

recommends, not surprisingly, that the chemical industry should strengthen its ties to academe, perhaps with the help of new federal tax incentives.

But then the committee moves on to its major finding, which is that the federal investment in chemistry is meager compared to the more glamorous big science disciplines such as physics and astronomy, and clearly incommensurate with the practical importance of the field. Unfortunately, as some committee members privately agree, this assertion is perhaps the weakest part of the whole report. As an example, consider one measure used to demonstrate the discrepancy: the number of federal basic research dollars invested in a given field in a given year, divided by the number of Ph.D.'s granted in that year. The discrepancy is indeed as much as an order of magnitude—\$205,000 per chemistry Ph.D. in 1983 versus \$1.09 million per physics Ph.D. and \$3.8 million per astronomy Ph.D. And yet, only one page later, the report goes on to point with pride to the fact that chemistry is still a

relatively small-scale, individualistic science—without ever trying to analyze how the aforementioned funding figures might reflect the different costs of doing physics or astronomy.

In any case, the committee recommends that the National Science Foundation (NSF) boost its support for chemistry—which currently stands at roughly \$350 million per year—by 25 percent per year for the next 3 years. These additional funds should go toward increasing the average size of individual grants to reflect the fact that research projects now tend to involve more people, and toward increasing the federal support of advanced instrumentation—the latter being an item that has absorbed virtually all of the growth in the federal funding of chemistry during the last decade.

The committee likewise urges the various mission agencies to recognize the importance of chemistry to their own program and to increase their support accordingly. The National Institutes of Health, for example, should increase its grants for chemical research related to

biomedicine, and should raise its support for chemical instrumentation in much the same way as recommended for the NSF. The Department of Energy, meanwhile, should plan a major initiative in those areas of chemistry relevant to energy technologies, with support for chemistry increasing by a factor of 2.5 over the next 5 years. Examples might include detergents to be injected into oil-bearing strata to aid tertiary oil recovery, or improvements in the utilization of low-grade fuels.

Similar increases were recommended for the Departments of Defense and Agriculture, the National Aeronautics and Space Administration, and the Environmental Protection Agency.

It is anyone's guess whether this increase in support will actually materialize, especially given the size of the federal deficit and the competition for the federal research budget by other disciplines. Even if it does not, however, the committee can still hope that the report will change the current pattern of funding chemistry.—**M. MITCHELL WALDROP**

On the Origin of Insect Wings

Experimental data on thermoregulation and aerodynamics give the first quantitative test of a popular hypothesis for the evolution of flight in insects

The evolution of insect wings, like the origin of flight in vertebrates, has long been a challenge to the explanatory powers of evolutionary biologists. Both cases present essentially the same problem: how do you pass from a wingless ancestor to a flying descendant, when intermediate forms would be incapable of flight? Natural selection cannot work on structures that are as yet functionally incompetent.

This conundrum has spurred the elaboration of many imaginative and ingenious suggestions in the case of insects, including the initial evolution of "proto-wings" for gliding, for courtship display, for gill ventilation and aquatic locomotion, and for thermoregulation, but direct experimental tests of hypotheses have been few. In an elegant series of studies Joel Kingsolver, at Brown University, and M. A. R. Koehl, at the University of California, Berkeley, have obtained data that should allow a more secure assessment of certain insect flight hypotheses than has previously been possible (1).

Kingsolver and Koehl's experiments focused on the proposal, first developed

in detail in the late 1970's (2), that insect wings derived from thermoregulatory structures that projected laterally from the body. The proposal was that natural selection worked first on the heat exchange benefits endowed by "proto-wings" (3) and then, when aerodynamic effects began to be felt, on the benefits of flight. There was, in other words, a shift of function, an exaptation (4), that allowed the development of fully fledged flight from structures that readily served as wings but had initially evolved for other purposes.

