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Evidence of Heterochronic Evolution: A Nasal Bone in the Olympic Salamander, *Rhyacotriton olympicus*

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those found in August or September generally contained larvae or well developed embryos. The earliest date that newly hatched larvae were found was August 10 and 11. I have collected or examined more than 30 additional *D. fuscus* females and their clutches in the field at a variety of other localities from northwestern to southwestern Pennsylvania. Clutches were found during July, August and September and possessed temporal developmental sequences similar to those from the Laurel Ridge region. Therefore, it appears that July represents the peak month for clutch deposition in western Pennsylvania and hatching takes place in August and September, probably peaking during the first half of September. A similar phenology has been reported for *D. fuscus* in Massachusetts (Wilder, 1913, 1917), Maryland (Danstedt, 1975), and Ohio (Dennis, 1962; Orr and Maple, 1978).

Although the additional clutches discussed above, from Laurel Ridge and western Pennsylvania, were found in a variety of habitats from many localities, microhabitat selection for clutch deposition was relatively consistent, as described above; shallow depressions excavated in a moist muddy or silty sand substrate, almost always less than 50 cm from the edge of a stream or spring. The most common exception was the deposition of eggs in seepage areas or the heads of springs, where clutches were brooded in cavities formed in a gravelly substrate through which a thin stream of water percolated continuously. One clutch was attached just above the surface of the water to a large rock in the center of a shallow and narrow riffle.

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EVIDENCE OF HETEROCHRONIC EVOLUTION: A NASAL BONE IN THE OLYMPIC SALAMANDER, *RHYACOTRITON OLYMPICUS*

Since its discovery, the Olympic Salamander, *Rhyacotriton olympicus*, has been an enigma for taxonomists and morphologists. Dunn (1920) illustrated the anterior cranial elements of an adult

Rhyacotriton olympicus of unstated size. The specimen as figured had large prefrontals and somewhat smaller yet well developed lacrimals, but no nasals or septomaxillaries. Dunn clearly stated his view that the absence of nasals might be due to "arrested development" (paedomorphosis, see Alberch et al., 1979), since the bones appear late in the larval life of *Dicamptodon*, a form considered to be a close relative of the monotypic *Rhyacotriton*.

In his designation of the monotypic subfamily Rhyacotritoninae, Tihen (1958) emphasized that *Rhyacotriton* was unique (among all metamorphosed salamanders) in its lack of nasals. He judged the bone as truly absent, not simply fused with an adjacent bone, and he, too, argued that this was paedomorphic "partial neoteny". Tihen noted that the bone is present in the permanent larvae of other ambystomatids, but, like Dunn, he argued that since the bone was one of the last to ossify it might be one of the first to disappear phylogenetically.

The views of Dunn and Tihen stand in contrast to those of several other workers. For example, Noble (1921), who corrected Dunn by showing that septomaxillaries were present in *Rhyacotriton*, questioned Dunn's account of the absent nasals. Without being explicit, Noble suggested that the bone labeled prefrontal by Dunn might in fact be the nasal (or, implied, a fusion of the nasal and the prefrontal, such as he reported in the same paper for some neotropical salamanders), since it was large and occupied much of the area occupied by the nasal in other salamanders. Cloete (1961) made a detailed description of cranial morphology in *Rhyacotriton* based on serial sections of two adult specimens (46.6 and 51.3 mm, snout to vent). She found no nasals, but suggested that the bones might be fused with the frontal processes of the premaxillaries. Her argument is indirect and convoluted. In 1962, Srinivasachar reported "nasal ossifications", seemingly continuous with an ossification surrounding the nasolacrimal duct. He believed that the lacrimal was fused to the nasal, and he reported this composite structure to lie between the dorsal extension (frontal process) of the maxillary and prefrontal (the normal position for a lacrimal).

In an earlier study of the ontogeny of *Rhyacotriton*, Worthington and Wake (1971) reported two centers of ossification which soon fuse to form the lacrimal, but argued that since these were both closely associated with the nasolacrimal duct there was no reason to consider one of them to be the nasal. Further, no evidence was found of two centers of ossification of the prefrontal or of the premaxillary. Since heterochrony is a theme of some importance in *Rhyacotriton*, the absence of the nasals was cited as one of several paedomorphic characters of the genus (i.e., the arguments of Dunn and Tihen were accepted).

