The delayed rise of present-day mammals

Olaf R.P. Bininda-Emonds[1,*], Marcel Cardillo[2], Kate E. Jones[3], Ross D.E. MacPhee[4], Robin M.D. Beck[5], Richard Grenyer[6], Samantha A. Price[7], Rutger A. Vos[8], John L. Gittleman[9] & Andy Purvis[2,10]

[1]Lehrstuhl für Tierzucht, Technical University of Munich, 85354 Freising-Weihenstephan, Germany. [2]Division of Biology, Imperial College, Silwood Park campus, Ascot SL5 7PY, UK. [3]Institute of Zoology, Zoological Society of London, Regents Park, London, NW1 4RY, UK. [4]Division of Vertebrate Zoology, American Museum of Natural History, New York, NY 10024 USA. [5]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia. [6]Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK. [7]National Evolutionary Synthesis Center (NESCent), Durham, NC 27705, USA. [8]Department of Zoology, University of British Columbia, Vancouver, B.C., V6T 1Z4, Canada. [9]Institute of Ecology, University of Georgia, Athens, GA 30602 USA. [10]NERC Centre for Population Biology, Imperial College, Silwood Park campus, Ascot SL5 7PY, UK

[*]Present address: AG Systematik und Evolutionsbiologie, Carl von Ossietzky Universität Oldenburg, 26111 Oldenburg, Germany.

Did the end-Cretaceous mass extinction, by wiping out non-avian dinosaurs and most of the existing fauna, trigger the evolutionary radiation of present-day mammals? Here we construct, date and analyse the first species-level phylogeny of nearly all extant Mammalia to bring a new perspective to this question. Our analyses of how extant lineages accumulated through time show that net per-lineage diversification rates barely change across the Cretaceous-Tertiary boundary. Instead, rates spike significantly with the origins of the currently

recognized placental superorders and orders ~89 million years ago before falling and remaining low until accelerating again throughout the Eocene and Oligocene. Our results show that the phylogenetic fuses leading to the explosion of extant placental orders are not only very much longer than suspected previously, but also challenge the hypothesis that the end-Cretaceous mass extinction event had a major, direct influence on the diversification of today's mammals.

Molecular data and the fossil record can give conflicting views of the evolutionary past. For instance, empirical paleontological evidence by itself tends to favour the Explosive Model of diversification for extant placental mammals[1], in which the orders with living representatives both originated and rapidly diversified soon after the Cretaceous-Tertiary (K-T) mass extinction that eliminated non-avian dinosaurs and many other, mostly marine[2], taxa 65.5 million years ago (Ma)[1,3,4]. By contrast, molecular data consistently push most origins of the same orders back into the Late Cretaceous[5–9], leading to alternative scenarios in which placental lineages persist at low diversity for some period of time after their initial origins ('phylogenetic fuses'; ref.[10]) before undergoing evolutionary explosions[1,11]. Chief among these scenarios is the Long-Fuse Model[1], which postulates an extended lag between the Cretaceous origins of the orders and the first split among their living representatives (crown groups) immediately following the K-T boundary[8]. Some older molecular studies advocate a Short-Fuse Model of diversification[1], where even the basal crown-group divergences within some of the larger placental orders occur well within the Cretaceous[5–7].

A partial molecular phylogeny of deep placental divergences suggested that over 20 lineages with extant descendants (henceforth, 'extant lineages') survived the K-T boundary[8]. However, the total number of extant lineages that predate the extinction event and whether or not they radiated immediately after it remain unknown. The fossil record alone does not provide direct answers to these questions. It does reveal a strong pulse of diversification in stem eutherians immediately after K-T[4,12], but few of the known Paleocene taxa can be placed securely within the crown groups of extant orders comprising Placentalia[4]. The latter only rise to prominence in fossils known from the Early Eocene onwards (~50 Ma) after a major faunal reorganisation[4,13,14]. The geographic patchiness of the record complicates interpretations of this near-absence of Paleocene crown-group fossils[14–16]: were these clades radiating throughout the Paleocene in parts of the world where the fossil record is less well-known; had they not yet originated; or did they have very long fuses, remaining at low diversity until the major turnover at the start of the Eocene?

