Chapter 3
Dispersal of Vertebrates from Between the Americas, Antarctica, and Australia in the Late Cretaceous and Early Cenozoic

Abstract The early Paleocene diversity of metatherians in Tiupampan faunas of South America and the pre-Tiupampan Paleocene polydolopimorphian *Cocatherium* speak in favor of an earliest Paleocene or Late Cretaceous dispersal of metatherians from North America. No Late Cretaceous metatherian or eutherian mammals have been recovered to date in South America, but the late Campanian to Maastrichtian hadrosaurine dinosaurs in Argentina, as well as the late Maastrichtian of the Antarctic Peninsula, is evidence of a biotic connection to North America. Placental 'condylarths' in the Tiupampan may have been related to, and dispersed southward relative to, Puercan taxa in North America and perhaps reflect a somewhat later event in comparison to metatherians. Other than hadrosaurine dinosaurs, Late Cretaceous vertebrates of South America are basically Gondwanan in affinities and reflect (and survived) the pre-106 Ma connection between South America, Africa, and Antarctica. The potential for a Late Cretaceous dispersal of metatherians would be compatible with a continued dispersal to Australia at that time, also supported by plate tectonic relationships, notwithstanding the basically endemic coeval Australian dinosaur fauna, and recognizing the essential absence of a Late Maastrichtian land vertebrate record there. An early Paleocene connection between at least Antarctica and South America is documented by the presence of a monotreme in the Peligran fauna of Patagonia. This, coupled with the fact that post-Peligran mammal faunas in South America and the Antarctic Peninsula (from at least 52 Ma in that location) are composed of derived metatherian as well as placental mammals, suggests that dispersal of metatherians to Australia had been achieved prior to the Eocene. Such timing is compatible with the still plesiomorphic level of Australian metatherians from the early Eocene Tingamarra fauna of Australia, the marine sundering of the Tasman Gate at about 50 Ma and the development of a continuously marine southern coastline of Australia from about 45 Ma effectively foreclosed overland mammal and other vertebrate dispersal to Australia thereafter.

Keywords Metatheria · South America · Late cretaceous · Paleogene · Dispersals · North America · Australia · Antarctica

3.1 Introduction

Woodburne and Case (1996) and Case et al. (2005) presented a dispersal scenario
that utilized contemporaneous plate tectonic and faunal comparisons to suggest a
biogeographic connection between North and South America in the Late
Cretaceous, based largely on the record provided by metatherian mammals (to
South America) and snakes (to North America). The initial dispersal apparently was
followed in the early Paleocene by eutherian mammals expanding their range to
South America. These events set the stage for the subsequent endemic evolution of
South America's unique therian mammal faunas, with episodes of later immigration
of placental mammals during the Neogene (summarized in Woodburne 2010;
Woodburne et al. 2014). The appraisal also suggested that the most likely dispersal
of metatherians to Australia took place prior to 64 Ma when the South Tasman Rise
was considered to be flooded.

   The following provides an update of faunal and plate tectonic information to
move toward a more complete understanding of biogeographic and tectonic aspects
of mainly mammalian dispersal between North and South America, Antarctica, and
Australia. To this end, considerable recognition is given to the excellent portrayal of
these aspects in Lawver et al. (2013).

3.1.1 Definitions and Abbreviations

EECO   Early Eocene Climatic Optimum. This is the interval of highest mean
         ocean temperature of the Cenozoic Era (Wolfe 1978; Zachos et al. 2001,
         2008). It began about 53 Ma and persisted to about 50 Ma (Tsukui and
         Clyde 2012), and occurred in the contexts of generally warm conditions
         that characterized the early Cenozoic Era from the Paleocene to about
         middle Eocene
k.y.   A segment of geologic time one thousand years in duration or the age of
         an event (e.g., ten thousand years ago), without reference to a point or
         set of points on the radioisotopic time scale
Ma   Megannum. One million years in the radioisotopic time scale (e.g.,
         10 Ma refers to the ten million year point on the time scale)
MAT   Mean Annual Temperature (as inferred from paleobotanical leaf margin
         and other data)
MECO   Mid-Eocene Climatic Optimum; a hyperthermal warming event at about
         41.6 Ma (Zachos et al. 2008; Figueirido et al. 2012)
m.y.   A segment of geologic time one million years in duration or the age of
         an event (e.g., ten million years ago) without reference to a point or set
         of points on the radioisotopic time scale

NALMA   North American Land Mammal Age (Woodburne 2004); an interval of
        time based on mammalian biochronology. Units discussed here are
        Puercan and Torrejonian
PETM   Paleocene–Eocene Thermal Maximum. A short-term hyperthermal pulse
        of global warming at the Paleocene–Eocene boundary (Zachos et al.
        2008; McInerney and Wing 2011). This is the earliest Eocene
        hyperthermal event, calibrated at 55.33 Ma (Westerhold et al. 2009). It
        had a duration of 120–220 k.y. (Murphy et al. 2010), with an initial pulse
        of about 10 k.y. during which global sea surface temperatures rose 5–9 °C
SALMA   South American Land Mammal age; comparable to NALMA; see
        Pascual et al. (1965), Simpson (1971), Patterson and Pascual (1972),
        Marshall et al. (1983). Units discussed here include Tiupampan,
        Peligran, "Carodnian," Itaboraian, Riochican, and "Sapoan." Units such
        as "Sapoan" are given between quotation marks due to their currently
        informal status.

3.2   Dispersals Between North and South America

3.2.1   Cretaceous Background

Prior to about 106 Ma (late Albian) when South America and Africa finally broke
apart (Lawver et al. 2013), Gondwana was still essentially intact, and land verte-
brate dispersal was basically possible throughout South America, Africa,
Madagascar, India, Australia, and Antarctica. Figure 3.1 shows a late Aptian
reconstruction of continental positions, after Lawver et al. (2013; Fig. 4a).
Figure 3.2 shows the stratigraphic disposition of faunal-bearing successions in
Patagonia during the Late Cretaceous and Paleocene. Land vertebrates are recog-
nized from the Brazilian Baurú Group in the Turonian/Coniacian to Santonian
(Adamantina and Uberaba formations, ca 93–83 Ma) and the late Maastrichtian
(Marília Fm., ca 67–65 Ma; 1 Fig. 3.3), as well as from the Late Cretaceous of
Patagonia. The taxa in the Brazilian assemblages were basically endemic to South
America (Candeiro et al. 2004, 2006, 2008; de la Fuente et al. 2007; Candeiro and
Rich 2010), with a diversity of fish, lepidosaurian frogs, aniloid snakes, podocne-
mid turtles, mesoeucrocodylians, spinosaurid, carcharodontosaurid, abelisaurid, and
titanosaurid 'dinosaurs,'enatiornithine birds, and a mammal of uncertain allocation.
Overall, the assemblage is typically of Gondwanan affinity and is closely related to
coeval biota in Madagascar, India, and continental Africa (Candeiro et al. 2004;
Candeiro and Rich 2010). Even though a trans-Caribbean pathway to North
America may have been available during at least parts of the Albian-Santonian
interval (Pindell and Kennan 2001), little northern affinity was developed as regards
these faunal elements. Candeiro and Rich (2010) note a possible northern origin for

Fig. 3.1 Reconstruction of Aptian continental positions at 120 Ma. Modified from Lawver et al. (2013: Fig. 4a)

a Turonian (ca 90 Ma) carcharodontosaurid from Argentina. The depauperate late Maastrichtian Marília Formation contains no hadrosaurian dinosaurs or mammals of North American affinity.

Gayet et al. (2001) discussed the land vertebrate fauna from the early Late Maastrichtian Pajcha Pata site, El Molino Formation, Bolivia (7, Fig. 3.3), correlated to about 69 Ma. The fauna includes frogs, salamanders, turtles, snakes, crocodiles, coelurosaur and sauropod saurischians, and indeterminate mammals. As yet, there is no evidence in the fauna of taxa having affinity beyond South America.

The Campanian–Maastrichtian vertebrate record of Argentina is considerably more diverse than that of the partly coeval Marília Formation of Brazil and has many of the same vertebrate groups found in the Uberaba–Marília formations to the north. These include frogs, turtles, lepidosaurs, mesoeucrocodilians, abelisaurids, carcharodontosaurids, spinosaurids, and titanosaurids recorded in the Allen and Los Alamitos (2, Fig. 3.3), and La Colonia (3, Fig. 3.3) formations (LA, LC in Fig. 3.2). Leanza et al. (2004) considered that Allen Formation hadrosaurine and lambeosaurine ornithopods and ankylosaurine ornithischians likely to be of northern origin and to have immigrated to Argentina at that time (late Campanian or early Maastrichtian), ca 75–70 Ma. Salgado and Gasparini (2006) reviewed the presence of Campanian ankylosaurian dinosaurs from the Antarctic Peninsula, but refrained from proposing a South American connection, which is comparable to Agnolin et al. (2010). Case et al. (2007) recorded the early Maastrichtian presence of an Antarctic Peninsula dromaeosaur, considered it to be endemic and of Gondwanan origin, comparable to the Santonian megalasaurid theropod, a late Campanian nodosaur, and early Maastrichtian hypsilophodontid and a similarly aged
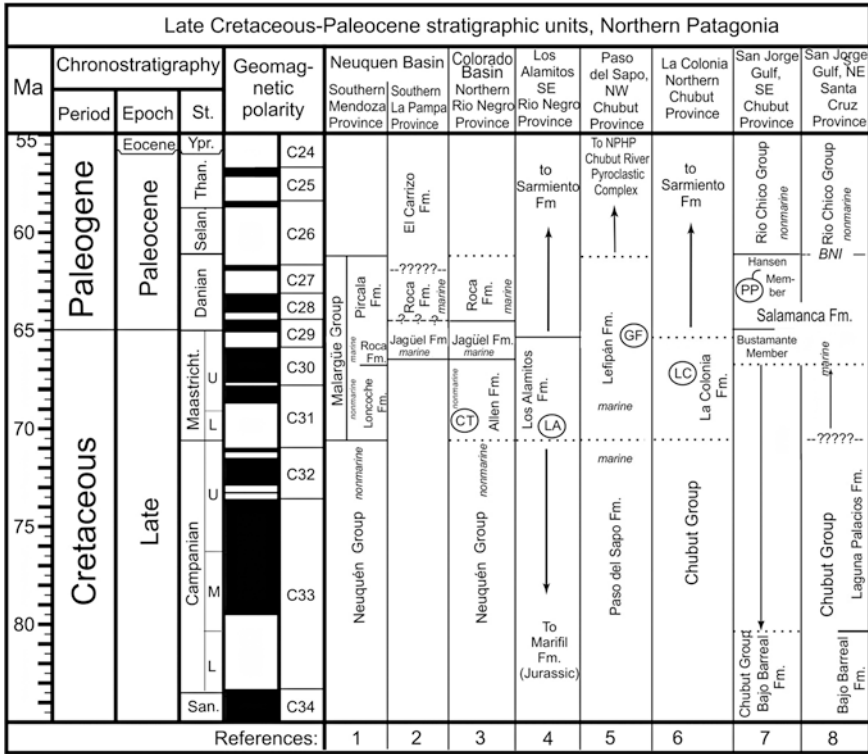
Fig. 3.2 Late Cretaceous stratigraphic units, Northern Patagonia. Modified from Woodburne et al. (2014: Fig. 3). Peligran after Clyde et al. (2014). *References* (1) Neuquén Basin (Leanza et al. 2004, Massabie 1995); (2) Northern Río Negro Province (Rougier et al. 2009a); CT = Cerro Tortuga mammal site. (3) Los Alamitos, southeastern Río Negro Province, (after Bonaparte 1987; Spalletti et al. 1999); LA = Los Alamitos mammal site; (4) Paso del Sapo, NW Chubut Province (after Ruiz 2006); GF = Grenier Farm mammal site; (5) La Colonia, northern Chubut Province (after Pascual et al. 2000); LC = La Colonia mammal site; (6) Golfo San Jorge Basin, SE Chubut Province (after Andreis et al. 1975; Iglesias et al. 2007; Clyde et al. 2014 for the age of the Bajo Barreal Formation); (7) Golfo San Jorge Basin (Clyde et al. 2014, for the age of the Bajo Barreal Formation)

