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Christopher A. Emerling

Michael Westerman


Carey Krajewski

Benjamin P. Kear

Lucy Meehan

See next page for additional authors

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Authors

Christopher A. Emerling, Michael Westerman, Carey Krajewski, Benjamin P. Kear, Lucy Meehan, Robert W. Meredith, and Mark S. Springer



Phylogenetic relationships of dasyuromorphian marsupials revisited

MICHAEL WESTERMAN^{1*}, CAREY KRAJEWSKI², BENJAMIN P. KEAR³,
LUCY MEEHAN¹, ROBERT W. MEREDITH⁴, CHRISTOPHER A. EMERLING⁴ and
MARK S. SPRINGER⁴

¹Genetics Department, LaTrobe University, Melbourne, Vic. 3086, Australia

²Zoology Department, Southern Illinois University, Carbondale, IL 62901, USA

³Paleobiology Programme, Department of Earth Sciences, Uppsala University, Villavagen 16, SE-752 36 Uppsala, Sweden

⁴Department of Biology, University of California, Riverside, CA 92521, USA

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We reassessed the phylogenetic relationships of dasyuromorphians using a large molecular database comprising previously published and new sequences for both nuclear (nDNA) and mitochondrial (mtDNA) genes from the numbat (*Myrmecobius fasciatus*), most living species of Dasyuridae, and the recently extinct marsupial wolf, *Thylacinus cynocephalus*. Our molecular tree suggests that Thylacinidae is sister to Myrmecobiidae + Dasyuridae. We show robust support for the dasyurid intrafamilial classification proposed by Krajewski & Westerman as well as for placement of most dasyurid genera, which suggests substantial homoplasy amongst craniodental characters presently used to generate morphology-based taxonomies. Molecular dating with relaxed molecular clocks suggests that dasyuromorphian cladogenesis began in the Eocene, and that all three dasyuromorphian families originated prior to the end of this epoch. Radiation within Thylacinidae and Dasyuridae had occurred by the middle to late Oligocene, consistent with recognition of primitive thylacinids (e.g. *Badjcinus turnbulli*) in the later Oligocene and of putative dasyurids (e.g. *Barinya wangala*) by the early Miocene. We propose that all four extant dasyurid tribes were in existence by the early Miocene and that most modern dasyurid genera/species were established before the later Miocene. This is in marked contrast to the popularly accepted advocacy of their origins in the latest Miocene–early Pliocene.

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INTRODUCTION

The marsupial order Dasyuromorphia represents the principal radiation of endemic insectivorous mammals within Australasia. They range in body size from the 2–10 g *Ningauai* spp. and *Planigale* spp. to the ~ 10 kg Tasmanian devil (*Sarcophilus harrisi*: Cuvier, 1837) and a maximum of about 30 kg for the

recently extinct thylacine or ‘marsupial wolf’ (*Thylacinus cynocephalus*: Harris, 1808). Dasyuromorphia, as currently understood taxonomically, comprises the largely fossil-based Thylacinidae, the monospecific Myrmecobiidae, and the speciose Dasyuridae. These long-recognized family-level clades have been the focus of numerous morphological and molecular phylogenetic studies and yet their higher-level systematics remains unclear. Moreover, the ubiquitous retention of plesiomorphic dental and basicranial character states, specialized diets, and an inadequate fossil record [particularly for key taxa such as the numbat (*Myrmecobius*

*Corresponding author.

E-mail: m.westerman@latrobe.edu.au

fasciatus: Waterhouse, 1836)] have further confounded attempts to resolve evolutionary patterns.

Krajewski & Westerman (2003) provided a detailed summary of dasyuromorphian inter-relationships (their classification is augmented in Table 1) and reviewed existing hypotheses derived from morphological (mainly craniodental) data. Archer (1982, 1984) and Aplin & Archer (1987) placed Thylacinidae as sister group to Myrmecobiidae and Dasyuridae. This was later contradicted by the studies of Marshall, Case & Woodburne (1990) and Wroe (1997), who considered Myrmecobiidae to be outside of a monophyletic Thylacinidae + Dasyuridae clade. More recently Wroe & Musser (2001), Wroe (2003), and Murray & Megirian (2006) advocated compatible assignments using fossils; however, both bootstrap (< 55%) and Bremer decay (1) support were weak throughout their parsimony trees, and no rigorous testing of alternative topologies was carried out.

Genus- and species-level placements within the various families were likewise weakly resolved. Indeed Wroe & Musser (2001) generated only 69% bootstrap support for Thylacinidae, and this clade was completely destabilized by the addition of new fossils (see Murray & Megirian, 2006). Resolution of Dasyuridae, which constitutes the bulk of extant dasyuromorphian taxa, was similarly ambiguous. The group is usually subdivided into the extinct Barinyinae and two living sister lineages, Dasyurinae and Sminthopsinae (see Krajewski & Westerman, 2003 and references therein). Surprisingly, none of these named radiations derived strong nodal support. Indeed, morphological studies have persistently failed to establish monophyly for any constituent dasyurid subgroup (see Wroe & Musser, 2001: 503: fig. 8; Van Dyck, 2002: 324: fig. 44; Murray & Megirian, 2006: appendix fig. 2). For example, Wroe & Musser (2001) recognized the genus *Antechinus* (Phascogalini) as sister to *Sminthopsis* (Sminthopsini) and placed *Neophascogale* (Dasyurini) with phascogalins (*Murexia* and *Phascogale*). By contrast, Murray & Megirian (2006) resolved *Neophascogale* with *Dasyurus* + *Sarcophilus* but found that the plesiomorphic thylacinid *Mutpuracinus archibaldi* could be returned as a dasyurid. Conversely, Van Dyck (2002) nested *Phascogale* within *Antechinus* and derived a polytomy incorporating Planigalini, Dasyurinae, and Sminthopsinae.

Molecular approaches to dasyuromorphian family relationships have fared little better. Lowenstein, Sarich & Richardson (1981) and Krajewski *et al.* (1997, 2000a, 2003) identified Myrmecobiidae as the most divergent family-level taxon within Dasyuromorphia but this was derived using only small (< 1 kb) DNA sequence databases, which concomitantly produced low node support. By contrast, Miller *et al.* (2009) used complete mtDNA sequences for the numbat (*Myr. fasciatus*),

Table 1. Suprageneric classification of Dasyuromorphia after Krajewski & Westerman (2003) modified in accordance with this study

