An emerging consensus in the evolution, phylogeny and systematics of marsupials and their fossil relatives (Metatheria)

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ABSTRACT

Marsupials and their fossil relatives, which collectively comprise the Metatheria, have been of scientific interest for centuries, with many aspects of their evolution and systematics subject to intense research and debate. Here we review progress over the last 25 years, which has included the description of many new species (modern and fossil), and major improvements in understanding of their phylogenetic relationships, as well as the overall evolutionary history and biogeography of Marsupialia (crown-clade) and Metatheria (total-clade). Significant advances have included the deployment of increasingly sophisticated molecular, morphological and total evidence analyses, which have resolved most previously disputed relationships amongst and within the modern marsupial orders. A broad systematic consensus is now emerging, although several major areas of contention remain, particularly among fossil metatherians. New modern species continue to be described at an impressive rate, with almost 50 named in last 25 years, and many more await discovery. There has also been an explosion in the discovery and description of fossil marsupials and non-marsupial metatherians (~270 species), principally from Australasia and the Americas but also from Antarctica, Europe and Asia. Most are represented by dental specimens only, but some consist of complete and well-preserved material, which has led to major improvements in our understanding of the evolution of cranial and postcranial morphology. Improvements in the fossil record and advances in methods for inferring divergence times have helped clarify when and where key events occurred in metatherian evolution and the patterns of subclade diversification. We also have improved understanding of biogeographical relationships among metatherians on different landmasses. Despite enormous progress, numerous key uncertainties remain due to major gaps in the fossil record (e.g. Antarctica, late Cretaceous and early Paleogene of Australia) and a comparative lack of studies that directly combine

molecular and fossil data. Future advances will largely depend on improvements in the fossil record and studies that better integrate neontological and palaeontological evidence.

INTRODUCTION

Although the marsupials (crown-clade metatherians) represent a much smaller radiation than their placental (crown-clade eutherian) counterparts, they have fascinated Western science ever since their discovery in the 16th and 17th Centuries (Tyndale-Biscoe 2005). This is due to a variety of factors, including their ancient evolutionary divergence, their current almost exclusively Gondwanan distribution, their distinctively specialized reproductive biology, and the many examples of convergent evolution between them and placentals (Weisbecker and Beck 2015). Although modern marsupials are confined to the Americas and Australasia, metatherian fossils are known from every continent (Beck in press). Metatherians diverged from eutherians at least 125 million years ago, and perhaps 160 million years ago or earlier (Luo et al. 2011; Bi et al. 2018). Metatherians appear to have been confined to Laurasia until at least the latest Cretaceous, before dispersing into Gondwana, presumably from North America to South America (Case et al. 2005; Beck 2017a). Gondwanan metatherians, including crown-clade marsupials, diversified enormously over the course of the Cenozoic (Long et al. 2002; Goin et al. 2016), in contrast to the far more limited diversity observed in Laurasian (non-marsupial) metatherians that survived the K-Pg mass extinction (Crochet 1980; Korth 2008; Bennett et al. 2018b).

Today, marsupials are more diverse in Australasia (Australia, New Guinea and Wallacea) than they are in the Americas, with four orders, 18 families, and >248 species in the former region compared to three orders, three families, and >111 species in the latter (Wilson and Mittermeier 2015) (Table 1). In the Americas, most diversity is found in South and Central America; only a single species (*Didelphis virginiana*) occurs north of Mexico (Wilson and Mittermeier 2015), the result of a recent (<1 Ma) dispersal event (Woodburne 2010). Although the fossil record is far from complete, both Australasia and South America once hosted a far more extensive marsupial fauna (Long et al. 2002; Goin et al. 2016) (Table 1).

Since their discovery by Western science, much debate and controversy has surrounded systematics, taxonomy, and evolution of marsupials, with many different techniques employed to unravel their relationships including anatomy (cranial, dental and postcranial osteology, as well as soft tissue morphology), chromosomes, proteins, and DNA (Tyndale-Biscoe 2005).

A revolution during recent decades in genetic/genomic methods and computing power has seen many increasingly large and sophisticated molecular studies examining relationships within modern marsupials. These studies have progressed from examining single genes (e.g. Retief et al. 1995; Jansa and Voss 2000), to 5-10 genes (e.g. Meredith et al. 2009b; Potter et al. 2012), to whole mitochondrial genomes (Phillips et al. 2001; Nilsson et al. 2003), and now partial nuclear genomes comprising thousands of loci (Duchêne et al. 2018; Nilsson et al. 2018). Whole nuclear genome sequences of marsupials are now also beginning to accumulate (Mikkelsen et al. 2007; Renfree et al. 2011; Murchison et al. 2012; Feigin et al. 2017; Johnson et al. 2018). The greater information content and power of these analyses, as well as improved taxon sampling, have transformed our understanding of modern marsupial relationships; a consensus is now emerging, with higher order systematics beginning to stabilize. In addition, these molecular techniques have proved instrumental in the recognition of additional, often morphologically cryptic, species (e.g. Baker et al. 2014; Potter et al. 2014).

As well as revolutionary developments in molecular techniques, there have been major advances in our knowledge of the morphology of marsupials and other metatherians, and in phylogenetic analyses that incorporate morphological data. This is partly the result of dramatic improvements in the fossil record of marsupials and other metatherians in recent years. These have included the discovery of numerous new taxa (see below), some of them known from extremely well-preserved remains, in a few cases even including ontogenetic series (Marshall et al. 1995; Sánchez-Villagra et al. 2007; Black et al. 2010; Ladevèze et al. 2011; Black et al. 2012c; Travouillon et al. 2015b; Maga and Beck 2017). The increasing use of screen-washing techniques has greatly improved the recovery of more fragmentary fossils, particularly isolated teeth and partial jaws (Goin et al. 2010). However, numerous major gaps remain in the metatherian fossil record, and most taxa are known only from dental remains. Particularly frustrating is the near total lack of Australian fossil sites preserving mammals from the early Paleogene, as this is the period during which the Australian marsupial radiation probably began to diverge (Meredith et al. 2011; Mitchell et al. 2014; Duchêne et al. 2018). Currently, only the early Eocene Tingamarra Local Fauna is known from this period in Australia (Godthelp et al. 1999; Long et al. 2002; Beck et al. 2008b).

Our knowledge of the comparative morphology (particularly the skull and postcranial skeleton) of modern marsupials has improved thanks to monographs, taxonomic studies, and new phylogenetic analyses incorporating morphological characters (Horovitz and Sanchez-Villagra 2003; Wible 2003; Flores 2009; Flores and Díaz 2009; Voss and Jansa 2009). Methodological advances have included widespread use of non-destructive imaging techniques such as CT-scanning, which allow internal structures to be reconstructed in 3D and examined in unprecedented detail (Sánchez-Villagra and Schmelzle 2007; Schmelzle et al. 2007), and refined methods of phylogenetic analysis that incorporate morphological data and fossil evidence (Lee and Palci 2015); these include model-based methods for morphology (Lewis 2001), “total evidence” approaches for combining morphological and molecular data (Asher et al. 2004; Kealy and Beck 2017; Travouillon and Phillips 2018), and more sophisticated methods for inferring divergence times by directly incorporating information from fossil taxa, rather than simply using them to calibrate divergences among modern taxa (Ronquist et al. 2012; Zhang et al. 2016).

The major advances in marsupial systematics of the last 25 years, as well as the remaining areas of uncertainty, are now outlined below.

Description of new taxa (modern and fossil)

A major advance in our knowledge of metatherian and marsupial diversity and systematics over the last 25 years has been the continued discovery and description of new taxa, both modern and fossil. This includes 16 new modern species from Australasia and 24 from the Americas (Table S1), as well as 274 new fossil species from all continents (Table S2). Whilst many newly described modern taxa belong to small, morphologically cryptic genera (e.g. *Antechinus, Marmosops, Monodelphis*), new species have also been described from amongst larger genera such as *Dendrolagus* (tree-kangaroos; 8-9 kg) and *Trichosurus* (brush-tailed possums; 2-4 kg) (Table S1). Some of these newly described taxa also remain controversial (e.g. Martin 2018; Suárez-Villota et al. 2018). At least 17 additional taxa have been raised from synonymy to species status based on detailed genetic and morphological studies (Table S3). These studies demonstrate that species diversity within many marsupial genera remains seriously underestimated, not just in poorly surveyed and researched regions such as New Guinea, and that the steady stream of newly recognized species will continue for some time (Reeder et al. 2007; Burgin et al. 2018).

Origin of Metatheria and Marsupialia

The last 25 years has seen a remarkable improvement in the mammalian fossil record, including the discovery of many new fossils that provide key information on the origin and early evolution of Metatheria and Marsupialia (Table 1; Table S2). The improvement in the Mesozoic record has been particularly striking (Kielan-Jaworowska et al. 2004; Luo 2007), most obviously with the description of spectacularly well-preserved specimens from fossil sites in China (Meng 2014). One of these, *Sinodelphys szalayi* from the Early Cretaceous (~125 Ma) Jehol biota of northeastern China, was originally identified as the oldest known metatherian (Luo et al. 2003), but has now been reinterpreted as a eutherian (Bi et al. 2018); if so, then the oldest known metatherian fossils are isolated teeth from the Aptian-Albian (~110 MYA) of North America, among them the earliest known members of Deltatheroida (Davis et al. 2008; Davis and Cifelli 2011). Deltatheroidans are small, carnivorously-adapted mammals that were long of uncertain affinities (Bi et al. 2015; Rougier et al. 2015); in the 1990s and 2000s, the description of well-preserved deltatheroidan specimens from the Cretaceous of Asia revealed that they are likely members of Metatheria, as they exhibit several derived features characteristic of marsupials (Rougier et al. 1998; Bi et al. 2015).

Although the oldest known metatherians are ~110 Ma old, the presence of eutherians such as *Sinodelphys*, *Eomaia* and *Ambolestes* in the Jehol biota demonstrate that the Metatheria-Eutheria split must be older than 125 Ma (Bi et al. 2018). In 2007, *Juramaia* was described from the early Late Jurassic Tiaojishan Formation of northeastern China and interpreted as a eutherian (Luo et al. 2011); if this age estimate is accurate, it would push the Metatheria-Eutheria split back to >160 Ma, in line with recent molecular clock estimates (Phillips 2016; Tarver et al. 2016; Liu et al. 2017). However, doubts have been raised regarding the stratigraphic provenance (and therefore age) of *Juramaia* (Meng 2014; Bi et al. 2018). Therefore, 125 Ma currently represents a conservative, paleontologically-informed minimum age for the divergence between metatherians and eutherians.

We restrict the name Marsupialia to the crown-clade here (Table 1), following most recent studies (e.g. O'Leary et al. 2013; Williamson et al. 2014; Wilson et al. 2016), whereas other, mostly older works (e.g. Kielan-Jaworowska et al. 2004), have applied it to a more inclusive clade that is now known as Marsupialiformes (Vullo and Gheerbrant 2009; Beck 2017a). The origin of (crown-clade) Marsupialia, appears to have been a much more recent event, as phylogenetic analyses published within the past several years indicate that all known Mesozoic metatherians fall outside the crown-clade (Ni et al. 2016; Wilson et al. 2016; Bi et al. 2018; Engelman et al. 2018; Beck in press). It seems likely that Marsupialia originated in Gondwana (but see Wilson et al. 2016 for an opposing view), and metatherians probably did not enter Gondwana (presumably dispersing from North America to South America via a land bridge or island chain; Case et al. 2005) until the latest Cretaceous or earliest Paleocene (Beck 2017a); if so, this puts an upper bound on the likely time of origin of Marsupialia. However, Marsupialia might be younger still. Some authors have argued that some of the oldest known metatherians from South America are members of the crown-clade (e.g., *Khasia cordillierensis* and *Roberthoffstetteria nationalgeographica* from Tiupampa; Muizon et al. 2018: 365), whereas others contend that these taxa either fall outside Marsupialia or lack features that unequivocally identify them as members of the crown-clade (e.g. Beck 2017b). Arguably the oldest unequivocal marsupials are from the early Eocene Tingamarra Local Fauna of Australia, which has been radiometrically dated as 54.6 million years old (Godthelp et al. 1992); these marsupial remains include australidelphian-type tarsals that have been referred to the taxon *Djarthia murgonensis* (previously named based on dental remains only; Godthelp et al. 1999; Beck et al. 2008b) and an un-named taxon represented by an isolated calcaneus [ankle bone] transitional between "ameridelphian" and australidelphian morphologies (Beck 2012). Similarly, the oldest unequivocal marsupials from South America are isolated australidelphian tarsals from the early–middle Eocene (45-47 million year old) La Barda locality in southern Argentina (Lorente et al. 2016), although, as noted above, some metatherians from Tiupampa and early Eocene sites slightly older than La Barda have been proposed as early members of the marsupial orders Paucituberculata and Microbiotheria (Goin et al. 2009; Tejedor et al. 2009; Woodburne et al. 2014; Muizon et al. 2018).

Depending on their exact age (either early or middle Eocene; see Goin et al. 2018), fossil microbiotherians from the La Meseta Formation of Seymour Island, western Antarctica (see below), may be older than the oldest known South American marsupials (Gelfo et al. 2017). It is therefore possible that the earliest divergences within Marsupialia occurred in Australia or Antarctica (Beck 2017b), although this is difficult to test given the poor fossil record from these regions. Recent molecular clock and total evidence "tip-dating" studies suggest that Marsupialia originated in the Late Cretaceous or early Paleocene (Meredith et al. 2011; Jansa et al. 2014; Mitchell et al. 2014; Beck et al. 2016; Maga and Beck 2017; Duchêne et al. 2018), a finding that would be closely congruent with the fossil record if some of the metatherians from Tiupampa and other early Paleogene South American sites do indeed pertain to the crown clade.

Relationships among American and Australasian marsupials

Although the number of orders of modern marsupials was unstable for well over a century, seven extant orders are now well accepted (Wilson and Reeder 2005; Meredith et al. 2011; Mitchell et al. 2014; Wilson and Mittermeier 2015) (Table 1). These form two distinct biogeographic clusters: members of Didelphimorphia (opossums) occur in South and Central America (and, to a much lesser extent, in North America), and Paucituberculata (shrew-opossums) and Microbiotheria (monito del monte, *Dromiciops gliroides*) are both exclusively South American (although fossil microbiotherians are known from the Eocene of Antarctica - see below); Dasyuromorphia (carnivorous Australasian marsupials, such as quolls, dunnarts, antechinuses, Tasmanian Devil, numbat and thylacine), Notoryctemorphia (marsupial moles), Peramelemorphia (bandicoots and bilbies), and the Diprotodontia (kangaroos, possums, koala, wombats) are confined to Australasia (Wilson and Mittermeier 2015).

