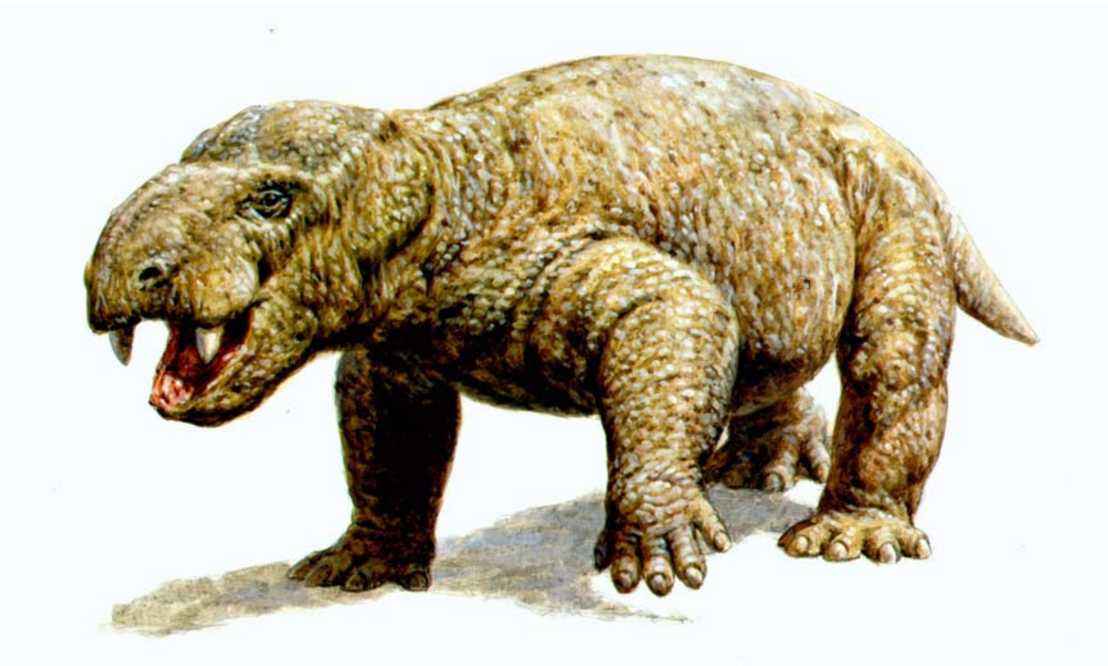
A History of Problem Solving:

Evolutionary Trends in Adaptation and Specialisation of Antarctic Vertebrates



A Review by Michael Tubby 43407116

1. Abstract

The modern Antarctic environment is typified by extremes in temperature and light. However extreme temperatures only developed within the last 35 million years. Before this Antarctic supported a temperate-climate vertebrate fauna which possessed few adaptations to extreme cold. However, dinosaurs, dicynodonts, marine reptiles and pterosaurs may have possessed adaptations for sustained darkness such as migration, hibernation and highly developed vision for remaining active in low light. After the K-T extinction event Antarctica began to cool gradually, eventually becoming too cold for its native mammals, birds and other terrestrial vertebrates which became extinct. Notothenioids thrived in the oceans and diverged significantly over a great length of time. New vertebrates have colonised Antarctica, though the extreme conditions promote bradytelic, R-selected taxa and convergent evolution. The adaptations of the modern Antarctic fauna generally can't be attributed to Antarctica's ancient vertebrates as conditions are too dissimilar, there is not relatedness and the modern animals are relatively 'new'.

3. Introduction

Antarctica is a land of challenges. Challenges so extreme that they demand an incredible degree of adaptation and specialization from any animal attempting to survive, let alone thrive, in this harsh environment. Yet animals do thrive, and appear to have done so throughout natural history. Granted, the Earth is not static, and conditions may not always have been as they are now, but geological evidence shows that Antarctica has been a challenging place to live for a significant amount of time, several hundred million years at least. This great expanse of time has seen the rise and fall of many ecosystems and associated vertebrate faunas, portions of which have been preserved in the fossil record to offer the slightest glimpse of life long gone. These remains are full of clues to the survival techniques and adaptations of extinct vertebrates, and are thus comparable to the modern vertebrate fauna of the Antarctic ecosystem. Adaptive traits required for Antarctic conditions can evolve on many different scales; molecular, physiological, morphological and behavioural. Evolution by natural selection has a tendency to retain features that work well in a given environment, and given the same stresses, the same adaptations commonly arise in unrelated organisms – convergent evolution. Conversely, the unique environmental pressures encountered in Antarctica could foster unique and novel adaptations found no-where else in the natural world. Divergent evolution creating the novel adaptations required for Antarctic life and convergent evolution reflecting the ‘success’ of such traits. One would expect that both these evolutionary trends work in unison to shape Antarctic vertebrates both now, and in the past.

