<u>Atmospheric Oxygen Level Controls on Insect Body size during the Late Paleozoic to Early Mesozoic Eras</u>

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Abstract

Alive today are a multitude of insect species spread across the reaches of the globe. In the history of life on Earth, there has never been a more diverse clade of organisms (Nel, 2015). During the Carboniferous and Permian periods, certain insect species grew much larger than modern counterparts. The cause of this insect gigantism, as it is referred to, was a high concentration of oxygen in the prehistoric atmosphere. Although the primary cause and effect of increased levels of oxygen on insects is debated, experiments on insects' anatomy demonstrate positive correlation to hyperoxic environments; for example, the wing sizes of flight insects have shown this positive correlation. Insect gigantism has not occurred in geologic history since the Carboniferous and Permian. However, insect taxonomy has been able to persist through time, with some species resembling those from the Carboniferous and Permian gigantism. Assessing how insects reacted to hyperoxic environments in the past can help scientists to evaluate the sensitivity insect classes have to a changing environment.

Introduction

In swamp environments of today, insects are ubiquitous. Modern insects are smaller than vertebrates. However, fossils found in the Carboniferous and Permian layers show that insects were at one time much larger than today, rivaling the size of some mammals. Although cinematography and some paleoart depict insects the size of buses, elephants, and trains, such large insects never existed on Earth. For example, Arthropleura was an extinct relative to modern-day millipedes that grew to six times the size of millipedes today, which is about 2 meters long. Insect gigantism during the Carboniferous and Permian periods was the only time that insects grew to such sizes. Smaller variations in insect size through time did occur, but insects remained smaller than vertebrates of their time. Multiple theories exist as to the cause of insect gigantism. One theory is that insects evolved into a specific niche that allowed them to grow to large sizes but were eventually displaced by vertebrates that filled that same ecological niche (Harrison, Kaiser, VandenBrooks, 2010). Another theory is that lower temperatures could have caused insect sizes to increase, as insect families tend to be larger in lower temperature environments (Harrison, et al., 2010). As the fossil record of insects is incomplete for the periods under study, theories for insect gigantism are controversial. One reoccurring controversy is that insects and other organisms are influenced by a wide range of abiotic and biotic factors that can limit their maximum sizes. During the Carboniferous and the Permian periods, one of the primary causes for insect gigantism is increased levels of oxygen in the early Earth atmosphere.

Geologic setting

During the Mississippian period, the supercontinent Pangea had not been fully formed (Fig. 1 and 2) (Lucas, Schneider, Nikolaeva, Wang, 2022). A rheic ocean separated the supercontinents Gondwana and Laurentia, that began to close during the Pennsylvanian period to form Pangea. The supercontinent began to rift apart in the Triassic as the continents started to move their current positions (Lucas, et al., 2022). Insect fossils of the late Paleozoic and early Mesozoic era are found spread across the globe, as the continents have moved since their burial. For example, some fossilized insects can be found in middle Jurassic volcanic ash of Inner Mongolia, China, and early Cretaceous Formations in Brazil (Nel, 2015).

Fossils of insects are grouped based on their family due to practical reasons of compiling endless databases of fossil taxa. These fossils can be found in lacustrine rocks, fluviatile rocks, and amber (fossil resins); though fossil resins hold small and relatively young fossils (Nel, 2015). Exceptional insect fossils can be preserved in selenite, salts, gypsum, cave stalactite, and sedimentary quartz.

Origin of insects

Looking at the fossil record to see where the class *Insecta* in the arthropod subphylum *Hexapod* originated explains how insects became so large during the Carboniferous and Permian periods (Glenner, Thomsen, Hebsgaard, Sørensen, and Willerslev, 2006). In freshwater environments, molecular research shows the origin of Hexapods 460 million years ago rather than in the Late Devonian (Glenner, et al. 2006). The authors also comment Hexapods being more closely related to freshwater brachiopods, a group of crustaceans (Fig. 3) (Glenner, et al., 2006). The subphylum is proposed to have transitioned to land dwelling due to a time of long-term arid conditions in the Devonian, possibly forcing Hexapods to migrate onto land as the freshwater habitats became scarce (Glenner, et al., 2006).

