
SEXUAL SYSTEMS OF NEW CALEDONIAN *ARALIACEAE*: A PRELIMINARY PHYLOGENETIC REAPPRAISAL

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A preliminary analysis of New Caledonian *Araliaceae* has shown varying degrees of support for previous hypotheses on sexual system evolution in the family. Andromonoecy, rather than hermaphroditism, is strongly supported as the ancestral sexual system for the *Araliaceae*. Derivation of hermaphroditism from andromonoecy in *Delarbrea harmsii* R. Vig. and *Polyscias bracteata* (R. Vig.) Lowry, ined. is also strongly supported. Support for the derivation of dioecy from andromonoecy in several New Caledonian species of *Polyscias* J. R. Forst. & G. Forst. depends in part on an assumption that andromonoecy cannot be secondarily derived from dioecy. The derivation of hermaphroditism from andromonoecy in *Schefflera candelabra* Baill. and *S. pseudocandelabra* R. Vig. is equivocal. The hypothesis that the immediate ancestors of *Arthrophyllum* Blume were andromonoecious is not supported.

Keywords. Andromonoecy, *Apiaceae*, *Apiales*, dioecy.

INTRODUCTION

Over the past decade, the availability of robust cladograms based on molecular data has spurred development of explicitly phylogenetic methods to reconstruct ancestral character states and to test hypotheses about the sequences of evolutionary steps that have produced extant biological diversity. Members of *Apiales* exhibit a wide variety of sexual systems, including hermaphroditism, andromonoecy, dioecy and gynodioecy (Schlessman *et al.*, 1990; Koul *et al.*, 1993). Unfortunately, because the taxonomic literature rarely reflects this diversity, obtaining sufficient data for broad comparative studies has been somewhat difficult. For example, a recent attempt to use MacClade (Maddison & Maddison, 1992) to trace the evolution of sexual systems on a molecular cladogram for 44 taxa of *Apiaceae* and *Araliaceae* produced ‘ambiguous results’ (Plunkett *et al.*, 1996).

Perhaps the most extensive single study of sexual systems in *Apiales* is that of Schlessman *et al.* (1990), which included 76 species representing all eight genera of *Araliaceae* that occur on the south-west Pacific island of New Caledonia (*Apiopetalum*

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Baill., *Arthrophyllum* Blume, *Delarbreia* Vieill., *Meryta* J. R. Forst. & G. Forst., *Myodocarpus* Brongn. & Gris., *Polyscias* J. R. Forst. & G. Forst., *Pseudosciadium* Baill. and *Schefflera* J. R. Forst. & G. Forst.). In that study, andromonoecy was the most common sexual system (41 species in six genera), followed by dioecy (25 species in two genera) and hermaphroditism (10 species in three genera). Citing the near ubiquity of andromonoecy in the generic group comprising *Delarbreia*, *Myodocarpus* and *Pseudosciadium*, and the apparent monophyly and great age of that group, they hypothesized that andromonoecy was the ancestral sexual system not only for each of the six New Caledonian genera in which it is found, but probably also for *Araliaceae* and for *Apiales* as a whole. They also presented a scheme of specific changes in inflorescence structure and patterns of floral dichogamy associated with the derivation of hermaphroditism or dioecy from andromonoecy in particular species of *Delarbreia*, *Polyscias* and *Schefflera*. We are now in the process of evaluating these hypotheses with molecular phylogenetic data. Our purpose in this brief communication is to report preliminary results on sexual systems.

METHODS

We used nuclear rDNA ITS sequences from 81 taxa including 25 genera of tropical and temperate *Araliaceae*, with as many New Caledonian species as possible. *Eryngium* L., *Sanicula* L. (both *Apiaceae*) and *Pittosporum* Gaertn. (*Pittosporaceae*) were used as outgroups. Details of the molecular phylogenetic methods are given in Plunkett *et al.* (2001). From Schlessman *et al.* (1990) and our own subsequent observations, we obtained data on sexual systems for 67 species: 37 native to New Caledonia (44% of the c.85 native species of araliads, all eight native genera were represented), and 30 non-New Caledonian, representing 16 mostly tropical genera. We scored variation in sexual systems as three discrete character states: andromonoecious (cosexual, all individuals with both perfect and staminate flowers), hermaphroditic (cosexual, all individuals with perfect flowers), and dioecious (sexually dimorphic, individuals with either staminate or functionally pistillate flowers, but not both). We used MacClade 3 (Maddison & Maddison, 1992) to find the most parsimonious mapping of character state transitions for sexual systems on the topology of a parsimony cladogram representing the strict consensus of 10,000 trees (total number of steps=1190, CI excluding uninformative characters=0.469, RI=0.800).

