A PHYLOGENETIC REEVALUATION OF THE OLD WORLD SPECIES OF *FUCHSIA* (ONAGRACEAE)[1]

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Abstract

The four Old World species of *Fuchsia*—*F. cyrtandroides*, *F. excorticata*, *F. perscandens*, and *F. procumbens*—form a monophyletic group (sect. *Skinnera*) defined by blue pollen and the presence of flavones in all species. Data on foliar flavonoid compounds in the section were reanalyzed, and additional nonflavonoid characters were employed to make a phylogenetic reevaluation of the group, using the rest of the genus as the outgroup. Of 17 characters used, 7 were phylogenetically informative, resulting in two equally most parsimonious cladograms 23 steps long. Both have a consistency index of 0.75 when all noninformative characters are excluded. The two trees differ in the position of the Tahitian *F. cyrtandroides* and the New Zealand *F. procumbens*, each of which appears as the sister group of the other species in the respective cladograms. In both trees, *F. excorticata* and *F. perscandens* form a clade defined by constricted floral tubes. These results differ from a prior cladistic analysis of the section based primarily on flavonoids, which placed *F. cyrtandroides* unambiguously as the sister species of the rest of the section and grouped *F. procumbens* in a clade with *F. perscandens*.

Fuchsia is a genus of about 105 species found primarily in mountainous regions of the Neotropics. Four species comprising the distinctive sect. *Skinnera* are confined to the Old World, however, with three species in New Zealand and one on the island of Tahiti. This section is of considerable biogeographical interest for its marked disjunction from the American species and the presence of closely related taxa on distant islands in the South Pacific.

As part of a study of foliar flavonoid compounds in sect. *Skinnera*, Williams & Garnock-Jones (1986) presented a cladistic analysis of the group, based on their flavonoid results and several other characters. A single shortest tree resulted from their analysis, in which the Tahitian *F. cyrtandroides* is the sister species of a clade comprising all the New Zealand taxa, and the arborescent *F. excorticata* is the sister species of a clade formed by *F. procumbens* and *F. perscandens*, a creeping and a scandent species, respectively.

Independently, Averett et al. (1986) conducted a comprehensive survey of foliar flavonoids in the entire genus, including a greater number of samples in sect. *Skinnera* than in the earlier study by Williams & Garnock-Jones. Their study resulted in the detection of several compounds not previously found in the same taxa by Williams & Garnock-Jones (1986). This and new information derived from a revision of the section by Godley, Berry, and Smith (in prep.) prompted us to reassess the phylogenetic relationships within sect. *Skinnera*, using a reevaluation of flavonoid characters as well as a larger number of nonflavonoid characters.

Materials and Methods

We recognize four species as terminal taxa in sect. *Skinnera* (Table 1). Three occur in New Zealand: the widespread tree fuchsia, *F. excorticata*, the lianoid *F. perscandens*, and the rare creeper, *F. procumbens*, which is restricted to the northern third of the North Island. Following Allan (1927, 1928), we treat *F.* ×*colensoi* as a series of interspecific hybrids between *F. excorticata* and *F. perscandens* and do not include it in our anal-

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TABLE 1. Taxa and geographical distributions in *Fuchsia* sect. *Skinnera*.

Taxa	Geographical distribution
F. cyrtandroides J. W. Moore	Tahiti (Society Islands)
F. excorticata (J. R. & G. Forster) Linnaeus f.	Throughout New Zealand, Chatham Islands, Stewart Island
F. perscandens Cockayne & Allan	New Zealand: throughout South Island, in southern half of North Island
F. procumbens R. Cunningham	New Zealand: restricted to northern third of North Island

ysis. The fourth species, *F. cyrtandroides*, grows as a small tree and is endemic to a few high peaks on Tahiti, in the Society Islands.

Character polarity was determined by the outgroup comparison method (Watrous & Wheeler, 1981; Maddison et al., 1984), collectively using the other sections of the genus as the outgroup since there is no single section that is a clear sister group. If sect. *Jimenezia* is used as the outgroup, based on the preliminary results of Sytsma & Smith's (1988) survey of chloroplast DNA restriction site mutations in *Fuchsia*, there are no differences in polarity assignment from using the other sections collectively.