The pattern of diversification rates through time, to which little attention has been paid so far, might hold the key to answering these questions. If the Cretaceous fauna inhibited mammalian diversification as is commonly assumed[1], and all mammal lineages were able to radiate after their extinction, then there should be a significant increase in the net per-lineage rate of extant mammalian diversification, r (the difference between the per-lineage speciation and extinction rates), immediately after the K-T mass extinction. This hypothesis, along with the Explosive, Long-, and Short-Fuse models, can be tested using densely-sampled phylogenies of extant species, which contain information about the history of their diversification rates[17–20].

Using modern supertree algorithms[21,22], we construct the first virtually complete species-level phylogeny of extant mammals from over 2500 partial estimates, and estimate divergence times (with confidence intervals) throughout it using a 66-gene alignment in conjunction with 30 cladistically robust fossil calibration points. Our analyses of the supertree indicate that the key splits underlying the diversification of the extant lineages occurred 1) from 100–85 Ma with the origins of the extant orders and 2) in or after the Early Eocene (agreeing with the upturn in their diversity known from the fossil record[4,13,14]), but not immediately post K-T where diversification rates are unchanged. Our findings—that more extant placental lineages survived the K-T boundary than previously recognised and that fewer arose immediately after it than previously suspected—extend the phylogenetic fuses of many extant orders and indicate that the end-Cretaceous mass extinction had at best a minor role in driving the diversification of the present-day mammalian lineages.

A supertree of extant mammals and a timescale for diversification

The supertree contains 4510 of the 4554 extant species in ref.[23], making it 99.0% complete at the species level (Fig. 1; Supplementary Fig. 1; Supplementary Table 1). Most major clades have complete taxonomic coverage and all are more than 90% complete except Afrosoricida (tenrecs and golden moles; 78.6%). The supertree is 46.7% resolved compared to a fully bifurcating tree, with poorly resolved areas being generally found closer to the tips of the tree, particularly within Muridae and other rodent families (Supplementary Table 1). Roughly 63% of the 2108 nodes in the tree were dated based on one or more estimates from molecular sequence data and/or cladistically robust fossil estimates (Supplementary Table 2).

The two earliest splits in the phylogeny established Monotremata by 166.2 Ma, and then Marsupialia and Placentalia by 147.4 Ma (Table 1). After nearly 50 million years (Myr) without the origination of any further extant groups, all four placental superorders (Afrotheria, Euarchontoglires, Laurasiatheria and Xenarthra) arose within 2.4 Myr of one another shortly after 100 Ma. This period seems to mark the start of a temporal hotspot of eutherian diversification: nearly all extant placental orders originated by 85 Ma, and all had appeared by 74 Ma, some 10 Myr before the K-T boundary. This interval of rapid eutherian radiation from 100–85 Ma is also notable for many other events in earth history (e.g., rise of angiosperms, general reduction in worldwide temperatures to the Campanian low at 75 Ma, the Cenomanian / Turonian boundary ocean anoxic event at 93.5 Ma), but whether the co-occurrence is more than coincidence is beyond the scope of this work. The phylogeny suggests that 40 placental lineages with extant descendants survived the K-T boundary, nearly twice as many as previously identified[8]. This taxic diversity is consistent with the hypothesis that placentals diversified ecologically in the Cretaceous (Model 5 of ref.[11]), although phylogenies alone are mute about ecological diversity[12]. Marsupialia did not diversify until 82.5 Ma, nearly 20 Myr after placentals, with four lineages crossing the K-T boundary. Diversification of the surviving Monotremata is even later, with the single lineage crossing the boundary first diversifying shortly thereafter (63.6 Ma).