In order to make our conclusions as robust as possible, we sought to minimize assumptions about character state transitions. On the other hand, we felt that being overly conservative might reduce the heuristic value of our analysis or lead us toward incorrect conclusions. In particular, we felt that reversions from dioecy to either andromonoecy or hermaphroditism would be highly unlikely. In a trial analysis allowing all possible transitions, there were no possible cases of hermaphroditism evolving from dioecy, so the question of restricting that transition became moot. There was, however, one potential case of andromonoecy evolving from dioecy. When all possible transitions were allowed, andromonoecy and dioecy were equally parsimonious states for the internal branch leading to the clade comprising *Polyscias dioica* (Vieill. ex Panch. & Sebert) Harms, *P. cissodendron* (C. Moore & F. Muell.) Harms and *P. sambucifolius* (Sieb. ex DC.) Harms (see Fig. 1). We chose to fix the character state for that branch to andromonoecy, thus excluding the possibility that andromonoecy in *P. sambucifolius* was derived from dioecy. We feel that this restriction is well justified as we have

found no theoretical predictions for, or documented examples of, the derivation of andromonoecy from dioecy.

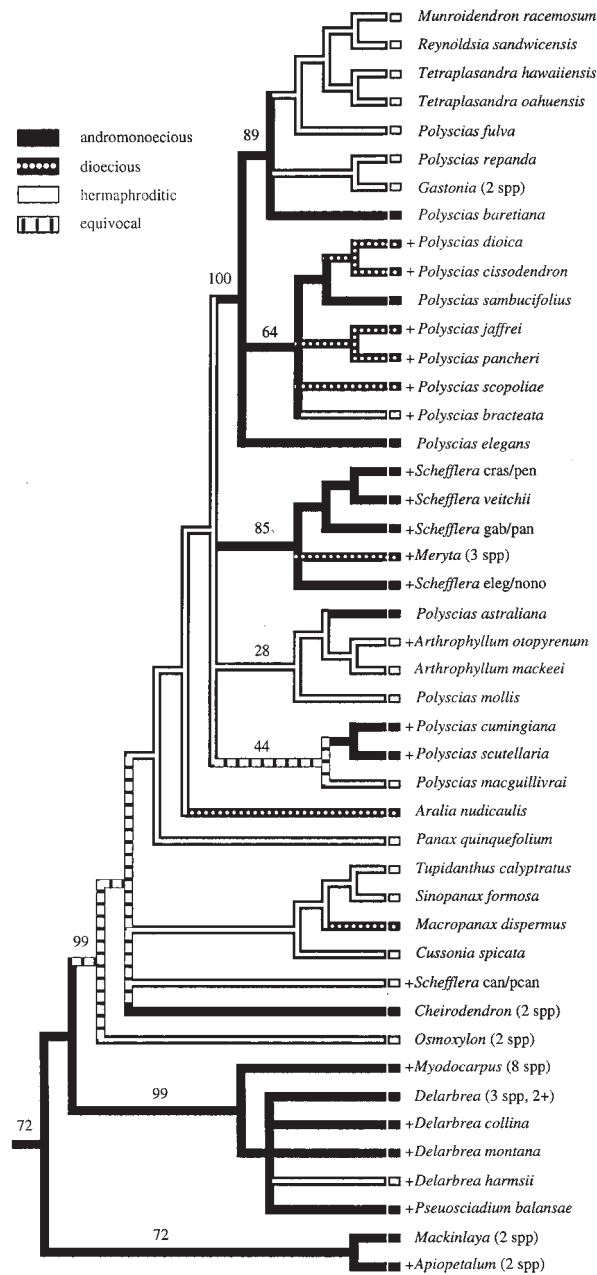
RESULTS

Figure 1 shows the most parsimonious mapping of sexual systems onto our molecular cladogram. New Caledonian taxa are dispersed throughout the tree. They are present in all of the larger clades except two: a terminal one comprising Hawaiian endemics (*Munroidendron* Sherff, *Reynoldsia* A. Gray and *Tetraplasandra* A. Gray) plus an African *Polyscias* J. R. Forst. & G. Forst.; and a more basal one comprising Asiatic *Tupidanthus* Hook.f. & Thomson, *Sinopanax* Li, *Macropanax* Miq., and the African *Cussonia* Thunb. For the 65 species represented in Fig. 1, andromonoecy is the most common sexual system (33 species, 51%), followed by hermaphroditism (22 species, 34%) and dioecy (10 species, 15%). The evolution of sexual systems cannot be fully resolved, due to several polytomies and a number of internal branches for which andromonoecy and hermaphroditism are equally parsimonious character states (those branches are labelled equivocal). Because our purpose here is to evaluate the scheme of Schlessman *et al.* (1990), the remainder of this section parallels their discussion.

