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Amphibian Evolution

The Life of Early Land Vertebrates

Rainer R. Schoch



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Amphibian Evolution

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Preface

This book focuses on the first vertebrates to conquer the land, and on their long journey to become fully independent from the water. It will trace the origin of tetrapod features and try to explain how and why they transformed into organs that permit life on land. The classic idea of early land vertebrates is that they were similar to modern amphibians. Right or wrong, the vast majority of early tetrapods are therefore classified as amphibians (or more precisely their stem taxa). Accordingly, this book is centered on early amphibian evolution, a topic that effectively includes all early tetrapods, and it will also analyze facts and opinions on the origins of modern amphibians. The major part of the story covers events that occurred over the past 370 million years, but it is far from restricted to paleontology.

My own motivation to study the amphibian fossil record derives in large part from a fascination with the development, ecology, and evolution of their modern representatives. Therefore I consider many topics that can only be covered by examination of extant animals: features of the soft body, functions of organs that mediate breathing, feeding, hearing, and locomotion, the morphogenesis of body parts, larval development, metamorphosis, and ecology.

The aim is to achieve a comprehensive picture of amphibian evolution. This requires a walk through several dimensions, and I cannot claim to be an expert in all the fields to be covered. Nevertheless, I hope that the outcome will be worth reading, even though some data may become quickly outdated as new finds are made, and some concepts may change with new insights. The following research questions illustrate the central problems of amphibian evolution as understood here:

1. How did fishes evolve the necessary structures and organs to survive on land?
2. What was the life of early tetrapods like?
3. Are modern amphibians a good model to understand early tetrapods?
4. How did modern amphibians acquire their complex life cycles, encompassing an aquatic larva, drastic metamorphosis, and a terrestrial adult?
5. How diverse were early land vertebrates, and which evolutionary strategies did they employ?
6. What were the major factors of amphibian evolution, and how did mass extinctions affect them?

We should not expect to find equally complete or satisfactory answers to all of these questions, as the problems remain at very different stages of research. Research questions that involve examining many fossilized hard parts may be relatively easy to solve, while others require inference from extant taxa and will always remain more hypothetical. Yet other problems date back such a long time that the fossil record is too poor and ambiguous to permit decisive answers – and in such cases we shall have to consider alternative solutions and discuss their plausibility.

The diversity of questions relates also to the different research fields addressing them, and that leads me to the second major focus of the book, which is to consider the various current approaches and perspectives of paleobiology. The study of amphibian morphology and paleontology exemplifies many aspects of evolution. This topic offers a great opportunity to deepen our understanding of how organisms survive under the most diverse range of conditions, as both extant and

extinct amphibians have been studied extensively. It sheds light on the pathways taken by evolution to alter developmental systems, phenotypes, and ecological relations in the amphibian world. Excellent fossils allow breathtaking insights into deep time: fishes with limb-like appendages, early tetrapods with gills and eight fingers, fossils of 1 cm larvae with bushy gills and dark eye pigments cast in stone, and spectacular skeletons of predators more than 5 m in length, with skulls

exceeding a meter and hundreds of teeth in their jaws. Paleontology, zoology, developmental biology, histology, and evolutionary biology all meet in this area. The book outlines how these fields are integrated and how they come together to analyze aspects of early amphibian evolution.

Rainer Schoch
Stuttgart, Germany
October 20, 2013

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Writing this book has been a joy, because it has allowed me to write down ideas that had accumulated over two decades. However, composing a book is also hard work, and it is never clear in the beginning what the manuscript will be like when the chain of thoughts has been laid down. In planning the framework of the book I have been influenced by many friends and colleagues, and although I have attempted to list them all below I suspect that some names may have been inadvertently omitted, for which I apologize.

My parents encouraged me to start the adventure that led to me becoming a paleontologist, and they contributed all they could. My family patiently accepted my devotion to the subject and always support me with their interest and critical appraisal. Hence, the present book is dedicated to my family.

When I was still at school, David Wake and Kevin Padian provided invaluable encouragement. Jürgen Boy was most supportive in bringing his critical eye and admirable experience to bear on my work when I wrote my first scientific paper. My academic teachers at Tübingen, Wolf-Ernst Reif (†) and Frank Westphal, were the most open-minded and supportive academics I ever met. Wolf, who became a close friend over the years, challenged my thoughts by asking the most unexpected and difficult questions. That he believed in me provided invaluable support. Dolf Seilacher was always ready to give my thoughts a new spin, and he would do this by asking the simplest questions. Andrew Milner has been a friend from early on; he was more ready than others to accept this would-be colleague, bringing order into my fuzzy thoughts and incomplete texts and dealing with my impatience whenever he worked with me – I owe him a lot.

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Finally, I am most grateful to Mike Benton for suggesting that I write this book, Delia Sandford

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1

Introduction

The study of amphibians – both extinct and extant – makes a significant contribution to our understanding of how organisms develop and evolve. Like few other vertebrate groups, amphibians have been studied extensively from an early historic phase until today. Their modern exemplars have made an essential contribution to our understanding of phenomena such as morphogenesis, plasticity, larvae, metamorphosis, heterochrony, viviparity, feeding, ecology, speciation and microevolution, and – most recently and sadly – extinction. Their rich fossil record provides unique insights into ontogeny and paleoecology, phylogeny and macroevolution. Hence, the knowledge of amphibian evolution holds a pivotal position in the study of vertebrates.

Admittedly, amphibians are neither the most speciose, nor particularly spectacular vertebrates. They are often sluggish and slow, with a cold and moist skin covered with mucous and venom glands. Most of them are not very large, and many species are so tiny that they are easily overlooked. At the same time, amphibians are often the preferred objects for studies in development, ecology, and evolution. What, then, makes them such prominent study taxa? Why should their evolutionary history be of such wide general interest to biologists? There are historical reasons, influenced by their ready availability for study and the relatively easy breeding conditions of some laboratory taxa. However, amphibians are also special among vertebrates in many ways, not least in their capacity to survive and propagate in unstable environments, as well as in their ability to change from one habitat to a profoundly different one. Some amphibians have mastered the regeneration of organs in a way unthinkable in most other vertebrates, and they have repeatedly evolved live-bearing species, each time with different features. Some amphibians breathe with lungs, others with gills, and yet others

through their skin – and many amphibians employ a combination of all these respiratory mechanisms. Finally, amphibians are a group whose evolutionary history dates back as far as the Early Carboniferous, a time span encompassing 330 million years of change and stasis, diversification and extinction, and fascinating examples of evolutionary innovation. It is the purpose of the present book to trace this history, seeking to understand features of amphibian evolution in the frameworks of development and ecology, the two major foci of modern evolutionary biology. It is the interdisciplinary questions that are the most fascinating in this field, and therefore the second major theme of the book is the question of how we conduct studies on the fossil record, development, ecology, and evolution of amphibians and beyond.

