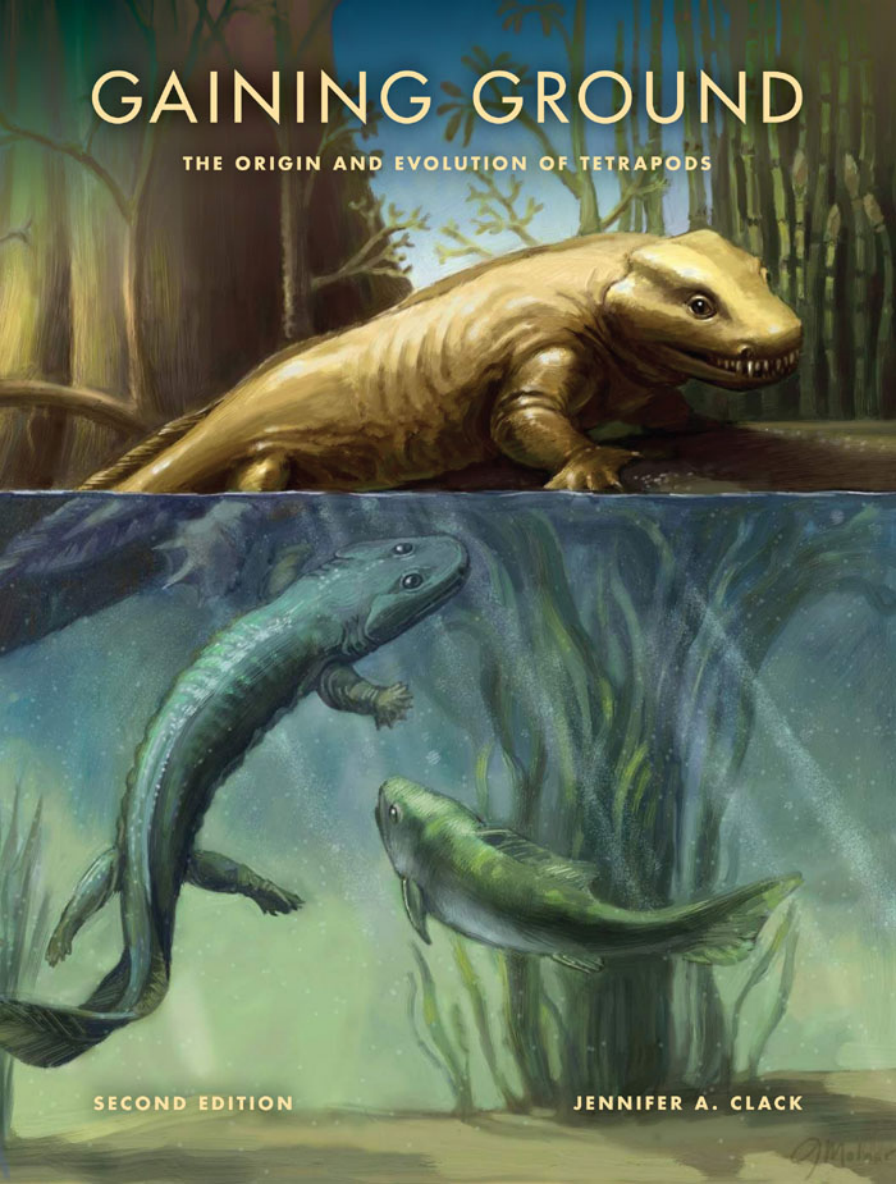
# GAINING GROUND

## THE ORIGIN AND EVOLUTION OF TETRAPODS



SECOND EDITION

JENNIFER A. CLACK

# GAINING GROUND

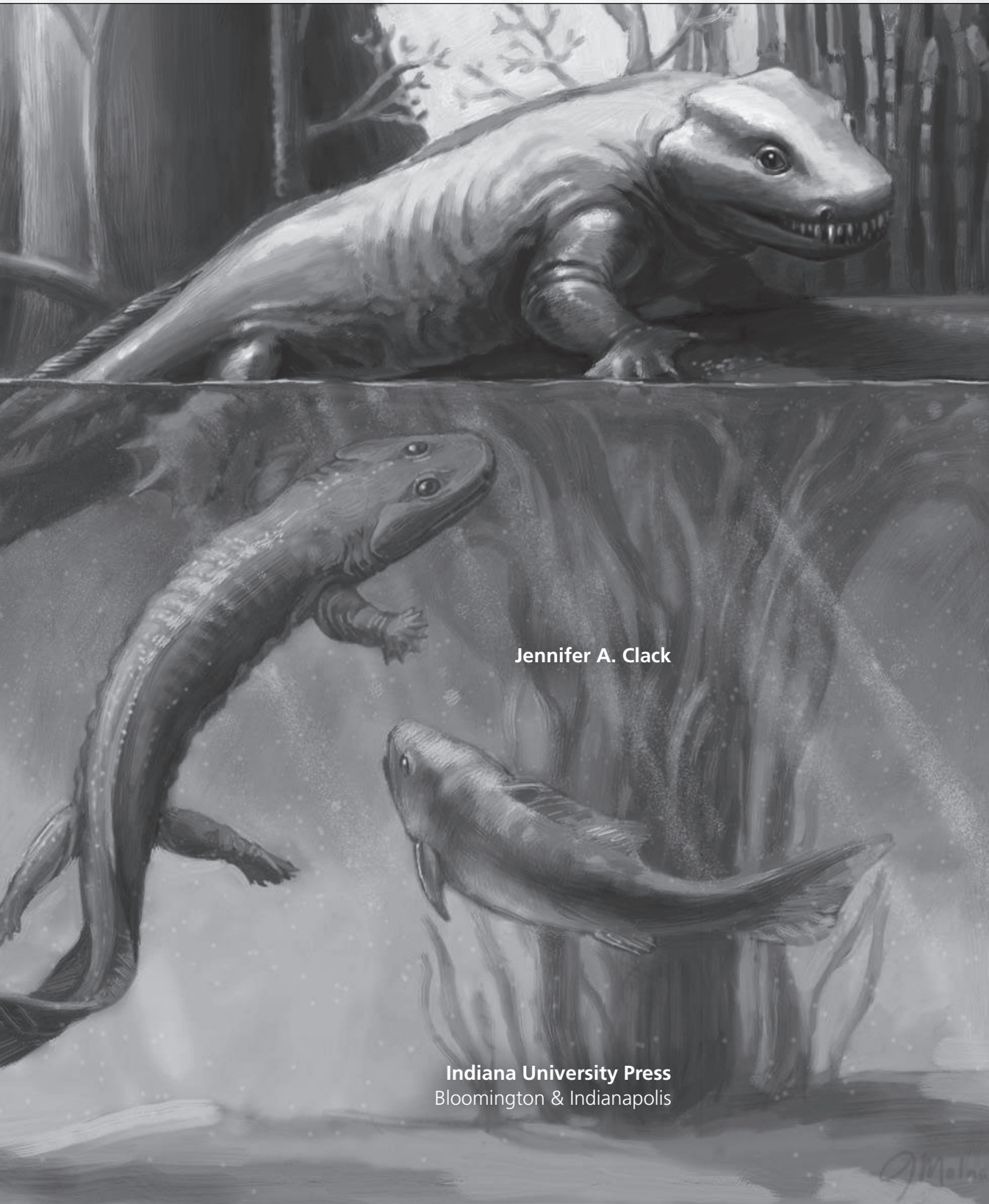


**Life of the Past** James o. Farlow, editor



# GAINING GROUND

**The Origin and Evolution of Tetrapods** Second Edition



**Jennifer A. Clack**

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# Preface to the Second Edition

Since the first edition of *Gaining Ground* was completed, much has happened in the field of early tetrapod paleontology and in the wider world that has affected not only the ideas and conclusions presented in the first edition, but also what paleontologists are able to do with material, the techniques that they use, and how easily and quickly things can be done.

One of the most significant events worldwide has been the global spread of the Internet, which has not only allowed discoveries to be published more quickly, but has enabled rapid searches for material and references. The ease and speed of access to references by electronic means and Internet search have improved enormously, allowing information and citations to be readily found at the touch of a button. It's hard to remember that in the late 1990s and the first couple of years of the 21st century, when the first edition was written, online connections were often slow and limited. Today, the ease and availability of electronic techniques has greatly affected many aspects of producing and delivering a wide range of scientific output. I personally have been most affected by my familiarity with software packages such as Photoshop, which permits manipulation of scanned images to produce diagrams. Some of the diagrams in the first edition were admittedly clumsy, and I hope that readers will find these improved in the second. Digital photography, of course, is another boon.

Technological advances have affected many areas of study, and paleontology is no exception here. One of the techniques that has improved in availability, cost, and degree of resolution is that of X-ray computed tomography (CT), or micro-CT scanning. This is becoming the technique of choice for examining new aspects of fossil material previously inaccessible. Software programs build the serial sections produced by scans into three-dimensional images that can be easily manipulated and dissected. These have become more sophisticated but at the same time more amenable to being run on a moderately powerful desktop computer, as well as becoming more intuitive to use. Such advances have allowed new questions to be framed and answered. One stage up from micro-CT scanning with X-rays is the use of a synchrotron. This allows minute examination of tissue structure inside fossil material, from which, for example, three-dimensional images of growth patterns of bone can be built. For really high-resolution scanning to get these results, at present, the limitation of this technique is the small size of sample that can be examined at any one time. Larger specimens can be scanned at lower resolution, often higher than with micro-CT machines, but results still depend on the geological makeup of the material.

Micro-CT images of fossils are increasingly being used in biomechanical studies using an engineering technique known as finite element analysis (FEA). This allows study of the relative degrees and directions of stress that a structure, such as a skull, can withstand, thus permitting function to be inferred. Although FEA has not yet been widely applied to very early tetrapods, such analysis of lower jaw function, for example, should help reveal what the implications are for the changes in dental patterns seen across the fish–tetrapod transition. Such work is in progress.

Digital imaging and suitable computer programs allow quantitative studies of, for example, skull proportions, or the way in which different bones contribute to skull structure in different groups. This study, known as geometric morphometrics, is being applied to groups of fossil tetrapods. It can help tease apart differences in shapes among a range of taxa to reveal phylogenetic or morphological relationships, and some of the results are included in this new edition.

New electronic techniques have also been brought to bear on climate modeling and atmospheric composition in past periods of Earth's history, and these are highly relevant to understanding the late Paleozoic and events that occurred during that time.

Computers' increased memory, faster processing power, and lower cost have allowed increasingly large data sets of taxa and characters to be used in phylogenetic analyses, and new search protocols and methods are beginning to provide alternative ways of processing the information. Some of these advances have been made in the field of molecular phylogenetics and in the incorporation of morphological and molecular data into combined analyses.

Cladistic matrices and the trees they generate are now being interrogated further in metadata analyses to produce hypotheses of overall evolutionary patterns: diversity and disparity curves, effects and results of evolutionary constraints or restrictions on taxa, episodes of "character release" (i.e., increasing the number of potentially varying characters) or decreased rates of character change, evolution of body size among clades, and many others (e.g., Ruta et al. 2006; Wagner et al. 2006; Laurin 2004).

The electronic age has seen a veritable explosion of information in the field of evolutionary developmental biology, or "evo-devo." In its infancy in the early 1990s, it has more recently been asking questions in a phylogenetic context, incorporating ideas and data from phylogenies that have been drawn by means of both molecular and morphological data and that include fossil taxa. Paleontology has much to contribute to that endeavor, but similarly, researchers in evo-devo fields have been addressing questions on the basis of phylogenetically relevant species. Sharks, lungfish, and nonteleost fish are examples of these species, which have provided key information in studies such as the origin of limbs and digits.

Within the field of early tetrapod vertebrate paleontology, there have also been major developments of a more traditional kind. People have gone out and found more fossils. The number of recognizably different taxa of Devonian tetrapods has increased more or less exponentially since

the mid-1990s, and discoveries are still going on. It is true that similarly explosive expansion has occurred in other fields of vertebrate paleontology as well, so my field appears to be part of a general trend. In fact, this probably applies to all aspects of scientific discovery, and a good part of the explanation is embodied in the electronic advances outlined above. But for the field covered in this book, there are particular areas in which major steps have been taken. The increasing information on elpistostegalian fish, like the discovery of *Tiktaalik* and micro-CT scanning of parts of *Panderichthys* and *Ichthyostega*, has added excitement, complexity, and some frustration to the field. The recent announcement of apparently tetrapod-like trackways in deposits 18 million years before tetrapod-like animals were supposed to exist is another surprise whose implications need to be assessed.

Two other fossil tetrapod groups have been the subjects of revived interest, generating new finds and new analyses. One of these is the temnospondyls, and in particular the group called dissorophoids. For some members of this group, we now have significant and useable growth series, and for others, we simply have far more relevant taxa. The lepospondyls are another group on which attention has been focused, from both morphological and phylogenetic points of view. This is one reason why readers will find much expanded sections on both of these groups and why the review of their relationships is much more complex and perhaps more confusing than it was. It reflects the efforts of key researchers in these various fields, which has been quite intense and difficult to summarize.

As I was writing the first edition, very little indeed was known about the environmental conditions in which early tetrapods lived. A review of the first edition commented on the lack of information about the faunas with which early tetrapods were associated. The reason for that was simple. Little comparative information was available at that time. Since then, several meetings and much exchange of information on the topic have allowed meaningful comparative faunal studies to be carried out for the first time. We are now a little closer to understanding the circumstances in which the fish–tetrapod transition took place. I have expanded these sections of the text accordingly. That said, our information is still limited to a few sites that are reasonably informative.

In short, early tetrapod paleontology continues to be a field of great excitement and possibilities. Some of the predictions of the first edition have been proved incorrect, some show early signs of success, and some have come about.



# Acknowledgments

This work essentially represents a summary of my research career in early tetrapod paleontology. Throughout this period, I have worked with, been guided and helped by, learned from, and been supported morally and financially by a large number of people and institutions whom it is now my opportunity to thank.

I begin with my late father, Ernest Agnew, who unfortunately did not live to see my election as a Fellow of the Royal Society. He and my husband, Mr. Rob Clack, have both been instrumental in encouraging me on this road, and have helped reduce the rather long odds against my arriving where I am. My mother, Alice, died in 1983, and so was not able to see what she also helped me achieve. It is also a delight to acknowledge the encouragement and understanding of my late mother-in-law, Mrs. Molly Clarke.

I belong to the Panchen school of early tetrapod paleontology, and thanks must go largely to Dr. Alec Panchen for having taken me on as a mature research student after several years working in a provincial museum. My boss at that time, Mrs. Anna Meredith, deserves my eternal thanks for having encouraged me to take the plunge and return to academia, as well as providing the opportunity that led to that outcome. I returned to museums after my postgraduate years, although not in the way I expected. When appointed to a post in the University Museum of Zoology, Cambridge (UMZC), in 1981, in a sense I returned to my ancestral home, since Alec was a student of Rex Parrington, whose work in early tetrapod paleontology is the foundation of the collections and research effort of the UMZC.

During my subsequent career, several colleagues have been key sources of advice, discussion, intellectual challenge, and stimulation, as well as sources of specimens and general paleontological and social fun: Drs. Mike Coates, Andrew Milner, Angela Milner, and Tim Smithson, all Panchen school graduates; my own research students, but particularly Prof. Per Ahlberg, whose research overlaps in a most satisfactory and fruitful way. In the UMZC, I am indebted to Dr. Ken Joysey, a former director, for crucial help in mounting the first Greenland expedition, and to Prof. Michael Akam, the previous director and now head of the Zoology Department; and to the former Curator of Vertebrates, Dr Adrian Friday, and the former head of the Department of Zoology, Prof. Malcolm Burrows, for continuing support both for my research and my personal progress. Mr. Ray Symonds, the former collections manager of UMZC, has been a source of practical support; he remained good-humored in even the most

trying of circumstances. Several people have assisted practically with the project over the years, including Ms. Rosie Rush, Dr. Nick Fraser, and Dr. Henning Blom, as a postdoctoral associate. Most recently, my collaborators on an early tetrapod locomotion project have been Dr. John Hutchinson (Royal Veterinary College, London) and Dr. Stephanie Pierce. Ms. Julia Molnar is our scientific illustrator, and she has helped me enormously with the figures for this book, especially the front cover.

My expeditions to Greenland could not have even begun had not Rob "mithered" me until I gave in, and nothing would have progressed without the help of Dr. Peter Friend of Cambridge's Department of Earth Sciences, and the unwitting help of his former student Dr. John Nicholson. The expeditions were supported logistically by the GGU/GEUS (Greenland Geological Survey of Denmark) led by Dr. Neils Henricksen (Oscar) and facilitated by the late Dr. Svend Erick Bendix Almgreen of the Geological Museum Copenhagen (MGUH). I thank both of these for the part they played in our expeditions' successes. Ms. Sally Neininger (now Dr. Thomas) and Dr. Becky Hitchin were two of my gallant field assistants in 1998. More recent collaboration with MGUH through the good offices of Dr. Minik Rosing, its former director, Dave Harper, Professor of Paleontology, and Dr. Gilles Cuny, Curator of Vertebrate Paleontology, have allowed my team to continue working on the Devonian tetrapods we find so rewarding and fascinating.

In the UK, much of my material has been provided by the collector Mr. Stan Wood, and I record here the debt British vertebrate paleontology owes to him.

Further abroad, many colleagues have helped me by generously discussing their own research and allowing access to collections, and providing support in more subtle ways. I particularly wish to thank Prof. Eric Lombard and Dr. John Bolt from Chicago, for ongoing collaboration and lots of gin and tonics, Profs. Bob Carroll and Robert Reisz in Canada, and Drs. Anne Warren and Susan Turner in Australia. Other museums and their staff have given me generous access to their collections and specimens: in the UK, Drs. Mike Taylor and Bobby Paton formerly of the National Museums of Scotland, Dr. Neil Clarke of the Hunterian Museum Glasgow, Dr. Steve McClean and Mrs. Sylvia Humphrey of the Hancock Museum, Tyne and Wear, Ms. Sandra Chapman of the Natural History Museum, London; in the United States, Dr. Dave Berman of the Carnegie Museum Pittsburgh, Dr. Ted Daeschler of the National Academy of Sciences in Philadelphia, Dr. Gene Gaffney of the American Museum of Natural History in New York, Dr. Farish Jenkins of the Museum of Comparative Zoology, Harvard; in Eastern Europe, Dr. Erwins Luksevics in the Natural History Museum in Riga and Dr. Oleg Lebedev of the Paleontological Institute in Moscow. Many other colleagues and friends helped directly or indirectly in my work on early tetrapods, and I thank them all.

The other side of my research interest, the evolution of hearing, was greatly influenced by two people, Dr. Arthur N. Popper, who encouraged

me into the world of auditory neurophysiology, and Dr. Christopher Platt, my close friend and colleague. I thank them both for welcoming a paleontologist into their world.

My research has benefitted from funding from the following bodies, which I gratefully acknowledge: Natural Environment Research Council, UK; National Geographic Society; Newnham College; and the Department of Zoology, University of Cambridge; UMZC, Isaac Newton Trust Fund, Cambridge; Copenhagen Biosystematics Centre.

Specific thanks in the production of this book go to Dr. Chris Berry for help with Devonian plants, Prof. Mike Coates for help with *Hox* genes, Drs. Andrew Milner and Jason Anderson for helpful comments on Chapter 9, and my editors, Dr. Jim Farlow and Bob Sloan.

Finally, I would like to draw particular attention to the part played by my former preparator for more than a decade, Mrs. Sarah Finney, without whose patient, exquisite, and delicate work on the fossil material this work could hardly have happened. She also produced many of the photographs that enhance this book. Early tetrapod paleontology owes her a great debt of gratitude.



# Abbreviations

# A

| | |
|---|---|
| **add foss** | adductor fossa |
| **ang** | angular |
| **ant pal fossa** | anterior palatal fossa |
| **ant tect** | anterior tectal |
| **artic** | articular |
| **bas art** | basal articulation |
| **bocc** | basioccipital |
| **bpt proc** | basipterygoid process |
| **branch ser** | branchial series |
| **bsphen** | basisphenoid |
| **ceratoh** | ceratohyal |
| **cleith** | cleithrum |
| **coron** | coronoid |
| **dent** | dentary |
| **dpcr** | deltopectoral crest |
| **ectepic** | ectepicondyle |
| **ectopt** | ectopterygoid |
| **entepic** | entepicondyle |
| **ethmosphen** | ethmosphenoid |
| **exocc** | exoccipital |
| **extra-scap ser** | extrascapular series |
| **fac** | facet |
| **fen vest** | fenestra vestibuli |
| **fiss** | fissure |
| **fro** | frontal |
| **hyom** | hyomandibula/r |
| **infradent ser** | infradentary series |
| **intemp** | intertemporal |
| **internas font** | internasal fontanelle |
| **jug** | jugal |
| **jug for** | jugular foramen |
| **lacr** | lacrimal |
| **lat comm** | lateral commissure |
| **lat ot fiss** | lateral otic fissure |
| **ldpr** | latissimus dorsi process |
| **llc** | lateral line canal |
| **max** | maxilla |
| **med ros** | median rostral |
| **nas** | nasal |
| **nas cap** | nasal capsule |
| **nas mos** | nasal mosaic |
| **oper ser** | opercular series |
| **operc** | opercular |
| **opisth** | opisthotic |
| **otocc** | otoccipital |
| **pal** | palatine |
| **par** | parietal |
| **par for** | parietal foramen |
| **pofro** | postfrontal |
| **popar** | postparietal |
| **porb** | postorbital |
| **pospl** | postsplenial |
| **posttemp foss** | posttemporal fossa |
| **preartic** | prearticular |
| **prefr** | prefrontal |
| **premax** | premaxilla |
| **preoperc** | preopercular |
| **psphen** | parasphenoid |
| **pteryg** | pterygoid |
| **quad** | quadrate |
| **quadjug** | quadratojugal |
| **rad** | radius/radial |
| **scapcor** | scapulocoracoid |
| **spir** | spiracle/spiracular |
| **splen** | splenial |
| **squam** | squamosal |
| **SSproc** | Säve-Söderbergh's process |
| **stap footplate** | stapedial footplate |
| **subtemp foss** | subtemporal fossa |
| **supclei ser** | supracleithral series |
| **supocc** | supraoccipital |
| **surang** | surangular |

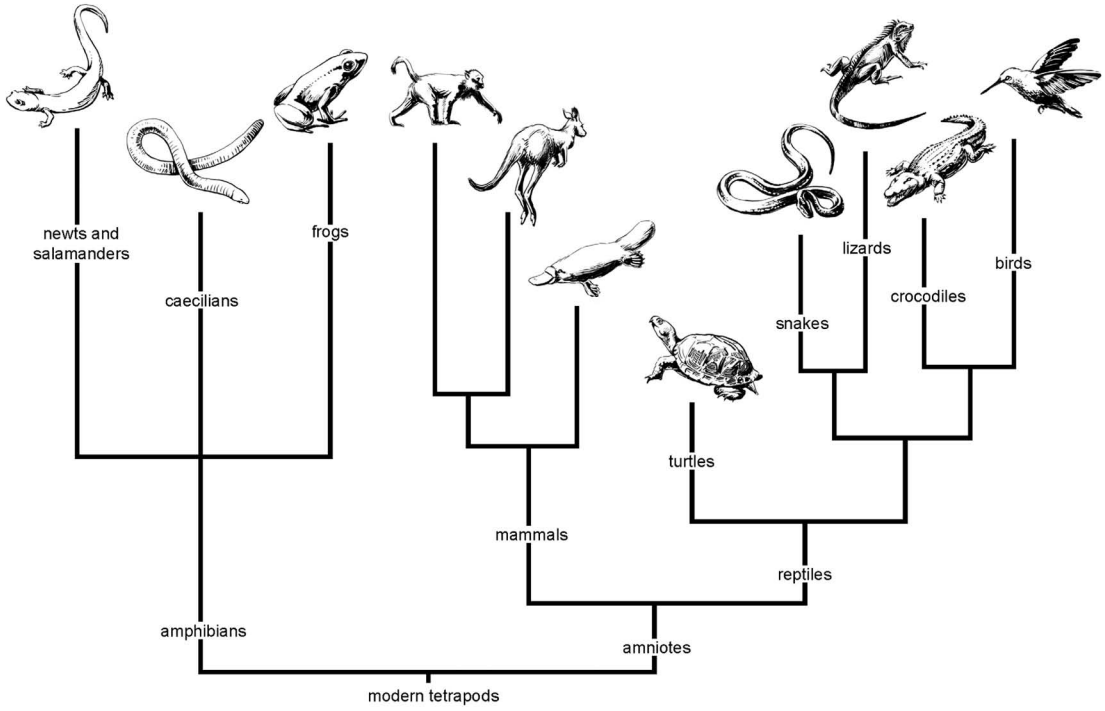
| | |
|---|---|
| **sutemp** | supratemporal |
| **tab** | tabular |
| **v cran fiss** | ventral cranial fissure |
| **vest font** | vestibular fontanelle |
| **vom** | vomer |
| **X** | tenth cranial nerve (vagus) |

## Abbreviations of People and Institutions

| | |
|---|---|
| **AMNH** | American Museum of Natural history, USA |
| **A.R.M.** | Andrew Milner |
| **CM** | Carnegie Museum, USA |
| **GLAHM** | hunterian Museum, Glasgow, Uk |
| **J.M.** | Julia Molnar |
| **MCZ** | Museum of Comparative Zoology, harvard, USA |
| **MGUH** | Museum Geologicum Universitatis hafniensis (= Geological Museum, University of Copenhagen): f.n.—field number; vP vertebrate Palaeontology collections |
| **NEWHM** | hancock Museum (now the Great North Museum), Tyne and wear, Uk |
| **NMS** | National Museums of Scotland, Edinburgh, Uk |
| **R.N.G.C** | Robert Clack |
| **S.L.N.** | Sally Neininger |
| **S.M.F.** | Sarah Finney |
| **UCLA** | University College of Los Angeles, USA |
| **UMZC** | University Museum of Zoology, Cambridge, Uk (GN—gnathostome; T—tetrapod) |
| **W.D.I.R.** | Ian Rolfe |
| **YPM** | Yale Peabody Museum, USA |

# GAINING GROUND






**1.1.** Family tree of the living tetrapod groups.

# Introduction

# 1

## The Origin and Evolution of Tetrapods

Approximately 380 million years ago, something strange and significant happened on Earth. That time is part of an interval of Earth's history called the Devonian period by scientists such as geologists and paleontologists, but in more popular imagination, it is known as the Age of Fishes. The reason for this is that after about 200 million years of earlier evolution, the vertebrates—animals with backbones—had produced an explosion of fishlike animals that lived in the nearshore lagoons, river estuaries, and lakes of the time. The strange thing that happened from the middle to the later parts of the Devonian period is that some of these fishlike animals evolved limbs with digits—fingers and toes. Over the ensuing 350 million years, these tetrapods gradually evolved from their aquatic ancestry into walking terrestrial vertebrates. These have dominated the land ever since this initial explosive radiation allowed them to colonize and exploit the land and its opportunities. The tetrapods, with their limbs and fingers and toes, include ourselves as humans, so that this distant Devonian event is profoundly significant for humans as well as for the planet.

Today, the modern descendants of these early pioneers are divided into two major groups (Fig. 1.1). The modern amphibians include frogs (anurans—jumping, tailless amphibians), salamanders (urodeles—tailed amphibians), and caecilians (apodans—elongate, limbless amphibians). The modern amniotes include mammals (usually animals with fur and that produce milk, humans among them), turtles, crocodiles and their relatives the birds, and lizards and their relatives the snakes. (Note that the term "reptile" can be used to include all amniotes except mammals, provided birds are included in this group.) In practice, tetrapods include any animal with four legs or whose ancestor had four legs. (The situation is a bit more difficult with fossils, as will be shown.) These two major radiations of vertebrates also had many relatives that are now extinct, notably the dinosaurs, whose closest living relatives are the birds.

Because becoming terrestrial was apparently a slow process, I have called this book *Gaining Ground*, to suggest that it was achieved with some difficulty. At the same time, this evolutionary development has led to enormous innovations in evolutionary terms, and I hope to suggest not only something of the breadth of possibilities that it opened up, but also the contingent nature of the transition. In other words, much of this change occurred because of happenstance—being at the right place at the right time. It was not a directed process.

The origin, early evolution, and relationships of tetrapods form the focus for the interaction of several disciplines. Paleontology (the study of fossils) and the related studies of paleoecology, taphonomy (how the creatures died and became fossilized), and paleobiogeography (where the creatures lived and how they were distributed in time and space), as well as modern zoology, anatomy, physiology, and developmental and molecular genetics, all contribute various aspects to the understanding of past life. Most people are aware that at some stage creatures crawled out of the water and came onto land, and so can relate to the contents of this book. I hope this book will show how much more can be said than that—and how much more there is to know.

The study of the origin of tetrapods has gone through many phases in its history, but none has been more exciting than that of the present day. Over the last few years, more fossil material from this crucial period has been unearthed than at any time in the past (this is even more the case than when the first edition of this book was being prepared 10 years ago), and these discoveries have helped to reshape ideas about when, where, how, and even possibly why the transition occurred at all. In the not-too-distant past, there was almost no fossil material, and ideas were based largely on informed guesswork. Speculation was intense, and as is often the case, this speculation was in inverse proportion to the amount of data. To be truthful, there is still not a large amount of real data, so speculation is still active, and whatever is concluded today may be overturned by discovery of a new fossil tomorrow. In some ways, this is to be hoped for, because only in that way can guesses be falsified and tested as scientific hypotheses. Indeed, much of this has gone on since the first edition of this book, as subsequent chapters will testify.

This book tells the story of the evolution of tetrapods from their fish ancestry and puts the sequence of events into its ecological context. The story is founded on an understanding of the evolutionary relationships between tetrapods and their fishy relatives—their phylogeny—and traces the family tree of tetrapods from its roots to the point at which the major groups of modern tetrapods branch off from its original trunk. The tetrapod family tree is in fact more like a bush, with several main branches, some of which have died out during the course of evolution and some of which have become large and important from small beginnings.

This book looks at the changes that occurred in the transition from creatures with fins and scales to those with limbs and digits in an attempt to understand how and when the changes occurred, and to do this, it is necessary to understand something of the anatomy of the animals involved. Chapters 2 and 3 are devoted to these parts of the story. Chapters 4, 5, and 6 set out what is currently known of the earliest tetrapods and their lifestyles. By careful analysis of what is known of them from fossils, and by comparison with modern animals that live at the transition between water and land, it may be possible to understand a little of how the early tetrapods worked as animals. After the tetrapods had become established, they radiated into a range of forms requiring modifications to

the original tetrapod pattern. Chapters 7, 8, and 9 carry the story forward from the origin of tetrapods to their ultimate conquest of terrestrial living. The final chapter draws together some of the threads that have been taken up in the preceding chapters and shows how they impact the study and understanding of tetrapods today.

A cautionary note should be added here. Many of the skull reconstructions, derived from the literature, have freely duplicated left or right sides to present a complete, but artificially symmetrical, picture. These reconstructions are therefore not suitable for use in morphometric studies. Also, in many cases, the dermal ornament on the skull roofs has been omitted.

I hope that this book brings the excitement of this field of study to a wider public, shows something of how paleontology progresses and what it can and cannot do, and, of course, most importantly, shows people a little more of how they fit into the broader picture of evolution.

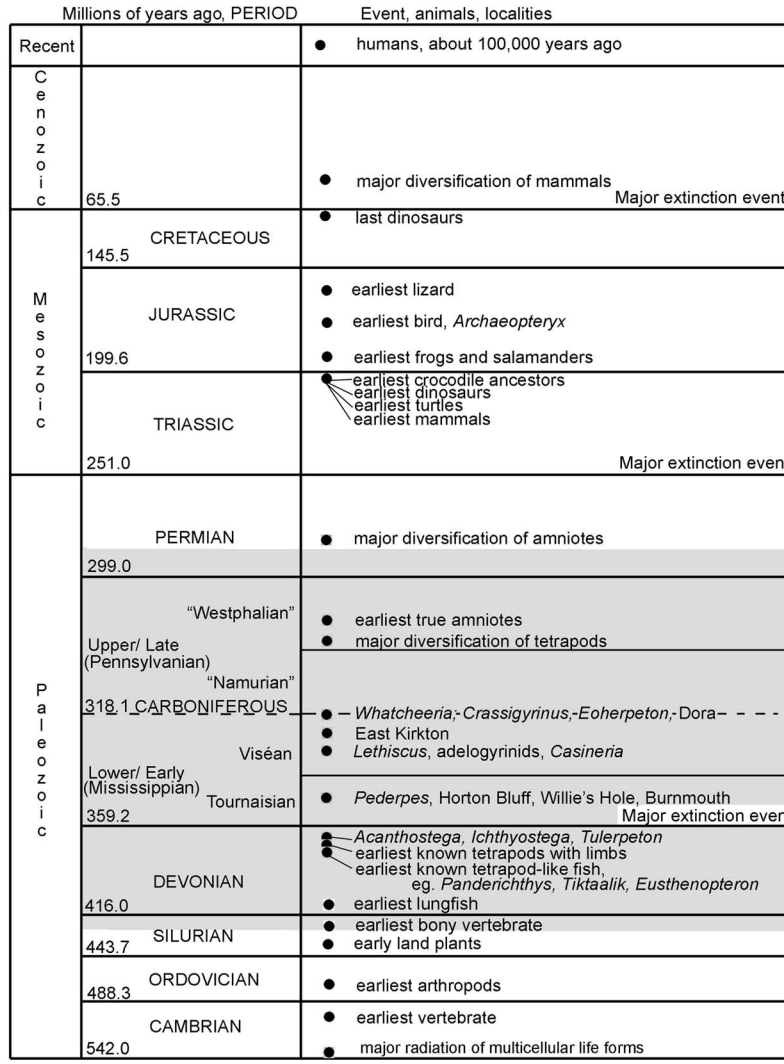
## Tools of the Trade: The Geological Framework, Fossilization, and Family Trees

### The Geological Framework

To put the evolution of terrestrial tetrapods in its context, it is necessary to have an understanding of Earth's history in general outline. This is not the place to discuss dating methods or techniques of stratigraphic correlation. These can be found in readily available geological textbooks such as that by Briggs and Crowther (2001) or Raup and Stanley (1979). However, it is necessary to explain the approximate dates and approximate lengths of time over which the story takes place, so that it can be put in the context of other major events in the story of evolution.

The geological column is the name that scientists give to the succession of times, dates, and names into which Earth's history is divided. There are several ways of expressing this. It can be expressed in a way that accords each time interval a space proportional to its length, usually as a vertical column, always with the oldest at the bottom. Or it might be depicted as a sort of clock face. The problem with this method is that only a small proportion of Earth's known history is represented by an abundant fossil record. The planet is estimated to be about 4,500 million years old, and the first signs of life (fossil bacteria) are dated at about 3,500 million years. Complex multicellular animals first appear commonly in the fossil record only about 550 million years ago, so that to use the clock face method has practical problems, in that most of it would effectively be empty. Another way is simply to set out the list of dates and names in their relative order, again with the oldest at the bottom, as shown in Figure 1.2. The numbers show the dates of the boundaries between the divisions and the lengths of time they have lasted.

The idea that the Earth is as old as this is a relatively recent one, dating back only to the early 19th century, and its appreciation has changed the perspective from which we view our place in its history. The concept has been called "deep time." As an example, one of the important factors that study of deep time reveals is the complexity of climate change




**1.2.** Timescale showing the time of origin of major groups, and other events in Earth's history. The shaded area indicates the period covered in this book. Dates from Gradstein et al. (2004).

through Earth's history, culminating in the appreciation of the possibility of human-induced global warming. This would not be possible without study of the Earth's climate over the past few million years. Talking of perspectives, when considering the period in Earth's history covered by this book, climate changes far more radical than recent ones are obvious. If global warming continues as predicted, eventually the climate may become something like it was about 15 million years ago in the Miocene period, but it will still be a long way from that which current study suggests prevailed when early tetrapods were alive.

The interval for which there are abundant fossils in the rocks is called the Phanerozoic, meaning "visible life," and it represents a time of about 600 million years. The Phanerozoic is divided into three eras, originally named according to what proportion of its biota resembled that of the modern world. These divisions are named the Paleozoic ("ancient life"), Mesozoic ("middle life"), and Cenozoic ("recent life"). The ages are

divided into periods, and the periods into stages. To a large extent the boundaries of the divisions are based on the fossils of animals and plants that lived at that time, although the names they receive do not necessarily reflect this. Names of the stages, for example, are often based on places where the representative strata were first found or where they are most clearly seen. These large time periods, rock sequences and their names, and the basic faunal complement of each were worked out during the 19th century, and they have not changed very much since then. The subsequent decades have seen a process of refinement, increasing resolution of time intervals, and precision of dating and correlation between sequences in different parts of the world.

Geologists and paleontologists usually date their finds by reference to an independently produced and well-established timescale. One of the most recent in use at the present time is that by Gradstein et al., published in 2004, and has used many different and complementary techniques in its construction. It is enormously detailed for the whole Phanerozoic.

The story of the origin and early evolution of tetrapods and the time frame of this book takes place almost entirely within the later part of the Paleozoic, during the Devonian, Carboniferous, and Permian periods (Fig. 1.2). More details of the stages into which these periods are divided are given in the relevant chapters. The story as we have come to understand it really begins about 380 million years ago, although some recent work suggests that an earlier date is likely. Some chapters set the scene by describing the history of plants and animals that were already present as the tetrapods started their evolutionary journey. It takes the story through about 132 million years to a time about 248 million years ago as the Permian period comes to a close. For comparison, the first dinosaur is dated at around 225 million years, while the last died out 65 million years ago, a comparable period of time. The earliest tetrapods that feature in this story are nearly twice as old as the oldest dinosaur. Humans can trace their lineage back to a split from the common ancestor of apes and humans about 5 million years ago, while *Homo sapiens* as a species is currently reckoned to be about 100,000 years old.

## Fossils, Fossilization, and Techniques of Study

The only means of finding out about animals and plants that lived so long ago is from fossils. These are the preserved remains or traces of these ancient organisms, and to understand the story more fully, it is necessary to look at how and under what circumstances these remains are preserved and discovered.

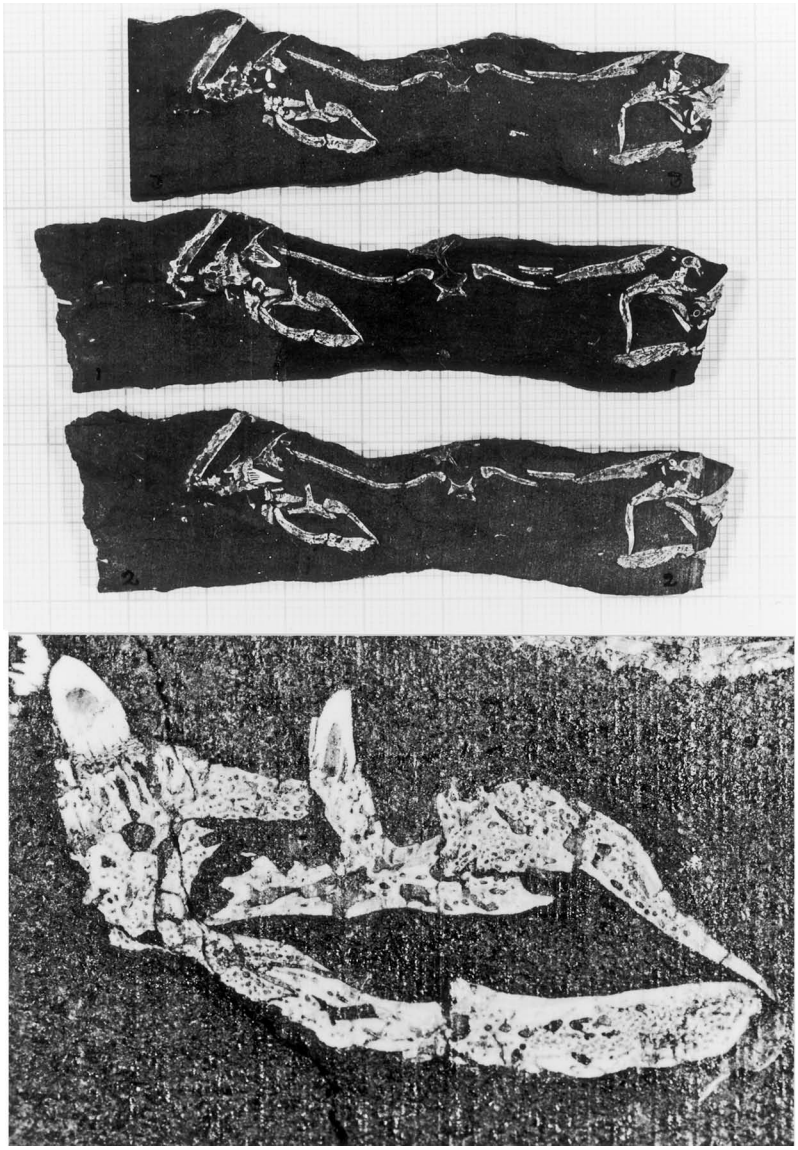
Types of fossils can be categorized in a variety of ways according to what is preserved, or how it is preserved. What is preserved is usually the harder parts of an animal or plant, so for example bones and shells make good fossils. This type of fossil is often called a body fossil, to distinguish it from another category, that of trace fossil. Trace fossils are preserved impressions of features that an animal (usually an animal,

although occasionally plants leave trace fossils too) has made—for example, footprints or burrows. Body fossils show the anatomy of the plant or animal it preserves, and from this it is possible to work out something of its evolutionary relationships and functional morphology. Trace fossils can sometimes be even more telling in that they can provide information about the behavior of the animal and clues to its lifestyle that body fossils cannot give. Both kinds of fossil are known in the story of the origin of tetrapods.

Body fossils are preserved in many different ways. Usually the process involves water to a large extent, and fossils of aquatic animals are much more common than those of terrestrial animals. Fossils of terrestrial animals are usually found only when the creatures' bodies have been accidentally washed into bodies of water. Generally, the animal sinks to the bottom of the lake or sea and the soft, fleshy parts usually decay quite rapidly. The remains may be scavenged by other animals and disintegrate so that bones become isolated, but gradually they are covered with sediment that over the millennia hardens to preserve the bones. Most favorable to preservation are deep, still waters where the sediment particle size is small. Sediments can then take up small details of the bones or shells by filling in even the smallest crevices, and then not being disturbed again. If decay happens more slowly—for example in water low in oxygen, where predators are few and bacterial action slow—the carcasses may be preserved in a more complete form.

The remains may be subsequently preserved in a variety of ways. They may be more or less unaltered. Shells made of calcium carbonate, for example, may retain the same chemical structure they had in life if they are preserved in limestone. Bones, which are the main concern here, are formed of calcium phosphate, which may also be unchanged chemically in many instances. However, bones are not solid but have pores or spaces in them, for blood vessels, nerves and fluid or even air, to allow them to grow and to make them lighter and stronger than solid bone would be. During fossilization, these spaces are often suffused with solutions of chemicals that later precipitate out and harden, so that the fine internal structure of the bone is preserved. This is why fossil bone is often much heavier than recently dead bone. Figure 1.3 shows sections through part of the skull of *Acanthostega*, a Devonian tetrapod, to show how well the internal structure of the bone can sometimes be preserved. This sort of detail can be used to explore aspects such as cell size, growth rates, annual or seasonal cycles, and microarchitecture.

Sometimes even the hard parts of the bone are dissolved away, leaving a natural mold of the original. This may be preserved as a space in the rock, or it may be replaced by another mineral to form a natural cast. Other hard parts of organisms that can be preserved are the teeth of vertebrates, whose enamel layer is often completely unaltered chemically even in ancient specimens, the chitin of arthropods, the silica spicules of sponges, or the woody (cellulose) parts of plants.



**1.3.** Photograph of sections through a skull of *Acanthostega* (MGUH f.n. 1604), shown on centimeter graph paper for scale. The palate and both lower jaws can be seen in the sections, but the skull roof is missing. The enlargement below shows dentary and coronoid with their teeth and the denticles on the prearticular. *Photograph from UMZC archives.*

Occasionally the remains have been buried and preserved so rapidly or in such unusual circumstances that decay has not had time to occur fully. Such occasions may result from a flash flood, inundating a river basin, or by an underwater avalanche in which soft sediment pours rapidly down an incline onto the organisms below. In some exceptional cases, even the softer parts of the organism may be fossilized. Some fish fossils, for example, retain details of the gill structure, and in such cases, muscle tissue shows such fine detail that individual cells can be identified. More commonly, soft tissue may be colonized by bacteria in the decay process (e.g., Fig. 9.15), and they may take up the shape of body outlines, fur or feathers, or gut contents. In recent years some spectacular examples of

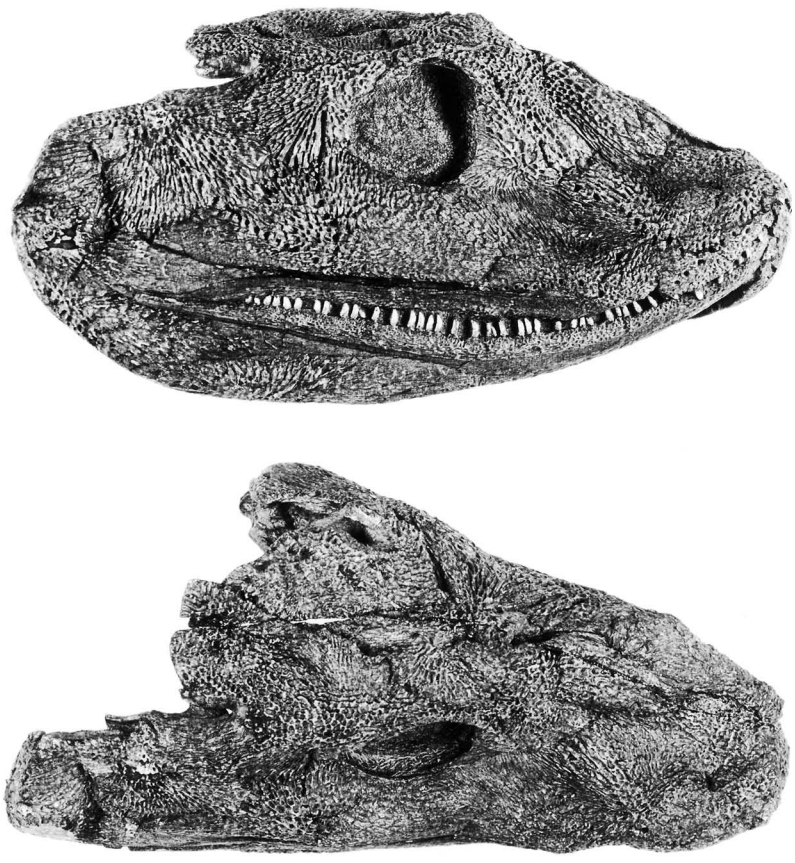
soft tissue preservation have come from China. Late Jurassic and Early Cretaceous dinosaurs with feather impressions have been found in large numbers, alongside many species of true bird, documenting the relationships between these groups of animals (Xu et al. 2003; Hou et al. 1996). From the same geological formations, early mammals with fur (Luo et al. 2007), salamanders, fish, and insects showing remains of color patterns have also been found (Chang et al. 2003). Even Early Cambrian and Precambrian fossils, also from China and preserved in exceptional circumstances, have provided new evidence not only of some of the earliest vertebrates (Shu et al. 1999, 2003), but also of embryonic animals consisting only of minute balls of cells (Donoghue et al. 2006).

For very ancient fossils such as those from the Paleozoic, the risk is high that during the period from their preservation to their discovery the fossils will have been altered in many different ways: by dissolution by acids that remove calcium and allow bones to bend into unnatural shapes without breaking; or by rock movements, faulting, or heat from igneous activity, which can distort and fracture them; or by exposure of the sediments to erosion in the air, which may remove or degrade them. Figure 1.4 shows a skull of *Acanthostega* distorted by crushing and twisting (compare this with the reconstruction based on examination of several specimens shown in Chapter 5, especially Fig. 5.21). Fossils may have disappeared when their sediments were subducted under other continental plates by tectonic movements. In short, fossils from earlier periods in Earth's history are usually rarer and less well preserved than those of more recent periods.

Sometimes fossils can be preserved without the aid of waterborne chemicals or sediments. Amber is a resin produced by certain trees that occasionally traps insects or even small vertebrates such as frogs or lizards. When the amber is eventually hardened and preserved (again, usually in a water-laid sediment), access is even sometimes possible not only to the molecular structure of the animals, but also the chemical composition of the atmosphere in which they lived. Unfortunately for the story of early tetrapods, amber-producing trees had not evolved in the Paleozoic.

Sometimes animals die in very arid conditions, such as deserts, and their bodies become mummified (completely air-dried) before being buried in sand. When the sand hardens to sandstone, the soft tissue is sometimes preserved as well as the bones. Several kinds of dinosaur skin are known from this type of preservation, but so far, no early tetrapods have been found with soft tissue preserved in this way. Further details of how animal remains can be fossilized can be found in general textbooks.

When a fossil is found, it often remains in its surrounding rock, called matrix, and this has to be removed before study of the animal can begin. This special skill, called preparation, requires dedication and patience because it may take many years to complete a large or difficult specimen. Preparation may be done by mechanical means, such as a fine needle used under a binocular microscope, or by chemical means, such as dissolving away matrix by use of dilute acid. Sarah Finney (Fig. 1.5) used



**1.4.** Two photographs of Grace (MGUH f.n. 1300, *Acanthostega*). Anterior is to the right. Top, right lateral view; bottom, dorsal view. Scale bar = 10 millimeters. *Photographs by S.M.F.*

mechanical tools to remove the matrix from the fossils from Greenland. In this case, a dental mallet was used to chip tiny particles of rock off the fossil. The handpiece converts the drill action of this dentist's apparatus into a reciprocating one, and both the "throw" and rate of the action can be adjusted. Some matrix that adheres strongly to the fossil may require finer work with a handheld mounted needle (or pin vice), as she is holding in the photograph, to remove the last particles grain by grain. For large tracts of bulk matrix, a pneumatic pen, like a tiny road drill, is the tool of choice. A skull of *Acanthostega* was bisected by the diamond wire saw to allow preparation of the internal surface, exposing the palate and internal surface of the lower jaw (Fig 1.6). The wire in this case had a diameter of only 0.3 mm, so very little of the original specimen was lost in the process.

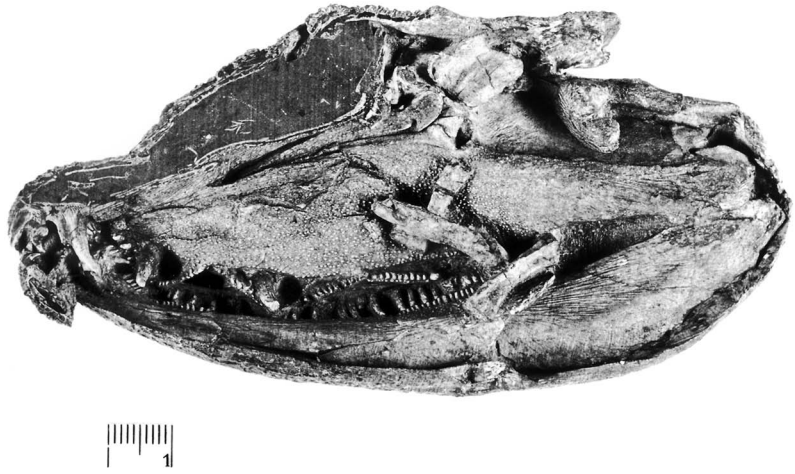
In the case of natural molds, specimens may be prepared by using a form of silicone or latex rubber to make casts from the original. Sometimes bone is badly preserved, in which case it is occasionally more useful to dissolve away the bone artificially and use a rubber peel from the



**1.5.** Sarah Finney, the preparator who has done most of the work on the Devonian tetrapod *Acanthostega* and many of the early Carboniferous forms described in this book. The photograph is taken in the Paleontological Laboratory in the Department of Zoology, University of Cambridge, UK. Sarah is holding a skull specimen of *Ichthyostega,* and in the background is a life reconstruction of *Acanthostega* by Mike Coates. *Photograph from UMZC archives.*

resulting mold to perform the study. Some of the Carboniferous fossils described in Chapter 9, such as those from Linton, Ohio, are treated in this way. The surface detail obtained by this method is sometimes so fine that images produced by a scanning electron microscope can give valuable information.

Good, articulated (i.e., those still joined together) fossil skeletons of Devonian and Carboniferous tetrapods, some of which are described in this book, are rare. Only a handful of animals are represented by more or less complete skeletons; the rest are represented by individual bones such as lower jaws, partial skull roofs, or limb fragments. Usually the matrix in which they are preserved is hard, and the specimens have taken

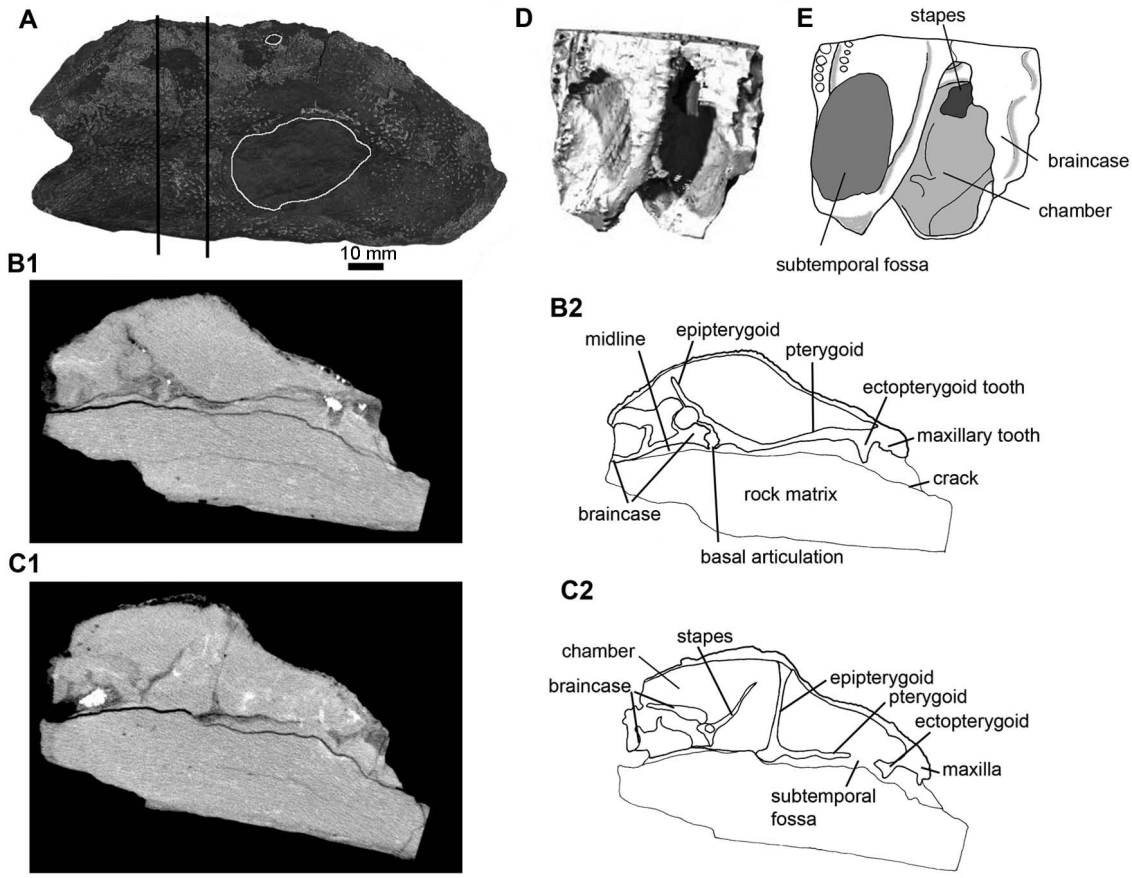


**1.6.** Photograph of Grace (MGUH f.n. 1300, *Acanthostega*, same specimen as in 1.4) showing the palatal surface prepared. Note the details of the teeth on the palate and the gill bars. Anterior is to the left. Scale bar = 10 millimeters. *Photograph by S.M.F.*

many hours of effort to extract. Occasionally, this general rule is broken: some early tetrapod fossils from the Baltic states are preserved in sandy material so soft that it can be washed off. The bones from these localities are three-dimensional and pale in color, so that they look almost like modern bone. The downside of this is that because the consolidation of the matrix is so poor, so is the consolidation of the fossil, and this creates a problem of conservation. It is difficult to extract them for the reverse reasons, in that they frequently fall apart without great care and use of consolidating plastics.

A newly developed technique, increasingly used since the late 1990s, is that of computer-assisted tomography, or micro-CT, in which a specimen is scanned in three dimensions by X-ray or other ionizing radiations. This technique, originally developed for medical purposes, has been refined for use in materials science and other physical studies, such that fine details of rock structure can be detected. The medically applied machines cannot usually use radiation of high enough energy to penetrate rock, although they have been used with great success in some cases, especially where the rocks and the enclosed bones are of contrasting densities. The rock-penetrating machines can now in many cases even cope with material containing iron compounds. Nonetheless, the material of *Ichthyostega* (Fig. 1.7), as illustrated in Chapters 5 and 6, was described as "a challenge" by the expert team at the University of Texas CT scanning unit. CT scanning can also be used for obtaining extremely fine detail from tiny specimens, allowing views of the internal structures of otherwise inaccessible parts, even distinguishing different cells and tissues at a histological scale.

An advance in the field of tomography has been the development of very fine-scale scanning with a synchrotron. Millimeter-scale portions can be scanned at quite large resolution, although one problem in dealing with larger specimens is that it is sometimes difficult to know where exactly the scan has been taken. The synchrotron can "see" almost to the cellular level, so that it is possible to build three-dimensional pictures of




**1.7.** Micro-CT scans of *Ichthyostega*. (A) Specimen of right half of a skull that has been scanned; lines show location of sections in (B) and (C). (B1) and (B2), respectively, photograph and interpretive drawing of more anterior section. (C1) and (C2), respectively, photograph and interpretive drawing of more posterior section. (D) Three-dimensional model of rear part of skull. (E) Interpretive drawing of model. Scale bar is for (A) only.

the internal microarchitectural structures of bone. In this way, successive growth surfaces have been revealed in bones showing changes to their shape and construction. Even the directions and areas of muscle fiber attachments can be made out, allowing muscle volume and direction of operation to be inferred. Larger specimens can also be scanned, although at lower resolutions, giving somewhat less detail. In some cases, however, depending on the characteristics of the matrix, better detail can be obtained using the synchrotron than with a more conventional CT machine.

The advantages of CT scanning techniques are that they do not require full mechanical preparation of the specimens or they can act as a guide to how to prepare such material. The disadvantages of the technique are that first, it is still relatively expensive, and second, further expense is sometimes required to obtain the sophisticated software necessary to reconstruct the CT images into three-dimensional models, and to pay for the time of the researchers who are able to perform this process. It takes a lot of skill and knowledge to translate what may be a poorly resolved image into a credible model. Even with these new techniques, a level of interpretation is still involved in understanding the material.

Once a three-dimensional image has been obtained in this way, under certain conditions, it may be possible to investigate it more deeply. For

example, a 3-D micro-CT scan reconstruction of a skull can be subjected to virtual analysis by engineering programs that allow the researcher to assess the stress forces that the skull can withstand. Finite element analysis has been used in this way to investigate dinosaur skull mechanics, although as yet not much has been done on early tetrapods. That is in part because the material is not always very amenable to scanning, or that it is too crushed to make a good 3-D model from.

Such new techniques have allowed completely new questions to be framed and answered, taking the investigation of fossil material to a more fundamental level.

Once the fossil is obtained and has been prepared and analyzed as far as it can, the time has come to describe it. To pass on the discovery to other researchers, so that they can use the information, is one of the most important parts of the scientific process. With fossils, other workers must have access to an accurate description of the material because many fossils are unique and are located in museums in distant parts of the world. The description is usually presented in a professional journal, in which a good clear verbal description is given alongside illustrations of the actual specimens and interpretive drawings and diagrams that explain how the describer sees and understands them. Ideas about the significance of the material, how it fits in to current knowledge, and what new hypotheses it challenges or presents are an important part of the scientific communication that results from such work.

## Understanding Phylogeny

One of the first clues to the idea that life on Earth had evolved by a gradual process of change over time was the discovery that animals and plants could be placed in groups showing a hierarchical order. Small groups of forms showing detailed similarities could be placed with other small groups into larger ones showing more generalized similarities. The arrangement resembles a family tree, and it was this that first suggested the idea of descent with modification—that is, the realization that the similarities existing between more and more inclusive groups of animals result from ancestor–descendant relationships. Although the hierarchical classification of animals and plants had been recognized since the 18th century, and the idea that animals had changed throughout time had been suggested several times, what this meant remained mysterious and debatable until the mid-19th century. At that time, Darwin and Wallace finally realized that it could be explained by genealogical relationships, and they put forward compelling evidence for the idea. They also independently suggested a mechanism—known as natural selection—that could have brought about the changes. Everything that has been discovered since in modern genetics and developmental biology has only served to strengthen the evidence for this kind of relatedness among animals and plants. Many recent books discuss the patterns and processes involved in descent with modification, such as that by Jones

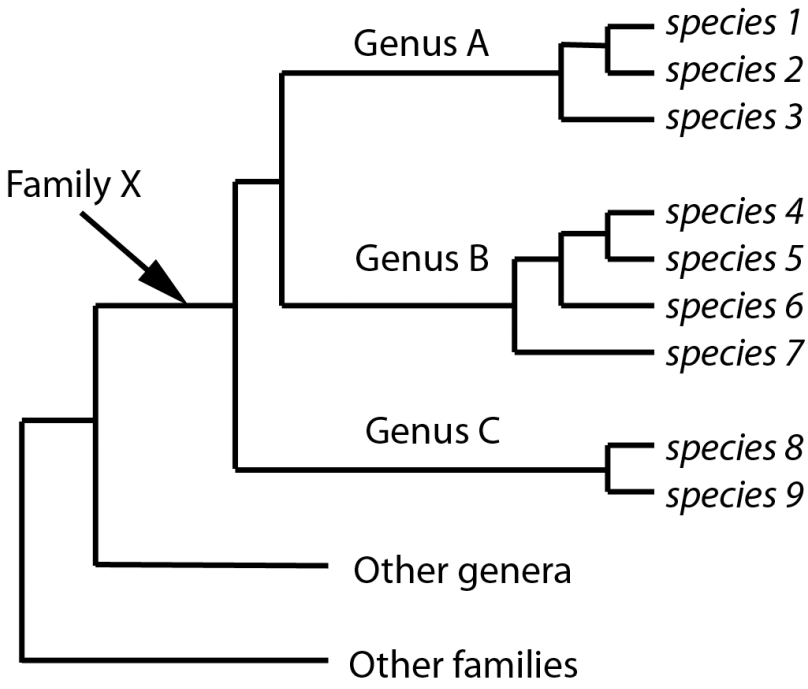
(1999). This book updates Darwin's original observations and expands the evidence he presented to include such topics as genetics, development, and plate tectonics. Others, perhaps more technical, are those by Barton et al. (2007), Futuyama (2005), and Ridley (2004).

The groups are given names to express these relationships. A species is the smallest group, usually meaning a group of organisms that can and do reproduce with one another. (This is not possible for extinct animals, of course, so paleontologists try to use other criteria. It is sometimes very difficult, especially if only fragments of an animal or plant are known.) Each species is given its own unique name. Species are grouped into genera (singular, genus) and share a generic name. Genera can be grouped into families, families into orders, and orders into classes (Fig. 1.8). In practice, in recent years, categories higher than genus are less used than formerly because they are in many ways incompatible with new methods of classification, such as cladistics.

An animal or plant species will have two names—a binomial. The first is the generic name and the second is the specific name. For example, one of the animals that features in this book is *Panderichthys rhombolepis*. *Panderichthys* is its generic name and *rhombolepis* is its specific name. Other species of the genus *Panderichthys* exist, such as *stolbovi* and *bystrowi*. Usually the first scientist to describe a new species will name it, unless it turns out to be a member of a genus that is already known, in which case the discoverer will only have to think up a new specific name. Each combination is unique to a species, and the name is designed to reflect something about the animal, such as who found it, where it came from, or some interesting feature of its anatomy. Scientists who name animals often have great fun doing so, although the international rules preclude facetious or vulgar names. Recently there have been suggestions to abandon this system because it was not designed to fit with recently developed methods of working out relationships between groups. However such suggestions are not universally accepted, and it remains to be seen whether they will stand the test of time and usefulness (e.g., Benton 2000; de Queiroz and Gauthier 1992; and other references listed in Chapter 3). Defining and naming higher categories is not always straightforward. Whether groups should be defined by reference simply to other taxa of apparently stable taxonomic relationships, by reference to living taxa, or by possession of certain suites of characters remains controversial. Examples of this are given in Chapter 3.

To understand the course of evolution, the evolutionary relationships between different groups must be worked out. Phylogeny is the name given to the evolutionary relationships and history of the animal in question, and the practice of working this out is called phylogenetics. The system of groupings in which an animal is placed is called its classification, and one of the main goals of evolutionary studies is to make classification reflect phylogeny.

Two major problems are encountered here. The first is that of discovering the best way of working out the phylogeny, and the second is that

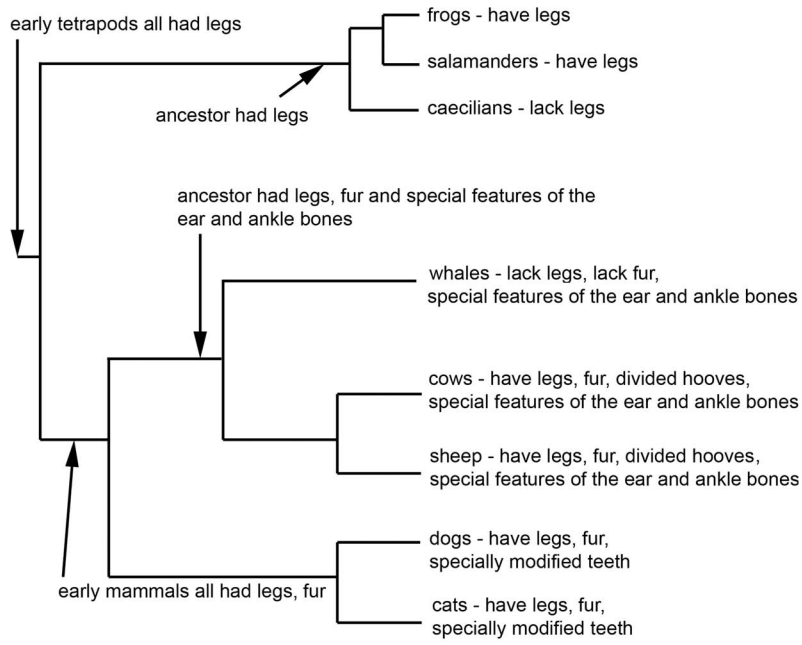



**1.8.** Chart showing Linnaen hierarchy of species grouped into genera, and genera into families.

the phylogeny that is finally decided to be the best by scientists is often at odds with the classification used in everyday language.

In recent times, one method for working out phylogeny that has become widely accepted is called cladistics. Named from the Greek word for "branch" (a clade), cladistics has some fairly strict rules about how to judge relationships between organisms, and it has its own language in which to express them. Often, commonly used words have a subtly different meaning in cladistics from those in everyday use, which may be confusing for the lay reader. One of the main rules is that only features (characters) that the groups (taxa) share uniquely (shared, derived characters) should be used to assess the relationship between them. This is in contrast to using characters that are more generally present in the larger grouping to which the organism might belong (shared primitive characters).

To give an example of this, in a classification of dogs and cats, possession of fur would not be a character used to unite them into a clade, because fur is found in many kinds of other animals. Fur is a character unique to a much larger group, the mammals. Dogs and cats instead share features of dentition only seen in members of the mammalian order Carnivora. Recently, it has emerged that whales show some specialized characters of the inner ear and anklebones that are otherwise found only in ungulates—cows, sheep, hippopotamuses, and their relatives. It is thought the most likely explanation is that they arose in a common ancestor of all these groups and have been inherited by all the descendants (Fig. 1.9). Another example might be to consider the three modern amphibian orders: frogs, salamanders, and caecilians. The fact that frogs




**1.9.** Chart showing use of derived characters in phylogeny: even though frogs and salamanders all have legs, it is not these characters that are used to unite them, but a suite of others such as specialized receptors in the inner ear and glands in the skin unique to all modern amphibians; although whales lack legs, they are more closely related to ungulates such as sheep and cows than to carnivores, as shown by shared characters of the ear that are only found in that clade.

and salamanders have legs, while caecilians do not, would not be used to suggest that frogs and salamanders were more closely related to each other than either one is to caecilians (Fig. 1.9). Legs are the common property of tetrapods (the main subject of this book) and have been lost by the ancestors of caecilians. (Indeed, some fossil caecilians are now known that have legs; Jenkins and Walsh 1993). Modern amphibians share a number of soft tissue characters, such as mucus glands in the skin, that are not found in other tetrapods.

Problems arise with this method for two reasons. One is the means by which primitive characters are distinguished from derived ones, and the other is how genuinely shared derived characters (homologies) are distinguished from similarities derived independently (analogies). An example of an analogous character might be the lack of limbs in snakes and caecilians. Such characters may show something about lifestyle, but nothing about relationships.

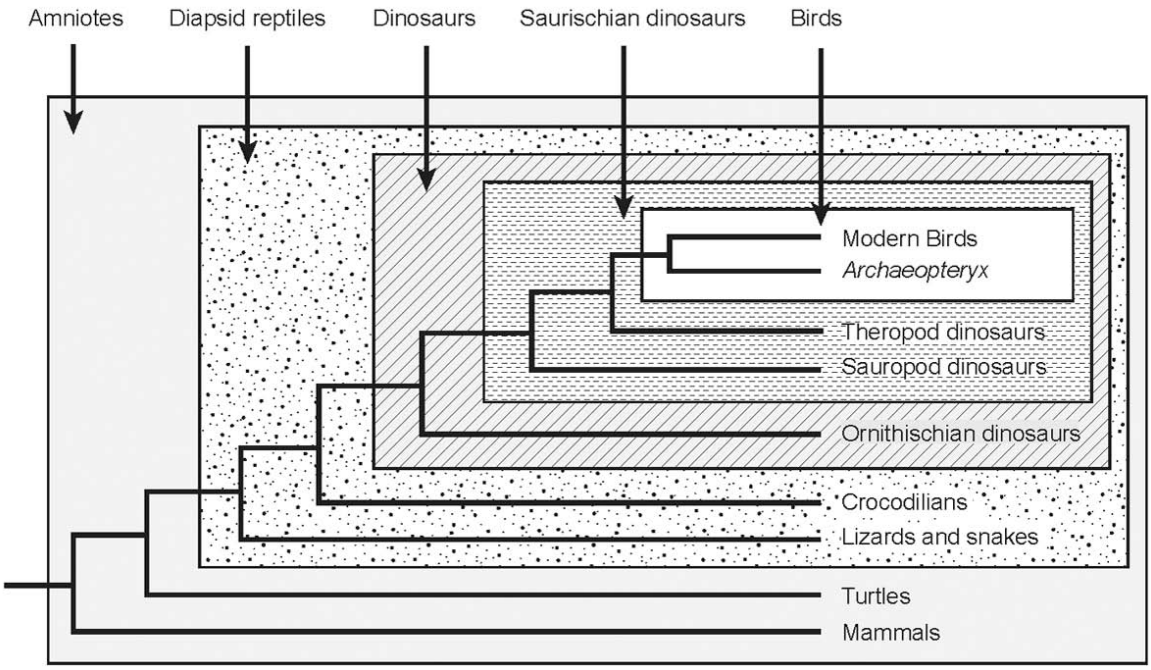
These problems can get very complicated, especially when large numbers of extinct taxa are involved. In such animals, there are usually many characters for which no data exist, and many characters show conflicts (incongruence) in their distribution. In other words, the distribution

of primitive and derived characters does not always overlap cleanly and simply in the way one might expect. This is partly because many of the taxa in question have had separate evolutionary histories, often of very long duration, during which each has undergone its own modifications. The answer these days is to use a computer. A table is drawn with the taxa listed along one axis, usually the columns, and the characters along the other, usually the rows. Each resulting square is filled in, showing the state of each character found in each taxon. The resulting table is called a matrix, not to be confused with the rock matrix enclosing fossils. Then the computer can find the branching arrangement (tree) of the taxa that involves the least incongruence and implies the fewest evolutionary changes (the most parsimonious). The tree or trees that are discovered represent the best available hypotheses of relationship drawn from the data used, but they are very much provisional. They will be subjected to much testing and are quite likely to be overturned by the addition of new data. Developments in cladistic analysis have recently included new methods that use likelihood or probability rather than parsimony as a basis for building phylogenetic trees. For morphological data, the results of this kind of analysis, known as Bayesian analysis, are not usually too far different from those obtained by parsimony analysis. In cases where an analysis includes extant forms, phylogenies based on molecular sequences can be used for comparison, although for early tetrapods, results from such studies have been ambiguous (see Chapter 3).

When a tree like this is drawn up, the task is then to name some of the branches. Because the animals are believed to be united into a clade by shared derived characters, all the members of the clade should be united by the same name to express this relationship, rather than arbitrarily split off some members from their closest relatives. This has led to some problems. For example, most paleontologists now believe that birds are most closely related to a group of small theropod dinosaurs (Fig. 1.10). In other words, birds *are* dinosaurs, evolutionarily speaking. Therefore they should not be promoted to a higher taxonomic status than dinosaurs and distinguished by being called a new class of vertebrates. In old classifications, this was what happened. The new method takes the evolutionary relationships of an animal group to be more important in its classification than its physical appearance.

A similar problem directly concerns the animals in this book. Because I will be dealing with a group of animals (tetrapods) that evolved from within a group of fishes (the lobe-finned fishes or sarcopterygians), technically, tetrapods are members of the lobe-finned fishes (Figs. 1.11, 1.12). Perhaps counterintuitively, a lungfish (a lobe-finned fish) is more closely related to a cow (a tetrapod) than it is to a salmon (a ray-finned fish); classifications should reflect this. The results of this will be explored in later chapters.

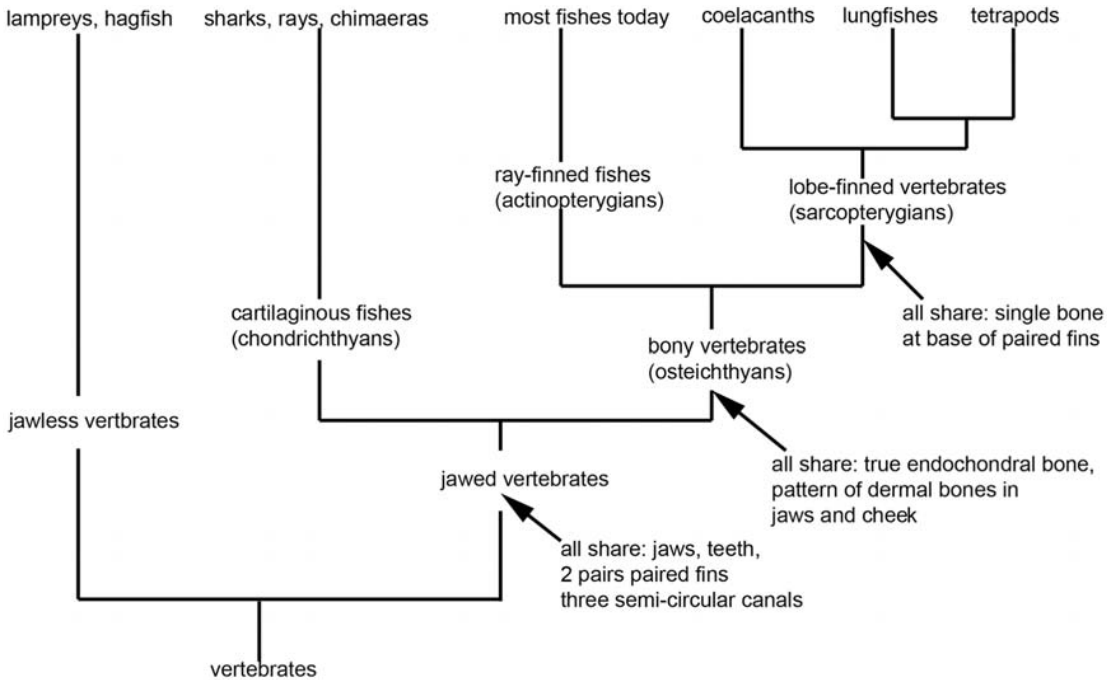
Yet another problem of phylogenetic classification arises because evolution is a continuous process. This means that it is sometimes difficult to know where to draw a line on the classification and give the branch




**1.10.** Chart showing the phylogeny of birds as a nested group within the dinosaurs, and the relationship of dinosaurs to other amniotes.

a new name. With tetrapods, the problem has not arisen until recently. Tetrapods share a number of unique derived characters, most notably limbs with digits, by which they have previously been distinguished. However, this is no longer such an easy distinction, and problems arise in deciding exactly where tetrapods begin (see Chapter 3). There are useful chapters on cladistics and its methodology in Briggs and Crowther (2001) and Kitching et al. (1998) that provide more detailed treatment.

Finally, a further problem is beginning to emerge that will complicate the process of working out phylogenetic relationships. The philosophy and practice of cladistic methodology is founded on the premise that evolution proceeds by speciation in a dichotomously branching pattern. It admits of no other kinds of process, and the algorithm underpinning the various phylogeny-generating computer programs are built on this idea. However, it is becoming increasingly clear that this is not really how nature does things. We know, for instance, that hybridization is much more common that was suspected in the past; certainly this is true for plants, but it is also true for animals, if not to the same degree. More recently, however, as a result of detailed investigations of DNA, it is becoming evident that lateral gene transfer does occur. It is common in bacteria and other unicellular organisms, but it is also known in multicellular ones. This appears to include arthropods, but it could also occur in vertebrates, most likely mediated by viruses (e.g., Dupré 2010). The number of apparently convergently acquired characters—or the amount of homoplasy, in technical terms—that always seems to appear in any cladogram may indicate that a network, or web, actually underlies the pattern of phylogenetic relationships. Cladistic analysis, therefore, is




**1.11.** Broad phylogeny of vertebrates, showing how lobe-finned and ray-finned vertebrates are all part of the bony vertebrates known as osteichthyans and how these nest into the larger picture of vertebrates. Some of the shared characters uniting the larger groups are indicated.

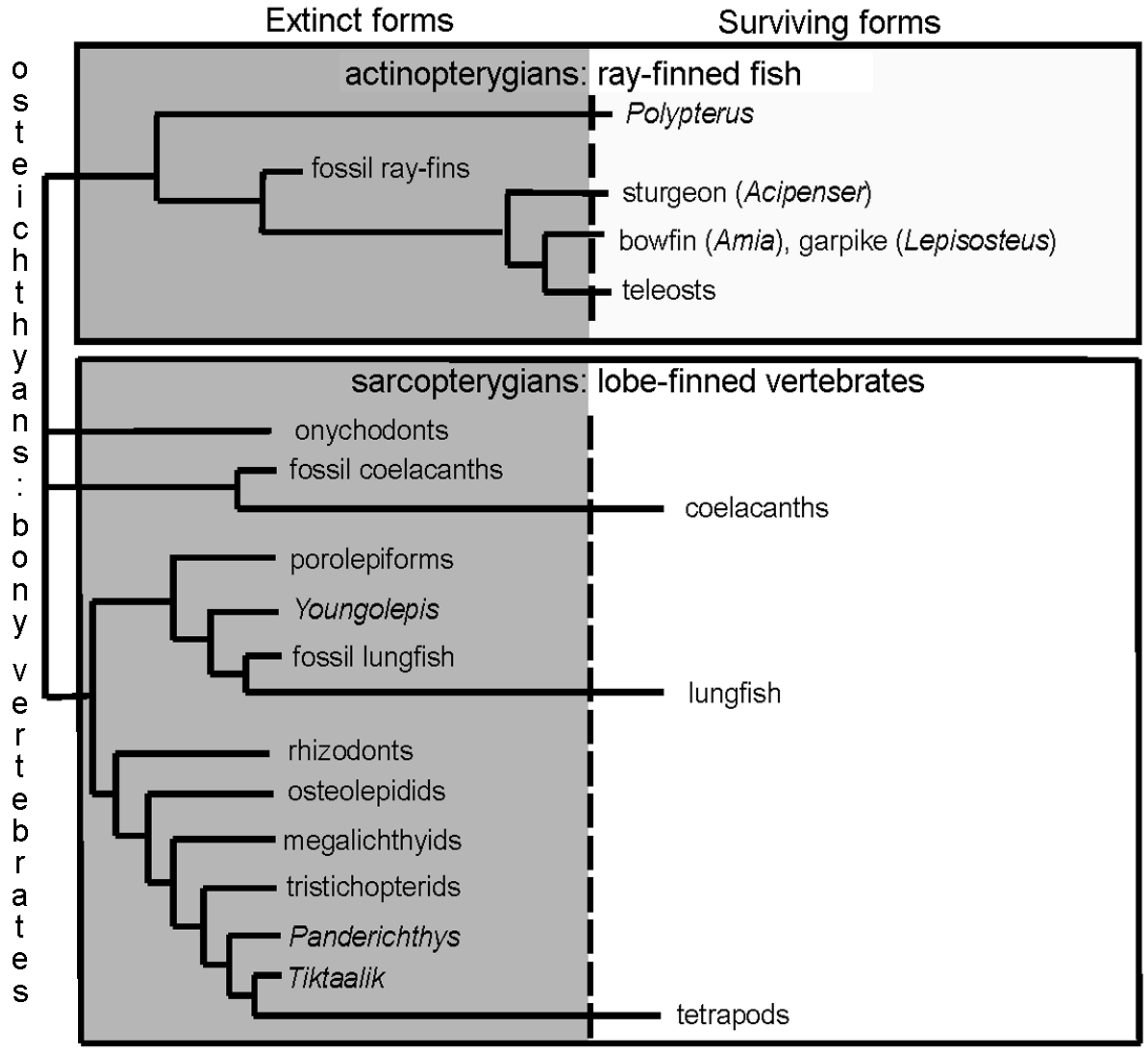
a currently useful but temporary solution to working out relationships between organisms.

### The Tetrapods and Their Place in the Family Tree

To understand how tetrapods fit into the pattern of evolution, the first requirement is to understand a little of their relatives, living and extinct. To see which features are unique to tetrapods, distinguishing them from all other vertebrates, it is necessary to recognize those that they share with others. These common features are the ones that betray their ancestry and relationships and are the basic material upon which the forces of evolution have acted to produce all the new features that tetrapods display.

Tetrapods belong to a once large and numerous group of vertebrates known as the Sarcopterygii, or sarcopterygians. This name literally means "fleshy-finned fishes," although the group is better known as the "lobe-fins." To put these animals into context among their relatives, the wider family tree of the vertebrates as a whole must be considered (Fig. 1.11).

Most fishes, including most modern and extinct ones, carry two pairs of paired fins (except where they have been lost through specialization), a fore pair—the pectorals—and a hind pair—the pelvics—carried on bony supports called girdles. These paired fins contrast with the midline fins such as the dorsal, anal, and tail fins, which are single. More details of this construction are provided in Chapter 2. Paired appendages such as these are in fact characteristic of a larger, more inclusive group of vertebrates, those whose defining characters also include possession of jaws and teeth. These are the gnathostomes ("jaw-holes").




**1.12.** Phylogeny of bony vertebrates showing how the modern groups fit with some of their extinct relatives. To the left are extinct forms and to the right, surviving members. This cladogram shows onychodonts in an uncertain relationship to coelacanths and the remaining lobe-fins. Compare this with Figures 3.1 and 3.15.

The gnathostomes share a whole suite of complex features not found anywhere else among the animal kingdom, which seem to be innovations related to their adoption of an active predatory lifestyle. Intimately connected with the evolution of jaws is the possession of a series of jointed gill bars used in the ventilation of a series of paired gill slits piercing the throat or pharynx. The gill filaments used for collecting oxygen from the water lie within pouches, each with its gill bar and set of muscles, nerves, and blood vessels to operate the system. The gill pouches open via holes in the pharynx, or throat region, that are opened and closed by operation of the gill bars. The holes are formed as the embryo grows: dimples in the external body wall grow inward to match similar dimples in the throat. Eventually the dimples meet and coalesce, forming complete tubes through the pharyngeal region through which water can pass.

The gnathostomes include fishes such as sharks, which form their skeletons from cartilage and are called chondrichthyans (cartilaginous

fishes), and those such as carp, which form their skeletons from bone and which are known as the osteichthyans (bony vertebrates), or more formally, Osteichthyes. Figures 1.11 and 1.12 provide more details of the osteichthyan family tree.

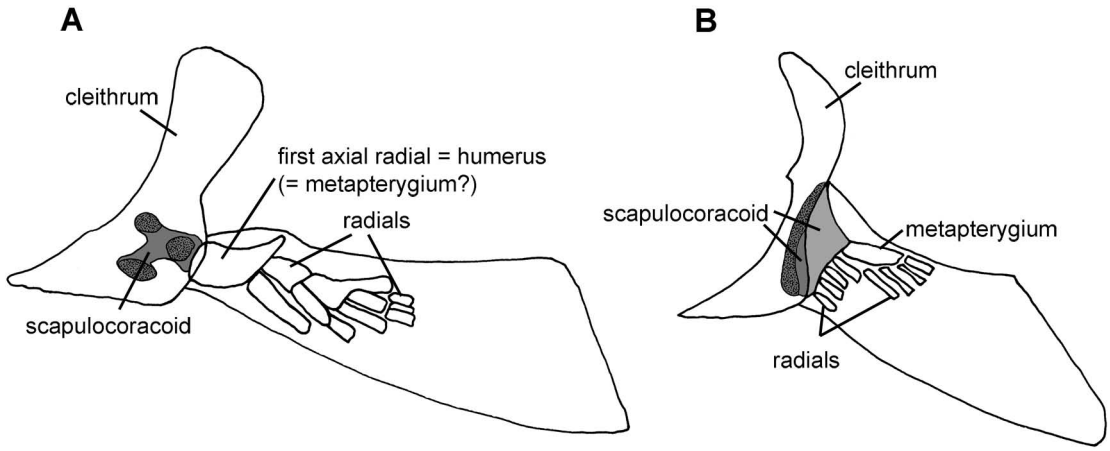
Bony vertebrates comprise the majority of vertebrate species alive today, and they are united by the fact that their skeletons are composed at least in part of a special kind of bone. This is known as endochondral bone because it has been formed by replacement of a cartilaginous precursor. The bones of human arms and legs, spinal column ("backbone"), and most of the skull are formed from this kind of bone. It contrasts with a bone formed in the skin without a cartilaginous precursor, called dermal bone. Even the most primitive known vertebrates have some form of this latter kind of bone, although in true osteichythans, it is arranged into distinctive patterns that can be recognized throughout the group. Humans retain some of these, such as the tooth-bearing jawbones, the maxilla and dentary.

Another feature that it seems early bony vertebrates shared was the ability to form an extra pair of pouches behind the standard set of gill pouches in the throat. This pair was used as an air chamber, and in many early bony vertebrates, they were essentially lungs. Some of these animals retained the lungs and used them regularly for breathing air. This needs to be borne in mind when considering the evolution of tetrapods. Air breathing was and is common among bony vertebrates; it is not unique to land-living ones.

The animals that belong in the bony vertebrates fall into two groups: the ray-finned fishes (the actinopterygians or Actinopterygii), and the lobe-fins. The difference between them is for the most part quite straightforward and easily recognized. In the ray-finned fishes, the paired fins articulate with the shoulder girdle through a series of parallel bones called radials. These in turn support the bony fin rays, or lepidotrichia. At least in early fossil forms, the fins had a broad base and were not very maneuverable, although this is no longer the case in most modern forms. This group encompasses almost all modern fishes.

The lobe-fins, by contrast, attach their paired fins by a single radial to the shoulder girdle, and the main axis of the fin is formed by stringing the rest of the radials in a chain growing outward from the body. The radials bear muscles running between the bones, thus making the lobe of the fin both segmented and muscular, and giving it a narrow, flexible base that allows it to rotate as well as be raised and lowered. It is this formula that humans and other tetrapods share most obviously with their lobe-finned relatives and one you can contemplate each time you look at your own arm or leg (Fig. 1.13).

Although humans do not usually think of themselves as fishes, nonetheless, they share several fundamental characters that unite them inextricably with their relatives among the fishes. If one of the aims of classifying animals is to reflect their relationships and phylogeny, then inevitably humans and other tetrapods fall within the same grouping as



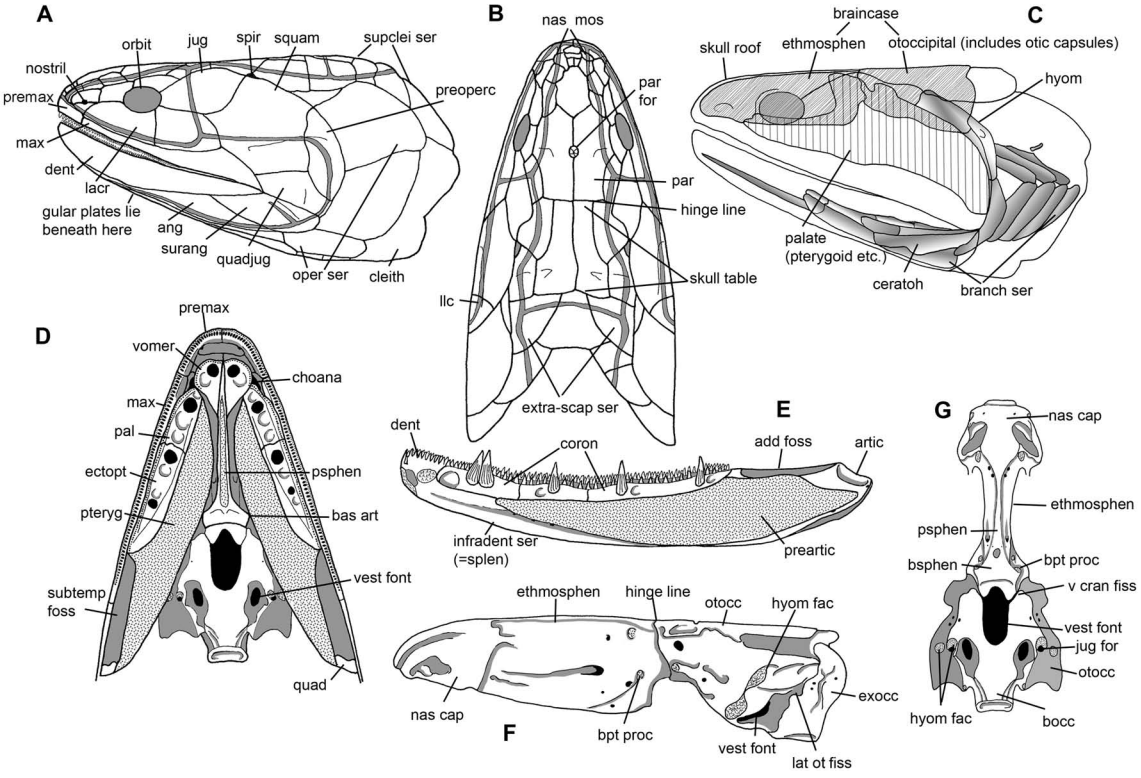

**1.13.** Diagram of contrasting fin-support structure. (A) Lobe-finned fishes. (B) Ray-finned fishes. The pattern in (A) is that which is found in tetrapods. Dark gray indicates areas of the scapulocoracoid situated interiorly to the cleithrum; lighter gray indicates area exposed in lateral view in the ray-finned fish. Stippled areas indicate regions of attachment to scapulocoracoid.

other members showing these characters and sharing the same common ancestor. Thus, humans are mammals and are defined as belonging within mammals, despite what might be seen as a suite of distinguishing characters. In the same way, mammals are tetrapods, because they have four legs (or their ancestors did) and a set of other characters that unite them with other tetrapods (amphibians plus amniotes). So humans are also tetrapods. So far so good. But the next step often causes a problem. In phylogenetic classification, tetrapods are sarcopterygians (lobe-fins). They belong with other forms, the lungfishes and coelacanths and a range of extinct forms, within the lobe-fins. Because "sarcopterygian" is usually translated as "lobe-finned fish," it is sometimes a problem to appreciate that tetrapods really belong here. "Sarcopterygian" is better translated as "fleshy-limbed vertebrate," so this can be more easily understood. Tetrapods did not evolve *from* sarcopterygians, they *are* sarcopterygians, just as one would not say that humans evolved from mammals, they *are* mammals. Similarly, sarcopterygians, along with their sister group the actinopterygians (ray-fins), both belong within the osteichthyans or bony vertebrates, and thus humans are also osteichthyans, even though this word is sometimes translated as "bony fish" (Figs. 1.11, 1.12).

This concept has recently been elegantly and clearly expressed in *Your Inner Fish* by Neil Shubin (2008). It looks not only at the fish–tetrapod transition, a subject in which Shubin and his colleagues have made some exciting discoveries (see Chapters 3 and 6), but expands on the theme of the nested sets of characters shared throughout the vertebrate family tree and beyond.

Any speculation about how evolutionary changes ("processes") took place must be set in the context of a testable phylogenetic hypothesis to derive the pattern. If not, any ideas about such matters will be set at the level of storytelling and have little or no scientific validity. They may, of course, precipitate a new look at fossil material that may eventually end up with more characters to add to the data matrix and thus a revised phylogeny. This kind of reciprocal enlightenment certainly goes on.

However, each time, the phylogeny into which the ideas are nested must be explicit and testable by other people. Discussions of the detailed phylogenies followed here will be found in the appropriate chapters, as will some examples of how different phylogenetic ideas can influence how fossil material is interpreted.




**2.1.** Skull of *Eusthenopteron* to show structures. (A) Left lateral view of skull roof and lower jaw. (B) Dorsal view. (C) Lateral view with skull roof bones shown transparent, and palate, braincase, and gill arches visible beneath. (D) Ventral (undersurface) view with braincase in position. (E) Medial (internal) view of lower jaw. (F) Lateral view of braincase. (G) Ventral view of braincase. *Based on Jarvik (1980).*

# Skulls and Skeletons in Transition

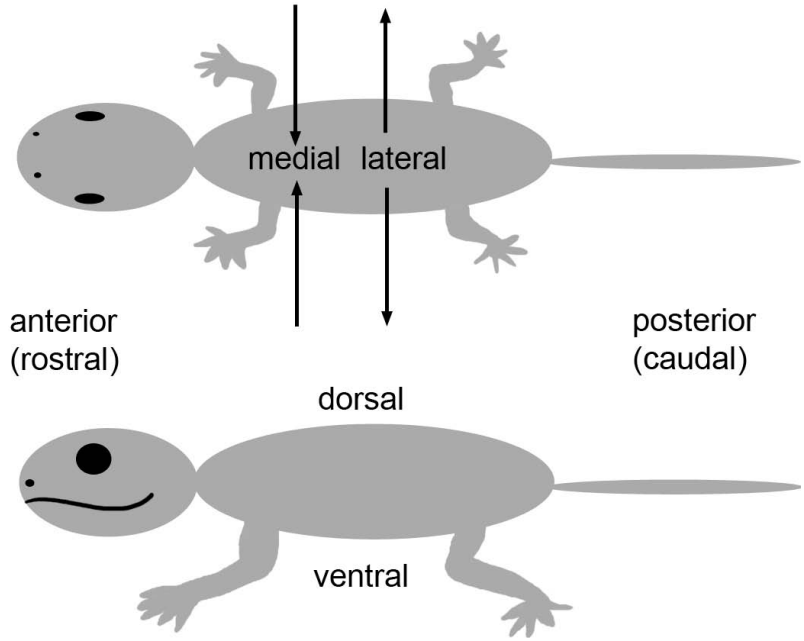
# 2

This chapter is an introduction to the skeletal anatomy of animals that exemplify the fish–tetrapod transition. The first part examines how the skulls and skeletons of lobe-finned fishes and tetrapods were built, and will introduce the terminology used for the bones. Unfortunately, many of the terms will be unfamiliar to the nonspecialist reader, but at least some of them need to be assimilated because in most cases, there simply are no other words available to describe them. It is probably a good idea to refer constantly to the diagram of skull structure (Fig. 2.1).

One particularly important set of terms is that referring to the orientation of diagrams and their relationship to the whole animal that they describe: top, bottom, front, back, and so forth. These everyday terms are not accurate or precise enough for explaining anatomical structures. Figure 2.2 shows some of these terms. One thing to note is that in humans, because of their upright stance, words describing front and back mean different things from those that mean nose to tail. Human and veterinary anatomists have therefore coined separate words for them. For human anatomy, the terms anterior and posterior are ambiguous, so front to back is described by the terms ventral to dorsal, whereas nose to tail is described by rostral (toward the top of the head or snout) and caudal (toward the tail). However, dealing exclusively with four-legged tetrapods or fishes, there is no such distinction. In this case, front to back is the same as nose to tail; anterior to posterior are used for these, and the terms ventral to dorsal are used for top to bottom.

Throughout the book, reference will also be made to the embryonic origins of certain tissues, so the second part of the chapter sets out the basics of how a vertebrate embryo forms, where various tissues come from, and what structures each becomes. A section on recent work in developmental genetics, especially on *Hox* genes, is necessary for understanding certain aspects of tetrapod evolution, where work on living animals has had an impact on paleontological studies.

Once the basic anatomy of a fish, such as the Devonian lobe-finned fish *Eusthenopteron*, and a tetrapod such as the Devonian *Acanthostega* or the Carboniferous temnospondyl *Dendrerpeton* is understood, the differences that came about at the fish–tetrapod transition can be approached. These are outlined in the last part of the chapter. However, the features that fish and tetrapods share must be dealt with before those that separate them can be appreciated. Many of these features can be found in modern vertebrates as well as in very early ones.




**2.2.** Diagrams explaining anatomical terms of orientation. Medial means looking toward the midline of the body, lateral means looking away from the midline.

## Understanding Skeletal Structure

### The Skull

#### DERMAL SKULL ROOF

Figure 2.1 shows the skull of the Devonian lobe-finned fish *Eusthenopteron*, which will be used as an exemplar to show fish skull anatomy. Early bony fishes, early tetrapods, and some modern ray-finned fishes share some common features of skull construction that are considered to be primitive. In these animals, the skull is built of an outer covering of bony armor called the dermal skull roof, while the braincase is a separate, relatively small box containing the brain proper, the ear capsules, and the roots of the nerves serving the other sense organs. Hinged to the back of the dermal skull roof is the lower jaw, while the palate forms the roof of the mouth. In most modern fishes and tetrapods, much of the dermal skeleton found in Paleozoic members has been lost, which is why their skulls look rather different from those of these more ancient creatures.

The dermal skull roof can be divided into several regions. At the top and back lies a flat, more or less rectangular lid called the skull table. It is made up of paired bones, sometimes given different names in fish and tetrapods. Reaching out from the front of this and running between the eye sockets, or orbits, runs a series of paired bones forming the interorbital region. In *Eusthenopteron*, the main bones in this region are the parietals, surrounding the parietal foramen, sometimes called the pineal foramen. The parietals attach at the front to the snout, which has the external nostrils on each side of it. In *Eusthenopteron*, the snout region is made up of a mosaic of small bones (Fig. 2.1A, B).

In most fishes, there are two small holes on each side of the snout. These are the nostrils or nares (pronounced as two syllables; singular, naris): the anterior one allows water into the nasal capsule for olfaction (sense of smell) and is called the incurrent nostril, and the posterior one allows the water to pass out again, called the excurrent nostril. *Eusthenopteron* has a different arrangement that will be described later (see Chapter 3).

Running back from the snout beneath the orbits and the skull table is the cheek region. The main cheekbones are the lacrimal, jugal, squamosal, and quadratojugal. At the back of the cheek, which is usually drawn backward well beyond the hind edge of the skull table, is the region where the lower jaw hinged to the skull roof, and this whole back portion of the cheek is sometimes called the suspensorium. Each of these regions consists of several mostly flat platelike dermal bones joined or sutured together. These form in the skin as the animal grows. The skull roof protects the braincase, which is suspended beneath the skull table. It also encloses the eyes and nasal capsules, and anchors some of the muscles responsible for closing the jaws. Of critical importance, it also bears the marginal arcade of teeth, on the premaxilla and maxilla.

Behind the main part of the skull in fishes and running beneath the lower jaw is a series of dermal bones called the operculogular series. Two or more large dermal bones form a flaplike extension to the back of the cheek, protecting the gill (or opercular) chamber and forming a seal for use in the ventilatory cycle. This flap is extended downward as a flexible covering to the throat through an interlinked chain of dermal plates, ending with the gular plates under the chin.

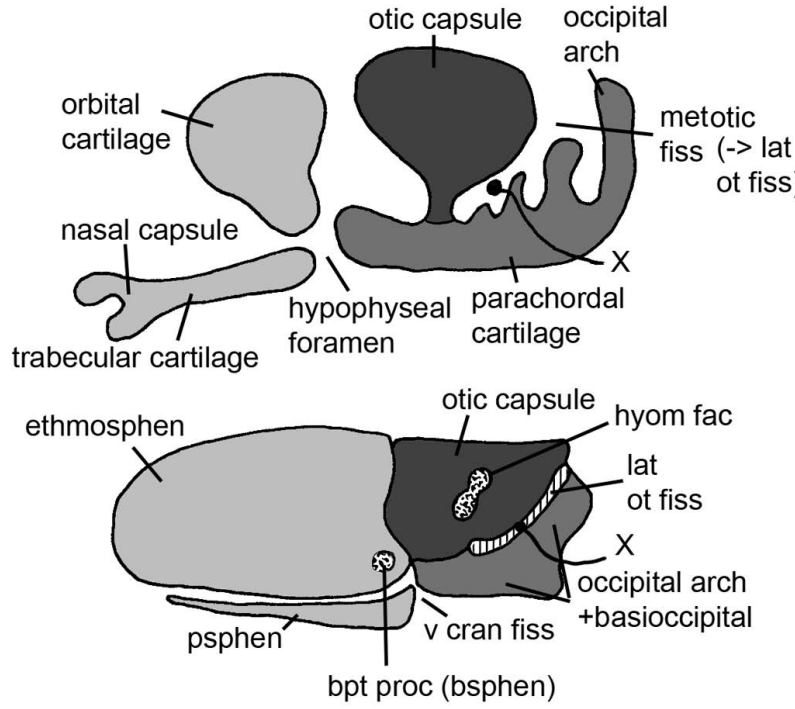
Between the opercular bone and the skull table is a notch where, in *Eusthenopteron*, as in some modern ray-finned fishes, the opening of the spiracle is found. The spiracle is the remnant of the gill pouch once associated with the hyoid arch.

Running over the skull bones at certain points are the lateral line canals. This sensory system is explained in detail in Chapter 6.

## BRAINCASE

The braincase is a complex structure formed from many different embryonic and anatomical components; readers unfamiliar with anatomy may wish to defer attempting this section and come back later if they need to. Unlike the skull roof, the braincase is made of bone that forms from the ossification of a cartilage precursor (Fig. 2.1F, G). This is endochondral bone, and the braincase is part of the endoskeleton.

The structure (Figs. 2.1, 2.3) consists of two main parts. The back part is formed from the ear capsules and the occipital region, with which the vertebral column articulates. These form from separate units in the embryo, seen in all modern jawed vertebrates and implied by the construction seen in fossil forms (Fig. 2.3). The ear (otic) capsules house the vestibular system and semicircular canals for monitoring posture,




**2.3.** Diagram of embryonic braincase components (top) and the regions of the braincase that they become in the adult (bottom). X marks the exit point and course of cranial nerve X, the vagus.

balance, and movement, and the sensory cells for hearing, when these are present. Bones of the otic capsules in the adult are called the pro-otics and opisthotics. Underlying this complex is the occipital arch complex, consisting of the paired parachordal cartilages, and growing up from them a series of arches or columns that may or may not join up with the otic capsules. In the adult, these structures form the basioccipital, exoccipital, and supraoccipital bones. The otic capsule and occipital arch are separated by a gap called the lateral otic fissure. The complete unit of otic capsules plus occipital regions is called the otoccipital region. It bears facets at which the hyomandibular articulates, and a large unossified gap called the vestibular fontanelle separates the otic and occipital regions.

The front part of the braincase consists of a midline partition separating the eyes and carrying the olfactory nerves to the front of the snout, where the nasal capsules, also part of the braincase, are situated. The front part consists of the ethmosphenoid (in fishes) or sphenethmoid (in tetrapods) and a more posteriorly lying portion called the basisphenoid. This bears articulations by which the braincase and palate link up, called the basipterygoid processes. Underlying these components lie a pair of rods known as the trabeculae. The front and back parts of the braincase are separated by a gap called the ventral cranial fissure.

### PALATE

A third component of the skull is probably the most difficult to explain and visualize, perhaps because it has several different jobs, and its structure is

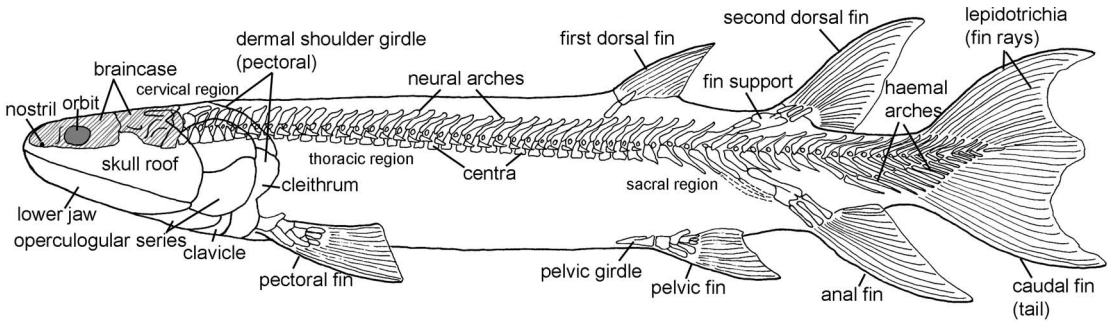
a reflection of its complex history. This is the palate region (Fig. 2.1D). At the front, the palate forms the roof of the mouth and supports the nasal capsules in the snout region. Along its outer edges, it fastens to the inner margins of the cheek. Moving back along the skull, just behind and internal to the eyes, a socket in the palate houses the basipterygoid process, a peg from the braincase, supporting the braincase at a crucial point. Behind the basal articulation, the palatal complex sends a process, the epipterygoid, upward to contact either the otic region of the braincase or the underneath of the skull roof. In this region, the palate curves in cross section from an approximately vertical component near the midline of the skull to a much less steeply angled or even nearly horizontal plane at the edges. The vertical part stretches backward, in contact with the back edge of the suspensorium, while the more horizontal one leaves its contact with the cheek to form a gap between the two regions, through which the jaw muscles pass downward. This is called the subtemporal fossa. At the very back, it is part of the palatal complex that provides the hinge where the lower jaw attaches, called the quadrate.

The palatal complex is a mixture of dermal and endochondral components, and in fishes it is even more complex, with more separate bones, than in early tetrapods. This has meant that fossil fish specialists use more and different names for the parts than do fossil tetrapod specialists. For the purposes of this chapter, the tetrapod structures are described and their names used. The major contributor is the dermal pterygoid. This forms the main plate of the palate and the part which clasps the quadrate, called the quadrate ramus. Bordering the pterygoid and linking the palate to the cheek on each side, a row of bones bears an inner row of teeth—the vomer, palatine, and ectopterygoid, from front to back. The front end of the palate in some species embodies a small endochondral component, but the main endochondral elements are the epipterygoid forming both the vertical (otic) process and the socket for the basal articulation, and the quadrate.

A midline dermal element called the parasphenoid underlies the braincase and forms part of the palate. Like the rest of the palate, it may bear teeth or denticles. At the junction between the premaxilla, maxilla, vomer, and palatine is a hole in the palate; this is the internal nostril or choana.

### LOWER JAW

The lower jaw is essentially a tube formed from dermal bones, some of which bear the teeth (Fig. 2.1E). An outer arcade of teeth on the dentary opposes those of the premaxilla and maxilla, and an inner row on a series of coronoids opposes those of the vomer, palatine, and ectopterygoid. Beneath the dentary on the outside lies a series of bones known as the infradentary series in fish, or the splenial series in tetrapods. On the inside the main bone is the prearticular, and it is often covered with denticles, to match those on the palate. As with the upper part of the jaw hinge, the



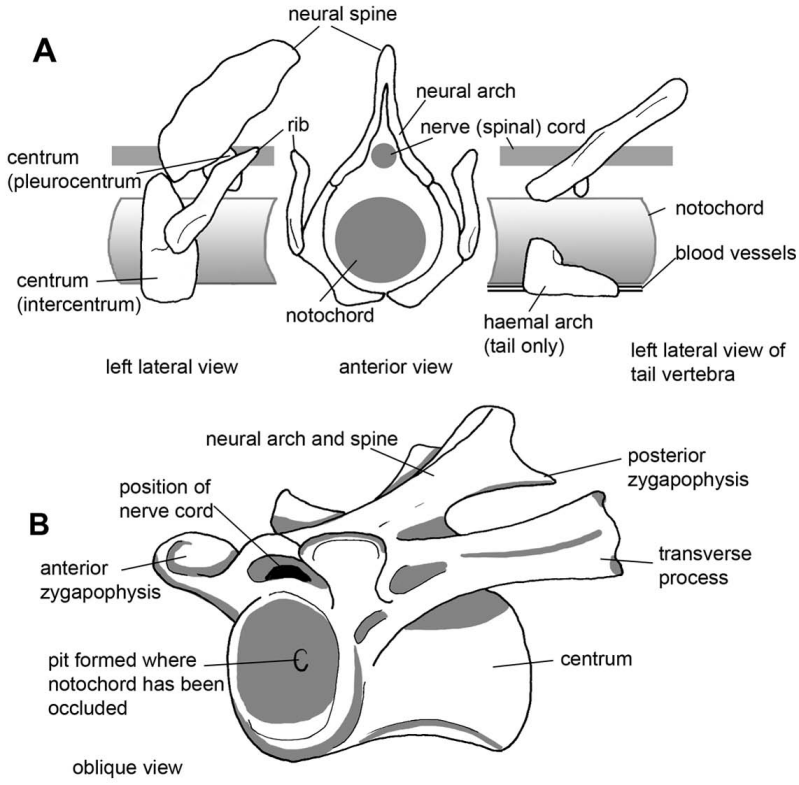

**2.4.** Skeleton of *Eusthenopteron* to show main features of the skeleton and body.

lower part is also an endochondral bone called the articular, sandwiched between inner and outer faces of the dermal jaw bones. In front of the articular is a hollow between the inner and outer faces, called the adductor fossa, into which the jaw muscles inserted. Within the tube in some cases lies a bar of endochondral Meckelian bone.

### Hyobranchial Skeleton and Gill Openings

The hyobranchial skeleton (Fig. 2.1C) is another term for the gill-supporting bones and their associated structures. In fishes, there is usually a series of five jointed gill bars, or branchial arches, supporting the gill filaments. The first couple of the series hinge onto the braincase and the rest attach to the more anterior ones. They join at the base, under the "chin" of the fish, to a midline bone. This structure provides a flexible, elastic basket that allows the gills to move in and out and the gill chamber to expand and contract as the fish breathes. In front of the standard set of gill arches, there lies a larger and highly modified set called the hyoid arch. The uppermost element of this set is called the hyomandibula, and the lower part the ceratohyal. Each gill arch is associated with an opening from the throat region (the pharynx), to the outside, though which water passes as it is processed by the fish during breathing. The hyomandibula has a crucial and literally pivotal job to do in the architecture of the skull of most fishes. It was associated in most early fishes with a modified gill opening called the spiracle. In tetrapods, the form of the bone and its function changes, and it is known as the stapes. These functional and anatomical differences are explained in more detail below.

The gill and hyoid arches are formed, as with the braincase, from endochondral bone, although in this case the embryonic origin of the cartilage is different from that of most other endoskeletal elements. Its formation is initiated by a unique vertebrate embryonic tissue called neural crest. This tissue is also responsible for bringing about the formation of the trabeculae of the braincase, and the quadrate, articular, epipterygoid, and other endochondral parts of the palate, which may ossify. For this and other reasons, scientists consider these jaw elements to be members of the same series as the gill arches.



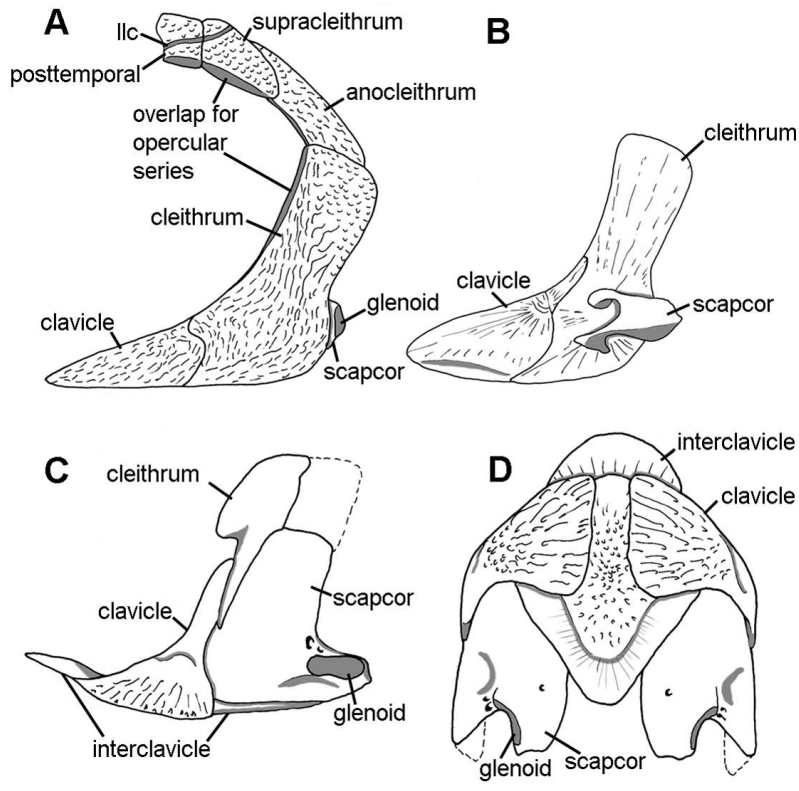

**2.5.** Construction of vertebrae in *Eusthenopteron* and a tetrapod. (A) Vertebrae of *Eusthenopteron* in three views: left to right are left lateral and anterior views of trunk vertebra, left lateral view of tail vertebra with hemal arch. (B) Oblique view of a tetrapod vertebra, *Andrias japonicus,* the Japanese giant salamander, showing a unitary centrum in which the rib attaches only to the neural arch via the transverse process.

## Postcranial Skeleton

The postcranial skeleton in all fishes and tetrapods consists, like the skull, both of endochondral and dermal elements. It can be divided into different regions, shown in the skeleton of *Eusthenopteron* in Fig. 2.4.

### AXIAL SKELETON

The axial skeleton consists of the vertebrae and associated structures including ribs, and in the case of fishes, the midline fins. A vertebra consists of a neural arch that sits over the spinal or nerve cord and rests on a centrum, which forms round the embryonic supporting bar called the notochord (Fig. 2.5). Centra may be simply formed from a single element, or they may be a compound of single and paired elements. Neural arches may be joined to one another or not. Ribs may be present, articulating with a neural arch and/or a centrum. In the tail, hemal arches may be present under the centra, allowing passage of blood vessels serving the posterior part of the body. There may be differentiation of different regions of the vertebral column, such as the cervical region at the front, thoracic in the middle, and sacral near the pelvis, though in fishes, the differences are minimal and the terms not really applicable. All these elements are endochondral in origin.




**2.6.** Shoulder girdles of *Eusthenopteron* and a generalized early tetrapod. (A) Left lateral view of cleithrum and clavicle of *Eusthenopteron.* (B) Medial view of right cleithrum and clavicle of *Eusthenopteron* showing the scapulocoracoid on the internal face (supracleithral series omitted). (C) Left lateral view of the shoulder girdle of an early tetrapod—note the reduced cleithrum and enlarged scapulocoracoid. (D) Ventral view of the shoulder girdle of an early tetrapod—note the large interclavicle.

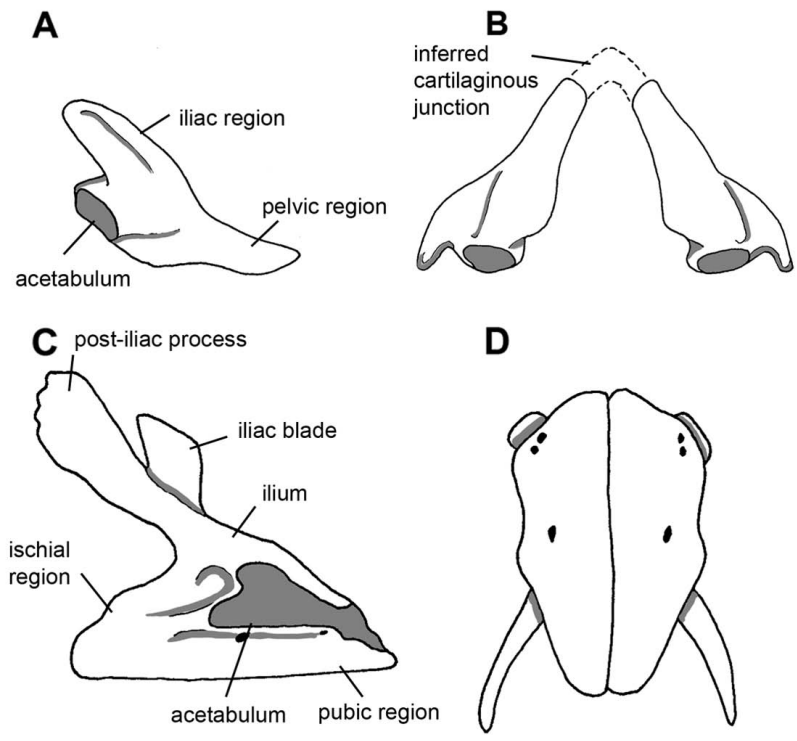
## APPENDICULAR SKELETON

The appendicular skeleton comprises the limbs and girdles, at the front the shoulder or pectoral set, and at the back, the hip or pelvic set. Figure 2.6 shows views of the shoulder, and Figure 2.7 shows the hip girdles of *Eusthenopteron* and a tetrapod.

The pectoral girdle is a mixture of elements, consisting of dermal bones such as the cleithrum, clavicle, and interclavicle, and the endochondral scapulocoracoid. It is this latter bone that provides the articulatory socket, or glenoid, for the pectoral appendages, and it fits within and behind the sheathing series of dermal bones. The pectoral girdle is not attached to the vertebral column except indirectly by soft tissue or through other linking bones. The pelvic girdle is entirely endoskeletal in origin and carries the socket, or acetabulum, for the pelvic appendage.

## DERMAL SKELETON OF THE BODY

Fishes also have an additional part to the skeleton, the body scales and the bony fin rays or lepidotrichia, which support the fin web. These are all dermal in origin. In most primitive fish, the tail was heterocercal—that is, they were asymmetrical, with the body lobe running up the leading edge of the fin and the main part of the fin webbing suspended below it as a flag from a pole, and in some, a lesser fringe grew above the body lobe.




**2.7.** Pelvic girdles in *Eusthenopteron* and a tetrapod (*Acanthostega*). (A) Right lateral view of *Eusthenopteron*. (B) Ventral view of *Eusthenopteron*. (C) Right lateral view of *Acanthostega*. (D) Ventral view of *Acanthostega*.

Scales primitively bore a layer of thick enamel-like tissue; this imparts a glossy look to their fossilized remains.

All the features mentioned in this section are common not only to all lobe-finned fishes and tetrapods, but also to ray-finned fishes. These are the shared inheritance of all bony fishes, the osteichthyans.

More details of the structure of the appendages and of the girdles will be dealt with in the section on differences between fishes and tetrapods. A summary of anatomical terms, along with their location and type, is provided in Table 2.1.

## Tissues and Skeletal Structures

### Developmental and Embryonic Origins

To understand the physical and developmental relationships among the various types of skeletal tissues and the features that they form, an explanation of their embryonic origins is necessary. Some of the characteristics that demonstrate the phylogenetic relationships between animals are best seen in the embryos of the animals, and the developmental history of some skeletal elements shows something of their commonality of descent. More details of this early stage in animal development may be found in standard textbooks on vertebrate biology, such as that by Kardong (2009), or in textbooks on developmental biology and embryology, such as those by Raff (1996), S. B. Carroll et al. (2004), and Wolpert et al. (2007).

Each animal starts out as a single cell, which, when fertilized, grows into a ball of cells (Fig. 2.8A–D). After it reaches a certain size, the

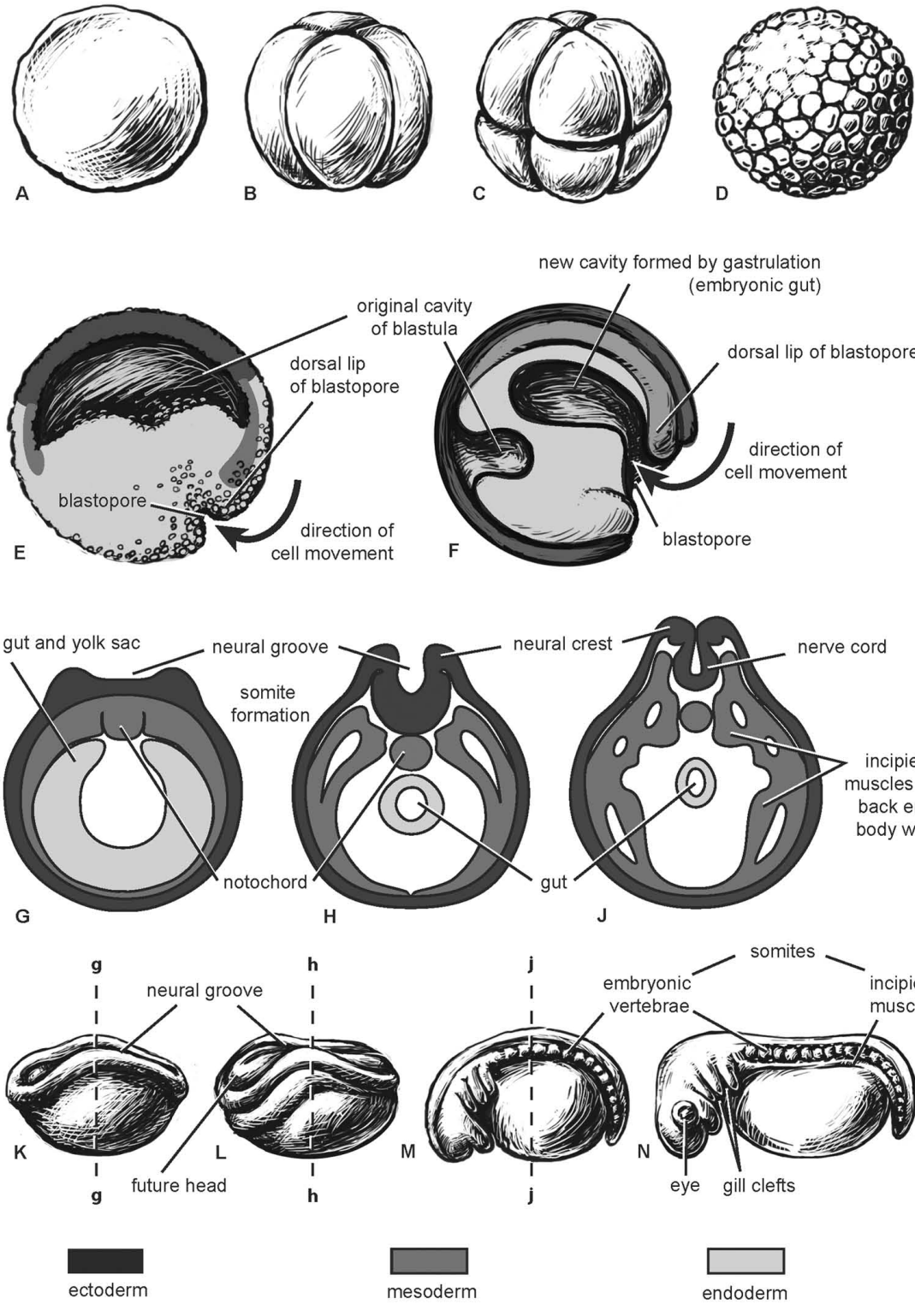
**Table 2.1.**

- Skull
  - Dermal skull roof
    - Snout
      - nasal
      - lacrimal
      - frontal
      - prefrontal
    - Cheek/suspensorium
      - jugal
      - quadratojugal
      - squamosal
      - postorbital
    - Skull table
      - postfrontal
      - parietal
      - postparietal
      - intertemporal
      - supratemporal
      - tabular
    - Marginal tooth-bearing bones
      - premaxilla
      - maxilla
  - Palate
    - Dermal bones
      - pterygoid
      - vomer
      - ectopterygoid
      - palatine
    - Endochondral bones
      - epipterygoid
      - quadrate
  - Braincase
    - Otic capsule
      - pro-otic
      - opisthotic
    - Occipital arch
      - (supraoccipital in a few forms)
      - exoccipital
      - basioccipital
    - Ethmoid region
      - sphenethmoid
      - basisphenoid
      - basipterygoid process (links to palate via basal articulation)
  - Lower jaw
    - External (lateral) face
      - dentary
      - splenial
      - postsplenial
      - angular
      - surangular
    - Internal (mesial) face
      - parasymphysial plate
      - coronoids (usually three)

**Table 2.1., continued**

- Postcranial skeleton
  - Axial skeleton
    - vertebrae
      - neural arch
      - centrum
      - hemal arch (in tail only)
      - zygapophyses
    - ribs
    - supraneural radials (primitively)
  - Appendicular skeleton
    - Pectoral girdle and limb: dermal components
      - anocleithrum (primitively)
      - cleithrum
      - clavicle
      - interclavicle
    - Pectoral endochondral components
      - scapulocoracoid
      - forelimb
        - humerus
        - radius
        - ulna
        - carpus
        - metacarpus
        - manus
    - Pelvic girdle and limb
      - ilium
      - ischium
      - pubis
      - hind limb
        - femur
        - tibia
        - fibula
        - tarsus
        - metatarsus
        - pes

- Bones of fish skull lost in early tetrapods
  - Skull roof
    - extrascapular series
    - multiple nasal bones
    - lateral rostral (except Devonian forms)
    - anterior tectal (except Devonian forms)
  - Opercular series
    - opercular
    - subopercular
    - submandibular series
    - gular plates
  - Pectoral girdle
    - posttemporal
    - supracleithrum
      - prearticular


A
B
C
D
new cavity formed by gastrulation
(embryonic gut)
original cavity
of blastula
dorsal lip
of blastopore
dorsal lip of blastopore
direction of
cell movement
blastopore
direction of
cell movement
blastopore
E
F
gut and yolk sac
neural groove
neural crest
nerve cord
somite
formation
incipient
muscles of
back end
body wall
notochord
gut
G
H
J
g
h
j
neural groove
somites
embryonic
vertebrae
incipient
muscles
K
L
M
N
future head
eye
gill clefts
g
h
j
ectoderm
mesoderm
endoderm

surface-to-volume ratio comes into effect, and to get nutrients into and waste products out of the ball of cells, it has to change shape. It does this by invaginating. In this process, a small hole appears in the ball of cells, and the cells surrounding the hole are swallowed into it, first creating a dimple, then followed by a deeper and deeper hole, called a blastopore (Fig. 2.8E). Cells continue to pour into this hole until eventually the ball of cells is no longer solid, but hollow (Fig. 2.8F). Even by this early stage, most of the cells have already had their future fates decided, and the ball already has a defined top and bottom, front and back. One important landmark in the ball of cells is the upper region of the margin of the hole, the dorsal lip of the blastopore. As cells pass over this lip to the inside, they are marked out for particular duties in the growing embryo, and the whole of this part of the animal's development is called gastrulation. It is probably the most crucial moment of the animal's life, during which much of its developmental fate is decided. This part of the developmental process in some form is common to all multicellular animals.

The ball of cells to begin with consists of two layers, and some animals, like sea anemones, stop there. However, in most animals (called triploblastic), a third region of cells arises in the space between the inner and outer layers. The three cell "layers" (the middle one is more than just a layer) form different parts of the developing embryo: in vertebrates, the outer layer is called the ectoderm and forms the thin outer layer of skin called the epidermis and a number of other features; the inner layer is called the endoderm and forms the lining of the gut and other outgrowths from it such as the liver; the tissue in the middle is called mesoderm, and it forms most of the structures of the body, such as most of the bones, the muscles, and most of the internal organs such as kidneys, blood vessels, heart, and glands (Fig. 2.8 G–J).

The next stage in the development of the embryo is called neurulation, and it is at this point that some of the most basic features of all vertebrates develop (Fig. 2.8 G–N). From each side of the embryo, two ridges of tissue begin to gather up into parallel crests, with the blastopore at one end (it becomes the anus in vertebrates and a few other animal groups related to them, such as echinoderms). Cells from the outer, ectodermal, layer stream toward the ridges and gather up like waves. The two waves eventually meet and zip together along the embryo's length, forming a loop at one end and petering out at the other. As the two waves meet, they enclose a tube beneath. The tube is the nerve cord and the loop becomes the head, with its swollen end becoming the incipient brain. The ridges are formed within the ectodermal layer, so the odd fact is that the brain and nerve cord are part of the outer surface or ectoderm of the embryo that has become enclosed (Fig. 2.8 G–J).

As the embryo grows, beneath the ectodermal nerve cord, the middle layer forms a midline structure of its own. The rodlike notochord forms here, circular in cross section and stretching the length of the embryo except for the front part of the incipient head end. To either side of the notochord, and to an extent regulated by it, the middle layer of mesoderm

**2.8.** Embryonic development of an amphibian from egg to neurula. (A) Single-cell stage. (B) Four-cell stage. (C) Eight-cell stage. (D) Multicell stage before invagination. (E) Invagination stage showing the blastopore and direction of cell flow into it. (F) Section through the embryo at a slightly later stage than (E), showing a section through the blastopore region, the invaginating cells, and the incipient outer and inner layers of the embryo. (G, H, and J) Sections through a later embryonic stage equivalent to those in (K), (L), and (M), at which the neural tube begins to form and the three germ layers are established. (N) Neurula, a stage at which the neural tube is complete, and body segments (somites) with incipient vertebrae, muscles, and nerves as well as gill slits have formed. *Illustration by J.M. based on information in Gilbert (2000) and Kardong (1998).*

**2.9.** *Hox* genes in vertebrate development. (A) The relative sphere of influence of eight of the *HoxB* series of genes in the head and anterior part of the trunk, and the more anterior body segments (as well as parts of the hindbrain) affected by more anteriorly situated genes. (B) Comparable segments of *Hox* genes in the fruit fly *Drosophila,* the primitive chordate *Amphioxus,* and the mouse (an amniote). *Drosophila* and *Amphioxus* each have one set of such genes, while the mouse has four, labeled A, B, C, and D. Homologous genes in *Amphioxus* and the mouse are shown shaded. Equivalent genes in the fly are shown with a diamond, and the abbreviations of the gene names are shown above. *J.M. based on information in Gilbert (2000).*

begins to divide into segments, starting from the head end and working backward (Fig. 2.8). The segments, called somites, become the muscle blocks that lie beside the vertebral column and control its movements. Nerves and blood vessels follow. The limbs or fins develop later from buds out of the lateral wall of the embryo. Bones of the internal limb skeleton, vertebral column (usually), some parts of the skull and braincase, the ribs, and some parts of the limb girdles are formed first in cartilage originating in the mesoderm that is then replaced by bone as the animal grows. Around the same time that the limb buds form, the gill pouches appear just behind the mouth of the growing embryo (see Chapter 1).

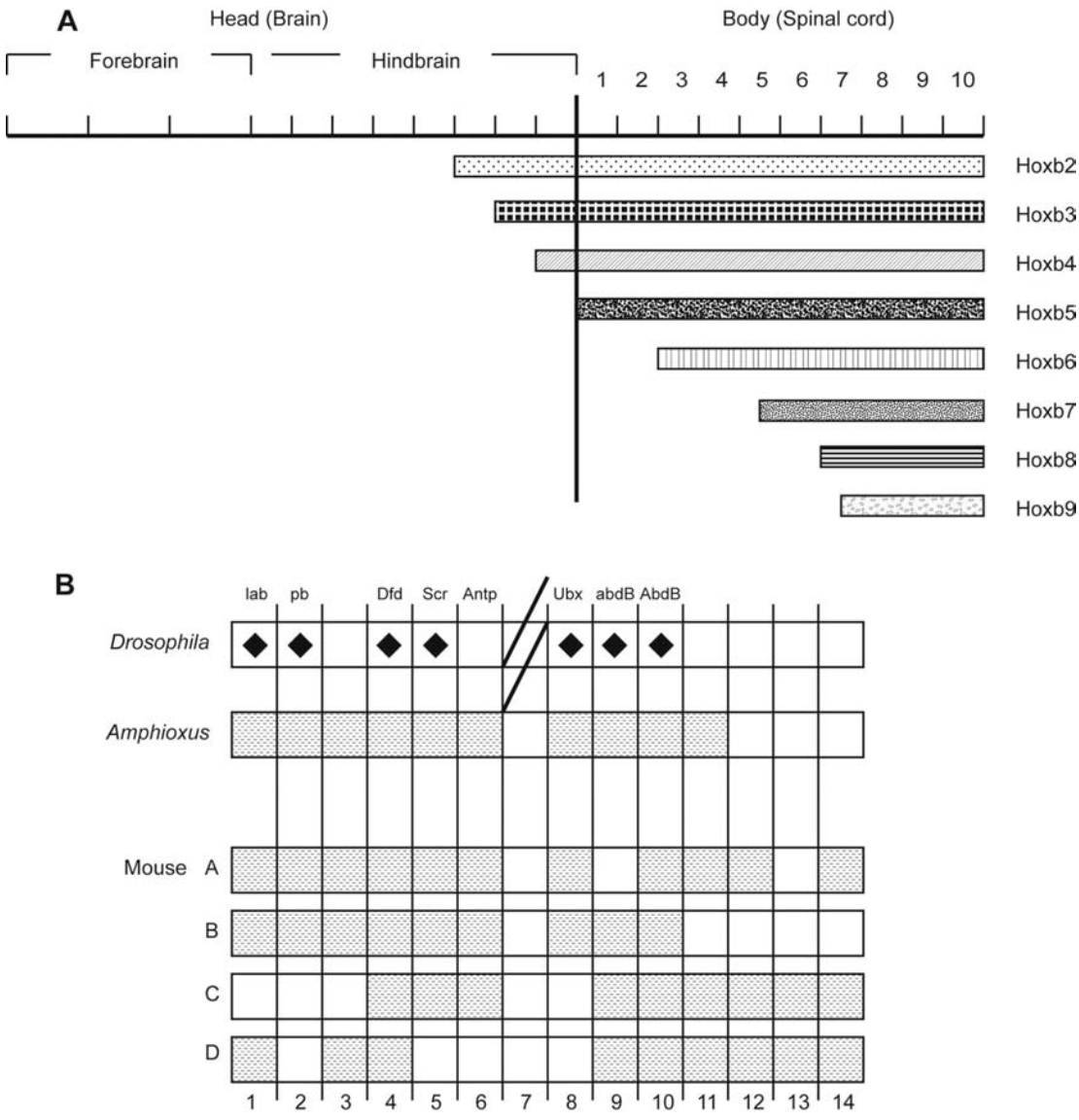
Although most of the cells of an embryo essentially stay put, obey instructions, and follow an orderly pattern, one population of cells, especially active in the head region, undertakes rather unexpected behavior: they begin to migrate around the body. These are called the neural crest cells (Fig. 2.8J). They are formed just where the embryonic ridges meet and touch, so they are ectodermal in origin, but they migrate into mesodermal or endodermal structures to reach their destinations. Here they initiate the development of a whole range of structures that turn out to be unique to vertebrates. The evolution of this highly active tissue probably accounts for the development of vertebrates as a diverse and successful group of animals. Neural crest initiates the jaws, the gill arches (including the hyomandibula), the trabecular cartilages of the braincase, the sensory capsules housing the sense organs, the sensory placodes that form the nasal, optical, ear-related sense organs and lateral lines, pigment cells, and, acting in concert with mesoderm and normal ectoderm, the teeth, scales, and dermal bones. They also form important structures around the heart.

The difference in origin between dermal and endochondral bone is important, as is the difference between bone formed by neural crest and that formed by mesodermal tissue (all dermal bone is neural crest in origin, but not all neural crest–derived bone is dermal). Their different roles and fates in evolution will become evident as the story of the origin of tetrapods unfolds.

## *Hox* Genes

Some of the insights into changes occurring during the fish–tetrapod transition have come not from fossils or from studies of embryonic development in modern animals, but from discoveries at an even more fundamental level of organization: the genes. Studies of developmental genetics can now be integrated with those of phylogeny and paleontology to reveal a whole realm of new ideas and interpretations. Reference will be made to some of these in Chapters 6 and 10, so at this stage, it is necessary to introduce some of the terminology and explain the concepts (Fig. 2.9A, B). More details will be found in textbooks on developmental biology, such as those mentioned above.

Among the most far-reaching discoveries of the past two decades has been the existence and function of homeobox genes. These are genes




that coordinate some of the most basic processes during the early development of almost all organisms. They determine such basics as front-to-back and top-to-bottom axes of embryos, and the order and position in which certain organs and structures appear. These genes occur on a particular chromosome (or chromosomes), like beads threaded on a string, and some of them are known as *Hox* genes. The genes themselves appear to be related to one another biochemically, but more surprising is that the order in which they occur corresponds to the order in which their effect is seen (technically, the order in which they are expressed) in the animal. For example, genes which occur at the front end of the chromosome (known as the 3-prime or 3' end) have their effect mainly at the front end of the animal, while those at the back (known as the 5-prime or 5' end)

have their effects further posteriorly. Figure 2.9A shows how members of the *HoxB* cluster act in sequence along the head and body, in the same order as they appear on the chromosome.

It has turned out that most animals have one or more clusters of such genes, and plants too have comparable (though not necessarily homologous) ones. Among animals (though only a few have been studied in detail, these genes have been found in a wide variety of invertebrates as well as vertebrates), the genes making up these sequences can be equated quite closely from one animal to another, and groups with similar structure and function have been given names or numbers. Vertebrate *Hox* genes are made up of around 13 groups. Each group is given its own number so that, for example, *Hox6* in a vertebrate can be compared with its equivalent in a worm or a fly (Fig. 2.9B). These are known as paralogue groups. Quite often, similarly positioned paralogue groups have comparable functions in different animals, even those not very closely related. For example, the instruction "make legs" uses a similar paralogue group in the fly *Drosophila* and in tetrapods. The implication is that the genetic instructions go far back in animal evolutionary history at least to the most recent common ancestor of insects and vertebrates, which cannot be more recent than about 600 million years ago.

Most organisms only have one such cluster of *Hox* genes, but during the evolution of vertebrates, some extraordinary events took place resulting in duplication of the *Hox* string. All modern jawed vertebrates have at least four copies of the string (e.g., mouse, Fig. 2.9B), while some, like zebra fish, have up to seven. The lamprey, a primitive jawless vertebrate, has only three sets (Sharman and Holland 1998), and one possibility is that there were some duplication events that increased the number of sets in the history of jawed vertebrates (Holland and Garcia-Fernàndez 1996; Cohn 2002). Surprisingly, it has recently been discovered that hagfish have up to seven duplications of one paralogous group, though fewer of others, and some appear to be missing (Stadler et al. 2004).

There have also been duplications of the individual genes. It looks as though the duplications have meant that while one set carries out its original function, the new set can go on to acquire new ones without disrupting the development of the animal. This might have allowed more rapid and more profound evolutionary events to have occurred than would otherwise have been possible. In mammals and birds, because of these additional duplications within each set, the four sets each differ very slightly from one another and they are given letters to distinguish them: *HoxA*, *HoxB*, *HoxC*, and *HoxD*. Each set has its own subtly different paralogue groups—*Hoxa13* is different in structure and function from *Hoxb13*, for example. Alongside gene or cluster duplication, sometimes genes have been deleted during the process of evolution.

Each gene makes the instructions for the production of a specific protein whose presence can be detected, by means of several different techniques, in the embryonic animal. It is detection of these proteins that makes it possible to work out the order and position in which the genes

are expressed. There are many other subtleties to the system, however, because whether the products of the *Hox* gene are expressed at any particular point depends on the interplay of several other chemicals. These may be other proteins, such as those known as transcription factors, or more simple chemicals called morphogens. Details of how these work is beyond the scope of this book but may be found in any modern text on developmental biology. As will be seen, it seems to be changes to the *Hox* genes that have been largely influential in evolutionary events such as the acquisition of limbs with digits.

## How to Turn a Fish into a Tetrapod

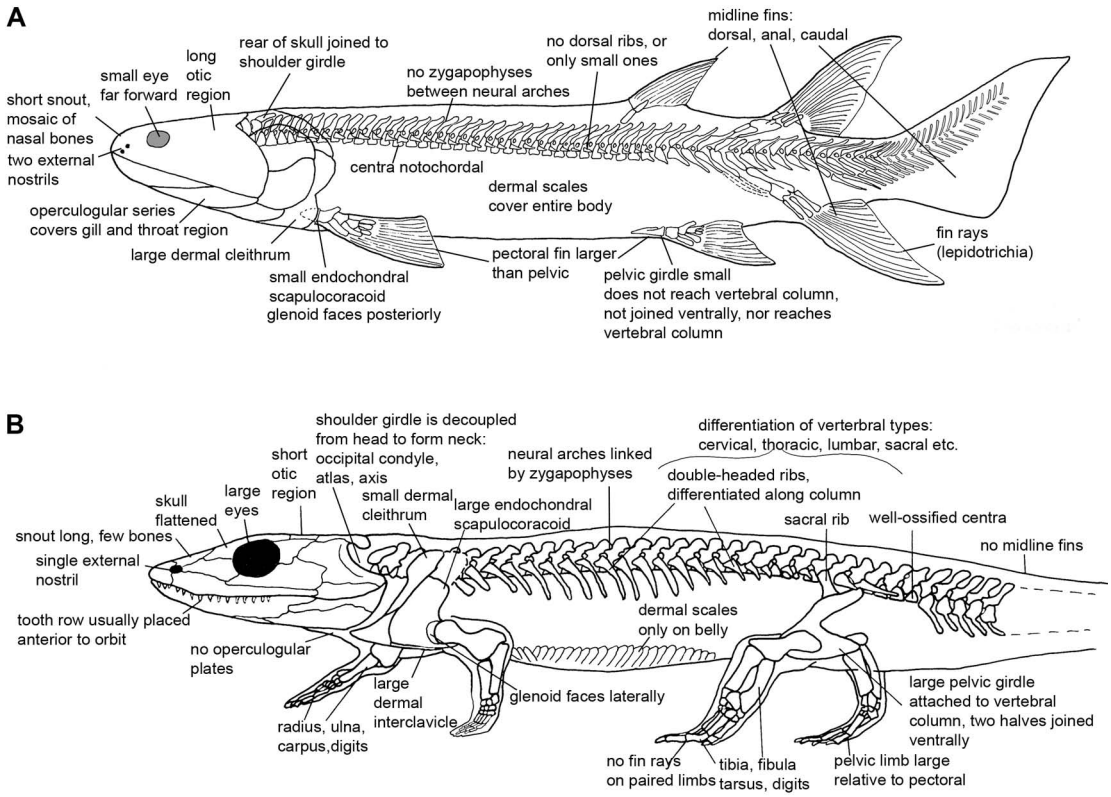
In the following section, the basic features of a fish skeleton are compared with those of a tetrapod to see what modifications were made during the transition. The contrasting features of a fish such as *Eusthenopteron* and a tetrapod such as the Devonian tetrapod *Acanthostega* (see Chapter 5) or the early tetrapods *Dendrerpeton* or *Pholiderpeton* (see Chapter 9) can be used to illustrate each end of the spectrum encompassed by the fish–tetrapod transition.

Not surprisingly, many of the characters that show the most difference in the comparison between fishes and tetrapods are those concerned with locomotion, and the contrasting needs of movement in water and on land. However, by no means are all of the differences connected with locomotion and support, nor are the most profound changes associated with the postcranial skeleton. Some of the most important differences between fishes and tetrapods lie in the skull structure and have to do with the related needs of breathing and feeding. Other differences are harder to account for and may result from some unknown mechanical, behavioral, or genetic reorganization.

Figure 2.10 summarizes the differences between a sample fish skeleton (similar to but not actually *Eusthenopteron*) and a tetrapod such as the Carboniferous *Dendrerpeton*. Some of these changes took place in a coordinated way and are interdependent, but for others, timing and sequence remain unknown. These will be discussed in later chapters. The anatomy of *Eusthenopteron* is based on Jarvik (1980), and that of *Dendrerpeton* on Holmes et al. (1998). In some cases, comparisons are made between a *Eusthenopteron*-like fish and the early tetrapod *Acanthostega*, based on the work of the author, and of Coates (1996).

### Skeletal Changes to the Skull and Shoulder Girdle

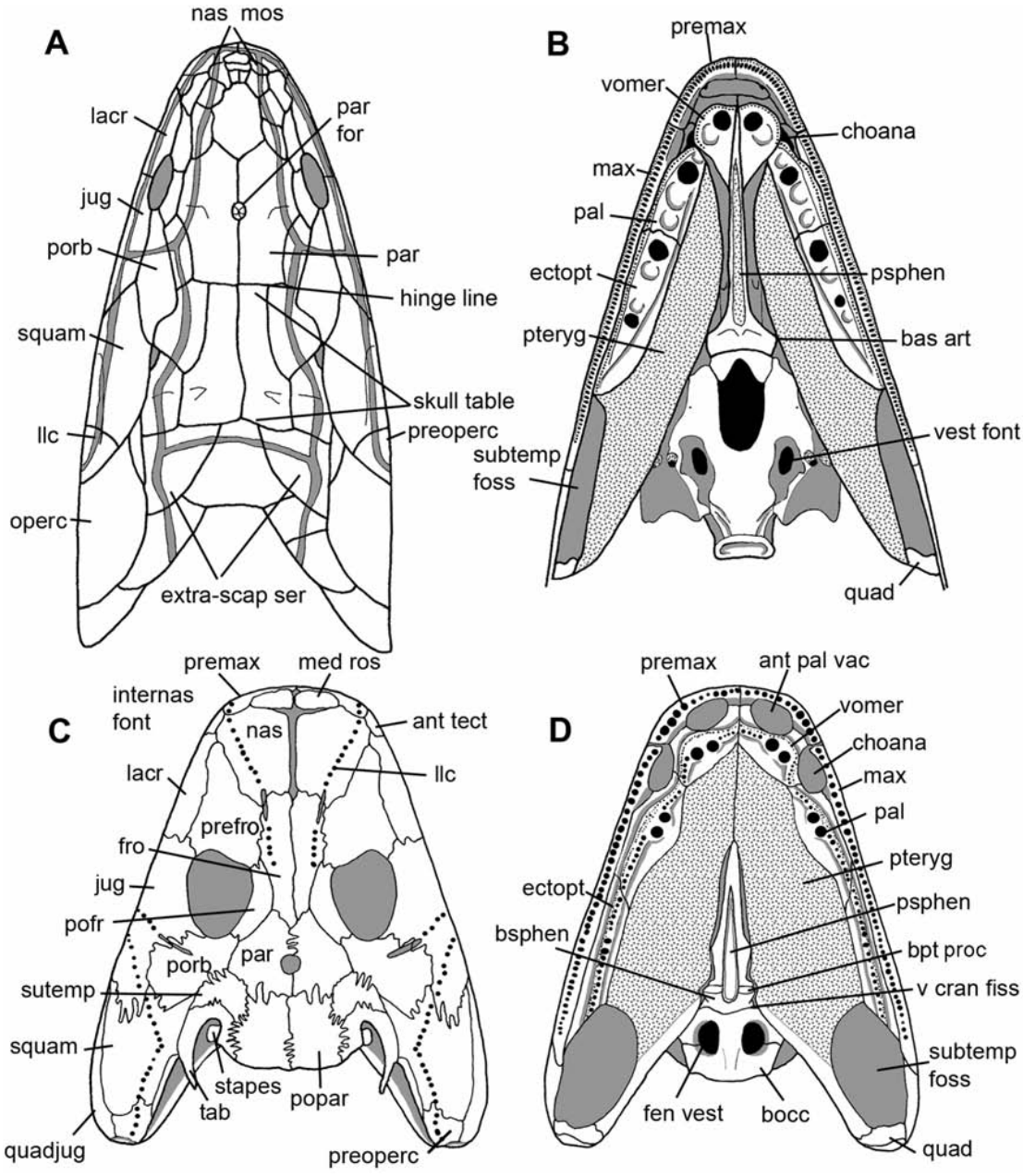
Some of the changes that are seen in skull construction are obvious, but some are subtle and involve changes in proportion. Figure 2.11 shows the skull of *Eusthenopteron* compared with that of the Devonian tetrapod *Acanthostega*. Probably the most obvious differences concern the bones covering the gill chamber and throat region in fishes, the operculogular series. This whole series was lost in tetrapods. It is tempting to think that the loss was related to abandonment of gill breathing, but for reasons put




**2.10.** Skeleton of (A) a fish (similar to *Eusthenopteron* or *Osteolepis*) compared with (B) a tetrapod such as *Dendrerpeton,* with the major differences highlighted.

forward in later chapters, this is not necessarily the case. However, it was an important change because it occurred in conjunction with a suite of others. Although it is not yet clear which of these changes occurred first, new finds are beginning to suggest the order of appearance of some of them.

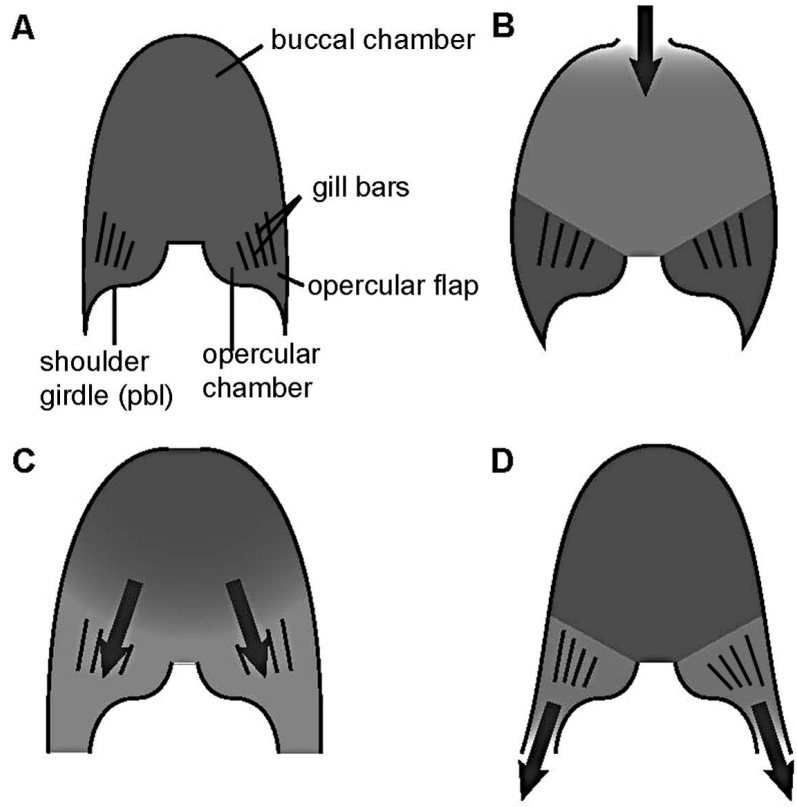
The opercular series plays a key role in the operation of the pump mechanism by which a fish ventilates its gills—that is to say, in the series of movements that cause water to pass across the gills to oxygenate the blood. It is appropriate here to describe this mechanism because it is one of the functions of the skeleton that changes during the fish–tetrapod transition. Understanding this mechanism will help to explain some of these changes as they are described later. The pumping mechanism is powered by movements of the mouth (buccal) chamber and opercular system, and is known as the buccal pump. It operates in distinct phases, illustrated in Figure 2.12. Flexible joints between the skull roof and cheeks in ray-finned fishes, and as was also true of primitive lobe-finned fishes, facilitate expansion of the buccal chamber and opercular chamber as they expand and contract, slightly out of phase with each other. This permits pressure differentials to exist between the buccal and opercular chambers, causing water to move from one to the other. In tetrapods, gill breathing is first reduced and then lost altogether in adult, metamorphosed amphibians, and all amniotes. To begin with, lungs were




**2.11.** Skulls of *Eusthenopteron* in (A) dorsal and (B) ventral views and *Acanthostega* in (C) dorsal and (D) ventral views compared to show some of the contrasts.

ventilated by a version of the buccal pump that used the hyoid skeleton, as in modern amphibians, but eventually, it is taken over by the body wall muscles. The hyoid skeleton is converted for other uses.

As well as losing the operculogular series, the tetrapod skull lacks another series of bones found in fishes. That is the series called the extrascapulars and supracleithrals, which in fishes join the dermal shoulder girdle to the skull roof at the back. The extrascapulars are the bones at the back of the skull table—usually three, as in *Eusthenopteron*—and the supracleithrals are the bones that lie above the cleithrum in the shoulder

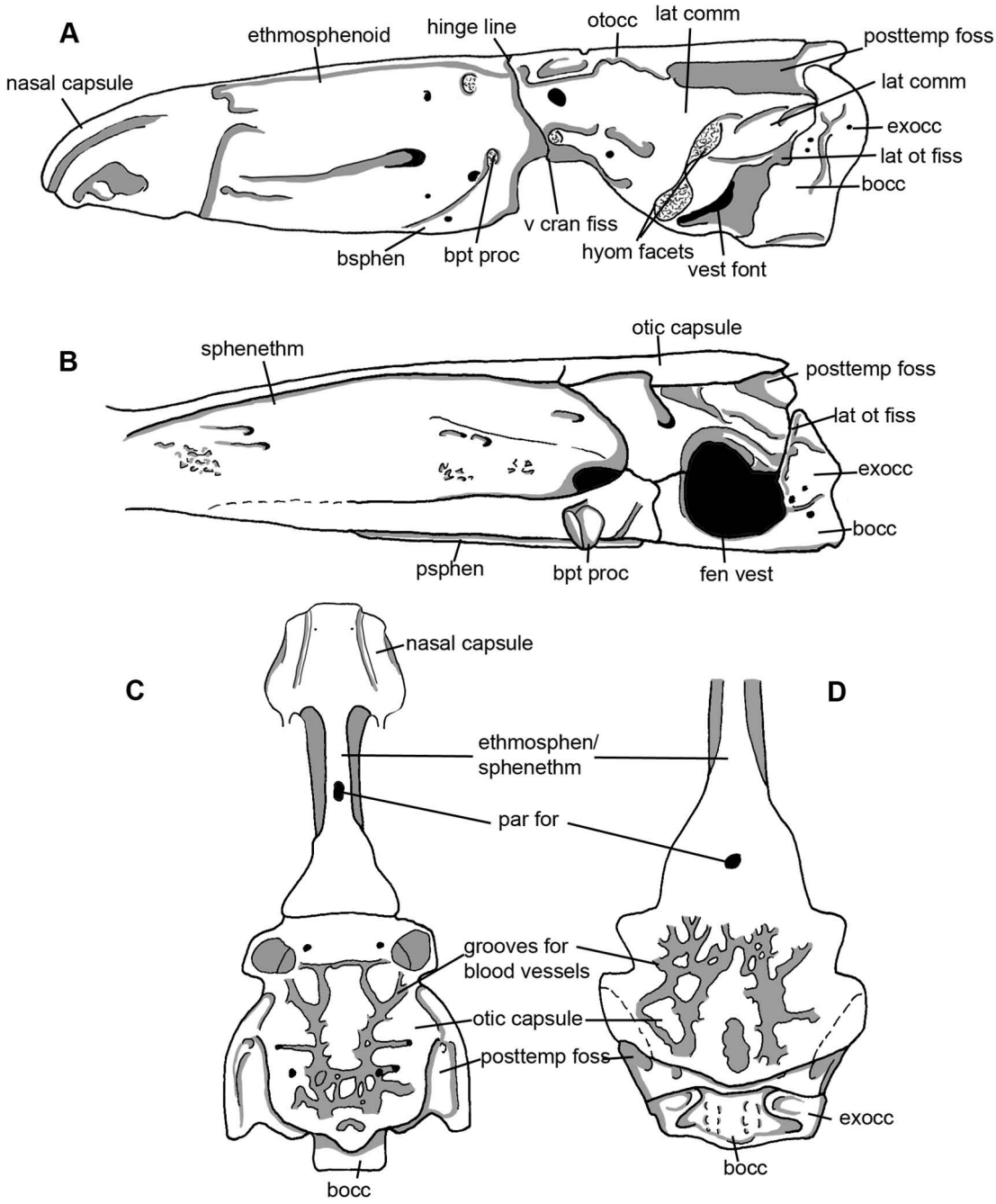



**2.12.** Operation of the buccal pumping mechanism. Diagrammatic horizontal sections through a fish's buccal and opercular chambers. (A) System at rest. (B) Mouth opens and buccal chamber expands, lowering the pressure, so water enters the mouth. Pressure in the opercular chamber is also lowered, and the spaces between the gill arches expand. (C) Opercular chamber opens, while the mouth begins to close, raising the water pressure and forcing water through the gill curtain. (D) Mouth closes and buccal chamber contracts, forcing the remaining water out from the opercular chamber, and the system comes to rest again. Postbranchial lamina (pbl) of the shoulder girdle forms the seal against which the opercular flap closes. *Illustration by J.M.*

girdle. In *Eusthenopteron*, these bones link to one another at the back of the head (Figs. 2.1, 2.4, 2.11). Loss of the operculogulars, extrascapulars, and supracleithrals results in a space being made between the suspensorium and the shoulder girdle. In effect, the head is no longer supported by the shoulder girdle, so the vertebral column and its muscles must do the job instead. Thus tetrapods have necks.

Construction of a neck itself involves a number of changes. Muscles that hold the head up must have a solid foundation for their origin. The back of the tetrapod head became gradually adapted to provide anchorage and space for these muscles to attach. One of the threads that this book will follow is that of how changes to the back of the skull took place in tetrapod evolution. It did not happen all at once. The neck muscles require strong insertion points along the spine, and elaboration of the neck vertebrae is another such gradual change to be seen in tetrapod evolution. Some of the muscles supporting the head and joining it to the vertebral column insert into pockets at the back of the skull called the posttemporal fossae (Fig. 2.13). The neck joint or occiput, built to allow the head to move freely on the vertebral column, was yet another feature whose evolution will be followed, and it too involved gradual changes to the back of the skull and the front of the vertebral column.

Other changes to the braincase are associated with the development of a neck. Running through the vertebral column and into the braincase




**2.13.** Braincases of *Eusthenopteron* and *Acanthostega* compared. (A) *Eusthenopteron* in left lateral view. (B) *Acanthostega* in left lateral view. (C) *Eusthenopteron* in dorsal view. (D) *Acanthostega* in dorsal view. *Based on Clack (1998c).*

of a fish is the notochord. It helps the body to return to shape after the bending produced during swimming by the muscles of the body wall. In a fish's vertebral column, the notochord is sheathed by the serially arranged centra, and it runs forward right into the braincase through an opening below the foramen magnum. In most tetrapods, the notochord is replaced by bone in each centrum and no longer runs into the braincase. This process can be traced in the transition between fishes and tetrapods,

because like the evolution of the neck joint, it occurred gradually. Figure 2.13 provides diagrams of the braincase of *Eusthenopteron* compared with that of *Acanthostega*.

Perhaps associated with this change are a number of others concerning the braincase. One is the elimination of the hinge found between the front and hind parts of the braincase seen in *Eusthenopteron*. Most current estimates of the phylogeny of these animals show that this feature was lost among advanced tetrapod-like fishes. In fishes, the dermal parasphenoid bone underlies only the front (ethmosphenoid) part of the braincase. In tetrapods, however, the former hinge line was sealed by the elongation of the dermal parasphenoid to underlie the back part of the braincase as well as the front. Along with sealing of this braincase hinge went the elimination of the hinge across the skull roof, as can be seen by comparing the dorsal views of *Eusthenopteron* and *Acanthostega* in Figures 2.11 and 2.13.

Moving forward in the skull, a number of changes are seen in the part that lay behind the eyes. As a general statement, the back part of the fish's skull is longer than the equivalent part of an early tetrapod's. This applies both to the braincase and the skull roof. If a series of early tetrapod skulls from the Devonian to the Permian were taken and assembled in chronological order, a trend of shortening of the back of the skull can be found. The reason for this appears to be that the otic capsules, which lie under the skull table, get gradually smaller in tetrapods relative to the rest of the skull. The beginnings of this trend can be seen even in very early tetrapods, though the reason for it is less clear. More details of this process and possible reasons for it are put forward in Chapter 6.

One of the more mysterious changes that took place in the braincase was possibly associated with this shortening of the otic region. The part where the hyomandibula attached to the otic capsule in most fishes, called the lateral commissure in *Eusthenopteron*, disappeared in tetrapods (Fig. 2.13). The head of the hyomandibula came to occupy the resulting hole, inserting instead into the sidewall of the braincase. At this point, the bone becomes known as a stapes, and the hole into which it inserted is the fenestra vestibuli.

The hyomandibula in fishes performs several jobs. From its articulation on the braincase wall, this long, flattened bone runs down the back of the palatoquadrate and supports the bones that form the roof of the mouth. The roof of the mouth has to be moveable to accommodate the expansion and contraction of the buccal cavity that occur during the fish's breathing cycles and in the movements of its feeding mechanism. These movements are controlled by the hyomandibula. This bone is also attached to the gill covers, the operculogular series, that also operate during the breathing cycle, so the hyomandibula also coordinates their movements with those of the palate. The palatoquadrate also joins to the braincase at other points: at the front and around the middle of its length at the basal articulation. However, these joints are all mobile. In fishes, then, the palatal bones are only loosely attached to the braincase,

chiefly through the hyomandibula, and this type of skull is described as hyostylic.

In many later tetrapods, this kind of flexible skull construction is eliminated, and the joints become firm and sutured together. The palate has its own firm attachments to the braincase and skull roof bones, so it does not have to be hung from the hyomandibula. This may be one of the reasons why the stapes in tetrapods is so much smaller than the hyomandibula of fishes. Tetrapod skulls with this firm kind of construction are described as autostylic. Instead of disappearing, the hyomandibula took on a new role in tetrapods: that of a hearing ossicle. This change did not happen quickly or all at once, and Chapter 10 describes how it may have happened in different tetrapod groups.

This change ties up with others that occurred in the branchial system. Gill breathing was finally lost in tetrapods, and the gill arches became not only reduced in number but in size. However, the bones that support the gill arches and the muscles that move them did not disappear. Instead, they were redeployed in the formation of the tongue supports and musculature. Tetrapods, once they became terrestrially feeding organisms, could not use the water to support food while they grasped it, or use its force in suction feeding as many fishes do. Instead, that uniquely tetrapod invention, the grasping and manipulating tongue, was built from the former gill arch components. Probably this could only occur once gill breathing had been entirely lost, and it may explain why modern amphibians use such a different tongue operational mechanism from that in amniotes. Amphibians retain the gill system for breathing in juveniles.

At the back of the skull of a fish such as *Eusthenopteron*, the spiracle opened into the apex of the slot known as the spiracular notch or cleft. Most early tetrapods, though not all, had a rounded or V-shaped embayment at the same location in the skull, which has been variously called the otic notch, the spiracular notch, and the temporal notch. The function of this embayment has been debated by paleontologists for years, and the story behind it is tied up with the change from gill to air breathing and in the function and form of the hyomandibula/stapes. It is set out in more detail in Chapters 6 and 10.

Although the back of the skull was generally shorter in tetrapods than in comparable fishes, in early tetrapods, the snout appeared to grow longer, resulting in the eyes appearing further back. One associated consequence was that more of the tooth row came to lie in front of the eyes in tetrapods compared to its position in fish. The eyes also seem to have increased in size and became positioned closer to the top of the head in early tetrapods than in fishes. Proportional changes like these are difficult to explain and are hard to separate from each other. They may be linked with changes to both sensory and feeding requirements.

Lengthening of the snout seems to have been associated with stabilization of the bone pattern of the front part of the skull and a reduction in the number of component bones. Where fishes had a mosaic of small bones in the nasal region, tetrapods evolved a single pair of nasal

bones, with remnants of this mosaic remaining only in the earliest ones. These—the lateral and median rostrals and anterior tectal bones—were lost early in tetrapod history.

Other, more subtle changes, such as those to the cheekbones, the internal and external nostrils, the spiracular notch, the dentition, and the aquatic pressure sensory system called the lateral line, which occurred during the fish–tetrapod transition, are best seen by studying particular fishes and tetrapods in context, as shown in later chapters.

Profound changes to the shoulder girdle occurred during the fish–tetrapod transition, associated with a shift in emphasis of the role which the complex played, and these can be seen in Figure 2.6. In fishes, the shoulder girdle is integral with the skull, continuing the profile of the skull back along the body in a smooth line, producing the hydrodynamic torpedo shape typical of many fishes. It consists mainly of dermal elements, the supracleithral bones, the cleithrum itself, the clavicle, and a small ventral midline interclavicle. This series of bones attaches to the skull at the top via the lateral extrascapular bones and forms a hoop around the body. Under the body, muscles run from the midline of the shoulder girdle to the gill arches and jaws to control their movements. Along the anterior edge of the cleithrum and clavicle, a groove and an internal flange called the postbranchial lamina (Fig. 2.12) (see also Chapter 5) not only helps direct water flow out of the gill chamber, but also helps to form a seal against which the operculum closes during breathing movements.

A small endochondral scapulocoracoid is wedged on the inner surface of the cleithrum, bearing a small, backwardly facing articulation point for the fin. In *Eusthenopteron*, the scapulocorocoid is a small tripod of bone with its three "legs" attached to the cleithrum.

In almost complete contrast, the shoulder girdle of all but the most primitive tetrapods consists mainly of an enlarged scapulocoracoid (Fig. 2.6), which later in tetrapod evolution may be divided into two or three separate ossifications: the scapula above, and one or two coracoids below. The scapular portion is clasped along its anterior margin by a slender dermal cleithrum, although this too is lost in most later tetrapods. The clavicle remains in most tetrapods. In early ones, it consists of a broad triangular ventral plate whose apex, positioned at the side of the body, is produced into an upwardly projecting prong. This sheathes the coracoid portion of the girdle and contacts the slender cleithrum. The dermal interclavicle may be a large shield-shaped plate of bone or a rather more slender T-shaped one, but in early tetrapods, it is always larger than that of the corresponding bone in fishes. The scapulocorcoid in tetrapods bears a large concave articulation surface for the limb, which faces outward from the body.

The shoulder girdle in fishes is mainly concerned with hydrodynamics, but it also provides anchorage for gill- and jaw-moving muscles. Bearing the pectoral fins seems a relatively minor role. In tetrapods, bearing the limbs and providing anchorage for the muscles that move them are

the most important jobs. The shoulder girdle is detached from the skull, which allows the limbs and the head greater freedom of movement than in fishes. Correspondingly, the outer dermal components are larger in fishes, while in tetrapods, these are reduced in favor of the inner endochondral elements. The shoulder girdles of the earliest tetrapods are not obviously halfway in structure between those of fishes and those of later tetrapods, but rather have some unique and some unexpected characters.

## Skeletal Changes to the Pelvic Girdle, Limbs, and Axial Skeleton

In the rear half of the animals, one of the biggest structural contrasts between a fish and a tetrapod lies in the size and function of the pelvic girdle. In most fishes, exemplified by *Eusthenopteron*, the pelvis is a relatively small simple ossification, which is anchored in the body wall without any bony connection to the vertebral column. In *Eusthenopteron* it consisted of a single pair of boomerang-shaped elements orientated apex downward, which did not meet each other at the midline—there was no symphysial junction. The pelvis bore the articulation for the fin at about the apex of the boomerang. These can be seen in Figures 2.4, 2.7, and 2.10.

Even in the earliest known tetrapods, the pelvic girdle had become far different in structure from that of a fish. It was a large robust element with a long ventral edge, along which both halves of the girdle met to form the pelvic symphysis. The articulation point for the hind limb, the acetabulum, was longer than the head of the femur, to allow movements of the hind limb. Most characteristically, there were long processes dorsally, internal to which one of the ribs articulated to form a sacral joint. Muscles to move the legs and tail inserted on these processes and on the enlarged platelike region below the acetabulum. The region surrounding the acetabulum was strengthened by various buttresses. In tetrapods from the Carboniferous onward, each half of the pelvic girdle consisted of three separate ossifications: the ilium dorsally, to which the sacral rib attached, and below it the pubis anteriorly and ischium posteriorly (Fig. 2.7). These regions were not separately distinguishable in the earliest tetrapods.

The differences in girdle structure between fishes and tetrapods reflect the differences in limb construction and differences in the emphasis placed on the different parts of the body used in locomotion. In fishes, the main muscles used for propulsion are those of the body wall, attached to the axial skeleton. The axial skeleton is flexible and the musculature complex. In tetrapods, the emphasis shifts to the appendicular skeleton—that is, to the limbs and girdles—for propulsion. The limbs and girdles are correspondingly enlarged, and their musculature more differentiated, while the body-wall musculature is relatively reduced and the axial skeleton is stiffened. The neural spines bear articulations one with another, called zygapophyses (Fig. 2.5), and provide anchorage for

substantial ribs. Fishes' ribs are usually thin and flexible, and true zygapophyses are absent. The vertebral centra in fishes are relatively poorly ossified and often remain hollow cylinders around the notochord; in tetrapods, they become more solidly constructed and often completely replace the notochord. In terrestrial tetrapods, this construction allows the vertebral column to function as bridge between the girdles, keeping the body off the ground.

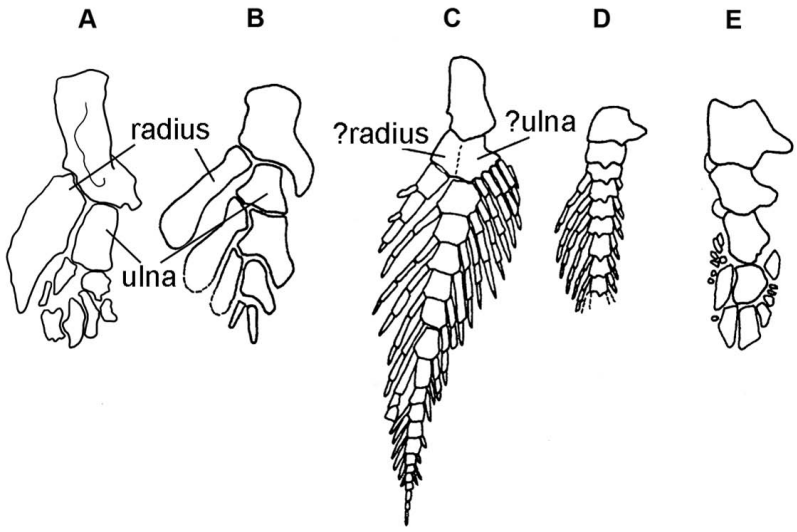
In fishes, where much of the propulsion comes from the tail and body, the fins are largely used only for steering and braking. Usually the pelvic fins are small, and in fossil lobe-finned fishes, they were usually smaller than the pectorals. By contrast, in unspecialized tetrapods from the Paleozoic onward, the hind limbs provide most of the thrust and are larger than the forelimbs. That was not the case in the very earliest tetrapods, for reasons to be explored later.

The feature that many people would pick to distinguish fishes from tetrapods is that which gives the name to the group: the structure of the limbs and the possession of digits. As set out in the previous chapter, there are some technical problems with this, but it is appropriate here to consider the similarities and differences in structure between the paired appendages of fishes and tetrapods.

The fore and hind sets of paired fins of a lobe-finned fish such as *Eusthenopteron* consist of similar bones. Figure 2.14 shows the pectoral fin skeletons in a range of lobe-finned fishes to illustrate their common features as well as their differences. In common is the single element called the first axial radial, which attaches to the girdle, identifying the animal as a sarcopterygian. In tetrapods, these are called the humerus and femur in fore- and hind limbs, respectively.

