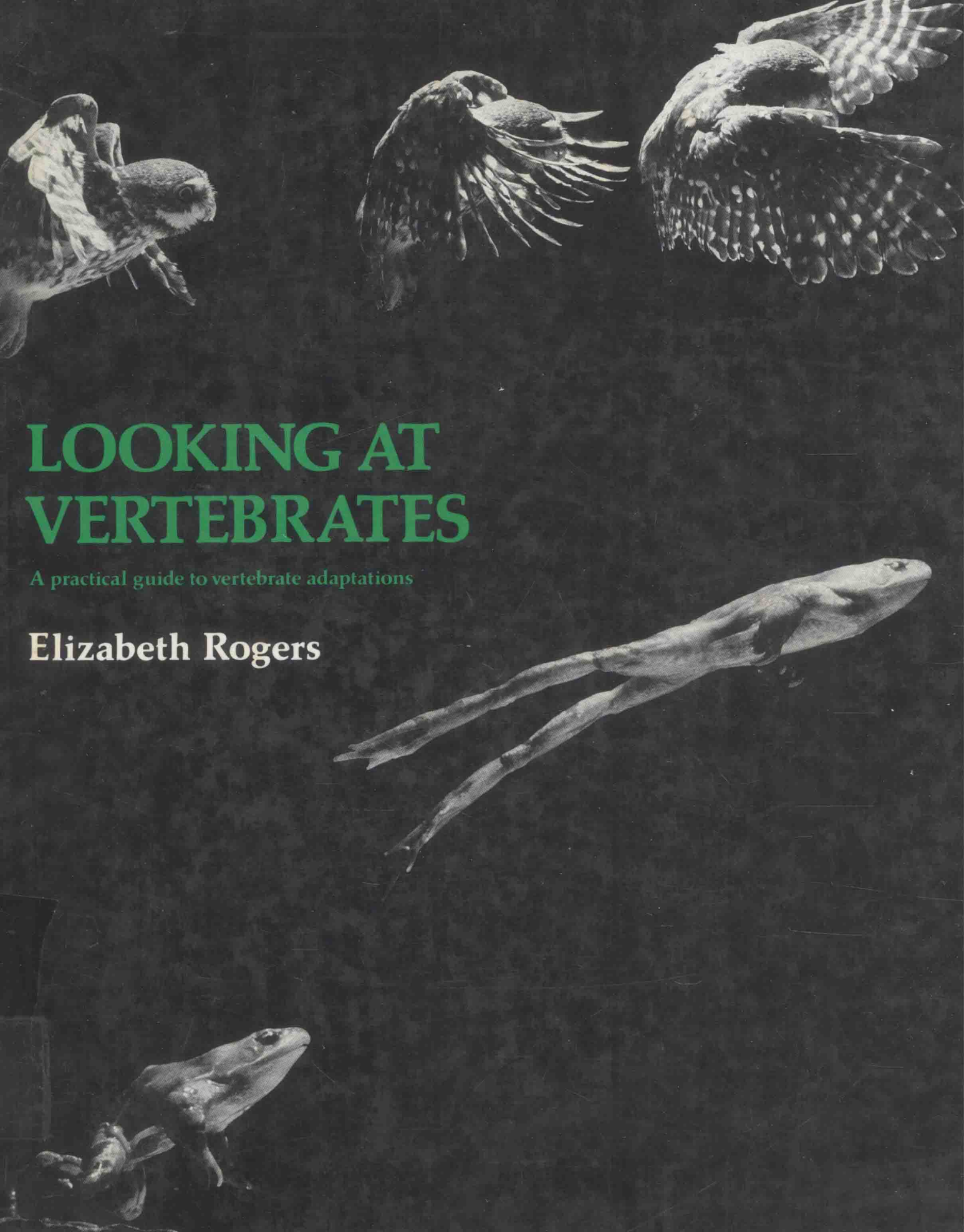

LOOKING AT VERTEBRATES

A practical guide to vertebrate adaptations

Elizabeth Rogers

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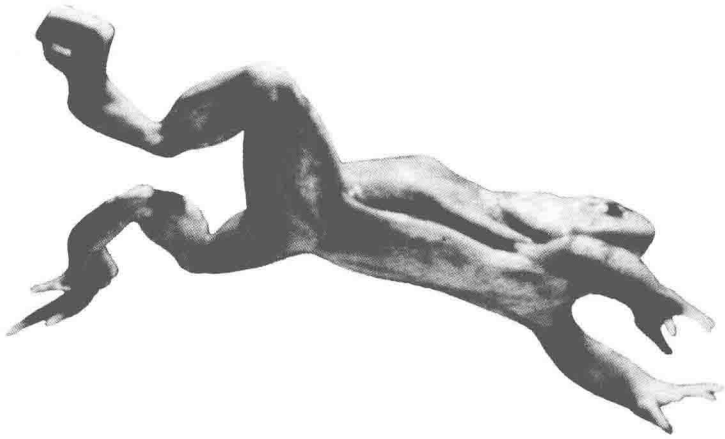

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Looking at Vertebrates

Elizabeth Rogers

Preface

This book is designed to fill a niche for a short practical course on vertebrate functional morphology for general biologists – whether students or school pupils. The idea is to observe certain aspects of vertebrate form, and then to offer explanations as to their functional value. Few existing practical books on vertebrates make any attempt to explain the structures they describe. For this, the student must use a general textbook, which may not be available during the practical class. Yet, on-the-spot explanations bring a new dimension to a dissection, making it much more than just a mechanical chore. Students start to see animals as whole functional units rather than collections of organ systems, and often as a result become more motivated.

