

SEED DISPERSAL BY ANIMALS: A ROLE IN ANGIOSPERM DIVERSIFICATION?

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The astounding diversity of angiosperms, and their prevalence in most present-day terrestrial habitats, has often attracted the attention of evolutionary biologists, and a number of factors have been proposed to explain the success and extraordinary radiation of this group, particularly in relation to gymnosperms (see, e.g., Stebbins 1974, 1981; Raven 1977; Regal 1977; Doyle 1978; Mulcahy 1979; Burger 1981; Queller 1983; Crepet 1984; Kubitzki and Gottlieb 1984; Doyle and Donoghue 1986). Seed dispersal by animals has been sometimes considered one of the factors helping to explain angiosperm diversification (Baker 1963; Regal 1977; Burger 1981; Crepet 1984; Tiffney 1984), although this hypothesis has gone essentially untested to date.

If seed dispersal by animals contributed significantly to angiosperm diversification, one should expect to find (1) that this seed-dispersal method was either a significant innovation of angiosperms (a feature unique to this group) or that it occurs proportionally more often in angiosperms than in gymnosperms; (2) that extant groups exhibiting this feature tend to be taxonomically more diverse than sister groups lacking it; and (3) that biotically dispersed groups were of greater proportional significance during the early, critical periods of angiosperm diversification. The objective of this paper is to test these simple predictions.

Seed dispersal by animals (biotic dispersal) takes place through a variety of mechanisms (van der Pijl 1982), including endozoochory (dispersal by vertebrate guts; Janzen 1983), epizoochory (dispersal by adhesion; Sorensen 1986), and dyszoochory (dispersal through scatter hoarding and related behaviors; Vander Wall and Balda 1977; Bossema 1979). I consider only endozoochory, because it seems the most genuine and widespread method of biotic dispersal among extant plants (Ridley 1930; van der Pijl 1982; Howe 1986) and among plants from the more distant past, since "[fruit] flesh has long been the primary attractant of biotic dispersal agents" (Tiffney 1986*b*, p. 300). Furthermore, endozoochory has been the method of biotic dispersal generally implied in the explanations of angiosperm diversification quoted above.

Apart from these considerations, methodological reasons also suggest confining the analyses to endozoochory. The assignment of taxa with imperfectly known dispersal ecologies to seed-dispersal categories must rely on consideration of diaspore morphology. It is for endozoochory that the most reliable inferences

about function (type of dispersal) can be made from consideration of the morphology of the diaspore alone. Among extant plants, the presence of nutritious tissues surrounding the seed(s) has been invariably associated with endozoochory in all instances where appropriate observations have been conducted (Ridley 1930; van der Pijl 1982; Howe 1986). In contrast, studies of epizoochorous and dyszoochorous plants reveal contrasting diaspore morphologies (and associated structures) within each group (see, e.g., van der Pijl 1982; Sorensen 1986). Thus, there seems to be no reliable, universally applicable indicator that can be used unequivocally to assign taxa to these two categories of dispersal on the basis of morphology alone. Accordingly, although examination of endozoochory alone has the drawback of neglecting other (although comparatively minor) methods of biotic dispersal, it has the obvious advantage of high reliability in those cases where one must assess dispersal method by inference from morphology (e.g., fossil taxa or extant taxa with poorly known dispersal ecologies).

OCCURRENCE OF ENDOZOOCHORY AMONG SEED PLANTS

Animal Seed Dispersal Not Unique to Angiosperms

As pointed out by Crepet, “attempts to explain angiosperm diversity might be directed logically at explaining the potential benefits of *unique, basic angiosperm features* (i.e., synapomorphic features at the level of ‘Angiospermae’)” (1984, p. 607; italics added). Endozoochorous seed dispersal is not a synapomorphy of angiosperms; in other words, angiosperms did not invent seed dispersal by animals.

