

## Growing up with dinosaurs: molecular dates and the mammalian radiation

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**Dates of divergence derived from molecular data have been used to place the beginning of the radiation of modern mammalian orders in the Cretaceous, long before the final extinction of the dinosaurs. These molecular dates have been used to challenge the idea that the ordinal diversification of mammals was triggered by the availability of 'empty niches' left vacant by the disappearance of the dinosaurs. However, the broad discrepancies between molecular date estimates from different studies warn that molecular dates should not be accepted uncritically. Consideration of the wide confidence intervals around molecular date estimates, and the potential for geographic bias in the fossil record, could lessen the discrepancy between molecular and palaeontological data but might still prompt a re-evaluation of the timing and causes of the mammalian radiation.**

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The study of mammal phylogeny has been revolutionized by molecular systematics<sup>1</sup>. Novel relationships have been suggested, such as the whales as the sister group to hippos<sup>2</sup>, and marginal hypotheses supported, such as grouping marsupials and monotremes into Marsupionta to the exclusion of the placentals<sup>3</sup>. Also, the presumed stochastic nature of molecular evolution has led to the prediction that changes should accumulate approximately linearly with time, so the divergence time between taxa can be estimated from their genetic distance. Some of the earliest applications of 'molecular clocks' were to mammalian evolution<sup>4,5</sup> and the technique continues to be widely applied.

Recent molecular phylogenetic studies<sup>3,6-9</sup> have presented surprisingly old dates for the origin of many mammalian orders. These dates have been proclaimed as the death knell of the idea that the radiation of modern mammals occurred in the early Tertiary, as mammals evolved into niches left vacant by the end-Cretaceous extinction of the dinosaurs. A radiation of mammalian orders after the Cretaceous-Tertiary (K-T) boundary 65 million years ago (Mya) has been supported by the relatively low diversity of Mesozoic (245-65 Mya) mammals, with few fossils unambiguously attributed to modern orders. This low Mesozoic diversity combined with the increase in mammal fossil diversity in the Palaeocene (65-60 Mya) following the apparently sudden disappearance of the dinosaurs from the fossil record

at the K-T boundary, and the 'bush-like' phylogeny of mammals, were interpreted as the signature of a rapid radiation.

Although some researchers in palaeontology accept a late Cretaceous origin of many lineages of modern mammals<sup>10</sup>, fossil evidence of modern orders before the K-T boundary is restricted to only a few lineages: monotremes, marsupials, insectivores and, possibly, primates. The molecular dates are controversial because they suggest that most mammalian orders crossed the K-T boundary, and that the divergences between these lineages are surprisingly deep<sup>11</sup> (Fig. 1). Are the molecular dates accurate, and can they be reconciled with the fossil record?

