Letter to the Editor

The dating game: a reply to Heads (2010)

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In a recent paper, Heads (2010) argued for the use of continental break-up dates as calibration points for molecular clocks when the taxon of interest is widely distributed but dispersal across open oceans is considered improbable. Using this method, he estimated that the placental mammal clade Primates originated in the Early Jurassic, requiring a 130 million year ghost lineage before the first euprimate fossils appear in the record. We demonstrate that this argument is flawed for several reasons: 1) Heads's description of the "transmogrification" of fossil calibration dates is inaccurate; 2) the dispersal abilities of primates are not known or estimated in any way; 3) transoceanic barriers can form over long periods, and modern ocean current regimes do not necessarily, or often, reflect past conditions; 4) continental breakup times are more poorly constrained than fossil occurrences; and 5) Heads's descriptions of the mammalian fossil record, the affinities of several fossil mammals, and evolutionary rates are erroneous. While we agree that palaeogeography is a valuable subject for evolutionary studies, the methodology described by Heads is problematic and unlikely to improve the accuracy of divergence time estimates. Consequently, Heads' conclusions concerning primate evolution are unsubstantiated and probably incorrect.

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Estimating the dates of divergence of evolutionary lineages is an important but tricky business. Thus far, the main sources of information available have been molecular data from living taxa and occurrence data from fossils (the latter dated by several methods, including biostratigraphy, radiogenic isotopes, and paleomagnetic analysis). The strengths and weaknesses of divergence time estimates from molecular or palaeontological data, and discrepancies in these estimates, have provided rich topics of research and discussion for decades. In a recent paper in this journal, Heads (2010) dismisses the validity of this previous work and proposes an alternative dating method based on biogeography. The basis of his method is that the dates of continental breakup events offer superior calibration points for divergence time estimates in terrestrial and globally-distributed modern clades. This use of continental breakup dates results in extreme range extensions for several mammalian lineages, including Primates, so that these lineages supposedly diverged during the Jurassic. Such a scenario implies an extraordinary amount of missing data in the mammalian fossil record, and

Heads accounts for this via a number of doubtful claims concerning the rates of evolution among mammals and the identities of certain Jurassic fossils. Here, we outline briefly some of the most significant problems with Heads' analysis and argue that strong support remains for more orthodox scenarios of mammalian evolution in which Primates diverged from other lineages during the Late Cretaceous or earliest Paleocene.

(1) Divergence dates

Heads argues that both fossil and molecular clock dates provide minimum divergence dates for clades, and he repeatedly claims that other workers 'transmogrify' their dates into maximum or absolute dates, without providing evidence of this. While certainly some people may mistakenly treat fossil or fossil-calibrated molecular dates as maximum divergence estimates, the vast majority of workers realize that they are in fact minimum divergence dates (Donoghue & Smith 2003). However, we can constrain a realistic range of divergence times for a clade provided we

have a suite of phylogenetic nodes where the minimum divergence time has been estimated. For example, if the earliest known euprimate fossil is the approximately 56 million years old (Mya) *Altiatlasius koulchii* from Morocco (Sigé *et al.* 1990; Bloch *et al.* 2007), and the earliest known eutherian mammal is the 125 Mya *Eomaia scansoria* from China (Ji *et al.* 2002), it seems probable that the first true primate originated somewhere between 56 and 125 Mya. This has led to the development of sophisticated Bayesian methods in which multiple fossil-based calibration points are used to provide 'hard minimum' and 'soft maximum' constraints on node ages in molecular phylogenies (e.g. Zhang & Wake 2009; Inoue *et al.* 2010). Thus, the suggestion that fossil-calibrated divergence times are generally treated as absolute, rather than minimum, dates is something of a 'straw man'.

