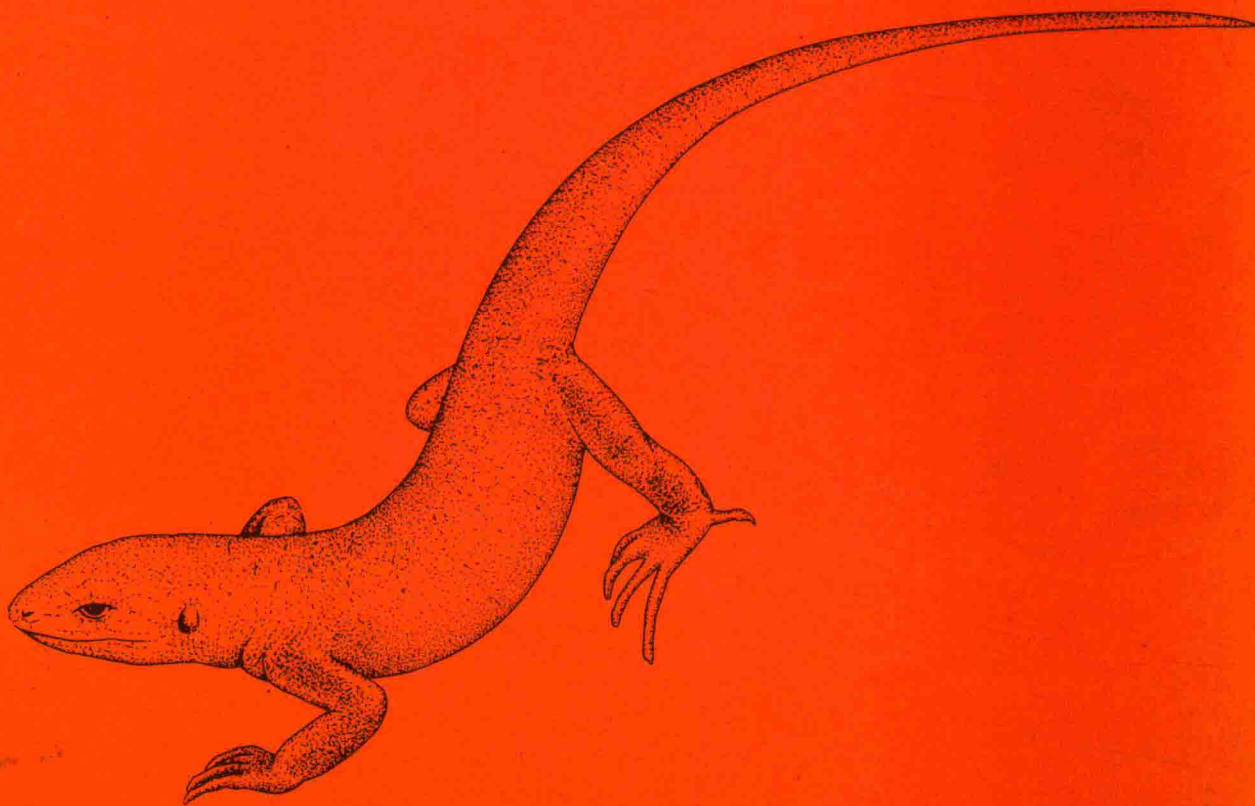


**Ronald Pearson &  
John N. Ball  
Lecture Notes on  
Vertebrate Zoology**



**Blackwell Scientific Publications**

# Lecture Notes on Vertebrate Zoology

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# Lecture Notes on Vertebrate Zoology

# Preface

This book is intended to serve a similar purpose to *Lecture Notes on Invertebrate Zoology* by M.S. Laverack and J. Dando. However, the vertebrates, as members of a single phylum, clearly form a more cohesive unit than do the thirty or so invertebrate groups. It is partly for this reason that we have not considered it appropriate to use the fully 'note' format employed by Laverack and Dando in their treatment of the extreme diversity found amongst invertebrates. Furthermore, the teaching of vertebrate biology varies greatly between institutions and we accept that no one textbook will satisfy all the requirements of all undergraduate students. We have, therefore, attempted to provide in this book a balanced account of vertebrate biology and evolution which will form a background for various kinds of elementary course and thereby provide a sound basis for later specialization in various directions.

We have deliberately placed greater emphasis on anatomy than has become usual in recent years, believ-

ing that it is desirable to correct what could become a swing away from the thorough grasp of structure that is surely an essential prerequisite for understanding physiology, evolution, behaviour, and all those other aspects of biology for which morphological and anatomical information can so usefully act as a conceptual framework. Another feature is the amount of attention given to the nervous and muscular systems, too often skimmed in undergraduate teaching. In these trends we have followed Laverack and Dando in aiming, as they put it, 'to release the teacher from the drudgery of simply reproducing anatomy' and to create 'a platform for profitable expansion on innumerable other topics'.

We hope that our platform is soundly enough constructed to be useful to both teacher and student, and to permit expansion in a variety of ways. If the book encourages students to appreciate the full panorama of vertebrate biology, we will feel that our intentions have been achieved.

R.P., J.N.B.

# Acknowledgments

We wish to express our appreciation to our colleagues in the Zoology Departments of Liverpool and Sheffield Universities for countless stimulating discussions over many years. We would also like to thank Miss Anita Callaghan and Mr Bryan V. Lewis of the Department of Zoology, Liverpool, for, respectively, typing the manuscript and assisting with the illustrations. Needless to say they are in no way responsible for any inadequacies which the book may have.

