

'Living fossil' vertebrates and rates of morphological evolution



Graeme T. Lloyd



Background



Conference on Genetics, Paleontology and Evolution held at Princeton, January 1947

Thomas Stanley Westoll

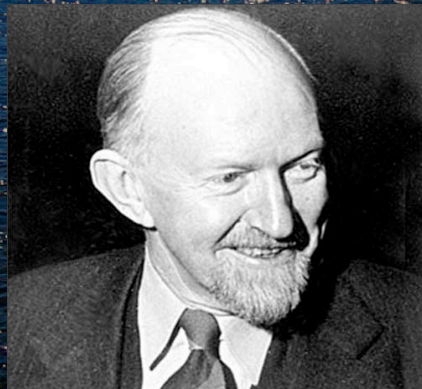


George Gaylord Simpson

Background



George Gaylord Simpson



1902 – 1984

- T&M published 1944
- Confirmed that rates vary
- Three basic tempos:
 - Tachytely (fast)
 - Horotely ('normal')
 - Bradytely (slow, living fossils)
- Only looked at single characters

Background

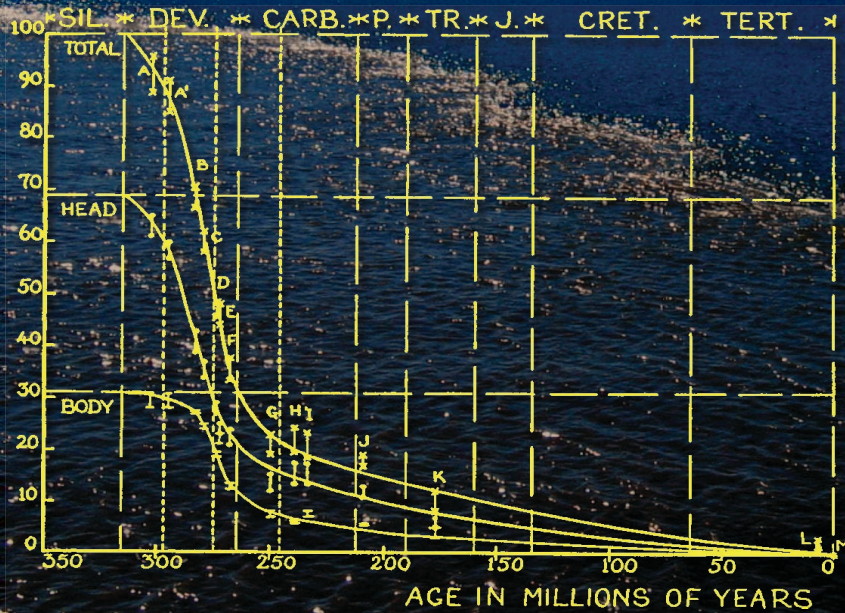


Thomas Stanley Westoll

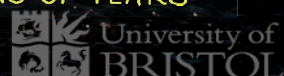


1912 – 1995

- Devised a method to investigate tempo in multiple characters
- Constructed character-taxon matrix and added states ('scoring' taxa)
- 14 dipnoan genera and 26 ordered multi-state characters
- Plotted scores vs. time



(Westoll 1949)



Problems with Westoll's methodology:

- Ancestor artificial (Schopf 1984)
- Only well known taxa can be included (Knoll *et al.* 1984)
- Error bars required (constrain interpretation)
- Reversals ignored (Derstler 1982)
- Assumes stratigraphically ordered ancestor-descendant sequence

Previous Solutions

- Derstler 1982 and Forey 1988
- Used cladistic (character-taxon) matrices
- Scored internal nodes of phylogeny (which are complete)
- Scored as number of character changes between nodes (i.e. include reversals)

But:

- These authors were calculating rates

The Problem With Rates I

- Divisor in rate calculation (time) is often zero (rate = ∞)
- Solution: add arbitrary value to divisor
 - Derstler 1982 1Ma
 - Cloutier 1991 2Ma
 - Forey 1988 5Ma
- Problem: predicts earlier origin of clade, e.g. Forey value necessitates pre-Cambrian lungfish

The Problem With Rates II

- Rates also suffer from the problem of comparability
- Solution:
- Use the desirable properties of scoring internal nodes, incorporating reversals and a phylogenetic context, but...
 - ...retain Westoll's plotting method
 - Reduces assumptions (e.g. anagenesis/cladogenesis)

Revisiting Lungfish Evolution

- Compiled 'supermatrix' from six published matrices
- 85 dipnoan taxa, 2 outgroups and 132 characters
- 4118 MPTs
- MPTs assessed using a MSM (Siddall 1998)
- Best-fit and worst-fit trees almost identical



Artefact?