What is an amphibian? The phylogenetic definition that I will use is straightforward: any member of the three modern groups salamanders (Caudata), frogs (Anura), and caecilians (Gymnophiona) is an amphibian (Figure 1.1). The correct systematic name for that group is **Lissamphibia**, and all lissamphibians share a common ancestor that lived sometime in the Late Paleozoic (~330–290 myr).

There is a large gap between lissamphibians and the manifold Paleozoic and Mesozoic taxa commonly referred to as “amphibians.” Some of these must rank among the ancestors of lissamphibians, but authors still debate which taxa fall into the lissamphibian stem-group. To avoid confusion, it is reasonable to distinguish between the lissamphibian relatives (phylogenetically called “stem-amphibians”) and all other taxa. The others are referred to here as “early tetrapods” when their relationships to Lissamphibia and Amniota are uncertain, and as “stem-amniotes” if their affinity with amniotes can be made plausible. Here, I follow the majority view on the origin of Lissamphibia, which holds that **temnospondyls**, members of a speciose clade encompassing almost 300 species, form the stem-group of lissamphibians (Bolt 1969; Milner 1993; Ruta and Coates 2007; Sigurdson and Green 2011; Maddin *et al.* 2012).

Therefore, when speaking of Paleozoic and Mesozoic amphibians, I refer to temnospondyls, and thus I employ a scheme in which Lissamphibia forms a subgroup within a larger clade Amphibia. The alternative views will be discussed in depth in Chapter 9 (phylogeny). Whereas this book deals mainly with

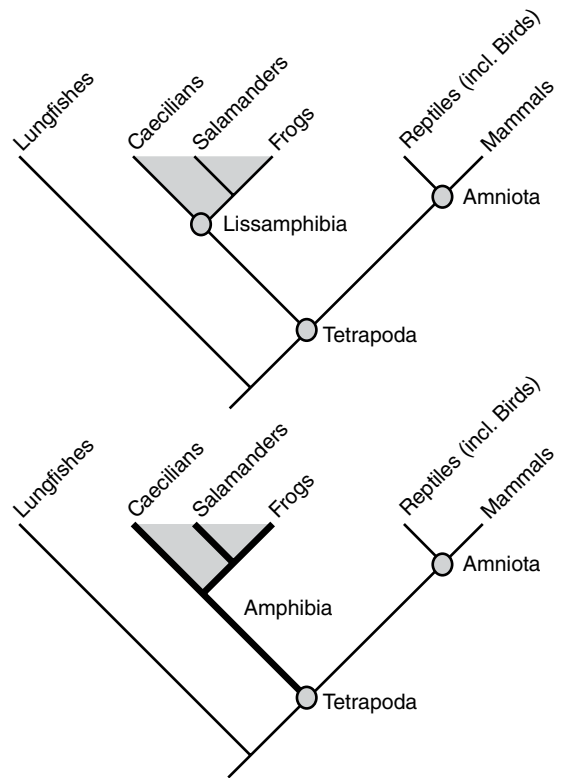


Figure 1.1 The relationships of extant tetrapods and their nearest relatives. Lissamphibians are probably a monophyletic group (clade), containing the limbless caecilians, salamanders, and frogs. Amphibia is a more inclusive name, here used to include all stem-group taxa, among which are many Paleozoic and Mesozoic forms (“early amphibians”).

lissamphibians and amphibians, it also tackles many problems concerned with early tetrapods.

1.1 Changing paradigms in amphibian evolution

Amphibians bear a most appropriate name in several respects, and the scientist who coined the term was probably not aware of all of them. Literally meaning “living on both sides,” the name points to the capacity to transform and adapt to divergent living conditions. In the narrow sense, the two sides are freshwater and land: the stereotyped amphibian life cycle includes the water-born newt or tadpole transforming into an adult land salamander or frog. Yet there are many other ways of amphibian existence, exemplified by the limbless caecilians, most of which live in the soil, the lungless and live-bearing salamanders, some of which ably climb trees, or the non-transforming axolotl, which is effectively a hypertrophied, sexually mature salamander larva. There are many more such cases, and on closer inspection one may even think there are as many different life cycles as there are species. These amazingly varied life histories differ far more than the slight variations in ontogeny known from other vertebrates. They often harbor built-in switches, responding to environmental inputs. Water conditions, temperature, food availability and properties, and oxygen form some of these factors, but there are many others, often confined to individual species or populations.

Amphibians are also peculiar because their fossil record is extraordinarily good. Although relatives of modern amphibians are often too small and delicate to be well preserved in most sediments, Paleozoic and early Mesozoic deposits yield a wealth of other, much larger amphibian fossils. These fossils tell us about a bizarre and alien world, playing in an exotic geographical setting and climate, and revealing highly unusual aspects of development and ecology. The abundance of early amphibians and their presence in numerous different deposits has made them preferred study objects for paleontologists ever since their first discovery in the 1820s. The most striking feature of these ancient forms is their

huge size – ranging between 0.5 and 6 m. Compared with living amphibians, they had a very different morphology, many of them resembling modern crocodiles, while others reveal convergences to modern flatfishes, moray eels, giant salamanders, caecilians, and lizards.

In recent decades, discoveries of many new fossils have changed our view of early amphibians profoundly. Fossils are usually interpreted within the framework of phylogenetic hypotheses, spanned by well-known extant organisms. This procedure arrives at extant groups that give the best model for the understanding of the extinct group. In the case of amphibians and early tetrapods, the classic living model organisms were the modern salamanders, because of their apparently plesiomorphic appearance and the biphasic life cycle (larval–metamorphic). One might call this a central dogma in the study of tetrapod origins. Indeed, salamanders appeared to be perfect model organisms: their general body architecture, their “primitive” mode of locomotion on land, and the capacity of water-living larvae to transform into a terrestrial adult were seen as essential features of all early tetrapods. The central assumption was that the first tetrapods conquered land in the same way as many modern salamanders do it – namely, during metamorphosis.

Is the evolutionary conquest of land recapitulated in each baby salamander and frog? Formulations like that may be elegant, but have little to do with what really happened. There is no simple parallelism between ontogeny and phylogeny, let alone in such developmentally complex organisms as amphibians. The underlying processes are entirely different: stochastic selection on the evolutionary level, genetic and developmental mechanisms on the organism level. The whole issue of heterochrony, first triggered by such extraordinary cases as the axolotl, has become a multifaceted issue to analyze in recent years. New fossils, including those of Paleozoic baby amphibians, shed light on the life cycles of early amphibians (Boy 1974; Schoch 2009). These data amounted to the insight that metamorphosis was not shared by most of these early taxa, and that the salamander model is far from appropriate for the understanding of early tetrapods (Schoch 2002).

This model has also been challenged by many finds that indicate a more aquatic, fish-like habit of many early tetrapods (Coates and Clack 1990, 1991). These taxa (see Figure 1.2 for examples) retained lateral lines and gills as adults, and their skeletons were hardly capable of supporting longer excursions on land. The available evidence from fossil footprints confirms this, revealing that these animals were extremely slow when forced to cross dry land. They did not undergo a metamorphosis like modern amphibians. In many cases, adults are found in the same environments as their juveniles.