The contents are based on six practical classes taught by me at the University of Edinburgh. In these, students concentrate on some of the main adaptations of each of the classes of living vertebrates. I had to make painful decisions on what to leave out, and my selection of topics will inevitably differ from that of others. It was heavily influenced by considerations of what material was readily available, and readily demonstrable to a large class in the lab. But I make no apology for lack of comprehensiveness – new ideas are constantly needed on how to teach abbreviated courses. I have omitted most conventional dissections; these are dealt with very adequately by existing practical books. I also do not restrict myself to the 'type' animals beloved of school syllabuses – a class on functional morphology is much more stimulating if a variety of animals is introduced. Adopting this approach also means that one can use some serendipity and opportunism in gathering lab material, and avoid using enormous numbers of any one species.

The style of the text is meant to provoke a questioning attitude. I want it to stimulate readers to talk to each other and their instructors. Many questions are posed: some are answered immediately, answers to others may be found by reading other parts of the book, and some are left unanswered. References at the end of each chapter show where further information can be found. Suggestions are made where measurements could be done and numerical data collected in the lab. The illustrations are hopefully comprehensive enough to allow users who do not have access to large zoological collections to see something of the animals being discussed. I have included pictures of live animals too, because I regard them as an absolutely essential part of any practical zoology class – whether they are seen in the lab, on field trips, in zoos, or on film. To understand function, animals must be observed living and moving.

This book is intended for biology students beginning university, or in their last years at school. If non-biologists read it too, then I will be delighted; it is certainly not intended only for specialist zoologists. I hope it will appeal to both the teachers and the taught. If it makes people look at animals and ask themselves why they look the way they do, then it will have achieved its purpose.

Elizabeth Rogers.

Edinburgh
1985

Acknowledgements

General Acknowledgements

Numerous people have helped with various aspects of this book. They have unearthed bones, bodies, and pictures; read my rough drafts; printed photographs; offered advice on all sorts of things; typed and photocopied, drawn and designed. I thank them all for giving so generously of their time, and hope that the finished product does justice to them – I could not have done it without them, and part of the fun lay in this extensive collaboration. I have not, needless to say, always followed their advice, so any defects are my responsibility alone.

The following helped me with material, often spending enormous amounts of time on my behalf: Catherine Cremer, Colin Whitelaw and Pete Grantham of the Zoology Department, Edinburgh; Ian Lyster, Geff Swinney, Bob McGowan, Alan O'Berg, Mahala Andrews, Arthur Clarke and Pat Macdonald, of the Royal Scottish Museum; Miranda Stevenson and Edwin Blake, of the Royal Zoological Society of Scotland; Andrew Loudon, now at the Institute of Zoology, London; Ronnie Rose, of the Economic Forestry Group; the Forestry Commission; Bud Finlayson and assistants at the Universities Marine Station, Millport; Alec Panchen and Tim Smithson, of the Zoology Department, University of Newcastle; Professor Ian Beattie of the Pathology Department, Royal (Dick) School of Veterinary Studies, Edinburgh; Mr. A. Yeoman of the Anatomy Department, Edinburgh Medical School; Marilyn Renfree, of Monash University, Australia; John Kirsch, formerly at the Museum of Comparative Zoology, Harvard, who was kind enough to give me accommodation and specimens while I wrote the chapter on marsupials; Norman Heglund, of Harvard University; Carsten Niemitz, of Free University, Berlin; Simon Bearder, David Chivers, Bill McGrew, Anthony Collins, Chris Mylne, Eric Hosking, and Stephen Dalton, who all helped with photographic material.

People who read rough drafts of each chapter were: Aubrey Manning, Chris Inchley, and Anthony Collins of Edinburgh's Zoology Department; Peter Jones and Steve Barbour, of the Department of Forestry and Natural Resources, Edinburgh; Marilyn Renfree and Roger Short, of Monash University, Australia; and John Kirsch, then at Harvard. Two anonymous reviewers, who read my manuscript, made some very helpful comments, and corrected several errors.

With so many illustrations, the book has demanded great efforts of photographers and artists. Pat Macdonald, Dennis Cremer, and Tom Scott-Roxburgh offered early advice on lenses and lighting. Eric Lucey filmed brachiating gibbons for me and helped with tracings from film of them and of a kangaroo hopping. Vernon French and Bernard Matthews allowed me to photograph specimens under their microscopes. Dennis Cremer loaned equipment, and he and Crispin Sadler patiently made quantities of prints from my negatives. Nancy Bryce, Steve Gibson, and Pat Macdonald did the drawings, and Pat Macdonald designed the book. The three of them have been a pleasure to work with. They made it possible to do all the drawings from original material, and brought their superb artistic talents and powers of observation to bear on them. Pat Macdonald's careful, imaginative, and professional approach to design has conquered my amateurishness on numerous occasions, and has created a book that is good to look at, and, we hope, a pleasure to use.