We are very grateful to the following authors and publishers for generously granting us permission to use the illustrations cited: Professor L.B. Halstead for Fig. 3.6 from *The Pattern of Vertebrate Evolution*, published by Oliver and Boyd; Professor A.I. Dagg for Fig. 6.15 from *Running, Walking and Jumping*, Wykeham Publications; Professor A.S. King and Dr. J. McLelland for Fig. 8.1 from *Outlines of Avian Anatomy*, Baillière and Tindall; Dr C.H. Tyndale-Biscoe for Fig. 9.18 from *Life of Marsupials*, Edward Arnold; Dr. C.J. Pennycuik for Fig. 8.4 from *Animal Flight*, Edward Arnold; Masson, Editeur, s.a., Paris, for Figs 2.7, 2.18, 8.28, 10.6–10.10 and 10.20 from the *Traité de Zoologie*; Cambridge University Press for Figs 3.12, 4.11 and 4.12 from Alexander R. M<sup>c</sup>, *The Chordates*, and Fig. 3.22 from Fridberg G. & Bern H.A. (1968). The urophysis, *Biol. Rev.* **43**; The University Tutorial Press for Figs 3.17 to 3.19 and 3.24 from *Animal Biology* by Grove A.J. & Newell G.E.; Academic Press Inc for Fig. 3.20 from

Jasinski A., *Gen. Comp. Endocrinol.* suppl. 2, pp. 510–521, for Fig. 7.8 from Kochva E., *Biology of the Reptilia*, C. Gans (ed.) Vol. 8, for Fig. 3.21 from Copp D.H., in *Fish Physiology*, Hoar W.S. & Randall D.J. (eds) Vol. 2., and together with the *Journal of Comparative Neurology*, for Figs 4.18 and 7.14 which are modified versions of Figures in Heric T.M. & Kruger L. (1965) *J. Comp. Neurol.* **124** and Schwassman H.O. & Kruger L. (1965) *J. Comp. Neurol.* **124** as used by Pearson R., *The Vertebrate Brain*, Academic Press Inc; W.H. Freeman and Co., for Fig 6.1 from Goin C.J., Goin O.B. & Zug G.R. (1978) *Introduction to Herpetology*, and Fig 9.19 from Eckert R. & Randall D. (1978) *Animal Physiology*; Sidgwick and Jackson for Fig 7.11 from Carter G.S., *Structure and habit in vertebrate evolution*; both Macmillan Publishing Co., Inc., and Kendall/Hunt Publishing Co., for Figs 3.15, 6.13, 9.4, 9.5, 9.14 from Holmes, *Manual of comparative anatomy*; Alan R. Liss Inc., for Fig. 8.7 from *J. Comp. Morphol.* **142**; Queensland University Press for Fig. 9.10 from May A.D.S., *Anatomy of the sheep*; Holt, Rhinehart and Winston for Fig. 9.11 from Villee *et al.*, *General Zoology*; W.B. Saunders and Co., for Fig. 9.12 from Miller H.E., Christensen G.C. & Evans H.E., *Anatomy of the dog*; McGraw Hill Book Co., for Figs 6.19 and 6.20 from Weichert C.K., *Representative Chordates*; Kindler Verlag GmbH, for Fig. 8.27 from Grzimek's *Animal Life Encyclopaedia*.

# Contents

Preface	vii
Acknowledgments	viii
1 Introduction	1
2 The Superclass Agnatha	4
3 Class Chondrichthyes	22
4 Class Osteichthyes: 1. Actinopterygii	47
5 Class Osteichthyes: 2. Crossopterygii and Dipnoi	66
6 Class Amphibia	72
7 Class Reptilia	92
8 Class Aves	109
9 The Mammals	131
10 Mammalian Diversity	153
Indexes	169

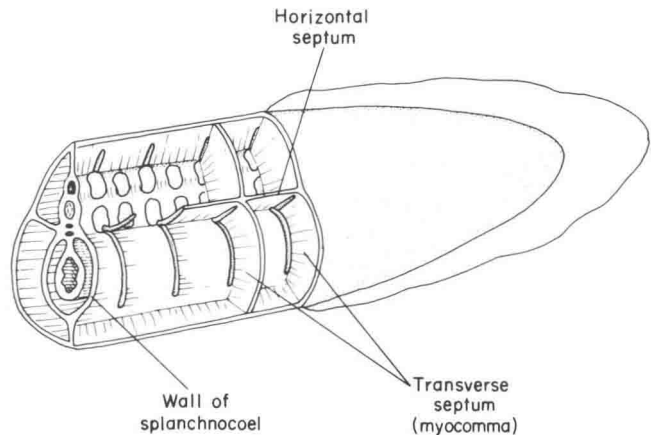
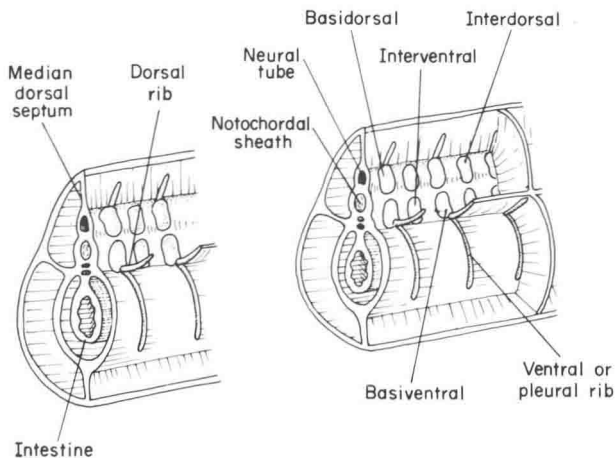
# 1 • Introduction

