The emergence of comparative biomechanics

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Synopsis In recent years, comparative biomechanics, while anything but a new subject, has by an odd concatenation of circumstances emerged from obscurity to become a widely recognized and active area of biology—remarkably diverse in questions asked and techniques employed but with clear intellectual coherence. In North America the Society for Integrative and Comparative Biology currently represents the center of gravity in this field.

Emergence . . . 3. "*an unpredictable development, as in evolution*" [Random House Dictionary of the English Language, College Edition, 1968]

Biomechanical metaphors pervade our speech—"put the bite on," "get in the swim," "twist his arm," "bent out of shape," "keep your head up." No area of biology, not even mating behavior, is as close to our everyday, intuitively familiar world. Or perhaps, in this viagrified world, biomechanics can lay claim to sex itself. So the subject of biomechanics is nothing if not close to home. In its comparative—read "biological"—version, biomechanics pervades the Society for Integrative and Comparative Biology as well. During the 1990s the fraction of contributions to the annual meeting that I identify as biomechanical rose from about 5% to around 25%; it has remained at that latter level since then and has just acquired its own division. In Britain, the Society for Experimental Biology (SEB) has experienced an analogous increase. Books at all levels have become common; a related, applied field, biomimetics, draws ever-increasing attention; science museums are discovering its appeal; and a biomechanical piece is a regular feature of each issue of *Natural History*.

This ever wider swath cut by biomechanics makes it at this point the most visible and fashionable versions of both comparative physiology and functional morphology. How has this happened? Why now? Where to from here? A bit of reflection might be timely, even from someone who must use intimacy with the subject to excuse his lack of credentials as historian or sociologist of science.

First, if comparative biomechanics asks such obvious questions, why did its widespread pursuit not begin earlier? Part of its tardiness may rest with the physics courses traditionally taken by neonatal biologists. In them, we encounter a world of rigid bodies making perfectly elastic collisions in vacuums—a start, perhaps, but one lacking an adequate bridge to our world of complexly flexible creatures comporting themselves in their viscous media. We have been disadvantaged by an accident of academic organization—would that colleges of arts and sciences provided berths for mechanical engineers! Student evaluations of my course repeatedly commented that they were startled to find physics relevant to biology—in a class that prerequired a year of college physics. Of course such self-serving off-loading of blame ignores the almost equal antipathy of traditional biologists to immersion in other obviously relevant fields such as chemistry and mathematics.

In fact the field has ancient roots and has suffered no period of total eclipse or inattention. We might pass over Aristotle's *De Motu Animalium* (Nussbaum 1978) as a set of largely incorrect shots-in-the-dark, but one can recognize proper biomechanical work by both Galileo (1564–1642) and William Harvey (1578–1657)—the former on solids, the latter on fluids. I think the key event, though, was publication of Giovanni Alphonso Borelli's isonymic *De Motu Animalium*, in 1680, 327 years ago. A fine volume on terrestrial locomotion appeared early in the 19th century (Weber and Weber 1825). Later in that century Samuel Haughton (1873) tackled a variety of familiar problems including a serious analysis of the biomechanics of death by hanging, undertaken to ensure properly humane procedure. By publicly doubting Darwin, Haughton just happened to lose in posterity's sweepstakes. Several people measured the power output of humans in the 18th century, and by the

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end of the 19th century reliable data were available on the outputs of common draft animals as well (see, for instance, Thurston, 1894) and on load carriage by soldiers (see Lothian, 1921, 1922). Until recently such things were of practical significance, not just, as now, aspects of athletic fanaticism. Another ancestral line looked at the shapes of biological entities from geometric and mechanical viewpoints—besides the well-known one by D'Arcy Thompson (1917) we might note books by James Bell Pettigrew (1908) and Theodore Andrea Cook (1914). But I think it fair to say that, for one reason or another, none of this interest initiated a mainstream discipline.

Only following the impetus provided by James Gray, at Cambridge University in the 1930's, can we recognize a discrete field in an operational as well as an intellectual sense. We might mark that as our effective founding in person, place, and time, in the same way that geneticists can point to Morgan and Sturtevant at Columbia University in the first decade of the 20th century. A remarkable fraction of the people now active in field can trace some sequence of formal links back to Gray's Zoology Department at Cambridge. At the same time, comparative biomechanics has been enriched by people from traditional comparative physiology and, most notably, from various areas of engineering.

As much as anything the present emphasis reflects a peculiarly prolific branch of that Cambridge trunk; this subsidiary efflorescence deserves a few words—which should be read with the special grain of salt reserved for anything at all autobiographical. During the late 1960s, Steve Wainwright and I worked together in an introductory course in biology in the Zoology Department at Duke, and we remained close professional and personal associates through the 1970s. Wainwright did solid mechanics and functional morphology using marine invertebrates; I did fluid mechanics and physiology, mainly with terrestrial insects and trees. It now seems inexplicable that we never explored a possible relationship between the two kinds of activities. We even gave separate courses derived from our interests, he with a radiation biologist as physical biology and I in a seminar course on fluids in biology.

In the 1970s, one of Wainwright's graduate students, Mimi Koehl, produced a remarkable doctoral thesis that looked at how the peculiarities of the solid mechanics of some sea anemones reflected their fluid mechanical interactions with their habitats (Koehl 1976). As I recall it, almost 30 years later, her thesis examination triggered the conversation that led us to give, in the following year, a course we called "biomechanics," renamed ten years later, "comparative biomechanics." In all, the course was given 26 times; by the time Wainwright retired, I felt adequately prepared by him to continue what had been his portion, solids. While I mention the course on account of my direct participation, the larger contribution came from Wainwright's peculiar genius in stimulating students in tutorials and other direct interactions. I have not met his equal in sensing the special talents of diverse individuals and gently launching and effectively supporting them as they defined and explored their separate domains. They did appear to benefit from exposure to both of us—in particular to our quite different scientific styles. My own contribution has most likely come more from words written than from direct interaction and dialog.

