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Ontogenetic evidence for the Paleozoic ancestry of salamanders

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SUMMARY The phylogenetic positions of frogs, salamanders, and caecilians have been difficult to establish. Data matrices based primarily on Paleozoic taxa support a monophyletic origin of all Lissamphibia but have resulted in widely divergent hypotheses of the nature of their common ancestor. Analysis that concentrates on the character states of the stem taxa of the extant orders, in contrast, suggests a polyphyletic origin from divergent Paleozoic clades. Comparison of patterns of larval development in Paleozoic and modern amphibians provides a means to test previous phylogenies based primarily on adult characteristics. This proves to be highly informative in the case of the origin of salamanders. Putative ancestors of salamanders are recognized from the Permo-Carboniferous boundary of Germany on the basis of ontogenetic changes observed in fossil remains of larval growth series. The entire developmental sequence from hatching to metamorphosis is revealed in an assemblage of over 600 specimens from a single locality, all belonging to the genus *Apateon. Apateon* forms the most speciose genus of the neotenic temnospondyl family Branchiosauridae. The sequence of ossification of individual bones and the changing configuration of the skull closely parallel those observed in the development of primitive living salamanders. These fossils provide a model of how derived features of the salamander skull may have evolved in the context of feeding specializations that appeared in early larval stages of members of the Branchiosauridae. Larvae of *Apateon* share many unique derived characters with salamanders of the families Hynobiidae, Salamandridae, and Ambystomatidae, which have not been recognized in any other group of Paleozoic amphibians.

INTRODUCTION

The origin and interrelationships of frogs, salamanders, and caecilians (collectively termed the Lissamphibia) remain among the major unresolved problems in the phylogeny of vertebrates. As recently summarized by Laurin (2002) and Schoch and Milner (in press), three divergent hypotheses are currently being debated. First, many authors believe that extant amphibians form a monophyletic clade that diverged from a single group of Paleozoic amphibians, the temnospondyls (Gauthier et al. 1988; Bolt 1991; Trueb and Cloutier 1991; Milner 1993; Ahlberg and Milner 1994; Schoch 1995). Second, in sharp contrast, Laurin and Reisz (1997) and Laurin (1998) present data supporting a common ancestry from a very distinct lineage, the lysorophid lepospondyls. Finally, others have argued that the modern amphibians are diphyletic, with the caecilians allied with lepospondyls, the frogs with temnospondyls, and the salamanders suggested as having affinities with either the lepospondyls (Carroll and Holmes 1980; Carroll et al. 1999) or with temnospondyls (Anderson 2001; Carroll et al. in press).

PHYLOGENETIC PROBLEMS AND APPROACHES

An underlying reason for the uncertainty regarding the relationships of extant amphibians is the insufficient knowledge of the fossil record during two important periods in the history of tetrapods. Specific to the modern taxa are gaps lasting from 80 to 100 million years that separate the oldest known representatives of the extant orders from any plausible ancestors in the late Paleozoic (Carroll 2001a). The oldest known fossils of stemgroups frogs (Salientia), caecilians (Gymnophiona), and salamanders (Caudata), dating from the Lower to Upper Jurassic, are essentially similar to their living descendants, and no fossils are known from the Paleozoic that are obvious ancestors (Jenkins and Walsh 1993; Jenkins and Shubin 1998; Gao and Shubin 2001).

Equally troublesome in establishing an informative phylogeny of amphibians is an approximately 30 million year gap at the base of the Carboniferous, during which time the initial radiation of the later Paleozoic and Mesozoic tetrapods is presumed to have occurred (Coates and Clack 1995; Clack 2002). As a result of this hiatus, very few data are available to document the specific interrelationships of the major lineages of land vertebrates (Carroll 2002). Recent phylogenetic analyses by Clack (2002) and Clack and Ahlberg (in press), based on newly recognized species from the Lower Carboniferous, show very poor resolution of sister-group relationships among Paleozoic tetrapods. Tetrapods from the Upper Devonian, Lower Carboniferous, and Upper Carboniferous appear as a succession of radiations, each of which are characterized by unresolved polytomies (Clack and Ahlberg in press).

Most of the taxa studied by Clack belong to an assemblage long referred to as "labyrinthodonts," which are assumed to include the stem taxa of all other tetrapods. These animals are generally large, up to a meter or more in length, with proportionately large skulls and a skeletal anatomy generally similar to that of the sarcopterygian sister-group of tetrapods, the tristichopterids (characterized by *Eusthenopteron*) and panderichthyids (Ahlberg and Johanson 1998). Unfortunately, the scarcity of fossils from the Lower Carboniferous makes it difficult to determine the specific interrelationships among the several orders included within the labyrinthodonts or between any of these and more derived tetrapods. Here, the term labyrinthodonts is used in reference to the eight tetrapod taxa known from the Upper Devonian, of which the best known are *Acanthostega* and *Ichthyostega*; an assemblage of archaic Carboniferous families, the Whatcheeriidae, Crassigyrinidae, and Baphetidae (Clack 2002); and two major clades that dominated the Upper Carboniferous and Lower Permian and continue into the lower Mesozoic, the temnospondyls (Holmes 2000) and anthracosaurs (Smithson 2000) (which may have a sister-group relationship with the Seymouriamorpha [Laurin 2000]). Among the labyrinthodonts, only the temnospondyls are currently considered as plausible ancestors of some or all of the Lissamphibia.

