The role of vertebrate herbivory in the evolution of land plants

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Land plants have evolved in the selective context of their surrounding environment. Climate has long been discussed as a selective force, but the effects of vertebrate herbivores may also be significant. Four phases of vertebrate herbivory may be recognised in the fossil record. The Silurian-Late Carboniferous apparently lacks vertebrate herbivores. The Early Permian-Late Triassic is dominated by low-feeding therapsids. The Late Triassic-K/T boundary is dominated by large archosaurian herbivores. The Tertiary-Present is dominated by small birds and mammals. Recognition of these changing forces of vertebrate herbivory will aid in understanding the evolution of vascular plants.

Key-words—Palaeontology, Palaeoclimate, Herbivory, Evolution.

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साराँश

स्थली पौधों के विकास में कशेरुकी शाकभक्षीयों की भूमिका

बूस एच० टिफ़नी

स्थली पौधों का विकास उनके आस-पास के वातावरण के अनुसार हुआ है और इसमें जलवायु की महत्वपूर्ण भूमिका रही है लेकिन कशेरुकी शाकभक्षीयों का प्रभाव भी उल्लेखनीय है। जीवाश्मी अभिलेखों में कशेरुकी शाकभक्षण की चार अवस्थायें अभिनिर्धारित की गई हैं। सिलूरी-अन्तिम कार्बनीफरी में कशेरुकी शाकभक्षी नहीं थे। प्रारम्भिक परमी-अन्तिम त्रिसंघी कल्प में कम खाने वाले थिरेप्सिडों की बाहुल्यता थी। अन्तिम त्रिसंघी-क्रीटेशी/तृतीयक सीमा पर बृहत आकार वाले आर्केसोरियन शाकभक्षीयों का बाहुल्य था। तृतीयक-वर्तमान कल्प में छोटी चिड़ियों एवं स्तनधारीयों की बाहुल्यता थी। इन कशेरुकी शाकभक्षीयों में निरन्तर परिवर्तन के आधार पर संवहनी पौधों के विकास के रहस्यों को जानने में सहायता मिलेगी।

PALAEOBOTANISTS have long interpreted the evolution of clades as influenced by individual plant biology, and secondarily, as a plant response to climate. However, the selective environment within which plants evolve also includes the surrounding biological community and ecosystem. Past communities and ecosystems are interpreted by analogy to living processes and systems, assuming biological uniformitarianism. However, the use of these modern biological relationships to interpret the past has the potential to trap palaeobotanists into thinking that the present is the past, that while organisms differed and evolved, communities and ecosystems, and the selective forces they harbour, have not fundamentally changed through time. In the past two decades there has been increasing recognition that a uniformitarianism of biological or geological process does not preclude vastly different past worlds, as rates and interactions of processes can yield different outcomes (cf. Behrensmeyer *et al.*, 1992). This insight has significance for the palaeobotanist studying individual fossils or clades. The terrestrial ecosystem forms the environment in which individual lineages evolve, and dissimilarities in ecosystems through time are differences in selective pressures faced by coeval plants. This dissimilarity of terrestrial ecosystems and the selective pressures they generate, particularly in plant-vertebrate interactions, is my focus.

This emphasis on vertebrate herbivores and vascular plants is not to deny the importance of arthropods as a selective force in the evolution of terrestrial plant lineages. Indeed, they have played

an early and central role (Rohdendorf, 1970; Wootton, 1990), and probably are the premier herbivores of the present day. However, their fossil record is relatively incomplete, and it is presently possible to provide a greater diversity of supporting observations from the record of vertebrates and plants.

Terrestrial vertebrates have clear interactions with vascular plants. Plants both provide the basis for a food chain and, perhaps more importantly, modify the moisture, light and heat regimes of the habitats occupied by animals. Further, plants define the three-dimensional environments in which animals live, influencing locomotory adaptations, size, and thus absolute numbers of vertebrates. In turn, vertebrates, depending on size and diet, may act as everything from dispersal agents to a source of disturbance affecting the successional status of the plant community. All of these relationships have changed through time, as particular combinations of plants, herbivores and environments have joined to form unique ecosystems, unlike those of the present. With these changes, the selective pressures faced by plants have altered.

SOURCES OF DATA

Interpretation of past plant-vertebrate interactions is largely inferential, suffering from the compounded uncertainties inherent in each of the fossil sources examined. Perhaps the best data come from the animal remains, including the structure of teeth and the biomechanics of jaws. Slightly further afield, vertebrates occurring in large numbers, relative to coeval forms, may suggest herbivory. Truly "hard" evidence such as gut or faecal contents are rarely found, and in the latter case, are often difficult to ascribe to specific taxa. From the perspective of plants, evidence is inferred from standard descriptions (e.g., Taylor, 1981; Stewart, 1983; Thomas & Spicer, 1987). While mechanical defences such as thorns or thorny leaves suggest non-insect herbivore pressure, other characters are more equivocal. Height may serve as an escape from herbivory, but may equally well be selected for wind pollination or seed dispersal (Tiffney & Niklas, 1985; Niklas, 1986). Tough bark and foliage can equally well indicate adaptations to drought or to the prevalence of fire (Robinson, 1989, pers. comm.), as they can deter herbivory. A detailed discussion of these and other data may be found in Behrensmeyer et al. (1992). However, while inferential in individual details, the summed patterns suggest an overall evolution of terrestrial systems from a beginning without herbivory to the present complex angiosperm-bird-mammal system.

