Invertebrate Biology

A FUNCTIONAL APPROACH

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PREFACE

Courses on the invertebrates have two principal aims: (1) to introduce students to the diversity of animal life and (2) to make them aware that organisms are marvellously integrated systems with evolutionary pasts and ecological presents. This text is concerned exclusively with the second aim and assumes that the reader will already know something about the diversity and classification of invertebrates. Concepts of whole-organism function, metabolism and adaptation form the core of the subject-matter and this is also considered in an ecological setting. Hence, the approach is multi-disciplinary, drawing from principles normally restricted to comparative morphology and physiology, ecology and evolutionary biology.

Invertebrate courses, as with all others in a science curriculum, also have another aim – to make students aware of the general methods of science. And these I take to be associated with the so-called hypothetico-deductive programme. Here, therefore, I make a conscious effort to formulate simple, some might say naive, hypotheses and to confront them with quantitative data from the real world. There are, for example, as many graphs in the book as illustrations of animals. My aim, though, has not been to test out the principles of Darwinism, but rather to sharpen our focus on physiological adaptations, given the assumption that Darwinism is approximately correct. Whether or not I succeed remains for the reader to decide.

As an aid to understanding the equations and graphs that are in the text and to identifying animals referred to by species the reader will find a glossary of symbols and a taxonomic index at the back of the book.

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1 INTRODUCTION

1.1 Functional Biology – What Is It?

This book is about how invertebrate animals function – not just about *how* they work but also about *why* they work in the way they do. The term *function* means 'the work a system is designed to do', but in a biological context *design* is not quite the correct word, for organisms are not intelligently conceived nor are they intelligently selected. The characters we now see associated with organisms are the ones that, having arisen in the first place by chance, have persisted because they are better than others at promoting the survival of their bearers and their ability to reproduce. John Ray (1627-1705) and William Paley (1743-1805) thought that they saw evidence for the work of an intelligent designer in the organisation of living things but Charles Darwin (1809-82) replaced all that with a process based simply on mutation and a 'struggle for existence'. He called it *natural selection.* By *functional biology,* then, I mean the search for explanations of the success of particular traits in given ecological circumstances; or why, in other words, those traits which have turned up by chance have then been naturally selected. There is also a very important predictive side to the programme. What traits would be expected to evolve in particular ecological conditions?

In approaching this problem I have made a conscious effort, where possible, to apply the well-tried methods of science – formulating hypotheses and testing their predictions against data from the real world. Later in this chapter we focus on a number of general hypotheses concerning the way that natural selection is likely to have influenced the functioning of invertebrates, and these will be used as a basis for data-collection and data-evaluation throughout the rest of the book. The aims, however, are not to refute natural selection as a basis for explaining adaptation, but rather to use this hypothetico-deductive approach to sharpen our understanding of the functional biology of invertebrates. We assume, therefore, that evolution has occurred by natural selection and then attempt to discover what this means for how animals work.

1.2 The Invertebrates

'The line traditionally drawn in zoological teaching between the vertebrates (*animals with backbones*) and invertebrates (*animals without backbones*) is an unfortunate one; it obscures the fundamental unity that underlies the organization of living material' (*my italics*). Thus wrote E.J.W. Barrington in the preface to the first edition of his *Invertebrate Structure and Function* (Barrington, 1967). The line is, nevertheless, a convenient one since it separates a relatively small taxonomic group of animals with limited diversity (the vertebrates) in which a great deal is known about a few species from one of great diversity (the invertebrates) in which a little is known about many species. Since the adaptive *raison d'être* of structure and process is often made most clear by comparing species with widely differing life-styles and ecology, the diversity presented by the invertebrates is helpful for the functional approach.

A very brief classification of the invertebrates that will be discussed in this book is given in Table 1.1 and a scheme of possible relationships is given in Figure 1.1. For a more comprehensive treatment the reader must refer to more classical, zoological texts. Two good and complementary books are Russell-Hunter's *A Life of Invertebrates* (1979) and Fretter and Graham's *A Functional Anatomy of Invertebrates* (1976).