The other major assemblage of Paleozoic amphibians are the lepospondyls, which can be differentiated from labyrinthodonts by a host of skeletal characters, many of which can be associated with their much smaller body size. Lepospondyl skulls are generally less than 4 cm in length and show a diversity of specializations (Carroll 2000a). All lepospondyls have spool-shaped vertebral centra in contrast with the multipartite vertebrae of the labyrinthodonts. Six lineages of lepospondyls are recognized, ranging in time of first appearance from Lower to Upper Carboniferous, none of which can be reliably linked to any of the labyrinthodont lineages by convincing synapomorphies. Among this assemblage, the microsaurs (Carroll et al. 1998) and the Lysorophia (Wellstead 1998) are currently considered as possible sister-taxa of one or more of the lissamphibian orders.

The phylogenetic position of the lepospondyls relative to the temnospondyls is especially critical because members of these groups are most frequently cited as possible sister-taxa of one or all of the lissamphibian orders. In Clack's (2002) cladogram of primitive tetrapods, lepospondyls appear at two possible positions, dependent on whether the crown group is located at one or another node.

The radical differences in the hypothesized sister-taxa of the modern amphibian orders among Paleozoic tetrapods suggest limits to the effective use of particular approaches to phylogenetic analysis. This is not to suggest that phylogenetic analysis as elaborated by Hennig (1966) is inherently flawed (in fact, it is an extremely effective means of establishing relationships in most instances), but that there may be limits to the amount of missing data that can be accommodated (especially when there are extensive periods during which major morphological changes must have occurred but for which there are no data from the fossil record).

In addition, this particular problem has been approached in a manner that may have made it especially difficult to solve using routine methods of phylogenetic analysis. All the recent attempts to establish the ancestry of lissamphibians have concentrated primarily on Paleozoic taxa, with very little data incorported from the modern orders. This is especially evident in the analysis by Laurin and Reisz (1997), in which so few characters of frogs, salamanders, and caecilians were included that not even the sequence of their divergence from one another could be established. Most characters in their data matrix pertain to Paleozoic taxa but are of little or no help in solving the problems of lissamphibian ancestry. The number of steps that define the resulting cladogram are dominated by dichotomies involving Paleozoic taxa, only a small percentage of which are significant to the relationships of the lissamphibians. Because only a few nodes determine the position of the lissamphibians, they are very sensitive to changes in other parts of the tree.

On the other hand, a much more direct approach to this problem would be to concentrate on derived characters that distinguish each of the three extant orders and attempt to identify some of them in Paleozoic taxa. Instead of trying to solve a myriad of phylogenetic problems involving the entirety of tetrapod radiation in the Paleozoic, we can begin with the well-established monophyly of each of the extant amphibian orders. This leaves only three key nodes to establish: the sister-group relationships of frogs, salamanders, and caecilians with one another and with one Paleozoic lineage (if the Lissamphibia is a truly monophyletic assemblage) or with two or three groups of archaic amphibians (if the lissamphibians are polyphyletic).

The skeletal apomorphies of each of the modern groups have been listed by many authors (Carroll and Currie 1975; Carroll and Holmes 1980; Milner 1988, 1993; Trueb and Cloutier 1991; Carroll et al. in press). We need only look for the initiation of those characters among the Paleozoic forms. This was the approach taken by Parsons and Williams (1963) in their effort to identify the common ancestry of the Lissamphibia. They determined the common features of the modern orders (concentrating on frogs and salamanders, with less consideration of caecilians) and looked for such a morphotype in the Paleozoic, without success. This suggests that most of the defining characters of the modern orders evolved subsequent to the Paleozoic. We now have additional knowledge of early Mesozoic forms that makes it possible to begin assembling a sequence of nested synapomorphies leading toward the modern crown groups. In addition we can make use of considerable ontogenetic information from Paleozoic forms that was not considered in previous analyses.

PLESIOMORPHIC SISTER-TAXA OF THE EXTANT CROWN GROUPS

Recent analyses of the fossil record of the modern orders have revealed numerous synapomorphies that are expressed in the most primitive known members of each: for anurans (Sanchiz 1998; Gao and Wang 2001), for urodeles (Milner 2000; Gao and Shubin 2001), and for caecilians (Carroll 2000b; Carroll et al. in press).

Only two genera are known that are plausible plesions along the stem lineage leading to crown-group anurans, the Lower Triassic *Triadobatrachus* (known from a single but nearly complete skeleton) and *Czatkobatrachus* (known from numerous disarticulated elements) (Roček and Rage 2000). *Triadobatrachus* shares the following synapomorphies with anurans: fused frontoparietals, skull wider than long, deeply embayed squamosal notch, dentary edentulous, iliac blade elongate and anteriorly directed. However, this genus is primitive in retaining caudal vertebrae and conservative limb proportions. Small temnospondyls from the Carboniferous and Permian share with *Triadobatrachus* and anurans the deep embayment of the squamosal and the slender stapes, as well as very large interpterygoid vacuities. The Lower Permian *Doleserpeton* is unique among Lower Permian temnospondyls in having a frog-like unipartite, bicondylar atlas, and cylindrical pleurocentra fused to the neural arches (Bolt 1969).