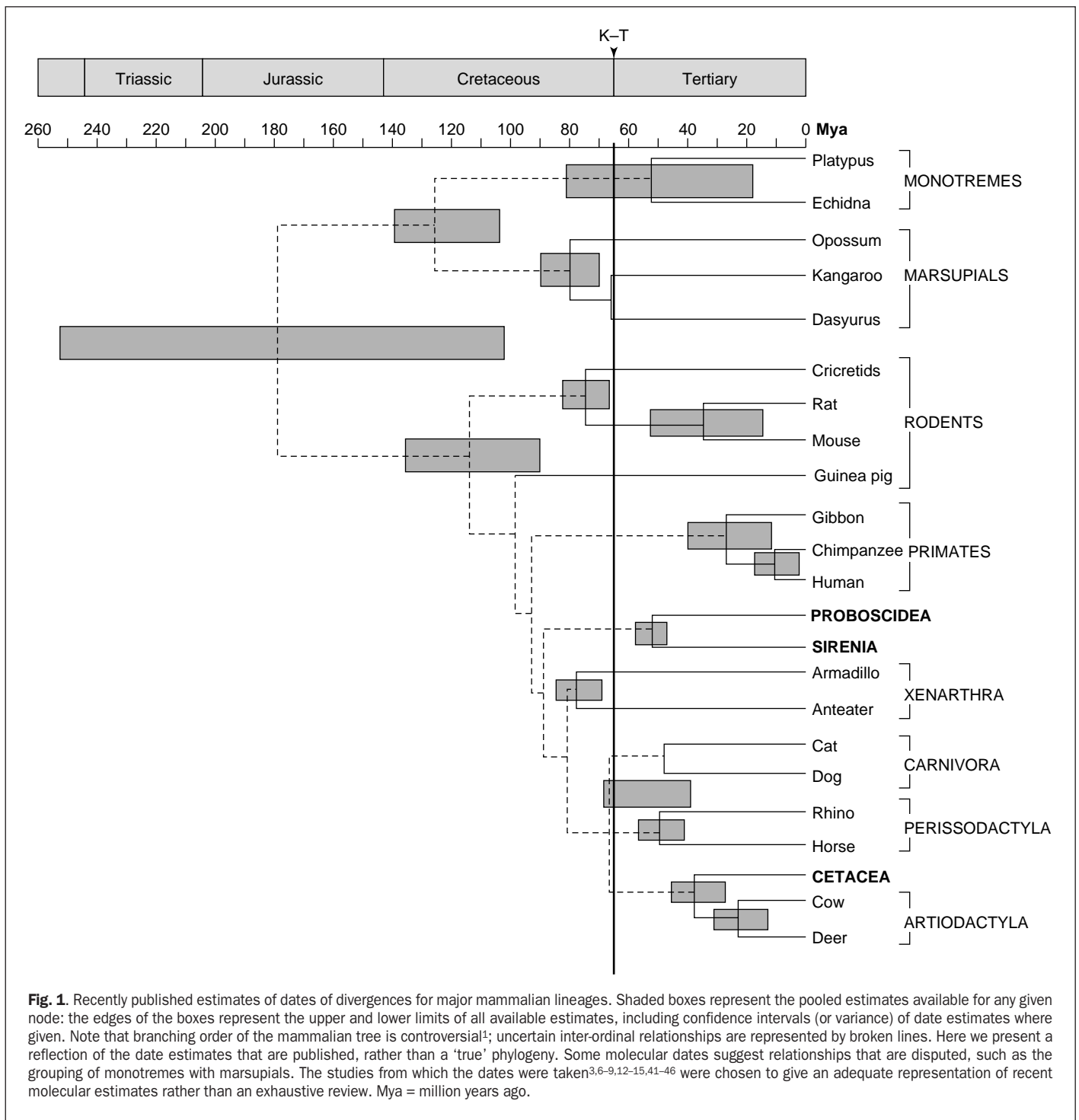
### Dating mammalian origins

The time-honoured way of estimating the age of a lineage uses the first appearance of a taxonomic group in the fossil record (Box 1). This not only marks the minimum age of that taxon, but also puts a minimum age on its sister groups (or outgroups). Fossil-based divergence dates are subject to various sources of error, owing to the temporal incompleteness of the fossil record, uncertainty in identifying specimens and difficulty in establishing absolute age. The size of the gap between the origin of a lineage and its first identifiable fossil will vary with location, age and type of organism. Despite these difficulties, fossil dates are irreplaceable as the primary means of assigning a minimum age to a taxon.

Molecular dates are obtained by converting estimated genetic distance between lineages to time since divergence using a calibration rate (the expected substitution rate; i.e. amount of molecular change per unit time), which has been calculated for some lineage with a 'known' date of origin (usually a palaeontological estimate). Molecular dates should mark the actual point where lineages split, and so are often earlier than the corresponding palaeobiological estimates, but not always – for example, the considerably younger estimates for the divergence of the great apes<sup>12,13</sup> and monotreme families<sup>14</sup>. Molecular data can be used to circumvent some of the natural biases of the fossil record, by inferring the presence of lineages in periods for which the fossil record of that taxon is poor or non-existent. Using sequences from extant taxa removes the difficulties associated with identifying early members of a lineage (such as stem groups that do not have all the defining features of the crown group: Box 1) from fragmentary evidence. However, molecular dates, like fossil dates, are subject to various sources of error. The accuracy of molecular date estimates depends on the data and methods used, which is why estimates of the same node from different studies can differ so dramatically (Table 1).

