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A Phylogeny and Timescale for Marsupial Evolution Based on Sequences for Five Nuclear Genes

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Abstract Even though marsupials are taxonomically less diverse than placentals, they exhibit comparable morphological and ecological diversity. However, much of their fossil record is thought to be missing, particularly for the Australasian groups. The more than 330 living species of marsupials are grouped into three American (Didelphimorphia, Microbiotheria, and Paucituberculata) and four Australasian (Dasyuromorphia, Diprotodontia, Notoryctemorphia, and Peramelemorphia) orders. Interordinal relationships have been investigated using a wide range of methods that have often yielded contradictory results. Much of the controversy has focused on the placement of *Dromiciops gliroides* (Microbiotheria). Studies either support a sister-taxon relationship to a monophyletic Australasian clade or a nested position within the Australasian radiation. Familial relationships within the Diprotodontia have also proved difficult to resolve. Here, we examine higher-level marsupial relationships using a nuclear multigene molecular data set representing all living orders. Protein-coding portions of ApoB, BRCA1, IRBP, Rag1, and vWF were analyzed using maximum parsimony, maximum likelihood, and Bayesian methods. Two different Bayesian relaxed molecular clock methods were employed to construct a timescale for marsupial evolution and estimate the unrepresented basal branch length (UBBL). Maximum likelihood and Bayesian results suggest that the root of the marsupial tree is between Didelphimorphia and all other marsupials. All methods provide strong support for the monophyly of Australidelphia. Within Australidelphia, *Dromiciops* is the sister-taxon to a monophyletic Australasian clade. Within the Australasian clade, Diprotodontia is the sister taxon to a Notoryctemorphia + Dasyuromorphia + Peramelemorphia clade. Within

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the Diprotodontia, Vombatiformes (wombat + koala) is the sister taxon to a paraphyletic possum group (Phalangeriformes) with kangaroos nested inside. Molecular dating analyses suggest Late Cretaceous/Paleocene dates for all interordinal divergences. All intraordinal divergences were placed in the mid to late Cenozoic except for the deepest splits within the Diprotodontia. Our UBBL estimates of the marsupial fossil record indicate that the South American record is approximately as complete as the Australasian record.

Keywords Marsupialia · Phylogeny · Fossil record · Molecular divergence dates · Ameridelphia · Australidelphia · Unrepresented basal branch length

Introduction

Marsupialia and Placentalia comprise the two major groups of living mammals. Marsupials are taxonomically less diverse than placentals by an order of magnitude, but their long, and often isolated, evolutionary history has resulted in an assemblage of species whose morphological and ecological diversity is nearly comparable to that seen in placental mammals (Springer et al. 1997a). Notable exceptions include the absence of marsupial analogs to Cetacea and Chiroptera.

There are more than 330 species of recent marsupials (Wilson and Reeder 2005). Wilson and Reeder (2005) divide these species into three American orders [Didelphimorphia (17 genera, 87 species), Microbiotheria (1 genus, 1 species), Paucituberculata (3 genera, 6 species)] and four Australian orders [Dasyuromorphia (23 genera, 71 species), Diprotodontia (39 genera, 143 species), Notoryctemorphia (1 genus, 2 species), Peramelemorphia (8 genera, 21 species)]. Szalay (1982) proposed a division of these orders into the cohorts Australidelphia and Ameridelphia based primarily on the distinction between the continuous lower ankle joint pattern (CLAJP) and the separate lower ankle joint pattern (SLAJP). CLAJP is the derived condition and characterizes Australidelphia, which is comprised of the four Australasian orders plus the American order Microbiotheria. SLAJP is the primitive condition and characterizes Ameridelphia, which includes the American orders Didelphimorphia and Paucituberculata. Australidelphia has subsequently been corroborated by analyses of morphological (Luckett 1994; Szalay and Sargis 2001; Horovitz and Sánchez-Villagra 2003), molecular (Kirsch et al. 1991, 1997; Springer et al. 1998; Phillips et al. 2001, 2006; Amrine-Madsen et al. 2003), and mixed data sets (Asher et al. 2004). Molecular data sets confirming Australidelphia are diverse and include single-copy DNA hybridization (Kirsch et al. 1991, 1997), mitochondrial genome sequences (Phillips et al. 2001; Nilsson et al. 2003, 2004; Munemasa et al. 2006), concatenations of nuclear gene segments (Amrine-Madsen et al. 2003), and mixed mitochondrial–nuclear data sets (Phillips et al. 2006).

Resolving relationships within Australidelphia has proved difficult and the above-mentioned data sets offer contradictory results. For example, some analyses nest microbiotheres within the Australasian radiation (Kirsch et al. 1997; Burk et al. 1999; Szalay and Sargis 2001; Nilsson et al. 2003, 2004), whereas in other studies microbiotheres are the sister-taxon to a monophyletic Australasian clade (Amrine-Madsen et al. 2003; Phillips et al. 2006). Resolving the relationship of microbiotheres relative to other australidelphians is critical for understanding the early biogeographic history of Australidelphia (Kirsch et al. 1991; Springer et al. 1998; Szalay and Sargis 2001; Nilsson et al. 2004).

Subsequent to the proposal of Ameridelphia by Szalay (1982), Temple-Smith (1987) suggested that this cohort might be a monophyletic sister-group to Australidelphia based on the occurrence of epididymal sperm-pairing in the former. Alternatively, analyses of mitochondrial genomes (Nilsson et al. 2003, 2004) and concatenated nuclear gene sequences (Amrine-

Madsen et al. 2003) suggest that Ameridelphia is paraphyletic, with a basal split between Didelphimorphia versus Paucituberculata + Australidelphia. Statistical tests reported by Amrine-Madsen et al. (2003) could not discriminate between rooting Marsupialia between Didelphimorphia and other marsupials and between Australidelphia and Ameridelphia. However, Asher et al. (2004) found significant statistical support for rejecting a root between Australidelphia and Ameridelphia. Resolving the root of the marsupial tree remains critical for inferring the geographic provenance of the last common ancestor of Marsupialia.

The construction of a molecular timescale for marsupial evolution requires the integration of fossil dates and molecular sequence data. Studies employing fossil-calibrated molecular clocks were previously the standard for estimating molecular divergence times. The divergence between marsupials and placentals is minimally 125 Ma based on the oldest undisputed metatherian fossil (*Sinodelphys*; Luo et al. 2003). Kumar and Hedges (1998) estimated that marsupials and placentals diverged 173 Mya using a molecular clock for multiple nuclear genes that was calibrated against the split between birds and mammals at 310 Ma. Penny et al. (1999) obtained a similar estimate for this split (176 Ma) using two calibrations (horse to rhino at 55 Ma; birds to mammals at 310 Ma) and linear interpolation along the backbone of the mammalian tree. The last common ancestor of crown-group metatherians (i.e., Marsupialia) is ostensibly much younger. Kirsch et al. (1997) obtained a date of 72 Ma for the last common ancestor of marsupials based on rate-calibrated DNA–DNA hybridization data. Springer (1997) used rate-adjusted 12S rRNA distances and concluded that cladogenesis between marsupial orders was mostly centered on the Cretaceous/Tertiary (K/T) boundary at approximately 65 Ma. Recent fossil discoveries suggest that crown-group Metatheria has a minimum age of Lancian (~69–65 Ma) or possibly Judithian (~79–73 Ma) depending on the phylogenetic position of polydolopimorphs (Case et al. 2005; Goin et al. 2006).

More recently, parametric (e.g., Thorne et al. 1998; Kishino et al. 2001) and semi-parametric (e.g., Sanderson 2002) divergence dating methods that relax the molecular clock assumption have been employed to examine marsupial divergences (Hasegawa et al. 2003; Nilsson et al. 2003, 2004; Woodburne et al. 2003). These methods often perform better than methods that assume a strict molecular clock (Yang and Rannala 2006; Smith et al. 2006; Benton and Donoghue 2007). Reliable calibration points are essential for obtaining accurate estimates of divergence times with relaxed clock methods and this topic has received considerable attention (Yang and Rannala 2006; Benton and Donoghue 2007). Minimum constraints on divergence times require (1) a fossil with diagnostic apomorphies for a particular group, (2) an accurate phylogenetic tree, and (3) a minimum geologic date for the fossil-bearing stratum. If all of these conditions are met, then the probability of an earlier divergence time drops immediately to zero (Benton and Donoghue 2007). Benton and Donoghue (2007) advocate a "hard" bound for minimum divergence age constraints when these conditions are satisfied. Alternatively, a "soft" bound for minimum ages may be more appropriate if there are potential problems with fossil identification, tree robustness, and geologic dates for the fossil-bearing stratum. Maximum constraints on divergence times are more difficult to specify (Benton and Ayala 2003; Hedges and Kumar 2004; Reisz and Müller 2004; Benton and Donoghue 2007). Reisz and Müller (2004) and Müller and Reisz (2005) suggest the use of phylogenetic bracketing to constrain maximum fossil divergence dates. Benton and Donoghue (2007, p. 28) advocate soft bounds for maximum divergence ages and suggest a pluralistic approach that combines phylogenetic bracketing with stratigraphic bounding (e.g., "consideration of the absence of fossils from underlying deposits"). These authors urge that both minimum and maximum constraints be fully substantiated so that as new fossils are found and geologic dates are refined, new analyses can reflect the new information. Yang and Rannala (2006) have shown that soft and hard bounds yield similar results when fossil

calibrations are consistent with each other and with molecular data. However, soft-bounded constraints perform better than hard-bounded constraints when poor fossil calibrations are used. This is because soft-bounded constraints allow sequence data to correct poor fossil calibrations, whereas hard-bounded constraints are fixed and are impossible to overcome with any amount of sequence data.

Woodburne et al. (2003) used the *estbranches* and *divtime5b* programs of Thorne et al. (1998) and Kishino et al. (2001) with hard constraints and amino acid sequences for two proteins (BRCA1 and IGF2) and obtained point estimates of 182–190 Ma for the split between marsupials and placentals. Nilsson et al. (2003, 2004) used Sanderson's (2002) penalized likelihood approach to estimate divergence times among marsupial orders and obtained a date for the base of Marsupialia slightly after the K/T boundary at 64 Mya (Nilsson et al. 2003) or just prior to the K/T boundary at 69 Ma (Nilsson et al. 2004). Nilsson et al. (2003, 2004) used three fixed calibration points, including 135 Ma for the split between marsupials and placentals. They also used a tree on which marsupials and monotremes are sister taxa. Hasegawa et al. (2003) employed the relaxed molecular clock method of Thorne and Kishino (2002) with mitochondrial genome data and hard constraints and obtained a date of approximately 100 Ma for the split between didelphimorphians and australidelphians. Hasegawa et al. (2003) cautioned that this seemingly too old split may have resulted from sparse marsupial sampling in their study and/or a model for changes in evolutionary rates that did not well describe marsupial history.

In the present paper we examine higher-level marsupial relationships using a molecular data set that builds on the concatenation of multiple nuclear gene segments presented by Amrine-Madsen et al. (2003) and present a timescale for marsupial evolution based on the relaxed molecular clock approaches of Thorne and Kishino (2002) and Drummond et al. (2006) with these nuclear gene sequences. These estimated dates of divergence are then used to estimate the unrepresented basal branch length (UBBL) of the marsupial fossil record following Teeling et al. (2005).

Materials and methods

Taxon sampling

Our study included 22 marsupials and nine placental outgroups, all of which are indicated in Table 1. Four of 22 marsupial taxa were chimeric above the genus level (Table 1). We follow the classification of Wilson and Reeder (2005) for marsupial orders and families, with the exception that we recognize two families (Didelphidae and Caluromyidae) within the Order Didelphimorphia (Kirsch and Palma 1995). Marsupials included in our study represent all extant orders (*sensu* Wilson and Reeder 2005); placental taxon sampling included representatives of the four major clades (i.e., Afrotheria, Euarchontoglires, Laurasiatheria, and Xenarthra; Murphy et al. 2001) (Table 1).

Gene sequences

DNA was extracted using DNeasy Tissue extraction kits from QUIAGEN or using the methodology of Kirsch et al. (1990). Portions of exon 26 of ApoB (Apolipoprotein B), exon 11 of BRCA1 (breast and ovarian cancer susceptibility gene 1), exon 1 of IRBP (interphotoreceptor retinoid binding protein gene), intronless Rag1 (recombination activating gene-1), and exon 28 of vWF (von Willebrand factor gene) were amplified as described elsewhere (Amrine-Madsen et al. 2003). External forward and reverse primers new to this study

Table 1 Ordinal representation of genera included in this study

- Marsupialia (Infraclass Metatheria)
  - Order Didelphimorphia
    - Didelphidae
      - Didelphinae (*Didelphis*/*Lutreolina*)
      - Marmosinae (*Monodelphis*)
    - Caluromyidae (*Caluromys*)
  - Order Paucituberculata
    - Caenolestidae (*Caenolestes*, *Rhyncholestes*)
  - Order Microbiotheria
    - Microbiotheriidae (*Dromiciops*)
  - Order Dasyuromorphia
    - Dasyuridae
      - Sminthopsinae (*Planigale*/*Sminthopsis*)
      - Dasyurinae
        - Phascogalini (*Phascogale*, *Antechinus*)
        - Dasyurini (*Dasyurus*)
  - Order Peramelemorphia
    - Peramelidae
      - Peramelinae (*Perameles*, *Isoodon*)
      - Echymiperinae (*Echymipera*)
  - Order Notoryctemorphia
    - Notoryctidae (*Notoryctes*)
  - Order Diprotodontia
    - Vombatiformes (*Vombatus*, *Phascolarctos*)
    - Macropodiformes
      - Potoroidae (*Aepyprymnus*)
      - Macropodidae (*Macropus*/*Dendrolagus*)
    - Phalangeriformes
      - Phalangeroidea
        - Phalangeridae (*Phalanger*)
        - Burramyidae (*Cercartetus*)
      - Petauroidea
        - Petauridae (*Petaurus*)
        - Pseudocheiridae (*Pseudochirops*/*Pseudocheirus*)
- Placentalia (Infraclass Eutheria)
  - Order Primates (*Homo*)
  - Order Dermoptera (*Cynocephalus*)
  - Order Chiroptera (*Pteropus*/*Tadarida*)
  - Order Artiodactyla (*Lama*)
  - Order Eulipotyphla (*Talpa*/*Uropsilus*)
  - Order Perissodactyla (*Equus*)
  - Order Proboscidea (*Elephas*/*Loxodonta*)
  - Order Xenarthra (*Bradypus*)

Commas separate taxa that correspond to distinct terminals in phylogenetic analyses; slashes indicate chimeric taxa that correspond to a single terminal in phylogenetic analyses.

are given in Supplementary Information. These genes were chosen because they have demonstrated their phylogenetic utility in resolving marsupial interrelationships (e.g., Amrine-Madsen et al. 2003).

PCR products were cleaned using QIAGEN QIAquick PCR purification kits and were then sequenced in both directions at the University of California Riverside's Core Genetics Institute, which uses an automated DNA sequencer (ABI 3730xl). When necessary, internal sequencing primers were designed. Accession numbers for previously published sequences and the 19 sequences that are new to this study are given in the Supplementary Information.

DNA alignments, data compatibility

New sequences were manually aligned to the Amrine-Madsen et al. (2003) data set after taking into account amino-acid residues using the program SE-AL (Rambaut 1996). A 63 bp region of BRCA1 was excluded from phylogenetic analyses following Amrine-Madsen et al. (2003). A partition homogeneity test (Farris et al. 1994; Swofford 2002) with 1,000 replications and 100 taxon input orders per replicate indicated that it was appropriate to combine the five gene segments into one multigene data set (p=0.114: ambiguous regions removed; p=0.113: ambiguous and parsimony uninformative characters removed). In addition, the bootstrap compatibility method (De Queiroz 1993; Teeling et al. 2002) found no conflicting nodes at 90% bootstrap support for the individual genes. The length of the concatenated alignment that included all five gene segments was 6,303 bp (Supplementary Information).

