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FRUIT CHARACTERISTICS, LIFE FORMS, AND SPECIES RICHNESS IN THE PLANT FAMILY RUBIACEAE

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Abstract.—We investigated how fruit types, or combinations of fruit types and life forms, affect species number in the large, mostly tropical plant family Rubiaceae. The aim was to test the hypothesis that animal dispersal promotes species diversification in plants. Information was compiled for 427 of the 630 genera in the family. Analyses were based on genera and on groups of taxa derived from a cladistic study of chloroplast DNA variation in the family. The results demonstrated that no single trait explains variation in species number. Instead, certain combinations of dispersal modes and life forms promote species richness. Genera consisting of (1) herbs with abiotic dispersal, (2) shrubs with animal dispersal, and (3) shrubs and trees with winged seeds were all characterized by comparatively large species numbers. These results imply an association between seed dispersibility and rate of species diversification.

After an extensive survey of fruit types and species number among gymnosperms and angiosperms, Herrera (1989) concluded that there exists no general support for the hypothesis that seed dispersal by animals promotes species diversification in angiosperms. Species diversification is the rate at which the number of species in a given taxon increases over time (Stanley 1979). It has long been thought that angiosperms' diversity is causally related to their reproductive characteristics (Grant 1949, 1981; Stebbins 1971, 1974; Raven 1977; Mulcahy 1979; Crepet 1983; Bond 1989), although the suggestions of key features vary. The animal-dispersal hypothesis is one of several related hypotheses initially aimed at explaining why angiosperms replaced gymnosperms as the dominating group of land plants during the late Cretaceous and early Tertiary periods. The hypothesis predicts increased species diversification in animal-dispersed taxa, but since not all angiosperms are so dispersed, the hypothesis also predicts a variable diversification rate among angiosperms. Raven (1977), Regal (1977), Burger (1981), and Crepet (1984) advocated the theory that the efficiency of insect pollination in populations with widely scattered individuals, in combination with animal-dispersed seeds promoting such a population structure, enabled angiosperms to gain competitive superiority over wind-pollinated and wind-dispersed gymnosperm taxa. Snow (1981) and Tiffney (1984, 1986a, 1986b) suggested that animal dispersal per se, particularly by birds, increases the diversification rate. Animal dispersal would increase the likelihood of propagules' founding new, isolated populations in which speciation may take place.

Some authors have argued that no single trait is the sole cause of angiosperm diversification (Stebbins 1981; Niklas et al. 1985; Tiffney 1986a). Different features may enhance diversification in different lineages. It has been suggested that, in addition to pollination and seed-dispersal modes, the life forms of plants affect the diversification rate. Herbs are expected to possess a comparatively high rate because of their short life cycle (Tiffney 1986a) and because of the population structure occurring among short-lived plants (Levin 1984).

When evaluating the hypotheses it is important to distinguish between "dominance" and "diversification" (Bond 1989). The hypothesis advocated by Raven (1977), Regal (1977), Burger (1981), and Crepet (1984) is mainly one of angiosperm dominance. Angiosperms are suggested to have gained competitive superiority over gymnosperms because of their capability of maintaining viable populations at a lower density than wind-pollinated and wind-dispersed gymnosperms. However, as pointed out by Stebbins (1981), the ability of widely scattered individuals to become cross-pollinated is expected to hinder rather than to promote speciation. It is therefore questionable whether that mechanism could apply to species diversification as well. Furthermore, an explanation for the replacement of gymnosperms by angiosperms during the late Cretaceous period should be kept separate from hypothesized causes of variation in species diversification among angiosperms. There may exist mechanisms that promote diversification in angiosperms that do not explain why they replaced gymnosperms as the dominant land plants.