(2) Primate dispersal ability
A key aspect of Heads' argument is that primates are not capable of dispersing across ocean barriers. This factor, when combined with knowledge of palaeogeographic history, means that the simplest way to explain past and current distributions of primate clades is via vicariance driven by continental break-up during the Jurassic and Cretaceous. Heads states that many authors do not believe that primates could disperse across oceans, but cites only one reference to support this (Simons 1976). Even if limits can be placed on the distance or duration of an oceanic crossing that could be achieved by primates, Heads does not deal with the issue that both ocean current regimes and the distances between continental fragments during the Jurassic and Cretaceous were rather different from those of today. For example, it might be unreasonable to propose that primates can disperse across the present 2000 km width of the Central Atlantic between South America and Africa, but this distance would have been substantially smaller during the Late Cretaceous just after these two continents separated. Similarly, modern oceanic currents in the Indian Ocean make it unlikely that mainland African mammals, clinging to rafts of vegetation, would be transported to Madagascar; however, a recent study that modelled 50 Mya oceanic current regimes suggests that such trans-oceanic dispersal would have been much more feasible at this time (Ali & Huber 2010). The dangers of categorical assertions about the dispersal abilities of organisms are further illustrated by a recent example from frogs. The volcanic Comoros islands apparently formed *in situ* in the Indian ocean, approximately 300 km from both Madagscar and the African mainland, and are surrounded by water depths of up to 3500 m. One of these islands has a fauna of endemic frogs, even though amphibians are generally regarded as salt-water intolerant. This observation cannot be explained via either vicariance related to rifting from the mainland nor the formation of a land-bridge via a drop in sea level: thus trans-oceanic dispersal of frogs remains as the most plausible explanation (Vences *et al.* 2003).

(3) Problems with dating continental breakup
The suggestion that continental break-up and other tectonic events provide a suite of tightly constrained absolute dates for calibrating molecular clocks is very doubtful. This is because palaeogeographic maps are hypothesized reconstructions of ancient land and sea areas based on multiple (sometimes conflicting) lines of evidence. There are disagreements and different interpretations resulting from missing data and the application of alternative analytical approaches and assumptions. For example, there are often insufficient data to enable a complete and accurate reconstruction of palaeocoastlines. Palaeogeographers have therefore utilized simplifying assumptions, such as 'maximization of sea area', when filling in areas of uncertainty on palaeogeographic maps (Smith *et al.* 1994). Thus, the date at which an area of ocean first appears between two continents might actually reflect a lack of data rather than a genuine tectonic separation or an increase in sea level. These uncertainties surrounding palaeogeography are well illustrated by the history of the Gondwanan supercontinent whose break-up plays such a key role in the vicariance-based explanation of primate evolution advocated by Heads. A recent review of Gondwanan palaeogeographic history (Upchurch 2008) identified four competing models for the sequence and timing of the supercontinent's break-up during the Jurassic and Cretaceous. These models include: (1) 'Samafrica', in which West Gondwana (South America and Africa) separated from East Gondwana (Antarctica, Australia and Indo- Madagascar) during the Middle Jurassic; (2) 'Africa-first' in which Africa became isolated from the rest of Gondwana during the Cretaceous while South America maintained a connection with East Gondwana until the Late Cretaceous; (3) 'multistage', combining elements of both the Samafrica and Africa-first models; and (4) 'Pan-Gondwana', in which the major southern continents remained in contact with each other until the Late Cretaceous. There are also considerable error margins around the estimated dates of separation between continental areas. For example, Heads dates the separation of Madagascar from Africa (via the opening of the Mozambique Channel) rather precisely to 160 Mya. In fact, the splitting of Gondwana into western and eastern portions along this channel and through the Weddell Sea area commenced approximately 172 Mya, and complete separation may not have occurred until around 140 Mya (Smith *et al.* 1994; Reeves & de Wit 2000; de Wit 2003;

Scotese 2004). Similarly, Heads himself mentions a study by de Wit (2003) in which the separation of India from Madagascar is dated as taking place between 96 and 84 Mya. Part of the difficulty with the use of tectonic events as divergence time calibration points is that millions of years can elapse between the onset of rifting and the final separation of two new continental areas by an oceanic barrier (Upchurch 2008). These substantial margins around the dates of tectonic events contrast with many fossil-based calibration points that can be dated accurately to the nearest million or even a few hundred thousand years (Benton & Donoghue 2007).

(4) Implied evolutionary rates

In order to strengthen the proposed ancient origin of mammalian clades (such as Primates) during the Jurassic, Heads also presents evidence that there were mid-Cenozoic mammal taxa that were virtually identical to those of today. The implication seems to be that such slow rates of morphological change are consistent with the greater amount of time available for primate evolution under the 'Jurassic origin' scenario. However, this line of reasoning is flawed both logically and in terms of its underpinning evidence. First, even if it were true that mid-Cenozoic primates were little different from those of today, this in no way precludes the origin of this clade in the early Tertiary or Late Cretaceous. All that is required to reconcile both observations is a relatively more rapid rate of morphological evolution during the first part of primate history, followed by relative stasis over the latter part of the Cenozoic.