The oldest known caecilian, *Eocaecilia*, from the Lower Jurassic, shares numerous synapomorphies of the cranium and lower jaws with primitive living caecilians but retains trunk intercentra and vestigial front and rear limbs, as well as most of the dermal bones of the skull roof common to Paleozoic amphibians, in strong contrast with frogs and salamanders (Jenkins and Walsh 1993; Carroll 2000b; Carroll et al. in press). The only Paleozoic genus that shares synapomorphies of the skull, vertebrae, and limbs with *Eocaecilia* is the Lower Permian lepospondyl microsaur *Rhynchonkos*.

Sister-taxa of the urodeles, but included in the more encompassing Caudata, include *Karaurus*, known from a complete skeleton from the Upper Jurassic (Ivachnenko 1978), and several genera from the Middle Jurassic of Great Britain (Evans and Waldman 1996) and Kirghizstan (Nessov 1988), all reviewed by Milner (2000). *Karaurus* and *Kokartus* show extensive dermal sculpturing on the dorsal portion of the squamosal, indicating that the adductor mandibulae internus superficialis did not yet extend over the otic capsule, as is the case in crown-group salamanders. This supports earlier suggestions that the definitive form of the orbitotemporal opening was achieved separately in frogs and salamanders (Carroll and Holmes 1980). Caudate atlas vertebrae from the Middle Jurassic also lack perforations for spinal nerve openings, which are found in all crown-group salamanders. Although somewhat more primitive than extant taxa, these Jurassic salamanders show no specific synapomorphies with adults of particular Paleozoic tetrapods. However, extensive, phylogenetically significant information can be gained through study of larval stages of both extant and Paleozoic amphibians.

EVIDENCE FROM ONTOGENY

Amphibians are unique among terrestrial vertebrates in having biphasic life histories in which there is commonly a free living larva showing early stages in development, before the elaboration of the adult anatomy. Fossil larvae are common in many Carboniferous and Permian localities, but surprisingly, little use has been made of changes that occur during ontogeny in the major phylogenetic studies of amphibians.

Although larval stages are common to the primitive members of all three extant orders, only two groups of Paleozoic amphibians are known to have had larval forms, distinguished by external gills and a long period of aquatic growth and development. There are the temnospondyls and the seymouriamorphs, the larvae of which are referred to collectively as branchiosaurs (Boy and Sues 2000). No gilled larvae are known of anthracosaurs, but immature specimens show a low degree of ossification, suggesting an extensive period of aquatic development.

The best known sister-taxon of tetrapods, *Eusthenopteron*, has recently been shown to have had direct development, with the smallest specimens, approximately 3 cm in length, having the same proportions as the adults (which reached a meter or more in length) and no trace of external gills (Cote et al. 2002).

The origin of gilled larvae among temnospondyls and anthracosaurs was presumably associated with their entrance into closed bodies of fresh water—ponds and coal swamps—where oxygen may have been severely depleted as a result of the large amount of rotting plant material, which was to give rise to the coal deposits within which the remains of many Carboniferous amphibians are found. Prolonged development in the water was necessary for most temnospondyls because of their large adult size and necessity of a long period of growth after hatching from tiny anamniotic eggs.

Lepospondyls show an entirely different pattern of development (Carroll 2000a, Carroll et al. in press). All the Carboniferous genera are much smaller than labyrinthodonts, and even the smallest known specimens, approximately 2 cm in skull–trunk length, were almost fully ossified and of essentially adult form. None showed any evidence of external gills, although many are known from deposits in which gilled larvae of temnospondyls are known. Two factors obviated the necessity for external gills: small body size and a high surface-to-volume ratio facilitated cutaneous respiration, and presumably short periods of development and growth enabled them to leave the water more quickly than the adults of most temnospondyls. It should be noted, however, that some genera (e.g., *Microbrachis*) were apparently neotenic, to judge by the presence of cranial sulci in the largest specimens.

The absence of recognizable larval stages among lepospondyls, first emphasized by Baird (1965), makes them improbable ancestors of frogs and salamanders, among whom nearly all the primitive members have gilled larvae. Primitive caecilians have distinct larval stages, but they loose the gills on hatching from the egg, so that they would be unlikely to be preserved in the fossils. On the other hand, it is possible to make comparisons between larvae of both frogs and salamanders with those of temnospondyls. Similarities of vertebral development in frogs and the branchiosaur larvae of temnospondyls provide strong evidence for their affinities (Carroll et al. 1999). Carroll (2001b) also pointed out detailed similarities of the hyoid apparatus and its probable function between ambystomatid salamanders and a particular group of branchiosaurs, the temnospondyl family Branchiosauridae. Much more striking similarities of development are evident in the skull. These observations are based on hundreds of specimens discovered at a locality near Kusel, Saar-Nahe Basin in southwestern Germany, including not only adults but extensive growth series (Schoch 1992).

This locality dates from the Lower Rotliegend, close to the Permo-Carboniferous boundary, between 290 and 300 million years ago (Boy and Fichter 1982). A recent dating of tuffs immediately below the fossiliferous layers yielded an age of 297 million years, which would fall within the uppermost Carboniferous (Königer et al. 2002). The exquisitely preserved larvae provide detailed information on early development within the temnospondyl family Branchiosauridae, which Trueb and Cloutier (1991) placed as a sister-taxon of all Lissamphibia on the basis of adult anatomy. These specimens, all belonging to the genus *Apateon*, document a continuous ontogenetic sequence from hatching to metamorphosis that demonstrates many unique derived characters comparable with those of primitive families of modern salamanders.

