Early diversifications of angiosperms and their insect pollinators: Were they unlinked?

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Glossary

ANA grade: the angiosperm lineages *Amborella*, Nymphaeales, and Austrobaileyales, which form successive sister taxa to a group comprising all other angiosperms.

Acrogymnosperms: monophyletic group that includes all living gymnosperm taxa, i.e., *Ginkgo*, Cycadophyta, Gnetophyta, Pinaceae, and Cupressophyta. The acrogymnosperms comprise approximately 1,100 living species, most of which are pollinated by wind.

Anemophilous: describing plants whose pollen is transported by wind.

Codiversification: the simultaneous evolutionary diversification of two lineages. This might be due to direct interaction between the lineages, an external factor influencing both, or by coincidence.

Cospeciation: the simultaneous speciation of two lineages because of direct interaction between them, possibly as a consequence of coevolution.

Coevolution: where evolutionary changes in one species occur in response to changes in another species.

Crown age: the age of the most recent common ancestor of the living members of a clade.

Crown angiosperms: the monophyletic group that includes the most recent common ancestor of living angiosperms and all of its descendants. Present-day members of crown angiosperms are the ANA grade, magnoliids, monocots, eudicots, and the less speciose *Ceratophyllum* and Chloranthaceae. The crown angiosperms are the most diverse extant clade of land plants.

Cretaceous Terrestrial Revolution: the rapid codiversification of angiosperms and their insect pollinators, proposed to have occurred during the Cretaceous.

Gymnosperms: the paraphyletic group of all seed plants other than angiosperms, including both living (acrogymnosperms) and extinct lineages, such as Peltaspermales and Bennettitales.

K–Pg (Cretaceous-Paleogene) extinction: a mass extinction event that occurred 66 Ma, caused by the Chicxulub asteroid impact in the Yucatán Peninsula of Mexico. This mass extinction event was responsible for the extinction of non-avian dinosaurs.

Long-proboscis: an elongated, tubular mouthpart frequently used to siphon nectar or other plant secretions by insects. This mouthpart is a common feature amongst extant pollinators that visit pollinators, such as butterflies, moths, flies, and bees.

Phytophagous: describing animals, mostly insects, that feed on plants.

Pollinivory: the consumption of pollen by animals, mostly insects.

Seed plants: also referred to as Spermatophyta, the group of seed plants. This clade includes gymnosperms and angiosperms.

Abstract

The present-day ubiquity of angiosperm-insect pollination has led to the hypothesis that these two groups coevolved early in their evolutionary history. However, recent fossil discoveries and fossil-calibrated molecular dating analyses challenge the notion that early diversifications of angiosperms and insects were inextricably linked. In this article we examine *(i)* the discrepancies between dates of emergence for major clades of angiosperm and insect lineages; *(ii)* the long history of gymnosperm–insect pollination modes, which likely shaped early angiosperm–insect pollination mutualisms; and (*iii*) how the K–Pg mass extinction event was vital in propelling modern angiosperm-insect mutualisms. We posit that the early diversifications of angiosperms and their insect pollinators were largely decoupled, until the end of the Cretaceous.

Keywords

angiosperms, codiversification, Cretaceous–Paleogene mass extinction, gymnosperms, insects, pollination

Angiosperm–insect pollination: a classic case of coevolution?

Insects pollinate an estimated 70% of species of flowering plants (angiosperms) [1]. This relationship is significant ecologically, with the angiosperms and their insect pollinators dominating terrestrial ecosystems [2–4]. Both groups are extremely biodiverse; for instance, the angiosperms are the most species-rich group of land plants, comprising at least 295,000 known species [5]. Similarly, the chief pollinator orders of insects, namely the Coleoptera (beetles), Lepidoptera (butterflies and moths), Hymenoptera (bees and wasps), and Diptera (flies), are the most speciose [2,4].