Peak size: Tracheal systems

At the initial evolution of insects around 460 million years ago, diversity among the class was limited, yet the sizes of individual species were not. This could be explained by recent atmospheric models that point to a period of high atmospheric oxygen levels reaching 27-35 kPa during the Carboniferous and Permian periods (Fig. 4) (Harrison, et al., 2010). Oxygen in Earth's atmosphere would not reach these high levels again (Fig. 4) (Harrison, et al., 2010). This time span of a hyperoxic atmosphere also saw the largest insects in Earth's history. Giant dragonflies had wingspans of 70 cm (about 2.3 ft) and thorax widths five times that of today's dragonflies (Harrison, et al., 2010). However, this was not the common size of all insects during that time. Some species developed into giant insects, but it is still unclear if the average insects during the Carboniferous and Permian periods were gigantic. In some species of insects, living in prolonged hyperoxic environments results in increased average and mean body sizes, whereas those same species exhibit decreased body sizes when living in prolonged hypoxia (Harrison, et al., 2010).

Insects “breathe” air through a system of tubes called trachea that extract oxygen out of the atmosphere and distribute it to their blood stream. In experiments exposing the fruit fly (*Drosophila melanogaster*) to prolonged hypoxic conditions, *D. melanogaster* evolved to have larger tracheae. Whereas in prolonged exposure to hyperoxic conditions, *D. melanogaster* evolved smaller tracheae. These results point out that tracheal development has significant expenses of materials, space, or energy and leads to a natural selection against a surplus of tracheal structures. Therefore, a smaller trachea caused by hyperoxic environments, such as during the Carboniferous and Permian periods, would be evolutionarily favorable for certain insect species.

Peak size: Large wings

Ancient coal swamps of the Carboniferous period are similar to today’s tropical and warm weather swamps. Similar to modern swamps, the coal-forming swamps of the carboniferous were filled with different kinds of insects, but hyperoxic atmospheric conditions caused insect gigantism. For example, a dragonfly relative with a 70 cm wingspan. Flying insects naturally have a higher demand for oxygen due to high energy demands of their musculature (Clapham and Karr, 2012). Therefore, flying species of insects are more susceptible to changes in oxygen levels of the atmosphere (Clapham and Karr, 2012). Since wing lengths of insects during the Carboniferous and Permian periods were the largest in the insect taxonomy record (Fig. 5) (Clapham and Karr, 2012), it suggests that having an hyperoxic environment likely triggered an increase in wing and associated body sizes of certain species. The increased wing sizes allowed for more of a gliding style of flight, which meant the larger the wingspan, the less nimble the insects were.

Decline of insect size after Permian

As the atmospheric levels of oxygen began to decrease by the end of the Permian, so did the sizes of insects, further supporting the correlation of insect body size to atmospheric oxygen levels. Although other smaller spikes of increased oxygen levels occurred, insects slowly decreased in size after the Permian (Fig. 5) (Clapham and Karr, 2012). This points to other constraints on insect size. Biotic factors, like predation, may have superseded oxygen's role in insect body size (Clapham and Karr, 2012). A great diversification of birds in the early Cretaceous corresponded with the disconnect of high atmospheric oxygen levels and large insect body sizes (Clapham, and Karr, 2012). The pressure exerted from birds hunting insects may have caused them to evolve to become smaller in size. For example, the large wings proved to be an evolutionary disadvantage, as maneuverability was later favored, and insects evolved to have smaller wing and body sizes (Clapham and Karr, 2012). This same logic can be applied to ground dwelling insect species who experienced insect gigantism. Early bird-like species that hunted insects inhabiting the ground were more likely to spot a large insect from the sky rather than a smaller one, whereas small insects were able to hide under foliage better than larger ones. As these bird-like species evolved and diversified, natural selection favored smaller insects, thereby overcoming the effect of oxygen on insect sizes.