Based purely on the timings of the interordinal and first intraordinal splits, all three diversification models are present in mammals (Table 1). The Short-Fuse Model is found for all placental crown groups that include at least 29 species, where the basal split within each clade occurs shortly after their origins (average fuse length = 11.7 Myr or 13.2%), and average some 10 Myr before the K-T boundary (76.0 Ma; range = 63.4–84.5 Ma). Crown-group marsupials instead approximate the Explosive Model, with the K-T boundary being within the confidence intervals of the dates of origin of most orders (although two orders did arise significantly earlier and most intraordinal divergences are significantly later). Finally, the Long-Fuse Model characterizes Monotremata, the depauperate placental superorder Xenarthra, and the less diverse extant placental orders. For many of these groups, the long fuses (average = 49.7 Myr or 60.4%) reflect that these taxa have often been more diverse in the past, with the present crown group encompassing little of their early evolutionary history (e.g., Proboscidea, Perissodactyla, Monotremata).

The tempo of mammalian diversification

To identify times of unusually rapid net diversifications (‘evolutionary explosions’), we use lineages-through-time plots[17] to gain insight into the history of mammalian diversification rates. If speciation and extinction rates have been constant through time, the logarithm of the number of phylogenetic lineages with extant descendants should rise linearly with time for much of a clade's history[19], with a slope that estimates the net rate of diversification, r. An increase in slope at the K-T boundary would indicate that r rose at that point, whereas a step-like increase would signify a burst of speciation[18]. Lineages-through-time plots from the supertree (Fig. 2a), however, show no evidence of any significant upturn in r at any time around the K-T boundary. This result is confirmed by two-tailed γ tests[20], which show that no significant temporal trend in r exists for mammals as a whole from the origin of crown-group mammals to 48.2 Ma ($\gamma = -0.769$, $P = 0.44$), with placental diversification actually slowing significantly over this period ($\gamma = -2.216$, $P = 0.03$). However, the placental data are more consistent with a step-change in diversification rate than a gradual trend ($\mathrm{AIC_c} = 222.94$ and 228.88, respectively; evidence weight for step-change = 95.1%), with the rate decrease inferred to have taken place at 82.5 Ma. Although marsupials do show a jump at the K-T boundary, the number of lineages involved (from three to six lineages) is very small, making firm conclusions difficult (see Supplementary Results).

Regression models in which r is a smooth function of time substantiate these findings (Fig. 2b). The temporal variation in r prior to 25 Ma is highly significant ($\chi^2_9 = 29.5$, $P < 0.001$). There is a peak at 89.3 Ma coincident with the Turonian/Coniacian boundary, after which r declined to a minimum around K-T. Post K-T, r remained low until the late Paleocene, after which it increased more or less continuously until the Miocene. Net diversification rates did not rise suddenly at any time around the K-T event: no significant rate difference exists between the latest Cretaceous (Maastrichtian) and earliest Tertiary (Danian) ($z = 0.368$, $df = 93$, $P = 0.71$). Results from parallel analyses broken down according to the major lineages of mammals or based on the 95% confidence interval dates are very similar (see Supplementary Results and Supplementary Figs 2–4).

The supertree therefore contains no evidence that the diversification rate of the extant mammalian lineages increased soon after non-avian dinosaurs went extinct. Although there is strong paleontological evidence that mammalian diversity, driven by a massively elevated rate of speciation, generally rose rapidly immediately post K-T[4], in fact there is no conflict between the paleontological and neontological interpretations of the known facts. Most diversifications immediately post K-T were in groups such as multituberculates, plesiadapiforms and 'archaic' ungulates[4] as plots of the numbers of genera known in each sub-epoch indicate (Fig. 2c). These groups declined or went extinct early in the Cenozoic and so are barely, if at all, represented in the phylogeny of living species. The continuing low rates of extant mammalian diversification through this period imply that the dearth of Paleocene crown-group fossils is a real reflection of the low diversity of those clades. The low rates are also consistent with (but not direct evidence for) the hypothesis that extant lineages were inhibited in some manner by the diversity of the predominantly Paleocene groups, and only started to diversify with the decline of the latter (Fig. 2c). However, like most other proposed competitive exclusion scenarios (e.g., refs[24,25]), this conjecture is based purely on the negative correlation of taxon diversities rather than direct evidence of exclusion.

