Heterochrony: response of Amphibia to cooling events

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ABSTRACT. As suggested by the palaeontological record from periods subsequent to global cooling events, Anura and Urodela (two major groups of modern Amphibia) may (but not necessarily must) respond by shortening their somatic development associated with normal gonadal development. There are two modes of heterochrony recognizable in fossil amphibians according to the degree of ossification and degree of metamorphosis of their hyobranchial skeleton: neoteny (resulting in a larva capable of breeding) and paedomorphosis (adult in juvenile but postmetamorphic phenotype). It was found that the Oligocene cooling provoked neoteny in some forms (Brachycormus), but was not efficient enough for some other closely related, and perhaps even ancestral forms (Chelotriton). In contrast, the Plio-Pleistocene temperature drop led to either the extinction of some groups (Palaeobatrachidae), the withdrawal from the original area of distribution to geographically restricted refugia, combined with paedomorphosis (Chelotriton → Tylototriton and Echinotriton, Palaeopleurodeles → Pleurodeles, Latonia → Discoglossus) or the withdrawal from the original area of distribution and subsequent re-immigration when the climatic conditions improved (Ranidae, Bufonidae). The severe global cooling event at the Permian/Triassic boundary seems to be a plausible explanation for paedomorphic nature of the Anura in general. Thus, heterochrony as a response to cooling events could have been manifested at a wider range of taxonomic levels (genus, order).

Introduction

The term heterochrony usually means a shift or displacement of ontogenetic appearance of some organ with respect to another in phylogenetic descendants. In other words, this is a change in the timing of development in the course of phylogeny. Several various modes of heterochrony were recognized (see Gould 1977 for discussion). One of them occurs frequently in Amphibia, namely the retention of formerly juvenile characters in adult descendants produced by retardation of somatic development. This may be developed to various degrees. Sexual maturity is attained in either the premetamorphic (neoteny, Kollman 1885) or the postmetamorphic but not the ultimate (paedomorphosis, Garstang 1922) stages of somatogenesis. In other words, neoteny involves a sexually mature individual with larval phenotype (often hypermorphosed), whereas paedomorphosis involves a mature adult with phenotype of postmetamorphic juvenile.

Both neoteny and paedomorphosis can be recognized also in fossil amphibians, provided that they are preserved as articulated skeletons including the hyobranchial part. That the individual was sexually mature is suggested by its fully ossified skeleton. If such fully ossified skeleton is accompanied by larval branchial skeleton (consisting of unmetamorphosed branchial arches), then it may be concluded that the individual in question was a neotenous larva. If a completely ossified skeleton is associated with a hyobranchial skeleton exhibiting various degrees of metamorphosis, and if a comparison with related taxa reveals that somatogenesis has not yet reached its ultimate stage, then it is obvious that the individual bears paedomorphic features.

In the Amphibia (i.e. ectotherms without thermoregulation), neoteny and paedomorphosis are the phenomena usually associated with climatic changes, especially drop of temperature. Even if the drop in mean annual temperature is seemingly inconspicuous (several degrees Celsius) it may provoke an increase in seasonality which may lead to the precocious onset and prolongation of the period of hibernation. This, in turn, reduces the time available for normal larval development. Since amphibian larvae are able to correlate their metabolic rate to temperature changes, they can hibernate in water and complete their development the following season. Such overwintering can even be repeated for several years, and may be accompanied with hypermorphosis (continuing increase in size). Survival of larvae over periods of long-term deterioration of climate has some positive aspects, but can also have disadvantages for the rate of reproduction is retarded. The only compensation for this is the resulting shift in breeding ability to the larval, premetamorphic stage.

It should be noted that neoteny may not only be a response to a temperature drop (due to ectothermy of amphibians) but also to aridization (amphibians are poorly protected against evaporation). If the surroundings of a breeding water body become dry, larvae may stay in the water because conditions on dry land have become lethal for postmetamorphic individuals. Moreover, neoteny is not only a way to survive long-term periods of climatic deterioration, but apparently has another function as well. It has been shown that the timing of reproduction is significantly different in modern urodele populations, where some individuals are metamorphosed, whilst others are neotenous. For example, when exposed to the same living conditions, the neotenous adults of *Ambystoma* lay eggs about 6 weeks earlier than their metamorphosed terrestrial counterparts. Early egglaying and subsequent growth of hatchlings results in a significant size advantage for larvae from neotenous parents (Scott 1993). Hence, the rate of reproduction is another important factor emphasizing role of neoteny in the evolution of the Amphibia (Whiteman 1994), besides being an adaptation to a temperature drop.

