

Skull of the Neotenic Salamandrid Amphibian *Triturus alpestris* and Abbreviated Development in the Tertiary Salamandridae

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ABSTRACT The skull of neotenic individuals of the Alpine Newt *Triturus alpestris* from the locality Drakolimni (Greece) is described on the basis of models made from magnified serial frontal sections. In order to recognize features associated with neoteny and paedomorphosis, the results were compared with normal development of contemporary *Triturus* and of other Caudata. The neotenic larvae from Greece correspond to advanced stages of metamorphosis in normal development of *Triturus alpestris*. Comparison with salamandrids from the Tertiary of Europe in which the hyobranchial skeleton was preserved, namely *Brachycormus noachicus*, *Chelotriton paradoxus*, and *Palaeopleurodeles hauffi*, revealed that both latter taxa were completely metamorphosed adults anatomically similar to their contemporary relatives *Tylotriton*, *Echinotriton*, and *Pleurodeles*, whereas *Brachycormus*, though apparently related to *Chelotriton*, was a neotenic amphibian. This is suggested by its incompletely metamorphosed but ossified hyobranchial skeleton. © 1996 Wiley-Liss, Inc.

The Alpine Newt *Triturus alpestris* is a common newt distributed in Europe west from the eastern foothills of Carpathians. It is absent only from Scandinavia and the Russian Plateau. Since its altitudinal distribution extends from sea level to about 2,500 m in the Alps (Grossenbacher, '88), it may be considered a species inhabiting habitats over a wide altitudinal range. Originally it may have been associated with forests of moderate climate. Its contemporary distribution only avoids areas with intensive agriculture. The limiting factor is aridity, suggested by isolated vestigial occurrences in high altitude areas originally covered by forests in the Balkan Peninsula and Appenin Peninsula (Sotiropoulos et al., '95). The Alpine Newt lives close to its ecological limits in this part of its distribution, evidenced by some percentage of individuals in these isolated populations which do not metamorphose and remain as neotenic larvae (described earlier as subspecies *lacusnigri*, *montenegrinus*, *serdarius*, and *piperanus*) or paedomorphic adults (subspecies *reiseri*). It is noteworthy that some individuals in these populations can reach normal postmetamorphic stage and that the neotenic larvae, if they are transferred into other environmental conditions, are able to metamorphose. Breuil and Guillaume ('85) found that there is no genetic

difference between metamorphosed individuals and neotenic larvae in these populations, and that the neotenic larvae cannot be considered separate subspecies. The environment of the Mediterranean populations of the Alpine Newt deteriorated, with increasing aridity resulting from cutting of forests during the Medieval Age. Some individuals may have responded to this deterioration by somatic development blocked at the phenotype stage of larva living permanently in water. Since sexual maturity is normally attained, this phenomenon may be described as neoteny, though not genetically fixed (Roček, '74b).

Abbreviated somatic development may also be recognized in fossil amphibians. Their maturity may be evidenced by complete ossification (including carpals and tarsals, but even in adults of some taxa these elements remain cartilaginous, as may be illustrated by *Andrias*; Westphal, '58; Böttcher, '87). Among numerous kinds of heterochrony (Gould, '77), two may be recognizable in fossil amphibians, according to the ultimate stage of their somatogenies. The first is neoteny (Kollman, 1885), defined as somatic development blocked in premetamorphic stages so that sexual maturity is associated with larval phenotype. The second is paedomorphosis (Garstang, '22), usually defined (Gould, '77) as retention of ancestral juvenile characters

by later ontogenetic stages of descendants; in such case maturity is attained in postmetamorphic, though not ultimate, stages of somatogenesis, which means that juvenile characters may be found in an adult.

There are four families of contemporary Caudata known to include exclusively neotenic forms, namely Amphiumidae, Cryptobranchidae, Proteidae, and Sirenidae. However, neoteny or at least persistence of juvenile characters in metamorphosed individuals may also be found in other families of the Caudata, e.g., in the Plethodontidae and Salamandridae. The same phenomena are recognized in some groups of fossil Caudata as well, by their incompletely developed but fully ossified skeletons. They have been found in the Tertiary urodeles, such as *Andrias Tschudi* (Cryptobranchidae), *Orthophylax Meyer* (? Proteidae), *Opisthotriton Auffenberg* and *Palaeoproteus Herre* (Batrachosauroididae), *Habrosaurus Gilmore* (Sirenidae), and others (Estes, '81). In the Mesozoic urodeles like *Karaurus* from the late Jurassic (Ivakhnenko, '78) and *Hylaeobatrachus* from the early Cretaceous (Dollo, 1884), some parts of the hyobranchial skeleton are preserved but not to a degree that would allow one to determine whether they are larvae or adults. In *Triassurus* from the late Triassic (Ivakhnenko, '78), faint imprints of the epibranchials are preserved, but judging from the incompletely ossified vertebrae this is a larva rather than a perennibranchiate adult.

What was the reason for the comparatively frequent occurrence of somatic underdevelopment in mentioned fossil and recent Caudata and does this phenomenon play any significant role in their evolution? The aim of the present paper is to describe the skull in a living neotenic form, to recognize the attained degree of its somatogeny, and to use these data for interpretation of the developmental status of closely related fossil taxa in which the hyobranchial apparatus and some other anatomical features have not reached their ultimate adult stage. The Alpine Newt is especially suitable for this purpose because it is a member of the family Salamandridae that is well represented in the Tertiary of Europe, and it can respond to deterioration of living conditions on a broad scale, from overwintering to neotenic larvae.

