Molecular dates and the mammalian radiation

In a perspectives article, Bromham *et al.*[1] raise some important concerns about the use of both molecular and paleontological data in assessing the timing of diversification of extant mammalian orders. In Box 1, they describe well the need to differentiate crown (or more generally, node-based) taxa from stem-based taxa. Unfortunately, their Fig. 2 is not clearly explained and thus confuses these kinds of taxa. As they note, the paleontologically based orders of extant placental mammals (except, perhaps, Insectivora) are recognized as appearing soon after the Cretaceous–Tertiary (K–T) boundary (thick lines in their Fig. 2). These dates are based on apomorphy- or node-based *intraordinal* diversifications for the order in question. In contrast, the extensions into the Late Cretaceous of clades shown in their Fig. 2 (the thin lines), estimated by molecular data, are *interordinal* separations. Thus, in at least this comparison, the molecular data indicate nothing about ordinal origination and diversification, but rather argue only that stem-based clades extend into the Late Cretaceous. Furthermore, the possible Cretaceous record of primates they mention in their text is a single tooth originally assigned to the primatomorph *Purgatorius*, which was discovered at a site now regarded as Paleocene in age[2].

The authors' biogeographical assessment of fossil taxa requires updating. The possible placental for the early Cretaceous of Australia is now regarded by most as symmetrodont[3] or early therian. Thus, although marsupials are known for the early Eocene of Australia[4], non-chiropteran placentals do not appear until the Pliocene[5]. In South America, all definite pre-Tertiary mammals are non-therians, with both marsupials and placentals appearing only after the K–T boundary[6]. As the authors note, the Late Cretaceous of North America and Asia have a good record of mammals, but except for, perhaps, Insectivora, no modern orders of placentals are known. In fact, the latest Cretaceous record[7] is better known than the earliest Paleocene[8]. Europe is not well known but echoes what is known in Asia for placentals[9]. As the authors also note, Africa is a cipher. Unless, however, one wishes to make the unsubstantiated argument that all 18 orders of extant placentals arose in Africa, the claim is not valid that the biogeography of placentals is too poor to help in deciphering ordinal appearances.

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Reply from L. Bromham, D. Penny and M.J. Phillips

Molecular and palaeontological dates for the radiation of modern mammals appear at odds because molecular studies propose a Cretaceous origin of many eutherian orders, but there are no uncontroversial Cretaceous fossils from modern eutherian orders, a point emphasized by David Archibald in his letter. This conflict might be partly due to different definitions of the 'origin' of an order – palaeontologists tend to focus on the appearance of members of a defined crown group, whereas molecular dates mark the split between lineages, long before they develop crown-group features[1]. Both definitions are interesting and important, particularly if the timing of lineage divergence and morphological diversification are not tightly linked. We currently cannot distinguish a long Mesozoic 'phylogenetic fuse'[2] from a true Cretaceous radiation. Perhaps, higher phylogenetic resolution or new fossil finds could shed light on this conundrum.

To explore the apparent discrepancy between molecular and palaeontological dates, we must ask: 'If the molecular dates are true, then where are the missing fossils?' The most plausible place to hide them is Africa, or perhaps Australia or Antarctica[3]. We do not suggest this is necessarily true, and we certainly don't expect that 18 eutherian orders arose in Africa. Molecular evidence suggests only some eutherians 'crossed the K–T boundary'[1], which is compatible with the suggestion that a handful of basal eutherian orders form an 'African clade'[4,5]. If the molecular dates are true, we have to hide the Cretaceous eutherians somewhere, and Africa seems the best candidate. Conversely, if the palaeontological dates are true, why are the molecular dates too old? Lineage-specific rate variation across mammals[6] could cause consistent overestimation of the dates of divergence of mammalian orders[1]. So, we are left with the conclusion that although the discrepancy between molecular and palaeontological dates seems large, at this stage neither can confidently exclude the other.

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Phase locking: another cause of synchronicity in predator–prey systems

In a recent *TREE* article, W.D. Koenig reviewed the patterns and causes of temporal synchronicity in spatially extended populations[1]. Synchronicity can have different causes, one of these, spatial correlation of environmental disturbances, was extensively discussed in a news & comment in the same *TREE* issue[2]. This mechanism, which has become known as the Moran effect, occurs when two populations are regulated by the same (linear) density dependence and are exposed to environmental disturbances. If these environmental disturbances are correlated, the fluctuations of population sizes will also be correlated. A further mechanism for synchrony is dispersal of individuals; both papers assumed that dispersal cannot counteract the desynchronizing effect of uncorrelated disturbances beyond the range of dispersal of the organisms under study. It was concluded that spatial correlations at larger spatial scales are likely to be caused by the Moran effect.

Some of the examples of spatial synchronicity in the review[1] were predator–prey or host–parasite systems, which have an intrinsic propensity to oscillate. For such systems, synchronicity can be caused by phase locking. Phase locking occurs if the populations are coupled through dispersal and can act at distances exceeding the typical dispersal distance.

This can be demonstrated with a deterministic mathematical model for predator and prey populations in two connected patches, in which the local dynamics are described by a standard predator–prey model (e.g. the Lotka–Volterra or McArthur–Rosenzweig model[3]). If the parameters are chosen such that the populations exhibit regular oscillations when isolated, the smallest amount of dispersal results in synchronous oscillations in a system of connected patches. Even if either prey or predator does not migrate, phase locking occurs. Such results can be extended to systems with more patches: some dispersal to neighbouring patches can result in phase-locked population dynamics in large groups of patches[4]. The dispersal range in this case is small but the correlation can work at distances exceeding the dispersal range of an individual. This effect can withstand the desynchronizing effect of uncorrelated disturbances to a certain extent (Fig. 1).

The effect of phase locking will be weaker for patches that are at a larger distance. If uncorrelated noise is superimposed on such a deterministic model, it can result in a correlation that decreases with distance, resulting in a typical

