The Palaeozoic Ancestry of Salamanders, Frogs and Caecilians

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The relationships of frogs, salamanders, and caecilians (Gymnophiona) with one another and with the vast assemblage of Palaeozoic amphibians remain highly contentious phylogenetic problems. Cladistic analyses support a common ancestry of the three modern orders, but fail to achieve a consensus regarding their affinities with Palaeozoic amphibians. The most exhaustive phylogenetic analyses that have been applied to the ancestry of lissamphibians have recognized few, if any, biologically significant characters differentiating the living orders. These results can be attributed to limiting the database primarily to characters common to Palaeozoic amphibians and including few features that distinguish the modern orders. Making use of the numerous derived characters that are expressed in either the larvae or adults of extant salamanders, frogs, and caecilians provides the basis for recognizing a nested sequence of synapomorphies that support a common ancestry of salamanders and anurans with temnospondyl labyrinthodonts to the exclusion of caecilians. The larvae of Carboniferous and Permian temnospondyl labyrinthodonts provide strong evidence for their being members of the stem group of urodeles. This is based primarily on the great similarity in the sequence of ossification of the bones of the skull and appendicular skeleton, but is also supported by detailed similarities of the hyoid apparatus. Recognition of a sister-group relationship between Permo-Carboniferous branchiosaurids and crown-group salamanders makes it possible to determine the sequence of changes in the anatomy and ways of life that occurred during the origin of urodeles, and to determine their time of divergence relative to that of frogs and caecilians. The Lower Triassic salientian *Triadobatrachus* exhibits early stages in the evolution of the anuran skull that enable close comparison with Palaeozoic dissorophoid amphibians and point to the early evolution of anuran hearing and vocalization. The Lower Jurassic caecilian *Eocaecilia* shows few if any unique derived characters in common with salientians or caudates, but the anatomy of the skull and the elongate body form point to affinities with the Permian microsaur *Rhynchonkos*. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150** (Suppl. 1), 1–140.

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INTRODUCTION

Living amphibians differ fundamentally from other terrestrial vertebrates – the reptiles, birds, and mammals (collectively the Amniota) – in that primitive members of all three orders have a biphasic life history. Typically, these species have obligatorily aquatic larval stages possessing lateral-line sensory organs, but facultatively terrestrial adult stages. Amphibian larvae and adults are commonly highly distinct from one another, with different body forms, modes of locomotion, and ways of feeding. Most show a clearly recognizable metamorphosis between larvae and adults. The free-living larvae are subject to different selective regimes from the adults, and have distinct evolutionary trajectories. Functional complexes such as feeding and locomotion must be described separately for the larvae and adults in order to understand their patterns of evolution and relationships.

The amphibious way of life of frogs, salamanders, and caecilians has long been thought to result from a retention of characteristics of animals transitional between fish and amniotes. With the discovery of Palaeozoic tetrapods with lateral-line canal grooves and gilled larval stages, they were grouped with the modern orders in the Class Amphibia. However, it was soon recognized that the Palaeozoic amphibians were very different from the modern orders in nearly all aspects of their skeletal anatomy, and provided very little evidence of specific relationships.

Many different hypotheses of relationships between various groups of Palaeozoic amphibians and the three modern orders were proposed in the mid-20th century, but the fossil evidence was not sufficient to support a

consensus (e.g. Gregory, Peabody & Price, 1956; Eaton, 1959; Szarski, 1962; Reig, 1964). The basic problem was the almost total absence of fossils from beds of intermediate age that provided anatomical links between any of the many lineages of archaic amphibians and the highly derived frogs and salamanders known from the Mesozoic. There was also, until recently, a complete absence of fossil caecilians.

A central question has been whether frogs, salamanders, and caecilians are monophyletic in terms of having an immediate common ancestor that can be distinguished from all other known groups of Palaeozoic amphibians. This question remains difficult to answer because of the fundamental differences between frogs, salamanders, and caecilians at their first appearance in the fossil record, as well as the distinction of all three from any known Palaeozoic groups. Molecular evidence is also lacking, due to the absence of surviving sister taxa of any basal Palaeozoic lineages.

Parsons & Williams (1962, 1963) initiated the modern analysis of extant amphibian relationships with their search for specialized anatomical characters that were present in two or three of the modern orders, but were not known in Palaeozoic amphibians or in amniotes [see Appendix 1 for synapomorphies listed by Parsons & Williams (1963)]. Although they did not cite Hennig's prior publications (Hennig, 1950, 1953, 1956) emphasizing the importance of using unique, shared, derived characters (synapomorphies) rather than primitive features for establishing relationships, this was clearly the approach taken by Parsons and Williams. Their concept of the monophyly of the three extant orders (collectively termed the Lissamphibia) continues to serve as the most generally accepted hypothesis of their relationships.

One of the reasons for the investigation of Parsons and William into the monophyly of the modern amphibian orders [also emphasized by Szarski (1962)] was to counter the hypotheses of Holmgren (1933, 1949) and Jarvik (1942, 1954, 1960), who argued for a diphyletic origin of all tetrapods that was reflected in divergence of the lineages leading to frogs and salamanders at the level of their fish ancestors. On the basis of conspicuous differences in the mode of limb development, Holmgren argued that salamanders were unique among tetrapods in having evolved from lungfish, whereas frogs and all other terrestrial vertebrates shared a common ancestry from extinct lobe-finned fish related to *Eusthenopteron*. Jarvik, in contrast, stressed differences in the anatomy of the snout region, which he felt demonstrated close affinities between salamanders and a very primitive group of lobe-finned fish, the porolepiforms. On the other hand, he agreed with Holmgren that frogs and all other tetrapods were more closely related to osteolepiform fish

such as *Eusthenopteron*. Although the monophyletic origin of tetrapods from among the osteolepiforms, more specifically the tristichopterids and panderichthyids, is now broadly accepted (Gaffney, 1979; Panchen & Smithson, 1988; Ahlberg & Johanson, 1998; Heatwole & Carroll, 2000; Clack, 2000, 2002a), there remain very serious problems in recognizing an immediate common ancestry for frogs, salamanders, and caecilians.

In addition to providing evidence for the monophyletic origin of frogs, salamanders, and caecilians, Parsons & Williams (1963) attempted to visualize a model of the anatomy of a plausible common ancestor, but they were unsuccessful in identifying any Palaeozoic tetrapod with an appropriate combination of characters. At the time, an outline of the relationships of Palaeozoic tetrapods was fairly well established, as reviewed by Romer (1945, 1947). Two major groups of Palaeozoic amphibians had been recognized, the labyrinthodonts and the lepospondyls.

The labyrinthodonts were generally of large size, from 20 cm to a metre or more in length, and united primarily by primitive characters, recognizably similar to those of choanate fish, such as *Eusthenopteron*, generally considered to be the sister taxa of land vertebrates.

These include multipartite vertebrae and retention of most of the primitive complement of bones of the skull and lower jaw. Three broad groups of labyrinthodonts can be recognized: (1) a stem assemblage present in the Upper Devonian and Lower Carboniferous, mostly without obvious relationships to any later tetrapods; (2) the anthracosauroids, which may include the ancestors of amniotes; and (3) the temnospondyls (Fig. 1A), which are most often cited as being related to the lissamphibians (Carroll & Holmes, 2007).

The lepospondyls include an assortment of lineages, distinguished from labyrinthodonts by a number of derived features, including their generally smaller size, less than 20 cm in body length, the presence of spool-shaped vertebral centra frequently fused to the neural arch, variable loss of skull bones, and reduction or loss of limbs (Carroll *et al.*, 1998; Carroll, 1999). Five highly distinct orders are recognized: microsaurs, nectrideans, lysorophids, adelelospondyls, and aïstopods. Microsaurs are a relatively conservative assemblage; all of them retain fully developed limbs and most of the skull bones of more primitive tetrapods. The nectrideans are distinguished by the elongation of the neural and haemal arches and their fusion to the centra to form a nearly symmetrical caudal fin. Most were aquatic, with the limbs being relatively poorly ossified, but none elongated the trunk region. The Lysorophia, Adelospondyli, and Aïstopoda all had a greatly elongated vertebral column. The Lysorophia
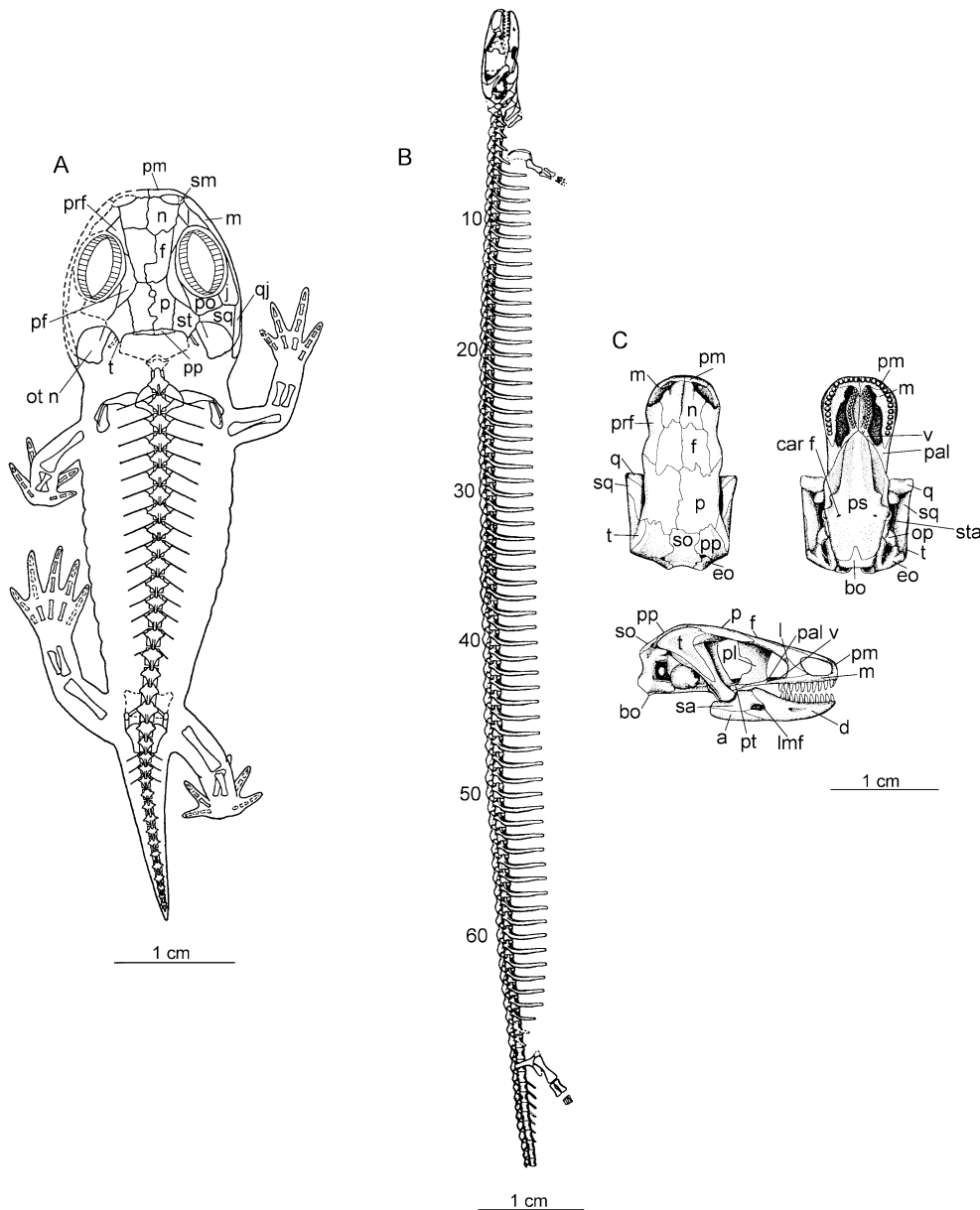
Figure 1. Reconstructions of two types of Palaeozoic amphibians that have been hypothesized to be the sister taxa of modern amphibians (Lissamphibia). A, the Upper Carboniferous temnospondyl labyrinthodont *Amphibamus grandiceps*. Reproduced from Gregory (1950). B, skeletal reconstruction of the Upper Carboniferous lysorophid lepospondyl *Brachydectes elongatus*. C, dorsal, lateral, and palatal view of the lysorophid *Brachydectes elongatus*, from the Lower Permian. B, C, modified from Wellstead (1991). Abbreviations used in figures listed on pages 8, 9.

retained diminutive limbs, but had a highly fenestrate skull (Fig. 1C). Adelospondylids retained the dermal shoulder girdle, but no other elements of the appendicular skeleton. The Aïstopoda retained only the cleithrum, and had a highly fenestrate skull, but of a very different pattern from that of the Lysorophia. Because of the many differences between even the most primitive members of each of these groups, their specific interrelationships are still not clearly established (Carroll, 2000a). In contrast to anthracosaurs and temnospondyls, no lepospondyls are known to have had larval stages distinguished by external gills. In all orders, the smallest known specimens had well-ossified cylindrical centra.

Subsequent to the work of Parsons and Williams, Bolt (1969, 1977) described a Lower Permian temnospondyl amphibian, *Doleserpeton*, that he argued might be a common ancestor of all lissamphibians, on

the basis of the presence of bicuspid, pedicellate teeth, nearly monospondylous trunk vertebrae, and a holospondylous, biconcave atlas vertebra. However, the large orbits and interpterygoid vacuities and the presence of a frog-like otic notch suggested specific affinities with anurans.

Numerous papers from the l980s and early 1990s supported the monophyletic origin of modern amphibians from temnospondyls on the basis of the anatomy of fossil and living species (Milner, 1982, 1988, 1993, 2000; Bolt, 1991; Trueb & Cloutier, 1991; Ahlberg & Milner, 1994). Monophyly of the modern orders (separate from amniotes) was also supported by molecular studies (Hedges, Nussbaum & Maxson, 1993; Hay *et al.*, 1995; Zardoya & Meyer, 2001; San Mauro, 2005). These studies, of course, cannot be extended to establishing relationships with any of the extinct Palaeozoic clades.

Carroll (1995) provided the first extensive phylogenetic analysis of Palaeozoic tetrapods based on parsimony, using PAUP. This was done essentially as a null hypothesis, to see what patterns might be revealed by using long-recognized skeletal characteristics. However, strong reservations were raised regarding the biological significance of the results. Numerous ques-

tions arose regarding the likelihood of various character state changes implied by the most parsimonious trees. When this paper was published, it was recognized that the skeletal features used to characterize lepospondyls would probably result in their being classified as sister taxa of the lissamphibians, but this was not investigated at that time. Inclusion of the lissamphibians was carried out by Laurin & Reisz (1997), who performed a more extensive analysis, based on much the same data for Palaeozoic tetrapods, but adding a few taxa and characteristics of lissamphibians (Fig. 2A). This yielded a monophyletic origin of lissamphibians (in common with most previous papers), but identified a surprising sister taxon – the Lysorophia (Fig. 2B), among the lepospondyls – rather than any labyrinthodont (Fig. 1A).

More recently, Ruta, Coates & Quicke (2003) published an even more exhaustive analysis, based on 319 characters and 90 taxa (Fig. 2B). Much of their cladogram showed the same arrangement of Palaeozoic taxa – a sequence of stem labyrinthodonts, followed by a similar succession of temnospondyls, anthracosauroids, and lepospondyls. As in the cladogram of Laurin and Reisz, the lepospondyls appeared in close proximity to amniotes. However, the cladogram of Ruta *et al.*

Figure 2. Cladograms hypothesizing the relationships of Palaeozoic and modern amphibians. A, reproduced from Laurin & Reisz (1997). B, reproduced from Ruta *et al.* (2003); one of the fundamental trees deriving from the original parsimony run. Numbers at nodes refer to bootstrap percentage values for clades with bootstrap support greater than 50%. Note the widely divergent taxa identified as the sister taxa of the modern amphibian orders, and the limited resolution among the Lissamphibia.

(2003) placed the lissamphibians as the sister taxon of the temnospondyls rather than lepospondyls. The lissamphibians were separated from the Lysorophia by approximately 20 nodes. In the cladogram of Laurin and Reisz, 33 extra steps were required to find a sister-group relationship between derived temnospondyls and lissamphibians.

It is striking that the two analyses found such different affinities for the lissamphibians, whereas the remainder of the cladograms remained nearly congruent. The higher degree of consistency regarding the Palaeozoic taxa can be attributed to the nature of the characters and taxa chosen for the data matrix. There is close correspondence between the Palaeozoic taxa chosen, despite the smaller number used by Laurin and Reisz. In contrast, the lissamphibian taxa chosen for analysis in the two studies differed considerably. Laurin and Reisz chose a combination of modern and
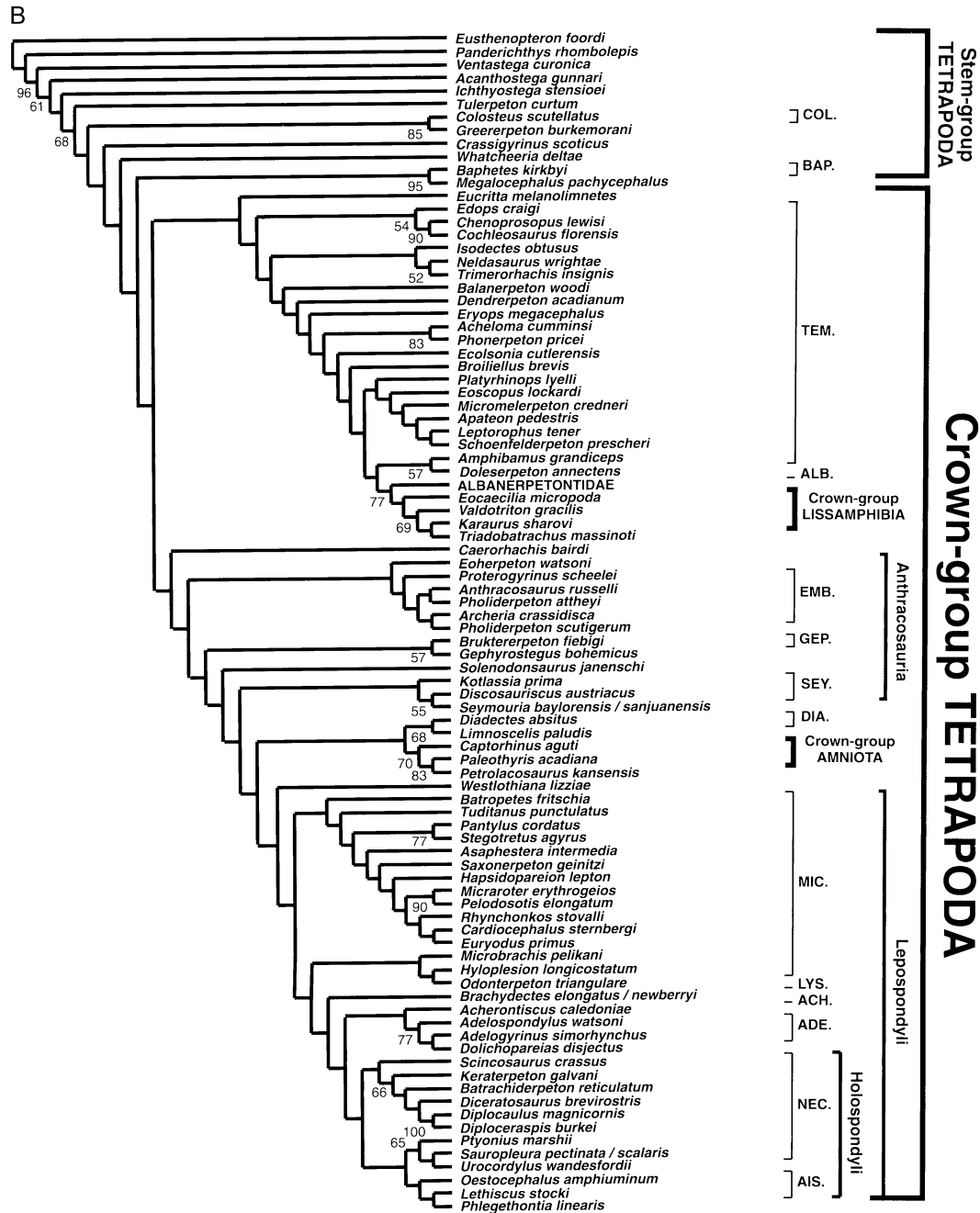

Figure 2. *Continued*

extinct taxa: the Lower Triassic salientian *Tria-dobatrachus*, representatives of two basal anuran families (Discoglossidae and Pipidae), three urodele families (Hynobiidae, Sirenidae, and Proteidae), the Lower Jurassic caecilian *Eocaecilia*, and two living families (Rhinatrematidae and Ichthyophiidae). Of these taxa, only *Triadobatrachus* and *Eocaecilia* were also chosen by Ruta *et al.* The other taxa that they studied were two extinct salamander genera, *Karaurus* and *Valdotriton*, and two species of the enigmatic Mesozoic and Cenozoic Albanerpetontidae (commonly allied with urodeles). Although the characters selected for the two analyses differed somewhat in terms of which parts of the skeleton were emphasized, they resembled one another in being based primarily on anatomical features of Palaeozoic tetrapods, with very few that were characteristic of any lissamphibians.

A further problem seen in these cladograms is that neither resolves the pattern of interrelationships among the three modern amphibian orders. The cladogram of Laurin & Reisz (1997) shows an unresolved pentacotomy, including three families of salamanders, as well as lineages leading to caecilians and salientians. Subsequent cladograms of Laurin and his colleagues (Laurin, 1998a, b; Laurin & Reisz, 1999; Vallin & Laurin, 2004) do show some apparent resolution among the modern amphibian orders, but they were not based on any synapomorphies that clarify our understanding of the pattern of divergence of the highly distinctive frogs, salamanders, and caecilians.

One of the cladograms published by Ruta *et al.* (2003) found a terminal sequence in which a stem-group caecilian is a sister taxon of (in succession) a crown-group urodele, a stem-group urodele, and a stem-group salientian (a taxon including crown-group anurans plus the Triadobatrachidae). In another cladogram, a stem-group caecilian was the sister taxon of an unresolved trichotomy consisting of a stem-group salientian, a stem-group caudate (urodeles plus their immediate sister taxa), and a urodele. Despite the manifest adaptive and morphological differences between primitive frogs, salamanders, and caecilians, these cladograms failed to establish their sister-group relationships. Other aspects of recent analyses of lissamphibian relationships have been discussed by Schoch & Milner (2004).

Two conspicuous problems are evident in the cladograms generated by Laurin and his colleagues and Ruta *et al.* (2003): (1) they postulate Palaeozoic sister taxa that differ radically in their anatomy; and (2) they fail to recognize a nested sequence of biologically significant derived characters leading to the widely divergent extant amphibian orders.

What could be the cause of these problems? One question that is rarely considered in undertaking a phylogenetic analysis is the nature of the characters that should be entered into the database. In most analyses, the answer seems obvious: include all the taxa in question, and as many as practical of the anatomical and/or molecular data that are common to all the taxa being studied. In most cases, the number of taxa and their morphological and genetic disparity are sufficiently limited for relatively consistent results to be achieved. However, the wider the diversity of forms, the more difficult it becomes to achieve consensus, especially when using anatomical data that may not be uniformly applicable across all taxa.

Recent efforts to establish the phylogenetic position of the modern amphibian orders have included all major groups of Palaeozoic tetrapods and their putative sister taxa among sarcopterygian fish in a single database. All have in common the basic elements of the vertebrate skeleton, but their expression from fish to frogs is so different that very few characters can be effectively compared between Palaeozoic and extant taxa. As a result, frogs, salamanders, and caecilians appear as a monophyletic assemblage simply because they all have characters that are not expressed in Palaeozoic tetrapods.

It is clear that the characters chosen for these analyses were inadequate to establish the nature of the relationships of the modern amphibian orders. More generally, this specific example should serve to indicate the necessity of choosing characters that are appropriate for the specific phylogenetic problem being investigated. This concern becomes increasingly critical as the assemblages under study increase in anatomical diversity. This problem was noted by Clack (2002b) and Clack & Finney (2005) in their attempts to establish the affinities of the oldest known Carboniferous tetrapod, *Pederpes*. Clack stated specifically that she was restricting her analysis to other, very early, tetrapods, which would provide the closest basis for comparison with *Pederpes*. However, this approach led to the grouping of diverse later tetrapods in an unresolved polytomy, as did a previous study based on the lower jaws of very early tetrapods (Ahlberg & Clack, 1998).

Analysis of the affinities of the modern amphibian orders requires a database that includes a substantial number of characters whose character states can be recognized among both frogs, salamanders, and caecilians, and their putative ancestors from the early Mesozoic and Palaeozoic. This essentially reverses the basis of character choice from that in previous analyses from an emphasis on data from Palaeozoic taxa to those of the extant orders.

One may argue that characters unique to crown taxa are autapomorphies, of no value in establishing sister-group relationships. They are, however, of great value in determining the monophyletic nature of crown-group anurans, urodeles, and caecilians, and

for establishing the polarity of character changes within each order and their included families. More importantly, what appear as autapomorphies of the extant orders when compared with one another may serve as synapomorphies to determine sister-group relationships with Palaeozoic lineages. Hence, all derived characters of frogs, salamanders, and caecilians should be evaluated in any phylogenetic analysis of their broader relationships.

The problem being investigated in this article is not whether frogs, salamanders, and caecilians shared an ultimate common ancestry among early tetrapods, which they must have done if tetrapods as a whole are a monophyletic assemblage. Rather, the problem is to determine how the characters that distinguish these groups may have evolved from among one or more of the numerous antecedent clades. To solve this problem, a necessary preliminary step is to characterize the anatomy and ways of life of each of the extant clades as thoroughly as possible. Rather than continuing to concentrate on the few synapomorphies that suggest an immediate common ancestry, distinct from that of any known Palaeozoic clades, we should look in detail at the many anatomical, functional, and adaptive attributes that distinguish the primitive members of the three orders.

Phylogenetic studies of lissamphibians have an advantage over those involving affinities among Palaeozoic taxa, in that one can use essentially all the characters of living frogs, salamanders, and caecilians to establish their relationships. Both the orders and families are based on numerous synapomorphies, only a few of which were included among the small number of lissamphibian characters used by Laurin & Reisz (1997) or Ruta *et al.* (2003). The synapomorphies of the individual orders have already been used to determine their monophyly, for which a solid consensus has been reached (Milner, 1988; Cannatella & Hillis, 1993a; Sanchiz, 1998; Gao & Wang, 2001; Carroll *et al.*, 2004) (Appendix 2). The monophyly of the individual families within each order is also well established, although some interrelationships among the families remain unresolved, especially among advanced anurans (Ford & Cannatella, 1993; Hedges & Maxson, 1993; Hedges *et al.*, 1993; Larson & Dimmick, 1993; Cannatella & Hillis, 1993b; Gao & Shubin, 2001; Pough *et al.*, 2004; Nishikawa, 2000). The polarity of character change within the individual orders and the capacity to recognize the most primitive character states provide a solid basis for evaluating their possible relationships with each other and with the various clades of Palaeozoic tetrapods.

Frogs, salamanders, and caecilians are unique among extant terrestrial vertebrates in having a biphasic life history, and this was almost certainly the case for the most primitive members of each order. To establish their phylogenetic positions, one must incorporate data from both their aquatic larval stages and their adult morphotypes, as well as knowledge of the patterns and sequences of change during metamorphosis between these two ways of life. Structural and behavioural adaptations for two different modes of life can provide a much more extensive database than that available for organisms that remain in only a single general environment throughout their life. Knowledge of early stages in development based on fossil larvae also provides a uniquely informative basis for determining the mode of evolutionary change that is not available for other terrestrial vertebrates.

From the standpoint of evolutionary biology, the question of the origin of the characters that distinguish the modern orders is certainly as important as the specific sequence of their ultimate divergence. Whether or not frogs, salamanders, and caecilians do share an ultimate common ancestry, the distinctive features of the stem taxa of each extant order, now known from as early as the Middle to Lower Jurassic, point to a significant degree of prior divergence.

Middle and Lower Jurassic salamanders, frogs, and caecilians are separated from their living descendants by 150–180 million years. However, their skeletal anatomy is so similar to that of primitive living descendants that there is no question regarding their membership in the same monophyletic orders, and their achievement of the same basic ways of life. Anatomical and adaptive differences between living members of the modern orders closely reflect evolutionary changes that had already occurred by the beginning of the Jurassic, and thus constitute a highly informative basis for investigating the directions of evolutionary change from among their Palaeozoic antecedents.

The approach of this analysis will be as follows:

1. to describe and compile derived characters present in crown-group salamanders, frogs, and caecilians
2. to determine the most primitive character states of these characters in each of the extant orders, on the basis of the polarity of character state changes observed among and between extant families within each order
3. to search for comparable characters among Early Mesozoic and Late Palaeozoic amphibians
4. to establish the succession of nested synapomorphies on a tentative phylogeny including Palaeozoic and extant amphibians
5. to enter characters into a database and conduct a formal cladistic analysis

As we are investigating relationships between living taxa and clades represented only by fossil remains, data will be restricted primarily to characters that can be directly or indirectly studied from fossil remains. Fortunately, we do have considerable fossil evidence of

larval as well as adult stages of both living and extinct taxa, as far back as the Carboniferous. Fossils of larvae show many elements of the soft anatomy, and also demonstrate growth sequences that are critical for establishing relationships with modern frogs, salamanders, and caecilians. Among features that are represented in the fossil record are body outlines, gills, eyes, and cartilage of the hyoid apparatus. Muscles are not preserved as such, but their relative positions and associations with specific bones are sufficiently conservative that their probable expression in extinct taxa can be plausibly reconstructed. From the bony skeleton of the fossils and detailed knowledge of living taxa, the nature of functional complexes, including feeding, locomotion, hearing, respiration, reproduction, and even calling (in plausible antecedents of anurans), can be reconstructed with variable degrees of confidence. The sequence of development and life-history traits can be hypothesized on the basis of information from growth series including both juveniles and adults.

ANATOMICAL ABBREVIATIONS USED IN FIGURES

BONES

a, angular; a co, anterior coracoid; ansp, angulosplenial; apq, ascending process of quadrate; art, articular; art-q, articulating surface for the quadrate; art st-q, articulating surface for the stapes–quadrate; bb, basibranchial; bo, basioccipital; bo-eo, fused basioccipital–exoccipital; bq, basal process of quadrate; c (1–4), centrale; car f, carotid foramen; cb, ceratobranchial; ch, ceratohyal; cl, clavicle; clei, cleithrum; co, coronoid; cor, coracoid; cv, caudal vertebrae; d, dentary; eb, epibranchial; ect, ectopterygoid; enls, endolymphatic sac; eo, exoccipital; epi, epipterygoid; f, frontal; fch, fenestra choanalis; fe, femur; fi, fibula; fib, fibulare; f im, intermandibular foramen; fo, fenestra ovalis; f-p, frontoparietal; ftr, fetal tooth rows; glen, glenoid; h, humerus; hb, hypobranchial; hbp, hypobranchial plate; hh, hypohyal; hy, hyomandibular; i, intermedium; ic, intercentrum; icl, interclavicle; il, ilium; int, intestine; int na, internal naris; int p, internal process; irc, infrarostal cartilage; isch, ischium; j, jugal; j art, articulating surface for lower jaw; l, lacrimal; lc, laryngeal cartilage; lmf, lateral mandibular foramen; lon, lamina orbitonasalis; m, maxilla; mc, Meckel's cartilage; mce, medial centrale; mco, medial coronoid; m-f, meckelian foramen; m-pal, fused maxilla and palatine; mm, mentomeckelian; m-p, fused maxilla and palatine; mppq, muscular process of palatoquadrate; mrc, median process of suprarostral cartilage; n, nasal; nc, nasal capsule; nld, opening for nasolacrimal duct; n-pm, fused nasal and premaxilla; ob, os basale; oc, orbital process; odp, odontoid process; of, optic foramen; onf, orbitonasal foramen; op, opisthotic; oper, operculum; ot, otic capsule; otc, otoglossal cartilage; otn, otic notch; p, parietal; pa, pseudoangular; pac, paracordal; pag, processus ascendens quadrati; pal, palatine; p art, posterior surface of jaw articulation; pc, pleurocentra; pco, posterior coracoid; pd, pseudodentary; pf, postfrontal; ph, parahyoid; phc, pharyngeal cavity; pi, pineal opening; pl, pleurosphenoid; pl f-p, posterolateral process of frontoparietal; pm, premaxilla; pmp, posteromedial process; po, postorbital; pp, postparietal; pq, palatoquadrate; pre art, prearticular; prf, prefrontal; prh, prehallux; pro, prootic; pro-ex, fused prootic and exoccipital; prp, prepollex; ps, parasphenoid; psp, postsplenial; psyp, parasymphyseal plate; pt, pterygoid; ptp, pterygoid process of palatoquadrate; pu, pubis; q, quadrate; qj, quadratojugal; r, radius; ra, radiale; rc, radial cartilage; rcon, radial condyle; ret p, retroarticular process; sa, surangular; sac, sacrum; sc, scapulocorocoid; scap, scapula; scf, suprascapular foramen; scr, sacral rib; sl, sublingual rod; sm, septomaxilla; smf, submeckelian fossa; sn, septum nasi; so, supraoccipital; sph, sphenethmoid; spl, splenial; spp, postsplenial; spsc, suprascapula; sq, squamosal; sqnt, squamosal notch; src, suprarostral cartilage; st, supratemporal; sta, stapes; stf, stapedial foramen; stom, stomach; st-q, fused stapes and quadrate; sur, surangular; t, tabular; ten g, tentacular groove; th, trabecular horn; ti, tibia; tib, tibiale; ti-fi, tibiofibula; tm, taenia marginalis; tp, trabecular plate; tro, trochanter; trp, posterior trabecula; u, ulna; uh, urohyal; ul, ulnare; ul-ra, fused ulna and radius; ur, urostyle; v, vomer; vert, vertebrae; v g, ventral groove; v-pal, vomeropalatine; 1, distal carpal or tarsal; 2, distal carpal or tarsal; 1–2, fused distal carpals or tarsals 1 and 2 (basal commune); 3, distal carpal or tarsal; 4, distal carpal or tarsal; 5, distal carpal or tarsal.

MUSCLES

Am, adductor mandibulae complex
Ame, adductor mandibulae externus
Ami, adductor mandibulae internus
Ami (pro), deep head of adductor mandibulae internus
Ami (pt), pterygoideus head of adductor mandibulae internus
Ami (sup), superficial head of adductor mandibulae internus
Amp, adductor mandibulae posterior
Amp (longus), longus head of adductor mandibulae posterior
Bh, branchiohyoideus
Bm, branchiomandibularis
Cb I–IV, constrictor branchialis muscles
Chi, ceratohyoideus internus
Cm, coracomandibularis

Db, diaphragmato-branchialis
Dm, depressor mandibulae
Dma, depressor mandibulae anterior
Dmp, depressor mandibulae posterior
Ep, epaxialis
Gg, genioglossus
Ggb, genioglossus basilis
Ggl, genioglossus, lateral division
Ggm, genioglossus, medial division
Gh, geniohyoideus
Gm, genioglossus medialis
Gmd, genioglossus medialis distalis
Ha, hyoangularis
Hg, hyoglossus
Hs, hebosteoypiloideus
Hy, hypaxialis
Hym, hyomandibularis
Ih, interhyoideus
Ihp, interhyoideus posterior, also termed constrictor colli
Im, intermandibularis
Ima, intermandibularis anterior
Imp, intermandibularis posterior
Lab I–IV, levatores arcuum branchiarum muscles
Lc, longus capitis
Lq, levator quadrati
Lv, levator scapulae
Mhl, mandibulohyoid ligament
Ml, mandibulobabialis (segment of intermandibularis)
Oh, omohyoideus
Orh, orbitohyoideus
Ph, petrohyoideus
Pt, pterygoideus
Qa, quadratoangularis
Ra, rectus abdominis
Rb, retractor bulbi
Rc, rectus cervicis (also termed Sh, sternohyoideus)
Sa, suspensorioangularis
Sar I–IV, subarcualis rectus muscles
Sh, sternohyoideus (also termed rectus cervicis)
Shy, subhyoideus
Sm, submentalis
So, subarcualis obliquus
Sph, suspensoriohyoideus
Sv, subvertebralis
Tp, tympanopharyngeus
Tv, transversus ventralis

NERVES AND THEIR FORAMINA

V, opening for trigeminal nerve
V_1, ophthalmic profundus ramus of trigeminal nerve
V_2, maxillar ramus of trigeminal nerve
V_3, mandibular ramus of trigeminal nerve
II, optic
X, vagus

FEATURES DISTINGUISHING SALAMANDERS, FROGS, AND CAECILIANS

ADULTS AND LARVAE

Despite the common possession of a biphasic history, all known salamanders, frogs, and caecilians are highly distinct from one other in the nature of the body form of both the larvae and the adults. The most conspicuous features that distinguish the adults of frogs, salamanders, and caecilians concern their general body shape, which is closely associated with their means of locomotion (Fig. 3). Salamanders are clearly the most primitive, in that nearly all species retain a moderately long vertebral column and a quadrupedal mode of locomotion associated with sinusoidal undulation of the trunk, in common with most early tetrapods. All frogs retain four limbs, but they are used in highly specialized saltatory locomotion that is reflected in major changes throughout the postcranial skeleton. The vertebral column is greatly shortened, and has very limited lateral mobility (Jenkins & Shubin, 1998). Caecilians are the most divergent. Modern species lack all trace of girdles and limbs, but have a greatly elongated trunk, with ~70–285 vertebrae. All caecilians are capable of burrowing; even the primarily aquatic typhlonectids burrow in the substrate of the water bodies in which they live (Summers & O'Reilly, 1997; O'Reilly, Summers & Ritter, 2000). In the earliest known caecilians, from the Lower Jurassic (Jenkins & Walsh, 1993), the skull was already modified for burrowing, in being as narrow as the trunk, with the braincase highly consolidated and the orbital openings reduced.

The basically different body forms of salamanders, frogs, and caecilians are associated with numerous other aspects of their anatomy and ways of life, from their sensory structures to their modes of feeding and the nature of their reproduction, larval stages, and patterns of development. Most of these derived features may already have been apparent when the modern orders first appeared in the fossil record of the Jurassic, but their origins must be sought even earlier, in the Palaeozoic and Triassic.

Overall, the larvae of frogs, salamanders, and caecilians can be readily distinguished from one another, with no obvious intermediates (Fig. 4). This does not necessary preclude their having had an ultimate common ancestry, but the distinctive features of the larvae must have resulted from significant periods of independent evolution (Duellman & Trueb, 1986; Hall & Wake, 1999; McDiarmid & Altig, 1999).

The larvae of salamanders and caecilians are more similar to the adults than is the frog tadpole, and undergo a less dramatic metamorphosis. The larvae of salamanders appear to be the most primitive, with the early appearance of limbs, a moderately elongate
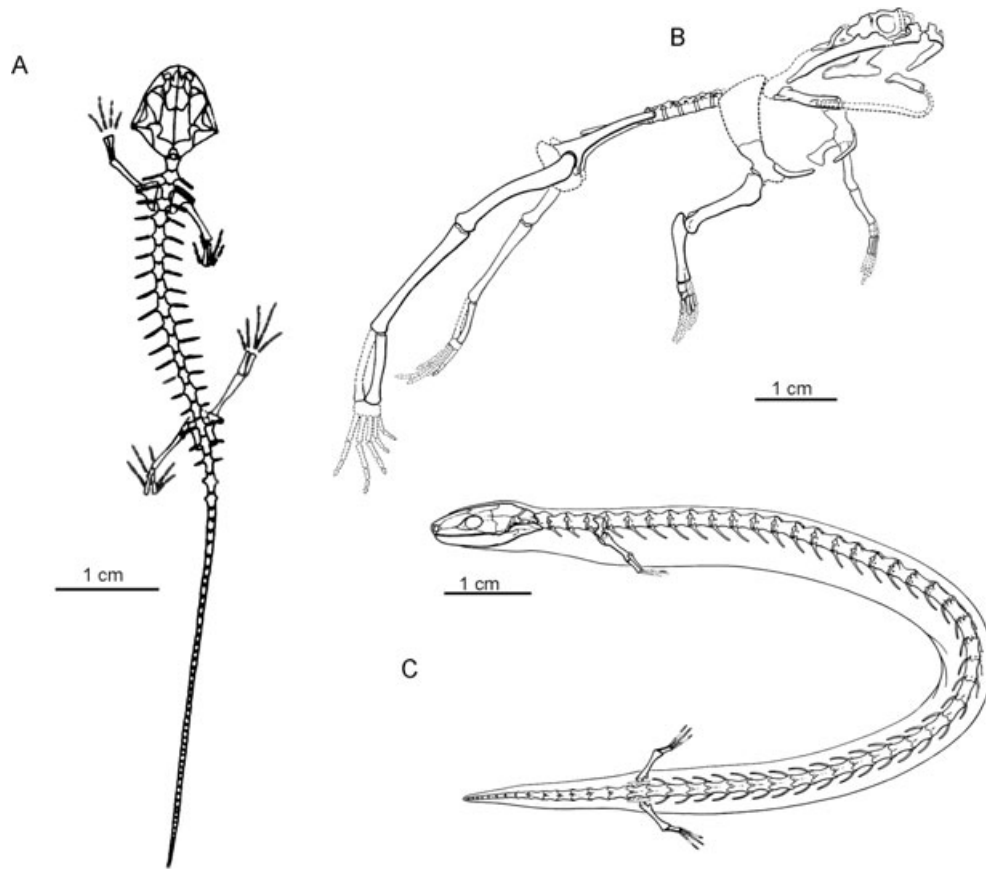
Figure 3. Reconstructions of Mesozoic representatives of the modern amphibian orders. A, the Lower Cretaceous salamander *Valdotriton gracilis*. Reproduced from Evans & Milner (1996). B, the Lower Jurassic anuran *Prosalirus bitis*. Reproduced from Shubin & Jenkins (1995). C, the Lower Jurassic caecilian *Eocaecilia micropodia*. Reproduced from Jenkins & Walsh (1993).

trunk, and conspicuous external gills, as in the larvae of Palaeozoic amphibians. The period of development within the egg is generally longer than that of frogs, and results in advanced organogenesis of the feeding, digestive, and locomotor apparatus, approaching the adult condition. Salamander larvae that undergo metamorphosis are distinguished from the adults by the presence of external gills and open gill slits, a caudal fin, and the absence of a mobile tongue. They are characterized by their capacity for highly effective gape-and-suck feeding, and are active predators soon after hatching.

Caecilian larvae differ little from the adults, except for their smaller size, retention of open gill slits, and, for those that transform to terrestrial adults, a caudal fin. The tentacle only develops at metamorphosis. Unlike frogs and salamanders, the external gills, which are highly elaborated within the egg or oviducts, are lost at the time of hatching or live birth. Caecilians are active predators soon after hatching or birth, as the result of more rapid development than occurs in either salamanders or frogs.

Frogs have the most highly derived larvae of the living orders. Tadpole locomotion depends almost entirely on undulation of the trunk and tail until near the time of metamorphosis. Feeding and digestion in most species requires specialized structures for suspension feeding on tiny plant particles. The intestine is greatly elongated for a primarily herbivorous diet, and occupies most of the body cavity. The head region is highly modified, with unique mouthparts for scraping food from the substrate. Metamorphosis is rapid, and affects nearly all parts of the body. Whereas many groups of salamanders have evolved a neotenic lifestyle, with reproduction occurring among essentially larval forms, no frogs are known to undergo neoteny, and reproductive organs only appear after metamorphosis (Wassersug, 1974, 1975).

In order to recognize possible Triassic and Palaeozoic antecedents, it is necessary to review in some detail the comparative and functional anatomy of each of the modern orders. The sequence of discussion of particular elements of the anatomy is not entirely consistent among the three orders, because their function
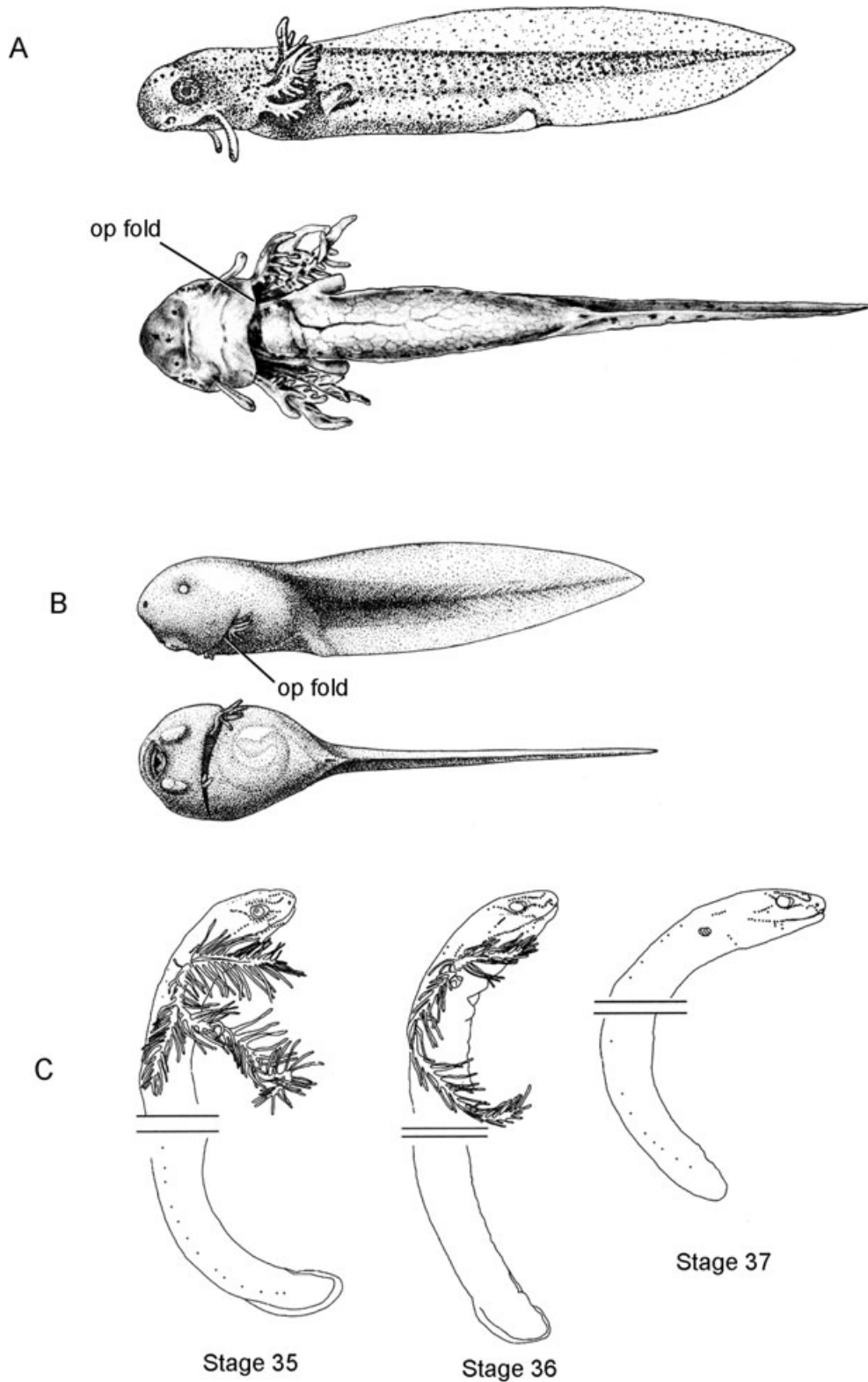
Figure 4. Larvae of modern amphibian orders. A, stage 25 of the salamander *Ambystoma maculatum*. Modified from Harrison (1969). Note conspicuous external gills and the balancers, extending from the back of the lower jaws. op fold, opercular fold. B, stage 24 of the neobatrachian frog *Rana pipiens*. Modified from Shumway (1940). C, the primitive caecilian *Ichthyophis kohtaoensis*; two late embryonic stages showing external gills and a hatchling, in which the external gills have been lost. Modified from Wake & Dickie (1998).

and mode of development may differ so dramatically that this is not practical. Description will begin with salamanders, because their skeletal anatomy and ways of life appear the most similar to those of Palaeozoic tetrapods.

SALAMANDERS

Salamanders are common elements of the North Temperate biota that appear to represent the most primitive level of organization of all extant terrestrial vertebrates. Most salamander families retain a primitive mode of reproduction, in which the eggs are laid in the water and the young hatch as aquatic larvae, as might be expected of the oldest terrestrial vertebrates. Among living amphibians, their pattern of terrestrial locomotion is clearly more primitive than those of the saltatory anurans or the limbless, snake-like caecilians (Gymnophiona).

Despite detailed knowledge of the anatomy and way of life of all groups of living salamanders, the nature of their relationships with other living amphibians and their ancestry among Palaeozoic tetrapods remains unresolved. This results from their marked differences from frogs and caecilians, and the long gap in the fossil record between the oldest known members of the crown group and any plausible antecedents in the Palaeozoic.

Living salamanders are grouped in ten families, including 60 genera and approximately 515 species. Most of the families are limited to temperate regions of North America and Eurasia, but about 200 species of the advanced family Plethodontidae have radiated into Central America and northern South America (Pough *et al.*, 2004). There is general agreement regarding classification at the family level (Fig. 5), on the basis of both anatomical and molecular data (Wiens, Bonett & Chippindale, 2005). Two superfamilies have been recognized, the Cryptobranchoidea (which are primitive in practising external fertilization), and the more advanced Salamandroidea, in which spermatophores are taken up by the female, except, perhaps, in the Sirenidae.

Cranial anatomy
The general anatomy of the skull and lower jaws among lissamphibians may be divided into two categories – that of caecilians, in which its configuration is strongly constrained by the burrowing habitus of all taxa within the order, and that of frogs and salamanders, in which this constraint does not apply (Figs 6, 7). Many bones present in the skull of the earliest known caecilian are absent in both frogs and salamanders. The skulls of most frogs and salamanders resemble those of one another and differ
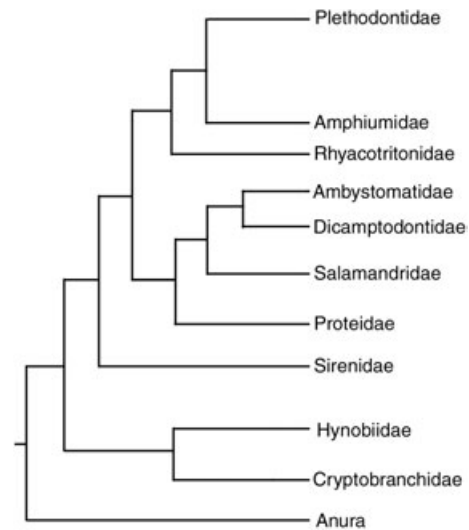

Figure 5. Phylogeny of salamanders. Reproduced from Wiens *et al.* (2005).

from those of caecilians in being relatively open, with the orbits not closely surrounded by bone. The skull is more or less parabolic in dorsal outline, and is typically wider than deep; the lateral wall of the braincase is nearly always less solidly ossified than in caecilians.

Among the most conspicuous features that distinguish the skulls of all salamanders from those of most frogs is the absence of a posterior squamosal embayment supporting a tympanum, and in many, a long gap in the bony margin of the skull between the maxilla and the jaw suspension. Salamanders also differ in having the jaw articulation at the level of the otic capsule, or further forwards, whereas that of most frogs is near the level of the occipital condyles.

If all salamander families are examined (Carroll & Holmes, 1980; Trueb, 1993; Rose, 2003), there is considerable diversity in anatomical details. However, for investigating the ancestry of salamanders, one may concentrate on conservative members of the families Hynobiidae (Fig. 6), Ambystomatidae, and Salamandridae, which share many features and retain the largest number of bones in common with Palaeozoic tetrapods. Of these, the hynobiids are generally accepted as the most primitive of terrestrial salamanders (Larsen, Beneski & Miller, 1996). Sirenids have been considered by some authors as the sister taxon of all other urodeles, partially on the basis that they have not evolved internal fertilization (Larson & Dimmick, 1993; Pough *et al.*, 2004), but the skull is highly derived, and cannot contribute to our understanding of the ancestral condition in salamanders.

Salamanders are clearly more primitive than frogs in the retention of separate, paired frontals and parietals, but resemble anurans in the loss of the posterior bones of the skull roof that are common to most
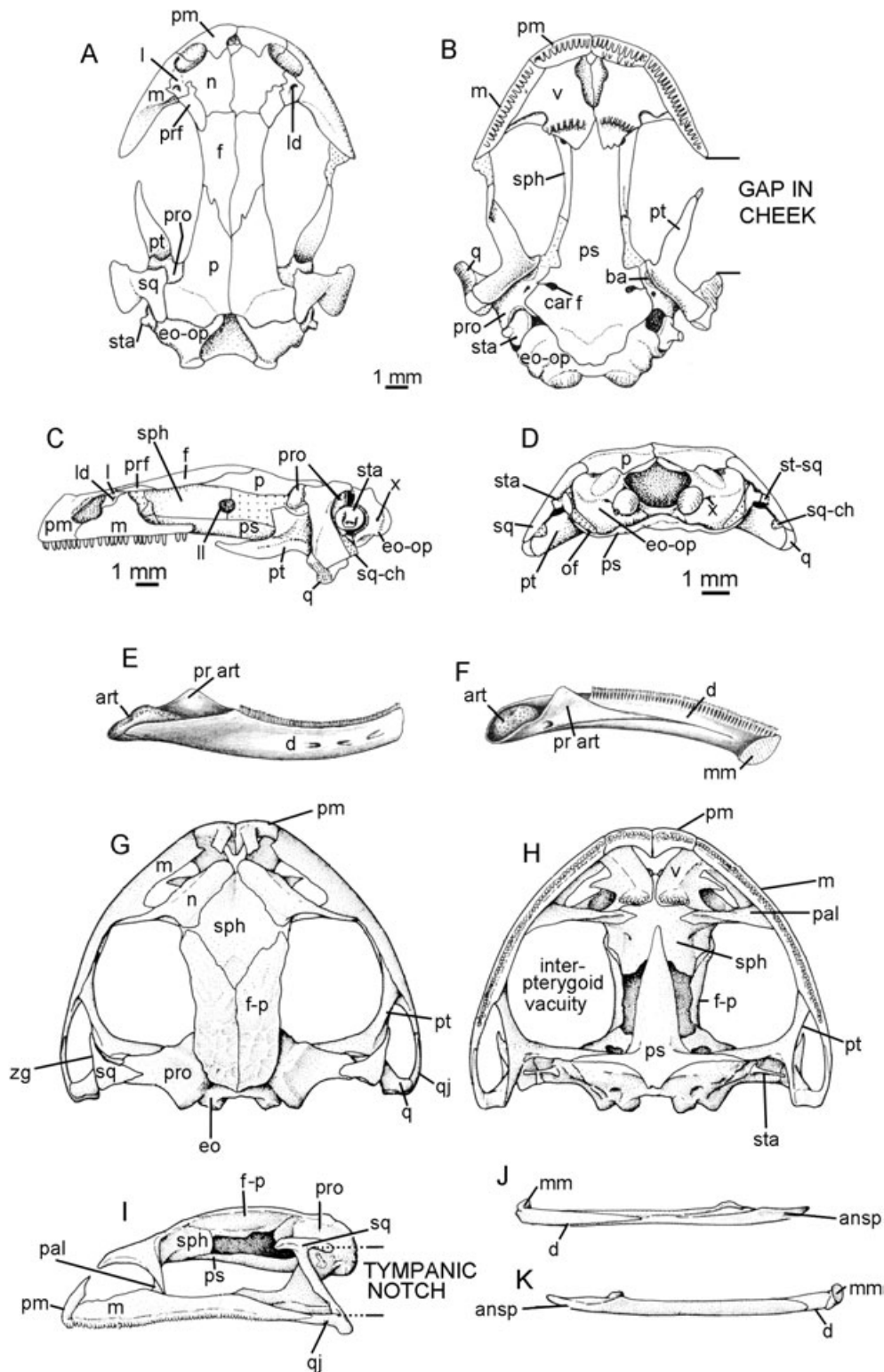
Figure 6. Skulls of extant salamanders and frogs. A–D, skulls of the most primitive family of terrestrial salamanders, the Hynobiidae. A–C, dorsal, palatal and lateral views of *Batrachuperus sinensis*. D, occipital view of *Hynobius naevius*. Reproduced from Carroll & Holmes (1980). E, F, lateral and medial views of the lower jaw of *Salamandra*. Reproduced from Francis (1934). G–K, skull and lower jaws of the hylid frog *Gastrotheca walkeri*. G, H, I, dorsal, palatal, and lateral views of skull. J, K, lateral and medial views of lower jaw. Reproduced from Duellman & Trueb (1986).
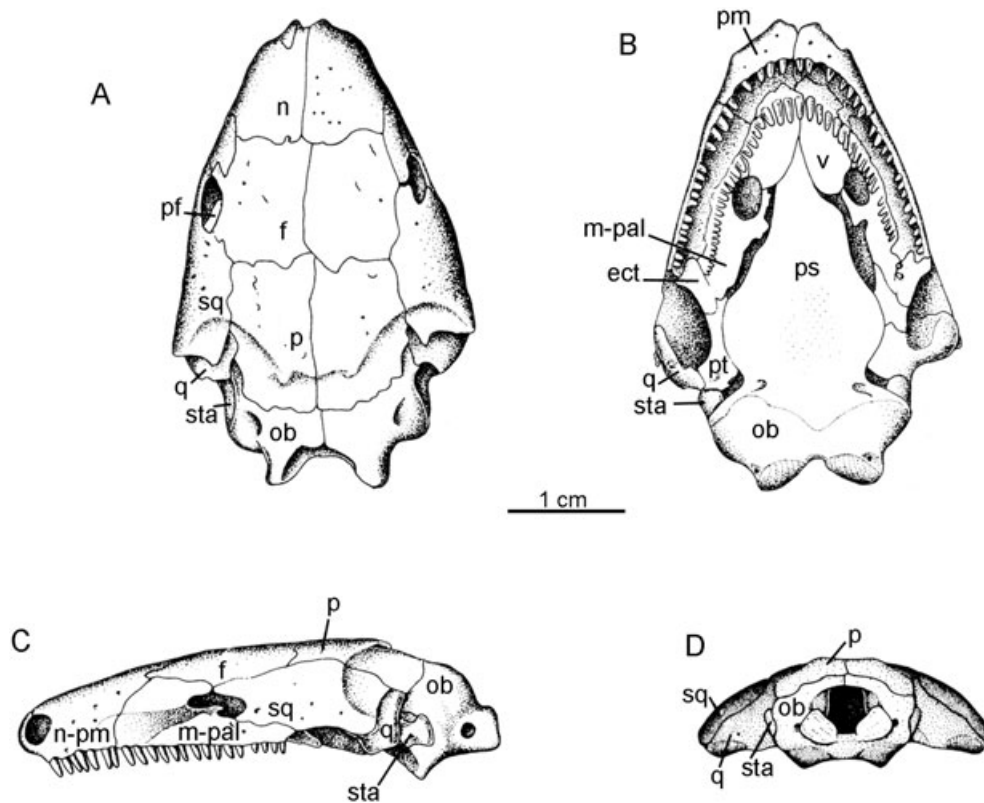
Figure 7. Caecilian skulls. A, B, C, dorsal, palatal, and lateral views of the caecilian *Grandisonia alternanas*. D, occiput of *Hypogeophis rostratus*. Reproduced from Carroll & Currie (1975).

Palaeozoic amphibians – the postparietal, tabular, supratemporal, and intertemporal – as well as the posterior circumorbital elements – postorbital, postfrontal, and jugal (Fig. 1A). The quadratojugal (present in most frogs) is missing, except as a remnant in some primitive salamanders (Trueb, 1993; Rose, 2003). Primitive salamanders differ from anurans in the retention of the lacrimal and prefrontal.

Functionally, the skulls of primitive salamanders differ from those of anurans in having a hinge-like line of articulation between the dorsal end of the squamosal and the top of the skull. In hynobiids and *Salamandra atra*, the area of articulation includes a posterolateral lappet of the parietal, as well as the adjacent exposures of the prootic and fused opisthotic–exoccipital. In *Ambystoma*, the extent of the parietal is reduced, and articulation occurs only with the otic capsule. Ventrolaterally, the squamosal is solidly attached to the quadrate and pterygoid, forming a distinct suspensorium for articulation with the lower jaw. In salamanders with a primitive cranial architecture, the pterygoid forms a synovial joint with the base of the braincase, suggesting that the jaw suspension could move in a mediolateral arc, enabling the space between the back of the jaws to be expanded during aquatic feeding and respiration. Mediolateral mobility of the jaw suspension is further enabled by the lack of bony attachment with the maxilla, and the absence of the posterior circumorbital bones. Such mobility would presumably be precluded in frogs with an impedance-matching middle ear, as it would result in the tympanum being pierced by the stapes. Mediolateral mobility of the jaw suspension in primitive salamanders may be associated with their particular mode of aquatic feeding, especially among larvae (see below).

Mobility of the jaw suspension is lost in a variety of more derived salamanders, including cryptobranchids, in which there is an interdigitating sutural joint between the squamosal and the parietal, and the anterior portion of the pterygoid is confluent with the parasphenoid. Loss of mobility also occurs in the derived salamandrid *Notophthalmus*, in which the squamosal is suturally attached to the frontal (Francis, 1934). The neotenic proteids, amphiumids, and sirenids are too derived for direct comparison.

It has long been assumed that the large orbitotemporal opening in salamanders is homologous with that of frogs. However, Carroll & Holmes (1980) pointed out that the identity of the major muscle that extends out

of the opening and across the otic capsule differs in the two orders. According to the terminology of Luther (1914), in salamanders it is the superficial branch of the adductor mandibulae internus, but in frogs, it is the longus branch of the adductor mandibulae posterior. In the primitive caecilian *Epicrionops*, which has a large gap between the cheek and the skull table, it is the adductor mandibulae externus that extends over the braincase (Fig. 8). This suggests that the opening in the skull roof may have evolved separately in all three orders. Separate elaboration of the orbitotemporal opening in salamanders is also suggested by the retention of the sculptured dorsal surface of the squamosal in the plesiomorphic sister taxa of the Urodela: the Middle Jurassic *Kokartus* from Kirghizstan, and the Upper Jurassic *Karaurus* from Kazakhstan (Milner, 2000).

In contrast, Haas (2001) has argued that the major muscles that extend out of the adductor chamber in salamanders, frogs, and caecilians are homologous, but that their position relative to the nerves has changed. There is a high degree of consistency of the relationships between the jaw muscles and nerves [as designated by Luther (1914)] throughout the evolution of both mammals (Barghusen, 1973) and squamates (Rieppel, 1980). However, it is extremely difficult to establish the positional homology of the nerves and jaw muscles during early development in anurans, because of the drastic changes in the position and orientation of the muscles during metamorphosis. Whatever the names that are applied to the muscles, the relative position of the branches of the trigeminal nerve and the specific muscles that extend out of the adductor is different between salamanders, frogs, and
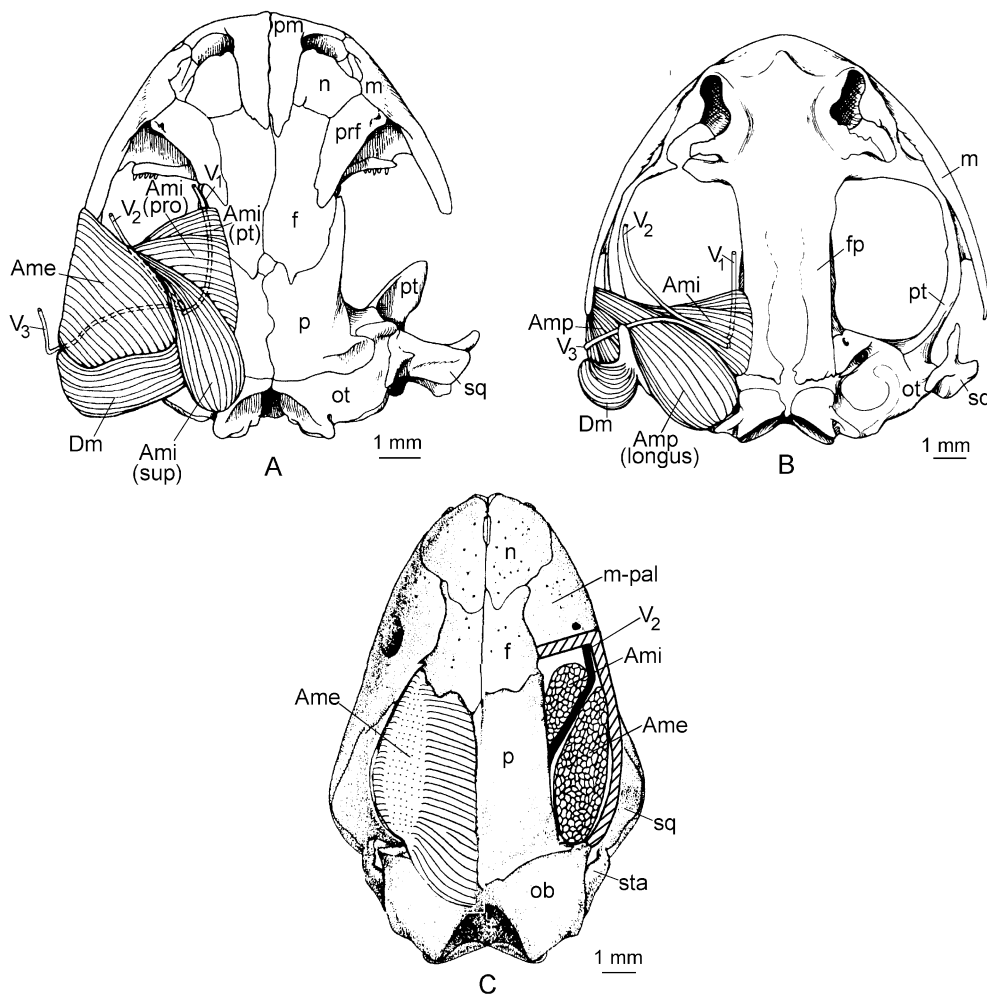

Figure 8. Configuration of the adductor jaw musculature in primitive representatives of the Urodela, Anura, and Gymnophiona. A, the salamander *Ambystoma maculatum*. B, the frog *Ascaphus truei*. C, the caecilian *Epicrionops petersi*. Muscles, distinguished on the basis of their position relative to the rami of the trigeminal nerve, are different in each of these groups. A, B, reproduced from Carroll & Holmes (1980). C, drawn on the basis of serial sections of Lousiana State University Museum of Zoology specimen 27324.

caecilians. This suggests divergent evolutionary pathways from the ancestral condition, in which the temporal region was covered with dermal bones.

Salamanders generally have a much larger mass of adductor jaw muscles than do frogs, with a very large adductor mandibulae externus, which is missing in many anurans. These differences may be associated with the large size of the middle ear cavity in frogs, which occupies much of the area adjacent to the adductor chamber.

In all lissamphibian orders, the parasphenoid serves as a solid bony support for the braincase and occupies a substantial portion of the palate. In primitive salamanders, it may be overlapped by the pterygoid, or be separated from that bone by a portion of the prootic. Neither frogs nor salamanders retain an ectopterygoid, but this bone is present in some caecilians (Taylor, 1969; Carroll & Currie, 1975, Wake, 2003). Frogs definitely retain a palatine, as do caecilians, but the identity of this bone has been uncertain in modern salamanders. A separate bone between the pterygoid and the vomer has been identified as the palatine in sirenids, and the presence of an anterior toothed region of the pterygoid in proteids and the plethodontid *Eurycea* suggests incorporation of a palatine (Trueb, 1993). Well-resolved histological series show the palatine arising as a separate ossification in *Ranodon*, *Pleurodeles* and *Salamandrella*, but it becomes fused to the pterygoid immediately after forming in the latter two genera (Rose, 2003). Presumably, the palatine was present in the ancestors of salamanders, and the capacity for its development was retained, even among more derived families.

The vomers are retained as large elements forming the anterior portion of the palate medial to the premaxillae and maxillae in all lissamphibian orders. The vomerine dentition is an important feature among all salamanders, and its configuration is taxonomically distinctive. The primitive condition may be that seen in *Hynobius tsuensis*, in which it forms a short, transverse row.

The pterygoid in primitive salamanders is a triradiate bone, the midportion of which articulates with the base of the braincase via either the parasphenoid or a synovial joint with the prootic (Carroll & Holmes, 1980). The quadrate ramus supports the quadrate, and the palatal ramus extends anterolaterally but does not form a bony contact with the anterior margin of the palate or the maxilla as it does in caecilians and anurans. There is commonly a ligamentous connection with the maxilla. An endochondral epipterygoid is retained in primitive hynobiid salamanders (Rose, 2003), but is not reported in caecilians or anurans.

In common with other lissamphibians, all terrestrial salamanders have pedicellate teeth as adults, but this condition is not expressed in the larval stage. In some fossil sirenids, in which the blunt cusps suggest a crushing role, teeth are not pedicellate in the adults (Gardner, 2003). The function of pedicellate teeth has never been satisfactorily explained.

The three elements at the back of the braincase in primitive tetrapods, the exoccipital, opisthotic, and prootic, develop separately but co-ossify to a variable degree in the adults. The hynobiids fuse the exoccipital and opisthotic, but the prootic remains distinct. The area occupied by the basioccipital in primitive tetrapods is not ossified in hynobiids, but is in *Ambystoma mexicanum* (Rose, 2003) and in *Trituris* (Stadtmüller, 1929). In primitive salamanders, the XIIth cranial nerve passes through the exoccipital, as in Palaeozoic tetrapods. In both frogs and salamanders, there is a gap in the lateral wall of the braincase of variable length between the prootic and the thin (variably paired or fused at the ventral midline) sphenethmoids that extend anteriorly towards the nasal capsules. This contrasts conspicuously with the braincase of all caecilians, in which all posterior elements of the braincase are fused into a unified os basale that articulates with a massive sphenethmoid anteriorly (Wake & Hanken, 1982).

Cranial sensory structures
Amphibians inherited the range of sensory capabilities of their fish ancestors: smell, sight, balance, and sensitivity to vibrations and electrical currents in the fluid environment. Among these, different systems were either augmented or reduced in the lineages leading to salamanders, frogs, and caecilians, depending on their highly distinctive ways of life.

All three orders retain the basic structure of the semicircular canals common to bony fish. The larvae of frogs, salamanders, and caecilians also have a similar structure and arrangement of the mechanoreceptors (neuromasts) of the lateral-line system exposed at the surface of the integument of the head and trunk. Neuromasts are sensitive to water currents and probably to pressure. They are retained in the adults of aquatic salamanders and pipid frogs. Ampullary organs, which are electroreceptors restricted to the head region, are present in larval caecilians and aquatic salamanders but have never been reported in anurans or in plethodontid salamanders that undergo direct development (Duellman & Trueb, 1986). The common presence of these structures in the modern orders is almost certainly indicative of an ultimate common ancestry, but this might lie at the level of strictly aquatic stem tetrapods.

Salamanders seem to be the least specialized of modern amphibians, in retaining electrosensory structures lost in anurans, and normal vision, much reduced in caecilians, and in lacking the impedance-

matching middle ear of anurans. Their olfactory system is the most primitive of the extant orders (Jurgens, 1971). Both salamanders and frogs are more advanced than primitive tetrapods in the presence of the operculum–opercularis system, which is sensitive to low-frequency sounds from the air, water, or ground. Frogs and salamanders have green rods (of uncertain function) in the eye, not present in caecilians or amniotes (Parsons & Williams, 1963).

Anurans are unique among living amphibians in having an impedance-matching middle ear capable of transmitting high-frequency vibrations from the air. The burrowing caecilians have reduced or completely lost the sense of sight, depending on the species, but much of the anterior portion of the skull is occupied by greatly enlarged nasal sacs and Jacobson's organ for detection of olfactory signals. In addition, they have an entirely new sensory organ, the tentacle, involved in chemical reception.

The mosaic of primitive retention, loss, and augmentation of specific elements of the sensory system does not provide a clear signal for establishing the specific pattern of relationships among the living taxa, but some features are useful in indicating affinities with particular Palaeozoic clades.

Structure and function of the salamander ear
Salamanders differ significantly from frogs in the absence of external evidence of the capacity to respond to airborne sounds. They lack a tympanic membrane, and have no middle ear cavity, and the potential for mobility of the stapes is greatly limited by its distal attachment to the squamosal.

The capacity of amphibians to respond to different frequencies varies from order to order (Fritzsch *et al.*, 1988). Only anurans, with an impedance-matching middle ear, can detect high-frequency airborne vibrations (1000 Hz and above). This capacity is critical for the acoustic communication that most frogs depend on for species recognition. Neither urodeles nor caecilians make use of acoustic communication. However, all three extant orders have an area of reception in the inner ear, the amphibian papilla, thought to be unique to these orders. This papilla is sensitive to low-frequency sound (up to about 200 Hz). Information from caecilians (discussed below) provides information regarding the homology of the amphibian papilla. Primitive living amphibians also retain the basilar papilla, the only papilla present in amniotes. Most members of all three orders have a stapes, homologous with that of amniotes, but most frogs and salamanders also have a second ear ossicle, the operculum, adjacent to the footplate of the stapes, occupying the posterior portion of the fenestra ovalis. The operculum is typically linked to the scapula via the opercularis muscle.

In both frogs and salamanders, the operculum–opercularis system transmits low-frequency sound from the air, water, and substrate.

This system is consistently formed at the initiation of terrestrial activity in both orders, and develops independently of the tympanum–stylus complex in anurans. It has been suggested that extant caecilians may have fused the operculum with the footplate of the stapes (Goodrich, 1930), but this has not been confirmed. Modern species have no shoulder girdle to which an opercularis muscle could be attached.