MATERIALS AND METHODS

Neotenic larvae of *Triturus alpestris* (Laurenti, 1768) were collected in the locality Drakolimni (Tymfi Mts., Greece; altitude

2,150 m), September 1988. These larvae bear partly larval characters (broad skull, vestiges of external gills, extensive tail fin) and partly characters of adults (color pattern on the ventral side of the trunk and tail, cloacal region). They are not only larger than normal larvae in about the same developmental degree (cf. Roček '74a, Fig. 5) but moderately larger than adults as well (Smirina and Sofianidou, '85, Fig. 2; see also Roček, '74b, Figs. 1–4). They are sexually mature and reach the individual age of 6–7 years (Smirina and Sofianidou, '85). The heads of two individuals not differing externally by degree of their development were sectioned (thickness 12.5 μm) and magnified ($\times 40$). Models of their skulls were constructed from the magnified frontal sections (every second section was used so magnified sections were 1 mm thick). Results were compared with published data on the normal development of the skull in *Triturus alpestris* and other recent and fossil Caudata.

The Tertiary urodeles in which the hyobranchial skeleton was preserved, namely *Brachycormus noachicus* (Goldfuss, 1831), *Chelotriton paradoxus* Pomel, 1853, and *Palaeopleurodeles hauffi* Herre, 1941, were investigated with regard to degree of metamorphosis of the hyobranchial skeleton, and the degree of overall ossification. Some specimens were studied both as negative imprints in matrix and as latex casts. Few were preserved as real skeletons. Two specimens of *Chelotriton paradoxus* from Enspel (JGUM 5809 and 5810) could be investigated from dorsal and ventral sides during the process of preparation carried out in the Landesamt für Denkmalpflege, Mainz. The skeletons examined are deposited in the Geologisches-Paläontologisches Institut der Universität, Bonn (GPIBO), Johannes Gutenberg Universität, Mainz (JGUM), and Urwelt-Museum Hauff, Holzmaden (UMH).

When appropriate, reference is given to papers in which full definition or first use of an anatomical term appears (both in case of synonyms, i.e., when different terms are used for the same structure, or homonyms, i.e., when same names are used for different structures).

RESULTS

The skull in neotenic Triturus alpestris Neural endocranium

Nasal capsules are comparatively well developed, though separated from the posterior part of the neural endocranium by a gap in the orbital region (see below) (Figs. 1, 2).

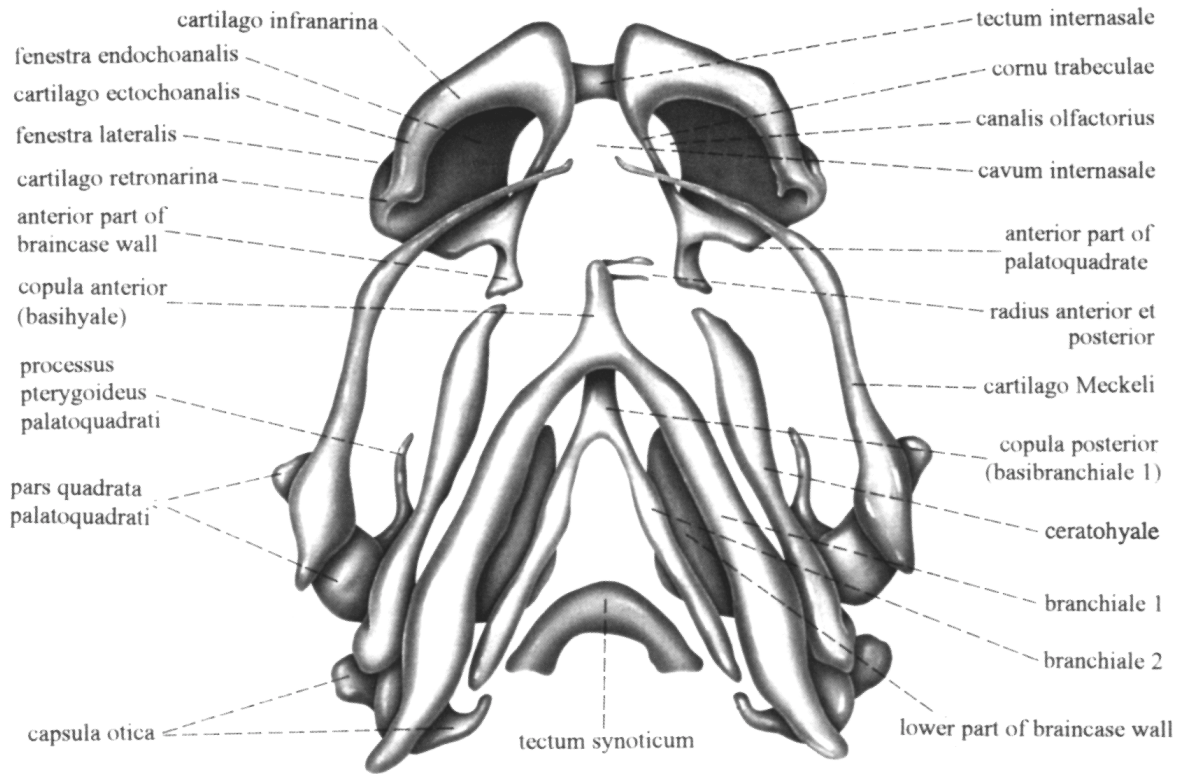


Fig. 1. Ventral view of neural and visceral endocranium of neotenic *Triturus alpestris*.