The evolutionary relationships amongst these orders has proved difficult to resolve. However, there is now compelling evidence supporting Szalay's (1982) revolutionary proposal that the South American order Microbiotheria forms a clade with the four modern Australian orders, which he named Australidelphia (Szalay 1982). All recent molecular and total evidence phylogenies strongly support this arrangement (e.g. Kirsch et al. 1997; Springer et al. 1998; Palma and Spotorno 1999; Amrine-Madsen et al. 2003; Asher et al. 2004; Nilsson et al. 2004; Beck 2008; Meredith et al. 2009a; Meredith et al. 2009b; Mitchell et al. 2014; Beck et al. 2016)), as do most, but not all, morphological phylogenies (Horovitz and Sanchez-Villagra 2003; Sánchez-Villagra et al. 2007; Beck et al. 2008b; Horovitz et al. 2009; Ladevèze and Muizon 2010; Beck et al. 2014; Wilson et al. 2016). Robust molecular evidence further indicates that the four modern Australian orders form a clade, Eomarsupialia (note that the name "Euaustralidelphia" proposed by Nilsson et al. (2010) for this grouping is a junior synonym), to the exclusion of Microbiotheria (Phillips et al. 2006; Nilsson et al. 2010; Mitchell et al. 2014; Duchêne et al. 2018); thus, Microbiotheria is sister to all modern Australasian orders, a topology that has led to the suggestion that the presence of marsupials in Australasia is the result of a single dispersal event from South America, via Antarctica (Nilsson et al. 2010), but see below.

Still unresolved is the position of the root within Marsupialia, with three possible alternatives: between Didelphimorphia and Paucituberculata+Australidelphia, between Paucituberculata and Didelphimorphia+Australidelphia, or between Didelphimorphia+Paucituberculata (= Ameridelphia) and Australidelphia. Molecular sequence data and morphological evidence fail to unambiguously favor one of these three options, although some datasets do reject a root between Ameridelphia and Australidelphia (Palma and Spotorno 1999; Amrine-Madsen et al. 2003; Nilsson et al. 2003; Asher et al. 2004; Nilsson et al. 2004; Beck 2008; Meredith et al. 2009a; Meredith et al. 2009b; May-Collado et al. 2015). However, analyses of retroposon insertions provide relatively strong evidence that Didelphimorphia was the first order to diverge (Nilsson et al. 2010; Gallus et al. 2015), an interpretation potentially congruent with tarsal evidence (Beck 2017b; but see Szalay and Sargis 2006). Thus, a root between Didelphimorphia and Paucituberculata+Australidelphia seems most the plausible arrangement at present, but this requires further corroboration.

Relationships within the American marsupial radiation

The vast majority of modern American marsupial species diversity is within Didelphidae, the sole extant didelphimorphian family. One hundred and thirteen species are recognized as of this writing, 19 of which have been named within the past 25 years (Table S1), a ~20% increase in species diversity (Burgin et al. 2018). Most of these new species are within *Monodelphis* and *Marmosops* (Table S1), making these the two most species-rich didelphid genera, with 23 and 20 species, respectively (followed closely by *Marmosa*, with 19 species). Four new *Philander* species have also been named within the past 25 years (Table S1), more than doubling the species diversity of this genus.

Didelphidae and the extinct family Sparassocynidae collectively comprise the superfamily Didelphoidea (Reig et al. 1985; Reig et al. 1987; Goin 1997a; Forasiepi et al. 2009). Sparassocynids were small (< 500 g), probably mesocarnivorous species that apparently occupied carnivorous ecological niches during the late Miocene and Pliocene, after the extinction of small sparassodont metatherians but before the arrival of placental carnivorans (Reig and Simpson 1972; Engelman and Croft 2014; Zimicz 2014). However, ongoing phylogenetic studies suggest that sparassocynids may nest within Didelphidae, possibly close to *Monodelphis* (Beck and Voss 2012; Engelman and Croft 2014)(Beck and Taglioretti, in prep), which would warrant their demotion to a didelphid subfamily or tribe or, alternatively, recognition of more than one extant didelphoid family (see also below). The family

Sparassocynidae included a single genus, *Sparassocynus*, until the genus *Hesperocynus* was erected (Forasiepi et al. 2009) to accommodate a species, *H. dolgopolae*, previously referred to the didelphid genus *Thylatheridium* (see Reig 1958).

We recognize only a single family of extant didelphoids here, Didelphidae, following most recent classifications (McKenna and Bell 1997; Gardner 2005a; Gardner 2007; Voss and Jansa 2009; Astua 2015). However, some authors have recognized two (Caluromyidae, Didelphidae (Kirsch and Palma 1995) or four (Marmosidae, Caluromyidae, Glironiidae, Didelphidae) (Hershkovitz 1992) extant families, but including variable numbers of subfamilies and tribes. Molecular clock studies disagree as to whether this clade originated during the Oligocene/early Miocene (Jansa et al. 2014) or earlier, during the Eocene (Steiner et al. 2005; Vilela et al. 2015). Based on paleontological evidence, a divergence prior to the Oligocene appears unlikely given that rich middle to late Eocene metatherian faunas have been recovered from Amazonia in recent years, and no unequivocal didelphoids have yet been recorded (Goin and Candela 2004; Antoine et al. 2016). However, this interpretation is complicated by the metatherian fossil record being largely dental, and the lack of unequivocal dental synapomorphies of Didelphoidea or Didelphidae (Voss and Jansa 2009). Currently, the minimum paleontological age of Didelphidae (or Didelphoidea) is early Miocene (~20 Ma), based on fossils from the Colhue Huapi Member of the Sarmiento Formation of Patagonia (Goin et al. 2007a; Dunn et al. 2013). Didelphid fossils from this site include putative members of Didelphinae and Caluromyinae; if correctly identified, these specimens would indicate that the modern subfamilies (which should perhaps then be recognized as distinct families) had already diverged from one another by this time.

Within Didelphidae, a combined morphological, genetic, and karyotypic study found strong support for four subfamilies (Voss and Jansa 2009): Caluromyinae (comprising the genera *Caluromys* and *Caluromysiops*), Glironiinae (for *Glironia* only), the Hyladelphinae (for

Hyladelphys only), and the much more diverse Didelphinae (the remaining genera). There is strong support for Hyladelphinae+Didelphinae, but the branching pattern between this clade and the other two subfamilies (which corresponds to the root) has yet to be confidently resolved (Voss and Jansa 2003, 2009). The number and composition of tribes within Didelphinae remains a topic of debate. Voss and Jansa (2009) recognized four tribes within Didelphinae, all of which received strong support from their combined phylogenetic analysis: Marmosini (*Marmosa*, *Monodelphis*, and *Tlacuatzin*), Metachirini (*Metachirus* only), Didelphini (*Chironectes*, *Didelphis*, *Lutreolina*, and *Philander*), and Thylamyini (*Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, *Marmosops*, and *Thylamys*). This classification largely parallels that of Reig et al. (1985, 1987), except for the separation of Thylamyini from Marmosini, and is gaining acceptance (e.g. Astua 2015). Integrating fossils into phylogenetic analysis of didelphid relationships will be an important area of future research, particularly regarding the timing of diversification. For example, several extinct didelphid species from the middle Miocene of Colombia have been referred to extant genera (*Thylamys* and *Micoureus*/*Marmosa*) (Goin 1997a) and so provide minimum ages for the origin of these taxa (Jansa et al. 2014). Ongoing phylogenetic work also suggests that, among known fossil didelphid genera, *Thylophorops* is probably a member of Didelphini, *Thylatheridium* is closely related to *Monodelphis* (as may be sparassocynids – see above), and *Hyperdidelphys* belongs to Didelphinae (Voss and Jansa 2009).

Four new didelphid genera have been recognized since 2000: *Chacodelphys*, *Cryptonanus*, *Hyladelphys*, and *Tlacuatzin* (Voss et al. 2001; Voss and Jansa 2003; Voss et al. 2004; Voss et al. 2005). These genera have been erected for species previously placed in *Gracilinanus* (*Hyladelphys* and *Cryptonanus)* and *Marmosa (Chacodelphys* and *Tlacuatzin*). *Chacodelphys* and *Hyladelphys* are currently monotypic (Voss and Jansa 2009), but five species of *Cryptonanus* and five species of *Tlacuatzin* have been recognized (Astua 2015). The most phylogenetically divergent of these taxa is *Hyladelphys kalinowskii*, which is placed in its own subfamily, Hyladelphinae, and represents the sister-taxon to the bulk of the didelphid radiation (Didelphinae) (Flores 2009; Voss and Jansa 2009). *Chacodelphys formosa* is probably the smallest extant South American marsupial (Voss et al. 2004); its previously uncertain phylogenetic relationships within Thylamyini were recently clarified using DNA extracted from a nearly century-old skin (Díaz-Nieto et al. 2016), indicating that it is the sister-taxon of *Cryptonanus*.

Additional, currently unnamed species-level diversity is known or seems likely to exist within several didelphid genera, including *Chironectes*, *Glironia*, *Gracilinanus*, *Hyladelphys*, *Metachirus*, and *Thylamys* (Voss et al. 2005; Voss and Jansa 2009; Giarla et al. 2010; Palma et al. 2014). Given the relatively recent recognition of the genera *Chacodelphys*, *Cryptonanus*, *Hyladelphys*, and *Tlacuatzin* (Voss et al. 2001; Voss and Jansa 2003; Voss et al. 2004; Voss et al. 2005), it seems feasible that supraspecific diversity will also continue to be discovered within Didelphidae in future. Particularly intriguing in this respect is *Sairadelphys tocantinensis*, which was described in 2011 based on late Pleistocene dental specimens from Gruta dos Moura cave, Tocantins state, northern Brazil (Oliveira et al. 2011). *Sairadelphys* was referred to Hyladelphinae by Oliveira et al. (2011), but its dentition differs markedly from that of *Hyladelphys* (and that of all other known didelphids), and ultimately it may warrant distinction at the subfamilial level, or even higher (RMDB, pers. obv.). Given the comparatively young age of known *S. tocantinensis* material, this taxon may still be extant, in which case its discovery would be of considerable interest.

Like didelphids, caenolestids are the sole extant representatives of their order, Paucituberculata. However, they are far less speciose, with only seven extant species currently recognized (Patterson 2015). Of these, two were named since 1995, a 40% increase in diversity (Burgin et al. 2018)(Table S1). Both new caenolestids pertain to the genus

Caenolestes and were collected in the Ecuadorean Andes (Albuja and Patterson 1996; Ojala-Barbour et al. 2013). Ojala-Barbour et al. (2013) also conducted the first phylogenetic analysis of all extant species, finding that *Caenolestes* species form a clade separate from that of *Rhyncholestes raphanurus*+*Lestoros inca*. This result supports recognizing *Lestoros* as a genus distinct from *Caenolestes*, as argued by most recent authors (e.g. Myers and Patton 2007; Timm and Patterson 2007; Martin 2013). Interestingly, this analysis did not provide support for dividing the genus *Caenolestes* into taxonomic groups that reflect long-observed ecological differences among species (e.g. Anthony 1924): the larger, mid-elevation species (*C. caniventer*, *C. condorensis*, and *C. convelatus*) do not constitute a monophyletic group exclusive of the smaller, high-elevation *C. fuliginosus*. Rather, *C. fuliginosus* appears to represent a lineage that diverged after *C. convelatus* but prior to the divergence of *C. caniventer* and *C. condorensis*. *C. sangay*, which represents another relatively large, mid-elevation species, is clearly part of the *C. caniventer*+*C. condorensis* clade, but its position within this clade is not well resolved. Caenolestids are comparatively poorly studied, and many basic aspects of their biology remain unknown or only partially understood (Gardner 2007; Patterson 2015). It seems probable that additional species-level diversity within the family will be revealed with further fieldwork and taxonomic revision of currently known specimens.

The order Microbiotheria has the smallest geographic range of any extant mammalian order and has generally been recognized as including a single species, *Dromiciops gliroides* (Gardner 2005b; Palma and Valladares-Gomez 2015). Two subspecies have been recognized by some authors (e.g. Marshall 1982), one corresponding to a mainland (southern Chile) population and the other to the population on Chiloé Island, but this distinction has not been accepted by others (e.g. Patterson and Rogers 2007). A phylogeographic analysis did not find support for a mainland-island division within *Dromiciops*, but did recognize northern and southern populations (the latter including Chiloé Island), and also a third, small and geographically intermediate, population (Himes et al. 2008). A subsequent cranial morphometric study found patterns congruent with those of Himes et al. (2008) and proposed two new species (*D. bozinovici* and *D. mondaca*; Table S1), reserving *D. gliroides* for the Chiloé Island and southern mainland population (D'Elía et al. 2016). However, Martin (2018) rejected this proposal based on a morphological and morphometric study of nearly 150 specimens, concluding that the differences observed represented intraspecific variation. Similarly, Suárez-Villota et al. (2018) concluded *Dromiciops* was monotypic based on a multi-locus DNA sequencing study. In contrast to didelphids and caenolestids, it seems unlikely that further species will be recognized within *Dromiciops*, as it has been relatively well-sampled across its modern (very restricted) range (D'Elía et al. 2016; Martin 2018; Suárez-Villota et al. 2018).

Relationships within the Australasian marsupial radiation

Many molecular studies in the last 25 years have examined higher order relationships within modern Australasian marsupials (Retief et al. 1995; Kirsch et al. 1997; Springer 1997; Springer et al. 1998; Nilsson et al. 2004; Phillips et al. 2006; Meredith et al. 2009a; Meredith et al. 2009b; Mitchell et al. 2014; Duchêne et al. 2018). These studies have become increasingly large, both in terms of genomic coverage and taxon sampling, with near complete taxon sampling now appearing within reach. As a result, we now have a much-improved understanding of the relationships among and within the orders and families of the Australian marsupial radiation. Many morphological studies have also been conducted examining relationships amongst marsupials, including studies that have focused on Australian groups (Wroe and Musser 2001; Horovitz and Sanchez-Villagra 2003; Murray and

Megirian 2006a; Sánchez-Villagra et al. 2007; Horovitz et al. 2009; Prideaux and Warburton 2010; Beck 2012; Beck et al. 2014; Beck et al. 2016; Beck 2017b). These have also dramatically improved our understanding of relationships and have enabled fossil taxa to be included, although some uncertainties remain, particularly regarding the affinities of several fossil groups.

While the monophyly of the four modern Australasian orders is now well established, relationships amongst these orders have proved difficult to resolve until recently. Two major groupings are apparent: Diprotodontia, and a clade comprising Notoryctemorphia, Peramelemorphia and Dasyuromorphia (Phillips et al. 2006; Beck 2008; Meredith et al. 2009a; Beck et al. 2014; Mitchell et al. 2014; Duchêne et al. 2018). These three polyprotodont orders have recently been placed in the newly created superorder Agreodontia (Beck et al. 2014). A major issue within Agreodontia has been determining the relationship of the highly morphologically derived marsupial moles (Notoryctemorphia) to Peramelemorphia and Dasyuromorphia. Several morphological assessments, particularly those that have used postcranial evidence, have supported a relationship with Peramelemorphia (Szalay 1994; Horovitz and Sanchez-Villagra 2003), but others that have focused on cranial characters have suggested closer affinities to Dasyuromorphia (Ladevèze et al. 2008). Molecular and total evidence studies, meanwhile, have variously placed Notoryctemorphia as sister to Peramelemorphia (Beck et al. 2016), Dasyuromorphia (Springer et al. 1998; Nilsson et al. 2004; Beck 2008; Phillips and Pratt 2008; Meredith et al. 2009b), or a combined Dasyuromorphia+Peramelemorphia clade (Phillips et al. 2006; Meredith et al. 2009a; Mitchell et al. 2014; May-Collado et al. 2015; Maga and Beck 2017). However, a recent phylogenomic data set combining data from over 1500 loci strongly supports placement of the Notoryctemorphia as sister to the Peramelemorphia (Duchêne et al. 2018). Only one Australian marsupial order is entirely extinct, Yalkaparidontia (Archer et al. 1988; Beck et al.