The sources of the flavonoid data were Williams & Garnock-Jones (1986) and Averett et al. (1986). Where the two studies differed in the flavonoid profile of a particular species, the presence of a compound was employed in our analysis rather than its absence, since lack of detection can be due to presence in low concentrations, inadequate amounts of sample material, environmentally induced flavonoid changes, developmental differences, or natural intraspecific variation (Harborne, 1975; Bohm, 1987). Data on the sexual systems of the species were taken from Godley (1955, 1963, 1979). Field observations and analysis of preserved specimens were used to define the remaining floral and vegetative characters.

The data matrix used in this analysis is contained in Table 2. The data set was analyzed using the HENNIG86 phylogenetic package (version 1.5, Farris, 1988; Platnick, 1989), run on a Dell 200 computer applying the implicit enumeration option for calculating trees. We also used the successive weighting procedure (Farris, 1989), which calculates weights from the best fits to the most parsimonious trees and applies them in the weighting procedure until there are no changes in successively produced trees.

CHARACTER DEFINITION AND CODIFICATION

1. *Flavones:* the different biochemical pathway leading to the synthesis of flavones makes the presence of this class of compounds an important distinguishing character from taxa that have only flavonols (Gottlieb, 1975). The presence of flavones is generally an advanced trait (Harborne, 1975), but the secondary loss of such compounds can also constitute a third, highly advanced stage in flavonoid evolution (Gornall & Bohm, 1978; Averett & Raven, 1984). In view of this situation, we use the overall presence or absence of the flavone class in *Fuchsia* as a character, rather than treating each flavone compound individually. Presence of flavones is considered apomorphic in sect. *Skinnera*, since they are absent in sect. *Jimenezia* and in nearly all the other species of the genus. Absence = 0, presence = 1.

2. *Pollen:* blue pollen is very rare in the angiosperms and is found in *Fuchsia* only in sect. *Skinnera*. Anthers of *F. excorticata* are rich in three different anthocyanins (Crowden et al., 1977) and probably form a blue metallo-flavone-anthocyanin complex in living flowers (N. H. Fischer, pers. comm.). Cream-colored pollen = 0, blue pollen = 1.

3. *Ovule number:* all other sections of *Fuchsia* have fewer than 200 ovules per ovary, with ovules arranged in two rows per locule. This is also the case for *F. procumbens*, but the other three species in sect. *Skinnera* have more than twice the maximum number of ovules found in the other sections and have more than two rows of ovules per locule. < 200 ovules/ovary = 0, > 200 ovules/ovary = 1.

4. *Flavone sulphates:* these compounds are unusual among angiosperms (Harborne & Williams, 1982) and occur in *Fuchsia* only in sect. *Skinnera*. Absence = 0, presence = 1.

5. *Flavonol diglycosides:* flavonol monoglycosides were detected in all 80 taxa of the genus studied by Averett et al. (1986), whereas flavonol diglycosides occur in only a few taxa, including *F. excorticata* in sect. *Skinnera*. Absence = 0, presence = 1.

6. *Eriodictyol 7-glucuronide:* this uncommon flavanone has only been found within the genus in

TABLE 2. Data matrix for the taxa of *Fuchsia* sect. *Skinnera*; the other sections of *Fuchsia* are used as the outgroup. Character 7 is additive; characters 14 and 15 are nonadditive.

Taxa	Character																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F. cyrtandroides	1	1	1	0	0	0	0	0	0	0	0	0	1	2	0	1	0
F. procumbens	1	1	0	1	0	0	2	1	1	1	1	0	0	0	2	0	1
F. perscandens	1	1	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1
F. excorticata	1	1	1	1	1	1	1	0	0	0	0	1	0	2	0	1	1

F. excorticata (Williams et al., 1983). Absence = 0, presence = 1.

7. *Sexual system:* gynodioecy is derived from hermaphroditism in *F. procumbens* and *F. excorticata* by the presence of a dominant gene for male sterility. The addition of a linked gene dominant for female fertility in *F. procumbens* then leads to subdioecy. The other sections of *Fuchsia* are hermaphroditic or else have male sterility determined by a recessive gene (Breedlove et al., 1982). Hermaphroditic = 0, gynodioecious = 1, subdioecious = 2; additively (= sequentially) coded.

8. *Flower position:* hanging flowers characterize all but one other section of *Fuchsia*, with erect flowers in *F. procumbens* clearly derived. Hanging = 0, erect = 1.

