MISSOURI BOTANICAL GARDEN

EARLY EVOLUTION OF DALECHAMPIA (EUPHORBIACEAE): INSIGHTS FROM PHYLOGENY, BIOGEOGRAPHY, AND COMPARATIVE ECOLOGY[1]

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ABSTRACT

Dalechampia contains over 120 species and occurs throughout the lowland tropics of Asia, Africa, and the New World. Most species in both the Old and the New World secrete terpenoid resin from large glandlike aggregations of bractlets in the pseudanthial inflorescences (blossoms) and are pollinated by bees that collect resin for use in nest construction. Using comparative chemical, morphological, and ecological data and phylogenetic analyses, I attempt to ascertain the early evolutionary and biogeographic events that led to the present distribution of species, character states, and pollination systems throughout the tropics. Available evidence suggests the genus originated in western Gondwana or South America in the mid Cretaceous or early Tertiary, respectively, and spread throughout the tropics by the rafting of land masses, or by migration across higher latitudes when they had subtropical climates, or both. There is some evidence for two migrational events between the Old and New Worlds. The original pollination system may have involved pollination by pollen-collecting insects or by fragrance-collecting male euglossine bees. The origin of pollination by resin-collecting bees appears to have been a consequence of a preadaptation (exaptation): the earliest *Dalechampia* apparently used triterpene resins to defend flower parts against attack by herbivores and/or microbes, and resin secondarily assumed the role of pollinator reward. The mutualistic relationship with resin-collecting bees may have originated independently in the Old and New Worlds.

Trans-oceanic disjunctions of similar plant species have intrigued plant biologists since the earliest botanical explorers began to report them. We have long wondered how such disjunctions arose, when and how dispersal occurred, and how populations evolved in isolation from each other. Disjunctions create natural evolutionary experiments in which two or more populations of similar genetic stock evolve independently in response to local environmental conditions. An interesting challenge is to unravel the history of disjunctions and reconstruct the evolutionary events that have occurred since the isolation of plant populations.

Research on this topic has rarely proceeded beyond the phase of description of the distributions of disjunct sister taxa and their taxonomic relationships. This is because research on historical phenomena, especially those as ancient as the events creating trans-oceanic disjunctions, is extremely difficult, and until recently required a detailed fossil record. The development of powerful computer-assisted methods of phylogeny reconstruction, however, now makes it realistic to attempt retrospective analysis of ancient biogeographic and evolutionary processes in the absence of a fossil record (see Donoghue, 1989). The field of vicariance biogeography represents one such approach in its attempt to use analyses of phylogenetic relationships of several independent taxa as an aid to ascertaining the processes that affected the distribution of those taxa (see review in Humphries & Parenti, 1986).

In the present paper I consider four questions about the early evolutionary and biogeographic events that affected the members of the pantropical euphorb genus *Dalechampia*: (1) Where and when did the genus originate? (2) What series of events led to the present geographical distribution of species, character states, and pollination systems? (3) What was the original pollination system in the

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genus, and how did the early diversification of pollination systems occur? (4) How, when, and where did the novel mutualism with resin-collecting bees arise? Using the cladistic method of phylogeny reconstruction, I develop explicit hypotheses addressing the four historical questions. I evaluate the hypotheses by considering independent data on the relationships between the plants and their herbivores and pollinators.

NATURAL HISTORY AND DISTRIBUTION OF *DALECHAMPIA*

Dalechampia is distinctive within the Euphorbiaceae: the ca. 120 species have pseudanthial inflorescences (blossoms) in which usually 3 pistillate flowers and usually 4–16 staminate flowers are united into subterminal and terminal cymules, respectively. Close examination of the *Dalechampia* inflorescence, however, indicates that its arrangement is probably homologous to that of the inflorescences of *Tragia* and *Plukenetia* (although in these taxa the inflorescences are not pseudanthial, i.e., do not function as single pollination units as in *Dalechampia*) (Webster & Webster, 1972). These three taxa are also similar in habit. Unlike most other euphorbs, *Tragia* and *Plukenetia* comprise viny species and *Dalechampia* comprises mostly viny species. *Tragia* and *Dalechampia* are also similar in having urticating, crystaliferous trichomes of virtually identical morphology (Webster & Webster, 1972). For these reasons, Webster (1994) has recently proposed that *Dalechampia* be included in tribe Plukenetieae (with *Tragia* and *Plukenetia*) rather than isolated in its own tribe as in earlier treatments (e.g., Webster, 1975). The striking similarities among these three genera and their inferred close relationship make it possible to use, with considerable confidence, *Tragia* and *Plukenetia* as candidate outgroups in the phylogenetic analyses described below.

Despite the relatively uniform blossom morphology in *Dalechampia*, there is considerable variation in the reproductive biology. Most species in both the Paleotropics and Neotropics offer resin as a pollinator reward and are pollinated by female or worker bees that collect resin from a variety of plant sources and use it in nest construction (Cammerloher, 1931; Armbruster & Webster, 1979; Armbruster, 1984; Armbruster & Mziray, 1987). The resin is secreted by a cluster of modified bractlets (the "resin gland") associated with the staminate flowers (Webster & Webster, 1972). About a dozen species in the New World offer fragrances as a pollinator reward and are pollinated by fra-

grance-collecting male euglossine bees (Apidae: Euglossini) (Armbruster & Webster, 1979; Armbruster et al., 1989; Armbruster et al., 1992). These bees apparently use fragrances as precursors in the biosynthesis of sex pheromones (Dressler, 1982; Whitten et al., 1989). Several species in the Neotropics and in Madagascar appear to produce no reward for pollinators other than pollen; these species are pollinated by pollen-collecting bees and beetles (Armbruster et al., 1993).

Species of *Dalechampia* are found throughout the lowland tropics of Asia, Africa, and the New World, although the greatest diversity is expressed in South America (Fig. 1). Species bearing resin glands (and pollinated by resin-collecting bees) are by far the most widespread; they occur in every major region where *Dalechampia* is found, except Madagascar. Those species pollinated by male euglossine bees are necessarily restricted to the Neotropics, because euglossines are endemic to the New World. Species lacking the resin gland and pollinated by pollen-seeking insects are most diverse in Madagascar, but are also found in northern South America and southern Central America.

Several authors have concluded that the glandless species found in Madagascar form the most basal species group in the genus (Michaelis, 1924; Magin, 1987), while Webster & Armbruster (1991) considered the glandless species of northern South America (sect. *Rhopalostylis*) to form probably the most basal group. It is possible that the Madagascan and South American glandless species, which share numerous characteristics, form a single basal monophyletic or paraphyletic cluster of species. This raises the possibility that *Dalechampia* has a complex biogeographic history, with multiple migrations among the continents and independent evolution of the mutualism with resin-collecting bees in the Old and New World tropics (Armbruster & Mziray, 1987). Alternatively, if the resemblance between Madagascan species and members of section *Rhopalostylis* is the result of homoplasy (character convergence and/or reversals), there may be no reason to reject a very simple biogeographic history involving an origin in the New or the Old World, followed by dispersal to the other hemisphere.