At the beginning of this whole project, I should probably not have

persevered without the interest and encouragement of Howard Moore, then at Longman. Since then, many others at Longman have been a constant source of encouragement in their various capacities. The manuscript was typed by Elizabeth Begley, whose accuracy and patience I gratefully acknowledge.

Last, but not least, I thank my students, who over the years have listened, looked, and offered comments on my vertebrate lectures and practicals. And my family, who have kept me going with their interest. They will be relieved to discover that they need no longer ask "When is your book coming out?" But, in the final analysis, it is to the animals that this book is dedicated; for the marvellous variety of their forms and functions remains as fascinating as it ever was to those who care to look and wonder.

Elizabeth Rogers.

Edinburgh
1985

Picture Acknowledgements

All photographs are by the author unless otherwise stated. I am grateful to the following for permission to photograph live animals or museum specimens on their premises:

Marine Biological Station, Millport: Figs 1.1, 2.19, 2.26, 2.28 and 2.29.
Royal Zoological Society of Scotland, Edinburgh: Figs 4.2, 4.5, 8.1, 8.30 and 8.35.
Royal Scottish Museum, Edinburgh: Figs 6.16, 6.18, 6.22, 7.4, 7.6, 8.2, 8.5, 8.7–8.9, 8.11–8.14, 8.22–8.25 and 8.28.
Museum of Comparative Zoology, Harvard University: Figs 7.5, 7.8–7.11, 7.15, 7.17, 7.18, 7.20(a), 7.21, 7.22, 8.3 and 8.4.
Anatomy Department, University of Edinburgh Medical School: Figs 8.18–8.20.
Fig. 1.5, Heather Angel, Biofotos; Fig. 2.5, Hans Reinhard, Bruce Coleman; Fig. 2.27, Heather Angel, Biofotos; Figs 3.1, adapted from original drawings by Tim Smithson; Fig. 3.13, adapted from various sources including photographs by Stephen Dalton, Oxford Scientific Films; Figs 5.2 and 5.3, I. Lyster and A. O'Berg; Fig. 5.15, Don Smith, Nature Photographers Ltd; Fig. 5.16, Eric Hosking; Fig. 5.17 and 5.18, Chris Mylne; Fig. 5.19, G. L. Carlisle; Fig. 6.1, Kim Taylor, Bruce Coleman; Fig. 6.15, from *Vertebrate Life* by W. N. McFarland *et al.*, Collier Macmillan, by permission of authors and publisher; Fig. 7.1, G. Pizzey, Bruce Coleman; Fig. 7.2, J. Markham, Bruce Coleman; Fig. 7.7, B. P. Kent, Oxford Scientific Films; Fig. 7.24, drawn from film supplied by N. Heglund; Fig. 7.25, M. Renfree; Fig. 8.6, Des Bartlett, Bruce Coleman; Fig. 8.10, Peter Steyn, Ardea London Ltd; Fig. 8.15(a) adapted from sketches provided by Professor C. Niemitz; Fig. 8.15(b) drawn from photographs supplied by S. Bearder; Fig. 8.16, L. L. Rue III, Bruce Coleman; Fig. 8.21, D. A. Collins; Fig. 8.26, D. A. Collins; Fig. 8.27, I. Vandermolen, Oxford Scientific Films; Fig. 8.30, drawn from film taken by E. Lucey.

Cover and title page photographs by Stephen Dalton.

Sources of Vertebrate Material

This book is not meant to encourage people to kill a lot of animals, nor to order vast quantities of pickled dogfish, frogs, and rats from suppliers. However, it does require students to look at animals. Thus, some dissection is necessary but this should be complemented by film, field trips, visits to zoos and museums, and by observation of prepared specimens. The illustrations in the book are supposed to fill in any gaps where actual specimens are lacking.

Some information on sources of material might be helpful, particularly for teachers planning courses for large numbers of students. Rather than attempting to supply every student with the same specimens, I have found it more stimulating to have students work in groups with several different things. It is unnecessary for every student to have one of everything. This reduces the numbers of any one species that are required, and provokes students into teaching each other while observing and commenting on differences between species.

Live animals

- Mostly demonstrated through the use of film, but large numbers of students can see birds in the wild, and field trips are worth the effort of planning in order to see flight patterns, variety of species in a habitat, behaviour, etc.
- Zoos may lend live animals, such as reptiles and amphibians, for demonstration in a class. Or collect a few locally yourself, once you have checked whether the species you want is scarce, protected, or endangered. If it is any of the latter, do not take any at all, even if the animals in question are common in your own locality.
- Some animals can be bought live from reputable suppliers, and are easy to keep in the laboratory provided the proper diet and living conditions are observed.