### Variation in molecular date estimates

The degree of variation in molecular date estimates is striking. Published estimates of the same node by different researchers can vary by as much as 100% (Table 1). The variation between dates indicates that differences in the data or methods used can substantially alter the results. Unfortunately, because studies differ in many aspects of data and methods, it is difficult to isolate specific causes of the discrepancy. For example, two recent studies<sup>3,7</sup> give disparate estimates of the marsupial-eutherian split (Table 1), and this discrepancy could be because of differences in the choice of sequences (concatenated mitochondrial protein genes versus many individual nuclear sequences), calibration date (artiodactyl-whale split at 60 Mya versus bird-mammal split at 310 Mya) or phylogenetic method (maximum likelihood and mt-REV distances versus 'Poisson corrected' distance). Note that because some sources of error will produce consistently biased results, these estimates might not be normally distributed about the true value, so averaging all published estimates will not necessarily give a more reliable estimate. One potential source of consistent bias in molecular studies, which is a particular cause for concern in dating mammalian



divergences, is the difficulty in establishing an appropriate calibration rate.

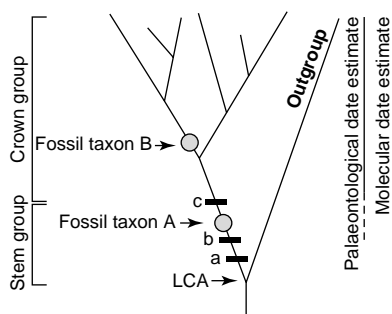
The accuracy of fossil dates used for calibration has been a focus of criticism<sup>13,15</sup>, because different calibration dates produce different estimates of rate of substitution<sup>16,17</sup>. The importance of the calibration date to the accuracy of date estimates is illustrated by comparing the dates for hominoid divergence times obtained in two studies using similar data and methods but different calibration dates (Table 2). A biogeographical estimate of the age of a radiation of seal species (*Phoca*) gave date estimates that were approximately half the age of those

given by a fossil-based estimate of the whale-artiodactyl split. To minimize the error resulting from fossil calibration dates, two opposite strategies can be adopted: use as many fossil dates as possible<sup>9</sup>, to spread the risk of error, or place your faith in one date deemed to be especially reliable. For example, Arnason *et al.*<sup>14</sup> suggested that primate fossil dates were so unreliable that it was preferable to use a well constrained fossil date from another taxon to date primate divergences. Hedges *et al.*<sup>6,7</sup> used a similar argument in adopting the split between mammals and birds (310 Mya) as a calibration for dating mammalian ordinal

divergence times. In contrast, Easteal *et al.*<sup>13</sup> aimed to avoid the error inherent in fossil dates by developing a fossil-free approach, applying a range of possible rates to pairwise distances and selecting the one that gave the most reasonable answers for the nodes tested. However, this approach served to illustrate the difficulty in using a single substitution rate to date all mammalian divergences. The intermediate rate chosen was much slower than previous estimates of the rate in rodents and much faster than previous primate estimates<sup>13</sup>, with the result that the rodent divergence dates were surprisingly old and the primate dates unusually

### Box 1. Stem and crown groups

Estimates of molecular and fossil dates mark different points in the history of a lineage, which can complicate their comparison. A taxonomic group might be defined as: (1) all of the taxa that show a defining set of characters; or (2) all of the members of a lineage. Molecular dates mark the point at which two lineages last shared a common ancestor (LCA), so estimate the age of the stem + crown group. The palaeontological age of a taxon marks the appearance in the fossil record of a specimen with the diagnostic characters of that group, which could be a member of the crown group or the stem lineage. In the example below, a taxon is defined as a monophyletic group (i.e. descended from a single ancestral taxon) consisting of species with three defining characteristics (a, b and c). Fossil B marks the known minimum age of the crown group because it has all the defining features. Fossil A has some but not all of the features, so might be recognized as a member of the ancestral lineage of the taxon. The palaeontological age might also represent an earlier fossil of a known sister group. In this review, we refer to the origin of a mammalian order as the point at which it diverges to form a separate lineage (i.e. stem → crown).



(Online: Fig. 1)

**Table 1. Comparison of some molecular date estimates published in the last five years for three mammalian divergence events of varying 'depth'<sup>a</sup>**

Node	Estimated date of split (Mya) <sup>b</sup>	Refs
Marsupial–Eutherian	133–175	12
	218–257	13
	120–160	3
	104	17
	161–185	7
Primate–Rodent	118–150	12
	112–133	13
	88–202	6
	97–126	42
	106–141	3
Human–Chimpanzee	109–116	7
	8.5–16.2	12
	5.2–6.9	15
	3.2–4.5	13
	5.3–5.7	7

<sup>a</sup>Depth is a broad term for the approximate age of a lineage.