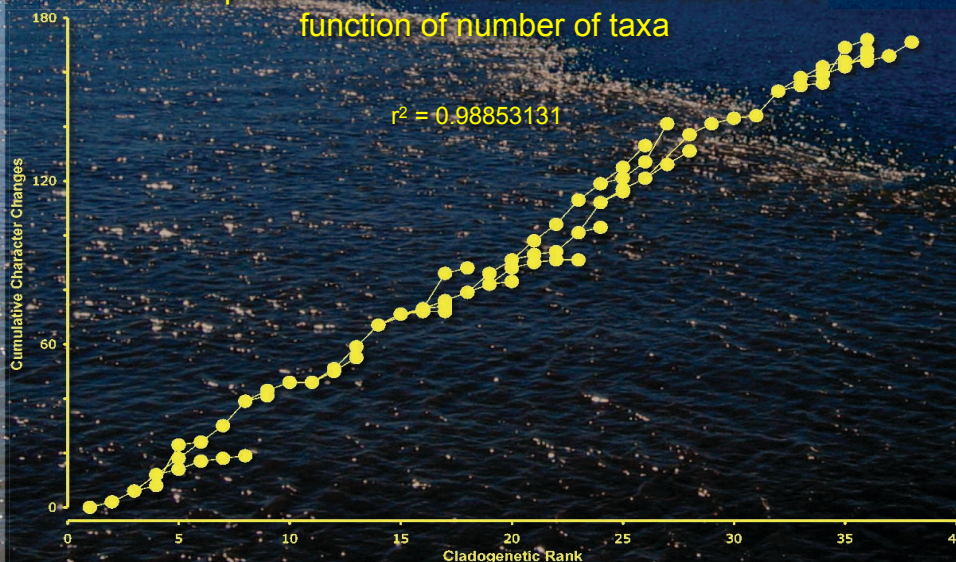
“it appears possible that the pattern of scores follows directly from the method of analysis” (Schopf 1984)

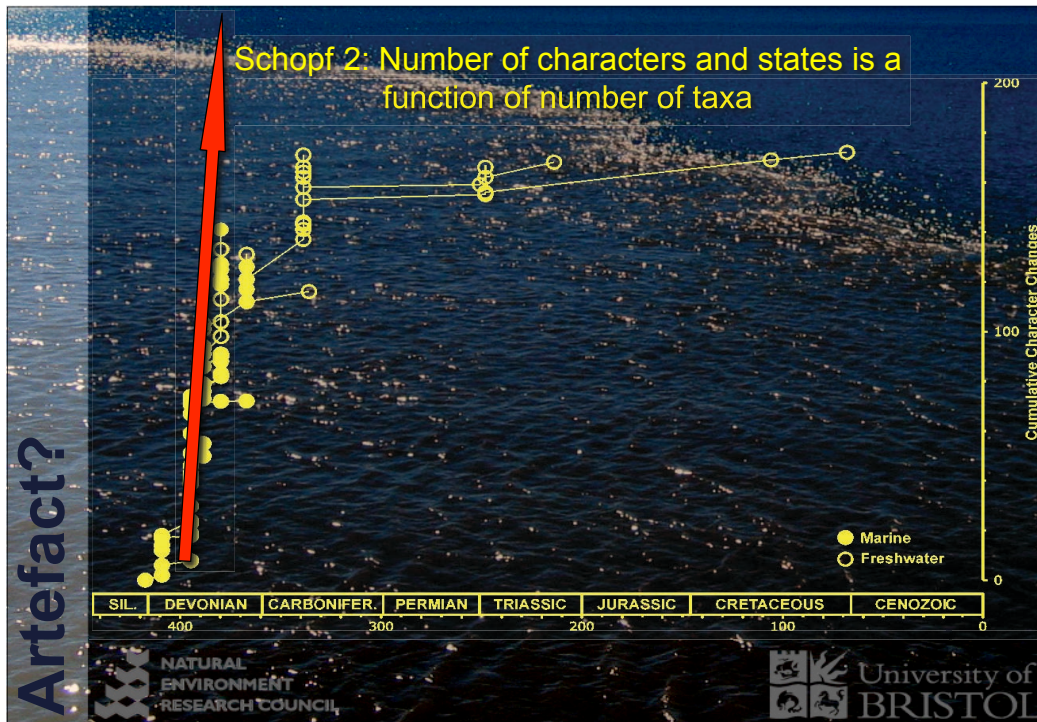
1. Artificial ancestor
2. Number of characters and states recognised a function of number of taxa (most of which are Devonian)