Animals for dissection

- Fish: local fish shops, fishermen, markets and marine biological stations. Use a variety of local species, freshwater or marine. Five or six individuals of several species will supply a large class.
- Amphibians and reptiles: if possible, use animals commonly bred in laboratories such as *Ambystoma*, *Xenopus*, and *Rana*. There are plenty of good suppliers of these animals, and you could set up your own breeding stock without very much trouble. Always ensure that humane killing methods are used when preparing animals for dissection.
- Birds: choose common species that are always available because they are considered as pests, and are therefore culled locally; or use birds bred for food (e.g. in the UK, pigeons, rooks, seagulls, and chickens).
- Mammals: some of us are never going to see much of marsupials and primates, so use museums and zoos as much as possible. But also be opportunistic and use as sources road kills, slaughter houses, and organisations or individuals that cull mammals regularly. One specimen of an interesting mammal can make a fascinating demonstration. Even if you cannot obtain whole animals, you will often find ready suppliers of heads, limbs, or internal organs for demonstrating feeding and locomotory adaptations. The pathology departments of veterinary colleges are another occasional source of material – they may pass things on to you after post-mortem examinations.

Skulls, skeletons, and skins
If you do not have a collection of these in your department, I suggest four possible solutions:

- Buy material in from a supplier.
- Borrow from a local museum – many will lend a great range of items. Or go to the museum with students and use specimens on the premises.
- Get students to prepare their own skulls and bones from material they have dissected.
- An eccentric and interesting collection can be made locally. For example, seabird skeletons can frequently be found on the beach, and small mammal skulls are not uncommon inland.

General Reading on Vertebrates

Several general textbooks have been useful sources during the preparation of this book. Reference is not made to these particular books after each chapter unless they were of special importance as source material, but information about most of the topics discussed here is available in one or other of them. They would be important companions for anyone aspiring to a knowledge of vertebrate form and function.

Alexander, R. McN. *The Chordates* (2nd ed). Cambridge University Press (1981).

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Contents

1 Protochordates: Vertebrate Relatives

Phylum: **CHORDATA**

Subphylum: **UROCHORDATA**

Class: **ASCIDIACEA** (sea squirts)

Class: **THALIACEA** (salps)

Class: **LARVACEA**

Subphylum: **CEPHALOCHORDATA**

Subphylum: **VERTEBRATA**

This book is about vertebrates, which, as you will see if you look at the classification above, are one of three groups within the phylum Chordata. To put them in context within the Animal Kingdom as a whole, we shall use this chapter to describe some animals which are chordates, but not vertebrates, for they throw some light on the origin of vertebrates themselves.

Urochordates and cephalochordates are often known collectively as 'protochordates'. How can living protochordates be useful in determining vertebrate origins, which must lie millions of years in the past? The assumption is that if evolution proceeds by modification of pre-existing groups, then living animals should reflect their ancestry. Zoologists search for structures with the same origin in a group of animals; such structures are said to be 'homologous' to each other. The problem lies in determining which structures are truly homologous and which are simply similar for functional reasons. What zoologists do is to combine the study of comparative anatomy, morphology, and embryology of living animals with data from the fossil record. From this, a set of characteristics can be defined which is common to, in this case, all members of the phylum Chordata. It is then possible to look for these essential characteristics both in fossils and in other groups of living animals – invertebrates, for example. Hypotheses have gradually emerged about the origin of vertebrates from protochordates, and of protochordates from other invertebrates. This chapter concentrates on those features of protochordates that seem to be most relevant to vertebrate origins.

Material required

- Live *Ciona* and *Ascidiella* (or other appropriate solitary sea squirts) for observation. (The structure of the pharynx is easier to see in *Ascidiella*.)
- Slides of the ascidian tadpole.
- Whole, preserved adult *Branchiostoma*.
- Slides of whole mounts of larval *Branchiostoma*.
- Slides of transverse sections of the pharynx of *Branchiostoma*.

Chordate Characteristics

Members of the phylum Chordata have five distinguishing characteristics:
1. The pharynx at the anterior end of the gut is perforated by gill slits, and

has a ventral groove called the endostyle, which produces mucus and sequesters iodine. The endostyle is thought to be the forerunner in protochordates of the thyroid gland of vertebrates.
2. There is a long dorsal rod called the notochord (hence 'chordate'), running from head to tail and providing the main support for the body in primitive chordates.
3. A dorsal hollow nerve cord lies above the notochord.
4. A post-anal tail is present.
5. Primitive chordates are deuterostomes; that is, the coelom develops as pouches pushing out from the embryonic gut, and the blastopore of the embryo forms the anus, not the mouth which is a new opening.

If we add onto these five features a sixth – the presence of an internal skeleton around brain and spinal cord – we have defined not only a chordate, but a vertebrate.

Urochordates

We shall concentrate here on the ascidians (also called tunicates), because they are most obviously relevant to discussions about vertebrate origins. Live sea squirts can readily be studied in the laboratory. They are at first sight unlikely looking chordates, being sessile and sac-like, but they have one important feature – the large perforated pharynx, which they use for filter feeding. The best way to study its structure and function is to allow live animals to take in a suspension of particles, which can then be seen either with the naked eye or under a microscope. Dissection of the pharynx reveals the destination of the particles after filtration, and it is then possible to deduce certain aspects of the filtering process.