Two species of *Apateon*, *A. caducus* and *A. pedestris*, are present in this locality. Both are well known from other sites (Boy and Sues 2000) and are distinguished by differences in skull proportions and adult body size (Schoch 1992). The two species show similar sequences of ossification of the cranial bones, although ossification is initiated earlier in *A. pedestris*. *Apateon caducus* shows a much more continuous growth sequence and therefore serves as the primary example of this process.

One might question the likelihood of two closely related species of a single genus living in the same locality, but this is not uncommon among modern salamanders (Fraser 1976; Griffiths 1996, pp. 91–94). Although collected from a single small deposit, they may actually have occupied the area at different times of the year or in different years or may have been preserved together even if they had lived in different parts of the water body or fed on different prey. The latter possibility is supported by the fact that adult *A. caducus* had much larger and stronger teeth than *A. pedestris* and achieved a firm consolidation of cheek and maxilla much earlier in ontogeny (Schoch 1995).

ONTOGENETIC CHANGES IN THE SKULL OF PALEOZOIC BRANCHIOSAURIDS AND SALAMANDERS

Two highly distinct patterns of skull development can be recognized among Paleozoic temnospondyls. In most, all the dermal bones of the skull roof ossify very early in ontogeny, well before the limbs and vertebrae, forming a closely integrated skull roof (Fig. 1). The primitive nature of this condition is demonstrated by its occurrence in the immediate sister-group of land vertebrates, the tristichopterid fish (Ahlberg and Johanson 1998), represented by *Eusthenopteron* (Schultze 1984). In marked contrast, members of the family Branchiosauridae, typified by *Apateon,* ossify the bones of the skull over a considerable period of time (to judge by the corresponding increase in body size), resulting in marked changes in cranial morphology (Fig. 2). The specific sequence of bone development (Table 1) and the resulting configuration of the skull in early larvae of *Apateon* are very similar to those of the larvae of primitive living salamanders (Figs. 2 and 3) (Erdmann 1933).

In both modern salamanders and *Apateon*, ossification of the skull begins with palatal and marginal tooth-bearing elements, typically parasphenoid, pterygoid, palatine, vomer, premaxilla, maxilla, and lower jaw. These are followed by the midline bones of the skull roof and later by the circumorbital bones. The most striking feature of *Apateon* is the early elaboration of the squamosal (relatively 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 recently described basal salamanders from the

Upper Jurassic and Lower Cretaceous of China (Carroll 2001a; Gao and Shubin 2001). 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 and the basipterygoid process of the pterygoid 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, which would have allowed the oropharyngeal chamber to expand laterally in the course of suction feeding.

The retention of mobile joints between the jaw suspension and the skull roof and base of the braincase in hynobiids (Fig. 2C), ambystomatids, and some salamandrids suggests that expansion of the cheek may be possible in the larvae of living salamanders. In 2000, Deban and Wake stated that early development of larval feeding in salamanders remained completely unstudied. Since then, Deban and 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. The lateral expansion contributed only slightly to the increase in buccal volume.

More mature larvae of branchiosaurids and ambystomatid salamanders also have similarities in the feeding apparatus (Carroll 2001b). Both groups have a large number of narrowly triangular gill rakers (pharyngeal denticles) associated with the ceratobranchials. They are arranged so as to fit together like the teeth of a zipper to close the external gill openings. As shown by Lauder and Schaffer (1985), this helps to maintain an effective vacuum during suction feeding in modern salamanders, as was presumably the case for branchiosaurids. The shape and arrangement of the pharyngeal denticles in *Apateon* and other branchiosaurids is derived compared with those of other temnospondyls (Boy and Sues 2000) and their antecedents among the sarcopterygian fish (Jarvik 1980), in which the ceratobranchials support flat oval plates of bone covered with small denticles that could not have served to seal the gill slits.