Order Dasyuromorphia (Gill, 1872)
Family Dasyuridae (Goldfuss, 1820)
Subfamily Dasyurinae (Goldfuss, 1820)
Tribe Dasyurini (Goldfuss, 1820)
<i>Dasyercus</i> (Peters, 1875)
<i>Dasykaluta</i> (Archer, 1982)
<i>Dasyuroides</i> (Spencer, 1896)
<i>Dasyurus</i> (Geoffroy, 1796)
<i>Myoictis</i> (Gray, 1858)
<i>Neophascogale</i> (Stein, 1933)
<i>Parantechinus</i> (Tate, 1947)
<i>Phascolosorex</i> (Matschei, 1916)
<i>Pseudantechinus</i> (Tate, 1947)
<i>Sarcophilus</i> (Cuvier, 1837)
Tribe Phascogalini (Gill, 1872)
<i>Antechinus</i> (Macleay, 1841)
* <i>Murexia</i> (Tate & Archbold, 1937)
<i>Phascogale</i> (Temminck, 1824)
Subfamily Sminthopsinae (Archer, 1982)
Tribe Sminthopsini (Archer, 1984)
<i>Antechinomys</i> (Krefft, 1867)
<i>Ningau</i> (Archer, 1975)
<i>Sminthopsis</i> (Thomas, 1887)
Tribe Planigalini (Archer, 1984)
<i>Planigale</i> (Troughton, 1928)
Family Myrmecobiidae (Waterhouse, 1836)
<i>Myrmecobius</i> (Waterhouse, 1836)
Family †Thylacinidae (Bonapart, 1838)
† <i>Thylacinus</i> (Bonapart, 1838)
Order Dasyuromorphia incertae sedis
†, ‡, § <i>Apoktesis</i> (Campbell, 1976b)
† <i>Maygriphus</i> (Wroe, 1997)
Family Thylacinidae incertae sedis
† <i>Badjcinus</i> (Muirhead & Wroe, 1998)
† <i>Maximucinus</i> (Wroe, 2001)
† <i>Muribacinus</i> (Wroe, 1996)
† <i>Mutpuracinus</i> (Murray & Megirian, 2006)
† <i>Ngamalacinus</i> (Muirhead, 1997)
† <i>Nimbacinus</i> (Muirhead and Archer, 1990)
† <i>Tjarrpecinus</i> (Murray & Megirian, 2006)
Family Dasyuridae incertae sedis
†, †† <i>Barinya</i> (Wroe, 1999)
†, **, †† <i>Archerium</i> (Wroe & Mackness, 2000)
†, **, †† <i>Ganbulanyi</i> (Wroe, 1998)

*Includes the monospecific phascogalin genera *Micromurexia*, *Murexechinus*, *Paramurexia*, and *Phascomurexia* following Armstrong *et al.* (1998) and Krajewski *et al.* (2007); also incorporates the additional species *Murexia aspera*. † Extinct. ‡ Close to *Dasyurus* (*sensu* Campbell, 1976a, b). § Dasyuromorphia incertae sedis (*sensu* Long *et al.*, 2002). ** Dasyurinae (*sensu* Long *et al.*, 2002). †† Dasyuridae (*sensu* Wroe, 2003).

several dasyurid sequences (*Dasyurus hallucatus*, *Phascogale tapoatafa*, and *Sminthopsis crassicaudata*), and *T. cynocephalus*, the latter species based on alcohol-preserved museum specimens. This substantially larger (> 16 kb) mitochondrial DNA sequence matrix yielded well-resolved nodes (87–100%) but generated a contrasting tree structure, with Thylacinidae returned as the sister lineage to Myrmecobiidae + Dasyuridae.

The monophyly of Dasyuridae is endorsed by molecular studies (e.g. Krajewski & Westerman, 2003), as are its subdivisions into the subfamilies Dasyurinae (containing tribes Dasyurini and Phascogalini) and Sminthopsinae (comprising tribes Sminthopsini and Planigalini) based on a combined analysis of mitochondrial [*12S* and *cytochrome b* (*cytb*)] and nuclear [*protamine P1* (*ProtP1*)] genes. Krajewski *et al.* (2004, 2007, 2012) and Westerman, Young & Krajewski (2008) subsequently explored genus-level affinities within Dasyuridae via extended mitochondrial (*cytb*, *12S rRNA*, *tRNA valine* + *16S rRNA*) and nuclear [*ProtP1*, *interphotoreceptor binding protein exon 1* (*IRBP*), and *beta-fibrinogen intron 7* (*bfib7*)] gene sequences. Their results variously confirmed the monophyly of the dasyurid genus *Pseudantechinus* (including *Pseudantechinus bilarni*), the sister placement of *Neophascogale* + *Phascolosorex* ('Phascolosoricinae' *sensu* Archer, 1982, 1984) and *Dasyurus* + *Sarcophilus*, as well as the close relationship between *Dasyercus* and *Dasyuroides*. In addition, a robust clade comprising *Dasykaluta*, *Parantechinus apicalis*, and *Myoictis* was returned by Westerman *et al.* (2008), although the other dasyurid genera could not be reliably placed. Krajewski *et al.* (2007) showed Phascogalini to be a valid tribe, with the monophyletic New Guinean *Murexia* species nesting with *Phascogale* (but only deriving 60% bootstrap support), which together resolved as sister to *Antechinus*. Sminthopsini and Planigalini appear to be robust groupings within Sminthopsinae, but sminthopsin species-level arrangements are still unclear (see Krajewski *et al.*, 2012).

The fossil record of dasyuromorphians is generally patchy, comprising fragmentary dental specimens augmented by a few exceptionally preserved cranial and, more rarely, identifiable postcranial remains (see Long *et al.*, 2002; Wroe, 2003; Black *et al.*, 2012 for reviews). Evidence for Myrmecobiidae is entirely lacking from the fossil record prior to the late Pleistocene and the almost exclusively late Oligocene to Miocene diversity of thylacinids is contentious in terms of their relationships (Wroe, 2003; Murray & Megirian, 2006). The currently oldest recognized dasyurid is the early middle Miocene *Barinya wangala* (Wroe, 1999), which has been placed in its own subfamily – Barinyainae – because of primitive dental features and skull morphology. By contrast, most other extinct dasyurids are middle–late Miocene or younger in age, which led to

proposals for the emergence of modern dasyurid genera only after a middle–late Miocene 'bottleneck' extinction of archaic thylacinids (and bandicoots) and the contemporaneous onset of aridification in Australia (Archer & Hand, 2006: 581). Incongruously, some putative dasyurids are known to pre-date this critical timeframe, with several obscure taxa established on the basis of late Oligocene fossils from South Australia (Campbell, 1976a, b). However, these remains have never been formally described and their placement within Dasyuridae is unclear; only a single genus and species, *Apoktesis cuspis*, has been recognized in the literature and is considered either close to *Dasyurus* spp. (Campbell, 1976a, b), or *Dasyuromorphia incertae sedis* (Long *et al.*, 2002). Other potential dasyurid fossil taxa include *Ankotarinja tirarensis*, *Keeunia woodbournei*, and *Wakamatha tasselli*.

In view of these ongoing uncertainties, we compiled a 17 kb combined nuclear + mitochondrial gene DNA sequence database comprising previously published and new nuclear genes (see Supporting Information Table S1) from *Myr. fasciatus* as well as from representatives of the majority of living dasyurid species. Our primary objectives were to provide a robust classification and divergence timescale for Dasyuromorphia, as well as to establish a coherent phylogenetic framework for future diversity assessments.

MATERIAL AND METHODS

MOLECULAR DATA AND APPROACHES

More than 40 novel sequences for five nuclear genes [*breast cancer early onset gene 1* (*BRCA1*), *apolipoprotein B gene* (*ApoB*), *recombination activating gene 1* (*RAG1*), *von Willibrand Factor gene* (*vWF*), and *embryonic globin gene intron 1* (*ε-globin*)] were added to previously published information for these and other nuclear genes (*ProtP1*, *interphotoreceptor binding protein* (*IRBP*), *bfib7*) to yield over 8.7 kb of nuclear gene data. Seven mitochondrial genes [*cytb*, *12S rRNA*, *tRNA valine plus 16S rRNA*, *nicotinamide dehydrogenase* (*NADH*) *genes 1* and *2*, and *cytochrome oxidase* (*CO*) *genes 1* and *2*] were also incorporated to provide a total DNA sequence database of over 17 kb. This database is the most extensive data set available for dasyuromorphian species. Taxon coverage for the individual mitochondrial genes employed in this study varied from a high of 72 of the 73 dasyuromorphian species (*12S rRNA*) to a low of 27 species (*CO2*) (see Table S1). Coverage of the eight nuclear genes was generally less, ranging from 62/73 species for *IRBP* and *bfib7* to 15/73 species for *ApoB*. We were thus able to include sequences for one or more genes from the majority of extant species of Dasyuromorphia except for the following: *Phascolosorex doriae* for which we could obtain only partial *12S rRNA*