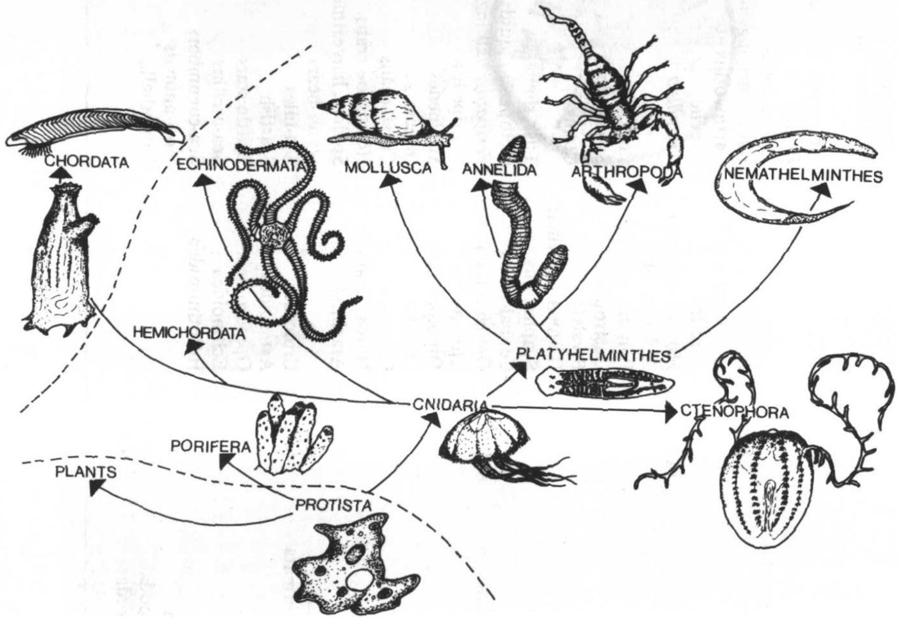
1.3 The Physiological Approach

Most of the processes seen in a phenotype involve the use of time and energy for personal survival and reproduction. The form of the phenotype depends on how resources from the food are allocated between different tissues and organs. Dynamic processes, such as metabolism and consequent growth and movement, depend similarly on a supply of resources. A study of the acquisition and allocation of resources by invertebrate organisms will form a framework for all that follows and the model illustrated in Figure 1.2 should be kept in mind throughout. This approach differs from more classical ones which either consider physiology on a group-by-group (Alexander, 1979) or system-by-system (Barrington, 1967) basis. Systems will certainly be considered here but only from the point of view of the way they are related to metabolic schemes of acquisition (Chapter 2), allocation (Chapters 3 to 6) and integration (Chapter 7). Control systems will be referred to throughout in so far as they are involved in the control of metabolism. However, the reader will not find detailed expositions on neurophysiology, sense

Table 1.1: A List of Major Invertebrate Phyla

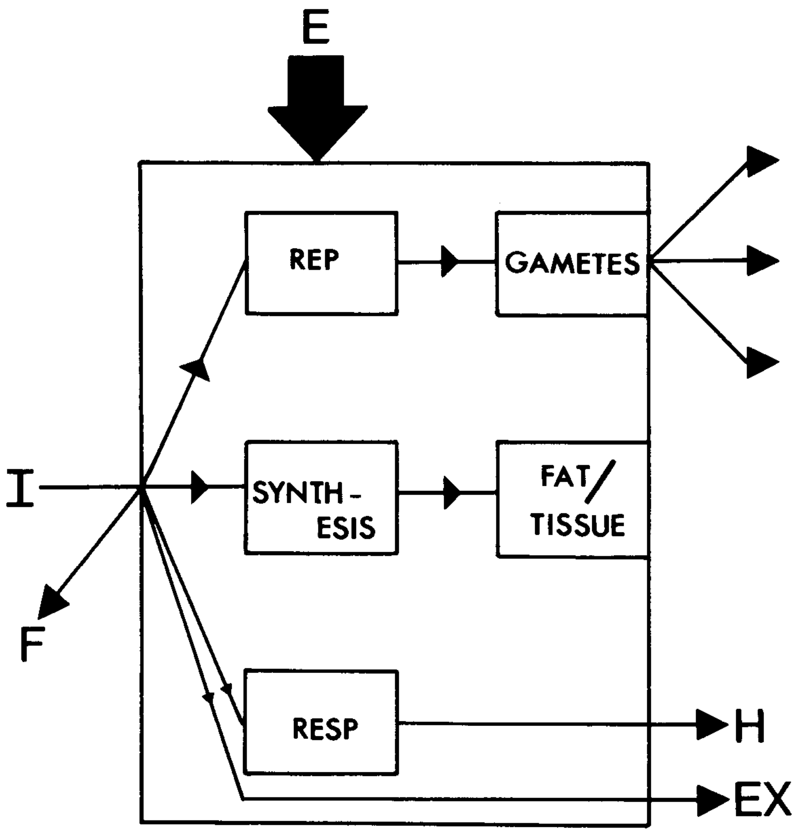
Phylum	No. of species x 10^3	Major classes	Common name(s)
Porifera	4.2	Calcarea	Sponges
		Hexactinellida	
		Demospongia	
Ctenophora	0.08		Comb jellies
Cnidaria	11	Hydrozoa	Hydroids
		Scyphozoa	Jellyfishes
		Anthozoa	Anemones, corals
Platyhelminthes	15	Turbellaria	Flatworms/planarians
		Monogenea	Flukes
		Trematoda	
		Cestoda	Tapeworms
Nemertea (= Rhyncocoela)	0.6		Ribbon-worms
Rotifera	1.5		Wheel animalicules
Nemathelminthes (= Nematoda)	80		Round-worms, nematodes
Annelida	8.8	Polychaeta	Ragworms, lugworms etc.
		Oligochaeta	Earthworms etc.
		Hirudinea	Leeches
Mollusca	110	Monoplacophora	*Neopilina*
		Aplacophora	
		Polyplacophora	Chitons
		Gastropoda	Snails, slugs
		Bivalvia (Lamellibranchia)	Clams
		Scaphopoda	Tusk shells
		Cephalopoda	Octopuses, squids
Arthropoda	800	Onychophora	*Peripatus*/walking-worm
		Chilopoda	Centipedes
		Dipolpoda	Millipedes
		Insecta	Insects
		Crustacea	Crustaceans
		Merostomata	Horseshoe crabs
		Arachnida	Spiders, harvestmen etc.
Tardigrada	0.17		Water-bears
Echinodermata	6	Crinoidea	Sea-lilies
		Asteroidea	Starfish
		Ophiuroidea	Brittle stars
		Echinoidea	Sea-urchins
		Holothuroidea	Sea-cucumbers
Bryozoa	4		Moss animals
Brachiopoda	0.31		Lampshells
Hemichordata	9.1		