## GENERALITIES

Vertebrates comprise a series of adaptive radiations from ancestral forms whose fossil remains first appear in rocks dating from some 450 million years ago. The precise invertebrate origins of the vertebrates remain unknown but they clearly shared a distant common ancestor with the echinoderms, a more recent one with the other non-vertebrate chordates, and themselves exhibit variations on a common plan. It is a study of these variations which forms the basis for courses in vertebrate zoology. This book considers each class in turn. Although a relatively uniform approach is used in each case some topics only relate to certain classes, and others, which relate to more than one class, are dealt with in detail on the first occasion. For information on the related phyla of invertebrates the reader is referred to Laverack & Dando (1979).

## GENERALIZED STRUCTURE

*i* Fig. 1.1 is an exploded stereogram of a generalized vertebrate body. In general terms the body is supported throughout by an all-pervading framework of connective tissue which binds the organ systems together. There is always, at least during embryonic development, a notochordal rod which underlies the tubular, dorsal central nervous system. The central and peripheral nervous systems which are of ectodermal origin, together with the dorsal musculature and kidney ducts, which are of mesodermal origin, are all primitively arranged in a metamerically segmented pattern. This segmentation may be obscured in the adult but it is always present in the embryo. Broadly speaking, all the mesodermal structures arise during ontogeny as paired outgrowths from the embryonic gut, or archenteron,



**Fig. 1.1** An exploded stereogram showing the connective-tissue systems in an idealized craniate and the disposition of notochord, nervecord, etc. (After Goodrich.)



and the archenteric walls then rejoin beneath them and complete the lining of the gut.

ii Each coelomic outgrowth derived in this way, whether hollow or solid, becomes divided into dorsal and ventral moieties. The dorsal moiety subsequently gives rise to the segmentally arranged muscles, myotomes, and to the sclerotomes that give the bony or cartilaginous axial skeleton. The ventral moieties are never truly segmental and soon join to form a continuous longitudinal coelomic chamber, the splanchnic coelom, which surrounds the viscera. The intermediate mesoderm in the region linking these dorsal and ventral

components is the source of the primitive kidney structures.

iii The paired origin of the coelomic derivatives leaves the body divided into left and right halves by a median longitudinal, vertical septum. This septum persists as a suspension for the gut.

iv The sclerotome gives rise to vertebral components, around or near the notochord, and to ribs. These last extend out from the sides of the vertebrae and usually lie between the dorsal and ventral muscles but fish possess two sets of ribs.

**Table 1.1** The vertebrate succession through geological time together with the predominant known vegetation and the ages as determined by radiometric methods.

Era	Period	Age from beginning (million years B.P.)	Type of vegetation	Vertebrate succession
CENOZOIC	Quaternary	2.5	Modern	Mammals
	Tertiary	65	Modern	
MESOZOIC	Cretaceous	136	Gymnosperms dominant in the Lower Cretaceous	Diapsid reptiles, plagiaulacid and ptilodontid multituberculates, marsupials, and placentals
	Jurassic	195	Luxuriant forests of gymnosperms and ferns	Diapsid reptiles, triconodonts, symmetrodonts and pantotheres
	Triassic	225	Sparse desert flora giving way to luxuriant forests of gymnosperms and ferns.	Diapsid reptiles, tritylodonts and ictidosaur
PALEOZOIC	Permian	280	Tall swamp forests with early gymnosperms, <i>Calamites</i> and ferns giving way to desert flora of conifers and Bennettitales	Cotylosaurs, pelycosaurs and therapsidans
	Carboniferous	345	Early gymnosperms, tree lycopods and ferns	Cotylosaurs and labyrinthodonts
	Devonian	395	Herbaceous marsh plants, e.g. <i>Psilophyta</i> and <i>Zosterophyllum</i> . <i>Rhynia</i> vegetation in Middle Devonian	Acanthodians, antiarchs and ichthyostegalian
	Silurian	440	Marine algae	Agnathans
	Ordovician	500	Marine algae	Agnathans
	Cambrian	570	Marine algae with some evidence of land plants	

## The environment and time-scale

The time-scale over which vertebrate evolution has occurred is summarized in Table 1.1. It is, however important to emphasize the great changes which have occurred in the environment during this period of some 450 million years. The continents have split, separated and reassembled. Climatic deteriorations and ameliorations have come and gone. In particular we have extensive evidence that glaciation occurred around the end of the Ordovician, during the Carboniferous and Permian, and during the last two million years. Complementarily we have the immense coal measures that record swamp conditions in the Carboniferous. These are not isolated events but reflect the persistent environmental variations to which vertebrates, and all other groups, have been exposed. Such changes undoubtedly greatly influenced the tempo of evolution by varying the precise nature and intensity of the selective factors acting at given moments of world history.

## FURTHER READING

Suggestions for further reading follow many of the subsequent chapters. We provide here a list of textbooks that can be consulted for the purposes of essay writing, etc.

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## 2 • The Superclass Agnatha

### Synopsis

- \*Class Pteraspidomorpha — *Pteraspis*
  - Class Cephalaspidomorpha
    - \*Subclass Osteostraci — *Tremataspis*;
    - \*Subclass Anaspida — *Birkenia*;
    - Subclass Cyclostomata — *Petromyzon* the lamprey and *Myxine* the hagfish
- \* = Fossil forms

N.B. The relationships of the hagfish are controversial. Some authors affiliate it to the pteraspidomorphs, whilst others deny its relationships to known fossil forms.