sequences; *Sminthopsis fuliginosus* recognized by Groves (2005) but otherwise not usually adopted as a distinct taxon; and *Antechinus arktos*, *Antechinus mysticus*, *Antechinus argentus*, *Antechinus adustus*, and *Antechinus subtropicus* (Van Dyck & Crowther, 2000). *Antechinus arktos* is a recently described species closely related to *Antechinus swainsonii* (Baker *et al.*, 2014); *A. mysticus* and *A. argentus* are close relatives of *Antechinus flavipes* (Baker, Mutton & Van Dyck, 2012; Baker, Mutton & Hines, 2013); *A. adustus* and *A. subtropicus* are part of the *Antechinus stuartii* species complex but are currently known only from partial mitochondrial control region sequences that proved difficult to align. We deemed the omission of these seven taxa to have little impact on our assessment of dasyurid interspecific relationships. We note also that prior to the revisions of *Myoictis* (Woolley, 2005) and *Dasyercus* (Woolley, 2008) our sequences for *Myoictis wavicus* and *Dasyercus blythi* were attributed to *Myoictis melas* and *Dasyercus cristicauda*, respectively.

Meredith *et al.* (2008, 2009, 2010), Krajewski *et al.* (1997), and Springer *et al.* (1997, 2011) clearly resolved the ordinal affinities of Dasyuromorphia as lying proximal to marsupial moles (Notoryctemorphia) and bandicoots (Peramelemorphia), the Agreodontia of Beck *et al.* (2014). We therefore designated *Notoryctes typhlops* and representatives of extant bandicoot genera as outgroups. *Dromiciops gliroides* was used to root trees because it is divergent from all other Australidelphian taxa (Nilsson *et al.*, 2010). Molecular dating exercises included representatives of the marsupial orders: Didelphimorphia, Microbiotheria, Dasyuromorphia, Peramelemorphia, Notoryctemorphia, and Diprotodontia. The DNA sequence matrix was analysed using maximum likelihood (ML) as implemented in RAxML 7.2.8 (Stamatakis, 2006) and Bayesian methods in MrBayes v. 3.2 (Ronquist *et al.*, 2012). Data were alternatively treated as either a single unpartitioned block or separated into 15 gene partitions (*BRCA1*, *ApoB*, *IRBP*, *RAG1*, *vWF*, *ProtP1*, *bfib7*, *ε-globin*, *cytb*, *12S rRNA*, *tRNA valine+16S rRNA*, *NADH1*, *NADH2*, *CO1*, *CO2*) each with its own model of sequence evolution. In addition we further partitioned protein coding genes into the three codon positions (first, second, and third) and the two rRNA genes into stems and loops to determine whether this had an effect on resolution in the phylogenetic tree. The general time-reversible + Γ + I (GTR + Γ + I) model was allocated for all partitions in RAxML. Other best-fit models were chosen using the Aikake Information Criterion as implemented in jModeltest (Posada, 2008). Node support was estimated by 1000 bootstrap pseudoreplications for RAxML. Bayesian analyses utilized random starting trees and two simultaneous runs of four Markov chains (one cold and three heated using default heating values) applied for 5×10^6 generations with sampling every

1000th generation. The first 1.25×10^6 generations were discarded from each run as burn-in. The remaining trees were used to construct a majority-rule consensus with posterior probabilities (PP) > 0.95 deemed as strong, and PP = 0.90–0.95 as moderate support, respectively (see Kolaczkowski & Thornton, 2006). To examine particular alternative phylogenetic relationships, we used Shimodaira–Hasegawa (SH; Shimodaira & Hasegawa, 1999) and Kishino–Hasegawa (KH; Kishino & Hasegawa, 1989) tests implemented in PAUP* v. 4.0b10 (Swofford, 2002) to compare our best ML trees against the following constraints: *Myr. fasciatus* (*T. cynocephalus* + Dasyuridae); *T. cynocephalus* (*Myr. fasciatus* + Dasyuridae); *Pa. apicalis* and *Ps. bilarni* are congeneric species (*sensu* Archer, 1982) and Parantechini (*sensu* Archer, 1982). We note that these tests were carried out in a likelihood framework implemented in PAUP* with a single model for the complete concatenation as PAUP does not allow full partitioning of multigene data sets.

MOLECULAR CLOCK ANALYSES

Time-tree analyses were performed using BEAST v. 1.8 (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) with the uncorrelated lognormal relaxed molecular clock. Two didelphimorphians (*Caluromys* spp. and *Didelphis virginiana*), together with multiple diprotodontian and peramelemorphian outgroups were chosen for which fossils are known. We used minimum and maximum calibration ages for 12 nodes in Marsupialia from Westerman *et al.* (2012: their electronic supplementary table 2). Minimum ages from Westerman *et al.* (2012) are based on the oldest crown fossils for each clade, and maximum ages are based on a combination of phylogenetic bracketing and stratigraphical bounding as described by Meredith *et al.* (2010) and Springer *et al.* (2011). The minimum age for Peramelemorphia was increased from 4.46 to 14.17 Myr (middle Miocene) in light of new fossil peramelid and thylacomyid fossils from Riversleigh (Travouillon *et al.*, 2014) including Crash bandicoot, which has a minimum age of 14.17 Myr (i.e. 14.64 ± 0.47 Myr) based on radiometric dates for the AL90 site (Woodhead *et al.*, 2014). We also included a 13th calibration for Dasyuromorphia from Meredith *et al.* (2009). Specifically, we used a minimum age of 24.7 Myr for this clade based on *Badjcinus turnbulli*, which is the oldest known thylacinid fossil. This minimum age also conforms to the inferred placement of *Apoktesis cuspis* as the most ancient dasyurid (*sensu* Campbell, 1976a, b). The maximum age was changed to 54.65 Myr rather than the more conservative 65 Myr used previously.

Modelling of upper and lower constraints followed a normal prior distribution, assigning 95% of the prior

to the interval between the maximum and the minimum. Markov Chain Monte Carlo analyses were run for 50×10^6 generations with a burn-in of 10×10^6 generations, and sampling every 1×10^4 generations [by which time effective sampling size (ESS) values were > 200 for all parameters estimated]. We used TreeAnnotator v. 1.6.1 from the BEAST package to summarize the sample of trees generated by BEAST.

RESULTS

PHYLOGENETIC STRUCTURE OF DASYUROMORPHIA

The phylogenetic trees obtained for individual gene loci (Fig. S1) showed no conflict for nodes with $> 70\%$ bootstrap support. Individual mitochondrial genes (the only ones including sequences for the recently extinct *T. cynocephalus*) gave trees unlike the one obtained from complete mitochondrial genomes (Miller *et al.*, 2009). Rather than showing Thylacinidae as sister to Myrmecobiidae + Dasyuridae, two of them (*12SrRNA* and *tRNA valine + 16S rRNA*) showed Thylacinidae and Myrmecobiidae as sister taxa with moderate to strong (81%) bootstrap support. Within Dasyuridae, all individual genes as well as the combined nuclear and mitochondrial genes resolved the two currently recognized subfamilies. As there were no major conflicts, the data sets were concatenated for all subsequent analyses.