EARLY ECOSYSTEMS

Terrestrial vegetation was certainly established by Middle to Late Silurian, and possibly earlier (Stebbins & Hill, 1980; Gray, 1985). By the Early Devonian, this flora began to diversify. By the Middle Devonian, increasingly larger plants were appearing, creating a complex, three-dimensional, terrestrial vegetation including seed plants (Chaloner & Sheerin, 1981). This plant "invasion" of land was paralleled by an arthropod invasion (Wootton, 1990), but one initially involving almost entirely detritivores and carnivores (Almond, 1985; Shear, 1991). Evidence for insect herbivory, and for plant responses to it, accumulate through the latest Devonian and Carboniferous (e.g., Scott & Taylor, 1983; Scott et al., 1985; Niklas, 1986; Jarzembowski, 1987), but it appears that arthropod herbivores were not a major force until the later Carboniferous (Shear, 1991; Behrensmeyer et al., 1992). It also appears that early insect herbivores concentrated on the nutrient-rich reproductive structures of land plants (Shear, 1991; but see also Kevan et al., 1975), perhaps seeking an energy content similar to that of previous animal prey items. With time, digestive adaptations evolved to allow insects to move their attentions to other, chemically-different, plant organs.

Vertebrates arrived on land with the Late Devonian amphibia Ichthyostega and Acanthostega (Carroll, 1988), and amniotes followed in the Lower Carboniferous (Smithson, 1989). These groups diversified through the rest of the Carboniferous (see Carroll, 1988), but it is not until the end of the Upper Carboniferous that the first clear vertebrate herbivores appear. Evolution of the teeth of Diadectes and Bolosaurus (reptiles) and Edaphosaurus (synapsid) indicates that they ate terrestrial plants (Olson et al., 1991). Thus, from the latest Upper Carboniferous through the Early Permian there were a small, but growing, number of vertebrate herbivores, although Milner (1987) assumes earlier, undiscovered, ancestral herbivores. By the later portion of the Early Permian, at least in North American assemblages, herbivores start to outnumber carnivores (Olson, 1971, 1986; stratigraphy after King, 1990). These early herbivores were low-feeding, representing a threat to herbaceous plants and young trees.

The significance of these observations is two-fold. First, the early terrestrial ecosystems were quite unlike those which existed from the Permian onwards. Insects evolved herbivory gradually, and

vertebrates evolved "serious" herbivory only in the latest Carboniferous. Before this time, plants existed in a relatively "herbivore-free" environment. Given the biomass of arthropods, and subsequently vertebrates, found in Devonian and Carboniferous deposits, how did solar energy find its way into the ecosystem from terrestrial photosynthesis? Three, by no means mutually-exclusive, routes are possible. First, it is likely that aquatic plants supported aquatic herbivores which were then consumed by amphibian carnivores who carried energy to land. This corresponds to Olson's (1971, 1986) "Permo Carboniferous chronofauna" trophic system. Second, many of the early arthropod groups show signs of being detritivores, and as detailed by Shear (1991), much photosynthetic energy may have been consumed by detritivores in a "semi-digested" form, and made available to terrestrial carnivores. Third, as herbivorous arthropods evolved, they may have become the prey of carnivorous arthropods and/or adult terrestrial vertebrates or aquatic larval vertebrates (Niklas, 1986).

Why did a transition to vertebrate herbivory take so long? Central to the plant invasion of land was the derivation of lignin as a gravity-resistant cell wall component. Lignin is both a refractory substance in its own right, and increases the physical effort required to break the cell walls it impregnates. The vertebrate clades which invaded land were initially carnivorous (Carroll, 1988). Thus a would-be terrestrial vertebrate herbivore was faced with the hurdle of evolving a dentition capable of breaking lignin-rich cell walls, and cultivating a gut microbiota capable of digesting cellulose and tolerating lignin. One contributing factor to success may have been size—that vertebrates may have had to achieve a certain minimum size to allow for a gut of sufficient length to hold enough fodder to have made bacterial fermentation an economical means of obtaining energy.

What brought a carnivore to consider herbivory? The process may have been quite similar to the postulated transition in insect herbivory. The later Carboniferous is marked by several relatively large seeds with strong testas and fleshy sarcotestas (e.g., *Pachytesta, Cardiocarpus*). It is possible these were vertebrate-dispersed, possibly by mimicking dead prey (Tiffney, 1986a). These could have eased carnivores into an herbivorous habit, much as arthropod "herbivory" possibly commenced with pollen consumption.

