

Perhaps the most unscientific statement in Graur's review is the proposal that gundis (Ctenodactylidae) have no known extinct recent relatives – a pessimistic remark which ignores important classic studies^{21–23} on fossil and recent ctenodactylids.

Each of us should keep in mind the words of Murray L. Johnson²⁴, a pioneering mammalogist interested in biochemical systematics: 'the best judgement will be made by the taxonomist with data from many fields at his disposal, not by the specialist in some other field, even

though it is he who may discover exciting new data'.

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Reply from D. Graur

Because of space limitations, I cannot refute all of Novacek's arguments in detail. Instead, I shall illustrate the invalidity of his claims by discussing one conspicuous error, a case of self misrepresentation, and four inconsistencies. But, first, I wish to correct three typos in my review¹: (1) Tubulidentata has been misplaced in my Fig. 1, (2) the word 'Artiodactyla' in Fig. 3(j) should be replaced by 'Proboscidea' as in the text, and (3) the labels (a) and (b) in Fig. 4 have been transposed. However, unless one is endowed with an inordinate fondness for dashed lines, there is no need to redraw nine trees.

Novacek claims that Allard *et al.*'s 12S rRNA data⁷ 'strongly support rodent monophyly'³. This claim reflects a lack of understanding of the differences between rooted and unrooted trees^{19,25}. Allard *et al.*'s unrooted tree, shown here in Fig. 1(a), is consistent with both rodent monophyly, shown in trees 1–3 in Fig. 1(b), and rodent paraphyly shown in trees 4 and 5 in Fig. 1(b). This is clearly stated by Allard *et al.* who wrote 'Graur *et al.*²⁶ also support this arrangement'. To test the monophyly of Rodentia, the tree in Fig. 1(a) was rooted with an outgroup sequence from chickens. The resulting rooted tree is inconsistent with traditional rodent monophyly. The fact that this tree is shorter than the traditional tree by only one substitution is immaterial. The tree may be said to add only weak support to rodent paraphyly, but it clearly does not uphold rodent monophyly. All Novacek's other 'corrections', such as his rendition of Irwin *et al.*'s tree²⁷, can be similarly discarded, as he confuses binary trees with consensus trees, and gene trees with species trees.

Novacek misrepresents not only the work of others but also his own work³. What I wrote was that Novacek is of the opinion 'that the fundamental features of eutherian evolution will prevent us from ever identifying the true phylogenetic

tree'. Novacek's exact words were: 'There is no reason to expect that all the basic lines among, for instance, the placental mammal orders will be teased apart. And there may be some truth in Simpson's remarks that the great burst of radiating mammalian orders more than 65 million years ago will not completely yield to [morphological and molecular] probes.' Elsewhere, in discussing the two possible explanations for the bushiness of the eutherian tree, i.e. that the bush may simply represent a 'lack of information necessary for finer resolution', or that it represents an 'emphatic statement' that 'a nearly simultaneous polytomy of major clades *actually* occurred', Novacek concludes that the truth 'lies somewhere between the two perspectives'²⁸.

Novacek claims that Pettigrew's tree is based not on morphological data, but on 'Pettigrew's version of those data'. This is silly, because conclusions are always based on interpretations – should I say that Novacek's trees are based not on paleontological data, but on Novacek's 'version' of those data? And why should disputes between Novacek and Pettigrew be interpreted to mean that Pettigrew's data are 'highly contested'? Novacek's other inconsistency concerns his demand that percentages be attached to my claim that 'many' morphological characters are problematic, while in his next sentence, he uses the term 'most biologists' without quantification. Finally, nowhere did I claim that the skepticism on the notion of bushiness was spawned by molecular work; however, self-citations regarding priority, even when irrelevant, are probably too strong a temptation to resist.