Ciona and *Ascidiella* are two genera of solitary sea squirts found around the British Isles (Fig. 1.1). Small individuals of *Ciona* often reveal details of their internal anatomy because the tunic is transparent. Much can therefore be seen by transmitted light under a low-power dissecting microscope. *Ascidiella* has a more opaque tunic, and less of its internal structure can be seen without dissection. Before proceeding, allow your animals to take in a suspension of carmine particles in sea water (India ink or algal suspensions are other possibilities). This can be introduced by discharging the suspension gently from a pipette, near the inhalant siphon (avoid touching the animal – it will close up). As you then watch your animal, a red line of accumulated carmine particles should appear down one side of the pharynx. But meanwhile, look at the general layout of the animals.

Fig. 1.1 Live Ciona intestinalis, *a solitary sea squirt.*

General features

1. Notice that the animals have two siphons at one end – one inhalant and one exhalant. Find out which is which. The other end of the animal is the attachment point.
2. The inhalant siphon passes into a large pharynx, which takes up most of the volume of the body. Water passes through the slits in its wall into the surrounding space or atrium, and so out via the exhalant siphon.
3. Down one side of the pharynx is a deep groove, heavily ciliated, called the endostyle. This sometimes appears (e.g. in small *Ciona*) as a wavy line visible through the tunic and body wall. It allows you to orientate the animal, as do the siphons – the endostyle is ventral, the exhalant siphon is dorsal.
4. Below the pharynx, at the base of the animal, are the intestine, the reproductive organs, and the heart. The intestine loops around and runs up one side of the pharynx to open into the atrium below the exhalant siphon. You can usually see it through the tunic. Ascidians are hermaphrodite, and have a single ovary and testis lying in the intestinal loop. The genital ducts also open below the exhalant siphon, but beyond the anus.
5. The heart and circulatory system are interesting, because the direction of blood flow reverses from time to time. You will not see the heart without

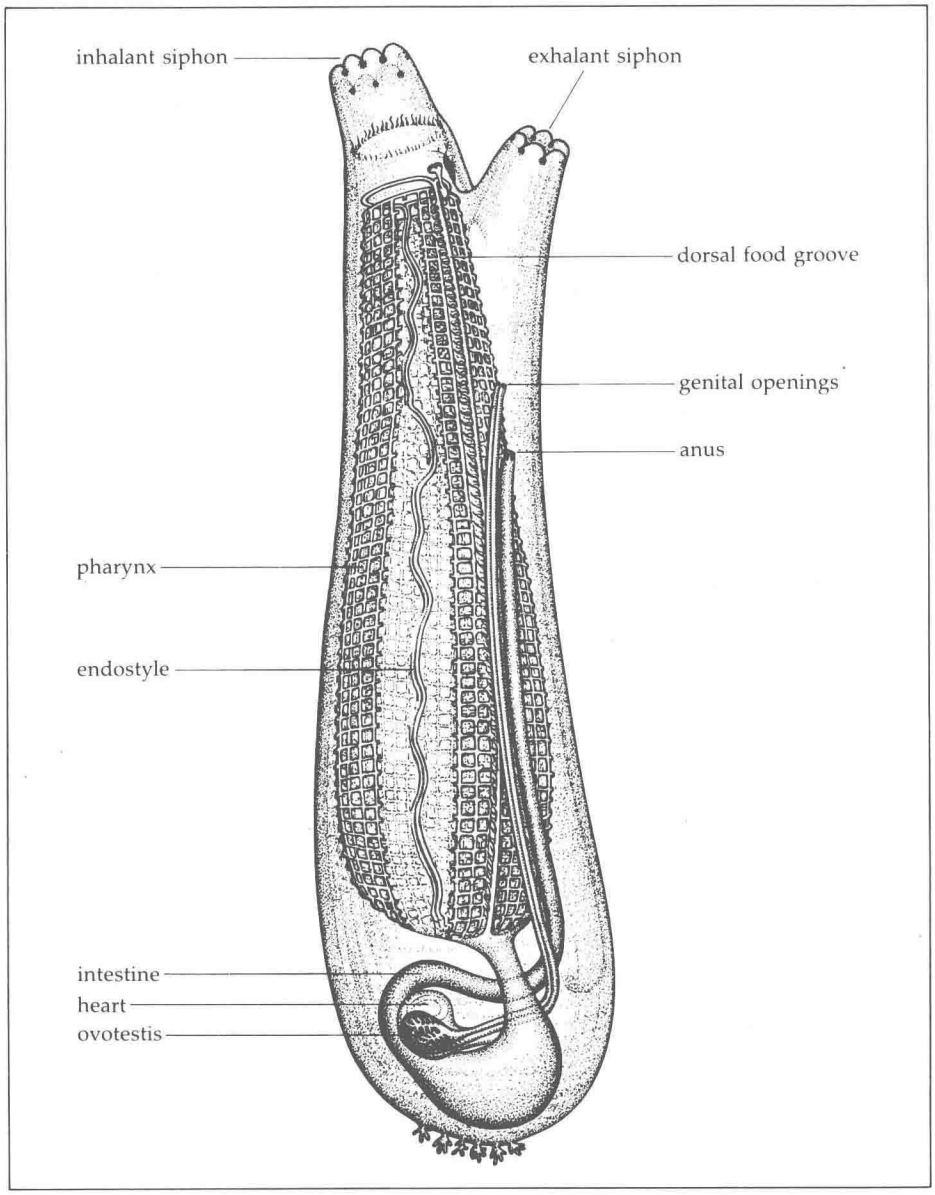


Fig. 1.2 General anatomy of Ciona.

