METAMORPHOSIS AND NEOTENY: ALTERNATIVE PATHWAYS IN AN EXTINCT AMPHIBIAN CLADE

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Abstract.—The Branchiosauridae was a clade of small amphibians from the Permo-Carboniferous with an overall salamander-like appearance. The clade is distinguished by an extraordinary fossil record that comprises hundreds of well-preserved specimens, representing a wide range of ontogenetic stages. Branchiosaurids had external gills and weakly ossified skeletons, and due to this larval appearance their status as neotenic (perennibranchiate) forms has long been accepted. Despite their extensive fossil record large specimens with an adult morphology appeared to be lacking altogether, but recently two adult specimens were identified in a rich sample of *Apateon gracilis* collected in the 19th century from a locality near Dresden, Saxony. These specimens are unique among branchiosaurids in showing a high level of ossification, including bones that have never been reported in a branchiosaur. These highlight the successive formation of features believed to indicate terrestrial locomotion, as well as feeding on larger prey items. Moreover, these transformations occurred in a small time window (whereas the degree of size increase is used as a proxy of time) and the degree of concentration of developmental events in branchiosaurids is unique among tetrapods outside the lissamphibians. These specimens are compared with large adults of the neotenic branchiosaurid *Apateon caducus* from the Saar-Nahe Basin, which despite their larger body size lack the features found in the adult *A. gracilis* specimens. These specimens give new insight into patterns of metamorphosis (morphological transformation) in branchiosaurids that are believed to be correlated to a change of habitat, and clearly show that different life-history pathways comparable to those of modern salamanders were already established in this Paleozoic clade.

Key words.—Amphibians, Branchiosauridae, development, developmental pathways, evolution, metamorphosis, neoteny, Temnospondyli.

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The evolutionary origin of metamorphosis in amphibians is still very poorly understood. The three extant clades, salamanders, frogs, and caecilians, reveal widely divergent patterns and processes usually referred to as metamorphosis, and the homology of metamorphosis-related features across these clades is far from clear. During metamorphosis, the remodeling of the skeleton as well as changes in the crucial organ systems have been found to be quite different in the three extant clades (Fox 1984; Duellman and Trueb 1986; Fritzsch 1990; Rose and Reiss 1993; Hall 2003; Rose 2003). However, the underlying system of endocrine control appears to be rather conservative (Gundernatsch 1912; Norris 1997; Shi 2000), and common features of morphological transformation have been mentioned among the three extant clades (Reiss 1996, 2002). It is therefore unclear which aspects of amphibian metamorphosis were actually inherited from a common ancestor and which evolved in parallel. Most generally, the origin of metamorphosis in the evolutionary history of amphibians is puzzling.

Here, we approach the problem from the perspective of the fossil record. In Paleozoic amphibians, or more precisely early anamniote-grade tetrapods, ontogeny has been studied in various clades. These studies were mostly based on different size classes of specimens from the same taxon and horizon, revealing particularly detailed information on the ontogeny of the skull (Boy 1974; Schoch 1992, 2003, 2004; Boy and Sues 2000). Regarding the problem of metamorphosis, these analyses arrived at a rather surprising result: a morphological transformation that would indicate some sort of metamorphosis is rarely found among these extinct groups. Instead, many clades appear to have included predominantly

aquatic animals, which underwent neither a change of habitat nor a significant morphological transformation during ontogeny. Notably, the most characteristic and feature-independent criterion for metamorphosis is not observed, namely the concentration of developmental events into a short phase of development (Alberch 1989).

Recently, one of us reviewed the evidence for metamorphosis in temnospondyls, the largest clade of Paleozoic amphibian-like tetrapods (Schoch 2002a). The emerging picture is that major morphological transformations occurred only in three small clades, which all had more or less terrestrial adults. However, in only one of these clades there was a substantial concentration of developmental events, the Permo-Carboniferous family Dissorophoidea. The family includes mostly small species with adults having well-ossified and long limbs suggesting a terrestrial existence. However, most species of dissorophoids are known by few size classes, which leaves major gaps in their ontogenetic trajectories. The group with the best-known fossil ontogenies, the Branchiosauridae, was until recently known exclusively from larval specimens.

In the present study, we report on the discovery of metamorphosed adults in a particular branchiosaurid species and analyze the transformations that characterize this previously unknown type of metamorphosis. Unlike all other temnospondyls, these changes were dramatic and rapid, that is, the crucial developmental events occurred in a small time window, whereas the degree of size increase is taken as a proxy for time. This recalls the situation in modern amphibians, in which metamorphosis is a short phase with drastic morphological changes. This is contrasted by other branchiosaurid

species, which merely extended the larval trajectory to form neotenic adults. The latter are throughout similar to larvae, although having a higher level of ossification.

