Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores

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ABSTRACT

The origins of interactions between angiosperms and fruit-eating seed dispersers have attracted much attention following a seminal paper on this topic by Tiffney (1984). This review synthesizes evidence pertaining to key events during the evolution of angiosperm–frugivore interactions and suggests some implications of this evidence for interpretations of angiosperm–frugivore coevolution. The most important conclusions are: (*i*) the diversification of angiosperm seed size and fleshy fruits commenced around 80 million years ago (Mya). The diversity of seed sizes, fruit sizes and fruit types peaked in the Eocene around 55 to 50 Mya. During this first phase of the interaction, angiosperms and animals evolving frugivory expanded into niche space not previously utilized by these groups, as frugivores and previously not existing fruit traits appeared. From the Eocene until the present, angiosperm–frugivore interactions have occurred within a broad frame of existing niche space, as defined by fruit traits and frugivory, motivating a separation of the angiosperm–frugivore interactions into two phases, before and after the peak in the early Eocene. (*ii*) The extinct multituberculates were probably the most important frugivores during the early radiation phase of angiosperm seeds and fleshy fruits. Primates and rodents are likely to have been important in the latter part of this first phase. (*iii*) Flying frugivores, birds and bats, evolved during the second phase, mainly during the Oligocene and Miocene, thus exploiting an existing diversity of fleshy fruits. (*iv*) A drastic climate shift around the Eocene–Oligocene boundary (around 34 Mya) resulted in more semi-open woodland vegetation, creating patchily occurring food resources for frugivores. This promoted evolution of a 'flying frugivore niche' exploited by birds and bats. In particular, passerines became a dominant frugivore group worldwide. (*v*) Fleshy fruits evolved at numerous occasions in many angiosperm families, and many of the originations of fleshy fruits occurred well after the peak in the early Eocene. (*vi*) During periods associated with environmental change altering coevolutionary networks and opening of niche space, reciprocal coevolution may result in strong directional selection formative for both fruit and frugivore evolution. Further evidence is needed to test this hypothesis. Based on the abundance of plant lineages with various forms of fleshy fruits, and the diversity of frugivores, it is suggested that periods of rapid coevolution in angiosperms and frugivores occurred numerous times during the 80 million years of angiosperm–frugivore evolution.

Key words: coevolution, fleshy fruits, bats, birds, megafauna, multituberculates, primates, rodents.

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I. INTRODUCTION

This review concerns the major transitions in the interactions between angiosperms and vertebrate seed dispersers, focusing on the diversification of seed and fruit traits associated with the evolution of frugivores from the late Cretaceous and during the Palaeogene and Neogene. The main topic is seed-dispersal by animals which are attracted by soft tissue associated with the seeds, so-called fleshy fruits. The term fleshy fruits is here used in a broad sense, including any structure enclosing seeds and surrounding them with a fleshy, edible, pulp layer (Jordano, 2000), thus including also structures that morphologically are not parts of the fruit, but function in that way (e.g. a strawberry, where the juicy part is not the fruit). Although there are suggestions that fleshy tissue surrounding seeds originally evolved as a defence structure (Mack, 2000), most discussion on fleshy fruits has assumed that they are functionally adapted to attract seed dispersers. The same argument has been made for a special form of granivory (seed predation) which may be considered as functionally similar to frugivory on fleshy fruits. This is when the animal, despite being attracted by the seed itself rather than by a fleshy tissue, by scatter-hoarding actively contributes to seed dispersal. As advocated by Hulme (2002) and Vander Wall & Beck (2012), frugivory and scatter-hoarding dispersal systems have much in common. In both systems, the plants provide a nutritional reward (soft juicy tissue, or seeds) for the service of seed dispersal by a vertebrate. Scatter-hoarding implies that a fraction of seeds harvested by the animal is not consumed, and thereby functions as dispersed propagules. Both these plant–animal interactions may be considered as mutualistic, they include a reward for the animal and they promote seed dispersal, and the interaction is potentially subject to coevolution.

Vertebrate-dispersed seeds occurred long before the origin of angiosperms (reviewed by Tiffney, 2004), and fleshy tissue surrounding seeds occur in for example cycads, *Ginkgo* spp., Gnetales and several groups of conifers (Friis, Crane & Pedersen, 2011). However, the origins of interactions between angiosperms, specifically, and fruit-eating seed dispersers have attracted special attention following a seminal paper on this topic by Tiffney (1984). A crucial question for interpreting these origins is the timing of the events. When did seed size start to diverge in angiosperms? When did fleshy fruits and scatter-hoarded nuts originate? Which were the animals that may have been involved in these interactions? As pointed out by Friis *et al.* (2011), studies on the explosive angiosperm diversification of plant–animal interactions are important for understanding the origin of modern ecosystems, and inferences on causal mechanisms regarding these interactions depend critically on coincidence of timing. A summary of evidence on timing of events relating to the angiosperm–seed disperser interaction should thus be in order, and is the rationale behind this review. The goal is to discuss these questions and provide a summary of evidence concerning the origins and diversification of fleshy fruits and frugivores throughout the evolutionary history of angiosperms, from their origin in the early Cretaceous. An additional goal is to discuss evolutionary implications of the interactions between angiosperms and animal seed dispersers, once these had become established.

II. BACKGROUND HYPOTHESES

Today, the interactions between angiosperms and vertebrate seed dispersers are among the most prominent in terrestrial ecosystems. Fleshy-fruited plants account for 36–42% of woody species in temperate forests and 22–56% in Mediterranean scrublands (Jordano, 2000), and 70–94% of woody species in tropical forests (Fleming, Breitwisch & Whitesides, 1987; Jordano, 2000). Taxonomically, fleshy fruits occur in a wide range of plant families (Vander Wall & Beck, 2012). Fruits of several angiosperm families, e.g. Icacinaceae, Lauraceae and Vitaceae, have a well-documented fossil record going back to the Eocene forests more than 50 Mya, and for Arecaceae, Cornaceae and Menispermaceae even to the late Cretaceous (Collinson & Hooker, 1991; Harley, 2006; Wang *et al.*, 2012). Figure 1 provides an account of the geological timescale. Scatter-hoarded fruits (mainly large nuts) are common in the temperate zone, for example in the Betulaceae, Fagaceae and Juglandaceae (Vander Wall & Beck, 2012), but are also important in the tropics, particularly in neotropical forests (Forget *et al.*, 2002).

Tiffney (1984) presented data on fruit and seed size throughout angiosperm evolution that constitutes the basis for most accounts on coevolution between plants and frugivores (e.g. Wing & Tiffney, 1987*b*; Sussman, 1991; Wing & Boucher, 1998; Tiffney, 2004; Sussman, Rasmussen & Raven, 2013). In his figure 2 (Tiffney, 1984, p. 560) seed volume is plotted against time, from the early Cretaceous
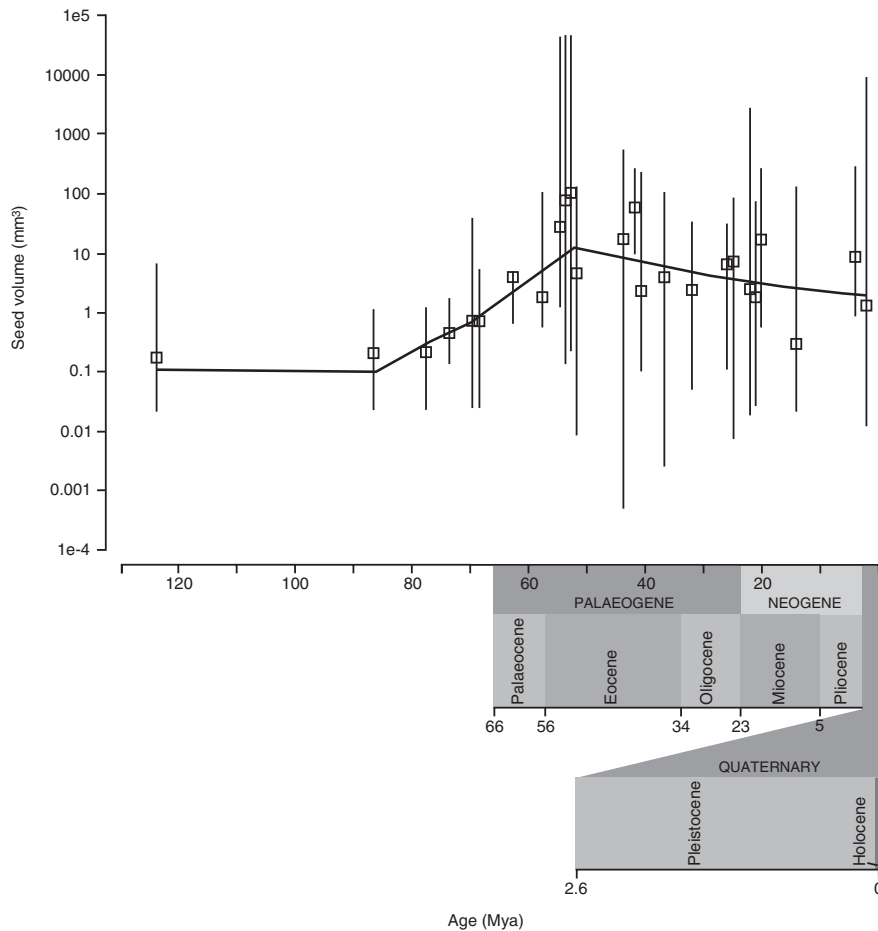
Fig. 1. Average and range of seed size in angiosperms since the origin of angiosperms around 130 Mya. The figure is based on Eriksson *et al.* (2000*a*), where details on data sampling and analyses are described. Seed size increases from around 80 Mya to the early Eocene, when palaeocommunities with the greatest maximum and average seed size are clustered, followed by a weak tendency of declining seed size. The geological timescale follows Cohen *et al.* (2013) and depicts the Cretaceous, and the Palaeogene, Neogene and Quaternary epochs.

onwards. Seed size did not change much during the Cretaceous and most angiosperms had rather small seeds that were abiotically dispersed. Later studies on seed size in relation to angiosperm phylogeny have confirmed that basal angiosperm lineages generally have small seeds (Sims, 2012). According to Tiffney (1984), seed size started to increase around the Cretaceous–Palaeogene (K–Pg) boundary, approximately 66 Mya. Seed size and fruit types diversified drastically during the following epoch, the Palaeocene, and peaked during the early Eocene (55 to 50 Mya). Tiffney (1984) remarked that there was a tendency, albeit non-significant, for a decline in average seed size from the Oligocene, reaching a level that has remained until the present.