dissection, but you may come across it as you investigate pharyngeal function. It is a transparent structure, shaped like a blunt finger, and lies in the intestinal loop, between intestine and gonad. The blood is also transparent, but has cells floating in it, which you can see moving as the heart beats. It is by looking at them that you will see the reversal of blood flow.

Internal features

The object of this section is to see the structure and extent of the pharynx, and to gain an idea of how it functions. Sea squirts obtain their food entirely by filtering vast quantities of water through the pharynx – hence its size. The best animal to use for investigation is *Ascidiella* because its pharyngeal structure is very clear upon dissection.

1. By the time you have looked at external features, your animal will have been able to take up some carmine particles and concentrate them in its pharynx. This will help you to see what is going on when food is processed.
2. Cut off the thick outer covering, or tunic, around the animal. Note its consistency as you do so – there is a cellulose-like substance in the tunic.
3. The general distribution of organs will now be clearer. Note the arrangement of siphons, pharynx, intestine, and gonads.
4. Cut open the pharynx from anterior to posterior end, passing half way between the exhalant siphon (dorsal) and the opposite side of the animal (ventral). The orientation of sea squirts is confusing, so look at Fig. 1.2 first.
5. Carefully pin out the pharynx, so that you can look at one complete side of it (Fig. 1.3). Using a dissecting microscope, locate the following:

(a) The endostyle. Can you see that it is a groove? It contains cilia, and secretes mucus, which passes out of the groove and onto each side of the pharynx as a continuous sheet. (You are unlikely to see this, because mucus secretion is usually interrupted as soon as an animal is disturbed.)
(b) The gill slits in the walls of the pharynx (Fig. 1.3b).
(c) The dorsal food groove, where food is collected into a mucous string for passing back into the intestine. You should see a string of carmine particles in the dorsal groove if your animal has processed them. Does the dorsal groove have the same appearance as the endostyle?
(d) The entrance from pharynx to intestine. This is dorsal. Follow the dorsal groove back until it passes into the intestine.

6. Filter-feeding involves a combination of ciliary currents and mucus secretion. The presence of a cord of accumulated carmine particles in the dorsal groove tells you that food particles are filtered by the pharynx, and concentrated dorsally. The food cord is then moved back along the dorsal groove to the intestine. What filters the food out of the water? And where are the cilia? You can investigate to some extent by cutting out a small piece of the pharynx wall, and mounting it on a slide, stretched under a coverslip. Look at it under a microscope with a ×20–40 phase-contrast objective. You may see cilia beating, but in any case, you will see their arrangement on the edges of the pharyngeal slits. The fine filter is actually the mucous sheet, not the slits, and it is the endostyle that is responsible for secreting it. Cilia then move it up over the sides of the pharynx, so that water has to pass through it in order to exit through the gill slits. It is collected, with its filtered food particles, in the dorsal food groove. This feeding process is a fundamental chordate characteristic. Feeding occurs in a very similar way in the cephalochordate, *Branchiostoma*, and also in larval lampreys.

Ascidian larvae

Clearly, the organisation of adult sea squirts is dominated by the large surface area of the pharynx required to collect enough food. Apart from the perforated pharynx, little else qualifies these animals for membership of the chordates. However, if we look at their development, an altogether different picture emerges.

The fertilised egg of ascidians develops into a swimming, tadpole-shaped larva with a dorsal tubular nerve cord, a notochord, and a post-anal tail (Fig. 1.4). Living larvae are hard to observe and collect, because they are tiny and may be very short-lived. Look at a prepared slide instead. Note the

general structure. The tadpole larva shows, at a very basic level, some important features of chordate organisation. These are the presence of a post-anal tail, supported by a notochord, which provides the force for locomotion; and a dorsal nerve cord running along into the tail above the notochord. Rows of muscle cells surrounding the notochord contract and,