Armbruster & Mziray (1987) proposed four alternative dispersal hypotheses that could explain the present distribution of *Dalechampia* species: (1) recent long-distance dispersal of species among continents, (2) migration across mid- to high-latitude land bridges during the Tertiary, when these latitudes had subtropical climates, (3) a nearly continuous western Gondwanan distribution in the mid
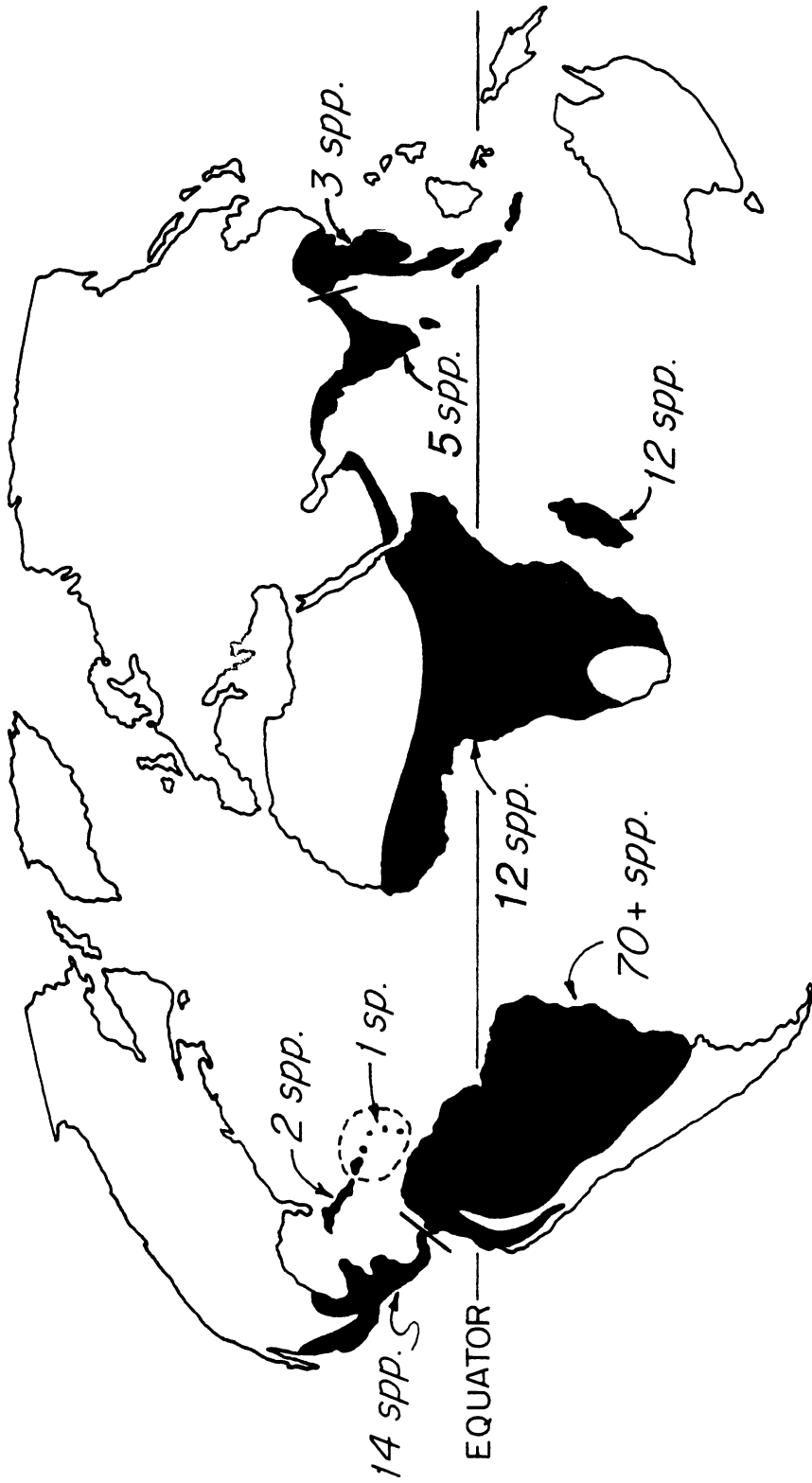
FIGURE 1. Approximate distribution and number of species of *Dalechampia* in the Paleo- and Neotropics.

to late Cretaceous disrupted by subsequent conti-
nental drift, and (4) distribution of primitive *Dal-
echampia* in South America, Africa, and Mada-
gascar by continental drift, followed by extinction
of primitive species in Africa and a second migra-
tion (either by long-distance dispersal or migration
via higher latitudes) of more derived species be-
tween South America, Africa, and Asia. Circum-
stantial evidence they provided supported the sec-
ond, third, and fourth hypotheses, but not the first.
They did not attempt to identify the site of origin
of the genus nor the direction dispersal events. The
purpose of the present study is to use phylogenetic
analyses of the New and Old World species to
refine these biogeographic hypotheses and specify
possible sites of origin of the genus, directions of
dispersal, pollination ecology of the earliest species,
and the site(s) of origin of the novel mutualism
with resin-collecting bees.

PHYLOGENETIC INFERENCE

METHODS

To reconstruct phylogenetic relationships among
Old and New World species of *Dalechampia*, I
conducted cladistic analyses on a data set of 46
morphological characters (Table 1) from 25 neo-
tropical, 4 African, and 3 Madagascan species of
Dalechampia and representatives of two sister
genera, *Tragia* and *Plukenetia*, to serve as possible
outgroups (Appendix). The species of *Dalecham-
pia* were chosen to represent the major species
groups in the genus. I used the heuristics algorithm
of PAUP 3.0 (see Swofford, 1993) on a Macintosh
microcomputer to find the shortest trees. In this
analysis ancestral states were not specified (i.e.,
characters were not polarized). Instead, PAUP de-
termined the ancestral states through global par-
simony (Maddison et al., 1984), selecting the more
parsimonious of the two sister taxa to be the out-
group. I used MacClade 3.0 (see Maddison & Mad-
dison, 1992) to explore alternate tree topologies,
analyze character evolution, assess tree congru-
ence with alternative biogeographic hypotheses, and
produce graphics.

After an initial run with the full set of taxa
(including the sister genera), I eliminated all but
one member of each stable, well defined clade of
neotropical species and all but two of the very
similar taxa in the paraphyletic section *Rhopalo-
stylis*. This reduced the number of New World
taxa to 11 and Old World taxa to 4. The decreased
number of taxa greatly reduced PAUP run time
on the computer. To further reduce run times the
results of the initial cladistic analysis were used to

polarize characters and specify ancestral character
states, and the outgroups were eliminated. These
procedures left unaltered the relative positions of
Old and New World taxa.

Iterative cladistic runs were conducted to de-
termine the sensitivity of cladistic results to initial
assumptions about character reversibility (Table 2).
I varied the assumption of character reversibility
(reversible vs. irreversible between plesiomorphic
[primitive] and apomorphic [derived] states) for
each of three selected characters, and in all possible
combinations of the three characters.

I then examined each of the numerous maxi-
mally parsimonious trees to determine the simplest
biogeographic and evolutionary scenarios that could
explain the distribution of taxa, character states,
and pollination systems and were consistent with
the tree. This was accomplished by manually map-
ping distribution and pollination ecology data onto
each tree using the parsimony assumption (see
Maddison & Maddison, 1992).

RESULTS

When all characters were assumed reversible,
cladistic analysis of the set of 34 taxa yielded 436
equally parsimonious trees (120 steps, consistency
index [CI] = 0.47). The large number of equally
parsimonious trees reflects instability in the place-
ment of a few similar taxa (Fig. 2). The gland
characteristics, pollination ecology, and geograph-
ical distribution of the various ancestral taxa (nodes
of the tree) were inferred by parsimony from the
distribution of these characteristics across the ex-
tant taxa (Maddison & Maddison, 1992). "Map-
ping" of characteristics onto the consensus tree
allowed inference of the history of these ecological
and biogeographic features. Despite the abundance
of equally parsimonious trees, the evolutionary and
biogeographic implications of this cladistic analysis
generally supported Hypothesis 1 (Table 3): *Dal-
echampia* originated in the Neotropics or western
Gondwana, and the earliest species were initially
pollinated by either fragrance-collecting male eu-
glossines or pollen-collecting insects (Figs. 2, 3).
Dalechampia evolved a mutualistic (pollination)
relationship with resin-collecting bees in the Neo-
tropics, and relatively recently in the genus's evo-
lutionary history a resin-reward species colonized
Africa. More recently, there occurred a migration
from Africa to Madagascar. The colonists of Mad-
agascar apparently evolved pollination by pollen-
collecting bees and/or beetles just after they col-
onized Madagascar.

Cladistic analysis of the reduced set of taxa

TABLE 1. Characters and character states used in phylogenetic analyses. The "0" character state is the ancestral condition, as determined by global-parsimony outgroup analysis. * indicates character was not used in the phylogenetic analysis.

