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Insect Morphology Above the Molecular Level: Biomechanics

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ABSTRACT In contrast to what is suggested by Gupta (Gupta, A. P. 1994. Insect anatomy-morphology: quo vadis? Ann. Entomol. Soc. Am. 87: 147-156), insect morphology does not have to be pursued at the molecular level to be cutting edge. For example, biomechanical analyses of morphology allow new knowledge and predictive relationships from new interpretations of morphology.

KEY WORDS biomechanics, morphology, mechanics

GUPTA (1994) PREDICTED that in upcoming decades new knowledge in insect anatomy-morphology will come primarily from studies at the molecular level. Gupta hastened to add that "classical anatomy-morphology at the gross, macro and micro, ultrastructural, and subcellular levels" will still be needed and relevant but primarily as "pre-requisites" for the molecular-level studies. Although I agree with Gupta that we should expect interesting new findings from molecular-level morphological studies, morphological studies above the molecular level certainly do more than just provide context for molecular-level morphology. For example, biomechanical analyses of morphology at all levels of magnification do nothing less radical than change the way we think about structures.

Biomechanics is the application of mechanical principles to biological systems (for outstanding introductions to the field see Wainwright et al. 1976, Alexander 1983, Pennycuik 1992, Vogel 1994). Biomechanical studies can run the gamut from morphology to physiology, but for purposes of responding to Gupta it is most useful if we follow his definition of morphology, which is a good one: the conceptualization of form in an anatomical, functional, and evolutionary context. Thus, morphology contrasts with purely descriptive anatomy. Gupta pointed out that this view of morphology may tend to "blur the traditional boundaries between morphology and physiology"; like Gupta, I do not see this as a problem.

Results from a biomechanical analysis of morphology can be both surprising and powerful. Results can be surprising because many mechanical phenomena are nonintuitive or even counterintuitive, especially to those not trained in the physical sciences. Can one look at the size and shape of an insect antenna and know anything a priori about its capacity to intercept chemical signals from the air; or look at the size and shape of an insect wing and know anything about its capacity to produce

lift and thrust? The power of a biomechanical analysis results from its ability to generate testable functional hypotheses about the performance of a structure. Obviously, the movement of the structure, its material properties, and the physical properties of the surrounding medium (e.g., air or water) also determine its function; but a biomechanical analysis of form can predict under what conditions a structure will function in a particular way.

A major reason why our own intuition is so unreliable when it comes to interpreting the insect world, is that smaller organisms inhabit a different physical world than we do; different physical processes scale differently with size. These differences lead to a number of interesting morphological trends (and interesting books on scaling, e.g., McMahon & Bonner 1983). For example, gravity and so-called inertial forces (resulting from changes in momentum) tend to be less important for smaller organisms than they are for larger organisms, and viscous forces and surface tension tend to be more important. Size affects function in addition to, and independently of, shape. One simple instance of a curious phenomenon affecting small objects is *critical radius* in heat transfer. For a body below a certain size (critical radius), the addition of insulation may in fact *increase* heat exchange rather than reduce it. Imagine getting colder after putting on a coat! This reversal occurs when the increase in surface area that follows from adding insulation more strongly promotes heat exchange than the change in thermal conductivity reduces it. The relevance of critical radius for heat exchange in very small insects is still unknown (Turner & Schroter 1985), although the (ordinary) insulating properties of hairs on caterpillars has been documented (Casey & Hegel 1981).

Below are three examples of studies in which biomechanical analysis has changed the way in

which we view particular structures: wings, sucking mouthparts, and antennae.

Wings. The ability to fly using wings influences many aspects of the lives of most insects. Therefore, there has been a great deal of interest both in understanding the functional significance of wing morphology in extant forms and in the evolution of wings in the insect groups (Wootton 1990). For example, recent biomechanical studies have evaluated competing hypotheses for the adaptive significance of hypothetical small winglets in the evolution of wings (Kingsolver & Koehl 1985, 1994; Wootton & Ellington 1991). Kingsolver & Koehl (1985) evaluated competing thermoregulatory and aerodynamic hypotheses for these hypothetical small winglets. Using physical modeling, they were able to show that short wings seem to confer no aerodynamic advantage relative to the wingless state, although significantly affecting thermoregulatory processes. In contrast, increasing wing length beyond a certain point no longer affected thermoregulatory capacity but did enhance aerodynamic performance. Thus, the authors hypothesized that in geological time, insect wings may have initially served a thermoregulatory function and were (later) used for aerodynamic functions at larger sizes. Furthermore, the authors pointed out that an isometric increase in wing and body size (i.e., no change in shape) could bring about a change in function of the wings from primarily thermoregulatory to primarily aerodynamic.

