

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.

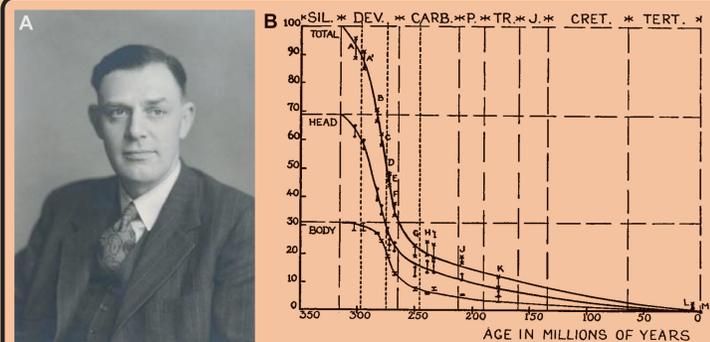


Figure 1 A classic work in macroevolution. **A** Thomas Stanley Westoll (1912 - 1995) **B** The results of Westoll's study of the evolution of the lungfish character complex. Sixteen dipnoan taxa (A - M) were scored from 100 (primitive ancestor) to 0 (the extant *Lepidosiren* and *Protopterus*). The slope of the graph represents the rate of evolution, with the steep rapid phase contained within the Devonian.

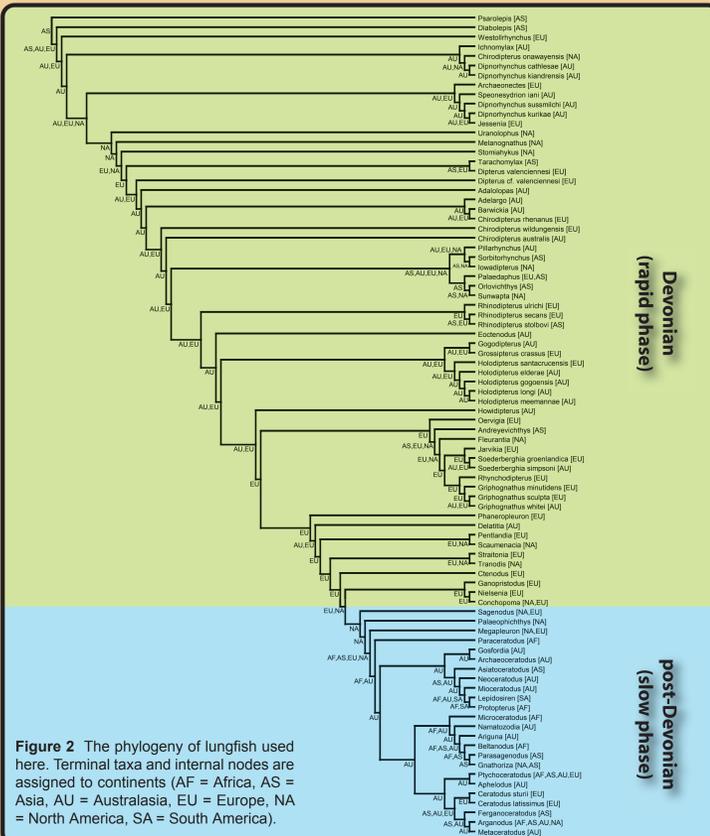


Figure 2 The phylogeny of lungfish used here. Terminal taxa and internal nodes are assigned to continents (AF = Africa, AS = Asia, AU = Australasia, EU = Europe, NA = North America, SA = South America).

Methods and Materials

Aside from the inevitable addition of new taxa and refinements to the geological timescale since 1949 there are some significant flaws in Westoll's method: 1) the ancestor is purely hypothetical, 2) a selective suite of taxa was used, 3) error bars (missing data) constraint 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 complete 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 retained a tolerance to marine conditions (Schultze 2004). Ancestral distributions were then reconstructed using Fitch (1972) parsimony. Each branch was then classified as either: a) a range expansion (e.g. a change from an Australasian distribution to an Australasian plus Asian distribution), b) a range contraction (e.g. a Eurasian distribution to an Asian distribution) or, c) no change.

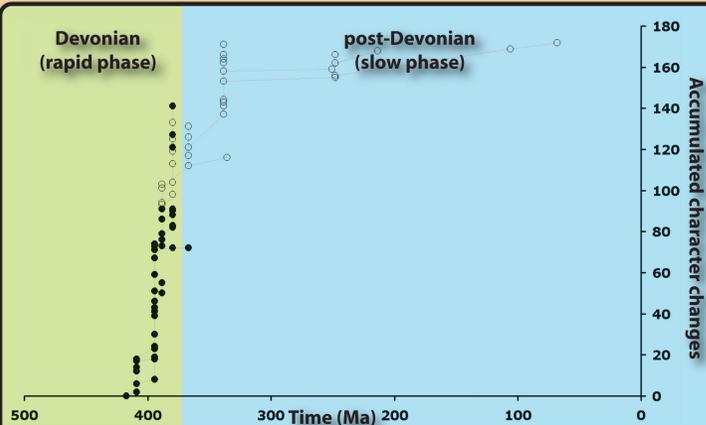


Figure 3 The results of the application of the cladistic modification of Westoll's (1949) original method. Note the broad congruence with Westoll's original results and the split between the two tempos of lungfish evolution. (Open circles indicate freshwater habits and closed circles marine habits; grey lines describe the branching structure of the phylogeny in Figure 2).

