Dinosaurs and the Cretaceous Terrestrial Revolution

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Talking about dinosaurian evolution

Discourse about dinosaurian evolution has moved through several stages of increasing clarity and quantification:

1. Story telling (up to 1980s)
2. Cladistics (1980s ->)
3. Comparative method (2000s ->)

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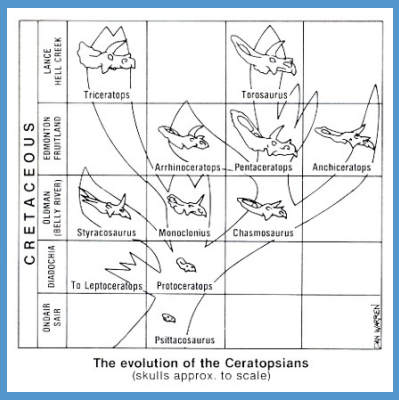
1. Story telling

- Colbert, Romer, Charig, Ostrom, and others used their broad knowledge and insights to present narratives of evolution - both in professional and popular works
- These accounts combined a knowledge of time (fossils in the rocks) and phylogeny
- But there was no chance of testing anything; a new find could change the narrative entirely



The evolution of the Ceratopsians
(skulls approx. to scale)

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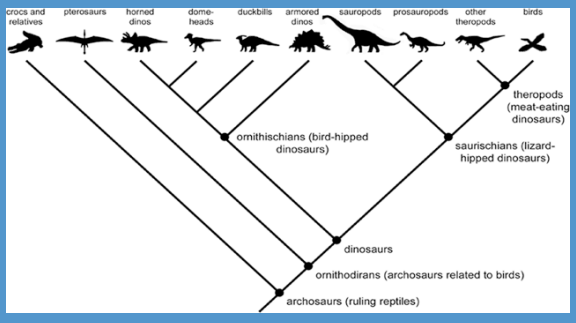
2. Cladistics

- The application of cladistics to dinosaurs, from the early 1980s, provided a framework for discourse about phylogeny
- Cladistics gave a convincing resolution of many debates, such as polyphyly vs. monophyly of Dinosauria; birds as theropods; relationships of key ornithischian clades…



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3. Comparative method

- *The comparative method in evolutionary biology* (OUP, 1991) by Paul Harvey and Mark Pagel presented a new approach to the use of phylogenetic trees in evolutionary study
- Their proposals to quantify the shapes of phylogenetic trees have been augmented and applied widely to trees by molecular biologists, ethologists, conservationists, and others
- Some themes, such as the geometry of tree shape have been considered by palaeontologists, but there are many other methods we could use

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Harvey & Pagel (1991)

- The comparative approach in evolutionary biology involves looking for correlations in characters between different members of a taxon.
- Using each species as an independent data point for statistical purposes is not valid, since species are often not independent because of a shared evolutionary history.
- *The Comparative Method in Evolutionary Biology* discusses several ways of using phylogenetic trees to separate the different components of the variation, thus allowing the use of simple statistical methods.
- Different methods are given for coping with discrete character variables, continuous character variables, and allometric relations.

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Dinosaurian phylogeny

- There have been many phylogenies of all, or parts of, Dinosauria since the 1980s
- Early efforts are Benton (1984), Gauthier (1984, 1986), Norman (1984), Gauthier and Padian (1985), Sereno (1986), Benton and Clark (1988)
- Since 1984, there have been 500 or more papers offering partial or complete cladistic coverage of Dinosauria
- As a first effort to summarise this information, we produced a supertree in 2002

