

# VERTEBRATE DISPERSAL OF SEED PLANTS THROUGH TIME

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■ **Abstract** Vertebrate dispersal of fruits and seeds is a common feature of many modern angiosperms and gymnosperms, yet the evolution and frequency of this feature in the fossil record remain unclear. Increasingly complex information suggests that (a) plants had the necessary morphological features for vertebrate dispersal by the Pennsylvanian, but possibly in the absence of clear vertebrate dispersal agents; (b) vertebrate herbivores first diversified in the Permian, and consistent dispersal relationships became possible; (c) the Mesozoic was dominated by large herbivorous dinosaurs, possible sources of diffuse, whole-plant dispersal; (d) simultaneously, several groups of small vertebrates, including lizards and, in the later Mesozoic, birds and mammals, could have established more specific vertebrate-plant associations, but supporting evidence is rudimentary; and (e) the diversification of small mammals and birds in the Tertiary established a consistent basis for organ-level interactions, allowing for the widespread occurrence of biotic dispersal in gymnosperms and angiosperms.

## INTRODUCTION

The dispersal of seeds and fruits by vertebrates (Corlett 1998, Wenny 2001, Clark et al. 2001) and invertebrates (Beattie 1985, Handel & Beattie 1990) is central to individual species biology and modern ecosystem function (e.g., Howe & Smallwood 1982, Murray 1986, Sallabanks & Courtney 1992, Cain et al. 2000, Nathan & Muller-Landau 2000, Herrera 2002, Levey et al. 2002, Wang & Smith 2002). Dispersal allows escape from predators, location of favorable growth sites, and reduction of parent-offspring and sibling competition. It further influences the structure of plant communities and the distribution of individual taxa. Thirty percent of angiosperm families are biotically dispersed, and another 22% possess biotic and abiotic dispersal; 14% of species are biotically dispersed, and 42% possess both biotic and abiotic dispersal (Tiffney & Mazer 1995). This factor has been implicated in the diversification of individual clades (Eriksson & Bremer 1991, Charlesdominique 1993, Tiffney & Mazer 1995, Smith 2001), although other

factors also play an important role (see Midgley & Bond 1991, Dodd et al. 1999, Magallon & Sanderson 2001). Biotic dispersal is also present in 64% of gymnosperm families (Herrera 1989a) and 46% of gymnosperm species [another 39% of species use both biotic and abiotic dispersal (B. Tiffney, unpublished data)]. Biotic dispersal also has an important effect on individual gymnosperm species success (e.g., Tomback & Linhart 1990, Vander Wall 1992, Willson et al. 1996).

Extant dispersal commonly involves endozoochory—the consumption of the disseminule, including its passage through the disperser’s gut. In a variant, the disperser may consume external flesh without eating the contained disseminule—for example, monkeys consuming large-sized fruits (Lambert & Garber 1998) or ants dispersing small seeds bearing external attractant bodies (Beattie 1985, Beattie & Hughes 2002). If the flesh is the reward, the embryo and nutritive tissue are generally not damaged by the disperser. Active seed predation may also accomplish dispersal but with substantial disseminule mortality. Less frequently, biotic dispersal involves exozoochory, in which the disseminule attaches by hooks, barbs, or glue to the surface of the dispersal agent (Sorensen 1986).

Dispersal mode also has broad links to seed size. Small disseminules may be dispersed by either biotic or abiotic means, but larger ones tend to move through biotic dispersal (Hughes et al. 1994a). Smaller seeds are generally assumed to characterize plants of early successional, light-rich environments, inasmuch as their small nutritional reserve requires that they become photosynthetically self-supporting shortly after germination. Larger seeds possess greater reserves and can generate a larger leaf surface area before becoming self-sufficient. Thus, larger seeds tend to characterize closed communities with lower light intensities (Salisbury 1942, Harper et al. 1970). Grubb & Metcalfe (1996) argue that large seed size may also occur in closed communities as an adaptation for germination through dense leaf litter. In either model, larger seed size is associated with a more closed forest, which, in turn, is associated with a greater frequency of biotic dispersal.

Although contemporaneous biotic dispersal has received substantial attention (e.g., van der Pijl 1982, Herrera & Pellmyr 2002, Levey et al. 2002), its historical evolution has been less studied (e.g., Tiffney 1986a,b; Fleming & Lips 1991; Collinson & Hooker 2000; Eriksson et al. 2000a,b; Labandeira 2002). In part, this discrepancy reflects the necessary parochialism of scientific specialization, but it is also a function of a more intractable problem—taphonomy. Paleontologic evidence provides only a snapshot in time, generally based on the morphology of one organ or organism. Rarely is an investigator presented with a fossil animal with a gut full of identifiable fruits or seeds. However, dispersal is by its nature a dynamic process involving two or more players (Herrera 2002). Thus, elucidation of dispersal relations from the fossil record requires the application of “biological uniformitarianism,” which is the use of morphological features of known ecological function in the present day as indicators of dynamic relations in the past. This approach is inherently antievolutionary because it assumes little change over time. However, the frequency with which convergence (the acquisition of similar morphological features by unrelated organisms facing similar ecological challenges)

occurs and can be identified in the modern day strongly suggests that certain morphological features are reasonable—but not failsafe—guides to the interpretation of past plant-animal interactions.

Classically, it was assumed that dispersal involved “coevolution,” the reciprocal selective influence of the dispersing animal and dispersed disseminule (Tewksbury 2002). Furthermore, it was assumed that this ongoing evolutionary interaction tightly bound the two organisms together, to the point that the extinction of one member would greatly reduce the fitness or cause the extinction of the other (Howe 1977). Recent experiments and observations, together with evidence from the fossil record, clearly indicate that such “tight” coevolution is rare if it exists at all (Schemske 1983, Witmer & Cheke 1991, Herrera 1995, Jordano 1995, Eby 1998, Wenny 2001; but see Tralau 1968, Janzen & Martin 1982, Tiffney 1984). Rather, the norm is “diffuse” coevolution, in which a distinct interaction exists between classes of dispersers and plants (e.g., between birds or mammals and fleshy fruits or seeds of a certain size). The dispersal agent may influence certain aspects of the disseminule (e.g., seed shape in some bird-dispersed plants; Mazer & Wheelwright 1993), but the disperser and disseminule are not tightly coadapted.

Finally, a word to the nonpaleontologist. The fossil record is wonderfully informative, but its data are not without biases. Particular to this paper, I must note three. First, paleontology is dominated by data from the modern temperate latitudes. These zones spawned the industrial revolution and the commensurate growth of an academic infrastructure that can spend the time to study the natural world. Furthermore, the modern tropics present difficulties in finding rocks buried beneath luxuriant greenery. Additionally, rocks that are found in such climates are often deeply weathered, and fossil evidence has been destroyed. Thus, with some very useful exceptions, most of the data come from the present-day latitudes 35° N to 50° N. Second, continents have moved over time. At the time of the probable initiation of vertebrate dispersal of plants, most modern Eurasian and North American localities were at or possibly slightly south of the paleoequator (Smith et al. 1981). Subsequent plate motion has influenced terrestrial environments at any one geographic point. Third, global climate has changed over time (Crowley & North 1991). If the incidence of vertebrate dispersal syndromes is related to climate, as the data suggest, the fossil record will not provide us with a global picture, but only with regional snapshots from successive time periods and paleoclimates.

