Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism?

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Relatively few studies have examined the evolution of the mutualism between endozoochorous plants and seed dispersers. Most seed dispersal studies are ecological and examine the role of fruit pulp in promoting seed dispersal. This interaction is often assumed to have originated due to selection stemming from seed dispersers. Here I suggest a "defence scenario" wherein fleshy fruits originated as mechanisms to defend seeds and secondarily became structures to promote seed dispersal. I suggest that frugivory followed from herbivores that specialized on consuming seed defensive tissues and that enhanced seed dispersal was initially a consequence of seed defence. The proposed defence scenario is not posited as an explanation for the sequence that led to all modern frugivores. However, it is suggested that seed predation was the initial source of selection that led to fleshy fruits; the necessary precursor to frugivory. Support is described from the fossil record and from modern structures and interactions. Testable predictions are made in hope that greater interest will be focused on the defensive role of fleshy fruit pulp both in modern interactions and historically.

1. Introduction

Endozoochory, the interaction between fleshy-fruited plants and the animals that ingest and disperse their seeds, has been the subject of many ecological studies (e.g., Estrada and Fleming 1986; Fleming and Estrada 1993). Ecological and evolutionary studies have emphasized examination of fleshy fruit pulp as a means of promoting seed dispersal and de-emphasized the role of fruit pulp in protection of seeds. The evolutionary history of the plant-disperser mutualism has been rarely examined. Understanding the evolution of fleshy fruit pulp, endozoochory, and the mutualism between plants and dispersers will require greater examination of the defensive role of fruit pulp. Here, I suggest plant adaptations for seed defence may have led to the evolution of endozoochory in -some lineages. This "defence scenario" challenges some currently held views and offers new avenues of investigation by generating testable hypotheses.

Fleshy pulp, forming or derived from several tissues (e.g., aril, sarcotesta, pericarp), in endozoochorous fruits, is widely recognized as an attractant and reward for seed dispersers. However, a second important function, defence of the seed, has received relatively little attention (Cippolini and Stiles 1992a). Possibly seed dispersal, the widely recognized function, may have evolved from seed defence, the less-studied function in most cases. Palaeoecologists often infer past interactions based on the similarity of the fossil record to modern structures and current ecological interactions. Hence, relationships with animal dispersal agents are often inferred from fossil fleshy fruits (e.g., Tiffney 1986a). However, in modern fruits, pulp often serves a protective function independent of any role in dispersal (Herrera 1982; Cippolini and Stiles 1992b). In the defensive scenario proposed here, fleshy fruits, frugivory and endozoochory evolved in that sequence. It is teleological to propose seeds developed pulp to promote dispersal because before the advent of fleshy fruits, frugivores did not occur to affect dispersal.

2. The proposed role of seed defence in the evolution of fruit pulp

The proposed "defence scenario" does not imply a single, linear progression of steps leading to the modern fleshy

Keywords. Endozoochory; evolution; frugivory; seed dispersal: seed predation

fruit. Endoxoochorous fruits arose independently many times; this general sequence might have transpired several times, but not in every instance that led to fleshy fruits. Depending upon when and where the sequence of evolutionary steps occurred, the components – plants, seed predators and seed dispersers – differed. The relative importance of these different components varied in different pathways but the general progression did not.

Naked seeds, the plesiomorphic state, were vulnerable to seed predators, pathogens, fungi and desiccation and later (c. mid-Permian) herbivores that incidentally killed seeds when consuming foliage. I hypothesize that initially a defensive layer evolved enclosing the seed in response to such selection (Stebbins 1970). A fleshy, defensive layer could inexpensively (relative to the plant's investment in a temporary structure) exclude pathogens and prevent seed-predatory insects from reaching seeds. A fleshy layer containing distasteful compounds could cause herbivores, that incidentally killed seeds while consuming foliage, to avoid fleshy seeds. Plants that evolved chemical defences in response to herbivory could substantially increase fitness by enveloping their progeny with the defence because the fitness cost of losing seeds could be greater than that of losing foliage (Ehrlen and Eriksson 1993).

A tleshy defence of immature seeds is more flexible than a hard, lignified coating. Fleshy coverings can accommodate and respond to the changing morphology of seeds as they mature whereas hard integuments cannot. 'Fossil fruits containing both heavily lignified seeds and fleshy sarcotestas cannot reveal which morphological trait developed first. In the "defence scenario" fleshy tissue protected the seed as it grew, then the seed lignified when full-sized within the fleshy enclosure.