The common presence of the amphibian papilla in all three orders and the operculum–opercularis system in frogs and salamanders have long been cited as evidence for the monophyly of lissamphibians (Parsons & Williams, 1963). If the three orders had a common ancestry, the impedance-matching middle ear of frogs might either be a new structure, or have been lost in urodeles and caecilians. There is some evidence of the loss of key structures of the ear region within both caecilians and urodeles.

Although the basilar papilla is present in the primitive members of all three groups, it is absent in all sirenids, proteiids, and plethodontids, as well as in some salamandrids. Within the genus *Triturus*, it is present in more terrestrial species, but is reduced or lost in those that are primarily aquatic (Duellman & Trueb, 1986). Schmalhausen (1968: 189) presented evidence from early developmental stages of the primitive urodeles *Hynobius* and *Ranodon* that suggested the initial elaboration of tissue (later lost) that forms in the area of the middle ear cavity of frogs, but this has not been confirmed in these or other salamanders. Hynobiids also retain other features of the ear region that are primitive for urodeles. The stapes is unique, in that it develops anteriorly and ventrally towards the palatoquadrate, eventually assuming a configuration similar to that of a fish hyomandibular (Hetherington, 1988). In 40% of the specimens of *Ranodon sibiricus* examined by Schmalhausen (1968: 183), a stapedial artery passed through a fenestra in the shaft of the stapes; in others, the orbital artery passes anteriorly, below the columella, as in other salamanders. *Salamandrella keyserlingi* and *Onychodactylus japonicus* have no muscular attachment from the fenestral plate to the shoulder girdle, and no element that can be considered to be an operculum. *Batrachuperus pinchonii* lacks a distinct operculum, but has a cartilaginous area of the otic capsule ventral to the fenestra vestibuli to which is attached the opercularis muscle (Monath, 1965). This variation may be interpreted as a series of stages in the origin of the operculum–opercularis complex common to more derived terrestrial salamanders, or as indicating progressive reduction and loss within the Hynobiidae.

There is no direct evidence that the crown-group urodeles ever possessed structures of hard or soft anatomy that would have enabled responses to high-frequency airborne vibrations. Not surprisingly, salamanders also show no evidence of ever having possessed a sound-producing apparatus comparable to that of frogs. Schneider (1988) notes that *Salamandra* and various species of *Triturus* are capable of sound production, although this ability apparently has no major significance in their lives. Both male and female salamanders can produce sounds, both in and out of the water, by expiration of air from the lungs when they are roughly handled, but without any discernible pattern.

If salamanders did share an immediate common ancestry with frogs, then they must have lost not only the capacity for the reception of high-frequency airborne sound, but also, presumably, the capacity for the generation of high-frequency calls.

It may be significant that the stapes develops in salamanders much earlier than in frogs, in which it does not appear until after metamorphosis. In larval salamanders, the stapes is freely movable within the fenestra ovalis, but it may become solidly integrated into the otic capsule in the adult, at which time the operculum, attached to the opercularis muscle, takes its place as a mobile element in the fenestra ovalis. In plethodontids, what appears to be the stapes remains within the fenestra ovalis, but is attached to the opercularis muscle (Hetherington, 1988). Fritzsch & Wake (1988), following Lombard & Bolt (1979), suggest that regression of the basilar papilla in caecilians and urodeles is related to the apparently primitive lack of a tympanic ear.

Lower jaws
As in primitive bony fish and the immediate ancestors of tetrapods, the lower jaws of amphibians are formed from two types of tissue – endochondral bone that is preformed in cartilage, and the more superficial dermal bone that forms without a cartilaginous precursor. The first to form in the embryo is the rod-shaped Meckel's cartilage. This is subsequently enveloped by dermal bones that form the bulk of the jaw in the adult. In choanate fish and most Palaeozoic tetrapods, there is a multitude of dermal bones. The long, tooth-bearing dentary makes up most of the lateral surface and forms the symphysis. The angular forms the posterior lateral and ventral surfaces, and is succeeded dorsolaterally by the surangular. The medial surface is formed by the prearticular, two splenials, and three tooth-bearing coronoids. Of Meckel's cartilage, only the posterior articular bone is ossified in the adult.

The lower jaws of salamanders and frogs retain the superficial appearance of their Palaeozoic anteced-ents, but those of caecilians are highly modified. All groups of modern amphibians have greatly reduced the number of dermal bones in the adults. Salamanders have a maximum of four dermal bones (Trueb, 1993; Rose, 2003). Only two are present throughout the order – the dentary and the prearticular. Two others are consistently expressed only in primitive families. A distinct angular is present only in crypobranchids and hynobiids, where it occupies the posteroventral surface of the jaw. In more advanced salamanders, it fuses with the prearticular. A bone termed alternatively the splenial or coronoid is frequently present in the larvae, but typically lost in adults. As it bears teeth, as does the coronoid in Palaeozoic amphibians, it is more plausibly homologous with that bone than with the splenial, which does not.

As in Palaeozoic amphibians, the posterior portion of Meckel's cartilage ossifies late in development as the articular bone. Either it ossifies in continuity with the prearticular, or the two bones may subsequently become fused. In contrast to any known Palaeozoic amphibians, all three modern amphibian orders have a second area of Meckel's cartilage, the mentomeckelian bones, that ossify on either side of the jaw symphysis. In salamanders, they may form in continuity with the dentary bones or become fused to them. Mentomeckelian bones are found in all salamander families except the structurally highly derived Plethodontidae, Sirenidae, and Amphiumidae. The Jurassic cryptobranchoid described by Gao & Shubin (2001) has the full complement of dermal elements, but they did not recognize a mentomeckelian bone.

Hyobranchial apparatus and aquatic feeding
Although the dermal bones of the adult skull and jaws provide much of the fossil evidence for the history of the head, knowledge of the both the larval and adult anatomy is necessary for understanding the evolution of the hyobranchial region. The fish ancestors of tetrapods were obligatorily aquatic feeders throughout their life history, but most amphibians rely on different structural and functional complexes for aquatic feeding as larvae and terrestrial feeding as adults. Hence, both the evolution of amphibians since the Devonian and the individual life histories of modern species express transformations in the nature of their feeding apparatus.

Modern amphibian larvae have inherited the basic structure and function of the hyobranchial skeleton from their fish ancestors as a result of the common practice of aquatic feeding and respiration. The overall similarity of the hyobranchial apparatus in *Eusthenopteron*, *Acanthostega*, and the larvae of *Ambystoma* (Figs 9, 10) shows that conservative salamanders retain the most primitive configuration
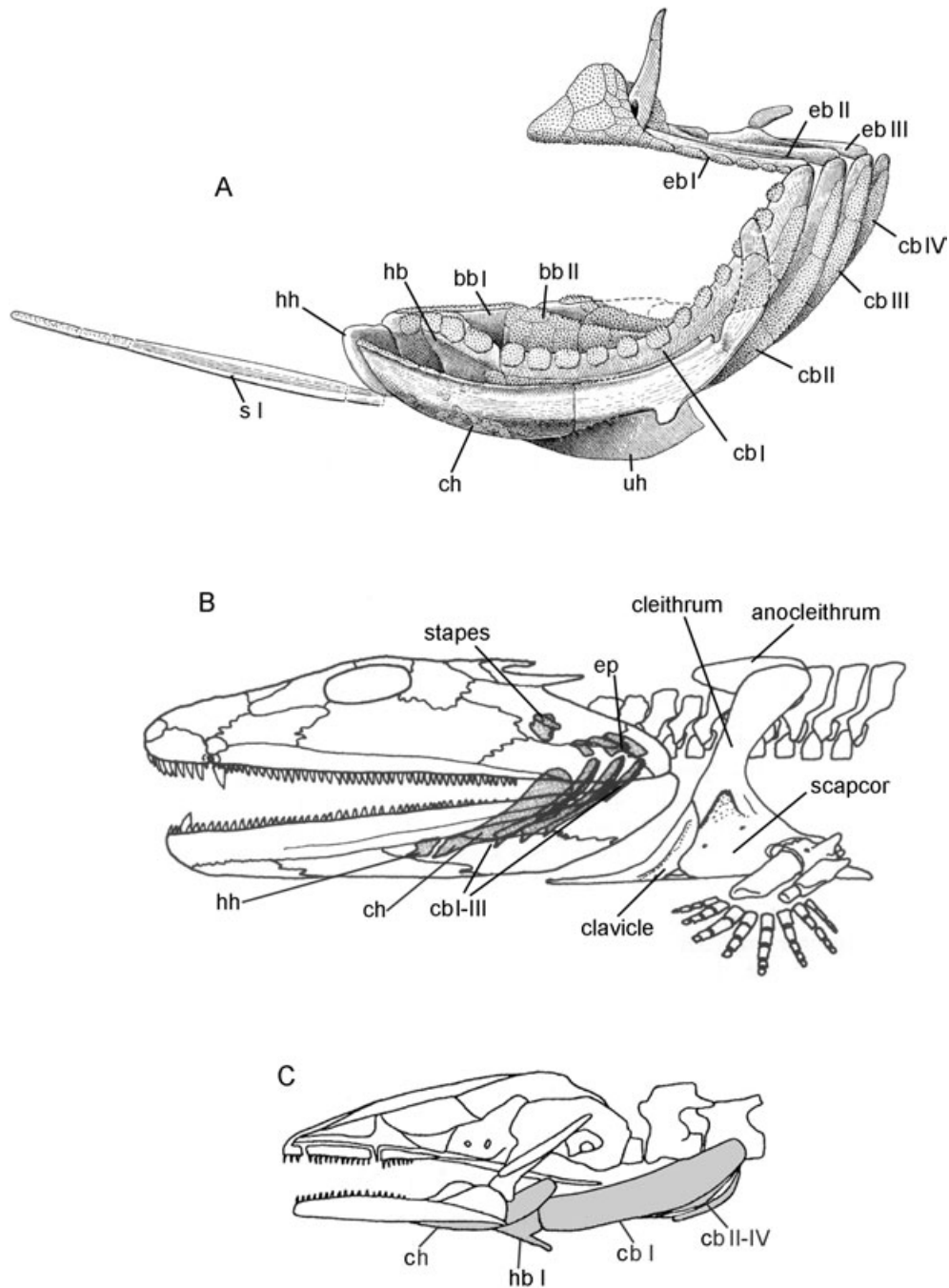
Figure 9. A, lateral view of the hyobranchial apparatus of the Upper Devonian osteolepiform fish *Eusthenopteron*. Reproduced from Jarvik (1954). B, lateral view of the hyobranchial apparatus of the Upper Devonian amphibian *Acanthostega*. Reproduced from Clack (2000). C, lateral view of the hyobranchial apparatus of the larva of a modern salamander. Reproduced from Deban & Wake (2000).

among living amphibians. All of these genera may be assumed to have had a comparable mode of suction feeding in the aquatic juvenile or larval stage.

However, specific aspects of larval feeding appear so different in salamanders, frogs, and caecilians that it is difficult to see how they could have evolved from an immediate common ancestor. For this reason, it is necessary to describe the specific anatomy of the bones and the function of the muscles in the three groups in some detail. Comparison is further complicated by questions of the homology of these element among frogs, salamanders, and caecilians, and the use of dif-
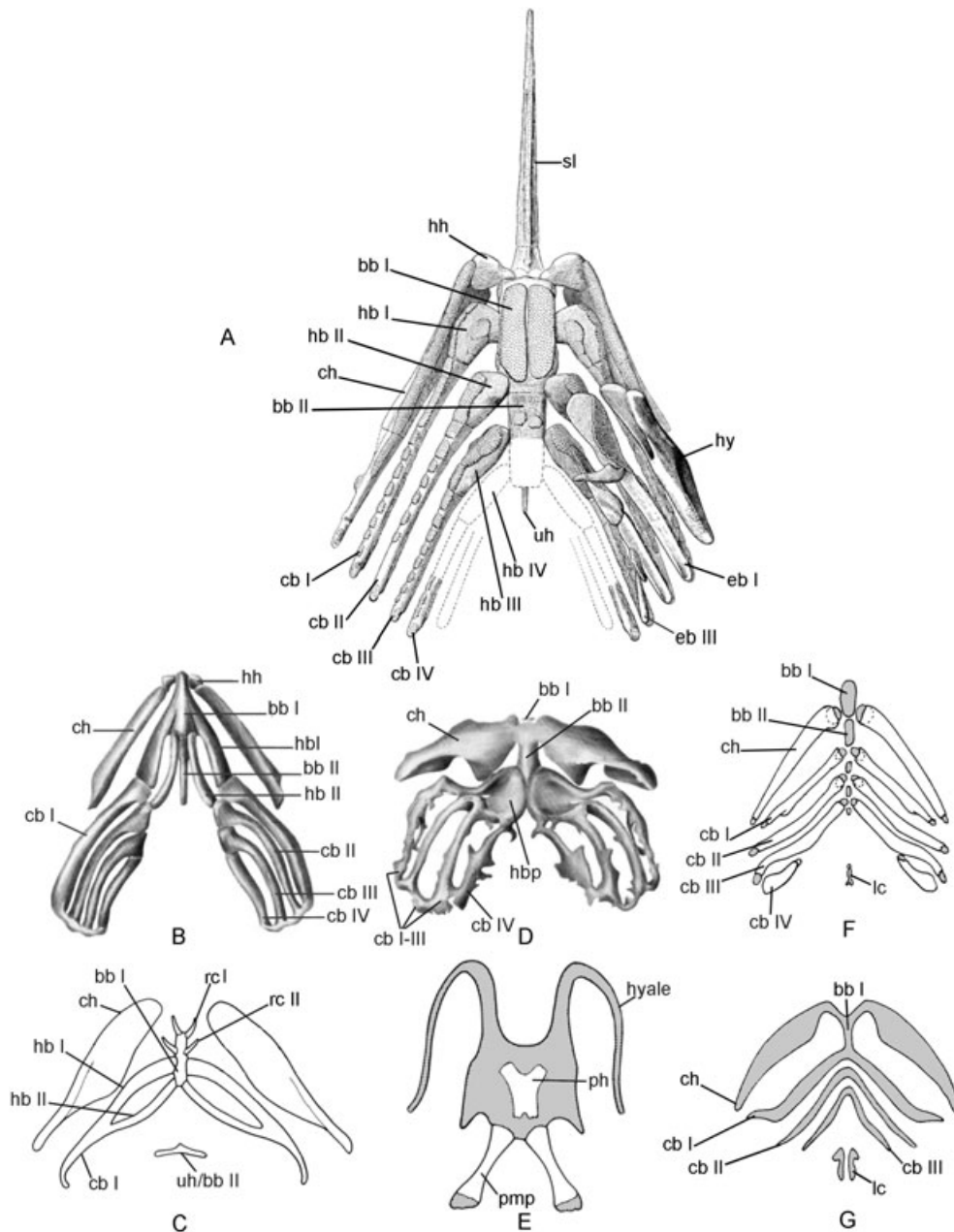
Figure 10. A, dorsal view of the hyobranchial apparatus in the Upper Devonian osteolepiform fish *Eusthenopteron*. B, C, ventral views of hyobranchial apparatus of larval and adult *Salamandra salamandra*. D, ventral view of hyobranchial apparatus of larval *Rana temporaria*. E. Hyoid plate of adult *Leiopelma hochstetteri*. F, G, hyobranchial apparatus of larval and adult individuals of the primitive caecilian *Epicrionops*. A, reproduced from Jarvik (1954). B–E, reproduced from Duellman & Trueb (1986). F, G, reproduced from Wake (1989). Coarse stippling is indicative of cartilage. It should be noted that the names of the more distal elements of the hyobranchial apparatus differ from those used by some modern authors (e.g. Deban & Wake, 2000), who refer to the hyobranchials and ceratobranchials as basibranchials and epibranchials. Reilly & Lauder (1988) discussed the homology of these elements and the historical reasons for the use by some authors of a unique terminology for salamanders.

ferent names both between and within the three orders (Schwenk, 2000; Rose, 2003).

The mechanics of feeding in the aquatic larvae of hynobiids, ambystomatids, and salamandrids have been studied intensively by Lauder (1985), Lauder & Shaffer (1985), Reilly & Lauder (1990), Larsen *et al.* (1996), and Deban & Wake (2000). They resemble the suction or 'gap-and-suck' feeding of generalized bony

fish. The buccopharyngeal cavity is expanded ventrally and laterally by contraction of pharyngeal and hypaxial musculature as the mouth is opened and water and suspended food are drawn in. Prominent labial lobes occlude the sides of the mouth, narrowing the oral opening and focusing the point of suction. To prevent influx of water through the gill slits, they are closed by interdigitation of the gill rakers. Closure of the jaws and elevation and protraction of the hyoid apparatus force the water posteriorly into the pharynx as the gill slits are opened. Prey is trapped by the gill rakers, and water is expelled.

Most elements of the hyobranchial apparatus can be directly compared from *Eusthenopteron* through the primitive tetrapod *Acanthostega* to conservative living salamanders (Figs 9, 10). An anterior central axis is composed of one or more basibranchials. Short, squarish or rounded hypohyals articulate with the rostral surface of the anterior basibranchial in *Eusthenopteron* and a range of primitive salamanders – *Cryptobranchus*, *Salamandra*, *Dicamptodon*,

Ambystoma, and *Amphiuma* – but are lost in others (Duellman & Trueb, 1986; Deban & Wake, 2000). Attached either to the hypohyals, or directly to the basibranchials, are the large, blade-shaped ceratohyals. More posterior are two pairs of hypobranchials that articulate distally with ceratobranchials I and II. Two further pairs of ceratobranchials are more posterior in position. The gaps between the ceratobranchials mark the position of the gill slits. A small bone, termed a urohyal or second basibranchial, may be present between the distal ends of the ceratobranchials. Both bones are present in *Eusthenopteron* (Jarvik, 1954). The ventral portion of the hyobranchial apparatus of larval salamanders is broadly similar to that of *Eusthenopteron*, but clearly distinct from those of any of the lepospondyl groups (Fig. 11), none of which have been described as having ossified basibranchial elements (Andrews & Carroll, 1991).

Eusthenopteron and other bony fish have an additional set of hyobranchial elements, the epibranchials, that extend dorsally and anteriorly from the cerato-
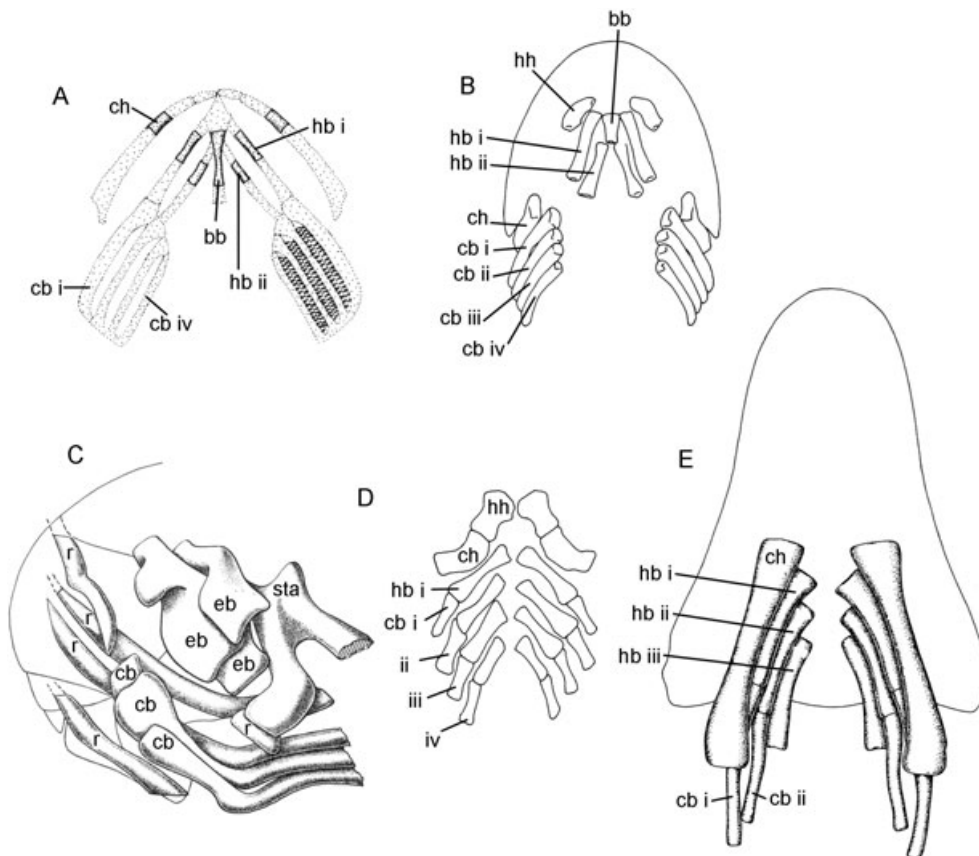

Figure 11. Hyobranchial apparatus of Palaeozoic amphibians. A, hyobranchial apparatus of the Permo-Carboniferous branchiosaurid *Apateon*. Reproduced from Boy & Sues (2000). B, the neotenic Upper Permian labyrinthodont *Dvinosaurus*. Reproduced from Bystrow (1938). C, the large, terrestrial Lower Permian microsaur *Pantylus*. Reproduced from Romer (1969). D, the Lower Permian lysorophid *Brachydectes elongatus*. E, the Lower Carboniferous adelogyrinid *Adelogyrinus*. D, E, reproduced from Andrews & Carroll (1991).

branchials. They are retained in *Acanthostega* and also in the lepospondyl *Pantylus* (Romer, 1969). These are not normally expressed in salamanders, but do occur as a rare atavism in a single population of the salamandrid *Notophthalmus viridescens* (Reilly & Lauder, 1988; Rose, 2003). Their presence and configuration in this population demonstrate conclusively that the larger elements present more ventrally in all salamanders are the ceratobranchials, not the epibranchials, as these bones have been designated by some authors (e.g. Larsen *et al.*, 1996; Deban & Wake, 2000).

The hyobranchial apparatus lies within the soft tissue between the lower jaws. The ceratohyals are attached posterolaterally to the lower jaws by the mandibulohyoid ligament. Most of the hyobranchial apparatus remains cartilaginous in the larvae, but may become ossified or mineralized at metamorphosis.

Feeding in aquatic salamanders involves complex interactions between the movements of the skull, lower jaws, and hyobranchial elements (Lauder, 1985; Lauder & Shaffer, 1985; Deban & Wake, 2000). As viewed laterally (Fig. 12), the elements can be drawn as a polygonal lattice, with the skull as an upper, horizontal unit that hinges posteriorly with the atlas vertebra. The lower jaw articulates with the skull somewhat posterior to midway in its length. The medial axis of the hyobranchial apparatus, made up of the basibranchials, remains essentially horizontal, whereas the paired ceratohyals and ceratobranchials change orientation from nearly horizontal, when the basibranchials are elevated, to almost vertical when their anterior extremities are depressed and retracted

posteriorly. All of these elements are in motion during gap-and-suck feeding, involving coordinated contraction of muscles that commonly affect the movements of more than one of the bones because of their mechanical linkage.

Opening of the mouth and expansion of the oropharyngeal cavity are achieved through the action of three sets of muscles. The dorsal epaxialis, which originates along the dorsal midline of the body and inserts on the posterodorsal surface of the skull, raises the head. The depressor mandibulae, running from the squamosal to the lower surface of the articular or prearticular and the geniohyoideus (also known as the coracomandibularis), which originates from the base of the shoulder girdle and the urohyoid and inserts at the front of the mandible, lower the jaws. The rectus cervicis (also termed the sternohyoideus) attaches laterally to the midline at the front of the hyoid apparatus and pulls it ventrally and posteriorly, while expanding the ceratobranchials laterally.

Another very important set of muscles, the branchial abductors (the branchiohyoideus and the transversus ventralis), move the ceratobranchials apart to open the gill slits. The gill slits are closed by subarcularis rectus 2–4, which span the ceratobranchials and move them towards one another. Subarcularis rectus 1 originates on the ventral surface of the ceratohyal and inserts on the first ceratobranchial. With metamorphosis, this muscle becomes an important in tongue protrusion.

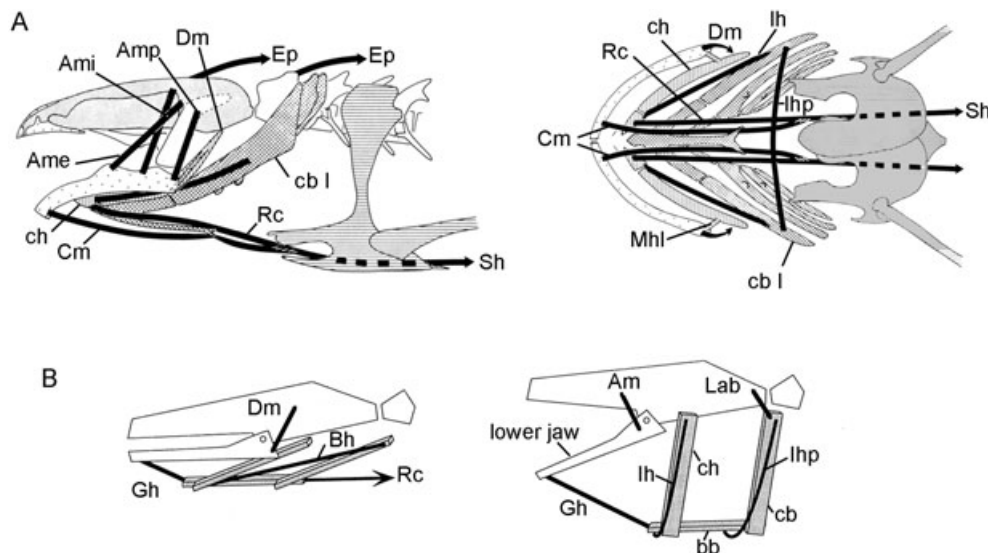The major force for jaw closure in salamanders and most other tetrapods is provided by the adductor

Figure 12. The mechanics of feeding and respiration in larval salamanders. A, B, diagrams of the bones and major muscles of the oropharyngeal region of *Ambystoma mexicanum* in lateral and ventral views. Reproduced from Lauder (1985). C, D, mechanical models in lateral view showing posteroventral expansion of the buccopharyngeal cavity during inspiration. Reproduced from Deban & Wake (2000).

(or levator) mandibulae, situated in the adductor chamber of the skull. Following the terminology of Luther (1914), three major groups of adductor muscles are recognized by their positions relative to branches of the Vth (trigeminal) nerve (Fig. 8A): the adductor mandibular internus, medial to the maxillary branch of the Vth nerve; the adductor mandibulae externus, between the maxillary and mandibular branch; and the adductor mandibulae posterior, posterior to the mandibular branch. As the jaw is closed by these adductors, the geniohyoideus can reverse its role as a jaw-opening muscle, and pull the hyobranchial apparatus anteriorly and dorsally.

As the mouth is closed, a number of other muscles cradle the hyobranchial apparatus and serve to lift and move it forwards. The intermandibularis posterior originates on the medial aponeurosis, and runs laterally to insert on the dentary and prearticular. The interhyoideus also originates on the medial aponeurosis, but extends caudally to insert on the posterior tip of the ceratohyal or on the hyoquadrate ligament. The interhyoideus posterior (also referred to as the interbranchialis or sphincer colli) runs from the medial aponeurosis of the throat to insert on the distal tip of the first ceratobranchial (Fig. 12).

Ontogeny of the skull
Correlated with larval growth in salamanders, there is progressive ossification of the dermal skull that may be associated with the mode of feeding (Fig. 13). All of the modern amphibian orders ossify the dermal bones of the skull and lower jaws in a sequential manner, although the specific sequence varies significantly from group to group. Such sequential ossification is in strong contrast to primitive tetrapods and their sister taxa among lobe-finned fish. The dermal bones of the skull and lower jaw of osteolepiform fish such as *Eusthenopteron* (Schultze, 1984) and the majority of Palaeozoic amphibians ossified nearly simultaneously in very small individuals. The entire complement of

bones formed an integrated mosaic in the smallest known specimens of all species (Schoch & Carroll, 2003; Witzmann, 2006).

Salamanders show a broadly consistent sequence of ossification over all species that have been studied (Fig. 13). The general sequence is as follows: (1) tooth-bearing bones of the palate and marginal dentition (with variable delay of the maxilla); (2) squamosal; (3) the midline bones of the skull roof; and (4) circumorbital bones. Rose (2003) tabulated the sequence of ossification of the skull and jaw bones for 24 species in all ten families, and Boisvert (2004), using many of the same sources as Rose, compiled a single list that she proposed as a universal staging table for all families (Table 1).

The early ossification of the tooth-bearing bones suggests the necessity for feeding at as early a stage as possible. During early development, the skull is a latticework of slender elements, only loosely connected with one another. This suggest a very flexible skull, capable of expanding to engulf large prey. Such a pattern is also seen in a Middle Jurassic salamander larva illustrated by Gao & Shubin (2003) from China, whose gut was filled with relatively large conchostracans. At this stage, the squamosal in primitive salamanders has a moveable joint with the parietal or the otic capsule that would permit the lateral extremity to swing laterally, allowing for expansion of the cheek and lateral movement of the back of the jaws. This would facilitate gap-and-suck-feeding, especially in smaller larvae.

Suction feeding continues into the sexually mature adult stage in neotenic salamanders, including cryptobranchids, amphiumids, proteids, and sirenids, much as in the larvae. Hynobiids, ambystomatids, and salamandrids that undergo metamorphosis to facultatively terrestrial adults may also use suction feeding when in the water, but this is less efficient, as their gill slits are permanently closed and the water must be expelled through the mouth (Lauder & Reilly, 1988). The bones of the adult skull of most hynobiid,

Table 1. Summary of sequence of ossification of skull bones common to most modern salamanders (from Boisvert, 2004)

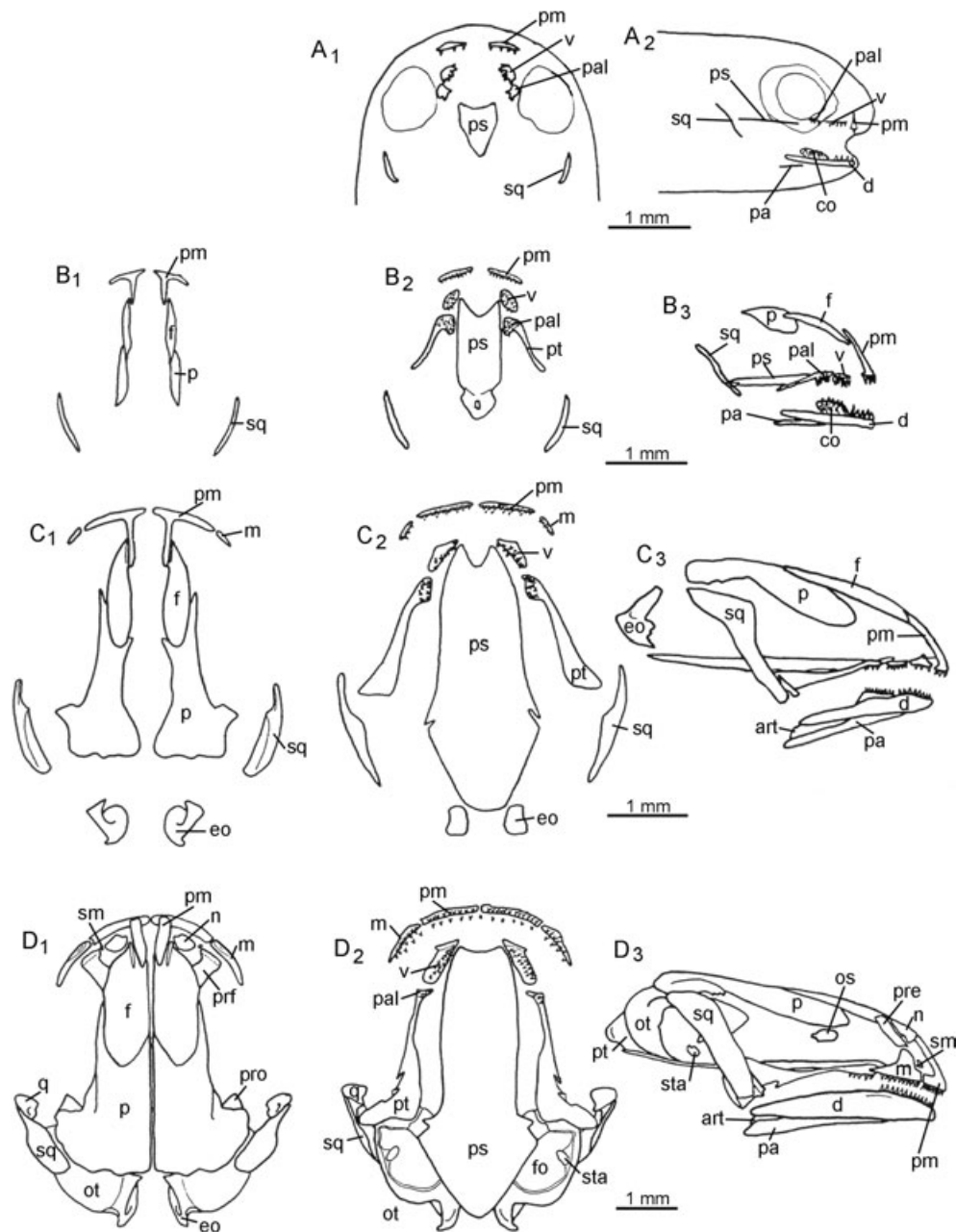| Stage	Bones newly ossified
I	Coronoid, dentary, palatine, vomer
II	Premaxilla, squamosal, prearticular
III	Parasphenoid, pterygoid
IV	Parietal, frontal
V	Exoccipital
VI	Quadrate, maxilla, orbitosphenoid
VII	Opisthotic, prootic
VIII	Prefrontal, operculum, nasal, articular, lacrimal, septomaxilla

Figure 13. Sequence of ossification of the bones of the skull of *Ambystoma texanum*. Reproduced from Bonebrake & Brandon (1971). A₁, A₂, dorsal and lateral views of stage II skull. B₁, B₂, B₃, dorsal, ventral, and lateral views of stage III. C₁, C₂, C₃, stage V. D₁, D₂, D₃, stage VII.

ambystomatid, and salamandrid species that feed on land are much more highly integrated than those of the larvae; this is related to feeding on larger and more resistant prey.

Terrestrial feeding
Salamanders feeding on land must use an entirely different means of prey capture. In all urodeles with a terrestrial stage in their life history, this involves a tongue (not developed in the larvae) that is projected from the mouth by the muscles and bones of the hyobranchial apparatus (Larsen *et al.*, 1996; Larsen & Guthrie, 1975; Wake & Deban, 2000). Even the most primitive of terrestrial salamanders, the Hynobiidae, use lingual (tongue) prehension for terrestrial prey capture, indicating that this capacity had evolved in the stem taxa of crown-group salamanders.

The tongue, as an important feature of feeding, is a unique structure of terrestrial vertebrates. Sala-

mander larvae, like fish, have a small fold of tissue in the floor of the mouth that surrounds the anterior medial elements of the hyoid apparatus. This is referred to as the primary tongue. At metamorphosis, the secondary part of the tongue develops anteriorly, and unites with the primary structure. The secondary tongue is distinguished by longitudinal furrows and an underlying glandular field.

According to Larsen *et al.* (1996), the adult configuration of the hyolingual skeleton in primitive terrestrial salamanders consists of one basibranchial, one pair of radials, two pairs of hyobranchials, and two pairs of ceratobranchials. The radials are newly formed, the hyobranchials fuse distally, and the more posterior ceratobranchials of the larvae are lost. A median element between the ceratobranchials is alternatively designated as either basibranchial II or the urohyal.

The metamorphosed tongue in *Ambystoma* is supported internally by two pairs of radiales, an otoglossal cartilage (Fig. 14), most of the basibranchial, and the first hypobranchial, but not by the underlying ceratohyals. In hynobiids, ambystomatids, and primitive salamandrids, the tongue is attached anteriorly.

As shown for *Ambystoma* by Larsen & Guthrie (1975), prey capture begins with a lunge towards the prey, after which the lower jaws are lowered and pressed to the ground by the geniohyoideus and the rectus cervicis superficialis, which extend from between the lower jaws to the base of the shoulder girdle. In addition to the epaxial muscles and (with the lower jaw immobilized) the depressor mandibulae, the cranium is raised by the cucullaris major, which extends from the base of the pectoral girdle to the top of the otic capsule. Frogs also have a cucullaris muscle (which is the only muscle extending between the skull and the pectoral girdle for which there is an obvious homologue in salamanders), but because of its different geometry, it lowers rather than raises the skull.

Movement of the tongue is simultaneous with jaw opening. The genioglossus, the major muscle of the tongue, has open spaces (sinuses) that can be filled with fluid, giving the tongue an effective shape for the capture of prey. It is reshaped from a small mound of tissue to form a broad surface with a dorsal depression. It is impossible to determine whether there is an independent hyoglossus muscle, as there is in anurans. The subarcualis rectus 1 is the prime mover in tongue projection. It originates on the anteroventral surface of the ceratohyal, and inserts around the posterior portion of the first ceratobranchial. Its contraction, and that of the genioglossus, propels the central portion of the branchial apparatus anteriorly. Contraction of the geniohyoideus, which originates from the mandibular synthesis, draws the rectus cervicis superficialis and the urohyal anteriorly, resulting in

buckling of the anterior radial cartilages so that they form a ridge supporting the leading edge of the tongue. When the prey is struck by the tongue, the lingual divisions of the genioglossus contract, resulting in the expulsion of a sticky secretion that holds the prey to the tongue.

Tongue retraction results primarily from contraction of the rectus cervicus profundus and lateral divisions of the rectus cervicis superficialis. Jaw closure involves the adductor mandibulae and the subvertebralis muscles, the latter of which originate ventral to the trunk vertebrae and insert on the base of the otic capsules.

Although the adult hyobranchial apparatus of primitive terrestrial salamanders is clearly distinct from that of their larvae and their ultimate fish ancestors, the changes during metamorphosis are readily accounted for by loss of and change in function from the pattern of the larvae. The ceratohyal retains its primitive position and configuration, but becomes separated from the basibranchials and so can remain essentially stationary while the rest of the branchial apparatus is protruded.

In all terrestrial salamanders that retain lungs, the hyobranchial apparatus has a dual role. It serves as a buccal pump in respiration, and as the main mechanism for tongue protrusion. In two genera of salamandrids and the entire family Plethodontidae, lungs are lost. According to Wake & Deban (2000), the loss of lungs frees the hyolingual apparatus from constraints common to all of the more primitive salamanders, and the hyoid apparatus can reach a much higher level of specialization. The single pair of ceratobranchials become enormously elongated, so that the tongue can be thrust out of the mouth by contraction of the subarcualis rectus to distances equal to 80% of the body length (Fig. 15). The anterior attachment of the tongue seen in primitive salamanders is lost.

In contrast to the well-documented independent origin of a protrudable tongue in advanced salamanders and frogs, another distinctive aspect of their feeding may be a common trait shared by primitive members of both groups. In adult frogs and salamanders, food is pushed backwards into the oesophagus by retraction of the large eyeballs into the buccal cavity. This action is mediated by the retractor bulbi muscles, which pull the eyes down through large palatal vacuities (Schwenk, 2000: 54) (Fig. 16). An antagonistic eye muscle, the levator bulbi, lifts the eyeball after swallowing.

Such an open palate is not present in any caecilians. They lack both tongue and eye mobility, but the large vascular spaces within the tongue and palate can be inflated and deflated as a means of prey manipulation. Caecilians have a muscle that is homologous with the levator bulbi, but its function has shifted to manipulation of the tentacle (Duellman & Trueb, 1986: 385).
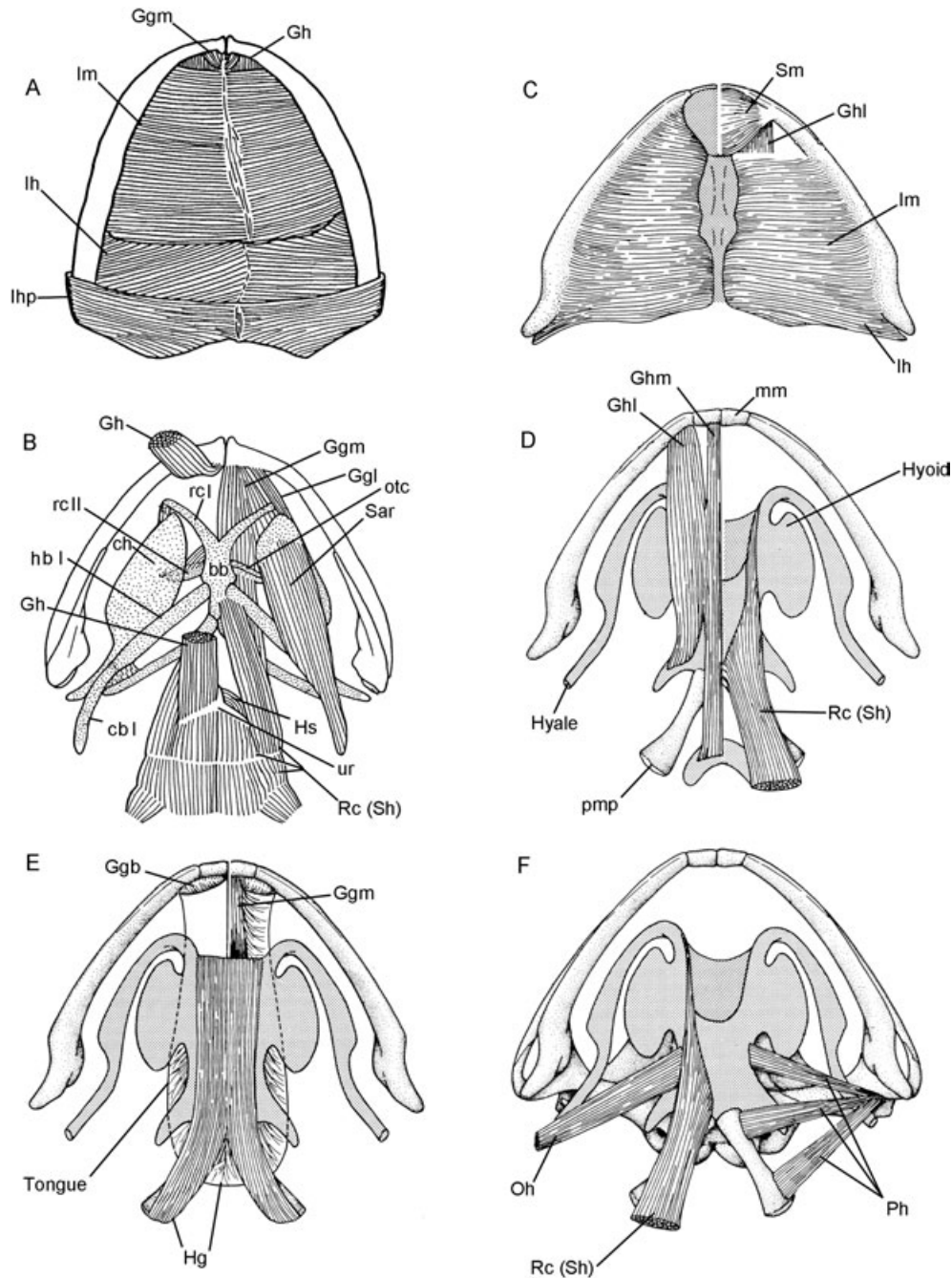
Figure 14. Musculature of the lower jaw and hyoid apparatus associated with feeding in terrestrial salamanders and frogs. A, ventral transverse throat musculature of *Ambystoma tigrinum*. B, hyobranchial apparatus and longitudinal throat and tongue musculature of *Ambystoma tigrinum* in ventral view. C–F, mandibular and hyoid musculature of *Bufo marinus*. C, superficial mandibular musculature, with medial raphe removed in upper right to expose deeper muscles. D, superficial (left) and deeper (right) hyoid musculature. E, tongue muscles. F, deep hyoid muscles (all in ventral view). A, B, reproduced from Larsen & Guthrie (1975). C, F, reproduced from Duellman & Trueb (1986).

Vertebrae and ribs
In the adult, the vertebrae of frogs, salamanders, and modern caecilians each appear as a single unit, in contrast to a sutural division between arch and centra and the presence of more than a single central element per segment that is common in many Palaeozoic taxa. The atlas (Fig. 17) is distinctive in having widely separated cotyles that articulate with the occipital condyles of the skull. The hinge-like geometry of this articulation limits the movement of the skull to the
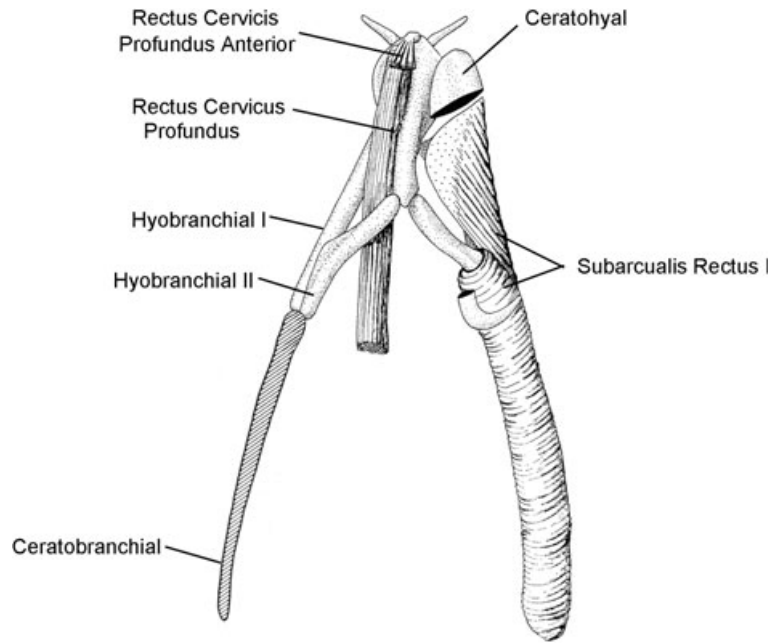
Figure 15. Hyobranchial skeleton and musculature of the plethodontid salamander *Eurycea bislineata*. Note the great length of the ceratobranchial. Modified from Bramble & Wake (1985).

vertical plane, without the possibility of rotation or lateral flexion that is common to Palaeozoic labyrinthodonts and amniotes.

The number of trunk vertebrae differs greatly among the three orders, from between six and ten in frogs, to 11 to ~60 in salamanders, and ~70 to 285 in caecilians (Duellman & Trueb, 1986). The configuration of the individual vertebrae and the pattern of their development also differ from group to group, so that those from different orders are readily distinguished from one another. The vertebrae of adult terrestrial salamanders follow a fairly stereotyped pattern (Fig. 17). A tuberculum interglenoideum (or odontoid) extends from the base of the atlas, and articulates with the medial surface of the exoccipitals (Trueb, 1993). In contrast to Palaeozoic microsaurs, in which an odontoid process of the atlas articulates with the basioccipital, the latter bone is not commonly expressed in salamanders. There is little regional variation among the trunk vertebrae. Salamanders never have more than a single sacral vertebra, but two or more may be present in frogs. Living caecilians show no evidence of a pre-existing sacrum (Wake, 2003).

All three modern amphibian orders have very short ribs, as compared to those of amniotes. This reflects the fact that amphibians do not use their ribs for respiration, but rely on a buccal pump, retained from their fish ancestors, and practise cutaneous respiration. The ribs of extant amphibians are even shorter than those of most of their Palaeozoic antecedents, in which they may have had a more important role in supporting the trunk. This may have been especially important in large, primitive genera, in which the elements of the individual vertebrae were not well integrated. Salamanders have ribs on all the trunk vertebrae except the atlas.

In the primitive salamander *Hynobius nigrescens* (Museum of Comparative Zoology, no. 22513), the sacral ribs are somewhat enlarged relative to those that are more anterior, but not greatly expanded distally. The surface that articulates with the ilium extends posteroventrally. A few proximal caudal vertebrae bear short ribs. Haemal arches, fused midway along the length of the centra, occur posteriorly to those bearing ribs.

Salamanders and frogs both have long structures that broadly resemble the transverse processes of amniotes, extending from the vertebrae to support the ribs. These seem to be unitary structures in frogs, but in salamanders they are clearly developed from separate dorsal and ventral elements. Ventrally, the parapophysis projects from the centrum, and dorsally, the diapophysis arises near the midpoint of the neural arch. The processes extend posteriolaterally, parallel to one another in the vertical plane. They are joined to one another by a narrow sheet of bone. In vertebrae 2–7 of *Hynobius nigrescens*, this sheet is pierced proximally by an opening that transmits the vertebral artery. From the 8th vertebra to about the 13th, this opening lies between the articulating surfaces of the parapophysis and the diapophysis and the adjacent rib heads, which is the common position for the pas-
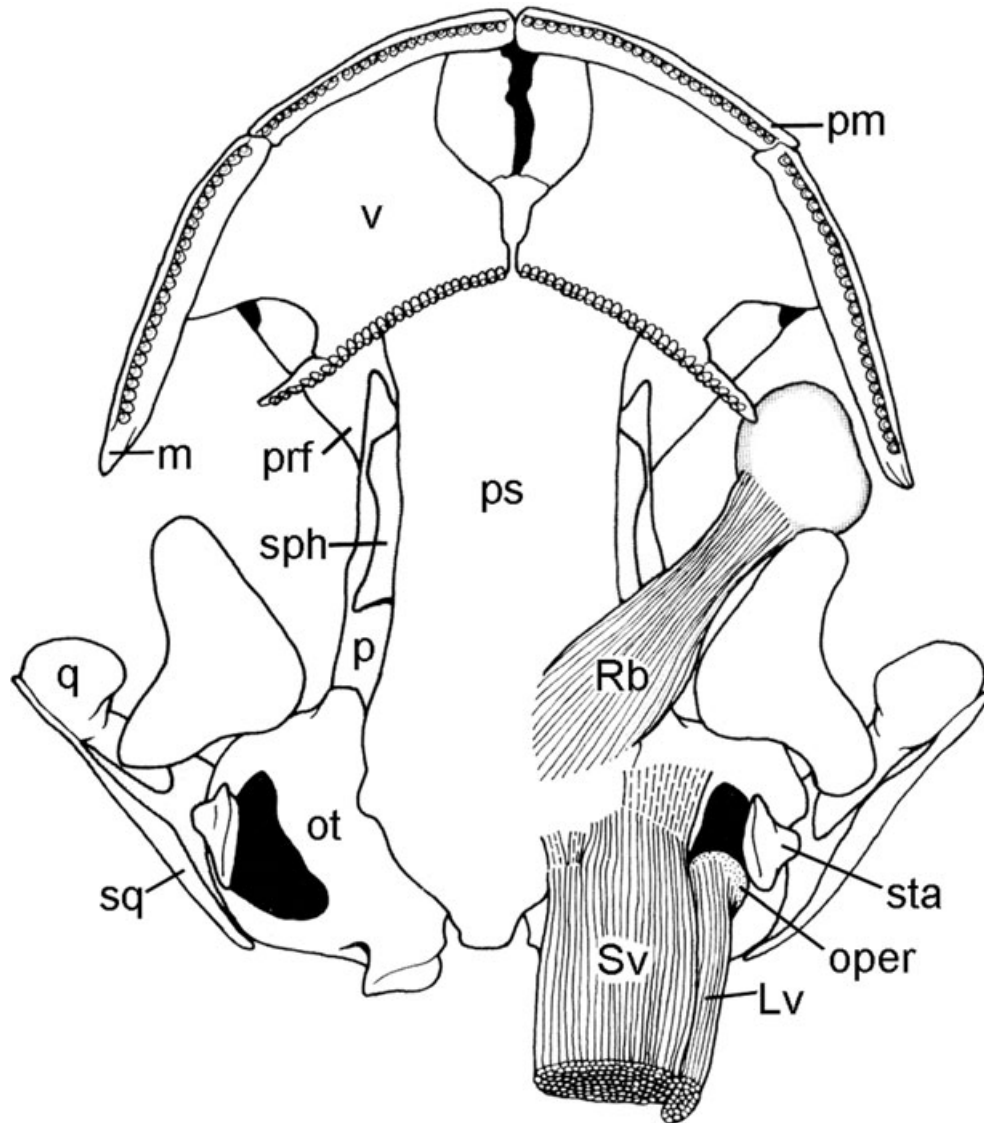
Figure 16. Ventral view of *Ambystoma tigrinum* showing subvertebralis and retractor bulbi musculature. Reproduced from Larsen & Guthrie (1975).

sage of the vertebral artery in most salamanders. There are 16 presacral vertebrae in this specimen.

Most salamanders have a clear separation between the capitular and tubercular rib heads, but this is not the case in cryptobranchids. Hynobiids exhibit both conditions. It is not certain whether coalescence or separation of the rib heads is primitive for salamanders.

Both individually and in terms of their number, the vertebrae of primitive salamanders are clearly distinct from those of both frogs and caecilians. However, all extant members of the three groups are clearly derived from all Palaeozoic labyrinthodonts in having no evidence for more than a single central element,

and from most in having a unipartite atlas with a clearly bicondylar articulation with the skull.

The manner of vertebral development in frogs and salamanders has long been recognized as being distinct from that in amniotes in the absence of clear evidence of resegmentation. Recent research by Wake & Wake (2000) clearly documents resegmentation in caecilians, but they argue that this can be attributed primarily to the much larger number and denser concentration of cells that make up the sclerotome at this early stage in development. They do not feel that this difference is of major taxonomic significance.

Carroll, Kuntz & Albright (1999) suggested that salamanders differ from frogs in the development of
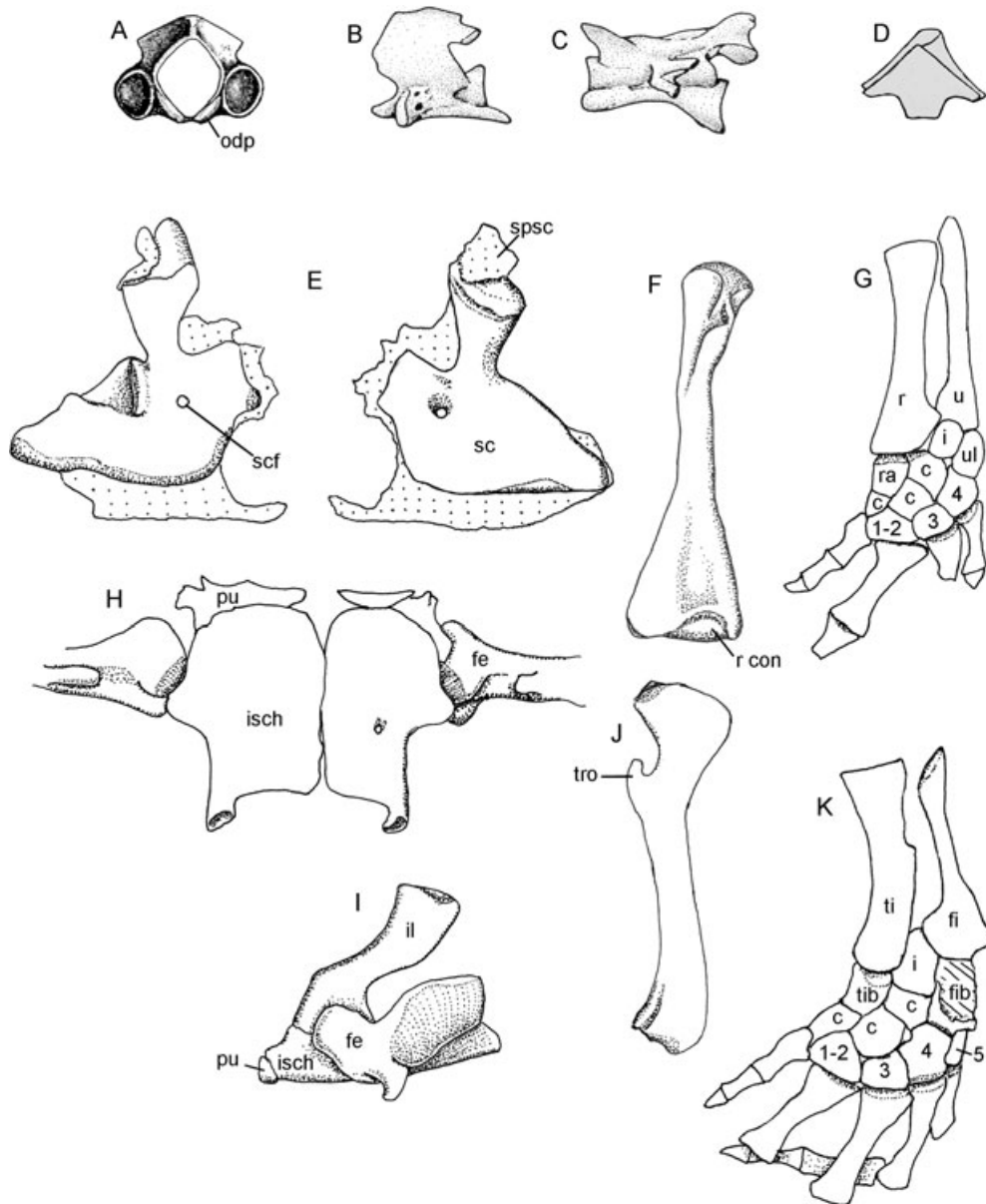
Figure 17. Vertebrae and appendicular skeleton of salamanders. A, anterior view of the atlas of *Salamandra salamandra*. Reproduced from Francis (1934). B, C, lateral views of atlas and seventh trunk vertebra of *Ambystoma opacum*. Reproduced from Duellman & Trueb (1986). Note separate articulating surfaces for articulation with double-headed ribs. D, cartilaginous sternum of *Salamandra salamandra*. Reproduced from Francis (1934). E–K, appendicular elements of *Hynobius nigrescens*, specimen no. 22513 in the Herpetology Collection of the Museum of Comparative Zoology, Harvard. E, lateral and medial views of the fused scapula and coracoid; the dorsal, anterior, and ventral surfaces are extended in cartilage (coarse stippling). F, ventral view of left humerus. G, left lower forelimb in ventral view. H, I, pelvic girdle in ventral and left lateral view, with femur in place. J, right femur in ventral view. K, left lower hindlimb in dorsal view.

their vertebrae by the chondrification of the centra prior the neural arches. In all frogs in which vertebral development has been studied, the arches both chondrify and ossify long before the centra. Neither develop at all in the tail, except for the proximal portion of the developing urostyle. Carroll *et al.* had based their argument on the description of Wake & Lawson (1973) of development in the plethodontid *Eurycea bislineata*, and on an early larval stage in the hynobiid *Salamandrella keyserlingii*. Subsequent research by Boisvert (2002, 2004), based on cleared and stained specimens representing all salamander families, demonstrated that this pattern does apply to most families, but not to all. Of all the specimens examined in

this study and by previous workers, only three species, belonging to two hynobiid genera (*Ranodon tsinpaensis*, *Ranodon sibericus*, and *Hynobius nebulosus*), were found to chondrify and/or ossify their arches before the centra, in a pattern broadly resembling that of anurans. That this was an ancestral pattern for salamanders was strongly supported by the illustration of Gao & Shubin (2003) of a primitive (presumably cryptobranchoid) salamander from the Middle Jurassic of China, in which both the neural and haemal arches clearly ossified well before the centra, and the tail remained notochordal. These recent discoveries provide strong evidence that the most primitive crown-group salamanders had a sequence of vertebral development that is common to frogs and labyrinthodonts (but distinct from that of lepospondyls), and that early ossification of the vertebral centra was a characteristic that evolved within urodeles.

Appendicular skeleton
The limbs and girdles of salamanders (Fig. 17) are broadly similar to those of Palaeozoic amphibians. In comparison to frogs, there are few features that show specialization towards a more derived mode of locomotion than that of Carboniferous tetrapods. The most obvious skeletal difference is the loss of all dermal elements of the pectoral girdle. In most species, much of the scapulocoracoid remains cartilaginous, as does the area of the pubis. A neomorphic endochondral sternum, which articulates with the medial margin of the coracoids (in a manner analogous to the sternum of lizards), forms in the position of the interclavicle in Palaeozoic tetrapods. A series of bones make up the ventromedial portion of the shoulder girdle in frogs that function to absorb the force of impact on the forelimbs from jumping.

The limb bones are more gracile than those of the most primitive and later large labyrinthodonts, but do not differ so greatly from those of smaller labyrinthodonts and small lepospondyls that have retained unreduced limbs (Carroll & Holmes, 2007; Shubin & Wake, 2003). Obvious differences seen among salamanders are the large size and nearly hemispherical configuration of the proximal articulating surfaces of the humerus and femur, and the absence of an entepicondylar foramen of the humerus.

The carpals and tarsal of hynobiids, as represented by *Hyn. nigrescens*, are readily compared with those of particular Palaeozoic amphibians, including the primitive temnospondyl *Balanerpeton* (Milner & Sequeira, 1994) (Fig. 70). As commonly described (Francis, 1934; Duellman & Trueb, 1986), the names given to some of the individual bones suggest significant anatomical differences, but the actual position of the elements relative to one another indicates close homology.

Salamanders have long been thought to be highly distinctive in the presence of a basal commune at the base of the metacarpals and metatarsals I and II, but these elements are clearly homologous with distal carpals and tarsals 1 and 2, as strongly emphasized by Francis (1934). The bones designated prepollex and prehallux in modern salamanders are in the position of the lateral centralia of Palaeozoic tetrapods, and although they differ in the nature of their surface texture (absence of periosteal bone), are almost certainly homologous. The wide range of variation in the patterns of the carpals and tarsals of more derived salamanders is well documented by Shubin & Wake (2003).

In common with temnospondyls and most microsaurs and nectrideans, salamanders have four digits in the manus and five in the pes. What is much more striking is the very high degree of consistency in the phalangeal number within both salamanders and frogs, and between both of these groups and Paleozoic temnospondyls (Table 2). This is surprising, and suggests a high degree of constraint in a portion of the skeleton that is notable for its variability and evolutionary potential in other taxa, such as dinosaurs, birds, and cursorial mammals. One may, however, contrast this variability with the stability in primates, such as ourselves, which retain the same phalangeal count as in some Cretaceous placentals (2,3,3,3,3) and (2,3,3,3,3). The importance of the retention of a primitive character such as the similarity of phalangeal counts in primitive frogs and salamanders and some Palaeozoic tetrapods cannot, of course, be recognized by phylogenetic analysis (which deals only with shared derived characters), except at the point where it can be recognized as a unique shared derived character among a particular group of Palaeozoic tetrapods.

The unusual pattern of limb development in salamanders is discussed in relationship to their ancestry in a subsequent section.

Locomotion
The general pattern of locomotion among salamanders is certainly the most primitive of the three modern amphibian orders, and probably close to that of the conservative Carboniferous tetrapods. O'Reilly *et al.* (2000) point to the similarity of the axial musculature of salamanders and lungfish in contrast to the divergent specializations of frogs and caecilians. Their cladogram shows an unresolved trichotomy of the functional transitions among the three orders. Comparable subdivisions into epaxial, hypaxial, and ventral axial muscles are also recognized in primitive living amniotes (Romer & Parsons, 1977). This general similarity among most tetrapods supports the assumption that the pattern in salamanders is close to that of primitive land vertebrates.

Table 2. Phalangeal counts of frogs, salamanders, and a variety of Palaeozoic tetrapods

	Manus	Pes
Most primitive known temnospondyl		
Balanerpeton woodi (Milner & Sequeira, 1994)	2,2,3,3	2,2,3,4,3
Superfamily Dissorophoidea		
'Branchiosauridae (Nyřany, (pers. observ.)	2,2,3,3	2,2,3,4,3
Amphibamus grandiceps (pers. observ.)	2,2,3,3	2,2,3,4,3
Eoscopus lackardi (Daly, 1994)	–	2,2,3,4,3
Micropholis (Broili & Schröder, 1937)	2,2,3,3	2,2,3,4,3
Micromelerpeton credneri (Boy & Sues, 2000)	2,2,3,3	2,2,3,4,3
Apateon (Royal Ontario Museum, no. 44276)	2,2,3,3	2,2,3,4,3
Apateon pedestris (Boy & Sues, 2000)	2,2,3,2	2,2,3,4,3
Apateon caducus (Boy & Sues, 2000)	2,2,3,2	2,2,3,4,3
Jurassic and Cretaceous salamanders		
Chunerpeton tianyiensis (Gao & Shubin, 2003)	2,2,?,2	2,2,3,4,3
Karaurus sharovi (Ivachnenko, 1978)	2,2,3,2	2,2,3,4,3
Jeholotriton paradoxus (Wang, 2000)	2,2,3,2	2,2,3,3,2
Valdotriton gracilis (Evans & Milner, 1996)	2,2,3,2	2,2,3,4,2
Mesozoic and Tertiary frogs		
Vieraella herbsti (Roček, 2000)	2,2,3,3	–
Notobatrachus degiustoi (Roček, 2000)	2,3,3,3	2,2,3,4,3
Notobatrachus degiustoi (Sanchiz, 1998)	2,2,3,3	2,2,3,4,3
Eodiscoglossus santonjae (Roček, 2000)	2,2,3,3	2,2,3,4,3
Palaeobatrachus grandipes (Sanchiz, 1998)	2,2,3,3	2,2,3,4,3
The albanerpetontid *Celtedens* (McGowan, 2002)	2,3,3,2	2,3,4,4,3
'Lepospondyls' (Carroll *et al.*, 1998)		
Microsauria		
Tuditanus	2,3,4,3	2,3,4,5,4
Batropetes	2,3,3,2	2,3,3,4,1
Microbrachis	2,3,3	2,3,4,4,3
Hyloplesion	2,3,3	2,3,4,5,?
Odonterpeton	2,4,3	–
Lysorophia and Nectridea		
Brachydectes	3,?,3,2	2,3,3,3,2
Urocordylus	2,3,?,?,2	2,3,4,4,2
Ptyonius	2,3,4,3	2,3,4,3
Sauropleura scalaris	2,3,4,3	2,3,4,4,2
Keraterpeton	2,3,3,3	2,3,3,3,3
Diceratosaurus	2,3,4,3	2,3,3,?,3
Other early tetrapods (Carroll & Holmes, 2006)		
Embolomeres	2,3,4,5,4	2,3,4,5,5
Seymouria	2,3,4,5,3	2,3,4,5,4
Limnoscelis	2,3,4,5,3	2,3,4,5,4
Early amniotes	2,3,4,5,3	2,3,4,5,3

Salamanders presumably resemble the pattern of the earliest tetrapods in utilizing a basically undulatory motion of the vertebral column for both aquatic and terrestrial locomotion. Salamanders can walk along the bottom, but swimming is similar to that of elongate fish. Travelling waves are propagated posteriorly along the body, increasing in amplitude towards the tail. The limbs are held against the trunk. On land, salamanders may move by lateral undulation, walk at slow speeds with at least three feet in contact with the ground, or walk at a trot, with only two feet providing simultaneous support (right front foot and left hind foot alternating with left front foot and right hind foot). Movement of the limbs is accompanied by

propagation of standing waves along the trunk. The length of each step is extended as the girdle of the pro-tracted limb is rotated forwards by movement of the trunk. Speed is limited by postural collapse if the animal attempts to trot too rapidly. The problem of coordination of their limbs by salamanders may be attributed to the fact that they lack the encapsulated stretch receptors of the appendicular muscles that characterize frogs and amniotes (Bone, Ridge & Ryan, 1976).

Two major subdivisions of the axial musculature are evident: the epaxial muscles, dorsal to the horizontal septum, and the more ventral hypaxial muscles. Three epaxial muscles are recognized: the dorsalis trunci, which inserts on the transverse myosepta and bodies of the vertebrae; interspinalis, which originate and insert on the spinous processes of the vertebrae; and the intertransversarii, which originates and inserts on the transverse processes. The hypaxial muscles include a dorsal group, the subvertebralis pars ventralis, which runs between the ventral surfaces of adjacent vertebrae, and the subvertebralis pars transversalis, which runs between the ribs. The fibres of the muscles so far named all run essentially longitudinally. There are also two to four sheets of hypaxial muscles that make up the body wall. The obliquus externus (which may be divided into the obliquus externus superficialis and obliquus externus profundus) has fibres running craniodorsally to caudoventrally. More medial is the obliquus internus and commonly a separate transversalis, in which the muscle fibres run from cranioventral to caudodorsal. A further muscle, the rectus abdominus, runs along the ventral midline.

Both epaxial and hypaxial muscles bend the trunk laterally in swimming and undulatory movement on land. In quadrupedal terrestrial locomotion, the hypaxial muscles also serve to resist torsional forces. The inner and outer layers of the lateral hypaxial muscles are functionally divided into two units as a result of their differing fibre orientation. As a result, one pair resists clockwise torsion, and the other resists counter-clockwise torsion. With each stride, the outer layer on one side is activated at the same time as the inner muscles on the opposite side.

The basic arrangement of the axial muscles in salamanders is logically ancestral to that of frogs and caecilians, but their function during locomotion has been drastically altered.

Reproduction and larvae
The mode of reproduction among primitive salamanders is certainly plesiomorphic among the lissamphibians, with an absence of any copulatory organ, and external fertilization in cryptobranchoids and probably sirenids. The laying of eggs in the water, with obligatorily aquatic hatchlings, is almost certainly primitive for all tetrapods.

The larvae of salamanders hatch from eggs less than 10 mm in diameter. The forelimbs appear within the egg in slowly developing species that breed in still water, but those that live in streams show both forelimbs and hindlimbs with well-formed digits at hatching. Limbs are typically held against the body, and swimming results from lateral undulation of the trunk and tail. Conspicuous external gills occur in all species (Fig. 4A). Suck-and-gape feeding begins soon after hatching (Hanken, 1999).

Unfortunately, no fossils are known of larval stages of the most primitive described tetrapods. However, very small juveniles are known of the tristichopterid *Eusthenopteron* as part of a very extensive growth series leading up to adults (Cote *et al.*, 2002). The juveniles lack any trace of external gills, and even individuals as small as 5 cm in total length have the same body proportions and relative position of the paired fins as in adults. There is no period that can be identified as metamorphosis as that term is defined for both fish and amphibians (Hall & Wake, 1999). It seems probable that external gills would not have been necessary in the well-aerated coastal waters in which these fish developed (Schultze & Cloutier, 1996).

The first evidence of juvenile labyrinthodonts is from the Lower Carboniferous (Viséan) locality of East Kirkton, in which specimens resembling the young of later temnospondyls and anthracosaurs have been described (Clack, 1994; Milner & Sequeira, 1994). Thousands of gilled larvae of both of these groups are known from the Upper Carboniferous and Lower Permian (Boy & Sues, 2000). Like most amphibians from the Carboniferous, many of these labyrinthodonts are known from isolated, shallow-water deposits, such as oxbow lakes, which were filled with rotting vegetation (Behrensmeyer *et al.*, 1992). These water bodies, at a high altitude but in a subtropical region, almost certainly had a reduced oxygen content that may have made external gills obligate in labyrinthodonts, most of which grew to large size via a protracted period of larval growth (Schoch & Milner, 2004). Tiny juveniles of lepospondyls are common in the same deposits, but show no evidence of external gills. They may not have needed external gills because of their very small body size, even as adults, and their very rapid development, indicated by a high degree of ossification of the vertebrae even in the smallest known specimens with the individual centra less than 1 mm in diameter (Carroll *et al.*, 1998). Of the two patterns of development observed among Carboniferous and Permian amphibians, only that of labyrinthodonts corresponds with that of extant salamanders.

ANURANS

Although details of skeletal anatomy and the manner of terrestrial feeding among living salamanders are considerably altered from those known or presumed to have characterized Palaeozoic amphibians, their general anatomy, physiology, and life history can be readily accounted for by progressive evolution from those of conservative early tetrapods. In contrast, anurans, from as far back as the Lower Jurassic, had evolved a unique mode of saltatory terrestrial locomotion that has no parallel among any Palaeozoic taxa. Even more striking is the evolution of an extremely highly modified larva, the tadpole, specialized for suspension feeding on plant material. Both of these attributes are accompanied by a host of changes in the skeletal anatomy and behaviour relative to those known or assumed to have been present in any plausible Palaeozoic predecessor. As a result of these radical modifications, it is difficult to recognize the few possible synapomorphies that may link anurans to either basal urodeles or to any recognized lineages among Palaeozoic tetrapods.

Anurans are the most numerous, globally widespread, and well known of all modern amphibian orders, with nearly 5000 species in 24 families (Duellman & Trueb, 1986; Pough *et al.*, 2004). However, in strong contrast to the numerous evolutionary changes relative to any known Palaeozoic lineages, the general body form and underlying skeletal anatomy of anurans has been the most conservative of all the lissamphibians throughout their evolutionary history. This is especially evident in the postcranial skeleton.

The fossil record of anurans extends back to the Lower Jurassic (Shubin & Jenkins, 1995; Sanchiz, 1998; Roček, 2000; Gao & Wang, 2001), and indicates the early establishment of most of the conspicuous skeletal features seen in extant species, while documenting some primitive character states that are useful in determining affinities with more primitive salientians and Palaeozoic tetrapods. However, a detailed analysis of the soft anatomy and behaviour of modern anurans is also necessary to establish the manner of their evolutionary divergence from salamanders and caecilians.

Figure 18. Phylogeny of anuran families based on morphological and molecular characters. Reproduced from Pough *et al.* (2004). The characters of each node are indicated in the original.