iguanodontid also known from the James Ross Island area of the Antarctic Peninsula (4, Fig. 3.3). The lambeosaurine (Powell 1987) was included in a new hadrosaur genus, *Willinakage*, by Juárez-Valieri et al. (2010), so the presence of lambeosaurs in South America is not supported. Case et al. (2000) reported the late Maastrichtian presence of a hadrosaurian dinosaur from the Antarctic Peninsula and viewed it in the context of an ultimate dispersal from North America. Based on the above considerations, the reptilian dispersal to from North to South America appears to have been accomplished in the late Campanian-early Maastrichtian and involved only hadrosaurs.
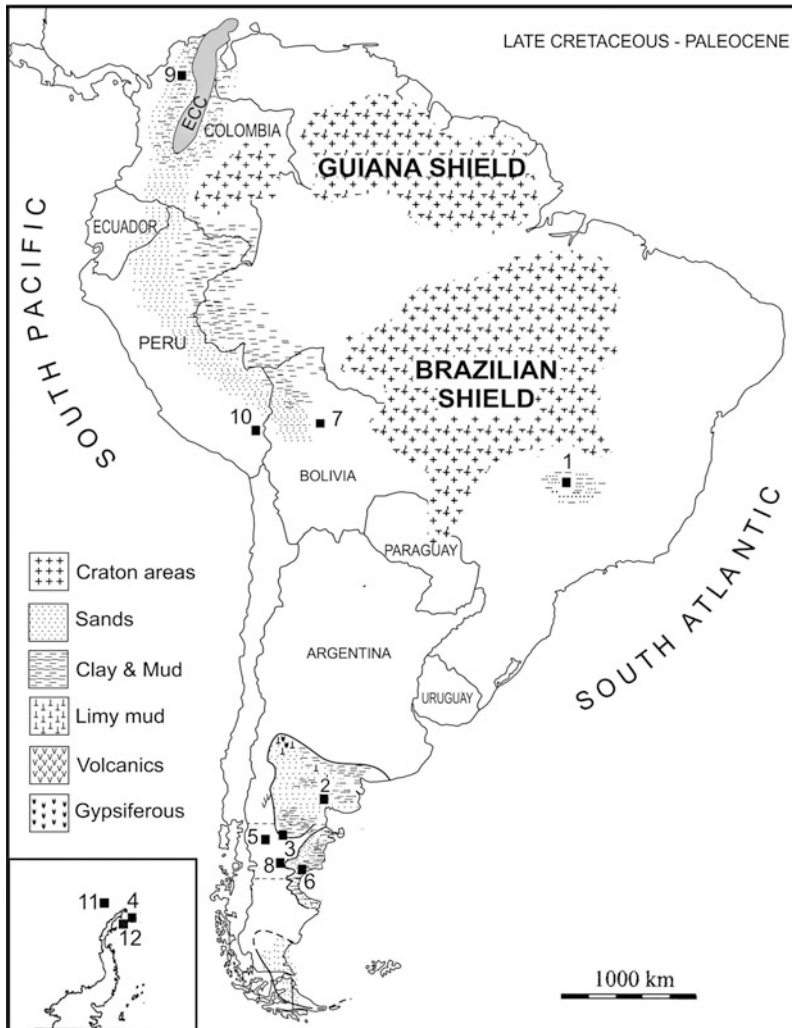
Fig. 3.3 Map of South America showing localities discussed in the text. Modified from Woodburne et al. (2014), Fig. 2B. (1) Baurú Basin, Adamantina and Uberaba formations (Santonian–Coniacian), and Marília Formation (Late Maastrichtian). (2) Allen and Los Alamitos formations (Maastrichtian). (3) La Colonia Formation (Maastrichtian). (4) La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula. (5) Grenier Farm site, early Paleocene, Chubut Province, Argentina. (6) Punta Peligro, Peligran SALMA, Paleocene, Argentina. (7) Tiupampa Fauna, Paleocene, Bolivia. (8) Palacio de los Loros flora, Salamanca Formation, Paleocene, Argentina. (9) Cerrejón flora, Paleocene, Colombia. (10) Laguna Umayo, late Paleocene or early Eocene, Peru. (11) South Shetland Islands, Antarctic Peninsula; Eocene plants (Poole et al. (2005). (12) James Ross Basin, Antarctic Peninsula, Late Cretaceous to Paleocene plants (Poole et al. (2005)

3.2.2   Alamitan SALMA

As reviewed by Woodburne et al. (2014) and paraphrased here, the Late Cretaceous Alamitan SALMA is based on the mammals of the Los Alamitos and Allen formations, Río Negro Province, as well as the La Colonia Formation, Chubut Province, Argentina, (LC, Figs. 3.2 and 3.3; see also Pascual and Ortiz-Jaureguizar 2007). The Alamitan is considered to be of Campanian-Maastrichtian (Bonaparte 1987) or Maastrichtian, but not latest (LA, Fig. 3.2) Maastrichtian age (Pascual et al. 2000; Rougier et al. 2009a, b). The Alamitan fauna contains 17 genera of mammals, all pertaining to non-tribosphenic groups that include a 'symmetrodont' 13 dryolestoids, and a sudamericid as well as a ferugliotheriid gondwanatheria (Pascual and Ortiz-Jaureguizar 2007; Rougier et al. 2009a, 2011; see Table 3.1). A single multituberculate also was recorded (Kielan-Jaworowska et al. 2007; but see Gurovich and Beck 2009). Even though the number of dryolestids may be reduced, their meridiolestid order is a distinct South American group (Rougier et al. 2011) and illustrative of the general pattern in which all Alamitan taxa are of endemic origin, with no antecedent and very few subsequent forms known.

The Alamitan fauna is clearly dominated by the 13 dryolestoids, distributed among seven families. Of these, casamiquelids comprise the most diverse family (3 genera), with mesungulatids, dryolestids, and barbereniids each represented by two genera. The Sudamericidae is of Gondwanan distribution in the Late Cretaceous through the mid-Paleocene in South America (and mid-Eocene of the Antarctic Peninsula; Goin et al. 2006). This, along with the Late Cretaceous South American endemic Ferugliotheriidae, reflects a major gondwanatheria influence here (Goin et al. 2012b). If correctly identified, the Alamitan multituberculate recovered from levels of the La Colonia Fm. (LC, Fig. 3.2) would reflect—along with those of the Early Cretaceous of Australia (Rich et al. 2009)—the rare Gondwanan occurrence of the group that is much better known in faunas of Jurassic and Cretaceous age in North America (and Holarctica; McKenna and Bell 2002). The Early Cretaceous record of the group in Africa (Morocco; Sigogneau-Russell 1991; Hahn and Hahn 2003) has been disputed (Hahn and Hahn 2006).

With the possible exception of multituberculates, this diverse group of non-tribosphenic taxa had its origin in late Jurassic faunas of Gondwana and underwent a successful radiation in the Cretaceous (Rougier et al. 2009a), during an interval termed the Gondwanan Episode by Pascual and Ortiz-Jaureguizar (2007). Goin et al. (2012a) suggested that the radiation of these endemic mammals was a Late Cretaceous (Cenomanian–Maastrichtian) event (their "Late Gondwanan Phase"), and that it was triggered by the global warming that developed since the Cenomanian. Bertini et al. (1993) and Candeiro et al. (2006) noted the presence of a potentially therian mammal from the Turonian–Santonian (ca 85 Ma) Adamantina Formation of Brazil (1, Fig. 3.3), but this awaits further verification.

Table 3.1 Late Cretaceous-Early Eocene record of South American mammals, at the generic level. 1, presence; 0, absence. Abbreviations: Ala., Alamitian SALMA; Tiu., Tiupampian SALMA; Pel., Peligran SALMA; Car., Carodnia biozone; Itab., Itaboraian SALMA; Rio., Riochican SALMA; Sap., Paso del Sapo mammalian association. The GABI record

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
Superfamilial taxon	Family	Genus							
Multituberculata									
"Symmetrodonta"	Bondesiidae	*Bondesius*	1	0	0	0	0	0	0
Dryolestoidea		*Paraungulatum*	1	0	0	0	0	0	0
		Austrotriconodon	1	0	0	0	0	0	0
	Dryolestidae	*Groeberitherium*	1	0	0	0	0	0	0
		Leonardus	1	0	0	0	0	0	0
	Mesungulatidae	*Mesungulatum*	1	0	0	0	0	0	0
		Coloniatherium	1	0	0	0	0	0	0
	Peligrotheriidae	*Peligrotherium*	0	0	1	0	0	0	0
	Regitheriidae	*Reigitherium*	1	0	0	0	0	0	0
	Brandoniidae	*Brandonia*	1	0	0	0	0	0	0
	Casamiguelidae	*Casamiguelia*	1	0	0	0	0	0	0
		Alamatherium	1	0	0	0	0	0	0
		Rougeritherium	1	0	0	0	0	0	0
	Barbereniidae	*Barberenia*	1	0	0	0	0	0	0
		Quirogatherium	1	0	0	0	0	0	0
Gondwanatheria	Sudamericidae	*Sudamerica*	0	0	1	0	0	0	0
		Gondwanatherium	1	0	0	0	0	0	0
	Ferugliotheriidae	*Ferugliotherium*	1	0	0	0	0	0	0
Gondwanatheria, Indet.		New genus	0	0	0	0	0	0	1
Monotremata	Ornithorhynchidae	*Monotrematum*	0	0	1	1	0	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
Metatheria									
"Ameridelphia"	Pediomyidae	Khasia	0	1	0	0	0	0	0
	Pucadelphyidae	Pucadelphys	0	1	0	0	0	0	0
		Andinodelphys	0	1	0	0	0	0	0
		Mizquedelphys	0	1	0	0	0	0	0
	Jaskhadelphyidae	Jaskhadelphys	0	1	0	0	0	0	0
	Mayulestidae	Mayulestes	0	1	0	0	0	0	0
	Protodidelphidae	Carolocoutoia	0	0	0	0	1	0	0
		Guggenheimia	0	0	0	0	1	0	0
		Protodidelphis	0	0	0	0	1	0	1
		Periprotodidelphis	0	0	0	0	1	0	0
		Zeusdelphys	0	0	0	0	1	0	0
	Derorhynchidae	Derorhynchus	0	0	1	0	1	0	1
		Pauladelphys	0	0	0	0	0	0	1
	Sternbergiidae	Carolopaulacoutoia	0	0	0	0	1	0	0
		Itaboraidelphys	0	0	0	0	1	0	1
		Didelphopsis	0	0	1	1	1	0	0
	Family indeterminate	Incadelphys	0	1	0	0	0	0	0
		Tiulordia	0	1	0	0	0	0	0
		Szalinia	0	1	0	0	0	0	0
		Eobrasilia	0	0	0	0	1	0	0
		Marmosopsis	0	0	0	0	1	0	1
		Gaylordia	0	0	0	0	1	0	0
		Minusculodelphis	0	0	0	0	1	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Monodelphopsis	0	0	0	0	1	0	0
		Sternbergia	0	0	0	0	1	0	0
Sparassodonta	Basal Sparassodonts	*Allqokirus*	0	1	0	0	0	0	0
		Nemolestes	0	0	0	0	1	0	1
		Patene	0	0	0	0	1	1	0
Marsupialia									
Didelphimorphia	Peradectidae	New genus	0	0	0	0	0	0	1
		Peradectes	0	1	0	0	0	0	0
	Caroloameghiniidae	*Procaroloameghinia*	0	0	0	0	1	1	1
		New genus	0	0	0	0	0	0	1
Paucituberculata	Family indeterminate	*Riolestes*	0	0	0	0	1	0	0
		Bardalestes	0	0	0	0	0	0	1
Australidelphia									
Microbiotheria	Microbiotheriidae	*Eomicrobiotherium*	0	0	0	0	0	0	1
		Mirandatherium	0	0	0	0	1	0	0
Polydolopimorphia	Family indeterminate	New genus and species	0	0	1	0	0	0	0
		Bobbschaefferia	0	0	0	0	1	0	0
	Glasbiidae	*Palangania*	0	0	0	0	0	1	1
	Bonapartheriidae	New genus	0	0	1	0	0	0	0
		Epidolops	0	0	0	0	1	0	0
	Gashterniidae	*Gashternia*	0	0	0	0	1	1	1
	Family indeterminate	*Roberthoffstetteria*	0	1	0	0	0	0	0
	Polydolopidae	*Amphidolops*	0	0	0	1	0	0	1
		Archaeodolops	0	0	0	0	0	1	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Pliodolops	0	0	0	0	1	1	1
		New genus	0	0	0	0	1	0	1
Eutheria									
Cingulata	Dasypodidae	Prostegotherium	0	0	0	0	0	1	1
		Riostegotherium	0	0	0	0	1	0	1
		Astegotherium	0	0	0	0	0	0	1
		Stegosimpsonia	0	0	0	0	0	0	1
	Peltephilidae	New genus	0	0	0	0	0	1	0
Astrapotheria	Astrapotheriidae	Eoastrapostylops	0	0	0	0	1	0	0
		Shecenia	0	0	0	0	1	0	0
		Tetragonostylops	0	0	0	0	1	0	0
	Trigonostylopidae	Trigonostylops	0	0	0	0	0	1	1
"Condylarthra"	Mioclaenidae								
	Kollpaniinae	Molinodus	0	1	0	0	0	0	0
		Tiuclaenus	0	1	0	0	0	0	0
		Pucanodus	0	1	0	0	0	0	0
		Silmoclaenus	0	1	0	0	0	0	0
		Andinodus	0	1	0	0	0	0	0
	Didolodontidae	New genus	0	0	0	0	0	0	1
		New genus	0	0	0	0	0	0	1
		Escribania	0	0	1	0	0	0	0
		Raulvaccia	0	0	1	0	0	0	0
		Ernestokokenia	0	0	0	0	1	1	0
		Lamegoia	0	0	0	0	1	0	0

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Paulacoutoia	0	0	0	0	1	0	0
		Umayodus	0	0	0	0	1	0	0
Pantodonta	Alcidedorbignyidae	*Alcidorbignia*	0	1	0	0	0	0	0
Litopterna	Protolipternidae	*Miguelsoria*	0	0	0	0	1	0	0
		Protolipterna	0	0	0	0	1	0	0
		Asmithwoodwardia	0	0	0	0	1	0	1
	Anisolabdidae	*Wainka*	0	0	0	1	0	0	0
		Anisolambda	0	0	0	0	1	1	0
	Notonychopidae	*Notonychops*	0	0	0	0	1	0	0
		Requisia	0	0	1	0	0	0	0
	Sparnotheriodontidae	*Victorlemoinea*	0	0	0	0	1	1	1
Notoungulata		*Satshatemnus*	0	0	0	0	1	0	0
	Perutheriidae	*Perutherium*	0	0	0	0	1	0	0
	Archaeopithecidae	*Archaeopithecus*	0	0	0	0	0	1	1
		Acropithecus	0	0	0	0	0	1	1
	Henricosborniidae	Genus indet.	1	0	0	0	0	0	0
		Henricosbornia	0	0	0	0	1	1	1
		Othnielmarshia	0	0	0	0	0	1	1
		Peripantostylops	0	0	0	0	1	0	0
		Simpsonotus	0	0	0	0	1	0	0
	Interatheriidae	*Notopithecus*	0	0	0	0	0	1	0
	Isotemnidae	*Isotemnus*	0	0	0	0	1	1	1
	Notostylopidae	*Brandmayria*	0	0	0	0	0	1	0
		Edvardotrouessartia	0	0	0	0	0	0	1

