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Authors: Rich, Thomas H., Vickers-Rich, Patricia, Flannery, Timothy F., Kear, Benjamin P., Cantrill, David J., et al.

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An Australian multituberculate and its palaeobiogeographic implications

THOMAS H. RICH, PATRICIA VICKERS-RICH, TIMOTHY F. FLANNERY, BENJAMIN P. KEAR, DAVID J. CANTRILL, PATRICIA KOMAROWER, LESLEY KOOL, DAVID PICKERING, PETER TRUSLER, STEVEN MORTON, NICHOLAS VAN KLAVEREN, and ERICH M.G. FITZGERALD



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A dentary fragment containing a tiny left plagiaulacoid fourth lower premolar from the Early Cretaceous (Aptian) of Victoria provides the first evidence of the Multituberculata from Australia. This unique specimen represents a new genus and species, *Corriebaatar marywaltersae*, and is placed in a new family, Corriebaataridae. The Australian fossil, together with meagre records of multituberculates from South America, Africa, and Madagascar, reinforces the view that Multituberculata had a cosmopolitan distribution during the Mesozoic, with dispersal into eastern Gondwana probably occurring prior to enforcement of climatic barriers (indicated by marked differentiation in regional floras) in the Early Cretaceous.

Key words: Mammalia, Multituberculata, Cimolodonta, Cretaceous, Gondwana, Australia.

Thomas H. Rich [trich@museum.vic.gov.au], David Pickering [dpick@museum.vic.gov.au], Peter Trusler [ptart@optusnet.com.au], Nicholas van Klaveren [Nicholas.VanKlaveren@goldfields.com.au], and Erich M.G. Fitzgerald [efitzgerald@museum.vic.gov.au], Museum Victoria, PO Box 666, Melbourne, Victoria 3001, Australia; Patricia Vickers-Rich [pat.rich@sci.monash.edu.au], Patricia Komarower [Patricia.Komarower@sci.monash.edu.au], and Lesley Kool [koolasuchas@bigpond.com], School of Geosciences, Monash University, Victoria 3800, Australia; Steven Morton [Steven.Morton@sci.monash.edu.au], School of Physics, Monash University, Victoria 3800, Australia; Timothy F. Flannery [tim.flannery@textpublishing.com.au], Macquarie University, New South Wales 2109, Australia; Benjamin P. Kear [b.kear@latrobe.edu.au], Department of Genetics, La Trobe University, Victoria 3086, Australia; David J. Cantrill [david.cantrill@rbg.vic.gov.au], Royal Botanic Gardens Melbourne, South Yarra, Victoria 3141, Australia.

Introduction

Multituberculata is the longest-lived order of mammals, first appearing in the Middle Jurassic (Bathonian) and persisting until the late Eocene (Kielan-Jaworowska et al. 2004). Members of this group were particularly widespread in Laurasia (Kielan-Jaworowska et al. 2004). They were unknown from the Gondwanan landmasses until Sigogneau-Russell (1991) described *Hahnodon taqueti* based on a single m2 from the Early Cretaceous (Berriasian) of Morocco. Hahn and Hahn (2003) subsequently reported three more similar teeth from the same locality, which they also attributed to Multituberculata. Butler and Hooker (2005) referred the Moroccan material to Haramiyidae, but Hahn and Hahn (2007) disagreed with this interpretation. Another potential Gondwana multituberculate is an indeterminate multituberculate tooth fragment from the Late Cretaceous (Maastrichtian) of Madagascar (Krause et al. 2006). Most recently, Kielan-Jaworowska et al. (2007) described a possible cimolodontan multituberculate, *Argentodites coloniensis*, based on an isolated ?left

p4 from the Campanian–Maastrichtian (Late Cretaceous) middle part of the La Colonia Formation of Chubut Province, Argentina. Taken together, these records of Gondwanan multituberculates and their potential relatives are rather sparse. Thus, the discovery of a well-preserved and morphologically complex multituberculate tooth in the Early Cretaceous of Australia is of considerable palaeobiogeographic significance and has implications for the dispersal pathways of the group into eastern Gondwana by the Early Cretaceous.

Institutional abbreviations.—NMV C, Comparative Anatomy Collection, Museum Victoria, Melbourne, Australia; NMV P, Palaeontology collection, Museum Victoria, Melbourne, Australia.