Phylogenetic analyses

Maximum-likelihood (ML) and maximum parsimony (MP) analyses were performed on the concatenated alignment set using PhyML (Guindon and Gascuel 2003) and PAUP 4.0b10 (Swofford 2002), respectively. The best fit model of molecular evolution and associated model parameters were chosen under the Akaike Information Criterion (AIC) using Modeltest 3.06 for the ML analyses (Posada and Crandall 1998). Models chosen were TrN+I+Γ (ApoB); GTR+I+Γ (BRCA1, IRBP, Rag1, and concatenation); and TVM+I+Γ (vWF). Heuristic searches using 1,000 randomized addition orders with tree-bisection and reconnection (TBR) branch-swapping were used for MP analyses. The ML analyses were started from a neighbor-joining tree. In all analyses gaps were treated as missing data. Bootstrap analyses employed the aforementioned options with 500 replicates (ML) or 1,000 replicates and 1,000 random input orders (MP).

MrBayes v3.1.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), which carries out Metropolis-coupled Markov chain Monte Carlo sampling, was used to calculate Bayesian posterior probabilities. Two Bayesian analyses were performed. In the first Bayesian analysis, each gene segment in the concatenation was allowed to have its own model of sequence evolution (models as above). In cases where models were not available under MrBayes (e.g., five substitution types), we selected a more general model (e.g., GTR). In the second Bayesian analysis, we used a single model (GTR+Γ+I) for the concatenated data set. We used default settings for priors, random starting trees, and four Markov chains (three hot and one cold). Chains were sampled every 1,000 generations. Analyses were run until the average standard deviation of split frequencies for the simultaneous analyses fell below 0.01.

Statistical tests

Alternative phylogenetic hypotheses of phylogenetic relationships were evaluated using Kishino-Hasegawa (KH), Shimodaira-Hasegawa (SH), and approximately unbiased (AU)

statistical tests (Kishino and Hasegawa 1989; Shimodaira and Hasegawa 1999; Shimodaira 2002). Each of these tests has disadvantages and can bias tree selection. KH tests can place overconfidence in the wrong tree; SH tests can be over conservative; and the AU tests compensate for these tree selection biases although it is only approximately unbiased (Shimodaira 2002). CONSEL was used to perform all three tests (Shimodaira 2002). We evaluated a priori hypotheses for (1) the root of Marsupialia; (2) the monophyly or paraphyly of Australasian taxa; (3) the placement of *Notoryctes*; (4) the basal split within Dasyuridae; (5) the monophyly or paraphyly of Phascogalini; (6) the sister group of *Echymipera*; (7) the sister group of *Cercartetus*; (8) the monophyly or polyphyly of Petauroidea (represented by Petauridae and Pseudocheiridae); and (9) the placement of Macropodiformes.

Molecular dating analyses

We tested the molecular clock hypothesis using the likelihood ratio statistic and it was strongly rejected ($p<0.001$) for each of the five genes and for the concatenation. As a result, divergence times were estimated using two Bayesian methods that employ a relaxed molecular clock and permit the incorporation of multiple constraints from the fossil record. The use of multiple fossil constraints provides anchor points throughout the tree, which in turn helps to determine patterns and degrees of rate variation. *Multidivtime* (version 9-25-03) (Thorne et al. 1998; Kishino et al. 2001; Thorne and Kishino 2002) assumes autocorrelation of molecular rates among lineages, requires a rooted tree topology, and allows for fixed (i.e., hard) minimum and maximum constraints on selected divergence times. BEAST v.1.4 (Drummond and Rambaut 2003; Drummond et al. 2006) simultaneously co-estimates both the phylogeny and divergence times, does not assume that lineage rates are autocorrelated, and allows node constraints to be treated as hard or soft (*sensu* Hedges and Kumar 2004; Yang and Rannala 2006). Following Yang and Rannala (2006), we plotted the widths of the 95% confidence intervals against the mean estimates of divergence times to determine whether the addition of more sequence length will improve the precision of our molecular divergence estimates. A strong linear relationship suggests that the addition of more data will have little effect on the precision of the estimates.

Multidivtime

We used the Bayesian phylogeny shown in Fig. 1 for the five-gene concatenation. Branch lengths were estimated using the program *estbranches* (Thorne et al. 1998; Kishino et al. 2001; Thorne and Kishino 2002); *Multidivtime* (Thorne et al. 1998; Kishino et al. 2001; Thorne and Kishino 2002) was used to estimate divergence times. Two different data sets were created from the five-gene concatenation. In the first data set all of the genes were assumed to change rate by a common factor on each branch, i.e., the concatenation was treated as a single gene. In the second data set each gene was allowed gene-specific rate trajectories over time (Thorne and Kishino 2002). In both *Multidivtime* analyses we used the F84 (Swofford et al. 1996) model of sequence evolution with an allowance for a Γ distribution of rates with four discrete categories. The F84+Γ model was chosen because this is the most complex model implemented in *Multidivtime*. The transition/transversion parameter and estimates of the rate categories of the Γ distribution were calculated with PAUP 4.0b10 (Swofford 2002) based on the tree shown in Fig. 1. We used an age of 75 Ma for the mean of the prior distribution for the root of Marsupialia, which is 6–10 Ma older than the oldest crown-group metatherian fossils (Case et al. 2005). The mean of the prior distribution for the rate of molecular evolution at the ingroup root node was set equal to the median amount of evolution from the ingroup root to the ingroup tips divided by the mean of the prior distribution for the root of Marsupialia. Markov Chain

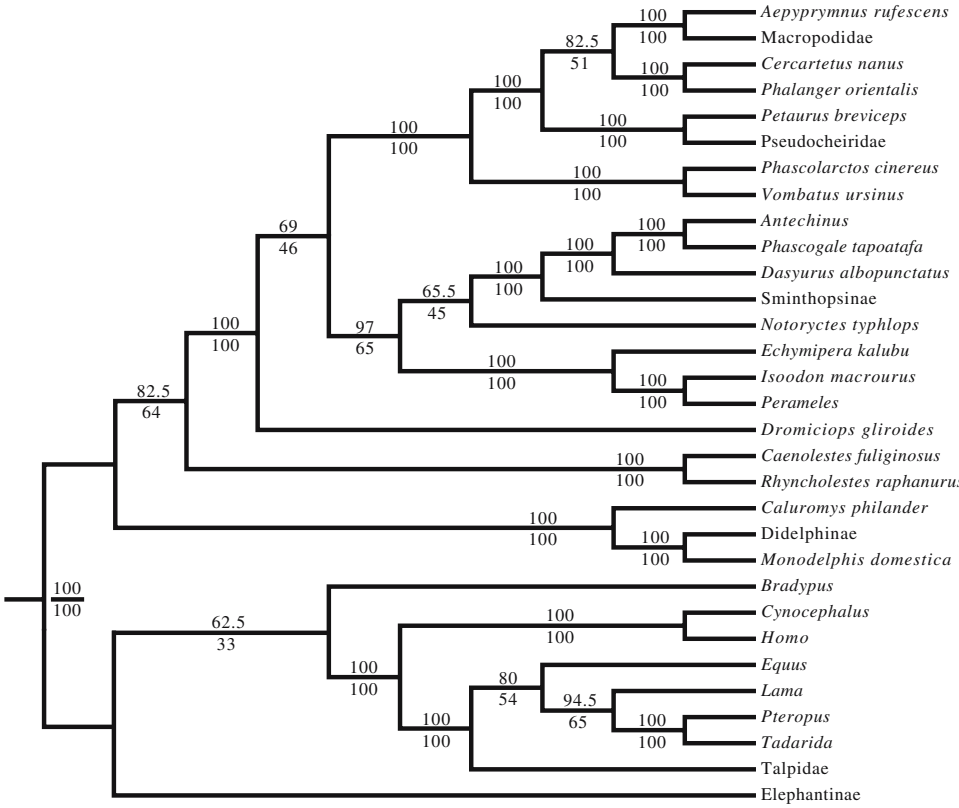

Fig. 1 Bayesian tree with each of the five genes modeled separately for the 6.4kb concatenation. Values *above* and *below* branches correspond to the mean percentage Bayesian posterior probabilities based on the two simultaneous runs and the ML bootstrap support percentages, respectively.

Monte Carlo analyses were run for one million generations after a burnin of 100,000 generations to allow Markov chains to approach stationarity before chains were sampled; chains were sampled every 100 generations.

We employed 26 hard constraints based on both the fossil record and previous phylogenetic analyses for taxa that were included in our analysis. These constraints were as follows (node numbers refer to Fig. 2):

(a) Node 7. The 54.6 Ma old Murgon deposit in southeastern Queensland (Godthelp et al. 1999) is the oldest terrestrial vertebrate bearing deposit in Australia to produce marsupial taxa. As of yet no crown group diprotodontians have been recovered. However, since this is the only Eocene terrestrial mammal bearing deposit in Australia, the absence of fossil taxa cannot be considered as "hard" evidence that they are not present. The late Oligocene contains several families of diprotodontians that are morphologically derived in being similar to the living genera. This is in contrast to both the Peramelidae and Dasyuridae. Therefore, we performed two different analyses with different maximums for the base of Diprotodontia. In the first analysis we used a maximum of 65 Ma, which allows for a slightly earlier origin than suggested by Murgon and in the second analysis we used 54.6 Ma. We used 25.5 Ma as the minimum. This is based on the oldest described fossil diprotodontians from Zone A of the Etadunna Formation (see nodes 3 and 4).

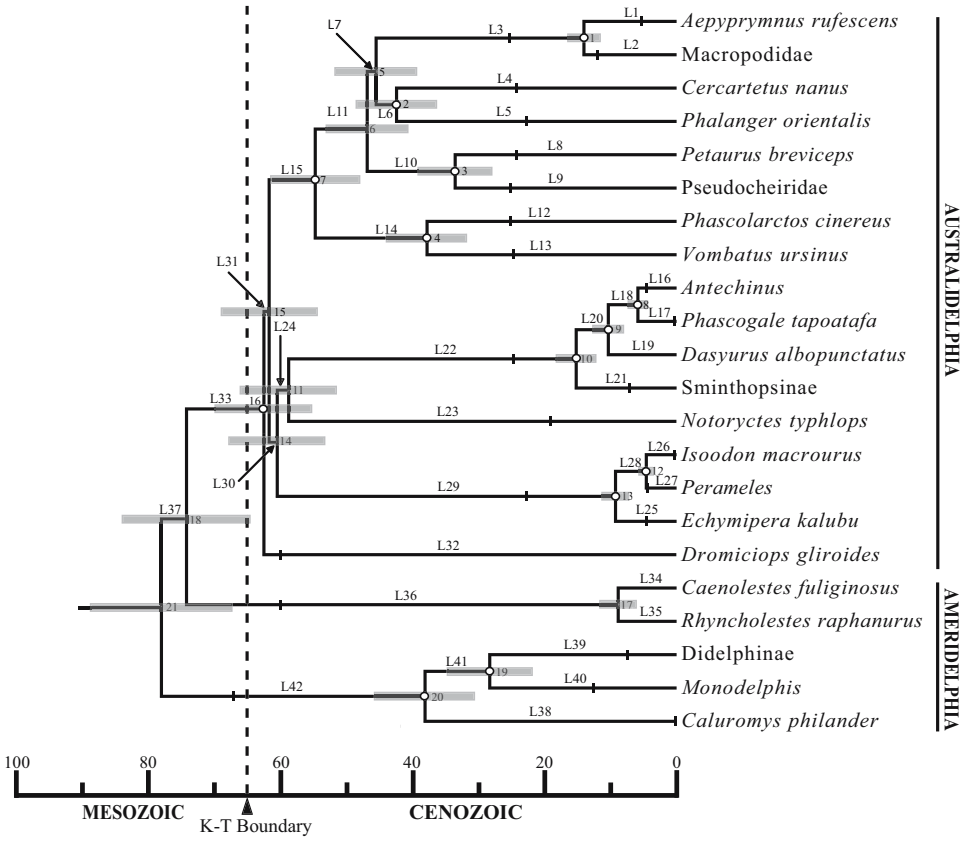

Fig. 2 Timeline in millions of years before present for marsupial evolution based on the *Multidivtime* partitioned analysis (diprotodontian maximum=65 Ma). *Node numbers* refer to those given in Table 5; *grey bars* indicate confidence intervals; *filled rectangles* indicate the oldest known fossil on a given lineage; and fossil constrained nodes are indicated with *open circles*. L = lineage; K–T = Cretaceous–Tertiary Boundary.

(b) Node 1. The Oligo-Miocene deposits of both central Australia and Riversleigh have produced several genera of kangaroos. However, there is disagreement over the taxonomic assignment of these taxa. Case (1984) and Woodburne et al. (1993) treat *Purtia mosaicus* as a potoroid, *Nambaroo* species A and B and macropodine genus P sp. A as macropodids. These specimens come from Zone C (25.0–25.5 Ma; Woodburne et al. 1993) of the Etadunna Formation. By contrast, other authors treat *Nambaroo* as a balbarine kangaroo (Long et al. 2002; Cooke 2006) and *Purtia* as a macropodoid *incertae sedis* (Long et al. 2002) or even a bulungamayine (Prideaux 2004). These same workers consider Balbarinae (Balbaridae) the sister group to all other macropodiforms (i.e., stem macropodiforms) and treat the Bulungamayinae as ancestral to the lophodont kangaroos (e.g., macropodines and sthenurines) even though this group might be paraphyletic. By contrast, Flannery (1989) considered the balbarines as ancestral to the lophodont kangaroos. Given the uncertainty in both the taxonomic assignment and placement of the Oligo-Miocene fossil taxa we used a conservative minimum of 12 Ma for the macropodid-potoroid split. This minimum is based on the presence of sthenurine-like, postcranial material (Prideaux 2004) and a small, high crowned molar tooth (Murray and Megirian 1992) from the middle Miocene Bullock Creek Local Fauna from the Camfield

Beds in the Northern Territory (~12 Ma; Woodburne et al. 1985; Murray and Megirian 1992; Long et al. 2002).

Bulungamayines and balbarines are known from Riversleigh's System A and B deposits (Archer et al. 1999; Cooke 2006), the former of which have been correlated with the Ngama Local Fauna (Zone D; 24.7–25.0 Ma; Woodburne et al. 1993) of the Etadunna Formation by Myers and Archer (1997). Zone A of the Etadunna Formation has produced a highly plesiomorphic kangaroo, "Kyeema" (Woodburne et al. 1993), that is not easily assigned to any kangaroo (sub)family. Given that late Oligocene/early Miocene macropodiforms show little morphological divergence from each other, and that the oldest kangaroo taxon from Zone A of the Etadunna is highly plesiomorphic and is not clearly associated with either the macropodid or potoroid lineage, we used the base of the Oligocene (33.9 Ma; Gradstein et al. 2004) as a maximum for the macropodid–potoroid split.

(c) Node 2. Burramyids are known from the late Oligocene to early Miocene deposits of both central Australia and Riversleigh. *Burramys wakefieldi* is from Zone D of the Etadunna Formation; Woodburne et al. (1993) proposed a date of approximately 24.7–25.0 Ma for this zone based on magnetostratigraphy. The burramyid genus *Cercartetus* is known from the late Oligocene Geilston Bay deposits of Tasmania (Tedford and Kemp 1998), which is at least 23 Ma old (Tedford and Kemp 1998). The Geilston Bay deposits have also yielded a phalangerid fossil that Tedford and Kemp (1998) classify as Phalangeridae *incertae sedis*. Other phalangerids have been described from the middle Miocene of Riversleigh but their affinities are debated (e.g., Crosby et al. 2004). We used 24.7 Ma as the minimum and either 54.6 or 65 Ma as the maximum for node 2.

(d) Node 3. The oldest pseudocheirid fossils belong to *Paljara* sp. A from Zone A (~25.5 Ma; Woodburne et al. 1993) of the Etadunna Formation. The oldest putative petaurid fossil is *Djaludjangi yadjana* from the middle Miocene of Riversleigh (Brammall 1998). However, it has also been suggested that this taxon is Petauroidea *incertae sedis* (Brammall 1998; Crosby et al. 2004). We used 25.5 Ma as a minimum and either 54.6 or 65 Ma as the maximum for node 3.

