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# THE BIGGEST BUGS: AN INVESTIGATION INTO THE FACTORS CONTROLLING THE MAXIMUM SIZE OF INSECTS

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## Introduction

Modern insects are much smaller than their prehistoric counterparts. The largest extant insect is three times smaller in mass than the heaviest of ancient insects. Whether there are indeed factors that have changed over the 400 million years of insect evolution leading to their smaller size and whether there is a single limiting factor are unsolved questions. In entomology, these two subjects are met with numerous conjectures; a proper analysis of them all would require a lengthy treatise. For the sake of brevity, this review looks at some of the most familiar suspects: the insect tracheal system, changes in atmospheric oxygen content over earth history and the evolution of flight. Other perhaps less common theories such as the changes in ecology in insect habitats, the insect exoskeleton, and the evolutionary advantage of being small are also topics of discussion.

In this paper, "largeness" and "smallness" will refer to mass as opposed to length, width or volume. However, one cannot often determine mass from insect fossils since some fossils only contain wings or other pieces of an insect's body. In some articles that have been cited here, only the body length is reported. In these cases, one can only assume that a larger wingspan or longer body means a more massive insect. When the comparison of size switches to wing length, or length, I will make that distinction. I will discuss only adult insects, even though the larval stages of a given species are commonly larger than the adult stage.

## Oxygen and Protodonata

The largest modern insect recorded for its weight was a "Giant Weta", or *Deinacrida heteracantha*, at 71g. Even in this case, it was an exception: a pregnant female with an exceptionally large brood (Williams 2001). 300 million years ago, the *Meganeura monyi* roamed the skies (Atkinson 2005). It had a 71cm wingspan, with a body 30cm long and 3cm wide (Maina 2005). Assuming its body was roughly cylindrical and had a density about equal to that of water, it weighed in approximately at 210g. This mass would make it the largest insect known in history (Atkinson 2005).

A common theory circulating in paleontology is that the massive oxygen changes over the past 500 million years of earth's history have contributed to change in insect size (Butterfield 2009; Okajima 2008). Insects distribute oxygen to their cells through a tracheal system. This system depends on diffusion to a greater extent than other oxygen distribution systems, such as our own circulatory system. For diffusion of oxygen, the higher the concentration of oxygen in the atmosphere, relative to the inside of the organism (the concentration gradient ΔC), the faster the rate of diffusion of that oxygen (Fick's First Law):

$$dm/dt = DS\Delta C/x$$

D is the diffusion coefficient, m is mass, S is surface area, x is distance, and t is time. This one-dimensional equation assumes that the concentration gradient doesn't change throughout the diffusive distance, but is a good approximation of many biological systems (Vogel 2003).

A simple approximation shows how diffusion can limit insect size. As the length (l) of an insect doubles, the surface area of its body increases by $l^2$. If the surface area of the spiracles, or tracheal openings, is proportional to the surface area of the insect, then these openings also increase by $l^2$. By Fick's law, then, rate of diffusion increases by 2. However, since volume and therefore mass scale approximately proportionally to $l^3$, the insect is fully eight times more massive. The new tissue now needs more oxygen. The metabolism of an insect scales approximately with surface area, $l^2$ (Alexander 2002), so has increased by 4. The diffusive rate of oxygen cannot keep up with the new energy needs.

A large insect like *Meganeura sp.* would need faster diffusion to make up for its great size, assuming that it also had a tracheal system. Since a higher amount of atmospheric oxygen means a larger concentration gradient, it follows that the ~30% atmospheric oxygen in the Carboniferous period, the time of *Meganeura*, would have allowed for faster diffusion, and thus, larger insects (see Fig 1).

The theory is further substantiated by the often-large size of decapods (e.g. lobsters and crabs). Members of this arthropod order have an oxygenated circulatory system and can reach considerably larger sizes than insects (Schmidt-Nielsen 1997). The largest land crab, the coconut crab (*Birgus latro*), can reach sizes of 4kg – almost 20 times larger than the largest insect in history (Terrestrial Ecoregions 2010). Despite having a similar body plan to insects in their segmented body and chitin-based exoskeleton, decapods can reach much larger sizes (Elzinga 2004). Since a key difference between insects and decapods is the tracheal system, perhaps the oxygenated circulatory system is the limiting factor of maximum size in insects.