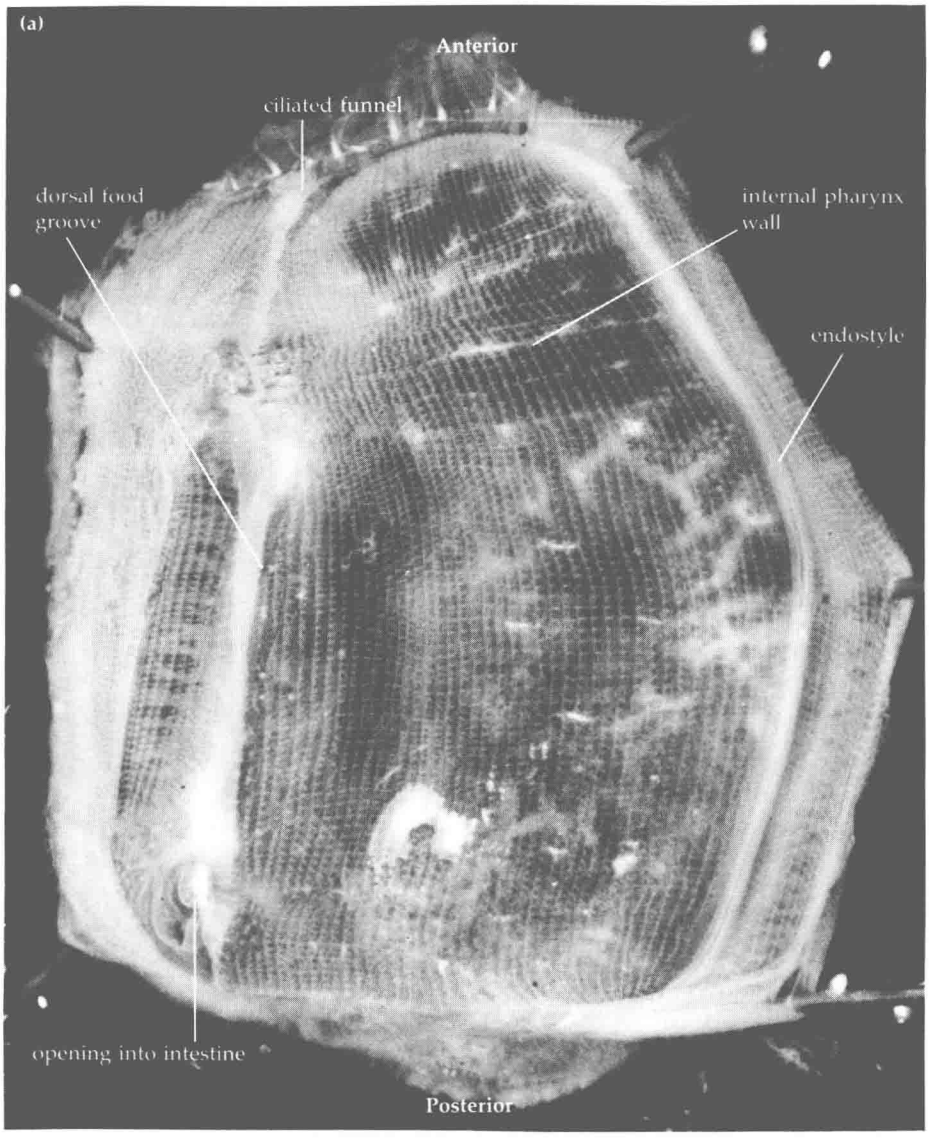


Fig. 1.3 Dissected pharyngeal region of Ascidiella: *(a) whole pharynx and (b) detail of pharyngeal wall (approx. ×60).*

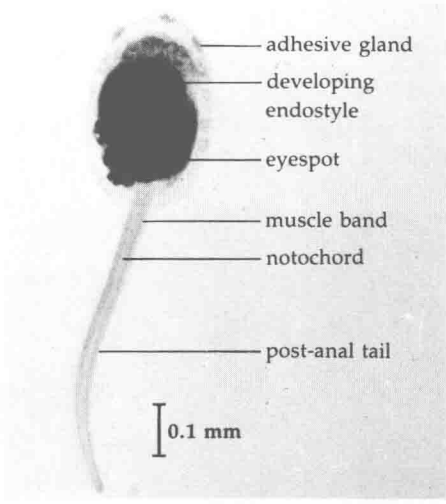
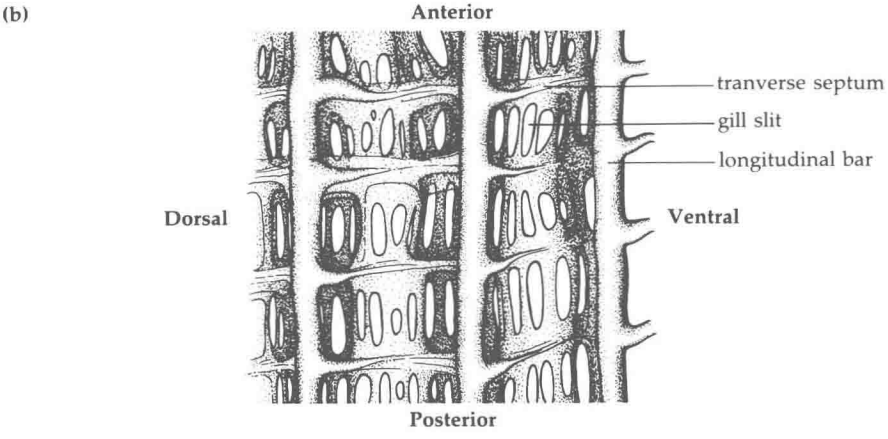


Fig. 1.4 Ascidian tadpole larva.



because the notochord is incompressible, their forces are translated into undulations of the tail. Structures concerned with feeding and other bodily functions are concentrated at the anterior end in chordates, and do not extend into the tail, whose function is to move the animal through the water.

