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## **An Overview of Hypotheses and Supporting Evidence Regarding Drivers of Insect Gigantism in the Permo-Carboniferous**

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## An Overview of Hypotheses and Supporting Evidence Regarding Drivers of Insect Gigantism in the Permo-Carboniferous

# Abstract

Insects provide powerful examples of the responses of organisms to environmental change. For example, insect body size gives us insight into the consequences of climate change due to shifts in atmospheric composition, both in the present and in the past. Indeed, one common hypothesis behind the enormous sizes of insects during the late Carboniferous to early Permian (323.2 to 265.0 million years ago) is that such sizes were enabled by elevated oxygen levels (hyperoxia) during the Permo-Carboniferous, when atmospheric oxygen was as high as 60% greater than its present-day concentration. To examine whether the giant body sizes of insects were solely a response to a high partial pressure of oxygen, I assess the strengths and weaknesses of studies to date and address the need for further research that would allow for more robust tests of this hypothesis. Conclusions from the growing body of literature on geomagnetic polarity reversal, insect physiology, paleoecology, paleoclimatology, and paleoentomology suggest that even present-day oxygen levels might have been enough to induce gigantism, but can no longer, due to more recent selection against large insects that has limited their maximum body sizes since the Permo-Carboniferous. Additionally, more definitive studies on long-term evolutionary changes of insect size in high oxygen levels are needed before the question of whether high oxygen levels drive insect gigantism can be adequately answered.

# Introduction

In popular culture, giant insects have played a huge role, from works like *Them!* to *Jurassic Park* to *Mysterious Island*. Prehistoric insect gigantism was nowhere near this scope, but its cause continues to fascinate paleontologists and entomologists alike. This phenomenon is seen in insect fossils primarily from the late Carboniferous to the early Permian (323.2 to 265.0 million years ago). This time period, the Permo-Carboniferous, was a turning point in insect diversification (Nicholson et al., 2015; Cannell 2020). Specifically, an analysis of rates of extinction and origination of insect families showed the highest peak of origination was during the Pennsylvanian (a subperiod in the late Carboniferous) at 0.45 new families per existing family per million years, while all the other peak origination rates are at or well below 0.1 new families per family per million years (Nicholson et al., 2015). Because these estimates are, by necessity, based on only those families preserved as fossils, they are likely conservative estimates. During the Bashkirian to Moscovian (within the Pennsylvanian), winged insects made their first appearance and were quick to proliferate across heavily forested biomes. Subsequently, insects began to colonize wider environments during the early Permian, corresponding with the rise of Paraneopteran (lice, thrips, and true bugs) and Endopterygote (complete metamorphosis) insects. Insect gigantism was present in both ages.

In the interest of not getting swept away by the charisma of giant insects, it is imperative to note that they were not the norm in the Permo-Carboniferous, but rather the exception (Table 1). However, what cannot be denied is that this phenomenon has not been seen again in history,

or at least not to the extent that it occurred during this Paleozoic time period (there was some gigantism during the Jurassic). What caused this exception to take place, and why? After all, understanding trends from our geologic past is paramount to making sense of the world we live in. Does hyperoxia drive insect gigantism (VandenBrooks et al., 2011)? Why are insects more tolerant to hypoxia than us vertebrates (Klok et al., 2016)? These are just some of the exciting questions that the field of paleoentomology seeks to answer.

Table 1. Insect orders that existed during the Carboniferous and subsequently the early Permian. From Daly et al., 1998 and Zicha, 2020. Not included are the families Syntonopteridae and Bojophlebiidae, which both experienced gigantism, but are yet to be placed within an order, as they did not belong to Palaeodictyoptera nor Ephemoptera, as many papers, such as VandenBrooks et al. (2011), seem to suggest (Sroka et al., 2014).