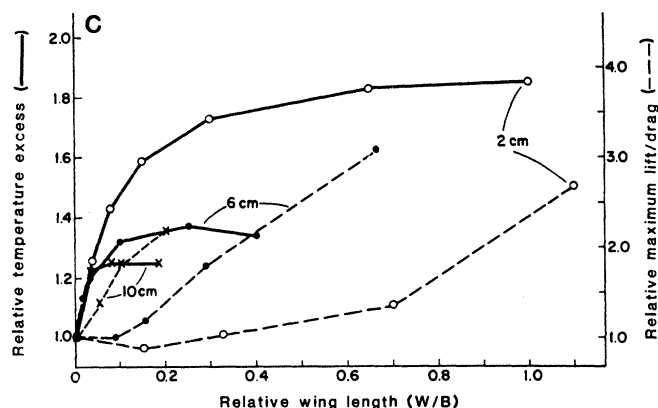
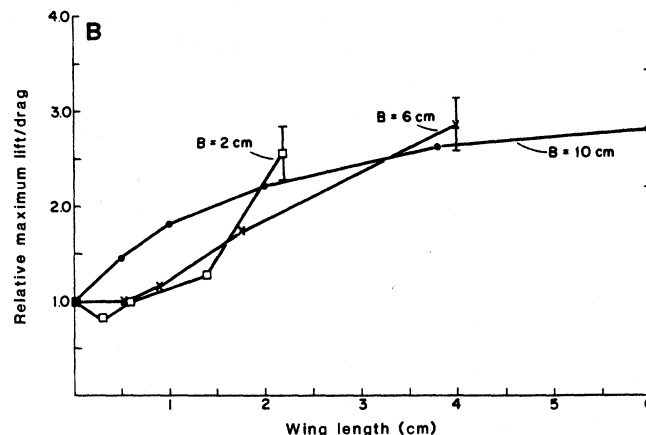
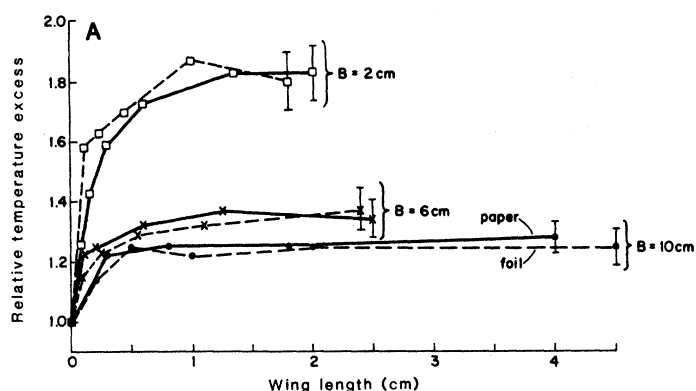
The idea sounded attractive enough in principle, and, judging from Kingsolver and Koehl's quantitative data, it turns out to be feasible too. Of particular interest in these results is the potential evolutionary importance of a simple increase in body size as compared with a modification in body geometry.

One reason why Kingsolver and Koehl addressed the plausibility of the thermoregulation and aerodynamic hypotheses is, simply, that they are amenable to experimental test. By contrast, it is very difficult to see how one might critically

examine the idea that "proto-wings" might have functioned initially in courtship display.

By building various models of putative ancestral insect bodies, Kingsolver and Koehl were able to ask the following questions: What size of wing is effective in thermoregulation? At what size do "proto-wings" become aerodynamically effective at particular body sizes? And how do these two relate to each other, particularly to a potential transition from one function to the other?

