Chapter 9

Long-Term Trends in Lineage 'Health' of the Australian Koala (Mammalia:Phascolarctidae): Using Paleo-diversity to Prioritize Species for Conservation

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Abstract Understanding phylogenetic diversity over large temporal scales as afforded by the fossil record allows for the identification of the history of taxonomic diversity in extant taxa. Identification of such long-term trends in lineage 'health' is a critical, but commonly underutilized method for helping to prioritize species for conservation. The modern Australian koala (*Phascolarctos cinereus*) is a case in point. It is widely debated whether the modern koala should be an immediate candidate for conservation. Although modern populations have seen recent declines in some regions, in other areas koalas are overabundant, with translocation, contraceptive, and evening culling programs suggested as population control measures. The view from the fossil record is that koalas (family Phascolarctidae) have suffered a dramatic, progressive long-term decline in diversity (e.g., four genera and eight species in the late Oligocene, compared to only one genus and species at present). At no time in the known history of the Phascolarctidae has phylogenetic diversity been as low as today. Climate change, leading to enhanced variability in seasonality, increased aridfication, and habitat change has had a negative impact on phascolarctid diversity through time, and has been a determining factor in the geographic range of the modern koala. Do such observations warrant adding the modern koala to the list of threatened species? Although the answer to this question remains outside the scope of this chapter, it should be remembered that extinction of the extant koala would mark the loss of not only of a single species, but also of an entire family of endemic Australian marsupial.

Keywords Climate change • Extinction • Koala • Lineage health • Phascolarctos • Phylogenetic diversity

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9.1 Introduction

The ability to reliably identify species most at risk of extinction is a challenge of modern conservation. Typically, understanding changes in population size, genetic diversity and geographic range adjustments (Dunham et al. 1999; Celdran and Aymerich 2010; Richards et al. 2011; Ando et al. 2011) are but a few of the key factors that help inform the conservation status of extant forms. Ecological and biological monitoring of contemporary populations is the key to differentiating those species that may face extinction in the near future, versus those that are the least at risk. In a world of limited resources, developing priorities for conservation becomes critical.

The difficulty with existing approaches is that most species are poorly studied, especially on extended temporal scales. In some cases well-known animals (e.g., pandas) are the targets of intense conservation studies and their vulnerability to short-term environmental and climatic perturbations may be reasonably well understood (Isaac et al. 2007). However, population dynamics of the majority of known species remains comparatively poorly known due to a paucity of ecological and biological investigation (Leader-Williams and Dublin 2000). In fact, a large number of species lack significant ecological monitoring of any kind. Furthermore, several species are known only as specimens that have been curated in museum collections and hence their ecological role in nature is poorly understood (Burbidge et al. 2009). Therefore it is not possible to accurately determine either the conservation status or vulnerability of the majority of known species to even short-term environmental perturbations and climate change. Without such information, it is simply not possible to set reasonable goals for conservation or identify those species that are the most at risk of extinction.

The fossil record provides a powerful tool for understanding ecological change at varying spatial, and most importantly, temporal scales. A key research focus of several contemporary paleocological studies has been the investigation of how species respond, both on individual and community scales, to past environmental perturbations. For example, Blois et al. (2010) examined the response of a North American small mammal community to global warming associated with the late Pleistocene–Holocene transition. The results suggest that despite the fact that no extinctions were observed over that time period, the diversity of the local community changed dramatically in terms of evenness and richness. Several species, such as the mountain beaver (*Aplodontia rufa*) and pocket gopher (*Thomomys* sp. cf. *mazama*) underwent dramatic geographic range shifts and were not recorded locally in the younger deposits, and hence the time coinciding with the period where temperatures were at their warmest. Understanding such patterns of change in the past is critical for our ability to reliably predict how such species may respond to hypothesized future global warming.

The fossil record also allows for assessment of deep-time lineage ‘health’ of extant groups. It is widely recognized that the species amongst the most vulnerable to extinction are those that are found within the most taxonomically depauperate groups (Russell et al. 1998; Brooks et al. 2005; Isaac et al. 2007; Rolland et al. 2011). Indeed, phylogenetic diversity may actually be a better measure of biodiversity than species

Fig. 9.1 The only extant koala, *Phascolarctos cinereus*, is closely associated with open eucalypt woodlands

richness (Rolland et al. 2011). In any case, understanding phylogenetic diversity, not only today, but over longer temporal scales as afforded by the fossil record, allows the identification of extant taxa that might appear to be relatively abundant, but who have suffered long-term, progressive declines in taxonomic diversity. Understanding deep time trends in diversity is a critical, but commonly underutilized method for helping to prioritize candidates for conservation.

The modern Australian koala, *Phascolarctos cinereus*, may be a case in point (Fig. 9.1). Commonly a target of conservation measures and ecological monitoring (Penn et al. 2000), the koala has undergone significant geographic range contractions since European colonization in the late 1700s (Fig. 9.2). Multiple factors, such as habitat loss, disease (e.g., Chlamydia), vehicular traffic, and introduced predators (e.g., domestic dogs), are commonly cited as threats to modern koala populations (Dique et al. 2004). However, despite the apparently dramatic decline in geographic range, it remains difficult to reliably predict the number of wild koalas (Melzer et al. 2000), with recent estimates ranging anywhere from 43,000 to over 300,000 (The Australian Koala Foundation 2010; Parliament of Australia 2011). The ability to accurately determine the physical number of wild koalas is paramount to determining the conservation status of the species. In any case, the spatial pattern of modern koala population density is quite complex, with some populations being at historic lows in certain regions, but occurring in overabundance in others (Melzer et al. 2000). In fact, in those regions where koalas are in overabundance, contraceptive based management strategies have been introduced to limit population size (Middleton et al. 2003; Tanaka et al. 2009; Hynes et al. 2010). Such factors have, in part, been influential for policy makers declining recent nominations for the modern koala to be listed in the Australian Government's Environment Protection and Biodiversity Conservation Act 1999 (Natural Resource Management Ministerial Council 2009).