Wootton & Ellington (1991) also used physical models to evaluate aerodynamic performance of hypothetical winglets relative to a wingless state and also found that the absolute size of the insect model made a large difference in the aerodynamic capabilities conferred by the winglets (greater aerodynamic performance at larger sizes). However, unlike Kingsolver & Koehl (1985), Wootton & Ellington found that even small winglets (length 5% of body length) would improve the gliding performance by decreasing the terminal velocity (the insect would not hit the ground so hard) and make it more likely that the insect would land the right way up; these aerodynamic enhancements would occur only if the winglets were positioned at a certain angle relative to the body and were measured for larger models in faster air flows than used in the Kingsolver & Koehl study. Therefore, the interpretation of events that occurred during the evolution of wings in insects is completely dependent on assumptions made about the body-size range in the protopterygote populations and the ability of the insects to change the positions of their winglets (Wootton & Ellington 1991, Kingsolver & Koehl 1994). These biomechanical studies have changed the way we think about wing morphology and wing evolution because they have delimited some of the functional consequences of changes in wing structure or size as well as alerted us to the potential of nonaerodynamic functions

(see Kingsolver & Koehl 1994 and references therein for more discussion).

Sucking Mouthparts. Many insects feed on fluids through mouthparts that resemble small hollow tubes (e.g., butterflies, mosquitoes, lice, and aphids). Biomechanical analyses of feeding on different fluids (blood and nectar) predict that the primary anatomical feature of the mouthparts that will affect the flow rate of fluid material is the inner radius; this is because the flow rate of fluid through a cylinder increases with the *fourth* power of the radius of the tube (Hagen-Poiseuille Law) (Bennet-Clark 1963, Kingsolver & Daniel 1979, Daniel & Kingsolver 1983). Thus, an insect feeding with mouthparts half the (lumen) diameter of another insect will generate only 6% of the volume flow rate of the other insect, all other factors remaining equal. It follows that from mouthpart anatomy, it is possible to predict the rate of fluid intake for a given pressure differential and fluid or conversely to estimate the sucking pressure drop from the observed feeding rate (Bennet-Clark 1963, Kingsolver & Daniel 1979).

One might assume that, the more concentrated the fluid an insect is sucking (such as a greater hematocrit for blood or a greater sucrose concentration for nectar), the greater the rate of nutrient uptake the insect would achieve. In fact, a more concentrated solution is more viscous, and will, therefore, flow more slowly along tubular mouthparts at a given sucking pressure differential. Daniel & Kingsolver (1983) argued that the mathematical nature of the relationship between viscosity and concentration (viscosity tends to increase exponentially with concentration of solute or suspended particle) will produce an intermediate (optimal) concentration that will maximize food intake. Specifically, they predicted that a sucrose concentration in the range 35–45% for nectar will tend to maximize the rate of sucrose intake for the anatomical range of butterfly mouthparts they investigated, whereas a hematocrit of 0.60–0.65 will tend to maximize the total protein uptake for the anatomical range of the blood feeders investigated (Kingsolver & Daniel 1993). Laboratory studies measuring nectar uptake rates by butterflies have found maximal energy intake rates at sucrose concentrations in the range 35–50%, consistent with these predictions (Kingsolver & Daniel 1993). The authors note that the hematocrit range predicted to maximize protein uptake by blood feeders (0.60–0.65) exceeds the normal range in humans (0.30–0.45); thus, the rate of protein intake by a mosquito feeding on human blood, for example, will tend to increase with increasing hematocrit. Blood in humans with blood parasite infections can differ in fluid properties from blood in healthy humans (both in hematocrit and in red blood cell properties); therefore, if blood feeders can behaviorally discriminate among hosts with and without blood parasite infections, this could have important implications for the evolution of disease transmis-

sion (Daniel & Kingsolver 1983, Kingsolver & Daniel 1993).