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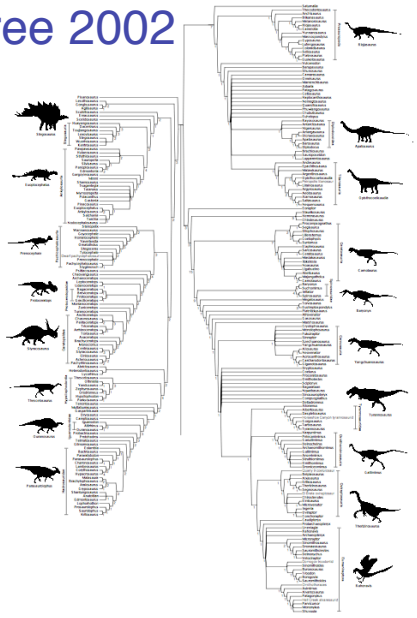
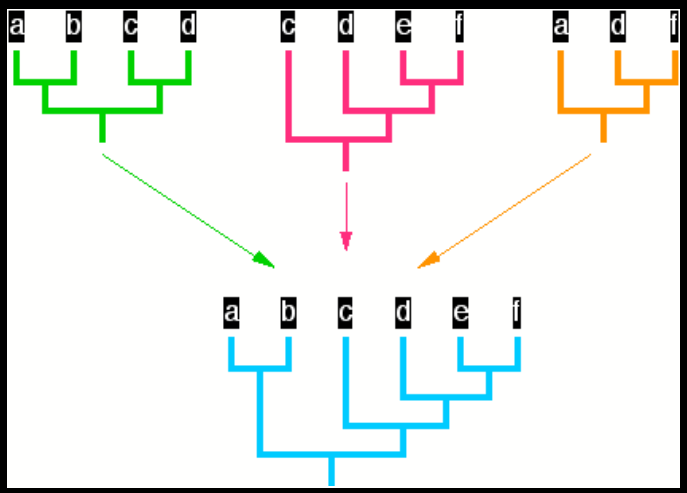
Dinosaur supertree 2002

- 126 trees and 227 genera
- The biggest supertree yet attempted (at that time)
- Provided a summary phylogenetic framework for half of the then-valid dinosaurian genera



Pisani, D., Yates, A. M., Langer, M., and Benton, M. J. 2002. *Proceedings of the Royal Society, Series B*, 269, 915-921

The supertree method



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Supertrees - critique

1. The supertree is democratic, not scientific (in other words, it relies on popularity of a conclusion, not rigorous testing)
2. The work of one person or team can dominate, or skew, the result, if they publish early and often
3. There are practical problems in deciding which trees to include and which to exclude

Responses

1. Supertrees are not meant to offer novel hypotheses; they are meta-analyses, or summaries of the current position
2. All practitioners correct for bias by using only the latest offering by a worker/ team, or constructing a single tree of all their contributions
3. Protocols include limiting the search to the past ten years, or excluding non-numerical trees, for example

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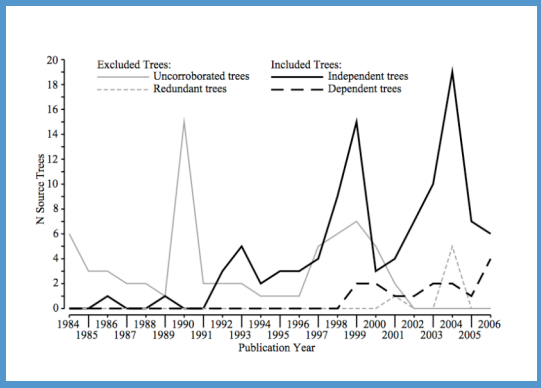
Dinosaur supertree 2008

- We looked at all trees published since 1984
- Many early trees were excluded (either unsupported by numerical analysis, or redundant with later efforts by same people)
- 'Dependent trees' were identified - those that related to other published trees - these were weighted in groups to be equivalent to single independent trees
- So what does the new supertree look like?