Order	Part of Carboniferous alive (358.9–298.9 Ma)	Status	Gigantism?
Microcoryphia	358.9–298.9 Ma	Extant	No
Monura	323.2–298.9 Ma	Extinct	No
Zygentoma	323.2–298.9 Ma	Extant	No
Diaphanopteroidea	323.2–298.9 Ma	Extinct	No
Palaeodictyoptera	318.0–298.9 Ma	Extinct	Yes
Megasecoptera	323.2–298.9 Ma	Extinct	No
Ephemeroptera	323.2–298.9 Ma	Extant	No
Meganisoptera	323.2–298.9 Ma	Extinct	Yes
Orthoptera	358.9–298.9 Ma	Extant	No
Protorthoptera	323.2–298.9 Ma	Extinct	No
Blattoptera	358.9–298.9 Ma	Extinct	No
Blattodea	358.9–298.9 Ma	Extant	No
Coleoptera	318.0–298.9 Ma	Extant	No
Miomoptera	318.0–298.9 Ma	Extinct	No

In the context of climate change research, insects have been an increasingly enticing model for studying the effects of a changing environment, as their body size over different geological periods is thought to be influenced by environmental factors such as temperature and concentration of gases in the atmosphere (Verbek & Bilton, 2011). A recent study by Tseng and Sarai (2018) examined the effect of climatic temperature change on body size of ground beetles in Vancouver, BC. They found that larger-bodied species are particularly sensitive to increasing temperature, with 95% of laboratory-reared beetles decreasing in size with increased rearing temperature. Furthermore, by examining the body sizes of beetle specimens spanning 30 to 100 years of collecting, they found that larger beetle species have become smaller over time in association with climate change. Larger body sizes are thought to be reached in insects in colder conditions because in contrast, warmer temperature causes insects to develop quicker, reaching their last molt into adulthood prematurely. Because global temperatures were low during the late Carboniferous before rising again during the Permian (Harrison et al., 2010), this link between cool temperatures and larger body size may have exacerbated the gigantic morphology of Carboniferous insects.

Another important potential driver of insect gigantism is elevated atmospheric oxygen, which would release insects from limitations imposed by their respiratory system (Ward, 2006).

Insects, as with all arthropods, have an open circulatory system, which means that their hemolymph (blood) is not sealed in arteries and veins. This makes respiration a more diffusion-dependent process than in species, such as humans, that have closed circulatory systems with veins and capillaries that can supply oxygen deeper into bodily tissue. Body size is restricted in insects because diffusion is only efficient over very short spatial scales. With increasing body size, the scale over which any such diffusion would need to happen would increase as well.

Both of these factors that may influence insect body size vary with altitude. However, temperature decreases with increasing altitude, and  $pO_2$  decreases with increasing altitude, so predicting the physiological response of insects to increasing altitude is messy and likely unique to its lifestyle or niche (Horne et al, 2018). Disregarding the variable of altitude and focusing on the effects of different  $pO_2$  on insect size at one elevation is a little simpler. For example, previous experiments have found that insects are consistently smaller when reared in hypoxia (low oxygen levels), but the effects of hyperoxia (high oxygen levels) on body size are non-linear and depend on the order to which the insect belongs (Harrison et al. 2010, VandenBrooks et al. 2011). For example, dragonflies increase in size under hyperoxia; cockroaches, grasshoppers, and fruit flies seem to not be affected; and sphinx moths even decrease in size.

Other studies have found that the impact of oxygen levels on body size and selection for gigantism might be more significant in aquatic environments than on land, as oxygen is limited underwater. Atmospheric oxygen partial pressure ( $aPO_2$ ) likely played a role in selecting for gigantism during the Pennsylvanian to mid-Permian (Permo-Carboniferous). Data from previous studies show that smaller freshwater nymphs are more sensitive to oxygen toxicity than larger freshwater nymphs. Consequently, larger body size may have been an adaptation to escape oxygen toxicity, as it would allow for a less dense distribution of oxygen molecules within cell tissues—meaning that hyperoxia did not merely *allow* for larger body sizes, but rather *necessitated* it, and larger body sizes in some taxa were selected for as a result (Verberk & Bilton, 2011). This causal hypothesis is consistent with the observation that gigantism was limited to insects with certain niches, such as those with aquatic juveniles (see Table 1—Meganisoptera, Syntonopteridae, and some species of Palaeodictyoptera all had aquatic nymphal stages [Prokop et al., 2019 and Sroka et al., 2014]. It is unknown whether Bojophlebiidae had aquatic nymphs [Bechly, pers. comm.]). This putative relationship would suggest that an insect's niche is important when considering how their body size responded to paleo-oxygen levels. Because niche occupancy (e.g. terrestrial vs. aquatic habitat) varies among orders, selection for gigantism during the Carboniferous may have varied depending on the order to which an insect belonged. This same logic would suggest that the degree of gigantism may vary among insect families within an order. Notwithstanding, the relationship between niche occupancy and hyperoxia is key in reconstructing the evolution of insect body size.