With those caveats, I briefly review various lines of evidence for vertebrate dispersal of plant disseminules through time and scenarios for its origin, followed by a summation of this evidence from the Paleozoic, Mesozoic, and Cenozoic. I conclude with a consideration of outstanding patterns and future possible directions of inquiry. I intentionally exclude ant dispersal because of a lack of fossil evidence for ant-dispersed disseminules until the later Tertiary, and then only through inference from related living genera and species. It is potentially significant because ants are present in the Late Cretaceous and become important members of the terrestrial ecosystem in the early Tertiary (Grimaldi & Agosti 2000).

## THE NATURE OF THE EVIDENCE

The evidence available for scrutiny using biological uniformitarianism comes from two sources: the fossil record of animals and that of plants.

### From the Disperser's Viewpoint

**COPROLITES AND GUT CAVITY FOSSILS** Coprolites (fossil feces) give an insight into diet but are often difficult to attribute to a source (Thulborn 1991, Chin 1997), whereas gut contents are animal specific but open to varied interpretation (Barrett & Willis 2001). The oldest evidence of either form is from the Permian. Weigelt (1930) reported nearly 60 seeds in the gut cavity of a Late Permian rhychocephalian *Protorosaurus* from Germany. He initially allied the seeds with the Podocarpaceae, but Schweitzer (1968) ascribed them to the primitive conifer *Pseudovoltzia*, which is wind dispersed (Taylor & Taylor 1993). This evidence leads one to suspect that the association was spurious or that the ingestion was accidental. However, Munk & Sues (1993) report the occurrence of similar seeds in the gut cavity of a second specimen of *Protorosaurus*. This finding suggests that the seeds were consumed in the absence of any morphological adaptation to vertebrate dispersal. Post-Permian coprolites and gut contents confirm continuing consumption of gymnosperm and angiosperm disseminules (Harris 1945; Hill 1976; Richter 1987, 1988; Nambudiri & Binda 1989; Rodriguez-de la Rosa et al. 1998; Collinson & Hooker 2000).

**DENTITION** Tooth structure and the arrangement of teeth within the mouth can be used to distinguish vertebrate herbivores from carnivores in a general sense (Sues 2000). Mammals possess a particularly complex tooth structure, which allows identification of specialized herbivory (i.e., granivory, frugivory, folivory, etc.) (Janis 2000, Rensberger 2000). In one case, this specialization has allowed direct association of disseminule and potential disperser (Collinson & Hooker 2000). Tooth marks on an Eocene *Stratiotes* (Hydrocharitaceae) seed can be attributed to a coeval rodent. However, this report is unusual, and the inference of diet from dentition has two substantial pitfalls.

The first pitfall is Janzen's (1984) hypotheses that "the foliage is the fruit," wherein animals with grazing or browsing dentition disperse fruits or seeds inadvertently while consuming foliage [for example, *Trillium* (Liliaceae), which is normally ant-dispersed, may also be moved by deer (Vellend et al. 2003)]. The second pitfall is that fruits and seeds may be effectively distributed by organisms with carnivorous dentition (Herrera 1989b), including bears (Rogers & Applegate 1983), coyotes and raccoons (Cypher 1999), foxes (Milton & Dean 2001), and even wolves (Motta-Junior & Martins 2002). The Permian *Protorosaurus* noted above (Munk & Sues 1993) has carnivorous dentition. Similarly, the absence of teeth in early birds could be associated with some form of herbivory, but living toothless birds range from frugivorous (e.g., parrots) to omnivorous (e.g., crows)

to carnivorous (e.g., owls). Thus, although we have an instinctive tendency to associate biotic fruit and seed dispersal with herbivores, reference to living forms indicates a far greater fluidity of resource use. Reliance on dentition may lead us astray in the fossil record, although not wildly so. Rather, the reliability of dentition is a matter of degree. In the absence of herbivorous dentition, dispersal may still be occurring, but in the presence of herbivorous dentition, or of specialized frugivorous or granivorous characters, dispersal is certainly more common. With rare exceptions (e.g., gnaw marks; Collinson & Hooker 2000), distinguishing simple dispersal from that associated with seed/fruit predation in the fossil record will be impossible.

### From the Plant's Viewpoint

The structure of fruits and seeds provides (sometimes ambiguous) clues to their mode of dispersal (van der Pijl 1982, Tiffney 1986a). Very small disseminules (Hughes et al. 1994a), or those with well-developed wings, suggest dispersal by wind; those with well-developed corky tissue suggest dispersal by water. Disseminules with surficial hooks suggest exozoochorous dispersal.

The most common indication of biotic dispersal is external flesh. Occasionally, preservational circumstances (permineralization; less commonly, compression or impression fossils) allow retention of the fleshy layer, but in most cases, it is degraded before final preservation. Even when flesh is present in fossil compressions and impressions, distortion can limit one's ability to estimate whether the surface was attractive or simply tough and leathery. Often, the interpretation of endozoochory is made by reference to the nearest living relatives. The preserved sclerotestas of Mesozoic cycads and *Ginkgo* generally lack evidence of flesh, but we assume its presence from their modern descendants. Similarly, in the absence of preserved flesh, many Tertiary fruits and seeds are interpreted as having been fleshy [e.g., *Vitis* (Vitaceae), Annonaceae, etc.] on the basis of nearest living relatives.

In some disseminules, largely nuts, the reward to the disperser is the contents of the disseminule. The "adaptation" to biotic dispersal is relatively large size (e.g., Juglandaceae, Fagaceae; Vander Wall 2001), although large size may also favor barochory or hydrochory. Occasionally these disseminules may show direct evidence of association with animals (e.g., gnaw marks; Schmidt et al. 1958) or scatter hoarding [e.g., cached hickory nuts from Miocene sediments of Washington (see figure 34a in Manchester 1987) or cached *Castanopsis* from the Miocene of Germany (see Gee et al. 2003)].

## ORIGINS OF VERTEBRATE DISPERSAL

How did vertebrate dispersal arise, and did it arise independently in separate lineages, as seems likely within the rubric of "diffuse coevolution"? The fossil record is not likely to answer these questions, but it can inform the inquiry. Tiffney (1986a)

suggested the dispersal of fleshy seeds of seed ferns by early herbivorous synapsids (*Edaphosaurus*) and the dispersal of cordaitalean seeds by fish. This implies the direct evolution of flesh for purpose of dispersal.