1. Nature of proximal involucral bract: 0 = stipuliform; 1 = involucral.
2. Nature of distal involucral bract: 0 = stipuliform; 1 = involucral.
3. Position of proximal involucral bract: 0 = separated from pistillate cymule; 1 = adjacent to pistillate cymule.
4. Stipels on proximal involucral bract: 0 = present; 1 = absent.
5. Number of basal veins of involucral bracts: 0 = 3; 1 = 5 or more.
6. Color of involucral bracts: 0 = white to pale green; 1 = pink; 2 = yellow; 3 = brown; 4 = deep green.
7. Shape of base of involucral bracts: 0 = cuneate; 1 = cordate.
8. Shape of tip of involucral bracts: 0 = entire, acute; 1 = lobed.
9. Persistence of involucral bracts: 0 = deciduous shortly after anthesis; 1 = persistent into fruiting.
10. Number of pistillate sepals: 0 = 5–6; 1 = >7; 2 = 4.
11. Margins of pistillate sepals: 0 = entire; 1 = lobed.
12. Presence of distal pistillate involucellar bractlets: 0 = present; 1 = absent.
13. Size of distal pistillate involucellar bractlets: 0 = small, stipuliform; 1 = large, enveloping.
14. Shape of pistillate sepals (excluding lobes): 0 = ovate; 1 = linear.
15. Style shape: 0 = cylindrical to slightly dilated at tip; 1 = clavate; 2 = strongly dilated at tip; 3 = umbraculiform; 4 = deeply lobed.
16. Number of stamens: 0 = 5–10; 1 = >11.
17. Fusion of staminate involucellar bracts: 0 = free; 1 = connate.
18. Symmetry of staminate pleiochasial arms: 0 = decussate; 1 = bilateral.
19. Number of staminate pleiochasial arms: 0 = 4; 1 = 5.
20. Arrangement of staminate bractlets: 0 = symmetrically distributed; 1 = clustered into "gland."
21. Tip of staminate bractlets: 0 = acute; 1 = truncate.
22. Margins of staminate bractlets: 0 = entire; 1 = laciniate.
23. Resin secretion by staminate bractlets: 0 = absent; 1 = present.
24. Resin color: 0 = clear, whitish; 1 = yellow, orange; 2 = maroon; 3 = blue.
25. Staminate sepal color: 0 = green to whitish; 1 = pink.
26. Stigma color: 0 = pale to deep green; 1 = pink to maroon.
27. Habit: 0 = vine; 1 = shrub.
28. Relative petiole length: 0 = >¼ limb length; 1 = <¹/₁₀ limb length.
29. Leaf shape: 0 = simple, entire; 1 = compound; 2 = simple, 3–5-lobed.
30. Leaf venation: 0 = palmate; 1 = pinnate.
31. Leaf stipules: 0 = stipuliform; 1 = foliose.
32. Involucral bract stipules: 0 = stipuliform; 1 = foliose.

TABLE 1. Continued.

33. Pollen shape: 0 = prolate; 1 = subspherical.
34. Seed surface: 0 = smooth; 1 = rugulose; 2 = tuberculate.
35. Seed shape: 0 = round; 1 = 3-angled; 2 = lenticular; 3 = slightly flattened.
36. Petiole of proximal involucral bract: 0 = present; 1 = absent.
37. Pollen exine: 0 = reticulate; 1 = psilate.
38. Relative size of pistillate sepals in fruit: 0 = <½ capsule length; 1 = approximately capsule length; 2 = fully enveloping capsule.
39. Stinging crystalliferous trichomes: 0 = absent; 1 = present.
40. Number of carpels: 0 = 3; 1 = 4.
41. Number of sterile arms in staminate pleiochasium: 0 = 0; 1 = 1; 2 = 2.
*42. Pollination: 0 = pollen-collecting bees (*Trigona* workers) or cetoniine beetles; 1 = resin-collecting bees (*Hypanthidium* females, *Trigona* workers, *Euglossa*, *Eulaema*, and *Eufriesea* females); 2 = fragrance-collecting male euglossine bees (*Euglossa*, *Eulaema*, *Eufriesea*).
43. Fusion of distal pistillate bractlets: 0 = free; 1 = connate.
44. Presence of leaf stipels: 0 = absent; 1 = present.
45. Leaf nectary: 0 = absent; 1 = present.
46. Inflorescence condensation: 0 = not condensed; 1 = highly condensed.
47. Expression of leaf stipules: 0 = well developed; 1 = reduced to absent.

yielded 50 equally parsimonious trees (70 steps, CI = 0.61). All of these were consistent with the biogeographical and evolutionary conclusions drawn from the analysis of the full set of taxa (Table 2, Fig. 4).

How reasonable is it to assume that all characters can evolve forward and backward repeatedly? Is it realistic to expect that structures are regained as easily (frequently) as they are lost? For certain characters at least, the answer may be "no." Upon reflection I became uncomfortable with allowing characters 17 (fusion of male involucel), 20 (presence of a "resin gland"), and 41 (presence of sterile pleiochasial arms) to revert to the plesiomorphic state as they do in all 436 (first analysis) and 50 (second analysis) maximally parsimonious trees. It seemed unlikely (although not impossible) from a developmental perspective for these characters to revert from the derived (apomorphic) condition back to the primitive (plesiomorphic) condition. For example, consider character 17: whether the involucellar bracts of the staminate subinflorescence (pleiochasium) are free, each subtending a pleiochasial arm, or are connate (fused). Based on outgroup comparisons, the former state appear to be plesiomorphic and the latter derived. Al-

TABLE 2.   Consequences of varying initial assumptions of reversibility of characters upon the biogeographic/ evolutionary conclusions drawn from the most parsimonious trees obtained by cladistic analysis of the reduced list of *Dalechampia* taxa. Numbers indicate biogeographic/evolutionary hypothesis(es) with which the most parsimonious trees were consistent (see Table 3). Numbers in parentheses indicate the proportion of maximally parsimonious trees consistent with each hypothesis.

Character assumed irreversible	Alone	In combination with character		
		20	41	17, 20
17. Fusion of staminate bracts	2 (96%)[1]	3 (60%)[2]	3 (100%)[3]	
	4 (3%)	2, 3 (33%)		
	3, 4 (1%)	5 (4%)		
		2, 5 (4%)		
20. Presence of resin gland or its vestige	3 (60%)[2]	—	3 (100%)[3]	—
	3, 5 (33%)			
	5 (4%)			
	2, 5 (4%)			
41. Presence of sterile arms in staminate pleiochasium	3 (100%)[3]			3 (100%)[3]
None	1 (100%)[4]	—	—	—

[1] N = 252 equally parsimonious trees.
[2] N = 114 equally parsimonious trees.
[3] N = 42 equally parsimonious trees.
[4] N = 50 equally parsimonious trees.

though the shift to the connate condition may not be expected to occur frequently, it seems even less likely that the connate involucre would split up into the "correct" number of bractlets, in the arrangement that recreates the original relationship between bracts and pleiochasial arms. Thus if there is homoplasy in this character, it seems more likely to reflect convergence than reversal.

The assumption of irreversibility was applied to each of these characters in turn and in all possible combinations. The cladograms from the seven different runs generated hypotheses 3, 2, 5, and 4 in order of frequency (Tables 2, 3). By far the most commonly supported hypothesis was H₃, with H₂ a distant second. For example, the assumption that a sterile pleiochasial arm cannot readily become fertile again resulted in 42 equally parsimonious trees that all support H₃: *Dalechampia* originated in the Neotropics or western Gondwana, a glandless lineage colonized the Paleotropics (by the breakup of Gondwana or migration via higher latitudes), mutualisms with resin-collecting pollinators evolved separately in the Old and New Worlds, followed by recolonization of the Neotropics by Old World gland-bearing (resin-producing) species, extinction of the glandless species from most of Africa, and their persistence in Madagascar (Fig. 5).

The assumption that the fusion of staminate bracts is irreversible, when taken alone, produced

252 maximally parsimonious trees, 96% of which supported H₂ (Table 2). In this hypothesis, *Dalechampia* originated in the Neotropics or western Gondwana, a glandless stock colonized the Paleotropics (by the breakup of Gondwana or migration via higher latitudes), the mutualism with resin-collecting bees originated in the Neotropics, followed by one or more additional colonizations of the Old World from the New by gland-bearing (resin-producing) species (Fig. 6).