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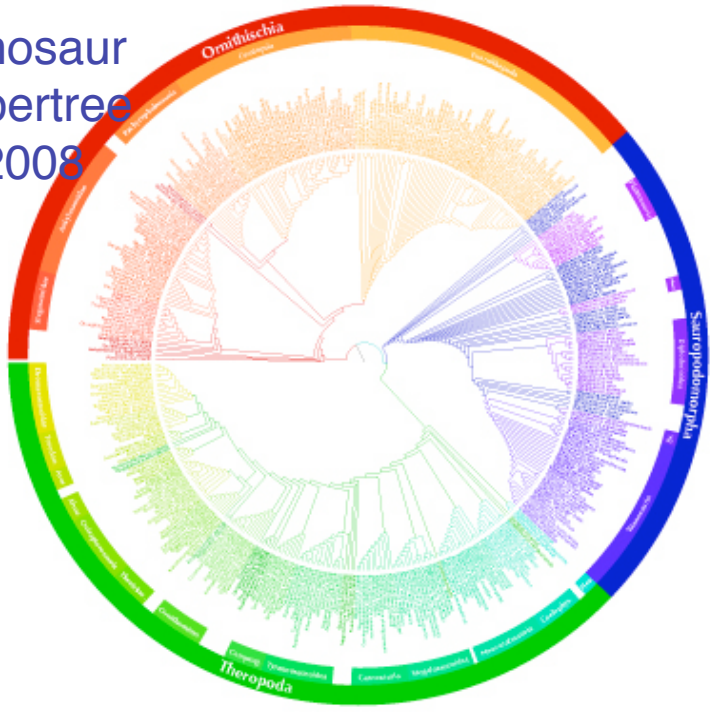
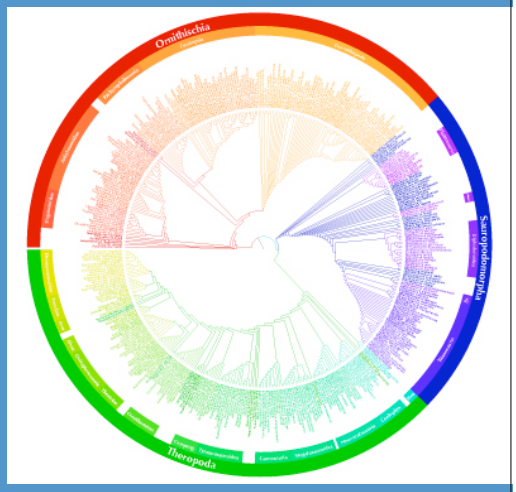
Dinosaur supertree 2008



Dinosaur supertree 2008

- 155 trees and 440 species
- The most comprehensive single phylogeny of Dinosauria
- Provides a summary phylogenetic framework for 75% of currently valid dinosaurian genera



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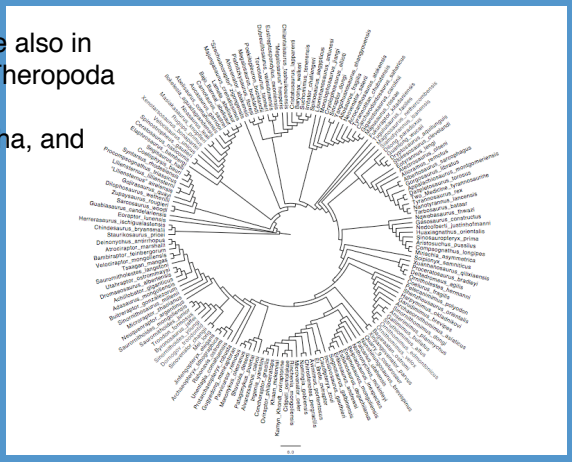
Dinosaur supertree 2008

The tree is available also in three sections: Theropoda (shown), Sauropodomorpha, and Ornithischia



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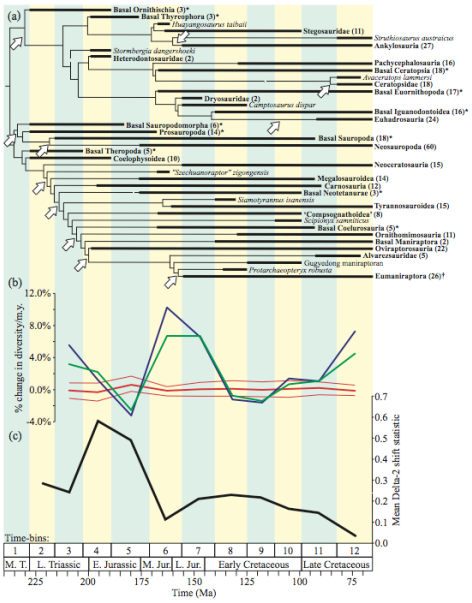
Dinosaurian evolution

(a) 11 statistically significant diversification shifts (Δ_2; open arrows)

(b) Diversification rates (blue), with ghost ranges (green), and sampling-corrected (red)

