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Publication Date: Fall 1999

Big Ideas About Big Bugs

By Danika Painter

They did not hunt humans because there were no humans to hunt, but insects of gargantuan proportions really did exist 300 million years ago.

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Typical supermarket tabloid headlines? Perhaps. But for decades, frightening mythical images such as these have been prime fodder for monster movies and late night television. The images prey on our fascination and fear of insects.

The enormous insects depicted in bad B movies exist mostly in the realm of science fiction. However, insects of giant proportions really did exist 300 million years ago. They were not as big as dump trucks, but some insects achieved masses many times greater than those of their modern relatives.

The fossil evidence is abundant. Scientists know that dragonflies with wing spans as wide as a hawk's and cockroaches big enough to take on house cats thrived during the Paleozoic era (245-570 million years ago). At the same time, mammoth millipedes longer than a human leg skittered across prehistoric soil.

Hundreds of different huge species evolved during the late Paleozoic era. The first dinosaurs appeared just about the time the giant insects disappeared.

These ancient giants fascinate Jon Harrison. A physiologist and professor of biology at Arizona State University, Harrison wants to know why giant insects evolved, and why they then disappeared.

The answer may lie in how insects breathe, according to research findings by Harrison and his colleagues. The ASU scientists are busy studying how the respiratory physiology of modern insects affects their body size.

Recent geologic findings opened a new window of thought on this issue. Some researchers are analyzing the composition of ancient soils. Their findings seem to comply with theoretical models. The findings indicate that there was a “pulse” in the concentration of environmental oxygen during the Paleozoic era.

In other words, there was much more oxygen in the atmosphere 300 million years ago than there is today. During this period, the oxygen concentration in the air reached 35 percent, almost double the present level of 21 percent. Oxygen concentration stayed high for about 100 million years, then dropped precipitously to about 15 percent.

Scientists think that the then-recent evolution of oxygen producing land plants caused this oxygen peak. Interestingly, the rise and fall of atmospheric oxygen also coincided with the evolution and extinction of giant insects.

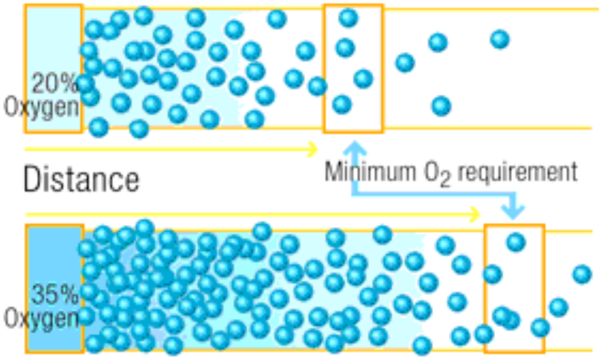
Harrison’s colleagues include Robert Dudley from the University of Texas at Austin, and Jeffrey Graham of the Scripps Institution of Oceanography in La Jolla, Calif. They propose that the temporary overlap between the oxygen peak and the appearance of giant insects was more than just coincidence.

Other researchers had speculated that oxygen availability might limit the ultimate body size for insects. Harrison and his colleagues took the idea a step further. They hypothesized that high ambient oxygen could have permitted the existence of giant species. The demise of winged monsters and behemoth beetles 100 million years later may be explained partly by the simultaneous decrease in the air's oxygen content.

Harrison says that the amount of available oxygen limits insect body size because of how the creatures' respiratory systems are made. Instead of lungs, insects breathe with a network of tiny tubes called tracheae. Air enters the tubes through a row of holes along an insect's abdomen. The air then diffuses down the blind-ended tracheae.

The distance oxygen can travel down the tracheae depends on its concentration in the air. If atmospheric oxygen is doubled, theory says that it should be able to make it twice as far.

According to Graham and Dudley, escalating Paleozoic oxygen levels may have helped speed oxygen transport in the longer tracheae of bigger insects. The environment itself could have opened the respiratory door for Paleozoic insects, allowing giant species to evolve.



Insects do not breath the same way that we do. Oxygen travels to insect tissues through tiny openings in the body walls called spiracles, and then through tiny blind-ended, air-filled tubes called tracheae. For a given tube diameter and temperature, gas molecules diffuse over distance at a rate proportional to the source concentration. In other words, air that contains more oxygen allows the minimum amount needed for metabolism to reach farther into the insect’s tracheae. Some insects canincrease oxygen delivery by a mechanical pumping action of their bodies. Humans and other vertebrates are less likely to be affected by atmospheric oxygen concentration, since oxygen is delivered by blood that is pumped through the tissues.

Harrison’s personal research interest is focused on insect respiratory physiology. The ASU scientist always wondered whether respiration could have been the limiting factor in insect gigantism. Shortly before Graham and Dudley’s hypothesis was published, Harrison learned about the Paleozoic oxygen pulse from Dudley himself.

The two were chatting at a national biology conference. “He told me about the oxygen pulse over a beer. I was stunned and excited by the idea,” Harrison says. “At the time, it was a shock to most of us to think that atmospheric oxygen concentrations could vary. If it did, it seems likely that there would be some fairly strong and interesting physiological consequences.”

The focus of Harrison’s research is Graham and Dudley’s most fundamental assumption: that available oxygen actually limits body size.

