

## ONTOGENY AND PHYLOGENY OF THE GNATHOSTOME BRANCHIAL SKELETON

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The branchial skeleton of gnathostomes is characterized by its metameric arrangement of dorsoventrally segmented elements. Developmentally, the arch skeleton is derived from neural crest streams that descend bilaterally. Studies have confirmed this for the dorsal elements within an arch, but not for the ventral elements. The basibranchials in extant taxa are unpaired. Goodrich (1958) assumed a neural crest origin for these ventral elements, although, he argued that they were primitively paired. Supporting a paired origin, Holmgren (1940) noted transient paired chondrogenic condensations in the development of several chondrichthyans. However, a recent study on *Bombina* (the flame toad) noted that the basibranchial was not derived from primary neural crest (Olsson & Hanken 1996). This finding challenges Goodrich's hypothesis for the origin of the basibranchials.

In the absence of direct observation, a neural crest origin can be determined by a skeletal element's association with hypobranchial musculature. Köntges & Lumsden (1996) note a specificity between these muscles and neural crest attachment sites. Thus, indirect evidence for a neural crest origin includes documentation of paired structures and their attachment to hypobranchial muscles. These criteria are met by *Cowralepis mclachlani* Ritchie 2005 (Placodermi, Phyllepidi). An ontogenetic series is preserved detailing the anatomy of the basibranchials with paired elements present in juveniles that persist into the adult. Unlike extant chondrichthyans where hypobranchial muscle attachments are displaced laterally, extensive attachment sites characterize the basibranchials in *Cowralepis*. The presence of paired elements in placoderms and in the development of some extant chondrichthyans suggests that the unpaired elements in extant fishes represent a peramorphic heterochronic shift from the ancestral gnathostome condition.

Goodrich, E. S. 1958. *Studies on the Structure & Development of Vertebrates. Volume 1*. Dover Publications, Inc., New York: 485 pp.

Holmgren, N. 1940. Studies on the head of fishes. Part 1: Development of the skull in sharks and rays. *Acta Zoologica* 21:52–267.

Köntges, G., & Lumsden, A. 1996. Rhombencephalic neural crest segmentation is preserved throughout craniofacial ontogeny. *Development* 122: 3229-3242.

Olsson, L., & Hanken, J. 1996. Cranial neural-crest migration and chondrogenic fate in the Oriental fire-bellied toad, *Bombina orientalis*: Defining the ancestral pattern of head development in anuran amphibians. *Journal of Morphology* 299: 105-120.