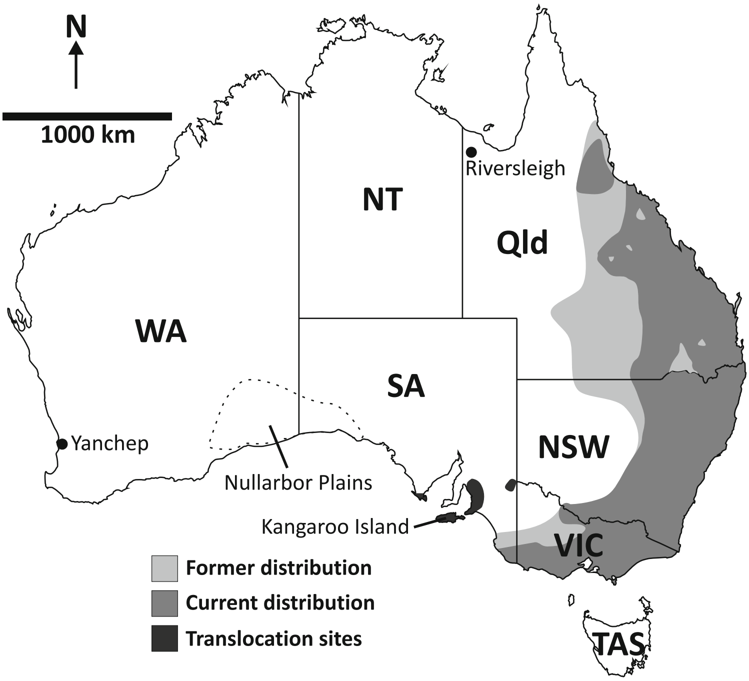

Fig. 9.2 Map of Australia indicating the modern and historic geographic distribution of the extant koala, *Phascolarctos cinereus*, as well as other sites mention in the text

Considering such a situation, and playing the role of 'Devil's Advocate', Flannery (1990, p. 174) asked the question, "What priority should we give koala conservation?" arguing that several other endemic Australian species are at higher immediate extinction risk than the koala and therefore deserving of greater attention. Archer et al. (1991) addressed the same question but from the view of the fossil record, and in particular, long-term trends in koala taxonomic diversity. On the basis of the completeness of the fossil record at the time of their study, they argued that koalas (members of the Phascolarctidae) are a taxonomically depauperate group with only a couple of species present at any one time during their 20+ million year history. Thus, Archer et al. (1991) suggested that the apparent low diversity of koalas today (i.e., one genus and one species) is not particularly unusual for the broader family and hence, the phylogenetic diversity of the group appears to be stable.

More recent fossil discoveries have drastically improved our understanding of prehistoric phascolarctid diversity. Since 1991, several new genera and species have been discovered, bringing the total number of known forms to at least 20. Coupled with improvements in our understanding of biostratigraphic relationships between geographically disparate fossil deposits, as well as new and improved dating methods, our understanding of the temporal occurrences of koalas has also greatly improved. The purpose of this study is to build on the approach of Archer et al. (1991) and provide a revised view of phascolarctid diversity through time.

Ultimately, an understanding of phascolarctid lineage 'health' may be useful for policy makers in determining emphasis, and the setting of priorities, for the conservation of the modern koala.

9.2 Members of the Phascolarctidae

Phascolarctids are typically medium- (ca. 3 kg) to large- (ca. 30 kg) bodied arboreal mammals. All known species, including both the modern koala and all extinct fossil forms, are interpreted to be folivores and endemic to Australian forests. The modern koala is a species that is closely associated with forests dominated by eucalypt trees (*Eucalyptus* spp.), where it relies almost exclusively on its leaves as a source of food (Fig. 9.1).

To date, eight phascolarctid genera and 20 species have been described. The fossil record dates back to at least the late Oligocene (>23 Ma). Although several relatively derived forms have been recorded from deposits of that age, earlier, more plesiomorphic phascolarctids are unknown due to a paucity of vertebrate-bearing pre-late Oligocene fossil deposits. On the basis of molecular studies, koalas are thought to have originated sometime in the middle-late Eocene (Beck 2008). However, a lack of appropriately aged fossil deposits from that Epoch precludes testing this hypothesis.

9.2.1 Priscakoala Black et al., 2012

Although the monotypic *Priscakoala* is considered to be the most plesiomorphic phascolarctid, it is not the geologically-oldest member of the family (Fig. 9.3) (Black et al. 2012). Represented by cranial and dentary remains, the type species *Priscakoala lucyturnbullae* is known only from early to middle Miocene deposits of the Riversleigh World Heritage area of northern Australia (Fig. 9.2). Its phylogenetic position, coupled with the geological age of the taxon and temporal relationship to other more derived koalas, suggests that older, more plesiomorphic ancestors of *Pr. lucyturnbullae* must have existed at least in the late Oligocene and possibly before.