One of the main problems when testing hypotheses about diversification rates is that the phylogeny of the investigated taxa is inadequately known. Using the number of extant species as a measure of diversification rate is justified only if we assume that the compared taxa are of equal age. Because of the uncertainty of angiosperm phylogeny (Dahlgren and Bremer 1985; Doyle and Donoghue 1986), it is difficult to evaluate this assumption in studies that compile information for angiosperms as a whole. One way to handle the problem, used in the present study, is to consider cladograms as phylogenetic hypotheses (Donoghue 1989). However, because of the scarcity of such information, this approach implies that only selected angiosperm taxa can be investigated.

In this study we examine how fruit characteristics, and combinations of fruit characteristics and life forms, affect species diversification in the angiosperm family Rubiaceae. The Rubiaceae are one of the largest angiosperm families, with 10,400 species in 630 genera (Mabberley 1987), mainly in the tropics. A majority of the species (ca. 98%) are insect pollinated (Puff 1986), whereas the family comprises a wide array of different fruit types and life forms. Thus, we assume that any effect of insect pollination on diversification is held constant. As units of comparison we use genera, or groups of genera, selected on the basis of a phylogenetic tree derived from an analysis of the variation in chloroplast DNA in the Rubiaceae (Bremer and Jansen 1991).

MATERIAL AND METHODS

In all, 427 of the 630 genera, comprising about 9,900 species, are included in this study. For each of these genera, information on species number, fruit

characteristics, and life form was gathered. The sources of information were floras from different parts of the world (Hooker 1880–1881; Schumann 1881–1888, 1888–1889; Pitard 1922–1924; Hutchinson and Dalziel 1931–1935; Steyermark 1974; Dyer 1975; Tutin et al. 1976; Verdcourt 1976; Dwyer 1980; Bridson and Verdcourt 1988), handbooks (Schumann 1891; Willis 1973; Mabberley 1987; Robbrecht 1988), and monographs (Hallé 1961; Ridsdale 1975, 1978a, 1978b, 1982; Bridson 1978; Aiello 1979; Bremer 1979, 1984, 1989; Kirkbride 1979; Robbrecht 1980, 1984; Tirvengadum 1983; Bridson and Robbrecht 1985; Puff 1986; Robbrecht and Puff 1986; Axelius 1987). In the following we do not repeat these references when we exemplify or discuss specific information. The complete data set is available from the authors on request.

Five different fruit types were distinguished: capsules, nuts, berries, drupes, and *Gardenia* fruits. This classification is a simplification of the existing fruit variation in the Rubiaceae, but it is sufficient for the purpose of this study. Most capsules in the Rubiaceae are considered homologous. Generally they contain a large number of small, abiotically dispersed seeds. All kinds of fruits with a hard, dry pericarp that does not open were classified as nuts. Fleshy fruits were divided into three classes. Drupes are characterized by a fleshy mesocarp and a hard endocarp. In berries the mesocarp is also fleshy, but the endocarp is thin and membranous. In *Gardenia* fruits, the seeds are embedded in a juicy or fleshy pulp, while the endocarp and mesocarp are more or less leathery, fibrous, or even woody.

The dispersal modes were defined only on the basis of fruit morphology. Fleshy fruits were considered to be dispersed by animals. According to Snow (1981), fleshy fruits of the Rubiaceae are among the most important food sources for frugivorous birds in the tropics. *Gardenia* fruits, however, are often dispersed by mammals, and occasional examples of dispersal by lizards and ants also occur (van der Pijl 1969). Seeds from capsules and the generally small nuts were considered to be abiotically dispersed, although epizoochory exists infrequently among the latter. This mode of dispersal is poorly known, and therefore we decided to consider only endozoochory.

The life forms recognized were herbs, shrubs, and trees. A covering life-form system for tropical plants does not exist, and there are many different kinds of shrublike plants. In this study, "herbs" also incorporates plants with basal woodiness if most parts are herbaceous. Almost all included herbs are perennial. Plants that were described as "small trees or shrubs" in the literature were classified as shrubs. A classification of genera according to their dominant life form showed that 22.0% of the investigated genera were dominated by herbs, 10.5% by trees, and 67.5% by shrubs. The small proportion of epiphytic genera (2.3%) was included among the shrubs.