Neoteny and paedomorphosis in fossil urodeles and anurans

Most fossil urodeles were described on the basis of disarticulated vertebrae. However, some were fossilized as more or less complete articulated skeletons. Those which have larval branchial skeleton include *Andrias scheuchzeri* (Holl, 1831), *Orthophyia longa* Meyer, 1845 and *Brachycormus noachicus* (Goldfuss, 1831). Their earliest palaeontological records are from the late Oligocene or early Miocene. *Andrias* is the only representative of the family Cryptobranchidae in the European Tertiary. It was thoroughly reviewed by Westphal (1958) and Böttcher

(1987). *Orthophyia* is based on a single specimen from the Lower Miocene of Öhningen (Meyer 1845); unfortunately, it was destroyed during World War 2 and its phylogenetic relations remain obscure.

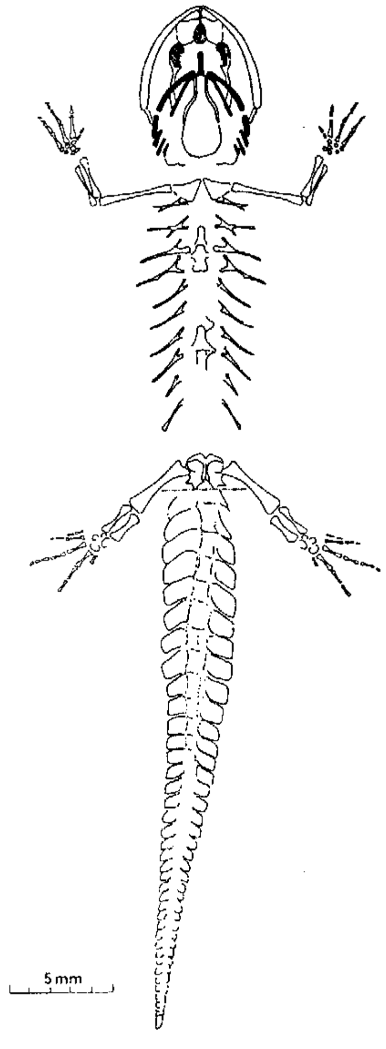

Figure 1 *Brachycormus noachicus* (Goldfuss, 1831). Reconstruction of the complete skeleton based on available material. In agreement with the mode of preservation, the tail posterior to the broken line is twisted ninety degrees along the long axis. After Roček (in press).

Brachycormus (Fig. 1) (Salamandridae) is, similar to *Andrias*, anatomically well documented (Roček in press). Its developmental status of neotenous larva can be seen by the incompletely metamorphosed branchial arches, the fully ossified skeleton (including carpals and tarsals) and the dilated neural and haemal arches of the caudal vertebrae (which undoubtedly supported the tail fin). It is closely related to *Chelotriton* which occurs as early as the Middle Eocene in England (Milner et al. 1980) and possibly also the Upper Eocene of Geiseltal in Germany (*"Tylototriton" weigelti* of Herre 1935). Both *Chelotriton* and *Brachycormus* bear principal diagnostic characters of the Salamandridae but the former is heavily ossified (seen by the well developed ornamentation of the dermal skull roof, the co-ossification of dermal and chondral bones, and the observation that the majority of dermal bones are in broad contact with each other) and its hyobranchial skeleton is completely metamorphosed. If these two amphibians are compared (Fig. 2) then *Brachycormus* can be taken as derivate of *Chelotriton*, provided that the somatic development of the latter was blocked at the praemetamorphic stage.

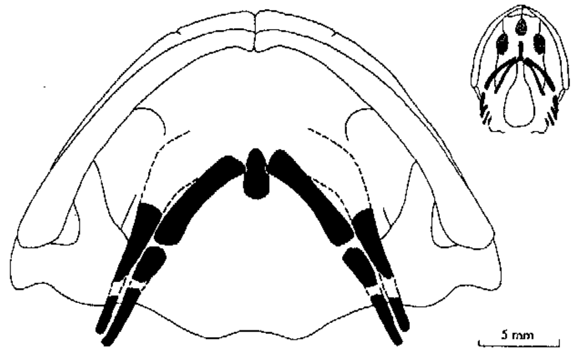

Figure 2 Reconstruction of the skull of *Chelotriton* (left) and neotenous *Brachycormus* (right) in ventral view. Ossified parts of the hyobranchial skeleton are in black. Drawn to scale.