Bayesian and RAxML analyses of the concatenated nuclear and mitochondrial gene sequences consistently resolved the base of the dasyuromorphian tree (Fig. 1). Both partitioned and unpartitioned analyses suggested that *Myr. fasciatus* is sister taxon to Dasyuridae although support for this relationship was weaker for the RAxML approach [67% (gene + position), 78% (gene only), and 80% (unpartitioned), respectively, see Table 2]. As some earlier work (see above) has suggested a sister relationship between Thylacinidae and Dasyuridae, we tested the goodness of fit of both alternative topologies using KH and SH tests. It is clear from Table 3 that the KH and SH tests positing *Myrmecobius* as sister to (*Thylacinus*, Dasyuridae) were not a significantly worse fit to the data ($P = 0.536$ and 0.655 , respectively). Thus, although our results support the suggestion that *Thylacinus* is sister to a clade comprising *Myrmecobius* + Dasyuridae, this might simply be a function of the retrieved sequences for *T. cynocephalus* being essentially limited to mtDNA (see below).

Monophyly of Dasyuridae and of the two constituent subfamilies Dasyurinae and Sminthopsinae (*sensu* Krajewski & Westerman, 2003) were consistently resolved by our data set, as were the tribes Dasyurini, Phascogalini, Planigalini, and Sminthopsini (see Table 2). There was also support for some particular intergeneric relationships within each tribe. Thus, within Dasyurini,

four generic groupings were consistently recovered: (1) *Sarcophilus* + *Dasyurus* + *Neophascogale* + *Phascolosorex*; (2) *Myoictis* + *Pa. apicalis*; (3) *Pseudantechinus* (including *Ps. bilarni*); and (4) *Dasyercus* + *Dasyuroides*. Only the sister relationship of *Dasykaluta* remains unresolved. Whereas the unpartitioned Bayesian analysis suggested a closer relationship with *Dasyercus* + *Dasyuroides* [0.73 Bayesian Posterior Probability (BPP)], all other analyses (partitioned BAYES and both partitioned and unpartitioned RAxML) indicated a closer relationship to *Myoictis* plus *Pa. apicalis*. However, support for this association was weak [55% bootstrap support unpartitioned RaxML, 59% partitioned (gene only), 85% partitioned (gene + Pos); 1.0 BPP partitioned].

It is clear from Figure 1 and Table 3 that there is no molecular support for Archer's (1982) suggestion that the southern (*Pa. apicalis*) and northern dibblers (*Ps. bilarni*) are congeneric species. Rather, the former consistently resolved as sister to the New Guinean endemic genus *Myoictis*, whereas the latter associated (albeit distantly) with members of *Pseudantechinus*, as suggested by Cooper, Aplin & Adams (2000). Neither was there any support for Archer's (1982) suggestion that *Pa. apicalis*, *Ps. bilarni*, *Dasykaluta rosamondae*, and the other *Pseudantechinus* species constitute a taxonomic unit 'Parantechini' ($P \ll 0.001^{***}$, Table 3).

Within Phascogalini, *Murexia* (*sensu* Armstrong, Krajewski & Westerman, 1998) mostly resolved as sister to *Phascogale*, although support for this association was not strong (0.91 BPP partitioned by gene, 0.51 BPP partitioned by gene and codon, 1.00 BPP unpartitioned, 73% bootstrap support for RaxML partitioned by gene, 74% partitioned by gene and codon).

In contrast to Dasyurinae, although all analyses robustly recovered the tribes Sminthopsini and Planigalini within Sminthopsinae (see Table 3), there was no support for a monophyletic *Sminthopsis*. This finding was in marked contrast to the complete resolution of every other dasyurid genus. As shown by Woolley *et al.* (2007) and Krajewski *et al.* (2012), *Sminthopsis* was rendered paraphyletic by both *Ningau* and *Antechinomys*. All analyses recovered a strongly supported sister relationship between *Antechinomys* and *Sminthopsis longicaudata* (see Table 2) as well as two well-supported groups of *Sminthopsis* species – the *Sminthopsis murina* and the *Sminthopsis crassicaudata* species complexes. *Ningau* is more closely related to the *S. murina* complex.

TIMING OF MOLECULAR DIVERGENCES

The results of our relaxed molecular clock BEAST analyses (Fig. 2; Table 4) indicate that all estimates of dasyuromorphian divergences, including those within Dasyuridae, are very old, with the initial split of Dasyuromorphia into the constituent families

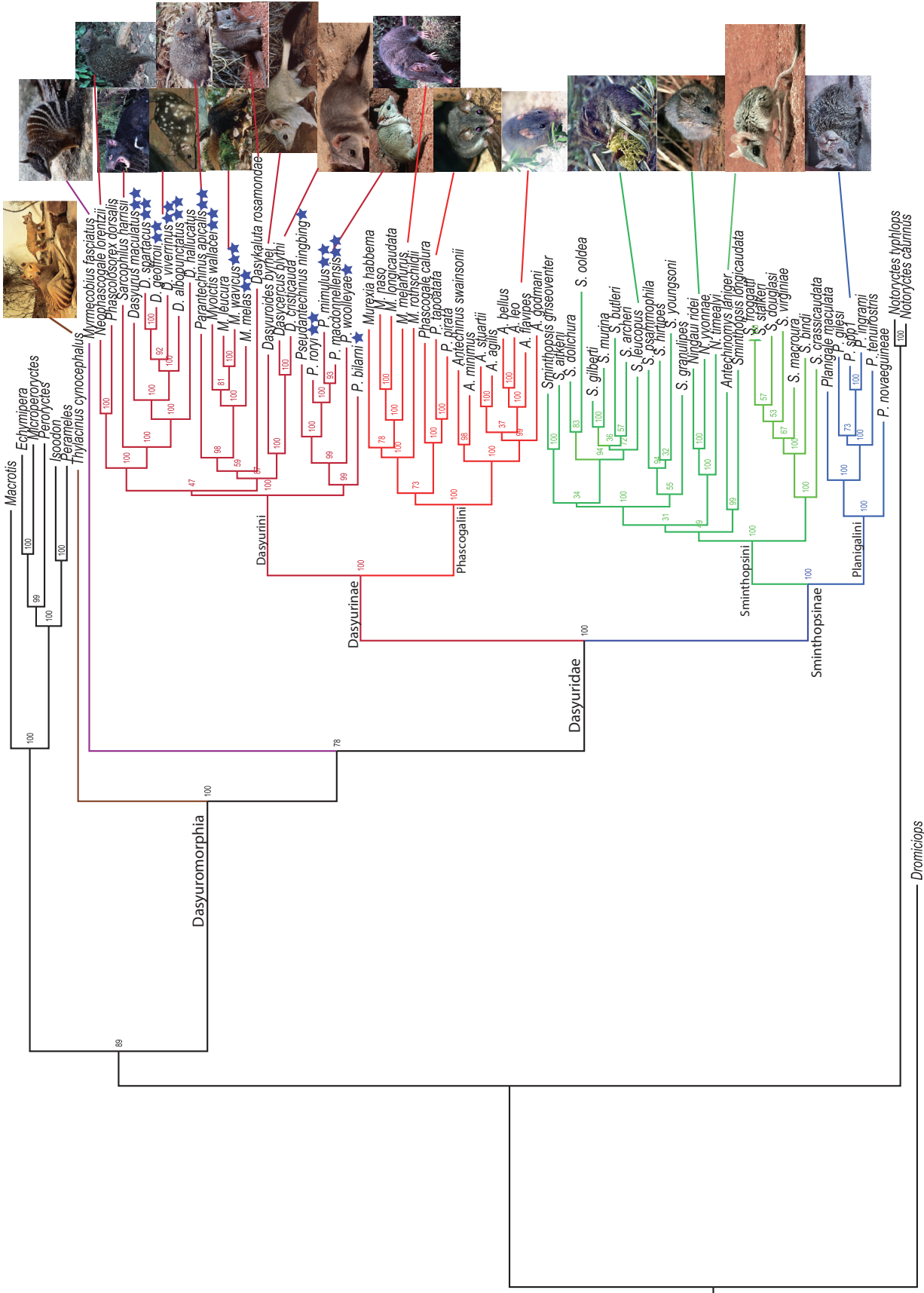


Figure 1. RAxML tree of phylogenetic relationships of dasyuromorphians obtained from the combined nuclear plus mitochondrial DNA sequences in which each gene was given its own model of sequence evolution. Bootstrap values are shown. (See Table 2 for Bayesian posterior probability values and the unpartitioned RAxML analysis.) Double stars indicate those species with penis appendages containing accessory erectile tissue derived from the corpora cavernosa; single stars indicate those species with accessory corpora cavernosa but without an appendage.