What influences could these factors have on plant evolution? The early history of land plants was free of selective pressures to protect foliage from vertebrates, or (until the later Carboniferous) to attract dispersal agents. To suggest one possible significance of this situation, the advent of vertebrate herbivores would have selected against low-growing plants lacking vegetative reproduction (an active means of re-sprouting following predation). One under-recognised feature of vascular plant evolution is that pteridophytes and gymnosperms pursued two very different strategies—the pteridophytes one of "phytoamphibious" sexual reproduction with the capability for vegetative reproduction, the gymnosperms one of the seed, associated with very limited or nonexistent capabilities for vegetative reproduction (Tiffney & Niklas, 1985). To what degree could the advent of vertebrate herbivores have influenced this dichotomy? Another unconsidered aspect involves atmospheric chemistry. Herbivory results in the oxidative destruction of plant material, using the O_2 released to the atmosphere by photosynthesis, and releasing CO_2 in its stead (e.g., Robinson, 1990, 1991). What effect on this equation, and on the atmosphere, does the relative absence of herbivores have on the O_2-CO_2 balance?

THERAPSID HERBIVORES

The first fully-established terrestrial vertebrate-plant ecosystem was carried forward by the synapsid successors to *Edaphosaurus*. Most important among these were the dicynodonts, aided by the dinocephalia. The dicynodonts have been described in detail by King (1990); Hotton (1986) has reviewed the herbivorous adaptations of the group, and Benton (1983) has examined the dicynodont-rhynchosaur-archosaur transition of the Triassic (but see also King, 1991). Zavada and Mentis (1992) have looked at some aspects of their herbivory.

The Permian dicynodonts were beaver to bear-sized herbivores, several of which exhibited adaptations for digging. While many dicynodonts browsed on low-growing ferns, sphenopsids, etc., the digging dicynodonts may have excavated the relatively starch-rich rhizomes of the same plants. Alternatively, the digging adaptations may have been partially or entirely used to find shelter from seasonal climatic changes. Microscopic tooth wear patterns (Hotton, 1986) indicate that the interpretation that dicynodonts tore open cycad-like trunks for food (Watson & Romer, 1956) is unlikely. *Lystrosaurus* carried the general pig-like morphology of dicynodonts into the Early Triassic, but the Middle and Late Triassic dicynodonts become increasingly large and specialised towards cutting and shredding of foliage (King, 1990). Dicynodont diversity decreases through the Triassic,

until they disappear in the Late Triassic. During this time, archosauromorph rhynchosaurs and synapsid "gomphodont" herbivores became increasingly common, filling the pig-like niche vacated by the dicynodonts.

The success of dicynodonts as terrestrial vertebrate herbivores is underscored by their adaptations and numbers. They appeared to dominate Late Permian terrestrial systems, comprising" ...90% of the individuals in the rich and diversified therapsid faunas of South Africa" (Hotton, 1986 : 71). This adaptive radiation of the Late Permian was partly based on biomechanical adaptations including the replacement of teeth with horn-covered jaws, and a flexible jaw hinge structure and a secondary palate, which combined to permit a sliding action of the jaw, allowing the grinding of food (King, 1990). This comminution of plant material meant larger surface areas exposed to the fermentative activity in the gut, and more efficient nutritive reward per amount of food consumed. These adaptations allowed dicynodonts to be the first vertebrates to have full access to the use of terrestrial plants. This is not to deny the reality of edaphosaurs, dinocephalia or caseids as herbivores, but to recognise that, with the rise of the dicynodonts, an herbivorous contingent of the terrestrial fauna is firmly established, and the transition from the initial, herbivoreless, stage completed.

The interaction betwixt dicynodont herbivores and coexisting vegetation is clouded by an excess of variables. The dicynodonts appeared affiliated with low-latitude floras, but by the Middle Permian, dicynodonts invaded higher latitudes, particularly in Gondwana, as warmer climates led to the poleward spread of mesic conditions (King, 1990). These conditions persisted through the later Permian and Early Triassic, associated with a vegetational change from a *Glossopteris*-dominated flora to a *Dicroidium*-dominated one, a transition which possibly contributed to the decline in dicynodont generic diversity (Benton, 1983; Weishampel & Norman, 1989; King, 1990, 1991). In the Middle and Late Triassic, continued global warming led to the decline of the *Dicroidium* flora, and its replacement by conifer-cycadophyte-dominated floras derived from palaeoequatorial and Northern Hemisphere sources. Associated with this floristic change was a substantial change in the nature of the vegetation. The *Glossopteris* and *Dicroidium* floras included trees, shrubs and pteridophytic herbs with fairly mesic foliage. However, in the later Triassic vegetation, arborescent forms became increasingly important, pteridophytes increasingly restricted to

moist sites in a drying environment. The gymnosperm trees and shrubs often featured an armour of old leaves (e.g., Araucariaceae) or old leaf bases (e.g., cycadophytes) and hard (sclerophyllous) foliage, often armed with marginal or apical spines.