Based on these characteristics, branchiosaurids are the first extinct lower tetrapod group to document the complete neotenic and metamorphosing trajectories in closely related species. They are indeed the first group for which a lissamphibian-like metamorphosis can be proven.

Branchiosaurids were first mentioned by Meyer (1844) and later recognized as a distinct group by Fritsch (1879), who also coined the family name (meaning ''gilled lizards''). Originally the group was used as a repository for immature specimens with poorly defined features. Despite their exquisite preservation, which includes skin remains and external gills, branchiosaurids have posed problems, that have not yet been surmounted. Since Fritsch, they have been referred to as a stereotype of larval amphibians in the Paleozoic.

Romer (1939) hypothesized that branchiosaurids were nothing but larval morphotypes of well-known, 2 to 3 m long temnospondyl amphibians such as *Onchiodon* or *Sclerocephalus*. This was indeed an attractive explanation, because larval specimens of these groups during that time were otherwise unknown and by analogy with extant amphibians, metamorphosis should have involved major transformations in Paleozoic amphibians as well.

Boy (1972) was able to reject Romer's hypothesis by identifying true larval specimens of *Sclerocephalus* and *Onchiodon* and by recognizing autapomorphic larval specializations of branchiosaurids, which distinguished them from both larvae and adults of all other temnospondyls. Boy (1972) concluded that members of the Branchiosauridae formed a clade of their own, being closely related to dissorophoids such as *Amphibamus*, *Micropholis*, and *Micromelerpeton*.

Further work on branchiosaurid ontogeny showed that the group differs from all others in the way the skull was modeled in early larval development, involving the sequence of ossifications as well as spatial growth patterns (Schoch 1992, 2002b, 2004). Some regions of the skull roof remained unossified or poorly ossified as compared to *Micromelerpeton*, *Sclerocephalus* or *Onchiodon*, while many postcranial bones were growing at an accelerated rate in contrast to those of other temnospondyls (Schoch and Carroll 2003; Schoch 2004). In sum, these findings have added much to our understanding of early branchiosaurid ontogeny, whereas little is known on the later stages, particularly metamorphosis (Boy 1974; Schoch 2001, 2002a).

To the present day, the main question that could not be resolved on the basis of the available material is whether branchiosaurids transformed into some adult (terrestrial) morphotype, or whether they were obligate neotenes similar to the extant axolotl. There is now substantial evidence for both pathways, metamorphosis and neoteny, to have occurred in branchiosaurids. In addition, the tempo and mode of metamorphosis differed from that of all other extinct lower tetrapods and shares features with that of extant amphibians. The scope of the present study is to report on these findings and analyze the alternative ontogenetic pathways now revealed in branchiosaurids.

We reexamined material collected in the 19th century by the mining director of the state of Saxony, Hermann Credner.

Recently, Werneburg (1991) reexamined the branchiosaurid material of this collection and correctly identified the adults of *Apateon gracilis* (referred to as *Melanerpeton gracile* in his study). The collection consists of an extensive body of material collected at just one locality and horizon, the Plauenscher Grund at Niederhäslich near Dresden. The material comprises an extensive growth series of several taxa, among them *Onchiodon labyrinthicus*, *Acanthostomatops vorax*, *Branchierpeton amblystomum*, and the species of interest here, *A. gracilis* (Boy 1987; Werneburg 1991). The main objectives of the present study are therefore to describe the unique features of the large specimens and to assess which changes characterized the latest events in the ontogeny of *A. gracilis*. These data will be compared with that from large adults of the neotenic branchiosaurid *Apateon caducus* from the Saar-Nahe Basin, based on material not described before.

MATERIAL

The material referred to in this paper is housed in the following institutional collections: Institut für Geowissenschaften, University of Mainz (Germany): GPIM-N 1230–1840; Landesamt für Denkmalpflege, Mainz (Germany): LDM-N-9u2; Landesamt für Umwelt und Geologie, Freiberg (Germany): LFUG-SS 13958, 13962, 13964, 13965, 13976, 13986, 14011, 14015, 14032, 14037, 14064, 14045, 14072, 14073, 14048; LFUG-RS 14770, 14775, 14782, 14783 (*A. gracilis*); Museum für Naturkunde, Humboldt Universität zu Berlin (Germany): MB.Am.55, 363, 364, 370, 374, 376, 398, 399, 402–406, 412, 413, 945 (*A. gracilis*); Staatliches Museum für Mineralogie und Geologie, Dresden, (Saxony, Germany): SGD 2144, 2149 (*A. gracilis*); and Staatliches Museum für Naturkunde in Stuttgart (Baden-Württemberg, Germany): SMNS 91016–91028 (*A. gracilis*).