9.2.2 Koobor Archer, 1976

The origins and familial relationships of *Koobor* have remained controversial since its discovery in 1976. Although Archer (1976, 1977) considered that *Koobor* was an undoubted koala, subsequent researchers have questioned its phylogenetic position within the Phascolarctidae, instead suggesting that it may either be better placed in the enigmatic extinct marsupial family, the Illiaridae (Pledge 1987a; Tedford and

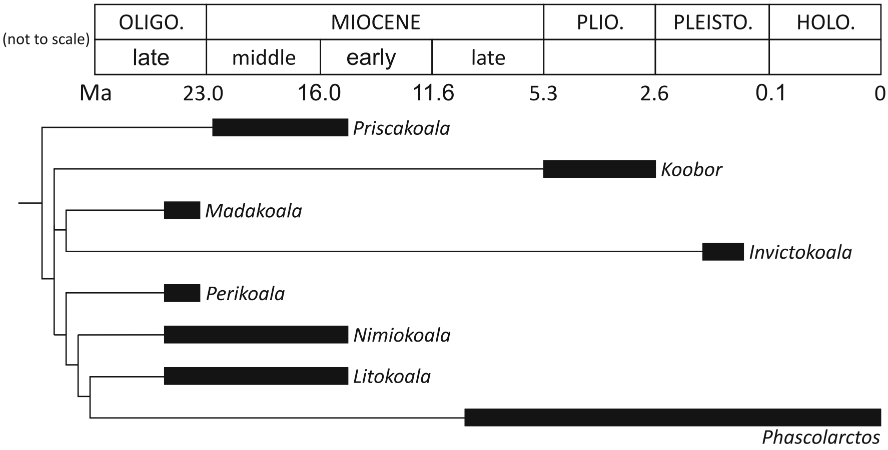

Fig. 9.3 Stratocladgram of phascolarctid inter-relationships (Modified from Black et al. in press)

Woodburne 1987), or may actually represent a new family altogether (Myers and Archer 1997). The most recent phylogenetic analysis of the broader Phascolarctidae suggests that *Koobor* is indeed a primitive koala, and second most plesiomorphic of the known genera (Fig. 9.3) (Black et al. 2012). In fact, Black et al. (2012) considered that *Koobor* may be a sister taxon to *Priscakoala*. If that interpretation is correct, then older, hitherto unknown and more plesiomorphic members of the clade must have been present between the Pliocene and at least the middle Miocene. *Koobor* is comprised of two species, *K. jimbaratti* and *K. notabilis*, from Pliocene deposits of central eastern and northeastern Australia (Archer 1976, 1977).

9.2.3 *Madakoala* Woodburne et al., 1987

Madakoala is thus far known only from late Oligocene deposits of central Australia. Three distinct species have been identified, *M. devisi*, *M. wellsi*, and an undescribed species, *Madakoala* sp. (Woodburne et al. 1987).

9.2.4 *Invictokoala* Price and Hocknull, 2011

The monotypic *Invictokoala* is known only from a maxillary specimen from the middle Pleistocene Mt. Etna fossil deposits of central eastern Australia . The type species *I. monticola* possesses a similar dental morphology to the geologically-older *Madakoala*, alluding to a close phylogenetic relationship between both forms (Price and Hocknull 2011). The implication of that interpretation is that the *Madakoala*-*Invictokoala* lineage represents a 'ghost' lineage within the broader Phascolarctidae.

That is, there are no known fossil representatives of the group between the late Oligocene and middle Pleistocene (Fig. 9.3). Consequently, if that interpretation is correct, there must be unknown transitional members of that lineage from intermediately-aged deposits (i.e., between the late Oligocene and middle Pleistocene).

9.2.5 *Perikoala* Stirton, 1957

Although the type locality of *Perikoala* was originally considered to be Pliocene in age (Stirton 1957), subsequent biostratigraphic and geochronological studies have supported a late Oligocene period for deposition (Woodburne et al. 1993). Two species have been recognized, *Pe. palankarinnica* and *Pe. robustus*, both known only from central Australian deposits (Stirton 1957; Woodburne et al. 1987).

9.2.6 *Nimiokoala* Black and Archer, 1997

Nimiokoala is one of the better and more completely preserved extinct members of the Phascolarctidae. Represented by isolated teeth, cranial and mandibular specimens, two species are presently recognized: *N. greystanesi* from early to middle Miocene deposits of Riversleigh, and the undescribed but distinct *Nimiokoala* sp. (Black and Archer 1997) from the late Oligocene of central Australia.

9.2.7 *Litokoala* Stirton et al., 1967

Litokoala is a diverse genus within the Phascolarctidae, second only to *Phascolarctos*. Four species are presently recognized: *L. kutjamarpensis*, *L. thurmerae*, *L. garyjohnstoni*, and *L.* sp. nov. (Stirton et al. 1967; Louys et al. 2007, 2009; Pledge 2010; Black et al. submitted). The poorly known *L. thurmerae* is represented by only a single worn molar tooth from a late Oligocene deposit of central Australia. *Litokoala garyjohnstoni* and *L.* sp. nov. are known only from early Miocene deposits of Riversleigh. *Litokoala kutjamarpensis* has the greatest geographic and temporal range of all *Litokoala* species, known from deposits of both central Australia and Riversleigh, spanning the early to middle Miocene.