An alternative and perhaps more likely possibility is that biotic dispersal arose through a transfer of function; flesh evolved for one purpose and was subsequently co-opted for biotic dispersal. Could oil-rich flesh assist in water dispersal (Tiffney 1986a)? Although precise modern analogs are lacking, abiotic dispersal can be common in modern riverine communities (Gordon 1998), but this hypothesis could be difficult to test in the fossil record.

Building on observations of C. Herrera (1982), J. Herrera (1987), Cipollini & Stiles (1992), and Cipollini & Levey (1997) (see also Willson & Whelan 1990, Tewksbury 2002), Mack (2000) suggested that fleshy coverings on fruits or seeds could have originated to retain chemicals to defend the fruits or seeds against invertebrate predation or fungal attack, as well as to serve as a mechanical barrier in its own right. Cipollini & Levey (1997) additionally note that the same chemicals could help define the time of germination through inhibition. Perhaps such chemicals could have been first degraded by insects or bacteria, a role taken over by passage through the gut of the herbivore.

The interaction of disseminules, vertebrate dispersers, and insects is complex in the present day (Sallabanks & Courtney 1992), and the evolution of such interaction in the fossil record is unstudied. Many authors have surmised that glandular structures commonly found on Paleozoic seed plants and ovules/seeds may represent an insect deterrent (e.g., Scott & Taylor 1983), and insects certainly attacked Pennsylvanian seeds (Baxendale 1979, Scott & Taylor 1983, Hilton et al. 2002, Labandeira 2002). Further, insect herbivory was more pronounced in Permian communities than in the present day (Beck & Labandeira 1998). Thus, fleshy fruits or seeds might not be an accurate indicator of biotic dispersal within a group but rather of an initial defense against insects and, possibly, pathogens. If surficial flesh were established for such a purpose, it could have then imitated carrion and attracted opportunistic tetrapod carnivores. The elaiosomes of ant-dispersed seeds have a chemical makeup similar to insect prey and thus attract predatory ants (Hughes et al. 1994b).

Mack (2000) argues that such a transfer of function may have occurred independently in several lineages and most recently within angiosperms. Certainly, fruit structure and dispersal mode is flexible within angiosperms (Tiffney 1984, Knapp 2002) and warns against using phylogenetic affinity to predict a particular dispersal solution.

## FOSSIL EVIDENCE

The fossil record of terrestrial animals and plants spans three geologic eras; although these geological units are defined by biological changes, in some cases patterns transgress era boundaries.

## Paleozoic Era

**PLANT DATA** Seeds first appeared in the late–Middle or Late Devonian (Bateman & DiMichele 1994, Marshall & Hemsley 2003). The initial seeds were small, but their size and morphological diversity rapidly expanded through the Mississippian and Pennsylvanian to encompass a wide range of winged, spinose, plumose, and fleshy forms (Sims 1997, 2000). Thus, many of the morphologies associated with major dispersal modes were established early in the history of the seed. This rise in morphological diversity was paralleled by a rise in seed plant diversity (Sims 1999).

Early seeds were likely dispersed by wind or water (Gensel & Skog 1977, Tiffney 1986a). Although the seeds of some seed ferns bore flattened wings suggestive of wind dispersal (Vega & Archangelsky 2000), similar to coeval conifers (Taylor & Taylor 1993), by the Pennsylvanian, large, flesh-covered seeds had evolved in both seed ferns and cordaitaleans (conifer relatives) (Tiffney 1986a, Taylor & Taylor 1993). Among medullosan seed ferns, the average seed ranged from 20,000 mm<sup>3</sup> to nearly 50,000 mm<sup>3</sup>, and one species exceeded 300,000 mm<sup>3</sup> (sizes range from a pecan to a mango; see Taylor 1965, Tiffney 1986a, Taylor & Taylor 1993). These disseminules are some of the largest reported in the fossil record until the radiation of large angiosperm fruits in the early Tertiary. Smaller, fleshy seed fern seeds also existed (Tiffney 1986a, Taylor & Taylor 1993) and could have been dispersed by vertebrates. Thus, Klavins et al. 2001 observe that fleshy appendages on the apex of a Permian seed could have attracted an arthropod or vertebrate. However, early seeds often attained large size prior to pollination, and these appendages could also have served an earlier role in pollination (see Krasilov 1999). Cordaitalean seeds were smaller but still large, ranging from 122 mm<sup>3</sup> to over 12,000 mm<sup>3</sup> in volume.

**ANIMAL DATA** The initial terrestrial herbivores were insects (Scott & Taylor 1983, Taylor & Scott 1983, Milner et al. 1986, Labandeira 1998). Hotton et al. (1997) have advanced evidence for the presence of low-fiber herbivory and omnivory evolving in later Mississippian and Early to Middle Pennsylvanian tetrapods. The supporting evidence is largely inferential and involves (a) analogy to living carnivorous lizards known to eat vegetation and fruit, (b) predicted jaw mechanics, (c) tooth-wear patterns, and (d) head-body ratios. Although the individual points are debatable, the resulting conclusion is not refutable in light of the often generalized diet of many living taxa.

Dedicated generalized herbivorous tetrapods radiated in the Early Permian (Carroll 1988; Modesto 1992, 1995; Modesto & Reisz 1992). The edaphosaurs were the earliest diverse herbivorous tetrapods, appearing in the Late Pennsylvanian and diversifying in the Early Permian before giving way to caseids and diadectids. Caseids and diadectids were succeeded in the Middle and Late Permian by the radiation of herbivorous therapsids, the dicynodonts. The latter group included small to large herbivores, many of which showed adaptations to digging,

either for food or shelter (King 1990, Cox 1998, Ray & Chinsamy 2003). Whereas earlier studies suggested a great diversity of dicynodonts, including some portrayed as frugivores (see illustration on p. 57 of Czerkas & Czerkas 1990), recent studies suggest that dicynodonts occurred with much lower diversity and in smaller numbers than originally thought and were generalist herbivores (Cox 1998) that possessed slicing teeth and fed close to the ground, perhaps on herbaceous sphenopsids (Rayner 1992). Dicynodonts were accompanied by other less diverse herbivorous reptiles, including procolophonids and pareiasaurs, a few of which also crossed into the early Mesozoic era (King 1996).

**SUMMARY** A wide range of seed morphologies had evolved by the end of the Pennsylvanian. Van der Pijl (1982) was the first to suggest that reptiles dispersed the large, fleshy forms. Hotton et al. (1997) elaborated that some amphibia, reptiles, and early synapsids could have provided dispersal sources in the latest Mississippian through later Pennsylvanian but that dedicated “high-fiber” vertebrate herbivores did not appear until the latest Pennsylvanian. Seed dispersal may also have been accomplished by fish (W. Chaloner, personal communication, 1981) because many plant taxa clearly lived adjacent to river and estuarine channels, and fish dispersal is an important feature in some situations in the present day (Goulding 1980).

