of compound fruits is soft and sweet, unlike the tart or bitter flesh of dogwood fruits in general. [See the front-cover foldout.]

When P. F. Maevskiĭ (1881) examined fruits of *Cornus capitata* microscopically, what he saw misled him. Seeing—he thought—free individuals, each set in a cup-like hollow, he concluded that adjoining fruits do not really unite, that they sink into an expanding fruit stalk as the complex ripens. Museum technician Stan Yankowski and I repeated Maevskiĭ's work with a modern microtome—the anatomist's precise slicer—and a modern microscope, taking pains to look at all stages of growth, and we found true developmental fusion of the ovaries. (Dogwood ovaries are inferior; that is, petals, calyx lobes, and stamens are above the ovary, out of union's way.) Indeed, the stages can be seen at different levels in a half-ripe compound fruit. Stained serial sections through a fused region show normal epidermal cells, one layer for each of the adjoining ovaries, only at the fruit's surface. Within the fruit, the corresponding cells show signs of repeated division. They no longer have their typical rectangular outlines, and they interdigitate: cells from each epidermis penetrate the other. There are, in some places where epidermises once were, nests of the thick-walled, heavily staining cells called sclereids. As the cluster ripens to a sphere roughly half the diameter of a golf ball, tissues tear and cavities develop near the sclereids, hence the illusion of nonunion that Maevskiĭ saw.

Evolutionists from Darwin on have studied the selective pressures that make flowers so diverse, but only recently have they taken note of pressures working on the fruits of temperate regions (Thompson and Willson, 1979; Stiles, 1980, 1982, 1984; Stiles and White, 1982; Morden-Moore and Willson, 1982; Willson, 1983, Borowicz and Stephenson, in press). Thus, evolutionists have overlooked the fact that compound-fruited dogwoods pose the following problem: any reasonable diagram connecting *Cornus* to a neighboring group, and subgroups of *Cornus* to each other, shows that ancestral dogwoods had open flower clusters, that dogwoods with bunched flowers and ordinary fruits came later and gave rise to those with compound fruits. The change to bunched flowers likely had to do with pollinating insects, but the further change to compound fruits must have been dispersal-linked. What new means of dispersal would have made a compound fruit a betterment? And why are dogwoods with such fruits found only in the Old World?

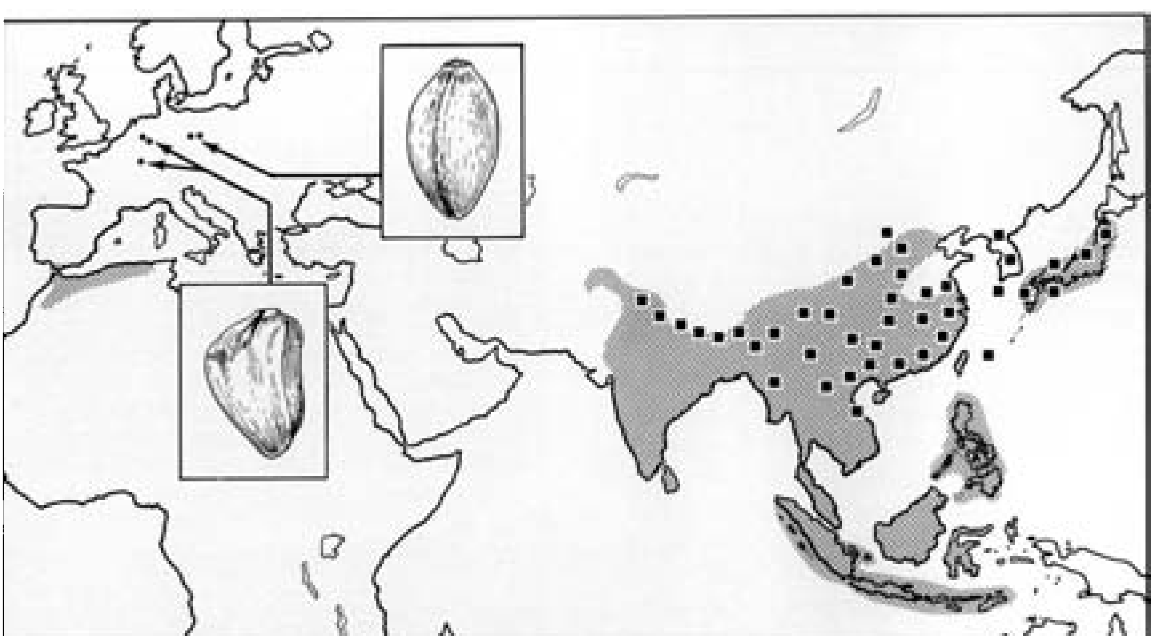
Robins and other migratory birds are the principal dispersers of the flowering dogwood (Baird, 1980). They also peck at fruits of kousa dogwoods introduced to gardens. By tearing up a compound fruit, they doubtless spread some of its seed-containing stones. (As in peaches, inner cell layers of the fruit wall turn into a "stony" housing for the seed. Most dogwoods have two seeds per stone, and a compound fruit has several stones.) But birds the size of robins, which are so well fitted to the bean-sized individual fruits of New World dogwoods, can hardly have provided pressure for the change to compound fruits. Grouse eat dogwood fruits, but tests with quails and pheasants indicate the gallinaceous gizzard does a dogwood stone more harm than good (Krefting and Roe, 1949). In Asia, hornbills and fruit pigeons spread large-fruited plants efficiently, but the birds are tropical, and Asiatic dogwoods, like our own, are largely temperate. Mice, raccoons, and bears disperse some dogwood stones (Martin *et al.*, 1951; Rogers and Applegate, 1983; Borowicz and Stephenson, in press) but not enough to cause an evolutionary change. Furthermore, the beasts are color-blind: the redness of a fruit means nothing to them.