Conclusions

As unquestionably useful as molecular data have been for untangling mammalian evolutionary history[26], no current molecular phylogeny is sufficiently complete to provide a clear view of dynamics so far in the past. Our analysis of a near-complete, species-level phylogeny of extant mammals sheds new light on how one of the best-known mass extinctions in earth history affected their macroevolutionary dynamics. In particular, we challenge the widely accepted importance of the K-T extinction event for the origin and diversification of extant mammalian lineages. The pulse of mammalian diversification immediately after K-T was mainly or wholly in groups that declined subsequently or died out, without contributing markedly to those lineages with extant descendants, where the rate at which the latter appeared remained flat across the boundary. Only selected marsupial orders agree with the Explosive Model to any extent, and then only in their times of origin. Instead, the pivotal macroevolutionary events for extant mammal lineages occur either well before the boundary (significant decrease in diversification rate at ~82.5 Ma following establishment and initial radiations of the placental superorders and major orders at ~89 Ma) or well afterward from the Early Eocene onwards (when net diversification began to accelerate). The supertree and fossils provide different parts of this picture, attesting to the value of using both approaches together: the supertree provides no information about the dynamics of extinct lineages, whereas the fossil record likely underestimates the timing of crown-group diversification in the past. Together, both lines of evidence indicate that the phylogenetic fuses throughout mammals, but especially in placentals, are much longer than previously suspected.

Therefore, the demise of the non-avian dinosaurs, and the K-T mass extinction event in general, do not seem to have had a substantial direct impact on the evolutionary dynamics of the extant mammalian lineages. What, then, was delaying the diversification of present-day mammals? Clearly, the priority is to now identify why net rates of diversification remained low for so long after the major lineages became established. Time lags are also known for other groups[10,27]; however, our values are much longer. Future tests are needed to see if the time lag might involve inhibition by not only the Cretaceous fauna, but also by the major Paleocene mammal groups. Net diversification rates might also have been shaped in part by abiotic factors that were more favourable for the modern groups: r starts to rise around the time of the Cenozoic thermal maximum and subsequent Early Eocene Climatic Optimum (~55–50 Ma)[28]. Discriminating among all these scenarios will be demanding, requiring a highly integrative approach combining phylogenetic, paleontological, paleoclimatic and geographic data at both regional and global scales.

Methods

The supertree was constructed in a hierarchical framework, combining pre-existing supertrees for Carnivora, Chiroptera, "Insectivora" (split into Afrosoricida and Eulipotyphla), and Lagomorpha with new ones for the remaining groups, including the base supertree of all extant families (see Supplementary Table 1). All new supertrees were built using an explicit source tree collection protocol[29] to minimize both data duplication (e.g., where the same data set underlies more than one source tree) and the inclusion of source trees of lesser quality (e.g., taxonomies or those based on appeals to authority). Species names in the source trees were standardized to those found in ref.[23] and extinct taxa (following the 2004 IUCN Red List; http://www.redlist.org) were pruned from the final supertree. All supertrees were obtained using Matrix Representation with Parsimony (MRP[30,31]), with the parsimony analyses for the new supertrees being performed in PAUP* v4.0b10[32].

Recognising that fossils provide minimum divergence-time estimates[33], divergence times throughout the entire supertree were either estimated by a combination of fossil and/or molecular dates under the assumption of a local molecular clock[34] (1322 of 2108 nodes) or interpolated from these empirically dated nodes using a pure birth model[34] (786 nodes) using the Perl scripts relDate v.2.3 and chronoGrapher v1.3.3, respectively (http://www.uni-oldenburg.de/molekularesystematik/33997.html). The interpolated dates were not used in any of the statistical analyses reported here. Because of the crucial nature of fossil calibration points, we restricted ourselves to fossils placed within crown groups of major lineages (generally orders) on the basis of one or more shared derived features as demonstrated in robust cladistic analyses. The 30 fossil dates so obtained represented minimum age constraints for their respective nodes

(Supplementary Table 3). The root of the mammalian tree (age of the crown group) was estimated at 166.2 Ma based on the Middle Jurassic (Bathonian) Malagasy fossil *Ambondro mahabo*[35].