All other assumptions and combinations of assumptions of irreversibility of characters yielded shortest trees that supported H₃ either all or most of the time (Table 2). Thus it appears that the most likely biogeographic/evolutionary hypotheses are H₁, H₃, and H₂. Which of these one favors depends not only on whether one assumes characters in general are reversible or irreversible, but also on which particular character or combination of characters are assumed irreversible. Assumptions about the irreversibility of certain characters have stronger effects on biogeographic conclusions than others. That is, assumptions of irreversibility of certain characters appear to be dominant, in their effects, over others. The "pecking order" apparent in Table 2 is Character 41 > Character 20 > Character 17.

All of the phylogenetic hypotheses derived from the cladistic analyses lead to two basic conclusions. (1) *Dalechampia* originated in the Neotropics or
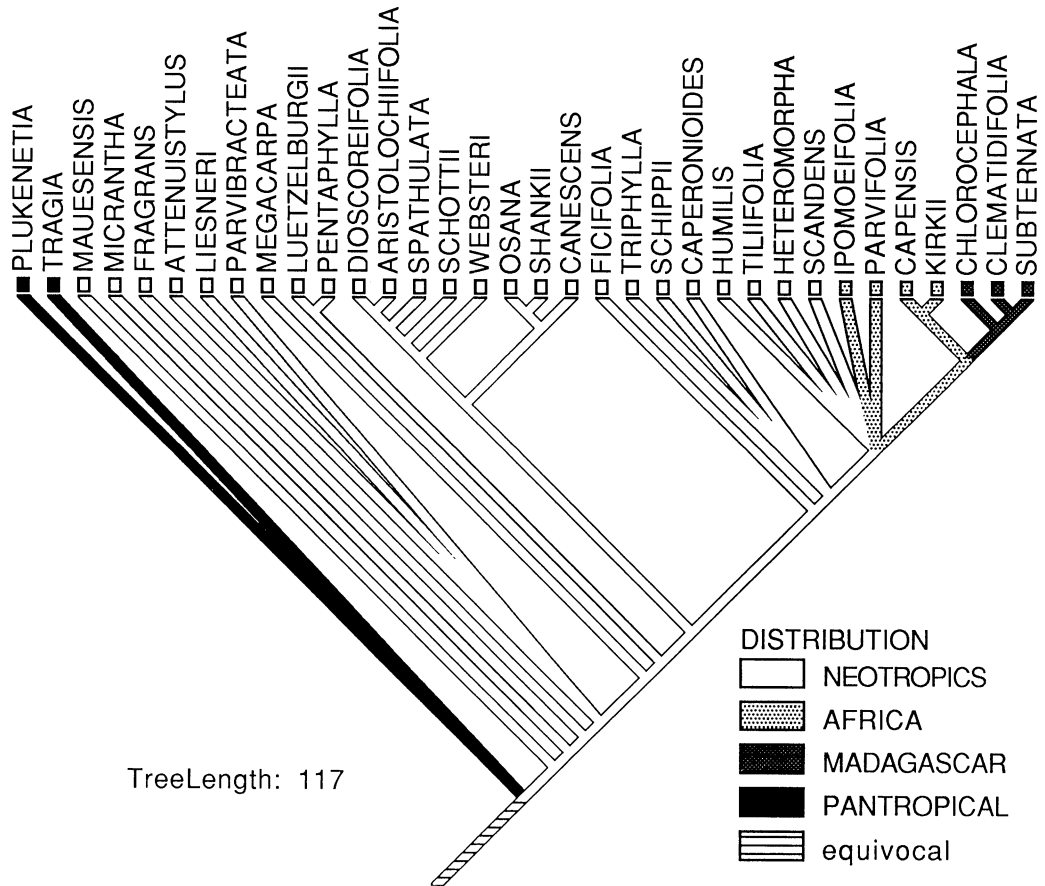
FIGURE 2. Consensus tree for set of 32 *Dalechampia* species and two candidate outgroups (*Tragia* and *Plukenetia*) based on assumption that all characters are reversible. Taxa with unstable arrangements in the 436 maximally parsimonious trees are indicated by polytomies (points of branching of more than two taxa).

western Gondwana. (2) The earliest species were pollinated by pollen-collecting insects or fragrance-collecting male euglossine bees. Uncertainty remains as to when and in which direction dispersal between the Old and New Worlds occurred.

TESTS OF HYPOTHESES

There are several sources of independent data that could be used to evaluate the biogeographic/evolutionary hypotheses generated by phylogenetic analyses. These include information on the relationships among specialist insect herbivores on Old and New World *Dalechampia*, the chemical defense systems that *Dalechampia* uses against herbivores, details of pollination biology of Old and New World *Dalechampia*, and morphological details of the resin gland of Old and New World species.

SPECIALIST HERBIVORES ON *DALECHAMPIA*

There are several genera of nymphalid butterflies whose larvae appear to be specialist folivores on New and Old World *Dalechampia*. The phylogenetic relationships among the New and Old World butterflies may give us some clues about the history of their and their host plants' migrations among the Neotropics and Paleotropics.

Assuming that specialist *Dalechampia* folivores feed only on *Dalechampia*, one can make several specific predictions about the phylogenetic relationships between those of the New and Old Worlds, depending on the biogeographic scenario used to account for their present distribution. (1) If the initial dispersal of *Dalechampia* from the New World to the Old occurred by long-distance dispersal after the continents achieved close to their present positions, the butterfly herbivores in the
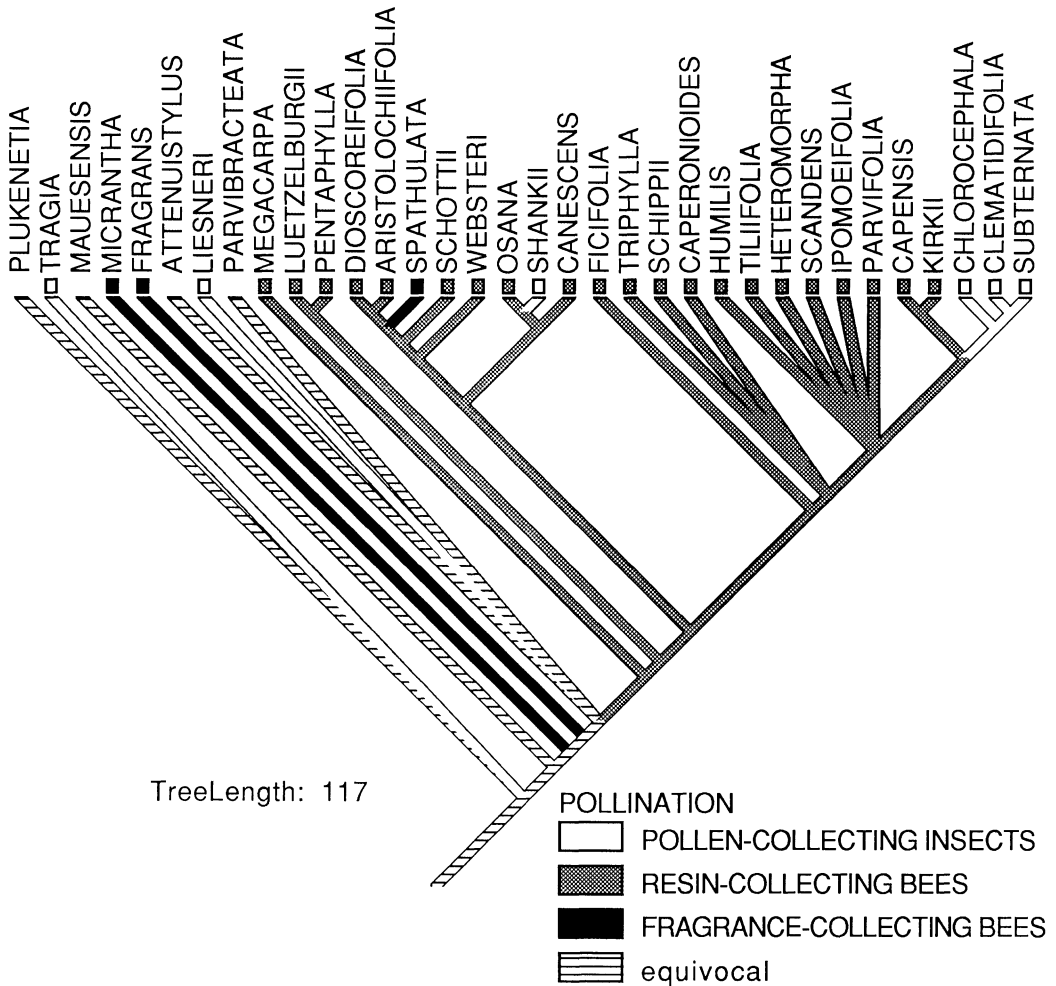
FIGURE 3.   Same cladogram as is in Figure 2, with pollination systems mapped onto the branches.