However, there is a suite of major problems with this hypothesis. First of all, the mathematical model relating insect wingspan to atmospheric oxygen does not always correlate with one another, as a study by Okajima showed

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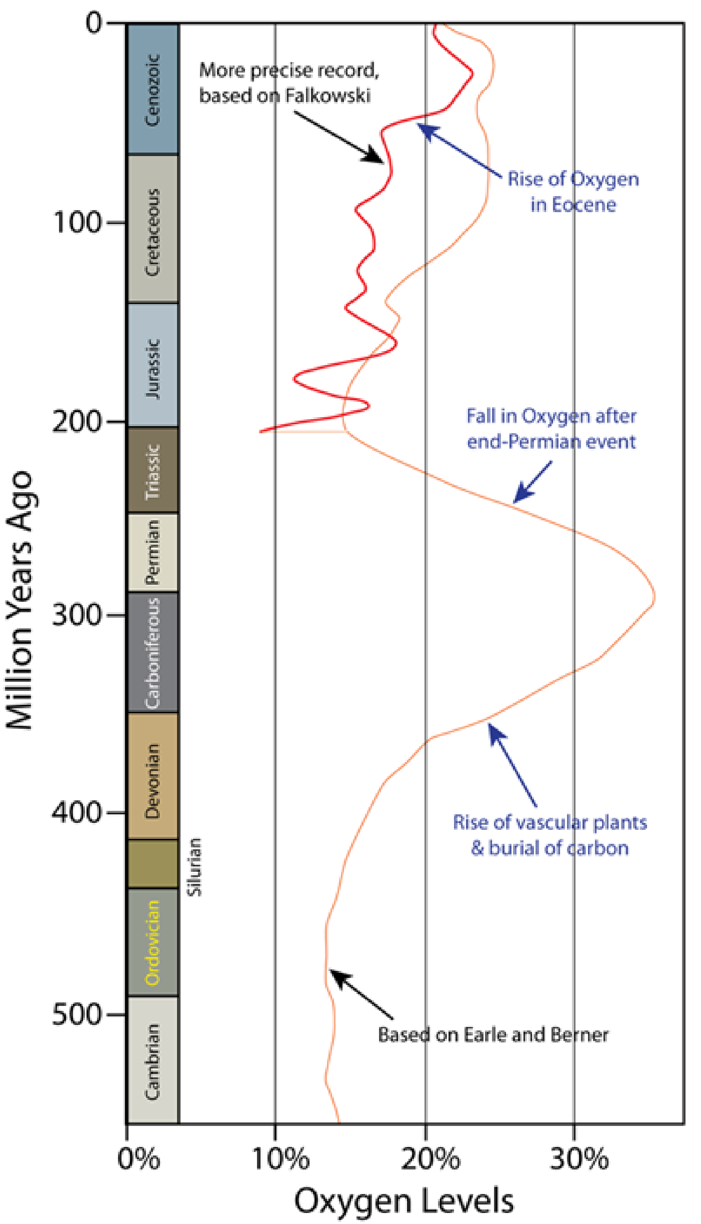

**Figure 1.** Atmospheric Oxygen Levels through geological time [source:essayweb.net/geology/timeline/phanerozoic.shtml]

in 2008. For example, dragonfly fossils from the Triassic and Jurassic show an insect with a wingspan double that of the largest dragonfly today, but atmospheric oxygen levels were one-half to three-quarters of modern levels. Secondly, modern insects have ways to compensate for low oxygen levels. A study by Loudon (1989) showed that when modern dragonflies were reared in different oxygen levels, the cross sectional area of their trachea increased with lower oxygen levels. Since, by Fick's law, mass of oxygen over time depends also on surface area, the increased surface area of the dragonflies' trachea compensates for the lower concentration gradient. Furthermore, diffusion is not the only tool of distributing oxygen in insect tracheal systems. Weis-Fogh (1964) analyzed the tracheal system in the flight muscles of insects. His conclusion was that in order to allow for passive diffusion to account for the metabolic needs in flight, the maximum diameter of a dragonfly's thorax should be approximately 0.5cm. Because thoraxes exceeding 0.5cm exist in modern dragonflies, he attributed these excesses to non-diffusive mechanisms. A study by Miller (1966) showed that a thoracic pump in beetles contributes to a large portion of their oxygen demand in flight. Similarly, thoracic pumps are believed to contribute heavily to the in-flight oxygen demand of dragonflies, moths, and many other insects (Weis-Fogh 1964; Miller 1966).