The extraordinary species diversity of the angiosperms and their insect pollinators is often attributed to their mutualistic interaction [3,6]. Ultimately, angiosperm diversification clearly had a major impact on insect pollinator diversification. However, to accurately assess whether **coevolution** (see Glossary) drove the early radiations of these two groups, the dates of the emergence and diversification of angiosperms and their insect pollinators must be established. A close correspondence between the ages of the **crown angiosperm** and insect lineages would suggest that **cospeciation** was responsible for the simultaneous emergence and rapid diversification of both groups. However, matching **crown ages** are a necessary, but not a sufficient, condition for cospeciation. It must then be shown that the earliest interactions between insects and angiosperms generated morphological and species diversity in both groups.

In this article, we argue that the early diversifications of angiosperms and their insect pollinators were decoupled. To support our argument, we first examine the evidence for matching dates of origination for crown angiosperms and key insect pollinator lineages, including the orders Hymenoptera (bees and wasps), Lepidoptera (butterflies and moths), Coleoptera (beetles), Thysanoptera (thrips), and Diptera (flies). We then explain how the evidence for coevolution must be assessed by considering how **gymnosperm**-insect interactions in the Paleozoic and Mesozoic acted as a ‘primer’ for angiosperm pollination modes. Finally, we discuss the importance of the **K–Pg extinction event** in the context of angiosperm and insect cospeciation.

Dates of emergence and diversification

Matching ages of angiosperms and insect pollinators, inferred from fossil-calibrated molecular phylogenetics, are often used to defend a narrative of rapid cospeciation occurring during or prior to the Cretaceous period. Here we critically examine fossil-calibrated molecular date estimates for crown angiosperms and key insect pollinator groups.

Age of angiosperms

The age of crown angiosperms has not been resolved with confidence, despite the ecological prominence of the group [7]. The first undisputed crown angiosperm fossils appear ~125 Ma, at the Barremian-Aptian boundary [9]. Although no unambiguous fossil evidence of pre-Cretaceous angiosperms exists [9,10], the vast majority of recent fossil-calibrated molecular dating studies have inferred that crown angiosperms originated in the Jurassic, Triassic, or even earlier [11–13] (Figure 1). Despite this lack of consensus, comparisons between recent estimates for the ages of crown angiosperms and major insect pollinators can still be made (Figure 1).

Ages of major insect pollinators

Hymenoptera include the iconic pollinating insects, Anthophila (bees), and certain wasp lineages that have highly specialized interactions with angiosperms [6,14]. For example, all 20,000 bee species rely on floral products, from the larval to the reproductive stages [6]. Similarly, fig wasps engage in an exclusive, obligate pollination mutualism with *Ficus* [15]. Crown Hymenoptera is inferred to have emerged close to the Paleozoic–Mesozoic boundary, with recent estimates between ~330 and 240 Ma [16–19]. This considerably predates most estimates for the timing of the initial diversification of angiosperms. Molecular studies infer that bees emerged during the Early Cretaceous (145–100 Ma), with most estimates falling around ~125–100 Ma [14,16,19–21]. These molecular estimates post-date the age of angiosperms by at least 20 million years, but they must also be viewed cautiously, given that the first crown bee only appeared in the fossil record much later, ~65 Ma [22].

Crown Lepidoptera appeared in the Permian, between ~300 and 270 Ma [17,18,23]. These recent fossil-calibrated molecular studies, as well as the discovery of unambiguous lepidopteran wing scales from the latest Triassic [24], contradict the young Jurassic age that