Tiffney (1984) associated the increase in seed size in angiosperms with the development of angiosperm-dominated forest communities and advocated the idea that angiosperms required biotic dispersal agents to attain dominance. He suggested that the coinciding radiations of birds and mammals were instrumental in allowing dispersal of large, animal-dispersed propagules, thus promoting the

development of angiosperm-dominated forest systems. In a later review, Tiffney (2004, p. 19) stressed that 'the radiation of birds and mammals established dispersal agents scaled to move organs, which, in turn, allowed larger disseminule size and ultimately the establishment of closed forests...'. However, Wing & Tiffney (1987*a*,*b*) incorporated also other aspects such as generalized herbivory and competition for light in successively more closed vegetation. They suggested that during the main part of the Cretaceous, large herbivores (dinosaurs) inflicted strong disturbance on vegetation. Angiosperms were '*r*-selected' and adapted to disturbance. Thus angiosperms were small-seeded and lacked adaptation to seed dispersers. During the late Cretaceous, some seeds became dispersed by vertebrates, but it was not until after the K–Pg boundary, when dinosaur herbivory ceased, that angiosperms became '*K*-selected' and adapted to dispersal by frugivores. Wing & Tiffney (1987*b*) suggested a complex relationship where coevolution between plants and dispersers is involved in a positive feedback with vegetation development, such that increasing seed size and increased

fraction of fleshy fruits results from both coevolution and a closed forest vegetation structure (figure 5 in Wing & Tiffney, 1987*b*, p. 201).

Eriksson, Friis & Löfgren (2000*a*) made an additional analysis of seed size and fruit types in angiosperms based on fossil floras from the early Cretaceous onwards. Their results differed from Tiffney (1984) in that the increase in seed size commenced earlier, by approximately 80 Mya, during the late Cretaceous (Fig. 1). The peak in seed size and fraction of animal-mediated seed dispersal in Eriksson *et al.* (2000*a*) agreed with Tiffney (1984), i.e. palaeocommunities with the greatest maximum and average seed size cluster in the early Eocene (*c.* 55 to 50 Mya). The fraction of angiosperms with animal-mediated seed dispersal systems increased in association with the increase in seed size (Eriksson *et al.*, 2000*a*; Eriksson, 2008), suggesting that fleshy fruits started to become more abundant at the same time as seed size started to increase. However, a detailed study of one of the earliest angiosperm floras (*c.* 124 Mya) showed that about a quarter of the fruits already at that time were fleshy (drupes and berries), although the size of the seeds and fruits was small (Eriksson *et al.*, 2000*b*). Eriksson *et al.* (2000*a*) suggested that the initial driver behind the increasing seed size in the late Cretaceous and early Tertiary was the structure of the vegetation. Angiosperm-dominated tropical forests expanded from the late Cretaceous and reached a maximal distribution in the early Eocene (Morley, 2000, 2011). In these forests, large seeds were favoured due to competition for light. Increased selection for animal-mediated dispersal resulted from the increased seed size. The increasingly common food source provided by fruits led to new animal groups exploiting this new food source, and plants were favoured by seed-dispersing animals which were capable of transporting large seeds. In this scenario, specialized frugivores were not the drivers behind the diversification of seed size and fruits types, but rather a consequence of the availability of a new food source.

The early interactions between angiosperms and seed-dispersing animals have also been discussed in the context of evolution of one of the putative disperser groups, the primates. Sussman (1991) and Sussman *et al.* (2013) suggested that euprimates ('modern' primates), evolved during the early Eocene in a close coevolutionary relationship with angiosperms: 'The evolution of modern primates, as well as that of fruit bats and fruit-eating birds, may be directly related to the evolution of improved means of exploiting (...) the fruits and seeds of flowering plants.' (Sussman *et al.*, 2013, p. 101).

The implications of the timing of the diversification of seed size and fruit types in relation to various suggested seed-dispersing animals is still an open question. For example, primates may not have been an important coevolutionary agent for the initial angiosperm diversification of seeds and fruits, since this took place considerably earlier than the radiation of primates. A similar discrepancy in timing has been noted for other frugivores, such as birds and bats (Eriksson, 2008; Fleming & Kress, 2011). Fleming & Kress (2011) even suggested that evolution of 'bird-fruits' may have facilitated evolution of frugivory in primates (thus, frugivorous birds would have evolved before frugivorous primates). Several of the above-mentioned papers on angiosperm seed size evolution (e.g. Tiffney, 1984; Wing & Tiffney, 1987*b*; Eriksson *et al.*, 2000*a,b*) are in fact quite vague on the identity of the interacting animals, referring mostly to a poor fossil record. An important issue is thus to identify which groups of extant and extinct animals were most likely involved in angiosperm–seed disperser interactions.

III. A RATIONALE FOR A FOCUS ON BIRDS, BATS, PRIMATES AND RODENTS (AMONG EXTANT SEED DISPERSERS)

Before summarizing evidence related to the timing of origin of the fleshy fruit/seed disperser interactions, one has to decide which extant animal groups should be considered as frugivorous. This is not a trivial problem, since fruit eating is a very common phenomenon, even among animals which do not have fruits as the main part of their diet. In his review on the biology of figs (*Ficus*, Moraceae), Janzen (1979, p. 40) posed the rhetorical question 'Who eats figs?' and answered: 'Everybody.' Figs are often considered the single most important genus of fleshy-fruited plants from a present-day fruit consumption viewpoint. Figs may also be among the first plants which were domesticated by humans (Kislev, Hartmann & Bar-Yosef, 2006). Shanahan *et al.* (2001) concluded that the animals known to eat figs include 10% of the world's bird species and 6% of the world's mammals. The major fig eaters among birds are fruit pigeons, parrots and passerines, and the major fig-eaters among mammals are bats, primates and squirrels (Shanahan *et al.*, 2001). This list of animal groups, birds, bats, primates and rodents, provides a reasonable starting point for discussing major groups of frugivores in the extant fauna. Birds, bats and primates constitute a trio most commonly mentioned as the animal groups which have fleshy fruits as their main source of nutrition, and thus being the major players in the seed disperser interaction, especially in the tropics (e.g. Fleming *et al.*, 1987; Chapman, 1995; Jordano, 2000; Gómez & Verdú, 2012; Sussman *et al.*, 2013). Rodents should be included both because some groups rely strongly on fleshy fruits (in a strict sense), e.g. squirrels (Shanahan *et al.*, 2001), but also since scatter-hoarding of large nuts is here considered as functionally similar to frugivory of fleshy fruit, and rodents play an important role in scatter-hoarding (Vander Wall & Beck, 2012).

This restricted list of animal groups should not be seen as downgrading the occurrence, and at least locally, the importance of frugivory involving also other groups of animals, for example elephants (e.g. Chapman, Chapman & Wrangham, 1992; Nchanji & Plumptre, 2003), carnivores (e.g. Willson, 1993; Motta-Junior & Martins, 2002), and opossums, kangaroos, lemurs, ungulates, reptiles and fish (Jordano, 2000; Herrera, 2002), or in geologically recent times, members of the now-extinct 'megafauna' (e.g. Donatti *et al.*, 2007; Guimarães, Galetti & Jordano, 2008; Hansen

& Galetti, 2009). Thus, frugivory should be described as an interaction between a large number of plant species and a diverse array of animals.

We will return to the interactions involving the Pleistocene megafauna in Section VII, and here focus on the extant animal groups suggested as most important for a long-term perspective of plant–frugivore interactions: birds, bats, primates and rodents. However, for examination of timing of origin in relation to angiosperm seed and fruit diversification, additional qualification is needed to identify focal taxa of these animals. In his list of 'specialized' tropical frugivorous birds, Snow (1981) included oilbirds (Caprimulgiformes), trogons (Trogoniformes), turacos (Cuculiformes), mousebirds (Coliiformes), hornbills (Coraciiformes), fruit pigeons (Columbiformes), and several groups of passerines (Passeriformes), e.g. barbets, cotingids, manakins, starlings, broadbills, corvids, honeybirds, birds of paradise and toucans (now usually placed in Piciformes, e.g. Patané *et al.*, 2009). Extracting similar information from Fleming *et al.* (1987) confirms the list by Snow (1981), but adds also parrots (Psittaciformes), cracids (Galliformes), and cassowaries (Struthioniformes). Among bats, two groups are mainly frugivorous, Old World fruit bats (megabats; Pteropodidae) and New World fruit bats (leaf-nosed bats; Phyllostomidae). In extant primates, the majority is mainly frugivorous (Gómez & Verdú, 2012), qualifying use of the order primates as a whole. For scatter-hoarding animals the list becomes more limited, including mainly rodents and some passerine birds, particularly corvids (jays, rooks, nutcrackers) (Vander Wall & Beck, 2012).