This touches the core of a second dogma on the fish–tetrapod transition, the ecological argument. The classic ecological scenario holds that tetrapods were attracted by food outside the water, that there must have been selection pressures driving their ancestors onto land. However, fossil evidence counters this idea by showing that early tetrapods and amphibians lived primarily in the water, retained many fish-like features and organs, and preyed on fish or other water-dwelling animals. New evidence from histology supports this conclusion, because many early tetrapods retained

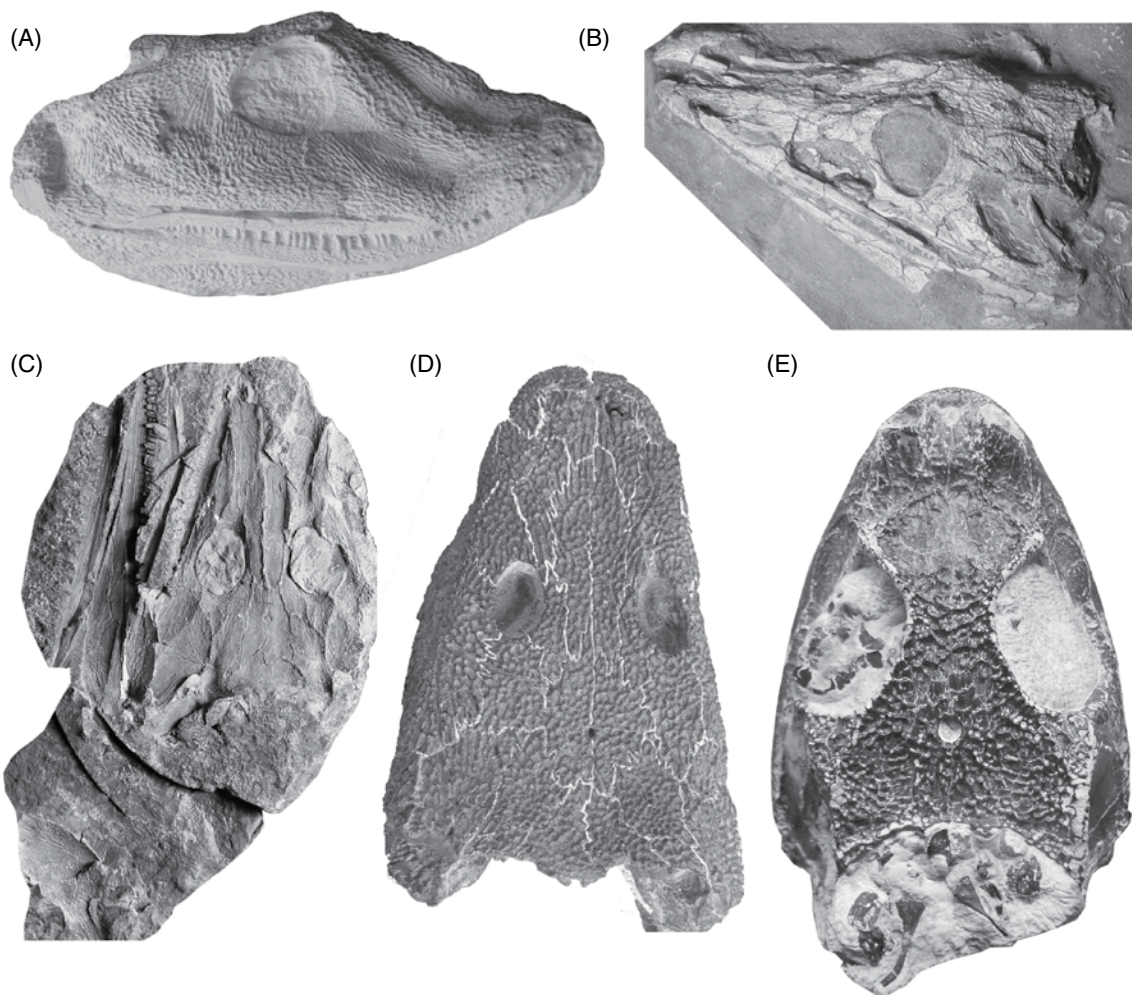


Figure 1.2 Skulls of different Paleozoic taxa: (A) the stem-tetrapod *Acanthostega*; (B) the chroniosuchian *Chroniosaurus*; (C) the temnospondyl *Archegosaurus*; (D) the colosteid *Greererpeton*; (E) the dissorophoid *Cacops*.

calcified cartilage inside their long bones to make their bodies heavier, while others had lightly built bones, providing excellent swimming but very poor walking abilities. In all of these taxa, the internal structure of limbs was not adapted to meet torsional stress such as that caused by locomotion on land (Sanchez *et al.* 2010). The old ideas of Alfred Sherwood Romer (1956, 1958), a pioneer in the study of early tetrapod evolution, are revived: then regarded as an oddity rather than mainstream opinion, his suggestion was that the origin of tetrapods took place under water, and that true land vertebrates appeared substantially later. Clearly, the salamander is not a reliable model for these long-extinct taxa. In turn, modern amphibians as a whole appear much more alien and interesting when these results are borne in mind. They form a separate, successive strategy to generate a land vertebrate, with many fascinating adaptations that were not features of early tetrapods, but evolved in the 330-million-year history of amphibian evolution after their split from the amniote ancestors. We are also more fully able now to trace some key aspects of this evolutionary pathway, although many problems are still unresolved.

The study of amphibian evolution – of extinct as well as extant taxa – reveals another very interesting aspect: ontogeny. In stark contrast to other groups of tetrapods, but similar to various fishes, amphibians are subject to profound ontogenetic change, reflecting a broad range of responses to environmental parameters. Although ancient taxa had very different ontogenies, they were sometimes as complex as modern ones. This reaches a stage at which it becomes necessary to consider the whole life cycle as a unit of taxonomy, phylogeny, ecology, and evolution. In paleontology, this concept has been put forward only recently. One outcome of these efforts is the present book, summarizing recent work and numerous still-unpublished observations. For paleontology, the life cycle concept means that single ontogenetic stages are not sufficient to trace evolutionary changes. Many problems in phylogenetic analyses result from the unsettled questions raised by ontogenies and developmental evolution. Fortunately, the preservation of different size classes in fossil amphibians provides insight into

this field, permitting detailed comparisons between extant and fossil ontogenies. The old and troubled concept of heterochrony comes into mind almost automatically here: neoteny, in its classic example of the axolotl as a sexually mature larva. Yet the new field of developmental evolution (evo-devo) is much more than the study of ontogeny and phylogeny. As pioneered by Ivan Ivanovich Schmalhausen and Conrad Hal Waddington, it focuses on the phenotype as an active player, responding to environmental changes, resisting perturbation from inside and outside, and being able to remain remarkably stable throughout evolution if required. However, the more obvious capacities of amphibian phenotypes are their flexibility and plasticity. This covers the important aspect of the *reaction norm*, a concept uniting development and ecology under the evolutionary umbrella.