Terminology.—The term “exodaenodont” is used here sensu Krause (1977), “. . . is used throughout the paper in reference to the portion of enamel on p4 that labially overlies and extends ventrally down the anterior root.” Also see Kielan-Jaworowska et al. (2004: 277) for a fuller discussion of the exodaenodont condition.

Systematic paleontology

Allotheria Marsh, 1880

Multituberculata Cope, 1884

Cimolodonta McKenna, 1975

Family Corriebaataridae nov.

Type genus: *Corriebaatar* gen. nov.

Diagnosis.—As for species *Corriebaatar marywaltersae*.

Genus *Corriebaatar* nov.

Type species: *Corriebaatar marywaltersae* gen. et sp. nov.

Etymology: *Corrie*, in honour of Dr. Corrie Williams for her discovery of a Gondwana multituberculata; *baatar*, “hero” (Mongolian) a common suffix used for the names of multituberculates.

Gender: Following precedent with regard to the suffix *-baatar*, to be regarded as masculine.

Diagnosis.—Same as for only known species.

Corriebaatar marywaltersae sp. nov.

Figs. 1, 2.

Etymology: In honour of Mrs. Mary Walters who found the holotype in 2004.

Holotype: NMV P216655, a fragment of a left dentary bearing a complete plagiulacoid p4 and the anterior root of m1 (Figs. 1, 2).

Type locality: Flat Rocks fossil site on the marine shore platform in the Bunorong Marine Park near Inverloch, Victoria, Australia (38° 39' 40±02" S, 145° 40' 52±03" E, World Geodetic System 1984). Three other mammalian taxa are known from this locality: two possible eutherians/australosphenidians, *Ausktribosphenos nyktos* (Rich et al. 1997) and *Bishops whitmorei* (Rich et al. 2001a) and a monotreme, *Teinolophos trusleri* (Rich et al. 2001b).

Type horizon: Wonthaggi Formation (Strzelecki Group), Aptian (late Early Cretaceous) in age (Rich et al. 1997).

Diagnosis.—Distinguished from the non-multituberculata mammals with plagiulacoid premolars in that the base of the enamel on the labial side of the anterior root extends far ventral to the remaining tooth crown, the exodaenodont condition (Figs. 1A, 2B). Distinguished from all multituberculates in the Plagiulacida with the exception of *Pinheirodon pygmaeus* in lacking either a buccal cusp or cusps or a row of

buccal pits on the p4 (Kielan-Jaworowska and Hurum 2001) (Figs. 1A, 2B). Although the single known specimen of the p4 of *Pinheirodon pygmaeus* lacks a distinct buccal cusp, Hahn and Hahn (1999: fig. 26a) indicate an area in the posteroventral buccal region of the crown setting it off from the immediate surrounding region of the tooth, suggestive of the former presence of a cusp that had been abraded. *Corriebaatar* is distinguished from all other multituberculates by its “double exodaenodont” condition on the p4 (see Description) and an excavation on the lingual side of the posterior root of the p4 (Figs. 1B, 2A).

Description.—The p4 of *Corriebaatar marywaltersae* (Fig. 2) is 3.4 mm in length. It can be uniquely differentiated from all other multituberculates by at least three key features.

(1) Restriction of the crown ridges to two on the labial side and one on the lingual. Typically, the ridges on the p4 in multituberculates densely cover the entire crown; however, in some taxa their number may be reduced. For example, *Cimolomys gracilis* has eight or nine serrations on the crest of the tooth but only three or four external ridges and two or three internal ridges (Clemens 1963).

(2) Presence of both labial and lingual excavations into the roots of the p4. The anterolabial excavation possibly accommodated the p3, as in *Cimolodon nitidus* (Clemens 1963: fig. 23a). Note that the anterior edge of the dentary fragment in NMV P216655 is broken posterior to where the p3 alveolus would be expected, thus presence or absence of the p3 cannot be confirmed with certainty. The posterolingual excavation does not conform to the tooth positions in any other known multituberculata, so consequently its function remains unknown. The excavation may have been occupied by an anterior projection of the m1, a remnant of which is preserved as a root fragment well posterior to the p4.

(3) The ventrally directed lobe of enamel on the labial surface of the posterior root. This condition is here termed “double exodaenodont” taking into account the presence of an accompanying enamel lobe on the labial surface of the anterior root. The “double exodaenodont” state has not been noted in any other previously reported multituberculata (Kielan-Jaworowska et al. 2004: fig. 3).