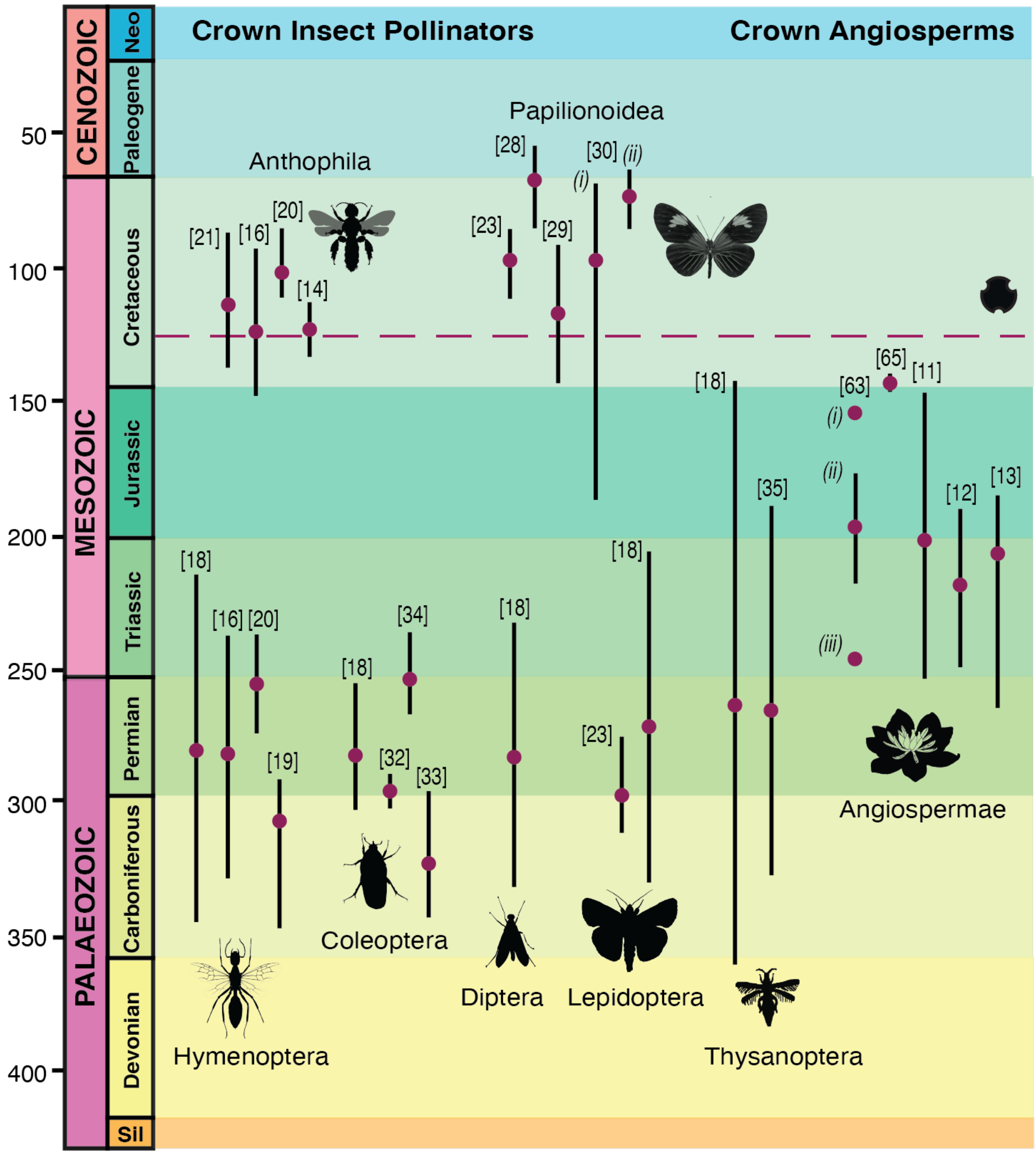

Figure 1. Timescale of the major appearances of crown angiosperms and insect pollinator clades. This figure depicts the results of recently published studies that used fossil-calibrated molecular dating techniques to estimate the timing of the emergence of the crown angiosperms and insect pollinators. The dashed line at ~125 Ma represents the appearance of the first undisputed angiosperms in the fossil record (e.g., eudicot tricoplate pollen). Two age estimates from Condamine *et al.* [30] are included, *(i)* without partitioned clocks and *(ii)* with partitioning. Similarly, three age estimates from Ramirez-Barahona *et al.* [63] are described, using *(i)* constrained, *(ii)* relaxed, and *(iii)* unconstrained calibrations. Silhouettes are either in the public domain or CC BY 3.0 (https://creativecommons.org/licenses/by/3.0/) – Anthophila and Hymenoptera (Melissa A. Broussard), Coleoptera (Camilo Julián-Caballero), and Thysanoptera (Joseph Hughes) available at http://www.phylopic.org. The angiosperm silhouette was adapted with permission from Benton *et al.* [54].