IV. TIMING OF ORIGIN AND RADIATION OF FRUGIVOROUS BIRDS

The origin and radiation of 'modern birds', Neornithes, has been subject to much debate, and remains controversial (e.g. Feduccia, 1996, 2003; Hedges *et al.*, 1996; Cooper & Penny, 1997; Dyke & van Tuinen, 2004; Ericson *et al.*, 2006; Ericson, 2012; Mayr, 2013). The main disagreement is whether lineages of Neornithes radiated and diversified during the Cretaceous, which is suggested by molecular analyses, or after the K–Pg boundary in the early Palaeogene, which is suggested by fossil evidence. Birds have often been considered very poorly represented in the fossil record, making conclusions on plant–disperser interactions involving birds difficult. This view has been questioned by Bleiweiss (1998) and Lindow & Dyke (2006), suggesting that the fossil record should be useful to assess the broad temporal relationships between the diversification of seed size and fleshy fruits and the diversification of various groups of potentially frugivorous birds. For example, of 33 recognized ordinal-level clades of extant Neornithes, 11 have been found from the Fur formation (early Eocene) in Denmark (Dyke & Lindow, 2009).

The most diverse and widely distributed group of birds during the Cretaceous, judged from the fossil record, is the now extinct Enantiornithes, some of which were relatively small and probably arboreal (Padian & Chiappe, 1998; Chiappe & Dyke, 2002). Not very much can be concluded about their feeding habits, although it seems likely that some included seeds and fruits in their diet. There is some direct evidence suggesting granivory in birds from the Cretaceous. Zhou & Zhang (2002) found traces of seeds in the fossil of an early Cretaceous bird of unknown affinity. Zheng *et al.* (2011) reported evidence that early Cretaceous birds had a well-developed digestive system with a crop, a feature that in modern birds usually is associated with granivory. Among modern bird orders, fossil evidence suggest a Cretaceous origin for only a few (e.g. Anseriformes, Charadriiformes, Gaviiformes, Procellariiformes) (Padian & Chiappe, 1998), but this evidence has been questioned (Dyke & van Tuinen, 2004). Assuming that these bird orders really did evolve during the Cretaceous, it seems unlikely that they were frugivorous, based on their extant representatives.

Very little evidence on fossil birds is known from the Palaeocene (Lindow & Dyke, 2006; Mayr, 2007; Dyke & Lindow, 2009). The bird groups that are found from this time (e.g. Anseriformes, Ralliformes, Gruiformes, Strigiformes) are not likely to have been frugivorous (e.g. Hwang, Mayr & Bolortsetseg, 2010; Mayr, Alvarenga & Clarke, 2011), and arboreal birds appear to be generally rare or even absent (Mayr, 2007). Although it has been suggested that the diversification of the crown groups of modern avian families did not take place before the Oligocene (Mayr, 2005), it seems that some of the groups potentially relevant for frugivorous interactions may have originated in the Eocene. Much of the relevant information comes from the Fur formation in Denmark which was previously interpreted as late Palaeocene, but has later been placed as early Eocene (Lindow & Dyke, 2006).

Kristoffersen (2001) described findings of trogons (Trogoniformes) from the Fur formation as morphologically quite similar to extant species, and she noted that some of the plant genera whose fruits are part of the diet of extant trogons, e.g. *Ocotea* (Lauraceae) and *Hasseltia* (Flacourtiaceae), have been found in the early Eocene London Clay (Collinson, 1983). Several other groups of birds which include extant frugivores have records from the Eocene, for example Caprimuligiformes, including extant oilbirds (Dyke & van Tuinen, 2004) and Coliiformes, including extant mousebirds (Lindow & Dyke, 2006). Coliiformes was particularly diverse during the Eocene (Dyke & van Tuinen, 2004; Mayr, 2005) but no evidence indicates whether they were frugivorous. Several studies describe Eocene records of Psittaciformes (parrots) (Dyke & van Tuinen, 2004; Mayr, 2005; Lindow & Dyke, 2006; Waterhouse *et al.*, 2008) but the earliest parrots may have been more generalized in their feeding habits, and only later evolved specialized frugivory (Mayr, 2005). For Cuculiformes (including extant turacos), and Coraciiformes (including extant hornbills), the fossil record is meagre, and it seems unclear whether they existed in the Eocene (Dyke & van Tuinen, 2004; Mayr, 2005). An exception may be the insectivorous rollers (Coraciiformes), which are known from the Eocene (Feduccia, 1996). Columbiformes (including extant fruit pigeons) are not known from fossils older than

the Miocene (Dyke & van Tuinen, 2004; Mayr, 2005). Evidence is equivocal for Galliformes. Even though the stem group may have occurred in the Eocene, the crown groups including the frugivorous cracids evolved much later (Dyke & van Tuinen, 2004; Mayr, 2005; Lindow & Dyke, 2006). Cassowaries (Struthioniformes) are not known before the Pliocene (Feduccia, 1996). For the toucans (Piciformes), their origin and diversification in the neotropics is not likely to have commenced before the middle Miocene (Patané *et al.*, 2009).

The bird order including most extant species and also the most diverse array of extant frugivores is the passerines (Passeriformes). The phylogeny of passerines is controversial, but it is known that passerines occurred in Australia already in the early Eocene (Boles, 1995). This finding is consistent with the hypothesis that passerines originated and diversified in the southern hemisphere, and later dispersed to the northern hemisphere (Ericson, Irestedt & Johansson, 2003; Barker *et al.*, 2004; Jønsson *et al.*, 2011), which would have been colonized during the Oligocene (Mayr & Manegold, 2004). No fossil of passerines in Europe is older than the Oligocene (Dyke & van Tuinen, 2004; Mayr, 2005), and Lindow & Dyke (2006) remarked that the rich fossil bird fauna from the early Eocene Fur formation in Denmark would have contained passerines, if there were any passerines present. Despite these indications of a late arrival to the northern hemisphere, recent molecular evidence suggests origins of major passerine lineages already in the late Cretaceous and diversification of the clade Oscines ('songbirds', containing most extant frugivores) in the Palaeocene or Eocene (Ericson *et al.*, 2014). However, Mayr (2013) strongly disagreed with suggestions of a Cretaceous origin of passerines. He remarked that passerines have a generally uniform morphology, and thus that '...a Cretaceous divergence of crown group passerines would imply an unprecedented evolutionary stasis for more than 80 million years in one of the most species-rich group of endothermic vertebrates' (Mayr, 2013, p. 7). Furthermore, Mayr (2013) pointed out that the oldest undisputable oscine fossils in the northern hemisphere are from late Oligocene.

Summarizing evidence of the origin and radiation of frugivorous birds (Fig. 2) leads to the conclusion that some seed- and fruit-eating birds (most likely the now extinct Enantiornithes) were present already in the Cretaceous. No evidence suggests that this feeding strategy was common, however. There is no strong evidence suggesting that there were 'modern' groups of frugivorous birds in the Palaeocene. A radiation of several lineages of modern groups of birds took place during the Eocene, and many of these lineages contain frugivores in the extant fauna, for example trogons,
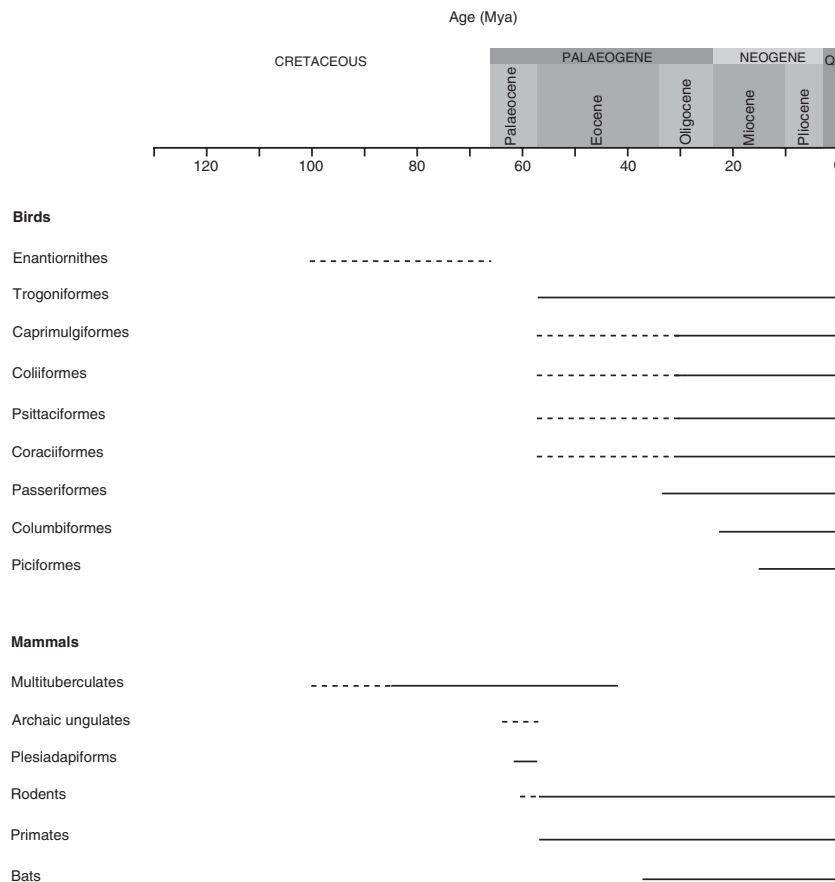

Fig. 2. Time lines for frugivorous birds and mammals. The time lines show temporal occurrence of frugivory during the last 100 million years, in major frugivorous bird and mammal groups for which there are evidence of frugivory prior to the Pliocene. A dotted line indicates that the evidence is weak.

mousebirds and parrots, but except for trogons the inference that these really were frugivorous at that time is weak. Most likely, passerines did not arrive to the northern hemisphere before the Oligocene, and perhaps they replaced earlier birds using frugivory niches (Harrison, 1979). Even if passerines originated earlier in the southern hemisphere, they are not likely to have been involved in plant–disperser interactions from the late Cretaceous to the Eocene in the northern hemisphere, from where most data on fossil seeds and fruits are derived (Tiffney, 1984; Eriksson *et al.*, 2000*a*).