Relative molecular date estimates were obtained by fitting sequence data to the topology of the supertree under a ML framework in PAUP* to determine the branch lengths (following ref.[36]). Sequence data were mined from the mammal section of GenBank release 144 (October 15, 2004) using the Perl script GenBankStrip v2.0 (http://www.uni-oldenburg.de/molekularesystematik/33997.html). Individual gene data sets were post-processed to retain only those sampled for at least 50 species and meeting minimum length and quality requirements before alignment (see Supplementary Methods). The final data set consisted of 51 089 bp from 66 genes (32 nDNA, 19 tRNA, and 15 other mtDNA), distributed across a total of 2182 mammalian species (Supplementary Table 4). Representative outgroup sequences from the chicken (*Gallus gallus*) and/or either of the African or western clawed frogs (*Xenopus laevis* and *Xenopus tropicalis*, respectively) were added to each data set. Variation among the relative molecular date estimates provided by each gene was used to establish 95% confidence intervals for each divergence time estimate (see Supplementary Methods).

Two-tailed γ tests[20] based on a lineages-through-time plot[17] of the dated supertree were used to test the significance of any trends in the net diversification rate, r, over time in placentals, marsupials, and mammals as a whole; under the null distribution γ has a standard Normal distribution. This test requires the tree to be highly resolved[20]; we therefore used it only for the time window in which our tree is more than 85% resolved (prior to 50 Ma for placentals and all mammals, Fig 2a; all dates within this portion of the tree were also estimated directly, rather than interpolated). On finding a trend within placentals, we compared the goodness-of-fit of linear and stepwise regression models to test whether the change in r was gradual or sudden. An additional test used only those lineages for which neither the beginning nor end dates were interpolated, and which did not start at a polytomy. These lineages can be informative about dynamics over a wider range of times (here, from the root of the tree up to about 25 Ma, after which point artefacts become increasingly important; see Supplementary Methods). Survival analysis[37] was used to estimate r within each geological age (pre-Pleistocene) or subepoch (Pleistocene). Temporal constancy in rate was tested by modelling r (as estimated from the number of speciation events per unit branch length within 0.1 Myr bins) as a function of time using generalized additive models (GAMs)[38]. All analyses were repeated using the 95% confidence interval dates. All statistical analysis was performed in R[39] using the packages ape[40] and mgcv[41].

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Author information The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to O.R.P.B-E. (e-mail: olaf.bininda@uni-oldenburg.de).

