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LEAF FLAVONOIDS AND OTHER PHENOLIC GLYCOSIDES AND THE TAXONOMY AND PHYLOGENY OF *FUCHSIA* SECT. *SKINNERA* (ONAGRACEAE)

CHRISTINE A. WILLIAMS and PHILIP J. GARNOCK-JONES*

Botany Department, Plant Science Laboratories, The University, Whiteknights, Reading, Berks., RG6 2AS, U.K.; *Botany Division, DSIR, Private Bag, Christchurch, New Zealand

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Key Word Index—*Fuchsia*; Onagraceae; flavonol glycosides; flavone glycosides; flavone sulphates; eriodictyol; galloylglucose sulphate; biochemical systematics; hybrid identification; phylogeny; biogeography; evolution; cladistics.

Abstract—In a leaf flavonoid investigation of all species and one hybrid of *Fuchsia* sect. *Skinnera* flavonol glycosides were found in all except *F. procumbens* and *F. perscandens*. Flavone glycosides and their sulphates previously characterized in *F. excorticata*, *F. procumbens* and their hybrid were found additionally in *F. perscandens* and *F. colensoi* but were absent from *F. cyrtandroides*. However, the rare *Fuchsia* constituents diosmetin 7-glucuronide and eriodictyol 7-glucoside were identified only in *F. excorticata*, *F. excorticata* × *F. procumbens* and *F. colensoi*, supporting the suggestion that the latter species is of hybrid origin with *F. excorticata* as one of the parents. The chemical evidence also indicates that sect. *Skinnera* is monophyletic with the Tahitian *F. cyrtandroides*, a sister species to a clade incorporating all the New Zealand species and thus not necessarily derived from a New Zealand ancestor.

INTRODUCTION

In his revision of the genus *Fuchsia* L. Munz [1] recognised six species in sect. *Skinnera*. Of these, *F. colensoi*, *F. excorticata*, *F. perscandens*, and *F. procumbens* are endemic to New Zealand, and *F. kirkii* is a synonym of *F. procumbens*, being based on a male plant of that species [2]. The remaining species, *F. cyrtandroides*, is endemic to the island of Tahiti, but has been thought to be very closely related to *F. excorticata*.

Morphological evidence suggests that some if not all forms of *F. colensoi* may be of hybrid origin, probably the progeny of *F. excorticata* × *F. perscandens* [2]. In a previous report of leaf flavonoid and phenolic glycosides from six *Fuchsia* species and their hybrids [3], *F. excorticata*, *F. procumbens* and an artificial hybrid from the cross *F. excorticata* × *F. procumbens* were examined. In that survey *F. excorticata* was clearly separated from *F. procumbens* by the presence of seven flavonol glycosides, eriodictyol 7-glucoside and diosmetin 7-glucuronide. Most of these parental compounds were found in the hybrid. However, two glycosides, kaempferol 3-arabinoside and 3-rhamnoside, were detected only in the hybrid.

In the present study we have analysed the remaining species of sect. *Skinnera*, two from New Zealand, *F. perscandens* and *F. colensoi*, and one from Tahiti, *F. cyrtandroides*. These results have been combined with those from the previous survey [3] and the taxonomic and biogeographic implications of the combined data are considered.

RESULTS AND DISCUSSION

The combined results of the leaf flavonoid analyses in this and a previous survey [3] of five species and one artificial hybrid from *Fuchsia* sect. *Skinnera* are presented in Table 1. Flavonol glycosides were found to be characteristic of *F. excorticata*, *F. excorticata* × *F. procumbens*, *F. cyrtandroides* and *F. colensoi*, but were absent from *F. procumbens* and *F. perscandens*. Flavone glycosides and flavone glycoside sulphates were identified in all taxa except *F. cyrtandroides*. Flavone glycoside sulphates have not been reported from other species of *Fuchsia* [3, 4]. A galloylglucose sulphate was universally present but is not confined to sect *Skinnera*. The characterization of luteolin 7-glucuronide sulphate and two other unusual flavone sulphates has been previously described [3].