<sup>b</sup>Mya = million years ago.

**Table 2. Comparison of estimated dates of hominoid divergences calculated from two different calibration dates**

Divergence	Calibration date	
	A/C-60 <sup>a</sup> (Mya)	<i>Phoca</i> standard <sup>b</sup> (Mya)
Human–Orangutan	24.5 ± 2.7	18.1 ± 1.6
Human–Gorilla	18 ± 2.9	8.4 ± 1.1
Human–Chimpanzee	13.5 ± 2.5	6.1 ± 0.9
Common chimp.–Pygmy chimp.	7 ± 1.8	3 ± 0.6

<sup>a</sup>Fossil-based estimate of the split between cetaceans and artiodactyls at 60 million years ago (Mya): whole mitochondrial genomes for 14 species analysed at the nucleotide and amino acid level by maximum likelihood and neighbour joining<sup>12</sup>.

<sup>b</sup>Radiation of *Phoca* (seal) species at 2.7 Mya, inferred from climatological data: whole mitochondrial sequences for eight species, neighbour-joining branch lengths<sup>15</sup>.

young. This pattern is consistent with previous claims that rodents have a faster rate of evolution than primates<sup>18–20</sup>. Such lineage-specific rate variation casts doubt on the use of a single calibration rate, whether produced by cross-taxon calibration or other means, to date all mammalian divergence times. A corollary of this observation is that the adequacy of a calibration rate cannot be established by referring to the reasonableness of the date estimates it gives for some nodes.

### Rate variation affects date estimates

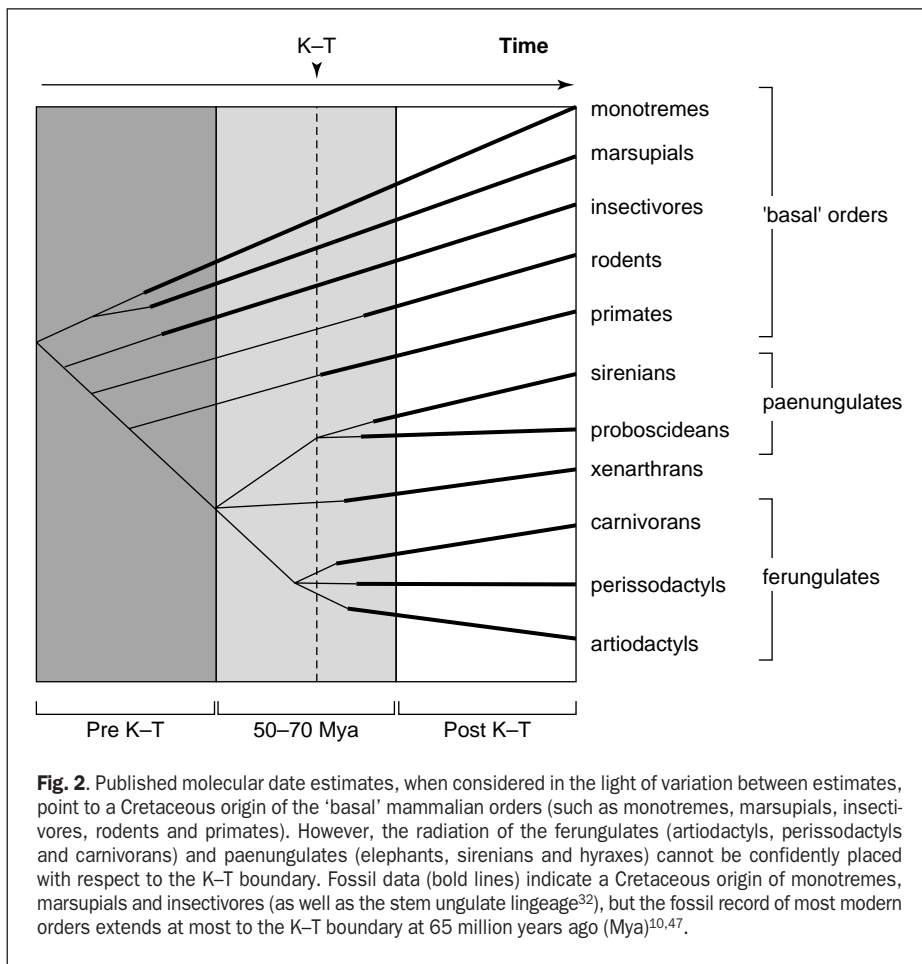
The common reliance on rate uniformity is one of the greatest stumbling blocks in the production of accurate molecular date estimates for mammalian orders. The existence of established cases of lineage-specific rate variation, whether for specific taxa (e.g. between hominids and murid rodents<sup>18–20</sup>), particular sequences