The significance of fossil amphibians for the understanding of evolution is obviously manifold: their own evolutionary history is full of detailed stories, their relationship to modern amphibians is complex and reveals many perplexing convergences, their paleoecology has many unique features and provides insight into habitats, environments, and climates long ago, and the connection between evolution and development has been studied extensively in some Paleozoic and Mesozoic clades. This leads to the recognition of metamorphosis, a key feature of modern amphibians, as a life history strategy that evolved some 300 million years ago. Finally, the bearing of early tetrapod fossils on the fish–tetrapod transition is profound and has the potential to further shift the picture.

1.2 Paleobiology: data, methods, and time scales

Although there is *one* true history of early land vertebrates that needs to be found, only aspects of this story can be studied by any one approach at a time. Methods, time scales, and the data themselves differ substantially between approaches. These are often complementary by nature – only when they are used in combination does a comprehensive picture come within reach. Although

efforts to make this picture clearer have met with tremendous success in the last few decades, there are inherent limitations and problems that will ensure that it remains forever incomplete. Understanding these problems is crucial for any successful contribution to this field.

Each of the research questions outlined in the Preface addresses complex and multifaceted problems. They require the integration of fossil data with those from embryology, genetics, physiology, developmental biology, and ecology. In concert, they form an inclusive research program of evolutionary biology, focused on early land vertebrates. The short list of questions leaves no doubt that different problems concerning the biology of early tetrapods require different research fields to be involved. But how this can be achieved is a far from trivial question, to be outlined as follows.

Despite their different problems and methods, scientists live in one world and want to grasp the whole story. To do that, interdisciplinary research is essential and inevitable. However, this often proves to be more difficult than it appears at first sight, especially when it concerns the integration of pattern- and process-focused disciplines. Paleontology and zoology are clearly centered on *patterns* – morphology, histology, embryology, and phylogeny dominate these fields. Description, statistics, and phylogenetic analysis are major approaches here, aimed at understanding the evolutionary history of the particular group. History, of course, is a sequence of unique events, it does not repeat itself in a predictable way, and has many causes. Consequently, zoology and paleontology are dominated by patterns that are historical, although it would be too simple to call them historical sciences.

On the other hand, genetics, developmental biology, ecology, and evolutionary biology study the *causes* of organismal structure and the reasons for its change. Genes and development are the domains where *mechanisms* of heredity act and the generation of organismal form takes place. These mechanisms are active within each and every organism, and they operate on microscopic scales of space and time. The actors in this play are cells, which gather in populations to coordinate movements, produce substances, and form tissues and hard parts. In the past two decades, genetics

and developmental biology have increasingly worked together to find unexpected levels of similarity between widely divergent taxa – referred to as deep homology. One facet of this very fruitful approach is that the new field of developmental genetics is able to bridge gaps between morphologically disjunct clades. It seems to hold one of the keys to *understand* major features of body plan evolution. The origin of tetrapod limbs from fish fins is one example where such novel approaches proved to be useful (Shubin *et al.* 1997, 2009). For instance, the tetrapod hand and foot have recently been found to be novel structures, without homologs among extant bony fishes (Clack 2009).

Conversely, ecology and evolutionary biology focus on markedly larger scales: the *processes* they study require much more time – from days to years in ecology, from years to thousands of millennia in evolution. The actors on this stage are not single individuals, but populations. Admittedly it is still not well understood how species are formed and what makes a population a species. After all, species are much more fuzzy and messy than atoms or molecules are in physics and chemistry. In sexually reproducing organisms, species boundaries are established (and maintained) by various mechanisms of reproductive isolation. In the long run, requiring at least 10^5 – 10^6 years, a given species transforms into a new one. This is the crucial gap between micro- and macroevolution. Rather than a principal difference, this gap is caused by the fact that our own time frame allows us to study the microscopic time scale of development, or the ecological time scale of predator–prey relationships, but not the evolutionary time scale at which species change.

How species form, by means of splitting (*cladogenetic*) or simple transformation within a lineage (*anagenetic*), is often unclear. Most probably, a broad range of modes exists, considering the enormous diversity of evolutionary rates and patterns known across the organismic world. Although paleontology cannot offer direct insight into processes, it reveals patterns of evolutionary transformation. However, it must be emphasized that it needs exceptional preservation, extraordinarily large samples, and a sequence of time slices that are not too distant in geological time, in order to

permit evolutionary studies. Unfortunately, this reduces the number of possible cases, especially in vertebrate paleontology, to very few. Even then, it must be remembered that all we get is a sequence of snapshots of the evolutionary transformation of a given species, which cannot be compared to the data a developmental biologist or ecologist operates with. More than in other fields, evolutionary biology handles fragmentary data – and this is true not only in paleontology, which is so used to dealing with pieces of a puzzle.

In paleontology, a single exceptional deposit (*Lagerstätte*) often reveals more data on the ecology and microevolution of its fauna than dozens of other localities that yield only fragments. In the case of early amphibians, lake deposits rank first among such highly informative sites. When undisturbed by erosion, such lakes preserve hundreds to thousands of years of continued deposition, permitting the identification of changes on a small scale. Unfortunately, such lake deposits, even if preserved in close succession in the same area, are often separated by long time intervals undocumented or destroyed by erosion. When paleontologists put together data from the fossil record, they always have to consider how many sources of uncertainty remain.

To conclude, the study of evolutionary history – for instance, that of early land vertebrates – requires integration of data from various disciplines. This can only be achieved when (1) the nature and significance of data from each field are understood, (2) the strengths and limitations of the different methods are considered, and (3) the integration of results from different disciplines acknowledges the different levels (pattern versus process, time scales, levels of complexity).

1.3 Concepts and metaphors: how scientists “figure out” problems

“Words matter in science, because they often stand for concepts” (Wake 2009). Scientists need a theoretical platform on which to work and a framework of ideas and concepts into which they can fit their observations. In paleobiology this platform is evolution, a vast theoretical framework shared with other life sciences. While working on

this platform, the developmental biologist, evolutionary biologist, ecologist, or paleontologist has to invent further concepts. These concepts build a framework within which problems are viewed and discussed. Such frameworks are essential for science, because they provide firm ground for hypotheses. The theory of evolution, with its constituent concepts of *natural selection* and *descent with modification*, provides the most general and stable pillars in the framework of modern life sciences.