(continued)

Table 3.1 (continued)

Biochron			Ala.	Tiu.	Pel.	Car.	Itab.	Rio.	Sap.
		Homalostylops	0	0	0	0	0	0	1
		Notostylops	0	0	0	0	0	1	1
		notostylopid indet.	0	0	0	0	1	0	0
	Oldfieldthomasiidae	*Colbertia*	0	0	0	0	1	0	0
		Itaboraitherium	0	0	0	0	1	0	0
		Kibenikhoria	0	0	0	0	1	0	0
		Maxschlosseria	0	0	0	0	0	1	0
		Oldfieldthomasia	0	0	0	0	0	1	0
Xenungulata	Carodniidae	*Carodnia*	0	0	0	1	1	0	0
		Notoetayoa	0	0	0	1	0	0	0
		Etayoa	0	0	0	0	1	0	0
Total number of genera			17	19	10	4	51	21	34
Number of FADs			17	19	10	4	48	13	12
Number of LADs			17	19	8	3	31	2	16
Through going			0	0	0	0	1	8	13
Number of taxa		Total	17	19	10	4	51	21	34
		FADs	17	19	10	4	48	13	12
			0	0	0	0	0	0	0
		LADs	−17	−19	−8	−3	−31	−2	−16
		Through going	0	0	0	0	1	8	13
Percent of taxa		FADs	100	100	100	100	94	62	35
			0	0	0	0	0	0	0
		LADs	−100	−100	−80	−75	−61	−10	−47
		Through going	0	0	0	0	2	38	38

The Alamitan mammal genera are basically unique to South America (Woodburne et al. 2014). Some of their higher-level groups indicate a Gondwanan influence and, with the possible exception of the multituberculate, none are clearly of North American origin. As discussed below, however, the Paleocene mammalian evidence favors a Late Cretaceous dispersal to South America. The conundrum may be partly alleviated by noting that Alamitan faunas do not extend into the late Maastrichtian (LA, Fig. 3.2), and it is to be hoped that mammals of this age will be discovered.

Pindell and Kennan (2001: Figs. 11, 13; 2009: Figs. 11, 12) reconstructed the Caribbean region to show that the Aves Ridge and adjacent areas of the Caribbean Arc experienced both volcanic and plutonic activity in the Campanian and early Maastrichtian. As shown in Figs. 3.4 and 3.5, this activity is considered here to have provided a pathway compatible with the above dispersals. In addition, Crawford and Smith (2005) performed a nuclear gene phylogenetic analysis of leptodactylid frogs that point to a northward dispersal of the subgenus *Craugastor* from South America to Central America (Costa Rica) in the Late Cretaceous or early Paleogene (77–63 Ma, contra Heinicke et al. 2007). These reconstructions are consistent with the proposed dispersal to South America of polydolopimorphian (Goin et al. 2006) as well as other metatherians (Woodburne and Case 1996; Case et al. 2005) to account for their early Paleocene diversity in South America.

3.2.3 Mammalian Immigrations

Woodburne et al. (2014) reviewed the Late Cretaceous to early Paleocene immigration of marsupial and placental mammals to South America, from which the following is paraphrased and updated. The earliest therian mammal is represented by the early Paleocene *Cocatherium*, from the pre-Tiupampan, earliest Paleocene, Grenier Farm fauna (GF, Fig. 3.2; 5, Fig. 3.3; Grenier Farm, Fig. 3.6) and is considered (Goin et al. 2006) to be a polydolopimorphian. Goin et al. (2009) suggested that polydolopimorphians are members of the Australidelphia clade (Szalay 1982, 1994), as are the microbiotheria (Nilsson et al. 2010). Along with the Tiupampan polydolopimorphian, *Roberthoffstetteria*, the clear early Paleocene presence of this relatively derived group contributes to the evidence in favor of there having been a Late Cretaceous entry and evolution of metatherians in South America. Whether or not Paleogene South American polydolopimorphians and microbiotheria have affinities with Australian taxa (see Chap. 5), the likely Late Cretaceous presence of these australidelphians in South America would provide a potential early biotic link between the two continents (Muizon 1991; Muizon and Brito 1993; Woodburne and Case 1996; Nilsson et al. 2010; Beck 2012). As discussed further below, this link also may be reflected by the early Paleocene presence of monotremes (Pascual et al. 1992) in the Punta Peligro fauna (6, Fig. 3.3; Peligran SALMA, Fig. 3.6) of Patagonia (Table 3.1).
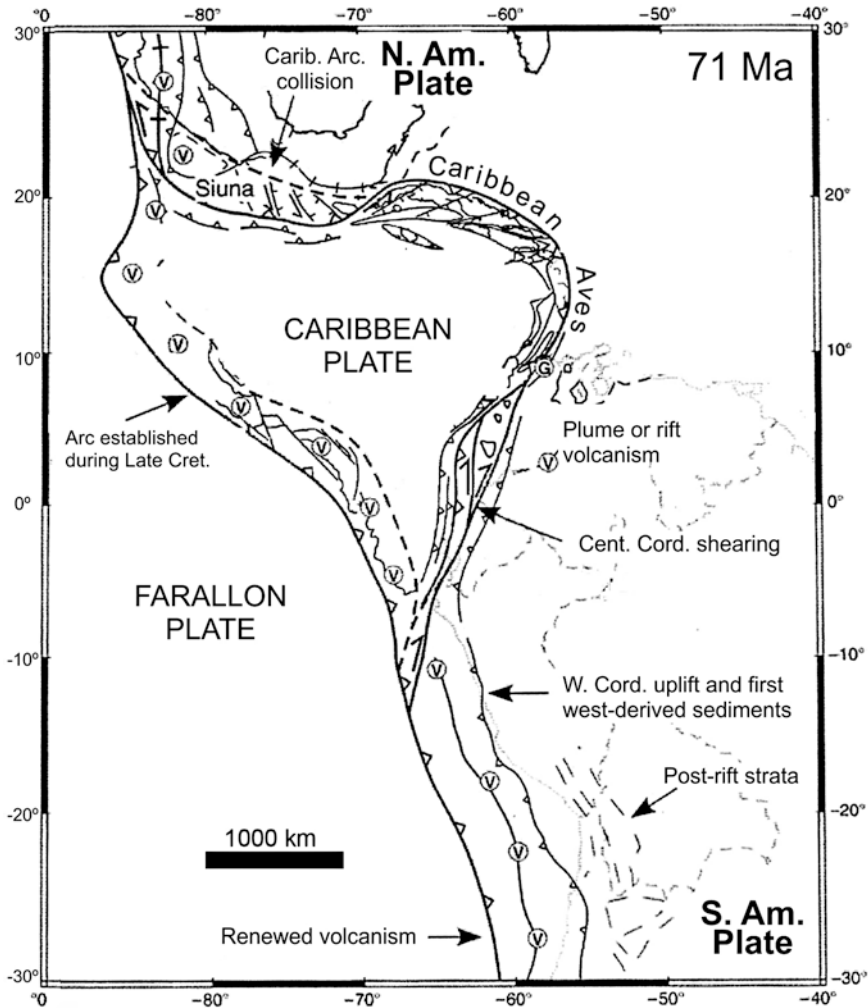
CAMPANIAN RECONSTRUCTION OF CARIBBAN REGION ARC ACTIVITY
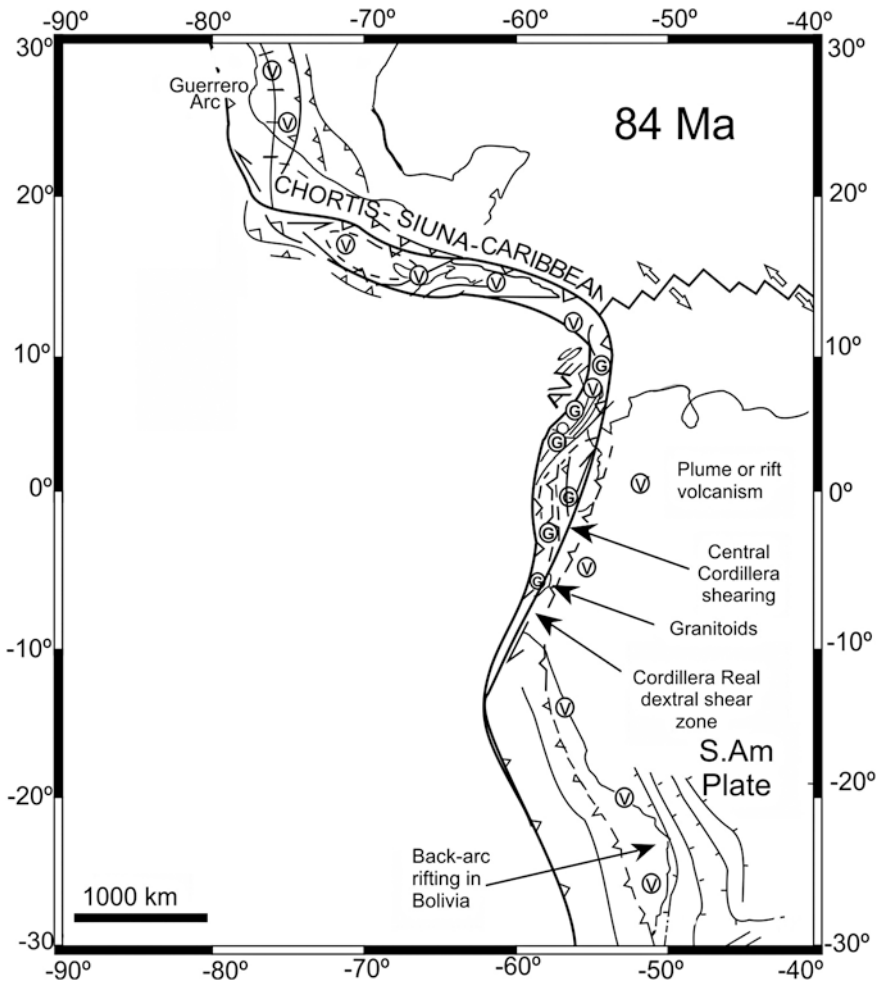
Fig. 3.4 Campanian reconstruction of Caribbean region arc activity. Modified from Pindell and Kennan (2009: Fig. 11)

The great metatherian diversity in the Tiupampan (7, Fig. 3.3) supports the inference of there having been a strong prior endemic radiation of the group. In Table 3.1, a majority of the 'ameridelphians' is considered to reflect this South American radiation (three pucadelphyids, a jaskhadelphyid, and a mayulestid). *Mayulestes* was once regarded as the earliest, and basal-most, sparassodontan (Muizon 1991, 1998), whereas it now is considered as a basal taxon to other South

MAASTRICHTIAN RECONSTRUCTION OF CARBBEAN REGION ARC ACTIVITY

Fig. 3.5 Maastrichtian reconstruction of Caribbean region arc activity. Modified from Pindell and Kennan (2009: Fig. 13)

American metatherians (e.g., Forasiepi 2009). The other, indeterminate 'ameridelphians,' *Incadelphys*, *Tiulordia*, and *Szalinia*, further broaden the endemic Tiupampan diversity, as does the sparassodontan *Allqokirus* (Table 3.1) all of which points to a pre-Tiupampan radiation of the group. The 'ameridelphian' *Khasia* is an enigmatic taxon whose precise affiliations are still to be proven (see Chap. 5).

Fig. 3.6 Paleocene and Eocene time scale showing North American and South American mammalian biochronologic units. After Woodburne et al. (2014: Fig. 1). Age, Epoch, Stage and Polarity Chrons follow Luterbacher et al. (2004). Global Temperature curve is after Zachos et al. (2001)

Originally regarded as a microbiothere (Muizon 1991), more recently it has been argued to have pediomyid affinities (Goin et al. 2013, Woodburne et al. 2014: Table 1; see Chap. 5). If the latter is the case, it would also argue in favor of close affinities between South American and North American early metatherians (Case et al. 2005). The didelphimorphian *Peradectes* (Horovitz et al. 2009) is the last element of that archaic marsupial clade from North America (but see Goin and Abello 2013). Pediomyids are not known from younger deposits in South America. In summary, the basic ancestry of South American metatherians lies in North America. The early Paleocene South American diversity of the group suggests its Late Cretaceous entry.

Regarding placental mammals, *Molinodus* and four other taxa (Table 3.1) provide not only a major, but also nearly final, diversity of kollpaniine 'condylarths,' which have a lingering presence in the "Barrancan" (*Pascualodus*). The archaic placental group, Pantodonta, is last represented in South America by the Tiupampan *Alcidedorbignia*. Muizon and Cifelli (2000) noted the basic similarity between Puercan-aged North American 'condylarths' and those of South America, and suggested a close temporal link between them. Williamson and Carr (2007) reviewed the mioclaenid condylarths from North America, concluded that the group is monophyletic, endemic to western North America, and gave no support for a specific relationship with South American ungulates. They concluded that the mioclaenids are basically known only from New Mexico, but provided no suggestions as to the origin of South American 'mioclaenids.' The point taken here is that regardless of not being related to North American Mioclaenidae, the South American 'condylarths' unequivocally still had a North American ancestry, most likely from Puercan (Fig. 3.6) taxa (Williamson and Carr 2007: Fig. 12-1; compare taxa with ages in McKenna and Bell 2002), so the dispersal signal they contain still is relevant and pertinent. The Tiupampan henricosborniid signals the beginning of the no-toungulates, a conspicuous group in Itaboraian (Fig. 3.6) and later Paleogene faunas (Table 3.1), as well as continuing into the Pleistocene (McKenna and Bell 2002).