### INTRODUCTION

The cyclostomes are the most primitive living vertebrates and their fossil relatives, the ostracoderms, were the first animals with backbones to appear in the fossil record. The absence of jaws is itself a distinctive characteristic serving to distinguish the agnathans from all the jawed vertebrates or gnathostomes. However, they possess a number of other unique features:

- their sucking or rasping mouths;
- the unpaired olfactory organ of cephalaspidomorphs;
- the absence of paired fins;
- the absence of both pectoral and pelvic girdles;
- the presence of only one or two semicircular canals in the inner ear.

They have well-developed anal fins but bending the body by serial contraction of the myotomes provides the principal motive force. The presence of paired fin-like structures in some fossil forms, and the presence of paired olfactory capsules in pteraspidomorphs, coupled with the fact that the unpaired olfactory organ of cyclostomes is associated with two olfactory nerves, implying a dual origin during phylogeny, demonstrates that the modern genera combine primitive and specialized characteristics.

### GENERAL FEATURES AND THE LIFE CYCLE OF MODERN FORMS

- i At least two distinct lineages are clearly represented

by the fossil forms that are known collectively as ostracoderms. The Pteraspidomorpha, Diplorhina or Heterostraci, possessed two nostrils and are therefore envisaged as approximating most closely to the ancestral stock. The Cephalaspidomorpha or Monorhina, including both the Osteostraci and Anaspida, have a single nostril (Fig. 2.1 and 2.2). The anaspids, in particular, have been viewed as representing a form which is closely similar to that of the putative ancestors of modern genera.

ii Known from the Ordovician, Silurian and Devonian periods the three groups underwent extensive adaptive radiations during the Upper Silurian and Lower Devonian only to decline rapidly thereafter. Apart from lineages which may be ancestral to the cyclostomes, the majority became extinct by the early Carboniferous. They exhibit a variety of buccal adaptations. These suggest that their methods of feeding ranged from microphagous ciliary feeding, comparable with that in *Amphioxus* or the ammocoete larva of lampreys, to swallowing larger food masses, as do the majority of vertebrates. Spoonlike adaptations were presumably for shovelling up bottom detritus which was then exposed to pharyngeal filtration mechanisms.

iii The two groups of living cyclostomes are variously ascribed to distinct orders or superorders by different workers. In broad terms they are the Petromyzontoidea, or lampreys, and the Myxinoidea, or hagfishes (Fig. 2.3). The latter comprises three genera—*Myxine*, *Paramyxine* and *Eptatretus*. They are marine forms that either burrow into dead or dying fishes, or eat marine invertebrates. Their lateral eyes are functionless, rudimentary organs, and they lack a pineal eye, but horny teeth are well developed.

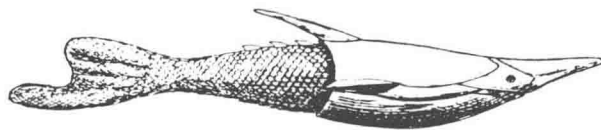
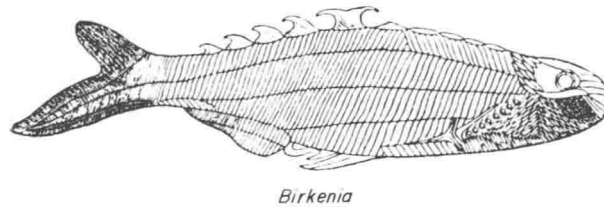
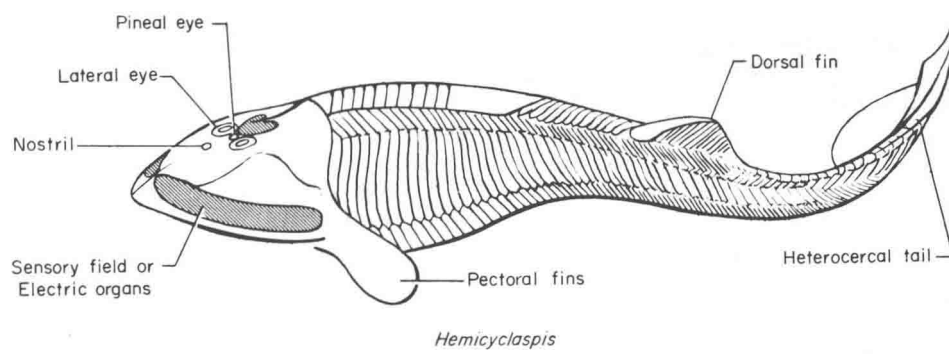
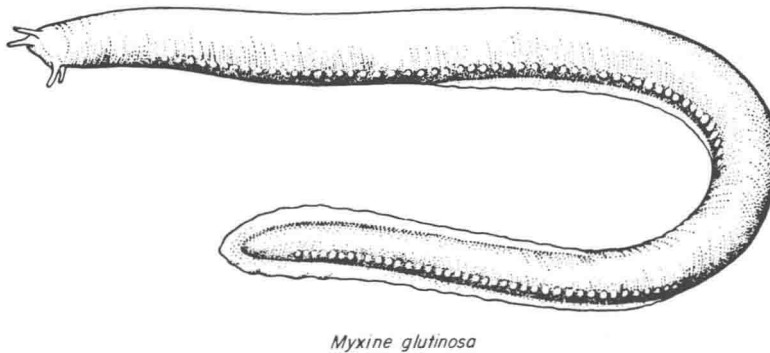
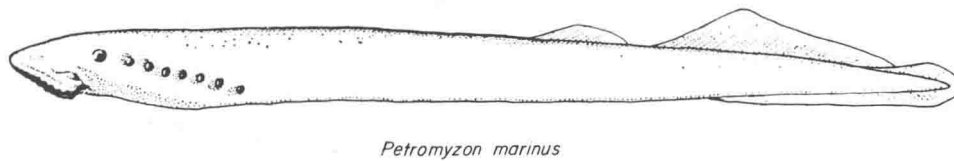


Fig. 2.1 Lateral view of a pteraspidomorph.