In the second stage of this scenario, herbivores overcome the plant's fleshy defence and consume the fleshy tissue without killing the enclosed seeds. These first "proto-frugivores" and putative seed dispersers would have dispersed seeds of pulp-defended plants better (e.g., greater dispersal distances, in greater numbers, greater escape from seed predators, or to more favourable establishment sites) than the abiotic dispersal of naked-seeded plants or abiotic dispersal of unpalatable pulp-defended seeds. At this stage the opportunity for diffuse coevolution (Herrera 1984a) between plants and dispersers began. Plants could incorporate rewards (e.g., sugars, lipids) into pulp in response to selection by seed-dispersing proto-frugivores. Plants could evolve ripening signals (e.g., colour changes), presentations (e.g., position on the plant), even phenological traits to promote dispersal. Such traits or behaviours are unlikely to have evolved before the existence of a reliable coterie of frugivores that increased plant fitness through seed dispersal. Alternatively, the second stage could have resulted through senescence of the pulpy tissue after the seed matures and hardens (E W Stiles, personal communication). In this case, herbivores did not "overcome" the defences, but the defences degraded and became more edible, leading to enhanced dispersal. Regardless. the primary tenet remains – tleshy tissues arose initially as defences.

As the mutualism developed, rapid evolution could occur among both plants and animals. The advantages accrued by biotically-dispersed plants might have enabled them to colonize new habitats, out compete abiotically-dispersed taxa, and increase effective breeding population size, leading to rapid speciation (Regal 1977). However, the importance of biotic dispersal in the angiosperm rise to dominance remains controversial (Midgeley and Bond 1991). Likewise among animals, as a new, nutritious food source appeared in more plant species and communities, specialization and divergence could occur. Past radiations, convergences, and trophic-switching among herbivores, seed predators and frugivores obfuscate the historical pathways. Pijl (1 982) postulated that endozoochory arose from accidental ingestion of seeds by folivores. Even if such folivores increased plant fitness by accidental ingestion of seeds, this behaviour is unlikely to lead to the evolution of conspicuous, fleshy fruits. Rather, folivore behaviour would have selected for seeds concealed in foliage that are protected from mastication and gastric mills (Janzen 1984). If incidental seed consumption by folivores reduced fitness, seeds would be expected to become spatially separated from foliage and chemically or physically protected.

3. Support for the "defence scenario"

The proposed sequence, defence before dispersal, may have occurred several times, from the early gymnosperms of the Carboniferous that had fleshy propagules (Retaltack and Dilcher 1988) through the Tertiary when the fleshy-fruited angiosperms radiated (Tiffney 1984). The fossil record cannot clearly reveal the evolutionary history of previous plant-animal interactions. However, existing fossil evidence is consistent with defence before dispersal.

Fossil evidence does indicate that early plant reproductive structures suffered insect herbivory and these instances precede records of fleshy fruits or frugivory. The earliest Devonian seeds were small, naked and possibly polyphyletic in origin (Tiffney 1986a). Limited evidence indicates that sap-feeding arthropods existed in the early Devonian (Chaloner *et* al 199 I) and that insects fed on plant spores (Scott 1977; Chaloner *et* al 1991), megaspores, and seeds (Smart and Hughes 1973; Scott and Taylor 1983) during the Carboniferous. Because of the higher nutrient value of seeds compared with foliage (Janzen 1978a), it is likely early herbivores and pathogens would have fed upon undefended seeds whenever possible. Thus the early record indicates naked, potentially vulnerable and probably nutritious seeds at a time when herbivores were numerous.

Middle Pennsylvanian fossil seeds of many gymnosperms and seed ferns exhibit hard and thick sclerotestas

(Tiffney 1986a), perhaps as defence against seed predators or desiccation. Progressing through the fossil record there are many instances of seeds being surrounded or partially enclosed in sterile tissues (Dilcher 1979) that could have served a defensive function. Some fossil genera (e.g., *Cordaicarpon*, *Nucellangium*) also exhibited a fleshy sarcotesta. Perhaps these early fleshy sarcotestas contained deterrent compounds rather than rewards for seed dispersers.

During the Permian, glossopterids dominated in Gondwana whereas Cordaitales were more numerous in Laurasia. The upland Cordaitales mostly had winged seeds whereas lowland forms had thick-walled seeds. often with fleshy sarcotestas (Tifl'ney 1986a). Some fossil evidence indicates herbivores consumed foliage, twigs and seeds indiscriminately and a late Permian coprolite contained seeds (Tiffney 1986a).