V. TIMING OF ORIGIN AND RADIATION OF FRUGIVOROUS MAMMALS

Mammals originated in the late Triassic (*c.* 200 Mya) (Carroll, 1997; Novacek, 1999), or possibly later during the Jurassic (*c.* 166 Mya) (O'Leary *et al.*, 2013), and the earliest mammals are thought to have been generalized, small, noc-turnal predators or scavengers. Estimates based on molecular methods suggest origins of extant mammal orders during the Cretaceous (e.g. Bininda-Emonds *et al.*, 2007; Meredith *et al.*, 2011), and there is some fossil evidence of eutherian mammals (including all extant placental mammals) from the Cretaceous (Ji *et al.*, 2002; Goswami *et al.*, 2011). However, recent studies based on a compilation of various data (O'Leary *et al.*, 2013), and most fossil evidence, is in accor-dance with the long-held opinion that 'modern' mammal orders radiated during the Palaeocene after the K–Pg mass extinction event (e.g. Alroy, 1999; Meredith *et al.*, 2011) or close to the Palaeocene–Eocene boundary, possibly causally related to the Palaeocene–Eocene thermal maximum. This period of exceptional global warming is associated with the appearance of primates and modern 'hoofed' mammals (Perissodactyla and Artiodactyla) (Gingerich, 2006), and also with a rapid geographical spread of several modern mammal groups (Bowen *et al.*, 2002; Smith, Rose & Gingerich, 2006).

During the Cretaceous, before the radiation of modern mammal orders, other mammal groups have been suggested as potential candidates of frugivorous seed-dispersing interactors with angiosperms, such as multituberculates and didelphoid marsupials (Collinson & Hooker, 1991; Agustí & Antón, 2002). In particular, the multituberculates (which went extinct in the late Eocene) are likely to have been important interactors with angiosperms. Multituberculates radiated profoundly from around 85 Mya, concerning body size and feeding habits (Wilson *et al.*, 2012) and became the most successful clade of late Cretaceous mammals (Novacek, 1999). Average body mass approximately tripled between 85 Mya and the K–Pg boundary; the largest species weighing up to 5 kg (Wilson *et al.*, 2012). Some species were arboreal (Jenkins & Krause, 1983; Collinson & Hooker, 1991), a life habit that has been suggested to be associated with longer life spans (Shattuk & Williams, 2010). The multituberculate radiation included adaptive shifts towards increased herbivory, including frugivory, and their dentition

suggests that seeds and fruits were an important part of the diet (Wilson *et al.*, 2012).

During the Palaeocene, average body mass in herbivores (including also 'archaic ungulates') increased (Wing & Tiffney, 1987*a*; Janis, 2000). Herbivores at this time were not specialized folivores; this feeding habit disappeared along with the dinosaurs, not to become common until later during the Eocene (Janis, 2000). Plant reproductive parts, flowers, seeds and fruits, were likely to have been important components of the herbivore diet. Thus, interactions between mammals and fleshy-fruited plants most likely had a long history before the radiation of modern mammals. Figure 2 summarizes the timing of origin and radiation of frugivorous mammals; a more detailed description of early frugivory in rodents, primates and bats is given below.

(1) Rodents

The stem group of rodents (and lagomorphs), Glires, probably originated close to the K–Pg boundary (Asher *et al.*, 2005), and there are several fossil findings of Glires from the Palaeocene (e.g. Meng *et al.*, 2005, 2007). The rodent lineage is believed to have evolved during the Palaeocene (Gingerich, 2006; Blanga-Kanfi *et al.*, 2009; O'Leary *et al.*, 2013), and some animals were 'squirrel-like and arboreal' (Agustí & Antón, 2002), thus potentially eating seeds and fruits. Although many extant rodents also are frugivorous, e.g. squirrels (Shanahan *et al.*, 2001), rodents are particularly important seed dispersers due to scatter-hoarding of nuts and large seeds (Vander Wall & Beck, 2012). A key adaptation is their ever-growing incisors, making rodents exceptionally suited to handling hard fruits such as nuts. Collinson & Hooker (2000) suggested that granivory and hoarding behaviour in rodents evolved and became common during the late Eocene along with climate deterioration, whereas rodent frugivory on soft fruits was more common earlier during the Eocene. Angiosperm families producing typically rodent-dispersed nuts today, Betulaceae, Fagaceae and Juglandaceae, had rather small dry-winged fruits in the early Eocene and large nuts did not become abundant until the late Eocene (Collinson & Hooker, 1991, 2000), or perhaps even later during the Oligocene (e.g. Daghlian & Crepet, 1983).

(2) Primates

The origin and early evolution of primates has long been controversial, and opinions diverge on the delimitation of primates, the timing of their origin, and the ecological conditions favouring characteristic features of primates such as grasping extremities, nails instead of claws, optic convergence, and brain enlargement. It has been suggested that the ancestral primate lineage diverged during the late Cretaceous (Tavaré *et al.*, 2002; Soligo & Martin, 2006; but see Silcox *et al.*, 2007). However, fossil evidence of euprimates ('modern' primates) is not known before the early Eocene, and a recent estimate including molecular data suggests that

euprimates originated 55.8 to 50.3 Mya, i.e. in the early Eocene (O'Leary *et al.*, 2013).

It has been considered likely that primate origin is related to an arboreal habit. Developing this idea, Cartmill (1974, 1992) suggested the 'visual predation hypothesis'. The key adaptation in the earliest primates, according to this hypothesis, was visually guided predation on insects in the understorey and canopy of tropical forests. An alternative hypothesis was suggested by Sussman (1991) who argued that early primates were omnivorous, and consumed 'small objects' in the forest canopies, including insects, but primarily flowers, seeds and fruits. This 'angiosperm–primate coevolution hypothesis' has recently been elaborated in more detail by Sussman *et al.* (2013).

These different opinions partly reflect a disagreement of how an extinct group of primates or primate-like mammals, the Plesiadapiformes, are related to euprimates. Plesiadapiforms were abundant during the Palaeocene (e.g. Silcox & Williamson, 2012), and went extinct during the Eocene. In contrast to Cartmill (1974), who did not consider plesiadapiforms as primates, later studies support that they should be included in primates (Bloch *et al.*, 2007). Furthermore, well-preserved fossil remains of a plesiadapiform from the Palaeocene indicate that grasping abilities evolved before orbital convergence (Bloch & Boyer, 2002). Although not altogether conclusive for distinguishing between these two hypotheses, this finding is not in line with what we should expect from Cartmill's (1974, 1992) visual predation hypothesis.

For the question of timing between the diversification of frugivores and angiosperm seed sizes and animal-dispersed fleshy fruits, the disagreement on whether plesiadapiforms should be regarded as primates is however not essential. Irrespective of whether plesiadapiforms should be considered as primates, they are undoubtedly good candidates as frugivorous seed dispersers during the Palaeocene. Plesiadapiforms had a wide range of feeding habits, including folivory (Boyer, Evans & Jernvall, 2010; Boyer, Costeur & Lipman, 2012) and frugivory (Bloch & Boyer, 2002; Sargis, 2002; Bloch *et al.*, 2007; Chester & Beard, 2012). A balanced conclusion may be that they were omnivores, but that fruits were an important part of their diet. After the Palaeocene–Eocene boundary, euprimates radiated (Gingerich, 2006). Based on reconstruction of diet of fossil primates from the Eocene and early Oligocene, Strait (2001) concluded that the majority were frugivorous (e.g. Silcox, Dalmyn & Bloch, 2009), but the diet repertoire included also insectivory (e.g. Ni *et al.*, 2003). Palaeocene plesiadapiforms thus seem to have had a range of feeding habits similar to the euprimates in the Eocene. It is thus possible that euprimates replaced plesiadapiforms within a similar range of feeding niches after the Palaeocene–Eocene boundary (Boyer *et al.*, 2012).

(3) Bats

Bats constitute about 20% of extant species of mammals, and together with rodents they are the most diverse mammal orders. Bats have traditionally been divided into two main groups, Megachiroptera, comprising the mostly frugivorous family Pteropodidae (megabats, or Old World fruit bats), and Microchiroptera, comprising the remaining families, including a range of different feeding strategies, for example insectivory, frugivory and sanguivory (Baker *et al.*, 2012). The main rationale for the separation of megabats from the remaining bat families is that megabats lack echolocation (apart from being generally bigger). However, a comprehensive analysis based on molecular data (Teeling *et al.*, 2005) suggests that megabats are actually nested within the other lineages of bats. This implies that either echolocation has evolved at least twice, or it has been lost in the lineage comprising megabats. Based on indirect evidence, the second alternative seems most probable (Simmons, 2005; Teeling *et al.*, 2005). The fossil record of bats has been considered poor (e.g. Eiting & Gunnell, 2009). Nevertheless, there are several recent studies examining combined fossil and molecular evidence, suggesting that we now have a rather consistent picture of when bats evolved, how the different bat lineages are related phylogenetically, and how early evolution of bats is related to the environmental conditions during the Palaeogene (e.g. Simmons, 2005; Teeling *et al.*, 2005; Almeida *et al.*, 2009, 2011; Dumont *et al.*, 2012).