9.2.8 *Phascolarctos Blainville, 1816*

Phascolarctos is the only extant member of the Phascolarctidae (Fig. 9.3). The oldest member of the genus, the undescribed *Phascolarctos* sp. from Riversleigh is thought to be late Miocene in age (Myers et al. 2001). *Phascolarctos maris* is a poorly represented species, known from only a single tooth from a probable Pliocene deposit in southern Australia (Pledge 1987b). The largest-bodied koalas, the 'megafaunal' *Ph. yorkensis* and *Ph. stirtoni*, are known from Pliocene and Pleistocene deposits of southern and eastern Australia (Pledge 1992; Archer et al. 1997; Price et al. 2009a, b). The extant *Ph. cinereus* has a fossil record extending back until at least the middle Pleistocene (Price 2008). *Phascolarctos cinereus* was originally considered to have been a late Pleistocene-Holocene dwarf of the extinct *Ph. stirtoni* (Archer 1984; Archer and Hand 1987; Murray 1984), thus implying that the later taxon did not suffer extinction in the late Pleistocene as a suite of other large-bodied 'megafauna' did (e.g., Price and Sobbe 2005; Price et al. 2011). However, Price (2008) demonstrated that the dwarfing hypothesis is not supported due to significant morphological differences between the two forms (and hence, warranting specific distinction), and the fact that the earliest known temporal occurrence of the supposed 'dwarf', *Ph. cinereus* (>350 ka), significantly predates the late Pleistocene. On the basis of those observations, the extant *Ph. cinerus* is considered to be a species distinct from the extinct *Ph. stirtoni* (Price 2008).

9.3 Phascolarctid Diversity Through Time

The combination of direct fossil records and an understanding of phylogenetic (Fig. 9.3) relationships between known forms, both coupled within a reliable geochronological framework, allows for the tracking of long-term trends in koala diversity. On the basis of the available evidence, it is clear that phascolarctids have suffered a dramatic long-term decline in diversity over the middle to late Cenozoic (Fig. 9.4). Phascolarctid diversity was greatest in the late Oligocene (ca. 22–24 Ma) with at least five genera present (*Litokoala*, *Nimiokoala*, *Perikoala*, *Madakoala*, and the hypothesised ancestor of the plesiomorphic *Priscakoala*). Eight species are evident from that time (*L. thurmerae*, *Nimiokoala* sp., *Pe. robustus*, *Pe. palankarinnica*, *M. wellsi*, *M. devisi*, *Madakoala* sp., and the ancestor of *Priscakoala*).

Leading into the early Miocene (ca. 16.4–23.0 Ma), the two central Australian taxa, *Madakoala* (three species) and *Perikoala* (two species), suffered extinction (Fig. 9.4). Overall, generic diversity decreased from five to four (with only *Litokoala*, *Nimiokoala*, *Priscakoala*, and the transitional member of the *Madkoala-Invictokoala* lineage present in the early Miocene). Species level diversity decreased from eight to six (including only *L.* sp. nov., *L. garyjohnstoni*, *L. kutjamarpensis*, *N. greystanesi*, *Pr. lucyturnbullae*, and the transitional *Madakoala-Invictokoala* taxon during the early Miocene).

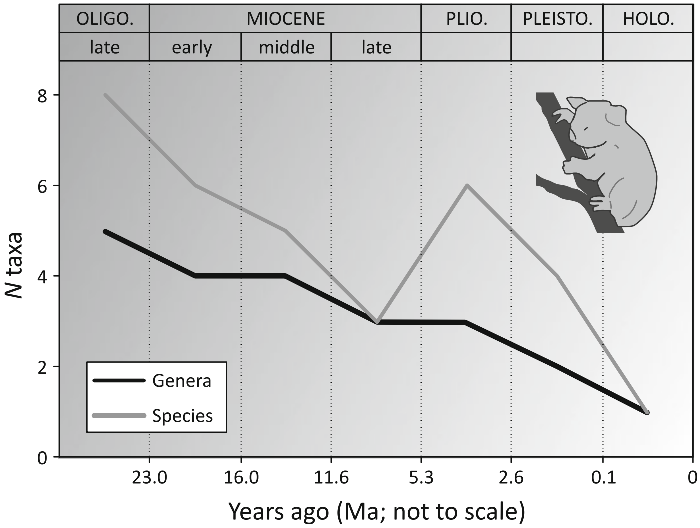

Fig. 9.4 Late Oligocene to recent trends in phascolarctid phylogenic diversity

Phascolarctid generic diversity remained steady between the early and middle Miocene (10.4–16.4 Ma) with no apparent extinctions (Fig. 9.4). However, species diversity decreased from six to five taxa (with *L. kutjamarpensis*, *N. greystanesi*, *Pr. lucyturnbullae*, transitional member of the *Madkoala-Invictokoala* lineage, and the ancestor of *Koobor* all present in the middle Miocene), including the apparent extinctions of *L.* sp. nov. and *L. garyjohnstoni*.

Our understanding of phascolarctid diversity in the late Miocene (5.3–10.4 Ma) is limited due to a paucity of appropriately-aged fossil deposits (Black 1999). At face value, diversity appears to have declined from four to three genera between the middle and late Miocene (earliest *Phascolarctos*, transitional member of the *Madakoala-Invictokoala* lineage, and the ancestor of *Koobor* present at that time). Three genera, *Priscakoala*, *Litokoala*, and *Nimiokoala* have not been recorded in post-middle Miocene deposits (Fig. 9.4). Species diversity appears to have decreased from five to three between the middle and late Miocene (taxa as for generic level above).

