



Fig. 1. (a) A cladogram for nine taxa (A-I). (b) A pectinate reduction of (a) using the method of Benton¹. (c) and (d) Pectinate reductions of (a) using the method of Norell and Novacek^{3,4}. (e) The stratigraphic ranges of taxa A-I. Age ranks are on the right column and clade ranks corresponding to reductions (b), (c) and (d) are shown below. For reductions (b) and (c) the underlined clade rank of 1 corresponds to group F-I (reduction c) and group A-E (reduction d).

new modifications are not always beneficial or necessary, especially when they violate basic principles of phylogenetic structure, like the temporal equivalence of sistergroups and the integrity of monophyletic groups.

Mark A. Norell

Dept of Vertebrate Paleontology,
American Museum of Natural History,
Central Park West at 79th Street,
New York, NY 10024, USA

References

- 1 Benton, M.J. (1994) *Trends Ecol. Evol.* 9, 181-185
- 2 Gauthier, J., Kluge, A.G. and Rowe, T. (1988) *Cladistics* 4, 105-209
- 3 Norell, M.A. and Novacek, M.J. (1992) *Science* 255, 1690-1693
- 4 Norell, M.A. and Novacek, M.J. (1992) *Cladistics* 8, 319-337
- 5 Fisher, D.C. (1992) in *MacClade* (Maddison, W.P. and Maddison, D.R., eds), pp. 124-129, Sinauer
- 6 Benton, M.J. and Storrs, G.W. (1994) *Geology* 22, 111-114

Reply from M.J. Benton

Norell makes one substantive point in his letter, that we^{1,2} used an invalid technique for assessing branching order in cladograms. He is right that our figure explained the technique imperfectly, and we fully support the approach he clearly outlines, and illustrates in his Fig. 1c,d. Our 'error' was, however, only in the explanatory figure. In our calculations, we applied the technique precisely as he describes.

Clade collapse, a prerequisite for clade ranking, was followed by analysis of the oldest clade '1' only, *not* each individually as mistakenly assumed by Norell. Independent analysis ('two phases') of each primary bifurcation of the cladogram as in Norell's Fig. 1c,d was the practical result. Thus, our S value for the synapsid half of Gauthier and colleagues' reptile cladogram³ is 0.950, close to Norell's value of 0.978 (small differences inevitably arise through differences in the precise choice of taxa, and in the choice of stratigraphic data points). The raw data upon which our published analyses^{1,2} were based will be published shortly⁴ and we stand by our conclusions.

Norell¹ comments further that 'many of Benton's methods fall short of those previously proposed'. In fact, all of the methods recounted in my review article in *TREE*³ had been presented previously by other authors, many by statisticians and palaeontologists working in concert, so the basis of Norell's sweeping statement is unclear. Indeed, we have followed, not modified, Norell's own work. Norell states that 'new modifications are not always beneficial or necessary, especially when they violate basic principles of phylogenetic structure'. Of course, he is correct in the second half of his assertion, but the former implies that the comparison of rank orders of clade age and stratigraphic age is an adequate test. This is not the case. Indeed, it is rather a crude test since it takes no account of the time duration between adjacent nodes in a cladogram: a more subtle test is required.

Michael J. Benton

Dept of Geology, University of Bristol,
Bristol, UK BS8 1RJ

References

- 1 Benton, M.J. and Storrs, G.W. (1994) *Geology* 22, 111-114
- 2 Benton, M.J. (1994) *Trends Ecol. Evol.* 9, 181-185

- 3 Gauthier, J., Kluge, A.G. and Rowe, T. (1988) *Cladistics* 4, 105-209
- 4 Benton, M.J. and Storrs, G.W. in *Aspects of the Genesis and Maintenance of Biological Diversity* (Hochberg, M., Clobert, J. and Barbault, R., eds), Oxford University Press (in press)

The emergence of behavioural ecology

In the 100th issue of *TREE*, Mart Gross wrote about the way the field of behavioural ecology has evolved¹. I was surprised that he made no mention of the three editions of *An Introduction to Behavioural Ecology and Behavioural Ecology: an Evolutionary Approach*, respectively written and edited by John Krebs and Nick Davies. Those books surely defined and motivated the field of behavioural ecology, especially in North America and Europe. The first edition of the edited book appeared in 1978 and the co-authored book in 1981. To claim that the *discipline* of behavioural ecology was founded in 1986 (see the first sentence of Gross's concluding remarks) is wide of the mark.

Paul H. Harvey

Dept of Zoology, University of Oxford,
South Parks Road, Oxford, UK OX1 3PS

References

- 1 Gross, M. (1994) *Trends Ecol. Evol.* 9, 358-360

Reply from M.R. Gross

While I agree with Paul Harvey that the Krebs and Davies books were influential in the emergence of behavioural ecology, I am not sure that the founding of the discipline can be pegged to any particular publication. Many other researchers, including R.D. Alexander, J.L. Brown, E.L. Charnov, W.D. Hamilton, G.H. Orians, R.L. Trivers and E.O. Wilson, also set the tone and pace for behavioural ecology before Krebs and Davies.

I chose 1986 because in that year an international meeting was held with the specific purpose of fostering behavioural ecology as a distinct discipline. The meeting was a watershed because for the first time it brought together a large number of like-minded people. The lively and sometimes heated debates resulted in the creation of a new scientific society - the International Society of Behavioral Ecology - and also the journal *Behavioral Ecology*, and the biennial congresses in behavioural ecology.

Because a discipline is a social as well as an intellectual phenomenon, its starting point cannot, in the nature of things, be measured exactly. A romance is usually well advanced before the marriage is celebrated.

Mart R. Gross

Dept of Zoology, University of Toronto,
Toronto, Ontario, Canada M5S 1A1