RESULTS

Size Classes of Apateon gracilis

Branchiosaurids were among those temnospondyls with the smallest adult size, ranging from 100 to 150 mm total body length. Yet even compared with these standards, *A. gracilis* was a small species. The largest adult specimen has a skull length of only 18 mm, while the bulk of the material falls in the 6–12 mm range (Fig. 1A, B). The adults thus reached a body length of only 80 mm. Features probably correlated with small size are the unusually poor level of ossification in larvae as compared with other *Apateon* species, and especially in contrast to the heavily ossified adults of *A. gracilis*. Some elements, such as the ectopterygoid and pterygoid, are particularly slender in large specimens. Further characteristic features of the taxon are the relatively large size of the orbits, the unusual width of all skull roofing elements (especially the supratemporal, squamosal, postorbital, and jugal) that goes well beyond the state in other species of *Apateon*, the great width of the basal plate combined with an unusual shortness of this region, and the unusually large tympanic embayment as indicated by a large unsculptured area on the medial margin of the squamosal. The latter two characters are unique among the Branchiosauridae, but appear in the distant relative *Amphibamus grandiceps*.
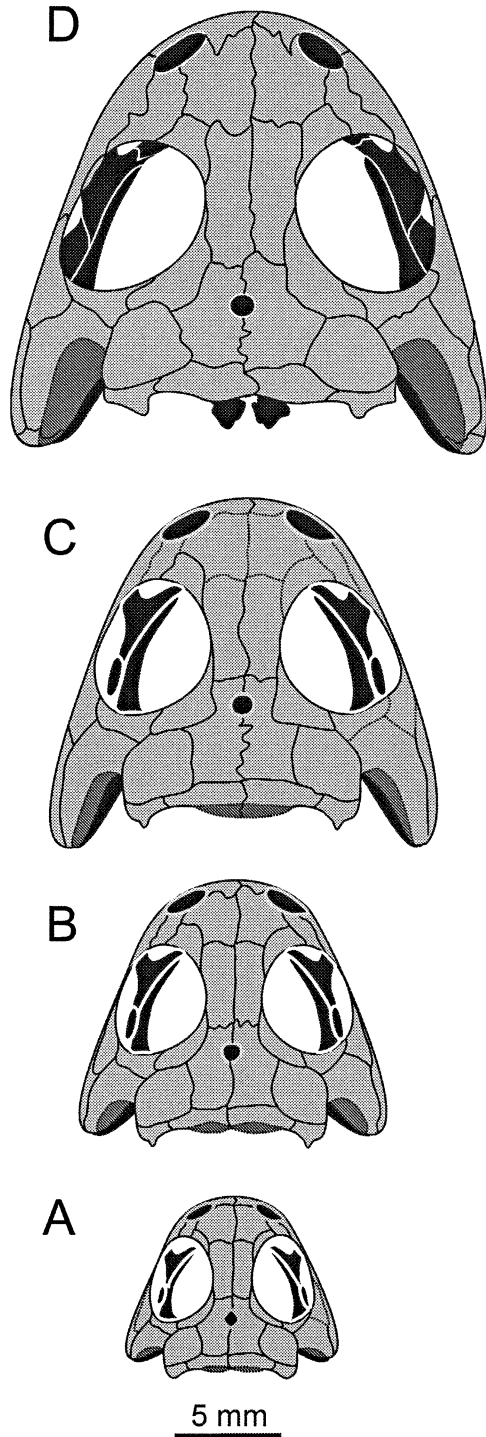
FIG. 1. Reconstruction of four skulls of *Apateon gracilis* representing larval (A, B), metamorphosing (C), and adult animals (D), all drawn to the same scale.

5 mm

The chronological succession of morphological changes in the adult phase of *A. gracilis* was as follows: (1) by 8–9 mm skull length, the maxilla reached further back than in larvae, suturing with the jugal, squamosal, and quadratojugal; (2) by about 12 mm, the dentition of premaxilla, maxilla, and dentary changed from needle-shaped, small, to conical, large

teeth (Fig. 1B); the teeth show no indication of being pedicellate. (3) by 16.5 mm (SGD 2144, 2149), the quadrate condyles were located well behind the occiput, and dermal ornamentation consisted of polygonal ridges (Fig. 1C); and (4) by 18 mm (LFUM-SS 13612), the quadrate, exoccipitals, coracoid, and trunk intercentra were ossified, the pterygoid had developed a transverse process, and the squamosal embayment formed a much enlarged otic notch for the attachment of the tympanum (Fig. 1D).

Developmental Trajectories

In branchiosaurids, ossification sequences of the skull and postcranial skeleton have been analyzed in and compared between *A. caducus*, *A. pedestris*, and *Melanerpeton humbergense* (Schoch 2004). Despite different size ranges and divergent adult morphologies, these taxa are remarkably similar in their cranial development. Only in the largest specimens does the sequence of bone formation become more variable between taxa—some events changed their relative position in the sequence.