Artefact?

Schopf 2: Number of characters and states is a function of number of taxa





- Artefact?
- "It appears possible that the pattern of scores follows directly from the method of analysis" (Schopf 1984)
1. Artificial ancestor
 2. Number of characters and states recognised a function of number of taxa (most of which are Devonian)
 3. If changes were late we would recognise a new group instead (e.g. birds from reptiles)
 4. A pedomorphic trend (Bemis 1984) in lungfish would limit the number of available character states as time progressed
- NATURAL ENVIRONMENT RESEARCH COUNCIL
- University of BRISTOL

Artefact?

Paedomorphosis as an explanation for the lungfish pattern

- Paedomorphosis can be obligate and irreversible (Bonett & Chippindale 2006)
- Bemis' (1984) hypothesis for a paedomorphic trend in lungfish can be tested as 5 of his 7 characters appear here
- However, all 5 have low CI's (0.2-0.4) and most include reversals (under ACCTRAN)
- Peramorphic trends also known in lungfish (Long 1993)



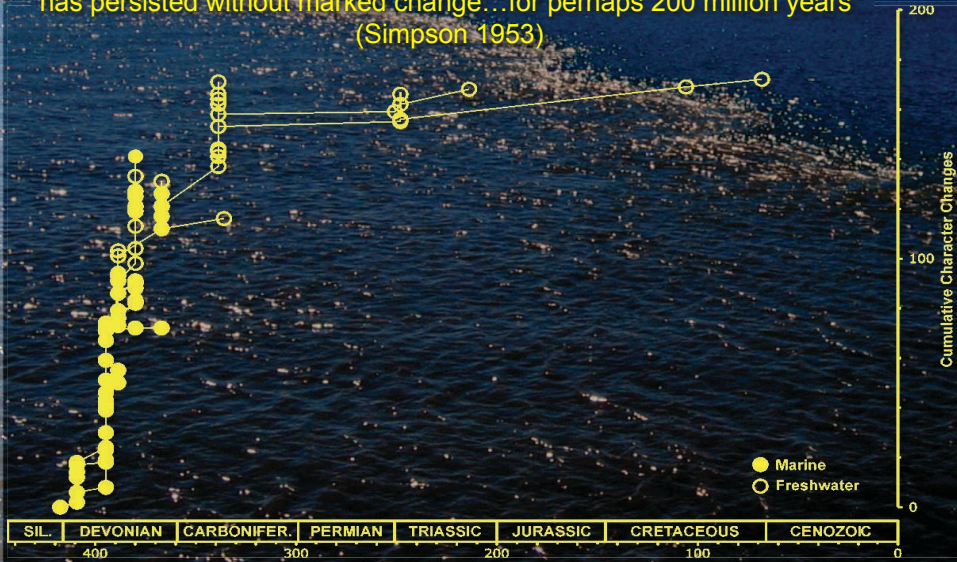
Biologically Real?