Further suggestion in favor of a Paleocene overland dispersal is provided by the record of the menispermaceaean podocarp, *Palaeoluna*, from the Cerrejón flora of Colombia (9, Fig. 3.3). *Palaeoluna* also is found in ∼60 Ma Paleocene sites in Wyoming, and thus is considered to reflect trans-Caribbean Paleocene connections between those places (Herrera et al. 2011). In addition, the Cerrejón genus, *Stephania*, is a possible precursor of modern Australian members (Herrera et al. 2011), but this dispersal scenario is hindered by the lack of information regarding fossil occurrences of the group in India and southeastern Asia, as well as Australia.

In contrast to Rage (1978), Rage (2005) proposed no snake genus as having dispersed northward from South America in the Late Cretaceous or early Tertiary, so the current vertebrate record favors north to south dispersal at those times. On the other hand, based on nuclear gene phylogenetic analysis, Crawford and Smith (2005) recently inferred a northward dispersal of the an ancestor of the leptodactylid

subgenus *Craugastor* from South America across the Caribbean region to Central America (Costa Rica) in the Late Cretaceous or early Paleocene (77–63 Ma), perhaps facilitated by low sea levels at that time. Consistent with this hypothesis, *Craugastor* is considered to have begun a rapid diversification in the Chortis Block (present day Guatemala) at about the Paleocene–Eocene transition.

Overall, the Tiupampan fauna appears to have been dominated by metatherian insectivorous–omnivorous taxa of minute to small size. All insectivores are below 50 g in body mass, and a very small taxon of 5 g (*Jaskhadelphys*) occurs in this trophic category (Zimicz 2012). The carnivore niche is also filled by metatherians, the small sparassodontan (*Allqokirus*), and the medium-sized 'ameridelphians' *Mayulestes* and *Andinodelphys*. Other small-sized metatherians occupy the mixed insectivory–frugivory niche (e.g., *Roberthoffstetteria*). The remainder of the fauna appears to have been adapted to largely browsing herbivory. The Bolivian Tiupampa fauna (7, Fig. 3.3) occurs far to the north of Argentina, but a review of its distribution and paleoecology (Woodburne et al. 2014) suggests that its climate would have been tropical to subtropical and similar to that of the Palacio de los Loros flora of Argentina (8, Fig. 3.3), or the Cerrejón flora of Colombia (9, Fig. 3.3).

None of the 19 Tiupampan genera is related to any genus or higher taxonomic category of Alamitan age (Gelfo et al. 2009; Table 3.1). The totally new fauna can only have been derived by immigration from North America in the latest Cretaceous or earliest Paleocene (as discussed above). A similar statement applies to the basal polydolopimorphian, *Cocatherium*, from the earlier Paleocene Grenier Farm Local Fauna (GF, Fig. 3.2, Lefipán Formation of Chubut Province, Argentina and 5, Fig. 3.3; Case et al. 2005; Goin et al. 2006). As a likely derived, rather than stem, metatherian, its early Paleocene age supports the interpretation that 'ameridelphian' and other stem-group metatherians, as well as their more derived lineages now found in the Tiupampa fauna, reflect a Late Cretaceous dispersal from North to South America. The 'condylarths' support an early Paleocene dispersal from North America as well. Except for the possible therian from the Adamantina Formation of Brazil (see above) relevant mammals have not been found in South American Late Cretaceous faunas as currently known, so the matter remains undocumented, at least.

Taking all of the above into consideration, the present record provides a growing list of taxa that seem most compatible with an overland dispersal pathway between North and South America that is better established than a "sweepstakes" model, but not as fully developed as a "corridor." The Caribbean-Aves Ridge arc volcanism (Figs. 3.4 and 3.5) apparently produced a succession of relatively closely spaced, but probably not completely interconnected, terranes suitable for land animal dispersal during an interval of about 20 m.y. The GABI (Great American Biotic Interchange) occurred over a comparable (although shorter) interval in the Neogene with better documentation of dispersal episodes (Woodburne 2010) than now possible for the Late Cretaceous. The GABI record may be instructive as to there having been a Late Cretaceous pattern of dispersal intervals, as well.

3.2.4 Xenarthran Problem

The oldest Xenarthra in South America is of early Eocene age (Itaboraian; Bergqvist et al. 2004; Woodburne et al. 2014), but the group is considered to be ancient and fundamentally a sister-taxon to virtually all other placental mammals (Magnorder Xenarthra; McKenna and Bell 2002; comparable to O'Leary et al. 2013). In that context, it has been advocated that the group is fundamentally related to the Afrotheria and thus an association with the Gondwana continent of Africa, and its South American occurrence likely represents an association prior to the time of final separation of those continents at ca 106 Ma (Lawver et al. 2013). In addition, some South American notoungulates have been proposed as having Afrotherian affinities (Agnolin and Chimento 2011; O'Leary et al. 2013), but this has been soundly discounted by López et al. (in press).

Stanhope et al. (1998) defined the new mammalian superorder, Afrotheria, based on an analysis of nuclear and mitochondrial genes. Afrotheria includes Proboscidea, Sirenia, Hyracoidea, aardvark (Tubulidentata), elephant shrews (Macroscelidea), tenrecs (Tenrecidae), and golden moles (Chrysochloridae), and Stanhope et al. (1998) suggested that the group originated in Africa in the mid-Cretaceous (105–90 Ma). This was followed by a number of articles in support of the concept (Springer et al. 1997, 1999; Tabuce et al. 2007, 2008), and others suggested a phylogenetic relationship with Xenarthra (Amrine-Madsen et al. 2003; Hallström et al. 2007).

Whereas the major input was derived from molecular analyses, Sánchez-Villagra et al. 2007) found that Afrotheria can be characterized as having 23 or more thoracolumbar vertebrae (TLV), which is an increase from the 19 seen in marsupials as well as many placental groups. Using the placental mammal phylogeny proposed by Amrine-Madsen et al. (2003), Sánchez-Villagra et al. (2007) recorded that within Afrotheria, only Macroscelidea (20) and Tubulidentata (21) had fewer than 23 TLV. Interestingly the Xenarthra, considered to be the next-closest clade to Afrotheria, also has a range of 14–29 TLV. Comparably high numbers for other placental mammals are achieved only in Primates (15–24) and Perissodactyla (22–24), groups otherwise not considered phyletically near afrotheres. Asher and Lehmann (2008) also determined that afrotherians share a retarded eruption of the permanent dentition and Seiffert (2007) noted unifying features of the ankle bones. See O'Leary et al. (2013) for additional discussion of Afrotherian morphological characters.

As reviewed by Tabuce et al. (2008) the best known fossil record for Afrotheria is represented by early Eocene Hyracoidea and Proboscidea in Africa which (at 56 Ma; Vandenberghe et al. 2012, and extended to about 60 Ma for proboscideans by Gheerbrant 2009) is compatible with older molecular clock-based proposals for its origin (>80–80 Ma; Bininda-Emonds et al. 2007; Springer and Murphy 2007; Springer et al. 1997; Hällstrom et al. 2007). If Afrotherians are related to xenarthrans (Atlantogenata of Waddell et al. 1999; Amrine-Madsen et al. 2003; Murphy et al. 2007; Hällstrom et al. 2007; Churakov et al. 2009; dos Reis et al. 2012), then their

phyletic separation most likely was prior to the ca 106 Ma separation of Africa and South America (Lawver et al. 2013). If so, their distribution apparently was a vicariant, rather than dispersal , event.

The phyletic and geographic portrayals of Nishihara et al. (2009) considered the African-South American connection having been severed shortly after 120 Ma. The timing is illustrated in greater detail by Jacobs et al. (2011) who indicated initial separation of coastal South America and Africa [Sergipe(SA)-Gabon (AF) and Campos (SA)-Kwanza (AF) basins] began about 115 Ma and was completed (deep water facies) by 90 Ma. This is generally compatible with the geophysical separation of the continents at about 106 Ma (Lawver et al. 2013). Nishihara et al. (2009) considered that the three major placental groups, Boreoeutheria, Afrotheria, and Xenarthra also were present by about 120 Ma. Whereas this has not been borne out by other work (above paragraph), the 106 Ma separation of Africa and South America requires that at least the ancestors of Xenarthra were present in Africa prior to that time, especially if they are considered as basal placental mammals. Meredith et al. (2011: Fig. 1) illustrated the basal node (Atlantogenata, but not named) for Xenarthra and Afrotheria as having been about 100 Ma old, arguably compatible with the 106 Ma Africa–South America separation, as could be the 98 Ma Atlantogenata age of Hallström et al. (2007). Other estimates for a younger Afrotheria age (see Tabuce et al. 2008; O'Leary et al. 2013) would require post-separation dispersals across the widening Atlantic Ocean which are here considered unlikely or at least not supported by other evidence. Inclusion of North American Paleocene leptictids in the Afrotheria (O'Leary et al. 2013) is the latest of a number of proposals (Asher et al. 2003; Zack et al. 2005; Penkrot et al. 2008) for including non-Gondwanan taxa in that group. In view of the strong Gondwanan integrity of the Afrotheria, such proposals seem best explained by homoplasy in both morphological and molecular data (e.g., Springer et al. 2013; characters in *Leptictis*; O'Leary et al. 2013; Supplemental Information, p. 31), and are not followed here.

3.2.5   Summary

The late Campanian to late Maastrichtian record of hadrosaurian dinosaurs in Patagonia and the Antarctic Peninsula suggests dispersal from North America within that interval. Such a dispersal is compatible with the early Paleocene diversity of metatherians, also of purported northern origin, and the northward dispersal of leptodactylid frogs. Plate tectonic reconstructions of the Caribbean region suggest that volcanism and related tectonic episodes provided an array of volcanic arcs sufficient to support those dispersals. The pathway apparently still was functional in the early Paleocene as implied by the North American origin of placental mammals to account for their Tiupampan record in South America, and the presence of the menispermaceaean podocarp, *Palaeoluna*, in Wyoming and Colombia at ∼60 Ma.

3.3 Dispersal Between South America, Antarctica, and Australia

3.3.1 Geological Overview

Woodburne and Case (1996) reviewed the plate tectonic evidence relative to the separation of Antarctica and Australia and concluded that such dispersal would have been increasingly unlikely from about 64 Ma when the South Tasman Rise was considered flooded. This is reviewed and updated, beginning with a summary of the tectonics and stratigraphy of main sedimentary basins along the southeastern margin of Australia.

Exon et al. (2004) indicated that sea floor spreading in the Late Cretaceous resulted in Australian moving northward relative to Antarctica such that the Australo-Antarctic Gulf (AAG) developed and extended eastward over time to finally cross the southern end of the South Tasman Rise (STR) by the beginning of the Oligocene. Lawver et al. (2011) noted that if not actually originating at about 95 Ma (Cenomanian), then sea floor spreading in the Great Australian Bight was well underway by that time.

As indicated in Fig. 3.7, the main basins from west to east are Otway (and Sorell), Bass, and Gippsland. Norvick (2000: Fig. 7) showed that crustal thinning developed during the late Jurassic (Tithonian, 145 Ma) along the line of the future Australian Bight through the Duntroon , Otway and Gippsland active rift basins, with the Otway, Bass, and Gippsland basins (Fig. 3.7) contiguous in the Aptian (110 Ma; Norvick 2000: Fig. 10). At this time, and into the Albian, the Gippsland Basin (Fig. 3.8) was filled by the nonmarine volcaniclastic sandstones of the Strzelecki Group (Norvik et al. 2001), apparently associated with volcanic centers to the east. The Otway and Gippsland basins are portrayed as possibly interconnected active sag basins receiving nonmarine and volcaniclastic sediment by Norvick (2000, enclosures 5, 6, 13, 14), a condition which continued to the late Albian (100 Ma). Cummings et al. (2004: Fig. 3) show a similar condition for the Bass Basin (Crayfish and Otway Sequences, comparable to those of the Otway; Figs. 3.9 and 3.10).

A Cenomanian hiatus (ca 95 Ma) saw the Otway and Gippsland basins (Figs. 3.8 and 3.10) experience uplift and inversion (Hofford et al. 2011) with reorganization of the Otway and Bass basins, and a hiatus is present at this time in the Bass Basin, as well (Cummings et al. 2004; Fig. 3.9). Turonian sedimentation then produced a succession of nonmarine and lacustrine coal-bearing deposits in the Gippsland Basin (Kipper Shale), with the Bass and Otway basins being active as well (Figs. 3.8, 3.9 and 3.10; Norvick et al. 2001: Fig. 6). At this time, the Otway Basin was aligned with other active basins that extended southeastward along the western border of Tasmania (e.g., Sorell Basin; Exon et al. 2004), a pattern that continued into the Santonian (ca 85 Ma). During these intervals, active basins also were present from southern and southeastern Tasmania to the northeast along the weakening crust of the Lord Howe Rise along the eastern coast of Australia, as the Tasman Sea began to open (Norvick 2000: Fig. 15).