The general pattern shared by all three species was the rapid development of girdles and limbs and the delayed development of certain sets of skull bones, such as the circumorbitals. These patterns were quite distinct from outgroups (*Sclerocephalus*: Schoch 2003; *Micromelerpeton*: Witzmann and Pfretzschner 2003), in which the skull formed in the early larval phase, whereas the postcranial skeleton required much more time until it attained a comparable degree of ossification.

Despite the aforementioned, the larval trajectories of branchiosaurids ended at a relatively early stage. The vertebral centra and the endochondral bones in the braincase, palatoquadrate, and shoulder girdle remained cartilaginous throughout development, freezing the late larval state of primitive dissorophoid temnospondyls such as *Micromelerpeton* (Boy and Sues 2000; Witzmann and Pfretzschner 2003). In the metamorphosed adults of *A. gracilis*, all these bones were ossified, and further developmental events were also added to the trajectory, such as the formation of a polygonal pitting and the posterior shift of the quadrate condyles. The latter events did not occur in most populations of *Micromelerpeton*, which was therefore considered a partial neotene as an adult (Boy 1972; Boy and Sues 2000).

The most striking feature of the newly recognized type of metamorphosis is the strong concentration of developmental events, the almost simultaneous expression of novel features in adult development. After a relatively long and stable phase in late larval life, in which an increase in body size, but hardly any recognizable new developmental events occurred, a remarkable morphological transformation gave way to a distinct adult morph. If compared with other temnospondyls, the adult morphology falls within the miniaturized dissorophoids *Amphibamus* and *Doleserpeton*, rather than larval branchiosaurids or other temnospondyls. Such a drastic metamorphosis has been postulated for *Amphibamus* but has never been proven because many intermediate size classes are missing (Milner 1982; Schoch 2001). Thus, adult *A. gracilis* forms the first unequivocal evidence for both mode and tempo of metamorphosis in a dissorophoid, much more so than pre-
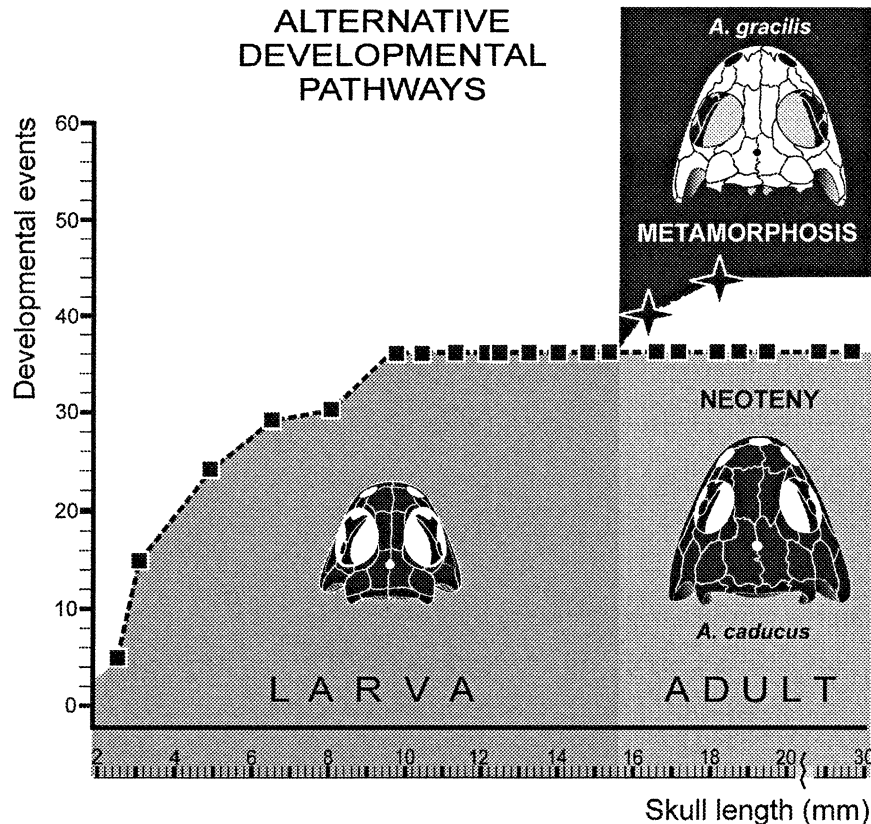
FIG. 2.   Alternative developmental pathways in the Permo-Carboniferous branchiosaurid temnospondyl genus *Apateon* as proposed in this paper. Developmental events (successive stages of bone formation) are mapped against size (skull length), giving three principal phases: (1) a continuous increase in the number of bones in the skeleton squares; (see Schoch 2004); (2) a phase of stagnation where no more elements are added (continued in the neotenic pathway of *Apateon caducus*; circles); and (3) a final phase of rapid bone formation and morphological changes, here identified as metamorphosis (*Apateon gracilis*; asterisks). For a detailed description of developmental events see Schoch (2002b, 2004).

vious assessments had conceived (Werneburg 1991; Schoch 2002a). In particular, the discovery of braincase ossifications and intercentra was not expected in a branchiosaurid, because in other temnospondyls these bones formed much later than all others.

