Rates of morphological evolution and ‘living fossils’

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Introduction

Our understanding of major evolutionary events is intrinsically linked to our knowledge of the rates involved. In the single figure in his *Origin of Species* Darwin predicted that rates of evolution would vary over time, but it wasn’t until almost 100 years later - with the advent of radiometric dating - that quantitative studies began in earnest, pioneered by Simpson’s *Tempo and Mode* (1944). Since then a proliferation of methods for examining evolutionary rates have appeared (Fenster and Sorhannus, 1991). One such method developed by Westoll (1949) utilised a character-taxon matrix to show that lungfish underwent rapid morphological evolution early on in their history before rates slowed dramatically (Figure 1). This has become a textbook example (literally) of evolution in a ‘living fossil’. Westoll’s method has also been used (with various minor modifications) to investigate actinistan (Schaeffer, 1952a,b), carpoid (Derstler, 1982) and angiosperm evolution. Various authors have also reinvestigated Westoll’s results (e.g. Martin, 1987). Despite this scrutiny Westoll’s method, and his results, have stood unchallenged (but see Schopf, 1984). Here Westoll’s method is modified for use with cladistic datasets.

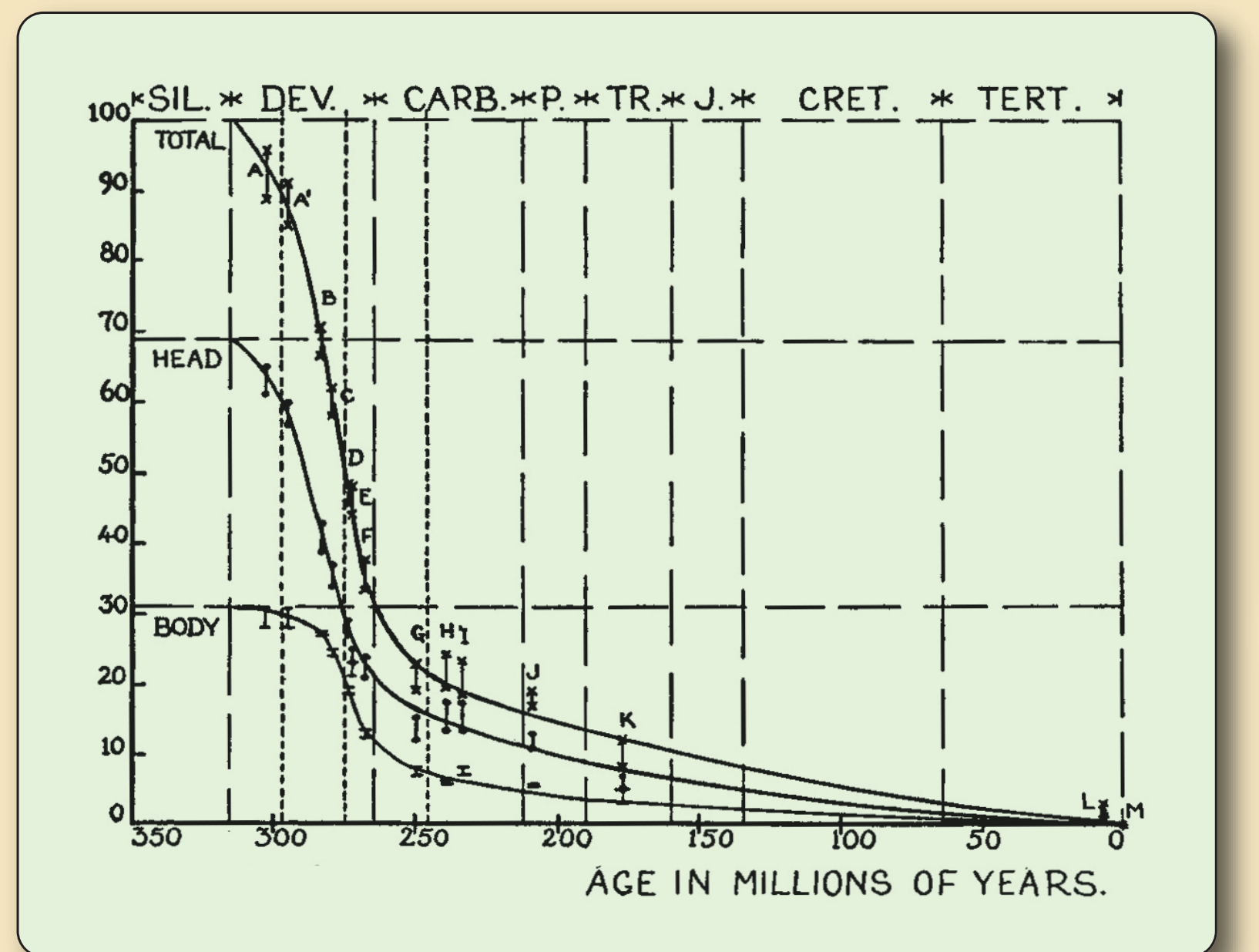

Figure 1 (left) - Results of Westoll’s (1949) original analysis. He coded 15 dipnoan taxa from 100 (hypothetical ancestor) to 0 (the extant *Lepidosiren*). The slope of the line represents the rate of evolution which is highest in the Mid. to Late Devonian, but tails off markedly into the Mesozoic. When the matrix was partitioned it can be seen that the exponential phase for cranial characters proceeded that for postcranial characters.