9. *Petals:* petals are present in all but one other section of the genus. In sect. *Skinnera*, the petals are either much reduced or completely lacking in *F. procumbens*. Present = 0, lacking = 1.

10. *Stamens:* all species in the genus except *F. procumbens* have the stamens in two whorls of conspicuously different lengths. Distinct whorls = 0, stamens subequal = 1.

11. *Sepals:* sepals are spreading at anthesis in all but a few species of the other sections of the genus. In sect. *Skinnera*, *F. procumbens* is the only species with completely reflexed sepals doubling back against the floral tube. Spreading = 0, reflexed = 1.

12. *Floral tube:* floral tubes with little or no constriction is the prevalent condition in the outgroup. In sect. *Skinnera*, the tubes are either strongly constricted above the nectary and then abruptly widened above, or else cylindrical. Unconstricted = 0, strongly constricted = 1.

13. *Leaf texture:* membranous or subcoriaceous leaves occur in the rest of the genus, with *F. cyrtandroides* unique in its considerably thicker, crassate leaves. Membranous = 0, thick-crassate = 1.

14. *Leaf underside:* the presence of a silvery-white leaf underside is caused by the absence of chlorophyll in the spongy parenchyma of *F. excorticata* (Suckling, 1914) and is more specialized than the normal green leaf underside in the genus. *Fuchsia perscandens* has chlorophyll in the spongy parenchyma but also has a whitish underside. Green = 0, whitish = 1, silvery-white = 2; nonadditive (= unordered).

15. *Habit:* the outgroup is primarily shrubby and is here taken to include the small to medium-sized trees found in two species of sect. *Skinnera*. The unique creeping habit of *F. procumbens* and the unusual lianoid habit of *F. perscandens* are both specialized for the genus. Shrubby or tree = 0, lianoid = 1, procumbent creeper = 2; nonadditive.

16. *Flower color change:* flowers in three species of the section pass through an abrupt floral color change from green to red (Delph & Lively, 1985; Berry, unpublished). 0 = no distinct color phases, 1 = two distinct color phases.

17. *Leaf phyllotaxis:* leaves are initially opposite in all species of the section at the seedling stage, but in three species they become alternate soon thereafter. Opposite = 0, alternate = 1.

RESULTS

Two equally most parsimonious hypotheses were generated by our data matrix, designated here as cladogram A and cladogram B (Fig. 1). Both have 23 steps, with a consistency index of 0.75 after the noninformative characters were excluded. The successive weighting procedure did not discriminate either of the two trees, which differ only in the placement of *F. cyrtandroides* and *F. procumbens*. In cladogram A, *F. cyrtandroides* is the sister species of the three New Zealand species, while in cladogram B, *F. procumbens* is the sister species to *F. cyrtandroides*, *F. excorticata*, and *F. perscandens*. In both cladograms, *F. excorticata* and *F. perscandens* form a clade characterized by the presence of constricted floral tubes.