In these outgroups, the formation of centra and the partial ossification of endochondral elements in the braincase required a much longer period and often occurred long after the change in ornamentation or the shift of the jaw articulation. In *Sclerocephalus*, for instance, these changes occurred in a rather long period correlating with the 20–60 mm size range (skull length), see Schoch (2003) and Witzmann (2006). In contrast, *A. gracilis* developed all these features in a size range of 14–18 mm skull length.

According to our findings, the developmental trajectory of the genus *Apateon* was triphasic, involving: (1) a phase of a steadily increasing bone count in the skeleton as described by Schoch (2004); (2) a phase of stagnation marked by an incremental morphological change throughout the skeleton and increase of size, but no further addition of elements (Boy 1978; Schoch 1992); and (3) a short phase of rapid formation of new skeletal elements (without a comparable increase of body size), which we identify as metamorphosis (Fig. 2). While phase 1 appears to have been rather similar at least in branchiosaurids (Schoch 2004), phase 2 was highly variable

in duration (measured by size), and development of morphological features. All neotenic branchiosaurids remained in phase 2 (Fig. 2).

Fossil Evidence of Metamorphosis

Boy (1974) characterized temnospondyl larvae particularly by the absence of crucial ossifications, the quadrate and braincase, coracoids and pubes, as well as the carpals and tarsals. In turn, the presence of a larval-type hyobranchial apparatus has been traditionally viewed as an indication of a larval or neotenic state (Bystrow 1938; Boy 1972, 1974), although this has been restricted to hyobranchial apparatuses similar to those of extant salamander larvae (Schoch 2001). The presence of other types of hyobranchial ossifications (e.g., *Micropholis*, *Sclerocephalus*) have more recently been interpreted as adult (Boy and Sues 2000).

So far, branchiosaurids appeared to be perfect larvae because they fulfilled both of the criteria cited above. The adults of *A. gracilis*, however, had practically all features by which adult temnospondyls are recognized, and they clearly lacked both a larval hyobranchial apparatus and branchial denticles. In addition, some of the features present in the largest specimen of *A. gracilis* indicate that these animals were well capable of a terrestrial existence, especially since these char-

acters are as clearly established as in other small, terrestrial dissorophoids (*Micropholis*, *Eoscopus*, *Amphibamus*). Biologically, these changes have been argued to indicate the transition from an aquatic to a terrestrial environment, involving the following observations (Boy 1972; Schoch 2002a).

The firm integration of the marginal tooth-bearing arcade into the cheek indicates stronger resistance to forces generated by a stronger bite, and the posterior extension of the tooth arcade of the maxilla and dentary as well as the formation of larger, more solid teeth enabled the engulfing of larger prey items and eventually the crushing of more solid exoskeletal materials such as insect integument. The backward shift of the quadrate condyles probably also reflects the trend for gape enlargement, while the ossification of the occipital condyles indicates stronger forces involved in the elevation of the skull during the opening of the mouth.

In all temnospondyls, orbit size decreased proportionately with growth. This is even found among branchiosaurids, although in that clade the trend is very weak (Boy 1972). In *A. gracilis*, the orbits grew at an isometric rate, probably because the eyes became substantially larger and more differentiated, while growth terminated at a very small adult size. A similar pattern is seen only in *A. grandiceps* (Milner 1982). Given that enlarged eyes were the reason for the large size of adult orbits, this could indicate an increased significance of the optical sense, triggered by a change to a terrestrial environment.

The ossification of the coracoid and glenoid portions of the pectoral girdle and the advanced formation of muscle support documented by the limbs indicates a stronger muscle support for limbs as is required for an effective, limb-generated locomotion on land. Branchiosaurids were rather short-bodied forms, which could not rely on lateral undulation of the trunk while on land, hence the importance of the limbs must have been greater than in micromelerpetontids or stereospondylomorphs. Branchiosauridae had short trunks and long limbs like many amphibamids and dissorophids, which could indicate that the clade including these three taxa underwent a fundamental switch from a trunk-based locomotion to a limb-based ''striding locomotion'' (A. Milner, pers. comm.).

Changes in the ornamentation of dermal bones have puzzled many workers (e.g., Bystrow 1935; Boy 1974; Schoch 2001), but despite numerous extant examples (anurans), there seems to be no clear explanation at hand. Cutaneous respiration as well as shedding of skin, both practised on land rather than under water, have been mentioned but are not clearly correlated with dermal ornamentation.

The ossification of intercentra highlights the increasing importance of the axial skeleton in supporting the trunk region. Again, this suggests a change to a locomotion on land, or at least the capability to support the trunk during land excursions.