An essential platform in evolutionary biology is the concept of homology (Hall 1994). First formulated by Richard Owen in 1840, it went through different phases of interpretation. First viewed as reflecting a divine body plan or *archetype*, it was then seen from the perspective of Darwin’s theory of evolution. Shared features were now interpreted as based on *common ancestry*, whereas analogy was the outcome of independent evolution, highlighting the power of natural selection. The hands and feet of tetrapods go back to the last common ancestor of Tetrapoda, no matter how different they are in modern land vertebrates, or whether they have eventually disappeared, as in snakes or caecilians. More recently, the homology concept has been enriched by the addition of *homoplasy*, which embraces convergence, parallelism, and reversal. Originally, homology and homoplasy were viewed as a dichotomy. Today, the two are increasingly considered end points on a continuum (Hall 2007). After all, homology, reversal, and parallelism are just different evolutionary stages of common ancestry. A central theme of modern genetics and evolutionary biology is *deep homology*, or the observation that disparate organisms share fundamental genetic and regulatory similarities behind their divergent morphologies (Shubin *et al.* 2009). These new insights of developmental genetics, entirely unforeseen, have made an adjustment of the homology concept necessary. The historical transformation of this concept exemplifies the important point that scientific frameworks need to be sufficiently flexible to adjust to new ideas and changed paradigms.

The downside of scientific concepts is that they often employ metaphors – *descriptive images* based on *analogy*. Metaphors help researchers to

figure out a complicated problem more clearly and in simple terms, but they may be easily over-stretched and overinterpreted. This is the point where the researcher has to perceive the difference between his metaphor and the process which it stands for – otherwise, the metaphor becomes the problem rather than the solution.

Like any science, paleobiology cannot work without metaphors, and knowing that one should always be aware of their existence and their limitations. It is appropriate to use the terms “homology,” “selection,” “genetic code,” or “diversity” if we keep in mind that they represent much more complex phenomena than we are able to describe. In a complicated text, they may serve as handy abbreviations. Viewed in this sense, metaphors can be powerful tools, naming the unspeakable. They reduce a complex phenomenon of the biological world (which we often only know inadequately) to a situation resembling the human world. The crucial point is that we should never forget that – otherwise we might confuse description with reality.

1.4 Characters and phylogenies

Characters form the basis of any phylogenetic analysis, and thus play a crucial role in evolutionary biology. Cladistics treats characters as the “atoms” of phylogeny, but that requires an essential property: to become a useful character, a feature must be divisible into distinct character states. Here’s why. A cladogram is a sequence of dichotomies or branching nodes. Each node is defined by at least one character that “supports” it. It forms the evidence that a given group has a common ancestor. Such evidence is provided only by exclusive (= derived) character states, the apomorphies.

What then makes a given feature a phylogenetic character? Although characters provide crucial evidence in the analysis of evolutionary history, they are still defined by researchers. It is quite common that newly published characters are disputed and their definition and coding subject to discussion and modification. In the long run, most proposed characters survive this test, albeit often with substantial reformulation and almost universally with recoding.

Reliable or “good” morphological characters are essential for phylogenetic analyses. But how can a character be recognized in an objective way? The reliability of morphological characters is difficult to assess because there are no objective, universally accepted criteria. The reality of characters itself is far from understood. Whereas it is undisputed that, for instance, a protein or cell really exists, there is no consensus on whether characters do. Organisms are modular, they fall into a nearly infinite number of units (Riedl 1978). Some units are obvious, but others can be very subtle and subject to scientific dispute (Wagner 2001). Some characters may be such modules, others are not. After all, characters are hypotheses of homology, not simple facts or undisputed building blocks of organisms.

Here are a few characters believed to be of some significance in early amphibian phylogeny (Figure 1.3):

- Presence of fingers and toes (yes/no).
- Number of fingers (8-7-6-5-4). This is a character that falls into more than two states.
- Shape of the occipital condyle. This character may be defined differently: either simple (one- or two-headed) or complex (contribution of basioccipital and surface area of facets). Depending on this, the character may have two states or be multistate.
- Length of ribs (short and straight/long and curved).

These four characters and their various states define major nodes in tetrapod phylogeny: (1) the limbed tetrapodomorphs, (2) the transition between limbed tetrapodomorphs and crown tetrapods, (3) the stem-group of modern amphibians, and (4) the stem-group of amniotes. These characters make most evolutionary considerations possible, thus forming the backbone of this book.

1.5 What’s in a name?

There are two different ways to name monophyletic groups (*clades*), and despite much debate there is no consensus on which way should be preferred. Effectively, each author needs to make a decision which definition to use for a particular taxon