The role of the tadpole larva is to select a site for the adult to settle. It is also a dispersal mechanism, because the adult does not move. Attachment occurs by adhesive glands at the anterior end; the tail and notochord are resorbed, and eventually the adult form develops. Note that a functional perforated pharynx is not present in the larva, which does not feed, although gill slits begin to appear. The larva is quite different from the adult, and its development up to metamorphosis is very like that of the next group – the cephalochordates – to which we shall now turn.

Cephalochordates

Cephalochordates – lancelets – used to belong to the genus *Amphioxus* until it was discovered that the name *Branchiostoma* had precedence. Many people still use 'amphioxus' as a common name for these animals.

Branchiostoma looks like a small, laterally flattened fish, pointed at both ends (Fig. 1.5). It spends its adult life semi-embedded in sand with its head sticking out into the water. It possesses all the features that are considered basic to chordate organisation, but it is not a vertebrate because it has no internal skeleton like theirs. *Branchiostoma* is a difficult animal to dissect successfully, but a combination of whole preserved adults and prepared slides of younger stages should reveal most of the essential aspects of its structure.

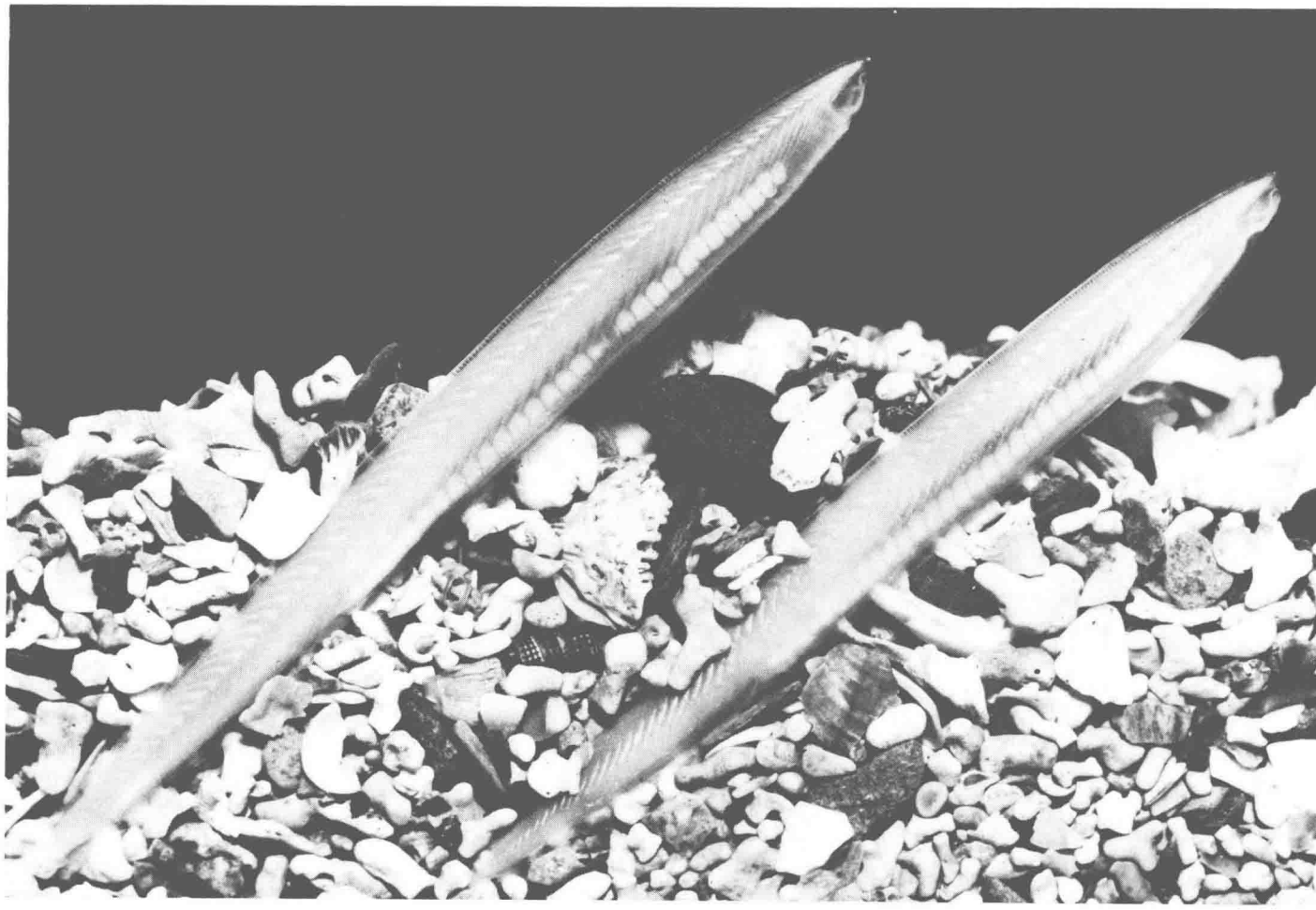


Fig. 1.5 Adult Branchiostoma *in gravel.*