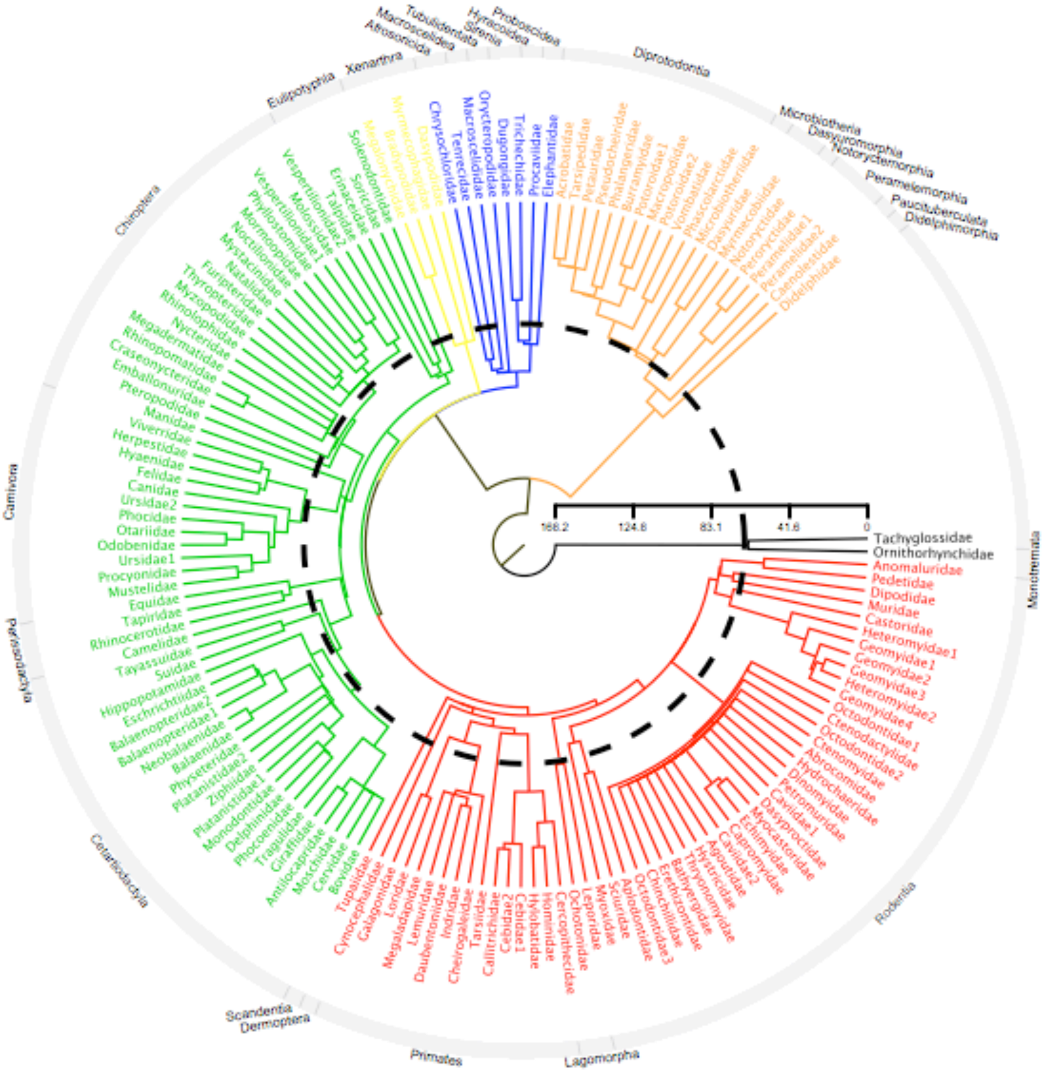

Figure 1 | Partial representation of the mammal supertree showing the relationships among the families (following ref.[23]). All orders are labelled and major lineages are coloured as follows: black, Monotremata; orange, Marsupialia; blue, Afrotheria; yellow, Xenarthra; green, Laurasiatheria; and red, Euarchontoglires. Families that were reconstructed as non-monophyletic are represented multiple times and numbered accordingly. Branch lengths are proportional to time, with the K-T boundary indicated by a black, dashed circle. The base tree was drawn using FigTree v1.1.2 (http://evolve.zoo.ox.ac.uk/software.html?id=figtree).

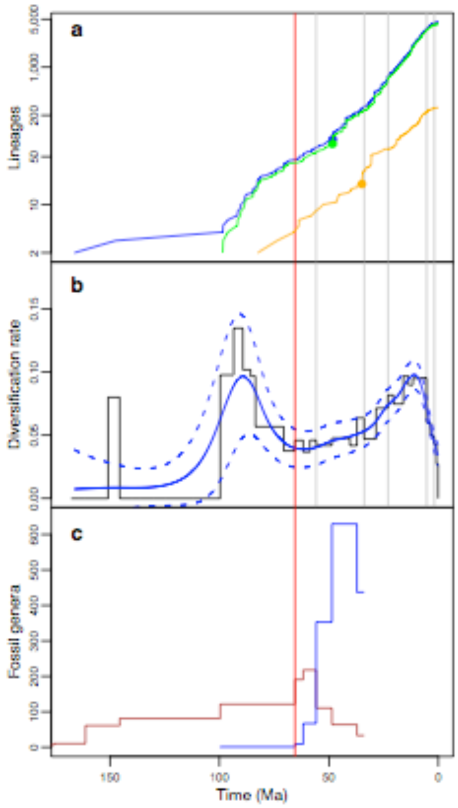

Figure 2 | Temporal patterns of mammalian diversification. a) Lineages-through-time plot for all (blue), placental (green), and marsupial (orange) mammals. Filled circles indicate when resolution in the phylogeny dropped below 85%. b) Net diversification rates: stepped line, rate in each age or subepoch; solid blue line, rate inferred from a GAM of rate against time (χ^2 = 108.2, estimated *df* = 9.35, *P* << 0.001, adjusted R^2 = 68.4%, deviance explained = 12.4%); dashed curves, 95% confidence intervals. c) Counts of mammalian genera in each sub-epoch (Late Triassic to Late Eocene) according to the Unitaxon database (based on ref.[42]). Red and blue lines represent genera whose families diversified predominantly before or after the Paleocene/Eocene boundary, respectively. Throughout, the red vertical line is the K-T boundary and grey lines separate Cenozoic epochs.

