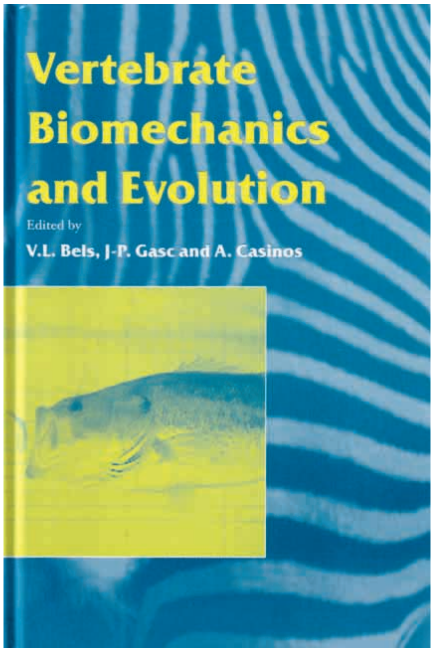
Book Review

# DOCTOR PANGLOSS RETIRES FROM BIOMECHANICS



## Vertebrate Biomechanics and Evolution

### Edited by V. L. Bels, J.-P. Gasc and A. Casinos

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“*The idea that animals are designed is dead, killed by Hume, buried, perhaps unwittingly by Darwin, but however comprehensively it is disposed of, like the walking dead it haunts us still.*” (Ollason, 1987)

Biomechanics has often come in the guise of adaptationism. What could be more intuitive than the question “*What is this structure good for?*” Biomechanics has also become the classic tool with which to explain form and function in organisms. In 19 chapters, the fruits of a conference on ‘Evolution and Biomechanics’ in Canterbury 2000, the book shows how studies of modern biomechanics address ‘design’ in animals: what determines how vertebrates propel themselves, process food or breathe? The contributing authors show how modern biomechanics can be used to dispel quite a few just-so stories. For example, our human ancestor Lucy might have been just as efficient a walker as modern humans, despite her relatively short legs. Lucy has a similar body shape to children, which Heglund (chapter 17) finds are just as efficient walkers as adults. Heterocercal fish tails were supposed to generate a torque that pitches the body nose-down, and the pectoral fins counteract this torque. But Lauder and colleagues (chapter 8) find that this is only partly true for sharks, and not at all for sturgeons. According to van Damme and colleagues (chapter 16), this type of biomechanical study contributes to evolutionary biology by focussing on the ‘performance gradient’, the connection from genes to morphology to performance. The focus often lies on the latter step: two chapters show how bird skulls cope with the forces and movements necessary to crack seed pods; other chapters relate respiration, suction feeding or locomotory performance to mouth, muscle and body morphology.

Evolutionary biomechanics, just like evolutionary biology, needs to address two important questions: first, is a particular trait heritable; and second, is this trait adaptive or random? The first question requires phylogenetic data or selection experiments. The second question requires context information from other disciplines (e.g. biochemistry, ecology) to understand the problems and constraints faced by the organism. To explore heritability, biomechanists have learnt much from evolutionary biology: many chapters proudly feature phylogenetic trees that help to order biomechanical data. But biomechanics has also much to give: Garland’s selection studies (chapter 3) on wheel-running mice inform not just about biomechanics, but also evolutionary biology. Biomechanists also help to expel the Panglossian ghost from functional and ecomorphology by addressing the second question: is a particular trait random or adaptive? To assume, like Voltaire’s Dr Pangloss, that everything in nature is ‘*designed*’ to create the ‘*best of all possible worlds*’, is to ignore random events like genetic drift. But, as Alexander points out in his chapter on fossil biomechanics, even if we use the adaptive hypothesis only as a starting point, biomechanics is not the magic wand that makes sense of any biological structure. Reverse-engineering a fossil requires context information (what did the organism eat, what was its habitat?) that has mostly disappeared along with the extinct species. And without context, hypotheses about a function cannot be tested. There are also more proximate problems: any knowledge gleaned from fossils comes with huge error bars. Alexander uses the scaling laws of walking as an example. The size of a dinosaur’s footprint can tell us its body size. But it is also true that on soft soils the size of a footprint initially increases with depth. If the top layer had eroded, and only the lower substratum were preserved, this would lead to an overestimate of the animal’s size, and such distorted data would not help to test ideas about the dynamic similarity of walking vertebrates.

Biomechanical explanations of extant structures also depend on knowing the context. Homberger (chapter 13) combined ecology, behavioural studies and botany with biomechanics to explain the unique structure of parrot beaks: parrots evolved a system of joints and grooves to crack Eucalyptus fruits. Deban (chapter 10) shows how biological and abiotic constraints as well as multi-functional demands often preclude optimal designs: only lungless salamanders that skip the suction-feeding larval stage are freed from ontogenetic and morphological constraints to develop the most impressive ballistic tongues. Domenici (chapter 9) points out that some fish developed high bodies to reduce vulnerability to gape-limited predators, despite the hydrodynamic costs. The water flow in elasmobranch gill cavities is not uniform enough to warrant the elegant counter-current system of their teleost cousins (Summers et al., chapter 6). The low degree of functional modularity in organisms disallows evolutionary scientists from ‘*atomising the phenotype*’.

Selection experiments (chapter 3) provide another nail in Pangloss’s coffin: some strains of mice increase their wheel-running performance by developing ‘mighty mini-muscles’: shorter diffusion distances help maintain high aerobic activity. Other strains only increase running speed. Garland asks “*if multiple solutions to an adaptive ‘problem’ are identified, then is it useful to think of some of them as being ‘more optimal’ than others?*”. Selective breeding is only one approach that can be used to map possible solutions to an adaptive problem. A more commonly used technique is to map the parameter space, of which Kardong’s mechanical models of viperid skulls are just one example (chapter 5).

The book is divided into three parts. The first part deals with conceptual issues. Here, authors point out the pitfalls of evolutionary biomechanics and present new techniques and concepts to avoid them. The other parts of the book contain case studies about locomotion, breathing and feeding in a terrestrial, aquatic or aerial environment. A conference volume cannot provide the ‘great unified theory’ of biomechanics. Instead, the diverse contributions from many leading biomechanists provide an excellent overview of the current trends and techniques, which will help fellow researchers to identify new questions. On the other hand, university teachers and students will appreciate the review format, which allowed the authors to place their work into the larger context of evolutionary biology, and elevates the book over a mere collection of scientific papers. The conceptual chapters and commentary in many case studies provide valuable seminar material for readers who want to learn more about modern ecomorphology and biomechanics.

The Panglossian days of evolutionary biomechanics are clearly numbered, and many chapters advocate more critical thinking. However, Ollason’s warning against teleological biology has not yet reached all biomechanists, even in this book. Nevertheless, a higher level of integration has largely replaced a simple adaptationist approach. Garland’s trail-blazing chapter on selection experiments makes biomechanics more than the engineering science of organisms. It shows how biomechanics is a valuable tool with which to study natural selection and adaptation.

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