Relationships

The large-scale pattern of anuran relationships is fairly well established (Sanchiz, 1998; Gao & Wang, 2001; Pough *et al.*, 2004) (Fig. 18). Approximately 20 advanced families, including ranoids, bufonoids, hylids, and leptodactylids, are placed in the Neobatrachia. No fossils of neobatrachians are known prior to the Upper Cretaceous, when leptodactylids appear in South America. Fossils of other families from t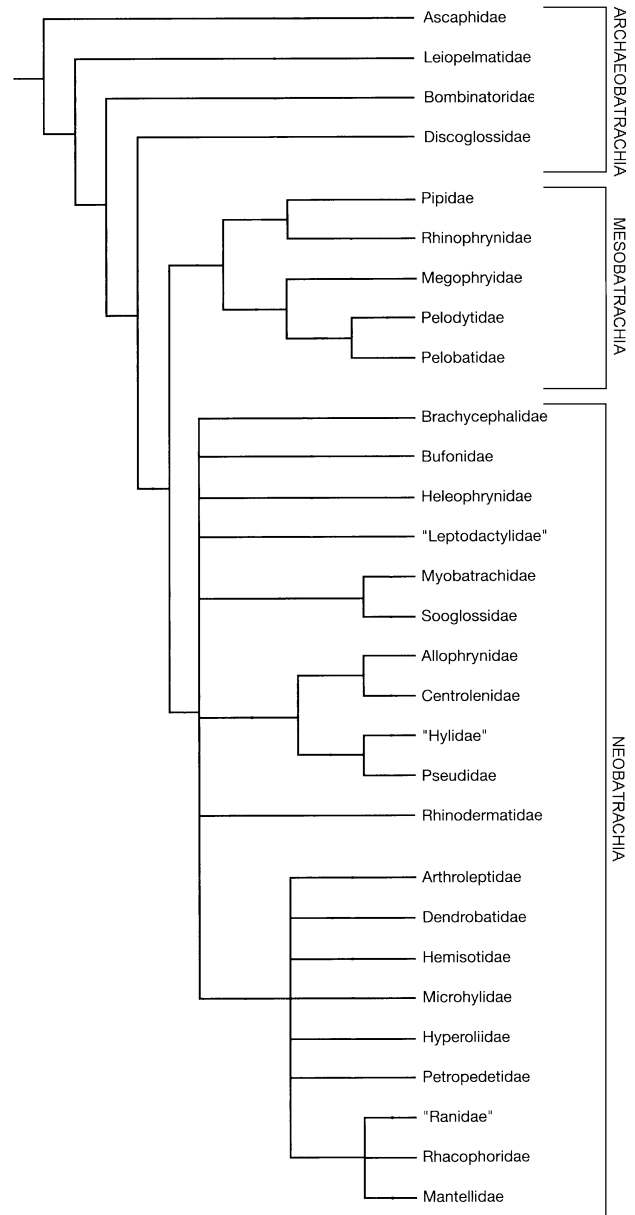he early Tertiary indicate that the primary radiation of neobatrachians had occurred by that time. A more primitive assemblage of extant families, designated the Mesobatrachia by Laurent (1979), composed of the Pipidae, Rhinophrynidae, Megophryidae, Pelodytidae, and Pelobatidae, may also have a common ancestry, but within the Late Jurassic or Early Cretaceous, to judge by the diversity of pipid-like genera in the Lower Cretaceous.

The most primitive living anurans, the Ascaphidae, Leiopelmatidae, Bombinatoridae, and Discoglossidae

(the latter two known from the Middle Jurassic), are placed as a series of successively more primitive sister taxa of all other families. *Ascaphus*, from the north-western USA and adjacent Canada, and *Leiopelma*, with four species from New Zealand, are unquestionably the most primitive of modern frogs on the basis of the retention of nine notochordal, amphicoelous, presacral vertebrae and free ribs (Green & Cannatella, 1993). This taxonomic position is supported by molecular data (Ford & Cannatella, 1993; Hillis *et al.*, 1993). Unfortunately, the fossil record of these families is restricted to disarticulated remains of three subfossil species of *Leiopelma* from the Pleistocene (Worthy, 1987). Ascaphids and leipelmatids were long categorized as sister taxa of one another, but Green & Cannatella (1993) were unable to find any derived characters that were uniquely shared by the two living genera.

Leiopelma and *Ascaphus* provide important information regarding primitive patterns of skeletal development, soft anatomy, and behaviour that are not available from fossil evidence, but each has some characteristics that were almost certainly not present in the immediate ancestors of crown anurans. Hence, neither *Leiopelma* nor *Ascaphus* can be relied upon to serve as such close models for the ancestral pattern for anurans, as was the case for hynobiids among the salamanders. Specific features that these modern genera possess that are unlikely to have been present in the common ancestors of other anuran families are as follows.

Ascaphus is unique in having a copulatory structure (or intromittent organ), formed from a highly vascularized extension of the cloaca that gives the appearance of a tail. It is supported by cartilaginous rods, the postpubes, and can be moved by muscles homologous with those that move the tail in the tadpole stage (Duellman & Trueb, 1986). *Ascaphus* also has a flat prepubis, anterior to the ischium. *Leiopelma* and some pipids also have a prepubic element, which is referred to as an epipubis, but is probably homologous with the structure in *Ascaphus*. The evolution of means for internal fertilization in *Ascaphus* is attributed to its specialization for life in fast-running mountain streams, which may also have led to selection for its well-developed sucker for attachment to the substrate. Life in this environment may also account for the loss of all features of the middle ear that are common to most other frogs, including genera from the Jurassic. Loss of middle ear structures also occurs among other small anurans.

Surprisingly, none of the larvae of the four extant species of *Leiopelma* are active feeders, and they lack many of the structures of the mouth and pharynx that are associated with suspension feeding in other anurans. This led Stephenson (1955) to suggest that the immediate ancestors of anurans did not possess a typical tadpole, but that the highly derived aspects of this type of larva evolved within the order. This hypothesis has been recently investigated by Bell & Wassersug (2003). Two distinct lifestyles and types of larvae can be recognized among the four species. *Leiopelma archeyi*, *Leiopelma hamiltoni*, and *Leiopelma pakeka* are the more terrestrial, living in forests and open ridges. They lay their eggs in moist depressions on land, or under rocks or vegetation, where they are protected by the adult males. The young hatch out with a larval body form, but the forelimbs are free of the operculum and face anteriorly. The limbs are used to clamber onto the back of the male, where they remain attached until they mature. The larvae neither feed nor swim. This pattern of life history is referred to as direct development, but might better be described as marked abbreviation of the larval period, during which the young does not feed but depends on the resources of the yolk sac. In contrast, *Leiopelma hochstetteri* lives alongside creeks and damp water courses, and the eggs are laid in wet seeps. The hatchlings are mobile and adept swimmers, relying on the tail. The forelimbs are enclosed in the operculum and the eyes are very poorly developed. None of these species feeds in the water, but Bell and Wassersug demonstrated that *Leiopelma hochstetteri* retains many relicts of the feeding system of typical tadpoles. This was not the case for the more terrestrial species. Most significantly, during early development, *Leiopelma hochstetteri* shows the formation of a greatly elongate, spiral-shaped digestive tube that occurs in typically herbivorous tadpoles. The number of loops increases in early stages, and then decreases as they mature. In contrast to the more terrestrial species, dye injected into the mouth during a restricted period of development passes out through the gill slits, suggesting the retention of the water-circulating system common to most tadpoles.

Stephenson (1955) argued that the more terrestrial species represent the primitive condition for the genus, but it is difficult to accept that the condition illustrated by *Leiopelma hochstetteri* could represent a transition towards the evolution of a typical anuran tadpole. Rather, it seems much more plausible that evolution proceeded from a form such as *Leiopelma hochstetteri* towards the condition seen in the more terrestrial genera, and thus possession of a highly evolved tadpole was a primitive heritage of anurans. *Leiopelma* is also distinguished by a series of endochondral structures embedded in the ventral body musculature, termed inscriptional ribs, that are unique among anurans, but may be serially homologous with the epipubis (Duellman & Trueb, 1986).

In both *Ascaphus* and *Leiopelma*, the jaw articulation is well anterior to the occipital condyles, which makes the skull resemble those of salamanders. How-

ever, this may be associated with the low degree of ossification and the small size of these genera as adults (~50 mm, snout–vent length), both of which suggest that they have retained characteristics of juvenile individuals, in which the quadrate is anterior in position. The absence of the quadratojugal in these genera may also be attributed to paedomorphosis, for this is among the last bones to ossify, at or beyond the end of metamorphosis (Roček, 2003). Among Jurassic frogs, *Eodiscoglossus* and *Notobatrachus* have the jaw articulation at the level of the occiput, but it lies in front of the occipital condyles in *Vieraella* (Báez & Basso, 1996).

Fortunately, knowledge of fossil anurans from the Lower, Middle, and Upper Jurassic (Shubin & Jenkins, 1995; Báez & Basso, 1996; Sanchiz, 1998; Roček, 2000; Gao & Wang, 2001) provide a consistent model for nearly all of the probable skeletal features of the common ancestors of subsequent crown-group anurans, and so serve as the most informative guide to their probable ancestors.

If leiopelmatids and ascaphids diverged from all other extant families by the Early Jurassic, the lineages including *Leiopelma* and *Ascaphus* had more than 180 million years to evolve a relatively small number of derived characters. Their basic conservatism demonstrates that they, like all other anurans, have maintained a basically similar skeletal anatomy, implying a very similar way of life, for a period nearly as long as the entire history of therian mammals.

Cranial anatomy

The skulls of most anurans, fossil and living, retain a common configuration (Fig. 6). The skull roof is dominated by fused frontoparietal bones that form a rigid longitudinal support between the very large orbitotemporal openings. The skull is generally much wider than deep, and has a conspicuous posterior embayment of the squamosal for support of the tympanic annulus (Trueb, 1993). The jaw articulation is commonly posterior to the occipital condyle, and there is a continuous bony margin to the cheek. In common with salamanders, the bones forming the back of the skull table in Palaeozoic amphibians (Fig. 1A), the postparietals, tabulars, supratemporal, and intertemporal, as well as the jugal, postorbital, and postfrontal, have been lost, but so have the prefrontal and lacrimal. However, the quadratojugal is typically retained and serves to join and stabilize the maxilla and jaw suspension.

The only other cheek bone that is retained is the squamosal. It is joined to the otic capsule and/or frontoparietal dorsally, and typically has an anteroventrally extending zygomatic process that lies lateral to the adductor jaw musculature. The ventral portion of the squamosal is firmly sutured to the quadrate ramus of the pterygoid to form the posterodorsal margin of the adductor chamber and separate it from the middle ear cavity.

The interpterygoid vacuities are extremely large in anurans, with the maxilla forming only a narrow lateral margin of the palate. The large size of these openings serves to accommodate the eyes, which are retracted through the palate during swallowing (Schwenk, 2000: 54). Trueb (1993) argued that the bone that occupies the position of the palatine in neobatrachian frogs is actually a neomorph, which may have arisen as a process from the maxilla. It seems to be absent in mesobatrachians (Wiens, 1989), and it not evident as a separate area of ossification in *Ascaphus*. In *Leiopelma*, it fuses with the vomer (Roček, 2003). A palatine is recognized in the Late Jurassic/Early Cretaceous frog *Neusibatrachus* (now considered a synonym of *Eodiscoglossus*) (Seiffert, 1972). There is no evidence for the presence or absence of a palatine in *Vieraella* (Báez & Basso, 1996) or *Prosalirus* (Jenkins & Shubin, 1998). However, a bone in the position of the palatine is present in *Triadobatrachus*, a salientian from the Lower Triassic (Roček & Rage, 2000). Where present, the palatine appears as a transverse bar, lying posterior to the vomers. Anurans from *Ascaphus* to neobatrachians show variable expression of denticles on the vomers, frequently arranged in a transverse row. The ectopterygoid is never expressed (Trueb, 1993).

The parasphenoid forms a strong ventral support for the braincase. In most anurans, it is firmly attached to the broadly overlapping medial ramus of the pterygoid, rather than forming a synovial joint at the base of the braincase, as in primitive salamanders. Iordansky (1990) has argued for a degree of kinesis at this joint in frogs, but it is difficult to understand how any measurable mediolateral movement of the cheek relative to the braincase could be accommodated without the stapes being forced through the tympanum. As in salamanders, the pterygoid commonly has a distinct posterior ramus that extends around the medial surface of the quadrate. In contrast to what is found salamanders, the anterior ramus of the pterygoid has a long overlapping attachment with the maxilla that serves to stabilize the jaw suspension.

As in salamanders, the posterior portion of the braincase develops from two separate areas of ossification, a posterior exoccipital, incorporating part of the opisthotic, and an anterior prootic, which remain separate from one another into the adult stage in primitive genera. Together, the latter bones form a conspicuous otic capsule that extends laterally to support the squamosal. The more anterior lateral walls of the braincase remain as thin, insubstantial elements in many species, but some, especially burrowing frogs,

may form a massive sphenethmoid. The sphenethmoid, as in some caecilians, frequently extends dorsally between the anterior extremities of the frontoparietals to occupy an area of the skull roof.

Sequence of cranial ossification

It is difficult to compare the sequence of ossification between larval and metamorphosed anurans with that of either salamanders or caecilians, because of the extremely highly derived tadpole stage, in which both the structure and function of the skull and hyoid apparatus are unique.

The sequence of ossification of the dermal bones of the salamander skull begins at an early stage in larval development, and continues into metamorphosis. The first bones to appear are the tooth-bearing elements, which are widely separated from one another. This configuration results in a very flexible skull in the smallest animals, allowing them to expand their buccal cavity for suck-and-gap feeding on large prey. The skull of the terrestrial adults is much more rigid, enabling them to apply a strong grip to struggling prey.

In contrast, very little of the anuran skull ossifies prior to metamorphosis, as the larval feeding apparatus consists almost entirely of cartilaginous elements. The first bones to ossify in the mesobatrachian frog *Spea bombifrons* (stage 36) are the frontoparietal, exoccipitals, and parasphenoid, followed by small areas of the prootic, premaxilla, maxilla, septomaxilla, and nasals (Wiens, 1989) (Fig. 19). In the direct-developing frog, *Eleutherodactylus coqui* (Hanken *et al.*, 1992), the sequence is very different, starting with the angulosplenial, squamosal, parasphenoid, and premaxilla, and continuing with the protoparietal, pterygoid, dentary, maxilla, and exoccipital. However, neither of these sequences is likely to be close to the condition in the Palaeozoic ancestor of anurans, which presumably did not have a highly derived larval stage. This question will be further investigated in the section 'Ancestry of anurans'.

Middle and inner ear of anurans

Frogs are unique among living amphibians in their capacity for reception of high-frequency airborne vibrations. Nearly all anuran species depend upon auditory communication for species recognition associated with reproduction (Duellman & Trueb, 1986; Fritzsch *et al.*, 1988; Webster, Ray & Popper, 1992; Pough *et al.*, 2004). Although low-frequency airborne vibrations, transmitted through the operculum–opercularis system, can be detected by the sensory cells of the amphibian papilla, high-frequency vibrations can only be transmitted through the impedance-matching system of the middle ear (Fig. 20). Its most conspicuous expression is the large tympanic membrane supported by the cartilaginous tympanic annulus that lies within the posterior embayment of the squamosal. The tympanum forms the external surface of the air-filled middle ear cavity, which is in the shape of a cone, focused on the fenestra ovalis.

Two elements transmit the vibrations of the tympanic membrane into the inner ear: the elongate bony stapes, or columella, whose footplate rests within the fenestra ovalis, and a complex, cartilaginous extrastapes partially embedded in the membrane of the tympanum that serves as a lever to magnify the force of the stapes. The ventral edge of the footplate of the stapes fits against the margin of the fenestra ovalis, where it forms a line of articulation that acts as a hinge (Bolt & Lombard, 1985; Lombard & Bolt, 1988). The essentially horizontal force of the airborne sound waves impinges on the middle of the tympanum, where it is augmented by the extra collumella and transmitted to the obliquely oriented stapes, whose footplate directs the force against the membrane covering the fenestra ovalis. The tympanic membrane is much larger than the fenestra ovalis, and this difference results in matching of the acoustic impedance of air to the higher impedance of the fluid in the inner ear (Duellman & Trueb, 1986).

The rocking motion of the footplate of the stapes on the margin of the fenestra oval is unique to frogs among extant terrestrial vertebrates. In contrast, the footplate of the stapes of modern amniotes acts as a piston, whose force is delivered at right angles to the plane of the fenestra ovalis. However, the particular relationship between the surface of articulation of the footplate of the stapes and the ventral margin of the fenestra ovalis is matched very closely by one group of Palaeozoic amphibians, the temnospondyls (Robinson, 2005).

Like salamanders, frogs have an operculum–opercularis systems, in which the opercularis portion of the levator scapulae extends from the operculum to the suprascapula. Contraction of the opercularis immobilizes the operculum, but frees the columella to vibrate. Contraction of the columellaris has the reverse effect, allowing frogs to control the relative inputs of the two auditory pathways. Like the opercularis of salamanders, the columellaris of frogs is a derivative of the levator scapulae (Duellman & Trueb, 1986).

Vibrations from the two auditory pathways are received by two auditory organs within the inner ear that are sensitive to different frequencies (Fig. 20). Frequencies below 1000 Hz from the operculum–opercularis system are received by the papilla amphibiorum, and the papilla basilaris responds to frequencies above 1000 Hz transmitted by the columella. The importance of having two systems is illus-
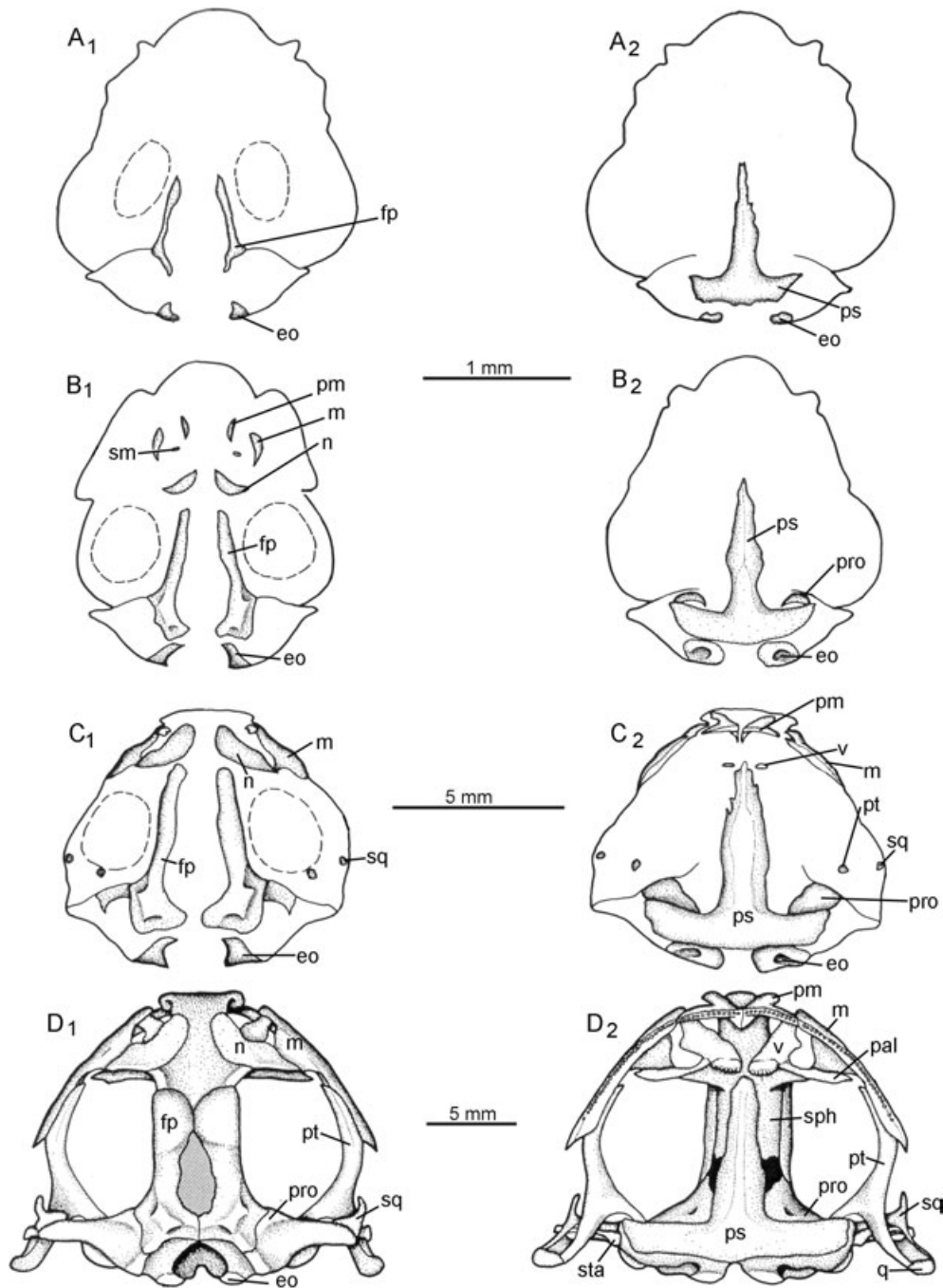
Figure 19. Sequence of ossification of the cranial bones of the pelobatid frog *Spea bombifrons*. Reproduced from Wiens (1989).

trated by their joint use in call reception in bull frogs. Their call notes are transmitted at widely spaced frequencies, with hair cells of the amphibian papilla being activated by frequencies in the area of 200 Hz and by the basilar papilla for those around 1500 Hz (Wilczynski & Ryan, 1988).

The presence of both a stapes and an operculum–opercularis system in frogs and salamanders, and the presence of both basilar and amphibian papillae in primitive salamanders, strongly support a common ancestry of these two groups. However, the presence of middle ear structures capable of receiving high-frequency vibrations (from 1000 Hz to 5000 Hz) throughout the crown-group anuras, relative to the absence of the middle ear in salamanders, suggests a long period of divergence. Anurans are the only living amphibians
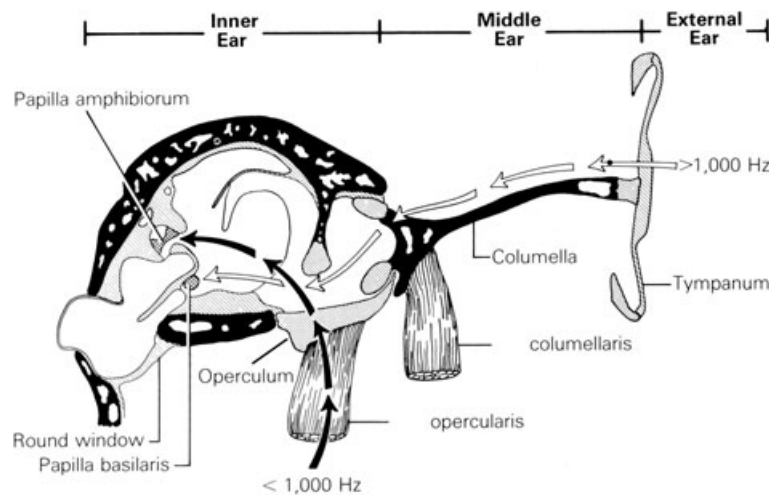
Figure 20. Diagram of the anuran auditory system. Reproduced from Duellman & Trueb (1986).

that engage in acoustic communication, but evidence from the fossil record suggests that this ability may be traced to the Lower Carboniferous (see 'Ancestry of anurans').

The large size and particular position of the middle ear cavity in anurans must have a significant influence on the pattern of the adjacent jaw adductors. In contrast to salamanders, most frogs have a continuous bony margin of the temporal region from the maxilla back to the jaw suspension, typically including the quadratojugal. This greatly limits the lateral expansion of the adductor muscles, especially the adductor mandibulae externus, as compared with the condition in salamanders (Fig. 8). Where it is present, as in *Rana*, its origin is restricted to the posteriorly sloping lateral surface of the squamosal and adjacent medial surface of the tympanic annulus. In contrast, this muscle is much larger in salamanders, and originates along much of the lateral surface of the vertically oriented squamosal. In addition, anterior elaboration of the jaw muscles is restricted by the large size of the orbits. Generally speaking, frogs have a small mass of adductor jaw musculature, located close to the jaw joint, which provides a wide gap but little power relative to that of the large mass of muscles and their more anterior extension in salamanders.

Lower jaw
The lower jaws of adult frogs show a further reduction in the number of dermal bones beyond that seen in salamanders, with the retention of only two separate ossification centres – the large dentary, which is edentulous (except in the hylid *Gastrotheca guentheri*), and the angulosplenial (Trueb, 1993). In addition, there are two areas of ossification of Meckel's cartilage, the posterior articular and the mentomeckelian bones,

which lie on either side of the symphysis (Fig. 6). The latter are known as early as *Vierella* from the Lower/Middle Jurassic boundary (Báez & Basso, 1996).

Structure and function of the hyoid apparatus in adult frogs
In describing the hyoid apparatus in primitive salamanders, the pattern seen in the larvae could be readily traced to that of the adults, making use of the same general structures, modified for use out of the water. Metamorphosis in anurans is much more drastic, involving a nearly total reorganization of the entire body. In particular, evolution of the larval feeding apparatus is so divergent that it bears almost no resemblance to that seen in the adult frog. For this reason, the larval feeding apparatus will be discussed with other aspects of the highly derived tadpole larvae.

The hyoid apparatus of adult anurans (Fig. 10) is also the most highly derived of any lissamphibians (Duellman & Trueb, 1986). As in salamanders, it is involved in feeding and respiration, but it also supports the larynx and so has an important role in vocalization. Rather than being made up of a number of separate elements, the hyoid of adult anurans consists primarily of a large, median cartilaginous plate that is attached to the ventral surface of the otic capsule by paired, slender, recurved processes termed hyale that extend from the anterolateral margins of the plate.

Primitively (as seen in *Leiopelma*), there are three bony elements, a Y-shaped parahyoid bone near the middle of the plate, and two posteromedial processes. Although the cartilage is unlikely to fossilize, the bony elements have been described in a number of Mesozoic fossils. These include *Notobatrachus* (Báez & Basso, 1996) from the boundary of the Middle and Upper
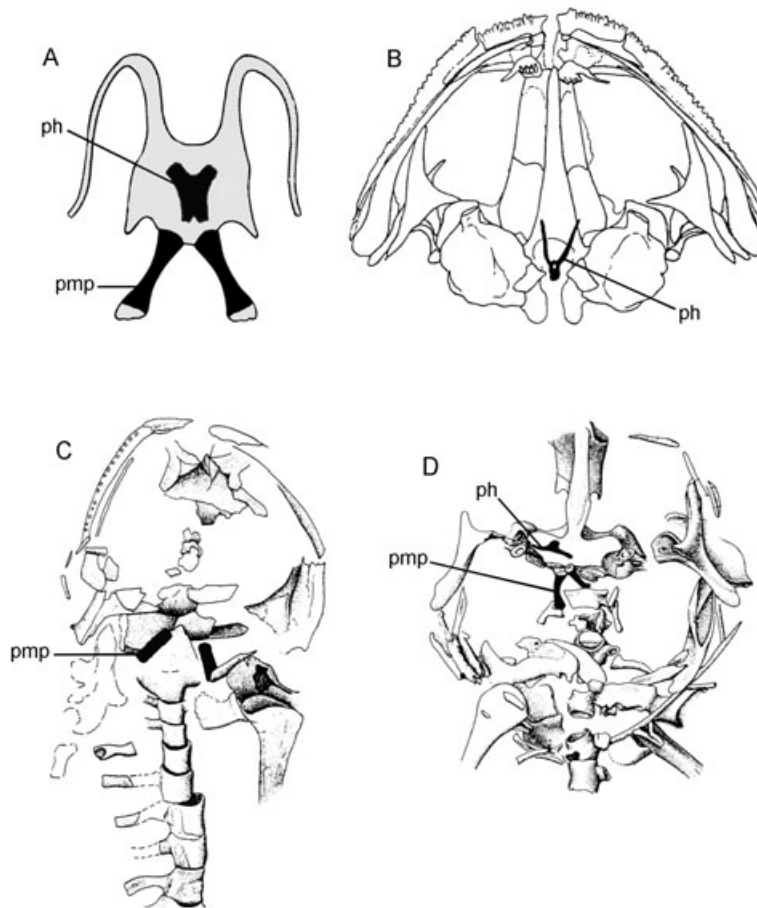
Figure 21. Evolution of the anuran hyoid over 245 million years. A, the primitive living frog *Leiopelma* (Duellman & Trueb, 1986). B, the Lower Cretaceous *Eodiscoglossus*. Reproduced from Roček (2000). C, the Lower Jurassic *Vieraella*. Reproduced from Báez & Basso (1996). D, *Triadobatrachus*, from the Lower Triassic. Reproduced from Roček & Rage (2000).

Jurassic, in which there are large, anteromedially expanded posteromedial processes, and a thick, crescent-shaped parahyoid. A V-shaped parahyoid, closely resembling that of the primitive living genera *Alytes*, *Pelodytes*, *Ascaphus*, *Discoglossus*, *Bombina*, *Pelobates*, *Rhinophrynus*, and *Xenopus*, is also known in *Eodiscoglossus* [illustrated by Roček (2000) as *Neusibatrachus*] from the Jurassic/Cretaceous boundary (Fig. 21B). The posteromedial processes of *Vieraella*, from the Lower/Middle Jurassic boundary, were described by Báez & Basso (1996), but they did not recognize a parahyoid.

It is of particular importance that both a Y-shaped parahyoid and slender, elongate posteromedial processes were illustrated by Roček & Rage (2000) in *Triadobatrachus*, a salientian from the Lower Triassic (Fig. 21D). The great similarity in position and configuration of the parahyoid and posteromedial processes between primitive living frogs and *Triadobatrachus* suggests the similar appearance of the cartilaginous portion of the hyoid plate as well. Certainly, the nature of the posteromedial processes indicates a comparable manner of support for the larynx. A similar mode of attachment of the tongue and the mechanism of the buccal pump, of which the hyoid plate is the most important element, may also be hypothesized.

If the structure and function of the hyoid apparatus at metamorphosis were similarly derived relative to those of the larvae, the configuration of the bony elements of the adult hyoid may suggest that *Triadobatrachus* had a larval stage that fed and respired like those of modern tadpoles. If so, the major changes in larval feeding and respiration may have evolved prior to the elaboration of the skeletal structures responsible for jumping in crown-group frogs (Jenkins & Shubin, 1998).

In modern frogs, the adult hyoid apparatus lies in the floor of the mouth and serves as the site of insertion for muscles associated with its movement as well as the origins of the hyoglossus and genioglossus mus-
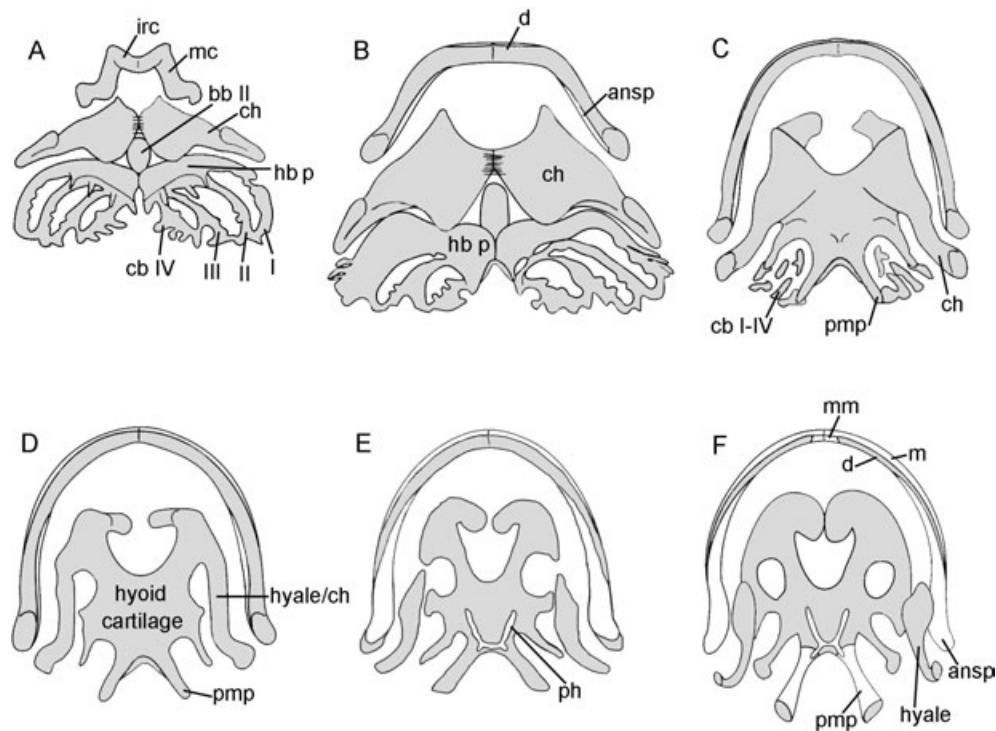
Figure 22. Changes in the hyobranchial apparatus during metamorphosis in the primitive living frog *Pelodytes*. Reproduced from Cannatella (1999).

cles that constitute the main body of the tongue. The primitive role of the adult anuran hyoid was probably terrestrial respiration, in which its function, if not the structure, resembled the general pattern of primitive salamanders. The sternohyoid (rectus cervicus) muscle, as in salamanders, attaches to the posterior margin of the hyoid plate, serving to retract and lower the hyoid, thus expanding the buccal cavity and lowering the pressure in order to draw air in through the nostrils. The geniohyoideus, primitively a single muscle, as in salamanders, but later divided into medial and lateral portions, originates from the jaw synthesis and attaches to the anterior surface of the hyoid, by which it pulls it anteriorly and dorsally. Also as in salamanders, the intermandibularis, located between the lower jaws, elevates the hyoid, thus reducing the volume of the buccal cavity and driving the air into the lungs. Exhalation in both frogs and salamanders occurs through rebound of the elastic tissue surrounding the lungs and the musculature of the body wall.

Frogs differ, however, in having a unique set of muscles, the omohyoideus and the petrohyoideus, that attach to the hyoid plate and the posteromedial processes (Figs 14, 23). The petrohyoideus muscles have a common origin at the base of the quadrate. Two insert at the extremities of the posteromedial process of the hyoid, and so can alter the orientation and tension on

the larynx. The omohyoideus muscle originates on the ventral margin of the scapula and inserts on the lateral edge of the hyoid plate, and moves it dorsally and posteriorly. The omohyoideus cannot be compared to any muscle in salamanders, but the petrohyoideus is derived from the branchial arch musculature, although its exact homology cannot be established (Duellman & Trueb, 1986).

The general appearance of the adult hyobranchial skeleton is similar in a wide range of modern anurans (Duellman & Trueb, 1986: figs 13–21), but provides little basis for comparison with the configuration in the larvae. However, developmental sequences from one of the most primitive living frogs, *Leiopelma archeyi* (Stephenson, 1955), the mesobatrachian *Pelodytes* (Cannatella, 1999) (Fig. 22), and *Rana* (deBeer, 1985: plate 77) show how this transformation occurs. The element termed hyale in the adult is unquestionably derived from the ceratohyal (deBeer, 1985). The posteromedial process develops more or less in the position of ceratobranchial 4, but does not replace it directly in development. During the course of both evolution and ontogeny, the function of the hyobranchial apparatus of anurans changes from acting to support the gills between open gill slits to supporting the larynx and the front of the trachea and serving for attachment and movement of a protrusile tongue.
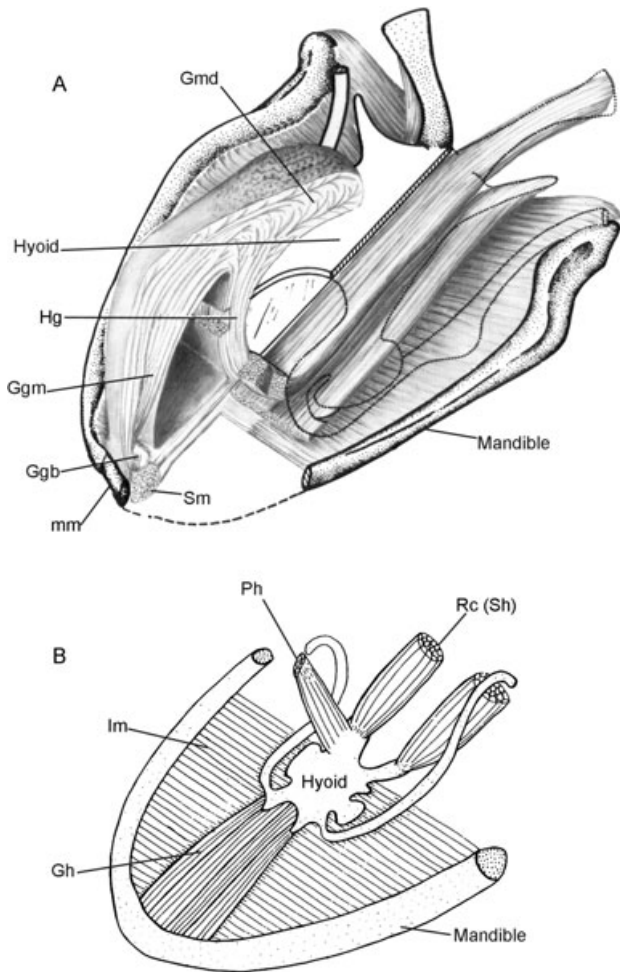
Figure 23. Tongue and hyoid apparatus in frogs. A, cut-away of hyoid and tongue musculature of *Bufo marinus* at the beginning of the tongue-flip sequence. Reproduced from Gans & Gorniak (1982). B, major muscles of the buccal floor of frogs in oblique dorsal view. Reproduced from Liem (1985).

The tongue
In common with salamanders, frog ancestors evolved a tongue for terrestrial feeding. However, these structures evolved independently, making use of some comparable elements, but others that are unique. As we have seen, the hyoid apparatus of adult frogs has almost no resemblance to that of salamanders. The presence of posteromedial processes and a parahyoid in *Triadobatrachus* suggests that a cartilaginous, plate-like hyoid had already evolved by the beginning of the Triassic, and presumably supported the muscles that make up the tongue, although it may not have been an effective, protrudable organ at that time, as judged by its limited mobility in the most primitive living frogs.

Frogs made use of some of the same muscles as those in salamanders, e.g. the genioglossus and the hypoglossus, which arise from the hyobranchial apparatus, and the geniohyoideus and the sternohyoideus (rectus cervicus), which protract and retract the hyoid. However, the relationships of the fleshy portion of the tongue and the hyobranchial apparatus are entirely different (Figs 14, 23). In salamanders, the anterior portion of the multipartite hyobranchial apparatus is inserted within the flesh of the tongue, and, together with muscles attached to the ceratohyal and ceratobranchial, forms a lever system that thrusts the tongue out of the mouth. In contrast, the hyoid of adult frogs is an unarticulated cartilaginous plate, to which are attached the muscles of the tongue. The geniohyoid and the sternohyoideus (rectus cervicus) move the hyoid plate anteriorly and posteriorly for a short distance within the oral cavity, but this does not contribute substantially to the protrusion of the tongue. Rather, the genioglossus medialis, whose anterior end is attached at the symphysis of the lower jaws, and the more posterior, underlying hyoglossus, are arranged so that their integrated movement flips the tongue out of the mouth, with the original dorsal surface becoming ventral in position (Gans & Gorniak, 1982). This flipping of the tongue is augmented by another muscle located close to the symphysis of the lower jaw, the submentalis. The submentalis, derived from the anterior fibres of the intermandibularis, is attached to two small elements on either side of the symphysis, the mentomeckelian bones, that are movable relative to the dentary. Their anterior surface is rotated ventrally so as to pull down on the anteroventral extremity of the dorsal surface of the genioglossus. The hyoglossus, which arises on the posterior ventral surface of the hyoid, forms the posteroventral portion of the tongue. It is relaxed as the tongue is protracted, but its contraction pulls the tongue, and its attached prey, back into the mouth. As in salamanders, the tongue exudes a sticky substance that adheres to the prey.

The basic structure and function of the tongue appear to be an ancient heritage of frogs. Although some primitive living frogs, including pipids and discoglossids, were once grouped as tongueless or aglossid frogs (Porter, 1972), recent work by Peters & Nishikawa (1999) has shown that the most primitive living frog, *Ascaphus*, has the same basic structure and function of the tongue as that just described for the neobatrachian frog *Bufo marinus*.

Basal frogs such as *Ascaphus* have a broad tongue, attached both posteriorly and anteriorly, that shortens during protraction and emerges only a short distance from the mouth (no more than 5 mm beyond the tip of the mandibles). More derived frogs have improved this capacity by modifications of the same basic tongue structure. Bufonids and phyllomedusine hylids have long, narrow tongues that elongate dramatically (up to 180% of jaw length), due primarily to the inertia from

mouth opening that is transferred to the tongue (Peters & Nishikawa, 1999). Microhylids and the termite specialist *Hemisus* employ a hydrostatic mechanism (somewhat comparable to that in primitive salamanders) in which fluids within the muscles force the tongue to elongate as dorsoventrally oriented fibres are shortened. As a result, the tongue may be protruded up to 200% of jaw length. The very different structures and mechanisms clearly show that tongue protrusion evolved separately in frogs and salamanders.

The jumping habits of frogs and the high degree of specialization of their larvae may be considered the most conspicuous specializations of frogs, but the feeding habits of the adults also involved a broad spectrum of their anatomy.

Vertebral column and ribs
Although the skulls of all frogs can be readily distinguished from those of other amphibian groups, it is the postcranial skeleton that sets frogs apart from all other vertebrates. No frog has more than ten presacral vertebrae, which allow for little if any lateral or dorsoventral mobility. Adult frogs have one or more sacral vertebrae with very widely expanded transverse processes (diapophyses) for articulation with the ilium, but none has a tail; in the adults, the anterior caudal vertebrae are fused into a long, rigid rod, the urostyle (Fig. 24).

As in salamanders and caecilians, the atlas of anurans has widely separated cotyles, which have a hinge-like articulation with the paired condyles of the skull, restricting movement to dorsoventral flexion in the sagittal plane. However, in contrast to salamanders and primitive caecilians, they do not have an odontoid process. As in salamanders and caecilians, the atlas never bears ribs. Except for the atlas, all the trunk vertebrae have long transverse processes. Ribs are absent from all the vertebrae in most anurans, but vestiges are retained of those articulating with the more anterior vertebrae of the primitive taxa *Leio-*
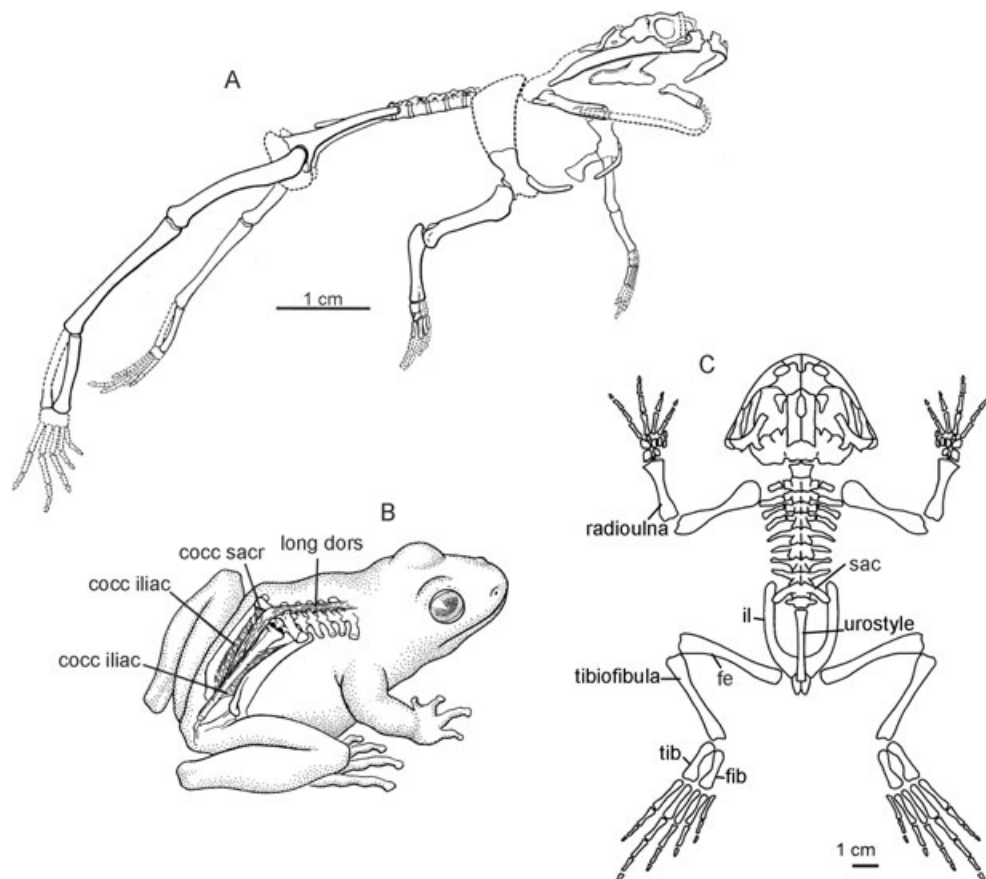

Figure 24. Jurassic frogs. A, lateral view of the Lower Jurassic frog *Prosalirus bitis*. B, diagram of the jumping musculature of anurans. A, B, reproduced from Jenkins & Shubin (1998). C, dorsal view of the Upper Jurassic anuran *Nothobatrachus*. Reproduced from Sanchiz (1998). Abbreviations specific to this figure: cocc iliac, coccygeo iliacus; cocc sacr, coccygeo-sacralis; long dors, longissimus dorsi.

pelma, *Ascaphus*, discoglossids, and pipids, as well as some Mesozoic fossils.

There is considerable variation in the nature of the articulating surfaces between the trunk vertebrae of anurans. Jurassic frogs and the primitive living genera retain the primitively amphicoelous configuration common to primitive salamanders and caecilians, with retention of extensive notochordal tissue. More advanced frogs may be either opistocoelous (in which the posterior surface of the centrum is recessed for articulation with the convex surface of the next more posterior vertebra), as in discoglossids and pipids, or procoelous (in which the anterior surface of the centrum is recessed for articulation with the convex surface of the next more anterior vertebra), as in the extinct palaeobatrachid frogs, some pelobatids, and all more advanced frogs.

According to Nicholls (1916), a rare variation occurs in the pelobatids *Phaneroglossa fuscus* and *Phaneroglossa cultripes*, in which the intervertebral articulation surfaces fail to unite with the centra, and the amphicoelous condition of the embryo persists into maturity. Duellman & Trueb (1986) refer to this articulating element as an intervertebral disc. This suggests a distinct area of calcification or mineralization that is comparable to the intercentra of Palaeozoic tetrapods. However, no such areas of calcification occur during development in either *Ascaphus* or *Leiopelma* (pers. observ.), although the centra are widely separated from one another until late in development.

Various patterns of chondrification and ossification of the vertebrae of advanced anurans have been described by Mookerjee (1931), Griffiths (1963), Kluge & Farris (1969), and Gardiner (1983). Duellman & Trueb (1986) comment on 'the distressing lack of concordance among the various schemes', and cast doubt on their evolutionary significance. On the other hand, a much more widespread phenomenon, common to all anurans, is the difference in timing of chondrification and ossification of the arches and centra. In contrast with all caecilians that have been studied and all but a very few salamanders, representatives of all frog families that have been studied chondrify and ossify the arches well before the centra (Carroll *et al*., 1999). This is in common with the pattern of all Palaeozoic amphibians for which larval stages have been described, as well as for most groups of primitive bony fish.

Anurans typically have a single sacral vertebra, but it may be fused with one or more anterior vertebrae. It primitively retains posterior zygapophyses, but these are lost in more advanced frogs. In most anurans, the urostyle bears a bicondylar articulation with the sacrum. However, the most primitive frogs, *Leiopelma* and *Ascaphus*, lack a distinct articulating surface, and the elements are connected by fibrocartilage.

Appendicular skeleton

All living frogs and their ancestors going back to the Lower Jurassic have a unique saltatory mechanism characterized by fusion of the proximal caudal vertebrae into a rod-like urostyle, a vertical hinge joint between the sacral vertebrae and the urostyle, an elongate, anteriorly directed ilium securely attached to the urostyle via the cocygeo-illiacus muscles, and a rotational joint between the sacral diapophyses and the more ventrally situated iliac blade. Extension of the trunk during jumping occurs through the contraction of the longissimus dorsi and coccygeo-sacralis muscles, accompanied by the thrust of the forelimbs (Jenkins & Shubin, 1998). Movement involves rotation at the iliosacral joints and extension at the sacrourostylic joint. This system has no parallel in salamanders or any Palaeozoic tetrapods.

When swimming, as when jumping, most frogs kick synchronously and symmetrically with both hindlegs. Abourachid & Green (1999) demonstrated that the most primitive frogs, *Leiopelma* and *Ascaphus*, always retain the primitive, asymmetrical movement of the rear limbs in swimming, in contrast with all other genera that have been studied. During swimming, the body swings from side to side, as is the case for tadpoles.

In relationship to saltatory locomotion, the configuration of the pelvic girdle is unique among vertebrates. The most conspicuous element is the ilium, which extends anteriorly from the acetabular as a long, laterally compressed rod. Instead of having a firm attachment with the sacrum, the massive diapophyses of the sacral vertebra overlay the dorsal surface of the ilia near its anterior end, so as to act as the axis for rotary movement of the pelvis relative to the vertebral column. The ischium is an oval element that makes up the posterior surface of the acetabulum. The pubis, which is not ossified, forms the anteroventral margin of the pelvis.

Although the force for saltatory locomotion is provided primarily by the hindlimbs, the pectoral girdle and forelimbs of frogs are also much modified to resist the impact of landing. The pectoral girdle shows a combination of primitive and derived features (Fig. 25). In contrast to salamanders, frogs retain two dermal elements, the cleithrum and clavicle, from their Palaeozoic ancestry. The clavicle serves an obvious role in maintaining the connection between the medial and lateral elements of the girdle, somewhat as in primates in association with our arboreal ancestry. A bony area on the anterior margin of the cartilaginous suprascapula is recognized as a remnant of the initially separate cleithrum. Unlike salamanders and Palaeozoic tetrapods, the scapula and coracoid are clearly distinct structures. Although the glenoid is formed jointly by the two bones, the scapula is typi-
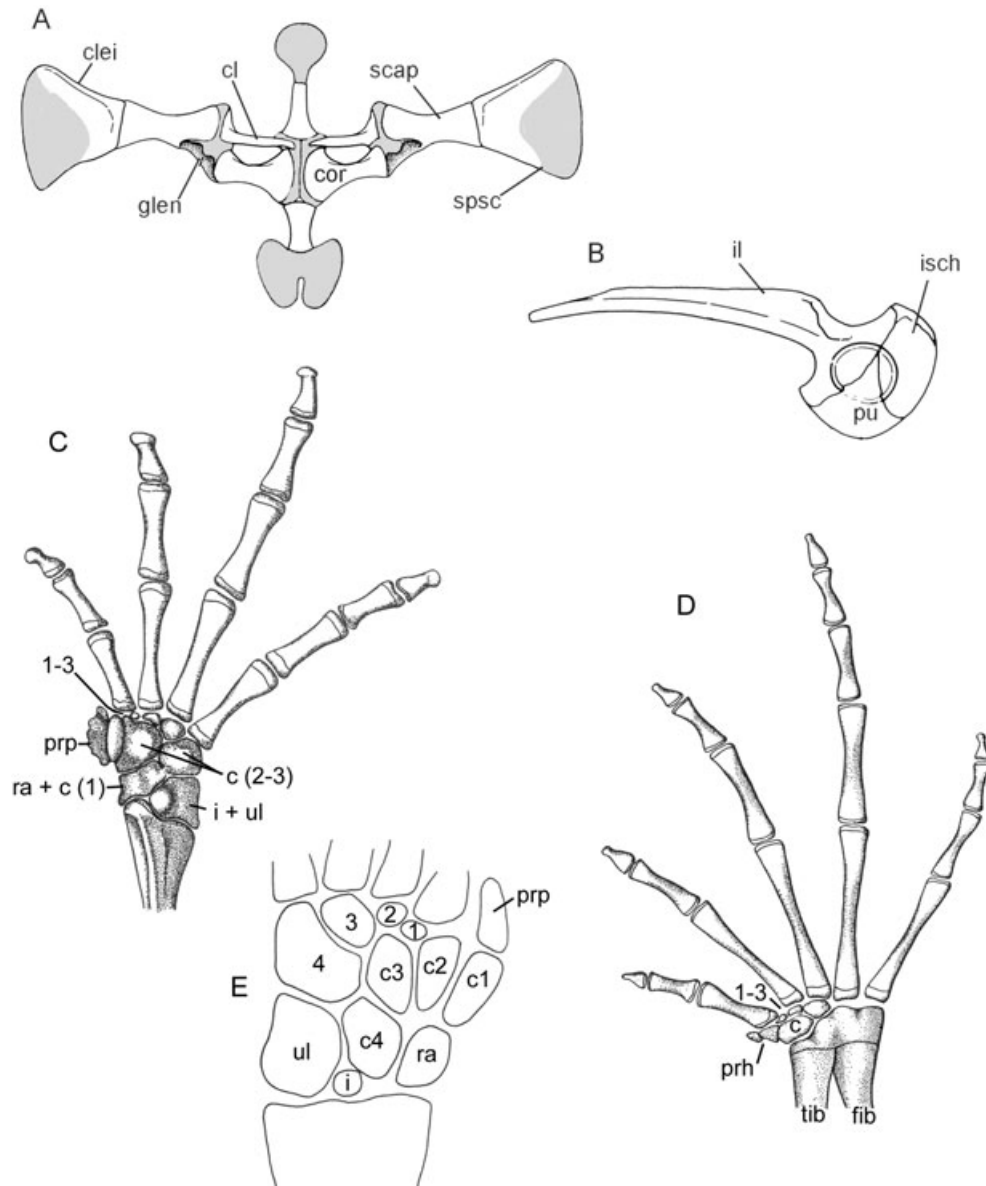
Figure 25. A, B, pectoral and pelvic girdles of modern anurans. Reproduced from Duellman & Trueb (1986). This general pattern applies back to the Jurassic. C, D, manus and pes of the primitive living anuran *Ascaphus truei*. Reproduced from Ritland (1955). E, carpus of the Late Jurassic *Notobatrachus degiustoi*. Reproduced from Estes & Reig (1973).

cally a flat element, exposed laterally, whereas the coracoid is more rod-like, and extends ventrally towards the midline. It is commonly separated from the more anterior clavicle by a large fenestra (Duellman & Trueb, 1986). Most anurans have a complex of elements along the ventral midline. None shows obvious homology with the interclavicle of primitive tetrapods, but, in common with the sternum in salamanders, mammals and birds, they are assumed to be endochondral neomorphs. A great diversity of patterns is seen among these medial units, which have long been assumed to be important in the classifica-

tion of frogs, but Emerson (1988) argued that the phylogenetic distributions of the two most commonly recognized patterns, firmisterny and arcifery, are not congruent with well-accepted systems of classification based on other traits, but appear to show extensive homoplasy.

The proximal elements of the forelimbs and hindlimbs, the humerus and femur, retain the general configuration of gracile Palaeozoic tetrapods, except for the loss of the entepicondylar foramen, the more hemispherical proximal articulating surface, and the distal condyle modified for articulation with the fused

radioulna and tibiofibula. The carpus retains a multi-plicity of elements common to Palaeozoic tetrapods, with the addition of a prepollex (Fig. 25). The carpus of one specimen of the Late Jurassic discoglossid *Notobatrachus* has 11 carpals – radiale, intermedium and ulnare, four centralia, and four distal carpals, plus a prepollex. However, a second specimen shows fusion of radiale–centrale 4 and centrale 2–centrale 3 (Estes & Reig, 1973). *Ascaphus* (Ritland, 1955; Romer & Parsons, 1977) shows even more extensive fusion – ulnare + intermedium, radiale + centrale 4, centrale 3 + distals 4 and 5, centrale 1 + 2, distal 1–3. A similar degree of fusion is seen in *Rana* (Duellman & Trueb, 1986). Using the known carpi of Palaeozoic amphibians as a plausible outgroup, the condition seen in *Notobatrachus* may be primitive for anurans, with extensive fusion being common.

The tarsus of anurans is highly derived in the great elongation of the tibiale and fibulare so that they have the general characteristic of long bones. The remaining tarsals are frequently fused and reduced in number to as few as a single centrale, one to three distal tarsals, and a prehallux. In contrast with the fusion and loss of proximal elements, the number of digits, metapodials, and phalanges is highly conserved among both fossil and living species. The number of digits and the phalangeal count retain a pattern that is very similar to that of small Palaeozoic temnospondyls. Counts of 2,2,3,3 in the manus and 2,2,3,4,3 in the pes are retained from *Notobatrachus* (Estes & Reig, 1973) to *Rana* (Duellman & Trueb, 1986) (Table 2).

Reproduction and larvae

As is the case among primitive salamanders, most frogs rely on external fertilization, lay their eggs in the water, and have free-living larvae. With the striking exception of *Ascaphus*, no anuran has a copulatory organ, although at least two species of the direct-developing *Eleutherodactylus* practise internal fertilization via cloacal apposition. Approximately 500 species, largely confined to the Leptodactylidae and Microhylidae, undergo direct development without a larval stage (Duellman & Trueb, 1986), but most others have a highly distinctive tadpole. Sanderson & Kupferberg (1999) pointed out that only among anurans is the feeding larva the dominant life-history strategy, with approximately 90% of the ~250 anuran genera having free-living tadpoles. Whereas neoteny is common among salamanders, it has never been observed in anurans, and is probably physiologically impossible (Wassersug, 1975).

It is now generally accepted that a highly derived, herbivorous larval stage was primitive for crown-group anurans (Sokol, 1975; Pugener, Maglia & Trueb,
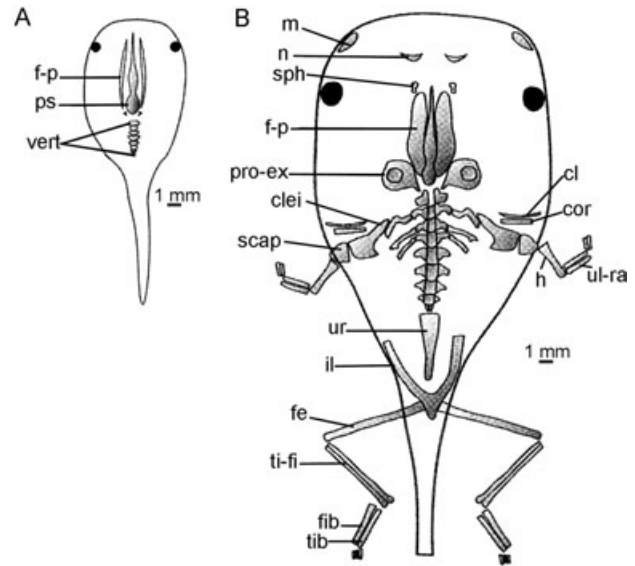

Figure 26. Two larval stages of the Lower Jurassic pipoidea frog *Shomronella jordanica* from the Lower Cretaceous. Reproduced from Chipman & Tchernov (2002).

2003; Pough *et al.*, 2004), and that the condition seen in pipoids and some microhylids, which have simpler larval jaws (Orton, 1957; Starrett, 1973) is derived, rather than primitive. Fossil larvae, known as early as the Lower Cretaceous (Chipman & Tchernov, 2002), already exhibit the general form of modern tadpoles (Fig. 26). The head and trunk form a globular structure, and the tail appears as a narrow appendage. The great expansion of the head and trunk are associated with the unique mode of feeding and digestion of tadpoles (Viertel & Richter, 1999).

The tadpole has the appearance of a totally neomorphic organism, highly divergent from the juveniles of any other amphibians, that must undergo a spectacular metamorphosis to achieve adulthood. In contrast to the situation in salamanders and caecilians, the diet and mode of feeding change drastically. With the exception of members of the Pipidae, adult frogs almost never feed in the water, but return to it only as a means of escape and for reproduction.

Feeding primarily on aquatic plant material and other particulate organic matter required extensive modifications of the structure and function of the tadpole mouthparts, means of circulating water and suspended food material, entrapment of food particles, and digestion. These changes involved nearly all aspects of the functional anatomy of the head, pharynx, and trunk, and must have occurred prior to the divergence of any of the modern anuran families. There must have been very strong and uniformly directional selection to achieve these changes, which transformed the entire body. What may have

been the selective advantage of these evolutionary changes?

Studies of modern tadpoles show that they are highly adapted to rapid growth in ephemeral water bodies, and early metamorphosis to primarily terrestrial adults (Harris, 1999; McDiarmid & Altig, 1999; Sanderson & Kupferberg, 1999). The ephemeral nature of the larval habitat reduces the problem of predation from typical aquatic predators, which require more permanent bodies of water to mature and reproduce, but also necessitates the rapid growth and early metamorphosis of tadpoles, which are incapable of surviving out of the water. Feeding on plant matter enables them to benefit from the much higher yield from primary production, as opposed to the predaceous feeding of other amphibian larvae. Sokol (1975) pointed to the much greater number of tadpoles than larval salamanders that can inhabit small, ephemeral bodies of water. This has remained the primary strategy of anuran larvae for at least the last 180 million years. It is more difficult to determine how or when tadpoles first evolved.

Early larvae of fish and amphibians are capable of absorbing at least small amounts of organic molecules through the skin and gut lining prior to active feeding (Sanderson & Kupferberg, 1999). For example, Ahlgren & Bowen (1991) showed that, under laboratory conditions, early, non-feeding tadpoles of *Bufo americanus* filtered precipitates of dissolved organic matter at a level that was sufficient for survival, but not for growth. Small particles of organic matter, of both plant and animal origin, can be ingested through the mouth as a result of buccal respiration, and would also have been available from the bottom sediments. The same actions could also have led to the assimilation of bacteria, some of which would have had the capacity to produce enzymes that would have facilitated the digestion of plant material.

One can hypothesize this mode of feeding being extended into later and larger larval stages in the early ancestry of salientians by primarily behavioural means, if there was a rich source of organic matter available. On the other hand, effective feeding on a diversity of unicellular and multicellular aquatic plants and particulate organic matter required a large number of integrated changes in anatomy and physiology. (1) In the ancestry of anuran tadpoles, the periodic use of suck-and-gape feeding in the larvae of Palaeozoic amphibians, such as the branchiosaurs (Boy & Sues, 2000), was replaced by a much more complex pumping system that delivered a continuous flow of water. This involved three successive pumps, in the mouth, the pharynx, and the gill chamber. (2) Instead of the gill slits opening directly to the exterior, as in salamanders, they open into paired chambers formed by the operculum, which grows posteriorly from each

hyoid arch and joins at the ventral midline (Sokol, 1975). (3) The requirements for entrapping tiny particles of food led to substantial modification of the surface of the oropharyngeal cavity (Viertel & Richter, 1999). (4) The digestive system was greatly elongated to provide more space for retention and breakdown of the organic matter with the help of symbionts (Pryor & Bjorndal, 2005). (5) An entirely new set of larval jaws evolved, anterior to the palatoquadrate and Meckel's cartilage, for the detachment and comminution of multicellular aquatic plants (Cannatella, 1999). (6) Finally, the cartilaginous larval brain case, or chondrocranium, was much modified in relationship to support of the larval jaws and primary pumping system.

It is difficult to establish a probable sequence for the appearance of these novel structures, which may have evolved more or less simultaneously, but perhaps either gradually or sporadically, over millions of years. Discussion of these changes will begin with the chondrocranium, because it is a basic structural unit, to which the mouthparts and the hyobranchial apparatus are attached.

Chondrocranium and palatoquadrate
The chondrocranium has a fairly conservative configuration during early development in primitive jawed vertebrates (deBeer, 1937, 1985). Its evolution can be only indirectly traced over geological time, as cartilage is only exceptionally preserved in the fossil record. However, the evolution of the chondrocranium can be roughly reconstructed on the basis of study of phylogenetic sequences of extant species in which the embryos or larvae can be directly studied. In the case of extant amphibians, the configuration of the salamander chondrocranium would be expected to represent a more primitive pattern than that of either anurans or caecilians, in view of the more plesiomorphic features of other aspects of the skull, both cartilage and bone. This is broadly supported by comparison with the chondrocranium in both actinopterygian and sarcopterygian fish with living representatives, e.g. *Polypterus* and *Ceratodus* (deBeer, 1985).

One may also look at differences in the configuration of the chondrocranium of living anurans as shown by a phylogenetic sequence (Wassersug & Hoff, 1982). Major differences in skull proportions are seen between one of the most primitive living frogs, *Ascaphus*, and the neobatrachian *Rana* (Fig. 27). Although the proportions of the chondrocranium of *Ascaphus* do somewhat more closely resemble those of primitive salamanders than do those of *Rana*, the major changes in the support of the larval jaws and the articulation with the ceratohyal had already reached a functionally modern level. Throughout anuran evolu-
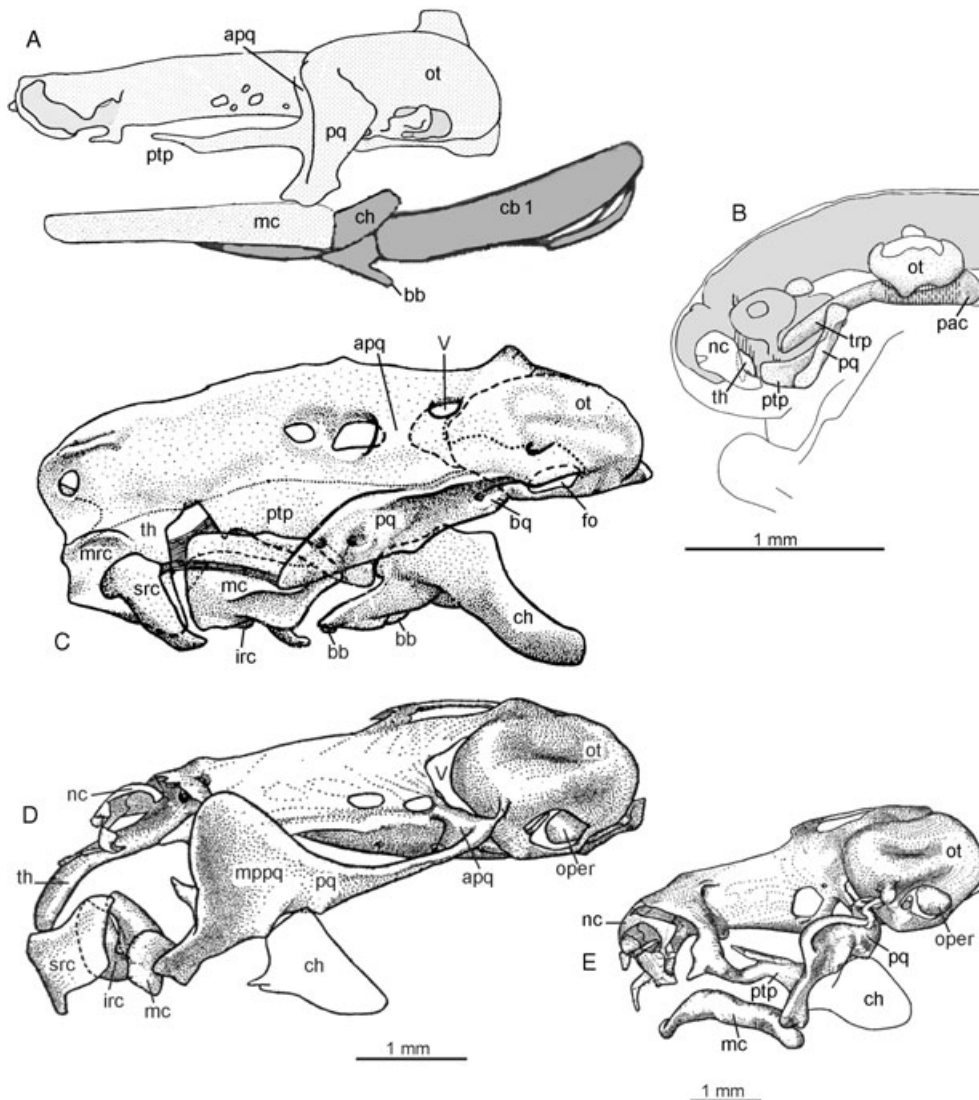
Figure 27. Chondrocrania, palatoquadrate, and Meckel's cartilage of a salamander and anurans. A, the chondrocranium, lower jaw, and branchial apparatus of a late larva of the hynobiid *Ranodon*. Modified from Rose (2003). This presumably represents a primitive pattern for amphibians, as it retains plesiomorphic features of extant members of basal actinopterygian and sarcopterygian groups (deBeer, 1937, 1985). B, an early stage (21) of the primitive anuran *Ascaphus truei*, showing some resemblance to early larvae of salamanders. Reproduced from Reiss (1997). C, advanced larval stage of *Ascaphus truei*, showing the anterior extension of the palatoquadrate and Meckel's cartilage, and the large suprarostral and infrarostral cartilages. Reproduced from Pusey (1943). D, advanced tadpole of *Rana temporaria*. Reproduced from Pusey (1938). E, larva of *Rana temporaria*, approaching metamorphosis, showing features in common with the larva of *Ranodon*. Reproduced from Pusey (1938).

tion, the anterior portion of the chondrocranium, specifically the trabeculae, became much increased in length relative to the size of the otic capsule, so that the larval jaws are extremely far forward in the skull, and the gape is much reduced.

One of the most significant changes in the ancestors of anurans was the modification of the palatoquadrate. In primitive bony fish and salamanders, its posterior extremity has an extensive dorsoventrally oriented portion that extends from just anterior to the otic capsule down to the posterior end of Meckel's cartilage, where it forms the jaw articulation. A more narrow anterior (pterygoid) process extends forwards to form the embryonic precursor of the upper jaw. This general configuration is retained in larval salamanders, and is re-established during metamorphosis among anurans (Fig. 27E). Among tadpoles, however, the palatoquadrate as a whole is oriented nearly horizontally, and its

articulation with Meckel's cartilage is far anterior, thus much reducing the gape. In addition, the poster-oventral surface of the palatoquadrate forms an extensive, longitudinally orientated surface for articulation with the ceratohyal, which forms the basis for the primary pumping element of the water-circulating system.

Hyobranchial skeleton
The hyobranchial skeleton of tadpoles superficially resembles that of salamander larvae (Figs 10, 28), but it functions in quite a different way (Cannatella, 1999). Most of the elements present in the hyobranchial skeleton of tadpoles can be homologized with those of *Eusthenopteron* and primitive salamanders, but there are significant differences in their proportions and nature of articulation. The ceratohyals are clearly comparable, but are considerably larger and have evolved a new articulation dorsally with the palatoquadrates that does not exist in salamanders or any Palaeozoic amphibians. The basibranchials (copulae) are integrated into a firm medial axis, with which the medial edge of each ceratohyal articulates in the manner of a hinge (Fig. 29). The articulation of the ceratohyals with the palatoquadrate and copulae are key to the larval pumping system.

Posterior to the ceratohyals are two plates of bone that apparently represent the fusion of homologs of the hypobranchials of salamanders. In the primitive anuran *Bombina* (Fig. 28C), these plates articulate distally with the conjoined proximal ends of the ceratobranchials (Roček, 2003), but these elements are fused in more derived anurans. In all frogs, the four ceratobranchials on each side are fused proximally and distally to form the branchial basket, which serves as an external framework for the support of the gills and entrapment of suspended food particles.

In all salamanders, larvae and adults, the hyobranchial elements function as a series of rods that articulate with one another, and together form a pumping and feeding apparatus. In tadpoles, the pumping function is concentrated on the anterior ceratohyals and hyobranchial plates, which move primarily dorsoventrally, without the strong anteroposterior component seen in larval salamanders. Homologies can be recognized between the muscles that move these elements in frogs and salamanders, but their functions are quite distinct.