**Fig. 2.2** Lateral views of the osteostracan *Hemicyclaspis* and the anaspid *Birkenia*.



**Fig. 2.3** *Petromyzon marinus*, the marine lamprey, and *Myxine glutinosa*, a hagfish.

iv The Petromyzontoidea includes eight genera. The life cycle consists of a filter-feeding larval phase, the ammocoete larva, possessing many anatomical features

reminiscent of *Amphioxus*, and a fish-like adult which is parasitic on fishes. This adult phase is achieved after a larval period of some three to seven years spent in the

mud of freshwater lakes and streams. Some species then migrate to the sea whereas others remain in freshwater environments. In either case, fully sexually mature adults migrate to freshwater streams for spawning. They have an anterior sucker bounded by a series of lips with which they attach themselves to the host fish. They then rasp away at the body surface of the fish by means of their tongues. Apparently they live primarily upon the host's blood and, having fed, detach themselves and swim away.

## THE AMMOCOETE LARVA

*i* The body of the ammocoete is metamerically segmented. During development the coelom and mesoderm originate from dorsolateral pouches which become nipped off from the archenteron, or embryonic gut, during the gastrula stage. The notochord arises as a third outgrowth in the mid-dorsal line at a slightly later stage. This method of forming the coelom and mesoderm is referred to as enterocoelic. Each somite then becomes differentiated into a dorsal myocoel and a more ventral splanchnocoel. The former is segmentally organized but the latter is not, and instead forms the continuous cavity surrounding the gut. On each side an intermediate component of the coelom, the nephrocoel, retains its opening into the splanchnocoel, the coelomostome, and gives rise to the kidney rudiments.

*ii* The median wall of the original myocoel differentiates in three ways. The majority of it forms the segmental muscle blocks, myotomes, which grow out into the original cavity and more or less occlude it. Growing ventrally they then attain a position in the body wall outside the splanchnocoel. A small ventral component of the original wall grows between the myocoel and the notochord, is known as the sclerotome, and subsequently develops into skeletal tissue. A further dorsal part is associated with skeletal tissue in the fin.

*iii* In the cranial region the early segmentation is obscured later by the development of the organs in the head. In the ammocoete, as in the embryos of all other vertebrates, the following cranial segments can be detected. The first segment lies in front of the mouth, is 'premandibular', and its myotomal derivatives form those extrinsic eye muscles that are innervated by the third, or oculomotor, nerve. These are the inferior oblique, the superior, inferior and internal rectus muscles. Behind this segment, but in front of the ear, there are two further segments (2 and 3) whose

myotomes also contribute to the eye musculature. As the eyes of ammocoetes are small, lying below the skin, these myotomes are also small. Segments 4 and 5 are in the ear region and their myotomes are displaced backwards but behind the otic capsule the sixth and subsequent segments form a regular sequence.

Gill clefts form on each side in the visceral plate region of segments 3–10, but those in segment 3 soon close. There are, therefore, some seven functional gill clefts which grow backwards behind their segments of origin during development. The ventral parts of their homologous myotomes grow back with them and displace the ventral parts of the myotomes in the segments behind. These ventral myotomal components then approach the mid-ventral line and form the hypobranchial musculature.

*iv* The cranial nerves are summarized in Table 2.1. The ventral nerve roots of segments 1–3, the oculomotor (III), trochlear (IV) and abducens (VI) nerves, supply the extrinsic eye muscles formed from the myotomes of these pre-otic segments. The ventral roots of segments 4 and 5 do not develop, although the myotomes are present and are innervated by more posterior roots. The ventral roots of segments 6–10 are typical nerves to the myotomes and those of 11–18 supply the hypobranchial musculature.

