

Early specializations in the branchial apparatus of jawless vertebrates: a consideration of gill number and size

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Abstract

The number of gill units and gill compartments in fossil and living agnathans shows an important interspecific and individual variation in living hagfish, but is quite stable in living lampreys and gnathostomes. In Palaeozoic agnathan taxa, interspecific variations seem to occur essentially in galeaspid, anaspid and two anaspid-like taxa, but galeaspid can display up to forty-five pairs of gill compartments, a number unequalled among vertebrates. Current vertebrate phylogenies suggest that the occurrence of “polybranchy” (i.e. a large number of gills, exceeding ten) in agnathans is homoplastic. At any rate, it is certainly a derived character within galeaspid, and it is probable that the generalised condition in most “ostracoderm” taxa was about seven to ten gill compartments. Osteostracans and possibly pituriaspid show that the posterior expansion of the branchial apparatus was constrained by the paired fins and girdles, and the former taxon solved this problem by expanding its branchial apparatus forward, far beyond the level of the optic capsules. Current data on the developmental genetics of the branchial apparatus offer no explanation to the process that leads to polybranchy, except for the fact that the anterior portion of the endoderm plays a major role in patterning the pharynx and that the production of pharyngeal pouches is theoretically unlimited within this region, as long as the individual pouches can become reduced in size without losing their respiratory function. It is assumed that the common ancestor to all fossil and living vertebrates probably possessed from five to possibly ten gill units, and that polybranchy, though vaguely recalling the numerous pharyngeal slits of cephalochordates, is not a primitive character for the vertebrates.

Introduction

The reconstruction of the hypothetical ancestral morphotype; that is, an assemblage of the most generalised character states for a particular clade, is one of the results that can be expected from phylogenetic analyses. In the case of the vertebrates as a whole, this quest is particularly difficult, because of the small number of reliable, anatomical homologues shared by this clade and its most likely sister group, the cephalochordates, and thus the difficulty for assigning a polarity to many of the multi-state vertebrate characters. Nevertheless, any consideration or scenario of the origin of the vertebrates should rest on a preliminary hypothesis about their ancestral morphotype. Since LØVTRUP's (1977) theory of craniate interrelationships, current reconstructions of the vertebrate morphotype are also largely based on the assumption that hagfishes are the sister group of all other vertebrates, and thus that some of the characters they share with lampreys are in fact general vertebrate characters (see e.g., DONOGHUE & SANSOM 2002, for an update of this question). Recent results of molecular phylogenetics, however, now seem to provide strong support for the classic cyclostome clade (hagfish + lampreys) and thus raise questions about the presumed plesiomorphic state of certain characters in the vertebrate morphotype, as inferred from their condition in hagfish and lampreys. This kind of question is exemplified here with the case of the morphology and size of the branchial apparatus in the vertebrates, with particular reference to the earliest known taxa, in which may occur considerable variations in the development of this major structural component of the vertebrate head.

Living jawed vertebrates generally have five posthyoidean gill arches, with a few exceptions, such as

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