From the other end of this element, further elements arise and articulate with it, forming a chain called the metapterygial axis. In *Eusthenopteron* and tetrapods, there are two elements that articulate with this first axial radial. In tetrapods, these are known as the radius and ulna in the forelimb, and tibia and fibula in the hind limb. In *Eusthenopteron*, the more posteriorly situated of these paired elements in turn gives rise to two more. The precise pattern varies among lobe-fins. Fins of the various lobe-finned fish groups differ more in structure further along the fin than they do nearer the base. Some groups, such as lungfishes, have elongated paired fins supported by a long series of segments, each with a branching radial springing from it. In most lobe-fins, the branches occur mainly on the anterior (leading) edge of the fin and are called preaxial radials. In lungfishes, both pre- and postaxial radials are found. In early members of the line leading to tetrapods, the fin skeleton is shorter but branches more profusely (Fig. 2.14).

The first axial radial—the humerus—of the forefin has flanges and foramina for muscle attachments and passageways for nerves and blood vessels. Several of these features are common to the humerus of *Eusthenopteron* and those of early tetrapods. On the uppermost surface of the



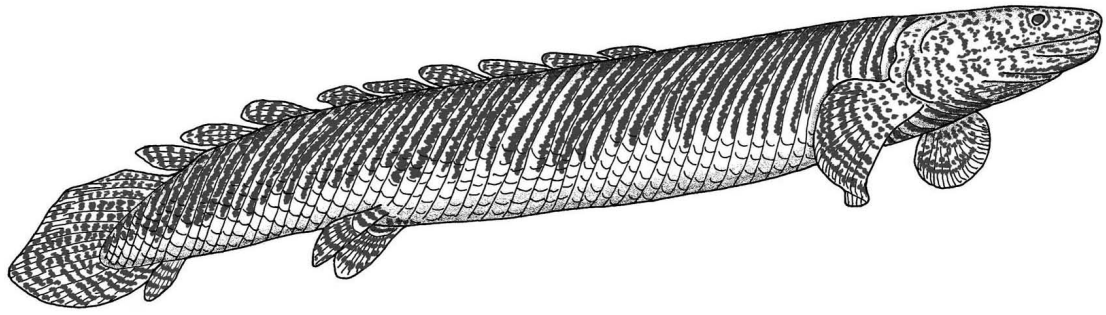

**2.14.** A selection of lobe-fin pectoral fin skeletons. (A) The elpistostegalian fish *Panderichthys*. Based on models in Boisvert et al. (2008). (B) The tristichopterid tetrapodomorph *Eusthenopteron*. (C) The Australian lungfish *Neoceratodus*. (D) The porolepiform *Glyptolepis*. (E) The coelacanth *Latimeria*.

bone is a ridge running most of the length of the bone, called the ectepicondyle. From it, muscles run to the radius. From about halfway along the length of the bone, growing from the posterior edge, is a flange called the entepicondyle, from which muscles run to the ulna. The muscles from these processes control movement of the lower arm or distal part of the fin. On the underside of the bone, there is a ridge called the ventral ridge, which in fish runs diagonally across most of the length of the bone from the humeral head to the entepicondyle. It is often pierced by a number of foramina.

Bounding the outer rim of the fish fin is a fringe of bony elements derived from the skin (and thus dermal in nature) called fin rays, or lepidotrichia.

The similarities in construction of tetrapod limbs and certain lobed fins lie in the first three skeletal elements. The pattern of a single element attaching to the body is common to all lobe-fins, whereas the more distal pattern in which this element gives rise to two more from its far end is characteristic of the line leading to tetrapods. Further along the fin skeleton, the resemblance breaks down. The divergence in skeletal pattern further away from the body seen among lobe-finned fishes is exaggerated in the contrast between fins and limbs.

In most tetrapod limbs, the two elements, ulna and radius or tibia and fibula, articulate distally with each other and with a series of blocklike bones connected by complex joint surfaces that allow much freedom of movement. These produce the characteristic elbow and knee or wrist and ankle joints (Fig. 2.10). They allow the ends of the limbs to be brought into contact with the ground at appropriate angles for bearing weight and transmitting thrust. At the ends of each limb, digits arise by sequential budding of a number of radial elements. More details of this will be found in Chapter 6.



**2.15.** *Polypterus bichir.* *Illustration by J.A.C.*

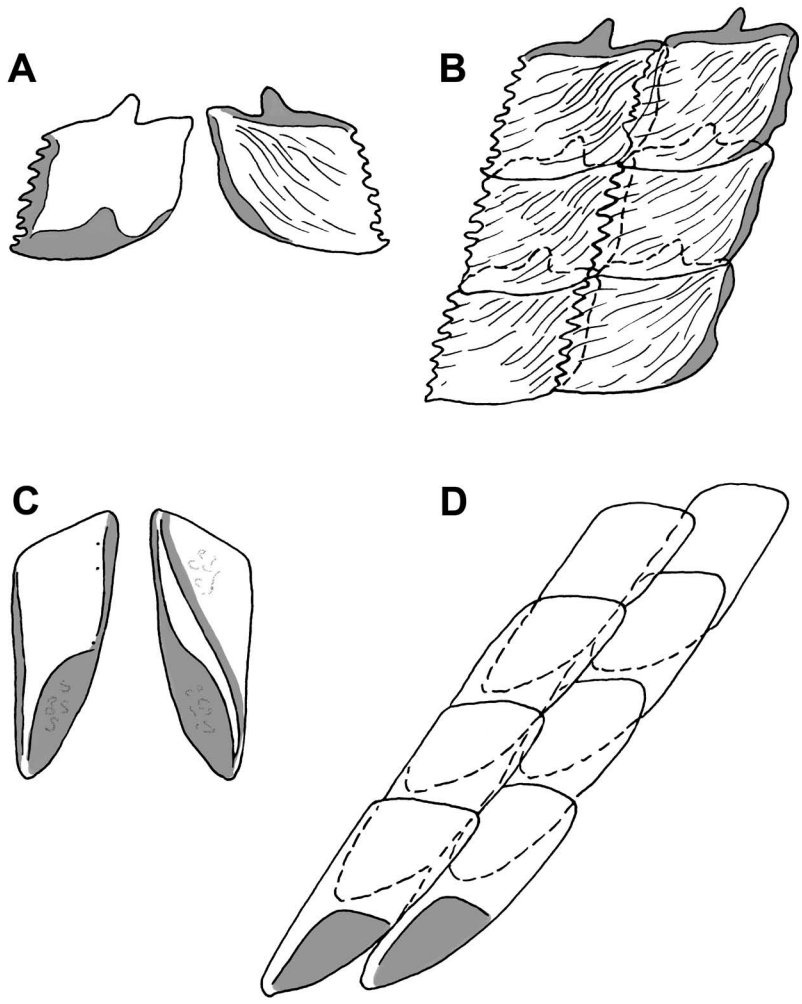
## Changes to Body Scales and Fin Rays

Two more kinds of structures need to be considered in the contrast between fishes and tetrapods. These are both formed from the dermal component of the bony skeleton and are, respectively, the body scales and the fin rays.

In fishes, scales are formed within mainly the middle layer of the skin, called the dermis, which is the part of the skin containing structures such as blood vessels, touch or pressure sensors, glands, and some superficial muscle tissue. In early lobe-finned fishes the scales were bony in texture, and in some species they were covered in shiny enameloid material matching the dermal bones of their skulls, to which the external layer, the epidermis, also contributed. The modern ray-finned fish *Polypterus* shows bony, enameloid-covered scales (Fig. 2.15) similar to those of many Paleozoic forms. In almost all modern fishes, however, the bony layer has been lost, leaving the scales only as thin proteinaceous sheets.

The scales in the early lobe-finned and ray-finned fishes were interlocked in diagonal rows that encompassed the body and met each other dorsally and ventrally at an acute angle (Fig. 2.16). Each row articulated with the one in front of and behind it, and along a line running down middle of each side of the body, each scale bore a segment of tube containing part of the lateral line organ.

In the early tetrapods, much of this scale cover was lost, especially those on the back, and the remaining parts were modified. The scales of the early tetrapods are known as scutes or gastral scales, and the flexible armor that they formed covered only the belly and parts of the sides. The gastral scales were bony but bore no enameloid layer. They can be oval, spindle, or rhomboid in shape, bearing an internal ridge and groove where each element articulated with the ones dorsal and ventral to it, but not with those either side of it (Fig. 2.16). The rows met ventrally in a forward-pointing V, except around the shoulders and interclavicle, where the orientation was reversed and the V pointed backward. Some early tetrapods are also known to have had dorsal scales, but these are usually rounded and tend to be much less well ossified, so they do not fossilize well. Some modern amphibians belonging to the group known as caecilians still retain vestiges of these primitive dermal scales. However,




**2.16.** Scales and gastral scales of fish and tetrapods. (A, B) Actinopterygians scales. (A) Internal (left) and external view (right). (B) Intercalating series. (C, D) Tetrapod gastral scales. (C) External (left) and internal (right). (D) intercalating series, with overlapped areas indicated by dotted lines.

gastral scales or scutes are not equivalent to the scales of modern reptiles. Because gastral scales in early tetrapods were dermal, they would have been covered by a thin layer of outer skin called epidermis. In modern reptiles, the scales are formed in the epidermis itself.

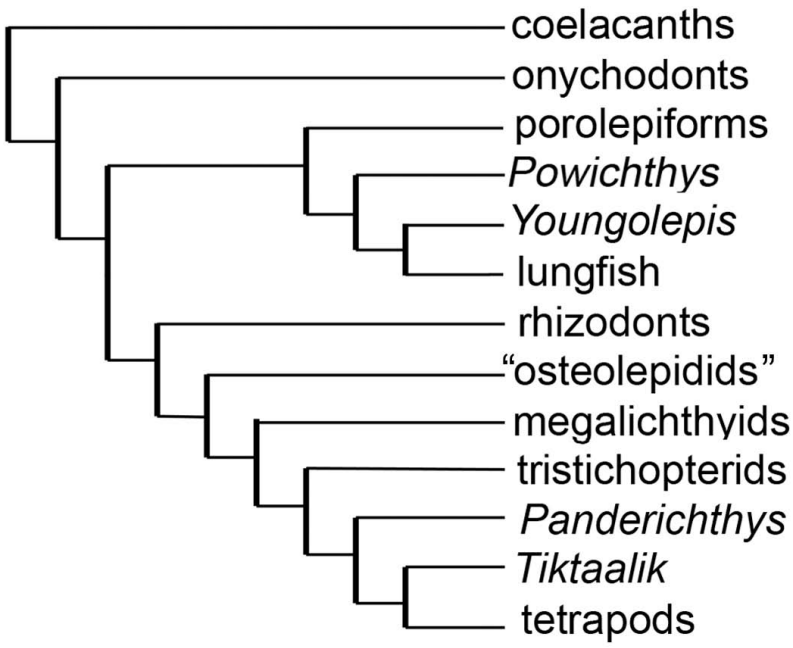
An ontogenetic sequence of scale morphology has been demonstrated in one group of early tetrapods, the temnospondyls (Witzmann 2007). Scales begin as relatively thin round elements, and during growth, they change to interlocking spindle-shaped scales that allow flexibility in the scale cover, then to a more rhomboid shape in which the interarticulations are more rigid. This sequence can be modified, and some taxa retain a juvenile morphology as a pedomorphic trait. Dorsal scales, if present, tend to retain the juvenile round morphology. Oval or spindle-shaped scales are also found in nontemnospondyl taxa, and similar growth patterns may be involved.

The fins of bony fishes are supported by dermal rays, which are essentially narrow, elongated scales forming a fringe suspending a thin web

of skin. In early lobe-finned fishes, narrow fringes of fin web surrounded each paired fin, the tail, an anal fin, and two dorsal fins. Dorsal and anal fins were additionally supported by a series of radials, the pattern of which varied according to the family. In tetrapods, almost all the fin webbing disappeared, along with all traces of dorsal and anal fins. The only remnants are seen in the two earliest known tetrapods, in which some tail fin web was still retained, and in a single specimen from an embolomere (see Chapter 9) in which supraneural spines have been found.



**3.1.** Cladogram of lobe-fins from Cloutier and Ahlberg (1997).



# Relationships and Relatives: The Lobe-Fin Family

# 3

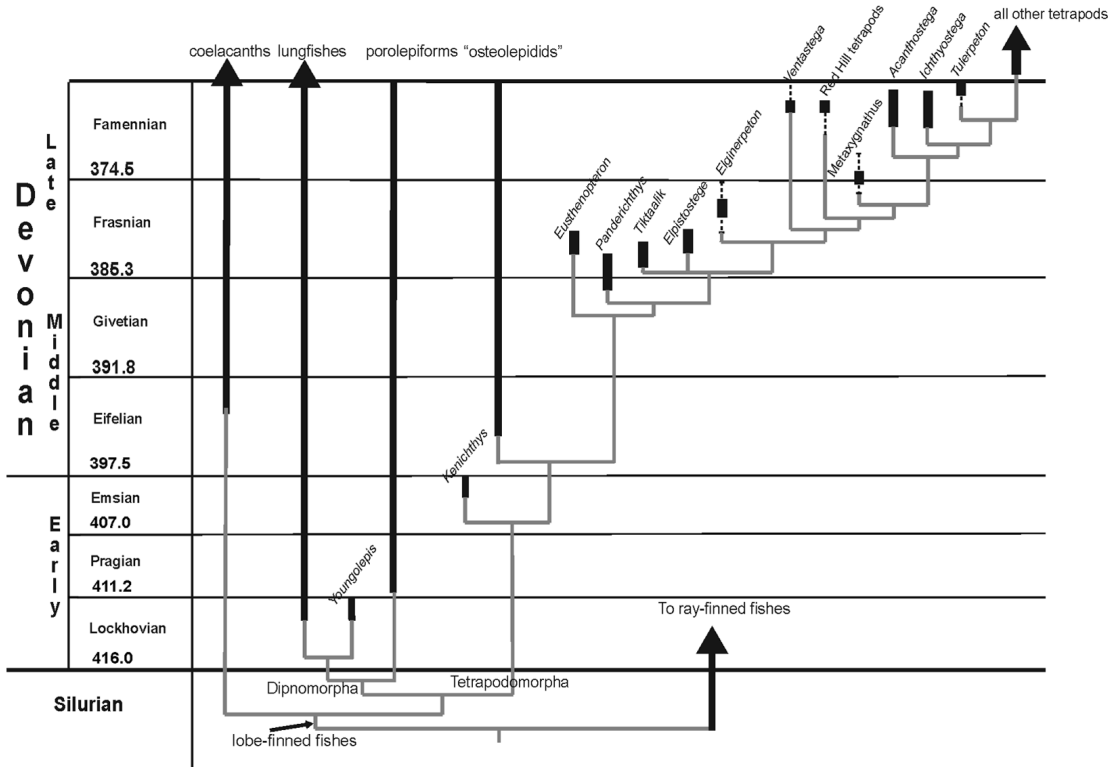
## Introducing the Lobe-Fins

This chapter introduces the tetrapods' closest relatives, explains how tetrapods fit into the scheme of relationships with other lobe-fins, and explores how ideas about the ancestry of tetrapods have evolved with changing perspectives.

There are a few characteristics of lobe-fins that distinguish them as a group, but the most conspicuous is the eponymous lobed fin, described more fully in Chapters 1 and 2, in which the paired fins are anchored to the respective limb girdle by a single bone. The structure appears to be a true shared, derived character of the group. Another shared feature is the possession of two dorsal fins, instead of the single one found in early ray-fins, and a third is the occurrence in the tail of a second series of fin rays growing above the body portion. This has enabled lobe-fins to evolve symmetrical tails without too much modification of the existing pattern, and they have done so in a number of separate lineages. The latter two features may after all be primitive for gnathostomes, but this is not clear. In addition, most early members of the lobe-finned group show an intracranial joint or hinge line. A hinge linked the front and back parts of the skull roof just behind the eyes, reflected in a matching hinge across the underlying braincase (see Chapter 2). The hinge line occurs at the point where the otoccipital portion of the braincase meets the ethmosphenoid dorsally, and the ventral otic fissure separates them ventrally (see Figs. 2.1, 2.3, 2.11, 2.13), an important landmark in building the vertebrate skull. The hinge itself is not seen in ray-finned fishes, and it is also lost from several of the lobe-finned groups independently, including tetrapods.

Most early lobe-finned "fish" were moderately sized animals. Although a few grew to enormous size, few small species are known, so it does not appear that there were lobe-finned equivalents of anchovies, for example. It is not at all clear why this should be the case. Early lobe-fins lived in both marine and freshwater conditions, but almost always in relatively shallow water.

Today there are few lobe-finned "fishes" remaining, as distinct from tetrapods (also lobe-fins). The surviving "fish" species are the coelacanth *Latimeria* and three genera of lungfish. In the Paleozoic, however, lobe-fins were dominant fishes for many millions of years, both in number of species and in size. Several lineages died out at the end of the Devonian, though some survived into the Early Permian. By the end of the

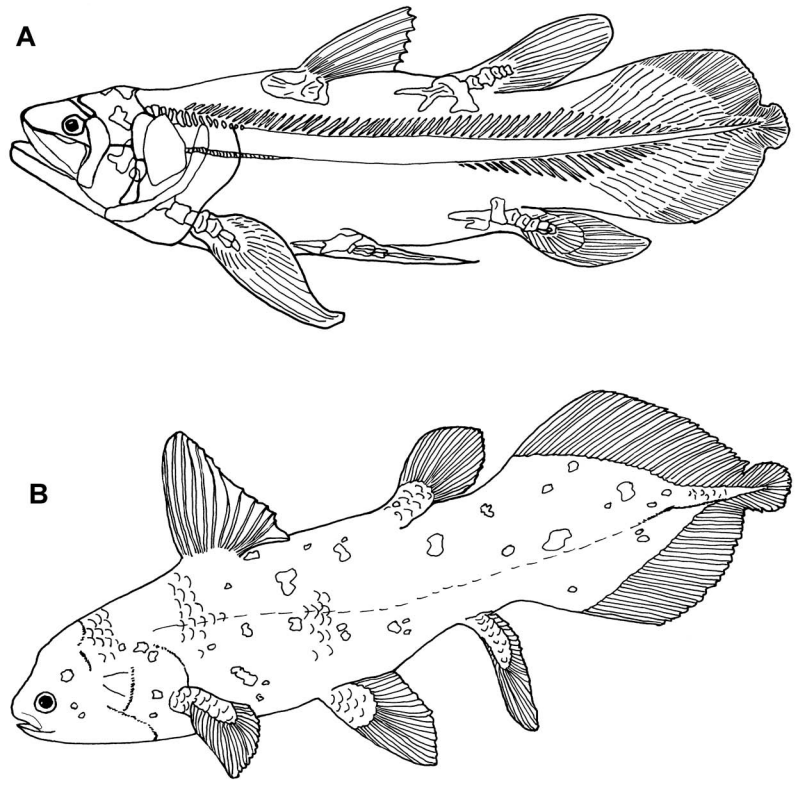



**3.2.** Timescale of the Devonian period with a phylogeny of lobe-finned vertebrates superimposed to show the times of origin and relationships of the main groups. *Dates from Gradstein et al. (2004).*

Paleozoic, only the lungfishes, coelacanths, and tetrapods remained, and the ray-finned fishes took over dominance of the water.

Figure 3.1 gives one idea of the relationships of lobe-finned fish groups (Cloutier and Ahlberg 1997), including tetrapods, to one another, and that is the scheme that will be followed in this book. Only with an explicit phylogeny behind it can any ideas about what occurred in evolution have any validity. The phylogeny must take precedence in drawing up scenarios about what went on in the distant past; otherwise, any possible story can be put forward, but it will not be a scientific one. However, readers must bear in mind that not all paleontologists agree with this particular phylogeny, and it is subject to change as new finds and ideas emerge. This implies that should a different phylogeny emerge for the relationships of tetrapods, some of the conclusions drawn throughout this book might be refuted.

Figure 3.2 puts the animals on a timescale of the Devonian period. Note the subdivisions or stages into which the Devonian is divided.




**3.3.** *Latimeria chalumnae* (A) skeleton and (B) whole animal.

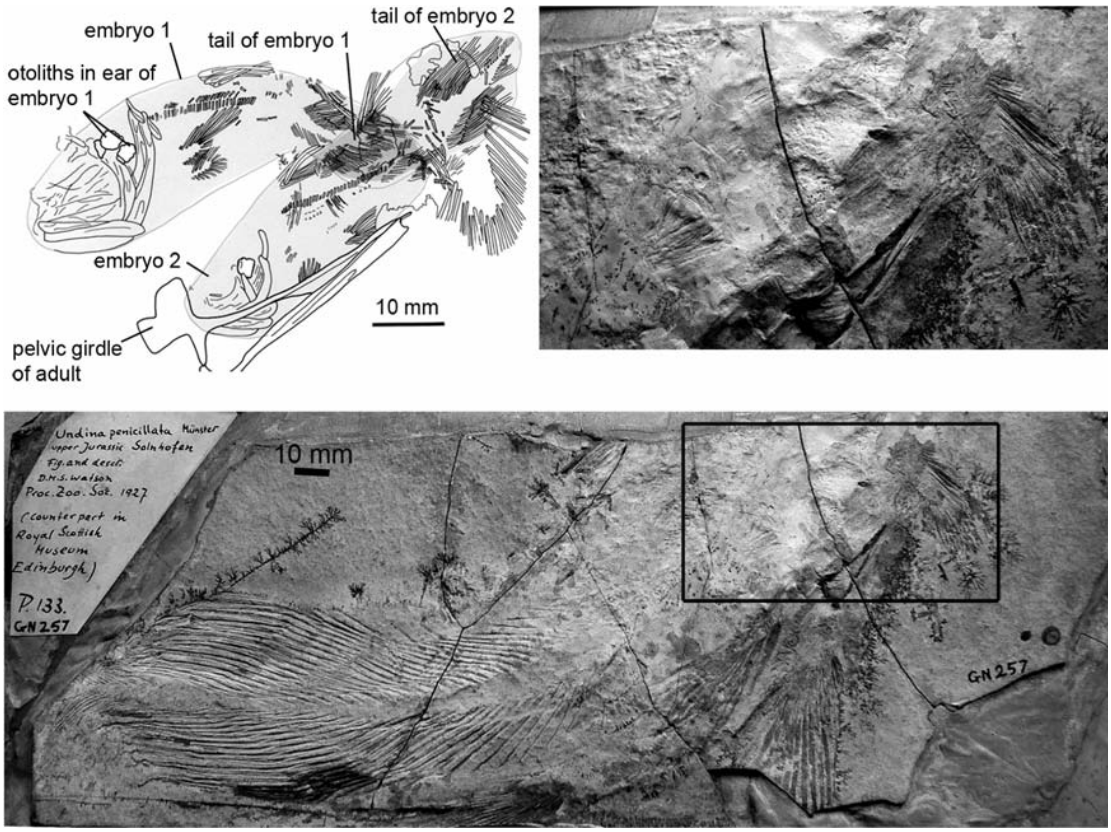
## Survivors

### COELACANTHS

Getting to Know the Lobe-Fin Groups

Until about 60 years ago, the coelacanths (the name means "hollow spine" and the group is formally known as Actinistia) were considered to have become extinct during the Cretaceous period, probably at the end of it, along with the dinosaurs. In 1938, however, the first modern coelacanth was recognized (Smith 1956). It was named *Latimeria*, after Marjorie Latimer, who worked at the museum in East London (South Africa) and was the first to recognize its importance. Since then, knowledge of it has increased greatly from the several specimens that have been recovered, preserved, and dissected (e.g., Millot and Anthony 1958), and from video footage taken from deep-sea submersibles (e.g. Fricke et al. 1987, 1991). These have shown that *Latimeria* does not use its fins in any kind of "walking" activity, but for slow propulsion in swimming. They have also shown how the fishes rest together in caves, in mixed groups of different-aged individuals. The composition of each group appears to remain relatively stable, and it is likely that they recognize each other. Each individual has a unique pattern of spots on its flanks.

The species *Latimeria chalumnae* (Fig. 3.3) is found predominantly around the east coast of the Comoro Islands in the Indian Ocean, where it is fished up from depths of about 300 meters by line fishermen. More

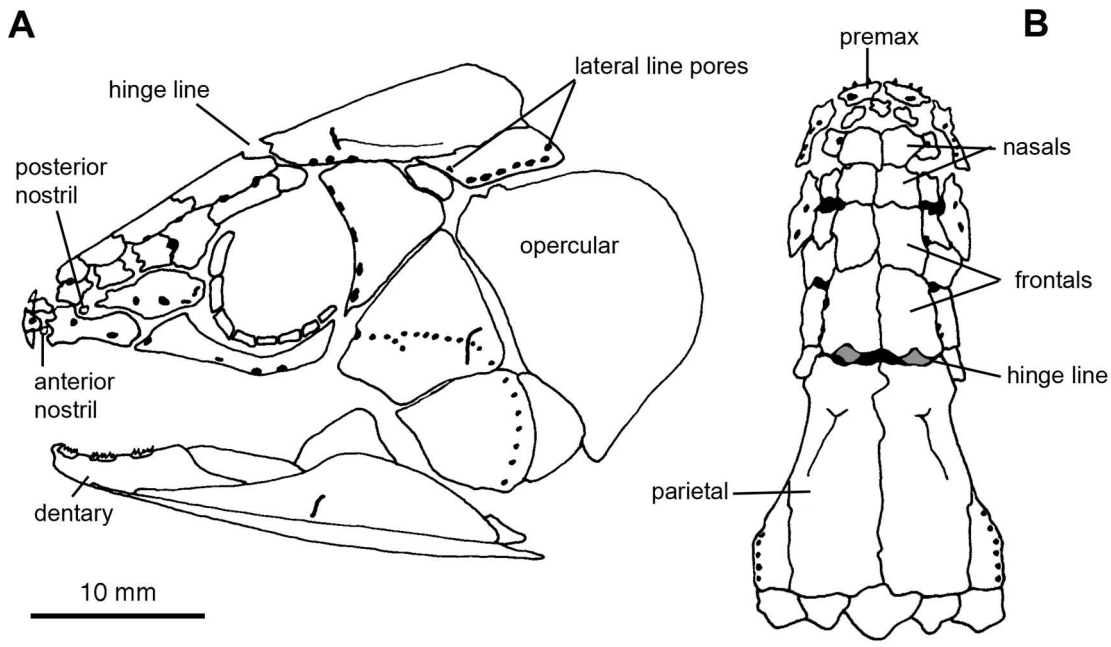



**3.4.** Photograph of a specimen of *Undina* showing embryos inside. Box shows area where embryos are found, with a close-up photograph and interpretive drawing of the embryos above. UMZC specimen GN.257. *Photograph by J.A.C.*

recently, coelacanths have been found off the Indonesian island of Sulawesi, representing a second and potentially important population of these intriguing fish, perhaps a separate species from the Comoro Islands form (Erdmann et al. 1998).

Because coelacanths were known first as fossils, ideas about them and their relationship to tetrapods were challenged by discovery of a living form. Some ideas were proved correct, whereas others, not surprisingly, were wrong (Musick et al. 1991; Forey 1998). One of the ideas that was tested concerned the nostrils. *Latimeria* proved to have a pair of nostrils on each side of its face, one for incurrent water and one for excurrent, and these are used for olfaction—smelling—and not for breathing. This it shares with most other fishes, both bony and cartilaginous. By contrast, certain other fossil lobe-fins and all tetrapods, to which *Latimeria* was supposedly closely related, have only a single nostril on each side, connected to an internal one inside the mouth on each side. In many other features of its physiology, *Latimeria* has proved unusual and more like sharks than bony fish. Most scientists take these features to show a general gnathostome condition rather than a direct relationship to sharks.

One feature suggested by fossils and confirmed by *Latimeria* is that coelacanths were ovoviviparous—they produce large eggs, maintained in the body cavity, until fully formed young are released. One fossil coelacanth from the Jurassic, called *Undina*, was described by D. M. S.

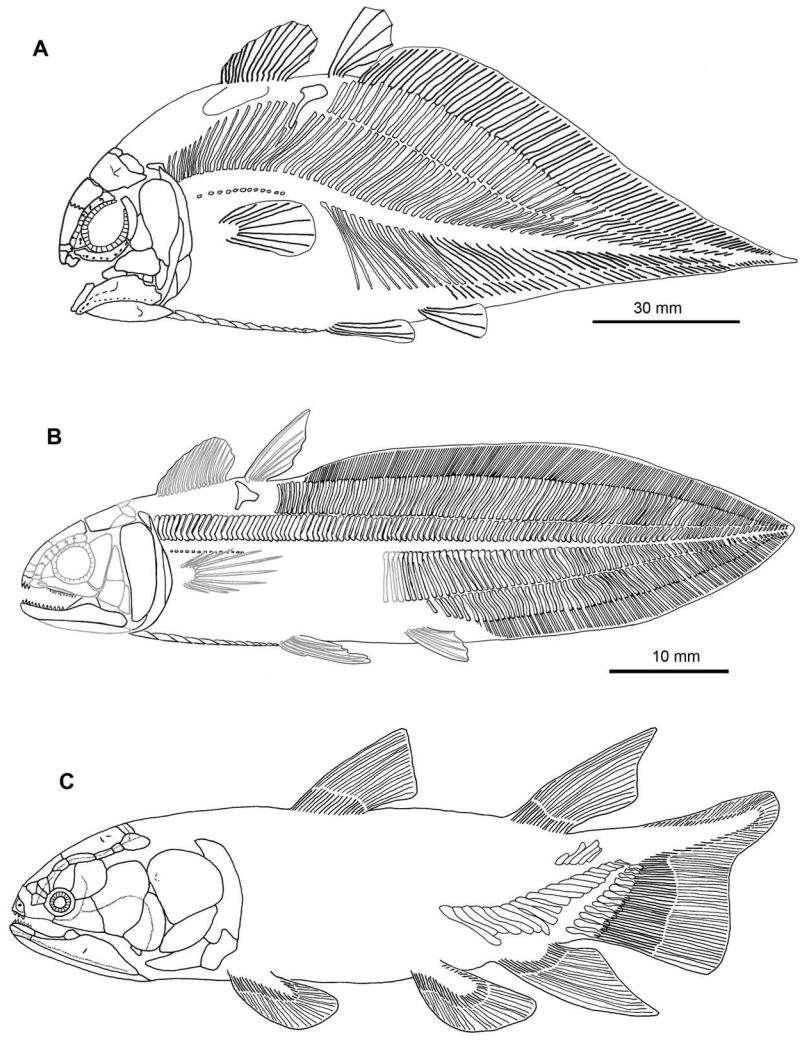



**3.5.** Skull roof of *Rhabdoderma elegans*. (A) Left lateral view. (B) Dorsal view. *Based on Forey (1998).*

Watson in 1927 within which two tiny coelacanths are preserved (Fig. 3.4), and though at the time they were considered to be embryos, another possibility was that they were stomach contents, with an adult having eaten the small fry. Discoveries of advanced embryos within female specimens of *Latimeria* have confirmed the observation of embryos in the fossils (Atz 1976).

In common with other bony fishes, coelacanths possess a derivative of the swim bladder, an outpocketing of the pharynx behind the gill pouches. In many bony fishes, this is an air sac and is used as a lung, while in others it acts as a gas-secreting bladder to control buoyancy. In some fossil coelacanths, this structure has extremely thin but strong bony walls, suggesting that it could resist changes in water pressure as the animal dived. In *Latimeria* instead, this bladder is filled with fat, which would have the same effect (Forey 1998). Although the swim bladder is not gas filled in *Latimeria*, it possesses a pulmonary circulation similar in some details to that of tetrapods and lungfish (Millot et al. 1978). One possible implication is that early in their history, coelacanths did have an air-filled swim bladder.

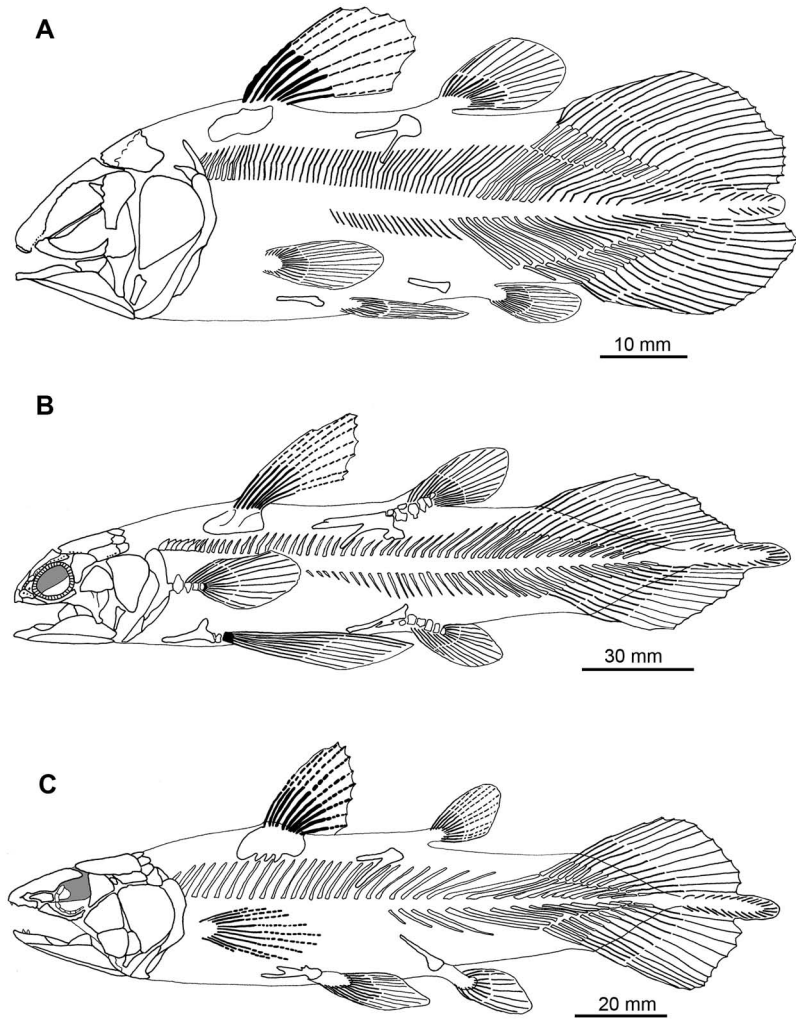
Coelacanths have some peculiarities of skull structure seen in both living and fossil forms (Figs. 3.3, 3.5). They have lost the maxillary bones of the upper jaw so that all their upper teeth are borne on the palate. Throughout their evolution, many other skull bones, present in early forms, are lost or reduced. Across the top of the skull and through the braincase runs the intracranial joint that they share with many fossil lobe-finned fishes, and which is characteristic of the whole group in its early history (see Chapters 2 and 6). This device has been studied in some detail and seems to provide coelacanths with added impetus to their




**3.6.** Three very early coelacanths showing extreme modifications (A, B) or primitive features (C). (A) *Allenypterus montanus,* Early Carboniferous, USA. Based on Forey (1998). (B) *Holopterygius nudus* mid–Late Devonian, Germany. Courtesy M. Friedman. (C) *Miguashaia bureaui* Late Devonian, Miguasha, Canada. Animal up to 450 mm long *Based on Cloutier (1996).*

method of suction feeding (Thomson 1967, 1969). With their deep tails, the coelacanths can produce a sudden surge of movement as they lunge at passing prey, usually small fish.

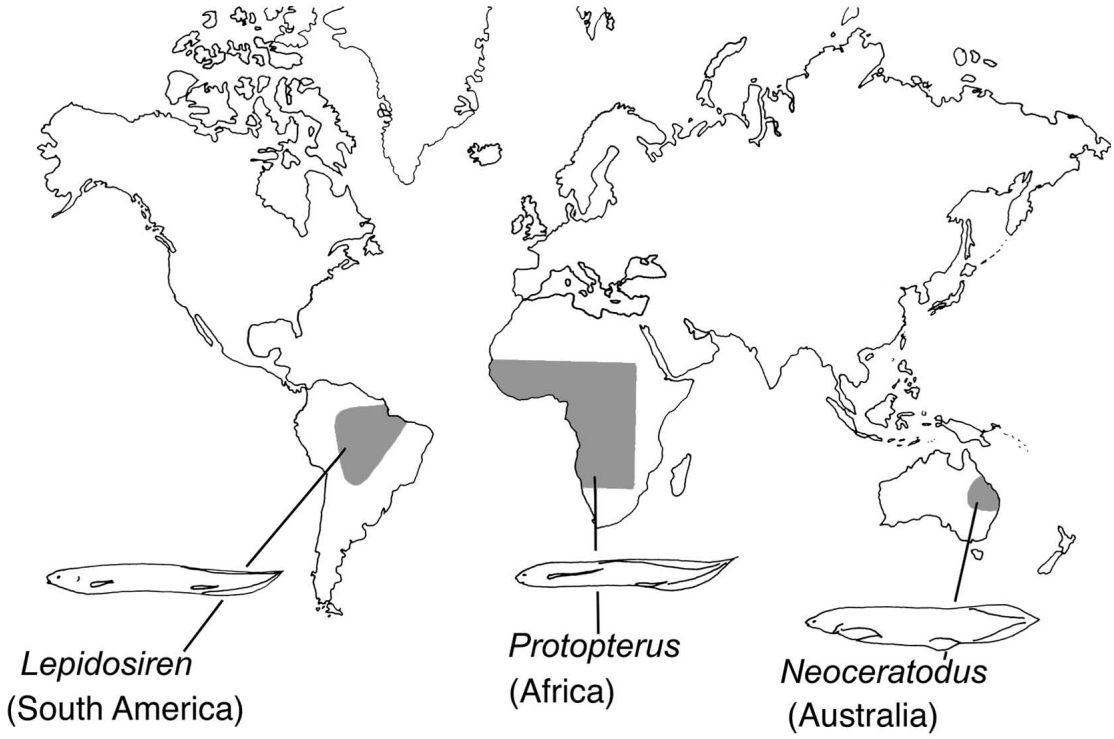
*Latimeria* has the characteristic fleshy lobed fins of its group, which it moves alternately or independently in a way that resembles the limb movements of a tetrapod (Fricke et al. 1987). However, at some time during their evolution, coelacanths developed a second dorsal and an anal fin that have an almost identical structure to the paired fins, each complete with half a girdle (Ahlberg 1992). The tail looks as though it has been duplicated, mirror fashion, along a line running horizontally halfway along the body (Fig. 3.3). Perhaps some strange genetic accident duplicated the paired fin structure where midline fins should be, and also duplicated the structure of the tail. It is possible to put a rough date to the time at which this occurred. The most primitive known coelacanths, *Gavinia* from the Middle Devonian locality of Mount Howitt in Australia and *Miguashaia*




**3.7.** Three fossil coelacanths. (A) *Macropomoides orientalis,* Late Cretaceous, Lebanon. (B) *Laugia groenlandica,* Early Triassic, Greenland. (C) *Rhabdoderma elegans,* Late Carboniferous, USA, and Europe. *Laugia* shows modifications to the position of the pelvic fins. They are placed much further forward than in any other genus of coelacanth and in this way parallel modifications found in teleost ray-fins. *Based on Forey (1998).*

from the Late Devonian Canadian locality of Miguasha (see Chapter 4), do not show this unique feature but instead retain the primitive form of tail (Fig. 3.6C). *Miguashaia* has midline fins with a structure similar to those found in most early lobe-fins and ray-fins (those of *Gavinia* are not known) (Cloutier 1996; Long 1999). Even *Gavinia* shows the characteristic skull constructions of other coelacanths, however, showing that skull modifications appeared some time before those to the tail and fins. The genetic changes to the tail and fins that characterize all later coelacanths happened around this time because in other Late Devonian coelacanths, they had already occurred.

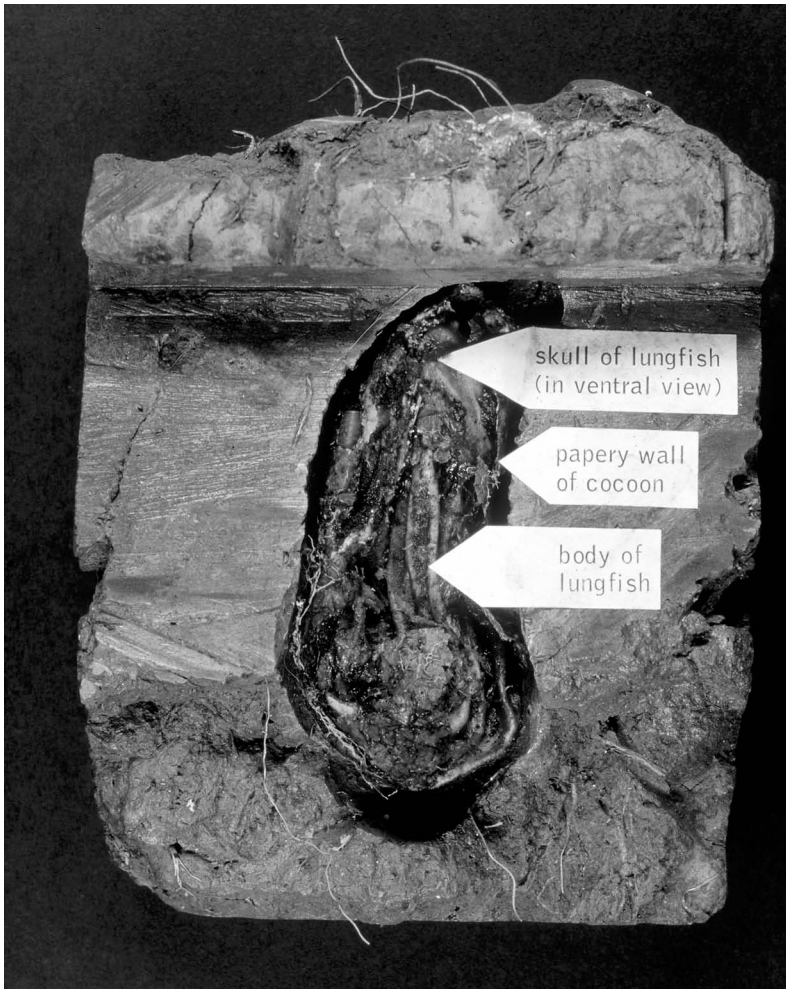
The earliest coelacanth so far described is known only from a single isolated dentary bone from the middle Early Devonian of Australia (Johanson et al. 2006), but it is sufficiently distinct not only to recognize it as a coelacanth, but sufficiently different from other coelacanths to give it a name: *Eoactinistia*. Unfortunately, because it gives no clues to its




**3.8.** Map showing distribution of modern lungfish genera.

postcranial skeleton, it is not possible to say whether it had the distinctive fin structure of later coelacanths.

Although only one genus of coelacanth remains, they were numerous and varied throughout the Paleozoic and Mesozoic eras. Paleozoic forms seem to have been euryhaline—that is, they could migrate between freshwater and seawater, and at least some, such as *Rhabdoderma* (Fig. 3.7C), lived in shallow water much of the time (Forey 1981, 1998). In contrast, the modern form lives exclusively in deep marine waters. Most Mesozoic coelacanths look similar in most ways to *Latimeria*—for example, *Macropomoides* from the English chalk (Fig. 3.7A)—and this led to the idea that coelacanths are more or less conservative morphologically. However, during the later Paleozoic, variations in body form are found. For example, one of the earliest coelacanths, *Holopterygius* from the Middle/Late Devonian boundary, had merged all its midline fins into a single one running all the way around the body (Friedman and Coates 2006) (Fig. 3.6B). A similar morphology is partially replicated in the Early Carboniferous form *Allenypterus*, although it is not especially closely related to *Holopterygius* (Fig. 3.6A). Other variations involved shifts in positions of the paired fins, paralleled later by ray-finned fishes (Lund and Lund 1985) (e.g., *Laugia*, Fig. 3.7B), in which the pelvic fins had moved forward to lie almost beneath the pectorals. During the late Mesozoic, some coelacanths reached enormous sizes; for example *Mawsonia* grew to lengths of over 10 feet (over 3 meters). A comprehensive review of fossil



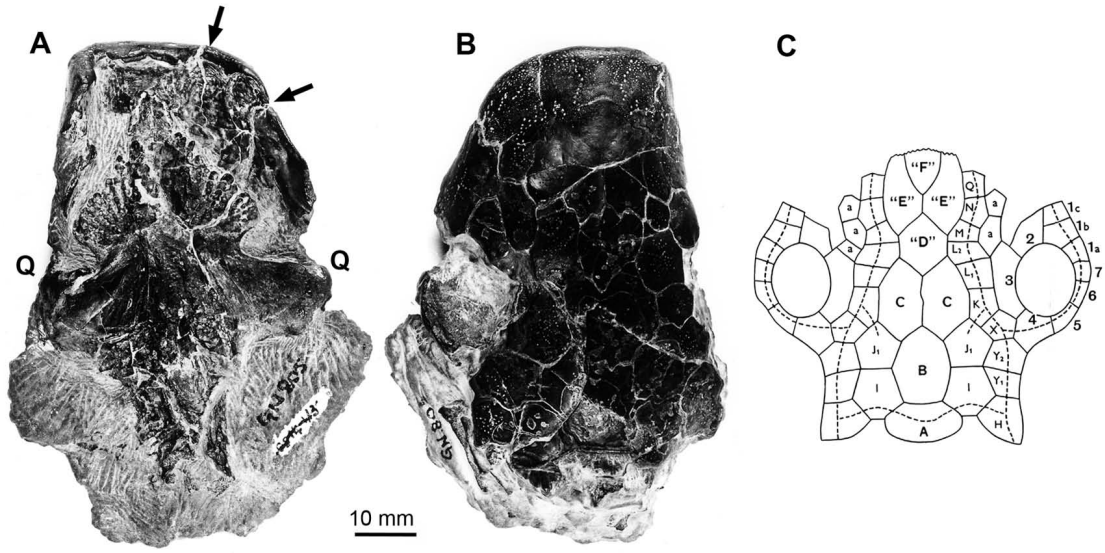

**3.9.** Preserved lungfish cocoon. *Photograph from UMZC archives.*

and extant coelacanths as well as a discussion of their relationships may be found in Forey (1998).

Although the living coelacanth was hailed as Old Four Legs, in fact it now appears that the similarities between coelacanths and tetrapods are not as close as once appeared. In the last section of this chapter, the evidence behind these ideas will be explored.

## LUNGFISHES

In contrast to coelacanths, the lungfishes or dipnoans (formally Dipnoi) were first known from their living representatives, and only in 1871 was it realized, by Günther, that the fossil forms from the Paleozoic were related to the modern forms. (They had been described many years previously but not recognized as related to living animals.) There are three modern genera, all living exclusively in freshwater. *Neoceratodus* inhabits a few river basins around the east and south coasts of Australia, whereas *Protopterus* in Africa and *Lepidosiren* in South America inhabit lakes



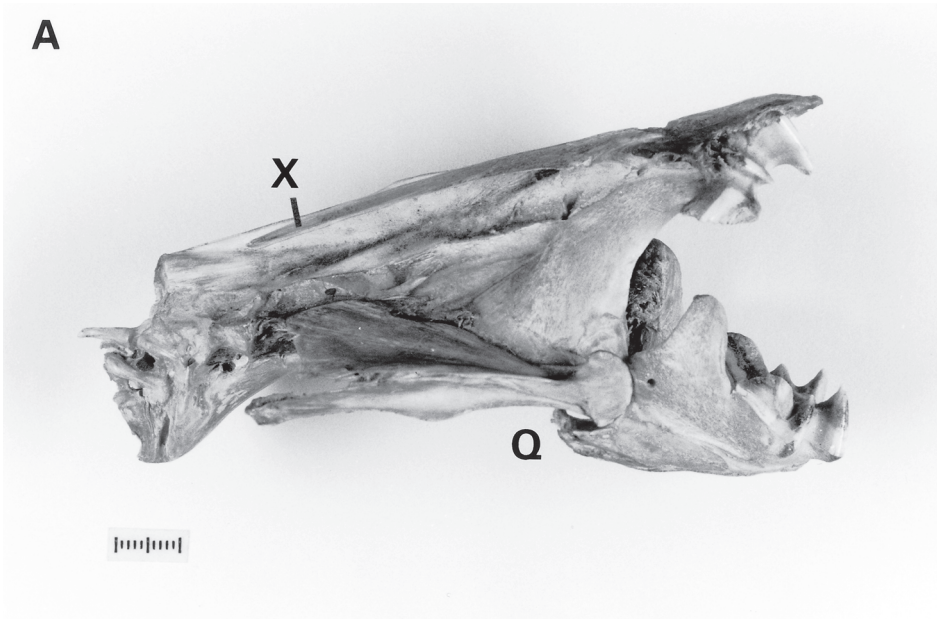

**3.10.** Skull of the fossil lungfish *Dipterus* in (A) palatal view and (B) dorsal view. Note the hopscotch pattern of the skull roofing bones, and the ridged tooth plates on the palate. Note also the incurved bony upper lip of the skull, which is toothless, lacking the premaxilla and maxilla. Arrows mark the notches for the anterior and posterior nostrils. Q marks the position of the quadrate. Scale bar = 10 millimeters. UMZC specimen GN.805. *Photograph by S.M.F.* (C) The alphanumeric scheme of bone identification put forward by Forster-Cooper (1937).

and rivers that periodically dry up. Of these, *Protopterus* and *Lepidosiren* are closely related, bearing witness to the close geographical position of South America and Africa before the two continents split apart in the Jurassic, carrying their cargo of lungfishes with them (Fig. 3.8).

All three species have lungs as well as gills, but of the three, *Neoceratodus* is least dependent on air, breathing with lungs only when the water becomes too anoxic or when it has been particularly active. The other two may drown if deprived of air and are capable of estivation, which means they go into a kind of suspended animation to survive the dry season. They form burrows of mucus in the drying mud at the bottom of their lake or river. This then dries to make an impervious seal, and the fish in effect sleeps through the hot dry season in a cocoon (Fig. 3.9). When the rains return and fill the basin again, the mud-and-mucous cocoon dissolves, and the fish swim away after a new gulp of air. Features interpreted as estivation burrows are known for some fossil lungfishes from the mid-Carboniferous period (Garcia et al. 2006), though it is also possible that these are nesting burrows.

The skull of a lungfish, living or fossil, has a suite of unique features that make it physically unlike the more conventional skulls of other lobe-fins or indeed ray-fins (Figs. 3.10, 3.11, 3.12). Because lungfishes have featured heavily in the struggle to understand the relationships and origin of tetrapods, it is necessary to understand this strange structure in some detail.

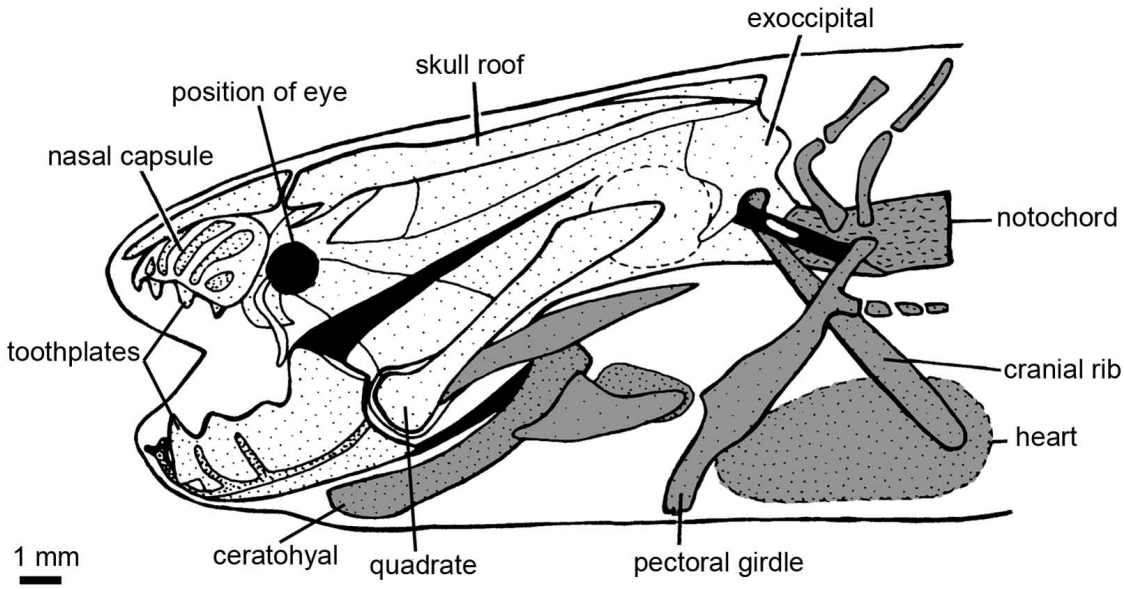
Among the most commonly found and most characteristic of fossil lungfish elements are their tooth plates (Figs. 3.10—3.13). These are usually more or less triangular structures carrying sharp-crested, radiating ridges. There are two pairs in the lower jaw that bite against corresponding pairs in the upper jaw, with the ridges meeting in a scissorlike action. Occasionally, rather than radiating ridges, the plates are equipped with







**3.11.** Skull of the modern lungfish *Protopterus* in (A) right lateral and (B) dorsal views. Note the ridged, scissorlike tooth plates, and the forward position of the quadrates (Q). Most of the dermal skull bones have been lost. X marks one of the remaining elements. Scale bar = 10 millimeters. UMZC specimen. *Photograph by S.M.F.*

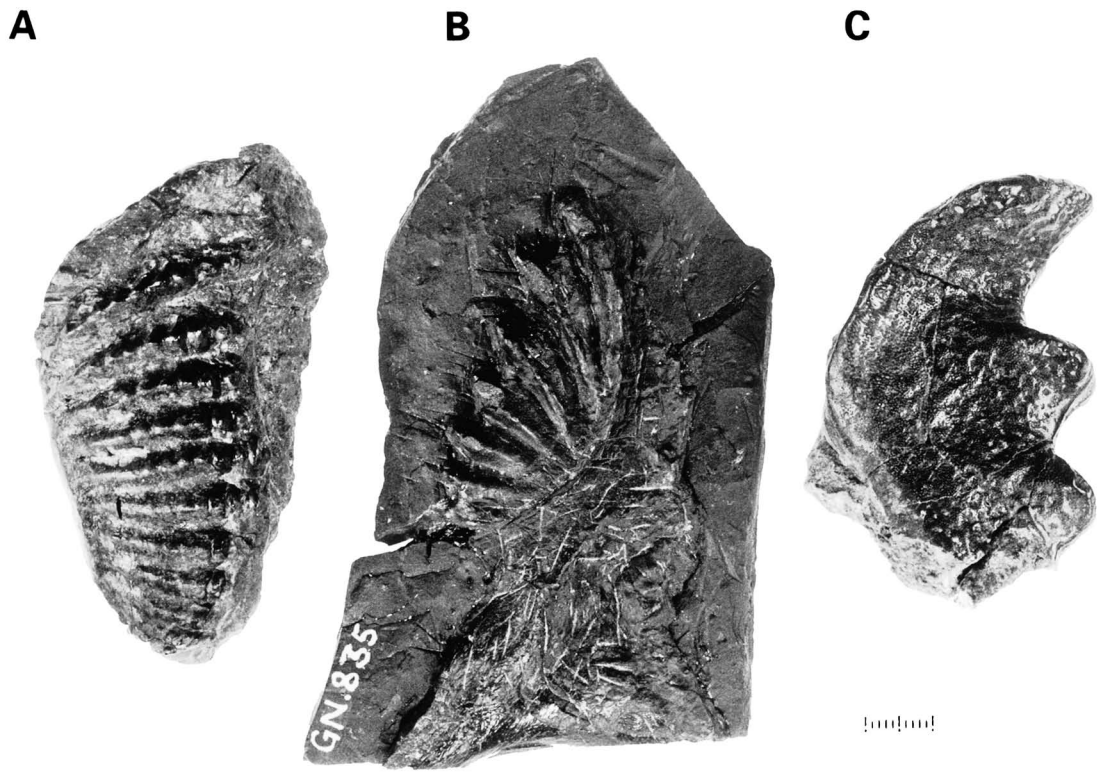



**3.12.** Diagram of the skull of *Protopterus* to show the cranial rib. Elements not present in the skull in Figure 3.11 are shaded. From Long (1993).

denticles, either forming a uniform surface or organized into radiating rows. The pattern of ridges or denticles is characteristic of their genera or species (for a range, see Fig. 3.13). The occurrence of the tooth plates attests to the loss of the marginal teeth that would normally be found in the maxilla, premaxilla, and dentary around the mouth of most other bony vertebrates. Lungfishes lack all trace of the maxilla and premaxilla, and only the most primitive have the remnants of the dentary. In fact, *Neoceratodus* does possess dentary bones—as an embryo—but they are resorbed when the animal grows (Ahlberg et al. 2006). The tooth plates form on the prearticular of the lower jaw and the pterygoid of the upper jaw (see Chapter 2).

Lack of the maxilla and premaxilla, as well as other modifications to the skull roof bones and palate, have had an impact on the nostrils of lungfishes. Both nostrils in lungfishes appear in the roof of the mouth, inside a fleshy (in modern forms) or bony (in fossil forms) lip (Fig. 3.10). There is an anterior pair for water intake and a posterior pair for water outlet after the water has passed over the olfactory membranes. The identity of these nostrils and their equivalence to those of other vertebrates have been a source of debate and confusion since the early part of the 19th century, as they have featured in the debate about how lungfishes are related to tetrapods.

The tooth plates appear adapted for a crushing action to use on hard prey items, and this, it has been suggested, correlates with other specializations of the lungfish skull. The skull roof of fossil forms, unlike those of most other bony vertebrates, has its bones arranged in a pattern best described as hopscotch—that is, a single bone alternates with a pair, in the sequence from the back to the front of the skull. Each bone tends to have a polygonal shape as a result. It has been a problem to see how

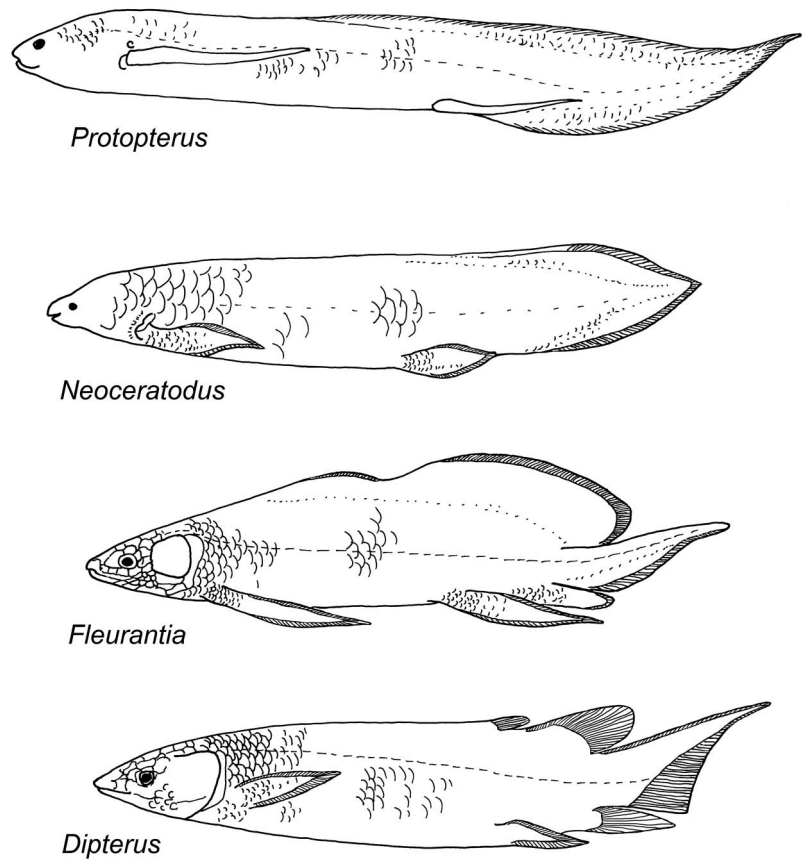



**3.13.** Fossil lungfish tooth plates. (A) *Ctenodus,* Lower Carboniferous, Scotland. (B) *Sagenodus,* Upper Carboniferous, Northumberland, UK. (C) *Ceratodus,* Upper Triassic, Gloucestershire, UK. Scale bar = 10 millimeters. UMZC specimens. *Photograph by S.M.F.*

lungfish skull roof bones equate to those of other lobe-fins, to the extent that most authors gave up the attempt to apply the bone names used for other groups and instead simply use a system of letters and numbers (Forster Cooper 1937) (Fig. 3.10). This system, though envisaged as temporary when it was proposed, is still in general use today. In consequence of this polygonal pattern, the lungfish skull roof lacks any trace of the lobe-fin hinge line, but rather is a solidly constructed unit in most early fossil members. Modern forms have lost most of the dermal roofing bones, making it even more difficult to homologize their skull bones with those of other lobe-fins. In the same way that they have reduced or lost their skull bones, lungfish have also lost much of their scale cover during their evolutionary history (Figs. 3.11, 3.14).

Other features tie in with this overall consolidation of the skull. The palate is a solid unit, with the plate-bearing pterygoids sutured to the braincase, while the jaw joint, formed by the quadrate, lies well forward in the skull rather than at the rear, as in most lobe-fins (Figs. 3.10, 3.11). It too is solidly attached directly to the braincase. Because of this, the hyomandibula, normally the bone responsible for providing the link between quadrate and braincase, is reduced or lost. This is an example of an autostylic skull, in which the quadrate and braincase are securely integrated with the palate. A parallel case occurs in most tetrapods.

Lungfishes have a specialized method of inhaling air by gulping it from the surface of the water. It involves the use of a cranial rib unique




**3.14.** Body forms of some extinct and extant lungfishes. Top to bottom: *Protopterus* from Africa; *Neoceratodus* from Australia; *Fleurantia* from the Upper Devonian of Canada; *Dipterus* from the Middle Devonian of Scotland (from Ahlberg and Trewin 1995). *Protopterus* and *Neoceratodus* can grow up to a meter in length, *Fleurantia* up to 420 millimeters, and *Dipterus* up to about 275 millimeters.

to lungfishes and a highly modified shoulder girdle that swings around beneath the chin as the buccal cavity expands (Fig. 3.12). At least some of the modifications to the palate described above, and others to the floor of the mouth, may be associated with the unique way in which they form a seal as the gulped air is swallowed, rather than with the requirements of a crushing dentition. On the other hand, some of the modifications to the shoulder girdle and cranial rib that are involved with air breathing are also involved in the lungfishes' sophisticated suction-feeding mechanism.

The development of these adaptations can be followed in the fossil record, and it is clear that the earliest lungfishes did not have them (Long 1993). This may mean that they did not breathe air at all, for they seem to have been marine forms that lived in relatively deep water (Campbell and Barwick 1987). For example, the Gogo lungfish *Griphognathus* has a fully developed gill skeleton with a complement of five gill arches, as in other gill-breathing fishes. However, because it is thought that all bony fishes were originally equipped with lungs or their equivalent, it may have been that early lungfishes, like *Neoceratodus*, breathed air only occasionally, and then in a relatively unspecialized way, with the deep-water marine forms reducing their facility for air breathing.

There are many features of soft tissue anatomy and physiology in which lungfishes resemble tetrapods, causing many people to believe the two groups to be closely related (Rosen et al. 1981). However, it is true that most of these features are concerned with air breathing and were quite likely to have been absent in the earliest lungfishes. If so, at least these similarities must have evolved in parallel among lungfishes and tetrapods. The fossil evidence nonetheless still seems to point to a closer relationship than that between tetrapods and coelacanths, although more evidence from modern forms needs to be gathered before this debate can finally be settled.

Early lungfishes show the lobed fin in almost an idealized form, with long lobes formed of many radials. This is seen today almost unmodified in *Neoceratodus*. As well as the series of branches that run along the anterior, preaxial, edge of the fin in other lobe-fins, lungfishes have another set postaxially. In the modern lungfishes *Protopterus* and *Lepidosiren*, the paired fins have become whiplike appendages used in steering and upon which they sometimes have been seen to support themselves and "walk" on the bottom of the lake bed. Early lungfish tails were heterocercal. During their evolution, lungfish tails changed from this early asymmetrical heterocercal form to a symmetrical form in which upper and lower lobes became equal, and the upper lobe merged with the anal and dorsal fins to form a single long fin (summarized in Long 1993) (Fig. 3.14). Another feature of lungfish evolutionary history is the gradual loss of ossification from the internal skeleton, so that braincases, vertebrae, and fin supports were nearly entirely cartilaginous from about the Late Carboniferous onwards. This makes it difficult to track changes to these systems in the fossil record from that time on (Clack et al. 2011).

## Extinct Lobe-Finned Fishes

During the Paleozoic, many lobe-finned families of diverse form and lifestyle existed that have no direct living descendants. The structure and relationships of some of these forms will put tetrapods and other modern lobe-fins into closer context.

According to some modern analyses, the lobe-finned lineage produced, as well as some less speciose groups, two major branches, one that is more closely related to lungfishes and another that is more closely related to tetrapods (Figs. 3.1, 3.2). Most members of the latter group were for many years known as osteolepiforms, but this name is no longer considered valid taxonomically. An alternative idea of relationships is that coelacanths are closer to tetrapods (Zhu and Schultze 1997, 2001), but more details of this debate are discussed later in the chapter.

In the scheme of relationships used here, the tetrapods belong with a suite of families and individual genera in a group that has been named the Tetrapodomorpha. With the lungfishes belong the porolepiforms and their relatives in a group called the Dipnomorpha. The coelacanths are usually placed outside this dichotomy, having split off from the family

tree earlier on, along with a small group called the onychodonts, a group whose anatomy and relationships are even more mysterious.

The tetrapodomorphs consist of several families: some primitive forms often referred to as osteolepidids; the rhizodonts; the megalichthyids; the tristichopterids; and some individual genera including *Livoniana*, *Panderichthys*, *Elpisostege*, and *Tiktaalik*, all of which feature in the story of tetrapod origins.

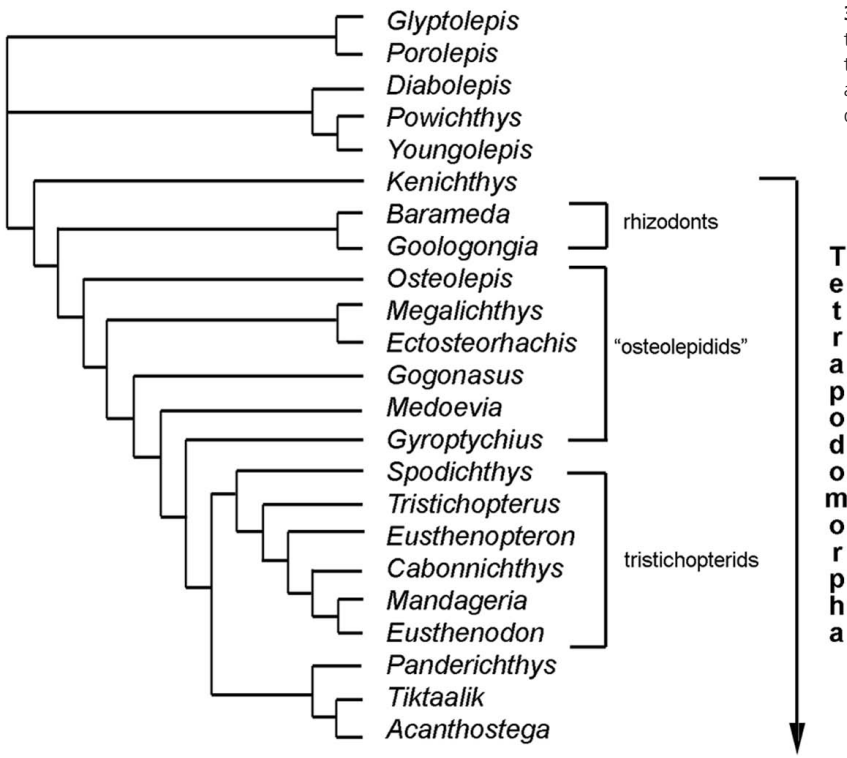
## Tetrapodomorph Lineage

The heyday of fishlike tetrapodomorphs spanned the Middle Devonian to the Early Permian. Over the last decade, many new genera of this lineage have been described from different parts of the world, including China, Canada, Kazakhstan, and Australia. Indeed, the number of described genera has approximately doubled in the last 15 years. Known since the 19th century, the familial relationships of tetrapodomorphs have only been worked out using modern techniques in the last decade or so (Ahlberg and Johanson 1998), and they are the subject of ongoing review. The most recent is that by Snitting (2008) (Fig. 3.15).

Tetrapodomorphs share a number of features that tie them together, along with the limbed tetrapods, as a natural group. One unique feature uniting tetrapodomorphs is the form of the excurrent nostril, known as the choana. Instead of incurrent and excurrent nostril pairs sitting on either side of the head, as is found in most fishes, the excurrent nostril has been repositioned to lie within the mouth and appears as a hole, known as the choana, in the roof of the mouth. For many years, the picture was confused by the fact that some researchers thought that porolepiforms had three nostrils on each side of the head—incurrent, excurrent, and an internal choana; furthermore, rhizodonts were thought not to have a choana. Now, both these perceptions have been proved incorrect, clarifying the situation and demonstrating a consistent, unique shared feature of tetrapodomorphs. Lungfishes have a superficially similar situation, though there, both sets of nostrils lie just inside the mouth as described above, but this condition is almost certainly achieved in parallel to that in tetrapodomorphs.

How and when the tetrapodomorph condition arose may be exemplified by the most primitive known member of the group, *Kenichthys*. This fish is from the Early Devonian of China. The snout is known in some detail, and it can be seen that the excurrent nostril lies right at the edge of the skull, so that it is effectively half in and half out of the mouth cavity (Zhu and Ahlberg 2004).

Another feature is seen in the paired fins. Having two radials (homologues of the tetrapod radius and ulna or tibia and fibula respectively) of almost equal width, that articulate with the first axial radial (humerus or femur in tetrapods), is a conspicuous feature among tetrapodomorphs. Something similar is seen in the embryonic development of *Neoceratodus*, but in that fish, the two elements fuse to form a single unit. All




**3.15.** Cladogram from Snitting (2008). The term in quotation marks is paraphyletic and does not include all the descendants of the clade.

fossil dipnoans where the fin skeleton is known have a single main radial articulating with the first, with or without pre- and postaxial radials coming off that. In the apparently primitive group of sarcopterygians called onychodonts, the humerus shows facets for the articulation of a narrow radius and a broader ulna, though those elements, and thus their lengths, are unknown (Andrews et al. 2006). A recent study of a partial fin skeleton of an early coelacanth has suggested that the tetrapodomorph pattern might be more widely spread and perhaps primitive among lobe-fins. However, the specimen on which it is based may be subject to different interpretations (Friedman et al. 2007).

Rhizodonts are a group of forms whose anatomy is only just being worked out. They are considered to be basal members of the tetrapodomorph lineage, likely to have branched off from this clade quite early in its history. Known from the middle of the Devonian period to the end of the Carboniferous, they are most notable for having produced the largest bony fish predators of their day and estimates suggest that some individuals reached 7 meters in length, with teeth to match. (The name rhizodont means "root-tooth.") Isolated teeth—long, curved, and bladelike, and not a bad match for those of *Tyrannosaurus rex*—have been found up to 15 centimeters long (excluding the root).

Characteristics of rhizodonts include a unique pattern of folding of the tooth enamel, so that a cross section will easily establish whether a tooth belongs to a rhizodont or not. Also unique are some features of

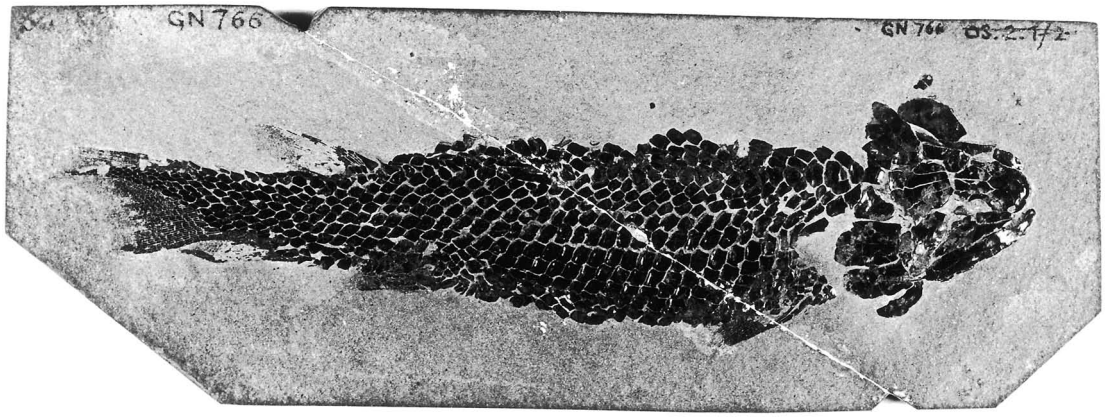
the shoulder girdle, so that one isolated shoulder girdle and fin from the Devonian of the United States called *Sauripterus* is put with reasonable certainty in this family. This specimen is important because it gives a good indication of the fin skeleton, and when first found, it was used as the model for the kind of fin structure that might have given rise to the limbs and digits of a tetrapod (e.g., Gregory 1915, 1935). Over the course of the succeeding decades, that idea changed and the fin of *Eusthenopteron*, a tristichopterid, was used instead.

Recent work on rhizodonts has helped to clarify their relationships a little. In Australia, a primitive rhizodont called *Goologongia* has been described from almost complete specimens (Johanson and Ahlberg 1998). New specimens of *Sauripterus* have been discovered in the United States, and work on the Carboniferous forms from Scotland has helped to throw light on their later evolution (Daeschler and Shubin 1997; Jeffery 2001, 2003). The complex pectoral fin skeleton seen in rhizodonts is currently thought to demonstrate a parallel elaboration to that seen in limbed tetrapods themselves. It may reflect a common mechanism of development among bony vertebrates, discovered recently in the primitive ray-finned fish *Polydon* that has been lost in more advanced ray-finned fish (see Chapter 6). On the other hand, should additional characters of the pectoral fin and girdle be included in the analysis, as well as other, now better-known features of the skull, the phylogenetic position of rhizodonts may change (Coates et al. 2002), perhaps to one in which they are indeed closer to tetrapods than are tristichopterids.

With their substantial skeletons, rhizodont pectoral fins are all relatively broad and fanlike (see Fig. 6.23), which may have supported the front end of the body either in water or with the head slightly lifted out of the water (Davis et al. 2001, 2004). In some cases, the humerus is so peculiar that it is hard to see the equivalence between it and those of other tetrapodomorphs (Davis et al. 2004, *Sauripterus*). These extra-strong fins may have helped stabilize the fish waiting in its stealth mode as an ambush predator.

One striking feature of all rhizodonts is the elaboration of the lateral line system (for the structure and function of lateral lines, see Chapter 6). In all of them, it is exceedingly well developed both on the skull and body, and in the more derived forms, it has branches that ramify onto the shoulder girdle, a unique condition. A triple or possibly quintuple row of lateral-line pores seems to have been present along the flanks of the fish, which may have been used as a phased array of detectors to give an accurate picture of pressure waves in the water around them. On the other hand, some studies of teleosts have likewise found an array of five parallel lateral lines along the flank of *Hexagrammos*, a modern teleost fish, but only one of these contained neuromasts. The other lateral lines did not contribute to the sensory function of the system (Wonsettler and Webb 1997). Thus, caution should be used when interpreting fossils.

During their evolution, changes to the body form and increase in size can be seen in the rhizodontids, paralleling those in tristichopterids,



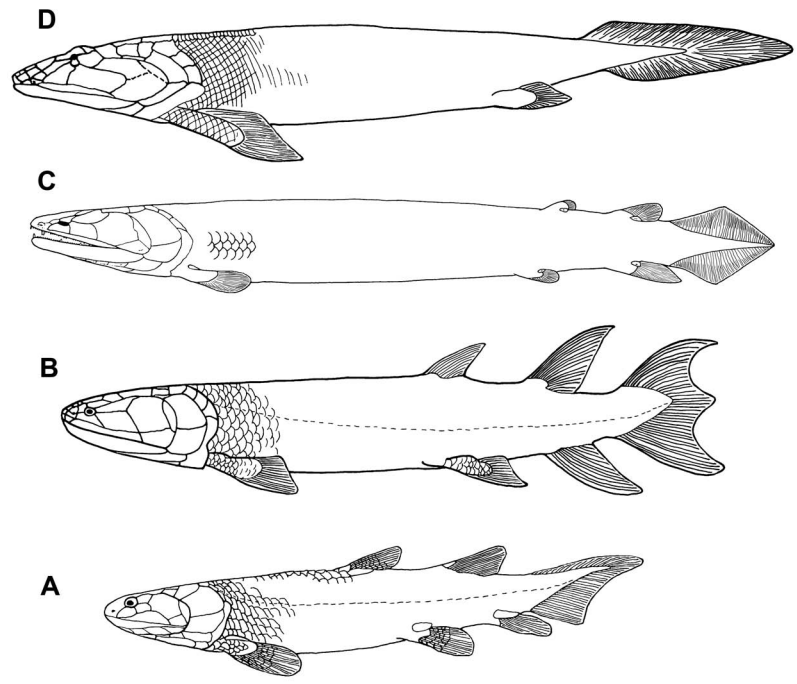

**3.16.** *Osteolepis macrolepidotus* from the Middle Devonian of Scotland. Scale bar = 10 millimeters. UMZC specimen GN.766. *Photograph by S.M.F.*

suggesting that both groups adopted similar modes of life. The changes to the head morphology and reduction in fin size seen in tristichopterids were also echoed in the evolution of tetrapods, suggesting that such a predisposition characterized the whole tetrapodomorph lineage (Johanson and Ahlberg 1998).

Recent cladistic analyses of tetrapodomorphs have shown that the family once known as osteolepidids is paraphyletic (Ahlberg and Johanson 1998; Snitting 2008). These have now been teased apart into a number of genera and smaller families spread through the tetrapodomorph family tree. One of the more specialized families, called tristichopterids and including *Eusthenopteron*, is currently placed at the crownward end of the tree nearer to the tetrapods (Fig. 3.15).

*Osteolepis*, one of the most primitive osteolepidids from the Middle Devonian, is known from deposits in Scotland and exemplifies early members of the group (Figs. 3.16, 3.17A). It had the characteristic intracranial joint and a heterocercal tail. Like other early lobe-fins, *Osteolepis* had two dorsal fins. Its scales and head bones were covered in cosmine, the glossy-looking enamel-like substance seen in other early lobe-fins as well.

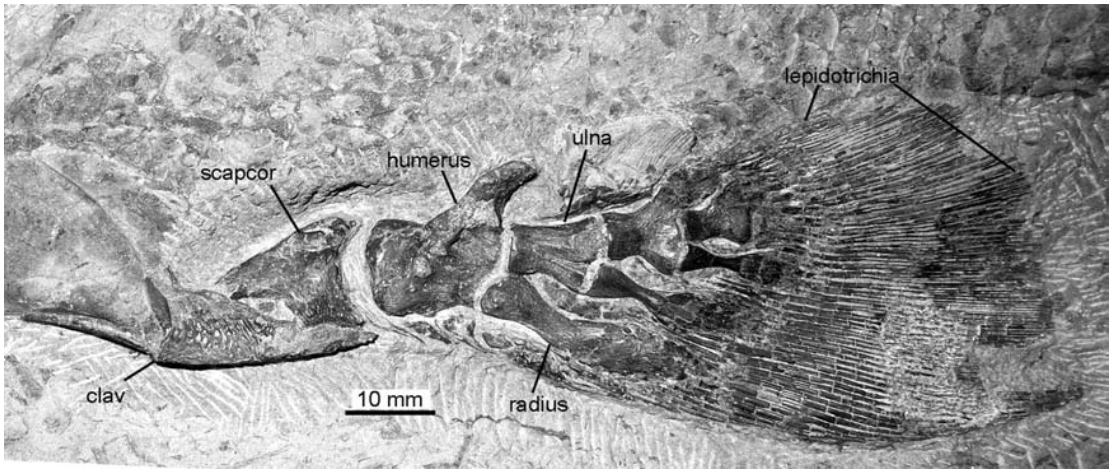
One of the best-preserved "osteolepidids" is from the locality of Gogo in Australia. This locality represents a deep-water environment situated between reefs, and the fishes are found in nodules of limestone. When the limestone is dissolved away with dilute acid, the fossils are left behind as near-three-dimensional remains that look almost like modern bone. Micro-CT scanning can reveal astonishing details of their internal bony structure. *Gogonasus* has recently been described from an almost complete uncrushed specimen. Originally thought to be an osteolepidid, its current phylogenetic position is debatable, as it shows both primitive and derived features. It retains cosmine on its bones, but has a large spiracular opening and robust pectoral fin skeletons (Long et al. 2006). Work on this fish and on other "osteolepidids" is currently undergoing a resurgence of interest, with some new ideas of their relationships to each




**3.17.** Drawings of some tetrapodomorph fishes. (A) *Osteolepis,* Middle Devonian, Scotland, about 250 millimeters long. (B) *Eusthenopteron,* Late Devonian, Canada, up to 1.5 meters long. (C) *Cabonnichthys,* Late Devonian, Australia, up to 80 millimeters long. (From Ahlberg and Johanson 1997). (D) *Panderichthys,* Late Devonian, Baltics, and Russia, up to 2 meters long.

other and to tetrapods emerging as a result. The most recent cladistic analysis places *Gogonasus* well outside the tristichopterids, in a much more basal position (Snitting 2008).

Another Late Devonian locality in Australia, Canowindra (the locals pronounce it "Canowndra"), has provided a spectacular number of fossil fishes in extensive bedding planes that probably represent mass mortality events. Most of the fishes are placoderms, but several lobe-fins were also present. All of the lobe-fins there were large predators, up to a meter long. Three tetrapodomorph genera have been described, two of them only discovered in the last few years of the 20th century. They are *Canowindra* (the fish's name is often pronounced as written), *Cabonnichthys* (Fig. 3.17C), and *Mandageria*. *Canowindra* is the most primitive of the three, whereas *Cabonnichthys* and *Mandageria* are both highly specialized members of the Tristichopteridae (Johanson and Ahlberg 1997; Ahlberg and Johanson 1997). They are both long-bodied forms with relatively small but almost symmetrical tail fins, and dorsal and anal fins positioned near the rear end of the body. The shape suggests that they had evolved into ambush predators, characterized by the ability to accelerate quickly, but not designed for sustained swimming. *Mandageria* shows a peculiarity of the back of the skull and its attachment to the vertebral column that suggests it had evolved the ability to raise its head with respect to the column. Though formed in a different way from the neck joint of tetrapods, it suggests that the animals were using the arrangement for a similar function (Johanson et al. 2003). *Cabonnichthys* and *Mandageria* are both quite closely related to a similar-shaped form, *Eusthenodon*, from Greenland and Russia, showing that the tristichopterids were a wide-ranging




**3.18.** Photograph of the fin skeleton of *Eusthenopteron foordi,* showing part of the clavicle and scapulocoracoid, and the humerus, radius, ulna, more distal radial elements, and lepidotrichia. UMZC specimen GN.787. *Photograph by J.A.C.*

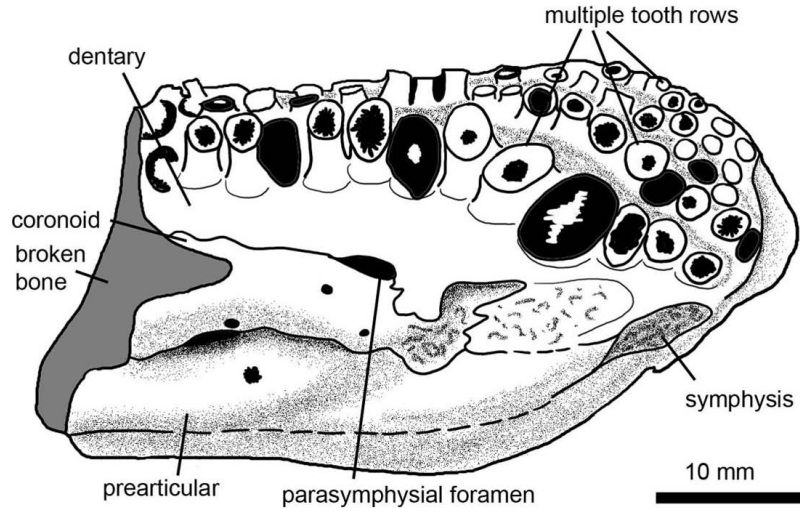
group, not restricted to a small part of the world. The tristichopterids as a whole show an evolutionary increase in size through the Late Devonian, and the proportions of the head show matching changes in which the anterior part of the skull became progressively longer with time.

*Eusthenopteron foordi*, probably the best-known tristichopterid, comes from a rich Frasnian locality called Miguasha in Quebec, Canada, which has also yielded many other species of fish (see Chapter 4). The survey of the skeleton of a lobe-fin in Chapter 2 is based on *Eusthenopteron*, so its anatomy is described in more detail there. However, this fish has its own unique features. One of them is the shape of its tail, which, rather than being asymmetrical like that of *Osteolepis*, is symmetrical, somewhat similar to that of a coelacanth, though different in detail (Fig. 3.17B).

*Eusthenopteron* is sometimes figured as crawling out of the mud of a Devonian lake, apparently with the intention of finding another pool to swim in. There are two main reasons for this picture relating to the origin of tetrapods, and they will be discussed in more detail in Chapter 4. But briefly, because *Eusthenopteron* was once cast in the role of the ancestor of tetrapods, tetrapod-like behavior was attributed to it. Second, the form of the fin skeleton was rather chunky, and its first three radials bear close comparison with the humerus, radius, and ulna of tetrapods (Fig. 3.18). Taking the whole morphology of *Eusthenopteron*, with its streamlined torpedo shape and with its dorsal, anal, and pelvic fins placed near the back of the body, it seems that its lifestyle was much more like that of a modern pike (*Esox*), a fully aquatic ambush predator.

The megalichthyids, one of the longest surviving tetrapodomorph families, include the widespread Carboniferous form *Megalichthys*. One of the last members, *Ectosteorhachis* from the Early Permian of the United States, is surprisingly a rather primitive member of that lineage, and both are cosmine-retaining forms. The anatomy and relationships of this group relative to other tetrapodomorphs is in need of review.

*Livoniana multidentata* is a recently recognized Frasnian tetrapodomorph (Fig. 3.19) (Ahlberg et al. 2000). It is known from only two

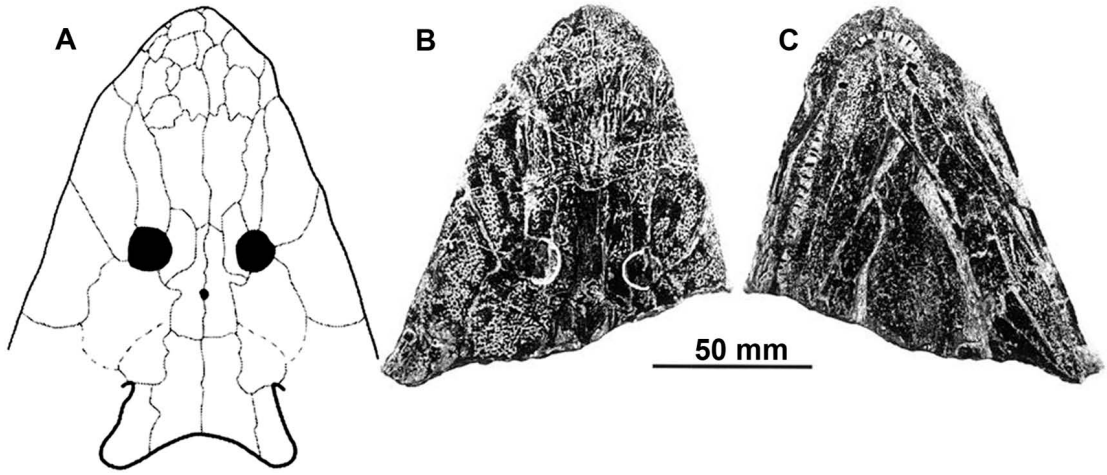



**3.19.** Specimen drawing of *Livoniana*. *Based on Ahlberg et al. (2000).*

fragments, both of the anterior end of the lower jaw. It comes from the area around the border between Latvia and Estonia, an area whose ancient name was Livonia. The most striking thing about the jaws is their multiple rows of small, rounded teeth, which give the appearance of a portion of corn on the cob. There are up to five rows of teeth, a feature not known in any other tetrapodomorph. The jaws do, however, show two or three features that are otherwise only found in animals close to true tetrapods like *Acanthostega*. When all the available information is pooled and put into a computer analysis, *Livoniana* appears sharing a node with two near tetrapods, *Elpistostege* and *Obruchevichthys*, on the tetrapod stem lineage. It was probably not a full tetrapod in the sense of having limbs with digits, but it was probably close to the cusp of tetrapod evolution, and so is one of the few concrete pieces of evidence for the range of animals that actually existed between truly fishlike stem tetrapods and more fully tetrapod-like ones. Its peculiar dentition suggests that there was a radiation of specialized animals at the boundary, one of which went on to produce tetrapods proper.

### *PANDERICHTHYS RHOMBOLEPIS, ELPISTOSTEGE WATSONI,* AND *TIKTAALIK ROSEAE*

These three genera are the "fish" most closely related to limbed tetrapods. All three genera are placed on successive nodes of the stem lineage close to tetrapods. Initially, *Panderichthys* and *Elpistostege* were placed together in a family called the Panderichthyidae. However, as more research and further finds have been made, it has become clear that the original family name is meaningless because these two are not uniquely related to each other; rather, all three are successive branches off the tetrapod stem lineage. The term Elpistostegalia has been suggested as a term uniting all these three genera plus limbed tetrapods (Daeschler et al. 2006), though



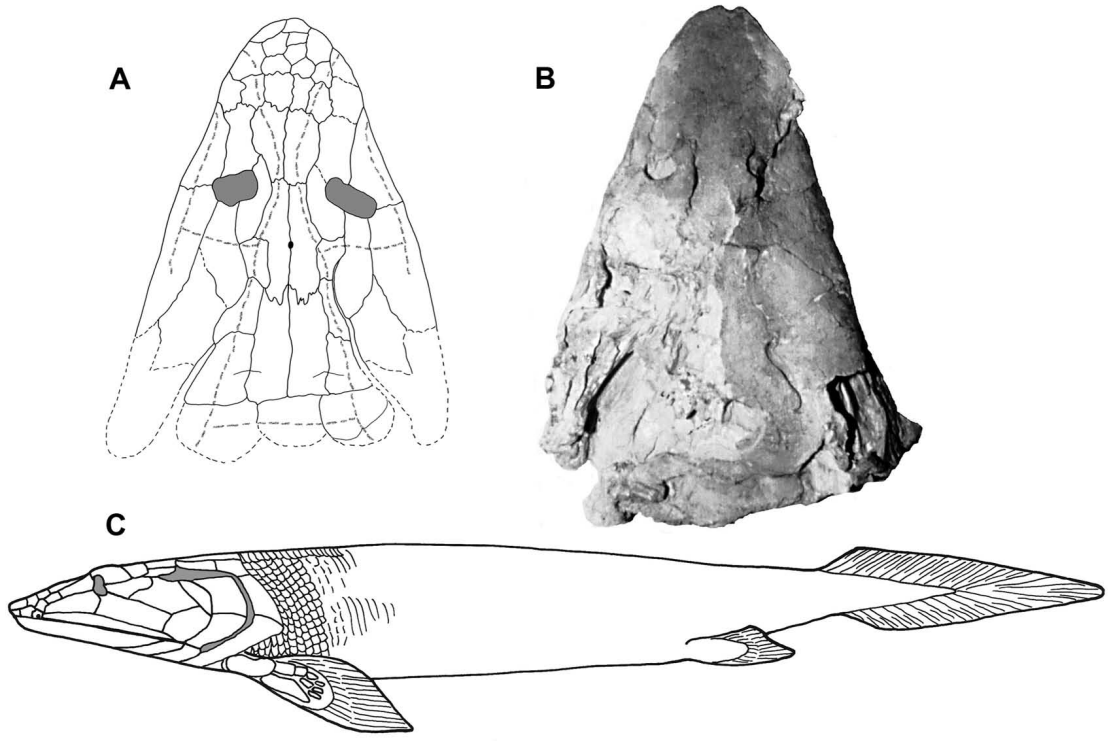

**3.20.** *Elpistostege watsoni.* (A) Skull drawing. (B) Specimen in dorsal view. (C) Specimen in ventral view. *From Schultze and Arsenault (1985).*

the informal terms "near tetrapods" or "elpistostegalian fish" are useful to encompass these three "fishes."

*Elpistostege* was originally described from just a partial skull roof, but in a remarkable piece of insight, the proportions of this small piece suggested to its describer that it was indeed close to a tetrapod (Westoll 1938). Confirmation of its true status came when a second, more complete specimen was discovered in the 1980s (Schultze and Arsenault 1985). *Elpistostege* comes from the same locality and time period as *Eusthenopteron*, the Frasnian deposits of Miguasha. Because it is still only represented by two skull specimens and a small section of vertebral column, its anatomy is not very well known (Fig. 3.20).

*Panderichthys* (Figs. 3.17D, 3.21) comes from a number of localities in Eastern Europe, the most remarkable specimens being from the Frasnian of Lode in Latvia. They include some more or less complete animals. Because these are still covered in their scales, the internal skeleton cannot be seen from the outside, so much of their bone structure remains unknown. However, recent work using micro-CT imaging is beginning to elucidate important features, such as the internal structure of the pectoral (Fig. 2.14A) and pelvic fins.

*Panderichthys* was quite a large fish, with a skull about 300 millimeters long and a total body length of over a meter. Its body and skull were somewhat flattened and the snout rather pointed. The eyes were placed quite close together on the top of its head and were set beneath ridges, giving the impression of eyebrows and creating a subjectively tetrapod-like appearance. Other characters of the skull were also tetrapod-like (Vorobyeva and Schultze 1991). It had a large spiracular chamber, between that of *Eusthenopteron* and *Acanthostega* in size and form (Brazeau and Ahlberg 2006), though its pelvic fin was somewhat specialized with no particular resemblance to a tetrapod hind limb (Boisvert 2005). Its pectoral fin skeleton, however, has recently been described from micro-CT scans of an undistorted specimen, and it shows



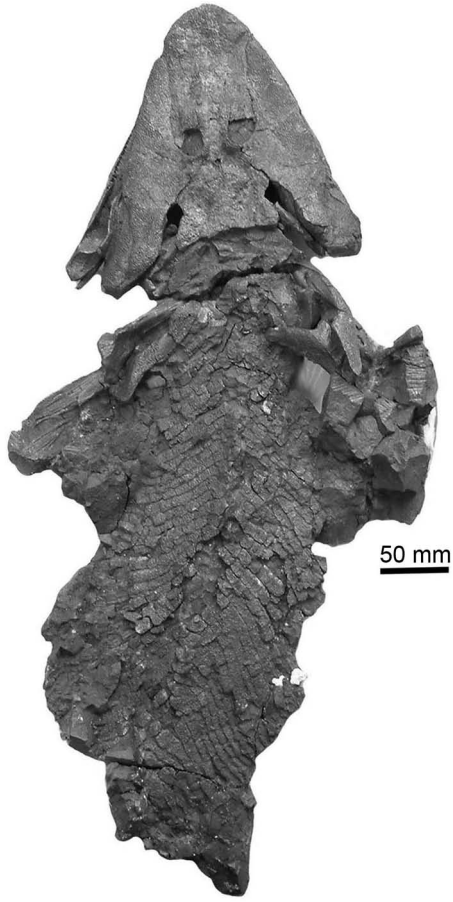

**3.21.** *Panderichthys rhombolepis.* (A) Skull reconstruction. From Vorobyeva and Schultze (1991). (B) Photograph of a specimen in the Institute of Evolutionary Morphology in Moscow. *Photograph by J.A.C.* (C) Reconstruction of *Panderichthys.* Length up to 2 meters.

some intriguingly tetrapod-like features, described in Chapter 6 (Boisvert et al. 2008).

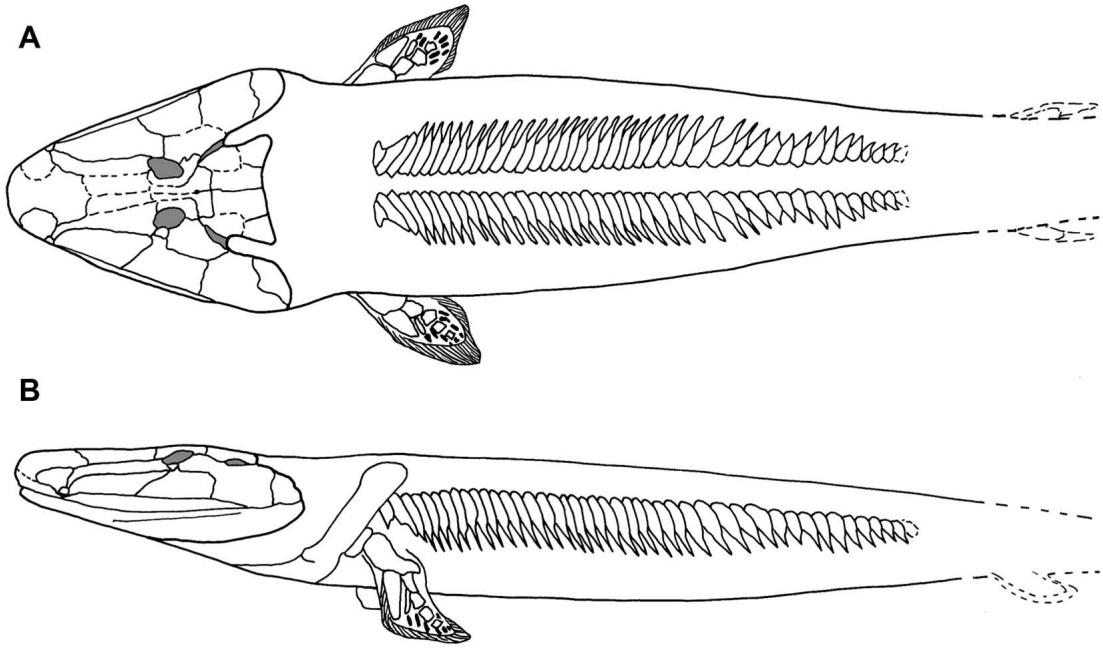
Most recently, almost complete three-dimensional specimens have been found of another animal, *Tiktaalik roseae,* that are similar to *Elpistostege* in many respects. These have been found in Upper Devonian deposits in the Canadian Arctic. *Tiktaalik* is known from a single locality, again Frasnian, but there, many specimens representing differently sized individuals, and showing most features of the anatomy, have been found. *Tiktaalik* has proved to be one of the most important finds in the story of the fish–tetrapod transition to have been made in recent years. It has a combination of characters that placed it in an intermediate position between *Panderichthys* and an early tetrapod like *Acanthostega.* Like *Panderichthys, Tiktaalik* grew to quite a large size, and jaws have been found up to 310 millimeters long. The skull was similar in shape to those of *Panderichthys* and *Elpistostege,* though its snout was a little longer and its eyes a little larger (Figs. 3.22, 3.23, 3.24).

There are two remarkable features of the postcranial skeleton of *Tiktaalik.* One is the long, broadly expanded, overlapping ribs that it possessed. The other is the number of vertebrae found in the most complete specimens. Although the vertebrae themselves are not ossified—in itself surprising—the number can be calculated from the ribs. There were at least 45, an unusually high number for either a fish or a tetrapod.

Although it bore heavy rhomboid scales on its body, and long, thick fin rays on its paired fins, *Tiktaalik* shows other characters in which it is




**3.22.** Photograph of a specimen of *Tiktaalik roseae*. *Photograph by J.A.C.*




**3.23.** Reconstruction of *Tiktaalik roseae*. *Modified from Daeschler et al. (2006).*



**3.24.** Photograph of an exhibit from the Museum of Evolution in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, showing a reconstruction of a Devonian swamp with *Tiktaalik*. *Courtesy of M. Machalski. Photograph by J.A.C.*

more tetrapod-like than *Panderichthys*. The dorsalmost series of bones, the extrascapulars that in fish, including *Panderichthys*, link the shoulder to the head, have apparently been lost, as have the opercular bones, meaning that *Tiktaalik* had the beginnings of a neck. The supracleithral series was still present, so the conversion was not quite complete. It also had robust pectoral fins, and the bones are so well preserved in some specimens that they could be prepared out from the matrix and manipulated against one another to reveal the possible ranges of movement in their joints. It appears that the "wrist" was able to rotate and flex in a way similar to that of a tetrapod, and that suggests a supportive role, raising the forequarters out of water. Additionally, the long imbricating ribs presumably must have borne muscles to keep the body rigid as it did so. Whether it could actually leave the water using its fins as "legs" is not certain. Crucially, the pelvic fin and girdle remain unknown.

For understanding the story of the origin of tetrapods, *Panderichthys* and *Tiktaalik* together provide most illuminating guides. Comparing the differences between *Panderichthys*, *Tiktaalik*, and an early tetrapod such as *Acanthostega* gives some ideas about the order and timing of the appearance of some tetrapod characters, and these will be considered in Chapter 6.

Looking at the tetrapodomorph radiation as a whole, there is a picture of much parallelism among the groups toward the role of ambush

predators in shallow water. The enlarged pectoral fins and lengthening of the snout in rhizodonts and tristichopterids, the evolution of a more elongate body, symmetrical and low-aspect-ratio tail in tristichopterids, the alterative way of forming a mobile occipital joint in *Mandageria*, and the tetrapod-like fin skeletons of the epistostegalian fish attest to such a lifestyle.

## The Dipnomorph Lineage

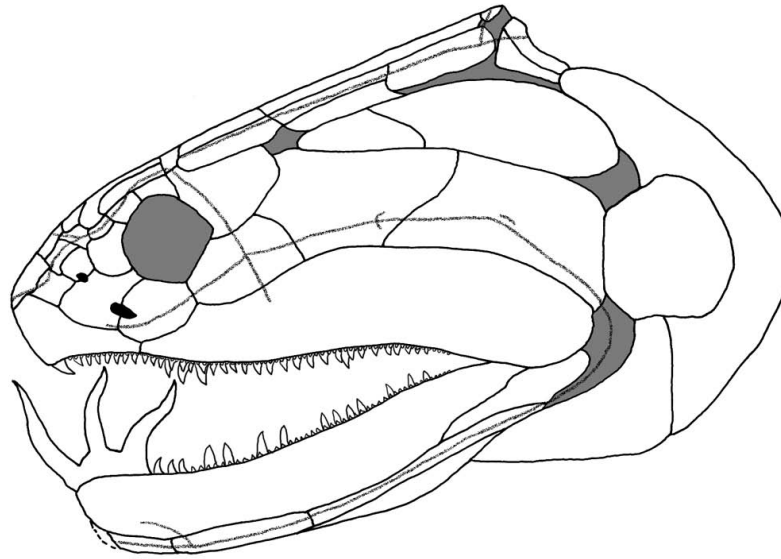
Members of the dipnomorph lineage include the entirely extinct porolepiforms ("hollow scale forms"), and a few basal members as well as the dipnoans. The earliest member of the porolepiforms comes from the Early Devonian of Canada, and it is thus one of the earliest lobe-finned fishes for which other than scattered remains are found. This genus is called *Powichthys*, named after Prince of Wales Island, where it was found. The best-known members of the group include *Glyptolepis* and *Holoptychius*, from the Middle Devonian of Scotland and Late Devonian of East Greenland, respectively (Ahlberg 1991a). Porolepiforms are not found beyond the end of the Devonian.

There are several differences between tetrapodomorphs such as osteolepidids, rhizodonts and tristichopterids, and porolepiforms, though their superficial similarity once caused them to be put together in a group known as the Rhipidistia. However, because they are not each other's closest relatives, this name has fallen into disuse. Both groups retain the intracranial joint in the braincase as well as the skull roof, and one of the easiest differences to spot is that whereas osteolepidids and tristichopterids have four bones ranged across the skull table behind the hinge line, porolepiforms have only two. Where osteolepidids and tristichopterids have short, compact pectoral fin skeletons, porolepiforms have long, lanceolate fins like early lungfishes. Indeed, this is but one of the characters linking porolepiforms to lungfishes.

A couple of primitive genera, *Youngolepis* and *Diabolepis* from the Early Devonian of China, corroborate this relationship by providing glimpses of what the common ancestor of these two groups was like (Chang and Smith 1992; Chang 1995). *Youngolepis* is generally regarded as a basal dipnomorph, whereas *Diabolepis* is usually placed as a basal member of the Dipnoi.

## Onychodonts

This final "fish" group is one that, along with coelacanths, cannot be slotted into the lobe-fin family tree easily. Excellently preserved specimens have been found in Devonian marine sediments of Gogo, Australia, and the skull structure is known in considerable detail (Andrews et al. 2006). However, the postcranial skeleton is not well known, and the onychodonts have only recently been included in any phylogenetic analysis of lobe-finned fishes following the discovery of more braincase material



**3.25.** Reconstruction of a skull of *Onychodus.* Skull is about 170 millimeters long. *Based on Andrews et al. (2006).*

(Lu and Zhu 2010). They were resolved as the sister group to coelacanths in that analysis. The earliest onychodont so far found, *Bukkanodus*, is middle Early Devonian in age and comes from Australia, in the same formation that yielded the earliest coelacanth (Johanson et al. 2007a). Onychodonts did not survive past the end of the Devonian.

Their most characteristic feature is the spiky whorl of teeth that the fish bore at the front of each lower jaw ramus (Fig. 3.25). These teeth are S shaped and would have been hard to dislodge once engaged in their prey. The pattern of growth of these teeth seems to be among the most primitive found among jawed vertebrates, and similar tooth whorls are found in early porolepiforms, the "spiny sharks" or acanthodians, and in the first chondrichthyans. The recently discovered posterior braincase material suggests that they may have had a biting mechanism like that of coelacanths. Most onychodonts were small, although some large tooth whorls are known (Janvier 1996).

## What Is a Tetrapod, and How Is the Group Defined?

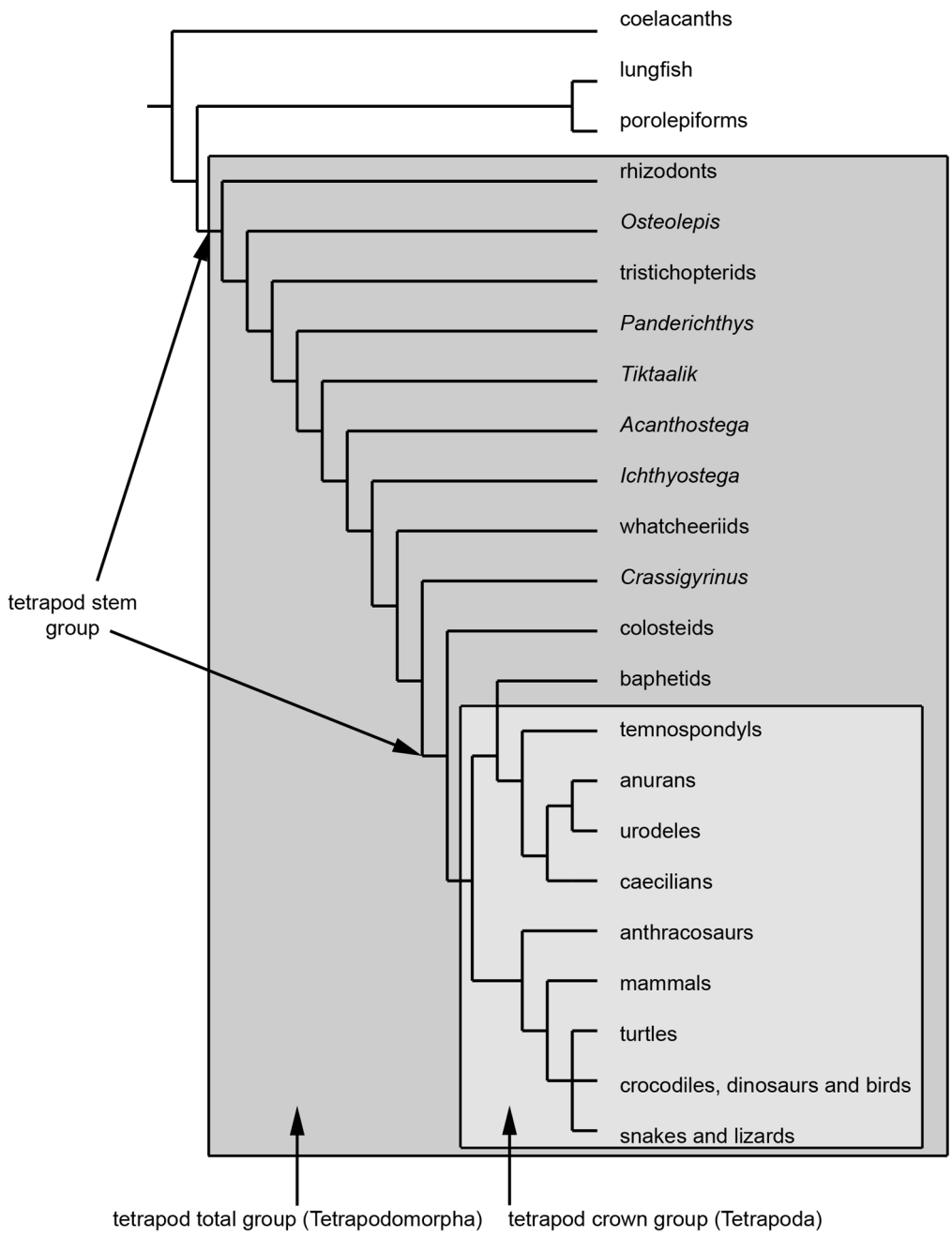
This review of the lobe-finned fish groups is not complete without the tetrapods, because this is where—evolutionarily speaking—they (and humans) belong. Modern tetrapods include on the one hand the amphibians (frogs, newts, caecilians, and their kin) and on the other the amniotes, mammals plus the "reptile" groups (turtles, lizards and snakes, and crocodiles, and their closest living relatives, the birds). It includes creatures that, although they do not have legs (limbs with digits) themselves, are descended from some that did. So bats and whales are tetrapods, as are birds and snakes. It also includes all the fossil forms such as dinosaurs, flying or swimming reptiles, and many other more bizarre and less well-known kinds, so long as they are descended from ancestors with legs (Figs. 1.1, 1.9, 1.11).

Most current views maintain that tetrapods are a natural group, tied together by numerous unique characters showing that the group had a single common ancestor. Among the unique features that tetrapods share is the possession of limbs with digits; the structure of these was explained in Chapter 2.

Although there is a suite of characters unique to most known tetrapods, as this book emphasizes, not all these characters evolved at once, and the sequence of their evolution is unknown in many cases. This is to be expected if tetrapods evolved by a gradual process, which is what most scientists accept. Furthermore, the same must be true of limbs and digits—that they evolved gradually by stages. Thus, difficult questions arise: when can an appendage really be called a limb, and so at what point does a tetrapod really become a tetrapod? In fact, if evolution is gradual, then there is no precise point in the continuum at which a line can be drawn to distinguish indisputably a limb from a fin, or indeed a tetrapod from a fish. What exactly would one choose? Loss of the fin rays? The evolution of wrist or ankle bones that interarticulate? The evolution of multiple, jointed radials? If so, how many would be the critical number? To add to the difficulties, because there are so many unique characters known for tetrapods, limbs and digits may not be the key feature that most usefully separates them from fishes. Some people might, for example, make the case that the evolution of a neck with loss of the operculogular series makes a more biologically significant character to separate the groups. Or others may choose the changes to the braincase that resulted in the stapes penetrating the wall of the otic capsule.

Until recently, the distinction between fossil fish and fossil tetrapods was usually easy to make, once the position of lungfishes had been resolved. However, the discovery of more fossils representing fishlike tetrapods and tetrapod-like fishes, such as *Tiktaalik*, and the discovery of fragments of such creatures for which the limbs are not known, such as *Livoniana*, has raised issues of some importance. The problem has now become even more severe as the transitional series has become better known. Arguments over what exactly a tetrapod is have become highly contentious, and use of the formal taxon Tetrapoda has different meanings for different researchers

In an attempt to sidestep the problems and provide a more stable means to define the limits of key groups of animals, such as mammals, birds, or tetrapods, methods have recently been proposed that are thought to be entirely independent of any single key character. These make use of the phylogenetic relationships of fossil forms to recent ones and are called the node-based and stem-based methods (Fig. 3.26). Both of these more recent methods rely on a cladistic analysis of overall character distribution that is ultimately a statistical process. Thus, no single key character may support some of the more important nodes. Each form has its problems, and as yet, there is no general agreement about which should be used, or even if either form is really more stable or more useful than the old one




that used key characters (e.g., Patterson 1993; de Queiroz and Gauthier 1992, 1994; Lee and Spencer 1997; Benton 2000).

In brief, both forms look at the relationships of modern representatives and define tetrapods in terms of these forms. Amphibians and amniotes must have had a common ancestor at some stage among the early tetrapods that was related equally to both but strictly belonged to neither. (Readers should note that because the earliest tetrapods are not always or

easily referred to either of these modern lineages, they are referred to as tetrapods and not as amphibians.) Although this common ancestor will probably always remain hypothetical, it would lie at the node where the lineages of amphibians and amniotes join. Any fossil form that can be shown to belong to either one of these lineages is said to lie above the node, within the crown group of tetrapods. Any creature that does not belong to either lies below the node in the stem group of tetrapods.

At this point, the crown-group definition would admit only creatures above the node into the formal taxon Crown Group Tetrapoda, with those falling outside it being relegated to stem tetrapods, even though they have four legs. The stem-based method, also known as the total-group method, would admit not only the crown group into Tetrapoda, but also a whole suite of other creatures below the crown on the cladogram, but above the node that admits its nearest living relative. For example, with respect to modern tetrapods, this method would look at the nearest living relative of crown-group tetrapods, in this case most likely (but not certainly) the lungfishes, and pinpoint the node at which these groups separated as being the next most significant. All animals belonging to the tetrapod stem lineage and falling above the split between lungfishes and crown group tetrapods—such as osteolepidids and rhizodonts—would be admitted into the formal taxon Tetrapoda, even though they do not have four "legs" (Fig. 3.26). Coates and colleagues insist that the taxon Tetrapoda should refer to the total group, with animals such as *Osteolepis* included as stem tetrapods (see, e.g., Coates et al. 2008). Others, such as Ahlberg (1991a), Ahlberg et al. (2008), Daeschler et al. (2006), and I use a separate term for the total group: Tetrapodomorpha. This is more in line with researchers in other areas of vertebrate paleontology, who also coin terms for total groups to distinguish them from crown groups, such as Archosauromorpha for the total group and Archosauria for the crown group that includes crocodiles, dinosaurs, and birds. For the purposes of this book, and with the recognition that it can be criticized, the informal term *tetrapod* will continue to be applied to animals with four legs bearing digits.

Other examples of the possibly unintended consequences of using a crown clade definition may be understood by consideration of lungfishes and coelacanths. Crown Group Dipnoi (i.e., lungfishes) would include only the extant genera *Neoceratodus*, *Protopterus*, and *Lepidosiren*, and any other fossil genera that lie on their respective stems. *Neoceratodus* and the other two split from each other around the Early Cretaceous, so that is the time at which Crown Group Dipnoi originated. All lungfishes earlier than that are therefore not members of the crown group. Taking a stance equivalent to that adopted by some with respect to Tetrapoda would mean that none of these creatures could be considered Dipnoi. Similarly, and perhaps an even more extreme example, Crown Group Actinistia consists only of *Latimeria*. No other coelacanth genera could be included in the crown group, so some would not admit them into the Actinistia. Another objection might be made to the possibly undue emphasis that this method gives to living taxa, as if they were more important than

**3.26.** A cladogram showing the differing definitions of Tetrapoda according to the crown group and total group definitions. Note that definition of tetrapods by the key character of limbs with digits would include at least *Acanthostega* and everything more crownward (i.e., more derived than *Acanthostega*.) Because it is not known for certain that *Elpistostege* had digits, its position within the tetrapods would be uncertain. Note also that this is cladogram of the tetrapods is notional. Chapter 9 shows how by some definitions temnospondyls and anthracosaurs would be excluded from the crown group. Under the crown-group definition, all the animals that fell outside the crown group (i.e., those directly related to modern tetrapods) would become members of the stem group, or the tetrapod stem lineage. The term "tetrapodomorphs" can be used to indicate this lineage, and "Tetrapodomorpha" can be an acceptable term for the total group.

extinct ones. People may argue that we can understand the phylogeny of extant taxa more accurately than that of extinct ones, but a glance at the problems figuring out the interrelationships of coelcanths, lungfish, and tetrapods, or anurans, urodeles, and caecilians to each other will quickly show that this is often not the case.

A further complication arises from attempts to date the origin of tetrapods from phylogenetic trees on the basis of molecular data. Clearly this kind of information can only be gleaned from extant animals—that is to say, from tetrapods that define Crown Group Tetrapoda. Thus, the crown-group definition is implicitly used by those building molecular trees, and the dating has to be calibrated on the origin of the crown group. This is almost certainly quite separate from and later than the time of origin of limbs and digits. It is therefore important to be explicit, rather than implicit, about which definition of Tetrapoda is being followed in this case, and also to understand that which fossils are included in Crown Group Tetrapoda is a controversial matter whose resolution may significantly affect the calibration points on the tree (see Chapter 9).

## Historical Background and the Debate about Tetrapod Relationships

Ideas on what tetrapods are, where they came from, and who their closest relatives are have gone through a series of phases over the years, echoing the main concerns, interests, and preoccupations of those who studied the problem. It is revealing to study the history of these ideas as much for what it shows about science and its progress as for what it says about tetrapods.

The first phase belongs to the naturalists of the early to mid-19th century, in the days before Darwin introduced his ideas of descent with modification, or evolution, as it is now better known. In those days, one of the main jobs of the naturalist, who was often not a professional scientist but might be a cleric, a medical practitioner, an explorer, a military man, or a person (there were a few notable women) of independent income, was to classify the inhabitants of the natural world. The hierarchical ordering of groups within groups outlined in Chapter 1 was already well established, and there were few organisms that could not be fitted comfortably into known groups, despite the speed at which new ones were being found. This was a time of expansion and exploration brought about by the Industrial Revolution. Even fossils at that time were recognized as the remains of once-living animals, and most of these were readily fitted into the scheme of things. The natural order was considered to be a manifestation of the order in the mind of the Creator when He made the world. The idea that species could become extinct, however, was new and not accepted by everyone. Thus it was that vertebrates could easily be classified as fish or reptile, mammal or bird. (The distinction between amphibians and reptiles was not yet clearly defined, but for the purposes of discussing the origin of tetrapods as a whole, this is a peripheral issue. What are now known as amphibians were then included within the term

"reptile." This old amalgamation is reflected in the term "herpetology" for the study of amphibians and reptiles.)

The trouble started with the discovery of the lungfish *Lepidosiren* from South America in 1837. Here was an animal that breathed both with lungs like a tetrapod and gills like a fish, that had little in the way of fins, and that had soft tissue resembling in many ways that of tetrapods. This was followed by the discovery of the African and Australian genera. Where did they fit? The earliest work described them as amphibians, but Richard Owen, at the institution that he largely founded and that is now called the Natural History Museum (London), came down on the side of fish. The basis of his decision was the state of the nostrils, because he did not believe that the posterior nostril in lungfishes was equivalent to the choana or internal nostril of tetrapods (Owen 1841). Because Owen was so influential, for a time, this view held sway. The arguments concerned the affiliation of the animals in question, and the problems arose because lungfish did not fit neatly into any of the previously recognized categories. It was a matter of trying to pigeonhole the animals each into its appointed place; the idea of phylogenetic relationships had not yet arisen.

When Darwin published his work on the *Origin of Species* in 1859, it became clear that the hierarchically arranged, nested sets of groups into which the animals fitted was in effect a family tree, and it resulted from the fact that the animals were related to one another by descent. The word "descent" here is crucial because it produced a search not only for immediate kinship relationships, but ancestor–descendant sequences. The search therefore began for tetrapod ancestry. This had two effects. One was to relegate the question of where lungfishes fitted to a side issue: because evolution predicted intermediate forms, it was no longer a surprise to find that some animals could not be slotted into conventional groups. The other effect was to shift the search from among living forms to fossil ones.

One of the first people to classify fishes after the publication of Darwin's book was T. H. Huxley. He coined the term "crossopterygian" for a number of fossil fishes that had fleshy fins, and in 1861, he included fossil lungfishes (not yet recognized as related to living ones), coelacanths (not yet known from living forms), and a number of others. It was the grouping of these forms together that paved the way for the recognition that their fin structure shared certain characters with tetrapod limbs (Fig. 3.27). In 1892, however, E. D. Cope suggested that lungfishes were too specialized to have given rise to tetrapods, and the tetrapods' ancestor should be sought elsewhere among the crossopterygians. However, he spotlighted the crossopterygians as the group from which tetrapods probably arose.

In the early years of this second phase, ideas varied about which animals belonged where among the crossopterygians, and several genera were cast in the role of model for a tetrapod ancestor at different times. For example, the rhizodont *Sauripterus* supplied a model fin from which the tetrapod limb might have arisen. D. M. S. Watson chose *Osteolepis* as a crossopterygian whose skull appeared not only sufficiently unspecialized

**Huxley's Classification of Fishes (1861)**

Ordo Ganoidei
Subordo I—Amiadae (*Amia*)
Subordo II—Lepidosteidae (*Lepisosteus*)
(These two are now both put among ray-finned fishes)
Subordo III—Crossopterygiidae
Fam 1. Polypterini
Dorsal fin very long, multifid; scales rhomboidal
*Polypterus*
(This is also now considered to be a primitive ray-finned fish)
Fam 2. Saurodipterini
Dorsal fins two; scales rhomboidal, smooth; fins subacutely lobate
*Diplopterus, Osteolepis, Megalichthys*
Fam 3. Glyptodipterini
Dorsal fins two; scales, rhomboidal or cycloidal, sculptured; pectoral fins acutely lobate; dentition dendrodont
Sub-Fam. A with rhomboidal scales
*Glyptolemus, Glyptopomus, Gyroptychius*
Sub-Fam. B with cycloid scales
*Holoptychius, Glyptolepis, Platygnathus, [Rhizodus, Dendrodus, Cricodus, Lammodus]*
Fam. 4. Ctenodipterini
Dorsal fins two; scales cycloidal; pectorals and ventrals acutely lobate, dentition ctenodont
*Dipterus,* [*Ceratodus?, Tristichopterus?*]
Fam. 5. Phaneropleurini
Dorsal fin single, very long, not subdivided, supported by many interspinous bones; scales thin, cycloidal; teeth conical; ventral fins very long, acutely lobate
*Phaneropleuron*
Fam. 6. Coelacanthini
Dorsal fins two, each supported by a single interspinous bone; scales cycloidal; paired fins obtusely lobate; air bladder ossified
*Coelacanthus, Undina, Macropoma*
Subordo IV—Chondrosteidae (*Acipenser, Polyodon*)
Subordo V—Acanthodidae ("spiny sharks"; a fossil group now entirely extinct; see Chapter 4)

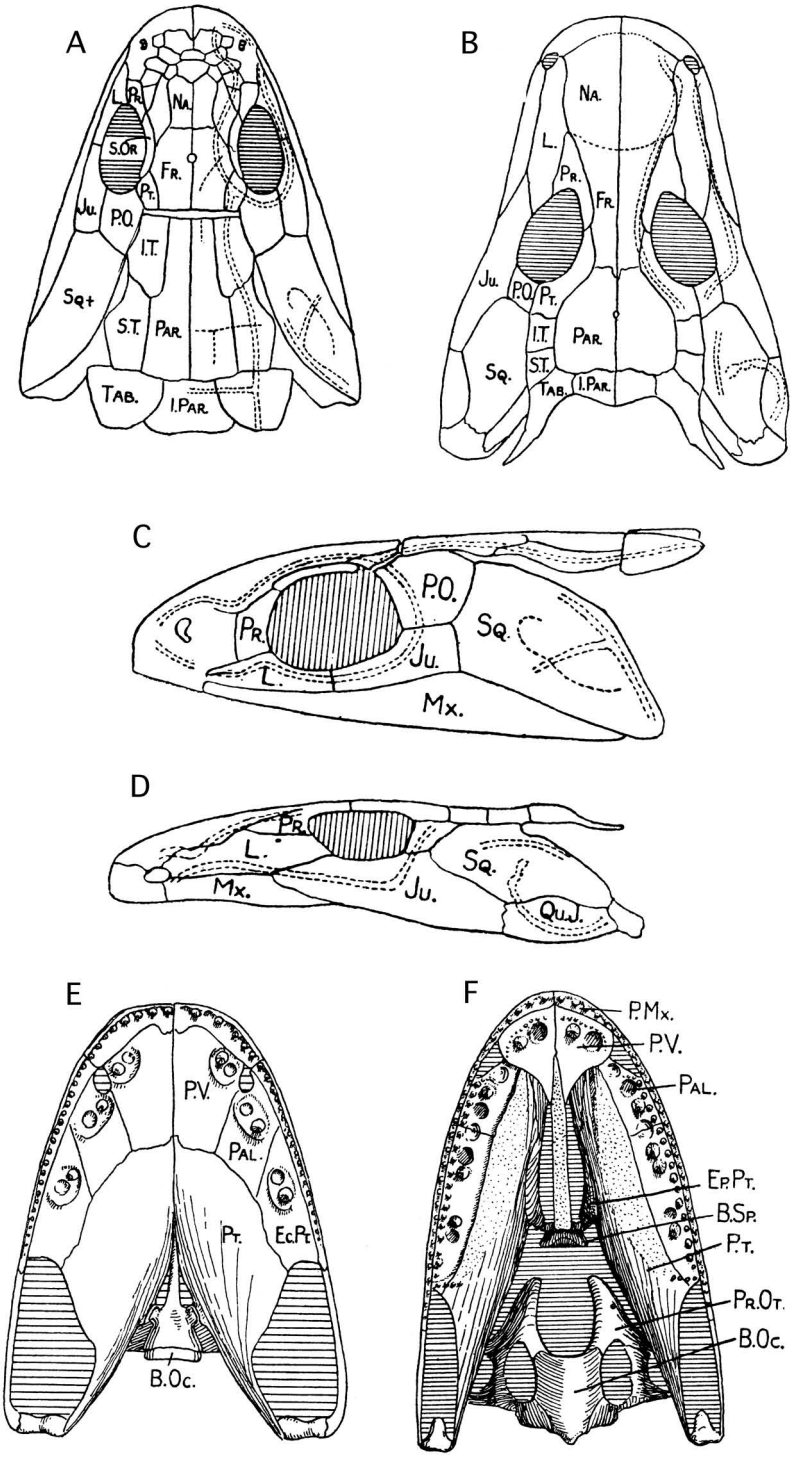
My comments are in parentheses.

Note that this scheme places together animals that we would now separate into lungfishes, porolepiforms. and tetrapodomorphs (e.g., in Fam. 4, the tristichopterid *Tristichopterus* appears in the same family as the lungfish *Dipterus*). However, tetrapodomorphs, porolepiforms, coelacanths, and lungfishes are all included in the crossopterygians.

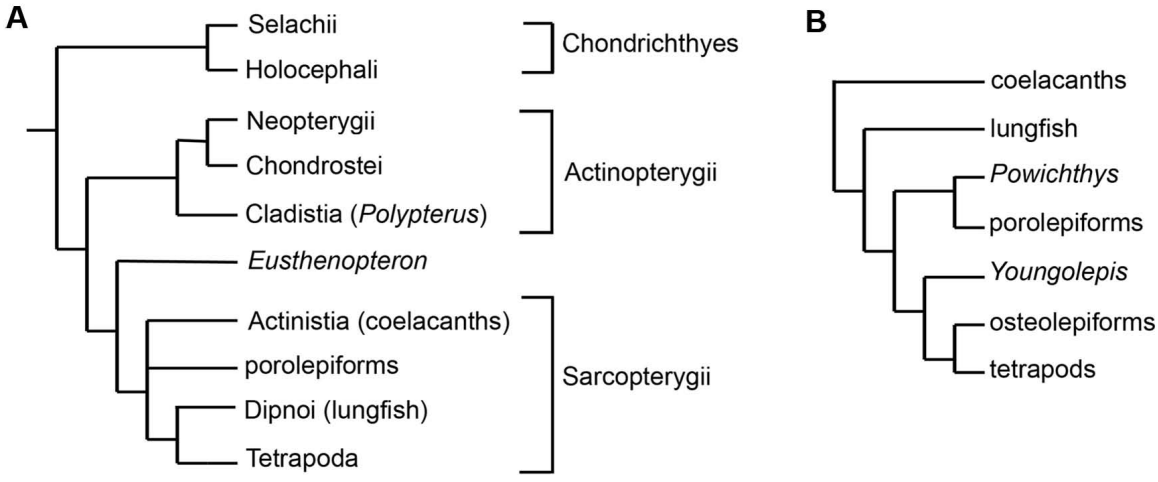
**3.27.** Table showing Huxley's classification of fishes from 1861.

to be a tetrapod ancestor, but also showed a number of similarities in bone pattern and skull construction to the Carboniferous tetrapods that he also described (Fig. 3.28) (Watson 1926). At that time, these were the earliest tetrapods known, and the inferences seemed reasonable to make. However, it was the detailed descriptions of *Eusthenopteron* from Canada that were to make the real impact, and its legacy as a putative tetrapod ancestor has shaped ideas and hypotheses about tetrapod origins to the present day.

Once the lungfishes had been removed from consideration, two or three groups remained among the crossopterygians: the osteolepiforms and porolepiforms, placed together as rhipidistians, and alongside them, the coelacanths (e.g., Romer 1966). Hence, when the modern coelacanth *Latimeria* was found, as a living crossopterygian, it was hailed as the surviving embodiment of a tetrapod ancestor. The problems that its anatomy eventually posed for this theory have been outlined above. Nevertheless, because of how coelacanths had been classified, for most people, *Latimeria* appeared much more closely related to tetrapods than did lungfishes.




**3.28.** D. M. S. Watson's comparison of fish and tetrapod skull structure. (A) Dorsal view of *Osteolepis.* (B) Dorsal view of "*Palaeogyrinus*" (now *Palaeoherpeton*). (C) Left lateral viewof *Osteolepis.* (D) Left lateral view of "*Palaeogyrinus.*" (E) Ventral view of *Baphetes.* (F) Ventral view of *Osteolepis.* B.Oc. = basioccipital; B.Sp. = basisphenoid; Ec.Pt. ectopterygoid; Ep.Pt. = epipterygoid; Fr. = frontal; I.Par. = interparietal; I.T. = intertemporal; Ju. = jugal; L. = lacrimal; Mx. = maxilla; Na. = nasal; P.Mx. = premaxilla; P.O. = postorbital; P.T./ Pt. = pterygoid; P.V. = prevomer; Pal.= palatine; Par.= parietal; Pr. = prefrontal; Pr.Ot. = pro-otic; Pt. = postfrontal; Qu.J. = quadratojugal; S.Or. supraorbital; S.T. = supratemporal; Sq. = squamosal; Tab. = tabular. Some of these names (such as "prevomer") are no longer used, and the bone equivalents recognized by Watson are not universally agreed upon.

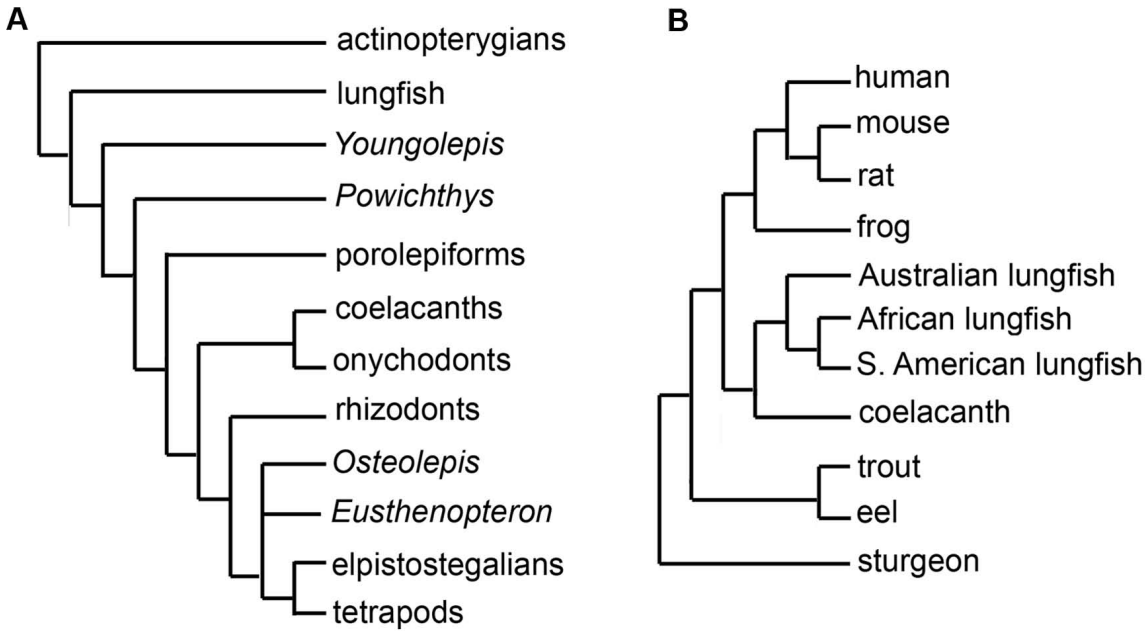



**3.29.** (A) *Cladogram from Rosen et al. (1981).* Note that *Eusthenopteron* falls outside of the sarcopterygians in this cladogram because it lies below the node that unites tetrapods, lungfishes, and coelacanths, the crown-group sarcopterygians. (B) *Cladogram from Panchen and Smithson (1987).*

Because people were interested in ancestry during this phase, the emphasis was on finding more and more primitive or generalized forms to provide the base for an ancestor–descendant sequence. Sometimes this meant erecting hypothetical ancestors that were really combinations of primitive characters never actually found together in any animal, living or fossil. They could be constructed according to taste on the basis of the reasoning and hypotheses that the particular worker favored. The schemes of relationships that were drawn up during this phase were also often based on primitive or generalized similarities—in other words, on the absence of specialized characters. Absence of characteristics, in retrospect, was an unsatisfactory criterion on which to base a classification.

The next phase began in 1981, when a group of workers, who came to be known as the Gang of Four, became discontented with this way of thinking. As a result of the impact of cladistics, they returned to the question of the relationships of tetrapods to living and fossil forms and subjected it to a radical reassessment (Rosen et al. 1981). The philosophy they followed was to take the living animals first, establish their relationships on the basis of shared derived characters, and then slot the fossils into the scheme. If the relationships between the living animals are correctly worked out, this should be a feasible proposition. (Unfortunately, the relationships between lungfishes, coelacanths, and tetrapods are not so easily established as they first appeared, and the jury is still out 30 years later.)

The main conclusion of the work of Rosen et al. (1981) was that lungfishes were more closely related to tetrapods than were coelacanths, in an echo of the original ideas of the mid-19th century (Fig. 3.29A). More surprising still was that they suggested lungfishes and all their fossil kin to be more closely related to tetrapods than any of the so-called crossopterygians. *Eusthenopteron* was relegated to a lowly and primitive branch on the tree of lobe-fins. The years that have followed have proved this work, although flawed, to be one of the most influential in the subject. Its first




**3.30.** (A) *Cladogram from Zhu and Schultze (1997).* The database supporting this cladogram with coelacanths closer to tetrapods than are lungfishes, varies by only a few data points from that of Cloutier and Ahlberg (1997) (3.1). (B) *Cladogram from Zardoya and Meyer (1996), based on molecular data.*

effect was to galvanize other workers to spring to the defense of the more traditional views, and to reassess their own ideas in cladistic terms (e.g., Panchen and Smithson 1987) (Fig. 3.29B). These efforts have culminated in complete reworking of the relationships of lobe-fins, such that terms like "crossopterygian" and "rhipidistian" are no longer used with their original meanings. As they had come to be defined over the years, they embraced what cladists call paraphyletic groups held together only by what they lacked, and part of this problem was caused by the exclusion of the lungfishes. The lungfishes were now returned to the fold, and in most recent cladistic analyses, it is the lungfishes rather than the coelacanths that emerge as the tetrapods' closest living relatives. However, in contrast to the 1981 analysis, a stem lineage of tetrapodomorph lobe-fins including rhizodonts, *Osteolepis*, and *Eusthenopteron* has been established, with many newly described fossil taxa adding support to this idea (Ahlberg and Johanson 1998). Taking account of fossil evidence, many of the lungfishes' soft tissue characters in which they resemble tetrapods appear to be parallel developments, showing not only the danger of using only the living forms for analysis, but also the usefulness of fossil ones.

To sound a final note of warning to end this phase, not all cladistic analyses produce the same result; a few have produced the alternative grouping of coelacanths as more closely related to tetrapods than are lungfishes (Zhu and Schultze 1997, 2001) (Fig. 3.30A). However, the data sets that produced this result were different in only a few details from that producing the lungfish–tetrapod grouping, and they show the fragility of both analyses. Part of the problem stems from the fact that all three groups—lungfish, coelacanths, and tetrapods—have a long evolutionary history separate from one another, which means that they are all rather

different from their early ancestors. The impact of this fact rebounds into the next phase of enquiry.

With the advent of molecular analysis, it might have been hoped that the problem of the interrelationships between tetrapods and their two closest living relatives would be quickly and decisively solved. One could have expected that a straightforward comparison between the structure of a molecule such as the DNA or RNA of each would yield definitive results, and that there would no longer be any need to resort to fossil data. Events have proved otherwise. There are a number of reasons for this. To begin with, the analyses that have been done by different research groups have not used comparable molecular data, or a comparable set of taxa, in their analyses. In order to work out the relationships of tetrapods to lungfish and coelacanths, it is first necessary to compare their molecular structure with those of "fish," to represent the basal or outgroup condition—and here, the choice has varied widely. Then there is the problem of which tetrapod or tetrapods to use as representative, and again, the choice and the number of taxa has varied. No two analyses have used the same set—indeed, most analyses have used either the lungfish or the coelacanth to test against other "fishes" and tetrapods, but not both. Nor have all the analyses used the same molecules; the early ones used amino acids, but some of the more recent studies have used nuclear genes from ribosomal RNA—but again, from different examples. Not surprisingly, not only did the analyses produce different results, but the results were not easily compared with one another. For example, in a study by Stock et al. (1991), the coelacanth and tetrapods emerged as sister groups, but disconcertingly, ray-finned fish and sharks were found nested within tetrapods! This result was tested for its robustness and was found (thankfully) to be only weakly supported by the statistics in any case.

Zardoya and Meyer (1996) tested the most representative sample of taxa using nuclear genes. That study found lungfishes and coelacanths to be sister groups—in other words, neither one was the sister group or closest relative of tetrapods (Fig. 3.30B). This result has some support from a small set of soft-tissue characters, but none at all from fossil data. Other studies using mitochondrial genes suggest lungfishes to be the tetrapods' sister group, but generally the analyses are poorly supported statistically. In 2001 Zardoya and Meyer reviewed the analyses that treated this question using molecular techniques up to that date, and they concluded that some molecular data are probably more reliable than others because some molecules evolve faster than others. The 28S rRNA analysis placed coelacanths and lungfishes as sister taxa, whereas the mitochondrial tRNA analysis failed to resolve the three taxon case of coelacanth–lungfish–tetrapod.

One of the reasons why these molecular analyses have been so inconclusive stems from the fact noted above that the three groups in question have been separate from each other for a very long time. This can be shown in the fossil record incontrovertibly. Their molecular structure has therefore had several hundred millions of years in which to diverge. Even

though coelacanths might be thought to be conservative anatomically, it has already been shown that at least some profound genetic changes, affecting the fins, occurred early during their evolution. Similarly, the lungfishes have evolved adaptations of the skull extreme enough to debar them for decades even from consideration as part of the tetrapod story. Not only that, but the modern forms are different in external appearance, and probably internal appearance, from their Devonian forebears. As for tetrapods, whether one takes modern amphibians or any particular amniote, one is dealing with an animal whose ancestors split from the common tetrapod stock over 300 million years ago. Furthermore, the tetrapods typically used in the analyses (for example, a mammal such as a mouse, or a frog such as *Xenopus*) belong to groups that came into existence no earlier than the Triassic.

Thus, it seems that on the evidence from molecular studies, the question is still unresolved. What about analyses of soft tissue anatomy in the three living groups? Does that fare any better or give firmer clues? The problem here is that analyses have tended to concentrate on individual features or systems. For example, Fritzsch (1987) found an inner ear receptor in coelacanths that appeared to match one found in a similar position in tetrapods and that was not found in lungfishes or anywhere else. Because of this, he suggested that coelacanths were more closely related to tetrapods than were lungfishes. But this is only one character, and the resemblance between the two receptors is not perfect. The two might equally well represent parallel developments.

Since then, a form of nonrespiratory circulatory system has been identified in coelacanths that resembles those of ray-fins and chondrichthyans, but that is not present in lungfishes or tetrapods. This could be read to support a closer relationship between lungfishes and tetrapods (Vogel et al. 1998). The range of circulatory and related features in which lungfishes and tetrapods resemble each other has already been mentioned, but the evidence now suggests that they must have been developed in parallel. Northcutt (1986) found some features of the brain in which lungfishes and coelacanths were more similar to each other than to tetrapods, and though this is difficult to explain away, it remains one of the few pieces of evidence for the grouping.

Recourse to fossils, then, seems inevitable. Despite the distance in time from the split between these three groups, the fossil record is improving all the time with more finds of relevant taxa. For the moment, many of the new discoveries are in fact making things even more confused because they represent animals that span apparently separate groups. For example, *Psarolepis* from the Early Devonian/Late Silurian of China has characters found in placoderms, chondrichthyans, ray-finned fishes, and lobe-fins (Zhu et al. 1999, 2009; Zhu and Yu 2009). At present, the balance of evidence is in favor of its being a primitive lobe-fin, especially on the basis of its newly described pectoral fin structure, which shows the sarcopterygian type of shoulder joint. However, opinions may change as more of its contemporaries are found. Such discoveries will

assuredly affect how the relationships between coelacanths, lungfishes, and tetrapods are viewed in the future. For the moment, it is hard to see that opinion will be swayed away from the idea that tetrapods are the descendants of a tetrapodomorph lineage including fish such as *Tiktaalik*, *Panderichthys*, *Eusthenopteron*, and *Osteolepis*.

One other aspect of the relationships of tetrapods deserves mention here. Throughout this book, the assumption is made that tetrapods are what is called a natural group—that the group had its origins in the Middle to Late Devonian, and that all modern forms are descended from a unique common ancestor appearing somewhat later, perhaps in the Early Carboniferous. This idea is almost universally held today, but it has not always been so.

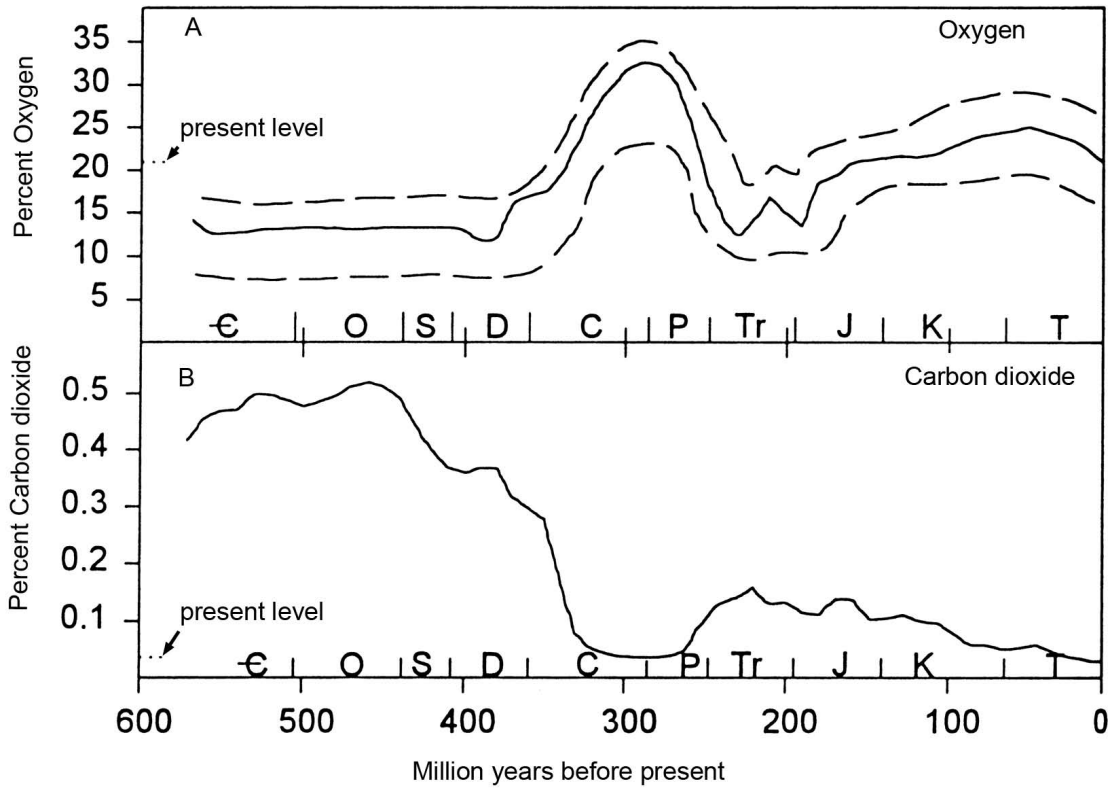
In the 1930s and 1940s, thinking about evolution was only just beginning to take the shape that it has today, in a move called the New Synthesis. This brought together the new sciences of genetics and its spin-off, population genetics, with the older discipline of paleontology. Evolution was seen in terms of adaptive radiation, with adaptation to certain environments more important than their phylogenetic descent in determining animal forms. This permitted the idea that, for example, many vertebrate groups could have been descended from more than one ancestor. Mammals, birds, and particularly teleost fishes were considered by some in this way. There was also an implicit concept of a kind of internal drive to evolve. In this atmosphere, one school of thought became convinced that tetrapods were the product of at least two separate radiations. This school was founded in Stockholm, and its ideas were quite widely taken up in Eastern Europe. There were two versions of the idea, but both recognized a divergence between salamanders on the one hand, and all other tetrapods on the other. Holmgren (1933) suggested that dipnoans gave rise to salamanders, while all other tetrapods were descendants of osteolepiforms (i.e., tetrapodomorphs). Indeed, there is an intriguing number of soft tissue and molecular characters in which salamanders and lungfishes closely resemble each other, though the main thrust of Holmgren's argument was based on the apparently different order in which salamander digits develop compared to those of all other tetrapods. This meant, to Holmgren, that salamanders could not share their limb structure with other tetrapods but must have acquired it separately. Recent reanalysis of salamander embryology has suggested that they have a specialized developmental program for digit production but are not fundamentally different from other tetrapods (see, e.g., Hinchliffe et al. 2001). They may retain some developmental features that are primitive for tetrapods (Johanson et al. 2007b). Furthermore, the apparently unique order of digit development in salamanders has recently been identified in a group of Paleozoic tetrapods, the branchiosaurs (Fröbisch et al. 2007).

By contrast, Jarvik (1942) suggested that salamanders were the descendants of porolepiforms, while frogs and all other tetrapods arose from a fish like *Eusthenopteron*. This, he maintained, was supported by detailed resemblances in the structure of the nasal capsules in the two lineages.

Not many people outside the Stockholm school could accept this conclusion, not least because it seemed that the soft tissue structures, upon which so much reliance was placed, had been reconstructed in the fossil representatives according to the preferred model. Another curiosity was that Jarvik considered tetrapod diversification, as exemplified by mammals, to have sprung directly from *Eusthenopteron* with no recognizable intervening stages. Thus, he viewed the skull and soft tissue of a mammal as having its exact counterpart in *Eusthenopteron*, whose soft anatomy could thus be reconstructed.

Today, overwhelming majority of workers accept that the long list of characters held in common by all living and, where known, by almost all fossil tetrapods is evidence that they form a monophyletic clade with a single common ancestor. It is now realized that not all these common characters arose at once, and some of the new preoccupations include questions of which arose first, along with when and how. Much of this book is devoted to how some of these questions are currently being answered.

Further information on some of the topics covered in this chapter can be obtained from the following books. For coelacanths, Smith (1956) gave his original account of the finding of the first and second coelacanths. Weinberg (1999) updated this with the story of more recent finds. Musick et al. (1991) covered aspects of the biology of *Latimeria*, and Forey (1998) provided a detailed account of all fossil coelacanths as well as aspects of the biology of *Latimeria* and the problems of determining the relationships of coelacanths to other lobe-fins. For lungfishes, Bemis et al. (1987) provided details of the anatomy, physiology, and ecology of modern lungfishes as well a bibliography of fossil forms, with a recent update (Jørgenson et al. 2010) providing more data. For a less technical account of Paleozoic and other fossil fishes, Long (1995) is both entertaining and well illustrated.




**4.1.** Graph of (A) and (B) levels through time from Graham et al. (1997). C = Carboniferous; Є = Cambrian; D = Devonian; J = Jurassic; K = Cretaceous; T = Tertiary; Tr = Triassic; O = Ordovician; P = Permian; PAL = present atmospheric levels; S = Silurian.

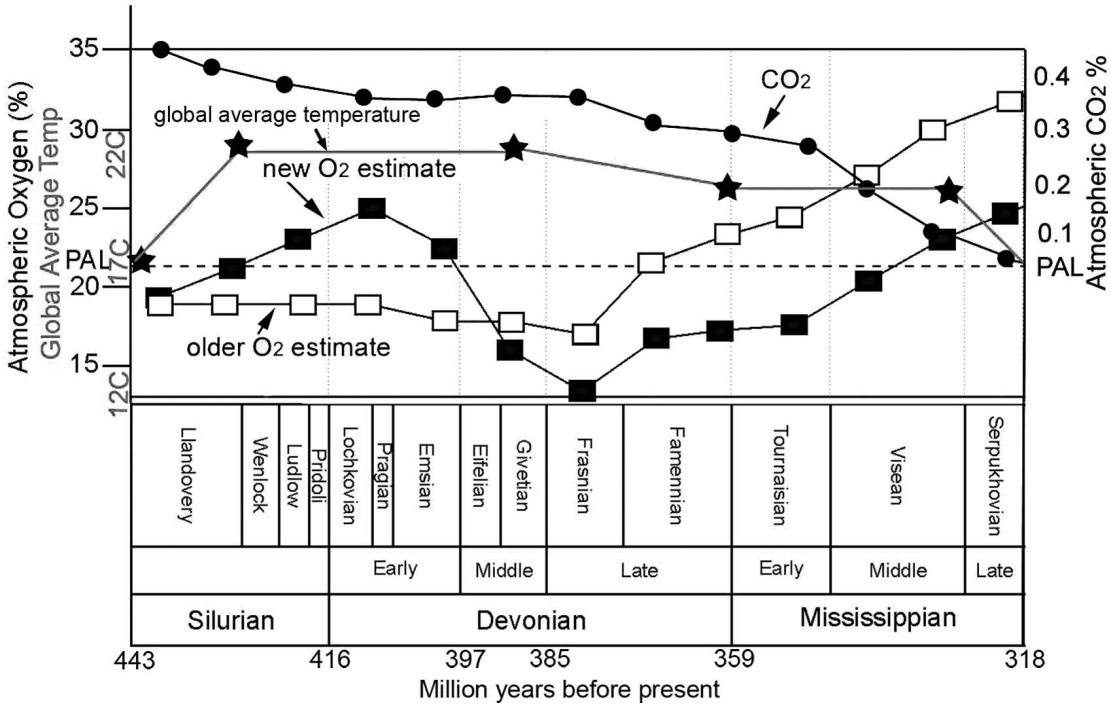
# Setting the Scene: The Devonian World

# 4

## Devonian Biogeography and Climate

The Devonian period opened onto a world far different from the present day. In the earliest stages, over 400 million years ago, even the oxygen content of the air was different from today. According to some models, at the beginning of the Devonian, the air contained about half the present levels of oxygen ($O_2$) but about 10 times the present amount of carbon dioxide ($CO_2$) (Fig. 4.1). Estimates of $O_2$ and $CO_2$ levels were produced by Berner and colleagues (Berner 1993, 1999) based on factors including increasing radiation from the sun over the last 570 million years and how that has affected weathering rates of carbonates and silicates, and how the increase in plant cover changed the rate of weathering as well as the uptake of $CO_2$ from the air. The models were backed up by evidence from carbon isotope studies of fossil soils. The effects mean that because $CO_2$ is less dense than $O_2$, the total air density was less than it is now. Generally speaking, the levels of $CO_2$ are estimated to have been higher than present levels throughout the Devonian, dropping from about 0.35% in the Early and Mid Devonian to about 0.3% by the end of the Famennian. Causes for this drop are suggested to be the increased rates of burial of organic carbon and enhanced weathering of silicates. These processes also had an effect on climate cooling (Algeo et al. 2001). Present atmospheric levels of 0.03% were reached by the mid-Carboniferous (late Mississippian) (Fig. 4.1). It is an example of the influence of the increase in land plants covering the Earth, using $CO_2$ and giving out $O_2$.

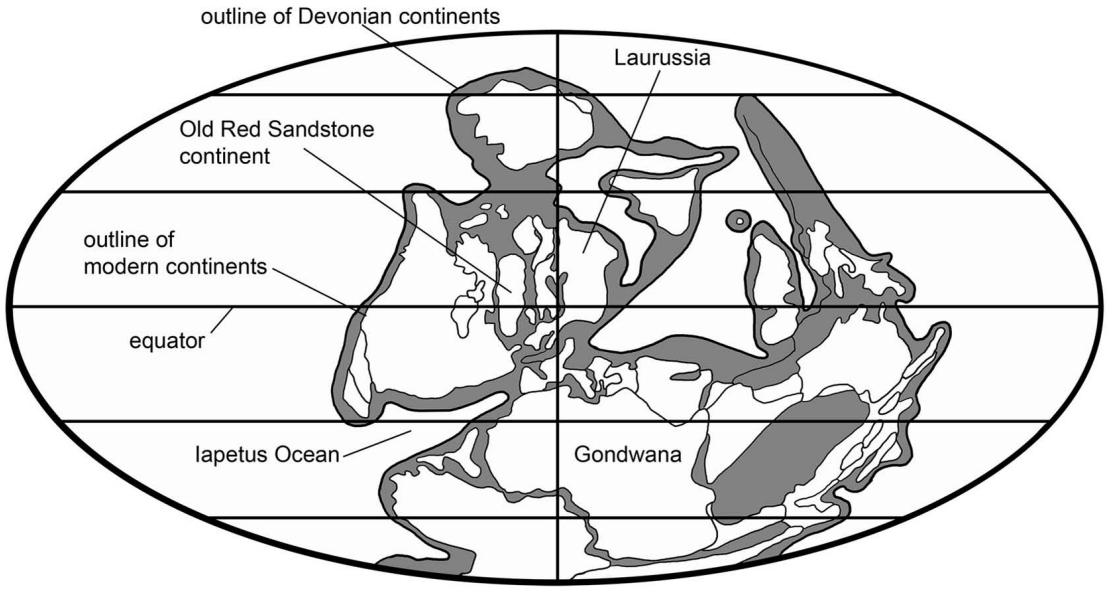
Those estimates suggested that during the Early and Middle Devonian, $O_2$ levels were somewhat lower than the present 21%, dropping slightly from about 19% to about 17% by the middle of the Frasnian, then rising steadily throughout the Mississippian to reach about 33% by the end of that period (Fig. 4.1) (Berner 1999; Berner et al. 2003). However, a new model for estimating $O_2$ levels has been produced that combines and refines previous models; it gives a new estimate for the Devonian. These are based on a GEOCARBSULF model (Berner 2006). This computer-based model uses factors such as weathering rates of calcium and magnesium silicates and pyrite, organic matter decay, degree of exposure of coastal lands, and the variability of volcanic rock weathering, to obtain its estimate. In contrast to earlier estimates, the new figures suggest that during the Early Devonian, $O_2$ levels first rose from about 22% to nearer 25%, but then dropped precipitously through most of the rest of the Devonian until the end of the Frasnian, at which point they were as low as 13%. Levels then rose slowly to reach about 16% by the end of the Famennian, reaching present levels by the mid-Viséan (Fig.




**4.2.** Graph of $O_2$, and $CO_2$ levels, and global average temperature during the late Paleozoic from Berner (2006). PAL = present atmospheric levels.

4.2). The result of these changes profoundly influenced the rest of life on Earth in ways that are only recently beginning to be appreciated (e.g., Dudley 1998; Graham et al. 1997; Ward et al. 2006; Clack 2007). It must be stressed that these are only models and thus provisional. Techniques can change and different data can be used, and other conclusions can be reached. Future research may suggest new views of the Paleozoic climate and atmospheric régimes.

The continents as they are today did not exist in the Devonian or preceding periods, but separate chunks lay scattered around the oceans. Even the length of the day was different. The Earth has been steadily and gradually slowing down since its origin, and so in the Devonian it was spinning faster than today, making the days shorter. At that time, however, the sun seems to have been less bright. From essentially bare beginnings in the Early Devonian, life on land underwent explosive evolution throughout the late Paleozoic, so that by the middle of the Carboniferous period, forests with essentially modern ecological structure flourished, with plants and animals showing comparable interactions with each other as they do today, except that until the latest Carboniferous, there were no terrestrial vertebrate herbivores. A comprehensive summary of terrestrial ecosystems through the Paleozoic can be found in DiMichele and Hook's (1992) chapter in the volume *Terrestrial Ecosystems through Time* edited by Behrensmeyer et al. Details have changed since it was published several years ago, but the overall sweep of the conclusions still paints a good picture of the times. A volume of collected papers, *Wetlands through Time*, edited by Greb and DiMichele (2006) provides




**4.3.** Paleogeographic map of Devonian continents during the Late Devonian (about 370 million years ago).

an updated picture with details of intensively studied sites, mainly from the late Paleozoic. Another volume, *Plants Invade the Land*, edited by Gensel and Edwards (2001), includes studies of Silurian and Devonian floras and faunas.

Throughout the period from the Late Devonian to the end of the Paleozoic Era, which closed at the end of the Permian period, the world went through enormous, though gradual, changes. This whole long episode of time is marked by movements of the continents into new configurations, which in turn affected the climate. Different continents experienced glaciations as they slid slowly over the poles. Continents sitting over the poles means much greater thicknesses of ice are possible than when just the sea lies over them (the same is seen today in comparing the present-day Antarctic with the Arctic, with the latter covered only by sea ice), and in turn this affects the climate of the whole Earth (Erwin 1995, 2006; Erwin et al. 2002). The changed positions also had profound effects on the circulation of water currents around the globe, which in turn affects the distribution of warm or cold water, thus affecting climate.

By the Early Devonian, the continents had coalesced into two major land masses, Laurussia to the north and Gondwana to the south, separated by a sea that geologists call the Iapetus Ocean (Fig. 4.3). When continents coalesce, the total length of seacoast decreases, limiting the available areas and habitats for marine animals to live in. At the same time, more communities are brought into more direct contact. The effect of this is to decrease the diversity of species. When communities are isolated, they tend to evolve away from each other into local specialized and unique species, but when they are brought together, each species has the opportunity to colonize greater areas, and communities become more cosmopolitan. The effect on marine species during the late Paleozoic was

thus a gradual decrease in species diversity, with a corresponding increase in the area of distribution of those remaining (Briggs and Crowther 2001).

Throughout the Devonian, Laurussia and Gondwana were gradually moving together, a process that ultimately ended in the Permian with the formation of the supercontintent Pangaea, and the inevitable squeezing out and eventual closure of the Iapetus Ocean. This had a number of profound consequences for life on Earth.

The gradual closure of Iapetus with the loss of marginal marine or nearshore habitats may have had the indirect result of forcing many organisms into terrestriality. Certainly more terrestrial habitats became available with the accompanying reduction of aquatic ones. The process of continental collision and loss of coastline habitats seems to have been going on throughout the Devonian, and in the Middle Devonian, present-day North America and northwestern Europe were brought together into what is known as the Old Red Sandstone Continent, or Laurussia. Vast areas of terrestrial sediments are associated with this continent, and in them are found fossils of the first known vascular plants and insects. It is here that Devonian tetrapod remains were first found, in Greenland. However, more recently, not only have they turned up in eastern North America, also part of Laurussia, but they are now also known to have been present in both Australia and China by this time. Australia lay far away on the eastern end of the southern continental landmass, and China lay on an isolated northeasterly positioned one.

With the position of large continental masses (today's Antarctica, South America, and South Africa) in polar regions, the world experienced glaciations on an episodic but gradually increasing scale throughout the late Paleozoic. In their turn, the development of large ice caps tied up water and lowered sea levels generally. This was another cause of reduction of marine habitats throughout the interval. Toward the end of the Permian, the glaciation gradually came to an end, and the supercontinent Pangaea had formed by the coalescence of the northern continents with the southerly Gondwana. This produced a huge area of land that experienced continental climates of extremes of temperature, because land gets hotter than water, and in turn, this affected the global climate, producing desert conditions over much of the land surface.

The Earth also experiences periodic fluctuations in its position relative to the sun. Combinations of circumstances in its orbit and declination, added to cyclical changes in the sun itself, combine to create slowly repeating cycles in the Earth's temperature and insolation. These are known as Milankovitch cycles after their discoverer, and they still operate today. They are responsible for cyclical changes to climate with effects such as periodic glaciation, and their periodicity is recorded in the rocks. For example, they can be seen in the cycles of alternating red and green bands in the so-called red-bed deposits of the Devonian of East Greenland (Fig. 4.4) (Olsen 1994; Astin et al. 2010), as well as being partly responsible for the cyclic deposition seen in coal deposits (see Chapter 7). These relatively short-term cycles, over timescales of tens or

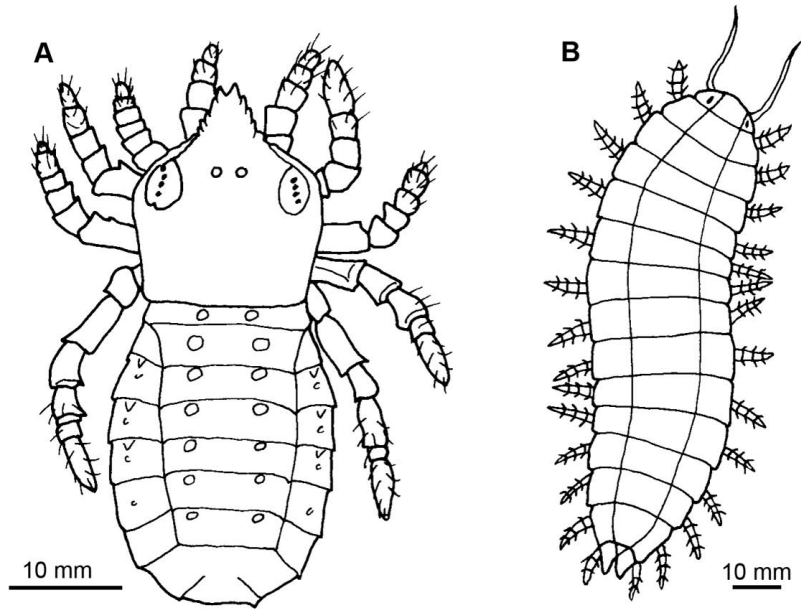


**4.4.** (Color Plate 1) Stensiö Bjerg in Greenland showing alternating red and green strata. These layers represent repeated cycles of depositional circumstances, probably influenced by globally occurring events such as the Milankovitch cycles. *Photograph by J.A.C.*

hundreds of thousands of years, must be added to the effects of changing oceanic currents and continent positions taking place over millions of years during the Paleozoic.

## Early Evolution of Plants and Animals

It is hard for people today to imagine the world as it must have been in the middle of the Paleozoic. We can scarcely envisage a world without birds and insects in the air, or grass covering the hills, or even familiar land animals, small or large. These are so much part of everyday life that we take them for granted. But when the story of tetrapods opens,

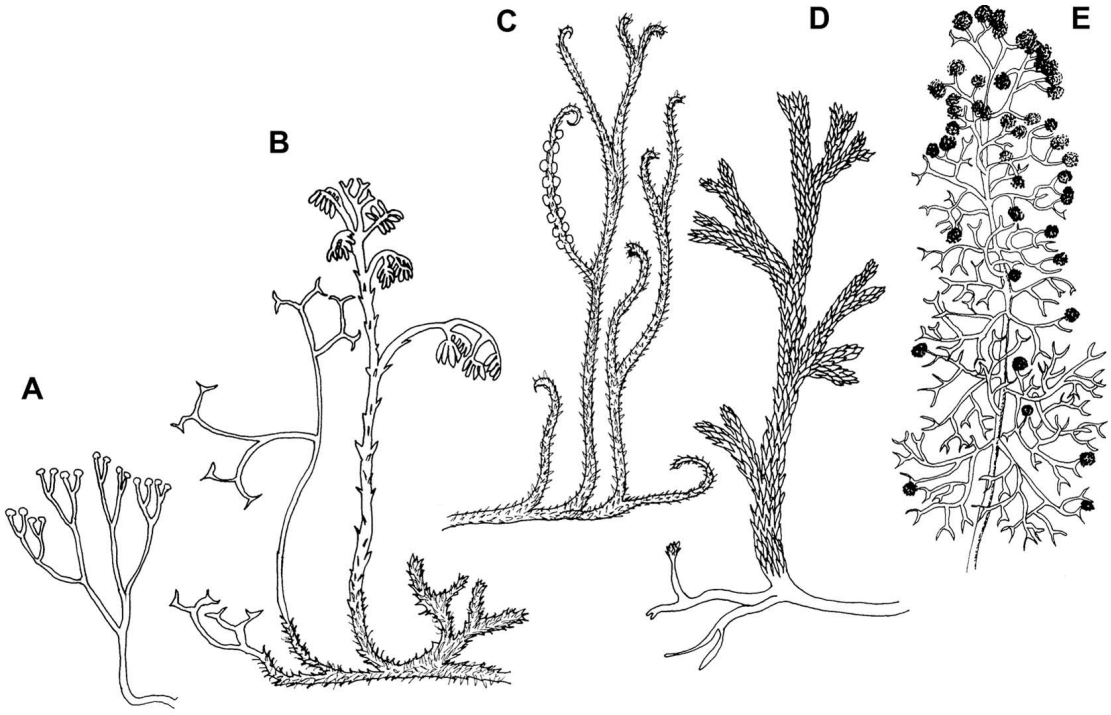



**4.5.** Drawings of Early Devonian arthropods. (A) Trigonotarbid from the Rhynie Chert. (B) Arthropleurid myriapod. *From Rolfe (1980).*

nothing moved on the land except water and wind through low-growing plants. Nothing moved in the air except dust and occasional dead plant stems—leaves had yet to evolve. Apart from the wind, the world would have been not only still, but silent.

The earliest record indicating the existence of land plants dates from the Late Ordovician (Wellman et al. 2003) and consists of spore-containing plant fragments thought to be from liverworts. Apart from this, little is known about what grew or moved on the land surface before the beginning of the Silurian. During the Silurian period, organisms such as liverworts, lichens, fungi, and mosslike plants existed that could inhabit humid nearshore habitats (Kenrick and Crane 1997), and there is evidence of terrestrial arthropods from late in this interval (Jeram et al. 1990). Leafless, sticklike plants without true roots, such as *Cooksonia*, could grow around the shores of shallow lakes and rivers. Only close to the water's edge and in shallows would there have been significant vegetation, and here, deposits of decaying plant matter may have formed sufficient organic debris to provide footing for plants to send up stems into the air, allowing invertebrates to climb in and around them. By the end of the Silurian, quite complex plant communities are known from some sites (Tomescu and Rothwell 2006).

The earliest known body fossils of terrestrial arthropods, are millipedes from the mid-Silurian, among the earliest known air-breathing animals of any kind (Wilson and Anderson 2004). Trackways of probable millipedes are recognized from earlier rocks and suggest that even as early as the Ordovician, some arthropods were terrestrial for at least part of the time, and may have breathed air (Shear and Selden 2001). The evolution of true vascular plants with water-conducting tissues and pores for gas exchange had happened by the end of the Silurian. Arthropods




**4.6.** Drawings of Early Devonian plants (not to scale). (A) *Cooksonia caledonica,* Late Silurian through Early Devonian, a primitive vascular plant a few centimeters high. (B) *Psilophyton crennulatum,* latest Early Devonian, a trimerophyte up to 1 meter high. (C) *Sawdonia ornata,* a zosterophyll showing fruiting bodies, stems up to 1 meter high. (D) *Asteroxylon mackei,* a prelycopsid, stems up to 1 meter high. (E) *Pertica quadrifaria,* a trimerophyte up to 2 meters high, and probably one of the tallest plants of the period.

such as millipedes, scorpions, and trigonotarbids—distant relatives of spiders—appear in numbers in the fossil record during the Devonian and were living among the plants (Fig. 4.5) (Rolfe 1980; DiMichele and Hook 1992). However, none of the plants grew very large, and they formed little cover for animals to hide in. Each type of plant tended to grow in its own small colony, and there was little interaction between plant types, unlike the situation today.

By the beginning of the Devonian and throughout the early part of the period, the vegetation expanded and diversified, and by the middle of the period, the flora can be divided into provinces according to latitude. The story of the Devonian period is one of diversification by land plants and invertebrates so that by the end of the period, a rich and diverse flora and fauna existed. The increase in plant cover seems to have been sufficient to change the balance of the atmosphere so that $CO_2$ decreased as it became tied up in plant tissues.

### Early–Middle Devonian Plants and Animals

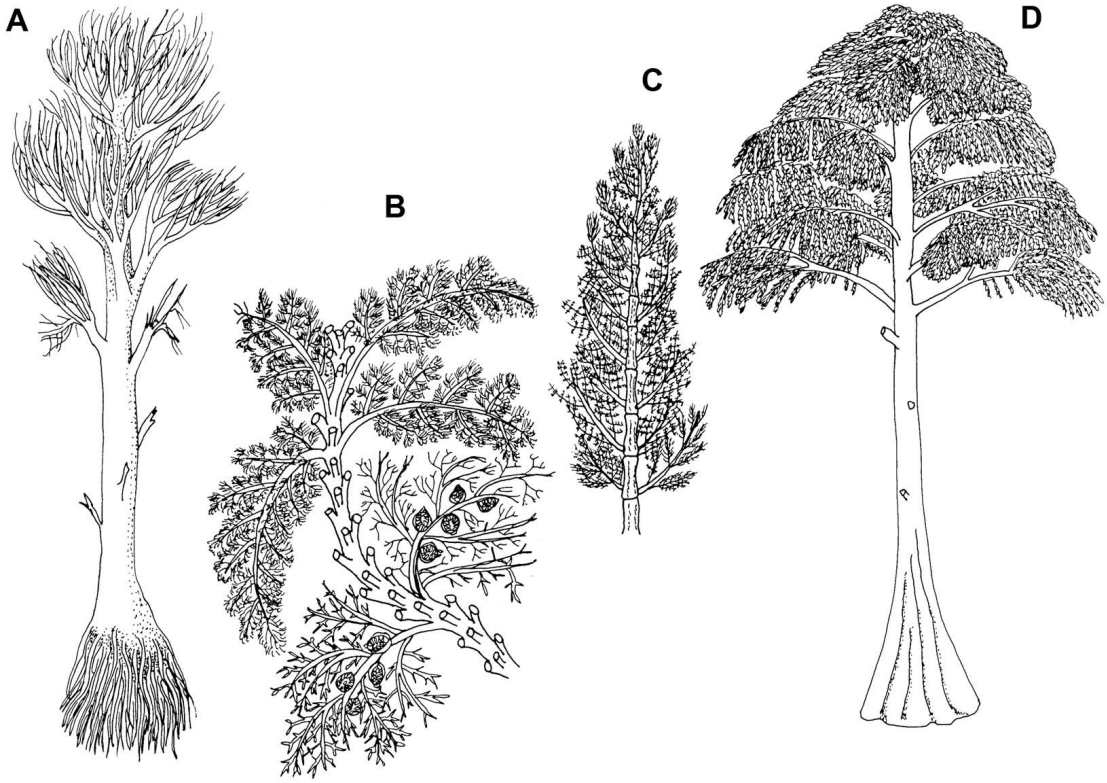
During the early parts of the Devonian, plants evolved into more complex forms, with at least three new major groups appearing for the first time, such as the extinct zosterophylls and trimerophytes, or becoming more diverse, such as the lycopsids or club mosses, which are still around today. Instead of simple stalks, these new forms developed branching stems with small leaflike structures, and some were up to 2 meters tall. One of the tallest of these was the trimerophyte *Pertica* (Fig. 4.6). Lycopsids lived

only in wet places, though there is evidence of specialization to different habitats among them. They may even have grown thickly enough to stabilize the courses of streams, limiting flooding (DiMichele and Hook 1992). From some sites, there is evidence that such plants grew in coastal habitats, either in brackish water or in sites that were periodically flooded by marine incursions (Hotton et al. 2001).