Old and New Worlds should be completely unre-
lated. This is because it is extremely unlikely that
both host plant and herbivore would have become
established in the Paleotropics by long-distance dis-
persal from the New World, and the Old World
herbivore fauna would more likely be the result of
members of the local butterfly fauna evolving to
feed on *Dalechampia*. (2) If the initial dispersal
from the New World to the Old occurred by mi-
gration of a semi-continuous population stretching
across North America and Europe or Asia in the
early to mid Tertiary, when these continents had
subtropical climates, the butterfly herbivores in the
Old World should be closely related sister taxa of
the New World species. This is because a semi-
continuous population of host plants across the
higher latitudes should have allowed a semi-con-

tinuous population of the herbivores to also disperse
into the Old World. (3) If the initial dispersal from
the New World to the Old occurred by a continuous
population being split into two or more populations
by the rafting apart of the continents (the breakup
of Gondwana) in the Cretaceous, the Old and New
World herbivores should again be sister taxa, but
not as closely related as in the second scenario.

There is some ecological information available
on butterfly herbivores that feed on *Dalechampia*
(Table 4; see Armbruster, 1983; Armbruster &
Mziray, 1987; DeVries, 1987). Unfortunately there
is not yet detailed information available on their
phylogenetic relationships. The systematic (Table
4) and phylogenetic information that is available
indicates a close phylogenetic relationship between
Old and New World taxa, possibly forming two

TABLE 3. Five most parsimonious biogeographic hypotheses derived from the cladistic analyses under varying assumptions about character reversibility.

H_1.	The genus and the resin-collection mutualism originated in the New World, with a subsequent migration to the Old World from the New and the loss of the resin-collection mutualism in Madagascan taxa.
H_2.	The genus originated in the New World or western Gondwana; an initial migration (or rafting) to the Old World from the New was followed by the evolution of the resin-collection mutualism in the New World, and then by a second migration to the Old World by gland-bearing species.
H_3.	The genus originated in the New World or western Gondwana; an initial migration (or rafting) to the Old World was followed by the independent evolution of the resin-collection mutualism in Old and New Worlds, followed by a migration of gland-bearing species to the New World from the Old.
H_4.	The genus and the resin-collection mutualism originated in the New World, followed by a migration of gland-bearing species to the Old World, loss of the mutualism in Madagascar, and finally recolonization of the New World by gland-bearing species.
H_5.	The genus and the resin-collection mutualism originated in the New World, followed by two or more migrations of gland-bearing species to the Old World and subsequent recolonization of the New World by gland-bearing species.

groups with vicariant genera in both areas (Jenkins, unpublished manuscript; Armbruster & Mziray, 1987; Otero, 1990; Ackery, 1988). This observation generally supports the predictions of the hypotheses of early *Dalechampia* "migration" by continental drift and migration in the Tertiary via higher latitudes. It does not support the hypothesis of recent long-distance dispersal (see Armbruster & Mziray, 1987, for additional discussion). Thus the evidence from the relationship among the lepidopteran herbivores of the Old and New Worlds supports the hypotheses that show a fairly early colonization of the Old World from the New.

The observation that many of the lepidopterans that feed on *Dalechampia* may sometimes also feed on *Tragia* (Table 4), however, raises another possibility. It is possible that *Tragia* and its herbivores achieved a pantropical distribution prior to *Dalechampia*. If this were true, then the lepidopterans now specializing on *Dalechampia* in the Old

World could be derived from *Tragia*-feeding ancestors. In this case phylogenetic relationships among lepidopteran herbivores may yield insights into the biogeographic history of *Tragia*, but not of *Dalechampia*.

EVOLUTION OF THE RESIN REWARD SYSTEM

How likely is it that an unusual pollination system such as pollination by resin-collecting bees could have originated more than once within *Dalechampia*? Elsewhere in the plant kingdom it has apparently originated only one other time, in *Clusia* (Guttiferae) (Armbruster, 1984). Therefore, it seems at first highly unlikely that pollination by resin-collecting bees would have arisen multiple times in the genus. Any biogeographic scenario invoking this would also seem improbable. Consideration of how the system arose, however, makes multiple origins of the relationship seem more probable.

TABLE 4. Provisional phylogenetic classification and host-plant associations of lepidopteran herbivores feeding on *Dalechampia* and related genera. Systematic relationships and host plant information from Jenkins (unpublished manuscript), Armbruster & Mziray (1987), Ackery (1988), Otero (1990), and D. Lees (unpublished data).

Neotropics	Paleotropics
Nymphalidae	
Subfamily Eurytelinae	
Tribe Neptini	
	Neptis (T[1], A, others)
Tribe Eurytelini	
Biblis (T)	*Byblia* (D, T, P)
Mestra (T, D)	*Mesoxantha* (T)
	Neptidopsis (D, T)
	Ariadne (T, R, D, Te, Ac)
	Eurytela (T, R, D, Te)
Tribe Epicaliini	
Hamadryas (D, T)	*Sallya* (D, T, others)
Ectima (D)	
Panacea (D??)	
Batesia (D??)	
Catonephele (A, D, V)	
Myscelia (D, Ad)	
Nessaea (P, A)	
Tribe Dynamini	
Dynamine (D, T)	

[1] Abbreviations for host plants: A = *Alchornia*, Ac = *Acalypha*, Ad = *Adelia*, D = *Dalechampia*, P = *Plukenetia*, R = *Ricinus*, T = *Tragia*, Te = *Tetracarpium*, V = *Veconcibea*.
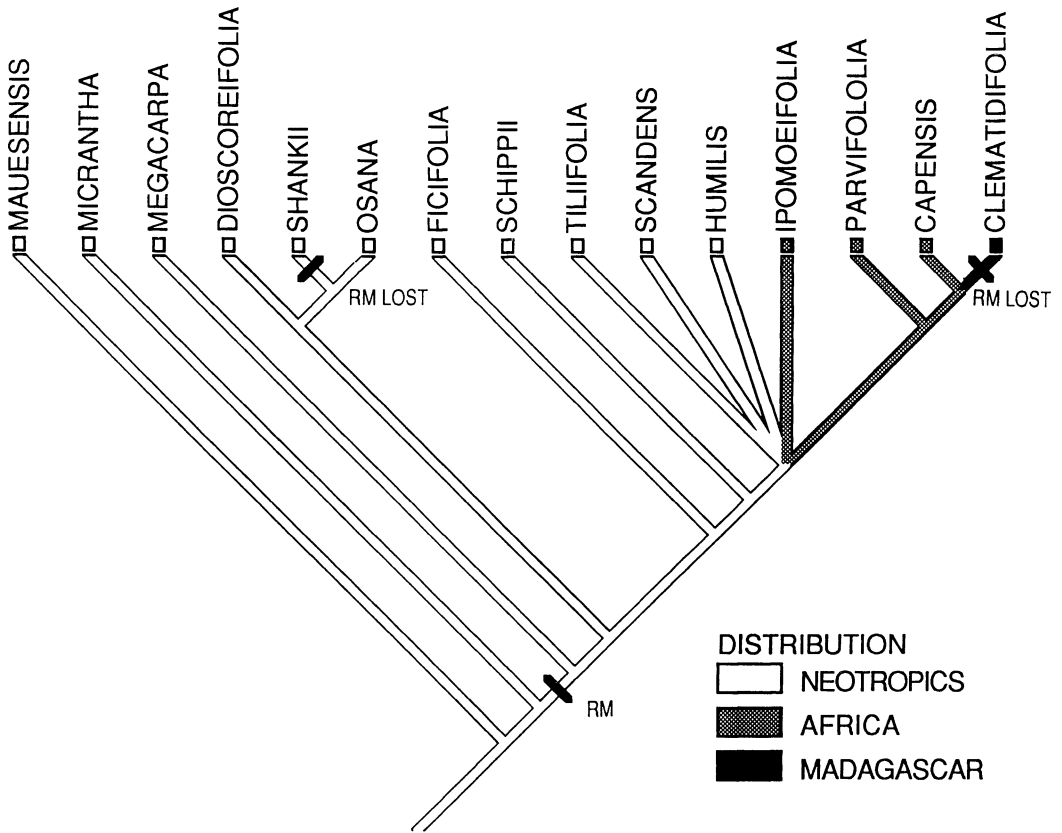
FIGURE 4.   Consensus tree for the simplified set of taxa, assuming that all characters are reversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 50 maximally parsimonious trees are indicated by polytomies.