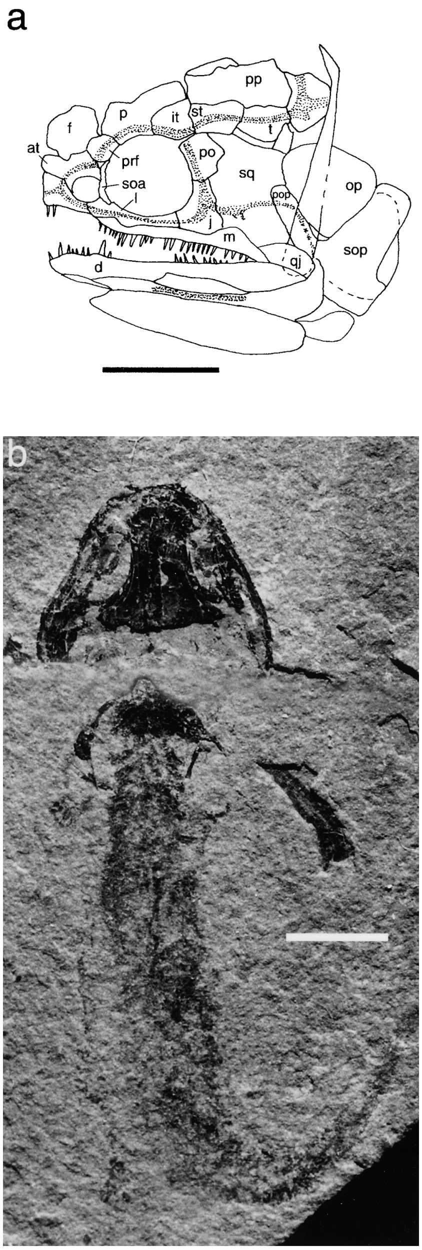


Fig. 1. Pattern of skull roof ossification in the smallest adequately known specimens of the osteolepiform fish *Eusthenopteron* (a) (from Schultze 1984) and the temnospondyl *Micromelerpeton* (b) (specimen no. 51326, Staatl. Museum f. Naturkunde, Stuttgart). At this stage, there is little if any ossification of the endochondral elements of the postcranial skeleton, but the bones forming the skull roof appear to ossify very rapidly and essentially simultaneously. Those surrounding the orbit in *Eusthenopteron* carry the lateral line canals (stippled), which must function soon after hatching. Scales bars, 5 mm. Abbreviations used in this and following figures: a, angular; at, anterior tectal; ba art, basicranial articulation; c, coronoid; car f, carotid foramen; cb, ceratobranchial; d, dentary; ect, ectopterygoid, eo, exoccipital; es, endolymphatic sac, filled with calcium carbonate; f, frontal; it, intertemporal; l, lacrimal; m, maxilla; n, nasal; op, operculum; op-eo, opisthotic-exoccipital; ot, otic capsule; p, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pop, preoperculum; pp, postparietal; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; soa, anterior supraorbital; sop, suboperculum; sph, sphenethmoid; sq, squamosal; sq art, articulation between squamosal and parietal or supratemporal; st, supratemporal; stp, stapes; t, tabular; v, vomer.

Table 1. Sequence of ossification of dermal skull bones in the branchiosaurid *Apateon caducus* and the hynobiid *Ranodon sibiricus*

Apateon caducus	*Ranodon sibiricus*
Parasphenoid, pterygoid	Parasphenoid, pterygoid
Palatine	Question of homology of palatine
Premaxilla, vomer	Premaxilla, vomer
Maxilla	
Squamosal, parietal, frontal	Squamosal, parietal, frontal
Supratemporal, ectopterygoid	(Not ossified in salamanders)
Postparietal	? Posterior parietal
Quadratojugal	Quadratojugal in *Salamandrella*
Nasal	Nasal
	Maxilla
Prefrontal, lacrimal	Prefrontal, lacrimal
Postfrontal	(Not ossified in salamanders)
Tabular	(Not ossified in salamanders)
Postorbital	(Not ossified in salamanders)
Jugal	(Not ossified in salamanders)
Septomaxilla	Septomaxilla

The sequence of ossification of bones common to *Apateon and Ranodon* is very similar, except for the much later ossification of the maxilla in *Ranodon* (data from Schoch 2002a).

During later larval development in *Apateon*, the postfrontal, postorbital, and jugal ossify in succession, while the maxilla extends posteriorly to make contact with the quadratojugal, greatly reducing mobility of the jaw suspension. In the final stage of development, the skull acquires the rugose ornamentation of adult temnospondyls, and the ceratobranchials become ossified or calcified (Fig. 4a). 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. But in large specimens of *Apateon,* the marginal teeth acquire the pedicellate structure of adult salamanders (Fig. 4b).

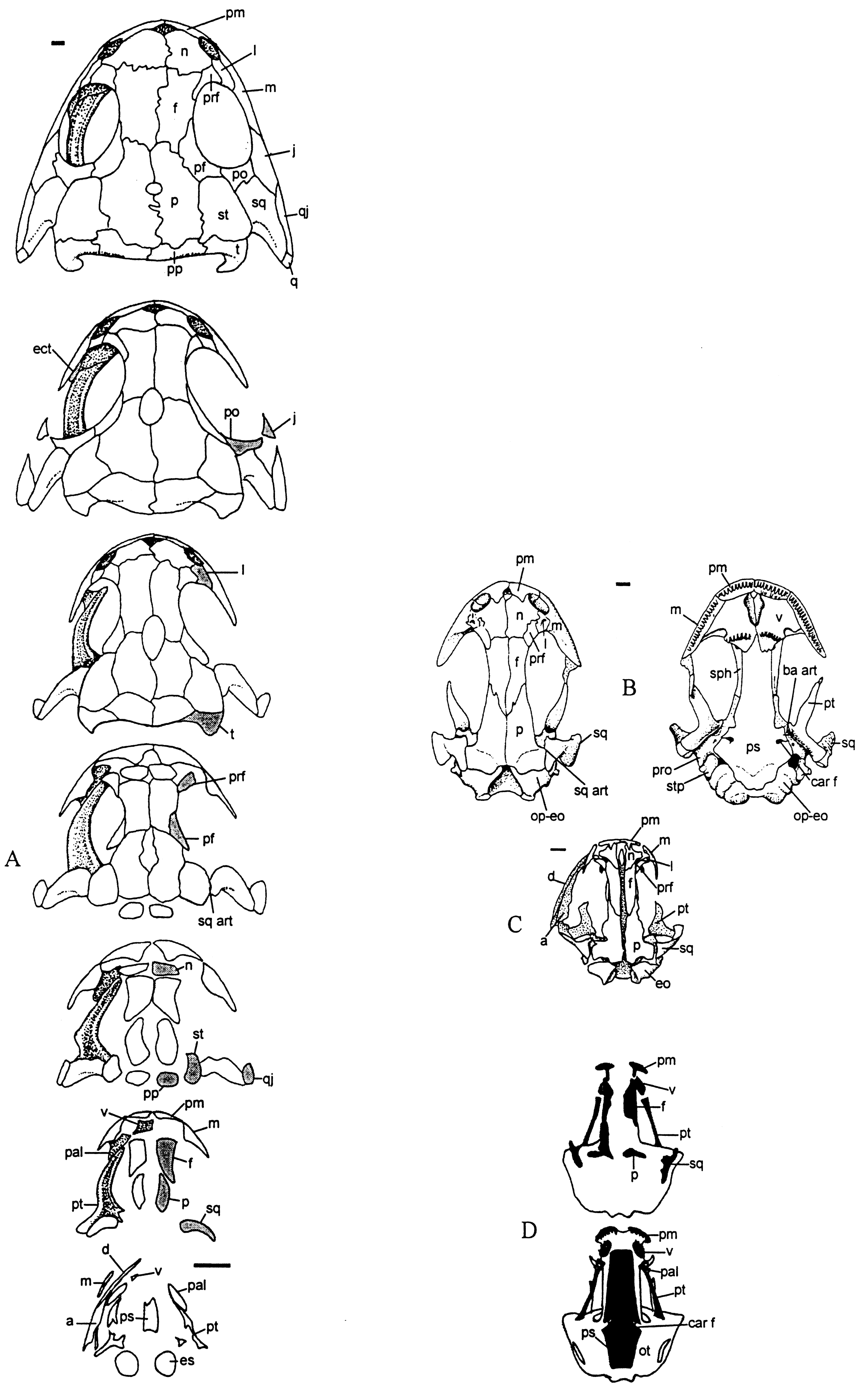
The adult cranial anatomy of modern hynobiids, ambystomatids, and salamandrids could have evolved from animals resembling *Apateon* by truncating ossification early in development, before the appearance of the posterior circumorbital bones and those of the posterior margin of the skull table, while retaining the gap between the maxilla and the squamosal. Although the larvae of *Apateon* provide an excellent model for the mode of development expected in salamander ancestors, the final achievement of their adult morphology must have occurred at a later time. Branchiosaurids were common in many large long-surviving lakes (on an ecological time scale) from the Upper Carboniferous and Lower Permian of central Europe. No comparable fossil deposits are known from the Upper Permian or Triassic, and crown-group salamanders do not appear in the fossil record until the Upper Jurassic (Milner 2000; Gao and Shubin 2001).