2014). This order, known only from Oligo-Miocene fossils of a single genus - the bizarre, dentally specialized, possible “mammalian woodpecker” *Yalkaparidon* (Archer et al. 1988; Beck 2009; Beck et al. 2014) – from the Riversleigh World Heritage Area (WHA), is probably an australidelphian, but its affinities otherwise remain obscure (Beck et al. 2014).

Dasyuromorphia

Within Dasyuromorphia, three modern families are recognized: Thylacinidae, containing a single modern species, the now extinct Tasmanian tiger or thylacine (*Thylacinus cynocephalus*); Myrmecobiidae, also containing a single modern species, the numbat (*Myrmecobius fasciatus*); and the highly diverse and speciose Dasyuridae, containing 17 genera and over 70 species of carnivorous and insectivorous Australasian marsupials (Wilson and Mittermeier 2015). Although the distinction of these three families is well supported (Mitchell et al. 2014; May-Collado et al. 2015), their interrelationships had historically proved difficult to resolve with either molecular or morphological data (Krajewski et al. 1992; Krajewski et al. 1997b; Krajewski et al. 2000; Wilson and Mittermeier 2015; Westerman et al. 2016b). Phylogenetic studies now indicate that Thylacinidae is probably the sister lineage to a combined Myrmecobiidae+Dasyuridae clade (Krajewski et al. 1997b; Mitchell et al. 2014; May-Collado et al. 2015; Westerman et al. 2016b; Feigin et al. 2017; Kealy and Beck 2017). However, conflicting retroposon insertion patterns suggest that incomplete lineage sorting complicates uncovering relationships among the three families (Feigin et al. 2017).

Despite many studies that have substantially improved our understanding of dasyurid relationships, the subfamilial and tribal systematics of this large and diverse family remained unsettled until recently, with multiple competing arrangements proposed (Archer 1982; Kirsch et al. 1997; Krajewski et al. 2000; Van Dyck 2002; Groves 2005a; Baker 2015;

Westerman et al. 2016b; Kealy and Beck 2017). Molecular studies consistently recognize two major clades (usually considered to be subfamilies) within Dasyuridae, both then divided into two further subclades (usually considered to be tribes) (Kirsch et al. 1997; Krajewski et al. 1997a; Krajewski et al. 2000; Mitchell et al. 2014; May-Collado et al. 2015; Westerman et al. 2016b); this overall arrangement was also supported by the total evidence analyses of Kealy and Beck (2017). The first major clade, Sminthopsinae, comprises four genera (*Sminthopsis, Antechinomys, Ningaui, Planigale*), with *Planigale* (the sole member of Planigalini) sister to the other three (=the tribe Sminthopsini). The second major clade, Dasyurinae, comprises 13 genera, with *Antechinus, Murexia* and *Phascogale* (= Phascogalini) forming a well-supported subclade that is sister to the other ten genera (*Dasyurus, Sarcophilus, Dasycercus, Dasyuroides, Dasykaluta, Parantechinus, Myoictis, Pseudantechinus, Neophascogale,* and *Phascolosorex* (= Dasyurini). More recently, an alternative classification has been proposed, which is broadly similar but with Phascogalini raised to subfamilial level as Phascogalinae (Baker 2015).

Despite this overall consensus regarding suprageneric relationships within Dasyuridae, generic nomenclature and limits remain somewhat unsettled, with additional changes likely to be required as data continues to accumulate. In 2002, four new monotypic genera (*Micromurexia, Murexechinus, Paramurexia, Phaschomurexia*) were proposed for the morphologically distinct species of New Guinean dasyurids previously assigned to '*Antechinus*' (Van Dyck 2002). Although these new genera have been adopted by some authors (Groves 2005a), they have not been widely accepted (Helgen 2007; Baker 2015) as these species have been shown to be monophyletic in molecular analyses with the species traditionally placed in the genus *Murexia*, and so it has been recommended that *Murexia* be expanded to accommodate them (Armstrong et al. 1988; Krajewski et al. 2007).

The generic position of the sandstone dibbler/sandstone false antechinus (*Pseudantechinus bilarni*) has also been unclear. Although this species has been placed in *Parantechinus* (Archer 1982), molecular data indicated that it is not closely related to the dibbler (*Parantechinus apicalis*) (Krajewski et al. 1997c). In 2000, *P. bilarni* was moved to *Pseudantechinus* but with the concern that this might make the genus paraphyletic with respect to other genera, such as *Dasyuroides* and *Dasycercus* (Cooper et al. 2000). However, subsequent molecular analyses have demonstrated that *P. bilarni,* while divergent, is sister to other *Pseudantechinus* species (Westerman et al. 2008; Mitchell et al. 2014; Westerman et al. 2016b; Kealy and Beck 2017). Intriguingly, these studies also suggest that the southwest Australian *Parantechinus apicalis* is the sister taxon to the New Guinean genus *Myoictis* (Westerman et al. 2016b; Kealy and Beck 2017).

Expanded taxon sampling within *Sminthopsis* also indicates that this speciose genus is paraphyletic as currently defined, with the genera *Ningaui* and *Antechinomys* clustering within it in molecular phylogenies (Mitchell et al. 2014; May-Collado et al. 2015; Westerman et al. 2016b), making future taxonomic changes inevitable. There is also uncertainty about status of the monotypic genus *Dasyuroides* (kowari), which some authors have suggested should be synonymised with *Dasycercus* (mulgaras) (Cooper et al. 2000; Groves 2005a). This proposal has received variable support from molecular analyses (Mitchell et al. 2014; May-Collado et al. 2015). Although it appears *Dasyuroides* and *Dasycercus* are sister genera (Westerman et al. 2008; Westerman et al. 2016b; Kealy and Beck 2017), whether they are sufficiently distinct to be retained as separate genera remains debated.

Many of the new marsupial species and subspecies described or recognized over the last 25 years are within the family Dasyuridae (Table S1), including six new species of *Antechinus* from Australia (Baker et al. 2012; Baker et al. 2013; Baker et al. 2014; Baker et al. 2015) and an additional species of *Myoictis* from New Guinea (Woolley 2005). However, ongoing research is likely to uncover additional species within many dasyurid genera, including *Sminthopsis, Planigale, Pseudantechinus, Phascolosorex, Murexia* and *Myoictis* (Baker 2015; Westerman et al. 2016a). This reflects the small size and morphological conservatism of many genera, limited sampling and, perhaps most importantly, a lack of recent concerted taxonomic research effort for many genera..

Peramelemorphia

Phylogenetic relationships and systematics within Peramelemorphia have been the subject of ongoing uncertainty for decades, but recent studies have seen a consensus beginning to emerge. There have been debates about whether bilbies (genus *Macrotis*) are closer to Australian bandicoots (Groves and Flannery 1990), or if Australian and New Guinean bandicoots form a clade to the exclusion of the bilbies (Kirsch et al. 1997). This debate appears to have been resolved by recent molecular studies, all of which have recovered bilbies as a distinct clade, warranting familial distinction as Thylacomyidae (Westerman et al. 1999; Pacey et al. 2001; Westerman et al. 2012; Travouillon and Phillips 2018), an arrangement that has been widely accepted (Groves 2005b; Van Dyck and Strahan 2008; Wilson and Mittermeier 2015; Travouillon 2016). The enigmatic pig-footed bandicoot, *Chaeropus ecaudatus,* was also found to be sufficiently genetically divergent from other peramelemorphians (Westerman et al. 1999) to warrant familial status as Chaeropodidae (Groves 2005b). This status was confirmed in all subsequent molecular studies (Meredith et al. 2008b; Westerman et al. 2012; Mitchell et al. 2014; Travouillon and Phillips 2018) and has also been widely accepted (Groves 2005b; Van Dyck and Strahan 2008; Wilson and Mittermeier 2015; Travouillon 2016). The family Peroryctidae (containing the mainly New Guinean genera *Echymipera, Rhynchomeles, Peroryctes* and *Microperoryctes*), was proposed by Groves and Flannery (1990) as distinct from the mainly Australian Peramelidae (genera *Isoodon, Perameles*) and was recognized by some subsequent authors (e.g. Strahan 1995).

However, the molecular study of Westerman et al. (1999), which was based on a single gene (12S rRNA), found Peroryctidae to be paraphyletic; as a result, the family was not recognized by some authors (Groves 2005b; Helgen 2007). However, this paraphyly has not been recovered in subsequent molecular studies using multiple genes (Meredith et al. 2008b; Westerman et al. 2012; Mitchell et al. 2014; Kear et al. 2016), nor in any morphological studies (Travouillon et al. 2010; Travouillon et al. 2013; Travouillon et al. 2013b; Gurovich et al. 2014; Travouillon et al. 2014; Travouillon et al. 2015b; Chamberlain et al. 2016). Consequently, Travouillon and Phillips (2018) reinstated the family Peroryctidae as the fourth family of modern peramelemorphians.

Recent molecular and total evidence analyses have typically found that Chaeropodidae (*Chaeropus*) was the first modern family to diverge, followed by Thylacomyidae (*Macrotis*), with Peramelidae and Peroryctidae as sister-taxa (Westerman et al. 2012; Mitchell et al. 2014; Kear et al. 2016; Travouillon and Phillips 2018). Within Peroryctidae, *Peroryctes* appears to be sister to the other genera, which have therefore been classified as the subfamilies Peroryctinae (*Peroryctes* only) and Echymiperinae (the remaining genera) respectively (Travouillon and Phillips 2018). Within Echymiperinae, the position of *Rhynchomeles* (known from a single species, the possibly extinct Seram bandicoot, *R. prattorum*) is uncertain; it may nest within *Echymipera*, in which case it should probably be synonymized with this genus.

Two modern peramelemorphian species, namely *Microperoryctes aplini* (Helgen and Flannery 2004a)and *Perameles papillon* (Travouillon and Phillips 2018), have been described in the last 25 years (Table S1), and several others have been raised from synonymy (Table S3) or will be in the future (e.g. *Perameles bougainville* appears to comprise multiple species-level taxa (Travouillon and Phillips 2018)). In addition, most of the New Guinean genera appear to contain currently unrecognized species-level diversity (Warburton and

Travouillon 2016). This trend of increasing species diversity therefore seems likely to continue, although most of the as yet undescribed Australian species have probably gone extinct post-European settlement (Travouillon and Phillips 2018).

Diprotodontia

Diprotodontia is the most speciose and morphologically disparate of the Australasian marsupial orders. It contains 11 modern families, with 41 modern genera and ~148 extant species (Wilson and Mittermeier 2015); recent molecular clock studies suggest that most of these families originated in the Eocene and early Oligocene (Mitchell et al. 2014). Relationships amongst these families have been controversial, but molecular studies are increasingly bringing clarity (Kavanagh et al. 2004; Phillips and Pratt 2008; Meredith et al. 2009b; Meredith et al. 2009c; Mitchell et al. 2014; May-Collado et al. 2015; Duchêne et al. 2018). The suborder Vombatiformes, containing two families, Vombatidae (wombats) and Phascolarctidae (koala), has been consistently resolved as the sister lineage to the other nine families. Amongst the remaining nine, three monophyletic groupings are now well established. Firstly, the suborder Macropodiformes (sometimes referred to as Macropodoidea), comprising three families, namely Hypsiprymnodontidae (musky rat-kangaroo), Potoroidae (potoroos and bettongs) and Macropodidae (kangaroos and wallabies), although potoroids and macropodids are sometimes combined into a single family, Macropodidae (e.g. Prideaux and Warburton 2010); secondly, the superfamily Phalangeroidea, comprising two families, Phalangeridae (cuscuses and brushtail possums) and Burramyidae (pygmy possums); and thirdly the superfamily Petauroidea, comprising four families, Petauridae (gliding and striped possums), Pseudocheiridae (ringtail possums), Tarsipidae (honey possum), and Acrobatidae (feathertail possums). The relationships between Macropodiformes, Phalangeroidea and Petauroidea has proved especially difficult to resolve, an apparent consequence of their rapid divergence in the mid-Eocene (Mitchell et al.

2014; Duchêne et al. 2018). A monophyletic grouping of all “possums” (Phalangeroidea+Petauroidea), referred to as the suborder Phalangeriformes was initially supported by DNA hybridization data (Kirsch et al. 1997) and has been followed by some authors (Groves 2005c). However, this arrangement has received little support in subsequent molecular studies. Instead these analyses have allied Macropodiformes with either Phalangeroidea (Phillips and Pratt 2008; Meredith et al. 2009a; Meredith et al. 2009b; Meredith et al. 2009c), consistent with some morphological evidence (Szalay 1994), or with Petauroidea (Meredith et al. 2011; Mitchell et al. 2014; May-Collado et al. 2015), but without strong support for either arrangement. Recently, a phylogenomic study of >1000 nuclear loci has provided moderately strong support for Macropodiformes and Petauroidea being sister taxa, but a subset of loci provided some support for the alternative arrangement (Duchêne et al. 2018).

Over the last few decades, the two families in the Phalangeroidea have displayed contrasting patterns of systematic stability within Burramyidae and considerable instability within Phalangeridae (Helgen and Jackson 2015; Jackson 2015a). Subfamilial classification and generic limits within Phalangeridae have been unstable for decades, but consensus is now beginning to emerge with the increased use of molecular data (Helgen and Jackson 2015). Based primarily on morphological analyses, two subfamilies were traditionally recognised within Phalangeridae: Ailuropinae, containing the genus *Ailurops* (Bear Cuscus, restricted to Sulawesi), and Phalangerinae, with the latter further separated into the tribes Phalangerini (genera *Phalanger, Spilocuscus*) and Trichosurini (genera *Strigocuscus, Trichosurus, Wyulda* (Flannery et al. 1987; Groves 2005c; Jackson and Groves 2015). However, a series of molecular studies have consistently demonstrated that this arrangement is incorrect; in particular, they revealed that *Strigocuscus* as then recognised is not monophyletic (Kirsch and Wolman 2001; Ruedas and Morales 2005; Raterman et al. 2006; Meredith et al. 2009c).