was previously estimated for the Lepidoptera [25]. Within the Lepidoptera are the Papilionoidea (superfamily of butterflies), which are highly effective **long-proboscis** pollinators [26]. The Papilionoidea emerged around the Late Cretaceous, most likely between ~110 and 90 Ma [23,27–30]. A Late Cretaceous age is also in line with the fossil record, given that the first crown butterfly fossil dates to the Eocene ~55.6 Ma [31].

The Coleoptera is the most speciose insect order, comprising over 380,000 known species. The crown group likely emerged between ~340 and 250 Ma, during the Permian [18,25,32–34], potentially tens of millions of years prior to the diversification of angiosperms. The Thysanoptera, with their unique punch-and-suck feeding mechanism, are estimated to have emerged in the late Permian ~266 Ma [17,18,35]. Diptera are similarly inferred to have emerged between the late Carboniferous and the Early Triassic, with estimates centred on ~280 Ma [17,18]. These Paleozoic dates of emergence show that the early beetles, thrips, and flies had a large window of evolutionary time to adapt to their environment prior to the diversification of angiosperms.

Overall, even when accounting for the approximate 100-million-year age range for crown angiosperms, there is little overlap with the diversification dates of insect groups that are now essential pollinators (Figure 1). Insect pollinator orders emerged substantially earlier than crown angiosperms, suggesting that their early diversification was not reliant on the angiosperms. Instead, many of these insect lineages were likely interacting with gymnosperms, which dominated the terrestrial landscape of the Paleozoic and Mesozoic [4,36–39]. Furthermore, highly specialized pollinators such as the bees and butterflies only appeared during the Late Cretaceous–Paleogene. This indicates that the initial rise of angiosperms in the Early Cretaceous was a necessary but not sufficient condition for the emergence and diversification of their insect hosts.

Gymnosperm-insect interactions

The extant gymnosperms (**acrogymnosperms**) are represented by five depauperate lineages: the monotypic *Ginkgo*, Cycadophyta, Gnetophyta, Pinaceae, and Cupressophyta [40]. These extant gymnosperms are disproportionately pollinated by wind and water, except for cycads and gnetophytes. Despite the reduced diversity of gymnosperms today, the fossil record has captured highly specialized interactions from the Triassic to the mid-Cretaceous [37–39], between gymnospermous plants and their insect pollinators (Figure 2). These interactions showcase the widespread existence of gymnosperm–insect pollination modes before or at the same time as the emergence of angiosperms, somewhat diminishing the 'uniqueness' of present-day angiosperm–insect pollination mutualisms.