At one locality in Scotland, the flora and fauna are spectacularly well preserved because silica-bearing water mineralized plant and animal remains. The rock formation is known as the Rhynie Chert, and it has provided an immense amount of information about Early Devonian life. The site seems to have been a wetland area in a hydrothermal basin, and several types of habitat—floodplains, ponds, and lakes, and marshlike areas—are represented. A site at Gilboa in New York State, which is a little younger, has provided comparable information about the Middle Devonian (Shear et al. 1984; Shear and Selden 2001).

From these and a few other the Middle Devonian localities, it is known that a variety of arthropods were living among these marginal plants. These included the millipede-like arthropleurids, centipedes, scorpions, pseudoscorpions, mites, and large predatory trigonotarbids (Rolfe 1980) (Fig. 4.5). Close relatives of the modern crustaceans, *Triops*, the tadpole shrimp, and *Artemia*, the brine shrimp, are known from Rhynie, though these were purely aquatic. The first spiders to show evidence of silk production are known from Gilboa, and the earliest insect is known from the Early Devonian of Canada. Springtails, wingless hexapods, are known from Rhynie, and recent work has shown that remains of true insects (perhaps even ones with wings, though that remains speculative) were also present there (Engel and Grimaldi 2004). However, generally throughout the Devonian, the fossil record of insects is poor. Most of the arthropods were predators who presumably fed on each other, though some plant fossils show damage to leaves and stems, indirect evidence of limited herbivory in arthropods. However, it is also possible that this damage resulted from the plants being chewed after they died and became part of the detritus. True herbivory among arthropods may not have arisen until later, in the Early Carboniferous.

During the early and middle parts of the Devonian, the climate was warm and seasonally dry, at least in some parts of the world. It was during this period that large plants first came to dominate the landscape. During the Middle Devonian, several groups of plants achieved bushy, shrublike forms and small treelike statures, including primitive fernlike types (Fig. 4.7), primitive ancestors of the conifers and horsetails of today. Lycopsids and progymnosperms such as *Archaeopteris* attained treelike morphologies, the latter up to 18 meters tall, for the first time. They would have produced a significant canopy layer, thus providing shade for early terrestrial animals. Figure 4.8 shows a habitat dominated by ferns and lycopsids on the island of Santiago (San Salvador) in the Galápagos Islands today. They are miniature representatives of the sort of landscape that would have existed in the Middle Devonian.




**4.7.** Drawings of Late Devonian plants (not to scale). (A) *Calamophyton* sp., a primitive lycopsid several meters high. (B) *Rhacophyton ceratangium,* an early prefern, about 1.5 meters tall. (C) Top part of *Pseudobornia ursina,* a sphenopsid (early horsetail) up to 20 meters high. (D) *Archaeopteris* sp., a progymnosperm up to 20 meters high.

The Middle and Late Devonian were times of unprecedented change in the appearance of land surfaces across the planet. It saw the expansion of size (both height and average axis diameter), taxonomic and morphological diversity, and habitats and area of ground cover occupied by land plants. This had a profound effect on the entire global system (Algeo et al. 1995; Algeo et al. 2001; Algeo and Scheckler 1998). The increase in plant productivity increased consumption of $CO_2$, contributing to a lowering of atmospheric levels of the gas and indirectly or directly, this led to a cooling of global temperatures and ultimately an end-Devonian glaciation.

During the middle of the Late Devonian, at the boundary between the Frasnian and Famennian stages, significant changes are seen in the flora. By this time, plants were diversifying and adapting to different types of landscape, some to the wetter, waterlogged places such as *Archaeopteris,* and some to the drier, better-drained uplands. *Archaeopteris* became a dominant form, as it remained until the beginning of the Carboniferous (Fig. 4.7). It contributed to a great increase in plant density at this time (Algeo et al. 2001). After its origin in the Givetian, it dominated the land surface until about the mid-Famennian, after which it began a slow decline, followed by extinction in the Carboniferous. At its peak, it reached heights of 30 meters, with trunk diameters of 1.5 meters. *Archaeopteris* produced many species throughout the interval and into the Early Carboniferous. These assumed many different habits, the best known



**4.8.** (Color Plate 2) Photographs of ferns and lycopsids on the island of Santa Cruz, Galápagos. Ground cover vegetation in the Middle Devonian may have looked something like this. *Photograph by R.N.G.C.*

forming extensive forests of trees with woody trunks of up to 1 meter diameter, especially in wetter places such as floodplains and stream valleys.

Ferns like *Rhacophyton* were common in peaty swamps, while the lycopsids evolved huge treelike forms called lepidodendroids, dominating wetland forests so densely that their remains formed the first coal deposits. The lycopsids maintained their dominance in these swamp forests until nearly the end of the Carboniferous. However, these types of plant, reproducing by spores and confined to the wetlands, were by the end of the Devonian essentially ancient relict species. In the drier regions, new forms were evolving that reproduced by true seeds with tough coats. This allowed them to cope with periodic environmental disturbances and reproduce in seasonally dry conditions. These plants were the seed ferns or pteridosperms, which became dominant during the Carboniferous (Fig. 4.7). The Famennian saw the initiation of the first forests with a structure analogous to modern ones.

Other plants that contributed to plant expansion were tree lycopods such as *Lepidodendropsis* and *Cyclostigma*. Cladoxylalean ferns such as *Pseudosporochnus* and the zygopterid fern *Rhacophyton* were also substantial plants that occupied wetland habitats. *Rhacophyton* seems to have been able to tolerate a wide range of conditions that allowed it to be a pioneer plant in the creation of marshy conditions (Greb et al. 2006). All these plants produced complex root systems, but particularly in the progymnosperms they were massive and deep, disturbing the land surface and creating deep soils for the first time. Additionally, these plants shed leaves and branches (DiMichele and Hook 1992), creating surface litter that was home to detritivores, bacteria, and fungi.

Some specimens of *Archaeopteris* from the late Frasnian show growth rings, indicating seasonal stress (DiMichele and Hook 1992). Growth rings in trees today form when times of slowed growth during climatic stress (possibly annual, essentially winter) alternates with more rapid growth in better times (spring and summer). *Pseudosporochnus* from the Eifelian of Belgium and *Wattiezia* from the Givetian of New York State are some of the first plants known to have had abscission layers at the bases of their leaves, and the leaves were shed as these treelike forms grew (Berry and Fairon-Demaret 2002). Effectively, they became deciduous, presumably as another response to the climatic deterioration.

In turn, the increase in plant activity along the water margins and on nearby land may have influenced the evolution of air breathing in vertebrates. Several factors may have contributed to this. As plants grew larger, their roots became correspondingly larger, so their root activity increased, forming deeper organic soils. Algeo et al. (1995) showed a 100-fold increase in the average diameter of fossil plant stems during the Devonian that occured contemporaneously with the decline of oxygen levels during the same time interval. The evolution of resistant seeds allowed the plants to penetrate further inland and increase the ground cover and biomass of plant material. All these developments led to an increase in leaf litter and decaying plant matter falling into the shallow waters in which the vertebrates lived. Such developments changed the face of the land surface and the production of soils. They influenced erosion from land surfaces, slowing the rates of runoff as well as changing its character and content. Acidic products of plant decomposition and solutes from the soil leached into the water, meaning that lakes and rivers received increasing quantities of carbon-based compounds and soluble nutrients that encouraged the growth of algae (Algeo et al. 2001), and importantly for water-dwelling vertebrates, they used much of the dissolved oxygen in the water. Combined with high temperatures, this would have produced periods of low oxygen concentration in the water. Algeo and his colleagues have suggested that this produced anoxia in all water systems, including marine environments, and have shown that the events are linked to recurrent black shale horizons throughout the Middle and Late Devonian (Algeo and Scheckler 1998; Algeo et al. 1995, 2001). They suggested, in what they described as the "Devonian plant

hypothesis" (Algeo et al. 2002, 233) , that this was directly related to the increase in plant cover seen during that time. They suggest that "elevated river-borne nutrient fluxes may have promoted eutrophication of semi-restricted epicontinental seas" and could have "stimulated algal blooms," with this high marine productivity resulting in the black shales. The shales represent "intense anoxia on an intercontinental scale." They also link this with the fate of the contemporary stromatoporoid and tabulate coral reefs that "declined rapidly through the mid-late Frasnian" (Algeo et al. 2001, 227, 233).

The fallen leaves seem to have had other effects as well. From the end of the Late Devonian, fire became a routine aspect of floral ecology, perhaps exacerbated by the fallen leaves and branches creating a fire hazard in drier regions (DiMichele and Hook 1992). Scott and Glasspool (2006) showed that the record of fossil charcoal accords with the more recent models of atmospheric composition produced by Berner (2006). Plant material requires a certain minimum level of atmospheric oxygen to burn. In the Early Devonian, there is a small but significant record of fossil charcoal, but no charcoal has ever been found in the Middle or early parts of the Late Devonian, a time when, according to Berner's model, oxygen levels were below that required to ignite plant material. Fossil charcoal is again found in the late part of the Late Devonian (Rowe and Jones 2001) and then in abundance from the Early Carboniferous onward. This finding neatly, though indirectly, corroborates Berner's model for atmospheric composition.

Plant form and growth were also affected by changing atmospheric conditions in other ways. Until the Late Devonian, few, if any, plants have been found with broad planar leaves, such as most modern plants have. Despite the length of time between the origin of terrestrial plants and the Late Devonian, this is surprising. However, the phenomenon has recently been explained by the protracted decrease in the percentage concentration of $CO_2$ in the atmosphere at the same time as the increased efficiency of plant stems to transport water upward (Beerling et al. 2001). This must have been another factor influencing the amount of plant debris accumulating in water bodies and lowering its oxygen content.

As the plants recovered from the extinctions during the Famennian, they underwent renewed radiations into many more habits and habitats. It was at this time that the whole range of modern ecological types first became established. Ground cover plants, vines, scramblers, shrubs, and forest trees arose. From the air, the landscape would not have seemed unlike a modern rain forest, though of course the constituent plants were vastly different (DiMichele and Hook 1992).

Little is known of terrestrial arthropods from the period between the Frasnian and the middle of the Carboniferous. Their evolution has to be inferred by comparing what is known of the Mid Devonian forms with those from the Late Carboniferous. This huge gap in the invertebrate fossil record is unfortunate because the radiation of terrestrial invertebrate faunas undoubtedly influenced that of vertebrates. Ward et al. (2006)

suggested that their absence was a real phenomenon, and that they—and tetrapods—were confined to water during this period because of the low oxygen levels in the atmosphere (see Chapter 7).

These changes to the terrestrial environment largely preceded a similar change in marine faunas. Many species became extinct, to be replaced by others, at what is known as the Frasnian–Famennian extinction event (McGhee 1989). This was one of the major extinction events to have shaped Earth's history, the most catastrophic of which occurred at the end of the Permian period. The Frasnian–Famennian extinction may have been caused by the movements of the continents so that the large landmass of Gondwana became glaciated, changing the world's climate and lowering the overall temperature, though changes to Earth's atmospheric composition and anoxia in the waters probably also contributed. Corals were particularly hard hit.

The Givetian through Famennian is known as a time of major biotic crisis exemplified by the Frasnian–Famennian extinction event. However, this is only one of several crises evident among marine organisms during that time. The geological record is marked by a series of black shale horizons initiated in the Givetian that represent anoxic events in marine waters. The last of these, known as the Hangenberg event, occurred at the end of the Famennian.

This extinction event occurred at the boundary between the Devonian and Carboniferous. A thin black shale layer at the stratigraphic boundary (Caplan and Bustin 1999) seems to have been caused by a rise in water level, disruption of water stratification, increase in organic content, and presumably decrease in oxygen content of the waters. A black shale layer has also been found at the Devonian/Carboniferous boundary in East Greenland (Marshall et al. 1999). It is one of the series of black shale layers found through the Late Devonian that Algeo et al. (1995) interpreted as being associated with increased organic runoff from plant material. Though most of the localities in which the Hangenberg event is recorded are marine in origin, the deposits of East Greenland are generally regarded as freshwater sediments. The Hangenberg event may have been much more general and widespread than previously realized. It certainly correlates with an unprecedented turnover in vertebrate faunal components, and a recent study by Sallan and Coates (2010) has documented this in detail (see Chapter 7).

### Late Devonian Fish Faunas

As far as the vertebrates are concerned, the Devonian period is rightly named the Age of Fishes. Many Late Devonian localities have provided us with detailed information about fish faunas in a variety of different habitats. In the north of Western Australia, the locality known as Gogo is one of the most intensively studied. Although the area has been known and collected from since the 1940s, excavations in recent years have produced astonishing finds, including many fishes with minute details



**4.9.** The locality of Escuminac Bay where many specimens of *Eusthenopteron* and other Late Devonian fishes have been found. *Photograph by J.A.C.*

of their soft tissue preserved inside them. Embryos of placoderms and their reproductive apparatus have been described (Long et al. 2009; Ahlberg et al. 2009)—particularly amazing finds that show evidence of internal fertilization in these fish. The fossil fish of Gogo and the story of the expeditions and finds there are vividly described by Long (2006) in *Swimming in Stone*. The locality was a marine tropical reef in the Devonian. So far, the closest relative to a tetrapod that has been found there is *Gogonasus* (see Chapter 3). None of the usual complement of genera found in tetrapod-yielding deposits has so far been found at Gogo, suggesting that it preserves a rather different environment from those in which tetrapods were living.

To provide a picture of the kinds of fishes that lived alongside elpisostegalian fish and the environments they lived in, one of the richest localities of all for Devonian fossil fishes is that of Miguasha, or Escuminac Bay, in eastern Canada. The locality, near the town of Nouvelle, is now a World Heritage Center in recognition of the importance of its fossil fauna (http://whc.unesco.org/en/list/686). A museum and interpretive center gives insights to its history and paleontology. A section through the sequence of strata has been excavated at one point, shown in a photograph taken during an international conference on early vertebrates in 1991 (Fig. 4.9). The sequence dates from early Frasnian times, and recent work has provided a detailed picture of this locality and its fauna (Schultze and Cloutier 1996; Cloutier et al. 1996). Geochemical and faunal studies show that the sediments represent a coastal brackish water to marine environment, though earlier interpretations suggested that it

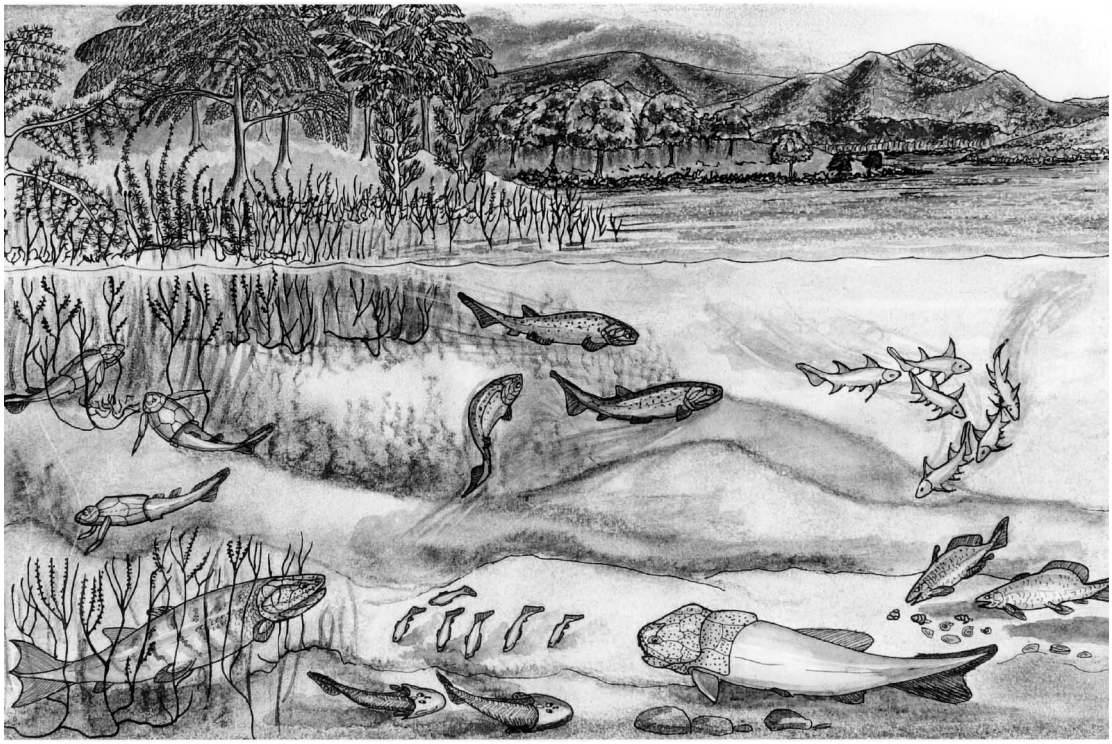
was freshwater (Chidiac 1996). The fauna and flora were described in a compendium volume edited by Schultze and Cloutier in 1996.

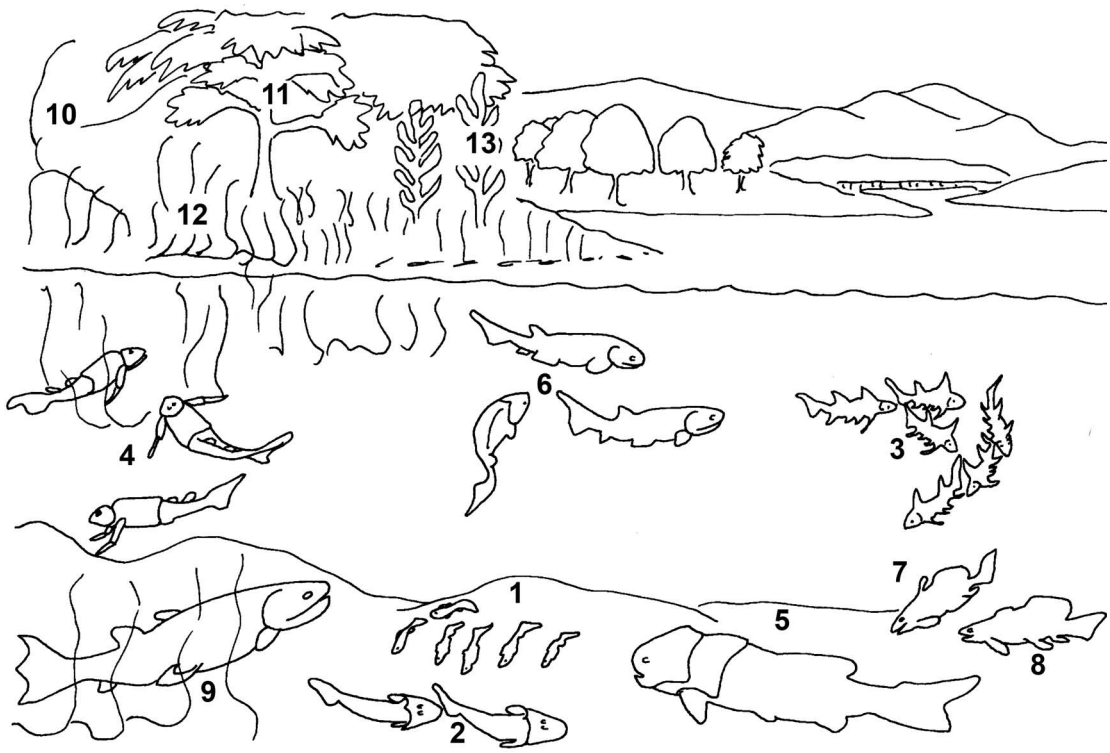
Representatives of all the major groups of vertebrates except chondrichthyans were present in Miguasha (Fig. 4.10). Jawless fishes, primitive relatives of today's lampreys, are represented by both the anaspids and the osteostracans. Anaspids were elongated and rather narrow-bodied forms with downturned tails. They had no paired fins and are thought to have been filter feeders. The osteostracans such as *Alaspis* had flattened, almost semicircular head shields formed of bony plates up to 300 millimeters across. Paired eyes were situated close together on the top of the shield, along with a single median nostril. In some osteostracans, the head shield bore fields of what might have been electric organs. They had a pair of flaplike pectoral appendages attached to the back of the head shield; the rest of the body was covered by scales. It is thought that they were bottom dwellers, perhaps detritus feeders.

Common at Miguasha were the heavily armored placoderms. Placoderms fall roughly into two groups, the antiarchs and the arthodires, though it has been suggested recently that placoderms as a whole may not be a natural group (Brazeau 2009). Both forms had heavily armored head shields that featured a joint between the head armor proper and a shoulder region. One of the best-known antiarchs is *Bothriolepis*, a moderately sized form about 200–250 millimeters long in total. The genus is found all over the world at comparable sites, and it is the most common fish at Miguasha. In antiarchs, the head shield was short compared to the shoulder shield, and just by the junction, paired appendages articulated at a complex shoulder joint. The appendages themselves were externally armored and jointed in the middle, giving them the appearance of crabs' claws. These animals had jaws but no true teeth and were probably scavengers. Preservation of some *Bothriolepis* specimens from Miguasha has led to the suggestion that antiarchs had lungs, though this is disputable (Denison 1941).

Arthrodires were, in contrast to antiarchs, major predatory forms. Some grew quite large, with heads nearly a meter long and bodies perhaps a further 2 meters long. Their mouths were armed with enormous jaws with built-in toothlike pincers or scissors. They had unarmored pectoral appendages and pelvic girdles, though their pelvic fins are poorly known. Much of the body appears to have been scaleless. At Miguasha, the arthrodire present was called *Pleurdosteus*, and it was up to 250 millimeters long.

Placoderms are jawed fishes, but their relationships to other fishes with jaws (gnathostomes) are unclear. They are now all extinct, as is another group of early gnathostome, the acanthodians or spiny sharks. There were several genera at Miguasha, some larger (up to 150 millimeters long), long-bodied, small-finned forms, and some with shorter bodies and longer fins, up to 80 millimeters long. The fins of acanthodians are their most notable feature. Both midline and paired fins were supported along the leading edge by a bony spine. Some acanthodians had more than two pairs of paired fins ventrally.




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Of the true osteichthyan groups, all except tetrapods are represented at Miguasha. Ray-fins are represented by the primitive form *Cheirolepis* up to 500 millimeters long, while of the lobe-fins, lungfishes, coelacanths, porolepiforms, and osteolepiforms, are all found there. The lungfishes were short-bodied forms with elongated second dorsal fins. *Fleurantia*, 420 millimeters in maximum length, had a long snout and a denticulated palate, while *Scaumenacia*, with a maximum body length of 645 millimeters, had a short one bearing tooth plates on the palate, indicating different habits and diets in the two. *Scaumenacia* is the fourth most abundant genus at Miguasha, occurring throughout the sequence, but *Fleurantia* is rather rare and only occurs in the lower half of the sequence (Cloutier et al. 1996). The primitive coelacanth *Miguashaia* (up to 450 millimeters long) did not show the characteristically modified tail, dorsal, and anal fins seen in all other later coelacanths (see Chapter 3). *Holoptychius* is the best-known porolepiform from the locality (up to 470 millimeters), while *Eusthenopteron*, the most common tristichopterid, is found throughout the sequence and is one of the most famous and best-known fossil fish in the world (see Chapters 2 and 3) (Figs. 2.4, 3.17, 4.10, 4.11). This species is known from individuals of a wide range of sizes, up to about 500 millimeters long. Finally, although only three incomplete specimens are known, for this review of tetrapod origins and relationships, one of the most significant fishes in the fauna is *Elpistostege*—the closest Escuminac Bay comes to a tetrapod (see Chapter 3). Its skull is a little smaller than that of *Panderichthys*, at about 210 millimeters. It occurs only near the top of the sequence. For further details of the fishes, see Schultze and Cloutier (1996).

This overview of Miguasha gives an idea of the range of vertebrates around during the Middle to Late Devonian, against which to view the record of the earliest tetrapods.

**4.10.** Drawing of Escuminac scene. 1, Anaspid jawless vertebrate, *Endeiolepis;* 2, osteostrachan jawless vertebrate, *Escuminaspis;* 3, acanthodian *Diplacanthus;* 4, antiarch placoderm *Bothriolepis;* 5, arthrodire placoderm *Pleurdosteus;* 6, actinopterygian *Cheirolepis;* 7, lungfish *Fleurantia;* 8, lungfish *Scaumenacia;* 9, tristichopterid *Eusthenopteron;* 10, fern *Rhacophyton;* 11, "seed fern" *Archaeopteris;* 12, early sphenophyll; 13, early sphenopsid horsetail *Archaeocalamites. Illustration by J.A.C.*

## The First Tetrapod Trackways: Traces and Tantalizing Fragments

The Late Devonian provides the first unequivocal evidence of the existence of tetrapods. There are two kinds of fossil material that provide different perspectives on the animals they represent. One is that provided by fossils of the animals themselves (body fossils), and the other is that presented by tracks and trails left by these creatures (trace fossils). This chapter surveys both kinds, starting with the body fossils.

### The Earliest Body Fossils

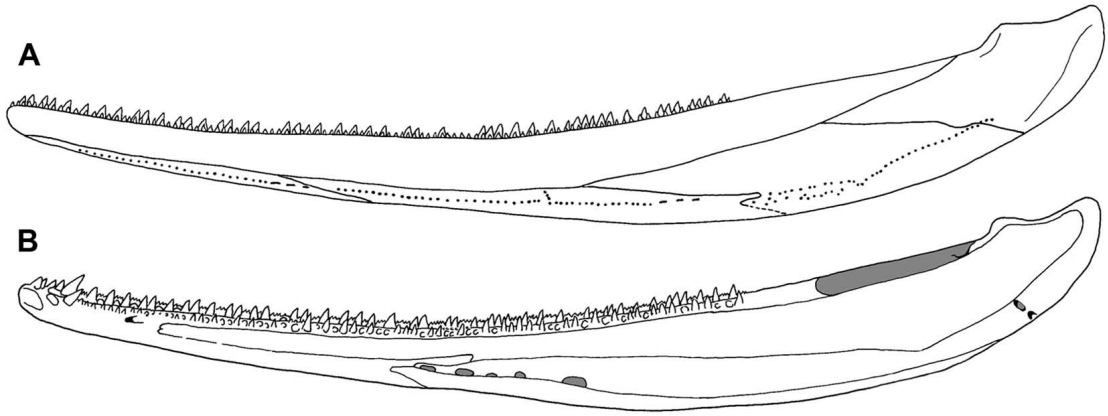
To date, the earliest occurring tetrapod genera are Frasnian in age and are known from fragmentary body fossils, chiefly of lower jaws, and in one case, some limb and girdle material. They are called *Obruchevichthys* and *Elginerpeton*. They have been recognized relatively recently from material that has existed in museum collections since the last century, but that has had to wait for discoveries of other, better-preserved Devonian tetrapod material before its identity could be appreciated (Fig. 4.12).




**4.11.** *Eusthenopteron foordi,* a specimen from Escuminac Bay showing a dorsoventrally crushed skull. Scale bar = 10 millimeters. UMZC specimen GN.790. *Photograph by S.M.F.*

*Obruchevichthys* was originally described as a more conventional sarcopterygian fish from the Frasnian of Latvia and western Russia (Ahlberg 1991b). It is known only from lower jaw fragments belonging to an animal with a skull length of about 400 millimeters. The slender, elongate jaws suggest an animal with a rather flattened skull, though the shape of the head can only be guessed at. The remains occur along with many fishes typical of the Late Devonian, such as placoderms, lungfishes, acanthodians, and some other fragmentary lobe-fins. Although no limb or girdle material is known from this animal, its lower jaw shows some features now considered to be characteristic of tetrapods. Even if it proves in the future not to have had true limbs or digits, its position on the cladogram is likely to remain close to animals that do. Recognized as a tetrapod, with *Elginerpeton*, it constitutes the earliest known body fossil evidence of the group.

*Elginerpeton* is known from a greater number of fossils than *Obruchevichthys*, which allows a more complete picture to be built (Ahlberg 1991b, 1995). Many of these specimens lay in museum drawers in the United Kingdom until 1991, where they had been labeled as "undetermined sarcopterygian" and had not been described or in some cases even cataloged. The material comes from a tiny locality called Scat Craig, where the rocks are exposed in a stream cutting near Elgin in Scotland (Fig. 4.13). An excavation in 1992 collected more material from this locality, but unfortunately, little of it proved to be of *Elginerpeton*. Like *Obruchevichthys*, it is late Frasnian in age.




**4.12.** Lower jaw of *Elginerpeton*. (A) External and (B) internal views. The posterior part of the jaw including the articular is mostly reconstructed. The jaw is estimated to be 270 millimeters long. *From Ahlberg (1998) and Ahlberg et al. (2005).*

The material consists of both upper and lower jaw fragments (Fig. 4.12), including a premaxilla, and some limb and girdle elements. Thus, this is the earliest tetrapod that is known to have had limbs. Among these elements is a tibia, a femur, pectoral and pelvic girdle fragments, and, less certainly identified, a humerus (Ahlberg 1998). The skull material shows an animal with a skull length of about 400 millimeters, with flat head and a somewhat pointed snout. Both pectoral and pelvic girdle elements are massive and are in accord with the size of the skull. The pelvic girdle in particular is comparable in morphology to that of the better-known *Ichthyostega*. The femur is short and flattened, and its shape suggests that it was held in such a way as to be unlikely to have supported weight, but was rather used as a paddle. The humerus, assuming it belongs to the same animal (and there is some doubt as to whether it is even a humerus), seems to fall somewhere between that of *Panderichthys* and a juvenile *Ichthyostega* in its morphology.

*Elginerpeton* occurs in coarse sandstone, and the bones are disarticulated and water worn, so their place of origin cannot be established. It seems certain that they were transported from another locality before the fossilization process. Other remains from the locality include some typical Devonian fishes such as placoderms, a lungfish, a porolepiform, and some jawless fishes. Little information about the habitat or lifestyle of *Elginerpeton* can be gained from the sediments in which it occurs, but the limbs suggest that it was an aquatic animal.

Late Devonian vertebrate material has also been found in other quarries not far from Scat Craig, in the Elgin area. One of these is Rosebrae Quarry. It has yielded lungfish, in particular *Rhynchodipterus*, which is known from an almost complete individual. Typically, bone material from this quarry is preserved as holes or natural molds in the rock where the bone has dissolved away. Because of the nature of the rock, this kind of preservation is amenable to magnetic resonance imaging techniques if the specimen is immersed in water. There is also a large tetrapodomorph jaw from this locality, suggesting that more tetrapodomorph fossils could exist there. However, the circumstances of the quarry mean that finding



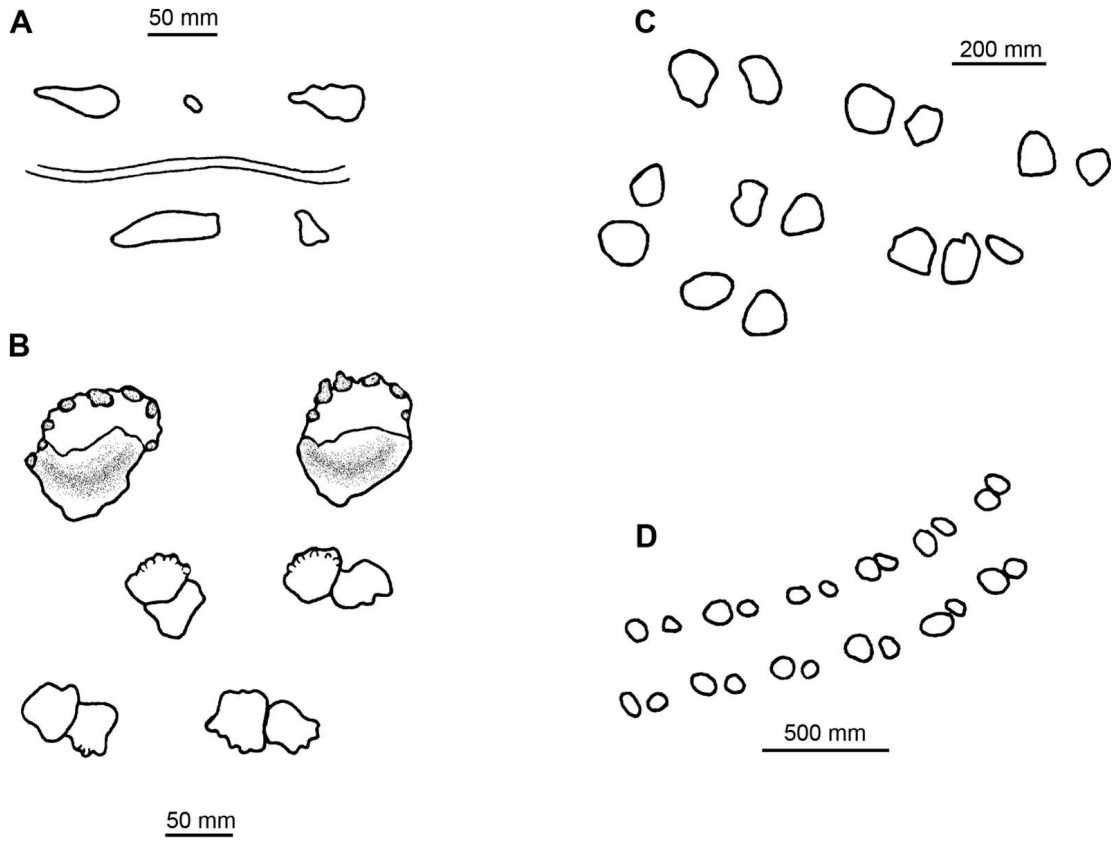
**4.13.** (Color Plate 3) The site at Scat Craig near Elgin in Scotland where *Elginerpeton* was found. Foreground, Per Ahlberg; at the cliff face, Bob Reekie and Bill Baird from the National Museum of Scotland. *Photograph by R.N.G.C.*

them would be expensive and not cost-effective in terms of the likelihood of finding them.

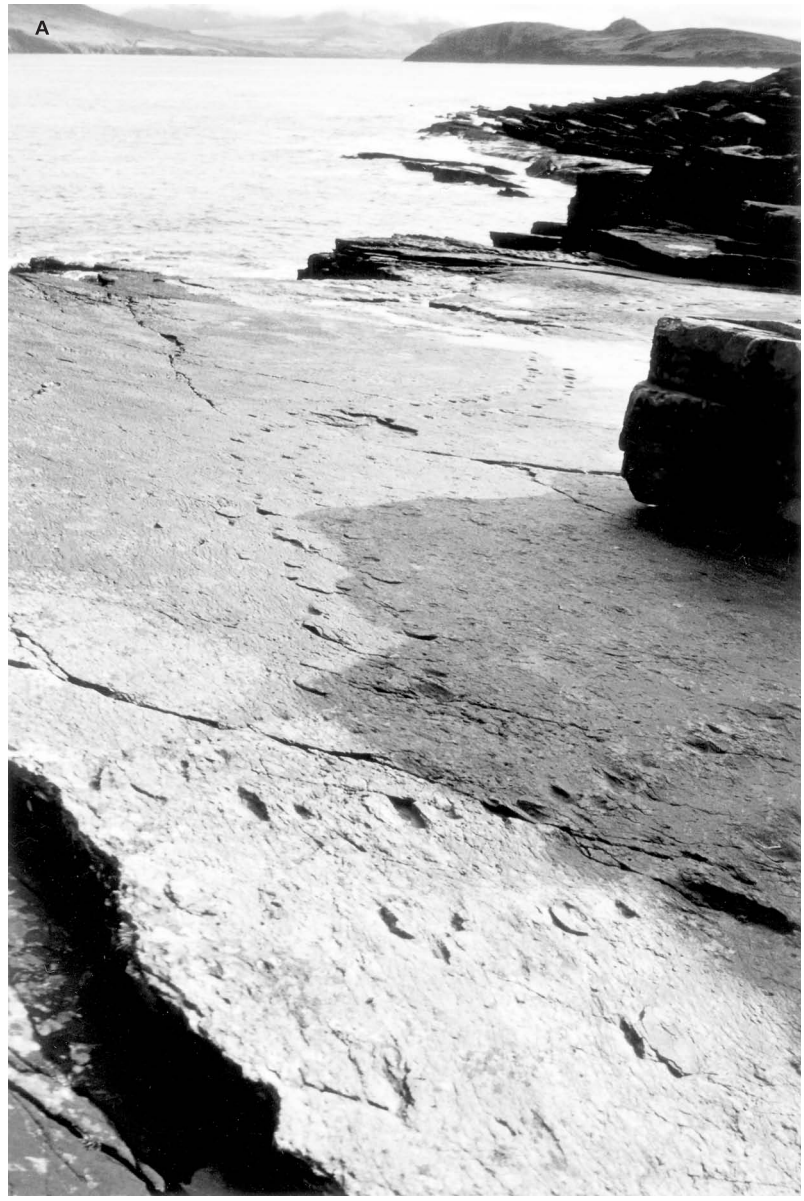
Intriguingly, in this quarry, the Devonian rocks, which are formed of a coarse yellow-brown sandstone, are overlaid unconformably by Triassic rocks, which coincidentally are also formed of a coarse yellow-brown sandstone. It is almost impossible to see where the division lies simply from observing the sedimentary sequence. Why these two series of rocks, so far removed in time from each other, should look so similar is something of a mystery, but it created a great deal of confusion for paleontologists in the nineteenth century. Crocodile-like and mammallike reptiles appeared to have come from Devonian rocks, and it was some time before the anomaly was resolved and they were shown to be Triassic. The similarity may be explained by the fact that both kinds of sediment were laid down in deserts.

## Trackways

It is notoriously difficult to interpret footprint trackways, meaning that trackways cannot always reliably be used as evidence of the habitus of the earliest tetrapods. Another problem is that the kind of fossilization process that preserves trackways seems incompatible with the preservation of bone. It is not clear why this should be, but it makes the identification of the trackway makers a matter of indirect evidence and inference. It is also sometimes difficult to determine whether prints are original (impressed



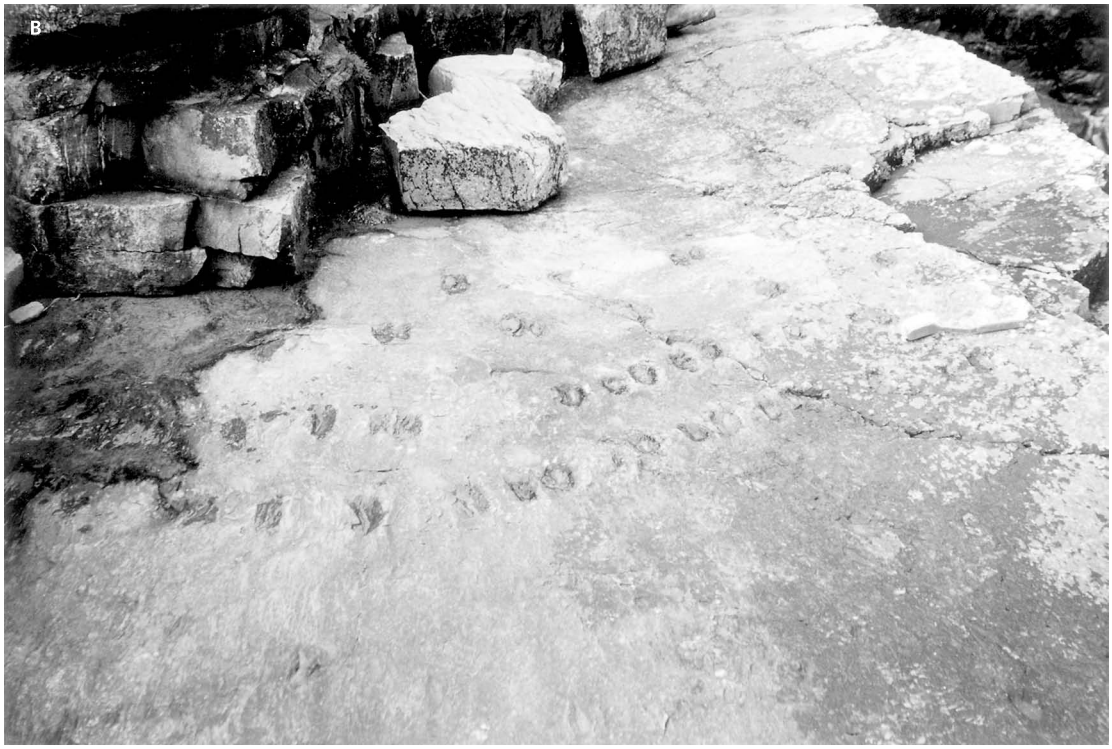

**4.14.** Drawings of Devonian tetrapod trackways. (A, B) Genoa River tracks; in (B), two of the prints from the second trackway are enlarged. (C) Tarbat Ness tracks. (D) Valentia Slate tracks. (E) Genoa River tracks. Note the digit impressions on the outer edge of the print at top right; this is the print figured at right in Figure 4.14B. *From a resin replica, photograph by J.A.C.*




**4.15.** (Color Plate 4) The Valentia Slate tracks in southern Ireland. (A) Overview of the main trackway in the background, a shorter trackway in the foreground—this one shows a shallow groove made by the animal's body, while the footprints themselves are raised on a ridge where the sediment has been forced upward. (B) Close-up of some of the shorter tracks showing different print spacing; the track in the foreground is the same as that in the foreground above; note the closer spacing of prints than in the track behind it. *Photographs by J.A.C.*

into the surface where the animal actually walked) or underprints at various levels (where the top layer has been eroded away to reveal impressions from lower down in the sediments). The latter case often results in overestimates of the size of the original print.

There are several trackway fossils described as having been made by Devonian tetrapods. A further problem that most of them share is that of their dating. The dates of all but one of these trackways can only be placed within rather broad ranges, so that it is not really possible to treat them in a strict time sequence. The easiest way to deal with them is by the date when their descriptions were published.




The first described are a pair of trackways on the same block from the Genoa River in Australia (Fig. 4.14A, B, E). These were described in 1972, and the date of the block is given as "probably Frasnian" by the authors (Warren and Wakefield 1972). Thus, the trackways are probably contemporary with *Obruchevichthys* and *Elginerpeton*.

The two trackways were apparently made by two rather different animals, or at least differently sized animals moving in contrasting ways. One trackway shows a series of foot impressions in which hind footprints overlap fore footprints in an alternating sequence on left and right sides. This pattern is characteristic of tetrapods and is produced when the animal moves its fore- and hind limbs alternately, as a dog would do, trotting on the beach. The prints show some digit impressions that are situated to the side of the print rather than in front, as they would be in a modern mammal. There are at least five digits represented by these impressions, though there could be more.

The animal left no tail or belly drag, and this has been interpreted to mean that the animal was walking with its body supported well clear of the ground. A rough calculation based on the separation of the prints gives the animal a body size of about 220 millimeters, minus the tail.

The second trackway runs parallel to the first, and in this, a small print from one foot, probably the forefoot, alternates on each side with a larger print, presumably from the hind foot, which left a drag mark behind it. Down the center of the trackway runs a sinuous body or tail

trace, suggesting that in this case, at least part of the body was not being supported. The animal was apparently somewhat smaller than the one that made the first track.

Although these trackways are supposedly from animals walking on the land surface, there is little independent evidence presented to support this assumption, other than the fact that they were made by tetrapods. Other trackways made by invertebrates occur on the same bedding plane, but these have not been described. Comparing the footprints with what is known of the earliest tetrapods suggests that none of the known forms is likely to have made these tracks unless they had formed at least partially under water (Clack 1997a). The next chapter deals with the morphology of some better-known Devonian tetrapods, and readers can compare them with these tracks for themselves. Nonetheless, these Genoa River trackways still constitute some of the best substantiated evidence for locomotion by a tetrapod with digits.

Trackways from the Valentia Slate Formation from the west of Ireland were also certainly made by tetrapods (Stössel 1995) (Figs. 4.14D, 4.15). The trackways are more extensive than those from Genoa River, though the individual prints are less clear. These trackways consist of several series of footprints made by more than one animal, all preserved on the same bedding plane. Despite having been distorted when the rocks were stretched and pulled by nearby geological events, they still show the typical alternating sequence of prints, with fore and hind footprints distinguishable. Computer techniques were used to restore the original shape of the prints and trackways.

There is one long, sinuous trackway and several shorter stretches, clearly made by different individuals. One of the trackways shows broad shallow furrows between the footprints, made by the body as it was pulled along the ground not supported fully by the limbs (Fig. 4.15B). If all the trackways were made by the same kind of animal, this one is the best evidence that, unsupported by much water, the body dragged on the ground and the limbs lay to the side of it. Another trackway shows footprints with a much longer stride length, though the distance between left and right prints remains much the same in all tracks. The footprints show no digit impressions but are quite deep and rather egg shaped, with the pointed end at the outer edge. The suite of trackways suggests that the animals were probably supported to some extent by water, though some were more emersed than others. All the trackways seem to have been made at about the same time, and all the animals were heading in more or less the same direction, but it is not clear whether the differences between them result from animals that were moving at different speeds, or animals that were moving in different depths of water, or by differently shaped animals.

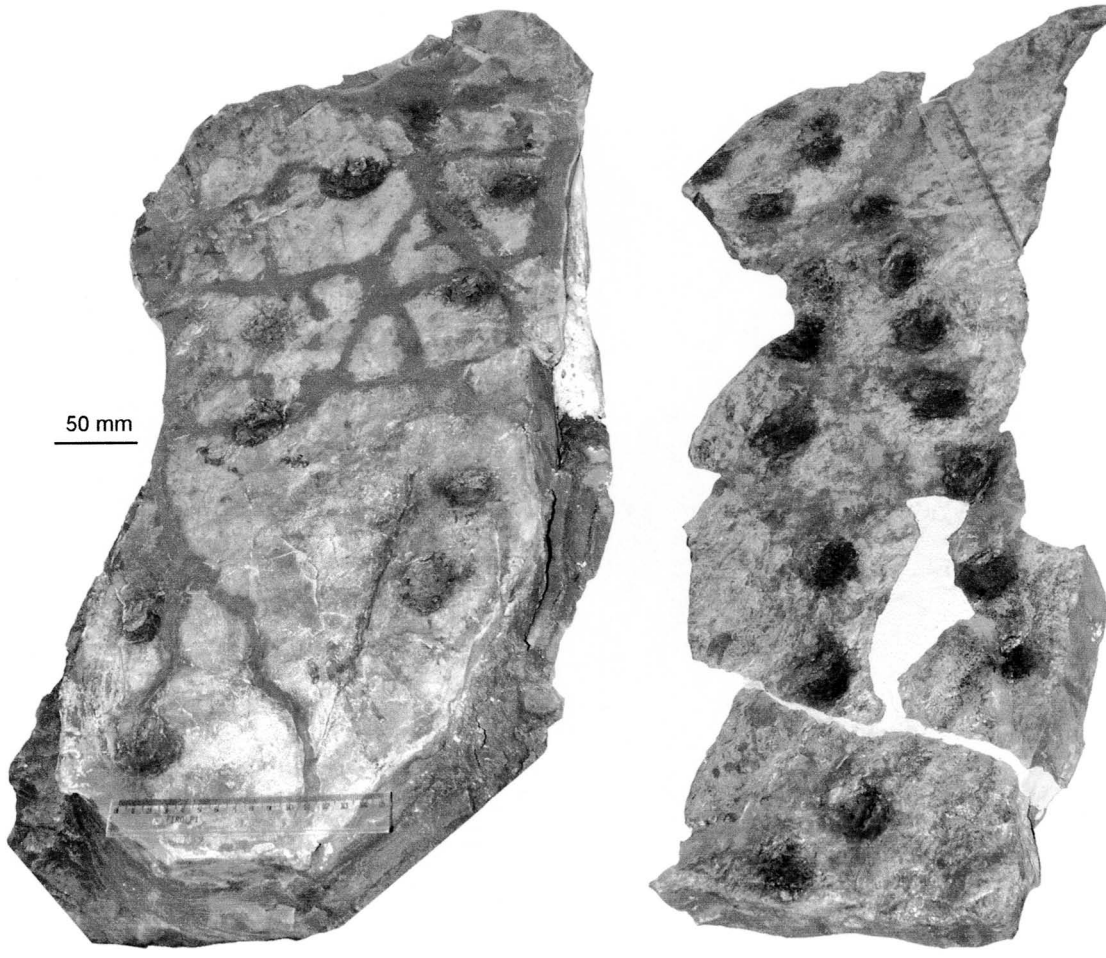
There are no other fossils that have been found in the same beds as these tracks and that might give clues to dating, nor have any spores been found in them. However, some placoderms have been found at a different point on the western Irish coastline in a nearby formation that probably

does not lie too far distant in time from those in which the tracks were found. These placoderms are consistent with a Frasnian age for the rocks, a date that would not be too surprising for these trackways. Perhaps they could have been made by an animal like *Elginerpeton*. However, a date around the Mid–Late Devonian boundary was supported by analysis of magmatic zircons from sediments just below the Valentia Slate Formation (Williams et al. 1997), and this implies an earlier date for the origin of tetrapods than indicated by the body fossil data.

Other trackways that have been described as tetrapod and dated within the Devonian are all subject to problems of interpretation, not only of date but of identity as tetrapod or as terrestrial in origin (Clack 1997a). These include a ladderlike trackway from the Grampian Mountains in Victoria, Australia, that the latest evidence suggests is Late Silurian or Early Devonian. Ladderlike trackways—similar-size individual prints in opposite pairs—are inherently unlikely to have been made by tetrapods, and some recently discovered evidence suggests that some kind of large invertebrate may have made them. Another interpretation, based on comparable ladderlike trackways from the Middle Devonian of East Greenland, is that they were formed under water by the forelimbs of a placoderm such as *Bothriolepis*. Certainly, a recent study has shown that the Greenland trackways are of exactly the right size to have been made by the fins of the contemporary placoderms. A trackway from Tarbat Ness in Scotland is more likely to have been made by a tetrapod; it is tentatively dated as Mid to Late Devonian, though it could be as late as Early Carboniferous (Rogers 1990) (Fig. 4.14C).

Though doubts may be cast on the dating and/or the origin of the Irish and Tarbat Ness trackways, they have to be viewed in a new context. The most recently described sets of trackways and imprints are the most astonishing yet. They give credence to the early dates given for such trackways. The latest discoveries are tracks and trackways from southeast Poland, in the Holy Cross Mountains, where rich sequences of rock from most ages from the early Paleozoic to the Triassic are found. The trackways were found in the disused Zachelmie Quarry, and the horizons in which they were found are well dated by conodont stratigraphy (Niedzwiedzki et al. 2010). They are early Eifelian in age, in absolute terms about 395 million years old. Furthermore, the sediments are representative of extremely shallow water within a coastal lagoonal environment. Desiccation cracks and raindrop impressions are also present.

The trackways include several series of paired or alternating prints in the form of oval depressions, the latter type of which are interpreted as having the typical alternating manus and pes sequence of indisputable tetrapods (Fig. 4.16). They vary in size, with animals from about 40 to 250 centimeters in length being indicated. There are also isolated single footprints that have been interpreted as being made by an *Ichthyostega*-like limb (see Chapter 5). Some of these isolated prints are large, about 15 centimeters across, and bear what appear to be prints of six or seven digitlike extensions.




**4.16.** Devonian trackways from Poland dated as early Middle Devonian, taken from casts. *Photographs by J.A.C.*

What is so unexpected about these trackways is first their age. They are about 18 million years older than the oldest tetrapod body fossils and even predate tetrapod-like sarcopterygians such as *Tiktaalik* and *Panderichthys*. The second surprising thing is their size. Although *Tiktaalik* has been estimated to have reached 2.75 meters, these much earlier trackways date to a time when the largest known sarcopterygians were animals like *Osteolepis* (see Chapter 3). The third surprising thing is the environment in which they were found. It represents a shallow water nearshore lagoonal environment that underwent occasional marine incursions. In the light of other recent finds of body fossils, this is perhaps not as surprising as it once would have been (see Chapter 5), but it raises questions about how the animals were living.

The whole scenario implied by these trackways shows that we may well have to rethink the whole question of timing, sequence, and circumstances of the origin of tetrapods. In the first edition of *Gaining Ground*, I wrote in Chapter 1 that "whatever is concluded today may be overturned by discovery of a new fossil tomorrow." This is one obvious and important example. If corroborated by bone material, there really will be a lot of rethinking to do.

## Timing of the Transition

The earliest evidence of body fossils of transitional forms between "fishes" and tetrapods are found in the early part of the Late Devonian, the Frasnian. These forms are represented by jaws that either were originally mistaken for fishes, or about which there was debate over identity. This was partly because they retain many fishlike characters, but also because the detailed differences between fishes and tetrapods with respect to the lower jaws had not been discovered. Even now, although some of these animals fall within the group usually called tetrapods, it is not clear that they had true limbs with digits in all cases. At this point, the difficulties of definition that were explored in Chapter 3 become significant.

Some things are clear, however. Both *Elginerpeton* and *Obruchevichthys* appear more closely related to tetrapods than was *Panderichthys* or *Tiktaalik*. They are also closely related to each other, sharing some details that cause them to be placed in the same family (Ahlberg 1995). This family was widely distributed in the Frasnian. They were also different from the slightly later Devonian tetrapods, which will be described in the next chapter. They may represent an early and specialized offshoot from the tetrapod branch.

*Panderichthys*, *Elpistostege*, and *Tiktaalik* flourished in the Givetian and early Frasnian and are some of the nearest relatives of tetrapods. But tetrapods, with limbs and digits, appear only about 5–10 million years later in the late Frasnian, by which time they were widely distributed and had evolved into at least several groups, including the lineage leading to the tetrapods of the Famennian. Given our current phylogeny, the transition from fish to tetrapod appears to have occurred rapidly within this restricted time span. Neither fishlike tetrapods nor tetrapod-like fish body fossils have so far been found in the record before this (Clack 1997a). Indeed, the only tetrapodomorphs found before the Mid Devonian is the primitive *Kenichthys*. The currently known body-fossil evidence conflicts with the interpretation of any pre-Famennian trackway as terrestrial. However, the recently described trackways from the Eifelian of Poland are strongly at odds with this interpretation. They imply that we may have to revise our ideas about the timing of the transition, which would appear to have begun much earlier than the phylogeny or the body fossil record suggest, with a long ghost lineage of tetrapodomorphs still waiting to be found.

Inference of a Mid Devonian date for the origin of tetrapods suggests that as plants and then invertebrates began to establish themselves in the marginal environment, vertebrates followed. In the Early Devonian, plant communities on land were limited in diversity and ecology, as were the terrestrial invertebrates, but by the Middle Devonian, considerable advances had been made by both plants and animals. Only when there was sufficient shelter and humidity under the plant canopy and sufficient invertebrates to supply them with food is it likely that vertebrates would have begun to explore the terrestrial environment.

Tetrapods had appeared by the Frasnian, but it is not clear whether they escaped the influence of the Frasnian–Famennian extinction event. As a result of more precise dating of some of the tetrapod discoveries and the still imprecise dating of others, the pattern can be interpreted in different ways, explored further in Chapter 5.

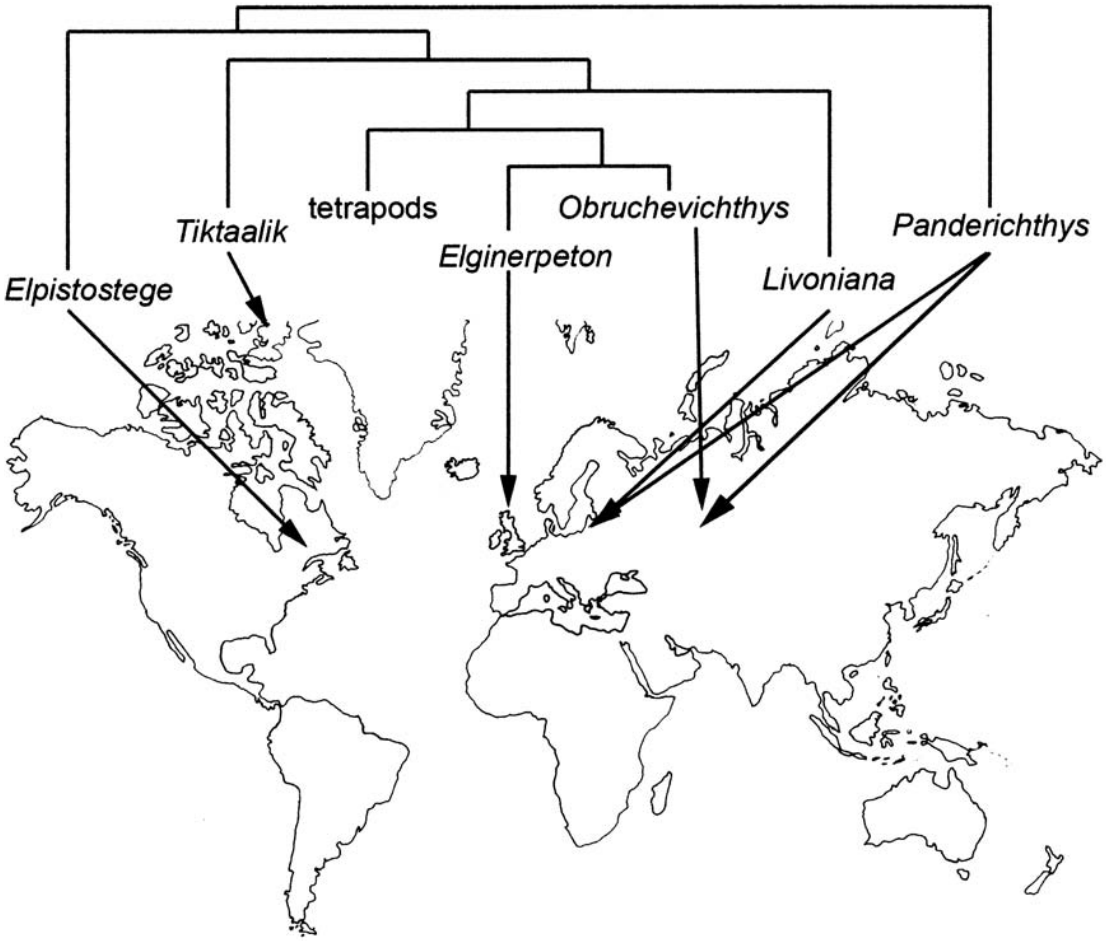
## Location of the Transition

The question of where tetrapods evolved is even more difficult to answer than that of when. It falls into two sorts of enquiry. The first is "where" in terms of geography and the second is "where" in terms of "in what type of conditions."

### GEOGRAPHY

Geographical evidence, so far as it goes, shows that the Frasnian tetrapods that have been found have all come from central Laurussia, but that by the Famennian, they had reached much further eastward into what are now Australia and China. The positions of those continents during the Late Devonian are still disputed, but most estimates place Australia near the equator, with the northern China block separately situated to the north. However, whether either was attached to other continents by land is not clear. Although the record of Frasnian tetrapods is still poor, it is possible to infer from biogeographical evidence that there was a major radiation of tetrapodomorphs in the middle to early Late Devonian of Laurussia (Ahlberg 1995; Ahlberg et al. 2000). *Livoniana* from Latvia exemplifies the kind of transitional form that is being found in the Laurussian region (Ahlberg et al. 2000). Most of the significant new finds from this area seem to slot into a reasonably well-resolved stem lineage for tetrapods, with the near tetrapods such as *Panderichthys*, *Tiktaalik*, and *Obruchevichthys* cropping up in the Baltic states and Russia (Fig. 4.17) (Ahlberg et al. 2008). The discovery of the apparently tetrapod trackways from Poland is not in conflict with this idea.

Tetrapodomorphs found in Australia are for the most part either rather far removed from the stem, such as rhizodonts like *Goologonia*, or are rather derived tristichopterids. The phylogenetic position of *Gogonasus* has been reinvestigated and appears to be a more primitive form than some of its recently discovered characters may suggest (Snitting 2008). Nonetheless, based in part on a possible redating of an Australian locality that has yielded Devonian tetrapod remains, Young (2006) suggested that a Gondwanan origin for the group might be a possibility to be considered. If these localities—and likewise a tetrapod-yielding locality from China—were Frasnian rather than Famennian, as usually considered, that hypothesis might stand. However, it fails to take into account the fact that *Elginerpeton*, an animal with a robust pelvic girdle, already existed in Scotland in the Frasnian. In addition, Blieck et al. (2010) dispute the Frasnian date for the Australian locality.




**4.17.** Cladogram of tetrapodomorphs showing the largely Laurasian distribution of the closest relatives of tetrapods. *From Ahlberg et al. (2000).*

## EARLY TETRAPODS AND THEIR ENVIRONMENTS

The middle Late Devonian, around Frasnian–Famennian times, was a period of great upheaval in the tectonic landscape of Laurussia (Blieck et al. 2007): the major crustal blocks of Laurussia, Gondwana, Kazakhstan, and Siberia were in the process of colliding. Mountains were thrown up worldwide, closing off previously existing oceans and uplifting wide continental areas. These events affected both continental and marine environments and may have contributed to the ongoing global cooling in addition to the $CO_2$ drawdown attributed to increased plant productivity. This is the background to the first major radiation of tetrapods, and it adds new perspectives to our consideration of the environments in which they lived.

Until quite recently, it had always been assumed that the earliest tetrapods—indeed, the earliest lobe-fins—lived in freshwater, and that tetrapods made their way onto land from rivers and swamps. Given the body forms of the best-known genera and the locality of East Greenland, from which the first-discovered examples were found, this is not a

surprising scenario. *Acanthostega* (see Chapter 5) appears to have been adapted for a more or less permanently aquatic existence, and its limbs and digits are thought to have been adapted for use in swampy waters where fins would be at a disadvantage. Other strands of evidence that have been used in favor of a freshwater origin for tetrapods include the fact that modern amphibians are unable to live in saltwater conditions. In the fossil record, only one fossil amphibian, a temnospondyl from the Triassic, has been found in indisputably marine conditions (see Chapter 9). Furthermore, it was always assumed that the lobe-finned ancestors of tetrapods were also freshwater animals, unable to cope physiologically with saltwater.

The assumption of a freshwater origin for tetrapods underlay many early scenarios to account for why tetrapods might have evolved in the first place, chief among these being the drying pool hypothesis. However, all these questions have been looked at again over the past two decades, and the assumption of a freshwater origin for tetrapods has been strongly challenged. Among more recent finds of early tetrapods are many that are now known to be from tidal, marginal marine, or brackish-water localities. These finding militate strongly against the suggestion made, for example by Graham and Lee (2004) on the basis of modern intertidal fishes, that the intertidal environment would have been quite unsuitable for the earliest tetrapods and was unlikely to have been the setting for their origin.

It now seems likely that some of the earliest lobe-fins, lungfish for example, were indeed marine (Campbell and Barwick 1987) and only moved into freshwater localities during the Late Devonian. Many other early lobe-fins seem to have been euryhaline, or possibly anadromous or catadromous—that is to say, they could move between freshwater and saltwater at different times in their lives (though the direction in which they moved and at which stages cannot be easily established), because some species appear in both kinds of paleoenvironments (e.g., the coelacanth *Rhabdoderma*, Forey 1981). By contrast, several sharks from the Paleozoic have been shown to occur in freshwater, so that they are unreliable as evidence for salt concentration. There is increasing evidence from modern fish that adjusting salt tolerance from marine dwelling to freshwater dwelling, or vice versa, is actually not difficult for many vertebrate types (Walsh 1997). If this was so for early lobe-finned fishes, maybe it was also true of tetrapods.

It is much more difficult than might be realized to differentiate between deposits laid down in freshwater and those laid down in marine conditions. The evidence for freshwater deposits is partly negative and consists of the absence of certainly marine fossils. These would be, for example, echinoderms, none of which has ever been found in freshwater deposits or lives in freshwater today; conodonts, usually found as tiny toothlike elements once regarded as useful only for correlating strata but now widely regarded as the remains of some primitive vertebrates; acritarchs, microfossils formed from the shells of tiny marine organisms;

or the shells of sedentary polychaete worms. Inferences from vertebrates, although one of the most widely used indicators of salinity conditions in the past, are now seen as the most prone to the dangers of circular reasoning. Other more independent evidence springs from geochemical analysis, in which the isotopic ratios of elements such as oxygen and carbon and the amounts of boron are found to be characteristically different in marine and freshwater deposits. The isotopic ratios of strontium within the bones of some fossil vertebrates can also be used in this way (Schmitz et al. 1991). Understanding the sedimentary sequence in which the fossils occur as well as their wider geological context will also give clues to their environmental origins.

As an example of how well-known Devonian deposits can be reinterpreted, Miguasha is one such locality that was previously assumed to have been freshwater in origin but is now regarded as brackish or marginal marine. One reason for this assumption was the high proportion of lobefins in its fauna, combined with an absence of sharks or any specifically marine invertebrates.

Looking at the localities in which early tetrapods were found provides some food for thought. The deposits of East Greenland where Devonian tetrapods were first found have almost universally been regarded as freshwater in origin. They are interpreted as having been laid down in a great river basin, surrounded by mountains and bounded by faults. No evidence of marine influence has ever been found there. The East Greenland faunas were highly significant in influencing the growth of ideas about the origin of tetrapods, and their freshwater environments accorded with then current ideas. The next section outlines some of these early ideas, to which discoveries of *Ichthyostega* contributed.

Other Devonian localities are also firmly interpreted as freshwater. The Australian localities yielding their fragmentary tetrapods are continental in origin—that is to say, they were laid down in small lakes or rivers in areas far distant from any marine influence. The Famennian tetrapods of the Catskill basin in the United States are associated with sequences of sediments representing a large river valley and its meandering channels, in many ways similar to those of in which the East Greenland faunas occur (Daeschler et al. 1994; Chapter 5).

However, by contrast, the locality of Tula, with its complement of tetrapods and fishes (see Chapter 5), has also yielded stromatolites, strongly suggesting at least some marine influence, and the geological conditions suggest that the site was rather far from the nearest land (Lebedev and Clack 1993). *Elpistostege*, *Tiktaalik*, and *Panderichthys* come from estuarine localities around the edges of the Old Red Sandstone Continent (Daeschler et al. 2006). The Baltic Frasnian sites from which *Panderichthys*, *Obruchevichthys*, and *Ventastega* (see Chapter 5) come are interpreted as marginal localities at the edge of a large marine basin on the east side of that paleocontinent (Kurss 1992; Lukševičs and Zupins 2004). Such estuarine or brackish water animals would have been in a good position to move around coastlines and river deltas.

The most recent evidence from animals such as *Tulerpeton* and *Ventastega* is that they seem not to have lived in purely freshwater habitats but in brackish or lagoonal ones, within the influence of the sea. In modern ecosystems, the intertidal zone is the richest in terms of ecological niches and diversity of forms, from the species to the phylum level, of any that exist. This is because the conditions are constantly changing, influenced by the tides and exposure to air, and this produces environmental stresses that put great evolutionary pressure on the animals that live there. These conditions have been important in the evolution of air-breathing vertebrates today—for example, teleosts such as mudskippers. It would therefore not be surprising to find the same diversity among intertidal animals in the Devonian, producing air-breathing, land-capable vertebrates.

Taking the tetrapod sites worldwide, one thing is obvious, and that is that they lie scattered over the globe in places that were remote from each other on separate continents, even in the Devonian. It is hard to see how the tetrapods could have reached these widely dispersed continents unless they could negotiate marine conditions (Thomson 1980). The alternative, that tetrapods radiated independently from lobe-fins that had originally been euryhaline and subsequently lost their salt tolerance, seems even more unlikely, and it is countered by the detailed similarities that are found in the tetrapods that are now known from over the world. The shallow swampy waters of marine lagoons, populated by emergent plants that were increasing in size and diversity, might have been the breeding ground for the earliest tetrapods.

## Theories and Speculation: Why Did Tetrapods Evolve?

Among the questions that interest many people is, "Why did the tetrapods come out of the water onto the land?" or, as an alternative, "Why did tetrapods evolve limbs with digits?" For many people, these questions would more or less express the same thing. Over the years during which people have been developing ideas about evolution of tetrapods from lobe-finned fishes, many theories have been put forward as possible answers to these questions. Often they involved hypothetical ancestors or hypothetical intermediates, such as the concept of a prototetrapod as envisaged by Gregory (1935; Gregory and Raven 1941). Several such ideas, most of which were put forward at a time when data were even scarcer than they are now, have often found their way into popular imagination, not to say mythology. It is time to examine some of these critically—not really to see which is correct, because there probably is no single answer to the question, but to see how many there have been, to examine some of the suggestions and see how they stand up to criticism and to recent discoveries about actual fossil animals.

### Historical Background

Scenarios to explain the evolution of limbs with digits were intimately tied to those speculating on the environment of the earliest tetrapods,

and it is difficult to tease the strands apart. Some of the earliest theories go back to the early years of the 20th century, when the observation was made that sediments from the Late Devonian period, the time when tetrapods were assumed to have evolved, consisted largely of red beds (Barrell 1916; Lull 1918). These are layers of sandstone that often have a reddish color as a result of the presence of iron, and such sediments are found all over the world from this period. The eastern United States, northern and eastern Europe, Australia, and China all have them. They have usually been interpreted as the result of arid or semiarid conditions. Indeed, comparable red beds are also found from other time periods such as the Permian and Triassic, which are likewise associated with deserts or semideserts, and the plant fossils they preserve support this interpretation.

Early theories of the origin of tetrapods suggested that these arid conditions caused a general drying up of the pools and lakes in which the lobe-finned ancestors of tetrapods lived, leaving the creatures stranded. As noted above, a freshwater origin for tetrapods is implied. The suggestion was that those that had lungs and were able to breathe air were the most likely to have been able to survive. One problem with this idea is that many lobe-finned fish types survived past the end of the Devonian into the Carboniferous period, and even into the Permian. Another is that all of the early lobe-finned fishes are thought to have had air bladders and some capacity for air breathing.

Building on the red-beds scenario, the next suggestion, by A. S. Romer (1933, 1945), was that those fishes whose fins were strongest and most resembled the structure of limbs, such as the lobed fins of *Sauripterus* or *Eusthenopteron*, were favored by a strong selective pressure on the animals to get back into the water. Those with more limblike legs were better able to struggle over the dry surface and so were more likely to reach another pool. According to this idea, limbs actually arose to enable the animals to get back into water, not to be better able to leave it, and Romer argued that it is not until the Carboniferous that truly terrestrial tetrapods are found (Romer 1958).

One of the most telling objections to the drying-pool idea is that on closer examination, red beds are found not to be invariably correlated with arid climates. In modern times, red beds are found in low-latitude, tropical climates, and they are always associated with oxidizing conditions. This was realized as long ago as 1957 (Inger 1957) and has been corroborated many times since. The red beds may be associated with rain forests or places where the rainfall is high but confined to monsoonal periods. The conclusion from this is that red beds are not really a good indicator of arid environments, even though they are frequently found along with evaporite deposits.

A good model for red bed–producing conditions today is the Amazon basin. Many of the fishes that live in the rivers there are air-breathing forms. As the season becomes drier, they simply move downriver to deeper water. This model prompted one worker to look at the behavior of air-breathing fishes today (Inger 1957). Inger pointed out that in many

cases, air bladders allow the fishes to remain in the water when the water becomes anoxic, rather than to allow them to make excursions on the land. Some of these fishes do feed on land, and some do leave the water to find other pools, but only when the climate is humid, and only to seek pools where the population is less dense (Goin and Goin 1956). Therefore, Inger suggested that one possible stimulus for early tetrapods to leave the water might have been population pressure. In addition, he pointed out that if the conditions in which the early tetrapods lived were indeed humid, then limbs with digits are unlikely to have evolved to dig estivation burrows, but could have helped them to migrate to new locations.

There is another point that the red-bed theory fails to take into account. Even if it were correct that the Devonian red beds were indicative of desert or semiarid conditions, that does not necessarily mean that these conditions are the ones in which the earliest tetrapods arose. By no means do all Middle or Late Devonian sediments consist of red beds. Some represent river and lake basins or nearshore deposits from lagoons that are rich in organic material, suggesting nearby forests. The earliest known tetrapod remains are Late Devonian in age, but presumably they actually evolved somewhat before that time, perhaps before the red beds were deposited. Furthermore, it is quite possible that they evolved in places other than those that the red beds represent.

The kinds of ecological conditions in which early tetrapods first arose are not certainly known, but if these tetrapods lived in brackish or lagoonal environments with a tidal influence, perhaps in an estuary or lagoon, the deposition of red beds elsewhere is of no consequence.

The drying-pool hypothesis was nevertheless widely accepted for many years. It gave rise to a variety of scenarios about how the changes to the limbs might have occurred, assuming that those changes took place between a fin like that of *Eusthenopteron* and a pentadactyl limb like that of the Permian temnospondyl *Eryops* (see Chapter 9). Some of these ideas are dealt with in more detail in the section on the evolution of limbs in Chapters 5, 6, and 10. One of the threads that unites ideas from this time is that because *Eusthenopteron* and its allies had fins with a bone structure like those of tetrapods, they must therefore have used them in a similar manner. Changes to the locomotory pattern were thought most likely to have evolved while the animals were still in water, but only excursions onto land would provide the selective pressure to lose the fin rays (Eaton 1951).

Over the middle decades of the 20th century, particularly during the 1950s, a whole series of papers addressed the question of the origin of limbs and terrestriality, putting forward objections to old ideas and coming up with new ones. Looking at modern amphibians gave one worker the idea that limbs might originally not have been for walking at all. Rather than walking away from drying pools, many modern amphibians, and indeed crocodiles as well, bury themselves in the mud at the bottom, where they stay until the rains come again. It was therefore suggested that

the limbs of early "prototetrapods" might have been evolved for burrowing into the mud (Orton 1954). However, even the proponent of this idea recognized that many animals that move or even burrow on land do not use limbs to do so, and some other explanation must be sought for why the animals eventually became terrestrial. It may also be pointed out that the lungfishes *Protopterus* and *Lepidosiren*, two of the tetrapods' closest living relatives, are noted for their ability to estivate in mud burrows. They are the lungfish genera with fins least like those of tetrapod limbs, and they do not use them for burrowing.

Arguments about the origin of limbs and terrestriality continued in the literature with the observation that most modern amphibians, rather than seeking new pools when their own dries up, congregate in the drying pools, and often die there. If they are disturbed for any reason, they may leave the pool, but the directions they take are random (Ewer 1955). Some may find new pools, but the selective pressure would be on those that could best withstand desiccation, not those with the strongest legs. The same would have been true in the Devonian. Population pressure in existing pools today may sometimes stimulate migrations in humid conditions, and in this case, the selective pressure may have been to favor those with limbs. If limbs had originally evolved for digging estivation burrows, he pointed out, it is hard to see why they would ever have been used for walking.

One contribution envisaged the pressure being on the larvae of these prototetrapods: "One must first be a successful tadpole before one can be a successful frog" (Warburton and Denman 1961). It was suggested that the animals laid their eggs in shallow water that then dried up, and the conditions favored those that could survive in temporary pools. The problem with this suggestion is that it is simply not known how these early prototetrapods reproduced. Study of modern amphibians suggests that their modes of reproduction are strongly tied to their ecology, and they show a greater variety of strategies than any other vertebrate group. Although most frogs lay large numbers of small eggs in spawn, which they then abandon, this is not necessarily a guide to what Devonian prototetrapods did. The most primitive frog genus has internal fertilization, as do all salamanders and caecilians, and most members of both these two latter groups produce their eggs and young internally. This idea will be developed further in Chapter 6, but it shows that theories about pressure on larvae may all be quite wrong.

This argument also fails to take into account that predatory forms too must have laid eggs and had young that sought small food, so that they too could well have been part of the marginal pool fauna, exploiting the prototetrapods that sought refuge there.

## More Recent Suggestions

Two major objections to the fin-to-limb scenarios outlined above have only recently become apparent. First, the modern coelacanth, with the

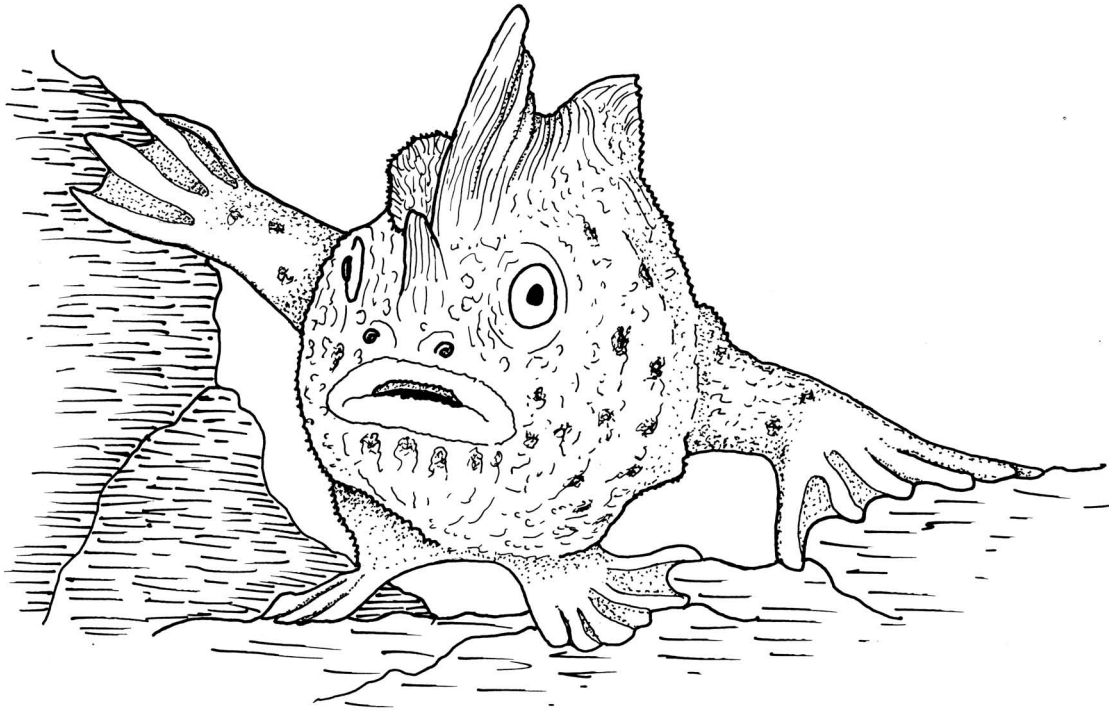
bony fin structure most like that of tetrapods among living fishes, does not use its fins for walking (Fricke et al. 1987, 1991). Before it was studied in its natural environment, many people predicted that its fin structure would mean that it used the fins for walking on the bottom of the sea or among the coral reefs where it lived. However, film of the fish in action shows that this is never the case; it uses its paired fins for slow paddling, albeit in an ipsilateral manner, one forefin moving in concert with the hind fin from the opposite side. This is the same sequence used by tetrapods and lungfishes, but not for the same purposes. The lungfish *Protopterus* has been observed to prop itself up on the substrate using thin whiplike appendages that are most unlimblike.

The second major objection to the fin-to-limb scenarios is that recent discoveries show that the earliest tetrapods were not pentadactyl after all, and the evolution of joints and digits did not proceed in the order or fashion that early theoretical studies assumed (see Chapters 5 and 6). The ideas that were put forward about how the changes took place do not fit the facts.

Some ideas about the acquisition of terrestriality and limbs may be gained from looking at modern ray-finned fishes that do show some adaptations for terrestrial excursions, as well as those that have evolved digitlike equivalents from fin rays. The first thing to notice is that these two groups are almost mutually exclusive—that is, those with digitlike fin rays by and large are not those that venture onto land, and conversely, those that do venture onto land do not necessarily do so by means of digitlike or limblike fins.

Fishes that have evolved limblike adaptations are often those that live in deep waters or that are habitual bottom dwellers. The Sargassum frog fish has developed perhaps the closest analog to tetrapod-digited limbs (Fig. 4.18). It uses its jointed, grasping fin rays to cling to the sargassum weed among which it lives, remaining stationary by this means until potential prey passes. Notably, there are eight of these jointed rays on each "foot." Batfish, with comparable adaptations, use their limblike fins for bottom walking, sometimes at abyssal depths. Gobies and blennies also develop digitlike fin rays, though these animals are often tide-pool species that do sometimes emerge from the water. However, their appendages are used for walking on the pool bottom, not on land. Eels, which make long journeys overland to reach their spawning grounds, not only have nothing in the way of limblike appendages, but their paired fins are reduced in size. *Periophthalmus* and its relatives, the mudskippers, of which there are many species in different parts of the world, do use modified fins for walking, but walking catfish may use modifications of the opercular series. Once again, there is little relationship between the origin of limblike appendages and terrestriality.

Fishes leave water and spend time on land under a wide range of conditions and circumstances (Sayer and Davenport 1991), but there is no link between those that do leave the water and those that have evolved digitlike structures. The emergence of tetrapods onto land may



**4.18.** Drawing of a frog fish, a ray-finned fish in which the pectoral and pelvic fins are adapted into jointed, digitlike fingers and toes. *Illustration by J.A.C.*

have involved any one or a combination of the sorts of conditions that induce terrestrial excursion in modern forms. Some of these are seen in marine fishes, some in freshwater forms, and some in intertidal or brackish water forms. Lowered oxygen concentration is one such factor. Low oxygen levels in waters today may occur for a variety of reasons, such as high daytime temperatures in tropical shallow freshwaters, low activity of photosynthetic organisms at night in tide pools, or decaying vegetable matter being oxidized by bacteria. Under these circumstances, many air-breathing fish increase the incidence of air gulping or the amount of body exposed to the air. Temperature may also be an influence in another way; some mudskippers, for example, only leave the water when the temperature on land is high enough, while some killifish will leave the water when the water temperature gets too low.

Biotic factors probably play a generally larger role in why fish leave the water. Increased competition for food or space sometimes plays a part, as for amphibians; so does avoidance of predation or aggression. However, one of the most common reasons is for feeding on terrestrial or semiterrestrial food sources. Associated with this, it has been shown that fish that feed on land and then stay there for a while actually experience an increased rate of digestion; indeed, some aquatically feeding fish leave the water after feeding to take advantage of this effect. Raised ambient temperature appears to be the key factor here. This idea has recently been developed by Carroll et al. (2005). A few fish leave the water in order to spawn. Some will leap out of the water to attach egg masses to leaves overhanging the water surface, while others deliberately seek places to

lay their eggs that are exposed to the air for at least half the time. There may be several reasons for this behavior: raised temperatures may speed development, or such places may be inaccessible to the most common predators, or the eggs may get an improved oxygen supply. The plethora of reasons for why modern fish leave the water demonstrates how difficult it would be to cite any one as the main stimulus for the tetrapods to have done so.

Many of these ideas about the origin of tetrapods have assumed that the origin of limbs was intimately connected with the origin of terrestriality. Some have tried to separate the two, such as Romer (e.g., 1958), who suggested that the limbs helped the animals to get back into the water. However, the problem actually consists of three parts: origin of limbs with digits, origin of walking, and origin of terrestriality. No one yet knows which came first, or which order they occurred in, though recent finds such as that of *Tiktaalik* have suggested some possibilities. Each aspect may require a separate explanation that is not necessarily dependent on the others. (Furthermore, the origin of the clade known as crown group Tetrapoda is a different issue again, not necessarily connected with limbs, walking, or terrestriality at all. Some of the problems associated with this are dealt with in Chapters 3 and 9.)

In recent years, further ideas have been put forward, each of which may have played a part. One is that tetrapods, either the adults or their eggs or young, were being pressured by predatory fish or arthropods to seek more and more marginal habitats where the predators could not follow (McNamara and Selden 1993). Certainly there were large predatory fish around during the Devonian, but they would not have been able to penetrate the shallow vegetation-choked water where the tetrapods are assumed to have lived. This explanation uses the timing of a rapid expansion in the diversity of fishes during the Devonian to suggest that competition for resources in the water grew rapidly, while the land offered new niches free from predation pressures.

During the Devonian, increase in diversity of fishes in the water occurred at the same time as the radiation of plants onto land, followed by an increase in the variety and numbers of arthropods that fed on them. By the Late Devonian, vegetation at the margins of lakes and rivers was dense and lush, with the appearance of forests whose structure resembled that of modern forests. The many arthropods living in and on this vegetation would have provided rich and unexploited resources for any vertebrate that could reach them. No competing vertebrate forms were on the land before them, so that any vertebrate that could in any degree survive partially or wholly out of water would find itself at an advantage, independent of what predation pressures might have existed in the water. Thus, access to an unexploited food resource constitutes another plausible explanation.

Carroll et al. (2005), exploiting the idea that raised body temperature would have been advantageous to a predator, recently suggested a new scenario as to why the tetrapods' immediate ancestors, or the earliest

tetrapods themselves, might have left the water. They posited the idea that these animals actively sought first warmer shallow water for increasing their body temperature, and that that led to them exploring the water margins and eventually the land to bask. This would have increased their metabolic rate and so made them faster and more effective predators when they returned to the water. Furthermore, they suggested that this could have been key to the evolution of large hind limbs and pelvic girdles. There are a number of objections that can be raised against this scenario, including the fact that it is more or less impossible to test, but nevertheless, the effect of increasing body temperature on leaving the water would have been inevitable and might have had some profound results for these animals, providing they could at the same time avoid the effects of desiccation.

Recently, a third scenario has been proposed (Clack 2007). It brings together recent evidence from the new models of atmospheric composition for the Devonian with the increase in plant size, land coverage, and diversity that occurred during that period, and new anatomical information from the evolution of tetrapodomorphs.

One conspicuous feature of the tetrapodomorph group is the spiracular notch, which lies between the skull table and the cheek. Whereas it is a simple slot in *Eusthenopteron*, the opening increases in width in some members of the tetrapodomorpha, notably *Panderichthys* and *Tiktaalik*. Brazeau and Ahlberg (2006) showed how the underlying spiracular chamber also increases in volume, approaching that of the early tetrapod *Acanthostega*. Subsequently, it was discovered that the condition in *Tiktaalik* was almost identical to that in the primitive tetrapod *Ventastega* (see Chapter 5). Brazeau and Ahlberg (2006), Daeschler et al. (2006), and Clack (2007) have associated the spircular cleft and its morphology specifically with an air-breathing mechanism, indicating increasing reliance on air breathing among the group. The timing of this increase corresponds to the period covering the Givetian–Frasnian, continuing into the Famennian.

In concert with the increasing spiracular volumes were changes to the pectoral region. The pectoral fin gained increasingly large areas for muscle attachments, which implies an enhanced ability to support the front end of the body and the head, seen in the modifications of the humerus and more distal elements of *Panderichthys*, *Tiktaalik*, and ANSP 21350, an isolated humerus from the Late Devonian of Pennsylvania (see Chapter 5). The reduction and loss of the opercular bones successively allowed the head to be raised more easily, and the wider skulls of these fish allowed a greater volume of air to be accommodated in gulping movements.

A look at other groups shows that the increased exploitation of air-breathing mechanisms may have occurred in them at about the same time, for example among lungfishes. The earliest lungfishes show no special adaptations for air breathing, but by the Late Devonian, lungfishes such as *Soederberghia*, which often occurs with early tetrapods, are

thought to have been air breathing. There is also a case for suggesting that early actinopterygians had this capacity.

The study by Algeo et al. (1995) on the increase in plant cover during the Mid and Late Devonian clearly shows that the average size of plant stems found in the fossil record increases by two orders of magnitude, from 1 to 100 millimeters. The second of these increases coincides with the rise of the first forestlike ecosystems and occurred during the Givetian–Frasnian stages. The consequences for land and water systems, though probably quite gradual, were profound.

This crucial period further coincides with the lowest levels of atmospheric oxygen under Berner's (2006) new model (though it also corresponds with his earlier models, which also suggested a low point during this period). Elevated $CO_2$ and temperature levels, compared with today's, also pertain to the Givetian–Frasnian period, both falling slowly during the Famennian and Early Carboniferous.

Such changes, though gradual, can hardly fail to have affected the evolution of animals both in water and out of it. Assuming that the models are correct, low oxygen levels in the atmosphere and anoxia in water systems as a result of plant decay, combined with high temperatures, must have produced gradually changing conditions, some of which were strongly adverse for vertebrates.

These conditions could well have favored animals that were tolerant of hypoxia, and today, those are often also air breathers. They are also the animals that can tolerate high levels of ammonia in their blood systems and a degree of desiccation (see Chapter 6). These are all qualities that one would associate with a group of animals exploring the water margins and swamps, and that could be expected in tetrapod-like fish and early tetrapods. The inference is that air-breathing animals would seek oxygen from the atmosphere in preference to the water, and that the environmental conditions of the Middle and Late Devonian contributed to the eventual origin of tetrapods as land-capable animals.

The discovery of the Eifelian trackways from Poland in deposits formed in a shallow sea has prompted yet another scenario for why tetrapods might have left the water. The suggestion is that in the intertidal zone, many fish might have been stranded as the tide retreated. Tetrapods may have evolved as scavengers exploiting this resource. Today, not many fish are thus stranded at any one time, except for short periods in certain parts of the world, where fish such as the North American alewife venture into shallow water to spawn once a year. Such conditions would not make a reliable food source for tetrapods. However, one has to remember that the fishes of the Devonian were unlike those of today, and there is no way of knowing how they would have behaved.

Nonetheless, it is difficult to tease apart all the influences that were at work in the Devonian to produce the appearance of tetrapods. Ideas are numerous, but evidence is equivocal. Most ideas can be countered by objections or alternative suggestions, or they are difficult or impossible

to test. Without a much more complete fossil record, they must remain speculative.

Other reviews of the questions and problems associated with the origin of tetrapods can be found in the following: Thomson (1991, 1993), Daeschler and Shubin (1995), Clack (2005, 2006, 2007, 2009a), and Coates et al. (2008).



**5.1.** Flying over Kejser Franz Joseph Fjord in a Twin Otter in July 1987. Ymer Ø and Celsius Bjerg in the foreground with some of the classic *Ichthyostega* sites on its northeastern side and Gauss Halvø in the background. *Photograph by R.N.G.C.*

# The First Feet: Tetrapods of the Famennian

# 5

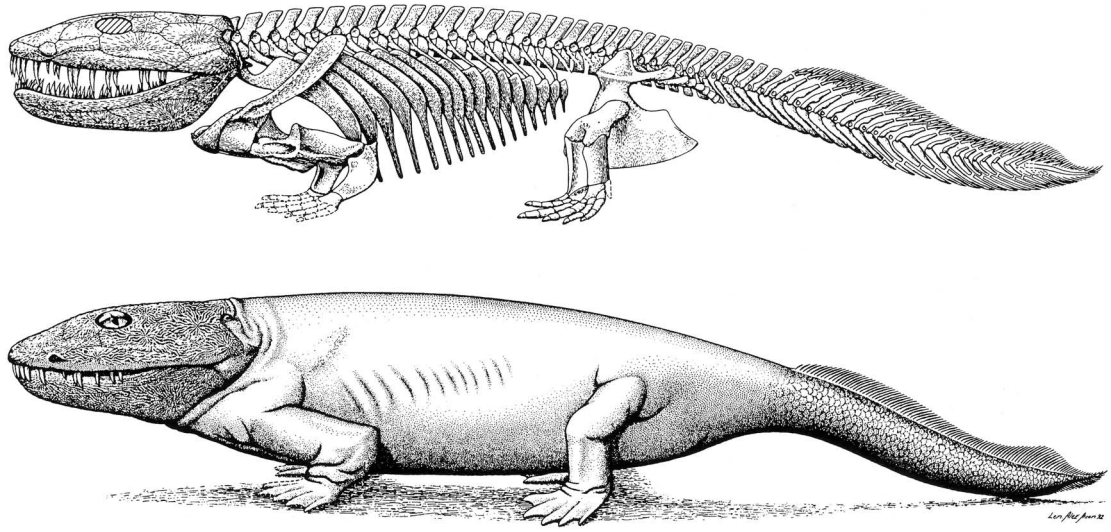
By the latter part of the Late Devonian, the Famennian, vertebrates with indisputable limbs bearing digits—tetrapods—had appeared. Some remarkably well-preserved material from several localities provides details of their anatomy and lifestyles. This chapter examines each of these in turn, and then goes on to see what pointers they may give to the origin of the group.

## Famennian Tetrapods from East Greenland

It is East Greenland that has provided the most detailed knowledge of Devonian tetrapods. East Greenland has been studied by geologists for many decades. One of the reasons is that the terrain lies within the polar semi-desert, so it is relatively sparsely vegetated and the geology can be seen during the short summer season, when the ice and snow melt around the coast. At the same time, in contrast to many desert areas, availability of water is not a problem for the visiting scientists, though they are often plagued by mosquitoes, and accessibility to the area is often hampered by bad weather. Most of the sites are usually only reached by helicopter, though in the past, icebreakers carried the scientific teams to the fjords from where they reached the sites by inflatable dinghies. Some of the most recent collecting expeditions have been carried out in collaboration with the Denmark and Greenland Geological Survey, who use as their base camp the Danish air force airstrip of Mestersvig.

Part of the central area of East Greenland is composed of rocks representing the Middle and Late Devonian period, and the area around Kejser Franz Joseph Fjord, which lies 400 kilometers north of the Arctic Circle, has been noted for yielding fossils of Devonian vertebrates since the early years of the 20th century. The main localities are gathered around Celsius Bjerg on Ymer Ø and the mountains of Sederholm, Smithwoodward, Stensiö, and Wiman Bjerg that make up the peninsula of Gauss Halvø (Fig. 5.1). All the East Greenland Devonian tetrapod localities and the specimens derived from them are documented in Blom et al. (2005, 2007).

From the late 1920s until the mid-1950s, a series of expeditions undertaken jointly by Danish and Swedish paleontologists brought back remarkable finds of fishes and what were then the earliest known tetrapods. Two genera of tetrapod from this area have become particularly well known from extensive collections. *Ichthyostega* was the first genus of



**5.2.** *Jarvik's (1996) reconstruction of* Ichthyostega.



**5.3.** (Color Plate 5) Three of the 1998 expedition members: from left to right, Becky Hitchin, Sarah Finney, and the author. *The photograph was taken by the fourth expedition member, Sally Neininger (S.L.N.).*



**5.4.** (Color Plate 6) I am seated in front of Stensiö Bjerg in 1998. *Photograph by S.L.N.*

Devonian tetrapod to become established in textbooks, scientific articles, and popular and children's books (Fig. 5.2). It is sometimes referred to as the four-legged fish. Many specimens of this creature were found during the early years of exploration of East Greenland, and these are vividly described by Jarvik (1996) in his monograph on the animal. *Acanthostega gunnari* was named and described from two specimens in 1952 (Jarvik 1952), but since then, it has become much better known thanks to collections made during the summer of 1987, when a joint expedition from Cambridge, England, and Copenhagen, Denmark, returned to the area (Bendix-Almgreen et al. 1990; Clack 1988). A follow-up expedition that I led in 1998 collected new ichthyostegid material, and we discovered a



**5.5.** (Color Plate 7) Photograph of Smithwoodward Bjerg and Stensiö Bjerg on Gauss Halvø showing the three formations of the Celsius Bjerg Group. At their base, the top of Aina Dal Formation is marked by an outcrop of harder rock forming a small cliff, running across from about 300 meters at the left of the photograph and dropping to about 100 meters on the right. The Wimans Bjerg Formation is the middle slightly grayer layer, while the uppermost Britta Dal Formation is marked by another slightly redder layer. *Photograph by J.A.C.*

bit more about the circumstances in which the tetrapods were deposited (Clack and Neininger 2000). This expedition was supported by the National Geographic Society. Figure 5.3 shows three of the expedition members on Gauss Halvø, on a reconnaissance trip, and Figure 5.4 shows me seated at the 1998 campsite under the brow of Stensiö Bjerg.

When *Ichthyostega* and *Acanthostega* were alive, Greenland would have been in tropical latitudes. The climate of the region seems to have been monsoonal, and the animals lived in an extensive river basin fed by meandering streams flowing from mountains to the south. These fed into a large freshwater lake or inland sea whose margins were determined by a series of faults, cutting a broad parallel-sided valley into the mountains of the Old Red Sandstone continent (Olsen and Larsen 1993; Olsen 1993; Larsen et al. 2008).

Along the peninsula now called Gauss Halvø, tetrapods have been found in two formations, a lower level called the Aina Dal Formation and an upper one called the Britta Dal Formation (Fig. 5.5). The formations represent two periods of seasonal deposition in the river basin. They are separated by another formation, the Wimans Bjerg, which has yielded few vertebrate fossils, though trace fossils and burrows have been found, indicating a rich fauna of bottom-dwelling invertebrates (Clack and Neininger 2000). These three formations constitute the Celsius Bjerg Group. The Wimans Bjerg Formation is thought to represent a drier period when a shallow lake or playa was all that remained of the once deeper lake of Aina Dal times. In succeeding Britta Dal times, the return to a wetter climate filled the lake and rivers once more. In other parts of

the Kejser Franz Joseph area, these separate formations cannot be distinguished so readily, suggesting slightly different geological conditions (Fig. 5.5) (Olsen and Larsen 1993; Olsen 1993).

Poorly preserved remains show that there were large plants growing in the region, probably along the riverbanks, but they do not give enough detail to be able to identify them precisely. One specimen shows a single, branched specimen as an impression; it has been likened to the fernlike *Rhacophyton* (Astin et al. 2010). The sediments have been oxidized in most regions, and most of the organic matter of the plants, including their spores, has been destroyed. Plant spores are useful for dating the sediments in which they occur, and until recently, the lack of spores in these Devonian rocks hampered precise dating.

Fortunately, spores unearthed in sediments above the Britta Dal Formation and below the Aina Dal formation demonstrate them to be unquestionably late Famennian (Marshall et al. 1999). *Acanthostega* and *Ichthyostega* are now some of the most securely dated of all Devonian tetrapods, with their occurrences bracketed between two marker bands defining quite a narrow range. Now that these spore dates have been worked out, they can be compared with similar spore data associated with other Devonian tetrapods. Blieck et al. (2007, 2010) reviewed the dating of Devonian tetrapod localities, based on European miospore zonation, finding that though *Acanthostega* and *Ichthyostega* are by no means the earliest to appear, they are the only ones to have definable stratigraphic ranges.

One small lens of rock contained numerous articulated skeletons of *Acanthostega*, and layers above and below contained disarticulated bones. Figure 5.6 shows the 1987 expedition at the small outcrop that yielded most of the *Acanthostega* material, about 800 meters up Stensiö Bjerg, which is reached only after several hours' climb. The first studies of the sediments in which it was found suggested that *Acanthostega* inhabited actively flowing river channels (Bendix-Almgreen et al. 1990). The deposit was interpreted as an accumulation of sediment on the bank of a river at the inside of a bend, called a point bar, where, perhaps during a flash flood, many individuals were heaped up together after they had died. Animal bones and carcasses were dumped on the bar, which was formed of fine silty sand, along with coarser sediments carried by the fast-flowing floodwater. From the good states of preservation of some of the skeletons, it does not look as though they had been transported far before they were fossilized.

A more recent interpretation has suggested that the environment resembled that of Cooper Creek in Australia (Astin et al. 2010). This is a multichannel ephemeral river system subject to rare but intense flooding. After the flood event, as the water gradually retreats, the remaining lake acts as a water hole, attracting local fauna. Astin and colleagues suggested that the animals in the *Acanthostega* horizon were transported or migrated downstream toward the remaining water, either during or after a major flood event. As the water receded, the animals could not or



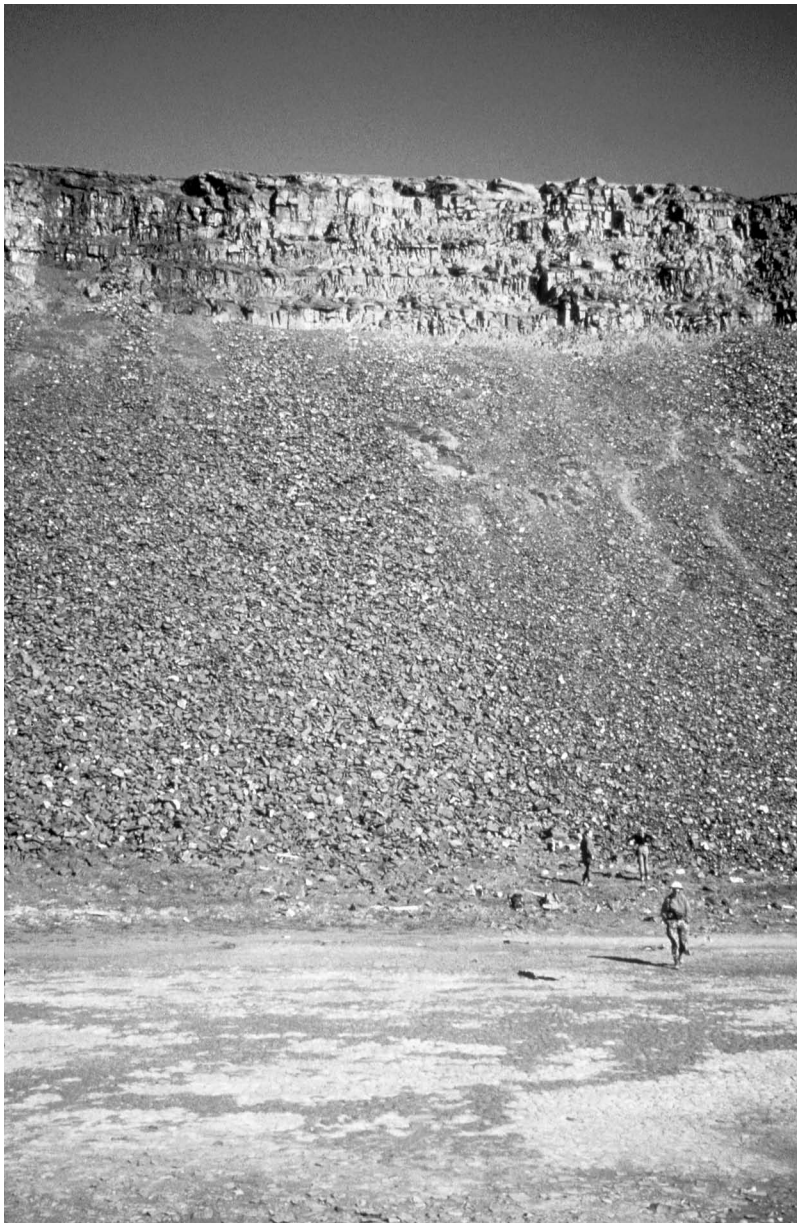
**5.6.** (Color Plate 8) The 1987 team on Stensiö Bjerg when they first encountered the *Acanthostega*-bearing horizon. The large block in front of me is that which provided the most complete articulated individual. At the base of the mountain, the campsite can just be seen. From left to right in the photograph: Jenny Clack and Per Ahlberg (kneeling), Birger Jørgenson, and the late Svend Bendix-Almgreen (standing). *Photograph by R.N.G.C.*

did not return upstream, and died in the channel as the water receded further. They suggested that the *Acanthostega* site represented two major flooding events in the same channel, separated in time. *Acanthostega* could therefore have been occupying the basin for some considerable period. It does seem clear that once the carcasses had been deposited on the point bar, they were exposed to the air for some time. Mud cracks subsequently filled by finer sediments run through the rocks, and in some places disrupt the skeletons.

The site that yielded most of the *Acanthostega* specimens also produced numbers of scales of fishes, such as the porolepiform *Holoptychius* and a lungfish, but the fish remains were all isolated, disarticulated elements. They almost all represented much larger animals than *Acanthostega*, and they could either have been living upstream in a lake of deeper water or fetched up where they did from a river or lake that flooded downstream.

The sediments in which *Ichthyostega* has been found vary from coarse red to fine-grained blackish-red sandstones, and they frequently contain fish scales and plates of placoderms. *Ichthyostega* is the most frequently found tetrapod in the Aina Dal formation, and it is usually encountered in massive blocks of ankle-breaking talus slope (Fig. 5.7).

Although fish scales such as those of *Holoptychius* and lungfish are found alongside remains of ichthyostegids, placoderms are, as often as not, found in different lenses of sediment from those preserving tetrapods. It is often the case that both placoderms and *Holoptychius* occur



**5.7.** (Color Plate 9) Aina Dal scree at the base of Stensiö Bjerg where many of the *Ichthyostega* specimens were found in the 1930s and in 1987. The figures in the picture give some idea of scale. *Photograph by J.A.C.*

in lenses or bedding planes containing only remains of those animals. Most ichthyostegid specimens are disarticulated and appear to have been preserved in flood deposits. A few specimens held together better and are partly articulated, and these may have been carcasses that dried out and became mummified before being caught up in the flood. It appears that the ichthyostegid specimens have all been carried quite a long way from their original habitat (Clack and Neininger 2000).

One of the most productive horizons for *Ichthyostega* lies at the base of the Britta Dal Formation. It is a thick sandstone layer, with abundant plant remains at its base (Blom et al. 2005). Several semiarticulated



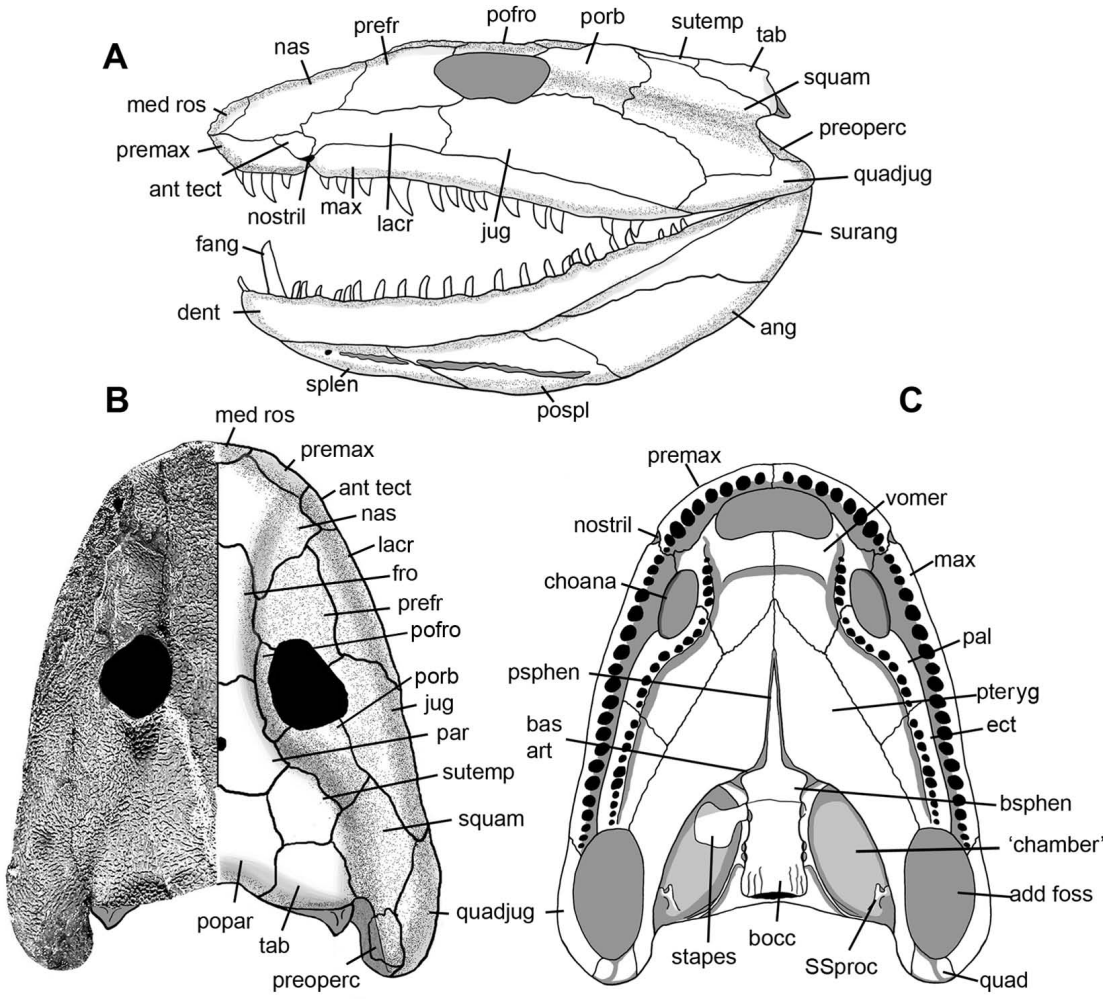
**5.8.** (Color Plate 10) Photograph of one of the skulls of *Ichthyostega* worked on by Jarvik (MGUH VP 6064). *Photograph by J.A.C.*

skeletons of *Ichthyostega* lie chaotically piled upon one another, along with isolated placoderm plates and *Holoptychius* scales. Again, these sediments are interpreted as resulting from a flood event (Astin et al. 2010).

*Ichthyostega* and *Acanthostega* represent two different kinds of animals, not particularly closely related to each other, and adapted in different ways. (The tendency in some literature to refer to them both as ichthyostegalians is mistaken and misleading.) Although they were contemporaries, they have not been found in exactly the same deposits; they most likely exploited contrasting environments. They show that by the end of the Famennian, tetrapods were already diverse in their body forms and modes of life.

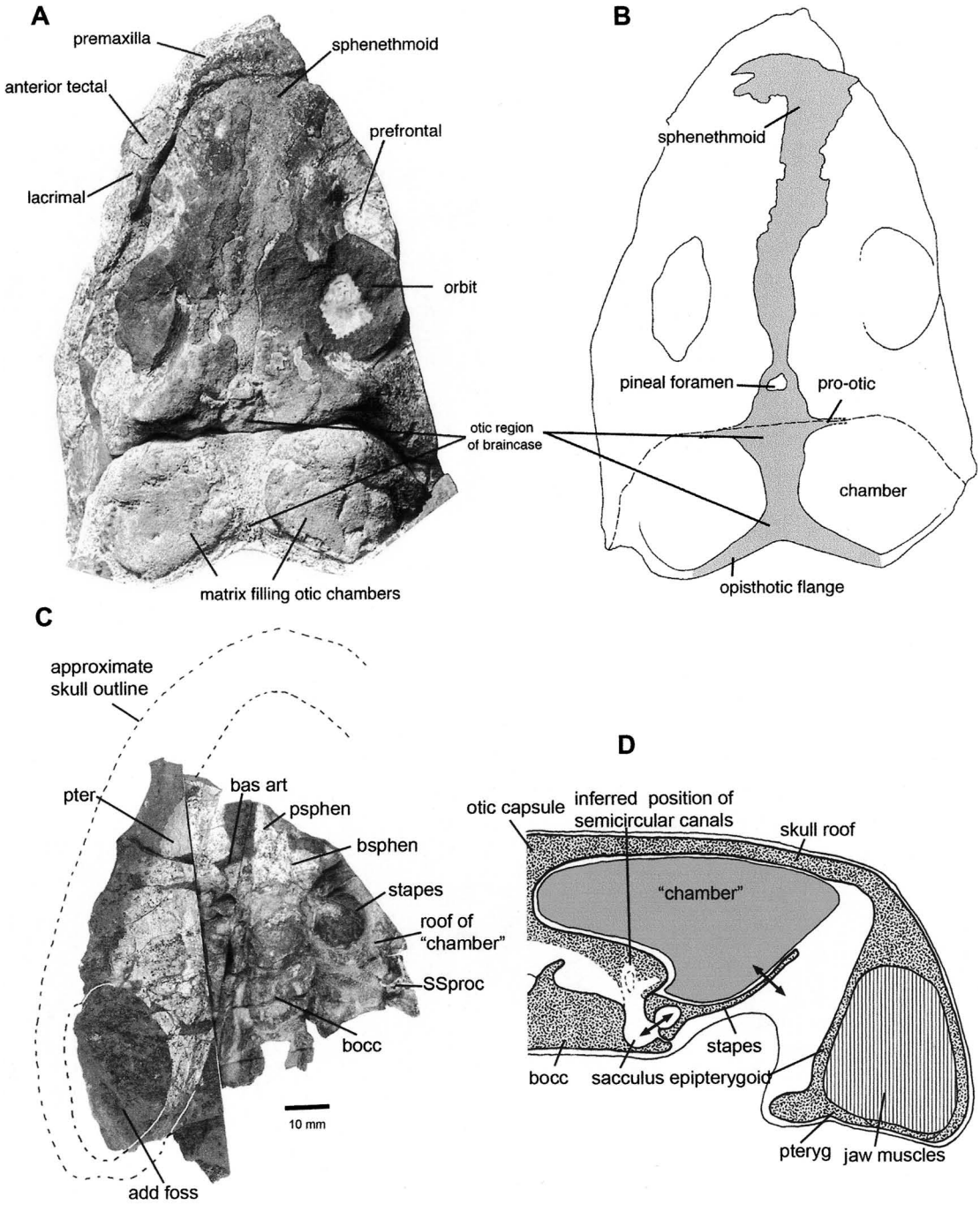
### *Ichthyostega*

*Ichthyostega* was first described in 1932 by Säve-Söderbergh and by Jarvik in a series of papers over many years, the most recent a 1996 monograph. Originally, four species were created, though their status as valid taxa remained uncertain for many years. Jarvik (1996) suggested that the name *I. stensioei* had priority over the others (correctly spelled *stensioi;* Snitting and Blom 2009). Recent work on studying the variability in skull morphology among the specimens and its relationship to the strata from which the material was collected has shown a consistent difference between those specimens from the Aina Dal Formation and those from the




**5.9.** New reconstruction drawings of skull of *Ichthyostega* based on specimen MGUH VP 6064. (A) Lateral view of skull roof and lower jaw. (B) Dorsal view of skull roof. (C) Ventral view with braincase and stapes.

Britta Dal Formation (Blom 2005). The later, Britta Dal, specimens show significantly shorter, broader skulls with consistently coarser ornament on the skull bones than those of the earlier, Aina Dal, specimens. It remains unknown what environmental conditions this difference may relate to, but the suggestion is that it represents a process of microevolution at work in *Ichthyostega* and that the two forms represent different species. Naming the species was problematic because most of the skulls studied derived from localities on Gauss Halvø, whereas most of Säve-Söderbergh's type specimens came from Celsius Bjerg. Two things further complicated the issue: first, these type specimens were all collected from talus, so it was impossible to say whether they were Britta Dal or Aina Dal derived; and second, those two formations are not so clearly demarcated on Celsius Bjerg as on Gauss Halvø. In the end, three of the old names were retained. The narrower Aina Dal specimens took the name *I. stensioi*, and the broader Britta Dal specimens took the name *I. eigili*, based on their resemblance to their respective type specimens. One skull, found


A
premaxilla
sphenethmoid
anterior tectal
prefrontal
lacrimal
orbit
otic region
of braincase
matrix filling otic chambers
B
sphenethmoid
pineal foramen
pro-otic
chamber
opisthotic flange
C
approximate
skull outline
pter
bas art
psphen
bsphen
stapes
roof of
"chamber"
SSproc
bocc
10 mm
add foss
D
otic capsule
inferred position of
semicircular canals
skull roof
"chamber"
stapes
bocc
sacculus
epipterygoid
pteryg
jaw muscles

at a lower level in the Britta Dal Formation than any of the others, had a form that was intermediate between the two morphologies and was given the name *I. watsoni*.

The skull of *Ichthyostega* ("fish armor") had a solid roof, like most vertebrates of its time. The head of the largest specimen is about 250 millimeters long (Figs. 5.8, 5.9). It had a bluntly rounded snout with a rather flattened profile, though at the back, the cheeks were quite steeply angled away down from the top of the head (Figs. 5.2, 5.9). The skull table, like those of many early tetrapods, had a hole for the pineal or parietal organ. The nostrils were near the edge of the snout, hardly separated from the mouth. Running through tubes in the bone of the head shield were the nerves and canals of the lateral line system, which opened to the outside by small pores. In this respect, *Ichthyostega* more closely resembles its fishy relatives than later tetrapods.

Though the braincase retains some primitive features, in others, it resembles that of no other known creature. Some recent work by myself and colleagues shows that its braincase was extremely narrow compared with any other contemporary fish or tetrapod. The regions to each side of the braincase appear to have been hollow chambers whose sides were specially strengthened by bony walls formed laterally by the palatal bones and posteriorly by downturned flanges of the skull roof (Fig. 5.10). The stapes has been identified as a thin, oval-shaped curved lamina of bone, convex ventrally, and attached to the braincase via a fairly narrow neck whose proximal end provided the stapedial foot plate. The foot plate region was divided into two portions that just met to enclose a large stapedial foramen. The lower part hinged against the braincase on the basisphenoid so that the upper part fitted against a foramen in the braincase wall.

The contents and function of this unusual construction could be debated, but they have been interpreted as being part of an ear system adapted for underwater audition, with the chamber being reinforced by bony walls and containing an air sac. The upper part of the stapedial foot plate could have responded to vibrations in the air sac, and by pivoting at its attachment to the basisphenoid, it could have transmitted those vibrations to the inner ear through the upper portion of the foot plate. It could have evolved from an air-filled spiracular chamber that was originally involved with air breathing. Thus, it could represent an early adaptation of this part of the anatomy as an auditory organ (Clack et al. 2003).

Where the cheek met the skull table was a deep embayment, bounded along the top edge by a downwardly turned flange from the skull table. Inside the skull, at the apex of the internal chamber so formed, was a curled tubular process known as Säve-Söderbergh's process. Its true function is unknown, but it has been suggested to be involved with a valvular mechanism for controlling air going in or coming out of the chamber.

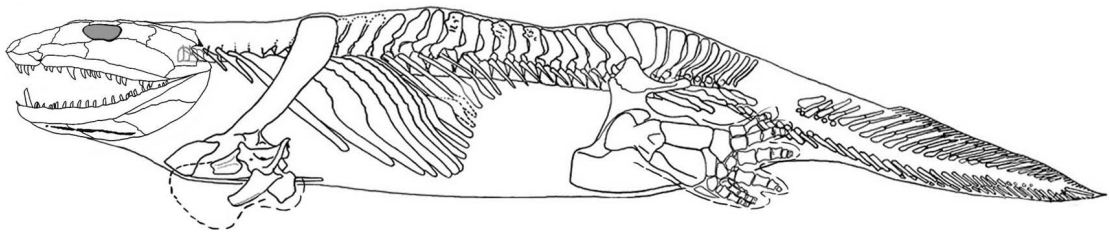
A well-ossified branchial system has now been identified in several specimens of *Ichthyostega*, and they show some resemblances to those of *Acanthostega* in being grooved (Clack et al. 2003). Both genera may therefore have retained some degree of gill breathing.

**5.10.** (A) Photograph of specimen MGUH VP 6158 of the skull of *Ichthyostega,* showing otic chambers. The dermal skull bones have been eroded away over most of the dorsal part of this skull. (B) Interpretation of the specimen. *(Photograph modified from Jarvik 1996.)* (C) Specimen MGUH VP 6018 showing the stapes. (D) Reconstruction of a section through the otic region based on the micro-CT scans of the specimen in Figure 1.7.

The mouth was armed with many robust and recurved teeth. In the upper jaw, there were two rows, an outer row of about 27–30 large ones and an inner row of about the same number of smaller ones, borne on the solid bony palate. The upper teeth contrast with those in the lower jaw, where surprisingly, in the outer row, rather than matching the upper teeth in size and number, there were more though smaller teeth. The reason for this discrepancy is not known, but *Ichthyostega* must have been capable of eating fairly large food items. It is likely to have fed on fish and invertebrates, though it is possible that it scavenged dead food as well as capturing live prey.

One of the more peculiar features of *Ichthyostega* was its ribs (Figs. 5.2, 5.11). It was a specimen containing the ribs of *Ichthyostega* that first gave paleontologists a clue that there were tetrapods to be found in the rocks of East Greenland, but it initially caused a great deal of puzzlement. In the trunk region, its ribs were greatly expanded, so that one rib would have overlapped three or four of the more posterior ones, forming a heavy, almost inflexible corset around its middle. It is not known what purpose the expanded ribs served. One suggestion is that they served to support the body in place of having well-ossified vertebrae (Thomson and Bossy 1970). *Ichthyostega* had vertebrae with quite well-formed neural arches, and the centra consisted of substantial horseshoe-shaped elements. Pleurocentra on which the neural arches would be expected to rest have not been positively identified in any specimen, and new computed tomographic scans suggest that they were absent. Another possibility is that the ribs were there to support the internal organs and stop them collapsing when the animal came onto the land, though they are not thought to have completely encompassed the body. They are unlikely to have been of use in helping ventilate the lungs, as those of mammals are, first because the overlap would effectively have prevented this. Second, although ribs are usually thought of as closely linked with ventilatory movements, in reality, it is mainly in modern amniotes (mammals, birds, reptiles; see Chapter 10) that ribs are used to bring about inhalation. They were not necessarily used like this in *Ichthyostega*. The arrangement does not appear to have allowed the animal to move in a sinusoidal motion, as might have been expected in an early tetrapod, and as can still be seen in lizards and salamanders.

A recent study (Ahlberg et al. 2005) has shown that an even more peculiar feature of its anatomy was its vertebral column. Whereas fishes—and most other Paleozoic tetrapods—had vertebrae whose shape varied little along the length of the spine, in *Ichthyostega*, the column was differentiated into clearly modified regions. There was a cervical region with short straight ribs, contrasting with a thoracic region bearing broad overlapping flanges, but with fewer of these broad ribs than previously suggested. The vertebrae in this region bore backwardly projecting and rather conventional neural spines. However, beyond that, there was a lumbar region in which the ribs became rapidly shorter and more backwardly projecting, and the neural spines gradually changed orientation



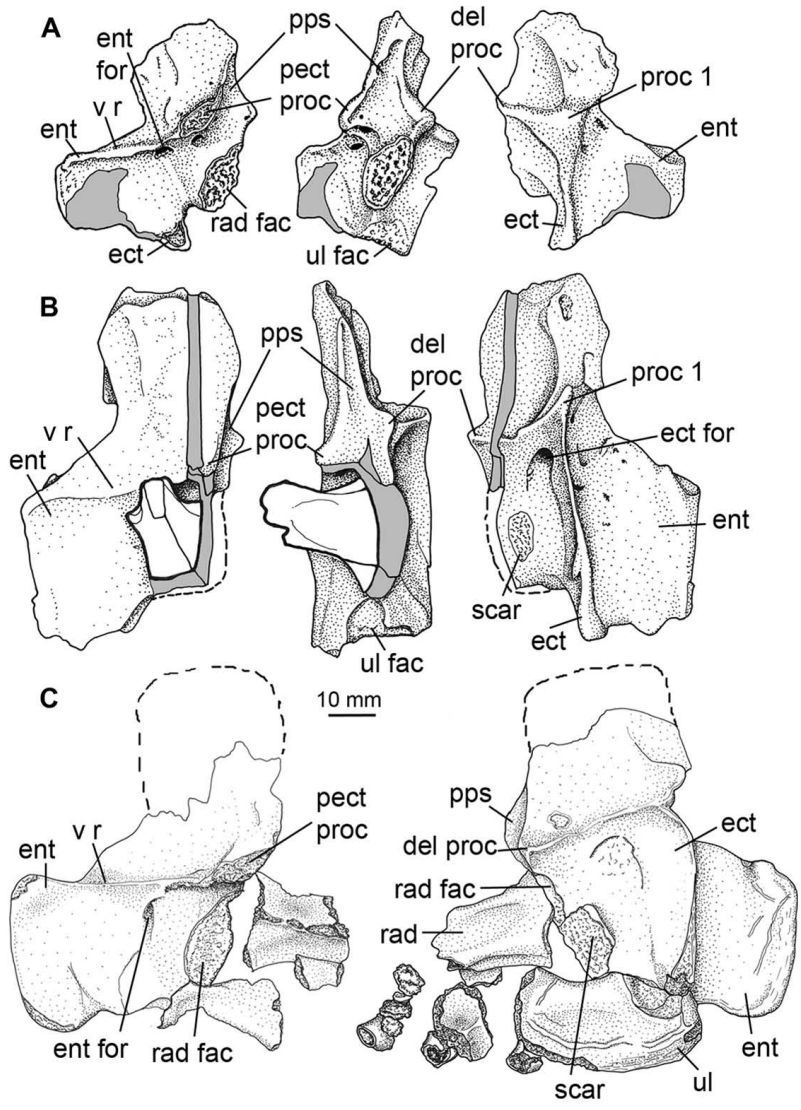
**5.11.** Skeletal reconstruction of *Ichthyostega*. *From Ahlberg et al. (2005).*

from backward to forwardly sloping. They also grew progressively longer in anteroposterior length, as well as somewhat taller, though an even more unusual feature was that in this region, the spines alternated in length and height, and some obviously bore scars indicative of muscle attachments. The orientation of the neural spines changed again over the sacrum, so that posterior to the pelvic girdle the neural spines were once again posteriorly sloping. The implications of this regionalization of the column are that different parts of the column were specialized to perform different functions and experienced different forces. That in turn means that the muscles that operated the column were also differentiated—surprising in such an early tetrapod, and not fully encountered again until the evolution of mammals.

The shoulders of *Ichthyostega* were massive for the size of its body, and recent restudy of the specimens suggest that Jarvik's (1996) restoration underestimates their relative size (Ahlberg et al. 2005). In early tetrapods, the shoulder girdle still retained parts of the dermal skeleton that was inherited from the fish, including a cleithrum (Fig. 2.6). This bone in *Ichthyostega* was large and fused with the cartilage-bone scapulocoracoid, where the articulation for the forelimb was placed. Judging from the size and position of this articulation point, the forelimb would have been fairly restricted in its range of movement. For example, it might not have been able to move forward further than about 90 degrees to the body, and could probably not have been pulled back into the side of the body when the animal was swimming.

The upper arm bone or humerus is known from both adult and subadult specimens. In adults, it was L shaped, fairly flattened, and with large processes forming attachment points for muscles to the shoulder girdle. At the outer end of the humerus were the attachment points for the forearm bones, the radius and ulna. In the adults, the facet at which the radius articulated was bifaceted and elongate, and it lay partly anteriorly and partly ventrally along the leading edge of the humerus, suggesting a complex range of movement for the radius. The ulnar facet is not well preserved in any specimen but appears to have wrapped around the end of the ectepicondyle.

Some information about the growth trajectory of the humerus has been gained from study of the subadult specimens collected in 1998 (Callier et al. 2009). This, combined with renewed study of earlier-collected material, has shown some remarkable changes in the morphology of the humerus during the life of the animal, as well as some features in which




**5.12.** Ontogeny of the humerus of *Ichthyostega*. From Callier et al. (2009). Adult and subadult humeri of *Ichthyostega* drawn to the same scale. (A) Specimen MGUH 29017a, left humerus in (left to right), ventral, preaxial (=anterior), and dorsal views, based on exposed region of specimen and a CT scan model. (B) Specimen MGUH VP 6115, left humerus in (left to right) ventral, preaxial, and dorsal views. Thick outline shows impacted radius, which obscures the entepicondylar foramen. (C) Specimen MGUH VP 6138, right humerus, reversed for ease of comparison, in ventral (left) and dorsal (right) views. Drawn from latex peels of part and counterpart. Radius, ulna and metacarpals are also present. Note that this humerus is flattened, with the ectepicondyle compressed into a posterior orientation. Gray infill represents broken or missing bone. In the case of MGUH VP 6115, this is in the form of a band saw cut that has removed the region of the radial facet. "Process one" is unique to *Ichthyostega*. del = deltoid; ect = ectepicondyle; ent = entepicondyle; fac = facet; for = foramen; pect = pectoralis; pps = prepectoral space; proc = process; rad = radius/al; ul = ulna/r; v r = ventral ridge.

it shows several unexpectedly primitive features (Fig. 5.12). The position of the facet that receives the radius moves relative to other parts of the bone: the more distal part of the bone seems to grow at a different rate from the proximal part, to make the radial facet occupy a position closer to the midpoint of the bone than it is in the subadult.

A prominent feature of the ventral surface in the subadults is the ventral ridge, which also changes its relative orientation on the ventral surface. In the subadults, it bears a conspicuous process at about its midpoint, which has recently been identified as the pectoral process. Muscles from the shoulder that pull the bone downward would attach to it. The ridge is also pierced by large foramina, including an ectepicondylar foramen. Specimens of about two-thirds of the known maximum size not only have the foramina seen in the adult, but these are also larger, and there

are more of them. In the adult, the whole ridge reduces in prominence, and the pectoral process migrates, along with changes to the orientation of the ventral ridge, across the bone. The pectoral process comes to lie close to the anterior edge of the humerus, closer to the radial facet. The foramina are reduced in size, or in some cases become completely occluded. On the upper side of the bone, a deltoid process lies at roughly the same distance from the head as the pectoral process, but there is gap between them, known as the prepectoral space. In effect, this means that in *Ichthyostega*, there is no deltopectoral crest. In other tetrapods, that feature is one that bears muscles from the shoulder to the humerus and controls anterior to posterior movements.

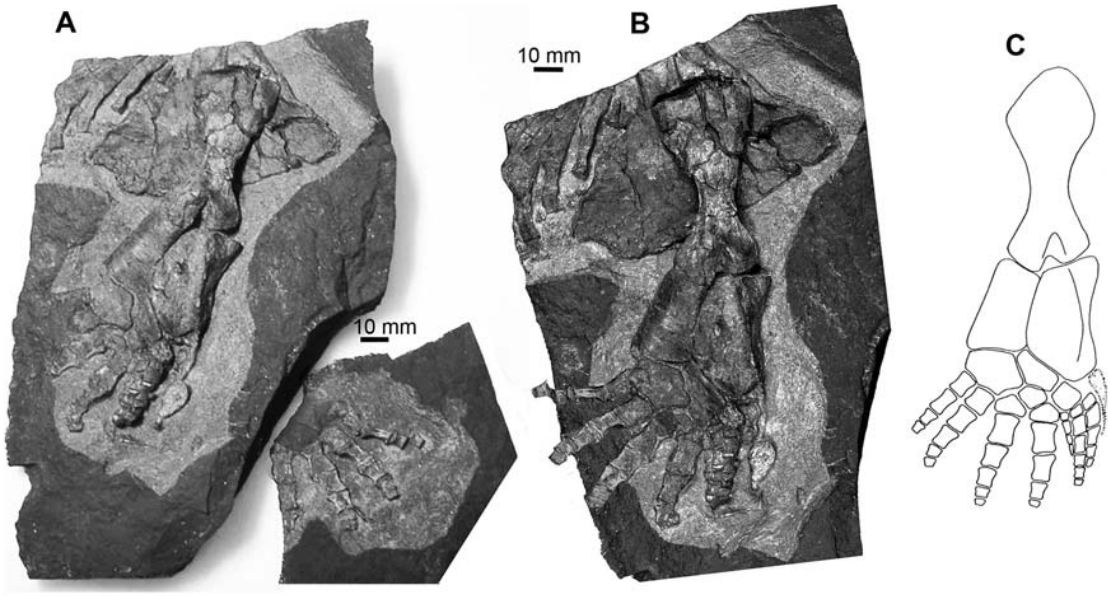
Both adult and subadult specimens lack some of the features found in later tetrapods but retain others that are equivalent to those in some tetrapodomorph fish. These features and their implications are discussed in Chapter 6.

The radius and ulna were rather short, stubby bones. The radius was short and broad, and bore a stout crest along its posterior surface. The ulna bore a process at the elbow, called the olecranon, to which muscles attached for raising the forearm. Because of the way the radius and ulna attached, the movement possible at the elbow seems to have been extremely constrained, but was probably not simple. Unfortunately, little is described of the wrists or hands of *Ichthyostega*, although some specimens do preserve incomplete material that remains to be fully investigated. First results from ongoing study suggest that the wrist and hand elements were broad and flattened, somewhat like most of those known for the feet.

When the postcranial skeleton of *Ichthyostega* was first described in detail, it was the tail that aroused the greatest interest because it was more fishlike than tetrapod-like. In many other respects, *Ichthyostega* is a strange animal, and parts of it are like no other tetrapod or fish. But the tail was unequivocally fishlike. Most obviously, it had bony fin rays supporting a web, as is found in fishes, but not at the time in any other known tetrapod (Figs. 5.2, 5.11). Extra supports called radials attached to the tips of the neural arches and helped stiffen the web. The fin web extended not just dorsally, but continued around underneath the end of the tail. Clearly this tail was one that was used in water to aid swimming, although recent reconstructions suggest that it was shorter than originally envisaged (Ahlberg et al. 2005).

Several specimens preserving tails are known, and some of them also preserve elements of the hind limb and pelvic girdle. The pelvic girdle was a large structure, robust and formed from a single bone on each side. It bore both a horizontally directed process oriented backward and a shorter, stouter one directed upward. It probably had a rib that was specially adapted to join to the pelvis on the internal face of this process, although this rib has not been found. The backwardly directed process almost certainly bore muscles that helped power the tail.

The hind limb is known from three or four specimens, the best preserved of which was found by the 1987 expedition (Figs. 5.13) (Coates



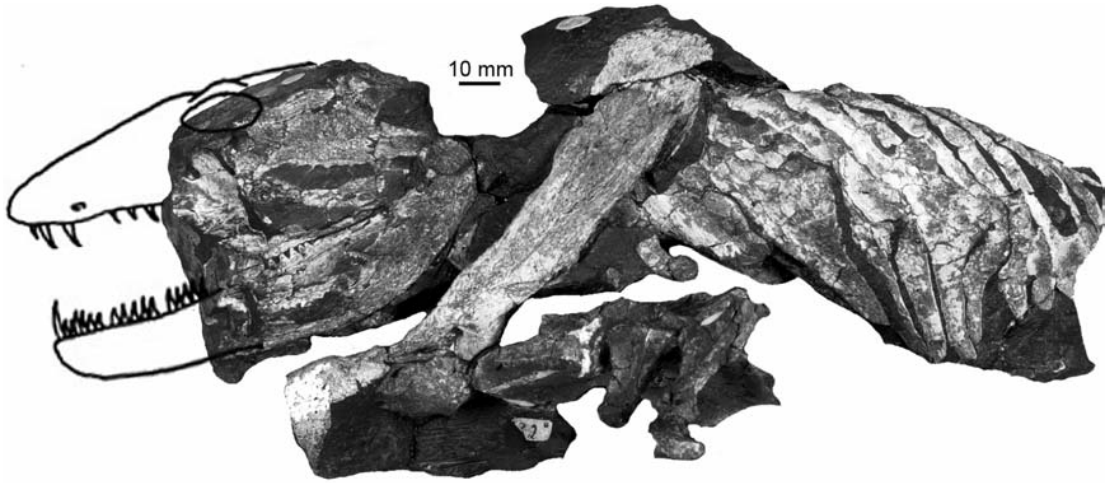

**5.13.** (A) The hind limb, pelvic girdle, and tail found in 1987, with the counterpart of the four largest toes placed at right (MGUH f.n. 1349). (B) The part and counterpart toes amalgamated using Photoshop. (C) Reconstruction drawing of the hind limb.

and Clack 1990). Its significance is discussed in Chapter 6. The femur was flattish in cross section, but it had a large flange on the side nearest the body carrying muscles that moved the limb inward and downward. At the outer end, the bone widened and provided attachment for broad and flat lower leg bones, the tibia and fibula. These in turn were attached to what seems to have been a rather inflexible ankle joint composed of fewer bones than those of modern tetrapods, though these, like those of the lower leg, were flat and quite large.

Perhaps the most surprising feature of all in *Ichthyostega* is the complement of toes. The 1987 specimen clearly shows that at the leading edge of the limb were three tiny toes, the smallest of them being the third one from the edge. Then followed four quite stout toes, giving a total of seven. The leading edge also seems to have been strengthened by a strip of a cartilage-like substance that was preserved along with the toes (Fig. 5.13).

The picture that emerged from putting together the material collected in 1987 and 1998 with some of the specimens collected by earlier expeditions was surprisingly different from the view that is found in textbooks and in the more popular literature for children and nonspecialists. What is more, over the years, the perception of *Ichthyostega* has changed. Though in 1952 it was restored as a semiaquatic animal with paddlelike hind limbs, by 1980 (Jarvik 1980) it was portrayed as a solidly terrestrial animal, with four stout, weight-bearing legs. The material collected in 1987 suggested that the earlier reconstructions of 1952, as well as a more recent one by Bjerring (1985), of a more aquatically adapted animal, were more correct.

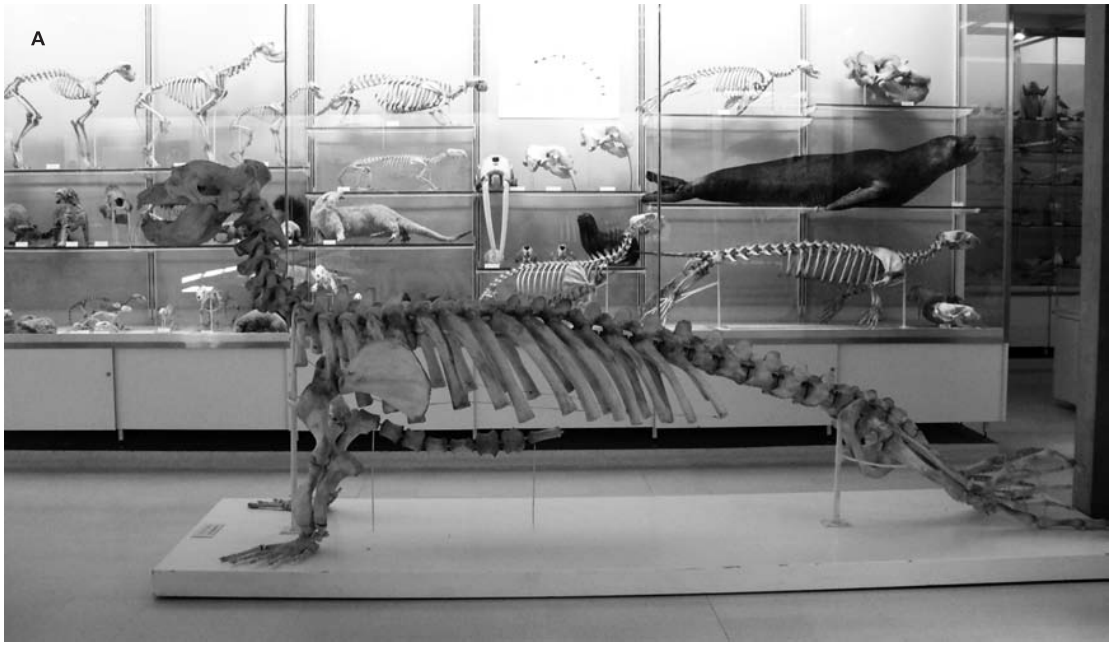
*Ichthyostega* is represented by many specimens, especially skulls, but articulated material tends to fall into two categories: heads with trunks, and hind limbs with pelves and tails. Very few show the whole animal, so it has been difficult to marry together front and rear halves. However,




**5.14.** An articulated specimen of *Ichthyostega* (MGUH VP 6115). The skull is broken off just behind the orbit. Half the left lower jaw can be seen. The specimen preserves both humeri and cleithra, and left scapulocoracoid, and this photograph shows the left shoulder girdle with the humerus tucked under the rib cage. The radius, ulna, and one wrist bone (ulnare) were preserved in articulation with it. The broad overlapping ribs of the anterior part of the body can be seen. *Photograph by S.M.F.*

there are a few that overlap in the crucial area. In the specimen on which Jarvik's original reconstruction was largely based (Fig. 5.14), the supposed association between a femur and a presacral column, head, and trunk are dubious, and they may not in fact belong to one individual. Thus, the proportions of the front of the animal to the rear have been quite problematic until recently, when restudy suggested a rather different appearance from the traditional one. The picture that emerged from the new work is an unexpected one for such an early tetrapod (Fig. 5.11), and this in itself may give grounds for questioning its accuracy. Ongoing work is attempting to test its validity by means of computed tomographic scanning techniques combined with virtual modeling of the skeleton. Nonetheless, the flattened hind limb bones and inflexible ankles were much more paddlelike than leglike, and the hind foot seems to have been held with the leading edge downward, to cut into the substrate and provide some anchorage. By contrast, the massive shoulders and forelimbs look adapted for supporting the head and lifting the front end of the body off the ground. It appears that in *Ichthyostega*, the forelimbs provided the motive power on land, although in the water, it would have been the tail and probably the hind limbs. The paddlelike hind limbs might also have aided steering and braking and perhaps stabilization, or might have given purchase against the ground on land.

It turns out that the skeleton of a modern seal, such as an elephant seal, compared with that of *Ichthyostega* shows a number of parallels that may provide clues about *Ichthyostega*'s lifestyle. In the elephant seal, the elbows are held at right angles when on land (Fig. 5.15A). The forelimbs are about twice the size of the hind limbs, which in turn are paddlelike. All the limbs can be tucked into the sides for speed swimming powered by the tail, or they can be used to steer the animal in directional changes. When the seal comes onto land, the forelimbs drag the body, hind legs, and tail, and they also tend to move together. It is possible to imagine *Ichthyostega* progressing in much the same way. Ongoing work in my







**5.15.** (A) Skeleton of an elephant seal skeleton in UMZC (B) Photograph of the paddlelike forelimb of a dolphin. *UMZC specimens, photographs from UMZC archives.*



**5.16.** Life reconstruction of *Ichthyostega*. The number of fingers on the manus is notional. *Illustration by J.M.*

laboratory with colleagues is hoping to test this idea and investigate the possible range of movmement in *Ichthyostega* and *Acanthostega*, and compare them with potential modern analogs such as seals, otters, crocodiles, and salamanders.

The skeleton of the paddlelike hind limb also has another parallel among modern forms, in its similarity to that of the forelimb of some dolphins, especially a river dolphin. In these animals, the bones are flattened, and there is a reduced number of them in the wrist. At the leading edge of the paddle is a small digit while the other four are stout, and all are bound together by a web (Fig. 5.15B). It is not known whether the digits of *Ichthyostega* were embedded in a web, but all of the known specimens of hind limbs have their digits present, tending to suggest that they might have been.

Figure 5.16 gives a life reconstruction of *Ichthyostega* based on the most recent information. In summary, *Ichthyostega* is a curious mixture of features, some of them primitive, some of them specialized and unique. Because of this, after its discovery, it did not lead to many new insights into the origin of tetrapods.

### *Acanthostega*

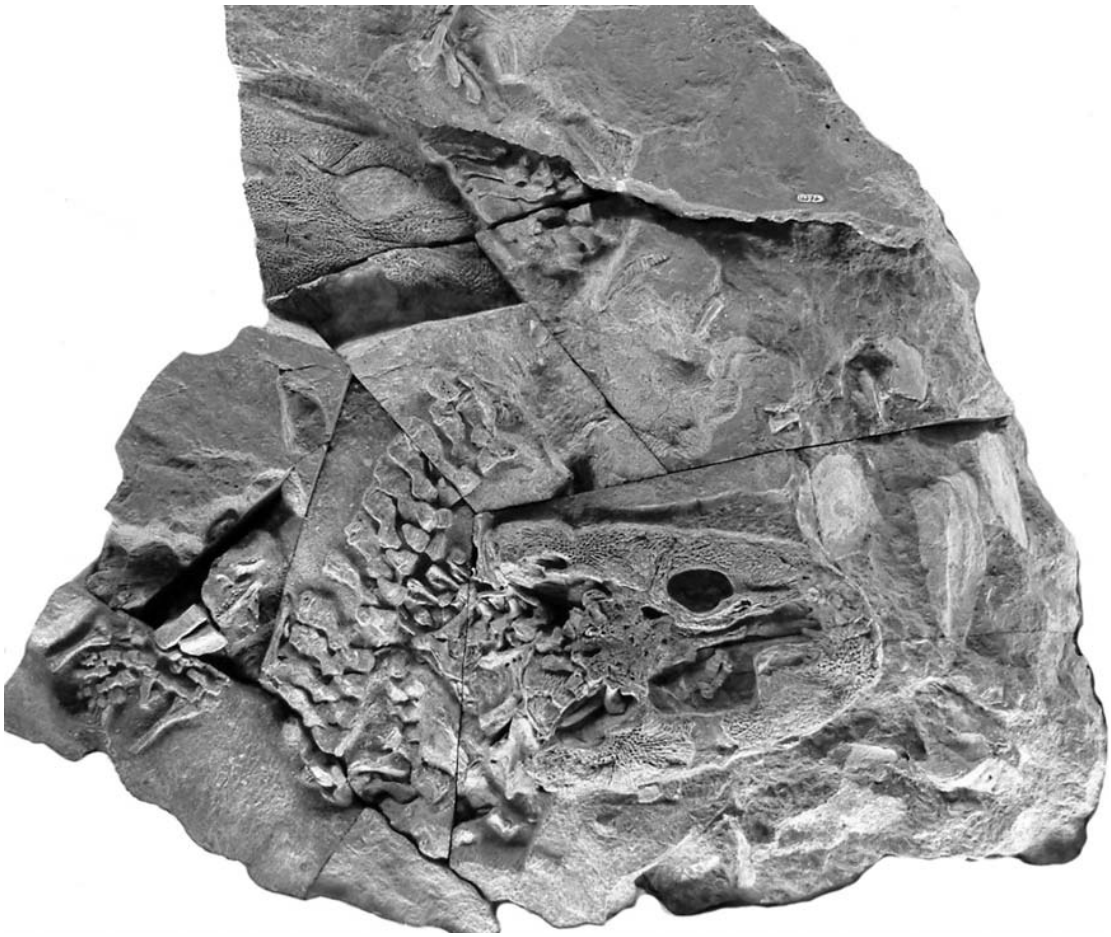
*Acanthostega* was the second Devonian tetrapod to be described from East Greenland (Jarvik 1952). For many decades, all that was known of this animal were two partial skull roofs, and from these it was clear that it was a very different animal from its contemporary. Figure 5.17 shows the holotype specimen on which the original description of *Acanthostega* was based. The specimen shows the right side and midline bones of the skull more or less complete, with the tooth-bearing maxilla somewhat detached from the rest of the cheek. The pattern of bones in the skull roof was in some respects different, in particular at the back edge of the skull table, where *Acanthostega* had a tabular bone that formed both a deep embayment and long pronglike tabular "horn." It is this distinctive structure that gives it its name: "spine armor."



**5.17.** The holotype specimen (MGUH VP 6033) of *Acanthostega* described in 1952 by Jarvik. *Photograph from UMZC archives.* Skull about 140 millimeters long.

Following up some accidental finds of *Acanthostega* material made in 1970 by a sedimentologist, the joint Copenhagen–Cambridge expedition succeeded in collecting what has turned out to be spectacular new material of this creature (Figs. 1.3, 1.4, 1.6, 5.18). Remarkably, among the specimens they collected in 1987 were the bodies of the animals whose skulls had been found in 1970 (Fig. 5.19). An account of this story is entertainingly told by Zimmer (1998). From these accumulated finds, almost the whole skeleton of *Acanthostega* is now known and has been described in a series of papers. The animal has emerged as much more what would be expected of a primitive tetrapod (Fig. 5.20) than is *Ichthyostega*. Study of this animal has led to some changed ideas about what early tetrapods were like and has also led to some new ideas about the development of limbs, the evolution of air breathing, and the subsequent radiation of tetrapods from the Devonian to the present day.

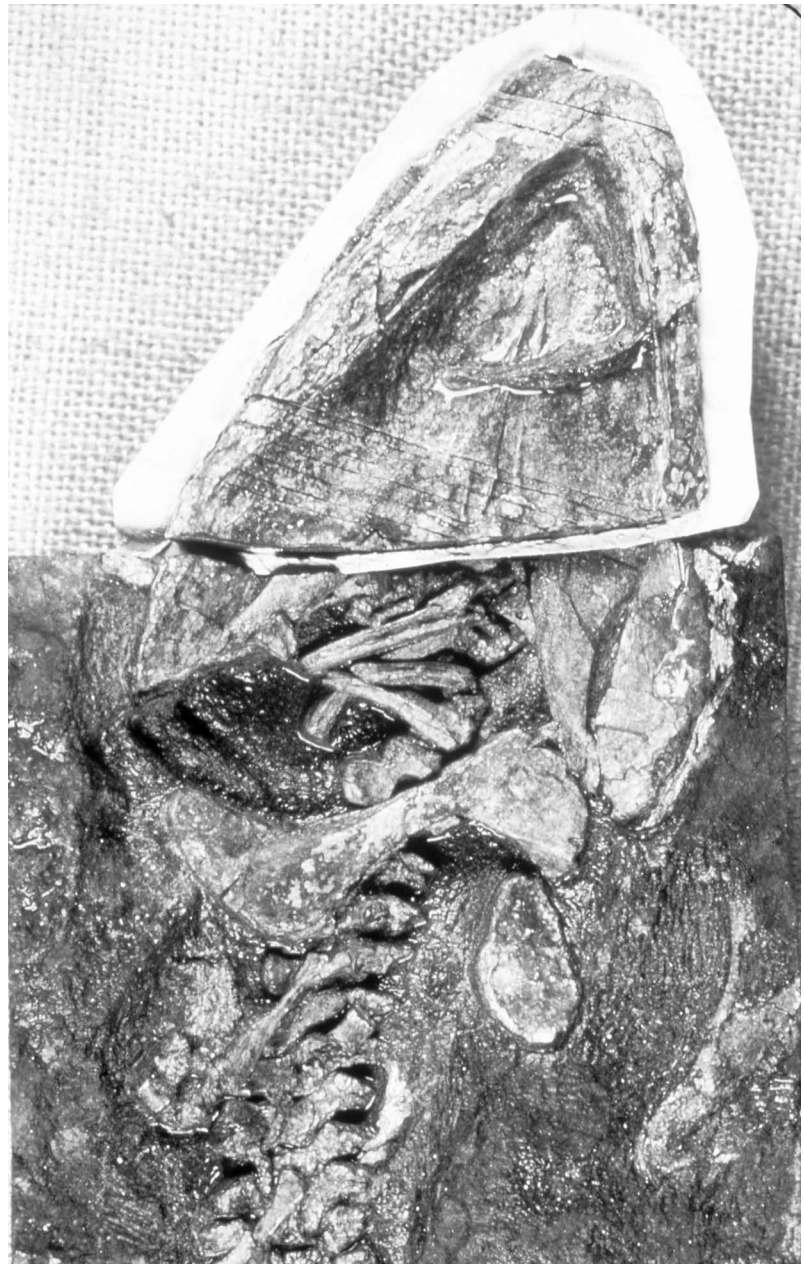
Apart from primitive similarities, *Ichthyostega* and *Acanthostega* have almost nothing in common. As in *Ichthyostega*, the skull of *Acanthostega* was quite shallow, with a bluntly rounded snout (Clack 1994a, 2002a, 2003a) (Fig. 5.21). Its palate was likewise formed of a bony sheet, though not so solidly attached to the rest of the skull as in *Ichthyostega*. As in *Ichthyostega*, the external nostril lay close to the edge of the mouth, and the lateral line organs were in most cases housed in tubes through the bone, although these merge into grooves in some places, and the pores through which they open to the outside are more conspicuous than in *Ichthyostega*. The skull and the dermal shoulder bones of both animals had a sculptured surface of pits, ridges, and furrows, in common with other early tetrapods and many contemporary fishes (see Figs. 1.4 and 6.6). The function of this ornament is unknown, but something similar is seen in certain modern fishes, especially catfishes.



**5.18.** (Color Plate 11) The most complete of the *Acanthostega* specimens found in 1987, after preparation was finally completed in 1998 (MGUH f.n. 1227). The skull is about 120 millimeters long. A second skull is seen to the top left. The forelimb with its eight digits lies at bottom left. *Photograph by S.M.F.*

*Acanthostega* was a rather smaller animal than *Ichthyostega*, with a skull of a maximum size of about 200 millimeters and a dentition suggesting a different diet. The marginal teeth of the outer row were much smaller than in *Ichthyostega*, while the inner row on the palate consisted of much smaller toothlets and denticles, plus some large fangs. The contrast in upper and lower teeth seen in *Ichthyostega* is less noticeable in *Acanthostega*. Almost all the features of *Acanthostega* that have been discovered suggest that it was pretty much totally aquatic, so that its dentition, resembling in some respects that of many of the contemporary lobe-finned fishes, was probably adapted for feeding in water.

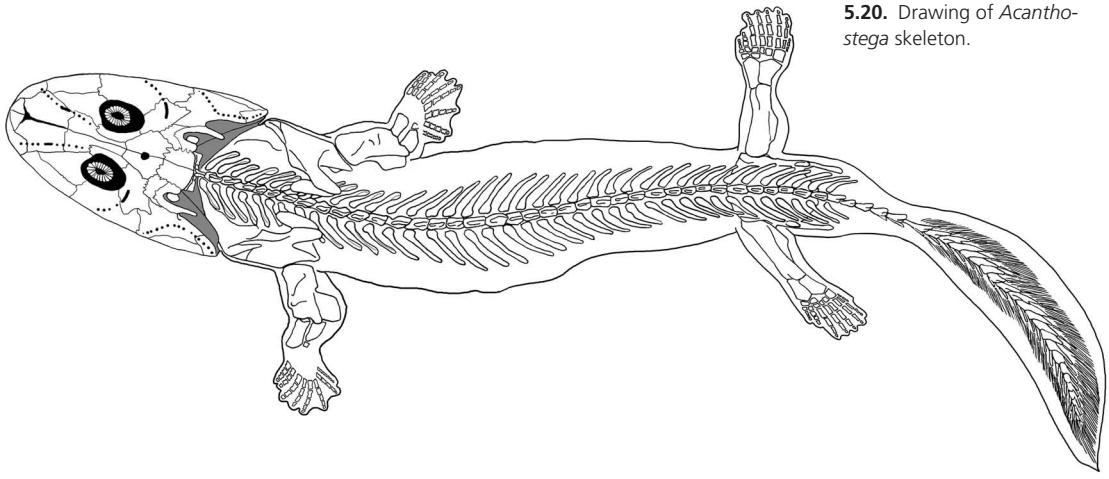
When collecting material in Greenland, we noticed that many of the skulls of *Acanthostega* had fallen apart along the midline, and we were curious as to why that happened. After new *Ventastega* material was collected in 2002, it became obvious that there was in fact little or no contact between the two nasal bones, or between them and the premaxillae. *Acanthostega* had an internasal fontanelle like *Ventastega*, but rather narrower, and unsuspected until the skull roof of *Ventastega*



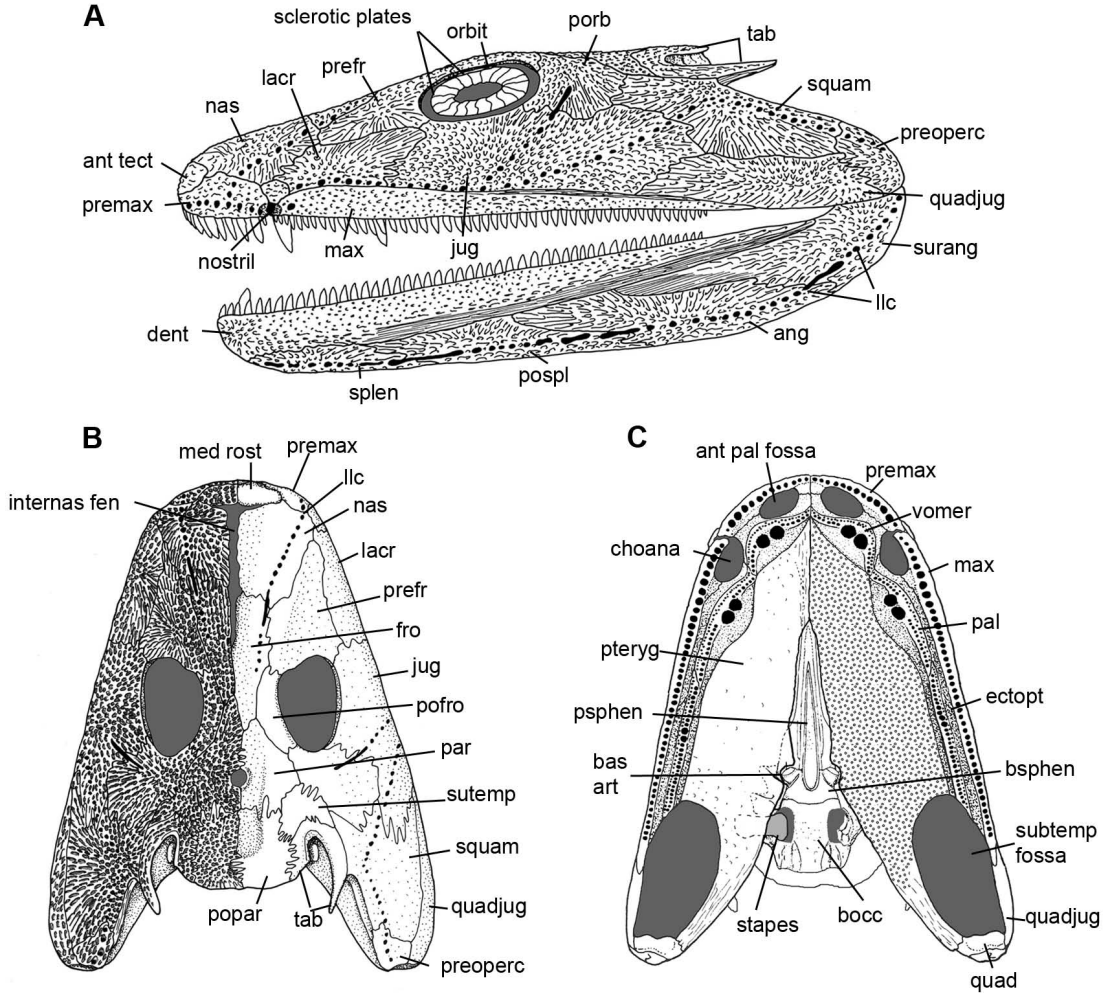
**5.19.** An *Acanthostega* specimen showing the skull in ventral view, with the gill skeleton underneath and shoulder girdle elements lying more or less in place (UMZC T.1300 and MGUH f.n. 1258). The skull was found in 1970 and the body in 1987.

was discovered. In other places in the skull roof—for example, the skull table—the suturing of the bones to each other is particularly secure, with interdigitations interfingering in three dimensions. On either side in the snout area, there are broad areas of overlap where the sutures are designed to resist twisting of the snout in feeding (Clack 2002a, 2003a). Recent work by Markey and Marshall (2007) has investigated the types of sutures found in different parts of the skull (discussed in Chapter 6).

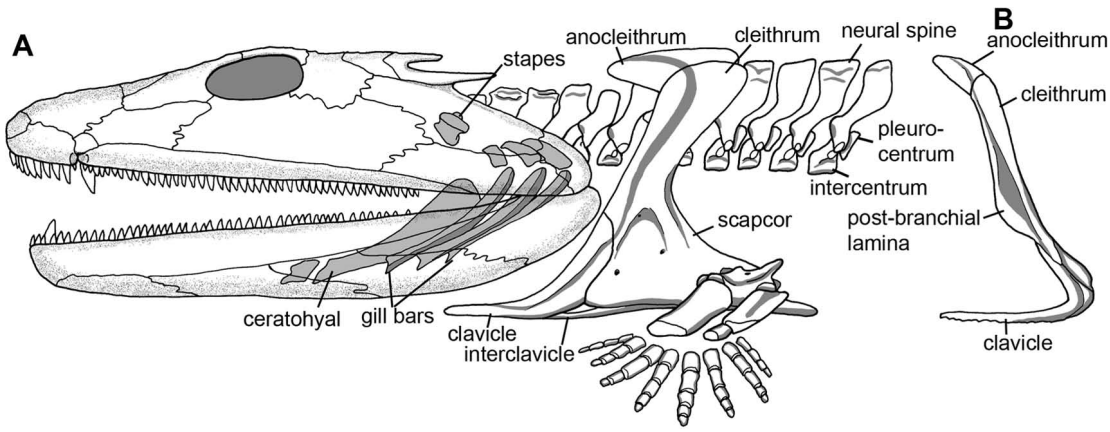
The remarkable preservation of several of the *Acanthostega* specimens has preserved parts of the skeleton, particularly the more delicate



**5.20.** Drawing of *Acanthostega* skeleton.



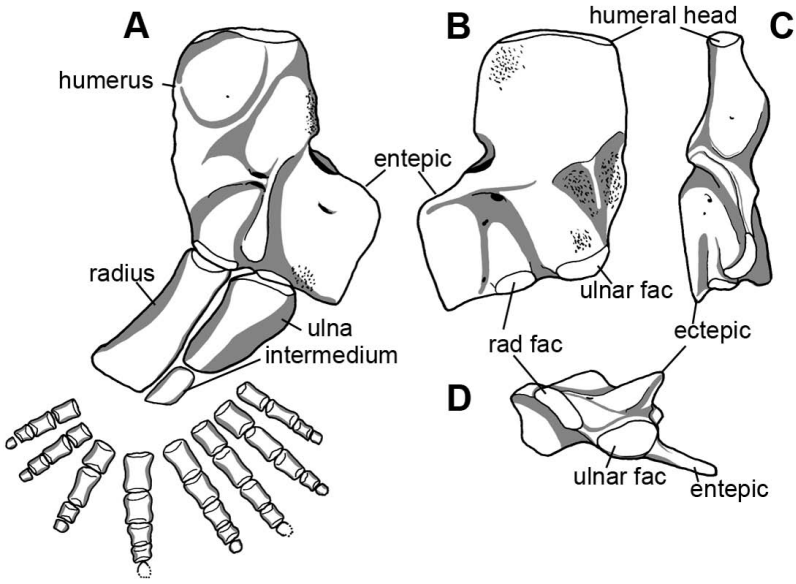

**5.21.** Drawings of skull of *Acanthostega*. (A) Left lateral view. (B) Dorsal view. (C) Ventral view. The anterior tectal is the small bone just above the nostril.




**5.22.** (A) Drawing of head and shoulders of *Acanthostega* with skull bones shown as transparent; gill skeleton restoration seen internally. (B) Anterior view of shoulder girdle showing postbranchial lamina.

ones, that are not often found. A good example of this is the preservation of the gill skeleton. In *Acanthostega* (Figs. 5.19, 5.22) the gill skeleton proved to be remarkably fishlike (Coates and Clack 1991). Each of the branchial elements was strongly ossified and had a deep groove running down the back. Elements from at least three and more likely four pairs of gill arches have been found. When compared with modern fishes, in which the gill structure is known, the gill bars of *Acanthostega* most closely resemble those of the Australian lungfish *Neoceratodus*. This fish uses internal gills for breathing in water like most fish, but also lungs for breathing air. There are three functional pairs of gill arches, as found in *Acanthostega*. The groove along the individual elements accommodates the afferent branchial artery, which takes blood to the gills for oxygenation. This is one piece of evidence to suggest that *Acanthostega* used internal gills like *Neoceratodus* as part of its breathing mechanism.

Another piece of evidence that supports this conclusion comes from the shoulder girdle (Fig. 5.22). In *Acanthostega*, as in *Ichthyostega*, the shoulder girdle consisted of a stout dermal cleithrum bonded to the endoskeletal scapulocoracoid. The whole unit was sheathed across the ventral surface and up the lower part of the leading edge by the dermal clavicle. Along the leading edge of the cleithrum in *Acanthostega* was an inturned flange, a little hollowed out from the front. This flange is the postbranchial lamina and is found in most fishes (Fig. 5.22B) (Coates and Clack 1991). (Next time you buy a whole fish to eat, look behind the gill flap at the rim of bone that receives the flap when the gills close. This is the postbranchial lamina.) This lamina does a couple of jobs. Its angled cross section gives the shoulder vertical strength, and it also forms the back of the gill chamber, where its shape helps to direct water out once it has passed over the gills (see Chapter 2). This, added to the evidence from the gill elements themselves, strongly suggests that *Acanthostega* still used internal gills for breathing. It would no doubt also have used lungs as well, as did *Neoceratodus*, because lungs or their equivalent appear to have been a common heritage of all bony fishes. *Acanthostega* also retained another fishlike character of the shoulder girdle, the presence




**5.23.** Drawing of forelimb of *Acanthostega*. (A) Complete left forelimb. Humerus in (B) ventral, (C) anterior, and (D) distal views.

of the anocleithrum, a remnant of the more extensive dermal shoulder girdle of fishes (Coates 1996). There was no postbranchial lamina in the shoulder girdle of *Ichthyostega*, and no anocleithrum has been found, though this may have more to do with the degree of ossification of the elements or the state of preservation of the specimens than with their actual absence in the living animal.

In contrast with *Ichthyostega*, in *Acanthostega*, the surface of the glenoid facet was not strongly contoured but rather was a relatively flat oval, directed to the side of the animal. This suggests that its forearm also was directed almost entirely sideways, though it may have had more freedom of movement to the front than that of *Ichthyostega*. It is the forearm of *Acanthostega* that has revealed a number of the most remarkable new facts about Devonian tetrapods (Coates and Clack 1990).

The humerus of *Acanthostega* is shaped like a broad L, as in most other early tetrapods, though as in *Ichthyostega*, a number of foramina and processes were present that disappear during the evolution of tetrapods as a whole. The same study (Callier et al. 2009) that looked at growth patterns in the humerus of *Ichthyostega* found that specimens of *Acanthostega* also represented a range of sizes from subadult to presumed adult (or again, the smaller examples were two-thirds of the size of known maximum). Unlike *Ichthyostega*, however, there was no evident change in shape or proportion, or reduction in the size of the foramina; the bone simply got larger and longer. On the other hand, the bone exhibited a number of features, including the presence of a latissimus dorsi process and a deltopectoral crest for muscles that attach to the shoulder (Fig. 5.23). These and the almost total lack of a ventral ridge in *Acanthostega* are features shared with Carboniferous tetrapods and *Tulerpeton*, but which are absent in *Ichthyostega* and tetrapodomorph fishes.

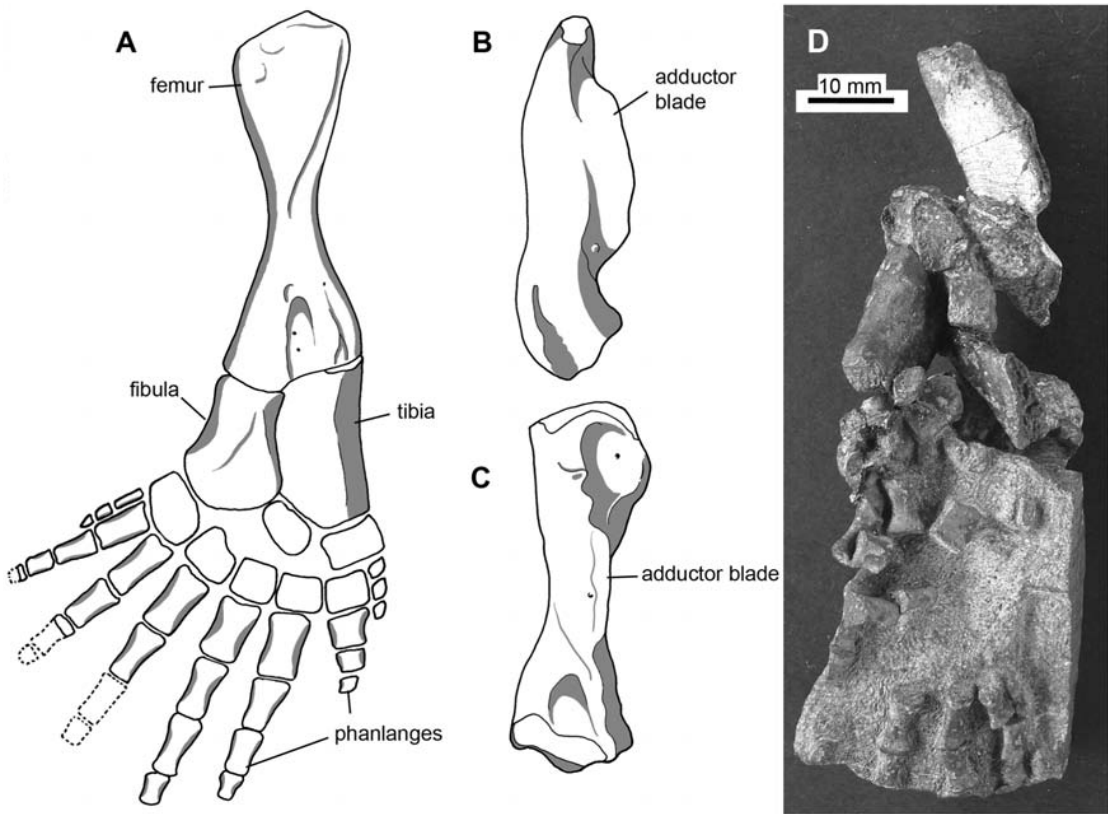
The bones of the lower arm, the radius and ulna, are different in several ways from those of any other tetrapod (Figs. 5.22, 5.23). First, the radius was an elongate element, cylindrical in section near the articulation with the humerus, but flattened and spatulate at the lower end. It was also nearly twice as long as the ulna. The ulna was a short, flattened bone with a strap-shaped articulation where it joined the humerus but a narrow articulation where it joined the wrist. The leading edge facing the radius was straight, but the back edge was curved. There was no prominent olecranon process like that in *Ichthyostega*.

These proportions and shapes are unique among tetrapods, but reflect those of a lobe-finned fish like *Eusthenopteron* or *Tiktaalik* remarkably closely. Therefore, the most plausible interpretation is that the shapes and proportions are those of a primitive forelimb that retains several fishlike features, rather than one that has been adapted from that seen in a more "conventional" tetrapod. This conclusion is important for interpreting many aspects of the morphology of *Acanthostega*, including what is probably the most surprising aspect of the animal: the hand and digits.

Only one true wrist bone is known, that which attached to the ulna, called the intermedium. Though a number of other possible elements were discovered that may be wrist bones, they were jumbled up and it is not possible to say where they were positioned. The wrist itself must have been broad and inflexible because of the discrepancy in length between the radius and ulna. It is difficult to see how that arrangement could have functioned as a weight-bearing joint.

More surprising are the digits. One specimen shows the digits in full articulation at the end of the arm. There are eight of them. Each is complete, and none is the duplicate of any of the others. They are arranged in a regular array, with three small ones at the leading edge and two slender ones at the rear. It is not clear whether these digits were enclosed in any kind of webbing, though the fact that they are still in articulation suggests that they might have been, at least to some extent. Each of the phalanges is basically a simple, slightly flattened cylinder in shape with little expansion at each end where it joins its neighbor. Taking into account the structure of the joints and the arrangement of the digits, the limb seems unquestionably to be adapted as a paddle rather than a walking leg. This discovery has proved significant in several ways, not only with respect to the original function of limbs with digits, but also for ideas on the embryogenic development of limbs. These implications will be discussed in later chapters.

The hind limb and pelvic girdle of *Acanthostega* are also known from a number of specimens (Fig. 5.24) (Coates 1996). The pelvic girdle was relatively small for a tetrapod, compared both with *Ichthyostega* and other somewhat later species from the Carboniferous. However, it was still large by comparison with that in any fish, and it was also more tetrapod-like than fishlike in other respects. It was a single element as in *Ichthyostega*, and similarly bore two dorsal processes, a short stout upwardly directed




**5.24.** Hind limb of *Acanthostega*. (A) Reconstruction of the hind limb of *Acanthostega* by Mike Coates (1996). Dashed lines indicate reconstructed elements. The position but not the number of tarsal bones has been inferred from the disarticulated specimen. Femur in (B) side and (C) internal views, showing the adductor blade. Adapted from Coates (1996). (D) Photograph of hind limb specimen MGUH f.n. 1375. *Photograph by S.M.F.*

one and a long and slender backwardly directed one. The backwardly directed one lay at an angle of about 45 degrees to the vertebral column. The more dorsally directed process would have been attached on its inner surface to the vertebral column, but there was no facet for the sacral rib to have articulated with it. Therefore, it seems as though the attachment must have been formed by ligaments. The sacral rib, which formed the link between girdle and vertebrae, was scarcely modified for the purpose, though it had a slightly expanded end to give a greater surface area for the attachment.