Lungfish Pattern as a Biological Phenomena

- Westoll/Simpson saw it as 'quantum evolution'

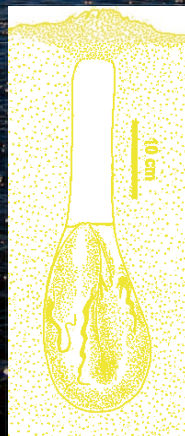


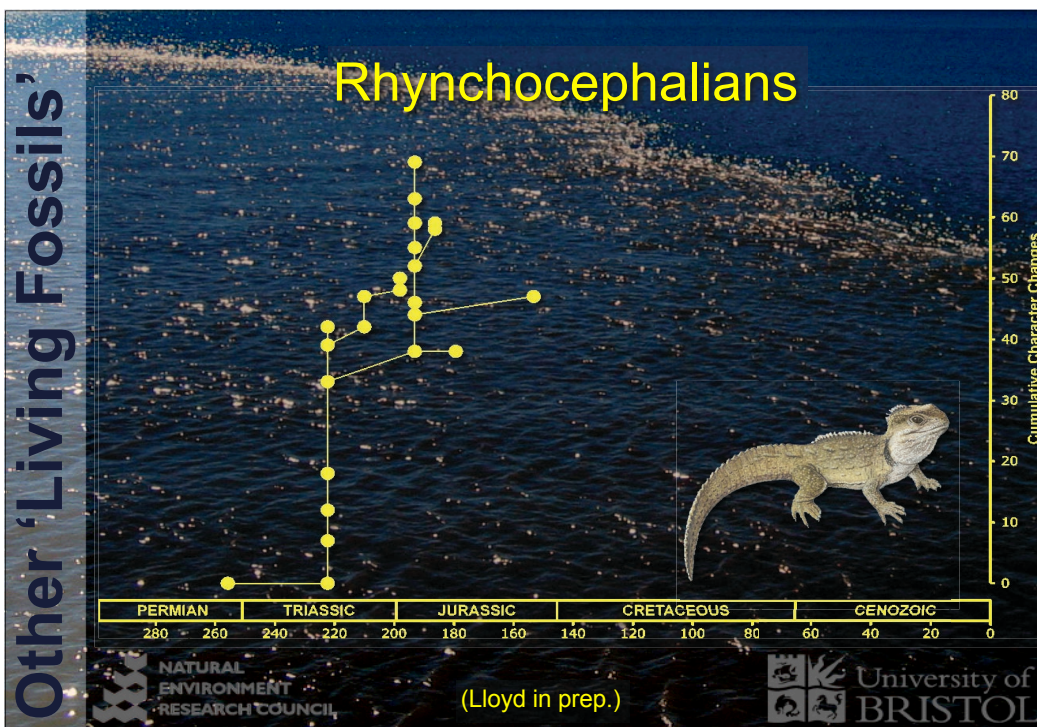
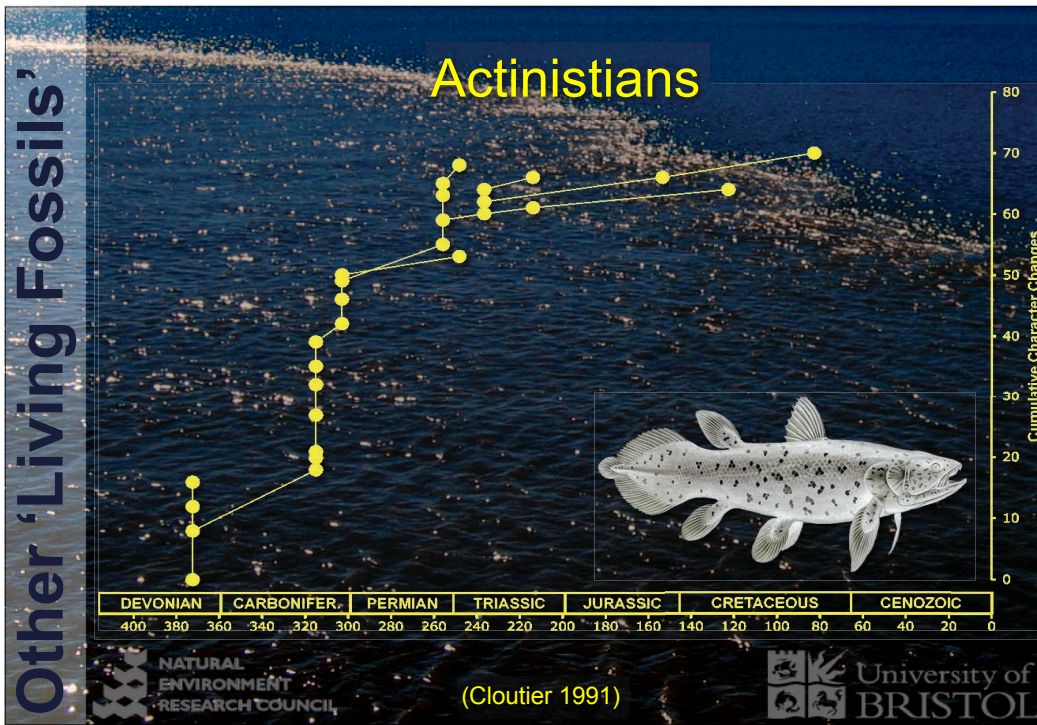
"The lungfish [adaptive] zone would seem to be quite narrow and yet it has persisted without marked change...for perhaps 200 million years"
(Simpson 1953)