All prior workers have agreed that a paired bone is missing in the snout of *Rhyacotriton*, but it might be truly absent ("undeveloped"—Dunn, Tihen), or fused with either the prefrontal (Noble), the premaxillary (Cloete), or the lacrimal (Srinivasachar). In this note I present data which lead to the rejection of the last three of these four hypotheses.

I have found nasal bones in members of two separate populations in the southern part of the range of *Rhyacotriton olympicus*. A recently metamorphosed (sexually immature) individual (36 mm snout to posterior angle of vent) from a seep along the Winchuck River, 6 mi E Highway 101, Curry Co., Oregon, has small but distinctly separate nasals. These bones have no articulations and are thin crescents, lying over the cartilaginous nasal capsules well removed from the nasolacrimal ducts. They are clearly evident in this alizarin-stained specimen, which also has well developed prefrontals, lacrimals, and septomaxillaries. The heads of 16 *Rhyacotriton* from Ti Creek, a tributary of the Klamath River in Humboldt Co., California, were removed, then cleared and stained with alizarin using standard techniques. The rest of each skeleton was macerated for study of the vertebral column. These individuals, all metamorphosed (and all sexually mature), ranged from 42.7–53.3 mm, snout-posterior angle of vent. All but one (48.2 mm) have at least some sign of independent mineralization in the nasal region, overlying the cartilaginous nasal capsule. In 7 individuals (including the largest and the smallest) the nasal is asymmetrical, absent on one side but present (ranging from extremely small to moderate in size) on the other. A specimen 43.2 mm in size has the bones moderately well developed bilaterally. The bones are only slivers on either side in a 44.2 mm animal, but moderately large elements, lacking articulations, are present in a 49.2 mm specimen (Fig. 1).

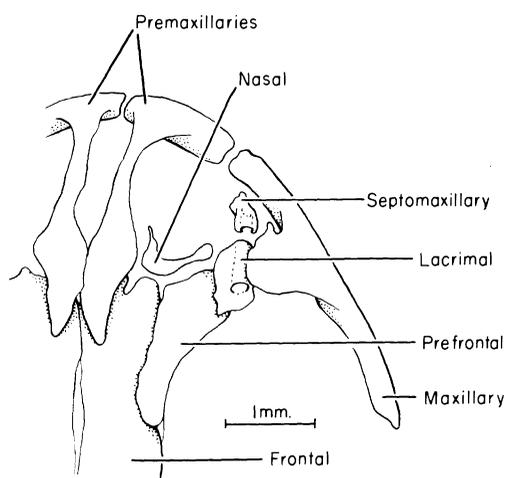


FIGURE 1. Anterior cranial elements in a metamorphosed adult female *Rhyacotriton olympicus* (49.2 mm snout-posterior angle of vent) from Ti Creek, Humboldt Co., California. Mainly the right side of the skull is illustrated. The nasolacrimal duct pierces the dorsal surface of the lacrimal; the path of the duct extends through the long axis of the lacrimal and the septomaxillary, then through the ventral surface of the latter bone into the nasal capsule.

history differences, with coastal versus inland, northern versus southern, or even general environmental temperature regimes being correlated with different life history patterns. The geographic variation in nasal appearance might be one manifestation of a more general phenomenon in which degree of differentiation is a function of developmental rate, whether determined by local, regional, or historical factors. Consequently, relatively slow development results in relatively more paedomorphosis. A detailed comparative investigation of ontogeny in this species throughout its range is currently in progress.