Among Paleozoic tetrapods, the branchiosaurid *Apateon* currently provides the best known basis for establishing the ancestry of salamanders. No other genus is known to possess such a large number of well-defined features that are comparable with uniquely derived characters of basal members of the crown-group Urodela: jaw suspension without a bony link to maxilla, at least in larval stages; ossification of posterior circumorbital bones much delayed in ontogeny or missing all together; squamosal with a hinge-like articulation with bones of the skull table and/or otic capsule; marginal teeth become pedicellate at the time of maturation; ceratobranchials become ossified or calcified at the time of metamorphosis in neotenic species; gill rakers capable of interdigitation so as to preclude flow of water through the gill slits during suction feeding; phalanges ossify from distal to proximal. These characters strongly support branchiosaurid temnospondyls as the sister-taxa of salamanders and indicate that the lineages leading to frogs and caecilians had diverged at an earlier time. The only unique derived osteological feature that is shared by all three living amphibians orders is the presence of pedicellate teeth; most other characters listed by Milner (1988) are of the soft anatomy and cannot be reconstructed from the fossil record. A more formal phylogenetic analysis awaits completion of ongoing studies of *Eocaecilia*, the oldest known caecilian, with Drs. Jenkins and Walsh; *Doleserpeton*, a putative sister-taxon of frogs, with Dr. Bolt; and further efforts to incorporate character changes that occur during development into a data matrix. Recent studies by Smith (2001) and Jeffery et al. (2002a,b) will be extremely helpful in providing analytical means for comparing different sequences of ossification of the skull bones in various taxa of salamanders and branchiosaurs.

DEVELOPMENT AND EVOLUTION

The sequence of ossification of the bones of the dermal skull in *Apateon* and other members of the family Branchiosauridae is unique among Paleozoic amphibians and directly comparable with that seen in modern salamanders. No other examples are known among vertebrates in which there is such strong evidence for direct relationship between changes in the sequence of the ossification of individual bones and major remodeling of both the structure and function of the skull.