(e) Node 4. The oldest phascolarctid fossils are specimens of *Perikoala robusta* from Zone A of the Etadunna Formation, which is approximately 25.5 Ma old following Woodburne et al. (1993). Vombatid fossils belonging to *Rhizophascolonus crowcrofti* are known from the Wipajiri Formation, which unconformably overlies the Etadunna Formation (Woodburne et al. 1993). Undescribed wombats are also known from the late Oligocene of Riversleigh (Archer and Hand 2006). We used 25.5 Ma as a minimum and either 54.6 or 65 Ma as the maximum for node 4.

(f) Node 10. The middle Miocene *Barinya wangala* of Riversleigh is the oldest fossil that can confidently be placed into the Dasyuridae (~11.6–23.0 Ma; Gradstein et al. 2004) (Wroe 1998, 2003). These specimens have been referred to their own subfamily (Barinyainae) and are thought to be the sister group to the living subfamilies (Wroe 1998, 2003; Archer and Hand 2006). The oldest dasyurids directly referable to the living subfamilies are from the Hamilton Local Fauna, which has been dated at 4.46 Ma (Turnbull et al. 2003). As a result, we used 4.46 Ma as a minimum for node 10. Dasyurids have been described from the Oligo-Miocene Etadunna Formation and several Oligo-Miocene Riversleigh sites but are quite different from living species (Godthelp et al. 1999; Wroe 2003). As a result these "dasyurid" fossils were reassigned to Dasyuromorphia *incertae sedis* (e.g., *Mayigriphus*; Godthelp et al. 1999; Wroe 2003) or even Marsupialia *incertae sedis* (e.g., *Wakamatha*, *Keeuna*, *Ankotarinja*; Godthelp et al. 1999; Wroe 2003). Unfortunately, the next fossil horizon to produce terrestrial mammals is Murgon (54.6 Ma). Therefore, there is a gap of almost 30 Ma in the fossil record, so putting a precise maximum is difficult. Known late

Oligocene to early Miocene dasyurids are archaic. Given this evidence, we use the base of the Oligocene (33.9 Ma; Gradstein et al. 2004) as a maximum for the Dasyuridae. This allows for the possibility that the late Oligocene to early Miocene dasyurids are directly related to the living dasyurids given that Wroe (1998) diagnoses the Dasyuridae using four cranial features not preserved on all of the Oligo-Miocene "dasyurids."

(g) Node 8. *Antechinus* sp. from the Hamilton Local Fauna (4.46 Ma; Archer 1982; Turnbull et al. 2003) is the oldest described member of the Phascogalini. We used 4.46 Ma as the minimum and base of the Miocene (23.03 Ma; Gradstein et al. 2004) as the maximum for the split between *Antechinus* and *Phascogale*.

(h) Node 9. *Antechinus* sp. from the Hamilton Local Fauna (4.46 Ma; Archer 1982; Turnbull et al. 2003) is the oldest described member of either the Dasyurini or Phascogalini. We used 4.46 Ma as the minimum and base of the Miocene (23.03 Ma; Gradstein et al. 2004) as the maximum for the split between the Dasyurini and Phascogalini.

(i) Node 13. The oldest fossil species referable to crown-group Peramelemorphia is cf. *Peroryctes tedfordi* from the early Pliocene Hamilton Local Fauna (4.46 Ma; Turnbull et al. 2003). *Perameles allinghamensis* is known from the Bluff Downs Local Fauna (Archer and Wade 1976). This fauna is derived from the Allingham Formation, which is overlain by basalt dated at 3.62 Ma (Mackness et al. 2000). We used 4.46 Ma as a minimum for node 13. The oldest described peramelemorphian is *Yarala kida* from the late Oligocene Kangaroo Well local fauna (Schwartz 2006), although a putative perameloid tooth has been reported from Murgon (Archer and Kirsch 2006; Archer and Hand 2006). *Yarala* is placed in its own monotypic superfamily and is currently regarded as a stem peramelemorphian (Archer et al. 1999; Archer and Hand 2006). Other fossil bandicoots are known from the late Oligocene to early Pliocene of Riversleigh, the Oligo-Miocene Etadunna Formation, and the Miocene Wipajiri Formation (Woodburne et al. 1993; Archer et al. 1999; Case 2001; Archer and Hand 2006). However, these fossils have not been formally described. Zone A and B Etadunna Formation bandicoots (25.0–25.7 Ma) are very different from living bandicoots in having tribosphenic molars (Case 2001). Case (2001) suggests that species from zone D of the Etadunna Formation (24.7–25.0 Ma; Woodburne et al. 1993) and the Wipajiri Formation (10.5–11.5 Ma; Langford et al. 1995) may be ancestral to living forms. The zone D species shows an enlarged metaconule, but retains many of the primitive stem peramelemorphian characters. Two of the three Wipijiri species are much more derived and appear quite modern but the other species is more similar to the zone D species. In view of this evidence, we use the base of the Miocene (23.03 Ma; Gradstein et al. 2004) as the maximum for the Peramelinae–Echymiperinae split.

(j) Node 12. The oldest described members of the Peramelinae are *Perameles allinghamensis* (Bluff Downs Local Fauna; Allingham Formation; Archer and Wade 1976) and *Perameles bowensis* (Bow Local Fauna; 3.62 Ma; Muirhead et al. 1997; Mackness et al. 2000). For the minimum we used 3.62 Ma and the base of the Miocene (23.03 Ma; Gradstein et al. 2004) as the maximum for split between *Perameles* and *Isoodon*.

(k) Node 15. The oldest definitive australidelphians come from the Murgon deposits in southeastern Queensland that have been dated at 54.6 Ma. Murgon fossils include a possible perameloid tooth (Archer and Hand 2006) as well as Marsupialia *incertae sedis* (*Djarthia*; Godthelp et al. 1999; Wroe 2003) specimens. We, therefore, used 54.6 as the minimum for the base of Australidelphia. The maximum age for Australidelphia is more difficult to constrain. The microbiothere *Khasia* is known from 60.4–59.2 Ma old Bolivian deposits, but there is ongoing debate about the putative microbiothere affinities of this genus (see Wroe et al. 2000). Whereas *Khasia* suggests the possibility of crown-

group australidelphians in the Paleocene, there are no marsupial fossils referable to Australidelphia from the latest Cretaceous (i.e., Maastrichtian). We therefore used the base of the Maastrichtian (70.6 Ma; Gradstein et al. 2004) as a cautious maximum for the base of Australidelphia.

(l) Node 20. Minimum of 12.2 Ma for the split between Didelphidae and Caluromyidae based on Laventan didelphid fossils described by Marshall (1976). These fossils are from the "Monkey Unit" of the Honda Group in Columbia (Marshall 1976) and are at least 12.2 Ma old (Czaplewski et al. 2003). Reig et al. (1987, Fig. 69) suggested a late Eocene date for the basal split between the Caluromyidae and other didelphimorphs. Recent cladistic studies suggest that Paleocene Tiupampan marsupials lie outside of crown group Metatheria (e.g., Muizon and Cifelli 2001; Sánchez-Villagra and Wible 2002; Horovitz and Sánchez-Villagra 2003; Luo et al. 2003). In light of this evidence we allow that the caluromyid–didelphid split may have occurred as early as the Paleocene–Eocene boundary (55.8 Ma; Gradstein et al. 2004) and used this date as a maximum for the base of Didelphimorphia.

(m) Node 19. Minimum of 6.8 Ma for the Didelphinae–Marmosinae (*sensu* Kirsch and Palma 1995) split based on the occurrence of late Miocene (Huayquerian 9–6.8 Ma) fossils referable to both Didelphinae and Marmosinae. Fossils from the medial Miocene (Laventan) have also been referred to Didelphidae (Marshall 1976), possibly to *Marmosa* (Marshall 1976), *Marmosops* (Reig et al. 1987), or *Micoureus* (Goin 1997), but whether these forms are stem or crown didelphids remains unclear. More recently, Cozzuol et al. (2006) have described the oldest species of *Didelphis* from the late Miocene Solimões Formation in Brazil, which has been assigned to the Huayquerian based on biochronology but the fossil locality has not been directly dated. Therefore, we used a cautious minimum of 6.8 and 55.8 Ma as the maximum for the Didelphinae–Marmosinae split.

BEAST

BEAST v1.4 allows for an uncorrelated lognormal distribution (UCLN) model, which independently draws the rate of each branch from a lognormal distribution. We performed two different BEAST v1.4 analyses with each of the diprotodontian maxima. In one analysis the genes were partitioned and in the second analysis the genes were not partitioned.

We used the mean prior distribution for the rate of molecular evolution at the root node as calculated in the *Multidivtime* non-partitioned analyses to estimate the mean substitution rate per year in the BEAST non-partitioned analyses. In the partitioned analyses we implemented the same technique to estimate the mean prior distribution for the rate of molecular evolution at the root node for each of the individual genes (see "Multidivtime" section). The Akaike Information Criterion as implemented in Modeltest 3.06 (Posada and Crandall 1998) was used to determine the appropriate model of molecular evolution for BEAST analyses. If the suggested model was nested within the GTR model, the GTR model was used. Branching rates were drawn from a Yule prior distribution and the starting tree was that shown in Fig. 1. Multiple Markov chain Monte Carlo analyses were run with a burnin equivalent to the first 10%. These independent runs were then combined (30–40 million generations in total) until the estimated sample size was at least 100. The chains were sampled every 1,000 generations.

Tracer 1.2 (Rambaut and Drummond 2003) was used to visually check for mixing/stationarity. Bounded ranges were used to calibrate the molecular divergence estimates. We employed hard-bounded constraints that were compatible with those used in the *Multidivtime*

analyses to allow for direct comparisons. We also explored the affect of using soft bounds. For these analyses, the prior node constraint followed a standard normal distribution with 95% of the distribution between the upper and lower bounds and 2.5% of the distribution in each tail. Minimum and maximum constraints on divergence times for BEAST analyses were the same as those that were used in *Multidivtime* analyses (above).

Unrepresented basal branch lengths

We estimated the fraction of the marsupial fossil record that is missing using methods described in Teeling et al. (2005). We compiled a list consisting of every definitive fossil for every marsupial lineage present on our phylogeny (Fig. 1). We attempted to use unequivocal fossils known from more than one element, but sometimes this was not possible (Table 2). A lineage is defined to include any taxon on that branch as well as any "off-shoots" from that branch (22 terminal taxa and 43 internal branches). The oldest fossil representative for each sister-lineage pair was then compared to the corresponding Bayesian molecular date estimate to determine the unrepresented basal branch length (UBBL) for each branch (Teeling et al. 2005). No missing data (UBBL=0) were recorded for a given lineage when the molecular and fossil age estimates were the same or if the molecular age estimate was younger than the fossil estimate. If the fossil age estimate was younger than the molecular age estimate, UBBL was determined by subtracting the age estimate of the fossil from the molecular age estimate.

Results

Phylogenetic analyses

Figure 1 shows the average posterior probabilities for the two Bayesian analyses that allowed each gene segment to have its own model of sequence evolution and the ML bootstrap support percentages. Table 3 summarizes posterior probabilities for Bayesian analyses and bootstrap support percentages for ML and MP analyses.

The root of Marsupialia was not well resolved, although a basal split between Didelphimorphia versus Australidelphia + Paucituberculata was favored in Bayesian and ML analyses. Bayesian posterior probabilities for Australidelphia + Paucituberculata ranged from 0.82 to 0.89; the ML bootstrap support for this clade was 64%. The monophyly of Ameridelphia was not well supported (posterior probabilities=0.06; ML bootstrap support=13.6; MP bootstrap support=0), although the American orders Didelphimorphia and Paucituberculata were each monophyletic in all analyses. Within Didelphimorphia, didelphids grouped to the exclusion of *Caluromys* (posterior probabilities=1.00; ML and MP bootstrap support=100).

Australidelphia was strongly supported in Bayesian (posterior probabilities=1.00), ML (bootstrap support=100), and MP (bootstrap support=100) analyses. Within Australidelphia, Bayesian and ML analyses also support the monophyly of Australasian taxa (Diprotodontia, Peramelemorphia, Dasyuromorphia, Notoryctemorphia) to the exclusion of the South American order Microbiotheria (posterior probabilities=0.69–0.87; ML bootstrap=46; MP=43). Within the Australasian moiety, Peramelidae + *Notoryctes* + Dasyuridae formed a clade to the exclusion of Diprotodontia in Bayesian and ML analyses (posterior probabilities=0.97–0.99; ML bootstrap support=65; MP=51.0). All of the non-monotypic Australasian orders were recovered as monophyletic with strong support (posterior probabilities and bootstrap support of 1.00 and 100, respectively). Within Peramelidae, *Isoodon* and *Perameles* grouped to

Table 2 Estimation of the missing fossil record per lineage

Branch Number	Taxon	Oldest Fossil[a]	Molecular Age	Duration of Lineage	Total Missing per Lineage	Percent Missing per Lineage	Reference
	AUSTRALIDELPHIA						
	Diprotodontia						
	Macropodiformes						
L1	*Bettongia moyesi*[b]	5.33	13.8/16.1	13.8/16.1	8.5/10.77	61.5/66.9	Woodburne et al. 1993
L2	Macropodine gen. P sp. A[b]	12.0	13.8/16.1	13.8/16.1	1.8/4.1	13.2/25.5	Woodburne et al. 1993
L3	Riversleigh Balbaridae[c]	25.25	44.9/45.6	31.1/29.5	5.8/4.3	18.8/14.4	Cooke and Kear 1999
	Phalangeroidea						
L4	*Burramys wakefieldi*	24.85	41.9/45.5	41.9/45.5	17.0/20.6	40.1/45.3	Woodburne et al. 1993
L5	Geilston Bay phalangerid	23.00	41.9/45.5	41.9/45.5	18.9/22.4	45.1/49.3	Tedford and Kemp 1998
L6	Unknown		44.9/45.6	3.0/0.2	3.0/0.2	100/100	
L7	Unknown		47.6/45.6	2.7/0.0	2.7/0.0	100/100	
	Petauroidea						
L8	Riversleigh petaurid	24.85	33.1/28.4	33.1/28.4	8.2/3.6	24.9/12.5	Brammall and Archer 1999
L9	*Paljara* sp. A	25.60	33.1/28.4	33.1/28.4	7.5/2.8	22.6/9.9	Woodburne et al. 1993
L10[d]	*Pilkipildra taylori*	25.60	47.6/45.6	14.5/17.2	14.5/17.2	100/100	Woodburne et al. 1993
L11	Unknown		54.1/53.8	6.4/8.2	6.4/8.2	100/100	
	Vombatiformes						
L12	*Perikoala robusta*	25.60	37.3/31.7	37.3/31.7	11.7/6.1	31.4/19.2	Woodburne et al. 1993
L13	EtadunnaVombatoids	25.60	37.3/31.7	37.3/31.7	11.7/6.1	31.4/19.2	Woodburne et al. 1993
L14	Unknown		54.1/53.8	16.8/22.1	16.8/22.1	100/100	
L15	Unknown		62.2/62.8	8.1/9.0	8.1/9.0	100/100	
	Dasyuromorphia						
	Dasyuridae						
	Phascogalini						
L16[e]	*Antechinus* sp.	4.46	5.7/7.7	5.7/7.7	1.3/3.2	22.2/42.1	Archer 1982; Turnbull et al. 2003