The production of fleshy fruits (berries, drupes)—in a strict morphological sense, structures resulting from an enlarged ovary—is restricted to angiosperms. In this sense, therefore, fleshy fruits are unique to angiosperms. Nevertheless, neither the production of structures functionally playing the same role as fleshy fruits nor seed dispersal by vertebrate animals is a unique feature of this group. Many extant gymnosperms produce diaspores consisting of one or a few seeds fully enclosed or partly surrounded by nutritious tissue, which serves as the reward to the animal frugivores that disperse their seeds. The fleshy portion of these “fruits” (throughout, quotation marks distinguish functional from true, anatomical fruits) originates not from ovary walls but from the modification of bracts or other ancillary floral structures (van der Pijl 1982). The “fruit”-producing habit occurs in all the four extant orders of gymnosperms, including the most primitive ones. Species in the Cycadales (e.g., *Cycas*, *Zamia*, *Macrozamia*), Ginkgoales (*Ginkgo*), and Gnetales (*Gnetum*, *Ephedra*) are endozoochorous (van der Pijl 1982). In the Coniferales, endozoochory is absent from only three of its seven families (Pinaceae, Taxodiaceae, and Araucariaceae). Species in the Taxaceae (*Taxus*, *Torreya*), Cephalotaxaceae (*Cephalotaxus*), Podocarpaceae (*Podocarpus*, *Dacrydium*), and Cupressaceae (*Juniperus*) produce “fruits.” Among extinct gymnosperms, “fruits” (seeds with well-developed fleshy sarcotestas or embedded in fleshy structures) were similarly well represented, occurring in at least the Medullosales, Caytoniales, and Cordaitales (Dilcher 1979; Tiffney 1986b).

Gymnosperm "fruits" are functionally equivalent to the fruits of angiosperms, and frugivorous animals eat them and disperse the enclosed seeds in exactly the same way as they do angiosperm fruits (see, e.g., Ridley 1930; Hartley 1954; Livingston 1972; Eckenwalder 1980; Burbidge and Whelan 1982; Poddar and Lederer 1982; van der Pijl 1982; Holthuijzen and Sharik 1985; Obeso 1986; Tang 1987*b*). Furthermore, evidence from fossils indicates that this also occurred during the earlier history of gymnosperms. Gymnosperm "fruits" were produced by ancestors of extant groups and by extinct taxa at least since the Jurassic and consumed by animals that dispersed the enclosed seeds (as revealed by coprolites; Harris 1964; Dilcher 1979; van der Pijl 1982; Weishampel 1984; Tiffney 1986*b*). Gymnosperm seeds surrounded by a fleshy sarcotesta have been reported since the late Carboniferous, and gymnosperm "fruits" seem to have existed uninterruptedly since then (Tiffney 1986*b*).

In short, the appearance of biotically dispersed, fleshy-fruited angiosperms did not bring about any *functional* novelty with respect to animal-dispersed, preexisting gymnosperms. It must be further stressed that the functional homogeneity of angiosperm and gymnosperm fleshy diaspores in spite of marked anatomical differences also occurs within the angiosperms themselves. The fleshy "fruits" of many angiosperms originate not from an enlarged ovary but from accessory structures or seed walls, as found in Magnoliaceae, Rosaceae, Myristicaceae, and Moraceae, to mention a few of the many possible examples (for more details on the anatomical diversity of angiosperm "fruits," see van der Pijl 1982). Therefore, anatomical differences between angiosperm and gymnosperm fleshy diaspores are also widely represented within the angiosperms themselves.

Relative Frequency of Endozoochory among Gymnosperm Families

Most of the diversity of angiosperms seems attributable to the large number of families, rather than to high diversity within individual families (Stebbins 1981; but see below). If endozoochory had actually played a role in angiosperm diversification, one should expect an increase in the relative frequency of this dispersal habit among angiosperm families relative to gymnosperms. This prediction assumes that an (extant) family of gymnosperms is phylogenetically "equivalent" to an extant family of angiosperms. Perhaps this is not the case (Van Valen 1973), but the commonly held notion of greater diversity of angiosperms (mostly because of familial diversity, as noted above) similarly (but implicitly) makes this assumption. Since the test is ultimately aimed at examining one specific hypothesis advanced to explain that very notion, it seems logically valid to assume a phylogenetic "equivalence" of extant angiosperm and gymnosperm families. In other words, if the possible nonequivalence of angiosperm and gymnosperm families invalidates the test, this would also automatically cast doubts on that fraction of increased angiosperm diversity that is attributed to greater familial diversification.