Instead, three subfamilies are now recognized: Phalangerinae (genera *Phalanger, Spilocuscus*); Trichosurinae (genera *Trichosurus, Wyulda*) and an expanded Ailuropinae that comprises the genus *Ailurops* and a redefined *Strigocusus* that now only includes the Small Sulawesi Cuscus (*Strigocuscus celebensis*) and the Small Sangihe Cuscus (*Strigocuscus sangirensis*) (Helgen and Jackson 2015). Ailuropinae and Phalangerinae have been resolved as sister taxa, to the exclusion of Trichosurinae (Raterman et al. 2006; Meredith et al. 2009c; Mitchell et al. 2014; May-Collado et al. 2015). In addition, the Peleng Cuscus, previously *Strigocuscus pelengensis*, and the Ground Cuscus, previously *Strigocuscus gymnotis*, have both now been transferred to the genus *Phalanger* (Helgen and Jackson 2015). Beyond this, species limits within the Phalangeridae continue to be in a state of flux, with new species continuing to be described (Table S1); including *Trichosurus cunninghami* (Lindenmayer et al. 2002) from southeastern Australia and two remarkable island endemics, *Spilocuscus wilsoni* (Helgen and Flannery 2004b) and *Phalanger alexandrae* (Flannery and Boeadi 1998) from eastern Indonesia. Ongoing research will likely result in the recognition of additional phalangerid taxa (Helgen 2007; Helgen and Jackson 2015). This is also likely to be true for the burramyid genus *Cercartetus* (Osborne and Christidis 2002).

Relationships within Petauroidea are now well established, with Petauridae and Pseudocheiridae being strongly supported as sister taxa to the exclusion of Tarsipedidae, and Acrobatidae being sister to these three families (Meredith et al. 2009c; Mitchell et al. 2014; May-Collado et al. 2015). Within Petauridae, two well supported subfamilies are recognized, Petaurinae (wrist-winged gliders) and Dactylopsilinae (striped possums) (Kirsch et al. 1997; Meredith et al. 2009c; Meredith et al. 2010; Mitchell et al. 2014). However, the subfamilial associations of Leadbeater's Possum (*Gymnobelideus leadbeateri*) continues to be unresolved, as morphological data indicate an association with petaurines (Archer 1984; Flannery 1994; Van Dyck and Strahan 2008), while most (Edwards and Westerman 1992;

Kirsch et al. 1997; Osborne and Christidis 2001; Meredith et al. 2009c; May-Collado et al. 2015) but not all (Springer et al. 1994; Meredith et al. 2010; Mitchell et al. 2014) molecular studies have indicated a closer relationship to dactylopsilines. Additional studies are required to resolve this uncertainty. The composition of the dactylopsiline genus *Dactylopsila* has also been unsettled, with some authors suggesting that the Long-fingered Striped Possum (*Dactylopsila palpator*) is sufficiently distinct to be placed in its own genus, *Dactylonax* (Helgen 2007), as was proposed in its original description (Thomas 1910). Additional phylogenetic studies including all current members of the genus *Dactylopsila* will be needed to resolve this. A significant development is the recent discovery that the Arfak Striped Possum (*Dactylopsila kambuayai*), originally described based on fragmentary Quaternary (perhaps late Pleistocene) subfossil remains (Aplin et al. 1999), is still extant (Jackson 2015b). In addition, it is likely that species diversity within the Petauridae and Acrobatidae is currently underestimated (Helgen 2007; Aplin 2015a; Jackson 2015b).

Three subfamilies are recognized within Pseudocheiridae: Hemibelidinae (genera *Hemibelideus, Petauroides*), Pseudocheirinae (genera *Pseudochirulus, Pseudocheirus*) and Pseudochiropsinae (genera *Petropseudes, Pseudochirops*) (Groves 2005c; Jackson 2015c). These are supported by molecular data. with Pseudochiropsinae being sister to Hemibelideinae+Pseudocheirinae (Kirsch et al. 1997; Meredith et al. 2009c; Meredith et al. 2010; May-Collado et al. 2015; Duchêne et al. 2018). Although the monotypic genus *Petropseudes* (Rock Ringtail) was initially included in Pseudocheirinae (Groves 2005c), phylogenetic analyses indicate that it is a member of Pseudochiropsinae, and furthermore is nested within *Pseudochirops*, making the latter paraphyletic (Meredith et al. 2009c; Meredith et al. 2010; May-Collado et al. 2015). Future taxonomic adjustments will be required to resolve this anomaly. Ongoing research is likely to uncover additional species within several pseudocheirid genera, including *Petauroides* and *Pseudocheirus* (Jackson 2015c).

Macropodiformes (sometimes referred to as superfamily Macropodoidea) is a large and diverse suborder of the Diprotodontia, comprising at least 75 modern species in 18 genera (Wilson and Mittermeier 2015). As one might imagine, the relationships among macropodiforms have been the focus of much research and debate over the last 25 years. These studies have dramatically improved our understanding of systematics and resolved some major issues, but areas of uncertainty remain. Macropodiformes had traditionally been divided into two modern families, Potoroidae (potoroos, bettongs) and Macropodidae (kangaroos and wallabies) (Aplin and Archer 1987; Walton 1988). However, in the late 1990s, it was proposed that the enigmatic Musky Rat-kangaroo (*Hypsiprymnodon moschatus*) be removed from Potoroidae and placed in its own family, Hypsiprymnodontidae, on account of phylogenetic analyses that placed it as sister to other modern macropodiforms (Kirsch et al. 1997; Burk et al. 1998); congruent with this position, *H. moschatus* differs markedly from other macropodiforms in terms of its morphology, behavior, reproduction and ecology, with many of these features likely plesiomorphic. Hypsiprymnodontidae has been widely accepted (Groves 2005c; Van Dyck and Strahan 2008; Jackson and Groves 2015; Wilson and Mittermeier 2015). Some authorities have treated the remaining modern macropodiforms as a single family, Macropodidae (e.g. Prideaux and Warburton, 2010), but we recognize Potoroidae and Macropodidae as separate families here.

Within the family Macropodidae, only a single modern subfamily, Macropodinae, has traditionally been recognized (Van Dyck and Strahan 2008). However, in the last few decades, there has been much debate on the subfamily affinities of the diminutive Banded Hare-wallaby (*Lagostrophus fasciatus*). Originally placed in Macropodinae, it was later argued that *Lagostrophus* showed some derived morphological similarities to the otherwise extinct macropodid subfamily Sthenurinae (Flannery 1983). Several molecular studies then demonstrated that *Lagostrophus* was not closely related to any extant macropodine or potoroid, supporting the view that it represented a highly divergent evolutionary lineage (Westerman et al. 2002; Nilsson 2006; Meredith et al. 2008a). However, subsequent comprehensive morphological analyses (Prideaux and Warburton 2010) and comparison with ancient DNA extracted from fossil sthenurines (Llamas et al. 2015) suggest that *Lagostrophus* is not closely related to either sthenurines or macropodines, and that it is sufficiently distinct to be placed in a new subfamily, Lagostrophinae, along with the extinct fossil genera *Troposodon* and *Tjukuru* (Prideaux and Warburton 2010; Prideaux and Tedford 2012).

Relationships amongst the modern macropodine genera continue to prove difficult to resolve, presumably due to the rapid diversification of the modern macropodine genera during the late Miocene and Pliocene (Meredith et al. 2008a; Prideaux and Warburton 2010; Mitchell et al. 2014; Couzens and Prideaux 2018; Nilsson et al. 2018). This appears connected with the spread of drier, more open environments and, later, the appearance of grasslands in Australia, with several macropodine lineages evolving higher-crowned (hypsodont) teeth as an adaptation for feeding on more abrasive vegetation (Meredith et al., 2008; Couzens and Prideaux 2018). In addition to the long-recognized tribes Dendrolagini and Macropodini, two further tribes, the Dorcopsini (Prideaux and Warburton 2010) and the Setonichini (Jackson and Groves 2015) have recently been proposed. However, their validity, composition and internal relationships remain unsettled.

Within the Dendrolagini, the initially surprising grouping of the highly specialised rock-wallabies (*Petrogale*) with tree-kangaroos (*Dendrolagus*) is now well supported by molecular and morphological data (Kirsch et al. 1997; Meredith et al. 2008a; Prideaux and Warburton 2010; Mitchell et al. 2014). Although molecular data place the morphologically relatively unspecialised pademelons (*Thylogale*) as the sister genus to *Dendrolagus*+*Petrogale* (Kirsch et al. 1997; Meredith et al. 2008a; Mitchell et al. 2014), this is not well supported by morphological studies (Prideaux and Warburton 2010). Within rock-wallabies, molecular data indicate that the Nabarlek (previously classified as the only representative of the genus *Peradorcas, P. concinna*) nests within *Petrogale*, and so *Peradorcas* has now been synonymised with *Petrogale* (Potter et al. 2012; Potter et al. 2017).

Within Macropodini, *Macropus* (*sensu lato*) (comprising the subgenera *Macropus*, *Notamacropus* and *Osphranter*) and *Wallabia* appear to form a clade, with *Onychogalea* (nail-tail wallabies) and *Lagorchestes* (hare-wallabies) probably also part of this group, although their precise branching relationship varies amongst analyses (Kirsch et al. 1997; Westerman et al. 2002; Cardillo et al. 2004; Meredith et al. 2008a; Mitchell et al. 2014). The relationship of the Swamp Wallaby (*Wallabia bicolor*) to the other large wallabies and kangaroos of the genus *Macropus* (*sensu lato*) has also been the subject of much debate. While *Wallabia* is clearly distinct morphologically from all *Macropus* (*sensu lato*) species (Prideaux and Warburton 2010), many molecular analyses have nevertheless placed *Wallabia* within *Macropus* (*sensu lato*), rendering the latter paraphyletic (Kirsch et al. 1997; Westerman et al. 2002; Meredith et al. 2008a, 2009c; Phillips et al. 2013; Dodt et al. 2017; Nilsson et al. 2018). To resolve this inconsistency, it has been proposed to elevate each of the existing *Macropus* (*sensu lato*) subgenera (*Macropus, Notamacropus, Osphranter*) to full generic status (Meredith et al. 2008a; Eldridge 2010), a proposal that is gaining acceptance (Jackson and Groves 2015; Eldridge and Coulson 2015).

The relationship of the forest wallaby genera *Dorcopsis* and *Dorcopsulus* to other macropodines is also remains uncertain. It has recently been proposed that they, along with the extinct genus *Dorcopsoides*, should be recognised as a new macropodine tribe, Dorcopsini (Prideaux and Warburton 2010). While morphological data (Prideaux and Warburton 2010) and some molecular studies (Burk et al. 1998; Westerman et al. 2002; Cardillo et al. 2004; Mitchell et al. 2014; Llamas et al. 2015) support this proposal, placing

Dorcopsis and *Dorcopsulus* as sister to other macropodines, other molecular analyses do not (Kirsch et al. 1997; Meredith et al. 2008a). An alternative arrangement places *Dorcopsis* and *Dorcopsulus* along with *Setonix* in a newly proposed tribe, Setonichini (Jackson and Groves 2015). However, the relationships of the Quokka (*Setonix brachyurus*) are unsettled and have also been the subject of much speculation. Morphologically and genetically, *Setonix* does not appear to have any particularly close relatives amongst macropodines, although various studies have suggested some affinities with *Dorcopsulus*, *Thylogale, Onychogalea*, *Lagorchestes* and *Macropus* (*sensu lato*), or varying combinations of these (Kirsch et al. 1997; Westerman et al. 2002; Cardillo et al. 2004; Meredith et al. 2008a, 2009c; Prideaux and Warburton 2010; Mitchell et al. 2014; Llamas et al. 2015). Further studies are clearly required to resolve these and other relationships, and additional changes in macropodine systematics seem inevitable. Although only one new species of living macropodid has been described in the last 25 years (Table S1), the extraordinary 8-9 kg black and white terrestrial tree-kangaroo (*Dendrolagus mbaiso*) from West Papua (Flannery et al. 1995), ongoing research is likely to uncover additional species within several macropodid genera, in particular *Petrogale*, *Dendrolagus, Dorcopsis* and *Dorcopsulus* (Helgen 2007; Eldridge and Coulson 2015).

In contrast to the major systematic changes and continuing uncertainty within the speciose Macropodidae, relationships within Potoroidae have been more settled. Within Potoroidae, two tribes are recognised: Bettongini (bettongs and rat-kangaroos) and Potoroini (potoroos) (Jackson and Groves 2015; Eldridge and Frankham 2015). The composition of these tribes has been relatively uncontroversial, with the exception of uncertainty surrounding the affinities of the recently extinct Desert Rat-kangaroo (*Caloprymnus campestris*), which morphologically appears to belong to Bettongini (Flannery 1989) but may have affinity with Potoroini based on limited molecular data (Westerman et al. 2004). At the species level, recent molecular studies suggest that the taxonomy of *Bettongia* and *Potorous* is in need of revision, with the presence of cryptic, currently undescribed diversity (Frankham et al. 2012; Haouchar et al. 2016). In addition, the now extinct *Bettongia anhydra* was recently recognised as a separate species (McDowell et al. 2015); similarly to peramelemorphians (see above), it seems likely that further recently extinct potoroid species will be identified in future.

Palaeontology

Mesozoic record

As noted above, the oldest definitive metatherians appear to be from the Aptian-Albian (~110 Ma) of North America (Davis et al. 2008; Davis and Cifelli 2011). However, the affinities of some of these, which are known only from isolated teeth, are controversial; for example, *Holoclemensia* was originally described as a metatherian but has now been suggested to be a eutherian, whereas the reverse is true for *Pappotherium* (Davis and Cifelli 2011). Metatherians are now known to have been present in Asia, Europe and North America during the Late Cretaceous (Kielan-Jaworowska et al. 2004; Martin et al. 2005; Vullo and Gheerbrant 2009; Williamson et al. 2014), with numerous new taxa described in the last 25 years (Table S2). In North America, they were both taxonomically more diverse and morphologically more disparate than eutherians, whereas the reverse appears to have been true in Asia (Cifelli and Davis 2003; Wilson 2013, 2014). With an estimated body mass of ~5.0 kg, *Didelphodon vorax* is the largest known Mesozoic metatherian (Wilson et al. 2016), and an as-yet-undescribed skeleton suggests that it was probably semi-aquatic, as previously proposed by several authors (Szalay 1994; Longrich 2004) but see (Fox and Naylor 2006). The phylogenetic relationships of Mesozoic metatherians remain unclear, with most taxa still known only from isolated teeth; however, current phylogenies indicate that they fall outside the crown-clade, i.e. they are not members of Marsupialia (Williamson et al. 2014; Ni et al. 2016; Wilson et al. 2016; Bi et al. 2018).

In contrast to the extensive record from Laurasia, metatherians have not been found in the Mesozoic of Gondwana, except for a single tooth from the latest Cretaceous of Madagascar that was identified as a probable "marsupial" (= marsupialiform) (Krause 2001); however, this tooth was subsequently argued to be more likely a eutherian (Averianov et al. 2003). Of greatest significance is the absence of any metatherians or eutherians from the diverse mammal faunas now known from the Late Cretaceous of South America; instead, these faunas are comprised of non-therian groups such as meridolestidan "dryolestoids" and the superficially rodent-like gondwanatherians (Muizon 2011; Rougier et al. 2011a; Rougier et al. 2011b). Assuming that the lack of therian mammals from these faunas is not artefactual, and that the likely dispersal route of therians to Gondwana was from North America to South America (perhaps via the Aves Ridge, Case et al. 2005), these faunas provide an upper bound on the time of entry of metatherians into Gondwana (Beck 2017a; Beck in press).