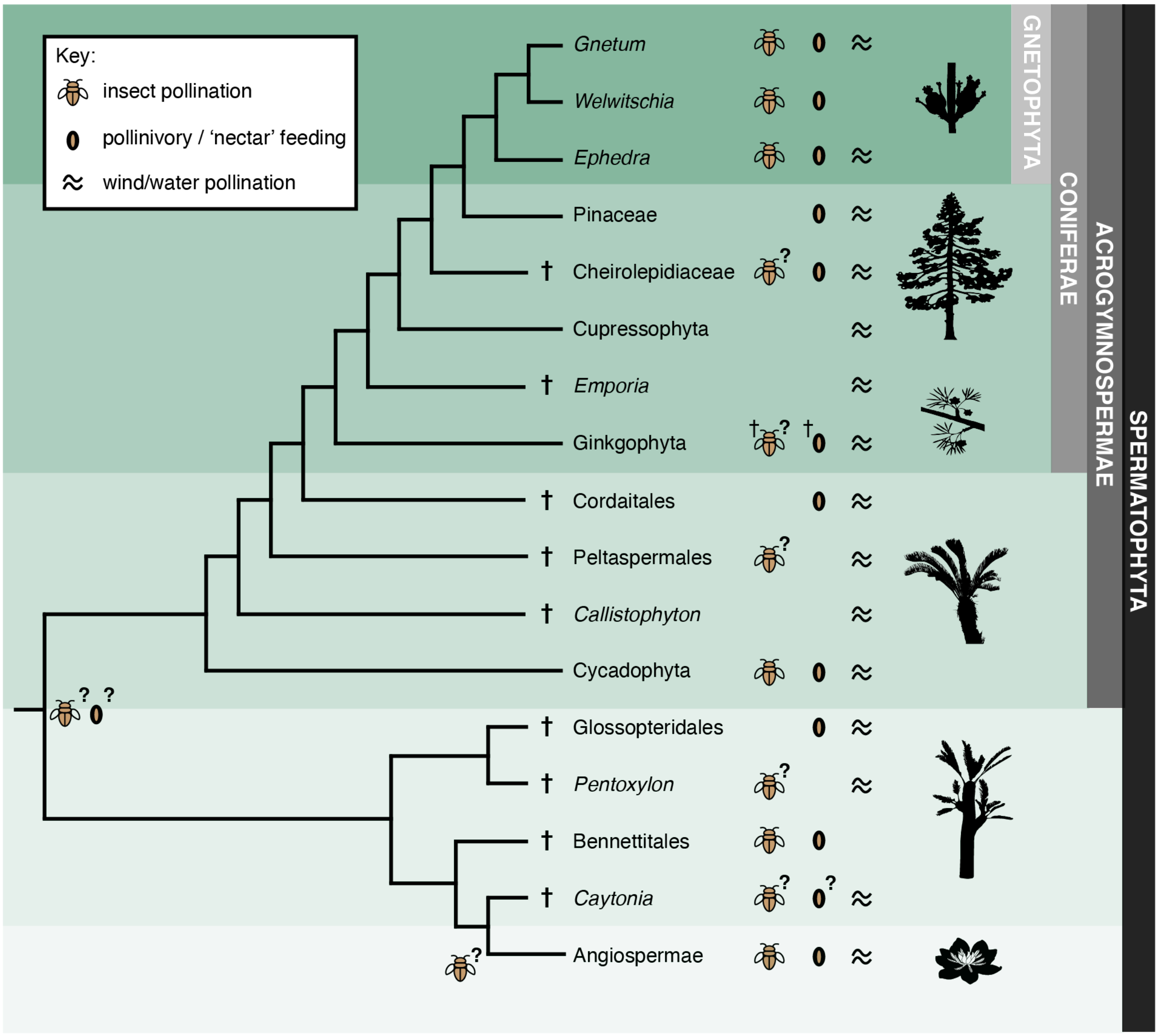

Figure 2. Phylogeny of seed plants, depicting pollination modes of both extinct and extant lineages. The phylogeny highlights the pollination mode of seed plants, focussing on extant and fossil gymnosperms (including angiosperm stem relatives). Phylogenetic relationships depicted here are based on Doyle [66] and Doyle [67]. '†' before a taxon name indicates that lineage is extinct. '†' before a pollination mode indicates that this is a historical pollination mode for a group, and is not found in extant species. Question marks indicate uncertain pollination modes, with some or limited support. The ancestral pollination modes of Spermatophyta and Angiospermae are also suggested. The pollination mode of extinct plants is based on plant reproductive biology, fossilized insects, and pollen size and ornamentation [37–39]. Silhouettes are either in the public domain, CC BY 3.0 (https://creativecommons.org/licenses/by/3.0/) – *Ginkgo* (Pollyanna von Knorring and T. Michael Keesey), or CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0/) – Gnetophyta (Curtis Clark and T. Michael Keesey) available at https://www.phylopic.org, and Bennettitales (Matteo De

Stefano/MUSE) available at https://commons.wikimedia.org/. The angiosperm silhouette was adapted with permission from Benton *et al.* [54].