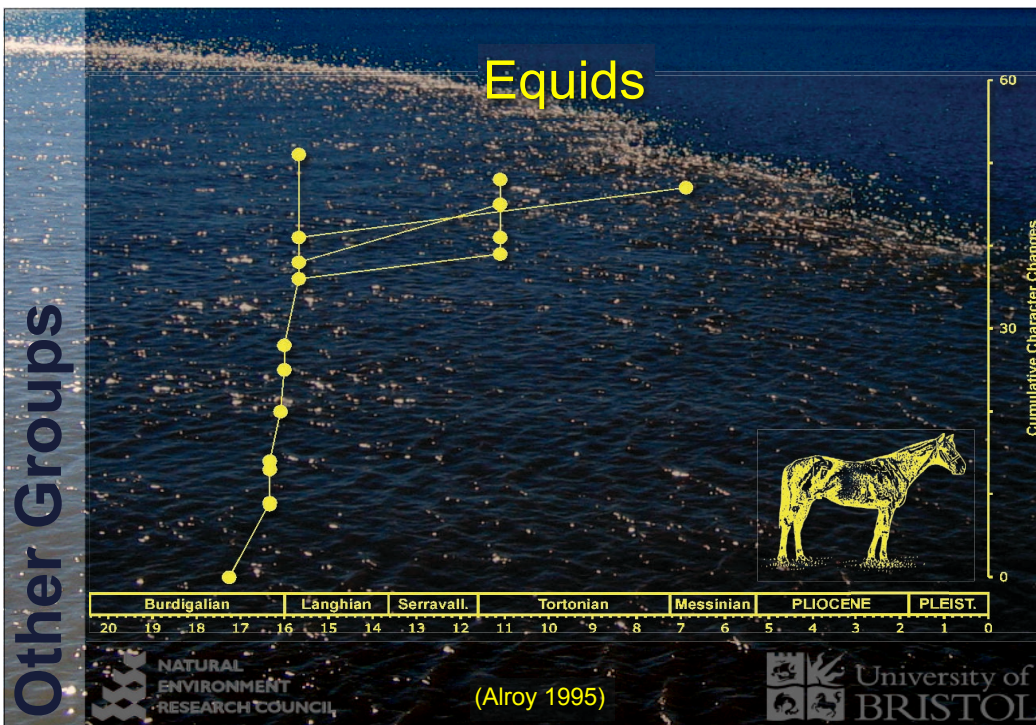
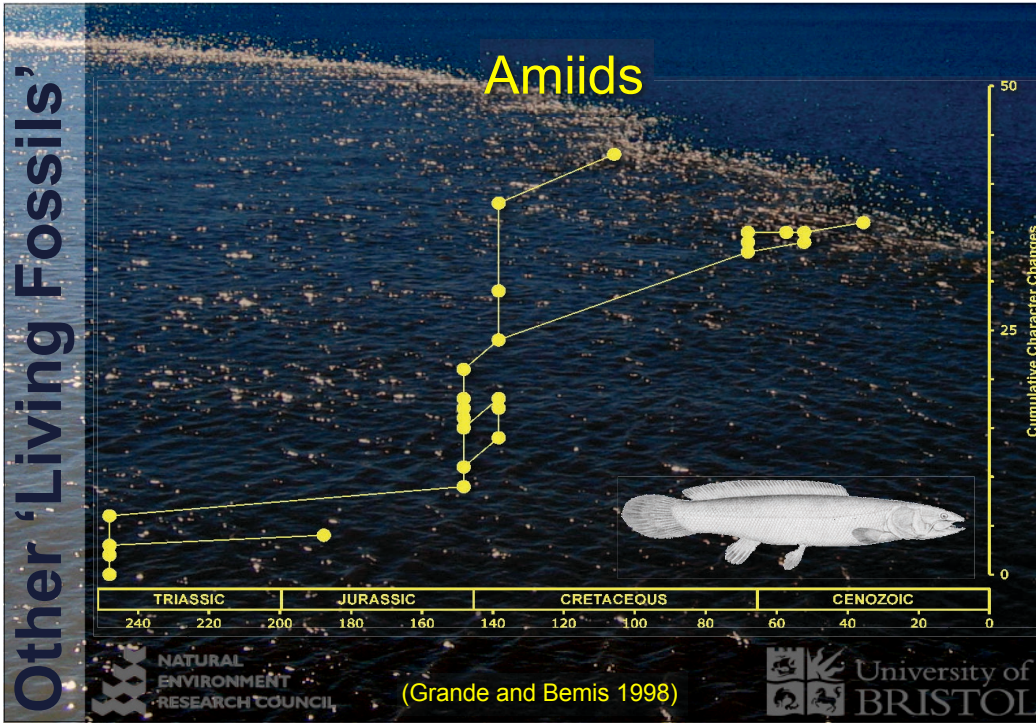