The Triassic witnessed the arrival of gingkoes, *Sphenobaiera*, fleshy-seeded cycads and *Caytonia*, though fossil seeds are rare. Reptiles are sometimes considered dispersers of these fruits (Pijl 1966), based on the assumption that fleshy tissues were rewards. It is equally plausible that gingko pulp originated as a defence. The sole remaining gingko species (*Ginkgo biloba*) has a foetid pulp that is unpalatable to most modern frugivores or herbivores. Gingkophytes, Coniferales, Nilssoniales. Caytoniales, Gnetales, cycads and Bennettitales radiated in the Mesozoic; many exhibit fructifications with mechanical defences against herbivores (Weishampel 1984). In one case they have been found in coprolites (Hill 1976).

Evidence suggests the prior existence of generalist herbivores consuming gymnosperm seeds with foliage (Tiffney 1986a) when the angiosperms radiated in the Cretaceous (Doyle 197X). The earliest angiosperm seeds were small and abiotically dispersed (Tiffney 1986a) shifting later to fleshy fruits. Some of the earliest fossil angiosperm fruits have glochids (Krassilov 1973), suggesting defence against seed predators. Fleshy-fruited angiosperms are rare in the Palaeocene fossil record (Collinson and Hooker 1991). The gradual development of a relationship between putative frugivores and angiosperms until the mid-Cretaceous might have helped set the stage for rapid diversification of angiosperm and frugivore lineages once the interaction became mutually beneficial in the late Cretaceous and Tertiary. Fleming and Lips (199 1) proposed that pterosaurs were one such group of frugivores in the Cretaceous. However, this does not necessarily imply a direct causal relationship between radiating plant and disperser lineages (Herrera 1989a; Eriksson and Bremer 1992).

Wing and Tiffney (1 987) documented a shift from large generalist herbivores to smaller specialist herbivores, including frugivores and granivores, across the Cretaceous-Tertiary boundary. The hamamelid families Juglandaceae, Fagaceae, Moraceae and possibly the Ulmaceae switched from abiotic to biotic dispersal in the late Cretaceous to early Tertiary (Tiffney 1986b).

Some early mammals probably were seed predators (Krause 1982). Collinson and Hooker (199 I) list fruit as a component in mammalian diets of the late Cretaceous but include both seeds and pulp as "fruit". Most of their specific examples refer to seed-eaters (Rensberger 1986) and the only two fossil specimens strongly indicating a diet of fleshy fruits are from the Palaeocene (Collinson and Hooker 1991). The early fossil record of frugivorous birds is sparse, but it appears that they diverged in the early Eocene (Tiffney 1984). Distinguishing the frugivorous habit in the fossil record is difficult because frugivory requires few morphological specializations (Herrera 1984b).

Evidence to support or refute the scenario can be sought among extant taxa. Basal plant groups might exhibit "primitive" traits, such as pulp chemistry and fruit morphology, that clarify the evolutionary history of fleshy fruits. Limited evidence from the primitive angiosperm families Idiospermaceae, Eupomatiaceae, Himantandraceae and Austrobaileyaceae is concordant with the defence scenario (Endress 1983). Other groups within the Magnoliales, particularly the Annonaceae (Schatz and Thomas 1993), also exhibit traits that could clarify the evolution of fleshy fruits with a phylogenetic analysis of fruit traits. Some examples of lignified defences of immature seeds exist (e.g., *Protomegabaria*, Euphorbiaceae) but these plants must produce a mature-sized capsule before the seeds can mature. In cases where ovules fail to develop, early investment in a hard capsule would result in greater loss and precludes the option of reabsorbing defence investments, whereas fleshy defences might present less loss. A relatively small number of endozoochorous taxa *(e.g., Cecropin, Fragaria, Piper)* have unenclosed seeds on fleshy accessory tissue. The relative rarity of such diaspores suggests there may be advantages to enclosing seeds independent of dispersal.

Substantiating evidence for the evolution of pulp to protect seeds should be sought from modern plant and seed predator interactions. Wright (1990) describes a system where insect seed predators are unable to oviposit on seeds enclosed with pulp, but do oviposit on exposed seeds. Herrera (1989b) suggested fleshy tissues reduced seed predation by rewarding herbivores that ingested seed predators. The thickness of the syconium wall of figs (*Ficus* spp.) restricts seed predators from ovipositing on fig seeds. The succulent pulp of *Gnetum* spp. is densely laced with sharp, glass-like urticating, "spicules." Rodents in New Guinea avoid intact *Gnetum* fruits, but avidly consume seeds where the pulp has been removed (A L Mack and D D Wright, unpublished data). The fact that other animals (e.g., the giant squirrel *Ratufa indica*) do consume *Gnetum* pulp (R M Borges, personal communication) is consistent in that it implies that some vertebrates overcame the defence and became effective dispersers. Herrera (1987) found fleshy-fruited species had lower seed predation rates than dry-fruited species. In these cases, a thick, watery exocarp is an effective, cheap defence against seed predators. Careful re-examination of plant-animal interactions will most likely reveal other cases where fleshy “reward” tissues act as a protective layer excluding seed predators or pathogens.