For instance, gymnospermous *Cycadopites* pollen dated to the Early Cretaceous (113–100.5 Ma) exuded a sticky substance similar to angiosperm pollenkitt, which allows insects to transport large quantities of pollen by clumping the grains together [41,42]. Gymnosperm lineages that exhibited this pollenkitt-like feature are now extinct [42]. Furthermore, *Cycadopites* pollen was found in association with thrips (family Melanthripidae). These thrips featured ring setae that appear to be analogous to the hooked structures that bees use to optimize their collection of pollen [42]. They were also found carrying much more pollen than that collected by present-day thrips, which primarily visit angiosperms. Similarly, a boganiid beetle (99 Ma) was found with clumped *Cycadopites* pollen on its body and with mandibular mouthparts specially adapted for pollen transport [43]. The fossil record has also frequently documented the existence of insects using a long proboscis to access ‘pollination drops’ – comparable to angiosperm nectar in nutritional content – in Mesozoic gymnosperms [37,38] (Box 1).

Box 1. Long-proboscid pollination before the rise of angiosperms

Long-proboscid insects began interacting with gymnosperms long before the rise of angiosperms [38]. The first recorded gymnosperm long-proboscid insect interactions consisted of **pollinivory**, **phytophagy**, and possible insect pollination of now-extinct seed ferns in the Early Permian [4,37–39]. After the Paleozoic, long-proboscid insect pollination of gymnospermous plants is prevalent, with long-proboscid insects found with clumped gymnospermous pollen on their bodies [68]. Furthermore, long-proboscid insects were likely using their mouthpart to access pollination drops [37,38]. Pollination drops first appeared in gymnosperms as a way for Carboniferous seed ferns to capture pollen, and by the mid-Mesozoic were delivered by gymnospermous plants using sophisticated mechanisms, secreted deep within gymnosperm ovules with narrow openings, well-suited to the long-proboscis mouthpart [37,38]. Gymnospermous plants that had such ovules include extinct lineages such as *Williamsonia* (Bennettitales), Caytoniales, Pentoxylales, Czekanowskiales, and Cheirolepidiaceae [38]. Significantly, Cheirolepidiaceae belongs to the now mostly **anemophilous** conifers, highlighting the disparity between extinct and present-day gymnosperms [38,42] (also see Figure 2).

The long-proboscid mouthpart is thought to have originated at least 13 times independently in Mesozoic insects, including in Mecoptera (scorpionflies), Neuroptera (kaligrammatid lacewings), Diptera (flies), and Lepidoptera (butterflies and moths) (Figure I) [50,69]. The Mecoptera, Neuroptera, and Diptera include 67 recognized species from the fossil record that feature the long-proboscid mouthpart from the mid-Jurassic to the Late Cretaceous [38]. This evidence starkly contrasts with Darwin's conjectures addressed to de Saporta in 1877, which stated that the absence of long-proboscid insects in the Jurassic explains why the angiosperms were unable to diversify earlier than the Cretaceous [38,70]. Deep-throated flowers suited to long-proboscid pollination only emerged in the Late Cretaceous, from 93.9–89.8 Ma, at least 40 million years after the angiosperms had established diversity [38,39,61].

There is evidence from pollen found in association with body fossils of long-proboscid kaligrammatids and scorpionflies that these insects visited Ginkgophyta, Cycadophyta, and Bennettitales [37,38,69]. In stark contrast to the complex morphological adaptations of ancient scorpionflies and kaligrammatids, modern scorpionflies very rarely pollinate angiosperms [26,71], and kaligrammatids disappeared from the fossil record ~120 Ma [26]. It appears that their 'niche' was overtaken by extant butterflies and bees, which use their long proboscises to extract nectar from floral tubes, akin to scorpionflies and kaligrammatids, which likely used their long proboscises to extract pollination drops from within gymnosperm strobili (cones) [26,38,71]. The wings of kaligrammatids also bear striking convergences with butterflies, particularly the family Nymphalidae [26].