(e.g.  $\psi$ / $\eta$  globins<sup>21,22</sup>) or related to life history characters (e.g. generation time<sup>18,23</sup>), indicates that rate uniformity cannot be taken for granted for any given set of sequences.

One way of dealing with the potential for inaccuracy caused by rate variation is to use a 'clock test' to select data that approximates rate uniformity. Clock tests are commonly based on the relative-rates test (which compares the amount of change in each of two ingroup sequences with respect to an outgroup<sup>5,24</sup>). Maximum likelihood can also be used to test how well a rate-constant model fits the data<sup>25,26</sup>. However, these clock tests are limited in power when applied to short sequences and are unlikely to detect moderate levels of rate variation for sequences of less than 1000 variable positions. Regression of observed genetic distance through palaeontological estimates to establish a linear relationship between distance and time<sup>7,9</sup> has the advantage of using a range

of fossil dates and species in the calibration. However, it is limited by the frequent use of nonindependent comparisons, which can give an overconfident impression of rate constancy.

The problems associated with selecting rate-constant sequences can be illustrated by a common approach to dating the frequently estimated primate–rodent split<sup>6,7,13</sup> (Table 1). A relative-rates test can be used to select rate-constant sequences with which to estimate the date of the split by multiplying half the pairwise distance by the calibration rate. However, relative-rates tests cannot reliably reject shorter sequences that show a realistic level of rate variation (e.g. rodent sequences with a rate 1.5 to 3 times faster than primate sequences<sup>18–20</sup>). Failure to reject sequences that evolve faster in rodents could result in an overestimation of the age of the split between rodents and primates, because the calibration rate will overestimate the number of years



required to produce the observed distance between rodents and primates. This discrepancy is expected whether the calibration rate is calculated from cross-taxon calibration (e.g. the artiodactyl-whale split<sup>12</sup>) or an external calibration point (e.g. the bird-mammal split<sup>6,7</sup>, although the discrepancy will be even greater if birds have a slower rate of molecular evolution than mammals<sup>27,28</sup>). If lineage-specific rate variation is a widespread feature of mammalian sequence evolution<sup>23</sup>, and if clock tests with limited power are used to screen sequences with relatively low numbers of variable sites, then failure to reject rate-variable sequences could potentially be a common cause of inaccuracy in molecular date estimates of the origins of mammalian orders.

**A sloppy clock is better than no clock**

Given the effect of choices of data and methods and the potential for error in molecular dates as a result of undetected rate variation, it might be unwise to expect a molecular clock analysis to give precise point estimates of divergence dates<sup>29</sup>. However, acknowledging the imprecision of molecular date estimates does not deny their usefulness in evolutionary biology.

Molecular dates considered in terms of confidence intervals, which reflect their imprecision, can be used to assess the compatibility of molecular dates with a given hypothesis<sup>26</sup>.

The variation in the date estimates presented in Fig. 1 and the potential inaccuracy resulting from rate variation prevent us from confidently placing the radiation of the ferungulates (artiodactyls, whales, perissodactyls and carnivores) and paenungulates (elephants, sirenians and hyraxes) on either side of the K-T boundary because most of these dates are in the region of 50-70 Mya. There is also insufficient resolution to determine if the radiation of mammalian orders occurred in a gradual, step-like or rapid, bush-like radiation. However, even allowing for a large margin of error in the range of dates in Fig. 1, molecular data support placing the divergence of primates from rodents, and monotremes from marsupials, before the K-T boundary. This also implies that any sister groups to these nodes, such as lagomorphs (rabbits and hares), insectivores and the lineage leading to the ungulate orders, must also have originated in the Cretaceous (Fig. 2).