We also investigated whether the occurrence of winged seeds among abiotically dispersed genera influenced diversification. Since most genera with winged seeds were shrubs or trees, only these life forms were analyzed in this respect.

The analyses in which genera were used as the unit of comparison assume that genera within the Rubiaceae are of a similar age. Even though this assumption is a necessary methodological simplification it is not currently amenable to testing.

TABLE 1

NUMBER OF SPECIES PER GENUS WITH DIFFERENT FRUIT TYPES IN THE RUBIACEAE

	FRUIT TYPE				
	Berry	*Gardenia* Fruit	Drupe	Capsule	Nut
$\overline{X}$	13.4	18.9	40.3	18.6	19.1
SE	3.0	7.8	8.8	3.5	7.2
N	92	34	113	143	44

NOTE.—The ANOVA was made on log-transformed data. $F = 2.36$, df $= 4, 421$, $P = .052$ (NS).

TABLE 2

NUMBER OF SPECIES PER GENUS WITH DIFFERENT DISPERSAL MODES IN THE RUBIACEAE

	DISPERSAL MODE	
	Animal	Abiotic
$\overline{X}$	26.9	18.7
SE	4.5	3.2
N	239	187

NOTE.—The ANOVA was made on log-transformed data. $F = 1.08$, df $= 1, 425$, $P = .298$ (NS).

In an attempt to alleviate this problem, one of the analyses was based on sister-group comparisons. Sister groups share a common ancestor and are, by definition, of equal age (Hennig 1966). One problem, however, is that the time of radiation need not necessarily equal the time of divergence. As a basis for sister-group comparisons, we used a phylogenetic tree derived from a cladistic analysis of variation in chloroplast DNA (Bremer and Jansen 1991). The phylogenetic tree (fig. 1), a strict consensus tree based on six equally parsimonious cladograms, includes 33 genera from 18 tribes. As far as possible, other genera were assigned to branches of the phylogenetic tree on the basis of the tribal classification of Robbrecht (1988). Of the 427 genera included in the study, 294 were assigned to branches of the phylogenetic tree.

A detailed presentation of the variation and evolution of fruit traits in the Rubiaceae will be published elsewhere (Bremer and Eriksson, in press).

RESULTS

The average number of species in the 427 investigated genera was 23.2 (SD $=$ 59.9). A comparison of species number among genera, grouped according to fruit types, yielded no significant between-group difference (tables 1, 2; ANOVA and Scheffé's multiple-range test), although P was close to .05. Despite a tendency toward a higher number of species in genera with drupes, a grouping of genera according to their dispersal mode does not suggest a higher diversity among genera dispersed by animals.

TABLE 3

NUMBER OF SPECIES PER GENUS IN THE RUBIACEAE IN RELATION TO DISPERSAL MODE AND LIFE FORM

	AVERAGE NO. OF SPECIES PER GENUS (SE)		
	Animal Dispersal	Abiotic Dispersal	Total Life Form
Herbs	9.9 (3.0)	44.0 (10.7)	35.7 (8.3) [62]
Shrubs	43.7 (7.5)	19.1 (3.4)	35.8 (5.3) [204]
Trees	11.6 (2.4)	11.8 (2.1)	11.7 (1.7) [24]
Total dispersal mode	37.8 (6.3) [168]	28.1 (4.6) [122]	

NOTE.—Two-factor ANOVA on log-transformed data. Only herbs and shrubs were analyzed. Monotypic genera were excluded from the analysis. For dispersal mode, $F = 0.34$ (NS); for life form, $F = 0.37$ (NS); for interaction of dispersal mode and life form, $F = 9.2$, $P = .003$. Numbers of genera are in square brackets.