Figure I. A butterfly (*Euploea corinna*) using its long-proboscis to access nectar of an angiosperm flower (*Spermacoce* sp.). Image courtesy of Thomas Mesaglio.

Clearly, insects that visited gymnospermous plants had accrued morphological diversity before the initial Cretaceous diversification of angiosperms. Studies of the fossil record have shown there is a plateau of insect family richness throughout the Cretaceous [44–46]; instead, insects accumulated a large proportion of family-level diversity early on in their history, by the Permian, with diversity later peaking in the Early Cretaceous [45,46]. However, this Early Cretaceous peak was likely caused by the evolution of parasitic insects and potentially morphological adaptations associated with pollination of gymnosperms [46]. Similarly, fossil and molecular analyses have revealed that insect families did not experience an increase in diversification rates during the Cretaceous [47]. Overall, these studies show that the diversification of insects, at the family level, was limited throughout the Cretaceous. This opposes the idea of a **Cretaceous Terrestrial Revolution** where insects rapidly codiversified with angiosperms.

The lack of increased family-level diversity of the Cretaceous entomofauna is better understood in the context of mid-Cretaceous ‘turnover’. This refers to the transformation of insect communities caused by the replacement of gymnosperms by angiosperms as the increasingly dominant component of the landscape [39,47–50]. Lineages that were closely associated with insect-pollinated gymnosperms, such as Mesopsycidae (scorpionflies) or Zhangsolvidae (flies), went extinct [50]. At the same time, new families and superfamilies originated, such as bees, whereas other lineages likely ‘switched’ from gymnospermous to angiospermous hosts [50,51]. Amber inclusions from the mid-Cretaceous provide additional evidence that insects that are now dependent on floral hosts were once pollinating gymnospermous plants. This includes false blister beetles [50], as well as a short-winged flower beetle that was found in association with hundreds of gymnosperm and angiosperm (**ANA-grade**) pollen grains [51]. Thus, the turnover of insect communities in the mid-Cretaceous explains why insect taxonomic diversity plateaued during this period, since insect lineages that were reliant on gymnosperms went extinct. Furthermore, it is easier to understand the pollination mode of the first angiosperms as likely generalist rather than specialist, pollinated by small mandibulate beetles and thrips [51,52].

Overall, evidence is lacking for a simple burst of insect diversity with the advent of the angiosperms during the Cretaceous. Insects also clearly accrued morphological innovations due to their interaction with gymnosperms, which might have ‘primed’ them for angiosperm pollination (Figure 2). The fact that multiple gymnospermous lineages that were likely pollinated by insects, such as Bennettitales and *Caytonia*, went extinct by the end of the Cretaceous suggests that insect pollination itself did not facilitate rapid cospeciation events or spectacular diversifications of their hosts [38,39,53]. We posit that the role of biotic pollination in the early diversification of angiosperms has potentially been overplayed. Indeed, insect pollination might have been driving the diversification of the seed plants since the Paleozoic.

Furthermore, it is possible that while insect pollination might have driven the diversification of seed plants as a whole, angiosperms eventually outcompeted most insect-pollinated lineages of gymnosperms given their unique physiology and the changed environmental conditions of the Late Cretaceous–Paleogene [54,55]. The harsh climates now occupied by conifers, which form the largest proportion of acrogymnosperm diversity, might have driven the move towards wind pollination of extant gymnosperms. This is especially pertinent given that many extant groups of cycads and conifers emerged in the Cenozoic, and are not evolutionary remnants of their Mesozoic ancestors [49,56,57].