Laurasian Cenozoic record

Metatherians are known from the Cenozoic of North America, Asia and Europe, but they are characterised by low species diversity and very limited morphological disparity (Crochet 1980; Korth 2008; Bennett et al. 2018a). They appear to have been much more strongly impacted by the KPg mass extinction event than were eutherians: in the well-studied North American record, only a single marsupialiform, the peradectid *Peradectes* cf. *P. pusillus*, is known from the earliest Palaeocene (Puercan 1), in contrast to at least ten eutherians (Wilson 2014). *Gurbanodelta*, from the late Palaeocene of China, may represent the youngest record of deltatheroidans, which would indicate that this group also survived the KPg extinction (Ni et al. 2016); if so, it is by far the smallest member of Deltatheroida, and one of the smallest known metatherians, with a mass of ~4 g (similar to the smallest modern marsupial (Van Dyck and Strahan 2008), the long-tailed planigale *Planigale ingrami*).

Besides *Gurbanodelta*, Laurasian Cenozoic metatherians are typically referred to one of two families, Herpetotheriidae and Peradectidae, based largely on differences in molar morphology; in particular, a v-shaped centrocrista has been considered characteristic of herpetotheriids, and a straight centrocrista characteristic of peradectids (Crochet 1980; Case et al. 2005; Korth 2008). However, recent phylogenetic analyses do not support monophyly of Herpetotheriidae and Peradectidae as currently recognised (Williamson et al. 2012; Williamson et al. 2014). Description and analysis of well-preserved fossil material reveals that herpetotheriids were probably relatively terrestrial and primarily insectivorous, whereas peradectids were probably more arboreal and may have been at least partially frugivorous (Kurz 2005; Sánchez-Villagra et al. 2007; Horovitz et al. 2008; Horovitz et al. 2009). Members of both families are characterised by small size, with the largest currently known taxa (the early Eocene North American peradectids *Mimoperadectes labrus* and *M. houdei*) probably weighing ~250 g (Williamson et al. 2012; Maga and Beck 2017). The very limited diversity and disparity of Laurasian metatherians during the Cenozoic, in comparison to the vastly more diverse and successful eutherians, has been used to support the hypothesis that metatherians are competitively inferior to eutherians (Lillegraven et al. 1987; Archibald 2011).

The discovery of new fossils from the middle Eocene Uzunçarşıdere Formation of Turkey has greatly expanded the known disparity of Laurasian Cenozoic metatherians (Maga and Beck 2017; Metais et al. 2018). These include *Anatoliadelphys maasae*, which is known from a nearly complete skeleton and partial skull that shows that this taxon was comparatively large (3-4 kg) and probably had a meso- or hypo-carnivorous diet (Maga and Beck 2017).

Another fossil metatherian from the same site, *Orhaniyeia nauta*, is probably related to *Anatoliadelphys*, but is known from dental remains only (Metais et al. 2018). A third taxon, *Galatiadelphys minor*, also known from isolated teeth, has been identified as metatherian (Metais et al. 2018), but the strongly invasive centrocrista of its upper molars is reminiscent of eutherians such as adapisoriculids and *Garatherium* (a possible early relative of tenrecs and golden moles; Seiffert 2010). The distinctive adaptations of *Anatoliadelphys*, *Orhaniyeia*, and (if indeed a metatherian) *Galatiadelphys* may be the result of evolving in the absence of potential eutherian competitors (Maga and Beck 2017; Metais et al. 2018). The region of Turkey where *Anatoliadelphys* was found was probably an island for at least part of the early Cenozoic (Sen 2013; Jones et al. 2018), and other fossil mammals from this fauna are highly distinctive and, in some way "relictual", suggesting that the fauna developed in relative isolation from adjacent landmasses (Maga and Beck 2017; Métais et al. 2017; Jones et al. 2018). If so, then the Uzunçarşıdere metatherians may provide further evidence that the diversity and disparity of Laurasian Cenozoic metatherians was constrained by competition from eutherians (Maga and Beck 2017; Métais et al. 2018).

The phylogenetic affinities of the Uzunçarşıdere metatherians are not well resolved. In the phylogenetic analysis accompanying its original description, *Anatoliadelphys* was identified as a non-marsupial marsupialiform (Maga and Beck (2018), but a later analysis by Carneiro (2018) found it to be a member of Protodidelphidae (a group otherwise known only from South America), within the marsupial order Didelphimorphia. Metais et al. (2018), meanwhile, found both *Anatoliadelphys* and *Orhaniyeia* to be closely related to Palaeogene bunodont taxa from South America and Australia, namely *Chulpasia*, *Palangania* and *Thylacotinga*, The uncertainty regarding the affinities of *Anatoliadelphys* and *Orhaniyeia* likely reflect high levels of dental homoplasy in dental features relating to a bunodont dentition (e.g. enlargement of stylar cusps B and D, reduction of molar crests), as discussed at length by Beck et al. (2008a).

Several recent phylogenetic analyses indicate that herpetotheriids, peradectids and other fossil Laurasian Cenozoic metatherians are not members of Marsupialia, or at least cannot be confidently placed within the crown-clade (Maga and Beck 2017; Beck in press). If so, then the origin and early diversification of Marsupialia probably occurred in Gondwana (Beck in press). However, other phylogenetic analyses suggest that the earliest divergences within Marsupialia may have occurred in North America (e.g. Wilson et al. 2016). The last records of Metatheria in Laurasia are from the Miocene (Bennett et al. 2018b), long before the appearance of *Didelphis virginiana* in the North American record <1 Ma (Woodburne 2010).

African Cenozoic record

A few enigmatic fossil taxa from Africa, all known from fragmentary dental remains, have at some point been identified as metatherian (Gunnell 2010). Of these, *Garatherium mahoubii* now appears to be a eutherian, perhaps a relative of modern tenrecs and golden moles (Seiffert 2010a, 2010b), whilst the late Eocene *Ghamidtherium dimaiensis* may be a bat (Gunnell 2010)(RMDB pers. obv.). *Peratherium* (previously "*Qatranitherium*") *africanum* is unquestionably a metatherian, and appears to be most closely related to *P. lavergnense* from the late Eocene-early Oligocene of Europe (Hooker et al. 2008). Finally, *Kasserinotherium tunisiense* (if it is indeed a metatherian; Gunnell 2010) shows intriguing, presumably derived, dental similarities to *Wirunodon chanku* from the ?Middle-Late Eocene of Peru and *Archaeonothos henkgodthelpi* from the early Eocene of Australia (Goin and Candela 2004; Beck 2015), although the significance of these resemblances has yet to be tested via phylogenetic analysis. Future fieldwork and additional fossil material will be required to clarify the evolutionary history of metatherians in Africa and their relationship to those of other landmasses.

South American Cenozoic record

Three main stages have long been recognized in the evolution of South American Cenozoic mammal faunas. Although traditionally referred to as strata I, II, and III (Simpson 1950, 1980; Flynn and Wyss 1998), more recent syntheses (Goin et al. 2012) have referred to these as the Early South American, Late South American, and Interamerican phases (Croft 2016; Goin et al. 2016). These intervals are characterized by marked differences in land mammal faunas, involving both eutherians and metatherians, and seem broadly related to large-scale temperature and/or precipitation trends in South America (Woodburne et al. 2014).

The first of these intervals, the Early South American Phase, encompasses early Cenozoic greenhouse conditions and extends from the late Cretaceous to the Eocene-Oligocene boundary. At many fossil sites of this age, metatherians are more taxonomically diverse (and were probably also more abundant) than eutherians (Croft 2016; Goin et al. 2016). One of the oldest probable metatherians from this phase is *Cocatherium lefipanum*, which was named in 2006 based on a single, bunodont lower molar from the early Paleocene (Danian) Lefipán Formation of southern Argentina and tentatively referred to the order Polydolopimorphia (Goin et al. 2006). A moderately diverse metatherian fauna is known from the "Banco Negro Inferior" at Punta Peligro in southern Argentina, which is also Danian in age (65.7-63.5 Ma) (Gelfo et al. 2009); most of this material remains to be described, but based on published information, none can be identified as representing unequivocal crown-clade marsupials (Forasiepi and Rougier 2009).

The most significant Paleocene South American metatherian fauna is from Tiupampa, Bolivia, within the Santa Lucía Formation. Originally discovered in 1982, the Tiupampa locality preserves a diverse range of vertebrates, including metatherian and eutherian mammals, lizards, crocodiles, lissamphibians and “fishes” (Muizon 1991; Suárez-Soruco 1991; Marshall et al. 1995). The age of Tiupampa is controversial: an early Palaeocene age has been proposed based on biostratigraphy (Muizon 1998; Gelfo et al. 2009), but a middle Palaeocene has also been suggested (Marshall et al. 1997; Sempere et al. 1997). Several of the Tiupampan mammals are represented by relatively complete, three-dimensionally preserved cranial and postcranial material and so represent critically important sources of information regarding early Palaeogene mammal evolution in South America (Muizon 1991; Muizon et al. 2015). Among the metatherians, *Pucadelphys andinus*, and *Mayulestes ferox* are known from nearly complete skeletons that have been described in detail (Marshall and Muizon 1995; Marshall et al. 1995; Muizon 1998; Ladevèze et al. 2011). A third metatherian, *Allqokirus australis*, is also known from relatively complete cranial remains (Muizon et al. 2018).

Pucadelphys was a small (~10-30 g) insectivore and, based on features of its postcranium, was probably relatively terrestrial (Argot 2002, 2003; Muizon and Argot 2003). Specimens of *Pucadelphys* were found at Tiupampa in two separate aggregations of multiple individuals, suggesting that it lived in groups, and the presence of strong sexual dimorphism (presumed males have longer and wider skulls and larger canines) implies a mating system characterised by male–male competition and polygyny (Ladevèze et al. 2011). *Mayulestes* was markedly larger, probably more carnivorous, and at least partially arboreal (Muizon 1998; Argot 2003; Muizon and Argot 2003). Recent phylogenies consistently place *Pucadelphys*, *Mayulestes* and another Tiupampan metatherian, *Andinodelphys*, outside Marsupialia (Forasiepi et al. 2015; Wilson et al. 2016; Engelman et al. 2018; Muizon et al. 2018), with *Pucadelphys* and *Andinodelphys* usually classified together in the family Pucadelphyidae (Muizon 1998; Ladevèze and Muizon 2007; Muizon et al. 2018). *Mayulestes* has been suggested to be an early, plesiomorphic member of the clade Sparassodonta (Muizon 1998), which includes carnivorous forms such as borhyaenids and the "sabre-toothed" thylacosmilids, but until recently, this had yet to receive clear phylogenetic support (Forasiepi et al. 2015; Wilson et al. 2016; Engelman et al. 2018). This changed with the study of Muizon et al. (2018), who described a digitally-reconstructed skull of *Allqokirus* from Tiupampa, which appears to be an early sparassodont. The accompanying phylogenetic analysis recovered a monophyletic Mayulestidae composed of *Mayulestes*, *Allqokirus*, and the Eocene sparassodont *Patene*, as the sister to all other sparassodonts, . Validating this topology will require reconciling the divergent character-taxon matrices of Muizon et al. (2018) and earlier phylogenetic analyses (Forasiepi et al. 2015; Wilson et al. 2016; Engelman et al. 2018).

Another key Early South American Phase fauna is from Itaboraí, southeastern Brazil. Fossil mammals from Itaboraí were first mentioned in the 1940s (Bergqvist et al. 2008), but the diverse mammal fauna collected from this site continues to be the subject of taxonomic, functional and phylogenetic studies (Szalay 1994; Szalay and Sargis 2001; Bergqvist et al. 2004; Oliveira and Goin 2006; Oliveira and Goin 2011; Beck 2017b). The age of the Itaboraí fauna has been successively revised downwards in recent years, with the most recent estimate being 50-53 Ma (Gelfo et al. 2009; Krause et al. 2017). More than 20 metatherian taxa have been described, although most are known only from isolated teeth and fragmentary jaws (Marshall 1987; Oliveira and Goin 2006; Oliveira and Goin 2011). The single best preserved metatherian specimen from Itaboraí is a skull of the polydolopimorphian, *Epidolops ameghinoi*, which is also by far the most common taxon at the site (Beck 2017b). The recent reanalysis of *Epidolops* by Beck (2017b) concluded that Polydolopimorphia as currently defined is polyphyletic, with *Epidolops* (and its probable relatives, such as polydolopids and bonapartheriids) falling outside Marsupialia, but argyrolagids (and possibly groeberiids and patagoniids) more closely related to Paucituberculata (which includes modern caenolestids), within Marsupialia. Several other recent studies, however, have recovered monophyly of a polydolopimorphian clade that includes polydolopids, bonapartheriids, argyrolagids and several other taxa, and have found this clade to be closely related to microbiotherians (e.g., Goin et al. 2009; Chornogubsky and Goin 2015). *Eobrasilia coutoi* was the first metatherian to be described from Itaboraí (Simpson 1947), and has recently been proposed to be a South American member of the family Stagodontidae (Carneiro and Oliveira 2017), which is otherwise known only from the Late Cretaceous of North America (see above); however, known material of *E. coutoi* is poorly preserved, and the resemblance to North American stagodontids may simply reflect convergent evolution of durophagous craniodental features (RMDB pers. obv.). A third Itaboraian metatherian, *Riolestes capricornicus*, was described in 2009 as the earliest known paucituberculatan, based on a single lower molar (Goin et al. 2009), but it has been suggested that this specimen may represent a deciduous third premolar of another taxon (Beck in press).

The significance of the Itaboraian metatherians for understanding the origin and evolution of crown-clade marsupials is debated. Beck (2017b) reviewed the Itaboraian metatherian fauna and concluded that there is no compelling evidence for the presence of crown-clade marsupials (contra e.g. Goin et al., 2009, 2016), a novel conclusion that will undoubtedly inspire much discussion and new analyses of Paleocene and early Eocene metatherians. Beck (2017b) concluded that the oldest known crown-clade marsupials are from the early Eocene Tingamarra Local fauna of Australia rather than Paleocene or early Eocene of South America: *Djarthia murgonensis* and an isolated calcaneus of a currently unnamed taxon, both of which appear to be stem-australidelphians (see below). If the metatherians from Itaboraí and older sites (e.g. Tiupampa) are not marsupials, the next oldest candidates from South America are from the La Barda locality; they include isolated tarsal remains that exhibit characteristic australidelphian apomorphies (Lorente et al. 2016) and *Bardalestes hunco*, which may represent an early paucituberculatan (Goin et al. 2009).