These adaptations (increasing dominance of long-lived, woody, plants with sclerophyllous foliage) correlate with the spread of warm, dry, climates in the Mesozoic, and may be seen as an adaptive response to climate (Tiffney, 1981). However, two alternative interpretations are possible. First, height, thick bark, and sclerophylly would be adaptive in environments in which fire had become prevalent. The evolution of atmospheric O_2 levels (Robinson, 1989, 1991) raises the possibility that forest fire might have been particularly important in the Mesozoic. Second, height, thick bark, sclerophylly and spinose leaves are excellent responses on the part of plants to increased herbivory.

I tend to suspect that the change in flora and vegetation was initially a response to climate and/or prevalence of fire. Triassic climatic changes probably drove a major evolutionary and vegetational shift which undermined therapsid communities, setting the stage for the radiation of the following archosaurian herbivores. However, the increased occurrence of herbivory, especially with the radiation of dinosaurian herbivores, would further select for height, thick bark and sclerophylly, plus the appearance of spines and herbivore-deterrent chemistries.

The transition to a world with vertebrate herbivores has implications for terrestrial plant evolution. Mechanical structures, height, and chemical composition take on a new importance, although possibly for several reasons (see above). The ability of some dicynodonts to dig (King, 1990) could initiate new selective pressures on low-growing, rhizomatous plants. "Fleshy" disseminules could have played an increased role in seed dispersal. These questions have been little considered (e.g., Zavada & Mentis, 1992), and deserve exploration. In such research, particular attention should be paid to the similarities and differences between the Permian and the Tertiary and present. Both periods involve small- and medium-sized herbivores in a vegetation including trees, shrubs and herbs. Certainly the Permo-Triassic vegetation and herbivore fauna are less taxonomically and morphologically diverse than the present. How does this limit the options of response of each group to the other? This is an untapped area for speculation and testing in the fossil record.

ARCHOSAURIAN HERBIVORES PHASE I

The change in vegetation of the later Triassic ushered in the third phase of terrestrial vertebrate herbivore—plant interactions. While some synapsid herbivores crossed through this transition (e.g., Tritylodonts), ecological dominance shifted to dinosaurian herbivores. These included the immense herbivorous saurischian sauropodomorphs and the variously sized (but smaller) members of the entirely herbivorous ornithischia (for sizes, see Norman, 1985). By contrast to the present day, dinosaurian faunas were skewed to large herbivores by several orders of magnitude.

The earliest dinosaur-dominated communities occurred in Late Triassic of the Northern Hemisphere and then rapidly spread to Gondwanan sites with the expansion of conifer-cycadophyte vegetation (Benton, 1983). These early dinosaur faunas included both large prosauropod herbivores (*Melanosaurus*—12 m long; *Plateosaurus*—8 m long) and smaller ornithischia such as *Lesothosaurus* and *Heterodontosaurus* (about 1 m long). Through succeeding dinosaurian history, this size relationship holds. Sauropodomorphs were immense herbivores (from the modestly sized *Apatosaurus* of about 20 tons up to *Ultrasaurus*, which may have weighed in excess of 100 tons). Ornithischia were generally smaller, providing some small herbivores (hypsolophodontids, early ceratopsians, some pachycephalosaurs of 2-3 m length, 100 kg weight) as well as many elephant-sized herbivores of the Jurassic and particularly Cretaceous (stegosaurs, iguanodonts, hadrosaurs, ceratopsians) of 5-10 tons weight (Hotton, 1980; Norman, 1985).

The physiognomic dominants of the Late Triassic, Jurassic and Early Cretaceous floras were gymnosperms. The most common of these included conifers (dominated by Araucariaceae and Taxodiaceae, among others), ginkgos, cycads and cycadeoids. Other gymnosperms including seed ferns, czekanowskians and more enigmatic forms were also present. With the exception of the ginkgos and perhaps czekanowskians, which tended to occur in moister communities at higher latitudes (Vakhrameev, 1991), these plants generally exhibited xerophytic vegetative characters of tough, lignin-rich, sclerophyllous leaves. By analogy to living forms, it seems reasonable to infer that the majority of these gymnosperms were relatively slow growing, and thus not resilient to the effects of herbivory. Further, vegetative reproduction in these groups is generally restricted to basal sprouting (Tiffney & Niklas, 1985), unlike the condition in pteridophytes which possessed excellent properties of vegetative reproduction. A possibly important exception to this general inference is the extinct conifer family Cheirolepidiaceae (Triassic-Cretaceous). These were widespread plants of low latitudes, apparently often of coastal sites (Alvin, 1982). The foliage appears succulent, and, without modern analogs, it is impossible to estimate damage resistance.