Table 3 presents the results from a two-factor ANOVA with genera grouped according to dispersal mode and life form. Among the investigated genera, 137 were monotypic, containing only one species. Monotypic genera are often established for aberrant species within otherwise monophyletic groups, and they do not have a separate phylogenetic status different from that of single species. In the analysis these genera were excluded. A preliminary analysis of a grouping of life form into herbs, shrubs, and trees revealed that the data were significantly heteroscedastic (Bartlett's test, $P = .009$). This was mainly due to comparatively low variances of species number among tree-dominated genera. A two-way ANOVA performed for only herbs and shrubs (a data set that was homoscedastic; Bartlett's test, $P = .07$) revealed no significant effects on species number per genus for the factors taken separately, but a significant interaction was found. Genera of herbs with abiotic dispersal and shrubs with animal dispersal consist of a larger number of species than other combinations of these traits (table 3).

Possession of winged seeds influenced species number per genus. In genera with abiotically dispersed shrubs and trees without winged seeds the average value was 15.9 (SD $= 29.3$, $N = 45$). The corresponding value for genera with winged seeds was 21.7 (SD $= 20.3$, $N = 30$). The difference was significant (log-transformed data, $t = 2.0$, $P < .05$).

The phylogenetic tree (fig. 1) was used to identify groups for comparison (table 4). Only the total number of species per branch was considered. There were some difficulties in assigning genera to branches, and, as a consequence, the species number per branch is probably underestimated. There is, however, no reason to suspect that the different dispersal modes are biased in this respect. In table 4, rows A and B, sister groups according to figure 1, were compared. In some cases it was not possible to perform sister-group comparisons, but closely related groups were compared (table 4, rows C, D, and E). In row A, the branch representing abiotic dispersal contains most species, in contrast to what is expected from the animal-dispersal hypothesis. Branches 3, 4, and 5 constitute a monophyletic group in which capsules are the plesiomorphic fruit type and fleshy fruits have originated twice (Bremer and Eriksson, in press). In branches 4 and 5, which

TABLE 4

NUMBER OF SPECIES AND DOMINANT LIFE FORM IN GROUPS OF TAXA
IN THE PHYLOGENETIC TREE OF THE RUBIACEAE

| | GROUPS WITH ANIMAL DISPERSAL | | | GROUPS WITH ABIOTIC DISPERSAL | | |
	Branch	No. of Species	Dominant Life Form	Branch	No. of Species	Dominant Life Form
A	1	61	Shrubs	2	106	Shrubs
B	4	367	Shrubs	3	53	Shrubs
C	5	2,487	Shrubs	3	53	Shrubs
D	7	112	Herbs	6 + 8	1,601	Herbs
E	9	1,865	Shrubs	6 + 8	1,601	Herbs

NOTE.—"Branch" refers to fig. 1. The following subfamilies, tribes, subtribes, and genera were incorporated: 1, Chiococceae; 2, Portlandineae; 3, Condamineae p.p. and *Calycophyllum;* 4, Iserteae; 5, Ixoroideae; 6, 7, 8, Rubioideae p.p.; 9, Psychotrieae. In all branches, the dominant life form occurred in at least 70% of the species.

possess fleshy fruits, the species number is higher than in 3 (rows B and C). In row D, taxa with different dispersal modes within the monophyletic group comprising branches 6, 7, and 8 were compared. Because of the difficulties of assigning genera to branches in this group, groups 6 and 8 were lumped together. In this comparison, most species are abiotically dispersed. Branch 9, which possesses fleshy fruits, comprises more species than branches 6 and 8 (row E). When the dominating life form in each branch was considered, we found that comparisons B, C, D, and E conformed to the results achieved in the genus-based analysis (table 3). In the comparisons of shrub-dominated groups (table 4, rows A, B, C, and E), those with fleshy fruits were the most species-rich in three of the four cases. In branches 6, 7, and 8 (table 4, row D), which are dominated by herbs, abiotic dispersal occurs in most species.

