their energetic masking components [11]. Modulation masking of speech has also been demonstrated and modelled using non-speech like stimuli (for example [12,13]). It will be an important question for future work to disentangle these different top-down/bottom-up effects.

One intriguing aspect of the data of Woods and McDermott [2] is that the temporal variation of the position of the vibrato signal did not vary detection performance — there appeared to be no 'build-up' of streaming over the course of the stimulus as has been reported in many streaming experiments using sequences of tones (for example [14]). This most likely results from the very different nature of the stimuli used here and may well have been exogenously driven, but it does suggest caution in the interpretation of previous results in the context of more ecological examples of auditory streaming, as tapped into by Woods and McDermott [2]. On the other hand, being able to rapidly form streams and focus attention would be critical for good performance in cocktail party listening where there is often also little to no gap in conversational turn-taking [15]. In that context it would be most interesting to explore the use of this most elegant and simple test as a diagnostic for various attentional disorders such as attentional deficit disorder and auditory processing disorder where speech understanding is also affected. Not only might it provide a very sensitive test of disability, it might reveal more of the underlying mechanism of dysfunction in these conditions.

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Mammalian Evolution: A Jurassic Spark

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There is increasing evidence that early mammals evolved rapidly into a range of body forms and habitats, right under the noses of the dinosaurs.

Mammals first appear in the fossil record at about the same time as the earliest dinosaurs (~220 million years ago), and so the first two-thirds of mammalian evolutionary history thus occurred during the Mesozoic 'Age of Dinosaurs' [1,2]. Mesozoic mammals were long portrayed as tiny, shrew-like creatures, unable to diversify due to severe competition and predation from dinosaurs and other reptiles. However, discoveries in the past two decades have greatly expanded the known diversity of Mesozoic mammals, revealing the existence of specialised gliders, climbers and burrowers, semi-aquatic forms and even badger-sized carnivores that ate small dinosaurs [1–4]. Evidence of extensive ecological differences has been found even between closely-related species [5,6], and quantitative analyses of the skulls and skeletons of Mesozoic mammals suggest a diverse range of diets and locomotor modes [4,7–9]. Although the ecological

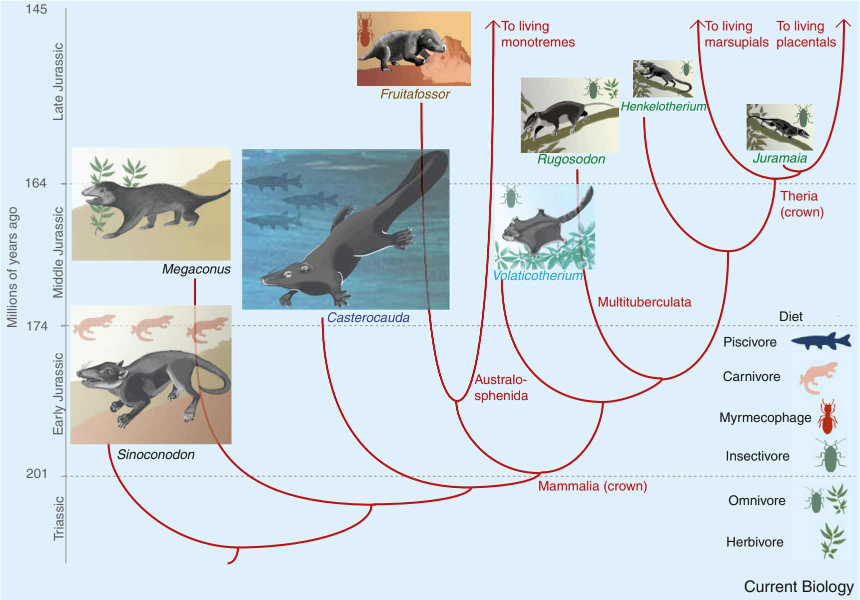

Figure 1. Early mammalian diversification.
Ecomorphological diversity [2] and phylogenetic relationships [5,10] of selected Jurassic mammals. Sizes of images are proportional to body size. Text colour refers to lifestyle: terrestrial (black), arboreal (green), fossorial (brown), aquatic (dark blue), volant (light blue); silhouettes in the background denote primary diet (see key). All illustrations by Katrina Kenny.

and functional diversity of Mesozoic mammals has received increasing attention, the tempo of their adaptive radiation has seldom been quantified. In a new paper in *Current Biology*, Close and colleagues [10] now show that, during the Mesozoic, mammals evolved very rapidly during the early and middle Jurassic (~201–164 million years ago), with the average rate of change during this period being twice as fast compared to the remainder of the Mesozoic.

This period of rapid evolution also broadly coincides with peaks in morphological disparity (as measured by the average morphological difference between contemporaneous species) and lineage diversity (as measured by the number of contemporaneous branches on the evolutionary tree). Together with previous studies which have highlighted the ecomorphological diversity of Jurassic mammals [1–5,7], these results demonstrate that mammals underwent a sustained and extensive adaptive radiation during the Jurassic, when dinosaurs also underwent a major increase in diversity and disparity [11]. The generally large size of dinosaurs during the early and middle Jurassic may have created a relatively permissive, low-competition environment for mammal diversification: small maniraptoran theropods, which might have interacted ecologically most strongly with early mammals, did not proliferate widely until the Cretaceous [12].