From these data it can be seen that all species of sect. *Skinnera* have distinctive phenolic profiles. Thus, *F. cyrtandroides* may be separated from all the other species of the section by the absence of flavone glycosides and their sulphates. Similarly, *F. excorticata* may be distinguished by the presence of quercetin 3-rutinoside. But it may be of more taxonomic significance that diosmetin 7-glucuronide and the relatively rare flavanone, eriodictyol 7-glucoside, previously shown to be good chemical markers for the latter species [3], have now been identified in *F. colensoi*, together with most of the other flavonol and flavone glycosides found in *F. excorticata* (see Table 1). As seen in the artificial hybrid of *F. excorticata* × *F. procumbens* not all the parental compounds are necessarily inherited and some extra constituents may be produced. Thus, the present evidence strongly supports the suggestion [2] of a hybrid origin for at least some forms of *F. colensoi* with *F. excorticata* as one of the parents. However, the presence of the other putative parent, *F. perscandens*, is not so clearly distinguished as only three of its four flavonoid constituents luteolin 7-glucuronide, apigenin 7-glucuronidesulphate and tricin 7-glucuronidesulphate were identified in *F.*

Table 1. Leaf flavonoid and phenolic glycosides of *Fuchsia* taxa from section *Skinnera*

Species or hybrid	Flavonol glycosides: Quercetin 1	2	3	4	5	Kaempferol 6	7	8	9	Flavone glycosides 10	11	12	13	14	15	Other glycosides 16	17
New Zealand taxa																	
F. colensoi Hook f.	+	+	+	+	–	+	+	–	–	+	+	–	+	+	+	+	+
F. excorticata (J. R. et G. Forst.) L.	+	+	+	+	+	+	+	–	–	+	+	–	–	+	+	+	+
F. excorticata × *F. procumbens*	+	+	+	+	(+)	+	+	+	+	+	+	+	+	+	–	+	+
F. perscandens CKn. et Allan	–	–	–	–	–	–	–	–	–	+	–	+	+	+	–	+	–
F. procumbens R. Cunn. ex A. Cunn	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	+	–
Tahitan taxon																	
F. cyrtandroides R. J. Moore	+	+	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–

Key: Quercetin glycosides: 1 = 3-glucoside, 2 = 3-galactoside, 3 = 3-rhamnoside, 4 = 3-arabinoside, 5 = 3-rutinoside; kaempferol glycosides: 6 = 3-glucoside, 7 = 3-galactoside, 8 = 3-rhamnoside, 9 = 3-arabinoside; flavone glycosides: 10 = luteolin 7-glucuronide, 11 = luteolin 7-glucuronidesulphate, 12 = apigenin 7-glucuronide, 13 = apigenin 7-glucuronidesulphate, 14 = tricin 7-glucuronidesulphate, 15 = diosmetin 7-glucuronide; other glycosides: 16 = a galloylglucose sulphate (R_f 15 in BAW and 53 in 15% acetic acid), 17 = eriodictyol 7-glucoside

colensoi and, of those, two were also found in *F. excorticata*. Also *F. perscandens* and *F. procumbens* have very similar flavonoid patterns (see Fig. 1) and are separated only by the presence of luteolin 7-glucuronidesulphate in the latter (Table 1). Therefore, it is not possible to use the present flavonoid data to decide which of these two lianoid species may be the other parent.

Some conclusions on cladistic relationships within sect. *Skinnera* may be drawn from the data presented here (Fig. 2). It is not entirely clear at present which section of *Fuchsia* is best considered to be the sister group of sect. *Skinnera*, and since Berry [5] has convincingly suggested that the section was one of the earliest evolutionary offshoots of *Fuchsia* we have taken the rest of the genus as an outgroup.

Firstly, sect. *Skinnera* can be considered a monophyletic group defined by its possession of blue pollen, not seen elsewhere in the genus. Second, the presence of flavone glucuronide sulphates is peculiar within the genus to the New Zealand species of sect. *Skinnera* and indicates that these are a monophyletic sister group to *F. cyrtandroides* of Tahiti. Previously *F. cyrtandroides* had been thought very closely related to *F. excorticata* of New Zealand [2]. However its chemical profile indicates that *F. cyrtandroides* in fact holds an isolated position in sect. *Skinnera* both phenetically, where there is only 31% similarity between *F. cyrtandroides* and *F. excorticata* (Fig. 1), and cladistically (Fig. 2). Probably assumptions of a close relationship between these two species have been based on symplesiomorphy, particularly as two of the other New Zealand species show unusual derived characters of habit.

It is thus not necessary to postulate a secondary loss of male sterility in *F. cyrtandroides* as did Raven [6]. Male sterility can be placed on the cladogram (Fig. 2) as a synapomorphy of the four New Zealand species of sect. *Skinnera*. Male sterility in other sections of *Fuchsia* has different characteristics [6, 7] and is thus not homologous with male sterility in sect. *Skinnera*.

The major biogeographic conclusion to be drawn from the cladistic analysis of flavonoid data (Fig. 2) is that the

	F. colensoi	F. excorticata	F. perscandens	F. procumbens	F. cyrtandroides
F. colensoi	100	86	29	36	31
F. excorticata	86	100	20	27	31
F. perscandens	29	20	100	83	13
F. procumbens	36	27	83	100	11
F. cyrtandroides	31	31	13	11	100

Fig. 1. Paired affinity diagram of *Fuchsia* sect. *Skinnera* based on flavonoid data from Table 1 expressed as percentage similarity.

