THE SCOPE AND AIMS OF
FUNCTIONAL AND ECOLOGICAL MORPHOLOGY

by

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SUMMARY

Functional morphology asks how animal structures work and whether observed structures are superior to possible alternatives. Ecological morphology examines the structures of different animals in relation to their various environments and ways of life. Some studies in both fields are concerned mainly with topography, but most make use of at least one of the branches of physics and engineering: examples involving kinematics, dynamics, fluid mechanics, acoustics, optics, heat exchange and diffusion are presented, together with some of the important experimental methods. Whichever branches of physics are used, allometry, optimization and the study of symmorphoses are likely to be illuminating. Functional and ecological morphologists should be more aware of evolutionary theory.

INTRODUCTION

This paper has three messages: that functional and ecological morphology are flourishing fields, that their subject matter and methods are very diverse and that they depend very heavily on physics and engineering.

The first two messages should be conveyed by the examples that I will present, without any need for them to be ordered in any particular way. I have therefore chosen to organize this paper around the third message, about the importance of physics and engineering. I will refer to most of the major branches of physics in turn, showing how each is used by morphologists.

The relationship between morphology, physics and engineering seems inevitable. Functional morphology tries to explain how the structures of animals' bodies work. It shows how particular designs have been favoured by natural selection because they work better than the alternatives, or are particularly economical of energy or materials. Engineering is the applied science of how things work, how they should be constructed to work best and how they can be made most economically. Physics is the basic science on which engineering is built.
The traditional tools of morphologists, the scalpel and the microscope, are still important, but functional and ecological morphologists need many other instruments as well. Different instruments and techniques are particularly useful, depending on the branch of physics that guides the investigation. I will refer to some examples in this review.

Functional morphology and ecological morphology are overlapping fields, so I will not attempt any sharp distinction between them. Ecological morphology emphasizes differences between species that relate to their different ways of life. Thus a study of the jaw mechanism common to all members of a group of species, would generally be regarded as functional morphology (Osse, 1969). A study of the jaws of a group of species, relating differences between them to the fishes' different lifestyles, is ecological morphology (Barel, 1983). A study of bat wing structure in relation to the mechanics of flight is functional morphology (Norberg, 1972) but a study of differences of wing design, between bats with different ways of life, is ecological morphology (Norberg & Rayner, 1987).

From this point I treat functional and ecological morphology together. I will discuss examples of both under a series of headings, most of which will be recognized as branches of physics or engineering: the first is the sole exception.

**TOPOGRAPHY**

Some studies in functional and ecological morphology are concerned principally with the sizes and shapes of parts of the body. They ask what the sizes and shapes of parts are, and how they relate to function or to differences in ways of life. For example, Barel (1983) studied the jaws and teeth of East African cichlid fishes. Some had pointed snouts and some had blunt ones. Some had upwardly-turned mouths and some had downwardly-turned ones. Some had long jaws and some short. Some had a few strong teeth and others had a brush-like array of fine, flexible teeth. The differences were related to the fishes' very diverse feeding habits: some ate zooplankton, some scraped algae off rocks, some ate molluscs and crushed their shells, and so on.

A question that often arises in topographical functional morphology is, how do the parts of the body fit together (Barel, 1984)? A nice example occurs almost as an aside in a paper by Otten (1981). The jaw muscles of fishes have to fit around the eye. In the cichlid *Haplochromis* section A1 of adductor mandibulae (the part closest to the eye) has the structure shown in fig. 1(a). Its belly is divided into two parts by an aponeurosis, and the tendon of insertion has a branch to