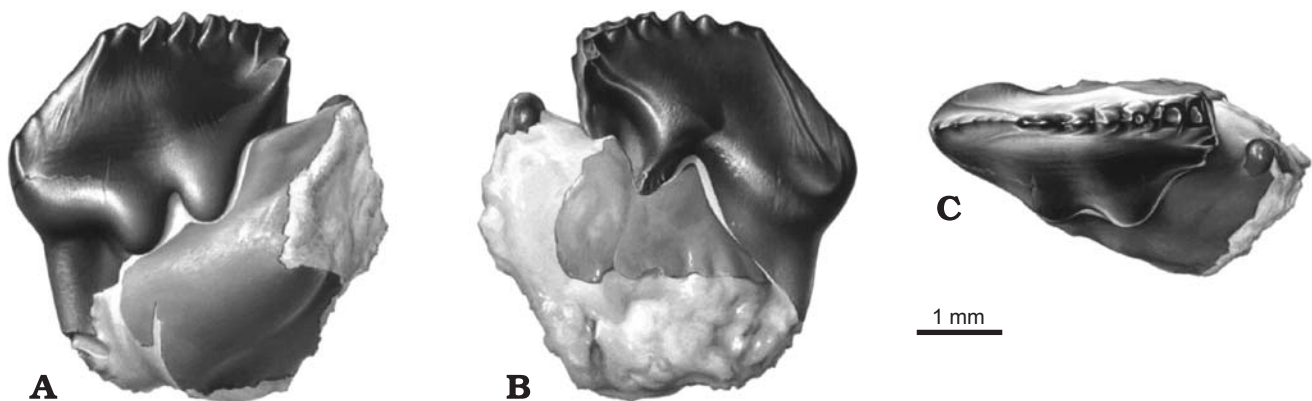


Fig. 1. Holotype of multituberculata mammal *Corriebaatar marywaltersae* gen. et sp. nov. from Flat Rocks, Wonthaggi Formation (Aptian), Australia (NMV P216655), a left dentary fragment with p4 and anterior root of m1 in labial (A), lingual (B), and occlusal (C) views. Artwork by P. Trusler.

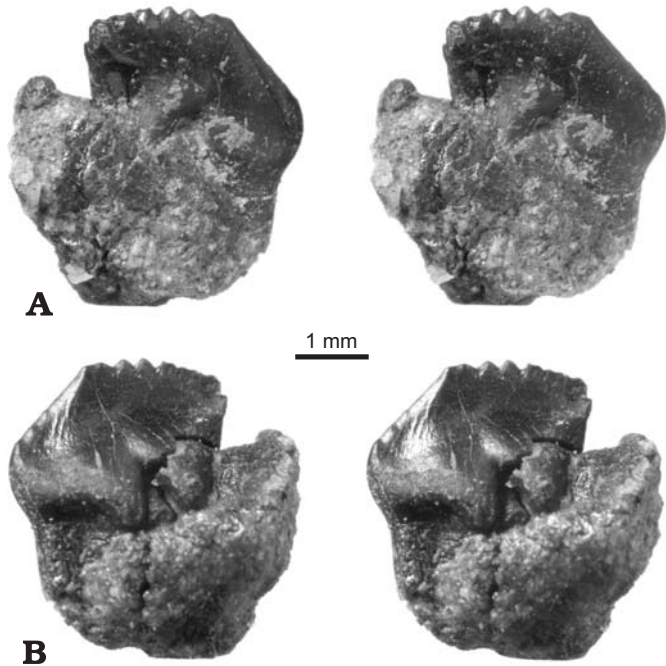


Fig. 2. Holotype of multituberculate mammal *Corriebaatar marywaltersae* gen. et sp. nov. from Flat Rocks, Wonthaggi Formation (Aptian), Australia (NMV P216655), a left dentary fragment with p4 and anterior root of m1 in lingual (A) and labial (B) views, stereopairs. Photographs by Steven Morton.

As Kielan-Jaworowska and Hurum (2001) pointed out, although the p4 of cimolodontans can be for the most part characterised as “arcuate” or “triangular” in profile while those of plagiulacids can be contrasted as “rectangular”, this is not a rigid distinction between the two groups. In any case, *Corriebaatar marywaltersae* has a p4 which is as “arcuate” as the unquestioned cimolodontan *Microcosmodon conus* (Jepsen 1940: pl. 5: 3).