Neoteny has never been found in the Anura and their tadpoles always metamorphose into postmetamorphic adults. However, if *Latonia*, a widely distributed and heavily ossified discoglossid frog from the European Neogene, is compared with the Holocene and contemporary *Discoglossus*, then adults of the latter genus correspond structurally to an incompletely developed *Latonia* and thus may be considered paedomorphic (Roček 1994).

Neoteny and paedomorphosis of amphibians may be manifested not only at the generic level but also at higher taxonomic ranks. For example, if the general structural scheme of the adult anuran skull is compared with that of the ontogenetic series in temnospondyl amhibians (Fig. 3), it is apparent that anurans may be interpreted as temnospondyls with shortened developmental period (Warren and Hutchinson 1988, 1990, Warren and Schroeder 1995). Also Bolt (1969, 1977, 1979) listed some structural paedomorphic features of a dissorophid amphibian *Doleserpeton*, which is considered to be phylogenetically linked with anurans. The paedomorphic nature of anurans is supported by findings of some additional bones in extraordinarily old individuals of various groups of frogs, mainly those which appeared early in the fossil record like Discoglossidae or Pelobatidae (Smirnov 1990, 1994, 1995). These cranial elements, for example the supratemporal, postfrontal, postorbital, tabular, etc., normally appear in the late developmental stages of temnospondyls but they are lacking in anurans because of a shortened period of somatogenetic development. It is not surprising that some of these elements have been found in *Triadobatrachus*, an amphibian from the Lower Triassic of Madagascar with anuran affinities (Roček 1988, Rage and Roček 1989). All these data support the view, which is now generally accepted, that anurans are paedomorphic descendants of labyrinthodonts.

Cooling events as reasons for neoteny and paedomorphosis

As previously mentioned, a long-term temperature drop, which is accompanied by an increase in seasonality, is an important climatic factor which can affect semiterrestrial ectotherms. If they are not resistent enough, they may respond in two ways. Either, the climatic conditions in a given region change to such a degree that these animals die out or survive only in some restricted refugia where original conditions persist, or they can adapt. It should be noted that ectotherms may not respond by shifting their temperature preferences but rather by changing their timing of development. It is theoretically possible that the entire somatogenetic development could be compressed into a shorter period of time. However, this seems to be the case only for gonadal development. Conversely, in somatogenetic development, the compression into a shorter period of time results in the subsequent reduction in number of stages as the terminal stages are not reached. This was supposedly the mechanism which affected some urodeles during the Oligocene cooling event, and is a possible explanation for the simultaneous appearance of such distinctly neotenous taxa like *Andrias* and *Branchycormus*.

However, the Tertiary fossil record of urodeles suggests that not all populations responded in this way. This can be seen in *Chelotriton*, whose stratigraphic distribution ranges from the middle Eocene to late Pliocene (thus covering periods of tropical climate with low seasonality in the Eocene, as well as significant cooling in the late Oligocene; Berger 1990, Cícha and Kováč 1990, Crowley and North 1991, Prothero 1985, Walther 1990, Wolfe 1978), *Chelotriton* was not affected by neoteny nor by paedomorphosis. Moreover, in the late Oligocene locality Rott, where two distinctly neotenous amphibians were recovered (*Andrias, Brachycormus*), an amphibian displaying normal development occurred too (*Chelotriton*, closely related to *Brachycormus*). This suggests that response of amphibians to cooling events may not be universal.

In contrast, the global cooling at the Pliocene/Pleistocene boundary influenced also those amphibians which apparently survived the Oligocene cooling event unaffected. *Chelotriton* disappeared from Europe and its close descendants (*Tylototriton, Echinotriton*) survived today only in the south-east Asia which may be considered their refugium. Thus, extensive glaciation in northern Eurasia resulted not only in the reduction of the formerly large area of distribution into a vestigial refugium, but also led to their survival as paedomorphic descendants of their Tertiary ancestral *Chelotriton*. The paedomorphic nature of these descendants can be seen by the reduced amount of ossification and the absence of dermal ornamentation. Thus *Chelotriton*, in its original state, disappeared. Curiously enough, *Andrias* (congeneric with *Cryptobranchus*), in spite of its neotenous nature, followed the same zoogeographic history as *Chelotriton-Tylototriton* and also survives in south-east Asian refugium. It should be noted in connection to this that *Brachycormus* did not survive the Pleistocene glaciation. Since it is anatomically very similar to modern *Triturus* and since the main difference between the two genera lies in the degree of development of the branchial skeleton, it is possible that *Triturus* is the evolutionary descendant of *Brachycormus*, providing that hyposomatic development was maintained but metamorphosis was completed (Roček, in press).