Because the potential for error in molecular date estimates cannot be ignored, these estimates should never be

accepted uncritically but should be examined in the light of other sources of historical information in biology, particularly palaeontology, biogeography and phylogeny. For example, biogeographical information can be used to put upper and lower bounds on the divergence of mammalian lineages by considering the presence of lineages on specific continents and the periods in which migration of mammals between continents was possible. Springer *et al.*<sup>9</sup> used the geographic isolation of Africa from South America from 80 Mya ago until after the K-T boundary to support a Cretaceous origin of an African clade of paenungulate lineages inferred from molecular data.

In particular, the proposed early diversification of modern mammals must be reconciled with the fossil record, which shows low diversity of modern orders in the Cretaceous, followed by a burst of diversity after the K-T boundary<sup>30</sup> (Fig. 2). Is it plausible to suggest that so many modern mammalian orders could have a long history before the K-T boundary but have so far largely failed to turn up in the Cretaceous fossil record?

**Mammals in the Cretaceous**

Fossil evidence for the history of modern mammals before the K-T boundary<sup>31,32</sup> is rare and often complicated by the difficulty of recognizing ancestral members of a lineage, which might not show the defining characteristics of the crown group - a problem compounded by the fragmentary nature of the specimens. Many species are known only from dental characters (sometimes only a single tooth), the phylogenetic stability of which can be questioned<sup>33</sup>.

Could early mammals have been hidden from the fossil record by consistent geological bias? Biogeography might hold the key to assessing the potential for a 'hidden' period of early mammalian evolution. For example, recent molecular phylogenies have promoted an 'African clade' deep within the mammalian tree, placing the origin of many lineages (such as paenungulates and some insectivore lineages) within the African continent<sup>9,34</sup>. But, as yet, there are no known African late Cretaceous beds of terrestrial vertebrate fossils that could provide information on the early members of these mammalian lineages. Similarly, recent finds suggest the presence of eutherian mammals in Australia as early as 120 Mya (Ref. 31), but there are no terrestrial vertebrate fossil-beds known from Australia between 100 and 55 Mya. Mammal fossils from stages just before the K-T boundary (Campanian-Maastrichtian, 83-65 Mya) are primarily from fossil beds of the western interior of North America<sup>35</sup> and the

central latitudes of Asia<sup>36</sup>, so if early mammal evolution occurred elsewhere, it could be effectively invisible to the fossil record.

Could the post-K–T burst in mammal diversity represent the movement of mammals from other continents into North America and Asia, rather than their rapid radiation within that region? The drop in sea levels in the late Cretaceous<sup>37</sup> could have brought together previously isolated faunas, and the Palaeocene burst in diversity in North America for terrestrial taxa other than mammals, such as amphibians and lizards<sup>38</sup>, might reflect a common biogeographical pattern of faunal movement. If the early history of modern mammals occurred in a region with an impoverished late Cretaceous fossil record, such as in Africa, then the absence of fossil evidence to support the molecular dates might be explained.

### Radiation of the mammals

So what do molecular dates tell us about the evolution of modern mammalian orders? If the molecular estimates are true, then many more modern orders had their origin in the Cretaceous and began radiating long before the dinosaurs disappeared. This might suggest that mammalian diversification was not primarily driven by release from the constraint of the presence of the dinosaurs, although the evolution of mammals into larger size and more conspicuous niches (such as large diurnal grazers and large carnivores) might have been limited until the demise of the larger dinosaurs, perhaps explaining the later radiation of the paenungulates and ferungulates. A Cretaceous divergence of mammalian orders also implies that many of the characteristics considered 'key innovations' of the mammalian radiation, such as aspects of brain function, reproduction or metabolism, evolved long before the extinction of the dinosaurs.

The coexistence of modern mammals with dinosaurs raises interesting questions about the nature of their interaction. If Cretaceous mammals, as a whole, were ecologically diverse as well as phylogenetically diverse (evidence from fossil dentition suggests possible mammalian insectivores, herbivores, granivores, carnivores and scavengers<sup>39,40</sup>), then it seems possible that the spectrum of resource requirements could have overlapped with that of the dinosaurs. It is intriguing to note that the projected rise of the modern mammals coincides with the disappearance of the smaller dinosaurs, those most likely to have been in direct competition with the new mammals (M.J. Phillips, unpublished).