Insect persistence through mass extinctions and to the present day

The fossil record indicates three mass extinctions occurred after the Carboniferous and Permian periods. The mass extinction at the end of the Permian (250 Mya), called the Permo-Triassic (P-T), included 96% of species, 56% of genres, and 55% of families of biota (Fig. 6) (Ritche, 2022). The mass extinction at the end of Triassic (200 Mya), included 80% of species, 47% of genres, and 23% of families (Fig. 6) (Ritche, 2022). The mass extinction when the dinosaurs died off was the Cretaceous-Paleogene (K-Pg) (66.1 Mya) in which 76% of species, 40% of genre, and 17% of families were lost (Fig. 6) (Ritche, 2022). Yet insects (subphylum *Hexapoda*) persisted through these major losses of species, and it is not clear how. For the P-T extinction event, taxonomy is not well documented for 5 million years before and after the event (Nel, 2015). Also, there may be species not recorded as living during the Permian and seen in the Triassic. Many taxa that are documented survived through the P-T boundary without noticeable problems (Nel, 2015). The K-Pg extinction event is slightly better documented because the fossil records are more complete for these more recent periods, but still uncertain (Nel, 2015). Evidence shows that at the K-Pg boundary all insect orders survived, as well as almost all Cretaceous families (Nel, 2015). It is possible that a great many insect species became extinct during the K-Pg boundary, but not so much as to eliminate an entire family (Fig. 7) (Nel, 2015). Therefore, the species that were left in a family could re-diversify (Fig. 8), keeping the insect family persistent in the geologic record (Nel, 2015). Additionally, changes in plant and insect relationships in the fossil record support the conclusion that Hexapods at the genus and species levels were negatively impacted at the K-Pg boundary (Fig. 9) (Labandeira, 2005). Despite impacts on the lower taxonomic levels, all the hexapod families survived through the extinction events, meaning that all their trophic level relationships with their environments persist in insects today (Nel, 2015). Modern insects rely on the same environmental factors to survive that insects did in the past, with the only difference being some species had larger body sizes due to hyperoxic environments.

Conclusion

One of the primary causes for insect gigantism during the Carboniferous and Permian periods was increased levels of oxygen in Earth's early atmosphere. Experiments on insects in hyperoxic environments have shown that certain species of insects increase their body size.

Having an excess of trachea is costly to an insect, therefore favoring a smaller tracheal system, which has been shown to occur in hyperoxic environments (Nel, 2015). The relationship between atmospheric oxygen levels and insect body and wing sizes began to diverge as the hunting of early bird-like animals on insects superseded the effect of oxygen. Statistical models of a positive correlation between atmospheric oxygen levels and maximal or average hexapod fossil sizes would be very helpful in strengthening the link between oxygen and insect size (Harrison, et al., 2010). The effect that atmospheric oxygen levels have on an organism's body size through geologic time is not just seen in insects, but also other independently evolved animals (i.e. mammals, reptiles). This further supports that atmospheric oxygen levels influence body sizes through evolution over geologic time (Nel, 2015).

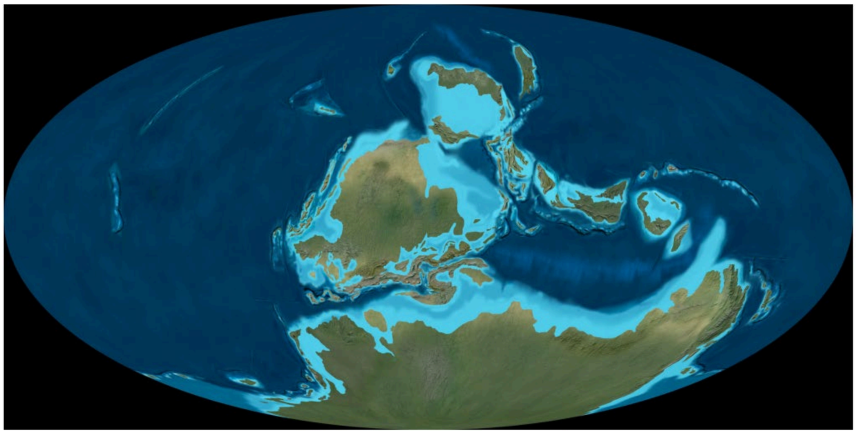


Figure 1: Mississippian paleogeography (Lucas, et al., 2022).

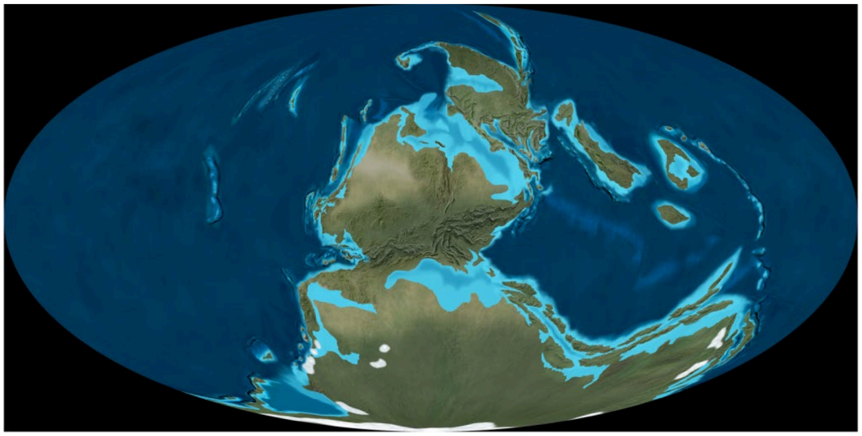


Figure 2: Pennsylvanian paleogeography (Lucas, et al., 2022).