In all *Dalechampia* species that reward pollinating bees with triterpenoid resins, the secretory bractlets are clustered into a glandlike structure in the staminate subinflorescence. Comparative morphological studies of gland-bearing and non-glandbearing species show that the bractlets of the gland are homologous to those that subtend the staminate flowers (and cover them in bud) in glandless species (Armbruster, unpublished obs.). The bractlets also secrete the same mixture of oxygenated triterpenes, even though the compounds play no role in pollination. These bractlets and their resinous secretions would instead appear to play a role in defending the staminate flowers from depredation by herbivorous insects or microbes. Also consistent with this idea is that some of the same compounds are also secreted by glands along the margins of young leaves, stipules, and/or sepals of many *Dalechampia* species, where they appear to play a role in defending those parts from herbivores (Armbruster, Howard & Debevec, unpublished data).

Species of *Dalechampia* identified in cladistic analyses as diverging early in the evolution of the genus do not use resin-collecting bees as pollinators, although they do produce resins from inflorescence bractlets. Character mapping indicates that the common ancestor of the rest of the genus also had this feature. This suggests that resin secretion in the genus first arose as a way of protecting reproductive tissues from attack by insect herbivores or microbes. Its presence in the inflorescence set the stage for resin-collecting bees to visit flowers to collect the resin for nest construction. These bees secondarily assumed the role of pollinators. The plant, in response, evolved higher rates of resin secretion, and the bractlets became organized into a gland from which the resin could be collected more efficiently. Thus the resin reward system probably evolved from a preadaptation (exaptation). Because the preadaptation was apparently "in place" very early in the evolution of the genus, it was probably present in the first *Dalechampia*
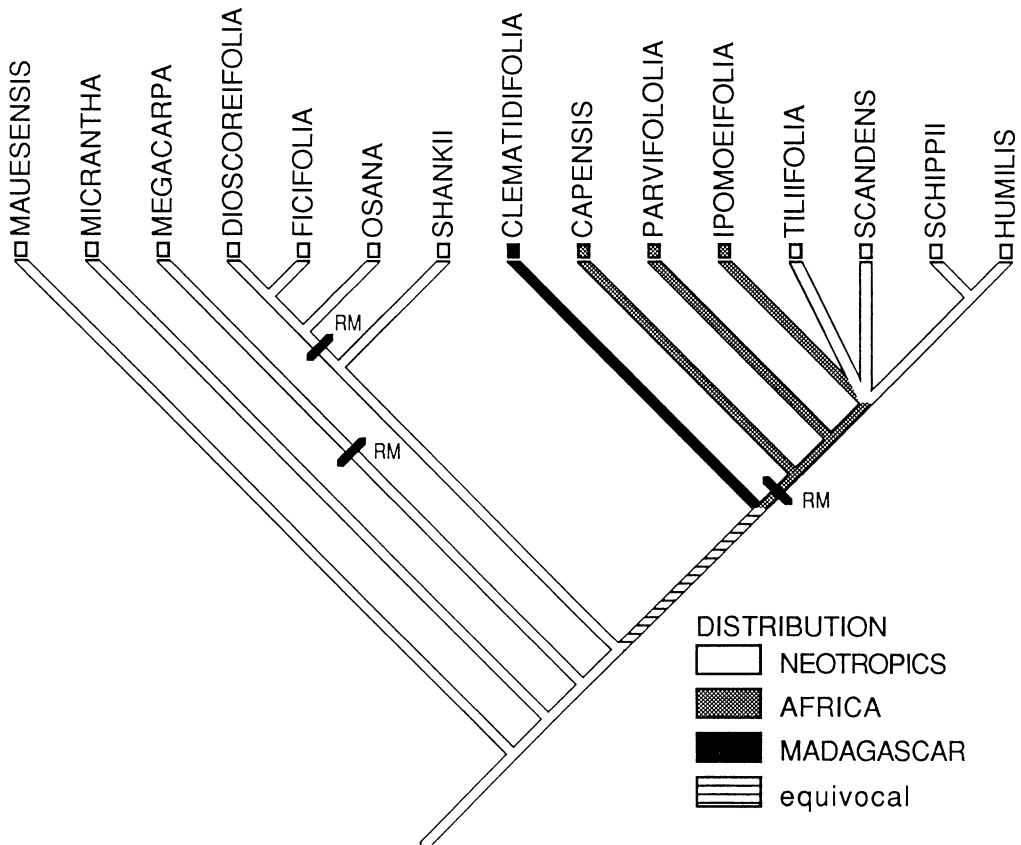
FIGURE 5. Consensus tree for the simplified set of taxa, assuming that all characters are reversible except character 41 (see Table 2), which was assumed irreversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 42 maximally parsimonious trees are indicated by polytomies.

to arrive in the Old World, as well as in the New World species. This is confirmed by the secretion of "defense" (non-reward) resins by many of the Madagascan species as well as several members of section *Rhopalostylis*. Thus the stage would have been set similarly in both the Paleotropics and Neotropics for the evolution of the mutualism with resin-collecting bees. Resin-collecting bees were probably already present in both the Paleo- and Neotropics (Michener, 1979). It thus seems not so unlikely that the resin-collecting mutualism might have originated independently in both places.

Another observation is consistent with two separate origins of the resin gland and resin-reward system. If the resin gland originated independently more than once, we might expect to see subtle differences in the structure of the gland. If the resin glands throughout the genus were of identical structure, it would suggest a single origin of the gland. There are actually two distinct kinds of resin gland. Members of sections *Dioscoreifoliae* and

Cremophyllum have resin glands composed of a single concentric whorl of resiniferous bractlets derived from three pleiochasial arms. The gland-bearing species of the Old World and most of the more derived species of the New World have resin glands composed of two rows of nearly parallel platelike bractlets which are apparently derived from four pleiochasial arms. The two forms of gland are consistent with two origins of the resin gland. The distribution of the two gland types is consistent with the phylogeny that supports biogeographic Hypothesis 3: one migration to the Old World, a separate origin of the resin gland in the Old and New Worlds, followed by a recolonization of the New World by species bearing the Old World gland type (Fig. 5).