The fossil record of the Pliocene is much more extensive than that of the late Miocene and hence there is a better understanding of phascolarctid diversity during that Epoch. Significantly, koala diversity at the generic level is much lower than that of the better sampled middle Miocene, with only three taxa present (*Koobor*, *Phascolarctos*, and the transitional member of the *Madakoala-Invictokoala* lineage). Despite relatively low levels of generic diversity during the Pliocene, six species have been recognized (*K. jimbaratti*, *K. notabilis*, *Ph. maris*, *Ph. yorkensis*, *Ph. stirtoni*, and the *Madkoala-Invictokoala* member), making it comparable in species diversity to the early Miocene (Fig. 9.4).

The transition to the Quaternary (encompassing the Pleistocene – 2.6 Ma to 11 ka, and Holocene – last 11 ky) marked the beginning of a sharp decline in phascolarctid diversity that appears to have continued to the present day (Fig. 9.4). Only two genera have been recorded (*Phascolarctos* and *Invictokoala*) in Pleistocene deposits. *Koobor* has not been recorded in deposits younger than Pliocene, implying its pre-Quaternary extinction. Diversity decreased from six to four species between the Pliocene and Pleistocene (with only *Ph. cinereus*, *Ph. stirtoni*, *Ph. yorkensis*, and *I. monticola* present).

The Pleistocene–Holocene transition represents the largest loss of diversity, at least at the species level, in the known history of the Phascolarctidae (Fig. 9.4). The rainforest-adapted *Invictokoala* has not been recorded after ca. 320 ka anywhere on the continent. The 'megafaunal' *Ph. stirtoni* has not been recorded in deposits after 53 ka (Price et al. 2009b), therefore pre-dating the hypothesised time of intense 'megafaunal' extinctions (e.g., Roberts et al. 2001). The extant *Ph. cinereus* is the only member of the Phascolarctidae that appears to have persisted through the Holocene to the present day.

9.4 Discussion

9.4.1 Driving Factors of Koala Diversity Through Time

The exact mechanisms and processes of prehistoric koala extinctions and broader changes in diversity is by no means clear, but almost certainly involved significant climate change, principally, a long-term trend towards aridification, enhanced seasonality and habitat change. The earliest known koalas thrived during warm and wet periods, and appear to have preferred habitats consisting of well-wooded vegetation including rainforest. Dental and cranial anatomy of the early koalas demonstrates a specialty for feeding on soft foliage, rather than the tough, leathery leaves of eucalypts – the near exclusive diet of the modern koala, *Ph. cinereus* (Louys et al. 2009).

Significant post-middle Miocene declines in rainfall and cool temperatures were largely responsible for a major reorganization of the distribution of Australia's central forests, leading to a major contraction of such habitats to the coastal fringes (Black et al. 2012). It was also at this time (i.e., late Miocene) that saw the origin of the extant genus, *Phascolarctos*, a taxon that is closely associated with the open, dry sclerophyll eucalypt forests of modern Australia. The teeth of *Phascolarctos* possess well-developed crenulations in molar enamel and are significantly higher-crowned than the ancestral koalas.

Although the traditional view is that koalas suffered extinction from rainforests in the late Miocene (Archer and Hand 1987), more recent discoveries of koalas in rainforest fossil deposits have suggested that koalas may have actually always been closely associated with such habitats (Price and Hocknull 2011). A paucity

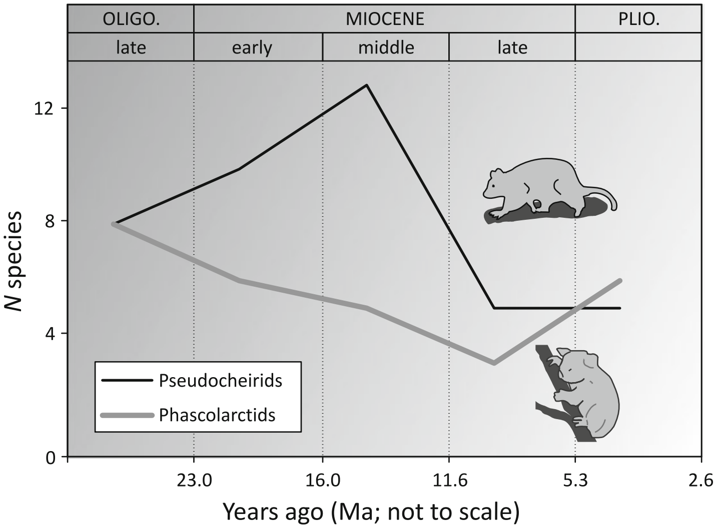

Fig. 9.5 Late Oligocene to Pliocene trends in phascolarctid and pseudochierid species diversity (see Long et al. (2002) for additional information on pseudochierid palaeodiversity)

of rainforest fossil deposits may reflect their post-Miocene rarity, and hence, may influence our understanding of koala-rainforest ecological relationships after that time. It is clear however, that koalas suffered extinction from rainforests of the continental fringe after the middle Pleistocene (Price and Hocknull 2011).

Archer and Hand (1987) also speculated that the loss of koalas from rainforests was associated with competition from other arboreal herbivores such as ringtail possums (Pseudochiridae), and principally, the large-bodied *Pseudokoala*. Again, a more complete picture of koala and ringtail possum diversity through time now allows the testing of such a hypothesis. At face value, fossil data suggests that while koalas suffered a long-term decline in diversity between the late Oligocene and Pliocene, ringtail possums diversified significantly at least until the middle Miocene (Fig. 9.5). However, significant differences in dental morphology and body size between those early koalas and possums suggests that both groups would have filled significantly different niches in the Oligo-Miocene forests, such it is likely that competition would have been minimal (similar factors also explain the niche partitioning of sympatric modern koalas and ringtail possums; Smith and Ganzhorn 1996). In any case, the giant ringtail *Pseudokoala* is thus far known only from Pliocene and Pleistocene deposits, and there is no evidence that it competed directly with the earlier rainforest koalas. The only post-Miocene rainforest koala known, *Invictokoala monticola*, has been recorded sympatrically with *Pseudokoala* from the middle Pleistocene rainforest deposits of Mt. Etna, central eastern Australia (Hocknull 2005; Hocknull et al. 2007; Price and Hocknull 2011). Neither taxon has been recorded from younger deposits locally, or anywhere else on the continent, after that time.