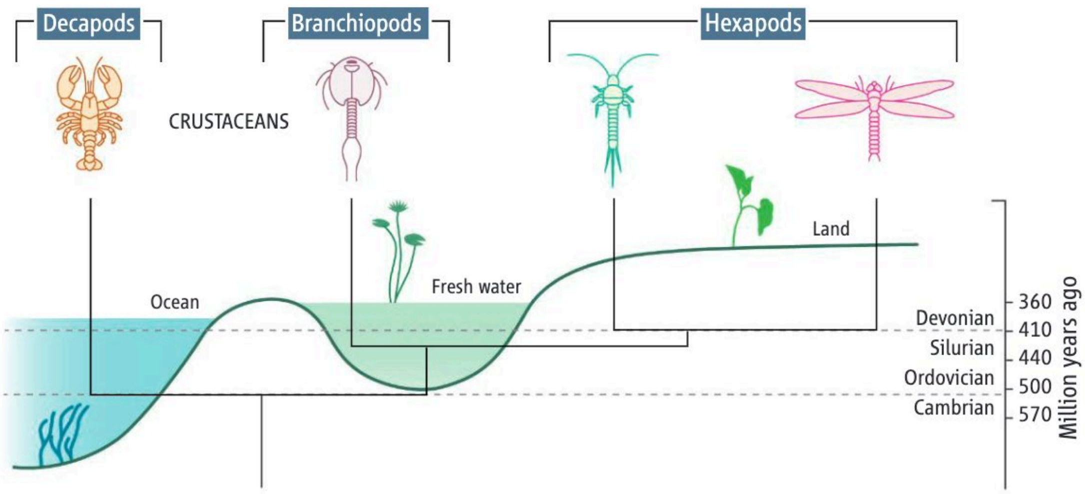


Figure 3: a phylogenetic tree depicting the evolution of Hexapods from a common ancestor overlaid by a drawing indicating which environments each subphylum of *Arthropoda* lived (Glenner, et al., 2006).

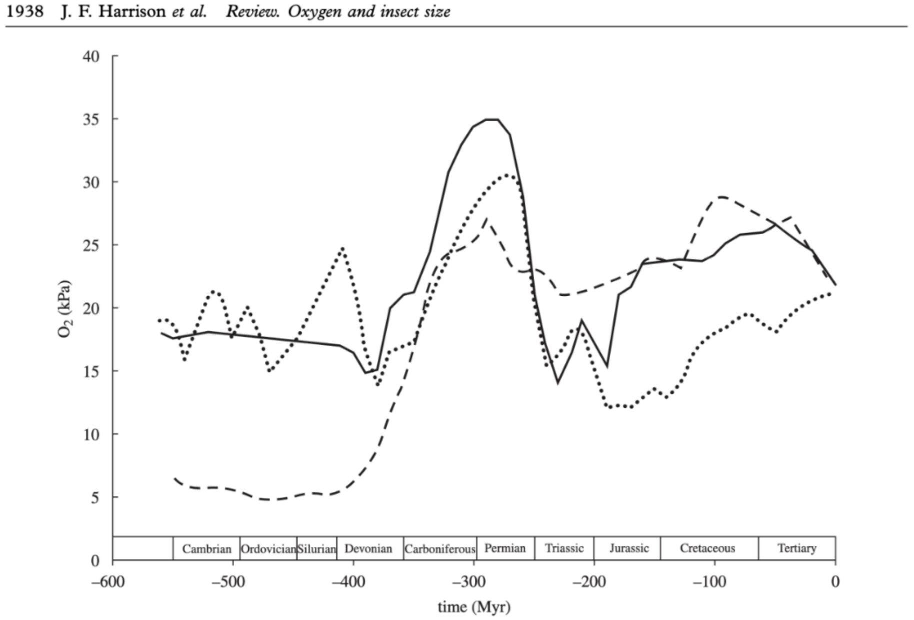


Figure 4: Various patterns of modelled atmospheric oxygen levels through the Phanerozoic. Solid lines are values measured by the balance of sedimentary rock abundance. Dotted lines are values measured from carbon and sulfur isotopic changes. Dashed line are values measured from feedback from atmospheric oxygen levels and fire on biogeochemical cycling (Harrison, et al., 2010).