Reconstruction of Australia and Antarctica at 53 Ma
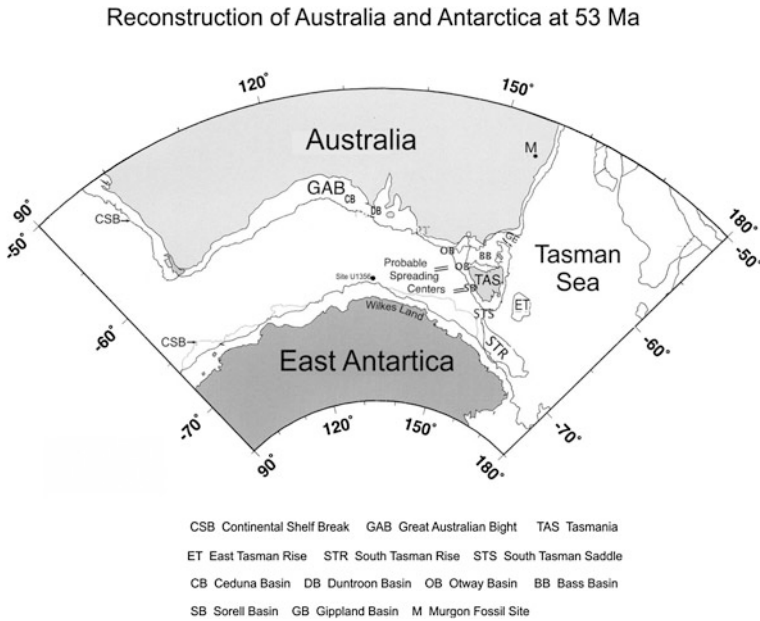
Fig. 3.7 Reconstruction of Australia and Antarctica at 53 Ma. After Lawver et al. (2011: Fig. 5). Shows opened seaway between Australia and Antarctica, with a connection to the Tasman Sea across the South Tasman Rise (STR). The Gippsland Basin is shown in a dashed line to indicate that whereas it opened at that time to the Tasman Sea on the east, there was no connection between the Gippsland and other basins to the west

Crustal thinning was occurring from the Australian Bight region (Ceduna Basin, Fig. 3.7) eastward through the above-named districts with active basins (Norvick 2000: Figs. 15, 16, enclosures 17–19) from the Turonian through Campanian (90–75 Ma), during which time the Tasman Sea opened by rifting along the eastern margins of Australia, Tasmania, and Antarctica. In the Coniacian and Turonian, the sequences begin with a marine unit, but these typically are followed by deltaic to regressive alluvial sequences.

Norvick (2000, enclosures 5 and 6) shows substantial marine sedimentation in the west-facing Ceduna and east-facing Gippsland basins from the Campanian through the Eocene which coincides with the progressive eastward transgression of the Southern Ocean on the one hand, and opening of the Tasman Sea on the other. Marine sedimentation in the Otway Basin was largely restricted to the early part of the sequence, again followed by deltaic regressive stratigraphically higher units. In fact, the Shipwreck through Sherbrook megasequences of Fig. 3.10 are considered to have been derived from both Australia and Antarctica at that time.

In the Paleocene, the Otway basin shelf mudstones and slope turbidites of the Wangerrip Group (Fig. 3.10) show northwestward progradation as marine conditions become more prevalent stratigraphically upward. By the middle Eocene, rapid marine transgression is recorded in the Nirranda megasequence (Fig. 3.10).
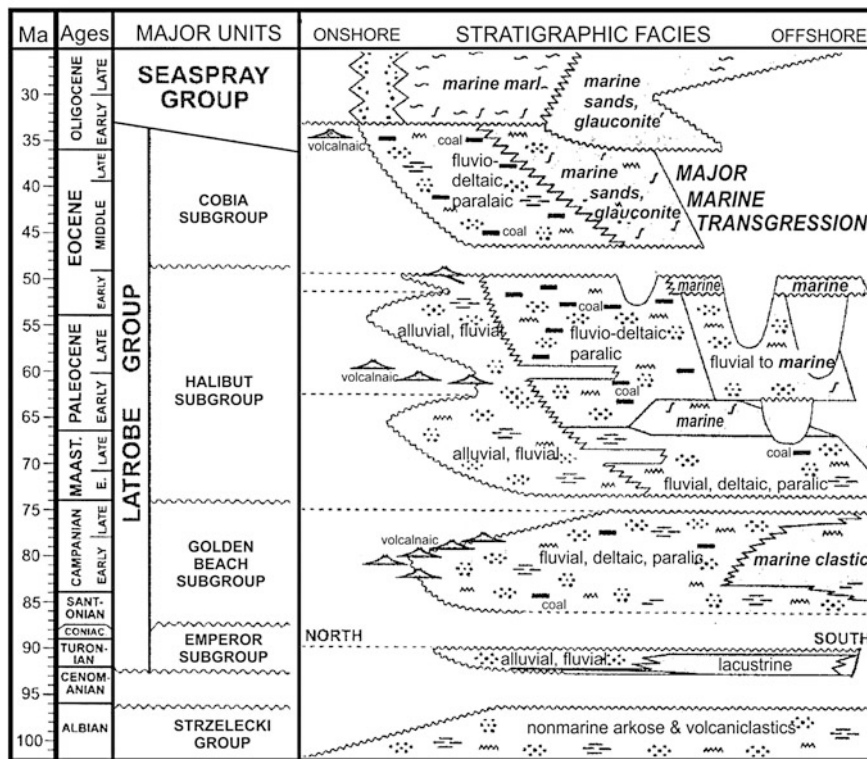
Fig. 3.8 Cretaceous and Paleogene stratigraphy of the Gippsland Basin, Australia. After Bernecker and Partridge (2001: Fig. 2)

During Campanian to Eocene, the Otway (and Bass) and Gippsland basins record the progressive separation of Australia and Antarctica along the Tasmanian-Antarctic shear zone, with final breaching of the South Tasman Rise by about 37 Ma (Exon et al. 2004). Certainly any overland dispersal of land animals between Antarctica and Tasmania (Australia) was severed from that time onward. The marine record on either side of the South Tasman Rise suggests that such may have begun by about the beginning of the Eocene, however.

The Bass Basin (Fig. 3.9) contains a stratigraphic record that extends from the Early Cretaceous (Berriasian) to the present (Cummings et al. 2004). From the Early Cretaceous to mid-Eocene (Lutetian), the sedimentary input is mostly nonmarine clastic, volcaniclastic, and alluvial to lacustrine facies, including lakes and

Fig. 3.9 Cretaceous and Cenozoic stratigraphy of the Bass Basin, Australia. After Cummings et al. (2004: Fig. 3)
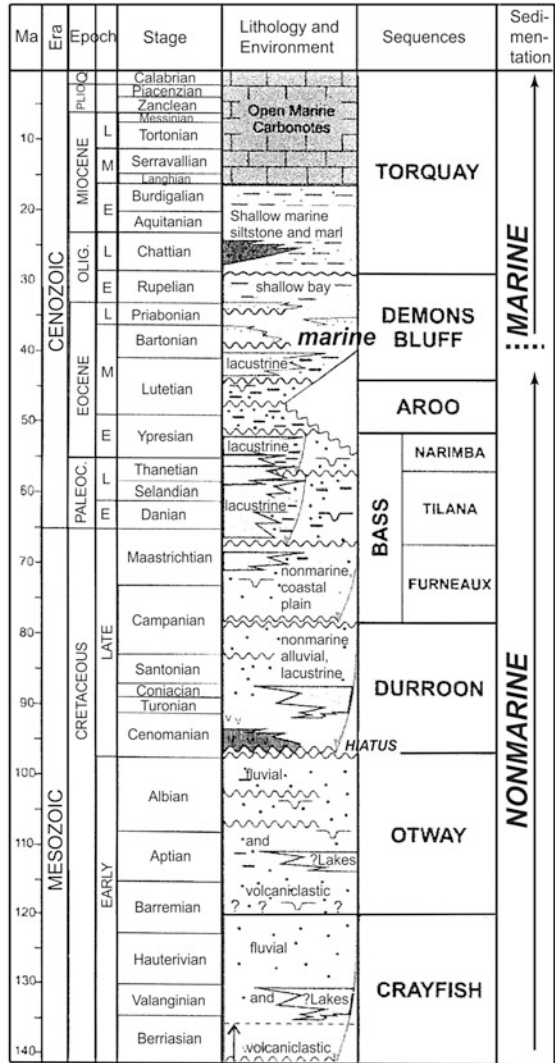
lacustrine coal beds. The Demons Bluff Megasequence [Mid-Eocene (mid-Lutetian) to early Oligocene (Rupelian), 44–30 Ma] records progressive drowning from west to east by a marine incursion that also affected the Otway and Sorell basins as well as western Tasmania, the South Tasman Saddle and South

CRETACEOUS AND PALEOGENE STRATIGRAPHY OF THE OTWAY BASIN, SOUTHEASTERN AUSTRALIA
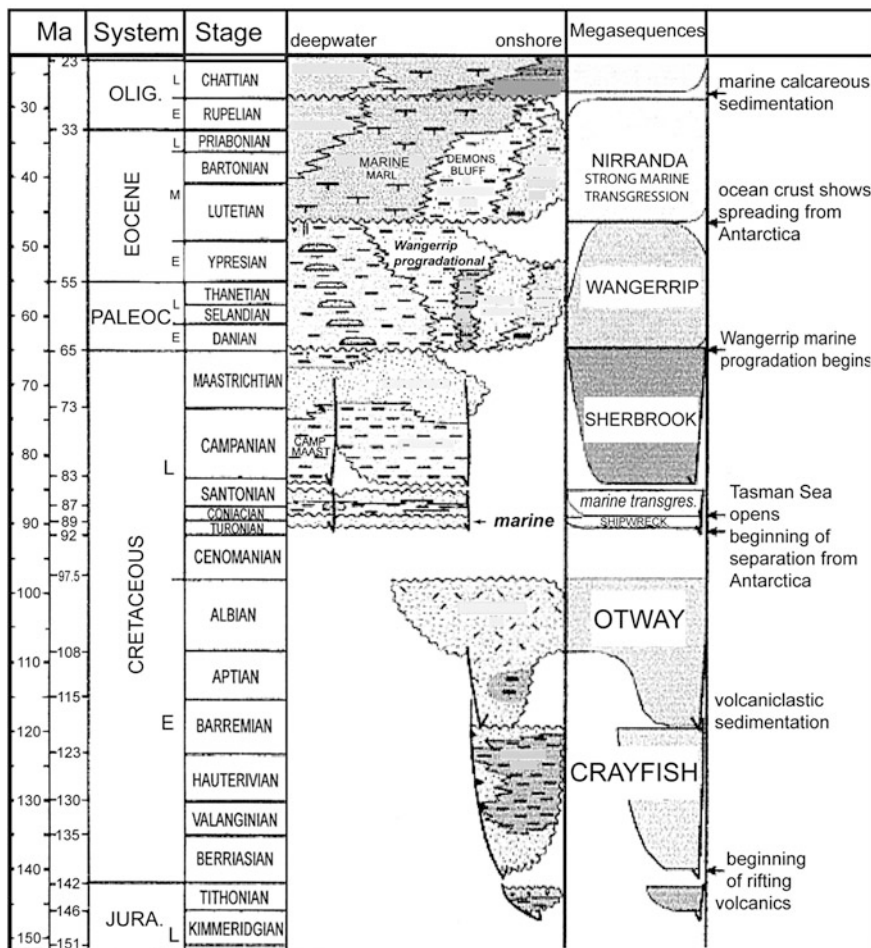
Fig. 3.10 Cretaceous and Paleogene stratigraphy of the Otway Basin, Australia. After Norvic (2000: enclosure 7)

Tasman Rise (Exon et al. 2004: Fig. F7A; Fig. 3.11). Apparently, the Durroon sub-basin of the southern Bass Basin made no connection to the opening Tasman Sea. The Demons Bluff is followed by the late Oligocene to Recent Torquay sequence of increasingly deeper marine conditions (Fig. 3.9).

Norvick et al. (2001) indicated that marine conditions prevailed in the offshore district of the Gippsland Basin from the Late Cretaceous well into the Neogene,

compatible with a connection to the developing Tasman Sea. According to Michael
Hall (personal communication To M.O. Woodburne in 2013), the Gippsland Basin
developed a marine seaway connection to the Bass Basin in the late Middle Eocene,
so that in conjunction with the connection between the Bass, Sorell and Otway
basins a marine barrier to overland mammal dispersal was present along the
southeastern coast of Australia from about 45 Ma (Fig. 3.11). Blevin et al. (2005)
indicated that such conditions deepened and persisted into the Oligocene in the
Bass Basin, by which time Australia and Antarctica were well separated.

   As suggested above, the region between Tasmania and Antarctica did support a
marine barrier to overland dispersal from the early Eocene, if not earlier. Lawver
et al. (2011) noted that the South Tasman Saddle (STS, Fig. 3.7) developed during

Fig. 3.11 Reconstruction of seaways between Australia and Antarctica at ca 45–40 Ma. Modified
from Exon et al. (2004: Fig. F7A). Addition of Otway (O), Sorell (S), Bass (B) and Gippsland
(G) basins after Norvick et al. (2001: Fig. 1). M = Murgon, southeast Queensland, after Godthelp
et al. (1992). Shows separation of Tasmania from the South Tasman Rise and restricted land access
between the Gippsland and Bass basins, southeastern Australia. AAG is Australo-Antarctic
Gulf; EAC is Eastern Australian Current

the Campanian and Maastrichtian, and the spreading center passed west of the Sorell Basin by 53 Ma (Fig. 3.7).