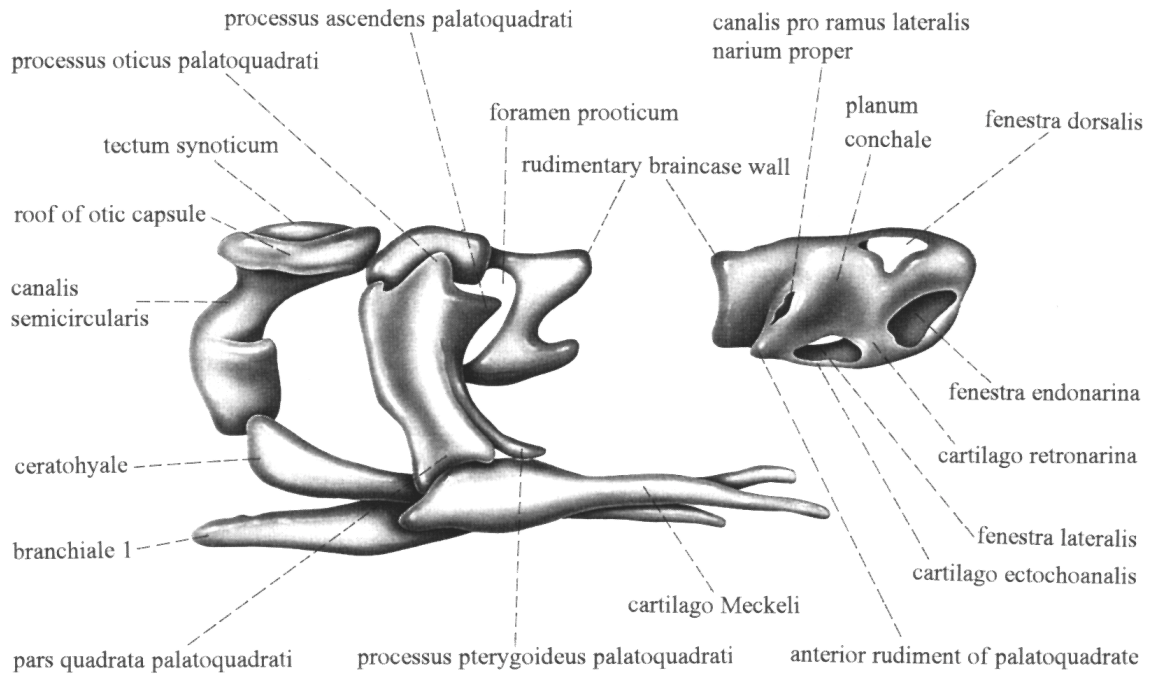


Fig. 2. Lateral view of neural and visceral endocranium of neotenic *Triturus alpestris*.

Both capsules are connected by a thin and comparatively narrow tectum internasale (*sensu* Stadtmüller, '36: 546) roofing dorsally in a very limited extent a space between both capsules (cavum internasale; "Intermaxillarraum" or "Internasalraum" of Born, 1876: 625). The floor is, however, beginning to develop as evidenced by a larger specimen (see below). The ventromedial part of each capsule is formed by a thickened crista confluent with the lower part of the braincase wall. It is considered homologous with the trabecular horn (Stadtmüller, '36: 546) or trabecula (Born, 1876: 630). Both cornua trabecularum diverge posteriorly in the ethmoidal region. In the larger individual there was a narrow thin connection between both capsules produced by both cornua at the level of the posterior margin of the canalis olfactorius. The capsule itself is a simple structure, the inner space of which is not subdivided. Its walls are pierced by several large and small foramina. One of the largest is facing posteromedially into the braincase cavity. This is a short canalis olfactorius (called fenestra olfactoria by Stadtmüller, '36: 546). It may or may not be confluent with the fenestra dorsalis piercing the roof of the capsule (in the specimens investigated, this opening was developed to various extents even in a single individual, and it was nearly completely obliterated in a larger specimen). The floor of the capsule is pierced by another large foramen, the fenestra endochoanalis (*seu* fenestra choanalis, fenestra basalis; Stadtmüller, '36: 547, 548, Fig. 405). It opens posteroventrally into the mouth cavity and its posterior part serves as the apertura choanalis of the nasal sac. Two other fenestrae are in the lateral wall of the capsule, the fenestra endonarina (*seu* narina, rostralateralis; Stadtmüller, '36: 547, Fig. 408) for the naris externa of the nasal sac and the ductus nasolacrimalis (Born, 1876: 628, 629), and the fenestra lateralis (*seu* infraconchalis; Stadtmüller, '36: 547, Fig. 409); both are separated by the cartilago retronarina. For further, more detailed description other terms were introduced—the cartilago infranarina for that part of the capsule between the fenestra endonarina and fenestra endochoanalis, and the cartilago ectochoanalis separating the latter from the fenestra lateralis (see Stadtmüller, '36: 548). The roof of the nasal capsule slants down lateroventrally, and is termed the planum conchale in its posterior part; the planum is distinctly depressed and

is called the impressio conchalis. The posterior wall of the capsule slants down posteroventrally, producing an indistinct outgrowth in the middle of its mediolateral extent; this is the anterior rudiment of the palatoquadrate (see below). The lower margin of the wall is the posterior margin of the fenestra endochoanalis. The wall is pierced by two foramina—a larger medial, the canalis pro ramus medialis n. ophthalmici (*seu* foramen orbitonasale mediale; Stadtmüller, '36: 547) and the smaller canalis pro ramus lateralis narium proper (foramen orbitonasale laterale; Stadtmüller, '36: 547). Detailed morphology of the most anterior part of the nasal capsule cannot be given because it was lost in the course of sectioning.

The orbital section of the neural endocranium is, regardless of the developmental stage of the neotenic larvae, restricted to the anterior and posterior parts of the braincase wall. In the smaller individual the wall ends abruptly, whereas in the larger specimen the anterior vestige of the wall decreases in height posteriorly so that its lower margin terminates in a posteriorly directed process. The posterior vestige of the orbital braincase wall produces two anteriorly directed processes—the larger is dorsal, forming part of the upper margin of the braincase wall; the smaller is ventral and is directed towards the similar process (mentioned above) on the anterior vestige of the braincase wall. The space between the anterior and posterior vestiges is not formed by any soft tissue. The posterior vestige of the braincase wall produces, besides the two anterior processes, two similar processes directed posteriorly. The dorsal one connects with the cartilaginous rudiment of the anterodorsal part of the otic capsule (though it seems that in the smaller individual this connection is not yet made); the lower is compressed dorsoventrally and ends freely at the level of the processus basalis palatoquadrati. The space between the two posterior processes is part of the foramen prooticum through which pass the trigeminus and facialis (probably also abducens) nerves.