These hypotheses lead to several intertwined possibilities. If we assume that only obligate herbivores are potential dispersal agents, then flesh clearly evolved for some purpose other than dispersal and assumed that role secondarily. However, large amphibian and reptilian carnivores and omnivores coexisted with these early fleshy seeds, and the possibility remains that these animals were the initial tetrapod dispersal agents, perhaps mistaking seeds for carrion. When synapsid herbivores radiated in the Permian, they supplanted the earlier forms, which were in decline because of drying climates—perhaps an early instance of diffuse coevolution.

The fleshy seeds of seed ferns and cordaitaleans appear to lack dormancy or germination deferment (fossils are found either empty of contents or germinated, but not ungerminated and containing an embryo). If dormancy was absent or poorly developed in these early forms, a trip through a gut may have spelled death. Furthermore, most reconstructions suggest that the early tetrapods were equatorial (Berman et al. 1997) and, thus, would have limited effects upon plant ranges. However, Permian synapsid and reptilian herbivores, although lacking apparent specific adaptations to seed dispersal, were both widespread and increasingly likely both to consume and to move seeds.

## Mesozoic Era

**PLANT DATA** Tiffney (1986a) summarized diaspore size and inferred dispersal modes for the Triassic, Jurassic, and Cretaceous. With the exception of the data for angiosperms, little has changed in this picture. Mesozoic gymnosperms involved a wide range of groups, some extant (conifers and cycads) and others extinct (various seed ferns and lesser known clades). The seeds exhibit a wide range

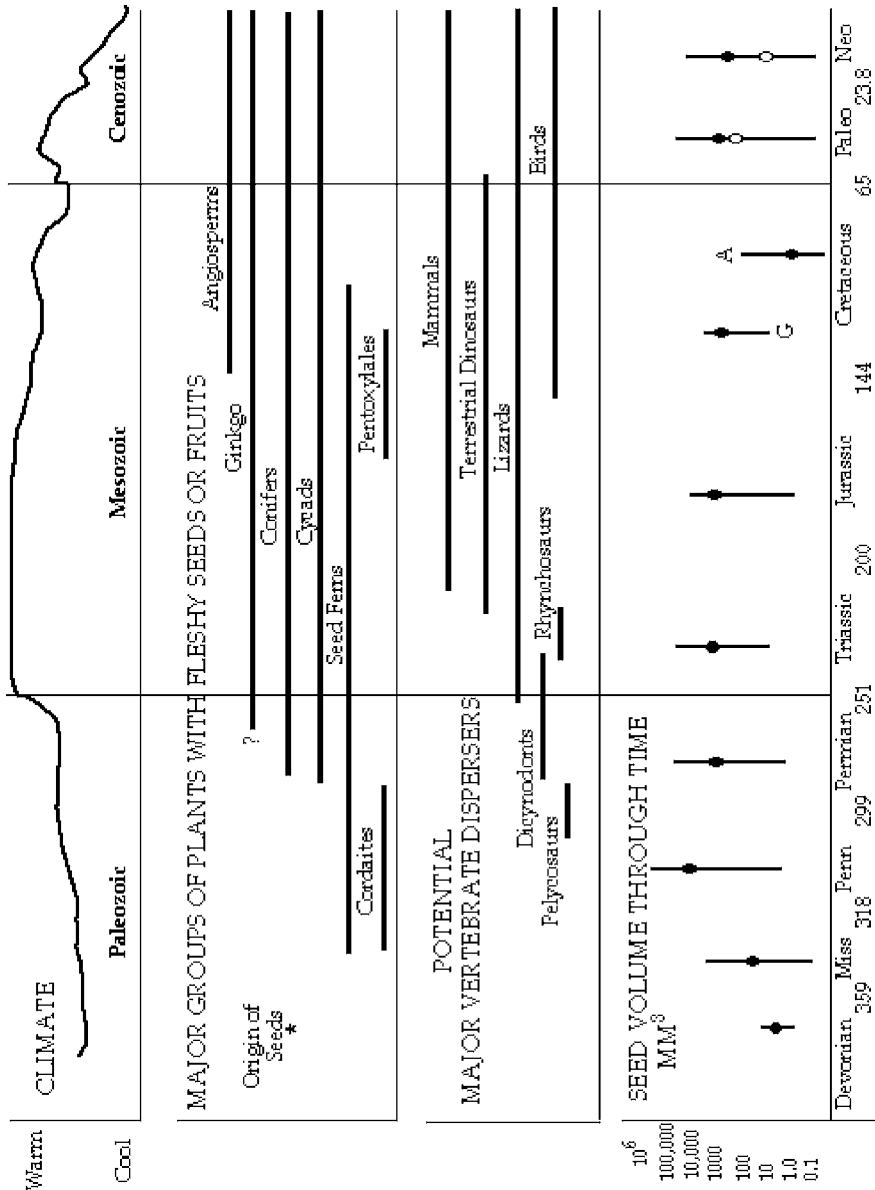


of sizes and dispersal modes (Tiffney 1986a) (Figure 1), including many large forms with fleshy exteriors suggestive of biotic dispersal such as cycads, *Ginkgo*, *Podocarpus* (Coniferae), and lesser known groups such as *Pentoxylon*, a Jurassic and Cretaceous plant of the Southern Hemisphere that possessed a head of fleshy seeds (Taylor & Taylor 1993, Howe & Cantrill 2001), *Caytonia*, which has fleshy “fruit” surrounding several seeds (Taylor & Taylor, 1993; but see also Reymanowna 1973), and the “*Brenneria*” plant, which had small, fleshy seeds (Pedersen et al. 1993). This evidence supports the inference of biotic dispersal in many Mesozoic gymnosperms (Weishampel 1984, Tiffney 1986a).

Angiosperms appeared and diversified in the later portions of the Early Cretaceous through the Late Cretaceous. The initial radiation involved shrubby or perhaps herbaceous plants growing in disturbed sites, particularly along rivers (Wing & Boucher 1998, Friis et al. 1999). Recent studies of floral material indicate the presence of many living families and orders (Crane & Herendeen 1996, Friis et al. 2000, Takahashi et al. 2002). However, a distinctive feature of these early angiosperms is the dominance (relative to the modern flora) of very small flowers, fruits, and seeds (Tiffney 1984; Crane & Herendeen 1996; Eriksson et al. 2000a,b). These seeds tend to range from less than 0.1 mm<sup>3</sup> to about 10 mm<sup>3</sup> (Eriksson et al. 2000a). Although many temperate floras of the present day have a similar mean seed mass (e.g., Leishman et al. 2000), the range includes seeds much larger than those observed in the Cretaceous. In a separate contrast, the mean seed volume of Mesozoic gymnosperm-dominated floras is generally two to three orders of magnitude greater than that of coeval angiosperm floras (Tiffney 1986a) (Figure 1). These distinctions suggest that Mesozoic and Cenozoic angiosperm communities are distinct and that strong differences exist in the ecology of dispersal and seedling establishment between Mesozoic angiosperms and many coexisting gymnosperms. On the basis of the small size and the structure of these seeds, Tiffney (1984) posited that Cretaceous angiosperms were dominated by abiotic dispersal. More recently, Eriksson et al. (2000b) described a diverse flora (106 angiosperm fruit and seed taxa) in which nearly 25% of the species were fleshy as interpreted by the presence of a nonmechanical external layer or a textured exocarp.