In salamander larvae, the primary force for expanding the buccal cavity is provided by the posteroventral pull of the sternohyoideus (rectus cervicus) and the geniohyoideus (coracomandibularis) on the basibranchials. In frog tadpoles, the sternohyoideus pulls posteriorly on the central portion of the branchial basket, but the primary expansive force is provided by the
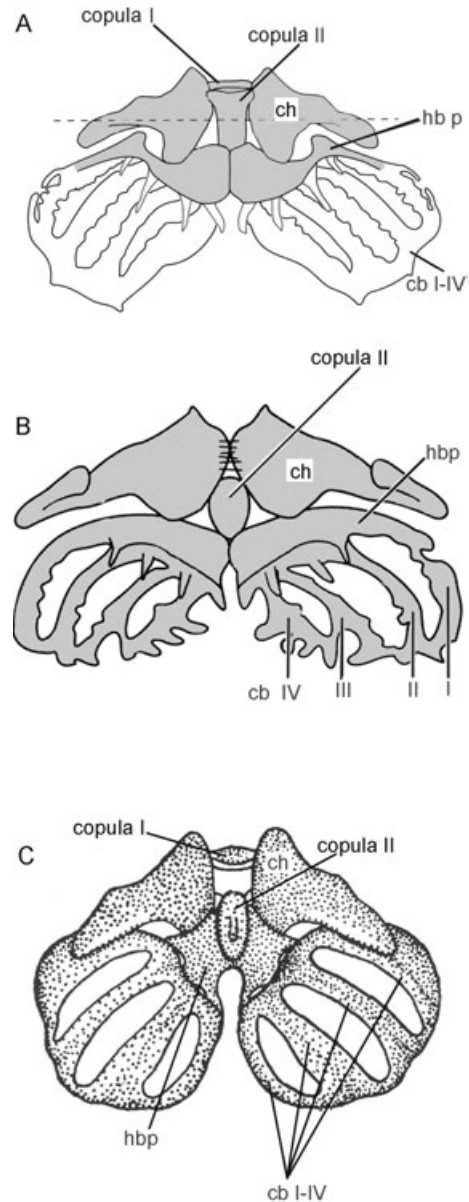

Figure 28. Progressive changes in the configuration of the hyobranchial apparatus among anurans. A, *Rana*. Reproduced from Cannatella (1999). B, *Pelodytes*. Reproduced from Cannatella (1999). C, *Bombina*. Reproduced from Roček (2003).

nearly vertically oriented orbitohyoideus and suspensoriohyoideus, which originate on the greatly expanded muscular process of the palatoquadrate and insert on the lateral margin of the paired ceratohyal cartilages that extend as lever arms beyond the line of articulation with the palatoquadrate. In contrast to the throat muscles that expand the buccal cavity in salamanders, the orbitohyoideus and suspensoriohyoideus of tadpoles are homologous with the depressor
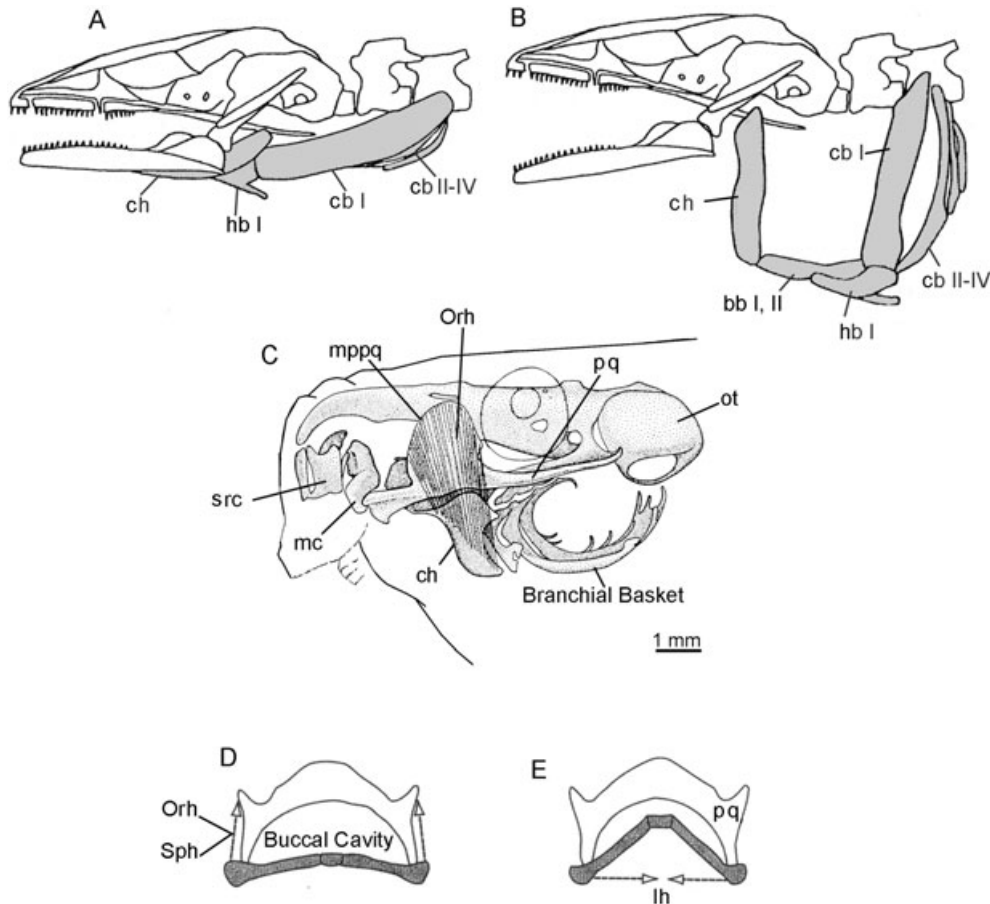
Figure 29. Mechanics of the buccopharyngeal region in salamanders and frogs. A, B, lateral views of the skull and branchial region of a modern salamander. The movement of the hyobranchial apparatus is primarily posteroventral during inspiration. Reproduced from Deban & Wake (2000). C, lateral view of the chondrocranium of the tadpole of the primitive living frog *Alytes obstetricans*, showing the essentially vertical orientation of the major muscles that lower the midportion of the ceratohyals and so expand the buccal cavity. Reproduced from Sanderson & Kupferberg (1999), after Wassersug & Hoff (1982). D, E, diagrammatic anterior view of the buccal cavity, showing the antagonistic actions of the muscles that drive the major pumping apparatus in tadpoles. Reproduced from Cannatella (1999).

mandibulae of the adult. Raising of the hyobranchial apparatus is achieved by muscles that run between the rami of the lower jaws in both groups; in salamanders, this is primarily the intermandibularis, but in anurans, it is the interhyoideus (Figs 30, 31).

Salamander larvae have only a single pump, involving the entire hyobranchial skeleton, for intermittent passage of water for suck-and-gape feeding. The external gills are aerated by their passage through the water. In contrast, tadpoles must maintain a continuous flow of water for feeding on suspended food particles and for uptake of oxygen by gills that are enclosed beneath the operculum. To provide a continuous flow, anuran larvae have three successive pumps, each partially separated from one another: (1) in the buccal cavity, involving the ceratohyals and hyobranchial plates; (2) in the pharyngeal cavity, involving the branchial basket; and (3) in the branchial cavity, involving the operculum (Fig. 32). The buccal pump draws in water through the nares, and forces it posteriorly towards the pharynx, from which it is separated by the ventral velum. When the buccal floor is depressed, the posterior edge of the ventral velum is pushed against the floor of the cavity, and so prevents flow of water into the pharyngeal cavity. When the buccal floor is elevated, the velum falls, and water is pushed into the branchial basket. The dorsal flaps of the ventral velum guide the water into the left and right gill filters.

The pharyngeal pump is powered by buccal floor elevation, simultaneously with expiration and contraction of the subarcualis obliquus, which enlarges the cavity and causes movements of the gills. Passive recoil of the buccal floor and contraction of the rectus
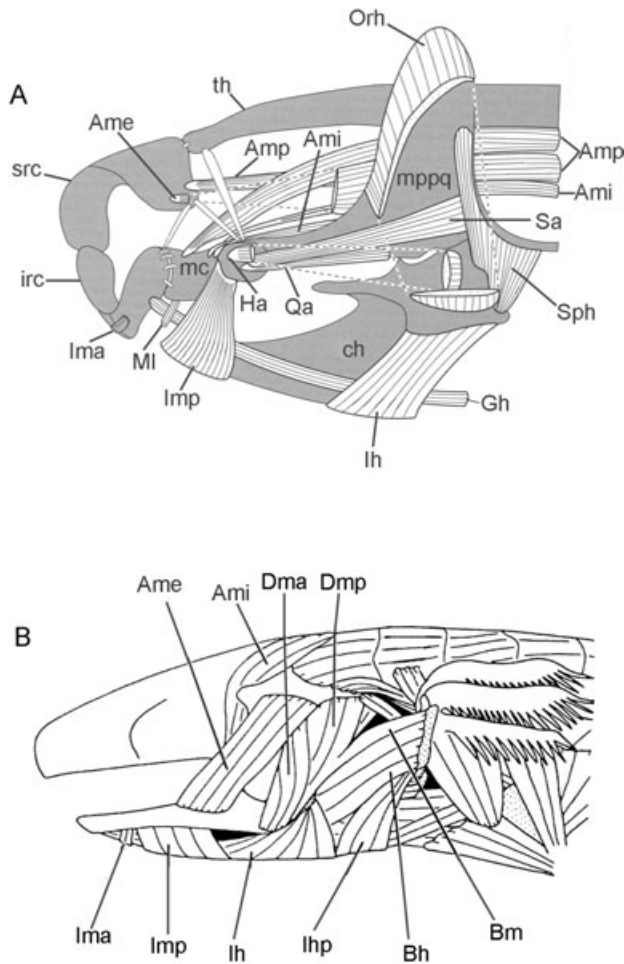
Figure 30. Patterns of the jaw musculature in the larvae of frogs and salamanders, as seen in lateral view. A, the tadpole of *Rana catesbeiana*. Reproduced from Cannatella (1999), after Gradwell (1972). B, the salamandrid *Taricha granulosa*. Reproduced from Deban & Wake (2000).

cervicus reduce the volume of the pharyngeal cavity. Food is trapped within the gills, and the water flows into the branchial chambers via three gill slits.

External to the gill slits is an enclosed space surrounded by the operculum. The operculum forms early in development from a sheet of tissue extended from the back of the hyoid arch, as in the case of the operculum in fish (Sokol, 1975). Such a structure is also observed in very early larval stages in salamanders, but in that group it quickly regresses to make way for the external gills. The gills are exposed externally in early tadpoles (Fig. 4B), but they are soon covered by the operculum. The formation of opercular tissue in the larvae of frogs and salamanders is probably a relic of their common aquatic ancestry, but might go back to the condition in sarcopterygian fish. The branchial pump, which involves the space beneath the opercu-

lum, is only active during hyperexpiration, when contraction of the interhyoideus posterior compresses the opercular chamber and forces water out the spiracle (Gradwell, 1972; Cannatella, 1999). It should be noted that nearly all the bones of the hyobranchial apparatus and their associated muscles are homologous in the larvae of frogs and salamanders, but the ways in which they function have followed widely divergent paths of evolution.

Larval jaws
Nearly all tadpoles, including those of the most primitive living genus, *Ascaphus*, feed primarily on attached aquatic plants such as algae, which must be cut, detached, or scraped from the substrate and reduced to fine particles. This is accomplished by unique, larval jaws, known in no other vertebrates, that are connected to the anterior end of the chondrocranium and Meckel's cartilage. Although the chondrocranium of *Ascaphus* (Fig. 27) is shorter than that of the more derived ranid and bufonid frogs, its larval jaws are already comparable to those of the most advanced tadpoles. Hence, this basic pattern almost certainly evolved prior to the radiation of the crown-group anurans. The upper and lower larval jaws are termed the suprarostral and infrarostral cartilages. Both are paired, at least in early development. The suprarostrals are formed exclusively from neural crest mesenchyme in the roof of the stomodeum, and are among the earliest structures to form in the anuran skull (Roček, 2003). In *Ascaphus*, *Discoglossus*, *Alytes*, and *Bufo*, two pairs of elements develop in the area of the suprarostrals, but whether this is a primitive or a derived condition for anurans has not been determined. The suprarostrals typically articulate with the trabecular horns, the most anterior processes of the chondrocranium.

The infrarostrals articulate with Meckel's cartilage (the anlage of the adult lower jaw). They are further integrated by a number of ligaments. In most frogs that have a larval stage (with the exception of pipoids and microhylids, which are midwater suspension feeders), the suprarostral and infrarostal cartilages are covered with keratinized jaw sheaths that act like a series of teeth, to scrape off and break up aquatic plant material (Cannatella, 1999). Most anurans augment the cartilaginous larval jaws and keratinized jaw sheath with keratinized denticles borne on the lips, to rasp algae down to particle size.

The larval jaw apparatus appears to be an entirely neomorphic complex, unique to anurans. However, some elements of this complex can be compared with those seen in salamanders and caecilians. In common with urodeles, frogs have ossified mentomeckelian bones adjacent to the symphysis in the adults. These
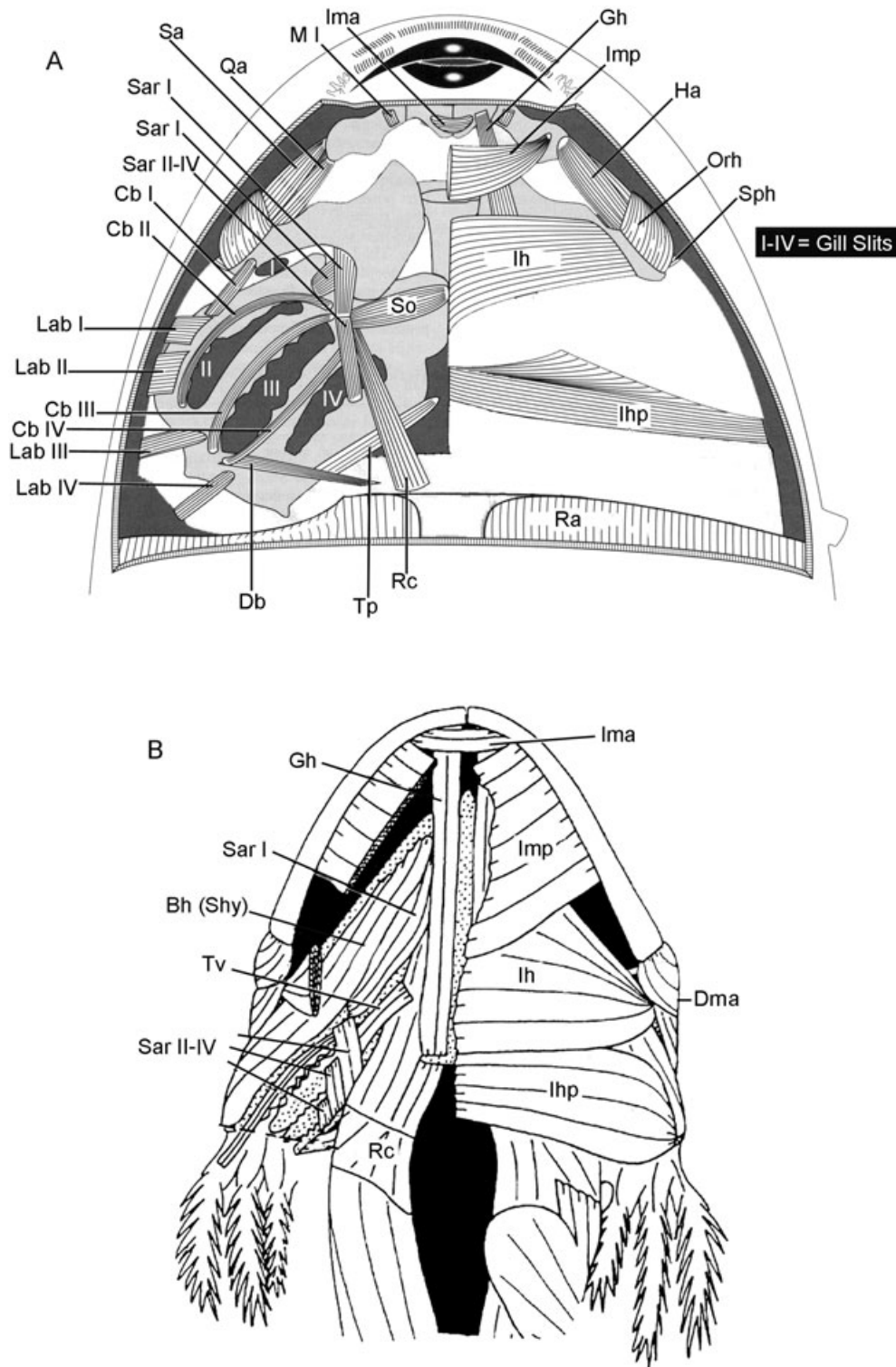
Figure 31. Patterns of the jaw musculature in the larvae of frogs and salamanders, as seen in ventral view. A, the tadpole of *Rana catesbeiana*. Reproduced from Cannatella (1999), after Gradwell (1972). B, the salamandrid *Taricha granulosa*. Reproduced from Deban & Wake (2000).
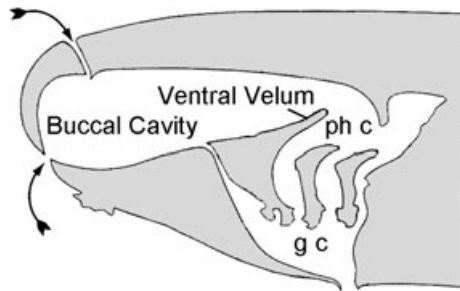
Figure 32. Sequence of pumps in anurans. Reproduced from Cannatella (1999). Abbreviations unique to this figure: phc, pharyngeal cavity; gc, gill cavity.
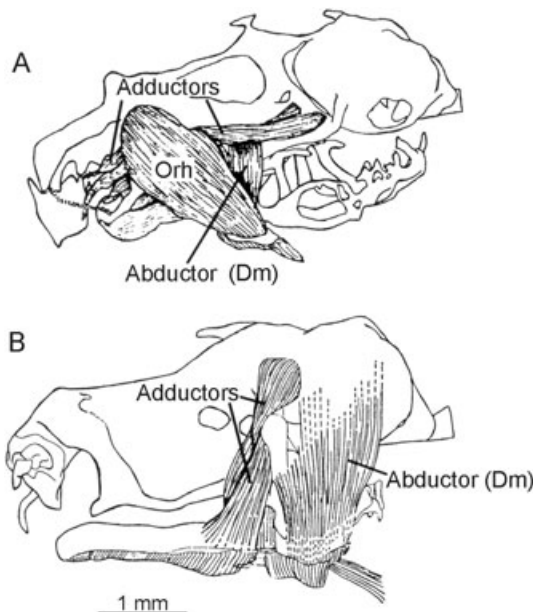

Figure 33. Lateral view showing the change in orientation of the jaw muscles of anurans between the larval condition (A), and a metamorphosed frog (B). Reproduced from de Jongh (1968).

bones are in the same position as the infrarostral cartilages, and develop in a similar manner – as an anterior expression of Meckel's cartilage. In adult frogs, they remain moveable relative to the dentary bones, and contribute to the mechanism of tongue protrusion. In contrast, neither salamanders nor caecilians have apparent homologues of the suprarostal cartilages, although they can be interpreted as extensions from the anterior end of the trabecular horns.

The geometry of the muscles that open and close the larval jaws is far different from that of the muscles that operate the adult jaws (Fig. 33). Recognition of their homology is further complicated by the use of different names for the muscles. In fact, the muscles are all broadly homologous, but their orientation and positions of insertion are drastically different, and adult muscles are subdivided into several smaller functional units in the larvae. In advanced anurans such as *Rana*, the larval jaws are located far anteriorly in a skull that is greatly modified in its proportions from those of Palaeozoic amphibians or salamanders (Fig. 27). The origins of both the adductor muscles and the depressor mandibulae remain at the back of the skull, but their insertions are transferred from the back of Meckel's cartilage to the new jaw elements, and become primarily horizontal rather than vertical in their orientation.

The problem of establishing specific homology is further complicated by the complete degeneration of the individual muscle fibres of the larval jaw muscles during metamorphosis. However, it has been recognized that most of the individual larval muscles are replaced by new fibres that develop from satellite cells of the same muscle groups that were present in the larvae (Alley, 1989). The homology of the larval and adult muscles is further demonstrated by the fact that association of the nerves with particular muscles is not broken during metamorphosis. Trigeminal motoneurons initially deployed to the larval myofibres are redirected to the new muscle fibres. Simultaneously, the cellular geometry and synaptic input to these motorneurons are reorganized. The original neuromuscular circuitry is updated during metamorphosis to establish the adult jaw motor activity, which is very different from that of the larva (Alley, 1990).

Opening of the larval mouth results from depression of the infrarostral cartilage, which is affected primarily by muscles that insert on the retroarticular process of Meckel's cartilage – the quadratoangularis, hyoangularis, and suspensorioangularis (Figs 30, 31). All are elements of the depressor mandibulae, which insert in a comparable position at the back of the lower jaw in adult frogs and salamanders. With their contraction, the infrarostral, to which Meckel's cartilage is attached by ligaments, is both lowered and thrust forwards. As the anterior end of Meckel's cartilage also has a ligamentous attachment to the posteroventral edge of the suprarostral cartilage, it too is protracted, and its anterior margin is raised. The geniohyoideus, which inserts on the mentomeckelian cartilage (or near the jaw symphysis) in adult frogs and salamanders, attaches to the anterior lower margin of the infrarostral cartilage to further widen the gape.

Closing of the larval jaws occurs more rapidly than their opening. This results from contraction of the levator posterior profundus and levator externus (homologous to elements of the adductor posterior and adductor externus of adult frogs and salamanders), which insert on the suprarostral, the levator posterior superficialis (homologous to the adductor mandibulae

posterior), and the levator mandibulae anterior (homologous to the adductor mandibulae internus), which insert on Meckel's cartilage, as well as elastic recoil of the associated ligaments. Opening and closing of the larval jaws is associated with both gill irrigation and feeding, but these functions involve different movements of the suprarostral and infrarostral cartilages (Cannatella, 1999).

The only jaw muscles that have more or less retained their primitive position relative to the long axis of the head are the intermandibularis anterior and posterior (between which is the mandibulolabialis), and the interhyoideus, but their functions have changed to variable degrees. The intermandibularis anterior has shifted to the neomorphic infrarostral cartilage. The intermandibularis posterior and interhyoideus both cradle the hyoid apparatus, as in salamanders. The interhyoideus retains the plesiomorphic area of origin along the midline between the lower jaws, but has a new area of insertion at the lateral margin of the ceratohyal that has a major role in elevating the floor of the mouth to drive the buccal pump.

Entrapment of food

Once food particles are drawn into the mouth and pharynx with the water, they must be filtered out of suspension. The large particles are trapped on the buccal papillae (Fig. 34). Smaller particles adhere to mucus secreted from the roof of the buccal cavity, the dorsal and ventral portions of the velum, and the ruf-
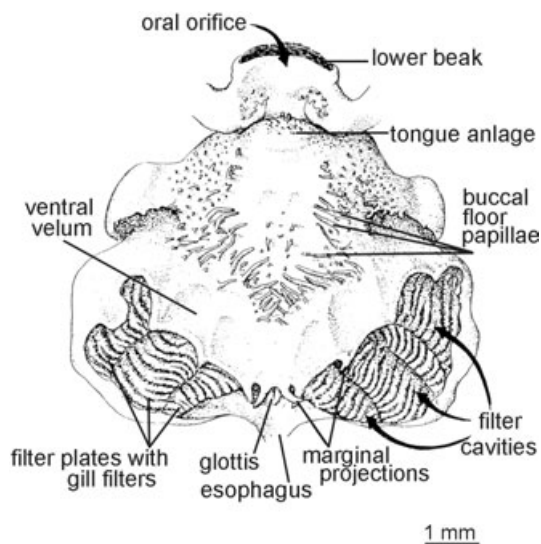

Figure 34. Floor of the mouth of an *Alytes* larvae showing the various structures associated with the entrapment of tiny food particles. These are common to all suspension-feeding tadpoles, except pipids. Modified from Sanderson & Kupferberg (1999).

fled epithelium of the gill filter plates. The mucus is transported to the oesophagus by cilia.

Digestion

Anuran larvae are the only amphibians known to be primarily herbivorous. Herbivory in members of other vertebrate classes is associated with a symbiotic relationship with microbial organisms. Pryor & Bjorndal (2005) recently demonstrated that this association also pertains to anurans, as represented by *Rana catesbeiana*. In both wild and laboratory populations, the colon of the tadpoles is inhabited by a diversity of bacteria, protozoa, and nematodes that occupy a thick mucous matrix lining the colon wall. The bacteria include bacilli, cocci, and spiral forms. The protozoans include *Opalina* spp. and *Nyctotherus cordiformes*. The nematode *Gyrinicola batrachiensis* is common in the colon, but is also found in the small intestine and rectum. The high levels of short-chain fatty acids (acetate, proprionate, and butyrate) result from the fermentation of complex structural carbohydrates by these microorganisms. The products of fermentation in the small intestine, colon, and rectum of bullfrog tadpoles represent 20% of their daily energy requirements. This is near the middle of the range reported for mammalian hindgut fermenters, higher than the range for avian hindgut fermentation, and at the low end of the range reported for reptilian hindgut fermenters. The retention of symbionts is facilitated by the very great length of the highly coiled intestinal tract, antiperistalsis distally, and the habit of extensive coprophagy (as in herbivorous mammals of comparable size).

Locomotion

Tadpoles are unique among terrestrial vertebrates in possessing a tail used in locomotion but retaining no remnants of vertebrae. Its axis consists only of an unrestricted notochord. Movement of the tail is effective for immediate evasion of predators, but less so for sustained locomotion (Wassersug, 1989; Hoff & Wassersug, 2000). No limbs are present in hatchling tadpoles. The forelimb develops beneath the operculum, which maintains the streamlined configuration of the trunk. The limbs only become functional just prior to the completion of metamorphosis.

Presumably, the evolutionary reduction and later absence of a tail in adult frogs was necessary for the optimal performance of the jumping apparatus. This assumption may be used to argue for a temporal association of the evolution of the specialized tail of the tadpole, as the absence of bony elements would presumably facilitate its loss at metamorphosis. If, as generally accepted, frogs evolved from temnospondyl

labyrinthodonts, it is easy to see how this condition could have evolved by the progressive reduction in the rate of the anterior-to-posterior ossification of the caudal vertebrae (already slow in branchiosaurs), until it stopped at the end of the trunk, beyond the end of the elements that are incorporated into the urostyle (Carroll *et al.*, 1999).

Metamorphosis

All anurans with a biphasic life history undergo a sudden and dramatic metamorphosis, which is necessary for achieving sexual maturity, as well as for switching from a primarily aquatic to a primarily terrestrial way of life (Wassersug, 1975). Metamorphosis, which in *Rana* is accomplished in 6 days, involves the following changes: hindlimbs appear and mature, forelimbs expand out of the branchial chamber, internal gills degenerate, the tail is resorbed, the skin thickens, the larval mouth degenerates and the adult mouth forms, the tongue and associated hyolaryngeal structures develop, the intestines shorten, the adult digestive tract differentiates, and gonads and their associated ducts develop (Duellman & Trueb, 1986). Metamorphosis is a period of extremely high mortality, as aquatic locomotion is severely compromised, and effective terrestrial locomotion is not fully achieved.

CAECILIANS

Caecilians are as highly derived from other amphibians as are anurans, but in very different ways.

Extant caecilians are unique among amphibians in the total absence of limbs and girdles, without even any developmental rudiments (Wake, 2003). They are greatly elongate, with from approximately 70 to as many as 285 trunk vertebrae, but no more than a vestige of a tail. Their habits are cryptic – living in the leaf litter, burrowing, or aquatic. Most of their anatomical attributes can be associated with burrowing. They are unique in the possession of a protrudable copulatory organ, called a phallodeum, and all practise internal fertilization. Their eyes are rudimentary, but they have evolved a sensory tentacle that protrudes from the eye region. Approximately 150 species are known from the wet tropics of the New World and Old World.

Phylogeny

Thirty-three genera of living caecilians are recognized (Pough *et al.*, 2004), and fossils are known from the Palaeocene of Brazil (Estes & Wake, 1972) and Bolivia (Rage, 1986), the Cretaceous of Sudan (Werner, 1994; Evans, Milner & Werner, 1996) and Morocco (Evans & Sigogneau-Russell, 2001), and the Lower Jurassic of
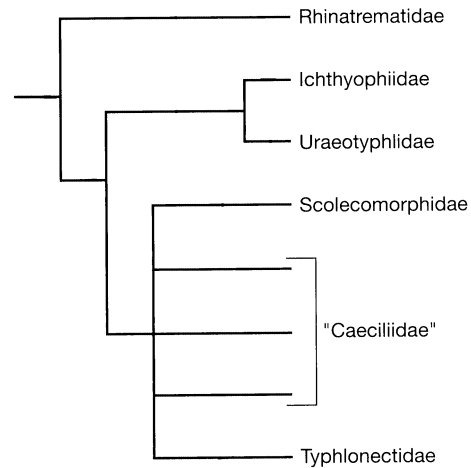

Figure 35. Phylogeny of extant caecilian families. Reproduced from Pough *et al.* (2004).

the western USA (Jenkins & Walsh, 1993). The modern genera are commonly grouped in six families. The Rhinatrematidae of northwestern South America, the Ichthyophiidae of Southeast Asia, and the Uraeotyphlidae of India are recognized as a series of stem taxa. They are succeeded by a large paraphyletic assemblage, the pantropical Caeciliidae, within which are assumed to lie the sister taxa of the more derived Scolocomophidae of East and West Africa and the primarily aquatic South American Typhlonectidae (Pough *et al.*, 2004; San Mauro *et al.*, 2004) (Fig. 35). The Lower Jurassic caecilian *Eocaecilia* (Jenkins & Walsh, 1993; Carroll, 2000b; F. A. Jenkins, D. Walsh & R. L. Carroll, 2007) is by far the oldest and most primitive caecilian, and the most likely to provide a close basis of comparison with Palaeozoic tetrapods.

Cranial anatomy

In strong contrast to frogs and salamanders (Fig. 6), nearly all caecilians have a solidly roofed skull, except for small openings for the orbits (completely covered in some species) and the nares (Taylor, 1969) (Figs 7, 36). Large, paired parietals, frontals, and nasals make up much of the dorsal surface of the skull. However, in many species, there is a narrow gap or apparent line of mobility between the frontal and parietal and the large squamosal, which makes up most of the cheek. In all members of the Typhlonectidae and the only genus within the Scolecomorphidae, there is a substantial opening in this position, but the jaw musculature does not usually extend out of the opening and over the surrounding bones, as it does in frogs and salamanders (Carroll & Holmes, 1980). On the other hand, members of the most primitive living caecilian
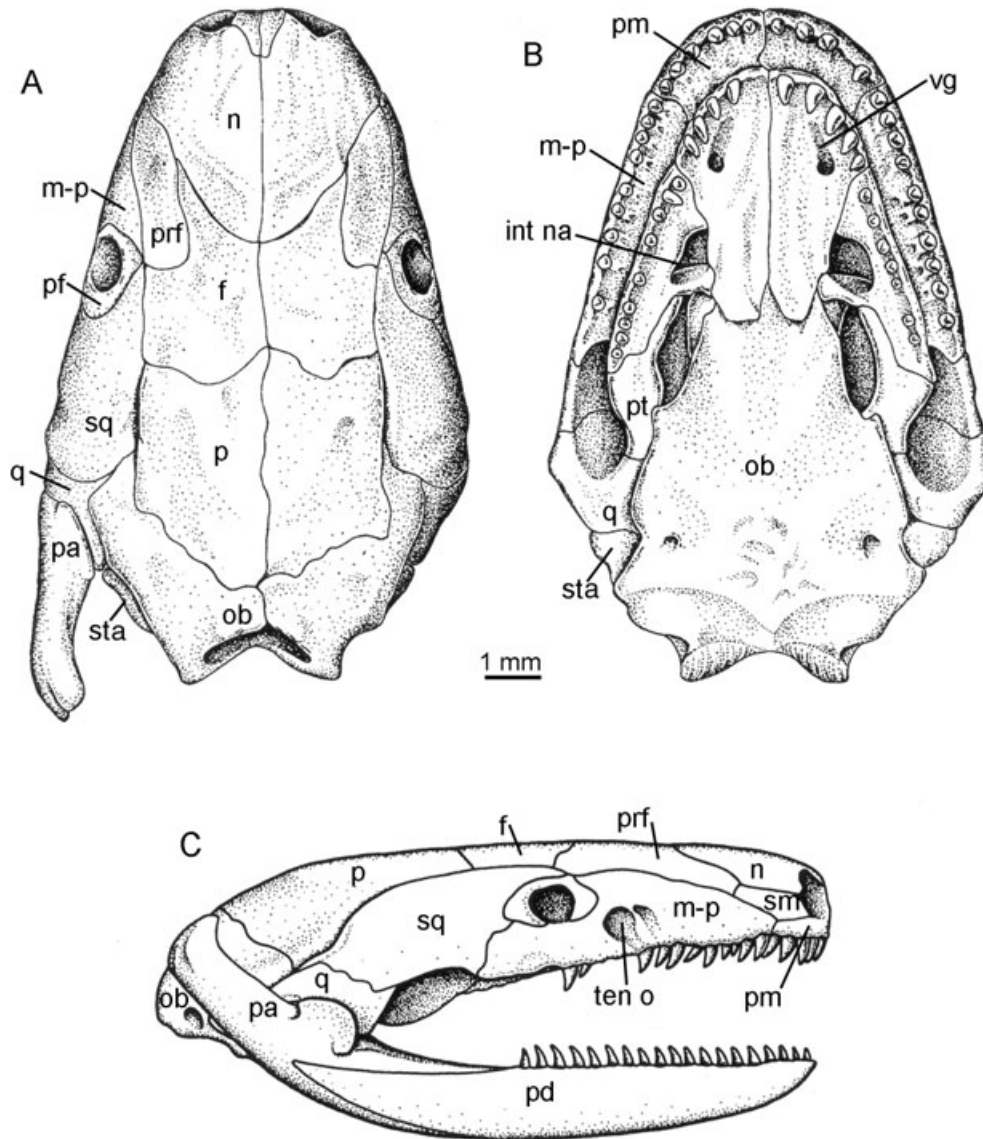
Figure 36. Skull of the conservative living caecilian *Ichthyophis glutinosis*, in dorsal, palatal, and ventral views. Reproduced from F. A. Jenkins, D. Walsh & R. L. Carroll, 2007 (in press).

family, the Rhinatrematidae, have a large temporal opening from which the adductor musculature does spread out over the braincase, as is also the case in the highly derived typhlonectid *Atretochoana* (Wilkinson & Nussbaum, 1997, 1999).

The lateral surface of the skull in extant caecilians is composed primarily of the squamosal and the maxillary portion of the fused maxillopalatine. Primitive genera have a large prefrontal bone and a substantial septomaxilla. Ichthyophids possess a nearly circular element that surrounds the orbit. It may be a neomorph, or a homologue of one of the circumorbital bones (e.g. postorbital or postfrontal) present in Palaeozoic tetrapods. In most genera, the premaxilla is exposed primarily ventrally, beneath the overhanging nasal region. There is a general tendency for more derived caecilians to exhibit further fusion of bones of the skull roof. Adults of extant caecilians never exhibit the quadratojugal or lacrimal bones that are variably seen in frogs and salamanders.

A unique feature of the caecilian skull is the presence of an opening for the tentacle (itself a unique sensory organ) between the margin of the orbit (in primitive genera, including *Eocaecilia*) and the narial opening (Fig. 37). There is a general tendency for the opening to be further forwards in more derived species. Another structural feature that distinguishes the caecilian skull from that of frogs and salamanders is
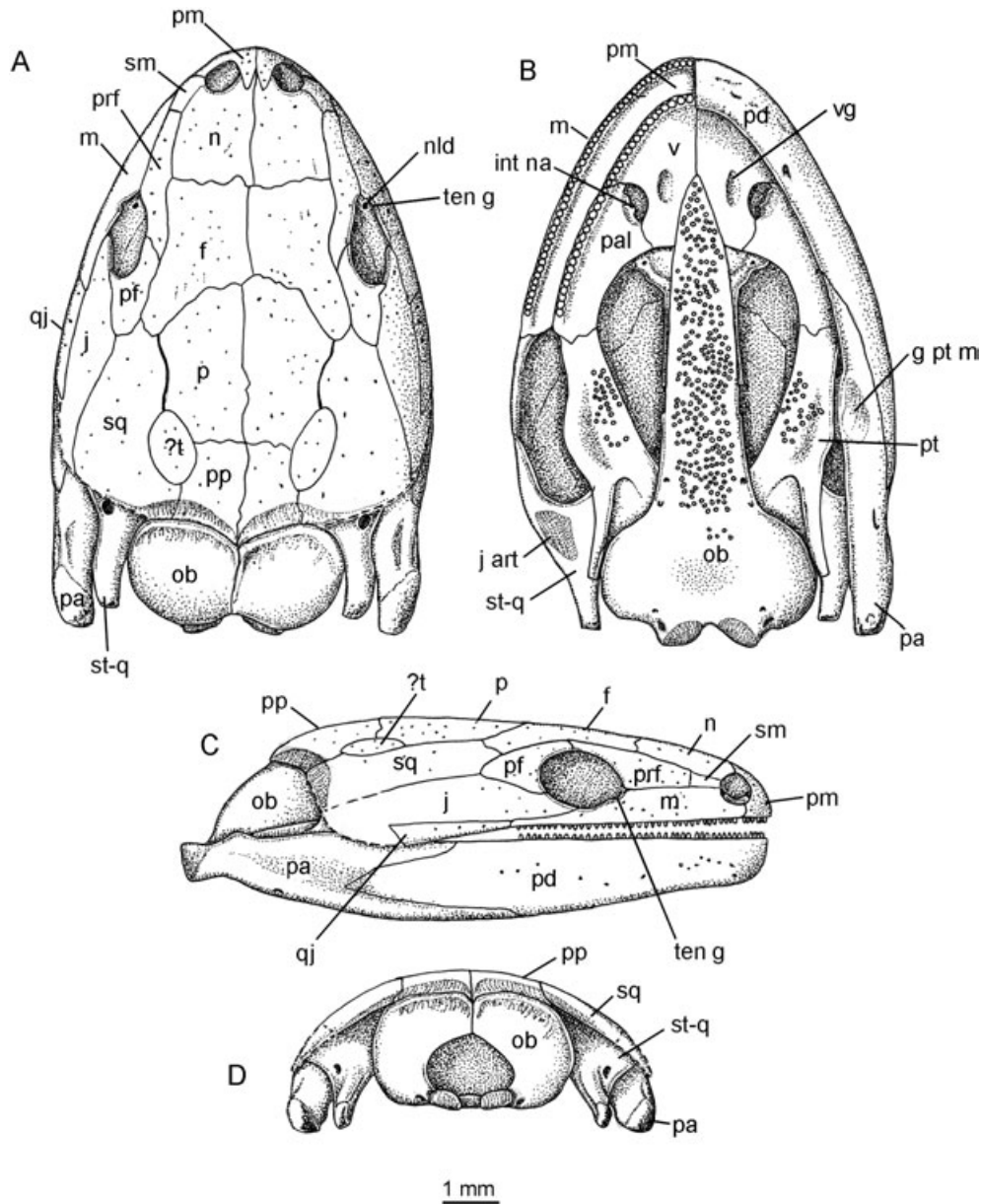
Figure 37. Skull of the most primitive fossil caecilian, *Eocaecilia*, from the Lower Jurassic of Arizona in dorsal, palatal, lateral, and occipital views. Reproduced from F. A. Jenkins, D. Walsh & R. L. Carroll, 2007 (in press).

the position of the jaw articulation anterior to the otic capsule. This is related to the unique nature of the jaw mechanics, which will be discussed below. In common with salamanders, no caecilian has any trace of an otic or squamosal notch, or other evidence of a middle ear cavity. The stapes, missing only in *Scolecomorphus*, is large and articulates closely with the back of the quadrate. The operculum is not present in extant caecilians, but a possibly comparable element has been described in *Eocaecilia* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007).

The palate of caecilians is distinct from that of frogs and salamanders in possessing a continuous row of teeth arising from the vomer and the maxillary portion of the maxillopalatine that runs parallel to the marginal tooth row, but extends further posteriorly. The internal nares are not bordered by the premaxillae anteriorly, but are more posterior in position. The maxilla and the palatine are distinct in the embryos and larvae, but fuse in the adults of all extant species, although not in the Lower Jurassic genus *Eocaecilia*. The ectopterygoid, not present in either frogs or sala-

manders, is variably expressed in a few caecilians (e.g. *Grandisonia alternanas*, BMNH 1974.958 (Carroll & Currie, 1975), *Geotrypetes*, *Microcaecilia*, and *Praslinia* (Wake, 2003). Because of the close integration of the lower jaws in all articulated specimens of *Eocaecilia*, it cannot be determined whether or not it possessed an ectopterygoid. The pterygoid may be a fairly large, distinct bone bordering a narrow interpterygoid vacuity, or it may be fused to the quadrate, or (in *Epicrionops*) be separated by a gap from the pterygoid process of the quadrate. There is a synovial joint between the pterygoid and the base of the braincase in *Dermophis* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007), somewhat comparable to that joint in salamanders. An articulating surface in this area of the braincase does not appear to be present in *Eocaecilia*. In extant caecilians, the narrow dorsal plate of the quadrate is tightly attached to the medial surface of the squamosal. The quadrate of *Eocaecilia* is bizarre

in being fused to the stapes without a trace of sutural attachment. It is described in more detail in 'Cranial sensory structures'.

Presumably in relationship to their burrowing behaviour, the braincase of caecilians is much better integrated that those of frogs and salamanders (Fig. 38). All the posterior elements of the occiput, otic capsules, and back of the braincase are fused into a single ossification, the os basale, including also the dermal parasphenoid (Wake, 2003). An ossification that is termed the pleurosphenoid in some early tetrapods forms the lateral wall of the braincase between the trigeminal foramen and the opening for the optic nerve, an area that is not ossified in either frogs or salamanders. The anterior portion of the braincase, including passages for the olfactory tracts, is fused into a massive sphenethmoid. In *Epicrionops*, the cartilaginous lamina orbitonasalis of the sphenethmoid extends laterally to form a posterior wall of the narial
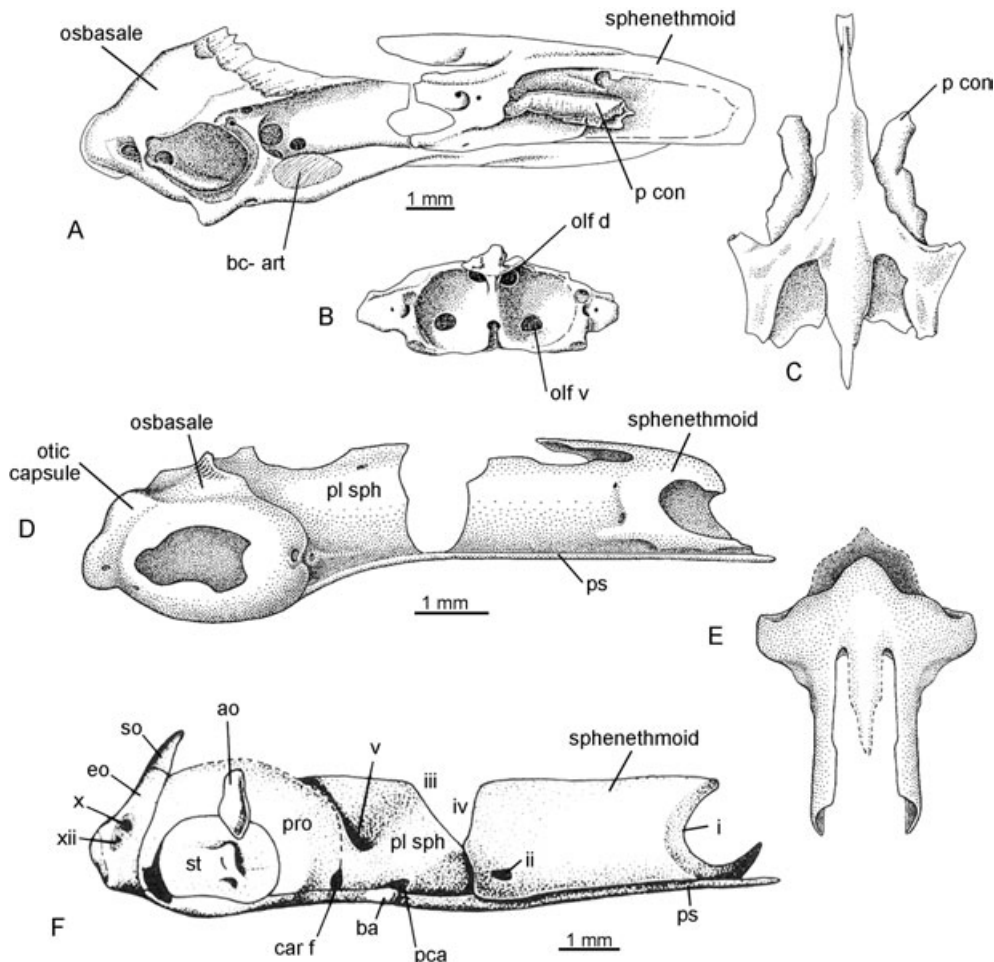

Figure 38. Comparative views of the braincase of the advanced modern caecilian *Dermophis* (A, B, C), the Lower Jurassic caecilian *Eocaecilia* (D, E), and the Lower Permian microsaur *Rhynchonkos* (F). A, D, F, lateral views. B, anterior view of sphenethmoid. C, E, dorsal views of sphenethmoid. Reproduced from F. A. Jenkins, D. Walsh & R. L. Carroll, 2007 (in press).

passage, possibly providing a buttress against the compressive forces of burrowing (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007). In some caecilians, as in some anurans, the sphenethmoid extends dorsally and is exposed at the midline of the skull. It is supported ventrally by the cultriform process of the parasphenoid.

Zygokrotaphy or stegokrotaphy?
It has long been assumed that the solidly roofed skull of most caecilians (a configuration termed stegokrotaphy) and the high degree of integration of the braincase were adaptations to burrowing. The open nature of the skull in the derived typhlonectids (termed zygokrotaphy) may be attributed to evolutionary reversal, related to their largely aquatic habits, but the temporal opening in the rhinatrematids *Rhinatrema* and *Epicrionops* might reflect an ancestral condition (Nussbaum, 1977). If caecilians originally had an open temporal region, it would support affinities with frogs and salamanders. However, evidence from the fossil record suggests that the stegokrotaphic condition is more likely to have been primitive. The Lower Jurassic caecilian *Eocaecilia* shows that generally more primitive caecilians had a solidly roofed skull, composed of numerous elements that are clearly homologous with the roofing bones of Palaeozoic amphibians (Fig. 37). There is unquestionably a pair of postparietals behind the parietal, as well as a second, smaller, and loosely attached temporal bone of uncertain identity that might be comparable to a supratemporal or tabular. That the parietal of modern caecilians has incorporated the area of a previously existing postparietal is suggested by the much greater length of the parietal relative to the frontal in primitive living genera, including *Epicrionops* and *Ichthyo-*

phis. There is also a clearly defined postfrontal bone, in contact with a large jugal (neither of which is present in frogs or salamanders). The ventral margin of the cheek is formed by an elongate quadratojugal. There is a small gap anterior to the orbit that may have marked the position of a lacrimal bone.

Information from *Eocaecilia* strongly supports the hypothesis that the closed skull roof common to most crown-group caecilians was inherited directly from that of primitive, solidly roofed Palaeozoic tetrapods. However, evidence from the sequence of ossification of the dermal bones of the skull is more equivocal.

Sequence of cranial ossification
In comparison to salamanders and frogs, there has been relatively little study of the development of the skull in caecilians. The classic study of the chondrocranium of the primitive caecilian *Ichthyophis* dates to Peter (1898) (Fig. 39), but a comparable pattern also occurs in the aquatic genus *Typhlonectes* (Wake, Exbrayat & Delsol, 1984), and the terrestrial *Dermophis* (Fig. 40) (Wake & Hanken, 1982), both of which bear live young. In comparison with the highly conserved configuration of the chondrocranium in bony fish and salamanders, that of caecilians appears to be highly derived, although in a manner very different from that of anurans (deBeer, 1985). Only the areas of the otic capsule, palatoquadrate, and Meckel's cartilage are comparable (Fig. 27).

The sequence of ossification of the dermal bones of the skull and lower jaw is also highly distinct from those in salamanders or frogs. The most detailed study has been that of Wake & Hanken (1982) on *Dermophis*. Unfortunately, this is a relatively advanced viviparous caecilian, without the aquatic larval stage that characterizes the more primitive gymnophionans.
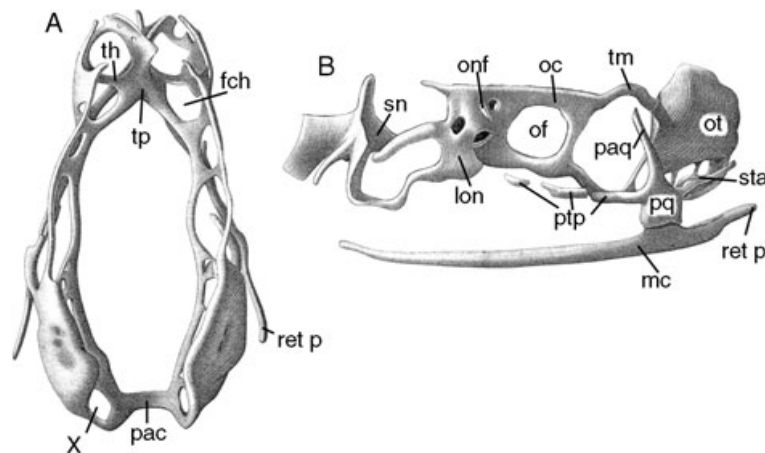

Figure 39. Chondrocranium of the primitive caecilian *Ichthyophis glutinosus*. Reproduced from Peter (1898). Note the striking differences from chondrocrania of frogs and salamanders (Fig. 27).
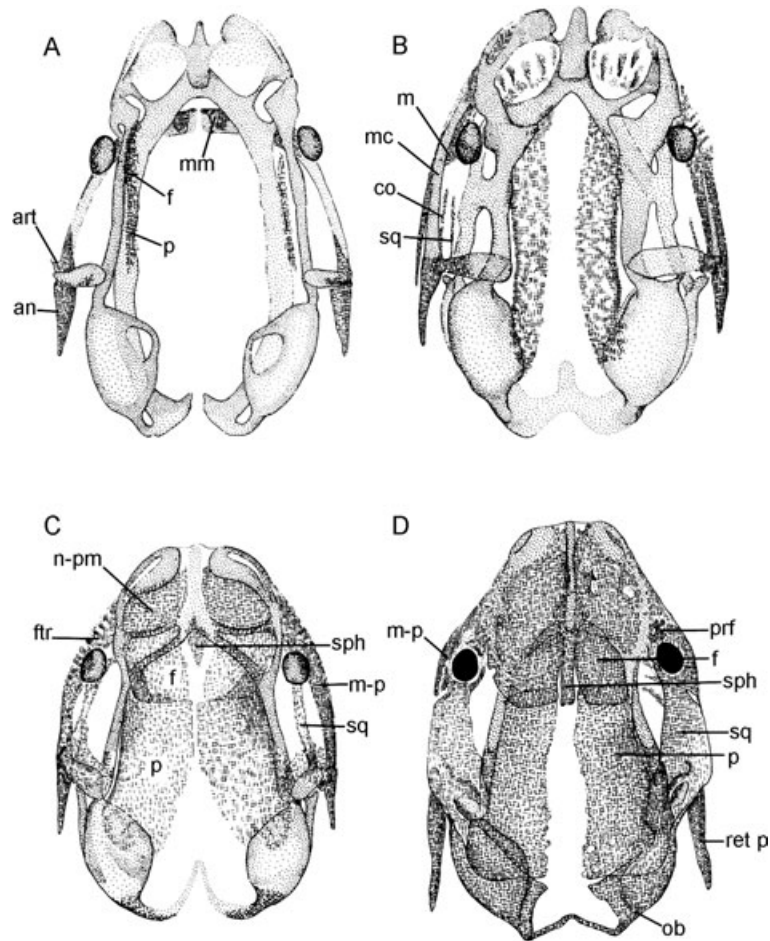
Figure 40. Sequence of ossification of the skull bones of the advanced caecilian *Dermophis*. Reproduced from Wake (2003).

The hyoid apparatus of the earliest developmental stage of *Dermophis* already resembles that of adults rather than larval rhinotrematids and ichthyophids (O'Reilly, 2000). Wake & Hanken (1982) and Wake (2003) argue that the particular sequence of chondrification and ossification of the *Dermophis* embryo, and the nature of its cranial kinesis, are related to its feeding on oviducal secretions and later on cells from the oviducal lining. Active feeding begins when the embryos emerge from the egg membrane, with a total length of 25 mm. The teeth, quadrate, and jaws ossify well ahead of the rest of the skull, followed by the occipital arch. The dorsal and lateral dermal bones ossify later, followed by the endochondral and dermal elements of the palate. The mouth is initially almost terminal, rather than subterminal as in the adult.

Analyses of earlier and less systematic studies of development in *Ichthyophis* show that it too ossifies the mentomeckelian, dentary, splenial, angular, articular, and quadrate early, although other bones, including the stapes, vomer, exoccipital, and elements of the braincase, ossify much later. The early ossification of the lower jaw and jaw articulation suggests that some aspects of the mechanics of feeding may be comparable in the ancestral free-living larvae of primitive caecilians and the embryos of derived viviparous genera. The overall sequence of development is clearly divergent from that of either the relatively conservative salamanders, or the highly divergent anurans, and provides no evidence for an immediate common ancestry.

Another striking feature of both the ontogeny and phylogeny of caecilians is the progressive fusion of initially independent areas of cranial ossification. In the dermal skull roof of *Dermophis mexicanus*, the maxillopalatine incorporates the nasal, premaxilla, septomaxilla, and sometimes the prefrontal. The pterygoquadrate is a further complex element. All the originally separate bones at the back of the braincase, the exoccipital, basioccipital, the area of the supraoccipital, otic capsule, basisphenoid, pleurosphenoid, and parasphenoid become integrated into the os basale. The sphenethmoids form from fusion of the orbitosphenoid, supraethmoid, and mesethmoid. In

the lower jaw, the pseudoangular results from fusion of the angular and articular. The pseudodentary forms in two stages, first by fusion of the dentary and mentomeckelian, and later with the incorporation of the splenial, coronoid, and complementale (an element of uncertain homology). The mentomeckelian elements are not expressed as separate bones in the adult, as is the case in frogs and salamanders.

Marcus, Stimmelmayr & Porsch (1935), in their work on *Hypogeophis*, attempted to demonstrate the incorporation during development of nearly all the bones that were originally present in Palaeozoic amphibians. Wake & Hanken (1982) could recognize only ~30 of the 36 distinct cranial elements (not including components of the lower jaw) postulated by Marcus *et al.*, but this nevertheless illustrates a phenomenon of development that is unmatched by either frogs or salamanders, and that is logically associated with both their small size and, more importantly, their burrowing way of life.

More recent studies by Wake (2003) show a surprising change in the degree of ossification of the cheek region in larvae and adults of the primitive caecilians *Epicrionops* and *Ichthyophis* (Fig. 41). In the larvae, nearly the entire cheek region is open, with only the anterior portion of the maxilla and the posterior segment of the squamosal ossified, exposing the braincase in lateral view. The squamosal and closely adhering quadrate appear to be attached only very loosely to the top of the braincase, and ventrally to the stem of the stapes. With metamorphosis, the cheek assumes the solid appearance (with only a small opening for the orbit) common to adult caecilians. A similar pattern of change is also seen during growth in the direct-
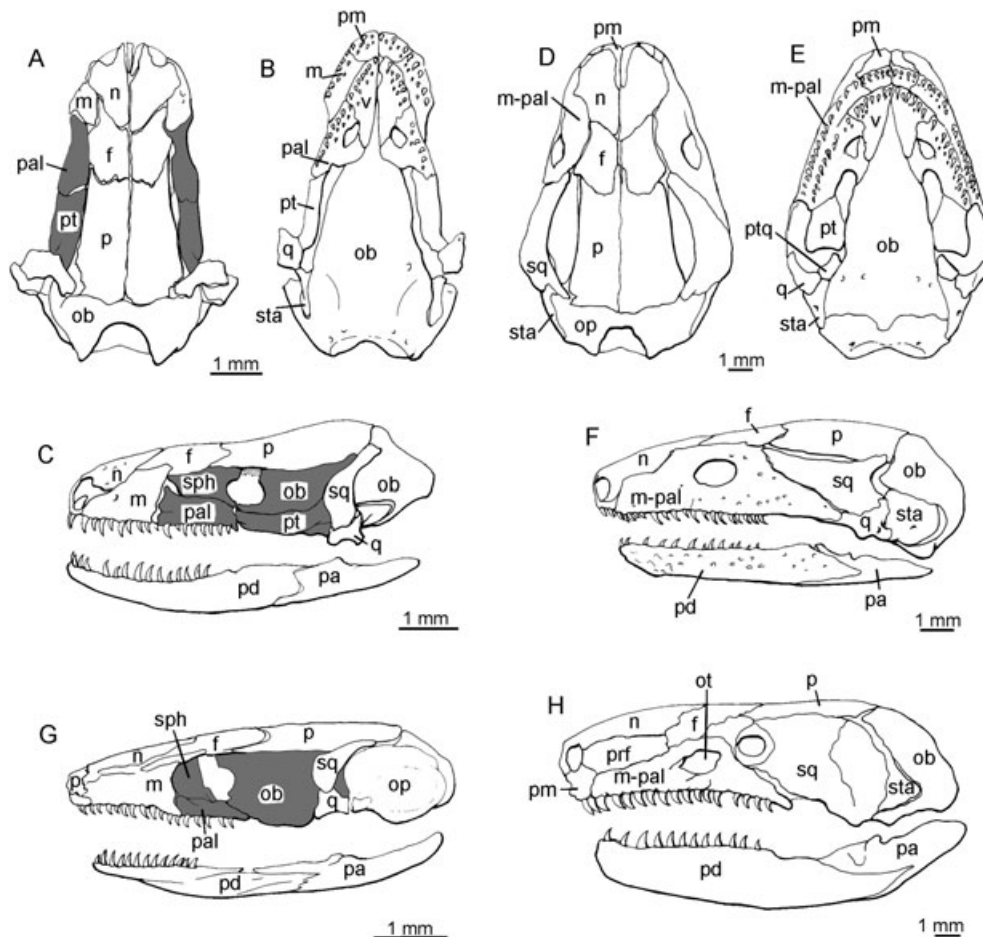
Figure 41. Changes in the ossification of the skull between advanced larvae and adults of primitive caecilians. A–C, dorsal, palatal, and lateral views of a larva of the primitive caecilian *Epicrionops bicolor*. Shaded areas show the bones that are exposed due to the long delay in ossification of the cheek region. D–F, dorsal, palatal, and lateral views of the adult of *Epicrionops bicolor*. Note the retention of a large dorsal opening between the squamosal and the parietal, and the posterior extension of the maxillary portion of the maxillopalatine. G, H, lateral views of the skull of the larva and adult of *Ichthyophis* sp. Modified from Wake (2003).

developing *Hypogeophis* (Reiss, 1996). The question is, does the slow ossification of the cheek indicate a retention of the ancestral pattern, or could it represent an example of larval adaptation? Unfortunately, no fossils are known of the larvae of extinct caecilians, or of any Palaeozoic tetrapods that might plausibly be considered as the sister taxa of caecilians. On the other hand, much information has been gained from Carboniferous fossils that have been postulated as the sister taxa of frogs and salamanders. The putative ancestors of salamanders and frogs (discussed in more detail in later sections) show very different patterns of development. The plesiomorphic sister taxa of frogs show little evidence of sequential ossification of the skull; rather, all the dermal bones appear to ossify at once. The putative sister taxa of salamanders (like their living descendants) do show a very clear sequence of ossification, but it is very different from that seen in caecilians.

Nearly all frogs maintain a continuous, although narrow, bar of bone along the ventral margin of the cheek made up of the maxilla and quadratojugal. Nearly all salamanders lack a bony connection between the maxilla and the quadrate, but a narrow ligamentous band is retained, lateral to the jaw muscles. This is clearly distinct from the changes apparent in primitive living caecilians. In addition, the 'temporal' openings of caecilians are surrounded by a very different pattern of bones from that seen in either frogs or salamanders (Fig. 8).

It is certain that the sequence and pattern of development of the skull in tadpoles and metamorphic anurans was the result of the insertion of a novel larval stage into the developmental sequence. Although the larvae of primitive caecilians are not nearly as specialized as the tadpoles of frogs, they nevertheless appear to have diverged from the primitive pattern seen in known Palaeozoic larvae, rather than reflecting an ancestral condition. The absence of a firm connection between the jaw suspension and the maxilla in caecilian larvae might have enabled the oral cavity to be expanded for suck-and-gape feeding, but this cannot be determined without additional knowledge of the mechanics of aquatic feeding in caecilians.

Cranial sensory structures
The relative importance of the cranial sensory structures of caecilians is very different from those of frogs and salamanders, and in fact from those of all other vertebrates. This is largely, if not entirely, linked to their high degree of adaptation to a burrowing way of life, as is clearly shown by the sense of vision. The eye is very much reduced, and in many genera is buried beneath the skin or dermal bone. On the basis of reduction of the retina and the optic nerve, and the

nature of the region of the brain for visual projection, it is doubtful that gymnophionans had the capacity for image formation (Fritzsch, Himstedt & Crapon de Caprona, 1985). Aquatic forms probably used electrical clues generated by their ampullary organs for tracking prey (Himstedt & Fritzsch, 1990; Deban, O'Reilly & Nishikawa, 2001).

Caecilians have remodelled many elements of the eye to form a new sensory structure, the tentacle, which has tactile and perhaps chemosensory functions (Fox, 1985). Its movements may also carry scents from the ground to Jacobson's organ, which is contiguous with the tentacular duct. The tentacle develops adjacent to the eye at the time of metamorphosis. Most caecilians, other than the plesiomorphic genus *Epicrionops*, can protrude the tentacle. In that genus, it exits from the skull just in front of the orbit. A groove in the maxilla of the Lower Jurassic gymnophionan *Eocaecilia* indicates a similar position for the tentacle.

Billo & Wake (1987) recognized the following homologies between elements associated with the primitive amphibian eye and the caecilian tentacle. The duct of the tentacle is remodelled from the lacrimal duct, and the extrinsic eye muscular is co-opted to extend and retract the tentacle; the retractor bulbi = the retractor tentaculi, the levator bulbi = the compressor tentaculi, the conjunctiva of the eye = the tentacle sac, the conjunctival sac = the tentacle sheath, the interpalpebral space = the tentacle aperture, and the lower eyelid = the tentacle fold.

In contrast with the eye, the sense of smell in caecilians is the most highly developed among any of the modern amphibian orders. The nasal capsule and the associated vomeronasal or Jacobson organ occupies a very large area of the skull anterior to the diminutive orbits (Badenhorst, 1978). Judging by the position and configuration of the sphenethmoid, this was already the case in *Eocaecilia* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007). According to Badenhorst (1978), the mode of development of the Jacobson organ of caecilians, as well as its innervation by the ventral ramus of the olfactory nerve, is undoubtedly homologous with that of the other amphibians and higher vertebrates in general. Because of their higher degree of terrestriality, the accessory nasal sacs of both frogs and caecilians are more complex than those of salamanders.

In common with salamanders, caecilians lack a tympanum and middle ear cavity, and have no sensory tissues that are responsive to high-frequency airborne vibrations. With the exception of *Scolecomorphus*, all have a stapes, which is connected to the quadrate by a synovial joint (Bemis, Schwenk & Wake, 1983). However, the living genera have no operculum, no opercularis muscle, and no shoulder girdle to which it might be attached. Wever (1978) has shown that caecilians

respond to low-frequency vibrations in the range that can be detected by salamanders: *Ichthyophis*, maximum sensitivity at 200 Hz; *Typhlonectes*, greatest sensitivity at 400 Hz; *Dermophis*, greatest sensitivity at 400 Hz, with a range up to ~1500 Hz.

The expression of the auditory papillae (also termed maculae) in the inner ear of gymnophionans shows considerable variation that may be useful for investigating their relationships with other tetrapods. Three types have been recognized among tetrapods. These include the papilla neglecta, the basilar papilla, and the amphibian papilla. Most vertebrates, going back to the lamprey, have a papilla neglecta, primitively located in the utriculus. In the shark *Carcharhinus*, this papilla has been shown to respond to a vibratory stimulus of 200 Hz (Fay *et al.*, 1974), but its function in amniotes is uncertain. Most terrestrial vertebrates, and the sarcopterygian *Latimeria* (Fritzsch, 1987), possess the basilar papilla, located in a medial recess of the lagena, which in frogs and amniotes responds to high-frequency vibrations (above 1000 Hz). Amphibians have long been thought to be unique among vertebrates in the possession of a separate area of sensitivity to low-frequency sound, the amphibian papilla, typically located in the sacculus. This was one of the most conspicuous synapomorphies cited by Parsons & Williams (1963) in support of the common ancestry of the modern amphibian orders. However, the pattern of its distribution among amphibians, and specifically gymnophionans, is open to different interpretations (Fritzsch & Wake, 1988).

Primitive frogs and salamanders have both an amphibian papilla and a basilar papilla. The basilar papilla is lost in more derived salamanders, but not in most frogs, where it plays a critical role in species recognition. Only caecilians have a macula neglecta. The primitive families Rhinatrematidae, Ichthyophidae, and Uraeotyphlidae retain a basilar papilla, but it is lost in more derived groups. Caecilians are the only group of vertebrates in which some species have both a macula neglecta and an amphibian papilla. As determined by Fritzsch & Wake (1988), these sensory tissues can be considered homologous on the basis of their common innervation from a single branch of the ramus of the VIIIth nerve to the posterior horizontal canal, the close association of the papilla neglecta and the amphibian papilla in some adult caecilians, and particularly positional changes during ontogeny. Early in the development of *Dermophis*, there is only a a single area of sensory epithelium in the utriculus (the area typically occupied by the papilla neglecta). However, this epithelium later divides, and one portion moves from the utriculus into the sacculus. Fritzsch and Wake argue that the amphibian-specific translocation of part of the papilla neglecta into the sacculus may be attributed to the dorsoventral flattening of the skull of amphibians, associated changes in the position of the utriculosaccular foramen, and the unique course of the amphibian periotic duct, which comes into close contact with the amphibian papilla.

If the amphibian papilla is homologous with the macula neglecta, the former tissue itself cannot be said to be a synapomorphy of the three amphibian orders. Nevertheless, the presence of two derivatives of the original macula neglecta in caecilians, frogs, and salamanders, one of which has a position that led it to be recognized as the amphibian papilla, does indicate a notable event that occurred within the history of the modern amphibian orders. However, if the subdivision occurred among caecilians, as is suggested by developmental data, their history must be different from that of frogs and salamanders, in which only one of these papillae is present, in a position distinct from that of the papilla neglecta.

The maintenance of the basilar papilla in anurans and its loss in caecilians and salamanders is clearly a reflection of the presence of an impedance-matching middle ear and the response to high-frequency vibration in frogs, but it should be noted that the basilar papilla was presumably retained also among primitive amniotes (including stem diapsids and stem synapsids), which did not evolve an impedance-matching middle ear until 50–90 million years after it had evolved in labyrinthodonts associated with the ancestry of frogs and salamanders. Judging from the different course of the periotic system, Fritzsch & Wake (1988: 214) suggested that the periotic labyrinth of tetrapods evolved at least twice, and reflects an independent adaptation to terrestrial hearing in amphibian and amniote lineages.

Knowledge of the Lower Jurassic amphibian *Eocaecilia* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007) provides interesting new information regarding the nature of the middle ear. *Eocaecilia* is unique among caecilians, and among tetrapods in general, in the fusion of the stapes and the quadrate into a single area of ossification that includes a large area for articulation with the articular bone together with a stapedial foramen and an extensive surface that overlays the fenestra ovalis. In contrast to the stapes of modern caecilians such as *Dermophis* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007), the 'footplate' of *Eocaecilia* does not fit closely within the fenestra ovalis, but overlaps a larger area of the otic capsule. The large 'columella' extends posteriorly, in parallel with the retroarticular process of the lower jaws. It is difficult to see how this massive element would have served the normal role of a stapes.

On the other hand, numerous specimens show a small, saucer-shaped ossification, either within the fenestra ovalis itself or in close association with the underside of the footplate of the fused stapes–

quadrate, that may be interpreted as an operculum. It is conceivable that an opercularis muscle extended from the margin of the operculum-like structure to the cartilaginous suprascapula, whose presence is indicated by the unfinished dorsal surface of the scapula (described with the appendicular skeleton). This ear ossicle might be homologous with the operculum of frogs and salamanders, but it is also possible that it was a uniquely evolved element that replaced the vibratory role of the stapes when it became fused with the quadrate.

Lower jaws

The lower jaws of adult caecilians are unique in being formed by the fusion of numerous separate bones common to primitive amphibians into two units, an anterior pseudodentary and a posterior pseudoangular, and in having a very long retroarticular process and an internal process medial to the jaw articulation (Fig. 42). These features are already fully expressed in the earliest known caecilian from the Lower Jurassic (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007).

The long retroarticular process is associated with a jaw-closing mechanism that is unique among vertebrates (Fig. 43). To facilitate burrowing, the skulls of caecilians are no wider than the trunk. This is achieved by having a very narrow adductor chamber, leaving little space for the normal jaw adductors. The main force for closing the jaws is provided by the interhyoideus posterior, a muscle that inserts at the back of the jaws in frogs and salamanders and serves to constrict the throat. In caecilians, this muscle is greatly enlarged and attaches to the extensive retroarticular process that acts as a first-class lever to raise the front of the jaw. Disarticulation of the lower jaw as a result of this ventral force is prevented by a complex jaw articulation and the presence of a large pterygoideus muscle that runs beneath the internal process and the lower surface of the back of the jaw like a sling.

As in frogs and salamanders, the jaw muscles that are located in the adductor chamber, the adductor mandibulae internus, adductor mandibulae externus, and adductor mandibulae posterior, can be recognized by their relationships with the rami of the Vth cranial nerve. In the plesiomorphic caecilian *Epicrionops*, the adductor mandibulae externus is the largest muscle, and it alone extends through the adductor fenestra and over the top of the braincase (Fig. 8). The levator quadrati is an enigmatic muscle unique to caecilians that may have separated from a portion of the adductor mandibulae internus, and inserts into a recess at the top of the quadrate (Fig. 43F). The quadrate appears to be strongly attached to the squamosal, so that contraction of the levator quadrati might serve to pull the cheek and jaw medially, thus closing the gap
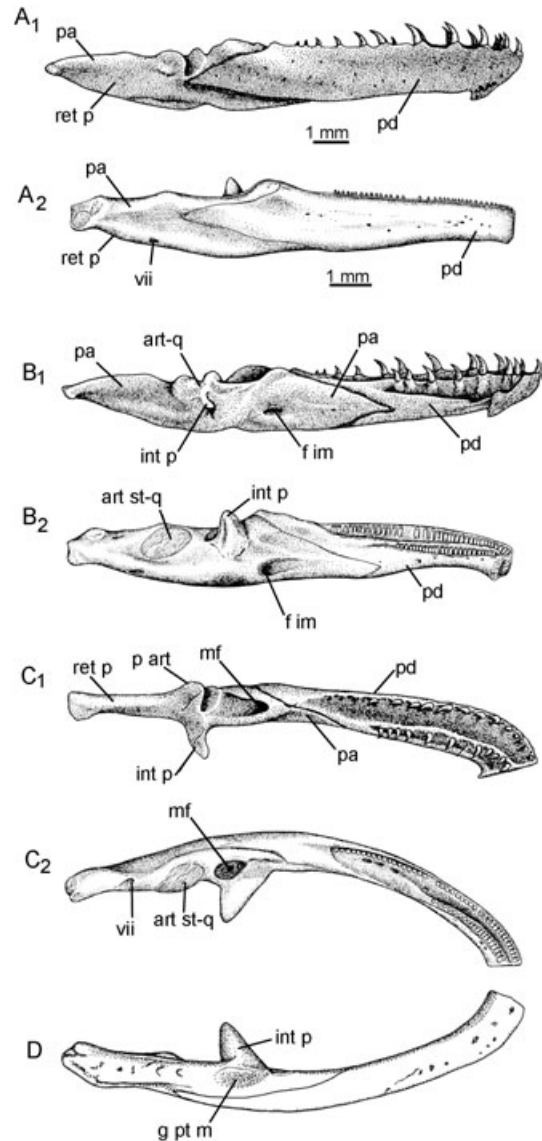

Figure 42. Comparisons of the lower jaws of the primitive living caecilian *Epicrionops*, A_1–C_1 [reproduced from Nussbaum (1977)], and the Lower Jurassic caecilian *Eocaecilia*, A_2–C_2 [reproduced from F. A. Jenkins, D. Walsh & R. L. Carroll, 2007 (in press)], in lateral, medial, and dorsal views. D, ventral view of the lower jaw of *Eocaecilia*, showing a groove for the passage of the pterygoideus muscle (g pt m), which extends under the lower jaw to maintain its attachment with the stapes–quadrate against the force of the interhyoideus posterior.

between the squamosal and the parietal. No function for such movement has been proposed.

The pterygoideus, which is generally agreed to have separated from the anterior portion of the adductor mandibulae internus, is a very important muscle in caecilians for holding the jaw articulation against the
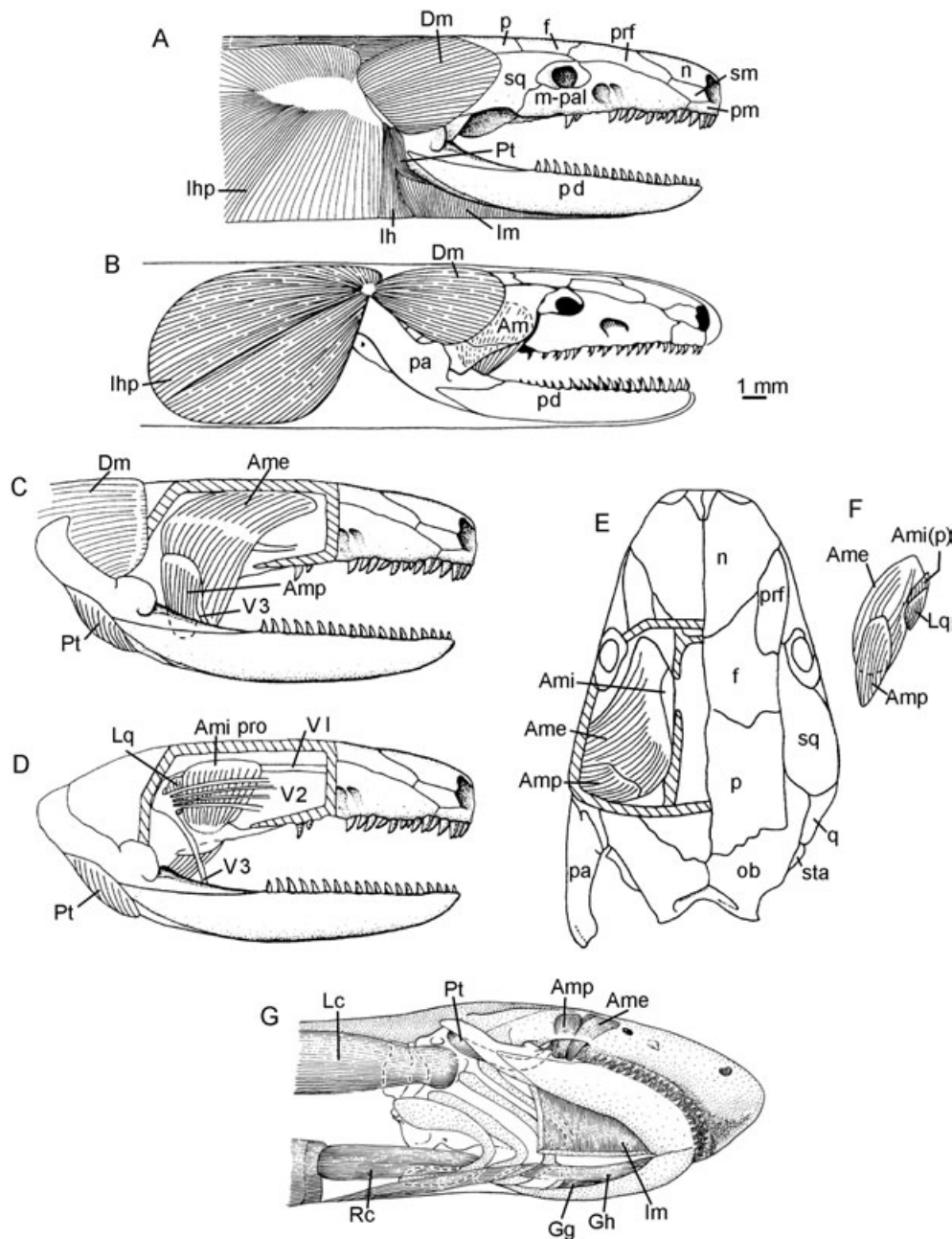
Figure 43. Jaw muscles of extant caecilians. A–F, the primitive genus *Ichthyophis glutinosus*. G, the caeciliid *Dermophis*. A, superficial view of all the major jaw muscles. B, diagrammatic view showing the major jaw-opening muscle, the depressor mandibulae, and the jaw-closing muscles, the very extensive interhyoideus posterior, and the much smaller adductor mandibulae complex. C, cutaway view of the adductor chamber, showing the extent of the adductor mandibulae externus and posterior. D, deeper view, showing the levator quadrati, adductor mandibulae internus (profundus), and the pterygoideus. E, dorsal view, showing the internus, externus, and posterior heads of the adductor mandibulae. F, posterior view of the adductor mandibulae complex. G, ventrolateral view of cranial, hyoid, and anterior trunk musculature of *Dermophis*. A, C–F, original drawings from specimens. B, reproduced from Nussbaum (1983). G, reproduced from Bemis *et al.* (1983).

quadrate in opposition to the strong downward force of the interhyoideus posterior. The pterygoideus in modern caecilians originates along the dorsal surface of the pterygoid, descends medial to the lower jaw, and inserts posteriorly on the ventral and lateral surfaces of the retroarticular process. It could serve both to open the jaw, in conjunction with the depressor mandibulae, and to pull it anteriorly. Nested within the

fibres of the pterygoideus is a massive ligament that inserts on the anterior, dorsal, and ventral surfaces of the internal process of the lower jaw, which would further assist in holding the lower jaw against the quadrate. The course of the pterygoideus in *Eocaecilia* can be recognized by a diagonal recess on the ventral surface of the retroarticular process in the position occupied by this muscle in living caecilians. Rugosities on the anterior surface of the internal process attest to the attachment of a ligament, such as those observed in the living species. In fact, it was knowledge of the recesses in the internal process of *Eocaecilia* that led to the search for a ligament in this position in *Ichthyophis* and *Epicrionops*.