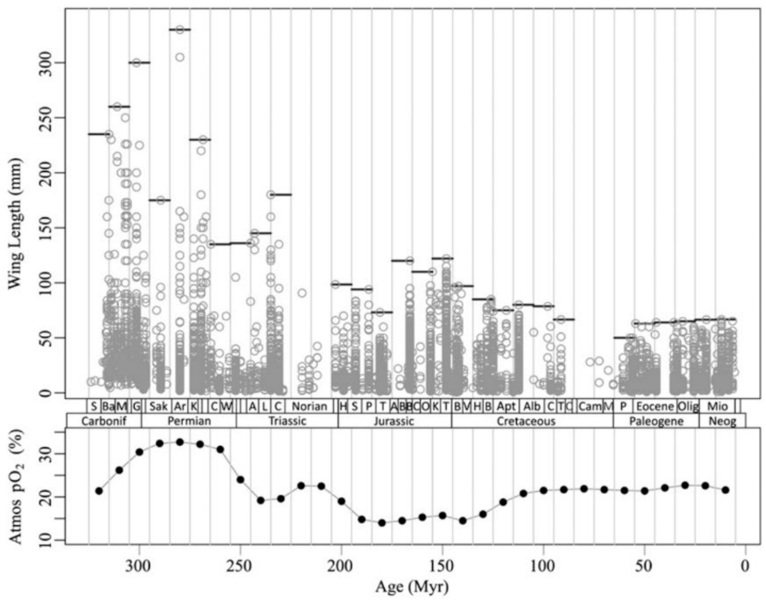
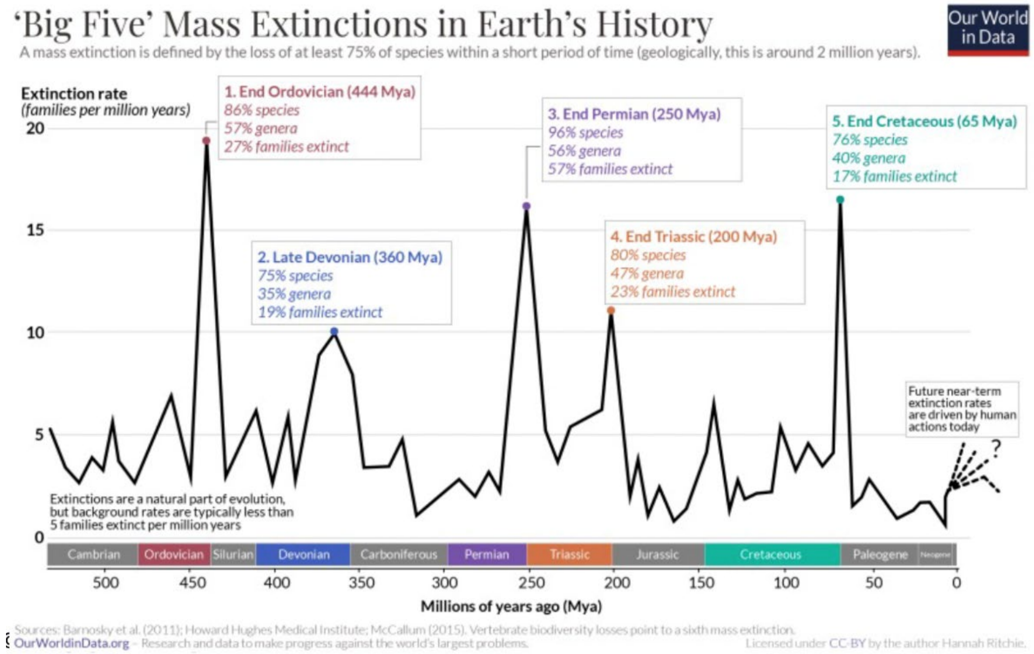


Figure 5: Phanerozoic trends in insect wing lengths and atmospheric pO2 (GEOCARBSULF model). The maximum size in each 10-Myr bin containing more than 50 measurements is indicated by black lines (Clapham and Karr, 2012).