The enlargement of the squamosal embayment, which formed the bony frame of the tympanum, indicates the capability to receive air-borne vibrations. This correlates with the ossification of the stapes, which started in smaller adults but attained its full size only during metamorphosis. The stapes of temnospondyls bears numerous similarities with that of modern anurans, and there is substantial evidence for the existence of an anuran-like middle ear, tympanum, and eustachian tube (Bolt and Lombard 1985; Schoch 2000).

Neoteny

With the exception of *A. gracilis*, the absence of features that would indicate metamorphosis is the normal situation in all other branchiosaurid species. This is documented by virtually thousands of specimens from numerous localities and stratigraphic horizons. Almost automatically, neoteny suggests itself as a biological explanation for this phenomenon (Boy 1971). Neoteny is here understood in the original sense, meaning that sexual maturity is reached while retaining larval somatic features. This definition includes adaptational aspects but can also be viewed as a process of developmental reprogramming that results in paedomorphosis, one of the major alternative modes of heterochrony.

Neoteny is documented from a wide range of extant salamander taxa (Duellman and Trueb 1986). Modern salamanders are known for an astonishing plasticity within their ontogeny and their capability to express different morphotypes, namely neotenic and metamorphosed morphs. Different environmental factors may lead to a different life-history pathway within one population or between populations of the same species. Facultative neoteny is a mode in which neoteny is an option alternative to metamorphosis (for an overview, see Duellman and Trueb 1986; Whiteman 1994). Obligatory neoteny is established in other taxa, where metamorphosis cannot be induced by any natural stimulus, for instance the axolotl (*Ambystoma mexicanum*). Facultative neoteny is controlled by complex ecological and developmental interactions and the threshold of the ecological stress that results in metamorphosis can vary considerably according to the long-term and short-term histories of the populations and species (Semlitsch et al. 1990; Newman 1992; Whiteman 1994; Denoel et al. 2002).

Ecological studies of extant salamanders, especially species of *Ambystoma*, which show the whole range of obligatory neoteny, facultative neoteny, and obligatory metamorphosis, show that neoteny, can generally be attributed to harsh terrestrial conditions (Sprules 1974; Patterson 1978; Whiteman 1994). Moreover, when the geographical distribution of *Ambystoma* was considered, neoteny occurred most frequently in populations inhabiting mountain lakes (Snyder 1956; Duellmann 1961; Dent 1968; Anderson 1971). Under laboratory conditions larvae collected at high-elevation localities metamorphosed less readily than those from low elevation (Snyder 1956). This shows that the environmental factors salamanders are exposed to high elevations do favor a neotenic life-history pathway. Most of the unfavorable parameters in a high-elevation terrestrial environment (temperature fluctuation, scarce cover, low humidity) are compensated by the aquatic environment (Sprules 1974).

Boy (1998, 2000) and Boy and Sues (2000) analyzed the ecological communities and food-web dynamics in fossil lakes of the Saar-Nahe Basin in southwestern Germany. These studies indicated that branchiosaurids were common in lakes with relatively unstable conditions regarding water influx, circulation, and eutrophication and with short food

chains. In these environments, developmental plasticity in the form of facultative neoteny is likely to have been advantageous.

The area of the Saar-Nahe Basin was situated in a tropical belt during the Late Carboniferous and Early Permian, whereas the lakes themselves were situated in intermontane basins within the Variscan Mountains (Boy and Sues 2000). Although located in a tropical environment, it has been estimated that the lakes may have been as high as 2000 m above sea level (Becq-Giraudon et al. 1996) and were exposed to monsoon weather conditions with pronounced differences in precipitation throughout the year (Patzowsky et al. 1991). The high elevation of the lakes may explain why neoteny apparently was the dominant pathway in most of the studied lakes.

Osteological correlates of neoteny are difficult to define (Boy 1971), especially when the full size range of an extinct species is unknown. In many species, it remains a realistic possibility that larger (metamorphosed) specimens were simply not preserved in the lake deposits, because adults visited the lakes only seasonally. Indeed, the temnospondyl-bearing deposits of the Permo-Carboniferous across Middle Europe corroborate this (Boy and Sues 2000). However, in the studied example of *A. caducus*, from which large specimens are known, we have found quite substantial evidence of neoteny.

Hypertrophic development of larval bones was mentioned by Boy (1971) as a correlate of neoteny, involving an accentuation of larval-type dermal ornamentation and the retention of a larval hyobranchial skeleton. More generally, neoteny is indicated by the accentuation of larval features, produced by the continuation of the larval developmental trajectory (Fig. 2). In branchiosaurids, isometric growth of many cranial bones resulted in the conservation of juvenile (i.e., late larval) cranial morphology even in the largest specimens (Schoch 1992). This contrasts strongly with metamorphosed *A. gracilis*, which underwent major proportional changes in the cheek and posterior skull table.