Figure 1.1: A phylogenetic tree giving a rough and very hypothetical summary of relationships between major invertebrate phyla. Broken lines delineate the sphere of interest for this book. Animals are not to scale.



Illustrations by L.J. Calow.

Figure 1.2: Acquisition and allocation of resources in an invertebrate. Large box = whole animal; small boxes = sub-systems. I = ingested resources, F = faeces (egesta), I-F = absorbed resources (A); Rep = reproduction; Resp = respiration; H = heat; Ex = excretory products (excreta); E = environmental variables such as temperature, humidity, pH, Po_2, etc. I, F and A are treated in Chapter 2, Resp in Chapter 3, Ex in Chapter 4, Synthesis in Chapter 5, Rep in Chapter 6. The integration between sub-systems is considered in Chapter 7.



organs and endocrinology, and again explicit information on these must be sought from other sources (e.g. Barrington, 1967; Alexander, 1979).

The resources used by invertebrates are many and varied (see Chapter 2), involving a variety of organic and inorganic chemicals. The use of each in morphogenesis and metabolism could be expressed in terms of mole equivalents. However, since carbon occurs in all organic molecules and potential energy occurs in everything, measurements of either of these can be used in a general way to describe body size, reproductive investment and metabolic expenditure. In this book all components of an organism's resources will be considered, but special emphasis will be put on the energetic aspects. There are a number of reasons for this. First, and as already indicated, energy is a very general measure and can be used to quantify activities (feeding rates, respiratory rates, excretory rates, etc.) as well as states (size, storage etc.). Secondly, it is, as we shall discover, relatively easy to determine. Thirdly, and following from these points, most information in the literature is expressed in terms of energy or can easily be converted to it. There are also drawbacks to the energy approach and some of these will be discussed in the next section.

1.4 Physiology and Fitness

The Darwinian interpretation of evolution can be summarised as follows: given finite resources and some degree of variability in traits and heritability, then those traits which best promote the survival and reproduction of their bearers will become most numerous in subsequent generations. Hence organisms become adapted to, i.e. able to live and reproduce in, a particular environment. Given the premises in this argument, the conclusions follow automatically. However, a number of non-obvious, refutable assumptions concerning the nature of variation (it is non-directed) and heredity (e.g. it does not include characters acquired by the phenotype) are also written into the argument, so that it cannot be dismissed as a mere tautology. The success of a trait in this process of natural selection is often referred to as its fitness and will depend on: (1) individual survivorship; (2) the speed at which offspring are themselves able to reproduce; (3) reproductive output.

In principle, therefore, judging the adaptational significance of a particular trait requires that we should be able to assess its influence on these components of fitness; that is, we should be able to redefine its effects in terms of individual survivorship, and life-time reproductive success. However, it is usually very difficult, if not impossible, to translate short-term physiological processes (which may operate on a minute-by-minute basis) into their long-term demographic effects (which may operate on a year-by-year basis). More immediate if less direct measures of fitness are therefore required, preferably derived from the physiological processes themselves. One which has been used widely in this context is the 'net resource returns' from a particular process; i.e. the total gain credited to the process less the cost of effecting it. The rationale behind this is that the more resources that are

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