A survey was made of all extant gymnosperm and angiosperm families, scoring them for presumed seed-dispersal method on the basis of production of fleshy fruits or functionally analogous structures ("fruits" as used here). Families were assigned to one of three categories: "endozoochorous," if all or the vast majority of genera produce fleshy diaspores (estimated percentage of genera with fleshy diaspores, >90%; e.g., Annonaceae, Lauraceae, Magnoliaceae, Myristicaceae);

TABLE 1
RELATIVE FREQUENCY OF ENDOZOOCHOROUS SEED DISPERSAL IN GYMNOSPERM AND
ANGIOSPERM FAMILIES

GROUP	NUMBER OF FAMILIES	DISPERSAL METHOD (% OF FAMILIES)*		
		Endozoochory	Mixed	Others
Gymnosperms	14	64.3	7.1	28.6
Angiosperms	277	27.1	23.8	49.1
Dicots	241	27.4	24.1	48.5
Monocots	36	25.0	22.0	52.8

* See the text for definitions of categories.

“mixed,” if both fleshy and non-fleshy diaspores are well represented in the family (10%–90% of genera; e.g., Apocynaceae, Ericaceae, Oleaceae, Rosaceae); and “others,” for families in which fleshy diaspores never occur or are extremely rare (<10% of genera; e.g., Bombacaceae, Compositae, Labiatae, Orchidaceae). The taxonomic treatment for families was that of Heywood (1978) for angiosperms and of Givnish (1980) for gymnosperms. Assignment of families to seed-dispersal categories was based on information of Strasburger et al. (1970), Heywood (1978), Davis and Cullen (1979), Givnish (1980), and Hora (1981) and was checked whenever possible against Ridley’s (1930) and van der Pijl’s (1982) treatises on seed dispersal. For angiosperms, the survey was restricted to terrestrial plants, excluding exclusively aquatic families. A few families for which assignment could not be made confidently on the basis of the literature available to me were omitted from the analyses. A complete listing of families, including assignments to categories and other pertinent data used later in this paper, is available from the author.

Monocot and dicot angiosperms do not differ ($G = 0.22$, $df = 2$, $P = 0.89$) in the relative distribution of extant families among the three seed-dispersal categories considered (table 1) and are thus treated together. Angiosperms and gymnosperms differ significantly in the proportion of families falling in different dispersal categories ($G = 7.96$, $df = 1$, $P = 0.005$; “mixed” and “others” categories combined for the test, to increase the size of the gymnosperms-mixed cell). Endozoochorous families are proportionally much more important in gymnosperms (64.3%) than in angiosperms (27.1%). Non-endozoochorous families (“others”) are most frequent in angiosperms. At the familial level, therefore, the endozoochorous habit is more representative of extant gymnosperms than of angiosperms, thus contradicting expectations from the hypothesis of its role in angiosperm diversification.

ENDOZOOCHORY AND DIVERSIFICATION

Taxonomic Diversity and Dispersal Method

Numbers of genera and species were gathered from Heywood (1978) for angiosperms and from Givnish (1980) and Hora (1981) for gymnosperms, for all families

TABLE 2
TAXONOMIC DIVERSITY OF PLANT FAMILIES WITH DIFFERENT SEED-DISPERSAL METHODS

GROUP	DISPERSAL METHOD*			HETEROGENEITY†	
	ENDOZOOCHORY	MIXED	OTHERS	<i>H</i>	<i>P</i>
	\bar{x} (SD)	\bar{x} (SD)	\bar{x} (SD)		
Gymnosperms					
<i>N</i> (families)	9	1	4		
Genera per family	3 (4) ^a	—	6 (4) ^b	4.13	0.04
Species per family	43 (53)	—	72 (94)	0.05	0.82
Species per genus	14 (13)	—	11 (10)	0.05	0.82
Angiosperms					
DICOTS					
<i>N</i> (families)	66	58	117		
Genera per family	16 (28) ^a	71 (113) ^b	37 (118) ^a	45.37	<0.0001
Species per family	361 (542) ^a	1321 (2406) ^b	650 (2397) ^a	30.76	<0.0001
Species per genus	31 (62)	19 (17)	26 (39)	0.69	0.41
MONOCOTS					
<i>N</i> (families)	9	8	19		
Genera per family	43 (69)	60 (75)	89 (211)	2.99	0.22
Species per family	745 (928)	1204 (1034)	1873 (4349)	3.27	0.20
Species per genus	48 (70)	33 (29)	23 (24)	2.40	0.30
All					
<i>N</i>	75	66	136		
Genera per family	19 (36) ^a	70 (109) ^b	44 (137) ^a	47.62	<0.0001
Species per family	407 (614) ^a	1307 (2284) ^b	821 (2786) ^a	33.80	<0.0001
Species per genus	33 (63)	21 (20)	25 (37)	1.31	0.52