### Prospects

Phylogeny has an important role to play in resolving the tempo and mode of the radiation of the mammals. Higher resolution of internodes would distinguish between two modes of diversification: explosive radiation versus stepwise divergence. Phylogeny can also allow the inference of past states, by providing relative timing of evolution of traits based on lineages sharing homologous characters. In addition, the estimation of divergence dates from molecular data will play a critical role in forming hypotheses concerning the origins of mammal diversity, particularly as the accuracy and precision of molecular phylogenetic methods develop. If date estimates with appropriate confidence intervals that reflect the uncertainty in molecular dating are combined with palaeontological data (as the only direct evidence of past forms) and biogeography (which gives a global view of mammal evolution), molecular data could help us understand the early evolution of modern mammals.

### Acknowledgements

This work was supported by the New Zealand Marsden Fund, the Australian Research Council and the Rhodes Trust.

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## Longhurst Areas

### Ecological Geography of the Sea

by A. Longhurst

Academic Press, 1998.

\$79.95 hbk (xiii + 398 pages)

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We were all waiting for this book. As pointed out in its introduction, a 'geography of the sea' – that is, a rigorous definition of 'provinces' suitable for describing, in standardized fashion, the distribution of all marine organisms – did not exist despite a history of oceanographic research starting with the Challenger Expedition (1872–1876). Numerous maps did exist in which this or that oceanographic parameter or the distribution of a few organisms had been used to draw provinces or 'Large Marine Ecosystems' (LME) of some sort. However, no test had been conducted of the ability of these proposed maps to predict distributions other than those from which they were derived: circularity reigned supreme.

Reasons for this are easy to imagine, from the excessive preoccupation of various specialists with their favorite taxonomic groups, to the absence, before the recent computer revolution, of analytical tools up to the task. However, the real reason is probably that developing a truly synoptic vision of the ocean was impossible before the advent of satellite-based oceanography.

Satellites cannot see very deep into the sea, nor can they see very much – at least as far as those satellites are concerned that civilians know about. However, what satellites do see is the very stuff that generates

fundamental differences between ocean provinces: sea surface temperatures and their seasonal fluctuations, and pigments such as chlorophyll, and their fluctuations. Marine systems differ from terrestrial ones in that their productivity is essentially a function of nutrient inputs to illuminated layers. This gives a structuring role to the physical processes that enrich surface waters with nutrients from deeper layers, such as wind-induced mixing, fronts, upwelling, etc. Thus, the location, duration and amplitude of deep nutrient inputs into different oceanic regions (as reflected in their chlorophyll standing stocks, and described in *Ecological Geography of the Sea*) largely define the upper trophic level biomasses and fluxes that can be maintained in these regions. This is the reason why satellite images reflect fundamental features of the ocean, whereas maps based on the distribution of various organisms – even 'indicator' organisms – can only reflect second-order phenomena.

Alan Longhurst is among the very first to have fully realized these implications of satellite oceanography, and to have followed up on them. This led to an estimate of global marine primary production much superior to earlier attempts<sup>1</sup>, based on a stratification by 'provinces' defined in another major contribution<sup>2</sup>. Then Alan Longhurst went into retirement to run an art gallery in southern France with his wife.

The book presented here was written thereafter, largely by popular demand: many colleagues adopted the provinces proposed in these earlier works as standard for work now published<sup>3</sup>, or still in preparation, but wanted more details on what it was obvious to call 'Longhurst Areas'<sup>4</sup>. For example, Longhurst Areas will provide the architecture for several projects in which I am involved, whose products are expressed on a global basis. This will involve stratifying

global marine fish biodiversity in forthcoming releases of FishBase<sup>5</sup> (<http://www.fishbase.org>). It will also involve replacing the 18 'FAO Statistical Areas' currently used for raising upper trophic level biomass fluxes from local ecosystem models to regional estimates, and thence to the global ocean<sup>6,7</sup> (<http://www.ecopath.org>).

This work will be aided not only by the existence of Longhurst's classification of ocean provinces – whose reliability can be assessed in the first 98 pages of the book, which discusses conceptual and methodological issues – but also by the detailed description of the 51 neritic and oceanic provinces presented in the next 300 pages. The work of various research groups will undoubtedly modify these descriptions. However, most of this follow-up work will only add details to one or other Longhurst Area. The excellence of this book guarantees that the overall structure will remain, and that the well deserved eponym will stick.

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