White (2004) addressed the Eocene deposits recorded in ODP (Ocean Drilling Program) cores on the west, south, and east of Tasmania (sites 1168, 1170–1172, Fig. 3.12). He reported that not only did marine conditions prevail in all four drill sites but also that early to middle Eocene glacioeustacy may have affected the Australo-Antarctic Seaway between Antarctica and Tasmania. It is apparent, as well, that the Tasmanian sections were interconnected with those of the Otway Basin to the northwest and, through them, to those of the Ceduna and other basins along the Great Australian Bight on the one hand, to the Ross Sea on the other. As indicated in Fig. 3.12, site 1172 is on the east margin of Tasmania and records events in the Eocene Pacific Ocean. Sites 1171 (farthest south) and 1170 occur on the western margin of the South Tasman Rise (the so-called Tasmanian Land Bridge), and site 1168 is located on the western margin of Tasmania. These three sites are part of the Australo-Antarctic seaway. White (2004, p. 13) observed that whatever processes were operational in the Pacific Ocean basin also seem to have affected the Australo-Antarctic seaway.

This includes a marine flooding surface interpreted to be present at the Paleocene/Eocene boundary at sites 1171 and 1172 (White 2004). Numerous flooding surfaces are present, with peaks at 55, 50, 39, and 36 Ma. According to White (2004), these peaks were caused by glacioeustasy, but it also means at least intermittent marine separation of Australia from Tasmania during this time, beginning at least by 55 Ma. This is compatible with mid-Eocene (ca 43 Ma) sea floor spreading that led to the separation of the South Tasman Rise from Antarctica along the Tasman Fracture Zone (Hill and Exon 2004) and the initiation of subsidence from about 52 Ma that led to the development of a westbound Antarctic Counter Current across the southern Tasmanian Gateway at 49–50 Ma (Bijl et al. 2013). From these data, it seems probable that overland dispersal between Antarctica and Australia was rendered very unlikely from at least 50 Ma, and possibly as early as 55 Ma (Fig. 3.11; Exon et al. 2004: Fig. F7A). Recall also that Lawver et al. (2011) noted that sea floor spreading in the South Tasman Saddle may have been active from 74–66 Ma, so the sea floor there at the beginning of the Eocene would have been at least 1000 m deep. In summary, the body of evidence indicates the presence of a marine barrier across the South Tasman Saddle by at least the late early Eocene.

Figure 3.7 also reconstructs the presence of marine embayments of mid-Eocene and later age north of Tasmania, at the South Tasman Saddle. Figure 3.11 is based on Fig. F7A of Exon et al. (2004), with addition of coastlines relative to the Otway, Bass, Sorell, and Gippsland from Norvick et al. (2001: Fig. 1). The Tingamarra Local Fauna, of Murgon, Australia (M, Fig. 3.7) is the only early Paleogene (55 Ma; Godthelp et al. 1992) mammal fauna of Australia. As discussed below, it is most likely that the taxa of that fauna likely reflect the results of a prior overland dispersal to Australia of Paleocene age.
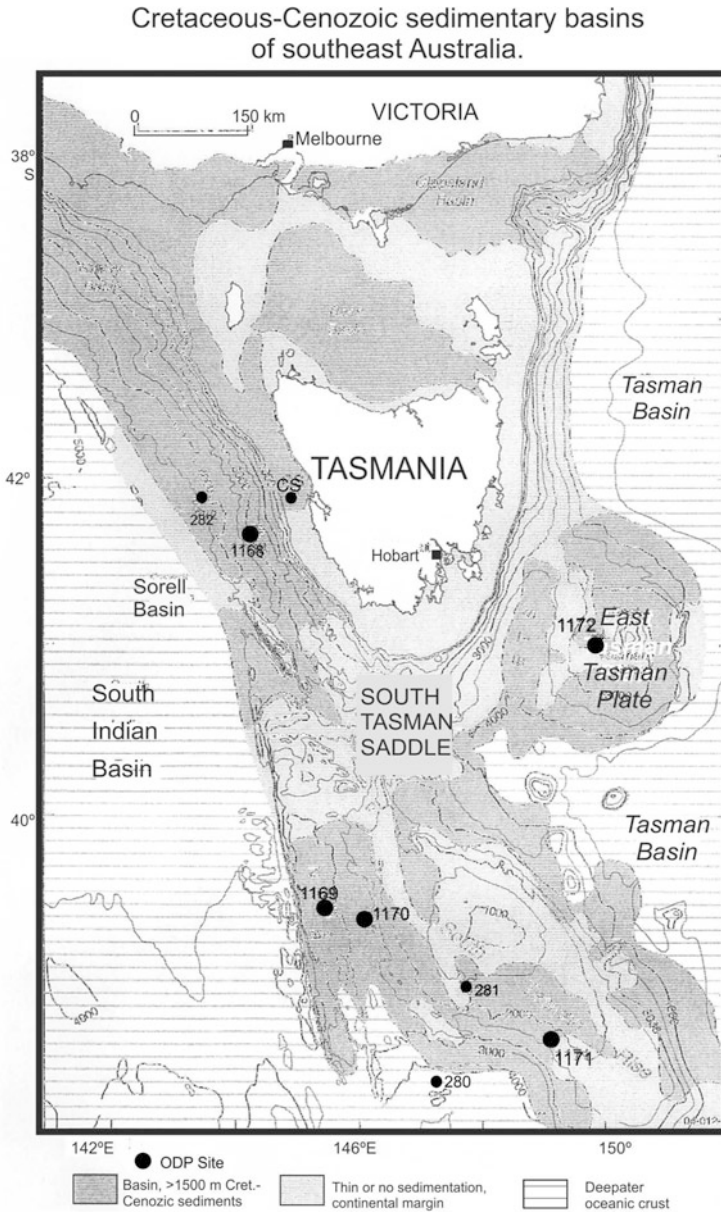
Fig. 3.12 Cretaceous-Cenozoic sedimentary basins of southeast Australia. After Exon et al. (2004: Fig. F1)

3.3.2 Tingamarra Local Fauna

As regards its geology and age, Godthelp et al. (1992) initiated the reports on the Tingamarra Local Fauna from Murgon, southeastern Queensland (Fig. 3.7). The fossils occur in greenish claystones considered to be part of the Oakdale Sandstone which crops out in an area of 36 km north of Murgon, about 140 km northwest of Brisbane (Murphy et al. 1976). The Oakdale Sandstone is about 100 m thick, unconformably overlies Permian and Triassic rocks and "may be overlain by Tertiary volcanics" (p. 57). The unit consists of poorly consolidated sandstone, mudstone, and conglomerate. Sandstone is buff colored, medium to coarse grained, quartzofeldspathic and quartzose, poorly bedded, and massive. Clasts are dominantly angular to subrounded granules of quartz. The matrix of both the conglomerate and sandstone is kaolinitic. Mudstone is light colored and grades into siltstone. Most outcrops are deeply lateritized.

Gaffney and Bartholomai (1979) reported fossil trionychid turtle material from a locality near Boat Mountain (152°E. longitude, 26°S. latitude), about 11 km NNE of Murgon. This also is the site of the Tingamarra Local Fauna, which includes the mammals, *Tingamarra porterorum* and *Thylacotinga bartholomaii* (Godthelp et al. 1992; Archer et al. 1993) as well as other taxa (below).

Regarding the age of the unit, note that Gaffney and Bartholomai (1979) pointed out the unlateritized nature of the fossil-bearing green clay beds at Boat Mountain and suggested on that basis that the beds might be Pliocene in age rather than the early Tertiary age they accepted, with reservation. Godthelp et al. (1992) reported an age of 54.6 ± 0.05 m.y. for the green clay beds, apparently the same as those reported by Gaffney and Bartholomai (1979). The radioisotopic age is derived from a single K-Ar date on illite and its analytical parameters have not been published. As noted by Woodburne and Case (1996), multiple samples of illite need to be analyzed in order to determine whether it is authigenic or detrital. Such samples have never been reported. Godthelp et al. (1992) noted that the basalts that apparently overlie the fossil beds at Boat Mountain are considered to be 29 Ma old.

The Undifferentiated Tertiary Volcanics that "may" overlie the Oakdale Sandstone are not dated. Murphy et al. (1976) chose the term, may, due to the fact that both the sediments and the volcanic rocks in the Murgon area are heavily lateritized and the contact between the two units is nowhere preserved. Based on the outcrop pattern presented on the geologic map in Murphy et al. (1976), it is reasonable that the volcanic rocks post-date the Oakdale Sandstone.

In summary, the geologic evidence appears to be potentially compatible with the isotopic age determined for the beds that produced the Tingamarra mammal fauna. Whether or not this can be clarified, the composition of the fauna appears compatible with an age earlier than Oligocene, at least. With that caveat, the approximately 55 Ma age for the Tingamarra Local Fauna is retained in the present discussion.

As regards the Tingamarra metatherians, the initial description of *Tingamarra* by Godthelp et al. (1992) was followed to include an 'ameridelphian' based on a

calcaneus (Beck 2012), the australidelphians *Djarthia* (Godthelp et al. 1999; Beck et al. 2008), and *Thylacotinga* (Archer et al. 1993; Sigé et al. 2009). *Tingamarra* was initially regarded as a possible condylarth eutherian mammal (Godthelp et al. 1992), but this was called into question by Woodburne and Case (1996), who considered the single lower molar to be a metatherian, with some resemblance to the plesiomorphic metatherian, *Kokopellia*. Wroe and Archer (2006) noted that more material is needed before the actual affinities of the taxon can be determined.

Djarthia was originally based (Godthelp et al. 1999) on dentary and maxillary fragments with a dentition represented by lower p2-m4 and upper C1, P1 or P2, and P3-M4. Informal character analysis suggested it to be a plesiomorphic taxon with some derived characters that posed possible affinity with both ameridelphians and australidelphians. Beck et al. (2008) assigned cranial and postcranial materials to the genus and proposed that it was an australidelphian, with a chief character in that regard being the distinctive features of the ankle bones. Assessment of all its characters resulted in a hypothesis that *Djarthia* was a relatively plesiomorphic australidelphian and positioned on a phylogenetic tree (Beck et al. 2008: Fig. 3B) prior to the origin of extant Australian groups. In that illustration, *Djarthia* was closely associated with the living South American microbiotheriid, *Dromiciops*, as shown in Fig. 3.13. If accurate, this relationship suggested that *Dromiciops* not only was an australidelphian—as then understood—but also could represent (along with the mid-Miocene *Microbiotherium*) a post-*Djarthia* dispersal to South America, under the concept that all Australia's marsupials ultimately were derived from a taxon that had originally dispersed to Australia from South America.

Goin et al. (2006) reported on the early Paleocene polydolopimorphian marsupial *Cocatherium* from Argentina and suggested affinity with the Australidelphia and an alliance with the Tiupampan (later early Paleocene) genus *Roberthoffstetteria*. If australidelphians, these taxa pre-date *Djarthia* on the one hand and are part of a strong diversity of South American metatherians on the other. As part of that diversity, Goin et al. (2010) allied the Itaboraian *Mirandatherium*, which is approximately contemporaneous with *Djarthia,* with the Australidelphia. At this time, it appears that *Djarthia* may not be the oldest australidelphian, but is still a very plesiomorphic taxon.

In that context, the Tiupampan (early Paleocene of Bolivia) genus *Khasia* has been taken as a South American australidelphian, and to document the early presence of the group. Beck et al. (2008) and Woodburne et al. (2014) noted, however, that *Khasia* is an enigmatic form, the precise affiliations of which are still to be proven. Originally regarded as a microbiothere (Muizon 1991), more recently it has been argued to have pediomyid affinities (see Chap. 5 and Woodburne et al. 2014: Table 1). If the latter is the case, it would also argue in favor of close affinities between South American and North American early metatherians (Case et al. 2005). If *Khasia* has South American affinities, analysis of the timing and context of that relationship is still limited by the lack of other Eocene or older mammal faunas in Australia.