The otic capsules are developed to a much lesser extent, compared to the nasal capsules. Their medial wall is nearly completely lacking and only very small precursors are formed by soft tissue. Several chondrified parts of the capsule may be discerned. The posterior part of the roof is present, distinctly depressed, and includes that part roofing the

canalis semicircularis lateralis. The medial wall of this canal is chondrified in a short extent and it is confluent with the ventrolateral wall of the vestibulum (the main cavity of the capsule). Anterolaterally is a rudiment of the otic capsule. The palatoquadrate is adjoined to its ventrolateral surface. Both are separated by a distinct slit. The dorsomedial part of the capsule appears as a slender rod directed posteromedially towards the chondrified part the tectum synoticum (*seu* tectum posterius; Stadtmüller, '36: 526) which occupies the space between developing roofs of both capsules but is not confluent with them. It should also be noted that chondrification of the otic capsules may be rather irregular, as is suggested by the fact that in the larger specimen the capsules were chondrified in a lesser degree. However, the chondrified parts basically correspond to the described scheme.

Visceral endocranium

The palatoquadrate consists of five parts: 1) The pars quadrata which, together with Meckel's cartilage, forms the jaw joint; 2) the processus pterygoideus (processus pterygopalatinus; Stöhr, 1880: 505) which is thin, slightly sigmoid, and ends free anteriorly. It is worthy of note that Stadtmüller ('36: 571) considered it present, though not connected with the postnasal wall in all *Triturus* species but mentioned its absence in neotenic *Triturus*; 3) the processus ascendens which extends anteriorly parallel to the processus pterygoideus but dorsally to it. In the investigated specimens the ascending process did not fuse with the braincase wall; 4) the processus oticus which adjoins the lateral surface of the developing otic capsule; and 5) the processus basalis ("Palatobasalfortsatz" of Stöhr, 1880: 500) which may be distinguished in the investigated specimen as an outgrowth towards the bases of the not yet fully cartilaginous otic capsule. According to Stadtmüller ('36: 575–576) there is some variation in the connection of this process with the otic capsule. He mentioned that in the neotenic *Triturus alpestris* the processus basalis can be confluent with the capsule on one side and separate on the other. This condition is undoubtedly associated with the degree of chondrification of the otic capsules. The postnasal wall ends in a distinct process directed posteroventrally, interpreted as the rudiment of the palatoquadrate (Fig. 2), towards the anterior tip of the processus pterygoideus palatoquadrati. Both these structures may represent vestigial palatoquadrate.

The mentomandibular was not found. However, Stadtmüller ('36: 643) mentioned that this element is developed in *Triturus alpestris* and other *Triturus* species, and that in the neotenic *Triturus alpestris* it appears as a perichondral ossification. Meckel's cartilage (mandibular) is slender anteriorly (pars fibularis) but stout posteriorly (pars articularis). Both mandibulars were asymmetrical in size and shape in one investigated specimen. The mandibular of its left side reached the midline whereas that of its right side was much shorter and its anterior tip was turned slightly laterally. In any case, both elements were not in touch and consequently connected neither syndesmotically nor synchronotically.

In the hyobranchial apparatus (consisting of all postmandibular branchial elements; see Fig. 1), the most anterior is an element independent of the more anterior Meckel's cartilage and other elements. That part of the hyoid arch is termed the ceratohyal in the complete larval branchial skeleton (Tarapani, '09: 70, Plate 6, Fig. 4a,b). It is called the hyale in those taxa in which the larval hyoid arch consists of a single element, or the ceratohyale in those Caudata in which the hyoid arch consists of the hypohyal and ceratohyal. In metamorphosed *Triturus* it is separated anteriorly from the basihyale (=copula anterior) and is termed the cornu hyale. The posterior part of this element in the specimens examined is bent dorsally towards the ventrolateral part of the otic capsule (the area of the future foramen ovale). At the level of the anterior end of the ceratohyal (=cornu hyale) there is an unpaired median element which is the basihyale (=copula anterior). It is confluent posteriorly with the next arch that is formed by a stout cartilaginous bar (cornu branchiale I; Tarapani, '09: 74, Plate 6, Fig. 5a) that ends freely beneath the otic capsule. It is moderately swollen anteriorly as well as in the border of the posterior two thirds of its length but one cannot precisely distinguish the border between the hypobranchial and ceratobranchial. However, Tarapani ('09: 74) found a broad syndesmotic connection between the two in normal development of *Triturus alpestris*. From the dorsal part of the posterior end of the copula anterior runs another, slightly thinner median element which is the basibranchiale of the second posthyoid arch (=copula posterior). This element also bifurcates posteriorly into two cartilaginous bars

(cornua branchialia II; Tarapani, '09, Plate 6, Fig. 5b) similar to those of the first posthyoid arch but smaller. The hyobranchial skeleton thus consists of two basibranchials (see also Stöhr, 1880: 484, Plate 29, Fig. 5; however, it should be noted that Tarapani, '09: 74–75, Plate 6, Fig. 5a,b considered the unpaired median element a single copula consisting of ventral and dorsal parts) and three branchial arches. All these arches terminate freely posteriorly, i.e., their commissurae terminales are absent. The copula anterior produces on its anterior tip two thin perpendicular outgrowths termed by Stadtmüller ('36: 665) the anterior and posterior radius (or "Bügelknorpel"). In the specimen investigated they are not yet fully developed (they are present on one side only) and they do not reach the anterior end of the cornu hyale, as is the case in the hyoid of, e.g., metamorphosed *Triturus cristatus*. Tarapani ('09: considered them vestiges of the hypohyals, whereas Stadtmüller ('36: 665) considered them neomorphs. The urobranchial (*sensu* Stöhr, 1880: 485; "Copulastiel" of Tarapani, '09: 75, Pl. 6, Fig. 5a,b) was not found in either of the specimens investigated.