The herb layer was provided by pteridophytes, dominantly ferns. Again modern analogs may be identified, which suggest that pteridophytes were probably restricted to seasonally moist or continuously moist areas, and were thus not ubiquitous elements of the landscape. The Cretaceous genus *Weichselia* is a possible exception, having xerophytic features, but seems restricted in distribution (Alvin, 1974). Some have suggested that "fern prairies" (e.g., Coe *et al.*, 1987) constituted important sources of dinosaur fodder. This term has the potential to conjure images of fern-dominated communities occupying the mid-continental regions of the Mesozoic, much as grasslands do in the present day. I would consider such a conclusion an example of assuming that the past is the present. Certainly ferns were common in the Mesozoic, and indeed may have formed fern-dominated communities much as they do in some temperate and tropical moist areas in the present day. Further, many ferns are both fast-growing and possess subterranean growing points (Coe *et al.*, 1987) suiting them to serving a forage for herbivores. However, there is no *a priori* reason to assume that ferns occupied the ecological niche of midcontinental grasslands. Thus, unless actual fossil evidence of pteridophyte homologs of grasslands is found, I find it more conservative to assume that elevated continental interiors were largely devoid of plants, or occupied by scattered vegetation in moister sites. At the very least this interpretation should be entertained as an alternative hypothesis to that of "fern prairies" analogous to modern grasslands.

The importance of the foregoing is that, while ferns may have been an important food element, they were not as extensively distributed as the communities that support modern grazers. Thus, for many dinosaurs, cycadophytes and conifers were extremely important food items. This intuitively fits with the extended necks of many sauropodomorphs, apparently designed for giraffe-like feeding high in the canopy. Some suggest on the basis of osteological and physiological data (Dodson, 1990a), that long-necked dinosaurs were unable to hold their necks erect for extended periods of time,

instead feeding with the neck extended horizontally. Bakker (1978) dismisses these objections as ignoring other aspects of dinosaurian structure. From a botanical perspective, the resistant nature of Mesozoic tree foliage and the mode of feeding of living giraffes suggest that the most conservative interpretation is that the great sauropodomorphs frequently fed on forest trees.

The large sauropodomorphs possessed peg-like teeth unsuitable for chewing, but presumably used to strip vegetation from branches. This was swallowed, possibly passed through a gizzard analog, and fermented in the stomach (Coe et al., 1987; Dodson, 1990a). The basic adaptation to herbivory appears to have been immense size, allowing protracted fermentation of huge quantities of food material, enabling an "efficient" return of energy for effort expended. Ornithischian herbivores, by contrast, evolved an increasingly complex tooth morphology and jaw dynamic, allowing effective chewing prior to swallowing (Weishampel & Norman, 1989), possibly accounting for their smaller body size.

The relative food quality of pteridophytes versus conifers is difficult to assess. Weaver (1983) concluded that gymnosperms generally yielded more calories per unit weight than pteridophytes, and suggested that *Brachiosaurus* would find selective energetic advantage in feeding on gymnosperms. However, he obtained the estimate of caloric value by igniting samples of leaf tissue. Gymnosperms are higher in lignin content than pteridophytes (Robinson, 1990), and lignin is generally indigestible. Thus Weaver may simply have been measuring differences in lignin content which did not yield differences in calories available to the animal. I suspect there was little difference in food value between pteridophytes and gymnosperms, and that their relative importance as a food item was far more dependent on availability and disturbance tolerance.

The structure of middle Mesozoic plant communities is conjectural. However, those of lower latitudes were probably fairly open in many cases. This is suggested both by analogy to living araucarians and cycads, and by the observation that larger herbivores tend to occupy open habitats in the present day (Wing & Tiffney, 1987). This is not to deny the occurrence of closed communities. Higher latitude *Ginkgo* forests may have been closed, and forests of Cheirolepidiaceae or *Czekanowskia* are conjectural. However, reconstructions depicting large sauropods within closed forests seem inappropriate.

The smaller ornithischian herbivores of the Mesozoic likely fed on organs and influenced pollination and dispersal. Large seeds assigned to cycads and to *Ginkgo* in the fossil record suggest biotic dispersal (Tiffney, 1986a). van der Pijl (1982) considers the armoured sclerotestas and brightly coloured sarcotestas of living members of these groups to be adapted for reptilian dispersal. However, the ecologically dominant herbivores of the period were the large sauropodomorphs, and in the Cretaceous, increasingly the large ornithischia.

From the herbivore's perspective, huge quantities of foliage must be consumed, which would quickly deplete resources in one area. Given that many gymnosperms were ill-suited to deal with intense herbivory, or at least slow to repair the resulting damages, large herbivores would have to keep migrating to find adequate food. A patchy distribution of fern-dominated communities would force the same response. The scale of the herbivore and the dynamic of its fodder could result in herbivore "home ranges" of a sub-continental scale. Herbivore size and food quality also suggest that there were limits to dinosaur numbers, commensurate with the modern observation that there is a lower population density in species of large body size than in those of small body size (Peters, 1983).