Results

A phylogenetic tree was derived from the 'supermatrix' (based first on parsimony analysis and then on stratigraphic 'fit') and ancestral distributions added (Figure 2). Despite the various modifications made here the results for lungfish (Figure 3) are broadly congruent with Westoll's original analysis (Figure 1; note Westoll's graph can be considered as 'upside-down' as he was investigating a loss of primitive characters whereas here the focus is on acquired characters). Using this data the tree was split into two parts reflecting the two evolutionary 'tempos' (a rapid Devonian phase and a much slower post-Devonian phase). The results here (Figures 4B and 5B) show that the slower phase actually reflects an increase in range expansion at the expense of both range contraction or continuity of range. However, a chi-squared test shows that there is no significant difference (p 0.99-0.975) between the relative proportions of expansion, contraction and continuity between the two evolutionary tempos.

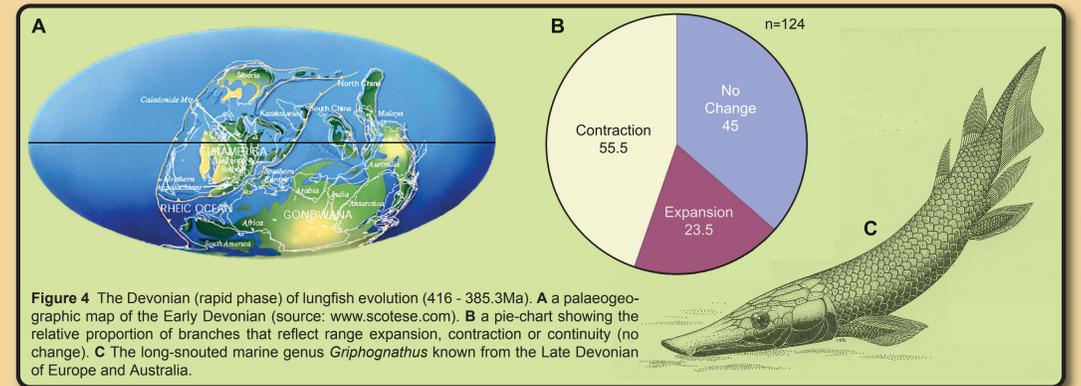


Figure 4 The Devonian (rapid phase) of lungfish evolution (416 - 385.3Ma). **A** a palaeogeographic map of the Early Devonian (source: www.scotese.com). **B** a pie-chart showing the relative proportion of branches that reflect range expansion, contraction or continuity (no change). **C** The long-snouted marine genus *Giphognathus* known from the Late Devonian of Europe and Australia.

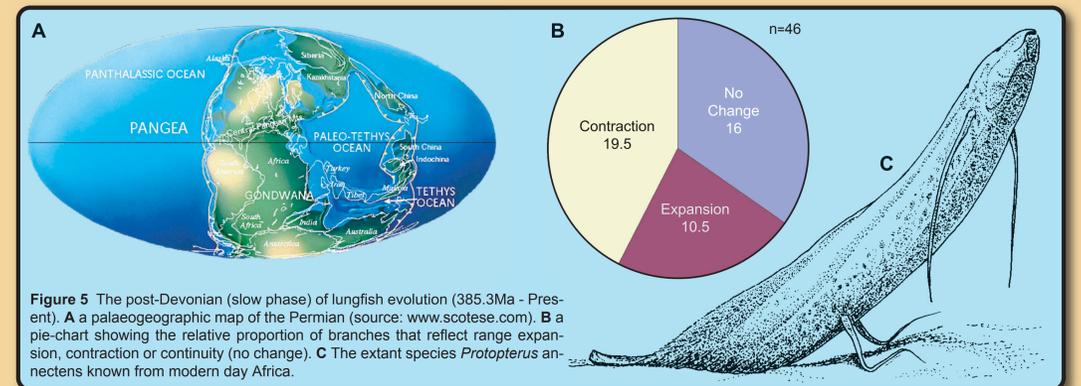


Figure 5 The post-Devonian (slow phase) of lungfish evolution (385.3Ma - Present). **A** a palaeogeographic map of the Permian (source: www.scotese.com). **B** a pie-chart showing the relative proportion of branches that reflect range expansion, contraction or continuity (no change). **C** The extant species *Protopterus annectens* known from modern day Africa.

Discussion

The broad congruence between the results presented here and those of Westoll suggest either that the pattern of two evolutionary tempos 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 retardation 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 larger spans of time. The three extant genera (*Lepidosiren*, *Neoceratodus* and *Protopterus*) are more closely related to each other than almost all of the extinct 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 endemic distribution, and the last intercontinental dispersal, didn't occur until the Cretaceous period, some 200 million years after evolutionary rates dropped off dramatically.

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