Stained microtome sections of developing Cornus *sp fruits.*

a A somewhat oblique slice through the entire fruit of *Cornus capitata*, magnified 11 times (See the front cover foldout of this issue of *Arnoldia*) *b* The area marked with a rectangle in *a*, enlarged to about 70 times (Liquid-preserved specimen taken from a wild tree in Nepal [D H Nicolson 2371]) *c* A section like that in *b*, but thinner and from a developing fruit of *Cornus kousa* (Liquid-preserved specimen from a cultivated dogwood on the grounds of the Smithsonian Institution) Groups of sclereids (arrows) have differentiated where ovaries have fused

That leaves monkeys. Monkeys disperse seeds and stones of fleshy fruits by spitting and by voiding (Hladik and Hladik, 1967, 1972; Lieberman *et al.*, 1979). Macaques, the northernmost of monkeys, see color much as human beings do (De Valois and Jacobs, 1968); they eat *Cornus* fruits, both simple and compound (Uehara, 1977; Maruhashi, 1980), and they once ranged almost everywhere within the range of compound-fruited dogwoods. A critic could object that matching the ranges of macaques and dogwoods merely shows that both of them are creatures of the deciduous forest. Taking fossils into account, however, boosts the case for monkey-mediated evolution. Macaque remains are found in the Pliocene and Pleistocene of Asia as far north as Beijing and Korea and at sites in Europe dating back almost to latest Miocene, when macaques are thought to have emerged from Africa (Delson, 1980; Sohn, 1983, 1984*a*, 1984*b*). Lately, European specialists have also learned to spot the remains of dogwood subgroups that have disappeared from Europe. Some of the Miocene impressions once called "persimmon calyxes" are now thought to be the four bracts of *Cornus* (Gregor, 1982), and fossil fruits, when they are well preserved, can be identified more accurately than that. Size, shape, surface features, and internal structure mark a fruit stone as belonging to the big-bracted subgroup. Then, if it is ovoid or ellipsoid, it must be from a solitary fruit like that of *C. florida.* Such stones occur in Oligocene and Miocene brown-coal deposits of the German Democratic Republic (Mai and Walther, 1978). If, however, a stone is asymmetrical, tapered to the base, and faceted, it is from a compound fruit. Only younger beds have yielded



The natural ranges of macaques (hatching) and compound-fruited dogwoods (squares).

Fruit stones like those of flowering dogwood (upper inset) occur as fossils in East Germany, stones from compound-fruited dogwoods occur at younger sites in Alsace and near the Dutch-German border Compound fruited dogwoods likely came to some sites—the Ryukyus, for example—with birds or people Five thousand years of tilling made the blank spot in the Yellow River basin

The macaque range is from Zhang *et al* (1981), Fooden (1982), and Wolfheim (1983) The dogwood range is from the Herbarium of the Arnold Arboretum, the Gray Herbarium, the U S National Herbarium, and all germane floristic works such: a mid-Pliocene locality near Cologne (Burgh, 1978, 1983), another in Alsace (Geissert and Gregor, 1981), and a later Pliocene locality at Tegelen in the Netherlands (Mai, 1976). The Tegelen beds have also yielded bones of a macaque (Schreuder, 1945; see Berggren and Van Couvering, 1979, for information on the age of the Tegelen beds).

Big-bracted dogwoods formerly extended round the Northern Hemisphere, and all had ordinary fruits until monkeys came in contact with them about five million years ago. Selection for a better monkey meal meant better scattering of seeds; so compound fruits replaced the simple ones, but only in Eurasia. America retains the older kind because the New World monkeys, blind to red (Terborgh, 1983) and tied to warmer regions, never took up foraging on dogwoods. The behavioral side of this scenario is testable. China and Japan have monkeys, dogwoods of both kinds (our kind in cultivation), and primatologists to do the testing.

Acknowledgments

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