In *A. caducus*, larval features retained in adults are most pronounced, which is highlighted by specimens in the 30-mm skull length range. The find of a previously undescribed, well-preserved *A. caducus* at Niederkirchen in the Pfalz region of southwestern Germany is particularly remarkable (specimen LDMN-N-9u). These giants have entirely conserved the trajectory of juveniles, and not a single one of the events recognized in metamorphosing *A. gracilis* had occurred (Fig. 2). In contrast, large *A. gracilis* departs from the larval trajectory by adding up to eight postlarval developmental events. In giant *A. caducus*, mineralized branchial denticles were retained, indicating the presence of open gill slits. This is the most clear-cut evidence we have of an aquatic mode of life in extinct amphibians (Schoch 2001). Its discovery in large branchiosaurids exceeding the size of metamorphosed *A. gracilis* by more than 10-mm skull length is a strong argument for neoteny in these large specimens. In addition, the deposit where the giants were collected yielded hundreds of branchiosaurid specimens but not a single one with a more adultlike appearance, despite the presence of larger, adult temnospondyl *Sclerocephalus* and *Micromelerpeton* at the same locality and horizon (Boy and Sues 2000).

Morphologically, neotenic giants of *A. caducus* can hardly be distinguished from smaller juveniles. The main differences are the accentuated larval-type ornamentation, the comparatively high degree of ossification, and the development of uncinate process on the anterior trunk ribs, otherwise neither found in larval nor metamorphosed branchiosaurids. The ornamentation of the skull roof elements differs from the pattern of strong polygonal ridges and roundish pits found in the adult *A. gracilis*. In giant *A. caducus*, all preserved skull-roofing elements possess an ornamentation that consists of small, irregularly shaped pits, which are particularly dense in the medial region of each skull roof element, and shallow elongate ridges that radiate out from the densely pitted centers.

Although the skeletal elements of giant *A. caducus* are well ossified in comparison to smaller, larval individuals of this species, it clearly lacks ossifications of the endocranium as well as ossified intercentra as found in metamorphosed *A. gracilis*. In addition, the girdle elements are small and slender and the limb bones lack distinct processes. The appendicular skeleton of giant *A. caducus* was most likely not suitable to permanently support the animal on land and to provide the frame for effective terrestrial locomotion.

An obvious size difference exists between the adult *A. gracilis* with a skull length of 18 mm and the large, neotenic *A. caducus* with a skull length of 30 mm. *Apateon caducus* generally grew to a larger size than *A. gracilis*, but this significant difference in adult size may at least partially result from the different life-history strategies of the two animals. It is known from facultatively neotenic salamander taxa that neotenic animals of a population grow to a distinctly larger body size than their metamorphosing members (Powers 1907; Semlitsch et al. 1990; Whiteman 1994; Denoel et al. 2002).

CONCLUSIONS

The discovery of metamorphosed specimens of *A. gracilis* shows that branchiosaurids were not exclusively paedomorphic, but that at least some members of this species underwent a transformation into terrestrial adults. In addition, neoteny has also been established in branchiosaurids as exemplified by large *A. caducus* specimens that clearly exhibit neotenic features, including a weakly ossified appendicular skeleton, a larval-type cranial morphology, and open gill slits even at the largest stages.

Our findings reveal that different life-history strategies (i.e., metamorphosis and neoteny) had already been established in branchiosaurids by the Upper Carboniferous. As in the case of extant facultative neotenic salamanders (Semlitsch et al. 1990; Whiteman 1994; Denoel et al. 2002), branchiosaurids were probably responding to environmental parameters rather than being obligate neotenes.

Among the places where branchiosaurids have been found, the Niederhäslich locality is the only one falling in the lowland belt of the Variscan orogen. Evidently, terrestrial conditions at the Niederhäslich lake were more favorable than in other known Permo-Carboniferous lakes, because two other temnospondyl amphibians represented there (*Onchiodon* and *Acanthostomatops*) are known by metamorphosed specimens in addition to their larvae (Schoch 2002a).