## Hypotheses

### General

The reason why environmental changes have such striking effects on insect size is thought to be due to their body plan. Insects have an open circulatory system with hemolymph containing proteins that evolved from copper-containing hemocyanins (Gullan & Cranston, 2014). Hemolymph is not very efficient at transporting oxygen—instead, the tracheoles of the respiratory system are responsible for this process. Tracheoles are dissimilar to lungs in that they

deliver oxygen directly to bodily tissues, shortening the interface between environmental conditions and insect cells, relative to us vertebrates. The limitations of this diffusion-dependent system are particularly acute for insects capable of flight, an activity which demands high metabolic capacity. High metabolic capacity in turn requires a greater amount of oxygen diffusion, a process which creates substantial metabolic waste in the form of free radicals, heightening sensitivity to high oxygen levels while simultaneously requiring oxygen (Riley, 1994). Insects have very specific oxygen needs, which make them sensitive to environmental fluxes involving oxygen deficiency and oxygen toxicity.

Prior research has shown that oxygen supply limits the heat tolerance of certain exopterygote (incomplete metamorphosis) insects, especially those nearing the maximum size of their particular instar (a developmental stage; insects must molt to proceed to the next instar), when they are especially susceptible to oxygen limitation (Youngblood et al. 2019). This is because oxygen demand increases as the animal grows and with increasing body temperature. Because stress is put on the tracheae as an insect begins to outgrow its exoskeleton, hypoxia is used as a signaling mechanism for molting. Exopterygote insects may molt sooner in hypoxic conditions, but this is not always consistent with experimental results. Furthermore, the process of molting itself temporarily disables gas exchange, as the lining of the trachea are stripped along with the rest of the exoskeleton (Camp et al. 2014). Naturally, this would be significantly more fatal—let alone more challenging—in a hypoxic atmosphere.

Given the above reactions to hypoxic conditions, it comes as no surprise that paleoentomologists would hypothesize that hyperoxia would induce the opposite effect. Because gas exchange is a diffusion-dependent process in insects, hyperoxia would allow a greater amount of oxygen to penetrate more deeply into larger body systems (Harrison et al., 2009). Klok et al. (2016) put it best when they said, “a reduction in the need for tracheal investment might facilitate larger insects by allowing greater investment in nonrespiratory tissues,” though this does oversimplify the selective pressures brought upon by oxygen toxicity.

## Specific

Studying geomagnetic reversal yields valuable insights into the patterns of hyperoxia and hypoxia seen in paleoclimatology research. Wei et al. (2014) investigated the curious relationship between geomagnetic polarity reversal rate, atmospheric oxygen concentration, and genus-level diversity (albeit for marine invertebrates, although this relationship should translate nicely to insects as well, given the shared open circulatory systems) and found that these three factors were tightly correlated. A hypothesis was formed: High rates of geomagnetic reversal cause O<sub>2</sub> levels to drop via planetary outgassing, causing global hypoxia and subsequently contributing to mass extinctions. Earth’s magnetosphere typically protects our ionosphere from being stripped away by harsh solar winds, but as dipoles begin to switch places, the magnetosphere is significantly weakened, and solar winds can penetrate closer to the planet. This phenomenon conveniently allows for radioisotope dating to confirm the chronology of these events: Ion escape favors lighter isotopes, which would have potentially increased global <sup>18</sup>O/<sup>16</sup>O ratios.

To investigate this supposed link between geomagnetic reversal (GMR) events and global hypoxia, Wei and colleagues (Wei et al. 2014) simulated a GMR event by mathematically conducting a reversing field to estimate rate of oxygen ion escape. Their results supported the hypothesis that a significant proportion of the drop of atmospheric oxygen levels throughout the Phanerozoic Eon was caused by the high GMR rate. If it is true that volatiles escape the planet

during GMR events, it would follow that during superchrons—or geologically lengthy periods of stable polarity—these volatiles accumulate, raising atmospheric density, pressure, and oxygen concentration to hyperoxic levels. The relation to insect body size has been examined by Cannell (2020), who proposes that the elevated air density would allow insects to invest less energy in staying aloft and more energy into physical growth. The co-occurring hyperoxia would increase the upper limits to which insect body size could evolve under such conditions. Put another way, an understanding of the geologic phenomena recorded during the Permo-Carboniferous provides both an explanation for why the maximum body size could become higher during that time, and a selective basis for why body size might be expected to increase.