The femur in *Acanthostega* was somewhat longer than the humerus, and on the surface nearest the body was a large rectangular adductor blade (Fig. 5.24). This flange would have carried the adductor muscles to pull the leg inward and backward. The size of the flange suggests large, powerful muscles, but the position of the adductor blade suggests that they were used in swimming. The lower leg bones, the tibia and fibula, like those of *Ichthyostega*, were flattened with a slight overlap between them along their length. As in *Ichthyostega*, the ankle was formed of flattened elements. Although only known from one disrupted specimen, the number of digits is likely to have been eight, as in the forelimb, based on a rather conservative judgment. In this case, small digits are placed one at each edge of the foot, with a second small one contributing to the leading edge (Fig. 5.24).

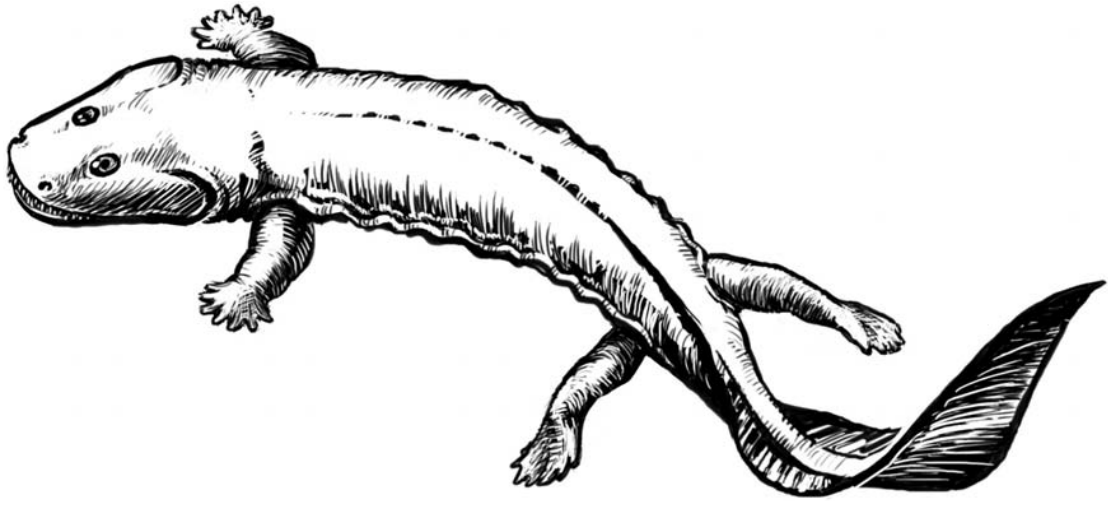
This structure strongly suggests that as in *Ichthyostega*, the hind limb was used largely as a paddle, and the powerful action produced by the adductor muscles was used in swimming, not in walking. Support for this idea comes from some modern aquatic salamanders, in which a large adductor blade is placed further down the shaft of the femur than it is in terrestrial ones (Coates 1996).

Almost the complete vertebral column of *Acanthostega* is preserved, including the most anterior elements forming the neck and those in the region where the pelvis attaches (Coates 1996). Also preserved are many of the ribs of the neck and those just behind the pelvis. One of the striking things about the column is how little variation there is along its length. In this respect, it was similar to a fish such as *Eusthenopteron* or an aquatic tetrapod from the Carboniferous such as *Greererpeton*. The processes on the neural arches, the zygapophyses, were poorly developed in *Acanthostega*, though in a few cases the arches had additional articulations between them instead. The centra were essentially husks surrounding the notochord and were formed from two halves that remained unfused in the midline, except for the atlas and sacral intercentra. This lack of differentiation and lack of zygapophyses is consistent with an animal whose head and body were routinely supported by water, rather than by the limbs and girdles that transmitted forces to the vertebral column by specialized muscles.

Although the cervical ribs of *Acanthostega* are well preserved and found in articulation with the vertebral column, most of the trunk ribs are missing or disarticulated. The cervical ribs were scooped out at the ends and broadened to provide seating for neck muscles and those that supported the shoulder. The trunk ribs were about the same length as the cervicals; they were short and straight, and their heads were only weakly differentiated into upper and lower processes for articulation with the vertebrae. They were quite unlike the heavy, flanged, overlapping ribs of *Ichthyostega*. These and the highly specialized vertebral column probably constitute the clearest evidence of the differences between them in body form and lifestyle.

Although in *Ichthyostega* the tail fin was relatively modest, in *Acanthostega* it was substantial, most closely resembling that of a lungfish (Fig. 5.20). The fin rays were longer, more numerous, and reached further around beneath the tail than in *Ichthyostega*. This is the tail of an ambush predator, which was able to produce and control fine rippling movements of the fin by means of the fin rays while the animal lay stationary in the water, but could have produced a fast, powerful thrust to provide rapid acceleration when it lunged to catch prey. This is not the tail of an animal that ventured regularly onto land. More details of the postcranial skeleton can be found in Coates (1996).

The postcranial skeleton of *Acanthostega* shows numerous features that clearly mark it as an aquatic animal that rarely if ever made forays onto dry land, and whose legs would have almost certainly been incapable of supporting its body had it done so (Fig. 5.25). However, the more important question is whether this aquatic adaptation was a primitive



**5.25.** *Life reconstruction of* Acanthostega *by J.M.*

relict of its fish ancestry or was secondarily derived from more terrestrial tetrapod ancestors (Clack and Coates 1995; Coates and Clack 1995).

In addition to the hyobranchial and postcranial skeleton of *Acanthostega*, there is another key region of the skeleton that has provided important insight into the events of the fish–tetrapod transition, and this is the braincase and associated structures. In contrast to that of *Ichthyostega*, the braincase of *Acanthostega* is directly comparable to that of related fishes such as *Eusthenopteron* and *Panderichthys*, and also to those of Carboniferous tetrapods. The otoccipital region shows several similarities to that of *Eusthenopteron*, especially its dorsal and posterior parts (Fig. 2.13). However, the sidewall of the braincase is penetrated by a large hole, the fenestra vestibuli, which in part incorporates the vestibular fontanelle of a fish like *Eusthenopteron*. Crucially, in *Acanthostega*, the part of the sidewall known as the lateral commissure in the fish is missing. Instead of having the hyomandibula pivot against the commissure, in *Acanthostega*, the equivalent bone, the stapes, fits into the hole. The stapes of *Acanthostega* is relatively much smaller than the hyomandibula of *Eusthenopteron*, though by comparison with the stapes of later tetrapods it is robust, with a large foot plate that almost filled the fenestra vestibuli, and more distally was a flattened platelike element. The similarities and differences between these animals are particularly instructive and will be considered in Chapter 6.

Several factors of the anatomy of *Acanthostega* imply that it is a primitively aquatic form, with no ancestors that were more terrestrial than itself. Among such features are the proportions of the bones of the forearm, which are, among all known vertebrates, most similar to those of *Eusthenopteron*. Only one, specialized group of Mesozoic secondarily aquatic tetrapods (some pachypleurosaurs, relatives of plesiosaurs) have a radius that is substantially longer than the ulna, but it is the rule in tetrapodomorphs. Thus, its condition in *Acanthostega* is far more likely to be primitive than secondary.

Another of these is the existence of the large, deep tail webbed with long lepidotrichia. The dermal fin skeleton seems unlikely to have reevolved once it had been lost, but it seems equally likely that any more terrestrially adapted form would have lost such a fin. It can be argued that a finned tail would be a liability on land; it would be eroded or torn by contact with the ground and subject to drying out or infection as a result.

It is at least as difficult to imagine a terrestrial animal retaining a tail fin like *Acanthostega* as it is to imagine a primitively aquatic one having evolved a large pelvis and femur. Possession of a pelvis in contact with the vertebral column supporting a large femur is a conspicuous feature of terrestrial tetrapods, and it has been argued that because *Acanthostega* had these, it must have evolved from a more terrestrial ancestor. Any early tetrapod of the Devonian presumably produced young that lived at least the early part of their lives in water, whatever their adult status might have been. It can thus be argued that the juveniles of even a fully terrestrial adult might have retained fin rays until metamorphosis. Therefore, it is not impossible to imagine a pedomorphic juvenile of such a more fully terrestrial adult evolving into an adult animal like *Acanthostega* with a fully finned tail. This is discussed in more detail in Chapter 6.

Something like this may be what we see in the growth of the humerus of *Ichthyostega*. The more primitive, fishlike nature of the subadult humerus could indicate a relatively long period of growth as an aquatic form, with more terrestrial capabilities developing later. By contrast, *Acanthostega* shares some characters of the humerus with later, more terrestrial, tetrapods, which *Ichthyostega* never develops.

Another region of *Acanthostega*'s anatomy that might point to the existence of terrestrial forebears is the hind part of the skull, where *Acanthostega* has lost the operculogular series of bones. The argument runs that if the animal were still as aquatic as a fish, these bones would still be present and functional in the movements associated with gill ventilation. Under this view, the gill skeleton and associated shoulder-girdle characters that are seen in *Acanthostega* would be primitive, but no longer functional, relicts.

As far as loss of the operculogular series in *Acanthostega* is concerned, we can now see a similar situation in *Tiktaalik*. Its gill skeleton is known in some detail and differs very little from that in more basal tetrapodomorphs (Downs et al. 2008), but the opercular bones seem to have been completely lost. The situation in lungfishes is also comparable. They have lost this series yet retain the use of gills, though they complement gill breathing with lungs and air breathing, just as envisaged for *Acanthostega*. Like lungfishes, *Acanthostega* and other early tetrapods probably gulped air too, by raising the snout out of the water and swallowing the air. Loss or reduction of the operculogulars is found in a variety of modern fishes, some air breathers and others not, such as the Moray eel.

The evolution of a pelvis and femur can be accommodated in a number of imaginative scenarios. A predator lurking in underwater weed may require thrust by a hind paddle to force it through the plant growth,

as in the Sargassum frog fish (Fig. 4.18) or one of the gurnards (which have their pelvic girdles attached to their shoulder girdles); it may need increased power and more accurate changes of direction that an enlarged hind limb might produce. The pelvis was the site of origin for muscles controlling tail movements used in swimming, so the elaboration of the girdle may be related to increasing use of the tail to provide the rapid thrusts that a lurking predator used.

As a primitive tetrapod, *Acanthostega* provided clues to the problem of how limbs with digits might originally have been used before they became adapted for walking on land. It certainly suggested that they evolved while tetrapods were still aquatic for most of the time, and so their major function was an aquatic one. Several models for what such a use might have been can be put forward based on modern fish with digitlike fins. Some of these have been suggested in Chapter 4, such as clinging onto weed to help maintain position in vegetation-rich waters, or to permit slow bottom walking. Other possible uses include pushing through weed-choked swamps or feeling about among the plant stems and debris. Finally, as an example of the lengths to which such scenarios can be taken, if the spawning behavior of fishes and amphibians are compared, one of the most conspicuous differences lies in the amphibians' use of amplexus, in which the male's limbs are wrapped round the female's body to ensure that fertilization is completed. Perhaps this was the reason for the invention of limbs. Other ideas to explain invention of limbs have been put forward and discussed in Chapter 4, but of course, none of them is currently testable as a scientific hypothesis.

If *Acanthostega* really is a good model for a primitive tetrapod, then its anatomy can provide a great deal of information about the order in which some events took place throughout the transition. For example, limbs with digits appear to have evolved before walking. *Acanthostega's* wrist was quite unlike the wrist of subsequent tetrapods. Because the radius and ulna were such different lengths, the ends could not have formed an effective bearing surface on which the animal's weight could be balanced. This can be said with some confidence, even though the wrist bones themselves are not ossified. However, *Acanthostega* obviously had digits, if somewhat unusual ones, so that digits must have evolved before wrists. There is some evidence for this order of events from recent developmental genetic studies of lungfish fins (Johanson et al. 2007b; see Chapter 6). Similarly, the ankle joint was also unsuitable as a weight-bearing joint, being rather inflexible, so that hind-limb digits also evolved before the ankle joint.

Apart from the possession of limbs with digits, a number of the supposed tetrapod-like characters found in *Acanthostega* that are often linked with terrestriality can actually be found among modern fishes that have no reputation as land dwellers. The air-breathing *Arapaima* of the Amazon basin is one such fish. It has a substantial endoskeletal coracoid portion to its shoulder girdle, there is an enlarged pelvis (though it is not attached to the vertebral column), there are zygapophyses in the

well-ossified vertebral column and large ventral ribs, and it has a tail fin of a similar shape to that of *Acanthostega*.

### A Third Tetrapod from East Greenland

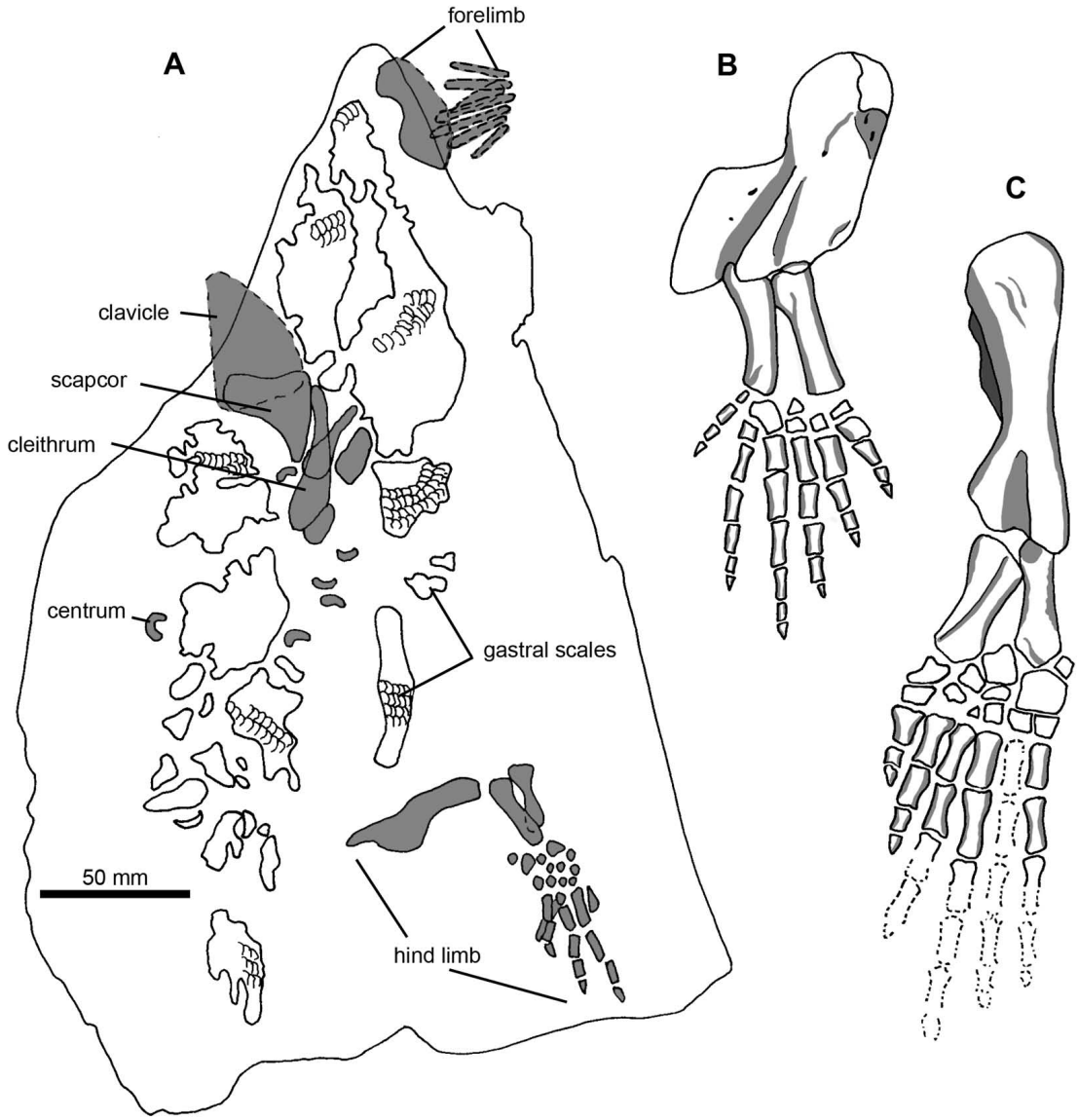
Among the specimens that the Danish and Swedish expeditions of the 1940s collected was a partial skull from the south side of Celsius Bjerg. It showed the lower jaws, dentition, and partial palate of a tetrapod, but Jarvik could not be certain of its identity. Recent study has been undertaken and more of the dentition and jaws have been revealed, and more information has been gained about the lower jaws and dentitions of *Acanthostega* and *Ichthyostega* (Clack et al. In Press). It is obvious from a glance that this specimen is not that of *Acanthostega* because it has far too few teeth, but it is similar to *Ichthyostega* in some ways. However, there are several differences between those two. In the new specimen, the dentary and maxillary teeth are about the same size as each other, whereas the upper teeth are larger than the lower in *Ichthyostega:* the coronoid teeth are about the same size as the maxillary and dentary teeth in the new specimen, whereas they are much smaller than the marginal teeth in *Ichthyostega*, and furthermore, where *Ichthyostega* has distinctive rose-thorn-shaped coronoid teeth, they are simple cones in the new specimen. The new specimen has much less marked dermal ornamentation than in *Ichthyostega*, and it has denticles on the prearticular of the lower jaw where *Ichthyostega* does not. This makes a total of five species of tetrapod recognized from the Devonian of East Greenland, making it probably the richest known locality for Devonian tetrapods and further indicating the diversity that the group had reached by that time.

## Famennian Tetrapods Worldwide

### *Tulerpeton*

*Tulerpeton curtum* is the third Devonian tetrapod genus for which articulated postcranial remains are known (Fig. 5.26). It comes from the Late Devonian, from a site called Andreyevka-2, near Tula in Russia, and is dated as latest Famennian (Alekseyev et al. 1994; Blieck et al. 2007). The site has yielded many taxa of fishes, including the almost ubiquitous placoderm *Bothriolepis* and its relative *Remigolepis*, and the porolepiform *Holoptychius*, almost equally ubiquitous in Late Devonian tetrapod localities. The dipnoan *Andreyevichthys*, acanthodians, an osteolepidid, and an actinopterygian have been found there, as well as a few invertebrates such as bivalves and serpulid worm tubes (Lebedev and Clack 1993).

When it was first described, it was unique among localities that had yielded Devonian tetrapods in showing clear evidence of marine influence in the sediments. Serpulid worms and stromatolites, the latter of which are accretions of calcite and limestone laid down in layers by algae, are characteristic of marine or brackish sediments. Charophytes, which are a form of primitive plant probably intermediate between vascular plants and algae, are also known from this site. The chemical




**5.26.** *Tulerpeton curtum.* (A) Diagram of specimen showing disposition of elements on the block. Limb and girdle elements are shaded; elements on underside of block shown drawn outside block edge and outline is dashed. (B) Forelimb and (C) hind limb reconstructions. *Based on information in Lebedev and Coates (1995).*

makeup of the sediments shows signs that the salinity of the water fluctuated widely, and the geological evidence suggests that the Andreyevka-2 site was situated about 200 kilometers from the nearest landmass (Alekseyev et al. 1994). Since that time, several tetrapod-bearing localities have been discovered that represent marginal marine or brackish water localities.

*Tulerpeton* is represented by a nodular block containing the belly scales, right hind limbs and forelimbs, and left shoulder girdle of a single individual, along with a premaxillary bone and its attached vomer. This specimen is the only one from the site that was preserved as an articulated series of bones. Many other vertebrate bones have been recovered from the site, but all of them have been found by using acid to digest the rock

away, leaving the bones behind. Other tetrapod elements are among these bones, including further isolated skull bones, vertebrae, ribs, interclavicles, and part of a pelvic girdle. It is not certain that all these belong to the same taxon. Two patterns of tabular bone in the collection that has been made from Andreyevka-2 suggest the presence of two distinct species at the site. Found alongside a fairly typical complement of fish taxa at the site, the existence of two tetrapod taxa would appear to refute the suggestion by Long and Gordon (2004) that the carcass of *Tulerpeton* had been carried out to sea from its original habitat.

When *Tulerpeton* was first found and described, it was considered aberrant in having six digits on the forelimb and almost certainly six on the hind limb (Lebedev 1984, 1985). Now that other Devonian tetrapods have been found similarly showing more than five digits, *Tulerpeton* is seen as fitting into a pattern of polydactylous (having more than five digits) early tetrapods. The implications of this are discussed in Chapter 10. In addition to the development of digits, several other important aspects of the early evolution of tetrapods are shown by *Tulerpeton* (Lebedev and Clack 1993; Lebedev and Coates 1995).

The first impression of its limbs is that apart from the digits, they resemble those of more conventional and later tetrapods. The humerus resembles most closely that of a group called anthracosaurs known from the Carboniferous (see Chapters 7 and 8). The radius and ulna, and to a lesser extent the tibia and fibula, are relatively more elongate and slender than those of the other known Devonian tetrapod limbs, those of *Ichthyostega* or *Acanthostega*. These give it the appearance of a more terrestrially adapted animal. However, the wrist construction bears some resemblance to those of *Ichthyostega* and *Acanthostega* in having fewer bones than those of later tetrapods. The tibia and fibula still retain some of the flattened structure seen in the two other Devonian genera, making the foot more of a paddlelike appendage rather than one that was used for walking. Furthermore, as in *Ichthyostega* and *Acanthostega*, the femur bore a large quadrangular adductor blade placed about halfway down the bone, the construction found today associated with swimming muscles in aquatic salamanders.

The shoulder girdle shows several primitive features, including retention of the anocleithrum, but unlike those of *Ichthyostega* and *Acanthostega*, the dermal cleithrum had become separated from the scapulocoracoid. *Tulerpeton* lacks a postbranchial lamina, which was still present in *Acanthostega*, though that does not necessarily mean that it did not use gills at all for breathing. *Ichthyostega* has no postbranchial lamina on the cleithrum, but it is known to have had a grooved, ossified branchial skeleton.

Although so little of the skeleton of *Tulerpeton* has been found, it has proved possible to generate some hypotheses about where it fits phylogenetically among other early tetrapods. Using postcranial characters, Lebedev and Coates (1995) found that it appeared more similar to the lineage of animals normally associated with the origin of amniotes than

to the lineage usually thought to have given rise to modern amphibians. However, these results have not been borne out by further studies. Several more recent ones have placed *Tulerpeton* as a stem tetrapod above *Ichthyostega*, or with the Early Carboniferous whatcheeriids (see Chapter 7) (Ruta et al. 2003; Warren 2007; Ruta 2009).

### *Ventastega*

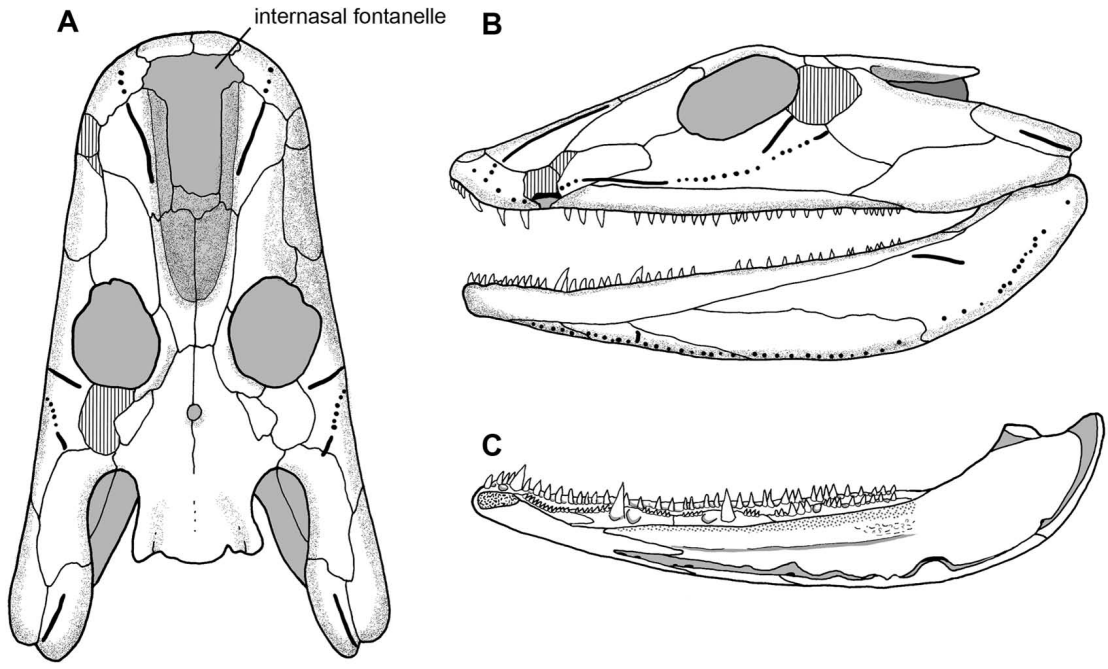
*Ventastega curonica*, one of the more recently discovered of the Devonian genera, comes from Latvia near the Venta River, from which its name derives (Ahlberg et al. 1994). This locality is dated as latest Famennian, though more precision is not possible at present. The potential time range would place *Ventastega* either as a contemporary of the Greenland tetrapods or slightly later than them, at the end of the Famennian (Blieck et al. 2007). The site represents a marginal marine locality, probably a low-tidal nearshore environment, that also preserves lungfish, the placoderm *Bothriolepis*, and the porolepiform *Holoptychius* (Lukševičs and Zupins 2003, 2004).

*Ventastega* is another example of an animal that was first recognized as a tetrapod from bones in a museum collection labeled as "unidentified sarcopterygian." Study of *Acanthostega* allowed its lower jaw to be picked out from its drawer and relabeled as a tetrapod.

The bones occur as beautifully preserved three-dimensional specimens, embedded in a light sandy matrix that can be excavated with a kitchen knife and is easily washed off. Rather than the long, slow preparation that has to be used for *Acanthostega*, *Ventastega* material can be prepared with a brush and mounted needle to reveal remarkable detail. In excavations that took place in 2004, exquisite material of the skull roof and some of the braincase, as well as additional portions of the postcranial skeleton, was found (Ahlberg et al. 2008).

The skull and palate of the animal resemble those of *Acanthostega* in some ways, especially in the known parts of the postcranial skeleton. However, it is evidently not the same animal (Fig. 5.27). For example, in the lower jaw, the inner row of tooth-bearing bones, the coronoids, each carry a fang pair as well as a row of smaller teeth (Ahlberg et al. 1994). These are similar to, though smaller than, those seen in fish such as *Panderichthys*, but they are absent in *Acanthostega* and *Ichthyostega*. Fang pairs are also carried on the palate in *Ventastega*, a feature also seen in *Acanthostega* and many later tetrapods. Their presence seems to be a fishlike and primitive character, perhaps associated with feeding in water, and gradually lost among tetrapods.

Key parts of the skull and braincase have been described recently, showing some unique features and some primitive ones (Ahlberg et al. 2008). The snout exhibited a large and obvious internasal fontanelle. In *Acanthostega*, there is a narrow slit between the nasals and median rostrals along the midline, but in *Ventastega*, the slot is much more widely open. The purpose of this fontanelle is unclear, but it has been suggested that




**5.27.** Reconstruction drawings of skull of *Ventastega (from Ahlberg et al. 2008)*. (A) Dorsal view. (B) Left lateral view. (C) Lower jaw in internal view. Skull is about 190 millimeters long.

it may represent the area in fish where a mosaic of small bones is found, and that the hole might result from the loss of some of these.

The skull table, rather than being similar to that of *Acanthostega*, instead bears close comparison with that of *Tiktaalik*. It retains some of the projections and notches along the posterior margin seen in *Tiktaalik*, but more conspicuously, it possesses a widely open, oval spiracular notch. A comparison between *Tiktaalik*, *Ventastega*, *Acanthostega*, and *Ichthyostega* shows that not only is *Ventastega* more similar to *Tiktaalik* than to either of the tetrapods, but also that the differences between *Tiktaalik* and *Ventastega* are largely only ones of proportion (Ahlberg et al. 2008).

Underneath the skull table, a key specimen retains the attached otic capsules and parts of the sphenethmoid region of the braincase. These, though incomplete, show some important features. The slots for the anterior and posterior semicircular canals can be seen, and the walls of the otic capsule show that it had a fenestra vestibulae. In other words, it had lost the fish lateral commissure where the hyomandibula attaches, and instead can be inferred to have had a stapes, probably like that in *Acanthostega*. The part of the sphenethmoid that is preserved shows one interesting difference from that of *Acanthostega*, in that it was more or less a solid wall pierced by a few small foramina for cranial nerves and blood vessels instead of the large interorbital foramen in *Acanthostega*. In this, *Ventastega* is the more primitive.

Parts of the postcranial skeleton that have been found include the cleithrum with a small portion of the scapulocoracoid integrated at its base, showing the condition found in most other Devonian tetrapod shoulder girdles. Not much of the scapulocoracoid portion is preserved,

unfortunately. The clavicle is well represented by several specimens, and it shows a broad triangular base with the typically narrow stem angled at about 90 degrees to the basal plate. The interclavicle was large and lozenge shaped, as in *Acanthostega*, with similar dermal ornament. The complete shoulder girdle has been reconstructed from these remains, and it is in many ways similar to that of *Acanthostega*. A partial ilium is also similar to that of *Acanthostega*, so that the assumption is that the limbs bore digits, though it remains uncertain as to how many there would have been.

On the basis of its complement of characters, *Ventastega* appears in a phylogeny as a more primitive animal than *Acanthostega* (Ahlberg and Clack 1998; Ahlberg et al. 2008) (see Chapter 10), even though it is a contemporary or even possibly later.

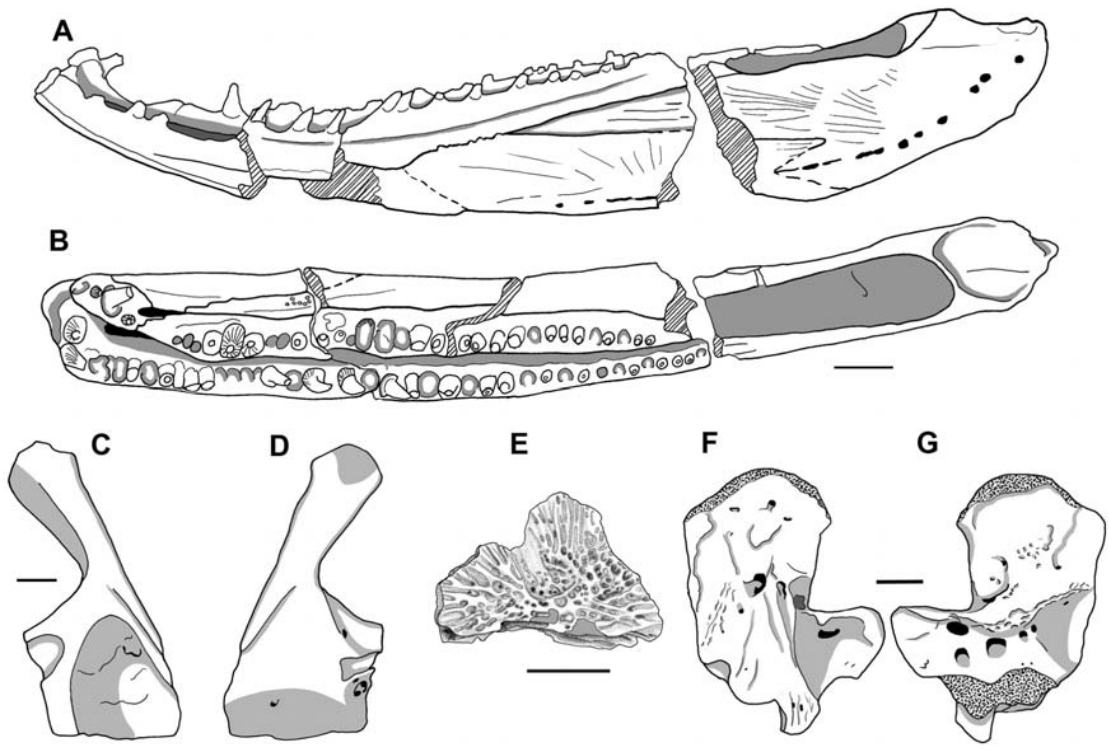
Fragments from the same locality in Latvia as yielded most of the *Ventastega* material indicate the possible presence of a second taxon in these sequences (Ahlberg et al. 1994).

### *Hynerpeton*, *Densignathus*, and the Red Hill Tetrapod Fauna

The discovery of *Hynerpeton bassetti* and *Densignathus rowei* demonstrate that Devonian tetrapods are waiting to be found in areas that have apparently been thoroughly surveyed geologically many times. They come from the middle of a popular tourist region of Pennsylvania in the United States. However, the sediments are only visible in road cuts, and they are not readily accessible. The rocks are of Late Devonian age, probably latest Famennian, but the dating is still imprecise (Blieck et al. 2007).

This locality is the richest of Late Devonian sites in terms of the broadness of the flora and fauna that it represents. Extensive paleoecological studies have been carried out, especially on the flora and environment. The layer that yielded the most plant fossils appears to have been a floodplain pond in a seasonally wet and dry environment. By the time of this assemblage, fossil charcoal is again common, showing that forest fires were quite frequent. *Archaeopteris* grew on well-drained areas. *Rhacophyton* was common, as were lycopsids and the gymnosperm *Gillespiea* (Cressler 2006). Essentially, this was a wetland community, in which fish and tetrapods lived in the floodplain pond and in shallow marginal channels. Tetrapods seem to have been mainly aquatic, and if they came onto land, it was probably only in the humid season.

Among the fishes were numerous placoderms of at least three genera, chondrichthyans, acanthodians, a single genus of ray-finned fish, and several lobe-finned fishes. *Holoptychius* was one of the most common, but large tristichopterids and other tetrapodomorphs and a lungfish were also present. A few arthropods are also represented. As for the tetrapods, two examples of shoulder girdles and one lower jaw have been attributed to *Hynerpeton* (Daeschler et al. 1994), and a second, larger, lower jaw (Daeschler 2000) has been named *Densignathus* on the basis partly of




**5.28.** Tetrapod specimens from Red Hill Pennsylvania. (A, B) Lower jaw of *Densignathus* in lateral and dorsal views. (C, D) Drawings of the shoulder girdle of *Hynerpeton* in medial and lateral views. (E) Lacrimal bone with similarity to that of *Pederpes* (see 7.6). (F, G) Humerus ANSP 21350 in dorsal and ventral views. All scale bars = 10 millimeters.

its size and robustness, but also its dentition, in which it differs from *Hynerpeton* (Fig. 5.28A, B).

The shoulder girdles were found in the same part of the same bed as the *Hynerpeton* jaw, as well as being of about the right size to go with it. They are robust and clearly carried large, strong muscles for powering the forearm (Fig. 5.28C, D). However, no limb bones are yet known to be associated with it, so it is not possible to say whether *Hynerpeton* walked or swam using these muscles. Taking the shoulder girdle alone, *Hynerpeton* shows some differences from both *Acanthostega* and *Ichthyostega*, including some in which it is more advanced. For example, it lacks a postbranchial lamina, but the cleithrum and scapulocoracoid are still bonded together as in these two forms, and this seems to be a primitive feature of the earliest tetrapods.

More recently, material from the original "*Hynerpeton* lens" has been further investigated, although a major excavation to expose more of this lens failed to discover any more tetrapod remains. In the original collection, a humerus, tetrapod gastral scales, and scattered skull bones including jugals, a postorbital, and a lacrimal (Fig. 5.28E) were found. The latter two are significant because they most closely resemble those of the Early Carboniferous form *Pederpes* (see Chapter 7). This means that for the first time, a link has been found between Devonian and Carboniferous tetrapod faunas, with a single family appearing to span the gap between these periods. However, the jugals do not particularly resemble those of *Pederpes* or of its sister taxon *Whatcheeria*, and whereas

*Hynerpeton* has a co-ossified cleithrum and scapulocoracoid, *Pederpes* and *Whatcheeria* do not. Thus, it is unlikely that the shoulder girdles belong to the same species as the postorbital and lacrimal (Daeschler et al. 2009).

Even stranger is a humerus, known as ANSP 21350 (Fig. 5.28F, G). It is unlike any other early tetrapod or near-tetrapod humerus, and has many unique features (Shubin et al. 2004). It has nonetheless proved informative about the evolution of the humerus and its functions. Although it is not possible to say what attached to the end of it, the angle of the radial and ulnar facets show that those bones must have been quite sturdy and oriented downward at about 45 degrees. The processes for muscle attachment to the lower limb were large, suggesting substantial muscles that may have provided some potential for raising the front part of the body. There were many large foramina through the bone, more than in *Ichthyostega* or *Acanthostega*, and the ventral ridge, though prominent, ran across the width of the bone transversely to its long axis, rather than diagonally across the length of the bone as in tetrapodomorph fish (see Chapter 6). It remains in many ways a mystery, and we cannot say whether it belonged to a true limb with digits or a fin with remaining fin rays.

Because of the shape of the humeral head, compared with the shape of the socket in the shoulder girdle of *Hynerpeton*, it is unlikely that they belonged together. It is also quite unlike the humeri of *Pederpes* or *Whatcheeria*, and so is unlikely to have belonged with the lacrimal and postorbital. Therefore, there is a question about how many types of animals may be represented in that one small lens. At least three and more likely four seems to be the current estimate. Figure 5.29 shows Ted Daeschler, the discoverer of *Hynerpeton*, standing on the site where the specimens of *Hynerpeton* and *Densignathus* were found.

### *Metaxygnathus*

*Metaxygnathus* was described in 1977 (Campbell and Bell 1977), but for many years, there was debate about whether or not it really was a tetrapod. Because the fossil consists only of a single lower jaw, it was naturally difficult to confirm its identity at first. However, with the description of the better-preserved lower jaws of *Acanthostega* and *Ventastega*, paleontologists have realized that there are some characters of the lower jaw unique to tetrapods that can be used to identify isolated jaws as tetrapod or not.

*Metaxygnathus* comes from the Devonian of New South Wales, Australia, at a locality that has yielded placoderms but no other tetrapod remains. The dating of the rocks from which it comes is not particularly precise, giving a range from latest Frasnian to earliest Famennian (Blieck et al. 2007). The specimen occurs along with plates of placoderms and the lungfish *Soederbergia*, but offers no clue about the ecology or lifestyle of the animal, and almost none about the anatomy. Its importance lies in showing that tetrapods were widely distributed by this time.



**5.29.** (Color Plate 12) The locality of Red Hill near Hyner, Pennsylvania, where *Hynerpeton* was found, with its discover, Ted Daeschler, standing at the level from which the specimens came. *Photograph by J.A.C.*

### *Sinostega*

Devonian tetrapods have recently been found more widely spread around the world even than previously thought. *Sinostega* is a partial lower jaw from northern China that can be attributed to a tetrapod with reasonable certainty from a number of characters it shares with *Acanthostega*. Its dating is uncertain, but current estimates suggest a Frasnian age. The fauna in which it occurs includes, like so many other early tetrapod localities, the placoderms *Bothriolepis* and *Remigolepis*, as well as a new, undescribed sarcopterygian. Though it adds little to our knowledge of early tetrapod morphology, it adds much to our understanding of their

distribution (Blieck et al. 2007), showing that even by this early stage, recognizable tetrapods had reached areas remote from Laurussia, the region in which they appear to have originated.

### Unnamed Ichthyostegid-Type Jaw from Belgium

On the basis of its recurved teeth and coarse ornament, a partial lower jaw from the mid-Famennian of Strud in Belgium has recently been identified as tetrapod (Clement et al. 2004; Blieck et al. 2007). It is another case of a specimen that was found in the 19th century, but which was thought to be from a fish. Though it is not sufficiently diagnostic to receive a scientific name, it is sufficiently distinctive to be considered related to the Greenland genus *Ichthyostega*. Its significance lies mainly in its biogeographic implications. The Old Red Sandstone continent, of which East Greenland was a part in the Late Devonian, was separated by a narrow, shallow seaway from that which now forms most of northern Europe. The presence of ichthyostegids on both these continents suggests that they could cope with crossing marginal marine environments, probably using near-coastal routes. Other fauna represented at Strud and other contemporary sites in Belgium include placoderms, tristichopterids, rhizodonts, megalichthyids, and gyracanthids. The latter three groups seem to have originated in Gondwana, further south, and migrated northward during the Late Devonian, replacing older placoderm-dominated faunas (Clement et al. 2004).

### *Jakubsonia*

Skull and jaw fragments, girdle, and possible limb elements constitute the material of *Jakubsonia livnensis*, described from the early Famennian of the Oryol region of Russia (Lebedev 2004). The remains are much eroded and could have been transported into the deltaic sediments in which they were found. They do, however, occur alongside a typical Late Devonian fauna that includes the placoderm *Remigolepis* and the porolepiform *Holoptychius*.

### Sosnogorsk Tetrapod Site on the Izhma River, Russia

Pavel Beznosov and colleagues have recently discovered a new Devonian tetrapod site in northern Russia. It is dated as early Famennian and has also yielded *Bothriolepis jeremejevi*, *Holoptychius* sp., and microremains of tetrapodomorphs, onychodonts, and juvenile dipnoans. This layer is almost completely composed of calcareous microremains of charophytes. The tetrapod remains include lower jaw elements, skull roof and palatal bone, including an almost complete pterygoid and three skull tables, and a cleithrum. The animal shows a combination of primitive and derived characters. It inhabited a shallow lagoon with dense thickets of aquatic vegetation (Ahlberg et al. 2010).

## Overview of Devonian Tetrapods

The above survey outlines the range of fossils available to represent the fish–tetrapod transition. The next task is to interpret this evidence. To do this, the phylogeny of the animals in question must be established. This can then be used to infer the sequence and timing of changes that took place during the origin of tetrapods.

By means of the methods of computer-aided cladistic analysis, the state of each of a wide range of characters is itemized and stated in as unambiguous a way as possible. These are then compared to those found in an outgroup. In the case of early tetrapods, this in practice means *Eusthenopteron*, *Panderichthys*, and *Tiktaalik*. This exercise has been done several times for early tetrapods in different ways by different people and for different regions of the body. Some used a range of features from the whole skeleton, some used only the postcranial skeleton, some the skull roof with the palate, and one used only the lower jaw. Almost all analyses produced the result that *Acanthostega* was the most primitive of the Devonian forms, with *Ichthyostega* being more derived (Lebedev and Coates 1995; Coates 1996; Clack 1998a, 1998b, 2001a; Ruta et al. 2003). In contrast, in the analysis of the lower jaws, *Ichthyostega* appeared as more primitive than *Acanthostega* (Ahlberg and Clack 1998). Only a few place them together as sister groups (Laurin and Reisz 1997; Laurin et al. 2004). A recent study incorporating new data from *Ichthyostega* and early tetrapod humeri showed that, depending on which characters were ordered versus unordered and which taxa were included or excluded, different results were obtained. In other words, the phylogeny of Devonian tetrapods was unstable (Callier et al. 2009), suggesting that there was substantial parallel evolution occurring among these animals. For the time being, however, most phylogenetic analyses place *Acanthostega* consistently above *Ventastega* when that taxon is included, and usually below *Ichthyostega*.

The tetrapodomorphs of the Frasnian—*Obruchevichthys*, *Elginerpeton*, and *Livoniana*—although not known from extensive material, hint at a level of diversity that exceeds that found in the tetrapods known from the Famennian. This is shown by the differences among their dentitions, with patterns not seen anywhere else among the lineage. This picture is muddied somewhat by the fact that the Chinese lower jaw named *Sinostega*, initially thought to have been Famennian, has subsequently been redated as Frasnian. *Metaxygnathus* may also turn out to be Frasnian. However, both these forms seem to resemble Famennian forms that show a striking conservatism in jaw, palate, skull roof, and girdle structure. They are all about the same size and have similar broad, flattened head shapes. Contrasting with the elongate shape seen in *Elginerpeton* and *Obruchevichthys*, this could be taken to mean that the specialized Frasnian forms suffered during the Frasnian–Famennian extinction event, to be wiped out in favor of the more conservative forms. However, the record is so sparse that it is probably wise not to read too much into this evidence.

Only subtle differences mark the lower jaws of, for example, *Acanthostega*, *Ventastega*, *Metaxygnathus*, and *Hynerpeton*, though they are

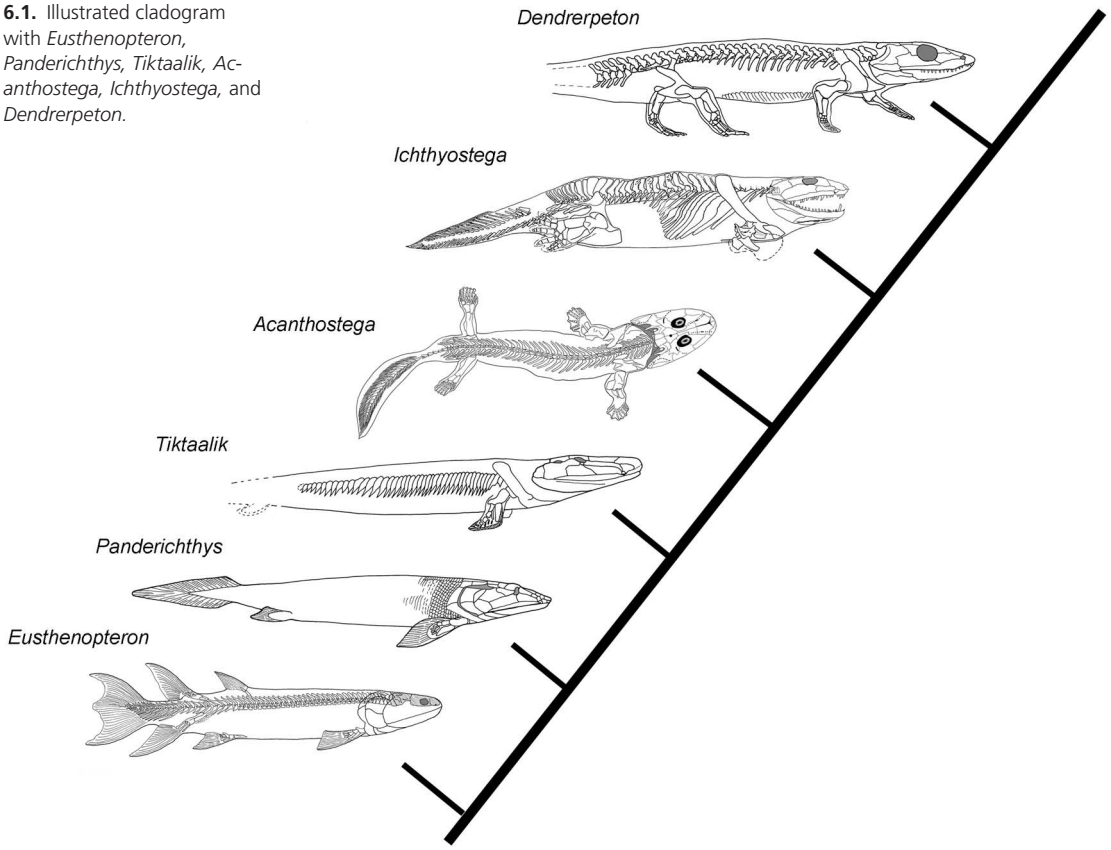
still clearly different animals. The minor differences in tooth complement suggest a degree of divergence in their habits and food preferences, though these cannot have been great. *Ichthyostega* is somewhat of an outlier in terms of morphology, whose lifestyle we are still struggling to understand. The probability is that all these animals were fairly slow moving most of the time, but capable of bursts of energy when catching moving prey. All may have fed in water (see Chapter 10), though perhaps with a snapping and biting action rather than a suction mechanism, which allowed them occasionally to feed on land. This conservative radiation of tetrapods nevertheless succeeded in colonizing widely separated parts of the world.

Placed on a paleogeographical map of the Devonian world, it seems clear that all the tetrapod localities occurred within 30 degrees of the equator, mainly in what would appear to have been an arid zone, although some were bordering on tropical zones (Scotese 2002; Averbuch et al. 2005). The localities where many of them lived, at the water margins of lakes, deltas, or coasts, might have ameliorated the climates in their habitats.

Although the environments in which the early tetrapods were found are now known to vary quite widely, from unequivocally freshwater through estuarine and deltaic to marginal marine or even to high salinity, a certain consistency exists among the fish faunas with which they are found. The same genera of placoderms, *Bothriolepis* and *Remigolepis*, are the most conspicuous, followed in ubiquity by the porolepiform *Holoptychius*, and almost all have a complement of lungfishes. These sites include other taxa less consistently, variously one or more tristichopterid, a few acanthodians (usually fragmentary), and occasionally rhizodontids and osteolepidids. It is therefore tempting to attribute euryhaline capabilities to these animals too. For further discussion of early tetrapod environments, see Lebedev (2004), Clack (2006), and Blieck et al. (2007, 2010).

As new information comes to light, many of these ideas will be tested and may have to be rethought. Examples of this have already begun to raise questions about when and how terrestriality was acquired, such as the existence of the trackways of tetrapodomorphs from the early Middle Devonian, and the primitive, fishlike characteristics of the humerus of *Ichthyostega*. Clearly the story is more complicated than the current range of fossils indicates.

**6.1.** Illustrated cladogram with *Eusthenopteron, Panderichthys, Tiktaalik, Acanthostega, Ichthyostega,* and *Dendrerpeton.*



# From Fins to Feet: Transformation and Transition

# 6

Reading the Evidence: *Eusthenopteron*— *Panderichthys*— *Tiktaalik*— *Ventastega*— *Acanthostega*

Chapter 2 looked at opposite ends of a spectrum. At one end was the structure of a fish such as *Eusthenopteron*, and at the other end was that of a tetrapod such as *Dendrerpeton*, an early tetrapod belonging to the group known as temnospondyls (see Chapters 8 and 9). The problem embodied in the phrase "the fish–tetrapod transition" is how evolution proceeded from one to the other. One of the ways to study this is to look at intermediate forms, but what makes a suitable intermediate form? In the past, a temnospondyl such as *Eryops* would have been featured in the role of primitive tetrapod, and *Ichthyostega* would have been seen as an intermediate between *Eusthenopteron* and *Eryops*. Recent analyses, however, have suggested that *Ichthyostega* has some highly specialized features that may make it unsuitable as a representative Devonian tetrapod; it is now also clear that *Eryops* is a highly specialized and unrepresentative temnospondyl. Although *Eusthenopteron* is not as close a relative of tetrapods as used to be considered, it still provides good information about basal tetrapodomorph structure.

Since the first edition of this book was published, several discoveries of tetrapods and tetrapod-like fish have been made that help to fill out the story, showing it to be more rich and complex than first suspected. Some parts of the story have been amplified, whereas others have had to be reconsidered in many details. The animals that have contributed most information to the story are *Tiktaalik* (Daeschler et al. 2006; Shubin et al. 2006; Downs et al. 2008) and *Ventastega* (Ahlberg et al. 2008), and with renewed study of *Ichthyostega* (Clack et al. 2003; Ahlberg et al. 2005; Callier et al. 2009) well under way, it needs to be fitted into the picture. For the most part, the new data fit into a consistent story, but now there are additional complexities that are not so easily explained.

In the first part of this chapter, *Eusthenopteron*, *Panderichthys*, *Tiktaalik*, *Ventastega*, *Acanthostega*, and, where relevant, the skull of *Elpistostege* are considered more closely for the light they shed on skeletal changes across the transition between fish and tetrapods. *Panderichthys*, *Tiktaalik*, and *Elpistostege* share a number of characters, though they do not appear to form a clade. All these animals and *Dendrerpeton* are featured in the cladogram in Figure 6.1. This sequence may justifiably be used to infer the order in which some of the changes occurred because it reflects their phylogenetic relationships as inferred from most modern analyses. In turn, understanding the order of events may provide

clues to the underlying processes. The second part looks at what can be inferred about the changes to soft tissue anatomy across the fish–tetrapod transition from studying modern fish and also from the differences between living amphibians and amniotes. Aspects of soft anatomy and other nonfossilizable information such as sensory systems, respiration and breathing, the origin of limbs and digits, locomotion, and reproduction fall into this category.

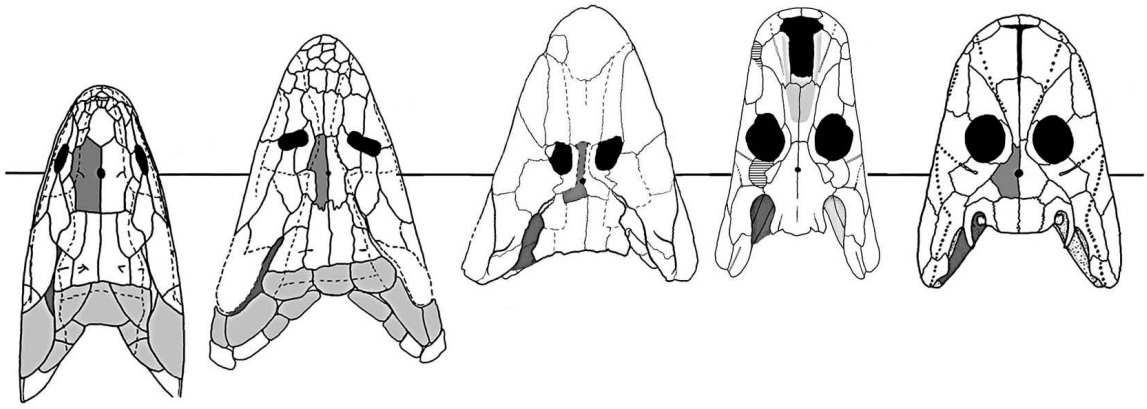
## Skull

### SKULL ROOF AND LOWER JAW

Figure 6.2 presents the skulls of *Eusthenopteron*, *Panderichthys*, *Tiktaalik*, *Ventastega*, and *Acanthostega* drawn to the same snout–quadrate length and lined up on the position of the parietal foramen. Some of the changes to the skull can be seen immediately; others are less obvious. To begin with, changes to the external part of the skull, the dermal skull roof, will be considered.

Early studies of the fish–tetrapod transition had little data on which to base ideas. Skull structure in *Eusthenopteron*, the tetrapods of the Late Carboniferous and the Early Permian, and the little that was known of *Ichthyostega* were all that were available. One of the problems that exercised several workers on the subject in the middle years of the 20th century was the problem of bone homologies in the skull roofs of these animals. In fishes and tetrapods, though the pattern of dermal bones in the skull roof of each is broadly similar, it differs in several important details. Another aspect of the problem stemmed from the fact that workers whose interest was mainly in fish tended to use a different system of nomenclature from those whose interest was mainly in tetrapods. Many papers tried to deal with the questions of which bones of fishes became which bones of tetrapods, and argued about the rationale behind the different answers that were produced. The problem arose partly because of the different proportions of parts of the skull between fishes and tetrapods, and because some of the bones appear to have been lost in the transition, making it difficult to draw up a one-to-one correspondence between them. Other factors in the argument were differences in the position of the lateral line grooves and the placement of the pineal foramen, often either or both being used as landmarks from which to work out the relationships of the surrounding bones (Jarvik 1944, 1980; Parrington 1956, 1967; Watson 1926; Westoll 1938, 1943a, 1961; Klembara 1992, 1994a).

The arguments were never really reconciled, and though several attempts were made to bring the two systems together, none was generally taken up (e.g., Borgen 1983). However, more recently, the whole issue has subsided in view of advances in developmental genetics. It is now clear that strict one-to-one homologies between two such disparate systems are difficult to draw and may not be meaningful. As will be shown in the case of limbs, what probably does underlie the development of the



**6.2.** Skulls of *Eusthenopteron, Panderichthys, Tiktaalik, Ventastega,* and *Acanthostega* (left to right) drawn to the same length from snout to quadrate and lined up on the parietal foramen. Opercular and supracleithral series of *Eusthenopteron* and *Panderichthys* in light gray shading. Spiracular clefts and left parietal bones in dark shading. Note that the posterior limit to the parietal in *Ventastega* is unknown, so the bone is shown unshaded. Hatched, unknown areas.

skull roof in both fishes and tetrapods are fundamental ground rules of formation, applied in different circumstances to produce different end results. In fact, only a few skull regions are affected by such problems—the snout, midline, and temporal series—and for most other bones, it is fairly clear where the equivalents lie in fishes and tetrapods, even though their shapes have changed, often quite radically. This in itself might be food for thought about the developmental processes controlling different parts of the skull.

The palate is among those regions least affected by changes to the complement of bones present across a range of tetrapodomorph fishes and tetrapods. By and large, they can be equated quite easily (see Chapter 2), the major modification being one of shape associated with a change from a deeper, narrower skull in fish like *Eusthenopteron*, to a broader, flatter skull from *Panderichthys* onward. Nevertheless, a study by Kimmel et al. (2009) of the shapes of palatal bones in early tetrapods has indicated that there may be well be developmental processes underlying their varying morphologies and proportions, and their relationships to the braincase and sensory tissues that lie above them in the skull.

As was noted in Chapter 2, one of the most conspicuous differences between the skull of *Eusthenopteron* and that of *Acanthostega* is that of proportion. In *Eusthenopteron*, the snout region is relatively short, with the eyes placed nearer the front than the rear, and the region behind the eyes and overlying the braincase and otic region is relatively long. The eyes are placed laterally and are relatively small. In *Acanthostega*, the opposite is true, with the snout being long and the otic region short, while the eyes are large and placed dorsally. The elpistostegalian fish present an almost exactly intermediate series, with the snout gradually increasing in length in relation to the postorbital region. Because the skull was flattened, their eyes looked dorsally. In *Panderichthys* and *Tiktaalik*, they have a curious shape, rather more elongated than circular, which may suggest they looked laterally as well as dorsally.

*Eusthenopteron* shows the mosaic of snout bones common to most early lobe-finned fish, but *Panderichthys* has a single pair of enlarged bones making up much of the snout and interorbital region, the

equivalent of the tetrapod frontal bones. *Panderichthys* is the most basal tetrapodomorph to show these bones, and this is thought to be a character shared with tetrapods (Vorobyeva and Schultze 1991). *Elpistostege* also shows this pattern, but where it has been included in cladistic analyses, it appears above *Panderichthys*. The suture pattern of *Tiktaalik* is difficult to make out in this region, although there is reason to suspect it may have been similar. To either side of the snout region, between the prefrontal and lacrimal bones, *Tiktaalik* has a broad, uninterdigitated, overlapping suture that invites the suggestion that it was flexible. There are fewer bones in the rest of the snout mosaic in *Panderichthys* than in other tetrapodomorphs, though there are still more than in tetrapods. Again, the suture pattern there in *Tiktaalik* is unknown, but this may be because the bones were in fact tightly bound together.

The snout of *Ventastega* provides some ideas about the significance of the internasal fontanelle, the midline gap between the paired nasal bones: it may represent the region where the mosaic of bones in fish has been lost. A similar fontanelle was found in *Acanthostega*, and subsequently smaller but definite fontanelles have been identified in some Early Carboniferous animals including *Crassigyrinus*, *Eoherpeton*, and *Greerepeton* (see Chapter 7). They may add weight to this suggestion.

The fact that tetrapods reduced the total number of bones in the snout may be related to its overall lengthening, in which the presence of fewer larger bones might have been stronger than a collection of many smaller ones. If the snout were habitually raised out of the water, either to feed or to gulp air, this may have been an advantage as the impact of gravity was brought to bear. However, the situation was evidently somewhat variable, and inferences from *Tiktaalik*, in which the snout is consolidated, seem to contrast with those from *Ventastega*, in which the bones do not even meet in the midline.

The external nostrils of *Panderichthys*, *Tiktaalik*, and *Elpistostege* are similar to each other, and larger than those of *Eusthenopteron*. They also lie closer to the jaw margin. They are still bounded by the anterior tectal and lateral rostral bones where it can be determined, as in *Eusthenopteron*. Reports that *Ichthyostega* retained a lateral rostral cannot be substantiated. *Acanthostega* has lost the lateral rostral, and all other tetrapods seem to have lost both bones. But the position and size of the nostril in the elpistostegalian fish is similar to that in many early tetrapods. It can be inferred that the nostril assumed the tetrapod-like size and position—that is, larger in size and low on the snout, before the bones surrounding it changed their relationships, with some of them being lost. It is difficult to explain why this change in topology took place in the tetrapod external nostril because it seems likely that it was doing the same job in them all, from *Panderichthys* to *Acanthostega*, that is to say, as an intake for water or air for chemosensing and olfaction, rather than for intake of air for breathing.

The internal nostril—the choana—has an almost identical arrangement of bones defining the opening in all the elpistostegalian fish and

*Acanthostega*, although in *Acanthostega* the hole is somewhat larger. Although many people have assumed that *Acanthostega*, being a tetrapod, used its nose to take in air for breathing, the external nostril is small enough to suggest that this was not the case, but that it remained fishlike in its nasal function. The next section discusses further aspects of the nose and its functioning during the transition.

Early tetrapods are consistent in the pattern of bones of the cheek region and are consistently different from tetrapodomorph fishes. In most tetrapodomorph fishes, the squamosal at the back of the cheek meets the maxilla, and this pattern prevents the quadratojugal from contacting the jugal. In tetrapods, the quadratojugal contacts the jugal, so that the squamosal cannot meet the maxilla. In one specimen of *Panderichthys*, one cheek is described as showing the fish pattern, while the other shows the tetrapod pattern (Vorobyeva and Schultze 1991). The condition in *Tiktaalik* is not described, and the cheek is missing in the fossil of *Elpistostege*. This seemingly insignificant change in cheek pattern cannot easily be explained in functional terms, though it correlates with a great increase in the size of the jugal in tetrapods that also impacts the size of the orbit. An isolated jugal bone from an early tetrapod can consistently be distinguished from that of a fish by its size and the proportion of the orbit margin that it provides. In *Panderichthys*, *Tiktaalik*, and *Elpistostege*, the jugal sometimes does and sometimes does not contribute to the orbit margin, and where it does, the contribution is small.

Some regions of the skull roofs of modern fishes frequently show a range of variation within species that does not seem important to the fishes themselves (Grande and Bemis 1998). Perhaps the variation in cheek pattern was one of those that became variable among the tetrapods' closest relatives and later stabilized in a different pattern among tetrapods themselves. Until more is known about tetrapod-like fish and fishlike tetrapods such as *Obruchevichthys*, *Elginerpeton*, and the others that are known only from scraps, it will not be possible to test this idea.

In the skull roof, one feature of more basal tetrapodomorphs conspicuously absent in the elpistostegalian fish forms is the hinge between front and rear halves (see Figs. 2.11, 6.2). In *Eusthenopteron*, this lies at the suture between the bones known as the parietals and postparietals. Although in *Eusthenopteron* it may not have been functional as a hinge, the position of this feature is clear. In *Panderichthys*, *Tiktaalik*, and *Elpistostege*, there is no sign of it, and the parietals and postparietals are joined by interdigitating sutures, just as they are in tetrapods. In all primitive tetrapods except *Ichthyostega*, in which there is the anomalous situation of having a single ossification there, the postparietals are much shorter than the parietals, but in the elpistostegalian fish, these two pairs of bones are about the same length, as they are in *Eusthenopteron*. This can be read to mean that the hinge line was lost before the rear of the skull became shortened.

Some workers have suggested that the loss of the cranial hinge line was connected with emergence onto land. Once the head was out of the

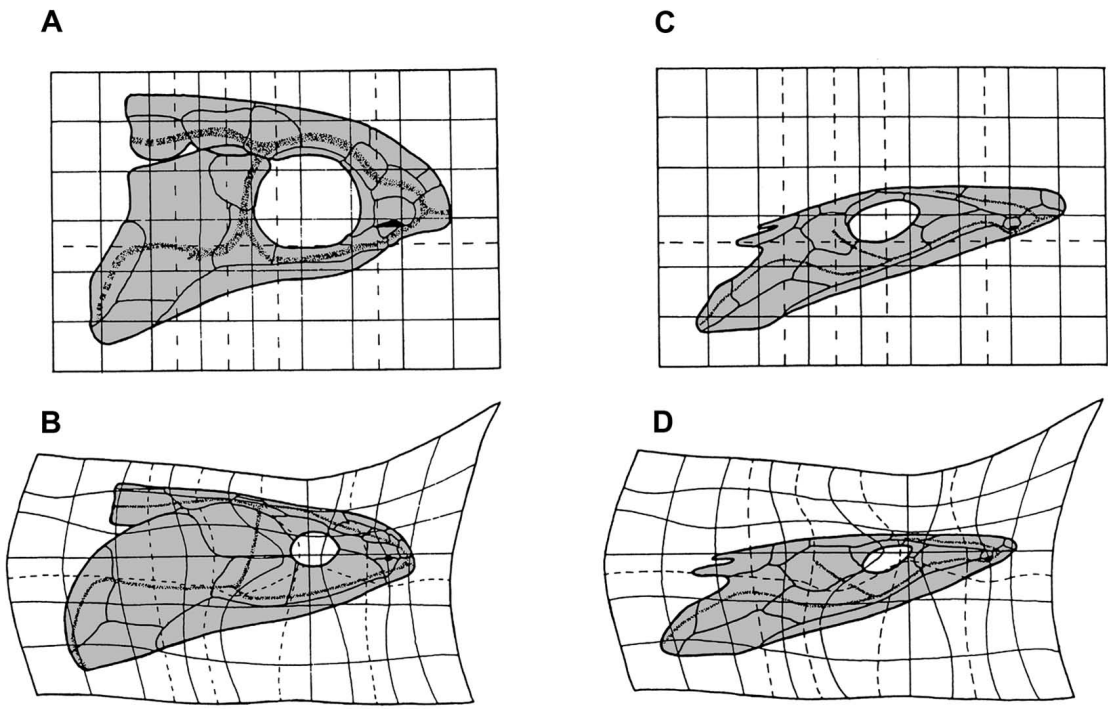
water, it becomes effectively much heavier, and to shift the bulk of the components closer to the neck joint would make it easier to lift. While maintaining the length of the tooth row, it would bring the teeth to a position in front of the eyes, allowing the animal to see more fully what it was catching, and allowing the tooth row to be longer relative to the length of the head (Thomson 1967). The proportions of *Panderichthys*, which are almost exactly intermediate between *Eusthenopteron* and *Acanthostega* in this respect, do not really help answer this question because nothing can be known about how much time it spent feeding with its head out of water. Alternatively, the head may well have been raised out of the water for air gulping.

Thomson (1967) made a study of the effects on intracranial kinetics of lengthening the anterior part of the skull at the expense of the posterior. He showed that as the front part of the skull became elongated, so the range of movement possible at the intracranial joint must necessarily have been reduced, until at a certain point it became completely ineffective. This kind of change in proportion is that seen across the fish–tetrapod spectrum, with *Eusthenopteron*, the elpistostegalian fish, and early tetrapods showing a progressive increase in snout length, and a corresponding loss in the features associated with intracranial movement.

Changes to the size of the orbit may be explained in a quite different way. In a series of *Eusthenopteron* skulls representing increase in size during growth, a sequence of changes can be seen. The eyes in the smaller, more juvenile individuals are relatively much larger than in the adults, although the snouts are relatively shorter. The relative size of the orbits in juveniles is much more like that of tetrapods than that of the adult fishes. This has led to the suggestion that increase in eye size at the fish–tetrapod transition may be caused by retention of juvenile proportions.

This idea was explored by Coates and Clack (1995). In an earlier study, Schultze (1984) had examined skulls of *Eusthenopteron*. The locality of Miguasha has provided a great size range of specimens from small juveniles to large adults. He examined the proportional changes that they underwent during growth by placing the outline drawing of a juvenile skull onto a grid. Points where the drawing and grid intersected were regarded as fixed. Then the positions of these same points were observed when the outline of an adult skull was placed on the grid. In order to make the grid lines pass through these same intersections, it has to undergo distortions. The amount and shape of the distortions gives a clue to the degree of proportional changes at various points in the skull. Coates and Clack (1995) used this technique in reverse. They placed an outline of the skull of *Acanthostega* on the undistorted grid, then subjected it to the same transformation that *Eusthenopteron* underwent in becoming adult. The skull shape that results looks much like that of *Panderichthys*. In other words, the skull shape of *Acanthostega* is much what would be expected if it had been the juvenile of a hypothetical *Panderichthys*-like ancestor (Fig. 6.3).

The skull table, the region behind the orbit consisting of the midline series of bones plus the flanking temporal series, is the region that




**6.3.** Diagrams to show Cartesian grid transformations of juvenile to adult *Eusthenopteron* applied to the skull of *Acanthostega*. (A) Juvenile *Eusthenopteron* placed on a plain grid. (B) How this grid is distorted by growth into the adult form. (C) Skull of *Acanthostega* placed on a plain grid. (D) Skull of *Acanthostega* after it has been subjected to the same distortion as from (A) to (B). *From Coates and Clack (1995).*

overlies the bulk of the braincase and the otic capsules. Another possible reason why it shrank in length relative to the preorbital region may be inextricably linked with corresponding changes to the brain and ear region below it. However, that is not the only modification that it underwent. As the movement between skull bones required by suction feeding and gill breathing became reduced in importance, the flexible joints between them were gradually sealed up. The skull table became more firmly attached to the cheek. At first, this occurred just behind the eyes. It involved the postorbital and postfrontal bones, but also the intertemporal, a bone that sat at what would be a pivotal point between the temporal and cheek series.

The intertemporal has a complex history. In *Panderichthys*, it can be identified as lying to either side and just in front of the junction between the postparietals and parietals. It is not identifiable as a separate element in *Elpistostege*, but its presence may be inferred in *Tiktaalik* (Ahlberg et al. 2008) on the basis of similarities to *Ventastega*, in which it can be identified. *Acanthostega* and *Ichthyostega* both lack it, as does the recently discovered tetrapod from Sosnogorsk in Russia. Its space is occupied by a junction between the supratemporal, parietal, and postorbital. In later tetrapods, the intertemporal is sometimes present and sometimes absent in different groups. Its presence used to be considered a primitive condition, but now the picture is less obvious.

At the back of the skull of almost any tetrapodomorph, the elpistostegalian fish being no exceptions, there is a notch situated between the cheek plate and the skull table. The notch, or cleft, is continued

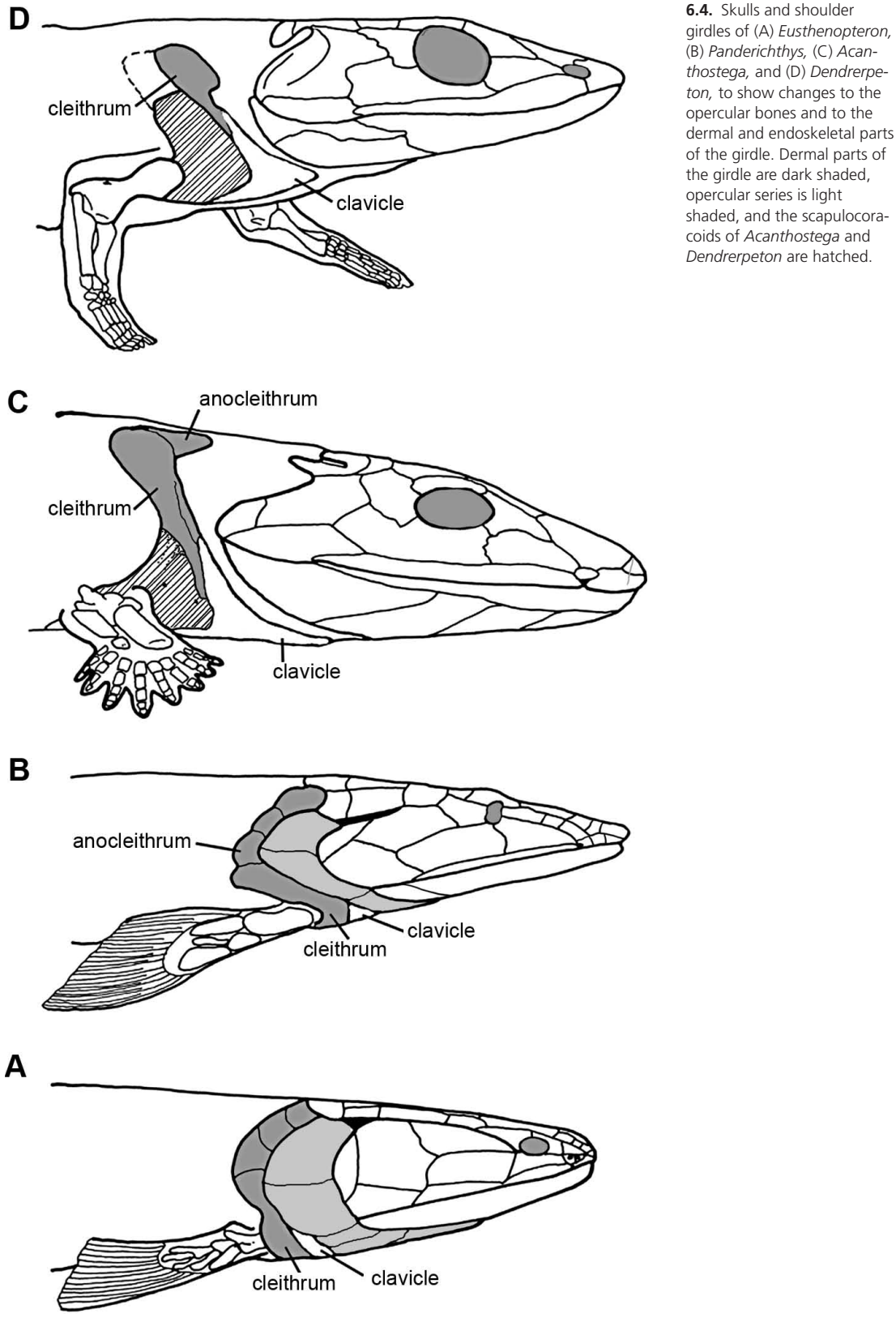
backward by the gap between the extrascapulars and the opercular series (see Figs. 2.1, 6.2). The apex of the notch is assumed to be the site of the opening of the spiracle, the external exit of the spiracular pouch. The spiracular pouch is the gill pouch associated with the hyoid arch and hyomandibula, and though no fully formed and functional gill has ever been found associated with the spiracular pouch, a rudimentary gill is sometimes found there in some modern forms. Other functions of the spiracular pouch (confusingly also sometimes known as the spiracular cleft) are as a chemosensory organ detecting the amount of oxygen or carbon dioxide in the water, or as an outlet for exhaled air in air-breathing forms such as *Polypterus*. In *Polypterus*, the spiracle can be used for taking in air without the rest of the fish breaking the water surface (Magid 1966, 1967; Thomson 1969). This observation has been disputed because it has not been replicated under experimental conditions (Brainerd et al. 1993), but has been seen by several observers, including myself and P. E. Ahlberg (personal communication 2007). A third use to which the spiracle is put is found in skates and rays, flattened chondrichthyans whose main gill openings lie entirely ventral to the animal. In these animals, the spiracle is the opening through which water enters the pharynx, to exit via the main gill openings in the usual way.

It is usually assumed that all early bony vertebrates had air bladders or functional lungs (Romer and Parsons 1986), and the possession of a functional spiracle is also attributed to them, especially because there is one in *Polypterus*. Early ray-finned fishes also show a groove in the side of the braincase wall, interpreted as the position where the duct leading to the spiracle would have run. The same is true of many early lobe-fins.

In *Acanthostega*, and indeed many other early tetrapods, a notch appears in the back of the skull in what is positionally the same place, between the skull table and the cheek. The function of such a notch has been disputed over the years. In earlier studies, it was called an otic notch and was assumed to have been part of an aerially adapted ear, holding the tympanic membrane. However, the braincase of *Acanthostega* has a groove in the same position as the spiracular groove in early ray-fins (Clack 1998c).

In the sequence of tetrapodomorphs from *Eusthenopteron*, through *Panderichthys*, *Tiktaalik*, and *Ventastega*, the spiracular notch is evident, and in each taxon, it is successively broader and more widely excavated. This is especially noticeable in the latter two, in which the configuration of the notch is conspicuously enlarged. In fact, there are many matches between landmarks on the skull tables of *Tiktaalik* and *Ventastega*, attesting to the primitive nature of the latter (Ahlberg et al. 2008). Clack (2007) suggested that the spiracle was open and involved with air breathing. If so, the increase in size may be attributed to the increase in importance of this capability among elpistostegalian fish and tetrapods.

The evolution of this whole region of the skull and its underlying braincase have been subjected to much change during the fish–tetrapod transition, and the structural and functional modifications that the region




**6.4.** Skulls and shoulder girdles of (A) *Eusthenopteron,* (B) *Panderichthys,* (C) *Acanthostega,* and (D) *Dendrerpeton,* to show changes to the opercular bones and to the dermal and endoskeletal parts of the girdle. Dermal parts of the girdle are dark shaded, opercular series is light shaded, and the scapulocoracoids of *Acanthostega* and *Dendrerpeton* are hatched.

has undergone are discussed in much more detail later in this chapter and in Chapter 10.

Moving back from the main part of the skull, one or two more things can be seen in the sequence through elpistostegalian fish to *Acanthostega*. *Panderichthys*, while retaining a full set of operculogular bones, nevertheless had these bones much reduced in anteroposterior length compared to *Eusthenopteron* (Fig. 6.4). This may be tied up with its much more consolidated skull and possibly indicates less complete reliance on gills for breathing. Modern fishes that habitually breathe air generally have reduced operculogular bones, though not all fishes that have reduced this series breathe air regularly (Coates 1996). However, lungfishes that are specialist air gulpers have lost this series of bones altogether. It may be that *Panderichthys* was a more regular air breather than *Eusthenopteron*.

Despite many similarities between *Panderichthys* and *Tiktaalik*, there are also significant differences. Both animals retained the bones beneath the lower jaws—the gulars and submandibulars—to which the opercular bones attach, but in *Tiktaalik*, the opercular series of bones appears to be completely missing. That is consistently the case in all the skull specimens that have been found.

One of the bones present in the fish cheek, but absent in most tetrapods, is the preopercular (compare Fig. 2.11 with, for example, Figs. 7.15, 9.5, or 9.8). In tetrapodomorph fish, this is an elongate bone clasping the rear of the squamosal and forming part of the rim against which the opercular series abutted. Its disappearance can be followed among early tetrapods. It remains present in *Ventastega*, *Ichthyostega*, and *Acanthostega*, where it is short and polygonal in shape, and it is also found in the Early Carboniferous forms *Pederpes* and *Whatcheeria* (see Chapter 7). However, in the latter two animals, it is a rather superficial element of the cheek, and in *Whatcheeria*, it is thin. Sometimes it is difficult to see at all, and in some specimens it appears to have been absent (Lombard and Bolt 1995). Loss of this bone was apparently gradual, its place taken by the meeting of the squamosal and quadratojugal bones underneath it, not by its sudden disappearance nor its fusion with other bones.

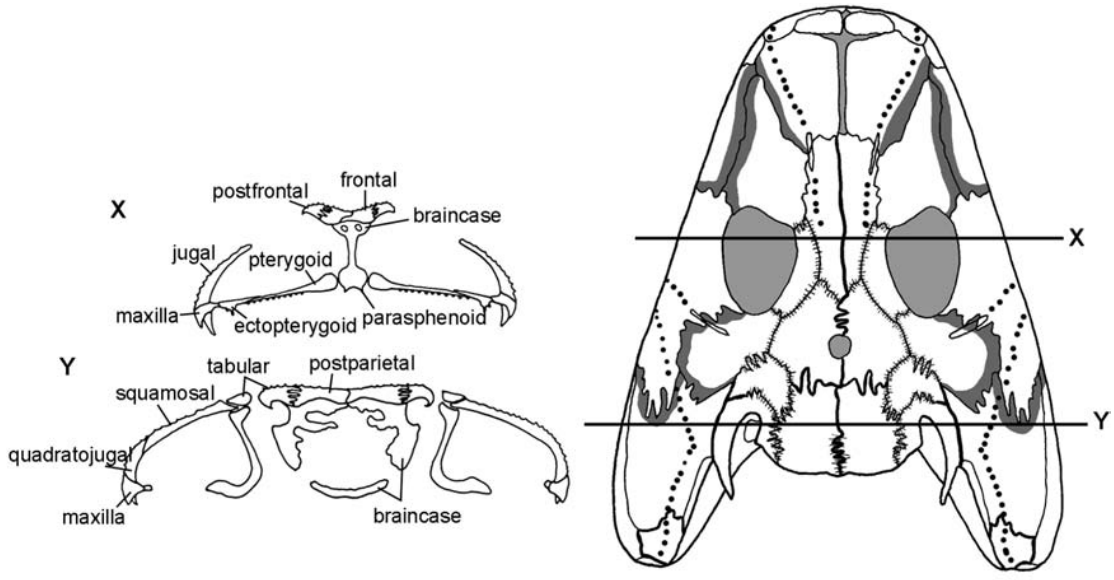
The extrascapular series meets the supracleithral series that in fishes joins the shoulder girdle to the head in fishes (Fig. 6.4). Both these series are lost in tetrapods. *Panderichthys* retains the extrascapular series, but it seems that *Tiktaalik* does not. At least they have never been found, although overlap areas on the back of the skull suggest some form of contact with the supracleithral bones. The latter bones do remain in *Tiktaalik*, attached to the cleithrum (Daeschler et al. 2006).

For many years, the lower jaws of early tetrapods and their close relatives were little studied, even ignored as uninformative. More recently, a series of characters has been found in which even the earliest tetrapods differ consistently from tetrapodomorphs, even the elpistostegalian fish. *Panderichthys* and *Tiktaalik* have very similar jaw construction to each other, and it is not very different from that of *Eusthenopteron*. Distinguishing characters of tetrapods include the presence of teeth versus

denticles on the parasymphysial plate, the presence or absence of a couple of foramina around the symphyseal area, the amount of ossification of the Meckelian bone in the body of the jaw, but more conspicuously in the relative sizes of the dentary and coronoid dentition. These characters in the dentition and structural makeup of the jaws must surely be related to changes in diet and the stresses under which the jaws operated. The subsequent changes among tetrapods show what looks to be an orderly sequence of appearance, and the significance of this will be dealt with in Chapter 10 (Ahlberg and Clack 1998).

This brings the discussion to consider the overall skull structure and the way it reflects differences in function at the fish–tetrapod transition. In fishes such as *Eusthenopteron*, the dermal bones are generally joined to one another rather loosely, by narrow under- and overlapping flanges. The margins of the individual bones appear straight or as simple curves in surface view. In some places, however, the bones fuse altogether, and the junctions between them are difficult to see at all. In early tetrapods, many of the bones are interdigitated—joined together with fingerlike interlinking processes—so that in surface view, the junctions are often highly irregular zigzags. The effect of this is to make many of the sutures between bones into strong junctions. Even in early forms such as *Acanthostega*, the range of sutural types seems to have increased, so that butt joints, scarf joints, tongue-and-groove joints, and three-dimensionally interdigitating joints are all found at different points in the skull (Fig. 6.5). This must reflect different stresses experienced by the skull at different points and may indicate that already the head was exposed to the air and thus to the effects of gravity. One of the regions to be most strongly integrated is the skull table, where tabular, postparietal, parietal, and supratemporal have the most complex mutual sutures in the skull. This part of the skull would have been to a great extent involved in the attachment of muscles from the vertebral column to hold up the head. One possible function for the tabular horn of *Acanthostega* is as an attachment point for a ligament or muscle joining the head to the shoulder girdle. Other parts of the skull of this animal show extensive overlapping sutures, good for resisting torsion perhaps created by catching or lifting prey out of the water (Clack 2002a). The contrast in skull integration between fishes and tetrapods may also indicate different feeding strategies, though this is not plainly reflected in jaw structure and dentition. The elpistostegalian fish show an intermediate form of construction, showing interdigitating sutures between some of the skull bones, visible in external view (Figs. 3.17, 3.21, 6.2) (see Chapter 10).

Work by Markey and Marshall (2007) looked at the types of sutures in relation to skull mechanics. The different types of suture, from simple overlaps to deeply interdigitated ones, relate to the kinds of stresses under which different regions of the skull operate, in turn related to the kinds of feeding that the animal uses. Markey and Marshall compared skull sutures in the primitive modern ray-finned fish *Polypterus*, *Eusthenopteron*, and the Permian tetrapod *Phonerpeton* with *Acanthostega*. They

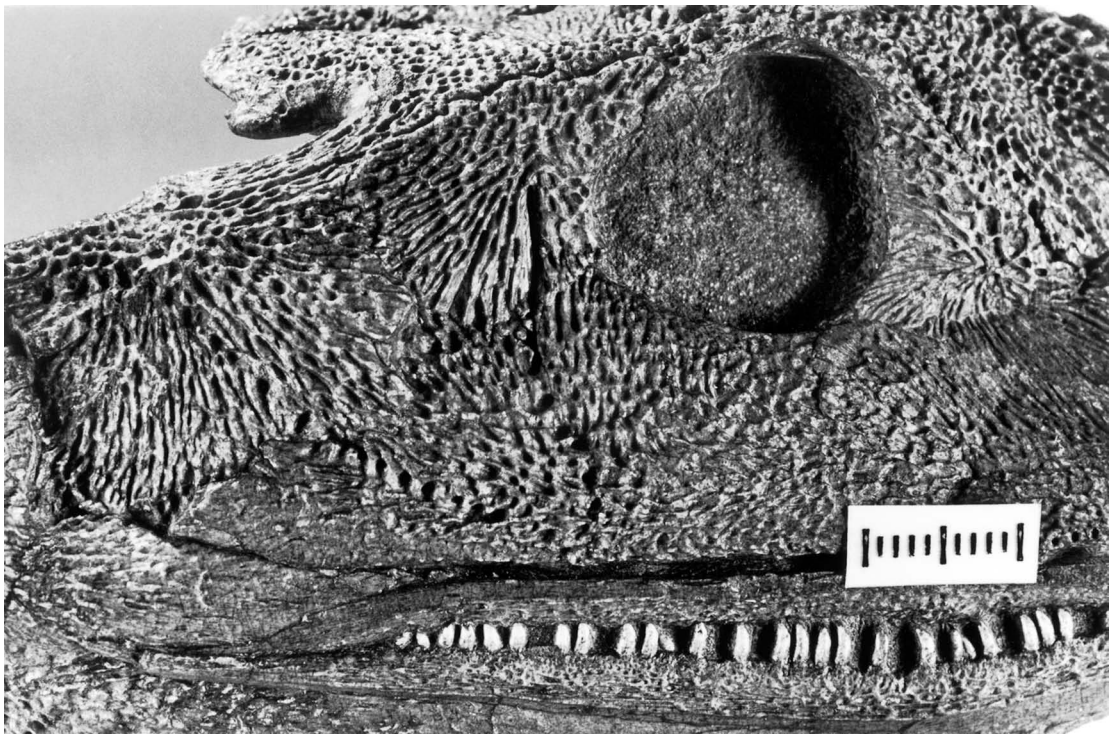



**6.5.** Skull roof of *Acanthostega* to show sutural types. Heavy lines indicate butt joints with no overlap; gray-shaded areas represent areas of sutural overlap (scarf joints); interdigitated joints are shown by hatching. To the left are shown sections through the skull at levels X and Y, illustrating some of the sutural types in section. *From Clack (2002a).*

examined which kinds of sutures occurred where in an attempt to discover which form *Acanthostega* more closely resembled. *Polypterus* and *Eusthenopteron* were evidently suction feeding in water, whereas *Phonerpeton*, a terrestrial tetrapod, was evidently biting. *Acanthostega* more closely resembled a biting form than a suction-feeding form, suggesting that it had moved to a less fully aquatic form of feeding.

With a bit of experience, early tetrapod paleontologists can usually distinguish isolated dermal bones of fish from those of early tetrapods, even when they are incomplete. The clues lie in the external surface of the bone. Most dermal bones carry sculpturing or ornament—that is, the surface is marked by wrinkles, pits, pustules, ridges, or grooves. By and large, in fishes, there is a recognizably different type of ornament. It tends to be quite fine, evenly distributed "pimple and dimple" texture, so that there is no obvious center of radiation. In tetrapods, the ornament tends to be coarser, to be higher profile, and to show a definite growth center (Figs. 1.3, 6.6). Usually toward the middle of the bone, the ornament is arranged in regular pits and ridges, often described as honeycomb, but toward the edges, the ridges are aligned more or less radially, with grooves fanning out between them. There are exceptions to the rule, but generally in early tetrapods, the ornament can be described as starburst. It was discovery of this type of ornament pattern that first alerted paleontologists to the existence of Devonian tetrapods in Scotland and Latvia.

The differences in ornament between fishes and tetrapods probably reflect differences in growth pattern, with the regions of elongated grooves and ridges in tetrapods indicating areas of more rapid growth. However, there may be other functional differences as well. In later tetrapods, there are characteristic differences between temnospondyls, in which the ornament tends to be quite regular, and anthracosaurs, in which it



**6.6.** Close-up of the dermal ornament of *Acanthostega*. Scale bar = 10 millimeters. *Photograph by S.M.F.*

becomes rather irregular or almost absent altogether (see Chapter 9). Again, reasons for this are unknown, but they could reflect physiological differences. Witzmann et al. (2010) studied differences among a substantial number of early tetrapods to try to establish common patterns. Where the ornament is clear and regular, it has been interpreted as indicating that the outer skin was quite closely applied to the surface, but where it becomes shallower in profile, the bone was more deeply buried below the surface. They suggested that the crests and protuberances may have provided protection for blood vessels that ran in the grooves between them. In histological studies, they also discovered numerous Sharpey's fibers, especially in the prominences. These fibers indicate the attachment of a significant layer of soft tissue to the underlying bone, implying a relatively thick skin. When they compared large and small tetrapods and aquatic and terrestrial forms, they concluded that cutaneous gas exchange through the skin was unlikely to be a major function of the dermal bone.

From a few cases in which growth series of early tetrapods are known, it seems that ornamentation changes and develops with age. In the youngest animals, ornamentation can be absent or inconspicuous, becoming more marked with increase in age and size. It may be that the lack of prominent ridges and tubercles in anthracosaurs could be a consequence of pedomorphosis, or retention of a juvenile condition.

The functional significance of dermal ornament remains to be studied in detail. There are a few modern animals that provide models, for

example catfishes, crocodiles, and some frogs. Some armored catfishes develop similar ornamentation patterns to those of early tetrapods. The ornament may increase the strength of the bones, or it may provide a greater surface area for attachment of the epidermis. It should be remembered that the skull bones of early tetrapods would have been covered in an outer layer of epidermis, as is the case with catfishes. In catfishes, the irregularities of the ornament are not visible externally in the living animal, though they are in crocodiles. In crocodiles, many of the pits in the skull bones house pressure-sensitive cells that inform the animal about movements in the water, analogous to the lateral line system in fishes (Soares 2002).

Sections through the dermal bone can provide information about growth patterns and even seasonal changes, though little work has yet been done on this.

### GILL SKELETON, BRAINCASE, AND OCCIPUT

A number of changes to the outer skull bones are evident across the series from *Eusthenopteron* to *Acanthostega*, but even more profound ones are seen internally, in the braincase. Changes to the skull roof appear gradual in this series, and whereas some changes to the braincase and other parts of the head seem to have occurred gradually, others seem to have occurred more rapidly (Ahlberg et al. 1996; Downs et al. 2008). Some of the changes are rather subtle but have important consequences for the subsequent evolution of the tetrapod skull.

The gill skeleton is a case that shows both apparently gradual and more rapid changes in various parts. *Panderichthys* and *Tiktaalik* both retain robust gill skeletons, and even in *Tiktaalik*, much of it is scarcely different from that in a more conservative tetrapodomorph such as *Gogonasus* (Downs et al. 2008). The indications are that the gill system was still important in the animal's life, though whether for gill breathing, air gulping, feeding, or some combination of all three cannot be determined. However that may be, there is a large difference between them and what is seen in *Acanthostega*.

By contrast with conservative form of the most of the gill skeleton, notable changes to the hyomandibula have been discovered in the last few years. Rather than the long, downwardly pointing hyomandibula of *Eusthenopteron*, which differs little from that of an early ray-finned fish such as *Moythomasia* (Gardiner 1984), in *Panderichthys* it is shorter, lacking any ossification distal to the opercular process (Brazeau and Ahlberg 2006). Rather than being ventrally oriented, it is more horizontal, which may be related to the flattened skull. It is associated with an expanded spiracular chamber compared to that of *Eusthenopteron*. In *Tiktaalik*, reduction of ossification in the hyomandibula seems to have proceeded further, and a relatively short proximal part is all that is preserved in that animal (Downs et al. 2008). Its proximal articulation with the braincase is a single strap-shaped facet, rather than the double facet

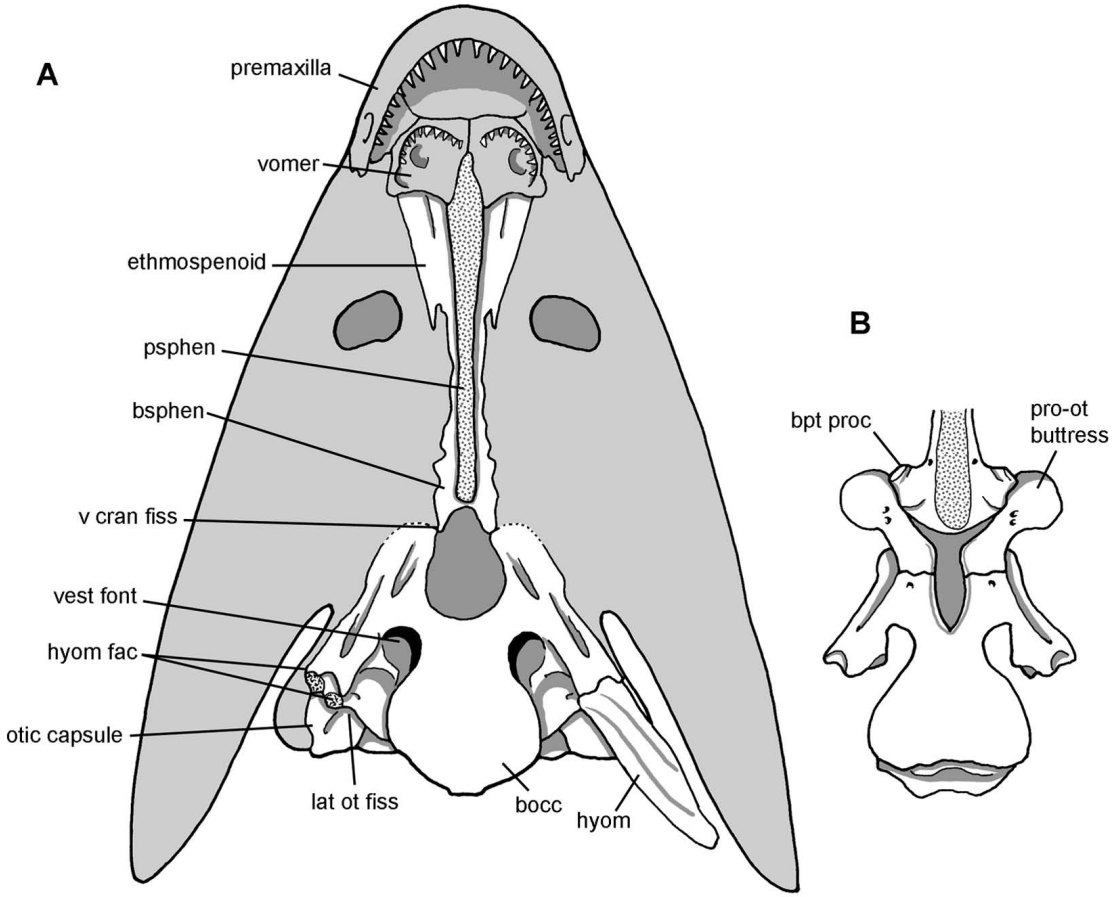
in *Eusthenopteron*. Its limited ossified extent no doubt has much to do with the lack of an opercular bone for it to contact.

Modifications to braincase construction include one of the points at which the braincase and palate are fastened together, the basal articulation. In fishes like *Eusthenopteron* and *Panderichthys*, this is an S-shaped joint in which the braincase and palate contribute more or less equally to the joint surfaces, each with a concave and convex component. There might have been some form of movement at this point to compensate for movements elsewhere in the skull between the skull roof and palate. In tetrapods, the form of the joint changes, so that even in *Ventastega*, the braincase contributes conspicuously bulbous faceted processes, the basipterygoid processes, that fit into recessed sockets on the palate (Figs. 2.11, 2.13, 6.7). Early tetrapods maintained this peg-and-socket arrangement, and although it was sealed up in at least one lineage, in another, it remained throughout evolution and can be seen even in modern forms such as some lizards. No one is really sure why the joint became as elaborate as it did, but it does seem to have allowed, or possibly constrained, some kind of skull kinesis. *Tiktaalik* shows a stage in the enlargement of the basipterygoid processes, in that they project prominently from the base of the braincase (Downs et al. 2008). The articular facets are not as complex as in *Acanthostega*, but they are much larger than in *Eusthenopteron* (Fig. 6.7B). Unfortunately, the basipterygoid processes of *Panderichthys* are not known.

Another modification affected much the same braincase regions. In tetrapods, the two halves of the braincase, the sphenethmoid in front and the otoccipital at the rear, instead of being separate as in *Eusthenopteron* and *Panderichthys*, became intimately joined to each other. The basisphenoid and basioccipital regions became integrated just at the point where the notochord would have ended inside the braincase. In *Acanthostega* and *Ichthyostega*, a suture can be seen at this point, although in all other known early tetrapods, the dermal parasphenoid has expanded over the ventral surface of the braincase and hides this suture from view. It is not clear from the preserved material whether the two portions were fully integrated in *Tiktaalik*, but there does not seem to have been an extensive gap between them.

In the restructuring of the braincase during the transition, two other regions are of especial interest, and they both concern sensory systems.

In all tetrapodomorphs, including both *Eusthenopteron* and *Panderichthys*, the nasal capsule is ossified in the adult, meaning that its fossilized remains can be found in good specimens. In all tetrapods including *Ventastega*, *Acanthostega*, and *Ichthyostega*, the nasal capsule never ossifies, and so there is no information about its construction (Fig. 6.8). However, this does not necessarily mean a complete lack of data. The inference is that for some reason, the former bony capsule was left in what may have been a more juvenile state, remaining as cartilage in the adult. A number of possible reasons can be suggested for this. Perhaps it was connected with weight reduction in the elongated, stronger snout

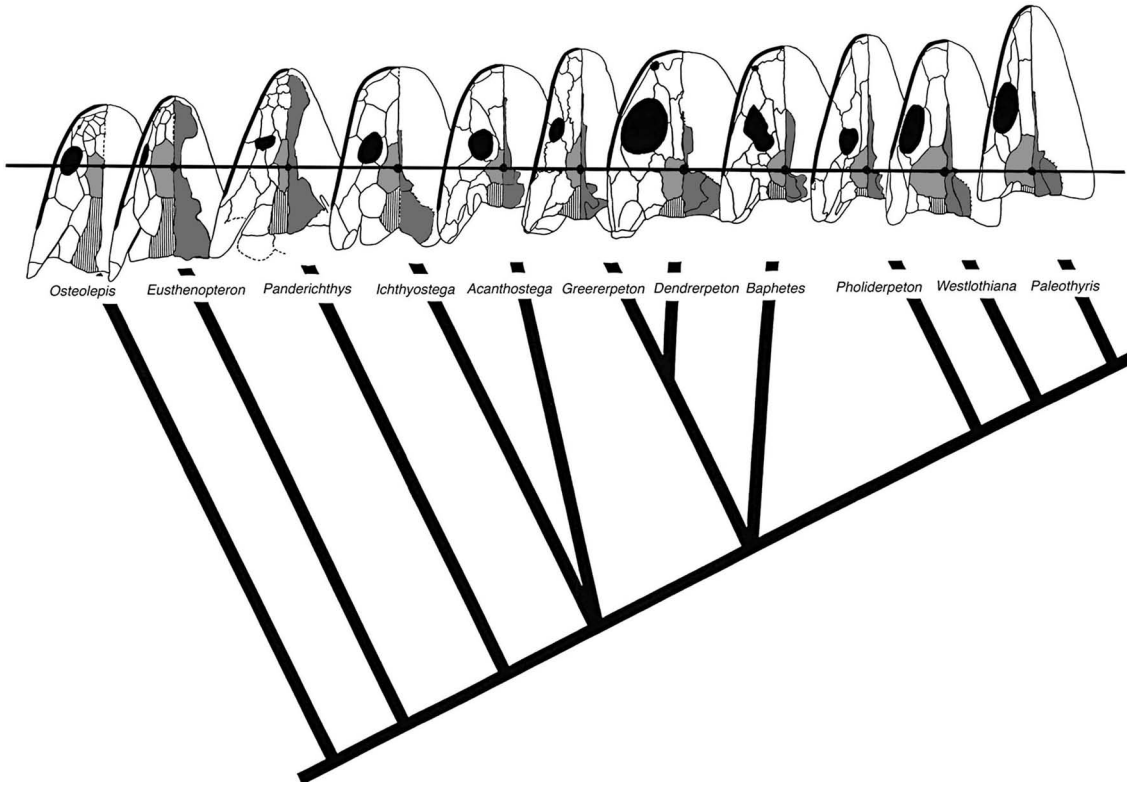



**6.7.** (A) Ventral view of the skull of *Panderichthys* showing braincase. Adapted from Ahlberg et al. (1996). Dermal elements light gray shaded. (B) Equivalent braincase region of *Tiktaalik*. *Adapted from Downs et al. (2008).*

of tetrapods, like the reduction in the number of bones seen earlier, in a snout that may have been habitually raised out of the water. If so, the condition in *Panderichthys* suggests that elongation and consolidation of the snout roofing bones began before the loss of bone from the nasal capsule. The condition in *Tiktaalik* remains unknown.

Reduction of ossification in skeletal structures is often associated with retention of the juvenile condition in animals, the process known as pedomorphosis. The nasal capsule is another instance, as suggested for changes to the proportions of the skull, orbit, and dermal ornamentation, of possibly pedomorphic processes occurring at the origin of tetrapods. Yet another may be connected with changes to the otic region of the braincase.

*Panderichthys* has a braincase construction similar in many ways to that of *Eusthenopteron*, despite the tetrapod-like features of its skull roof (Fig. 6.7). One of the most surprising things is that its braincase still shows many of the features associated with the division between the ethmosphenoid and oticoccipital parts that are seen in *Eusthenopteron*. It has the fishlike type of basal articulation and size and position of parasphenoid. It even shows some of the processes and facets that in *Eusthenopteron*

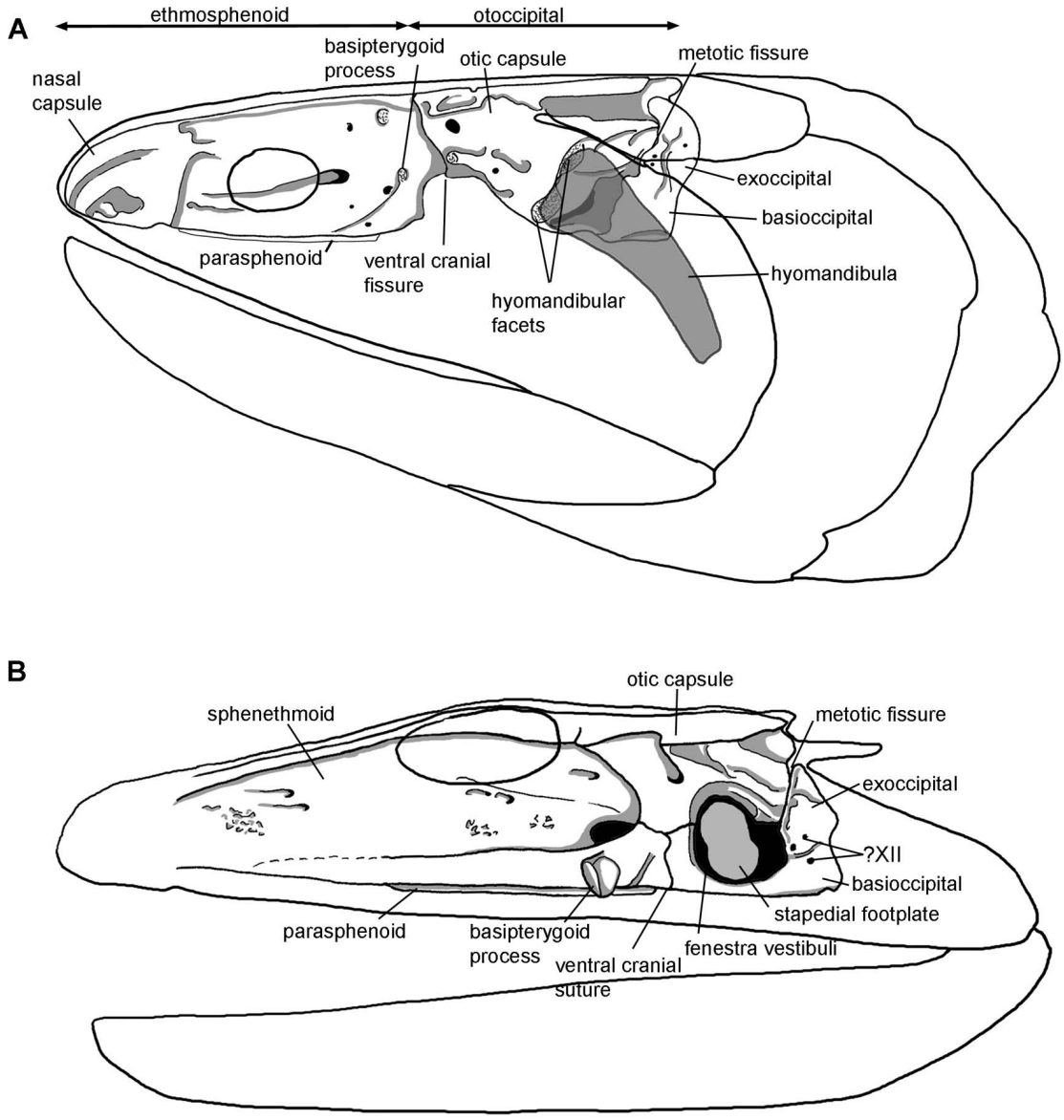



**6.8.** Cladogram of skulls of fish and tetrapods to show the changes in proportion to the snout, otic region, and eyes. In each skull, on the right, the ossified portions of the braincase are shown shaded. On the left, the postparietals in each are hatched and the parietals light gray shaded.

are associated with the hinge that exists between the braincase regions, despite lacking the corresponding hinge in the skull roof.

In the light of information from *Tiktaalik*, some changes to the braincase now also appear to be gradual. However, others may have been much more rapid. Some occurred between *Panderichthys* and *Acanthostega* (Ahlberg et al. 1996) or possibly even *Ventastega*, such as changes to the nasal capsule. Others seem to have occurred between *Tiktaalik* and *Ventastega*, such as the development of a fenestra vestibuli.

In all tetrapods, the hyomandibula, which in fishes functioned as a palate, jaw, and gill arch support, changed form and function and became the stapes. Though the bone is the same, the name is changed in response to an important and radical restructuring of the proximal end (Fig. 6.9). While in fishes, the head of the hyomandibula articulates against the sidewall of the braincase at a bridge of bone called the lateral commissure, in tetrapods, the head or footplate of the stapes fits into a hole in the braincase wall formed where this bridge used to be, in combination with an existing hole in the braincase wall known in fishes as the vestibular fontanelle (see Fig. 2.13). In later tetrapods, this hole reduces in size as the stapes itself becomes more slender and the footplate diminishes. The hole, covered by a membrane, is termed the fenestra vestibuli or fenestra ovalis, and this and the stapes change during evolution from a supporting bone to part of a hearing mechanism. The story of the evolution of the ear region is told in greater detail in Chapter 10.




**6.9.** Braincases and hyomandibula or stapes of (A) *Eusthenopteron* and (B) *Acanthostega* to show contrast in otic region construction. Outline of skull roof superimposed.

Neither *Panderichthys* nor *Tiktaalik* shows much sign even of the beginnings of this profound change. Both retain the lateral commissure against which the hyomandibula articulates. *Acanthostega* and *Ventastega* are in most respects "good" tetrapods. Crucial changes to the location of the stapedial head and the side walls of the braincase had already taken place in *Ventastega* and *Acanthostega*, with the footplate of the stapes inserted into the braincase wall. The stapes in *Acanthostega* and other early tetrapods was nevertheless still a stout bone with connections to the palate. It formed the only link between the ossified portion of the braincase and the palate except for that at the basal articulation (see Chapter 2), and so its main function could still have been as a support for the braincase.

The inside of the otic region and the side walls of the braincase are invariably poorly ossified in early tetrapods, and it is tempting to think that this might be a comparable pedomorphic state to the lack of ossification in the nasal capsule. The poor ossification may in some way be connected to the reconfiguration of the whole otic region, where instead of abutting against the braincase wall at solid facets, the head of the stapes had nothing to articulate against and so became in effect part of the wall.

In many living tetrapods, the embryonic development of the stapes suggests that the portion bearing the footplate is formed from parts of the otic capsule that become attached to the more distal parts of the stapes. On the other hand, there is some evidence that part of the otic capsule surrounding the fenestra vestibuli is derived from neural crest material (Couly et al. 1993), and therefore could have come from the hyoid arch. Perhaps during the reorganization at the fish–tetrapod transition there was some interchange between these tissues of different embryonic origins, though how and in which direction is still unclear. Fossils showing intermediate stages in the transformation may eventually provide clues to the course that events really took, and other evidence may come from looking further at the embryogenesis of the region among modern fishes and tetrapods.

As outlined at the beginning of this section, there was a shortening of the posterior part of the skull roof between *Panderichthys* and *Acanthostega*, especially in the postparietal region. This was noticed as long ago as 1937 by Romer, who pointed out that this region of the skull roof overlies the otic region of the braincase. The shortening of the postparietals reflects the reduction in size of the otic capsules, relative to the rest of the skull. That can be clearly seen in the lineup of skulls in Figure 6.8. The trend seems to continue into the origin of amniotes—that is to say, the radiation of tetrapods that led to reptiles, birds and mammals. Many ideas have been put forward to explain this shortening in the back of the skull.

In most tetrapodomorph fish, the area of the skull table that overlies the braincase appears to be consistent throughout the group, as if they were developmentally linked. However at some point, there seems to have been a developmental disconnection between the dermal roofing bones and the braincase itself. Even in the earliest tetrapods, it is no longer possible to gauge the size of the braincase from the areas of the parietal and postparietal bones, for example. How and when this occurred are questions that it would be interesting to answer, although this has not yet been studied in detail.

Romer (1937) thought that reduction of the posterior part of the braincase might be associated with a change in the configuration of the brain from fish to tetrapod, in which the brain becomes folded and takes up less space. This may apply to some amniotes, but it does not appear to apply to early tetrapods because it is not true of all amphibians and amniotes. The shortening seems to have occurred fairly steadily between *Panderichthys* and *Acanthostega*, with *Tiktaalik* and *Ventastega*

representing intermediate stages. It does seem to correlate with an underlying shortening of the braincase.

Another suggestion was that it might have been related to the development of a neck in tetrapods and the development of strong neck musculature on the occiput (Westoll 1943a). Muscles that move the head run along above and below the spine and insert onto the occiput and braincase in modern tetrapods, and presumably Paleozoic ones as well. In early tetrapods, shortening of the occipital region might have provided a mechanical advantage in a skull that was habitually raised on the occipital joint. The discovery that *Acanthostega* shows the shortened tetrapod condition while retaining a fishlike, notochordal occiput and braincase, argues strongly against this idea. The shortening had already occurred before the occipital condyle had evolved.

Yet a third suggestion to explain the shortening of the otic region was that the semicircular canals, which monitor posture and balance, became smaller and less sensitive once the head was separated from the body by the neck (Bernacsek and Carroll 1981). Jones and Spells (1963) had shown that sensitivity of the canal system was directly related to the cross-sectional radius of the semicircular canals and also to their radii of curvature. They showed that these dimensions increase only slowly compared to the body mass in living animals. They also showed that fishes tended to have larger, and thus more sensitive, systems than those of the tetrapods that were measured at the same time, namely a selection of mammals and reptiles. Bernacsek and Carroll added to this original data measurements of fossil fishes from a wide range of groups, including placoderms, ray-fins, lungfish, a fossil coelacanth, and three tetrapodomorphs, along with the temnospondyl amphibians *Edops* and *Eryops* (see Chapter 9). In the fossil amphibians, the canal sizes were slightly larger than those of amniotes but significantly smaller than any of the fossil fishes, which clustered with the living fishes. They suggested that the size decrease corresponded to a decrease in the sensitivity of the canals and their sensory apparatus at the transition. One possible explanation might be that once on land, the semicircular canals of tetrapods only had to monitor the head and not the body as well. At the initiation of terrestriality, the body was effectively moving only in two dimensions instead of the three exploited by animals living in water, so the semicircular canals would be doing a slightly different job. Once on land, the animals would have experienced the effects of gravity and would have needed to elicit a trip response to imbalance or falling. Fish don't fall. Perhaps the semicircular canals became less sensitive to edit out some of the noise that terrestrial experiences produced. The observations of Bernacsek and Carroll need to be augmented by measurements from the otic capsules of some of the more recently discovered early tetrapods to test the hypothesis of reduction across the transition.

If modern fishes are compared with modern tetrapods, broadly speaking, the difference in proportions is discernible. However, the rule is not general, and many exceptions can be found. Among modern fishes, it

is true that in some cases, those that engaged in walking on land have smaller or narrower semicircular canals than those that do not (Gauldie and Radtke 1990). However, it is difficult to judge from the fossils what the diameter of the semicircular canal tubes might have been, or whether it strictly possible to predict their sensitivity by knowing their diameter.

In this context, the condition in *Ichthyostega* is particularly intriguing. Its phylogenetic position is equivocal. On postcranial anatomy, it consistently appears above *Acanthostega* on a cladogram, but on braincase and jaw anatomy, it appears to be more primitive. Figure 6.8 shows this uncertainty by placing it at the same node as *Acanthostega* with respect to other tetrapods. According to its skull roof proportions, it shows a much more fishlike condition and has front and rear portions in much the same relation as *Panderichthys*. Like *Acanthostega*, it has a fishlike notochordal occiput, corroborating the suspicion that tetrapod-like limbs at least evolved before the occipital condyle. However, its braincase is peculiar, especially the otic region. It is not obvious how large the otic capsules were because they were poorly ossified. Work based on micro-CT scans of skull material (Clack et al. 2003) suggests that it did not have the tetrapod type of stapes seen so clearly in *Acanthostega* but had a unique spoon-shaped element that was part of an underwater auditory organ. Although the semicircular canals were not well represented in the scans, the saccular chamber was visible, and suggested that, if anything, the semicircular canals were smaller, rather than larger, than expected.

A possible confounding factor in the whole debate is that it is difficult to tell whether the reduction in relative size of the ear region is a real effect, or whether it results from the increase in the length of the snout. Only a full morphometric study could really tease apart the separate influences on proportional changes.

Changes to the back of the braincase and ear region were also affecting the way the head and body were joined. With the loss of the extrascapular series, from *Tiktaalik* through *Acanthostega* and other early tetrapods, the head was effectively disconnected from the body except via the occiput and surrounding fleshy tissue. However, a true neck joint or occipital condyle had not evolved in *Acanthostega* or *Ichthyostega*, which were still fishlike in this respect. The notochord still ran through the vertebrae and into the braincase in these animals, meaning that the neck must have had restricted movement. The notochord is bendable, but springs naturally back to a straight line unless muscular effort is exerted. The earliest tetrapods probably had little control over the attitude of the head and probably had to expend considerable energy to move it sideways or up and down.

The ongoing story of the tetrapod neck is one of consolidation of the bones at the back of the skull, increasing the surface area onto which to fasten these muscles and specialization of the joint surfaces. These did not happen all at once, and recent work suggests that they occurred differently and separately among amphibians and amniotes (see Chapter 10). None of these processes had yet begun in the earliest tetrapods so far known.

In their display of tetrapod-like characters, *Panderichthys* and *Tiktaalik* show that many of the changes in the skull roof seen between fish and tetrapods actually arose among animals that would still have been called fish—that is to say in animals that still had fins and that were still aquatic. Other characters, however, seem to be unique to tetrapods, so far as is known. These are, for example, changes to the braincase and limbs.

The reasons for the changes to the braincase wall are unknown, but they are profound, characteristic of tetrapods, and apparently occurred at the same time as those to the limbs that produced digits (Ahlberg et al. 1996). Only further research in paleontology and developmental biology will show whether these two events could be in any way connected, but it is tempting to speculate whether they, perhaps occurring simultaneously, account for a sudden evolutionary event that resulted in the appearance of tetrapods.

## The Postcranial Skeleton

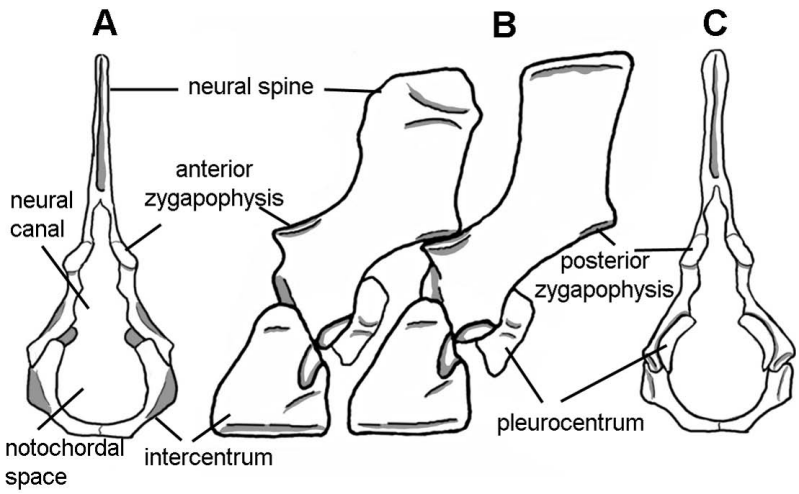
Unfortunately, the postcranial skeleton of *Panderichthys* is still not very well known, but there is sufficient knowledge about some parts to allow inferences about the order of appearance of some tetrapod characters. This section describes the changes that can be seen to the postcranial skeleton in the sequence *Eusthenopteron*—*Panderichthys*—*Tiktaalik*—*Acanthostega*.

### VERTEBRAL COLUMN AND RIBS

As with many other parts of this story, the discovery of *Tiktaalik*, and further study of *Ichthyostega*, have added layers of complexity to our understanding.

The arrangement of centra in *Eusthenopteron* is that called rhachitomous, with horseshoe-shaped intercentra, often formed from paired halves, and small, dorsally placed pleurocentra (Fig. 2.5A). The centra were essentially husks around the notochord, which was still patent even in the adults. There was little to distinguish the atlas or axis centrum from any other. The centra of *Acanthostega* were similar to those of *Eusthenopteron* in almost every detail (compare Figs. 2.5A and 6.10), except that the pleurocentra were slightly larger and the axis intercentrum was about twice the length of the other intercentra. No features distinguished the sacral centra from the others in *Acanthostega*, even though there was a recognizable, if only slightly distinctive, sacral rib (Coates 1996).

Taking this at face value, it seems reasonable to draw the conclusion that *Acanthostega* shows the primitive condition for an early tetrapod vertebral column. Neither centra nor neural arches have been found for *Tiktaalik*. *Ichthyostega* has robust horseshoe-like centra through which the notochord still ran, but micro-CT scans of key specimens suggest that pleurocentra were absent. It is unclear whether this represents a modified rhachitomous condition, but a similar arrangement can be seen in the Early Carboniferous tetrapod *Crassigyrinus* (see Chapter 7).




**6.10.** Diagram of *Acanthostega* trunk vertebra. (A) Anterior view. (B) Left lateral view. (C) Posterior view.

As far as the neural arches are concerned, a few more differences can be found. The atlantal and axial arches in *Acanthostega* are somewhat different from the trunk arches, with the atlas arch being rather smaller and the axis arch rather larger than those of most trunk vertebrae. The fourth cervical arch is rather reduced too. None of these distinctions can be made in *Eusthenopteron* (Fig. 2.4; see also Fig. 10.18). From about the sacral region to the end of the tail in *Eusthenopteron*, the arches become longer and more slender and take on a more acute posterior slope, while in *Acanthostega*, this shape is achieved at about the 12th arch past the sacrum. The arches of *Eusthenopteron* do not interarticulate except for a few at the anterior end of the column that touch each other. They do not have defined points of articulation. In *Acanthostega*, the arches of the trunk region do interarticulate in some places, via poorly developed zygapophyses and at an additional articulation more dorsally. However, even these are poorly defined and would hardly contribute to making the column a weight-bearing structure.

By contrast with *Acanthostega*, the extreme variation along the column seen in the neural spines of *Ichthyostega* is indicative of a highly specialized mode of locomotion and of a well-differentiated musculature to operate them. Both features are totally unexpected in such an early tetrapod. Current work is under way to test the accuracy of the two-dimensional reconstruction produced by Ahlberg et al. (2005), as well as to investigate possible ranges of movement that the column could produce.

Additional bony spines articulate at the end of the arches in the tail of both *Eusthenopteron* and *Acanthostega*, called caudal supraneural spines or radials, a fishlike feature retained in this early tetrapod (compare Fig. 2.4 with Fig. 5.20). They are present also in *Ichthyostega*. Until recently, supraneural radials were not known to occur in any other early tetrapod, but a specimen has now come to light (CM 34638) that clearly shows that at least one embolomere (see Fig. 9.20) had them. They may have been

a primitive feature retained more widely in early tetrapods than had previously been realized.

Substantial dorsal ribs articulating with the intercentrum and neural arch are one of the features that most clearly distinguish tetrapods from fish in general. *Panderichthys* and *Elpistostege* appear to have had some kind of accessory structure attached to the centrum, though it is not absolutely clear that they were the equivalent of tetrapod ribs (Vorobyeva and Schultze 1991; Schultze and Arsenault 1985). *Eusthenopteron* has short, dorsally pointing spinelike processes spanning the gap between the intercentrum and neural arch, but there was no equivalent of a rib shaft (Andrews and Westoll 1970). *Acanthostega*, by contrast, certainly had ribs in the tetrapod sense of a shaft articulating to the vertebral column at two points proximally, one on the transverse process of the neural arch and one on the intercentrum. Because the vertebrae of *Tiktaalik* are unknown and the proximal ends of the ribs not yet described, it is not possible to say whether they shared this construction.

In *Acanthostega* the shafts were short compared to almost any other tetrapod (Fig. 5.20). The cervical ribs had spoon-shaped expanded ends, but the trunk ribs were simply straight or had small dorsally placed triangular processes around their midlength (Coates 1996). They form a good intermediate morphology between *Eusthenopteron* and the ribs of later tetrapods such as the aquatic *Greererpeton* (see Chapter 7). They were almost as different as could be from the massive overlapping and distinctly double-headed ribs of *Ichthyostega* (Figs. 5.2, 5.11, 5.14), which thus seemed anomalous.

The discovery of the massive, imbricating ribs of *Tiktaalik* immediately raises the question of what condition might be primitive for tetrapods and what the function of ribs might be in their various different guises. The corsetlike rib cage of *Tiktaalik* was suggested by Daeschler and colleagues (2006) to provide support for the trunk as the head and front end of the body were raised off the substrate (Figs. 3.22, 3.23). Certainly broad ribs in the shoulder region seem to relate to enlarged shoulder musculature. On the other hand, the apparent lack of ossified centra or neural arches is very much at odds with this interpretation, or at least suggests that the vertebrae only contributed to support of the body at a later stage.

Some possible functional correlates of rib morphology are discussed in Chapter 10.

## SHOULDER AND HIP GIRDLES

In the shoulder girdle, there is a change in emphasis during the transition from fish to tetrapods in the contribution made by the different parts (Fig. 2.6). In fishes such as *Eusthenopteron*, the emphasis is on the dermal components, with a large dermal platelike clavicle strongly attached by a suture to the cleithrum. The ventral part of the clavicle consists of a broad plate, tapering into a dorsal process by which it is attached to the cleithrum. The cleithrum bears a small tripod-shaped endochondral

scapulocoracoid on its inside surface, carrying the socket where the fin articulated. A small midline dermal element, the interclavicle, was present in some forms. In limbed tetrapods, the emphasis shifts to the endochondral components, with the dermal elements becoming successively reduced.

One of the most striking changes to the dermal shoulder girdle seems to defy the overall trend toward reduced dermal elements. This is the development in tetrapods of the interclavicle (see Fig. 2.6). It is an important bone in even the earliest tetrapods. In *Acanthostega* it is shaped like an old-fashioned kite, or a lozenge in heraldic terms, whereas in *Ichthyostega* it has a rounded anterior component with a long narrow posteriorly pointing process. No modern tetrapod has an interclavicle of this type, but the function may in some ways have been similar to the sternum in modern animals, providing attachment for shoulder-girdle muscles, or it may have spread the weight of the animal across the chest in an animal that was belly crawling, taking pressure off the heart.

In fish, the supracleithral series links the shoulder girdle to the extrascapular series. In *Panderichthys*, there is a conventional "fish" complement. In *Tiktaalik*, these bones are still present, but because the extrascapulars seem to be absent, the link between head and shoulder is lost or weakened (Figs. 3.22, 3.23). One component of this series, the anocleithrum, is still present in *Acanthostega*, but it had no bony connection with the head. It is a small oval bone and is also known in a few other early tetrapods. It attached to the dorsal end of the cleithrum and internal to it, so that it lay below the skin and bore no ornamentation. *Acanthostega* and *Tulerpeton* both retained the anocleithrum, and the bone has also been found in a few Carboniferous forms. The embolomere *Pholiderpeton* and the seymouriamorph *Discosauriscus* (see Chapter 9) have both recently been discovered to retain this bone (Clack 1987a; Coates 1996; Klembara 2000), so like supraneural radials, it may be a primitive feature more widely retained in early tetrapods than was previously realized.

In tetrapods, the clavicle remained roughly the same general shape as in fishes, though the dorsally tapering process became rather more slender in most species, and the cleithrum was correspondingly narrower.

Another significant difference between fishes and tetrapods, probably related to the changes to the cleithrum, concerns the scapulocoracoid. This became greatly increased in size to accommodate the enlarged glenoid at which the forelimb articulated. Figure 6.4 shows some of these changes to the shoulder, including that of the Carboniferous *Dendrerpeton*.

In *Panderichthys*, the enlargement of the scapulocoracoid had begun, and this element was attached over much of its surface to the cleithrum, in contrast to *Eusthenopteron*, in which it attached at only three points. The cleithrum itself, however, was still much as it was in *Eusthenopteron*. *Tiktaalik* shows further development of the scapulocoracoid: it is enlarged and elaborated, and has increased in complexity relative to that of *Panderichthys*. The glenoid, though mainly facing backward, has a region

that faces laterally, a condition intermediate between *Eusthenopteron* and *Acanthostega*. Shubin et al. (2006) suggested that many features of the shoulder joint in *Tiktaalik* were adapted to provide stability, possibly at the expense of restrictions to the range of movement that it allowed.

In tetrapods, the glenoid was not only enlarged but changed its orientation to face laterally. Strengthening buttresses ran up its posterior margin and excavations on the internal surface provided housing for chest muscles. From Carboniferous forms onward, the scapulocoracoid acquired a dorsal component that occupied a similar area to that which the cleithrum did in fishes.

The Devonian forms, with the exception of *Tulerpeton*, are rather different in construction from either the fishes or the later Carboniferous forms and may provide clues to how the changes came about in terms of function, though it will require much more study to understand them fully. In *Ichthyostega* (Figs. 5.2, 5.11), *Acanthostega* (Fig. 5.20), and also in *Hynerpeton* (Fig. 5.28C, D) and *Ventastega*, the cleithrum was relatively reduced, though it was still a substantial dorsally extensive blade. Rather than a clavicle firmly sutured to the cleithrum, as in fishes, these animals had the cleithrum and scapulocoracoid fused into a unit so that the joint between them can sometimes only be seen in a cross section through the bone. The scapulocoracoid itself had a substantial platelike form equivalent to the coracoid portion of later tetrapods, but there was no endochondral component further dorsally equivalent to the scapular blade. This region was still the province of the cleithrum. However, the cleithrum was a much less superficial element than in fishes. In fishes, it carried surface ornament characteristic of dermal bone that is close to the animal's surface, whereas in the Devonian tetrapods, the ornament is almost totally absent, suggesting a layer of thicker skin or even muscle external to the bone. At the same time, the clavicle had become more loosely attached to the cleithrum, and the dorsal process had taken up the more gracile form found in later Carboniferous forms. *Tulerpeton* shows a more typical tetrapod-type relationship between the scapulocoracoid and the cleithrum. The bones were separate, as they are in later forms, but there was still no scapular blade. The inference is that the expansion of an ossified scapular blade followed the acquisition of the tetrapod-style anatomical relationship between the two.

Some of these changes must surely have been connected with a shift in the function of the shoulder girdle during the transition and in the changes in stress patterns imposed on it by the enlargement and changes to the use of the limbs. However, some of them may also have been associated with changes in breathing patterns and the reduction of reliance on gill breathing. Muscles used to operate the gills, which would once have been attached to the shoulder girdle, at some stage must have been reduced in importance and in the positions of their attachments. Several of these muscles today serve to operate the tongue and hyoid apparatus in living tetrapods. Matsuoka et al. (2005) were able to identify neural crest invoked muscle attachments for the hyoid musculature on the scapula

of modern tetrapods, which they inferred indicated that that area of the scapula was in fact a remnant of the cleithrum of ancient fishes (the cleithrum is a dermal bone and thus of neural crest origin).

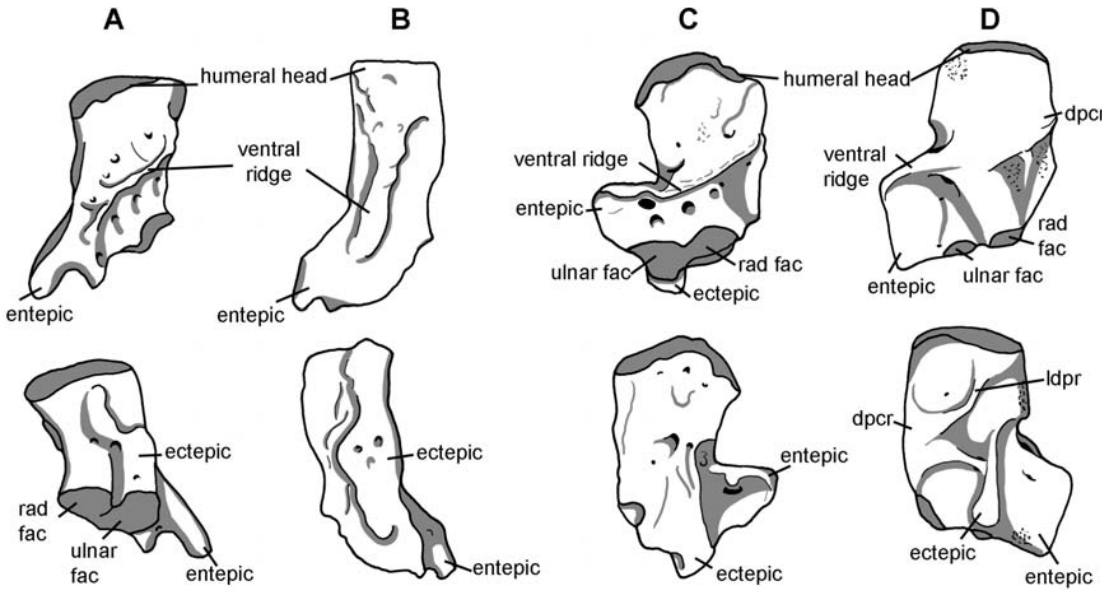
Chapter 2 outlined the profound differences in the construction of the pelvic girdle between fishes and tetrapods. The pelvic girdle of *Panderichthys* is known from a poorly preserved example in a single specimen (Boisvert 2005), but it shows no tetrapod-like features. The pelvic region is unknown in *Tiktaalik*, but it may be inferred to have been similar to *Panderichthys* because so far, further collecting has failed to find any significant remains: larger elements may have been easier to find, so their lack could be suggestive. By contrast, even in the earliest tetrapods known, such as *Elginerpeton*, the change had taken place, and that animal is known to have had a pelvic girdle very like that of *Ichthyostega*. However, the reason for having this large pelvis is less clear. Although in later tetrapods the hind limbs came to be substantially larger than the forelimbs, the evidence from the earliest tetrapods suggests that this discrepancy between front and rear had not yet evolved. In *Acanthostega* and *Ichthyostega*, where both limbs are known in some detail, the humerus and femur are of about equal length. In *Tulerpeton*, although the hind foot is larger and longer than the forefoot, humerus, radius, and ulna are just about the same length as the femur, tibia, and fibula. As outlined in Chapter 5, the early function of limbs with digits may have been more associated with aquatic habits, in which case the increase in size of the pelvis is puzzling.

## FIN AND LIMB SKELETONS

The humerus is the most robust element of the pectoral fin or limb, and fossils of it preserve well, even if they are sometimes flattened during preservation. The sequence of humeri from *Eusthenopteron*, the elpistostegalian fish, the isolated humerus from Pennsylvania (ANSP 21350), *Acanthostega*, and *Ichthyostega* show a series of changes that can be interpreted as providing a more supportive limb (Fig. 6.11).

The bone becomes relatively larger, with a longer proximal shaft. The humeral head that articulates with the shoulder becomes flatter, as seen in *Panderichthys* and *Tiktaalik*. The articular surface becomes more elongate rather than bulbous. This form of shoulder joint, as suggested by Shubin et al. (2006), would mean a more restricted range of movement for the forearm, limiting the potential for rotation but allowing some front-to-rear and up-and-down excursion. A longer proximal shaft allows a greater area for attachment of the muscles that stabilize the shoulder joint. At the same time, the more distal parts of the humerus, where muscles attach that operate the radius, ulna, and more distal parts of the appendage, become more elaborate and larger.

Now that CT scanning of a *Panderichthys* pectoral fin has proved possible, a picture has emerged that is rather different from earlier reconstructions (Boisvert et al. 2008) (Figs. 6.11, 6.12). These show that the

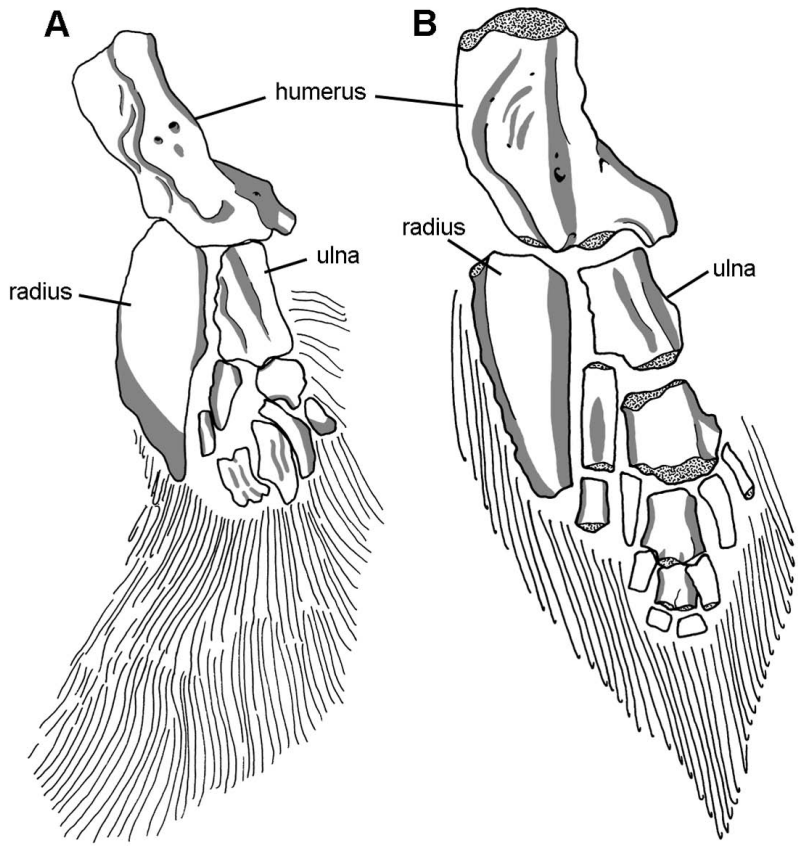



**6.11.** Left humeri of (A) *Eusthenopteron,* (B) *Panderichthys,* (C) ANSP 21350, and (D) *Acanthostega* in ventral view (top row) and dorsal view (bottom row).

large "ulna" described previously was in fact formed from a compaction of scales, whereas the actual ulna was short and stout, more comparable with *Eusthenopteron.* The radius was somewhat bladelike, with a curved leading edge. More significantly, the distal elements of the fin skeleton appear as a series of four or five short bones arrayed side by side, in a manner that is suggestive of the proximal elements of digits. The humerus also shows some tetrapod-like features, in that it has a relatively flat articular surface at the head, and it is a much more elongate bone than that of *Eusthenopteron.*

The humerus of *Tiktaalik* is quite similar to that of *Panderichthys,* but the more distal elements are better known because they have been extracted from the matrix and can be articulated with one another (Fig. 6.12). Shubin et al. (2006) experimented with the possible range of movement that the fin could undergo, and suggested that it showed wristlike joints. In many respects, the fin skeleton of *Panderichthys* is similar to that of *Tiktaalik,* but is arguably even more tetrapod-like.

Two conspicuous features of the dorsal surface of the early tetrapod humerus are a posteriorly positioned, rectangular blade called the entepicondyle, which bears muscles to the ulna and a dorsally positioned, vertically oriented ridge called the ectepicondyle, which bears muscles to the radius (see Chapter 2). In tetrapodomorph fish, the entepicondyle is smaller and triangular, and the ectepicondyle is little more than a rather diffuse ridge. The humerus ANSP 21350 shows a condition in which these two condyles are relatively larger than in fish, with a robust ectepicondyle whose distal end overhangs the rest of the bone, and an entepicondyle that, although triangular, is positioned on the shaft in a more proximal position and at a more acute angle to the shaft, like those of tetrapods (Shubin et al. 2004) (Fig. 6.11).




**6.12.** Fin skeletons of *Panderichthys* and *Tiktaalik*. *Information from Vorobyeva (2000) and Boisvert et al. (2008), and Shubin et al. (2006).*

On the ventral surface, other changes are equally distinctive. In tetrapodomorph fish, the ventral ridge runs from near the head, diagonally across the bone to end at or near the sloping edge of the ventral surface of the entepicondyle. The ventral ridge marks the point where muscles from the shoulder to the forearm, and from the forearm to the rest of the appendage, meet each other. In tetrapodomorph fish, the ridge is pierced by several foramina carrying blood vessels to the more distal parts of the appendage. From ANSP 21350 onward, the ventral ridge becomes reoriented to run more or less transversely across the bone at right angles to the length of the shaft, and in later tetrapods, it disappears more or less completely. Eventually, only the more anterior part of the ridge remains, as a process that probably bore muscles approximating to shoulder muscles—the deltoid and pectoralis—of more terrestrial tetrapods. The reorientation may correlate with the reorientation of the appendage from a more posterior alignment to a more lateral position. The foramina piercing the ridge also reduce and eventually disappear, suggesting that the blood vessels were freed from their bony tunnels, running instead through soft tissue, permitting a greater blood volume to pass through them (Lebedev and Coates 1995; Shubin et al. 2004) (Fig. 6.11).

Study of the subadult specimens of *Ichthyostega* compared with similar stages in *Acanthostega* have added complexity to the picture

(Fig. 5 .12). The humerus of *Ichthyostega* changes in several respects as it grows. The ventral ridge in the subadults bears similarities to those of *Panderichthys* and *Tiktaalik* in its position and in the number and size of foramina that pierced it. This might suggest that the subadults were still aquatic. There are differences, however. The pectoral process is absent as a distinct entity in the fishes, whereas it is prominent in the subadult *Ichthyostega* specimens. It is placed at about the midpoint along the ventral ridge in the subadult specimens. As an adult, *Ichthyostega* effectively loses the ventral ridge except as an inconspicuous feature, and its more distal portion is orientated transversely to the long axis of the bone, as in ANSP 21350 and later tetrapods. It does, however, retain the pectoral process, but that is now situated close to the anterior margin of the bone. Such changes must surely relate to locomotory modifications, and it is tempting to suggest that they were related to a move from more fully aquatic to more terrestrial capabilities.

*Ichthyostega* still has a proximal arm to the ventral ridge, running more or less up the anterior edge, but this segment is lost in *Acanthostega*. In *Ichthyostega*, between this arm of the ventral ridge and another ridge on the dorsal surface that bears the deltoid process is a concave triangular area known as the prepectoral space; these two ridges thus remain separated. This construction is maintained throughout growth, with the result that a deltopectoral crest, formed by the coalescence of those ridges, cannot develop. This is a primitive characteristic shared with tetrapodomorph fishes. *Ichthyostega* also lacks a latissimus dorsi process on the dorsal side of the bone. Muscles from the shoulder that raise the humerus would normally attach here, so its lack suggests that these muscles were not clearly differentiated in *Ichthyostega*.

By contrast, *Acanthostega* shares both a deltopectoral crest and a latissimus dorsi process with later tetrapods, which might hint that it is not as primitive as first suspected. As noted in the previous chapter, the phylogeny of early tetrapods is extremely fragile. The contrast between these two animals may indicate that there was much experimentation taking place among Devonian tetrapods.

Across the transition, modifications to the humerus appear in concert with others to the articular facets that bore the radius and ulna, which become more ventrally positioned, rather than entirely distal as they are in fin skeletons. They indicate the beginning of an elbow bend, bringing the radius and ulna to a downwardly sloping angle, though the hand would have been laterally positioned and not bent forward, as in later tetrapods. ANSP 21350 shows such a change in addition to enlarged epicondyles (Fig. 6.11).

This whole suite of changes implies an increase in muscle bulk and their differentiation into separate bodies, rather than the simple dorsal and ventral sheets found in fishes. With the reorientation of the radius and ulna that occurs in the sequence from *Tiktaalik* to *Ichthyostega* (Fig. 6.1), they further indicate that the limbs have an increasing role in support of the body and even in locomotion that requires muscular effort. They

could potentially raise the front end of the animal, especially the head, up and out of the water, helping the animal to breathe air. This would both allow for greater expansion of the mouth cavity and greater expansion of an air bladder in the act of air gulping (Clack 2006, 2007).

In studies that are still in their early stages, details of bone growth and histology have been obtained by both traditional methods using thin sections of bone under microscopic examination, and by a new technique: synchrotron phase contrast tomography. Humeri of *Eusthenopteron*, *Acanthostega*, and some Carboniferous tetrapods have been subjected to such studies. One of the problems that the use of thin sections has faced in the past has been the scarcity of relevant material, and the understandable reluctance of museum curators to permit what is an inevitably destructive technique. However, Laurin and colleagues (2007) realized that literally hundreds of specimens of *Eusthenopteron* existed, and some were made available to them by the Parc de Miguasha for this purpose. They were therefore able to conduct the first studies of histological thin sections from the pectoral fin skeleton of *Eusthenopteron* and compare them with those of some modern aquatic and terrestrial tetrapods. They discovered that although the histological components of the bones were similar to those of living tetrapods, their organization was quite different. The outer portion of all these bones consists of a layered structure known as cortical bone, and the inner part consists of bone with a spongy texture known as medullary bone. It is in the proportions of each type of bone that the differences lie. Although *Eusthenopteron* was more similar to modern aquatic tetrapods than it was to terrestrial ones, it was still rather different from any of the aquatic taxa that were studied. In the humerus, the outer layer of cortical bone was relatively thin, with the center of the bone completely occupied by medullary bone. The conclusion of the study was that *Eusthenopteron* was unlikely to have left the water to walk overland, although the authors suggested that some more crownward taxa, such as *Panderichthys*, might have done so on occasion.

The first synchrotron phase contrast tomography of humeri looked at subadult and adult humeri of *Eusthenopteron* to examine growth patterns, and found that the proportion of cortical to medullary bone changed as the animal grew (Sanchez et al. 2009). This work is in its initial stages, but some conclusions can be drawn. The humerus of a larger *Eusthenopteron* was more lightly, though more completely ossified than that of a subadult—the cortical layer became relatively thinner with growth. In *Acanthostega*, the cortical part was relatively much thicker, and the medullary region denser, than in *Eusthenopteron*, at least in the regions studied, and showed novel growth patterns and a more tetrapod-like histology.

The pelvic fin skeleton of *Panderichthys* was at least as small relatively as that of *Eusthenopteron* and shows no especially tetrapod-like features. The sequence *Eusthenopteron—Panderichthys—Acanthostega* as it stands suggests a rapid transition from a fishlike to a tetrapod-like condition, and there are more or less no clues to the intermediate forms.

The most obvious contrast between fishes and tetrapods is the evolution of digits and the associated limb joints, the wrists and ankles and elbows and knees. Some of the features of the earliest tetrapod limbs were described in the section on *Acanthostega*, and the evolution and development of these appendages are considered in the sections below on limbs and digits, with their subsequent modifications for terrestriality treated in Chapter 10.

### FIN RAYS AND SCALES

In fishes like *Eusthenopteron* and *Panderichthys*, each paired fin was bounded by a fringe of lepidotrichia. Lepidotrichia, being modified scales, are dermal in origin, with their formation controlled by neural crest tissue, so in *Panderichthys* and *Tktaalik* (Fig. 6.12), this tissue was still operating in the fin region of the skeleton. However, in tetrapods, the dermal components of the skeleton—fin rays and scales—are completely absent from the limbs. The jointed elements that form the digits are all endochondral. In other words, the digits are not formed from modified fin rays but rather are derived from a different embryonic source. An earlier idea that an animal could have either complex endoskeletal fin supports or a large array of fin rays is refuted by the presence of both in rhizodonts such as *Sauripterus* (see Fig. 6.23), as well as *Tiktaalik*, in which the fin rays are unusually robust, especially along the leading edge of the fin.

In fins such as those of the lungfish *Neoceratodus*, there are not only fin rays but also jointed radials present, some of which are in an equivalent position to digits. It is nevertheless true that in lobe-fins generally, the fin rays comprise a smaller proportion of the whole fin than they do in ray-finned fishes. The fin rays in lobe-fins usually form only a relatively narrow fringe around the fleshy lobe.

In *Panderichthys*, there was a tail fin formed of lepidotrichia, running above, below, and round the end of the rather straight tail. However, it had neither dorsal nor anal midline fins. This situation is just as in the earliest tetrapods, *Acanthostega* and *Ichthyostega* (unfortunately, like the pelvic region, the tail remains unknown in *Tiktaalik*). The inference is that the reduction in the activity of neural crest tissue that formed fin rays had begun in *Panderichthys* and was continued among the earliest tetrapods, until it was lost altogether in subsequent forms. The tail fin webbing in these three transitional animals was supported by additional endochondral elements, the supraneural spines or caudal radials. It is not clear whether the supraneural spines disappeared at the same time as the lepidotrichia in the tail. *Ichthyostega* and *Acanthostega* had both, but the appropriate regions are not preserved in the single embolomere specimen with supraneural spines.

This sequence is reflected in the gradual loss of dermal scales from the tetrapod skeleton, although the parallels cannot be taken too far. *Panderichthys* and *Tiktaalik* were both scaled all over with tuberculated, rhomboid scales in a typical fishlike pattern, whereas early tetrapods for

the most part retained only the belly scales. In general, the scalation in fishes is added front to back, echoing the front to back ossification of the axial skeleton (except in *Eusthenopteron*, in which it proceeds back to front; Cote et al. 2002). The tetrapod pattern of ventral to dorsal loss of ossification is rather different. Ventral armor did persist among tetrapods for much longer, however, and is found even among some reptiles as "gastralia" forming a ventral armor. Some dorsal scalation is found in a few Carboniferous tetrapods, but they are usually lightly ossified, if at all.

Looking at the patterns of skeletal evolution more broadly, it seems that in many different parts of the body, the dermal skeleton was lost at the expense of the endochondral skeleton. This sequence is seen in the evolution of the skull, the shoulder girdle, the limbs, and the axial skeleton, including the scales. The reasons for this must be related to the embryonic development of the animals, but as yet, there is little clue to the underlying causes. Nonetheless, one inference is that reduction of the scale cover and fin webbing in early tetrapods may have been a contingent effect of the decreasing role that neural crest–derived tissue played in the formation of the postcranial skeleton—a kind of domino effect from a developmental accident rather than a direct adaptation to becoming a tetrapod and eventually attaining terrestriality. Subsequent evolution may have been facilitated by such modifications so that tetrapods were eventually able to exploit them in a new environment. Similar effects took place in parallel in the skull among various groups of vertebrates, in that the dermal component of the skull was reduced while the endochondral elements became more structurally important. This kind of change seems to have allowed the opening up and lightening of the skull structure, facilitating skull kinesis and the exploitation of a whole range of previously unavailable morphologies and ecological niches among both tetrapods and ray-finned fishes.

## Inferences and Implications: How Did Early Tetrapods Work?

As has been suggested, the best clues about the sequence and timing of changes that came about during the fish–tetrapod transition come from reading the actual fossil evidence. These usually only involve hard parts of the skeleton, with occasional input from trackways and aided by study of the faunal and sedimentological context in which the fossils occur. However, there is another line of evidence that can be used in some cases, and that is the study of present-day animals. This can sometimes furnish ideas about the evolution of soft tissue characters if the characters are treated rigorously, with the foundations laid on phylogeny. Some of these have been touched on already in looking at skull structure—vision, olfaction, and hearing among sensory systems, and locomotory and breathing mechanisms among others.

A certain amount of caution must be used in this kind of study to try to ensure that the living forms chosen for comparison are suitable models. One technique that has been widely applied is that known as the extant phylogenetic bracket (EPB). This involves using inferences only from the

closest living relatives on either side of the phylogenetic node of an extinct group to infer the soft tissue structures or physiological makeup of fossil ones. The technique is intended to bring a certain rigor to the process. However, in some circumstances, it has its limitations, such as when the fossil animals in question are remote from any living relative. The study of early tetrapods and their fish relatives is a case in point. On one side, the nearest relatives are likely to be lungfish. In terms of behavior and physiology, the African and South American genera are intuitively more similar to early tetrapods than the Australian genus, but the Australian *Neoceratodus* is considered to be the more primitive. Neither may really provide a good model because lungfishes diverged from tetrapods more than 400 million years ago, and, for example, appear to have evolved their air-breathing specializations convergently with tetrapods. They can at best be analogs on the grounds of possibly similar habitus. However, even environmental analogs may be misleading: studies of modern air-breathing intertidal fishes have suggested that the intertidal environment would have been unsuitable for the earliest tetrapods (Graham and Lee 2004), and yet increasingly, marine and lagoon environments are where the fossils are being found. There is also the possibility that coelacanths may be closer to tetrapods than lungfishes: coelacanths appear to be even less tetrapod-like in their physiology than lungfishes, and in fact have some remarkably primitive and some remarkably specialized characters. It is impossible to say whether they resemble the extinct tetrapodomorphs in any physiological respect.

For the modern tetrapod models, many people turn to salamanders as being appropriate. As far as skeletal structure is concerned, they are far different from early tetrapods, and they have some developmental peculiarities not shared by other living tetrapods. On the other hand, in features such as circulatory systems, they do seem to approach modern fishes, especially lungfishes, more closely than other tetrapods. As far as the origin of salamanders is concerned, at best, their earliest appearance is Jurassic (although they may derive from Carboniferous branchiosaurs; Chapter 9). Among amniotes, it is hard to say which group best represents a more basal form, but *Sphenodon* is often cited. Rhynchocephalians first appear in the Triassic, and *Sphenodon* does not appear to be a primitive member of this group, so its use as a model may be limited. All things considered, it is clear that the extinct phylogenetic bracket is not a lot of help in understanding early tetrapods.

Nevertheless, by looking at modern animals, some gaps in the story may be filled. For such physiological aspects of early tetrapods as respiration and excretion, a range of possibilities may be inferred from modern animals that live in similar conditions, and some insight about locomotory patterns may be gained from looking at both modern tetrapods and some fishes that use walking motions underwater. For example, the transition from a swimming to a walking mode was achieved by a robotic salamander with an electronic spinal cord (Ijspeert et al. 2007). Study of modern animals' sensory systems should provide clues about what the

nervous system of early tetrapods might have been capable of, or at least suggest ideas about what questions to ask about modern animals in order to get some useful answers. However, much more work could be done in this context. There are still more questions than answers.

## Sensory Systems

The capabilities of the sensory systems are, inevitably, governed in large part by the complexity of the brain of the animal. To judge by modern fishes and amphibians, it would seem that the brains of early tetrapods were relatively simple. Those of lungfishes are distinctly simpler than those of teleosts, but then teleosts have specializations not found elsewhere. Although the brain of the coelacanth is relatively small, its relevance to early tetrapods is hard to interpret: it has some similarities to teleosts, some to chondrichthyans, and other characters in which it is unique (Collin 2007). The braincases of early tetrapods tend to be poorly ossified internally, so that a cast of the internal spaces—an endocast—may not be helpful in interpreting brain structures. Nonetheless, by studying modern animals, some inferences to brain evolution may be made.

The brains of modern amphibians are simpler than those of amniotes; for example, they lack a definitive cerebral cortex, and the cerebellum is small (Duellman and Trueb 1986). Zakon et al. (2011) showed that the number and type of voltage-dependent sodium channels—critical factors in electrical excitablility and neuronal processing in the cell—increased several times during early tetrapod evolution through duplications of the genes that controlled their formation. They associated this with an increase in the anatomical complexity of the amniote brain, which facilitated the appearance of new tactile sensory receptors and may in turn have facilitated the onset of terrestriality.

### VISION

Considering vision, there were changes to the position and size of the eye socket, so that in general, early tetrapods have larger sockets more closely spaced than in fishes and looking as much dorsally as laterally. There was a suggestion that the increase in size may have been connected with retention of a juvenile condition. However, this is not the only change that occurred to the eyes during the transition. Tetrapods whose heads were exposed to the air for any extended periods (whether or not they walked on the land) would have experienced several factors that were far different from life in water. First, the refractive index of water is similar to that of the eyeball, but different from that of air. The refractive index of a substance is a measure of the degree to which light is bent on entering the medium from air. When the eyeball is in water, it experiences little refraction because the eye is mostly liquid with a similar refractive index to water. When the eye is in air, the light is refracted as it moves from air into the fluid of the eyeball. Second, when it is in air, the eye is exposed

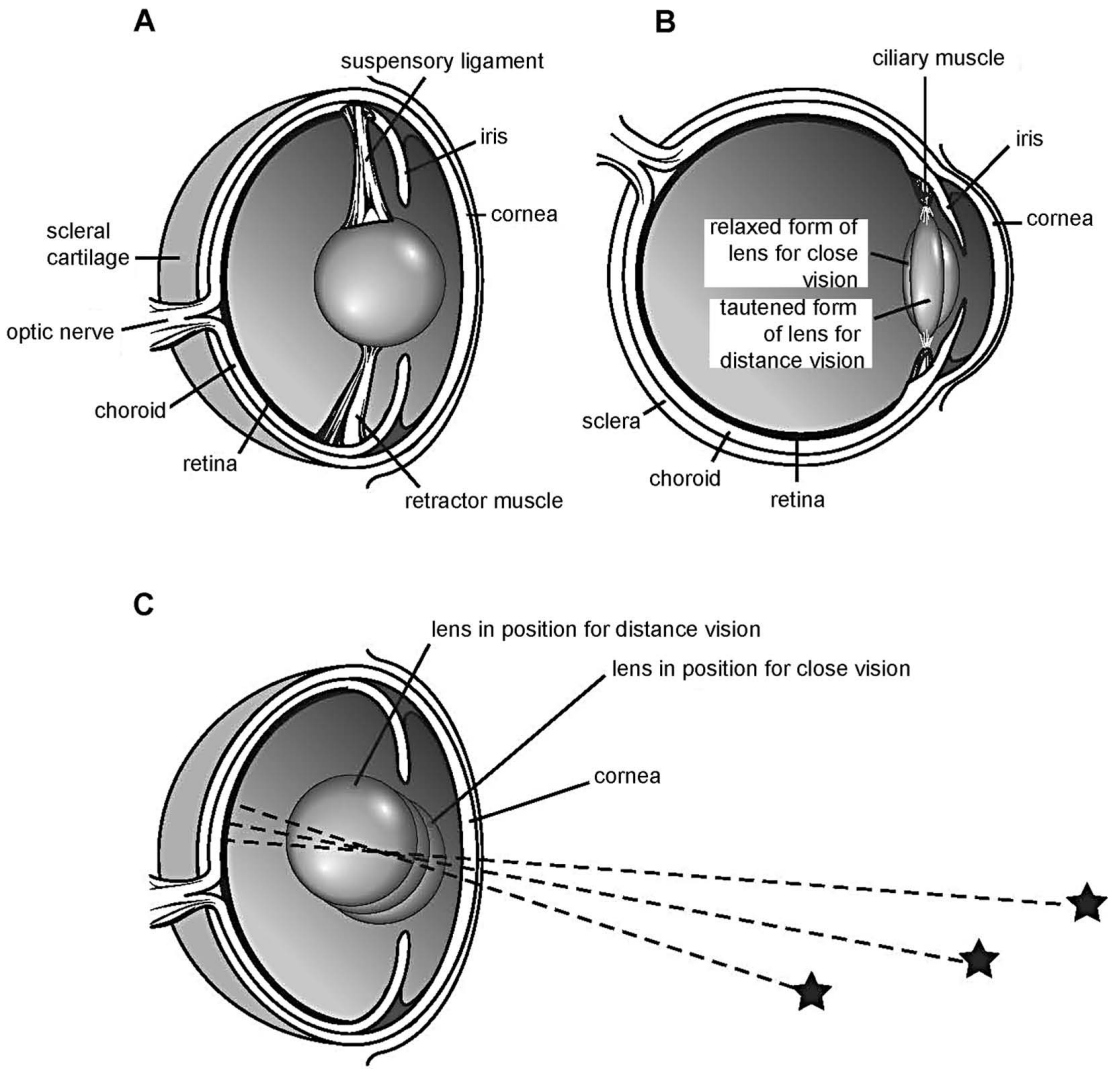
to drying conditions. However, it needs to retain its internal fluid and have a smooth surface if it is to function properly, both conditions being compromised by drying. It may also be subject to greater risk of damage from foreign bodies. Third, the transparency of air is much greater than that of water, especially turbid water or water full of organic debris, and it was in just such conditions that tetrapods may first have arisen. In air, therefore, vision can come to play a relatively more important part in the animal's appreciation of its surroundings.

These changed conditions are met by solutions that are the hallmarks of modern tetrapods, and it can be inferred that they evolved sometime during the process that produced tetrapods. In some cases, modern amphibians and amniotes have found different solutions, each of which probably arose after these two groups had split. In other cases, modern amphibians show characteristics similar to those of fishes, and many of these can be inferred to be primitive for tetrapods and so likely to have been present in the earliest forms.

Some of these differences lie in the methods of accommodation, that is, on how the lens changes its focal length to focus on images at varying distances from the animal (Fig. 6.13). Much anatomical work on vertebrate vision was published by Walls (1942), and his book still provides the standard reference for the subject. The following observations are derived from his work. In fishes, the lens is hard, incompressible, and spherical. Accommodation is brought about by moving the lens within the eyeball, though not all fishes are capable of this. The lens lies close to the surface of the eyeball, and the muscles that move it attach around the circumference of the lens. Some aquatic vertebrates such as lampreys and ray-finned fishes move the lens backward in the eyeball to accommodate to distant objects, while others, such as chondrichthyans, move it forward. Some tetrapods, including modern amphibians, also use this means in part. Lungfishes apparently have no powers of accommodation, though the condition in *Neoceratodus* is not known. It is thus quite uncertain which condition is primitive for jawed vertebrates, although perhaps the modern amphibians give us the best clue to that in the earliest tetrapods.

In amniotes, the lens is slightly flattened and compressible, and accommodation is usually achieved by muscles that change the shape of the lens while it remains stationary in the eyeball. Once in air, some focusing power can be delegated to the thickened corneal layer. As a result of this arrangement, in tetrapods, the lens can lie further back in the eye, which in turn means that it can sit behind the iris, allowing the pupil to be more flexible and to change its diameter. The reason for this is that if the fish's lens were more deeply sunk in the eyeball, without the corneal contribution to refraction, the visual field available to the eye would be restricted. Once the cornea becomes a significant refracting component, this restriction is lifted.

Changes to the shape of the lens itself in tetrapods are brought about by different means in amphibians, mammals, and all other amniotes. In amphibians, the lens is almost spherical like that of a fish,




and accommodation is brought about as in fishes by moving the lens. Muscles above and below the lens, the pro- and retractor lentis muscles, are present in frogs and salamanders, and are unique to these groups. They still use the fishlike method of accommodation but have specialized it in their own unique way. This distribution of characters can be read to imply that early tetrapods also used the fishlike means of moving the lens to accommodate the eye, but cannot help to show which muscles they used to do so.

Mammals use a different method from most other amniotes (and snakes are a special case in having a unique arrangement). In mammals, changes to the lens shape are brought about by relaxing the ciliary muscles around the eye, which reduces the tension in the suspensory ligaments supporting the lens. Most other amniotes, by contrast, squeeze the lens at its equator by contractions of the ciliary muscles, which are correspondingly large. If the last common ancestor of mammals and

**6.13.** Eye accommodation in fish and tetrapods. (A) Diagram of a fish eye in vertical section, showing spherical lens set well within the eyeball. (B) Diagram of a mammalian eye, showing compressible lens set close to the outer part of the eyeball, and the shape of the lens shown for close and distance vision. (C) Diagram of a fish eye showing how the eye moves for distance and close vision. *Adapted from Walls (1942). Illustration by J.M.*

other amniotes lived in the Mid–Late Carboniferous, this animal may not have developed either kind of amniote accommodation mechanism, but rather may still have been using the more primitive means of moving the eyeball, as in amphibians.

In amniotes such as lizards and birds, the sclerotic ring of bones lying around the eyeball plays a role in accommodation. Muscles attached on the inner surface help to squeeze the lens, but also the ring counteracts the increase in internal pressure in the eyeball that this squeezing brings about. Each plate may be flat or have its outer surface concave, and this means that the muscle is brought closer to the eyeball. Many early tetrapods, as well as many extinct lobe-finned fishes, also show this ring of plates, but here it is less clear what its role would have been, assuming they used the fishlike method of accommodation. The ring in early tetrapods is not concave but may be flat or slightly domed. Many sarcopterygians also have a similarly constructed ring, and they too presumably still moved the lens rather than squeezing it. It appears that amniotes (except mammals, where it is entirely absent) co-opted an existing feature and used it for another purpose.

Other features in which amphibians and amniotes differ can be seen in the sensory cells of the retina. Rods are the cells that respond best to light, dark, and movement, while cones are cells that respond best to color, and only work well in good light. Modern amphibians appear to retain some primitive features of their cone cells and can see some colors, but they have also evolved some unique retinal cells called green rods. Early tetrapods are likely to have been diurnal and would probably have had both rods and cones in their retinas, but perhaps they would have lacked the specializations of either amphibians or amniotes.

Tetrapods have a unique system of lacrimal glands and ducts that produce liquid to keep the eye moist and drain the fluid away again. Though sometimes it is possible to see the lacrimal duct in fossil material, there is no evidence of it in the earliest tetrapods. Jarvik (1980) suggested that it can be seen in the nasal capsules of *Eusthenopteron*, but because there is no nasal capsule in early tetrapods to compare it with, it cannot be easily checked. Tetrapods likewise have eyelids, another unique innovation connected with terrestrial life, and there is a muscle to move the eyelids that only tetrapods have. Bjerring (1987) suggested that *Eusthenopteron* had this muscle, but this depends on the interpretation of a small inpocketing in the braincase. Interpreting muscle insertions is hazardous at the best of times, but in this case, it is particularly fraught with difficulties. Other eye muscles, not unique to tetrapods, are equally likely candidates to insert in that small pocket. It is quite likely that it will never be certain when early tetrapods, or their fish relatives, evolved the eyelid or its muscles.

Another eye muscle that is unique to tetrapods pulls the eyeball down into the skull and is called the retractor bulbi. Some attempts have been made to interpret the position of origin of this muscle in early tetrapods and even in *Eusthenopteron* (Bjerring 1987), but this is made difficult

because its position in modern tetrapods is notoriously variable. Again, there are great difficulties in trying to assess whether it was present in early tetrapods.

When artists or museum curators try to make life reconstructions of early tetrapods, and *Acanthostega* is a good example, they often ask, "What kind of eyes did it have?" This is still an unanswerable question and is likely to remain so. The size of the sclerotic ring may tell something about the size of the eyeball, but not how much of the eye would have been visible in the living animal. It is not even obvious what sort of modern animal it would be best to use as a model. The eyes could have been large and prominent like those of a flatfish or frog, or they could have appeared small and relatively inconspicuous like those of a giant salamander or a lungfish. However, the large, prominent kind is associated with specialized lifestyles, and of the two styles, early tetrapods may have been more likely to have had the inconspicuous, unspecialized sort. But this is a guess.

## OLFACTION

The noses of early tetrapods show both similarities and differences compared to those of fishes. There are similarities in the openings of the nostrils but differences in the arrangement of snout bones and the state of the nasal capsule. Changes to the olfactory system seem to have happened at the transition, to judge from a contrast between living tetrapods and living fishes, and changes to the construction of the nasal capsule may have accompanied these. In fishes, the nose functions purely as an organ of olfaction, and it is not used in breathing. In modern tetrapods, and probably most fossil forms too, it is used for both. At some point during the fish–tetrapod transition, the change must have occurred. Because the nostrils—internal as well as external—are so similar between *Acanthostega*, *Tiktaalik*, and *Panderichthys*, it may be safe to assume they were doing the same job in each, namely olfaction only, though it is not obvious whether either or both were sampling air or water or both. Probably, however, sampling air chemically preceded taking it in through the nose to breathe. As has been suggested above, *Acanthostega* probably gulped air as lungfishes do, and the guess is that it did not breathe through its nose. This facility arose only later at some unknown stage during the evolution of tetrapods.

In tetrapods, there is a structure called the accessory olfactory bulb in the nasal capsule that is not present in any fishes. This structure, also called Jacobson's organ, is usually associated with detection of airborne chemical signals called pheromones, though that is not its only purpose. It is found in both aquatic and terrestrial forms, though it was once thought to be restricted to terrestrial ones (Eisthen 1992, 1998). It is possible to imagine that at the origin of tetrapods, some major change occurred to the construction of the olfactory organs, with the production of this accessory bulb, and that this coincided with the observed loss of

ossification. It may thus also coincide with increasing emersion of the snout. This organ may have been "invented" by the earliest tetrapods.

One more piece of evidence derives from examining the mechanisms by which amphibians and amniotes receive and process olfactory information. There is at least one system, that for detecting sour tastes, that differs fundamentally between modern amphibians and modern amniotes (for example, Kinnamon and Roper 1987 for the mud puppy and Gilbertson et al. 1992 for the hamster). The implication is that this system was evolved separately in the two groups, but probably sometime after the origin of tetrapods as a group.

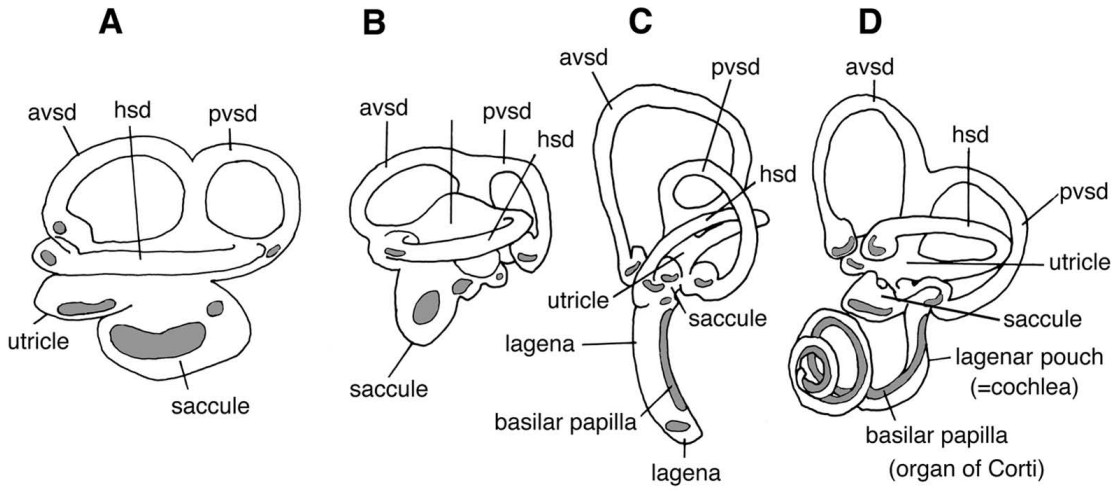
By contrast to the negative evidence on the sense of olfaction, two senses leave positive traces in the fossil record, these being the lateral line sense and the sense of hearing.

### INNER EARS

A number of differences can be seen in the soft tissue characters of inner ears in tetrapods as compared with any known fish. These concern the arrangement of pouches and the hair cells they contain. Such features of course cannot be seen in fossils, so inferences must be based on what can be seen in modern animals. Some of these differences may have been initiated at the same time as the reconfiguration of the otic region of the braincase described above.

The inner ear of all vertebrates (except lampreys) is composed of a set of three semicircular canals set at right angles to each other and filled with fluid whose movement informs patches of hair cells of movements in the body. This part of the inner ear is called the pars superior and is primarily concerned with posture control or balance in tetrapods that have gravity to contend with. Situated near the junction of the semicircular canals is a pouch called the utriculus, also part of the pars superior. Beneath this is suspended a further pouch or pouches, the sacculus and lagena, constituting the pars inferior (Fig. 6.14). A sacculus pouch is common to all vertebrates, but a separate lagenar pouch, budded off from the sacculus during development, is found in certain groups, including most tetrapods. Generally the lagena is associated with audition in tetrapods, though in teleost fishes, both sacculus and lagena may have auditory functions (Popper and Platt 1993; Collin 2007).

One of the differences between modern fishes and tetrapods lies in the structure of the pars inferior and in the contents of the sacs. Another name for these sacs is the otolithic organs. In teleosts and also in the extinct acanthodians, each of the sacs—utriculus, sacculus, and lagena—contains a solid crystalline calcium carbonate otolith, or ear stone (Schultze 1990). This rests on the hair cells in the sac and stimulates them when it is moved by gravity or sound waves. Because it has a gravistatic function, it is also called a statolith. Tetrapods and lungfishes lack solid crystalline otoliths (Carlström 1963). Instead, they have a large number of small crystallites bound together in a gelatinous matrix to form what is




**6.14.** Diagram of vestibular systems in different groups. (A) Lungfish. (B) Frog. (C) Bird. (D) Mammal. *From Romer and Parsons (1986).*

usually called a "pasty" statolith. Lungfishes do not have lagenae (Retzius 1881; Popper and Platt 1996), so there are only two of these statoliths. Pasty statoliths are rarely fossilized, and correspondingly, otolithic material has not been found in early tetrapods. By contrast, only single saccular statoliths have been found in fossil and living coelacanths even though they do have lagenae (Clack 1996).

Fossils of tetrapodomorphs show that, like lungfishes, they appear to have possessed pasty saccular statoliths but lacked lagenae, as shown in well-preserved material of *Ectosteorhachis* (Romer 1937). Lacking in their closest relatives, the lungfishes and tetrapodomorph fishes, the phylogeny suggests that the earliest tetrapods also lacked this lagenar pouch. Evidence for its existence in tetrapods only appears much later in their evolution.

In addition to differences in the otolithic composition (single crystal versus suspension of small crystals in a pasty matrix) in fishes and tetrapods, there are differences in the patterns in which the hair cells are arranged within the pouches. Though little studied as yet, it seems that, despite the fact that both groups possess lagenae in contrast to lungfishes, coelacanths resemble the more primitive ray-finned fish pattern in their hair cells rather than that of tetrapods (Platt 1994).

Lungfish lack any of the specialized inner ear receptors for processing sound signals that are seen in tetrapods, and that are also seen, independently derived, in teleost fishes (modern ray-fins). In tetrapods the main sound receptor is called the basilar papilla and is situated in the lagena. Fritzsch (1987) found a patch of cells in the coelacanth lagena that he considered to be a homologue of the tetrapod basilar papilla, that is, a feature derived in common in tetrapods and coelacanths, rather than as a parallel development (Fritzsch 1992). However, no experiments have been done on living coelacanths to confirm or refute whether the cells could respond to sound in the same way as in tetrapods. Conclusions

of homology would normally be based on more extensive studies of relationship (see Chapter 3).