Some modern insects (such as bumble bees) generate body heat by muscular contraction while others (including butterflies) use their wings to soak up the sun's warmth. In both cases a high body temperature is important for fast, powered flight. The investigators made the assumption that heat uptake was the principal function of "proto-wings." Measurements with the models show that increasing the size of the "proto-wing" increased the amount of heat that could be transmitted from the wings to the body by conduction, but an upper limit was quickly reached. The reason is



Flying by numbers

The increase in thermoregulatory capacity achieved by increasing "proto-wing" length quickly plateaus, as shown in diagram A. Natural selection for increased "proto-wing" length would cease after about 1 cm, in all body sizes ($B = 2$ cm, etc). Aerodynamic tests show that, except in very large insects ($B = 10$ cm), lift becomes significant once "proto-wings" exceed about 1.5 cm (diagram B). This means that for moderate- to small-sized insects, there is an adaptive vacuum between thermoregulation and aerodynamics; the gap is closed in larger insects. Diagram C puts the two sets of data together, showing the effects in terms of relative, rather than absolute, "proto-wing" sizes.

that beyond a "proto-wing" length of about 1 cm heat begins to be lost by convection.

The data from heat exchange experiments on the insect models clearly show a potential for natural selection to operate between minimal "proto-wing" length up to about 1 cm (see diagram A). This result, say Kingsolver and Koehl, is "consistent with the hypothesis that the initial evolution of wings from ancestors with small winglets was related to selection for increased thermoregulatory capacity, which would be particularly effective at the small body size of the earliest insects."

On, then, to aerodynamics. Some investigators have proposed that small "proto-wings" may have served as aerofoils by which insects could glide following prodigious leaps or by jumping from vegetation. However, Kingsolver and Koehl's data from wind tunnel experiments show that aerodynamic effects are minimal until the "proto-wing" significantly exceeds 1.0 to 1.5 cm in length, except at large body sizes (see diagram B). Now, as the first winged insects are thought to have been relatively small bodied (in the range of 2 to 4 cm), the aerodynamic hypothesis appears to be untenable. But how do these data fit with the thermoregulatory hypothesis?

First of all, the relationship between body and wing length and its effect on effective lift is clearly important. The smaller the insect, the larger its "proto-

wing" has to be before aerodynamic benefits can be enjoyed. If the first flying insects did indeed derive from ancestors of a mere 2 cm body length, then their wings would have to have been as much as 1.5 cm long before aerodynamic effects became significant. Less than this and natural selection for flight would have been inoperative. But 1.5 cm exceeds the length at which natural selection for thermoregulatory effects ceases in insects of this size. In other words, there would have been an adaptive vacuum, which would have blocked further "proto-wing" elongation.

A slightly larger-bodied insect, however, would close the gap between the adaptive canopies of thermoregulation on one side and flight on the other, and natural selection could begin to take effect, thus lengthening the "proto-wing" to full wing dimensions.

However, a different potential means of transition between "proto-winged" ancestor and winged descendant emerged unexpectedly from these figures. The means become clear if one considers two cases: The first is a 2 cm insect with 1 cm wings (that is, 50 percent of its body length), which is close to the upper limit of the thermoregulatory adaptive canopy but still short of the realm of aerodynamic effects. And the second is a 4 cm insect whose wings are also 50 percent of its body length. In this second case selection for flight can operate because the "proto-wings" are 2 cm

long, which is within the realm of aerodynamic effects.

Now, if there were a simple increase in the body size of the first insect, from 2 cm to 4 cm, perhaps for reasons totally unrelated to either thermoregulation or flight, such as fecundity or survivorship, the descendants would find themselves under a new adaptive canopy. The reason is that the concomitant doubling of wing size takes them out of the realm of thermoregulatory effects and into the realm of aerodynamics: they would now have the potential for flight. "This means that geometrically identical forms may serve different functions at different body sizes," note Kingsolver and Koehl.

The idea that a dramatic change in the function of a structure might come about *without* a change in geometry—in other words, a drastic redesign—is unfamiliar to most biologists. Instead, there has long been a considerable, and legitimate, fascination with developmental modifications that might lead to the alteration of the form of existing structures, which can then perform new functions. That the potential for functional modification results from a simple increase in size is a most exciting insight to have emerged from these data.—ROGER LEWIN

References

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