DISCUSSION

We found no consistent evidence from the Rubiaceae supporting the hypothesis that animal dispersal as such promotes species diversity. The same conclusion was reached when genera were analyzed as when a phylogenetic tree was used for sister-group comparisons. These results are similar to those presented by Stebbins (1981) and Herrera (1989). There are probably several features that, depending on ecological context, may enhance species diversification (Tiffney 1986a). There was a nonsignificant tendency, however, toward a high species number in genera possessing drupes. In a separate study (Bremer and Eriksson, in press), we found that drupes were overrepresented among genera with trans-oceanic distributions, as well as on islands. Assuming that these geographical patterns reflect dispersal ability, they indicate a positive relation between species diversification and dispersal ability.
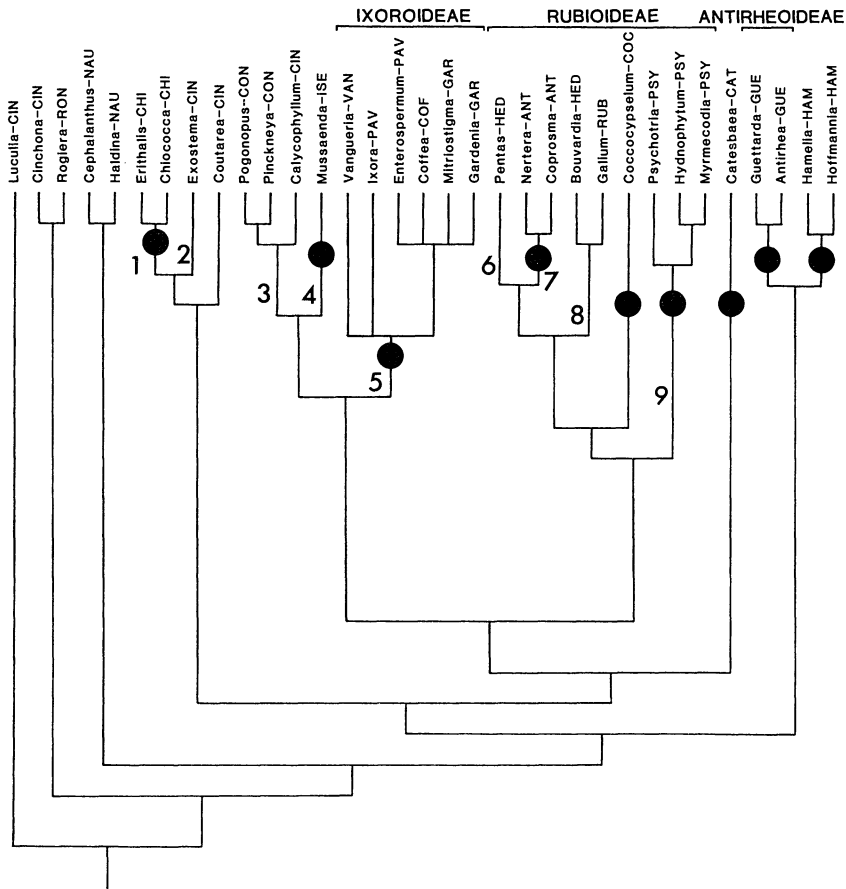
FIG. 1.—A phylogenetic tree of the Rubiaceae, based on restriction-site mutations of chloroplast DNA. The diagram is a strict consensus tree of six equally parsimonious trees 348 steps long with a consistency index of 0.46. The numbers mark the different branches discussed in the text. The origins of fleshy fruits (according to Bremer and Eriksson, in press) are indicated by the large dots. The tribal position (Robbrecht 1988) of each taxon is indicated by a three-letter suffix. (Redrawn from Bremer and Jansen 1991.)

Such a relation was also indicated by the main results from this study. Three combinations of dispersal mode and life form were characterized by comparatively high species diversity: herbs with abiotic dispersal, shrubs with fleshy fruits, and, among shrubs and trees with abiotic dispersal, the possession of winged seeds.