By the middle Eocene, eutherians were more diverse and abundant than metatherians (Croft 2016; Goin et al. 2016), and metatherian faunas were composed primarily of polydolopimorphians and sparassodonts (Woodburne et al. 2014). Most of these taxa are known only from teeth or fragmentary craniodental remains, though a conspicuous exception is the proborhyaenid *Callistoe vincei*, a moderately large sparassodont (~20-25 kg) (Argot and Babot 2011; Prevosti et al. 2013) represented by a virtually complete skeleton (Babot et al. 2002). These middle and late Eocene metatherians apparently occupied a variety of ecological niches: sparassodonts were terrestrial to scansorial mesocarnivores and hypercarnivores (Argot 2004; Prevosti et al. 2013; Croft et al. 2018); caroloameghiniid didelphimorphians were probably arboreal frugivores, potentially occupying primate-like ecological niches (Goin 2006); polydolopid polydolopimorphians likely consumed various proportions of insects, fruits, and/or vegetation depending on the species (Goin et al. 2016) (but see (Dumont et al. 2000)); and the unusual, short-faced groeberiids (still of uncertain higher taxonomic placement) may have filled an ecological niche similar to small rodents or even parrots, feeding on seeds and/or insects (Goin 1988; Pascual et al. 1994).

The transition from the Eocene to the Oligocene epoch marked a pronounced change in South American metatherian faunas and the beginning of the Late South American Phase of faunal evolution (Goin et al. 2012; Croft 2016). Groups last recorded during the early Oligocene include polydolopid and rosendolopid polydolopimorphians, as well as caroloameghiniid and sternbergiid didelphimorphians, whereas groups first recorded during this interval include argyrolagoids (other than *Groeberia* from Divisadero Largo, the age of which is uncertain but seems to be middle Eocene; (López 2010), notable for their hypsodont dentitions, and several families of paucituberculatans (Flynn and Wyss 1999; Flynn et al. 2003; Goin et al. 2010).

This shift in metatherian faunas (and other South American mammals) associated with the Eocene-Oligocene Transition has been termed the Patagonian Hinge ("Bisagra Patagónica" in Spanish)(Goin et al. 2012). It represents the South American equivalent of similar faunal turnover events seen on other land masses (such as the "Grande Coupure" of Europe, and the "Mongolian Remodelling" of Asia (Hooker et al. 2004; Kraatz and Geisler 2010)), and coincides with a dramatic drop in mean global temperatures (Zachos et al. 2001; Zachos et al. 2008; Woodburne et al. 2014), likely connected with the development of a permanent Antarctic icesheet. However, in South America (or at least in Patagonia, which has the most complete sedimentary record across this interval (Madden et al. 2010)), it may be more closely tied to arid conditions during the late middle Eocene that extended through the early Oligocene, as temperatures were relatively stable across this interval (Dunn et al. 2015; Kohn et al. 2015). The arrival of immigrant caviomorph rodents and platyrrhine primates from Africa during the Eocene (Antoine et al. 2011; Bond et al. 2015; Boivin et al. 2017) may also have had a major impact on South American mammal faunas through competition for ecological niches occupied by several Paleogene metatherian groups (e.g. polydolopimorphians and caroloameghiniids).

Some of the most impressive South American metatherians, modern or extinct, were the giant proborhyaenid sparassodonts of the late Oligocene. The largest of these, *Proborhyaena gigantea* of Argentina, likely had a body mass of 115-150 kg (Prevosti et al. 2013; Croft et al. 2018), making it one of the largest carnivorous metatherians known (Croft 2016). The evolution of these large sparassodonts may have been ecologically linked to the evolution of very large size in many herbivorous placental lineages during the same interval (Scillato-Yané 1977). Definitive members of the families Borhyaenidae (*Australohyaena antiqua*) and Hathliacynidae (*Notogale mitis*, *Sallacyon hoffstetteri*), two of the predominant groups of sparassodonts in Neogene faunas, are also first recorded in the late Oligocene (Forasiepi

2009; Croft et al. 2018). In addition to sparassodonts, late Oligocene metatherian faunas included the earliest argyrolagid (*Proargyrolagus bolivianus*) (Wolff 1984) and several lineages of paucituberculatans, including the earliest palaeothentids (*Antawallathentes* spp) (Rincón et al. 2015; Engelman et al. 2017). Many of these metatherians are known exclusively from the rich deposits of Salla, Bolivia, which has become one of the most important sites South America for remains of late Oligocene metatherians. A peculiar shrew-like metatherian from the late Oligocene of Mendoza, western Argentina, *Fieratherium sorex*, may be the sister-group to Paucituberculata (Forasiepi et al. 2014) or an early-diverging member of that clade (Engelman et al. 2017).

The early Miocene is among the best-sampled intervals for South American mammals (Marshall et al. 1983). Metatherian faunas were principally composed of sparassodonts (Forasiepi 2009; Prevosti et al. 2013) and a diversity of paucituberculatans, including palaeothentids, abderitids, and the oldest caenolestids (Bown and Fleagle 1993; Abello 2013, 2016). Paucituberculatans may have filled many of the insectivore-frugivore ecological niches occupied by polydolopids during the Paleogene (Pascual et al. 1996), whereas the precise breadth of ecological niches filled by sparassodonts remains a topic of investigation (Prevosti et al. 2012; Ercoli et al. 2014; Croft et al. 2018). Microbiotherians reached their peak diversity during the early Miocene (Marshall 1982) and, as noted previously, didelphids are first recorded during this interval, though only from very fragmentary remains (Goin et al. 2007a). A single tooth from the Cohue Huapi Member of the Sarmiento Formation in Patagonia represents the oldest record of saber-toothed (thylacosmilid) sparassodonts (Goin et al. 2007a).

One of the most significant Miocene metatherian sites in South America is that of La Venta, Colombia, which preserves a rich record of late middle Miocene (~13-11.5 Ma) mammals and other terrestrial and aquatic vertebrates from a lowland tropical forest environment (Kay et al. 1997; Croft 2016). The most recent analysis of La Venta's metatherians recognized 12 species, including five sparassodonts, four didelphids, and two paucituberculatans (Goin 1997a). None of these species has been recorded elsewhere in South America, even at the roughly contemporaneous site of Quebrada Honda, Bolivia, at which three sparassodonts, four paucituberculatans, and an argyrolagid have been identified (Sánchez-Villagra et al. 2000; Engelman et al. 2017, 2018). This illustrates the marked provinciality that had developed in South America by the early Miocene (Croft 2007; Croft et al. 2018), a phenomenon potentially related to significant variation in local climates and habitats, at least in the case of La Venta and Quebrada Honda (Catena et al. 2017). Unfortunately, the metatherians from sites of similar age in the Southern Cone (e.g. Villafañe et al. 2008; Pérez 2010; Brandoni 2014)) have yet to be described in detail, precluding comparisons across the length of the continent. Palaeothentoid paucituberculatans (including both palaeothentids and abderitids) apparently went extinct quite abruptly at the end of the middle Miocene, perhaps due to changes in precipitation patterns, leaving caenolestids as the sole representatives of the order (Engelman et al. 2017); microbiotherians also appear to have undergone considerable extinction at this time (Goin and Abello 2013). Sparassodonts peaked in taxonomic and morphological diversity during the middle Miocene, gradually decreasing in both thereafter (Croft et al. 2018).

By the late Miocene, South American metatherian faunas were composed primarily of didelphoid didelphimorphians: extinct species of several modern genera have been reported (*Lutreolina*, *Monodelphis*, *Thylamys* (Goin et al. 2010), as well as entirely extinct genera that nevertheless probably fall within the didelphid crown-clade (e.g. *Hyperdidelphys*, *Thylophorops*, *Thylatheridium*, "sparassocynids" (Voss and Jansa 2009; Beck and Voss 2012) – see above). Late Miocene sparassodonts included the large (50-120 kg) and well-known thylacosmilid, *Thylacosmilus*, the tiny hathliacynids *Borhyaenidium* and *Notictis* (both less than 3 kg), and the relatively large (15-30 kg)(Croft et al. 2018) and potentially more omnivorous *Stylocynus*, as well as a poorly-characterized borhyaenid (Forasiepi 2009; Croft et al. 2018). Only small hathliacynids and *Thylacosmilus* persisted into the Pliocene, with *Thylacosmilus* (the last surviving sparassodont) going extinct 3-4 Ma (Goin et al. 2016). Although terrestrial mammal dispersals between the Americas commenced during the late Miocene (the beginning of the Interamerican Phase), only procyonids have been recorded at South America sites that are older than late Pliocene in age (Woodburne 2010), making competition between placental carnivorans and sparassodonts an unlikely explanation for sparassodont extinction (Prevosti et al. 2013); a climatic explanation is more likely given overall trends in diversity and disparity (Croft et al. 2018). The appearance of more carnivorous didelphoids (“sparassocynids” and didelphids) during the late Miocene and Pliocene appears to represent a case of didelphimorphians filling niches vacated by small sparassodonts (hathliacynids) rather than competitive replacement of sparassodonts by didelphimorphians (Engelman and Croft 2014; Zimicz 2014).

Among the most unusual extinct South American metatherians were the argyrolagids *Microtragulus* and *Argyrolagus* from the late Miocene and Pliocene (Zimicz 2011). These small (40-60 g) (Zimicz 2011) metatherians, of which some very complete remains have been discovered, were bipedal and ricochetal and had ever-growing (hypselodont) cheek teeth (Simpson 1970). They may have occupied ecological niches similar to extant jerboas (Dipodidae) and kangaroo rats (Heteromyidae) (Simpson 1970), with suggestions that the lack of extant rodents filling similar niches in South America was attributable to the occupation of these niches by argyrolagids until relatively recently (Mares 1975, 1985). The affinities of argyrolagids have proven controversial; some authorities have placed them in the superfamily Argyrolagoidea in the order Polydolopimorphia (Goin et al. 2009; Forasiepi et al. 2014; Chornogubsky and Goin 2015), which includes dentally somewhat similar (i.e.

hypsodont or hypselodont) taxa such as groeberiids and patagoniids (Flynn and Wyss 1999; Goin et al. 2010), whereas others have concluded that they are members of Paucituberculata. (Sánchez-Villagra 2001; Beck 2017b). The survival of argyrolagids into the Pliocene means that it may be possible to obtain ancient proteins (such as collagen) from their fossils (Rybczynski et al. 2013), which should help clarify their phylogenetic relationships. The youngest sparassodont, *Thylacosmilus*, may also preserve ancient proteins, which may help confirm whether Sparassodonta falls outside Marsupialia, as current morphological evidence suggests (Forasiepi et al. 2015; Wilson et al. 2016).

Antarctic Cenozoic Record

Although data are still limited, recent fossil discoveries from Antarctica have highlighted the importance of this region in understanding metatherian and marsupial evolution (Reguero et al. 2013; Reguero 2016). These specimens are particularly significant because marsupials (and perhaps non-marsupial metatherians) presumably reached Australasia from South America, via Antarctica (Beck 2017a). Terrestrial fossil mammals from Antarctica have so far only been recovered from the La Meseta Formation of Seymour Island, which may span from the late Paleocene to the early Oligocene (Reguero et al. 2013; Gelfo et al. 2017) or, alternatively, the middle-to-late Eocene only (Douglas et al. 2014). All metatherian remains collected to date are from a single unit, the *Cucullaea I* Allomember, which may be early Eocene (Ypresian) or middle Eocene (Lutetian) in age (Reguero et al. 2013; Douglas et al. 2014; Gelfo et al. 2017). Among terrestrial Antarctic mammals, metatherians are the most species-rich group, accounting for at least 11 of the 17 taxa identified so far, including four “didelphimorphians,” two microbiotherians, four polydolopimorphians, and a species of uncertain affinities represented by an edentulous mandible (Goin et al. 1999; Reguero et al. 2013; Reguero 2016; Goin et al. 2018). The two species of *Antarctodolops* (Polydolopidae) described to date are also the most abundant mammals in the La Meseta Formation (Goin et al. 2007b; Reguero et al. 2013) . All of these metatherians pertain to typical South American groups, and at least two derorhynchids, are from genera (*Pauladelphys, Derorhynchus*) also recorded in mainland South America (Tejedor et al. 2009; Reguero et al. 2013; Goin et al. 2018) . It has been suggested that the metatherians of Antarctica arrived during the Paleocene via several waif dispersal events from South America (Reguero et al. 2013).

It has been proposed that some of the metatherian taxa known from the La Meseta Formation are related to modern Australasian marsupial groups (Reguero et al. 2013), specifically that derorhynchids may be peramelemorphians, the peculiar *Xenostylos* may be a dasyuromorphian, and that the polydolopimorphians may be related to diprotodontians. However, current evidence does not support a relationship between derorhynchids and peramelemorphians (Forasiepi and Rougier 2009; Beck in press), and polydolopimorphians do not appear to be closely related to diprotodontians (Beck 2017b). The affinities of *Xenostylos* have yet to be tested, but at present, the evidence linking this taxon (known from a single upper molar) and definitive dasyuromorphians does not appear compelling (RMDB pers. obv.). The closest faunal link between the Antarctic metatherians and Australian marsupials is provided by the La Mesetan *Marambiotherium glacialis* and *Woodburnodon casei*, which are microbiotherians and hence members of the marsupial superorder Australidelphia (Goin and Carlini 1995; Goin et al. 1999; Goin et al. 2007b), which also includes modern Australasian marsupials. However, definitive microbiotherians have not been described from Australia (putative microbiotherians from the early Eocene Tingamarra fauna have been reported but have yet to be described (Archer et al. 1999). Likewise, definitive Australasian marsupial groups have not been reported from Antarctica or South America, with the exception of isolated tarsals from southern Argentina that have been proposed to represent diprotodontians (Lorente et al. 2016). Although the evidence is currently inconclusive, the apparent absence of typical South American metatherians (e.g.

polydolopids, sparassodonts) and also eutherians (e.g. xenarthrans, notoungulates) from the Australasian fossil record hints at the presence of major barriers to dispersal between western Gondwana (South America and western Antarctica) and eastern Gondwana (Australasia and perhaps the part of Antarctica east of the Transantarctic Mountains) (Beck 2017a). The closest link between the South American and Australasian metatherian faunas is provided by *Chulpasia* (Sigé et al. 2009; Black et al. 2012b; Beck 2017a; see below).