* See the text for definitions.

† Kruskal-Wallis analysis of variance. For significant heterogeneity tests, entries in the same row sharing a superscript are not statistically different in paired comparisons (Mann-Whitney test, $P > 0.10$).

included in the survey. Particularly in very large families, these figures represent only estimates. Nevertheless, discrepancies between the figures given by different authors for the same family (for angiosperms, cf., e.g., Stebbins 1974 and Heywood 1978) are always comparatively unimportant in relation to the broad variation existing between families; thus, these figures may be used reliably for comparative purposes.

Not only do angiosperms have a much larger number of extant families than gymnosperms, but also they have, on the average, more extant genera per family (44 vs. 5; Mann-Whitney *U*-test, $z = 2.76$, $P = 0.006$) and species per family (825 vs. 57; $z = 2.95$, $P = 0.003$) than do extant gymnosperm families. The two groups do not differ significantly in the average number of species per genus (26 for angiosperms vs. 13 for gymnosperms; $z = 1.59$, $P = 0.11$); hence, the higher number of species per family in angiosperms is mostly due to a higher number of genera per family, not to a greater diversity of individual genera.

In gymnosperms, families in different seed-dispersal categories do not differ significantly in the number of species per family and species per genus (table 2). They do differ in the number of genera per family. Endozoochorous families are

less diverse at this taxonomic level than non-endozoochorous ones. Among monocot angiosperms, no significant differences were found among seed-dispersal categories at any of the three levels of taxonomic diversity considered. Among dicotyledons, no significant heterogeneity exists between seed-dispersal categories with regard to species/genus ratios. There are differences in genera/family ratios and species/family ratios. In these cases, families with "mixed" dispersal methods exhibit significantly larger values than endozoochorous and non-endozoochorous ("others") families. The latter two groups do not differ significantly. For all angiosperms combined, results are similar to those for dicots alone.

In summary, in none of the groups examined (gymnosperms, dicots, monocots), and at none of the taxonomic levels considered, are endozoochorous families more diverse than non-endozoochorous ones. For gymnosperms, the result is the opposite.

Analysis of Selected Families with Mixed Dispersal

In the context of the results above, the greater taxonomic diversity of dicot families with "mixed" seed dispersal (relative to both endozoochorous and non-endozoochorous families) should best be interpreted as an artifact. The larger and more diverse a family, the greater the likelihood of its being internally heterogeneous with regard to seed-dispersal method (or any other non-family-specific attribute) and thus to fall into the "mixed" seed-dispersal category. Nevertheless, families with both endozoochorous and non-endozoochorous genera provide an opportunity to investigate further the relationship between endozoochory and diversity, holding constant all family-specific attributes.

In this section, I compare the taxonomic diversity of genera with and without endozoochorous dispersal for all plant families belonging to the "mixed" dispersal category that are represented in the European flora. The survey was limited to native European families and species because of my greater familiarity with this flora, and was based on Tutin et al. (1964–1980). The European flora is diverse enough to provide sufficient data for the comparisons and to expect that patterns revealed are not seriously biased. I chose seven families (Santalaceae, Ulmaceae, Thymelaeaceae, Rosaceae, Ericaceae, Solanaceae, and Liliaceae) that had at least one genus in each dispersal category (endozoochorous and non-endozoochorous). The relative importance of endozoochorous genera varies broadly among families, from 17% in the Liliaceae to 70% in the Solanaceae. The results are summarized in table 3.