Successful dispersal is not only a question of having seeds widely scattered. It is also essential to consider the availability of suitable habitats. Very specialized plants may be limited by habitat availability rather than by seed dispersal. The herbaceous genera in the Rubiaceae that inhabit lowland tropical rain forests usually occur in restricted habitats such as near waterfalls and streams and on

small hills or mountains (Bremer 1984, 1989). A majority of the herbaceous genera with fleshy fruits included in this study live in such habitats. Even if we assume that the dispersal of fleshy fruits by birds is potentially more efficient over long distances than is abiotic dispersal, this may not be enough to overcome the limitations of suitable habitats. Furthermore, it is possible that fleshy fruits in rainforest herbs are dispersed by ground-dwelling mammals, which presumably have rather small home ranges. In contrast, most herbs with abiotic dispersal, belonging to the tribes Hedyotideae and Rubioideae, also inhabit environments outside tropical rain forests, including parts of the temperate regions.

A complementary and perhaps more general explanation for low dispersal ability in herbs with fleshy fruits is that herbs, as a result of their size, are able to produce relatively few fleshy fruits. As a consequence, their fruit display is not as efficient as in larger plants, shrubs, or trees. This incurs an inherent constraint on bird dispersal in herbs. In contrast, herbs with abiotic dispersal do not depend on fruit display for dispersal. Accordingly, herbs are probably most efficiently dispersed by abiotic means.

The situation is quite different for shrubs inhabiting tropical forests. Frugivorous birds are the main dispersers of tropical Rubiaceae shrubs, and these birds usually forage at the lower levels of the forests (Snow 1981). It seems plausible that the occurrence of fleshy fruits in shrubs enhances dispersal. In a similar way, enhanced dispersal is the most likely cause for the comparatively high species number among genera of abiotically dispersed shrubs and trees with winged seeds.

The trends of variation in species diversification found in the Rubiaceae thus suggest a positive relationship between dispersal ability and rate of diversification. These trends were revealed only when both fruit characteristics and life form were considered in combination. Any attempt to reduce existing patterns of diversification to a relationship with animal dispersal alone failed. In this respect our conclusion is similar to the one reached by Herrera (1989). However, his results do not exclude the possibility that dispersal mode is one of several factors that influence diversification. Moreover, our results seemingly contradict proposals by Mayr (1963) and Stanley (1979), who argued that, in widely dispersed taxa, gene flow would counteract the development of reproductive barriers and, hence, speciation. But since gene flow generally seems to be restricted in plants (Levin 1981, 1984; Ellstrand and Marshall 1985), it is likely that the effect of dispersal ability on the successful establishment of isolated populations, promoting speciation, dominates over the cohesive effects caused by dispersal between populations. Accordingly, our results support the notion of a predominant role of allopatric speciation in species diversification (Mayr 1963).

In conclusion, we suggest that life-cycle features promoting dispersal ability in the Rubiaceae enhance species diversification. Different combinations of fruit and life-form characteristics have this effect. In order to unravel the causes behind species diversification in angiosperms, an approach is needed that takes into account the specific ecological context relevant for the investigated groups. General explanations of diversification patterns that are based on single traits are not likely to be successful.

LITERATURE CITED

Aiello, A. 1979. A reexamination of *Portlandia* (Rubiaceae) and associated taxa. Journal of the Arnold Arboretum, Harvard University 60:38–123.

Axelius, B. 1987. The genus *Lerchea* (Rubiaceae). Blumea 32:91–114.

Bond, W. J. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biological Journal of the Linnean Society 36:227–249.

Bremer, B. 1979. The genus *Neurocalyx* (Rubiaceae—Argostemmateae) in Ceylon. Botaniska Notiser 132:399–407.

———. 1984. The genus *Steenisia* (Rubiaceae) and its taxonomic position. Nordic Journal of Botany 4:333–345.

———. 1989. The genus *Argostemma* (Rubiaceae—Argostemmateae) in Borneo. Annals of the Missouri Botanical Garden 76:7–49.