L17	*Phascogale* sp.	0.036	5.7/7.7	5.7/7.7	5.7/7.7	99.4/99.5	Pledge 1990
L18	Unknown		10.2/9.9	4.4/2.2	4.4/4.4	100/100	
	Dasyurini						
L19[f]	*Ganbulanyi djadjinguli*	13.79[g]	10.2/9.9	10.2/9.9	0.0/0.0	0.0/0.0	Wroe 1998
L20	Unknown		15.0/22.9	4.9/13.0	4.9/13.0	100/100	
	Sminthopsini						
L21[h]	*Planigale* sp.	4.4	15.0/22.9	15.0/22.9	10.6/18.5	70.8/80.8	Archer 1982
L22[i]	*Ankotarinja tirarensis, Keeuna woodburnei*	25.25	59.1/59.9	44.0/37.0	18.8/11.8	42.7/31.8	Woodburne et al. 1993
	Notoryctemorphia						
L23[j]	Riversleigh notoryctid	19.50	59.1/59.9	59.1/59.9	39.6/40.4	67.0/67.5	Archer et al. 1999; Warburton 2003
L24	Unknown		60.9/60.1	1.8/0.2	1.8/0.2	100/100	
	Peramelemorphia						
	Peramelidae						
L25[k]	*Peroryctes tedfordi*	4.46	9.1/13.3	9.1/13.3	4.6/8.8	51.0/66.5	Turnbull et al. 2003
L26	*Isoodon obesulus*	0.036	4.5/6.7	4.5/6.7	4.4/6.7	99.2/99.5	Price 2004
L27	*Perameles allinghamensis*	4.4	4.5/6.7	4.5/6.7	0.1/2.3	1.4/34.3	Archer and Wade 1976
L28	Unknown		9.1/13.3	4.6/6.6	4.6/6.6	100/100	
L29[l]	*Yarala kida*	23.03	60.9/60.1	51.8/46.8	28.8/23.8	55.5/50.8	Schwartz 2006
L30	Unknown		62.2/62.8	1.3/2.7	1.3/2.7	100/100	
L31	Unknown		62.9/62.8	0.7/0.0	0.7/0.0	100/100	
	Microbiotheria						
L32	*Khasia cordillerensis*	59.80	62.9/62.8	62.9/62.8	3.1/3.0	4.9/4.8	Marshall and Muizon 1988; Marshall et al. 1997
L33[m]	*Chulpasia mattaueri*	56.60	74.8/85.6	12.0/22.8	12.0/22.8	100/100	Goin et al. 2006; Sigé et al. 2004
	AMERIDELPHIA						
	Paucituberculata						
L34	Unknown		9.7/14.1	9.7/14.1	9.7/14.1	100/100	
L35	Unknown		9.7/14.1	9.7/14.1	9.7/14.1	100/100	

Table 2 (continued)

Branch Number	Taxon	Oldest Fossil[a]	Molecular Age	Duration of Lineage	Total Missing per Lineage	Percent Missing per Lineage	Reference
L36[n]	*Mayulestes ferox*	59.80	74.8/85.6	65.2/71.5	5.4/11.7	8.3/16.4	Goin et al. 2006
L37	Unknown		78.5/89.3	3.6/3.7	3.6/3.7	100/100	
	Didelphimorphia						
L38	*Caluromys derbianus*	0.01	37.5/35.4	37.5/35.4	37.5/35.4	100/100	Reig et al. 1987
L39[o]	*Hyperdidelphis pattersoni*	7.90	27.9/25.0	27.9/25.0	20.0/17.1	71.7/68.4	Reig 1952, 1958; Reig et al. 1987
L40	*Micoureus laventicus*	12.85	27.9/25.0	27.9/25.0	15.0/12.2	53.9/48.6	Goin 1997
L41	Unknown		37.5/35.4	9.7/10.4	9.7/10.4	100/100	
L42[p]	*Nortedelphys intermedius*	67.0	78.5/89.3	41.0/59.3	11.5/22.3	28.0/41.2	Goin et al. 2006

Analyses before and after slashes are based on the partitioned hard-bounded *Multidivtime* and BEAST analyses (Diprotodontia maximum set to 65Ma), respectively. Values are in millions of years. References refer to column 3 (age of oldest fossil).

[a] If possible only taxa from dated deposits were used. If a range was given, the midpoint date/value was used for column 3 (age of oldest fossil).

[b] As previously mentioned there is disagreement in regards to the exact identification and affinities of the Oligo-Miocene macropodiforms. For the purposes of the UBBL analyses we treated all of the Oligo-Miocene kangaroo species as stem macropodoids.

[c] Myers and Archer (1997) have correlated one of the oldest Riversleigh sites to the Ngama Local Fauna of the Etadunna Formation (24.7–25.0Ma; Woodburne et al. 1993). We used the middle of the estimated age of the Ngama Local Fauna for all Riversleigh System A deposits.

[d] Although considered *incertae sedis* by Archer et al. (1987) or a stem lineage of the phalangeroids (Marshall et al. 1990), the pilkipildrids are sometimes considered the sister group of the petauroids.

[e] We assigned a conservative date as the end of the Pleistocene. In a personal communication to Archer and Hand (2006), van Dyck has suggested that a phascogaline similar to *Antechinus* might be present in early Miocene of Riversleigh. However, it has yet to be described and this assignment can be viewed as highly questionable.

[f] This species comes from the middle to early late Miocene Encore Site in Riversleigh. There is dispute in regards to exact dates at Riversleigh (e.g., Megirian et al. 2004). As a result we use the middle of the medial Miocene (Gradstein et al. 2004) as reasonable approximation.

[g] In both the BEAST and *Multidivtime* analyses, the age of the fossil was older than the divergence estimates. *Ganbulanyi* might also be more closely related to *Barinya*, which is considered the sister taxon to the living dasyurid subfamilies (Wroe 2003), which is consistent with our younger age estimate for the Dasyurini Phascogalini split.

[h] The minimum age of the Bluffs Down Local Fauna (Allingham Formation) is 3.62Ma with a maximum of 5.2Ma based on potassium-argon basalt dates (Mackness et al. 2000; Archer and Wade 1976).

[i] Godthelp et al. (1999) and Wroe (2003) remove these genera from Dasyuridae and refer to them as Marsupialia *incertae sedis*. Even if these genera later turn out not to be members of the Dasyuromorphia, thylacinid fossils are known from the late Oligocene (Wroe 2003) and molecular studies have demonstrated a sister group relationship with the

Dasyuridae (Krajewski et al. 1997). Tedford and Kemp (1998) describe the proximal end of a femur from the late Oligocene Geilston Bay local fauna, which they refer to the Dasyuridae. However, since only one element is known and because of problems with morphological convergence, this assignment can only be regarded as tentative.

[j] Notoryctid specimens are known from several Riversleigh System B localities that are thought to be early to middle Miocene in age, but these have yet to be well correlated to any dated fossil deposit. As a result we used the middle Miocene dates of Gradstein et al. (2004).

[k] Assignment to *Peroryctes* was considered provisional by Turnbull et al. (2003).

[l] These specimens are from the Kangaroo Well Local Fauna which has not been directly dated, but Megirian et al. (2004) suggest a late Oligocene age based on biocorrelation. They suggest that the fauna is "slightly" older than the Wipajiri fauna (11.5–10.5 Ma; Langford et al. 1995) but "slightly" younger than Zone D of the Etadunna Formation (25–24.7 Ma; Woodburne et al. 1993). As a result we used the Oligo-Miocene boundary (23.03 Ma; Gradstein et al. 2004) as an age estimate for this specimen. It should be noted that a putative "perameloid" tooth is known from Murgon, but has yet to be described (Archer and Hand 2006), which would extend the record back to the Eocene.

[m] *Chulpasia* from the Late Cretaceous or Paleocene Umayo Formation of southern Peru has been associated with *Glasbius* (Crochet and Sigé 1993), *Thylacotinga* from the Murgon deposits of Australia (Sigé et al. 1995), and in the most recent study sister to the Microbiotheria (Goin et al. 2006). As a result we treat it as an australidelphian in all of the fossil completeness estimates. The Umayo Formation is a microconglomerate that is not age constrained, but new paleontological, paleomagnetic, and stratigraphic data favor chron 24 (latest Paleocene or earliest Eocene) over chrons 26 and 29 (Sigé et al. 2004). As a result we use the base of chron 24 (56.6 Ma) as its age. A closely related *Chulpasia* sp. may also be present in Murgon (Sigé et al. 2004).

[n] Kielan-Jaworowska et al. (2004) treat the Lancian Glasbiidae as a family within Paucituberculata. However, the most recent cladistic analyses do not find any association between *Glasbius* and the paucituberculates (Goin et al. 2006). Goin et al. (2006) recovered the Borhyaenoidea as the sister group to paucituberculates. However, it should be noted that Sánchez-Villagra et al. (2007) recover the Boryhyaenidae as outside of the living genera and other earlier studies (e.g., Rougier et al. 1998; Luo et al. 2003) suggest the Boryhyaenidae are not crown group marsupials as well.

[o] Reig et al. (1987) found a close association between *Hyperdidelphis* and *Didelphis*. Otherwise the oldest member of this lineage is *Lutreolina tracheia* from the late Miocene of Argentina (Simpson 1974) or *Didelphis solimoensis* from the late Miocene Solimões Formation (Cozzuol et al. 2006).

[p] Goin et al. (2006) recovered the recently named Lancian genus *Nortedelphys* (Herpetotheriidae) as the sister taxon to all other didelphimorphians. However, some workers suggest there are no crown group metatherians present/known in the Cretaceous (e.g., Rougier et al. 1998; Luo et al. 2003; Sánchez-Villagra et al. 2007).

Table 3 Summary of bootstrap and posterior probabilities

Hypothesis	MP	ML	Bayesian analyses			
			Partitioned		Non-partitioned	
			Run 1	Run 2	Run 1	Run 2
Ameridelphia (Didelphimorphia + Paucituberculata)	0	13.6	0.06	0.06	0.02	0.03
Australidelphia	100	100	1.00	1.00	1.00	1.00
All marsupials except *Dromiciops*	0	0	0.00	0.00	0.00	0.00
All marsupials except Paucituberculata	95	22.0	0.11	0.12	0.09	0.07
All marsupials except Didelphimorphia	4.9	64.4	0.83	0.82	0.89	0.89
Monophyly of Australasian taxa	43.2	46.2	0.69	0.69	0.87	0.87
Eometatheria (All Australasian taxa but Peramelidae)	0	0	0.00	0.00	0.00	0.00
Australasian possum monophyly	26.2	6.2	0.001	0.00	0.00	0.00
Notoryctes + Diprotodontia	0	0	0.00	0.00	0.00	0.00
Notoryctes + Dasyuridae	39.2	44.6	0.66	0.65	0.67	0.68
Notoryctes + Peramelidae	32.8	16	0.08	0.09	0.06	0.06
Peramelidae + *Notoryctes* + Dasyuridae	51.0	64.6	0.97	0.97	0.99	0.99
Peramelidae + *Notoryctes* + Dasyuridae + *Dromiciops*	31.5	9.2	0.04	0.04	0.00	.00
Peramelidae + Dasyuridae	27.4	35.0	0.26	0.26	0.27	0.26
Peramelidae + *Notoryctes* + *Dromiciops*	0	1.4	0.00	0.00	0.00	0.00
Peramelidae + Dasyuridae + Diprotodontia	0	0	0.00	0.00	0.00	0.00
Dromiciops + Diprotodontia	0	23.4	0.25	0.26	0.11	0.11
Dromiciops + Dasyuridae	30.9	6.8	0.00	0.00	0.00	0.00
Dromiciops + Peramelidae	12.0	7.8	0.00	0.00	0.00	0.00
Dromiciops + Dasyuridae + Peramelidae	0	0.2	0.00	0.00	0.00	0.00
Dromiciops + Dasyuridae + *Notoryctes*	0	10.2	0.02	0.01	0.00	0.00
Diprotodontia + Peramelidae	0	0	0.00	0.00	0.00	0.00
Paucituberculata	100	100	1.00	1.00	1.00	1.00
Didelphimorphia	100	100	1.00	1.00	1.00	1.00
Didelphinae + Marmosinae	100	100	1.00	1.00	1.00	1.00
Dasyuridae	100	100	1.00	1.00	1.00	1.00
Phascogalini	100	100	1.00	1.00	1.00	1.00
Dasyurini + Phascogalini	100	100	1.00	1.00	1.00	1.00
Peramelidae	100	100	1.00	1.00	1.00	1.00
Echymiperinae	100	100	1.00	1.00	1.00	1.00
Diprotodontia	100	100	1.00	1.00	1.00	1.00
Vombatiformes	100	100	1.00	1.00	1.00	1.00
Macropodiformes + Phalangeriformes	100	100	1.00	1.00	1.00	1.00
Burramyidae + Macropodiformes	2.4	1.2	0.00	0.00	0.00	0.00
Macropodiformes + Phalangeridae	10.2	4.2	0.00	0.00	0.00	0.00
Macropodiformes	100	100	1.00	1.00	1.00	1.00
Macropodiformes + Phalangeroidea	11.6	50.8	0.82	0.83	0.74	0.74
Petauroidea[a]	100	100	1.00	1.00	1.00	1.00
Macropodiformes + Petauroidea	48.2	38.2	0.18	0.17	0.26	0.26
Phalangeroidea	72.5	88.8	1.00	1.00	1.00	1.00

Partitioned each gene was partitioned to have its own model of molecular evolution, *Non-partitioned* concatenation was treated as a single gene, *MP* maximum parsimony, *ML* maximum likelihood

[a] Represented by Petauridae and Pseudocheiridae

the exclusion of *Echymipera*. Within Dasyuridae, Phascogalini (*Antechinus* and *Phascogale*) was monophyletic and Phascogalini and Dasyurini (*Dasyurus*) grouped to the exclusion of Sminthopsinae. Among diprotodontian marsupials, Vombatiformes and Macropodiformes + Phalangeriformes were reciprocally monophyletic clades. Macropodiformes was monophyletic whereas there was no support for the monophyly of Phalangeriformes. However, there was support for two distinct Australasian possum clades: a petauroid clade represented by Pseudocheiridae + Petauridae, and a phalangeroid clade represented by Phalangeridae and Burramyidae.

Statistical tests

Table 4 reports the results of the KH, SH, and AU tests. Four hypotheses were compared for the root of Marsupialia. The pairwise comparisons rejected rooting the tree between *Dromiciops gliroides* and other marsupials (Hershkovitz 1992) and rooting between Ameridelphia and Australidelphia. However, these tests could not discriminate between rooting the marsupial tree on Didelphimorphia or on Paucituberculata. No significant differences were found between Eometatheria (*Dromiciops gliroides* + all Australasian orders excepting Peramelemorphia; Kirsch et al. 1997); a monophyletic Australasian clade; and a *Dromiciops* + Diprotodontia clade as recovered by Drummond et al. (2006).

Four hypotheses were compared for the placement of *Notoryctes*. The pairwise comparisons rejected a sister group relationship between *Notoryctes* and the Diprotodontia, but failed to discriminate between a sister-taxon relationship to either the Dasyuridae, Peramelidae, or Dasyuridae + Peramelidae. Within Dasyuromorphia, we compared two different tree hypotheses for both the base of Dasyuridae and the sister taxon to *Antechinus*. There was statistical support for a basal split between the Sminthopsinae and other dasyurids as found by Krajewski et al. (2000) rather than a basal split between the Dasyurini and other dasyurids (Wroe et al. 2000). Phascogalini monophyly was also statistically supported, contrary to the results of Wroe et al. (2000) and consistent with Krajewski et al. (2000). Within Peramelidae, there was statistical support for an *Echymipera* + Peramelinae clade as compared to a sister group relationship to either *Isoodon* or *Perameles*.

Within Diprotodontia, there was statistical support for the Petauroidea (represented by *Petaurus* and Pseudocheiridae) as compared to a dichotomous split between either *Petaurus* (Horovitz and Sánchez-Villagra 2003) or the Pseudocheiridae (Woodburne et al. 1987) and the other diprotodontians.

We compared five possible positions for *Cercartetus* (Family Burramyidae). These tests rejected a sister-group relationship to all other diprotodontians except *Petaurus* (Horovitz and Sánchez-Villagra 2003) and a sister-group relationship to the Macropodiformes (rejected in all tests but the SH), but were unable to discriminate between a sister-taxon relationship to either the Petauroidea (Springer and Woodburne 1989), the Phalangeridae (Springer and Kirsch 1991), or a Phalangeridae + Macropodiformes clade. However, the tests favored monophyly of the Phalangeroidea.

Statistical tests failed to discriminate between three alternative hypotheses for the sister group of the Macropodiformes, i.e., Phalangeroidea (Springer and Kirsch 1991), Petauroidea (Amrine-Madsen et al. 2003), and Phalangeriformes (possum monophyly; Springer and Woodburne 1989), but favored the Phalangeroidea + Macropodoidea hypothesis.