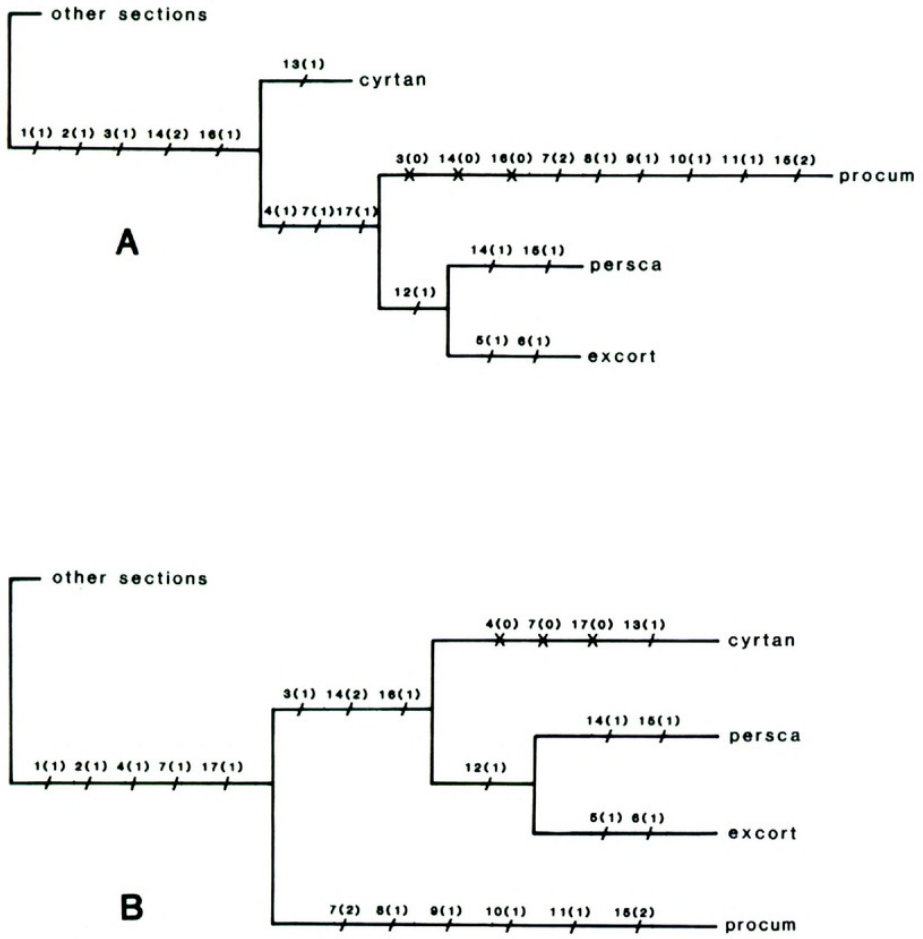

FIGURE 1. The two most parsimonious cladograms (length = 23; consistency index = 0.75 when noninformative characters are excluded) found from the analysis of the data matrix.—A. The topology in which *F. cyrtandroides* is the sister group of the New Zealand species.—B. The topology in which *F. procumbens* is the sister group of the rest of the section. Character state changes are superimposed on the cladograms; single lines = apomorphies, X = reversals.

Of the 17 characters used, 7 are informative in defining the phylogeny of the section. Only one of these remains as originally coded in both trees (#12, floral tube constriction), with the differences in the two trees determined by the evolution of the other six characters. In cladogram A, one extra step is required in each of three characters: 3 (ovule number), 14 (chlorophyll presence in spongy mesophyll), and 16 (floral color change), whereas in cladogram B the extra step occurs in characters 4 (flavone sulphates), 7 (sexual system), and 17 (leaf phyllotaxis). Characters 1 and 2 (flavones, blue pollen) are present in all members of the ingroup and define the section as a monophyletic group. Seven characters are autapomorphies (5, 6, 8, 9, 10, 11, and 13), with three additional autapomorphies in two multistate, nonadditive characters (14 and 15).

DISCUSSION

The main consequence of our reevaluation of flavonoid data in sect. *Skinnera* was a reduction in the number of flavonoid characters from seven (four informative) in Williams & Garnock-Jones (1986) to four in our analysis (only one of these informative). This was due to a more conservative choice of characters employed in our data matrix. We justify our use of flavonoid classes (instead of individual compounds) as being more congruent with current knowledge of flavonoid evolution, especially when the data are based on general surveys such as in *Fuchsia* (Gornall & Bohm, 1978; Richardson, 1983; Averett & Raven, 1984). Our matrix also reflects character state changes in some of the characters that were maintained in both studies, such as flavones in *F. cyrtandroides* and flavonol glycosides in *F. procumbens* and *F. perscandens*. These are "presences" of compounds that were not detected by Williams & Garnock-Jones (1986), but were found by Averett et al. (1986). Averett et al. (1986) examined 3–16 individuals per taxon in sect. *Skinnera* compared to 1–3 per taxon in Williams & Garnock-Jones (1986), which supports the use of larger sample sizes in

flavonoid surveys to more reliably detect the presence of compounds.

Our results differ considerably from the previous cladistic analysis of Williams & Garnock-Jones (1986), whose single shortest cladogram is shown in Figure 2. In their tree, *F. perscandens* forms a terminal clade with *F. procumbens*, whereas our results place *F. perscandens* in a terminal clade with *F. excorticata* (Fig. 1). Williams & Garnock-Jones used two flavonoid characters, presence of apigenin and loss of flavonols, as apomorphies defining their *perscandens-procumbens* clade, but the study by Averett et al. (1986) showed that both kinds of compounds are in fact found in all members of the section. Their third apomorphy for this clade, lianoid habit, is inappropriate, since it is unlikely that the creeping, barely woody character of *F. procumbens* is homologous with the woody, scandent habit of *F. perscandens*. The only character that defines our *perscandens-excorticata* clade is the strongly constricted floral tube, and this is probably associated with pollination by honeyeater birds (Meliphagidae) in these two species (Thomson, 1927; Delph & Lively, 1985). Bird pollination, on the other hand, is not known to occur in *F. procumbens*.