The skull in Tertiary Salamandridae
Brachycormus noachicus

A description of all the available skeletal parts of *Brachycormus noachicus* was given by Roček (1996); only a brief description of the hyobranchial skeleton and topographically associated structures will be given here (Fig. 3A). The skull is preserved as imprints in matrix but the ossified parts of the hyobranchial skeleton can be reconstructed from several individuals. There is one median element which can be interpreted as the basihyal (=copula anterior). Anteriorly, it extends to the level of the choanae. Its posterior end is associated with two posterolaterally directed slender elements that can be interpreted as the first ceratobranchials. In some specimens the copula and ceratobranchials are articulated and the border between them is distinguishable; in others they seem to be confluent. These differences may be ontogenetic or possibly due to preservation. Another pair of elements is situated laterally from the ceratobranchials; their anterior ends are directed towards the posterior half of the copula, whereas their posterior ends are directed to the vicinity of the jaw joint. These may be interpreted as the ceratohyals. It is noteworthy that the ceratobranchials are absent in PIUB-Ro 4243; interpretation of the

preserved element as the ceratohyal is based on the superimposed projection of this and other specimens in the same scale, a projection revealing that the first ceratobranchial is situated medially. The posterior ends of the ceratohyals were articulated with the epihyals which extend beyond the margin of the otic capsule. Similarly, there are several epibranchials. The most lateral of them is apparently associated with the first ceratobranchial and may be thus interpreted as the first epibranchial. All epibranchials are situated on the lateral margin of the otic capsule. The described elements of the hyobranchial skeleton are discernible as imprints in matrix which suggests that they were ossified or at least consisted of mineralized cartilage. The second and third epibranchials suggest that there were also other (2nd and 3rd) branchial arches present, probably as strips of cartilage.

In addition to the hyobranchial skeleton, the general proportions of the skull (e.g., the jaw joint located far anteriorly, the otic capsules prominent posteriorly) also suggest larval features. In contrast, ossified carpals and tarsals as well as ossified epiphyses of the long bones may be taken as evidence of sexual maturity and thus that the fossils represent adults. *Brachycormus noachicus* was thus apparently neotenic.

Palaeopleurodeles hauffi

The skull of *Palaeopleurodeles hauffi* is very similar to that of *Chelotriton*, but not as broad (Fig. 3B). The hyobranchial apparatus is also similar, consisting of a pair of bowed first ceratobranchials and pairs of distal parts of first epibranchials and distal parts of ceratohyals. In the holotype specimen (UMH) there are two parallel fragmentary rod-like elements underneath the otic capsule which most probably represent these latter elements of the hyobranchial skeleton.

Chelotriton paradoxus

The skull of *Chelotriton paradoxus* is broad and heavily ossified (the maxilla is in broad contact with the quadratojugal; all dermal bones are ornamented) (Fig. 3C). The copula is short, with a pair of stout, posterolaterally directed elements adjoining its anterior half. They may be interpreted as the first ceratobranchials because in JGUM 5809 there is another element laterally adjoining the posterior end of the first ceratobranchial. This may be the remnant of the ceratohyal. Its

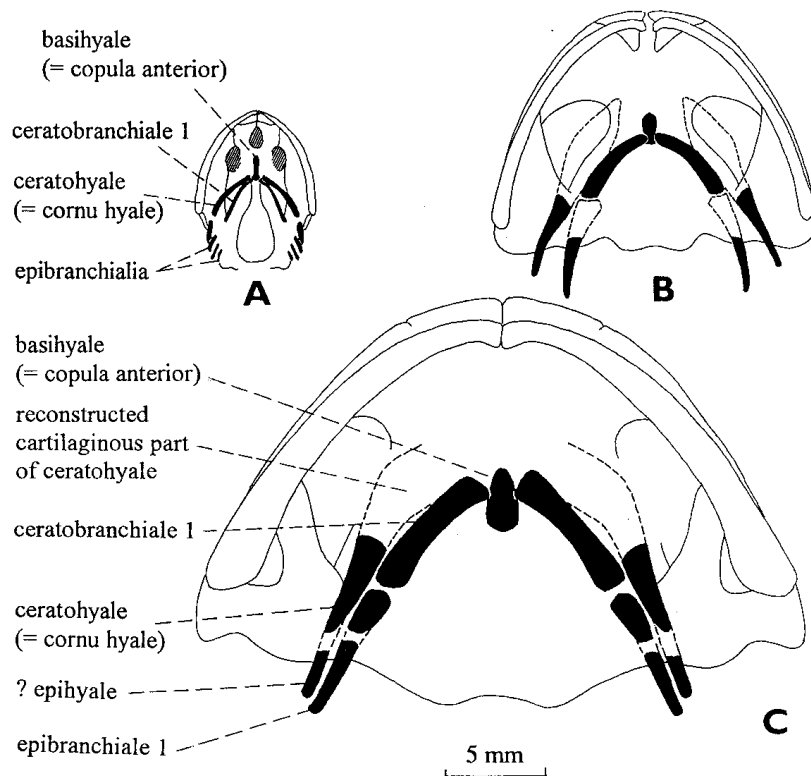


Fig. 3. Reconstruction of skull in ventral view of some Tertiary salamandrids. **A:** *Brachycormus noachicus* (late Oligocene, Rott near Bonn, Germany). **B:** *Palaeopleurodeles hauffi* (early Miocene, Randecker Maar, Germany). **C:** *Chelotriton paradoxus* (late Oligocene, Enspel, Germany). Ossified parts of hyobranchial skeleton are black. Broken line, cartilaginous part of ceratohyals. All drawn to the same scale.