Molecular dating

Figure 2 shows a timescale for marsupial divergences based on the results of a *Multidivtime* analysis in which each gene was allowed to have its own model of sequence evolution

Table 4 Results of statistical tests

Phylogenetic hypotheses	-ln likelihood	Δ	*P*		
			KH	SH	AU
Base of Marsupialia					
(a) *Dromiciops* and other marsupials	63840.24996	49.64288	0.000*	0.000*	0.000*
(b) Paucituberculata and other marsupials	63793.16680	2.55972	0.259	0.587	0.261
(c) Didelphimorphia and other marsupials (best)	63790.60708		0.741	0.868	0.744
(d) Ameridelphia and Australidelphia	63842.64640	52.03932	0.000*	0.000*	0.000*
Australasian taxa					
(a) Monophyletic (best)	63790.60708		0.656	0.797	0.699
(b) Eometatheria	63795.65829	5.05121	0.344	0.593	0.428
(c) *Dromiciops* + Diprotodontia	63792.32610	1.71902	0.262	0.329	0.273
Position of *Notoryctes* (sister taxon to)					
(a) Dasyuridae (best)	63790.60708		1.000	0.745	0.739
(b) Peramelidae	63792.87153	2.26445	0.505	0.612	0.261
(c) Diprotodontia	64074.21936	283.61228	0.000*	0.000*	0.000*
(d) Dasyuridae + Peramelidae (best)	63790.60708	0.000	1.000	0.745	0.739
Base of Dasyuridae					
(a) Sminthopsinae (best)	63790.60708		1.000	1.000	1.000
(b) Dasyurini (*Dasyurus*)	63863.15502	72.54794	0.000*	0.000*	0.000*
Antechinus (sister taxon to)					
(a) *Phascogale* (Phascogalini monophyly) (best)	63790.60708		1.000	1.000	1.000
(b) Sminthopsinae	63951.07986	160.47278	0.000*	0.000*	0.000*
Position of *Echymipera* (sister taxon to)					
(a) Peramelinae (best)	63790.60708		1.000	1.000	1.000
(b) *Isoodon*	63854.20520	63.59812	0.000*	0.000*	0.000*
(c) *Perameles*	63853.91710	63.31002	0.000*	0.000*	0.000*
Position of *Cercartetus* (sister taxon to)					
(a) Phalangeridae (best)	63790.60708		0.936	0.983	0.914
(b) Petauroidea[a]	63802.47924	11.87216	0.132	0.456	0.143
(c) all other Diprotodontia	64035.67588	245.06880	0.000*	0.000*	0.000*
(d) Macropodiformes	63802.12219	11.51510	0.039*	0.439	0.024*
(e) Macropodiformes + Phalangeridae	63800.86253	10.25544	0.064	0.473	0.089
Petauroidea[a] (monophyly)					
(a) *Petaurus* + Pseudocheiridae (best)	63790.60708		1.000	1.000	1.000
(b) *Petaurus* sister to other Diprotodontia	64001.15798	210.55090	0.000*	0.000*	0.000*
(c) Pseudocheiridae sister to other Diprotodontia	63922.33414	131.72706	0.000*	0.000*	0.000*
Position of Macropodiformes (sister group to)					
(a) Phalangeroidea (best)	63790.60708		0.596	0.718	0.637
(b) Petauroidea[a]	63792.06444	1.45736	0.404	0.543	0.462
(c) Phalangeriformes (possum monophyly)	63796.59513	5.98805	0.139	0.221	0.073

KH Kishino-Hasegawa, *SH* Shimodaira-Hasegawa, *AU* approximately unbiased

*P=<0.05

[a] Represented by Petauridae and Pseudocheiridae

(partitioned) and the maximum age for the base of Diprotodontia was fixed at 65 Ma. Table 5 shows point estimates of divergence times, 95% credibility intervals (*Multidivtime*), and 95% highest posterior densities (HPDs) for *Multidivtime* and hard-bounded BEAST analyses for all nodes in Fig. 2. Although the maximum of 33.9 Ma (nodes 1 and 10) can be considered arbitrary, the 95% HPDs and 95% credibility intervals are not bumping up against the maximum. As a result, the upper bound is not critical in informing these divergence dates. This is in contrast to the diprotodontian maximum, which is critical in informing the divergence estimates in that the 95% HPDs and 95% credibility intervals are bumping up against the maximum. In analyses that employed the 65 Ma maximum for the base of Diprotodontia, mean divergence dates obtained with *Multidivtime* were 1.5 Ma younger than those obtained with BEAST. In analyses that employed the 54.6 Ma maximum for the base of Diprotodontia, mean BEAST dates were 2.4 Ma older than *Multidivtime* dates. The diprotodontian maximum had less influence on the BEAST dates than on the *Multidivtime* dates. Mean BEAST dates were 0.87 Ma older with the 65 Ma maximum whereas mean *Multidivtime* dates were 1.8 Ma older.

Results of *Multidivtime* and BEAST analyses that employed a single model of sequence evolution for the entire concatenation of gene sequences (i.e., non-partitioned) are similar to results obtained with partitioned analyses and are provided in the Supplementary Information. Mean dates in the non-partitioned analyses (54.6 Ma diprotodontian maximum) were slightly older (≤1 Ma), but when the diprotodontian maximum was 65 Ma they were slightly younger (≤1 Ma) than the corresponding dates in the partitioned analyses. The results of the soft-bounded BEAST analyses (Supplementary Information) were similar to corresponding results that were obtained with hard bounds. Mean dates were ≤1 Ma younger in all analyses (Supplementary Information).

All point estimates (74–89 Ma), 95% credibility intervals, and 95% HPDs for the base of Marsupialia were in the Cretaceous (Table 5). Point estimates were also entirely in the Cretaceous for the split between Paucituberculata and Australidelphia (71–86 Ma). The most recent common ancestor of Australidelphia (node 16) was estimated at 60–66 Ma. Interordinal divergences within the Australasian clade (nodes 11, 14, 15) ranged from 56 to 64 Ma. All intraordinal divergence dates were placed in the Cenozoic. The deepest intraordinal splits were within Diprotodontia.

Figure 3 shows the widths of the 95% confidence intervals plotted against the mean estimates of divergence times for the hard-bounded *Multidivtime* analysis (Diprotodontia maximum set to 65 Ma). The *Multidivtime* analyses yielded a more linear relationship as compared to the BEAST analyses (other *Multidivtime* analyses and BEAST analyses not shown). The nearly linear relationship obtained in the *Multidivtime* analyses suggests that the addition of more sequence data will not significantly improve our *Multidivtime* estimated times of divergence. Put differently, the regression line for the partitioned *Multidivtime* analyses ($y = 0.2725x$) suggests that even with an infinite amount of sequence data each 1 Ma of species divergence will only add 0.2725 Ma to the 95% confidence interval. However, this relationship will only hold up if the constraints remain unchanged. BEAST plots (not shown) were non-linear, which suggests that more sequence data will improve estimates of divergence time obtained with BEAST.

After the exclusion of the burnin trees, the non-partitioned BEAST analyses recovered 65–80 different tree topologies with the MAP (maximum a posteriori) tree accounting for 64–65% of the posterior probability. These tree topologies for Marsupialia were identical to that of the MrBayes tree shown in Fig. 1. The covariance statistic indicated that there was virtually no autocorrelation of rates for all of the non-partitioned analyses (Supplementary Information) with a mean rate of evolution equal to 1.3E-3–1.4E-3 substitutions per site per million years

Table 5 Hard bounded partitioned BEAST and *Multidivtime* divergence estimates

Node[b]	Divergence Estimates[a]			
	Multidivtime		BEAST	
	Diprotodontia maximum			
	54.6 Ma	65 Ma	54.6 Ma	65 Ma
Macropodiformes (node 1)	13.4 (12.1–15.8)	13.8 (12.1–17.0)	16.0 (12.0–22.2)	16.1 (12.0–23.3)
Phalangeroidea (node 2)	39.8 (35.5–44.0)	41.9 (36.0–48.2)	43.4 (36.3–50.7)	45.4 (36.4–54.6)
Petauridae + Pseudocheiridae (node 3)	31.4 (27.2–35.7)	33.1 (27.7–38.9)	28.0 (25.5–32.5)	28.4 (25.5–34.0)
Vombatiformes (node 4)	35.4 (31.0–39.7)	37.3 (31.4–43.6)	30.8 (25.5–38.3)	31.7 (25.5–40.7)
Macropodiformes + Phalangeroidea (node 5)	42.7 (38.4–46.7)	44.9 (38.9–51.3)	43.7 (37.0–50.1)	45.6 (36.8–54.5)
Macropodiformes + Petauroidea[c] + Phalangeroidea (node 6)	45.2 (40.9–49.0)	47.6 (41.4–54.1)	43.8 (37.0–50.1)	45.6 (36.8–54.5)
Diprotodontia (node 7)	51.3 (46.8–54.4)	54.1 (47.3–60.9)	50.8 (45.8–54.6)	53.8 (44.6–62.8)
Phascogalini (node 8)	5.5 (4.5–7.0)	5.7 (4.6–7.5)	7.8 (4.5–11.3)	7.7 (4.5–11.4)
Dasyurini + Phascogalini (node 9)	9.7 (7.9–12.0)	10.2 (8.1–12.8)	10.0 (6.4–14.5)	9.9 (5.8–14.4)
Dasyuridae (node 10)	14.4 (12.0–17.2)	15.0 (12.3–18.3)	22.6 (16.6–29.3)	22.9 (16.6–29.7)
Notoryctes + Dasyuridae (node 11)	56.2 (51.2–61.3)	59.1 (51.7–66.4)	59.1 (51.9–67.1)	59.9 (52.6–67.9)
Peramelinae (node 12)	4.3 (3.6–5.5)	4.5 (3.6–5.8)	6.8 (3.6–11.2)	6.7 (3.6–10.8)
Peramelidae (node 13)	8.7 (7.1–10.6)	9.1 (7.3–11.3)	13.7 (7.7–20.1)	13.3 (7.2–20.1)
Peramelidae + *Notoryctes* + Dasyuridae (node 14)	58.0 (53.1–62.8)	60.9 (53.5–68.1)	59.3 (52.3–66.9)	60.1 (52.9–67.7)
Australasian taxa (node 15)	59.2 (54.4–64.0)	62.2 (54.7–69.3)	61.5 (54.9–67.9)	62.8 (56.9–70.6)
Australidelphia (node 16)	59.9 (55.0–64.8)	62.9 (55.3–70.0)	61.5 (54.9–67.8)	62.8 (56.9–70.6)
Paucituberculata (node 17)	9.2 (6.9–11.8)	9.7 (7.1–12.7)	13.9 (5.5–24.4)	14.1 (4.9–25.5)
All marsupials but Didelphimorphia (node 18)	71.3 (64.6–78.5)	74.8 (65.1–84.6)	83.3 (68.8–100.7)	85.6 (69.5–104.4)
Didelphini + Marmosini (node 19)	26.6 (21.3–32.5)	27.9 (21.8–34.8)	25.4 (13.4–41.4)	25.0 (13.5–39.9)
Didelphimorphia (node 20)	35.8 (29.6–42.5)	37.5 (30.4–45.6)	35.7 (21.1–52.1)	35.4 (21.5–51.6)
Marsupialia (node 21)	74.8 (67.0–83.0)	78.5 (67.8–89.4)	86.8 (71.8–103.8)	89.3 (72.1–108.3)

[a] Values are in millions of years

[b] Node numbers refer to Fig. 2

[c] Represented by Petauridae and Pseudocheiridae

(HPD=1.3E-3–1.5E-3). The partitioned BEAST analyses recovered thousands of unique tree topologies with the MAP tree for each gene accounting for less than 1–14% of the posterior probability. The mean of the covariance statistics for BRCA1, IRBP, and vWF in some of the analyses indicates that there was some autocorrelation of rates for these genes; ApoB and Rag1 showed no evidence of autocorrelation (Supplementary Information).

Unrepresented basal branch lengths

Tables 2 and 6 show the percentage of the UBBL for the lineages and clades based on the partitioned, hard-bounded *Multidivtime* and BEAST analyses (Diprotodontia maximum= 65 Ma). External lineages on the marsupial tree were on average 29% (BEAST) to 32% (*Multidivtime*) more complete than internal lineages (Table 6). In comparison to the Felidae and

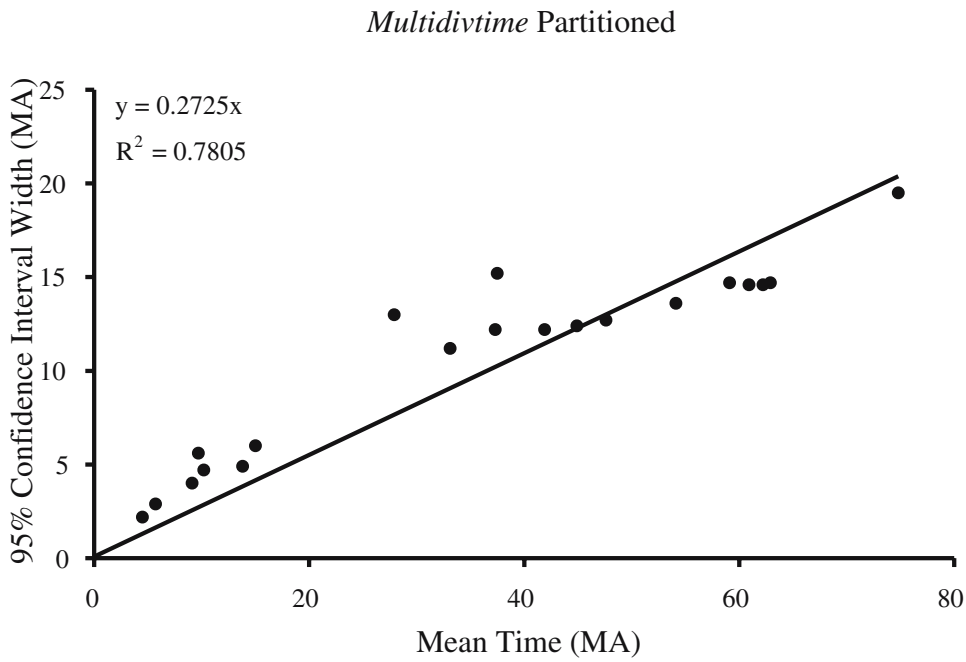

Fig. 3 Ninety-five percent confidence intervals plotted against mean for divergence date estimates for hard bounded *Multidivtime* analysis (diprotodontian maximum=65 Ma). Raw data are given in the Supplementary Information.

Chiroptera fossil records, the marsupial UBBL record is relatively more complete. The australidelphian UBBL is approximately 5% (BEAST) to 9% (*Multidivtime*) less complete than the ameridelphian fossil record. Of the seven marsupial orders, the notoryctemorphian UBBL is the most incomplete with over 67% missing and the Microbiotheria record is the most complete with no more than 5% missing. Among Australasian orders, the record for Diprotodontia is the most complete (42–43% missing).

Discussion

Phylogenetic relationships

Marsupial cohorts and the root of Marsupialia

The seven marsupial orders are currently divided into the cohorts Ameridelphia and Australidelphia (Szalay 1982). We found strong support for the monophyly of Australidelphia and its constituent orders, even with the addition of more australidelphian taxa to the Amrine-Madsen et al. (2003) data set. Australidelphian monophyly is in solid agreement with previous morphological (Luckett 1994; Szalay and Sargis 2001; Horovitz and Sánchez-Villagra 2003), molecular (Kirsch et al. 1991, 1997; Springer et al. 1998; Phillips et al. 2001, 2006; Amrine-Madsen et al. 2003), and mixed data sets (Asher et al. 2004). Hershkovitz (1992) suggested that the continuous lower ankle joint pattern used by Szalay (1982) to define Australidelphia is not a synapomorphy because it is present in some ameridelphian taxa. Szalay (1994) extended

Table 6 Estimation of the missing fossil record for marsupial, felid, and chiropteran lineages

	Percent missing[a]	Average of percentage missing per lineage
Marsupialia[b]		
All lineages	45.4/48.0	65.8/67.0
External lineages	45.5/46.9	50.5/52.7
Internal lineages	45.1/49.5	82.7/82.7
Dasyuridae	50.8/58.4	62.1/64.8
Diprotodontia	42.6/41.7	59.3/57.5
Notoryctemorphia	67.0/67.5	67.0/67.5
Peramelidae	57.1/60.1	61.4/70.2
Microbiotheria	4.9/4. 8	4.9/4. 8
Paucituberculata	29.2/40.0	69.4/72.1
Didelphimorphia	51.6/52.6	70.7/71.6
All Australidelphia but Diprotodontia	46.4/50.0	65.5/69.3
American taxa	39.8/44.6	69.7/70.8
Australasian taxa	48.7/50.2	63.3/64.5
Australidelphia	44.4/45.7	62.6/63.7
Ameridelphia	47.6/52.6	76.2/77.5
Felidae[c]		
All lineages	70	76
External lineages	70	72
Internal lineages	69	80
Chiroptera[d]		
All lineages	61	73
External lineages	59	58
Internal lineages	71	89

[a] Summed over all lineages

[b] Values for marsupial lineages are from *Multidivtime* and BEAST partitioned analyses, respectively, with the diprotodontian maximum set to 65.0 Ma. Raw data for marsupial lineages are given in Table 5.