Although it has been speculated that bats may have a Palaeocene origin (e.g. Teeling *et al.*, 2005), bats do not appear in the fossil record until the Eocene (Tabuce, Antunes & Sigé, 2009; Harrison & Hooker, 2010; Ravel *et al.*, 2011; Morgan & Czaplewski, 2012; Smith *et al.*, 2012). Fossil evidence suggests that the earliest bats were small and insectivorous (Baker *et al.*, 2012; Smith *et al.*, 2012). The diversity of bats was high already in the early Eocene, suggesting a rapid diversification (Simmons, 2005; Teeling *et al.*, 2005). This rapid diversification of bats has been associated with the Palaeocene–Eocene thermal maximum (Gingerich, 2006), during which insect abundance is thought to have increased drastically (Currano *et al.*, 2008). Key innovations such as a powered flight and echolocation were instrumental for the radiation and success of bats, exploiting a feeding niche based on insects (Simmons, 2005).

Frugivory in bats seems to have evolved later, first in Pteropodidae and then in some lineages of Phyllostomidae (Baker *et al.*, 2012). Although Pteropodidae was separated from other bat lineages already in the early Eocene, the crown group is more recent (Almeida *et al.*, 2011). Diversification of the crown-group Pteropodidae has been estimated to 38 to 24 Mya (Almeida *et al.*, 2009) and 28 to 18 Mya (Teeling *et al.*, 2005), i.e. during an interval from the late Eocene to Miocene. The ancestral condition of Phyllostomidae was probably insectivory (Rojas *et al.*, 2011), and it was not until the diversification of the crown group, estimated to have occurred during the late Oligocene–Miocene, 26 to 15 Mya (Teeling *et al.*, 2005), that frugivory appeared in some lineages. This diversification involved successive changes in skull morphology and biting performance, as adaptations to particular specialized diets (Dumont *et al.*, 2012). The subfamily Phyllostominae, including some frugivorous lineages, diversified in the middle Miocene 19.5

to 18.6 Mya (Hoffmann, Hoofer & Baker, 2008). For one genus of frugivorous phyllostomid bats, *Sturnira*, the initial diversification has been estimated to have occurred in the late Miocene 15.9 to 12.6 Mya, with divergence between the two major extant lineages 5.5 to 3.7 Mya (Velazco & Patterson, 2013). The suggested scenario is thus that some insectivorous lineages of phyllostomids during the Miocene evolved a successively more specialized frugivory, initially feeding on soft fruits and later feeding on harder and more fibre-rich fruits (Rojas *et al.*, 2012).

VI. TIMING OF ORIGIN OF ANGIOSPERM FLESHY FRUITS

Angiosperm seeds were initially generally small, and continued so from the origin of angiosperms somewhere around 130 Mya and during the following approximately 50 million years (Fig. 1). After this long period of stasis, seed and fruit size started to increase, commencing around 80 Mya, approximately coinciding with a general expansion phase of angiosperms (Lupia, Lidgard & Crane, 1999; Friis *et al.*, 2011). Angiosperm-dominated tropical rainforests expanded during the period from the late Cretaceous to the global warming maximum in the early Eocene (Morley, 2000, 2011; Wang *et al.*, 2012). At this time, tropical forests extended as far as 60°N (Morley, 2011). The environmental context, from a vegetation viewpoint, is thus clear. The diversification of angiosperm seed sizes and fruits took place along with expanding tropical forests.

Before summarizing evidence on timing of fleshy fruit origins, a few remarks on fruit evolution is useful. The ancestral condition for angiosperm fruits is apocarpy, i.e. free carpels, but the majority of extant angiosperms have evolved syncarpous fruits, i.e. where the carpels are fused (Endress, 1982). Fruits may be dehiscent, i.e. they open to release the seeds, or indehiscent, remaining closed, and they may be dry or fleshy. There are many different variants of fleshy fruits where the 'fleshiness' originates from other tissues than the

pericarp developed from the ovary wall, but two major types of fleshy fruits are often recognized, drupes and berries (e.g. Seymour *et al.*, 2013). Both these are indehiscent and usually syncarpous. Exceptions occur rarely, for example apocarpous berries in Apocynaceae (Simões *et al.*, 2007). Drupes are characterized by having few seeds, usually only one, and this seed is enclosed in a hard inner fruit layer, the endocarp. Berries have a thin often almost unnoticeable endocarp, and they usually contain many seeds, which then by necessity are smaller than what is regularly the case for drupes. Although there are one-seeded berries, for example in the Lauraceae (e.g. avocado), most extant berries contain many small seeds (e.g. Ericaceae and Solanaceae). Nuts are morphologically similar to drupes, but lacking a fleshy mesocarp (middle fruit layer), thus enclosing the seed within a hard or leathery fruit wall. A general conclusion is that fleshy fruits, if interpreted as an adaptation for attracting animal seed dispersers, are the result of convergent evolution occurring in many different plant lineages, and resulting in a wide array of morphologies.

Focusing on syncarpous fruits, drupes and nuts are the expected endpoints of selection acting on fruit structure to increase seed size. Due to a seed size/number trade-off, a consequence is reduced seed number per fruit. Thus, the major option to increase seed size is to evolve one-seeded drupes or nuts and enlarge them. This can be documented in the palaeofloras during the period commencing around 80 Mya, but the trend only concerns drupes (large nuts did not become abundant before the late Eocene; Collinson & Hooker, 2000). Based on fossil evidence, drupes dominated among the fleshy fruits during the expansion phase in the late Cretaceous and early Palaeocene. Berries are rarely documented in palaeofloras from the Cretaceous, but their occurrence may be underestimated since the structure of berries makes them more difficult to detect in fossils. Comparing the fraction of species with drupes in six palaeofloras spanning the period 87 to 63 Mya (Table 1) shows an increase from 5.6 to 33.3%. The corresponding values for early Eocene floras from the London Clay during the 'peak phase' of angiosperm seed and fruit size are similar,

Table 1. Fraction of 'species' with fruits interpreted as drupes based on fossil evidence from palaeofloras from the late Cretaceous to early Eocene. The floras are the same as those used in Eriksson *et al.* (2000*a*) for this period. Records of endocarps have been interpreted as drupes. Assuming conservatism of fruit types, many seeds from these floras indicate that the true fraction of drupes was higher, and also that berries were common, for example in the Vitaceae and Annonaceae

Flora	Age (Mya)	% drupes	N
Klikov-Schichtenfolge (1, 2)	87	5.6	71
Aachen (1, 3)	78	11.4	35
Horni Becva (1, 4)	74	7.4	27
Walbeck (1)	70	24.6	65
Eisleben (1)	70	30.4	46
Gonna-Walkmühlz II, IV (5)	58–63	33.3	36
London Clay, Herne Bay (6)	53	34.7	150
London Clay, Bognor (6)	53	30.6	134
London Clay, Sheppey (6)	53	33.3	327

Figure within parentheses after the name of each flora is a key to references: 1, Knobloch (1964), Nemejc (1971), Knobloch & Mai (1983, 1984, 1986); 2, Knobloch (1985); 3, Vangerow (1954); 4, Knobloch (1977); 5, Mai (1987); 6, Reid & Chandler (1933), Chandler (1961).

i.e. around a third of all species had drupes (Table 1). The floras used in Table 1 are the same as those used in Eriksson *et al.* (2000*a*), showing a continuous size increase of seeds and fruits during this period. Berries were also common in the London Clay floras, but many of these were one-seeded berries (Lauraceae), thus functionally similar to one-seeded drupes. However, based on seeds from families which today possess berries, for example those fossil seeds identified as Vitaceae and Annonaceae, the fraction of berries may have been quite high.

Transforming the structure of a fruit (for example evolving a large drupe from a capsule) means losing dehiscence, reducing the seed number per fruit in order to enable larger seeds, developing a fleshy mesocarp, enclosing the seed in a hard endocarp, and enlarging the seed and the fruit. Recent evidence on fruit development pathways shows that the genomic regulation of ontogenetic development of different kinds of fruit (capsules, berries, drupes) is similar (Seymour *et al.*, 2013), suggesting that a consistent directional selection would enable such a transformation without any need for fundamentally altering gene regulation of fruit development. Detailed studies combining phylogeny and diversification with analyses of fruit evolution, for Solanaceae (Knapp, 2002; Särkinen *et al.*, 2013) and Melastomataceae (Clausing, Meyer & Renner, 2000), suggest that changes in fruit morphology, both from dry to fleshy fruits, and among different forms of fleshy fruits, are ontogenetically 'easy'. Although likely to be much less common, there is evidence also for transitions from fleshy to dry fruits, for example in Solanceae (Knapp, 2002), Apocynaceae (Simões *et al.*, 2007), Ericaceae (Bush *et al.*, 2009) and Adoxaceae (Jacobs, Huysmans & Smets, 2010).

As indicated by the presence of plant families which today possess berries, this fruit type most likely was abundant in the floras from the Eocene, and the same holds for large nuts (Collinson & Hooker, 2000). Thus, as far as can be established from fossil evidence all the major dimensions of fruit type variation (Seymour *et al.*, 2013) concerning apocarpy/syncarpy, dehiscence/indehiscence, dry/fleshy fruits, and among the latter, both the main types, berries and drupes, as well as a full seed size range (in relation to present-day variation), were established in the early Eocene. Although not recognized in the fossil record, also the smallest existing angiosperm seeds, so called 'dust seeds', were most likely present in the Eocene (Eriksson & Kainulainen, 2011). This 'peak' of seed and fruit size diversification is thus not only referring to average seed and fruit size (Tiffney, 1984; Eriksson *et al.*, 2000*a*; Fig. 1), but also to variation in seed size and fruit types.