There are other ways through which insects can overcome diffusion, which are only recently being uncovered. Many species of insects have been shown to exhibit discontinuous gas exchange, where they close their spiracles for extended periods of time before opening them again. The "fluttering phase" of this process uses the slightly negative air pressure built up from oxygen use to suck in fresh oxygen. The process is thought to transport oxygen faster than diffusion (Nation 2008). The insect tracheal system is still poorly understood and more study may yet reveal processes not yet considered. Finally, some have argued that high oxygen levels would favour smaller insects, if any size at all, since smaller flying animals require a faster metabolism relative to their body size compared with large animals (Butterfield 2009).

Although atmospheric oxygen levels are not the only factor controlling insect size, they are still an important factor to consider. The insect tracheal system depends on diffusion to a greater extent than other systems and may still constrain insect size somewhat but certainly not by the amount supposed through pure diffusive processes (Dudley 2000; Weis-Fogh 1964). Currently, knowledge of past oxygen levels is the subject of much debate, and a better grasp on how atmospheric oxygen has changed may still shed some light on why insect size has changed (Butterfield 2009). However, oxygen levels are certainly not the only factor.

## Exoskeleton

The exoskeleton has also played a key role in insect development and diversity. Their hard shells saves them from dry conditions on land and can protect them from predators (Elzinga 2004). For a class of terrestrial animals that started small, an exoskeleton would be a wise choice.

Many scientists have studied whether the tracheal system limits insect size, but the exoskeleton - another key component of insect physiology - seems to have been mostly overlooked as a constraint to size. The biggest land animals in history all had an internal skeleton made of bone, such as a Mammoth or *Supersaurus,* a large dinosaur. Whether an exoskeleton made of Chitin that prevents insects from becoming large is an issue worth considering.

A study by Currey (1967) compared the endoskeleton to the exoskeleton, based purely on mechanical properties. He treated the legs like upright columns and applied formulae for buckling, rupture, compression, bending, and impact loading. The exoskeleton, he concluded, is the better choice for static loading, the kind of loading one's legs experience when one is standing still. The endoskeleton, with its surrounding soft tissue, is much better for dynamic loading, which is mostly experienced through activity, like running and jumping. Smaller organisms will experience less dynamic loading due to their lower momentum at normal activity speeds (Vogel 2003). Currey concluded that the endoskeleton is more advantageous for large organisms and the exoskeleton for smaller organisms. The insects' dependence on an exoskeleton makes them ideal for small sizes, but as they get bigger the exoskeleton is a burden. The opposite is true of tetrapods: their endoskeleton makes them adaptable to being large, but it keeps them from achieving the size of the smallest arthropods.

The constraint on the exoskeleton by itself cannot explain why the largest modern insects are so much smaller than the largest ancient insects. We don't know much of how the exoskeleton has changed over time. However, assuming that the materials of the endo- and exoskeletons have remained relatively constant over earth's history, one can come to an interesting hypothesis when one also consider the changes in ecology between the Carboniferous and now.

### Ecology

Atmospheric oxygen increased in the Jurassic and the wingspan of the Ordonata became smaller over the same time period. There was one major problem with models comparing atmospheric oxygen concentration to insect size. Okajima (2008) pointed out that the emergence of flying vertebrates could explain this particular case of shrinking. In the Paleozoic, insects were the only animals in the skies. However, Pterosaurs showed up in the Triassic and birds in the Jurrasic, competing with the insects for aerial space. Pterosaurs and birds can get much larger than insects, possibly due to their endoskeleton, hollow bones and oxygenated blood. The factors make them a more likely predator than the insect. A big insect is a more obvious prey for something much bigger. To adapt, insects became smaller.

Modern studies on butterfly larvae have agreed with the theory. In a laboratory setting, large caterpillars were selected preferentially by a *Picromerus bidens* predator (Berger and others 2006). In the experiment, two species of Lepidoptera were used. The results show that it did not matter which species were looked at or what colour they were. Larvae at the same size saw the same risk of predation, with larger larvae having a larger risk.

The largest of endoskeletal animals were all flightless varieties. One should think that the same would be true of insects. Indeed, Giant Wetas are flightless and the largest of modern insects. Uninhibited by the need to fly, one may question whether flightless insects in the Carboniferous can easily outgrow the flight-endowed species. On the ground, insects never reached the 30cm length that their flying cousins managed. In fact, the largest Paleozoic flightless insect found so far in the literature is a 6cm long silverfish called *Ramsdelepidion schusteri*. Perhaps instead of granting them girth, their inability to fly doomed them to a life of miniature.