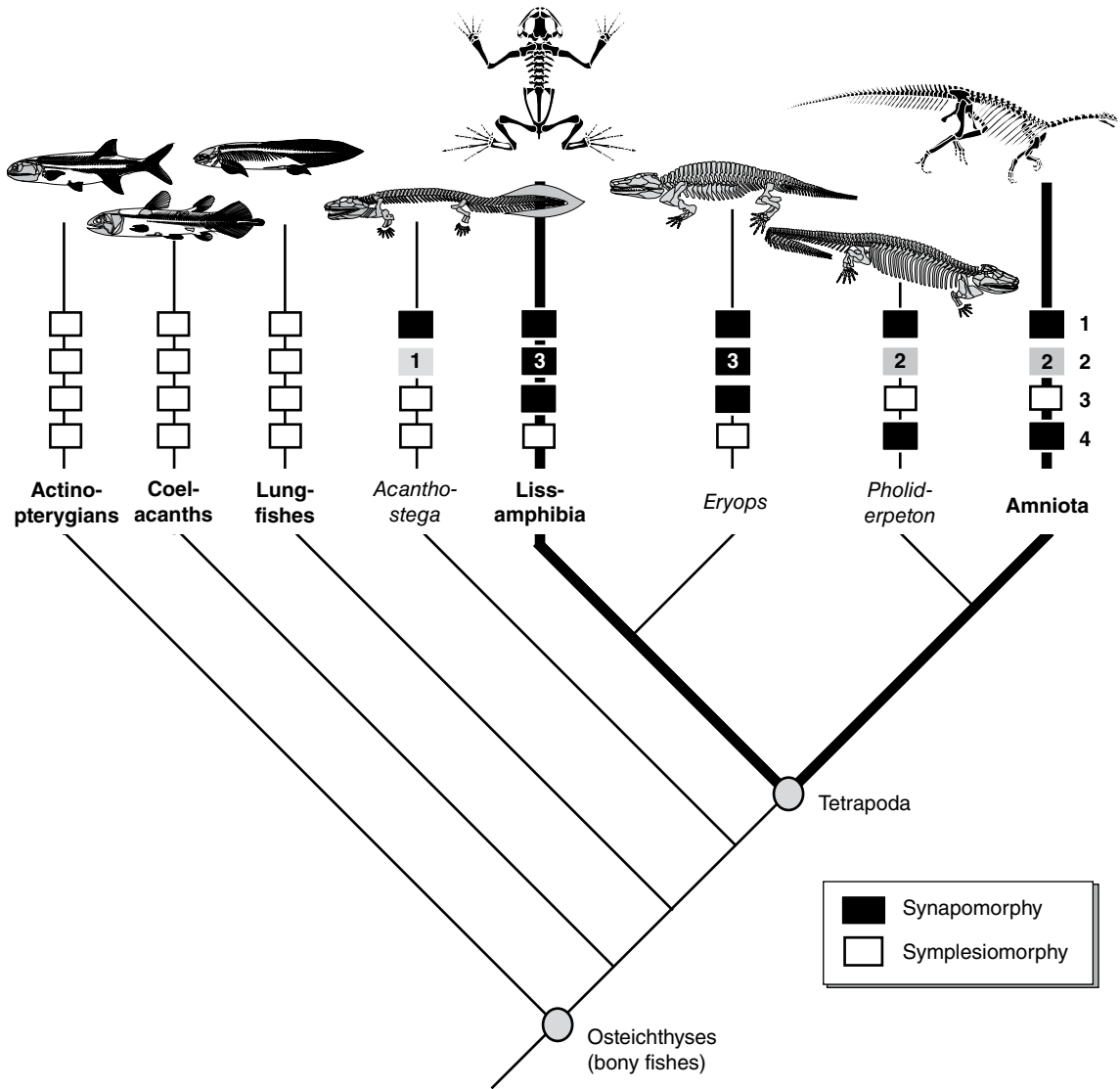


Figure 1.3 The importance of single morphological characters exemplified by early tetrapod phylogeny (see text). The presence of digits (1) is shared by some tetrapodomorphs. The number of digits varies from clade to clade: eight in *Acanthostega* (state 1) to five in stem-amniotes (state 2), and finally reduced to four in amphibians (state 3). The double occipital condyle (3) is a derived character of amphibians, whereas the long ribs characterizes amniotes and their stem (4).

name. It can only be hoped that in the long run authors will agree on a particular definition – but currently such agreement is not in sight. Without a clear statement by the author defining his/her use of taxa, much confusion can arise. The definitions of the names Amphibia and Lissamphibia have already been given. Here, I will briefly

explain the two alternative definitions as exemplified by the taxon Tetrapoda (land vertebrates), which includes Amphibia and Amniota.

The traditional way to define groups (predating cladistics) is to refer to key characters. It is called the *character-based concept*. Obviously, tetrapods have digits (fingers and toes) that their fish-like

relatives lacked. This seems to be a perfect case, giving a clear-cut morphological definition that even corresponds to the meaning of the name Tetrapoda: four-footed animals (Greek: *tetra* = four; *pous, podos* = foot). In phylogenetic (cladistic) parlance, the presence of digits is a synapomorphy of all tetrapods, whereas “fishes” retain the plesiomorphic character state, the absence of fingers and toes. (In the case that digits evolved from radials, currently an alternative hypothesis, the distinction would be a functional one, highlighting the difference between radials in a fin and digits in a hand or foot.) Apart from the obvious advantage of referring a taxon to its most significant character, supporters of the character-based concept emphasize that it preserves the original meaning of taxon names better, upholding tradition and minimizing complicated nomenclatural changes.

The alternative way to define a taxon is *phylogenetic nomenclature*. This was introduced by Willi Hennig, the founder of phylogenetic systematics, who also first defined Tetrapoda in this new way. Here, taxa are defined entirely by the structure of the cladogram, and remain independent of particular characters (Figure 1.4). This is not such a bad idea, because our perception of characters often changes with new evidence, and sometimes characters are even abandoned when it is shown that they are ill-defined in principle. Without using characters, Tetrapoda can be defined as the group encompassing exclusively extant amphibians and amniotes. These two largest extant clades of land vertebrates form the two branches of modern tetrapods. All phylogenetic analyses, both morphological and molecular, agree on this. In this definition, fossil taxa fall either within this comb (in which case they are true tetrapods) or on the stem lineage (in which case they are stem-tetrapods).

Currently, the name Tetrapoda is used with divergent meanings by different authors. For instance, Ahlberg and Clack (1998), Anderson (2001), and Clack (2012) preferred the character-based definition. They speak of *Acanthostega* as a “basal tetrapod” because it has hand and foot skeletons, whereas *Tiktaalik* is considered a “fish-like sarcopterygian” because it lacks them. On the other hand, Laurin (1998, 2004) applied the

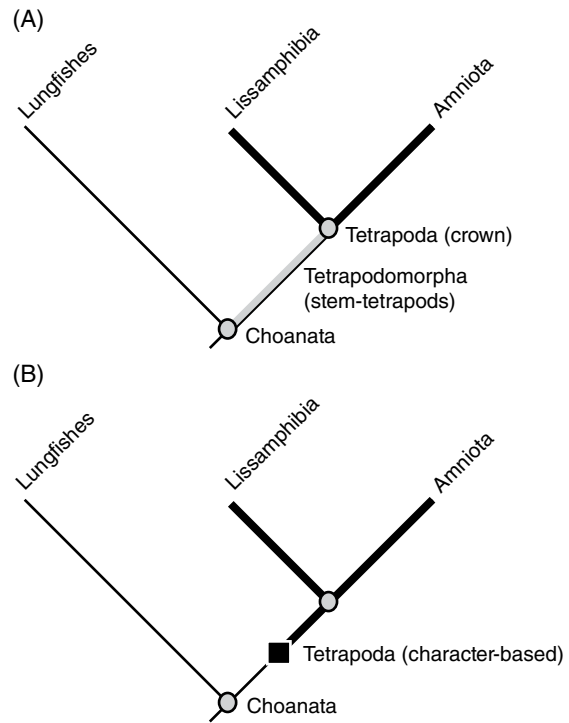


Figure 1.4 Two different ways to name a clade: (A) node-based versus (B) character-based.

phylogenetic nomenclature. This demands ranking both *Acanthostega* and *Tiktaalik* as stem-tetrapods (tetrapodomorphs). To acknowledge the presence of hand and foot skeletons in *Acanthostega*, Laurin (1998) has suggested naming all tetrapodomorphs with these features “stegoccephalians.” So far, this name has not been adopted by other authors because Laurin proposed a radically different phylogeny of lissamphibians which leaves numerous taxa traditionally regarded as crown tetrapods outside the Tetrapoda.

Throughout this book, I shall use phylogenetic definitions rather than those based on characters. My reasons for doing so are twofold: (1) my own experience has made me wary of character definitions, after even features long regarded as robust characters turned out (based on new evidence) to be poorly defined or, worse, impossible to define objectively; and (2) I agree with Hennig that there is a key difference between crown groups and other

taxa in that extant species permit countless more traits to be studied than fossils. The constituent taxa of crown groups should therefore be much better known in the long run than fossil taxa will ever be. This is why crown groups – as one example of node-based phylogenetic definition – may serve as anchors for cladograms. The crown group Tetrapoda is a good example, as the monophyly of amniotes and lissamphibians is more robust than all taxa defined on the basis of extinct taxa. For those interested in the details of this debate, I recommend Laurin and Anderson's (2004) exchange of arguments for and against phylogenetic nomenclature.