Dodson (1990b) concluded that there were between 900 and 1,200 genera of dinosaurs. Assuming the ratio of about 1.2 dinosaur species per genus (Dodson, 1990b), this implies about 1,100-1,500 species existed during 160 million years, or approximately 7-9 species per million years. By contrast, there are over 3,000 genera of mammals in the Tertiary (Padian & Clemens, 1985). Assuming approximately four species per genus of mammal (modern ratio; Nowak, 1991), this suggests between 3,000 (conservative) and 12,000 species of Tertiary mammals over 65 million years, or between 46 (conservative) and 185 species per million years. This discrepancy is one of the strongest indications of the difference between the Mesozoic dinosaurian terrestrial ecosystem, and the mammal-bird dominated ecosystem of the Tertiary and present. The lower diversity of dinosaur species and individuals raises questions about their evolutionary biology. Small population sizes generally imply a heightened potential for turnover and extinction. Such evolutionary instability might predispose the dinosaurs to fluctuations in diversity, and make them more susceptible to environmental perturbations, such as the supposed events of the Cretaceous-Tertiary boundary.

Summed, this combination of immense herbivores and fairly sparse, relatively disturbance-

intolerant, often lignin-rich, plants implies "whole plant predation", resulting in selection for mechanical defence, great size, or rapid re-growth in the plants. The effects of such selection on the clades of gymnosperms and pteridophytes which entered the Mesozoic has yet to be considered. It may help explain the appearance of angiosperms.

ARCHOSAURIAN HERBIVORES PHASE II

The second half of this third phase of vertebrate-plant interactions involves the continued dominance of big dinosaurian herbivores, but modified by the appearance of the flowering plants. The angiosperms became ecologically-significant members of the terrestrial flora in the Middle Cretaceous, diversifying to dominate world floras numerically, and probably physiognomically, by the later Cretaceous (Niklas *et al.*, 1985; Lidgard & Crane, 1990). Many features underwrote this diversification, but one aspect is of particular importance with respect to herbivory. While pteridophytes lack the "amniotic" advantages of the seed, many retain excellent powers of vegetative reproduction, enabling them to respond to herbivore damage. By contrast, gymnosperms possess the seed, but lack all but the most rudimentary abilities of vegetative reproduction save in a few isolated cases (Tiffney & Niklas, 1985). Thus, angiosperms embody the advantages of the seed in a plant capable of vegetative reproduction; they are essentially weedy, disturbance-tolerant, vegetatively-reproducing gymnosperms (Tiffney & Niklas, 1985).

The very appearance of angiosperms may in part be a function of the effect of dinosaurian herbivory. If dinosaurian herbivores were as destructive as suggested above, then vast areas of vegetation would repeatedly be reduced to early successional stages, favouring the spread of weedy forms. As Bakker (1978) suggested, dinosaurs may have selected for the appearance of angiosperms.

Swain (1976) suggested that the secondary chemicals characteristic of the angiosperms "poisoned" the dinosaurs, contributing to their demise. On the contrary, the radiation of angiosperms appears to have underwritten a secondary radiation of ornithischia. As food, angiosperms generally have lower lignin concentrations than gymnosperms (Robinson, 1990), suggesting greater digestibility and a greater food value per volume consumed. I cannot locate comparative data on the caloric content of angiosperm foliage sampled in a similar manner to Weaver (1983). I would expect that it would match

that of ferns, as there is no *a priori* reason why angiosperm foliage should be higher in starch or sugar than fern foliage. However, by virtue of their shrub to tree size and ability to grow in a wider range of habitats than ferns, angiosperms would offer a greater food resource than ferns. Thus an angiosperm-dominated world would be expected to support a greater herbivore biomass than a gymnosperm-fern dominated one.

The existing diversity record of the dinosaurs displays a dramatic upsurge in numbers of genera in the Cretaceous; almost 50 per cent of known dinosaur species are from the last 20 million years of the Cretaceous (Dodson, 1990b). The effect of this new, productive, food source is also apparent in the numbers of individual dinosaurs. Pre-angiosperm dinosaur species tend to be represented by few individual specimens and, in general, evidence does not suggest that they occurred in large herds. By contrast, several dinosaur species of the later Cretaceous appear to have occurred in large numbers (up to 10,000 individuals in a herd of *Maiasaurus*, Weishampel & Horner, 1990). That this diversification was underwritten by angiosperms is further supported by the observation that many of the newly evolved dinosaurs fed at 1-3 m off the ground, compared to the sauropodomorphs which fed at a much higher level consistent with life in a cycadophyte-conifer flora (Bakker, 1978). In one case where roughly coeval faunas could be associated with different floras, low-feeding ornithischia are associated with angiosperm-dominated floras, and the sauropod *Alamosaurus* with conifer-dominated floras (Lehman, 1987).

While overall herbivore size decreased from sauropodomorphs to ornithischians, the latter remained, by comparison with the present, immense. The dominant plant-animal interaction remained one of intense "predation", favouring the evolution and further spread of early successional angiosperms. In keeping with this situation, Cretaceous angiosperm seeds are generally quite small (Tiffney, 1984), typical of open, light-rich, communities. Such small seeds might have been dispersed abiotically, or as Janzen (1984) has suggested, perhaps biotically dispersed when inadvertently eaten by herbivores consuming large quantities of foliage. Janzen typified this as the "whole plant as attractant" syndrome, and it might explain the apparent anomaly that later Cretaceous angiosperms did not evolve a range of spinose and sclerophyllous leaves to deter herbivory.