(c) Mean value of Δ_2 statistic through time



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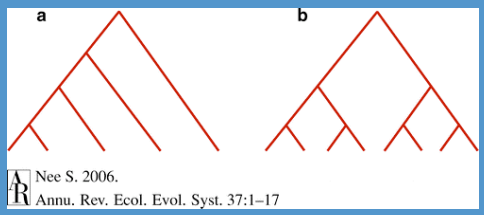
Diversification shifts (1)

- A diversification shift is a change in net speciation rate (i.e. rate of splitting of evolutionary lineages)
- Under the Equal-rates Markov Model (ERM), a tree splits equally to left and right - real trees tend to diverge from such a model assumption, and one branch will tend to split faster (or experience lower extinction) than the other
- This gives rise to unbalanced (a) and balanced (b) trees



Nee S. 2006.
Annu. Rev. Ecol. Evol. Syst. 37:1–17

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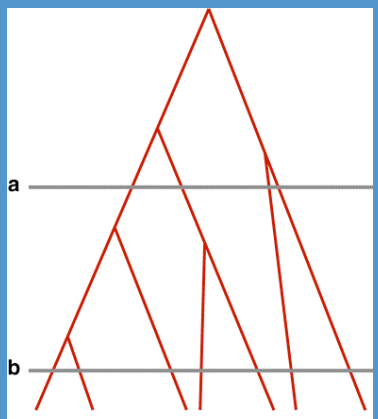
Diversification shifts (2)

- The question is whether, at time *b*, the number of lineages subtended by each lineage present at time *a* is equal or not?
- Here, the numbers are 3, 2, 1, 1 - so somewhat different from the 'equal rates'/ equal numbers assumption
- The diversification shift statistic (Δ_2) measures whether one or other lineage is statistically significantly more speciose than its sister - i.e. diverges sufficiently from a random walk expansion



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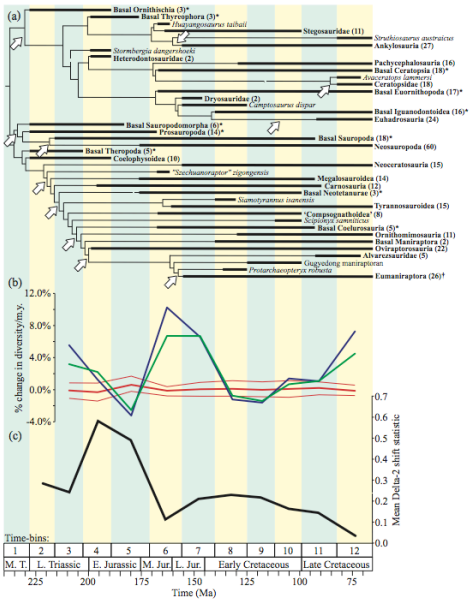
Dinosaurian evolution

- So, here we identify 11 (out of 416) nodes that show sufficient imbalance between diversities of the sisters to be deemed statistically significant
- Note the temporal distribution: Late Triassic (3), Jurassic (6), Cretaceous (2) - it is not a foregone conclusion that all d.s. fall low in a cladogram



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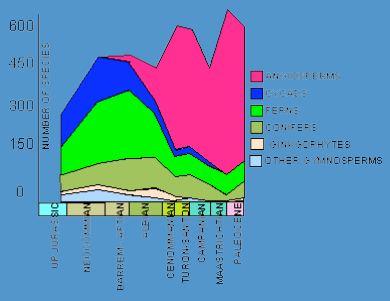
The Cretaceous Terrestrial Revolution (KTR)

- We name the KTR as an analogue of the Mesozoic Marine Revolution (MMR), a term devised by Vermeij (1987), both of which are associated with massive increases in global diversity.
- The MMR is the explosion of new life forms in the sea, both producers and predators
- The KTR is the explosive diversification of angiosperms, herbivorous and social insects, squamates, birds and mammals



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The Cretaceous Terrestrial Revolution (KTR)

- There were many new dinosaurian groups in the Early to mid Cretaceous, including euhadrosaurs, neoceratopsians, ankylosaurids, pachycephalosaurs, caracharodontosaurines, troodontids, dromaeosaurs, and ornithomimosaurs.
- Only euhadrosaurs and neoceratopsians are associated with statistically significant diversification shifts - the others are part of a diversification that did not exceed the expectations of an ERM process