Table 1 | Times of origin of, initial diversification within, and phylogenetic fuse lengths for major mammalian lineages (in Ma ± 95% confidence interval). See also Supplementary Table 2.

Taxon	Crown-group size	Time of origin	Time of basal diversification	Waiting time to first split	
				Absolute	%
Mammalia	4510	n/a	166.2 (fixed)	n/a	n/a
Monotremata	3	166.2 ± (fixed)	63.6 ± 11.4	102.6	61.7
Placentalia	4249	147.4 ± 5.6	98.5 ± 7.5	48.9	33.2
Euarchontoglires	2302	96.1 ± 2.8	91.8 ± 1.9	4.3	4.5
Rodentia	1969	88.9 ± 1.2	82.8 ± 2.6	6.1	6.9
Lagomorpha	79	n/a	64.3 ± 4.4	n/a	n/a
Primates	233	88.5 ± 2.6	84.5 ± 2.6	4.0	4.5
Dermoptera	2	88.5 ± 2.6	15 ± 4.9	73.5	83.1
Scandentia	19	91.6 ± 2.2	31.7 ± 2.4	59.9	65.4
Laurasiatheria	1851	96.1 ± 2.8	87.8 ± 2.8	8.3	8.6
Cetartiodactyla	290	83.4 ± 1.5	70.7 ± 3.1	12.7	15.2
Perissodactyla	17	83.4 ± 1.5	55.8 ± 4.7	27.6	33.1
Carnivora	268	81.4 ± 3.3	63.4 ± 3.7	18.0	22.1
Pholidota	7	81.4 ± 3.3	19.1 ± 19.8	62.3	76.5
Chiroptera	915	84.8 ± 1.9	71.2 ± 3.2	13.6	16.0
Eulipotyphla	354	87.8 ± 2.8	82.5 ± 2.8	5.3	6.0

Xenarthra	29	98.3 ± 3.4	70.5 ± 4.9	27.8	28.3
Afrotheria	67	98.5 ± 7.5	90.4 ± 3.2	8.1	8.2
Afrosoricida	39	88.3 ± 2.7	82.4 ± 4.1	5.9	6.7
Macroscelidea	15	88.3 ± 2.7	47.5 ± 7.9	40.8	46.2
Tubulidentata	1	90.2 ± 3.1	n/a	n/a	n/a
Sirenia	4	74.1 ± 3.9	52.2 ± 14.3	21.9	29.6
Hyracoidea	6	74.1 ± 3.9	18.6 ± 0.9	55.5	74.9
Proboscidea	2	75.8 ± 3.4	19.5 ± 11.9	56.3	74.3
Marsupialia	258	147.4 ± 5.6	82.5 ± 11.2	64.9	44.0
Diprotodontia	109	63.6 ± 0.7	54.1 ± 1.7	9.5	14.9
Microbiotheria	1	63.6 ± 0.7	n/a	n/a	n/a
Dasyuromorphia	61	57.8 ± 8.0	31.3 ± 19.8	26.5	45.8
Notoryctemorphia	2	57.8 ± 8.0	9.2 ± 1.0	48.6	84.1
Peramelemorphia	18	65.8 ± 4.9	36.2 ± 5.6	29.6	45.0
Paucituberculata	5	73.6 ± 2.8	33.2 ± 6.9	40.4	54.9
Didelphimorphia	62	82.5 ± 11.2	56.2 ± 10.9	26.3	31.9

Hierarchical nesting of taxa is indicted using an indented taxonomy. Waiting times indicate the temporal gap between the time of origin and of the basal diversification of the existing members of the crown group, both in absolute (Ma) and relative terms (%, relative to time of origin).