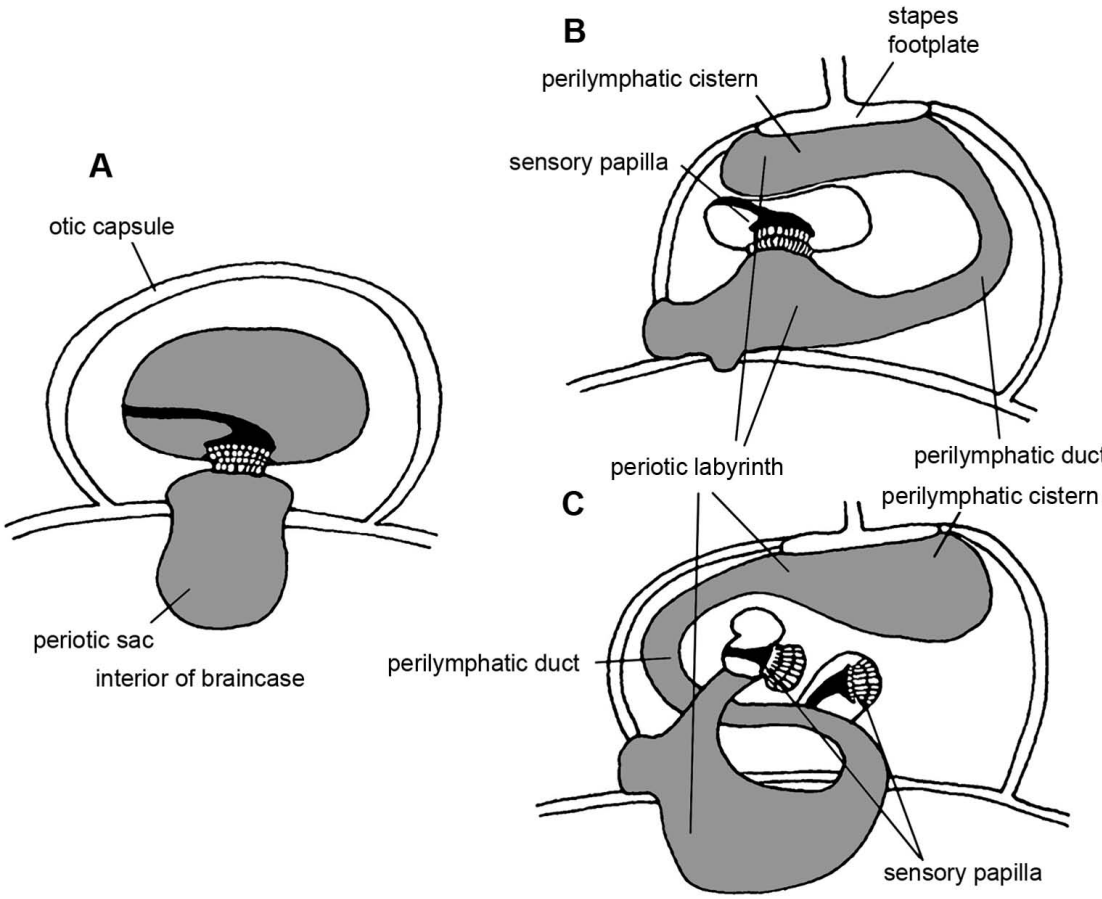
Another difference between tetrapods and all fishes relates to the way the inner ear pouches are suspended in the inner ear cavity. The fluid inside the inner ear itself is called endolymph, but the system is suspended within a chamber and surrounded by fluid called perilymph. In fishes, this is contained in a simple periotic sac, but in tetrapods, the perilymphatic space is organized into a system of tubes and sacs that run round and about the pars inferior (Fig. 6.15) (see Fritzsch 1992; Duellman and Trueb 1986). There is a main chamber called the perilymphatic cistern that is confluent with the periotic sac. They are connected by a tube called the perilymphatic duct. There is no way to know whether early tetrapods had the simple fishlike condition or the more complex one found in modern tetrapods, but it is clear that modern amphibians and modern amniotes have different arrangements from one another (Lombard and Bolt 1979). In amphibians, the duct passes posterior to the sacculolagena complex containing the sensory papillae (Fig. 6.15), but in amniotes, it passes anterior to it. These two conditions appear to be mutually exclusive. The implication is that each has been derived independently from a fishlike condition, so that the simple fishlike arrangement might still have been present in the earliest tetrapods. If so, the profound changes to the otic region of the braincase that occurred during the fish–tetrapod transition preceded rather than accompanied those to the inner ear.

Evidence from fossils preserving the bones surrounding the inner ear of the dissorophoid temnospondyl *Doleserpeton* (see Chapter 9) has shown that its perilymphatic duct took the amphibian route (Sigurdsen 2008). The possibility cannot be ruled out that this condition is primitive for tetrapods.

The middle ear and the evolution of tetrapod hearing mechanisms are described in more detail in the final chapter. Here, suffice to say that *Acanthostega* does not appear to have evolved some of the refinements that in later tetrapods are seen to be those associated with the reception of airborne sound, nor does it appear to have had the inner ear and brain structures associated with processing and interpretation of the signal. For a model of its hearing capabilities, the other living lobe-fins as well as the more primitive ray-finned fishes seem to provide better models than do modern tetrapods. A recent study of lungfish hearing suggested that they could receive low-frequency, substrate-borne sound, but not airborne sound, as suggested for early tetrapods (Christensen-Dalsgaard et al. 2011).

### LATERAL LINE SYSTEM

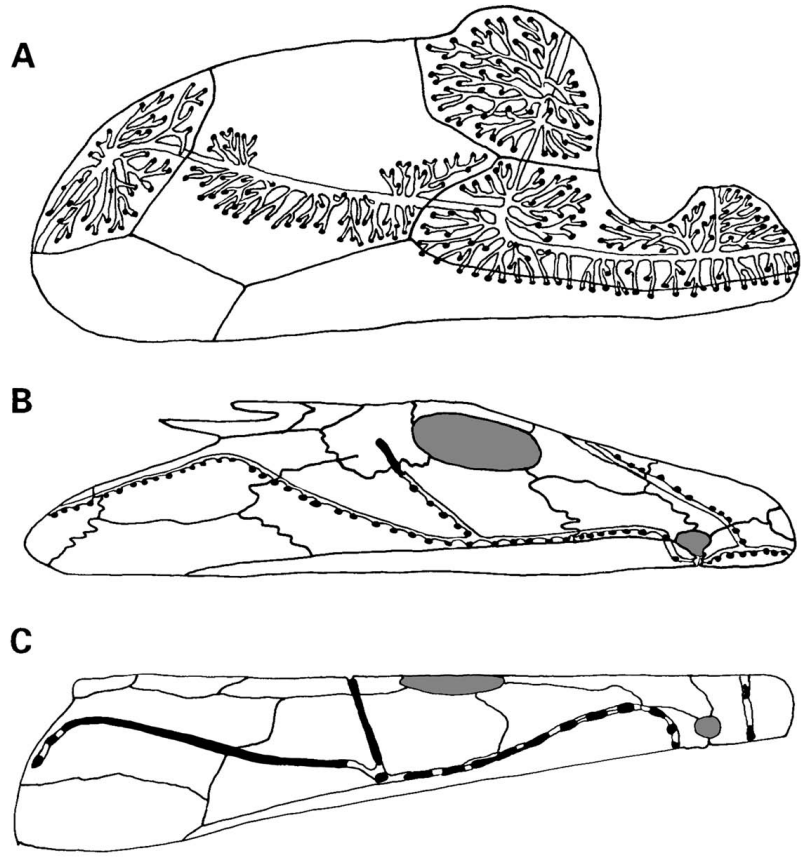
The lateral line system is one that, as mammals and members of the amniote group, humans are not well equipped to understand. Amniotes have lost all trace of the lateral line system, and people do not even have the language to describe the sensations that it must produce. The system consists of a tracery of tubes or canals running within or on the surface




**6.15.** Diagram of perilymphatic systems in (A) *Latimeria,* (B) amniotes, and (C) amphibians.

of the dermal bones or skin (Fig. 6.16). The canals or tubes are open to the outside and are filled with water, so the contents are affected by movement and pressure changes in the surrounding water. Inside them lie sensory hair cells or neuromasts, tipped by hairlike cilia, whose movements trigger nervous impulses. As they are moved around by pressure waves from the water, they send signals to the brain. This system can detect pressure changes in water up to about a meter or so away from its owner's body, and can inform the brain of the direction and size of the object that has created the pressure changes. The lateral line system can detect vibrations of up to about 1 Hz, whereas the inner ear responds to those above about 35–50 Hz. Although in the past there has been a suggestion that the inner ear somehow derived from the lateral line, this is not now accepted. They appear to be nonoverlapping systems though they both use hair cells (Collin 2007).

As a rule of thumb, in fossil lobe-finned fishes, the lateral line canals of the head lie within tubes in the dermal bone, opening by a series of pores to the outside. *Eusthenopteron* has a complex ramifying system of tubes with multiple small openings in wide bands on the bone (Jarvik 1980) (Fig. 6.16A). The system, as exemplified by coelacanths, becomes




**6.16.** Diagram of lateral line expression in different groups. (A) Cheek of *Eusthenopteron* showing numerous pores in a network connected to the lateral line canals within the bones. *From Jarvik (1980).* (B) Skull roof of *Acanthostega* in lateral view showing the single row of pores connected to the lateral line canal. (C) Skull roof of *Greererpeton* in lateral view showing most of the lateral line canal as open grooves (openings shown black). *From Smithson (1982).*

more elaborate as the animal grows, with the number of pore openings increasing and the tracery of the tubules becoming more racemose. *Panderichthys*, *Tiktaalik* and *Acanthostega* have a simpler system (Fig. 6.16B), and in each, a single series of somewhat larger pores can easily be seen. In most later tetrapods, by contrast, the lateral line canals run in open grooves on the surface of the skull (Fig. 6.16C). Although in the more primitive forms of tetrapod some of the canal's length may still be enclosed in the bone, it seems to be the case that most tetrapods show the open condition of the grooves, or no grooves at all. What the difference signifies is unknown. It is known that in modern animals, the lateral lines start as superficial structures and gradually sink into the skin or underlying bone as the animal grows. Thus, open grooves gradually become enclosed into tubes. The elpistostegalian fish, early tetrapods with fewer pores and later tetrapods with open grooves may be showing successively more pedomorphic conditions. It is possible to see among modern ray-finned fishes that some have enclosed neuromasts while others have superficial ones in the outer skin, but there seems to be no consistent explanation of this in terms of ecology (Webb 1989). It may relate to the amount of water movement or the water depth that the fish generally lives with, but this is by no means certain. So the differences among the

fossil animals can only be guessed at. There may be an ecological signal to be read here rather than a phylogenetic one, but more work needs to be done not only on fossil forms, but also on living ones.

There is a further possibility. As with certain teleost fish that have multiple lateral lines, not all the apparent lines contain neuromasts (see Chapter 3 on rhizodonts). It could be that the grooves seen on the skulls of Paleozoic tetrapods did not always house neuromasts either.

One thing is quite certain, however, and that is that the amniote lineage lost its lateral line system during the course of evolution. A whole region of the brain and some large nerves that served the lateral line system disappeared in amniotes. It is not clear whether the nerves and brain region were redeployed for other sensory input, or whether the structures atrophied (Fritzsch 1989). Nor is it known whether the loss of the lateral line system occurred suddenly at the origin of amniotes or bit by bit during their very early evolution. Modern amphibians do retain superficial lateral line organs (though not grooves) while they are tadpoles, and these are retained in perpetually aquatic forms (Fritzsch 1989). However, those that are predominantly terrestrial as adults lose the lateral line system at metamorphosis. No modern amniote shows any evidence of the lateral line system even in the egg stage, but whether this applied to the very earliest amniotes of all, those of the Late Carboniferous (see Chapter 9), remains a mystery. An analogous system has been discovered in aquatic crocodiles (Soares 2002), but these do not use hair cells and are innervated by a different nerve from the lateral line.

In many fishes, the lateral lines continue down the sides of the body borne by a row of specialized scales. No tetrapod gastral scales are known that carry such lateral line pores, though like modern aquatic amphibians, the lateral lines may have been carried down the body in the skin, so the presence of a trunk lateral line in early tetrapods cannot be ruled out.

### PINEAL ORGAN

The skulls of many fishes and tetrapods from the Paleozoic have a foramen situated in the center of the skull table, called the pineal or parietal foramen (Figs. 5.21, 6.2, 6.5). Some modern amphibians and reptiles have a similar hole, though by no means all. The hole houses the pineal organ, which in mammals is closely allied to the pituitary gland. In most nonmammals, the pineal is a separate organ from the pituitary, and in lizards, it is known to have a role in monitoring day length and in controlling the animal's daily and longer-term rhythms. It has also been shown to be sensitive to polarized light in salamanders, so that the animals can tell the direction of north and south, useful in migrations (Taylor and Adler 1978). In tetrapodomorph fishes, the hole is as a rule rather smaller than that in Devonian or Carboniferous tetrapods, where it can be a conspicuous feature. On the other hand, it is lacking entirely in some later tetrapods such as turtles. Even in modern tetrapods such as birds and lizards where there is no foramen, however, the pineal organ can

still function to monitor day length. It has been shown that in birds, light can penetrate to and stimulate the pineal either via the eyes, or directly (Barrett and Underwood 1991). Judging from the size of the foramen in early tetrapods, it may have been functioning differently in them from the way it was in fishes, and its size may reflect the fact that exposure to daylight was more important.

### OTHER MECHANORECEPTORS

Other receptors are found in the skin and muscles of modern tetrapods, such as stretch receptors and proprioceptors, for telling the brain the position and attitude of the limbs, for example. Fishes and tetrapods have proprioceptors in the paired appendages for informing the brain of what these are touching and their position, but most tetrapods also have receptors in the muscles, known as muscle spindles, that are not present in modern ray-finned fishes (Barker et al. 1974). However, there are simple branched sensory endings, something similar to muscle spindles, apparently found in the fin musculature of rays and lungfishes, as well as in the connective tissue at the base of the walking fins of the gurnard. Presumably there was a type of nerve ending found in the bodies of primitive vertebrates that has been variously adapted and developed in different groups. Muscle spindles are also apparently absent in newts, and it is not known whether caecilians have them or not. In frogs, these spindles are only present in limb and abdominal muscles and are absent from axial muscles. Muscle spindles have been closely studied in mammals and frogs, and in both of these groups, they are highly specialized. Mammals seem to have the most highly developed system of muscle receptor types of all tetrapods, while in frogs, the muscle receptors are particularly well developed to control the leg muscles, important in the jumping abilities of the animals. The spindles in amphibians and amniotes apart from mammals are supplied with two types of nerve endings, known as grape endings and plate endings, that may therefore be assumed to be the common inheritance of all tetrapods that have then been modified and specialized in mammals (Barker et al. 1974). Possibly these two types were developed early in tetrapod history at the time when legs were acquiring an increasingly important role in locomotion.

Much research into sensory systems and physiology in the past was dedicated to the basics of finding out how things worked and to the demands of medical application. This means that work has concentrated on mammals and on a few other easily available laboratory animals such as frogs and chickens. More recently, a broader range of animals has been studied, and the perspective of phylogeny and evolution has brought new questions that have shown how rewarding it can be to investigate other animals, such as nonteleost ray-finned fishes, lungfishes, and an even wider range of tetrapods.

Unfortunately, some of the most phylogenetically and evolutionarily interesting animals are difficult or impossible to rear in laboratory

conditions, the coelacanth being a prime example. However, a breeding program for the Australian lungfish has produced some exciting and revealing results (Joss and Joss 1995; Johanson et al. 2007b). A possible research program for the future might ask what sensory equipment an early tetrapod might have had, judging from what is present in their closest relatives, more primitive fishes, and what is most widely distributed among different tetrapod groups.

## Physiology: Breathing, Respiration, Excretion, Reproduction

### BREATHING AND RESPIRATION

One problem that early tetrapods might have faced was that of desiccation. If the climate was humid, this was not such a great problem, but there may have been a conflict of pressures to be met in any case with respect to the scaly armor of these pioneers. To make more efficient progress over land, it might have been an advantage to reduce weight by losing the body scales. On the other hand, to avoid the drying effects of air, it might have been advantageous to have kept them. The earliest known tetrapods had lost their dorsal scales but kept their belly scales, although several groups of later tetrapods produced dorsal scales again. Belly scales might have protected the undersides from abrasion or assisted them in keeping the body shape during movement, but loss of the dorsal scales would have meant that the part of the body most frequently lifted out of the water was most exposed to drying out. An alternative suggestion for the loss of dorsal scales was that when wholly or partially out of the water, this part of the body could be engaged in cutaneous gas exchange, or skin breathing.

In the past, it has been stated that early tetrapods had skins that were too thick and heavily ossified for any cutaneous gas exchange to have taken place through it. Not only that, but it was suggested that, being large, the surface-to-volume ratio of these animals was too poor to allow efficient use of cutaneous gas exchange. These ideas were put forward around 1970 (Gans 1970; Romer 1972a) but have been accepted by many recent physiologists trying to work out how early tetrapods breathed (Ultsch 1987). It is time to look again at the possibilities (e.g., Janis and Keller 2001), because some of the statements made about early tetrapods a few decades ago were based on several assumptions that have led to sources of error. First, they were based on theoretical properties of gas and skin, rather than on experiment and observation of living forms, and second, they were based on a view of early tetrapod structure that was limited and has been changed by recent discoveries. Third, the idea that the composition of the atmosphere might have been different from today had not then been put forward (see Chapter 4). Finally, there seems to be no real reason why early tetrapods should not have used all possible means of breathing; they might have used lung as well as skin breathing employing not just the outer body surface, but also that of the buccal

cavity. It is known that the palate of *Ichthyostega* bore large blood vessels running over it (Jarvik 1996), which may indicate a rich subcutaneous blood supply.

One of the main objections to the idea of skin breathing in early tetrapods was their possession of gastral scales over the belly and the evidence of dorsal bony scales in others. However, the gastral scales, as well as the dermal bones of the skull and shoulder girdles of early tetrapods, were dermal in origin and so had blood vessels running through them to the epidermis that lay external to bones and scales. Pores in the bones and vascular spaces throughout the bone are evidence of this (Bystrow 1947). Grooves for blood vessels are sometimes visible as well, but even without this, the structure and tissue relations of the dermal bone imply that epidermal tissue lay external to the bone. This means that capillaries carried blood close to the surface, where it could have received oxygen. The thickness of the epidermis is unknown (but see Witzmann et al. 2010 for a contrary view), of course, but in the case of heavily ornamented dermal bone, it may have followed the ornament pattern quite closely, and where the ornament was reduced, skin folds may have hung from it, as suggested for *Crassigyrinus* (see Chapter 7).

The scales were not similar to the cosmine-covered ones of primitive tetrapodomorph fishes in that they were not covered in enameloid of any kind, and in this sense they were not unlike the thinner scales of other tetrapodomorphs such as *Eusthenopteron*. By contrast, the skin of an early tetrapod was not like that of a modern amniote either. Amniotes have incorporated a keratin protein into their epidermis; in most amniotes, this is beta-keratin, while mammals have alpha-keratin in addition. This forms epidermal scales, fur, and feathers. Dinosaurs, crocodiles, or lizards with scaly skins, as well as mammals and birds, are effectively waterproofed. Despite this, however, studies on recent amniotes (Feder and Burggren 1985) have shown that even something as armored as a turtle exchanges 30% of its $CO_2$ and 20% of its $O_2$ through its skin (some of this in fact occurs through the cloaca and may not be comparable with the situation in other tetrapods). Similarly, lizards and snakes also perform a substantial part of their gas exchange through the skin, using the thin skin between the scales to do so (Feder and Burggren 1985).

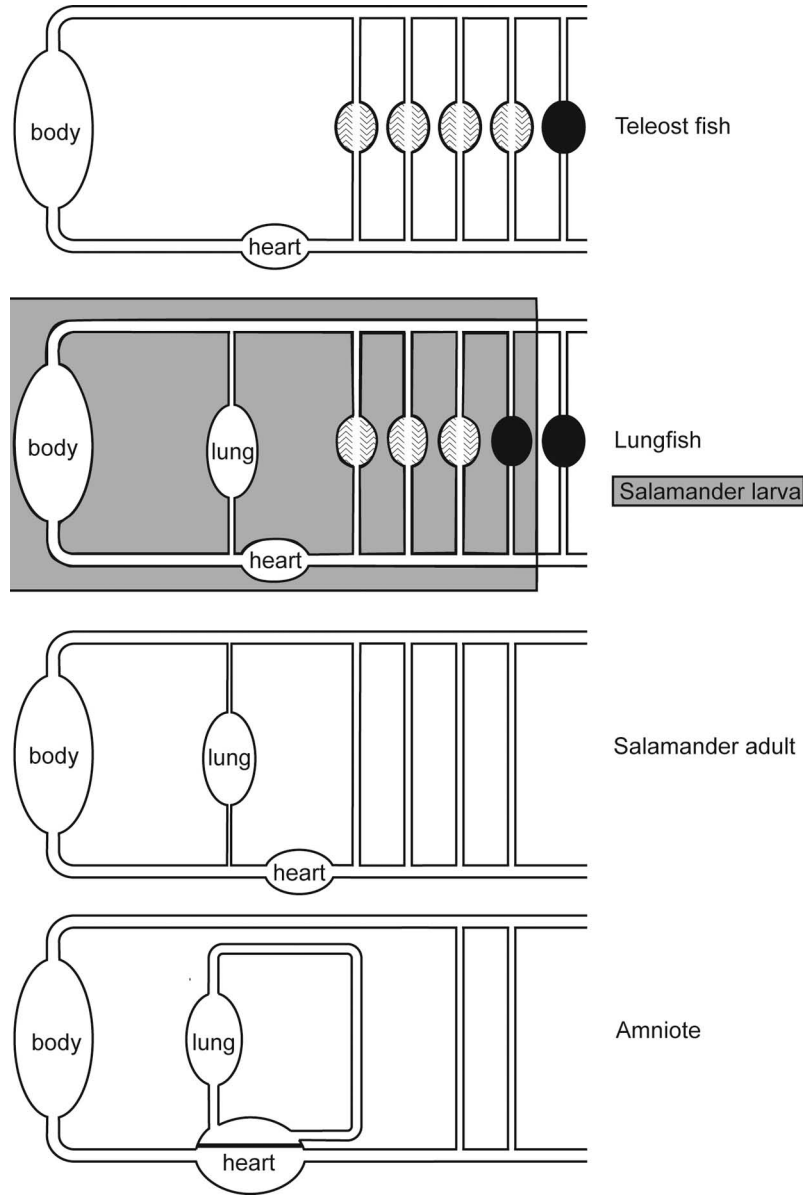
At the other end of the spectrum, the heavily enameled scales of the fish *Calamoichthys* do not prevent it from using its skin for about 30% of its gas exchange, though most of this might be involved with superficial servicing of the skin and scales. The large modern amphibian known as the hellbender (*Cryptobranchus*), a permanently aquatic form, also uses its skin for up to 90% of its gas exchange (Feder and Burggren 1985).

Since the first edition of this book, estimates of atmospheric composition, and the levels of oxygen in particular, have changed considerably. The emergence of tetrapods now has to be seen in the context of lowered oxygen levels in the Middle through the Late Devonian and even into the Early Carboniferous. Oxygen might well have been at more of a premium than previously realized, in which case it seems highly unlikely

that early tetrapods failed to exploit every possible means of taking up this vital resource, however theoretically inefficient. Furthermore, the metabolic rate of the animals is of course unknown, but it may not have been as high as that of modern tetrapods. A scenario linking low oxygen levels with the origin of the air-breathing specialists in the tetrapod stem group has been explored in Chapter 4.

Carbon dioxide metabolism might have posed more of a problem for early tetrapods than oxygen uptake. Accumulation of $CO_2$ in the body is more often a limiting factor in vertebrate physiology than lack of oxygen. With the higher levels of $CO_2$ in the air in the Devonian and Early Carboniferous, diffusion from body surfaces may have been more difficult than in today's atmosphere. However, if they maintained a high level of $CO_2$ in the blood, the gradient between body and air might still have allowed diffusion to take away the $CO_2$, provided the skin could stay moist. $CO_2$ is as easily dispersible in air as it is in water. Modern air-breathing fish provide a possible model here because they can tolerate quite a high level of $CO_2$ in the blood, more comparable with amniotes than modern amphibians or non-air-breathing fishes. They often live in water that has a high $CO_2$ content as well as low oxygen content (Randall et al. 1981). It has been suggested that early tetrapods, living in vegetation-choked environments, might have used a mode of $CO_2$ metabolism similar to these fish and thus have been preadapted to make the transition to land (Ultsch 1987). Most modern fishes get rid of excess $CO_2$ from the gills and skin, though few studies have been done to find whether or what proportion is excreted through the skin as distinct from gills. Some air-breathing fishes such as *Amia* do excrete a small proportion of $CO_2$ though their air-breathing organ (Brauner and Berenbrink 2007) and modern amphibians' lungs are likewise responsible for some, though only a little, $CO_2$ excretion. The ability to deal with $CO_2$ is important in the stabilization of body fluid acidity. The ability of lungs to cope with this function seems to have been fully accomplished in the amniote lineage only, though again, it must remain unknown at what point in the evolution of the group it evolved. Early tetrapods with gills such as *Acanthostega* may well have continued to use them for $CO_2$ loss. As the $CO_2$ levels fell during the Late Devonian and Early Carboniferous, it may have become less and less of a problem.

Nothing is known about the circulatory systems of the earliest tetrapods. In modern amphibians, much of the system is devoted to supplying the skin with blood for gas exchange, and modern amphibian skin is rich with blood vessels for this purpose, as well as glands to keep it moist. It is also much thinner than that of any amniote. Amphibians appear to have specialized in cutaneous gas exchange, elaborating a primitive mechanism into something more sophisticated. Early tetrapods were probably much less specialized in this respect, using skin breathing as only part of their repertoire. Salamanders, with the most fishlike circulatory system among modern tetrapods, and lungfish may provide clues about the circulatory system of early tetrapods (Fig. 6.17). This is despite the fact




**6.17.** Diagrams of the circulatory systems of a teleost fish, a lungfish, salamander larva and adult, and an amniote. The functional gills are shown wavy-hatched, nonfunctional gills black. In the teleost, there are four functional gills and a simple circulation from the heart, through the gills to the body, and back to the heart. In lungfish, there are three functional gills and two nonfunctional gills. In some, the blood from the body and the lung are partially separated (not shown). In the salamander larva, three functional gills have external filaments. These are resorbed in the adult and gas exchange occurs in the lungs and/or the skin. In amniotes, the blood to the lungs and body are kept separate so as not to mix oxygenated and deoxygenated blood. Early tetrapods may have had a circulatory pattern like a lungfish or salamander.

that one large group of salamanders has lost its lungs altogether, relying entirely on cutaneous gas exchange. However, these animals are all small creatures, and it is not likely that early tetrapods went to this extreme.

The circulation of a lungfish, a salamander, or indeed some amniotes uses a three-chambered heart with two auricles and a single ventricle. The system is unlike that of a mammal, in which the ventricle is also divided, to separate off the lung circulation from that to the body. By this means, in mammals, oxygenated blood is completely isolated from deoxygenated blood, and this is generally supposed to be more efficient than that of amphibians. However, because the single ventricle of an amphibian receives oxygenated blood not only from the lungs but also

from the skin, the system is not as inefficient as it appears at first sight (Fig. 6.17). If early tetrapods also had a three-chambered heart and used skin breathing as well as lungs, the system might well have worked in a way that was good enough.

More clues to the physiology of early tetrapods have come from study of air breathing in lungfishes and the so-called primitive ray-finned fishes such as *Polypterus*, *Lepisosteus*, and *Amia*. It is possible to get some ideas from them about the means of respiration in the earliest tetrapods and the circumstances under which air breathing took over from gill breathing. Because these cladistically primitive ray-finned fishes and lungfishes breathe air using lungs, lungs are usually assumed to have been present as a primitive feature in all bony fishes (see Chapter 2). *Lepisosteus* and *Amia*, for example, use mainly gills in low-temperature waters, but when the temperature rises, the percentage of oxygen taken up by the lungs increases dramatically, from about 25% to up to 75%. Early tetrapods probably evolved in warm waters. Even at higher temperatures, however, in these modern fish, the gills and skin remain the main site for $CO_2$ excretion (Randall et al. 1981).

In lungfishes, the dependency on oxygen from the air increases with age and size of the individual. Small, young animals seem to get all their requirements from the water, though where oxygen is in poor supply, they will often congregate at the water's surface (Randall et al. 1981). Lungfish do have some capacity for $CO_2$ exchange by the lungs, and they use this capacity during estivation. They also have hearts and circulatory systems very like those of amphibians (Fig. 6.17), and they have an epiglottis used to separate air and food passageways. In these respects, they probably make good analogs for early tetrapod soft anatomy, even though they may have achieved them convergently.

In practice, it appears that in addition to a function in gas exchange, the lungs of lungfish, and for that matter *Cryptobranchus*, operated also as a buoyancy aid, not unlike that of the swim bladder in some fishes (R. G. Boutilier, personal communication). Perhaps all these Devonian bony vertebrates, including the fishes like *Eusthenopteron*, had an all-purpose gas bladder, useful both as a lung and a swim bladder. Coelacanths certainly have, and had, gas bladders, and although they are used for buoyancy control rather than air breathing in modern and some fossil genera, their purpose in early coelacanths is not known. They do possess a pulmonary circulation with some similarities to that of lungfishes (Millot et al. 1978).

Early tetrapods almost certainly used a form of buccal pumping to ventilate their lungs, rather than using ribs in the way many amniote groups do. This is another idea that has been disputed by earlier workers, but again, it depends on views of early tetrapods that are oversimplified or have recently been proved wrong. Part of the argument concerns the structure of the ribs. This problem will be dealt with further in Chapter 10, when more of the animals that come into the equation have been described.

**6.18.** (A) Diagram of the body-wall muscles of a salamander to show which occur in which vertebrate groups. (B) Cladogram with ventilation mechanisms superimposed. *From Brainerd et al. (1993).*

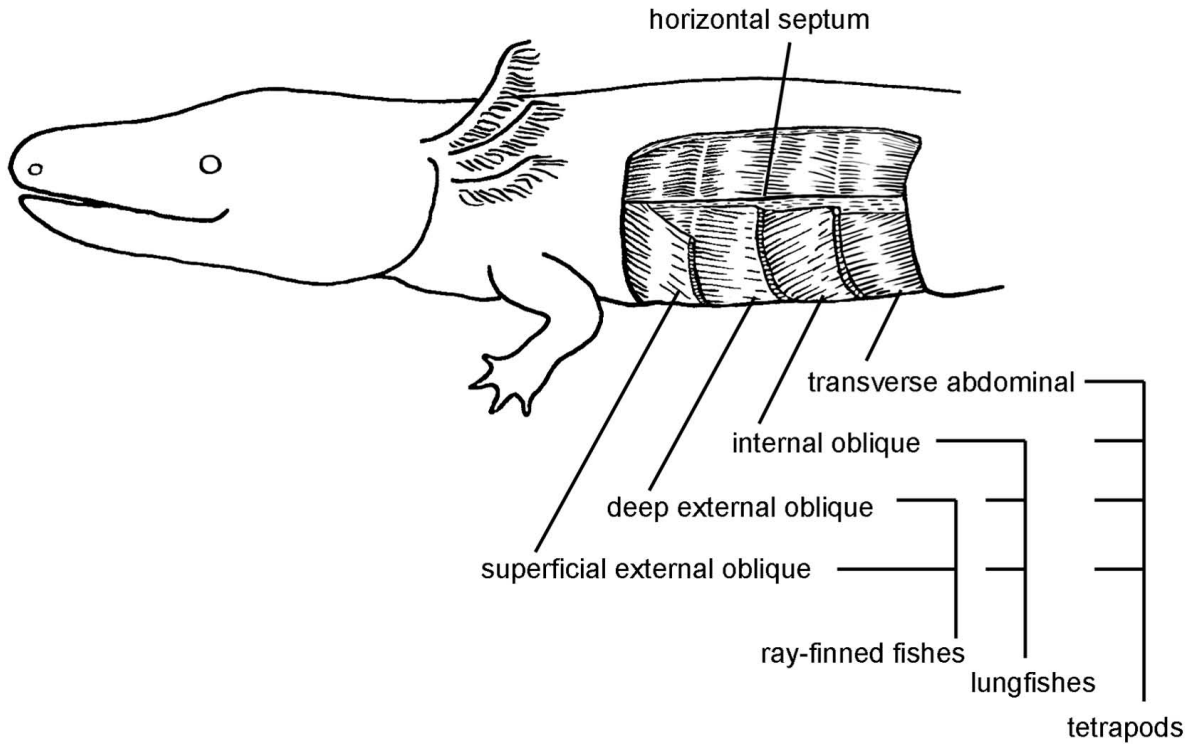
The loss of the operculogular system by even the earliest tetrapods and in *Tiktaalik* may relate to the buccal pumping mechanism, allowing a larger and more flexible gape for this purpose. Other groups of air gulpers, for example the lungfish, have similarly reduced or lost the operculogular series, and this seems to be related to the changed emphasis from lateral movements of the cheek to ventral movements of the buccal floor. Lungfish have the braincase fused to the palate, another factor that may correlate with air gulping. In many groups of later tetrapods, the palate and braincase likewise become solidly attached to each other, that is, they had autostylic jaw suspension like lungfishes. The flattened, broad heads of early tetrapods may have provided a greater area for movements of the buccal floor, as well as a large surface area for gas exchange.

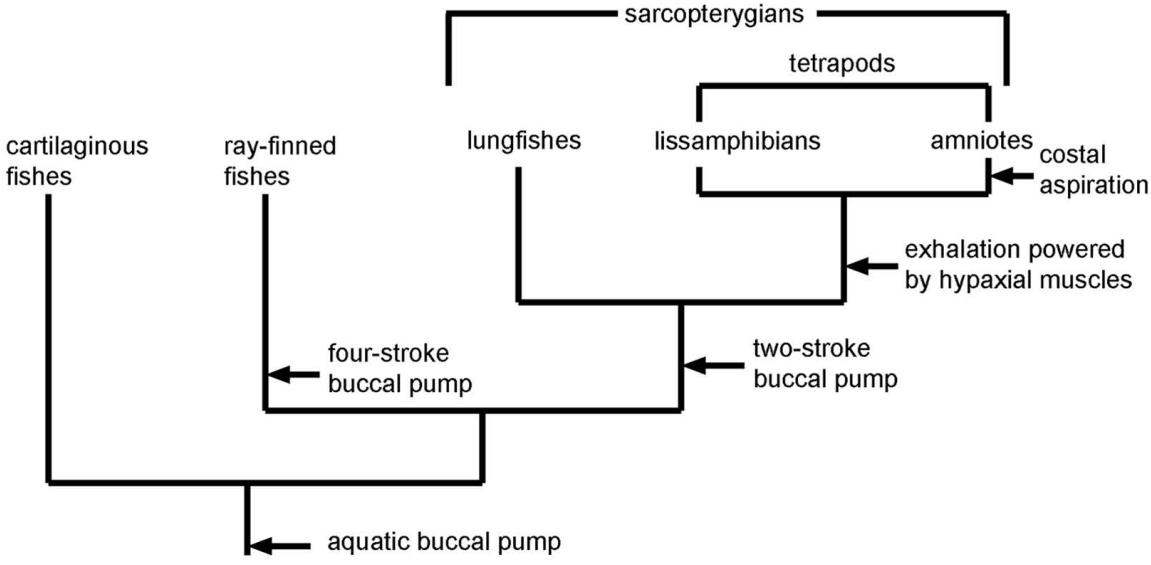
Lungfishes, salamanders, and frogs all use a form of lung ventilation called mixed-air buccal pumping. It appears to be primitive for tetrapods and does not involve the use of ribs. Comparing this mechanism in salamanders and lungfishes reveals some differences in the way that it is brought about, and it shows another character by which tetrapods differ from other vertebrates. Tetrapods have an extra layer of muscle in the body wall called the transverse abdominal muscle, and it is used in expiration (Brainerd et al. 1993) (Fig. 6.18). Contraction of this muscle helps to force air out of the lungs, and it is found in amniotes as well as amphibians. It will probably never be known when in history this extra muscle evolved, or whether it would have been present in early tetrapods such as *Acanthostega*.

Mechanisms of inhalation vary between amphibians and amniotes. In amphibians, inhalation happens by passive recoil of the lungs and abdomen when the muscles are relaxed, but in amniotes, another suite of muscles is used. It has been suggested that ventilation of the lungs in air-breathing tetrapods evolved in three stages. The first stage would have used pure buccal pumping; the second stage used muscles only for exhalation; and the third stage, reached only in amniotes, used muscles for both exhalation and inhalation. This is expressed in the cladogram in Fig. 6.18 (Brainerd et al. 1993). In some amniote groups, the inhalatory muscles were helped by the ribs, but different amniote groups use their ribs in different ways, or in some cases, such as turtles, not at all. The implication is that the specialized use of ribs in breathing evolved separately in different amniote groups.

### NITROGEN EXCRETION

Understanding the physiology of nitrogenous excretion, like respiration, among early tetrapods can be done best on the basis of what can be seen among modern animals. Neither function is directly reflected in skeletal anatomy. There are big differences between modern fishes and tetrapods in the metabolism of nitrogenous waste. In tetrapods, nitrogenous waste is almost exclusively processed by the kidney and is voided either as urine or a uric acid paste. In fishes, this is not the kidney's main function, which




is osmoregulation, although in a few fishes, it is responsible for a small proportion of nitrogen excretion. Its main function in fishes is to maintain the salt balance of the blood, while nitrogenous waste is processed and excreted mainly by the gills, with a small proportion excreted through the skin. In most modern ray-finned fishes, ammonia is the main excretory product, but some can produce urea instead (Walsh 1997; McKenzie et

al. 1999), especially those that are exposed to air on a regular basis, or those that live in water high in $CO_2$, and some even use quite different methods of dealing with ammonia and convert it to glutamine on exposure to air (Jow et al. 1999). Among those that do produce urea, the kidney can play a small part in nitrogen excretion via an active transport system, though this is always done when the fish is in water and not on land, as far as is known. Mudskippers have quite a high tolerance for ammonia, as do lungfishes. The latter produce urea especially while estivating, but it is not known where it is excreted, though it may be through the skin. There appears to be a correlation between ammonia and hypoxia tolerance in fishes, suiting them to adverse conditions (Wright 2007), a situation that might well have applied to early tetrapods. In modern amphibians, nitrogenous waste is excreted as ammonia via the gills (if present) and skin while the animals are in water, for example as tadpoles, but they convert products to urea and excrete them through the kidneys when on land (Wright 1995).

Gills were presumably the primitive site for excretion of nitrogenous waste. As for the excretory products, while the production of ammonia is easy for an aquatic animal because it is easily soluble in water, production of urea is also probably a capacity that was found widely among ancient vertebrates. The enzymes for doing this are found in invertebrates, chondrichthyans, and coelacanths, as well as some teleosts (Wright 1995). Little work on this matter has been done on primitive ray finned fishes such as *Polypterus* or *Lepisosteus*. For early tetrapods that lived in water high in $CO_2$, and that were to some degree exposed to the air or breathed air routinely, production of urea was probably the preferred option.

During early tetrapod evolution, the kidney acquired the capacity to process the urea and void it, though it was probably a rather gradual process. At first, as in modern air-breathing fish, the animals probably accumulated urea until they returned to water where it was lost, some via the gills, some via the kidney, and probably some through the skin (Walsh 1997; Wright 2007). Early tetrapods like *Acanthostega* that retained gills may have used them for nitrogenous excretion as in fishes, but quite possibly, *Acanthostega* may have already begun to use its kidney in addition.

Janis and Farmer (1999) suggested that if early tetrapods like *Ichthyostega* and *Tulerpeton* had really lost their gills, their ancestors must have been more terrestrial than these descendants were (gill bars have subsequently been discovered in *Ichthyostega*, but the argument may still apply to other taxa). The basis of this argument is that no modern fish, even an air-breathing one, uses its kidney to excrete nitrogen on land. Fish may retain gills for this purpose as well as for excreting $CO_2$ on their return to the water. It remains true that not many fishes have been studied in this context, however. Thus, gills were considered too valuable to lose in an aquatic animal. The argument runs that an early tetrapod that had lost its gills completely would only have done so if the kidney was already being used for its entire nitrogen excretion, and that this would only happen on land. However, because some modern fishes do use kidneys for part

of their nitrogen excretion, it may be that air-breathing early tetrapods used the kidneys to some extent in this way. They may have adopted this role gradually, along with reduction of reliance on gills for breathing, but while the animals were still aquatic. In any case, the evidence for lack of gills in early tetrapods is based entirely on negative evidence. Gill bars are cartilaginous in lungfishes and may have been so in early tetrapods like *Tulerpeton*, for which there is no evidence of gill bars.

## REPRODUCTION

It is usually assumed that early tetrapods had what is called an amphibious lifestyle. That means that they would have laid their eggs (many small ones, like frogs) in water, the eggs would have hatched into aquatic larvae that would probably have had external gills, and then at some stage, the larvae would have metamorphosed into the adult form. This is the kind of lifestyle seen today in many frogs and salamanders, and it is also seen in a diverse range of fishes. The lungfishes *Protopterus* and *Lepidosiren* as well as the ray-finned fish *Polypterus* use this strategy. Until the rise of cladistic or phylogenetic methods of classifying animals, the modern lissamphibians were defined as amphibians because they showed this lifestyle, and early tetrapods were also called amphibians because they too were assumed to have used it. If it is believed that the amphibian style of life history was present in the ancestors of tetrapods and that early tetrapods inherited it, of course that can no longer be used to define a group Amphibia because it is more generally distributed than just among amphibians. That is one problem, but not the only one.

For most of the early tetrapods there is no evidence concerning reproductive strategies, so that the froglike reproduction and metamorphosis is an assumption. Another problem is that reproductive strategy among modern animals is intimately connected to ecology. An animal may make more investment in production of large numbers of eggs or young that then receive little care, or it may make more investment in parental care of a small number of young (Gould 1977). Which strategy is used is governed by a combination of factors involving how stable the environment might be and the animal's place in the food web. These are sometimes difficult to disentangle, but they have meant that frogs, for example, use the whole range of possible options from the production of large quantities of frog spawn to production of a single offspring cared for till maturity. Sometimes these both occur in the same genus of frog, so that reproductive strategy has little connection with phylogeny. For this reason, it may be a mistake to think of early tetrapods as being like frogs that produce spawn in their reproduction strategies.

As for metamorphosis, it has become clear that an abrupt change from aquatic to terrestrial lifestyles with concomitant changes in skull morphology and degrees of ossification incorporates a suite of features that have evolved within temnospondyl amphibians and that are not found in more primitive members of the group (e.g., Schoch 2002b, 2004;

Schoch and Milner 2004). Other taxa show more incremental growth and a more gradual change in morphology. The morphological changes to the humerus of *Ichthyostega* show that even at quite a late stage in its life cycle, it still retained what appear to be aquatic adaptations, but whether this implies a later, more rapid change in morphology cannot be judged on this evidence alone.

The most primitive frogs, most salamanders, and all caecilians use internal fertilization. The coelacanths and the chondrichthyans do likewise, so that there is no good reason to suppose that early tetrapods might not have done the same. Indeed, coelacanths and many sharks are ovoviviparous, keeping the young inside the body until they are miniature adults. Again, some early tetrapods might have done so too. It is perhaps easier to envisage the development of an amniote egg from such precursors than from a spawn-producing animal (Skulan 2000).

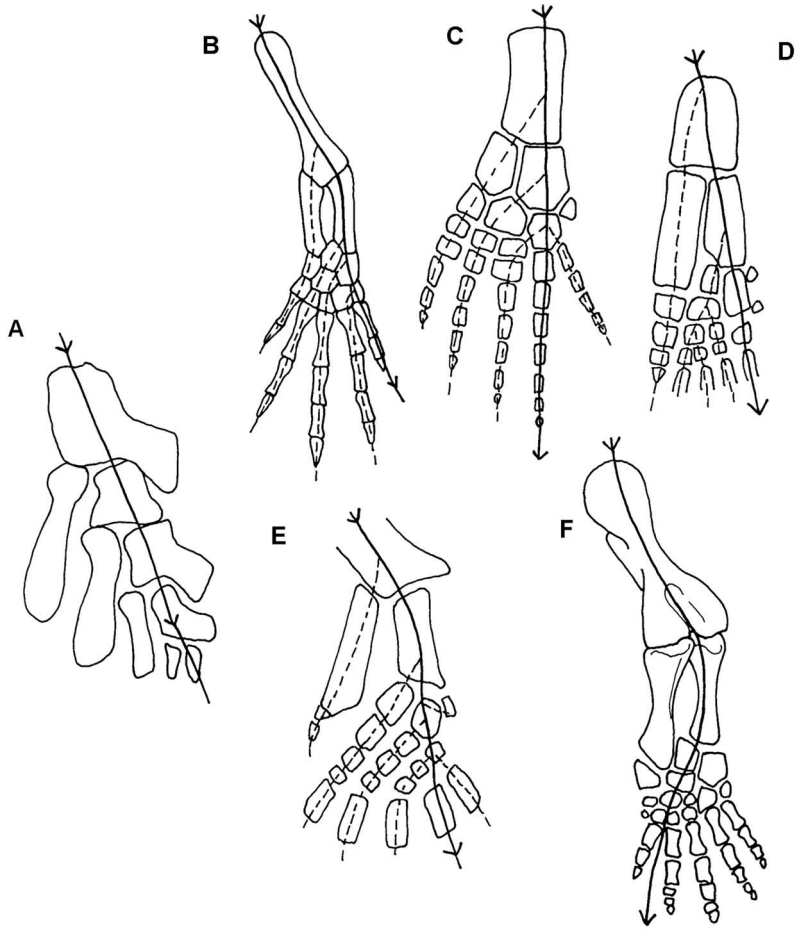
The only way these ideas could be tested would be if Devonian tetrapods were discovered in some deposit showing exceptional preservation. Such deposits in the past have yielded the Burgess Shale fauna of Early Cambrian soft-bodied animals. The feathered Jurassic protobird *Archaeopteryx* and the coelacanth *Undina* came from the Solnhofen Limestone. In the latter specimen, babies were preserved inside the mother. Perhaps one day a Devonian tetrapod may be found that also preserves babies inside an adult's body.

## Limbs, Digits and Their Development

Limbs with their fingers and toes and the act of walking are among the most conspicuous attributes of tetrapods, and the combination has given the group its name. In the first part of this chapter, some of the similarities and differences between fins and limbs were explored; the next part examines what is known about how some of those differences came about, using evidence from fossils and living animals, integrating paleontology with embryology and developmental genetics. More detailed accounts of this topic can be found in Coates et al. (2008) and Clack (2009b).

There are basic similarities between the fins of a lobe-finned fish and the limbs of a tetrapod in the means of attachment to the body by a single element (bone or cartilage), and in having a pair of further elements attached to that. However, further down the limb and the fin, the differences become more and more obvious, so that it is difficult to see the relationship between the two. In the past there have been various conflicting ideas put forward to try to reconcile them (Fig. 6.19).

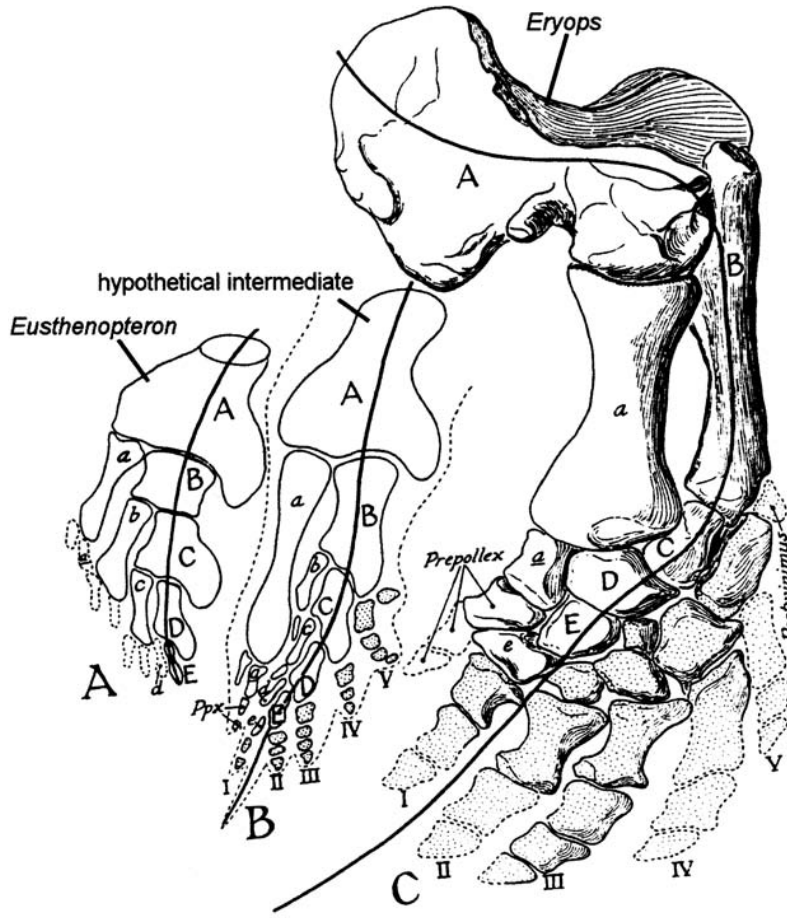
The fin of a lungfish or a tetrapodomorph is built with a main central axis from which elements branch off. This axis is called the metapterygial axis, meaning "middle of the fin." In the time from about the 1870s to the 1950s, people attempted to discover where the equivalent of the metapterygial axis ran in the tetrapod limb (Gegenbaur 1878; Watson 1913; Gregory et al. 1923; Gregory and Raven 1941; Steiner 1934; Westoll 1943b; Jarvik 1980). Because limbs evolved from fins, the axis should in theory still




**6.19.** Diagram to illustrate historical ideas of the position of the metapterygial axis (shown as an arrow). (A) *Eusthenopteron* fin for reference. (B) Gegenbaur (1878). (C) Watson (1913). (D) Gregory et al. (1923), Gregory and Raven (1941). (E) Steiner (1934), Jarvik (1980). (F) Westoll (1943b).

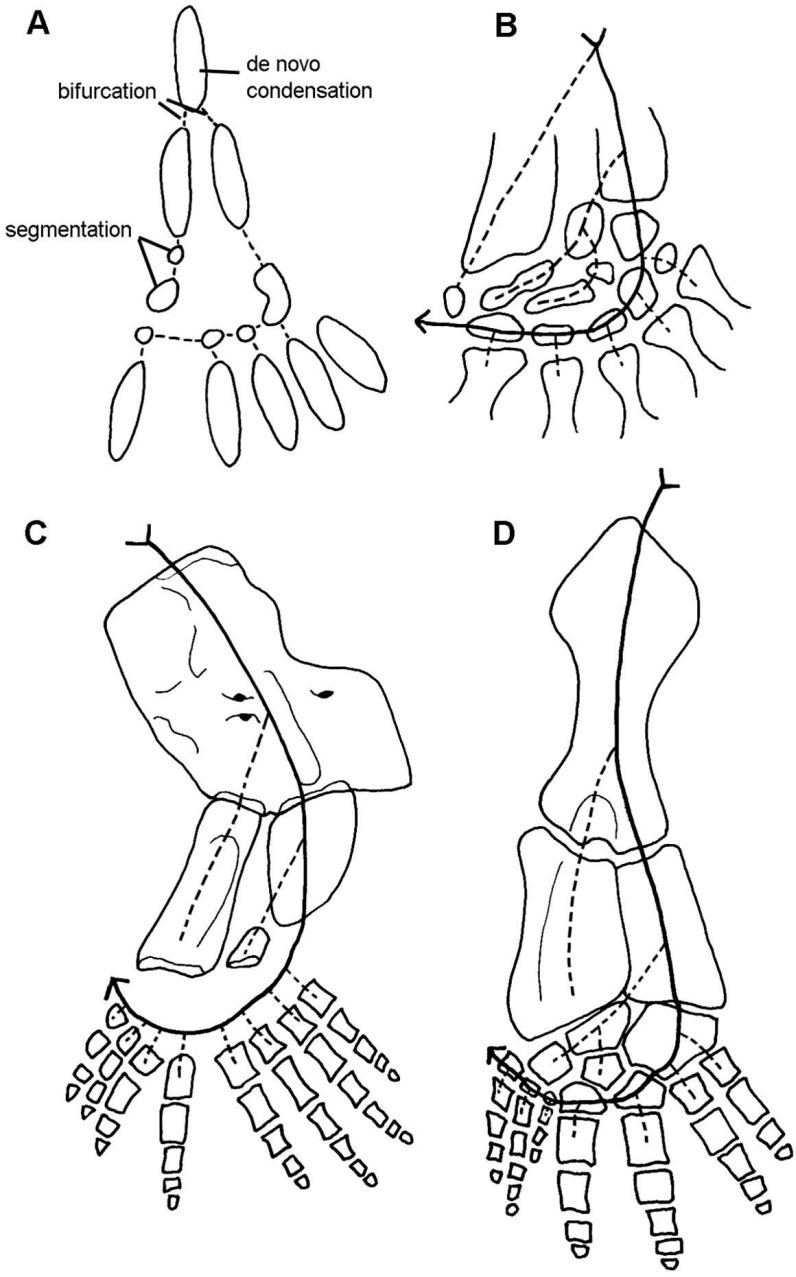
be recognizable. Because the axis runs more or less centrally in the fin, most people looked for it more or less in the middle of the limb, so that this hypothetical structure would run out either along the middle digit, or between two digits, with the digits branching off it in a pyramidal form. It was also thought that the early limb was equipped with a set number of elements or fundamental parts, called a canonical set, which ought to be equatable to a similar number of elements in the fish fin. Various hypothetical frameworks were derived to try to match them, but none of them completely succeeded, partly because it depended on which fish fin and which tetrapod limb was used as a model (Figs. 6.19, 6.20).

The problems produced by the hypothetical models were never resolved, and attention shifted away to the techniques of developmental biology, with interest focused on processes governing the formation of limb elements in the early limb buds of living forms. These studies were not particularly concerned with the evolutionary origins of limbs from fins; rather, they sought to learn how the limb grew from the embryo to the adult, and how the cells knew where they were, what to do, and when to do it.




**6.20.** Diagram of the fin skeleton of *Eusthenopteron,* the pectoral limb of *Eryops,* and a proposed hypothetical ancestor between them. *From Gregory and Raven (1941).* The heavy line denotes the proposed course of the metapterygial axis. Letters on the individual elements denote equivalent (homologous) structures. Roman numerals denote the digits. Note that *Eryops* has been reconstructed with the canonical five digits in its hand, plus theoretical elements called the prepollex and postminimus, whereas more recent work suggests that it had only four digits, as in all temnospondyls where the hand is known in detail.

Problems with early limb evolution surfaced again in the mid-1980s, when Shubin and Alberch looked again at the very early development of limbs in a range of amniotes and amphibians to find out in what order and pattern the elements actually appeared (Shubin and Alberch 1986). This work produced a suite of key discoveries about the order of events. It was already known that in the early limb bud, bones begin to form as cartilage precursors that appear by aggregation of cells from the embryonic cell matrix. This process is called focal condensation, and it produces a new potential limb element. The first condensation produces the nearest element to the body, the humerus or femur. A little later, the end of this element grows outward and produces two further new elements, in processes called segmentation and bifurcation. Shubin and Alberch followed these processes in very early embryos from a range of modern tetrapods. After the initial segmentation and bifurcation has produced the elements for the femur or humerus and the next two elements, the process is repeated once more, but only one of the two elements bifurcates further. The side that stops producing new elements forms the radius or the tibia and one or two more small dependent elements. The side that continues forms the carpus or tarsus on one side and the ulna or fibula




**6.21.** (A) Diagram to illustrate Shubin and Alberch's three embryonic processes in limb formation. (B) Shubin and Alberch's theory for the location of the metapterygial axis in the tetrapod limb *(from Shubin and Alberch 1986)*. Shubin and Alberch's idea applied to the (C) forelimb of *Acanthostega* and to the (D) hind limb of *Ichthyostega* *(from Coates and Clack 1990)*.

on the other. Springing from the ulnar or fibular bifurcation, a series of further elements arise that segment but do not bifurcate (Fig. 6.21).

The result of this is a chain of elements running around the hand or foot through the wrist or ankle, from which the digits spring along the side away from the body. This chain, called the primary axis or digital arch, could be envisaged as the old metapterygial axis, running not along or between digits, but forward, bending around the wrist or ankle. The last digit to form would be the thumb or big toe. There is some variation among the range of tetrapods studied and between fore- and hind

limbs, but the overall pattern was similar in all the taxa studied. Under this model, the digits would lie in a position equivalent to the postaxial radials of the fish fin, while most bones of the carpus or tarsus would be preaxial. Few lobe-finned vertebrates form postaxial radials, lungfish being the most obvious exception, so the appearance of digits appeared to be an unusual development.

It appears that these processes of focal condensation, segmentation, and bifurcation are the same in both fish fins and tetrapod limbs, and it can explain the similarities in those elements closest to the body in both. Further out, more differences are seen, not only between fishes and tetrapods, but among lobe-fins generally. The more distal parts of the limb or fin are those that form later in growth of the animal and may have reached their specialized condition most recently in evolution (see Fig. 2.14).

When the multidigited limbs of Devonian tetrapods were discovered, old ideas about the metapterygial axis and the canonical set of elements could not explain them. However, Shubin and Alberch's model describing the curved axis could accommodate them easily. All that would have to happen is that the axis keeps on segmenting and bifurcating longer than it now does in tetrapods (Fig. 6.21). In theory, any number of digits would be possible.

More recent work in developmental genetics has suggested that the Shubin and Alberch (1986) model is probably overly simple, though the existence of a primary axis has been corroborated in many cases. However, it may not equate to the metapterygial axis. In a review of limb formation and evolution, Wagner and Larsson (2007) summarized the arguments against Shubin and Alberch's idea. They noted that the patterns found by those authors were less universal than at first thought, with the appearance of digits often being independent of the digital arch. However, they also noted that there was good evidence for the existence of the primary axis, and that those digits of the hand or foot that derived from it were the most developmentally stable. They suggested that this developmentally stable region may be equivalent to the metapterygial axis.

In the years since Shubin and Alberch's paper redescribing the embryonic development of digits, much has been learned about the genetic control of early fin and limb development, so that it is becoming clearer which patterns are unique to tetrapods and which are shared by other vertebrates. Until recently, it was considered that the digits of tetrapods were a novel development (see, for example, the review by Wagner and Larsson 2007) that had no obvious precursor in the fins of fishes, at least as seen from studies of modern fishes. However, now that picture is beginning to change with the study of the genetic control of fins from a wider range of fishes, combined with the information from fossil forms.

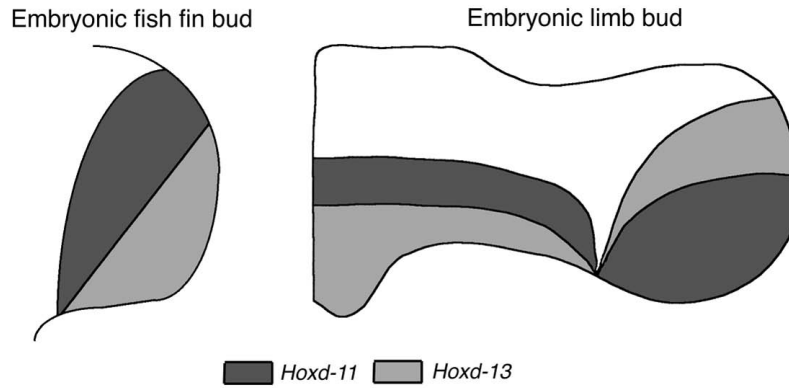
In recent years, the genetic and developmental control of limb formation (and fin formation by extension) has been the subject of an enormous growth of study, interest, and concomitant understanding. Some of the developmental findings reflect those that are seen in the fossil record, as well as generally among living vertebrates. More details can be found

in textbooks of developmental biology, such as those listed in Chapter 2. Though only a few modern animals, usually a chicken, a mouse, a frog, or a zebra fish, have been studied in detail, the conclusions that can be drawn have wide implications for all vertebrates. The interplay of *Hox* genes, morphogens, and transcription factors (proteins that moderate what cells do) (see Chapter 2) are now beginning to throw light on the evolution of tetrapod limbs.

Vertebrate fins and limbs begin to form in special areas at two pairs of points along the flank of the embryo. To begin the formation of a limb (or fin), cells from the general body wall (mesenchyme) migrate out to the limb-forming region and induce the outer body layer, the ectoderm, to produce a distinct string of cells along the flank called the apical ectodermal ridge (AER). This provides a major signaling center from which messages pass to and fro to the limb-forming cells, among which are messages defining the three axes that the limb must take up: proximal → distal; anterior → posterior; and dorsal → ventral. The proximal → distal axis defines the order in which humerus/femur, radius–ulna/tibia–fibula, wrist/ankle, and fingers/toes are laid down; the anterior → posterior axis defines, for example, that from thumb to little finger, and the dorsal → ventral axis defines the back of the hand versus the palm. Cascades of many genes are involved in patterning the limb, establishing the proximodistal, anteroposterior, and dorsoventral axes, without which the limb skeleton would be a disorganized and undifferentiated collection of cells. Tanaka and Tickle (2007) give a more detailed review of these early stages of limb development. *HoxA* and *HoxD* are key genes in control of appendage development, in concert with the gene called *Sonic hedgehog* (*Shh*), the cutely named equivalent of the *hedgehog* gene in the fly *Drosophila* (geneticists have as much fun naming genes as zoologists do naming animals), as well as an array of transcription factors and proteins.

In tetrapods, cells growing internal to the AER push it outward, first into a small pimplelike region round which the AER runs horizontally, and eventually elongating it as the limb grows. This is called the limb bud. Figure 6.22 explains where these regions appear and where the *Hox* genes have their influence. In most vertebrate embryos, forelimbs begin to develop before hind limbs. Here is a reflection not only of what is seen in the fins of fish, but also of what is seen in the evolution of fins generally among vertebrates—forefins are usually larger than hind ones in tetrapodomorph fish, and forefins are thought to have evolved before hind ones in early vertebrates (Coates and Cohn 1999).

In the proximal parts of the limb, there are similar mechanisms of *Hox* gene control acting in both fish and tetrapods. One of the critical regions in initiating limb development sits just at the back of the limb bud, where it joins the body wall. It is called the zone of polarizing activity, or ZPA. *Sonic hedgehog*, under the influence of *Hoxb8* establishes the ZPA and the anterior–posterior axis in fish fins and tetrapod limbs. In particular, this region defines digit or fin ray identity, also by means of the *Sonic hedgehog* gene. Without this posterior expression of *Shh*, digits




**6.22.** Diagram of *Hox* gene domains in the embryo fish fin and tetrapod limb bud. In the fish, *Hoxd13* is expressed distally and posteriorly to *Hoxd11* in the embryonic fin, and the fin itself never elongates. In the tetrapod limb bud, in the proximal end, the domains of *Hoxd11* and *Hoxd13* are stretched along the posterior margin of the fin in much the same relationship as they are found in the fish fin bud. However, distally, at the end of the limb where the digits form, there seems to have been a twist so that not only are their positions reversed, but also their expression domains curl round the end of the limb bud. It is possible that this may be responsible for the way the digits are formed around the digital arch in the embryonic limb bud. *From Gilbert (2000).*

will not form. Though for a while the activity of *Shh* here was thought to be a derived feature unique to osteichthyans (that is, all ray-finned fishes plus all lobe-finned vertebrates including tetrapods), it is now known to be present also in chondrichthyans (sharks and rays), performing much the same role (Dahn et al. 2007). Again, this appears to be an ancient function for this gene.

Toward the more distal parts of the limb, controlling the formation of fingers and toes, some *Hox* genes come into play in ways that have no equivalent function among teleost fishes like the zebra fish, giving the impression that these functions were a novel tetrapod development. These are the distally operating sequences of *HoxA* and *HoxD*, the paralog groups 11–13 in each gene.

Genes at the 5' end of the sequence of *HoxA* and *HoxD*—that is, *Hoxa11–13* and *Hoxd11–13*—are involved in patterning the fin or limb skeleton. In zebra fish and tetrapods, they are all initially expressed in a pattern that is collinear with the proximodistal axis of the appendage, with the *Hoxd11* paralog groups found more proximally than the *Hoxd13* paralog groups. The sequential action of these genes produces both the proximodistal and anteroposterior axes of the limb (Tarchini et al. 2006). In tetrapods, as the limb grows outward, these genes continue to be expressed, whereas in zebra fish, their expression soon ceases and the bud does not extend distally. In later stages of limb development, *Hoxa13* is found throughout the limb bud, with the boundary between *Hoxa11* and *Hoxa13* positioned at the junction between the main limb long bones and the wrist. *Hoxa13* and *Hoxd13* are both required for digit development, but curiously, the expression of *Hoxd13* is inverted at the tip. It is thought that *Hoxd13* is responsible for limiting the number of digits to five; the implication here is that this function is a late addition, absent or incomplete in Devonian tetrapods. The late-stage expression and inversion of *Hoxd13* was for long considered to be a unique tetrapod feature, and it was this that suggested that the evolution of digits was a produced by a genetic novelty (Wagner and Larsson 2007).

Davis et al. (2007) more recently discovered that a late expression of *Hoxd10–13* comparable to that in tetrapods was present in the

development of the fins of the living basal ray-finned fish *Polyodon*, the paddlefish. Not only that, but there is an inversion of *Hoxd13*, so that it is expressed more anteriorly in the fin bud. The implication of this is that, after all, this genetic twist is not unique to tetrapods but is a more generally distributed feature that has been lost in teleosts such as the zebra fish. *Polyodon* has a much more complex internal fin skeleton than any teleost, and its structure relates to its more complex genetic control. The potential existence of this genetic mechanism could underlie the presence of complex fin skeletons in the tetrapodomorph group, from rhizodonts to tetrapods.

A key strand of information about limb development has until recently been missing from the suite of experimental possibilities, and that is information from other living lobe-finned vertebrates. Only two groups apart from tetrapods are still extant, the coelacanths and the lungfishes, but no embryonic sequences are likely to be available for the deep-sea coelacanth in the foreseeable future. For the lungfishes, the situation has recently been improved by the ability of a research group in Australia to breed *Neoceratodus*, the most primitive of the three living lungfish genera. Now valuable genetic and developmental data are beginning to come through. These have provided some new hypotheses about the relationship of digits to the radials of the lobe-finned fish skeleton and the appearance of wrists and ankles (Johanson et al. 2007b).

Johanson et al. (2007b) noted the apparent developmental discontinuity between the digits and the wrist or ankle bones as seen in the embryogenesis of urodeles and the fossil record of Paleozoic tetrapods. To explore possible comparable patterns in the lungfish, they looked at the development of pre- and postaxial fin radials relative to those of the main fin axis. In lungfish, they found both a discontinuity between the formation of pectoral fin radials and the axial elements, and a pattern of *Hoxd13* activity in the fin bud comparable to that in tetrapods. *Hoxd13* is initially found on the anterior side of the fin, moving posteriorly only later. The preaxial radials first form independently of the axial elements, only coalescing to form joints with them after *Hoxd13* has ceased to be expressed there; postaxial radials appear once *Hoxd13* expression has passed through the posterior side of the fin, at which point they too coalesce with the axial elements. Johanson and her colleagues thus contended that this late-phase and anterior expression of *Hoxd13* is homologous to that in *Polyodon* and tetrapods.

Looking at the fin structure of fossil sarcopterygians suggests that a short fin axis is primitive for the whole group, and thus, as Johanson et al. (2007b) suggested, it is probable that the long fin in lungfishes is a derived condition. However, the genetic control mechanisms may be conserved across the whole group. Thus, they were able to put forward a hypothesis of independent development for the more distal parts of the sarcopterygian fin skeleton, of which the wrists/ankles and digits in tetrapods are one version. If correct, this would constitute further evidence that digits are not really an evolutionary novelty as previously considered,

but instead are developments of an existing mechanism. It further implies that the metapterygial axis in those with short fins and in limbs is curtailed, followed by elaboration of the independently developed distal elements; thus, there are only the most proximal parts of a metapterygial axis component to the tetrapod limb.

It remains to be said that most of the work on developmental mechanisms in vertebrates has been carried out on the pectoral appendage. Less attention has been paid to the pelvic limb, based on the assumption that they are similar. However, as Coates and Ruta (2007) pointed out, pectoral and pelvic limbs may in fact be differently formed. Coates et al. (2002) noted that in almost all fishes, including modern and fossil forms, pectoral fins are larger and more complex than pelvic fins. Fin modification toward weight bearing in tetrapodomorphs begins with the pectoral pair. Later, with the evolution of digited tetrapods from the Devonian onward, the hind limb acquires advanced features before the pectoral, and in tetrapod embryogenesis, it is the pelvic limb that (with the exception of marsupial mammals) appears and develops ahead of the pectoral.

Coates et al. (2002) performed a cladistic analysis based on characters of fins, limbs, and girdles. Taking pectoral and pelvic elements as separate entities, they found that among the tetrapod taxa examined, hind limb morphology of each taxon tended to cluster with the forelimb of the next most crownward in the phylogeny, supporting the hypothesis that hind limbs overtake forelimbs in evolution as well as development. They used a limited sample of taxa, however, that could not include more recent information from *Panderichthys* and *Tiktaalik*, whose pelvic fins and girdles would have been found to be less well developed than their pectoral equivalents.

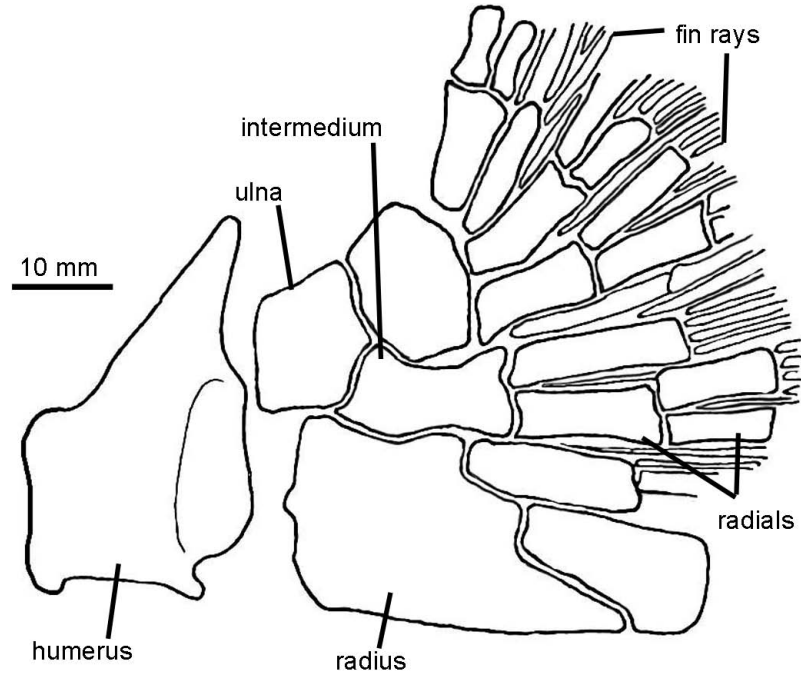
The points at which tetrapod limbs form correspond to the transitional zones where two *Hox* genes interact, in the case of the amniote forelimb, where *Hoxc6* meets the action of *Hoxc8*, the same point at which cervical vertebrae are modified into thoracic ones. These points correspond to different vertebral numbers in mammals and birds, but the *Hox* genes influencing the formation are the same. *Hoxc6* also specifies where the brachial plexus (the nerve ganglion controlling the pectoral appendage; see Chapter 10) forms in the zebra fish, so although in tetrapods it is involved with regionalization in the vertebral column, it has other functions as well. By comparing the occurrence of digits in the fossil record with the time at which vertebral specification occurs, it appears that the new regions of *Hox* genes *A* and *D* acquired their digit-forming functions before the precise operation of *Hoxc6* and *Hoxc8* came mutually to specify the cervical–thoracic boundary as found in amniotes. Although in the ray-finned fish *Danio Hoxc6* defines a similar boundary, there does not seem to be an equivalent region in early tetrapods or amphibians, or it occurs in a different place, judging from the position and lack of definition of the cervical thoracic boundary in these animals. It has also been suggested that *HoxA* and *D* came to operate as digit-invoking genes in two separate phases. *HoxA* might have controlled the appearance of

digits, while *HoxD* came into action later to specify a pentadactyl limb (Shubin et al. 1997). Such a suggestion would fit with the idea that the digits of an early tetrapod like *Acanthostega* cannot be matched one for one with those of a pentadactyl tetrapod (Coates and Cohn 1998).

One early suggestion in the quest for understanding digit evolution was based on the idea that there were five groups of digit-producing genes on *HoxD*, and there were five digits: one group per digit might be in operation. This suggestion carried the implication that for a polydactylous animal, there could only be five *types* of digit, and if there were more present, then at least some must be duplicates (Tabin 1992; Shubin et al. 1997). The idea is refuted by *Acanthostega*, in which of the eight digits, none is a duplicate in either size or configuration of any of the others. It remains a puzzle why so few animals have evolved polydactyly as a normal body form, and why, if extra digits are needed by an animal, they are almost always formed from co-opted material derived from elsewhere (see Gould's essay on "The Panda's Thumb"; Gould 1980). For example, most frogs have only four fingers on the hand, but some, which use their hands for digging, invent an extra digit from wrist bones.

Formation of independent digits can only happen by a process of orderly cell death (apoptosis), with cells that lie in the limb bud between where digits form being sacrificed to make the spaces between the digits. This process may not have been well established among Devonian taxa such as *Acanthostega* and *Ichthyostega:* the way their digits are preserved could suggest that they still retained a fleshy web that held the digits in place during fossilization.

Paleontology may not only be able to pose but also to answer some questions about the development and evolution of limbs. Once limbs with digits were established, generally speaking, changes that happen to one set in nature (as opposed to experiment) tend to happen to the other. For example, the reduction in the number of toes in horses and the increase in the number of phalanges in ichthyosaurs (marine dolphinlike amniotes of the Jurassic and Cretaceous periods) happen to both sets. This is manifestly not an invariable rule, and functional necessity dictates that birds and bats have only one set of paired limbs modified into wings. (Interestingly, among the first winged relatives of birds, the dinobird *Microraptor* had winglike feather arrangements on hind limbs as well as forelimbs.) The number of toes in early tetrapods may test the hypothesis of similarity between fore- and hind limbs. So far, it appears that there were the same number of digits on the fore- and hind limbs of *Acanthostega* and *Tulerpeton*. However, the hand of *Ichthyostega* is unknown. The hypothesis of similarity predicts that it will have seven digits on the forelimb. At the same time, its complement of toes on the hind foot is so unusual that it is hard to see how it could be combined with the format of the forelimb, which is so distinct from the hind in structure, proportions, and presumably, function. The most recent developmental work has, by contrast with the hypothesis of similarity, suggested that although fore- and hind limbs are specified by




**6.23.** Fin skeleton of *Sauripterus*. *From Daeschler and Shubin (1997).*

similar transcription factors, these factors, though closely related, are not identical (Coates and Cohn 1998).

The hypothesis of similarity also predicts that digits will appear on fore- and hind limbs at the same time, so, for example, no animal would have had digits on the forelimb while still retaining fin rays on the hind limb. Fossils would theoretically be able to refute this hypothesis. Something that appears to have happened in the evolution of limbs is the suppression of the dermal fin rays found in the lobe-fins and other fishes. No limb has yet been found with both fin rays and digits, though *Acanthostega* and *Ichthyostega* retain fin rays in the tail. The rhizodont *Sauripterus* retains fin rays at the same time as producing an enlarged endoskeletal fin skeleton, so the appearance of both together might not be impossible in a very early tetrapod (Fig. 6.23).

Fossils can also refute hypotheses of forbidden morphologies. That is, sometimes it appears that the way some developmental pathways work precludes the existence of certain morphologies. One such applies to the configuration of digits on the hand or foot. A theoretically forbidden morphology is to have the shortest digit in the middle of the set, rather than at one end or the other (Holder 1983; Thomson 1988). The hind foot of *Ichthyostega*, with its tiny digit as number three from the front, refutes this idea. However, it is also refuted by some living animals—some seals have small digits at the center of the hind flipper, with long ones forming each edge (Fig. 5.15A). Part of the problem of posing such theoretical ideas is that they are based on the study of such a limited sample of experimental animals. Zebra fish, mice, chickens, and the frog *Xenopus*, the most commonly studied laboratory animals in developmental biology, all belong

to species that are highly specialized members of their vertebrate groups. This means that they may not always be representative of tetrapods as a whole, and they certainly cannot account for many of the extreme specializations that some tetrapods show.

The variable number of digits seen among the Devonian forms does fit another observation of developmental biology. Early in the evolution of a number of systems, variability seems to be the rule, followed by stabilization only later, as the genetic mechanism controlling it tightens up and becomes to a degree canalized. This is seen in a wide range of systems: the number of segments found in arthropod bodies; the number of gill slits in the earliest of most primitive vertebrates; number of vertebrae in a tetrapod group; the number of vertebrae in each region of the mammalian vertebral column; pattern of lateral line systems; types and formation of hard tissues in vertebrates; morphology of the ear region. Stabilization may be forced by some functional necessity. In frogs, birds, and mammals, for example, the number of vertebrae is strictly controlled in response to the needs of their respective locomotory requirements. This may be true also of insect bodies. *Hox* genes may well be implicated in this tightening-up process.

Although it is still unknown why the tetrapod limb stabilized at five digits, two factors may play a part. The limb bud is a physically restricted area, so it may only be possible to make either larger numbers of smaller digits or a smaller number of larger digits, in combination with the material needed to make wrists and ankles. The amount of material available in relation to the demands of walking may predicate a smaller number of larger digits if a functional wrist or ankle is to be formed. Alternatively, perhaps five digits is the number that fits not only most economically but also most stably round the wrist or ankle for taking the weight of the animal, but that allows flexibility for the twisting movements of pronation and supination at the same time. Another suggestion is that it may be related to the neuromuscular coordination required for the operation of individual digits, once the fleshy webbing of early limbs had been lost. The answer to the question of why five will almost certainly remain elusive.

## Locomotion

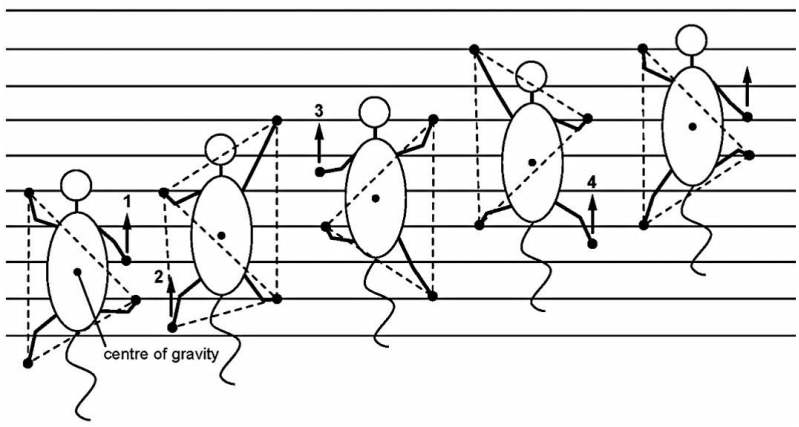
During the fish–tetrapod transition, along with the changes to the bone and muscle structure, the mode of limb movement must also have changed. A fish swims by moving its body in a sinusoidal wave that passes down the body and pushes against the water. The fins, attached to the sides of the body, are generally moved in coordination with the bending so that diagonally opposite pairs of fins move more or less together. Several groups of fish that walk on the bottom of the sea use this kind of movement to perform something like a walking trot (Pridmore 1995). These include chondrichthyans (sharks like the epaulette shark), teleosts such as batfish and frogfish, and even the coelacanth moves its fins in the same way, though it does not use them for walking. Early

tetrapods that moved primarily in water would probably have used this kind of movement to begin with, and it would probably require little if any rewiring of the neural pathways of the brain and limbs to control it. Modern salamanders use this movement in water today.

Ijspeert and colleagues (2007) built a model salamander that they could operate electronically by a computer that mimicked the action of the central pattern generators in the spinal cord and limbs of the living animal. Salamanders show a fairly simple and stereotyped range of body and limb locomotory movements that make them suitable for this experiment. By means of simple commands, the model could be made to produce both walking and swimming motions that paralleled those of the living animal quite closely. Walking movements produce slow standing waves in the body, whereas swimming produces faster traveling waves along the body. As more energy is put into the system, movements become faster and faster, until a walking mode changes quite abruptly into a swimming mode. This correlates with the fact that many salamanders, when forced to move quickly, in fact abandon use of the limbs and wriggle on their bellies instead. It would be interesting to know whether walking or swimming was more energetically expensive overall, though it also implies that neurologically, it might be quite simple to convert the system from swimming to walking.

There is a debate over which method of locomotion would have been used by early tetrapods moving out of the water (Edwards 1989). If the body were to be lifted off the ground, the animal would have needed three legs on the ground at any one time if it were not to fall over. To move one leg at a time in an orderly fashion is called the lateral sequence walk (Fig. 6.24). This may have required considerably more complex control by the brain than that produced by simple axial bending to move opposite corners at the same time, and so it may not have been achieved right away (Pridmore 1995). Early tetrapods may therefore have been belly crawlers on land, at first using limbs only for purchase against the ground and for steering and braking, much as fish fins are used. Limbs used as support structures probably evolved only later. When moving quickly on land, modern salamanders first change from the lateral sequence walk to the walking trot, but they eventually abandon the use of limbs and move by wriggling the body. Some have suggested that the walking trot may have been used by early tetrapods with substantial tails, such as *Acanthostega*, in which the tail could have functioned as a fifth leg, though this does not mesh with its extensive webbing.

The extraordinary picture that emerged from study of the axial skeleton of *Ichthyostega*, with its highly differentiated neural spines and deeply overlapping thoracic ribs, is one that needs to be tested. The reconstruction exists only in lateral view, for example, so three-dimensional images need to be produced. This done, an attempt may be made at interpreting its range of movement. A current study is making three-dimensional reconstructions of parts of the skeleton directly from fossil material using micro-CT scans, photographic laser scans, and imaging software. It is




**6.24.** Diagram of lateral sequence walk.

hoped that this may be built into a virtual skeletal model that can be manipulated and, within broad limits, soft tissue properties built onto it. By comparing it and other early tetrapods similarly treated to modern tetrapods such as seals, otters, and salamanders, the study aims to build a picture of modes of locomotion that would have been possible for these animals, as well as ruling out those that would not have been possible.

It is sometimes said that in tetrapods, the wrist and knee joints are simple hinges while the elbow and ankle joints are rotatory. This observation is based mainly on modern amniotes, though it also applies to modern amphibians. However, it does not apply to the earliest tetrapods. The wrist of *Acanthostega*, far from being a hinge, occupied a long arc from front to back, whose range of movement is hard to interpret. The knee joint was also unlike that of later tetrapods except *Ichthyostega*, in that tibia and fibula seem to have overlapped each other a little where they joined the femur. Both bones were rather flattened, and as with the wrist, it is hard to envisage their possible range of movements, but it seems unlikely that they would have walked in a conventional tetrapod manner with the body held well off the ground. This is discussed in more detail in Chapter 10.

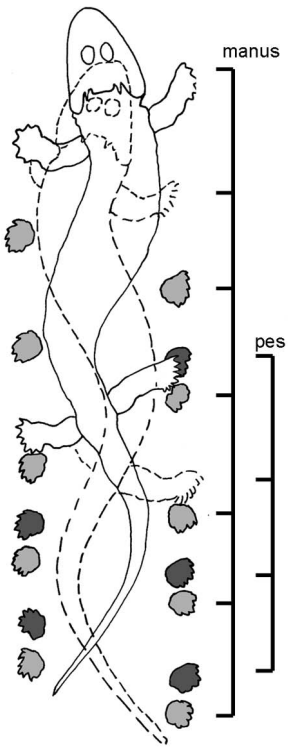
Unfortunately, the trackways left by Devonian tetrapods (see Chapter 4) are difficult to interpret (Clack 1997a). For example, because the proportions of the animals that made them are unknown, so is the gait they were using. Figure 6.25 shows how an *Acanthostega*-like animal might have produced tracks like those of the Genoa River sequence if its body were partly supported by water. However, it is not clear whether the tracks were made entirely on the land surface or whether the animals might have been partially submerged. Without knowing that, it is not possible to be sure that the apparently walking tracks from Poland, Australia, or Ireland, for example, were made by truly walking or paddling animals. Only more fossils will provide more information that will help us interpret the early evolution of land locomotion.

During the evolution of tetrapods and the development of walking, the emphasis in muscle power and bulk changed from preponderance

of axial or body-wall muscles to appendicular or limb muscles. (People tend to eat limb muscles of mammals and leg or flight muscles of birds, but the body-wall muscles of fish.) This was accompanied by changes not only to the limb bones, but also to the vertebral column and ribs, as they acquired means by which to support the body and constrain unnecessary twisting. Some of these have been outlined above. In Chapter 10, it will be suggested that these same changes also affected the means by which the animals breathed in air and by which they fed on land, with domino effects to hearing. Because the animals must have continued to work as a coordinated whole, each of the changes must have occurred in concert with the others. The suggestion here is that they began with breathing, which affected feeding, which in turn affected locomotion and hearing.

## Emerging Visions of the Fish–Tetrapod Transition

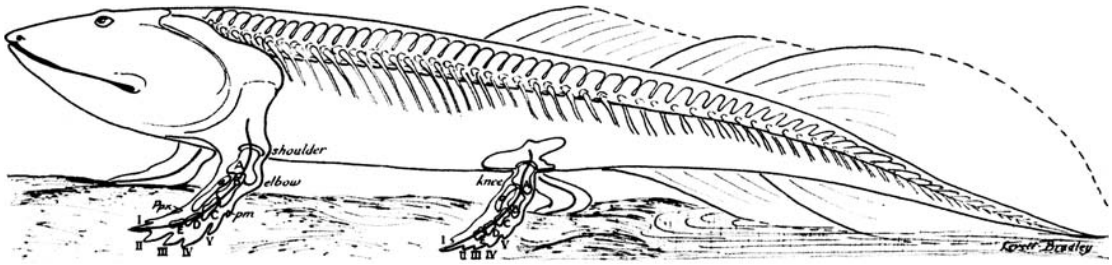
In 1941, Gregory and Raven put forward a suggestion as to the appearance of a "prototetrapod," with a combination of fishlike and tetrapod-like features (Fig. 6.26). This creature was envisaged as retaining the fishlike midline fins on the back and tail, with two dorsals and the caudal fin becoming incorporated into a single fin around the body, much as in a lungfish. It was viewed as having a fishlike skull shape—deep and by inference narrow, with a relatively short snout and with the skull bones still attached to the shoulder girdle at the back—consistent with *Eusthenopteron* and as is still seen in fish today. The elements of the vertebral column were thought to be more or less self-similar all along its length, though it was equipped with tall rectangular neural spines and a series of longish ribs, more tetrapod-like in nature. It was seen as having modified pectoral and pelvic fins that were equipped with the beginnings of digits and rotated to face anteriorly, raising the body off the ground. The pelvic fins were thought to be approximately the same size as the pectorals, though the pelvic girdle was seen as still essentially like that of a fish in shape and proportions. It was presumed to be a more or less terrestrial organism.




**6.25.** Diagram to show how an *Acanthostega*-like tetrapod might produce tracks like those of the Genoa River.

This vision incorporated a number of assumptions. These include the idea that the fins were among the first parts of the animal to develop tetrapod-like characteristics. Their anterior position and weight-bearing function corresponded to the locomotory limbs of tetrapods, and they were pentadactylous, possessing five digitlike extensions. However, they still did not have obvious joint surfaces for wrists and ankles. Other parts, such as the head–shoulder link and the midline fins, remained fishlike even though the animal was essentially landgoing. Tetrapod features such as the enlargement of the pelvic girdle and its attachment to the vertebral column were seen as developing only after the animal had already begun to move on land.

It is instructive to compare this vision with what is now known of creatures like *Tiktaalik* and *Acanthostega*. It shows how the discovery of relevant fossils can radically change apparently well-founded views on the origin of major evolutionary innovations. In contrast to the hypothetical form, *Tiktaalik* shows that one of the first changes to occur during the




**6.26.** Gregory and Raven's (1941) vision of a prototetrapod.

transition was the loss of the connection between the shoulder girdle and the head, allowing the development of a neck. Rather than the deep and narrow skull found in Gregory and Raven's prototetrapod, those of *Tiktaalik* and *Panderichthys* are dorsoventrally flattened and widened. The humeri of *Tiktaalik* and *Panderichthys* show elaboration of muscle attachments to allow support, but they were still horizontally and posteriorly orientated, in contrast to the more vertical and anterior orientation in Gregory and Raven's hypothetical prototetrapod. Changes to the humerus for a supportive role, along with those to the head, were among the first to occur. With respect to the more distal parts of the appendages, the anteriorly directed stance in the hypothetical prototetrapod contrasts with those of *Tiktaalik* and *Panderichthys* in which the posterior orientation was still maintained. The limbs become laterally orientated only later in the transition, and possibly only after the origin of digits, rather than before, as suggested by the hypothetical prototetrapod. Rather than having both appendages of equal size, enlargement of the pelvic girdle and limb appears to be a later development. The suggestion of two dorsal fins as well as an anal and a caudal (tail) fin is refuted by the discovery that from *Panderichthys* on, all the midline fins except the caudal had been lost.

Overall, the sequence of events leading to the emergence of tetrapods seems to have been the reverse of the old vision. The contrast seems to result from the preconception of the main pressures on tetrapods to emerge from the water. In the hypothetical model, it was those parts of the skeleton involved with locomotion on land that were seen as preeminent, so that reorientation of the limbs and the initiation of (five) digits were those thought to evolve first. With our current sequence of tetrapodomorphs, the story seems much more likely to begin with changes involved in improved air-breathing capabilities while the animals were still aquatic, adaptations for terrestrial locomotion being later developments, with the origin of pentadactyly being among the last to be completed.

Although this scenario makes a coherent story, it could be that our vision changes again in the future. The tetrapod-like footprints found in the Middle Devonian of Poland hint that there is much information missing from our picture. If body fossils are found to complement these trackways, it could change the scenario profoundly, or it could change our understanding of the timing. The outcome would really depend on where in the phylogenetic tree the body fossils were found to lie, and thus how they change what we understand about the evolution not only

of limbs, but also of skulls, brains, sensory systems, and physiology. Until they are found, interpretation of the trackways should be made with caution.

## Summary

Skeletal characters that changed over the transition can be summarized as follows (some are illustrated in Fig. 6.1):

From *Eusthenopteron* to *Panderichthys:*
Losses: median fins except for the tail; mosaic of frontal series of bones; cranial mobility across skull roof; reduction in relative size of opercular region; distal part of hyomandibula.
Gains: lengthening of snout; enlargement of eyes and change of location to lie more dorsally; lengthening and broadening of humerus.

From *Panderichthys* to *Tiktaalik:*
Losses: extrascapular series; opercular series; opercular process of hyomandibula.
Gains: enlargement of scapulocoracoid; flexible wrist joint; imbricating ribs.

From *Tiktaalik* to *Acanthostega:*
Losses: supracleithral series (except anocleithrum); dermal fin rays on paired appendages, dorsal scales; mosaic of nasal bones (except for median rostrals and anterior tectals); reduction of cleithrum.
Gains: consolidated braincase with suture between anterior and posterior units; fenestra vestibuli enclosing head of stapes; large bulbous basipterygoid processes; ribs attaching to neural arch and centrum; limbs with digits; enlarged scapulocoracoid; large dermal interclavicle; large pelvic girdle, sacral rib; enlarged femur, tibia and fibula, mosaic of ankle bones.

From *Acanthostega* to post-Devonian tetrapods (see Chapter 10 for further details):
Losses: dermal fin rays from tail; reduction in number of digits per limb to no more than five; lateral lines mainly in tubes opening by single pores.
Gains: occipital joint; elaborated zygapophyses; further elongation of ribs; radius/ulna and tibia/fibula form weight-bearing joint.

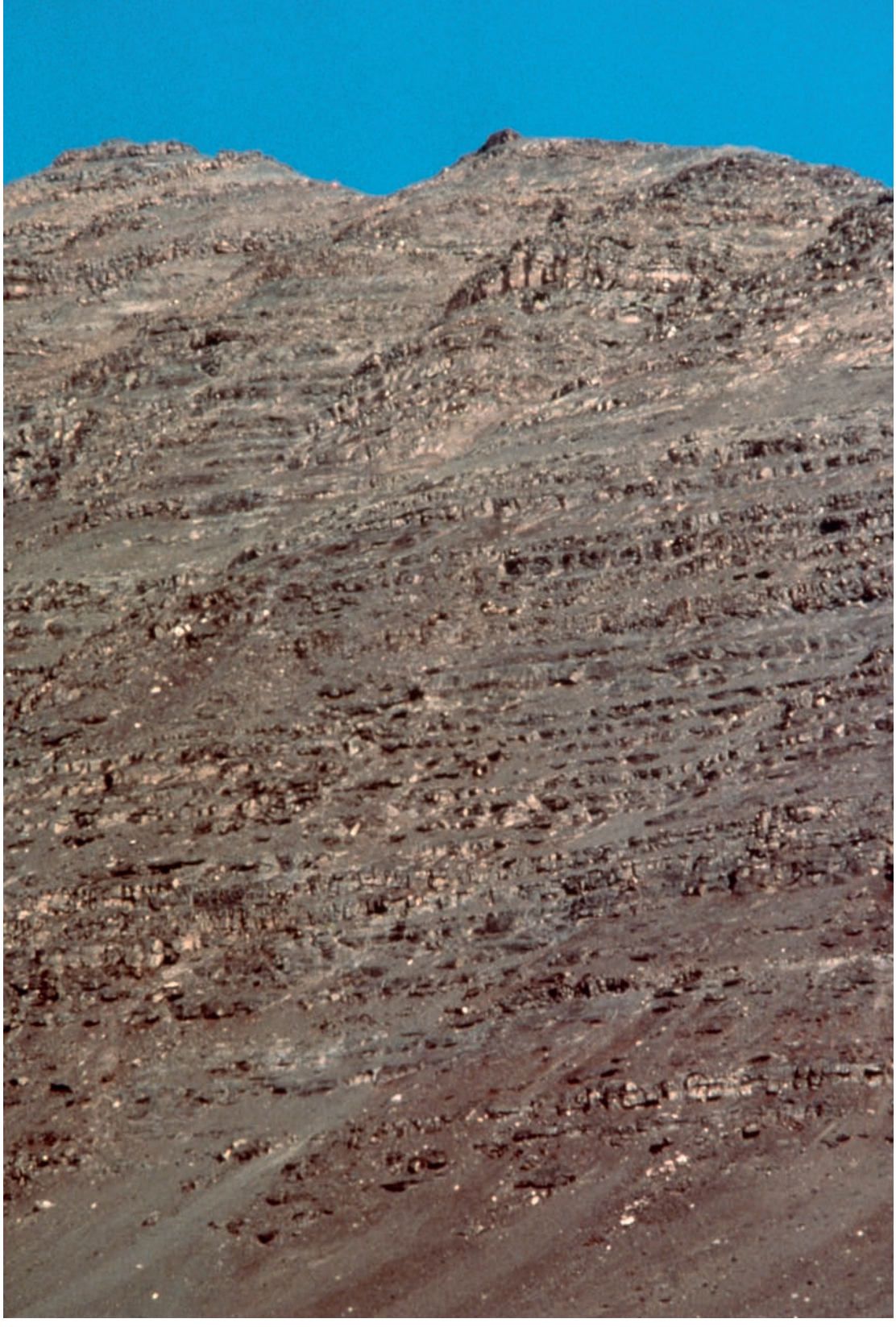


**Plate 1.** Stensiö Bjerg in Greenland showing alternating red and green strata. These layers represent repeated cycles of depositional circumstances, probably influenced by globally occurring events such as the Milankovitch cycles. *Photograph by J.A.C.*



**Plate 2.** Photographs of ferns and lycopsids on the island of Santa Cruz, Galápagos. Ground cover vegetation in the Middle Devonian may have looked something like this. *Photograph by R.N.G.C.*



**Plate 3.** The site at Scat Craig near Elgin in Scotland where *Elginerpeton* was found. Foreground, Per Ahlberg; at the cliff face, Bob Reekie and Bill Baird from the National Museum of Scotland. *Photograph by R.N.G.C.*





**Plate 4.** The Valentia Slate tracks in southern Ireland. (overleaf left) Overview of the main trackway in the background, a shorter trackway in the foreground—this one shows a shallow groove made by the animal's body, while the footprints themselves are raised on a ridge where the sediment has been forced upward. (above) Close-up of some of the shorter tracks showing different print spacing; the track in the foreground is the same as that in the foreground above; note the closer spacing of prints than in the track behind it. *Photographs by J.A.C.*



**Plate 5.** Three of the 1998 expedition members: from left to right, Becky Hitchin, Sarah Finney, and the author.
*The photograph was taken by the fourth expedition member, Sally Neininger (S.L.N.).*

**Plate 6.** I am seated in front of Stensiö Bjerg in 1998. *Photograph by S.L.N.*





**Plate 7.** Photograph of Smithwoodward Bjerg and Stensiö Bjerg on Gauss Halvø showing the three formations of the Celsius Bjerg Group. At their base, the top of Aina Dal Formation is marked by an outcrop of harder rock forming a small cliff, running across from about 300 meters at the left of the photograph and dropping to about 100 meters on the right. The Wimans Bjerg Formation is the middle slightly grayer layer, while the uppermost Britta Dal Formation is marked by another slightly redder layer. *Photograph by J.A.C.*



**Plate 8.** The 1987 team on Stensiö Bjerg when they first encountered the *Acanthostega*-bearing horizon. The large block in front of me is that which provided the most complete articulated individual. At the base of the mountain, the campsite can just be seen. From left to right in the photograph: Jenny Clack and Per Ahlberg (kneeling), Birger Jørgenson, and the late Svend Bendix-Almgreen (standing). *Photograph by R.N.G.C.*



**Plate 9.** Aina Dal scree at the base of Stensiö Bjerg where many of the *Ichthyostega* specimens were found in the 1930s and in 1987. The figures in the picture give some idea of scale. *Photograph by J.A.C.*



**Plate 10.** Photograph of one of the skulls of *Ichthyostega* worked on by Jarvik (MGUH VP 6064). *Photograph by J.A.C.*



**Plate 11.** The most complete of the *Acanthostega* specimens found in 1987, after preparation was finally completed in 1998 (MGUH f.n. 1227). The skull is about 120 millimeters long. A second skull is seen to the top left. The forelimb with its eight digits lies at bottom left. *Photograph by S.M.F.*



**Plate 12.** The locality of Red Hill near Hyner, Pennsylvania, where *Hynerpeton* was found, with its discover, Ted Daeschler, standing at the level from which the specimens came. *Photograph by J.A.C.*



**Plate 13.** Horton Bluff, also known as Blue Beach, in Nova Scotia, Canada, from which some Tournaisian tetrapod elements have been recovered. *Photograph by J.A.C.*

**Plate 14.** Photograph of the locality from which the specimen of *Pederpes* came, shown by the black arrow. Rob Clack is standing on the promontory called Lot's Wife. *Photograph by J.A.C.*



**Plate 15.** The East Kirkton Quarry site once clearance was complete and a section had been excavated through the sequence, with the author standing at the level of unit 82, where most of the best tetrapod specimens have come from. *Photograph by R.N.G.C.*



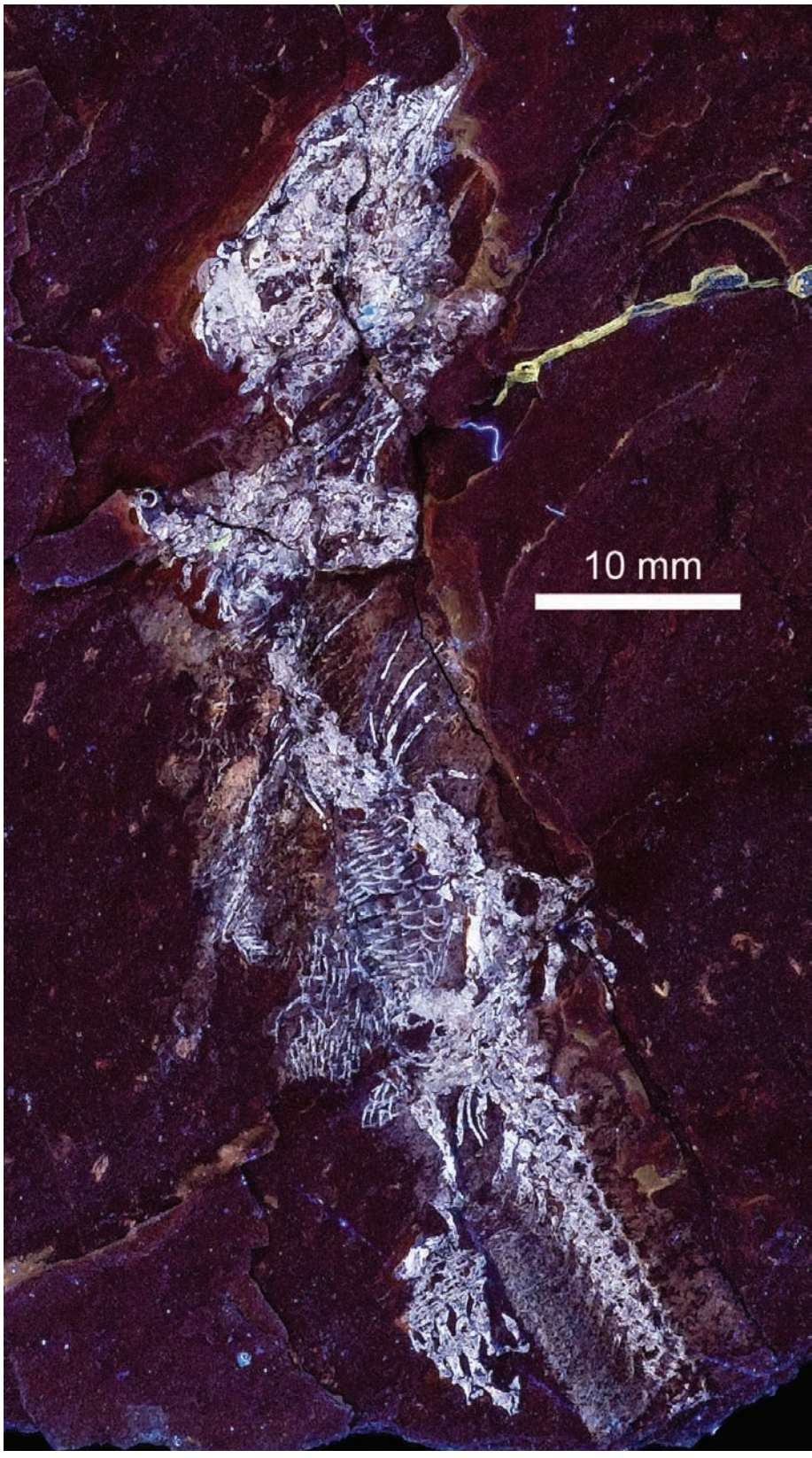


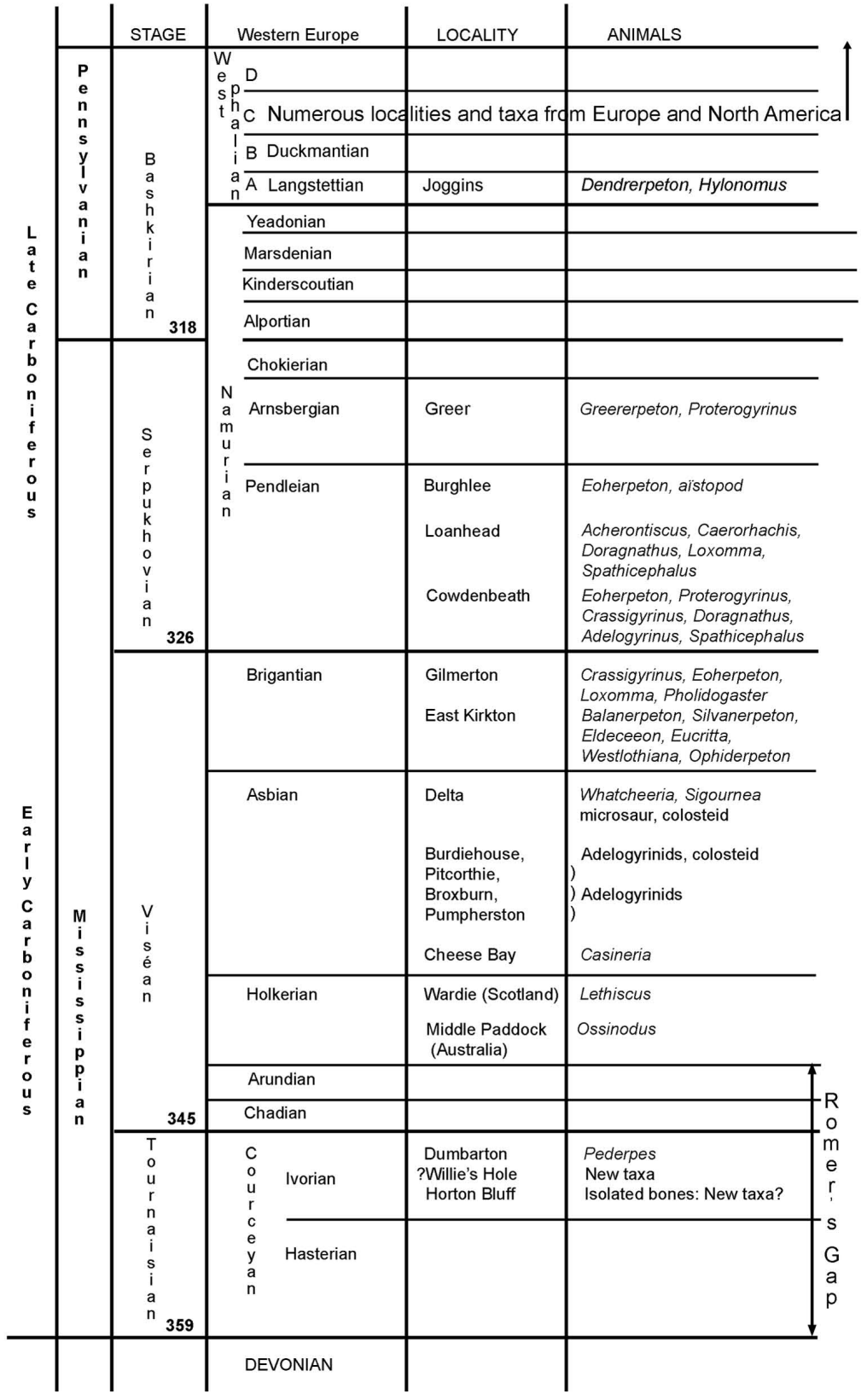


**Plate 17.** *Pulmonoscorpius kirktonensis,* one of the giant scorpions from East Kirkton, about 700 millimeters long. (NMS G1987.7.136). *Photograph by NMS.*

**Plate 16.** Detail of the tuff (fossilized volcanic ash) layers from which some isolated tetrapod bones have been recovered. *Photograph by J.A.C.*

**Plate 18.** Photograph in ultraviolet light of a probable microsaur from East Kirkton. *Photograph by P. Crabb (Natural History Museum, London).* UMZC specimen 2002.2.




STAGE
Western Europe
LOCALITY
ANIMALS
Late Carboniferous
Early Carboniferous
Pennsylvanian
Mississippian
Bashkirian
318
Serpukhovian
326
Viséan
345
Tournaisian
359
West Phalian
D
C Numerous localities and taxa from Europe and North America
B Duckmantian
A Langstettian
Joggins
Dendrerpeton, Hylonomus
Namurian
Yeadonian
Marsdenian
Kinderscoutian
Alportian
Chokierian
Arnsbergian
Greer
Greererpeton, Proterogyrinus
Pendleian
Burghlee
Eoherpeton, aïstopod
Loanhead
Acherontiscus, Caerorhachis, Doragnathus, Loxomma, Spathicephalus
Cowdenbeath
Eoherpeton, Proterogyrinus, Crassigyrinus, Doragnathus, Adelogyrinus, Spathicephalus
Brigantian
Gilmerton
East Kirkton
Crassigyrinus, Eoherpeton, Loxomma, Pholidogaster Balanerpeton, Silvanerpeton, Eldeceeon, Eucritta, Westlothiana, Ophiderpeton
Asbian
Delta
Whatcheeria, Sigournea microsaur, colosteid
Burdiehouse, Pitcorthie, Broxburn, Pumpherston
Adelogyrinids, colosteid ) Adelogyrinids
Cheese Bay
Casineria
Holkerian
Wardie (Scotland)
Lethiscus
Middle Paddock (Australia)
Ossinodus
Arundian
Chadian
Courceyan
Ivorian
Dumbarton
?Willie's Hole
Horton Bluff
Pederpes
New taxa
Isolated bones: New taxa?
Hasterian
Romer's Gap
DEVONIAN

# Emerging into the Carboniferous: The First Phase

# 7

## The Carboniferous World

At the end of the Devonian, a major extinction event hit most groups of vertebrates, both marine and nonmarine. Although an earlier extinction event at the Frasnian–Famennian boundary has been recognized for many years, it appears to have affected invertebrates, especially marine ones, with most vertebrate groups essentially passing through it unscathed. By contrast, a massive vertebrate faunal turnover at the end of the Devonian, associated with the geological phenomenon known as the Hangenberg event, saw the extinction of many groups of vertebrates such as placoderms, and most acanthodians and sarcopterygians (Sallan and Coates 2010). Of those acanthodians and sarcopterygians that did survive, most were represented by only a remnant of their former populations, and these too eventually became extinct. After the extinction, a few groups notably survived well. These included the ray-finned fishes, which had begun their radiation in the Late Devonian but which expanded greatly in numbers, species, and niches in the Early Carboniferous. The chondrichthyans, although they had been persistently present through the Devonian, again became more widespread and numerous, particularly later in the Early Carboniferous. Finally, the tetrapods really began their radiation at this stage. From this point on, the multidigited forms from the Devonian were rare or absent, and five-digited forms became dominant.

It was during this period that the advent of tetrapods onto the land really began, with their radiation into a wealth of body forms, niches, and families, among them fully terrestrial forms that were the forerunners of modern amniotes. Regrettably, the early parts of the period have a poor fossil record, not only for tetrapods but for plants and invertebrates too. By the time tetrapod fossils become at all common, during the later parts, they had already acquired many of the characteristics that mark them as terrestrial tetrapods, which makes understanding this sequence of events difficult. To place the tetrapods in context, it is necessary to survey what is known of their contemporaries in the plant and invertebrate world because it was these that paved the way for the tetrapods to follow.

The Carboniferous period is usually divided into two phases, called the Early and Late Carboniferous in Europe, and the Mississippian and Pennsylvanian in North America. Although the boundaries between these divisions have in the past not been considered equivalent on each side of the Atlantic, this seems to have been an effect of incomplete stratigraphic correlation, and more recently, these two boundaries have

**7.1.** Stratigraphic table of the earlier parts of the Carboniferous with localities and their faunas indicated. *Stratigraphic information from Gradstein et al. (2004), locality and taxa from Smithson (1985a), and other sources cited in the text.*

been reconciled. The terms "Mississippian" and "Pennsylvanian" are now used for European sequences as well (Heckel and Clayton 2006). One way to remember which term equates to Early and which to Late Carboniferous is to realize that M precedes P in the alphabet, indicating that Mississippian precedes Pennsylvanian in the stratigraphic sequence. For the current discussion, because ages rather than rock sequences are usually being described, the terms Early and Late Carboniferous convey the sense of relative time more immediately.

In turn, each of the two parts of the Carboniferous is further divided into stages, with the Early Carboniferous consisting of an earlier Tournaisian and a later Viséan stage. Among vertebrate paleontologists, the names widely used for the Late Carboniferous are Namurian for the earliest part, Westphalian for the middle, and Stephanian for the latest. Because of more detailed work by sedimentologists and stratigraphers, these names are no longer universally accepted because they are imprecise. For example, the earliest part of the Namurian is now considered to be part of the Early Carboniferous, while parts of the Stephanian may fall within the Permian. The older names are nonetheless convenient to use for the study of tetrapods because they seem, by and large, to coincide with changes to the faunas. Subdivisions divide some of these stages, applicable in broad geographical areas, to give more precision to the relative dating of faunas. As far as plants are concerned, the Namurian-stage flora shows more similarities to the Early Carboniferous than to the Westphalian and Stephanian. Figure 7.1 sets out a simplified stratigraphical table of the Early Carboniferous and indicates the localities at which some the animals described in this chapter are found.

## Biogeography, Paleoecology, and Coal

Much of the Carboniferous was a time of mountain-building activity. During this period, a huge chain of mountains was progressively pushed up, and the time was marked by periods of increased volcanic activity. The mountains stretched all across Laurussia, dividing it into two, and are possibly responsible for somewhat different, though comparable, faunas and floras in the two parts. These mountains, as they exist today, stretch all along the eastern United States—the Appalachians—across Europe and into North Africa—the Atlas and Alpine mountains—and on into Asia, forming the early stages of the Himalayas. This sequence of Carboniferous earth movements is called the Allegheny or Variscan orogeny. Throughout the Early Carboniferous, Gondwana was drifting southward away from the equator, while the regions now making up Siberia, Kazakhstan, and North China were isolated. No tetrapod remains from the Carboniferous period have been found there, though it is not necessarily because there were none living there at the time. They may simply not have been found.

Throughout the Carboniferous, the climate became gradually more humid and warmer, at least in equatorial and tropical latitudes.

During the Early Carboniferous in the United Kingdom, for example, at least the early and mid-Viséan are thought to have been seasonal, with periods of severe water stress for plants and animals (Falcon-Lang 1999). This can be read in sequences of sediments and also in the type of growth rings found in some of the larger plants. Glaciation still affected the southern continents, and the deposits from localities in their middle latitudes from this time show an impoverished flora and fauna. However, all across the lowlands around the northern shores of Iapetus, the ocean that separated the northern and southern continents, there flourished an increasingly dense and speciose forest, stretching across Laurussia from what is now the central United States through Europe, Russia, and China. It is this forest that has left its legacy in the form of coal deposits, as well as providing almost the entire record of Carboniferous tetrapods (Milner 1993a).

The trees and other plants found in the Late Carboniferous forest flourished because of the warm, humid climate that the whole of the equatorial region experienced at that time. Unlike the trees of the Early Carboniferous, they show no growth rings in their wood (DiMichele and Hook 1992) because there were no seasons to affect plant growth in this way. Trees flourished, and when individuals died, their remains fell into swamp water made anoxic by all the fallen vegetation. So instead of decaying totally, as they do in modern rain forests, they accumulated into peat, which was then turned into coal.

Throughout the Carboniferous, changes to the gas composition of the air continued the trends begun in the mid-Devonian. The changes appear to coincide with the vast expansion of the coal forest vegetation (Graham et al. 1997; Algeo et al. 1995). A large proportion of the carbon material that was used by the plants was apparently not recycled but became locked in swamp deposits as peat and later fixed as coal. The result was that by the end of the Carboniferous, $CO_2$ levels had dropped to about the same levels as today, that is, about 0.03%, while oxygen content had risen to about 24% (the modern level is about 21%) (see Fig. 4.2). The effects must have influenced in their turn the breathing and gas exchange capabilities of all animals, not just air-breathing ones, because the atmospheric gas content must also have had a rebound effect on the water. It is notable that the current increase in $CO_2$ in the atmosphere results in part from the release of this ancient source of stored carbon from 300 million years ago, as fossil fuel is burned. Why this carbon was stored in such quantities during the Carboniferous, rather than being recycled as decayed matter, as it would be today, remains unclear.

The Carboniferous period gets its name from the fact that much of the world's coal deposits derive from rocks of this age. Vast quantities of carbon are tied up in the remains of plants that lived during this time interval and that became the source of so much of the present-day world's fuel. A look at how, where, and why these coal deposits arose helps understand what happened to the tetrapods of the time, which in turn helps us understand the Carboniferous world in general.

One striking phenomenon seen in the formation of coal deposits is a regular repetition or cyclicity of layers. Like the Devonian red beds described in Chapter 4, this may partly be a result of Milankovitch cycles. It also seems to correlate with periodically increased glaciation of the southern continents, which in turn affected the global sea level.

The trees in the Carboniferous grew in a clayey, often iron-rich soil, and with their root remains, this layer is called an underclay or seat Earth. This layer always lies under the coal seam, which is formed by the decay of layer upon layer of plant material. While the land surface is exposed, the lowlands and marshy regions can support such extensive plant growth. Gradually, however, as the sea level rises as a result of the melting of the ice cap, the sea floods the land surface, and the forest dies. This may happen in a fairly restricted local region, or it may be a more extensive, large-scale event. Finally, however, the coal forest sediments are covered by marine deposits, first of shale from shallow waters and then of limestone from more fully marine conditions. Then as the glaciation resumes, the sea levels fall again, and the sediments become less marine in character, with nonmarine limestones and shales eventually giving way to terrestrially deposited sandstone. Eventually the land surfaces are recolonized by plants, and the whole sequence starts again. The series of deposits so formed are called cyclothems, and they are characteristic of coal forest deposits; some localities show up to 100 of them in a sequence.

Until recently, it was assumed that the coal swamps formed exclusively in freshwaters, partly because among modern trees, few are well adapted to tolerate saltwater. However, more recent investigations of some coal deposits have revealed tidal influences and faunas characteristic of marginal marine conditions (Schultze and Maples 1992; Schultze et al. 1994; Schultze 1995), discussed further in Chapter 9. This is a similar problem to that of interpreting Devonian paleoenvironments explored in Chapter 4.

### Early Carboniferous Plants and Invertebrates

Many great changes occurred to the flora between the Late Devonian and the later parts of the Early Carboniferous. This was the time of the first major radiation of modern plant groups such as true ferns and seed plants, the gymnosperms related to today's conifers. During this period, *Archaeopteris* and *Rhacophyton* became extinct. Although swamps were still dominated by the lycopsids, these plants were essentially conservative. New species colonized coastal swamps and lagoons, and *Calamites*, related to today's *Equisetum* or horsetails, grew along stream margins, while ferns and pteridosperms grew in better-drained places (DiMichele and Hook 1992). Much information about the Early Carboniferous floras has come from localities preserved under volcanic sediments (e.g., Rolfe et al. 1990, 1994), and Chapter 8 shows how this kind of preservation has

thrown light on the early evolution of tetrapods. Other sources of information include that from fusain, which becomes much more common in the fossil record from the Early Carboniferous. Which kinds of plant are preserved as charcoal, in contrast to those that are not, can give quite detailed information about plant ecology and climate. It appears that the Early Carboniferous in Laurussia was monsoonal and that fires were a regular occurrence; in some instances, even the regularity of forest fires can be estimated, suggesting periods of between 105 and 1,085 years between events (Falcon-Lang 2001).

The locality of Horton Bluff has provided a picture of a Tournaisian wetland biota. Known for its early tetrapod fauna, it also preserves numerous horizons representing in situ standing vegetation (Rygel et al. 2006). Forests of the arborescent lycopod *Lepidodendropsis*, fossilized in the form of its lobed bases, formed dense stands, with trunks up to about 80 centimeters in diameter. Evidence for marine influence has been found in some horizons at Horton Bluff. It is not clear whether the plants there were salt tolerant or were killed in marine incursions, but they certainly lived in coastal areas, perhaps behind a sandbank. Many trackways from invertebrates have also been found at Horton Bluff, and many ray-finned fishes.

The structure of Viséan stage forests was much like that of the preceding Tournaisian, though the constituent species were different. By this time, the forests showed a complex mosaic of habitats and communities, as they do today, with some plants adapted for wetlands, some for better-drained places, and some for uplands. However, in the Carboniferous, there was a link between ecology and taxonomy, with related groups of plants specializing in some habitats and other groups in other habitats. Nothing like this separation is seen today (DiMichele and Hook 1992). In modern floras, the same plant group has many different species in different habitats.

A Mid Carboniferous (basal Namurian) flora has been described from Arkansas (Dunn et al. 2006). Generally, the flora of this period is poorly represented in the fossil record, so this locality is of some interest. It is extremely rich in terms of numbers of species and classes represented: three canopy trees, three understory trees, seven herbaceous seed ferns, and two ferns are represented as whole plants. In the landscape as a whole, seed ferns are the most speciose, with at least 10 identified.

By the end of the Namurian, there is evidence of more distinct and varied interactions between plants and animals. Truly herbivorous arthropods had evolved, and winged insects flew in the trees. Plants evolved devices to combat herbivorous arthropods, such as hard coatings to their seeds, and the arthropods, mainly insects, would have evolved ways to get around them, such as stronger mouthparts. However, the vertebrates would have had little impact on the plants until toward the end of the Carboniferous. No vertebrate evolved the ability to deal with plant food until the Stephanian (DiMichele and Hook 1992).

## Tetrapods of the Early Carboniferous: Experimenting with Shape and Form

Among the forests, rivers threaded their way, forming pools and channels in which the water-dwelling tetrapods and fishes lived. Sometimes the channels became blocked off from the main stream, as in oxbow lakes today, and these blocked channel deposits are often those which produce the best record of fossil tetrapods (Hook and Ferm 1988). Other localities result from shallow water pools, whereas yet others preserve animals from deeper-water environments.

In any discussion of Carboniferous tetrapods, something to bear in mind is that almost all the information comes from a very few, but very exceptional, sites representing coal-swamp pools and channels. Almost nothing is known of more upland environments, and only a little is known of the more terrestrially adapted tetrapods of the time. Many of the fossils of coal-swamp tetrapods derive from coal deposits worked in deep mines in the 19th century by coal miners who dug coal by hand and noticed fossils as they dug. Many of the best are from such old, deep mines, no longer available to paleontologists, such as those of the Low Main Seam mined at Newsham in Northumberland, England, and those of the Scottish localities of Gilmerton, Loanhead, and Borough Lee. Today, most coal fossils go unnoticed as they are dug out by machines, unless they are spotted by enthusiasts searching open-cast sites. Some of the more recent discoveries of coal fossils have been of this sort, including the Namurian site of the Dora bone bed in Cowdenbeath (Andrews et al. 1977), Scotland, and a single specimen from the Coal Measures of Wigan, Lancashire, England (Milner and Lindsay 1998).

After the end of the Devonian, the fossil record of tetrapods becomes sparse, and until recently, only a few fragments of limb bones had been found from rocks representing the succeeding 30 million years. This significance of this gap in the record was noted during the early 1950s by paleontologist A. S. Romer, who pointed out that much of the evolution of terrestriality probably occurred during this period for which there is almost no information. It has been called Romer's Gap in his honor (Coates and Clack 1995). The interval covers the whole of the Tournaisian and most of the Viséan.

In a discussion of Romer's Gap, Ward et al. (2006) found that there seemed to be a parallel between the lack of fossil record of tetrapods and that of arthropods. They therefore inferred that the gap was the result of a real lack of animals to be fossilized, rather than a taphonomic artifact. Because this gap seemed to be bounded at its inception by terrestrialization of arthropods and at its close by the terrestrialization of tetrapods, they suggested that the lack of a fossil record in between signified that conditions were unfavorable for terrestrial animals. They pointed to the low oxygen levels expected under Berner's (2006 atmospheric model discussed in Chapter 4, and they inferred that this confined the animals to the water.

This suggestion does not really work for a number of reasons. First, fossil tetrapods at least are more commonly found in water-laid deposits such as lakes, rivers, and estuaries than they are in terrestrial ones, so that

should not affect the numbers in which they are discovered. Second, a low level of atmospheric oxygen in the air predicates an even lower level in the water, so that it might be expected that air-breathing, i.e., terrestrial, animals would be selected for. In any case, the idea of Ward et al. (2006) does not accord with the diversity that is seen at the end of Romer's Gap and the growing record of tetrapods during this period, to be discussed in this and the next chapter.

Since Romer's time, the record of tetrapods from the Viséan has been increased by some spectacular finds, so that now, several tetrapod genera represent the top part of this period. In the last year or so, as with the Devonian tetrapods in the early 1990s, the logjam that forms Romer's Gap is beginning to break as more Tournaisian and early Viséan tetrapods are being discovered. The most notable of these is the recent discovery of a whole Tournaisian ecosystem in Scotland, mentioned below. However, it seems clear that immediately after the end of the Devonian, there was indeed a period of low diversity representing a recovery period from an extinction event.

The interrelationships of early tetrapods constitute a problem that for the time being is unsatisfactorily resolved. There seems to be little obvious connection between the tetrapods of the Late Devonian and those of the Early Carboniferous. The Late Devonian forms share a suite of features that are at present regarded as primitive for all tetrapods, with the only possible exception to this being *Tulerpeton*. However, once over the Devonian–Carboniferous boundary, an almost completely different complement of taxa is found. There are two possible exceptions to this observation. First, a single example of a group that possibly crossed the boundary may be the mainly Carboniferous whatcheeriids, represented by a postorbital and a lacrimal bone from the Red Hill locality in Pennsylvania (Daeschler et al. 2009). There is also some suggestion that *Tulerpeton* may turn out to be a whatcheeriid if it were better known. Second, there are also *Acanthostega*-like and *Ichthyostega*-like elements that have been found at Horton Bluff (Anderson et al. 2009). It may nonetheless be that most of the Devonian forms became extinct at the end of the Devonian, as suggested in Chapter 4. By the time they are found in any numbers in the fossil record, Carboniferous tetrapods had reradiated into a wide range of morphologies and ecologies.

Some of the genera that are coming out of the Early Carboniferous challenge the present understanding of tetrapod evolution in that they do not readily fit into any scheme of classification based on the forms appearing later during the Late Carboniferous. They hint at a diversity of form and function among these earliest tetrapods representing ecologies and lifestyles no longer found on Earth today. For many of them, the part they played in the evolution of tetrapods can only be guessed at. How they are related to each other or to more recent forms, or even whether or not they were descended from more terrestrial ancestors, remains to be discovered.

When the tetrapods that lived throughout the early parts of the Carboniferous period, the Tournaisian, Viséan, and early part of the

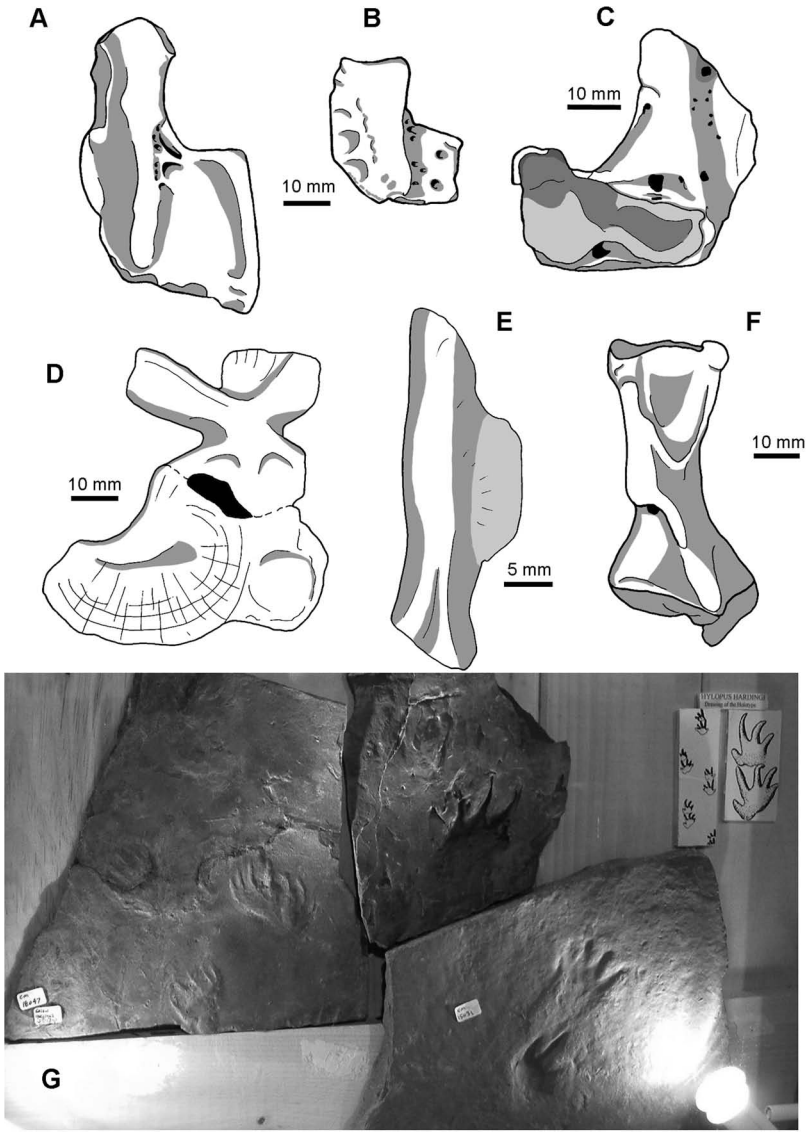


**7.2.** (Color Plate 13) Horton Bluff, also known as Blue Beach, in Nova Scotia, Canada, from which some Tournaisian tetrapod elements have been recovered. *Photograph by J.A.C.*

Namurian are compared, it seems there was a different complement of genera from those that lived during the Westphalian. Only one genus (*Loxomma;* see Chapter 9) crosses this boundary, and indeed, there is another noticeable gap in the tetrapod record from the middle part of the Namurian to the early part of the Westphalian (Smithson 1985a). The next sections describe these animals roughly in their order of appearance in the fossil record to try to convey some of the strangeness that stretches the imagination in trying to make sense of them.

## The Horton Bluff Tetrapods

Until recently, the only evidence of tetrapods from the earliest phase of the Carboniferous, the Tournaisian, consisted of a few isolated elements from a locality known as Horton Bluff, or Blue Beach, in Nova Scotia (Figs. 7.2, 7.3). They are at present the earliest post-Devonian tetrapod remains known, coming from the Ivorian stage of the Tournaisian (Rygel et al. 2006). Some specimens have been described and consist of limb and girdle fragments (Clack and Carroll 2000). At least three kinds of humeri are represented, one resembling that of an animal like *Tulerpeton* or possibly an early anthracosaur like *Eoherpeton*. Another is more like that of a juvenile colosteid, and a third resembles that of the whatcheeriid




**7.3.** Horton Bluff tetrapod elements. (A, B) Two tetrapod humeri of different types. (C) Scapulocoracoid resembling that of *Ichthyostega*. (D) Pelvic girdle, like that of *Pederpes*. (E) Femur like that of *Acanthostega*. (F) Second type of femur. (G) Photographs of tracks from Horton Bluff in the Blue Beach Museum, Nova Scotia. *Photograph by J.A.C.*

*Pederpes*. There is a partial shoulder girdle preserving the lower part of the scapulocoracoid, and this somewhat crescent-shaped bone shows one feature in which it resembles that of *Ichthyostega*. Partial interclavicles from Horton Bluff also resemble those of anthracosaurs in being kite shaped. Even by the Tournaisian, a range of tetrapod morphologies was present. Since 2000, more specimens have been discovered, including an *Acanthostega*-like femur, more elements of a *Pederpes*-like animal, and further unattributed humeri. These are currently being studied (Anderson et al. 2009).

In addition to body fossils, Horton Bluff has produced a wide range of tetrapod trackways, representing at least six morphotypes and a wide range of sizes. They occur on subaerially exposed substrates (Rygel et al. 2006). With their very early date in the Carboniferous, it is possible to



**7.4.** (Color Plate 14) Photograph of the locality from which the specimen of *Pederpes* came, shown by the black arrow. Rob Clack is standing on the promontory called Lot's Wife. *Photograph by J.A.C.*

infer from these trackways either that a rapid diversification occurred immediately after the end of the Devonian, or that a wider range of tetrapod morphologies was present in the Devonian that is not represented in the fossil record. It certainly shows that tetrapods were not confined to the water at that time.

### WHATCHEERIIDS

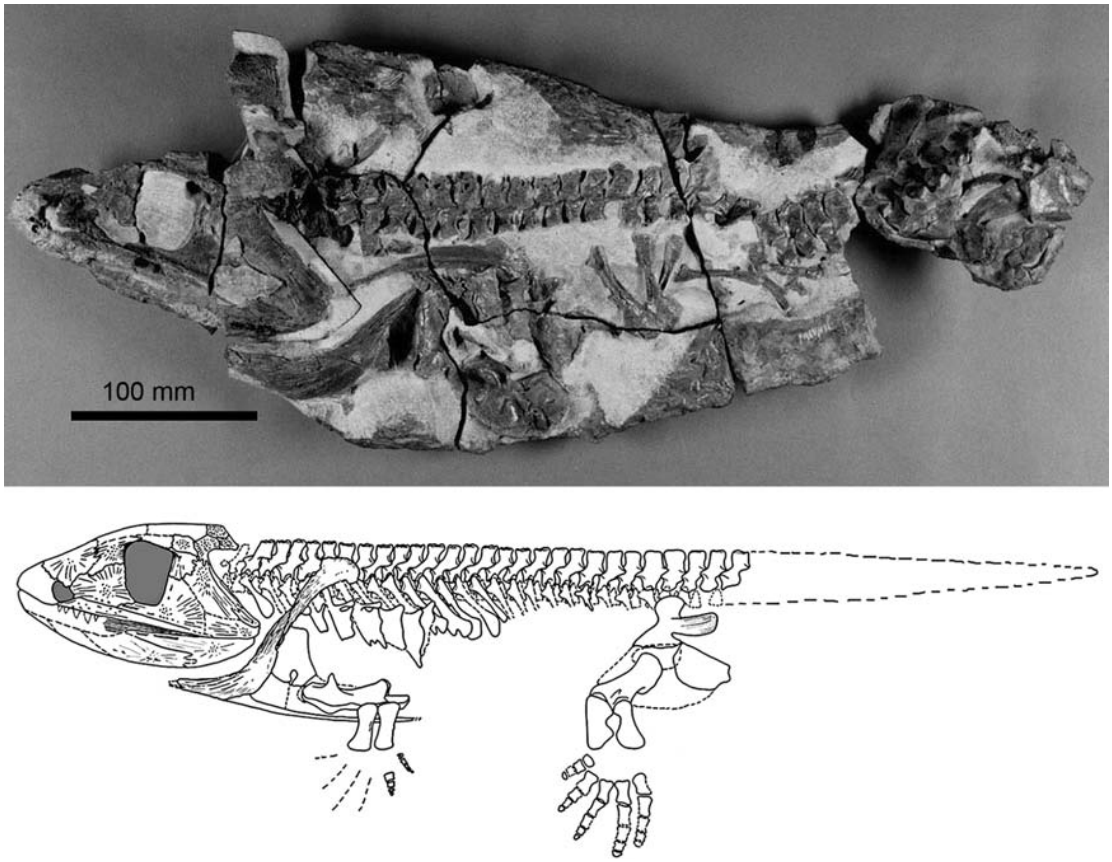
The whatcheeriids are the most recently recognized family of Early Carboniferous tetrapods that seem to range widely both geographically and temporally. Some of the taxa that have been ascribed to the group may eventually turn out not to belong here, and the family may represent something of a "grade group" encompassing various primitive taxa. The two best known are *Pederpes* and *Whatcheeria*.

*Pederpes finneyae* is a single specimen of a tetrapod from late Tournaisian deposits of western Scotland, and it is the only Tournaisian tetrapod so far to be preserved as an articulated specimen (Clack 2002b; Clack and Finney 2005). It is slightly younger than the specimens from Horton Bluff. It takes its name in part from its discoverer, Peder Aspen, linked to the Latin for foot, "pes." Peder, the Norwegian form of Peter, also means "rock." Coincidentally, the name *Pederpes* also breaks down into "ped" (also meaning foot), and "-erpes," which is Greek for "crawler." Thus it can mean "Peder's foot," "rock foot," or "foot crawler." The specific name is in recognition of the contribution of the preparator, Sarah Finney (see Acknowledgments and Chapter 1).

The sequence in which it was found, the Ballagan Formation, consists of shales, clays, and limestones that originated in marginal marine conditions (Fig. 7.4). The specimen was found in a limey clay nodule and is an almost intact skeleton, lacking only the tail, some parts of each limb, the top of the head, and most of the lower jaws (Fig. 7.5). Its intact preservation may suggest that the carcass had been mummified before burial, but as one of the only vertebrate fossils to have been found in the sequence, its isolation suggests that it had been washed in from elsewhere as an erratic. The only other vertebrate remains so far found in the sequence are a lungfish rib, a few small limb bones (P. Gavin personal communication), and a few unidentified microremains.

The skull profile was high rather than flattened, with deep cheeks and large orbits facing more sideways than upward (Fig. 7.6). The back part of the cheek extended far backward beyond the back of the skull table, which itself was relatively short, and a steep angle was formed between the skull table and cheekbones. Its lower jaw is poorly preserved, though there is information on the palate and braincase.

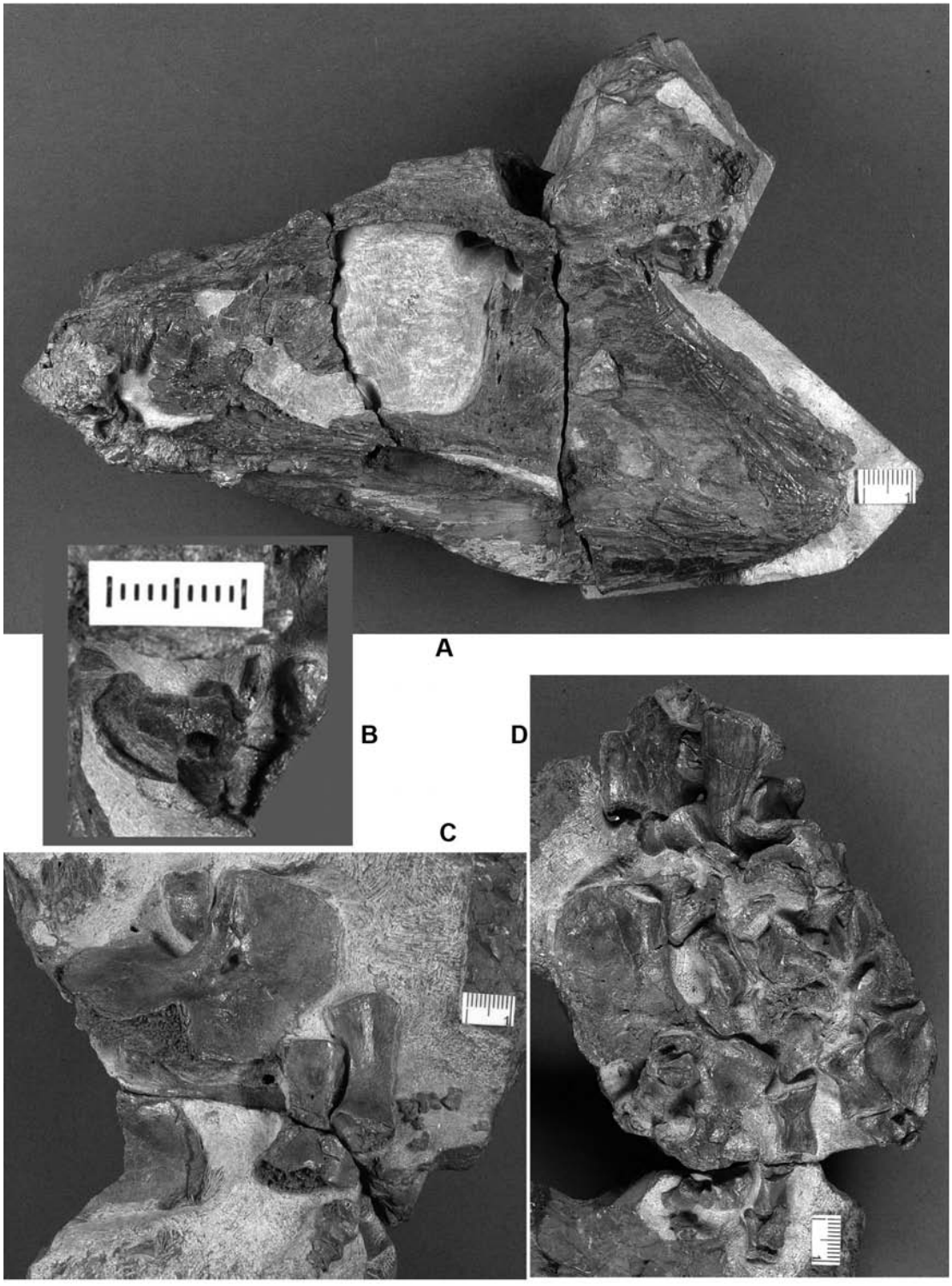
One stapes is present and well preserved and looks like a relatively smaller, but absolutely larger, version of that of *Acanthostega*—not surprising in a proportionately larger animal (Fig. 7.6A, B). However, the postcranial skeleton of *Pederpes* is different from that of *Whatcheeria* in many respects.




**7.5.** Photograph and skeletal reconstruction of *Pederpes finneyae*. *Photograph by S.M.F.*

The humerus resembles most closely that of the baphetid *Baphetes*, marked in particular by a prominent spikelike process for the latissimus dorsi muscle that attaches to the shoulder girdle and raises the forearm. Two forelimb digits only are preserved, of the right hand, but these two are rather different from each other. One is short and stubby, whereas the other is more slender and tiny (Fig. 7.6C). This tiny digit appears to be a more posterior one than the other, suggestive of the tiny digits at the leading or trailing edges of the hind limb of *Ichthyostega*, both limbs of *Acanthostega*, and the forelimb of *Tulerpeton*. Though the manus is incomplete, the inference is that it may have retained a polydactylous state like the limbs of the Devonian tetrapods.

Another feature suggestive of *Ichthyostega* is the form of the ribs. They have triangular flanges on the shafts, as indeed do some of those of *Whatcheeria*, but in the case of *Pederpes*, there is also a curious prong-like process separate from and dorsal to the triangular flange. This form of rib is also seen in some aquatic temnospondyls such as *Eryops* and *Sclerocephalus* (see Chapter 9), and it may be more widely distributed than has been appreciated up to now. Its functional significance remains unknown.


A
B
C
D

The hind limbs of *Pederpes* are quite robust. Five digits are preserved on the hind foot of *Pederpes*, which may be the full complement, although this cannot be taken for granted (Fig. 7.6D). In terms of the pedal morphology and the complement of phalanges, *Pederpes* resembles more conventional Carboniferous tetrapods such as colosteids, and the inference here is that it had a pentadactyl hind limb. If this is correct, taken together with the manual digits, it suggests that the hind limb achieved pentadactyly in advance of the forelimb. This is in accord with the suggestion that development of the hind limb became advanced over that of the forelimb in post-Devonian tetrapods (Chapter 6).

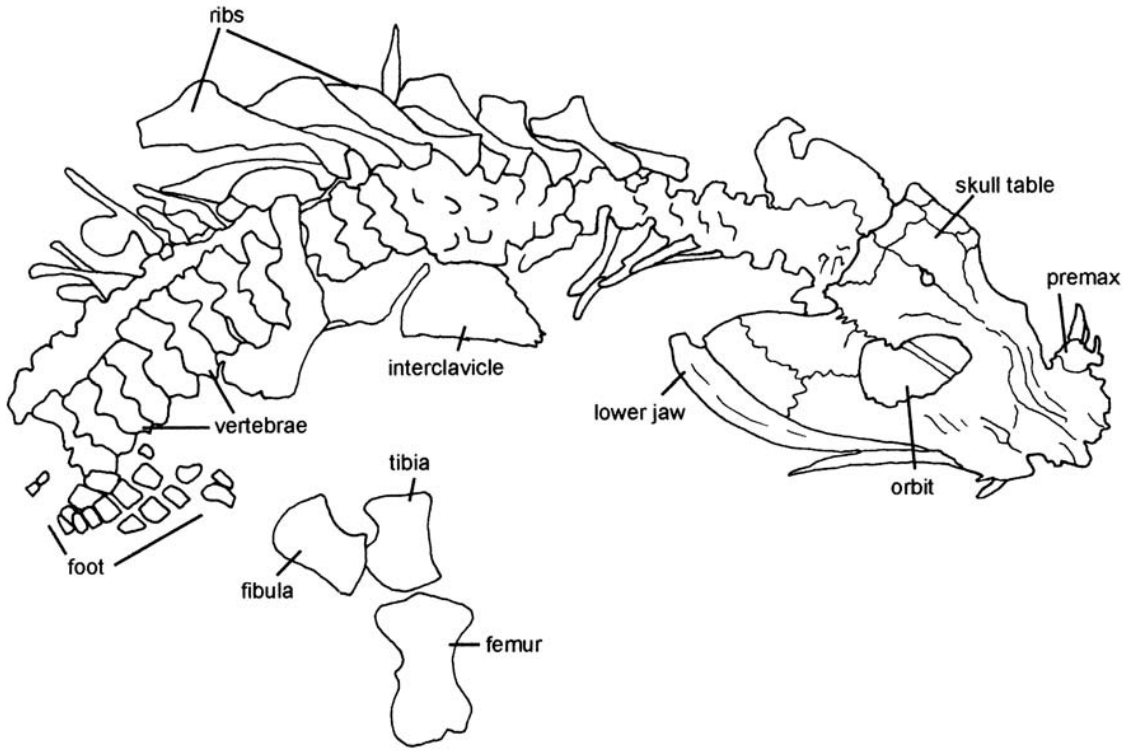
There is one more interesting feature of the hind limb of *Pederpes*. The metatarsals are clearly distinguishable from the phalanges, unlike the condition in Devonian tetrapods, and furthermore, they are slightly asymmetrical about their long axes. This asymmetry is also seen in post-Devonian tetrapods. It has been taken to indicate that the foot was beginning to be oriented with the toes pointing forward, rather than directed laterally as in *Acanthostega*, for example. In other words, *Pederpes* is the first animal to show evidence of a foot adapted for terrestrial locomotion.

The first whatcheeriid to be discovered and described was *Whatcheeria deltae*, after which the family is named. This creature, unlike almost all its near contemporaries, comes not from Scotland but from the United States. It was found near the town of What Cheer, near Delta, Iowa, in an abandoned limestone quarry (Bolt et al. 1988; Lombard and Bolt 1995; Bolt and Lombard 2000) whose deposits are mid-Viséan in age. The sediments in which it was found are thought to represent lake, river, and swamp environments in a coastal lowland setting, and it is possible that on occasions the water in the swamp was brackish as the sea made incursions into the area. *Whatcheeria* itself was the most common tetrapod found at the site, and several articulated and nearly complete skeletons were recovered. The locality also yielded colosteids and other fragmentary tetrapods, as well as fish and invertebrates. The fish fauna includes rhizodonts, osteolepidids, the lungfish *Tranodis*, and a few acanthodians, elasmobranchs, and actinopterygians (Lombard and Bolt 1995).

The skull of *Whatcheeria* is about 200–250 millimeters long and is armed with an array of large recurved teeth (Fig. 7.7). It is similar in shape to that of *Pederpes*, but there are a few detailed differences, for example in the shape of the orbit. The midline of the skull of *Whatcheeria* was strengthened by buttresses running along its length, but this portion is missing in the fossil of *Pederpes*.

As in *Pederpes*, the skull retains a number of primitive characters, such as the preopercular bone, and some characters of the lower jaw that are lost in later tetrapods. The latter include a row of small teeth along all three coronoid bones, and a row of meckelian fenestrae between the postsplenial and prearticular. This represents a stage in lower jaw construction between that of *Acanthostega* and *Ichthyostega* in which there was a single slotlike meckelian fenestra along most of the lower jaw margin, and that of later tetrapods in which the splenial bones became more or

**7.6.** *Pederpes finneyae.* (A) Photograph of the skull. (B) Close-up of the stapes. (C) Forelimb showing humerus, radius, ulna, and two disrupted small digits. (D) Hind limb showing femur and five digits along with other elements including intercentra and part of the pelvis. Scale bars = 10 millimeters. *Photographs by S.M.F.*




**7.7.** Drawing of one specimen of *Whatcheeria deltae.* Animal is up to 1 meter long.

less fully sutured to the prearticular (see Chapter 10). *Whatcheeria* also has a sheet of denticles on the prearticular, another primitive feature seen in *Acanthostega* and lost in most later forms (Lombard and Bolt 2006). The palate has not yet been fully described, but work is in progress (Bolt personal communication).

The postcranial skeleton of *Whatcheeria* is well preserved in most respects and shows an animal of up to about a meter long. The expanded ribs found in the thoracic region of the trunk resemble those of *Pederpes*, and like those, they are somewhat reminiscent of those of *Ichthyostega*. Its paddlelike limbs are more reminiscent of both *Ichthyostega* and *Acanthostega* than are those of *Pederpes*, which does not show the flattening of the tibia, fibula, and phalanges characteristic of *Whatcheeria*. The inference from this is that *Whatcheeria* was more aquatically adapted than *Pederpes*. The fossils show that at least five digits were present on the limbs, but none of the specimens is complete, and it is possible that more were present.

### *SIGOURNEA MULTIDENTATA*

As well as *Whatcheeria*, the Delta locality in Iowa has yielded partial remains of several tetrapods, some of which may represent new taxa. One of these that has been described is *Sigournea* (Bolt and Lombard 2006). This animal is known only from a single lower jaw specimen, but it is sufficiently distinctive to merit its own name. Now that lower jaw characters

are better understood, this can be done with some confidence. *Sigournea* retains several primitive characters also seen in *Whatcheeria*, such as a row of many small teeth along all the coronoids and the presence of a row of four small meckelian fenestra along the ventral margin of the jaw. It is distinguished from *Whatcheeria* by characters such as the form of the dentary teeth and the lack of denticles on the prearticular.

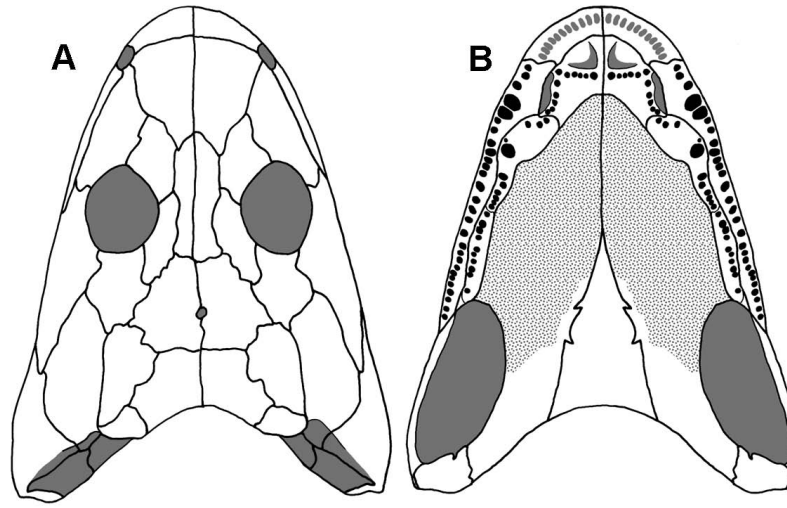
### *OSSINODUS PUERI*

Until recently, finds of Carboniferous tetrapods had been confined to Euramerica, despite the presence of Devonian tetrapods in Australia. In 1996, finds of tetrapods from a site in Queensland, Australia, known as Middle Paddock proved that they existed well outside the Laurussian continent, in Gondwana (Thulborn et al. 1996). The finds, from the Ducabrook Formation, are dated as the equivalent of early–mid-Viséan and are among the earliest of tetrapod fossils found anywhere. Other vertebrate material from the site includes chondrichthyan remains, actinopterygians, gyracanthid acanthodians, and a few rhizodont and lungfish elements. Shrimplike crustaceans, plant macrofossils, and a rich flora represented by spores are also present. The site is thought to represent a shallow fluviatile or lacustrine environment (Thulborn et al. 1996).

The tetrapod material consists of isolated, often broken bones that are difficult to identify as belonging to particular groups. Possible colosteids, temnospondyls, and anthracosaurs were identified at first, but more recent discoveries have suggested that these identifications might not be correct. The bones include a massively broad skull table bearing deeply pitted ornament. Its sutures are hard to make out, and various interpretations have been published, but the latest suggests that like *Ichthyostega* and *Acanthostega*, the skull did not include a separate intertermporal. The tabular region was excavated for a temporal notch. This skull table has been linked to one of the most recent finds, a more or less intact left half of a skull and palate (Fig. 7.8) (Warren and Turner 2004; Warren 2007). The palate is closed and denticulated, as in primitive tetrapods, and the dental pattern resembles that of the Devonian forms and the enigmatic *Crassigyrinus*. The posterior portion of the cheek was elongated, also as in *Crassigyrinus*. If they really belong together, this animal was a strange mixture of features, with a highly unusual skull pattern.

Some elements of the postcranial skeleton, such as the cleithrum, interclavicle, scapulocoracoid, and some of the ribs, resemble those of whatcheeriids, and in a cladistic analysis, *Ossinodus* grouped near *Pederpes* and *Whatcheeria* (Warren 2007). If that relationship stands the test of time, it adds to the picture of whatcheeriids as a group with a wide geographical range through the Early Carboniferous.

The exact identity and relationships of these Australian animals may remain obscure unless articulated material is found—unlikely given the type of preservation at the locality—but biogeographically, they are important in showing that tetrapods inhabited Gondwana at this early stage.

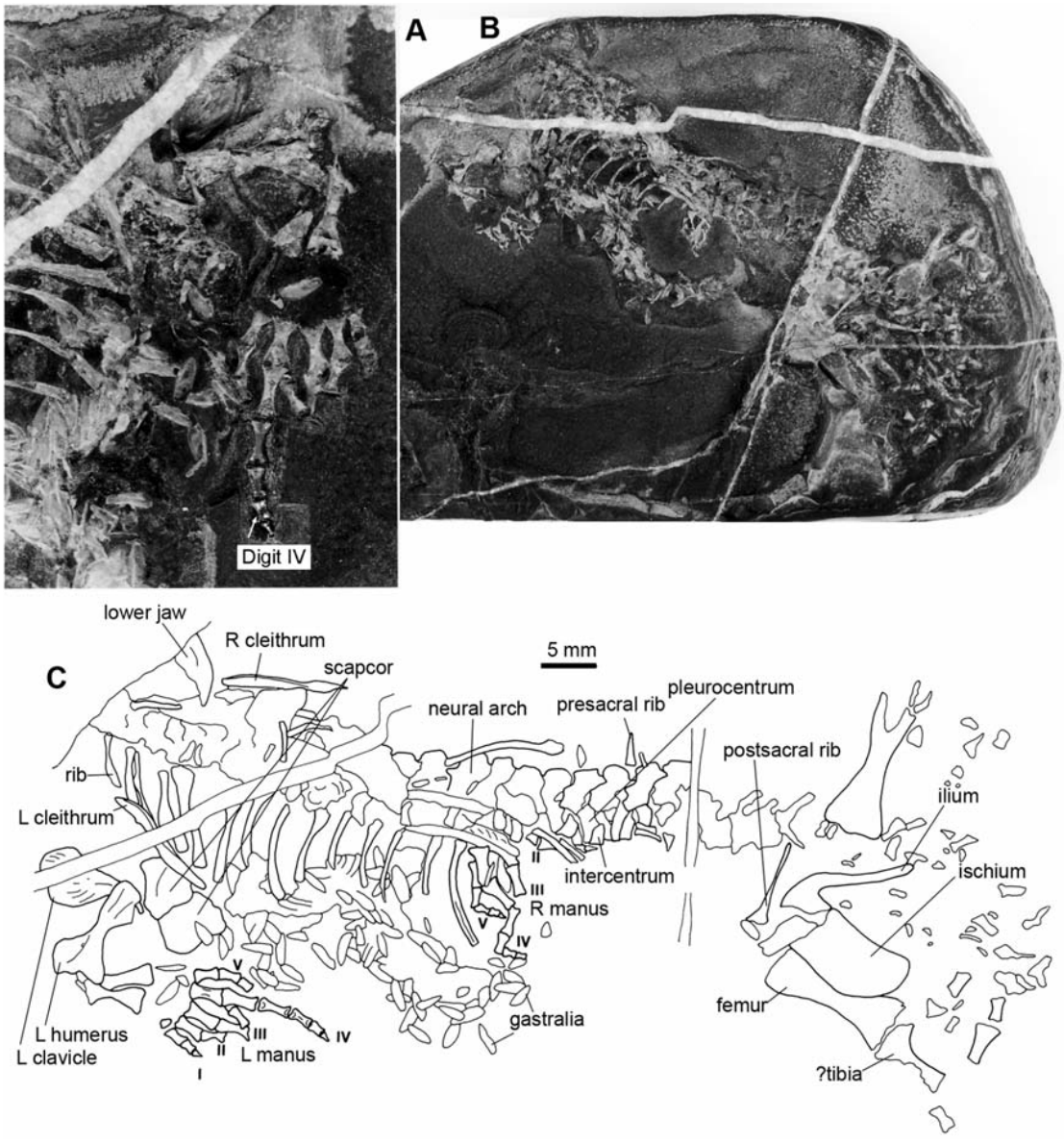



**7.8.** Reconstruction of the skull of *Ossinodus pueri*. (A) Dorsal view. (B) Ventral view. The braincase is unknown. Note that this reconstruction assumes that the skull and cheek region belong to the same species and are from individuals of a similar size. Skull is about 250 millimeters long. *Based on Warren (2007).*

### *CASINERIA KIDDI*

A single small specimen from a coastal locality not far from Edinburgh, Scotland, represents one of the most tantalizing finds from the Early Carboniferous (Paton et al. 1999). Found on the coast at Cheese Bay in Viséan age rocks, the name *Casineria* is derived in part from the Latin for "cheese." The specimen came from a horizon known as the Cheese Bay Shrimp Bed, which has yielded numerous specimens of the crustacean *Tealliocaris*. These are preserved in exquisite detail, suggesting that there was little postmortem disturbance of the fine-grained sediments. The fauna also includes scorpions and a few actinopterygians and hydroids, and recently a small lungfish has been found there (NMS G.2007.54.3).

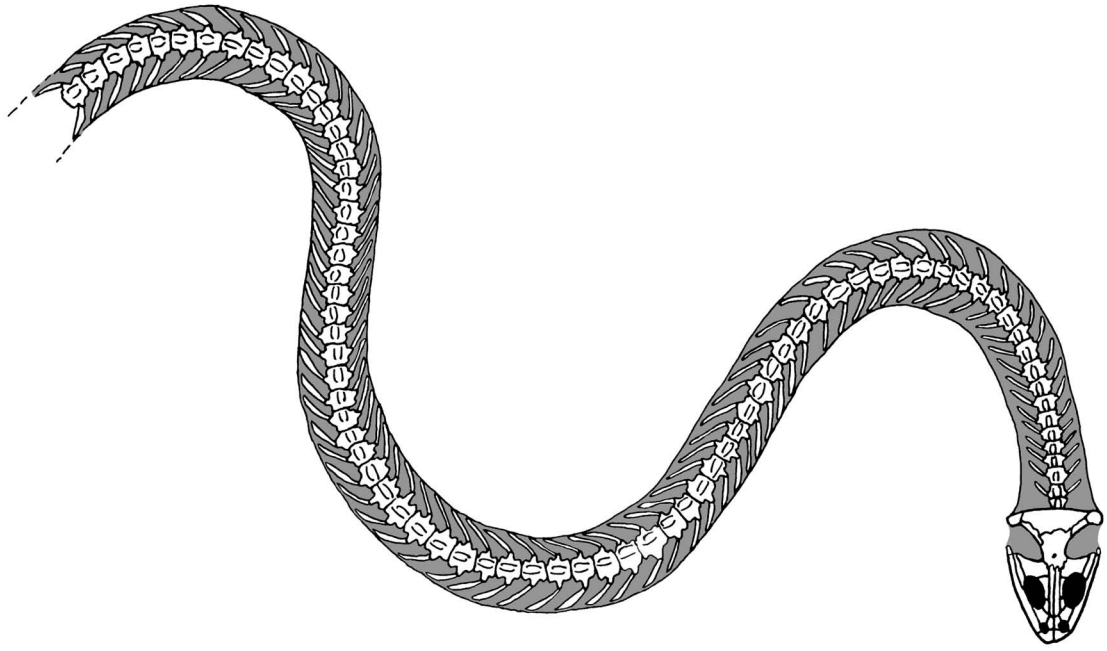
The tetrapod skeleton consists of a nodule in part and counterpart showing well-preserved vertebrae, ribs, and forelimbs, less well-preserved hind limbs (water worn and only on half of the specimen) and measuring only a few centimeters from neck to pelvis (Fig. 7.9). The vertebral column is solidly ossified and is of the form called gastrocentrous, having large pleurocentra. It has long, slender, curving ribs and oval-shaped gastral scales. Most remarkable, however, is the preservation of one of its forelimbs. This shows that the humerus is much more slender than that of any other Early Carboniferous tetrapod, having an obvious shaft and with the two ends set at different angles to each other (known as torsion). The radius and ulna are also slender, with an olecranon process on the ulna (though this is not easily visible in the figures). These features alone strongly suggest a fully terrestrial animal. However, in addition, the manus has five slender digits, with the fourth substantially longer than the others, and on the underside, the individual phalanges show tiny V-shaped grooves that would have housed ligaments to the next phalanx. The last phalanx on each digit (the ungual) is noticeably curved, and the whole arrangement suggests a hand capable of grasping. No other Early




Carboniferous tetrapod shows digits like this, but they are similar to those found in Late Carboniferous early amniotes. *Casineria*, however, comes from a deposit dated as early Viséan, about 20 million years before the earliest amniotes have been found!

Perhaps the most striking thing about *Casineria*, in view of it date, is its small size. Most Early Carboniferous tetrapods so far known are large, with skull lengths of 100–300 millimeters, and apart from a microsaur from East Kirkton (see Chapter 8; Clack et al. in press), *Casineria* is by far the smallest. It has been suggested that the origin of amniotes is connected with an evolutionary step involving small size (see Chapter 10), and here is a specimen that accords well with that theory.

**7.9.** *Casineria kiddi*. (A) Enlargement of the region around the hand (NMS G1993.54.1). (B) One of the blocks of the specimen of *Casineria kiddi*. *Photograph by S.M.F.* (C) Specimen drawing of *Casineria,* taken from part and counterpart. *From Paton et al. (1999).*



**7.10.** Skeletal reconstruction of *Lethiscus stocki.* The skull is about 30 millimeters long.

Unfortunately, the head of *Casineria* is not preserved, which makes it difficult to determine its relationships to other tetrapods. In some respects, the skeleton resembles the more terrestrial forms such as *Gephyrostegus* (see Chapter 9). Despite the lack of a skull, a phylogenetic analysis of a range of early tetrapods, including several amniotes, placed *Casineria* among the early amniotes of the Late Carboniferous (Paton et al. 1999). If this is its true position, it suggests that the origin of amniotes might have been much earlier than otherwise suspected, and furthermore, that fully terrestrial tetrapods had evolved soon after they had emerged from the water in the Late Devonian (Ruta et al. 2002).

### AÏSTOPODS

Until the recent discovery of the Tournaisian tetrapod *Pederpes*, the earliest articulated post-Devonian tetrapod was a creature called *Lethiscus*, a member of a group known chiefly from the Coal Measures, the aïstopods (Fig. 7.10) (Carroll et al. 1998). The name *Lethiscus* comes from the name of the River Lethe, the river of forgetfulness, one of the rivers in ancient Greek mythology that flowed into Hades. *Lethiscus* comes from Viséan rocks found at a locality near Edinburgh in a sequence called the Wardie Shales. This marine sequence of shales and ironstone nodules is more famous for its many fine fossil fishes, including many genera of ray-fins and sharks. *Lethiscus* is the only tetrapod to have been found there, suggesting that, like *Pederpes* and *Casineria*, it did not habitually live in the environment where it was preserved.

Although it is more primitive in some ways than its later relatives, *Lethiscus* is nonetheless highly specialized and scarcely recognizable as a tetrapod at all. Aïstopods were snakelike creatures that had lost all trace of limbs and girdles, and *Lethiscus* had increased the number of vertebrae to at least 80 (the specimen is incomplete). Aïstopod skulls were also strange, in some cases reduced to a series of struts and bars or a mosaic of small plates. These will be dealt with in more detail in Chapter 9.

In *Lethiscus*, the skull, which is about 60 millimeters long, shows several of the characters that distinguish aïstopods, but it is not as specialized as later members of the group. Its eyes are large and far forward on the skull; many of the bones of the cheek have been lost, their places represented by open spaces. The ribs, which evolved into unique K-shaped structures in later aïstopods, were more or less straight in *Lethiscus*.

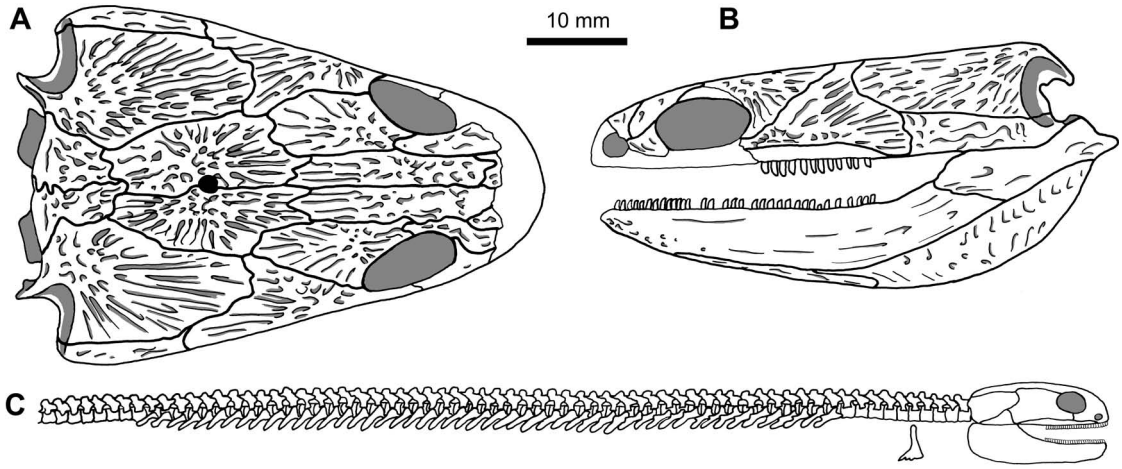
*Lethiscus* is acknowledged as a tetrapod even though it had no limbs because it shows features of the skeleton that are thought to characterize tetrapods. These include a skull in which a large part of the orbit margin is formed from the jugal bone, and in which the snout is formed by the expected series of paired bones, rather than the mosaic found in fish. The well-ossified vertebrae and ribs provide further evidence of its tetrapod nature.

The existence of such a specialized animal so early in the fossil record of tetrapods shows that a great deal of evolutionary diversification and adaptation must have taken place in the time since tetrapods first evolved. Presumably *Lethiscus* had ancestors with legs and digits, although it is impossible to say how many digits this ancestor might have had. The Devonian tetrapods are known to have shown variation in the numbers of digits, but with the discovery of *Casineria*, it is clear that by the mid-Viséan, at least some tetrapods had evolved the more usual five. *Lethiscus*, with none at all, provides a puzzling contrast.

How *Lethiscus* lived is a mystery. *Lethiscus* is the only tetrapod to have come from this much-collected site. Its occurrence is thought to have been erratic, meaning that its presence at Wardie was the result of accidental transport of the carcass from elsewhere, and its original habitat might have been either aquatic or terrestrial.

### ADELOGYRINIDS

Another group of limbless animals is found during the Viséan and early parts of the Namurian. These are the adelogyrinids (Fig. 7.11). Several specimens have been found in different localities, all in Scotland, and many seem associated with fish faunas, though they occur sporadically with other tetrapods. They are considered to have been mainly aquatic. There are four named genera, of which *Adelogyrinus* was the first named, but because each is incompletely preserved and all are restricted to a fairly limited geographical area, there is a question about whether they are all valid. They could all belong to the same taxon, preserved in different ways (Andrews and Carroll 1991).



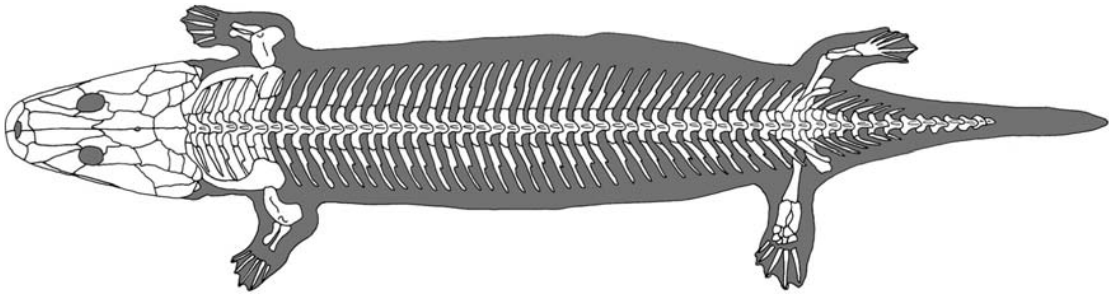

**7.11.** Adelogyrinids. (A, B) Skull of *Adelospondylus watsoni* in dorsal and left lateral views. (C) Skeletal reconstruction of an adelogyrinid. Scale bar for skulls = 10 millimeters. *Based on Andrews and Carroll (1991).*

Like the aïstopods, they have elongated bodies and highly modified skulls with the eyes placed far forward. Unlike the aïstopods, they retain a substantial dermal shoulder girdle, and though no limb elements have been recognized, such an extensive dermal girdle suggests that the limbs were present but that the bones remained as cartilage and so were not preserved. The vertebrae were holospondylous—single complete cylinders—but the ribs were not modified like those of aïstopods, but more like those of a conventional primitive tetrapod.

Unlike the aïstopod skull, that of the adelogyrinids was completely roofed with ornamented dermal bones, though the complement was different from any other tetrapods and appears reduced by comparison with more primitive tetrapods. At the back was a rounded embayment or temporal notch occupying the rear margin of the cheek.

They appear to have been capable of a large gape. The teeth were sharply chisel shaped and arranged in close order, like a hacksaw blade. These might possibly have been used as a filter-feeding device through which water could be expelled once the mouth was closed, and several specimens are found in strata that preserve numerous small crustaceans called ostracods. The teeth show no evidence of wear and are unlikely to have been used either for eating plants or subduing active prey. The hyoid apparatus was extremely well ossified and relatively large, though it does not show the grooving found in that of *Acanthostega*; more likely it contributed to a mechanism of suction feeding rather than breathing. This would be consistent with the tooth morphology and large gape and implies that the animals were aquatic.

Though adelogyrinids share several derived characters with other animals usually included among the "lepospondyls" (see Chapter 9), such as vertebral construction, and have elongate bodies with small or absent limbs, in other respects, they appear to be the most primitive members of this assemblage. In several recent phylogenetic analyses, they consistently cluster with colosteids such as *Greererpeton* (Ruta et al. 2003; Ruta and Clack 2006; Clack and Klembara 2009), though



**7.12.** Skeletal reconstruction of *Greererpeton* viewed from above. *Based on Godfrey (1989).* Animal is about 750 millimeters long snout to tip of tail.

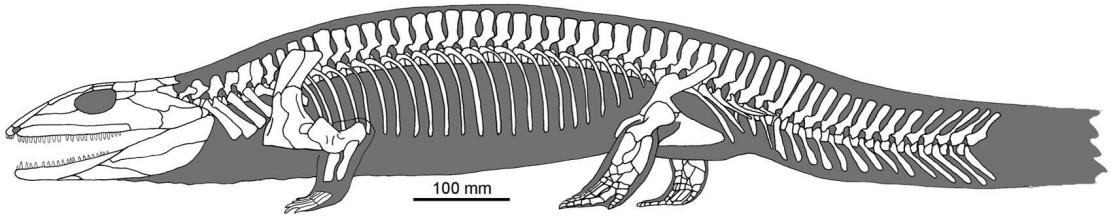
others place them with other lepospondyl groups (e.g., Laurin 2004), an intuitively more likely position.

### COLOSTEIDS

One group of Early Carboniferous tetrapods seems to be more commonly and more widely represented than most of the others. These are the colosteids. They are known from the United Kingdom and North America.