**Table 2.1** The segmental organization of the cranial region in the ammocoete larva.

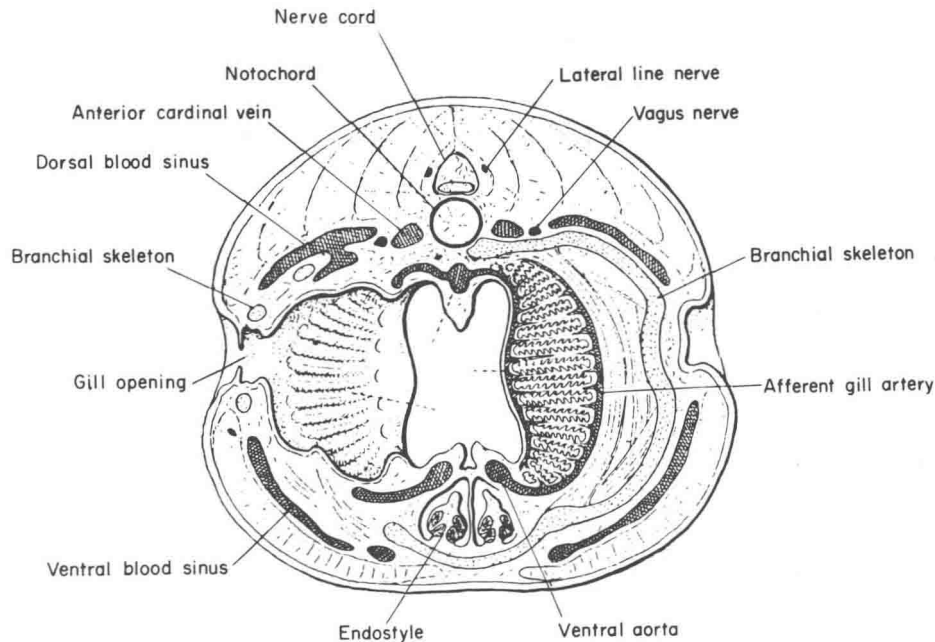
Segment	Dorsal root	Ventral root	Muscles served
1	Profundus (usually referred to as V <sub>1</sub> )	Oculomotor III	Inferior oblique, superior, inferior and internal recti
2	Trigeminal (V <sub>2</sub> and V <sub>3</sub> )	Trochlear or pathetic IV	Superior oblique
3	Facial VII	Abducens VI	External rectus
4	Glossopharyngeal IX	Absent	Displaced backwards behind the otic region
5	Vagus	Absent	
6–10	Vagus	Normal roots supplying myotomal derivatives of segments 4–10	Myotomes

The profundus nerve is apparently a branch of nerve V in most vertebrates. In the ammocoete it is free. It is the dorsal root of the first segment and supplies sense organs at the front of the head. The dorsal root of the second segment is the trigeminal nerve (V), that of the third segment is the facial (VII) which innervates cranial lateral-line sense organs. The glossopharyngeal (IX) is the dorsal root of the fourth segment and innervates the first functional gill slit. The dorsal roots of segments 5–10 combine to form the vagus nerve (X) which not only provides the innervation for the remainder of the gill clefts but also has a branch which innervates the lateral line sense organs on the side of the body. It can be seen that motor neurons travel in dorsal roots in the cranial region which therefore retains an ancient organization comparable with the trunk region in *Amphioxus*. The basic structure involves modification of an underlying, repetitive, metameric segmentation (see later Table 3.1).

v The ammocoete larva is a ciliary or microphagous feeder. Two ectodermal flaps on the sides of the head grow ventrally and form an oral hood. Around the mouth there are some papillae which both prevent large

particles from entering the pharynx and bear sense organs that test the inhalant water. The internal oral cavity is a stomodaeum lined by ectoderm and two muscular flaps—the velum—project backwards at the connection between the oral cavity and the pharynx. Rhythmical contractions of both these flaps and the pharyngeal wall result in a current of water passing into the pharynx and then out to the exterior via the gill clefts. In the mid-ventral line of the pharynx there is a ciliated groove which divides into two peripharyngeal bands that pass dorsally. Within this ciliated groove, and at the level of the second functioning gill slit, there is the opening of the endostyle, an organ which secretes mucus by which food particles are trapped and passed back into the oesophagus.

Between the pharyngeal wall and the external openings of the gill clefts lie the gill chambers (see Fig. 2.4) whose organization is more similar to that of fishes than are those of adult lampreys. Gill filaments develop on both the anterior and posterior walls as a series of horizontal folds. Above and below each filament a series of secondary folds is organized transversely to it and it is here that gaseous exchange occurs.



**Fig. 2.4** Transverse section of the branchial region of an ammocoete larva passing through a gill bar on the right and a gill opening on the left.

## THE INTEGUMENT

*i* Sections cut perpendicular to the surface reveal the structure of the body wall. In the pteraspidomorphs there was a superficial layer of dentine which tended towards enamel on the surface. Below this there was a reticular layer of bone. In the osteostracans an analogous dentine layer was penetrated by very fine canals, similar to those in the dentine of modern vertebrates and opening onto the surface by way of minute pores (Fig. 2.5). The superficial layer was also penetrated by much larger pores. It has been suggested that mucus was secreted through these in view of the great importance of mucus as both an osmotic control and a general protection in modern hagfishes. The layer was also very varied in its development. In some genera it is a prominent feature whilst in others it can either be restricted to the surface of tubercles or be completely absent. It was underlain by a layer containing large diameter anastomosing canals which contained a network of blood vessels, and, below this again, was a basal layer of laminated bone containing many spaces for cells and some large canals through which subcutaneous blood vessels coursed.

*ii* The skin of *Myxine* consists of a hypodermis rich in fat cells, a dermis with bundles of collagenous fibres, and an epidermis. These are, respectively, 240  $\mu\text{m}$ , 90  $\mu\text{m}$  and 90  $\mu\text{m}$  thick. The epidermis is unique. There are five types of cells—undifferentiated basal cells, small mucous cells, large mucous cells, thread cells and sensory cells (Fig. 2.6). Undifferentiated basal cells and small mucous cells comprise the bulk of the inner and outer halves of the epidermis respectively, and their numbers greatly exceed those of other types. Secretory canaliculi within the apical regions of the mucous cells

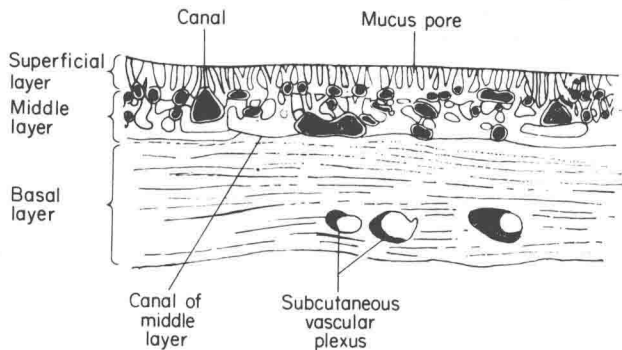


Fig. 2.5 Section through the carapace of an osteostracan.

give a striated appearance but it is the thread cells that are the most conspicuous individual units. They have a large central mass of dense granules and peripheral spiral threads which lie within an aqueous matrix. When discharged these form part of the slime.