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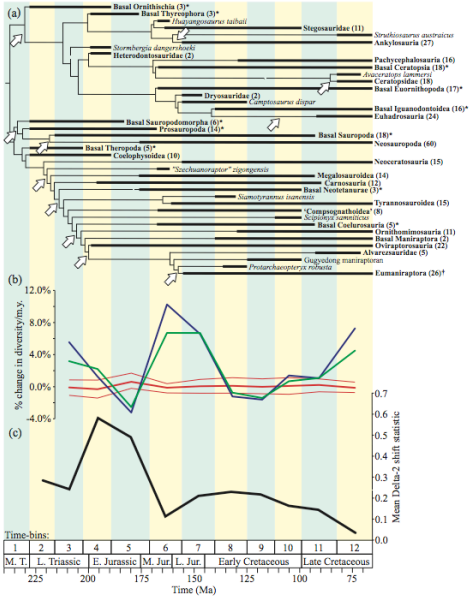
The end-Cretaceous 'burst'

- Fastovsky *et al.* (2004) identified a burst of dinosaurian evolution in the Campanian and Maastrichtian, the last 18 Myr of the Cretaceous
- This shows as a rise in (b) - blue/ green curves…
- … but, when subsampled/ rarefied to make each time bin of roughly equal sampling quality (red line), the peak disappears
- Perhaps there was no final burst of evolution…



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Subtleties of the message…

- Dinosaurs did not participate in the KTR - so they did not see an equivalent burst of speciation to match angiosperms, social insects, squamates, birds or mammals
- Further, the end-Cretaceous burst in radiation may be an artefact of intensive sampling (lots of fossil sites = lots of species)
- But neither of these findings in any way says dinosaurs had stopped evolving, or predicts the demise of the dinosaurs
- But, beware simplistic interpretation of these results…

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Subtleties of the message…

- But, beware simplistic interpretation of these results:
  - 'Dinosaurs stopped evolving 50 million years before they became extinct' - *Daily Mail*
  - 'Lloyd *et al.* suggested that dinosaurs' failure to diversify as ecosystems were changing doomed them to extinction' *Wikipedia - Dinosaurs.*
- Other examples of numerical analysis…

Dinosaurs 'ran out of evolutionary steam' before they became extinct

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Dinosaurs stopped evolving and taking advantage of their changing environment during their last 50 million years on Earth, scientists have learned.

They were not part of the Cretaceous Terrestrial Revolution around 100 million years ago, which saw the rapid expansion of many land animals and plants.

While flowering plants, lizards, snakes, birds and mammals evolved swiftly, the dinosaurs plodded behind. A short time later, they were extinct.

Researchers made the discovery after using powerful computer programs to produce a 'supertree' of dinosaur lineages.

The results showed the most likely pattern of evolution for 440 of the 600 known species of dinosaur.

Graeme Lloyd, one of the University of Bristol scientists who led the study, said: 'Supertrees are very large family trees made using sophisticated computer

Dinosaurs stopped evolving 50 million years before they became extinct

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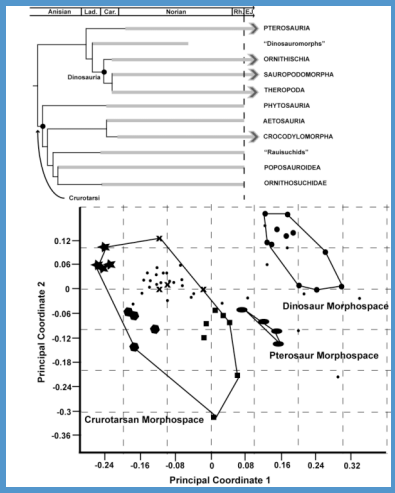
A numerical study of dinosaurian origins

- How did dinosaurs radiate in the Late Triassic?
- Earlier ideas were either a simple competitive vs. opportunistic model
- Numerical assessment of **disparity** shows that dinosaurs occupied a distinct, but small character space in the Late Triassic
- So, a two-step radiation, sauropodomorphs in the Late Triassic, following extinction of rhynchosaurs and dicynodonts, and larger theropods and ornithischians in the Early Jurassic, after extinction of crurotarsans



Brusatte, S. L., Benton, M. J., Ruta, M., and Lloyd, G. T. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science*, in press for September 12th.