Table 2. Support levels (MrBayes posterior probabilities; RAxML bootstrap %) for various nodes shown in Figure 1

Node	MrBayes unpart	MrBayes part (gene)	MrBayes part (gene + position)	RAxML unpart	RAxML part (gene)	RAxML part (gene + position)
Thylacinidae + Dasyuridae	–	–	–	–	–	–
Myrmecobiidae + Dasyuridae	1.00	1.00	0.95	80	78	67
Dasyuridae	1.00	1.00	1.00	100	100	100
Dasyurinae	1.00	1.00	1.00	100	100	100
Sminthopsinae	1.00	1.00	1.00	100	100	100
Dasyurini	1.00	1.00	1.00	100	100	100
Phascogalini	1.00	1.00	1.00	100	100	100
Planigalini	1.00	1.00	1.00	100	100	100
Sminthopsini	1.00	1.00	1.00	100	100	100
(<i>Dasyurus</i> + <i>Sarcophilus</i>), (<i>Neophascogale</i> + <i>Phascolosorex</i>)	1.00	1.00	1.00	100	100	100
<i>Dasyurus</i> + <i>Sarcophilus</i>	1.00	1.00	1.00	100	100	100
<i>Neophascogale</i> + <i>Phascolosorex</i>	1.00	1.00	1.00	100	100	100
<i>Myoictis</i> + <i>Parantechinus apicalis</i>	1.00	1.00	1.00	93	99	95
(<i>Dasyercus</i> , <i>Dasyuroides</i>), <i>Dasykaluta</i>	0.73	–	–	–	–	–
(<i>Myoictis</i> , <i>Pa. apicalis</i>), <i>Dasykaluta</i>	–	1.00	1.00	55	59	85
<i>Dasyuroides</i> + <i>Dasyercus</i>	1.00	1.00	1.00	100	100	100
(<i>Dasykaluta</i> + <i>Myoictis</i> + <i>Pa. apicalis</i> + <i>Dasyercus</i> + <i>Dasyuroides</i>)	1.00	1.00	1.00	82	87	100
<i>Pseudantechinus</i> (including <i>Pseudantechinus bilarni</i>)	0.97	0.97	1.00	97	99	98
<i>Phascogale</i> + <i>Murexia</i>	1.00	0.91	0.51	–	73	74
<i>Sminthopsis longicaudata</i> + <i>Antechinomys laniger</i>	1.00	1.00	1.00	98	99	99
<i>Sminthopsis murina</i> complex	1.00	1.00	1.00	100	100	100
<i>Sminthopsis crassicaudata</i> complex	1.00	1.00	1.00	100	100	100

Table 3. Likelihood scores and significance of some alternative relationships of dasyuromorphian families and species

Relationship tested	–lnL	Diff –lnL	KH test (P-value)	SH test (P-value)
Thylacinidae, (Myrmecobiidae + Dasyuridae)	234851.2249	(Best)	–	–
Myrmecobiidae, (Thylacinidae + Dasyuridae)	234864.3590	13.1341	0.536	0.655
<i>Pseudantechinus bilarni</i> + <i>Parantechinus apicalis</i> (sister to <i>Pseudantechinus</i>)	235099.3115	248.0866	<0.001***	<0.001***
Parantechini (<i>sensu</i> Archer, 1982)	235221.9854	370.7605	<0.001***	<0.001***

*** $P < 0.001$. KH, Kishino–Hasegawa; SH, Shimodaira–Hasegawa; –lnL, log likelihood, Diff –lnL, difference in log likelihood.

Myrmecobiidae, Thylacinidae, and Dasyuridae probably occurring in the later Eocene ~ 40 Mya. Myrmecobiidae and Dasyuridae also diverged before the end of the Eocene (~ 36 Mya). Radiations within Dasyuridae, giving rise to the two extant subfamilies and their constituent tribes, seem to have been serial events during the Oligocene (~ 31 and ~ 25 Mya). It would appear that all extant dasyurid genera were in existence by the middle Miocene, and that with a few exceptions (e.g. *Sminthopsis stalkerii* and *Sminthopsis*

froggatti), all modern species had appeared before the Pliocene and the onset of aridity in Australia (see discussion below).

DISCUSSION

PHYLOGENETIC RELATIONSHIPS WITHIN DASYUROMORPHIA

Previous assessments of dasyuromorphian inter-relationships, especially at the interfamilial level, have