Larger Cretaceous disseminules exist (Monteillet & Lappartient 1981, Krasilov & Martinson 1982, Lamb 2001). In two cases, these disseminules are littoral (Monteillet & Lappartient 1981, Lamb 2001), suggesting possible association with water transport. However, a bias is introduced by paleolatitude. Save for Chesters (1955) and Monteillet & Lappartient (1981), all of the reports of Cretaceous fruits and seeds come from Europe and North America, which lay at roughly 35° N to 55° N paleolatitude in the Cretaceous. We know almost nothing of Cretaceous equatorial floras.

**ANIMAL DATA** The primary herbivores in the Mesozoic era are reptiles. However, many of the smaller reptiles tend to be facultative rather than obligate herbivores (King 1996), making assured attribution of dispersal to a particular group difficult. As a result, much evidence is anecdotal or conjectural.



*Early to Middle Triassic* The dicynodonts carried from the later Permian into the Early Triassic and became extinct. These were followed by a Middle and Late Triassic radiation of generalist herbivorous archosaurs, the rhynchosaurs (Carroll 1988), accompanied by aetosaurs and lesser groups of reptilian herbivores (King 1996). In turn, this grouping became extinct, and their role was assumed by the herbivorous dinosaurs.

*Dinosaurs* Although dinosaurian tooth structure allows the separation of herbivores and carnivores, it is generalized enough to preclude identification of particular specializations (e.g., frugivory). Furthermore, most dinosaurs are sufficiently massive to suggest that they were generalist, rather than specialist, herbivores. Clear arguments have been made for their probable importance in dispersal (Weishampel 1984), but direct evidence is difficult to come by. Gut contents have been reported for herbivorous sauropods (Stokes 1964, Ash et al. 1992, Mohabey 2001) and ornithischians (Sternberg 1909, Kräusel 1922, Weigelt 1927), but the authenticity of some of these findings has been questioned (see Currie et al. 1995, Barrett & Willis 2001). The most interesting report is of an Early Cretaceous ankylosaur (Molnar & Clifford 2000, 2001) whose gut contents included three 4.5 mm long fruits and several 0.3 mm diameter seeds. From this and other data, the authors interpret this small (about 1.4 m long) ornithischian as engaging in the selective nipping of particular plant parts, although the presence of fern sporangia and much material interpreted as leaf remains suggests a facultative, not obligate, dispersal agent.

*Birds* The fossil record of birds commences in the Jurassic (Padian & Chiappe 1998) and involves two periods of radiation, one in the Cretaceous and a second, explosive one in the Tertiary (Chiappe & Dyke 2002, Feduccia 2003). The latter

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**Figure 1** Summation of major features and clades involved in the evolution of vertebrate dispersal from the Devonian through Tertiary periods. Climate: a relative track (cooler, warmer) of global climate (from Crowley & North 1991, Stanley 1999). Plant groups: geologic occurrence of major groups of seed plants that may possess fleshy disseminules (ranges from Taylor & Taylor 1993). Vertebrate dispersers: geologic occurrence of major groups of potential vertebrate dispersers (ranges from Carroll 1988). Seed volume: average seed volume in cubic mm by period from Tiffney (1986a) modified after Eriksson (2000a). Bar represents the full range; black dot represents the mean value. In the Cretaceous period, G = gymnosperms only, and A = angiosperms only. The Tertiary is broken into the Paleogene and Neogene; the white dots are data from Eriksson (2000a) that have slightly lower Tertiary values than data from Tiffney (1986a) because of different floras sampled. This illustrates the average decline in seed volume in the Northern Hemisphere as climates cooled. The horizontal axis is geologic time, with the boundaries between the periods noted in millions of years. Miss = Mississippian, Penn = Pennsylvanian, Paleo = Paleogene, Neo = Neogene.

diversification clearly involved many frugivorous and seed-eating birds, particularly among the passerines (Ericson et al. 2003). However, the role of birds in seed dispersal in the Cretaceous is less clear. Early birds were classically seen as toothed carnivores, particularly those associated with aquatic habitats. However, research in the past 20 years has demonstrated a greater diversity of Mesozoic birds and the existence of a whole clade (Enantiornithines) that became extinct at the end of the Cretaceous (Chiappe & Dyke 2002, Feduccia 2003). We have no living analogs by which to judge the habits of these latter organisms. Although the role of Cretaceous birds as dispersal agents is largely conjectural, two examples provide tantalizing evidence. Zhou & Zhang (2002) report a middle–Early Cretaceous bird of about 60 cm in length with remains of *Carpolithus* sp. (a form genus for seeds of unidentifiable affinity) in the area of its stomach. Because of the size of the plant objects and the associated vegetation (Zhou et al. 2003), the most parsimonious suggestion is that this bird was feeding on a gymnosperm. An associated genus from the same area, *Sapeornis*, possessed gastroliths and reduced teeth, suggesting it, too, fed on plants; the associated foot structure indicated that it could climb (Zhou & Zhang 2003).

**Smaller terrestrial reptiles** Many modern lizards are omnivorous (Barrett 2000) and are known to disperse fruits and seeds (e.g., Lord & Marshall 2001, Valido & Nogales 2003). Lizards were widespread in the Mesozoic era and could have played an important role in moving smaller disseminules. Similarly, turtles can be effective dispersal agents in the present day (Moll & Jansen 1995) and are likely the source of a Campanian age coprolite containing nearly 200 achenes of early Ranunculaceae (Rodriguez-de la Rosa et al. 1998).

**Pterosaurs** Fleming & Lips (1991) argued that pterosaurs were potentially important seed dispersers, particularly of early angiosperms. The majority of pterosaurs display a dentition suited to piscivory or insectivory; the few forms that are edentulous may be demonstrated either by stomach contents to be fish eaters (*Pteranodon*) or by their sheer size (*Pteranodon*, *Nyctosaurus*) unlikely to be effective seed or fruit dispersers because they would have had great difficulty perching on vegetation. The stratigraphic distribution of the major clades suggests that only the Pteranodontidae and Nyctosauridae radiated in the middle or later Cretaceous, in parallel with the appearance of angiosperms. One very odd group, the Barremian to Albian Tapjaridae, has an edentulous bill, relatively small size (although still large with an estimated 1.5 to 2.0 m wingspan), and an odd head shape reminiscent of a moa or an emu; it could have been involved in dispersal of larger seeds. Fleming & Lips (1991) and Wellnhofer (1991) argued that fruit-eating pterosaurs likely lived in more terrestrial settings with lower potential for fossilization. Wellnhofer concluded, “If there were fruit-eaters—which is highly probable—we are unlikely to ever find their fossil remains” (Wellnhofer 1991, p. 161). If this argument were valid, the fossil record of birds in the Cretaceous and Tertiary would be entirely of aquatic forms, which it decidedly is not. Although evidence suggests pterosaurs

were at best a minor source of biotic dispersal, caution must be exercised in light of evidence for “carnivores” consuming fleshy fruits or seeds in other groups.