anterior part is absent and most probably it was cartilaginous, as in most contemporary salamandrids. Also the distal tips of the ceratohyal and the first ceratobranchial were completed by cartilage (as suggested by their concave ends). The posterior end of the first ceratobranchial is associated with an imprint of another element that may be interpreted as the first epibranchial. This interpretation is supported by JGUM 5810 preserved in dorsal view, where two parallel elements project from below the squamosal; the shorter lateral and longer medial are no doubt distal ends of the epihyal and first epibranchial, respectively. The shape of the skull with the jaw joint shifted far posteriorly and the shape of the hyobranchial skeleton suggest that all specimens were adults.

"*Tylototriton*" weigelti

This taxon was described on the basis of a poorly preserved skeleton exposed in dorsal aspect, and it was referred to as *Tylototriton* before the complete skull of *Chelotriton* was

discovered. It probably belongs to the latter genus. Two parallel rod-like elements project from below the squamosal on the left side (Herre, '35, Fig. 19). They may represent distal tips of the ceratohyal and first epibranchial. Their size and position suggest that the hyobranchial skeleton was similar to that of *Chelotriton* and *Palaeopleurodeles*.

DISCUSSION

Comparison of neotenic and normal Triturus alpestris

Judging by the degree of development of the hyobranchial apparatus, both neotenic individuals agree with metamorphosing larvae (30 mm total length) of normal *Triturus alpestris* (Tarapani, '09: 73–75, Plate 6, Fig. 5a,b). Tarapani mentioned a vestige of the urobranchial and she was able to distinguish syndesmotomic division between the hypobranchial and ceratobranchial. These differences may be caused by the degree of chondrification. Such larval characters of the hyobranchial apparatus, like the connection of the

hypohyal to the copula, the presence of ceratobranchials 3 and 4 (i.e., four posthyoid arches), and the interconnection of the posterior ends of the ceratobranchials by the commissurae terminales, have already disappeared. On the other hand, the final developmental stage of the hyoid in the adult was not yet reached (Özeti and Wake, '69, Fig. 3C). One can thus conclude that the neotenic larva corresponds in structure of the hyobranchial apparatus to a normally developing larva, except for its size. The size of the neotenic larvae can reach that of a metamorphosed adult, so the most conspicuous (and the only) difference between the both kinds of larvae is the greater size of the neotenic one.

Little has been published about the rate of membrane bone formation in this newt. This, together with the fact that membrane bone formation had only begun in the investigated specimens, does not allow any comparison with data from the literature. A possible basioccipital was found in *Triturus alpestris* by Stadtmüller ('29a,b).

Comparison of neotenic Triturus alpestris with other Caudata

As in other Caudata, the neural endocranium of the neotenic individuals of *Triturus alpestris* is, when compared with the visceral endocranium, markedly retarded in its development. This concerns mainly the otic capsule which is chondrified to an extent corresponding to the earlier stages of normal development of other *Triturus* species (Stöhr, 1880: 505). However, apart from this retardation the chondrification modus of the otic capsule is the same as in other species; for instance, its medial wall is among the latest structures that chondrify within the otic capsule (Stöhr, 1880: 497–498).

Nasal capsules separated from the orbital region is a character that may be found in neotenic genera *Necturus* and *Proteus* (Stadtmüller, '36: 545) and may be ascribed to a lower ossification degree of the neural endocranium. However, in the course of normal development of other *Triturus* species the braincase side wall develops from the trabeculae by their upward growth (crista trabeculae of Stöhr, 1880: 490, Plate 19, Fig. 11), so that the opticus nerve is enclosed in a foramen. Only farther posteriorly, at the level of the ganglion Gessneri, is the wall absent but the trabeculae continuous—this is the condition found in investigated neotenic *Triturus alpestris*. A conspicuous feature in which the neo-

tenic *Triturus alpestris* differs from other *Triturus* species is that at the level of the anterior tip of the notochord, the bottom of the braincase is entirely absent (cf. Stöhr, 1880: 492–493).

Stadtmüller ('36: 571) lists those genera of the Caudata in which the processus pterygoideus palatoquadrati develops in early developmental stages as a continuous strip of tissue connecting the posterior part of the process with the nasal capsule (or, in this stage, with the trabecula). In only a few taxa it persists in its entirety into the cartilaginous stage (in larvae of various ages) but in all of them it loses its connection with the nasal capsule in adults. From this larval development one may conclude that the continuous palatoquadrate was the ancestral state and the condition found in neotenic and metamorphosed *Triturus* is derived. It also should be noted that in *Triturus cristatus* the processus pterygoideus originates as an independent cartilaginous center (Stadtmüller, '36: 572) much later than the pars quadrata (Stöhr, 1880: 511). The processus oticus is always well separated from the otic capsule, and a distinct slot was also found in large larvae of *Triturus cristatus* (Stöhr, 1880: 509–510). As in *Triturus alpestris*, in other *Triturus* species, and in *Ambystoma* the processus ascendens originates independently from the braincase wall. Later, the ascending process is retarded in its development and finally it fuses with the wall (Stöhr, 1880: 491, 510–511, Plate 19, Figs. 11, 12) but remains separated in the neotenic *Triturus alpestris*.