Bremer, B., and O. Eriksson. In press. Evolution of fruit characters and dispersal modes in the tropical family Rubiaceae. Biological Journal of the Linnean Society.

Bremer, B., and R. K. Jansen. 1991. Comparative restriction site mapping of chloroplast DNA implies new phylogenetic relationships within Rubiaceae. American Journal of Botany 78:198–213.

Bridson, D. M. 1978. A short revision of *Rutidea* (Rubiaceae). Kew Bulletin 33:243–278.

Bridson, D. M., and E. Robbrecht. 1985. Further notes on the tribe Pavetteeae (Rubiaceae). Bulletin du Jardin Botanique National de Belgique 55:83–115.

Bridson, D. M., and B. Verdcourt. 1988. Rubiaceae (part 2). Pages 415–747 *in* R. M. Polhill, ed. Flora of tropical East Africa. Balkema, Rotterdam.

Burger, W. C. 1981. Why are there so many kinds of flowering plants? BioScience 31:572, 577–581.

Crepet, W. L. 1983. The role of insect pollination in the evolution of the angiosperm. Pages 31–50 *in* L. Real, ed. Pollination biology. Academic Press, Orlando, Fla.

———. 1984. Advanced (constant) insect pollination mechanisms: pattern of evolution and implication vis-à-vis angiosperm diversity. Annals of the Missouri Botanical Garden 71:607–630.

Dahlgren, R., and K. Bremer. 1985. Major clades of the angiosperms. Cladistics 1:349–368.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences with examples from seed plants. Evolution 43:1137–1156.

Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. Botanical Review 52:321–431.

Dwyer, J. 1980. Flora of Panama. IX. Family 179: Rubiaceae. Annals of the Missouri Botanical Garden 67:1–256.

Dyer, R. A. 1975. The genera of southern African flowering plants 1. Department of Agricultural Technical Services, Pretoria.

Ellstrand, N. C., and D. L. Marshall. 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. American Naturalist 126:606–616.

Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. Evolution 3:82–97.

———. 1981. Plant speciation. 2d ed. Columbia University Press, New York.

Hallé, F. 1961. Contribution a l'étude biologique et taxonomique des Mussaendeae (Rubiaceae) d'Afrique tropicale. Adansonia 1:266–298.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Herrera, C. M. 1989. Seed dispersal by animals: a role in angiosperm diversification? American Naturalist 133:309–322.

Hooker, J. D. 1880–1881. Rubiaceae. Pages 17–199 *in* J. D. Hooker, ed. The flora of British India. Vol. 3. L. Reeve, London.

Hutchinson, J., and J. M. Dalziel. 1931–1935. Flora of west tropical Africa. Vol. 2. Crown Agents for the Colonies, London.

Kirkbride, M. C. G. 1979. Review of the Neotropical Iserteae (Rubiaceae). Brittonia 31:313–332.

Levin, D. A. 1981. Dispersal versus gene flow in plants. Annals of the Missouri Botanical Garden 68:233–252.

———. 1984. Immigration in plants: an exercise in the subjunctive. Pages 242–260 in R. Dirzo and J. Sarukhan, eds. Perspectives on plant population ecology. Sinauer, Sunderland, Mass.

Mabberley, D. E. 1987. The plant book: a portable dictionary of the higher plants. Cambridge University Press, Cambridge.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

Mulcahy, D. L. 1979. The rise of angiosperms: a genecological factor. Science (Washington, D.C.) 206:20–23.

Niklas, K. J., B. H. Tiffney, and A. H. Knoll. 1985. Patterns in vascular land plant diversification: an analysis at the species level. Pages 97–128 in J. W. Valentine, ed. Phanerozoic diversity patterns. Princeton University Press, Princeton, N.J.

Pitard, J. 1922–1924. Rubiaceae. Pages 20–442 in H. Lecomte and H. Humbert, eds. Flore générale de l'Indo Chine. Muséum National D'Histoire Naturelle, Paris.