4. Evolutionary implications and testable hypotheses

Secondary compounds are found in the ripe **fruits** of a broad and diverse array of modern plants. Some fruits are so toxic that frugivores avoid them (Herrera 1982). Defensive compounds in fruit serve a purpose that **must** balance the potential cost of losing dispersers with the benefits of protecting seeds (Herrera 1982; Cipollini and Stiles 1992b). Some plants reabsorb or de-toxify chemical defences of immature fruits upon maturation (Goldstein and Swain 1963; McKey 1979; Cippolini and Stiles 1992a). Such mechanisms were likely to have evolved after chemical defences arose – a sequence more parsimoniously explained by the defence scenario than in any explanation wherein fleshy pulp arises for dispersal and subsequently develops defences which later must be detoxified to retain dispersers.

Several authors have proposed that a fruit’s secondary compounds limit the quantity of fruit that frugivores will consume and the length of a single foraging bout, thereby prompting the frugivores to forage elsewhere, increasing seed dispersal efficacy (Janzen 1978b; Barnea *et al* 1993). Although secondary compounds in fruits may cause patch switching in some frugivores, such manipulation of frugivore foraging activity may merely be a fortuitous consequence of the original defensive role of such compounds (Mack 1990). Such secondary compounds might serve a defensive function; some might even be chemical relicts from historical interactions with past seed predators and pathogens. A stronger historical perspective might improve how we interpret modern fruit pulp chemistry.

The described scenario is plausible and incidental observations support it. Reconstruction of phylogenies and cladistic analyses of extant and fossil organisms might reveal the historical evolutionary paths of traits pertinent to the hypothesis (Brooks and McLennan 1991). For example, in the basal avian ratite lineage, the derived hypothesis predicts that herbivory and granivory are plesiomorphic traits and frugivory is the derived condition. This is supported by a recent phylogeny of the ratites (Sibley and Ahlquist 1990). However, disentangling the sequence of evolution in lineages with mixed trophic specializations including frugivory will be problematic, particularly for recently-evolved frugivores. Once plants had evolved fleshy fruits, vertebrate taxa with other trophic specializations could switch readily to frugivory as fruit consumption typically requires few special modifications (Herrera 1984b). Insectivorous vertebrate taxa might switch to fruit-eating more easily than frugivores could switch to insectivory because insects are often cryptic with sophisticated evasive strategies whereas fruits are usually the opposite.

Likewise, phylogenetic analyses of plant groups, particularly basal groups, may reveal whether defensive structures and chemistry preceded reward structures and chemistry (e.g., Janson 1992). Non-endozoochorous fruits exhibiting fleshiness might support defence being the plesiomorphic mechanism rather than dispersal; such taxa would be predicted to be basal to endozoochorous sister taxa. The defence scenario predicts that taxa having fleshy defensive tissues of immature fruits and non-fleshy, non-endozoochorous mature (e.g., leathery or dry) fruits will be basal in a clade containing endozoochorous relatives. Endozoochorous fruits will be an apomorphic trait in these clades. It is easy to envision fleshy mature fruits arising from fleshy immature-only fruits through heterochrony; the seed accelerates its maturation relative to the fruit wall, maturing before the immature fruit becomes dry or leathery. Some possible examples exist among the Annonaceae and Myristicaceae. Such a heterochronous transition could occur within any lineage; for example, *Parmentiera* (Bignoniaceae) has a fleshy indehiscent mature capsule containing dry, winged seeds (Gentry 1974).

Because fleshy fruits are widespread and have evolved independently several times, biologists have often assumed that selection favouring seed dispersal by animals must be strong and widespread. This assumption is weakened if we consider the defensive function of fleshy fruits. The widespread evolution of fleshy pulps could also be rooted in selection generated by seed predators and then subsequently modified by seed dispersers. The evolution of defences, in the form of a defensive layer around the seed, could have acted as an exaptation (Gould and Vrba 1982) for the evolution of a reward layer around the seed. In summary, it appears misleading to conclude that the observed morphology and chemistry of modern fleshy fruits is solely or, even perhaps, predominantly the evolutionary result of the mutualism with frugivorous seed dispersers.

Acknowledgements

I thank M L Cippolini, L Curran, D Levey, C M Herrera, D B McKey, E W Stiles, B H Tiffney and D D Wright for helpful comments on earlier drafts of this paper.

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MS received 18 August 1999; accepted 18 November 1999

Corresponding editor: RENEE M BORGES