*iii* In the midline the skin is produced into the fins—two on the back and one round the tail in lampreys. These are supported by fin rays. In the cephalaspidomorphs the one or two fins were a continuation of a dorsal crest and this was also carried over the tail to form a caudal fin.

## SKELETAL SYSTEM

### (a) Cephalic region

*i* In the pteraspidomorphs and osteostracans the anterior region of the body was encased within the heavily ossified carapace. In pteraspidomorphs this formed a

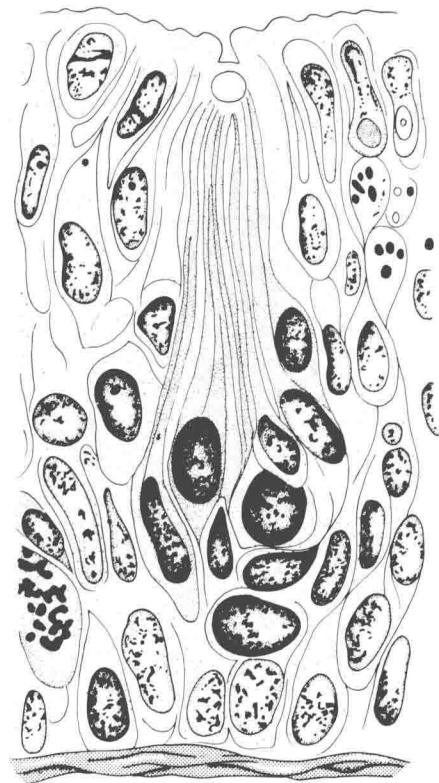


Fig. 2.6 Stylized drawing of secretory cells in the skin of *Myxine*.



relatively immobile unit of variable appearance. It was composed of large plates, which may have originated by the fusion of scales, and could be either rounded or pointed. Such distinct plates were lacking in osteostracans. However, in both cases the carapace enclosed both the cranial and branchial regions and, in the osteostracans, where it was more strongly flattened on the ventral side, it also encased most of the abdominal region. In contrast, the anterior of anaspids lacked a coherent carapace and was covered by small plates.

ii The internal skeleton of pteraspidomorphs was not ossified and is poorly known. The osteostracans had an ossified cranial skeleton whose composition contrasts with that of most vertebrates. Instead of a separate braincase and jointed branchial arches the dermal shield was underlain by a single unified structure. It has been suggested that this represents a primitive undifferentiated condition and that the establishment of separate

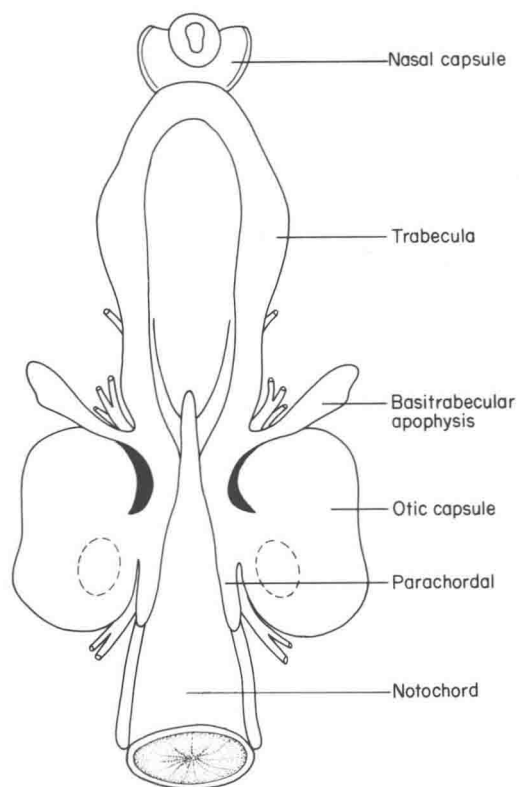


Fig. 2.7 Ventral view of cranial skeletal rudiments in *Lampetra*. (After Parker.)

units followed later, although it is probable that an early metameric organization occurred during development. The internal skeleton of anaspids is presumed to have been cartilaginous.

iii Modern cyclostomes have a skeleton of uncalcified cartilage which differs from that in other vertebrates in having relatively little matrix. The incomplete neurocranium which protects the sense organs and brain is similar in both the ammocoete larva and the adult lamprey—although more complete in the latter—but the splanchnocranium changes in association with the transition from larval microphagy to the adult parasitic way of life. In broad terms the neurocranium develops from paired rudiments (Fig. 2.7). These comprise paired trabeculae and olfactory capsules in front; parachordals on either side of the notochord; lateral basitrabecular apophyses and otic capsules. The trabeculae of gnathostomes have long been considered as representing the remnants of a gill arch in segment one. In the adult cyclostome they are overlain by the lateral cranial wall and a cranial roof forms between the otic capsules, but the fact that both the glossopharyngeal (IX) and vagus (X) nerves leave the brain behind the caudal limits of the skull shows that the occipital region is essentially incomplete by comparison with that in gnathostomes.

iv The splanchnocranium is a continuous cartilaginous structure known as the branchial basket (Fig. 2.8). Slender, irregular, cartilaginous bars lie external to the gill pouches and support the gill region but there are several reasons for not homologizing them with the typical visceral arches of gnathostomes, and such homologies remain controversial. Additional, anterior, dorsal and ventral cartilages provide support for the rasping tongue and sucker.