Sims (2010) examined the temporal trends in seed size described by Tiffney (1984) and Eriksson *et al.* (2000*a*) in relation to potential sampling errors due to the latitudinal location of palaeofloras. There is a strong latitudinal gradient in seed size in extant floras (Moles *et al.*, 2007), and if present during the Cretaceous and Palaeogene, it could produce a misleading picture of any temporal trend in seed size. However, Sims (2010) found that the large increase in seed size during the late Cretaceous and early Palaeogene, reaching a peak in the early Eocene, was

robust. Furthermore, both Tiffney (1984) and Eriksson *et al.* (2000*a*) noted a slight decrease in average seed size after the Eocene. This trend was weak, and should be viewed with caution.

The fact that a full range of variation with regard to fleshy fruits existed in the early Eocene does not mean that all extant fleshy-fruited angiosperm lineages had at that time evolved fleshy fruits. Even though many angiosperm families seem to have conserved fruit traits ever since the Eocene (Eriksson *et al.*, 2000*a*), e.g. the Icacinaceae (Stull *et al.*, 2012), both drupes and berries have evolved much more recently in many angiosperm lineages. Bolmgren & Eriksson (2005) found that clades where fleshy fruits originated were temporally distributed over the last 70 million years, and almost half the origins were younger than 40 Mya. In the Rubiaceae, different kinds of fleshy fruits, drupes, berries, and 'Gardenia-fruits' have evolved independently at least 12 times (Bremer & Eriksson, 1992). More detailed analyses of parts of the family (Kainulainen *et al.*, 2010) suggest that the number of origins is even higher. The divergence times of different tribes in the Rubiaceae have been estimated to span from 77.9 to 14.2 Mya (Bremer & Eriksson, 2009). Some of these tribes, e.g. Coffeeae (divergence time 33.3 to 21.3 Mya) generally possess fleshy fruits. Relatively recent origins of fleshy fruits are also found in the tribe Condamineeae, where most lineages have capsules (Kainulainen *et al.*, 2010). In Melastomataceae fleshy fruits have originated at least three times (Clausing *et al.*, 2000). One of these lineages, including the genus *Medinilla*, originated and diversified in the Miocene (Renner, Clausing & Meyer, 2001; Renner, 2004). Another example of diversification of fleshy fruits is from the palm family (Arecaceae). Palms are an ancient family with a fossil record from the late Cretaceous (Harley, 2006). Most palms have fleshy fruits (drupes) dispersed by a wide array of mostly mammalian and avian frugivores (Zona & Henderson, 1989). Although the crown group of palms diversified in the late Cretaceous (Baker & Couvreur, 2013*a*), a drastic increase in diversification rate occurred in the tribe Areceae much later, 38.1 to 23.6 Mya (Baker & Couvreur, 2013*b*). This tribe possesses relatively small and for frugivores attractive drupes (Baker & Couvreur, 2013*b*).

The most detailed information on timing of evolution of fleshy fruits within a single family is from the Solanaceae (Knapp, 2002; Särkinen *et al.*, 2013). This family comprises around 10000 species, of which about 2000 species belong to the cosmopolitan genus *Solanum*. Capsular fruits are the ancestral condition in the Solanaceae, and berries have originated in three separate lineages. The major lineage with berries, including *Solanum*, branched off from its sister branch (including *Nicotiana*) 26 to 23 Mya, and initiated a rapid diversification 18 to 13 Mya. The other two lineages with berries are likely to be of a more recent origin.

These examples, although far from exhaustive, suffice to conclude that in many angiosperm lineages fleshy fruits evolved much later than the expansion phase from the late Cretaceous to the peak in the early Eocene. A focus solely on the putative frugivores in the late Cretaceous

and early Tertiary, as is the case for most treatments of the evolution of angiosperm–frugivore interactions (e.g. Tiffney, 1984; Wing & Tiffney, 1987b; Sussman, 1991; Eriksson et al., 2000a; Fleming & Kress, 2011; Sussman et al., 2013), is thus incomplete. It may be necessary to distinguish between the evolutionary interactions occurring during the 'origination and expansion' phase of fleshy fruits, i.e. when dry dehiscent fruits in many lineages first started to evolve into fleshy indehiscent fruits, and the evolutionary interactions occurring when the fleshy fruits were already in place, providing a niche zone for frugivores to exploit.

VII. DISCUSSION

(1) Synthesis of evidence of timing

The evidence reviewed on fleshy fruits and frugivorous birds and mammals is summarized in Figs 1 and 2. Several of the modern frugivores, particularly birds and bats, can be excluded as part of any potential coevolutionary interaction with plants during the first phase of angiosperm seed size, fruit size and fruit type diversification from approximately 80 Mya, and continuing until it reached a 'peak' in the early Eocene. Although some bird orders which today include frugivores, e.g. Caprimulgiformes (including oilbirds), Coliiformes (including mousebirds) and Psittaciformes (parrots) were probably present from the Eocene, the only direct inference suggesting bird frugivory in the Eocene concerns trogons (Trogoniformes) (Kristoffersen, 2001). Passerines, which today comprise the bulk of frugivorous bird species, did not become potential agents in interactions with angiosperm seeds and fruits until the Oligocene, or perhaps even the Miocene (at least in the northern hemisphere). Also the other group of flying frugivores, bats, can be excluded as agents of interactions with angiosperms during this first phase. Although radiating in the early Tertiary, bats were initially insectivorous. Frugivorous lineages (Phyllostomidae, Pteropodidae) evolved later, in the late Oligocene–Miocene.

Evidence on timing suggests a somewhat more complex picture for the two other dominant groups of present-day mammals involved in disperser interactions with plants with fleshy fruits, primates and rodents. Plesiadapiforms existed during the Palaeocene, and are thus very likely candidates as causal agents influencing angiosperms during this period. Euprimates, which radiated in the Early Eocene, may also have become important interacting agents close to the peak of seed size and fruit size diversification. Rodents radiated in the Eocene, and although large nuts apparently did not become abundant before the late Eocene (Collinson & Hooker, 2000), it cannot be excluded that rodents were influential agents in interactions with angiosperm seeds and fruits close to the seed and fruit size peak in the Eocene. However, both primates and rodents can be excluded as interacting agents already from 80 Mya. Furthermore, the suggestion by Fleming & Kress (2011) that bird frugivory laid the basis for evolution of frugivory in primates because birds dominate

(quantitatively) the frugivore fauna today, is obviously not in accordance with the evidence presented here.

The strongest candidates as major agents of interactions with angiosperm seeds and fruits during the period from 80 Mya until the peak in the early Eocene are the multituberculates. This group of mammals which went extinct in the late Eocene has been considered ecological 'analogues' to rodents and has been suggested as putative seed dispersers during the Cretaceous (e.g. Wing & Tiffney, 1987b; Collinson & Hooker, 1991), but not based on much evidence. Recent studies highlight their potential importance in the context of angiosperm evolution. Multituberculates experienced a radiation during the last 20 million years of the Cretaceous (Wilson et al., 2012), i.e. coinciding with the initiation of the increase in seed size and fraction of fleshy fruits. Other frugivorous mammal groups may have been present at this time, e.g. marsupials, but multituberculates stand out as the prime candidate for early angiosperm–seed disperser interaction, potentially influencing seed and fruit diversity.

The global environment changed drastically at the end of the Eocene. According to Prothero (1994), the Eocene–Oligocene transition was the most significant period of change in the Earth's history since the K–Pg mass extinction. In several pulses, the Earth became much cooler, followed by marked changes in the diversity of organisms. In the northern hemisphere, tropical and subtropical forests were replaced by temperate deciduous forests, in both North America (Graham, 1999) and Europe (Mai, 1989). The forest cover in general disintegrated (Knobloch et al., 1993), thus implying that the landscape became more open, with patchy woodland, and with a larger element of smaller trees, shrubs and herbaceous vegetation (Graham, 1999). Over time, the cooling of the Earth gave way to the development of grassland biomes, which expanded during the early Miocene around 18–20 Mya in North America (Janis, Damuth & Theodor, 2002) and in Eurasia (Strömberg, 2011). The distribution of rainforest retracted, and rainforests remained only at low latitudes (Morley, 2011). The climate and vegetation changes resulted in a major transformation of the faunas, where many lineages of forest-dwelling 'archaic' mammals adapted to browsing, and mammals adapted to an arboreal life (e.g. many arboreal primates) went extinct (e.g. Collinson & Hooker, 1991; Prothero, 1994). The majority of these disappearing early euprimates were frugivores (Strait, 2001).

When viewing these drastic changes in climate, vegetation structure, and composition of faunas in the context of angiosperm–frugivore interactions, three features stand out as particularly important: (i) major groups of frugivores among arboreal mammals, the multituberculates, and many lineages of primates went extinct, opening niche space for arboreal frugivory by other groups of animals. (ii) All major morphological forms of fleshy fruits were present. Thus, the frugivore feeding niche space was available for new animal groups to exploit. (iii) The conditions for frugivory and seed dispersal may have been altered when the vegetation composition and structure became more open or semi-open.

A striking feature of timing of evolution of the major groups of extant frugivores is that flying frugivores, i.e. bats (Pteropodidae; Old World fruit bats, and lineages of Phyllostomidae; New World fruit bats), as well as the major group of extant frugivorous birds, the passerines, appeared during this second phase of plant–frugivore interactions, mainly after the Eocene–Oligocene cooling. Thus, these groups of frugivores exploited an existing feeding niche, previously occupied by now extinct frugivores (arboreal mammals), and they exploited a food resource that, at least outside the tropical rainforests, was likely to be more patchily distributed. Being able to fly would be an obvious advantage particularly in landscapes where the food resources were more scattered spatially (Fleming & Kress, 2011). Moreover, plants living in patchily distributed habitats were more likely to benefit from seed dispersal beyond the immediate surroundings of the mother plant.