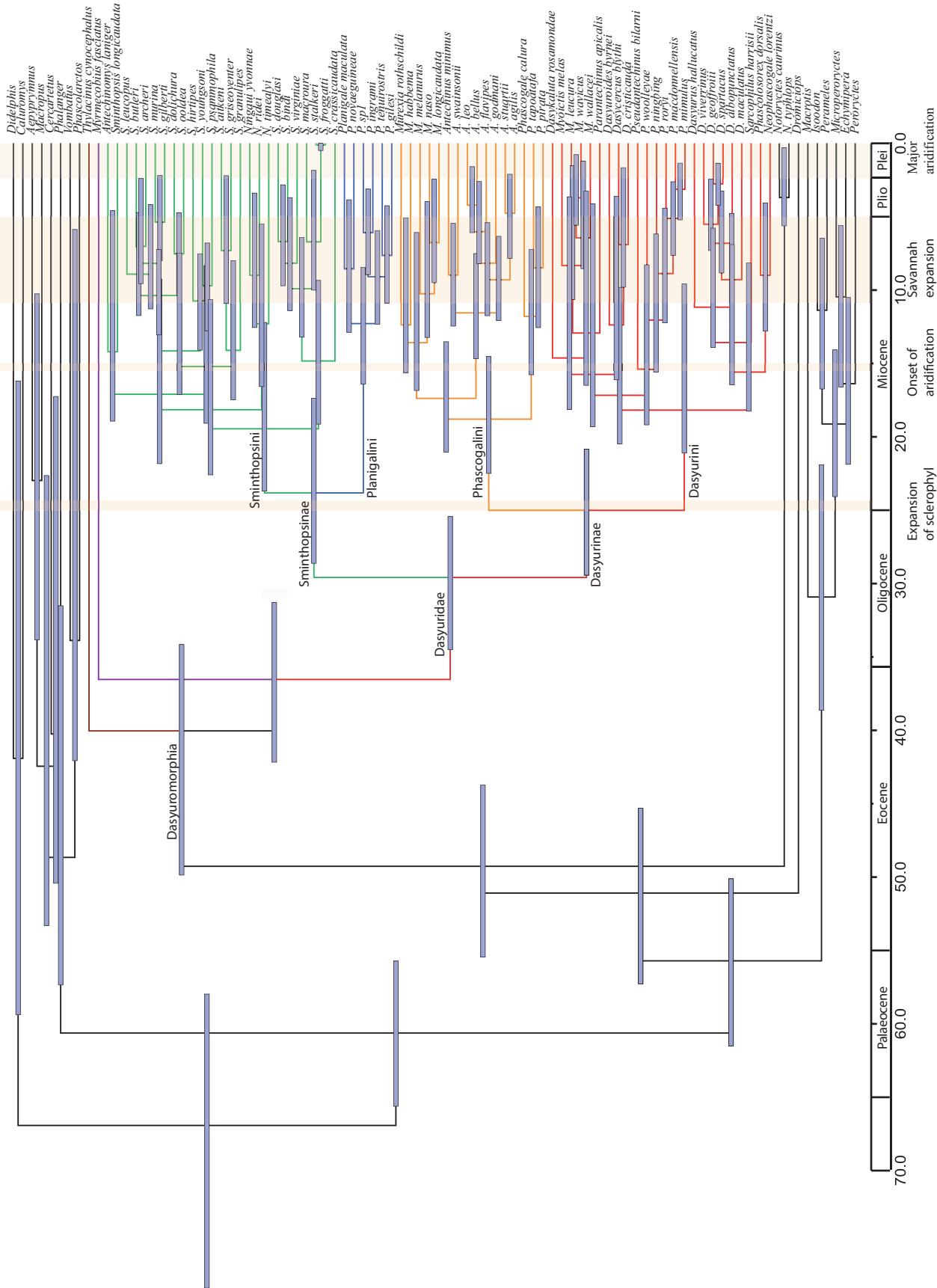


Figure 2. Molecular divergence times (in millions of years with 95% highest posterior intervals on the divergence estimates of each node) for dasyuromorphians based on the analysis of partitioned concatenated DNA sequences of nuclear and mitochondrial genes using BEAST v. 1.8.2. Maximum and minimum values for the nodes constrained in the molecular dating analysis are as described in the text. Vertical brown bars indicate timings of major phases of aridity in Australia over the last 30 Myr.

Table 4. Estimated average time of divergences within Dasyuromorphia (with 95% highest posterior intervals of divergence, HPD) in millions of years before present (Myr) for taxa in Figure 2

Divergence/origin	Mean divergence in Myr (95% HPD)
Dasyuridae	36.5 (32.1–41.0)
Dasyurinae v Sminthopsinae	29.3 (25.5–33.1)
Dasyurini v Phascogalini	24.5 (21.2–28.0)
Sminthopsini v Planigalini	24.1 (20.5–27.7)
(<i>Dasyercus</i> + <i>Dasyuroides</i>) v (<i>Dasykaluta</i> + <i>Parantechinus</i> + <i>Myoictis</i>)	15.7 (13.4–18.3)
<i>Dasykaluta</i> v (<i>Parantechinus</i> + <i>Myoictis</i>)	14.7 (12.4–17.2)
<i>Myoictis</i> v <i>Parantechinus</i>	13.0 (10.6–15.5)
<i>Myoictis</i>	8.4 (6.2–10.8)
<i>Dasyuroides</i> v <i>Dasyercus</i>	12.3 (9.7–15.0)
<i>Dasyercus</i>	7.1 (4.4–9.7)
<i>Dasyurus</i> v <i>Sarcophilus</i>	13.5 (11.3–15.3)
<i>Dasyurus</i>	11.2 (9.0–13.4)
<i>Pseudantechinus</i>	15.5 (12.7–18.6)
<i>Phascogale</i> v (<i>Murexia</i> + <i>Antechinus</i>)	18.8 (15.7–21.9)
<i>Murexia</i> v <i>Antechinus</i>	17.4 (14.6–20.4)
<i>Phascogale</i>	11.8 (8.2–15.2)
<i>Murexia</i>	13.7 (11.0–16.6)
<i>Antechinus</i>	11.9 (9.5–14.5)
<i>Planigale</i>	12.3 (9.4–15.5)
<i>Ningaui</i>	12.5 (9.1–15.9)
<i>Sminthopsis crassicaudata</i> species complex v other Sminthopsinae	19.7 (16.7–23.0)
<i>S. crassicaudata</i> species complex	15.1 (12.0–18.4)
<i>Sminthopsis murina</i> species complex	15.4 (12.6–18.3)

v, diverged from.

usually employed small databases of only a few mitochondrial genes (Thomas *et al.*, 1989), or craniodentally restricted morphological characters (Krajewski & Westerman, 2003). It is therefore perhaps not surprising that the final phylogenetic outcomes were often unclear and conflicting. Miller *et al.* (2009) attempted to address these issues via analysis of complete mitochondrial genomes for the extinct *T. cynocephalus*, *Myr. fasciatus*, and some representative dasyurids. Their tree presented a well-resolved Dasyuromorphia with Thylacinidae sister to Dasyuridae and Myrmecobiidae, a finding that is at odds with obverse hypotheses based on morphology/fossils (Wroe & Musser, 2001), serology (Lowenstein *et al.*, 1981), and limited mtDNA (Krajewski, Wroe & Westerman, 2000b). Our more extensive sampling of eight nuclear and eight mitochondrial genes (totalling over 16 kb DNA) confirms the topology reported by Miller *et al.* (2009) and, as reiterated by Mitchell *et al.* (2014), places

Thylacinidae as sister to Myrmecobiidae and Dasyuridae. However, we note that the DNA sequences currently available for the recently extinct thylacine are almost entirely mitochondrial in origin and so, until substantial nuclear gene sequences become available for *Thylacinus* to confirm this, we regard dasyuromorphian family-level relationships as ‘provisional’.

Our large DNA sequence data set gave a well-validated phylogeny of dasyuromorphians with robust support for the monophyly of Dasyuridae (Fig. 1), the intrafamilial classification advanced by Krajewski & Westerman (2003; see also Table 1), as well as strong evidence for four major groupings of genera within Dasyurini. These are: *Pseudantechinus* (including *Ps. bilarni*); *Myoictis* + *Pa. apicalis*; *Dasyurus* + *Sarcophilus* + *Neophascogale* + *Phascolosorex*; and *Dasyercus* + *Dasyuroides*. Although the relationships of *Dasykaluta rosamondae vis a vis* other dasyurines remain unresolved, it appears to be closer to *Myoictis* + *Pa. apicalis* than to other genera. The apparently large genetic difference seen between the northern dibbler, *Ps. bilarni*, and other members of *Pseudantechinus* reflects the difficulties that morphologists have had in ascertaining the phylogenetic affinities of this species (Cooper *et al.*, 2000).

The affinities of the two New Guinean rainforest-adapted genera *Neophascogale* and *Phascolosorex* are unequivocal. Previously, as with *Murexia* (see below), these two genera have been plagued by discordance between molecular and morphological data sets. On the basis of very limited dental evidence, Archer (1982) concluded that *Neophascogale* and *Phascolosorex* ‘... may be fundamentally distinct within the dasyuridae’ (Archer, 1982: 438) and consequently placed them in his ‘Phascosoricinae’. Although Wroe *et al.* (2000) only included *Neophascogale* in their matrix of craniodental characters, their tree alternatively depicted it nesting within Phascogalini as sister to *Murexia*. Our molecular data unequivocally resolve *Neophascogale* and *Phascolosorex* as sister to *Dasyurus* + *Sarcophilus* within Dasyurini. We therefore conclude that the limited craniodental (mainly dental) characters available for dasyurids in the Wroe *et al.* (2000) data set are influenced by homoplasy relative to these taxa.