The development of the hyobranchial apparatus in *Triturus alpestris* does not differ substantially from that in *Triturus cristatus* (Stöhr, 1880: 482–485, Plate 29, Figs. 1–3); consequently, the neotenic larvae of the former species correspond (as to the degree of development of the hyobranchial apparatus) to metamorphosing larvae of the latter. Slight differences may occur in the timing of separation of the hyoid arch from the basi-hyal. According to Stöhr (1880: 484, Plate 19, Fig. 3), the separation of both hyals from the copula anterior takes place in *Triturus cristatus* at the time when the urohyal (urobranchial according to Stöhr) and all posterior branchial arches are still present. Stöhr, however, investigated earlier, premetamorphic stages. The posterior end of the urohyal can ossify after metamorphosis in some *Triturus* species which means that this element does

not always disappear in adults (Tarapani, '09: 130; Stadtmüller, '36: 663, 666).

In the specimens investigated the operculum was not yet discernible, whereas Stöhr (1880: 500–501) found it in *Triturus cristatus* as early as in larvae of the total length of 24 mm.

*Comparison of the normal and neotenic
Triturus alpestris with
Tertiary salamanders*

Members of the family Salamandridae from the Tertiary of Europe in which the preserved and articulated skull also includes the hyobranchial skeleton are *Chelotriton* (extending from the Oligocene and possibly, as is suggested by "*Tylotriton*" *weigelti* which is probably *Chelotriton* too, from the middle Eocene through late Miocene), *Palaeopleurodeles* (from the early Miocene), and *Brachycormus* (from the late Oligocene). If these fossils are compared with the normal and neotenic *Triturus alpestris* as a contemporary representative of the family, one may state that *Chelotriton* and *Palaeopleurodeles* are no doubt adults. This is evidenced not only by their degree of both dermal bone formation and endochondral ossification but also by the shape of their hyobranchial skeleton, the ossified parts of which do not differ from those of adults of contemporary *Tylotriton* and *Pleurodeles* (possibly except for epiphyseals). The main difference between *Chelotriton* and *Tylotriton*, and *Palaeopleurodeles* and *Pleurodeles* is the lower degree of ossification in the cranial skeleton of the contemporary taxa. This is indicated, for example, by loss of ornamentation on the bones of the cranial roof, and by a narrow or interrupted connection between the maxilla and quadratojugal, and between the maxilla and pterygoid (present in some other contemporary taxa, e.g., *Pachytriton*). This hypo-ossification of the dermal skeleton is apparently caused by abbreviated somatogeny associated with the deterioration of climate during the Pleistocene. Özeti and Wake ('69: 116–117) correctly recognized the primitive status of *Tylotriton* and *Pleurodeles*, though they did not compare them with fossils.

In contrast, *Brachycormus* differs in exhibiting a hyobranchial skeleton similar to that of larval salamandrids. Especially the specimen GPIBO-Ro 4244b, in which both first ceratobranchials are confluent with the anterior copula, closely recalls the condition found in neotenic *Triturus alpestris* (Fig. 1) or in the final stages of metamorphosis of normal

development. Other specimens available suggest that the hyobranchial skeleton consisted of ossified elements separated by gaps which were filled with cartilage in living animals. This holds even for epibranchials (or for the distal sections of branchials, as may be judged from the condition in the neotenic *Triturus alpestris*) located laterally to the otic capsule. A similar condition may be found in living *Proteus* (Dolivo-Dobrowolsky, ex Stadtmüller, '36, Fig. 504). This suggests that *Brachycor-*

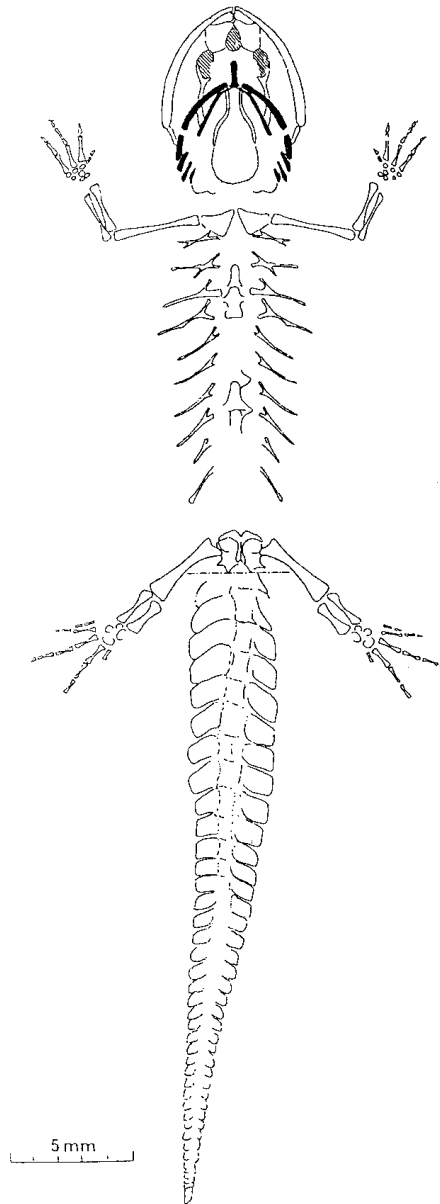


Fig. 4. Reconstruction of neotenic salamandrid *Brachycormus noachicus* (late Oligocene, Rott near Bonn, Germany) based on available elements. Tail twisted 90° along its longitudinal axis. Hyobranchial skeleton is black.

mus was a neotenic, permanent water dweller (this conclusion is supported by dilated spinal and haemal processes of the caudal vertebrae which no doubt supported the tail fin; Fig. 4).