Australasian Cenozoic Record

Although some significant progress has been made, our understanding of the early evolution of marsupials in Australia (and potentially non-marsupial metatherians, if they were ever present) is still hampered by an almost total lack of fossil sites of an appropriate age. The early Eocene Tingamarra Local Fauna provides our only direct fossil evidence prior to the late Oligocene (Godthelp et al. 1999). Godthelp et al. (1999) described *Djarthia murgonensis* from Tingamarra, and identified it as a possible “prototypical” Australian marsupial, but did not classify it beyond Marsupialia *incertae sedis*. In 2008, isolated petrosal and tarsal specimens from Tingamarra were referred to *Djarthia* and phylogenetic analyses showed that *Djarthia* is a plesiomorphic member of the marsupial order Australiadelphia (Beck et al. 2008a). Most strikingly, the tarsals referred to *Djarthia* show distinct australalidelphian apomorphies, namely a “continuous” lower ankle joint and a tripartite calcaneocuboid facet (Beck et al. 2008b). Subsequently, an isolated calcaneus from Tingamarra was described that lacked the “continuous” lower ankle joint but had a tripartite calcaneocuboid facet, suggesting it is transitional between the plesiomorphic non-australidelphian and derived australidelphian tarsal morphologies (Beck 2012). A third Tingamarran taxon, the bunodont *Chulpasia jimthorselli* was subsequently described based on isolated upper molars and identified as congeneric with *C. mattaueri* from the late Palaeocene or early Eocene of Peru (Sigé et al. 2009). This is the only metatherian genus currently known from both South

America and Australasia, and provides the closest biogeographic link between the metatherian faunas of the two continents. *Chulpasia mattaueri, C. jimthorselli* and another Tingamarran taxon, *Thylacotinga bartholomaii,* were referred to the same subfamily, Chulpasiinae (Sigé et al. 2009), but the higher-level relationships of this subfamily (including whether it belongs to Marsupialia or not) remain unclear; it may belong to the order Polydolopomorphia, or may represent an independent radiation of bunodont metatherians (Goin et al. 2006; Beck et al. 2008a; Black et al. 2012b). Most recently, the small, faunivorous metatherian *Archaeonothos godthelpi*, was described, based on a single upper molar from Tingamarra (Beck 2015). This distinctive taxon shows some (probably derived) similarities to *Kasserinotherium tunisiense* from the early Eocene of Africa and *Wirunodon chanku* from the ?middle–late Eocene of Peru, although whether these similarities are indicative of a close phylogenetic relationship remains unclear (Beck 2015).

In summary, Tingamarra preserves an intriguing, but still poorly known metatherian fauna that includes the oldest known definitive Australian marsupials (*Djarthia murgonensis*, and the unnamed transitional calcaneus), plus other taxa of more uncertain relationships. Given the lack of obvious relatives of some of these in later Australian sites, it seems that several marsupial (and possibly non-marsupial metatherian) lineages went extinct in Australia between the early Eocene and late Oligocene. It is also clear there was not simply a single dispersal of marsupials from South America to Australia (the scenario implied by phylogenies of extant marsupials only); instead, the fossil evidence from Tingamarra, South America and Antarctica suggests a much more complex biogeographical relationship between these landmasses, characterised either by multiple dispersals, differential extinctions, or a combination of these (Beck 2012, 2017a).

Oligocene

There are still no early Oligocene fossil sites containing terrestrial mammals known from Australia. However, the Pwerte Marnte Marnte Local Fauna (which preserves a diverse but highly fragmentary vertebrate fauna, including diprotodontians and a possible early notoryctemorphian) may be somewhat older than the other late Oligocene sites currently known (Murray and Megirian 2006b). The late Oligocene Australian fossil record as a whole has improved in the last few decades, thanks in particular to the continued work being done on the Etadunna Formation (South Australia), the Riversleigh World Heritage Area (WHA; Queensland), and Kangaroo Well in the Northern Territory.

Only one new dasyuromorphian has been described from the late Oligocene, *Badjcinus turnbulli*, a thylacinid from Riversleigh WHA (Muirhead and Wroe 1998), which, as a member of Thylacinidae, would appear to be the oldest generally accepted crown-clade dasyuromorphian. However, *Badjcinus* was not consistently recovered within Thylacinidae in recent phylogenetic analyses by Kealy and Beck (2017); instead, it was sometimes placed as sister to all other dasyuromorphians, and hence outside crown-clade Dasyuromorphia. As a consequence, Kealy and Beck (2017) recommended that *Badjcinus* be classified as ?Thylacinidae (Table S2). Kealy and Beck (2017) also consistently recovered two late Oligocene taxa that had previously considered to be members of Dasyuridae by some authors (Archer 1976; Murray and Megirian 2006a), but as Marsupialia *incertae sedis* by others (Godthelp et al. 1999; Wroe 2003), namely *Ankotarinja tirarensis* and *Keeuna woodburnei*, in a clade with the early Eocene stem-australidelphian *Djarthia murgonensis*; as a result, *Ankotarinja* and *Keeuna* should not be considered members of Dasyuromorphia.

The fossil record of Peramelemorphia has improved markedly in the last 25 years. Three genera (*Bulungu*, *Madju* and *Yarala*) are now known from the late Oligocene, with the oldest known species being *Bulungu muirheadae* from the Etadunna Formation (Muirhead and Filan 1995; Muirhead 2000; Travouillon et al. 2013b; Gurovich et al. 2014; Travouillon et al.

2015b). *Yarala* has been referred to its own family, Yaralidae, and superfamily Yaraloidea (Muirhead 2000), but *Bulungu* and *Madju* are not currently referred to a particular peramelemorphian family (Table S2). Species of *Bulungu* and *Yarala* differ from modern bandicoots in their smaller size (<150 g), shorter snouts and (based on their less specialised dentitions) presumably more insectivorous diets, and it seems likely that they filled the ecological niche that small dasyurids such as *Antechinus* occupy today (Muirhead and Filan 1995; Gurovich et al. 2014). *Madju variae*, from Riversleigh WHA is much more similar to modern bandicoots, with an elongated snout and omnivorous dentition, and is recognised as a crown peramelemorphian, in the suborder Perameloidea (Travouillon et al. 2015b).

The diversity of late Oligocene diprotodontians has also increased significantly, with 20 new species described (Table S2). Of these, only two are phascolarctids (koalas): *Nimiokoala greystanesi*, which is known from numerous dental remains and a well-preserved partial cranium (Black and Archer 1997b; Louys et al. 2009), and *Litokoala thurmerae,* from the Etadunna Formation, named based on a single upper molar (Pledge 2010), although Black et al. (2013) considered *L. thurmerae* to be a *nomen dubium*.

Within Thylacoleonidae (marsupial lions), *Priscileo roskellyae* was first described based on a partial cranium from the early Miocene of Riversleigh WHA (Gillespie 1997), but additional material has now extended its range back to the late Oligocene (Travouillon et al. 2011). Gillespie et al.'s (2017) description of the dog-size *Wakaleo schouteni* from the late Oligocene and early Miocene of Riversleigh WHA (including a very well-preserved cranium) has led to taxonomic revisions within Thylacoleonidae, with "*Priscileo*" *pitikantensis* from the late Oligocene Etadunna Formation at Lake Pitikanta in South Australia now assigned to *Wakaleo* (Gillespie et al. 2017).

An enigmatic vombatomorphian, *Marada arcanum*, was described based on a single lower jaw from the late Oligocene of Riversleigh WHA (Black 2007); although this taxon shows dental similarities to wynyardiids and diprotodontoids (diprotodontids and palorchestids), its relationships remain unclear, and hence it has been referred to its own family, Maradidae. This is the seventh family currently recognised within the infraorder Vombatomorphia; the apparent absence of maradids from the Miocene suggests that the family had gone extinct by the end of the Oligocene, similarly to ilariids (Black et al. 2012b). A new genus and two species of diprotodontids from the late Oligocene of Riversleigh WHA were described, *Silvabestius johnnilandi and S. michaelbirti,* with the former known from a mother and a pouch young that were found in close proximity (Black and Archer 1997a). *Silvabestius* appears to be a plesiomorphic member of the diprotodontid subfamily Zygomaturinae, and may be ancestral to the Miocene *Nimbadon* (Black and Archer 1997a). Our knowledge of the vombatiform family Wynyardiidae has also expanded with the description of 3 new late Oligocene species, all of which are known from well-preserved cranial and some postcranial material, namely: *Namilamadeta albivenator* and *N. crassirostrum* from Riversleigh WHA (Pledge 2005) and *Muramura pinpensis* from the Etadunna Formation (Pledge 2003).

Within Macropodiformes, *Wururoo dayamayi* and '*Nambaroo*' *couperi* from Riversleigh WHA (Cooke 1997a) were first described as balbarines, but this subfamily was later raised to family level, i.e. Balbaridae (Kear and Cooke 2001), and both of those species were assigned to the balbarid subfamily Nambarinae. However, subsequently it was found that *W. dayamayi* had closer affinities with *Balbaroo* (Balbarinae) (Black et al. 2014) and so '*Nambaroo*' *couperi* was reassigned to *Ganawamaya* (Butler et al. 2018), which phylogenetic analyses place as sister *Balbaroo+Wururoo* (Butler et al. 2018). *Ngamaroo archeri* was described from the Etadunna Formation (Kear and Pledge 2007), and identified as a basal "macropodoid" (= macropodiform here), but following the description of *Gumardee springae* from Riversleigh WHA (Travouillon et al. 2016), both of these taxa now appear to belong to Potoroidae (Table S2). ‘*Nowidgee matrix*’ now appears to be a junior synonym of *Bulungamaya delicata* (Cooke 1997b; Travouillon et al. 2014b). The relationships of *Bulungamaya* and other “bulungamyines” -for example, the recently described *Cookeroo bulwidarri* (Butler et al. 2016) - are uncertain, but recent published analyses consistently fail to recover them as monophyletic. Instead, at least some taxa fall on the stem leading to crown-clade Macropodidae (Travouillon et al. 2014b; Butler et al. 2016, 2018); if so, taxonomic revision will be required to ensure a monophyletic classification. Finally, a recent analysis has reaffirmed that *Palaeopotorous priscus*, from the Namba Formation, is likely to be sister to all other macropodiforms, based on its uniquely plesiomorphic dentition (den Boer and Kear 2018).

The oldest known burramyid, *Burramys brutyi*, was described from the late Oligocene of Riversleigh WHA, and seemed to have survived well into the Miocene (Brammall and Archer 1997). Kangaroo Well in the Northern Territory has yielded a new genus (*Barguru*) and 3 new species (*B. kayir, B. kula* and *B. maru)* of the extinct family Miralinidae (Schwartz 2006b), and a new ektopodontid, *Ektopodon tommosi* was described from the Etadunna Formation (Pledge 2016).

Miocene

The Australian fossil record provides evidence of a major increase in marsupial diversity from the Oligocene to the middle Miocene, probably as a result of the return of wetter conditions (Travouillon et al. 2006; Black et al. 2012b). There is also evidence of a major faunal turnover between the middle and late Miocene (also seen in the South American record – see above), coinciding with the middle Miocene Climatic Optimum, and probably reflecting the onset of drier conditions (Black et al. 2012b); this affected many Australian marsupial groups, with the apparent decline or extinction of many “archaic” lineages (such as wynyardiids, balbarids, pilkipildrids, miralinids, yalkaparidontids), and the appearance of representatives of several modern genera, such as *Phascolarctos* and *Bettongia* (Black et al. 2012b), although there are now doubts as to whether the fossil “*Bettongia*” *moyesi*, the earliest putative member of *Bettongia,* belongs to this genus (Travouillon et al. 2016).

Within Dasyuromorphia, thylacinids are now known to have been very diverse during the early and middle Miocene, with 9 new species described in the last 25 years (Table S3), from a variety of genera including *Maximucinus*, *Muribacinus, Mutpuracinus, Ngamalacinus, Nimbacinus*, *Thylacinus*, *Tyarrpecinus* and *Wabulacinus* (Wroe 1996a; Muirhead 1997; Murray 1997; Murray and Megirian 2000; Wroe 2001; Yates 2015). However, Kealy and Beck (2017) did not recover *Mutpuracinus archibaldi* within Thylacinidae, and argued that this taxon should be considered Dasyuromorphia *incertae sedis* pending further study. Known thylacinid diversity declines markedly from the middle to the late Miocene, from five to two genera (Kealy and Beck 2017). This decline coincides with the onset of diversification of three of the four modern dasyurid tribes (Dasyurini, Phascogalini and Sminthopsini) (Kealy and Beck 2017), in which case there may be a relationship between these phenomena, which seems plausible given that the smaller fossil thylacinids and larger modern dasyurids represent putative ecological competitors. However, other studies have concluded that modern dasyurids began to radiate earlier than this, during the early Miocene (Westerman et al. 2016b), suggesting that there is no connection with the observed reduction of thylacinid diversity and the radiation of modern dasyurids.

Barinya wangala was described the oldest and most plesiomorphic known dasyurid (Wroe 1999), but the analyses of Kealy and Beck (2017) failed to unequivocally support dasyurid affinities for this taxon, and suggested that it (similarly to *Mutpuracinus*) should be classified as Dasyuromorphia *incertae sedis*. Regardless, a second species of *Barinya, B.*

kutjamarpensis was recently described from the Wipajiri Formation in South Australia (Binfield et al. 2017). Two new species from Riversleigh WHA have been attributed to Dasyuridae, bamely *Ganbulanyi djadjinguli* from the middle Miocene (Wroe 1998) and the very large (20-25 kg), hypercarnivorous *Whollydooleya tomnpatrichorum* from middle or late Miocene limestone deposits to the southwest of Riversleigh (Archer et al. 2016a). Two other fossil taxa, namely the middle Miocene *Joculusium muizoni* and late Miocene *Mayigriphus orbus*, are currently classified as Dasyuromorphia *incertae sedis* (Wroe 1997, 2001a). The 2 bizarre ‘hammer-toothed’ marsupials, *Malleodectes mirabilis* and *M. moenia*, were originally described as being of uncertain relationships (Arena et al. 2011), but discovery of a juvenile specimen that preserves more of the dentition indicated that they are members of Dasyuromorphia; they have now assigned to their own family, Malleodectidae, the only entirely extinct dasyuromorphian family currently known (Archer et al. 2016b).

Miocene peramelemorphians include *Bulungu palara* and *Yarala burchfieldi* (both of which are also known form the late Oligocene – see above), but also the larger (~0.6-1.6 kg) short-snouted, and presumably more carnivorous *Galadi*, with 4 described species (*G. adversus, G. amplus, G. grandis* and *G. speciosus*), all known only from Riversleigh WHA (Travouillon et al. 2010; Travouillon et al. 2013b). *Kutjamarcoot brevirostrum,* is another short-snouted peramelemorphian, only distantly related to *Galadi*, that is currently known only Wipajiri Formation (Chamberlain et al. 2016). Another late Oligocene peramelemorphian species, *Madju variae*, is succeeded by *M. encorensis* by the late Miocene (Travouillon et al. 2015b). The Riversleigh WHA sees the oldest known members of Peramelidae (*Crash bandicoot*) and Thylacomyidae (*Liyamayi dayi* both from the middle Miocene (Travouillon et al. 2014). There are at least two additional peramelemorphian genera yet unnamed from Riversleigh WHA (Travouillon et al. 2006; Travouillon et al. 2011). Like thylacinids, several peramelemorphian lineages appear to go extinct between the middle and late Miocene, including *Bulungu*, *Yarala* and *Galadi* (although this may partly be due to a lack of late Miocene sites); given that the extinct lineages include taxa that were probably more insectivorous or carnivorous than modern peramelemorphians, their decline (again like that of thylacinids) may be connected with the diversification of modern dasyurids (Kealy and Beck 2017).