There are two final aspects of the pollination ecology that may have bearing on our biogeographic hypotheses. First, if *Dalechampia* had tight relationships with resin-collecting pollinators prior to its colonization of the Old World (as it apparently
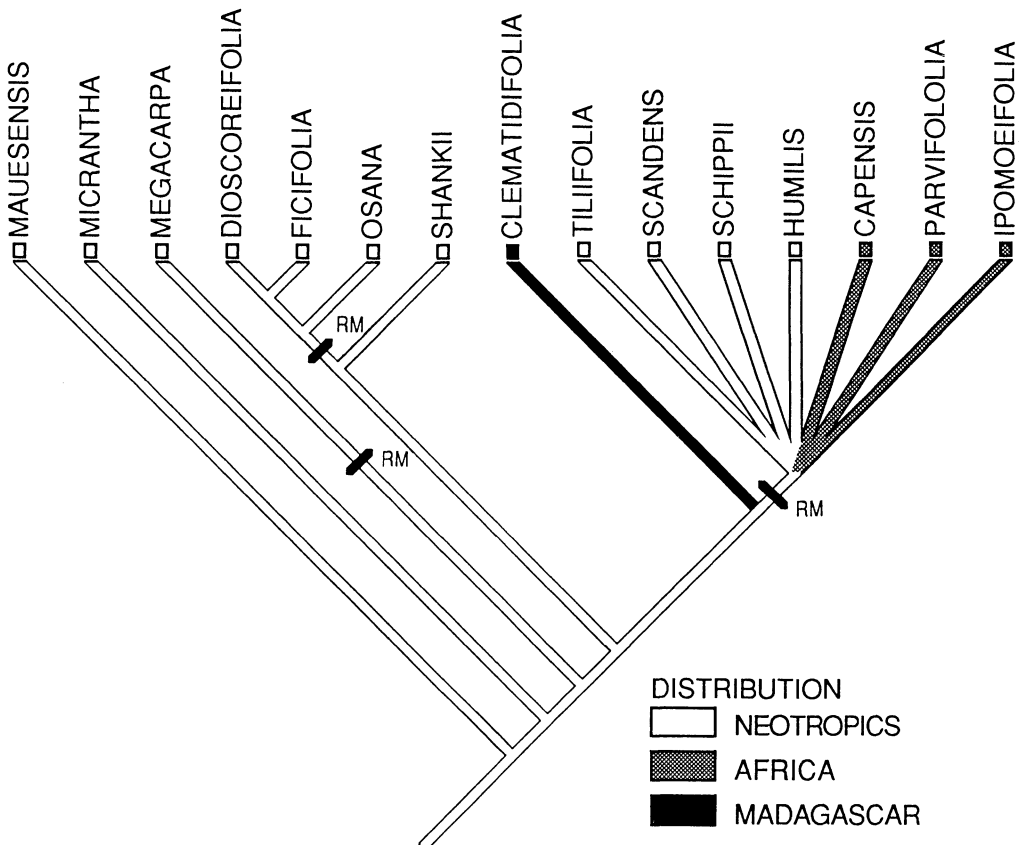
FIGURE 6. Consensus tree for the simplified set of taxa, assuming that all characters are reversible except character 17 (see Table 2), which was assumed irreversible. The figure shows the species distribution mapped onto the cladogram and origins of the mutualism with resin-collecting bees ("resin mutualism" = RM). Taxa with unstable arrangements in the 252 maximally parsimonious trees are indicated by polytomies.

did with lepidopteran symbionts), and it colonized the Old World by some mode other than long-distance dispersal, we might expect to see sister genera of bees visiting *Dalechampia* on either side of the Atlantic as we observed in the lepidoptera. We do not see this; there are not close phylogenetic relationships between the major pollinators in the New World and the Old. The most likely candidates, *Hypanthidium* on neotropical *Dalechampia* and *Pachyanthidium* on South African *Dalechampia* (Steiner & Whitehead, 1990; Armbruster & Steiner, 1992), are not particularly close within the Anthidiini (C. D. Michener, pers. comm.). This suggests dispersal between continents either was long-distance over oceanic barriers to bees, or occurred prior to the evolution of the resin mutualism (consistent with H_3 but not H_1), or somehow occurred without the bees "following" the plant.

A somewhat surprising feature of H_1 is that it has the *Dalechampia* that colonized Madagascar

abandoning pollination by resin-collecting bees and reverting to pollination by pollen-collecting bees and beetles. This is surprising because pollination by resin-collecting bees appears to be a very successful pollination system, as evidenced by its abundance in the genus (some 80% of *Dalechampia* species are pollinated in this way). If this occurred, we could expect there to be some disadvantage to pollination by resin-collecting bees in Madagascar. There might actually be such a disadvantage; according to C. D. Michener (pers. comm.), except for tiny *Trigona* spp., which are often too small to be effective pollinators (see Armbruster & Mziray, 1987; Armbruster, 1988), resin-collecting bees are notably uncommon in Madagascar.

DISCUSSION AND CONCLUSIONS

In this study I have tried to illustrate the advantages of using the results of cladistic analyses to develop and refine hypotheses about the bio-

geographic and evolutionary history of extant or-
ganisms for which there are no detailed fossil rec-
ords. However, many uncertainties remain, and it
is essential to explore through iterative analysis the
consequences of making different assumptions about
character evolution. The use of molecular data to
infer phylogeny may solve some of the problems
and uncertainties illustrated here, but even molec-
ular phylogenies often may be ambiguous (see San-
derson & Donoghue, 1989). Tests of phylogenetic
and historical hypotheses using independent data
(such as information on symbionts) are necessary
if we are to progress beyond the stage of hypothesis
generation.

In the present study, I used cladistic results to
generate and refine several hypotheses explaining
the present distribution of *Dalechampia* species
and their pollination systems. Three competing hy-
potheses seem most likely, and independent data
are needed to distinguish among these. In partic-
ular, information on the genetics and development
of flowers and inflorescences would be valuable,
because the phylogenetic and biogeographical in-
ferences made were sensitive to assumptions about
the reversibility to the primitive character states
of certain inflorescence characters.

Independent ecological information was used to
evaluate the likelihood of the hypotheses generated
from phylogenetic information. Data from insect
herbivores and pollination of *Dalechampia* best
support Hypothesis 3. The evidence, however, does
not exclude Hypotheses 1 or 2. Hypothesis 1 de-
pends on the assumption that all morphological
characters can revert to their primitive stages.
Whether this is realistic remains to be determined.

It appears that *Dalechampia* originated in the
Neotropics or western Gondwana. The earliest spe-
cies of *Dalechampia* probably employed fra-
grance-collecting male euglossine bees or pollen-
collecting insects as pollinators. The mutualism with
resin-collecting bees may have evolved separately
in the Old and New Worlds (Hypothesis 3), or may
have evolved only in the New World (Hypotheses
1 and 2).

The simplest biogeographic scenario is proposed
in Hypothesis 1: *Dalechampia* originated in the
New World, evolved a mutualism with resin-col-
lecting bees there, and subsequently colonized Af-
rica and Asia, and most recently, Madagascar,
where the mutualism with resin-collecting bees was
lost. This explanation is similar to explanations of
the dispersal history of a number of plant groups
(Raven & Axelrod, 1974). For example, the usual
explanation of pantropical distribution of the Mal-
pighiaceae is that the group originated in South

America in the late Cretaceous/early Tertiary,
evolved a mutualism with oil-collecting bees (based
on oil secretion by calyx glands), and more recently
colonized the Paleotropics, where the mutualism
was lost (Raven & Axelrod, 1974; Anderson, 1979).

A recent re-evaluation of floral morphology of
Malpighiaceae by Vogel (1990) leads to an alter-
native conclusion: the Malpighiaceae originated in
western Gondwana in the mid-Cretaceous, and con-
tinental drift resulted in primitively glandless spe-
cies occurring in both the Paleotropics and Neo-
tropics. One (or several?) lineage(s) in the Neotropics
evolved a mutualism with oil-collecting bees, and,
later, members of this advanced lineage recolonized
the Paleotropics (Vogel, 1990). This scenario is
similar to Hypotheses 2 and 3 for *Dalechampia*:
the presence of species with predominately ple-
siomorphic character states in the Old and New
Worlds is explained by a widespread, possibly
Gondwanan distribution of *Dalechampia* during
the mid-Cretaceous to early Tertiary. The close
similarity of some of the derived species of the Old
and New Worlds is explained by a second trans-
Atlantic dispersal event in both Malpighiaceae and
Dalechampia. It will be interesting to see if ad-
ditional evidence continues to support these earlier
origins and more complex biogeographic scenarios
for *Dalechampia*, Malpighiaceae, and possibly oth-
er plant groups.

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APPENDIX. List of specimens studied.

D. aristolochiifolia HBK: Armbruster et al. 87-128, 87-136 (ALA); Chavez 3067 (MO); Cook & Gilbert 1022 (F); Dillon & Turner 1703 (F, MO); Gentry et al. 44120, Hudson 1192, Hutchison & Wright 3852 (MO); Mac-Bride 3802 (F); Sagastegui et al. 8455, Stein & Todzia 2064 (MO); Stork & Horton 10093, Stork et al. 10563 (F); Vargas 131, Woytkowski 5720, 6564, 6834 (MO). *D. attenuistylus* Armbruster: Armbruster et al. 87-153, Armbruster 93-01 (ALA).