In testing this hypothesis, a slew of experiments has been performed that involve rearing various taxa in different oxygen concentrations that are reminiscent of Permo-Carboniferous  $aPO_2$ . These experiments focus on the phenotypically plastic response of insects to changing atmospheric conditions—as testing evolutionary responses is not feasible—but the value of observations of plastic responses cannot go overstated. For example, studies on both modern algal responses to changing ocean chemistry and stomatal density in plants in response to carbon dioxide levels have shown that we can study the phenotypic plastic results of organisms to specific environmental variables to accurately reconstruct paleoclimatic conditions—assuming that developmental responses of modern taxa are similar to their ancient counterparts (VandenBrooks et al., 2011). Therefore, plastic responses could be reflective of an insect's evolutionary history. The inference is that, for our fossil record of insects exhibiting gigantism, this spectacular trait was a result of selection toward insects that could tolerate hyperoxia by growing to larger sizes.

## Assessment of Evidence

### Paleontological

Although experiments focusing on phenotypic plasticity may be useful in reconstructing the evolutionary responses in insects because plastic responses themselves are an agent of evolution, there are certain evolutionary outcomes that cannot be gleaned via plastic responses. A plastic response involving minor increases in body size does not establish that dramatic increases in body size are possible, and the fact that phenotypic plasticity is a highly specialized trait to begin with inhibits an organism's ability to respond effectively to changing climate by limiting genetic variability in populations (Oostra et al, 2018). Furthermore, it is possible that historical shifts in atmospheric composition cannot be disentangled from other factors that may have influenced insect body size evolution. For example, is it merely a coincidence that, during the Permo-Carboniferous when insect gigantism was most prolific, there were no recorded vertebrate aerial competitors or predators (Klok et al. 2016)? Clapham and Karr (2012) analyzed the wing lengths of over 10,500 non-amber fossil insects from the early Carboniferous to the present for specimens from orders such as Odonata, Orthoptera, Blattodea, Hemiptera, Neuroptera, Meganisoptera, and Titanoptera. The authors found that, for each 10-million-year increment, the correlation between  $pO_2$  and maximum wing length was not significant after correcting for the effects of temperature. This statistical result is in spite of the data suggesting that insect wing length and atmospheric oxygen seem to follow the same trend during the Permo-Carboniferous. These factors do not correlate because this trend did not repeat during a part of

the Cretaceous in which atmospheric oxygen rose once more, to its present-day concentration. This inconsistent response to elevated oxygen led the authors to conclude that atmospheric oxygen did indeed have a substantial effect on insect body size in the early 150 million years of their evolution, but subsequent biotic interactions constrained the ability of insects to evolve large body sizes under conditions of elevated atmospheric oxygen (Clapham & Karr, 2012).

Clapham and Karr (2012) demonstrated that maximum insect wing length and atmospheric pO<sub>2</sub> both seem to have peaked in the late Carboniferous to early Permian and have steadily gone down since then, save for the small rise in oxygen in the early Cretaceous. Prior to this paleoecological research, one could not be blamed for being quick to assume that hyperoxia and insect wing size, rather than have a correlative relationship, have a causal one. And this still might be true—to an extent. First of all, while Clapham and Karr's (2012) aerial predation hypothesis is a compelling explanation, alternative to oxygen levels dropping, as to why insect gigantism receded, it does not account for the disappearance of giant ground-dwellers like *Arthropleura*, a 2.5 meter-long (8 feet) giant millipede that existed during the Carboniferous (Martino & Greb, 2008). The more likely culprit is loss of habitat and diet, since many of the millipede's natural predators, such as carabid beetles, birds, and mammals, only have records well after the time period that *Arthropleura* fossils are found. The case of habitat and diet loss could therefore be true for aerial insects as well. Secondly, temperature was much lower during the Permo-Carboniferous than the Cretaceous, and so it is possible that this was a stronger selecting factor for gigantism than the lack of aerial predators (Harrison et al., 2010). Lastly, having said that insect body size did not rise during the early Cretaceous, the rising oxygen levels during the time were not enough to recreate the conditions of extreme hyperoxia theorized to induce oxygen toxicity in insects. If insect body size and pO<sub>2</sub> did not have a 1:1 relationship, this decoupling should come as no surprise.