The other main difference in our cladistic analysis from that of Williams & Garnock-Jones is the ambiguous resolution of the sister species to the rest of the section (*F. cyrtandroides* or *F. procumbens*). With the Tahitian *F. cyrtandroides* as the sister species, our first hypothesis requires that *F. procumbens* (a) reverted back to a low ovule number, (b) regained chlorophyll in the spongy mesophyll (green leaf undersides), and (c) lost the derived floral color change. With *F. procumbens* as the sister species, *F. cyrtandroides* is required to have (a) lost flavone sulphates, (b) lost male sterility, and (c) reverted back to opposite leaves. This situation indicates that there must be extensive homoplasy in the section, but it is not yet evident from our results in which set of the above characters this has occurred.

The large number of autapomorphies in *F. procumbens* underscores how differentiated this species is from the rest of the section, yet does not help us determine if those characters are the result of a fundamental divergence or are a secondary development related to an unusual pollination syndrome or habitat type, for example. Because *F. procumbens* is now so rare in nature and its natural pollinators may have gone extinct, its pollination system remains unknown. The species is distinctive in *Fuchsia*, however, in occupying a seashore habitat, and it is restricted to the northern part of the North Island, an endemic-rich area of New Zealand (Craw, 1988).

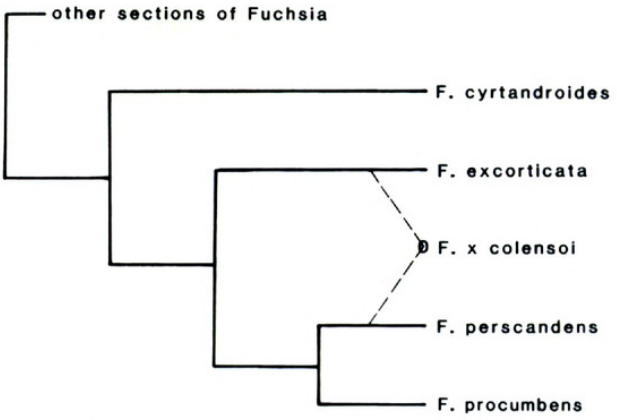

FIGURE 2. The single most parsimonious cladogram obtained by Williams & Garnock-Jones (1986); this differs from our hypotheses mainly in the position of *F. procumbens*.

Fuchsia's disjunct distribution between the New World and New Zealand and Tahiti has stimulated several hypotheses about its origin. Croizat, who opposed arguments of chance long-distance dispersal in *Fuchsia* and other groups, first considered the presence of the genus on Tahiti as an ancient one that exemplified the "trans-Pacific" track joining southeastern Brazil, south-central Chile, and the southwest Pacific (Croizat, 1962, p. 547). Later, Raven (1972, 1979a) suggested that *Fuchsia* reached New Zealand by trans-Pacific long-distance dispersal from South America, first to New Zealand by the mid-Miocene (to account for the fossil pollen of *Fuchsia* dated from that time; see Couper, 1960), then secondarily to Tahiti. More recently, Berry (1982) proposed an older, more direct connection from South America to New Zealand via Antarctica, with subsequent dispersal to Tahiti. This was based on older, Oligocene fossil records of *Fuchsia* from New Zealand (Mildenhall, 1980) and a newer understanding of the opportunities for direct migration across Antarctica until the Miocene (Raven, 1979b).

Most explanations for the presence of *Fuchsia* sect. *Skinnera* on Tahiti have been based on hypotheses of recent, probably bird-mediated dispersal from New Zealand (Carlquist, 1967, 1974; Fleming, 1976; Godley, 1979; Raven, 1979a; Berry, 1982). This view is based on the isolated oceanic position of Tahiti, its volcanic origin and recent age (less than two million years old; Dymond, 1975), and the fleshy fruit and small seeds of *F. cyrtandroides*. As a result of their cladistic analysis showing *F. cyrtandroides* to be the sister species of the rest of the section, Williams & Garnock-Jones (1986) dissented with this view, suggesting that *F.*