Endozoochorous and non-endozoochorous genera do not differ significantly in the number of species in the two largest families represented in the sample (Kruskal-Wallis analysis of variance: Rosaceae, $H = 1.33$, $P = 0.25$; Liliaceae, $H = 0.92$, $P = 0.66$). The remaining families do not have sufficient numbers of genera for separate statistical testing. In order to test for a general association between dispersal method and diversification, the average numbers of species per genus for endozoochorous and non-endozoochorous genera were compared using the Wilcoxon matched-pair test (Siegel 1956). No significant difference was found between the two groups ($P > 0.05$).

TABLE 3

COMPARATIVE DIVERSITY OF ENDOZOOCHOROUS AND NON-ENDOZOOCHOROUS GENERA OF EUROPEAN PLANT FAMILIES WITH MIXED SEED-DISPERSAL METHODS

FAMILY	ENDOZOOCHOROUS GENERA		NON-ENDOZOOCHOROUS GENERA	
	N	NO. OF SPECIES PER GENUS	N	NO. OF SPECIES PER GENUS
		\bar{x} (SD)		\bar{x} (SD)
Santalaceae	2	1.5 (0.7)	1	18
Ulmaceae	2	2.5 (2.1)	1	5
Thymelaeaceae	2	9.0 (11.3)	1	17
Rosaceae	13	17.2 (21.6)	16	15.6 (32.8)
Ericaceae	3	3.7 (2.9)	13	2.7 (4.2)
Solanaceae	7	2.6 (1.6)	3	3.0 (2.0)
Liliaceae	8	3.6 (4.8)	39	8.5 (18.4)

NOTE.—Families are listed in taxonomic order.

Analysis of Selected Angiosperm Orders

Here I compare, on a within-order basis, the taxonomic diversity (number of species) of endozoochorous and non-endozoochorous families. Only orders having at least one family in each category have been considered here. Families with "mixed" seed dispersal (as defined earlier) are not included in the analyses.

The average diversity of endozoochorous families exceeded that of non-endozoochorous ones in 11 orders, and the situation was the reverse in 9 orders (table 4). The number of families per order is generally too small for performing separate within-order statistical testing. A Wilcoxon matched-pair test does not reveal any overall significant difference in diversity between endozoochorous and non-endozoochorous families ($P = 0.70$).

ENDOZOOCHORY IN A HISTORICAL CONTEXT

One of the reasons for attributing to endozoochory a role in angiosperm diversification apparently stems from the observation that animal-dispersed taxa are particularly numerous in the most primitive living angiosperms (Magnoliidae). Fleshy fruits are effectively associated with comparatively primitive characters in angiosperm phylogeny. Using Sporne's (1980) index of advancement for dicot families (with amendments in Chapman 1987, table 1), non-endozoochorous families (mean \pm SD = 54 ± 13 , $N = 113$) score slightly, but significantly higher (Kruskal-Wallis test, $\chi^2 = 5.89$, $P = 0.015$) than endozoochorous and mixed families combined (50 ± 11 , $N = 121$; these groups are combined because they do not differ significantly, $\chi^2 = 0.32$, $P = 0.57$). Similar patterns, however, also occur among extant gymnosperms, in which the primitive Ginkgoales and Cycadales produce fleshy fruits, whereas many of the more recent Coniferales do not. The comparatively primitive character of endozoochory in living angio-

TABLE 4

COMPARATIVE TAXONOMIC DIVERSITY OF ENDOZOOCHOROUS AND NON-ENDOZOOCHOROUS FAMILIES IN ORDERS WITH CONTRASTING SEED-DISPERSAL METHODS

ORDER	ENDOZOOCHOROUS		NON-ENDOZOOCHOROUS	
	N	NO. OF SPECIES PER FAMILY	N	NO. OF SPECIES PER FAMILY
		\bar{x} (SD)		\bar{x} (SD)
Apiales	1	700	1	2500
Capparales	1	2	2	1506 (2113)
Caryophyllales	2	1011 (1399)	5	860 (849)
Celastrales	4	154 (187)	2	14 (18)
Dipsacales	2	226 (317)	2	375 (35)
Ericales	2	5 (1)	3	183 (193)
Euphorbiales	1	28	1	5000
Illiciales	1	47	1	40
Laurales	4	740 (1192)	1	76
Liliales	2	203 (243)	7	332 (655)
Magnoliales	6	437 (781)	2	1 (0)
Myrtales	2	6 (6)	3	317 (252)
Piperales	2	1033 (1368)	1	7
Primulales	1	1000	1	1000
Rosales	2	300 (141)	8	235 (518)
Santalales	1	1300	1	11
Sapindales	4	501 (373)	6	83 (91)
Scrophulariales	1	150	6	990 (1374)
Theales	2	363 (336)	4	167 (276)
Violales	4	183 (281)	12	210 (331)
Zingiberales	1	40	1	30