Neither frogs nor primitive salamanders have a conspicuous pterygoideus such as characterizes the most primitive caecilians. The pterygoideus has not been identified in *Hynobius*, and is only poorly differentiated from the adductor internus in *Ambystoma*. However, a large pterygoideus is present in neotenic genera with a more derived cranial configuration, including *Cryptobranchus*, *Siren*, and *Necturus*.

A further muscle that acts to produce a strong bite is the longis capitis et colli (subvertebralis), a large, paired ventral trunk muscle that originates on the basapophyses of the anterior vertebrae, inserts on the cranium below the otic capsules, and bends the skull ventrally (Fig. 43G). This muscle, also present in salamanders, but not in frogs, is also important in producing the ventral flexion of the skull during burrowing (Wake, 1993). Anurans lack any subvertebral musculature (Duellman & Trueb, 1986: 335). The high degree of specialization of the axial musculature in frogs suggests that the absence of the subvertebralis results from its loss, rather than representing a primitive condition.

Bemis *et al.* (1983) refer to caecilians as jaw feeders that utilize the bone and muscle systems of the head for both prey capture and most of their prey processing. Terrestrial feeding is achieved by jaw protrusion. The floor of the mouth is lowered as food is captured, but this is apparently a result of the bulk of the prey. In contrast to frogs and salamanders, caecilians have not evolved a protrudable tongue, although the oral cavity is filled with a large, sessile genioglossus muscle. Extensive blood sinuses in both the tongue and the palate help to hold the prey within the mouth cavity and may assist in swallowing.

Hyobranchial apparatus
The larval hyobranchial skeleton of caecilians is considerably simplified relative to that of frogs and salamanders (Wake, 2003) (Figs 10, 44). That of *Epicriniops* and *Ichthyophis* is a jointed structure, like that of *Eusthenopteron* and salamanders, but is missing significant elements. These caecilians have a medial series of two or three bones equivalent to the basibranchials of salamanders or the copulae of anurans. The ceratohyals are readily compared, but there are apparently no elements equivalent to the hyobranchials of salamanders or the hyobranchial plates of frogs. Rather, there are three pairs of elongate ceratobranchials and a smaller, lateral remnant of the fourth.

Epicrionops, although one of the most primitive caecilians in other respects, is unique among caecilians in ossifying the major paired elements of the hyobranchial skeleton early in larval development, but replacing the bone by cartilage at the time of metamorphosis (Wake, 1989). In other caecilians, the hyobranchial skeleton remains cartilaginous throughout their lives, but shows significant changes in its configuration at the time of metamorphosis.

The hyobranchial skeleton of the adults is highly conservative throughout the order in the loss or fusion of independent medial elements, fusion of the left and right halves of all the paired bones, and fusion at the midline of the ceratohyals and the first ceratobranchial. The remnants of the fourth ceratobranchial are fused to the end of the third. All the elements become flattened relative to their rod-shaped configuration in the larvae (Wake, 2003).

The aquatic larvae of *Epicrionops* and *Ichthyophis* have been observed to use suction feeding (O'Reilly, 2000), but the detailed mechanics of movements between the elements of the hyoid apparatus have not been described. Larvae of *Epicrionops* have only been observed using hydraulic transport, although Wake (1989) describes the tongue as being apparently manoeuvrable. Typhlonectids feed in the water as both juveniles and adults, but they use jaw prehension rather than suction feeding. The hyoid apparatus of the juveniles much more closely resembles that of the adults in this and other derived caecilians than it does in the more primitive families.

In contrast to the clearly distinct skeletal anatomy of the hyoid apparatus in caecilians, as compared with that of frogs and salamanders, most of the hyoid muscles can be homologized among all three groups (Edgeworth, 1935; Lawson, 1965). This points to an ultimate common ancestry, but perhaps not much above the level of tristichopterids and the most primitive tetrapods.

The adult hyoid is thought to function in respiration, but seems to play little part in feeding. Bemis *et al.* (1983) refer to several of the same muscles as seen in frogs and salamanders. The rectus cervicis and the geniohyoideus are connected in series as in salamanders, but electromyographic records indicate contraction during respiration but not during jaw depression. The levator arcus branchiales originates
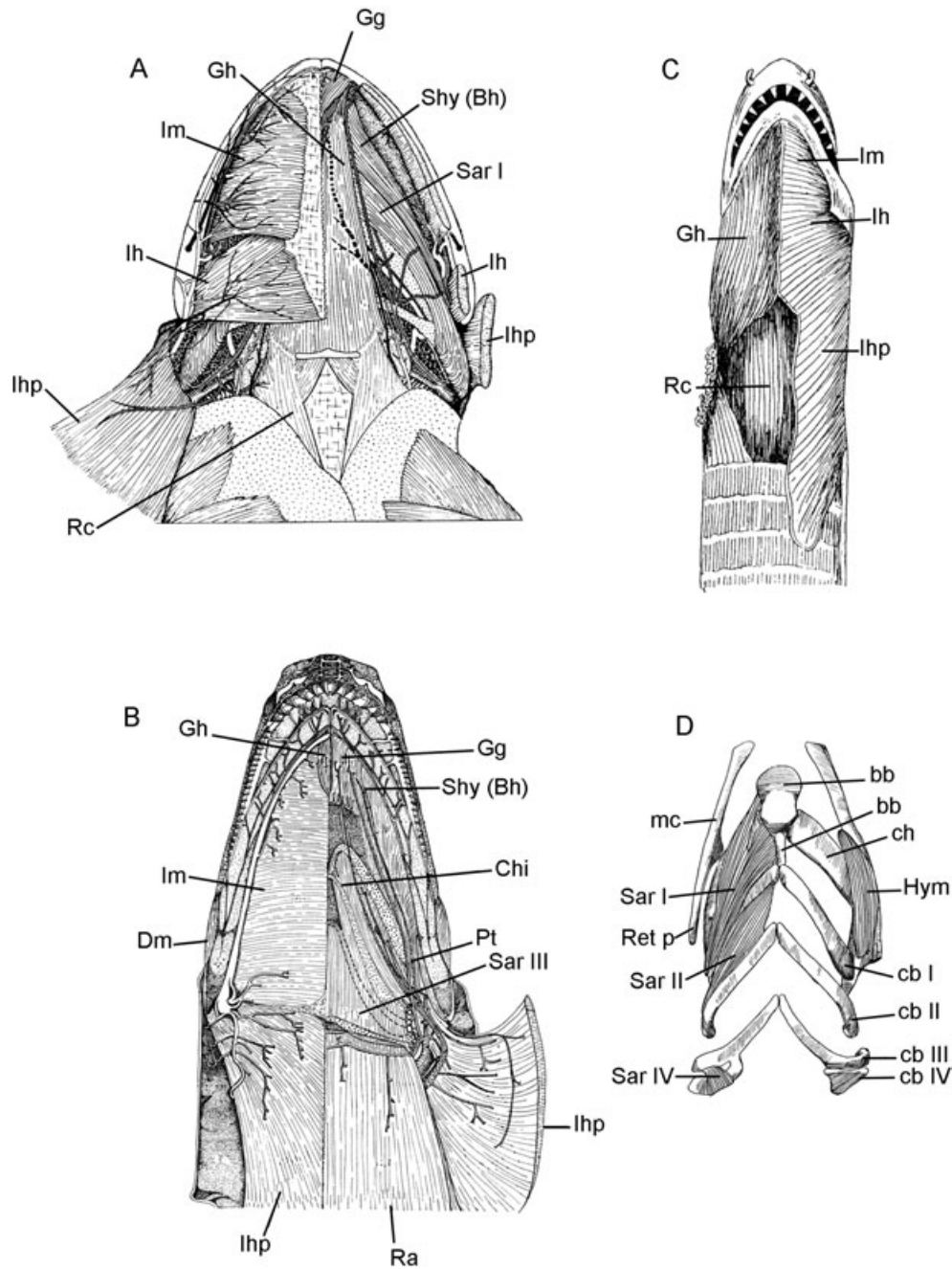
Figure 44. Hyoid musculature of *Salamandra* and caecilians. A, ventral view of the jaw musculature of *Salamandra*. Reproduced from Francis (1934). B, ventral view of the jaw musculature of *Hypogeophis rostratus*. Reproduced from Lawson (1965). C, superficial view of the ventral musculature of *Caecilia lumbricoides*. D, ventral view of hyobranchial skeleton and associated muscles of *Ichthyophis*. C, D, reproduced from Edgeworth (1935).

on the dorsal fascias of the trunk, passes ventrally beneath the interhyoideus posterior, and inserts on the hyoid apparatus, which it is thought to elevate during both respiration and feeding. This muscle is also present in the larvae, but not the adults, of salamanders and frogs. The intermandibularis elevates the buccal floor. None of the muscles that move the

individual elements of the hyoid apparatus relative to one another in salamanders has been studied in detail.

Respiration
In common with frogs and salamanders, all caecilians rely on cutaneous respiration. In association with their elongate body, only one lung (the left) is typical of

the group. The highly derived typhlonectid *Atretocho-ana* is unique in lacking lungs entirely, and the internal nostrils are sealed (Wilkinson & Nussbaum, 1999).

Vertebrae

The most conspicuous feature of caecilians is the great elongation of the vertebral column – in living genera, there are up to 285 vertebrae. Trunk elongation is not unique to caecilians among the Amphibia, but is conspicuous in sirenids and amphiumids among the extant urodeles, and is expressed in all members of the Aïstopoda, Adelospondyli, and Lysorophia, and some families of microsaurs among the Palaeozoic lepospondyls. The fossil record of Palaeozoic amphibians (Carroll *et al.*, 1998), and phylogenetic analysis of the modern families (Cannatella & Hillis, 1993a), demonstrate that increases in the number of trunk vertebrae occurred within most of these groups, and the large and consistent differences in the cranial anatomy of each argue against common ancestry of this character across this diversity of lineages. The great elongation of the vertebral column certainly differentiates caecilians from all anurans and from basal urodeles, and its functional ties to burrowing indicate a clear adaptive difference from the elongation that has evolved in sirenids and amphiumids.

The individual vertebrae of extant caecilians are unipartite structures, with amphicoelous centra firmly fused to the arches. They are clearly distinct from those of frogs and salamanders in the elaboration of greatly elongate parapophyses for articulation with the capitula of the ribs that extend far anteriorly from the base of the centra (Wake, 2003) (Fig. 45).

Caecilian vertebrae are known from fossils dating from the early and late Palaeocene (Estes & Wake, 1972; Rage, 1991) and the Late Cretaceous (Evans *et al.*, 1996) that closely resemble living genera. In contrast, an atlas vertebra of *Rubricacaecilia* from the early Cretaceous (Evans & Sigogneau-Russell, 2001) has a conspicuous interglenoid tubercule not present in modern caecilians, and trunk vertebrae that lack the long, anteriorly directed parapophyeal processes that characterize all living species.

Even more primitive, but much better known, is *Eocaecilia* from the Lower Jurassic (Jenkins & Walsh, 1993; F. A. Jenkins, D. Walsh & R. L. Carroll, 2007). Numerous specimens are known, from which many features of the vertebral column can be established. The total number of vertebrae is estimated as 64, including two sacrals and 13 caudals, close to the minimum of 70 presacrals recorded among living species (Nussbaum & Naylor, 1982). Five areas of regionalization can be recognized. Posterior to the atlas are four additional vertebrae that can be recognized as cervicals by the presence of intravertebral foramina in the pedicles for spinal nerves, and roughly by the position of elements of the shoulder girdle and forelimbs. Posterior to the five cervicals are approximately 44 trunk vertebrae. They lack intravertebral foramina, and show an increase in the angle of the zygapophyses from nearly horizontal to approximately a 45° angle. The length of the centra increases among the anterior dorsals, and decreases more posteriorly, as in the living *Dermophis*. Two vertebrae are recognized as sacrals by the elevation of the tubercular facets from the lateral surface of the pedicels, the shorter distance between the postzygapophyses, and the shorter length of the centra relative to that of the posterior dorsals. These vertebrae lay at the level of the rear limbs. There are approximately 13 caudal vertebrae, with perforated haemal arches and prominent, posteriorly directed spinous processes.
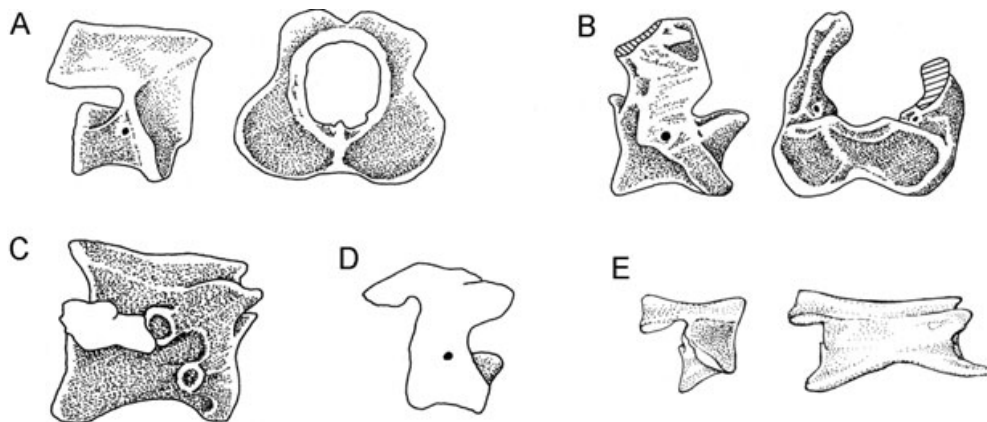
Figure 45. Caecilian vertebrae. A, atlas vertebra of *Ichthyophis mindanaoensis* in right lateral and anterior views. B, atlas of the Lower Cretaceous *Rubricacaecilia monbaroni*. C, right lateral view of anterior trunk vertebra of *Rubricacaecilia monbaroni*. D, atlas of the Lower Jurassic *Eocaecilia macropoda*. A–D, reproduced from Evans & Sigogneau-Russell (2001). E, lateral views of atlas and posterior trunk vertebra of *Typhlonectes natans*. Reproduced from Wake (2003).

The vertebrae of *Eocaecilia* differ fundamentally from those of living genera in the presence of intercentra in the position of the anteriorly directed parapophyses of all modern caecilians. Except for the first cervical rib (between the atlas and the axis), which articulates with both the intercentrum and the pleurocentrum, the remainder articulate with only the centrum.

The mode of vertebral development has long been thought to distinguish different groups of vertebrates. The most detailed study of caecilian vertebral development was undertaken by Wake & Wake (2000) on the advanced caecilian *Dermophis*. They note that development is strongly cephalized, so that the posterior-to-anterior sequence along the column shows a progressive sequence of developmental states. The anterior portion of the column becomes ossified before the adjacent portion of the otic capsules. Three stages of development of the arches and centra can be recognized: pre-cartilaginous condensation of cells, calcification, and ossification. Pre-cartilaginous condensation of the tissue that gives rise to the neural arch rudiments (basi-dorsals) is established before the perichondral tube is well formed, but calcification of the arches and centra occur at approximately the same time.

The early ossification of the entire column can also be seen in hatchlings of the primitive living caecilian *Epicrionops* and in *Schistometopum* (Carroll *et al.*, 1999). A comparable pattern can be seen in advanced salamanders, but is in strong contrast to the sequence in frogs, in which both chondrification and ossification of the arches occur well before that of the centra. The surfaces of the occipital condyle and the atlas vertebra become ossified at an early stage in caecilians, to facilitate effective feeding and locomotion. Ball-and-socket joints between the trunk vertebrae never develop among caecilians, as they do in frogs and salamanders.

Another developmental difference that distinguishes the vertebrae of caecilians from those of frogs and salamanders is the clear appearance of a sclerocoele within the sclerotomes of each somite, which provides strong evidence for the resegmentation of the tissue contributing to the vertebrae, as in amniotes. Resegmentation of the vertebral rudiments has not been demonstrated in frogs and salamanders, in which there is a much smaller number of cells in the scanty scleotomal tissue at a comparable stage of development. The phylogenetic significance of this difference cannot be determined, as there is no way for it to be studied from more primitive, fossil representatives of these taxa.

Appendicular skeleton
No extant caecilian shows a trace of girdles or limbs, even in early development [Wake (2003), in contrast to the claims of Renous, Exbrayat & Estabel (1997)]. Apart from the proximal end of a femur found in close association with elements of the axial skeleton of the Lower Cretaceous caecilian *Rubricacaecilia monbaroni* (Evans & Sigogneau-Russell, 2001), all our knowledge of the appendicular skeleton of caecilians stems from the Lower Jurassic genus *Eocaecilia*, as described in detail by F. A. Jenkins, D. Walsh & R. L. Carroll (2007). Remains of the pectoral girdle, forelimbs, and hindlimbs are found in close association with several skeletons, but few bones are complete or in immediate articulation.

The shoulder girdle is thought to be located at the end of the cervical series, at about the level of the fifth vertebra. Nothing is known of the dermal shoulder girdle. It was presumably lost, as was that of salamanders, by this time in their evolutionary history. The scapula and coracoid are sutured to one another, with evidence of their attachment in the area of the glenoid. The scapular blade narrows above its line of contact with the coracoid, and then expands dorsally. The dorsal margin is unfinished where a cartilaginous suprascapula may have attached. The anterior margin of the scapula is incised at its base, and may have enclosed a coracoid foramen. The glenoid is formed jointly by the scapula and coracoid. It retains the spiral configuration common to Palaeozoic tetrapods. Ventral to the anterior half of the glenoid is a circular fossa, similar in size and position to that seen in some microsaurs (Carroll & Gaskill, 1978; Carroll, 1991), but of uncertain function or homology.

The humerus, varying from 4.25 to 4.4 mm in length, or roughly equivalent to the length of two anterior dorsal vertebrae, has a large area of proximal articulation in the form of a spiral, extending from the dorsolateral to the ventromedial surface of the bone. A short shaft, round in cross-section, separates the proximal and distal surfaces of articulation. There is no entepicondylar foramen in the modestly expanded distal portion of the bone. There is a bulbous, hemispherical capitulum for articulation with the radius and a trochlea for the ulna. The radius, approximately 2 mm in length, has a round proximal facet at about a 20° angle to the long axis of the shaft. The ulna has a short but distinct olecranon. The distal end is slightly expanded and perpendicular to the shaft. Mesopodials, metapodials, and phalanges are associated, but so disarticulated that their natural arrangement cannot be restored.

Crushed bones in association with the sacral vertebrae and the rear limb may represent a pelvis, but its original shape cannot be determined. A complete femur is 4.4 mm in length. It is distinguished by a bulbous, approximately oval, head, in contrast with the elongated surface of the proximal articulation common to Palaeozoic amphibians. There is a prominent

triangular trochanter on the medioventral side of the shaft. It is expanded distally, with the condyles separated by an intercondylar groove. The tibia, approximately 2.1 mm long, is less than one-half the length of the femur. A slightly raised area of the shaft, proximal and anterior, may represent a cnemial crest. The proximal end of the fibula (which ranges from 1.9 to 2.1 mm in length) is at about a 45° angle with the shaft. Where in articulation, the expanded end of the fibula terminates short of the distal end of the tibia. The two bones bear facets for articulation with the fibulare, intermedium, and tibiale. At least some digits possess three phalanges each. Several specimens retained three digits.

The limbs are much reduced in size relative to those of most salamanders or Palaeozoic tetrapods, but the bones (including the mesopodials) are well ossified, with well-defined articulating surfaces. The limbs presumably continued to function in quadrupedal locomotion, as in long-bodied salamanders and lizards.

Locomotion

The elongate, snake-like extant caecilians rely entirely on their axial muscles for locomotion. In an aquatic medium, they are propelled by lateral undulation, generated by travelling waves propagated along the length of their bodies. They may also use lateral undulation on land and in vegetation. All caecilians have some capacity for burrowing, which appears to have influenced their anatomy throughout the history of this order. Studies by Summers & O'Reilly (1997) and O'Reilly *et al.* (2000) documented the importance of a particular mode of burrowing locomotion, internal concertina, in a wide range of living families, from the primitive Rhinatrematidae and Ichthyophiidae to the advanced caeciliid genus *Dermophis*. The only family (or subfamily) that does not practise internal concertina locomotion is the derived Typhlonectinae, an aquatic clade that has apparently lost this trait. Internal concertina locomotion is the capacity for the vertebral column to form a sinusoidal curve without this being reflected in the external curvature of the trunk. This is possible because of functional separation of the axial musculature from the overlying muscles of the body wall. Internal concertina locomotion enables caecilians to burrow through strongly indurated sediments without expanding the burrow beyond the diameter of the trunk.

The epaxial muscles, consisting of the dorsalis trunci and interspinalis, are similar to those of salamanders, without the specializations of anurans. The hypaxials are more complex. The subvertebralis and basapophyseal muscles are ventral to the vertebrae. The subvertebralis pars ventralis originates on the mid-ventral surface of the vertebrae and inserts on the lateral (hypaxial) body wall musculature. The external obliquus (pars profundus) and rectus lateralis make up the lateral and dorsal components of the lateral body musculature. There are three additional muscles with more vertical orientations. The external oblique (pars superficialis) and internal oblique (at a 90° angle to each other) both insert directly into tendinous fibres embedded in the body wall, and are organized in a crossed helical array surrounding the entire trunk. The transversus is vertically oriented, and runs from the ventral part of the subvertebralis to a tendinous sheet that holds the viscera in a transverse sling.

The vertebral and body wall muscles form separate functional units. The vertebral musculature functions to bend or stabilize regions of the vertebral column. The muscles form a travelling wave during swimming, and standing waves during lateral undulation on land and during vermiform or concertina locomotion. The body wall musculature is associated with a complex of tendons that generate hydrostatic pressure on the body cavity to maintain a rigid body shape, and play a key role in generating propulsive forces. The force for burrowing is generated by the vertically oriented muscles in the body wall. The superficial external and internal oblique muscles insert into fibrous tendons that form the stratum compactum of the dermis. Their contraction narrows and elongates the active portion of the body wall, moving the body forwards, beyond the level of the adjacent vertebrae, while the greater diameter of the more posterior portion of the trunk anchors it to the side walls of the burrow.

Scales

Dermal scales, somewhat resembling those of early bony fish, occur in many caecilians, but comparable structures are not known in either frogs or salamanders. Wake (2003) does not attribute any phylogenetic significance to their presence, but their retention suggests divergence of caecilians prior to the separation of the lineage or lineages leading to frogs and salamanders. The scales are set in pockets, and have a vague resemblance to those of Palaeozoic amphibians, but are not closely comparable to those in any known taxa. Detailed features described by Wake (2003) are apomorphic to the order.

Reproduction

There are several modes of reproduction among caecilians (Wake, 1992; Dünker, Wake & Olson, 2000). A common pattern among primitive species is for the eggs to be deposited on land, and for the hatchlings to wriggle into nearby streams, where they undergo a free-living larval period before metamorphosis. In strong contrast to most primitive frogs and sala-

manders, no caecilians are known to lay their eggs in the water. Those that have aquatic larval stages enter the water only after hatching (Wake & Dickie, 1998). Prior to hatching, they have extensive external gills that may serve for oxygen exchange within the egg, but these are lost at hatching or during metamorphosis. No more than rudiments of the gills persist in the larvae of the primitive species *Epicrionops petersi* and *Epicrionops bicolor*. The larvae feed with the help of electroreceptive ampullary organs. In contrast to those of anurans, larvae of caecilians closely resemble the adults, morphologically, physiologically, and trophically. Metamorphosis is a gradual process, involving loss of the caudal fin and lateral-line system, closure of the gill slits, and appearance of the tentacle. The morphology of the hyobranchial apparatus changes significantly between the aquatic larvae and the terrestrial adults of the primitive caecilians *Epicrionops* and *Ichthyophis*. Three gill slits are present in the larvae. Presumably, they remained closed when the pressure in the gill chamber dropped, and opened when water in the buccal cavity was forced through the gills.

Other, more derived, species undergo direct development within the egg, and have fully metamorphosed juveniles at hatching. In contrast to the situation in frogs and salamanders, viviparity is the predominant reproductive mode. Perhaps more than half of the living species, including the aquatic typhlonectids, retain the developing young in the female's oviducts, and nutrients are provided to the young after the yolk is exhausted (Wake & Dickie, 1998).

ANCESTRY OF SALAMANDERS

ESTABLISHING RELATIONSHIPS

Having discussed the structural and functional aspects of the anatomy that distinguish the modern orders, we can now look for evidence of these traits across the diversity of Early Mesozoic and Late Palaeozoic forms. This will be done initially for each of the extant taxa separately; after this, the relationships between these clades will be considered.

The fossil record shows a high degree of conservation of the skeletons of salamanders, frogs, and caecilians back to the Middle or Lower Jurassic. It is logical to assume a similar degree of conservation of the skeletal muscles and the general way of life, including a biphasic life history. The minimum time of achievement of the synapomorphies of the crown taxa must date well before the base of the Jurassic, but the actual time can only be determined on the basis of the fossil record. The problem is to extend recognition of more plesiomorphic character states of the crown-group characters into the Triassic and Palaeozoic. This involves using as many skeletal characters as possible

to recognize a nested sequence of synapomorphies going back to the Carboniferous. These synapomorphies may have evolved at a succession of levels: (1) those that support a monophyletic origin of each of the crown taxa; (2) those that support clades including any of the three possible pairs of the extant orders (i.e. frogs + salamanders; salamanders + caecilians; or caecilians + frogs); (3) those that support the monophyletic origin of all of the modern orders to the exclusion of any other Palaeozoic clades; or (4) those that support the sister-group relationship between any one of the Palaeozoic clades and one or two of the extant orders.

The major portion of this work has been devoted to establishing the character states that distinguish the phylogenetically most primitive members of the crown group of each of the extant amphibian orders. These characters will now be used to recognize putative sister taxa among the many lineages of Palaeozoic tetrapods. Attention will be focused primarily on the identification of unique derived characters known only in one or more of the extant clades and among individual taxa of early Mesozoic and Palaeozoic tetrapods. However, the probability of close relationships can also be supported by the retention of similar primitive characters. Attention will also be paid to the relative likelihood of the transformation of specific characters across potential transitions between Palaeozoic and extant lineages.

Knowledge of character transformations within well-known lineages of both Palaeozoic and extant clades provides a basis for judging the likelihood of transformations between these lineages. For example, loss and/or fusion of bones is generally more common than gain. Convergent loss of comparable bones is common in lineages without an immediate common ancestry. Elongation of the vertebral column and reduction of limbs is more probable than shortening of the column and re-elaboration of limbs. Among both Palaeozoic and extant orders, life-history traits (whether or not there are distinct aquatic and terrestrial stages) and general body form and way of life (whether terrestrial, aquatic, or burrowing) are associated with distinct character complexes that are resistant to (but not precluded from) major change within or between groups.

THE EARLY FOSSIL RECORD OF CROWN-GROUP URODELES

Detailed descriptions of the structural and functional anatomy of salamanders have been based primarily on extant species that are included in the crown taxon Urodela. However, the fossil record shows that many of the skeletal features of the extant families had been achieved by the Late Jurassic (Fig. 46). Certainly, the
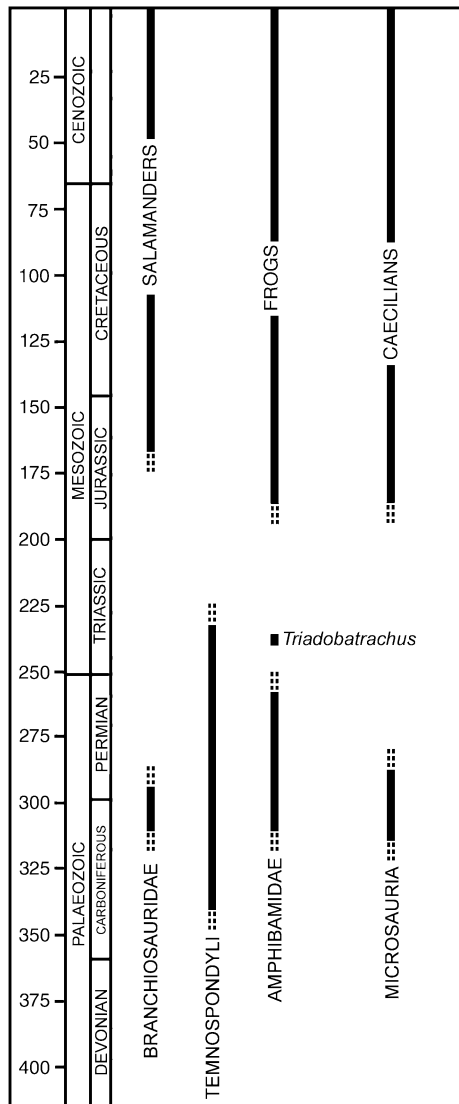
Figure 46. Geological time scale, showing temporal duration of taxa pertinent to the ancestry of the modern amphibian orders [time scale from Gradstein, Ogg & Smith (2004)].

two superfamilies, Cryptobranchoidea and Salamandroidea, were distinct before the end of the Jurassic, but the time of divergence among the salamandroid families remains less well resolved.

There is still some question regarding the age of Mesozoic salamanders from China, with estimates ranging from Middle Jurassic to Early Cretaceous (Evans *et al.*, 2005), but there is strong evidence for the occurrence of cryptobranchids and possibly hynobiids by the beginning of this sequence (Gao & Shubin, 2003). This is illustrated by superb specimens of the cryptobranchid *Chunerpeton tianyiensis*, which demonstrates the prior separation of this family from the

Hynobiidae (Fig. 47). Specific cryptobranchid characters of *Chunerpeton tianyiensis* include extensive flattening of the skull, the vomerine tooth row parallel and close to that of the premaxilla and maxilla, reduction of nasals, the anterolateral process of the parietal extending along the lateral border of the frontal, and retention of internal carotid foramina within the parasphenoid. The phalangeal count of the manus is 2,(2/3),3,2, and that of the pes is 2,2,3,4,3. The total length of the type specimen is 180 mm, but it still retains gill rakers, and the carpals and tarsals are not ossified, indicating that it was paedomorphic.

A smaller, early larval stage of another, unidentified urodele genus is known from the same area (Fig. 48A). This is unquestionably comparable to the early larvae of a wide range of primitive living salamanders in the sequence of ossification of the dermal bones of the skull, the nature of the external gills, and general body outline. The skull bones resemble those of a stage II larva of *Ambystoma texanum* in the ossification of tooth-bearing elements of the lower jaw, premaxilla, fragments of the palate, the frontal and parietal, and the squamosal angling forward to the jaw articulation (Fig. 13: C_{1-3}). One may also note the relatively great size of the conchostracan shells in the digestive tract that could only be accommodated by extensive expansion of the oropharyngeal cavity.

Especially important is the ossification of the neural arches prior to the centra, clearly shown in the anterior caudal region. This sequence is known only in the most primitive living salamanders, within the Hynobiidae. The tail fin is very deep, and extends forwards onto the trunk dorsally, as in pond-dwelling larvae of modern salamanders, including most members of the genus *Hynobius*, ambystomatids, salamandrids, and some plethodontids (Duellman & Trueb, 1986). This specimen shows that many features of primitive living salamander larvae had evolved by the Middle to Late Jurassic.

Iridotriton, from well-dated beds of the Morrison Formation of Utah, documents a primitive salamandroid from the Upper Jurassic (Evans *et al.*, 2005). In contrast to the neotenic nature of *Chunerpeton*, *Iridotriton* is a fully metamorphosed adult, although with a skull–trunk length of only 50–60 mm. It is not possible to classify *Iridotriton* in any of the extant salamandroid families, but it may occupy a stem position relative to the subsequent radiation of that superfamily. The centra are ossified as complete cylinders, without a trace of intercentra, even at small body size. One specific feature that *Iridotriton* shares with salamandroids is the fusion of the ulnare and intermedium, which remain separate in hynobiid cryptobranchoids. The squamosal articulates dorsally with the braincase, but not with the parietal, as it does in most hynobiids and cryptobranchids. On the other hand,

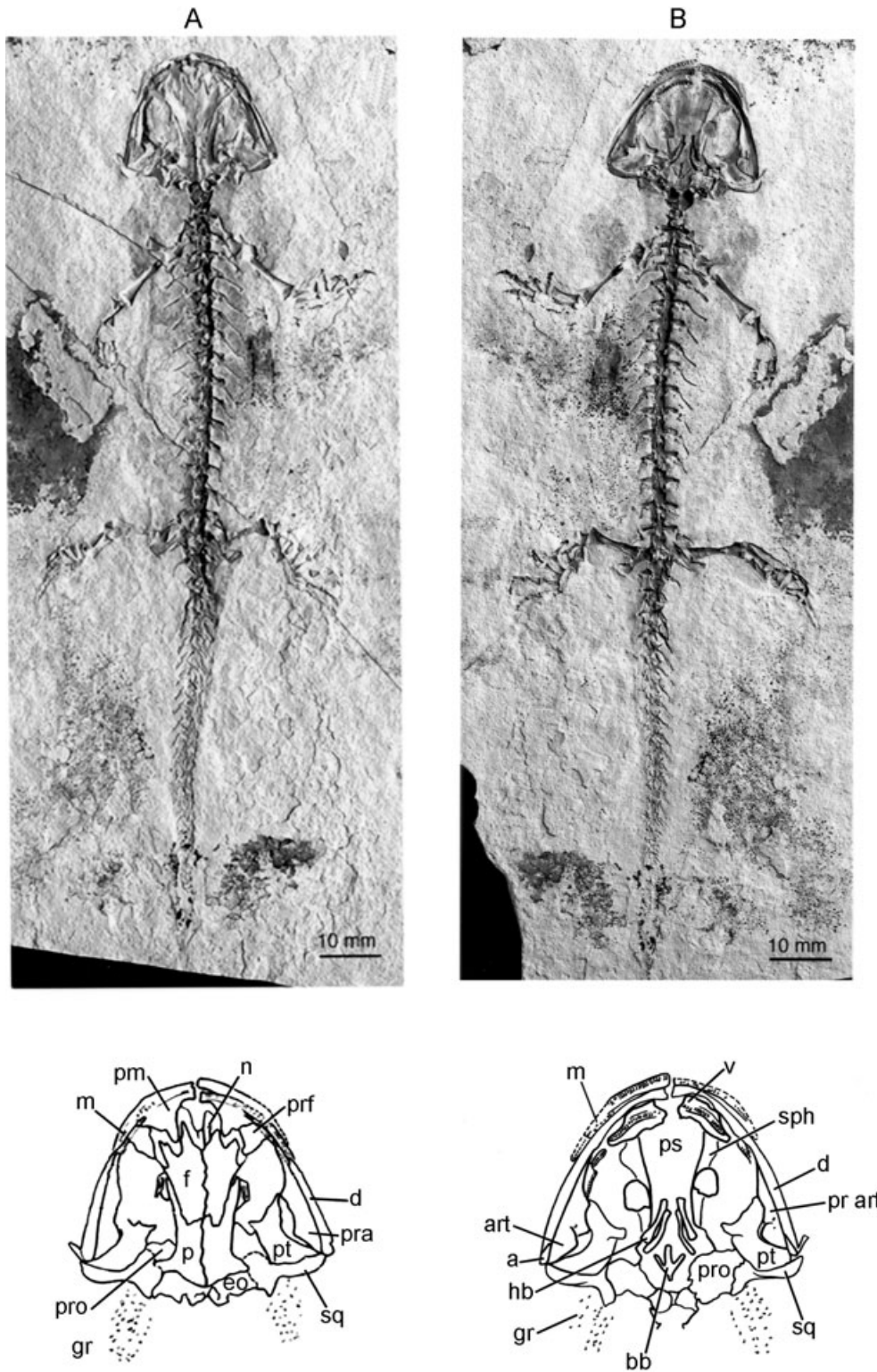**Figure 47.** *Chunerpeton tianyiensis*, a cryptobranchid salamander from the Middle Jurassic of China. Reproduced from Gao & Shubin (2003). A, skeleton and drawing of the skull in dorsal view. B, skeleton and drawing of the skull in ventral view.
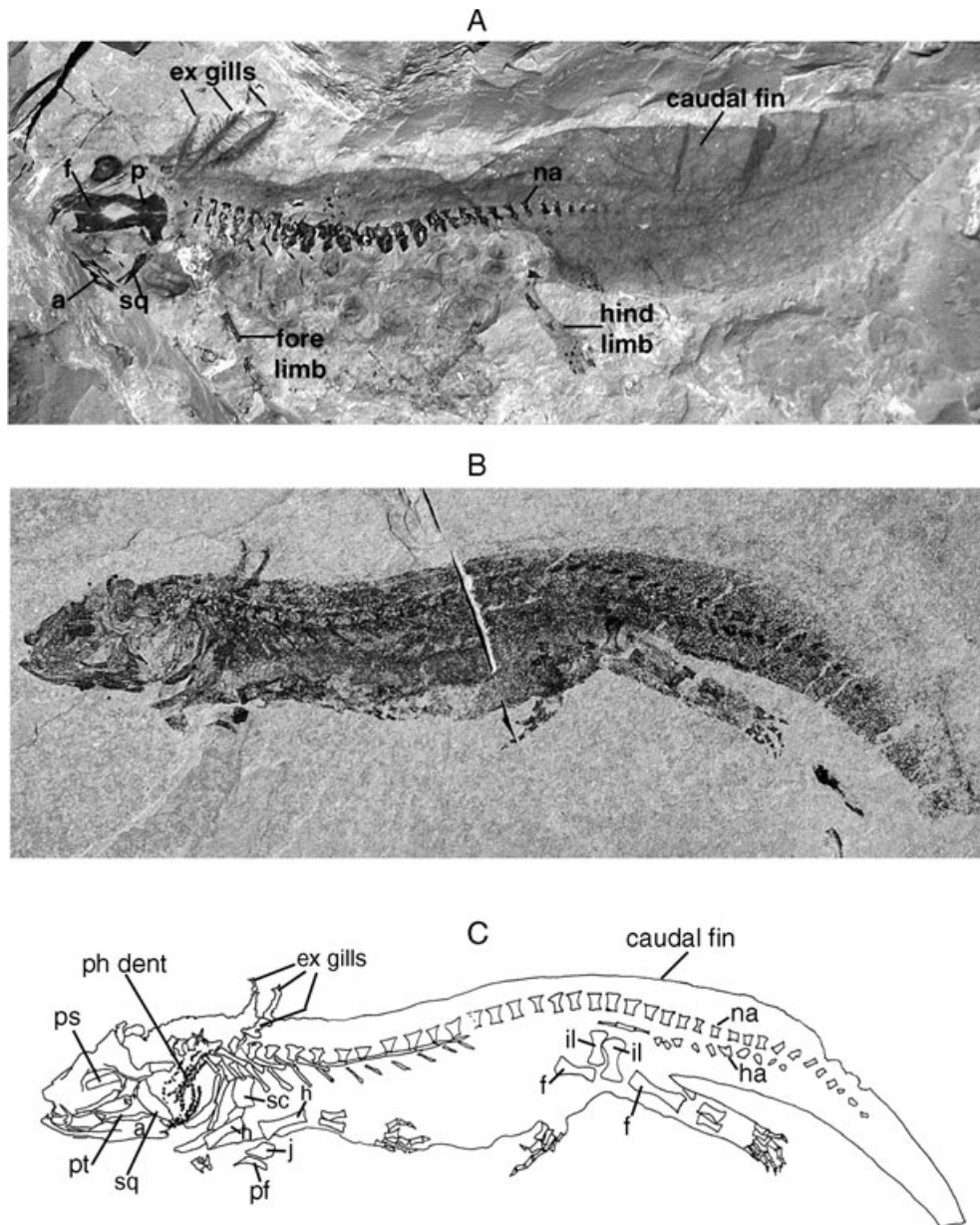
Figure 48. Salamandramorph larvae. A, the oldest described urodele larva, an unnamed genus from the Middle Jurassic of China; skull in primarily dorsal view, trunk and tail in primarily lateral view. Reproduced from Gao & Shubin (2003). B, advanced larval stage of the derived branchiosaurid *Apateon* (Royal Ontario Museum, no. 44276) from the lowermost Permian locality of Odenheim, Germany, in primarily lateral view. Two external gills are extended dorsally from the trunk. The third gill is lower in position, and pressed against the side of the trunk; a very delicate impression of the caudal fin can be seen above the central portion of the tail. C, sketch of the *Apateon* larva, emphasizing the outline of the bones. Note that the neural and haemal arches appear prior to the centra, which are not ossified in this specimen.

Iridotriton also possesses other features that are more primitive than those of the extant salamandroid families, including separate prearticular and angular bones in the lower jaw. They are already fused in the Lower Cretaceous stem salamandroid *Valdotriton* (Evans & Milner, 1996). In addition, the premaxillae remain paired, and their dorsal process is short.

Other characters of Jurassic salamanders that have been used to differentiate families have been shown to be variable within groups, and so of uncertain value in establishing specific relationships. These include the presence of single-headed or double-headed ribs, which have a variable expression among cryptobranchoids, and the distribution of spinal nerve foramina

in the vertebrae (Evans *et al.*, 2005). The family Karauridae, which may be the closest sister taxon to the crown-group urodeles, lacks spinal nerve foramina. The presence of a foramen in the atlas of cryptobranchoids may be a defining character of crown-group urodeles. The presence of nerve foramina in at least one of the caudal vertebrae may be a feature uniting salamandroids, because it occurs in *Iridotriton* and *Valdotriton* as well as in the extant *Dicamptodon* and *Rhyacotriton*. However, sirenids have them throughout the body, and proteids lack any foramina behind the atlas.

It is these primitive members of crown-group salamanders (Urodela) that provide most of the characteristics that can be used to evaluate their probable affinities among the Palaeozoic tetrapods. On the other hand, a few fossils are known that show many derived characters in common with crown-group salamanders, but cannot be placed within either of the extant superfamilies. These constitute a number of plesions that may be included in a total group, the Caudata, following the usage of Milner (2000).

The most informative of these are members of the family Karauridae from the Middle and Upper Jurassic of Kazakhstan and Kirghizstan. *Karaurus* is known from a complete articulated skeleton (Ivachnenko, 1978) (Fig. 49). It is clearly a salamander in the general anatomy of the skull and appendicular skeleton, but is apparently primitive in the retention of a heavily sculptured skull roof, with the external surface of the squamosal extending over the portion of the otic capsule that, in modern salamanders, provides for the passage of the superficial head of the adductor mandibulae internus. *Karaurus* also retains a lacri-
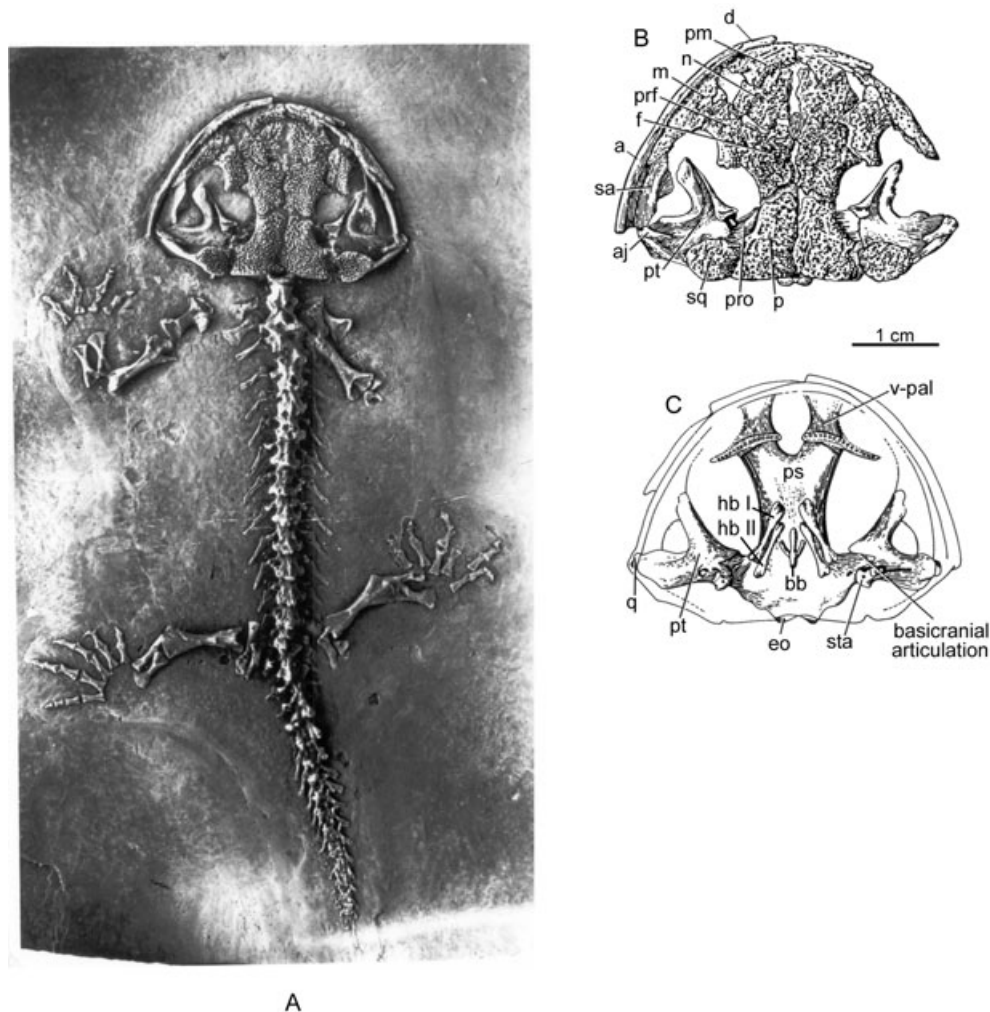

Figure 49. *Karaurus*, a caudate from the Upper Jurassic of Russia that lies outside the crown-group urodeles. Note sculptured surface of the squamosal, which would preclude the extension of the adductor mandibulae internus out of the adductor chamber. Note also the very close similarity of the configuration of the hyoid apparatus with that of *Chunerpeton* (Fig. 47B).

mal, as in some salamandrids, a quadratojugal, and a separate angular, as in stem cryptobranchoids and salamandroids. The related *Kokartus*, which may be paedomorphic, retains a tooth-bearing coronoid.

Numerous, disarticulated remains of caudates are known from the Bathonian of England (Evans & Milner, 1994). Some are primitive in lacking perforations in the atlas for the passage of the spinal nerve that are present in members of the crown group. Other elements are similar to those of *Karaurus*. *Triassurus*, from the Upper Triassic of Uzbekistan, has been described as either a larval temnospondyl (Estes, 1981) or an early salamander (Ivachnenko, 1978; Milner, 1994). If it is a salamander, it is primitive in the early ossification of the neural arches, relative to the centra. Similar fossils, expressing characters of both branchiosaurs and primitive salamanders, have also been reported from the Early Triassic of western China (Gao *et al.*, 2004).

The previous groups all have plesiomorphic features that might serve to link salamanders with more primitive late Palaeozoic or early Mesozoic predecessors. The following taxa [reviewed by Milner (2000)] are contemporary with Mesozoic and early Cenozoic salamanders, and may be included within the Urodela, but are divergent from any of the extant families. The Batrachosauroididae are mid-Cretaceous to lower Pliocene perennibranchiate forms with slender skulls resembling those of proteids. *Opisthotriton* and *Palaeoproteus* have 37–40 presacral vertebrae, and short forelimbs and hindlimbs. The ceratohyals and ceratobranchial are ossified; the atlas lacks an interglenoid tubercle. All appear to lack spinal foramina in the trunk or tail. They may be proteids, or convergent with that group. The vertebrae of *Batrachosauroides* are unquestionably of advanced salamandroid form.

The Scapherpetontidae include three genera from the Upper Cretaceous and Palaeocene of North America, of which *Piceoerpeton* extends into the Lower Eocene. They are neotenic, and resemble the cryptobranchoids in general appearance. They have spinal foramina in the caudal but not the trunk vertebrae.

ALBANERPETONTIDAE

The Albanerpetontidae (Estes & Hoffstetter, 1976; Fox & Naylor, 1982; McGowan & Evans, 1995; McGowan, 2002; Gardner, Evans & Sigogneau-Russell, 2003) are the most enigmatic of salamander-like animals. They are known from the Middle Jurassic to the Upper Miocene (a period of approximately 150 million years), from North America, Europe, Asia, and North Africa. Three genera with 11 species are currently recognized, but all retain a highly conservative morphology (Fig. 50). The complete skeleton of the Early Cretaceous *Celtedens ibericus* has a broadly salamander-like body form, with 22 presacral vertebrae and relatively long, slender limbs. The skull–trunk region is approximately 60 mm in length, but even in smaller specimens, the skeleton is highly ossified, including the braincase, carpals, and tarsals.

Superficially, the skull resembles that of salamanders in having a large orbitotemporal opening and anteriorly placed jaw articulation. The squamosal articulates dorsally with the braincase, and lacks a posterior embayment. There is a large bone in the position of the prefrontal and lacrimal in hynobiids that has been referred to as a lacrimal, but could be either a prefrontal or the result of fusion between these two bones. However, other features of the skull indicate divergence from salamanders from at least the Middle Jurassic. Unlike in any salamander, the frontals are fused at the midline, without a trace of suture. In contrast to the absence of a bony link between the maxilla and the jaw suspension in salamanders, a jugal is present in this position in the only well-articulated skull, that of the Lower Cretaceous *Celtedens ibericus* (McGowan, 2002). The paired bones of the palate are poorly known, but the cultiform process of the parasphenoid is unique among extant amphibians in being in the shape of either a short narrow spike or a long, very slender rod, rather than forming a broad supporting surface beneath the braincase.

The braincase is best known in the Miocene genus *Albanerpeton inexpectatum* (Estes & Hoffstetter, 1976). The posterior portion is fused into a solid unit, superficially resembling that of caecilians. It differs, however, in the fusion of the two sides of the occipital arch above the foramen magnum, but the retention of a suture between the otic region and the area of the basisphenoid and pleurosphenoid. The sphenethmoid portion of the braincase has not been described. There is a huge fenestra ovalis, described as showing separate areas for articulation with the head of the stapes and the operculum, although neither of these bones has been recognized. The occipital condyles and corresponding cotylar surfaces of the atlas are located primarily beneath the foramen magnum rather than more laterally, as in primitive salamanders, strongly resembling the position common to Palaeozoic microsaurs.

Well-preserved upper and lower jaws, known from the Middle Jurassic into the Miocene, bear teeth without a trace of pedicellate structure. The crown is chisel-shaped and typically bears three cusps. The lower jaws of the Miocene *Albanerpeton*, and apparently all earlier albanerpetontids, are highly derived in a manner distinct from that of frogs, salamanders, or caecilians. As in these groups, the number of bones is much reduced from that of Palaeozoic tetrapods, but their specific configuration is highly distinct. Almost
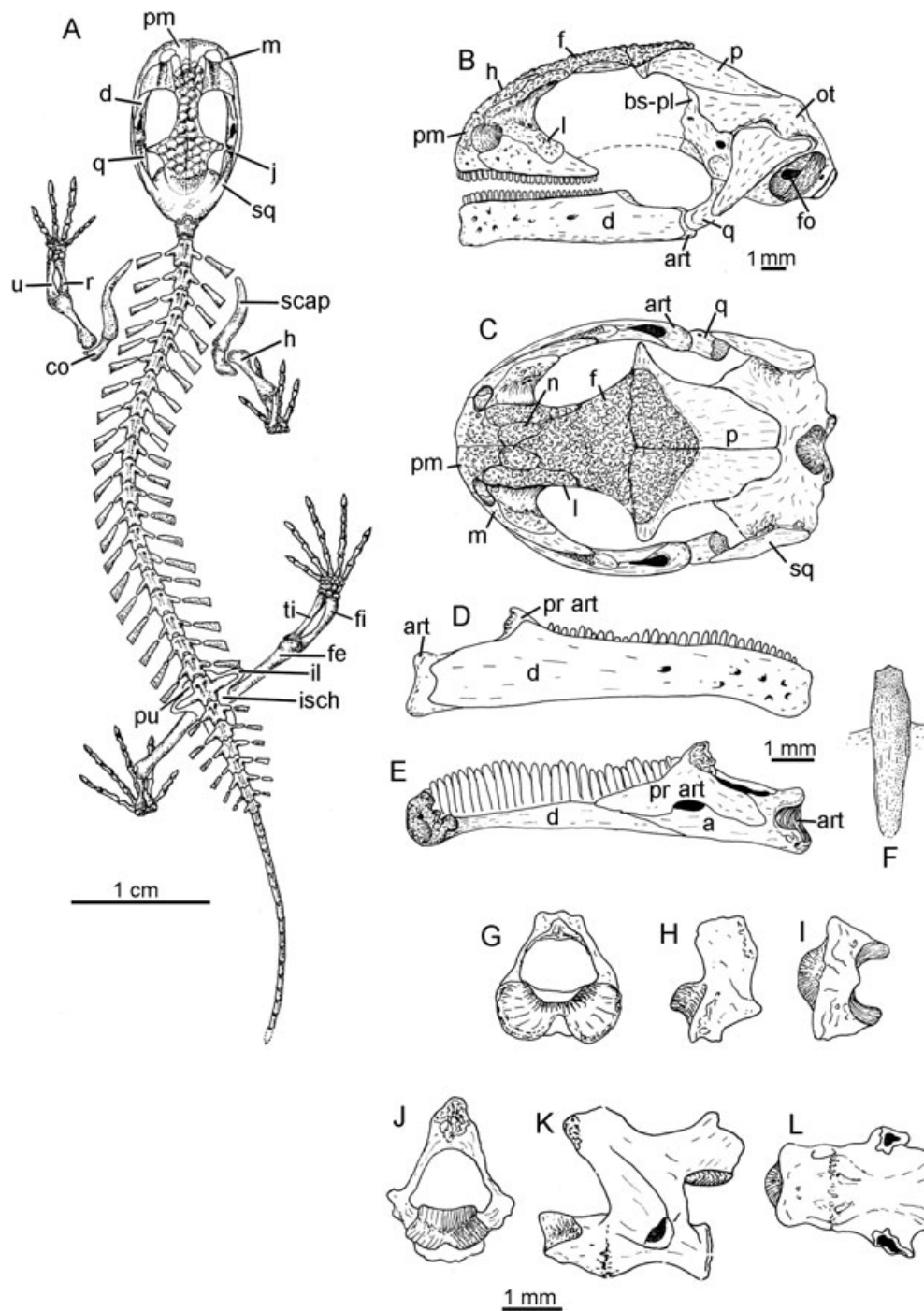
Figure 50. Albanerpetontids, an enigmatic clade known from the Middle Jurassic into the Miocene that has been suggested as being related to the extant amphibian orders. A, skeleton of *Celtedens megacephalus* from the Lower Cretaceous of Spain. Reproduced from McGowan & Evans (1995). B–L, *Albanerpeton inexpectatum* from the upper Miocene of France. Reproduced from Estes & Hoffstetter (1976). B, C, skull in lateral and dorsal views. D, E, lateral and medial views of lower jaw. F, single tooth (much enlarged). G–I, atlas vertebra in anterior, lateral, and ventral views. J–L, fused second and third vertebrae in anterior, lateral, and ventral views.

all the external surface is composed of the dentary, which occupies much of the area of lateral expression of the angular and surangular in Palaeozoic amphibians. The joint-forming surface of the articular is unique among all amphibians in being sharply concave and facing primarily posteriorly to receive the convex surface of the quadrate. The medial surface of the articular extends forward over much of the area occupied by the angular in early tetrapods. Presumably, these bones have become fused. The other major element exposed medially is a large, chevron-shaped prearticular that extends dorsally into the area primitively occupied by the coronoid bone, where its rugose texture suggests that it functioned as a major site of attachment for the adductor jaw musculature. The front of the jaw has an asymmetrical peg-and-socket joint that would have allowed some degree of movement between the right and left halves, in contrast to the essentially flat surface in salamanders. Mentomeckelian bones have not been recognized. The unique modes of articulation at the symphysis of the lower jaws and between the quadrate and articular suggest a very different mode of feeding from that of any salamanders.

An impression between the jaws of *Celtedens ibericus* (McGowan, 2002) has been tentatively identified as a hyoid element, but no details can be distinguished.

The cervical vertebrae, known from the Middle Jurassic into the Miocene, have a pattern that is unique among all terrestrial vertebrates (Fig. 50G–L). The atlas–axis complex (not recognized as a functional complex in any other putative lissamphibians) consists of a large bicotylar atlas and a small axis centrum lacking a neural arch. The clearly bicondylar articulation with the skull would have restricted movement to the vertical plane, as in frogs, salamanders, and caecilians. However, according to McGowan (1998), the configuration between the atlas and axis would have allowed movement in the mediolateral plane, which is not possible in any of the extant amphibian orders. Several authors (e.g. Gardner *et al.*, 2003) have referred to the atlas–axis complex of albanerpetontids as being structurally similar to those of mammals or amniotes in general, but this is not an appropriate comparison, as this implies rotational movement, provided by a very different configuration of these bones from that seen in albanerpetontids (Jenkins, 1971). Estes & Hoffstetter (1976) described a further unique character in *Albanerpeton inexpectatum*, in which the second cervical centrum is fused to the third. However, this fusion is not recognized among the many specimens of the axis that have been collected from the Jurassic and Cretaceous (McGowan, 1998).

Neither the atlas nor the axis bears ribs. The more posterior vertebrae of albanerpetontids are also distinct from those of any salamanders in the shortness of the transverse processes and the absence of bifurcated surfaces for articulation with the ribs. In fact, the trunk vertebrae of *Albanerpeton inexpectatum* closely resemble those of many microsaurs (pers. observ.), although they lack intercentra, which are found in several elongate microsaurs.

The girdles and limbs superficially resemble those of salamanders. No dermal or medial elements of the shoulder girdle have been recognized. The humerus bears conspicuous surfaces for articulation with the radius (a large spherical structure) and the ulna. The carpals and tarsal are all ossified, even in animals of very small size, and appear to retain most of the elements present in Palaeozoic tetrapods. However, they are notable in lacking the fusion of distal carpals and tarsals 1 and 2 that forms the basale commune in salamanders. In the fully articulated specimen of *Celtedens ibericus*, the phalangeal formula of the manus is 2,3,3,3, and that of the pes is 2,3,4/5,3,3; this is common to neither salamanders nor frogs.

Celtedens ibericus has a continuous covering of hexagonal dermal scales over the trunk and head, totally unlike the condition in frogs and salamanders (McGowan & Evans, 1995). Caecilians have scales, but not of a comparable pattern. This species is also unique in having patches of about 100 tiny spherules lying just above each femur. McGowan (2002) interprets these as being associated with glands concerned with courtship. In addition to the extensive scalation, the high degree of ossification of the entire skeleton, even in tiny specimens, and the well-developed appendicular skeleton suggest that all albanerpetontid species known were fully terrestrial animals.

The earliest discovered albanerpetontid material was originally assigned to previously named salamander taxa by Costa (1864), Estes (1964, 1969), Seiffert (1969), and Estes & Hoffstetter (1976). Only in 1982 did Fox & Naylor recognize that the configuration of the cervical vertebrae and the nature of the symphysis of the lower jaws were unique among all known terrestrial vertebrates (Fox & Naylor, 1982). They also listed several other features in which they were distinct from salamanders: nonpedicellate teeth; the parasphenoid a narrow midline spike; a highly convex quadrate fitting into a deeply concave articular; a labyrinthodont-like sculpture on the skull bones; frontals fused; and unicipital rib-bearers on trunk vertebrae. To these, we can now add the absence of fusion of distal carpals and tarsals 1 and 2, and retention of a large, ossified pubis.

Albanerpetonids have been classified as a separate clade within the Lissamphibia, as a doubtful sister taxon of either salamanders (Milner, 2000), or both salamanders and frogs (McGowan & Evans, 1995), or all other extant orders (Milner, 1988; Ruta *et al.*,

2003). Although much more has been learned of albanerpetontids since the paper by Fox & Naylor (1982), their conclusions regarding the probable ancestry of this family still apply today: 'The family may be derived from lepospondyls, from primitive lissamphibians, or even from labyrinthodonts, but available information provides no resolution of ultimate ancestry.' Whatever their specific relationships, they provide little if any evidence regarding the ancestry of the Caudata, whose first appearance in the fossil record is identical in time and place (Gardner *et al.*, 2003).

DERIVED CHARACTERS OF THE MOST PRIMITIVE CROWN-GROUP SALAMANDERS

The combination of the following shared derived characters (unless otherwise indicated) supports the monophyletic origin of salamanders, and distinguishes the most primitive members of the crown group Urodela and their immediate sister taxa from frogs, and/or caecilians, and/or most groups of Palaeozoic tetrapods:

Adults

Skull
 1. gap between the posterior extremity of maxilla and movable jaw suspension
 2. squamosal articulates dorsally with parietal and otic capsule
 3. absence of the following skull bones common to Palaeozoic amphibians: tabular, supratemporal, postparietal, postfrontal, postorbital, jugal, ectopterygoid
 4. large, confluent orbitotemporal openings separated by unfused frontal and parietal
 5. reduction of dorsal portion of squamosal to permit passage of superficial branch of adductor mandibulae internus out of adductor chamber
 6. presence of pedicellate teeth
 7. absence of an impedance-matching middle ear
 8. loss of sulci for lateral-line canals in skull roof
 9. presence of an operculum and opercularis muscles

Lower jaw
10. no more than five separately ossified bones: articular, angular, prearticular, dentary, mentomeckelian

Hyoid apparatus
11. one well-defined basibranchial
12. one pair of radial cartilages
13. distal fusion of two hypobranchials
14. protrudable tongue supported and propelled by hyoid apparatus

Vertebrae and ribs
15. no intercentra
16. spinal nerve foramen in the atlas vertebra
17. reduction of number of presacral vertebrae to ~17
18. elongate, typically double-headed transverse processes
19. double-headed ribs

Appendicular skeleton
20. absence of dermal elements of shoulder girdle
21. presence of endochondral sternum
22. reduction and eventual loss of ossification of pubes
23. basale commune of carpus and tarsus
24. digital number and phalangeal count of manus, 2,2,3,2 (derived; see Table 2)
25. digital number and phalangeal count of pes, 2,2,3,4,3 (primitive)

Reproduction and larvae

26. absence of internal fertilization (primitive)
27. eggs laid in the water (primitive)
28. larvae with conspicuous external gills throughout most of development (primitive)

Skull
29. progressive ossification of bony elements in approximately the following sequence: beginning with the tooth-bearing bones of the palate and upper and lower jaws, followed by the squamosal and midline bones of the skull roof, and finally the bones that form the anterior margin of the orbit (could be considered as a single character, or a series of characters for the specific sequence of each bone)

Lower jaw
30. presence of separate, toothed coronoid (primitive)

Hyoid apparatus
31. two pairs of rod-shaped hypobranchials (primitive)
32. early regression of fleshy operculum covering gills
33. six rows of columnar to triangular gill rakers, not joined to bony base, that interdigitate to prevent flow of water through external gills
34. ceratohyals become ossified or chondrified at the time of metamorphosis

Vertebrae
35. neural arches chondrify and/or ossify before centra (primitive)

Appendicular skeleton
36. limbs appear before or soon after hatching (primitive)

37. chondrification and ossification of distal limb elements of forelimbs and hindlimbs develop in an anterior-to-posterior direction, in contrast to the situation in all other tetrapods

38. ossification of terminal phalanges may occur prior to that of proximal phalanges

THE BRANCHIOSAURIDAE

Among which late Palaeozoic and early Mesozoic tetrapods can the largest number of these features be recognized?

Prior to the Middle Jurassic, we still lack fossils of any taxa that exhibit derived characters that are uniquely homologous with those of extant adult salamanders. However, thousands of specimens are known from the Upper Carboniferous and Lower Permian that resemble the larvae of modern urodeles. As primitive members of all extant salamander families have extensive periods of larval development, and several families are entirely neotenic, knowledge of early development among Palaeozoic amphibians is clearly of great importance in establishing their ancestry. In this regard, it is ironic that Laurin & Reisz (1997) specifically excluded evidence from larval stages in their attempt to establish the relationships of the modern amphibian groups.

Fortunately, the conditions of deposition during the Late Carboniferous and Early Permian favoured the preservation of early developmental stages of amphibians in a great number of lake deposits in Germany, France, the Czech Republic, and the UK, as well as at Mazon Creek in the USA (Milner, 1980, 1982; Shabica & Hay, 1997; Boy & Sues, 2000; Schoch & Milner, 2005). Both major groups of Permo-Carboniferous amphibians are represented. We will look first at the lepospondyls. Tiny juveniles (as small as 2 cm in skull–trunk length and with centra length less than 1 mm) of all major groups of lepospondyls are known (Carroll, 2000a; Anderson, 2002, 2003). Specimens of tiny aïstopods, adelogyrinids, lysorophids, microsaurs, and nectrideans resemble one another in precocial ossification of their vertebral centra as complete cylinders (Fig. 51). This mode of development is derived relative to that of the most primitive salamanders (e.g. the extant hynobiids *Ranodon tsinpaensis*, *Ranodon sibericus*, and *Hynobius maculosus*) (Boisvert, 2002; C. A. Boisvert, 2004) and a primitive Jurassic salamander (Fig. 48A), in which the arches ossify prior to the centra. Aïstopods, adelogyrinids, and lysorophids are particularly improbable sister taxa of salamanders, as their girdle and limbs are either completely absent or highly reduced, and the vertebral column is greatly elongated. Microsaurs and nectrideans have relatively normal limbs, but no specific synapomorphies with either frogs or salamanders.

Another distinctive feature of juvenile lepospondyls is that they lack evidence of external gills, although many are found in the same deposits as larval labyrinthodonts, in many specimens of which conspicuous external gills are preserved (Milner, 1980; Boy & Sues, 2000). It is because of the presence of external gills that larval labyrinthodonts have long been referred to as branchiosaurs. However, these gilled larvae clearly belong to two divergent clades, the temnospondyls and the discosauriscid anthracosauroids. These groups are distinguished by many features of their adult anatomy, including the dominance of intercentra and the presence of a four-toed manus in the temnospondyls vs. dominance of pleurocentra and a five-toed manus in the anthracosauroids (Boy & Sues, 2000). Both of these features preclude the close affinities of anthracosauroids and modern amphibians.

Among the temnospondyls, many larvae can be identified as representing early growth stages of previously recognized Palaeozoic amphibians that share few, if any, characters suggestive of salamanders. On the other hand, other larvae belong to distinct taxa that cannot be associated with particular adult labyrinthodonts, and metamorphose only very late, or not at all. These are grouped in two families, the Micromelerpetontidae and the Branchiosauridae (Fig. 52), belonging to the superfamily Dissorophoidea (Boy & Sues, 2000; Schoch, 1992, 2004; Schoch & Milner, 2005). Larvae of the Branchiosauridae, of which *Apateon* is the best known example, share a great many aspects of their development, especially that of the skull and hyoid apparatus, with modern salamanders (Schoch & Carroll, 2003).

The skull

Cranial development among Palaeozoic amphibians follows two distinct patterns. The vast majority, including most labyrinthodonts and lepospondyls as well as their sister taxa among Upper Devonian fish, ossify all the dermal bones of the skull roof, palate, and lower jaws essentially simultaneously (Schoch & Carroll, 2003; Witzmann & Pfretzschner, 2003; Witzmann, 2006). All the bones form a close-fitting mosaic, in even the smallest known fossils (Fig. 53). In contrast, most Late Carboniferous and Early Permian members of the Branchiosauridae ossify the dermal bones of the skull gradually during larval development in a relatively consistent sequence (Schoch, 1992, 2002). The first bones to ossify are those associated with grasping prey: the tooth-bearing bones of the palate, and the margins of the upper and lower jaws – the premaxilla, maxilla, vomer, palatine, pterygoid, dentary, coronoids, and anterior end of the parasphenoid. These are followed by the squamosal and midline bones of the skull roof, and later the cir-
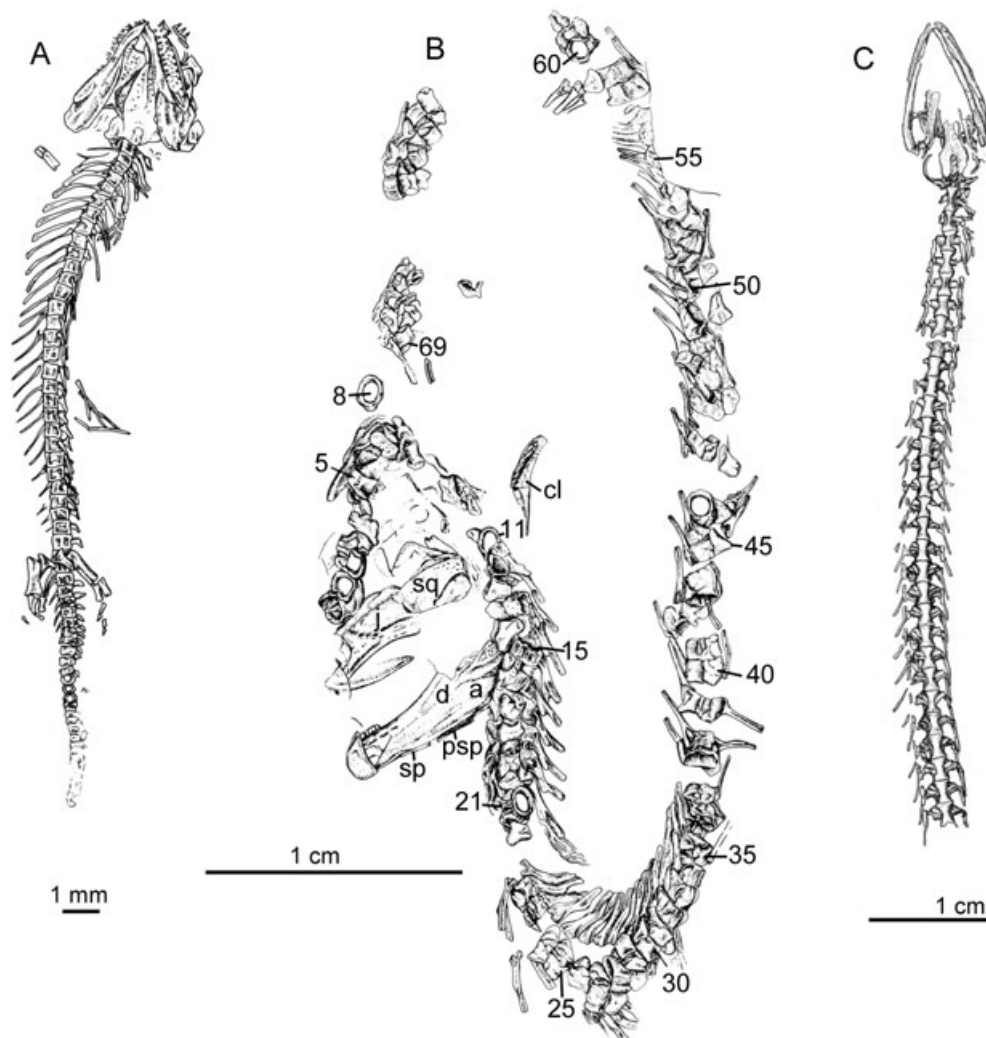
Figure 51. Skeletons of juvenile lepospondyls. A, the microsaur *Hyloplesion longicostatus*. Reproduced from Carroll & Gaskill (1978). B, an unnamed adelogyrinid. Reproduced from Carroll (1989). C, the aïstopod *Pseudophlegethontia turnulllorum*. Reproduced from Anderson (2003). In contrast to the larvae of labyrinthodonts, lepospondyls ossify fully cylindrical centra at a very early stage in development, but show no evidence of external gills.

cumorbital bones and those at the back of the skull table (Figs 54, 55; Table 1). This is essentially the same sequence as that of primitive living salamanders (Rose, 2003; C. A. Boisvert, 2004), but is very different from that of extant anurans or caecilians.