Selection for these changes in branchiosaurids must have been focused primarily on early stages in larval development, because the adult has reverted to the configuration common to primitive temnospondyls. The very early ossification of the squamosal and the toothed bones of the jaws and palate suggests that modifications in the mode of feeding or nature of the prey may have played a significant role in these changes. Presumably, the larger adult stages of branchiosaurids did not rely on lateral movement of the cheek for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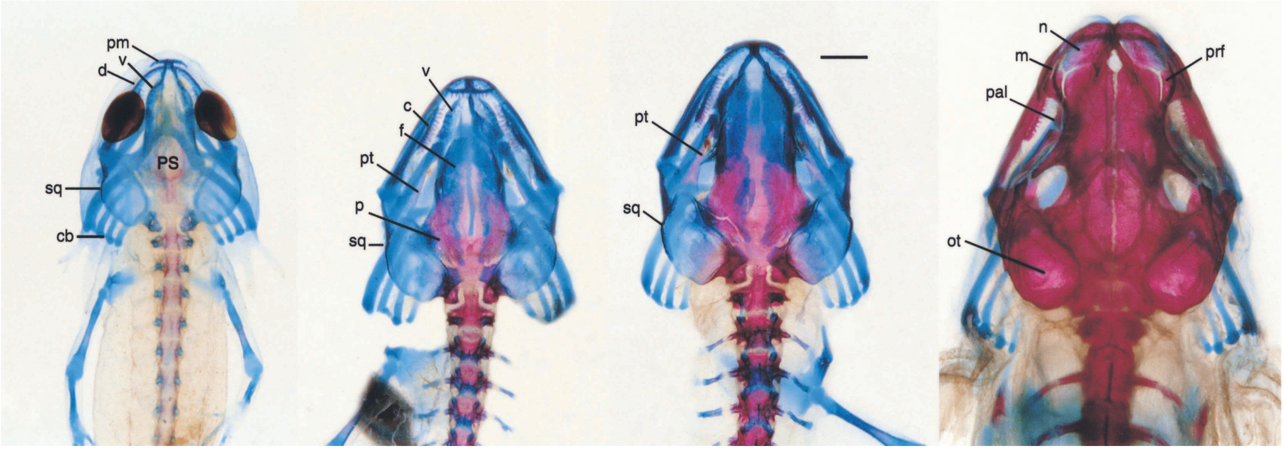

Fig. 3. Developmental sequence of cleared and stained specimens of the salamandrid *Notophthalmus viridescens* (Redpath Museum, McGill University, specimen nos. 5007, 5009–5011). Bone is red and, where viewed on edge, black; cartilage is blue. Note the very early appearance of the squamosal, when most of the surrounding skull is still cartilaginous. The maxilla, however, ossifies long after the premaxilla. Abbreviations are listed in Figure 1. Scale bar, 1 mm.

suction feeding but consolidated the cheek region in the manner of other primitive Paleozoic amphibians.

Although changes in the sequence of ossification leading to the skull configuration of modern salamanders have been well documented among larval branchiosaurids, it is more difficult to establish their molecular or genetic basis. A factor that may have been involved in the early ossification of the tooth bearing bones of the palate and jaws is the capacity for the rate of ossification to be accelerated as a result of stress placed on individual bones. It has long been recognized that growth of bones in mammals is influenced by movements in the womb and the stresses placed upon them by the associated musculature. Recent research on mammals demonstrates that mechanical stress placed on bones leads to increased expression of bone morphogenetic proteins (BMPs) 2 and 4, which are in turn associated with increased rates of ossification (Sato et al. 1999). Such a system may have been involved in establishing the early ossification of both the tooth bearing bones and the squamosal, which served as a major support for jaw articulation. We assume that additional genetic factors became involved at a later stage in the evolution of branchiosaurids that ensured the controlled sequence of bone development seen in the ancestors of salamanders. We are, however, not aware of any specific genes or proteins that might have a role in determining the overall sequence of ossification of the skull bones. Karsenty (1998, p. 303) specifically stated the following: “As of now, no clear genetic cascade has emerged to explain patterning of the head, the axial or the appendicular skeleton.” Except for many studies of premature closure of cranial sutures in mammals, this continues to be the case (Ducy 2001).

The capacity for delaying ossification of the circumorbital bones in the ancestors of salamanders requires a separate explanation. Except for members of the family Branchiosauridae, all Paleozoic temnospondyls for which ontogenetic sequences have been reconstructed (Milner 1982; Boy and Sues 2000; Steyer 2000; Schoch in press) ossify the dermal bones of the skull roof nearly simultaneously at small body size. None shows the sequence of ossification of individual elements observed in *Apateon*.

Among primitive living bony fish, the pattern of development of the cranial bones is exquisitely illustrated in *Amia*, as seen from the work of Grande and Bemis (1998, fig. 11). In this and other actinopterygian fish, ossification begins

Fig. 2. Ontogenetic changes in cranial ossification of the Lower Permian branchiosaur *Apateon* and modern hynobiid salamanders. (A) Growth series in *Apateon caducus*. From bottom to top, reconstructions of skulls of specimens of increasing size. Geological and Palaeontolological Institute of Mainz specimen numbers in sequence: 1310, 1387, 1442, 1779, 1249, 1335, 1601. The mm scale at the bottom applies to all but the largest skull. Only the palatal and jaw elements are ossified in the smallest specimen. Uniform gray shading identifies the successive ossification of bones in larger skulls. Palatal bones are omitted on the right side to emphasize progressive closing of gap in the skull margin between the jaw suspensorium and the maxilla. The sequence of ossification in *Apateon* parallels that seen in hynobiids, ambystomatids, and salamandrids. (B–D) Growth stages in hynobiid salamanders (according to Gao and Shubin, 2001), members of the most primitive clade of living 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 and Wake 2000). (D) Dorsal and palatal views of *Ranodon sibiricus,* redrawn from Lebedkina, 1979. Ossified bones indicated in black; surrounding areas are cartilaginous at this stage. Based on an animal 36 mm in length. Scale bars, 1 mm. Abbreviations are listed in Figure 1.