Antennae. Consider flow past arrays of tiny cylinders such as sensory hairs on antennae. The flow past arrays of tiny cylinders behaves in a very viscous manner, which means that the boundary layers around the cylinders are large relative to their diameters, and that much of the fluid (air or water) approaching the array is likely to be diverted around, rather than pass through, the array. This is important for chemical signal interception because air that is diverted around an antenna is unavailable for sampling. Vogel (1983) measured the reluctance of air to pass through antennae of the male luna moth, *Actias luna* (L.): only 8–18% of the air approaching an antenna passed through. Only recently has the functional significance of anatomical differences among antennae such as sensory hair length, diameter, spacing, and arrangement begun to be estimated theoretically and empirically by fluid mechanical methods. For the simplest possible case of flow through an array (two infinitely long hairs), Cheer & Koehl (1987) have shown mathematically that in very viscous air flow (corresponding to an ambient air flow of 1 cm s^{-1} and $2\text{-}\mu\text{m}$ diameter sensory hairs), barely >20% of the air approaching the gap between the two hairs would pass through (a leakiness of 20%) even when the gap is enormous (50 times the diameter of one of the hairs). In air moving faster, as at 1 m s^{-1} , viscous forces have less relative importance and smaller changes in hair spacing translate into bigger differences in leakiness; hairs 5 diameters apart have a leakiness close to 20%, whereas hairs 15 diameters apart now have a leakiness closer to 45%. An empirical study using physical modeling has confirmed the theoretical results for the faster flows and shown the importance of nearby structures in influencing the flow and thus the chemical signal interception (Loudon et al. 1994). Thus, there are some flow regimes (or air speeds) within which some anatomical differences (such as hair spacing) translate into large functional differences (such as leakiness), and other flow regimes within which the same anatomical differences are functionally neutral.

These three examples of biomechanical studies demonstrate the kind of new information available about the function of these particular insect structures. Biological structures are complex; thus, it is easy to become swamped in anatomical minutiae when describing or observing anatomy. What is important to report? And what do we tend to notice in the first place? The size of hairs or their spacing? The curvature? The distribution of surface irregularities or their size? The area (and would this be projected area or *wettable* surface area or cross-sectional area?)? We tend to think in simple proportional terms (if a structure is twice as big, does it have twice the effect?), but one of the important lessons coming from biomechanical studies is that sometimes a large anatomical change is without

functional correlation and sometimes a small anatomical change makes a huge difference. If morphology is truly "what you think you see with your mind" (from the delightful quote by Snodgrass repeated in Gupta 1994; p. 148), then biomechanical studies will focus our minds as well as our eyes on insect structures. This is how the application of biomechanics can generate new anatomical-morphological information—because it helps us to know where to look and how to look (e.g., is the length important or the length:width ratio?).

Although Gupta (1994) suggested that studies in *molecular anatomy-morphology* "will become the fountainheads to understand and elucidate many of the behavioral, functional, and taxonomic aspects of insects encompassing other subdisciplines of entomology," the comparable potential of biomechanical techniques should be evident from the three examples of biomechanical studies described above. Significantly, one of Gupta's own examples of recent cutting-edge studies in insect morphology was a biomechanical study by Henderson & Locke (1991). Henderson & Locke were able to interpret actin rings functionally (as support structures) because they drew explicitly on mechanical, not molecular, concepts. In fact, the rings could have been made of a different material entirely and had similar strengthening properties. Relationships between forces and geometry do not follow logically by extension from molecular biology; these predictive physical relationships come directly from classical mechanics or mechanical engineering. Thus, the science of mechanics provides a source of additional information with which to make interpretations of morphology.

Gupta is to be commended for encouraging morphological studies that place anatomy in a functional context. However, morphological studies that change the way in which we view or interpret form or structure are important studies whether the tools are molecular or biomechanical or something else entirely. As scientists we should focus primarily on the questions addressed by our studies rather than on the technological tools used. What then are the important outstanding questions in insect morphology, and are they most appropriately addressed using molecular techniques, as implied by Gupta? Certainly, morphological questions about development (e.g., cell lineage) and biosynthesis are often best addressed using molecular techniques. However, other important questions remain in morphology that are best addressed using biomechanical and phylogenetic techniques. These areas include the identification of functionally neutral and functionally significant morphological changes (including size changes), the recognition of changes in *nominal structure* by context (a structure can *behave* larger or smaller depending on different ambient flows, for example), the functional integration of different parts of the body, and the related issue of the evolution of complex structures and functions (such as seen in the

approach of Lauder 1991). Surely a recognition of the breadth of studies and questions that comprise insect morphology will help keep morphology an active, provocative, and interesting area, whereas narrowing the range of studies that are considered insect morphology will serve only to decrease the number of scientists who will interact and call themselves morphologists.

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