Even so, the hypothesis that aerial predation selected against large insect body sizes seems to be supported when considered in combination with other data. For example, Cannell (2020) superimposed the data from Figure 1 of Clapham and Karr (2012) and Figure 1a of Wei et al. (2014) to show the correlation between geomagnetic reversal rate and insect wing size. The duration of the Kiaman superchron, which lasted from the late Carboniferous to the mid-Permian, is associated with the lowest reversal rate (leading to a high accumulation of volatiles, raising pO<sub>2</sub>) and shows the highest peaks of maximum insect wing length. This relationship, however, does not continue into the next superchron, the Cretaceous Normal Superchron—incidentally where this increase in atmospheric oxygen, to the present-day concentration, occurred. However, what the graph does *not* show is the trend in pterosaur or bird abundance compared to the geomagnetic reversal data. Clapham and Karr might argue that wing size of insects went down during the Cretaceous because pterosaurs and birds, both of which potentially fed on flying insects, were increasing in number in the fossil record around that time.

## Experiments

If aerial vertebrate predators were at fault for decoupling hyperoxia and insect wing size during the Carboniferous, and not the fact that the small rise in oxygen was not enough to induce oxygen toxicity, there is another possibility. If winged vertebrates are the main factor selecting against large insects, as these data seem to imply, and *not* normoxia or even hypoxia, could insect size potentially rise in 21% oxygen if not for the constraint of small body size that has been selected for to evade predators? Is what we call “normoxia” actually hyperoxic relative to hyperoxia, at least in regard to an insect's plastic growth response?

The results of a phenotypic plasticity conducted by Harrison and colleagues (2009) indirectly support this hypothesis. After rearing a variety of insects in hypoxia (12% oxygen) and hyperoxia (31% oxygen), they saw that most orders raised in hypoxia exhibited linear responses, growing to smaller maximum body sizes than in normoxia. In contrast, under hyperoxia, growth responses were nonlinear (Table 2). Noting the decrease in tracheal size for the German cockroaches reared in hyperoxia despite not having a notable growth response, the authors realized that relative tracheal sizes of insects in amber can be measured to assemble information about paleo-oxygen levels. According to one of the authors (VandenBrooks, pers. comm.), a specific study on the application of insect tracheal sizes in amber is still in the works but is yet to be published as of May 2020.

Table 2. Developmentally plastic body size responses in hypoxia and hyperoxia from Harrison et al. (2009, 2010). Specimens belonging to orders that existed during the Carboniferous (Table 1) are marked with an asterisk. This does not, however, indicate that the species studied existed during the Carboniferous.

<b>Insect</b>	<b>Order</b>	<b>Family</b>	<b>Body size response in hypoxia</b>	<b>Body size response in hyperoxia</b>
<i>Hexagenia limbata</i>	Ephemeroptera*	Ephemeridae	Decrease	Not affected
Dragonflies	Odonata	Not specified	Decrease	Increase
<i>Schistocerca americana</i>	Orthoptera*	Acrididae	Not affected	Not affected
<i>Blattella germanica</i>	Blattodea*	Ectobiidae	Decrease	Not affected
<i>Zophobas morio</i>	Coleoptera*	Tebebrionidae	Decrease	Increase
<i>Tenebrio molitor</i>	Coleoptera*	Tenebrionidae	Decrease	Not affected
<i>Cotinus texana</i>	Coleoptera*	Scarabaeidae	Decrease	Increase
<i>Drosophila melanogaster</i>	Diptera	Drosophilidae	Decrease	Not affected
<i>Manduca sexta</i>	Lepidoptera	Sphingidae	Decrease	Decrease

The authors concluded that different insects have different oxygen delivery and growth regulation demands, so it is predictable that insects from different orders would exhibit such varying responses in hyperoxia. Additionally, the diversity of responses in different orders to hyperoxia may owe to the ability of changes in oxygen concentration to restructure communities to favor orders with traits that can better adapt in changing oxygen conditions. For example, grasshoppers (Orthoptera) are more capable of repairing oxidative damage due to their plant-based diet.