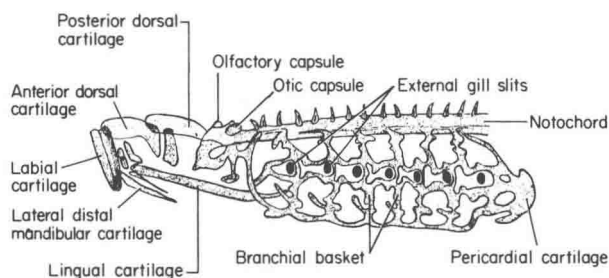


Fig. 2.8 Lateral view of chondrocranium and branchial basket of *Petromyzon*. (After Parker.)



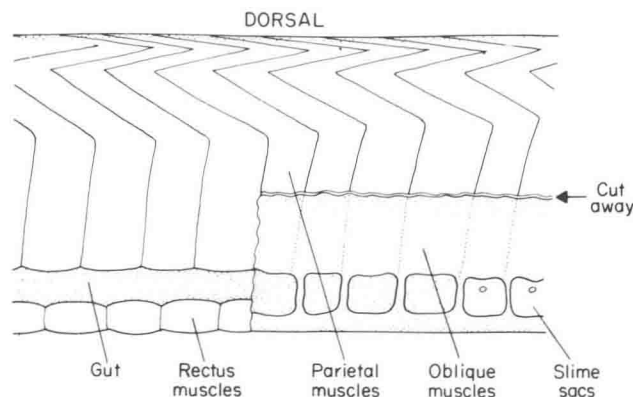
## (b) Axial skeleton

*i* As noted above, the internal skeleton of pteraspidiomorphs was not ossified and is poorly known. In osteostracans ossification took place in association with pre-existing cartilage. Perichondral ossification left the cartilage persisting within a bony sheath, whilst endochondral ossification transformed it into bone. The majority of genera had a pair of pectoral fins that were probably supported by fin rays and the tail was heterocercal with the vertebral elements in the dorsal lobe. In contrast the pteraspidiomorphs had hypocercal tails and, during swimming, the upward movement, resulting from the more flexible ventral lobe, depressed the front end of the body (see page 32). The tail of anaspids such as *Birkenia* tilted downward to give a reversed heterocercal tail. Amongst living forms this is only known in the ammocoete larva and not in any other vertebrate.

*ii* The axial skeleton of modern cyclostomes largely comprises the persistent notochord with its vacuolated cells. Its fibrous sheath is continuous with the connective tissue septa which separate the myotomes and it functions as an elastic rod flexed laterally by myotomal contractions. Various associated perichordal structures can be cartilaginous in adult petromyzontids but are fibrous or membranous in myxinooids. In each segment two pairs of peglike structures lie on each side of the notochord. The anterior pair is in front of the ventral nerve roots, the posterior in front of the dorsal root. They are analogous, if not fully homologous, with the interdorsal and basidorsal elements of other classes, extend dorsally, and, like the neural arches of gnathostomes, partially surround the spinal cord. Similar cartilages in the tail region extend ventrally to form haemal arches. Very slender fin rays support the median fins.

## MUSCULAR SYSTEM

*i* As cyclostomes lack paired fins the musculature of the trunk and tail has a very straightforward plan. The muscle blocks of lampreys are metamerically arranged myomeres or myotomes that are disposed almost vertically but curve forward slightly in both the dorsal and ventral regions giving a somewhat W-shaped structure. The component muscle fibres are not inserted onto the axial skeleton but onto the tough, connective tissue partitions called myosepta or myocommata which separate adjacent myotomes. The scale rows of osteostracans and anaspids are thought to reflect a com-



**Fig. 2.9** Lateral view of body musculature in *Myxine*. The oblique muscles underlying the parietal ones are shown on the right. (After Cole.)

parable myotomal plan. In adult hagfishes there is rather more differentiation. On each side there is a metamerically organized dorsolateral parietal muscle and a continuous ventrolateral sheet forming the oblique muscle. A mid-ventral rectus muscle completes the picture (Fig. 2.9).

*ii* The musculature of the cranial region is, of course, modified in association with feeding and sensory functions. In lampreys the somitic mesoderm gives rise to the extrinsic eye muscles, and eight other muscles, associated with the anterior cartilages, are involved in attachment to the prey. In hagfishes the eyes are rudimentary, eye muscles are lacking, and the greater part of the cranial musculature is involved with the dental plate but a number of smaller muscles move the tentacles, lips and velum.

## THE DIGESTIVE SYSTEM

### (a) The buccal region

The mouth of ostracoderms was situated at the anterior end of an orobranchial chamber and varied in shape from a circular opening to a transverse or longitudinal slit. The mouth of the microphagous ammocoete larva has already been described (page 7). When attached to its prey, the mouth of the adult lamprey is round, and numerous deciduous, horny teeth are distributed on the lips and rasping tongue. That of *Myxine* is horseshoe shaped, bordered by two pairs of tentacles, and bears some 33 permanent, horny teeth. A single, median, palatal tooth is situated dorsally, points backwards, and