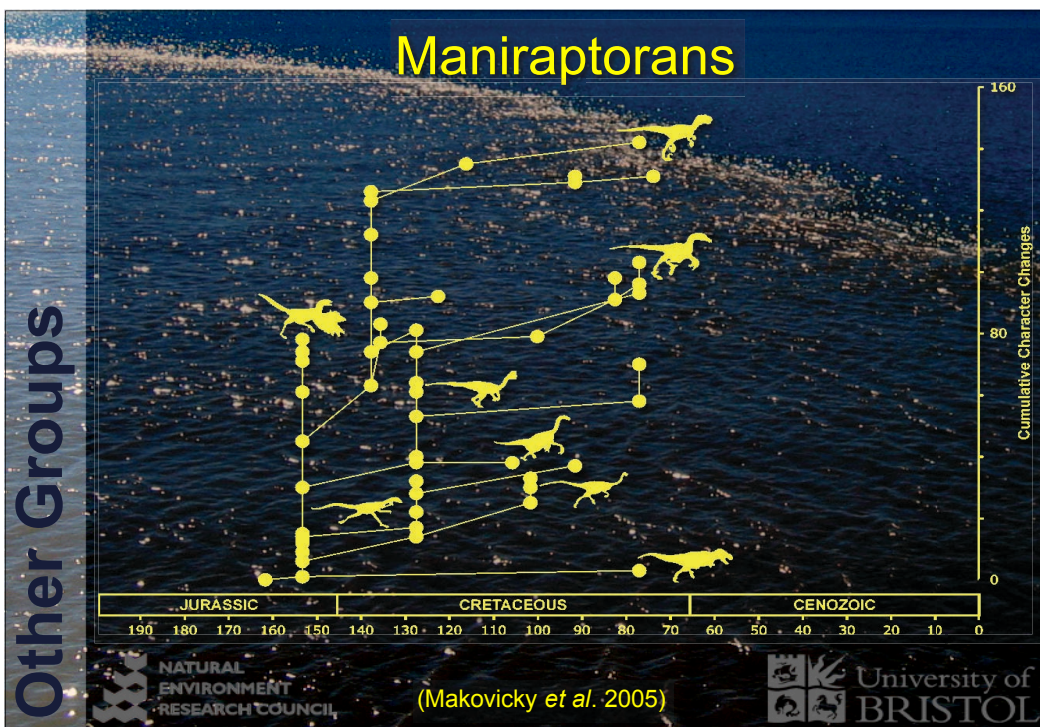
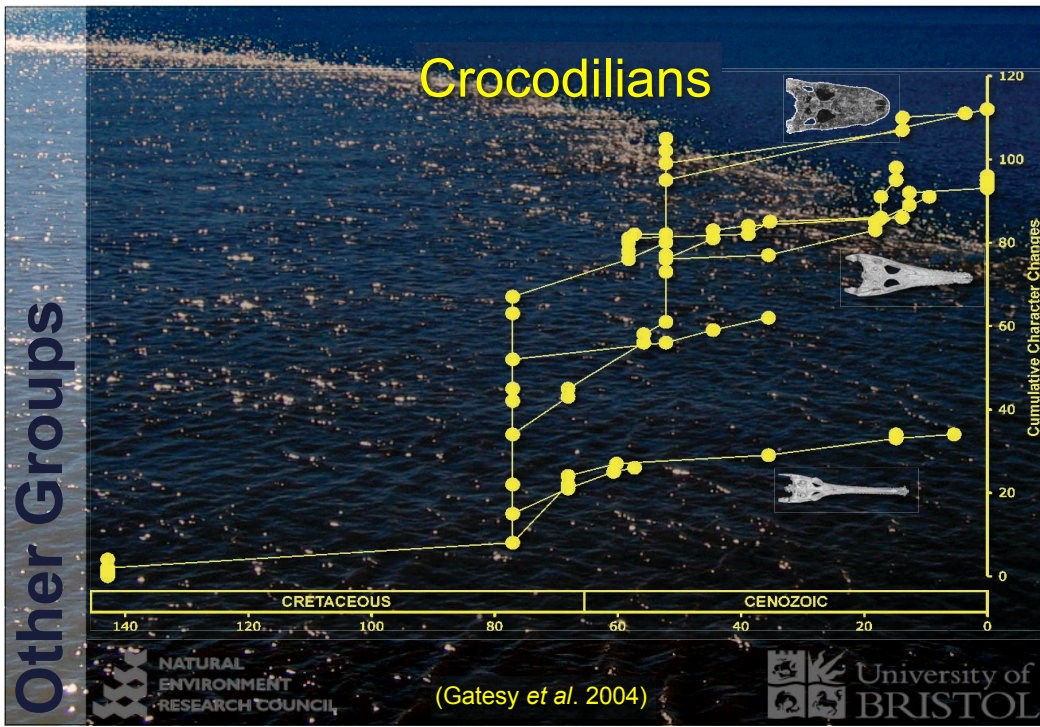
Lungfish Pattern as a Biological Phenomena