sperms is thus paralleled in gymnosperms. For this reason, the argument for a role of biotic dispersal in angiosperm diversification based on the endozoochory of primitive taxa alone could apply equally well to gymnosperms.

A more critical test is provided by examining the timing of the appearance in the fossil record of angiosperm families with different seed-dispersal methods. If biotic dispersal contributed decisively to the radiation burst of angiosperms, I would expect to find biotically dispersed taxa proportionally overrepresented in the early stages of angiosperm radiation (relative to non-biotically dispersed groups). In other words, endozoochorous families should display a trend toward earlier appearances in the fossil record relative to families with other seed-dispersal methods. The weakness of this test lies in its dependence on the assumption, untestable at present, that the dispersal method generally has remained constant over geologic time within individual families, and results are presented here with this explicit reservation. The time of first appearance in the fossil record for 130 angiosperm families is summarized in table 5, separately for endozoochorous, mixed, and non-endozoochorous categories, based on information given by Muller (1981). There is no significant heterogeneity between dispersal categories in central tendency (extended-median test, $\chi^2 = 1.28$, $df = 2$, $P = 0.52$; Siegel 1956), proportional distributions ($\chi^2 = 12.1$, $df = 10$, $P = 0.28$), or shape of

TABLE 5
DISTRIBUTION OF FIRST APPEARANCES IN THE FOSSIL RECORD FOR EXTANT
ANGIOSPERM FAMILIES WITH DIFFERENT SEED-DISPERSAL METHODS

PERIOD/EPOCH	NUMBER OF FAMILIES		
	Endozoochorous	Mixed	Others
Cretaceous	11	11	8
Tertiary			
Paleocene	3	5	9
Eocene	8	13	8
Oligocene	3	10	8
Miocene	7	6	14
Pliocene	3	2	1

cumulative curves over time (Kolmogorov-Smirnov two-sample tests, $P > 0.75$), of first appearances among geologic periods.

DISCUSSION

The hypothesis considered here, that biotic seed dispersal has contributed significantly to the diversity of angiosperms, is both functional (by conferring great significance on one interaction, that between animals and plants) and historical (by attempting to explain a past event) in nature. Since past interactions cannot be observed, but only inferred from what we know about present-day environments, the hypothesis is deeply rooted in uniformitarian principles. On the other hand, because of its historical nature (and the impossibility of actually observing the functional aspects), the hypothesis is untestable in a strict sense unless uniformitarian principles (in a broad sense) are also accepted for the test. Tests may be conducted using both neontological and paleontological data, as exemplified here (for a similar two-way approach, see Tiffney 1986a). Since the most important element of the hypothesis being tested (the interaction component) was ultimately provided by neontological data, it seems logically congruent to use neontological data for testing it (by "congruent" I mean that the same general set of assumptions applies to both the hypothesis and the tests).

In addition to specific limitations inherent in some of the tests performed, as noted earlier, a more general limitation is common to several of them: the absence of statistical independence between features of taxa, as a consequence of their linkage in a hierarchical system of relationship (phylogeny). As discussed in detail by Felsenstein (1985), the use of statistical methods that assume independence is inappropriate in these cases, because different taxa are not drawn independently from the same distribution. In the context of this paper, circumventing this problem would require an accurate knowledge of the phylogeny of angiosperms, a formidable requirement that is impossible to meet at the present. Violating the independence assumption, however, tends to overstate the level of statistical significance in hypothesis tests involving phylogenies (Felsenstein 1985). For this reason, and because the vast majority of statistical tests performed in this paper

did not reach significance, I believe that accounting for the effect of statistical dependence would not change the nature of the results presented here. Furthermore, the fact that the tests performed failed to reach significance in spite of increased Type 1 error adds reliability to the results obtained.