The way this particular ball got rolling might be held up as an object lesson for deans and other university administrators. A department, urged on by a few persuasive members, developed a tradition of hiring eclectic and interactive generalists, a tradition that became self-perpetuating as these people generated a spreading antipathy towards what they derided as hyperspecialized philistines. It hired young, and it supported its new members, but with only the gentlest directional guidance. The result was excellence by almost any relevant criterion—in teaching undergraduates, in attracting and launching graduate students, in initiating new lines of work, in a remarkable level of internal scientific hybridization, and in an extraordinarily long shelf of books. If the history of the Duke Zoology Department from about 1960 to 2000 says anything, it is that administrators should be facilitators and enablers, not instigators or, worse, directors. Appoint the right kind of people and then support any reasonable initiative—bottom-up rather than top-down management is especially appropriate for dealing with university faculty whom, after all, are picked for their initiative and creativity.

What might be said of comparative biomechanics at this juncture? Clearly its conjunction of solid and fluid mechanics has been seminal. In engineering the two areas represent obviously separate traditions; in biology, less obviously, one has emerged from morphology and the other from physiology. Combined, they give literal meaning to the scatological expression, "when the shit hit the fan." To the extent that institutions prefer the new and the interdisciplinary, we can make a credible claim to be both; deliberately cultivating visibility matters quite a lot in contemporary academia.

In a sense, comparative biomechanics carries the anachronistic odor of 19th rather then 20th or 21st century science—immature and underexploited.

One might adopt an ecological analogy to describe our present situation. Using variables from the standard logistic equation as labels, ecology texts distinguish between *r*-selected species and *K*-selected species. Individuals of *r*-selected ones, to remind ourselves, establish themselves in recently disturbed or otherwise underutilized habitats, and their populations expand rapidly. Their worlds are ones of minimal competition (beyond relative dispersal ability) and the positive feedback of exponential growth. By contrast, members of *K*-selected species deal with well-populated, severely competitive—essentially filled—worlds and the negative feedback of resource-limited growth. With more scientists active than ever before in human history, most areas of science resemble *K*-selected species, with success going to the narrow-niche specialist and the interpersonal competitor. By contrast, comparative biomechanics remains highly *r*-selected, an unfilled world in which good problems outnumber investigators.

That makes ours a particularly nice world. Situations that are *r*-selected, whether ecological or scientific, share some pleasant characteristics. Once up and running, the chance of success is high—whether in terms of reproduction or as significant advance and academic success. And competition—whether for sunlight or scientific priority—is low. So a graduate student, even an undergraduate, can stake a claim to a decent chunk of reality and can, to advantage, start by proclaiming rather than concealing the claim. We may slice things ever finer, but the slices remain agreeably thick compared with those in most other areas. And one doesn't have to fearfully keep ears to the ground and eyes on the literature, ever worried that someone has beaten you to the next step.

Additionally, that character permits, even encourages, the best of interpersonal relationships between colleagues and between mentors and students—it even blurs that last distinction. Still, permissiveness is far from assuredness, so we should account ourselves fortunate to have harbored some key individuals. I mean people not merely of high scientific acumen and productivity, but of what might be described as intellectual generosity. That senior figures can afford to give away promising problems does not mean that they will in fact do so. Similarly, discovering that some famous predecessor blundered may be a sign of one's own excellence, but it may be counterproductive career-wise—if those predecessors do not have that proper generosity, that largeness of personal, academic, and scientific spirit. Our founding generation has engendered not only a large number of academic offspring but a tradition of such generosity. As much as any area of science, we have been, as in the motto of the Society of Sigma Xi, "companions in zealous research."

I note this character, from which I have benefited and which I have tried to practice, not to pat our collective backs—a biomechanic will recognize the hazard of patting one's own back—nor to mourn its incipient deterioration. To invoke again the ecological analogy, populations grow and habitats fill; *r*-selected behavior carries ever less reward and *K*-selected behavior yet more. Or, adopting a Kuhnian view, revolutionary science becomes routine science. So academic practices that were at one stage, one might say, natural, must then be deliberately cultivated and intentionally perpetuated. We will need to exert ourselves to make sure that comparative biomechanics retains the spirit that, in effect, we celebrate here.

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References

Borelli GA. 1680. De motu animalium. 1989. P. Maquet (trans.). Berlin: Springer-Verlag. 1989.

Cook TA. 1914. The curves of life. London: Constable and Co.

Haughton S. 1873. Principles of animal mechanics. London: Longmans, Green and Co.

Koehl MAR. (1976). *Mechanical design in sea anemones*. [PhD Thesis]. Durham, NC: Duke University.

Lothian NV. 1921. The load carried by the soldier. J Roy Army Med Corps 37:241–263; 342–51; 448–58.

Lothian NV. 1922. The load carried by the soldier. J Roy Army Med Corps 38:9–24.

Nussbaum MC. 1978. Aristotle's de motu animalium. Princeton, NJ: Princeton University Press.

Pettigrew JB. 1908. Design in nature. London: Longmans, Green and Co.

Thompson DW. 1917. On growth and form. Cambridge, UK: Cambridge University Press.

Thurston RH. 1894. The animal as a machine and a prime mover and the laws of energetics. New York: John Wiley and Sons.

Weber WE, Weber E. 1825. Mechanik der Menschlichen Gehwerkzeuge P. Maquet and R. Furlong (trans.). Berlin: Springer-Verlag. 1992.