While insects in the air mostly had to worry about each other, insects on the ground had to compete with giant tetrapods. Like birds and pterosaurs, the endoskeleton and oxygenated respiratory system allows earth-bound tetrapods to get much larger than insects. Therefore, tetrapods became the major predators. As expected from the model, land-dwelling insects adapted to these new competitors by downsizing. Predation has helped to push both winged and wingless insects to the size one sees today.

Since predation pushes animals to become smaller, one may ask why can terrestrial crabs are so large. The coconut crab may be a case of island gigantism since they develop on isolated islands where no large terrestrial predators had been established (Gan and others 2008; Brockie and others 1988). Still, the answer in this case may indeed remind one of the oxygenated blood in these crustaceans and perhaps even in the harder Chitin and higher number of supporting legs in these animals.

The Giant Weta may also be a case of this sort of "island gigantism". They are endemic to New Zealand, an island country that has no native land mammals besides bats (McIntyre 2001). Because Giant Wetas are nocturnal, provide food for owls and distribute seeds much like small rodents in other ecosystems, Giant Wetas are the ecological analogue of mice in New Zealand (McIntyre 2001). This is a clear example of how the changes in ecosystem have affected insect size. Due to the lack of competitors in the niche occupied by mice, insects grew into that niche by evolution and thus began growing to sizes comparable to those of mice. When mice were introduced to New Zealand, the Giant Weta population declined drastically (McIntyre 2001). The same may be generally true of insects over their evolutionary history. Since the physiology of tetrapods makes them more adaptive to those niches occupied by large organisms, they out-competed the large insects. Because insects are more adaptive to niches occupied by small organisms, they better adapt to those niches.

### The Evolutionary Advantage of Small Size

In terms of animal species diversity, insects are the undisputed champions. Estimates for insect diversity range from as much as 80 million species to as few as 5 million species. Even at the lowest estimate, insects represent around half of global species diversity (Gullan and Cranston 1994). A major reason for this success is the fact that they are small. Gullan and Cranston (1994) convey a very good illustration for the phenomenon. Consider a single acacia tree. One tree can provide one meal for a giraffe but can also support the complete life cycles of dozens of insects. As an extreme example, a single tree surveyed in Uganda hosted 37 species of ants alone (Shulz and Wagner 2002).

The smallness of insects allows them to fill niches left vacant by larger organisms. It also may have helped them survive four major mass extinctions and survive on land (McKinney 1997). Warm-blooded species such as mammals and birds have increased difficulty at small sizes because they have to maintain an incredibly high metabolism (Alexander 2002). As previously mentioned, even cold-blooded tetrapods are at a serious disadvantage at small sizes because of their endoskeletons. The insects filled ecological vacuums that other organisms simply could not fill (Gullan and Cranston 2005). Evolution would have selected for those insects that kept their small size. This does not fully explain why there are no insects larger than 70g today, only that evolution makes such sizes less likely.

Indeed, there is some degree of overlap: large beetles can exceed the sizes of small mice, bats and reptiles.

## Conclusion

The issue of why ancient insects could be so big and modern ones are not is an area of fierce debate with many viewpoints. The tracheal system in insects is a likely contender but by how much is still under scrutiny. Their exoskeletons make them well suited to small sizes but not as much to larger sizes. Their ability to fly, in combination with their choice of skeleton, may have reduced their size somewhat. All these factors contributed to initially reduced sizes in comparison to endoskeletal competitors with oxygenated blood. Over time, insects evolved to occupy smaller niches where their endoskeletal competitors were at a disadvantage.

Not a single one of the above theories can by themselves explain the modern maximal insect size. By taking into account the limitations of insect respiration, skeleton and predation within the larger context of evolution, we've come up with a plausible explanation for the range of insect sizes discussed in this paper. A more detailed analysis of all the largest insects over time, along with any dramatic changes in the above factors contributing to their size, is required before any general conclusions can be made. An even more developed answer would take into account other factors, for example, geography, sexual selection, climate, and nutrition.

The small sizes of insects have enormously contributed to their success. It allows them to have faster reproduction times, enabling them to adapt quickly to change, and allows them to survive times of trouble when food is scarce. Perhaps the question we should be asking is not "why are insects small" but rather "why be big?" At over 5 million species, and having dominated *terra firma* longer than any other animals, insects seem to be doing quite nicely on this planet. Ironically, these little creatures are the true titans of planet Earth.

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