Thylacotinga was based on a broken LM2 or M3, to which a broken Lm2 (with damaged metaconid), RM4 or 5, and a fragmentary LM2 or 3 was assigned (Archer et al. 1993). It was considered to differ from Australian bunodont
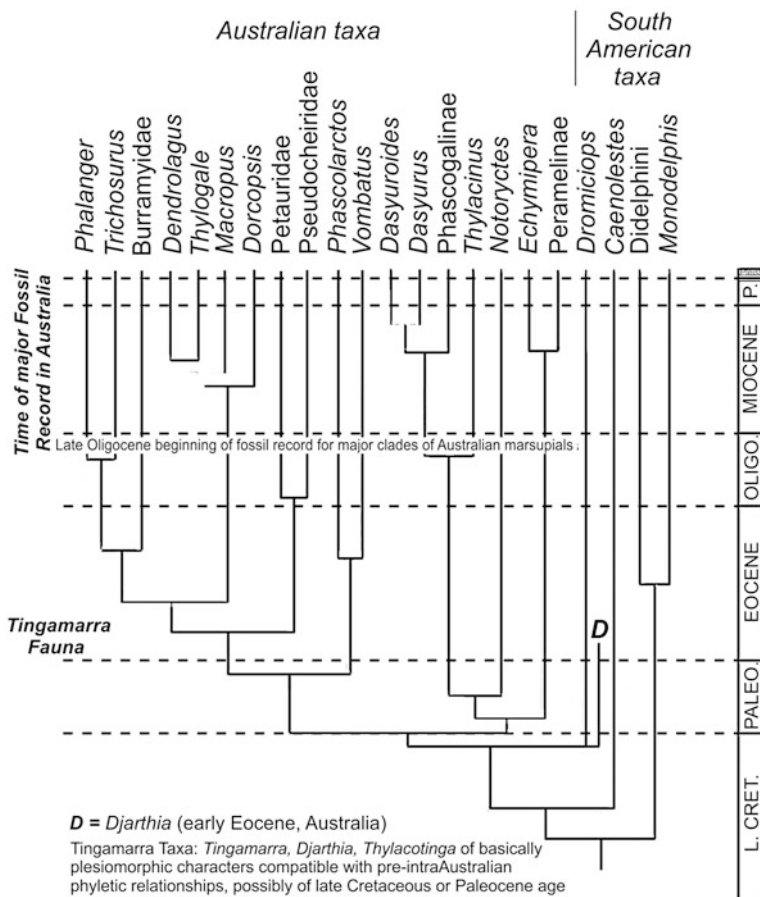
Fig. 3.13 Phyletic relationships of living Australian and South American marsupials and origination ages of taxon clades after Beck et al. (2008: Fig. 4). *Djarthia* added after Beck et al. (2008: Fig. 3b), coeval with the age of the Tingamarra Fauna. Whereas the fossils record of all other Australian marsupials begins in the late Oligocene, the timing of major groups is interpreted to have occurred prior to that time, in the Eocene and Paleocene. The Tingamarra Local Fauna is the only pre-Oligocene fauna in Australia and its genera, *Tingamarra, Djarthia,* and *Thylacotinga* are basically plesiomorphic taxa that show no relationship to intra-Australian taxa, but rather suggest affinities to South American groups. In that context it is possible that the Tingamarra Fauna is older than currently interpreted

metatherians and to share features found in South American forms. Sigé et al. (2009) described ten more specimens of *Thylacotinga* as well as a Tingamarra species of *Chulpasia, C. jimthorselli*, based on an isolated LM1 or 2. *Chulpasia* was previously known from Laguna Umayo, Peru (10, Fig. 3.3), considered to be of

late Paleocene or possibly early Eocene age (Sigé et al. 2004). On this basis Sigé et al. (2009) considered the genus *Chulpasia* to record an effectively instantaneous early Eocene dispersal from Perú to Australia. The Paleogene mammal record of South America is not yet complete. Nevertheless, Woodburne et al. (2014) recognized no South American elements referable to *Chulpasia* or to the new subfamily, Chulpasiinae, to which is has been assigned. The limited material upon which its Australian occurrence is based, as well as the lack of an empirical character analysis to support assignment of the specimens to which the two species are based to the same genus, leads to the present appraisal that this paleogeographic inference is at best a very weakly supported hypothesis.

Finally, Beck (2013) described *Archaeonothos* as a faunivorous Metatheria *incertae sedis* based on a single-upper molar. The specimen shares similarities to both South American and Tunisian genera, but not with any indigenous Australian taxa.

In summary, the Tingamarra metatherians discussed above represent the only fauna of pre-late Oligocene age in Australia (Megirian et al. 2010; Black et al. 2012) and thus provide a remarkable, but singular, glimpse into the evolutionary status of Australian marsupials. As currently presented, it is clear that the Tingamarra metatherians are of generally plesiomorphic status, compatible with their early Eocene age. On the other hand, it also is clear that none of them show any suggestion of relationship to the diverse clades of Australian marsupials recognized from the late Oligocene (Fig. 3.13). Based on examples from South America, the nearest southern Hemisphere continent with a relatively well-developed mammal fauna (Woodburne et al. 2014), it is reasonable to propose that a great diversity of Paleogene mammals is to be expected to have lived in Australia as well, and that even with dispersal from Antarctica having been impeded from the early Eocene (50 Ma), if not earlier, it can be suggested that Australia potentially could have received input of a diverse assemblage of marsupials from South America and Antarctica. The extremely important Tingamarra Local Fauna yet displays only a minor glimpse of this potential diversity.

3.4 Antarctic Dispersals to and from South America

Based on the available fossil record which may yet mask a prior occurrence, monotremes apparently dispersed from Antarctica (at least) to South America in the early Paleocene (Pascual et al. 1992). The Punta Peligro site (PP, Fig. 3.2; 6, Fig. 3.3) is now indicated as about 63 Ma (Clyde et al. 2014) and the Peligran SALMA that contains it is so correlated in Fig. 3.6. Subsequently, the middle Eocene La Meseta Fauna of Seymour Island (Fig. 3.3) of the Antarctic Peninsula gives the only other glimpse of Paleogene Antarctic mammals. The La Meseta Fauna (Reguero et al. 2002; Chornogubsky et al. 2009; Reguero and Marenssi 2010; Bond et al. 2011) is composed of mammals of South American, rather than Australian, affinity. The bulk of the fauna ranges in age from about 47–45 Ma, but the distinctive, large litoptern *Notiolofos*, is recorded from about 51.5 Ma. Whereas

some of the La Meseta mammals appear to reflect endemism (among microbio-theriid and prepidolopid metatherians and a sudamericid gondwanatheia) others, including the placentals *Notiolofos*, the astrapothere *Antarctodon*as well as the metatherian microbiotheriids *Marambiotherium* and *Woodburnodon*, and three derorhynchids, suggest derivation from early Eocene faunas of South America (Itaboraian, ca 53 Ma; Woodburne et al. 2014, which includes the initial diversity of astrapotheres, litopterns, and notoungulates; the "Sapoan" component includes taxa from the La Meseta fauna).

Overall, the La Meseta mammals represent derived elements of the groups to which they pertain, with those groups also being derived components of the South American mammal fauna. To the extent that it is representative, the La Meseta Fauna likely was characteristic of the contemporaneous land mammal fauna of the Antarctic continent, were it open to dispersal in the early Eocene. The lack of such a derived marsupial and placental mammal fauna in Australia can be laid in part to the sundering of the Tasmanian Gateway by about 50 Ma (Bijl et al. 2013), but the current absence of any input from derived South American mammals suggests that the dispersal window was closed prior to the Eocene, at least.

Based not only on the above, but also the diversity of metatherian, but not placental mammals, in the Paleocene of South America (Woodburne et al. 2014), the data further suggest that a dispersal to Australia was most likely to have occurred in that interval. As summarized above, metatherians are known in South America in the early Paleocene and, especially as recorded in the Tiupampan and Peligran SALMAs, were very diverse. This is shown (Table 3.1) by 12 genera distributed in eight Tiupampan families of largely insectivorous "Ameridelphians," a carnivorous sparassodontan, as well as a perhaps more omnivorous didelphi-morphian and a polydolopimorphian australidelphian (*Roberthoffstetteria*). This diversity compares with five mioclaenid 'condylarths,' and a pantodont in the Tiupampan, and with two 'condylarths,' and a litoptern in the Peligran. The number of "Carodnian" taxa is too small to be significant here.

The above pattern is changed markedly in the Itaboraian. Whereas marsupials are still numerous (23 genera), some of their original diversity has been lost (four families, Table 3.1), partly compensated by a caroloameghiniid and a microbiothere (*Mirandatherium*; Goin et al. 2010). In strong contrast to Paleocene faunas, the Itaboraian shows a major placental diversification, ranging from cingulates on the one hand to the first astrapotheres, notoungulates, and a major increase of litopterns on the other. Whereas the Itaboraian fauna is well suited to a relation with the La Meseta Fauna, it has effectively no similarity with any Australian clade. The aus-tralidelphian microbiothere *Mirandatherium* is a relatively derived taxon and the polydolopimorphians pertain to indigenous South American genera (*Bobbschaefferia*, *Epidolops*, and *Gashternia*). The Itaboraian cingulate, astra-potheres, 'condylarths,' litopterns and notoungulates are typical endemic South American placental taxa (Woodburne et al. 2014). Based on these particulars, it appears that the most likely interval of faunal dispersal to Australia is from the Late Cretaceous to early Paleocene (Fig. 3.14), in part contemporaneous with the Antarctic connection recorded by the apparently Peligran dispersal of a monotreme
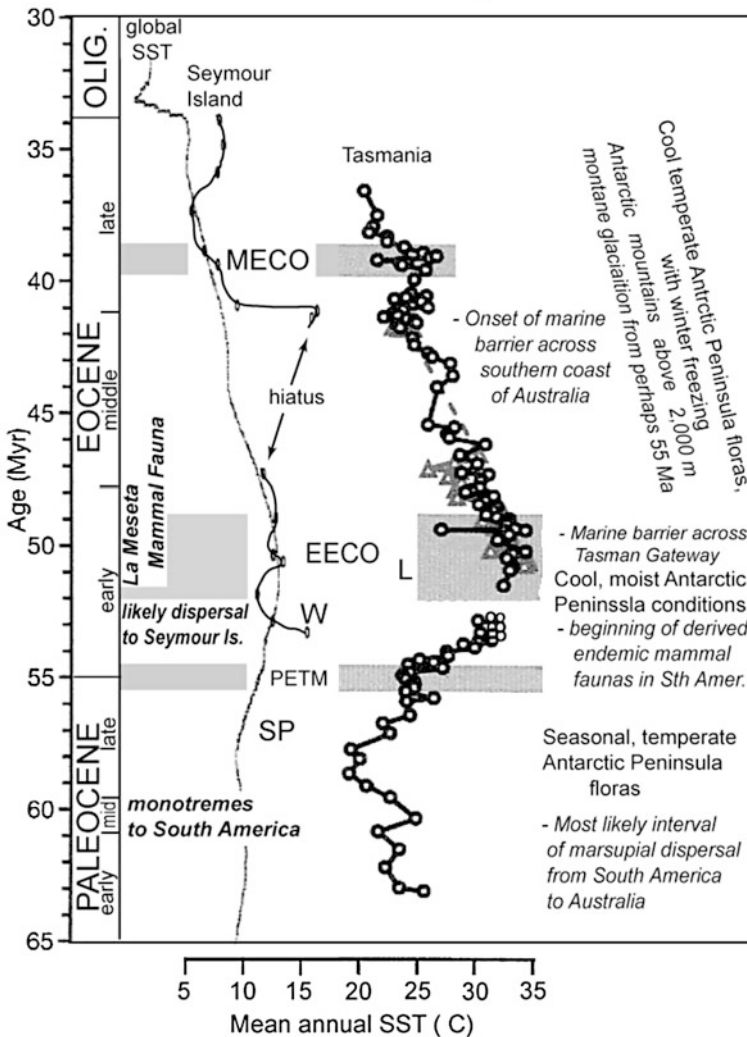
Fig. 3.14 Summary of temperatures, climatic events and mammal dispersals to South America and the Antarctic Peninsula. Tasmanian record after Bijl et al. (2009). Seymour Island record after Ivany et al. (2008). Global SST after Zachos et al. (2001). L = Leona Road, Tasmania, continental climate after Carpenter et al. (2012). W = Wilkes Land continental climates after Pross et al. (2012). SP = Seymour plants after Francis et al. (2008). PETM = Paleocene Eocene Thermal Maximum. EECO = Early Eocene Climatic Optimum. MECO = Middle Eocene Climatic Optimum La Meseta Mammal Fauna likely dispersed to Seymour Island about 53 M. Monotremes dispersed to South America from Antarctica at about 62 Ma. Antarctic glacio-eustatic activity possibly seen from 55 Ma in Tasmanian record (White 2004). See text

to Argentina (Pascual et al. 1992). If this is reasonable, it appears here that the Tingamarra Local Fauna most likely post-dates any dispersal from South America.

Additional context, derived from the Paleogene record of mammalian evolution and diversity in North and South America (Woodburne et al. 2009a, b, 2014), indicates that a comparably representative record in Australia would display strong diversity in its mammalian fauna, with numerous lineages representing a myriad of character states, potential homoplasies, and a general complexity that would include the evolution of the lineages that produced the Tingamarra metatherians on the one hand, and the extremely diverse and derived indigenous faunas of late Oligocene and later age (Fig. 3.13) on the other. In fact, Fig. 3.13 is overly simplified in that it stresses living taxa. It was not intended to include known fossil groups that do not survive to the present time, and which likely also would show ties to prior phyletic radiations, if patterns shown in other regions are a guide. Note that Black et al. (2012: Tables 1, 3) identified as many as 17 Australian mammal lineages that do not continue to the Recent. In this context, the resultant early mammal character matrix would be much more representative of Australian mammal evolution than now derivable from Tingamarra taxa alone, and questions of relationships both within and beyond Australia would be placed on a much firmer footing than now possible. The Tingamarra metatherians provide an extremely important, but still very limited glimpse of what must have been a much greater diversity of character development and evolution in Australia's metatherian fauna. It is to be hoped that the Tingamarra Local Fauna will become one of a number of Paleocene and Eocene mammalian faunas of Australia.

One way to perhaps reconcile, the Tingamarra taxa with their singular unity and separation from the Oligocene and younger Australian mammals would be to suggest that they actually are older than currently interpreted (also Black et al. 2012). The proposed phyletic pattern (Fig. 3.13) for the evolutionary steps leading to the Oligocene and later marsupials in Australia as proposed by Beck et al. (2008) could be accomplished in spite of the Tingamarra character conflict were that fauna of early Paleocene or even Late Cretaceous age. Assessments of the non-marsupial taxa from Tingamarra [placental chiropteran (Hand et al. 1994), anseriform birds (Elzanowski and Boles 2012), crocodiles (Willis et al. 1993; Stein et al. 2012) and snakes (Scanlon 2005)] apparently would be compatible with such an age. Whether a detailed lithostratigraphic-magnetostratigraphic analysis of the Tingamarra succession would result in a substantial revision of its age remains to be determined.