A couple of North American genera are well known from nearly complete skeletons: *Colosteus* after which the group is named, and *Greererpeton* (Fig. 7.12) (Romer 1972b; Carroll 1980; Smithson 1982; Hook 1983; Godfrey 1989a, 1989b). The two genera are similar, with *Greererpeton* the more completely known. The genus *Greererpeton* was named after the Greer quarry where the animals were first found, in West Virginia, United States, in the Mauch Chunk Group, which dates from around the Viséan/Namurian boundary. Several well-preserved and nearly complete skeletons from this quarry lay beside one another in the deposit, suggesting that the animals had died more or less simultaneously, perhaps in a drying riverbed. This locality has also yielded several other well-preserved genera, including *Proterogyrinus,* indicating that a rich fauna was living at the site. Articulated skeletons of the lungfish *Tranodis* suggest that those animals were living alongside the tetrapods, whereas spines of gyracanthid acanthodians, actinopterygians and sarcopterygian elements, and plant fragments appear to have been washed in from elsewhere (Holmes 1984). A single skeleton of a colosteid from Scotland, *Pholidogaster*, comes from the Gilmerton Ironstone, mined near Edinburgh. This locality is dated as Viséan and is also notable for having yielded specimens of *Crassigyrinus*, *Eoherpeton*, and *Loxomma* (see Chapter 9), as well as the rhizodont *Screbinodus*, lungfishes, and actinopterygians.

Most *Greererpeton* specimens are of animals with flattened shallow skulls, though some from southern Illinois, preserved in a different way, suggest that at least some of the flattening is preservational (Schultze and Bolt 1996). It is clear that colosteids were fully aquatic. They had short limbs with a robust ventral covering of gastral scales and also a dorsal covering of rounded scales. The length of the tail is not known, but it does seem to have been deep and flattened from side to side. The




**7.13.** Skeletal reconstruction of *Proterogyrinus. Based on Holmes (1984).*

skull outline was a smooth U shape whose arms diverge a little toward the rear. The large orbits looked dorsally, though the size of the eyeball is not known, nor whether they would have been flat inside the skull or bulged out above it. The lower jaw has been described in some detail from excellently preserved southern Illinois material, and lower jaw material has also been found at the Delta locality alongside *Whatcheeria* (Bolt and Lombard 2000; Lombard and Bolt 2006).

The skulls of most *Greererpeton* specimens measure from between 150 to 180 millimeters, but because of the abundance and size range of specimens, not only the basic anatomy of *Greererpeton* but also the growth stages have been studied. As in many animals today, in the smaller, younger forms, the eyes were relatively larger, though as the skull grew, the snout did not get progressively relatively longer as it usually does in other genera (Godfrey 1989a).

Unlike many early tetrapods, the skull of *Greererpeton* did not have a notch at the back between the cheek and skull table. This has been interpreted to suggest that early in tetrapod evolution, the notch found commonly among these early forms might not have housed a tympanic membrane for hearing, as was at one time assumed. In addition, the stapes of *Greererpeton* was robust and flattened, and appears in most specimens to rest against the dorsal part of the palate. In the southern Illinois material, this contact has been broken, though it is not clear that this was its life position. The condition of the Greer material gave rise to alternative theories about the early role of the stapes in tetrapods, suggesting that it originally did not have much to do with hearing but rather acted as a bracing member between the braincase and the palate (Carroll 1980; Smithson 1982). This idea is explained more fully in Chapter 10.

Subadult specimens of *Colosteus* have been found that show toothed ceratobranchial elements, which have been interpreted as gill rakers. Gill rakers in fish prevent large particulate debris from entering the gill chamber in aquatic filter feeders. The implication is that at least up to subadult size, *Colosteus* was not only aquatic, but a filter feeder in water. It is not known whether these elements were retained in fully adult specimens because of their preservation (Hook 1983). However, at least in the subadults, filter feeding implies that the buccal cavity was water filled and that the animals may have been using their gills to breathe.

The modern giant salamander *Andrias*, which lives in present-day Japan, gives an idea of colosteid ecology. This creature lives in streams and rivers at between 2 to 8 meters' depth, hiding in rock crevices. The

larger, older animals tend to favor the deeper water. *Greererpeton* seems to have had similar limb and body proportions to *Andrias*, and the disposition of specimens fits a similar ecological distribution. It was probably likewise an ambush predator feeding on whatever small vertebrates or invertebrates it could catch.

### *PROTEROGYRINUS*

*Proterogyrinus* belongs to a group more commonly found in the Late Carboniferous, the embolomeres (see Chapter 9). *Proterogyrinus scheeli* (Fig. 7.13) is known from numerous specimens from the same quarry as *Greererpeton* and is early Namurian. There is another species of *Proterogyrinus*, *P. pancheni*, that comes from the Dora bone bed near Cowdenbeath in Scotland. This open-cast mine has yielded a tetrapod fauna that also includes *Crassigyrinus* and *Eoherpeton*, as well as the lungfish *Uronemus*.

*Proterogyrinus* shows typical features of embolomere skulls such as contact between the tabular and parietal bones and a "horn" on the posteriormost corner of the tabular bone. Unlike *Eoherpeton*, it has a deep notch between the skull table and the cheek that is usually referred to as the otic or spiracular notch. The stapes is unknown. The lower jaw has two much enlarged meckelian fenestrae on the inner face, as in later embolomeres.

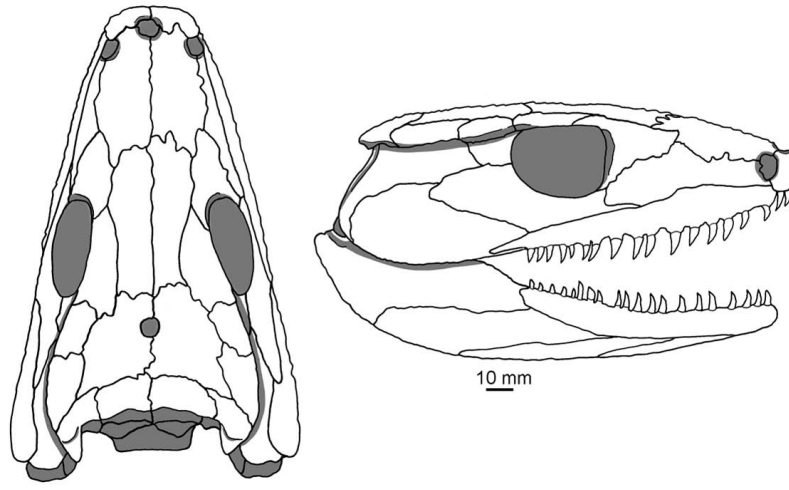
Characters of the limbs and girdles are similar to those of other embolomeres (see Chapter 9), but the vertebrae do not show the typical fully embolomerous centra—that is to say, it does not have completely ring-shaped pleuro- and intercentra. In *Proterogyrinus*, pleurocentra, though enlarged, do not form a complete hoop dorsally, and intercentra are wedge shaped. The length of the vertebral column from neck to sacrum, at 32, is shorter than most later embolomeres.

The overall morphology of *Proterogyrinus* is that of a semiterrestrial crocodile-like predator.

### *EOHERPETON WATSONI*

*Eoherpeton* is represented by several specimens, all from localities in Scotland, ranging in time from the late Viséan through the early Namurian. One of these is the Dora bone bed, found in an open-cast mine north of the Firth of Forth at Cowdenbeath. This locality has also yielded *Crassigyrinus*, *Proterogyrinus*, and *Doragnathus*, and the baphetoid *Spathicephalus*, as well as fragments of an adelogyrinid. The site was discovered by the fossil collector Stan Wood, who has also found a wealth of other early tetrapod and fish material from the Devonian and Carboniferous of Scotland. The preservation of tetrapods in the Dora bone bed is unusual in that they are found mainly in the seat earth, the level lying below the coal-bearing layer. More usually, tetrapod remains are found above the coal.

*Eoherpeton* has also come from the Scottish deep mine locality of Loanhead near Edinburgh. This particularly rich site has yielded several




**7.14.** Skull of *Eoherpeton*. (A) Dorsal view. (B) Lateral view.

adelogyrinids, the baphetoids *Spathicephalus* and *Loxomma*, *Caerorhachis*, various lepospondyl elements, the lungfish *Ctenodus*, and a variety of actinopterygians.

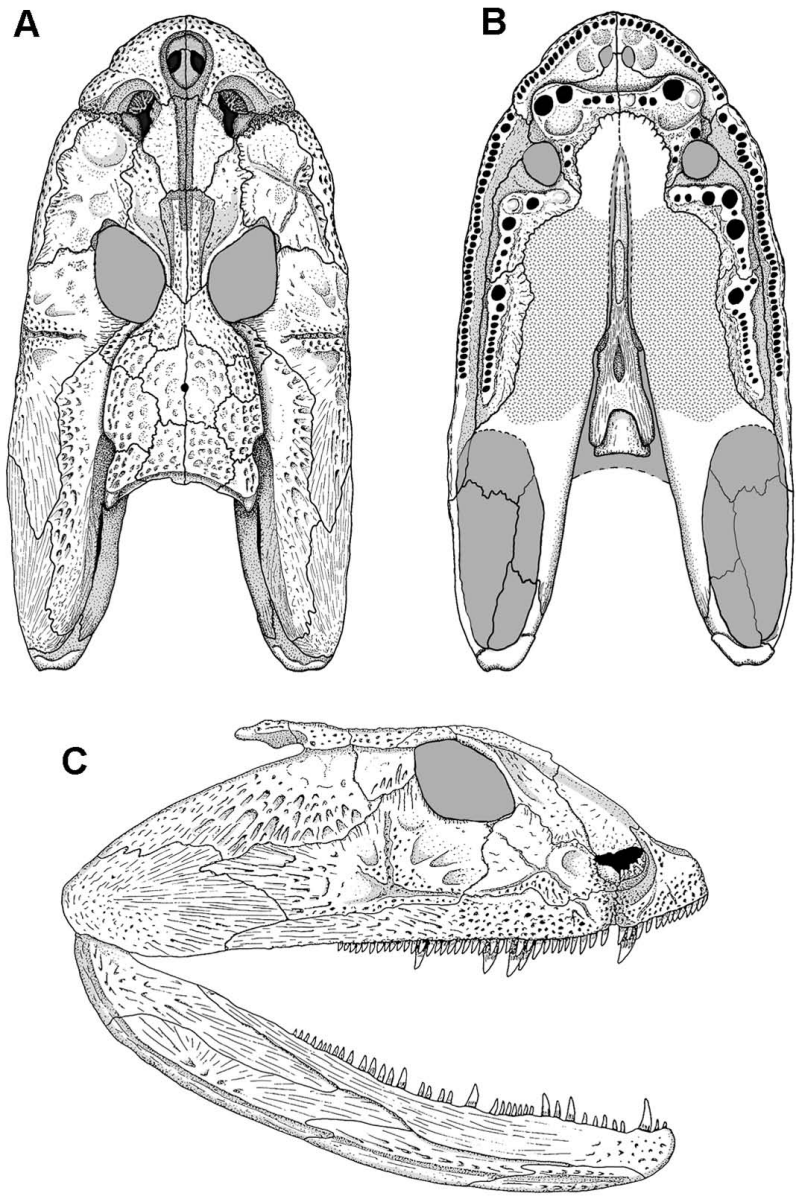
Remains of *Eoherpeton* include a complete, though flattened, skull, a partial skull retaining part of the braincase, and postcranial elements representing much of the skeleton (Fig. 7.14). Usually *Eoherpeton* is considered to be closely related to the embolomeres, in a wider group called anthracosaurs (see Chapters 8 and 9), though there is some debate whether anthracosaurs constitute a natural group. Its membership has varied over time, making the use of that term problematic.

The skull has been described in some detail (Panchen 1975; Smithson 1985b) and shows some of the derived characters thought to be characteristic of anthracosaurs: a contact between the tabular and parietal bones, and a tabular horn projecting from the posterolateral margin of that bone. There is no significant otic notch, and its stapes is unknown. Its braincase bears close resemblance to those of other anthracosaurs in the configuration of the basipterygoid processes and the region that sits just dorsal to them.

The vertebrae are gastrocentrous—that is, the horseshoe-shaped pleurocentra are larger than the wedge-shaped intercentra. This feature found in other anthracosaurs. It has long, slender, curved ribs. The humerus is L shaped and resembles those of anthracosaurs in key features. There is a robust pelvic girdle with a long, expanded puboischiadic plate, associated with a substantial hind limb. Overall, the morphology seems to be that of an animal that was a least semiterrestrial, and maybe fully terrestrial.

### *CRASSIGYRINUS SCOTICUS*

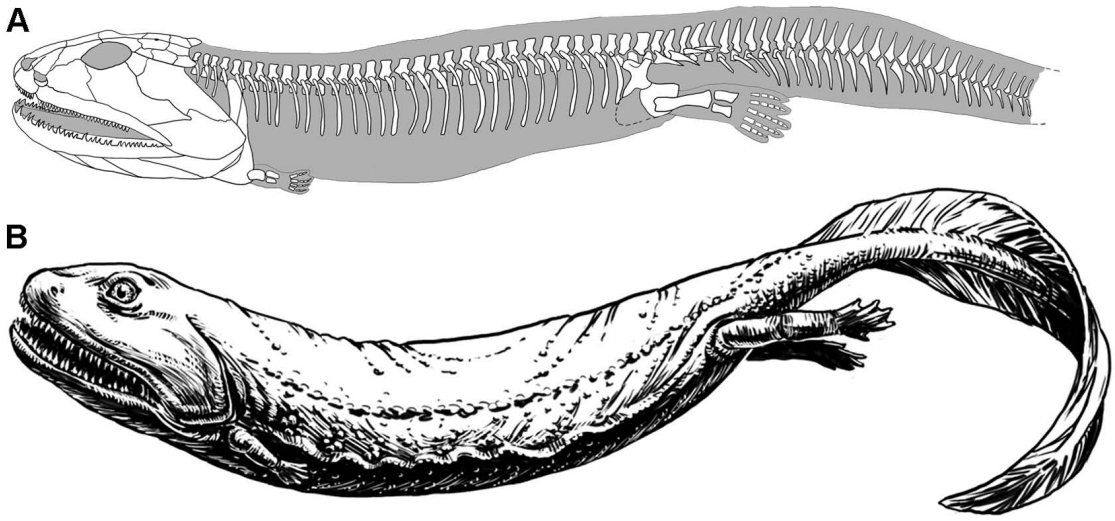
One of the most peculiar and least understood creatures from the early part of the Carboniferous is *Crassigyrinus scoticus*. Fossils of this creature




**7.15.** Skull reconstructions of *Crassigyrinus*. (A) Dorsal view. (B) Ventral view. (C) Lateral view. Skull is about 350 millimeters long. *From Clack (1998b).*

have been known since the first specimens of it were discovered in the 1850s, but they were not immediately recognized for what they were. This accounts for the name: *Crassigyrinus* means "shallow wriggler." This name was given because only half the skull was known and it was considered to have been a flat-headed animal—very far from the truth as it is now understood. In recent years, more material has been found, so most of its anatomy can now be described (Watson 1929; Panchen 1985; Panchen and Smithson 1990; Clack 1998b). Despite this, it remains a puzzling animal.

*Crassigyrinus* is known definitively only from Scotland and from only a couple of sites: the deep coal mine at Gilmerton near Edinburgh,




**7.16.** (A) Skeletal reconstruction of *Crassigyrinus*. (B) *Life reconstruction by J.M.*

and the Dora bone bed. These localities represent times around the Early to Late Carboniferous boundary. Some elements that may have come from a *Crassigyrinus*-like animal have been reported from Greer (Godfrey 1988).

The head of *Crassigyrinus* was about 320 millimeters long and was narrow and deep, with a short snout and long rear cheek region (Figs. 7.15, 7.16). The skull bones were ornamented around the mouth with deeply incised pits and grooves, but elsewhere, the ornamentation was shallow and irregular. The eye socket was rhomboidal in shape, and the deep skull ensured that the eyes looked laterally rather than dorsally. At the front, above the nose, lay what appears as a large hole in the snout, apparently connected to a hole in the palate, though it is not known whether these passages were separated by soft tissue in life. Running back from the hole in the snout was a groove, which seems to have become shallower toward the top of the head until it disappeared. The buttresses flanking the groove may have strengthened the snout. The existence of the hole and its groove are reminiscent of the internasal fontanelle in *Ventastega* and *Acanthostega* and could represent a primitive retention.

There were also buttresses on the inside of the skull running down the front rim of the orbit. Massive teeth, especially on the palate, may have required extra strengthening of the snout that bore them. The lower jaw received some of these teeth into special holes when the jaws closed. The length of the cheek means that the lower jaws hinged far back on the skull, allowing them extra swing as they closed like a trap.

Between the short skull table and the cheek, there was a deep spiracular notch, and though the nostril was large, a breathing hole on top of this high skull might have been useful to an aquatic animal.

*Crassigyrinus* was certainly aquatic. It had a long, narrow body, probably nearly 2 meters in length including the tail, which matched the skull in narrowness and tapered gradually toward the rear. A deep tail

has been reconstructed for it from a few postsacral vertebrae. Although its hind limbs were relatively small for the size of its body, its forelimbs were extremely reduced. The humerus or forearm bone was only as long as the long dimension of its orbit. From the limbs and body, *Crassigyrinus* is thought to have been an actively swimming, permanently aquatic animal, while the skull and dentition are those of a fearsome predator (Fig. 7.15).

*Crassigyrinus* is puzzling: it has many curious adaptations of its skull and limbs, and at the same time, it shows a number of primitive features. In particular, the pattern of bones in the palate is one of the most fishlike known among early tetrapods. The vertebrae were not well ossified, consisting of single hoop-shaped centra and neural arches that had only poorly developed articulations joining them together. Paleontologists have debated whether this combination of characters indicates that *Crassigyrinus* was a secondarily aquatic animal adapted from a previously more terrestrial form, or whether in fact it is a long-surviving relict of the earliest tetrapods that had not yet become fully terrestrial. Some analyses suggest that indeed it is a secondarily aquatic form, and that the fishlike features of its palate have been reacquired (Clack 1998b). This is because these computer-generated phylogenies placed it closer to anthracosaurs, baphetids, and *Whatcheeria*, none of which have these fishlike tooth arrangements. More recent attempts have either placed it above the whatcheeriids (Clack 2002b; Clack and Finney 2005) or below them and immediately above *Ichthyostega*, so that its true position still remains unresolved (Ruta et al. 2003; Ruta and Clack 2006).

### *DORAGNATHUS WOODI*

Another taxon represented only by lower jaws is *Doragnathus woodi*. It is known from many specimens, almost all from the Dora bone bed in Cowdenbeath, alongside *Crassigyrinus* and *Eoherpeton*, and thus late Namurian. The jaw is distinctively long and narrow, with large numbers of small teeth on the dentary and a complete row of even smaller teeth along the coronoid row. The tooth complement does not match any known taxon, and though it shares some similarities with the baphetid *Spathicephalus* in proportion, it is evidently not the same animal (Smithson 1980). The jaw appears to belong to an animal that fed on small, perhaps numerous prey, or was even a filter feeder.

### *ACHERONTISCUS CALEDONIAE*

This small animal is represented by a single specimen from Scotland and is named, as are several other serpentlike lepospondyls, after one of the rivers of Hades, tributaries of the River Styx. There are no data on locality or collector, and the dating remains in doubt. However, spore analysis performed in 1969 suggested that it was late Viséan or early Namurian (Carroll 1969a; Carroll et al. 1998). The bone in the specimen is poorly preserved, so the interpretation of the morphology is also in doubt. The skull appears to be that of a notchless, small-eyed, adelogyrinid-like form,

and it has an elongate vertebral column with reduced or absent limbs as in those animals. The vertebral column, however, is anomalous in that the centra consist of two more or less disk-shaped parts, somewhat like the later embolomeres (see Chapter 9). Informal suggestions include the idea that it might be a juvenile colosteid. It is another of those enigmatic forms that suggests a much greater diversity of early tetrapods in the Early Carboniferous than those that are currently known.

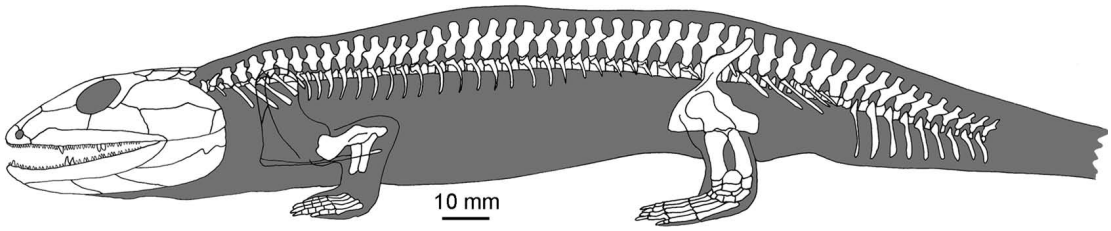
### *ANTLERPETON CLARKII*

The single specimen of *Antlerpeton* was found in a most unlikely place for an Early Carboniferous tetrapod. It comes from a talus slope in the hilly desert of central Nevada—the Antler Highlands after which it is named—and is the only early tetrapod to have been found in that part of the world (Thomson et al. 1998). The area has been little explored, and recent expeditions have failed to relocate the spot at which it was found. It appears to have been an erratic in that it was a totally isolated find, though somewhere as yet undiscovered there may be other such treasures waiting to be found. Because it was found as a loose block, it cannot be dated with certainty, but it appears to have come from Lower to mid-Carboniferous beds. The sediments in the area include some marine deposits, indicating the possible close proximity to the sea of this animal's habitat. The matrix in which the specimen was preserved is also unusual for a Carboniferous tetrapod, being an intractable red sandstone, quite different from the coal, shale, or ironstone in which they are typically found. The specimen was therefore prepared as a natural mold from which latex peels were made.

There is no skull preserved, nor much of the limbs or girdles, though there appear to be parts of the femora and pelvis. The remains chiefly consist of vertebral centra and ribs, preserved in an unusual ventral view that makes them difficult to interpret, and they were described as being unlike those of any other known early tetrapod. It remains possible that they were rhachitomous. This tantalizing specimen is another that hints of greater diversity than paleontologists are yet aware of.

### *CAERORHACHIS BAIRDI*

Originally interpreted as a type of temnospondyl, *Caerorhachis* 9 (Fig. 7.17) is another mid-Carboniferous animal known from a single, patchily preserved specimen (Holmes and Carroll 1977; Ruta et al. 2002). Limited data suggest that it was basal Namurian in age and thus within the Early Carboniferous, and study of the matrix suggests it was from Loanhead (Smithson 1985a). The skull, which is preserved as a natural mold, shows only a part of the external surface of the skull roof. Although some is represented by the internal surface, this is more difficult to make out, and it has been interpreted in different ways. The palate is also preserved as a natural mold, but half of it is almost complete. It has been interpreted as having the characteristic palatal vacuities of temnospondyls, but at the same time, the skull has been described as notchless. Both these




**7.17.** Skeletal reconstruction of *Caerorhachis*. *Based on Ruta et al. (2002).*

characters have been challenged by a more recent assessment that suggests a shallow notch and small interpterygoid vacuities were present in a relatively larger skull than suggested by Holmes and Carroll (Ruta et al. 2002). The pelvis appears to have the single dorsal process associated most closely with temnospondyls, though this may be an effect of uneven preservation. Ruta et al. (2002) suggested that the dorsal process may in fact have been present, represented by a broken base. Uncharacteristic of temnospondyls, the vertebrae of *Caerorhachis* are gastrocentrous, with large pleurocentra and small ventral intercentra (Ruta et al. 2002). Also uncharacteristic of temnospondyls, and indeed any other known early tetrapod, is the lining of denticulated shagreen that covers not only all of the palate, but the whole of the inner face of the lower jaw. Such a complete cover of shagreen on the lower jaw is distinctive and unique to *Caerorhachis*. Ruta et al. (2002) found that *Caerorhachis*, rather than being a peculiar temnospondyl, more consistently appears among the amniote stem lineage than elsewhere in their analysis. Other analyses have placed it back with temnospondyls.

### *OCCIDENS PORTLOCKI*

Like *Signourea*, which it resembles in some ways, *Occidens* is known only from a single lower jaw specimen, in this case incomplete. Only the middle section is preserved, but it is sufficiently distinctive to be confident that it does not belong to any known taxon (Clack and Ahlberg 2004). It was first described, in 1843, as "*Holoptychius*," but it is clearly the jaw of a tetrapod. It comes from Northern Ireland, but unfortunately, no precise locality was given in the original description, so there is some uncertainty about its date. A spore analysis gave equivocal results, but the construction of the jaw, combined with some knowledge of the geology of Northern Ireland, suggest an Early Carboniferous age, though whether Tournaisian, Viséan, or basal Namurian will have to remain uncertain unless further specimens are found. It is the only early tetrapod ever found in Northern Ireland, and it suggests that further excavations in that region might pay dividends.

Like *Sigournea*, it has a row of small coronoid teeth, but unlike *Sigournea*, these show somewhat enlarged teeth in the center of the middle coronoid row. Its dermal ornamentation is also rather different from *Sigournea*. Although its exact relationships must remain uncertain, it clusters with whatcheeriids in a cladistic analysis.

### Other Early Carboniferous Localities

There are a few other Early Carboniferous localities in the United States and the United Kingdom, explored in the late 20th century, that preserve fragmentary remains of a variety of tetrapods. The early Namurian locality of Grand Étang in Nova Scotia has yielded a fauna of embolomere, colosteid, and whatcheeriid elements as well as some of uncertain affinity (Holmes et al. 1995; the ilium illustrated in their figure 3 is undoubtedly whatcheeriid, a group unknown at the time of publication). The nearby locality of Parrsborough has yielded a rich fauna of trackways and a partial lower jaw (Godfrey and Holmes 1989). The lower jaw appears to be of a relatively primitive tetrapod of *Crassigyrinus*-like or whatcheeriid grade (J.A.C. personal observation). A relatively newly discovered site is that in Hancock County, Kentucky. Here, colosteids and embolomeres have been found in an oxbow lake environment, with other embolomeres, possible whatcheeriids, and some unidentified taxa found in a separate horizon representing a floodplain or lake facies. It is dated as early to mid-Namurian, approximately contemporary with Greer (Garcia et al. 2006). A partial skull of what appears to be a colosteid-like tetrapod has recently been discovered from the Viséan St. Louis Formation in Missouri (Clack et al. in preparation).

The island of Inchkeith in the Firth of Forth, Scotland, has produced a range of tetrapod fragments as well as fish remains from a steeply dipping ash band in rocks of mid-Viséan age. Unfortunately, this has proved difficult to collect from (Smithson 1985a). Still undescribed Early Carboniferous tetrapod material has also been found at the North Berwick site of Tantallon Castle. The prolific site, known as East Kirkton, near Bathgate, Scotland, has been one of the most informative, providing a window onto a terrestrial fauna of the late Viséan; it is dealt with in detail in Chapter 8.

Most recently, and still under investigation, are Tournaisian sites in southern Scotland. One site has yielded mainly isolated elements such as a neural arch, a femur, a lower jaw fragments, and a disrupted skull (Smithson and Wood 2009a), but also a partially articulated lungfish. Other localities, including a rich fauna from Willie's Hole near Chirnside in Scotland, have yielded almost complete tetrapod skeletons as well as many less complete remains, along with many fish, arthropods, and plants (Smithson and Wood 2009b). Further collecting at these sites is under way and should bring some exciting new finds.

## Early Carboniferous Tetrapods: An Overview

By the mid-Carboniferous, tetrapods had produced a wide range of body forms, skull shapes, and sizes of animals that far exceeded those of the Devonian, so far as is known. From tiny, mouse-size animals like *Casineria* to large predatory forms such as *Crassigyrinus* through to the limbless aïstopods, tetrapods broke away from the conservatism of their Devonian forerunners. This range also exceeds what is seen in the

lobe-finned fish of the Late Devonian, though by the Late Carboniferous, the rhizodonts had produced some of the largest bony fish that have ever evolved, and the ray-finned fishes were filling the water with small forms unparalleled among the lobe-fins. The diversity of form, size, proportion, and structure produced by this early radiation of tetrapods is matched only later by the diversification of amniotes in the Early Triassic and by the evolution of teleosts among the ray-finned fishes of the Late Jurassic and Early Cretaceous. It is as if some kind of threshold had been crossed that allowed the animals to colonize the new territory and exploit the variety of niches that were being newly provided among the plants and invertebrates. This explosion of diversity must have happened at some stage before it appears in the fossil record, and that must have been during the Tournaisian and early Viséan—that is to say, in Romer's Gap. More complex forest structure and the subsequent diversification of terrestrial invertebrates, including mollusks and insects, may have triggered this diversification, or the ecological niche may have become exploitable by tetrapods as a result of some structural or developmental innovation.

A suggestion for the apparently developmental breakthrough is provided by the observation that the Tournaisian saw the advent of cooler and drier conditions operating throughout the period. Vertebrate faunas, and likely plants and arthropods as well, were recovering from the end-Devonian extinction marked by the Hangenberg event. By the early Namurian, the climate had once more become monsoonal. The cooler, drier conditions of the Tournaisian stage could have led to two outcomes, both of which may be involved in the lack of a fossil record and the appearance of many groups of small tetrapods during that time. First, the conditions may not have favored preservation except in a few rare circumstances. After an extinction event, the animals might have been scarce in any case. But another possibility links the climate to developmental changes among tetrapods. Under environmental stress, many animals undergo a shortening of their developmental periods in order to reduce the risk factors of desiccation or predation in harsh conditions. This is a strategy seen today, especially by frogs that habitually live in temporary pools. By comparison with their relatives in more permanent water bodies, the frogs of ephemeral pools have larvae that are generally faster developing and adults that are rather smaller (Gould 1977). The process is known as progenetic dwarfing. It can result in modifications to skeletal and skull structure and proportions, including dermal skull roof bone reduction, reduction of the skull size relative to the braincase and ear regions, and reduction of endochondral ossifications. These are in many ways consistent with the differences seen among the first Carboniferous tetrapods compared with their Devonian relatives. The climatic stress of the Tournaisian period might have been a contributory factor in such changes. It is also possible that such processes might have played a part in changes to methods of breathing and feeding that had profound consequences for skull architecture, as suggested in the last chapter.

Many of the important questions about early tetrapod evolution and diversification, as well as about how they eventually became more fully terrestrial, can only be answered by discoveries of more fossils to represent this crucial period. Now that the picture of Devonian tetrapods is beginning to fill out and the late Viséan is becoming better known, the discoveries with most impact are going to come from the early Viséan and Tournaisian stages. That will depend on renewed collecting in these areas. Almost all the known Viséan tetrapods have been found in Scotland, and most of these are from long-known and now inaccessible localities. The Scottish Midland Valley has been one of the most productive and important areas for early tetrapod paleontology historically. However, this in itself makes the sample biased.

Much remains to be done in the Early Carboniferous of other parts of the world, and recent finds in Australia and North America emphasize the possibilities. The implications from the finds that have been made is that, rather than lack of fossils, or even lack of suitable rock sequences, Romer's Gap represents a lack of collecting effort from rocks of the right age and environments. Collecting from Early Carboniferous continental localities is probably one of the most potentially rewarding paleontological investigations that could be made at this time.



**8.1.** (Color Plate 15) The East Kirkton Quarry site once clearance was complete and a section had been excavated through the sequence, with the author standing at the level of unit 82, where most of the best tetrapod specimens have come from. *Photograph by R.N.G.C.*

# East Kirkton and the Roots of the Modern Family Tree

# 8

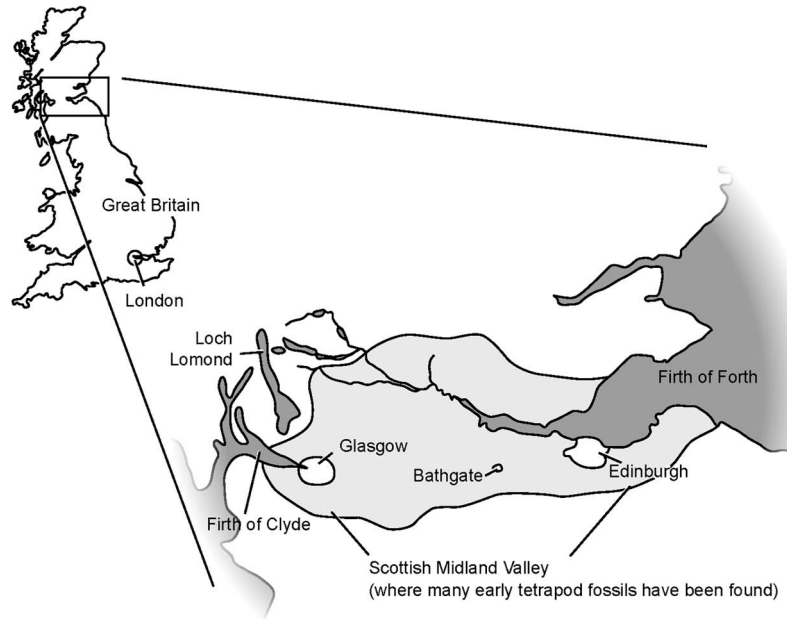
## Background to the East Kirkton Locality

A small former mining town called Bathgate, about 20 miles from Edinburgh, Scotland, has recently been made famous in the paleontological world for being the location of a window through which to view an extraordinary episode in evolutionary history. At the edge of a housing estate lies a quarry where in the 19th century a rock called the East Kirkton Limestone was dug out. It had some curious qualities that made it attractive as a building stone and hard wearing for making the local farm walls.

It is composed of thinly alternating bands of dark carbonaceous limestone, pale silica, and hardened gray volcanic ash called tuff, and often the bands are speckled with small white nodules or twisted and distorted into intriguing curls and waves. In the 1830s, fossil collectors also found some unusual specimens, which are now recognized as the carapaces of eurypterids or sea scorpions, as well as many plant remains. The quarry was closed in about 1844, and though geologists visited occasionally afterward, it was eventually forgotten and became grown over.

About 140 years later, in 1984, Stan Wood, the fossil collector who also found the Dora site near Cowdenbeath, Scotland, from which tetrapods like *Crassigyrinus* and *Eoherpeton* came (see Chapter 7), decided to investigate the East Kirkton Limestone again, first by investigating the now disused and neglected farm walls. It was here, after some years of searching, that he found the remains of tetrapods (Wood et al. 1985) among the stones forming field boundary walls on farmland in the Bathgate area. Among these were some completely articulated skeletons representing new species. However, that was only the first of a series of discoveries revealing unusual and important aspects of the fossils of East Kirkton. The quarry was subsequently relocated and opened up, with a section dug to expose the stratigraphic sequence (Fig. 8.1). Figure 8.2 shows a map of Scotland and the location of Bathgate.

The East Kirkton Limestone lies within a sequence called the Bathgate Hills Volcanic Formation, which gives a clue to its significance. This sequence dates from the later part of the Early Carboniferous, the Viséan, and the volcanoes forming it resulted from the mountain-building processes of the Variscan orogeny. Its age makes it one of the earliest known sites for tetrapod fossils, after those from the Late Devonian. It predates most of those that yielded the animals described in Chapter 7. The site subsequently yielded not only many new taxa of tetrapods, but also of invertebrates and plants. Many of these proved to be of exceptional interest by being the earliest known representatives of their groups to be




**8.2.** Main map shows the British Isles; inset shows the Scottish Midland valley and the position of Bathgate.

demonstrably terrestrial. In short, East Kirkton had yielded the earliest certainly terrestrial assemblage of animals, including tetrapods, yet discovered. The circumstances allowing the preservation of these animals have themselves proved extraordinary because the site itself represents remarkable physical and ecological conditions.

In the years after Stan Wood's discovery, much work was carried out on the sedimentology, stratigraphy, geophysics, geochemistry, paleoecology, and paleontology of the site, culminating in an international conference in 1992. Accounts from a wide range of experts were published in 1994 by the Royal Society of Edinburgh (Rolfe et al. 1994). The rest of this chapter is devoted to describing some of the findings and their significance for tetrapod evolution.

The Bathgate Hills to the south of Edinburgh are the remains of old volcanic uplands that rose during the latter part of the Early Carboniferous as a result of the Variscan orogeny, spilling basalts and other volcanic sediments over the surrounding region. The uplands and the active volcanoes lay not far from the coast, where rivers flowed out, forming estuaries, lagoons, and deltas, and where thick forests grew on the resulting rich soil. The East Kirkton Limestone formed as the bed of a predominantly freshwater lake, filling gradually by sediments derived from the surrounding country as well as by occasional volcanic outflows.

The nearby volcanoes had a number of different effects on the animals, plants, and sediments of the East Kirkton lake. The first was that after an eruption, sediments of volcanic ash settled and were then washed down into the lake, forming thick deposits of tuff (Fig. 8.3). The hot ash or lava appears to have set fire to the forests on occasion, as volcanic eruptions do today, and pieces of charred and broken wood are found in the



**8.3.** (Color Plate 16) Detail of the tuff (fossilized volcanic ash) layers from which some isolated tetrapod bones have been recovered. *Photograph by J.A.C.*

tuff layers. Poisonous gases and fires killed many nearby animals, so that as well as wood, the flowing ash picked up their carcasses, broke them up, and carried the bones into the lake. It is notable that the isolated bones found in the tuff layers are much the largest of the tetrapod specimens to have been found at East Kirkton, suggesting that they did not live in the lake itself.

Another, less direct, effect of the vulcanism was the production of mineral-rich water in the lake. Both the concentration of minerals and the temperature of the water fluctuated, perhaps seasonally or annually, and this had an effect on the fauna and flora inhabiting the lake waters. Calcium, silica, magnesium, iron, manganese, and sulfur are all found in



**8.4.** Sample of rock showing distorted layers and calcite bands in East Kirkton sediments. Scale bar = 10 millimeters. *Photograph by S.M.F.*

relatively high quantities in some of the layers. Some layers were formed almost entirely of calcite, while others were more highly carbonaceous. When the water became saturated with minerals, these precipitated out of the water, clinging to any available surface. Common in the sediments are small nodules of calcite, which apparently formed by accretion round single-celled algae, ostracods (small ovoid crustaceans), plant debris, or other minute cores, forming characteristic whitish speckles in the rock. It is thought that sometimes these accretions formed blankets that covered the surface or floor of the lake, choking whatever was underneath. Occasionally these accretions of calcite formed larger structures that distorted the over- and underlying layers to form waves and ripples in the sediments (Fig. 8.4). Mineral-rich water occasionally penetrated plant stems, replacing or impregnating the tissue cell by cell so that the fossils are able to reveal the stem structure in exceptional detail (Scott et al. 1994). Along with plant debris and broken fronds, fossilized charcoal, known as fusain, is frequently found in some levels. This is taken to indicate the activity of forest fires, perhaps caused by volcanic eruptions.

Many of the tetrapod specimens found at East Kirkton are complete or almost complete skeletons, but these are exclusively of relatively small animals, no more than about 400 millimeters long. This suggests that the animals were not transported far and that they died within close proximity to the water, if not in the water itself. Because the skeletal structure of many of these animals suggests terrestrial habits, one idea is that they fell into the water by accident, perhaps attempting to escape from the volcanic eruptions or influx of poisonous gases. Other possibilities are that the lake itself occasionally produced upwellings of poisonous gas, which overcame the creatures living nearby. Another suggestion is that the creatures ventured out onto algal mats that grew along the lakeshores, until they

reached the thinning edges over the water, whereupon they fell through the mats and drowned. Certainly, in many cases, bone structure is poorly preserved, and the animals may have been cooked before preservation.

The closest modern analogies to the East Kirkton of Viséan times might be the Yellowstone National Park in the United States and the Virunga National Park in the Ruwenzori Mountains at the headwaters of the River Nile in the Congo Republic. Here, volcanic activity produces places where hot streams can literally boil unlucky animals in seconds, and others where pockets of carbon dioxide, accumulating in the night, can asphyxiate unwary creatures that stray into them, followed by predators that attempt to scavenge their corpses. The bodies of both lie undisturbed and decay without being disarticulated.

The sediments of the East Kirkton limestone are about 15 meters thick, and a series of boreholes and careful excavations allowed the sequence of beds to be recorded. This survey showed some of the changes that occurred to the lake flora and fauna during its existence, demonstrating that toward the end of deposition in the lake, it became confluent with other nearby water bodies. The evidence also suggests a change from a drier to a wetter environment toward the top of the sequence, with fish remains found for the first time in the topmost levels. It is not clear what length of time the sediments represent, except that it was relatively short, geologically. A few hundred to a few thousand years seems most likely.

## The Plants and Invertebrates of East Kirkton

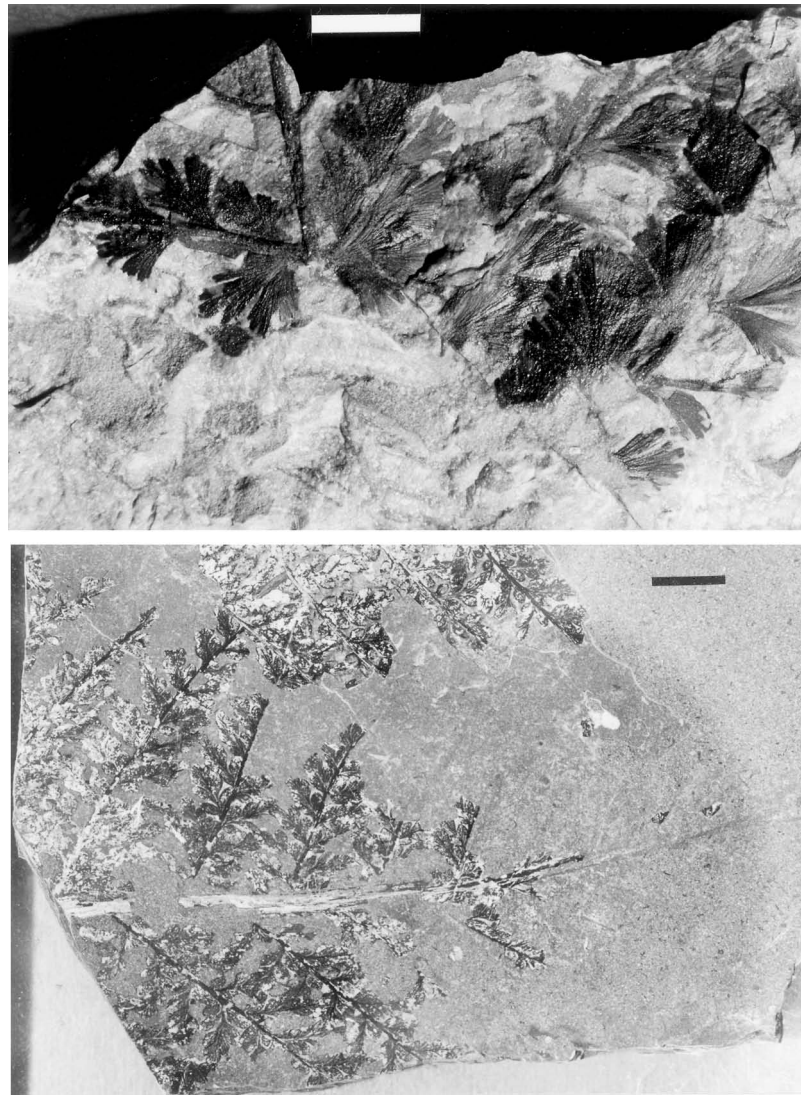
### Plants

Like the animals, the flora of East Kirkton shows a change in character through different parts of the sequence. Early on, the flora is dominated by treelike early relatives of modern conifers. These had large leaves, and their wood was dense and thus preserved well. These plants enjoyed well-drained soils, which suggests that early in the life of the lake, conditions were warm and dry. From the fact that none of the remains seem to have been transported far, it is inferred that they grew close to the lake. One genus of this kind is called *Stanwoodia*, for obvious reasons. These kinds of plants and conditions are associated with the base of the sequence from which most of the best vertebrate specimens have also come (Fig. 8.5) (Scott et al. 1994).

Later on in the history of the lake, represented by the East Kirkton limestone itself, so-called seed ferns and true ferns are found. At the top of the sequence, as the lake finally became silted up, there is a further change to the vegetation. Lycopsids (club mosses) become the most common component, and these plants suggest damper soils. This may mean that the climate became wetter, or that the land was beginning to sink again.

### Invertebrates

Much interest in the East Kirkton site has been generated by the invertebrate fauna. This includes not only the eurypterids (Jeram and Selden



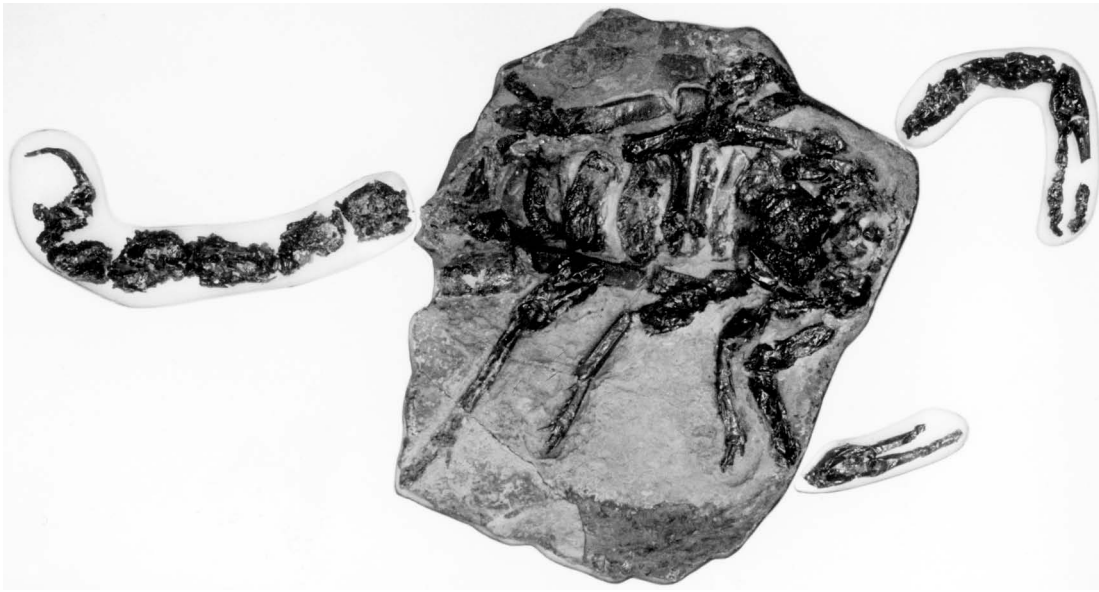
**8.5.** Two plants from East Kirkton (NMS specimens). Top, *Sphenopteridium crassum,* one of the most common pteridosperms at East Kirkton. Bottom, *Spathulopteris obovata,* a pteridosperm. Scale bars in each = 10 millimeters. *Photographs by NMS.*

1994), but also scorpions (Jeram 1994), myriapods (Shear 1994), and a single specimen of a harvestman.

## SCORPIONS

Probably the most important thing about the scorpions of East Kirkton has been their state of preservation. This has allowed much more detailed information to be gained than from any other previous site, and it has meant that not only the East Kirkton scorpions but also some of those from other sites can be interpreted more accurately. Another factor has been the large number of specimens recovered.

The Eask Kirkton scorpions are often preserved as isolated pieces of cuticle, the resilient skin in which the animals were covered. Like all arthropods, scorpions shed their skins periodically, and for some reason,



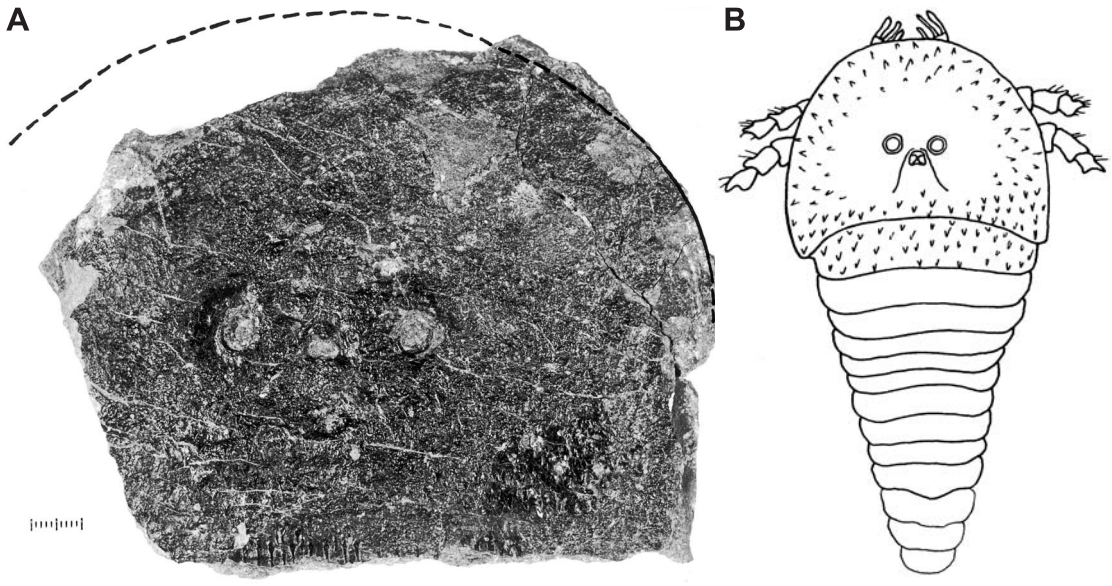
**8.6.** (Color Plate 17) *Pulmonoscorpius kirktonensis,* one of the giant scorpions from East Kirkton, about 700 millimeters long. (NMS G1987.7.136). *Photograph by NMS.*

at this site, many of these shed skins have been found. Instead of being preserved as compressed and blackened stains in the rock, which is usual for fossil scorpions, here they have been preserved almost in their original three-dimensional state, often with what appears to be their original brown or yellow color (Fig. 8.6). Because of the difference in the chemical nature between the rock and the scorpion cuticle, it has been possible to dissolve away the rock to leave behind fragments or larger pieces of scorpion material. Details of the claws, eyes, and bristles can be made out. Most of the specimens discovered appear to belong to a single species, *Pulmonoscorpius kirktonensis.* Several stages of growth are represented, from juveniles about 17 millimeters long up to one 700 millimeters long. A few other scorpion species are also present, represented by rarer material.

*Pulmonoscorpius* has proved important by establishing that it possessed an air-breathing mechanism called a book lung. This discovery shows that *Pulmonoscorpius* definitely breathed air, adding to the evidence that East Kirkton preserves a terrestrial fauna. *Pulmonoscorpius* also had large eyes, suggesting that vision played a significant role in its life. Modern scorpions have reduced eyes and are predominantly nocturnal, while this Paleozoic form seems to have been active during the day (Jeram 1994). It is not clear what *Pulmonoscorpius* would have eaten, but perhaps smaller arthropods formed part of its prey. With the characteristic scorpion sting at the end of its tail, a large *Pulmonoscorpius* was probably equipped to deal with small tetrapods that might have crossed its path.

### EURYPTERIDS

Eurypterids, sometimes known as sea scorpions, were not really scorpions at all. They were arthropods quite closely related to horseshoe crabs.

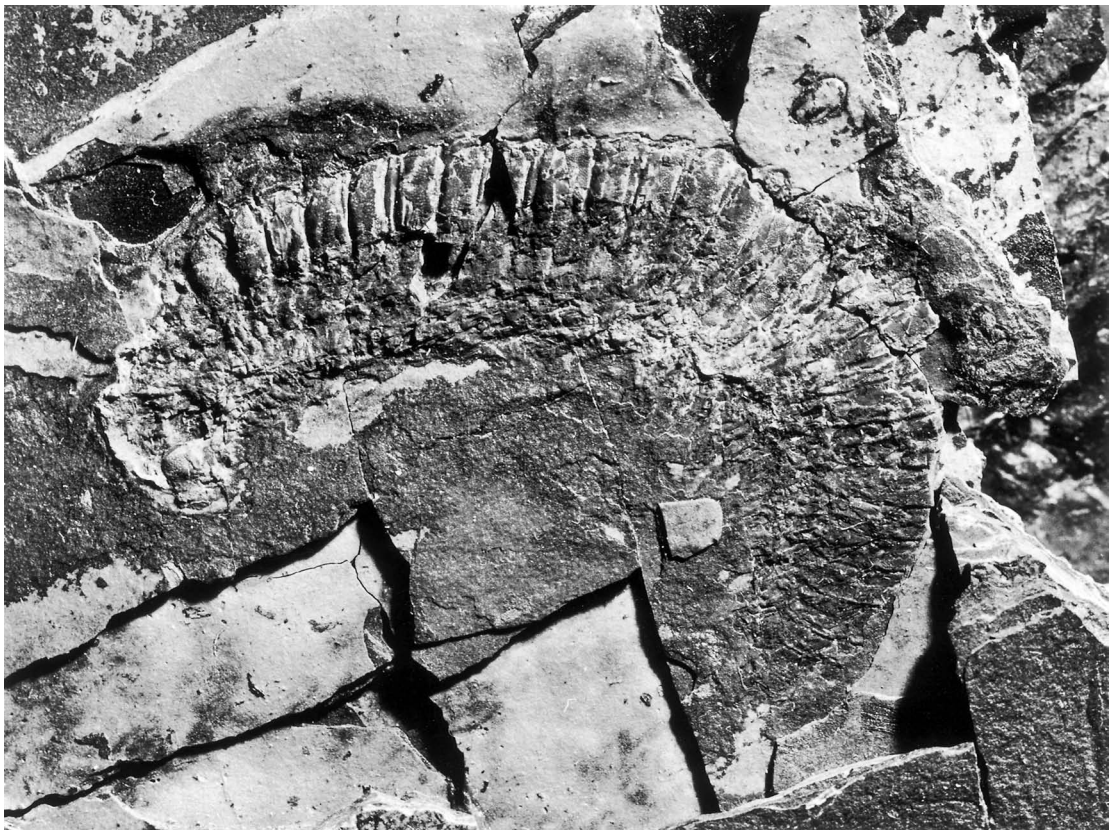



**8.7.** *Hibbertopterus scouleri.* (A) Head shield from East Kirkton. The dotted line shows the restored outline of the head shield. Note the eyes and the ornamented surface of the cuticle in this specimen (UMZC specimen) *Photograph by S.M.F.* Scale bar = 10 millimeters. (B) Life restoration of *Hibbertopterus. Hibbertopterus* grew up to about 650 millimeters across.

Though the early forms found in the Silurian were marine, those of East Kirkton were certainly not so, and like the scorpions, they have been shown to be largely terrestrial.

Three genera of eurypterid have been found at East Kirkton, the most common being *Hibbertopterus.* Specimens of *Hibbertopterus* have been found preserved most commonly in the tuff layers, where they occur as isolated fragments or more complete pieces of carapace with some remaining three-dimensional structure. Like the scorpions, sometimes the carapace can be dissolved from the rock to reveal clear detail. The head of *Hibbertopterus* was rounded in outline and slightly domed, with small eyes near the center (Fig. 8.7). The largest carapace found measures 650 millimeters across, making it one of the largest ever found. The anterior appendages that fixed to the underside of the carapace lack any evidence of specialization for swimming or predation, and for juvenile animals, it has been suggested that they raked through soft sediment with their anterior appendages. As the animals grew larger, their mode of feeding may have changed to a form of sweep feeding using comblike structures developed on their limbs (Jeram and Selden 1994).

No very small eurypterids are represented at East Kirkton, suggesting that they did not breed there. Where there is much broken-up plant material, an abundance of broken-up cuticle fragments is also found, both kinds of debris presumably being transported from elsewhere. Perhaps large hibbertopterids fed on small invertebrates at the lake edges, perhaps as a seasonal occurrence, while they moved elsewhere to breed.

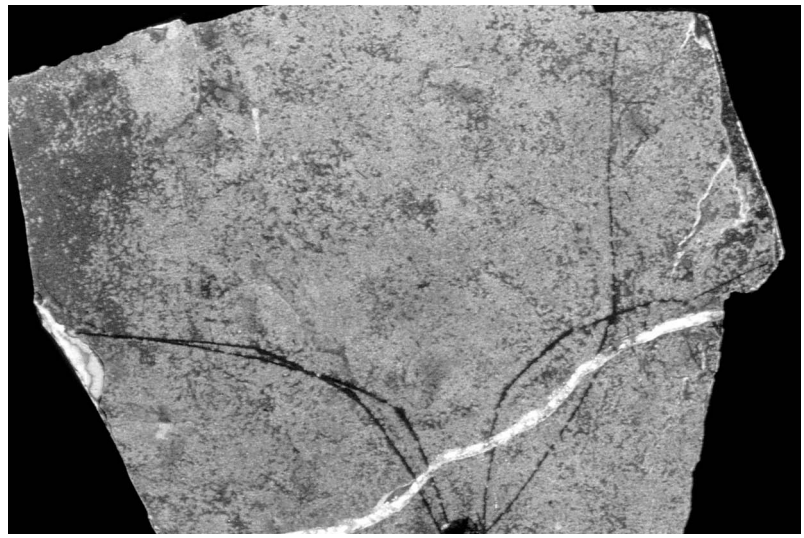


**8.8.** Unnamed myriapod specimen from East Kirkton (length of animal, about 6–8 millimeters). (NMS G1992.21.1p). *Photograph by NMS.*

## MYRIAPODS, HARVESTMAN, AND OSTRACODS

Although not particularly well preserved, a few specimens of myriapods have been found at East Kirkton. These are among the earliest Carboniferous fossils of millipede-like animals so far described, although representatives are known from the Silurian and Devonian. One of the East Kirkton specimens shows some of the earliest evidence for the kind of pores that modern millipedes possess to secrete noxious chemicals, effective in repelling predators. The substances that they produce are known to be effective against amphibians, and the tetrapods of East Kirkton would have attempted to feed on the millipedes of the day (Shear 1994) (Fig. 8.8).

One specimen of an opilionid—a harvestman—has been found at East Kirkton. It has only four remaining legs preserved, but many living examples lose one or more legs and yet function adequately, so it might have lost the other four while it was alive rather than after it had died (Fig. 8.9). Like modern opilionids, it had a single part to the body, and each joint of the legs bore a slight swelling. These and the long, thin legs make it recognizable as an opilionid rather than a spider, to which harvestmen are quite closely related. True spiders are known from the Devonian, but this Kirkton specimen is the earliest known opilionid. Unfortunately the specimen shows no detail other than those that identify it as a harvestman.



**8.9.** Opilionid (a harvestman) from East Kirkton. Specimen from the Hunterian Museum, Glasgow. *Photograph by W.D.I.R.*

Many layers of the East Kirkton Limestone are crowded with the remains of small oval-shaped organisms that look like tiny bivalve mollusk shells. However, they are not mollusks (whose shells are absent from the deposits) but small crustaceans called ostracods. Their shells are hinged like those of bivalves, but inside lived a little creature with feathery feeding arms like those of a tiny barnacle. Ostracod shells often have surface sculpture on the outside, and in well-preserved samples, they can be identified as to species by means of the details of this ornament. However, those from East Kirkton are not sufficiently well preserved to do this. The abundance of ostracods in the lake speaks of a rich food source for both invertebrates and tetrapods, and it suggests that at some periods at least, the water was rich in even smaller organisms, such as unicellular animals, on which the ostracods would have fed.

One group of invertebrate that has not been found at East Kirkton are insects. Though six-legged wingless insect relatives are known from the mid-Devonian, flying insects have not yet certainly been found before the Namurian. Their absence from the East Kirkton deposits is surprising given the type of preservation there, and it may mean that flying insects had indeed yet to evolve.

This brief survey of the variety of plants and invertebrates found at East Kirkton provides a view of a habitat rich in a diversity of niches for animals to live in, and a glimpse of what it must have been like for the tetrapods of the time. The invertebrates, as well as the vertebrates themselves, no doubt formed complex food chains, with the tetrapods and the larger invertebrates feeding in the forests surrounding the lake.

## Vertebrates of East Kirkton

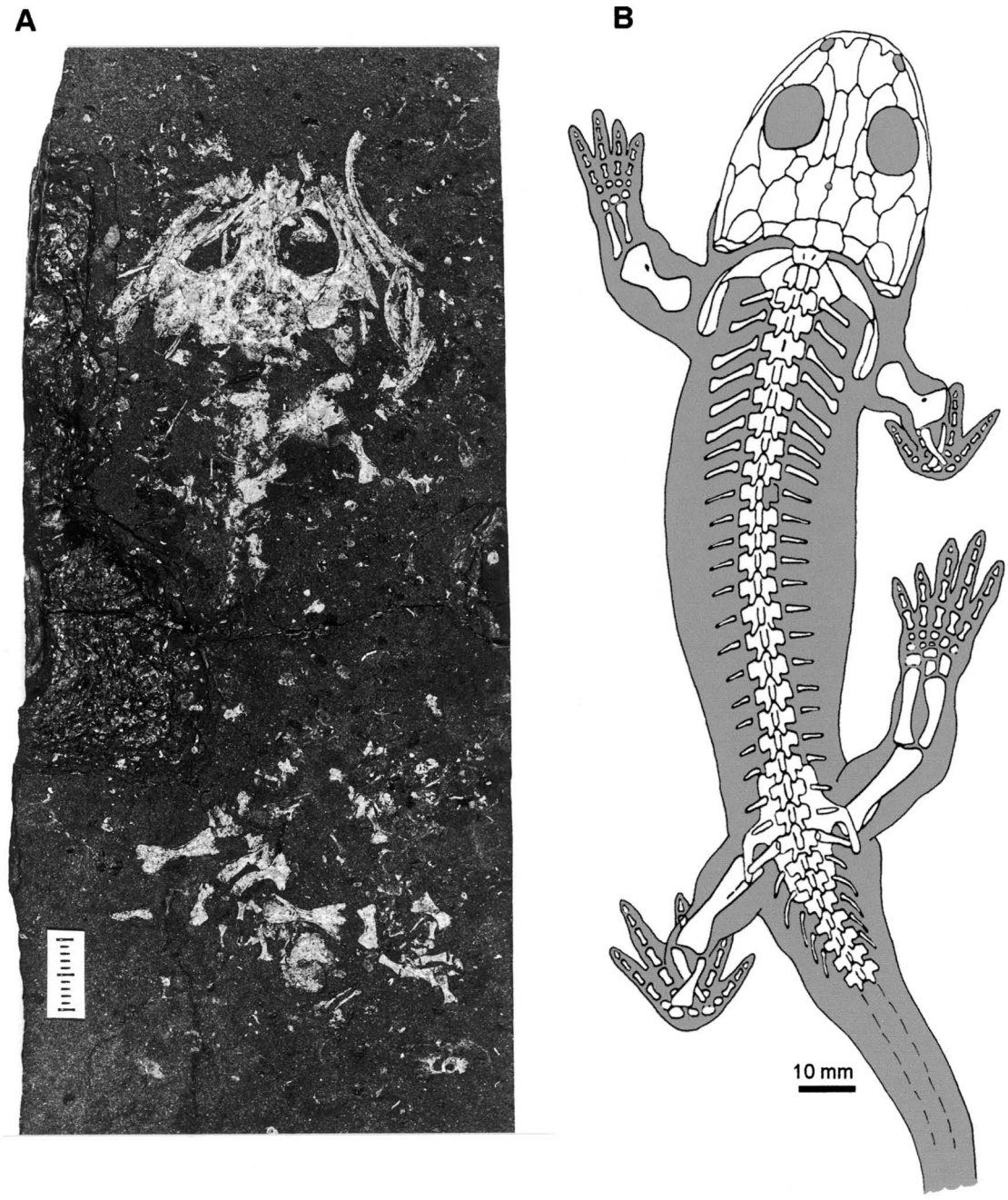
The vertebrate fauna of East Kirkton has proved most remarkable for its collection of tetrapods, which seems to represent the earliest undoubtedly terrestrial assemblage of species. Although many diverse tetrapods



**8.10.** Holotype specimen of *Balanerpeton woodi* (Hunterian Museum specimen GLAHM V2051). *Photograph by A.R.M.*

must have evolved before the period spotlighted at East Kirkton, there is only a sparse record of them. Furthermore, groups whose descendants come to play a significant role in the subsequent evolution of tetrapods are found for the first time in the rocks of the East Kirkton Limestone. There are others whose relationships remain obscure and that seem to have left no descendants.

In addition to the tetrapods, several kinds of fish are found in the sediments toward the top of the sequence suggesting a wetter period in which the lake was deeper. They include acanthodians, ray-finned fishes, and chondrichthyans. They are all fragmentary specimens, although some can tentatively be identified to genus.




The best specimens of tetrapods, including some quite small ones, come from a black shale horizon known as Unit 82, and this layer is also notable for producing the filter-feeding eurypterids. The fine grain of the rock and the high carbon content, together with the good preservation of animals, indicate that the water was deep and quiet enough for fine sediment to accumulate and for an undisturbed oxygen-depleted layer to develop at the bottom of the lake. This allowed the animals' bodies to be

covered over before they could rot, which would not have been possible if the water had been disturbed and oxygenated.

## Temnospondyls

The most common tetrapod by far to be found at East Kirkton is a creature called *Balanerpeton* (Milner and Sequeira 1994). Its name means "crawler from the hot spring or bath." Most specimens of this creature are quite small, with skulls ranging from 25 to 48 millimeters long. Although no complete specimens are known, if extrapolations are made from known specimens, body lengths of 175 to about 440 millimeters can be estimated (Figs. 8.10, 8.11). It had a rather flattened head with a rounded snout, and large circular orbits suggest that eyes looked dorsally.

*Balanerpeton* belongs to a group called the temnospondyls, and it represents the earliest record of the group. Temnospondyls became common and diverse during the Paleozoic and early Mesozoic; their story is continued Chapter 9. However, at this point, it is appropriate to introduce the group and some of its significant features.

One uniting character of temnospondyls is clearly seen in *Balanerpeton*, and that is found in the palate. All the animals described in this book up to this point have had what are called closed palates—that is to say, they are formed from a complete bony sheet, mostly contributed by the pterygoid. In all temnospondyls, by contrast, there are large openings or vacuities where the parts of the pterygoids lying near the midline of the skull have been embayed (this is illustrated in detail in Chapter 9; compare, for example, Fig. 9.5 with Figs. 9.9, 9.10). The feature can be seen in Figure 8.10. Fossils of some Carboniferous animals show that a mosaic of denticle-bearing bony platelets lay in skin that stretched over the vacuities, and it is assumed that in other temnospondyls, skin covered the vacuities in life.

The form of these palatal vacuities reflects a similar condition in frogs and salamanders today. In frogs, the flexible skin of the vacuities allows the eyeballs to be pulled down into the mouth cavity to help the animal swallow food. The same process is also used in breathing as the animal swallows air. It could be that in temnospondyls, the vacuities were used in the same way. Certainly the possession of these vacuities is one character that is thought to unite temnospondyls with frogs and salamanders.

Where the palate and braincase joined, at the basal articulation, *Balanerpeton* shows the beginning of a trend seen among all later temnospondyls, which is for the basal articulation to become a fixed, immobile joint. In early tetrapods, there appears to have been a mobile, cartilage-capped (synovial) joint at this junction, which persists among some groups and can still be seen in some modern reptiles. Although the joint was not sutured in *Balanerpeton*, the style of junction suggests that it was not movable (Fig. 8.10). One suggestion is that the joint no longer needed to move once the palatal vacuities were formed and allowed an alternative region of flexibility in the palate.

**8.11.** *Balanerpeton.* (A) Juvenile specimen of *Balanerpeton.* The skull is a little disrupted, and much of the vertebral column is missing. Three of the four limbs are represented. (B) Skeletal reconstruction of *Balanerpeton.* From Milner and Sequeira (1994). UMZC T1313. Scale bar = 10 millimeters. *Photograph by S.M.F.*

The bones of the palate itself, like those of most other early tetrapods, were covered with shagreen, a field of small denticles embedded in the skin. Where other early tetrapods have a row of teeth, only a pair of somewhat enlarged teeth was found on the vomers, palatines, and ectopterygoids. This seems to be true of most early temnospondyls. The parasphenoid had a narrow process at the front, but at the back, where it lay under the braincase, it was quite broad and bore a further patch of denticles. Again, this seems characteristic of early members of the group.

As with most temnospondyls, there was a rounded otic notch at the back of each cheek that might have supported a tympanic membrane. The stapes was a small bone, and though only part of it is preserved in any specimen, there is enough to show that it was probably slender and rodlike. The footplate fitted into the braincase, and a hole penetrated the base of the bone. In modern tetrapods, a small branch of the stapedial artery runs through such a hole, and it probably did so in these fossil creatures too. The combination of the embayment and the rodlike shape of the stapes suggest that *Balanerpeton*, like many other temnospondyls, had a reasonably good hearing system.

The teeth in the premaxilla and maxilla were numerous, small, and undifferentiated, although those on the dentary seem to have been somewhat larger. *Balanerpeton* does not seem to have been much of a predator and probably fed on small invertebrates. Indeed, some specimens have the remains of myriapods preserved in the position were the stomach would have been.

The limbs were quite short but sturdy, with the hind limbs somewhat longer than the forelimbs (Fig. 8.11B). The humerus was robust, waisted in the middle, and expanded at each end but with little true shaft. There are no well-preserved wrist bones, although there is some evidence that they were ossified. There were four fingers on the hand and five toes on the feet. The femur, like the humerus, was robust with expanded ends, while the ankle was more substantially ossified than the wrist. The pelvic girdle bore a single posteriorly directed dorsal process. The ribs were short, with little differentiation among them along the column, except for in the cervical region, where they are slightly expanded at the ends. It appears that a substantial tail was present, though its length is unknown. As with many early tetrapods, *Balanerpeton* had a covering of dermal gastral scales over its belly.

Almost as interesting as what is preserved of *Balanerpeton* is what is not preserved. For example, there is no evidence of any lateral line system or any branchial arches. This, along with the well-ossified ankle and limb bones and the possible presence of a tympanic ear, suggests that *Balanerpeton* was mainly a terrestrial creature.

Some large ribs of a second type of temnospondyl were also recognized at East Kirkton, though none of the rest of the animal has yet been found. This is a pity, because knowledge of early temnospondyls may help throw light on the origins of the modern frogs and salamanders. It is widely believed that temnospondyls gave rise to these two groups of

modern amphibians. Because East Kirkton provides the first evidence of temnospondyls in the fossil record, it could be said that the evolution of these modern groups started there.

### *Silvanerpeton*, *Eldeceeon*, *Eucritta*, and *Westlothiana*

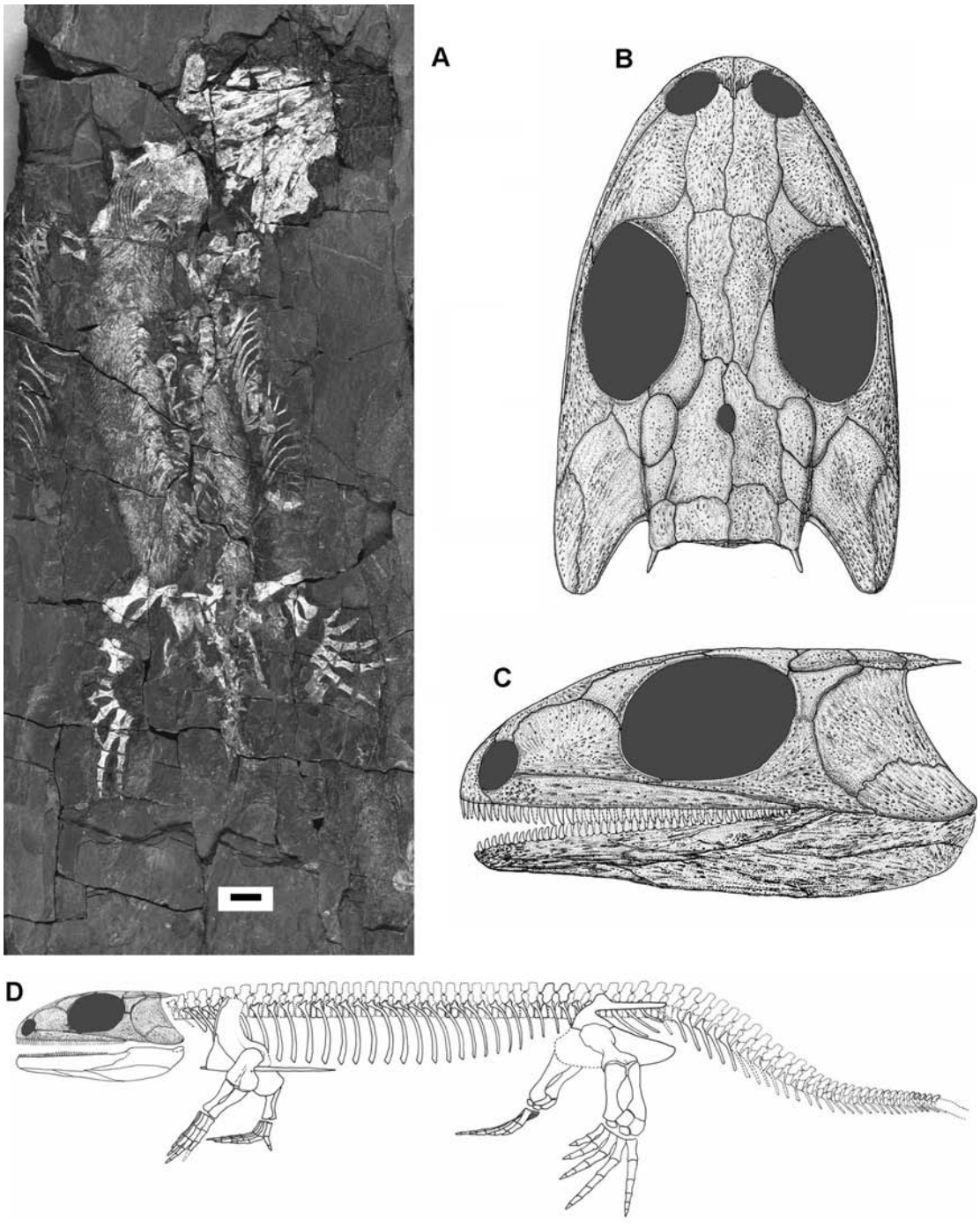
While by far the majority of tetrapod specimens (about 50) from East Kirkton are of *Balanerpeton*, there are about 20 specimens that show other kinds. Among these is a great diversity of forms, each represented by only a few fossils. It is curious that the temnospondyls should show such a limited diversity despite a large number of specimens, while other forms should show a much greater diversity despite only a few fossils. Perhaps the temnospondyls were more local inhabitants than some of the less common forms. Of these other forms, two in particular, *Silvanerpeton* and *Eldeceeon*, are the most numerous. They have both been placed in the group called anthracosaurs, but as noted in Chapter 7, this may not constitute a natural group. Other possible members of the group are described in Chapter 9. Whether or not anthracosaurs are a real group, its constituent members all appear more closely related to amniotes than to amphibians. This is also true of *Westlothiana*, described in the penultimate section of this chapter.

*Silvanerpeton miripedes* (Clack 1994b) and *Eldeceeon rolfei* (Smithson 1994) appear as sister taxa in recent cladistic analyses (Ruta and Clack 2006; Clack and Klembara 2009), though they are easily distinguished by a number of features, especially of the postcranial skeleton. Both are furthermore easily distinguished from *Balanerpeton*.

#### *SILVANERPETON MIRIPEDES*

The name *Silvanerpeton* derives from the Roman god of the woods, Silvanus. It was created to honor its discoverer, Stan Wood, and the fact that the East Kirkton quarry was a wood when Stan rediscovered the site. The specific name *miripedes* ("wonderful feet") refers to the fact that the holotype specimen is preserved with both hind feet intact and in beautiful detail, showing an extra toe bone in the fifth toe that is unique to those anthracosaurs in which the feet are sufficiently well known to observe it (Fig. 8.12).

Most of the *Silvanerpeton* specimens are quite small, showing an animal about 200 millimeters from snout to pelvis, with a skull about 44 millimeters long. The length of the tail, as with so many East Kirkton specimens, is unknown. Its body was covered ventrally by an armor of interlocking gastral scales, narrower than those of *Balanerpeton*, and unlike *Balanerpeton*, they were plain rather than striated. This feature is sometimes helpful in diagnosing incomplete specimens as one or the other. Its lozenge-shaped interclavicle was more elongate than that of *Balanerpeton*, and again, this is a useful distinguishing character. One of the most conspicuous differences between *Silvanerpeton* and *Balanerpeton*




lies in the ribs. In *Silvanerpeton*, the ribs were elongate and curved and must have reached at least halfway around the body, even quite far back along the abdomen. Where *Balanerpeton* had four, *Silvanerpeton* had five fingers on the hand, in common with most other early tetrapods except the Devonian forms.

One feature that anthracosaurs share lies in the skull, and in particular the relationship of the bones of the skull table to one another. In the skull table, rather than having the primitive pattern in which the postparietal stretches across the skull table to meet the supratemporal (see, for example, in *Acanthostega* and *Ichthyostega*), in anthracosaurs, an alternative and mutually exclusive pattern is found in which there is a contact between the tabular and parietal bones (see Chapter 9 for more details; this is also mentioned in Chapter 7). *Silvanerpeton* shows this feature. A detailed description of *Silvanerpeton*, based on recently collected material, was published in 2006, showing new details (Ruta and Clack 2006) (Fig. 8.12). Unfortunately, some of the other key features remain lacking or are not preserved well enough to be sure about. Therefore, the position of *Silvanerpeton* with respect to anthracosaurs is a bit uncertain. In some phylogenies, it appears as a sister taxon to the embolomeres; in others, it lies sometimes more crownward and sometimes more stemward than that group (Ruta and Clack 2006).

**8.12.** (A) *Silvanerpeton miripedes* holotype specimen (UMZC T1317) Photograph from UMZC archives. Scale bar = 10 millimeters. (B) Skull in dorsal view. (C) Skull in left lateral view. (D) Skeletal reconstruction. *Drawings by M. Ruta. From Ruta and Clack (2006).*

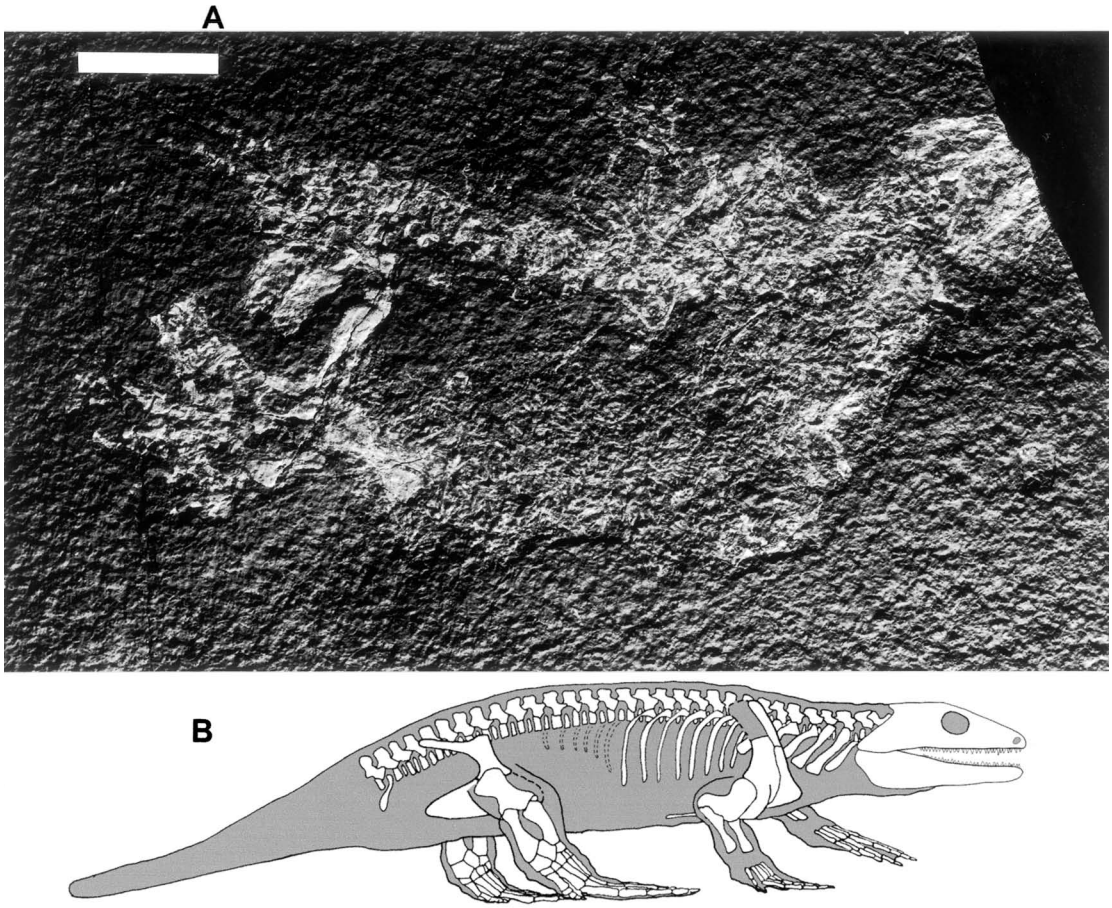
Some of the features that *Silvanerpeton* does share with anthracosaurs are apparently primitive features that might be expected in many early tetrapods, and that are seen, for example, in *Acanthostega*. These include a closed palate, without any of the large vacuities that characterize temnospondyls. At the point where the palate and braincase meet, the braincase sends out a prominent process that fits into a socket on the palate in what appears to have been a synovial joint. This contrasts with *Balanerpeton*, where this junction is considered to have been immobile. A moveable joint here may be a leftover from the condition found in tetrapodomorph fishes, although even in *Tiktaalik* and tetrapods as early as *Acanthostega*, the articulation had specialized to a degree.

Where the skull table joins the cheek, anthracosaurs have a conspicuous joint known as a kinetic line. This abrupt junction has been considered to have allowed a limited amount of flexibility between the two skull units, reflecting that which was found in some tetrapodomorph fishes at the same point, although it is not present in *Tiktaalik*, for example. It has been thought to be related to the presence of the mobile palatal articulation. *Silvanerpeton* shares this character with embolomeres.

The back of cheek sloped diagonally backward and downward from the corner of the skull table, in a manner that at one time would have been considered to have formed an otic notch as in *Balanerpeton*. For reasons addressed in Chapter 10, this interpretation now seems unlikely, and the notch might alternatively have been spiracular.

### *ELDEECEON ROLFEI*

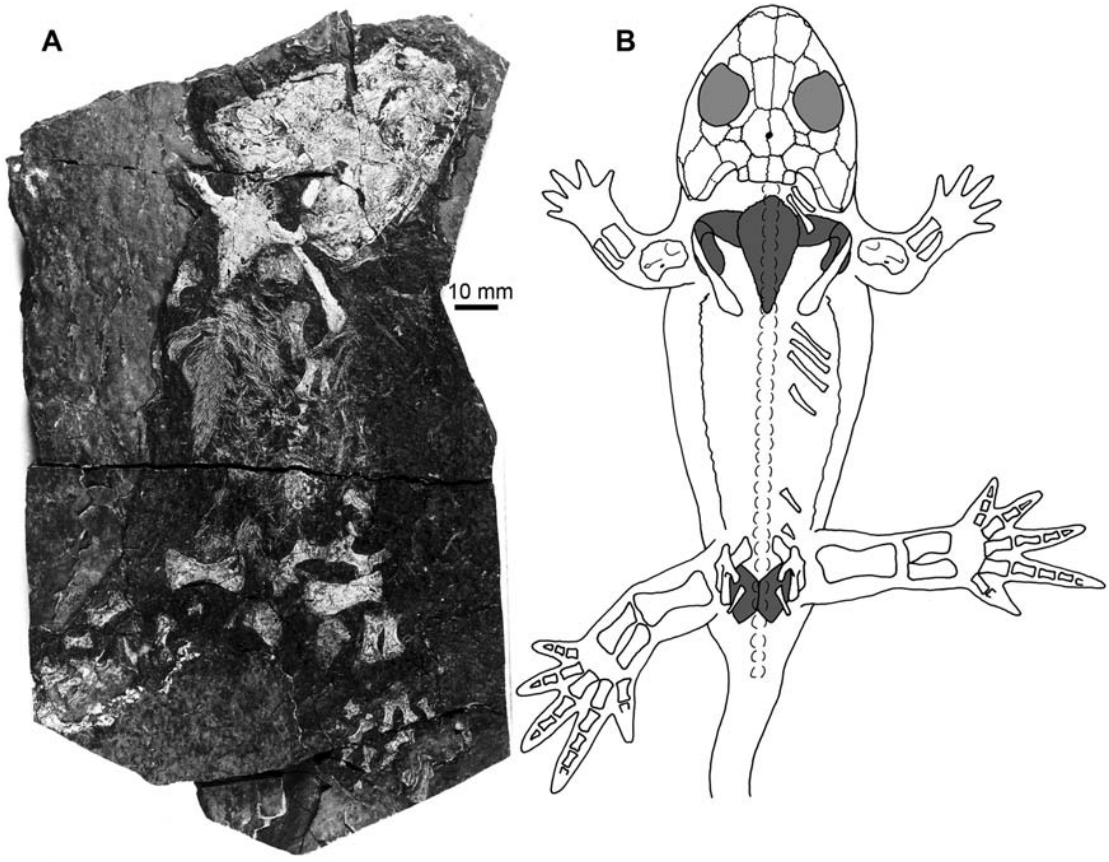
This animal is only known from four or five specimens, but they show a different animal from *Silvanerpeton*, despite being about the same size and apparently related (Fig. 8.13). *Eldeceeon's* name comes from the letters LDC, which stand for the Livingston Development Corporation, which contributed to the purchase of the specimen for the National




**8.13.** (A) Holotype specimen of *Eldeceeon rolfei* (NMS G1986.39.1p) *Photograph by NMS.* Scale bar = 30 millimeters. (B) Skeletal reconstruction of *Eldeceeon*. (There are no ribs preserved posterior to those illustrated.) *Based on Smithson (1994).*

Museum of Scotland. It has a much more robust skeleton than *Silvanerpeton*, with much more heavily ossified vertebrae and limbs. Like *Silvanerpeton*, it has elongate gastral scales, but its interclavicle, rather than being lozenge shaped, has a narrow posterior process. Other differences between the two include a shorter vertebral column anterior to the pelvis and a rib cage that seems only to have surrounded the anterior part of the trunk, much in the same way as it does in mammals, but in contrast to the more complete rib cage of reptiles such as lizards or crocodiles. The more posterior ribs, where they are preserved, appear to have been short and lightly ossified.

The most conspicuous difference between the two animals lies in the hind limbs. In *Silvanerpeton* they are relatively short, only a little over one-third of the length of the skull, whereas in *Eldeceeon* they are nearly half the length of the skull. The ankle is sturdily ossified, and the feet appear large for the size of the body. Whereas in some respects *Silvanerpeton* looks more like an aquatic form, or perhaps one for which only subadult and incompletely ossified individuals are preserved, *Eldeceeon* appears to have been unquestionably terrestrial. Its relationships are unclear because many details of the skull roof are poorly known, but some

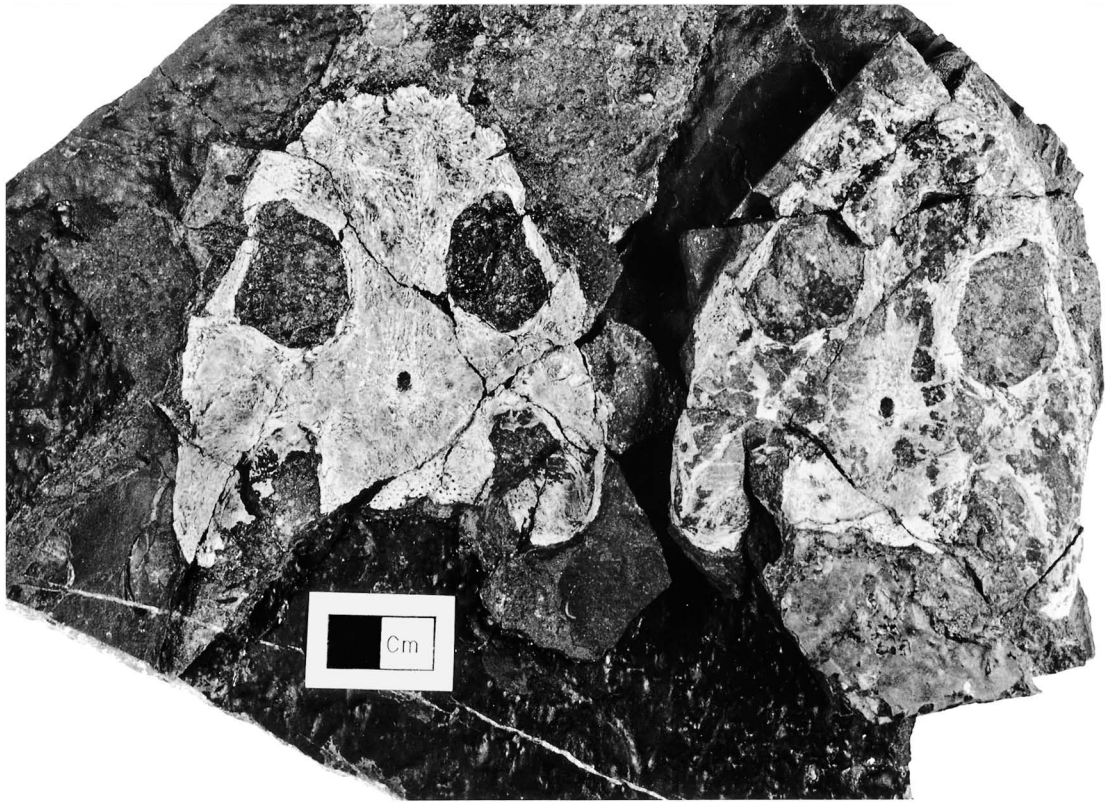



**8.14.** Holotype specimen of *Eucritta melanolimnetes:* (UMZC T1347). (A) *Photograph by S.M.F.* (B) Skeletal reconstruction of *Eucritta.* The inner surfaces of the girdles that are visible in dorsal view have been shaded. *Modified from Clack (2001a).*

features, such as the closed palate and kinetic line and the features of the vertebrae and pelvic girdle, suggest that it lies close to *Silvanerpeton*, probably with the anthracosaurs. For neither *Eldeceeon* nor *Silvanerpeton* is there evidence of what they might have eaten because the teeth of the jaws are unspecialized and those of the palate are unknown.

### *EUCRITTA MELANOLIMNETES*

One of the species from East Kirkton produced great puzzlement among the paleontologists who first looked at it. Those who worked on anthracosaurs shook their heads and thought, no, it is not an anthracosaur, it must be a temnospondyl—look at the shape of its head and its large otic notch. Those who worked on temnospondyls also shook their heads and said no, it is not a temnospondyl, it must be an anthracosaur—look at its closed palate, its lozenge-shaped interclavicle, its double-pronged ilium. This animal showed a mixture of characters normally associated with each of these two separate groups, but not normally found together. It was given the name *Eucritta*, based on the American vernacular word "critter," meaning "creature," but prefixed by "Eu" from the Greek meaning "beautiful" or "perfect." The latter is pronounced as "you" in Britain and




**8.15.** An isolated skull of *Eucritta* (NMS 1992.14) showing its similarity to *Balanerpeton*. *Photograph by S.M.F.*

North America, and so indicates some frustration over where the animal might belong phylogenetically. The specific name *melanolimnetes* means "from the black lagoon," a reference to the nature of the East Kirkton locality (Clack 1998a).

Eventually, five specimens were recognized, of different sizes in a growth sequence. The specimen chosen as the holotype was a medium-sized example, with some well-preserved postcranial material, though no vertebral elements (Figs. 8.14, 8.15). The skulls showed subtle but consistent differences from *Balanerpeton*, despite their superficial similarities, though the rounded shape, large open notch, large orbits and short snout were originally deceptive. The closed, denticulated palate and the long stylus-shaped parasphenoid were not those of temnospondyl. Significantly, the largest and best-preserved skull roof showed that the orbits had slight but clear anterior extensions, also unlike *Balanerpeton*.

The animal had quite a short body, with robust hind limbs and large feet, not unlike *Eldeceeon* in proportion, but its ribs were shorter and straighter, more like those of a temnospondyl than an anthracosaur. The forelimbs were badly preserved, so it was not possible to say whether it had four or five digits on the hand. Cladistic analysis has suggested that *Eucritta* may belong with a later Carboniferous group called the baphetids (see Chapter 9).

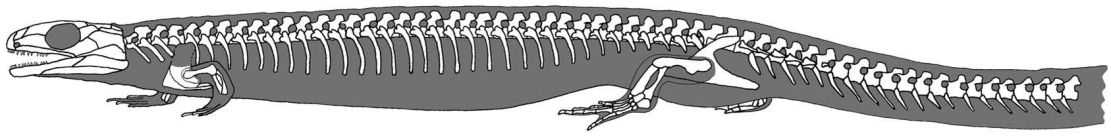


**8.16.** *Westlothiana lizziae.* Specimen in part and counterpart. (NMS G1990.72.1). Scale bar = 10 millimeters. *Photograph by NMS.*

### *WESTLOTHIANA LIZZIAE*

Among the many specimens from East Kirkton that were found by Stan Wood was one which caused particular excitement. When it was first discovered and studied, only one specimen was known, and preliminary results suggested that this animal was the earliest known reptile. It received the name Lizzy the Lizard from Stan. The reason for the excitement was that before this discovery, the earliest known reptile was *Hylonomus* (see Chapter 9) from a locality called Joggins in Nova Scotia, in rocks about 15 million years younger than those of East Kirkton. An amniote from East Kirkton therefore would put the known origin of this important group back by this considerable amount of time.

The specimen was purchased by the National Museum of Scotland, with help from West Lothian District Council, the district in which East Kirkton lies, and whose name was thus incorporated into the generic name of the animal, *Westlothiana*. It was given the specific name *lizziae*, after Stan Wood's nickname for it. Unfortunately, the specimen was not well preserved in some key areas that would truly establish the



**8.17.** Skeletal restoration of *Westlothiana*. Snout–vent length of animal about 115 millimeters. *Based on Smithson et al. (1994).*

creature's identity as an amniote. However, a little while later, a few more specimens came to light, allowing more thorough study of this species.

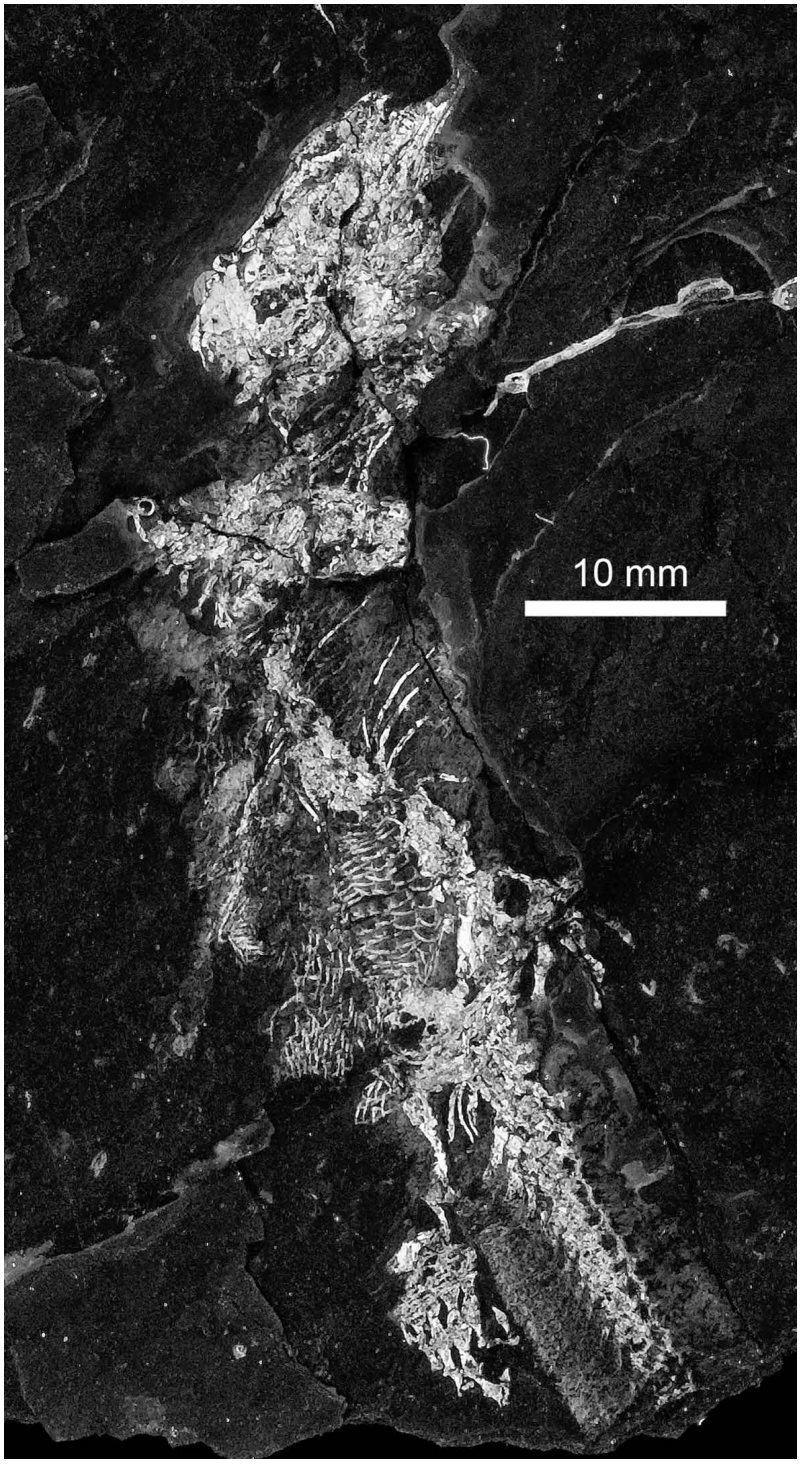
What all the information showed when put together was a small, rather long-bodied animal with short legs (Figs. 8.16, 8.17) (Smithson et al. 1994). The vertebrae are robust, with the centrum of each vertebra fused to its neural arch. This is one of the features that first made *Westlothiana* look like an amniote and is one generally associated with terrestrial forms. Although the limbs are rather short, the ankles are well ossified, and the bones of the limbs themselves gracile, rather than short and stubby. It was the form of the skull that helped form the first impression of an amniote, however. The back of the skull shows no otic notch (see Chapter 10), and there are fewer or smaller bones in the temporal region than in almost any other contemporary nonamniote group. The tooth row extends far forward in front of the eye but not very far behind it, and the eyes are large (Fig. 8.17).

The additional specimens showed some regions that were not visible in the first one. They showed that a feature such as a particular flange on the palate, diagnostic of early amniotes, was in fact not present. Most amniotes have two enlarged bones in the ankle, called the astragalus and calcaneum, but in *Westlothiana*, there were three smaller ones, a more primitive condition. The temporal series of bones was difficult to interpret, although they seemed most probably to be amniote-like, whereas other potentially diagnostic characters such as the form of the occipital condyle were not visible in any specimen.

When included with other amniotes and nonamniotes in cladistic analysis, the position of *Westlothiana* became a little clearer. Rather than being a true amniote, it slotted into the bottom of the family tree of the group containing amniotes; in other words, it belongs to the stem group of amniotes. This group also contains the anthracosaurs, though they slot in below *Westlothiana*.

If this analysis is correct, and the difficulties of studying this animal means that there is some doubt about this, it was an important find. It means that at East Kirkton, representing a period about 333 million years ago, members of both the lineage that gave ultimate rise to modern amphibians (*Balanerpeton*) and that which gave rise to amniotes (*Westlothiana*) were already present. The implications of this are that these two lineages must have separated before this time, and most likely well before it. The subsequent discovery of *Casineria* supports this view.

Despite the attractiveness of this hypothesis, there is an alternative that must be considered, and further study may resolve the problem in its favor. That is, that *Westlothiana* lies close to the microsaurs (see




**8.18.** (Color Plate 18) Photograph in ultraviolet light of a probable microsaur from East Kirkton. *Photograph by P. Crabb (Natural History Museum, London).* UMZC specimen 2002.2.

**8.19.** Reconstruction of the East Kirkton landscape and fauna. The scene shows two *Balanerpeton* in the foreground, with *Hibbertopterus* at the left, and a harvestman and a scorpion close by on the rocks. *Silvanerpeton* and *Eldeceeon* are seen in the background. *Illustration by J.A.C.*

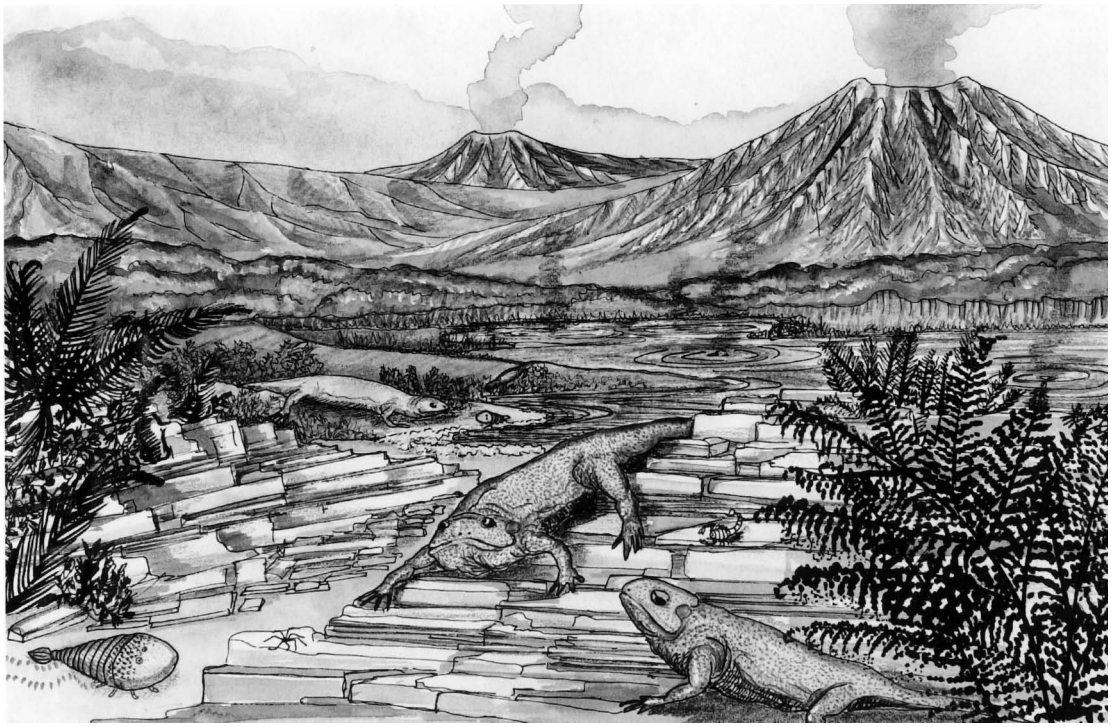
Chapter 9). Many of its features are consistent with its being a microsaur, but all the features that could resolve the issue one way or the other are either poorly preserved or not visible on the known specimens. However, in many recent phylogenies, microsaurs themselves emerge as stem amniotes, although slightly further away from crown amniotes than *Westlothiana* is usually placed. Only further specimens could really prove the case.

## Other Tetrapods

There are at least two other taxa of tetrapods from East Kirkton. One of them is a member of the specialized group called the aïstopods. Chapter 7 introduced *Lethiscus*, which is the earliest known member of the group, but at East Kirkton, the genus *Ophiderpeton* is represented by two or three poorly preserved specimens (Milner 1994). This genus is also found in rocks of the Late Carboniferous of Ireland and shows some features in common with other, later aïstopods that *Lethiscus* does not show. There is some degree of specialization of the teeth among aïstopods, with *Ophiderpeton* showing broad, conical, recurved, and widely spaced teeth, in contrast to later genera in which the teeth are narrow, straight sided, and closely packed in the jaw. However, the different niches that these peculiar creatures occupied are matters for speculation. It is thought that with their snakelike bodies and lack of limbs, they were terrestrial rather than aquatic.

The microsaurs may still be represented at East Kirkton, even if *Westlothiana* is not one. These creatures became quite common during the Carboniferous (see Chapter 9), and by the Permian they were highly specialized. A single specimen from East Kirkton is possibly their earliest known member, and the only one recognized in the United Kingdom (Fig. 8.18). The single specimen is poorly preserved, but one distinctively microsaur feature is the form of the gastral scales. These show the characteristic fine transverse striations found in microsaurs such as *Hyloplesion* and *Llistrofus* (Carroll and Gaskill 1978), but in no other groups. It has a short vertebral column of holospondylous centra. This specimen is unusual in having a deepened swimming tail. The caudal neural spines are low and rounded, but the anteriormost hemal spines are long and broad. Posteriorly, the hemal spines become progressively less well ossified, but a thin "skin" of bone persists, as shown by photographs taken in ultraviolet light. The tail is covered with a web of skin, preserved as a black carbonaceous layer showing fine striations and undulations that do not correspond with the number of vertebrae (Clack <in press>).

Among the many tetrapod specimens found at East Kirkton are many that preserve larger elements than those associated with the more fully articulated skeletons. Some appear to belong to temnospondyls, such as the ribs mentioned above. However, there are also large humeri, some incomplete lower jaws, interclavicles, gastral scales, a large isolated but fully articulated digit (probably a toe), and pelvic elements that are not

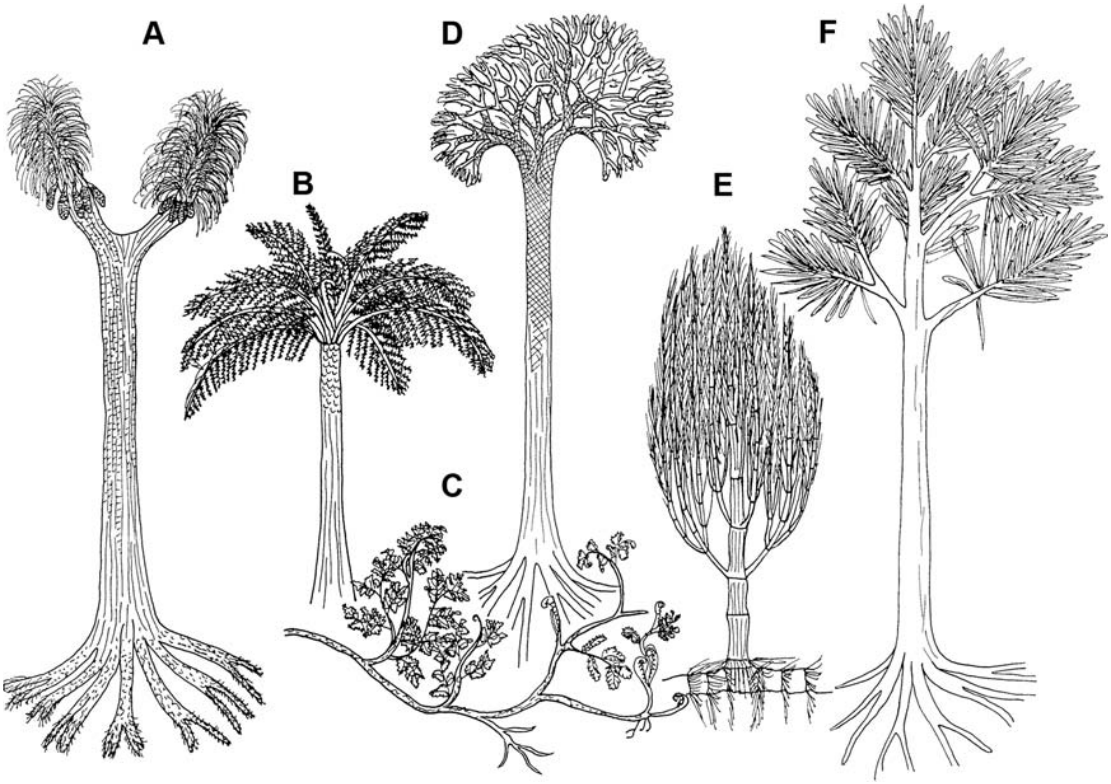


certainly associated with any taxon. Some may well be anthracosaurian, and it may be that they belong to adult individuals of taxa already known from the site, or they may belong to new species. Until more clues are found in the way of larger, more fully articulated skeletons, their identity will probably remain a mystery.

## Conclusions

The single locality of East Kirkton, with its unusual preservation, gives invaluable insight into the early diversification of tetrapods, as well as other terrestrial organisms. It provides minimum dates for the origin or separation of major tetrapod groups, which can be compared with results from molecular analyses of living forms. It gives a glimpse of some of the range of niches into which tetrapods had evolved by this early stage, as well as some of the interactions that went on between vertebrates and invertebrates. Whichever analysis of tetrapod interrelationships is accepted (see Chapter 9), the lineages leading to modern amniotes and modern amphibians had already split from each other by the time represented by the East Kirkton locality. Although excavations have finished for the present time, much of the tetrapod-bearing horizon that has been collected still remains to be studied, and it is likely that the locality has not ceased to yield previously unknown creatures and provide important surprises for early tetrapod paleontology.

Figure 8.19 shows a reconstruction of East Kirkton as it might have looked in the Early Carboniferous.




**9.1.** Drawings of Late Carboniferous plants. (A) *Sigillaria* sp., a lycopsid (club moss) with a trunk up to 1 meter in diameter. (B) *Psaronius* sp., a tree fern related to the modern family Marattiales. (C) *Callistophyton* sp., a trailing pteridosperm. (D) *Lepidodendron* sp., a lycopsid (club moss) up to 54 meters high. (E) *Calamites carinatus,* a horsetail (Equisetales). (F) A member of the Cordaites family, a gymnosperm with trunk diameter up to 1 meter.

# The Late Carboniferous: Expanding Horizons

# 9

## Late Carboniferous/ Early Permian Biogeography and Paleoecology

During the Late Carboniferous, the continents, which had slowly moved southward through the Devonian and Early Carboniferous, changed direction and began to rotate. Gondwana and Euramerica gradually collided, initiating the formation of the supercontinent Pangaea. The world's vegetation had differentiated into continental regions so that, for example, the Gondwana flora became quite distinct from those of Euramerica and of what are now China and Siberia. At this time, Euramerica, positioned in the tropics, was covered by a vast swamp forest, while to the north and south of it, evaporite deposits speak of arid climates (Milner 1993a).

The forest has provided an excellent fossil record of both plants and animals. There was a huge increase in diversity not only of plants but also of invertebrates and vertebrates. Partly this can be explained by the quality of the fossil record and the distribution of fossil collectors, but the increase of taxonomic diversity, body forms, and ecologies among the animals parallels but lags behind that among the plants, suggesting that the phenomenon is real, not simply an artifact. In the Late Carboniferous, more orders and classes of plants were contributing more diversity to the flora than at any other time in Earth's history. The swamp forests of the Late Carboniferous were not completely heterogeneous. Greb et al. (2006) describe and illustrate at least six different types of habitat, each with a different complement of floral types, varying according to distance from water margins, depth of standing water, depth of decaying vegetation (mires), and so on.

Most of the plants from this time are those of the lowland swamps, but a few localities preserve more upland floras showing adaptations to drier conditions. The dominant plants were still lycopsids in the form of lepidodendrons. These grew into huge trees up to 30 meters tall. They had a life history like no modern plants. In their prereproductive phase, they consisted of a single polelike trunk that, at a certain point in their growth, sprouted a crown of branches bearing conelike fruiting bodies. The branches consisted of thickened woody tissue, making them unappetizing to arthropod herbivores, but the cones containing a rich filling of spores would have been appreciated. Some of them were eaten by the large *Arthropleura* type of millipedes (see Chapter 7 and below). Probably only flying insects could reach the cones borne in the tops of the trees until these were shed (DiMichele and Hook 1992). Figure 9.1 shows a selection of Late Carboniferous plants.

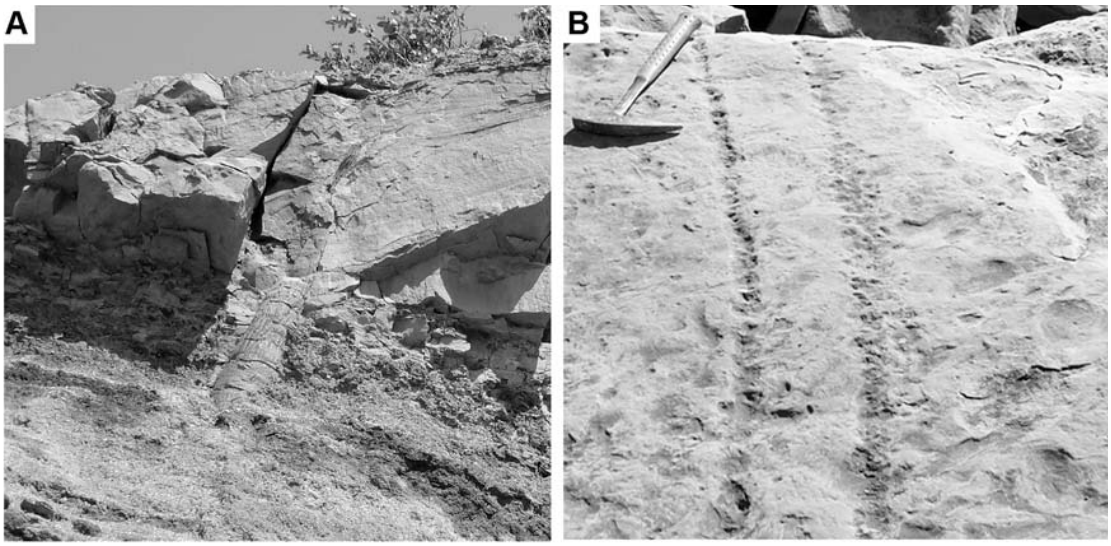
The lycopsid trunk was formed of a relatively thin but tough outer casing, while the inner tissue was soft and open, unlike the structure of woody trees today. When a lycopsid died, the inner material rotted faster than the outer, sometimes leaving a tall hollow cylinder standing upright after the rest of the plant decayed. This construction is important for vertebrate paleontologists because it has led to the occasional and unusual preservation of some small terrestrially adapted animals, in particular in Joggins, Nova Scotia.

Pteridosperms, or seed ferns, were diverse during the Late Carboniferous, and some reached heights of 6–10 meters. Individual leaves could be several meters long, and when they died, the fronds remained on the trees, drooping around the trunk in a skirt that would have provided important refuges for small arthropods or tetrapods (DiMichele and Hook 1992). As with the lepidodendroids, the stems and branches offered tough food for herbivores, but the fruiting bodies, once the protective outer coat had been penetrated, would have provided a rich source of food. As well as trees, scrambling or vinelike habits were common among pteridosperms. True ferns were also part of the flora, low in numbers but high in diversity. Both low-growing ground-covering forms and tree ferns were present, as well as climbing and vinelike forms. Their leaves were soft and might have been eaten by herbivores, but today's ferns produce toxins to deter this. Perhaps this ability evolved first in the Carboniferous with the first radiation of herbivorous insects.

Sphenopsids, relatives of modern horsetails, provided major ground-covering forms in the sphenophylls, while the calamites formed trees with trunks up to half a meter in diameter. The sphenophylls formed thickets with branches linked by hooks and barbs, much like brambles do today. The undergrowth would have been impenetrable to most large animals, but it formed cover for smaller ones.

Cordaites (pronounced Cor-DAY-tees) evolved and radiated explosively in the Westphalian. They were quite closely related to modern conifers, and like them, many of the Carboniferous forms are associated with drier environments. They had true seeds, sometimes winged, and sometimes with fleshy outer coats that could have attracted animals to eat them, a device used by many modern plants to aid dispersal. True conifers also evolved during this stage, and as with modern forms, many had needlelike leaves and were associated with drier environments. Many examples are preserved as fossil charcoal, or fusain, implying that the conifer forests were periodically burned.

A lot has been learned about Late Carboniferous arthropods from one or two exceptionally preserved sites. Mazon Creek in Illinois has produced nodules in which soft body parts are preserved, so there is information on soft-bodied invertebrates and vertebrates such as lampreys as well as arthropods (Shabica and Hay 1997). The diversity of terrestrial invertebrates increased greatly during this period, including the first appearance of land snails. Many of these invertebrates were feeders on detritus, both plant and animal, such as the arthropleurid millipedes. The latter grew up

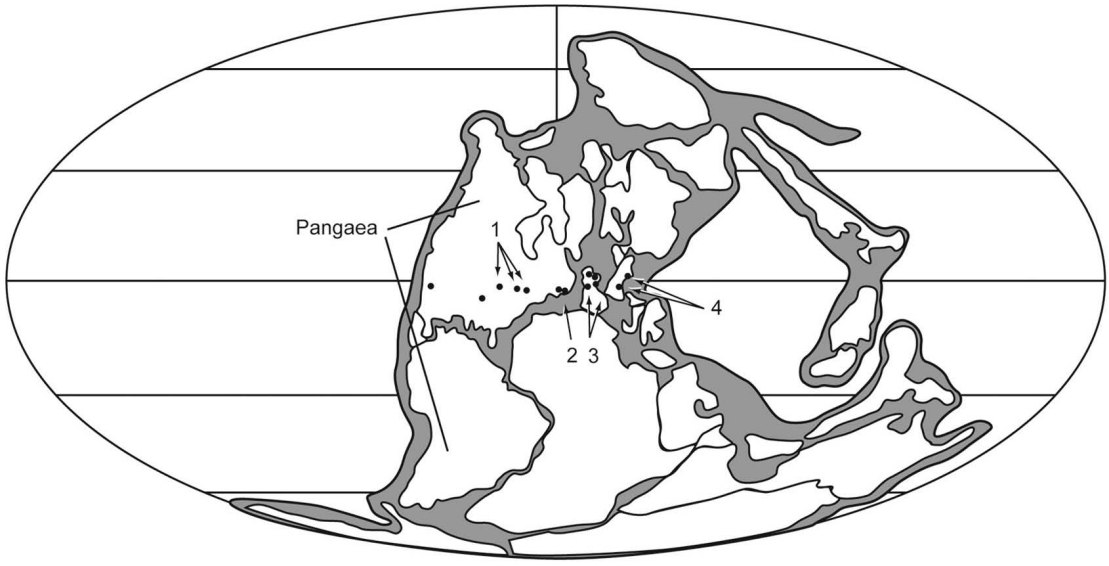



**9.2.** (A) Photograph of Joggins cliffs showing a fossil tree stump in situ. (B) Trackway of a giant arthropod found at Joggins. The geological hammer gives scale. *Photographs by J.A.C.*

to 2 meters in length, and their large size suggests that at this stage, they were not sharing their niche with tetrapods. Figure 9.2A shows the cliffs at Joggins with a lycopsid tree trunk in position, and Figure 9.2B shows the trail of a giant arthropleurid preserved on a slab of limestone there. As with the East Kirkton fauna, some of the millipedes were equipped with glands that produced toxic substances, and the smaller forms were eaten by tetrapods, as shown by fossilized gut contents in a few specimens.

Much evidence from chewed leaves and bored seeds, and the mouthparts of insects themselves, suggests that herbivory was well developed in many forms. It has been suggested that insect flight and herbivory coevolved, allowing insects to exploit the tops of the trees. Many Carboniferous insects reached large sizes, the most famous being a primitive form of dragonfly with a 430-millimeter wingspan. Its flight and landing abilities were probably quite limited. Primitive cockroaches and their relatives were common, and early relatives of grasshoppers and plant-sucking bugs made their first appearance. Many insects were predatory and could have been in competition with tetrapods, while some were big enough to have preyed on small individuals, such as juvenile amphibians (DiMichele and Hook 1992). Spiders and scorpions lurked among the plant debris. Many of the insects, perhaps most, had aquatic larvae, as do their modern descendants. The larvae may have formed food for tetrapods, but again, as today, large predatory forms such as dragonfly nymphs may have preyed on larval or hatchling tetrapods.

Recent models of atmospheric composition in the Carboniferous have suggested that the increase in oxygen content was both later and slower than in earlier models (Berner 2006). However, a link may still exist between this increased oxygen supply in the Late Carboniferous, the concomitant higher air density and the appearance of winged insects, and also the subsequent evolution of giant insects and other arthropods toward the end of the period (Dudley 1998). It has been suggested that the




**9.3.** Late Carboniferous paleocontinents with major tetrapod sites indicated: 1, North American sites including Mazon Creek, Illinois, and Linton, Ohio; 2, Canadian sites including Joggins and Florence (Nova Scotia); 3, English, Scottish, and Irish sites including Jarrow (Eire), Scottish Midland Valley sites, Newsham, and Yorkshire sites; 4, Czech and German sites including Nýřany and Tremosna. All are grouped around the equator, most to the south of it.

denser air had a direct effect facilitating the evolution of flight, that more oxygen in the air allowed the animals to be more active, and that their means of gaining oxygen by their system of minute tubes throughout the body (the tracheal system) was better able to distribute the oxygen under these conditions (Graham et al. 1997). Similarly, this would enable the animals to reach a much larger size than is possible in today's relatively oxygen-poor air. Not just air density is affected when the proportions of these gases change; so do the viscosity, diffusivity, and heat conductivity. Some of these would have had unknown effects on the evolution of the animals of the time. One of the effects of increased oxygen in the atmosphere might well have been to provoke the evolution in animals of mechanisms to prevent or deal with oxidative damage to tissues.

Another link has been suggested between increased oxygen levels in the Late Carboniferous and the prevalence of deposits of fusain: evidence of forest fires. Such a high level of oxygen is almost at the point at which organic matter spontaneously combusts, and certainly if a forest fire started, it would spread widely and rapidly (DiMichele and Hook 1992; Scott and Glasspool 2006).

The increasing diversity among tetrapods that began in the Early Carboniferous continued and intensified during the Late Carboniferous, so that by the end of the period, the foundations were laid for the appearance of most major groups, including those that remain today (Milner 1987). However, most of the information comes from a handful of especially productive Westphalian localities, most of which, except for Joggins and a similar site at Florence, Nova Scotia, preserve predominantly aquatic forms (Figs. 7.1, 9.3).

At those two localities, upright, hollow lycopsid trunks are preserved in extensive sequences of sediments (Fig. 9.2A). At Joggins, these represent about 4 million years' worth of accumulation; they have been studied by

Calder et al. (2006). At least 60 horizons in the sequence contain tree stumps. They were preserved as standing forests, killed probably en masse, as floodwaters periodically invaded the landscape: the area was a slowly sinking basin, and at the same time, sea levels were rising and falling in response to a series of ice ages. As the basin slowly refilled with sediment, plants returned and in some intervals formed coal beds. It is these particular sequences, known as the Fundy forests, that have yielded the remains of small tetrapods within the sediment that accumulated when the soft, pithy centers of the lycopsids decayed. The tree stumps have been known since the 1820s, but it was Sir Charles Lyell working with Sir William Dawson in 1853 whose description of some of the tetrapods that made them famous. The site was mentioned by Darwin in his *Origin of Species* in 1859, and the Joggins Cliffs have now been listed as a World Heritage Site.

One widely cited explanation for why the tetrapods were in the hollow stumps is that these hollow trunks stayed upright long enough for the sediment to accumulate around them until it was level with the top of the trunk cylinder. The hollow cylinders would then have become effective pitfall traps into which passing unwary small tetrapods fell and were unable to escape. This scenario has recently been shown to be unlikely. A more recent interpretation is that the hollow stumps might have served as refuges for the animals during forest fires. Fusain is often found in the sediments in the base of the stumps. Yet another interpretation is that the animals actually lived in the stumps, or that large predators might have used them as larders, or somewhere safe to eat their prey (Scott 2001). The unfortunate side effect for paleontologists was that the animal remains became almost totally disarticulated and mixed up, causing years of taxonomic confusion for those trying to understand them. Nevertheless, without these flukes of preservation, there would be almost nothing known about small, terrestrially adapted tetrapods of the Late Carboniferous. In more recent years, larger and more completely articulated specimens have been found at Joggins outside of the tree stumps, including an almost complete skeleton of the temnospondyl *Dendrerpeton* (Holmes et al. 1998) and a large embolomere (Holmes and Carroll 2010). Other horizons preserve evidence of plants such as seed ferns and gymnosperms, and many arthropod and tetrapod trackways, both small and large, are known. The Joggins Formation is dated as Westphalian A, now known as Langstettian, but it is quite close to the Namurian/Westphalian boundary.

At Linton, Ohio, and Nýřany in the Czech Republic are found the faunas of relatively shallow lakes. Linton shows the animals preserved in an abandoned river channel (Hook and Baird 1986), while Nýřany seems to have been a shallow pool that existed for perhaps no more than a few hundred years (A. R. Milner 1980). Despite some environmental differences and their geographical separation, the two share many genera in common. Newsham in Northumberland, United Kingdom, like Linton, was an abandoned river channel, but the fauna preserved there, consisting for the most part of larger animals than are found at Linton, is indicative of deeper water.

A few localities that have been investigated in recent years show clear indications that they experienced transitions from marine to freshwater sequences. For example, three localities in North America, called Robinson, Hamilton, and Garnett, all in Kansas, form a series showing increasing influence from marine or tidal conditions, yet they have all produced tetrapods and represent coal-swamp environments. They demonstrate that coal-swamp flora and fauna could tolerate at least some salinity, and that such assemblages cannot be assumed to be associated exclusively with freshwater (Schultze and Maples 1992; Schultze et al. 1994; Schultze 1995). It remains problematical to be certain whether the flora was actually salt tolerant, or whether it was living in freshwater pools close to the shore that were periodically invaded by the sea (Greb et al. 2006). Furthermore, freshwater is less dense than seawater, and it could have formed pools above a base of seawater in which plants and animals could live. When they died, however, they would sink to the bottom of the saltwater, as happens in many places today, including Mexico and Florida.

Westphalian and Stephanian tetrapod localities are more or less geographically restricted to Europe and North America. As yet, virtually nothing has been found from these periods in other parts of the world (Fig. 9.3). As far as Gondwana is concerned, the reason for this is that during this part of the Paleozoic, it was undergoing a prolonged period of glaciation; it was simply too cold for the tetrapods to live there (Milner 1993a). However, it is less clear why tetrapods from this time have not been discovered in what were the more easterly parts of the northern Paleozoic continents—today's Asia. Because the coal-bearing forests extended east as far as China, the reason for this may be historical and have more to do with collecting bias. Perhaps the tetrapods are there but are still waiting to be found. Alternatively, it may be that the Hangenberg event wiped out the far-eastern populations of tetrapods of Devonian times, and that Carboniferous forms did not reradiate into those regions until much later.

From the Early Permian, the climate had been slowly changing, so that by the end of this period, the coal swamps had all disappeared. A study by DiMichele et al. (2006) has tracked the changes to the vegetation and environment of a Late Carboniferous to Early Permian sequence in Texas. They showed how in the Late Carboniferous, forests of seed ferns, true ferns, lycopsids, and calamites, with an understory of ground cover and vinelike plants were present in an extensive coal swamp. Gradually the climate became drier and more seasonal, and the swamps reduced in size and eventually disappeared. In the equatorial region of the new supercontinent of Pangaea, such as that represented by the Texas study site, they were replaced by red beds and evaporites indicating the onset of a more arid climate. A number of localities in Texas preserve remains of tetrapods, known as the Texas red-bed fauna. They include terrestrial temnospondyls such as dissorophoids, as well as many varieties of early

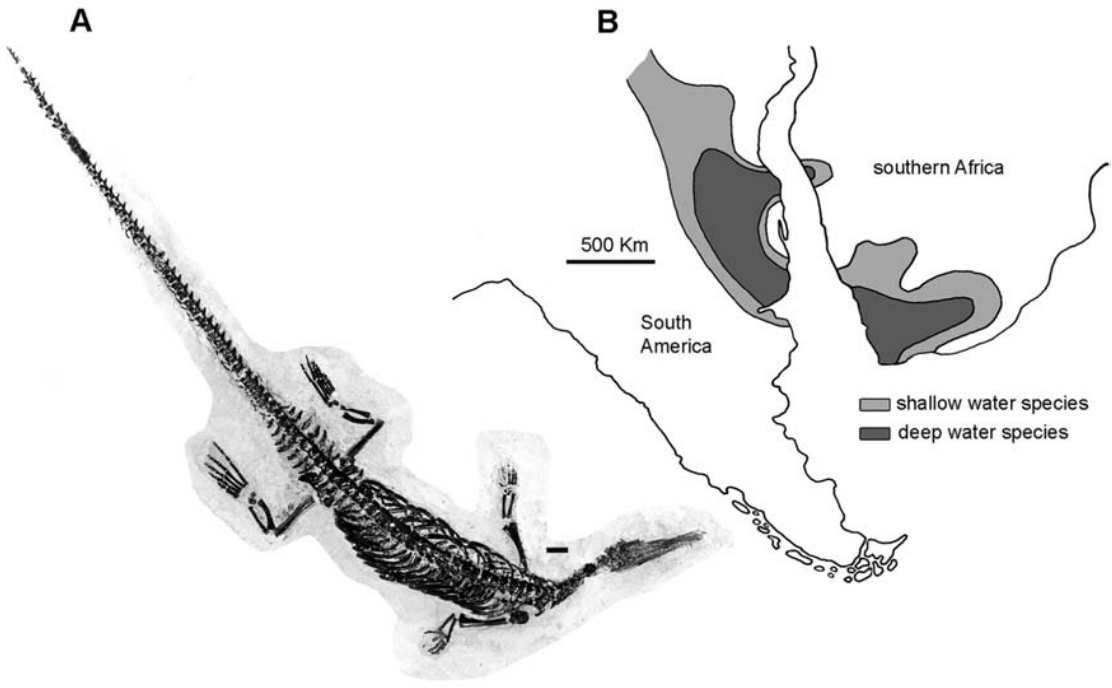
amniote. Several tetrapod families disappeared at this time, while at least one new one appeared (Milner 1993a).

Two Early Permian localities have produced particularly remarkable assemblages of fossil tetrapods that represent almost exclusively terrestrial faunas. One of them is the Dolese Brothers Quarry at Richard's Spur in Oklahoma, sometimes called Fort Sill. It is Early Permian in age, but because of the circumstances of its deposition, it is difficult to correlate its date with other localities. Here, fossils are found within sediments filling fissures that developed in Carboniferous limestone. Whether they fell into pitfall traps in the gullies and caves formed in the limestone or whether they lived there is not clear, but all of the tetrapods from the locality are small. The tetrapod material is usually disarticulated, but occasionally articulated specimens occur, and in most cases, bone preservation is exceptionally good, being three-dimensional and usually easy to free from the rock matrix. Among the commonest tetrapods at this site is the early amniote *Captorhinus* (Heaton 1979). The other locality is known as the Bromacker Quarry, in the Thuringian Forest region of Germany, and is the only site in Europe to produce a terrestrial fauna from the Early Permian. It has given us a wide variety of tetrapods, both amniote and nonamniote, and whereas the families represented are also found in North America, the species are unique to Bromacker. The main tetrapod-bearing deposits were formed in an upland setting in which ephemeral lakes and pools were subject to seasonal flooding (Eberth et al. 2000; Berman et al. 2004).

During the Early Permian, the tetrapods reached a kind of phylogenetic stability. About 60 families of tetrapods are known from the Late Carboniferous and Early Permian, and all except a very few occupied the same biogeographical region (Milner 1993a). This was the equatorial European and North American continental landmass.

There is some evidence that tetrapods lived beyond the limits of this Euramerican region by the later Late Carboniferous or early Early Permian. Two tetrapod footprint trails have been found from this period in South America, which would have been well into the Gondwanan continent at that time (Bell and Boyd 1986). By the Late Permian, one species of nectridean and a few temnospondyls had reached what is now northern and western Africa, which represent a more southerly radiation (Milner 1993a; Steyer and Jalil 2009).

One little group of tetrapods, the fully aquatic amniotes called mesosaurs, are known from Gondwana in the Early Permian, but they represent almost the only tetrapods from the Early Permian of Gondwana. They are significant in several ways. Not only are they the first amniotes known to have been marine, but also their distribution across South America and southern Africa was one of the first pieces of evidence to support the idea that these two continents had once been joined together. There are three genera in the group, and their distribution is known in some detail, with shallow-water forms found around the periphery of




what was an extensive seaway, and deeper-water forms more centrally (Oelofsen 1987; Modesto 1999, 2000) (Fig. 9.4).

The next sections of this chapter examine some of the major tetrapod groups of the Late Carboniferous and Early Permian to show how the roots of the family tree found at East Kirkton had produced a bush of many and varied forms (Fig. 7.1). Some of these are strikingly modern in appearance, while others resemble no creature living today.

## Tetrapods of the Coal Swamps

### Baphetoids

Among the most bizarre and enigmatic tetrapods of the Carboniferous period are the baphetoids. Although the earliest of them occurs in the Early Carboniferous, the majority are Westphalian. These animals are known from a few skulls and lower jaws, but almost no fossils of their vertebrae or other postcranial remains have been found. At this time, there is little known about their postcranial skeletons, except for two specimens that show some shoulder-girdle elements, one of which also preserves a humerus, a radius, and a few phalanges, and the other of which preserves some gastral scales. Baphetoids were among the first of the Carboniferous fossil tetrapods to be found and were first described by William Dawson (1863). They were discovered at a time when Paleozoic tetrapods were only just beginning to be studied and helped found ideas about what early tetrapods were like.

Five genera comprise the core of this group: *Loxomma*, *Baphetes*, *Megalocephalus*, *Kyrinion*, and *Spathicephalus*, with only one or two

species in each (Beaumont 1977; Beaumont and Smithson 1998; Milner and Lindsay 1998; Clack 2003b). A recent analysis found this to be a monophyletic grouping and gave it the rank of Family Baphetidae (Milner et al. 2009). They found that *Loxomma*, *Megalocephalus*, and *Kyrinion* grouped together as a subfamily named the Loxommatinae, whereas *Baphetes* stood outside this group in a subfamily of its own, the Baphetinae. Each of these five genera has its own peculiarities, and there are few unique characters tying them to each other. The one distinctive feature they share is one that is easily recognized and described, but much less easy to explain: in each member of the group, the eye socket has a forwardly directed extension, making what has been called a keyhole-shaped orbit.

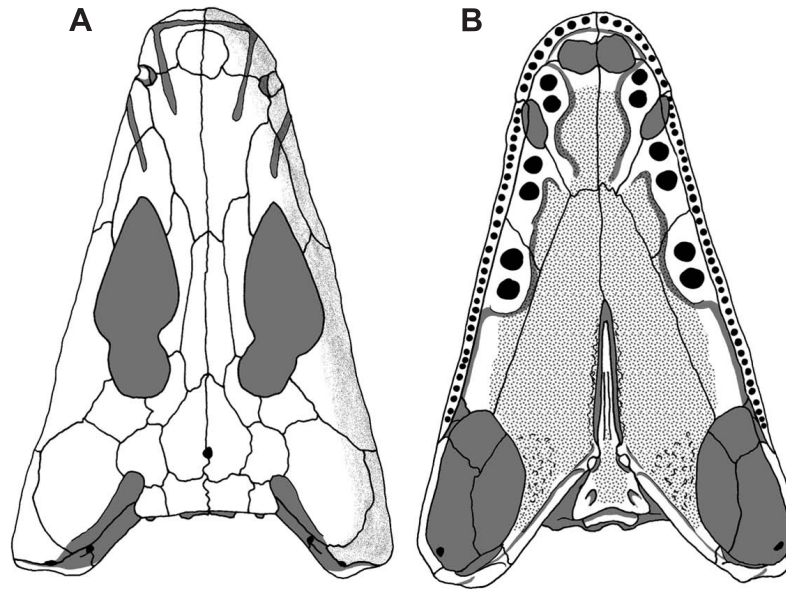
*Loxomma* ("slanting eyes") is the oldest member of the baphetids, from rocks of the Scottish Midland Valley dated between the Viséan and the middle of the Coal Measures. The skull was about 250 millimeters from the tip of its snout to the back of the cheek, with a bluntly rounded snout. It was rather flattened in profile, but the eyes would have been positioned quite high on the head, to allow it to look out of the water while the rest of the animal was submerged. The jaws and palate were armed with a battery of large, curved, and slightly keeled teeth, making the animal a formidable predator.

At the back of the skull, the skull table included the intertemporal bone, lost in most later tetrapods, including most of the other baphetoids. The skull table was marked off from the cheek region by a strongly defined embayment. This feature, often called an otic notch, may have had no connection to hearing and was more likely to be connected with breathing and to have housed a spiracle (see Chapter 10). It is often called a temporal notch to divorce its name from any functional implications.

*Megalocephalus* ("big head") is a later, larger, and more common relative of *Loxomma* known from the Coal Measures of Scotland, England, and Ireland. It had a longer, though relatively narrower and more pointed, head than *Loxomma*, reaching about 350 millimeters in length, possessing even larger teeth than *Loxomma*, and with an altogether more crocodile-like appearance (Fig. 9.5). Although nothing of its skeleton is known apart from the head, it must surely have been an active predator, perhaps occupying a similar niche to that of crocodiles today. It probably fed mainly on fish caught in the swampy waters of the coal-measures forest, though it presumably ate other tetrapods. No postcranial elements have ever been found, so whether it could venture onto the banks or marshy ground to catch more terrestrial prey remains speculative.

Figure 9.6 shows a baphetid skull representing a new genus and species, *Kyrinion martilli*. The name *Kyrinion* derives from combining the Greek for "to happen upon" with that for "neck joint." It was found as an erratic boulder by paleontologist David Martill on the coast of Northumberland, England, where it had fallen out of the overlying boulder–clay deposit. Presumably it had been picked up during the Pleistocene glaciation from some unknown locality and moved along until it eventually

**9.4.** (A) Specimen of one of the Brazilian mesosaurs (UMZC T1342). Scale bar = 10 millimeters. *Photograph by S.M.F.* (B) Map showing the distribution of the group during the Late Permian.




**9.5.** Drawing of skull of *Megalocephalus pachycephalus*. (A) Dorsal view. (B) Ventral view. Skull is about 300 millimeters in length. *Based on Beaumont (1977).*

eroded out of the cliff. It preserves a somewhat flattened but otherwise three-dimensional skull, complete with both stapes and a probable atlantal vertebral element. The palate is fused to the braincase at the basal articulation, making the skull exceptionally solid and robust. The stapes does not appear to have lain against the palate but rather was surrounded by a space that might have been filled with air. The stapes was certainly not acting as a bracing element, but to what extent it may have been involved with hearing is debatable. The specimen also preserves the occipital region, the first time that this has been found well preserved in a baphetid (Clack 2003b).

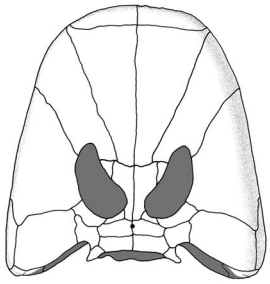
*Baphetes* was contemporary with *Megalocephalus*, but it seems to have occupied a different niche. Its head was much broader and flatter, though it possessed numerous large teeth like its relative and was also clearly predatory. Recent work has described a juvenile baphetine skull that shows some differences from the better-known larger specimens. From this, it has been inferred that during growth, the snout region of *Baphetes* not only grew longer but also wider, a rather different pattern from, for example, temnospondyls (Milner et al. 2009).

In the recent analysis, the genus *Spathicephalus* stands apart from all other baphetids as a sister group, and together, they all belong in a group known as the baphetoids. *Spathicephalus* ("spatulate head") occurs in some Early Carboniferous sites such as Loanhead and Dora, and there is one species from the United States. *Spathicephalus* had a skull that was almost totally flat and shovel shaped, and in this genus, the form of the eyeholes was taken to extremes (Fig. 9.7). The eye sockets were extremely close together in the middle of the skull, with the unique baphetid keyholes giving the face a strange appearance. It is possible to imagine its eyes raised above the surface of the skull, as for example in a flatfish or




**9.6.** Skull of *Kyrinion martilli* (NEWHM: 2000.H845). Scale bar = 100 millimeters.

a frog. It is not clear what *Spathicephalus* may have fed on, but its teeth were quite unlike those of the other baphetid genera. Rather than being large, lanceolate piercing teeth, those of *Spathicephalus* were small, chisel shaped, evenly sized, and numerous. They seem to have formed a comblike structure, which might have been used for filter feeding or for picking up large quantities of small, slippery invertebrates. Unlike almost all other Paleozoic tetrapods, most of the teeth were present in the jaw at the same time, forming a continuous band. In most other contemporary vertebrates, about one third of the tooth positions were empty or were being replaced at any one time. *Spathicephalus* must have had an unusual system of tooth replacement to furnish its specialized dentition, but the mechanism and the purpose are unknown (Beaumont and Smithson 1998). Its palate and braincase were fused at the basal articulation, as in *Kyrinion*.



**9.7.** Skull of *Spathicephalus mirus* in dorsal view. Skull is about 210 millimeters in length. *From Beaumont and Smithson (1998).*

The function of the anterior extension of the orbit in baphetids has given rise to much debate. Several theories have been suggested, but objections can be found to all of them. One of the suggestions is that the space was occupied by a salt gland, ridding the body of excess salt. The bone formation around the rim, however, suggests that whatever was situated there did not lie outside the skull roof, as would be expected of a salt gland, but was housed inside (Beaumont 1977). In most analyses, the coal swamps in which baphetids lived are considered to have been freshwater, an unlikely habitat for an animal to develop a salt gland. More recently, however, it has seemed less certain that these swamps were purely freshwater, and there is some suggestion of tidal or marine influence perhaps making the water brackish. If that were so, a salt gland might be a more likely explanation.

Another possibility is that the space was occupied by the mass of a muscle used for closing the lower jaw rapidly and powerfully, the pterygoideus muscle (Beaumont 1977). With the shallow skull characteristic of baphetids, there may have been little room for this muscle, which is thought to have run dorsally along the inside of the palate, to bulge during contraction. Extra room may have allowed the muscle to develop more power for snapping the jaws shut. Alternatively, the muscles may have originated around the rim of the hole, giving a firmer attachment. However, the course of the muscle is conjectural.

A third possibility is that the space was occupied by an electrosensory organ (Bjerring 1986). Such organs are not uncommon in modern fishes that live in murky, vegetation-choked water, and they help the animals to detect electrical impulses produced by the muscles of fishes or tetrapods, when vision is of limited use. All these hypotheses are, unfortunately, speculative and cannot be scientifically tested.

The relationships of baphetids to one another have been proving problematic to work out, and only recently has the group been subjected to cladistic analysis (Milner et al. 2009). *Spathicephalus*, despite being the most peculiar in appearance, appears as the most primitive. However, it is by no means the earliest, coming from the Namurian and early Westphalian of Scotland and Nova Scotia. *Kyrinion* was also early Westphalian, but it does not appear to be immediately related to *Spathicephalus*. Both appeared later than *Loxomma*, the most primitive of the loxommatinae, whose first appearance was Viséan, with *Megalocephalus* and *Kyrinion* from the Westphalian being successively more derived.

One other taxon that consistently clusters with the baphetoids in cladistic analyses is *Eucritta*, the problematical taxon from East Kirkton (see Chapter 7). The first analyses to place *Eucritta* phylogenetically have produced some equivocal results (Clack 1998a, 2001a). In these analyses, trees were found showing two major topologies. They placed *Eucritta* among the baphetids, but found this group clustering either with the anthracosaurs or with the temnospondyls. Milner et al. (2009) also placed *Eucritta* close to the baphetids, in the larger grouping of baphetoids.

Other recent analyses have also placed *Eucritta* within the baphetoids (Ruta et al. 2003; Ruta and Bolt 2006; Ruta and Clack 2006). *Eucritta* is only slightly older than *Loxomma*, but it does appear to be more primitive, suggesting that the baphetids arose from more terrestrially adapted forms. These patterns of relationship imply a long ghost lineage for baphetoids, perhaps going back to the Tournaisian stage.

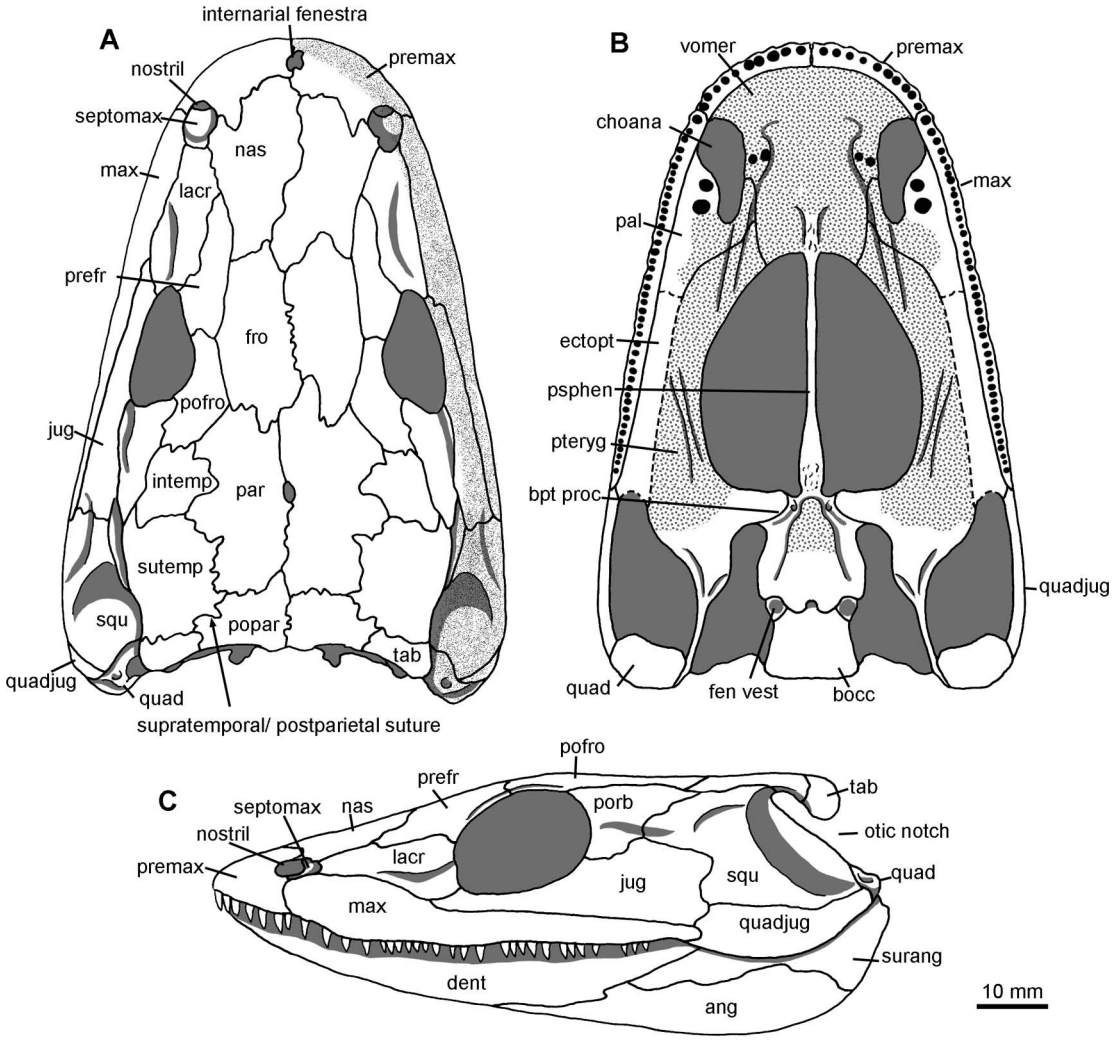
The baphetoids as a whole usually fall below temnospondyls and all stem amniotes (Ruta et al. 2003; Ruta and Bolt 2006; Ruta and Clack 2006). This result reflects the fact that they appear to be one of the most primitive groups of tetrapods. They retain a number of plesiomorphies, but they have also developed their own unique features.

If amniotes share their lineage with anthracosaurs, and lissamphibians with temnospondyls, baphetids appear to be basal tetrapods that show a mosaic of characters later stabilized in each of the two main tetrapod lineages (Clack 2001a).

## Temnospondyls

By the Westphalian, the temnospondyls, with their earliest known member found in the Viséan of East Kirkton (*Balanerpeton*, Chapter 8), had radiated into a diversity of forms that paleontologists place into about 15 different families. The temnospondyls were the largest group of fossil amphibians (see Chapter 8 and below for the justification of the term "amphibian" in this context), producing the largest number of species, the largest individuals, and the greatest diversity of body forms extending over the longest time range (Milner 1990, 1993b). The earliest temnospondyl, *Balanerpeton*, was a relatively small form, apparently predominantly terrestrial. Another relatively early form, *Dendrerpeton*, was also most likely terrestrial. Its name means "tree creeper," in honor of the fact that its remains are found among the tree stumps of Joggins (Fig. 9.8). Its skull and postcranial anatomy are well known from three-dimensional material (Holmes et al. 1998), and though there is some dispute about its exact phylogenetic position, it is generally considered fairly primitive. Its skeleton provides a useful model for understanding basic temnospondyl anatomy (see Chapter 2). Together, these animals suggest that temnospondyls arose from a terrestrial ancestor. However, later, the temnospondyls produced many aquatic forms, and the last ones of all to survive were entirely so.

The palatal vacuities, seen in *Balanerpeton* (see Chapter 8) and *Dendrerpeton* (Fig. 9.8), make one of the most conspicuous distinguishing characters of temnospondyls, and it is found throughout the group. In early temnospondyls such as *Balanerpeton*, they were relatively small, and the margins of the vacuities were formed mainly by the pterygoids and vomers or, in some cases, just the pterygoids. In some later ones, the vacuities enlarged even more, so that the palatines were involved as well. In yet others, the ectopterygoids disappeared altogether. Comparable vacuities are found elsewhere, so it is not, unfortunately for systematists,

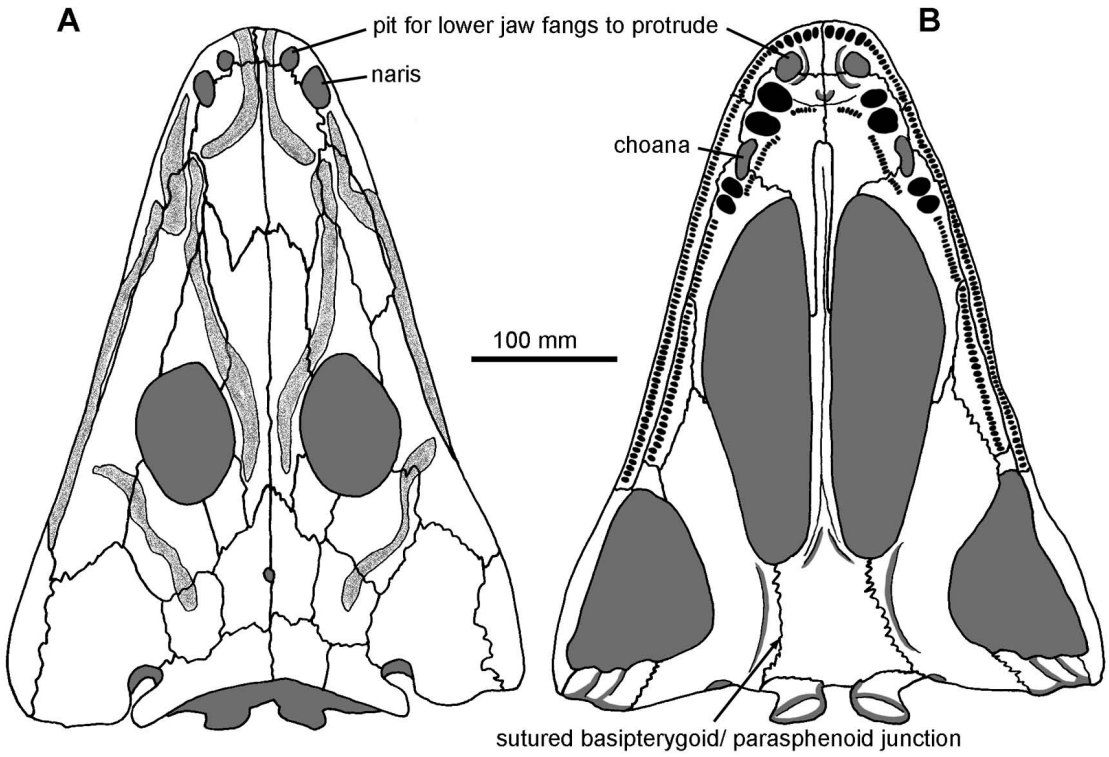



**9.8.** Skull of *Dendrerpeton*. (A) Dorsal view. (B) Ventral view. (C) Left lateral view. *Based on Holmes et al. (1998).*

exclusive to the group. However, they are found in frogs, and this is one of the features that has been used to link temnospondyls to modern amphibians.

Temnospondyl skull bones usually had characteristic dermal ornament of fairly regular pits and ridges, forming a honeycomb pattern at the growing points near the center of each bone and usually drawn out into ridges toward the margins. Lateral line grooves are usually conspicuous. Apart from losing the intertemporal in more derived forms, the skull roof retains an apparently plesiomorphic pattern in which the postparietal bone remains in contact with the supratemporal (Fig. 9.8).

Early temnospondyls such as *Dendrerpeton* retained the form of basal articulation found in primitive tetrapods such as *Acanthostega* and baphetoids, with a peg from the braincase fitting into a socket in the palate, and with a surface texture on the peg that suggested a cartilage cap. Some degree of mobility is often inferred. In later members of the

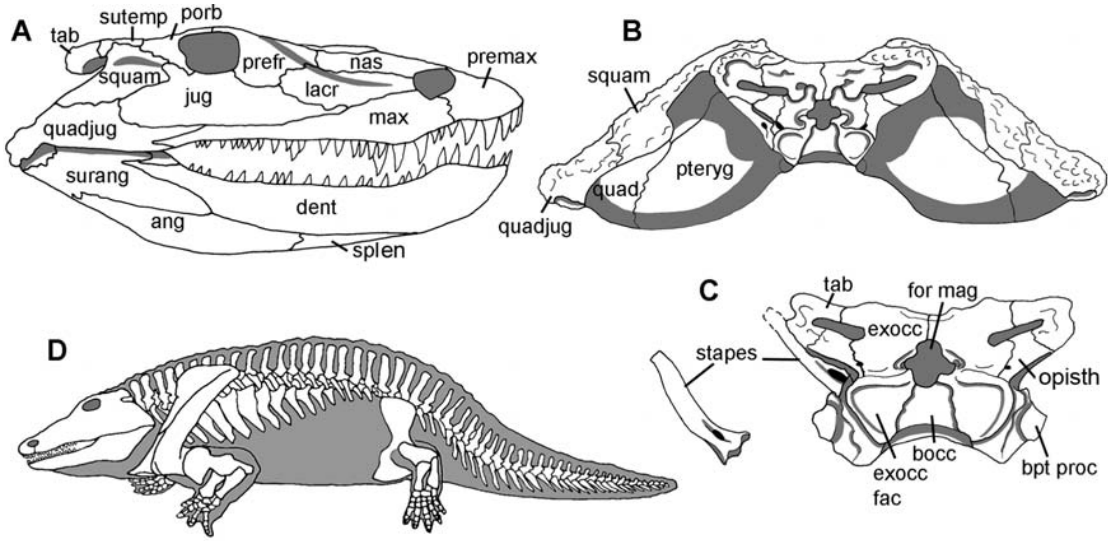



**9.9.** *Mastodonsaurus giganteus.* (A) Skull in dorsal view. (B) Skull in ventral view. *Based on Schoch and Milner (2000).*

group, this articulation was eliminated by a sutured junction between the dermal bones of the palate, the pterygoids, and that of the braincase, the parasphenoid. This is exemplified by the condition of the middle Triassic capitosaur *Mastodonsaurus* (Schoch 2002a) (Fig. 9.9). The effect of this was to make the posterior region of the braincase much more securely attached to the rest of the skull.

Other characteristics of temnospondyls include an occipital condyle formed only by the exoccipitals. During the radiation of temnospondyls, the midline basioccipital bone diminishes in size until it more or less disappears. The occipital condyle is thus left as a pair of facets contributed by the exoccipitals on each side. These bones also grow in importance to form most of the occipital surface of the skull, replacing territory formerly occupied by the opisthotics, as seen in *Eryops* and *Mastodonsaurus* (Figs. 9.9, 9.10). By contrast, much of the rest of the braincase remained unossified in many forms, even in large individuals.

Many temnospondyls, including the most primitive, have a form of ear region in which the stapes is rodlike, and is positioned so that it stretches dorsally toward the otic notch, seen in *Eryops* (Fig. 9.10). This construction is similar to that in frogs, where it forms part of an aerially adapted ear, the notch holding the tympanic membrane. A similar function is inferred for temnospondyls, and this form was once considered primitive for all tetrapods. Recent discoveries suggest that this is not the case (see Chapter 10).




**9.10.** *Eryops megacephalus.* (A) Skull in right lateral view. (B) Skull in posterior view. (C) Occipital region in posterior view, with dermal skull roof bones mostly removed and left stapes in posterior view. (D) Skeletal reconstruction. (E) Skeletal reconstruction of *Eryops.* Skull is about 430 millimeters long. *Based on Romer (1966).*

Robinson et al. (2005) took one rather unpromising skull specimen of *Dendrerpeton* and subjected it to micro-CT scanning. They discovered an exceptionally well-preserved braincase inside the skull, with one of the stapes tucked inside the brain cavity. It had evidently fallen there as the soft tissue of the head decayed. The stapes was long and rodlike, and although rather stouter than in later forms, it does seem to have been part of an early hearing mechanism. This construction does appear to be the primitive condition for temnospondyls. However, there are many instances in which it has been modified or lost. Tympanic ears do not function well in water, so the tympanum and its enclosing notch are often lost in permanently aquatic forms. Loss by retention of the aquatic larval condition is probably one of the chief mechanisms by which this occurred.

Temnospondyl vertebrae are usually rhachitomous, with substantial wedge-shaped intercentra ventrally and small paired pleurocentra dorsally. The pleurocentra support the neural arches, and the ribs are borne partly by the transverse processes of the neural arches and partly by facets on the intercentra. This form of vertebral construction seems to be primitive for tetrapods and is seen in *Acanthostega* (see Fig. 6.10). It may be associated with primarily aquatic locomotion (see Chapter 10). In later members of the group, the size of the intercentrum enlarged to become much the more dominant element, essentially a complete disk, and the pleurocentra became rudimentary or even disappeared altogether. This form of vertebra characterizes the large group of mainly post-Permian forms called stereospondyls. Another group evolved toward a form in which inter- and pleurocentra became complete, almost equally sized disks, a condition similar to that of the embolomeres, a group of elongate aquatic predators.

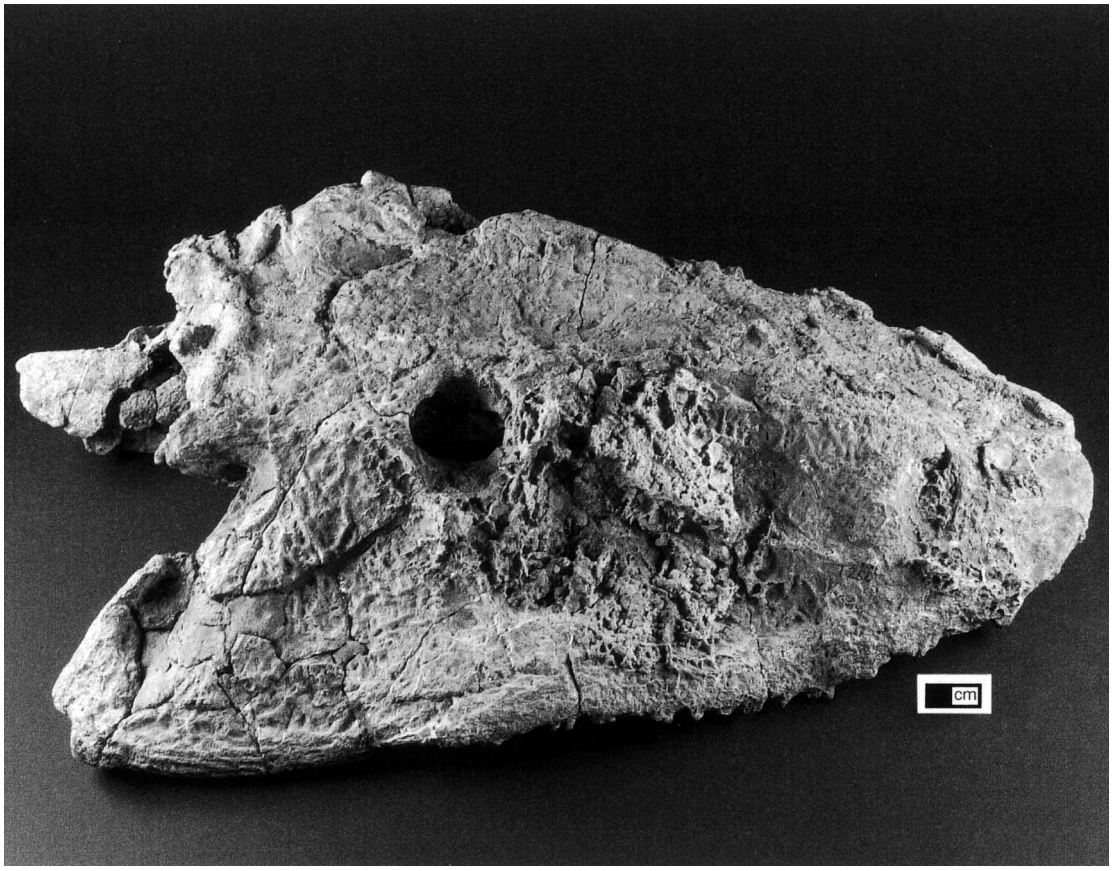
Temnospondyl ribs are usually short and more or less straight, though in a few forms, such as *Eryops* (Fig. 9.10) and *Mastodonsaurus*, they bear

flanges resembling those seen in *Pederpes* or *Whatcheeria*. Temnospondyls also have a relatively small, usually diamond-shaped interclavicle and an ilium with only a single dorsal process. None of these by itself is reliably diagnostic. No temnospondyl is known with more than four digits on the hand—again, a condition seen not only in frogs, but also in any modern amphibian.

It was during the Carboniferous and Early Permian that temnospondyls produced their greatest range of body forms and ecology (see Holmes 2000 for a review). The phylogeny of temnospondyls of this time has not been fully resolved. Most attempts have included only a few genera, and only recently has a more comprehensive cladistic analysis proved possible (Ruta and Bolt 2006). This is partly because of the numerous taxa erected during the 19th and early 20th centuries that have subsequently been found invalid and that had caused some confusion. Even now there is considerable controversy over the placing of certain groups and taxa. There is nonetheless an emerging consensus over some early temnospondyl relationships. Much work on the anatomy, systematics, and ontogeny of temnospondyls has been done in recent years.

The edopoids are generally considered to be the most primitive temnospondyls. *Edops* itself is from the Early Permian of the United States. It is only known from a single skull, multiple skull fragments, and a humerus. As an Early Permian genus, *Edops* is actually one of the latest known members of the group, although one genus of edopoid, *Nigerpeton*, is known from the Late Permian of Africa (Sidor et al. 2005). The earliest edopoid material may be the large ribs and some other isolated bones found at East Kirkton (Milner 1990). Edopoid skulls retain some primitive features, such as possession of the intertemporal and an unsutured basal articulation, as well as relatively small interpterygoid vacuities. However, they do also show some unique features. Their radiation includes a variety of skull forms. *Edops* was a broad-skulled form, *Cochleosaurus* and other Late Carboniferous genera were narrower-skulled forms, and the Early Permian *Chenoprosopus* was a longer-snouted form.

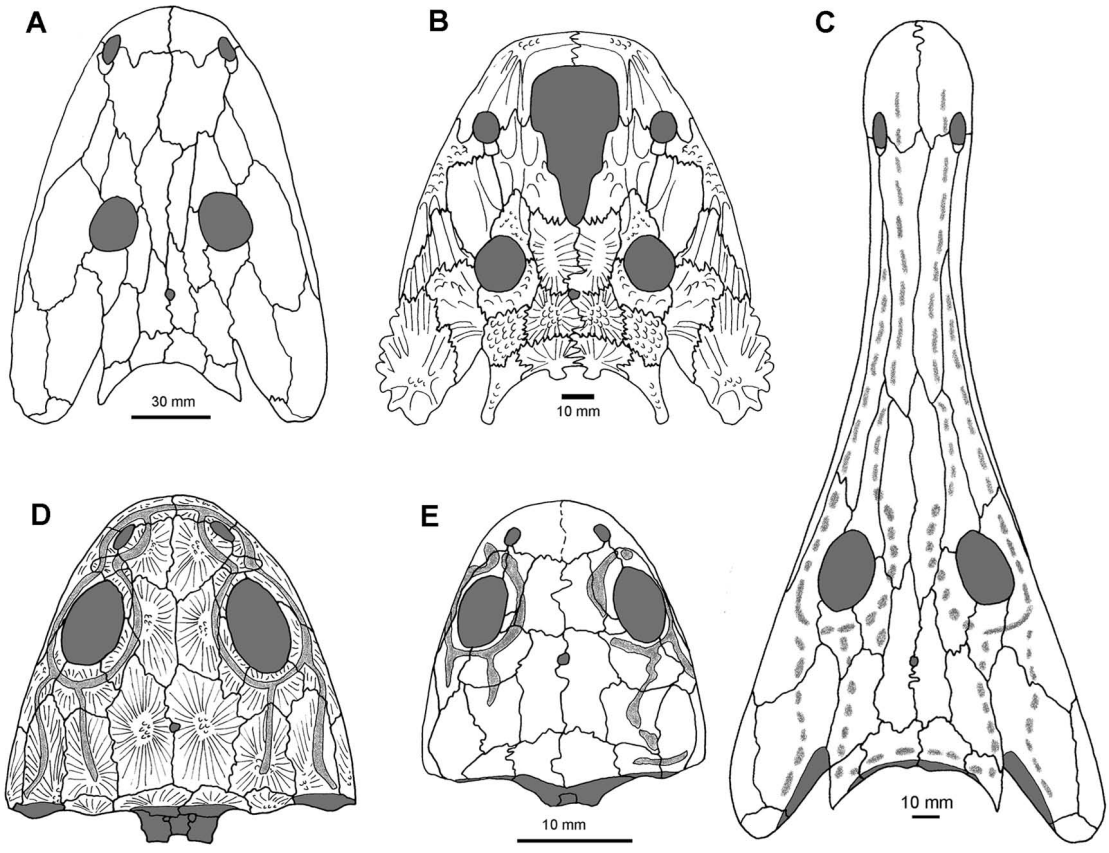
The next group, the eryopoids, includes the founder member of the group, *Eryops*, one of the first temnospondyls to be described from almost complete material (e.g., Sawin 1941). It is represented by many specimens preserved in the Lower Permian Red Beds of the United States (Figs. 9.10, 9.11). Before *Balanerpeton* and *Dendrerpeton* became better understood, *Eryops* was often viewed as the embodiment of not just a typical temnospondyl but as a generalized early tetrapod. Now, however, it is seen as rather unrepresentative and to have given a somewhat distorted view of the morphology and ecology of early tetrapods in general and temnospondyls in particular. *Eryops* is nonetheless interesting because recent studies have shown that several species of the genus replace each other in time and space throughout the area and span of the Early Permian of the southern United States. It could be one of the few vertebrates of use in stratigraphy (Milner 1996).




**9.11.** Photograph of the skull of *Eryops*. (UMZC specimen T.250).

Deposits in Germany and eastern Europe have yielded large numbers of temnospondyls from a series of shallow lakes that existed there in the Late Carboniferous and Early Permian. Several of these temnospondyls are included in the eryopoids. One of the best known is *Onchiodon*, now considered to belong to the same family as *Eryops*, in the Eryopidae (Schoch and Witzmann 2009). It is known from a large number of specimens that show growth stages from small juveniles to adults, and ossification sequences have been described for the skull, hyobranchial system, and postcranial skeleton (Boy 1990; Witzmann 2005). They changed from aquatic larvae with external gills to semiterrestrial juveniles and finally terrestrial adults in a gradual sequence, and the ossification pattern seems to be fairly plesiomorphic among temnospondyls.

Another group of eryopoids includes the unusual forms *Acanthostomatops* and *Zatrachys*. These genera are characterized by having numerous spines or processes growing from the rear of the skull around the quadratojugal and jugal bones (Fig. 9.12B). They lived in the Late Carboniferous and Early Permian of North America and in the Early Permian lake basins of Germany, and some are known from growth




sequences. The spines increased in length and number as the skull grew (Witzmann and Schoch 2006).

*Sclerocephalus* (Fig. 9.12A) is one of the best-known temnospondyls, again mainly from the Early Permian lake basins of Germany, and again, growth sequences from quite small larvae have been described (Schoch 2003). It is sometimes considered an eryopoid and sometimes a basal member of the clade known as Stereospondylomorpha that includes most post-Permian temnospondyls. The adult skull bears many similarities to that of an eryopid, but differences lie in the palate and dentition. These kinds of features are among those that distinguish stereospondyls as a whole from other temnospondyls. The phylogenetic relationships of eryopids and stereospondylomorph families are still under review, but the most recent is that by Schoch and Witzmann (2009).

The archegosaurids, stereospondylomorphs from the Late Carboniferous and Early Permian of Germany, present an interesting case. They are the first temnospondyls to produce a long and narrow-snouted skull form, and they are among the earliest tetrapods to do so. The appearance of long-snouted aquatic predators at this time may reflect some evolutionary changes or innovations among the contemporary ray-finned

**9.12.** Temnospondyl skulls. (A) The stereospondylomorph *Sclerocephalus haueseri. Based on Schoch and Milner (2000).* (B) The eryopoid *Zatrachys serratus. Fom Schoch (2002b).* (C) The stereospondylomorph *Archegosaurus decheni. Based on Schoch and Milner (2000).* (D) The dvinosaurid *Dvinosaurus amalitski.* Skull is about 170 millimeters long. *Based on Bystrow (1938).* (E) The tupilakosaur *Thabanchuia oomie. Based on Warren (1999).*

fishes. *Archegosaurus* (Fig. 9.12C) is known from a skull length of about 20 millimeters up to 280 millimeters. As it grew, it underwent extreme elongation of the rostrum. This skull shape is consistent with a piscivorous predator and is found today in gharials and the alligator gar. It permits a rapid snapping action through the water, though without a powerful closure to the bite. In *Archegosaurus*, study of the wealth of specimens has shown only a gradual change in the length of the rostrum during growth, indicating that there was no metamorphosis, such as is seen in modern amphibians, and that *Archegosaurus* remained an aquatic predator throughout its life. It lost its external gills, though at a relatively large size of 150 millimeters skull length, but this did not coincide with any major changes to the rest of the anatomy (Witzmann 2006a, 2006b; Witzmann and Scholz 2006).

Another grouping that appears fairly consistently in analyses is that of the Dvinosauria. This grouping encompasses a range of skull and body morphologies, but nearly all of them have lost the otic notch and have the eyes placed far forward in the skull. Somewhat controversially, Ruta and Bolt's (2006) analysis placed *Dendrerpeton* and *Balanerpeton* at the base of this clade. There is more consensus about other members. The trimerorhachids are a constituent family in this grouping, from the Early Permian of the United States. *Trimerorhachis* is another example of an aquatic piscivore that evolved a narrow, elongate skull in parallel with *Archegosaurus*, but has the dvinosaurid condition of a reduced otic notch and eyes placed well forward on the skull. The genera *Acroplous* and *Isodectes* are small dvinosauroids with short rounded snouts, also from the Early Permian of the southern United States (Sequeira 1998). One of the most derived members of the dvinosauroids is the perpetually aquatic *Dvinosaurus* (Fig. 9.12D) from the Late Permian of Russia. Its notchless skull was almost an equilateral triangle in shape, with eyes placed far forward, and it is known to have had well-ossified branchial bars (Bystrow 1938). A highly specialized group of dvinosaurs are the tupilakosaurids. These long-bodied forms with diminutive limbs are known from localities scattered almost worldwide. The most derived, the Early Triassic genera *Tupilakosaurus* from the Early Triassic of Greenland and India and *Thabanchuia* (Fig. 9.12E) from South Africa, had developed vertebrae similar to those of embolomeres, with ring-shaped inter- and pleurocentra (Warren 1999).