Relationships within the *Sarcophilus* plus *Dasyurus* clade are now completely resolved, with *Sarcophilus* sister to *Dasyurus*. Within the latter genus, the northern quoll (*Dasyurus hallucatus*) is clearly divergent from all others and *Dasyurus maculatus* is sister to a clade containing *Dasyurus viverrinus*, *Dasyurus albopunctatus*, *Dasyurus geoffroii*, and *Dasyurus spartacus* – as also suggested by Krajewski *et al.* (2004). Our expanded data set indicates with 100% bootstrap support that *Dasyurus albopunctatus* is sister to the other species in this group and that *Dasyurus viverrinus* is sister to *Dasyurus geoffroii* plus *Dasyurus spartacus*. This suggests that

the endemic quolls of New Guinea's rainforests (*Dasyurus albopunctatus*) and savannah woodlands (*Dasyurus spartacus*) are not particularly closely related to one another; the latter species being more closely related to the Australian mainland arid-adapted western quoll, *Dasyurus geoffroii*, as suggested in Woolley, Krajewski & Westerman (2015).

We derive no justifiable separation of presumably 'ancestral' rainforest-adapted taxa such as *Neophascogale* and *Myoictis* from dasyurid taxa found in xeric environments. Indeed, the seemingly disjunct emergence of arid-adapted dasyurid genera *Pseudantechinus*, *Parantechinus*, *Dasyercus*, *Dasyuroides*, and *Dasykaluta* infers multiple independent invasions of drier habitats and desert regions throughout the radiation of Dasyuridae. This concurs with previous assessments by Archer & Hand (2006), and more recently by Mitchell *et al.* (2014).

Our placement of *Pa. apicalis* with the New Guinean rainforest *Myoictis* advocates the generic distinction between *Pa. apicalis* and *Ps. bilarni*. *Pseudantechinus bilarni* is the most divergent species of *Pseudantechinus* (*sensu* Cooper *et al.*, 2000; Westerman *et al.*, 2006). Tate (1947) erected *Parantechinus* with a single species, *Pa. apicalis*, but Archer (1982: 434) interpreted the accessory erectile tissue derived from the corpora cavernosa of *Ps. bilarni* described by Woolley (1982: 780) as evidence that *Parantechinus* included *Ps. bilarni*, despite a predominance of symplesiomorphies. By contrast, Woolley (1982: 779–780) identified sufficient differences to warrant generic distinction. Certainly 15 of the 24 dasyurid species in our analysis possess accessory erectile tissue formed from the corpora cavernosa. In 12 of these it forms a ventral appendage to the penis enclosed in a pocket of preputial skin (Woolley & Webb, 1977; Woolley, 1982, 2011; Cooper *et al.*, 2000; Woolley *et al.*, 2015). These 15 species belong to three of the four dasyurid lineages outlined above, *viz.*: all species of *Pseudantechinus*, three of four species of *Myoictis* together with *Pa. apicalis* and all species of *Dasyurus* except *Dasyurus hallucatus* (Fig. 1). The penis morphology of *Myoictis leucura* and *Dasyercus cristicauda* has not yet been examined, and there is no information for *Ph. doriae* (P. A. Woolley, pers. comm.). Moreover, it is unclear whether the accessory structures seen in dasyurids are homologous. We therefore propose convergence given their absence from *Sarcophilus*, *Neophascogale*, and *Phascosorex dorsalis* (P. A. Woolley, pers. comm.), and from *Dasyurus hallucatus* (Woolley *et al.*, 2015), as well as from *Dasykaluta rosamondae* (as '*Antechinus*' *rosamondae*, Woolley, 1982), *Dasyercus blythi* (as *D. cristicauda*), and *Dasyuroides* (Woolley, 1987).

We found no support for the Archer (1982) grouping of *Pa. apicalis*, *Ps. bilarni*, *Dasykaluta rosamondae*, and *Pseudantechinus* species (his '*Parantechini*').

Pseudantechinus bilarni was genetically distinct from *Pa. apicalis* and only distantly related to other *Pseudantechinus* species. This is compatible with Cooper *et al.* (2000: 135), who stated that *Ps. bilarni* '... shows a complex mosaic of plesiomorphic and apomorphic characters making it phenotypically distinct from all other false antechinuses'. Although we advocate the retention of *Ps. bilarni* in the genus *Pseudantechinus*, we posit a caveat that both *Ps. bilarni* and *Pseudantechinus woolleyae* are genetically divergent from other *Pseudantechinus* species (*Pseudantechinus macdonnellensis*, *Pseudantechinus mimulus*, *Pseudantechinus ningbing*, and *Pseudantechinus roryi*) and specifically lack both a major insertion and a deletion in intron 7 of the beta-fibrinogen gene common to the latter four species (Westerman *et al.*, 2008).

We found no support for the contention that *Murexia* spp. are the most 'anatomically primitive' dasyurines (Archer, 1982, 1984). Rather, we derived a positioning of *Murexia* within Phascogalini as sister to *Phascogale* rather than as sister to *Antechinus* (following Archer, 1982; Kirsch *et al.*, 1990; Krajewski & Westerman, 2003). This suggests that the craniodental traits evident in *Murexia* are symplesiomorphic and that the derivation of 'Type 1' (annual male die-off) reproductive strategies in *Antechinus* and *Phascogale* (Krajewski, Woolley & Westerman, 2000) are likewise unrelated. All nodes within *Murexia* (*sensu* Krajewski *et al.*, 2007) are age equivalent to *Phascogale* and *Antechinus* (see below). We therefore reject generic subdivision of *Murexia* into *Micromurexia*, *Phascomurexia*, *Murexechinus*, and *Paramurexia* as proposed by Van Dyck (2002).

In contrast to Dasyurinae, taxon relationships within Sminthopsini are uncertain. Our inclusion of an additional nuclear gene (*ε-globin*) reiterated the primary tribe-level groupings: Sminthopsini and Planigalini (see Fig. 1) produced by Krajewski *et al.* (2012), and provides strong support for the deep divergence of *S. murina* and its related taxa (Woolley *et al.*, 2007). Interpolation of *Ningai* within *Sminthopsis* not only renders the latter genus paraphyletic (as intimated by Baverstock *et al.*, 1982), but also suggests that squamosal–frontal contact has been secondarily lost in *Ningai*. Moreover, the genetic disparity of *S. crassicaudata* + *S. macroura* + *S. virginiae* + *S. bindi* + *S. douglasi* + *S. froggatti* + *S. stalker* from all other *Sminthopsis* species as well as from *Antechinomys* and *Ningai* highlights the need for a broader taxonomic revision of Sminthopsinae.

MOLECULAR DIVERGENCE DATES

Our sophisticated molecular dating methodologies suggest dasyuromorphian cladogenic events during the later Eocene, with the establishment of Myrmecobiidae,

Thylacinidae, and Dasyuridae by the early Oligocene. Critically, there are as yet no fossils to validate these estimates although possible peramelemorphians inferring a dasyuromorphian split can be evidenced from the early Eocene (Black *et al.*, 2012). The oldest reported dasyuromorphian remains derive from the late Oligocene (Wroe, 2003). This situation is similar to the fossil record of peramelemorphians, which includes crown-group representatives (Thylacomyidae, Peramelidae) from at least the middle Miocene (Travouillon *et al.*, 2014), pointedly vindicating earlier arguments based on molecular clocks (Westerman *et al.*, 2012).