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Sampling and data quality

- A key question behind any numerical study of macroevolution is the quality of the data, and this is especially true of the terrestrial fossil record
- Some authors have suggested that much, or most, of some or all fossil records is geological rather than biological signal
- I think they exaggerate, but it is clearly crucial to demonstrate that a fossil record signal does not simply reflect sampling
- Some authors suggest we correct counts of dinosaurian diversity by removing the signal of number of dinosaur localities - but of course there is a correlation between number of taxa and number of localities (but which causes which?)
- Better perhaps to use a count of **all** terrestrial vertebrate localities, not just those with dinosaurs, or to use a subsampling/ rarefaction technique, as we did
- Also, there is a question about the validity of taxa - are the species or genera in a study all real or not?

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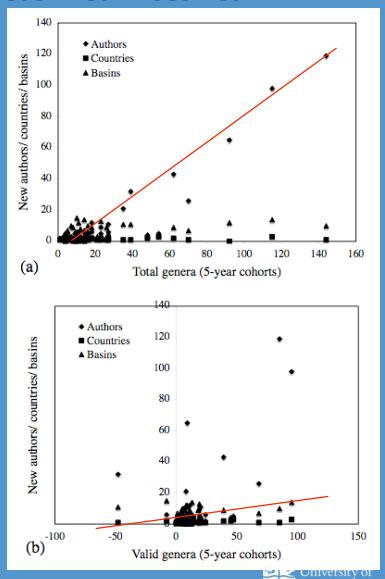
Validity of dinosaurian taxa

- Can we be sure that all the species and genera, and families of dinosaurs are real?
- Recent reviews (Dinosauria 2) relegate >50% to synonymy or improper naming (in fact more *nomina dubia* than synonyms)
- If you want to name a new dinosaur, put more palaeontologists on the job; if you want to name a *valid* new dinosaur, find a new sedimentary basin (best-fitting lines)
- I also present figures for the 'success rates' (valid: invalid taxa) of prolific namers of new dinosaurs…



Benton, M. J. 2008. How to find a new dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology*, in press for December 2008.

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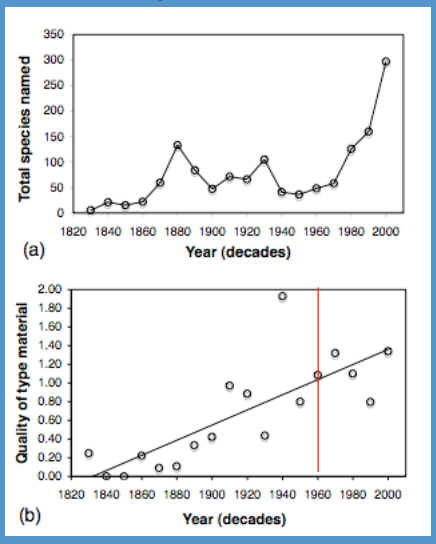
Quality of taxonomic practice

- Today, some 30 new species of dinosaurs are named each year - the highest ever level
- Are we driven by granting agencies, journals, and the media to name ever more useless little scraps as new species, or are all these likely to be valid?
- In an assessment of quality of type specimens for all 1047 species of dinosaurs named up to 2005, we collectively passed a Rubicon in 1960 - since then, most new species were based on more than fragments



Benton, M. J. 2008. Fossil quality and naming dinosaurs. *Biology Letters*, in press for October 2008.

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Conclusions

- Palaeontologists must use quantitative methods in studies of macroevolution, palaeobiogeography, and other fields - if they do not, their conclusions risk being little more than 'join the dots' narratives
- Our new studies show that
  - dinosaurs did not participate in the Cretaceous Terrestrial Revolution (KTR) - Lloyd *et al.* (2008)
  - the late burst of dinosaurian evolution at the end of the Cretaceous may be an artefact of sampling - Lloyd *et al.* (2008)
  - dinosaurs originated in a two-step process, each step following an extinction event - Brusatte *et al.* (2008)
  - the discovery of valid new species of dinosaurs depends on the discovery of new sedimentary basins - Benton (2008a)
  - practice in naming new dinosaurian species has improved markedly since 1960, and so most new species being named today are probably valid - Benton (2008b)

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