Second, and more importantly, Heads mentions, in the section about the modern appearance of mid-Cenozoic mammals, only a few examples from the late Cenozoic, including several platyrrhine primates from La Venta, Colombia dated to 12–14 Mya (Hartwig & Meldrum 2002) and then molecular clock estimates of Late Miocene to Pliocene divergences in various apes. These are not mid-Cenozoic examples, they are late Cenozoic, and a 12–14 million year old monkey of some modern aspect hardly supports his contention of a 160 million year old origin for platyrrhines. Heads also lists Cretaceous fossils of the monotreme clade Ornithorynchidae. The fossil record supports divergence of monotremes from therians (placentals and marsupials) by the Middle Jurassic, and the Jurassic origin of this distantly related clade has no bearing on the origin of Primates.

(5) Early Jurassic mammals and the missing fossil record of mammals

Heads notes that one difficulty with his proposal is that the origin of primates in the Early or Middle Jurassic implies an extraordinary gap in the fossil record. Indeed, this early date then requires that all of the placental super-orders and at least some of the other ordinal-level clades within Euarchontaglires were also present by the Early to Middle Jurassic. Furthermore, his vicariance model requires that some clades, like Primates, would have covered much of the globe at this time, suggesting unparalleled gaps in the fossil record.

Although the fossil record for Mesozoic mammals is certainly incomplete and biased geographically and temporally, there are at least 300 genera known from the Late Triassic to the K/T boundary (Luo 2007). As of yet, none of these species has been convincingly tied to crown placental mammals. While some gap between the origin of a lineage and its first appearance in the fossil record is expected, Heads is suggesting a gap of at least 130 million years, and not just for one clade, but for several lineages of mammals. This is an extraordinary amount of inferred missing data, given the presence of other mammals and other vertebrates in beds of that age. Furthermore, he offers no explanation for the sudden increase in mammalian fossil remains following the end-Cretaceous extinction.

Heads attempts to reduce the severity of this problem by hinting that some recently discovered Jurassic fossils may be relevant to the early origin of modern mammalian orders. For example, he mentions the Early Jurassic beaver-like docodontan mammaliaform *Castorocauda lutrasimilis* from China (Ji *et al.* 2006), as well as the late Jurassic fossorial mammaliaform *Fruitafossor windscheffeli* (Luo & Wible 2005). However, these Jurassic and Early Cretaceous examples are not therian mammals; they are instead representatives of separate Jurassic-Early Cretaceous radiations of mammaliaforms that convergently evolved superficially similar forms to those in modern clades. Their existence in the Jurassic and Early Cretaceous thus has no relevance for establishing the timing of origin for placental clades, a point firmly made by Luo & Wible (2005) in their original description of *Fruitafossor*.

In short, Heads states towards the end of his paper that the main issue with his conclusions are the dates. We strongly agree, but we also find many other problems with his conclusions. Continental break-up times are far more poorly constrained than are the dates of fossil occurrences. Trans-oceanic dispersal is documented in many extant clades, and there is little attempt to validate the claim that primates could not have dispersed to Madagascar and South America across narrower oceans during the Cretaceous or early Cenozoic. Where fossil data do not match Heads' expectations, he repeatedly dismisses their accuracy (e.g. 'plesiadapids may have existed in South America and Africa, even if we only have a record from the northern continents') or describes them

in a misleading fashion. Finally, most palaeontologists are well in tune with the molecular revolution (see Peterson *et al.* 2007), but they also have an appreciation for large units of time and what a gap of 130 million years implies for our understanding of the evolutionary process and for evolutionary rates. We agree with Heads that the mammalian fossil record is very incomplete and that the true divergence times of extant orders are likely to predate the earliest fossils known at present. We also agree that comparisons of estimated divergence times, phylogenetic topologies, geographic ranges and palaeogeographic history can yield some important insights into the causation and timing of certain cladogenetic events. However, the claim that tectonically calibrated divergence times necessitate the origin of Primates in the Early Jurassic runs counter to our understanding of the quality of the mammalian fossil record and is based on a methodology of doubtful merit.

Acknowledgements

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