**Synapsids** Early Triassic herbivore communities were dominated by dicynodont synapsids, carrying on the tradition of the Permian (Carroll 1988, Schwanke 1998). The dicynodonts became extinct in the Middle Triassic, and synapsids were represented for most of the rest of the Mesozoic era by insectivores, including mammals. A timely summary (Kielan-Jaworowska et al. 2004) allows access to the most recent thinking on Mesozoic mammalian diets. The multituberculates were classically identified as the most diverse and important mammalian herbivores of the middle and late Mesozoic based on their dentition. Their demise in the early Paleocene in the face of the explosive diversification of rodents was seen as further evidence of their occupying a rodent-like niche, although differences in reproductive features may better explain this extinction (Kielan-Jaworowska et al. 2004). More recent examination of the jaw mechanics and biology of modern analogs now indicates that multituberculates were omnivores (Clemens & Kielan-Jaworowska 1979, Kielan-Jaworowska et al. 2004). Del Tredici (1989) invoked them as dispersal agents for *Ginkgo*, but Wall & Krause (1992) demonstrated that at least *Ptilodotus*, an advanced multituberculate, would have been unable to crack the seed of *Ginkgo*. Similarly, some Cretaceous marsupials (e.g., *Turgidodon* of the later Cretaceous) were likely omnivorous and could have dispersed fruits or seeds. Only one species, the Late Cretaceous marsupial *Glasbius intricatus* of North America, is specifically identified as a possible early frugivore (Kielan-Jaworowska et al. 2004). A third group of generalist herbivores were the “zhelestid” eutherians, also referred to as archaic hoofed mammals (Nessov et al. 1998). These small herbivores of Central Asia possessed low crowned teeth that were appropriate for browsing.

**SUMMARY** Sparse evidence from gut contents and coprolites indicates seed and fruit dispersal occurred (Nambudiri & Binda 1989, Molnar & Clifford 2000, Zhou & Zhang 2002) and affected angiosperms (Rodriguez-de la Rosa et al. 1998). However, the relative frequency of the dispersal is unclear. Potential dispersal agents had been available to gymnosperms throughout the Mesozoic era, and the large size of many saurischian herbivores suggests that dispersal could occur in the absence of specific animal or plant adaptations. In the middle to Late Cretaceous the rise of angiosperms was paralleled by the diversification of ornithischian herbivores, at least in North America (Weishampel & Norman 1989; Tiffney 1992, 1997). This development suggests, but does not demonstrate, that the potential existed for generalized angiosperm dispersal by ornithischians, much as ungulates serve in this role in the present day (Carrano et al. 1999).

Fleshy fruits formed an important component of one Early Cretaceous flora (Eriksson et al. 2000b). This finding could indicate dispersal by smaller dispersal agents, or it could be related to aspects of germination ecology or plant pathogen deterrence (Mack 2000). If dispersers were involved, they might include lizards,

birds, and, in the Late Cretaceous period, multituberculates, “zhelestids,” and the occasional marsupial. However, no compelling evidence presently exists for obligate fruit or seed dispersal by mammals, although only the North American mammal record is known in detail (Clemens 2001); future discoveries may alter this conclusion.

## Cenozoic Era

**PLANT DATA** The angiosperms underwent a major burst of taxonomic and morphological diversification in the Tertiary period that involved the appearance of many modern genera (Niklas et al. 1985), often with fruit and seed sizes and morphologies close to those of their living descendants (Tiffney 1990, Dilcher 2000). This development is displayed in several Eocene fruit and seed floras (e.g., Chandler 1964, Collinson 1983, Manchester 1994). These floras are frequently associated with diverse mammalian faunas that contain potential dispersal agents; for example, the Paleocene-Eocene Dormaal locality of Belgium (Fairon-Demaret & Smith 2002) and the coeval faunas and floras of southern England (Collinson & Hooker 1987).

The initial Tertiary radiation generally involved plants of closed communities, often with large disseminule sizes (Tiffney 1986a, Eriksson et al. 2000a). Cooling and drying climates of the later Paleogene led to the evolution of more open communities in middle latitudes, and by the middle Tertiary another angiosperm radiation involving annual and biennial herbs and grasses was underway (Friis 1975; Tiffney 1984, 1986a; Jacobs et al. 1999). Although large, animal-dispersed disseminules were present in virtually all of these communities, the overall trend was toward a reduction in fruit and seed size (Tiffney 1986a, Eriksson et al. 2000a). Many of these smaller disseminules (e.g., Compositae) could be as easily spread by wind as by granivorous birds or rodents. Indeed, the seeds of most herbs do not exhibit clear morphological adaptations to vertebrate dispersal.

This second radiation is well encompassed by the north temperate fossil record, but we have no evidence from the tropics to tell whether the climatic deterioration of the mid-Tertiary had an influence on the structure of tropical forests or their associated dispersal syndromes. Thus, the evidence from the fossil record for the rise of abiotic dispersal mechanisms in the later Tertiary is a regional, not global, feature.

**ANIMAL DATA** The radiation of birds in the Tertiary (Feduccia 1995, 2003) suggests a strong escalation of bird-plant interaction. Initially, this interaction involved several lineages focused on larger, fleshy fruits, but in the middle Tertiary, the radiation of the passerines layered on a major group of frugivores and granivores.

Recent phylogenetic studies may place a twist on this story. Passerines originated in Australia (Ericson et al. 2003) and spread to the rest of the world as Australia drifted north, starting in the Eocene. As a result, passerine-plant interactions could have early Tertiary or Late Cretaceous roots in Australia.

Similarly, many important mammal groups radiated in the early Tertiary. Several of these groups displayed clear adaptations to frugivory and granivory (e.g.,

Collinson & Hooker 1991). Primates in particular showed early adaptations to frugivory (Szalay 1968), radiated in the early Tertiary (Sussman 1991, 1995), and serve an important role in dispersing modern tropical angiosperms (Sussman 1995, Lambert & Garber 1998, Regan et al. 2001). Organ-specific biotic dispersal agents also became important in more temperate lineages as families with small Cretaceous fruits (Juglandaceae, Fagaceae) evolved larger nuts in the early Tertiary (Tiffney 1986b, Vander Wall 2001). Bats first appeared in the Eocene (Jepson 1970, Benton 1993) and diversified through the Tertiary. The earliest forms were clearly insectivorous. The oldest frugivorous bat is a middle Oligocene megachiropteran, and the oldest microchiropteran frugivore is from the Miocene (University of Michigan Museum of Zoology 2004). Because frugivorous bats are essentially tropical and because of the relative paucity of fossil material from the equatorial portions of Earth, this adaptation possibly evolved earlier in the history of the group.