In addition to providing food, plants also create the three-dimensional environment in which animals live. Modern observation suggests that larger

animals tend to inhabit more open environments, smaller animals more closed environments (e.g., figure 2, Wing & Tiffney, 1987). The largest modern animals in question are elephants, roughly equivalent to small- to medium-sized duckbills or ceratopsians. Thus we might expect the spatial environment of later Cretaceous dinosaurs to be fairly open. We have no direct evidence of the past spatial distribution of plants save through the very rare "fossil forest", and via analogy to living forms. However, given the lower and more shrubby habit of angiosperms relative to gymnosperms, it is reasonable to expect angiosperm communities to be more closed than gymnosperm communities. While herbivore pressure and climatic features may have maintained open vegetation in some areas, on a global scale the evolution of angiosperms must have created an increasingly closed three-dimensional environment in which herbivores lived. Given the tendency for larger herbivores to inhabit open vegetation, this change may have increasingly fragmented and isolated dinosaurian populations, rendering them more susceptible to other environmental changes and possibly extinction, an idea first suggested by Krassilov (1981).

The majority of Mesozoic mammals were insectivores, but in the later Cretaceous, new herbivorous forms evolved, and mammalian diversity began to increase (Clemens & Kielan-Jaworowska, 1979; Wing & Tiffney, 1987). Thus, the radiation of angiosperms was as significant to mammals as it apparently was to dinosaurs, but for different reasons. First, the angiosperms generated an increase in insect diversity. From their earliest appearance many angiosperms were insect pollinated (Dilcher, 1979; Crepet & Friis, 1987). Further, insect herbivores of the present day predominantly focus on angiosperms, and it is reasonable to assume this coevolutionary relationship commenced in the Cretaceous. Jointly, these features spelled a resource boom for insectivores. Second, the small size of mammals suited them to live *within* the angiosperm vegetation, rather than on its "surface", thereby increasing the scope of their environment. In so doing, mammalian insectivores apparently replayed the events involved in the origin of insect and vertebrate herbivory in the Palaeozoic. Much as insects apparently passed from carnivory to feeding on the "high energy" food of pollen, and as vertebrates may have passed from carnivory to facultative consumption of late Palaeozoic seeds, so apparently mammals initially consumed insects attracted to angiosperms, but in time began to feed on energy-rich fruits and seeds, as suggested by the

teeth of multituberculates (Clemens & Kielan-Jaworowska, 1979).

In sum, from the plant's point of view, the age of dinosaurs was not an extension of Permian herbivory, nor a duplication of the present. While smaller herbivores duplicated some aspects of the preceding and following time, the immense herbivores imposed a unique selective force on the physiognomy and life history strategies of Mesozoic plants. Initially, these forces were met by a limited diversity of genetic lineages of plants, but by the end of the Mesozoic, gymnosperms with efficient vegetative growth and abilities to recover from damage (= angiosperms) had evolved. Much of the morphology and biology of Mesozoic plants should be considered in the light of this substantial herbivore pressure.

MAMMALS AND BIRDS :
THE TERTIARY AND PRESENT

The fourth, and modern, plant-vertebrate ecosystem dynamic found its roots in these later Cretaceous interactions of angiosperms and mammals, but became fully established with the demise of the dinosaurs at the Cretaceous-Tertiary boundary. The importance of this boundary, and the distinction between the later Mesozoic and the Cenozoic, was one of scale. While the dominant herbivores of the later Cretaceous weighed several tons to tens of tons, the survivors of the boundary event weighed kilograms to tens of kilograms, creating a several order of magnitude drop in herbivore size over a very brief time (Tiffney, 1989, figure 3). This established an ecosystem where the herbivores were scaled to fit "within" the vegetation, feeding on plant organs, rather than "outside" of it, feeding on whole organisms. We tend to think of these smaller herbivores in terms of mammals (e.g., "The Age of Mammals"), however, it is more properly the "Age of Birds", which outnumber mammalian species 9,000 to 4,400 in the present day (Feduccia, 1980; Nowak, 1991). Thus, one might be more correct to think of the Tertiary and present as the "Age of Small Herbivores". Very large herbivores did evolve in the Oligocene (e.g., *Indricotherium, Baluchitherium*) and the open habitats of the later Tertiary hosted moderately large herbivores (deer, horses, camels, etc.). However, by contrast to the herds of ceratopsians or duckbills which had been their predecessors, the size of Tertiary and Recent mammalian and avian herbivores is relatively small.

The small average body size of the herbivores of this fourth guild stems both from their own biologies, and from the nature of the angiosperm

community they evolved into. Mammals have far more effective teeth than most dinosaurs, allowing them to break up tough vegetable material, thereby reducing the stomach volume (and body size) required for efficient digestive fermentation. Birds lack teeth, but have gizzards serving the same function. The small size and endothermic physiology of both birds and mammals led many of them to focus on energy-rich food sources. Indeed, birds may have followed mammals in first preying on angiosperm-feeding insects, and then assuming energy-rich fruits and seeds as an alternative food. In time this led to the diversification of facultative or obligately herbivorous birds (Tiffney, 1984).