Catzeflis demands objectivity and completeness. However, as most morphological references had already been reviewed in *TREE*²⁹, I promised and delivered a 'far from exhaustive' review. As to my ignoring 'important classic' studies, we all know

from Gregor Mendel's example that papers published in journals such as *Paleontologica Sinica* or *Journal of the Paleontological Society of India* tend to remain unknown for long periods. In fact, none of these papers is listed in the new reference guide to mammalian species³⁰. I also do not subscribe to the myth of scientific objectivity. Rather, I believe in the veracity of Søren Kirkegaard's words: 'To exist is to be subjective.' However, I must protest Catzeflis' claim that Novacek's review³ is more 'objective' than mine. Novacek either ignored the molecular studies (e.g. Refs 31,32) or else ignored their conclusions (e.g. Refs 26,33). Novacek even downplayed Gingerich *et al.*'s paleontological inferences, so that in his review, the cetacean-artiodactyl association 'so well illuminated by the fossil record' is deemed 'ambiguous'. Finally, his review purported to 'shake' the mammalian phylogenetic tree, but the

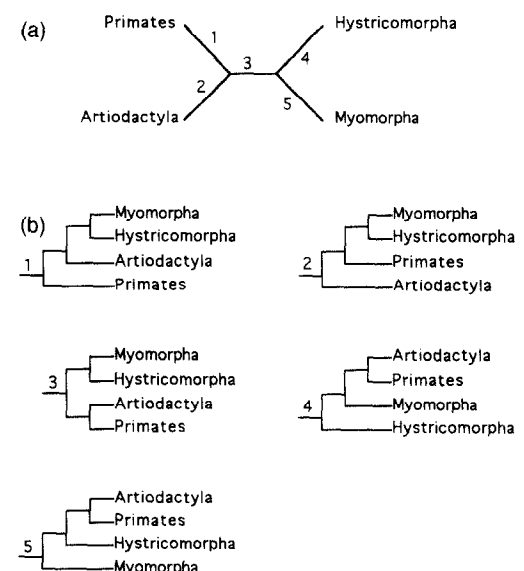


Fig. 1. (a) Allard *et al.*'s unrooted tree for Hystricomorpha, Myomorpha, Primates and Artiodactyla'. Depending on the position of the root (arabic numerals), five rooted trees (b) can be obtained. Allard *et al.*'s 12S rRNA sequences support tree 4, which is identical to the one obtained in Ref. 5.

similarities between his 1992 tree and that of Simpson from 1945 indicate that the tree was barely stirred.

I agree with Catzeflis that many methodological problems in molecular phylogeny are not yet resolved. However, many of the difficulties, such as multiple alignment, statistical testing of trees and weighting procedures, have been solved wholly or partially in recent years^{34,35}. Moreover, errors in molecular phylogeny are predictable. The dynamics of molecular evolution can be simulated by varying parameters, such as the rates and patterns of substitution, and we can define the conditions under which topological errors may occur³⁶. Try to do that with morphological character states defined as narrow, pronounced, developed, large, reduced, flattened, elongated, compressed or strong³⁷.

Whether rodent paraphyly²⁶ is an artifact of elevated rates of substitution is an open question. However, in this case we must assume that the evolution of the guinea-pig lineage is characterized by an extraordinary combination of high rates of substitution, on the one hand, and a remarkable retention of primitive characters, on the other. Evidence in support of rodent paraphyly continues to accumulate from many unrelated fields, and we have recently shown that the New World hystricomorphs (guinea-pigs) and the Old World hystricomorphs (porcupines) are monophyletic³⁸.

This exchange leaves me with the impression that paleontologists fear the possibility of being relegated secondary; their studies mere 'Christmas ornaments' on molecular trees. Actually, a Christmas tree would not be a Christmas tree without the ornaments. However, while as a molecular biologist I felt no constraint in giving advice to paleontologists, I

do not feel qualified to comment on matters of Christmas.

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Book Reviews

Chiropteran Stochasticity

Bats: A Community Perspective

by James S. Findley, *Cambridge University Press, 1993. £27.95 hbk (xi + 167 pages) ISBN 0 521 38054 5*

Bats appear to live in a MacArthurian world. They have exceptionally long life spans, long gestation periods and low fecundities. Among mammals, bats are dramatic outliers to established relationships between

body size and these life history traits. Also, the population sizes of bats appear stable and probably are close to carrying capacities. Although most small mammals are at the opposite end of the *r*-*K* continuum, bats are classical *K*-strategists. Bats are also a rich taxon with nearly a 1000 extant species. In most places, bat communities consist of suites of

closely related species with similar ecological requirements. In tropical habitats, single localities often contain dozens of such species. Thus, bats provide diverse assemblages of *K*-selected organisms living in stable environments – apparently ideal models, argues Findley, for studying how community structure may be controlled by interspecific interactions.