'Big Five' Mass Extinctions in Earth's History

A mass extinction is defined by the loss of at least 75% of species within a short period of time (geologically, this is around 2 million years).

1. End Ordovician (444 Mya)
86% species
57% genera
27% families extinct

2. Late Devonian (360 Mya)
75% species
35% genera
19% families extinct

3. End Permian (250 Mya)
96% species
56% genera
57% families extinct

4. End Triassic (200 Mya)
80% species
47% genera
23% families extinct

5. End Cretaceous (65 Mya)
76% species
40% genera
17% families extinct

Extinctions are a natural part of evolution, but background rates are typically less than 5 families extinct per million years

Future near-term extinction rates are driven by human actions today

Sources: Barnosky et al. (2011); Howard Hughes Medical Institute; McCallum (2015). Vertebrate biodiversity losses point to a sixth mass extinction.
OurWorldinData.org – Research and data to make progress against the world's largest problems. Licensed under CC-BY by the author Hannah Ritchie.

Figure 6: When mass extinction events occurred compared to how many families went extinct. Each mass extinction event show percentages of species, genre, and families of life died off (Ritche, 2022).

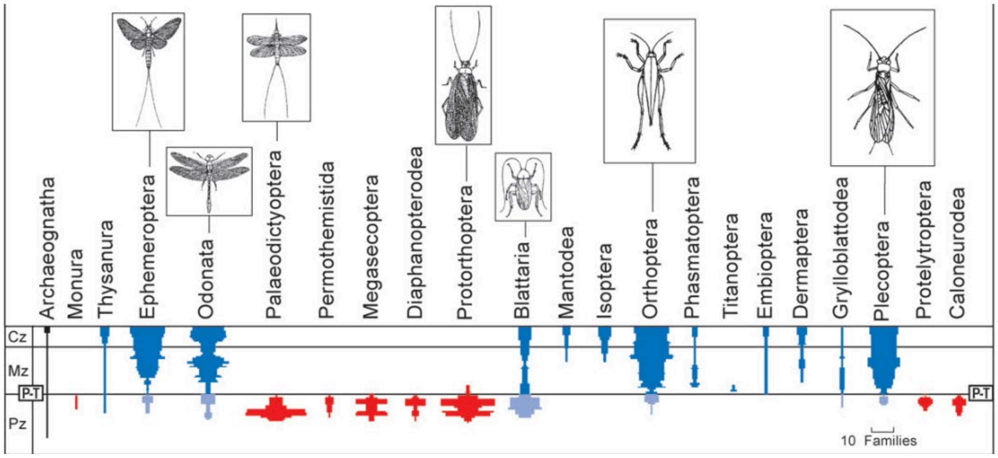
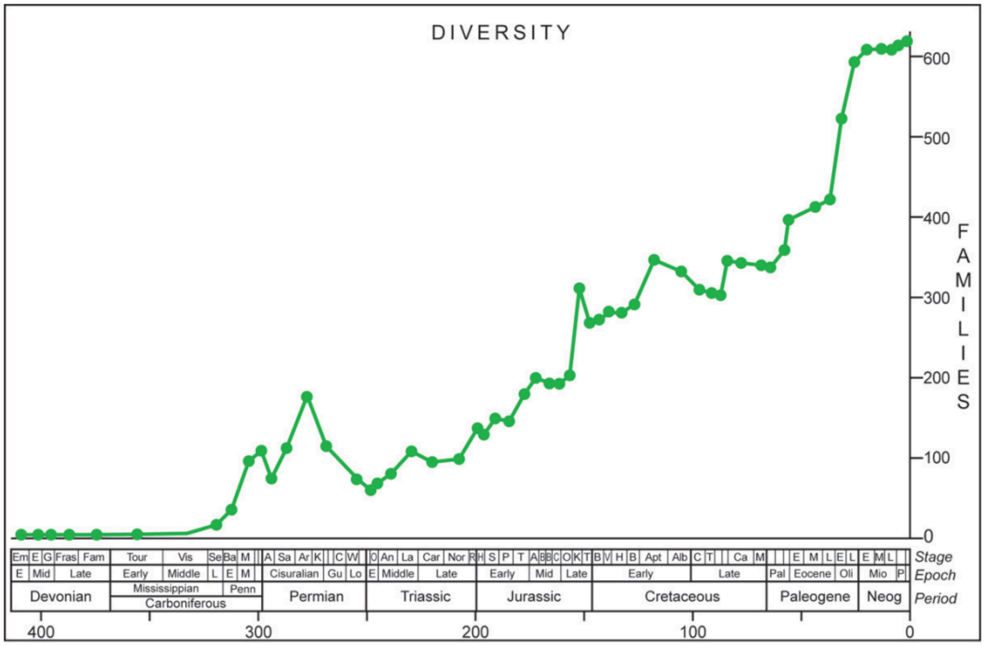


