EVOLUTIONARY BIOLOGY

A New Theory of Insect Wing Origins Takes Off

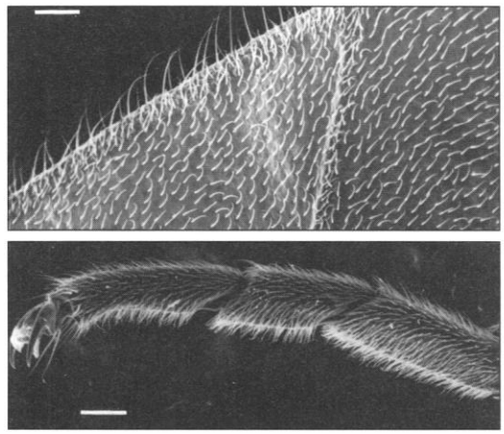
Evolutionary biologist James Marden set out on a routine fly-collecting task two winters ago, but returned with something extraordinary. As his students at Colgate University searched for mayfly nymphs in an Adirondack stream, Marden's attention wandered to stoneflies skimming across the icy waters—and he realized the creatures might hold an answer to one of biology's oldest puzzles: the origin of insect wings.

Wings are relatively large, complex structures, and as Charles Darwin himself pointed out 118 years ago, such features don't come out of nowhere. They have to start out small. But a small wing can't bear a body aloft, so rudimentary wings must have given their owners some other advantage, or natural selection would not have pushed them to become larger and more powerful. Marden's streamside inspiration was that early wings were probably good for skimming across water.

After conducting experiments with *Taeniopteryx burksi*, a species of stonefly, Marden, now at Pennsylvania State University in University Park, and undergrad Melissa Kramer have come up with support for this suggestion. On page 427 of this issue, they report that artificially shortened wings are good for skimming, and the bigger these wings get, the better the flies skim. Their conclusion: Skimming could be the impetus for a rudimentary wing evolving into one with the size and power needed for flight.

Other scientists who have wrestled with this problem—and come up with different answers—are intrigued. "[It's] a mechanism that involves the use of wings in locomotion, but it avoids the problem, literally, of getting off the ground," notes University of Washington evolutionary ecologist Joel Kingsolver, who has championed the idea that insect wings got their start as biological solar panels. Adds Robin Wootton, an insect morphologist at the University of Exeter in the United Kingdom: "I think it's something which, curiously, has escaped the attention of people thinking about the origin of flight." But he and others caution that Marden and Kramer will have an even sounder hypothesis if they can find support for their idea from the fossil record.

It's the lack of fossil evidence, however, that's kept wing development shrouded in mystery for so long. Fossils show insects had fully developed wings big enough for flight in the late Carboniferous, or 330 million years ago. But when paleontologists search farther back in the fossil record, they find the next oldest insect fossils are completely wingless; the intermediate forms are missing. But scientists perusing those wingless bodies—led by Jarmila Kukalova-Peck, a paleoentomologist at Carleton University in Ottawa—have, at least, found evidence that wings probably originated as gills that were used for swimming or gas exchange.



J. MARDEN AND M. KRAMER

Hairborne. Wet-resistant hairs on stonefly wings *(top)* and legs help the fly to swim—a trait that could explain early insect wing evolution.

Scientists have tried to fill in the gap between gills and wings with theories. In the early 1980s, University of California, Berkeley, evolutionary biologist Mimi Koehl and Kingsolver, then a postdoc in Koehl's lab, used models of insects with tinfoil or paper wings to show that small wings could collect heat and might have been selected to keep an insect warm. As the wings got larger, the duo found, the heat they collected began to dissipate before it reached the body—but at that size, the wings were big enough for gliding and turning.

But Marden found gaps in this theory and some other ideas, such as the notion that wings grew larger to attract mates. These ideas explain increasing size, he says, but they don't account for how the appendages developed the muscular and neural complexity required for flying; solar collectors, for instance, don't demand a high-powered motor. Then he noticed the skimming stoneflies, and "it all just clicked."

Stoneflies are an ancient family of insect that differ little from their ancestors in the Carboniferous. "They're good candidates because they're extremely primitive," says Kukalova-Peck, which means they are likely to still manifest ancient behavior or anatomy. Marden and Kramer began lab experiments with *T. burksi*, which, as an adult, moves by flapping its way across water with its legs touching the surface; its wings are too weak for more than feeble attempts to fly. Marden and Kramer cut back *T. burksi* wings to as much as 20% of their original length, and found that the stoneflies could still skim. And they got progressively more adroit as their wing size increased. That meant even small wings could have allowed skimming, and natural selection would have favored larger wings as the stoneflies evolved.

The two scientists thus propose the following scenario: Ancestors of winged insects were aquatic creatures with gills. To escape water's drag, insects began using their gill plates to row across the water. Rowing gave way to skimming, and eventually these wings became large enough and strong enough for the insects to take flight.

Marden and Kramer have made "a strong argument for [skimming as] an evolutionary stage," notes John Lighton, an insect physiologist at the University of Utah. But he also notes that this interpretation relies on using the skimming stoneflies as living fossils, representative of earlier insect evolution. And there's a chance that, just as some current cave-dwelling creatures have lost the ability to see, stoneflies actually flew earlier in their history and only recently reverted to being nonfliers. Marden and Kramer would have a "stronger case," Lighton says, if researchers can show that primitive stoneflies skimmed.

Marden and Kramer think they may have a way to do just that. *T. burksi* wings, they note, have hairs that seem to help the insects float on water, but would be a hindrance for flight. And young mayflies—stonefly cousins—have these hairs and move by skimming, but lose them when they become flying adults. If scientists were to re-examine Carboniferous insect fossils and find these hairs, that would support the notion that skimming was a primitive trait.

Koehl says that another potential test of the theory would be to examine many modern species and establish if only the skimming insects have wing hairs. Indeed, she says, one of the major attractions of the skimming notion is that it's "a neat new idea that suggests a lot of ways to test it." No matter what further experiments show, she and other scientists say, Marden and Kramer have already made a big splash in a field heavy on armchair theorizing and short on experimental data. "This is one of those papers that we call heuristic," Lighton agrees. "Even if it turns out to be wrong, we've learned something."

–Jocelyn Kaiser