9.4.2 Climate Change and Influence on the Geographic Distribution of the Modern Koala

The modern koala, *Ph cinerus*, has a fossil record dating back to at least 350 ka. Strikingly, it is the only koala that survived through the period of intense late Pleistocene megafaunal extinctions (hypothetically 50–40 ka); earliest human arrival (ca. 45–50 ka); enhanced seasonality over the last 50 ky; intense aridification associated with the last glacial maximum (30–18 ka); post-glacial global warming (18–11 ka); and through the period of European colonization (late 1700s). Yet the fossil record demonstrates that it was not entirely resilient to such impacts through the Pleistocene–Holocene transition. Fossil records demonstrate that the modern koala once had a near continent-wide distribution (Price 2008), being found not only through eastern and southeastern Australia (including its modern geographic range), but also across southern central and southwestern Australia (e.g., Archer 1972; Lundelius and Turnbull 1982; Prideaux et al. 2010). For example, late Pleistocene fossils of *Ph. cinereus* have been recorded from Madura Cave, part of the Nullarbor Plains ('the treeless plains') (Lundelius and Turnbull 1982) (Fig. 9.2). The occurrence of the extant koala in the late Pleistocene indicates the former existence of local eucalypt woodlands. In contrast, the modern Nullarbor Plains is dominated by chenopod shrubs (Morton et al. 2011). Independent paleohabitat evidence from nearby offshore pollen cores has demonstrated a progressive, long-term reduction in eucalyptus forest in the region (Van der Kaars et al. 2007). Although forests appear to have been locally widespread at Marine Oxygen Stage (MIS) 5E (around 130 ka), and hence, implying an episode of high effective precipitation, *Eucalyptus* decreased significantly after this time. A considerable decline in charcoal abundance at the MIS 5–4 boundary (around 74 ka), and depressed charcoal-pollen counts after that time also suggests a progressive decline in the biomass available for burning. A paucity of charcoal and decline in *Eucalyptus* abundance strongly suggests a more open, sparser habitat after 74 ka (Van der Kaars et al. 2007), similar to today (e.g., Morton et al. 2011). Other southern Australian palynological records demonstrate similar MIS 5–4 declines in eucalypt forest (Singh and Geissler 1985; Harle 1997; Harle et al. 1999). It is those late Pleistocene changes – tending towards greater seasonality, droughts, a decline in rainfall, aridification and habitat change (see also Hesse et al. 2004) – that likely contributed to the demise of the region's late Pleistocene koala populations. It is also important to point out that such changes pre-date human colonization of the continent by >20,000 years, thus humans cannot be instigating factors in such long-term trends. Pre-human climate changes leading to the decline of local forests may also be implicated as the cause of extinction of numerous forest mammals, such as browsing kangaroos, arboreal tree kangaroos, and forest wallabies, recorded from older middle Pleistocene deposits of the region (e.g., Prideaux et al. 2007).

This newly refined understanding of late Pleistocene climatic changes, its influence on the decline of eucalypt forest habitat, and subsequently, local koala

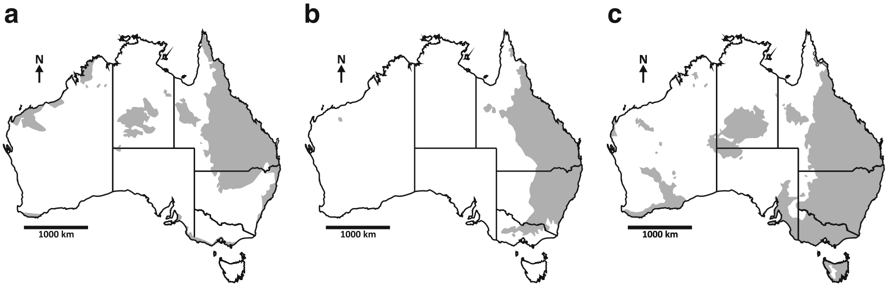

Fig. 9.6 Bioclimatic models based on the distribution of the modern koala. (**a**) potential koala distribution with a 6°C drop in temperature and 20% decline in rainfall; (**b**) potential koala distribution with an additional 40% decline in rainfall; and (**c**) regions that today fall within the bioclimatic envelope of the extant koala (Modified from Adams-Hosking et al. 2011)