Figure 2 (right) - Results of the application of the modified Westoll method (see text for explanation). For each graph the clade, source and ‘r-squared’ value (based on a plot of ‘score’ (see text) against cladogenetic rank) are given.

Materials and Methods

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) 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 often contain a real outgroup (answering points 1 and 2 above) missing data is still a major issue. Here a phylogenetic tree derived from the matrix was used to code character states for *internal* nodes (which are complete). This obviates the problem of missing data (point 3 above). In order to take into account both phylogeny and reversals the internal nodes were scored as the total number of character changes from the root to that node. Here DELTRAN was used as it places 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 that node.

This modified method was first applied to lungfish (using a ‘supermatrix’ of 88 taxa and 250 characters) for comparison with Westoll’s original results. Next other ‘living fossil’ groups (coelacanths, sphenodonts, horseshoe crabs etc.) were examined using published (and unpublished) matrices. For comparison a selection of other, non-‘living fossil’ groups were also analysed.

Results

Despite the various modifications made here the results for lungfish (Figure 2, top left) are broadly congruent with Westoll’s original analysis (Figure 1). An interesting observation is that the group exhibit a second minor radiation at the base of the Triassic. When the additional ‘living fossil’ groups are compared, similar results are also obtained - i.e. relatively rapid early character acquisition followed by lengthy periods of little or no character change. However, the rapidity of the initial phase does vary between groups. Rhynchocephalians, linguloids and amiids share a very rapid early phase with dipnoans, but xiphosurans and actinistans are slower ‘out of the blocks’. Significantly the non-’living fossil’ groups examined here can be assigned to similar patterns.

An acknowledged problem with Westoll‘s method (and it’s modified form presented here) is that it is not strictly a calculation of rate. Consequently other authors have attempted to produce a cladistic rate calculation, adding either one (Derstler, 1982), two (Cloutier, 1991), or five (Forey, 1988) million years to branch durations in order to avoid dividing by zero. However, when these values were applied to lungfish they necessitated moving their origin from the Early Devonian back to the Silurian, Ordovician or pre-Cambrian respectively. Instead, separate graphs (not shown) were produced where scores were plotted against cladogenetic rank and ‘r-squared’ values calculated. In almost all cases a strong linear correlation was observed, suggesting that morphological change is correlated with speciation, and hence the patterns observed here reflect a fall off in speciation rates as a clade ‘ages’. For artiodactyls and crocodiles the lower ‘r-squared’ value represents a basal dichotomy in the tree with two or three main branches exhibiting different rates of character acquisition. This is most obvious in the Crocodylia (Figure 2, bottom right).

Discussion

The pattern of character acquisition observed by Westoll is upheld here despite various modifications to the method, major changes to the geologic time scale, and a doubling of known lungfish taxa. For actinistians, the close relatives of dipnoans, the early rapid phase is drawn out until the close of the Palaeozoic. This result contradicts that of earlier workers (Schaeffer, 1952a,b; Forey, 1988; Cloutier, 1991; Schultze, 2004), who stressed a stronger similarity with the lungfish pattern. Xiphosurans have an even slower initial phase and appear to have always exhibited low evolutionary rates. Whereas linguloids and rhynchocephalians show the most extreme differences in rate, with the early phase extremely rapid followed by an apparent complete halt in evolution, with the last recorded speciation event much closer to the origin of the group than to the present. Amiids have the longest ‘fuse’ of the ‘living fossil’ groups, but undergo a very rapid phase in the Early Cretaceous which drops off into the Cenozoic.

However, notions of a ‘living fossil’ pattern of evolution are false as the non-’living fossil’ groups show similar results. Artiodactyls and reptiles have a pattern similar to rhynchocephalians, with a rapid phase early in thir history and a large gap since the last branching event. Equids more closely match the results for linguloids with an extreme difference between a near vertical early phase followed by a near horizontal later phase. Although the only extinct group here, mosasaurs also exhibit an s-shaped pattern of evolution. Tetraodontiform fish seem to exhibit a long ‘fuse’, similar to amiids, and have a less pronounced rapid phase, but still show the levelling off seen in the other groups. Finally, the Crocodylia show an interesting pattern, with the three lineages (gavials, alligators and crocodiles) all levelling off at the same time.

‘Living fossils’ cannot therefore be circumscribed as slowly evolving groups and another explanation is required if the concept is to remain. However, what these results show is a deeper, more universal pattern of evolution - that of early acquisition of characters followed by periods of relative morphological stasis. A search for a biological explanation must be postponed until worker biases can be ruled out. A potential explanation is an excessive number of sympleisomorphic characters. I hope to test this hypothesis by combining dipnoan and actinistian matrices in a sarcopterygian ‘supermatrix’ to see if the two branches exhibit the differing pattern seen here, or if they combine as crocodylians do. Another potential explanation is the use of higher taxa. Reptiles and artiodactyls exhibit the lungfish pattern, but perhaps this is due to the use of more derived representatives (by selecting for more complete, or even extant specimens) which give a false picture of rapid evolution.

Conclusions

A common pattern of rapid evolution early in a clade’s history followed by extended periods of much lower evolutionary rates is observed in both ‘living fossil’ and non-’living fossil’ groups. Although this is consistent with a punctuationist or ‘quantum’ model of evolution it must first be shown that this is a biological pattern and not a worker bias. The notion of ‘living fossils’ as ‘bradytelic’ or slowly evolving groups must be abandoned, and hence (potentially) the concept as a whole.

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