Andromonoecy ancestral?

In our expanded analysis here, andromonoecy is the most common sexual system (33 of 65 species, 51%), although it occurs less frequently in non-New Caledonian species (nine of 28, 32%) than in New Caledonian ones (24 of 37, 65%). With just one exception, all species of the genera *Apiopetalum*, *Delarbrea*, *Mackinlaya*, *Myodocarpus* and *Pseudosciadium* are andromonoecious. All of these groups, except *Mackinlaya* F. Muell., are either endemic to, or geographically centred on, New Caledonia. The *Apiopetalum*–*Mackinlaya* and *Delarbrea*–*Myodocarpus*–*Pseudosciadium* clades have strong bootstrap support (72% and 99%, respectively), and their separation from the remainder of *Araliaceae* (the core *Araliaceae*) is consistent with the results of other studies using morphological, anatomical and molecular data (Plunkett *et al.*, 1997; Lowry *et al.*, 2001). In the simple parsimony analysis presented here, the basal positions of these two clades, coupled with the ubiquity of andromonoecy in the five genera comprising them, leads to the unequivocal result that andromonoecy is the ancestral sexual system for the entire tree. We obtained the same result in our trial analysis that allowed all possible character state transitions.

Andromonoecy is also found in two Hawaiian species of *Cheirodendron* Seem. and several species of the apparently polyphyletic genera *Polyscias* and *Schefflera*. These taxa are dispersed among five different clades. Two of those clades include hermaphroditic and dioecious species as well, and in those instances andromonoecy is the ancestral state. However, the ancestral states for *Polyscias cumingiana* C. Presl)



Fern.-Vill.—*P. scutellaria* (Burm.f.) Fosberg and for *Chierodendron* are equivocal, and andromonoecy in *Polyscias australiana* (F. Muell.) Philipson appears to be secondarily derived from hermaphroditism.

Derivation of hermaphroditism from andromonoecy

For the 65 species in Fig. 1, hermaphroditism is much more common elsewhere (17 of 28 species, 61%) than it is on New Caledonia (five of 37 species, 14%). We believe that our sample of non-New Caledonian taxa is representative in the sense that hermaphroditism is indeed more common outside of New Caledonia (Lowry, pers. observ.). It appears that at some point after the divergence of the *Macinklaya*–*Apiopetalum* and *Delarbrea*–*Myodocarpus*–*Pseudosciadium* clades, there was an early evolution of hermaphroditism followed by two or more reversions to andromonoecy. Schlessman *et al.* (1990) hypothesized five specific cases of the derivation of hermaphroditism from andromonoecy in New Caledonian groups. Four of those can be addressed here. Hermaphroditism is clearly derived from andromonoecy in *Delarbrea harmsii* R. Vig. and in *Polyscias bracteata* (R. Vig.) Lowry, ined., but for *Schefflera candelabra* Baill. and *S. pseudocandelabra* R. Vig. our results are equivocal. Our analysis does not support the evolution of hermaphroditism from andromonoecy in the immediate ancestors of *Arthrophyllum*.

Evolution of dioecy

Dioecy is the least common sexual system in our sample, occurring in the genera *Aralia* L., *Macropanax*, *Polyscias* and *Meryta*. *Meryta* is entirely dioecious, while the other three genera are polymorphic with respect to sexual systems. Schlessman *et al.* (1990) addressed only the evolution of dioecy in *Polyscias*, hypothesizing that it was derived from andromonoecy rather than hermaphroditism. Although the results presented here depend in part on our assumption that andromonoecy cannot be secondarily derived from dioecy, they tend to support that view. Our analysis also suggests that there were at least two independent origins of dioecy in ancestors of the genus. It appears that dioecy in *Meryta* is derived from andromonoecy as well.