D. canescens HBK: Armbruster & Herzig 85-119, 85-127 (ALA); Haught 1832, Plowman & Vaughan 5354 (F); Webster & Armbruster 23651 (ALA). *D. capensis* Spreng.: Armbruster & Steiner 90-202, Armbruster et al. 90-203 (ALA); Bayliss 5294, Coetzee 1328, Dahlstrand 1952, Germishuizen 233, Huntley 79, Kemp 760, Kerfoot K7301, Strey 11185, Zeyher 245 (MO). *D. caperonioides* Baill.: Webster et al. 25245 (ALA). *D. chlorocephala* M. Denis: Armbruster et al. 90-151; Dorr & Koenders 2987, 2987A, 3024 (ALA, MO). *D. clematidifolia* Baill.: Armbruster et al. 90-148 (ALA); Croat 29424, 30130, 31463, 32153 (MO).

D. dioscoreifolia Poepp.: Armbruster 79-212, Armbruster et al. 85-117, 87-139 (ALA); Beekman 59, Feuillet 417 (CAY); Gentry 6365 (ALA, MO); Gentry et al. 18696 (MO); Granville et al. 7292 (B, CAY, MO, P); Guanchez & Huber 4742 (ALA, VEN); Maas et al. 2226 (CAY, U); Oldeman 2067 (CAY, MO, NY, P); Oldeman B.3227 (CAY, NY, U); Poncy 89 (ALA); Proctor et al. 27384 (F); Raynal-Roques 20006 (CAY); Revilla 1710 (MO).

D. ficifolia Lam.: Hatschbach 44381 (F); Webster et al. 25007, Webster & Armbruster 25101, 25161 (ALA). *D. fragrans* Armbruster: Armbruster & Herzig 85-101 (ALA, NY); Armbruster & Herzig 85-104 (ALA); Maas et al. 2320 (MO); Mori et al. 8693 (NY, P).

D. heteromorpha Pax & Hoffm.: Armbruster 77302, 77306, 77405, 78414, 78422, 79-201, 79-210, 79-217, Armbruster et al. 87-119, 87-134, 87-135 (ALA); Foster 11920 (ALA, F); Webster & Armbruster 22073 (ALA). *D. humilis* Muell. Arg.: Webster et al. 25275 (ALA).

D. ipomoeifolia Benth.: Ash 2422, Dalziel 1270, de Wilde 5955, 6872, Grant 4024, Harris 1784, Katende & Lye K440, Westphal & Westphal-Stevens 3497 (MO).

D. kirkii Prain: Lavranos 4915, Story 1663 (MO).

D. liesneri Huft: Armbruster et al. 87-142, 87-143 (ALA). *D. luetzelburgii* Pax & Hoffm.: Luetzelburg 132 (MO).

D. "mauesensis" sp. nov.: Murça Pirez 50 (VEN). *D. megacarpa* Armbruster: Armbruster et al. 85-115, 87-151 (ALA). *D. micrantha* Poepp.: Armbruster et al. 85-113, 87-150, 87-156 (ALA); Byron & Coelho 443 (MO); Garcia-Barriga 14103 (NY); Gentry et al. 29955 (F); Lindeman et al. 214 (U); MacRae & Ruiz 80 (F); Nee 31877 (MO); Poeppig 2807 (P); Poeppig 7200 (MO); Prance et al. 24587 (NY); Revilla 87 (F, MO, NY); Rimachi 323 (NY); Schomburgk 783 (P); Spichiger & Encarnacion 1014 (MO, NY); Spichiger & Encarnacion 1037 (MO); Vasquez et al. 666 (F, MO, NY); Wessels Boer 454 (K, NY, U); Williams 3629 (US).

D. osana Armbruster: Burger & Liesner 7278, Burger & Gentry 8962, 9011 B, Gomez 19672, Liesner 1869, Utley & Utley 1214 (F).

D. parvibracteata Lanj.: Jenman 4088 (US); McDowell & Gopaul 2264 (ALA, US). *D. parvifolia* Lam.: Armbruster et al. 90-168, Armbruster & Steiner 90-195 (ALA). *D. pentaphylla* Lam.: Hatschbach 11840, Mexia 4149, Regnelli 1051 (F); Webster et al. 25215 (ALA); Woytkowski 35147 (F).

D. scandens L.: Alexandre 227 (CAY); Armbruster & Herzig 85-107, 85-124, Armbruster et al. 87-103, 87-107, 87-115, 87-140 (ALA); Benoist 835, 1262 (P); Billiet & Jadin 4332 (BM, CAY); Broadway 444 (US); Cremers & Hoff 10608, Feuillet 538, 2969 (CAY); Gentry & Revilla 16246, Gentry et al. 22702 (MO); Gillespie & Persaud 1046, Gillespie et al. 1654, 1655, 1781 (ALA, US); Granville 6940 (B, CAY, P); Harrison 714 (K); Harrison 1769 (K, NY); Hekking 1049 (U); Hitchcock 16770, Irwin BG-71 (US); Irwin et al. 55831 (MO, NY, U, US); Kappler 1888 (P, U); Lall 312 (U); Lanjouw & Lindeman 1114, 1807 (NY, U); L.B.B. (J.T. Serringa) 12534 (U); Maas et al. 7222 (B, US); Prevost 1456 (CAY); Reitsma & Reitsma 852 (NY); Sagot 512 (BM, P); Schomburgk 610 (BM); Service Forestier 3077 (U); Service Forestier 4328 (CAY, P, U); Skog et al. 7427 (CAY, NY, P, U, US); Solomon 8899 (MO); Solomon & Escobar 12486 (ALA, MO); Wachenheim 25 (P); Webster 24143 (NY, U); Webster & Armbruster 23508, 23523, 25105 (ALA). *D. schippii* Standley: Armbruster 77-303, 78-416, 79-204 (ALA). *D. schottii* Greenm.:

Armbruster 77-305, 78-409 (ALA). *D. shankii* (Molina) Huft: Armbruster 79-213, 91-102, Armbruster & Berg 85-128 (ALA); Cuatrecasas 21512, Davidson 6828, Shank & Molina 4427, 4475, Standley & Valerio 48588 (F). *D. spathulata* Baill.: Croat 20306, Poeppig 2380, Vigo 6480, 7693 (MO); Williams 4189 (F). *D. subternata* Muell. Arg.: Armbruster et al. 90-144, 90-150, Armbruster & Hines 90-158, 90-160, 90-162, 90-164 (ALA); Croat 30708, 30744, 31022, 31065, Dorr 3050, Gentry 11801 (MO); Gillespie 4180, 4181 (ALA, US); Lorence 2097 (MO); Miller & Keating 4527, Phillipson 2492, 3050 (ALA, MO).

D. tiliifolia Lam.: Armbruster et al. 85-108, 85-111, 87-111, 87-125, 87-138, 87-141 (ALA); Barthelemy 145 (CAY); Broadway 631 (NY); Cremers 9429 (B, CAY, MO, NY, P, US); Feuillet 1754 (CAY, P); Forest Dept. Brit. Guy. 5978 (K, NY); Granville 260 (CAY, P, U); Granville 265 (CAY); Hoff 5357 (B, CAY, NY, P, US); Mori et al. 15026 (CAY, P); Oldeman B-802 (CAY, U); Picon et al. 1524 (ALA, VEN); Poncy 4 (P); Prevost 1808 (CAY, U, US); Sagot 513 (P); Solomon 3248, 7586 (MO); Webster & Armbruster 23712 (ALA). *D. triphylla* Lam.: Armbruster & Herzig 85-103 (ALA); Barreto 5058, Henschen 1052 (F); Webster & Armbruster 25182, 25189, 25218 (ALA).

Plukenetia spp.: Armbruster 78-420, Armbruster et al. 85-106, 87-110, 87-113, 87-144, Webster & Armbruster 23412 (ALA).

Tragia spp.: Armbruster et al. 90-146, Armbruster & Hines 90-157, 90-159, 90-163 (ALA); Maas 6231 (MO).