At the end of the Permian, most families of temnospondyl appear to have been wiped out in the mass extinction that occurred at that time. The reradiation of the group seems to have arisen from only a few survivors, though there is controversy over how many. The tupilakosaurs were certainly one of them. However, it is the stereospondyls that constitute the major radiation, and they are considered to be a monophyletic group (see the reviews by Schoch and Milner 2000; Warren 2000; Warren and Marsicano 2000), though with fewer or more constituent families. A cladistic analysis was attempted by Yates and Warren (2000). Whereas

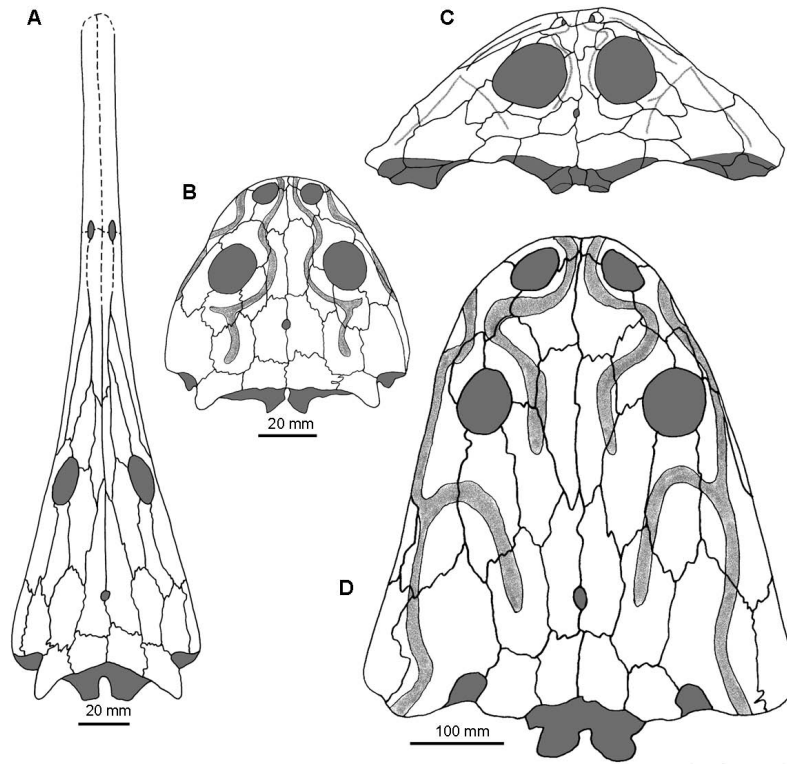
many early temnospondyls had reduced the number of palatal teeth, the palatal dentition in stereospondyls generally seems to have reversed to a form similar to that in primitive tetrapods like *Crassigyrinus* with an almost continuous row of small teeth as well as fang pairs on the marginal palatal bones. Almost all had deeply incised lateral line grooves on the skull roof.

The earliest true stereospondyls were the rhinesuchids. This family lived in the Late Permian and Early Triassic of the Gondwanan continents of southern Africa, Madagascar, and India. Among the best-known and speciose stereospondyls are the mastodonsauroids, also known as capitosaurs. This group is large in many senses, and includes some of the giants of the temnospondyl radiation, as well as the greatest number of genera, and Damiani (2001) has provided a cladistic analysis. Most mastodonsauroids were large and had flattened skulls, sometimes over a meter in length, with enlarged palatal vacuities and reduced ossification of the braincase. The limbs were generally small, and many forms must have been permanently aquatic. The metoposaurs are another group of large aquatic predators, but in that group, exemplified by *Buettneria* (Fig. 9.13D), the eyes lay far forward in the skull. The effect of that was to enlarge the pharyngeal region and buccal cavity for a more effective gulping action.

In most stereospondyls, the skull was broad with a more or less rounded snout, but some, notably among the trematosaurids such as *Aphaneramma*, the rostrum was extremely elongate (Fig. 9.13A)—so much so that in some species, the tip has never been found. They are known to reach at least 60 centimeters in skull length. *Aphaneramma* is known from the Early Triassic of Svalbard, South Africa, and Pakistan. Trematosaurids are also notable for having been capable of living in marine conditions and have been found in indisputably marine sediments on Svalbard. By contrast, another family, the lydekkerinids, produced small terrestrial forms with heavily ossified postcranial skeletons in the Early Triassic of South Africa (Pawley and Warren 2005).

The last family of stereospondyls to survive was the chigutisaurs. This was a family with rather short, broad heads that seem to have been pedomorphic (Fig. 9.13B). The chigutisaur *Koolasuchus* is known from partial remains from the Early Cretaceous of Australia and is the last temnospondyl so far found in the fossil record (Warren et al. 1997).

There is still controversy over the affinities of a number of families in which the short, broad skull form was developed. Two families exploited this morphology apart from the chigutisaurs. These are the brachyopids and the plagiosaurs. In some cases, for example in the plagiosaur *Gerrothorax*, this morphology became extreme, with skull width exceeding more than twice the dimensions of its length (Fig. 9.13C). *Gerrothorax* was also extremely flattened, with enormous eye sockets, a well-ossified gill skeleton, and a large dermal shoulder girdle. It was covered dorsally in ornamented, overlapping scutes. It was almost certainly a fully aquatic

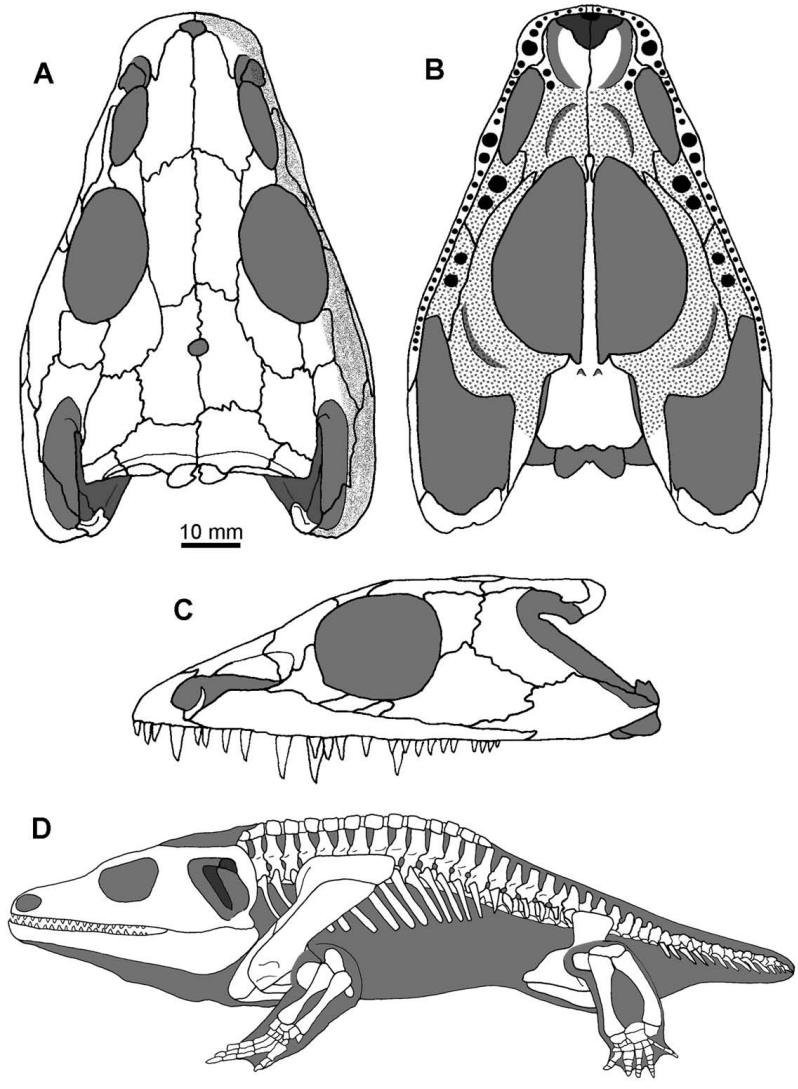



**9.13.** Temnospondyl skulls. (A) The trematosaurid *Aphaneramma rostratum.* (B) The chigutisaur *Keratobrachyops australis.* (C) The plagiosaur *Gerrothorax pustuloglomeratus.* Skull is about 164 millimeters wide. (D) The metoposaur *Buettneria perfecta.* (C) *Based on Hellrung (2003); others based on Schoch and Milner (2000).*

form living on the riverbed, and was probably pedomorphic in retaining not only external gills as a larva, but also internal gills as an adult (Hellrung 2003). By studying the occipital and jaw joints, Jenkins and colleagues (2008) were able to show that the short, broad head of this animal, in combination with the precise shape of these joints, allowed it to raise its skull to about an angle of 50 degrees while at the same time protruding its lower jaw.

The relationships of these forms are uncertain, but whereas Milner (1990) and Schoch and Milner (2000) did not include plagiosaurs among the stereospondyls, Yates and Warren (2000) placed them close to the chigutisaurs. As for the brachyopids, Milner (1990) placed them close to the tupilakosaurs and other dvinosauroids, whereas Yates and Warren (2000) and Damiani and Kitching (2003) suggested a sister-group relationship with the chigutisaurs. The situation remains unresolved. Brachyopids may not be a coherent group as currently formulated, and it is still unclear whether the similar morphologies arise from relationships or have evolved in parallel. However that may be, it was these short-faced aquatic gulpers that survived the longest among temnospondyls, perhaps exploiting a niche that neither amniotes nor teleosts had invaded during the late Mesozoic (Milner 1990).

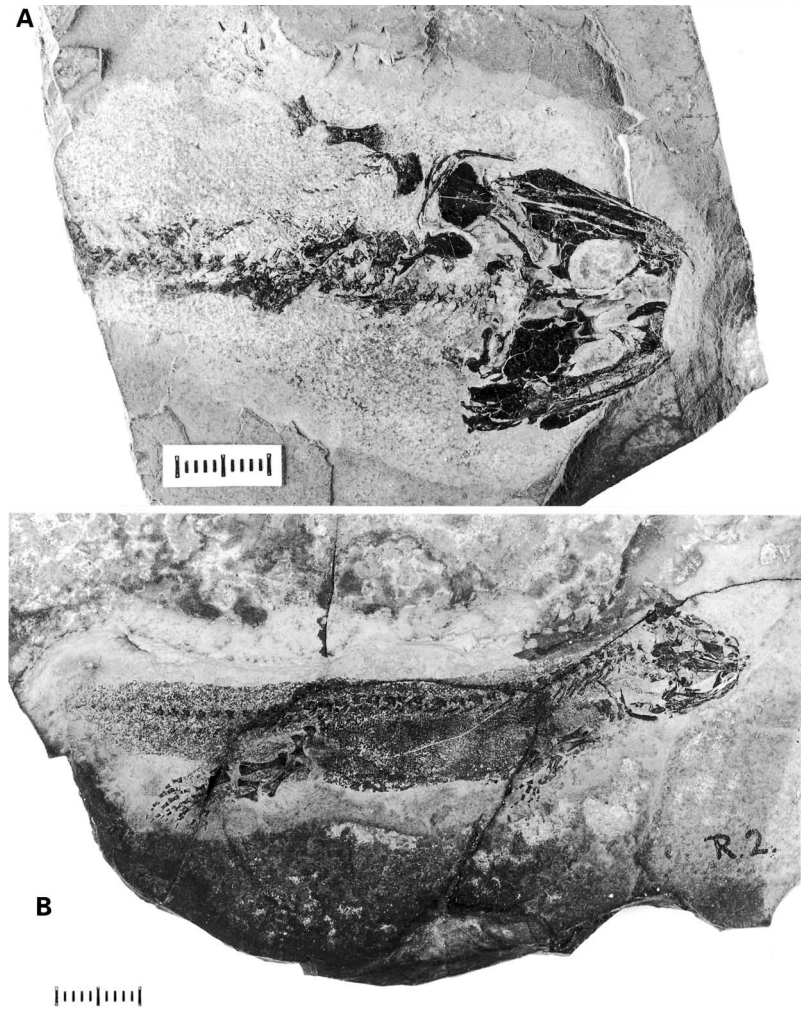
One further group of temnospondyls is of particular significance and has recently been subject to increased interest and study. This group, the dissorophoids, appears to be closely related to the origin of modern




**9.14.** Skull of the dissorophoid *Phonerpeton*. (A) Dorsal view. (B) Ventral view. (C) Left lateral view (lower jaw omitted). Based on Dilkes (1990). (D) Skeletal reconstruction of the dissosorophid *Cacops*. Skull is about 150 millimeters long.

amphibians. The families included in this group fall roughly into three morphotypes.

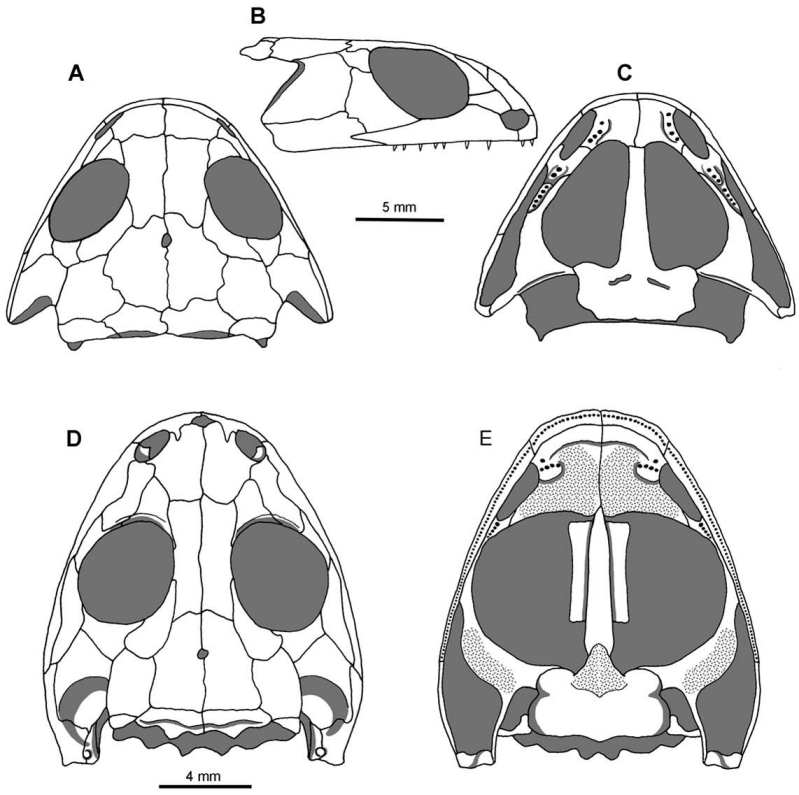
The robustly built dissorophids, trematopids, and the genus *Ecolsonia* comprise a radiation of small- to medium-sized terrestrial forms, mainly from the Early Permian of the United States but recently recognized in Europe (Sumida et al. 1998). They usually have well-ossified limbs, wrists, and ankles, as well as specialized nasal regions suggesting adaptations for dry or even desert conditions (Dilkes 1993). The vertebral column was usually strengthened by dermal armor plates along the back (e.g., *Cacops*, Fig. 9.14D), that assisted in locomotion (Dilkes and Brown 2006). Most have broadly open more or less hemispherical otic notches like that of *Phonerpeton* (Fig. 9.14A–C), though in some, the notch is closed posteriorly by a bar of bone, as in *Cacops*, or compressed into a narrow slot, as in *Acheloma*. This branch of the dissorophoids has




**9.15.** Branchiosaurs. (A) *Micromelerpeton credneri* showing some soft tissue preservation; note the faint close ridging on the animal's left side (UMZC T.970). (B) *Apateon pedestris,* not only showing body-wall and tail outline (note the close ridging round the abdomen), but also tiny strings of ossicles from the gill filaments just behind the skull (UMZC T.955). Scale bar = 10 millimeters. *Photographs by S.M.F.*

been named the Olsoniformes (Anderson et al. 2008a). Dissorophoids as a whole show similarities to frogs in the construction of the ear region (Bolt and Lombard 1985).

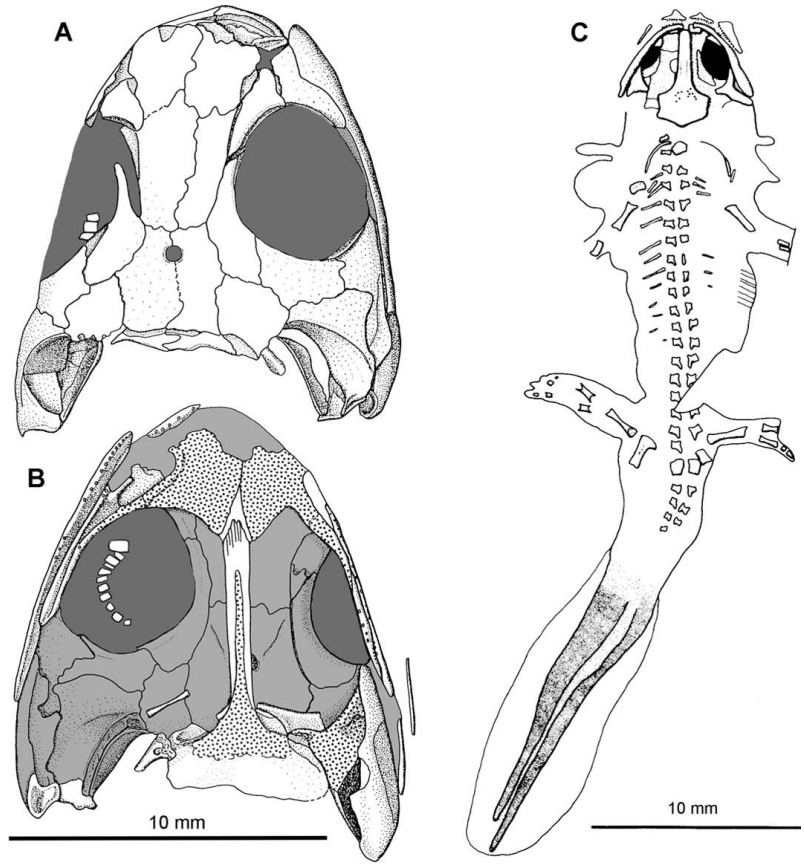
The other two morphotypes include small, probably perpetually aquatic and pedomorphic forms informally known as branchiosaurs (Fig. 9.15), and a group of small, more terrestrial, gracile forms known as amphibamids (Figs. 9.16–9.18). The branchiosaurids probably branch off from within the amphibamids. The branchiosaurs are usually taken to include two families, the branchiosaurids and micromelerpetontids, but they may not be monophyletic. In some analyses, the micromelerpetontids appear as among the most plesiomorphic dissorophoids, falling below the split between amphibamids and dissorophids. The interrelationships of these groups to each other have been the subject of intense debate in recent years, as much more information has come forward regarding their anatomy and ontogeny, and as a result of their likely relationship to modern amphibians.




**9.16.** Amphibamid temnospondyls. (A), (B) and (C), dorsal, lateral and palatal views of the skull of the branchiosaur *Apateon pedestris*. From Boy (1974). Skull of *Doleserpeton annectens* in (D) dorsal view and (E) ventral view. *Based on Sigurdsen and Bolt (2010).*

The branchiosaurids are known mainly from thousands of specimens from the Permo-Carboniferous lake basin systems of Germany, which have also yielded many other temnospondyls (Boy and Sues 2000). They are known from high-resolution series representing growth stages. Branchiosaurids developed a mechanism for filter feeding using branchial denticles housed in the gill clefts, and delayed the ossification of the upper jaw. This facilitated manipulation of the mouth in a suction feeding mechanism that they used to capture plankton (Schoch and Milner 2008). A branchiosaur from Russia called *Tungussogyrinus* is the latest so far known in the fossil record and may be Early Triassic (Wernerberg 2009).

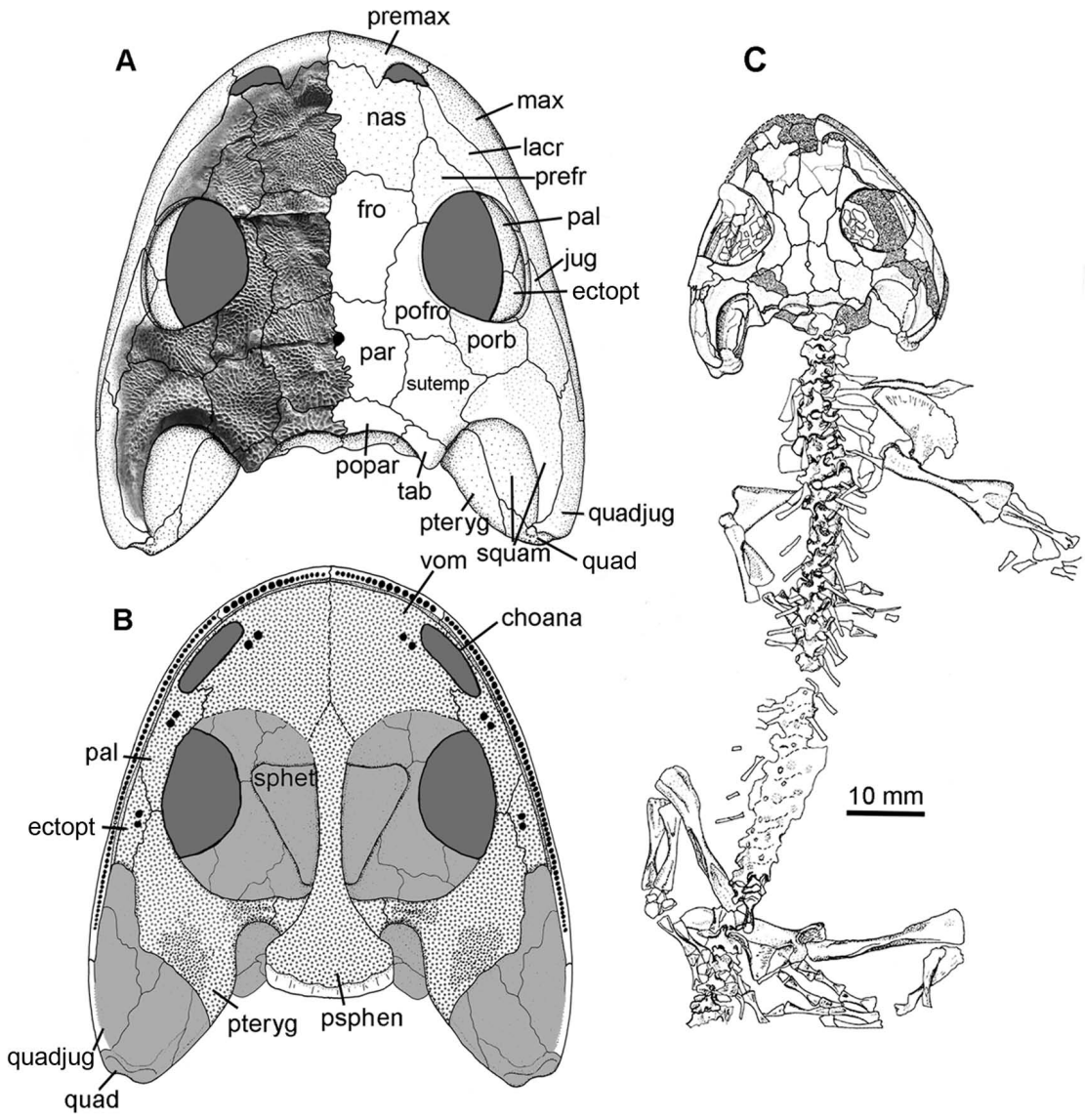
Details of the sequence of ossification in both skull bones and postcranial elements have been described for a number of genera and species of branchiosaurid. Some of them show more or less conservative patterns, similar to those of other temnospondyls in that they show only gradual changes from larva to adult (for example, *Micromelerpeton*, Witzmann and Pfretzschner 2003). Others, especially the genus *Apateon*, show more divergent patterns. All species of *Apateon* show a larval phase during which they add ossfications in a sequence. Unlike most larval temnospondyls, the shoulder girdle ossified early during this phase. After this early phase, essentially the animals grew in size but did not modify their morphology much further, and they remained as neotenic forms.




**9.17.** *Amphibamus grandiceps* (Y.P.M. 794). (A) Skull in dorsal view. (B) Skull in ventral view. *Original.* (D) Drawing of a larval specimen of *Amphibamus grandiceps* as preserved. *From Milner (1980).*

However, for *A. gracilis*, metamorphosed adults are known. The adults had large eyes, the otic notch was particularly large, and the limbs were well ossified, even at the relatively small size of about 16 millimeters in skull length. They bore a close resemblance to adults of amphibamids and were evidently terrestrial animals. This is the only instance in which a concentrated metamorphosis event can really be demonstrated among Paleozoic tetrapods (Schoch 2002b; Schoch and Fröbisch 2006).

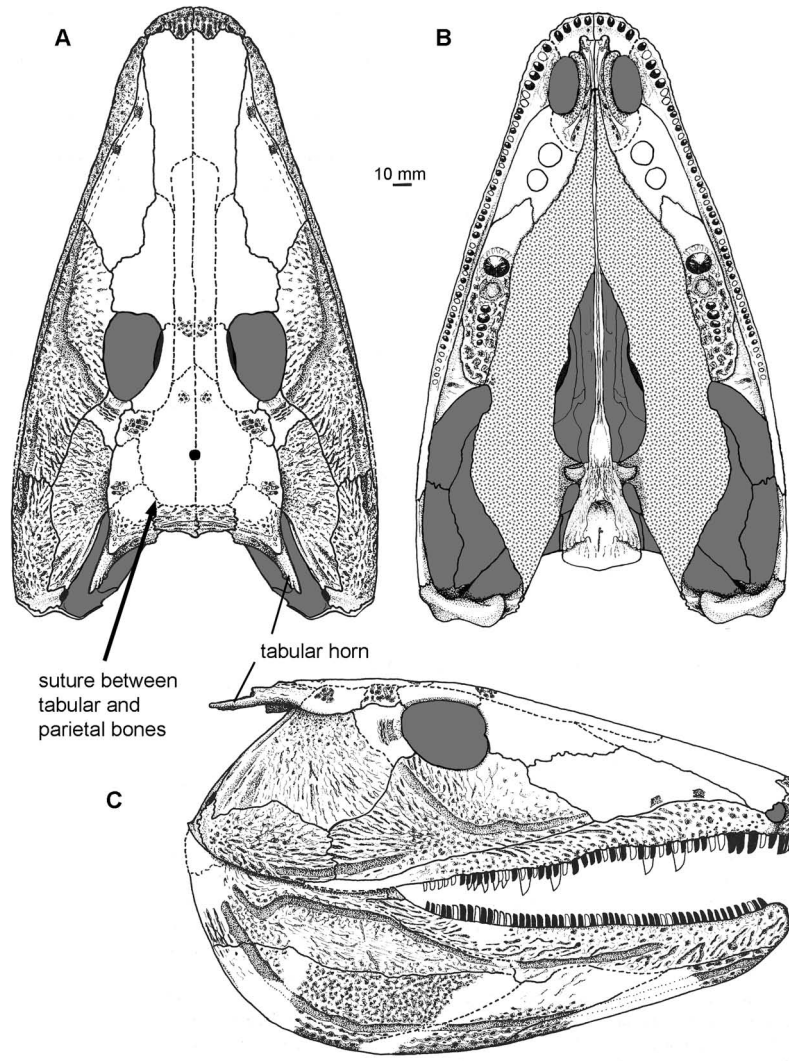
The amphibamids are a group known almost entirely from adults, though it has been suggested that at least some branchiosaurs may be the juveniles of amphibamids, as for example with *A. gracilis*. However, *Amphibamus* larvae are known and are recognizably different from any branchiosaur (Milner 1982). Amphibamids were small terrestrial forms with relatively long, gracile limbs and generally short vertebral columns. They all had large eye sockets and short skull tables. *Amphibamus grandiceps*, from the Late Carboniferous of the United States, has long been associated with the origin of modern amphibians (Watson 1940; Bolt 1969, 1979, 1991). At a skull length of 11 or 12 millimeters, it was much more robustly ossified than any of the larval branchiosaurs at a similar size. *Platyrhinops lyelli* from Linton, Ohio, is known from several specimens showing growth stages (Carroll 1964b; Clack and Milner 2010) (Fig. 9.18).




**9.18.** *Platyrhinops lyelli.* (A) Skull in dorsal view. (B) Skull in ventral view. (C) Drawing of articulated skeleton of *Platyrhinops lyelli. From Clack and Milner (2010).* (AMNH 6841). Light shaded areas, internal exposures of skull roofing bones.

Although the amphibamid genus *Doleserpeton* (Fig. 9.16D, E) has been known for many years, detailed descriptions are only just appearing; they show that it possessed some remarkable features that it shares uniquely with modern amphibians, as discussed in the last section of this chapter. Amphibamids generally are becoming much better known, and new species have been described recently. *Georgenthalia* comes from the Early Permian Bromacker Quarry (Anderson et al. 2008a). *Georgenthalia* has a particularly short skull table and extremely large eye sockets. *Plemmyradytes* is another recently described genus from the Early Permian of Nebraska (Huttenlocker et al. 2007), and *Pasawioops* is from the Permian locality of Richard's Spur (Fröbisch and Reisz 2008).

The youngest amphibamid in the fossil record is Early Triassic *Micropholis*, from South Africa. This has been known since the mid-19th century,



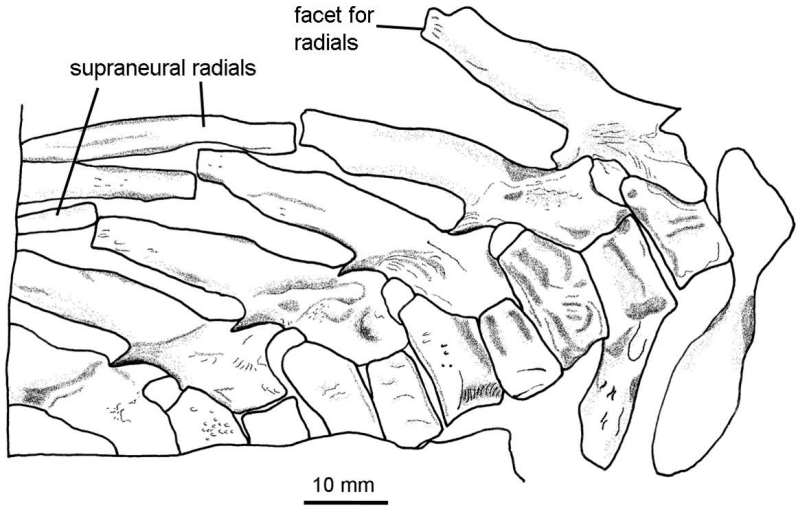

**9.19.** Drawing of skull of *Pholiderpeton scutigerum*. (A) Dorsal view. (B) Ventral view. (C) Right lateral view. *Based on Clack (1987a).*

but recent restudy has placed it phylogenetically among the amphibamids (Schoch and Rubidge 2005; Anderson et al. 2008a). Two distinct morphs have been found in the population, a long-headed and a broad-headed form, though it is not clear whether this represents sexual dimorphism or potentially two separate species (Schoch and Rubidge 2005).

One of the most exciting finds in recent years is that of *Gerobatrachus hottoni*. This single specimen, from the Early Permian of Texas, has the shortest skull and shortest vertebral column of any amphibamid. It also shows many features with specific resemblances to both frogs and salamanders (Anderson et al. 2008b).

### Anthracosaurs and Their Kin

Large crocodile-like predators called embolomeres inhabited the waters of the Late Carboniferous coal swamps (see Smithson 2000 for a review).

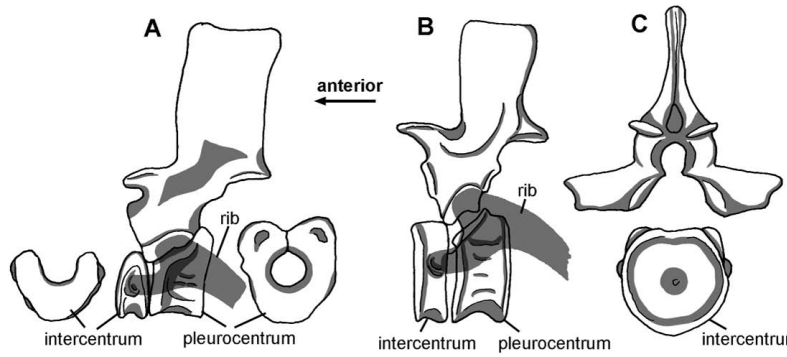



**9.20.** Sketch of embolomere tail vertebrae from a peel provided by the Carnegie Museum (CM 34638). The specimen is a natural mold.

They have been placed with a few other genera in a group known as the anthracosaurs. Whether or not the anthracosaurs form a monophyletic group has been debated, but for example Laurin (2004) recovered a clade that included embolomeres and *Gephyrostegus*. If their relationships are correctly understood, it seems that they radiated from small- to medium-sized, more or less terrestrial forms into larger, more fully aquatic forms paralleling some of the temnospondyls. *Silvanerpeton* (see Chapter 8) has been allied with these forms, suggesting that their origins go back at least to the Viséan, though their success was more limited than that of temnospondyls and they are much less common in the fossil record. *Eoherpeton* from the Namurian of Scotland is a semiterrestrial form that usually clusters with embolomeres (see Chapter 7), and together, they form the main constituent members of the anthracosaurs. *Eoherpeton* gave the first hint that early anthracosaurs may not necessarily have had the so-called otic notch that was long associated with all early tetrapods (Smithson 1985b) (Fig. 7.14).

Anthracosaurs are characterized by contact between the tabular and parietal bones in the skull table (Fig. 9.19) (see Chapter 8), in combination with the presence of an intertemporal, a closed palate with small or no vacuities in the midline, and often a skull table that is separated from the cheek plates by a noninterdigitating suture called a kinetic line. In the past, this has been considered to be a primitive character related to the kinetic skull roofs of primitive sarcopterygians, though now, with more early tetrapods having been discovered that lack this type of junction, the story appears not to be so simple.

Often there is a knob or small button, or in some groups a bladelike process, growing from the back of the tabular bone, called the tabular horn. The embolomeres, which form a coherent clade within the anthracosaur grouping, are characterized by the elaboration of such a process, often in the form of a blade growing from the unornamented posterior portion of the tabular (Fig. 9.19). Its form is distinctive, and it is quite different from the prong on the tabular found in *Acanthostega*. Its



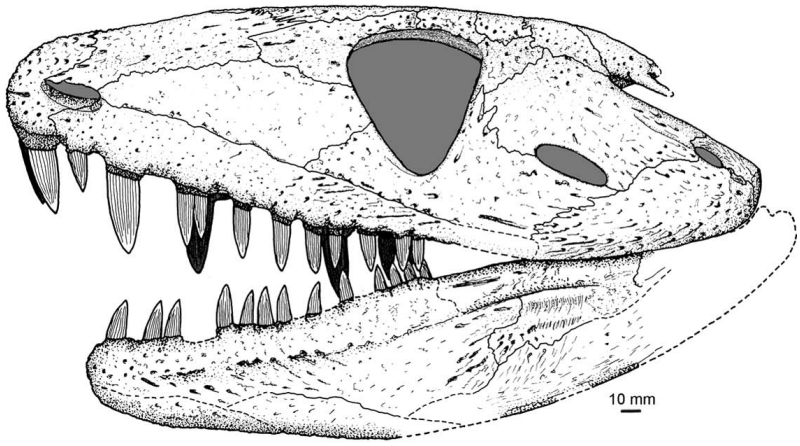

**9.21.** Embolomerous vertebral construction. (A) *Proterogyrinus,* neural arch with centra. Intercentrum in anterior view at left, pleurocentrum in anterior view at right. (B) *Pholiderpeton,* neural arch with centra. (C) *Pholiderpeton,* neural arch and intercentrum in anterior view. Arrow indicates orientation of neural arches in (A) and (B). Rib shown as transparent, with articulations to transverse process and intercentrum.

function is not clear, but it may have formed an attachment point for a ligament that passed to the shoulder girdle, possibly to the anocleithrum. This dermal bone of the shoulder girdle is usually lost in tetrapods, but *Acanthostega* and the embolomere *Pholiderpeton* are both known to retain it. It constitutes one of the primitive characters that at least some embolomeres retain. Another such primitive character appears in a specimen of an embolomere tail that shows supraneural radials like those of *Acanthostega* (Fig. 9.20).

The braincases of embolomeres are quite characteristic, having large, bulbous basipterygoid processes, with complex saddle-shaped faces, were set close to the midline, with a narrow crestlike cultriform process of the parasphenoid that runs between them. More posteriorly the parasphenoid forms a pair of ridges that stand proud of the basioccipital and that formed the housing for insertion of hypaxial muscles (Clack and Holmes 1988)

The embolomeres were long-bodied, crocodile-like piscivores whose remains are known from sites in the United Kingdom and the eastern United States (Panchen 1972b). The most primitive embolomere is *Proterogyrinus*, known from several early Namurian sites in the United States and also Scotland (Holmes 1980, 1984; Smithson 1986) (see Chapter 7). Its vertebrae, like those of *Eoherpeton*, were not the fully embolomerous type found in more typical forms such as *Pholiderpeton* (Clack 1987a) (Fig. 9.21), though they were gastrocentrous, with pleurocentra forming almost complete rings. In fully embolomerous forms, pleuro- and intercentra both formed complete rings, though the pleurocentrum is always the larger (Fig. 9.21). There seems to be a morphocline in vertebral construction, from animals like *Eoherpeton* in which neither the pleurocentrum nor intercentrum were complete rings, through forms like *Proterogyrinus* in which the pleurocentrum was a nearly complete ring, to those in which both were (Panchen 1966, 1967). The significance of this is discussed in Chapter 10.

*Anthracosaurus* was probably the most fearsome predator of its day, but it is only known from its skull (Panchen 1977; Clack 1987b) (Fig. 9.22). It had a massive skull with a dentition in which, compared to other embolomeres, the marginal teeth were fewer in number but greatly enlarged.

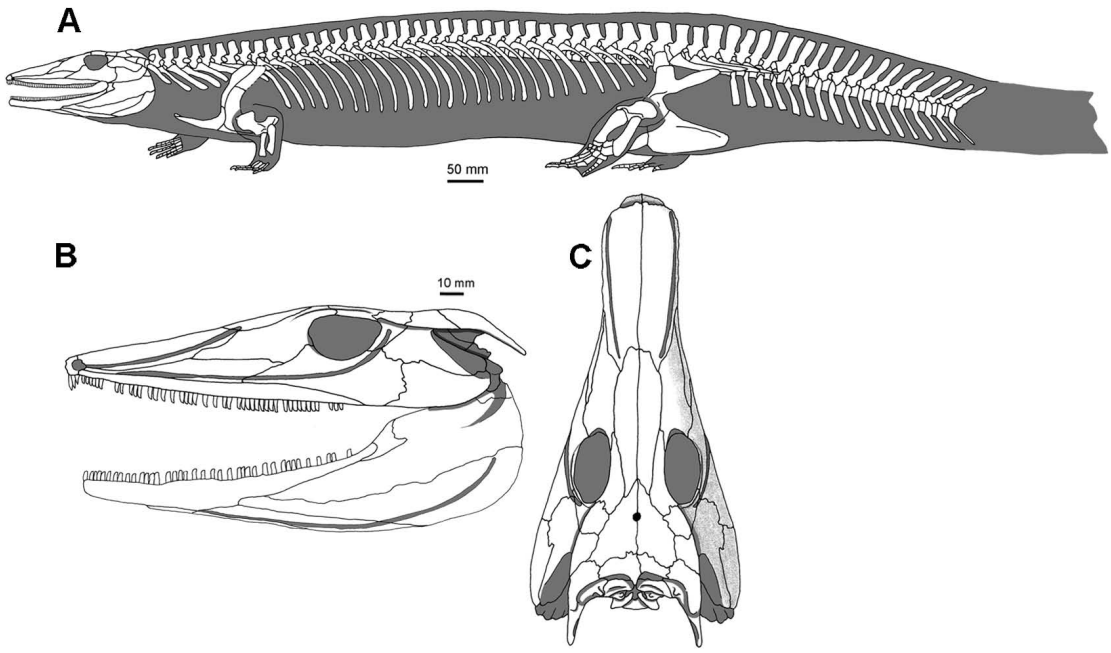



**9.22.** Skull of *Anthracosaurus russelli*. *From Clack (1987b).* Skull is about 400 millimeters long.

*Carbonoherpeton* is a Late Carboniferous embolomere from Florence, Nova Scotia, found in tree-stump preservation similar to that of Joggins (Klembara 1985). *Calligenethlon* is another embolomere known from small elements from the Joggins tree stumps (Carroll 1967), though other, larger, embolomere material from that site has been found outside of the tree stumps and has been described recently (personal observation 2007; Holmes and Carroll 2010).

Only one genus of embolomere, *Archeria*, is known from the Early Permian of the United States (Holmes 1989a) (Fig. 9.23). This is the only fully embolomerous form known from more or less complete skeletons and for which the number of presacral vertebrae is certainly known. It had about 40, and also had a long, deep tail supported by elongate neural and hemal spines, both features that are associated with agile swimmers. It is one of the earliest tetrapods to develop a long-snouted skull, though not to such an extreme extent as the temnospondyl *Archegosaurus*. It had a large number of small chisel-shaped teeth along its jaw margins and may have eaten small, slippery aquatic prey.

Until recently, only a few fragmentary specimens from Russia suggested that embolomeres persisted as rare, specialized members into the Early Triassic. These animals are now better known, with the description and analysis of new material and comparisons made with existing collections. These animals, called chroniosuchians, resemble small- to medium-sized crocodiles. *Chroniosaurus dongusensis*, from the Late Permian of Russia, is the best known (Fig. 9.24). Chroniosuchians have dorsal scutes that lock together over the vertebral column and limb bones that are much less complex than those of typical embolomeres. They have characteristic anteriorly placed vacuities in the snout, they lack an intertemporal, and some of the skull bones are strengthened by ridges. The kinetic line seen in more typical embolomeres has become elongated in chroniosuchians to run between the postorbital and squamosal bones. However, they retain a number of features in which they resemble other embolomeres: the vertebral centra including the atlas–axis complex,



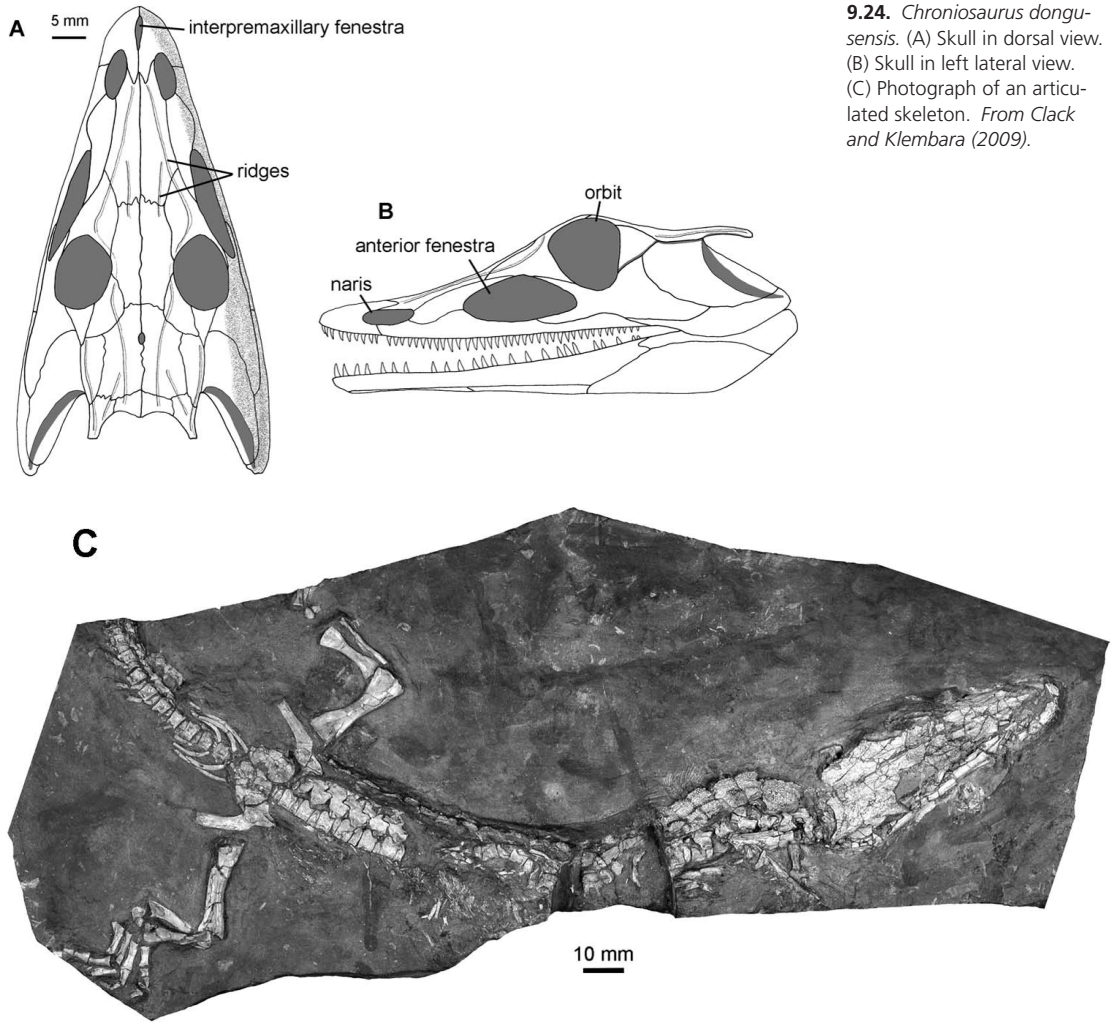

**9.23.** Skull of *Archeria*.
(A) Skeletal reconstruction.
(B) Skull in left lateral view.
(C) Skull in dorsal view. *Based on Holmes (1989a).*

and particularly the braincase (Clack and Klembara 2009). By the Early Triassic, chroniosuchians had radiated as far as China and Germany.

One other genus of animal often placed within the anthracosaurs is known from substantial remains. This is *Gephyrostegus* (Fig. 9.25), known from a number of specimens from Westphalian localities in the Czech Republic. Material of this taxon is currently undergoing restudy because some features of the published reconstructions are inconsistent, and further material that has recently been identified as *Gephyrostegus* could help resolve these problems. Also some of the many postcranial remains that have been attributed to it may not belong, whereas others that have been given other names may in fact belong to it and indicate that it occurs at sites in North America such as Linton.

In the early 1970s, *Gephyrostegus* was seen as a possibly "ancestral to reptiles" (Carroll 1970, 268). Its body form has been interpreted as very like that of some of the early amniotes from Joggins, having a relatively short presacral vertebral column and robust limbs. It has gastrocentrous vertebrae, though some specimens suggest that the tail was fully embolomerous and that the animal was at least partially aquatic. It has the typical embolomere bone contact pattern in the skull table. *Brukterepeton* is a poorly known form from the Namurian of Germany that resembles *Gephyrostegus* (Boy and Bandel 1973). It has gastrocentrous vertebrae and slender limbs, suggesting it was mainly terrestrial.

Anthracosaurs in general share many features with early amniotes that have been considered to show a phylogenetic relationship between them (Panchen 1972a, 1972b). Amniotes also, for example, show tabular–parietal contact in the skull roof, though they have lost the intertemporal.

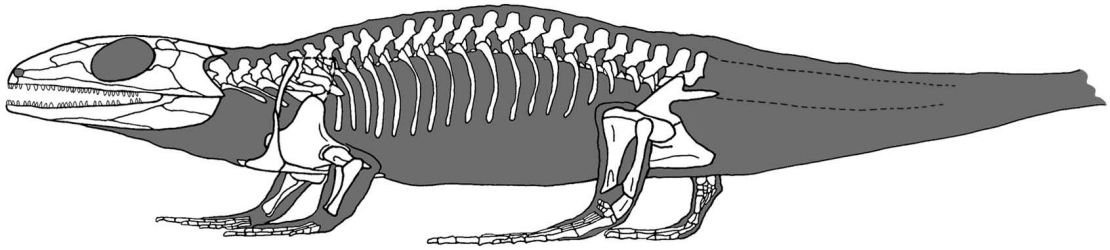



**9.24.** *Chroniosaurus dongusensis.* (A) Skull in dorsal view. (B) Skull in left lateral view. (C) Photograph of an articulated skeleton. *From Clack and Klembara (2009).*

Anthracosaurs and amniotes have gastrocentrous vertebrae in which the pleurocentrum is the dominant element (see Chapter 10), and most of them have two dorsal blades to the ilium. Anthracosaurs are still considered to be more closely related to amniotes than they are to temnospondyls, though the relationship is now considered to be more distant than was once thought. They may not form a natural group, and *Gephyrostegus* often falls one node above a monophyletic group formed by the embolomeres. *Silvanerpeton*, usually considered to be an anthracosaur, also sometimes appears as a separate taxon outside the embolomeres. In a recent redescription, it fell below the embolomeres (Ruta and Clack 2006).

### Seymouriamorphs

*Seymouria baylorensis* is the best-known seymouriamorph, represented by many specimens found from the red beds of the Late Permian deposits in Texas and other southern states of the United States. Its name derives



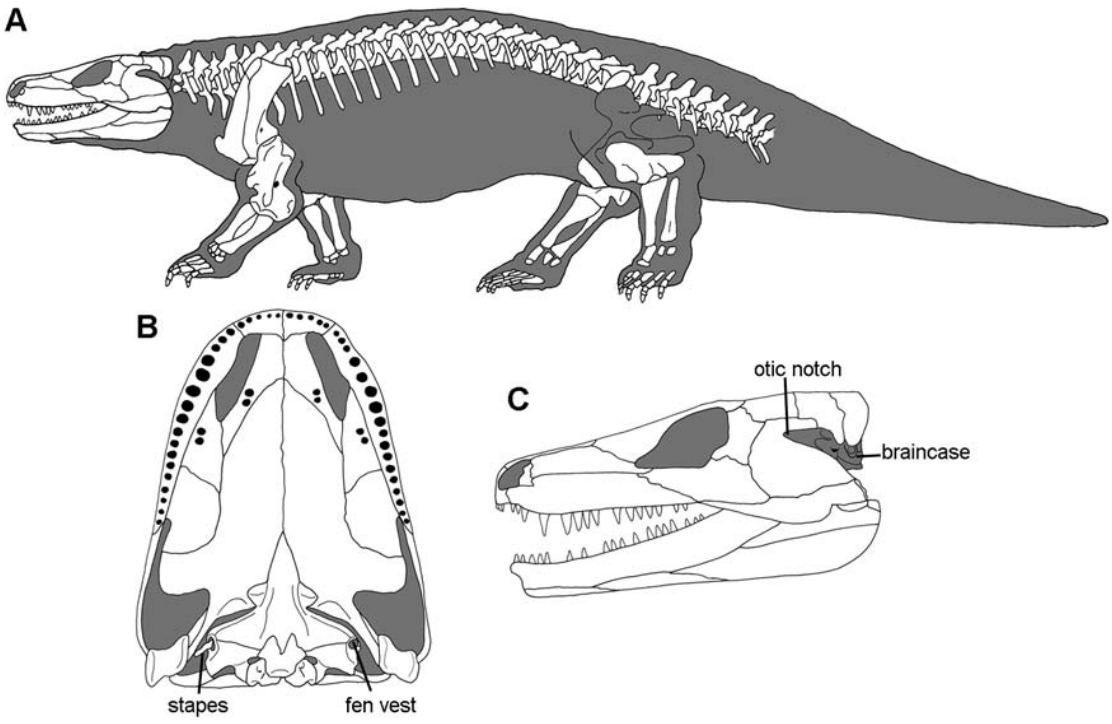
**9.25.** Skeletal reconstruction of *Gephyrostegus. Based on Carroll (1970).* Snout–vent length about 100–120 millimeters.

from two counties in Texas, Seymour and Baylor, where many of the first specimens were discovered. For several decades during the 1920s to 1960s, a debate took place over whether *Seymouria* was a "reptile" or an "amphibian" (Watson 1919; White 1939). The reason for the confusion was that while its skull resembled that of an anthracosaur in some ways, its postcranial skeleton was very like that of some early reptiles (Figs. 9.26, 9.27). The skull retained an intertemporal, a primitive feature, while the skull table showed tabular–parietal contact. It is no longer clear that the amniotes inherited this contact from an anthracosaur ancestor or whether they acquired it separately, because of the loss of the intertemporal in amniotes.

The seymouriamorphs also share with anthracosaurs a palatal structure that, like those of very early tetrapods, is closed—that is to say, it lacks the palatal vacuities of temnospondyls. However, the closed palate is clearly a primitive feature, not indicative of close relationship.

The postcranial skeleton is quite heavily built with robust limbs. The most reptilelike feature of the skeleton lies in the structure of the vertebral centra and neural arches. The centra are composed mainly of a solid pleurocentrum, attached firmly to the overlying neural arch by a suture. The intercentrum is small in seymouriamorphs and lost in most amniotes. The neural arches of seymouriamorphs are broader than they are long, and the interarticulations are set on horizontally placed, broad zygapophyses (see Chapter 10). The neural spines are domed rather than the more commonly found elongate rectangle. This domed shape is found in some groups of early reptiles, but not all, so its significance is a puzzle.

The feature that for some people decided the issue was the ear region. Seymouriamorphs have deeply embayed otic notches, and the stapes is interpreted (the evidence is not good) as a slender rod (Fig. 9.26). Though the otic region of the braincase is unique and specialized, the configuration of the notch and stapes suggested an ear like that of a temnospondyl rather than of an early amniote. Thus, seymouriamorphs were interpreted as amphibians. However, this is not the whole story. On the one hand, phylogeny suggests that the ear structure of seymouriamorphs is probably an independent development, not derived from that of a temnospondyl-like arrangement (see Laurin 1996, 2000). On the other hand, new evidence shows that larval seymouriamorphs retained external gills like most modern amphibians and like temnospondyls.




**9.26.** Drawings of *Seymouria*. (A) Skeletal reconstruction. (B) Skull in ventral view. (C) Skull in left lateral view. *Based on White (1939).* Skull is 115 millimeters long.

*Seymouria* itself has now been found in Germany, suggesting fairly close links among the faunas of Euramerica during the Early Permian (Berman and Martens 1993). In fact, the same species, *S. sanjuanensis*, has been found in Utah and New Mexico as well the Bromacker Quarry in Germany. Even so, juvenile seymouriamorph remains have been found there that resemble those of apparently aquatic juveniles of another genus of seymouriamorph, *Discosauriscus* (Klembara et al. 2006).

*Discosauriscus* is one of a number of seymouriamorph genera from eastern Europe that have been described recently. These animals, collectively known as discosauriscids, have been known for many decades from well-preserved remains showing traces of the body wall and, more significantly, of external gills like those of larval salamanders (Klembara 1995). They were eventually recognized as related to the seymouriamorphs of North America (Fig. 9.28). There are at least six recognized genera. *Discosauriscus* itself is known from a wealth of specimens that document growth stages, though even the largest known are thought still to be juveniles, with a skull length of 42 millimeters (Klembara 1994a, 1995, 1997, 2000). The material often shows three-dimensional preservation and has been extracted from the matrix by acid-preparation techniques (Klembara 1997, 2000). This process has revealed fine details of bone construction, including unusual pits with numerous foramina in their bases. These have been interpreted as having housed ampullary electroreceptive organs (Klembara 1994b). In one exceptional specimen, the remains of a smaller individual are found in the abdominal region of a larger one, and a coprolite also preserved in the larger specimen contains



**9.27.** Model of *Seymouria* skeleton (UMZC specimen). *Photograph by S.M.F.*

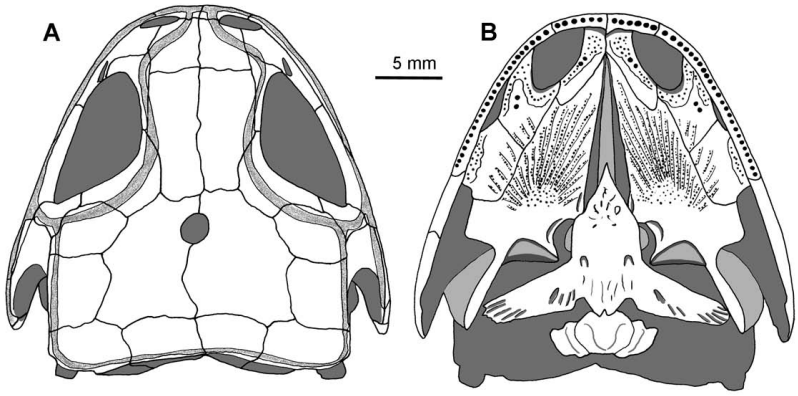
recognizable discosauriscid bones. An instance of cannibalism is strongly indicated (Klembara and Meszaros 1992), a feature that is also seen in some modern amphibians.

*Ariekanerpeton* from Tadzhikistan is also known from growth series and has similar growth characteristics to *Discosauriscus* (Klembara and Ruta 2005). *Utegenia* from Kazakhstan grows to a skull length of about 48 millimeters, but even at this relatively large size, its morphology and degree of ossification remained more similar to larval *Discosauriscus* (Klembara and Ruta 2004).

It has been shown conclusively that seymouriamorphs had an amphibian-type life history, with aquatic young stages that lost their external gills after metamorphosis. The lifestyle similarity between seymouriamorphs and temnospondyls cannot suggest a relationship, however, because reproductive strategies are strongly influenced by ecology, and in any case, larvae with external gills are found in many fishes, so the attribute is a probably a primitive one. Seymouriamorphs and anthracosaurs are usually considered to belong to the amniote stem lineage, but seymouriamorphs were definitely not amniotes themselves.

## Lepospondyl groups: Microsaurs, Lysorophids, Aïstopods, and Nectrideans

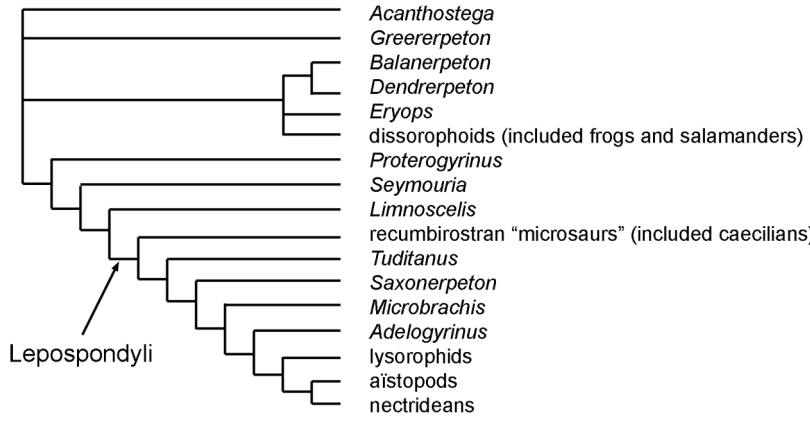
In older classifications, the groups of larger tetrapods such as temnospondyls and anthracosaurs were placed together in a group called the labyrinthodonts (Romer 1947, 1966). Current thinking has split the labyrinthodonts into disparate, more or less unrelated groups. Co-lateral to




**9.28.** Skull of *Discosauriscus*. (A) Dorsal view. (B) Ventral view. *Based on Klembara (1997, 2000).*

the labyrinthodonts was a second assemblage, this time of small animals, called the lepospondyls (Romer 1966; Carroll 1987; Carroll et al. 1998). The four main included groups—microsaurs, lysorophids, aïstopods, and nectrideans—show a number of common features that appear to be shared specializations. They include the absence of any kind of temporal notch, the reduction in the number of skull bones (though not exactly comparable conditions in each) and the consolidation of the vertebrae. In particular, the odontoid process, a knoblike process from the atlas arch that fits into the occipital condyle, is present in all groups (Anderson 2001). In all, a large cylindrical centrum is usually the sole central element. A few genera are known in which an intercentral element is present. The neural arches are either sutured or fused to their respective centra, making each vertebra a coherent unit. They also, with the single possible exception of *Microbrachis*, appear to ossify their bones at an early stage in their ontogeny, so that they appear more or less fully formed in even in the smallest known examples. The Early Carboniferous adelogyrinds are also usually included among the lepospondyls, though some of them have a temporal notch (see Chapter 7) and sometimes fall with colosteids in cladistic analyses (e.g., Ruta et al. 2003).

Opinions about the relationships of the lepospondyls to one another and to other tetrapods have differed widely. One suggestion, based on a large cladistic analysis of morphological characters, was that not only are they closely related to one another, but that they are also closely related both to modern amphibians and to amniotes (Laurin and Reisz 1997). Ruta et al. (2003), though they refuted the proposed relationship between modern amphibians and lepospondyls, nevertheless corroborated the suggestion that lepospondyls are closely related to one another and also supported the position of lepospondyls as closely related to amniotes. Anderson (2007) found a sister-group relationship between amniotes and a monophyletic Lepospondyli, but found that whereas caecilians emerged from within microsaurs, frogs and salamanders derived from temnospondyls, a situation that makes modern amphibians paraphyletic (Fig. 9.29). He also found microsaurs themselves to be paraphyletic.



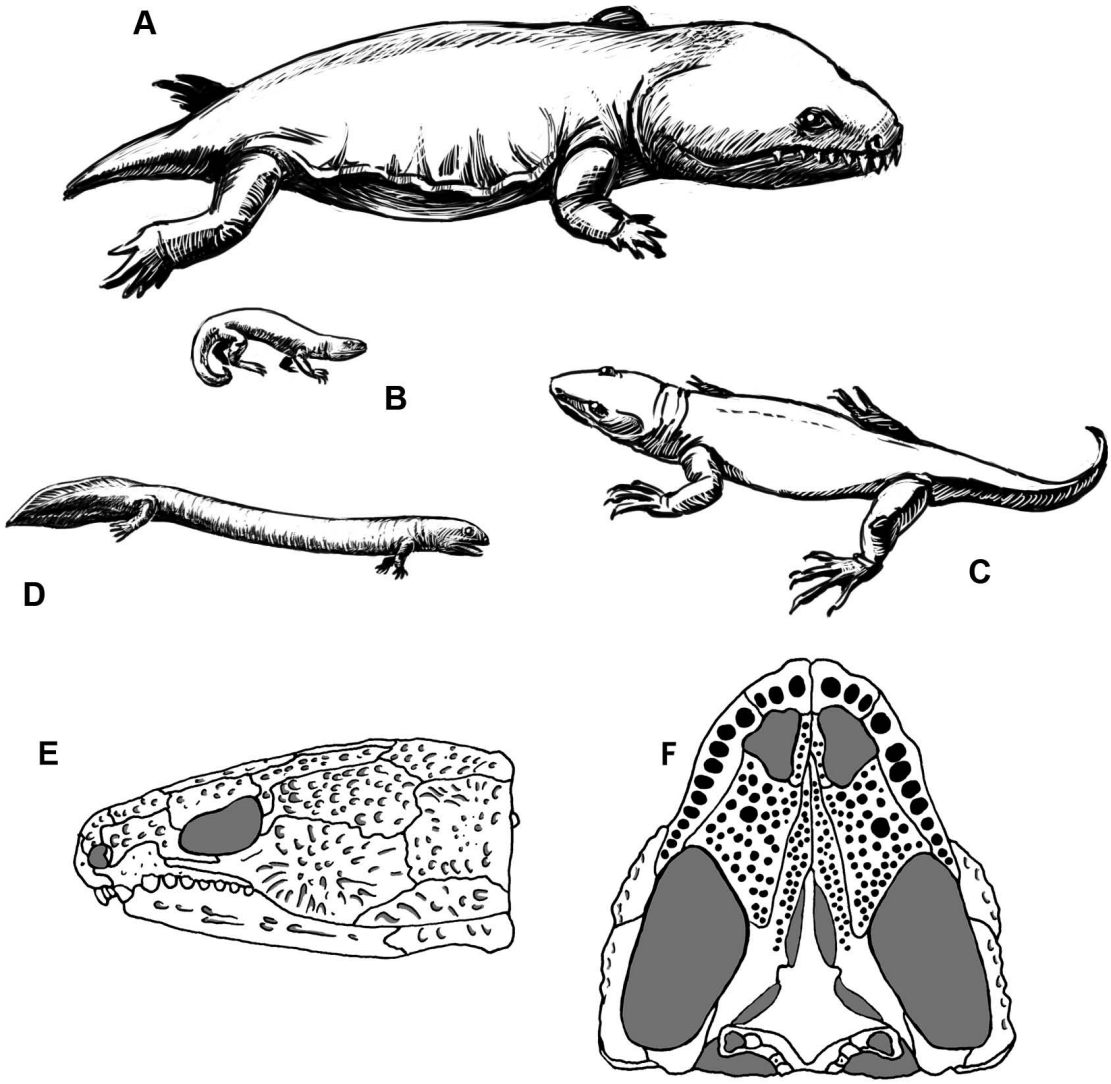

**9.29.** *Cladogram from Anderson (2007).*

One of the reasons for the difficulty in placing lepospondyls is that it is hard to tease apart morphological similarities deriving from relationship and those deriving from lifestyle and ecological similarities among small animals. The uniting features of lepospondyls are also characteristic of small early amniotes. Much interest is currently being taken in lepospondyl phylogeny and anatomy, so the picture could change rapidly over the next few years.

## MICROSAURS

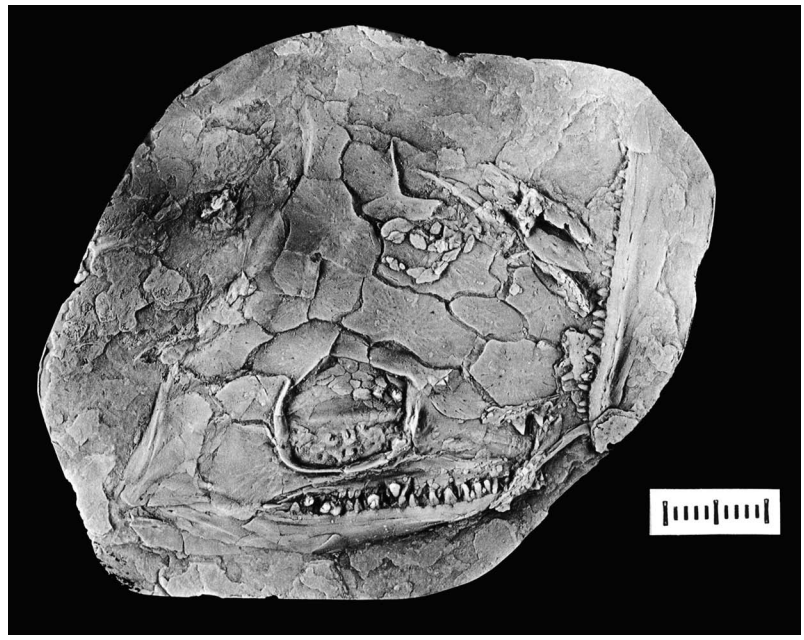
Some of the best-known lepospondyls have formerly been included in the group called microsaurs. The earliest member of this group is form from East Kirkton in Scotland (see Chapter 7) (Clack in press), with the next earliest being from the early Namurian of Goreville, Illinois (Lombard and Bolt 1999). The last microsaurs were Early Permian. Microsaurs have traditionally been divided into two rather different groups, one the predominantly terrestrial tuditanomorphs, and the other the mainly aquatic microbrachomorphs (Figs. 9.30, 9.31). They have different, and mutually exclusive, skull table bone patterns. Microsaurs as a whole are quite diverse, showing a variety of body forms, some lizardlike, some like salamanders, and several with long bodies and short limbs that may have been burrowers (Carroll and Gaskill 1978; Carroll et al. 1998; Carroll 2000a). It is unclear which of the two groups is the more primitive, and the microbrachomorphs have appeared as paraphyletic in some analyses (Anderson 2001, 2007), though not in others (Ruta et al. 2003).

Among the first microsaurs to be recognized were several genera from the tree stumps at Joggins, where their remains were jumbled together with those of genuine amniotes. This created confusion. Microsaur means "little reptile," and microsaurs are very like early amniotes in their anatomy, which was one of the sources of confusion, another being that fossils of the two types were difficult to disentangle physically. The similarity between microsaurs and early amniotes has led to suggestions over the years that they are closely related, with recent cladistic analyses




**9.30.** A selection of microsaurs. (A) *Pantylus.* (B) *Saxonerpeton.* (C) *Tuditanus.* (D) *Microbrachis.* To scale. *Pantylus* is about 270 millimeters long from snout to tail tip. (E) Left lateral and (F) ventral views of the skull of *Pantylus. Illustrations by J.M., based on Carroll and Gaskill (1978).*

being the latest of these. They have quite deep, compact skulls with no otic notch, and with short snouts bearing the tooth row well forward in the skull, as in early amniotes. However, there are several characters in which microsaurs differ substantially from reptiles, among them the pattern of skull roofing bones. Microsaurs have a skull table pattern involving a single temporal bone, where early amniotes have several, and of the two microsaur groups, the amniote pattern more closely resembles that of the aquatic microbrachomorphs. All microsaurs have a specialized atlas–axis vertebra that fits into a unique form of occipital condyle not found in reptiles. It bears more similarity to the occipital joint of temnospondyls. The vertebrae usually consist of a single centrum either sutured or fused to the compact neural arches, and the limbs are gracile. Headless skeletons of microsaurs and early amniotes are difficult to tell apart, one of the few distinguishing features being that where amniotes have five toes



**9.31.** Skull of the microsaur *Crinodon limnophyes*. Photograph of a replica in UMZC. Scale bar = 10 millimeters. *Photograph by S.M.F.*

on the forelimb, microsaurs never have more than four. In this, they again resemble temnospondyls rather than amniotes—one of the pieces of evidence once used to suggest that microsaurs and temnospondyls are closely related. Another is the condition of the occiput, in which both microsaurs and temnospondyls show an unusual condition where the exoccipitals contact the postparietal bones (Smithson 1982).

*Microbrachis* is the best-known microbrachomorph. It comes from the late Westphalian Nýřany locality in the Czech Republic. It has a long trunk of about 38 vertebrae, short limbs, and skull bones with dermal ornamentation and lateral lines, and some specimens show dental ossicles on the ceratobranchials (Carroll and Gaskill 1978). These could have been used in suction feeding rather than breathing, but this is not certain. Recent work has shown that it had a deep propulsive tail with a fleshy caudal fin (Milner 2008). The relative length of the tail apparently increased with growth, with the terminal vertebrae ossifying late in ontogeny.

Another genus generally considered to be a microbrachomorph is *Hyloplesion*, also from Czech Westphalian localities, and similar in overall appearance to *Microbrachis*. However, although Ruta et al. (2003) confirmed this relationship, Anderson (2001) did not, placing *Hyloplesion* as one of the most basal microsaurs and placing *Microbrachis* as closer to nectrideans than to other microsaurs. Anderson (2007) found that both *Microbrachis* and *Hyloplesion* are closer to nectrideans and aïstopods than to other microsaurs.

The tuditanomorphs usually seem to form a monophyletic group, although Anderson's (2007) analysis split them up with several of them apparently paraphyletic with respect to nectrideans and aïstopods. This

rather radical result remains to be tested further. Conventionally, tuditanomorphs are made up of several families. *Tuditanus* itself comes from the Westphalian of Linton, Ohio, and is a classically terrestrial form with a short vertebral column and substantial limbs. A subgroup of the former tuditanomorphs has been named the Recumbirostra by Anderson (2007). A number of these terrestrial forms developed embayments in the cheek margin near the back of the skull, such as *Pelodosotis* and *Microroter*, having reduced or lost the quadratojugal. These were both long-bodied forms with reduced limbs from the Early Permian of the United States. The most recent of this group to be described is a tiny skull from the Richard's Spur quarry in Oklahoma. *Nannaroter* shows the pointed snout and compact skull of the recumbirostrines, with tightly knit skull sutures (Anderson et al. 2009). The structure resembles that of the burrowing amphisbaenians and to a lesser extent that of the modern caecilians. *Pantylus*, also from the Early Permian of the United States, was the largest microsaur (Fig. 9.30). Its skull was robust and large relative to the size of its body compared with other microsaurs. It had numerous rounded teeth spread over the palate, and the marginal dentition was formed of blunt but strong teeth. The dentition appears adapted for crushing (Carroll et al. 1998).

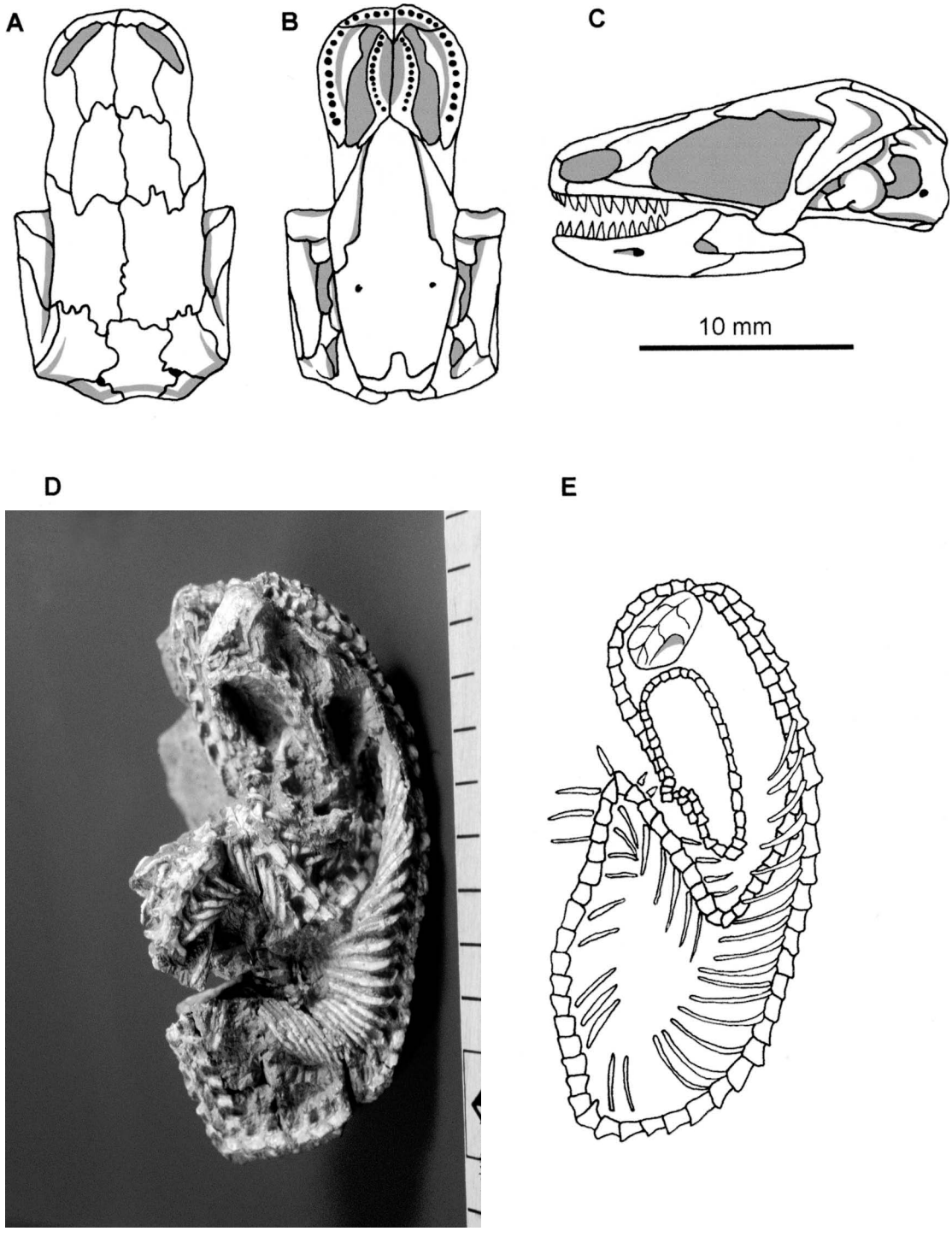
### LYSOROPHIDS

Lysorophids were once thought to be highly derived microsaurs, but not all recent cladistic analyses have borne this out. Instead, they have tended to cluster with nectrideans (Anderson 2001; Ruta et al. 2003). However, Laurin and Reisz (1997) and Vallin and Laurin (2004) found them to lie one node above the microsaurs, which thus appeared as a paraphyletic group, and lysorophids appeared as a sister group to modern amphibians.

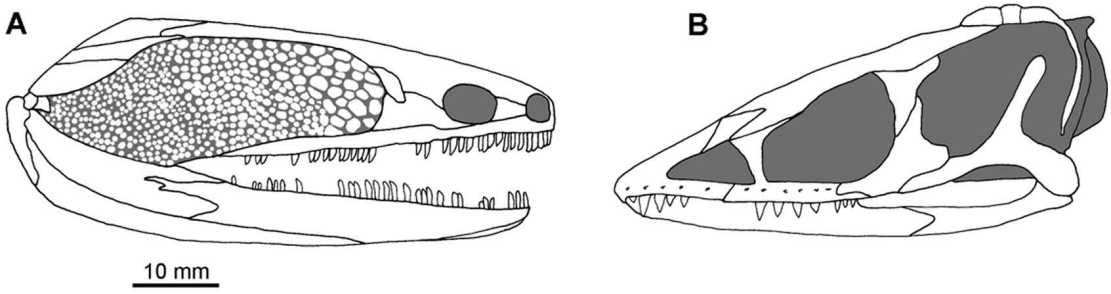
The earliest record of a lysorophid consists of a few vertebrae from the Late Carboniferous of Northumberland, England (Boyd 1980). The best known is *Brachydectes* from the Early Permian Red Beds of the United States. It had a long body containing up to 100 presacral vertebrae, small limbs, a unique pattern of skull roofing bones, and a braincase in which all elements are fused into a unit (Carroll and Gaskill 1978; Carroll et al. 1998; Carroll 2000a). The compact nature of the skull has been suggested to result from a burrowing habit, and the overall construction resembles that of modern burrowing amphisbaenians. Fossilized "cocoons" of *Brachydectes* have been found, showing that at least one group of tetrapods dealt with periodic aridity by estivating (Fig. 9.32) (Olson 1971).

### AÏSTOPODS

Aïstopods are extremely elongate limbless animals from the Carboniferous. Their relationships are obscure, but in two recent analyses (Anderson 2001; Ruta et al. 2003), they appear among the nectrideans. The first known aïstopods date from the Viséan of Wardie (*Lethiscus*, Chapter 7) and East Kirkton in Scotland (*Ophiderpeton*, Chapter 8), but by the




**9.32.** The lysorophid *Brachydectes elongatus.* (A) Skull in dorsal view. (B) Skull in ventral view. (C) Skull in left lateral view *(from Carroll et al. 1998)*. (D) Photograph of lysorophid specimen (UCLA VP2802). The specimen is about 100 millimeters long. *Photograph by ARM.* (E) Drawing of the same specimen preserved curled up in an estivation burrow *(from Olson 1971)*.



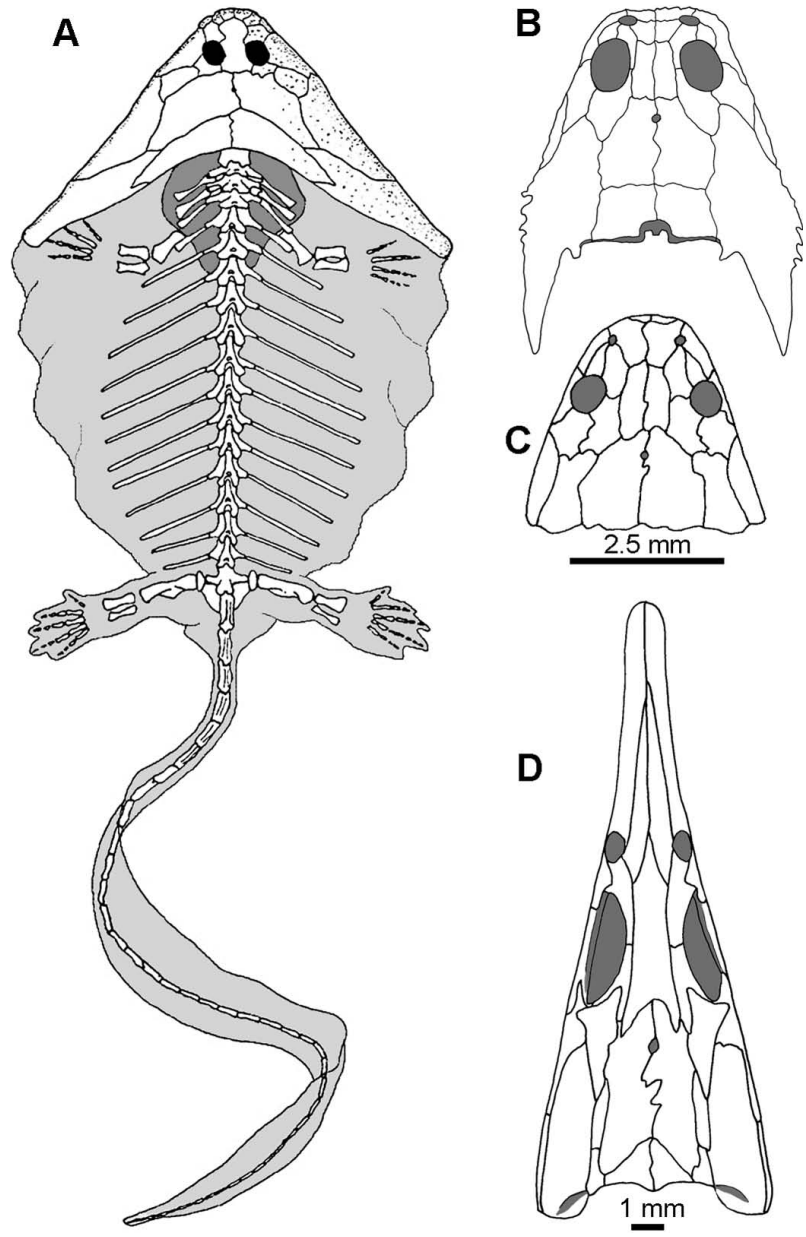

**9.33.** (A) Skull reconstruction of the aïstopod *Oestocephalus*. *Based on Carroll (1998).* (B) Skull reconstruction of *Phlegethontia*. Skull up to 15 millimeters long. *Based on Anderson (2002).*

Westphalian, they had become quite common and widespread (Carroll et al. 1998; Carroll 2000a). All had rather derived skull morphologies, though two patterns dominate. In one, exemplified by *Oestocephalus* and *Coloraderpeton*, the eyes were far forward and small, and the sides of the cheek were covered by a mosaic of small plates (Fig. 9.33). These would have been flexible enough to accommodate the huge jaw-closing muscles housed in the enormous adductor chamber that the skull incorporated. *Oestocephalus* and *Coloraderpeton* are Westphalian in age and come from Europe and the United States, respectively (Anderson 2003). In the other form, such as in *Phlegethontia* from the Westphalian of Europe and the United States, the skull proportions were more conventional, but the cheek bones formed a slender framework attached to a solidly ossified braincase (Anderson 2007).

Both groups had high numbers of vertebrae: about 100 vertebrae in *Oestocephalus* and up to 250 in *Phlegethontia* (Anderson 2002). None had any vestiges of limbs or girdles. Each had at least some ribs that were shaped like the letter K, and there have been some suggestions that these were used for rib walking, as in modern snakes, though other researchers disagree. By studying the ratio of caudal to presacral vertebrae, Anderson (2003) was able to show that aïstopods elongated their bodies in a manner more like that of the anguid lizard *Ophisaurus*, which has a long caudal region, and not like snakes, in which the caudal region is always short. It is not clear whether aïstopods were all aquatic or whether some might have been terrestrial burrowers. All bore a ventral covering of elongate ventral scales and a dorsal covering of rounded scales. In the past, the elongate gastral scales were mistaken for gill bars, but there is now great uncertainty about whether aïstopods retained any branchial elements at all (Carroll et al. 1998).

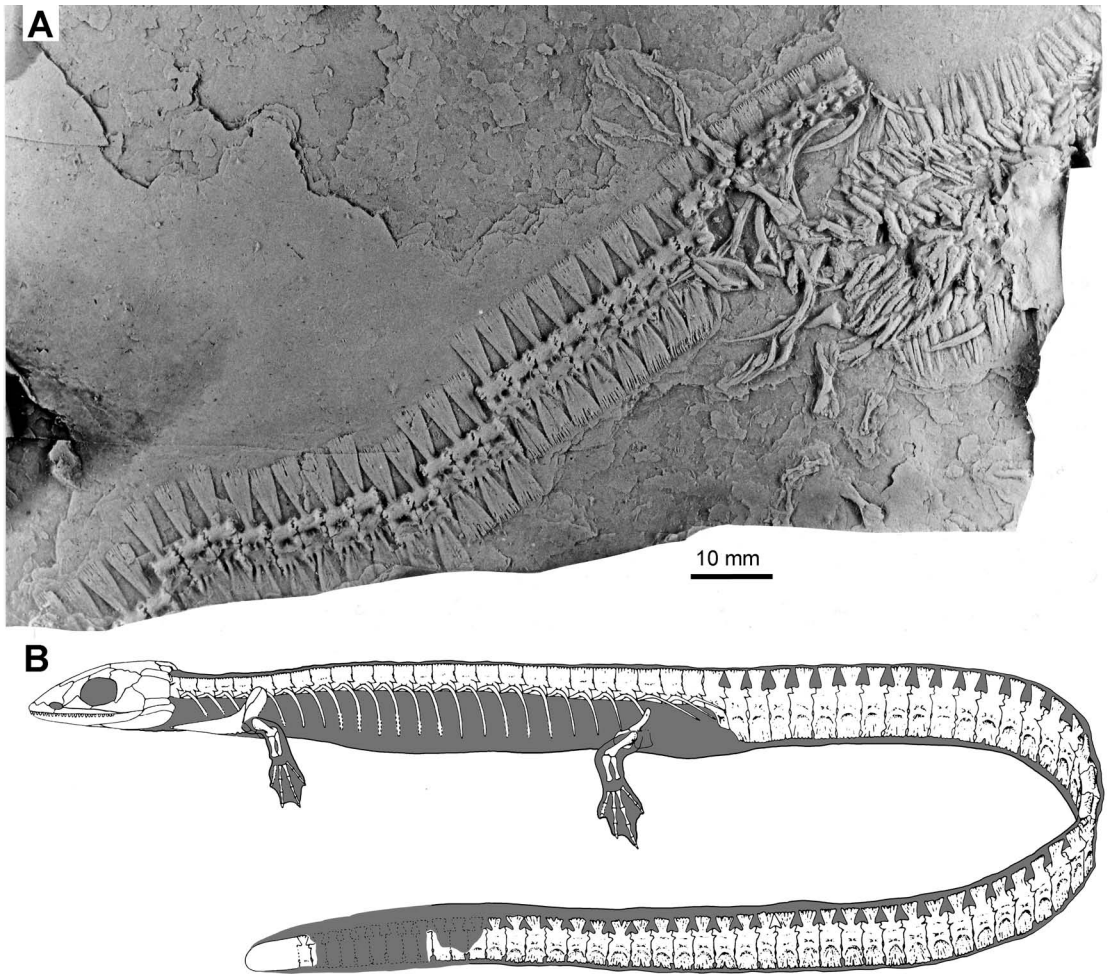
### NECTRIDEANS

Nectrideans are usually considered to be a monophyletic group linked by a number of apomorphies (Carroll et al. 1998), although recent cladistic analyses suggest that they are paraphyletic with respect to the aïstopods. Among their distinguishing features is the form of the neural and hemal arches of the tail. These are hatchet shaped from front to back, and the margins are marked by crinkled ornament, known as




**9.34.** Drawings of nectrideans. (A) The diplocaulid *Diplocaulus,* skeletal restoration with body outline based on resting trace fossil. Note that the forelimbs would be free from the skin flaps and held beneath it. Skull about 50 millimeters wide. (B) Skull of the diplocaulid *Diceratosaurus.* Skull up to 22.5 millimeters long. (C) Skull of the scincosaurid *Scincosaurus.* (D) Skull of the urocordylid *Sauropleura. (A, C, D) Based on Carroll et al. (1998).*

piecrust decoration, owing to its similarity in appearance to the way the edges of pastry cases are sealed (Figs. 9.34, 9.35). The effect of expanding the neural and hemal arches is to produce a tail flattened but strengthened to produce lateral bending used for propulsion in swimming, and a series of additional articulations between the vertebrae are also characteristic of this construction. Other features of the skeleton are fairly conservative; the trunk is short and the limbs relatively long and slender. Early nectrideans lost the intertemporal bone but acquired an anthracosaurlike tabular parietal contact, though they are not usually considered as anthracosaur relatives. Later nectrideans developed




**9.35.** (A) Tail of the nectridean *Ctenerpeton* (Carnegie Museum specimen CM 44777, from a replica in UMZC). Scale bar = 10 millimeters. *Photograph by S.M.F.* (B) Skeletal reconstruction of *Ptyonius.* Animal is about 220 millimeters long. *Based on Carroll et al. (1998).*

palatal vacuities like temnospondyls, but again, this is considered to be a convergent acquisition.

The earliest nectrideans are not found until the early part of the Westphalian, but by their demise in the Early Permian, they had evolved into some of the strangest tetrapods of all (A. C. Milner 1980; Carroll et al. 1998; Carroll 2000a). The implications from the diversity that appears among the Westphalian forms is that their origins must have been much earlier.

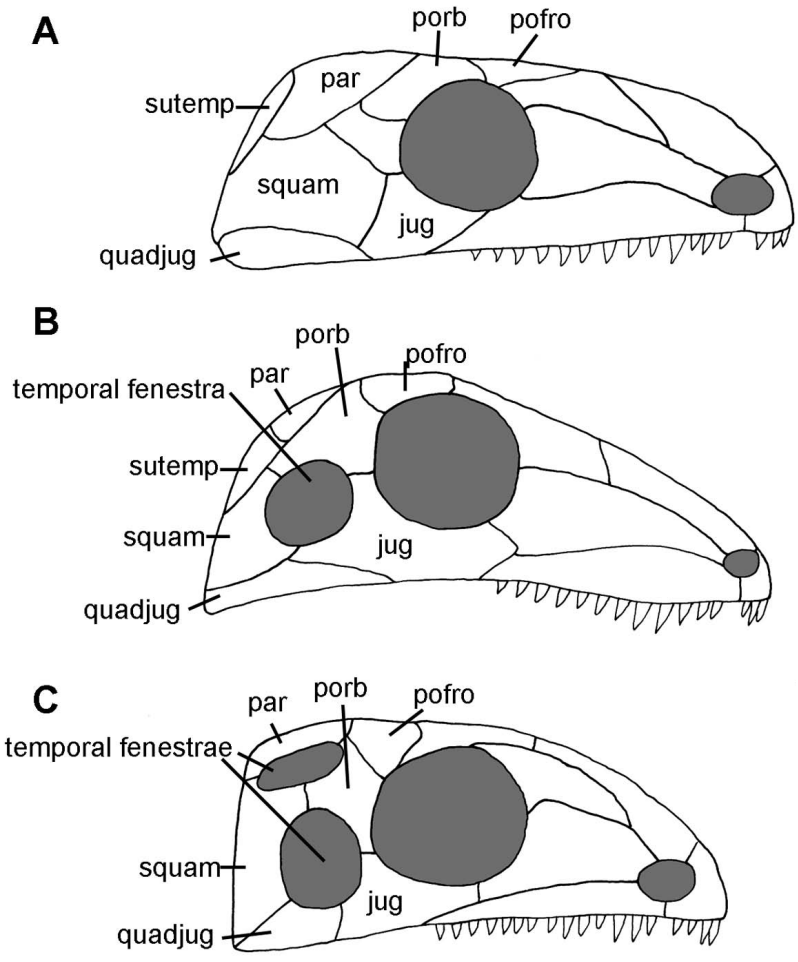
There are two main radiations of nectrideans: the urocordylids and the diplocaulids. The urocordylids, found in Europe and the United States, were Late Carboniferous to Early Permian in age. They are characterized by particularly long, flattened tails and high, narrow, and often long-snouted skulls that showed evidence of kinesis (Fig. 9.34D). The basal articulation was unsutured, and there were narrow interpterygoid vacuities. Limbs were small though always present. *Sauropleura* from the Westphalian of Linton, Ohio, had the most elongate skull, and *Ctenerpeton*, also from Linton, had the deepest tail (Fig. 9.35A).

The most primitive of the diplocaulids appears to be *Scincosaurus*, from the Westphalian of the Czech Republic and Early Permian of France. *Scincosaurus* is a small terrestrial form with a short, broad skull that had no tabular horn (Fig. 9.34C), a short vertebral column, and a robustly ossified postcranial skeleton. Unlike other nectrideans, the caudal vertebrae do not have expanded hemal arches. They do share some features of the tail with other nectrideans but are in many respects far different from other nectridean taxa (Milner and Ruta 2009). The other diplocaulids were perhaps the most bizarre of all Paleozoic tetrapods and have earned the name "hammerhead salamander." Nectrideans apart from scinosaurids elaborated the temporal region of the skull into horns or prongs, but in the totally aquatic Early Permian diplocaulids from the United States, this was taken to extremes (Fig. 9.34A, B). The corners of the skull were drawn back to an exaggerated degree, so that the skull formed a boomerang shape. One suggestion for the function of this shape was that it provided a hydrofoil section to the skull, providing lift for the animal as it attempted to lunge upward from the bottom of the stream or river where it lived to capture prey passing overhead (Cruickshank and Skews 1980). Trace fossils of nectridean resting places have shown that the corners of the skull were attached by sheets of skin to the body, which left the legs free (Fig. 9.34A). The function of the skin flap is not known (Walter and Wernerberg 1988).

For at least one species of nectridean, *Diplocaulus magnicornis*, there is a well-documented growth series showing how the "horns" change shape and orientation at a certain size of animal. This may indicate a period of metamorphosis or a change of lifestyle. From the subsequent growth pattern, it is possible to suggest that these nectrideans kept on growing, rather than reaching a determinate size (Olson 1951; Rinehart and Lucas 2001). For other lepospondyls, such as microsaurs, it seems clear that growth was determinate—in other words, the adults reached a final size and stopped growing—because for these animals, only small representatives have ever been found.

## The Earliest Known Amniotes and the Beginnings of Modern Amniote Groups

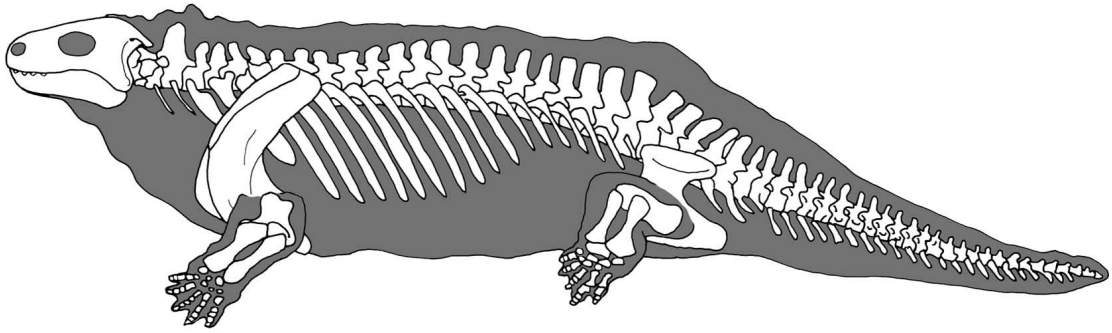
It is during the Westphalian that the first remains of animals that can be called reptiles with any degree of confidence are found—that is, basal members of the amniote radiation. (Note that the term "reptile" has recently been used in a cladistic sense to mean all amniotes other than the synapsid/mammal lineage, and including birds. In popular usage, it has meant amniotes that are neither mammals nor birds.) These animals share a number of osteological characters with each other and with modern amniotes that have been used as the basis for their classification, but whether they shared the physiological characters of the egg that the name "amniote" implies can never be established from fossils. The word is derived from the amnion, one of the three membranes that surround the egg




**9.36.** Amniote skull types. (A) Primitive type with no temporal fenestrae ("anapsid") as in *Captorhinus*. (B) Single temporal fenestra (synapsid) as in *Archaeothyris* (mammalian lineage). (C) Two temporal fenestrae (diapsid) as in *Petrolacosaurus*.

of an amniote, whether the egg is shelled like those of crocodiles, turtles, or birds, or not, as in most mammals. It is unlikely that their reproductive physiology will ever be known—for example, whether some of them retained reproductive life histories like seymouriamorphs, or whether some of them used mammallike egg retention. The best assessments of phylogeny of some of these entirely extinct groups must rely on skeletal characters, and integrating these studies with those from living forms has produced controversial results over the last many decades.

Amniotes can be divided into three main supergroups on the basis of the construction of the cheek region. The primitive condition is called anapsid because the cheek region is a platelike structure in which there are no holes in the side of the head. (The "aps" in anapsid actually refers to the arches bounding the holes rather than the holes themselves.) Figure 9.36 illustrates this kind of skull structure. This condition is that found in earlier tetrapods and is primitive, so it cannot be used to support any phylogenetic relationship between the animals possessing it. The synapsids, to which the mammals belong, had a single hole in the cheek, though it has become much modified during subsequent evolution of the



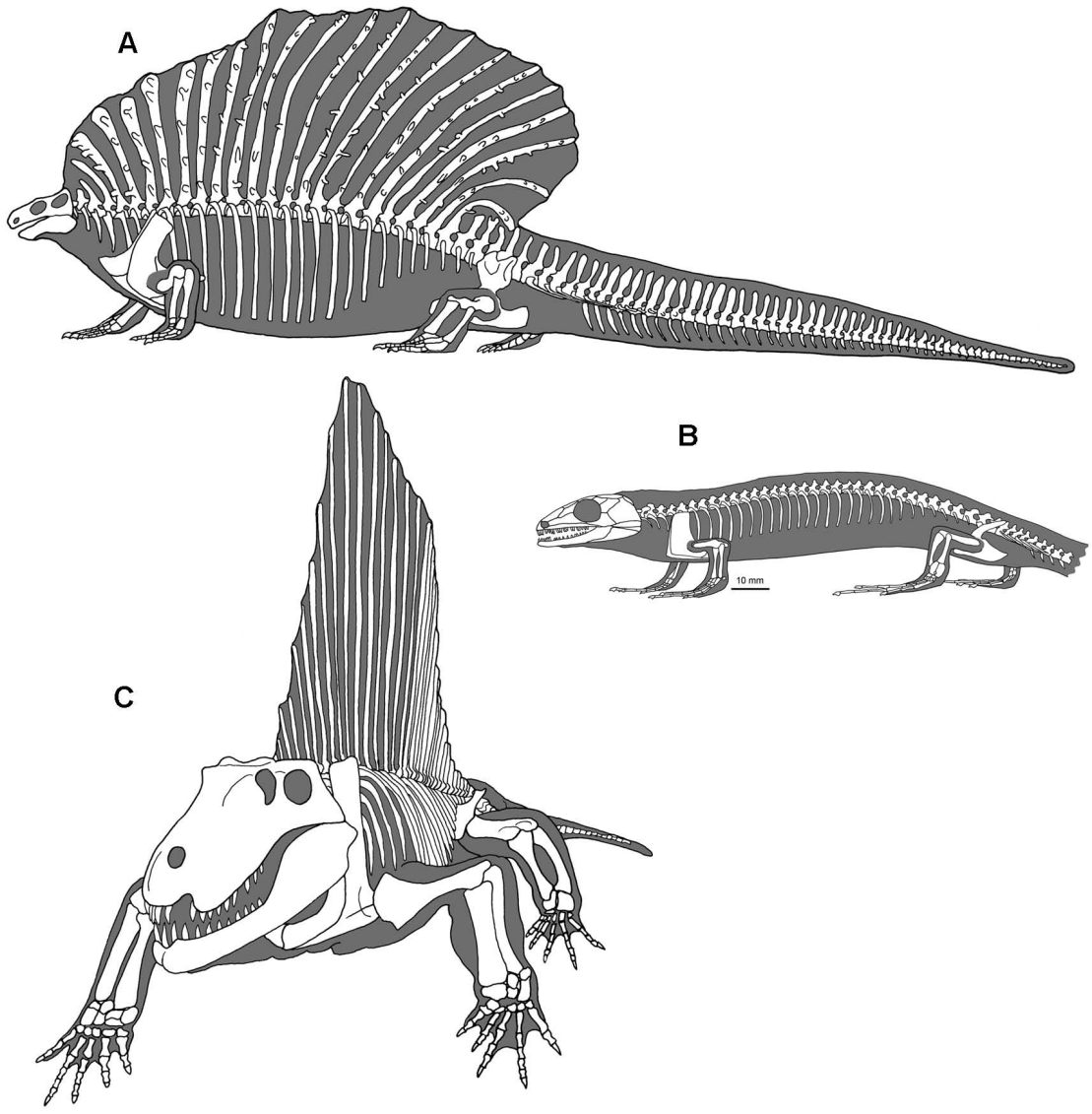
**9.37.** Drawing of skeletal reconstruction of *Diadectes. Based on Case (1907).* Animal is up to 2 meters long.

group. The diapsids, to which lizards and snakes, crocodiles, and birds belong, had two holes in the cheek.

Among Paleozoic tetrapods are a number of other entirely extinct forms that are not closely related to any modern survivors and that are probably basal to all amniotes. These include the large Permo-Carboniferous diadectomorphs (Fig. 9.37) (Case 1907). *Diadectes* is quite well known from the Early Permian of the United States. The relationships of diadectomorphs to other amniotes remain controversial, and some analyses have suggested a link with synapsids (Berman et al. 1992; Berman 2000) on the basis of characters of the occiput. By contrast, other studies have suggested that they are either the sister group to amniotes (Laurin and Reisz 1995), or are the most primitive amniotes, based on inferences with respect to physiology (Lee and Spencer 1997). Recently, the ankle construction of some diadectids has been shown to incorporate a large bone equivalent in position to the amniote astragalus. Other diadectomorph families retain the three separate bones in this position that are typically found in nonamniotes, whereas in diadectids the fusion of these bones can be traced. This shows conclusively that the amniote astragalus is formed of three bones (Berman and Henrici 2003), and it also corroborates the close relationship between diadectomorphs and amniotes.

The large, clumsy-looking diadectomorphs appear to have been one of the first tetrapod groups to have succeeded in adopting herbivory. Their barrel-shaped bodies and grinding teeth speak of the ability to process and digest large volumes of fibrous, poorly nutritious plant food. Like the other major amniote groups, the earliest member evolved in the Late Carboniferous. However, the most primitive diadectomorph, *Orobates*, is Early Permian in age and comes from the Bromacker Quarry (Berman et al. 2004). The group did not outlast the Permian.

The earliest representatives of synapsids and diapsids can both be traced to the Westphalian, and there is little controversy over the respective lineages of most modern groups. However, turtles are an exception to this, and which group forms their closest relatives is controversial. One idea in the past saw them as derived from a group called captorhinids (Gaffney 1980) at a time when this group was placed among the anapsids. Others have seen turtles as belonging to a separate lineage known as parareptiles with some extinct groups called procolophonids and pareiasaurs




(Lee 1995, 1997; Reisz and Laurin 1991; Fraser 1991). These all have the anapsid skull construction. Some molecular studies have suggested that they could be highly modified diapsids (Rieppel and DeBraga 1996; Iwabe et al. 2004), although a study based on embryology placed them as basal to diapsids (Wernerberg and Sanchez-Villagra 2009).

*Hylonomus* is generally considered to be one of the earliest animals in the fossil record to be a true amniote. It is one of the creatures found in the Joggins tree stumps, making it Westphalian A in age (Carroll 1964a). It was more advanced in its terrestrial features than *Casineria* (see Chapter 7), for example in having an even more gracile humerus, and unlike *Casineria*, its skull is well known. It was a small, lightly built animal, rather lizardlike in form, and it is one of several similar genera, such as *Paleothyris* (Fig. 9.38B), that appear at about this time or only a little

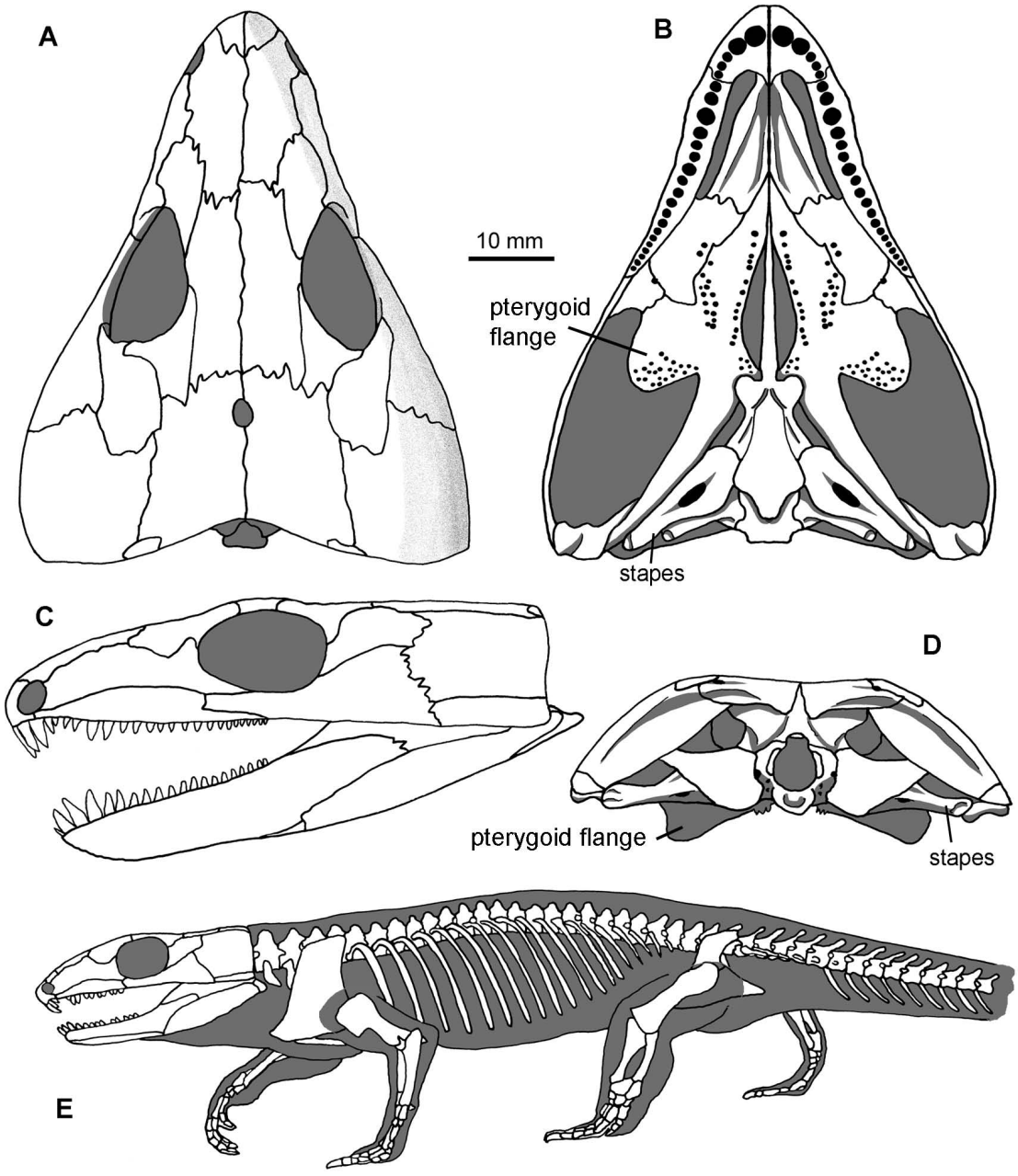
**9.38.** Skeletal reconstructions of early amniotes. (A) The herbivorous synapsid *Edaphosaurus,* from the Early Permian of Texas. Skeleton 3.26 meters long as reconstructed. *Based on Romer and Price (1940).* (B) The early amniote *Paleothyris* from the Late Carboniferous of Nova Scotia. *Based on Carroll (1969b).* (C) The carnivorous synapsid *Dimetrodon,* from the Early Permian of Texas. Skeleton is about 3 meters long.

later. They all had the anapsid type of skull. However, only a little later than *Hylonomus*, two forms appear that are superficially similar to it in skull shape and body form. One of them, *Archaeothyris*, has a single hole piercing the side of the cheek (Reisz 1972, 1975, 1986). This is one of the earliest members of the synapsids whose Triassic descendants produced the mammals, and the other is *Petrolacosaurus*, which had two holes (Reisz 1977). This is the earliest known form with a diapsid type of skull, and its descendants include not only modern lizards, snakes, crocodiles, birds, and perhaps turtles, but also the dinosaurs, the pterosaurs, and a wealth of early diapsid amniotes that dominated the tetrapod faunas of the land and sea throughout the Mesozoic.

Despite the early appearance of these fossils, cladistic analyses have suggested that they are not particularly primitive members of their respective clades. *Hylonomus*, for example, seems to sit more crownward than captorhinids as a stem diapsid in the Eureptilia, though it falls below *Petrolacosaurus* (Müller and Reisz 2006). Furthermore, though early, *Archaeothyris* is not considered to be the most basal synapsid (Sumida and Modesto 2001).

Some morphological characters unite all the Paleozoic amniote forms, though some of these characters may be paralleled in other non-amniote groups, such as the microsaurs. Some of these are exemplified by the Permian amniote *Captorhinus*, which, though anapsid, is now thought to be quite closely related to diapsids (Laurin and Reisz 1995). The most conspicuous skeletal feature of many amniotes is a flange of the ptergoid that is turned downward into the back of the throat and frequently bears a suite of teeth. The upper surface of this pterygoid flange is thought to have provided an attachment point for the pterygoideus muscle that closes the jaw (Fig. 9.39) (see Chapter 10). Early amniotes were exclusively carnivorous or insectivorous feeders on land, and a powerful bite required a reconfiguration of the mouth and jaws to facilitate this action. At the back of the skull, the skull table was reduced until first the postparietals and then the supratemporals and tabulars became small bones exposed mainly on the occipital surface of the skull. A midline ossification of the braincase called the supraoccipital developed. The cheek outline was smooth, with no hint of an otic notch, and the stapes, rather than being a slender upwardly directed rod, was a stout downwardly or horizontally directed strut, running between the braincase and the quadrate (Fig. 9.39). It appears that early amniotes did not have any form of specialized ear for terrestrial hearing, unlike the temnospondyls or seymouriamorphs.

In contrast to the paired exoccipital condyles of temnospondyls, amniotes had a convex condyle formed by the basioccipital (see Fig. 10.6), which attached to a specialized atlas–axis vertebra, similar to but different from that of microsaurs. In the postcranial skeleton, the most conspicuous amniote invention was found in the ankle, where three of the small tarsal bones fused into a single structure called the astragalus. This is presumably correlated with increasing facility for terrestrial locomotion. Associated with these adaptations, the limbs are gracile and slender, and




they have the muscle attachment points close to the joints. Gone is the flattened, L-shaped humerus of early tetrapods, replaced with something that looks much more like the humerus of a modern amniote. The vertebrae have cylindrical pleurocentra, firmly attached or sometimes fused to the neural arches; the intercentra are small; and the ribs are long and slender, and encompass most of the abdomen.

Ideas about the origin of amniotes have been widely discussed for many years. Some have focused on the origin of the amniote egg (e.g.,

**9.39.** Drawings of skull and skeleton of *Captorhinus*.
(A) Skull in dorsal view.
(B) Skull in ventral view.
(C) Skull in left lateral view.
(D) Skull in posterior view.
(E) Skeletal reconstruction.
*(A–D) Based on Heaton (1979).*
(E) *Based on information in Fox and Bowman (1966).*

Packard and Seymour 1997; Skulan 2000; Elinson and Beckham 2002), some on amniote locomotion (e.g., Sumida and Modesto 2001), and some on skull structure and the origin of herbivory. In the past, scenarios were based on the precept that small amniotes such as *Captorhinus*, or *Hylonomys* from Joggins and *Paleothryis* from Florence, Nova Scotia, represented the primitive amniote morphology. At the same time, small terrestrial anthracosaurs such as *Gephyrostegus* were envisaged to be the "ancestors" of reptiles (Carroll 1970). More recently, as discussed above, the suggestion has been that the large diadectomorphs are the amniotes' closest relatives. Connected with this, the idea has been put forward that herbivory, as seen in diadectomorphs, may have been a significant factor in the origin of amniotes (Reisz 1997).

It was not until the Late Carboniferous that skeletal adaptations for full herbivory appeared in tetrapods, though plant material could have formed part of the diet of earlier forms (Hotton et al. 1997). One of the first amniote groups to produce herbivorous forms was the synapsid lineage, and *Edaphosaurus* developed a battery of grinding teeth on the lower jaws and palate. It has been suggested that herbivory could not be evolved easily among tetrapods until parental care in the form of feeding allowed the gut flora necessary to digest plant food to be passed directly from adult to young (Modesto 1992). Another suggestion is that each of the several lineages of amniote to have evolved herbivory seems to have arisen from insectivorous ancestors, and the required symbiotic gut flora for cellulose digestion could have been picked up during this phase (Sues and Reisz 1998). *Edaphosaurus* and some of the other Early Permian synapsids such as *Dimetrodon* carried elongated neural spines on their backs (Fig. 9.38 A, C). It is thought that these supported a fin of skin, whose function is most plausibly explained as a radiator for collecting or dissipating heat from the sun. This may be the first skeletal indication of thermal regulation in the lineage that eventually led to the internally heated mammals.

By the Early Permian, many new forms of amniote had evolved, including the small procolophonids and large cowlike pareiasaurs and small lizardlike millerettids. All these forms are thought to belong to the group of amniotes known as parareptiles, and they seem to be mainly a Gondwanan radiation (Modesto 1999, 2000), though they later spread northward as far as Russia. One highly specialized member of the parareptiles is *Eudibamus*, from the Bromacker Quarry in Germany. It shows the first evidence of a bipedal form of locomotion in a parasagittal as opposed to an undulatory gait. It belongs to a family called the bolosaurids, known from throughout the Laurussian continent, including the United States, Russia, and China (Berman et al. 2000).

At the base of this parareptile clade are the earliest marine amniotes, the mesosaurs (Fig. 9.4). *Mesosaurus* and its relatives were small forms with flattened skulls and elongate rostra that bore a large number of long, slender teeth. They seem to have been adapted for capturing small shrimplike prey (Modesto 1999, 2006). The term "Anapsida" has recently

been used to encompass a monophyletic grouping of mesosaurs and parareptiles (Sumida and Modesto 2001).

Small amniotes such as *Captorhinus* as well as the parareptiles were common worldwide during the Early Permian, and the diapsids had diversified into a wide range of forms. They even produced strange forms with elongate bony struts sprouting from the trunk that supported flaps of skin on which they could glide (Evans and Haubold 1987). By the end of the Permian, many of the amniote innovations had evolved and the foundations laid for the subsequent history of the group.

At the end of the Permian, however, some disaster struck the Earth, and 95% of its fauna was wiped out. The end-Permian extinction event may not have been a single event, nor caused by a single phenomenon, but it nevertheless produced the most catastrophic series of extinctions in Earth's history, apparently within half a million years. The most recent ideas of the causes of this extinction are summarized in Benton (2003), Erwin (2006) and Erwin et al. (2002) and include evidence for anoxic conditions in both shallow and deep waters, massive eruptions of flood basalts in Siberia, and global warming at the end of the Permian. Some evidence also suggests a possible asteroid impact that might have contributed, though this is less likely. As far as the tetrapods are concerned, most of the temnospondyls, most of the anthracosaurs, all of the lepospondyls, and many of the stranger forms of amniote disappeared during this event. The tetrapods reradiated after the event from the few surviving families. In the case of the amniotes, they evolved with new vigor and by the end of the Triassic had produced many of the lineages whose legacy is familiar today. But that is part of another story.

## Phylogeny of Paleozoic Tetrapods

### The Interrelationships of Paleozoic Tetrapods and the Origins of the Modern Tetrapod Groups

Ideas about the interrelationships of early tetrapods have changed significantly over the last 20 years or so, largely as a result of the advent of cladistic analysis and more rigorous assessments of primitive versus derived characters. Up to about the early 1980s, most people accepted that almost all early tetrapods (or fossil amphibians, as they would have been more commonly called) fell into one of two large groups formalized and made popular by A. S. Romer: labyrinthodonts and lepospondyls. The scheme became widely known not only among paleontologists, but also among scientists remotely interested in any aspect of vertebrate evolution. It is worth discussing this classification because it still persists and has influenced ideas about many issues in the subject.

The term "labyrinthodont" derives from the structure of the teeth found in many early tetrapods, in which the enamel of the tooth crown has a complex folded appearance in cross section. It was first applied to the group that is now known as temnospondyls, because temnospondyls were among the first fossil amphibians to be found and recognized. Later, more creatures were discovered with this tooth structure, and they were also placed in the group. They included the animals now

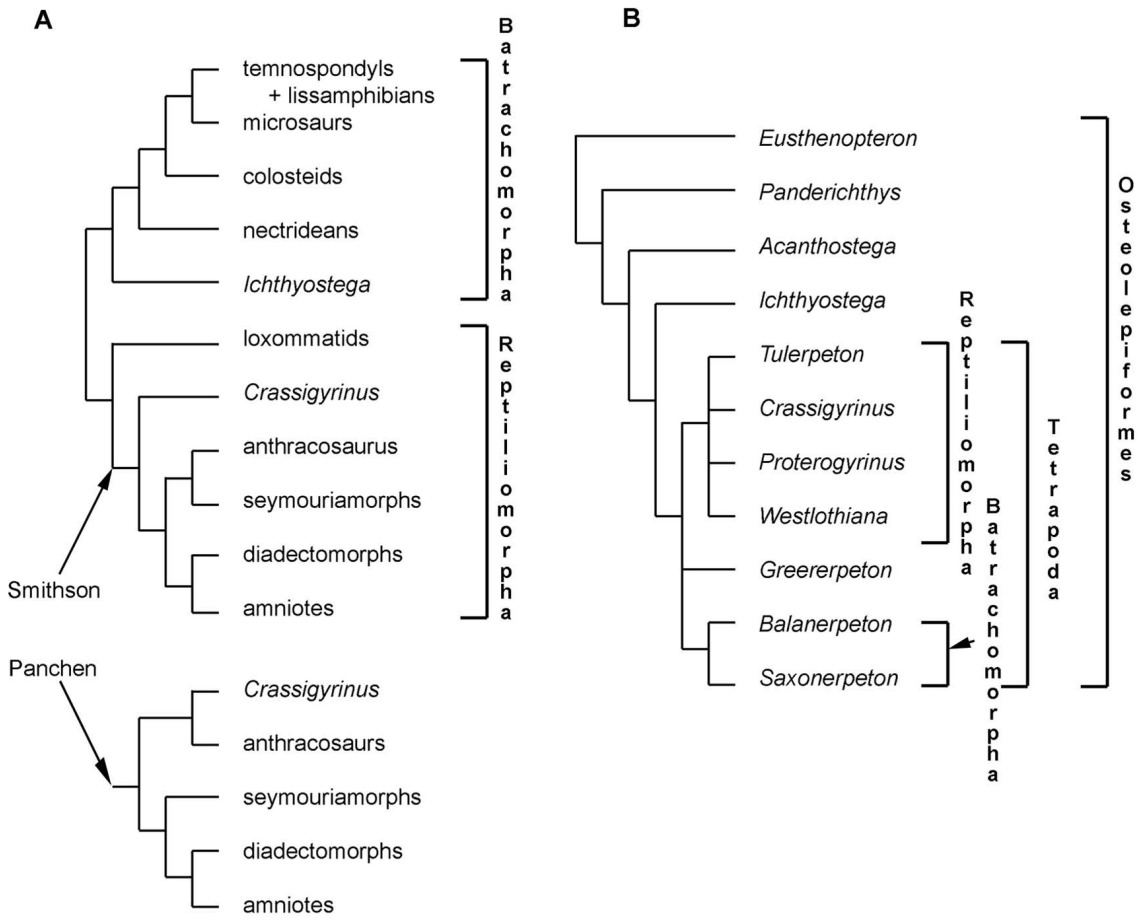
called anthracosaurs, colosteids, baphetids, and the problematic genera *Crassigyrinus* and *Ichthyostega*. As well as tooth structure, these animals also shared characters such as having multiple parts to their vertebral centra, and skull roofs with ornamented bone, of a fairly standard bone complement showing no openings other than those for the eyes, nostrils, and parietal organ, usually with lateral lines carried in open grooves, and often with heavily ossified braincases. Most of them also had closed palates covered with denticles, though it was recognized that temnospondyls were distinguished by their large palatal vacuities. Most of these creatures were relatively large—desktop sized, so to speak (Romer 1947, 1966).

The lepospondyls were distinguished first by their type of vertebral centra, which were usually formed of solid, spool shaped centra that lacked any of the separate elements seen in the labyrinthodonts. None of them had labyrinthodont teeth, and most of them were relatively small—laptop sized by comparison. The group included microsaurs (when these were eventually separated from early amniotes), aïstopods, nectrideans, adelogyrinids, and lysorophids. Skull construction was rather different in each of the groups because each appeared to lack one or more of the standard complement of bones found in labyrinthodonts (Romer 1966).

With the advent of cladistic analysis, it became obvious that at least the labyrinthodonts were united only by characters that were primitive for tetrapods, most of which were found also in the stem lineage, such as the fish *Eusthenopteron*. This was as true of the tooth structure as it was of the vertebral and palatal construction, though the skull roof pattern among the labyrinthodonts showed consistent differences from the fish, which created difficulties of homology between the two groups (as mentioned in Chapter 6). The skull roof pattern is now seen to distinguish tetrapods, but it does not serve to define a subgroup within tetrapods. The distinction between labyrinthodonts and lepospondyls might almost be thought of as one of size. Differences in the vertebral construction now seem to be less marked because some microsaurs are now known to have intercentra in the vertebrae (Carroll and Gaskill 1978).

As ideas about early tetrapod classification have changed, so it has become more obvious that lumping all the large forms together under the same collective title has camouflaged important differences between the individual groups. The danger lies in assuming that members were basically all the same in aspects of their anatomy and biology, which now seems not to be the case at all. A case in point will be discussed in Chapter 10.

One of the first people to try to place the classification of early tetrapods on a cladistic footing was Gaffney (1979) in a critique of scenario-driven taxonomy. He evidently realized the artificiality of the "labyrinthodonts" and does not even use the word. Smithson (1982) gave another early precomputer attempt at a cladistic analysis. He looked at the construction of the occiput and noted that temnospondyls and microsaurs shared an apparently derived feature in which the exoccipital bones became important, and were the main bones to tie the back of the

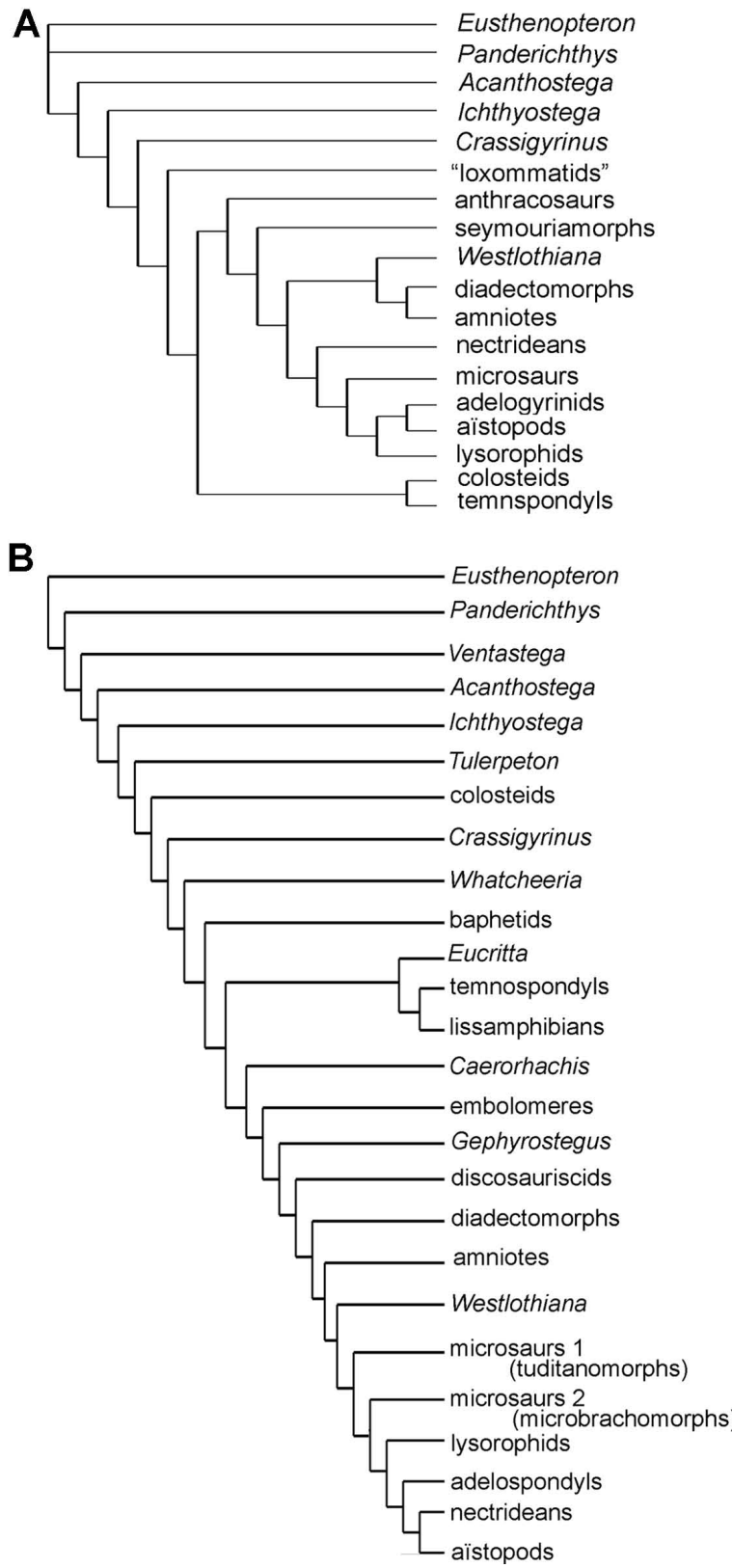



**9.40.** (A) *Cladograms from Panchen and Smithson (1988)*, showing the two authors' alternative groupings of the reptiliomorphs. (B) *Cladogram from Lebedev and Coates (1995)*, showing the division into reptiliomorphs and batrachomorphs.

braincase to the skull roof. In most other tetrapods, the exoccipitals were small, and the opisthotics, part of the otic capsules, provided this anchorage. This led him to separate the microsaurs from the other lepospondyls and place them in a clade with the temnospondyls and the colosteids. Thus, labyrinthodonts and lepospondyls became paraphyletic groups. He distinguished two lineages, with the temnospondyls, colosteids, and microsaurs sharing their occipital construction with modern amphibians and being part of a batrachomorph lineage, while anthracosaurs were placed with seymouriamorphs into a reptiliomorph lineage along with amniotes. In this lineage, the occipital construction was essentially primitive, but the members shared features of the vertebral column (Smithson 1985b). These conclusions were corroborated by a follow-up study by Panchen and Smithson (Fig. 9.40A), though in this paper, even the two coauthors could not agree on the details of interrelationships within the reptiliomorph lineage (Panchen and Smithson 1988).

In the years that followed, further cladistic analyses were carried out after the discovery of new genera, especially from the Late Devonian. Lebedev and Coates (1995) attempted a large-scale computer-assisted analysis, and they corroborated part of Smithson's scheme by showing a

**9.41.** (A) *Cladogram from Carroll (1995)*, one of the first large-scale cladistic analyses to include "lepospondyls." (B) *Cladogram from Ruta et al. (2003).*



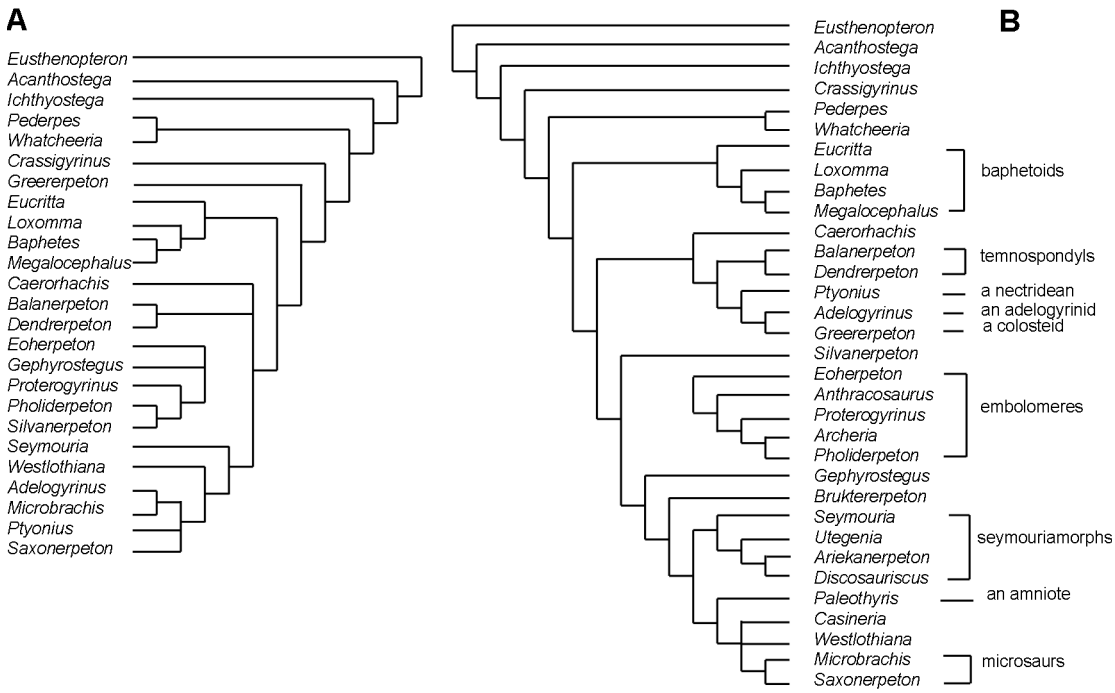
dichotomy between the reptiliomorph and batrachomorph lineages (Fig. 9.40B). They suggested that the split between these groups occurred in the Late Devonian and that *Tulerpeton* was the earliest known member of the reptiliomorph clade. That leads to the inference that modern amphibians and amniotes belong to separate lineages going back to the Late Devonian. Lebedev and Coates also showed that genera such as *Acanthostega* and *Ichthyostega* were stem tetrapods and had no especially close relationship either to each other or to the Carboniferous forms, other than the general one of being tetrapods. Like Smithson, they found that *Greererpeton* and the microsaurs grouped with temnospondyls. Their conclusion was reinforced in Coates's later work (1996) on the postcranial skeleton of *Acanthostega* (Fig. 9.40B), but only one, not particularly primitive, lepospondyl was included in the analysis.

A large-scale cladistic analysis was performed by Carroll in 1995, in which a wide range of taxa and a large number of characters were included (Fig. 9.41A). One of the main findings of this study was the reestablishment of the clade known as lepospondyls because they did appear to share many derived characters that united them into a monophyletic clade. The study placed the lepospondyls as the sister group to amniotes, with seymouriamorphs and anthracosaurs as successively more primitive taxa on that branch of the cladogram. As in Smithson's analysis, colosteids grouped with temnospondyls.

A larger cladistic analysis was performed by Laurin and Reisz, based on Carroll's 1995 scheme, but including modern forms alongside fossil ones. It produced controversial results that broke away from more traditionally accepted groupings, especially with respect to the origin, or origins, of modern amphibians (Laurin and Reisz 1997; Laurin 1998). Some of these results have been corroborated by subsequent work, though others have not. Particularly controversial was the conclusion that the elongate lepospondyl lysorophians were the sister group to all modern amphibians. It emerged that the majority of characters supporting this grouping were characters involving loss of features, rather than possession of uniquely shared morphological traits.

Since these controversial ideas were put forward, further cladistic analyses that incorporated further taxa and more data have reconfirmed more traditional ideas; for example, Ruta et al. (2003) (Fig. 9.41B) used a massive database of 90 taxa and 319 characters. This database has subsequently been refined and subjected to several tests that have corroborated its original findings. It reestablished the relationship between temnospondyls and modern amphibians, and the implications of that have been found and corroborated by recent detailed studies of several temnospondyl and lepospondyl groups (Anderson 2001, 2007).

A study to investigate the position of *Casineria* by Paton et al. (1999) also suggested a stem-group position for anthracosaurs, and like Carroll's analysis, it placed microsaurs alongside amniotes and seymouriamorphs. This study placed *Westlothiana* alongside the amniotes, but new studies may well suggest a rather different position, possibly among the microsaurs.

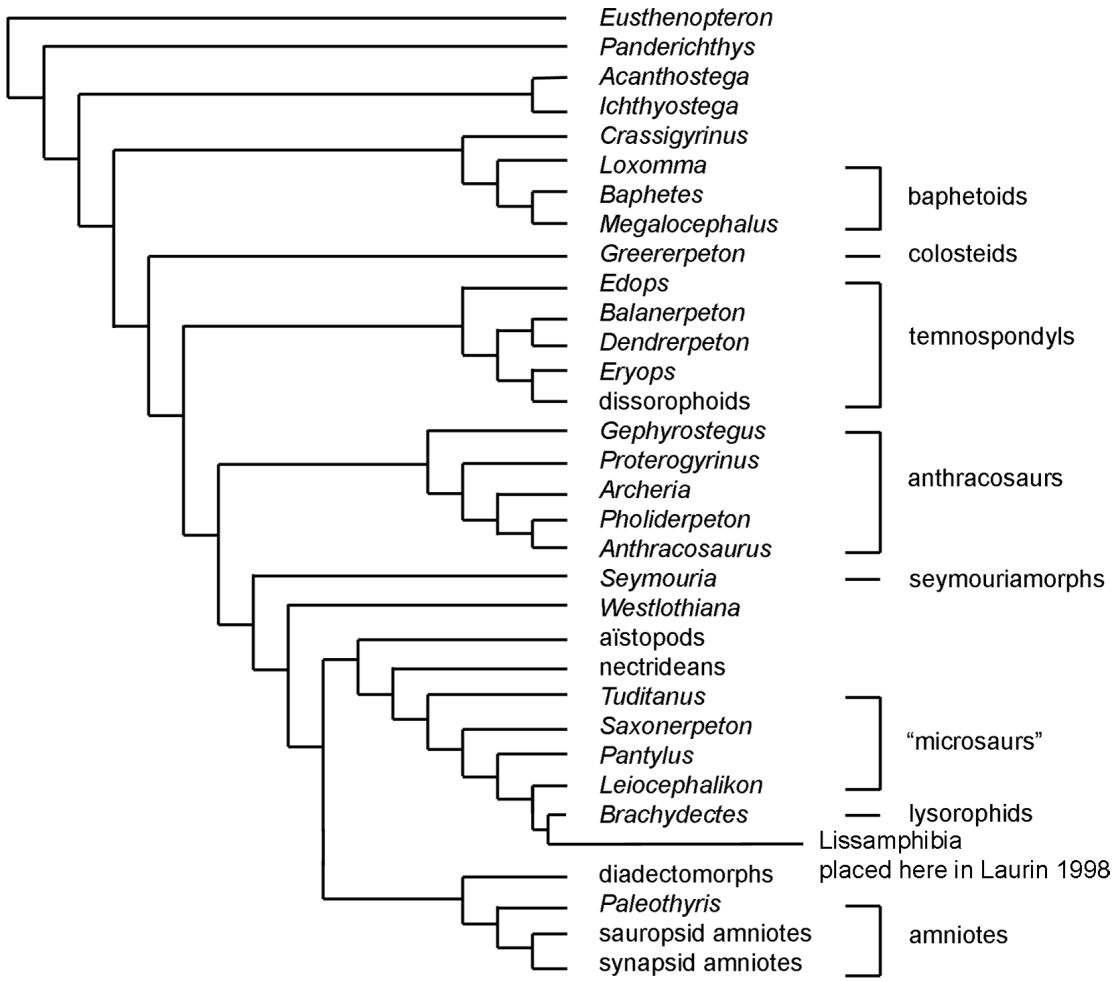



**9.42.** (A) *Cladogram from Clack and Finney (2005).* (B) *Cladogram from Ruta and Clack (2006).*

In a series of analyses to work out the relationships of genera such as *Crassigyrinus*, *Eucritta*, and *Pederpes*, Clack (1998a, 1998b, 2001a, 2002b; Clack and Finney 2005) performed analyses of most of the better known early tetrapod groups, though these analyses either excluded lepospondyls and early amniote taxa, or included only a few of them. This is because it was considered that the lepospondyls and amniotes would probably not affect the more basal parts of the cladogram that were the main focus of interest. In these studies, *Acanthostega* consistently appeared as the most primitive tetrapod, with *Ichthyostega* as more derived. In the analyses that tested the position of *Pederpes*, the whatcheeriids appeared as the next most basal taxon, with *Crassigyrinus* next. Anthracosaurs appeared as a monophyletic group, and *Westlothiana* and the microsaurs likewise (Fig. 9.42A).

In an attempt to test the position of *Silvanerpeton* among the anthracosaurs, Ruta and Clack (2006) built a new matrix by combining characters from Clack (2002b) and Ruta et al. (2003). They reduced the number of taxa from Ruta et al. (2003) to those that were used by Clack (2002b) and added the taxa that were used in those analyses by Clack (2002b) but not by Ruta et al. (2003) (Fig. 9.42B). This data set was further augmented later by the addition of *Chroniosaurus* (Clack and Klembara 2009). Both *Silvanerpeton* and *Chroniosaurus* fell close to the embolomeres, though *Silvanerpeton* did not form a clade with them.

The debate continues, with other studies by Laurin and colleagues (Laurin 2004; Marjanovic and Laurin 2008) continuing to recover a relationship between lissamphibians and lepospondyls rather than




**9.43.** *Cladogram from Laurin (2004).* The lissampibians are placed in the position found by Laurin (1998).

temnospondyls, and no relationship between amniotes and anthracosaurs (Fig. 9.43).

In recent years, studies based on the analysis of metadata—cladograms derived from databases of characters and taxa—have been increasingly common. Topics such as diversity and disparity curves of tetrapods through the Paleozoic, geometric morphometrics of skull shape, and distribution of body sizes among clades, have been worked on. Some interesting and sometimes controversial conclusions have been reached. The problem with such analyses, it seems to me, is that the researchers producing their analyses use their own databases, basing what can be rather profound conclusions on them. In addition, these databases can only include characters that are amenable to cladistic analysis. Subtleties of shape, size, or ontogeny are not easily or unambiguously factored into them, and thus potentially biologically important features are missed. The fact that alternative databases produce in some instances radically different cladograms suggests that such metadata studies are inherently unreliable.

One reaction to the problem of conflicting cladograms is to search more taxa for more characters, and to divide or "atomize" characters into increasingly detailed parts. A danger of this procedure is that the existence of related or correlated characters, those that are necessarily found together, is neglected. The influence of their individual parts is overemphasized while the significance of their relatedness is overlooked. Thus, the results are skewed one way or another.

In Chapter 10, the phylogeny that will be used is that which unites temnospondyls with frogs and salamanders, and places anthracosaurs on the stem of amniotes. The implications of alternative phylogenies will be considered where appropriate, but in many instances, the conclusions are unaffected by which phylogeny is chosen. In describing the evolution of tetrapods from fish and the subsequent acquisition of terrestriality, certain events perforce must have taken place. A well-founded phylogeny can help to show when these changes might have occurred, in what order, or how many times, but the fact of their occurrence can be inferred even without a phylogeny. In fact, the phylogeny of early tetrapods is still uncertain and controversial, so that the ideal of showing when and how often certain changes took place is still a long way off.

## Origin of Modern Amphibians

Modern amphibians, or Lissamphibia, are represented by three surviving groups, the anurans (frogs, toads), the urodeles (newts, salamanders), and the caecilians (apodans or gymnophionans). Until the advent of phylogenies based on molecular sequences, it was unclear whether these three formed a monophyletic group, but now it seems most likely that they are all each others' closest relatives. There is still no agreement, despite sequence data, about which group is sister group to which among the modern forms. This can be attributed in part to the fact that there is little consistency among the molecular analyses as to which taxa or which molecules have been used, a similar problem to that seen already in investigating the closest relatives of tetrapods as a whole. This uncertainty adds to the complexity of the problem of evaluating the evidence from fossil forms (Lee and Anderson 2006; Ruta and Coates 2007), whereas a definite answer from molecular studies could help choose between competing hypotheses based on fossil or morphological evidence.

The earliest fossil record of any animals that can be associated with any of the lissamphibian groups are dated as Early Triassic. *Triadobatrachus* is a protofrog from Madagascar known from a single specimen preserved in a nodule, and *Czatkobatrachus*, only slightly younger, is represented by isolated remains from Poland (Rage and Rocek 1989; Evans and Borsuk-Bialynicka 1998). The earliest salamander and caecilian are both Middle Jurassic in age: respectively, isolated salamander remains from England (Evans et al. 1988; Milner 2000) and *Eocaecilia* from the United States (Jenkins and Walsh 1993; Jenkins et al. 2007). The latter is notable for being the only caecilian with legs. The Late Jurassic

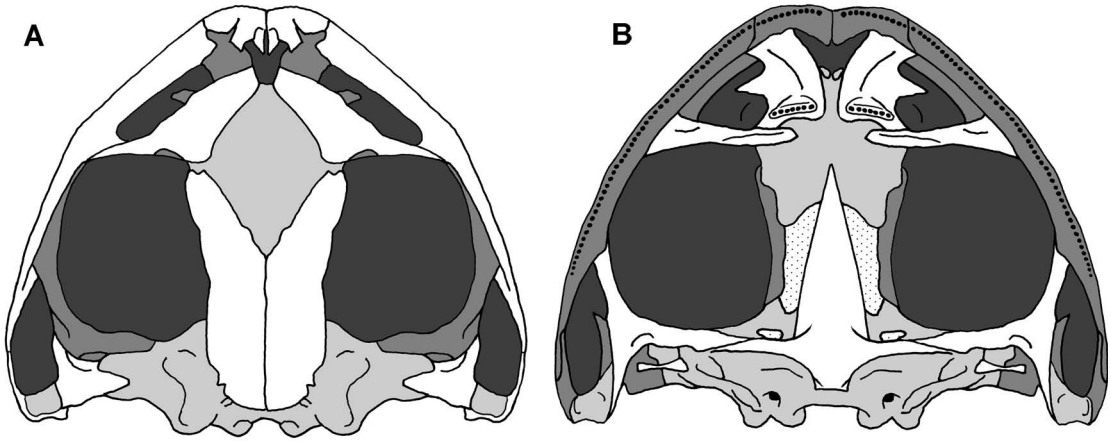
salamander *Karaurus* (pronounced as four syllables, "Kara" and "yurus," meaning "urodele from Kara") from Kazakhstan (Ivachnenko 1978) is the earliest known from more or less complete remains.

Since the amniote lineage is known to have appeared by at least the Late Carboniferous and is monophyletic to the exclusion of lissamphibians, it can be inferred that the lineage leading to lissamphibians must also have been distinct by that time. This leaves a long period of evolutionary history of the lissamphibians for which there is no fossil record. This is surprising, given the good fossil record for amniotes throughout that same period, and given the fact that one would expect amphibians to have lived and died in waterside or swamp conditions that would provide a relatively good chance of preservation (Milner 1993b). Part of the problem may reside in the small size of the animals involved, because of which they could have been overlooked in the past. Certainly more clues in the form of tiny broken and disarticulated elements belonging to lissamphibian-like animals are now beginning to come to light. However, because of this dearth of fossils, the origin of lissamphibians remains controversial, and it is now by far the least well documented and understood of any of the major vertebrate evolutionary transitions. Because the origin of lissamphibians must have occurred during the late Paleozoic, it is appropriate to consider some of the issues here.

D. M. S. Watson was one of the first people to point out similarities between frogs and small dissorophoid temnospondyls from the Late Carboniferous, specifying the genus now known as *Amphibamus* (Fig. 9.17) (Watson 1940). Other studies followed in the 1960s, and these too concluded that temnospondyls were the most plausible group to have given rise to frogs (at least) (Parsons and Williams 1963). They also concluded that lissamphibians were a monophyletic group on the basis of a number of apparently unique characters. Unfortunately, most of these are from the creatures' soft anatomy and cannot be verified or refuted by fossils.

Other opinions coexisted with the temnospondyl theory for a monophyletic lissamphibian origin, and these focused on a microsaur ancestry for caecilians, or urodeles, or both. Carroll and Currie (1975) pointed out a number of specific resemblances between one particular microsaur genus and one particular caecilian genus, which are compelling until the hypothesis is considered more widely, whereupon it appears that these similarities do not seem to apply to microsaurs or caecilians in general. The two chosen genera could equally likely resemble each other because of convergent evolution.

Temnospondyls share a number of characters with frogs especially, though some of them are also seen in salamanders and some even in caecilians too. Among the most striking are the large palatal vacuities, particularly well developed in frogs and dissorophoid temnspondyls, and the fact that the occipital condyle in all of them is formed by facets formed only from the exoccipitals (Fig. 9.44). Other general similarities have been noted in recent years, such as the shortness of the ribs in temnospondyls generally, the similarities of the stapes and otic capsule in




**9.44.** (A) Dorsal and (B) ventral view of a frog skull for comparison with that of a branchiosaur such as the dissorophoid *Apateon, Amphibamus,* and *Doleserpeton.* In (A), the bones of the palate are dark shaded; in (B), the bones of the skull roof are dark shaded. In both, braincase elements are light shaded. Cartilage is stippled and vacuities are shown in black.

temnospondyls and dissorophoids, the fact that some dissorophoids (such as *Amphibamus* and its close relative, *Platyrhinops*, Fig. 9.18) have the shortest vertebral columns of any tetrapods except frogs. Dissorophoids also include some families, the branchiosaurs, that show tadpolelike larvae and evidence of pedomorphosis in their development. Similarities in lifestyles and physiology between some dissorophoids and lissamphibians do not seem improbable, such as their mode of buccal pumping, their metamorphic life histories, and the prevalence of heterochrony in their ontogeny. This hypothesis was put on a more formal cladistic footing by studies such as those by Milner (1988, 1993b) and Trueb and Cloutier (1991), who showed a nested series of forms in which the attributes of lissamphibians are progressively acquired.

These early cladistic analyses that suggested temnospondyl affinities for lissamphibians were all based on a few selected characters, before the advent of computer-generated cladistic studies. Furthermore, they were all less than comprehensive in at least one important way. All omitted any lepospondyl groups. Subsequently, a series of studies has included not only lepospondyls but also representatives of most early tetrapod groups and some extant representatives of both lissamphibians and amniotes. Carroll's treatment in 1995 has been mentioned above, with his reestablishment of the lepospondyls as monophyletic. This was used as the basis of another study that added the living groups into the equation. Initiated by Laurin and Reisz (1997), their results were in many ways surprising. As described above, they found that lepospondyls, though monophyletic, were in fact the sister group to lissamphibians, and that amniotes were sister to that clade. Temnospondyls, they suggested, had no connection with lissamphibians, being an early offshoot from the tetrapod stem, and furthermore, anthracosaurs were not closely related to amniotes.

These results are intriguing but remain contentious, and they have been heavily criticized (e.g., Ruta et al. 2003; Ruta and Coates 2007; Schoch and Milner 2004). Despite the apparent rigor of the cladistic analysis that produced them, among the problems is that their cladogram implies that not only a large number of characters might be convergent

between lissamphibians and temnospondyls, such as those connected with breathing and hearing, but also that there are no positive characters that unite them: all of the uniting characters are losses of feature. This is true even of the most recent reworkings of the matrix (e.g., Vallin and Laurin 2004; Marjanovic and Laurin 2008). Most of the members of this lepospondyl–lissamphibian clade are small animals that show characters associated with miniaturization, and with forms so widely separated in time, even cladistics is hard put to distinguish resemblances on the basis of relationship from those resulting from convergent evolution (see Chapter 3).

In the last few years, much new data and several major analyses and reviews have dealt with this subject (Anderson 2001, 2007; Anderson et al. 2008a, 2008b; Carroll 2004, 2007, 2009; R. L. Carroll et al. 2004; Ruta et al. 2003; Ruta and Coates 2007; Schoch 2002b; Schoch and Carroll 2003; Schoch and Milner 2004), and though some consensus may be beginning to emerge, it is likely to be fragile. There is still much debate actively taking place.

Most of the argument centers on whether all lissamphibians arose from the same Paleozoic group or from different groups. Favored hypotheses are: (1) all lissamphibians from dissorophoid temnospondyls (Milner 1988, 1993b; Ruta et al. 2003; Schoch and Milner 2004); (2) frogs and salamanders from amphibamids, caecilians from microsaurs (Anderson 2007; Anderson et al. 2008a, 2008b); (3) frogs from amphibamids, salamanders from branchiosaurs, and caecilians from microsaurs (R. L. Carroll et al. 2004; Carroll 2007); or (4) all lissamphibians as sister group to lysorophians and microsaurs (Laurin and Reisz 1997; Laurin 1998). The first and last of these imply a monophyletic Lissamphibia, whereas the other two could imply para- or polyphyly, depending on the position of lysorophians or microsaurs. If recent phylogenies that place microsaurs and lysorophians close to amniotes are in fact correct, caecilians could be closer to amniotes than to other amphibians. The first of these effectively suggests a monophyletic Lissamphibia and is usually referred to as the temnospondyl hypothesis.

As far as the molecular evidence is concerned, most analyses suggest that frogs and salamanders are immediately related, with caecilians as the outgroup, although a few have suggested that salamanders and caecilians may be more closely related to each other with frogs as the outgroup. San Mauro et al. (2004) recently put forward a molecular analysis that suggested that caecilians and the other amphibians split from each other at a very early date, possibly in the earliest Carboniferous. Lee and Anderson (2006) suggest that this is supported by hypothesis 2, although Ruta and Coates (2007) have cast doubt on the dating suggested by San Mauro et al. (2004).

Among the evidence cited for a relationship between caecilians and microsaurs, apart from strict cladistic analysis, is the discovery of *Eocaecilia*. This earliest caecilian with legs from the Early Jurassic of the United States has been suggested to retain some characters uniquely

shared with microsaurs, specifically *Rhynchonkos*. Carroll (2000b, 2001, 2007; Carroll R. L. et al. 2004) has been the foremost proponent of this idea. It still suffers from the criticism that the similarities could result from convergent adaptations. Although the most recent full description of *Eocaecilia* (Jenkins et al. 2007) could find no definitive evidence for the relationship with microsaurs, they did conclude that *Eocaecilia* was probably not a burrower.

Much of the evidence for the relationship between salamanders and branchiosaurs comes from the discovery of growth stages of several species, notably *Apateon*. The sequence of addition of bones during the branchiosaurid larval phase has been shown to be similar to that of the salamander *Ranodon*, possible evidence for a relationship (Schoch 2002b; Carroll 2004), though Schoch (2004) and Anderson (2007) warned that the similarities could be plesiomorphic for all tetrapods. Carroll has noted similarities in the arrangement of branchial denticles between *Apateon* and larval salamanders, and has suggested that the arrangement is derived in common (Carroll 2001, 2007; R. L. Carroll et al. 2004). More compellingly, Fröbisch et al. (2007) showed that the ossification sequence of the forelimb digits in *Apateon* occurred in the preaxial-dominant pattern found only in salamanders among modern tetrapods. This apparently unique pattern among salamanders has been used in the past to mark them out as separately evolved from all other tetrapods (see Chapter 3), and it is hard to imagine that this quite profound genetic shift could occur in parallel in other groups.

In many phylogenies, frogs appear as the sister group of the amphibamid *Doleserpeton*, and the similarities included greatly enlarged palatal vacuities, eye sockets, and otic notches. There are also peculiarities of the vertebral column in *Doleserpeton* that could be interpreted to foreshadow the construction of anuran vertebrae. Rather than the primitive rhachitomous form, *Doleserpeton* has large unitary pleurocentra that fuse with the neural arch to form an almost cylindrical structure (Bolt 1969; R. L. Carroll et al. 2004; Sigurdsen and Bolt 2010).

Another feature that has played an important role in supporting the relationship between frogs and amphibamids is the presence in many frogs and several amphibamids of pedicellate teeth. Such teeth have a ring of weakness around their base that facilitates a clean breakage instead of uneven damage that could be incurred during biting. Many frogs as well as other lissamphibians have teeth with two cusps, known as bicuspid, and this too has been cited in support of a relationship. Neither of these features is consistently present in all amphibamids, though the similarity between the teeth of *Doleserpeton* and many modern amphibians is striking. Bicuspid teeth have also been seen in a microsaur (Anderson and Reisz 2003), but the configuration does not resemble that of lissamphibians (Sigurdsen and Bolt 2010).

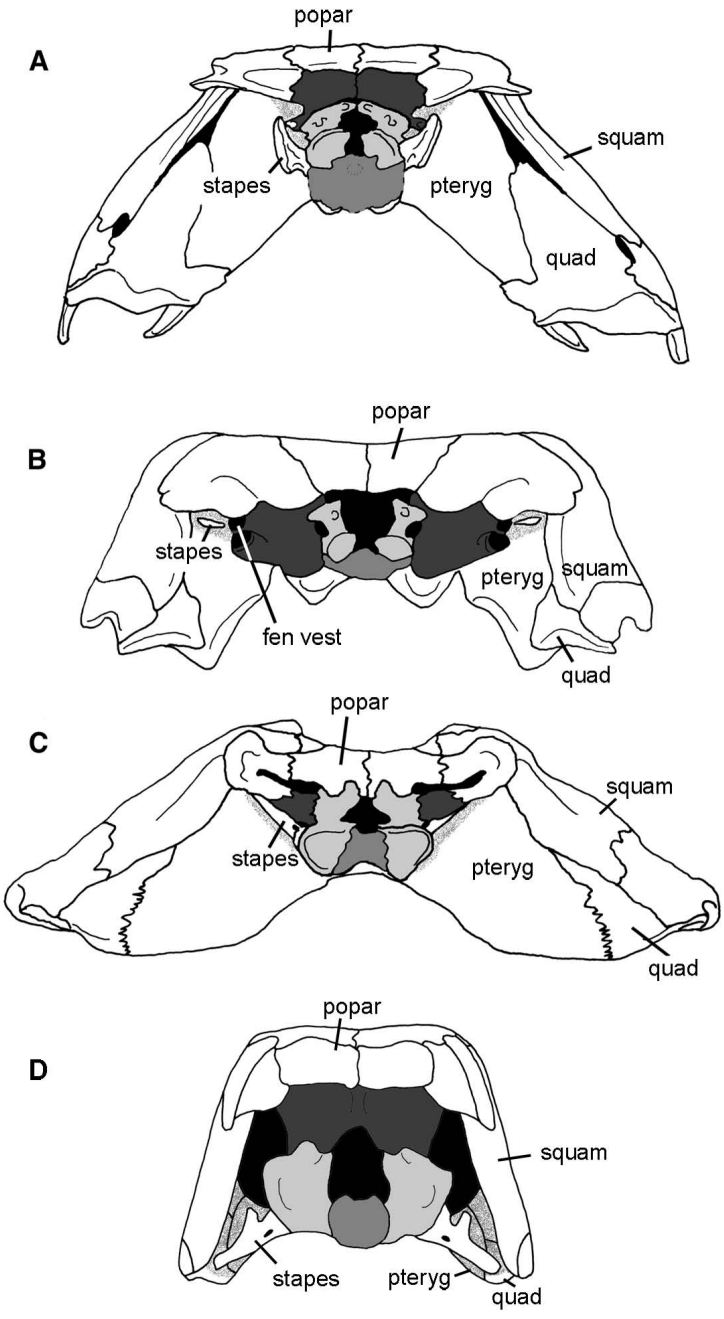
A recently produced full description and analysis of *Doleserpeton* has provided more evidence of the similarities between dissorophoids and lissamphibians in the shape of the elbow joint and in the construction

of the inner ear, both of which are otherwise unique to lissamphibians (Sigurdsen 2008; Sigurdsen and Bolt 2009, 2010) (see Chapter 10). Some features of the elbow joint are indeed found more widely in temnospondyls but nowhere else. These similarities are hard to explain away as convergences.

The discovery of the derived amphibamid *Gerobatrachus* has reinforced the relationship between amphibamids and both frogs and salamanders (Anderson et al. 2008b). Although this creature is convincingly froglike, it has been suggested to show the preaxial-dominant digit development thought unique to salamanders and branchiosaurids. Of course, the ontogeny of digit development is unknown for almost all amphibamids and branchiosaurs, so that this character could conceivably be characteristic of the whole clade. However, it would have to have been subsequently lost in frogs, with frogs regaining a more plesiomorphic, amniotelike developmental pattern—an idea that is hard to accept. On the other hand, if it were to be found convergently derived in amphibamids and branchiosaurs, it would undermine its credibility as a synapomorphy between branchiosaurs and salamanders. Some of the results of cladistic analyses—for example, that which places lissamphibians close to lepospondyls—seem to imply biologically implausible scenarios, such as the redevelopment of buccal ventilation from a previously costal aspiration mechanism.

One observation that comes out of all these attempts to unravel the origin or origins of modern amphibians is that the authors of the various ideas and analyses do not seem to be swayed by anyone else. Rather, they continue to retrieve their preferred hypotheses regardless of how many characters or how many taxa they include in their attempts. This probably says as much about the methods of cladistic analysis and the way they are used as about the intractability of the problem.






**10.1.** Occipital views of tetrapods. (A) The embolomere *Pholiderpeton*. (B) The seymouriamorph *Seymouria*. (C) The temnospondyl *Eryops*. (D) The early amniote *Paleothyris*. Opisthotic/supraoccipital, dark shading; basioccipital, medium shading; exoccipital, light shading.

# Gaining Ground: The Evolution of Terrestriality

# 10

## Steps toward Terrestriality

This extended survey of the anatomy and lifestyles of tetrapods throughout the Paleozoic has explored the evidence and speculation bearing on the advent of tetrapods onto land. This final chapter now goes on to consider the evolution of several key aspects of their biology and how they became truly adapted to terrestriality. The solutions that these early tetrapods arrived at laid the foundations for terrestrial living in a huge group of vertebrates that have ultimately become a highly conspicuous part of the fauna of the planet. How these changes were achieved over that time has influenced the anatomy, morphology, and evolutionary pathways of all subsequent tetrapods and is still reflected in our own anatomy.

The origin of terrestrial tetrapods is one of the few faunal events in the evolution of vertebrates that was evidently not some kind of faunal replacement: there were no vertebrate competitors preceding them. It is also clear that there was no single primary driver, but that a combination of circumstances and evolutionary responses to them fits with a model of correlated progression (Kemp 2006, 2007) in which gradual changes to many parts of the anatomy occurred in concert. This has been seen already in the evolution of the elpistostegalian fish and the earliest limbed tetrapods. Many of the other changes involved also took place gradually and can be followed from the early fossil lobe-finned fishes, through the earliest tetrapods, into the explosion of terrestrial forms in the late Paleozoic.

Some of the aspects that can be followed in most detail include those related to the interconnected mechanisms of feeding, hearing, breathing, and locomotion, and this final chapter draws together threads from new discoveries in paleontology and in the biology of living animals. The story of skeletal evolution is continued in this chapter from *Acanthostega* and its Devonian contemporaries, and it shows how parts of the skeleton were gradually adapted by Carboniferous forms for terrestrial living, how changes to one part affected those to another, and how different groups made these changes in different ways and at different times. The origin of tetrapods is demonstrably separate from the origin of terrestriality, in that tetrapods as a group appear in the fossil record in the Late Devonian, whereas the ensuing adaptations for terrestriality are first seen in the latter part of the Early Carboniferous, appearing bit by bit throughout the rest of the late Paleozoic.

## Changes to the Skull Roof

What is known of the skulls of Devonian tetrapods shows them to be essentially conservative. There are a number of consistent features marking them out as different from their fish relatives, such as the reduced number of snout bones, the pattern of the cheek and skull table, and the subtle characters of the lower jaw, but in other ways they show little variation. The Devonian forms all seem to be rather flat headed, with spade-shaped snouts and eyes placed about the midpoint in the skull, looking more or less dorsally. Only *Ichthyostega* shows much in the way of elaboration of the inside of the skull roof, in that it has produced elaborate flanges that attach to the braincase at the back and sides. In *Acanthostega*, there are no such flanges, and the internal surface of the skull roof is essentially smooth. The only parts of its skull roof to show specially thickened bone are two ridges running up the frontals and prefrontals above the eye. The skull roof of *Ventastega* is much the same.

Among Carboniferous forms, even those from the earliest parts, some striking modifications can be seen to the skull architecture. Several early forms such as *Pederpes* and *Whatcheeria* have skulls that are more deep than broad. *Whatcheeria* has specially thickened ridges inside the skull anterior to the eyes, and *Crassigyrinus* (Fig. 7.15) has taken both these modifications to extremes, with a particularly deep skull, elongated posteriorly, and with greatly thickened ridges running up the snout, between the eyes, and inside the prefrontal. Its eyes are relatively far forward, and furthermore the orbits are rhomboidal. Even in more conventionally shaped skulls such as those of baphetids, the eye sockets acquired forwardly extending embayments (Fig. 9.5).

Other examples of extreme modifications can be seen among some of the lepospondyls, in which the skull roof pattern of early tetrapods is scarcely recognizable. Many of the skull roof bones are lost, in some forms to be replaced by small platelets and in others by struts and braces. Eyes in some lepospondyls moved extremely far forward (Figs. 7.11, 9.33). The development of narrower-snouted and deeper skulls may have facilitated the development of binocular vision, especially in some of the smaller forms, such as microsaurs and amniotes.

Another region of the skull to undergo change was the external nostril. Rather a small opening in *Acanthostega* (Fig. 5.21) and *Ichthyostega* (Fig. 5.9), little different from that of *Panderichthys* (Fig. 3.21), it soon became modified, apparently quite rapidly, into the larger opening found consistently among Carboniferous forms. The maxilla and premaxilla both contributed, but the lacrimal and sometimes the nasal were also involved in forming the margin of the external nostril. In many forms, a bone known as the septomaxilla was located within the narial opening. In some modern tetrapods, the septomaxilla is a bone that bears muscles that open and close the soft tissue of the nostril.

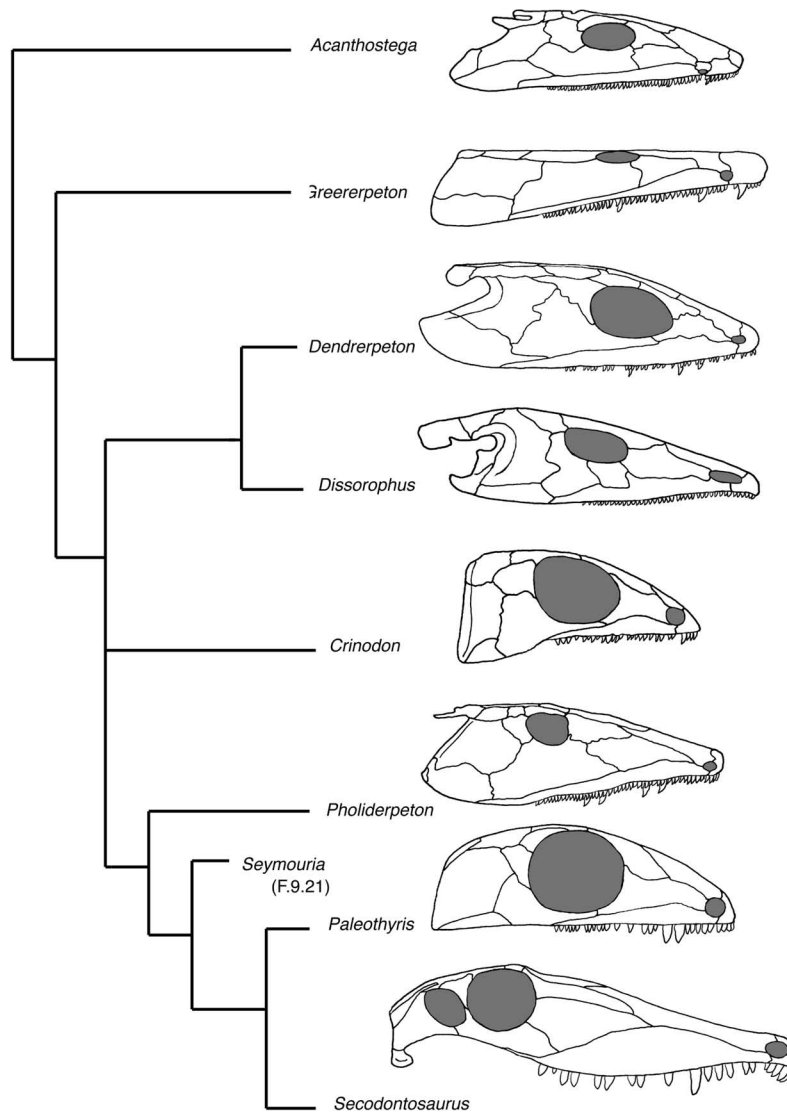
One of the most basic forms of this bone might be that found in baphetids, where a dermal bone occludes a large part of the narial opening

(e.g., *Megalocephalus*, Fig. 9.5). It is ornamented in the same manner as other dermal bones of the skull roof. In these forms, there is little to distinguish the bone from the anterior tectal, found in fishes such as *Panderichthys*, and so called in *Acanthostega* (Fig. 5.21). There have been arguments about the homologies of this bone between fish and tetrapods parallel to those concerning the skull table bones, and these arguments have not been satisfactorily resolved. Although there seems no compelling reason to doubt the homology between the baphetid bone and that of *Acanthostega*, in other tetrapods, the situation is more confused.

One such confusing animal is *Crassigyrinus*. The floor of its nasal opening includes a thickened, cushion-shaped bone, whose surface, judging by the bone type, appears not to have been exposed on the outside of the animal. Identification as a septomaxilla seems the most likely possibility, but whether this bone is a modified anterior tectal or something different is at this stage difficult to say (Fig. 7.15). Septomaxillae are found in many early tetrapods, usually internal to the nostril. In some cases, such as some early amniotes, they are simple curled or conical structures (Heaton 1979), and this seems to be paralleled in the temnospondyl family known as trematopids, terrestrial members of the dissorophoids. The feature is associated with a narial region that seems adapted for dry conditions (Dilkes 1993).

Another region where there is some diversity to be seen among early tetrapods is the way the skull roof and the palate are joined together at the back along the line formed where the back of the squamosal and quadratojugal meet the pterygoid. In *Acanthostega*, for example, there is no suture between these two plates of bone, which simply butt up against one another down the length of the cheek. In other forms, though there may have been a firmer union, it appears that it may have been a loose and possibly moveable one, for example as has been suggested for baphetids as part of a skull kinetic mechanism (Beaumont 1977). In some embolomeres like *Pholiderpeton*, there was hardly even a meeting between the two (Fig. 10.1) (Clack 1987a). In other forms, such as colosteids, some temnospondyls like *Eryops*, and animals like *Seymouria*, there was a firm seam running down the back of the cheek joining skull and palate in a solid union (Fig. 10.1). In microsaurs and some early amniotes, there was no ossified junction at all between these bones (see Fig. 9.39 for *Captorhinus*, Fig. 10.16 for a microsaur), but a large gap was left that may or may not have been filled with cartilage. Some of these differences may be connected with size, in that the junction seems to be absent in small forms. However, not all large forms show the sealed construction. Where the junction is sealed, it must mean that the skull was well on the way to being autostylic.

The presence of a spiracular notch at the back of the skull in early tetrapods has been mentioned before, and this constitutes another region of the skull where variability is seen early on in tetrapod history. In most forms, it is easy to say whether a notch was present or absent, though there are one or two exceptions. The exceptions are creatures like the anthracosaurs *Eoherpeton* (Fig. 7.14) and *Gephyrostegus* (Fig. 9.25), where the




**10.2.** Distribution of the temporal notch among a selection of early tetrapods, the Devonian tetrapod *Acanthostega,* the stem tetrapod *Greererpeton,* the primitive temnospondyl *Dendrerpeton,* the dissorophid temnospondyl *Dissorophus,* the anthracosaur *Pholiderpeton,* the microsaur *Crinodon,* the early amniote *Captorhinus* related to diapsids, the synapsid amniote *Secodontosaurus* related to mammals. (Not to scale.)

slope of the back of the cheek is shallow. However, notches do seem to be present in most anthracosaurs and their postulated relatives. Notches are consistently present in most of the earliest tetrapods but absent in *Greererpeton*, most "lepospondyls" (Figs. 9.30–9.35), all early amniotes (e.g., *Captorhinus*, Fig. 9.39), and a few temnospondyls, such as *Dvinosaurus* (Fig. 9.12). Putting the presence or absence of a notch onto a cladogram tells an interesting story (Fig. 10.2).

Three Devonian tetrapods are known from enough skull material to show the temporal region, and all three—*Acanthostega* (Fig. 5.21), *Ventastega* (Fig. 5.27), and *Ichthyostega* (Fig. 5.9)—had notches at the back. It is true that the notch structure is rather different in detail in each of these three, but in general terms, they occur in equivalent positions. That of *Ventastega* is most similar to that of *Tiktaalik* (see Chapters 5 and 6).

Among the next earliest tetrapods, *Pederpes* (Fig. 7.6) and *Whatcheeria*, each have deep notches, as do *Crassigyrinus* (Fig. 7.15) *Eucritta* (Figs. 8.14, 8.15), *Balanerpeton* (Fig. 8.11), *Silvanerpeton* (Fig. 8.12), and other early temnospondyls and anthracosaurs. The enigmatic adelogyrinids also have large rounded notches occupying the whole back margin of the skull (Fig. 7.11). Interpretation of the function of the notch has changed in recent years. Part of that story has been told in Chapter 6, and another part in a later section of this chapter below. However, a third part is considered next.

The potential function of the notch in the elpistostegalian fish and early tetrapods is intimately connected with the condition of other parts of the bony structure, such as whether or not there was an enlarged spiracular chamber or space for a middle ear cavity, and also whether or not the spiracular notch was open to the outside or closed by a membrane. The existence of a chamber is relatively easily established by looking at the bones of the back of the skull, such as the pterygoid, quadrate, paroccipital processes if present, and the relationship between the stapes and these bones. What is more difficult to establish is what the chamber contained—whether it was water or air. In modern tetrapods, it usually is air filled (when present), but in fish, the equivalent (if present) is water filled. The question arises as to when the chamber changed from water to air filled to attain the modern tetrapod condition. This is something that cannot easily be tested. As noted in Chapter 6, the extant phylogenetic bracket (EPB) is not very helpful for early tetrapods, and this is a case in point. The EPB is ambivalent, because in coelacanths the chamber is water filled and in modern tetrapods it is air filled (lungfish do not have a spiracular chamber).

A related problem is that of whether the chamber was open to the outside, as it is in the primitive ray-finned fish *Polypterus*, or closed, as it is in modern tetrapods. The tympanic membrane and middle ear cavity in modern tetrapods is formed somewhat differently in amniotes and amphibians, but they are both in part remnants of the spiracular chamber, with the tympanum being in effect the membrane that closes the notch. As explained in Chapter 1, gill openings are formed in the embryo when inpushings from outside of the pharynx meet similar ones from the inside, but just before they do, a thin wall separates the two. This is true of all gill pouches, including the spiracular pouch. The implication is that it is this remnant membrane that provides the basis for a tympanum, and that if it remained intact, it would be responsible for closing the spiracular notch. Strict application of the EPB would suggest that because the spiracular chamber is closed in coelacanths and in modern tetrapods, early tetrapods too would have had a closed spiracle. Another argument to suggest a closed spiracle would be that a closed chamber could be a retention of an embryonic condition, and thus is yet another example of pedomorphosis in the evolution of early tetrapods. All of this would argue against the spiracular chamber having any function in breathing, contrary to what was suggested in Chapter 6.

If the spiracle were not involved with breathing, what might be an alternative explanation? Again, this depends on what filled the chamber. If water, it is hard to see what the enlarged chamber and notch were doing. If air, on the other hand, it could be that early on, the chamber was more closely involved with audition, for example as suggested for *Ichthyostega*. However, the enlargement of the chamber and expansion of the notch do not obviously correlate with any modifications to the hyomandibula that could promote hearing, although a closed, air-filled chamber connect to the pharynx could have acted as an acoustically coupled ear that could receive directional sound at low frequencies (Christensen-Dalsgaard and Carr 2008). There is some evidence that the different groups of tetrapods developed a tympanum at different times and in different ways. Thus, the whole issue of the condition in early tetrapods and elpistostegalian fish remains moot. Circumstantial evidence, based on what else was going on around them at the time, seems to be the best we have at present to interpret structure and function in those cases.