However, what appears to be consistent in the results of this study is that linear effects of body size and oxygen concentration cease at about 21%—coincidentally, the present-day value (Harrison et al. 2009). The authors reasoned this was because at higher aPO<sub>2</sub>, oxidative stress poses more detriments against any advantages of higher oxygen availability—advantages such as larger body size to better diffuse oxygen molecules; which, as discussed earlier, seems to have been selected against due to aerial predation. Consequently, there seems to be very little difference between the plastic growth responses for insects in hyperoxia vs normoxia. Relative to hypoxic conditions, it is possible that even normoxia was enough to increase body size. This would be an interesting direction for future research to investigate, although difficult to quantify, given the negative selective pressures by means of aerial predation.



When evaluating the merits of these experiments on growth responses of insects to paleo- $aPO_2$ , it is important not to disregard viable past data, therefore limiting oneself in the types of interpretation that can be made. VandenBrooks and colleagues (2011) claimed that the Blattodea were of particular interest for understanding the evolution of insect gigantism because they had a substantial fossil record from the Carboniferous, and therefore would exhibit responses more in line with what insects were capable of during the Permo-Carboniferous. They argue that beetles, flies, and grasshoppers—orders that they studied phenotypic responses of two years prior (Table 2)—are not actually useful for reconstructive paleoentomological studies because “none of these groups have relatives that existed during the entirety of the major swings in oxygen.” This claim has no citation to ground it, probably because it is false.

Despite the fact that most insects from the Paleogene and Neogene belong to orders, families, and genera alive today (Daly et al. 1998), many of our modern orders have been recognized in fossils from Carboniferous and early Permian outcrops (see Table 1). Even if the claim of VandenBrooks et al. (2011) was true, this means they could not have studied dragonflies either, because the Odonata have no fossil records until the early Mesozoic (Grimaldi & Engel, 2005). Of course, it is not possible to study the phenotypic plastic responses of griffinflies belonging to the extinct Meganisoptera order, so dragonflies are a good proxy. Rather, the more important point of consideration would be whether orders that haven't shown gigantism have any relevance in these phenotypic plasticity experiments. As long as these researchers decide to cast doubt on themselves, we might as well question the worthwhileness of studying phenotypic plasticity to gain information on evolutionary responses.

As can be seen from Clapham and Karr (2012)'s work, an experimental approach cannot accurately recreate ecological relationships between predator and prey. These selective pressures may prove to be paramount in understanding the dynamics of insect body size, as it is the very mechanism of evolution. The studies thus far on phenotypic plasticity have showed that investigating plastic responses certainly is useful in understanding how insect physiology would have responded to paleo-oxygen conditions, but studies documenting the evolution of insect body size over multiple generations in such conditions would probably be more valuable in understanding long-term physiological responses.

Fortunately, something of evolutionary interest appeared in work by Harrison et al. (2010), who raised fruit flies in hyperoxia individually and found that mean or maximal body mass did not appear to change. In contrast, when raised in groups over multiple generations, the flies exhibited an increased mean and maximal body mass, which was different from an individual fly's plastic response. These results suggest that evolutionary changes across the generations may have been at play, at least for these specific insects. They suspect this is the case for only fruit flies because they are more likely to encounter hypoxic environments in a given lifetime, and the novelty of hyperoxia is sure to elicit evolutionary responses. However, body size evolution in fruit flies over just a couple of generations (in one article, they mentioned only *one* generation) is a hefty claim to make. Nevertheless, Harrison et al. (2010) appears to be the first publication—nay, the first *allusion* to something that maybe someday could be a publication—demonstrating evolutionary responses of insect body size to changing  $pO_2$ , although the speed at which they claimed their fruitflies were evolving casts doubt on any future experiments.