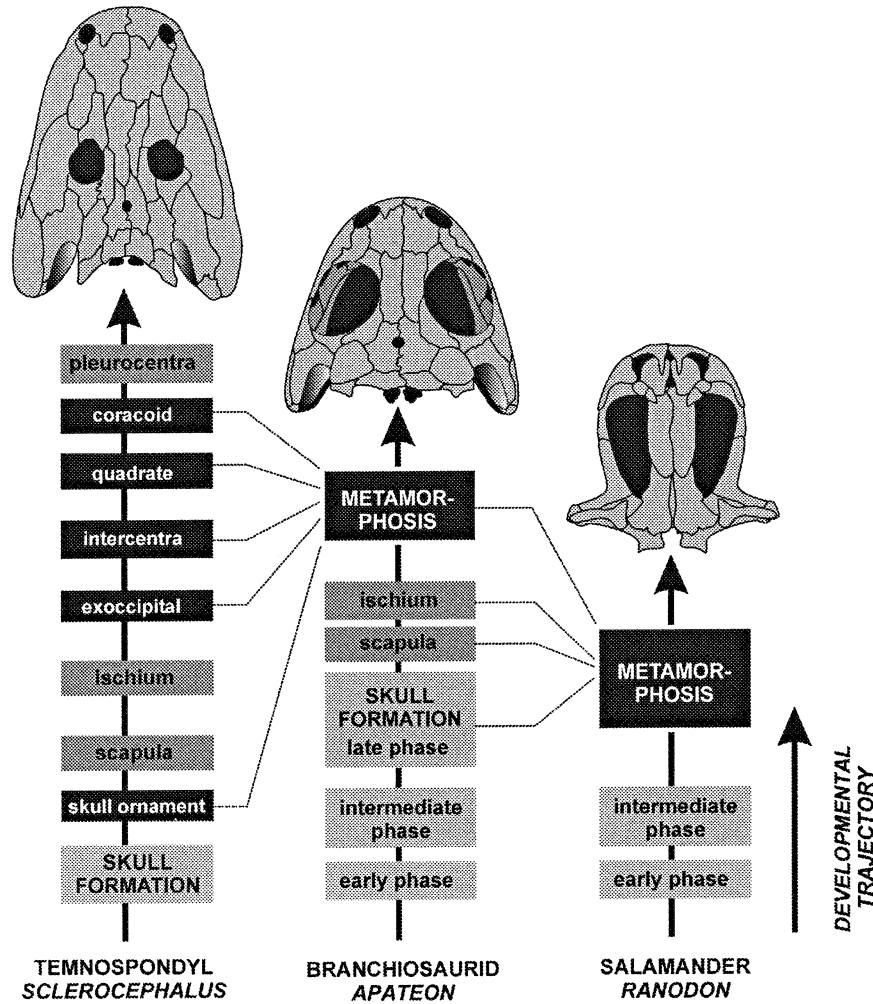Among extant amphibians, the branchiosaurid pattern of

FIG. 3. Comparison of developmental trajectories of a primitive temnospondyl (*Sclerocephalus*), a branchiosaurid temnospondyl (*Apateon*), and a primitive salamander (*Ranodon*). The gradual and slow ontogeny of *Sclerocephalus* did not involve rapid metamorphic changes, while in *Apateon gracilis* several events were condensed to a short phase (branchiosaurid metamorphosis, marked in black). In lissamphibians, here exemplified by *Ranodon sibiricus*, metamorphosis is even more inclusive, involving the metamorphic events of *Apateon* as well as additional events of the premetamorphic phase of *Apateon*.

both metamorphosis and neoteny is closest to that of salamanders, notably hynobiids, ambystomatids, and dicamptodontids. This shows that alternative life cycles of this type already had evolved by the late Paleozoic, roughly 300 million years ago. Short trunks and limb-based striding locomotion in the dissorophid-branchiosaurid-amphibamid clade implicates that these taxa were fundamentally terrestrial. A triphasic life history may have arisen in relation to this terrestriality and specialized filter-feeding larvae allowed for the exploration of permanent filter-feeding niches as seen in branchiosaurids (A. Milner, pers. comm.).

The degree of concentration of developmental events in branchiosaurids is unique among tetrapods outside the lissamphibians. The rapid formation of new bones is also typical of both anurans and salamanders, but this involves many more elements than in branchiosaurids. The ossification sequence of *Apateon* was recently found to be remarkably similar to that of salamanders (Schoch 2002b), although in the former skull formation was completed long before metamorphosis started. Extant salamanders complete skull for-

mation during or after metamorphosis. The most characteristic feature of salamander metamorphosis—the resorption of parts of the palate and the patterning of a new palate (Rose 2003)—is not observed in branchiosaurids. However, metamorphosis in the primitive salamander *Ranodon sibiricus* involves changes also noticed in *A. gracilis* (Schmalhausen 1968; Kuzmin and Thiesmayer 2001; Lebedkina 2004; Fig. 3). In *Ranodon* metamorphosis thus involves several events of the premetamorphic phase of *Apateon*, whereby the chronological order of some events has been retained (Schoch 2002b).

Alternatively, the concentration of developmental events may have evolved in parallel in branchiosaurids and lissamphibians. The relationship between temnospondyls and lissamphibians is still disputed; see Schoch and Milner (2004) for a summary of hypotheses. The common feature shared by both clades was their small size compared to that of most other metamorphosing Palaeozoic amphibian-grade tetrapods (Milner 1988). This suggests that a clear-cut, short, and drastic type of metamorphosis may also be influenced by size-

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