Discussion

Plagiulacoid or blade-like lower premolars are known to occur in several mammalian groups (Fig. 3; see also Kielan-Jaworowska and Hurum 2001; Simpson 1933): multituberculates (families Allodontidae, Zofiabaataridae, Paulchoffatiidae, Pinheirodontidae, Albionbaataridae, Eobaataridae, Arginbaataridae, Eucosmodontidae, Ptilodontidae); marsupials (Burramyidae, Hypsiprymodontidae, Balbaridae, Polydolopidae, Caenolestidae); and placentals (Carpolestidae). Synapomorphic with multituberculates, the Australian specimen is exodaenodont prompting referral to this group.

Corriebaatar marywaltersae can be plausibly interpreted as (1) an aberrant multituberculate endemic to Australia or Gondwana, or (2) less parsimoniously as a previously unknown mammalian lineage. Given the scanty record of Mesozoic mammals in Gondwana, either interpretation is reasonable. However, as a working hypothesis, here we suggest that *C. marywaltersae* was a cimolodontan, because in the structure of its p4, it appears to be a multituberculate that is

not a plagiulacidan, the only other principal subdivision of the Multituberculata as recognised by Kielan-Jaworowska and Hurum (2001).

Up to five Mesozoic mammal families can be identified from the stratigraphically restricted Aptian–Albian (late Early Cretaceous) occurrences in Australia: Ornithorhynchidae (monotreme) (Archer et al. 1985; Rowe et al. 2008); an unassigned non-ornithorhynchid monotreme family incorporating *Kryoryctes cadburyi* (Pridmore et al. 2005); Kollikodontidae (either a monotreme Flannery et al. 1995 or “a basal mammal of uncertain affinities” Musser 2003); Ausktribosphenidae (a placental Woodburne et al. 2003 or australosphenidan Kielan-Jaworowska et al. 2004); and now Corriebaataridae (multituberculate). Significantly, only one of these families has been recognised outside of Australia—the Ornithorhynchidae, based on a fossil “platypus” *Monotrematum sudamericanum* from the Palaeocene of Chubut Province, Argentina (Pascual et al. 2002).

Such unusually high family-level endemism is paralleled in the Late Cretaceous South American Los Alamitos assemblage [Campanian–Maastrichtian, Los Alamitos Formation, Rio Negro Province, Argentina (Bonaparte 1990)]. The absence of a single specimen of a tribosphenic mammal in the extensive collections from the Los Alamitos site suggests there had been no interchange of terrestrial (non-volant) mammals between South and North America for a significant period of geological time prior to when this deposit was formed. Certainly marsupials and placentals were well established in North America at that time (Kielan-Jaworowska et al. 2004). The Los Alamitos assemblage is characterised by both endemic forms quite unlike those known elsewhere, together with other taxa that have records extending back into the Jurassic, e.g., ?docodonts, an “archaic” symmetrodont, dryolestids, and eutriconodonts (Kielan-Jaworowska et al. 2004). Given the relative geographic positions of Australia and South America during the Mesozoic, it is reasonable to expect that were it then possible to do so, at least one of these terrestrial (non-volant) mammals would have traversed the Antarctic landmasses, in one direction or the other, and have been found on both continents; namely in at least one of the Aptian–Albian terrestrial vertebrate sites in Australia and in the Los Alamitos assemblage in Argentina. This is plausible because a number of the Los Alamitos forms have records elsewhere that significantly predate the earliest known records of mammals in Australia, i.e., Aptian–Albian, suggesting that they would have been in South America by that time as they are present on that continent later. Indeed, ornithorhynchids, known in Australia from before and after the Late Cretaceous, do not appear in South America prior to the Palaeogene (Pascual et al. 2002). Notably, this is also about the time that marsupials evidently reached Australia from South America (Beck et al. 2008). There is a questionably identified dryolestid from Lightning Ridge [Albian, Griman Creek Formation, New South Wales, Australia, Clemens et al. (2003)], the one tentative link between the Australian