Phylogeny suggests that possession of a notch is primitive for tetrapods, whatever its function may have been. However, animals lacking notches crop up at several points in tetrapod phylogeny (Fig. 10.2). In a number of cladistic analyses, *Greererpeton* comes out as the next most primitive tetrapod after the whatcheeriids and *Crassigyrinus*, suggesting that colosteids lost their notches early on. Notchlessness may be one character that unites lepospondyls, with the exception of adelogyrinids, and it seems also to unite early amniotes. Some phylogenies suggest that it unites lepospondyls and amniotes (Laurin and Reisz 1997). However, there may be functional or size correlates that suggest that convergence rather than shared history accounts for the lack of a notch in some groups.

The notch is lost in perennially aquatic temnospondyls, such as some of the Late Permian forms like *Dvinosaurus* from Russia. These are known to have been neotenous forms with well-developed gill bars (Bystrow 1938). Supposing the notch to have been originally spiracular rather than part of an ear, *Dvinosaurus* and colosteids could each have lost the notch because they no longer relied on air breathing and did not use the spiracle for exhalation. Gill rakers are known from colosteids. These are mineralized projections from the gill bars into the mouth. They are used in some fishes as a kind of filtering device for preventing food particles from entering the gill chamber and damaging gill filaments, for catching minute food particles for ingestion, or for helping to seal the buccal chamber during suction feeding. They are also found in filter-feeding larval salamanders, which are all aquatic. Their presence in fossil tetrapods suggests that these animals used their gills for feeding in water in some way, and perhaps for breathing as well. On the other hand, small forms like microsaurs and amniotes may have begun the evolution of costal ventilation, using body-wall muscles for inhalation as well as exhalation (see Chapter 6), and gradually abandoning the buccal pumping of early tetrapods. In their case, the spiracular notch may have

become redundant for a quite different reason from that in colosteids and some temnospondyls. Implication of changes to breathing mechanisms may be invoked.

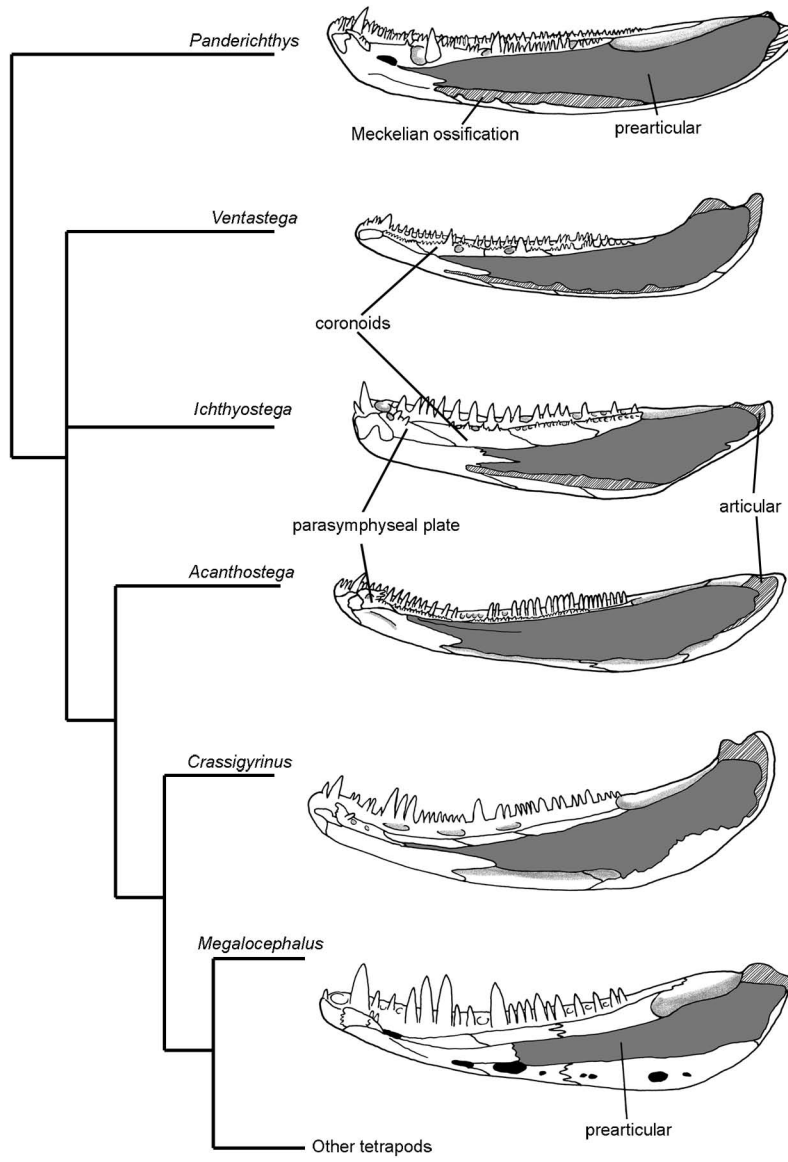
In summary, initial changes to the skull shape and architecture as well as to the shape and position of the orbit, the construction of the nostril, and the spiracular region preceded the origin of limbs with digits in appearance. However, after an initial period of tetrapod conservatism, a much wider range of shapes and sizes are seen; it is as if some constraint had been lifted that allowed the evolution of a much more radical suite of skull modifications. That constraint may have been connected to reduction of reliance on gill breathing, which may in turn have been affected by the final size to which the animals grew. Smaller animals may have been able to limit their reliance on gill breathing in favor of cutaneous gas exchange or buccal pumping. In turn, the changes affected the evolution of the neck and consequently the position of the heart.

## Jaws, Dentition, and Feeding

Lower jaws constitute the most commonly preserved parts of the anatomy of Devonian and Early Carboniferous tetrapods, and a fairly orderly series of changes to the lower jaws can be demonstrated among them. However, this was followed by a radiation of lower jaw shapes that suggests a rapid diversification among mid–Late Carboniferous forms (Ahlberg and Clack 1998). Lower jaw changes show a parallel story in this respect to those in already noted to skull shape and architecture, and many of them had to do with changes to feeding mechanisms. Figure 10.3 places the lower jaws of several Devonian and Carboniferous tetrapods onto a cladogram of their relationships.

Most fishes today feed using a suction mechanism of some kind. There are exceptions like the garpike, which has evolved long, narrow jaws for slicing quickly through water, but the majority of fishes have elaborate mechanisms to draw in as much food as possible with the water they suck in as they open their mouths. This often involves widening the gape as far as possible, brought about by loosening the connections between their skull bones to form a flexible framework for the jaw muscles. It is thought that even early fishes used this method, though their skull adaptations toward it were not as extreme as in later ray-finned fishes. The intracranial hinge (Figs. 2.1, 3.5) found in early lobe-fins is thought to be an example of an adaptation to make suction feeding more efficient, though it tends to disappear in longer-snouted forms (Thomson 1967, 1969).

*Panderichthys*, *Tiktaalik*, and *Elpistostege* had lost the hinge mechanism and appear to have been rather unspecialized gulpers, presumably still feeding in water. It seems that the lineage leading to tetrapods had found other methods for feeding, which might have been related to a possible adaptation to bottom dwelling or life in shallower waters (Ahlberg and Milner 1994). Markey and Marshall's (2007) study of suture patterns




**10.3.** Early tetrapod lower jaws; the stem tetrapodomorph *Panderichthys,* the Devonian tetrapods *Ventastega, Ichthyostega,* and *Acanthostega,* the primitive tetrapods *Crassigyrinus* and *Megalocephalus.* Prearticular gray shaded, Meckelian ossifications including the articular, hatched. (Not to scale.) *From Ahlberg and Clack (1998).*

in the skull of *Acanthostega* have suggested that it used a biting rather than a suction mechanism for feeding.

Changes to feeding mechanisms will naturally be reflected in changes to jaw structure and operation, so that the lower jaw, often the only clue there is to the existence of Devonian tetrapods, offers evidence of this shift. Accordingly, there are many similarities in the jaw structure and dentition of the earliest tetrapods to those of *Panderichthys* and *Tikaalik* and those of tristichopterids. Indeed, many specimens of lower jaws now known to have belonged to tetrapods were once thought to be those of tetrapodomorph fishes. The similarities are sufficient to suppose that the earliest tetrapods were, like these fishes, aquatically feeding animals. All of them would have been carnivorous, feeding on other fishes and

invertebrates, or scavenging anything edible that became available. The early tetrapods were probably gulpers like *Panderichthys*, and with their flattened, broad heads, they may have behaved like the giant Japanese salamanders of today.

In all primitive bony vertebrates, including early tetrapods, the lower jaw consisted of internal and external faces forming a tubular structure (Fig. 2.1). The number and arrangement of bones was the same in early tetrapods and other tetrapodomorphs, with teeth on the dentary and coronoids forming parallel rows. However, changes to the teeth and jaw structure in the evolution of tetrapods can be traced in such features as the relative size and number of teeth in each of these rows (Fig. 10.3). The bones and teeth of the palate change in concert with those of the lower jaw. The lower jaws of *Panderichthys* and *Tiktaalik* were nonetheless more similar to tristichopterids than they were to those of *Acanthostega*, especially in features of the dentition, indicating that some subtle changes had taken place to the means of feeding or the food being taken. Ahlberg and Clack's (1998) study of lower jaws of early tetrapods provided a perspective on the changes encountered in their structure. A cladogram based only on lower jaws produced a result comparable to that using all available characters, which presumably reflects modifications to changing mechanisms, food intake, and the effect of gravity produced by feeding in air rather than in water. The cladogram in Figure 10.3 shows these changes quite clearly. They were general to begin with, but among the tetrapods of the mid to Late Carboniferous, many more specializations can be seen that must relate to increasing adaptation to terrestrial feeding and to their radiation into different niches in the terrestrial habitat. They correspond to the wider range of overall skull shape seen among Carboniferous forms.

In animals like *Eusthenopteron* and *Panderichthys*, the outer marginal row on the dentary was made up of numerous small teeth, often a double row with even smaller teeth in an external row (Figs. 2.1, 10.3). The coronoid teeth, however, consisted of large fang pairs and their replacement pits, with perhaps a row of small toothlets or denticles running alongside external to the fangs. In the early tetrapods, the emphasis shifted away from the coronoid teeth, so that the large tusk pairs were replaced first by rows of small teeth in the earliest tetrapods, and then by a shagreen field of denticles in later ones, such as *Crassigyrinus* and the embolomeres. Most baphetids had lost even the shagreen (Fig. 10.3). Ultimately the coronoids lost their teeth as in microsaurs and amniotes, and the number of coronoid bones was reduced, to disappear completely in some tetrapod groups.

Among early tetrapods, a gradual strengthening of the tubular structure of the lower jaw started with loss of the spongy endochondral Meckelian bone that filled the tube in lobe-fins, present in *Panderichthys*, reduced in *Ventastega*, and absent in *Crassigyrinus* and *Megalocephalus* (Fig. 10.3). In its place, internal and external faces became sutured together along the back and lower edges. This can clearly be seen in the

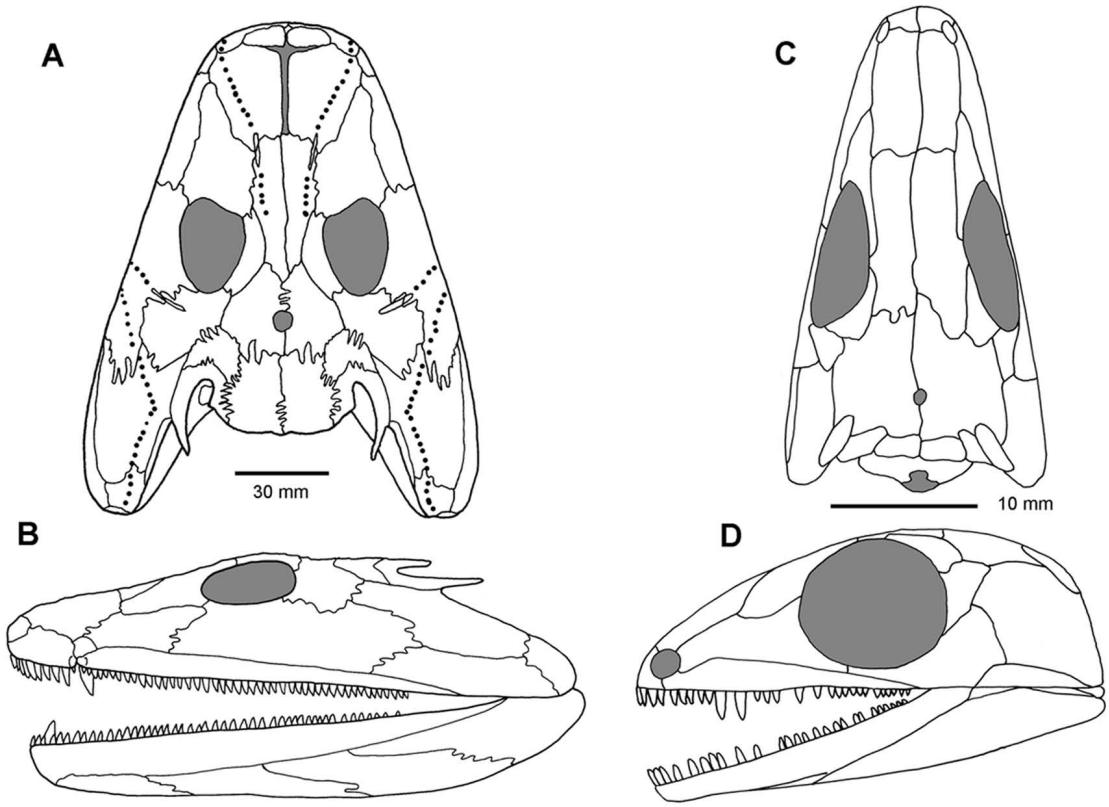
sequence from *Acanthostega*, through *Crassigyrinus* and the baphetids, and continued though into the anthracosaurs, temnospondyls, and amniotes.

There was also a change in the angle at which the jaw articulated, and the rather backwardly orientated joint in basal tetrapodomorphs gradually became more forward facing. This would have affected the muscles that opened the jaw and the angles at which they were most effective. The implications of these changes for jaw movements and function have not yet been explored.

In temnospondyls, for example, the lower jaw remained generally long and narrow, though it became gradually more consolidated, with some of the coronoid series being lost. In this case, changes to the lower jaw structure may have been constrained by its use in buccal pumping, where a light, narrow jaw may have been an advantage in this amphibian lineage (Szarski 1962; Janis and Keller 2001). Nonetheless, temnospondyls were the first group of tetrapods to produce a radiation of long, narrow-snouted forms, resembling the modern gharial in shape (Fig. 9.12, 9.13). This shape is exploited by animals that feed in water by rapid snaps. A narrow snout encounters less resistance to the water than a broader one. Like the modern garpike, the long-snouted temnospondyls must have been specialized aquatic snappers of fish. As with early tetrapods, a cladogram of temnospondyl lower jaws produced a result comparable to that using all available characters, suggesting that features of the lower jaw reflect changes to the whole animal (Ruta and Bolt 2008).

The tusk pairs of the palate also ultimately disappeared, but more gradually. For example, *Acanthostega* retained massive vomerine teeth like those of tetrapodomorph fish, but the other palatal teeth were small (Fig. 5.21). Many early tetrapod groups such as temnospondyls (Figs. 9.8, 9.14) and early anthracosaurs (Fig. 9.19) still had palatal tusk pairs, though again they were usually relatively small. A gradual reduction can be traced in the palatal teeth, especially clearly in the amniote lineage. No early amniote has palatal tusks or teeth on the vomers or palatines, and the ectopterygoid bone itself disappears entirely (Fig. 9.39), perhaps as a result of pedomorphic processes (Kimmel et al. 2009). The sheet of denticles found on the pterygoid of almost all early tetrapods also gradually disappears. In early amniotes, a few strips of denticulated tissue remain, and later most of these disappear. All that remain are a few teeth in rows on the pterygoid, but importantly, some of these are ranged across the downwardly turned pterygoid flange (Fig. 9.39). This is one of the few osteological characters that most early amniotes share and is one of the few skeletal clues to distinguish an amniote from a nonamniote. Its function will be discussed below.

By contrast to the coronoid and palatal teeth, the marginal dentition in tetrapods became more important. In the tetrapodomorph fish, the small, numerous dentary and maxillary teeth probably served mainly to anchor prey impaled on the massive palatal and coronid fangs. In tetrapods, from even the earliest forms, the dentary and maxillary teeth

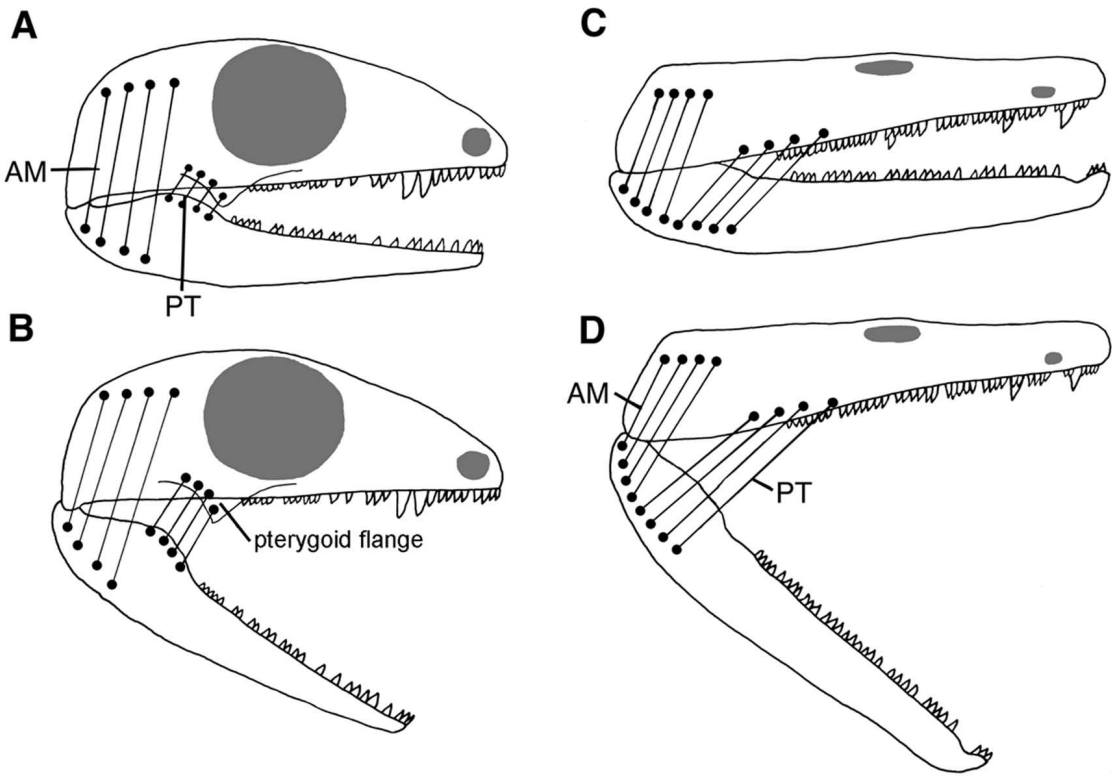



**10.4.** Early tetrapod skull shapes: (A, B) Dorsal and lateral views of the skull of *Acanthostega*. (C, D) Dorsal and lateral views of the skull of the early amniote *Paleothyris*. Note the difference in size between these two skulls.

had become larger though fewer than in the fish, and the palatal fangs smaller and more even-sized, with C*rassigyrinus* and later temnospondyls having reevolved a massive and specialized palatal dentition. The inference is that although these early tetrapods were largely aquatic animals still feeding mainly in water, they were using slightly different methods from their fish forebears or were eating different prey types. C*rassigyrinus* may represent another instance of this kind of adaptation, with its narrow and elongated skull adapted to slashing through water.

Whereas in most of the early tetrapods and most temnospondyls the skull was broad and flat, in the reptilomorph lineage of tetrapods, including the anthracosaurs, a different type of skull architecture is seen. Here the skulls tend to be high and narrow, with deep cheeks (Fig. 10.4). The contrast may be related to the interconnected needs of breathing and feeding on land.

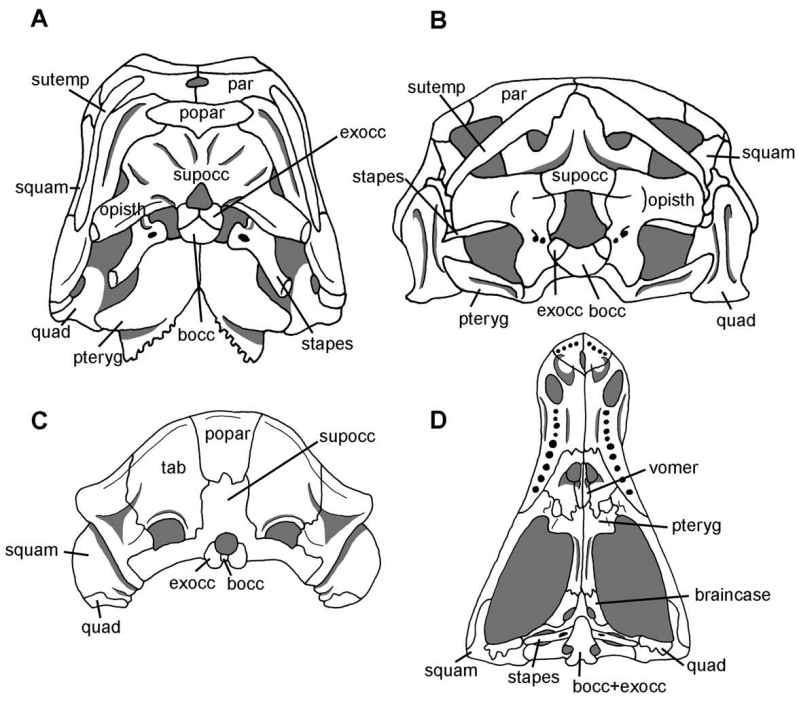
On land, two extremes of jaw closing mechanisms have been recognized, summarized in Figure 10.5 (Olson 1961). This scheme is certainly oversimplified, but it is a useful starting point. In animals with long skulls that have the jaw joint right at the back, the lower jaw is swung closed by muscles whose greatest force acts as the jaw begins its travel. By the time it closes, the jaw is moving with considerable speed and inertia so that the teeth impale the prey rapidly. The wider the mouth can be opened, the better. This is called the kinetic interial system. Essentially, this




**10.5.** Jaw closing mechanisms in early tetrapods: (A, B) Static pressure system in an early amniote. (C, D) Kinetic inertial system in an animal such as *Greererpeton.* AM = adductor mandibuli muscle; PT = pterygoideus muscle. Note the angle that the pterydoideus makes with the lower jaw when it is open in each case.

reflects the structure in primitive tetrapods, and it may be constrained by the requirements of a wide, shallow head, proximity of the head to the shoulders, and the maintenance of muscles for buccal pumping. In the other mode, called the static pressure system, the jaw muscles are arranged so that they exert their greatest force when the jaw is nearly closed and after it has shut. In this case, the prey can be held tightly, squeezed by the mouth and teeth. To achieve this, the point at which the muscles insert has to be moved further forward on the jaw, so that the muscles act at right angles to the articulation when the jaw is closed. Shorter tooth rows and a crest for muscle insertion behind the teeth are characteristic of this mode. A combination of both modes can be used by the same animal, or the jaw mechanism can fall between the two extremes. Such modifications involve differentiation of musculature into those whose action is slow and maintained, requiring a good, long-lasting blood supply, and those with a short, sharp action that require oxygen, and thus blood supply, for a shorter period.

Some anthracosaurs show some modifications toward this static pressure jaw system, including a crest on the surangular bone, but it is best seen in the amniote and microsaur lineages. These animals may represent the first indications of specialized terrestrial feeding. Some microsaurs evolved crushing teeth, which look as though they might have dealt with the shells of the first land snails, for example (Fig. 9.30), or thick-cuticled arthropods. Both groups produced small




**10.6.** (A) Occipital view of the basal synapsid *Ophiacodon*. The paroccipital process (opisthotic) meets the cheek, but the stapes is still strutlike. (B) Occipital view of a lizard ("advanced" diapsid) skull. The paroccipital process meets the cheek, and the stapes is a slender rod. (C, D) Occipital and ventral views of the skull of the "advanced" synapsid *Cynognathus*. The braincase, palate, and skull roof are closely integrated by sutures, and the role of the stapes as a bracing strut is reduced. Gray shading, posttemporal fossae and other skull fenestrae. Ophiacodon, Cynognathus *and lizard based on Romer (1966).*

forms with short tooth rows and reduced the number of coronoids to one. In the amniotes, the coronoid was produced backward into a crest onto which jaw closing muscles inserted. The downturned pterygoid flange that bore teeth also provided a point of origin for the powerful pterygoideus muscle, important in the static pressure method of jaw closure (Fig. 9.39).

In early amniotes, all these features are associated with a rather box-like skull. None of these animals had an embayment at the back of the cheek like temnospondyls or many other early tetrapods, and instead of being a somewhat triangular shape in occipital view, the amniote skull was often rectangular (Fig. 10.6). The stapes ran from the braincase, approximately at the center of the rectangle, to the lower corners of the skull, contacting the quadrate. In the early amniote skull, the basal articulation remained much like those of early tetrapods and probably acted as a shock absorber. The stapes was thus called on to help tie the braincase and skull roof together, as well as to counteract some of the inwardly directed forces acting at the jaw joint, produced by the static pressure feeding system. In early amniotes, therefore, the stapes was a structural member of the skull. In other words, they were still partially hyostylic. In diapsid groups, the stapes' role as a bracing member seems to have been gradually replaced by the development of the strutlike paroccipital process that gained a firmer and firmer attachment to the bones of the cheek at its distal end (Fig. 10.1D). In mammals, by contrast, the skull roof and braincase became more firmly tied to each other by elaboration of the occipital plate, and the palatal bones also gained firm attachments

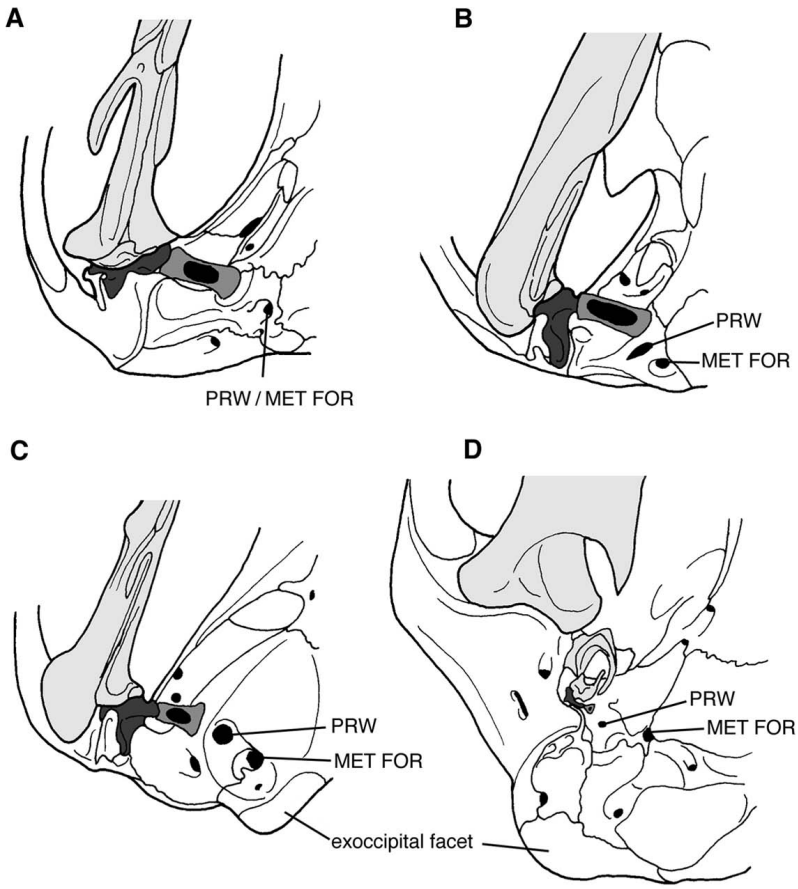
to the braincase in place of the old basal articulation (Fig. 10.6). Both groups became effectively autostylic, but they did it in contrasting ways. Only when this process was well under way could the stapes be finally freed from its structural role to be used instead as a hearing ossicle (Clack 1997b).

Returning to the lower jaw, the mammals, which were evolving in the Triassic, continued some of the changes that were begun by their Carboniferous ancestors and took them to further extremes. For example, they reduced the number of bones further, to just a single one on each side, the dentary. It articulated to the squamosal bone, and part of it formed an equivalent to the coronoid process seen in earlier amniotes. At the same time, consolidation of the skull architecture allowed the stapes to become reduced in size, while the bones of the former jaw articulation, the quadrate and articular, were incorporated with it into the middle ear (Allin and Hopson 1992). This helped to form the mammals' unique hearing system, once more connected to changes in skull structure, including the great expansion of the brain (Rowe 1996; Manley 2010) (Fig. 10.7). Herbivory in tetrapods could only occur once teeth and jaws were capable of being adapted to collect plant food. The static pressure system had to evolve before this could be achieved, and herbivorously adapted animals are first found in the Late Carboniferous, some among the synapsid lineage and some among the diadectomorphs. It has been suggested that the evolution of herbivory was an even more important development in amniotes than the evolution of the shelled egg, but whether or not this is true, it seems to be the case that herbivorous clades of animals seem to have been more diverse that those that feed only on animal food (Sues and Reisz 1998), and something about the acquisition of herbivory could have triggered the increase in diversity among amniotes that occurred early in the Permian. However that may be, it is possible that in order to develop the static pressure jaw mechanism that allowed herbivory, buccal pumping first had to be replaced by aspiration breathing, which used movements of the rib cage to expand and compress the lungs. Only then was it possible to change the shape of the head in the manner that the static pressure system required.

## The Ear Region and Hearing

Because of the interrelated changes to skull structure outlined in the previous section, a discussion of jaws and feeding connects closely with the evolution of hearing airborne sound. Both are connected with the early function of the stapedial bone, used in most modern tetrapods as a hearing ossicle.

To capture sound energy traveling through air, an animal must evolve the equivalent of an acoustic transformer. Because the air is more transparent to sound than the animal's body, most of the sound waves would normally bounce straight off the surface, so that an amplifier is needed to make the best use of what is left. A flexible membrane (the

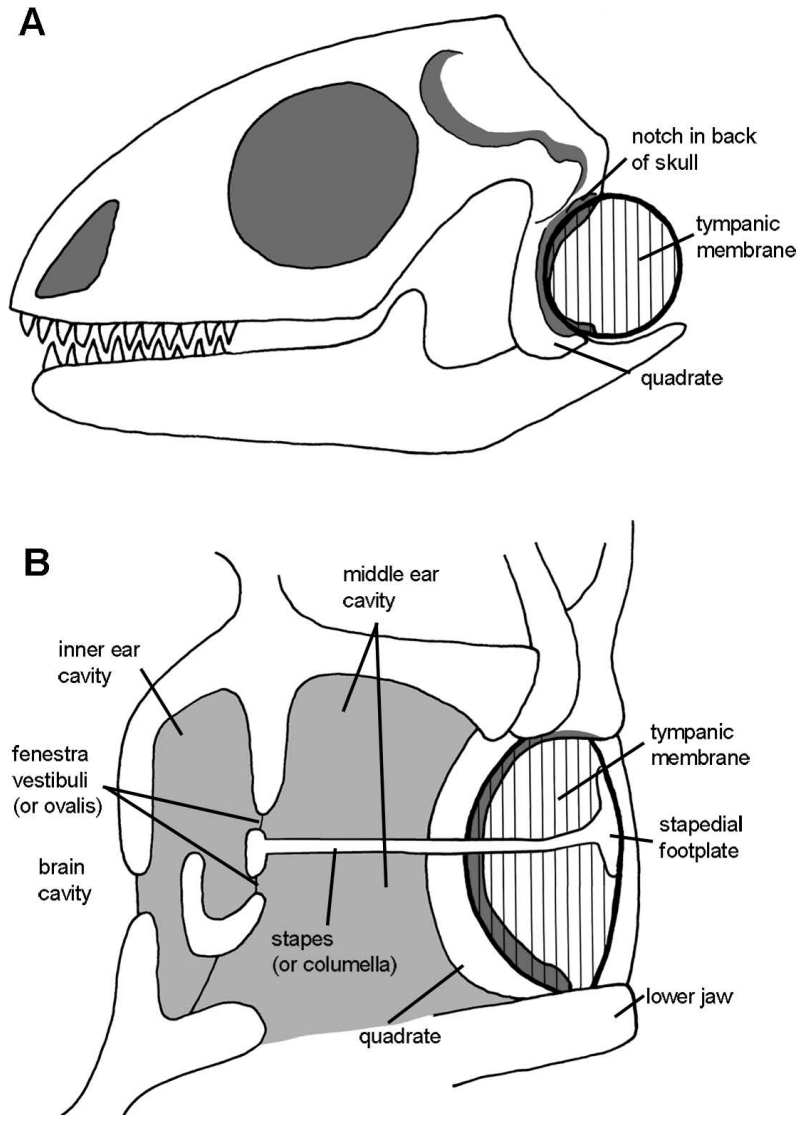



**10.7.** Mammal ear evolution. (A) *Thrinaxodon,* a cyndont synapsid. (B) *Pachygenelus,* a trithelodontid synapsid. (C) *Morganucodon,* a primitive mammal. (D) An opossum, a marsupial mammal. The figures show the ventral view of the posterior half of the skull with the lower jaw in place. Compare with Figure 10.6. Light shading, lower jaw bones and their derivatives in (D) the tympanic bone and malleus; medium shading, stapes; dark shading, quadrate and its derivative in (D) the incus. PRW = pressure relief window; MET FOR = metotic foramen. *From Allin and Hopson (1992).*

tympanum) collects the sound waves that impinge on it, and a freely vibrating lever system (the stapes) magnifies and transmits them across an air space (the middle ear cavity), where they are concentrated into the fenestra vestibuli (or ovalis), the opening into the animal's braincase. These are the main components of a tympanic ear (Fig. 10.8), which the ear of a lizard exemplifies well. Once inside the animal's head, the sound wave energy is picked up by receptors in the fluid of the inner ear and transmitted to the brain, where it is processed into usable information. Even nontympanic forms, such as secondarily aquatic frogs, do have some ability to hear low-frequency sound and can detect differences in sound pressure between the two sides of the head that give them some directional capability (Christensen-Dalsgaard and Carr 2008).

### EARLY TETRAPOD EARS AND THE FOSSIL RECORD

The history of ideas about the evolution of a terrestrial hearing mechanism in tetrapods illustrates a number of important principles in paleontology. First, it emphasizes how changed perceptions of phylogeny can radically alter views of the evolution of an organ system, and thus the functional interpretation of skeletal parts, and even how the relationships




**10.8.** Diagram of a lizard ear to show the elements of a tympanic ear. (A) Left lateral view. (B) Posterior view of right side.

of the skeletal parts to one another are seen. It illustrates how a system such as the ear, which appears similar in different groups, may on deeper examination differ in ways that have been at first overlooked. Finally, it provides a good example of how changed search images may suddenly reveal things that, although they had been there all along, were not recognizable for what they were without additional information. For this reason, it is worth spending a little time on the history of the middle ear in paleontological debate.

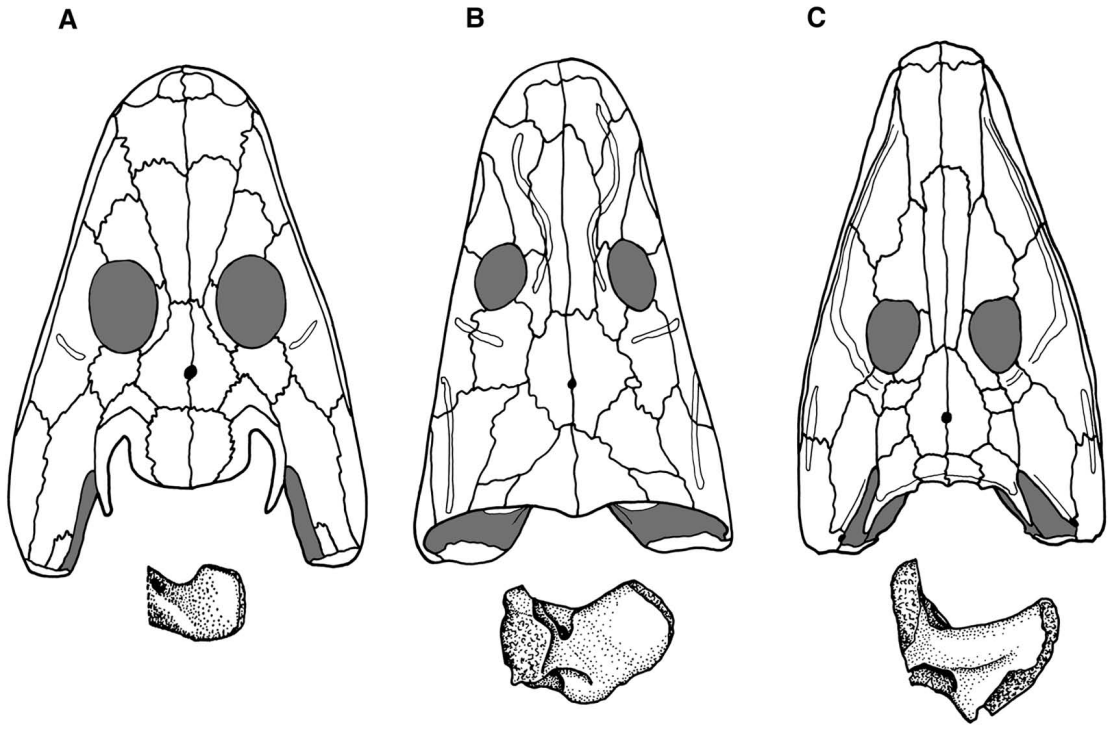
Because the middle ear is one of the only two sensory systems to leave a positive fossil record in tetrapods (the other being the lateral line, absent in amniotes), it has been of interest to paleontologists more or less since the science began (for reviews, see Clack 1993, 1997b, 2002c). One of the earliest observations concerning the ear region was that many early

tetrapods had an embayment at the back of the skull in a similar position to that of the spiracular cleft of tetrapodomorph fish. At first the embayment was interpreted as an otic notch, which would have supported a tympanic membrane, and by implication, the rest of the components of a tympanic ear. What are now known as temnospondyls were originally called labyrinthodonts, and they showed this ear structure well. In some, a rodlike stapes had a foot plate that fitted into the animal's braincase at the fenestra vestibuli, and it passed dorsally toward the center of the otic notch through the airspace of the middle ear cavity, toward a tympanic membrane that was presumed to have stretched across the notch. *Eryops* provided the exemplar for this structure (Fig. 9.10). The whole arrangement resembles the ear region of many frogs and lizards.

As discoveries of early tetrapods continued, other animals were added to the labyrinthodonts (see Chapter 9), including *Ichthyostega* and anthracosaurs such as embolomeres (Fig. 9.19) as well as *Seymouria* (Fig. 9.26). An ear region apparently similar to that of temnospondyls was present in *Seymouria*, though the structure of its braincase in the otic region is quite unlike that of any temnospondyl, and its stapes is rather poorly ossified and horizontally positioned (Fig. 10.1). Anthracosaurs, which also had otic notches, were assumed to have had stapes like those of temnospondyls, in a typically labyrinthodont ear. For many years, no anthracosaur stapes had been found, but they were reconstructed along these lines. The term "labyrinthodont ear" attests to the perceived phylogenetic relationships between the groups in question. Other early tetrapods with labyrinthodont-like characters also had notches at the back of the skull, such as baphetids (Fig. 9.5), *Ichthyostega* (Fig. 5.9), and *Crassigyrinus* (Fig. 7.15), and these too were placed among the labyrinthodonts. Their stapes were also unknown at this stage.

Because of its wide distribution in a range of primitive tetrapods, the labyrinthodont ear was perceived as a primitive feature common to them all, and the inference was that the tympanic ears found in modern animals would have been derived from this original early tetrapod invention. Other assumptions were tied up with this one. Terrestrial hearing would have evolved right at the outset of tetrapod evolution because the animals were seen as having been terrestrial from the beginning. The labyrinthodont ear would have evolved early in tetrapod history, as soon as the stapes' role in operating gills and the opercular system had been jettisoned. Once freed from this role, the stapes would also have become redundant as a lever tying the palate to the braincase. The tetrapod skull was considered to have become autostylic during the earliest days of their evolution.

Many recent discoveries about early tetrapods have refuted each one of these assumptions. Early tetrapods such as *Acanthostega* have been shown to be largely aquatic; indeed, on the basis of current evidence, limbs and digits arose while the animals still spent most of their time in water. Most importantly, from the early 1980s onward, it has become evident from finds of the stapes of the colosteid *Greererpeton* (Smithson

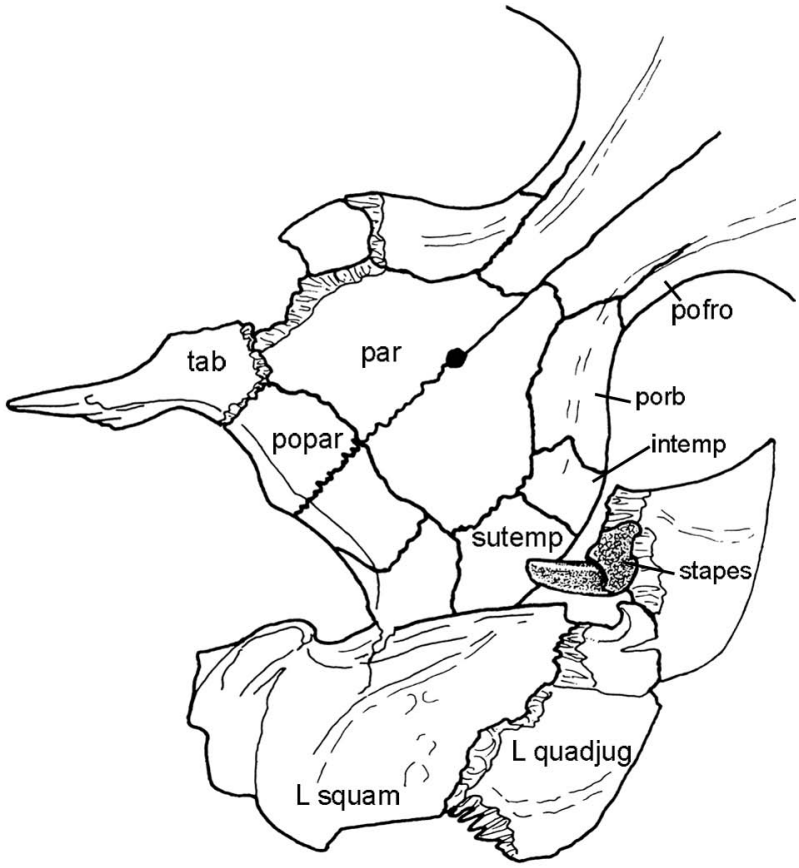



**10.9.** Skulls and stapes of early tetrapods—skull above with the left stapes below. (A) *Acanthostega*. (B) *Greererpeton*. (C) *Pholiderpeton*. (Not to scale.) *From Clack (1992).*

1982), from the anthracosaurs *Pholiderpeton* and *Palaeoherpeton* (Clack 1983), and from *Acanthostega* (Clack 1989, 1992) that early tetrapods did not have stapes that were lightly built or apparently freely vibrating, but were rather stout with flattened or wing-shaped ends (Fig. 10.9). With this knowledge, it was discovered that the stapes of the anthracosaur *Palaeoherpeton*, closely related to *Pholiderpeton*, had been present on the specimen since its first discovery in the 19th century, but it had been unrecognizable as such using the search image of a rodlike bone (Fig. 10.10) (Clack 1983).

Other reassessments suggested that the skulls of the earliest tetrapods were not fully autostylic after all, but that their stapes seem still to have been acting as a brace between braincase and palate (Carroll 1980; Smithson 1982); the basal articulation was probably mobile, while even connections between the skull roof and palate were loose or even kinetic. *Acanthostega* is now thought to have had functional internal gills, and the stapes may still have been involved with breathing (Coates and Clack 1991). Finally, and importantly, the group Labyrinthodontia is not now seen as valid phylogenetically (see Chapter 9).

Along with the new paleontological discoveries went a revised appreciation of the fine-detailed anatomy of the ear regions in modern tetrapods. It became clear through the work of Wever (1978) that in modern amniotes, though superficially similar, the tympanic ears of lizards, crocodiles, and turtles showed differences not only in construction of their stapes and tympanic membranes (see also Presley 1984), but also

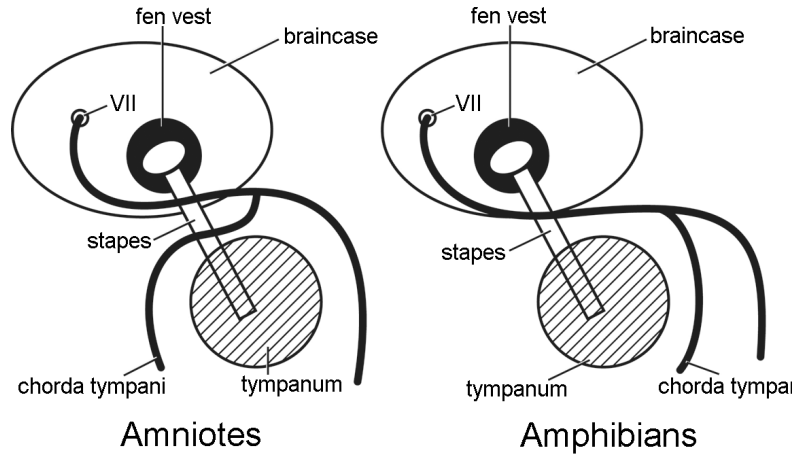



**10.10.** Specimen drawing of *Palaeoherpeton* showing where the stapes was preserved. The bone is similar to the stapes of *Pholiderpeton* (see 10.9).

in the inner ear and brain wiring. Birds show similarities to crocodiles (see also Carr 1992), while mammals are quite different from any other amniote group. These findings began to suggest the separate evolution of the tympanic ear in modern animals.

In 1979, around the same time that the stapes of *Greererpeton* and *Pholiderpeton* were first discovered, Lombard and Bolt made a fresh study of the evolution of the tympanic ear in the light not only of Wever's work, but also of Lombard's own work on frog ears (Lombard and Bolt 1979). It had become clear that the inner ear of frogs and amniotes showed fundamental differences that made it difficult to see how one could have evolved from the other (see Chapter 6). In addition to differences in the course of the perilymphatic duct (see Chapter 6), one of the nerves from the brain to the jaw follows a comparably incompatible route through the ear in frogs and amniotes (Fig. 10.11). Lombard and Bolt's study suggested that it was at least as parsimonious to assume a separate origin for the tympanic ear in several tetrapod groups as to assume a single origin as in the old view.

Since then have come the discoveries of the aquatic nature of early tetrapods, the flattened, robust form of the primitive tetrapod stapes, the likelihood of the role of the stapes in skull architecture, and the breaking

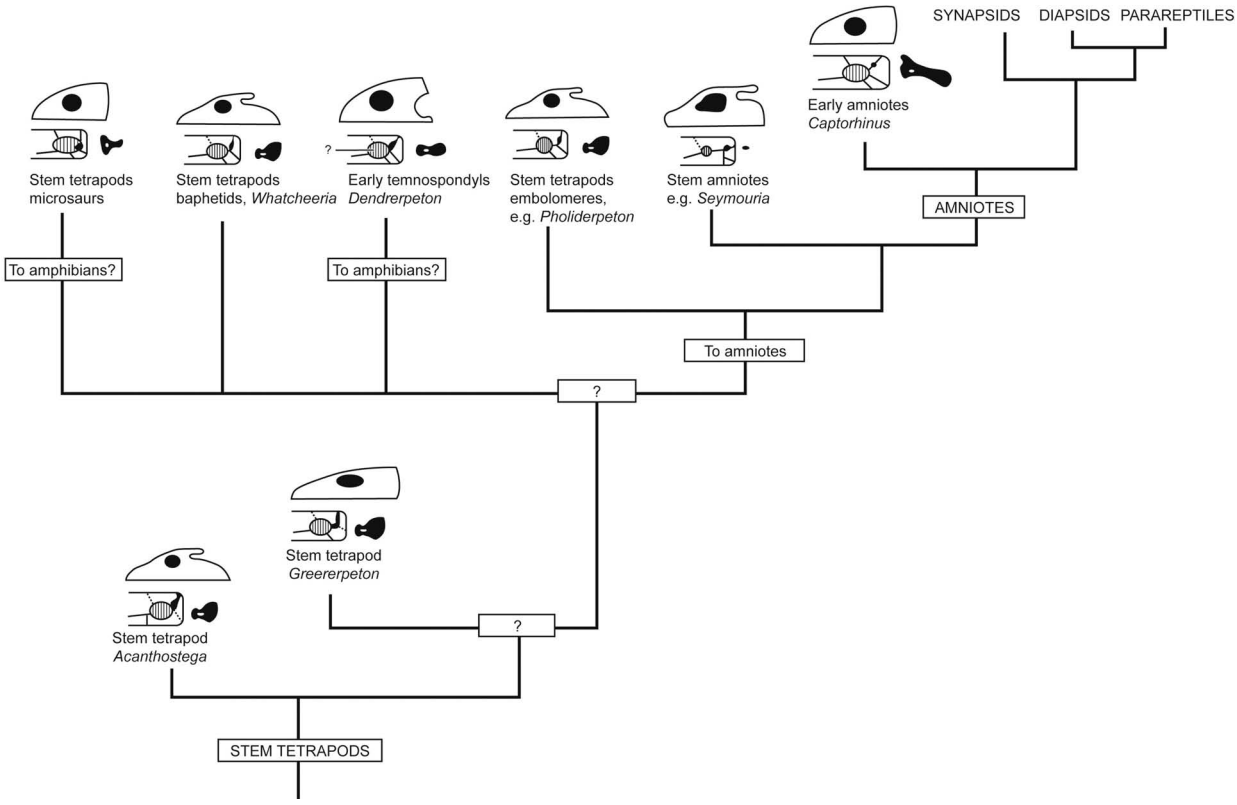



**10.11.** Diagram showing the contrasting course of the chorda tympani nerve in amphibians and amniotes.

up of the labyrinthodonts into a tetrapod stem lineage that gave rise to amniote and amphibian lineages. Following from this, a revised view of the evolution of the ear can be put forward (Fig. 10.12).

Apart from the fact that in tetrapods, the stapes fits into the fenestra ovalis in the side wall of the braincase, the otic regions of early tetrapods and tetrapodomorph fishes are rather similar (with the notable exception of *Ichthyostega*). The inner workings of the brain, including the receptors for sound, were also probably much the same, so it seems unlikely that tetrapods would have had the neural mechanisms for keen differentiation of sound stimuli. On the other hand, there is evidence that even modern fishes with no obvious adaptations to hearing in water do appear to perceive sound stimuli at least at low frequencies, and the same may therefore have been true of early tetrapodomorph fishes. By virtue of the close proximity of the stapedial foot plate to the saccular region of the braincase, there was doubtless some auditory function, perhaps to capture low-frequency waterborne or groundborne vibrations, but by and large, the best model for the hearing capacity of early tetrapods like *Acanthostega* is probably provided by lungfishes and primitive ray-finned fishes rather than any modern tetrapod.

The robust, flattened stapes of many of the earliest tetrapods, such as *Acanthostega*, *Greererpeton*, and embolomeres, appear to have been connected to the palatal bones in an echo of the way the tetrapodomorph hyomandibula was. The braincases of these animals were not well ossified, but it seems clear that they did not have many of the inner ear specializations of modern animals with tympanic ears. It has been suggested that instead of an otic notch, the embayment, positioned in the region of the old spiracular cleft, in fact still retained this original function and housed a persistent spiracular opening to the outside in forms such as *Acanthostega* (Carroll, in Panchen 1985; Clack 1989) (see Chapter 6). Because of this, the notch is better called something other than otic. The term "spiracular notch" is a possibility, but because its function cannot be ascertained, and may in any case have been different in different




**10.12.** Cladogram of early tetrapod and their ear characters. The fenestra vestibuli, shown hatched, starts as a hole bounded by otic capsule and occipital arch bones, and the dermal parasphenoid. The lateral otic fissure is open but the basi- and exoccipitals are co-ossified. The stapes, shown black, is a flat broad plate in early tetrapods, and is converted to a strut in early amniotes.

groups, a neutral term such as "temporal notch" has sometimes been used (Godfrey et al. 1987).

The first occurrence of what may have been a true tympanic ear is seen in the temnospondyl lineage, with *Balanerpeton* from the Viséan of East Kirkton (see Chapter 8). It had a broad embayment in the back of the cheek, but also the stapes is known to have been a relatively small bone. It is only known from the end nearest the braincase, but this suggests a relatively light bone directed toward the center of the embayment (Milner and Sequeira 1994). The arrangement bears close comparison with the ear region of frogs, and in Chapter 9, it was suggested that modern amphibians are the descendants of temnospondyls. If this is correct, the ears of frogs are a direct inheritance from this group of Carboniferous ancestors (see also Bolt and Lombard 1985; Sigurdsen and Bolt 2009). Evolution of a terrestrial hearing mechanism in temnospondyls may be consequent upon their development of the interpterygoid vacuities. If temnospondyls specialized as buccal pumpers, the vacuities could have allowed the roof of the palate a greater flexibility and facility for expansion. Given this, the basal articulation might have become redundant and immobile; thus, the skull became increasingly autostylic, eventually freeing the stapes from its bracing role, to be used instead as a specialized hearing ossicle (Clack 1992).

Alternatively, if lissamphibians are related to lepospondyls rather than to temnospondyls, the middle ear in frogs represents yet a further iteration

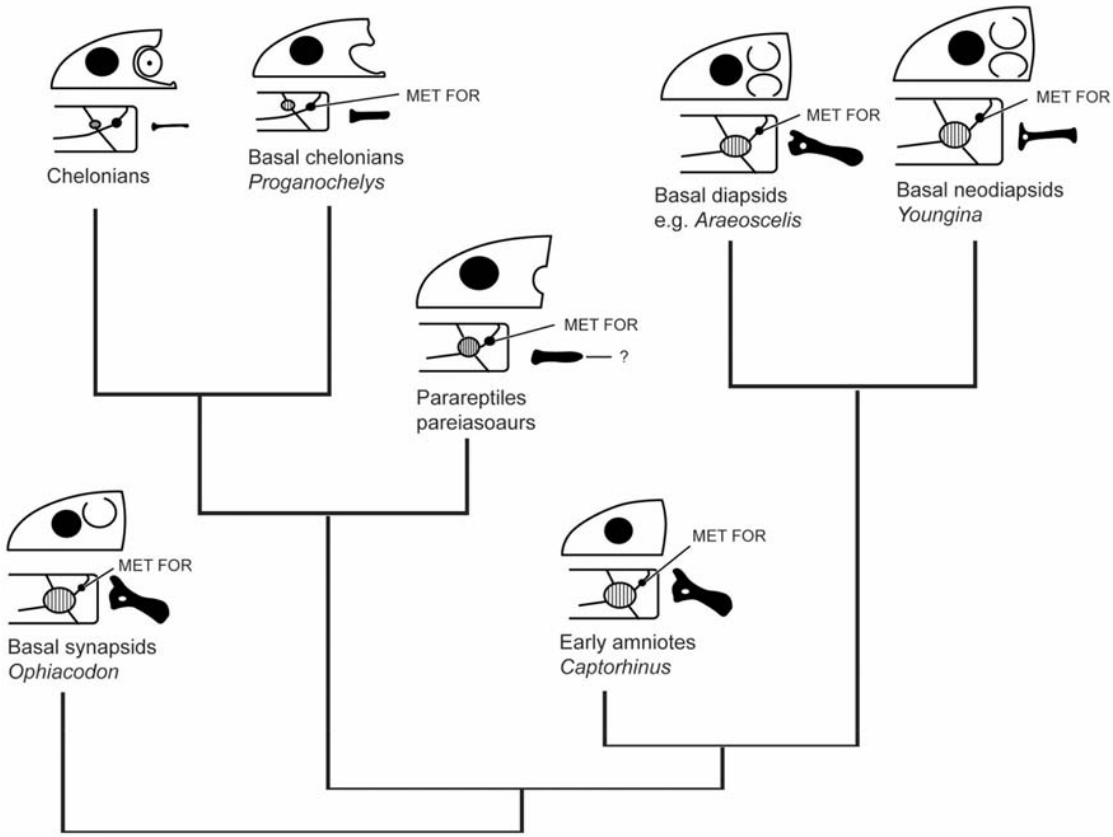
of the development of a tympanic ear because no such modification is seen in any lepospondyl (Laurin and Reisz 1997).

In this context, the otic region of *Eucritta* deserves mention (Figs. 8.14, 8.15). In the large baphetids *Megalocephalus*, *Spathicephalus*, and *Kyrinion*, the stapes is known to be of the stubby "winged" form seen in *Acanthostega*, *Greererpeton*, and *Whatcheeria*, a morphology not likely to be associated with a terrestrially adapted ear and tympanic membrane. However, the otic notch of *Eucritta* is of much the same shape and relative size as that of *Balanerpeton*, whose stapes is known to be like that of other small terrestrial temnospondyls that are assumed to have had tympanic ears. If *Eucritta* really is a baphetid, two explanations are possible. The first is that the earliest baphetids had tympanic ears like those envisaged in temnospondyls, and that in secondarily aquatic forms, this structure was lost. Alternatively, the notch of *Eucritta* was not otic but still spiracular. This carries the possible implication that the notches in early temnospondyls, similar in appearance to those of *Eucritta*, were not otic either. Unfortunately, the best way to test the strength of either of these hypotheses is to examine the stapes of *Eucritta*. It has not yet been found.

Some recent information on temnospondyls and baphetids may have a bearing on these questions. As described in Chapter 9, Robinson et al. (2005) discovered an undistorted stapes of the Carboniferous temnospondyl *Dendrerpeton*. It turned out to be relatively more slender than originally thought (Clack 1983) based on an incomplete example, and may well have been part of an early aerial auditory mechanism, though admittedly not one capable of receiving high-frequency sound. The stapes of *Kyrinion* (Clack 2003b) has the flattened shape of the stapes of *Pholiderpeton* and *Greererpeton*. However, it manifestly did not contact the palatoquadrate—indeed, because the braincase and palate were firmly united in this animal (see Chapter 9), there would have been no requirement for such contact. It appears to have been housed in some kind of free space, perhaps a potential middle ear cavity (Robinson 2005).

In some juveniles of the Triassic temnospondyl *Parotosuchus aliciae*, Warren and Schroeder (1995) have suggested that there was a persistent spiracle because of the association between the stapes and an oblique ridge running just in front of it beneath the cheek. This creates a wall that they suggested formed the boundary of a spiracular cleft, rather than a middle ear cavity. Second, some Late Triassic temnospondyls with otic notches have been discovered to have gill rakers preserved in their pharynxes (Van Hoepen 1915). The implications of this are that the animals, like colosteids, may have been feeding in water using gills. Whether they were breathing with the gills is unknown, but perhaps the existence of a tympanic ear in such cases is unlikely.

As described in the section on jaws, in all the early amniotes, there was no embayment at the back of the skull, and the stapes was acting as a structural brace between the jaw joint and the brain. The story of the



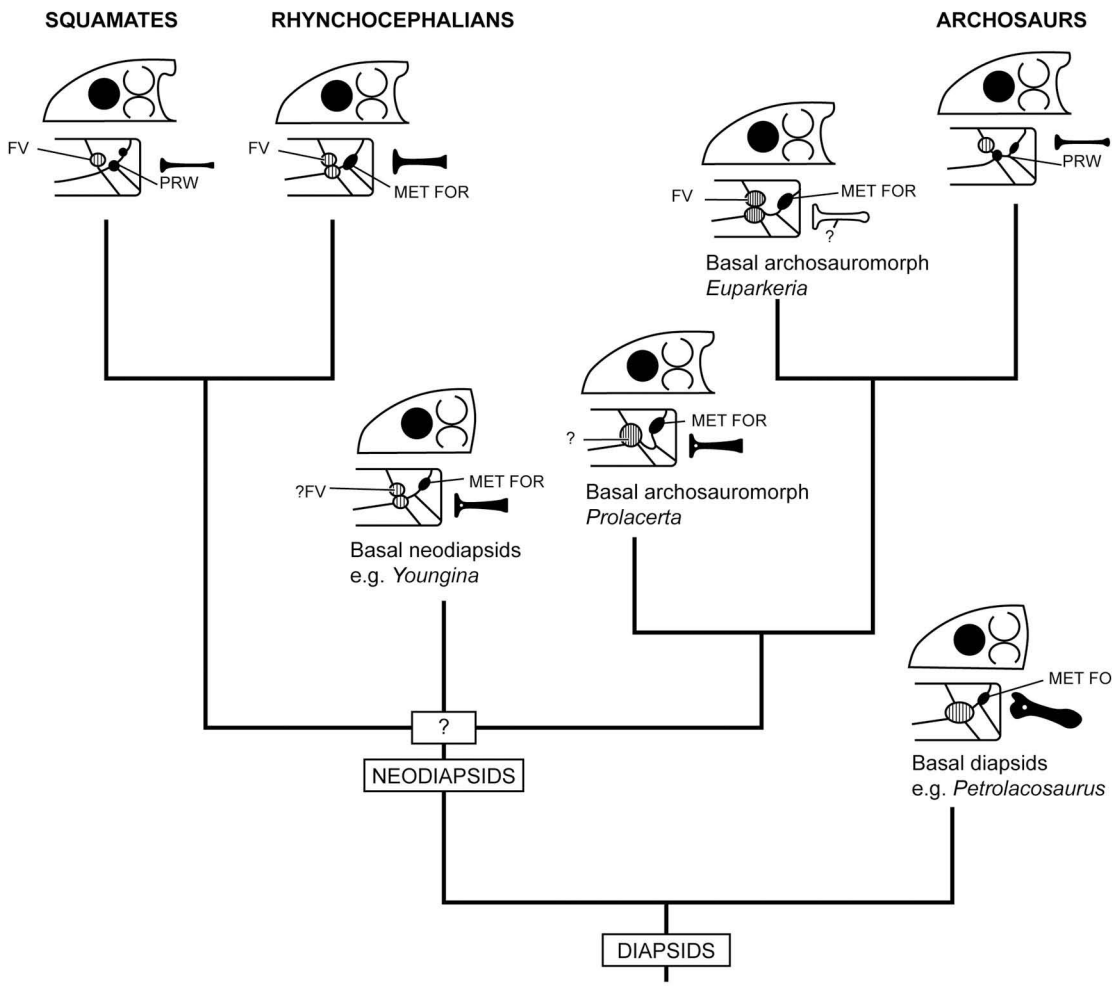

changes to the stapes, braincase, and skull architecture in amniotes is a complex one, but the fossil record of these features can be followed through evolutionary time in several different lineages, and some of these are summarized in Figures 10.12 and 10.13 (Clack 1997b). Turtles, mammals and diapsid reptiles can be shown to have evolved many crucial components of the tympanic ear separately from beginnings that all resemble those of early, effectively earless forms.

A critical stage in each lineage was the freeing up of the stapes from its early bracing function. This cannot be achieved without consolidating the skull by some other means, and these have been outlined in some amniote groups in the section on feeding.

Among early amniotes, a neat example demonstrates that it appears not to be difficult to evolve a tympanic ear from a nontympanic ear from scratch. In the parareptile group known as the nycteroleters, from the Permian of Russia, the most primitive forms lack any kind of notch. In the more derived forms such as *Nycteroleter*, a large tympanic notch is present, complete with a long, delicate rodlike stapes (Müller and Tsuji 2007).

Paralleling the changes to the stapes, there is a consistent pattern in the evolution of the fenestra vestibuli to be seen in the fossil record (Figs. 10.12, 10.13, 10.14). In the earliest tetrapods, the foot plate of the

**10.13.** Cladogram of amniotes and their ear characters. Same conventions as 10.12. The stapes reduces in diameter through the evolution of turtles and diapsids independently. MET FOR = metotic foramen. The metotic foramen is the remnant of the lateral otic fissure found in later tetrapods and diminishes further through their evolution. For mammalian ear evolution, see Figure 10.7.




**10.14.** Cladogram of diapsids and their ear characters. Same conventions as 10.12 and 10.13. PRW = pressure relief window. A reduced fenestra vestibuli and the PRW have appeared in archosaurs and lepidosaurs independently.

stapes is a relatively large component occupying a considerable part of the braincase wall. It contacts several of the braincase bones, including those of the otic capsule, the occipital arch and the sphenethmoid region, and in many cases also the parasphenoid. In fact, it lies more or less on the line of the embryonic metotic fissure that separates these discrete embryonic elements (see Chapter 2). This condition is found throughout early tetrapods, whether they be part of the stem lineage, reptiliomorphs, amphibian lineage, or lepospondyls, and there can be little doubt that it was primitive for tetrapods. Followed through the fossil record—which is especially good in amniotes—the relative size, but more importantly the position, of the fenestra vestibuli changes. It gradually shrinks relative to the braincase wall, and eventually its relationship to the occipital arch, sphenethmoid, and parasphenoid bones is broken and it becomes a hole that is completely defined by otic capsule bones. A small fenestra vestibuli indicates a small stapedial foot plate, which implies a more slender stapes, which in turn implies increased auditory refinement. These developments can be tracked as separate developments in each of

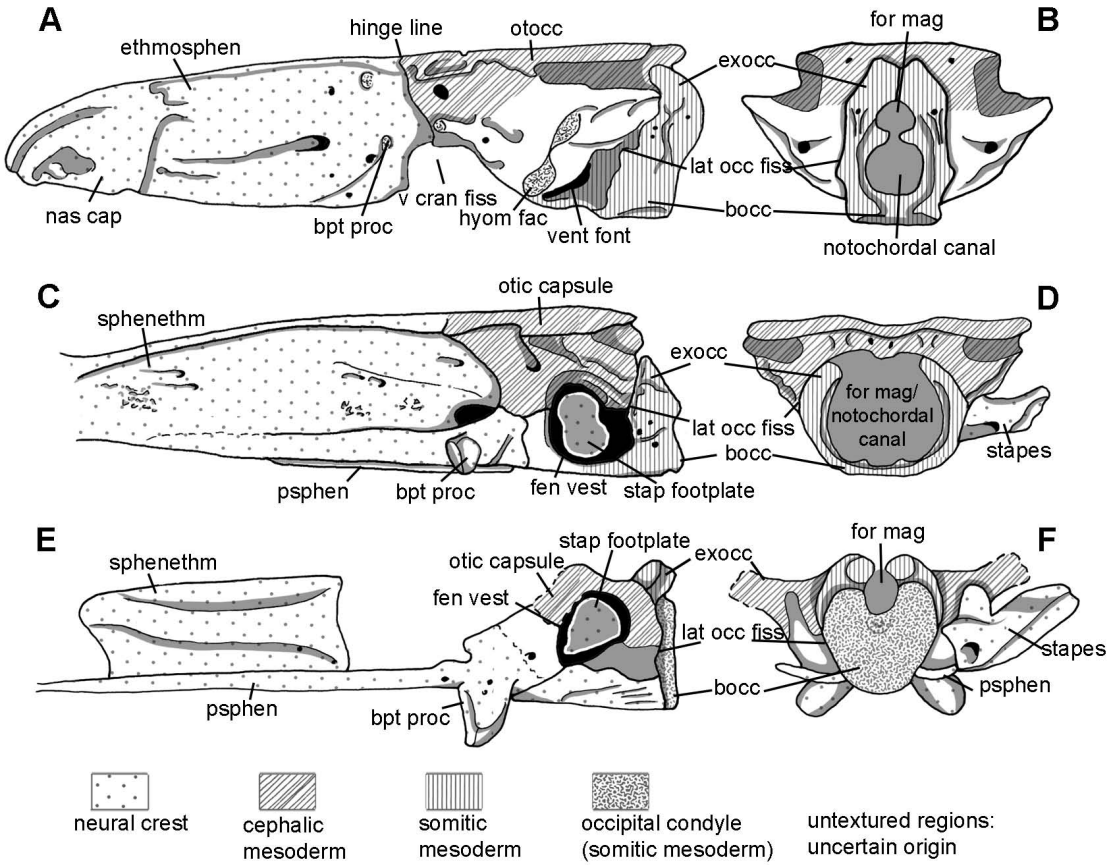
several amniote groups—diapsid amniotes (Fig. 10.14), turtles (Fig. 10.13), and mammals (Fig. 10.7).

A further stage in the refinement of higher-frequency reception was the evolution of a mechanism by which pressure waves, set up by sound vibrations impinging on inner ear fluids, could be relieved by the development of a separate window in the braincase wall. This is sometimes called the fenestra rotunda, or "round window." This pressure relief mechanism is an important part of the tympanic ear, and its evolution can be seen in the fossil record (Fig. 10.14). Like the changes to the role of the stapes, this one can be tracked separately in each of these amniote groups. All of them were apparently initiated only toward the end of the Permian, or possibly in the Early Triassic, in each of the groups. It has been suggested that the evolution of buzzing insects may have been one of the stimuli in developing an aerially adapted ear in amniotes (Clack 1997b). The timing of the evolution of the characteristics of an ear capable of receiving airborne sound well certainly corresponds to the huge radiation of insects that can be seen in fossil record of the Late Permian and Early Triassic. Alternatively, in some lineages such as mammals, with the evolution of nesting behavior, an additional stimulus might have been the ability to hear offsprings' higher-pitched cries.

The evolution of hearing in air was a slow and complicated process; far from being achieved and perfected by the earliest tetrapods, it was separately invented many times by different groups, and rather a long time after tetrapods first gained the land.

## EMBRYONIC ORIGINS AND EVOLUTION OF THE TETRAPOD OCCIPITAL AND OTIC REGIONS

Some insight into the formation of the tetrapod occipital region and its relationship to the otic capsule can be gained from consideration of the embryonic origins of the several braincase regions and how they have been affected differently during the fish–tetrapod transition. As outlined in Chapter 2, the braincase forms from a number of discrete components that contribute to the whole (Fig. 2.3). After their initial formation, the components may fuse to each other completely except for the necessary foramina for nerves and blood vessels, or gaps and fissures may remain even into the adult structure. The extent and pattern of fusion varies among different groups and taxa, but some key landmarks are usually identifiable, such as the ventral cranial fissure between the front and rear halves of the braincase in many early forms. In many lobe-fins, this fissure extends dorsally to the roof of the skull to contribute to the cranial hinge characteristic of certain groups (e.g., *Eusthenopteron*, Figs. 2.1, 2.11, 6.9). In the earliest tetrapods, the ventral cranial fissure can still be identified (e.g., *Acanthostega*, represented by a suture, Fig. 2.11), though it is eliminated in most later ones. The lateral otic fissure is another such landmark, visible during the embryonic development of all modern vertebrates and evident in many fossils, including fish such as *Eusthenopteron* and early




**10.15.** Braincases showing comparable structures and embryonic origins of tissues. (A, B) *Eusthenopteron* in left lateral and posterior views. (B, C) *Acanthostega* in left lateral and posterior views. (D, E) *Greererpeton* in left lateral and posterior views. *Based on Clack (2001b).*

tetrapods such as *Acanthostega*. Figure 10.15 shows the braincases of *Eusthenopteron*, *Acanthostega*, and *Greererpeton* for comparison.

The fissures appear to correspond to the junctions between tissues of different embryonic origins (Clack 2001b). In fossil forms, though the embryonic development of the animals cannot be directly observed, some of the boundaries are clear enough for one to infer that the same embryonic tissue contributed to the corresponding parts as in modern forms. Thus, for example, it appears that the otic capsule was formed by a type of mesoderm associated with purely cranial development (cephalic mesoderm), whereas the underlying parachordal cartilages and occipital arch material was formed from mesoderm that is more closely associated with the rest of the body (somitic mesoderm). The anterior parts of the braincase, including the trabecular cartilages, the sphenethmoid, and the basisphenoid, are formed from neural crest, as of course is the underlying dermal bone, the parasphenoid. The hyomandibula or stapes is also largely formed from neural crest, being a branchial arch element, and it appears that some of the otic capsule surrounding the foot plate of the stapes might also be of neural crest origin, though this is debated (see Chapter 6). Figure 10.15 shows the inferred domains of these components in three animals, *Eusthenopteron*, *Acanthostega*, and *Greererpeton*.

In Chapter 6 the point was made that in the sequence *Eusthenopteron—Panderichthys—Tiktaalik—Acanthostega*, some changes to the otic region of the braincase appear to have occurred rapidly between *Panderichthys*, and *Ventastega* and *Acanthostega*. Whereas *Panderichthys* and *Tiktaalik* retain fishlike relationships between the otic capsule and hyomandibula in possessing a lateral commissure, *Ventastega* and *Acanthostega* are essentially tetrapod-like. At the same time, it is apparent that *Acanthostega* had an occipital construction in most ways just like *Eusthenopteron*. This region remained conservative, changing little despite the radical restructuring going on in parts of the otic capsule. If the embryonic origins of these two regions are taken into account, some inferences can be drawn. Those parts of the braincase that underwent the most radical change are those associated with neural crest. Along with changes to the otic region affecting the hyomandibula/stapes are others to the front and mid parts of the braincase. The cranial hinge is eliminated, the basisphenoid joins up with the basioccipital, and large, bulbous basipterygoid processes are produced, a process that seems to have begun in *Tiktaalik*. These parts too are all of neural crest origin, an observation that carries the implication of increased activity of neural crest tissue in the early stages of tetrapod braincase evolution.

If another early tetrapod is added to the sequence—and only *Greererpeton* is known in sufficient detail to be useful—further developments of this change can be seen (Fig. 10.15). The parasphenoid has elongated to underlie both parts of the braincase, while the anterior portion of the braincase itself is longer with respect to the posterior, an effect also explored in Chapter 6. But there has been one further development. In *Greererpeton*, the occipital condyle has developed and become a solid articulating surface.

In modern animals (and caution must be exercised here because only birds have been examined in this context), the condylar part of the occipital complex is actually added at a later stage during the embryonic development of the braincase than the rest of the basioccipital. It forms from an extra segment of the somitic mesoderm that is incorporated into the braincase. Could the contrast between *Acanthostega* and *Greererpeton* reflect this addition of the extra segment, with *Acanthostega* lacking it, and later tetrapods from *Greererpeton* onward having gained it? Are the contrasts in occipital formation seen in the two ancient lineages reflected in the embryonic development of animals today? Such questions can only really be approached by looking at the embryonic development of modern animals, for instance by investigating how amniotes might differ from amphibians.

One of the critically affected regions at the fish–tetrapod transition was that where the head of the hyomandibula and its articulations to the braincase became transformed into the stapes and fenestra vestibuli (see Chapter 6 and Figs. 2.11, 6.9). The fenestra vestibuli is a gap in the bones lying just at the boundary between otic capsule, occipital arch, and neural crest domains. The subsequent evolution of this region and how

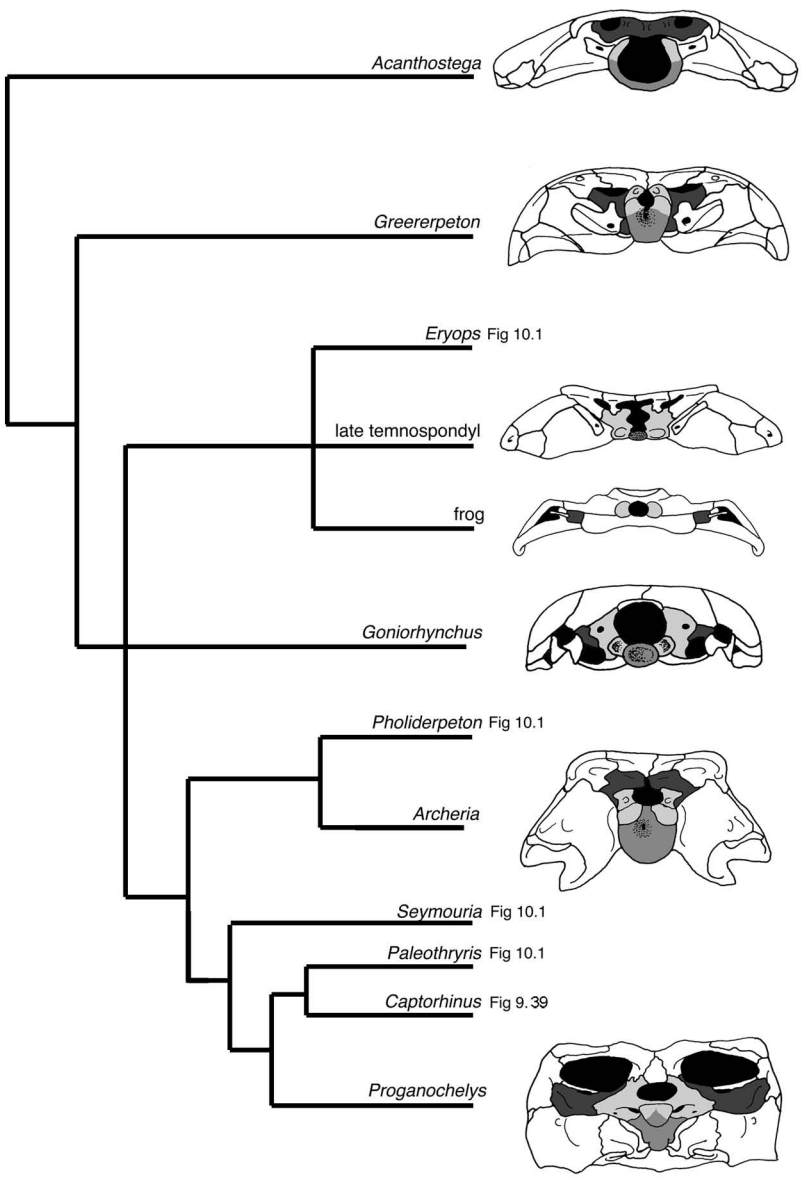
the gaps between these tissues are sealed is the key to the evolution of the tetrapod auditory apparatus. Because it involves modifications to the occipital region, the ear region was strongly affected by changes to the neck joint (Clack 2001b). For example, the size and extent of the exoccipitals and their relationship to the opisthotic bones affects the formation of the round window in diapsids. Other relationships between the occipital region and the ear are outlined in the next section.

### THE NECK JOINT

The evolution of a neck joint may well have gone hand in hand with increasing reliance on air breathing in early tetrapods and their forerunners. For example, the operculogular region in the tetrapod-like fish *Panderichthys* was relatively reduced, it was absent in *Tiktaalik*, and in modern lungfishes, it has also disappeared. The ability to raise the head and widen the mouth cavity to gulp air is increased by this means. *Acanthostega*, with an occipital region like that of *Eusthenopteron* (see Figs. 2.11 and 10.16), had not developed the flexible neck joint seen in later tetrapods, but it had lost the operculogulars and was probably an air gulper—a bit like a lungfish, which did not spend much time out of water.

It is possible to track changes to the neck region among early tetrapods, with interesting results. First, there is a consolidation of the braincase so that the front ethmosphenoid becomes more firmly attached to the rear occipital region. The notochord in fish like *Eusthenopteron* penetrates to about the midpoint of the braincase; in the earliest tetrapods, in which the posterior part of the braincase is much shortened, the notochord necessarily runs for a shorter distance inside it. Among Carboniferous forms, the space for the notochord becomes a shallow cone in shape. Eventually, only a dimple is left to mark the position of the front of the embryonic notochord. The resulting concave surface is used as the articulation surface, which is matched by a convex surface on the most anterior centrum (Fig. 10.16).

Above the basioccipital lie the exoccipitals, a pair of bones that flank the hole through which the spinal cord enters the brain. In some ways, they resemble paired halves of a neural arch. In *Eusthenopteron*, *Acanthostega*, and many early tetrapods, they are quite small and are loosely attached to the otic region of the braincase. In some early tetrapods, they articulate with the arch of the atlas vertebra or with the proatlas. Following the fate of these occipital arch elements shows that in the anthracosaurs and in the amniote lineage, they stay as relatively small, loosely attached bones. The exoccipitals do not make contact with any part of the skull roof, so that contact between the braincase and skull roof is made via the otic capsules (Figs. 10.1, 10.16). Through the gaps that remain separating the exoccipitals from the otic capsules, nerves such as the vagus and blood vessels such as the jugular vein pass out to the body. In early members of the amniotes, and in some modern ones such as turtles, part of each exoccipital joins with the basioccipital to form




**10.16.** Occipital construction in tetrapods. In *Acanthostega,* there is no occipital condyle, and basi- and exoccipitals are co-ossified; in the early tetrapod *Greererpeton,* the concave condyle is formed from the co-ossified basi- and exoccipitals. In temnospondyls, the occipital condyle is formed mainly or entirely from the exoccipitals, which contact the skull roof and exclude the opisthotics from the occiput. In frogs, the basioccipital is not distinguishable, and the paired condyles are formed from the exoccipitals. In microsaurs, the condyle is formed from basi- and exoccipitals in roughly equal proportions. In anthracosaurs, and seymouriamorphs, the concave condyle is formed mainly from the basioccipital with small exoccipitals that do not contact the skull roof. In the early amniotes *Paleothyris* and *Captorhinus,* the convex condyle is basioccipital, as in diapsids, but in turtles, it is formed from basi- and exoccipitals. Opisthotic, dark shading; basioccipital, medium shading; exoccipital, light shading. (Not to scale.)

the condyle with which the atlas vertebrae articulates. The condyle in amniotes is always convex, though even here, sometimes there is a small dimple representing the old course of the notochord. In mammals, the basioccipital's role diminishes, and the condyle becomes a double one formed only by the exoccipitals (Fig. 10.16). In all amniotes, it is the otic capsule, especially the opisthotic paroccipital process, that comes to form the main part of the rear of the skull bearing the muscles running to the vertebral column.

In the amphibian lineage of tetrapods, something quite different happens. The exoccipitals come to be important from an early stage. They increase in size among temnospondyls so that they grow over much of

the rest of the occipital surface, masking off the otic capsule from behind and growing upward to join the skull roofing bones (Figs. 10.1, 10.16). In these animals, it is material from the occipital arch that provides much of the anchorage between the braincase and the skull roof, while the otic capsules remain relatively poorly ossified. The basioccipital becomes gradually reduced in temnospondyls until it leaves a gap between the two exoccipital facets that remain to form the condyle (Watson 1926). The atlas vertebra has a matching paired articular surface. Here the back of the skull was strengthened by quite different means from that in amniotes (Smithson 1982) (see Chapter 9). A similar occipital formation is found among modern amphibians, which also have a double condyle like temnospondyls. Among microsaurs, the form of the occipital condyle is characteristic and highly specialized as a concave horizontally configured figure-eight shape (Fig. 10.16) (Carroll 2000a).

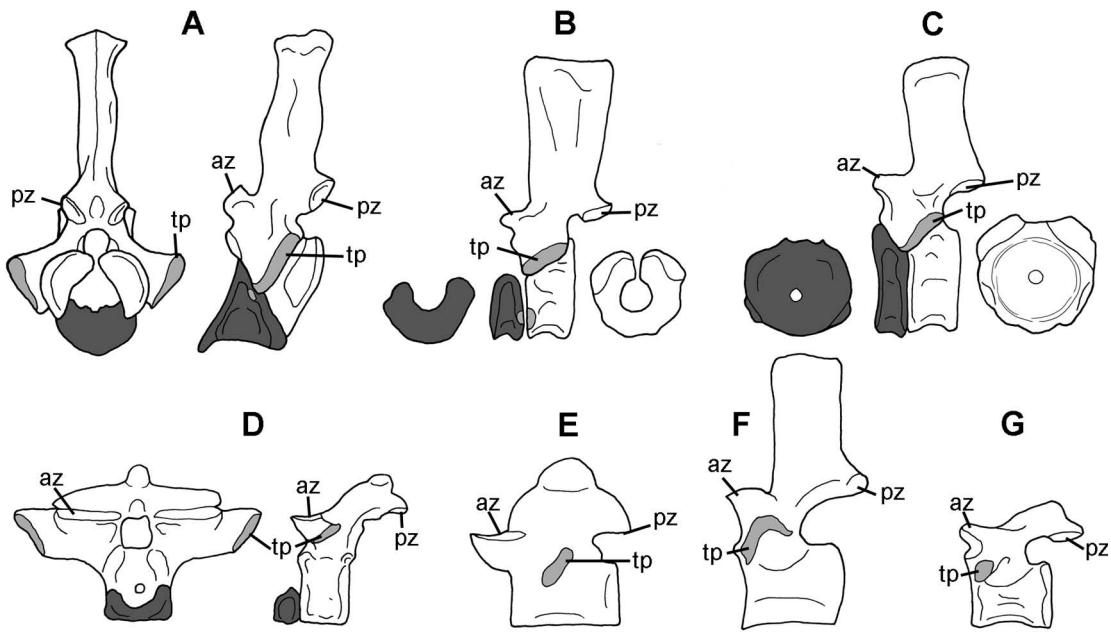
One inference from this is that the neck joint started from a structure that was relatively unstable for a terrestrial animal and became strengthened gradually as the animals became more and more adapted to life on land. It seems to have been achieved by a different method in each of the two groups of animals that have left living descendants. The way the back of the skull became strengthened to receive neck muscles also had an effect on the role the stapes played, and thus on the evolution of hearing. For example, in diapsids, the stapes began as a strengthening device for the back of the skull, but with the development of a paroccipital process, the stapes could be freed from its former role to become a freely vibrating ossicle. In mammals, the occiput was strengthened by increasingly firm connections between the opisthotics and palate, as well as between the opisthotics and skull roof. The fossil record shows an inverse relationship between the extent of these connections and the size of the stapes (Allin and Hopson 1992). In temnospondyls, the occiput was strengthened by a different method: the expansion of the exoccipitals and their intimate connection to the skull roof. In addition, the palate and skull roof became firmly tied to each other at the basal articulation and around the margins. Breathing by buccal pumping was enhanced by the palatal vacuities.

The formation of an occipital condyle gives another example of a terrestrial adaptation that was achieved convergently several times among tetrapods, with extant and extinct groups showing a range of patterns.

## Postcranial Modifications for Terrestriality

### Vertebral Column: Centra, Atlas–Axis, Vertebrae, and Ribs

It might be supposed that one of the parts of the skeleton to have been most affected at the fish–tetrapod transition would be the vertebral column. It is the vertebral column that supports the weight of the body when it is suspended between the pillars of the four limbs, so that in a terrestrial animal, adaptations to take this weight might be expected. The information now coming from creatures like *Tiktaalik* and *Ichthyostega* are giving mixed messages about the early evolution and functioning of the axial




skeleton during the transition, and it is no longer so easy to determine what kind of axial morphology is primitive.

**10.17.** Types of vertebrae in early tetrapods. (A) *Eryops,* a rhachitomous temnospondyl, posterior view at left to show paired pleurocentra, lateral view at right. (B) *Proterogyrinus,* a gastrocentrous anthracosaur, intercentrum at left, pleurocentrum at right. (C) *Archeria,* an embolomerous anthracosaur, intercentrum at left, pleurocentrum at right. (D) *Seymouria,* a gastrocentrous seymouriamorph, anterior view at left to show small intercentrum, lateral view at right. (E) *Captorhinus,* a gastrocentrous (or holospondylous) early amniote with domed neural spines. (F) *Archaeothryis,* a gastrocentrous (or holospondylous) early amniote with bladelike neural spines. (G) *Pantylus,* a gastrocentrous (or holospondylous) microsaur. All lateral views shown with anterior to the left. Intercentrum dark shaded, rib articulations light shaded. (Not to scale.) Note the sloping zygapophyses in the animals (A–C) and the almost horizontal ones in the animals (E–G). az = anterior zygapophysis; pz = posterior zygapophysis; tp = transverse process.

### CENTRA

In fishes such as *Osteolepis* and *Eusthenopteron*, the vertebral construction is that called rhachitomous—that is, the main element—is a horseshoe-shaped structure ventrally, usually single but in some circumstances with a split between two halves at the midline. This is the intercentrum. Dorsal and posterior to that lie smaller paired elements called pleurocentra. These elements lie beside the notochord and sheathe it to a greater or lesser extent, though the notochord would still have been present and relatively unconstricted (Figs. 2.5, 6.10). These elements appear to have ossified from a cartilage precursor that formed in the sheath around the notochord (Carroll et al. 1999). Often, though their external surfaces would be covered in smooth periosteal bone, the internal surfaces remained unfinished where the surfaces were covered only in cartilage. In the tetrapods, the intercentrum bore a laterally placed facet onto which one of the rib heads articulated.

This kind of construction is found more or less universally in the earliest tetrapods (Fig. 10.17). *Acanthostega* shows a textbook form (Fig. 6.10), though in *Ichthyostega* the centra are single hoops and are not of the typical rhachitomous type. *Whatcheeria* and *Pederpes* also have more or less classic rhachitomous centra, and the style is found throughout the majority of Paleozoic temnospondyls. There seems to be no doubt that this kind of centrum is primitive for tetrapods, and at least in the earliest forms, it was associated with an aquatic lifestyle.

Developments to the centra during the transition seem to lag behind those to the neural arches and ribs. Although *Acanthostega* has barely developed zygapophyses and has short, straight ribs (Figs. 5.20, 6.10), *Ichthyostega* and most other early tetrapods have more or less robust ribs and conspicuous zygapophyses. These are presumably associated with changes to locomotory patterns, though that may not be the whole story. The lack of ossified centra, or indeed neural arches, in *Tiktaalik* is curious given the broad, imbricating ribs, and it also frustrates attempts to understand vertebral evolution at this stage.

There are other forms of vertebral construction found among tetrapods from the late Early Carboniferous onward, and there seems to be a phylogenetic as well as a functional component to their distribution. Figure 10.17 summarizes the different types of vertebral construction seen in early tetrapods. Stem amniotes, or the reptiliomorph lineage, exemplified by anthracosaurs, seymouriamorphs, and amniotes, have what are called gastrocentrous vertebrae. In this form, the dominant element is the pleurocentrum, which is again a horseshoe-shaped structure, while the more anterior intercentrum is a small ventral wedge. The neural arch sat securely on the pleurocentrum supported by broad facets, or even sutured to it. In early anthracosaurs, the pleurocentrum was incompletely ossified dorsally, but in more specialized forms, it became a complete disk or cylinder. In some members of the lineage, the intercentrum became less and less conspicuous and eventually disappeared. Like the rhachitomous form, the gastrocentrous type ossified from a cartilaginous precursor, and the distribution of periosteal to unfinished surface is comparable (Carroll et al. 1999).

Another type of vertebral construction is found among the lepospondyls. Here, centra are almost universally single cylinders, often spool shaped, and always sutured or even fused to the neural arch, and this is called holospondylous (Fig. 10.17). In a few forms, an additional small wedge-shaped ventral element, presumed to be an intercentrum, is present, but these are exceptions. It is also notable that in later amniotes, the form of vertebral construction approaches that of the holospondylous groups (Carroll et al. 1999).

It is natural to try to attribute some functional interpretation to these varieties of vertebral types. Among the earliest was that by Parrington (1977), who built models of the various types and subjected them to a range of tests. He concluded that the rhachitomous type allowed the vertebral column to twist at the same time as bending laterally. Panchen (1966, 1967) took the matter further and suggested that the rhachitomous form was associated with use of the axial musculature for lateral movements and swimming. He postulated that in swimming or laterally flexing animals, the axial musculature, founded on the ribs, required good support from the column. With the emphasis on the intercentrum, the rhachitomous column would provide this better than the gastrocentrous, in which the intercentrum was small. Conversely, in the gastrocentrous column, emphasis would have been on the foundation for the neural

arch, that is to say on the pleurocentrum, and this made more sense in an animal that raised its body off the ground and relied on limb (appendicular) muscles for its locomotion. Thus, the rhachitomous type might be expected in more aquatic forms, such as *Acanthostega* and many temnospondyls, whereas the gastrocentrous type might be expected in more terrestrial forms such as amniotes and their kin.

The idea fits in with quite a number of observations in early tetrapods and is tested by some exceptions found in both temnospondyls and anthracosaurs. For example, in the secondarily aquatic embolomeres, the emphasis has almost been shifted back again, so that the intercentra become larger once more and they form complete disks like the pleurocentra (Fig. 10.17). This is known as embolomerous. The vertebral column becomes composed of a series of disklike central elements. By contrast, in some of the larger and more permanently aquatic temnospondyls, the pleurocentrum is reduced in size until it disappears in the later forms, while the intercentrum becomes a complete, often solid disk. These centra are described as stereospondylous. In the colosteids, there appears to have been another instance of the evolution of almost complete ring centra, where the pleurocentra are enlarged in an otherwise more or less rhachitomous column (Godfrey 1989a). *Crassigyrinus* seems to have had two more or less equal parts to its centra, though both seem to have remained cartilaginous dorsally (Panchen 1985). The evolution of disklike centra seems to have occurred commonly among swimming forms, and it is also found in the much later marine reptiles such as ichthyosaurs. By contrast, some of the more terrestrial temnospondyls, such as a peculiar animal called *Peltobatrachus* (Panchen 1959) and some of the dissorophoids including *Doleserpeton* (Bolt 1969; Sigurdsen and Bolt 2010, there has been the evolution of something approaching the gastrocentrous form of centrum. The little *Casineria* from the mid-Viséan of Scotland is the earliest known example of gastrocentrous vertebrae with cylindrical pleurocentra and small intercentra, and the creature appears to have been fully terrestrial (Paton et al. 1999) (Fig. 7.9). Fully gastrocentrous vertebrae are also found in the amniotelike creature *Westlothiana* from East Kirkton (Fig. 8.17).

Of course, there are some animals that do not fit into this neat scheme, one of the best known being *Eryops* (Fig. 9.10). This large temnospondyl appears to have been capable of land locomotion and of carrying its body weight entirely by limbs, but its vertebrae are rhachitomous (Moulton 1974). The story is probably more complex than that painted above, because several important factors, such as the angle that the zygapophyseal facets make to the column, have been left out of the equation (Holmes 1989b).

Because some growth series are known for a few early tetrapods, especially temnospondyls, it is possible to say a little about the way their vertebral centra became ossified. Centra in the earliest tetrapods, whether pleurocentra or intercentra, began as paired elements that often became co-ossified in the midline. The centra of younger individuals enclose a

larger space for the notochord, and the ossification of the centra gradually encroaches into the space to occlude the notochord to a greater or lesser degree. From the distribution of unfinished versus periosteal surface, it seems reasonably certain that the centra formed first from cartilage that was gradually replaced by bone during the animal's growth, as in typical endoskeletal development. The pattern can be described as ossification from the inside to the outside (Carroll et al. 1999).

Furthermore, it is also clear that ossification of the vertebrae began at the front of the column and increased backward as the animal grew. That order is in accord with the way the vertebral column is initiated in the embryo, with embryonic segmentation and somite formation starting from the front and working backward. There is evidence for this kind of development and vertebral form in most early tetrapods that at one time would have been called labyrinthodonts. At the same time, it is interesting to note that the reverse order applies to the fin rays and spines of the tail in *Eusthenopteron*, in that they start to ossify from the rear forward. Use of the tail in swimming from an early stage may be the operating factor here, emphasizing the changes that can be brought about by the needs of function in some cases (Cote et al. 2002).

In the lepospondyls, the situation is quite different. No lepospondyl is known in which the centra are not obviously cylindrical, even in the smallest and presumed youngest individuals ever found, and even in those forms where what appears to be an intercentrum is present. This is not simply a matter of size or maturity. Some of the smallest temnospondyls and anthracosaurs are smaller than many lepospondyls, and some lepospondyls are larger than some small temnospondyl species, but still this consistent difference pertains. It does seem, however, that although small, young lepospondyls had cylindrical centra, the centra were not well ossified. In the flattened fossil vertebrae, a clear X shape is often seen, representing the walls of a spool-shaped element in which the cone-shaped recesses for the notochord are outlined. The outer bony skin of the centrum was present, but the inside was still soft. This indicates a contrasting pattern of ossification from either temnospondyls or anthracosaurs in that it proceeds from the outside to the inside. It is not clear whether they were preformed in cartilage or ossified directly around the notochord, but the latter is the case in modern salamanders. In frogs and amniotes—though the vertebrae are in some ways similar in final appearance to those of lepospondyls—the centra form first in cartilage. However, the details of ossification and formation of vertebral centra are complex and different among many of the modern groups, so that homologies between the centra of fossil tetrapods and modern ones are almost impossible to be sure about. Although cylindrical centra in lepospondyls are something they all show in common, it remains uncertain whether this represents a single shared derived character. Its appearance among several other groups might give cause to suspect that it is a parallelism and that the constraints of making vertebrae in a small animal might be involved in all of them (Carroll et al. 1999).

It is true that modern amniotes end up with centra that are similar in appearance to those of some lepospondyls, while none shows anything similar to the centra of early tetrapods. This is one of the arguments that have been used in the debate about the relationships between amniotes and some lepospondyl groups. Nonetheless, there are sufficient similarities between the centra of early amniotes and animals such as seymouriamorphs to suggest that even though their developmental patterns might have diverged, the amniotes nevertheless had ancestors whose vertebrae were typically gastrocentrous.

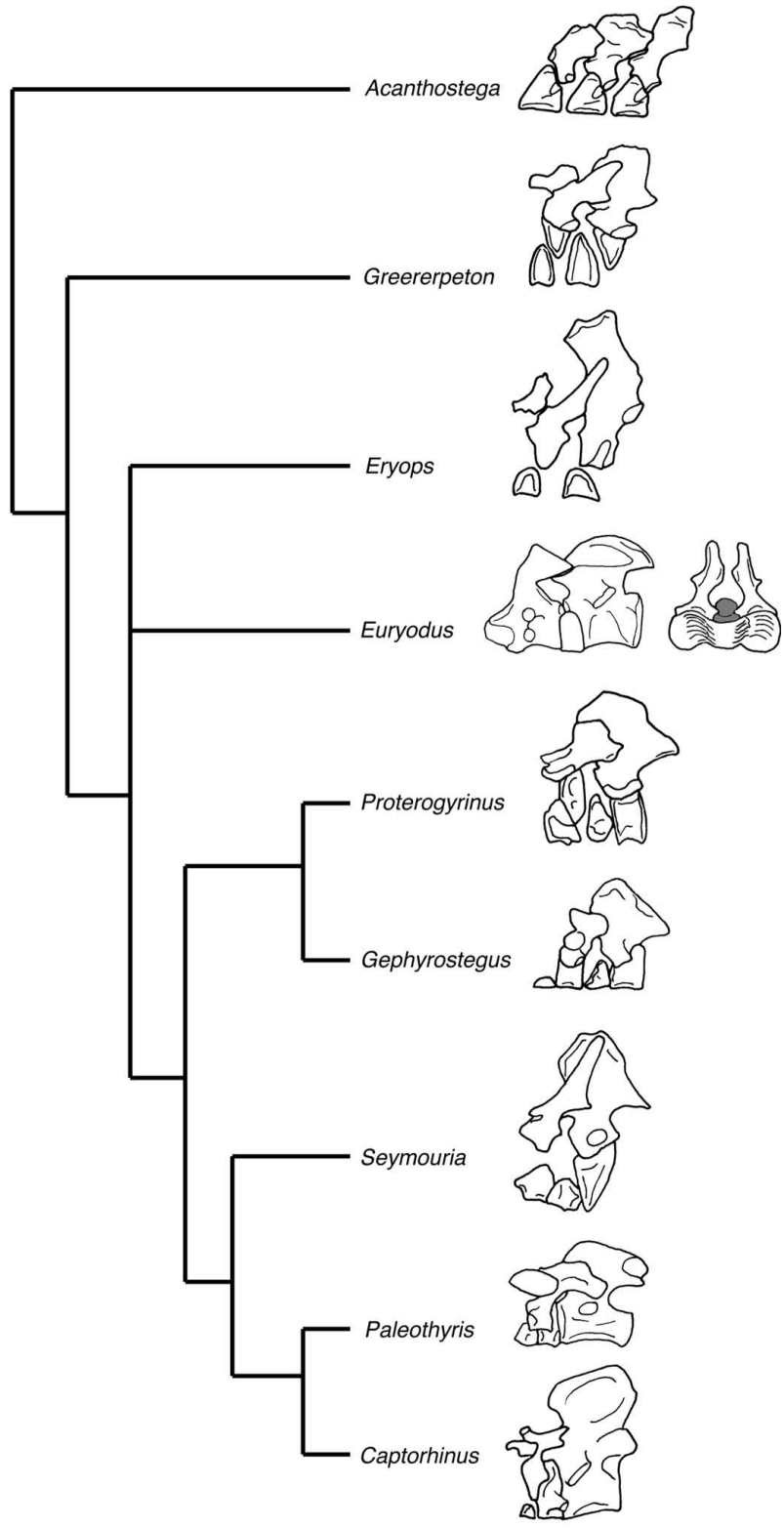
Something that has not been generally considered when trying to assess the function of early tetrapod vertebrae is the possible connection between vertebral construction, body wall musculature, and the movements of breathing and locomotion. In early tetrapods, the axial musculature, supported by the ribs, acts largely in locomotion. The same is true of modern salamanders. While it is so engaged, the part that both the muscles and the ribs can play in the operation of aspiration breathing may be constrained. Thus, it may be that rhachitomous animals using body wall muscles for locomotion had to remain buccal pumpers. With the development of gastrocentrous vertebrae, the freeing of axial musculature from their role in locomotion allowed the ribs and the intercostal muscles to be used in the movements of costal ventilation.

## ATLAS–AXIS

There is one region of the vertebral column that becomes differentiated from the rest early on in tetrapod history, and that is the most anterior part. The two most anterior vertebrae—the atlas and axis—become modified to provide support and flexibility for the neck joint, and their development echoes that of the occipital region of the skull (Fig. 10.18). In *Acanthostega*, even though there is little to distinguish most of the vertebrae from one another along on the column, at the front, the atlas and axis are already recognizable (Coates 1996). The atlas arch is quite small, whereas the axis arch has a neural spine that is longer than average front to back, though it is shorter than the other trunk neural spines. There seem to be no atlas pleurocentra, but the intercentrum is slightly longer than average, and furthermore, where other intercentra are usually formed from two separate halves, the atlas intercentrum is a robustly built single element.

Between *Acanthostega* and the tetrapods of the mid-Carboniferous, there is little information on the development of the atlas–axis complex. That of *Ichthyostega* is still unknown. The next early tetrapod that gives any clues is *Greererpeton* from the Namurian (Godfrey 1989a). In this animal, the atlas arch was relatively a little smaller than in *Acanthostega*, and its position was shifted so that the axis arch was clasped between each half (Fig. 10.18). There was a small proatlas; though this might also have been present in *Acanthostega*, it has not been found. Proatlases are such small elements that they are often lost in disrupted specimens, but

**10.18.** Atlas–axis construction in early tetrapods; the early tetrapods *Acanthostega* and *Greererpeton,* the temnospondyl *Eryops,* the microsaur *Euryodus,* the anthracosaurs *Proterogyrinus* and *Gephyrostegus,* the seymouriamorph *Seymouria,* and the early amniotes *Paleothyris* and *Captorhinus.* Anterior is to the left in each case. In *Acanthostega,* the third vertebra has been included to show its longer spine. The atlas–axis complex of the microsaur *Euryodus* is shown in anterior view at right. (Not to scale.)



it is thought that they articulated with the exoccipitals and the atlas arch. The axis arch in *Greererpeton*, as in most other subsequent tetrapods, had both its halves firmly fused together, reflecting its role in supporting occipital musculature. The atlas and axis centra looked little different from other trunk centra. There was no expanded bony surface to correspond to the large occipital condyle present in the skull of *Greererpeton*, so that it must be supposed that the joint was partly cartilaginous. There are few atlas–axis vertebrae fully described from early temnospondyls, one of the exceptions being, not surprisingly, *Eryops*. The reason for this may simply be lack of preservation, or it may be that the region was poorly ossified or only loosely articulated in the intact animal. There seems to be a contrast here with the amniote lineage.

In the lineage leading to amniotes, along with loss of the atlantal neural spine went the fusion of the atlantal pleurocentrum to the axial intercentrum, to form a compound central element supporting the atlas arch, while the axial neural arch became fused to its pleurocentrum (Fig. 10.18) (Sumida and Lombard 1991; Sumida et al. 1992). Some early amniotes still retained a proatlas articulating with the exoccipitals, for example in *Paleothryis*, *Captorhinus*, and the synapsid *Ophiacodon*. Axial neural arches in the amniote stem lineage in general tend to be taller in height and longer from front to back than other trunk arches. As in many early tetrapods, the facet on the atlas arch did not precisely match the shape of the occipital condyle of the braincase with which it articulated, so that there must have been cartilage present to complete the articulating surface.

A widely distributed feature of the anterior column in early tetrapods is that the neural spine of the third, or sometimes the fourth, vertebra is noticeably shorter than those either side of it. A possible explanation is that this helps in flexibility of the neck and the ability to raise the head. It prevents the three neural spines from fouling against one another as the spine flexes upward.

One group, the microsaurs, is more or less defined by the unique structure of the atlas–axis region and its occipital joint (Fig. 10.18). In this group, the occipital facet on the skull is a narrow horizontal figure eight in shape and is divided into three approximately equal parts. The outer two parts are contributed by the exoccipitals, the center part by the basioccipital. This central part is recessed relative to the outer parts. Corresponding to this the facet provided by the atlas–axis complex is also a narrow oval, but its central part is produced into a projecting knob called the odontoid that fits into the basioccipital recess on the skull. The facet is provided by the atlantal centrum, and in these animals there is a close match between the shape of the occipital condyle and the atlantal facet. The atlantal centrum is fused or sutured to the atlas arch, while the axis arch and its centrum are also sutured or fused together (Carroll et al. 1998; Carroll 2000a). Such a construction would seem to allow dorsoventral movement, but restrict lateral movement and rotation. This might stablize the head as the body yaws and rolls during walking.

With each modification of the atlas–axis vertebrae came increased flexibility of the neck joint, accompanied by increasing independence of the head from the shoulder girdle. Development of the joint may well be read in parallel to loss of reliance on the musculature and blood system used in fishlike buccal pumping.

### NEURAL SPINES AND ZYGAPOPHYSES

Before the discovery of regionalization in *Ichthyostega*, it could be said that in most early tetrapods, other regions of the vertebral column remain little differentiated from one another, quite unlike the obvious demarcation into cervical, thoracic, lumbar, and sacral seen in mammals (e.g., Fig. 2.4). *Ichthyostega* provides an important exception to this expectation, and its implications for function and phylogeny still have to be fully explored. The way in which the neural arches articulate to each other and the development of an attachment between the pelvic girdle and the vertebral column are nonetheless two of the areas of most importance in the evolution of terrestriality in tetrapods. The sacral region will be treated after the section on the pelvic girdle, but next, developments to the neural arches will be considered.

Fishes such as *Eusthenopteron* not only do not have much differentiation into regions along the column as many later tetrapods do, but also their neural spines do not articulate with one another (Fig. 2.4). However, they do support the axial muscles and tend to be long and at a steeper angle to the column than in tetrapods. The steep angle also reflects the cone-shaped segments into which the axial muscle blocks are arranged to facilitate control of swimming movements.

Zygapophyses, the joints between the neural arches, consist of paired oval facets facing upward at the front of the arch and downward at the back (a way to remember which is which it to think of the phrase "up front"). As with the slope of the neural spine, so the number of caudal vertebrae bearing zygapophyses also increases from about five or six in *Acanthostega*, through about 12 in *Greererpeton* to 22 or more in *Proterogyrinus* and other later tetrapods (Coates 1996). As one of the most primitive tetrapods, *Acanthostega* has barely differentiated zygapophyses, and in that respect is the most fishlike tetrapod. Those of *Ichthyostega* are more pronounced, but more detailed work is required on this animal to determine their exact nature. In *Crassigyrinus*, it is the anterior set of zygapophyses that are more conspicuous, whereas the posterior ones are no more developed than in *Acanthostega*.

In animals with well-developed sets of zygapophyses both front and rear, the angle at which the facets lie becomes important and can constrain the range of movement in the vertebral column (Holmes 1989b). Most early tetrapods, such as the temnospondyl *Eryops*, have the facets set at an angle to the vertical plane, sloping in toward the midline, but those in *Pederpes*, with typically rhachitomous centra, are approximately horizontal. In some animals, such as *Seymouria*, some early amniotes, and

some microsaurs, the angle is also horizontal (Fig. 10.17), but the contact surfaces are broadened, forming a column whose movement is more or less constrained to lateral bending. Presumably this restricts rotation at the same time. This kind of horizontal arrangement is usually found in conjunction with solid spool-shaped centra and low, dome-shaped neural spines. The functional implications of this are not well understood, but it seems to have arisen several times in early terrestrial tetrapods.

A few groups developed extra articulations between the neural spines of the trunk or tail. These are particularly conspicuous in nectrideans; indeed, this is a feature of the group. However, there are also less well-developed interarticulations even in some regions of the column in *Acanthostega*. They presumably function to reduce twisting of the column.

### RIBS

Substantial ribs attaching to the vertebral column via the neural arch and centrum are characteristic of tetrapods and are known even in the earliest forms. However, there is more contrast in rib morphology between *Acanthostega* and *Ichthyostega* than there is between any other two Paleozoic tetrapods, so it is difficult to draw general conclusions about what function the ribs may have had in these very early forms. *Acanthostega*, with its short and for the most part undifferentiated ribs, seems more like what might be expected of a primitive tetrapod, in contrast to the broad overlapping ribs of *Ichthyostega*. With the discovery of broad imbricating ribs in *Tiktaalik* combined with apparently poorly ossified neural arches and centra, the picture has become even more complicated (compare Figs. 3.23, 5.11, 5.20). *Ichthyostega* no longer seems such a specialized anomaly, at least in this respect. Micro-CT scans of several *Ichthyostega* specimens appear to show that whereas the centra are well ossified, the neural arches are not (Pierce and Clack work in progress). One explanation might be that the overlapping ribs provided rigidity to the trunk before such a role was developed by the vertebrae. More aquatic tetrapods such as *Acanthostega* presumably did not require such support for the trunk.

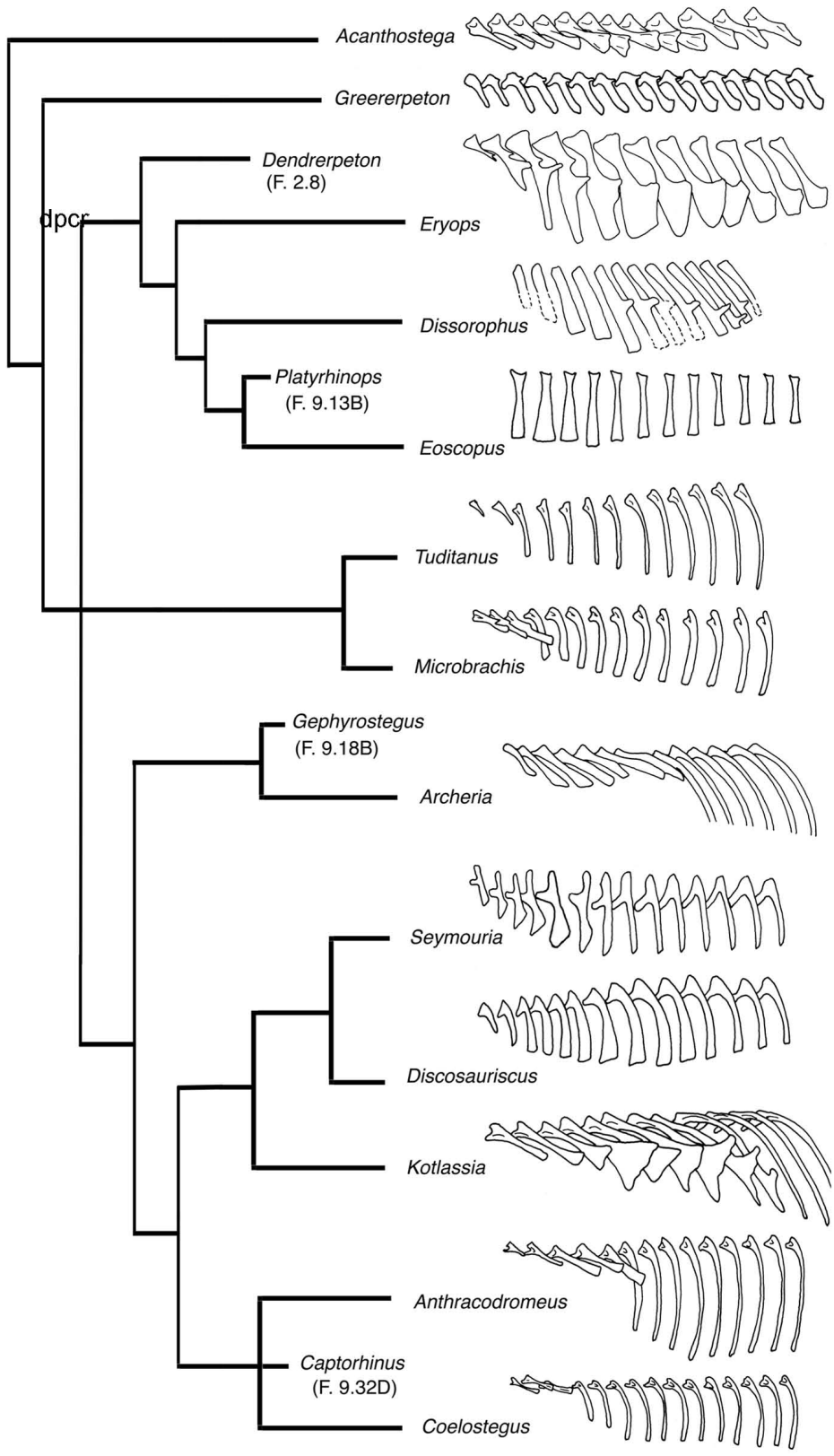
Even among apparently closely related forms, the ribs often differ remarkably. Figure 10.19 shows a selection of rib morphologies among early tetrapods. *Pederpes* and *Whatcheeria* both have flanged ribs, and although not as extreme as *Ichthyostega*, those of *Pederpes* share some features with it, including notches along the dorsal edge assumed to be for the passage of blood vessels. Among temnospondyls, the majority have short, more or less straight ribs that do not show much curvature around the body (e.g., *Platyrhinops*, Fig. 9.18, *Eoscopus*, Daly 1994) (Fig. 10.19), and in fact, they probably only extended over the dorsal part of the body wall. Most do not show much differentiation along the column, except that the cervical and immediately presacral ribs are somewhat shorter than the rest. Some appear to have no ribs on the axis or atlas vertebrae, but apart from that, no cervical ribs can readily be distinguished. However, by contrast,

**10.19.** Rib patterns in the cervical and thoracic region in early tetrapods; the early tetrapods *Acanthostega* and *Greererpeton,* the temnospondyls *Dendrerpeton, Eryops, Dissorophus, Platyrhinops,* and *Eoscopus,* the anthracosaurs *Gephyrostegus* and *Archeria,* the seymouriamorphs *Seymouria, Discosauriscus,* and *Kotlassia,* and the early amniotes *Anthracodromeus, Captorhinus,* and *Coelostegus.* Anterior is to the left in each case. In *Dissorophus* and *Eoscopus,* the atlantal and probably the axial ribs are missing. (Not to scale.) Eoscopus *from Daly 1994.*

some, such as *Dendrerpeton* and *Doleserpeton*, have slightly broadened ribs associated with at least some cervical vertebrae (the sequence is not fully known) (Fig. 2.10). The dissorophids show more variation in rib morphology than most temnospondyl families, perhaps associated with their production of more terrestrial forms such as *Dissorophus* itself (Fig. 10.19). In that animal, though there are no cervical ribs showing expansions, ribs associated with vertebrae 7 through 13 show small triangular flanges at about the midpoint of the shaft. These are sometimes called uncinate processes, though there is some disagreement about how such processes are actually defined. The temnospondyl that shows some of the most specialized rib morphology is *Eryops* (Fig. 9.10), though similar patterns are also found in other temnospondyls such as *Sclerocephalus* and *Mastodonsaurus*. Very like those of *Pederpes*, their ribs show a series of flanges and expansions, starting with short ribs on the atlas, axis, and first two cervicals that bear spiky processes. Thereafter, the ribs bear broadly expanded triangular ends that increase in size to about the seventh, and then gradually diminish to disappear at rib 13. Though the first four ribs may be described as cervicals, there is really no abrupt change between cervicals and trunk ribs. The flanges are sometimes assumed to have been associated with the muscles attaching the shoulder girdle to the body in what is taken for a more or less terrestrial animal, with a similar explanation for the uncinate processes of *Dissorophus*. Such an explanation is also sometimes given for the broadly expanded ribs of *Ichthyostega*, but the picture may not be so simple. A link with terrestriality may have to be reconsidered because both *Sclerocephalus* and *Mastodonsaurus* were evidently aquatic.

Rib flanges turn out not to be uncommon among many early tetrapods. In addition to *Ichthyostega*, *Pederpes*, and *Whatcheeria* (Figs. 7.5, 7.7), they are present in *Eucritta*, and (from the evidence of only a single known rib) in *Baphetes* (Milner and Lindsay 1998), though they are different in detail. Broadly triangular flanges set at the distal end of the ribs are also found in the seymouriamorph *Kotlassia* (Fig. 10.19) (Bystrow 1944). As far as one can tell, most of these animals were more aquatic than terrestrial, though *Kotlassia* was probably terrestrial. Other seymouriamorphs such as *Seymouria* itself and *Discosauriscus* show variations. The latter has slightly expanded anterior thoracic ribs, while in *Seymouria*, it is the cervicals that appear to be expanded (Fig. 10.19). No studies have yet been made of the possible function of such flanges, which in some cases are quite bizarre in form. They may have been concerned with musculature involved in axially driven locomotion and the added strain of performing such movements on land rather than in water.

Yet another variation is found in some animals such as *Greererpeton* (Figs. 7.12, 10.19). Though, like the majority of temnospondyls, it has no distinctive cervical ribs, most of its trunk ribs bore small processes about midway along the shaft, somewhat similar to the uncinate processes of *Dissorophus*. However, *Greererpeton* was an aquatic animal, as was *Acanthostega*, where modest processes appear on about vertebrae 10 to 13


Acanthostega
Greererpeton
Dendrerpeton
(F. 2.8)
dpcr
Eryops
Dissorophus
Platyrhinops
(F. 9.13B)
Eoscopus
Tuditanus
Microbrachis
Gephyrostegus
(F. 9.18B)
Archeria
Seymouria
Discosauriscus
Kotlassia
Anthracodromeus
Captorhinus
(F. 9.32D)
Coelostegus

following a slight expanded series more anteriorly. Again, the function of these processes is unknown, though in such predominantly aquatic animals, the needs of axial locomotion might be invoked.

In some early tetrapods, there is an abrupt change in rib morphology defining a cervical region. These are animals that have been traditionally placed in the reptiliomorph lineages such as anthracosaurs (see Coates 1996). *Archeria* and *Gephyrostegus* are among these (Fig. 10.19), though the seymouriamorphs *Seymouria*, *Kotlassia*, and *Discosauriscus* do not show an abrupt transition like this. In many of these forms, three or four ribs following the atlas and axis vertebrae bear ribs that are set at a narrow angle to the vertebral column, sometimes almost parallel to it. They are often broader than the trunk ribs, expanding gradually down the shaft to the distal end, though not showing distinct processes such as those in *Eryops*. This kind of differentiation is also seen in a range of early amniotes such as *Coelostegus* and *Anthracodromeus* (Carroll and Baird 1972) (Fig. 10.19).

Microsaurs show an intermediate condition, in which in most forms, the first three vertebrae only are distinguishable as cervical. They may or may not carry ribs, but thereafter the ribs tend to be simple curved bars with no additional processes. Exceptional cases can be found among both aquatic microbrachomorph forms and terrestrial tuditanomorph forms, in which up to five cervical vertebrae carry modified ribs (Fig. 10.19).

Rib and vertebral patterning in birds and mammals is known to be under the control of *Hox* genes. In these animals, the cervical series is characterized by the lack of ribs, and associated structural correlates. Cervical vertebrae occur where *Hoxc6* operates in the absence of *Hoxc8* (Burke et al. 1995), and that also specifies where the limbs will be formed. However, in early tetrapods, often all the anteriormost vertebrae carry ribs of some form. As detailed above, in some amniotes and amniote-like tetrapods, they are clearly distinct from other ribs in orientation or shape, but in other groups, they are often little different from trunk ribs. The pattern may indicate that the *Hox* gene control was less rigid in early tetrapods, and the interactions between the two *HoxC* genes less clearly defined. The variable patterns in early tetrapods may represent yet another instance of early variability followed by later stabilization in the early evolution of systems.

As well as having a role in locomotion, ribs are often thought of as being involved with breathing mechanisms. That is certainly true for most amniotes, but perhaps this is the place to consider the possible role of ribs in breathing among early tetrapods in general. In the past, most people considered that early on in tetrapod history, the ribs would have played a similar part to that which they play today in amniotes—that is to say, in helping to ventilate the lungs. The evidence for this was based in the main on two observations. One was that most early tetrapods were thought to have had substantial rib cages, in which the ribs surrounded the body cavity more or less fully, and the second was that where they were known in early tetrapods, the ribs had heads that consisted of two

separate articulatory facets set at an angle to each other (Gans 1970; Romer 1972a). In modern animals, this design ensures that when the ribs move in and out from the body, they change the volume of the cavity they enclose; thus, the lungs can be alternately expanded and contracted.

The early tetrapods that were used as examples in such studies were *Ichthyostega* and *Eryops*. The overlap of the ribs in *Ichthyostega* lies at the extreme end of the spectrum in early tetrapods and may not be helpful in drawing up a general picture. In Chapter 5 it was suggested that the ribs in *Ichthyostega* may have had a supporting role in locomotion, imparting rigidity rather than flexibility. Certainly the contrast could hardly be greater with the ribs of *Acanthostega*, whose short, straight ribs look most unlikely to have formed part of a ventilatory mechanism. In most temnospondyls, the ribs as a rule are not unlike those of *Acanthostega*, in being straight and relatively short. There seems to be no evidence in most of them of cartilaginous extensions carrying the rib ends around under the body so that they could meet each other or contact any midline structures (Janis and Keller 2001). In order to function in costal ventilation, such extensions appear to be necessary and are found in modern animals where the ribs have this role. In *Ichthyostega*, *Acanthostega*, most of the Early Carboniferous tetrapods and temnospondyls generally, the ribs have tapering ends finished in smooth periosteal bone. By contrast, some of the anthracosaurs such as *Pholiderpeton* have relatively much longer ribs that are curved, with ends bearing an unfinished facet suggestive of a cartilaginous end. If any early tetrapods had begun to use the ribs in ventilatory movements, it is likely to have been these animals, thought to be stem amniotes by most people. Other animals such as the more terrestrial microsaurs might also have begun this process.

Even the possession of long, curved ribs almost enclosing the trunk is not necessarily an indicator of costal aspiration. Carboniferous lungfish also possess them. These lungfish are specialized air breathers that used buccal pumping for air intake, and it appears that the ribs were more likely to have been involved in locomotion (Clack et al. 2011).

One of the key factors in the change of thinking about early tetrapods was the realization that they could not all be lumped together as a single unit known as labyrinthodonts, but that several lineages should be teased apart and treated independently. This is therefore another example showing the importance of ideas about phylogeny in determining how early tetrapods are interpreted.

From the evidence of head and shoulder structure, and from knowledge of breathing mechanisms and musculature of modern animals, it now appears more likely that most early tetrapods were probably air gulpers. Temnospondyls appear to have elaborated this system into a buccal pumping mechanism, assisted by the development of the palatal vacuities (Clack 1992). Modern amphibians use this method too. Not only do their breathing mechanisms not involve the use of ribs to ventilate the lungs (though they do involve body-wall musculature in exhalation; see Chapter 6), but in most frogs, the ribs have been lost altogether. In the

previous section on vertebrae, the connection between the structure of the centrum and the role of the neural arch and ribs in locomotion was pointed out, and the ideas mesh well with these new interpretations of breathing mechanisms in which rib musculature was not fully involved with aspiration breathing. Rhachitomous vertebrae, short ribs, and buccal pumping seem intimately related.

In amniotes, by contrast with temnospondyls, ribs are usually quite long and curved. Ribs may have become in some way involved in breathing among amniotes at an early stage in their evolution, bearing opposing sets of muscles to open and close the rib cage as they do in modern mammals. However, there is evidence that these early animals did not rely on them entirely to ventilate lungs. In modern amniote groups, lizards, crocodiles, turtles, and mammals all use quite different methods of lung ventilation that may not use ribs at all. In turtles, for example, the ribs have become incorporated into the shell internally, so it is hard to see how the turtles' ancestors could have done this if the lungs had been ventilated exclusively by rib movements. However, amniotes do have certain features in common that suggest at least the beginnings of costal aspiration may have been present in all of them. These features include intercostal musculature for moving the rib cage. It may be that early tetrapods, even including early amniotes, were using all possible means by which to aid gas exchange—air gulping, buccal pumping, and skin breathing, as well as an early version of rib movement.

A possible role for the elaboration of ribs in the earliest tetrapods may be one associated with the development of the transverse abdominal muscle, the extra muscle layer that tetrapods developed to aid exhalation during aspiration breathing (see Chapter 6). This appears to have arisen in the common ancestor of amphibians and amniotes and may therefore have been present in some of the earliest tetrapods. It is the innermost of the body-wall muscle layers in salamanders and presumably was so in early tetrapods too. Its appearance may herald the initiation of axial muscle involvement with ventilation. The flanges may have given this muscle an increased length of edge onto which to attach. At present, all that can be said is that these expanded trunk rib flanges are found in a number of the earliest tetrapods, as well as in some more derived ones, and that though they are more often found in aquatic forms than terrestrial ones, even some forms thought to be at least semiterrestrial, such as *Eryops*, have enlarged trunk flanges on their ribs.

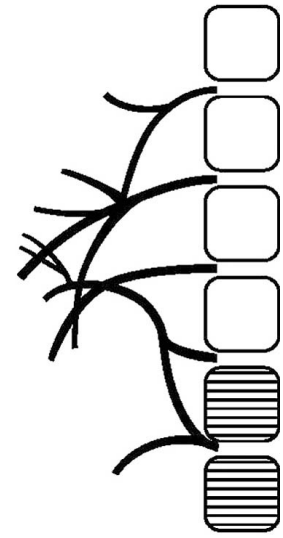
### Evolution of the Cervical Region and the Brachial Plexus

Movements of the limbs are controlled to a large degree by a complex of nerves that come together to form the brachial and sacral plexuses in the spinal column, in the cervical and sacral regions. In modern amphibians, spinal nerves near the anterior end of the column are involved; in frogs, spinal nerves 2 and 3 (corresponding to cervical vertebrae 2 and 3) and in salamanders nerves 3 and 4 (with a few fibers also from 2 and 5)

contribute to a simple brachial plexus. There is little or no enlargement of the spinal cord itself at this point in modern frogs (Huxley 1882) or salamanders (personal observation). Caecilians, which lack limbs, also lack the plexuses.

In amniotes, the situation is much more complex and variable. In lizards, for example, there are usually five (or more) nerves that contribute to the brachial plexus (Fig. 10.20). The most posterior of these nerves exits the vertebral column between the last cervical and first thoracic vertebrae, which means that the nerves pass out between cervical vertebrae 4 through 8. In crocodiles, the five nerves of the brachial plexus are associated with spinal nerves 7 through 11 (Giffin 1995).

The size and complexity of the brachial and sacral plexuses reflect the degree of coordination, range of movements, and refinements of limb control among amniotes. The variability seen in amniotes is also paralleled by the degree of differentiation seen along the length of the column. For example, cervical vertebrae in amniotes are usually distinct from those of the thoracic region, marked out by features such as the position of rib attachments (Giffin 1995). The situation contrasts with that in salamanders, where usually only the atlas vertebra, lacking a rib, is clearly distinct from any of the others. In its lack of distinct regions, the vertebral column of, say, a salamander like *Megalobatrachus* is similar to that of the early tetrapod *Acanthostega*. It is likely that, as in salamanders, there was little elaboration of the brachial plexus in early tetrapods like *Acanthostega*, and that the nerves serving the forelimbs were associated with more anterior vertebrae as in salamanders and frogs.



**10.20.** The brachial plexus of a lizard. Cervical vertebrae, plain; thoracic, hatched. Nerves to the pectoral region coalsce and intertwine to form a ganglion around cervical 3 and 4. Amphibians have no complex brachial plexus.

The position of the brachial plexus is of some interest because it reflects changes to the position of the shoulder girdle and forelimbs. Among modern animals, amniotes contrast with amphibians in having much longer cervical regions as well as having more differentiation of this region. A long neck is characteristic of amniotes (Janis and Keller 2001). In early tetrapods, the shoulder girdle remains tucked close up behind the head, so that the interclavicle often underlies the back part of the skull, between the lower jaw joints, and the clavicle and cleithrum likewise almost touch the back of the head. In *Acanthostega*, the shoulder girdle retained one of its fishlike functions, in providing a seal for the opercular flap (Fig. 5.22). Even in early tetrapods in which there is no clear evidence of internal gills, this close relationship between head and shoulders is still maintained. The reason may have to do with the retention of buccal pumping, whose musculature was essentially similar to that used in gill ventilation and was to a large extent inserted onto the shoulder girdle. A further implication is carried for the position of the heart. In fishes, the heart lies more or less amid the gill basket, between the operculars. Judging by the position of the shoulders, it still rested in much the same place in early tetrapods.

The inferences may be carried further to suggest that as buccal pumping was gradually abandoned, the shoulder girdle moved further back, the circulatory system lost its primitive gill-related structure, the

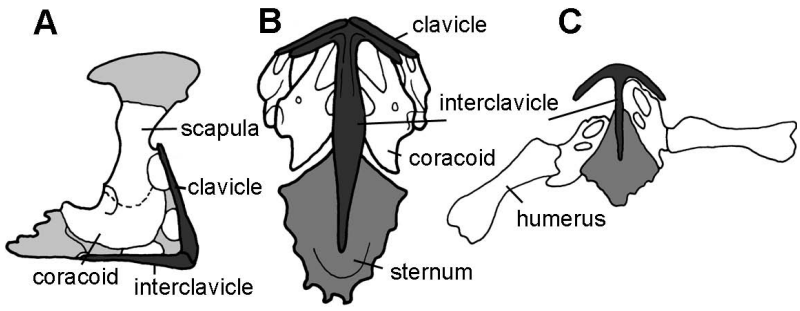
neck lengthened, and the brachial plexus increased in complexity. Thus, perhaps only in amniotes could fine control of the forelimbs be achieved. In this context, it is notable that frogs, which have maintained buccal pumping, have elaborated the function of the hind limbs but reduced the importance of the forelimbs. In salamanders, both sets of limbs are of relatively minor importance in locomotion and in some species have been reduced or lost altogether.

## Pectoral and Pelvic Girdles, Limb Bones, and Joints

### PECTORAL GIRDLE

Post-Devonian tetrapods show a consistency of construction in the shoulder girdle. After major changes during the fish–tetrapod transition, such as enlargement of the interclavicle and increase of the scapulocoracoid, most of the subsequent developments consist of a further general reduction of the dermal girdle. From the pattern seen in most Devonian tetrapods, in which the cleithum and scapulocoraoid are co-ossified, in the later forms, this connection is lost. The cleithrum and clavicle retain their interconnection, but the scapulocoracoid becomes a separate, and much larger, entity. It no longer has a bony connection to the dermal elements as it had in fishes. There are no facets on the internal surface of the cleithrum to receive it as there were in fishes, and it must have been held in place by soft tissue connections. Eventually, the scapulocoracoid seems to have taken over the area formerly occupied by the cleithrum and even ends up with a similar shape in some forms (compare, for example, the scapulocoracoid of *Dendrerpeton* with the cleithrum of *Eusthenopteron* (Figs. 2.6, 6.4).

As was mentioned in Chapter 6, the dermal elements in tetrapods became reduced in size, and the connections between cleithrum and clavicle became less intimate. The cleithrum is the bone that undergoes the most radical reduction, becoming first a narrow splint, as found in most post-Devonian tetrapods (Fig. 6.4), eventually disappearing altogether in many amniote groups. This could well be associated with the loss or reduction of branchial musculature and its decoupling from breathing. Clavicles in most early tetrapods remain remarkably conservative in form, only undergoing significant reduction among the more terrestrially adapted amniotes and microsaurs. In some such cases, the clavicle is reduced to a narrow splint more or less at right angles to the body and is often associated with an interclavicle that has taken on a T-shaped appearance. In such animals, the way was open for the development of movements of the shoulder girdle, so that not only could the girdle move relative to the body during each step, but also this movement could be amplified by movements of the bones relative to one another (Fig. 10.21). This kind of movement, called girdle rotation, is an important component of the locomotory cycle in animals like lizards and was presumably first developed among the early amniotes whose girdles were essentially similar in shape to those of lizards.




**10.21.** Pectoral girdle of a lizard in (A) lateral and (B) ventral views. (C) Relative movement between coracoid and sternum during the stride. This movement helps to lengthen the stride and is only possible because of the flexible attachments between the elements, and the relative reduction of the dermal bones. Dermal bones, dark shading; sternum, medium shading; cartilaginous elements, light shading. *From Carroll (1987).*

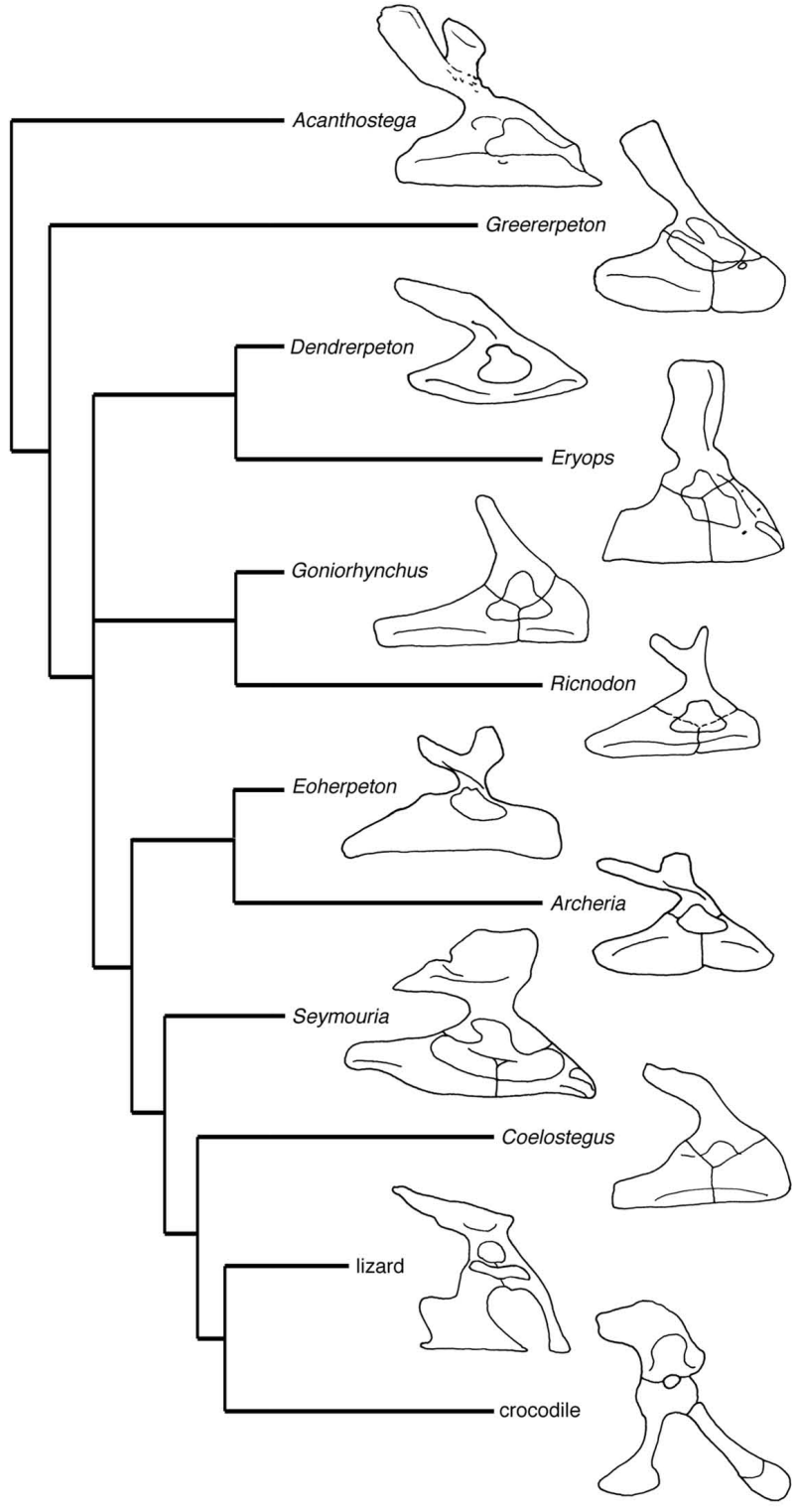
## PELVIC GIRDLE

A more or less orderly sequence can be seen in the evolution of the tetrapod pelvic girdle and sacrum, once the enlargement of the girdle bones typical of tetrapods had taken place. No pretetrapod lobe-fin shows any hint of the broad medially sutured pair of plates seen in even the earliest tetrapods. The earliest known tetrapod-like pelvic girdle elements belong to *Elginerpeton*, and these are similar in size and probably morphology (they are only known in part) to those of *Ichthyostega* (Ahlberg 1998). *Acanthostega* has a pelvic girdle that appears to be relatively smaller than that of *Ichthyostega*.

These early tetrapod pelvic girdles were typically single ossifications as they are found in the fossil record, which differs from the trinity of bones found in later forms: ilium, pubis, and ischium presumably were represented, but the limits of their respective regions cannot be distinguished in the earliest forms (Fig. 10.22). Some later tetrapods such as the anthracosaur *Eoherpeton* also had a unitary pelvis like the Devonian forms, but by and large, in most Carboniferous forms, the three separate ossifications are clear. The means by which this separation came about remains speculative. One possibility is a process of pedomorphosis, whereby in early tetrapods, the three contributory bones fuse early in life so that in the adult, only the solid structure is left. As tetrapod evolution proceeded, pedomorphosis delayed the fusion of the three into later and later stages, so that in some the fusion was never complete. To delay the fusion of separate bones in this way may have permitted longer periods of growth in the larger forms. Separate bones are found in all the small forms such as amniotes and microsaurs (Fig. 10.22).

The earliest tetrapods typically had a backwardly pointing postiliac process, thought to have carried muscles to operate the tail, as well as a dorsally projecting iliac blade, via the inner surface of which the girdle attached to the sacral region of the vertebral column. In *Ichthyostega* and *Elginerpeton* as well as in the early anthracosaur *Eoherpeton*, the postiliac process was oriented to lie more or less parallel to the vertebral column, whereas in *Acanthostega*—and indeed most early tetrapods—it lay at an angle of about 30 degrees to the horizontal. What the difference means is unknown, but it might signal differences in the use of the tail and the degree of emphasis in propulsion provided by the tail compared

**10.22.** Pelvic girdles in early tetrapods (lateral views); the early tetrapods *Acanthostega* and *Greererpeton,* the temnospondyls *Dendrerpeton* and *Eryops,* the microsaurs *Goniorhynchus* and *Ricnodon,* the anthracosaurs *Eoherpeton* and *Archeria,* the seymouriamorph *Seymouria,* the early amniote *Coelostegus,* and the diapsids, a lizard and a crocodile. Anterior is to the right in all cases. (Not to scale.)



to that by the limbs. In later tetrapods, one or other of the iliac processes may be lost. In temnospondyls, for example, only what appears to be the postiliac process remains, but in others, such as microsaurs and amniotes, the single process seems midway between the two in size and orientation, and its homologies are difficult to draw (Fig. 10.22).

Pubic and ischiadic regions in early tetrapods were triangular, hexagonal, oval or rectangular plates. The acetabulum (the articulation point for the femur) was situated at the junction of the three pelvic bones. In *Ichthyostega* and *Acanthostega*, the anterior margin of the acetabulum was carried forward in a curious extension to the articular surface, whose function is quite obscure. Nothing like it is seen in most later tetrapods, in which the acetabulum has settled into its more usual oval shape. It presumably means there was some locomotory function in the earliest tetrapods that was unlike that of more typical tetrapods, but it is difficult to investigate what that might have been.

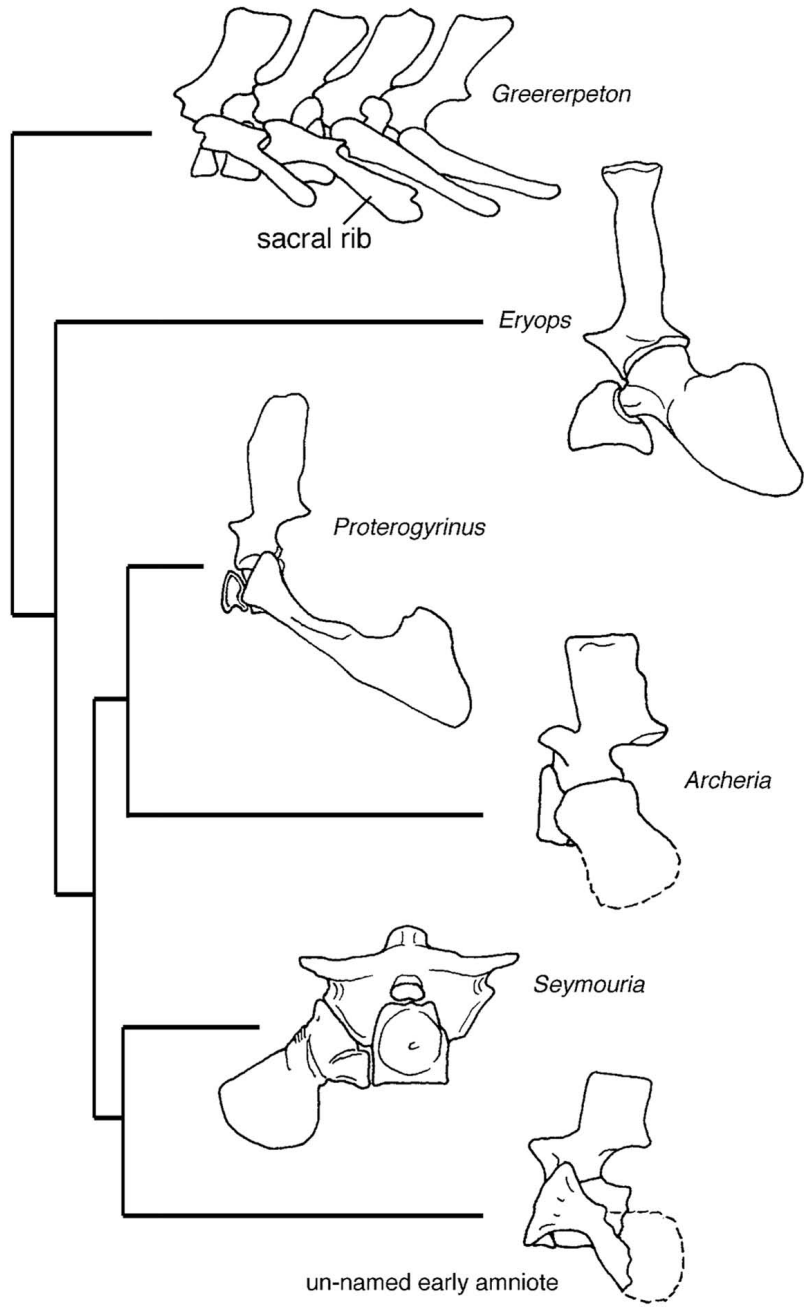
It is a strange fact that in many Carboniferous forms, particularly the early ones, the pubis apparently remained unossified throughout life. The ilium with its processes and dorsal contribution to the acetabulum, and the ischium with its almost triangular or oval shape are conspicuous features in animals such as *Silvanerpeton* (Fig. 8.12) and *Eucritta* (Fig. 8.14), but the pubis is missing. This may even have been the case in *Ichthyostega*, because one specimen shows an elongated anterior portion, complete with a couple of large obturator foramina, that is absent in most other specimens. The reason for such lack of ossification is obscure, especially given that in the fish girdle, the pubic region of the bone seems to be the most easily homologized with the corresponding region of the tetrapod girdle.

In other Carboniferous forms, such as *Crassigyrinus*, the pelvic girdle was composed of bones that apparently were joined only by cartilage in life. The ischiadic plate was a small triangular bone that shows no obvious joint surfaces to meet the other pelvic bones, but uniquely, it does show clear scars for a muscle insertion on the external surface.

During the evolution of more terrestrial tetrapods, the platelike form of the pelvic girdle of early tetrapods was modified, particularly in early amniotes, so that each bone was transformed into a slender strut. The girdle took on the characteristic triradiate shape of many later amniotes (Fig. 10.22).

### SACRUM

The sacral region by which the pelvic girdle is joined to the vertebral column follows a sequence that probably corresponds closely with increasing terrestriality (Fig. 10.23). The sacrum consists of the vertebra or vertebrae that carry the sacral rib or ribs attaching to the girdle. In *Acanthostega*, there appear to be no conspicuous modifications to any vertebra that clearly indicate that it was sacral. There is a sacral rib that shows some broadening of the distal end, but it is not otherwise much modified from




**10.23.** Sacral construction in early tetrapods; the early tetrapod *Greererpeton,* the temnospondyl *Eryops,* the anthracosaurs *Proterogyrinus* and *Archeria,* the seymouriamorph *Seymouria,* and a Carboniferous amniote. Anterior is to the left, except in *Seymouria,* which is shown in anterior view. (Not to scale.)

the presacral ribs, and the vertebra that bore it is not recognizably different from those fore and aft of it. The sacral rib of *Ichthyostega* has not been described. In *Acanthostega*, the ilium shows no joint surfaces for attachment of the sacral rib, though there is some scarring that might indicate its attachment by soft tissue. There are certainly no articular facets on the end of the sacral rib.

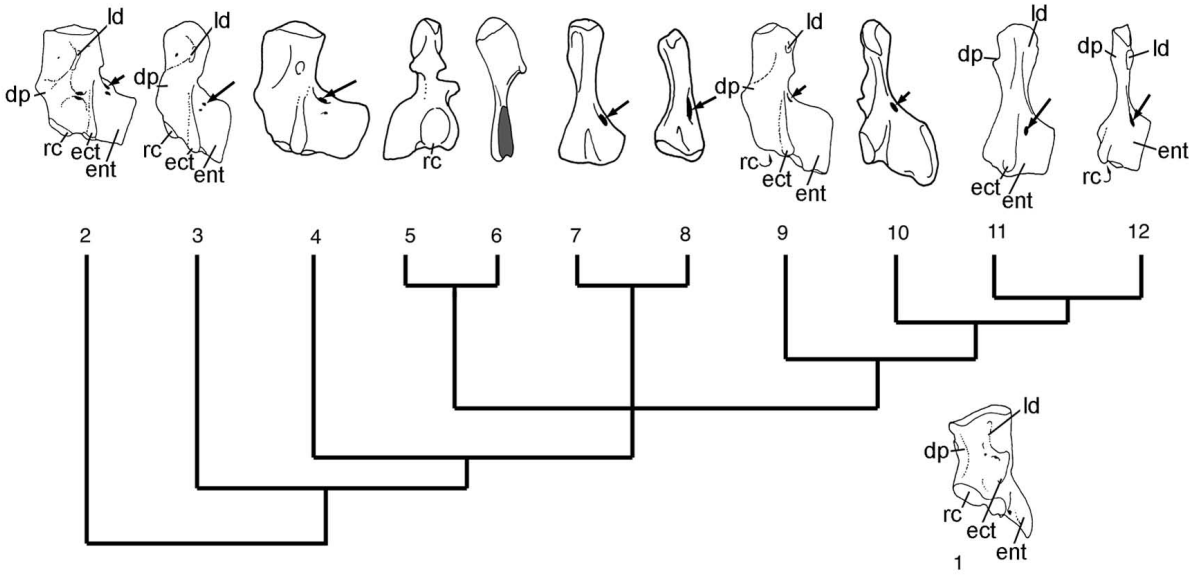
Like *Acanthostega*, *Greererpeton* has a recognizable sacral rib, but the sacral neural arch is not distinguishable from the rest (Godfrey 1989a).

The sacral rib of *Pederpes* is not preserved, and the sacral vertebra hardly distinct from the others. In *Whatcheeria*, the sacral rib is noticeably broader than the pre- or postsacrals, but is shorter than most of the trunk ribs, many of which are greatly expanded at the ends. The sacral neural spine appears to have a broadened transverse process to receive one of the sacral rib heads, but the sacral centrum, as in *Pederpes*, does not seem to be specially differentiated (Lombard and Bolt 1995; personal observation). In later Carboniferous forms, for example the anthracosaurs *Archeria* and *Silvanerpeton*, a short, stubby sacral rib has developed, but there is still no facet on the ilium to receive its distal end (Holmes 1989b; Clack 1994b). The junction must have been entirely supported by soft tissue. A sacral pleurocentrum is recognizable by being somewhat enlarged to support the sacral rib (Fig. 10.23). Here, then, changes in morphology can be seen that accord with both a temporal and a phylogenetic sequence: sacral rib first, sacral neural spine next, sacral centrum third. Thereafter, the sacral elements become modified in different ways in different groups.

In temnospondyls, there is some variation to be found. Most seem to have had a single sacral rib that was not sutured or fused to the pelvis but had an enlarged attachment to the sacral vertebra. The rib was sometimes expanded distally into a fan shape, but not always (Fig. 10.23). Among the terrestrial dissorophids, *Cacops* shows one of the more developed sacral regions in having two pairs of sacral ribs, though other dissorophids, such as *Doleserpeton* (Sigurdsen and Bolt 2010), had only one.

In the Late Carboniferous, amniotes such as *Coelostegus* and *Paleothyris* (Carroll and Baird 1972), the attachment of the pelvic girdle to the vertebral column is little different from that in an anthracosaur such as *Archeria*. The single sacral rib is quite distinctively shortened and broadened, as seen in an unnamed specimen of a Carboniferous amniote, but no articular facet is present on the ilium to receive it (Fig. 10.23). Rather, there is evidence of scarring for muscle and ligamentous attachments. The sacral joint of the earliest synapsid, *Archaeothyris*, has two sacral ribs that both attach to the ilium, probably by ligaments, but in more derived synapsids such as *Ophiacodon*, the more posterior of these is modified to support the first, rather than attaching to the girdle itself. About the earliest evidence of a bony connection between sacral rib and ilium seems to come from basal synapsids (Romer and Price 1940).

With the evolution of more terrestrial forms, not only did the link between sacral rib and ilium become firmer, but also the number of vertebrae that bore such sacral ribs increased, first to two and later to three and more. Among the earliest groups to do this include some microsaurs. Although most microsaurs resemble amniotes such as *Paleothyris*, a few have a series of three specialized sacral ribs, and the internal surface of the ilium shows an articular facet for them (Carroll and Gaskill 1978). The stoutly built terrestrial forms such as *Seymouria* (White 1939) and *Diadectes* (Case 1907) each had two vertebrae modified as sacrals. The first, more anterior of these was heavily built and broadened, and the associated ribs had greatly expanded ends that lined the inner surface of the



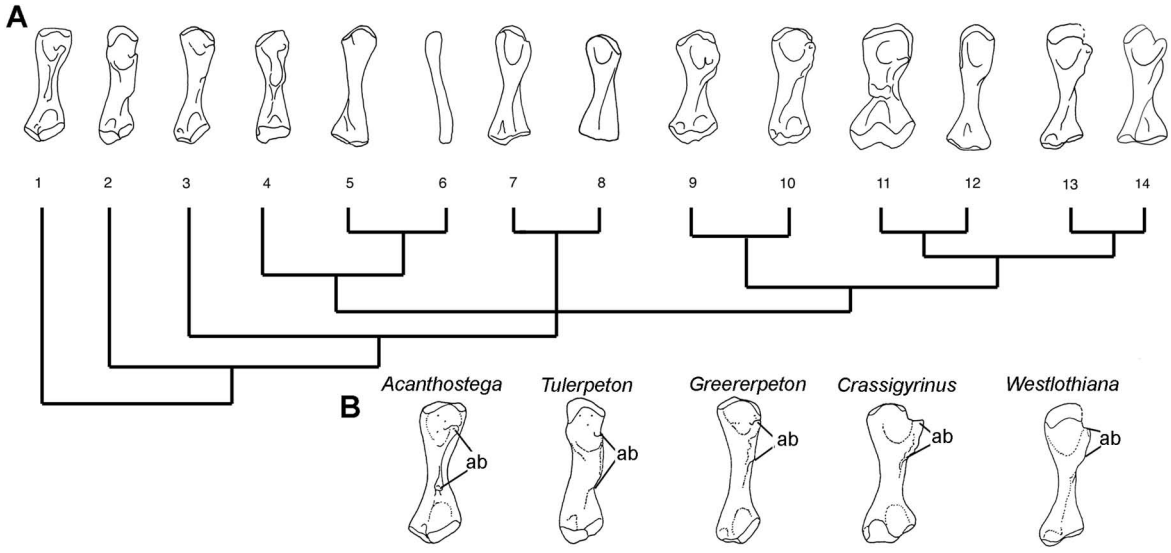

**10.24.** Tetrapod humeri. 1; (outgroup) *Eusthenopteron;* 2, *Acanthostega;* 3, *Tulerpeton;* 4, *Greererpeton;* 5, *Eryops;* 6, *Eoscopus* (shaded area not preserved); 7, *Pelodosotis* (tuditanomorph microsaur); 8, *Microbrachis;* 9, *Eoherpeton;* 10, *Seymouria;* 11, *Casineria;* 12, *Westlothiana.* Left humeri; not all in the same aspect; and not to scale. Straight arrow points to entepicondylar foraman. dp = deltopectoral crest; ect = ectepicondyle; ent = entepicondyle; ld = latissimus dorsi process; rc = radial condyle. *Adapted from Coates (1996).*

ilium to a large degree. The second sacral was much less modified, but still the distal end of the rib contacted the ilium. In the young stages of the aquatic larval forms of seymouriamorphs such as *Discosauriscus*, the sacral region was present only as a single unmodified vertebra, and the ilium alone was ossified in the pelvic girdle (Klembara 2000). However, as the animals grew, the remaining components of the girdle ossified, and two sacral ribs developed. The sacral vertebrae themselves are not so conspicuous, though they had extra articulations for the large sacral rib heads.

Once more, adaptation of the sacral region for terrestriality (that is to say, weight bearing and transmission of limb propulsion to the vertebral column) can be seen to have been a gradual process, with the earliest tetrapods having little in the way of a firm connection between the girdle and the vertebral column. Increasing the size of the sacral elements and the extent of the contact and its firmness can be shown to have occurred several times in different groups.

## Limb Bones and Joints

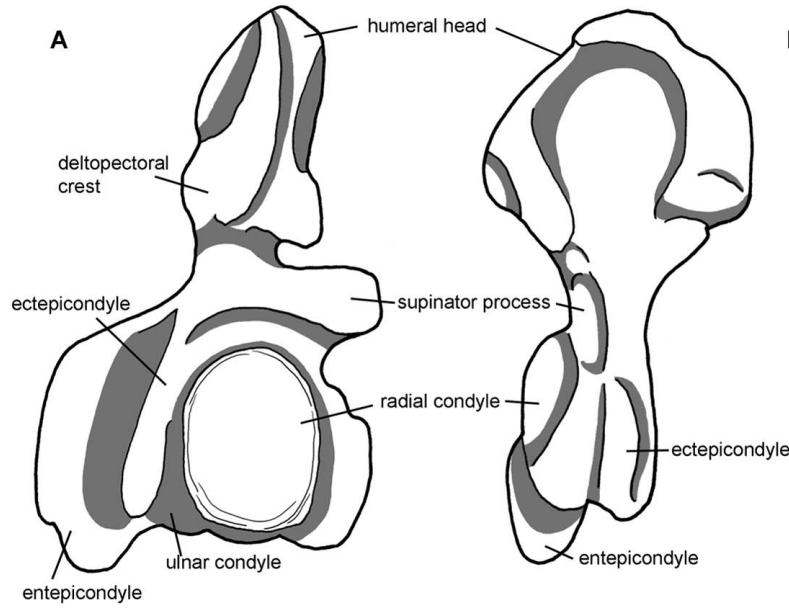
Early in tetrapod history, the limb elements were rather different in form from their equivalents in later forms. They tended to be bulky and flattened rather than gracile and elongate. The humerus of *Acanthostega*, for example, is shaped like a broad L. If the limbs of early tetrapods are ranged upon a cladogram, a number of significant directions of change are seen, especially to the humerus and femur. The humerus in early tetrapods has an L shape, with large epicondyles for muscles to attach and move the forelimb (Figs. 6.11, 10.24). The deltopectoral crest is the point where the adductor muscles attach to move the whole limb into the body. These are placed at about the midpoint of the bone, but there




**10.25.** Tetrapod femora. (A) Cladogram showing 1, *Acanthostega;* 2, *Tulerpeton;* 3, *Greererpeton;* 4, *Eryops;* 5, *Tersomius;* 6, *Platyrhinops;* 7, *Saxonerpeton* (tuditanomorph microsaur; 8, *Microbrachis;* 9, *Proterogyrinus;* 10, *Archeria;* 11, *Seymouria;* 12, *Discosauriscus;* 13, *Westlothiana;* 14, *Captorhinus.* (Not all in the same aspect and not to scale.) (B) Tetrapod femora aligned to show the reduction in the adductor blade. *Adapted from Coates (1996).*

is no recognizable shaft to the humerus. Similarly, on the femur of *Acanthostega*, there is a large adductor blade that extends more than halfway along the inside surface of the bone (Figs. 5.24, 10.25). During limb evolution, the deltopectoral crest and the adductor blade become reduced in size and moved toward the proximal (body) end of the bone. This seems to be connected with increasing efficiency of the muscles, whose insertion points come to lie closer and closer to the body. This process goes hand in hand with elongation of the bone and the production of a shaft to give the bone its more familiar shape. The whole system seems to be responding to changing locomotory needs, probably connected with the shift from swimming or paddling to truly terrestrial walking (Coates 1996). Figures 10.24 and 10.25 show humeri and femora on a cladogram, and show that slender, elongate long bones arose independently in several terrestrial lineages including temnospondyls, microsaurs, and amniotes. The picture of limb evolution parallels closely the pattern seen in jaw evolution. Among early tetrapods, the limbs sequentially acquire a suite of characters including those to the muscle insertions mentioned above and the elongation of the limb bones themselves. Thereafter, as tetrapods diversify, there is an explosion of convergent evolution as separate groups become more fully terrestrial.

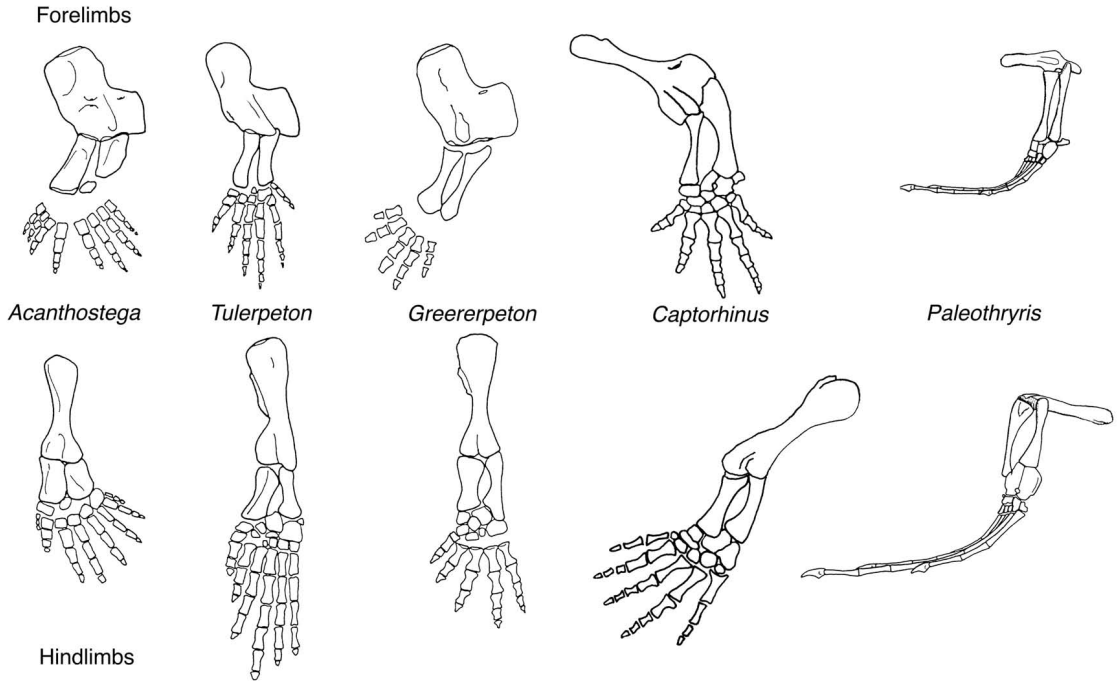
The humeri of *Ichthyostega* and *Acanthostega* retain a series of foramina that are also found in those of *Eusthenopteron* and *Panderichthys.* These are presumed to have been for the passage of blood vessels to and through the bones of the humerus (see Chapters 5 and 6). During the evolution of the tetrapod humerus, most of these were eliminated (Fig. 10.24). All except the entepicondylar foramen had disappeared in the humeri of most Carboniferous forms, one of the few exceptions being *Crassigyrinus.* It retains two or three of them, making it apparently primitive in this respect (Panchen 1985). Given the phylogenetic status of the




**10.26.** Humerus of *Eryops* showing supinator process, and the twist caused by head and condyles being set at 90 degrees to each other.

animal and its reacquisition of secondarily primitive features of the palate, those of the humerus could likewise represent reversals to the more primitive condition. The question remains, however, as to what brought about the loss of the foramina in most other tetrapods. One possibility is that as the humerus slimmed down from its primitive L shape, the blood vessels were simply left to travel in the soft tissue rather than in the bone. However, the loss of the foramina from even the L-shaped humeri of embolomeres argues against this. Another possibility might be that having the blood vessels pass through the bones restricted the amount of blood that could flow through them. While the limb muscles remained relatively small, this was not much of a problem, but as the muscles increased in bulk, having the blood vessels enclosed in foramina might have been restrictive. Releasing them into the soft tissue might have allowed a greater volume of blood to pass to more active limbs and bulkier muscles (see Chapter 6; Lebedev and Coates 1995).

Another conspicuous change to the humerus is evident. In very early tetrapods, the strap-shaped articulatory surface on the head is set at almost the same angle as that formed between the radial and ulnar condyles. In later tetrapods, the angle increases until it is about 90 degrees. In some humeri, such as those like *Eryops* (Fig. 10.26) or *Seymouria* (Fig. 10.24, number 10) that have relatively short shafts, this results in a shape like two triangles set at right angles to one another and it has been called tetrahedral. This twist, know as torsion, is also found in other humeri, such as the elongate bones of temnospondyls like *Doleserpeton*. The effect of this twist is to bring the radius and ulna down into the power stroke more easily and sooner than by a humerus that is not so twisted. It is also found in tandem with changes to the glenoid, which is altered from being a relatively flat surface to one with a distinct twisting curve. The head of




**10.27.** The evolution of limb joints in early tetrapods. Left limbs, anterior to the left. *Acanthostega, Tulerpeton,* and *Greererpeton* are shown with limbs extended, *Captorhinus* and *Paleothyris* with limbs bent. Captorhinus *based on information from Fox and Bowman (1966).*

the humerus can move along this curved surface, thus exaggerating the effects produced by the torsion of the humeral shaft. It has been suggested that the twisted form of glenoid constrains the path through which the humerus can travel to those movements that allow most efficient walking. The idea is that the bone shape governs the movement rather having it controlled by the brain, allowing the brain to be freer to perform other tasks (Jenkins 1971).

Along with modifications to the humerus and femur, the evolution of early tetrapods involves the development of elbow and knee joints (Fig. 10.27). Among conventional tetrapods, it has been said that while the elbow and ankle joints are always rotatory in form, the wrist and knee, by contrast, are always simple hinges (see Chapter 6; Romer 1962). This is true for most fossil as well as modern tetrapods and can be tested by trying to turn the hand over without using the elbow joint. The radius is so called because it allows for rotatory movement at the elbow. The wrist, however, has no power to twist as does the ankle. When it comes to very early tetrapods, however, the picture is not so simple.

It has been suggested that the beginnings of the characteristics of tetrapod elbow and knee joints can be seen in the fins of the lobe-finned fish *Ectosteorhachis* (Rackoff 1980), though this fish is rather a derived member of the tetrapod stem lineage and its adaptations may therefore represent an instance of convergent evolution rather than an ancestral condition for tetrapods. The pectoral fin skeleton of *Tiktaalik* likewise has been suggested to allow movements similar to those of the tetrapod wrist joints. On the other hand, *Acanthostega* shows no very clearly defined elbow and knee joints in the sense that neither joint was as mobile as it

became in later tetrapods. In *Acanthostega*, the radial and ulnar articulations lay at the extreme end of the humerus (Fig. 5.23). That might have allowed the forearm to be raised or lowered with respect to the upper arm, or it may have allowed some capacity for swinging the forearm toward or away from the body, but it was certainly not rotatory. In *Ichthyostega*, the elbow was a hinge, and although its actual range of movement has yet to be fully investigated, the curious shape and rather proximal position of the radial condyle indicates that it may not have been simple (Figs. 5.12, 5.14). The ulna itself bore a prominent olecranon process, testament to the presence of a large muscle to raise the forearm relative to the humerus. By contrast, the knees of both animals appear to have been to some extent capable of rotation, with a degree of overlap between the tibia and fibula when the limbs were at rest (Coates 1996). The rotation would have allowed the limbs to operate in a form of rowing motion while the animals were swimming.

In many later tetrapods, the pattern of limb maneuverability at the elbows and knees was counteracted by the presence of the opposite type at the wrist and ankle, so that the wrist became a hinge while the ankle became rotatory. Clearly these refinements evolved later in tetrapod history when the joints became further adapted for terrestrial locomotion. The rotatory component of the elbow joint first arose when the forearm had to be both raised and swung forward during the recovery stroke, to be brought down to the ground for the power stroke during which it took the weight of the animal and carried it forward, and at the same time allowed the foot to be placed forward instead of to the sides. To do this requires a motion called supination, and a process on the humerus, the supinator process, evolved to which the appropriate muscle attached (Fig. 10.24). Such processes are not present in the earliest tetrapods, but they can be seen in creatures like *Eoherpeton* and other animals with some terrestrial capability.

Recent work has shown that many temnospondyls, such as *Eryops*, and especially the dissorophoids show a feature of the humerus that is similar to one found in modern frogs and salamanders. This feature is an enlarged radial condyle that is developed into a bulbous structure called the capitulum. Part of the ulnar condyle is also incorporated into the capitulum, so that the radius and ulna have a common articulation point (Sigurdsen and Bolt 2009). The arrangement imparts a unique joint function to the elbow, a characteristic that appears to strengthen the dissorophoid–lissamphibian relationship.

Unfortunately, in almost all very early tetrapods, wrist and ankle bones tend to have been poorly ossified and hence were poorly fossilized. The ankles of *Ichthyostega* and *Acanthostega*, and both ankle and wrist of *Tulerpeton* (Fig. 5.26) constitute conspicuous exceptions to this observation. The ankles of *Ichthyostega* and *Acanthostega* are consequently known to be rather different from those of tetrapods from the mid–Late Carboniferous, having fewer bones and no obvious lines of flexibility that would have allowed the foot to be placed flat on the ground for weight

bearing (Bjerring 1985, 1988; Coates 1996). Even in *Tulerpeton*, it is not clear that the joints would have been as flexible as those of later, more terrestrial tetrapods (Fig. 10.27) (Lebedev and Coates 1995). As has been discussed in Chapters 5 and 6, the wrist of *Tulerpeton* is less similar to those of modern tetrapods than is the ankle, another feature that accords with the idea that the hind limb overtakes the forelimb in evolutionary development. Because the hind limb produces most of the thrust in locomotion, this is not particularly surprising.

The earliest known terrestrial tetrapod, *Casineria*, has few of its wrist bones preserved, though to judge from its digits and humerus the wrist must have been weight bearing (Fig. 7.9). The limbs of *Pederpes* do not have preserved wrist or ankle bones, though as indicated in Chapter 7, its metatarsals, with their asymmetrical shape, may indicate the beginnings of a foot that could be twisted forward.

Not only the bones of the wrists and ankles in early tetrapods remain elusive as fossils. In many animals, the ends of the limb bones themselves remained poorly ossified. In fully aquatic animals, this is no great surprise, and the skeletons of modern aquatic animals often remain wholly or partly cartilaginous. However, this also seems to be the case in what appear to be terrestrially adapted early tetrapods. An example of this is seen in the development, or lack of it, of the olecranon process. Exceptionally well developed in *Ichthyostega*, a well-ossified olecranon is not evident again in early tetrapods until it appears in early amniotes and some microsaurs. In the otherwise terrestrially adapted *Casineria*, the olecranon is not conspicuously ossified (Fig. 7.9). If nothing else, this makes one wonder whether or not the function of the olecranon in *Ichthyostega* was comparable with that in later tetrapods.

Because of circumstances such as these, the transition from the earliest and presumed non-weight-bearing joints to those that were more fully terrestrial is still poorly understood. Once these features are more closely reflected in the bony skeleton, it becomes possible to say more about terrestrial adaptation of limbs and vertebrae, and a review by Sumida (1997) takes this subject forward.

## Conclusions

Although a full understanding of the origin of tetrapods is still a long way off, recent discoveries in paleoecology, paleobotany, invertebrate paleontology, developmental biology, and physiology as well as invaluable finds of early fossil tetrapods and their relatives have led to a greatly improved picture of the events and processes involved.

It seems clear that the tetrapods did not invade the land but acquired adaptations to terrestriality slowly, sometimes in many diverse ways. It seems that the colonization of the land was first achieved by plants, then by the invertebrates. Only after that could the vertebrates follow. Changes to the vegetation involving the evolution of complex ecology were influenced by climatic and tectonic events in the early to mid-Paleozoic. Diversifying plant ecology facilitated the adaptation of invertebrates to

life on land, which in turn may have been a critical factor in the gaining of the land by vertebrates. In many circumstances today, this sequence of colonization is still echoed when there is newly exposed land to be exploited.

Looking at the fossils of early tetrapods and their relatives shows how changes to the skull, jaws, and dentition reflect adaptations to terrestrial feeding. They are also inextricably linked to changes to the ear and hearing, and to the neck, vertebral column, and breathing. Changes to the limbs and to locomotory patterns may have been among those that occurred last in the suite of adaptations seen in the transition from fish to tetrapod. Several of these kinds of modifications show fairly slow and gradual change to begin with and can be tracked sequentially from the tetrapodomorph fish through the Devonian and Early Carboniferous genera. However, when tetrapods are picked up again in the fossil record of the later Early Carboniferous, these features show an explosive radiation with numerous parallel developments to jaws, occiputs, ear regions, vertebrae, ribs, sacrum, pelvic and pectoral girdles, limb proportions, and joint anatomy in response to the demands of terrestriality. Hints of this diversity are reflected in the wide range of sizes and morphologies found in the trackway sequences of Horton Bluff and in the newly collected Tournaisian material from southern Scotland. Together, these finds imply that in fact, diversification of tetrapods happened significantly earlier than the poor record for the Early Carboniferous suggests.

These animals have left their differing legacies for modern forms in the differences between modern amphibians and amniotes, and among the diverse amniote groups. Although changes to soft tissues and anatomy can only be inferred from modern forms, these may not always provide useful models for understanding early tetrapods.

By the closing stages of the Carboniferous, however, it seems as though the foundations were laid for truly terrestrial living among vertebrates, with the development of the amniote egg and the evolution of herbivory well established, as well as adaptations for terrestrial locomotion. A huge diversity of forms had evolved, some of which are like nothing that exists today, and some of which have left no living descendants. Tetrapods appear to have reached some kind of peak in the Late Carboniferous and Early Permian, achieving more or less global distribution. Many groups are represented in far-flung parts of the world.

At the end of the Permian, something catastrophic for all animal life on earth occurred, which resulted in the almost complete extinction of most lineages. Some fortunate survivors of most vertebrate groups were left, though it is not clear that these were the ones with particularly advantageous adaptations. Whatever the truth of this, they were left to repopulate the Earth, building on foundations laid by their Devonian and Carboniferous forebears.



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