Subsequent middle Tertiary radiations of “whole-plant” grazers (even-toed and odd-toed ungulates and others) added a further layer of diffuse dispersal relationships (Janis 1993, Novacek 1999, Janis et al. 2002).

**SUMMARY** A clear upsurge occurred in the importance of biotic dispersal in the Tertiary. Central to this are birds and mammals that, because of their small size, have organ-level interactions with plants (Wing & Tiffney 1987a,b; Tiffney 1992), particularly in closed communities (Clark et al. 2001). The question of what the forcing factor is remains to be answered. Wing & Tiffney (1987a,b) and Tiffney (1992) postulated that the radiation of small vertebrates led to a rise in dispersal and the subsequent establishment of closed-canopy forests. Eriksson et al. (2000a) note that increased precipitation and warmer climates would favor closed forests, which, in turn, would favor larger disseminules and would thus drive the radiation of smaller vertebrates scaled to fit within this community. This hypothesis is considered in more detail below.

Fossil evidence suggests that subsequent climatic cooling led to the spread of herbaceous angiosperms, many of which possessed smaller seeds and fruits, amenable to biotic and abiotic dispersal. By the Tertiary the continents were near enough to their present positions that the fossil record, restricted to the temperate latitudes, provides evidence for only a portion of the evolution of Tertiary dispersal spectra.

## DISCUSSION

I have summarized the basic patterns of vertebrate dispersal within each of the geologic eras (Figure 1); here my focus is on common threads.

### Data Quality

Neontological studies delineate granivores, frugivores, and herbivores in contrast to carnivores, leaving the impression that feeding mode may be clearly recognized from morphological characters. In fact, the relationship between diet and dentition

appears as diffuse as coevolution—so diffuse as to greatly limit our ability to infer the absolute presence or absence of biotic dispersal from plant or animal morphology in the fossil record. Flesh could possibly serve purposes other than dispersal, either at its evolutionary inception or while dispersal is actively under way. Carnivorous dentition is no guarantor of diet because fossil gut contents of reptiles that would otherwise be considered carnivores indicate that they could serve as dispersal agents. In short, it is difficult to conclusively demonstrate the presence or absence of dispersal except through gut contents or coprolites. However, the relative frequency of herbivorous dentition, biotic dispersal-related fruit and seed characters, or both within a fossil assemblage allows us to establish probabilities. I suggest from present data that biotic dispersal has been with us from at least the Permian and possibly the later Pennsylvanian, but that it became more widespread and important in the Tertiary than in previous periods.

## Dispersal is Very Diffuse Coevolution

The foregoing observations, particularly the ability of carnivores to act as dispersal agents, strengthens Herrera's (1995) contention that coevolutionary dispersal relationships are diffuse. A broad perspective suggests that dispersal can be achieved by any organism with the ability to reach and manipulate the dispersal unit. That certain groups become important dispersal agents in particular environments (e.g., birds and primates in tropical forests) might primarily be a function of their ability to move within the canopy and secondarily of other morphological features related to frugivory.

**BIOLOGICAL UNIFORMITARIANISM TAKES US JUST SO FAR** We can use the morphology and associated ecological functions of living plants to infer function from the morphological remains of the past. I believe such inferences about dispersal are viable back to the beginning of the Tertiary. Beyond that, this approach may encounter a "stem group/crown group" problem.

Molecular and morphological systematists have battled in the past decade over the disconnect between molecular evidence that suggests a far earlier cladogenesis than is observed in the morphological fossil record. With time, most have agreed that the solution lies in disconnecting phylogenetic radiation from ecological radiation. The two may occur simultaneously, but more often (early metazoa, mammalian orders), phylogenetic diversification occurs within a stem group that is ecologically homogeneous (e.g., Knoll & Carroll 1999). Subsequent environmental change releases different taxa to pursue different ecological solutions, resulting in a later burst of crown group morphological diversification. These two alternatives are summed in the terms "pattern congruency" (simultaneous phylogenetic and ecological diversification) and "pattern lag" (ecological diversification follows phylogenetic diversification), coined by Wing & Boucher (1998) in their summary of Cretaceous angiosperm evolution. Although Cretaceous floras harbor many modern angiosperm families, structural features suggest the group occupied a far narrower ecological niche than in the Tertiary or in the present. Barring



future data to the contrary, inference of Cretaceous ecological function from living representatives of these families is thus fraught with uncertainty.

What if no living clade is available for reference? We then assume that morphological characteristics that cross clades reflect shared function; that is, flesh promotes biotic dispersal in the seeds of widely divergent clades. However, in examining the fossil record, we should remain alert to the possibility that some characteristics have changed function over time. I am increasingly dubious that the fleshy seeds of the Mississippian and Pennsylvanian evolved for the purpose of biotic dispersal, although the function of that tissue remains conjectural. At the very least, we should be careful in using the present as a guide to the past, lest we turn the past into a precise parallel to the present, just with different plants and animals plugged into their respective roles.

## FUTURE ENDEAVORS

### Early Dispersal

The time at which significant vertebrate dispersal of seeds first appeared is conjectural. Vertebrate dispersal was certainly in place by the Late Permian (Weigelt 1930, Munk & Sues 1993) and likely by the Early Permian, as indicated by the presence of obligate herbivores (Hotton et al. 1997). It could have occurred earlier, in the Pennsylvanian, accomplished by “soft tissue” herbivores and omnivores (Hotton et al. 1997) or even earlier by apparent carnivores. Resolution of this problem using present morphological data is not possible, but paleobiogeographic distributions may provide some insight.

Pennsylvanian and Early Permian herbivores occur within 10° N and 10° S of the paleoequator, and spread beyond this belt only in the Late Permian (Milner 1993, Berman et al. 1997). This development parallels the distribution of many groups with fleshy-seeded plants. However, if fleshy-seeded gymnosperms occurred beyond the paleoequatorial range of early tetrapods, then flesh evolved for a purpose other than dispersal, even if it was involved in facultative dispersal relationships where tetrapods existed.

### Seed Coat Thickness

Vertebrate dispersal required a seed coat that is light enough to be moved by a dispersal agent but resistant enough to protect the embryo from being consumed. An examination of trends in seed coat thickness (normalized for seed size to account for scaling effects) through time, particularly with reference to the evolution and demise of various potential disperser lineages, would be informative.

### Tropical Data: A Key Missing Element

A core requirement for a better understanding of the evolution of dispersal relationships is better fossil data from the tropics, particularly because modern vertebrate dispersal is so important in these communities (Herrera 2002). Tertiary

communities of Europe and North America began in a greenhouse world of subtropical environments that gave way to increasingly temperate ones. This circumstance enforces a bias in that we cannot track dispersal-mode changes within a single community type in one climate regime over time. Optimally, we would like to observe Eocene to present patterns within plant communities living under similar climates.