The tests performed here represent reasonably independent lines of inquiry; yet they have provided remarkably similar results. None of them supports a role of seed dispersal by animals per se in angiosperm diversification. This coincidence in the outcome of rather heterogeneous tests lends further support to the conclusion that endozoochory is unrelated to angiosperm diversification, and it tends to rule out any overwhelming influence of test limitations noted above. Not only is endozoochorous seed dispersal a feature shared by gymnosperms and angiosperms, but also it is proportionally most frequent among extant gymnosperm families. Furthermore, endozoochory is not significantly associated with increased taxonomic diversity in either the gymnosperm or angiosperm groups in which it occurs. Angiosperm families with different seed-dispersal methods do not differ significantly in the timing of the first appearance in the fossil record. Within angiosperm orders, endozoochory is associated with increased familial diversity as often as with decreased diversity. Assuming that individual orders represent monophyletic lineages and that in most cases the included families represent sister groups, this result effectively indicates that endozoochory does not confer any consistent diversification advantage to the lineages in which it appears.

The finding that endozoochory is not consistently associated with increased diversity is at variance with the results reported by Tiffney (1986a) for 22 families in the Hamamelidae. He found that biotically dispersed families had more extant species than abiotically dispersed ones. Carlquist (1974) found that biotically dispersed immigrants in Hawaii apparently have produced more descendant species than abiotically dispersed ones. These findings, along with some of the data presented in table 4, may indicate a direct relationship between diversity and seed dispersal by animals in some lineages or ecological circumstances, but this does not imply that such a relationship holds for the angiosperms as a whole because the reverse situation occurs nearly as often.

It has been argued that seed dispersal by birds, rather than endozoochory in itself, was one of the critical events in the initial rise of angiosperms to dominance (Regal 1977). The greater mobility of these seed vectors relative to frugivorous reptilian predecessors (the dispersers of early endozoochorous gymnosperms; Dilcher 1979; van der Pijl 1982; Weishampel 1984) would have increased the probability of long-distance dispersal and generated new patterns of local dispersal. Nevertheless, there are no reasons to suspect that early frugivorous birds would exclusively eat the fruits and disperse the seeds of angiosperms, while ignoring the available gymnosperm "fruits." This is not the pattern observed in present-day habitats, where frugivorous birds regularly feed on gymnosperm "fruits," sometimes to the near exclusion of coexisting angiosperm fruits (Hartley 1954; Livingston 1972; Poddar and Lederer 1982; Obeso 1986). Some of these bird-dispersed gymnosperms belong to genera that evolved in the late Cretaceous or early Tertiary (simultaneous with the rise of angiosperms), but others belong to much older lineages (e.g., *Taxus*, with arillate seeds that look remarkably like

those of *Palaeotaxus*, from the early Jurassic; Emberger 1968; Thomas and Spicer 1987). If the radiation of birds effectively opened new possibilities for dispersal that could translate into increased diversity and dominance opportunities, the derived advantages would have affected endozoochorous gymnosperms and angiosperms in analogous ways.

I have shown above that endozoochory occurs (and has occurred) in both gymnosperms and angiosperms and that the patterns of taxonomic diversity are similar in both groups. For this reason, endozoochory is best examined in the context of the Spermatophyta as a whole, not only of the Angiospermae. The evolution of fleshy diaspores (and endozoochorous dispersal) apparently has not constituted a sufficiently important evolutionary breakthrough to promote diversification in and of itself. The distribution of fleshy diaspores among and within plant taxa reveals that adaptations to endozoochory have evolved on innumerable occasions and in innumerable lineages in the phylogeny of seed plants, starting with seed ferns (pteridosperms) in the early Carboniferous (Dilcher 1979; Tiffney 1986b). The habit occurs in many unrelated (extant and extinct) groups, and the fleshy portion of the diaspore (the reward to the dispersal agent) may originate from a number of different anatomical structures, as noted earlier. When only extant taxa are considered, fleshy diaspores may occur over whole orders (e.g., Cycadales), groups of families within one order (e.g., Coniferales, Ranunculales), groups of genera within one family (e.g., Cupressaceae, Rosaceae), or groups of species within one genus (e.g., *Hypericum* in the Guttiferae, *Galium* in the Rubiaceae, *Clibadium* in the Compositae). Fleshy diaspores even occur sporadically in some very large families like the Compositae (*Clibadium*, *Chrysanthemoides*, *Wulffia*; Stuessy and Liu 1983) and the Poaceae (*Lasiacis*, *Olmeca*; Davidse and Morton 1973; Soderstrom 1981), which are largely characterized by other seed-dispersal methods. If we assume a reasonable degree of phylogenetic congruence in the taxonomic hierarchy, this extremely patchy distribution unequivocally points to a marked polyphyletism of fleshy diaspores within the whole of Spermatophyta. Furthermore, these observations suggest that the evolution of fleshy diaspores is not subject to consistent morphological and/or ontogenetic constraints and that this dispersal habit has been selectively advantageous many times in a variety of contrasting ecological scenarios.