range contractions, is also supported by independent bioclimatic modeling. Adams-Hosking et al. (2011) developed a bioclimatic envelope for the modern koala and explored a variety of scenarios mirrored to reflect the actual hypothesized changes in late Pleistocene temperature and rainfall. The resulting models suggest that a decline in temperature by 6°C and reduction in rainfall by 20% (relative to today) would result in the total loss of koala habitat in southern central Australia (Fig. 9.6a); a subsequent decline in rainfall by 40% is predicted to result in the total annihilation of koala habitat in the southwest (Fig. 9.6b). Although bioclimatic modeling based on modern conditions suggests that the extant koala could persist in southwestern Australia today (Fig. 9.6c), potential connective corridors (e.g., Nullarbor Plains) are too sparsely vegetated to allow natural koala dispersal into the region. In other potentially favorable areas, such as Kangaroo Island off southern central Australia (Figs. 9.2 and 9.6c), koalas, introduced from the mainland by Europeans in the 1920s, have thrived so successfully that they are now considered to be a pest species (Masters et al. 2004). Significant population control measures for the Kangaroo Island koalas such as culling have been considered (Tyndale-Biscoe 1997; Ross and Pollett 2007), while fertility contraceptive measures and translocations have been introduced (Duka and Masters 2005). Conversely, in regions that are not considered to be suitable for the modern koala today, such as Yanchep of southwestern Australia (approximately 300 km to the north of the southwestern favorable zone; Figs. 9.2 and 9.6c), introduced populations have failed to become established. In fact, the original population introduced to Yanchep in 1938 died out by 1941; and numerous other introductions have since occurred (Congreve and Betts 1978). Failure of the population to become well established may be explained, in part, by both inbreeding effects (Congreve and Betts 1978) and bioclimatic unsuitability.

Rainfall and availability of permanent sources of freshwater, in addition to general tree suitability, continues to have a strong influence on the distribution and survival of the modern koala. For example, Munks et al. (1996) noted that koalas more frequently used those trees that grew proximal to permanent water bodies versus those from more distal areas. Gordon et al (1988) observed that numerous koalas (ca. 63% of the population) from southwestern Queensland suffered mortality during a major drought and heat wave in the summer of 1979–1980. A later, extended drought between 2001 and 2009 from the same region resulted in an 80% decline of the local population (Seabrook et al. 2010). During the 1978–1980 event, mortality was greatest in those areas where food trees suffered leaf-fall and browning of the foliage, which, significantly, included those trees that were growing along dry stretches of the local watercourses. The cause of individual mortality was likely a combination of malnutrition and dehydration; the survivors from those areas were commonly observed in poor condition with anemia and high tick loads (Gordon et al. 1988). Gordon et al. (1988) also identified differential rates of mortality in the region during the 1979–1980 drought. High rates of survivorship were observed for those areas where the food trees grew adjacent to sources of permanent water (hence, such trees were least affected from drought conditions; a pattern also later observed by Seabrook et al. (2010) in the 2001–2009 drought). Demographically, mortality was greatest amongst younger animals that were excluded from optimal sites by older individuals (Gordon et al. 1988). Thus, a lack of recruitment into the breeding population, as well as ongoing local drought conditions over the subsequent few years drastically impeded the recovery of the population. During the 2001–2009 drought, despite a major population crash, there was only a minor change in overall koala distribution in the region. The ability of populations to migrate from the drought affected areas appears to have been significantly impeded by regional land clearing, thus reducing potential migratory connective habitat corridors (Seabrook et al. 2010).

Although such population crashes may be rare events (Gordon et al. 1988), it is easy to imagine a scenario where late Pleistocene koala populations of southern and central Australia were regularly exposed to similar drought conditions associated with the last glacial cycle. Where such climate events occurred frequently and populations were not able to adequately recover before the next event, local population extinctions would have been imminent, progressive and repetitive across the landscape, leading to a massive geographic distributional range shift.

Collectively, the view from the fossil record, independent paleoclimatic evidence, bioclimatic modeling, and observations of modern populations clearly demonstrates the vulnerability of koalas to prehistoric and recent changes in precipitation regimes, moisture availability, habitat change, and short and long-term variations in seasonality. Significantly, such climatic changes mirror those that are predicted to occur in the future, particularly in those regions where koalas currently persist (Intergovernmental Panel on Climate Change 2007; Dunlop and Brown 2008; Hamin and Gurran 2009; Seabrook et al. 2010). Thus, the long-term view is that climate change, associated with increased aridification, increased variability in seasonality, and habitat change, has had, and will likely to continue to have, detrimental impacts on the persistence of koala populations.

9.5 Should the Modern Koala Become an Immediate Priority for Conservation?

At present, koalas are listed as being of 'least concern' on the 2011 International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2011). Within Australia, they are not listed in the Environment Protection and Biodiversity Conservation Act 1999 (Natural Resource Management Ministerial Council 2009), although a ministerial position on a recent nomination to be included as 'vulnerable' in the Act is pending and will be announced in 2012 (Minister for Sustainability, Environment, Water, Population and Communities 2011). On a State-by-State level, koalas are: listed as 'regionally vulnerable' in the Southeast Queensland Bioregion, but 'of least concern' in other areas as per Queensland's Nature Conservation Act 1992; listed as 'vulnerable' under the Threatened Species Conservation Act 1995 for New South Wales; protected wildlife under Victoria's Wildlife Act 1975 but not listed under the Victorian Flora and Fauna Guarantee Act 1988; and protected under the National Parks and Wildlife Act 1972 of South Australia (Natural Resource Management Ministerial Council 2009). The key challenge faced by policy decision makers and their advisors is to determine whether the modern koala is truly a species on the brink of extinction, and therefore whether or not it should become a priority for conservation.