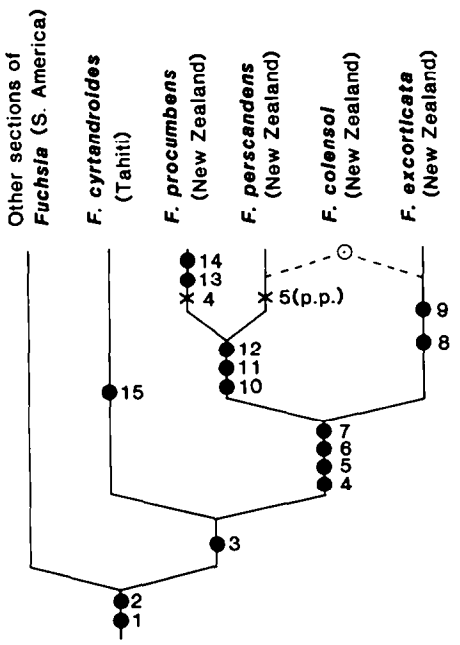

Fig. 2. Cladogram of *Fuchsia* sect. *Skinnera* based largely on appropriate flavonoid data from Table 1. Apomorphic character states employed are: 1, fruit a berry; 2, calyx corolloid; 3, pollen blue; 4, hypanthium swollen above ovary; 5, luteolin 7-glucuronide and its sulphate; 6, tricin 7-glucuronide and its sulphate; 7, male sterility; 8, diosmetin 7-glucuronide sulphate; 9, eriodictyol 7-glucuronide; 10, loss of all flavonol glycosides; 11, apigenin 7-glucuronide and its sulphate; 12, lianoid habit; 13, flowers erect; 14, petals absent; 15, loss of all flavone glycosides. The putative hybrid origin of *F. colensoi* is indicated by dotted lines. Apparent reversals of characters from apomorphic to plesiomorphic states are indicated by crosses (characters 4 and 5).

suggestion of Raven [6] that *F. cyrtandroides* probably spread to Tahiti from New Zealand receives no support. It appears to have been derived from the common ancestor of sect. *Skinnera* before the speciation events which led to the four species in New Zealand. Although there are several plant species in SE Polynesia clearly derived from New Zealand ancestors [8], each case must be analysed separately and the sister relationship between Tahitian and New Zealand *Fuchsia* does not necessarily imply a New Zealand origin for the section. However, Tahiti is a young volcanic island, probably less than 2 my old although the oldest presently emergent derivative island of its hot-spot is perhaps 4 my old [9]. *Fuchsia* is known from late Oligocene fossils (*ca* 25–30 my ago) in New Zealand [10] which led Berry [5] to suggest *Fuchsia* reached New Zealand via Antarctica and spread very recently to Tahiti. Like many other biogeographic conundrums this one will be solved not by victory of one or other vigorously competing methodological frameworks but by analytical methods which produce phylogenies with a time axis, such as DNA sequencing.

EXPERIMENTAL

Plant material. Leaf material of *F. colensoi* was collected by one of us (P.J. G.-J.) with H. D. Wilson from Dyers Pass, Lyttelton Port Hills, Canterbury, New Zealand in December 1982. Verified dried leaf material of *F. excorticata*, *F. procumbens* and a hybrid between these two species made by D. H. Percy were received from E. J. Godley, Botany Division, DSIR, Private Bag, Christchurch, New Zealand. Two further accessions of cultivated *F. procumbens* and *F. excorticata* were supplied by J. O. Wright of Lechlade Garden & Fuchsia Centre, Lechlade, Glos., U.K. Mr. Wright also supplied verified leaf material of *F. perscandens*. *Fuchsia cyrtandroides* was grown at DSIR, Botany Division, Christchurch, New Zealand from seeds collected in Tahiti by E. J. Godley. Vouchers are in CHR and RNG.

Identification of leaf flavonoids and phenolics. Flavonoid glycosides and phenolic glycosides were isolated and identified from 80% methanolic leaf extracts as previously described [3].

Cladistic methodology. The cladogram of sect. *Skinnera* was derived from inspection of the data, clades being defined only by synapomorphies. Character state polarity was decided by outgroup comparison [11] using the rest of the genus as an outgroup. Because of the absence of a reliable hypothesis of outgroup relationships, only characters thought to be invariate in the outgroup were used. For many characters the distribution of character states within the genus is poorly known and we emphasize that this cladogram is therefore provisional. Some congruent chemical character states were treated as one as they may reflect only one change at the gene level.

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