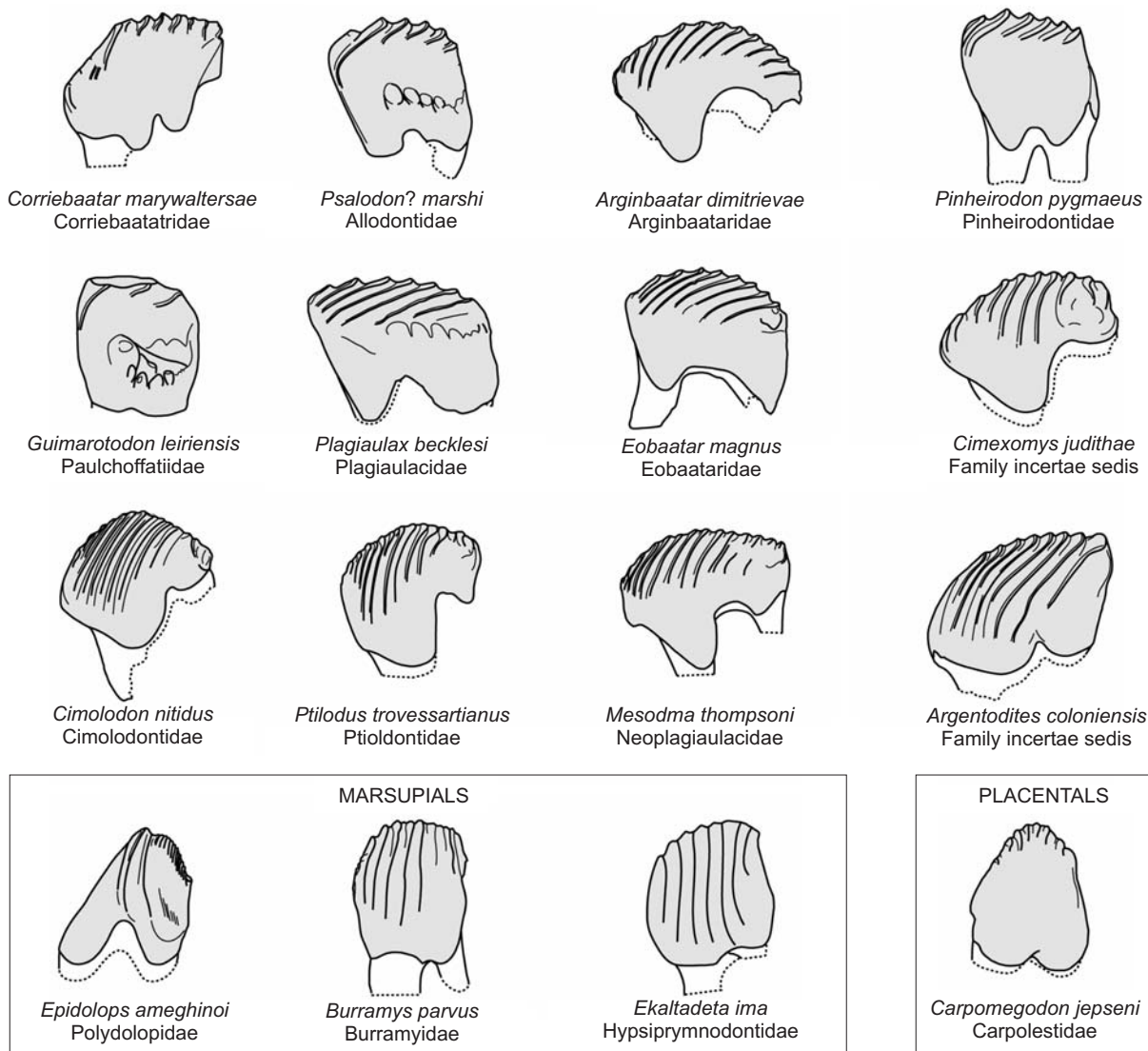


Fig. 3. Plagiaulacoid premolars (labial views) of selected multituberculates and other mammals. Illustrations: *Argentodites coloniensis* (Kielan-Jaworowska et al. 2007); *Burramys parvus* (NMV C22693); *Carpomegodon jepseni* (Bloch et al. 2001); *Cimexomys judithae* (Montellano et al. 2000); *Cimolodon nitidus* (Clemens 1963); *Ekaltadeta ima* (Archer and Flannery 1985); *Eobaatar magnus* (Kielan-Jaworowska et al. 1987); *Epidolops ameghinoi* (Paula Couto 1952); *Guimarotodon leiriensis* (Kielan-Jaworowska et al. 2004); *Mesodma thompsoni* (Clemens 1963); *Pinheirodon pygmaeus* (Hahn and Hahn 1999); *Plagiaulax becklesi* (Kielan-Jaworowska et al. 1987); *Psalodon? marshi* (Simpson 1929); *Ptilodus trovessartianus* (Granger and Simpson 1929). Compiled by Erich Fitzgerald.