Dunn (1920) and Tihen (1958) were correct in attributing absence of nasals to paedomorphosis. The nasals are the last of the cranial elements to appear in *Rhyacotriton*, and in many populations, including all of those that have been studied in the northern part of the range, sexual maturation is achieved before osteogenesis of the cranium is complete (in comparison with generalized patterns in metamorphosed salamanders). Cloete's (1961) specimens were from northwestern Washington, Srinivasachar's (1962) specimens were from Skamania and Mason Counties, Washington, and it is reasonable to assume that the specimens of both Dunn (1920) and Noble (1921) were also from northwestern Washington, since that is the only region from which the species had been reported at the time they worked. Tihen (1958) did not list his specimens. Worthington and Wake (1971) worked with material collected just across the Columbia River from Washington. I suggest that all populations of *Rhyacotriton* share a common developmental program, but one that has undergone heterochronic evolution (paedomorphosis in the sense of Gould, 1977, and Alberch et al., 1979), relative to more generalized salamanders such as its apparent relative, *Dicamptodon*. If the program is left "on", nasals appear, but if rate of differentiation is slow relative to rate of growth (increase in size of cells, number of cells, or both), sexual maturation occurs before the program is completed and nasals never appear. If my hypothesis is correct, one might expect nasals in the northern part of the range of the species in rare, very large animals, in animals which have shown post-maturational development, or in warm microclimates where the developmental program proceeds with relative rapidity. In warmer, more southerly or coastal regions, nasals will be more frequent in adults, regardless of their size.

Nasals are probably no more than markers of a complex interplay of environmental gradients, selection on reproductive parameters, and programs of development. Their discovery in some

I have also examined *Rhyacotriton* from more northern parts of its range, and none have nasals. The series of 35 cleared and stained specimens studied earlier (Worthington and Wake, 1971), from Wahkeena Falls, Multnomah Co., Oregon, was reexamined, and sexually mature, fully metamorphosed individuals from the same population were also studied (as large as 46.8 mm). No nasals were observed. One large (ca. 57 mm) individual from Lake Cushman, Mason Co., Washington, also lacks nasals. Apparently *Rhyacotriton* demonstrates geographic variation in the extent of cranial development.

Considerable differentiation of coastal (central Oregon) as compared with inland (the Wahkeena Falls population in northern Oregon) populations of *Rhyacotriton* has been reported in a number of important life history measures by Nussbaum and Tait (1977). Local habitat differences were cited as the selective forces for what were interpreted as life history adaptations. It is conceivable that there might be a more pervasive regional component to the life

populations of *Rhyacotriton* removes what was previously thought to be a unique taxonomic character and illuminates evolutionary processes in salamander phylogeny, but in no way changes the status of this unique genus.

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THE NORTHEASTERN RANGE LIMIT OF THE EASTERN MUD TURTLE *KINOSTERNON S. SUBRUBRUM* (LACEPEDE)

Kinosternon s. subrubrum is listed as ranging north into Connecticut by several recent authors: (Blair et al., 1968; Carr, 1952; Conant, 1975; Ernst and Barbour, 1972). In addition, older works including (Babcock, 1919; Lamson, 1935; Linsley, 1844; and Pope, 1939) indicate its possible occurrence in Connecticut. Linsley (1844) reports a specimen collected at Stratford, Fairfield County in 1843, and Babcock (1919) mentions a possible sighting at Sound Beach, Greenwich, Fairfield County. Neither of these records is substantiated by specimens or adequate descriptions, however.

To gather information on the status of *K. s. subrubrum* in Connecticut we made inquiries to 23 institutions with either major herpetological collections or collections specializing in northeastern specimens. Only the Yale University, Peabody Museum reported Connecticut specimens. The entire series (YPM 2948–2953), collected in 1936, proved to be incorrectly identified Musk Turtles, *Sternotherus odoratus* (Latrielle). Moreover, a specimen from Massachusetts (collected before 1881) in the British Museum (Natural History) (BM 1920.1.20.1891) also was a misidentified *S. odoratus*. These misidentifications suggest that earlier workers had difficulty separating these two species, and thus doubts must be expressed concerning the validity of Linsley's (1844) and Babcock's (1919) records. We conclude that no historical evidence of indigenous populations of *K. s. subrubrum* in Connecticut can be documented.

Only two recent Connecticut reports of *K. s. subrubrum* are known to us. N. S. Proctor, a reliable field observer, sighted an adult in Ansonia, New Haven County about 1960 and a single adult was collected at Bethel, Fairfield County in 1977 (E. Briggs, pers. comm.). This specimen is now in captivity at the Flanders Nature Center in Woodbury, Connecticut.