A striking feature of branchiosaurids is the early elaboration of the squamosal (relative to the circumorbital bones), which extends from the back of the skull table as a laterally oriented jaw suspension, much as in the salamander families Hynobiidae, Salamandridae, and Ambystomatidae, as well as the recently illustrated (but unnamed) larval salamander from the Middle Jurassic of China (Gao & Shubin, 2003) (Fig. 48). In common with these families, there is initially a long gap in the margin of the cheek between the maxilla and the jaw suspension, and both the squamosal and underlying pterygoid have a mobile articulation with the skull. In *Apateon*, the dorsal end of the squamosal loosely underlaps the supratemporal (which actually ossifies slightly later, along with the quadratojugal, postparietal, and nasal). The distal end of the squamosal is firmly attached to the quadrate and pterygoid, whose medial basipterygoid process has a V-shaped surface that would have permitted mediolateral movement relative to the parasphenoid. The configuration of these bones suggests that the distal end of the suspensorium could have moved in a mediolateral arc that would have allowed the oropharyngeal chamber to expand laterally in the course of suction feeding.
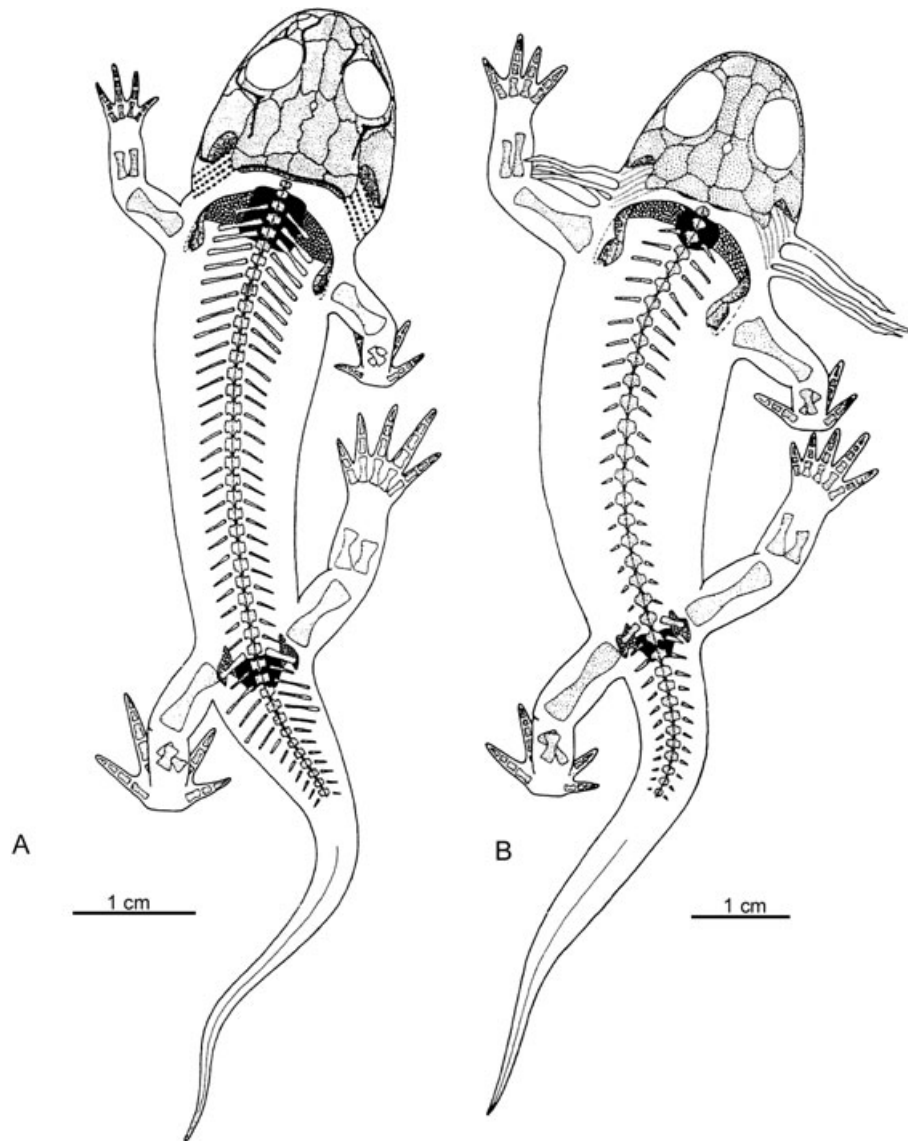
Figure 52. Skeletal reconstructions of branchiosaurs. A, the micromelerpetontid *Micromelerpeton credneri*, with four rows of gill rakers, attached to thin bony plates. B, the branchiosaurid *Apateon pedestris*, with six rows of gill rakers. Reproduced from Boy (1971).

The skull bones in the smallest known larvae (in which the endolymphatic sacs still retain a calcium reserve) form an open lattice that would allow the mouth and pharynx great flexibility to expand laterally and ventrally to accommodate prey during suck-and-gape feeding. In contrast, the most mature specimens of *Apateon* (Figs 54E$_1$, 56) have the same complement of dermal bones as other advanced temnospondyls, in which they form a highly integrated skull for grasping and biting prey.

The retention of mobile joints between the jaw suspension and the skull roof and base of the braincase in hynobiids, ambystomatids, and some salamandrids suggests that expansion of the cheek may be possible in the larvae of living salamanders. Deban & Marks (2002) reported that video sequences from a dorsal perspective in *Desmognathus marmoratus*, *Gyrinophilus porphyriticus*, and *Pseudotriton ruber* (all primitive plethodontids) revealed slight lateral expansion of the branchial region during suction feeding. However, the lateral expansion contributed only slightly to the increase in buccal volume.

During later larval development in *Apateon*, the prefrontal, postfrontal, lacrimal, postorbital, and jugal ossify in succession, after which the maxilla extends posteriorly to make contact with the quadratojugal, greatly reducing the mobility of the jaw suspension. In the final stage of development, the skull acquires the
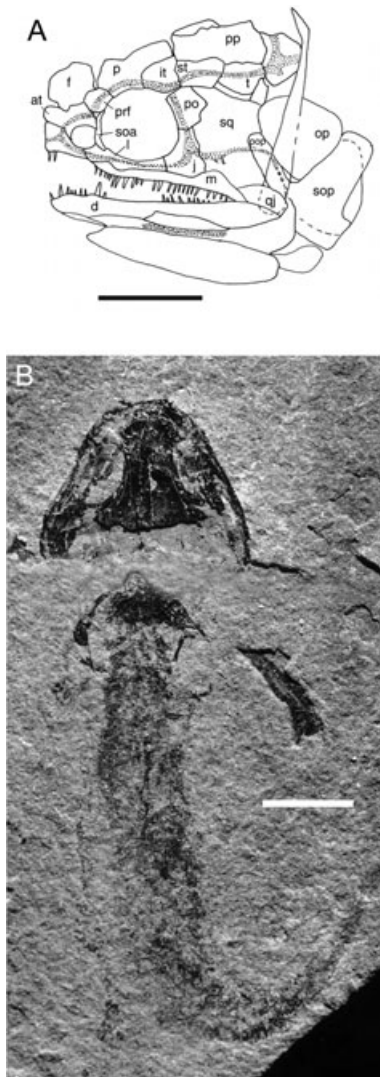
Figure 53. A, pattern of skull roof ossification in the smallest adequately known specimen of the osteolepiform fish *Eusthenopteron*, in which the dermal bones of the skull ossify essentially simultaneously. Reproduced from Schultze (1984). B, the skeleton of a very small specimen of the branchiosaur *Micromelerpeton*, in which the skull bones also ossify simultaneously. Scale bars 5 mm in length. Reproduced from Schoch & Carroll (2003).

rugose ornamentation of adult temnospondyls, and the ceratobranchials become ossified or calcified. An even more striking change occurs in the marginal dentition. During larval growth, the teeth of both *Apateon* and modern salamanders are long and slender, without the gap between the base and crown that characterizes the pedicellate teeth of the adults. However, in large specimens of *Apateon*, the marginal teeth acquire the pedicellate structure of adult salamanders (Fig. 56). Boy & Sues (2000) argue that the very large

size of the interpterygoid vacuities in more mature branchiosaurids, and their position beneath the expanded orbits, may have enabled branchiosaurids to use the retractor bulbi muscles, as in modern salamanders and frogs, to force the food down the throat.

The bones forming the anterior margin of the orbit are the last to ossify in modern salamanders, and the bones forming the posterior margin of the orbit and the back of the skull table in primitive tetrapods are lost completely. The adult cranial anatomy of modern hynobiids, ambystomatids, and salamandrids could have evolved from animals resembling *Apateon* by truncating ossification early in development, before the appearance of the posterior circumorbital bones and those at the posterior margin of the skull table, while retaining the gap between the maxilla and the squamosal. Ossification of endochondral bones of the skull, the quadrate, elements of the braincase (except the exoccipitals), and the articular of the lower jaw is long delayed in branchiosaurids, as in most Palaeozoic amphibians.

As was discussed in the descriptive sections, both frogs and caecilians show sequential ossification of the dermal bones of the skull roof, but each extant order has a different sequence, resulting in a succession of distinctive geometric patterns.

In contrast to other habitually aquatic temnospondyl labyrinthodonts, most branchiosaurids lack conspicuous lateral-line canal grooves on the skull bones. This does not indicate that they lacked the sensory structures associated with the lateral-line canal system, but simply that it did not sink into the bone but remained suspended in the overlaying soft tissue, as in modern salamanders (Duellman & Trueb, 1986). Postcranial lateral-line canals have been demonstrated in the branchiosaurids *Apateon* and *Melanerpeton*, where they are supported by rows of denticles (Werneburg, 2004).

Hyoid apparatus
Larvae of branchiosaurids and those of primitive living salamanders also have significant similarities in their hyoid apparatus. The endochondral elements of *Apateon* are only poorly ossified, but have been reconstructed by Boy & Sues (2000) (Fig. 57) as being comparable to those of ambystomatids. Both groups have columnar to narrowly triangular gill rakers (pharyngeal denticles) associated with the ceratobranchials. In modern salamanders, they are arranged so as to fit together like the teeth of a zipper to close the external gill openings. As shown by Lauder & Schaffer (1985), and Lauder & Reilly (1988), this is necessary to maintain an effective vacuum during suction feeding in modern salamanders, as was presumably the case for branchiosaurids. Gill rakers in modern salamanders
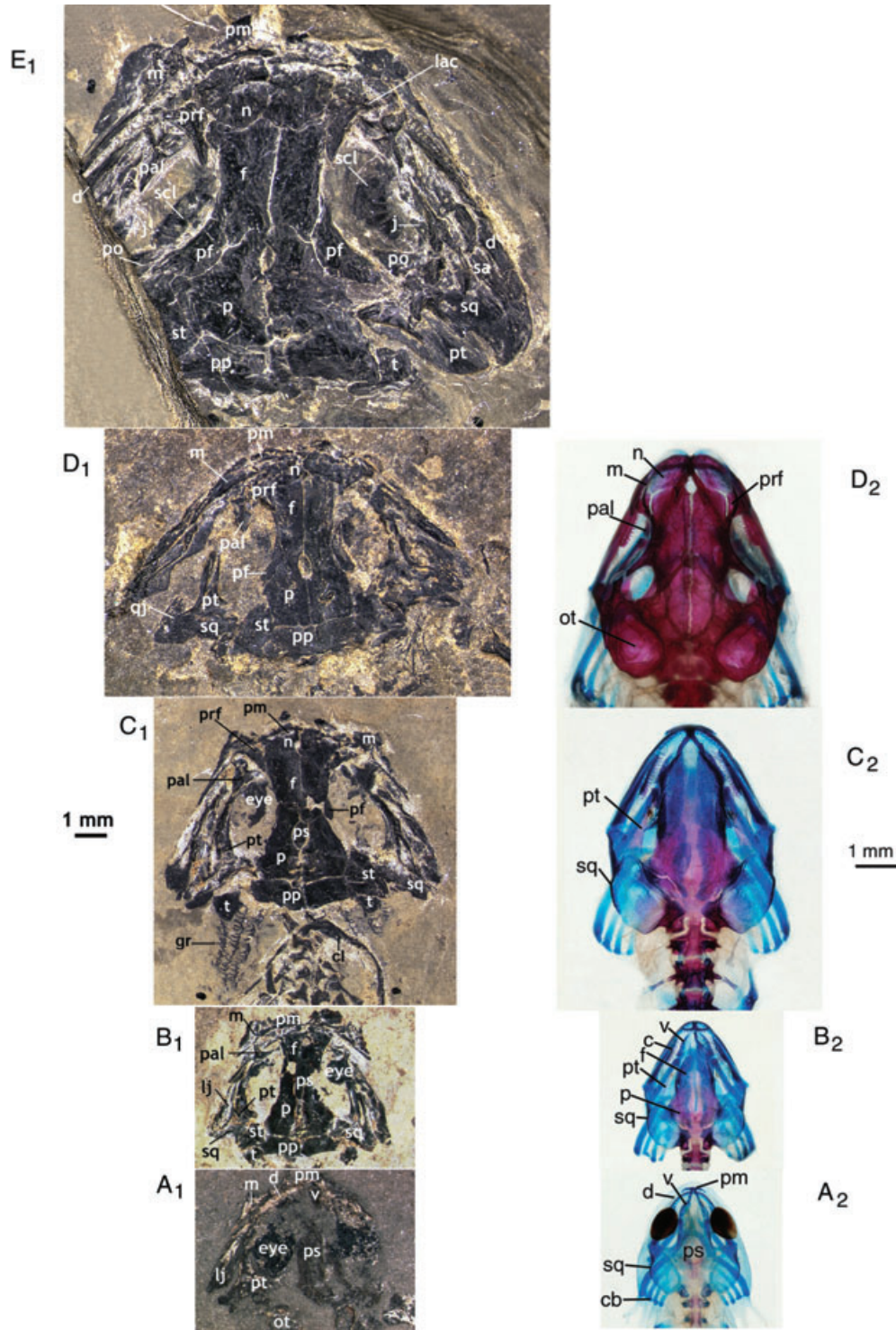
Figure 54. Comparative views of the sequence of ossification of the dermal skull bones of the uppermost Carboniferous branchiosaurid *Apateon caducus* (on the left), and the extant salamandrid *Notophthalmus viridescens* on the right. A₁–E₁, succession of growth stages illustrated in specimens from the Geological and Palaeontological Institute of Mainz; specimen numbers 1478, 1460, 1464, 1280, and 1530. A₂–D₂, developmental sequence of cleared and stained specimens of the salamandrid *Notophthalmus viridescens* (Redpath Museum, McGill University, specimen numbers 5007, and 5009–5011). Bone is red and, where viewed on edge, black; cartilage is blue. Note the very early appearance of the squamosal, when most of the surrounding skull is still cartilaginous. The maxilla, however, ossifies long after the premaxilla.
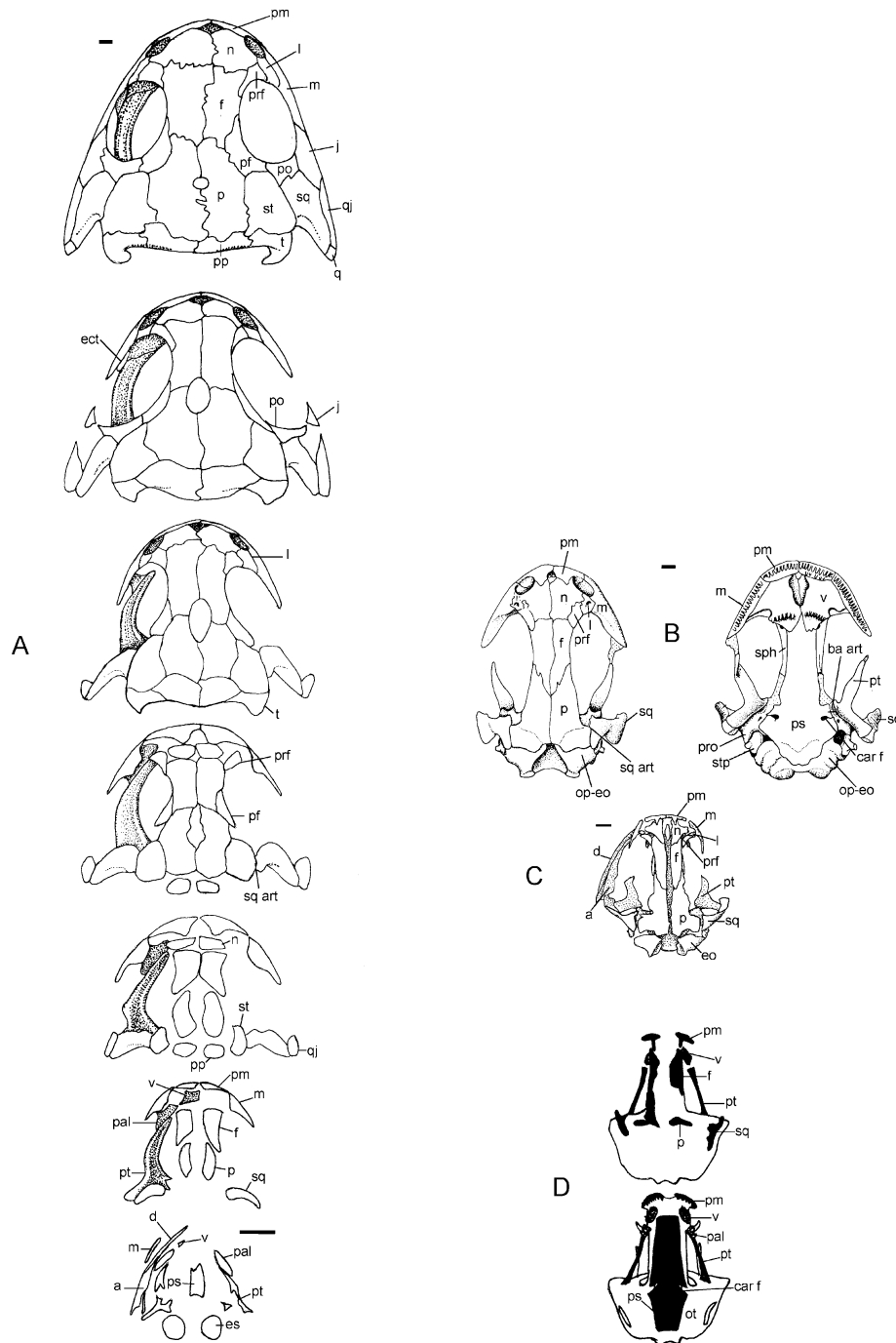
Figure 55. Diagrammatic illustrations of the sequence of cranial ossification of the uppermost Carboniferous branchiosaurid *Apateon caducus* on the left and modern hynobiid salamanders on the right. A, uniform grey shading identifies the successive ossification of bones in larger skulls of *Apateon*. Specimens from the Geological and Palaeontological Institute of Mainz, and numbers in accordance with increasing size: 1310, 1387, 1442, 1779, 1249, 1335, 1601. The millimetre scale at the bottom applies to all but the largest skull. Palatal bones are omitted on the right side to emphasize progressive closing of the gap in the skull margin between the jaw suspensorium and the maxilla. Reproduced from Schoch & Carroll (2003). B–D, growth stages in hynobiid salamanders. Only the palatal and jaw elements are ossified in the smallest specimen. B–D, growth stages in hynobiid salamanders. B, dorsal and palatal views of the skull of an adult specimen of *Batrachuperus sinensis* (Natural History Museum, London, no. 94-9-15-15). C, late larval stage of *Batrachuperus mustersi*. Redrawn from Deban & Wake (2000). D, dorsal and palatal views of *Ranodon sibiricus*. Redrawn from Lebedkina (1979). Ossified bones are in black; surrounding areas are cartilaginous at this stage. Based on an animal 36 mm in length. Scale bars, 1 mm.
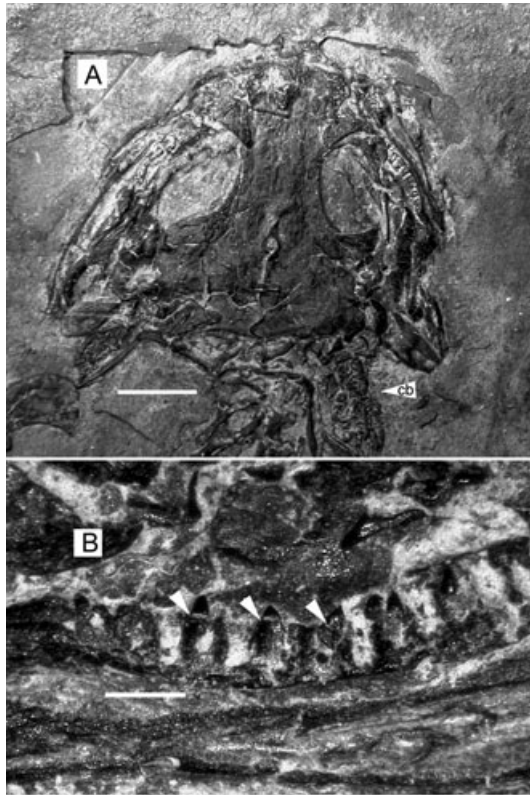
Figure 56. Neotenic adult of *Apateon* from the Lower Permian of Odernheim (Geological and Palaeontological Institute of Mainz, N800). A, complete skull showing calcified or ossified ceratobranchials (cb), with attached branchial denticles. B, enlarged view of teeth from the right dentary as seen through the orbit. Note the clear demarcation between the base and the crown (white arrows). The teeth in larval individuals are slender pegs, showing no trace of pedicellate structure. Scale bars: A, 5 mm; B, 1 mm.

The individual denticles of primitive branchiosaurids are typically in the shape of slender cones, narrowing to a single tip. Such a configuration closely resembles that of the pharyngeal denticles of modern salamander larvae. This is also the shape of the denticles in the most mature specimens of *Apateon*, in which the skull roof is fully ossified but the ceratobranchials are calcified or ossified, indicating that the specimen is a neotenic adult. In less mature specimens of *Apateon* and other advanced branchiosaurids, the shape of the denticles changes during growth. The smallest individuals have simple denticles, but as they mature, additional slender processes grow successively from near the base of the crown. The largest specimens of *Apateon caducus* have up to six, and some later branchiosaurids have as many as 11 Schoch & Milner (2004). Such subdivision of the crown produces an admirable structure for the filtering of tiny particles of food. Nothing equivalent has been described in modern salamanders. It may have been a unique adaptation to the apparently planktonic feeding of the Carboniferous branchiosaurs, living in the many large, but isolated, lakes of the 2000-m-high Variscian mountains of central Europe, as described by Boy & Sues (2000) and Schoch & Milner (2004).

are also described as being important in filtering out small particles of food, which are then swept back into the digestive tract (Deban & Wake, 2000).

In modern larvae (Fig. 57D), the gill rakers are arranged in six rows. Ceratobranchials I and IV each support one row, while ceratobranchials II and III each support two rows. Together, these form an interlocking pattern that closes the three gill slits. This is exactly the arrangement of the gill rakers observed in *Apateon* and other advanced branchiosaurids. In nearly all other Palaeozoic amphibians for which larvae are known, the branchial denticles are attached in patches to thin plates of bone that are arranged in four rows, each attached to separate ceratobranchials. This pattern is retained in the close sister taxon of the branchiosaurs, the Micromelerpetontidae, and can be traced back to their ancestors among sarcopterygian fish such as *Eusthenopteron* (Figs 10A, 57A).

Vertebrae

As is the case for the development of the skull, knowledge of the vertebrae of branchiosaurs is confined primarily to the larvae. As in other labyrinthodonts, the neural arches formed as paired elements that ossified in an anterior–posterior sequence. The intercentra and pleurocentra either ossified only very late in ontogeny, or remained cartilaginous throughout the life of the animal. Both the structure and sequence of development of the vertebrae were highly distinct from those of most extant salamanders, in which the centra both chondrify and ossify prior to the arches. If salamanders evolved from branchiosaurids, it must be assumed that the initially paired pleurocentra fused to form a cylindrical structure closely integrated with the neural arch, and that the intercentra were completely lost, at some time between the Lower Permian and the Middle Jurassic, by which time fully modern salamander centra had evolved.

The research of C. A. Boisvert (2004) has demonstrated that a major change in the sequence of development occurred within basal salamanders (the Hynobiidae), among which three primitive species retain the plesiomorphic sequence of chondrification and ossification of the neural arches prior to the centra. This supports other evidence that salamanders had evolved from labyrinthodonts rather than lepospondyls, in which the centra always ossified prior to the arches, at a very early stage of development.
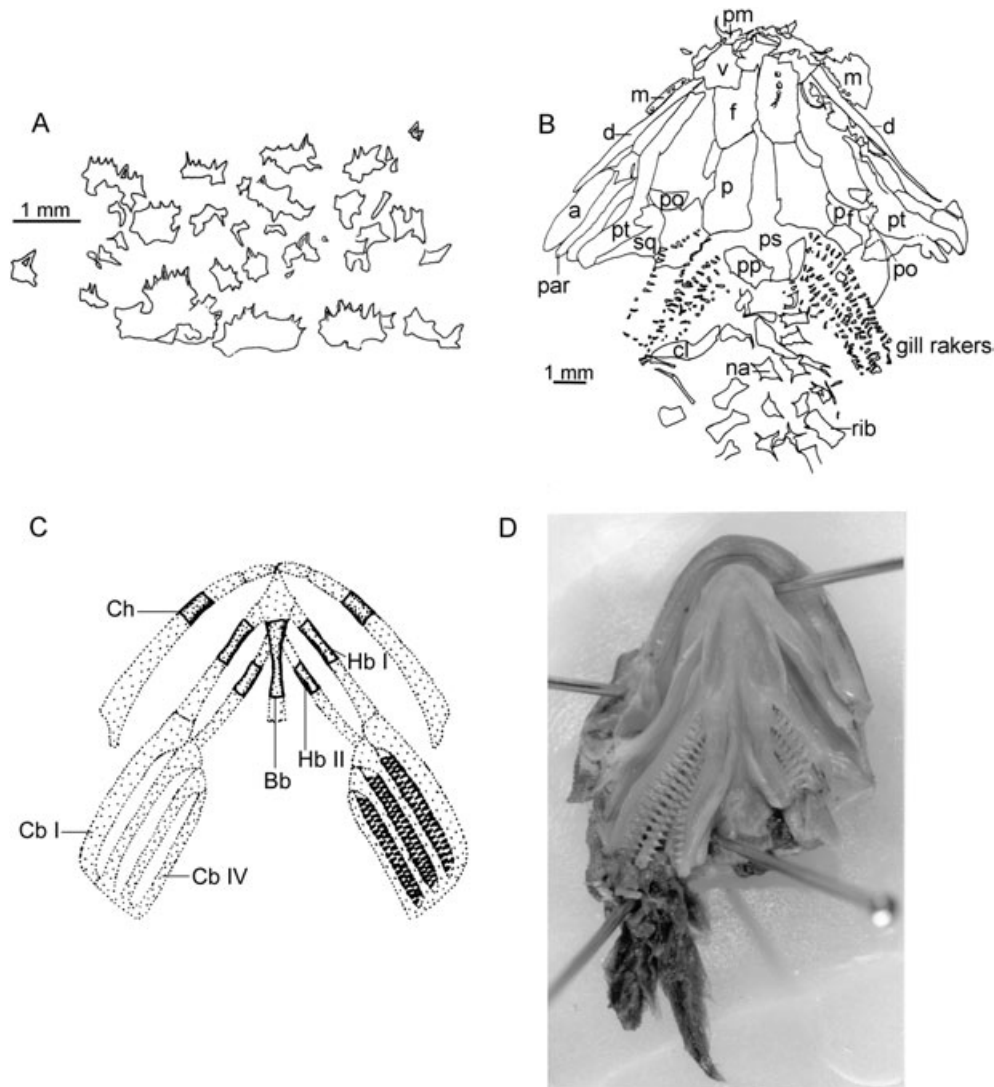
Figure 57. Branchial denticles in Palaeozoic branchiosaurs and a modern salamander. A, branchial tooth plates with attached denticles from the micromelerpetontid *Micromelerpeton credneri* from Odernheim, Geological and Palaeontological Institute of Mainz, specimen number N226. This typified the primitive pattern for temnospondyls. B, branchial denticles in the branchiosaurid *Apateon* (Royal Ontario Museum, Canada, 44276). C, reconstruction of hyobranchial elements and branchial denticles of the branchiosaurid *Apateon*. Reproduced from Boy & Sues (2000). D, branchial denticles associated with the gill slits in *Ambystoma tigrinum* (Canadian Museum of Nature, Ottawa, 7255).

Appendicular skeleton

As with the skull and vertebrae, sequential development is also evident in the appendicular skeleton of branchiosaurids, but this also occurs in other Palaeozoic labyrinthodonts. In most Palaeozoic tetrapods, the dermal shoulder girdle ossified essentially simultaneously with the dermal skull, and well before the endochondral girdles and other elements of the postcranial skeleton. In *Micromelanerpeton* (Fig. 53), which may be considered a plesiomorphic sister taxon of branchiosaurids, only the body outline is evident behind the pectoral girdle at an early larval stage. In branchiosaurids, the dermal bones of the shoulder girdle ossify more slowly and are of reduced size in the adults. This might be expected in a sister taxa of salamanders, in which these bones are lost entirely. The pubis is also slow to ossify in most branchiosaurids, as is the case in primitive living salamanders (e.g. *Hyn. nigrescens*, Fig. 17), and fails to ossify in others.

The limbs of all early tetrapods ossify in an essentially proximal-to-distal sequence, except for a delay

in ossification of the carpals, tarsals, and ends of the limb bones. Ossification of the carpals and tarsals is very much delayed in branchiosaurs, for which this part of the skeleton is known in very few specimens.

The most striking feature of limb development in branchiosaurids is the sequence of ossification across the digital arch (Figs 58, 59). As early as 1910, Schmalhausen recognized that salamanders were unique among living tetrapods in the sequence of development of the distal portion of the limbs (Schmalhausen, 1910). In all anurans and amniotes that have been studied, development occurs in a posterior-to-anterior (or postaxial-to-preaxial) direction – the ulna ahead of the radius, the fibula ahead of the tibia, and the digits and associated elements of the wrist and ankle from the fourth to the first. Salamanders alone chondrify and ossify these elements in the opposite direction (Erdmann, 1933; Shubin & Wake, 2003). Holmgren (1933, 1939) used this distinct pattern of development to argue that salamanders had evolved their limbs independently from all other tetrapods, as a result of their origin from a different group of fish, the Dipnoi.

A pattern very close to that of modern salamanders can also be recognized in the Palaeozoic branchiosaurid *Apateon* (Schoch, 1992; Fröbisch NB, Carroll RL, Schoch RR, 2007). At an early stage in development (Figs 58, 59), the radius is distinctly larger and more differentiated than the ulna, and the tibia is more advanced than the fibula. Carpals and tarsals

Figure 58. Sequence of ossification of the bones of the forelimb (top) and hindlimb (bottom) of *Apateon*. A, stage III, specimen number ATD 6. B, forelimb only, stage IV, ATD 106. C, stage V, ATD 290. D, stage V, ATD 231. Specimens in Figs 58 and 59 are from the Geological and Palaeontological Institute of Mainz. The darker the bones, the greater the level of ossification. *Preaxial side of limb.

Figure 59. Sequence of ossification of the bones of the forelimb and hindlimb of *Apateon*. A, stage V, ATD 264, hindlimb only. B, stage VI, specimen number 16258, Staatl. Museum für Naturkunde, Stuttgart.

are very slow to ossify in all branchiosaurids, if they appear at all, and their sequence cannot be determined. However, the metapodials and digits show a consistent pattern of ossification in the sequence II–III–I–IV–(V), uniquely comparable to that of modern salamanders. Surprisingly, the first elements of the autopodium (the hands and feet) to ossify in *Apateon* are the terminal phalanges of the manus. These appear at stage III (Fig. 58A), leaving a great gap distal to the ulna and radius. A similar pattern is seen in the living salamanders *Ranodon sibiricus*, *Salamandrella keyserlingii*, and *Ambystoma mexicanum*. It has been suggested that the early development of the

extremities of the manus and pes may help to keep the smallest larvae suspended above the sediments of the water bodies in which they develop. The next elements to ossify in *Apateon* are the metapodials, which also appear in the sequence II–III–I–IV–(V). They in turn are followed by the medial phalanges, in the same order. The preterminal phalanges ossify from proximal to distal.

No Palaeozoic taxa other than branchiosaurs are known to show this dominance of the preaxial elements of the limbs or the precocial ossification of the terminal phalanges. As such, this appears as an important synapomorphy with salamanders that is

logically associated with their life histories, based on great prolongation of the larval stage. However, despite the unique sequence of development, the anatomy of the most mature specimens, specifically the nearly identical phalangeal count, remains very similar to that of other dissorophoids and early temnospondyls (Table 2), and supports an ultimate common ancestry. Observations of primitive extant salamander larvae show the importance of the first and second digits in locomotion and attachment to vegetation, as well as their having a sensory role (Vorobyeva et al., 2000; Shubin & Wake, 2003), which may have served as a force of selection for the switch from postaxial to preaxial dominance in development of the digital arch in ancestral caudates.

Life-history traits
Although branchiosaurids are not unique among Palaeozoic amphibians in their prolonged retention of larval characteristics, they are the only group known to have larvae very similar to those of primitive modern salamanders. Their prolongation of an aquatic way of life can be associated with a long period of adaptation to the large lake system that existed in central Europe for millions of years in the Late Carboniferous. Most branchiosaurid fossils have been collected from a series of large, long-lasting (on an ecological time scale) lakes in the Czech Republic (Milner, 1980), France (Steyer, 2000), and Germany (Schoch & Milner, 2004, 2005). They suggest very long periods of larval life, and either very late metamorphosis, or neoteny.

One may postulate that the specialized cranial anatomy of the early larvae that characterizes *Apateon* evolved in response to adaptation to the rich and continuous food resources provided in these long-lasting lake systems. The adaptive advantage for prolongation of the span of larval life may have been the factor that selected for whatever genetic changes were responsible for the slow, sequential sequence of the ossification of the dermal bones of the skull, in contrast to the near synchrony of their ossification in more primitive tetrapods. Great extension of their period of larval life would eventually have had repercussions on other aspects of their anatomy and way of life.

Both branchiosaurids and micromelerpetontids are known almost entirely from larvae. The only branchiosaurid that has certainly reached the level of ossification of the skull and limbs common to the terrestrial adults of modern salamanders is *Apateon gracilis* from the Middle Autunian (R. R. Schoch & N. B. Fröbisch 2006). Most other branchiosaurids that have been described may have been fully neotentic, with few if any skeletal characters specifically associated with a terrestrial life stage. R. R. Schoch & A.

Milner (2004) point out that no specimens showing ossification of endochondral elements of the skull or the carpals and tarsals have been recognized among the hundreds of specimens of larvae of approximately a dozen other branchiosaurid species that have been recognized. In contrast, they cite continuous growth stages, from tiny larvae to highly ossified adults, of the genera *Onchiodon* and *Sclerocephalus*, which occur in other localities in Europe over the same time span. They go on to suggest that the apparent absence of adult branchiosaurids may be the result of the probable high altitude of many of the localities in which they have been collected, citing the tendency towards neoteny in some modern salamanders that live in cold environments. However, it should also be noted that the area near the margins of these lakes, where adults might be expected to come to breed, is almost never represented in the sedimentary record of these basins.

The most widely distributed branchiosaurids were small forms, the most common of which was *Apateon pedestris*. They occurred many kilometres from the shore in the pelagic zone of large, deep, eutrophic lakes with abiotic bottom layers. Prolongation of larval life may have been a very important selective factor in the origin of urodeles, in which the specific structure and function of the larval feeding apparatus is unique relative to all other amphibians.

Specimens that have been described as either branchiosaurs or larval salamanders from the Early Triassic (Gao et al., 2004) and Late Triassic (Milner, 2000) suggest that the antecedents of salamanders may have gone through a long period, from the Upper Carboniferous into the Jurassic, during which they were dominated by larval/neotenic forms that would have spent little if any time out of the water. A primarily aquatic way of life may explain the retention of the primitive sequence of vertebral ossification, with the long persistence of an unrestricted notochord running beneath the neural arches prior to the ossification of cylindrical centra. However, in contrast to primitive caecilians, there is no evidence for the retention of separate intercentra.

Synapomorphies of salamanders and advanced branchiosaurids
Although our knowledge of branchiosaurids is limited almost entirely to their larvae, they none the less share numerous synapomorphies with salamanders:

1. specific sequence of ossification of individual bones of the skull and postcranial skeleton
2. retardation in ossification of bones that are either slow to ossify or are lost in modern salamanders
3. jaw suspension without a bony link to the maxilla (at least during development)

4. squamosal with a hinge-like articulation with bones of the skull table and /or otic capsule

5. absence of lateral-lines grooves in the skull bones of late larvae

6. pedicellate teeth in adults but not larvae

7. ceratobranchials become ossified or calcified at the time of maturation in neotenic species

8. pharyngeal denticles not attached proximally to a bony plate, as in most Palaeozoic tetrapods, but appearing as separate elements

9. denticles arranged in six rows that interdigitate across the intervening gill slits

10. loss of bony ventral scales

None of these synapomorphies are known in other Palaeozoic amphibians, and only the presence of pedicellate teeth is also seen in frogs and caecilians.

Other character states, although of a primitive nature, shared between advanced branchiosaurids and primitive salamanders are the ossification of neural arches prior to the centra, a very similar phalangeal formula, and the same number of digits.

The gap between branchiosaurids and crown-group salamanders

Unfortunately, the long-lasting system of lakes, in which a plethora of salamander-like features evolved among branchiosaurids and which was also responsible for their preservation as fossils, did not persist long beyond the base of the Permian. Aside from two fossil assemblages, too poorly preserved to allow determination of whether the specimens were branchiosaurs or primitive salamanders, there remains a gap of approximately 100 million years before the first appearance of crown-group urodeles. We can only guess when, and under what conditions, the sequence of cranial ossification common to branchiosaurs was truncated, and the number of bones present in the larval cranium was retained in the metamorphosed adults.

Although the early larvae of branchiosaurids closely resemble those of Middle Jurassic cryptobranchoids, late larvae or neotenic adults of branchiosaurs retain all the dermal skull bones of other advanced temnospondyl labyrinthodonts. There is no evidence as to whether any branchiosaurids had acquired the anatomical or behavioural characters necessary for the mode of terrestrial feeding present in the most primitive of living salamanders, the hynobiids.

More generally, the changes between the Lower Permian and the Lower Jurassic were as follows:

1. re-emergence or prolongation of life on land

2. termination of growth prior to the development of the following bones of the skull: tabular*, postparietal*, supratemporal*, postfrontal*, postorbital*, jugal*

3. reduction of the sculptured dorsal portion of the squamosal to allow passage of the adductor mandibulae internus (superficialis) out of the adductor chamber and over the otic capsule

4. loss of the otic notch and middle ear cavity associated with the capacity to hear high-frequency, airborne vibrations

5. origin of tongue supported by a modified hyoid apparatus and capable of protrusion

6. change of configuration of the articulating surfaces of the exoccipitals and atlas to limit movement of the head to dorsoventral hinging in the sagittal plane

7. reduction in the number of presacral vertebrae from 20 to 17

8. reduction in the number of dermal bones in the lower jaw from about eight to four

9. formation of cylindrical centra, fused to the neural arch in adults

10. loss of intercentra

11. loss of *cleithrum, *clavicle, and *interclavicle

12. origin of endochondral sternum

13. fusion of distal carpals and tarsals 1 and 2 to form basale commune in the adult

It is important to note that few of these changes require reversal, and many cases of bone loss (*) are presaged by their delayed ossification in the Palaeozoic genera.

One characteristic that appears to change very near the base of the crown group is the loss of sculpturing on the dorsal portion of the squamosal, which allows passage of the adductor mandibulae internus (superficialis) jaw muscle over the otic capsule. This area of sculptured bone is still retained in the Upper Jurassic caudate *Karaurus*.

Another major change that occurred prior to the appearance of crown-group salamanders involved the nature of the middle ear and hearing. Adults of extant salamanders lack any evidence of the posterior embayment of the squamosal or the middle ear cavity that characterize frogs, or the capacity to respond to high-frequency, airborne sounds. In contrast, all branchiosaurids retain an otic notch, common to other temnospondyls, which appears to be structurally, and therefore presumably functionally, homologous with that of anurans (R. R. Schoch & N. B. Fröbisch (2006). A clearly defined otic notch and a stapes that broadly resembles that of modern frogs is a heritage of temnospondyls (Robinson, 2005), going back to the Lower Carboniferous, and those of the Lower Permian dissorophoid *Doleserpeton* are very close to the anuran pattern (Bolt & Lombard, 1985). *Apateon* differs only in having a somewhat shallower notch as a result of the more anterior position of the jaw suspension and delayed ossification of the quadrate. Stapes are known

for large individuals of *Apateon* that closely resemble those of small terrestrial temnospondyls, except for the partially unossified footplate. The shaft is compressed anteroposteriorly, and the straight ventral margin of the footplate is hinged or suturally attached to the parasphenoid. This evidence led Boy & Sues (2000) to argue that branchiosaurs were capable of detecting airborne sound. However, a well-developed stapes with a stapedial foramen is present in the stem-group urodele *Karaurus* and also in hynobiids. These latter species have no place for attachment of a tympanum, and hynobiids have no middle ear cavity.

The question is not whether branchiosaurs could hear airborne sounds, but how important hearing was to their way of life. The persistence of an aquatic way of life, indicated by the presence of external gills in most branchiosaurids over a period of at least 10 million years, and the high degree of specialization of their hyoid apparatus for suck-and-gape feeding, indicate that they had long larval stages, or were facultatively or obligatorily neotenic. As such, they might have found it difficult to make use of an impedance-matching middle ear. Despite the presumed selective value of response to high-frequency airborne sound in many Palaeozoic temnospondyls, the otic notch is reduced or lost in several other clades that show a high degree of aquatic adaptation (Holmes, 2000), and numerous cases of loss of the middle ear are known in modern frogs (Duellman & Trueb, 1986).

As can be seen in lateral views of the larvae of modern salamanders, their Middle Jurassic relatives, and *Apateon* (Fig. 48), the functioning external gills extend dorsally over the trunk, above the lateral surface of the skull, which was occupied by the tympanic membrane in terrestrial temnospondyls. These animals clearly could not respire in an aquatic medium and hear airborne sounds at the same time, and nor could they use their gills for respiration if they were exposed to the air.

Over the millions of years during which branchiosaurids adapted to a primarily aquatic way of life, where chemical means of species recognition might have been facilitated, the need to respond to high-frequency vibrations may have been reduced. If there were not strong selective pressures to maintain an impedance-matching middle ear, other forces of selection may have acted to reduce the large middle ear cavity. In modern frogs, this occupies the same general area of the head as the jaw muscles. Salamanders, in contrast, have used this space to greatly enlarge the area of the adductor jaw musculature relative to that of anurans.

It is interesting to note the salamander-like features of the skull that are evident in one of the most primitive of living anurans, *Ascaphus*. In contrast to most frogs, it has lost the impedance-matching middle ear and stapes, apparently as a result of its adaptation to life in fast-running streams, in which airborne sounds would be difficult to discern. As in hynobiids and ambystomatids, the jaw articulation is anterior to the level of the occiput, and there is no bony connection between the jaw suspension and the maxilla.

The strongest evidence for the presence of an impedance-matching middle ear structure in the ancestors of salamanders is provided by embryological studies of the primitive hynobiid salamanders *Ranodon* and *Hynobius* by Schmalhausen (1968:189–190):

The tympanic cavity of anurans is developed as an outgrowth of the dorsal wall of the first visceral fold in the form of an aggregated cellular mass, taking the form of a bubble set on a long pedicel. This cellular mass then loses its connection with the pharyngeal epithelium. The tympanic cavity proper is formed from these primordia only during metamorphosis. It is located anterior to the hyomandibular nerve. The Eustachian tube is formed anew. If one considers the features of the development of the tympanic cavity in anurans, then it is easy to recognize the same process seen in the development of urodele Amphibia.

In *Hynobius*, the anlage of the dorsal diverticulum of the first visceral fold is considerably larger than in the axolotl or *Triton*. Its general form is the same: it is a small pyriform formation set on a long pedicel. It is, however, retained much longer without reduction and its original connection to the pharyngeal epithelium sometimes persists until metamorphosis. In one case, in a larva of 33 mm length near metamorphosis, a well-preserved pear-shaped anteroposteriorly flattened mass of cells set on a long, flat, rather thick pedicel has been observed. In *Ranodon*, however, this formation is even more strongly developed although the connection of the primordium to the pharyngeal epithelium is broken earlier than in *Hynobius*.

The rudiments described and especially the epithelial formations developing from this in the larvae of *Ranodon*, are quite similar to the anlagen of the tympanic cavities of anuran Amphibia, both in their mode of development and in their position between the palatoquadrate cartilage and the hyomandibular nerve.

In summary, he states that evidence from *Ranodon* and *Hynobius* 'gives quite clear indication that in the ancestors of urodele Amphibia there was actually an apparatus for sound transmission from the air, i.e., a tympanic cavity and tympanic membrane'.

Acquisition of salamander characters among branchiosaurids

Although there remains a long gap in time and morphology between advanced branchiosaurids and the adults of crown-group salamanders, there are no other Palaeozoic tetrapods that are known to share as many synapomorphies with urodeles. If advanced branchiosaurs comprised the plesiomorphic sister taxon of urodeles, the next question to ask is how they are

related to other Palaeozoic amphibians. We may begin with consideration of the more primitive branchiosaurids (R. R. Schoch & A. R. Milner, 2004).

Although *Apateon*, and particularly the species *Apateon pedestris* and *Apateon caducus*, provide the best known models for comparison with salamanders, there are several other species of *Apateon* and other genera within the Family Branchiosauridae that should be considered in evaluating the ancestry of salamander characters.

All members of the Branchiosauridae were small, with skulls ranging from 15 to 35 cm in length. Correlated with their small skull size, the orbits were relatively much enlarged. The prefrontal and postfrontal narrowly overlap in primitive species, but are separated from one another to a variable degree in others, and the jugal and lacrimal are separated by the maxilla. The palate was also distinguished by very large interpterygoid vacuities and corresponding reduction of the surrounding bones. The anterior process of the pterygoid is very slender, and the palatine and ectopterygoid are short. In common with other dissorophoids, the anterior ramus of the pterygoid does not reach the vomer. Where there were fangs on the vomers, palatines, and ectopterygoids in more primitive temnospondyls, these teeth are reduced within the Branchiosauridae to the size of the marginal dentition or that of denticles. The squamosal embayment is relatively shallow in *Branchiosaurus*, but deep in *Schoenfelderpeton*. Except in *Melanerpeton*, the jaw articulation does not extend posterior to the level of the occiput.

The body proportions of branchiosaurids resemble those of terrestrial members of other dissorophoid families, with relatively large limbs, short trunk, and large manus. Even in the earliest species, the interclavicle and clavicle were much smaller than those of other temnospondyls. The ilium is slender in primitive genera, but more massive and more nearly vertical in more derived forms.

The most primitive branchiosaurid is *Branchiosaurus*, known from species from the Westphalian D in both North America and Europe, approximately 8 million years prior to the specimens of *Apateon* that have just been described (Milner, 1982). The first described material of *Branchiosaurus*, *Branchiosaurus salamandroides*, came from what is now the Czech Republic. This species resembles the more mature specimens of *Apateon* in the general configuration of the skeleton, but even in the smallest individuals, with skulls little more than 5 mm in length, most, if not all, of the dermal bones were ossified, as in the larvae of most Palaeozoic tetrapods (Fig. 60). That is, *Branchiosaurus* had not yet evolved the capacity for gradual, sequential ossification of the dermal skull. This genus was also primitive in retaining contact between the prefrontal
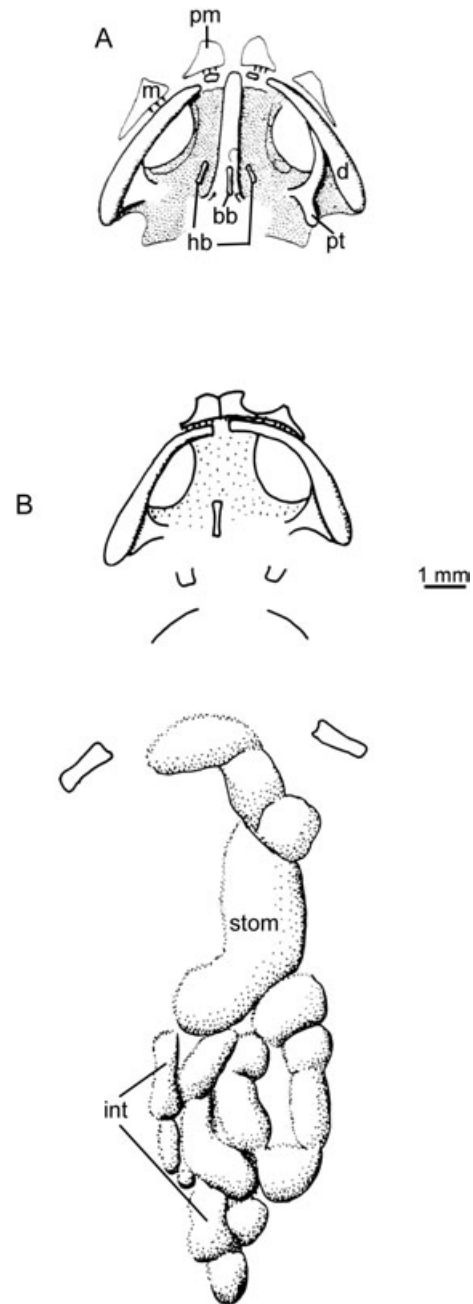

Figure 60. Two specimens attributed to the primitive branchiosaurid *Branchiosaurus* sp. from the Westphalian D of Mazon Creek, Illinois. Reproduced from Milner (1982). A, skull of United States National Museum 4400 in palatal view. Note the similarity of the hyoid elements to those of the Middle Jurassic salamander *Chunerpeton tianyiensis* (Fig. 47). B, Yale Peabody Museum 802, showing palate and infillings of the digestive tract.

and postfrontal bones, which are separated by the frontals in the adults of *Apateon*, and have a rugose area on the posterior plate of the parasphenoid that may reflect the prior presence of denticles that are

present in this position in sister taxa of the branchiosaurids, specifically the early amphibamids. *Branchiosaurus* also retained the bony ventral scales that were lost in later branchiosaurids. It has 24 presacral vertebrae, as opposed to 20–22 in later species.

However, *Branchiosaurus* did express several derived features shared with later branchiosaurids, including the loss of the bony plates that support the pharyngeal denticles in most primitive temnospondyls. The individual denticles are separate, as in later branchiosaurids, although they usually lack the multiple processes from the tip of the denticle that are elaborated during growth in later branchiosaurids. The jugal failed to reach the lachrymal, and the back of the skull table was reduced, as were the size of the clavicular blade and the interclavicle. *Branchiosaurus* had also achieved features of the hyoid elements that are similar to those of later branchiosaurs, with early ossification of the hypobranchials and basibranchial (Fig. 60). This condition also resembles that of the primitive caudates, *Karaurus* and *Chunerpeton*.

We see within the Branchiosauridae, over the roughly 10 million years between the Westphalian D and the beginning of the Permian, the accumulation of numerous characteristics leading towards salamanders. The most important was the evolution of the capacity to ossify the dermal bones of the skull in a sequential manner, in contrast with the nearly simultaneous mode of ossification in all other Palaeozoic tetrapods, in which nearly all the dermal bones are integrated into a tight-fitting matrix in the smallest known specimens.

Branchiosaurids are, in turn, strongly supported as members of the Superfamily Dissorophoidea (also including the Micromelerpetontidae, the Amphibamidae, and the Trematopidae) (Holmes, 2000) by the following synapomorphies: small size of early species compared with all other temnospondyls, very large orbits and interpterygoid vacuities relative to skull size, retention of a movable basicranial articulation, conspicuous otic notch, and a tendency to lose contact between the prefrontal and postfrontal and between the lacrimal and jugal (Milner, 1982). They share with eryopoids the loss of the intertemporal that is present in earlier temnospondyls. Going further back, the ancestry of dissorophoids, together with many other members of the Temnospondyli, are traceable to the Viséan *Balanerpeton* (Milner & Sequeira, 1994).

Of the characteristics of primitive members of the crown-group urodeles, a few can already be recognized in *Balanerpeton*: digital and phalangeal count, relatively small body size, arches ossifying before centra, large orbits and interpterygoid vacuities, and general proportions of trunk and limbs (Fig. 70). These, however, are enough to distinguish *Balanerpeton* from all other clades known from this or earlier time periods in the Palaeozoic, as a plausible sister taxon of salamanders. Thus, one may say with considerable confidence that salamanders have a closer sister-group relationship among the temnospondyls than with any of the other recognized clades of Palaeozoic tetrapods.

In the absence of any knowledge of temnospondyls earlier than *Balanerpeton*, no characteristics seen in older amphibians are plausibly homologous with any of the distinguishing characters of salamanders.

A nested sequence of synapomorphies leading from early temnospondyls to crown-group urodeles is shown in Fig. 61.

ANCESTRY OF ANURANS

MESOZOIC ANURANS

In contrast to the diversity of body forms and life-history strategies exhibited by crown-group salamanders, the general body plan of adult anurans has been essentially constant since the Lower Jurassic. This may be attributed to the strong constraints resulting from the mode of saltatory locomotion. Fossils of tadpoles are known no earlier than the Lower Cretaceous (Chipman & Tchernov, 2002), but the basic similarities of these tadpoles to those of the living *Ascaphus*, whose ancestors are thought to have diverged from other anuran clades by the beginning of the Jurassic, indicate a similar constancy of their larvae.

Fortunately, fossils from the Lower and Middle Jurassic provide an extensive basis for establishing which character states of the adult skeleton distinguish the basal members of the crown-group anurans. The most informative genera are *Prosalirus* (Jenkins & Shubin, 1998), known from disarticulated remains of several individuals from the mid-Lower Jurassic (Pliensbachian) of Arizona, *Vieraella*, represented by a single individual from the upper portion of the Lower Jurassic of southern Patagonia, and *Notobatrachus* (Fig. 62), from the transition between the Middle and Late Jurassic, also from Patagonia (Báez & Basso, 1996). Almost the entire skeleton of *Notobatrachus* is known from numerous well-preserved and nearly complete, articulated skeletons.

Ironically, it has remained very difficult to classify the earliest fossil anurans, or to establish their specific relationships with extant families, because most of their osteological character states are plesiomorphic for anurans as a whole. The problem of classification is particularly evident in the case of *Notobatrachus*, despite very complete knowledge of its anatomy. Estes & Reig (1973) placed *Notobatrachus* in the Ascaphidae, which at that time included both *Ascaphus* and *Leiopelma*. A strict consensus tree of Báez & Basso (1996) indicated a position between *Vieraella* and a clade including *Ascaphus* and *Leiopelma* as sister taxa, and an unresolved trichotomy including
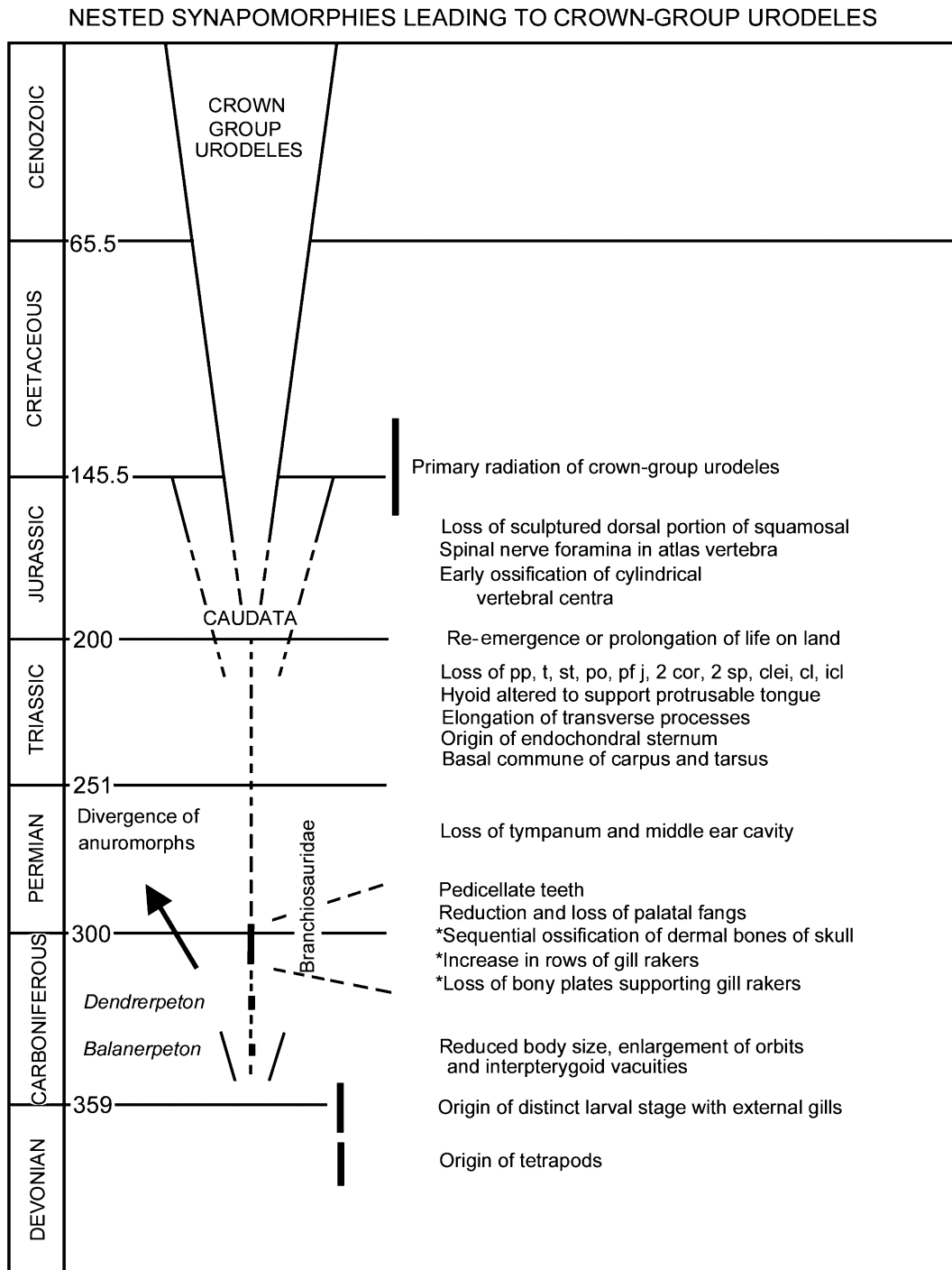
NESTED SYNAPOMORPHIES LEADING TO CROWN-GROUP URODELES

Figure 61. Nested synapomorphies leading to crown-group urodeles.

Bombina, *Alytes*, and *Discoglossus*. Roček (2000) assigned *Notobatrachus* to the Leiopelmatidae, used in the same sense as the Ascaphidae of Estes & Reig (1973). Sanchiz (1998) placed it in the Leiopelmatidae (to the exclusion of the Ascaphidae). More recently, a phylogenetic analysis by Gao & Wang (2001) united *Notobatrachus* and the very incompletely known

Lower Jurassic *Prosalirus* as sister taxa at the base of the Anura.

The fossil record of tadpoles goes back no further than the Lower Cretaceous (Chipman & Tchernov, 2002). The body form of the smallest individuals (Fig. 26) indicates that they had essentially modern proportions, with a globular head and trunk region,
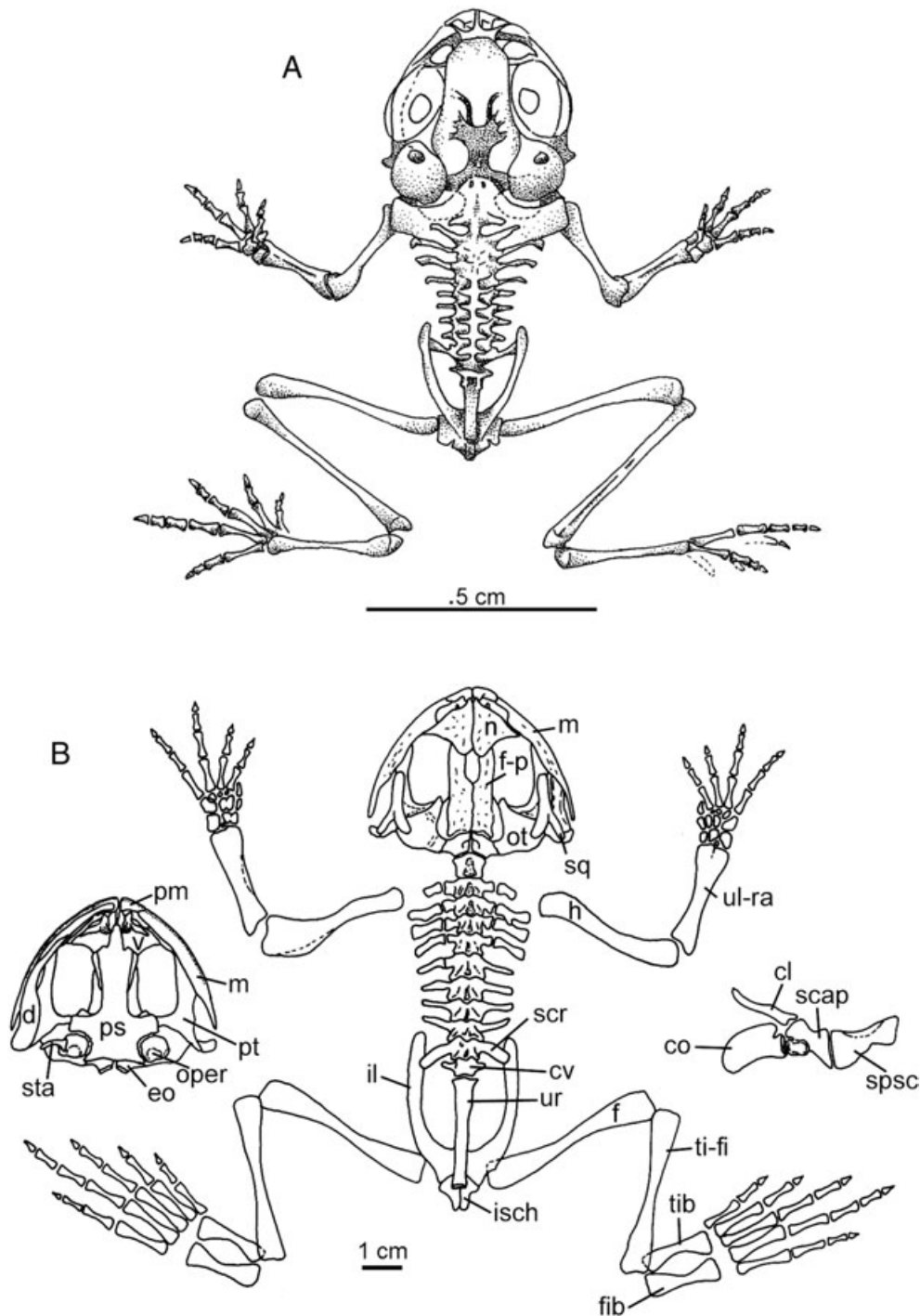
Figure 62. A, juvenile of one of the most primitive living anurans, *Leiopelma*; drawing by Cambell Rolian from cleared and stained specimen in the Redpath Museum. B, *Notobatrachus degiustoi*, a primitive anuran from the Late Jurassic of Argentina. Reproduced from Estes & Reig (1973).

succeeded by a much narrower tail. This implies an abdominal cavity like that of modern tadpoles, with a large, spirally arranged gut. Fossils retaining nothing more than body outlines from earlier in the Mesozoic or even the Permian could provide evidence of when stem salientians had first evolved a gut capable of feeding on plant material. Unfortunately, it is not likely that the cartilaginous larval jaws would be pre-

served in early frog larvae, as they are not evident in the numerous specimens collected from either the Cretaceous or the Oligocene (Špinar, 1972).

The reduction of the tail appears to have begun in the Lower Triassic *Triadobatrachus*, which, on the basis of the degree of ossification of the skeleton of the only known specimen, was an adult. Essentially modern-type pipoid tadpoles are known from the Lower Cretaceous. Larvae are known from the family of Palaeozoic amphibians that are most often suggested as sister taxa of anurans, the Amphibamidae; they do not have any visible characteristics that are comparable to those of tadpoles, but superficially resemble the larvae of salamanders and their putative Palaeozoic sister group (Milner, 1982). Presumably, the tadpole evolved no earlier than the Early Mesozoic.

The following characters of *Notobatrachus* and other Lower and Middle Jurassic anurans include synapomorphies uniting the crown-group anurans, and other features that can be used to establish their probable relationship among Palaeozoic tetrapods.

ANURAN SYNAPOMORPHIES

D: Derived at the level of basal anurans
Ds: Derived at the level of basal salientians (*Triadobatrachus*)
Da: Derived at the level of amphibamids
Dt: Derived at the level of temnospondyls
P: Present in primitive labyrinthodonts

Adults

Skull
 1. Ds. Large orbitotemporal openings separated by frontoparietal, and surrounded by the prootic, squamosal, maxilla, and nasals
 2. Ds. Area of ossification occupied by the frontal and parietal in other tetrapods formed as a single ossification, the frontoparietal. Frontoparietal paired in *Notobatrachus* and *Vieraella*; condition not certain in *Prosalirus*
 3. D. The frontoparietal of *Notobatrachus* and *Vieraella* lacks the posterolateral portion that extends over the otic capsule in most Palaeozoic tetrapods. It is retained in *Prosalirus* and *Triadobatrachus*
 4. Dt. Squamosal embayed above quadrate, presumably to support the tympanum
 5. D. Squamosal bearing anterior zygomatic process
 6. Ds. Loss of the following skull bones relative to Palaeozoic tetrapods: postparietal, tabular, supratemporal, postorbital, postfrontal, jugal, prefrontal, lacrimal, ectopterygoid
 7. Da. Absence of fangs on vomers and palatine
 8. Dt. Extremely large interpterygoid vacuity
 9. Da. Pedicellate marginal teeth

10. D. Fused opisthotic–exoccipital
11. Ds. Stapes imperforate
12. Dt. Ventral edge of stapedial footplate articulates with ventral margin of fenestra ovalis
13. D. Operculum (ear ossicle)
14. Da. Articulation between skull and first cervical vertebra via a bicondylar occipital condyle and bicotylar atlas

Lower jaw
15. D. Lower jaw consists of dentary, angulosplenial and mentomeckelian bones. Coronoid, splenial and prearticular no longer appear as separate areas of ossification
16. Ds. Loss of dentition on dentary

Hyoid apparatus
17. Ds. Bony parahyoid and posterior medial processes

Vertebrae and ribs
18. D. Number of trunk vertebrae: ten in *Vieraella*, nine in *Notobatrachus*, not known in *Prosalirus*
19. Da. Atlas a single ossification in the adult, two large cotyles, pointed odontoid process
20. D. Loss of transverse processes of atlas in *Prosalirus*, but not in *Notobatrachus*
21. D. Sacral vertebrae lacking postzygapophyses in *Prosalirus*, but not in most specimens of *Notobatrachus*
22. D. Loss of free ribs posterior to trunk vertebrae II–V, occasionally VI
23. Ds. Ribs with uncinate processes
24. D. Fusion of all but the most anterior caudal vertebrae into urostyle
25. D. Articulation between sacrum and urostyle, but without a bony condyle
26. D. Reduction of caudal vertebrae to one or two anterior to urostyle
27. D. Transverse process of sacral vertebra lies above the ilium, resulting in a rotary joint

Appendicular skeleton
28. D. Scapula with open ventral cleft (homologous with the supraglenoid foramen in Palaeozoic tetrapods) between the anterior portion of the scapula and the glenoid
29. D. Elongate coracoid, not fused with scapula
30. D. Slender cleithrum (forming anterior margin of suprascapula) and clavicle
31. Ds. Humerus with single articulating surface for fused ulna and radius

32. D. Ulna and radius fused into an elongate radioulna
33. D. Carpus consisting of ulnare, intermedium, radiale, large bone distal to radiale formed by two contiguous elements, two elements of the prepollex, distal carpals, I, II, III
34. Dt. Phalangeal formula of manus 2,2,3,3
35. Ds. Elongate, anteriorly directed iliac blade, with superior tuber
36. Ds. Pubis unossified
37. D. Fused and elongate tibiofibula
38. Da. Tibiale and fibulare elongate, but extremities not fused
39. D. Mesopodials reduced to one centrale and three distal tarsals
40. Dt. Phalangeal formula of pes 2,2,3,4,3
41. D. Presence of prehallux

Larvae

42. D. Extremely highly specialized tadpole form is known only among crown-group anurans, but some of these features probably evolved among earlier salientians
43. P. Modern anurans retain the primitive labyrinthodont trait of having a distinct larval stage
44. P. Development of neural arches long before centra

Most of the adult features in this list were based on *Notobatrachus*, but some differences can be noted in *Prosalirus* and *Vieraella*. *Prosalirus* appears to retain a pineal foramen. A few other characters states seen in Early and Middle Jurassic frogs probably represent apomorphies or may have undergone reversal in later anurans. These include the apparent absence of a quadratojugal bone in *Vieraella* and *Notobatrachus* (a condition not known in *Prosalirus*). A discrete palatine cannot be recognized in these early anurans, but is expressed in neobatrachians. Whether the sphenethmoid is paired or fused at the midline may be a factor of size and/or the degree of maturity.

LOWER TRIASSIC SALIENTIANS

An interval of approximately 50 million years separates the oldest known, unquestioned anuran, *Prosalirus*, from the only fossils that link them to any plausible Palaeozoic antecedents (Roček & Rage, 2000; Borsuk-Białynicka, Maryańska & Shishkin, 2003). Two species from the Early Triassic (Olenekian or upper Scythian) show numerous derived features in common with crown-group anurans – *Triadobatrachus* (Figs 63, 64), represented by a natural cast of a nearly complete skeleton from Madagascar, and *Czatkobatrachus*, known from isolated bones of several specimens from Poland. Most of the following characters are known only in *Triadobatrachus*.
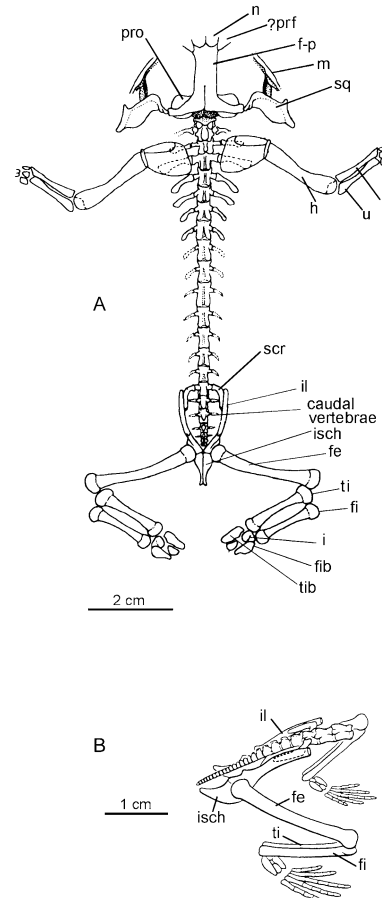

Figure 63. The Lower Triassic salientian *Triadobatrachus masslinoti* from Madagascar. A, skeleton. Reproduced from Roček & Rage (2000). B, lateral view of pelvic girdle and rear limb. Reproduced from Jenkins & Shubin (1998).

SALIENTIAN SYNAPOMORPHIES

Ds: Derived at the level of basal Salientia
Da: Derived at the level of amphibamids
Dt: Derived at the level of temnospondyls
P: Primitive for tetrapods

Skull

1. Ds. Large orbitotemporal openings separated by frontoparietal, and surrounded by the squamosal, maxilla, and nasal
2. Ds. Frontal and parietal fused to form a single frontoparietal
3. P. A pineal foramen is retained, as in *Prosalirus*
4. P. As in *Prosalirus*, the posterolateral portion of the frontoparietal extends over the otic capsule
5. Dt. Squamosal embayed above quadrate, presumably to support the tympanum
6. Ds. *Triadobatrachus* has lost all the dermal bones of the skull that are missing in *Notobatrachus*, except (perhaps) for the prefrontal. As in *Notobatrachus*, a quadratojugal is not evident
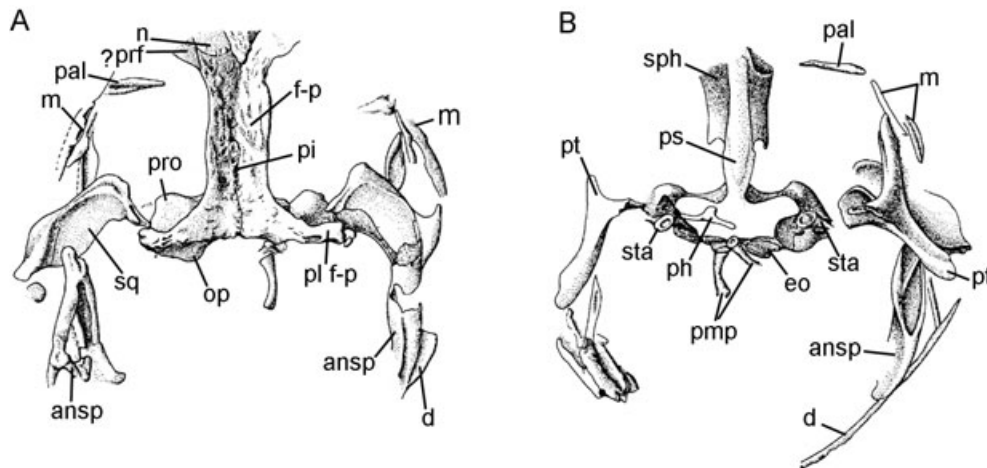
Figure 64. Skull of *Triadobatrachus massinoti* in dorsal and ventral views. Reproduced from Roček (2003).