Early Cretaceous and the South American Late Cretaceous (Los Alamitos) assemblages.

The possibility for a post-Albian interchange of mammals between South America and Australia is supported by evidence of the fossil vegetation in West Antarctica. Despite the proximity of the Antarctic Peninsula to southern South America, Early Cretaceous macrofloras exhibit greater similarities to macrofloras in Australia. Both Aptian (Cantrill 2000) and Albian (Falcon-Lang et al. 2001) floras of Australia and West Antarctica are rich in liverworts and ferns. Fern taxa found in West Antarctica also occur in both Australia and New Zealand (e.g., *Aculea*, Cantrill 1996, 2000; *Phyllopteroides*, *Sphenopteris warragulensis*, Cantrill and Nagalingum 2005). In contrast, relatively few South American taxa can be recognised within these floras (Cantrill and Nagalingum 2005).

The patterns exhibited by the macrofloras are mirrored by the microfloras (pollen and spores). The Antarctic Peninsula region occupies a transitional zone between two major floristic regions within the Trisaccate Province (Herngreen et al. 1996). Southern South American and African microfloras fall within the *Cyculsphaera*–*Classopollis* subprovince whereas Australia and India lie within the *Murospora* subprovince. The palynofloras of West Antarctica (e.g., Dettmann and Thomson 1987; Hathway et al. 1999) and New Zealand (e.g., Raine 1984) are most similar to the microfloras defining *Murospora* subprovince in composition despite lacking the key indicator taxon. Although a few South American species occur in West Antarctic Early Cretaceous palynofloras (e.g., *Interulobites pseudoreticulatus*, Hathway et al. 1999), they are low in diversity compared to the Australian taxa.

The contrast in composition between the palaeofloras of South America on the one hand and those of Australia plus West Antarctica on the other suggests a strong floristic gradient along the Antarctic Peninsula region (Dettman 1986; Cantrill and Poole 2002) likely largely controlled by climate. Recent modeling experiments (Valdes et al. 1996) has supported this idea. It has been further suggested that this gradient acted as a strong filter and barrier to migration of flora into West Antarctica from South America and vice versa (Cantrill and Poole 2002). Global warming to a peak of Cretaceous warmth in the Turonian may have led to latitudinal range expansions from low latitudes into the higher latitudes and thus modification of West Antarctic vegetation (Cantrill and Poole 2002). However, it was not until the Late Cretaceous, when global climates cooled, that the biota of the high southern latitudes was able to expand out into South America and more northerly regions of Australia. An example of this pattern is the Campanian appearance of *Nothofagidites* (Nothofagaceae) in the high southern latitudes (i.e., West Antarctica and southern Australia) with expansion and diversification in the Late Campanian and Maastrichtian into southern South America, Australia, New Zealand, New Caledonia, and New Guinea (Dettmann et al. 1990). Consequently, like the mammalian fossil record, that of the palaeofloras indicates little biotic exchange between West Antarctica and South America in the Early Cretaceous, giving way to significant interchange in the Late Cretaceous.

Using principal components analysis of data culled from the literature, Wilson and Arens (2001) reached similar palaeobiogeographic conclusions based on a review of the palynological record of the southern land masses and the southeastern United States between the Albian and the Paleocene.

The record of Early Cretaceous fossil mammals and plants from low temperature, high latitude Australia–Antarctica indicates that limited biotic exchange took place with the warmer climatic regions of South America at that time or somewhat prior. The migration of multituberculates between the Australian landmass and elsewhere was more likely to have occurred some time before the minimum low-temperature period in the Valanginian to Albian (Frakes et al. 1995). If the Mesozoic Gondwanan tribosphenic mammals known from three areas [Middle Jurassic of Madagascar (Flynn et al. 1999), late Middle–early Late Jurassic of South America (Rauhut et al. 2002; Rougier et al. 2007) and late Early Cretaceous of Australia (Rich et al. 1997, 2001a)] indeed form a monophyletic group, then some time during that interval (or even possibly somewhat prior) would most likely have been the time of interchange between those regions.

Unfortunately, our currently meagre understanding of Gondwanan Mesozoic mammals limits critical evaluation of this hypothesis. New discoveries could fundamentally change our interpretations of palaeobiogeography in the future (Rich 2008).

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