Scientists know that the flight muscle of an insect burns more oxygen than any other animal tissue. The amount of oxygen supplied to an insect’s muscles directly depends on the amount of oxygen in the air. Given these facts, it makes sense that giant insects would struggle to get by in a low oxygen atmosphere.

However, Harrison points out that the presumption that the Paleozoic oxygen pulse actually caused the evolution of giant insects rests more on inference than evidence. There are no living giant insects, or fossils of their tracheae.

As a result, biologists are forced to study the next best thing: related species still alive and crawling and flying today. A convincing test of the oxygen pulse hypothesis will depend on the weight of evidence from studies of several species. This takes time. Harrison and his students are contributing to the effort.

“Our work is important because it is the first research I am aware of to experimentally test Graham and Dudley’s hypothesis,” he says.

But until he and others produce the necessary data, Harrison’s good scientific sense requires him to take other possible explanations into consideration.

“There has been a lot of ‘gigantism gone extinct’ in other groups,” he explains.

Some well-known examples are the dinosaurs and the elephant-like mastodons of the Pleistocene era. In these groups, evolution has not been linked to atmospheric oxygen levels, Harrison explains.

“Obviously, there are other environmental or ecological reasons for gigantism and gigantism gone extinct,” he adds.

Some researchers might find this uncertainty unnerving. Harrison is excited by the opportunity to pursue a number of intriguing possibilities. Scribbling chalkboard figures to illustrate his points, he elaborates on numerous other evolutionary scenarios that also could have accounted for the existence of the puzzling giants.

Paleozoic insects may have been able to use other mechanisms, such as respiratory pumps, to increase airflow in their tracheae. If so, giant species could have maximized their ability to breathe even in low oxygen environments.

Ecological factors also could explain the pattern of prehistoric gigantism. For example, some insect biologists favor the idea that giant Paleozoic insects were successful because they were less likely to be eaten. Their massive bodies might have made them more powerful fighters, or made them too big to be considered feasible prey.

Another possible explanation is that increases in ecological diversity may have simply diversified body size options for insects. Being "giant" was just one of the alternatives.

Despite the abundance of competing ideas, the results of Harrison's experiments suggest that Graham and Dudley's ideas may well hold up.

In his ASU laboratory, Harrison studies grasshoppers and dragonflies, diminutive modern relatives of the prehistoric giants. He has found that these insects' activity is affected by the amount of oxygen in the atmosphere.

More importantly, the effect is more pronounced in the largest individuals, which is what the oxygen pulse hypothesis predicts. Since the biggest bugs have the longest tracheae, they should need the most oxygen to be able to breathe. Only when environmental oxygen is high will it push to the deepest reaches of the tracheae.

If this hypothesis is correct, the smallest bugs should be able to deliver adequate oxygen to the tissues even in an atmosphere with low oxygen, since their tracheae are very short.

This difference ought to be particularly apparent when the insects are challenged with an oxygen consuming activity, such as flying or jumping.

These results are precisely what Harrison sees in the laboratory.

Graduate student Scott Kirkton works with Harrison to test the aerobic performance of grasshoppers given controlled amounts of oxygen. They have found that smaller grasshoppers can hop nonstop in sub-atmospheric oxygen levels. In fact, the smallest ones are not even bothered when oxygen is as low as 5 percent.

In contrast, when larger grasshoppers are placed in the same environment, they can’t keep up. They wear out faster, and their hopping rates quickly drop to zero.

However, if Kirkton gives them an extra dose of oxygen—say 40 percent—large grasshoppers demonstrate their oxygen sensitivity by jumping more. The oxygen-stimulated boost in performance suggests that larger insects do require more oxygen.

A similar pattern emerges for dragonflies. As oxygen in the atmosphere is reduced, the dragonflies go from effortless flight to increasingly futile exertion. Eventually, when oxygen is set at a critically low level, they can’t even get off the ground. Like the hoppers, dragonflies perform better with increased oxygen, flying more energetically and breathing faster.

Whether or not the Paleozoic oxygen pulse actually triggered the rise of insect gigantism, Harrison is motivated by the more general applications of his work.

“We are most interested in defining broad scaling rules about how respiration changes with body size," he says. "There is a tight relationship between body size and metabolic rates in all animals, but no one has been able to determine why this is so."

From insects to elephants, the pattern is impressively consistent. Smaller species tend to live fast and die young. They have speedy metabolic rates and short life spans. Bigger animals are generally longer-lived, and they have more leisurely metabolic rates.

Since high metabolism demands high oxygen delivery, Harrison suspects that respiratory mechanisms may provide some valuable clues about the nature of this basic relationship.

Harrison plans to examine insect flight at higher altitudes, where oxygen naturally decreases. For this work, the record-setting metabolic rates and flight abilities of bees make them natural subjects.

Says Harrison, "What I'd really like to do is take the whole family on a drive up Pike's Peak Road. We'd throw bees out the window every 1000 feet to see if they can fly."—*Danika Painter*

The National Science Foundation supports ASU research on how the respiratory physiology of insects affects their body size. For more information, contact Jon F. Harrison, Ph.D., Department of Biology, College of Liberal Arts and Sciences, 480.965.9459. Send e-mail to J.Harrison@asu.edu

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