Puff, C. 1986. A biosystematic study of the African and Madagascan Rubiaceae—Anthospermeae. Plant Systematics and Evolution 3:1–535 (Supplement).

Raven, P. H. 1977. A suggestion concerning the Cretaceous rise to dominance of the angiosperms. Evolution 31:451–452.

Regal, P. J. 1977. Ecology and evolution of flowering plant dominance. Science (Washington, D.C.) 196:622–629.

Ridsdale, C. E. 1975. A synopsis of African and Madagascan Rubiaceae—Naucleeae. Blumea 22:541–553.

———. 1978a. A revision of Mitragyna and Uncaria. Blumea 24:43–100.

———. 1978b. A revision of the tribe Naucleeae s.s. (Rubiaceae). Blumea 24:307–366.

———. 1982. A revision of Badusa (Rubiaceae, Condamineae, Portlandinae). Blumea 28:145–150.

Robbrecht, E. 1980. The Hypobatreae (Rubiaceae–Ixoroideae) I. Delimitation and division of a new tribe. Bulletin du Jardin Botanique National de Belgique 50:69–77.

———. 1984. The delimitation and taxonomic position of the tropical African genera Leptactina and Dictyandra (Rubiaceae). Plant Systematics and Evolution 145:105–118.

———. 1988. Tropical woody Rubiaceae. Opera Botanica Belgica 1:1–271.

Robbrecht, E., and C. Puff. 1986. A survey of the Gardenieae and related tribes (Rubiaceae). Botanische Jahrbücher für Systematik, Pflanzengeschichte, und Pflanzengeographie 108:63–137.

Schumann, K. 1881–1888. Rubiaceae. In C. F. P. Martius, ed. Flora brasiliensis. Vol. 6 (part 5). Munich.

———. 1888–1889. Rubiaceae. In C. F. P. Martius, ed. Flora brasiliensis. Vol. 6 (part 6). Munich.

———. 1891. Rubiaceae. In A. Engler and K. Prantl, eds. Die natürlichen Pflanzenfamilien. Vol. 4 (part 4-5). Leipzig.

Snow, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13:1–14.

Stanley, S. M. 1979. Macroevolution—pattern and process. W. H. Freeman, San Francisco.

Stebbins, G. L. 1971. Adaptive radiation of reproductive characteristics in angiosperms. II. Seeds and seedlings. Annual Review of Ecology and Systematics 2:237–260.

———. 1974. Flowering plants: evolution above the species level. Belknap, Cambridge, Mass.

———. 1981. Why are there so many species of flowering plants? BioScience 31:573–577.

Steyermark, J. A. 1974. Rubiaceae. In T. Lasser, ed. Flora de Venezuela. Vol. 9 (part 1-3). Instituto Botanico, Ministeria de Agricultura y Cria, Caracas.

Tiffney, B. H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. Annals of the Missouri Botanical Garden 71:551–576.

———. 1986a. Fruit and seed dispersal and the evolution of the Hamamelidae. Annals of the Missouri Botanical Garden 73:394–416.

———. 1986b. Evolution of seed dispersal syndromes according to the fossil record. Pages 273–305 in D. R. Murray, ed. Seed dispersal. Academic Press, Sydney.

Tirvengadum, D. D. 1983. New taxa and name changes in tropical Asian Rubiaceae. Nordic Journal
    of Botany 3:455–469.
Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and
    D. A. Webb. 1976. Flora europaea. Vol. 4. Cambridge University Press, Cambridge.
van der Pijl, L. 1969. Principles of dispersal in higher plants. Springer, Berlin.
Verdcourt, B. 1976. Rubiaceae (part 1). Pages 1–414 in R. M. Polhill, ed. Flora of tropical East Africa.
    Whitefriars, London.
Willis, J. C. 1973. A dictionary of the flowering plants and ferns. 8th ed., rev. by H. K. Airy Shaw.
    Cambridge University Press, Cambridge.