Brachycormus is closely related to *Chelotriton* (both have the frontosquamosal arch which separates the postorbital vacuity from the orbit, bicapitate ribs, etc.). *Brachycormus* was recovered from the Late Oligocene locality Rott near Bonn in Germany. The Oligocene, especially its terminal part, was a period of global cooling and decreasing annual mean temperatures associated with increasing seasonality. This could be the main reason why this amphibian became neotenic. This shift could be preceded by the stage of "overwintering" larvae which were not able to complete their metamorphosis before hibernation due to shortened seasons. As a consequence, the breeding rhythm was retarded. This disadvantage was compensated for by a shift of ability to breed to a premetamorphic stage. Anatomically, such transition could be reconstructed if the somatogeny is blocked at the stage of advanced premetamorphic larva, or in larva before the end of metamorphosis. It should be noted that the earliest evidence of *Andrias scheuchzeri*, another late Oligocene neotenic amphibian, is from the same locality. This supports the hypothesis that late Oligocene deterioration of climate was the main reason for neoteny of these amphibians.

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LITERATURE CITED

- Born, G. (1876) Ueber die Nasenhöhlen und den Thränen-
nasengang der Amphibien. *Morphol. Jahrb.* 2:577-
646.
- Böttcher, R. (1987) Neue Funde von *Andrias scheuchzeri*
(Cryptobranchidae, Amphibia) aus der süddeutschen
Molasse (Miozän). *Stuttgarter Beitr. Naturk. [Ser. B]*
131:1-38.
- Breuil, M., and C.-P. Guillaume (1985) Étude électropho-
rétique de quelques populations de tritons alpestres
neoténiques (*Triturus alpestris*, Amphibia, Caudata,
Salamandridae), de sud de la Yougoslavie. *Bull. Soc.
zool. France* 109(1984):377-389.
- Dollo, L. (1884) Note sur le batracien de Bernissart. *Bull.
Mus. R. Hist. Nat. Belg.* 3:85-93.
- Estes, R. (1981) Gymnophiona, Caudata. In P. Welln-
hofer (ed): *Handbuch der Paläoherpetologie*, Part 2.
Stuttgart: Gustav Fischer, pp. 1-15.
- Garstang, W. (1922) The theory of recapitulation: A
critical restatement of the biogenetic law. *J. Linn. Soc.
Zool.* 35:81-101.
- Gould, S.J. (1977) *Ontogeny and Phylogeny*. Cambridge,
MA: Belknap.
- Grossenbacher, K. (1988) Verbreitung der Amphibien
der Schweiz. *Doc. Faunist. Helv.* 7:1-208.
- Herre, W. (1935) Die Schwanzlurche der mitteleocänen
(oberlutetischen) Braunkohle des Geiseltales und die
Phylogenie der Urodelen unter Einschluss der fossilen
Formen. *Zoologica (Stuttgart)* 33:1-85.
- Ivakhnenko, M.F. (1978) [Tailed amphibians from the
Triassic and Jurassic of Central Asia]. *Paleontol. Zh.*
12(3):84-88 (In Russian).
- Kollman, J. (1885) Das Ueberwintern von europäischen
Frosch- und Triton-larven und die Umwandlung des
mexikanischen Axolotl. *Verh. Naturf. Ges. Basel* 7:387-
398.
- Özeti, N., and D.B. Wake (1969) The morphology and
evolution of the tongue and associated structures in
salamanders and newts (family Salamandridae). *Copeia*
1969:91-123.
- Roček, Z. (1974a) Biometrical investigations of Central
European populations of the Alpine Newt—*Triturus*
alpestris alpestris (Laurenti, 1768) (Amphibia:
Urodela). *Acta Univ. Carol. Biol.* 1972:295-373.
- Roček, Z. (1974b) Beitrag zur Erkennung der Neotenie
des Alpenmolches *Triturus alpestris* (Laurenti, 1768).
Bull. Soc. Zool. Bohemoslov. 38:285-294.
- Roček, Z. (1996) The salamander *Brachycormus noachicus*
from the Oligocene of Europe, and the role of
neoteny in the evolution of salamanders. *Palaeontol-
ogy* 39(2):477-495.
- Smirina, E.M. and T. Sofianidou (1985) On life span of
the neotenic and metamorphosed Alpine Newts (*Tritu-
rus alpestris*) from high mountains of Greece. *Zool. Zh.*
64:311-315.
- Sotiropoulos, K., A. Legakis, and R.-M. Polymeni (1995)
A review of the knowledge on the distribution of the
genus *Triturus* (Rafinesque, 1815) in Greece. *Herpeto-
zoa* 8:25-34.

- Stadtmüller, F. (1929a) Nachweis eines Basioccipitale bei einem rezenten Amphibium. Verh. Anat. Ges. Suppl. Anat. Anz. 67(1929):219.
- Stadtmüller, F. (1929b) Studien am Urodelenschädel. II. Nachweis eines Basioccipitale bei einem rezenten Amphibium (*Triton alpestris*). Z. ges. Anat. [Abt. 1]. Z. Anat. Entwicklungsgech. 90:144–152.
- Stadtmüller, F. (1936) Kranium und Visceralskelett der Stegocephalen und Amphibien. In L. Bolk, E. Göppert, E. Kallius, and W. Lubosch (eds): Handbuch der vergleichende Anatomie der Wirbeltiere. Berlin: Urban & Schwarzenberg, pp. 501–698.
- Stöhr, P. (1880) Zur Entwicklungsgeschichte des Urodelenschädels. Z. Wiss. Zool. 38:477–526.
- Tarapani, H. (1909) Zur Entwicklungsgeschichte der Hyobranchialskeletts von *Salamandra atra* und *Triton alpestris*. Jena. Z. Naturwiss. 45:57–110.
- Westphal, F. (1958) Die tertiären und rezenten eurasiatischen Riesensalamander (Genus *Andrias*, Urodela, Amphibia). Palaeontographica Abt. A 110:20–92.