At a time of widespread confusion and concern on the possible fate of the koala, it may be useful to consider the deep-time history of another iconic family of Australian marsupial, the Thylacinidae, which includes the recently extinct *Thylacinus cynocephalus* (variously known as the Tasmanian tiger, Tasmanian wolf and thylacine). Strikingly, the long-term view of the Thylacinidae has many parallels with the patterns of diversity changes as seen in the Phascolarctidae. Nine genera and thirteen species have so far been described, with a fossil record dating back to the late Oligocene (Long et al. 2002). For at least the first 15+ million years of the known history of the Thylacinidae, there were a minimum of two distinct genera present at any one time (Fig. 9.7). Both genus and species diversity was greatest in the middle Miocene, before declining steadily, such that by the Pliocene, only one genus (*Thylacinus*) and one species (*Thylacinus* sp.; Mackness et al. 2003) remained (Fig. 9.7). The modern Tasmanian tiger has a fossil record dating back to the Pleistocene (Dawson 1982), and leading into the Holocene, was the sole survivor of the previously diverse family. The Tasmanian tiger was widespread across mainland Australia (e.g., Price and Webb 2006; Prideaux et al. 2010), Tasmania (Mooney and Rounsevell 2008) and New Guinea (Sutton et al. 2009), at least until the mid Holocene. The Tasmanian tiger suffered extinction from the Australian mainland and New Guinea following the introduction of the dingo (*Canis lupus dingo*) by humans around 3.5 ka (Gollan 1984). Although it is possible that additional factors other than competition with the dingo also contributed to the extinction of the Tasmanian tiger from such regions (Johnson and Wroe 2003), it is clear that Tasmania was its last refuge prior to European colonization.

During the 1800s and following the colonization of Tasmania by Europeans, the Tasmanian tiger was regarded as a significant killer of sheep, although this

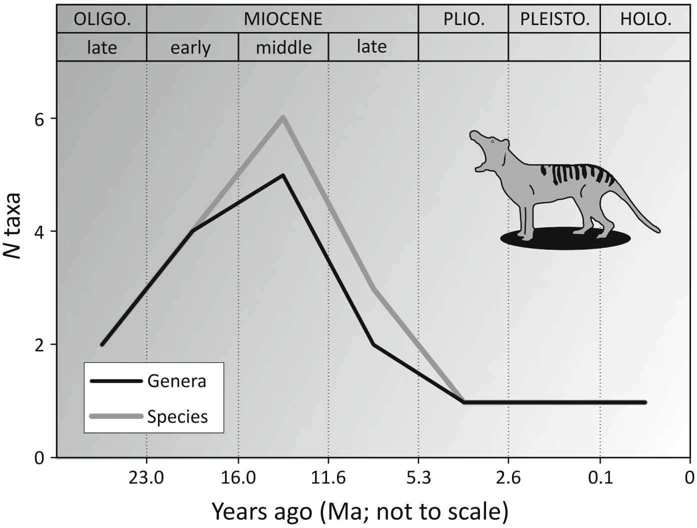

Fig. 9.7 Late Oligocene to recent trends in thylacinid phylogenic diversity (see Long et al. (2002) for a summary of key taxa)

reputation was greatly over-exaggerated (Paddle 2000). In addition to farmers killing Tasmanian tigers to protect their stock, a bounty scheme was also established to control their numbers (Paddle 2000). In addition to hunting, competition with introduced domestic dogs, habitat loss and disease played a significant role in the decline of thylacine populations (Paddle 2000). Although the Tasmanian tiger was recognized as a species vulnerable to extinction as early as 1901, it wasn't until the 10th of July 1936, that it became an officially protected species by the Tasmanian State Government. As Penn et al. (2000, p. 630) pointed out in relation to establishing policy-based conservation strategies for the modern koala, "the best time to consider conservation management is before the population has become so small that options are limited"; in the case of the Tasmanian tiger, the last known living individual died in captivity on the 7th of September 1936, just 59 days after the species became officially protected by legislation (Paddle 2000).

The long-term decline in diversity of the Thylacinidae coincided in time with intense late Cenozoic climate-driven environmental changes; humans, both directly (e.g., hunting) and indirectly (e.g., land clearing and introduced competitors) contributed to their ultimate extinction. Thus, the passing of the last Tasmanian tiger in captivity marked not only the extinction of a single species, but an entire family of endemic Australian marsupials. It remains tempting to speculate how the deep-time knowledge of lineage 'health' of the Thylacinidae may have influenced the decision of policy makers of the 1800s and 1900s in terms of prioritizing the Tasmanian tiger as candidate for conservation sooner; however this is outside the scope of this chapter.

Although the long-term trend in lineage 'health' of phascolarctids points to a steep, downward decline in diversity, does this alone warrant adding the modern koala to the list of threatened species? The answer to this question is far more complex than simply understanding the history of its phylogenetic diversity and must consider other external factors as well. However, it may be critical for environmental managers, conservationists, and perhaps most importantly, policy makers and advisers, to consider the following facts:

1. Koalas have declined dramatically in diversity over the last 20+ million years (four genera and eight species in the late Oligocene, compared to only one genus and species today);
2. At no time in the known history of the Phascolarctidae has phylogenetic diversity been as low as what it is today;
3. Climate change, principally a long-term trend towards increased aridification and seasonality, has not only shaped our past and present ecosystems and influenced the evolution of our biota, but has had detrimental impacts on koala diversity through time;
4. Climate change and associated habitat changes of the Quaternary – the last 2.6 Ma in the history of life on our planet, including the time period in which we currently live – has strongly influenced and caused major geographic range contractions and localized population extinctions of the modern koala;
5. Similar patterns of past Quaternary climate change are also predicted to occur in the future; and
6. Extinction of the modern koala will mean the loss of a species that has survived on the continent for at least the last 350 millennia; it will mark the demise of a genus that persisted for close on 9 Million years; and ultimately, it will result in the decimation of yet another endemic family of marsupials that previously ruled Australia's forests for over 23 Million years.

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