7. Ds. Transversely oriented palatine, as in advanced anurans
8. Dt. Extremely large interpterygoid vacuity
9. P. Opisthotic and exoccipital ossify separately
10. Ds. Stapes imperforate
11. Da. Articulation between skull and first cervical vertebra via a bicondylar occipital condyle and bicotylar atlas

Lower jaw
12. Ds. Fused angulosplenial
13. Ds. Loss of dentition on dentary

Hyoid apparatus
14. Ds. Bony parahyoid and posterior medial processes

Vertebrae
15. Ds. *Triadobatrachus* retains 14 trunk vertebrae
16. Ds. *Czatkobatrachus* has lost the transverse processes and ribs on the atlas, but they are retained in *Triadobatrachus*
17. Ds. Intercentra lost
18. P. Six caudal vertebrae are preserved in *Triadobatrachus*, but more were probably present

Appendicular skeleton
19. Ds. *Czatkobatrachus* shows ventral elongation of the supraglenoid foramen, which is presumably an intermediate stage in the formation of the scapular cleft common to anurans (Borsuk-Białynicka & Evans, 2002)
20. Da. The carpus consists of the radiale, intermedium, ulnare, and three centralia

21. Ds. The ilium is anteriorly directed and elongate. It has a superior tubercle in *Czatkobatrachus*
22s. D. Pubis unossified
23a. Da. The tibiale and fibulare are somewhat elongate

The hands and feet remain unknown; no knowledge of larvae.

Triadobatrachus remains primitive in that the sacral rib was not fused to the centrum. The blade of the sacral rib was attached to the medial margin of the iliac blade, with little likelihood of rotatory movement of the ilium on the sacrum. There is no evidence of an operculum.

Because of the many synapomorphies of the cranium shared with crown-group anurans, and key aspects of the locomotor apparatus suggestive of an early stage in the evolution of saltatory locomotion, there has never been any question regarding the anuran affinities of *Triadobatrachus*. It is now considered a sister taxon, within the total group Salientia (Sanchiz, 1998). *Czatkobatrachus* occupies a comparable, but perhaps slightly more derived, position on the basis of the limited elements of the skeleton that are so far known.

PALAEOZOIC ANTECEDENTS OF ANURANS

Unfortunately, knowledge of *Triadobatrachus* and *Czatkobatrachus* brings us little closer to understanding the relationships of the Salientia with urodeles or caecilians, or their probable affinities with Palaeozoic tetrapods, as indicated by the highly divergent hypotheses of Laurin & Reisz (1997), Laurin (1998a, b), Ruta *et al.* (2003), or Vallin & Laurin (2004).

Despite the claim by the above authors that frogs, salamanders, and caecilians share a unique common ancestry above the level of any of the primarily Palae-

ozoic clades, *Triadobatrachus* shares few, if any, obvious synapomorphies with either salamanders or caecilians. This is especially striking in view of the fact that both Ruta *et al.* (2003: 291) and Laurin & Anderson (2004: 69) illustrate the divergence of frogs, salamanders, and caecilians as having occurred at the base of the Triassic, immediately before the appearance of *Triadobatrachus*. In the absence of obvious synapomorphies between *Triadobatrachus* and either basal salamanders or basal caecilians, are there any character states that might be recognized as synapomorphies uniting *Triadobatrachus* (and/or basal anurans) with particular Palaeozoic clades?

As is the case for salamanders, most anurans resemble early temnospondyls rather than lepospondyls in having gilled larvae (even if tadpoles quickly extend the operculum over the gills), in the ossification of neural arches long before the centra, and in many other osteological characters. Among Palaeozoic amphibians, only dissorophoid temnospondyls have the very large orbital openings and interpterygoid vacuities of anurans, along with conspicuous otic notches, a short skull table, a short trunk, and well-developed limbs. These characters are most highly elaborated among the family Amphibamidae, known from *Amphibamus* (Fig. 1) in the Upper Carboniferous (Milner, 1982) to the Upper Permian *Micropholis* (Holmes, 2000). Cranial similarities are most apparent in the Lower Permian *Doleserpeton* (Bolt, 1969, 1977, 1991), in which the great size of the interpterygoid vacuities achieved an essentially anuran configuration (Fig. 65). In this genus, they exceed the area of the orbits, themselves relatively larger than those of any other Palaeozoic amphibians. The large size of the orbits in *Doleserpeton* may be partially attributed to the small size of the adult skull (approximately 12 mm in length), but the orbits of microsaurs with similarly small skulls are relatively, as well as absolutely, much smaller (Carroll & Gaskill, 1978: 154).

On the other hand, amphibamids lack the derived features of branchiosaurids that support affinities with the Caudata, such as the sequential ossification of the skull bones and prolongation of the larval stage, and retain the primitive four rows of pharyngeal denticles, although these have lost the primitively supporting bony plates (Milner, pers. comm.).

Although *Doleserpeton* differs significantly from *Triadobatrachus* and basal anurans in the retention of the primitive tetrapod complement of circumorbital bones (jugal, postorbital, postfrontal, prefrontal and lacrimal), all are reduced in size, and the resulting orbital opening has already achieved the general configuration of modern anurans. The large size of the orbits in *Doleserpeton* is reflected in the exposure of both the palatine and the frontal in the orbital margin. In contrast, the prefrontal and postfrontal meet at the dorsal margin of the orbit, and the lacrimal and jugal meet along the lower margin in most primitive tetrapods. On the other hand, all the primitive bones of the skull table present in other dissorophoids are retained.

In relationship to the large size of the interpterygoid vacuity, the marginal bones of the palate of *Doleserpeton* are much reduced. The ectopterygoid appears to be lost, and the palatine has only a small palatal exposure, although it is exposed dorsally in the orbital margin. Denticles are present at the base of the cultriform process and on the pterygoid where it extends around the opening for the adductor chamber. In addition, there is a patch of larger denticles around the anteromedial margin of the internal naris in the position of the vomerine fangs of more primitive temnospondyls, but of much smaller size. A patch of denticles remains in this general position in numerous groups of modern anurans (Trueb, 1993). This area of the palate is not preserved in *Triadobatrachus*. The large Upper Carboniferous amphibamid *Amphibamus* (*Platyrhinops*) *lyelli* retains fangs on the vomer and palatine, but they are not present in the smaller *Amphibamus grandiceps*. This suggests that the absence of fangs may result from the retention of the juvenile character state in species of smaller adult size.

Doleserpeton is unique among amphibamids in having pedicellate teeth (Bolt, 1969), although they are much more slender (and therefore more like those of modern genera) than those of the putative caudate sister taxon *Apateon* (Fig. 56). No other Palaeozoic tetrapods are known to have had pedicellate teeth.

Another very important characteristic of amphibamids, including *Doleserpeton*, is the presence of a conspicuous notch in the posterior surface of the squamosal, which in modern frogs supports the tympanic annulus. This is accompanied by a small stapes with a relatively long columella and a footplate whose ventral margin articulates with the ventral surface of the fenestra ovalis. Neither crown-group urodeles nor caecilians have a tympanum, or any other characteristic of an impedance-matching middle ear, present in nearly all anurans. The great diversity of Lower Permian dissorophoids at the level of genera and species, with many species being described from a single locality (Carroll, 1964), may be a reflection of their use of airborne sounds as a necessary means of species recognition, as in modern anurans. The only group of Palaeozoic amphibians other than temnospondyls that have an otic notch and a stapes of sufficiently small size to function as part of an impedance-matching system are the seymouriamorphs. However, seymouriamorphs share no other putative synapomorphies with either temnospondyls or anurans (Laurin, 2000).
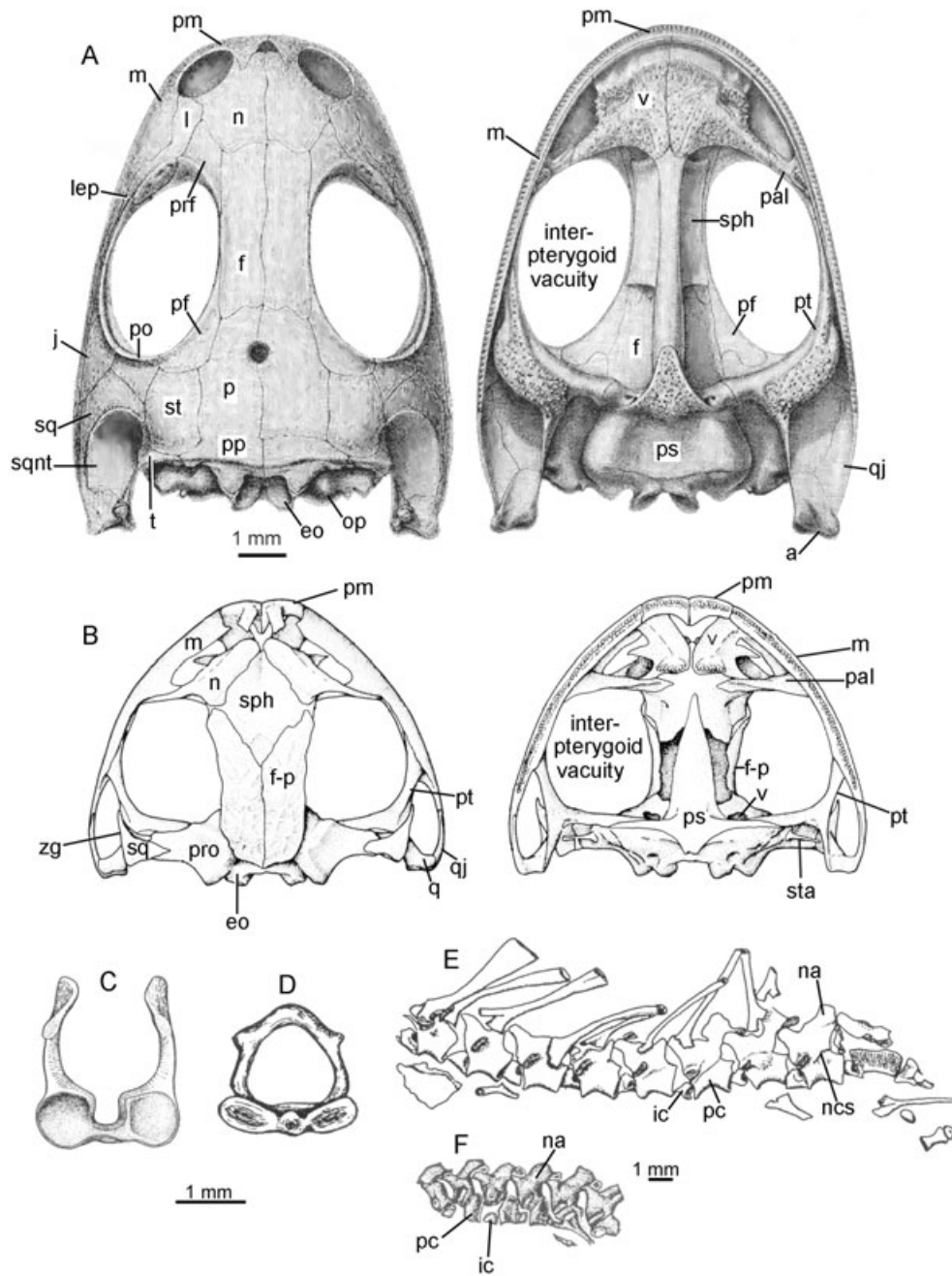
Figure 65. A, skull of the amphibamid *Doleserpeton* from the Lower Permian of Oklahoma in dorsal and palatal views. Reproduced from Bolt (1969). B, skull of the modern hylid frog, *Gastrotheca*, in dorsal and ventral views. Reproduced from Duellman & Trueb (1986). C, anterior view of atlas of *Doleserpeton*. D, anterior view of the atlas of the primitive anuran *Leiopelma hochstetteri*. Reproduced from Stephenson (1952). E, F, changes during development of the trunk vertebrae of *Doleserpeton*. E, close to maturity, when the centra and intercentra of the most anterior vertebrae are fused, without evidence of sutures, but the more posterior vertebrae still show evidence of their separation during earlier development. The intercentra are much smaller than the pleurocentra. F. Smaller individual in which the arches and centra are not suturally attached and the intercentra are nearly as long as the pleurocentra.

Doleserpeton differs from the close sister taxon of the amphibamids, the branchiosaurids, in the early ossification of the quadrate and the presence of a conspicuous dorsal process of that bone that Bolt & Lombard (1985) argue may be related to the elaboration of the tympanic annulus in modern anurans. Also shared by *Doleserpeton* and *Triadobatrachus* is the dorsomedial extension of the quadratojugal around the base of the dorsal process.

The presence of a double occipital condyle and a corresponding double cotyle on the atlas are comparable derived features of frogs, salamanders, and caecilians, and also occur in the lepospondyl orders Microsauria and Nectridea (Carroll *et al.*, 1998). A similar, but certainly convergent, structure is also characteristic of derived temnospondyls (the stereospondyls), known from the Late Permian into the Cretaceous (Warren, 2000). In all these groups, the configuration of this articulating surface constrains the movement of the cranium on the vertebral column to a dorsoventral arc in the sagittal plane. Although such a double condyle and cotyle is not reported in any other Permo-Carboniferous temnospondyls, it is clearly expressed in *Doleserpeton* (Fig. 65). A sequence of change with increasing size of the atlas of *Doleserpeton* shows that this element developed from distinct arch and central elements, as in other temnospondyls, into a uniquely shaped adult structure that shows no evidence of sutures (unpubl. data). This suggests that the anuran configuration of the atlas evolved among amphibamids, and that this compound structure is not strictly homologous with that in salamanders and caecilians.

No fully articulated skeletons of *Doleserpeton* have yet been found, so it is impossible to establish the specific number of trunk vertebrae, but the numbers found for other members of the Amphibamidae range from 18 in the Westphalian D species *Amphibamus grandiceps* (Fig. 1) (only four more than in *Triadobatrachus*) to 25 in *Amphibamus* (*Platyrhinops*) *lyelli* (Carroll, 1964). These numbers are far lower than the 69 reported in the shortest of lysorophians, the group that Laurin & Reisz (1997) identified as the sister taxon of lissamphibians.

As adults, frogs show no neurocentral sutures between the neural arches and centra, as is also the case with salamanders and caecilians. On the other hand, these structures show different patterns or sequences of development in each of the three groups. Developmental series of *Doleserpeton* trunk vertebrae (Fig. 65E,F) begin with separate intercentra, pleurocentra, and neural arches, in common with other Palaeozoic temnospondyls. However, in contrast to the situation in nearly all other genera, the pleurocentra are fused at the ventral midline, rather than remaining paired, and become fused with the neural arches during maturation. During development, the pleurocentra also increase in size relative to the intercentra. A similar pattern of vertebral development is also seen in *Leiopelma* (pers. observ.), in which the arches and pleurocentra form from separate cartilaginous elements. Initially, there is a wide gap between the pleurocentra in the position occupied by the intercentra in *Doleserpeton*, but this is subsequently filled by chondrification and ossification of the articulating surfaces of the centra.

As in the most primitive salamanders, the neural arches in anurans chondrify and ossify long before the centra. In contrast, the centra ossify extremely early in development in the juveniles of all lepospondyl groups and in the few caecilians that have been studied.

In contrast to salamanders and caecilians, anurans retain two of the dermal elements common to Paleozoic tetrapods, the clavicle and cleithrum. Frogs have lost the dermal interclavicle, but have replaced it with a complex of cartilaginous elements that help to constrain the lateral elements of the girdle during landing. As in branchiosaurs, the dermal elements of the shoulder girdle in amphibamids are slow to ossify, but retain a generally primitive position and configuration.

The endochondral shoulder girdle in *Doleserpeton* resembles that of most Palaeozoic amphibians in being co-ossified in the adult. In contrast, the scapula and coracoid are clearly separated by cartilage in the area of the glenoid in anurans. Anurans are also distinguished by a dorsoventrally elongate supraglenoid foramen. This opening is also elongated in *Triadobatrachus*, but the scapulocoracoid ossifies as a single element, as in temnospondyls.

The humerus of *Doleserpeton*, as in other small Palaeozoic tetrapods, has an elongate shaft between expanded articulating surfaces. There is no supinator process such as distinguishes larger labyrinthodonts and early amniotes, and nor is there an entepicondylar foramen. The ulna and radius are slender, and about half the length of the humerus. Strikingly, the carpus of *Doleserpeton* is fully ossified, even in animals only a few centimetres in snout–vent length. In the ankle, the tibiale and fibulare are approximately twice as long as wide, and ossified at small body size.

Neither the manus nor the pes are known in *Triadobatrachus* or *Doleserpeton*, but the number of phalanges is nearly identical across a wide range of dissorophoids and other small temnospondyls and in anurans in general. The counts for the manus and pes of 2,2,3,3 and 2,2,3,4,3 remain constant from *Amphibamus grandiceps* in the Upper Carboniferous to *Micropholis* in the Upper Permian. Such a consistent phalangeal count is not found in any other groups of Palaeozoic tetrapods (Table 2). This phalangeal formula is also similar to that of salamanders in which the limbs are not reduced.

Amphibamus grandiceps has ventral gastralia, but they were lost in later amphibamids and anurans. Small, incompletely ossified bones were found with the material of adult *Doleserpeton*, but none that could be considered as belonging to larvae.

LARVAE AND DEVELOPMENT

The similarity of the larvae between primitive extant salamanders and those of branchiosaurids provides the strongest evidence for a sister-group relationship between those taxa. Larvae are also known for early amphibamids. These, however, are very different from anuran tadpoles. The larvae of *Amphibamus grandiceps* (Fig. 66) are basically similar to those of

Figure 66. A, skull of the amphibamid *Amphibamus grandiceps* (Field Museum of Natural History PR664) from the Westphalian D of Mazon Creek, Illinois, showing the early ossification of most of the circumorbital bones, in contrast to (B), the comparably sized branchiosaurid, *Apateon* (see Fig. 54C₁), in which these bones are slower to ossify. C, skeleton of *Amphibamus grandiceps*, showing the long, salamander-like tail. Reproduced from Milner (1982).

Branchiosaurus cf. *salamandroides*, found in the same locality of Mazon Creek, from the Westphalian D (Milner, 1982). Most notably, they have an overall body shape comparable that of to the larvae of primitive living salamanders, including a long tail with a caudal fin, and roughly similar forelimbs and hindlimbs. The neural arches are ossified prior to the appearance of the centra, and the clavicles and interclavicles remain very small. However, they differ from later branchiosaurids in several important features. Most significantly, the dermal bones of the skull ossify nearly simultaneously at small body size, at a stage when the endolymphatic capsules still hold a large calcium reserve (Fig. 67). At the same absolute size, *Apateon* is still at a very early stage in the ossification of the circumorbital bones. The ventral margin of the otic notch (which presumably supported a tympanum) is elongated posteriorly during development in *Amphibamus grandiceps*, but not yet in *Branchiosaurus*.

Amphibamids differ in having only four rows of pharyngeal denticles, suggesting that they do not have an effective means of sealing the gill slits. The Mazon Creek specimens also lack any ossification of the hyoid apparatus, although it is preserved in similar-sized larvae of *Branchiosaurus* (Fig. 60). This suggests significant differences in the mode of feeding in the larvae of the oldest known species associated with the anuran and urodele clades. On the other hand, a specimen of *Amphibamus grandiceps* in which the alimentary canal is preserved as an infilling (Fig. 67) shows a robust stomach and an intestinal region similar to that of a predator, in strong contrast to that of anuran tadpoles, which lack a stomach and have a very long intestine, coiled in a tight spiral. Larval amphibamids show no hint of the origin of the anuran digestive system. They also retain external gills past the stage of development at which they are closed over by the operculum in anuran tadpoles.

In contrast, the high degree of ossification of the skeleton that is achieved at small body size in *Amphibamus grandiceps* and *Doleserpeton*, relative to *Apateon*, suggests a different life history from that of branchiosaurids. An overall similarity between *Doleserpeton* and most anurans is the achievement of an adult level of ossification of the endochondral bones of the skull, carpals, and tarsals at small body size. This implies early metamorphosis. According to Milner (1982), this occurs rapidly between a skull length of 7 and 14 mm. Like most modern anurans, these early genera appear to have passed rapidly from larvae to small, but highly ossified, adults. One may assume a rapid metamorphosis, although not as dramatic as that in anurans, for there would not have been significant changes in either the appendicular skeleton or in the mode of digestion.
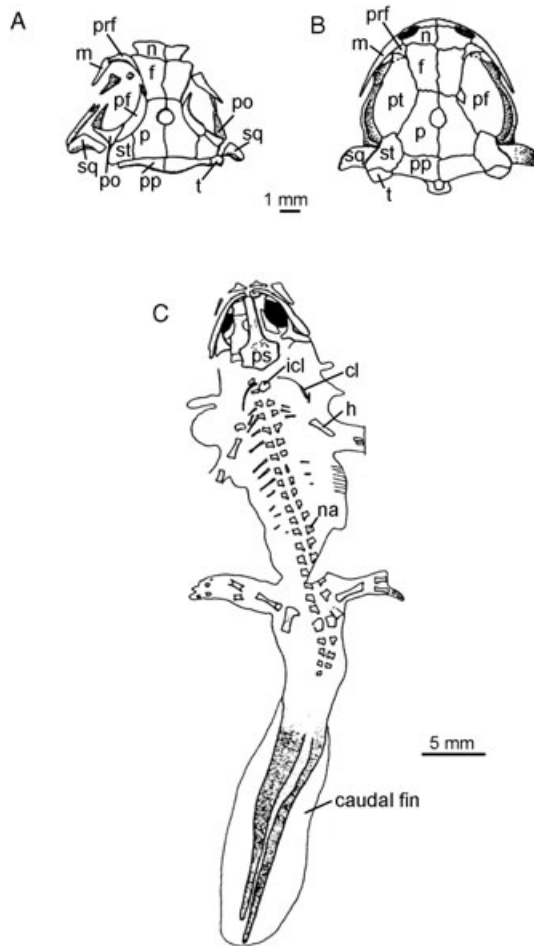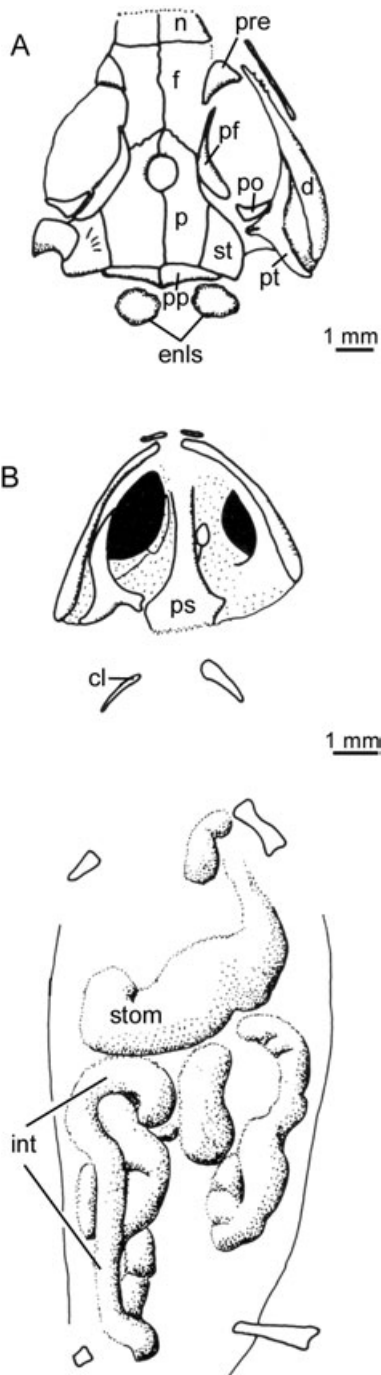
Figure 67. *Amphibamus grandiceps* (United States National Museum 4400). A, dorsal view of skull, showing ossification of the circumorbital bones prior to the breakdown of the calcium carbonate in the endolymphatic ducts. B, ventral view of skeleton, showing infillings of the stomach and intestine. Reproduced from Milner (1982).

SYNAPOMORPHIES OF BASAL SALIENTIANS AND THE AMPHIBAMIDAE

The following list outlines the synapomorphies between *Triadobatrachus* and amphibamids, as represented by *Amphibamus grandiceps* and/or *Doleserpeton annectens*.

1. large orbital opening bordered dorsally by the frontal or frontoparietal, and ventrally by the maxilla
2. deep squamosal embayment above the quadrate
3. stapes with slender columella
4. footplate articulating with the ventral rim of the foramen ovale
5. articulation between skull and the first cervical vertebra via a bicondylar occipital condyle
6. extremely large interpterygoid vacuities
7. loss of ectopterygoid
8. absence of fangs on vomers and palatine
9. atlas has a single ossification in the adult
10. pleurocentra cylindrical in the adult
11. short ribs
12. phalangeal formula of manus 2,2,3,3
13. tibiale and fibulare elongate
14. phalangeal formula of pes 2,2,3,4,3

Primitive similarities include the ossification of the neural arches prior to the centra and the retention of a distinct larval stage.

PEDICELLATE TEETH

Pedicellate marginal teeth are not recognized in Carboniferous amphibamids, but the nature of their palatal dentition may provide evidence of how pedicelly evolved. As a graduate student, I examined the palate of *Amphibamus* (*Platyrhinops?*) *lyelli* (Carroll, 1964). In American Museum of Natural History 6841, one can see a thick layer of denticulate tissue covering much of the palate. It does not conform exactly with the underlying bones, however, but has slipped out of plate to cover the internal nares. Such slippage indicates that the crowns of the denticles were not firmly attached to the bases, a pattern very clearly evident in the parasphenoid denticles of *Eocaecilia* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007). Such capacity for detachment might have resulted from nothing more than a delay in the integration of the portions of the tooth that had developed from the two embryonic primordia – the crown from an infolding of the ectoderm, and the base from the supporting bone. Although it remains difficult to hypothesize a functional advantage for pedicelly of either the palatal or marginal dentition, its evolution may have been initiated early in the batrachian stem, but only much later among caecilians.

Table 3. Differences between basal amphibamids and branchiosaurids

Amphibamidae	Branchiosauridae
1. Four rows of gill rakers	Six rows of gill rakers
2. Early larvae lack ossified hyoid elements	Hyoid elements ossified in early larvae
3. Metamorphosis at small body size, rapid achievement of terrestriality	Prolonged larval stage, facultative or obligatory neoteny
4. Rapid ossification of quadrate	Slow ossification of quadrate

THE DIVERGENCE OF SISTER TAXA

On the one hand, branchiosaurids and amphibamids from the Westphalian D show divergence in several anatomical features and in their probable life-history patterns. Of particular importance, amphibamids metamorphosed to fully terrestrial adults at relatively small body size, whereas branchiosaurids had a protracted period of larval growth and may have been either facultatively or obligatorily neotenic.

Differences between basal amphibamids and branchiosaurids are shown in Table 3.

On the other hand, these families share a number of synapomorphies that suggest a relatively close sister group relationship. Branchiosaurids and amphibamids have long been included, along with dissorophids, micromelerpetontids, and trematopsids, in the superfamily Dissorophoidea. However, as only the former two families show close affinities with salamanders and frogs, the latter three will be omitted from this comparison.

SYNAPOMORPHIES OF BASAL AMPHIBAMIDS AND BRANCHIOSAURIDS

1. Small body size as adults
2. Large orbits and interpterygoid vacuities
3. Absence of intertemporal
4. Conspicuous squamosal notch
5. Short skull table
6. Late larvae and adults lack lateral-line canal grooves on the skull
7. Loss of bony plates supporting pharyngeal denticles
8. Length of ribs reduced
9. Slow development of dermal elements of the shoulder girdle
10. Long, slender humerus without supinator process or entepicondylar foramen

Although the Late Carboniferous history of branchiosaurids and amphibamids shows the initiation of character states and ways of life that distinguish frogs and salamanders, the large number of derived characters that they share strongly supports a close common ancestry.

COMMON ANCESTRY OF ANURANS AND URODELES

Neither amphibamids nor branchiosaurids are known prior to the Westphalian D of Mazon Creek, Illinois, ~ 309 million years ago. Nor are any other amphibians known from earlier deposits that can be associated specifically with the ancestry of either of these families. However, two rich fossil horizons from earlier in the Carboniferous – Joggins, Nova Scotia, Canada, approximately 315 million years of age, and East Kirkton, West Lothian, Scotland, 328 million years of age – have yielded highly informative specimens of earlier temnospondyls.

From Joggins, Nova Scotia have come numerous well-preserved remains of *Dendrerpeton acadianum*. This is a moderate-sized temnospondyl, with the most complete skeleton having a snout–vent length of approximately 30 cm (Holmes, Carroll & Reisz, 1998) (Fig. 68). The largest skulls are at least ten times the length of those of *Doleserpeton*. Not surprisingly, the orbits and interpterygoid vacuities are relatively much smaller than those of *Doleserpeton*, but the otic notches are of comparable size. Recent studies by Robinson (2005), with the help of computed tomography scans, provide suburb illustrations of the braincase and stapes (Fig. 69). The stapes shares many features in common with that of *Doleserpeton*, including the retention of a stapedial canal, and a bipartite footplate. There is also a roughened area at the back of the stem that has been interpreted as the area of attachment of the columellaris muscle. Although more robust than the stapes of modern anurans, that of these Paleozoic temnospondyls has many of the functional features expected of an ancestral condition. *Dendrerpeton* and anurans have a near-identical configuration of the footplate of the stapes that involves a hinge-like articulation with the lateral flange of the parasphenoid in *Dendrerpeton* but with the base of the fenestra ovalis in anurans. This configuration suggests that pressure on the fluid of the inner ear is produced by a rocking movement of the distal end of the stapes, rather than a plunger-like movement of the base of the stapes as in amniotes (Lombard & Bolt, 1988). The otic notch of *Dendrerpeton* occupies nearly the entire height of the cheek.
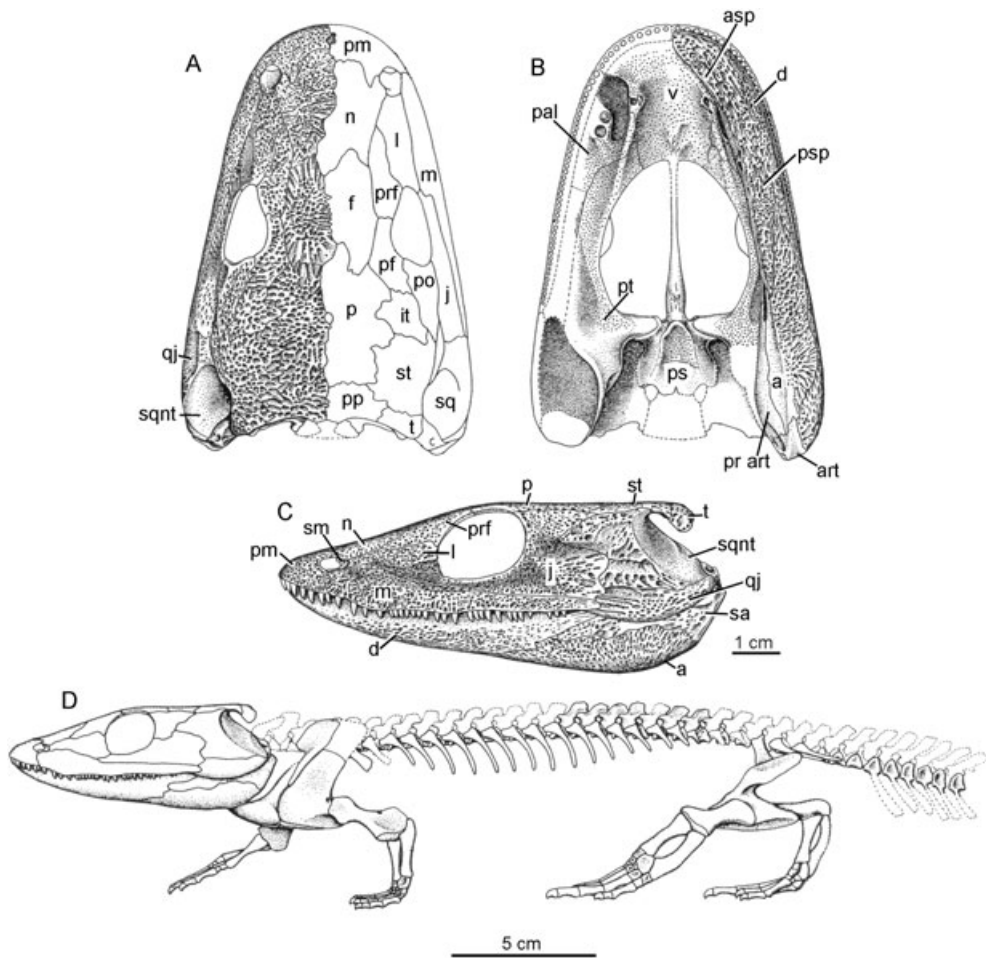
Figure 68. Skull and skeleton of *Dendrerpeton*, an early temnospondyl amphibian from the Westphalian A of Joggins, Nova Scotia. Reproduced from Holmes *et al*. (1998).

There is, however, no evidence for the presence of an operculum.

Balanerpeton woodi (Fig. 70), from the Viséan of Scotland, is not as well known as *Dendrerpeton*, but its small size (snout–vent length approximately 16 cm) gives it an appearance even closer to that of amphibamids, especially in the large size of the orbits and the relatively short snout. A high degree of terrestriality is indicated by the absence of lateral-line canals, and the high degree of ossification of the extremities of the limb bones, carpals, and tarsals. It too has a deep otic notch, and a relatively light stapes with a narrow stem and expanded footplate, strongly suggestive of an impedance-matching middle ear (Milner & Sequeira, 1994: fig. 6). This genus provides the earliest evidence for the evolution of a middle ear structure capable of responding to high-frequency airborne sound among vertebrates. *Balanerpeton* is not only a plausible plesiomorphic sister taxon of branchiosaurids and amphibamids, but also the oldest known temnospondyl.

In addition to these synapmorphies with later temnospondyls, *Balanerpeton* shows primitive character states, including the ossification of the arches prior to the centra, and the retention of an intertemporal bone (also seen in *Dendrerpeton*), that demonstrate sister-group relationships with other early labyrinthodonts, to the exclusion of lepospondyls. Although no gilled larvae of *Balanerpeton* have yet been discovered, a juvenile specimen (Milner & Sequeira, 1994: fig. 17) shows the early appearance of neural arches, the complete ossification of the dermal skull at a comparatively small size (skull length about 2.5 cm), a relatively large size of the dermal shoulder girdles, the retention of an entepicondylar foramen, and phalangeal formulae of 2,2,3,3 and 2,2,3,4,3.

Knowledge of *Balanerpeton*, *Dendrerpeton*, amphibamids, and branchiosaurids makes it possible to construct a nested sequence of synapomorphies that extends from the earliest recognizable temnospondyls, through the divergence of amphibamids and branchiosaurids, to the base of the crown groups Urodela and
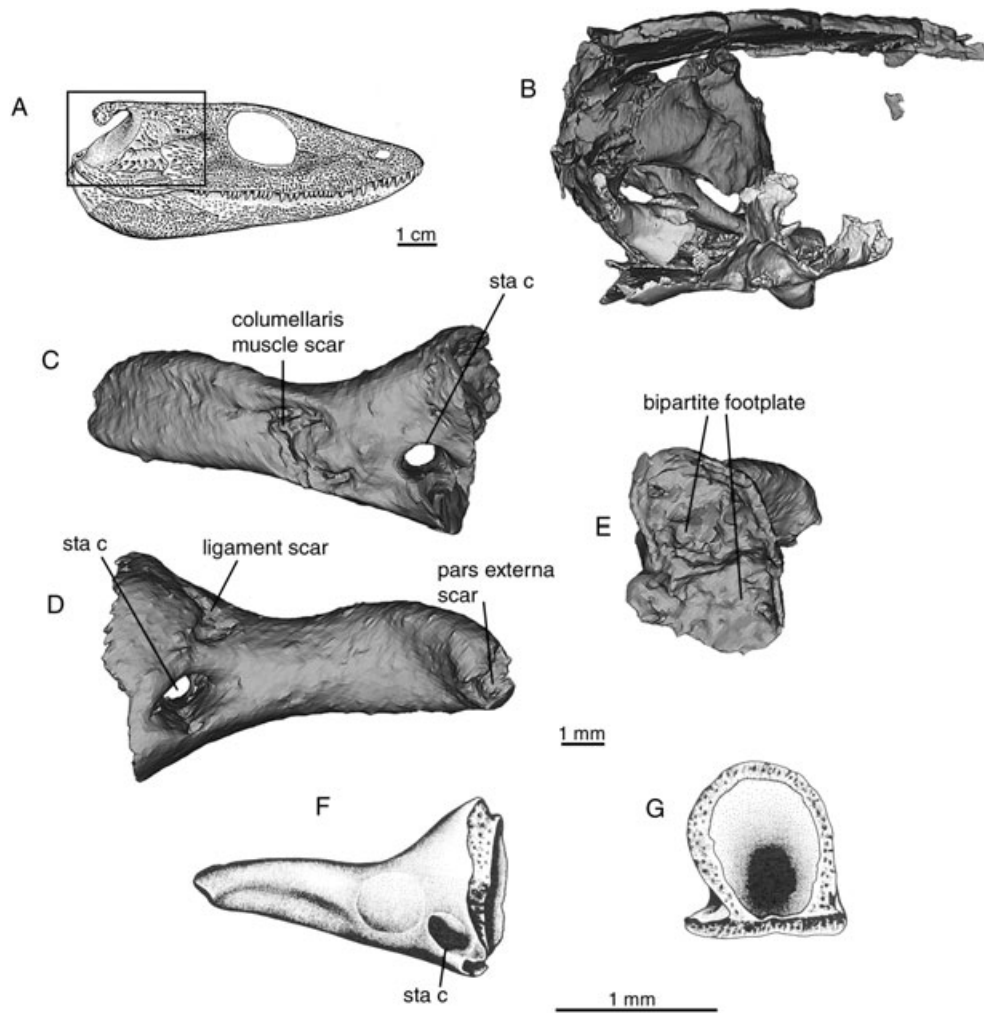
Figure 69. Middle ear of temnospondyls. A, lateral view of the skull of the Westphalian A *Dendrerpeton*, showing the area scanned to produce images B–E (unpublished images based on data from Robinson, 2005). B, lateral view of the braincase and right stapes, shown as if the right cheek were removed. C–E, left stapes in posterior, anterior, and medial views. F, G, posterior and medial views of the left stapes of the Lower Permian *Doleserpeton*. Reproduced from Lombard & Bolt (1988).

Anura (Fig. 71). Both derived and primitive features shared by the oldest known temnospondyls and primitive salientians and caudates can potentially be used as a basis for establishing the ultimate affiliations between the ancestors of frogs and salamanders and other early Palaeozoic tetrapod clades.

PUTATIVE ANCESTRY OF CAECILIANS

Apart from the occurrence of pedicellate teeth, and the presence of mentomeckelian bones during early development, there are few derived skeletal features that extant caecilians share with living frogs or salamanders, or their antecedents from the Lower and Middle Jurassic. Even the oldest members of the salamandramorph and anuromorph clades from the Car-

boniferous fail to reveal any obvious osteological synapomorphies with caecilians that would indicate a close sister-group relationship. On the other hand, the fossil record of caecilians does provide numerous characters that may be used to hypothesize affinities among a broader range of Palaeozoic tetrapods.

FOSSIL RECORD

The fossil record of caecilians is far less complete than that of urodeles or anurans, but it allows their history to be traced for approximately 185 million years, back to the Lower Jurassic. The first caecilian fossil to be recognized was a single posterior trunk vertebra from the Late Palaeocene of Brazil (Estes & Wake, 1972). It was named *Apodops pricei*, and was suggested to be
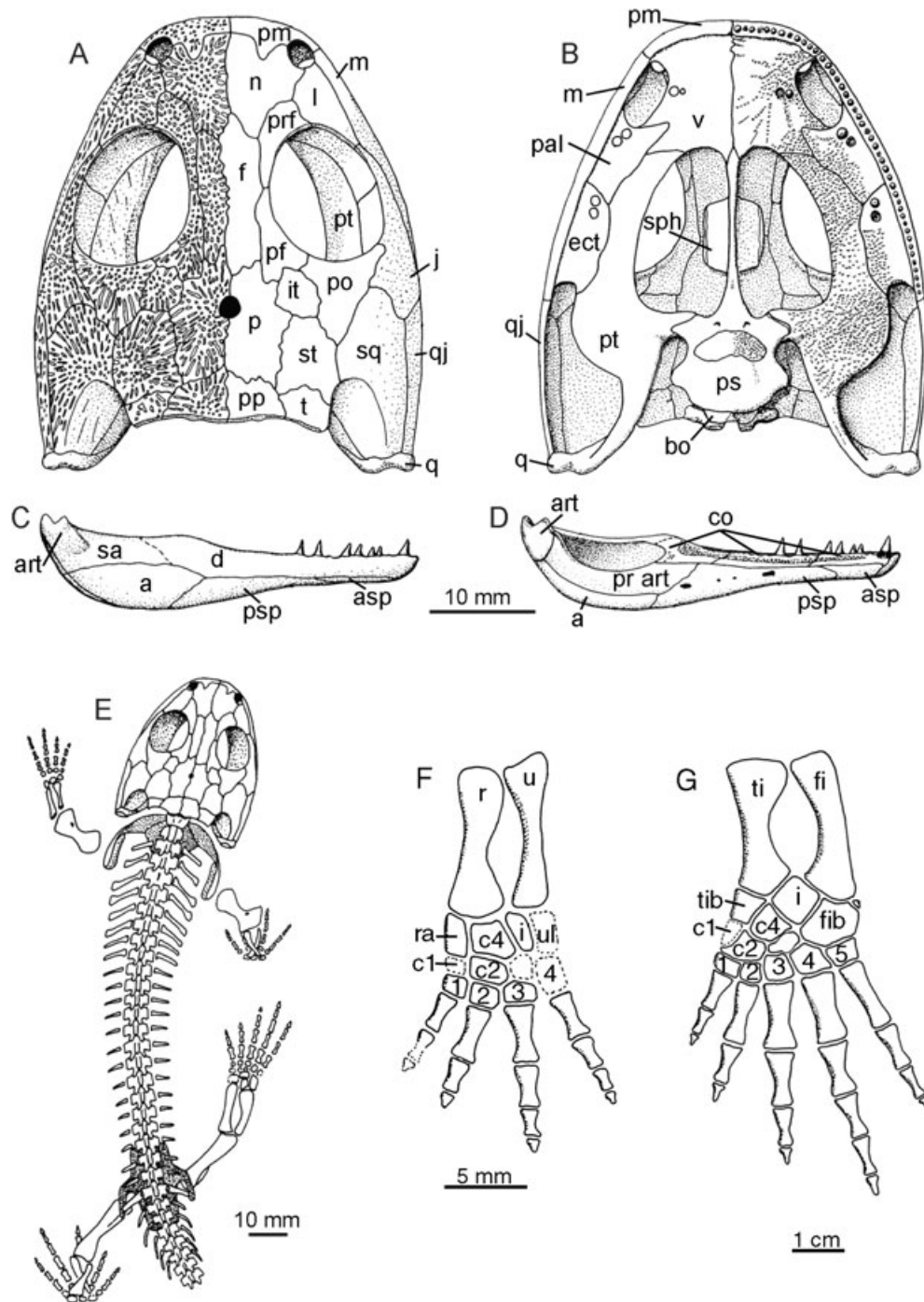
Figure 70. The Lower Carboniferous temnospondyl *Balanerpeton*. A, B, skull in dorsal and palatal views. C, D, lower jaw in lateral and medial views. E, reconstruction of skeleton. F, G, lower forelimbs and hindlimbs. Reproduced from Milner & Sequeira (1994).

most similar to those of the West Africa caeciliid *Geotrypetes*, although similarities with the Central American *Dermophis* were also cited. The general proportions are those of heavy-bodied terrestrial viviparous species. It differs little from the basic pat-tern of the trunk vertebrae of all extant caecilians, with an elongate, amphicoelous centrum, prominent anteriorly directed parapophyses, and low, posteriorly restricted neural spines. The centrum is markedly constricted medially, and bears a deep ventral ridge
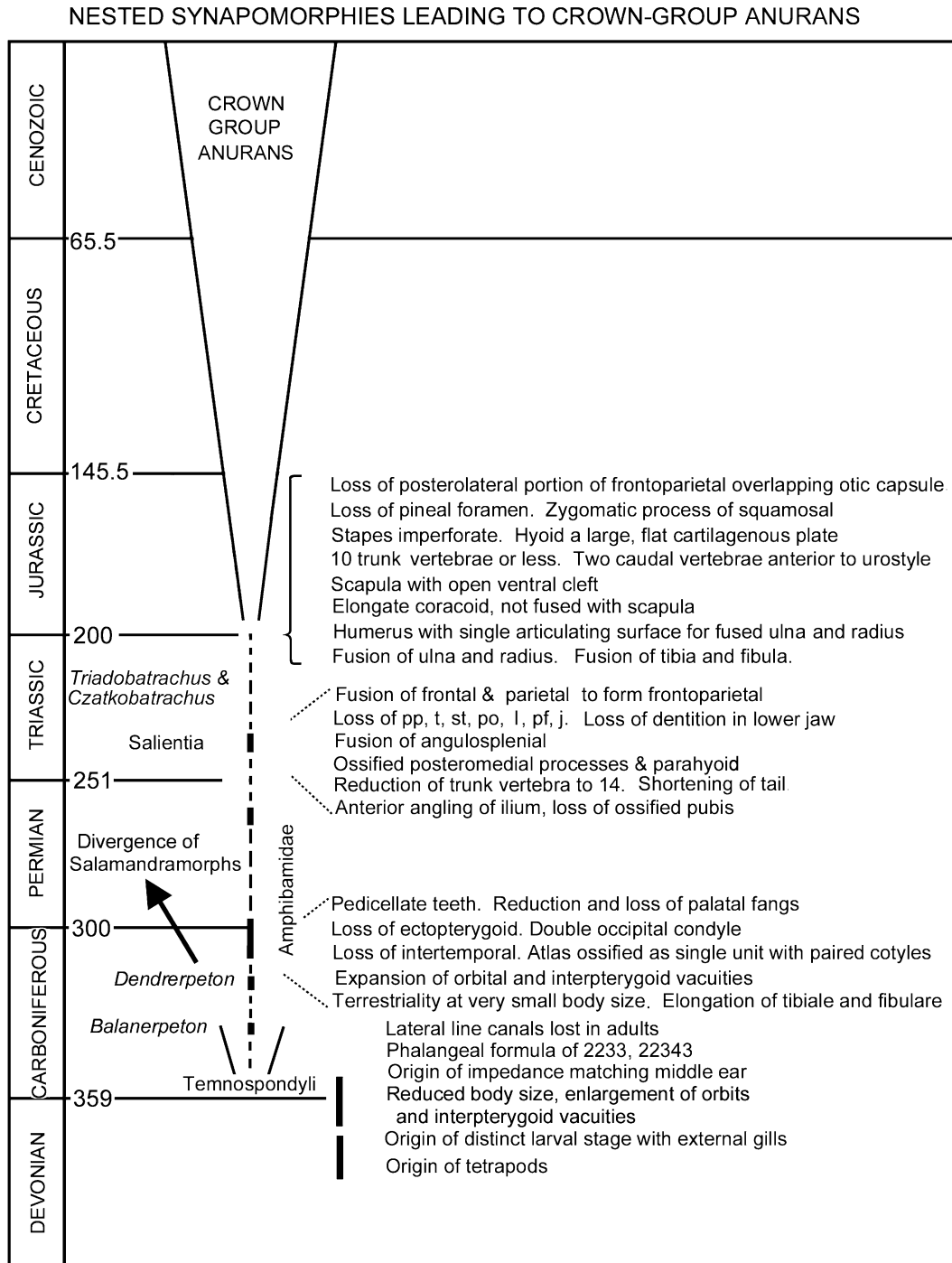
NESTED SYNAPOMORPHIES LEADING TO CROWN-GROUP ANURANS

Figure 71. Nested synapomorphies leading from primitive temnospondyls to crown-group anurans.

throughout its length. This individual bone indicates the achievement of a fully modern configuration by the late Palaeocene.

Another isolated vertebra was described by Rage (1986) from the Lower Palaeocene of Bolivia. It is much less well preserved that of *Apodops*, and, although clearly that of a caecilian, cannot be assigned

to any modern taxon, and nor are any features visible that contribute to our understanding of the earlier history of the group.

Four trunk vertebrae broadly resembling those of modern caecilians are known from the Cenomanian (base of the Upper Cretaceous) of Sudan (Evans *et al.*, 1996). These have not been named, and cannot

be confidently assigned to any extant family. Nevertheless, they bear all the distinctive caecilian features cited for *Apodops*. Notable is the clear expression of the areas of articulation for the widely divergent rib heads. The articulating facet for the ventral rib head resembles that of members of the Dermophinae.

Much more informative caecilian fossils have been described from the base of the Cretaceous (Berriasian) of Morocco (Evans & Sigogneau-Russell, 2001). They consist of lower jaw bones, numerous vertebrae, and a possibly associated femur. These remains contrast with the previously mentioned fossils in exhibiting several plesiomorphic character states that illustrate a more primitive stage in their evolutionary history. The caecilian nature of these specimens is clearly demonstrated by the presence of pseudodentary and pseudoangular bones with most of the features of extant taxa. In comparison to modern caecilia, they are distinctive in the nearly horizontal orientation of the retroarticular process, the apparently small internal processes, and the presence of only two teeth in the medial tooth row. *Typhlonectes natans* has three teeth in this position. The palatine appears not to have been fused to the maxilla, as it is in the adults of all extant caecilians.

The vertebrae are recognizable as belonging to caecilians in having a poorly defined neural spine and a low ventral ridge on the centrum, but are clearly distinct in other respects. The atlas has a conspicuous interglenoid tubercule (tuberculum glenoideum) not present in modern caecilians, and the trunk vertebrae lack the long, anteriorly directed parapophyseal processes that characterize all living species. The proximal end of a femur that broadly resembles that of the modern salamanders was found in association with the caecilian bones.

The oldest known, but by far the most informative, fossil caecilian is *Eocaecilia* from the Lower Jurassic (Pleisbachian) of Arizona. It was described in a preliminary manner by Jenkins & Walsh (1993), and a reconstruction of the skull was published by Carroll (2000b). A description of the entire skeleton will be published shortly (F. A. Jenkins *et al.*, 2007). The general anatomy of the skull and lower jaw demonstrates unequivocally its affinities with extant caecilians, although several skull bones, lost in modern caecilians, have been retained, including the postparietal, jugal, and quadratojugal, and a bone in the temporal region that might represent either a tabular or (less likely) supratemporal. One may note that the combined length of the postparietal and parietal in *Eocaecilia* is approximately as long, relative to the frontal, as the length of the parietal alone of later caecilians. This suggests that the postparietals have been incorporated into the parietals in the ancestry of modern caecilians.

The bony elements of the feeding apparatus suggest the same general function as that in living species. The palatine and maxilla are not fused with one another, as they are in all modern genera. A groove in the maxilla at the margin of the orbit indicates the passage for a tentacle in the position seen in the living genus *Epicrionops*. The teeth are clearly pedicellate and bicuspate. The braincase has already become consolidated into two units, the posterior os basale, including the parasphenoid and the pleurosphenoid, and the anterior sphenethmoid (Fig. 38).

The atlas has two large cotyles for articulation with the occipital condyles. Between the cotyles is a well-developed interglenoid tubercle, which occurs in microsaurs and salamanders, but is not present in living caecilians. The trunk vertebrae are primitive in the retention of intercentra, in contrast to any living amphibians. The centra lack the parapophyses of modern caecilians; their role in supporting the capitulum of the ribs was taken by the intercentra. Although no fully articulated specimens are known, reconstructions based on several overlapping segments of the column indicate the presence of approximately 49 presacral vertebrae.

The shoulder girdle retains the scapulocoracoid, but no dermal elements are known. Remains of the forelimb include a small but well-developed humerus, ulna, and radius, and remnants of digits. The pelvic girdle is not known, but the femur (broadly resembling that of salamanders), tibia, and fibula are well formed, but tiny. There may have been as many as three digits. Despite the early occurrence of *Eocaecilia*, it shows no significant features that support close affinities with frogs or salamanders, or their putative Palaeozoic antecedents.

SYNAPOMOPHIES OF BASAL CAECILIANS

Using *Eocaecilia* as a model for the most primitive caecilians, the following characters distinguish basal members of this order from frogs, salamanders, and/or most Palaeozoic taxa.

Skull
  1. skull solidly roofed, except for small openings for the eyes and nares
  2. line of loose attachment between the squamosal and the parietal
  3. groove to accommodate tentacle
  4. jaw articulation well anterior to occipital condyle
  5. internal naris not bordered by premaxilla
  6. pedicellate teeth
  7. absence of fangs on palatal bones

8. row of teeth on vomer and palatine parallel to those of premaxilla and maxilla
9. loss of some bones common to primitive Palaeozoic tetrapods (two of the original three bones in the skull table – intertemporal and either tabular or supratemporal), and reduction or loss of lacrimal
10. fusion of all bones of the braincase into two large areas of ossification, an os basale posteriorly, and sphenethmoid anteriorly
11. double occipital condyles

Lower jaw
12. Adults express only two elements, the pseudodentary, bearing the dentitions, and the pseudoangular, bearing the jaw articulation, a large internal process, and a long retroarticular process. Most of the bones common to the jaws of Palaeozoic amphibians co-ossified during development, and a very long overlapping joint formed between the resulting units
13. row of nonlabyrinthodont teeth medial and parallel to the marginal dentition borne by the pseudodentary
14. very narrow mandibular foramen

Vertebrae and ribs
15. atlas with double cotyles
16. cylindrical centra fused to arches
17. greatly elongate vertebral column; at least 49 presacral vertebrae

Appendicular skeleton
18. great reduction in size of girdles and limbs
19. reduction in digital count

On the other hand, *Eocaecilia* is clearly more primitive than crown-group caecilians in the following characters:

1. Retention of the following cranial bones common to Palaeozoic amphibians, but not extant genera: postparietal,?tabular, prefrontal, postorbital, jugal, quadratojugal
2. Lack of fusion in the adult of the maxilla and palatine
3. Presence of an interglenoid tubercle
4. Presence of intercentra throughout the trunk, and unfused haemal arches in the tail
5. Absence of elongate parapophyses
6. Slightly smaller number of trunk vertebrae, but more caudal vertebrae
7. Presence of two sacral vertebrae
8. Presence of pectoral and pelvic girdles
9. Retention of forelimbs and hindlimbs (although reduced)

How does this suite of characters compare with those of early Mesozoic or Palaeozoic tetrapods?

PLESIOMORPHIC SISTER TAXA OF CAECILIANS

In common with Jurassic urodeles and anurans, *Eocaecilia* had already attained many of the skeletal features of its living descendants. The elongation of its vertebral column and the high degree of similarity of the cranial anatomy indicate that adaptation to a burrowing way of life was already well established. Whereas basal frogs and salamanders resemble one another in having very open skulls, a relatively short vertebral column, and substantial limbs, basal caecilians were already highly divergent in these character complexes.

Although gaps of 150–180 million years separate stem-group anurans and urodeles from plausible Palaeozoic antecedents, Permo-Carboniferous amphibamids and branchiosaurids document the sequential origin of many of the key characteristics of the extant taxa. The degree of expression of these characters converges towards a similar morphology within the Westphalian, indicating an ultimate common ancestry of salamanders and frogs from among the oldest known temnospondyl labyrinthodonts. Among the early temnospondyls, *Balanerpeton* was already derived in its small body size as an adult, high degree of ossification, and loss of lateral-line canals on the skull, indicating a basically terrestrial way of life. Immature specimens of *Balanerpeton* suggest an aquatic larval stage, comparable to those of branchiosaurids and amphibamids, that probably had conspicuous external gills. In contrast, no early temnospondyl expresses any of the derived characters of caecilians. No temnospondyls, as that group is currently recognized (Carroll & Holmes, 2007), shows any tendency towards extensive elongation of the trunk or limb reduction, and all retain a conservative pattern of cranial elements, but have relatively large orbits and interpterygoid vacuities.

Double occipital condyles evolved separately among branchiosaurids and amphibamids, as did pedicellate teeth, in clades that otherwise show none of the unique derived characters of caecilians. Although extant caecilians have well-developed external gills in utero or within the egg, they are lost at the time of birth or hatching, and would probably not have been as capable of fossilization as are those of branchiosaurs. In contrast to salamandramorphs and anuromorphs, no larvae or juveniles are known from the Palaeozoic whose general appearance suggests them to be antecedents of caecilians.

The known Palaeozoic fossils provide no support for a sister-group relationship between caecilians and any temnospondyls. The other major group of Palaeozoic labyrinthodonts, the anthracosauroids (Smithson, 2000; Laurin, 2000), among which the discosauriscids (Špinar, 1952) also have gill-bearing larvae, also lack any obvious synapomorphies with caecilians.

This leaves the other major assemblage of Palaeozoic tetrapods, the lepospondyls, for consideration (Carroll et al., 1998). Lepospondyls share the following general similarities with caecilians. Even the smallest known specimens of the major orders show no evidence of external gills, but ossify cylindrical centra at a very early stage of development. No lepospondyl shows any evidence for the occurrence of an otic notch. Some members of all orders, except the Nectridea, evolved an elongate trunk region, and all show reduction or complete loss of limbs. All have cylindrical pleurocentra. Only microsaurs also have small crescentic intercentra. *Acherontiscus* is unique in having both intercentra and pleurocentra that are cylindrical (Carroll, 1969a).

Aïstopods and adelogyrinids had lost all trace of limbs by their first appearance in the fossil record in the Lower Carboniferous (Fig. 76), making them improbable sister taxa of a clade that still retained limbs in the Lower Jurassic. Lysorophids retain limbs of about the same proportions as those in *Eocaecilia*, but they had already attained 69 trunk vertebrae in the Upper Carboniferous and 97 by the Lower Permian, whereas *Eocaecilia* had only 49 in the Lower Jurassic. Lysorophids are otherwise highly improbable sister taxa of caecilians in light of their great reduction in the number of skull bones in all known genera (Fig. 1).

The only group of lepospondyls that includes genera that are sufficiently primitive to be plausible sister taxa of caecilians are the microsaurs (Carroll & Gaskill, 1978; Carroll et al., 1998). These are the most diverse assemblage of lepospondyls, with some 12 recognized families, 30 genera, and a fossil record extending from the upper part of the Lower Carboniferous (Lombard & Bolt, 1999) into the Lower Permian. Most early taxa had short vertebral columns, and fairly robust limbs, but more derived genera in the Lower Permian had more than 30 presacral vertebrae, and several lineages reduced their limbs. Tiny juveniles from the Upper Carboniferous are typical of lepospondyls in ossifying the vertebral centra as complete cylinders at a very early stage (Fig. 51).

Microsaurs have previously been suggested as possible antecedents of caecilians (Gregory et al., 1956) or salamanders (Carroll & Holmes, 1980), but the genus showing the most derived characters in common with caecilians is the Lower Permian genus *Rhynchonkos* (initially designated *Goniorhynchus*) (Carroll & Currie, 1975; Carroll, 2000b).

Rhynchonkos stovalli is known from numerous specimens from the Lower Permian of Oklahoma (Figs 72–74). None is fully articulated, but there are approximately 37 presacral vertebrae. The limbs are abbreviated to about the same extent as in *Eocaecilia*, but the girdles retain the typical elements of Palaeozoic tetra-pods. The ilium has a long, narrow dorsal process supported by two pairs of sacral ribs, as in *Eocaecilia*. Both carpals and tarsals are well ossified, and the rear limb appears to retain five digits, with the phalangeal count of the first three being 2,3,3.

The vertebrae resemble those of *Eocaecilia* in having cylindrical pleurocentra fused to the neural arch and crescentic intercentra. The atlas has a large odontoid (interglenoid tubercle) that articulated with the recessed basioccipital between double condyles.

The skull of *Rhynchonkos* broadly resembles that of *Eocaecilia* in its small size, relatively small orbits, and position of the jaw articulation well anterior to the occipital condyles. The palate and lower jaw both resemble those of caecilians in having medial rows of teeth on the vomer, palatine and ectopterygoid of the palate, and on the medial surface of the lower jaw. The dermal bones of the skull correspond almost exactly to those of *Eocaecilia*, except for the retention of a large lacrimal, and both a postorbital and a postfrontal behind the eye; only a single bone is retained in this position in the Jurassic genus. *Rhynchonkos* does differ in having small bony plates that presumably reinforced the eyelid.

Of particular importance is the high degree of ossification of the endochondral braincase (Fig. 38). In contrast to those of most other Palaeozoic amphibians, and certainly anuromorphs and salamandramorphs, it extends continuously from the occiput through the sphenethmoid. The Xth nerve is wholly incorporated into the exoccipital, perhaps as an early stage in the integration of all bones of the back of the braincase into a single os basale. Primitively, a separate supraoccipital is retained. The exoccipital, opisthotic, and prootic ossify separately, but the area surrounding the foramen for the Vth nerve is formed by an extensive pleurosphenoid that reaches anteriorly to link with the posterior margin of the sphenethmoid. Rather than passing between the pleurosphenoid and sphenethmoid as in *Eocaecilia* and extant caecilians, cranial nerve II apparently passed though a foramen near the posterior limit of the sphenethmoid. In contrast with modern caecilians, the parasphenoid is not fused with the other bones that make up the os basale; rather, as in *Eocaecilia*, it passes freely beneath the sphenethmoid. The footplate of the stapes of *Rhynchokos* is very large, but there is a clearly evident gap in ossification between the posteroventral margin of the footplate and the margin of the otic capsule in the position that is occupied by an operculum in frogs and salamanders. There is, however, no evidence of any ossification in this area. On the other hand, there is a small additional ossicle resting just above the stem of the stapes in this and several other microsaurs that has been called an accessory ear ossicle (Carroll &
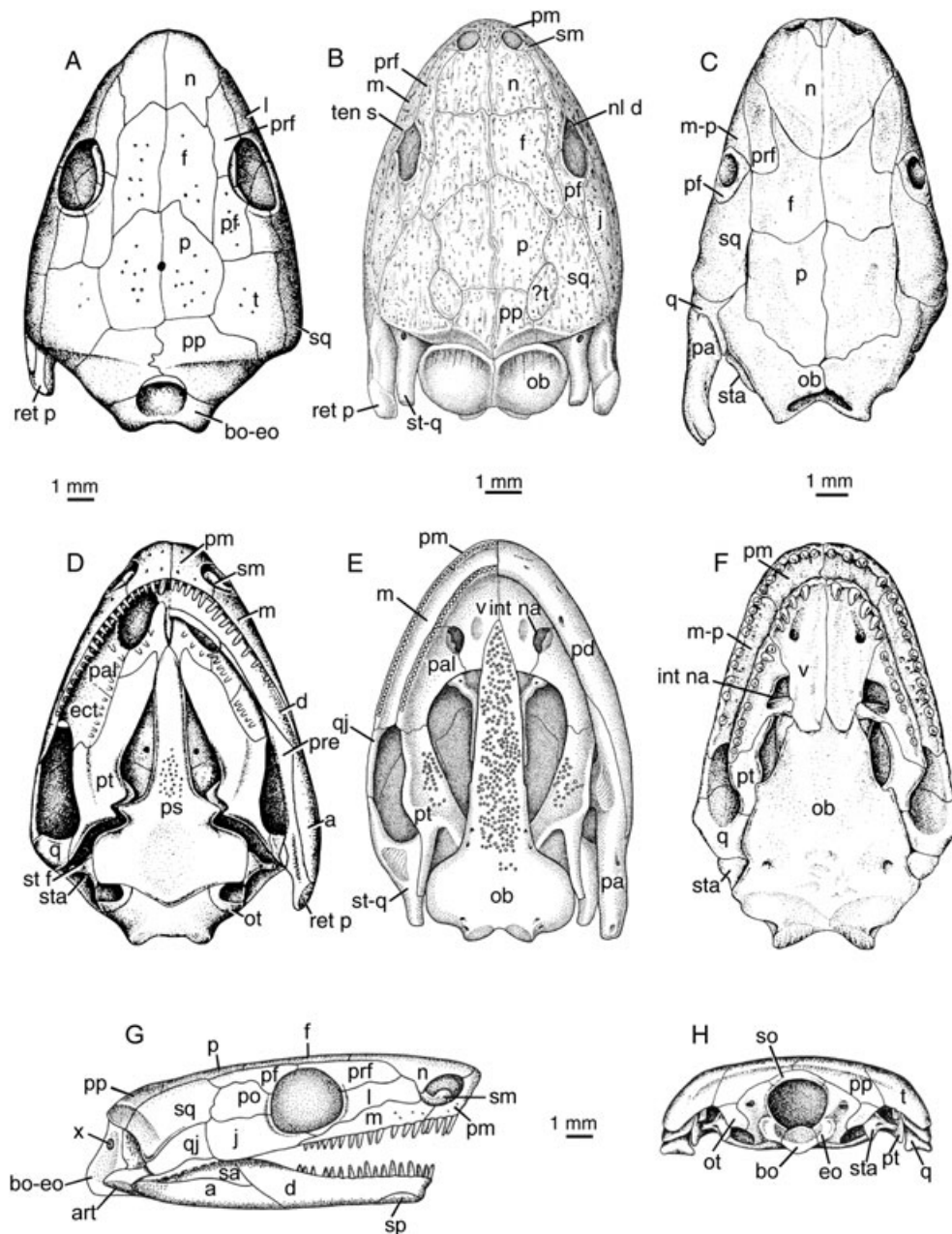
Figure 72. Comparative drawings of the Lower Permian microsaur *Rhynchonkos* (Carroll, 2000b), the Lower Jurassic caecilian *Eocaecilia*, and the primitive living caecilian *Ichthyophis* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007, in press). A, D, G, H, dorsal, palatal, lateral, and occipital views of *Rhynchonkos*. B, E, dorsal and palatal views of *Eocaecilia*. C, F, dorsal and lateral views of *Ichthyophis*.

Gaskill, 1978). An ear ossicle in the position of that of *Eocaecilia*, medial to the interior surface of the footplate of the stapes, has not been observed in *Rhynchonkos*.

The lower jaw of *Rhynchonkos* retains most of the elements common to primitive Palaeozoic tetrapods, except for the reduction in the number of coronoid bones from three to two. More importantly, it shows

the presence of a short, but clearly defined, retroarticular process.

In summary, the following characters, derived above the level of basal tetrapods, are expressed in both *Rhynchonkos* and primitive caecilians:

1. Orbital openings small relative to those of comparably sized early tetrapods
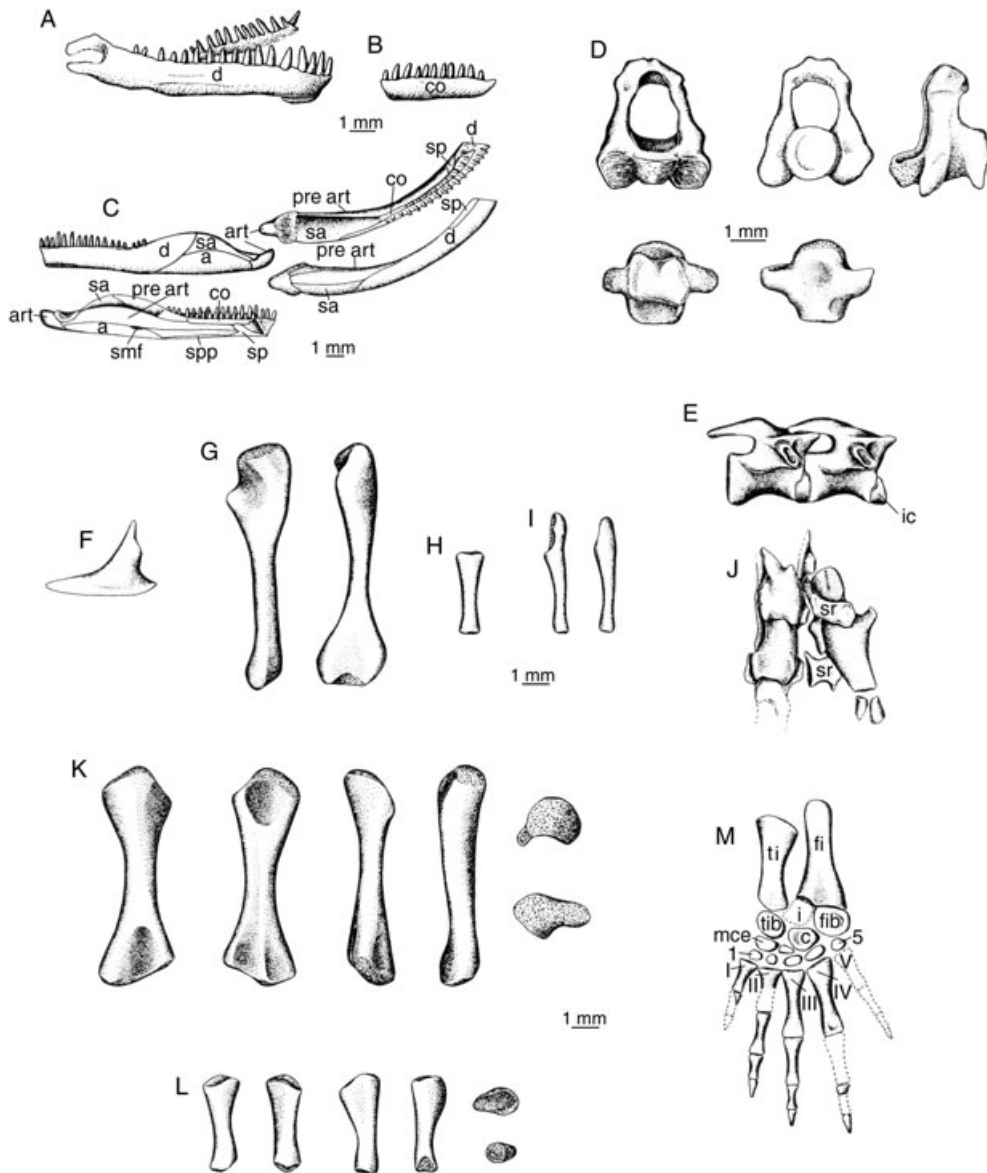
Figure 73. Jaw and postcranial elements of the Lower Permian microsaur *Rhynchonkos*. Reproduced from Carroll & Gaskill (1978). A, B, lateral and medial views of the lower jaw as preserved. C, lateral, medial, dorsal, and ventral views of the lower jaw as restored. D, anterior, posterior, lateral, dorsal, and ventral views of atlas. E, reconstruction of trunk vertebrae, showing crescentic intercentra. F, base of clavicle. G, humerus in anterior and ventral views. H, radius. I, left ulna in two views. J, sacral vertebrae, ribs, and head of right femur. K, right femur in dorsal, ventral, anterior, posterior, proximal, and distal views. L, tibia in six views. M, foot as restored.

2. Jaw articulation well anterior to occipital condyle
3. *Absence of fangs on palatal bones
4. Rows of teeth on vomer and palatine, parallel to those of premaxilla and maxilla
5. *Loss of intertemporal and supratemporal bones common to early temnospondyls
6. Ossification of pleurosphenoid
7. *Double occipital condyle, not present in Carboniferous temnospondyls or anthracosaurs

8. *Cylindrical centra fused to neural arch early in development, in contrast to labyrinthodonts
9. *Greater elongation of vertebral column than in any temnospondyls, anthracosauroids, nectrideans, or early amniotes

The characters indicated by an asterisk are common to lepospondyls, but not to temnospondyls or anthracosauroids.
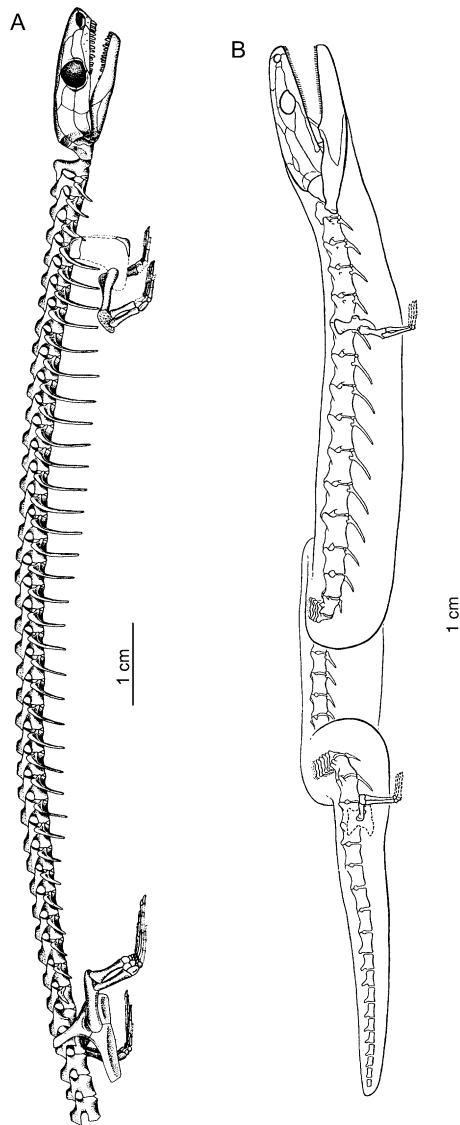
Figure 74. Comparative reconstructions of the skeletons of (A), the Lower Permian microsaur *Rhynchonkos* [reproduced from Carroll & Gaskill (1978)], and (B) the Lower Jurassic caecilian *Eocaecilia* [reproduced from F. A. Jenkins, D. Walsh & R. L. Carroll, 2007 (in press)].