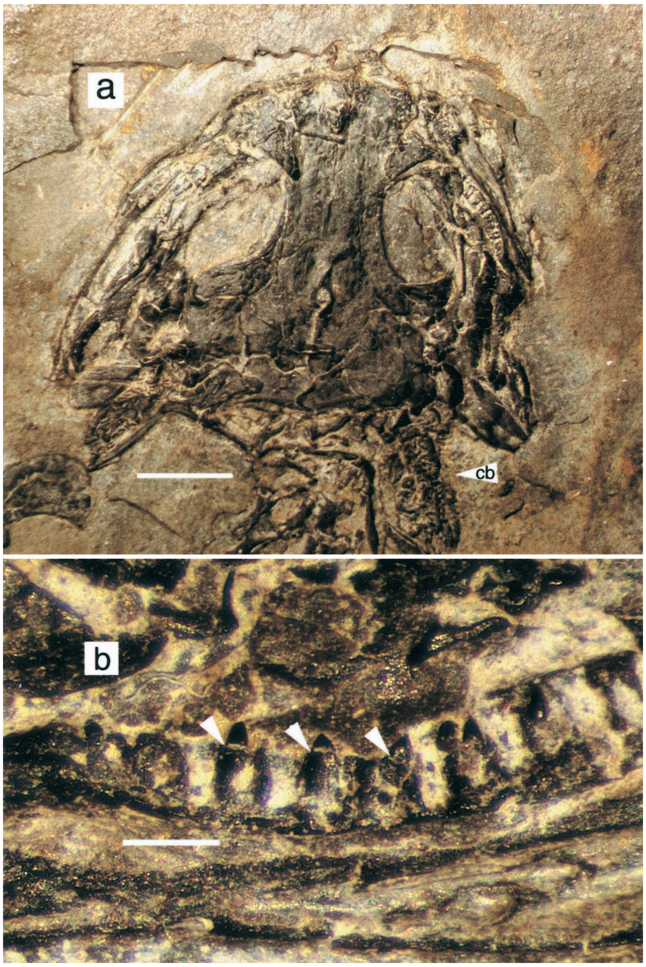

Fig. 4. Neotenic adult of *Apateon pedestris* (a) showing the entire skull. Institute of Palaeontology, University of Mainz, N800. The calcified or ossified ceratobranchials (cb), supporting the gill rakers, are seen extending posteriorly. Teeth from the right dentary can be seen through the orbit; they are enlarged in b. 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.

along the course of the lateral-line canals. Most cranial bones first ossify as simple tubes surrounding the sensory canals, with the rest of the bone forming later in ontogeny. The importance of the circumorbital bones in supporting the lateral line system is especially well-defined in *Eusthenopteron* (Fig. 1a), the best known of the sister-taxa of tetrapods (Ahlberg and Johanson 1998). In this and other osteolepiform fish, the sensory sulci are completely surrounded with bone but communicate with the surrounding water via small pores. Among Devonian and early Carboniferous tetrapods, the canals become intermittently open to the surface (Clack 2002). Within the adults of later Paleozoic amphibians, secondarily aquatic species have fully open lateral line sulci, whereas fully terrestrial species do not retain the canals after metamorphosis (Schoch 2002b). The larger group to which *Apateon* and other branchiosaurids belong—the Dissorophoidea (Holmes 2000)—includes primarily terrestrial forms that lack lateral line sulci as adults. The modern amphibian orders possess sensory canals during larval development, but they are supported by soft tissue and have no connection with the underlying dermal bones, perhaps as a consequence of their generally low degree of ossification.The oldest known dissorophoid, *Amphibamus grandiceps*, metamorphosed at very small size and apparently lost all trace of lateral line canals at an early stage in development (Milner 1982; Schoch 2002b). Reduced selection for formation of lateral line canals within the bones was a prerequisite for the very slow ossification of the circumorbital bones that primitively carried these canals. In branchiosaurids, this was presumably countered by selection for mobility of the jaw suspension associated with more effective suction feeding.

Another position at which selection may have been acting was in the specific timing and sequence of ossification of the individual skull bones. This is postulated on the basis of differences between the two species of *Apateon* described from the Kusel locality (Schoch 1992, figs. 7 and 20). Detailed comparison between these species is complicated by the less complete fossil sequence of *Apateon pedestris*, but some features are evident: Overall ossification begins and is completed at a much smaller size in *A. pedestris* than in *A. caducus*, presumably in relationship to the smaller adult size of *A. pedestris.* On the other hand, ossification of the squamosal and supratemporal (with which the squamosal articulates) is completed notably earlier relative to other skull bones in *A. pedestris*, as is that of the prefrontal and lacrimal (which are retained in salamanders). Although we are comparing differences between species rather than among members of a single species, similar forces of selection may have been acting at both taxonomic levels. Similar differences in relative timing of ossification of individual elements are also apparent among modern salamanders. For example, the maxilla begins ossification at a much later stage in the salamandrids *Triturus vulgaris* (Erdmann 1933) and *Nothophthalmus viridescends* (Fig. 3) and in *Ranodon* (Lebedkina 1979; Schoch 2002a) than in *Ambystoma* (Carroll, personal observation). Finally, the parasphenoid ossifies much later in *Triturus vulgaris* than in *Ranodon.*

The evolution of development in branchiosaurids is thus important not only as a model of how change in overall configuration of the skull could have resulted from differences in the timing of ossification of individual elements, but also as a model of how the expression of changes in developmental may be influenced by natural selection acting at the level of species and populations. The long delay in formation and final loss of many of the circumorbital bones among the ancestors of salamanders depended on changes in the genes and proteins controlling the timing of their ossification. However, such changes could not have been manifest as long as there was strong selection for the early formation of lateral line canals within these bones and/or until there was a selective advantage for the separation of the maxilla from the jaw suspension.

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