DISCUSSION

Our preliminary analysis provides varying degrees of support for six specific hypotheses advanced by Schlessman *et al.* (1990). Three are strongly supported:

FIG. 1. Topology of the strict consensus parsimony ITS sequence tree, showing character state transformations for sexual systems. For branches labelled equivocal, andromonoecy and hermaphroditism are equally parsimonious states. Numbers above internal branches are bootstrap support values for clades that are especially important in our analysis. Sixty-five species are represented. In several cases, terminal clades consisting of two or more congeners with the same sexual system have been collapsed into one terminal branch. Species that occur on New Caledonia are indicated by a plus sign in front of the generic name. For conciseness and clarity, the outgroups and the taxa for which we had no data on sexual systems are not shown; including them would not change our results or interpretations.

(1) andromonoecy, rather than hermaphroditism, is the ancestral sexual system for *Araliaceae*; and hermaphroditism in (2) *Delarobrea harmsii* and (3) *Polyscias bracteata* is derived from andromonoecy. Support for (4), the derivation of dioecy from andromonoecy in several New Caledonian species of *Polyscias*, depends in part on an assumption that andromonoecy cannot be secondarily derived from dioecy. With respect to (5) the derivation of hermaphroditism from andromonoecy in *Schefflera candelabra* and *S. pseudocandelabra*, our analysis is equivocal; and finally (6), the hypothesis that the immediate ancestors of *Arthrophyllum* were andromonoecious, is not supported.

Because most of the taxa in this study occur on islands, it is interesting to compare the frequencies of sexual systems with those of well-studied Pacific island floras. High frequencies of dioecy in certain island floras have been cited in support of some theories on the evolution of dioecy from hermaphroditism (Baker, 1967; Carlquist, 1974; Bawa, 1980; Thomson & Barrett, 1981). Although dioecy is the least common system in this study, the proportion of dioecious taxa (15%) is high relative to angiosperms as a whole (4%, Yamplosky & Yamplosky, 1922), and similar to those for the floras of New Zealand (12–13%, Godley, 1979) and Hawaii (14.7%, Sakai *et al.*, 1995). Thomson and Brunet (1990) noted that high frequencies of dioecy are not characteristic of all island floras (see for example Baker & Cox, 1984), and that when high frequencies do occur, the causes are 'almost certainly ... highly indirect'. In a detailed analysis of the Hawaiian flora, Sakai *et al.* (1995) showed that both colonization by dioecious species and the evolution of dioecy from hermaphroditic colonists have contributed to the high incidence of dioecy on those islands. Unfortunately, there is no published tabulation of the proportions of different sexual systems for the flora of New Caledonia.

In our study, the frequency of andromonoecy was very high (51% overall, 65% for New Caledonia). In the past, andromonoecy has been frequently overlooked by systematists, even in familiar groups such as the apioid umbellifers, where it has long been known to be common. Thus, we suspect that many estimates of the frequency of andromonoecy in angiosperms as a whole may be too low. For example, the percentage of strictly andromonoecious species in the pioneering, often-cited compilation by Yamplosky and Yamplosky (1922) is only 1.7, or approximately half that of dioecious species. Perhaps the most reliable estimates for a particular flora come from Sakai *et al.* (1995), who analysed the flora of Hawaii to report values of 2.5% (based on Carlquist, 1974) and 4.5% (based on Wagner *et al.*, 1990). In any case, the frequency of andromonoecy in this study is exceedingly high. In our view, this is due to our focus on the araliads of New Caledonia, where a large number of species belong to ancestral lineages and have retained the ancestral sexual system. Because andromonoecy is relatively uncommon in angiosperms as a whole and is usually thought to be derived from hermaphroditism (Bertin, 1982; Willson, 1983), our conclusion raises the intriguing question of how andromonoecy evolved in the common ancestor of araliads. We are in the process of evaluating our data with maximum likelihood methods for phylogenetic reconstruction. We are also

integrating data on other reproductive characters, such as inflorescence structure and patterns of floral dichogamy (cf. Schlessman *et al.*, 1990), so we can more fully elucidate the evolutionary forces that have produced the diversity of sexual systems in araliads. At present, one significant impediment to progress is a lack of reliable data on the sexual systems of relevant taxa, for which direct observations are almost always required. We encourage all those who conduct field studies on *Apiales* and their relatives to observe and record information on floral biology, documenting variation in inflorescence structure, floral morphology and floral phenology.

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