[c] Values calculated from those given in Johnson et al. (2006)

[d] Values from Teeling et al. (2005)

his pedal character analyses and demonstrated that virtually all australidelphians display this ankle joint pattern. Luckett (1994) agreed with Szalay (1982, 1994) and suggested that a double or triple faceted calcaneocuboid may also support Australidelphia. The continuous lower ankle joint pattern (Szalay 1982, 1994) and the 12 unambiguous cranial and postcranial characters listed by Horovitz and Sánchez-Villagra (2003) appear to be reliable morphological characters that define Australidelphia.

Sperm pairing is often cited in support of Ameridelphia, but in didelphimorphians it is side-by-side whilst in the paucituberculates it is head-to-head (Temple-Smith 1987). The morphological study of Horovitz and Sánchez-Villagra (2003) found no characters in support of Ameridelphia. Our results provide little or no support for Ameridelphia and suggest that the root of the marsupial tree is between Didelphimorphia and Paucituberculata + Australidelphia (ML, Bayesian) or between Paucituberculata and Didelphimorphia + Australidelphia (MP). A sister-group relationship between paucituberculates and australidelphians to the exclusion of

didelphimorphians is in agreement with results obtained using complete mitochondrial genomes (Nilsson et al. 2003, 2004), concatenated nuclear genes with fewer taxa (Amrine-Madsen et al. 2003), morphological data (Horovitz and Sánchez-Villagra 2003), and mixed data sets (Asher et al. 2004). Horovitz and Sánchez-Villagra (2003) cited eight cranial and skeletal characters in support of Paucituberculata + Australidelphia. Robust resolution of the root of the marsupial tree will likely await the discovery of rare genomic changes defining particular groups (e.g., indels).

Didelphimorphia

Our analysis included only three didelphimorphian lineages. We recovered *Caluromys* as the sister taxon to a Marmosinae + Didelphinae clade. This result is consistent with previous morphological and molecular studies (Reig et al. 1987; Kirsch et al. 1997; Steiner et al. 2005; Jansa and Voss 2005).

Australidelphia

Delineation of the basal split within Australidelphia has proven difficult to resolve. Several molecular and morphological studies have recovered microbiotheres as nested somewhere within the Australasian radiation (e.g., Kirsch et al. 1991, 1997; Burk et al. 1999; Szalay and Sargis 2001; Horovitz and Sánchez-Villagra 2003; Nilsson et al. 2003, 2004; Munemasa et al. 2006). This is in marked contrast to our nuclear gene results and to the most recent molecular studies (e.g., Amrine-Madsen et al. 2003; Phillips et al. 2006), which consistently recover microbiotheres as the sister-taxon to a monophyletic Australasian clade. This suggests that the Australasian clade can be defined by the presence of an epitympanic sinus in the squamosal above the auditory meatus (Woodburne 1984) and that the 15 supposedly unambiguous apomorphies uniting *Dromiciops* and Diprotodontia given by Horovitz and Sánchez-Villagra (2003) are either convergent and/or plesiomorphic for Australidelphia. Furthermore, our results have significance for understanding the biogeographic history of marsupials and suggest the need for only a single dispersal event from South America to Australia, presumably through Antarctica. A nested position of *Dromiciops* with Australidelphia would suggest multiple dispersion events and/or back migrations.

Within the Australasian clade, we find robust support for all recognized orders. There is also support for a basal split between Diprotodontia and a clade consisting of Peramelemorphia together with Notoryctemorphia and Dasyuromorphia. This result is consistent with the Amrine-Madsen et al. (2003) nuclear analysis and with the combined nuclear plus mitochondrial and mitochondrial only DNA analyses of Phillips et al. (2006).

Dasyuromorphia and Peramelidae

Within Dasyuromorphia we find strong support for Phascogalini (*Phascogale* + *Antechinus*), a sister-group relationship between Phascogalini and Dasyurini (*Dasyurus*), and a basal split between Sminthopsinae and the Dasyurini + Phascogalini clade. These results are consistent with those of nuclear, mitochondrial, and DNA hybridization studies (Kirsch et al. 1990, 1997; Krajewski et al. 2000). In contrast Wroe et al. (2000) recovered a basal split between the Dasyurini and the other dasyurids and Phascogalini paraphyly. Within the Peramelidae the split between Peramelinae (*Perameles* + *Isoodon*) and Echymiperinae (*Echymipera)* is robustly supported. This is consistent with mitochondrial (Westerman et al. 1999, 2001) and DNA hybridization studies (Kirsch et al. 1997).

Diprotodontia

Historically, relationships between sections of Diprotodontia, the largest and most diverse order of Australasian marsupials, have been difficult to resolve. Members of this order are united by several distinctive synapomorphies: diprotodonty, a superficial thymus, syndactyly, a fasciculus aberrans connecting the two hemispheres of the brain (Abbie 1937), and 22 additional morphological apomorphies given by Horovitz and Sánchez-Villagra (2003). Despite the overwhelming morphological evidence in support of this clade, robust molecular support has only recently been found (Amrine-Madsen et al. 2003). Our study adds one diprotodontian family (Burramyidae) to the Amrine-Madsen et al. (2003) data set and finds robust support for Diprotodontia.

The interrelationships of diprotodontian families and superfamilies remain controversial. Kirsch et al. (1997) and Wilson and Reeder (2005) recognized three suborders within the Diprotodontia: Macropodiformes (kangaroos and kin), Phalangeriformes (possums and kin), and Vombatiformes (wombats and koalas). Our results show robust support for Vombatiformes (*Vombatus* + *Phascolarctos*). Molecular support for the monophyly of Vombatiformes is consistent with their hook-shaped spermatozoa (Hughes 1965; Harding 1987), serological data (Kirsch 1968, 1977), DNA hybridization (Springer and Kirsch 1991; Kirsch et al. 1997; Springer et al. 1997a, b), mitochondrial DNA (Burk et al. 1999; Kavanagh et al. 2004; Munemasa et al. 2006), nuclear DNA (Amrine-Madsen et al. 2003), morphology (Horovitz and Sánchez-Villagra 2003), and combined molecular and morphological studies (Asher et al. 2004). We also find robust molecular support for Macropodiformes + Phalangeriformes (= Phalangerida of Aplin and Archer 1987), which is consistent with some morphological evidence, including posterior expansion of the alisphenoid tympanic wing (Winge 1941; Springer and Woodburne 1989), and a recent analysis of mitochondrial genome sequences (Munemasa et al. 2006).

Whereas the monophyly of Macropodiformes was strongly supported, we recovered no support for the monophyly of Australasian possums (i.e., Phalangeriformes). In contrast to DNA hybridization studies (Springer and Kirsch 1991; Kirsch et al. 1997), which supported Australasian possum monophyly (i.e., Phalangeriformes), our results argue against the monophyly of this clade. The lack of molecular support for Phalangeriformes suggests that morphological characters supporting this clade, such as a tube-like ectotympanic that is fused to other bones of the skull (Flannery 1987; Springer and Woodburne 1989), are convergent in phalangeroids and petauroids.

The association of pseudocheirids and petaurids (Petauroidea) has been recovered with molecular data sets (e.g., Kirsch 1977; Kirsch et al. 1997; Osborne and Christidis 2001; Osborne et al. 2002; Amrine-Madsen et al. 2003; Kavanagh et al. 2004), mixed data sets (Asher et al. 2004), and some morphological data sets (e.g., Archer et al. 1999). Kirsch et al. (1997) considered petaurids and pseudocheirids among the most closely related diprotodontian families. However, the morphological analysis of Horovitz and Sánchez-Villagra (2003) recovered *Petaurus* as the sister taxon to all other diprotodontians and Woodburne et al. (1987) suggested the pseudocheirids were the sister group to all other possums. All of our phylogenetic and statistical analyses unambiguously supported Petauroidea, albeit with limited taxon representation.

Determination of the phylogenetic affinities of the burramyids has been less forthcoming. Molecular studies have recovered them as the sister group to the Vombatiformes (Osborne et al. 2002), sister to all other possums (Edwards and Westerman 1995), or sister to the phalangerids (Springer and Kirsch 1991; Kirsch et al. 1997). Gunson et al. (1968) suggested an association with Acrobatidae based on chromosome number. Morphological studies have likewise been

ambiguous. Springer and Woodburne (1989) and Marshall et al. (1990) suggested an association with the petauroids but pedal morphology suggests an association with the acrobatids (Szalay 1994). In the absence of acrobatid exemplars, our analyses suggest that the burramyids are the sister group to the phalangerids, although statistical tests could not discriminate between different phylogenetic hypotheses.

Timeline for marsupial evolution

BEAST and multidivtime comparisons

For groups with a poor fossil record (e.g., Australasian marsupials), molecular estimates of divergence times are of critical importance in helping to understand the evolution, timing, and possible causes of radiation. The present study is the first to employ two different relaxed molecular clock methods to a marsupial nuclear gene data set that includes representatives of all marsupial orders in addition to multiple placental outgroups. Both of the Bayesian dating methods (BEAST, *Multidivtime*) employ a relaxed molecular clock assumption and allow the incorporation of multiple fossil constraints. The methods differ in that BEAST simultaneously estimates the phylogeny and divergence dates, and allows for soft-bounded constraints on calibration nodes, whereas *Multidivtime* requires an optimal tree to be specified and only permits hard-bounded constraints. Even with these differences, there is still good agreement between most divergence dates that were estimated by these methods.

Soft-bounded node constraints have the advantage of allowing sequence data to correct poor node constraints if they exist. We obtained similar divergence time estimates with soft and hard bounds in BEAST analyses, which suggest that fossils are not in conflict with either themselves or the molecular data (Yang and Rannala 2006).

Drummond et al. (2006) analyzed the Amrine-Madsen et al. (2003) marsupial data set. Their MAP topology obtained from a non-partitioned UCLN analysis is different from ours in that *Notoryctes* is the sister taxon to a Peramelidae + Dasyuromorphia clade, *Dromiciops* is the sister taxon to the Diprotodontia, and within Diprotodontia the petauroids are the sister group to the kangaroos. For all of the nodes that are directly comparable to our phylogeny (Fig. 1), the estimated divergence dates are similar (Table 7). Drummond et al. (2006) found that the fastest branch on their tree was evolving 2.7× faster than the slowest branch. Our results for all of the non-partitioned analyses indicate that the branch leading to the Dasyuromorphia (L22) is evolving 2.8× faster than the slowest branch (L15, branch leading to Diprotodontia). In the *Multidivtime* non-partitioned analyses, the *Dasyurus* rate (L19) was 4.7× faster than the *Cercartetus* rate (L4).

Nilsson et al. (2003, 2004) reconstructed phylogenetic relationships among marsupial orders using complete mitochondrial genomes and also inferred a timeline for marsupial evolution with relaxed clock dating methods. The phylogeny of Nilsson et al. (2003, 2004) differs from our Bayesian tree (Fig. 1) by supporting Marsupionta (monotremes plus marsupials), *Dromiciops gliroides* as the sister taxon to a Peramelemorphia + Dasyuromorphia + Notoryctemorphia clade, and Vombatiformes as the sister taxon to Macropodiformes. Nilsson et al. (2004) also used a maximum constraint of 135 Ma for the base of Mammalia, which is much younger than dates suggested by other molecular studies that do not constrain this node (Woodburne et al. 2003). Given these differences, it is not surprising that our estimated dates are generally older than the dates of Nilsson et al. (2003, 2004) (Table 7). Nilsson et al. (2004) estimate the root of Marsupialia at 69 Ma, which is younger than our estimates by approximately 6–20 Ma. They also suggest an age of only 42 Ma for the base of the

Peramelemorphia + Dasyuromorphia + Notoryctemorphia clade, whereas our estimate for this split is 57–62 Ma. The date suggested by our analysis is consistent with putative stem dasyuromorphian *incertae sedis* fossils and the "perameloid" tooth known from 54.6 Ma old Murgon deposits (Godthelp et al. 1999). Nilsson et al. (2003, 2004) also suggest that australidelphians last shared a common ancestor 50–51 Ma. This age is younger than the microbiothere fossil record, which extends as far back as the middle Paleocene (e.g., *Khasia*). Even if one does not accept *Khasia* as a microbiothere, definitive australidelphians from Murgon at 54.6 Ma (Godthelp et al. 1999) indicate an older age for Australidelphia than suggested by Nilsson et al. (2003, 2004).

All of our Bayesian estimates suggest that crown group marsupials had a most recent common ancestor in the Cretaceous, possibly as far back as 89 Ma. These estimates are younger than Hasegawa et al.'s (2003) estimate of ~100 Ma. Benton and Donoghue (2007) provide 30 hard minima and soft maxima fossil constraints for dating the tree of life. One of their proposed dates is the opossum–kangaroo split, i.e., the ameridelphian–australidelphian split. They suggest a hard minimum of 61.5 Ma and a soft maximum of 71.2 Ma. They base the minimum on the newly described probable Paleocene polydolopimorph, *Cocatherium* (Goin et al. 2006), and claim this is the oldest known crown-group marsupial. However, if these authors accept that *Cocatherium* is a polydolopimorph, and that polydolopimorphs are crown-group metatherians, then this cannot be the oldest member of crown-group Marsupialia as the polydolopimorph fossil record extends back to the Judithian (74–79 Ma; Case et al. 2005). In contrast, Goin et al. (2006) recovered Polydolopimorphia as stem metatherians rather than as members of the crown-group. Case et al. (2005) found that *Nortedelphys* (Lancian) was the oldest crown-group metatherian. Our estimated dates for the base of Marsupialia are consistent with younger fossil dates given that the fossil record usually underestimates the true time of divergence for a given node.

Our molecular data suggest an Eocene date for the origin of the living didelphimorphians. Our estimates are slightly younger than those obtained by Steiner et al. (2005) using a single nuclear gene (transthyretin), and approximately 14 Ma younger than complete mitochondrial genome estimates (Nilsson et al. 2004; Table 7). Steiner et al. (2005) attributed the middle Eocene origin of living didelphids to one of the first definitive phases of the Andean uplift, which caused a cooling and drying out of the woodland habitats. Our divergence time estimate for the Didelphinae + Marmosinae split is consistent with this interpretation.