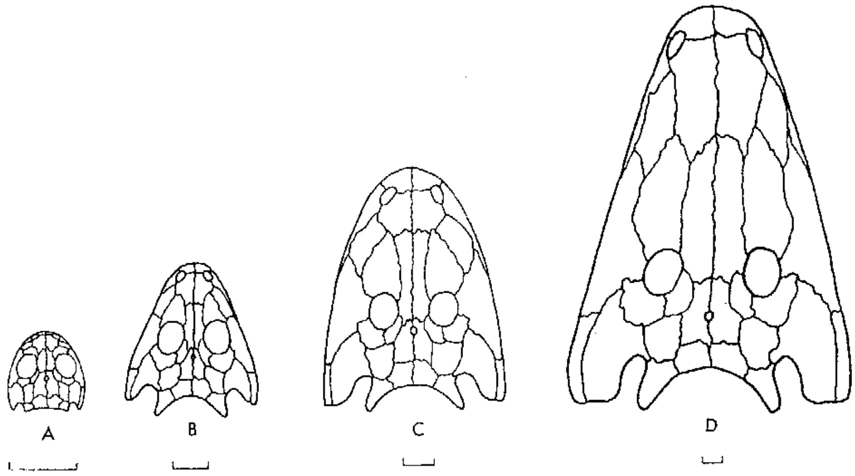

Figure 3. Changes in skull roof proportions during postmetamorphic growth of the early Triassic (Scythian A1) capitosaurid amphibian *Parotosuchus aliciae* (Warren et Hutchinson, 1988) from Queensland. A – at metamorphosis, B, C – intermediale growth stages, D – adult. Lines for scale are 10 mm. From Warren and Hutchinson (1988).

A similar evolutionary history holds for *Palaeopleurodeles*, which is another Tertiary salamandrid from Europe. Like *Chelotriton*, it survived the Oligocene cooling event unaffected but the Pleistocene cooling led to the development of a paedomorphic descendant *Pleurodeles* (restricted today to southern Iberian Penninsula and northern Africa).

Among anuran amphibians, *Latonia* from the European Neogene (Roček 1994) parallels *Chelotriton* and *Palaeopleurodeles* in that its paedomorphic descendant (*Discoglossus*) is currently restricted to a geographical refugium south of its original area of distribution. It seems that the modern anurans (e.g. Ranidae, Bufonidae), despite having followed the same zoogeographical history, have not changed their rate of development, and re-immigrated back after withdrawal of the continental glacier. In contrast, the Palaeobatrachidae did not survive the Pleistocene cooling and became extinct; this was most probably due to their prevailingly aquatic way of life. This is especially interesting in the context that they are the only family in the whole history of the Anura which became totally extinct.

With regard to the early Triassic appearance of some transitional forms to the modern Anura (like *Triadobatrachus*), which correspond structurally to the underdeveloped temnospondyls, one may suppose that their somatic underdevelopment was associated with the dramatic cooling event at the end of the Permian. This event is generally considered to be the greatest extinction of Earth's biota, when 75% of amphibian families and 80% of reptile families disappeared (Nevo 1995). It should be taken into account that this was the period when metabolic thermoregulation (i.e. endothermy) initially appeared in the evolutionary history of vertebrates among anatomically advanced reptiles (Therapsida). This may be understood as an adaptation to a sustained period of global cooling, and a long-term temperature drop may be taken as a similar plausible causal mechanism for paedomorphic nature of anurans.

Acknowledgements

I would like to express my sincere thanks to Susan Rehorek, University of Adelaide for the linguistic review of an earlier draft. The project "The role of neotemy and paedomorphosis in the evolution of the Amphibia: evidence from paleontological and embryological data" was supported by the Grant Agency of the Czech Republic (Grant No 204 / 94 / 3001) and by the Deutsche Akademische Austauschienst grant No 323 / 94.

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