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2

The Amphibian World: Now and Then

The amphibian world encompasses numerous groups of animals that evolved during the past 330 myr. Although most of them are long extinct, they played important roles in ancient ecosystems. The story begins with the first four-legged vertebrates (tetrapods), which were remarkably fish-like in many features – and only some of them fall within the ancestral lineage of modern amphibians. Lissamphibians and amniotes form the end points in an exciting sequence of early tetrapod evolution. Only the fossil record can shed light on how the extant groups formed and what the diversity of tetrapods was like in the Paleozoic, Mesozoic, and Cenozoic eras. The last few decades have produced many new and unexpected finds of these animals, and these discoveries have changed the big picture of early tetrapod evolution profoundly. Many of these taxa were radically different from all modern vertebrates, and there is no single extant model organism that can serve as a safe guide in understanding these animals. How was the fish skeleton modified to become that of a tetrapod? How many different tetrapod groups existed at a given time? How can they be identified, and what do we know about their evolution? Studying early tetrapods brings us face to face with fascinating and alien creatures whose reconstruction, life habits, development, and evolution pose major problems for paleobiology.

2.1 Tetrapoda

The land vertebrates form the starting point of the present book, which in many respects deals as much with early tetrapods as it does with amphibians. The origin of tetrapods matters here because the understanding of amphibian evolution requires a deep knowledge of early tetrapod characters themselves. It is a major argument of this book that the traditional idea of modern amphibians as a guide to understanding extinct amphibians needs revision. This notion has emerged primarily from the study of fossil taxa themselves, but has been complemented by insights into the functional morphology, physiology, and developmental biology of lissamphibians. On closer inspection, early tetrapods appear stunningly different from both extant amphibians and amniotes. It is therefore important to approach the topic by setting a framework within which all further thoughts and discussions may be placed. The crown-group concept first advocated by Hennig (1966) is such a frame, and it will serve this purpose throughout the book. In the following sections, major features of the tetrapod skeleton

will be described, followed by a discussion of the most important tetrapod characters.

2.1.1 The tetrapod skeleton

Tetrapod skeletons have evolved hundreds of very diverse forms, but they all share a common underlying architecture. This may be considered a coherent tetrapod *body plan* (a structuralist view) or it may be viewed as an *assemblage of characters* (a phylogenetic view). Either way, the hard parts of tetrapods are numerous and often highly complicated, but they all go back to a common ancestor. In turn, this ancestral stem-tetrapod inherited its bodily structure from bony fishes, that is, from aquatic vertebrates. Consequently, the tetrapod skeleton can be understood as a modification of the fish skeleton.

Skull structure. The tetrapod skull falls into three different units that can be defined under three entirely different aspects: embryology, phylogeny, and function. These include (1) the dermal skull (“outer skull”), (2) the endocranium (“inner skull”), and (3) the gill arches (visceral skeleton) (Figure 2.1). The different units are formed by cartilage or bone and serve many purposes: feeding,

BOX 2.1: VERTEBRATE PHYLOGENY AND RELATIONSHIPS

Gnathostomata: The jawed vertebrates include all fishes with jaws supported by a skeletal apparatus. They originated in the Early Silurian (~440 myr). Characters: (1) head skeleton composed of braincase, dermal skull, and gill arches plus jaws, (2) paired fins, (3) three unpaired fins (two dorsal, one anal), (4) teeth and bony scales. The gnathostomes include two large extant groups: the cartilaginous fishes (sharks, rays, and chimaeras) and bony fishes.

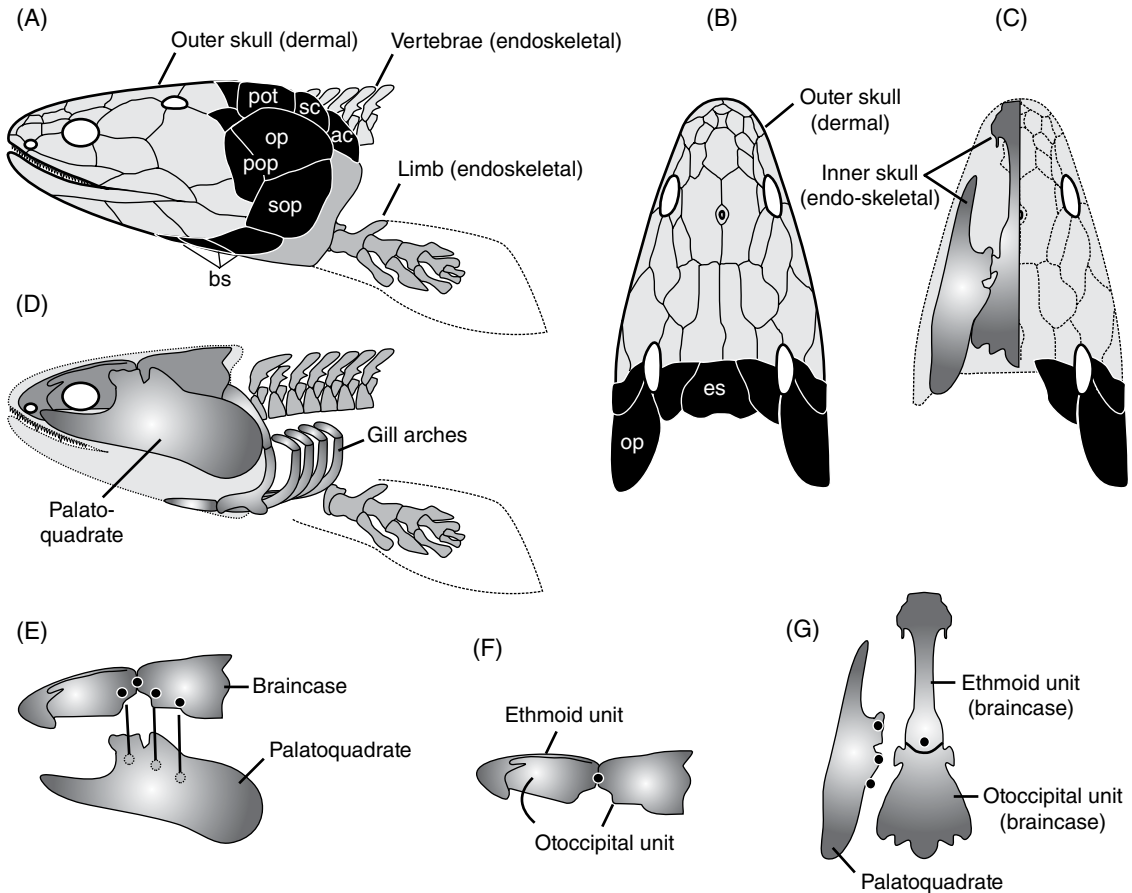
Osteichthyes: The bony vertebrates. The oldest osteichthyan fossils are from the Late Silurian (~428 myr). Characters: (1) lungs or swim bladder, (2) lepidotrichiae (bony fin-rays), (3) numerous new dermal bones in the skull and pectoral girdle. The Osteichthyes include two large branches, the ray-finned fishes (~30 000 extant species) and lobe-finned fishes and tetrapods (~24 000 extant species).