A secure phylogeny for Australidelphia is of paramount importance for understanding the early biogeographic history of this group. As previously mentioned, some molecular and morphological studies recover microbiotheres as nested somewhere within the Australasian radiation (e.g., Kirsch et al. 1991, 1997; Nilsson et al. 2003, 2004; Horovitz and Sánchez-Villagra 2003). The nesting of Microbiotheria within the Australasian marsupial radiation is in marked contrast to our results above and to other recent molecular studies (e.g., Amrine-Madsen et al. 2003; Phillips et al. 2006) that recover microbiotheres as the sister-taxon to a monophyletic Australasian clade. A sister relationship between microbiotheres and Australasian marsupials, together with our estimated dates of divergence (60–65 Ma) for this split, suggest that the paleobiogeography of Australidelphia involves a single dispersal event from South America to Australia via Antarctica. Monophyly of the Australasian marsupials makes for a much simpler biogeographic history and may explain the complete absence of Australasian taxa from the middle Eocene deposits of Antarctica—despite the postulated importance of Antarctica as a venue for the early diversification of Gondwanan marsupials. Furthermore, the necessity of a pan-Gondwanan distribution of marsupials before the separation of Antarctica and Australia with subsequent vicariance and extinction is not required. The most recent cladistic analysis of early metatherians has recovered the South

Table 7 Molecular divergence dates from other relaxed clock studies

	Nilsson et al. 2003[a]	Nilsson et al. 2004[b]	Drummond et al. 2006[c]
Node			
1. Macropodidae + Potoroidae	N/A	20	N/A
4. Vombatiformes	N/A	N/A	33
5. Macropodiformes + Phalangeroidea	33	N/A	N/A
6. Macropodiformes + Phalangeriformes	N/A	N/A	41
7. Diprotodontia	42	46	48
9. Dasyurini + Phascogalini	N/A	N/A	15
10. Dasyuridae	N/A	20	25
11. *Notoryctes* + Dasyuridae	N/A	39	N/A
13. Peramelidae	N/A	11	16
14. Peramelidae + *Notoryctes* + Dasyuridae	N/A	42	62
16. Australidelphia	51	51	66
17. Paucituberculata	29	31	16
18. All marsupials but Didelphimorphia	62	61	N/A
19. Didelphinae+ Marmosinae	52	52	29
20. Didelphimorphia	NA	NA	39
21. Marsupialia	64	69	85

Dates are in millions of years

[a] Dates are estimated from their Fig. 3

[b] Dates are estimated from their Fig. 3

[c] Nodes numbers correspond to our Fig. 1. Nodes not shown were not present in the data sets listed above.

American species *Chulpasia mattaueri* as a stem australidelphian (Goin et al. 2006) and there appears to be an undescribed species from the Murgon deposit (54.6 Ma) in Australia (Sigé et al. 1995). *Chulpasia mattaueri* is known from the Umayo Formation, which according to Sigé et al. (1995) is most consistent in age with chron 24 (latest Paleocene or earliest Eocene). These fossils are slightly younger than our expected date for stem australidelphians, but nonetheless are consistent with our study in that we would expect the fossil record to underestimate the true times of divergence.

Australasian marsupials

As currently understood the Australian plate migrated northward after its complete separation from Antarctica and by the middle Oligocene had collided with the Asian plate in the New Guinean region resulting in the emergence of New Guinea and the uplift of the New Guinean Highlands. By the late Oligocene the Sepik Province had docked with the emerging land mass. The rising of the New Guinean Central Cordillera along with the emergence of Timor and the establishment of the circumpolar current to the south of Australia had a major effect on climates across Australia and changed the drainage patterns of central Australia leading to a progressive drying. In Australia, the average temperature was lowered and the rainforests began to be replaced by drier forest types and more open country (White 1994; Heads 2002). By the late Miocene, xeric and mesic habitats predominated much of central Australia. By the late Pliocene there were periods of prolonged cooling.

Case (1989) suggested that all of the major lineages within the Diprotodontia were present in the Eocene. In the late Eocene the dominant podocarp forests began to be replaced by *Nothofagus* dominated forests, which "opened" up the forest canopy. This floristic change may have promoted the radiation of the arboreal possum species in the middle to late Eocene. Radiation of the terrestrial forms probably did not occur until the forests began to open up with an herbaceous angiosperm understorey in the Oligocene. Megirian et al. (2004) and Adam (1999) provide evidence that rainforests were almost certainly not the predominant vegetation in the North Territory, South Australia, and NW Queensland from the late Oligocene onward. It is then probable that the terrestrial australidelphians began to radiate before the late Oligocene. As the grasslands spread concurrently with the "drying out" of Australia in the late Miocene and early Pliocene, more specialized herbivores such as macropodine grazers evolved to occupy new ecological niches. Our estimated dates of divergence are congruent with such scenarios. The terrestrial dasyuromorphians and peramelemorphians radiate in the late Oligocene and early Miocene. All of the major diprotodontian lineages in our study were present in the early Tertiary. The clades of arboreal possums (Petauroidea and Phalangeroidea) emerged before the late Oligocene/early Miocene. The split between the terrestrial/fossorial vombatid ancestor and the arboreal phascolarctids again occurred before the canopy began to open up. Furthermore, the split between the potoroids (non-grazing kangaroos) and the predominantly grazing kangaroos occurred ~14–17 Ma, later than any of the other interfamilial divergences within Diprotodontia.

Unrepresented basal branch lengths

The UBBL technique for estimating the completeness of the fossil record has previously been applied to two mammalian clades—Chiroptera (Teeling et al. 2005) and Felidae (Johnson et al. 2006). A similar method has also been applied to the Echinoidea (Smith et al. 2006). Table 6 shows that the percentage of the UBBL that is missing, as well as the average percentage missing per lineage, is higher for Felidae and Chiroptera than for Marsupialia. Felids are carnivores and marsupials are predominantly herbivores and omnivores. In general, herbivores have a greater biomass (being lower on the food chain) and thus have a correspondingly higher chance of fossilization. In the case of bats, many taxa live in tropical environments where preservation rates are low. Small body size and fragile bones also help to explain the poor fossil record of bats.

Table 6 shows that the unrepresented basal branch length is more incomplete or approximately equivalent for both internal and external lineages in all three clades. This finding is consistent with the general rule that the fossil record becomes more incomplete further back in time. The lack of diagnostic characters for internal branches, which represent direct ancestors and/or extinct side branches, may also contribute to the greater unrepresented basal branch length for internal branches than for external branches.

Among marsupials, it is perhaps surprising that our estimates suggest that the Australasian marsupial record is approximately as complete as the South American record even though the literature is filled with claims that underscore the incompleteness of the Australasian fossil record. However, marsupials have inhabited South America for a longer period of time and, as noted above, the completeness of the fossil record decreases with increasing time spans. Also, estimates for the incompleteness of the South American record may diminish pending the phylogenetic placement of key fossil taxa. We recovered a date of 35–39 Ma for the didelphid–caluromyid split, which resulted in an estimate of 100% incompleteness for the long branch (branch L38, Fig. 2) leading to *Caluromys*. However, some authors (Reig et al. 1987; McKenna and Bell 1997) have suggested that the early Miocene genus *Pachybiotherium*

belongs to Caluromyinae, which would reduce the incompleteness of this lineage by approximately 50%.

Our estimates for the completeness of the South American record assume that several Late Cretaceous and early Paleocene fossils are crown group marsupials (Goin et al. 2006). If Rougier et al. (1998), Luo et al. (2003), Horovitz and Sánchez-Villagra (2003), and Sánchez-Villagra et al. (2007) are correct in their contention that there are no known crown group marsupials from the Late Cretaceous or early Paleocene, then the completeness of the record for South American orders becomes even more impoverished.

Among the South American marsupial orders, the apparent completeness of the microbiothere record is surprising if the single living species (*Dromiciops gliroides*) is taken as an analog for all microbiotheres. *D. gliroides* has a restricted geographic distribution and lives in an environment that is not conducive to fossilization. The completeness of the microbiothere fossil record is based on the genus *Khasia*, which is known from 60.4 to 59.2 Ma old Bolivian deposits. Although *Khasia* is believed to be a microbiothere (e.g., Woodburne and Case 1996; Marshall et al. 1997), Wroe et al. (2000) have called the identification of fossil microbiotheres into question. These authors argue that the characters used to diagnose microbiotheres are essentially symplesiomorphic or convergent and that microbiotheres are not well diagnosed dentally. If true, this would complicate the correct identification of fossil species such as *Khasia* that are known only from dental elements. However, Wroe et al. (2000) allow for the possibility that these fossils are microbiotheres.

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References

Abbie AA (1937) Some observations on the major subdivisions of the Marsupialia, with special reference to the position of the Peramelidae and Caenolestidae. J Anat 71:424–436

Adam P (1999) Australian rainforests. Oxford University Press, Oxford

Amrine-Madsen H, Scally M, Westerman M, Stanhope MJ, Krajewski C, Springer MS (2003) Nuclear gene sequences provide evidence for the monophyly of australidelphian marsupials. Mol Phylogenet Evol 28:186–196

Aplin KP, Archer M (1987) Recent advances in marsupial systematics with a new syncretic classification. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp xv–xxii

Archer M (1982) Review of the dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. In: Archer M (ed) Carnivorous marsupials. Royal Zoological Society of New South Wales, Mossman, New South Wales, pp. 397–443

Archer M, Hand SJ (2006) The Australian marsupial radiation. In: Merrick JR, Archer M, Hickey GM, Lee MSY (eds) Evolution and biogeography of Australasian vertebrates. Auscipub, New South Wales, pp 575–646

Archer M, Kirsch JAW (2006) The evolution and classification of marsupials. In: Armati PJ, Dickman CR, Hume ID (eds) Marsupials. Cambridge University Press, New York, pp 1–21

Archer M, Wade M (1976) Results of the Ray E Lemley Expeditions: part 1 the Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland Australia. Mem Qld Mus 17:379–398

Archer M, Tedford RH, Rich TH (1987) The Pilkipildridae, a new family and new species of? petauroid possums (Marsupialia: Phalangerida) from the Australian Miocene. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 607–628

Archer M, Arena R, Bassarova M, Black K, Brammall J, Cooke B, Creaser P, Crosby K, Gillespie A, Godthelp H, Gott M, Hand SJ, Kear B, Krikmann A, Mackness B, Muirhead J, Musser A, Myers T, Pledge N, Wang Y, Wroe S (1999) The evolutionary history and diversity of Australian mammals. Aust Mammal 21:1–45

Asher RJ, Horovitz I, Sánchez-Villagra MR (2004) First combined cladistic analysis of marsupial mammal interrelationships. Mol Phylogenet Evol 33:240–250

Benton MJ, Ayala FJ (2003) Dating the tree of life. Science 300:1698–1700
Benton MJ, Donoghue PCJ (2007) Paleontological evidence to date the tree of life. Mol Biol Evol 24:26–53
Brammall JR (1998) A new petauroid possum from the Oligo-Miocene of Riversleigh, northwestern Queensland. Alcheringa 23:31–50
Brammall J, Archer M (1999) Living and extinct petaurids, acrobatids, tarsipedids and burramyids (Marsupialia): relationships and diversity through time. Aust Mammal 21:24–25
Burk A, Westerman M, Kao DJ, Kavanagh JR, Springer MS (1999) An analysis of marsupial interordinal relationships based on 12S rRNA, tRNA valine, 16S rRNA, and cytochrome b sequences. J Mammal Evol 6:317–334
Case JA (1984) A new genus of Potoroinae (Marsupialia Macropodidae) from the Miocene Ngapakaldi Local Fauna, South Australia, and a definition of the Potoroinae. J Paleontol 58:1074–1086
Case JA (1989) Antarctica: The effect of high latitude heterochroneity on the origin of the Australian marsupials. In: Crame JA (ed) Origins and evolution of the Antarctic biota. Geological Society Special Publication 47, pp 217–226
Case JA (2001) Turnover of bandicoots in the Oligo-Miocene of South Australia. J Vertebr Paleontol Supp 21:39A
Case JA, Goin FJ, Woodburne MO (2005) "South American" marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. J Mammal Evol 12:461–494
Cooke BN (2006) Kangaroos. In: Merrick JR, Archer M, Hickey GM, Lee MSY (eds) Evolution and biogeography of Australasian vertebrates. Auscipub, New South Wales, pp 647–672
Cooke B, Kear B (1999) Evolution and diversity of kangaroos (Macropodoidea, Marsupialia). Aust Mammal 21:27–29
Cozzuol MA, Goin F, Reyes MDL, Ranzi A (2006) The oldest species of *Didelphis* (Mammalia, Marsupialia, Didelphidae), from the late Miocene of Amazonia. J Mammal 87:663–667
Crochet J-Y, Sigé B (1993) Les mammifères de Chulpas (Formation Umayo, transition Crétacé-Tertiaire, Pérou): données préliminaires. Documents Lab Géol Faculté Sci Lyon 125:97–107
Crosby K, Bassarova M, Archer M, Carbery K (2004) Fossil possums in Australasia: discovery, diversity and evolution. In: Goldingay RL, Jackson SM (ed) The biology of Australian possums and gliders. Beatty, Sydney, pp 161–176
Czaplewski NJ, Masanaru T, Naeher, TM, Shigehara N, Setoguchi T (2003) Additional bats from the middle Miocene La Venta fauna of Colombia. Rev Acad Colomb Cienc 27:263–282
De Queiroz A (1993) For consensus (sometimes). Syst Biol 42:368–372
Drummond AJ, Rambaut A (2003) BEAST version 14 [computer program] Available http://evolvezoooxacuk/beast Accessed January 2007
Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. PLoS Biol 4:699–710
Edwards D, Westerman M (1995) The molecular relationships of possum and glider families as revealed by DNA–DNA hybridisations. Aust J Zool 43:231–240
Farris JS, Kallersjo M, Kluge AG, Bult C (1994) Testing significance of incongruence. Cladistics 10:315–319
Flannery T (1987) The relationships of the macropodoids (Marsupialia) and the polarity of some morphological features within the Phalangeriformes. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 741–748
Flannery TF (1989) Phylogeny of the Macropodoidea; a case study in convergence. In: Grigg GC, Jarman PJ, Hume ID (eds) Kangaroos, wallabies and rat–kangaroos. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 1–46
Godthelp H, Wroe S, Archer M (1999) A new marsupial from the early Eocene Tingamarra local Fauna of Murgon, southeastern Queensland: a prototypical Australian marsupial? J Mammal Evol 6:289–313
Goin FJ (1997) New clues for understanding Neogene marsupial radiations. In: Kay RF (ed) Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia. Smithsonian Institution, Washington, DC, pp 187–206
Goin FJ, Pascual R, Tejedor MF, Gelfo JN, Woodburne MO, Case JA, Reguero MA, Bond M, Lopez GM, Cione AL, Udrizar Sauthier D, Balarino L, Scasso RA, Medina FA, Ubaldon MC (2006) The earliest Tertiary therian mammal from South America. J Vertebr Paleontol 26:505–510
Gradstein FM, Ogg JG, Smith AG, 39 co-authors (2004) A geologic timescale. Cambridge University Press, Cambridge
Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst Biol 52:696–704
Gunson MM, Sharman GB, Thomson JA (1968) The affinities of *Burramys* (Marsupialia: Phalangeroidea) as revealed by its chromosomes. Aust J Sci 31:40–41
Harding HR (1987) Interrelationships of the families of the Diprotodontia—a view based on spermatozoan ultrastructure. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 195–216