3.5 Antarctic Climate

The Late Cretaceous to late Eocene climate and paleoecology of Antarctica formed the context in which mammal dispersals took place between South America and Antarctica, and to Australia. Bijl et al. (2009) addressed the paleoclimatic regime of the southwestern Pacific Ocean and adjacent areas, based on ODP Leg 189 site 1172, adjacent to the East Tasman Plateau (Fig. 3.7), in a section that ranges in age

from 64 to 36 Ma. The data show that the SST (Sea Surface Temperature) was ~25 °C at about 63 Ma, and fell to ~20 °C at 58 Ma. Absent any pulse at the time of the PETM (55 Ma), the temperatures rose to about 34 °C during the EECO, 53–49 Ma, apparently about 10 °C higher than the continental climate in the same area (Carpenter et al. 2012; L, Fig. 3.14). The SST values declined thereafter to ~23 °C at about 42 Ma, and then rose briefly during the MECO (Middle Eocene Climatic Optimum) at ~40 Ma to ~27 °C. Subsequently SST declined to ~21 by 37 Ma. As indicated below there is some difference not only in continental temperatures during the Paleogene, but also SST values to the west.

With regard to the east Antarctic region, Carpenter et al. (2012) investigated foliar and pollen data from 53 to 50 Ma tidal channel deposits exposed along Lowana Road, Maquarie Harbour, in western Tasmania (near B in SB, Fig. 3.7). The results suggest that continental mean annual temperatures in southern Tasmania at that time were on the order of 24 °C, with warm temperatures indicated by dominance of entire-margined, probably evergreen, dicotyledonous leaves, and the presence of warm-water cysts of the dinoflagellate subfamily Wetzelielloideae. The presence of *Nypa*, cycads, and mangroves at the site also indicates winter temperatures above freezing. Epiphyllous fungal structures also reflect humid-rainforest conditions comparable to the subtropics and tropics, and pollen with warm-climate indications include *Alchornea*, Arecaceae, Cupanieae, *Diospyros ,and Ilex*. In fact, MAT may have been greater than 24 °C because the largest leaves were under represented.

Farther west, Pross et al. (2012) proposed a MAT of 16 ± 5 °C for the climate of continental Wilkes Land (Fig. 3.7; W, Fig. 3.14) for the 54–52 Ma interval based on materials recovered from ODP 318 site U1356 which is dominated by paratropical and tropical rainforest plants. These include dominant ferns, tree ferns and palms, with less frequent members of the Bombacoideae, including Malvaceae (cotton, hollyhock; shrubs) Strasburgeriaceae; Olacaceae (hog plum, African walnut), and Araceae (duckweed). The bombacoid group is insect-pollinated which is considered to reflect an areally interconnected forest. Winter temperatures were well above freezing. The presence of montane sporomorphs also indicates that a temperate rainforest inhabited more inland parts of Wilkes Land. The difference in Tasman SST and continental values versus those of Wilkes Land may reflect, in part, a local warm center in the Tasman—New Zealand region (Hollis et al. 2009).

The relatively cooler conditions shown by the Wilkes Land rainforest relative to that from Tasmania is continued farther west, to Seymour Island (Fig. 3.3) of the Antarctic Peninsula. The La Meseta Formation sampled for this study was assessed to range in age from 55 to 35 Ma. Based on $\delta^{18}O$ and $\delta^{13}C$ from aragonite in shells of two bivalve genera, Ivany et al. (2008: Fig. 10) documented a change from an early Eocene SST of ~15 °C at 53 Ma, likely reflective of the global EECO. The temperature then underwent a drop during 53–51 Ma to ~10 °C, recorded a short rise ~12 °C shortly after 51 Ma, and fell back to ~10 °C at about 48 Ma. After a 2 Ma hiatus, the temperature had risen again to ~15 °C by 42 Ma, likely coincident with the MECO. This pattern is also seen in the Southern Ocean on the Maud Rise and Kerguelen Plateau (Bohaty and Zachos 2003). Thereafter, sea temperature

underwent a sharp drop to ∼8 °C at about 41 Ma, and then fell further to ∼5 °C at 37.3 Ma during the global Middle Eocene Cooling interval. As another local example, mountain glaciation on the nearby South Shetland Islands occurred from 45 to 41 Ma (Birkenmajer et al. 2005; Francis et al. 2008). Subsequently, the SST rose slightly again to ∼7 °C from 36 to 34 Ma.

Paleofloras from the Antarctic Peninsula as represented by fossil wood, leaf, and pollen from the South Shetland Islands and James Ross Basin of the northern Antarctic Peninsula (Fig. 3.3) provide an indication of terrestrial climates of the region (Poole et al. 2005). Winter darkness is a pervasive factor affecting plant and animal life in high latitudes, but the plant community appears to have accommodated this overall. Growth-ring patterns reflecting winter darkness are found mostly in mid-Cretaceous conifer samples, whereas the pattern morphology of Paleocene and Eocene taxa appears to have resulted from seasonal variations in water availability, compatible with a change from warmer overall mid to Late Cretaceous climate to cooler conditions in the Paleogene.

The Coniacian–Campanian climate was warm and equable, during the Cretaceous Thermal Maximum (CTA; 100–80 Ma; Francis et al. 2008), more so than in the late Early Eocene. A MAP of 600 cm in the Campanian fell to 500 cm in the early Paleocene, and to 250 cm in the late Paleocene as conditions became drier and cooler. MAP increased to 400 cm in the early middle Eocene, but by the late middle Eocene had decreased to 100 cm. These data are based on fossil wood analyses and may be overestimated (Poole et al. 2005), although the overall trend is realistic. Comparable numbers based on leaf physiognomy are about 90 cm for Campanian to early Paleocene, 70–100 cm in the mid-Eocene (Poole et al. 2005: Fig. 2). Overall increased aridity through time was accompanied by a decrease in precipitation. MAT interpretations suggest that the Coniacian–Campanian reached 13.5 °C, cooled to 11 °C in the late Maastrichtian, ranged from 10 °C in the early Paleocene to about 15 °C in the late Paleocene (SP, Fig. 3.14), with cooling again in the Eocene (11–12 °C). The plant record contains a hiatus at the time of the EECO (50–53 Ma).

Together, the data indicate relatively warm and wet conditions in the Late Cretaceous, with higher rainfall during the growing season consistent with tropical to subtropical climates that lacked winter freezing. Angiosperm plants diversified strongly in the Santonian within the CTA (Francis et al. 2008). Conditions became much cooler and drier at the end of the Maastrichtian, and into the Paleocene. Dry conditions continued into the mid-Paleocene, becoming cooler but also wetter in the Eocene (Fig. 3.14).

A Late Paleocene flora of Seymour Island is represented by 36 angiosperms and two ferns, along with podocarp and araucarian conifers. The angiosperms are represented by Nothofagaceae (*Nothofagus*), Lauraceae (laurels) and Proteaceae, as well as by Myrtaceae (*Eucalyptus* family), Elaeocarpaceae (crinodendrons), Winteraceae (Winter's Bark), Moraceae (hemp), Cunoniaceae and Monimiaceae, collectively indicative of cool-warm temperatures and a mixed conifer-broad leaf evergreen and deciduous forest, dominated by large trees of *Nothofagus* and araucarian and podocarp conifers. Other angiosperms grew in the mid-canopy and

as understorey shrubs. A MAT of about 14 °C is indicated (SP, Fig. 3.14) with a strongly seasonal climate, winter cold still above freezing, and MAP of about 210 cm. The MAT is comparable to that for the Palacio de los Loros flora from Patagonia (Woodburne et al. 2014: Fig. 8), but the MAP is much higher (210 vs. 115 cm.).

Early Eocene plants on Seymour Island included araucarian conifers and angiosperms (Francis et al. 2008), with the latter being similar to living Lauraceae, Myricaceae, Myrtaceae, and Proteaceae. The conifers suggest a cool and moist climate (Fig. 3.14), with MAT of about 8–13 °C, comparable to the SST of 12 °C (Ivany et al. 2008).

Later, the mid-Eocene flora is reduced in diversity by 47 %, with 19 leaf morphotypes. *Nothofagus* is dominant, and the flora is comparable to those of cool-temperate conditions (Fig. 3.14). Substantial cooling over the interval is indicated thereby. A MAT is given as about 11 °C, freezing conditions in winter, and a MAP of 150 cm (Francis et al. 2008). Thus, as also indicated by Poole et al. (2005), Francis et al. (2008) concluded that late Paleocene floras of the Antarctic Peninsula were relatively warm and ice-free in winter. By the middle Eocene (47–44 Ma), conditions were much cooler, and winter ice was likely (Fig. 3.14).

Poole et al. (2005) suggest that the Antarctic Peninsula supported a central mountain range likely 2000–3000 m in elevation, with a probable rain shadow to the east. Due to the high paleolatitude (ca 60ºS) and relatively high atmospheric CO_2, vegetation would have experienced at least a month-long dormant phase due to reduced light intensity. In spite of the maritime influence, it is possible that winter frost might have been a factor in the growth cycle. Wilson and Luyendyk (2009) restored the paleotopography of West Antarctica in the late Eocene and early Oligocene and posited a reconstruction compatible with the elevation of the Antarctic Peninsula ranges. They also proposed that such elevations would have been present in the earlier Eocene, at least, and would have included much of East Antarctica having been at about 1000–2000 m (Queen Maud Land and adjacent parts of Wilkes Land as well as the Transantarctic Mountains). Lowland and coastal regions persisted in any case.

The cool mid to late Eocene climates derived from floral analysis is compatible with the presence of at least mountain glaciation on Antarctica including the Antarctic Peninsula (Birkenmajer et al. 2005), and White (2004) suggested a glacio-eustatic record at 55–50 Ma in Eocene ODP cores adjacent to Tasmania.

3.6   Summary

Based on SST and continental evidence, Late Cretaceous climatic conditions across the Antarctic region were warm and supported subtropical to tropical vegetation. As climate began to cool in the Paleocene, at least the Antarctic Peninsula records the persistence of cooler temperatures and a mixed conifer-broad leaf evergreen and deciduous forest that still lacked conditions of winter freezing, with no evidence of

mountain glaciation. Early Eocene plants suggest a cool and moist climate, with MAT of about 8–13 °C, comparable to a SST value of 12 °C. Dispersal of a derived component of mammals from South America to Seymour Island from about 53 Ma apparently took place under such conditions (Fig. 3.14). Later in the Eocene, the development of yet cooler conditions, winter freezing, and mountain glaciation likely present at higher elevations across the entire Antarctic continent, would pose increasing difficulties to mammalian dispersal from South America to Australia, although coastal and lowland routes still would have been available. The 50 Ma sundering of the Tasmanian Gateway (with earlier potential interruptions from about 55 Ma) would have made a major impact on overland dispersals of animals with that, in conjunction with the 45 Ma marine barrier across the entire southern coast of Australia, essentially terminating any potential for dispersal.

The dominance of diverse marsupials in the early Paleocene of South America and the presence of monotremes in South America by about 63 Ma combine to highlight the early to middle Paleocene as the most likely time for mammalian dispersal to Australia (Fig. 3.14). If the Tingamarra Local Fauna proves to be of Paleocene, rather than early Eocene, age, the regional affiliations of its taxa would be most compatible with dispersal at that time.

3.7 Conclusions

The early Paleocene diversity of metatherians in Tiupampan faunas of South America and the pre-Tiupampan record of the polydolopimorphian *Cocatherium* speak in favor of a Late Cretaceous or earliest Paleocene dispersal of metatherians from North America. Whereas no Late Cretaceous metatherians have been recovered to date in South America, the late Campanian to Maastrichtian presence of hadrosaurine dinosaurs in Argentina as well as the late Maastrichtian of the Antarctic Peninsula is evidence of a biotic connection to North America at that time, also compatible with a concurrent northward dispersal of leptodactylid frogs. Placental 'condylarths' in the Tiupampan may have been related to, and dispersed southward relative to, Puercan taxa in North America and perhaps reflect a somewhat later event in comparison to metatherians, also attested to by the presence of the menispermaceaean podocarp, *Palaeoluna* in Wyoming and Colombia at ∼60 Ma.

Other than hadrosaurine dinosaurs, Late Cretaceous vertebrates of South America are basically Gondwanan in affinities and reflect (and survived) the pre-106 Ma connection between South America, Africa, and Antarctica. The potential for a Late Cretaceous dispersal of metatherians would be compatible with a continued dispersal to Australia at that time, also supported by plate tectonic relationships, the basically endemic coeval dinosaurian Australian dinosaur fauna notwithstanding, and with the proviso that a late Maastrichtian Australian record of dinosaurian and other land vertebrates is effectively nonexistent. An early Paleocene connection between at least Antarctica and South America is suggested

by the presence of a monotreme in the fauna at Punta Peligro, Patagonia. This, coupled with the fact that post-Peligran mammal faunas in South America and the Antarctic Peninsula (from at least 52 Ma in that location) are composed of derived metatherian as well as placental mammals, suggests that the dispersal of metatherians to Australia had been achieved prior to the Eocene. This is compatible with the still plesiomorphic level of Australian metatherians from the early Eocene Tingamarra fauna of Australia, the only pre-late Oligocene mammal fauna of that continent. The sundering of the Tasman Gate by marine waters at about 50 Ma and the development of a continuously marine southern coastline of Australia by about 45 Ma, effectively foreclosed overland mammal as well as other vertebrate dispersal to Australia from then on. If a relationship between South American xenarthrans and the Afrotheria is sustained, it would appear to reflect a vicariant separation of the groups when South America and Africa separated at about 106 Ma regardless of certain studies that imply a younger age for the two groups.

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