In the Cretaceous, we lack clear evidence of what is occurring at the tropics. Perhaps lower-middle latitude communities were the tropics. If they were not, however, we might be missing an important part of the picture. The phylogenetic and ecological radiation of angiosperms might have occurred concurrently in a tropical setting we have yet to sample, but the results leaked stepwise to more temperate latitudes, simulating pattern lag.

## Palms

Palms appear in the Santonian stage of the Cretaceous, represented by wood and leaves (Uhl & Dransfield 1987). No unequivocal Cretaceous palm fruits have been found (excluding the dubious Aptian *Hyphaeneocarpon*; Vaudois-Miéja & Lejal-Nicol 1987), although fruits are widely known from the Tertiary (Mai 2000). Modern palms are almost entirely animal dispersed (Uhl & Dransfield 1987). Although excellent evidence suggests that dispersal modes changed from abiotic in the Cretaceous to biotic in the Tertiary in some angiosperm lineages (Tiffney 1986b), vestiges of the Cretaceous dispersal mode persisted in these groups in the Tertiary and in the present. Not so in palms. Either we are missing abiotically dispersed palm fruits in the Cretaceous and Tertiary, or we are missing biotically dispersed palm fruits in the Cretaceous. One possible exception is the enigmatic "*Ficus*" *ceratops* of the Campanian age of western North America (Shoemaker 1977), whose morphology is suggestive of a cast of an eroded palm fruit.

## Latitudinal Gradients

Climate influences the modes of dispersal within communities through its effect on vegetation. The cooling Tertiary climates in Europe and North America led to a radiation of smaller seeds and fruits with a higher incidence of abiotic dispersal (Tiffney 1984, Eriksson et al. 2000a). This same effect is observed in the latitudinal distribution of modern seed size; Moles & Westoby (2003) record that, for every roughly 23° distance from the equator, average seed mass decreases 10-fold, although some intraspecific variation exists (Hampe 2003).

If the ecological relationships between Cretaceous angiosperms, dispersal agents, and climates were similar to those of the Tertiary and the present, we would predict that a similar pattern would emerge from a time-limited, pole-to-equator summation of Cretaceous seed size. Available data do not allow such a summation, and this becomes another goal for future exploration. If a pattern emerges similar to that observed in the Tertiary and the present, then one might infer similar ecological relationships between seed size, dispersal, and community ecology. If the pattern (once corrected for the lower equator-to-pole temperature gradients of

the Cretaceous) is not comparable, it may suggest that Cretaceous and Tertiary angiosperm communities functioned differently.

This pattern should also be separately checked for gymnosperms. In the present day, the intuitive response is that the pattern is parallel to that of angiosperms (Pinaceae dominating the far northern latitudes, whereas larger-seeded *Ginkgo* is more temperate, and cycads are subtropical). However, will this pattern hold in the Cretaceous?

## Do Dispersers Structure Vegetation or Does Vegetation Drive Dispersers?

One of the most interesting historical questions raised with respect to biotic dispersal involves the Cretaceous-Tertiary transition. Disseminal size and the occurrence of biotic dispersal both markedly increase across this boundary; however, the cause is open to debate. Tiffney (1984) and Wing & Tiffney (1987a,b) suggested that the radiation of birds and mammals established dispersal agents scaled to move organs, which, in turn, allowed larger disseminal size and ultimately the establishment of closed forests with low-light germination regimes. Eriksson et al. (2000a) countered that these relations were inverted and that a warmer climate and increased precipitation allowed the establishment of closed forest, which shifted the ecological constraints on seed recruitment (Eriksson & Jakobsson 1999) and possibly seedling ecology (Ibarra-Manriquez et al. 2001) and led to larger seeds. The dispersal agents therefore tracked, not led, the increase in seed size.

Plant stature and community density have relationships both with prevailing climate and with mode of dispersal; disentangling the influence of these two forcing factors may prove difficult. However, I think that the basis of distinguishing the two will be found in examining two features of Cretaceous community function.

First, one must examine whether the rise in precipitation and warmth at the Cretaceous-Tertiary boundary is a valid trigger of the radiation of closed angiosperm communities. Certainly such a climatic change occurred at the boundary (Wolfe & Upchurch 1986, 1987). However, warm and wet climates existed in areas occupied by angiosperms earlier in the Cretaceous. White et al. (2001) and Ufnar et al. (2002) advance isotopic evidence that the western margin of eastern North America may have had as much as 2500 to 4100 mm of rain per year in the Albian through Cenomanian ages, distributed evenly throughout the year. Contemporaneous gravel-choked, low-gradient stream channels support this interpretation (Brenner et al. 2003). Although these data come from the eastern shore of the Mid-Continental Seaway, prevailing wind currents (White et al. 2001, Ufnar et al. 2002) would carry airmasses northeast, providing at least adequate rain to the east coast of North America, where moisture-indicating coals are recognized in the earlier Cretaceous (Ziegler et al. 1987). If the hypothesis of Eriksson et al. (2000a) is correct, floras from these areas (and others shown to have high rainfall; see Parrish et al. 1982) should display a tendency toward larger seed sizes. The data are presently limited, but the Santonian-Campanian floras of New Jersey and New England appear to exhibit small fruit and seed size (Tiffney 1977, Crepet

et al. 2001). If further exploration supports higher moisture being associated with small fruit and seed size, then moisture is unlikely to be the feature that triggered the evolution of larger fruit and seed size at the Cretaceous-Tertiary boundary.

Second, one must examine whether the ecosystem dynamic of the early Tertiary is homologous to that of the middle Cretaceous. Whereas Cretaceous angiosperms were dominated by small seed size, Cretaceous gymnosperm groups included taxa with both small (e.g., Bennettiales) and large (cycads, *Ginkgo*, several conifers) (Figure 1) seeds. Unless a different ecologic metric exists in seed recruitment and response to climate in gymnosperms and angiosperms, both groups should roughly parallel each other in seed size and dispersal mode when growing in similar climates. This disparity may provide clues to the Cretaceous-Tertiary transition and involve coevolution on a very broad scale. Reptiles and gymnosperms both radiated in the Triassic and held sway through the Mesozoic. Terrestrial dinosaurs and enantiornithine birds became extinct at the boundary, ending approximately 150 million years of association. Mammals, modern birds, and angiosperms then radiated, establishing new and broad coevolutionary relationships in the Tertiary (Wing & Tiffney 1987a,b; Tiffney 1992, 1997). I suggest that, although the Mesozoic and Cenozoic eras both involved plant-animal interactions, the Mesozoic dynamic was dominated by reptile-gymnosperm interactions to which the angiosperms were newcomers. Only with the demise of terrestrial dinosaurs at the Cretaceous-Tertiary boundary did an angiosperm-bird-mammal dynamic become fully established. In short, the terrestrial Mesozoic and Cenozoic had different ecological dynamics, much as Bambach et al. (2002) have demonstrated for the marine realm. Further research can test both of these contentions.

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