Hasegawa M, Thorne JL, Kishino H (2003) Time scale of eutherian evolution estimated without assuming a constant rate of molecular evolution. Genes Genet Syst 78:267–283
Heads M (2002) Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. J Biogeog 29:261–283
Hedges SB, Kumar S (2004) Precision of molecular time estimates. Trends Gen 20:242–247
Hershkovitz P (1992) Ankle bones: the Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. Bonn Zool Beit 43:181–213
Horovitz I, Sánchez-Villagra MR (2003) A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19:181–212
Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755
Hughes RL (1965) Comparative morphology of spermatozoa from five families. Aust J Zool 13:533–543
Jansa SA, Voss RS (2005) Phylogenetic relationships of the marsupial genus *Hyladelphys* based on nuclear gene sequences and morphology. J Mammal 86:853–865
Johnson WE, Eizirik E, Pecon-Slattery J, Murphy WJ, Antunes A, Teeling E, O'Brien SJ (2006) The late Miocene radiation of modern Felidae: a genetic assessment. Science 311:73–77
Kavanagh JR, Burk-Herrick A, Westerman M, Springer MS (2004) Relationships among families of Diprotodontia (Marsupialia) and the phylogenetic position of the autapomorphic honey possum (*Tarsipes rostratus*). J Mammal Evol 11:207–222
Kielan-Jaworowska Z, Cifelli RL, Luo Z-X (2004) Mammals from the age of dinosaurs: origins, evolution, and structure. Columbia University Press, New York
Kirsch JA (1968) Prodromus of the comparative serology of Marsupialia. Nature 217:418–420
Kirsch JAW (1977) The comparative serology of Marsupialia and a classification of marsupials. Aust J Zool, Supp Ser 52:1–152
Kirsch JAW, Palma RE (1995) DNA/DNA hybridization studies of carnivorous marsupials. V. A further estimate of relationships among opossums (Marsupialia: Didelphidae). Mammalia 59:403–425
Kirsch JAW, Krajewski C, Springer MS, Archer M (1990) DNA–DNA hybridization studies of carnivorous marsupials. II. Relationships among dasyurids (Marsupialia: Dasyuridae). Aust J Zool 38:673–696
Kirsch JAW, Dickerman AW, Reig OA, Springer MS (1991) DNA hybridization evidence for the Australasian affinity of the American marsupial *Dromiciops australis.* Proc Natl Acad Sci USA 88:10465–10469
Kirsch JAW, Lapointe F-J, Springer MS (1997) DNA-hybridisation studies of marsupials and their implications for metatherian classification. Aust J Zool 45:211–280
Kishino H, Hasegawa M (1989) Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data and the branching order in Hominoidea. J Mol Evol 29:170–179
Kishino H, Thorne JL, Bruno WJ (2001) Performance of a divergence time estimation method under a probabilistic model of rate evolution. Mol Biol Evol 18:352–361
Krajewski C, Young J, Buckley L, Woolley PA, Westerman M (1997) Reconstructing the evolutionary radiation of dasyurine marsupials with cytochrome b, 12S rRNA, and protamine P1 gene trees. J Mammal Evol 4:217–236
Krajewski C, Blacket MJ, Westerman M (2000) DNA sequence analysis of familial relationships among dasyuromorphian marsupials. J Mammal Evol 7:95–108
Kumar S, Hedges SB (1998) A molecular timescale for vertebrate evolution. Nature 392:917–920
Langford RP, Wilford GE, Truswell EM, Isern AR (1995) Palaeogeographic atlas of Australia, Volume 10 Cainozoic. Australian Geological Survey Organization, Canberra
Long J, Archer M, Flannery TF, Hand SJ (2002) Prehistoric mammals of Australia and New Guinea: one hundred million years of evolution. University of New South Wales Press, Sydney
Luckett WP (1994) Suprafamilial relationships within Marsupialia: resolution and discordance from multidisciplinary data. J Mammal Evol 2:255–283
Luo Z-X, Ji Q, Wible JR, Yuan C-X (2003) An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302:1934–1940
Mackness BS, Whitehead PW, McNamara GC (2000) New potassium–argon basalt date in relation to the Pliocene Bluff Downs local fauna, northern Australia. Aust J Earth Sci 47:807–811
Marshall LG (1976) New didelphine marsupials from the La-Venta Fauna Miocene of Colombia South America. J Paleontol 50:402–418
Marshall LG, de Muizon C (1988) The dawn of the age of mammals in South America. Natl Geograph Res 4:23–55
Marshall LG, Case JA, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. In: Genoways HH (ed) Current mammalogy, Vol 2. Plenum, New York, pp 433–506
Marshall LG, Sempere T, Butler RF (1997) Chronostratigraphy of the mammal-bearing Paleocene of South America. J South Am Earth Sci 10:49–70
McKenna MC, Bell SK (1997) Classification of mammals above the species level. Columbia University Press, New York

Megirian D, Murray P, Schwartz L, Vonderborsch C (2004) Late Oligocene Kangaroo Well Local Fauna from the Ulta Limestone (new name), and climate of the 'Miocene oscillation' across central Australia. Aust J Earth Sci 51:701–741

Muizon C de, Cifelli RL (2001) A new basal "didelphoid" (Marsupialia, Mammalia) from the early Paleocene of Tiupampa (Bolivia). J Vertebr Paleontol 21:87–97

Muirhead J, Dawson L, Archer M (1997) Perameles bowensis, a new species of Perameles (Peramelemorphia: Marsupialia) from the Pliocene faunas of Bow and Wellington Caves, New South Wales. Proc Lin Soc NSW 117:163–173

Müller J, Reisz RR (2005) Four well-constrained calibration points from the vertebrate fossil record for molecular clock estimates. BioEssays 27:1069–1075

Munemasa M, Nikaido M, Donnellan S, Austin CC, Okada N, Hasegawa M (2006) Phylogenetic analysis of diprotodontian marsupials based on complete mitochondrial genomes. Genes Genet Syst 81:181–191

Murphy WJ, Eizirik E, O'Brien SJ, Madsen O, Scally M, Douady CJ, Teeling E, Ryder OA, Stanhope MJ, de Jong WW, Springer MS (2001) Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294:2348–2351

Murray PF, Megirian D (1992) Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. Beagle 9:195–218

Myers TJ, Archer M (1997) *Kuterintja ngama* (Marsupialia, Ilariidae): A revised systematic analysis based on material from the late Oligocene of Riversleigh, northwestern Queensland. Mem Qld Mus 41:379–392

Nilsson MA, Gullberg A, Spotorno AE, Arnason U, Janke A (2003) Radiation of extant marsupials after the K/T boundary: evidence from complete mitochondrial genomes. J Mol Evol 57:S3–S12

Nilsson MA, Arnason U, Spencer PBS, Janke A (2004) Marsupial relationships and a timeline for marsupial radiation in south Gondwana. Gene 340:189–196

Osborne MJ, Christidis L (2001) Molecular phylogenetics of Australo-Papuan possums and gliders (Family Petauridae). Mol Phylogenet Evol 20:211–224

Osborne MJ, Christidis L, Norman JA (2002) Molecular phylogenetics of the Diprotodontia (kangaroos, wombats, koala, possums, and allies). Mol Phylogenet Evol 25:219–228

Penny D, Hasegawa M, Waddell PJ, Hendy MD (1999) Mammalian evolution: timing and implications from using the log determinant transform for proteins of differing amino acid composition. Syst Biol 48:76–93

Phillips MJ, Lin Y-H, Harrison GL, Penny D (2001) Mitochondrial genomes of a bandicoot and a brushtail possum confirm the monophyly of australidelphian marsupials. Proc R Soc Lond B 268:1533–1538

Phillips MJ, McLenachan PA, Down C, Gibb GC, Penny D (2006) Combined mitochondrial and nuclear DNA sequences resolve the interrelations of the major Australasian marsupial radiations. Syst Biol 55:122–137

Pledge NS (1990) The upper fossil fauna of the Henschke fossil cave, Naracoorte, South Australia. Mem Queensl Mus 28:247–262

Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution. Bioinformatics 14:817–818

Price GJ (2004) Fossil bandicoots (Marsupialia, Peramelidae) and environmental change during the Pleistocene on the Darling Downs, southeastern Queensland, Australia. J Syst Palaeontol 2:347–356

Prideaux G (2004) Systematics and evolution of the sthenurine kangaroos. Univ Calif Pub Geol Sci 146:i–xvii, 1-623, Berkeley, University of California Press

Rambaut A (1996) Se-Al: sequence alignment editor [computer editor]. Available at http://evolvezoooxacuk/

Rambaut A, Drummond AJ (2003) Tracer version 12 [computer program]. Available http://evolvezoooxacuk Accessed August 2006

Reig OA (1952) Descripcion previa de nuevos ungulados y marsupiales fosiles del Plioceno y del eocuartario Argentinos 1:119–129

Reig OA (1958) Notas para una actualizacion del conocimiento de la fauna de la formacion Chapadmala II Amphibia, Reptilia, Aves, Mammalia (Marsupialia: Didelphidae, Borhyaenidae). Acta Geol Lilloana, 2:255–283

Reig OA, Kirsch JAW, Marshall LG (1987) Systematic relationships of the living and Neocenozoic American "opossum-like" marsupials (Suborder Didelphimorphia) with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 1–90

Reisz RR, Müller J (2004) Molecular timescales and the fossil record: a paleontological perspective. Trends Gen 20:237–241

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574

Rougier GW, Wible JR, Novacek MJ (1998) Implications of *Deltatheridium* specimens for early marsupial history. Nature 396:459–463

Sánchez-Villagra MR, Wible JR (2002) Patterns of evolutionary transformation in the petrosal bone and some basicranial features in marsupial mammals, with special reference to didelphids. J Zool Syst Evol Res 40:26–45

Sánchez-Villagra MR, Ladevèze S, Horovitz I, Argot C, Hooker JJ, Macrini TE, Martin T, Moore-Fay S, Muizon C de, Schmelzle T, Asher RJ (2007) Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. Biol Letters 3:318–322

Sanderson MJ (2002) Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Mol Biol Evol 19:101–109

Schwartz L (2006) A new species of bandicoot from the Oligocene of Northern Australia and implications of bandicoots for correlating Australian Tertiary mammal faunas. Palaeontol 49:991–998

Shimodaira H (2002) An approximately unbiased test of phylogenetic tree selection. Syst Biol 51:492–508

Shimodaira H, Hasegawa M (1999) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol Biol Evol 16:1114–1116

Sigé B, Archer M, Godthelp H, Hand S, Crochet J-Y (1995) Peruvian–Australian Paleogene mammal connection. Cavep's 95, Fifth Conference on Australian Vertebrate Evolution, Palaeontology and Systematics, Canberra, Programme and Abstracts, 2

Sigé B, Sempere T, Butler RF, Marshall LG, Crochet J-Y (2004) Age and stratigraphic reassessment of the fossil-bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record, and paleomagnetism. Geobios 37:771–794

Simpson GG (1974) Notes on Didelphidae (Mammalia, Marsupialia) from the Huayquerian (Pliocene) of Argentina. Am Mus Novitates 2559:1–15

Smith AB, Pisani D, Mackenzie-Dodds JA, Stockley B, Webster BL, Littlewood TJ (2006) Testing the molecular clock: molecular and paleontological estimates of divergence times in the Echinoidea (Echinodermata). Mol Biol Evol 23:1832–1851

Springer MS (1997) Molecular clocks and the timing of the placental and marsupial radiations in relation to the Cretaceous–Tertiary boundary. J Mammal Evol 4:285–302

Springer MS, Kirsch JAW (1991) DNA hybridization, the compression effect, and the radiation of diprotodontian marsupials. Syst Zool 40:131–151

Springer MS, Woodburne MO (1989) The distribution of some basicranial characters within the Marsupialia and a phylogeny of the Phalangeriformes. J Vertebr Paleontol 9:210–221

Springer MS, Kirsch JAW, Case JA (1997a) The chronicle of marsupial evolution. In: Givnish TJ, Sytsma KJ (eds) Molecular evolution and adaptive radiation. Cambridge University Press, New York, pp 129–161

Springer MS, Burk A, Kavanagh JR, Waddell VG, Stanhope MJ (1997b) The interphotoreceptor retinoid binding protein gene in therian mammals: implications for higher level relationships and evidence for loss of function in the marsupial mole. Proc Natl Acad Sci USA 94:13754–13759

Springer MS, Westerman M, Kavanagh JR, Burk A, Woodburne MO, Kao DJ, Krajewski C (1998) The origin of the Australasian marsupial fauna and the phylogenetic affinities of the enigmatic monito del monte and marsupial mole. Proc R Soc Lond B 265:2381–2386

Steiner C, Tilak M, Douzery JP, Catzeflis FM (2005) New DNA data from a transthyretin nuclear intron suggest an Oligocene to Miocene diversification of living South America opossums (Marsupialia: Didelphidae). Mol Phylogenet Evol 35:363–379

Swofford DL (2002) PAUP* Phylogenetic analysis using parsimony (*and other methods), Version 4. Sinauer Associates, Sunderland, Massachusetts

Swofford DL, Olsen GJ, Waddell PJ, Hillis DM (1996) Phylogenetic inference. In: Hillis DM, Moritz C, Mable BK (eds) Molecular systematics, 2nd edn. Sinauer, Sunderland, MA, pp 407–514

Szalay FS (1982) A new appraisal of marsupial phylogeny and classification. In: Archer M (ed) Carnivorous marsupials. Royal Zoological Society of New South Wales, Sydney, pp 621–640

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge University Press, New York

Szalay FS, Sargis EJ (2001) Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaborai (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas 23:139–302

Tedford RH, Kemp NR (1998) Oligocene marsupials of the Geilston Bay local fauna, Tasmania. Am Mus Novitates 3244:1–22

Teeling EC, Madsen O, Van Den Bussche RA, de Jong WW, Stanhope MJ, Springer MS (2002) Microbat paraphyly and the convergent evolution of a key innovation in Old World rhinolophoid microbats. Proc Natl Acad Sci USA 99:1431–1436

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584

Temple-Smith PD (1987) Sperm structure and marsupial phylogeny. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 171–193

Thorne JL, Kishino H (2002) Divergence time and evolutionary rate estimation with multilocus data. Syst Biol 51:689–702

Thorne JL, Kishino H, Painter IS (1998) Estimating the rate of evolution of the rate of molecular evolution. Mol Biol Evol 15:1647–1657

Turnbull WD, Lundelius EL Jr, Archer M (2003) Dasyurids, perameloids, phalangeroids, and vombatoids from the early Pliocene Hamilton fauna, Victoria, Australia. Bull Am Mus Nat Hist 279:513–540

Warburton NM (2003) Functional morphology and evolution of marsupial moles (Marsupialia; Notoryctemorphia). Thesis, The University of Western Australia

Westerman M, Springer MS, Dixon J, Krajewski C (1999) Molecular relationships of the extinct pig-footed bandicoot *Chaeropus ecaudatus* (Marsupialia: Perameloidea) using 12S rRNA sequences. J Mammal Evol 6:271–288

Westerman M, Springer MS, Krajewski C (2001) Molecular relationships of the New Guinean bandicoot genera *Microperoryctes* and *Echymipera* (Marsupialia:Peramelina). J Mammal Evol 8:93–105

White ME (1994) After the greening: the browning of Australia. Kangaroo, New South Wales

Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference. The Johns Hopkins University Press, Baltimore

Winge H (1941) The inter-relationships of the mammalian genera, Vol 1. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata. CA Reitzels Forlag, Copenhagen

Woodburne MO (1984) Families of marsupials: relationships, evolution, and biogeography. In: Broadhead TW (ed) Mammals: notes for a short course. Univ Tenn Dept Geol Sci Stud Geol 8, pp 48–71

Woodburne MO, Case JA (1996) Dispersal, vicariance, and the Late Cretaceous to early Tertiary land mammal biogeography from South America to Australia. J Mammal Evol 3:121–161

Woodburne MO, Tedford RH, Archer M, Turnbull WD, Plane MD, Lundelius EL Jr (1985) Biochronology of the continental mammal record of Australia and New Guinea. Spec Publ S Aust Dept Mines Energy 5:347–364

Woodburne MO, Tedford RH, Archer M (1987) New Miocene pseudocheirids (Pseudocheiridae: Marsupialia) from South Australia. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty and Sons, Chipping Norton, New South Wales, pp 639–679

Woodburne MO, MacFadden BJ, Case JA, Springer MS, Pledge NS, Power JD, Woodburne JM, Springer KB (1993) Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (late Oligocene) of South Australia. J Vertebr Paleontol 13:483–515

Woodburne MO, Rich TH, Springer MS (2003) The evolution of tribospheny and the antiquity of mammalian clades. Mol Phylogenet Evol 28:360–385

Wroe S (1998) The geologically oldest dasyurid, from the Miocene of Riversleigh, north-west Queensland. Palaeontol 42:501–527

Wroe S (2003) Australian marsupial carnivores: recent advances in palaeontology. In: Jones M, Dickerman C, Archer M (eds) Predators with pouches: the biology of marsupial carnivores. CSIRO, Collingwood, Australia, pp 102–123

Wroe S, Mackness BS (2000) Additional material of *Dasyurus dunmalli* from the Pliocene Chinchilla Local Fauna of Queensland and its phylogenetic implications. Mem Queensl Mus 45:641–645

Wroe S, Ebach M, Ahyong S, Muizon C de, Muirhead J (2000) Cladistic analysis of dasyuromorphian (Marsupialia) phylogeny using cranial and dental characters. J Mammal 81:1008–1024

Yang Z, Rannala B (2006) Bayesian estimation of species divergence times under a molecular clock using multiple calibrations with soft bounds. Mol Biol Evol 23:212–226