## Altitudinal patterns

A crucial distinction was made about oxygen concentrations in Ward (2006): Partial pressure of oxygen is lower at high elevations, which means that growth responses may be varied along elevational gradients. Ward describes how the hypoxic conditions of the Mesozoic granted the common ancestor of avians with a body plan that better accommodated life in—literally—thin air. As a result, many birds can withstand the hypoxia of high-altitude flight. Cannell (2020) describes how atmospheric pressure and air density must have been substantially higher during the Permo-Carboniferous to accommodate such large flying insects. These are both factors that decrease with increasing altitude; but so does temperature, which seems to favor larger insect body sizes. Which variables have a more substantial effect? Does this likewise imply that smaller, more hypoxia-tolerant insects such as fruit flies and some beetles can be found in greater quantity at higher elevations?

The research seems to be conflicted. Dillon et al. (2006) described how, because temperature, air density, and oxygen partial pressure vary with altitude, so too does insect body size. They used weather balloon data from sites across the globe and found that temperature decreases by about 6°C with each kilometer in elevation (though the amplitude of this shift varies seasonally), compromising insect thermoregulation at high altitudes (insects can manipulate their operative temperature to some degree). Air density decreases by about 0.083 kg/m<sup>3</sup> with each kilometer. Oxygen partial pressure decreases by about 1.5% with each kilometer in elevation and results in smaller body size in Coleoptera, Diptera, Neuroptera, and Orthoptera. They noted that higher temperature exacerbates the effect of hypoxia. The implication is that hypoxia will have a greater cost for heterothermic insects with high metabolic demands, such as bees, large flies, and moths. As for decreasing air density, flying insects have mechanisms for altering their wing or thoracic morphology to accommodate this, resulting in a downsizing of power requirements to sustain a certain aerial velocity.

What is interesting is that the authors saw a trend after studying elevation and body size data of 29 species from 4 different orders (what those species were, they did not say): Most insects are actually smaller at colder, high-altitude sites than at warmer, low-altitude sites, which contradicted predictions that larger insects are found at higher latitudes—likely due to the cold, more than anything. The combined downsizing effects of a decrease in pO<sub>2</sub> and air density trump the upsizing effect of a decrease in temperature. However, Horne et al. (2018) saw slightly different results. Coleoptera and Orthoptera decreased in body size with increasing altitude, whereas Diptera, Hymenoptera, and Lepidoptera increased in body size with increasing altitude. Other groups that increased in size were flying species and freshwater species. Flightless insects decreased in size, and terrestrial insects seemed to not change in dry mass. This doesn't necessarily invalidate the study of Dillon et al. (2006), but the inconsistency in insect body size relative to elevation suggests niche-specific adaptations of these orders. Had Dillon and colleagues analyzed their data based on these different lifestyles, they might have seen similar results. Ultimately, studies on this topic provide mixed evidence that body size along elevational gradients is consistent with the hypothesis that higher oxygen availability is associated with increased body size.

## Conclusions

The field of paleoentomology could benefit from further research to better understand the drivers of insect gigantism, primarily studies demonstrating evolutionary changes in insect body

size over multiple generations as a function of changing oxygen level. Current available research does not firmly establish hyperoxia as the primary cause of large mean and maximal insect body sizes. As it stands, the existing experiments on rearing insects in paleo-oxygen levels have so far distinguished 12% pO<sub>2</sub>, 21.4% pO<sub>2</sub>, and 35% pO<sub>2</sub> into the categories of hypoxia, normoxia, and hyperoxia respectively, and have approached statistical analysis with three variables in mind. To test the hypothesis that normoxia (21.4%) was enough to raise mean and maximal insect body size, definitive studies must be performed to discern whether there is a statistical difference between growth responses in hypoxia compared to normoxia and hyperoxia.

Additionally, Wei and colleagues (2014) mentioned that there is a lack of global-scale ancient field records, and as such, the intensity and morphology of reversing fields during the Paleozoic is not clear. A good starting point to flesh out their hypothesis on geomagnetic reversal events contributing to global hypoxia would be to gather more geomagnetic polarity studies on the late Paleozoic, as this type of data is far more available for preceding eras. Furthermore, it would be fascinating to confirm the combined hypothesis of Cannell (2020), Wei et al. (2014), and Clapham and Karr (2012) about superchrons enabling, and aerial predation limiting, insect gigantism. Unfortunately, as the complexity of the factors contributing to insect gigantism are brought to light, so too is the complexity of statistical tests and the experimental challenges that must be overcome to verify these relationships.

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