Post-Cretaceous revolution

The importance of Early Cretaceous angiosperms for generating insect diversity might also have been overstated. Instead, unique environmental conditions during the Late Cretaceous, and especially following the K–Pg extinction event 66 Ma, could have played a significant role in accelerating insect–angiosperm codiversification. It is evident from molecular studies and the fossil record that during the Late Cretaceous–Paleogene interval multiple lineages of pollinating insects, such as the weevils, bees, and butterflies diversified into families that have survived to the present day [27,34,58,59]. Rates of diversification of insect families also accelerated at 80 Ma, in the Late Cretaceous, and at the beginning of the Paleogene [47]. Specialized morphological adaptations for pollination also appeared in both floral hosts and insects around the same time period [60,61]. For example, whilst phytophagous scarabs emerged in the Early Cretaceous, flower-feeding lineages appeared much later, at the K–Pg boundary [59].

The late diversification of key pollinator groups indicates there was a delayed colonization on angiosperms [62]. This might be because pollinators required the complex niches and high nutrient resources proffered by the litterfall of angiosperm-dominated forests, which only appeared at the end of the Cretaceous [48,54,63]. Similarly, the origin of pollinivory in bees, a behaviour that is associated with pollination, is decoupled from the diversification of bees in the Cretaceous [53]. Plainly, the most prominent insect pollinators were not able to exploit their floral hosts until the end of the Cretaceous. The increased diversification of phytophagous and pollinating insects at the end of the Cretaceous also matches the timing of the diversification of angiosperm families. Angiosperm families diversified in two distinct periods, the first occurring in the mid-Cretaceous with the origin of the family (stem group), and a second period of diversification into extant lineages (crown group) beginning in the Late Cretaceous–Paleogene [63].

Critically, the present-day, closed-canopy rainforest was only able to form after the K–Pg extinction event, and angiosperms similarly became ecologically dominant at this time too [48]. These angiosperm-dominated rainforests today harbor megadiverse lineages of pollinating beetles [64]. The ashfall from the asteroid impact is likely to have enriched the soil, which was highly favorable to angiosperms since their growth is bolstered by added resources. Contrastingly, extant gymnosperms, such as conifers, fare best under low-resource conditions, and in cool, high-latitude climates [48,58]. Thus, there is clear support for a delayed cospeciation of insect pollinators and angiosperms, which was prompted by the K–Pg extinction event clearing the open-canopy forests of the Mesozoic. Major attributes of present-day terrestrial ecosystems, including angiosperm-insect pollinating mutualisms, only developed and became important in the early Cenozoic [54].

Concluding Remarks and Future Perspectives

In this article, we have shown that there is a gaping mismatch between the emergence and initial diversification of angiosperms and the origin and diversification of their key insect pollinators. Many pollinating orders emerged in the Paleozoic or early Mesozoic, potentially pre-dating the angiosperms by tens of millions of years. Moreover, there is considerable fossil evidence demonstrating that these insects already had mutualistic interactions with gymnosperms before angiosperms started to diversify. Evidently, biotic pollination played a significant role in the evolution of seed plants as a whole, which has been little appreciated. The pre-existing diversity of insects that developed in tandem with gymnosperms might have been a useful springboard by which more efficient adaptations arose with the diversification of angiosperms, which replaced gymnosperms as the dominant terrestrial vegetation by the end of the Cretaceous. It was only in the post K-Pg environment that the diversifications of angiosperms and of insects had explosive impacts on each other through their mutualistic interactions, including pollination. Future studies should focus on the role of insect pollination in seed plants overall, including the evolution of pollination mode in seed plants (see Outstanding Questions).

Outstanding Questions

- When did morphological synapomorphies (shared, derived characters found in members of a clade) of the crown angiosperms first appear? For instance, when did the closed carpel and double fertilization originate?
- What were the pollination modes of the most recent common ancestors of seed plants and of clades such as the acrogymnosperms?
- How has the pollination mode of present-day gymnosperms been shaped by their reduced diversity and occupation of harsh climates? Has climate driven the abiotic pollination of pines and cupressophytes?
- How much host switching occurred in the early evolutionary history of flowering plants and their insect pollinators?
- How were the diversification dynamics of insect-pollinating clades shaped by climatic and abiotic factors in the Cretaceous and Paleogene?

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