Our results demonstrate that splits between extant subfamilies and tribes of Dasyuridae had occurred by the late Oligocene (~ 29 and ~ 24 Mya, respectively). This is consistent with dates obtained from *12S rRNA* gene and single-copy DNA hybridization studies (Springer *et al.*, 1997) but somewhat earlier than the early Miocene timeframe postulated by Meredith *et al.* (2009). In addition, our estimates concur with the identification of both late Oligocene primitive thylacinids (*Bad. turnbulli*: Muirhead & Wroe, 1998) and putative dasyurids (e.g. *Bar. wangala*: Wroe, 1999) in the early Miocene. Furthermore, intratribe diversification was obviously well underway by the middle Miocene, with most modern dasyurid genera and species in existence well before the latest Miocene (Table 4). The only post-Miocene dasyuromorphian divergences occurred between *Murexia longicaudata* and *Murexia aspera*; *Dasyurus spartacus* and *Dasyurus geoffroii*; *Ps. macdonnellensis* and *Ps. mimulus*; *S. stalker* and *S. froggatti*; and *Planigale ingrami* and *Planigale* sp1. More recent (post-Pliocene) lineage splits seemingly took place entirely *within* currently recognized species such as *Dasyurus hallucatus*, *Antechinus swainsonii*, *A. flavipes*, *A. stuartii* and the *S. macroura* and *S. murina* species complexes. Such results imply that the origin of extant dasyurid genera was at least a middle Miocene event. This contrasts with popular suppositions otherwise describing the modern dasyurid clade as an entirely post late Miocene or early Pliocene event; a premise grounded on the lack of suitable fossils (see Wroe, 2003; Archer & Hand, 2006). Plesiomorphic dasyurid-like remains have nonetheless been documented from late Oligocene to early Miocene sediments (e.g. *Apoktesis cuspis* and putative *Antechinus*-like teeth: Campbell, 1976a, b; Archer, Hand & Godthelp, 1991; Woodburne *et al.*, 1994; Van Dyck, 1996), but these have not been formally described and are best regarded as *Dasyuromorphia incertae sedis*. No demonstrable traces of extant dasyurid genera have yet been reported from before the terminal Miocene, although the coeval occurrence of at least five discrete lineages in the early part of the middle Pliocene (see Black *et al.*, 2012) would imply ghost lineages

that need to be tested against the presently limited Australian late Miocene fossil record.

Travouillon *et al.* (2009) argued that evidence for open forest environments based on late Oligocene mammal assemblages in northeastern Australia might explain the apparent dearth of thylacinids as a characteristic element of early–middle Miocene rainforest faunas. This under-representation of xeric/arid palaeocommunities, in conjunction with ambiguous character state interpretations (see Murray & Megirian, 2006), could likewise account for the absence of abundant Miocene dasyurids, which perhaps proliferated in the more erosional Mallee-like scrublands evinced for central Australia from the middle Miocene (Metzger, 2007; Metzger & Retallack, 2010). Certainly, similar ‘environmentally biased’ Neogene distributions have been mooted for other Australian marsupials including peramelemorphians (Westerman *et al.*, 2012), macropodiforms (Meredith *et al.*, 2008), and pseudocheirid possums (Meredith *et al.*, 2010), as well as for reptile, amphibian, and bird groups including Australian diplodactylid geckos (Oliver *et al.*, 2012), sphenomorphid skinks (Skinner, Hutchinson & Lee, 2013), snapping turtles (Todd *et al.*, 2014), Australian toadlets (Catullo & Keogh, 2014), and birds (Toon *et al.*, 2012; Joseph *et al.*, 2014).

What factors might then have influenced the archetypal radiation of dasyurids? The separation of Australia and Antarctica, which culminated in the middle–late Eocene (~ 45–38 Mya: Veevers, 1991; Veevers, Powell & Roots, 1991), and establishment of the Antarctic Circumpolar Current following the opening of Drake’s Passage in the early–middle Oligocene (~ 30 Mya), dramatically altered climates within the Australasian region (Martin, 2006), and presumably likewise affected terrestrial biotas. Increasingly temperate conditions and decreased rainfall also seem to have facilitated the spread of sclerophyllous woodlands throughout central Australia in the Oligocene (Martin, 2006). Northward tectonic motion of the Australian plate simultaneously decreased from ~ 71 to ~ 26 km Myr⁻¹ in the late Oligocene–earliest Miocene (26–23 Mya) as a result of collision with the Ontong-Java Plateau (Knesel *et al.*, 2008). The direction of this movement became progressively more westerly, and was accompanied by massive volcanic outpourings in the Tweed Shield area. A resumption of the faster motion (~ 61 km Myr⁻¹) and decreased volcanism was initiated from the early to middle Miocene (23–16 Mya) and would have profoundly affected both climate and vegetation, at least locally, possibly fostering the spread of drier habitats, and the radiation of *Eucalyptus/Casuarina* woodlands. These events could have favoured diversification of Dasyuridae as part of a broader xeric biota (see also Skinner *et al.*, 2013), and specifically coincided with the internal split of

Sminthopsinae and Dasyurinae as well as their various constituent subclades.

Although much warmer and wetter environments re-established during the early–middle Miocene, climates became progressively cooler and drier, leading to a vegetation mosaic (Martin, 2006). Concurrent turnover in marsupial taxa appears to have been minimal (Travouillon *et al.*, 2009), yet radical change affected Late Miocene and Pliocene biotas, where arid-adapted open savannah grasslands proliferated (Hill, 1994), and ‘modern’ marsupial clades made their first appearance (e.g. macropodines: Prideaux & Warburton, 2010). Elevation of the New Guinean Central Cordillera and the Timor Rise also created new altitudinally segregated habitats within New Guinea that were in turn colonized by vicariant lineages (e.g. peramelemorphians: Westerman *et al.*, 2012). The timing of dasyurid cladogenesis therefore appears to have been manifold, with initial diversification following mesic habitat differentiation in the Oligocene accompanied by progressive radiation within Thylacinidae and Dasyuridae. Further intraclade divergences occurred in the early and middle Miocene, including the appearance of extant dasyurid genera, which were apparently all in existence by the end of the epoch. Most extant species splits coincide with the spread of arid woodland-grassland habitats and dispersals into New Guinea from the late Miocene. These proposed clade inceptions pre-date the fossil record. However, we emphasize that much of the ‘evidence’ for relationships between and within extinct dasyuromorphians rests upon the interpretation of a limited subset of craniodental characters. Not only might these traits manifest extensive homoplasy but they may not even be ‘independent’ as is frequently assumed. Growing evidence from genetic and developmental studies indicates that both cranial and dental data modules can be profoundly affected by subtle changes in activity levels of only a few genes and/or their controlling elements (Jernvall, Keranen & Thesleff, 2000; Kangas *et al.*, 2004). This must have a concomitant effect on cladistic interpretations, which can only be alleviated by the discovery of more complete fossil material and further integration of the rock record with molecular divergence dates to eliminate remaining discrepancies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Individual and combined gene Bayesian trees. A, *apolipoprotein B (ApoB)*, *breast cancer early onset gene 1 (BRCA1)*, *beta-fibrinogen intron 7 (bfib7)*, *embryonic globin gene intron 1 (ϵ -globin)*. B, *interphotoreceptor binding protein (IRBP)*, *protamine P1 (ProtP1)*, *recombination activating gene 1 (RAG1)*, *von Willibrand Factor (vWF)*. C, *cytochrome oxidase 1 and 2*, *nicotinamide dehydrogenase (NADH) 1 and 2*. D, *cytochrome b*, *12S rRNA*, *tRNAvaline+16S rRNA*. E, combined nuclear genes.

Table S1. GenBank accession numbers for taxa and gene sequences included in this study. New sequences indicated by light red shading; sequences with <50% of the longest sequence are indicated by darker shading. A, nuclear genes. B, mitochondrial genes.