Thus, a speculative suggestion is that the drastic changes initiated during the late Eocene and Oligocene paved the way to the evolution of flying frugivores, bats and birds. Concerning birds, it has been proposed that small non-passerine birds before the Oligocene utilized similar niches as those later filled by modern passerines (Harrison, 1979; Mayr, 2005). There is unfortunately not much evidence available to examine this suggestion. Although exploiting the fruit-eating feeding niche was important, the success of passerines was not only related to frugivory. For example, passerines include several radiations of granivorous birds that are among the most successful within the entire class of birds (Ericson *et al.*, 2003), and passerines may have benefitted from their cognitive abilities, useful for example in food hoarding (Jönsson *et al.*, 2011). Passerines are exceptionally common and widespread among frugivores throughout the world, and they are the most species-rich order of frugivores today. It may thus be possible to consider an Oligocene–Miocene 'passerine take-over' of a feeding niche based on fleshy fruits. Although this food source initially evolved through interactions with other, now extinct, mammal frugivores, birds managed to exploit an existing feeding niche under conditions where food resources due to climate change became more widespread and scattered, and when the earlier occupants of this niche were largely gone. Only fruit-bats challenged the birds in this 'flying frugivore niche'.

(2) Implications for plant–frugivore coevolution

There is a general understanding that today most interactions between fleshy-fruited plants and their frugivorous seed dispersers are weak and 'diffuse'. This idea emerged as a critique of early interpretations of relationships between plants and frugivores where these were seen as similar to coevolutionary interactions between plants and pollinators (e.g. van der Pijl, 1972). Advocated by Wheelwright & Orians (1982) and Herrera (1985), and supported by several studies (e.g. Herrera, 1987, 1998; Jordano, 1995*a*,*b*; Jordano *et al.*, 2007), the picture emerged that plants are generally weakly, if at all, influenced by the identity of frugivores, or by where and when animal fruit-eating occurs, and that fruit-trait variation

has minor impacts on plant fitness. There is a correspondingly weak relation when the interactions are viewed from the animal's side. Most frugivores consume numerous different fruits, and their dependence on particular species, or fruit traits, is negligible (e.g. Jordano, 2000; Herrera, 2002). Plant–frugivore interactions act 'group-wise'; many species of frugivores interact simultaneously with many plant species with fleshy fruits.

With the exception of large nuts dispersed by scatter-hoarding birds and rodents (Vander Wall & Beck, 2012), hypothesized 'dispersal syndromes', i.e. complexes of fruit traits that converge into clusters with different trait clusters for plants interacting with different groups of frugivores, are only weakly supported (Gautier-Hion *et al.*, 1985; Fischer & Chapman, 1993; Herrera, 2002). There is a strong phylogenetic signal in fruit-trait variation, i.e. much of the variation in fruit traits occurs between different plant lineages (Jordano, 1995*a*). When the phylogenetic effect is removed, the main remaining effect is a trend that larger frugivores tend to feed on larger fruits (e.g. Janson, 1983; Jordano, 1995*a*; Dew & Wright, 1998; Pizo, 2002; Lomáscolo, Speranza & Kimball, 2008; Flörchinger *et al.*, 2010). Furthermore, the largest fleshy fruits occur in the Old World tropics where frugivores are on average larger than in the New World tropics (Mack, 1993; Lomáscolo *et al.*, 2008). Fruits consumed by birds have been found relatively more integrated in trait space than fruits consumed by mammals, possibly a result of the fact that birds have generally better vision than mammals, enabling them to exert stronger selection on visual cues (Valido, Schaefer & Jordano, 2011). Mammal-dispersed fruits have been found to be generally 'dull-coloured' (Dew & Wright, 1998; Dominy, Svenning & Li, 2003), in contrast to bird-dispersed fruits which are often brightly coloured (e.g. Poulsen *et al.*, 2002; Lomáscolo *et al.*, 2008).

Even though transformation of fruits, for example from capsules to berries, and from berries to drupes is likely to be ontogenetically 'easy' (as reviewed in Section VI), it seems reasonable that transformation of fruit structure, related to dehiscence, seed size and number, occurrence of a hard endocarp, and 'fleshiness', would necessitate a consistent directional selection. Animals would also have been subjected to consistent directional selection to evolve into specialized frugivores. Suggested adaptations for fruit-eating, for example dentition in Cretaceous mammals (Wilson *et al.*, 2012), trichromatic vision in primates (Dominy *et al.*, 2003), social behaviour in primates (Müller & Soligo, 2005), and various form of bill shapes, e.g. in toucans (Patané *et al.*, 2009), all indicate strong directional selection. Under what conditions could group-wise coevolution lead to such directional selection during the formative periods when these traits evolved?

Theoretical studies of complex species-rich mutualistic networks suggest that such networks may provide a basis for strong selection of coevolving traits (Guimarães, Jordano & Thompson, 2011; Nuismer, Jordano & Bascompte, 2012). Loss of species in complex mutualistic networks may alter the selection gradients, resulting in rapid changes in trait distribution. For example, a study by Galetti *et al.* (2013)

found seed size reduction in a palm species following local extinction of large toucans, suggesting that fruit traits may be directly and rapidly responding to changes in frugivory. Could it be that the weak and diffuse interactions, so often found in field studies, may have been misinterpreted as evidence that reciprocal selective influence between fleshy-fruited plants and frugivores is always weak?

A suggestion is that periods associated with significant changes in environmental conditions, for example in vegetation structure or in the identity of the interacting frugivore groups, induce strong and formative coevolutionary plant–frugivore interactions. These changes result in altered mutualistic networks, in turn initiating directional and reciprocal selection on fruit and frugivore traits. Periods of strong interactions resulting in diversification may also occur when unoccupied ecological niche space becomes available. Sims (2012) proposed that this is a general explanation for the diversification in seed size in seed plants; both the earliest diversification that occurred in 'gymnosperms', from the Devonian to the Late Carboniferous (Pennsylvanian), and for the angiosperms later during the Cretaceous and the Palaeogene.

These mechanisms would imply that angiosperm–frugivore coevolution occurs in pulses, interspersed by periods where weak and diffuse interactions dominate, corresponding to a macroevolutionary manifestation of the mosaic theory of coevolution (Thompson, 1994, 2005). Figure 3 provides a conceptual summary of this suggestion. Althoff, Segraves & Johnson (2014) suggested that use of new environments, for example niche expansion mediated by coevolutionary interactions (Joy, 2013) may initiate a cascade of processes ultimately resulting in diversification of lineages of the interacting partners. Over time, as the new niche zone becomes occupied, the resulting networks of interacting plants and frugivores stabilize and the interactions become weaker. Although plant–frugivore networks have been found to vary in stability, they are nevertheless relatively stable (e.g. Schleuning et al., 2011; Menke, Böhning-Gaese
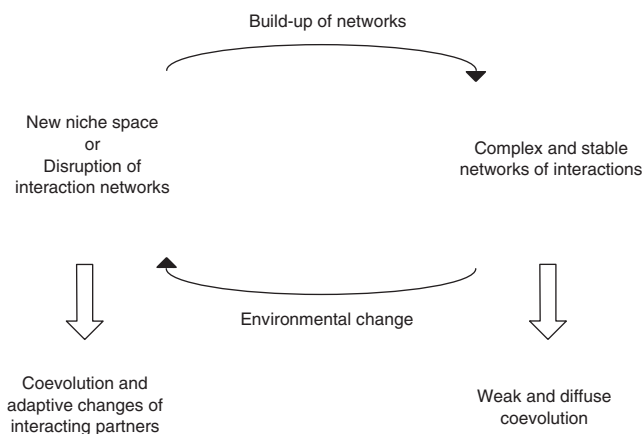

Fig. 3. A conceptual model of shifts between periods of coevolution leading to reciprocal adaptive changes in fruits and frugivores, and periods of weak and diffuse coevolution.

& Schleuning, 2012; Plein et al., 2013), suggesting that only substantial changes in the network (e.g. Galetti et al., 2013), or environmental changes affecting the structure of vegetation, may spur a new period of coevolutionary interactions strong enough to alter trait distributions. The ubiquity of different lineages of fleshy fruits with various morphologies suggesting convergent evolution, as for example in Rubiaceae (Bremer & Eriksson, 1992; Kainulainen et al., 2010), Melastomataceae (Clausing et al., 2000), Solanaceae (Knapp, 2002), Apocynaceae (Simões et al., 2007) and Rosaceae (Potter et al., 2007), indicate that such localized pulses of coevolution may in fact have been common.

What evidence is there for an association of general environmental changes, and periods of diversification among fleshy-fruited angiosperms and their frugivores? Answering this question necessitates a lot of speculation, as there is not much evidence available. Overall, the diversification period from the late Cretaceous to the early Eocene, for angiosperm seeds and fruits, multituberculates, and, in the latter part of the period, primates, occurred along with an expansion of tropical rainforests (Morley, 2011). Changing vegetation structure may thus be one environmental driver. Further support for this explanation comes from Bolmgren & Eriksson (2005) who found a significant association between the evolution of fleshy fruits in different angiosperm lineages and vegetation change towards forest vegetation. But this evidence only concerned plants, as no simultaneous radiations of frugivores were assessed. Moreover, there is a striking similarity between the angiosperm seed and fruit diversification during the late Cretaceous and early Palaeo-gene, and the diversification of seed size in non-flowering seed plants in the Pennsylvanian, a diversification which also took place during a period of rapid vegetation change (Willis & McElwain, 2002; Tiffney, 2004; Sims, 2012).