The size and physiology of these small herbivores resulted in a complete change in the selective environment in which plants evolved. By example, the development of frugivory in both mammals and birds is reflected in a shift in angiosperm fruit and seed morphology from smaller to larger disseminules. Early Cretaceous angiosperm disseminules are generally quite small (Tiffney, 1984). In the Late Cretaceous, disseminules assignable to modern angiosperm families start to appear (Knobloch & Mai, 1986), but are still smaller than those of more recent relatives. By the Early Tertiary, larger disseminules begin to appear, and by Eocene, the present range of disseminule sizes are present. I (Tiffney, 1984, 1986b) interpreted this pattern to reflect the growing importance of mammalian and avian frugivory. Together with insect pollination, vertebrate dispersal can influence gene flow, and thus diversification of angiosperms, and likely contributes to (but is not solely responsible for) the high diversity of angiosperms compared to pre-existing vascular plants (Niklas *et al.*, 1985; Lidgard & Crane, 1990). This interaction was reciprocal, and the increased diversity of three-dimensional structure of vegetation and of consumable resources created by angiosperms is reflected in the high diversity of vertebrates in the Tertiary. While existing surveys of vertebrate diversity (Padian & Clemens, 1985; Benton, 1987) may be fraught with taphonomic biases, they agree in depicting a 3-5 fold increase in the diversity of higher taxa in the Tertiary.

In summary, the very beginnings of the rise of birds and mammals roughly coincides with the rise to dominance of angiosperms. When events still under debate caused the demise of the dinosaurs, the pace of bird-mammal diversification accelerated. These animals were small, and established a different ecosystem dynamic and selective environment than that which dominated the Mesozoic. In a very real sense, the transition from the Mesozoic to the Cenozoic was a transition of whole ecosystems, based on the scale of the plants and animals involved. It was not a sharp transition, passing as it did through the later Cretaceous (Wing & Tiffney, 1987), but the two end point ecosystems were very different. The ecosystems, and selective environments, of the Tertiary and present are thus a recent phenomenon, and not representative of the selective environment in which pre-Tertiary plants evolved.

CONCLUSIONS

There have been four distinct terrestrial ecosystems involving vascular plants and herbivores. In the first phase from the earliest land plants through the latest Carboniferous—Early Permian, vascular plants evolved in an environment with slowly developing insect herbivory, but free of vertebrate herbivory. Vertebrate herbivory was introduced in the second phase, becoming an important feature in the later Permian and Early Triassic, with the diversification of low feeding dicynodonts and associated vertebrates. Changing vegetation introduced the third phase, dominated by archosaurs. This third phase is divided into two parts, before and after the origin of angiosperms, both featuring the dominance of extraordinarily large herbivores. The beginnings of the final phase overlap with the end of the third phase, as smaller mammals and birds commence to radiate in the later Cretaceous, coming to dominate plant-herbivore interactions in the fourth phase of the Cenozoic and Recent.

What is the significance of the foregoing to the palaeobotanist interested in the concrete record of individual taxa or clades? The vegetative and reproductive features of morphology that palaeobotanists track in the fossil record are influenced by both the physical and biological environments in which the parent plant lived. Palaeobotanists have long perceived the selective importance of the physical environment in affecting the course of plant evolution. By example, the rise of gymnosperms is recognized as associated with the transition from the warmth and moisture of the late Palaeozoic to the dry, continental climates of Pangaea. The point is, the evolution of plants has been similarly affected by grand changes in the prevailing environment of vertebrate herbivory. Plants which evolved in an environment dominated by massive herbivores faced different selective regimes than did plants evolving without vertebrates at all, or evolving with dominantly small vertebrates. This would influence the form and position of

foliage and reproductive structures, chemistry, growth habit, etc. Recognition of these additional selective forces will complicate our evolutionary scenarios. Where before the sclerophylly of many gymnosperms might be attributed to water stress, we may now recognise the potential additive influence of the low-level dicynodont herbivores of the Permian, or the great archosaurian herbivores of the Mesozoic. Where we have focussed on insects and angiosperms in the Cretaceous, we may now add the insight of the effect of constant grazing disturbance. The selective environment in which land plants have evolved is dictated by coeval biota as much as it is by abiotic factors, and we need to integrate this insight into palaeobotanical thinking.

I do not mean to convey fixed, static conclusions. Much of what I say pulls together real patterns, but is inferential and subject to revision. Unresolved questions remain. What factors determined the appearance of the first vertebrate herbivores? What can be determined of dicynodont-plant interactions, and how similar was this ecosystem to that of the Tertiary and present day? Why did dinosaurian herbivores become so large, so early in their history? My interpretations of, and hypotheses about, the course of vertebrate-plant interactions may be altered or disproven by future data, but I am convinced that a better understanding of the history of vertebrate-land plant interaction and the evolution of terrestrial ecosystems will strengthen our knowledge and understanding of the evolution of their components, including land plants.

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