No larval forms of any taxa have been found in the Texas–Oklahoma redbeds in which *Rhynkonkos* was discovered.

Rhynkonkos exhibits more derived characters in common with caecilians, especially *Eocaecilia*, than any other Palaeozoic genus that has been described. Most of the osteological differences recognized between these genera can be attributed to continuation of evolutionary trends that can be observed between more primitive microsaurs and *Rhynchonkos*, such as further elongation of the trunk, reduction of the limbs,

extension of the retroarticular process, and further consolidation of the braincase. Only the lower jaws have undergone a major reorganization.

Few, if any, skeletal changes would be considered reversals, and all may be attributed to continuing specialization for a burrowing way of life. There remains a long gap in time, and a substantial change in morphology, but *Rhynkonkos* provides the best known example of a Palaeozoic amphibian that could have been close to the ancestry of caecilians. However, it provides no support for close affinities with anurans or urodeles.

Rhynkonkos stovalli is the only species within the Goniorhynchidae. This family resembles the much more diverse and widespread Gymnarthridae, which extends from the Westphalian A of the Upper Carboniferous into the Lower Permian of North America and Europe. Among the Lower Permian gymnarthrids, *Cardiocephalus peabodyi* is known to have had 37 presacral vertebrae and two sacral vertebrae, exactly as in *Rhynkonkos stovalli*. However, a well-articulated specimen of another genus of the same family from the Upper Carboniferous of the Czech Republic, *Sparodus* (Carroll, 1988), has approximately 25, indicating the general time frame within which trunk elongation has occurred in a related clade of microsaurs (Carroll, 2000a).

An unnamed genus from the Namurian E2 (Serpukhovian) of Illinois demonstrates the earliest known occurrence of microsaurs (Lombard & Bolt, 1999). Although none of the eight intertwined specimens are fully exposed or articulated, a minimum of 34 presacral vertebrae is well established, as is the presence of strap-shaped intercentra, similar to those of both *Rhynchonkos* and *Eocaecilia*. In contrast to any other lepospondyl, this species retains paired proatlas elements and clearly defined areas for their articulation with the atlas arch, as in the primitive tetrapod *Acanthostega*, but in no other microsaur. The centrum of the atlas is expanded laterally to form a bicotylar articulation with the occipital condyles, as in all other microsaurs. Not all of the limb elements are preserved, but the humerus and femur are approximately the length of three trunk vertebrae, as is also the case for *Rhynchonkos*. The humerus, however, is more primitive in retaining the entepicondylar foramen, as in other primitive microsaurs. This is the earliest known species that expresses some derived traits uniquely shared with the oldest known caecilian, *Eocaecilia*. The nested sequence of synapomorphies leading towards caecilians is shown in Fig. 75.

The microsaur described by Lombard & Bolt (1999) is about 5 million years younger than the horizon from which *Balanerepton* has been described. Hence, the age of the earliest currently known species that show some derived characters in common with
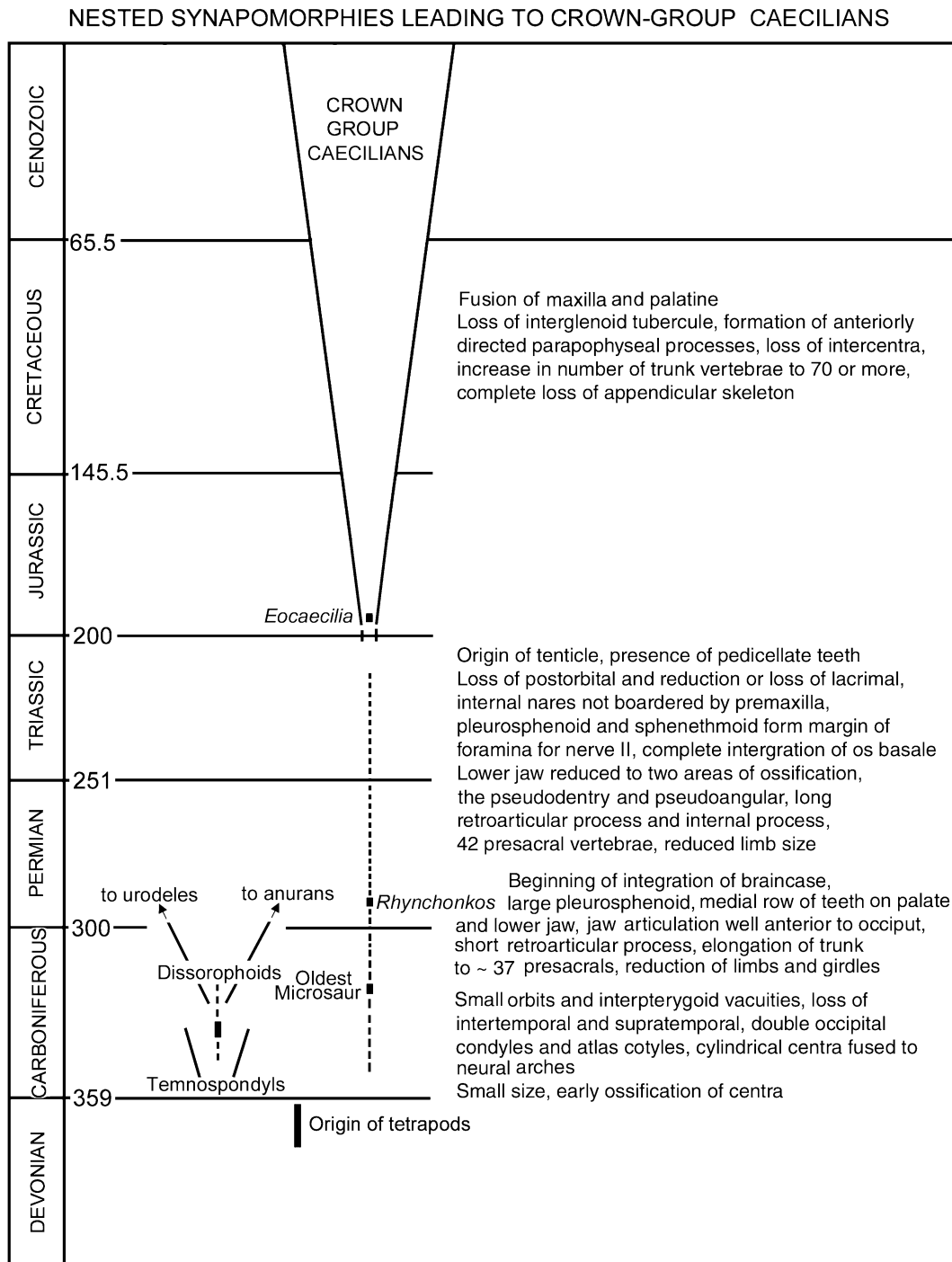
NESTED SYNAPOMORPHIES LEADING TO CROWN-GROUP CAECILIANS

Figure 75. Nested synapomorphies leading from the oldest known microsaur to crown-group caecilians.

caecilians is approximately as great as that of the temnospondyls that exhibit characters in common with frogs and salamanders. This implies that the time of initial divergence of the clades leading to batrachians and caecilians was within the first 30 million years of the Carboniferous. This brings us back to a time for which the fossil record is very poor, and provides little evidence for the interrelationships among any of the major tetrapod clades (Coates & Clack, 1995).

AMPHIBIAN RELATIONSHIPS

Although plausible antecedents of batrachians (frogs and salamanders) can be traced to the temnospondyls
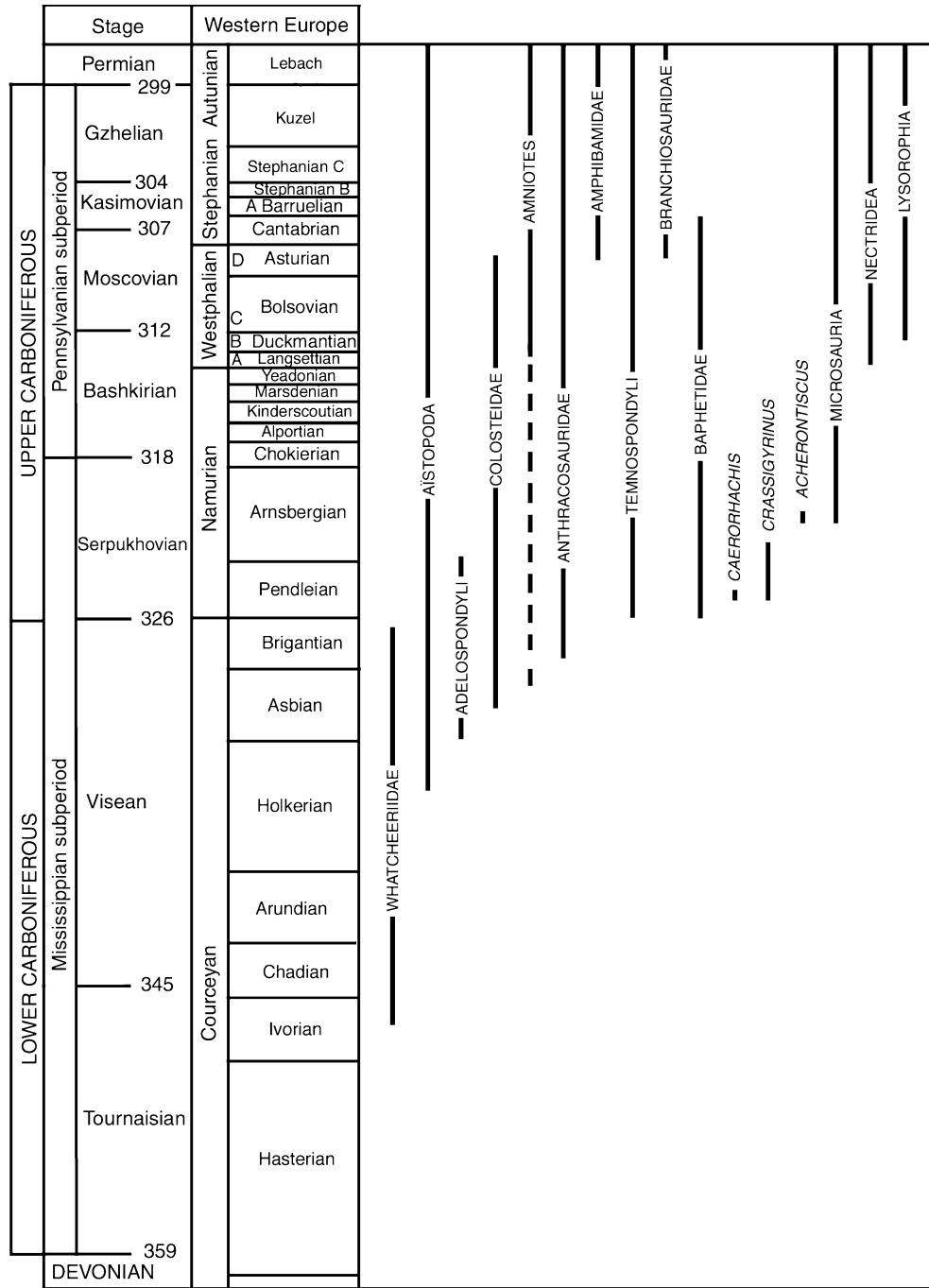
Figure 76. Ranges of occurrence of major Carboniferous amphibian clades, based on the 2004 geological time scale of Gradstein *et al.* (2004).

of the Brigantian, and those of caecilians to the microsaurs of the Arnbergian (Fig. 76), few if any definitive characters of these clades can be recognized in earlier tetrapods. In fact, very few tetrapods of any sort are yet known from earlier in the Carboniferous. From the first 30 million years of the Carboniferous, only four clades have been described: the labyrinthodont families Whatcheeriidae (Lombard & Bolt, 1995;

Warren & Turner, 2004; Clack & Finney, 2005) and Colosteidae (Panchen, 1975), and the lepospondyl families Oestocephalidae (Aïstopoda) (Anderson, Carroll & Rowe, 2003) and Adelogyrinidae (Andrews & Carroll, 1991). None of these families has obvious synapomorphies with any lineages that survived the Palaeozoic. The appearance of 12 more lineages in the later Carboniferous indicates that many more taxa

must have existed during the late Tournaisian and early Viséan, but have not yet been discovered. In the absence of such fossils, it is extremely difficult, if not impossible, to establish the pattern of interrelationships among the Late Carboniferous lineages, making it unlikely that a definitive answer can be found to the question of the temporal sequence of divergence of the basal lineages leading to the modern amphibian orders. Nevertheless, it may be informative to attempt a formal cladistic analysis of Palaeozoic tetrapods on the basis of what is currently known, even if only to show the possible limits of this procedure.

METHODOLOGY

Although the combined use of skeletal data and knowledge of the soft anatomy, physiology, and behaviour of extant taxa was effective in evaluating the putative ancestry of modern amphibian orders among a limited number of late Palaeozoic clades, this approach cannot be carried further to determine their possible affinities among earlier Carboniferous amphibians or ancestral amniotes. This is the result of the absence of comparable, derived osteological features, and the impossibility of making use of extraskeletal attributes of Lower Carboniferous tetrapods. Consequently, a different methodology and emphasis on different characters must be used to establish relationships of lissamphibians to Upper Devonian and Early Carboniferous taxa with no surviving direct relatives. In this respect, the following analysis closely parallels the approach of Laurin & Reisz (1997) and Ruta *et al.* (2003). However, as emphasized in the introduction to this article, previous phylogenetic analyses of primitive tetrapods have resulted in highly disparate hypotheses regarding their affinities with one another and with the lissamphibian orders. The approach taken here differs in several respects. First, it concentrates on establishing the probable ancestry of the modern amphibian orders, rather than engaging in a detailed analysis of all Palaeozoic tetrapods. For this reason, the number of amniote taxa is reduced to one: the single assemblage that can be traced to a monophyletic origin within the Carboniferous. Second, the number of non-amniote taxa was reduced by concentrating on a small number of clearly identifiable groups, each of which had a demonstrably common ancestry, based on a unique combination of derived characters that permit the earliest known members to be clearly distinguished from members of all other clades. The distinction between these clades is further emphasized by our very incomplete knowledge of the fossil record of relevant groups in the Palaeozoic, and the rarity of intermediates between any of the major groups.

The data matrix was limited to only 23 taxonomic units, in comparison with 38 of Laurin & Reisz (1997)

and 90 of Ruta *et al.* (2003). This was achieved by concentrating on species that exhibited the most primitive character states of each clade, as determined by the polarity of character changes observed within the clades in question, and comparison with generally more plesiomorphic outgroups. Limiting the dataset to taxa exhibiting only the most primitive character states within each clade is justified by the reasoning that variation that occurs within groups with a monophyletic origin should not be used to determine affinities with other clades whose apomorphies support a separate ancestry. For example, no changes that evolved among amniotes *s.s.* can be homologous with those that evolved among distinct clades of non-amniotes, on the basis of prior understanding of their dichotomous origins. Reliance on the probably monophyletic origin of the non-amniotic clades is based on recent reviews of all major taxa (Heatwole & Carroll, 2000; Carroll *et al.*, 1998; Anderson, 2001). Sarcopterygian taxa, used as outgroups by Laurin & Reisz (1997) and Ruta *et al.* (2003), were omitted from formal analysis to avoid the inclusion of characters of the paired fins and other structures restricted to fish but not present in any tetrapods.

As a monophyletic taxon, each of the recognized clades was assumed to have arisen from a single species with a particular suite of characters, although it is unlikely that fossils of such unique taxa have yet been recovered, considering the extremely incomplete record from the Palaeozoic. Rather, the best known or presumably most informative taxa have been chosen to document the plausibly most primitive character states of the basal members of each of the clades. The clades vary greatly in size, from a single relatively well-known specimen or species, to entire orders or higher taxa.

MONOPHYLY AND PARAPHYLY

The term monophyly has been used in this discussion in the sense of Simpson (1961) to refer to the ancestry of a clade, in contrast to that of Hennig (1966), who specifies that a monophyletic clade must also include all of its descendants. Although Hennig's use of the term can be considered more objective, as it precludes the arbitrary separation of ancestors and descendants, his usage makes it difficult to discuss evolutionary processes that inevitably involve sequential changes among assemblages of organisms that are sufficiently different to have been placed in different species, genera, or even families and orders. In the case of the origin of the modern amphibian orders, their degree of distinction from putative antecedents is such that their ancestry among Palaeozoic non-amniotes is still not satisfactorily resolved. For this reason, primitive Palaeozoic non-amniotes continue to be referred to as members of taxonomic groups that are assumed to be

paraphyletic (non-monophyletic) in the sense that they may include the ancestors of either amniotes or one or more of the modern amphibian orders. The anthracosaurs have long been assumed to include the sister taxa of amniotes, and the temnospondyls are presumed to be ancestral to some, if not all, of the modern amphibian orders. However, it remains impractical to develop a new (phylogenetic) taxonomy for Palaeozoic tetrapods when the specific nature of their relationships to extant tetrapods remains unresolved, or even unresolvable on the basis of our current knowledge of the fossil record.

This problem is reflected in the choice of particular taxa and characters for this data matrix. Although many of the clades recognized in this study are monophyletic in the sense of both Simpson and Hennig, i.e. they almost certainly became extinct without descendants, several consist of species that appear to be linked to other recognized clades. These include the basal temnospondyls, branchiosaurids, amphibamids, and microsaurs, as well as the genera *Rhynchonkos* and *Triadobatrachus*. These were treated individually because of the specific focus of this study on the origin of the modern amphibian orders. In contrast to the other clades, for which only the most primitive character states were tabulated, character states unique to more derived branchiosauridae, amphibamids, and microsaurs (as represented by *Rhynchonkos*) were also included, to enable more specific comparison with the modern amphibian orders. This is clearly an unorthodox approach, but necessary if sequential relationships are to be recognized. The selection of such specific taxa and character states might be viewed as arbitrary, if one considers that all characters and taxa should be treated equally, but this is clearly not the case in this study, which is directed specifically at establishing the probable nature of the taxa and character states that linked particular lineages of Palaeozoic amphibians to their living descendants.

Few individual species are sufficiently well known to illustrate all the characters under study. In most cases, two or more of the most primitive known species or genera have been used to provide the included data. These are as follows:

|	
Acanthostega	*Acanthostega gunnari* (Coates, 1996; Clack, 1998, 2002c, 2003a)
Whatcheeridae	*Whatcheeria deltae* (Lombard & Bolt, 1995), *Pederpes finneyae* (Clack & Finney, 2005), *Ossinodus pueri* (Warren & Turner, 2004)
Crassigyrinus	*Crassigyrinus scoticus* (Panchen & Smithson, 1990)
Anthracosauroidea	*Proterogyrinus scheelei* (Holmes, 1984), *Eoherpeton watsoni* (Smithson 1985), *Gephyrostegus bohemicus* (Carroll, 1970), discosauriscids (Špinar, 1952)
Baphetidae	*Baphetes kirkbyi* (Milner & Lindsay, 1998), *Eucritta melanolimnetes* (Clack, 2001), *Kyrinion martilli* (Clack, 2003b)
Caerorhachis	*Caerorhachis bairdi* (Holmes & Carroll, 1977; Ruta, Milner & Coates, 2002)
Colosteidae	*Pholidogaster pisciformis* (Panchen, 1975), *Greererpeton burkemorani* (Smithson, 1982; Godfrey, 1989), *Colosteus scutellatus* (Hook, 1983)
Basal temnospondyls	*Balanerpeton woodi* (Milner & Sequeira, 1994), *Dendrerpeton* (Holmes et al., 1998).
Branchiosauridae	*Branchiosaurus* sp. [from Mazon Creek (Milner, 1982)], *Apateon caudus* (Schoch, 1992; Schoch & Carroll, 2003), *Apateon dracyiensis* (Werneburg, 2001), *Apateon gracilis* (Schoch & Fröbisch, 2006), Branchiosauridae (Boy & Sues, 2000)
Amphibamidae	*Amphibamus grandiceps* (Gregory, 1956; Milner, 1982), *Doleserpeton annectens* (Bolt, 1969)
Rhynchonkos	*Rhynchonkos* (= *Goniorhynchus*) *stovalli* (Carroll & Gaskill, 1978)
Acherontiscus	*Acherontiscus caledoniae* (Carroll, 1969a)
Aïstopoda	*Lethiscus stocki* (Anderson et al., 2003)
Adelospondyli	All taxa (Andrews & Carroll, 1991)
Lysorophia	*Brachydectes elongatus* and *Brachydectes newberryi* (Wellstead, 1991)
Microsauria	*Utaherpeton franklini* (Carroll, Bybee & Tidwell, 1991); entire order (Carroll & Gaskill, 1978)
Nectridea	Entire order (Bossy & Milner, 1998)
Early amniotes	*Hylonomus lyelli* (Carroll, 1964), *Paleothyris acadiana* (Carroll, 1969b)
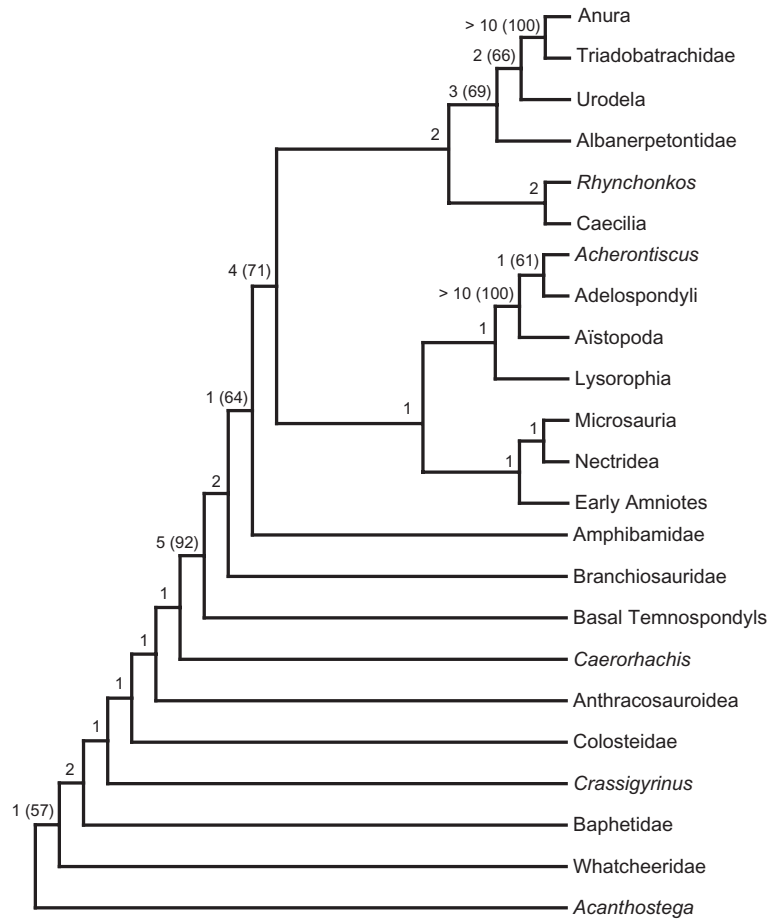
Figure 77. Single most parsimonious tree, of 530 steps, generated by PAUP, illustrating the phylogenetic relationships of the major amphibian clades. Numbers at nodes represent decay index values. Numbers in parentheses are bootstrap percentage values. Bootstrap support less than 50% is not indicated.

Albanerpetontidae   *Celtedens ibericus* (McGowan, 2002), *Albanerpeton inexpectatum* (Estes & Hoffstetter, 1976)

Urodela   Jurassic/Lower Cretaceous Caudata (Milner, 2000), *Chunerpeton tianyiensis* (Gao & Shubin, 2003)

Triadobatrachidae   *Triadobatrachus massinoti* and *Czatkobatrachus polonicus* (Roček & Rage, 2000)

Anura   *Prosalirus bitis* (Jenkins & Shubin, 1998), other Jurassic frogs (Báez & Basso, 1996)

Caecilia   *Eocaecilia micropodia* (F. A. Jenkins, D. Walsh & R. L. Carroll, 2007)

CLADOGRAMS AND ANALYSES

This analysis is based on 118 morphological characters (described in Appendix 3). All characters are unordered, equally weighted, and optimized using the DELTRAN option. All characters but five appear to be informative. The matrix includes 23 taxa, with a missing data percentage of 13.7% (Appendix 4). The analysis was performed in PAUP version 4.0.b10 (Swofford, 2001) with the heuristic search option, tree bisection-reconnection branch-swapping algorithm, ten random addition sequences, and holding 100 trees at each step. Support for internal nodes was assessed through 10 000 bootstrap replicates and by the calculation of decay index values (for example, how many extra steps are required to collapse the branches at each node?).

A single most parsimonious tree was obtained with a length of 530 steps (Fig. 77). This cladogram differs greatly in general appearance from the diagrams illustrating the patterns of nested synapomorphies leading to the modern orders (Figs 61, 71, 75). The latter include only the modern amphibian orders and their immediate sister taxa from the Early Mesozoic and Palaeozoic. All other taxa, which do not share synapomorphies with the modern orders, are omitted. On the

other hand, although all major taxa of Palaeozoic tetrapods were included in the PAUP analysis, most trace their origins to the Lower Carboniferous, and show no specific sister-group relationships with the extant orders. The morphological distance between taxa from *Acanthostega* through *Caerorhachis* presumably results from the very small number of clades known from the Early Carboniferous, and the paucity of characters supporting any specific patterns of relationship.

Two specific similarities between the results of these different methods of analysis are the close affinities of anurans (plus triadobatrachids) and urodeles, and the more distant relationship with caecilians (plus *Rhynchonkos*). Where the PAUP analysis differs most strongly is in the absence of close affiliations between either urodeles or salientians and any of the Palaeozoic taxa, and the great phylogenetic distance between *Rhynchonkos* and more basal microsaurs. On the other hand, the putative antecedents of frogs and salamanders (the basal temnospondyls) do appear as the immediate sister taxa of branchiosaurs and amphibamids in one cladogram only two steps beyond the most parsimonious tree (not shown), and have a bootstrap support of 23.6%. All of these differences reflect the great degree of anatomical distinction between Palaeozoic and Late Mesozoic and Cenozoic amphibians.

Support of relationships seen in the most parsimonious tree, at 530 steps, rapidly decays in slightly longer trees (Fig. 77). At 531 steps, little more than the clades including the modern orders and that uniting *Acherontiscus*, aïstopods, and adelogyrinids are maintained. Most other taxa occur within polytomies. At 532 steps, *Acherontiscus*, aïstopods, and the Adelospondyli remain as an unresolved tricotomy; Triadobatrachidae plus Anura is the only remaining sister-group pair, with albanerpetontids as an outgroup of batrachians. At 533 steps, urodeles and albanerpetontids fall into an extensive polytomy. The remaining groups of terminal taxa retain their distinction at 534 and 535 steps, but intermediate nodes are lost. Trees of length 534–540 retain this same pattern, after which the analysis was terminated.

The results of a bootstrap analysis essentially parallel those of the decay analysis (Fig. 77). Most of the archaic taxa fall below the 50% bootstrap value, but the node uniting basal temnospondyls and all more derived clades is supported by 92% of the trees. The clade of adelospondylids, aïstopods, and *Acherontiscus* is supported 100% of the time, as is the sister-group relationship of Triadobatrachidae and Anura. The Batrachia have a support value of 66%, and *Rhynchonkos* and caecilians are recognized as sister taxa in 48.5% of the trees.

The program Mesquite, version 1.05 (Maddison & Maddison, 2004), was used to manipulate the most parsimonious tree obtained in PAUP to estimate the number of extra steps required to establish the pattern of relationships determined through recognition of a series of nested synapomorphies (Fig. 78).

Working in stages: If branchiosaurids alone were placed as a sister taxon of temnospondyls, the resulting tree was 535 steps in length, only five steps more than the most parsimonious tree. However, if urodeles were added as well, the length increased to 560 steps. Adding amphibamids to temnospondyls required eight more steps than the most parsimonious tree, whereas adding both amphibamids and anurans + triadobatrachids required 25 extra steps. Adding both branchiosaurids and amphibamids to temnospondyls required only five steps more than the most parsimonious tree. Adding branchiosaurids, urodeles, amphibamids, and anurans + triadobatrachids to temnospondyls gave a length of 565 steps, 32 steps more than the most parsimonious trees. However, adding *Rhynchonkos* and caecilians to microsaurs (without rearranging any other branches) required only five more steps than the most parsimonious tree. Finally, if both caecilians and batrachians were placed with their putative Palaeozoic sister taxa, the number of steps increased to 566, 36 more than the most parsimonious tree. The number of extra steps that are required for Mesquite to accommodate the relationships indicated by the search for nested synapomorphies suggests a highly unparsimonious tree, but this requires only about a 7% increase in the number of steps. Nevertheless, the general configuration of the most parsimonious cladogram (Fig. 77) differs greatly from the conclusions reached by the search for nested synapomorphies.

LIMITATIONS OF MAXIMUM PARSIMONY IN ESTABLISHING RELATIONSHIPS

Why should the results of these two methodologies differ so greatly? The main reason is that these procedures stem from very different approaches to establishing relationships. Following Hennig (1966), PAUP serves primarily to recognize sister-group relationships rather than affinities between ancestors and descendants. This was based on the reasoning that ancestors could not be recognized as such simply by the absence of unique shared derived characters present in their putative descendants. The particular methodology for recognizing sister-group relationships is via a search for the most parsimonious pattern of character distributions, based on the minimum number of character state changes among all the taxa being investigated – broadly, an extension of Occam's razor. This procedure implies that evolution of unique derived character states is more frequent than reversals or convergence, but this has never been tested.

The search for nested synapomorphies also depends on the use of shared derived characters to recognize
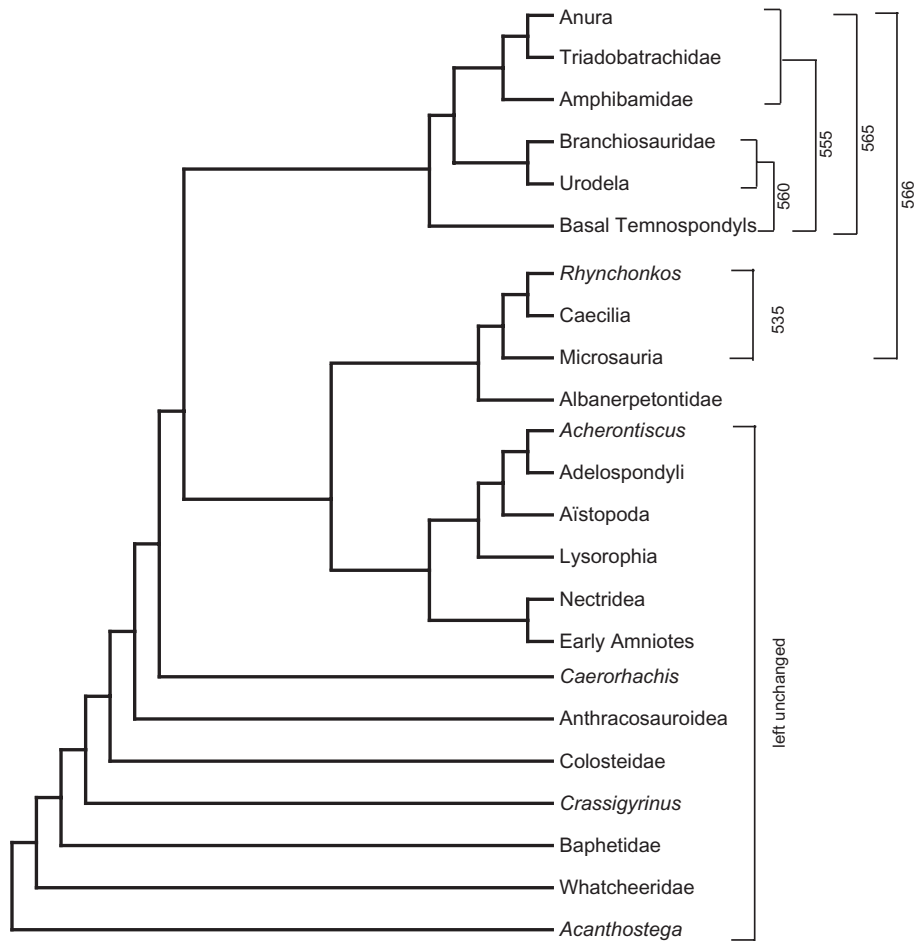
Figure 78. Tree resulting from swapping branches of the originally most parsimonious cladogram generated by PAUP to accord with the relationships based on the pattern of nested synapomorphies. Numbers of addition steps required for each swap calculated by Mesquite (Maddison & Maddison, 2004).

sister-group relationships, but these are investigated in a sequential manner, so that they may lead to the recognition of a series of putative ancestor–descendant relationships. Parsimony is not emphasized. The homology of characters present in distinct clades is not judged primarily on the basis of congruence (Grande & Rieppel, 1994), but should be dependent on the recognition of a putative common ancestor that already expresses the traits in question (Shubin, 1994).

With the development of mathematical algorithms such as those used in PAUP, it is possible to analyse very large datasets, which are now the standard means of phylogenetic analysis. Despite their wide usage and general acceptance, questions should still be raised as to the assumptions on which they are based, and the possible limits of their applicability.

Four factors, generally not encompassed by phylogenetic analysis, must be considered in determining the interrelationships of the major amphibian clades:

1. Major gaps in our knowledge of the fossil record
2. Different rates and/or patterns of evolution during different stages in the history of amphibians
3. The known temporal distribution of the available fossils
4. Homology

Relative completeness of the fossil record
There are two major gaps in our knowledge of the fossil record of amphibians, one in the Lower Carboniferous, lasting approximately 30 million years, during the period in which primitive tetrapods were undergoing their initial major radiation, and a second of 80–100 million years between the Lower Permian and the Jurassic, during which the most conspicuous attributes of the extant amphibian orders evolved. As a result of these long gaps, each clade can be readily differentiated by a number of autapomorphies, but relatively few synapomorphies can be recognized that link them with one another.

This is most clearly shown by the stepwise succession of primitive tetrapods from *Acanthostega* through *Caerorhachis*. Neither a search for maximum parsimony nor a search for nested synapomorphies can reveal reliable sister-group affinities on the basis of our very incomplete knowledge of the fossil record in the Lower Carboniferous, when these taxa first diverged.

However, even among taxa from the Upper Carboniferous, the lack of knowledge of primitive members of the more derived clades limits the number of characters that may be compared with putative antecedents or sister taxa.

Neither temnospondyls, amphibamids, nor branchiosaurids can be securely linked to any of the more archaic tetrapods. On the other hand, numerous synapomophies can be recognized linking amphibamids and branchiosaurs to each other and to temnospondyls, as detailed in the descriptive portion of this article. These are sufficient to link these taxa in some cladograms generated by PAUP, but these affinities are not recognized in the most parsimonious tree. This can be attributed to the fact that the earliest known temnospondyls, branchiosaurids, and amphibamids have each diverged sufficiently that the number of apomorphies that distinguish them from one another is greater than the number of synapomorphies that might reflect a series of sister-group relationships linking them with one or more of the more archaic tetrapod clades and/or with one another.

Even greater problems are recognized at the next level, between amphibamids and anurans, and between branchiosaurids and salamanders. Key evolutionary changes that may be recognized as synapomorphies linking a succession of clades, including temnospondyls, amphibamids, and anurans (e.g. the great enlargement of the orbits and interpterygoid vacuities, and the anatomy of the middle ear), may be numerically rare and swamped by global parsimony based on other features that distinguish the end groups, such as the number of dermal bones in the skull, and the configuration of the vertebrae. On the other hand, the large number of synapomorphies shared by the larvae of branchiosaurids and modern salamanders, especially the unique sequence of ossification of both the skull and the appendicular skeleton, as well as the specific configuration of the hyoid apparatus, are also not sufficient for PAUP to recognize their affinities. This may be because comparable assessment of development is not possible to code in other fossil taxa. If there are relatively few derived characters in common, or if they are difficult to compare from clade to clade, this may explain why relationships between Palaeozoic and extant clades are so difficult to recognize by a search for maximum parsimony.

The known temporal distribution of fossils
Other phylogenetic problems can be recognized if we take into account the earliest time of occurrence of taxa (Fig. 76). In the most parsimonious tree (Fig. 77), two assemblages of terminal taxa are recognized above the level of amphibamids, one including the batrachians, Albanerpetontidae, and caecilians, and the other grouping lepospondyls and amniotes. However, among the latter assemblage are two taxa, the aïstopods and the adelospondyls, that are, in fact, among the oldest tetrapods known from the fossil record, and that almost certainly diverged close to the base of tetrapod radiation. However, their morphology diverges so greatly that no sister-group affinities can be recognized with any of the archaic clades. The possible affinities of amniotes may also lie well down in the Carboniferous, especially if *Westlothiana* (Smithson *et al.*, 1994) and *Casineria* (Patton, Smithson & Clack, 1999) are the sister taxa of amniotes, but no well-established affinities have yet been recognized with any of the archaic clades.

Different rates and/or patterns of evolution during different stages in amphibian evolution
The problem of lacking sufficient evidence to establish reliable sister-group relationships would also be expected to be accentuated in the case of higher than normal rates of morphological change within lineages during periods of major radiation or adaptation to distinct environments or ways of life. This would result in short internodal periods, with little time for the accumulation of the synapomorphies necessary to recognize sister-group relationships. The greater the anatomical differences between the oldest known members of clades, the less likely it is that correct sister-taxa affinities will be correctly recognized.

Homology
Another very serious problem is the correct recognition of homology. The first step after selecting the taxa for phylogenetic analysis is to establish the characters and character states that are to be used and their distribution among the taxa. Anatomical characters that appear similar are nearly always coded in the same way in all taxa in which they are observed (e. g. presence or absence of particular bones or of foramina within or between the bones). In practice, little thought is given to the question of homology, because it is assumed that most changes in structures are uniquely derived rather than being the result of reversals or convergence (Grande & Rieppel, 1994), and so will be identified as such in a parsimony analysis. There are, however, conspicuous exceptions.

All clades of Palaeozoic amphibians for which the fossil record is known over a sufficient period of time show progressive changes in many aspects of their anatomy,

including modifications in the configuration, loss, or fusion of bones throughout the skeleton. Such changes are especially evident in clades that have undergone significant size reduction, including all the lepospondyl orders and the ancestors of amniotes (Carroll, 1999). If the resulting changes are sufficiently similar to be coded in the same way in all taxa making up a data matrix, they will hence be treated as homologous.

It has been common practice (Grande & Rieppel, 1994: 238) to assume that homology can be determined on the basis of the congruence of character distribution. If many similar derived characters are evident in two potential sister taxa, it is generally accepted that they are all homologous. However, there are certainly cases in which this is not true. One of the most strongly supported of all relationships found in this analysis is between aïstopods, adelospondylids, and *Acherontiscus*, all of which have greatly reduced or entirely lost the appendicular skeleton. In order to represent attributes of the appendicular skeleton in an equivalent manner for all taxa, the presence or absence of each bone was indicated for all clades. Animals with extensive loss of the same bones would thus have a great number of similar character states, and would therefore be recognized as sister taxa. In the absence of fossil evidence of plausible ancestors or sister taxa of aïstopods, adelospondylids, and *Acherontiscus*, there is no basis for determining whether limb reduction and loss had been initiated in a single common ancestor or whether this condition had been achieved by convergence.

On the other hand, there are many examples of convergent limb loss in other groups, most effectively documented in lizards by Greer (1991). He found that limb reduction had occurred at least 62 times in 53 clearly distinct lineages of skinks. None of these character changes can be considered as homologous, and they provide no evidence of close affinities between the individual species in these 53 lineages. However, scored simply as the loss of particular bones, they appear as homologues, and suggest a close relationship. Similar limb reduction, if coded for living caecilians (which are totally limbless), would have placed them within the same assemblage as the Palaeozoic aïstopods, adelospondylids, and *Acherontiscus*. This does not occur in this cladogram because the more primitive condition, shown by the basal caecilian *Eocaecilia*, demonstrates that limb loss occurred within this order, rather than being inherited from a more plesiomorphic antecedent.

Molecular phylogenies
There are clearly problems in depending on maximum parsimony as a means of establishing relationships if it is based on the patterns of distribution of changes in skeletal anatomy over long periods of geological time. This is an especially serious problem in establishing affinities between archaic and extant amphibian clades, which differ to a much greater degree than is evident within any of the extant orders. Fortunately, this is not the only system available for such an analysis. In contrast to the great amount of change over time seen in the skeleton between Late Palaeozoic and Early Mesozoic amphibians, a much more conservative pattern of variation can be seen in the evolution of genetic systems among all vertebrates. Comparable genes, with unquestioned homology, are maintained from primitive living fish to birds and mammals. A particularly well-studied system is the genome of the mitochondria, which plays the same vital role in cellular respiration in all vertebrates.

This was strikingly demonstrated by Zhang *et al.* (2005) in a molecular study of the origin and phylogeny of living amphibians. Zhang *et al.* analysed the complete mitochondrial genomes of 12 extant amphibians, including two caecilians, four salamanders, and eight anurans, using representatives of seven other vertebrate genera as outgroups. The mitochondrial genome is especially effective for this type of study, because nearly all amphibians have the standard gene component common to higher vertebrates (two rRNAs, 22 tRNAs, and 13 protein-coding genes). Hence, there is little if any doubt regarding the homology of all elements in all taxa. At the nucleotide level, 3953 sites were constant, 857 were variable, and 2849 were informative for parsimony.

A single most parsimonious cladogram was discovered that indicated the same sequence of branching of the extant orders as that established in this search for nested synapomorphies of the skeleton: frogs and salamanders as sister taxa, and caecilians as an outgroup. Close agreement was also established for the time scale of divergence of the immediate ancestors of each group: divergence of the caecilian lineage from batrachians between 353 and 321 million years ago (near the base of the Carboniferous), and divergence of anurans and urodeles between 328 and 289 million years ago, within the Upper Carboniferous and Lower Permian. On the basis of the degree of overlap between the proposed time of molecular divergence and the known fossil record, strong support was given for the temnospondyl origin for lissamphibians, but with the possibility of the origin of caecilians from microsaurs.

Unfortunately, none of the basal amphibian groups have living representatives, as is the case for some other vertebrate groups, including fish, so it will never be possible to use molecular means to establish the affinities of temnospondyls, microsaurs, or putative antecedents of amniotes. As stated by Zhang *et al.* (2005: 398), 'only paleontological data can provide direct evidence to support which extinct amphibian

group is actually most closely related to living amphibians'.

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Appendix 1. Lists of lissamphibian synapomorphies tabulated by Parsons & Williams (1963)

THOSE THAT CLEARLY AND UNIQUELY LINK THE THREE MODERN ORDERS

*1. Pedicellate teeth
*2. The operculum–plectrum complex
 3. The papilla amphibiorum
 4. The green rods
 5. The fat bodies
 6. The structure of the skin glands
 7. Cutaneous respiration and its attendant specializations

CHARACTERS THAT THE THREE MODERN ORDERS SHARE BUT THAT ARE KNOWN TO HAVE BEEN ACQUIRED OR APPROACHED BY OTHER TETRAPOD GROUPS

*1. The peculiar fenestration of the posterolateral skull roof
*2. The loss of the posterior series of skull bones
*3. The advanced type of palate
*4. The usual presence of only ten cranial nerves
*5. Two occipital condyles
*6. The characteristic atlas

CHARACTERS THAT MAY BE INDICATIVE OF SOME SPECIAL RELATIONSHIPS BETWEEN THE THREE MODERN ORDERS BUT THAT SHOW ENOUGH DIFFERENCES BETWEEN THE ORDERS TO BE AMBIGUOUS

*1. Reduction of ossification and simplification of bone structure
 2. Pattern of the nasal organ
 3. Simplification of brain structure.

These lists may be divided between skeletal features that can be recognized in the fossil record (indicated by asterisks) and those of the soft anatomy that cannot be studied directly from fossils.

Appendix 2. Selected skeletal synapomorphies supporting the monophyly of the extant amphibian orders (from Carroll *et al.*, 2004)

PART A. SYNAPOMORPHIES OF BASAL SALAMANDERS (HYNOBIIDS, AMBYSTOMATIDS, AND SALAMANDRIDS)

1. Jaw suspension without a bony link to maxilla
2. Ventral end of squamosal moves laterally relative to braincase via a hinge-like articulation with the parietal and/or otic capsule
3. Ceratobranchials become ossified or calcified at the time of metamorphosis in neotenic species (Gao & Shubin, 2001)

4. Gill rakers capable of interdigitation so as to preclude flow of water through gill slits during suction feeding
5. Absence of middle ear cavity
6. Stapedial foramen lost
7. Ligamentous attachment of stapes to squamosal or quadrate (Trueb, 1993)
8. Mesopodial bones 1 and 2 in wrist and ankle fused to form basale commune
9. Phalanges ossify from distal to proximal (Wake & Shubin, 1998)

PART B. SYNAPOMORPHIES OF BASAL ANURANS [LIST MODIFIED FROM THAT OF GAO & WANG (2001)]

 1. Skull wider than long
 2. Otic occipital composed of prootic and exoccipital
 3. Fusion of frontal and parietal
 4. Prefrontal lost
 5. Squamosal triradiate with anteriorly projecting zygomatic ramus
 6. Squamosal not in contact with dermal bones of skull table
 7. Squamosal deeply embayed posteriorly
 8. Stapes free distally
 9. Postchoanal process of vomer present
10. Palatine fused with vomer
11. Dentary edentulous
12. Vertebral column shortened to no more than ten presacral bones (14 in *Triadobatrachus*)
13. Free ribs greatly reduced in number; four pairs or fewer
14. Leading edge of scapula concave
15. Scapula reduced to less than half the length of the humerus
16. Rodlike urostyle
17. Epipodial elements fused to form compound radioulna and tibiofibula
18. Dorsal tubercle of ilium low or absent
19. Iliac blade elongate and anteriorly directed
20. Hindlimb lengthened with significant elongation of proximal tarsal elements
21. Highly derived tadpole larvae

PART C SYNAPOMORPHIES OF CAECILIANS (BASED ON THE LOWER JURASSIC GENUS *EOCAECILIA*)

1. Jaw articulation anterior to otic capsule
2. Orbits small relative to those of most other tetrapods of comparable skull size
3. Posterior portion of squamosal bone moveable laterally relative to skull table
4. Frontal bone in contract with squamosal bone
5. Tentacular groove or fenestra
6. Medial rows of teeth on vomer, palatine, and inner surface of lower jaw

7. Internal naris medial to suture between maxilla and premaxilla, and tooth rows on vomer and palatine

8. Close integration of quadrate and stapes

9. Vomerine eminence

10. Posterior portion of braincase fused into a single unit, the os basale

11. Massive sphenethmoid extending anterior from the opening for the optic nerve and incorporating the orbitosphenoid, mesethmoid, and basisphenoid

12. Planum anorbitale extends from sphenethmoid to upper jaw

13. Nasal capsule occupies all space anterior to planum anorbitale

14. Lower jaws composed of two centres of ossification, an anterior pseudodentary and a posterior pseudoangular, separated by an extensive oblique suture

15. Long retroarticular process

16. Large internal process of pseudoangular

17. Surface for articulation between lower jaw and skull nearly vertical and angled anteromedially

18. Forelimbs and hindlimbs greatly reduced (absent in all living species)

19. Thirty-six or more presacral vertebrae

20. Intercentra retained in Jurassic species

Appendix 3. Character descriptions

SKULL ROOF

1. Total skull length (cm): (0) > 10; (1) between 2 and 10; (2) < 2.

2. Ratio of skull to presacral column length (%): (0) between 45 and 60; (1) > 60; (2) between 35 and 45; (3) between 20 and 35; (4) < 20.

3. Skull length expressed in no. of anterior trunk vertebrae: (0) 14–16; (1) 13; (2) 9–10; (3) 7–8; (4) 4–6.

4. Ratio of skull height to skull width (%): (0) < 25; (1) 25–45; (2) 45–60; (3) > 60.

5. Ratio of orbit (or orbitotemporal opening) length to skull length (%): (0) < 20; (1) 20–25; (2) 25–40; (3) > 40.

6. Position of jaw articulation: (0) behind the occiput; (1) at the level of the occiput; (2) anterior to the occiput.

7. Relationship of skull table to cheek: (0) continuous arc; (1) sharp change of orientation and possible mobility; (2) does not apply.

8. Bones surrounding nostril (not including pm and m): (0) l, at; (1) l, n; (2) prf; (3) l, prf; (4) l, n, prf; (5) n, l + prf; (6) n.

9. Bones surrounding orbit: (0) prf, pf, po, j; (1) l, prf, pf, po, j; (2) l, prf, f, pf, po, j, m; (3) l, prf, pf, po, j, m; (4) l, prf, pf, j; (5) l, prf, p, integrated sq + t + m; (6) l, prf, f, pf, po, j; (7) m, fused l + prf, median f, p, sq, j; (8) l, prf, f, p, m; (9) prf or n, fused f + p, m; (10) m, prf, pf, j.

10. Orbit shape: (0) rounded; (1) square; (2) expanded anteriorly; (3) expanded posteriorly.

11. Orbit position: (0) intersecting midline of skull; (1) anterior to midline of skull.

12. Pineal opening: (0) present; (1) absent.

13. Posterior embayment of squamosal: (0) incised dorsally for spiracle; (1) without embayment; (2) large embayment supporting a tympanum.

14. Squamosal: (0) firmly integrated into cheek throughout development; (1) has mobile articulation dorsally with otic capsule and/or adjacent dermal bones of skull table.

15. Anterior zygomatic process on the squamosal: (0) lacking; (1) present.

16. Relationship between maxilla and jaw suspension in larvae and/or adults: (0) ventral margin of cheek continuous between maxilla and jaw suspension; (1) gap between maxilla and jaw suspension.

17. Temporal or orbitotemporal opening: (0) no temporal opening; (1) temporal opening; (2) orbitotemporal opening.

18. Sensory canals: (0) present, but largely open as lines of pores; (1) largely or entirely open as grooves; (2) no lateral-line canals incised in bone.

19. Bones of the skull roof: (0) all bones present (a condition not represented in the matrix); (1) it absent: (2) mr absent; (3) mr, preo absent; (4) mr, preo, it absent; (5) mr, preo, it, st absent; (6) mr, preo, it absent, fusion of st, sq, t; (7) mr, preo, it, j, pf, po, st absent; (8) mr, preo, it, st, pp, t, qj absent, l + prf fused, median f; (9) mr, preo, it, st, t, pp, pf, po, j absent; (10) mr, preo, it, st, t, pp, l, ±prf, j, pf, po absent, f + p fused; (11) mr, preo, it, st, po

20. Relationship between parietal and tabular: (0) parietal separated from tabular by supratemporal; (1) parietal in contact with tabular; (2) not applicable (e.g. tabular absent).

PALATE

21. Interpterygoid vacuity: (0) absent; (1) a conspicuous oval opening that extends anteriorly to the vomers.

22. Ectopterygoid: (0) present; (1) lost.

23. Parasphenoid extends beneath the level of bs and bo: (0) no; (1) yes.

24. Marginal dentition: (0) nearly uniform, moderate-sized teeth in pm and m: (1) huge fangs on pm; (2) distinct canine teeth in m; (3) a small number of bulbous teeth.

25. Palatal dentition: (0) fang and associated replacement pit on v, pal, and ect; (1) fang and associated replacement pits present on v and pal, but missing on ect; (2) palatal fangs on pal and ect, but missing on v; (3) large palatal teeth on v, pal and ect, but without associated replacement pits; (4) progressive reduction of fang and pit pairs to patches of denticles; (5) continuous rows of small teeth on v and pal and/or ect; (6) rows of teeth on v, but no other palatal bones; (7) row of teeth on pal; (8) patches of denticles on v; (9) covering of small denticles, but neither enlarged teeth nor rows of small teeth on v, pal, or ect; (10) no enlarged teeth on v, pal, or ect, but rows of large denticles radiating across pterygoid.

26. Tooth structure: (0) crown and base of teeth continuous in adults; (1) teeth pedicellate (crown and base separated by fibrous tissue).

JAW

27. Relationship between the ventral margin of the preart and the infradentary bones: (0) elongate gap where the meckelian bone was unossified; (1) sutural contact.

28. Parasymphysial plate: (0) present; (1) absent.

29. Number of coronoids: (0) 3; (1) 2; (2) 1; (3) 0.

30. Other jaw bones distinct in adults: (0) d, 2spl, a, sa, preart, art; (1) d, 1 spl, a, sa, preart, art; (2) d, preart, a + art; (3) d, a, preart, art, co; (4) d, ar, ansp (5) pa, pd.

31. Mentomeckelian bone: (0) not present in adults; (1) present in adults.

32. Dentition: (0) as in upper jaws; (1) loss of dentary dentition.

OCCIPUT

33. Supraoccipital: (0) not expressed as a separate element; (1) occupies position between pp and otic capsule.

34. Post-temporal fossa: (0) opens onto occipital surface; (1) not apparent.

35. Relationship between bo and eo: (0) partially or completely fused; (1) clearly distinct.

36. Relationship between otic capsule and t: (0) bony contact; (1) cartilaginous contact; (2) no contact; (3) does not apply.

37. Relationship between eo and pp: (0) eo not reaching pp; (1) eo does reach pp; (2) pp lost; (3) eo indistinguishably fused.

38. Otic capsules: (0) fused posteriorly at midline without suture; (1) meet at midline suture; (2) do not meet at midline posteriorly.

39. Articulation between occiput and vertebral column: (0) notochord extends anteriorly between thin husk of eo and bo with little if any bony articulation with atlas centrum; (1) loosely articulated, block-like bo, which did not form a finished occipital condyle; (2) closely integrated surfaces of eo and bo forming a shallow, more or less circular recess for articulation with atlas centrum; (3) articular surfaces of eo lateral to bo, forming a double occipital condyle; (4) fused bo and eo form a circular recess for the notochord – bony contact with the atlas only on the periphery of this structure; (5) bo but not eo in contact with atlas centrum; (6) broad recess formed by bo and eo; (7) hemispherical occipital condyle that forms a ball-and-socket joint with the multipartite atlas.

BRAIN CASE

40. Relationship between bo and eo: (0) no clear suture between bo and eo, complex separated from the otic capsule dorsally by lateral otic fissure; (1) clear sutural attachment between bo and eo, lateral otic fissure not evident; (2) secondary incorporation between bo, eo, and otic capsule into a consolidated otic–occipital unit.

41. Sphenethmoid region: (0) continuity dorsally and laterally between otic–occipital and sphenethmoid region; (1) wide separation between otic–occipital and sphenethmoid elements; (2) area of pleurosphenoid extends from exit of trigeminal nerve to sphenethmoid.

EAR OSSICLES

42. Distal end of stapes: (0) with large, spatulate portion in contact with the quadrate ramus of pt; (1) with long slender stem directed towards an area assumed or known to have been occupied by a tympanic membrane; (2) with short stem directed towards quadrate bone; (3) fenestra ovalis opens ventrally, and stapes may have no stem at all; (4) with short stem directed towards squamosal.

43. Stapes with stapedial foramen: (0) yes; (1) no.

44. Operculum: (0) stapes the only ear ossicle; (1) stapes accompanied by operculum; (2) accompanied by accessory ossicle above stem of stapes.

HYOID

45. Bony elements of hyoid appartus: (0) bb, hh, ch; (1) little if any ossification; (2)? ch; (3) hb and cb; (4) bb, two hh, ch, two hb, four cb; (5) plate-like cb; (6) ch, hb, cb; (7) h, ch, four hb, four cb; (8)? + cb, eb; (9) cb; (10) bb, hinged ch, fused hb blade, four cb; (11) bb, ch, four cb.

46. Pharyngeal denticles: (0) attached to thin bony plates associated with cb; (1) four rows not attached to plates; (2) six rows interdigitated with one another.

47. Function of hyoid apparatus: (0) no evidence of use for tongue protrusion in terrestrial adults; (1) tongue protrusion involving the basibranchial bone, first hypobranchial bone and ceratohyal bones; (2) hyoid plate with parathyoid and posteromedial processes serves for support of protrudable tongue.

VERTEBRAL COLUMN

48. Number of trunk vertebrae: (0) 21–30; (1) 31–40; (2) 41–50; (3) 51–70; (4) 71 and greater; (5) 11–20; (6) 1–10.
49. Neural arch fusion: (0) neural arches weakly attached medially in trunk region; (1) no medial fusion between neural arches; (2) medial fusion of all postaxial neural arches; (3) deep division between paired neural spines of trunk.
50. Neural arch articulation: (0) neural arches loosely articulated with intercentra; (1) neural arches articulated with pleurocentra; (2) neural arches articulated with both intercentra and pleurocentra; (3) neural arches fused to pleurocentra in adults.
51. Supraneural canals: (0) present; (1) absent.
52. Ossification of pleurocentra: (0) not ossified in the first seven presacral vertebrae or the posterior portion of the tail; (1) ossified throughout trunk; (2) no pleurocentrum ossified.
53. Pleurocentra shape: (0) paired; (1) fused ventromedially into a crescent or horseshoe shape; (2) cylindrical.
54. Intercentra: (0) paired throughout trunk except for atlas and sacral vertebrae, where they are fused medially; (1) fused ventromedially throughout trunk; (2) cylindrical; (3) lost.
55. Atlas–axis complex: (0) paired proatlas oberved or assumed on the basis of paired prezygopophyses on atlas; (1) fused medially; (2) lost.
56. Atlas arches: (0) paired; (1) fused medially.
57. Axis arches: (0) paired; (1) fused medially.
58. Articulation between atlas and axis centrum (0) not specialized relative to those of more posterior vertebrae; (1) posterior surface of atlas centrum is subhemispherical in outline and deeply concave to fit over the specialized axis centrum.
59. Number of sacral vertebrae: (0) one; (1) two; (2) none.
60. Number of caudal vertebrae: (0) 31–40; (1) 41–50; (2) 51–60; (3) 21–30; (4) 11–20; (5) 0–10; (6) area of caudal vertebrae forms urostyle.

PECTORAL GIRDLE AND FORELIMB

61. Anocleithrum: (0) present; (1) absent.
62. Cleithrum: (0) fused to scapula with postbranchial lamina; (1) a separate ossification with postbranchial lamina; (2) a separate ossification without postbranchial lamina; (3) bony element forming the leading edge of the suprascapula without postbranchial lamina; (4) lost.
63. Clavicle: (0) present; (1) absent.
64. Interclavicle: (0) present; (1) absent.
65. Scapula and coracoid ossification: (0) scapulocoracoid ossified as a single unit; (1) not co-ossified in adult; (2) neither ossified.
66. Scapula and coracoid openings: (0) numerous openings in variable positions, not readily homologized with those of later tetrapods; (1) two openings, the supraglenoid foramen and supracoracoid foramen; (2) supraglenoid foramen and two coracoid foramina; (3) two coracoid foramina, but no supraglenoid foramen; (4) suprascapular foramen only; (5) supraglenoid foramen elongated to form scapular cleft; (6) a single coracoid foramen only; (7) does not apply (scapulocoracoid bone not ossified).
67. Glenoid articulation: (0) strap-shaped, slightly helical (screw-shaped); (1) subcircular and evenly concave to articulate with hemispherical humeral head; (2) does not apply (glenoid not ossified).
68. Medioventral endochondral elements of the shoulder girdle: (0) none; (1) a single median element that articulates with base of scapulocoracoid; (2) a series of ventromedial elements (omosternum, epicoracoid and sternum) that serve to resist the force of striking the ground.

HUMERUS

69. Shaft: (0) humerus flattened, L-shaped bone with no evidence of shaft; (1) proximal and distal areas of expansion separated by a marked constriction presaging a distinct shaft; (2) substantial shaft; (3) does not apply (no humerus).
70. Articulating surface for articulation with scapulocoracoid: (0) surface covering the entire proximal end of bone; where well ossified, it has a spiral pattern; (1) surface in the form of a hemispherical condyle; (2) does not apply.
71. Articulation surfaces for radius and ulna: (0) separated and directed ventrolaterally; (1) adjacent and facing ventrally; (2) hemispherical radial condyle; (3) does not apply.
72. Torsion angle between the planes of the proximal and distal areas of expansion: (0) roughly 30°; (1) 40° to 50°; (2) approximately 90°; (3) does not apply.
73. Foramina: (0) entepicondylar and ectepicondylar canals, and two other foramina designated as C and D; (1) only entepicondylar foramen; (2)

entepicondylar foramen and foramen C; (3) loss of all foramina; (4) does not apply.

74. Ectepicondylar ridge: (0) present dorsally; (1) lost; (2) does not apply.

75. Entepicondylar process: (0) extensive, posteriorly directed; (1) lost; (2) does not apply.

76. Supinator process: (0) not clearly distinguished from deltoid chest; (1) distinct; (2) absent; (3) does not apply.

77. Latissimus dorsi process: (0) present; (1) absent; (2) does not apply.

LOWER FORELIMB

78. Ulna size: (0) shorter than radius; (1) equal in length to or longer than radius; (2) does not apply.

79. Olecranon on ulna: (0) lacking; (1) present; (2) does not apply.

80. Flange along shaft: (0) extensive; (1) absent; (2) does not apply.

81. Ulna and radius fused: (0) no; (1) yes; (2) does not apply.

82. Ventral radial crest: (0) present; (1) absent; (2) does not apply.

83. Ossified carpal bones: (0) intermedium only; (1) three ossified carpals, including first and second distal; (2) radiale, intermedium, ulnare, three or four centralia, four distals; (3) two proximals, three distals; (4) three proximals, one centrale, four or five distals; (5) pisiform, intermedium, radilae, ulnare, two or three centralia, five distals; (6) three proximals, three centralia, five distals; (7) three proximals, three centralia, three distals (first and second fused into basale commune); (8) tridiate, intermedium, ulnares, four centralia, four distals, one prepollex; (9) does not apply.

84. Ossification of the intermedium surface: (0) perichondrally; (1) only endochondrally; (2) does not apply.

85. Number of metacarpals and digits: (0) eight; (1) five; (2) four; (3) does not apply.

86. Manus phalangeal formula: (0) 3,3,3,4,4,4,4,3; (1) 2,3,4,5,3–4; (2) 1,2,2,3,2; (3) 2,2,3,3; (4) 2,3,3,3; (5) 3,?3,3,2; (6) 2,3,4,3,2; (7) 2,3,3,2; (8) does not apply.

PELVIC GIRDLE

87. Sutures: (0) co-ossified ilium, ischium and pubis, showing little if any trace of sutures; (1) distinct sutural contacts between ilium, ischium, and pubis (if present); (2) does not apply.

88. Time of ossification of pubis: (0) at the same time as the ilium and ischium; (1) slow to ossify or lost altogether; (2) does not apply.

89. Ilium shape: (0) clearly bifurcate dorsal and posterior processes; (1) only a single process, dorsally or posteriorly angled; (2) angled anterodorsally; (3) does not apply.

90. Position of acetabulum relative to base of iliac blades: (0) anterior; (1) posterior; (2) does not apply.

91. Unfinished surface of acetabulum: (0) extends anteriorly across much of pubis; (1) does not extend anteriorly (2) does not apply.

92. Puboischiadic plate: (0) extends the length of several centra; (1) greatly shortened; (2) does not apply.

93. Obturator canals on puboischiadic plate: (0) more than one; (1) only a single foramen; (2) no foramen; (3) does not apply.

FEMUR

94. Articulation with the acetabulum: (0) broadly curving surface extending over the entire proximal end of the bone; (1) concentrated on hemispherical condyle; (2) does not apply.

95. Plane of proximal articulating surface to the plane of the surface for articulation with the tibia and fibula: (0) at 60° to 90°; (1) in the same plane; (2) proximal surface not planar; (3) does not apply.

96. Intertrochanteric fossa: (0) large and facing anteriorly; (1) faces primarily ventrally; (2) lost; (3) does not apply.

97. Ventral ridge system: (0) proximally located internal trochanter, elongated fourth trochanter along the adductor blade [as in Coates (1996)] occupying ~50% of the length of the femur, succeeded by the adductor crest, extending to nearly the end of the shaft; (1) as in (0), but adductor blade and crest much reduced; (2) as in (0), but adductor blade much shortened, and adductor crest extended for much of the distal half of the shaft; (3) as in (0), but adductor blade extends to no more than half the length of the shaft; (4) ventral ridge system very poorly ossified; (5) diagonal ridge running the length of the shaft; (6) loss of adductor ridge system; (7) as in (0), but with internal trochanter merged with short adductor crest; (8) as in (3), but distinction between blade and crest lost; (9) as in (3), but with loss of fourth trochanter; (A) does not apply.

TIBIA

98. Size: (0) tibia longer than fibula; (1) fibula as long or longer than tibia; (2) does not apply.

99. Lateral margin of tibia: (0) straight and overlapped by fibula; (1) sharply concave; (2) gently concave; (3) does not apply.

100. Tibia shaft: (0) tibia nearly flat, with little or no shaft between widened proximal and distal extremities; (1) clearly apparent shaft; (2) does not apply.
101. Torsion between extremities: (0) no; (1) yes; (2) does not apply.
102. Cnemial crest along anterodorsal surface: (0) present; (1) absent; (2) does not apply.
103. Tibia and fibula: (0) ossified separately; (1) fused; (2) does not apply.

FIBULA

104. Shape: (0) slight concavity of medial edge of fibula and little or no concavity of lateral edge between expanded proximal and distal articulating surfaces; (1) narrow shaft between articulating surfaces; (2) very elongate shaft with little expansion of articulating surfaces; (3) does not apply.
105. Axial torsion of fibula: (0) ~25°; (1) ~0°; (2) ~45°; (3) 70–90°; (4) does not apply.

TARSUS

106. Proximal row of tarsals includes: (0) short, rectangular or rounded fibulare, intermedium, and tibiale; (1) tibiale and fibulare elongate; (2) fibulare (calcaneum) plus fused tibiale, intermedium and proximal centrale forming astragalus; (3) does not apply.
107. Number of centralia: (0) none recognized; (1) four; (2) three; (3) two independent; (4) one large centrale; (5) does not apply.
108. Distal tarsals: (0) five; (1) fusion of distal tarsals 1 and 2 to form basale commune; (2) three distal tarsals and support for prehallux; (3) does not apply.

METATARSALS AND DIGITS

109. Number of metatarsals and digits: (0) eight; (1) five; (2) three; (3) does not apply.
110. Phalangeal formula: (0) 1,2,3,3,3,3,3,2; (1) 2,3,4,4,>2; (2) 2,3,4,5,5; (3) 2,2,3,4,?; (4) 2,2,3,4,3; (5) 2,3,3,3,2; (6) 2,3,4,5,3; (7) 2,3,4,4,2; (8) does not apply.

LARVAE AND DEVELOPMENT

111. Larval stages: (0) lacking distinguishable larvae as identified by the presence of external gills and/or a period of metamorphosis between juveniles and adults; (1) distinct larval stage recognized by external gills and/or morphological changes leading from aquatic juvenile to terrestrial adult, such as loss of caudal fins; (2) knowledge of juveniles lacking external gills or metamorphic changes; (3) lack of evidence for any aquatic stage.
112. Larval feeding: (0) probable use of tooth plate attached to ceratobranchials to strain, crush, and hold prey in oropharyngeal cavity; (1) gap-and-suck feeding involving use of interdigitating gill rakers, not attached to bony plates, to block intake of water through gill openings; (2) suspension feeding on particulate matter and finely comminutated plants; (3) does not apply.
113. Larval pumping system: (0) intermittent posteroventral movement of hyoid apparatus to expand oropharyngeal opening, as judged by configuration of hyoid elements; (1) continuing dorsoventral pumping of ceratohyals; (2) does not apply.
114. Larval locomotion: (0) fish-like undulation of trunk and tail; (1) whip-like action of tail that lacks bony support; (2) does not apply.
115. Pattern of skull ossification: (0) essentially simultaneous ossification of dermal bones of skull roof, palate, and lower jaw as seen in tiny juveniles; (1) sequential ossification – tooth-bearing elements of the palate, upper and lower jaws, and sq–f, p, eo; circumorbital bones; (2) sequential ossification – frontoparietal, eo, ps–pm, m, n–v, pt, sq; (3) sequential ossification – m, f, pal, ps–l, v, eo–ps.
116. Ossification of vertebrae: (0) arches before centra; (1) centra before or simultaneous with centra.
117. Ossification of distal limb elements and autopodium: (0) from anterior to posterior; (1) from posterior to anterior.
118. Adult lifestyle: (0) facultatively terrestrial; (1) aquatic.

ABBREVIATIONS

a, angular; ansp, anguloslenial; art, articular; bb, basibranchial; bo, basioccipital; bs, basisphenoid; cb, ceratobranchial; ch, ceratohyal; co, coronoid; d, dentary; eb, epibranchial; ect, ectopterygoid; eo, exoccipital; f, frontal; hb, hypobranchial; hh, hypohyal; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; mr, medial rostral; n, nasal; p, parietal; pa, pseudoangular; pd, pseudodentary; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; preart, prearticular; preo, preoperculum; prf, prefrontal; pro, prootic; ps, parasphenoid; psyp, parasymphyseal plate; pt, pterygoid; qj, quadratojugal; sa, surrangular; so, supraoccipital; sph, sphenethmoid; spl, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer.

Appendix 4. Data Matrix

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                   1   1111111112  2222222223  3333333334  4444444445  5555555556
Taxon     1234567890  1234567890  1234567890  1234567890  1234567890  1234567890

Acanthostega        0000000000  0000000010  0000100000  0000010000  00000?0000  0000000000
Whatcheeridae       0002101111  0000000020  0010001000  000011001?  ????1?0000  010120100?
Crassigyrinus       0003001111  1000000130  0010000000  00??0?0?11  ????1?0010  ?2?100000?
Anthracosauroidea   0203101110  0000000131  0010201100  0001100021  00001?0121  0111001001
Baphetidae          101?200?12  0000000130  0010001000  0000100020  ?0?02?0?20  ???100?00?
Caerorhachis        1002100??0  00?0000230  0010001000  00????????  ??????0121  011101100?
Colosteidae         0311000210  0010000130  0011001000  0000110121  1000300221  0101001000
Basal temnospondyls 102?200110  0020000230  1010001100  0000101221  11004000?0  ?111001000
Branchiosauridae    2221210120  0021010240  1010411100  000?101?21  1100420000  ?001??000
Amphibamidae        1221021?0   0020000240  1010411100  0000101231  1100110520  ?111??1004
Rhynchonkos         2431020110  1010000251  0010501110  0011121231  2202??0123  112121101?
Acherontiscus       243?0103?0  1?100001??  ??13?0????  ?0????????  ????5?01?2  ?122???026
Aïstopoda           143?110?30  1010001240  0010701121  0000000240  ?3101?0423  1123111026
Adelospondyli       1??1010?40  1000000262  00109011?0  000013??51  ????6?0422  0123201026
Lysorophia          2433322453  1110012271  0110601131  0010101261  12107?0331  1123200004
Microsauria         233?210110  0010000251  0010301100  0010111231  22028?0023  1121211001
Nectridea           134?210410  0010000241  0010501121  0000101231  ????1?0523  1123211002
Early amniotes      1322210160  0010000241  0012A01111  0010120271  12009?0023  1121101012
Albanerpetontidae   2232222573  0110002282  ??10?01132  0001032032  ????1?0023  1123211103
Urodela             2341222183  0111012292  1110811123  1001132131  1411421523  1123211004
Triadobatrachidae   134?312?93  00200022A2  111????1??  ?101?3223?  111???2523  112?211005
Anura               113?322693  01201022A2  1110811134  1101132231  1111A?2623  1123211005
Caecilia            24410106A0  11110102B1  0010511135  0001033132  2201B?0223  1121211014


                                                        1   1111111111  11111111
          6666666667  7777777778  8888888889  9999999990  0000000001  11111111
Taxon     1234567890  1234567890  1234567890  1234567890  1234567890  12345678

Acanthostega        0000000000  0000000000  0000000000  0000000000  0000000000  ??0????0
Whatcheeridae       110001?000  0010000111  00????0001  0000110010  00011???11  ???????0
Crassigyrinus       120027?000  0000000011  0?????1101  ?0?0111121  00012?????  ???????1
Anthracosauroidea   0200020000  1110000111  011?110001  1000112110  1001001012  1???00?0
Baphetidae          11000??000  0010000111  00????1001  00?????120  0001???13   ?????0?0
Caerorhachis        1?00???0??  ????????11  0?????0001  00?0113?21  0101?0101?  ???????0
Colosteidae         1100030000  0020000111  00??121001  1010113121  1001301013  ?0?????0
Basal temnospondyls 1200010010  1110021111  0121231011  1010113111  ??01201014  10000?0
Branchiosauridae    1200??0020  113?121111  01??231111  ?0?0114021  ??010??014  11001001
Amphibamidae        1200020020  2231121111  0121231111  1010115021  ?10121?014  10?000?0
Rhynchonkos         1401???020  1231121111  0?31241011  10?0116121  110120201?  ???????0
Acherontiscus       1400272032  3342232222  2292382232  223233A232  3223435338  ???????1
Aïstopoda           1200272032  3342232222  2292382232  223233A232  3223435338  2??201?1
Adelospondyli       1200272032  3342232222  2292382232  223233A232  3223435338  2??201?1
Lysorophia          12000??020  ?031121011  01??25111?  ???0007121  11??0?0015  2??201?1
Microsauria         1200020010  ?211121111  0141241001  1010113110  0001302016  2??200?0
Nectridea           12000??000  ?01?001111  0141161011  1020112110  00012??017  2??201?0
Early amniotes      1200020020  2210011111  0151110011  1010118121  1001223016  3322?110
Albanerpetontidae   14111??020  2231121111  0161271011  10?011?121  ??01201011  ???????0
Urodela             1411040121  2231121111  0171271111  1020119121  1001202114  11001001
Triadobatrachidae   1201051021  2231121111  01?1??1121  1021226021  ?10121????  2?1????0
Anura               1301151221  2231121111  1181231121  1121226131  0112314214  12112010
Caecilia            1411060020  2130021111  01????????  ???1016121  ?10120??2?  1?003??0
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