During the early Miocene (23 to 16 Mya), the global climate again became warmer, resulting in a second phase of tropical rainforest expansion (Morley, 2011). In South America this period coincided with radiations of New World fruit bats (Hoffmann et al., 2008; Velazco & Patterson, 2013), New World monkeys (Opazo et al., 2006), caviomorph rodents (Opazo, 2005), and several lineages of frugivorous birds (Hoorn et al., 2010), e.g. toucans (Patané et al., 2009) and parakeets (Ribas, Miyaki & Cracraft, 2009). Some evidence also comes from Africa, where vegetation change during the Pliocene promoting distribution of forests versus open vegetation was associated with rapid radiation of forest robins (Voelker, Outlaw & Bowie, 2010).

In particular, the radiations of fruit bats are suggestive of coevolutionary interactions with fleshy-fruited plants. Seed dispersal by phyllostomid bats is linked to the recruitment niche of early successional plants in several angiosperm families, e.g. Solanaceae, Piperaceae and Moraceae (Muscarella & Fleming, 2007). One genus of phyllostomid bats, Sturnira, experienced a pronounced diversification in the Miocene (from 15.9 to 12.6 Mya) (Velazco & Patterson, 2013). These bats rely much on Solanum, and according to Velazco & Patterson (2013) radiation of Solanum in South
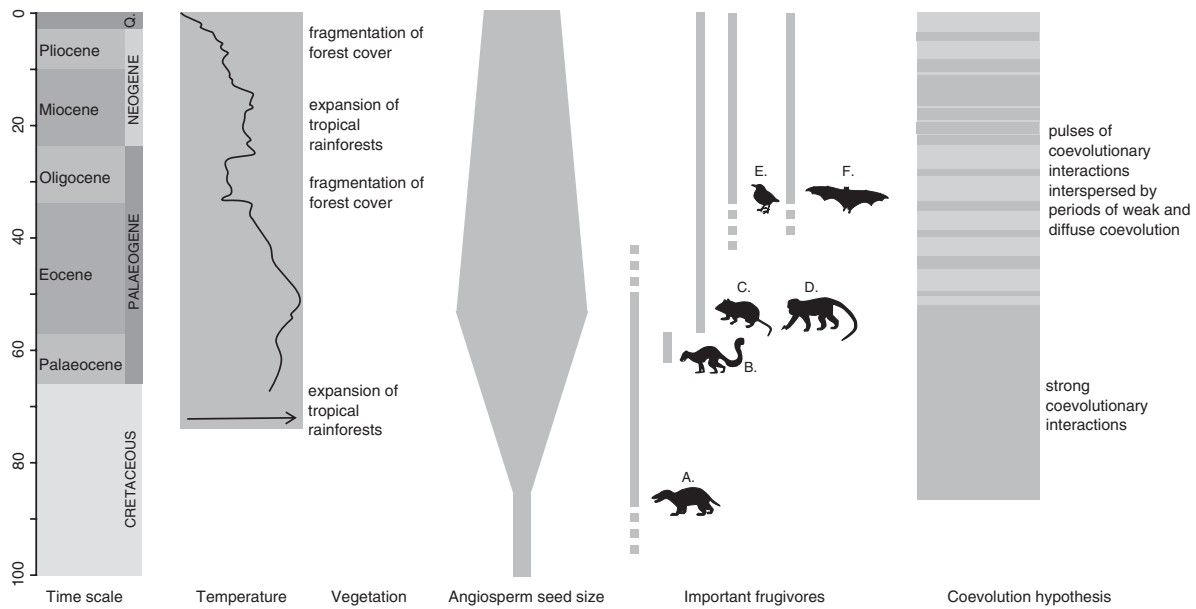
Fig. 4. An overview of the origin and evolution of coevolutionary interactions between angiosperms with fleshy fruits and their frugivorous seed dispersers, in relation to major changes in global temperature and vegetation. The temperature curve is adapted from Zachos *et al.* (2001). A, multituberculates; B, plesiadapiforms; C, rodents; D, primates; E, birds; F, bats.

America has depended on and been spatially congruent with the diversification of these bats. Their suggestion is supported by phylogenetic studies indicating that diversification of *Solanum* commenced 18 to 13 Mya (Särkinen *et al.*, 2013). *Solanum* berries vary in size (1–15 cm) and colour, black, red, orange, yellow and green; bats prefer yellowish berries (Knapp, 2002), and most likely the berries in the lower range of the size variation (due to the bat's own small body size).

Unfortunately, there are very few studies enabling comparisons such as that between *Sturnira* and *Solanum*, but such studies should be possible to perform as more detailed phylogenies of radiations of frugivores and fleshy-fruited plants become available (Althoff *et al.*, 2014). If pulses of coevolution between angiosperms and frugivores have driven the evolution of this interaction, it seems reasonable that the first phase during the period about 80 to 50 Mya witnessed particularly strong coevolutionary interactions. The trait space of seed and fruit traits changed drastically from relative stasis between 130 and 80 Mya, to an 'explosion' of seed and fruit traits, culminating in the early Eocene. From that time until the present, pulses of formative coevolution between angiosperms and frugivores may have been more localized, both in time and space, as the example on phyllostomid bats and *Solanum* suggests. Figure 4 illustrates this suggestion, and summarizes the major patterns of changing climate, vegetation and seed size, and major groups of frugivores, from the late Cretaceous to the present.

It might be that we are witnessing an ongoing formative coevolutionary process, and this relates to the megafauna which largely went extinct after the last glaciation, probably due to a combination of hunting by humans and climate change (Koch & Barnosky, 2006). Janzen & Martin (1982) advocated the idea that many fleshy fruits were adapted to dispersal by megafauna, and that such dispersal syndromes would be anachronisms in those parts of the world where megafauna no longer exists. This idea has been followed up recently by several authors (e.g. Donatti *et al.*, 2007; Guimarães *et al.*, 2008; Hansen & Galetti, 2009; Johnson, 2009) providing indirect support for the hypothesis of 'megafauna fruits'. These fruits are characterized by an 'overbuilt design' with large fruit mass, but with either few very large or many small seeds (Guimarães *et al.*, 2008). The megafauna had no counterpart during the early periods of fruit and seed size diversification, when mammals were generally small. Dinosaurs might have had a similar ecological role as megafauna during the Cretaceous, but this is not supported by the fact that angiosperm fruits and seeds remained small during more than 50 million years until the diversification began around 80 Mya. Thus, interactions with megafauna are likely to be evolutionarily rather recent. Still, the drastic change during the last 10–12 millennia in size structure of animals which included fruits in their diet might have induced not only decline and possibly extinctions of plants that depended on megafauna for seed dispersal, but also selection for smaller fruits and seeds. Fruit-eating is constrained by the dimensions of mouthparts, and in a recent study, Galetti *et al.* (2013) showed that the distribution of seed size in a palm species was strongly influenced by the size distribution of the frugivores present. Their study concerned large frugivorous birds, toucans, and they estimated that phenotypic selection after loss of the largest frugivores over about 100 years could be responsible for an about 30% reduction in seed mass. Even though these results reflect a tragic loss of biodiversity, the strongly transformed nature of the world may provide us with excellent opportunities to examine the potential for strong directional selection in

coevolutionary interactions between frugivores and plants with fleshy fruits.

VIII. CONCLUSIONS

(1) This review summarizes evidence on the timing of origin and diversification of fleshy-fruited angiosperms and their frugivores, and discusses the implications of this evidence for an understanding of plant–frugivore coevolution. Synthesizing evidence from major frugivore groups, combined with evidence from morphological and phylogenetic studies of several angiosperm families results in a partly new view of angiosperm–frugivore coevolutionary interactions.

(2) A drastic diversification of angiosperm seed size and fleshy fruits commenced around 80 Mya. The diversity of seed sizes, fruit sizes and fruit types peaked in the early Eocene around 55 to 50 Mya. During this phase of the interaction, angiosperms and animals evolving frugivory expanded into niche space not previously utilized by these groups, as frugivores and previously not existing fruit traits appeared. From the early Eocene until the present, angiosperm–frugivore interactions have occurred within a broad frame of existing niche space, as defined by fruit traits and frugivory. This indicates a separation of the angiosperm–frugivore interaction into two major phases, before and after the peak in the early Eocene.

(3) The timing of the origin and diversification of major frugivore groups suggests that now-extinct mammal groups, mainly the multituberculates, were the most important frugivores during the early radiation phase of angiosperm seeds and fleshy fruits. Primates and rodents are likely to have been important in the latter part of this first phase.

(4) Flying frugivores (birds and bats) evolved during the second phase, thus exploiting an existing diversity of fleshy fruits. The same holds for most extant primate lineages, since many of the arboreal primate groups during the Eocene went extinct around the Eocene–Oligocene boundary (around 34 Mya).

(5) The drastic climate shift around the Eocene–Oligocene boundary promoted more semi-open woodland vegetation, creating more patchily occurring food resources for frugivores. This may have promoted evolution of a 'flying frugivore niche' exploited by birds and bats. In particular, passerines became a dominant frugivore group worldwide.

(6) Fleshy fruits have evolved at numerous occasions in many angiosperm families, and many of the originations and diversifications of fleshy fruits occurred well after the peak in the early Eocene. Although evidence is scarce, it is suggested that evolution of fleshy fruit was particularly common during the Miocene.

(7) During localized periods in space and time, associated with altered interaction networks and opening of new niche space, reciprocal coevolution may result in strong directional selection formative for both fruit and frugivore features. Further evidence is needed to test this hypothesis. Based on the abundance of plant lineages with various forms of fleshy fruits, and the diversity of frugivores, it is suggested that such periods of rapid coevolution in angiosperms and frugivores have occurred numerous times during the 80 million years of angiosperm–frugivore evolution. One such formative period may be taking place today as a result of the loss of megafauna.

IX. ACKNOWLEDGEMENTS

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