Figure 7: Family level diversity for some Paleozoic orders through the Phanerozoic. Note: end-Permian mass extinction at the Paleozoic-Mesozoic era boundary. Some orders with distinctive Paleozoic clades are indicated by a lighter shade of blue (Labandeira, 2005).



Geochronologic abbreviations, in temporal order, from oldest to youngest, for this and the following figure are as follows (from Gradstein et al. 2004). The Paleozoic consists of the Devonian, Carboniferous and Permian; the Mesozoic consists of the Triassic, Jurassic, and Cretaceous; and the Cenozoic is the Paleogene and Neogene. The Mississippian and Pennsylvanian are subperiods of the Carboniferous Period. Some stages of short duration are listed below but not placed in Figures 3 and 4.

Figure 8: Family-level insect diversity for the Phanerozoic. For the latter half of the Permian, parts of the Jurassic (Bajocian and Bathonian), and much of the Paleogene and Neogene, data representing two or (less commonly) three stages are combined into a single point (Labandeira, 2005).

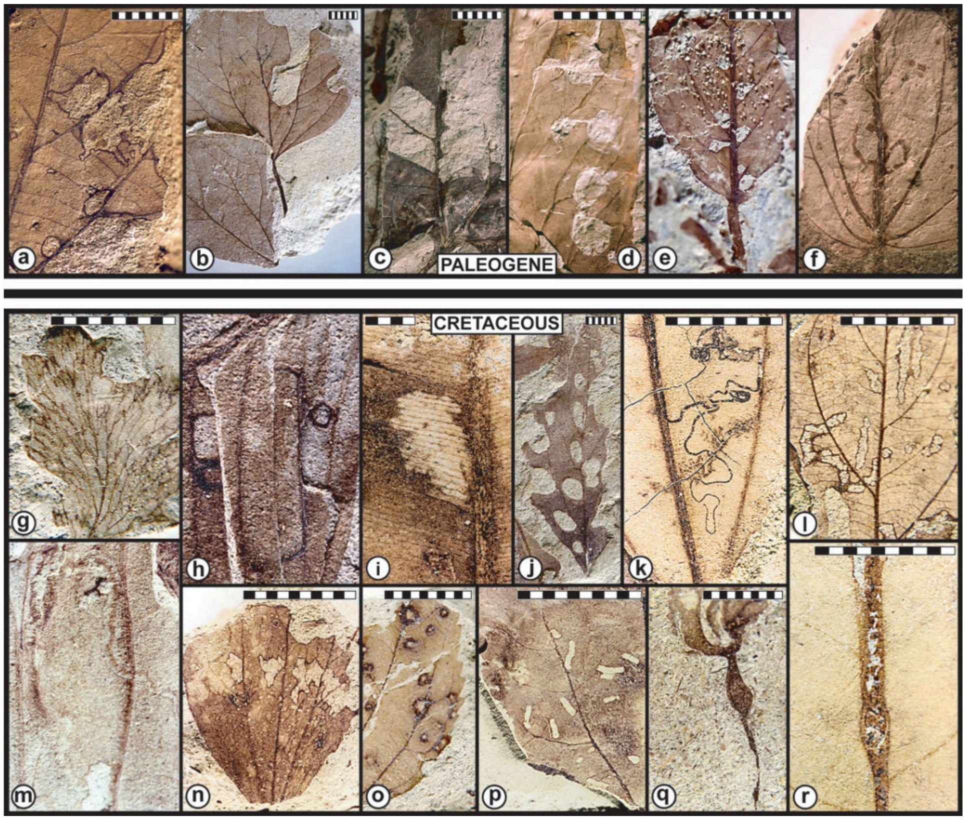


Figure 9: Insect and Plant relationships preserved in the fossil record (Labandeira, 2005).

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