Can palaeobiogeography explain low rates of morphological evolution in ‘living fossil’ lungfish?

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Introduction

In a classic work Westoll (1949) used a character-taxon matrix to show that lungfish underwent rapid morphological evolution early in their history followed by an extended period of morphological stagnation (Figure 1): a textbook example (literally) of evolution in a ‘living fossil’. Here I update Westoll’s method for use with cladistic datasets and place it in its correct phylogenetic context. One proposed explanation for the existence of living fossils is geographic isolation in refugia, where lack of competition negates the need for morphological change. Here this hypothesis is tested by comparing lungfish dispersal patterns during their rapid Devonian phase with their slower post-Devonian phase of evolution.

Methods and Materials

Aside from the inevitable addition of new taxa and refinements to the geological timescale since 1949 there are some significant flows in Westoll’s method: 1) the ancestor is purely hypothetical, 2) a selective suite of taxa was used, 3) error bars (missing data) constrain interpretation, 4) a stratigraphically ordered ancestor-descendant sequence was assumed, and 5) reversal (character loss) wasn’t taken into account. Although modern cladistic matrices are more inclusive and more often contain a real outgroup (answering points 1 and 2 above) missing data is still a major issue. To overcome this the internal nodes (rather than the taxa themselves) were scored as these are completely under a given phylogenetic hypothesis. Nodes were scored as the total number of accumulated character changes between that node and the root. Here DELTRAN was used as it dumps equivocal changes on the terminal branches (which aren’t used). Nodes were dated based on the stage mid-point (using Gradstein et al., 2004) of the oldest taxon stemming from it. Here this method is applied to a ‘supermatrix’ (of 86 taxa and 132 morphological characters) based on six published cladistic analyses of lungfish interrelationships.

Palaeobiogeographic analysis involved assignment of each taxon to a geographic region, in this case modern continents. Despite lungfish undergoing a change in habitat preference from marine to freshwater environments it is assumed that this didn’t significantly affect dispersal patterns, especially as Mesozoic taxa are thought to have maintained a tolerance to marine conditions (Schultze 2004). Ancestral distributions were then reconstructed using Fitch (1971) parsimony. Each branch was then classified as either a) a range expansion (e.g. a change from an Australian distribution to an Asian distribution), b) a range contraction (e.g. a Eurasian distribution to an Asian distribution) or, c) no change.

Discussion

The broad congruence between the results presented here and those of Westoll suggest either that the pattern of two evolutionary temps for lungfish is robust, and hence biologically real, or consistently biased, either by worker methodology or the fossil record. A more comprehensive discussion of the causes of this disparity is given elsewhere (Lloyd, in prep.). However, the results presented here present strong evidence that palaeobiogeographic processes do not impact on rates of lungfish evolution at all. Interestingly lungfish seem to show no retention of dispersal ability following their transition from marine to freshwater environments, although it seems likely that dispersal rates did drop off as the branches used in the post-Devonian phase represent longer spans of time. The three extant genera (Lepidosiren, Neoceratodus and Protopterus) are more closely related to each other than almost all of the extant taxa and are now restricted to freshwater habitats in the southern hemisphere (South America, Australia and Africa respectively). It seems probable that this shift towards a more aquatic lifestyle occurred after the Cretaceous period, some 200 million years after evolutionary rates dropped off dramatically.

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References cited