Actinopterygii: The ray-finned fishes, comprising more than 95% of living fishes. They are known from the Late Silurian onwards. Characters: (1) ganoid scales (containing the enamel-like substance ganoin), (2) crowns of teeth formed by acrodin, a transparent material, and (3) only one dorsal fin (which may be split to form two in some taxa). A plesiomorphic feature is the thin cross-section of the fins, in contrast to the lobe-finned fishes.

Sarcopterygii: The lobe-finned fishes have very few surviving aquatic taxa (only *Latimeria* and three genera of lungfishes), but they also include all living land vertebrates. They have been in existence since the latest Silurian (~420 myr). Characters: (1) strong paired fins or limbs with a single long axis, (2) teeth entirely covered by enamel, and (3) scleral eye ring with more than four plates.

Tetrapoda: The extant four-legged land vertebrates. They first appeared in the Early Carboniferous (~335 myr) and fall into two major clades: Lissamphibia (caecilians, salamanders, and frogs) and Amniota (mammals and reptiles, which include birds).

Figure 2.1 Essential units of the skull, exemplified by *Eusthenopteron*. Dermal bones in light grey, endoskeletal units in darker shades. All dermal bones marked in black were lost in tetrapods (opercular or gill-covering elements). ac, anocleithrum; bs, branchiostegal bones; es, extrascapular; op, operculum; pop, preoperculum; pot, posttemporal; sc, scapula; sop, suboperculum.



breathing, housing and protecting the brain and organs of sense, and the attachment of musculature, to name just the most obvious.

Although highly complex, the three units are found in all tetrapods, and indeed occur throughout vertebrates. Originally, each of these units was composed of numerous elements, but evolution has reduced the number and sometimes the complexity of elements in several major lineages. Comparing early tetrapods with modern amphibians reveals how far this reduction has gone: most salamanders retain just half of the skeletal elements possessed by the first tetrapods.

Structurally, the inner skull forms a cylindrical cover of the brain, while the outer skull in turn contains the inner skull – the two cranial skeletons are separated by thick sheets of musculature attaching at the jaws and eyeballs (Figure 2.2). The third unit is the gill arches, which form a basket primitively composed of five half-rings that contain the gills and permit the water to flow from the mouth through the gills; the gill openings are located between these half-rings. This basket is composed of rod-like elements formed of cartilage in the embryo, which may be replaced by bone in later life. Like the gill arches, the inner

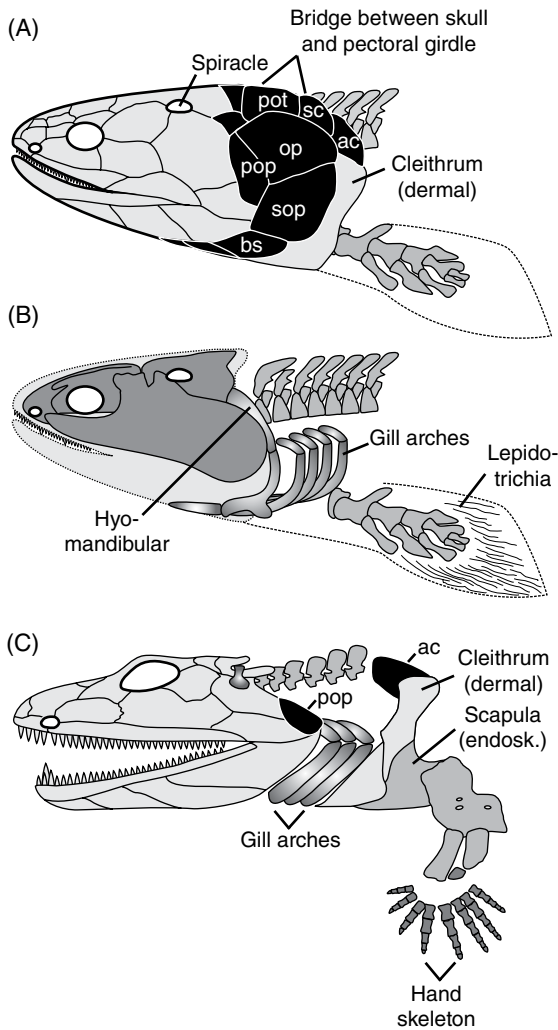


Figure 2.2 During the fish–tetrapod transition, the skull and forelimb underwent substantial modification: reduction of gill chamber, consolidation of skull, separation of pectoral girdle and forelimb, and the appearance of digits. (A, B) *Eusthenopteron*; (C) *Acanthostega*. Adapted from Jarvik (1980) and Clack (2002a). Abbreviations as in Figure 2.1.

skull originates as a cartilaginous structure in the embryo, but may be partially replaced by bone during later stages of ontogeny. In contrast, the dermal skull is bony from the start, it usually forms rather late, and cartilage is never involved.

Braincase and jaws. In the inner skull, the braincase forms an unpaired central unit encapsu-

lating the brain, whereas the endoskeletal jaws (palatoquadrate and mandible) form the paired upper and lower jaw halves, respectively. In bony fishes, the inner skull is moveable (kinetic) in itself: apart from the joint between upper and lower jaw, the upper jaw can also be moved against the braincase. This was already a functional property of early bony fishes and is retained in some extant bony fishes. Although long lost in most extant tetrapods, this kinetism is reflected by the embryonic patterning of the inner skull. In early tetrapods, the braincase was only partially replaced by bone, and only these portions are usually preserved in fossils. The most common bony portion is the region between the eyes (sphenethmoid), but the ear capsules may also be bony (otics), and especially the articulation with the first vertebra, originally composed of four elements (occipital bones).

The inner skeleton of the upper jaw (palatoquadrate) remains mostly cartilaginous in tetrapods, except for the jaw articulation, which ossifies as quadrate (upper jaw) and articular (lower jaw). Only in ancient lobe-finned fishes and early tetrapods, a second part of the palatoquadrate was bony: the epipterygoid. This element formed one of the joints by which the palatoquadrate hinged at the braincase. The inner part of the lower jaw is called Meckelian cartilage and ossifies only rarely and partially in some taxa.

Dermal skull. The outer skull is composed of numerous plate-like bones that grow within a more superficial layer of the skin (dermis). Referring to this developmental origin, they are called *dermal bones*. Figure 2.3 exemplifies the diversity of tetrapod skulls. Dermal bones are relatively thin but often form a complete shield, leaving only the openings for eyes (orbits) and nose (nares) uncovered. The dermal bones are often the only skeletal parts visible from outside, and they also bear the teeth, which also belong to the outer skeleton (Figure 2.4). The epidermis, or external layer of the skin, is never involved in bone formation and always covers the dermal bones. In bony fishes and their early tetrapod descendants, the dermal skull is composed of at least 43 elements, most of which occur in pairs. In modern salamanders, the number has been reduced to 21–23, in frogs to 19, and in gymnophionans to as few as 17.