In the context of this paper, the most interesting implication of the above examples is that the distribution of endozoochory among taxonomic categories is similarly polyphyletic in gymnosperms (extant and extinct) and angiosperms. Gymnosperms and angiosperms are not essentially different in the extremely patchy occurrence of endozoochory across taxonomic groups and hierarchical levels (and, by inference, across lineages). Polyphyletism presumably has afforded repeated occasions for evolutionary experimentation of this seed-dispersal method in different times and environments in both gymnosperm and angiosperm lineages. Despite this, there is not an overall, statistically significant association between endozoochory and diversity at various taxonomic levels in either of these groups, as shown in this paper. Furthermore, none of the 17 most species-rich angiosperm families (6.1% of total families in my sample), accounting for 51% of

species and 49% of genera in the group, is entirely endozoochorous (8 are entirely non-endozoochorous, 9 have mixed dispersal systems). The 75 entirely endozoochorous families in my sample (27.1%) account altogether for only 13% of species and 12% of the genera of extant angiosperms.

The similarities noted with regard to the pattern of occurrence of fleshy diaspores across gymnosperm and angiosperm lineages support the view that this seed-dispersal method is a feature occurring across the Spermatophyta as a whole (both living and extinct). From this perspective, then, there is little basis for attributing to biotic dispersal alone a central and driving role in angiosperm diversification, and the results presented in this paper are consistent with this interpretation. Biotic dispersal, however, may have been a contributing factor in angiosperm diversification acting in concert (synergistically) with insect pollination (Regal 1977; Burger 1981; but see Stebbins 1981). Nevertheless, if Mesozoic Gnetales were simultaneously insect-pollinated and animal-dispersed, as are extant species of *Ephedra* and *Gnetum* (Croat 1978; Faegri and van der Pijl 1979; van der Pijl 1982; Bino et al. 1984*a,b*), then the combination of biotic pollination and dispersal would again be a feature found in the Spermatophyta as a whole, not only in the angiosperms (fleshy diaspores and insect pollination also occur simultaneously in some extant cycads; Eckenwalder 1980; Tang 1987*a,b*). More important, this combination could hardly explain by itself the success of angiosperms in light of the limited success experienced by the closely related Gnetales (Muhammad and Sattler 1982; Crane 1985; Doyle and Donoghue 1986). This points to the need, already noted by Doyle and Donoghue (1986), for identifying more-specific angiosperm synapomorphies that might have resulted in this group's success over other seed plants.

SUMMARY

Seed dispersal by animals has sometimes been considered one of the factors helping to explain angiosperm diversification. Three predictions related to this hypothesis are examined here, namely, (1) biotic seed dispersal is a feature unique to angiosperms, or this group exhibits it proportionally more often than gymnosperms; (2) extant groups exhibiting this feature tend to be taxonomically more diverse than sister groups lacking it; and (3) the timing of the appearance in the fossil record differs for biotically and abiotically dispersed angiosperm taxa. The analyses have been confined to endozoochory, the most genuine and widespread of the various biotic seed-dispersal methods, and conducted on virtually the entire set of extant gymnosperm and angiosperm families. None of the tests supports a role for animal dispersal per se in angiosperm diversification.

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