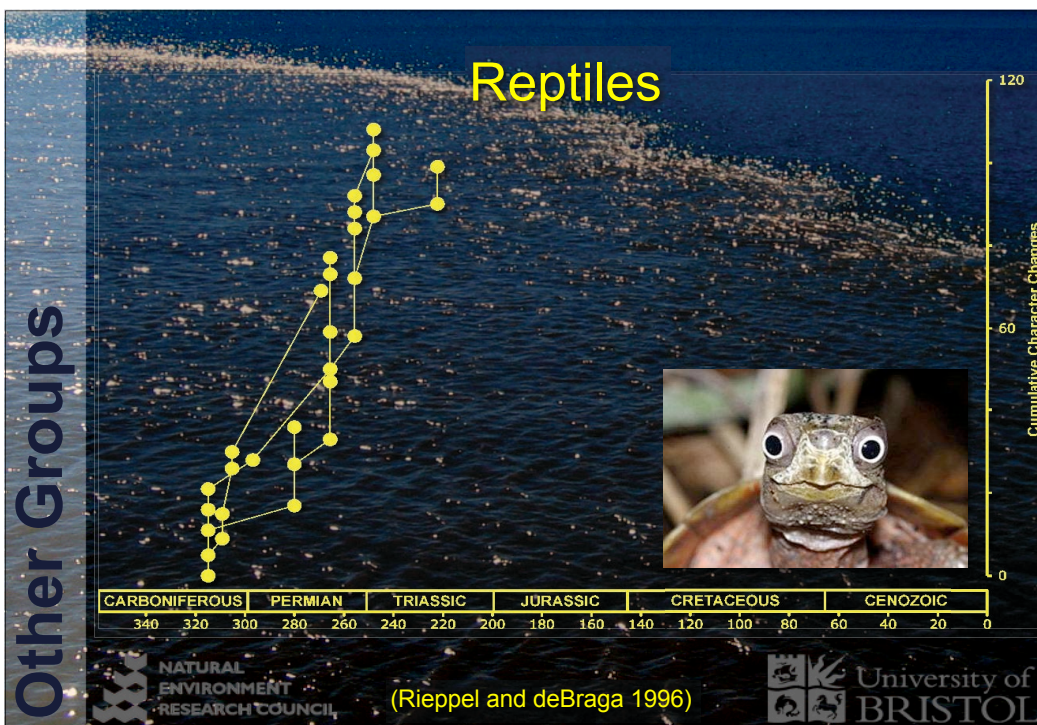
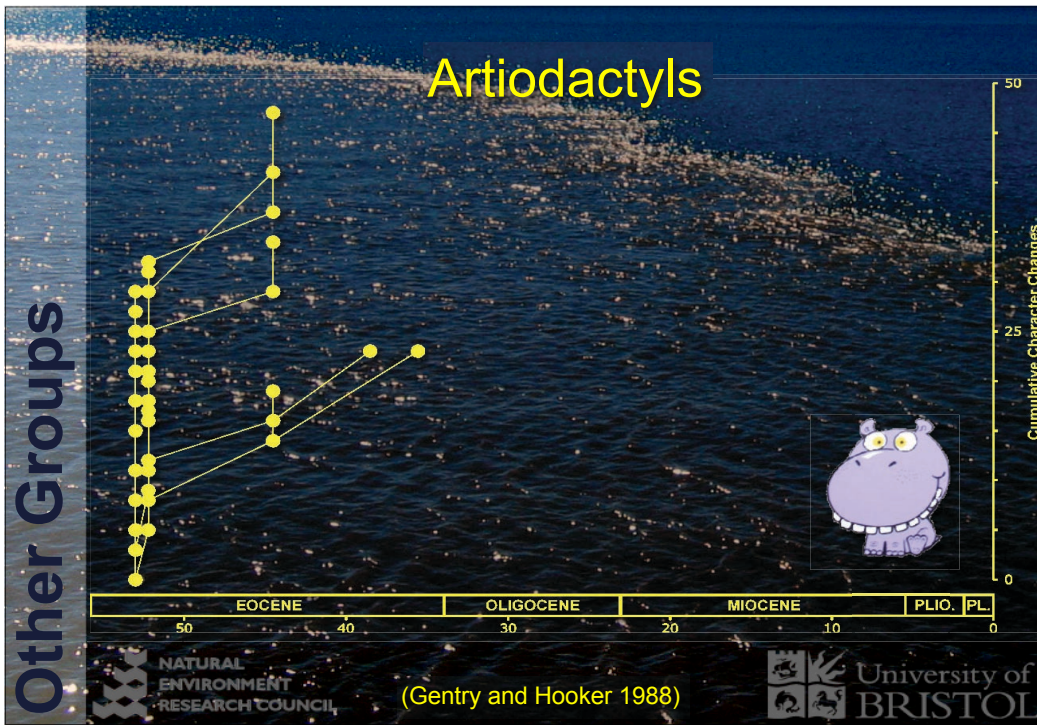
- Westoll/Simpson saw it as 'quantum evolution'
- Others argue for specialisation (aestivation/air-breathing)











Conclusions

- A (modified) Westoll methodology allows assessment of evolutionary tempo in cladistic matrices
- Application of this method to lungfish confirms a pattern of arrested evolutionary tempo
- However, a pattern of rapid character acquisition early in a clade's history seems to be a more general evolutionary phenomena

Conclusions



Acknowledgements



Hans-Peter Schultze (University of Kansas) provided me with a copy of his unpublished data matrix which was used in the lungfish study and Matt Friedman (University of Chicago) helped track down information on some of the more obscure lungfish taxa. This work represents part of my Ph.D. which is supported by a NERC studentship. Phil Donoghue provided useful comments and advice on an earlier version of this talk.