Besides a putative fossil notoryctemorphian specimen from the Pwerte Marnte Marnte Local Fauna (see above), the first fossil record of marsupial moles is *Naraboryctes philcreaseri* from the early Miocene of Riversleigh WHA (Archer et al. 2011). Perhaps surprisingly, *N. philcreaseri* shows postcranial adaptations for digging that are almost as extreme as in the modern, desert-dwelling species, even though Riversleigh WHA was probably covered in rainforest at this time (Beck et al. 2016). However, today several placental golden mole species occur in the rainforests of sub-Saharan Africa (Bronner 2013), and may represent reasonable modern analogs of *N. philcreaseri* (Beck et al. 2016). 2016). The estimated time of inactivation of the vision-related gene Interphotoreceptor Retinoid Binding Protein (a pseudogene in modern marsupial moles) in the notoryctemorphian lineage is ~5.4 Ma, and based on this, it has been concluded that *N. philcreaseri* may have retained functional vision (Beck et al. 2016).

Miocene vombatiforms are highly diverse. However, while one species of wynyardid is known the early Miocene, namely *Namilamadeta superior*, the family appears to have gone extinct by the middle Miocene (Pledge 2005). Five new species, and two new genera, of phascolarctids have been described from the Miocene in the last 25 years (Table S2). *Priscakoala lucyturnbullae,* from the early Miocene of Riversleigh WHA, is the most pleisiomorphic phascolarctid currently known (Black et al. 2012a). Three new species of *Litokoala, L. dicksmithi, L.* "*dicktedfordi*" and *L. garyjohnstoni* have been described from the early Miocene of Riversleigh WHA, but *L.* "*dicktedfordi*" was subsequently concluded to be a junior synonym of *L. kutjamarpensis* (Louys et al. 2007; Pledge 2010; Black et al. 2012a). The middle Miocene *Stelakoala riversleighensis* seems to represent a transitional form between *Litokoala* and the modern genus *Phascolarctos* (Black 2016). A new thylacoleonid was described from the early Miocene of Riversleigh WHA, *Microleo attenboroughi,* which is the smallest (~600 g) and most plesiomorphic species in that family, and was most likely an arboreal predator (Gillespie et al. 2016). The palorchestid *Palorchestes anulus,* from the late Miocene of Riversleigh WHA, is intermediate in size and morphology between the earlier *Propalorchestes novaculacephalus* and later *Palorchestes painei* (Black 1997). Two new diprotodontids have been described, *Neohelos davidridei* and *N. solus*, both from the middle Miocene of Riversleigh WHA (Black et al. 2013). *Neohelos davidridei* is proposed to be part of a chronological morphocline (*N. tirarensis-N. stirtoni-N. davidridei*), which has assisted with the biostratigraphy of the Riversleigh sites (Black et al. 2013). Within Vombatidae, Riversleigh WHA has yielded a new genus and three new species, *Nimbavombatus boodjamullensis,* the most plesiomorphic wombat known (Brewer et al. 2015), *Rhizophascolonus ngangaba,* which is closely related to *Rhizophascolonus crowcrofti* (the oldest known vombatid) (Brewer et al. 2018) and *Warendja encorensis*, the first known vombatid with open-rooted (hypselodont) molars (Brewer et al. 2007).

The diversity within Macropodiformes is at its highest in the early Miocene of Riversleigh WHA, decreasing slowly until the late Miocene (Butler et al. 2017). Three new species of *Hypsiprymnodon* were described from Riversleigh WHA (*H. dennisi, H. karenblackae, H. philcreaseri*) suggesting that at least two species in this genus co-existed at the same time, whereas only a single species survives today (Bates et al. 2014). *Ekaltadeta ima*, the propleopine, the so-called “carnivorous kangaroo”, was common during the late Oligocene to middle Miocene, but it was seemingly replaced by a larger species, *E. jamiemulvaneyi,* in the late Miocene (Wroe 1996b). Among potoroids, two new species of *Gumardee*, *G. richi* and

G. springae, have been described, with the more derived, early Miocene *G. richi* (and *G. pascuali*) replacing the late Oligocene *G. springae* (Travouillon et al. 2016).

Four new species of balbarid have been described: *Balbaroo fangaroo* from the early Miocene of Riversleigh, which is famous for its large upper canines (Cooke 2000), *B. nalima* from the middle Miocene of Riversleigh(Black et al. 2014), "*Nambaroo bullockensis*" from the middle Miocene of Bullock Creek, Northern Territory (Schwartz and Megirian 2004), and finally "*Nambaroo*" *gillespieae* (Kear and Pledge 2007). However, of these, "*Nambaroo bullockensis*" has been synonymised with *Balbaroo camfieldensis* (Black et al. 2014), and "*Nambaroo*" *gillespieae*, described based on the most complete balbarid specimen known to date, is now placed in the genus *Ganawamaya* (Butler et al. 2018). Balbarids decreased in diversity through the Miocene, but never recovered and went completely extinct in the late Miocene (Butler et al. 2017). Their extinction may have been due to competition from macropodids during a period of major climate change, with multiple macropodid species appearing at this time, including the recently described *Cookeroo hortusensis*, and *Ganguroo bilamina*, *G. bites* and *G. robustiter* (Cooke 1997b; Travouillon et al. 2014b; Cooke et al. 2015; Butler et al. 2016). The origin of sthenurines may have also played a part in the extinction of the balbarids: recently described Miocene sthenurines include *Rhizosthenurus flanneryi* from the late Miocene of Riversleigh WHA(Kear 2002), *Wanburoo hilarus* from the middle Miocene (Cooke 1999), which was first described as a bulungamayine but later reassigned to Sthenurinae (Prideaux and Warburton 2010), and *Wabularoo prideauxi* (Travouillon et al. 2015a) from the early Miocene, which is likely to be part of a chronomorphocline between the late Oligocene *Wabularoo naughtoni* and the middle Miocene *Wanburoo hilarus* (Travouillon et al. 2015a).

Among the various families of "possum", the known diversity of pseudocheirids has increased particularly significantly over the last 25 years (Table S2). All of these new species have been described from Riversleigh WHA, providing further support for the presence of rainforest at Riversleigh during the early and middle Miocene. Three new species of *Marlu* (*M. ampelos, M. karya* and *M. syke*) (Roberts et al. 2009), three new species of *Paljara* (*P. hushae, P. maxbourkei* and *P. nancyhawardae*) (Bassarova et al. 2001; Roberts et al. 2008) and a new genus *Gawinga* (see Roberts et al. 2007) have been described, with most species existing for long periods of time during the Miocene. Among phalangerids, *Strigocuscus reidi* was assigned to the new genus *Onirocuscus* by Crosby (2007), who also described a further three species: *O. inversus, O. rupina* and *O. silvicultrix* (Crosby 2007). The description of the first fossil scaly-tailed possum, *Wyulda asherjoeli*, from Riversleigh WHA (Crosby et al. 2001), is significant because the only modern species in this genus is now confined to the Kimberley region in Western Australia, and little is known about its biology or evolution (Van Dyck and Strahan 2008). Several other Miocene "possums" have been described from Riversleigh WHA, including, a new petaurid, *Djaludjangi yadjana* (Brammall 1998), two miralinids, *Durudawiri anfractus* and *D. inusitatus* (Crosby and Archer 2000), an ektopodontid, *Ektopodon litolophus* from the Wipajiri Formation in South Australia (Pledge et al. 1999), and, most recently, an entirely new family, Miminipossumidae (*Miminipossum notioplanetes*) (Archer et al. 2018)

Pliocene

The Australian fossil record of marsupials from the Pliocene is known from a wide range of sites, including Chinchilla and Bluff Downs Local Fauna (LF) in Queensland, Bow Local Fauna (LF), Wellington Caves and Fisherman Cliff in New South Wales, Hamilton Local Fauna (LF) and Portland Pliocene Beds in Victoria and the Tirari Formation in South Australia, which continue to be the focus of active research. Two new Pliocene dasyuromorphians have been described: *Dasyuroides worboysi* from Wellington Caves (Lawson et al. 1999), and a new genus and species from Chinchilla, *Archerium* *chinchillaensis* (Wroe and Mackness 2004). Two new species of *Perameles* have been described *Perameles bowensis* from Bow LF and Wellington Caves (Muirhead et al. 1997), and, *Perameles wilkinsonorum* (Travouillon et al. 2017). Both these species have been identified as as potential ancestors to the modern genera *Isoodon* and *Perameles* (Travouillon et al. 2017). The first fossil chaeropodid, *Chaeropus baynesi* from Chinchilla (Travouillon 2016) was described from Fisherman Cliff (Travouillon 2016). There is still a significant gap in the fossil record for this family, as it is estimated to have originated in the Oligocene (Westerman et al. 2012). The species "cf. *Peroryctes*" *tedfordi* from Hamilton LF was described as the oldest known peroryctid (Turnbull et al. 2003), but has now been reassigned to a new genus of archaic peramelemorphians, *Silvicultor*, along with two further species: *S. hamiltonensis* from the same locality, and *S. karae* from Bow LF and Wellington Caves (Travouillon et al. 2017). A surprising discovery from the Bluff Downs LF was the unusual *Numbigilga ernielundeliusi*, a newly described taxon referred it to its own family, Numbigilgidae, and considered to be of uncertain relationships (Beck et al. 2008a). The dentition of *Numbigilga* is bizarre and highly autapomorphic, but a relationship to Peramelemorphia is plausible, and seems more congruent with biogeography and stratigraphy than alternative possibilities (e.g. a relationship to the predominantly South American polydolopimorphians) (Beck et al. 2008a).

Within Diprotodonta, two new *Palorchestes* species have been described, *Palorchestes selestiae* from the Bluff Downs LF (Mackness 1995), and *Palorchestes pickeringi* from the Hamilton LF (Piper 2006). Among macropodiforms, *Protemnodon bandharr* from Wellington Caves (Dawson et al. 1999) was reassigned to a new genus, *Silvaroo*, along with a new species *S. bila* from Chinchilla (Dawson 2004b), a new dendrolagin, *Bohra wilkinsonorum* was described from Chinchilla (Dawson 2004a), and a new lagostrophine, *Tjukuru wellsi* was described from the Tirari Formation (Prideaux and Tedford 2012).

Among “possums”, a pseudocheirid, *Pseudochirops winteri* was been described from Bluff Downs LF (Mackness and Archer 2001), and an ektopodontid, *Ektopodon paucicristata* was described from Portland (Rich et al. 2006).

Quaternary

It is often assumed that only the megafauna went extinct in Australia during the Pleistocene and Holocene, but there is evidence that a number of small mammals also went extinct during this period. Two species of dasyurids, *Antechinus yammal* and *A. yuna* from the middle Pleistocene of Mount Etna in central Queensland, appear to have gone extinct (Cramb and Hocknull 2010) along with the disappearance of the rainforest in the region (Hocknull et al. 2007). Indeed many elements of the now extinct rainforest marsupial fauna that occurred at Mount Etna during the middle Pleistocene shows affinities with the modern New Guinea fauna rather than north Queensland (Hocknull 2005; Hocknull et al. 2007). Intriguingly, a Pleistocene koala, *Invictokoala monticola* described from Mount Etna (Price and Hocknull 2011), appears more closely related to late Oligocene koalas than to the modern species, suggesting the existence of a prolonged ghost lineage that is now extinct. A bandicoot from the Darling Downs, *Perameles sobbei* is also known to have gone extinct during the Pleistocene (Price 2002).

Within Macropodiformes, a potoroid, *Borungaboodie hatcheri* described based on a partial lower jaw from southwest Western Australia, was identified as the most plesiomorphic Pleistocene potoroid (Prideaux 1999). The most significant changes to our understanding of Quaternary macropodiform systematics have been within Sthenurinae, with the description of three new genera and nine new species (Table S2), including *Archaeosimos correllii, Metasthenurus newtonae, Procoptodon williamsi, Simosthenurus (Sthenurus) baileyi, Simosthenurus (Sthenurus) brachyselenis, Simosthenurus euryskaphus, Simosthenurus* *tirarensis, Sthenurus murrayi, Sthenurus stirlingi* (Wells and Tedford 1995; Prideaux and Wells 1997; Prideaux and Wells 1998; Prideaux 2000; Prideaux 2004). In addition, two new tree kangaroo species, *Bohra illuminata* and *Bohra nullarbora* (Prideaux and Warburton 2008, 2009), have been described from a dry open forest fauna from the middle Pleistocene of Western Australia, significantly altering our understanding of tree-kangaroo habitat requirements and ecology (Prideaux et al. 2007). Also of significance has been the successful amplification of ancient DNA from two Pleistocene macropodids: the sthenurine *Simosthenurus occidentalis* and the macropodine *Protemnodon anak* (the "giant wallaby"). This has confirmed that Sthenurinae is a highly distinct lineage within Macropodidae, separate from Macropodinae and Lagostrophinae, and that *Protemnodon* is most closely related to *Macropus sensu lato* and *Wallabia* among modern macropodines (Llamas et al. 2015).

Outside Australia, a new fossil bandicoot species, *Lemdubuoryctes aruensis*, was described based on late Quaternary specimens from the Aru Islands, Indonesia (Kear et al. 2016). Although Kear et al. (2016) identified it as a late surviving member of an archaic, stem-peramelemorphian lineage, Travouillon and Phillips (2018) argued that all its putatively archaic dental features were the result of wear, and instead reassigned this taxon to *Peroryctes*. Finally, two new species of possums, the pseudocheirid *Petauroides ayamaruensis* and dactylopsiline *Dactylopsila kambuayai* were described from Holocene material obtained from the Arfak Peninsula, West Papua (Aplin et al. 1999). Of these, *D. kambuayai* (the smallest known dactylopsiline) has recently been identified as still extant (Wilson and Mittermeier, 2015).

Conclusion

Many substantial advances in our understanding of marsupial diversity, evolution, phylogenetics and morphology have been made over the last 25 years, with a broad systematic consensus and taxonomic stability beginning to emerge. Although molecular and morphological research have largely continued in parallel, a true understanding of marsupial diversity, phylogeography, systematics and evolution will only be able to emerge with the integration of data from fossil, living and recently extinct taxa. We therefore welcome the increasing trend for total evidence analyses that combine morphological and genetic data, and the use of DNA extracted from museum specimens of recently extinct taxa and ancient DNA and ancient protein sequencing to generate molecular data from fossil material. The increasing use of these and other new technologies will enable many of the remaining issues in marsupial systematics to be resolved. The search for additional fossils must remain a priority, both in terms of finding new localities that fill large temporal and geographic gaps, as well as resampling classic localities to uncover new species and more complete specimens of species that are currently known. However, emphasis should also be placed on using recently-developed techniques such as CT scanning to extract as much information as possible from existing specimens so that larger and better datasets can be marshalled to understand the evolutionary history of this remarkable clade. We are optimistic that progress over the next 25 years will be at least as remarkable as that of the last 25.

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Table 1. Families of living and extinct metatherians.

SUPPLEMENTARY INFORMATION (uploaded as separate file)

Supplementary Table S1. Modern marsupial species and subspecies described since 1995.

Supplementary Table S2. Fossil metatherian species described since 1995.

Supplementary Table S3. Modern marsupial species newly raised from synonymy after 1995.

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