In addition to revealing the tempo of early mammal evolution, the work of Close and colleagues [10] highlights some broader methodological issues. It is the first study to directly compare the results of using two very different approaches to infer evolutionary dates and rates. The first approach sequentially infers tree topology, divergence dates and evolutionary rates [12]: an undated phylogenetic analysis is performed first, then the preferred trees are time-scaled by enforcing the shallowest divergence dates compatible with the age of the fossils and a specified minimum branch duration, in this case either 1, 2, 3 or 4 million years; finally, evolutionary rates are inferred using this dated tree. This method tends to minimise temporal gaps in the fossil record ('ghost lineages'), but has very little restriction on rates of evolution (all rates are equally possible *a priori*).

The second approach co-estimates tree topology, divergence dates and evolutionary rates [13]. This 'tip-dating' approach typically uses an overall evolutionary clock model, which smoothes rates of evolution by penalising extremely fast or slow rates, and can insert long ghost lineages if these help account for large amounts of evolutionary change. Despite their almost opposite assumptions, the two methods produced broadly concordant results: both identify a Jurassic peak in the rate of mammal evolution. However, as expected, the first, sequential method when used with short minimum branch durations yielded trees with shorter ghost lineages and also more branches with very fast evolutionary rates compared to tip-dating.

Regardless of the exact questions asked and methods employed, attempts to infer macroevolutionary dynamics in the fossil record using large-scale character matrices, as done by Close *et al.* [10], require unbiased sampling of morphological traits to accurately reflect disparity between taxa. While such character matrices are typically developed to infer phylogenetic relationships, rather than morphological disparity *per se*, studies have shown that they give results similar to other methods for measuring disparity (e.g. morphometric data [14,15]). This suggests that, in principle, such matrices are suitable for use in macroevolutionary studies. However, to yield accurate results, they need to sample morphological novelties that evolve on every branch, leading to every clade and terminal taxon, with the same intensity. Despite this, virtually all existing morphological character matrices suffer from two important biases. First, these matrices have usually been developed for phylogenetic analysis using parsimony, and so typically exclude specialisations unique to single terminal taxa (autapomorphies), as these do not influence tree topology under parsimony. Second, individual matrices often focus heavily on changes along the series of branches leading to clades of particular interest. The present study tackles these issues, respectively, by investigating the effect of excluding terminal branches, and by evaluating a range of datasets with varying taxonomic emphases. All of these different analyses retrieved the burst of diversification in the Jurassic.

Close *et al*. [10] found the fastest overall rate of morphological change in their focal analysis along the branch leading to therians — the clade comprising placentals, marsupials and their close fossil relatives (Figure 1). This rate was an order of magnitude faster than the average rate across the tree, and is likely due at least in part to the placement of the shrew-sized, insectivorous *Juramaia* from the Middle-Late Jurassic of China [16] as a placental relative and thus the earliest therian (Figure 1). Doubts have been expressed about the reported age of 160 million years for *Juramaia* [3], >35 million years older than the next oldest candidates; if *Juramaia* is younger, then this might reduce the inferred evolutionary rate on this part of the tree by allowing more time for therian characters to accumulate. Nevertheless, the proposed ancient age for *Juramaia* is consistent with recent molecular clock studies suggesting that living placentals and marsupials probably diverged early in the Jurassic [17,18]. In addition, the pattern of high rates of morphological evolution among mammals during the Early–Middle Jurassic found by Close *et al.* [10] is not driven by therians alone. High rates during this period were also inferred for branches within two clades that lie outside Theria: Multituberculata (a diverse and long-lived group of superficially rodent-like mammals) and Australosphenida (a Gondwanan clade that includes living monotremes; Figure 1).

Similar patterns were found in rates of evolution for characters from the entire skeleton, or from the tooth patterns only [10]. Future studies might consider whether different functional regions of the skeleton — such as the jaws and teeth, the ear region or the postcranial skeleton — show correlated or uncoupled evolutionary rates. Such studies will, however, face the challenge that the Mesozoic mammal fossil record is dominated by dental fossils, with cranial fossils exceptionally scarce and postcranial material rarer still [1]. Such uneven representation may pose difficulties for analyses of morphological disparity unless explicitly accommodated [19].

It is now increasingly evident that Jurassic mammals underwent extensive ecomorphological diversification, which in some ways presaged the more spectacular mammalian radiation after the demise of the dinosaurs [2]. This adaptive radiation also appears to have occurred at modest body size, with the largest known Jurassic mammals probably weighing less than a kilogram [1,2,8]. This is in obvious contrast to the modern fauna but also to the Cretaceous fauna, which included several taxa that exceeded 10 kilograms [2]. However, it is interesting to note that the typical (modal) body size for living mammals is still only ~100 grams [20], considerably smaller than a rat but rather similar to that of many Mesozoic mammals [1,2,8]. Among modern mammals, however, there is a secondary peak in body size at about 30 kilograms [20], which was never approached by the group during the entire Mesozoic. The Jurassic radiation of small mammals also underscores the prevalence of convergent evolution. Phylogenetic analyses of modern mammals have highlighted how similar ecomorphs (e.g. ant-eating forms, gliders, specialised burrowers and carnivores) evolved multiple times during the Cenozoic [17,18]. Ongoing studies of their fossil relatives are revealing that many of these ecomorphs also evolved repeatedly [1–3], and relatively rapidly [10], during the Age of Dinosaurs. Early mammals, despite living in the shadows of the dinosaurs, were diverse and successful.

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