4. Antarctic: An Overview

Two extreme environmental conditions typify modern day Antarctica; extreme cold and related dryness and windiness, and the presence of the polar night – midnight sun (extreme seasonality). These two stresses have not always been present on the Antarctic continent. Extreme seasonality initiated once the Antarctic continent entered the Antarctic Circle (60°S) during the Devonian period, after ca. 417 million years before present (BP) (Ziegler, Hulver & Rowley 1997)(Appendix A.). This has resulted in extreme seasonality – several months of continual darkness alternating with several months of continual day light. An effect which is strongest at the Southern Geographic Pole, but which is not as severe further north. For instance, polar nights are not present at 60°S because of twilight (Denton et al. 2005). Conversely, midnight sun is experienced throughout the Polar Regions.

Antarctica’s ice cap is the end result of a long cooling trend which has persisted throughout the Cenozoic Era (Siegert & Florindo 2008). This glaciations event wiped out Antarctica’s remnant Gondwana fauna, which were soon replaced by familiar taxa such as penguins, seals and whales. Yet before the ice cap formed, palynological evidence suggests a mild temperate climate for the Antarctic continent (Peat, Clarke & Convey 2007).

5. Adaptations

5.1 Molecular and Physiological

Antarctic conditions are such that vertebrates are affected at the molecular scale, forcing animals to adapt to gain energy, retain heat and avoid freezing. The group which seems to best exemplify the variety of molecular adaptations is undoubtedly the notothenioid fish (E.G. *Cryodraco antarcticus*). Living in waters with an average temperature of ca. -1.8°C, the notothenioids primary challenge is avoiding freezing, a feat achieved by the production of antifreeze proteins (AFP's) which are carried in the blood stream and inhibit the growth of ice crystals. All Antarctic notothenioid species posses similar AFP's which adsorb to ice crystals and inhibit growth, while most non-Antarctic species lack any cold-resistance adaptations, suggesting divergent evolution from a common notothenioid ancestor (notothenioids outside Antarctic waters are believed to have evolved from Antarctic ancestors (Cheng et al. 2003)). Notothenioid fish also produce AFP's in response to ambient water temperature, while non-notothenioid Antarctic fish species (like *Paraliparis devriesi*) and Arctic fish produce AFP's in response to light exposure (Woehrmann 1997), suggesting that Arctic fish and non-notothenioid Antarctic fish share a common ancestor, or that the evolution of AFP's was an instance of homoplasy. As yet fish are the only vertebrates know to produce AFP's (Cheng 1998) with the trait arising on several occasions throughout natural history.

Such low temperatures also have adverse effects on blood chemistry. One such effect is that blood plasma becomes a great deal more viscous, increasing the effort required to circulate blood around the body (Palenske & Saunders 2002). It is unclear whether this was the trigger for the loss of haemoglobin in the notothenioid family channichthyidae (icefish) was to reduce blood viscosity, or whether it was the extremely high concentrations of oxygen dissolved in the sea water which allowed for the loss of 'unnecessary' haemoglobin, and in some cases myoglobin as well (Sidell & O'Brien 2006). In any case, the result is a family of highly specialized vertebrates which are unique to the Antarctic.

Loss of haemoglobin and production of AFP’s are features which are shared by many vertebrates, indicating a common ancestor and divergent evolution. Unfortunately molecular characteristics are almost never preserved in fossil material, and the timing of divergences and the rise of specific adaptations can generally only be calculated using molecular clocks and genomics (Clark et al. 2004). As for the higher vertebrates, mammals and aves sustain high temperatures through endothermy, minimising the need for such specialized proteins, while lower vertebrates like amphibians and reptiles are currently absent from the continent. Even though the reptiles and amphibians have fossil records in Antarctica, as stated earlier, molecular traits are rarely ever preserved. Our knowledge of molecular adaptations is completely restricted to modern vertebrates, making projections of traits onto extinct life forms highly fallible.

5.2 Morphological and Anatomical

Once again, the major problem for any vertebrate is heat retention. Both penguins and pinnipeds have similar adaptations in place to conserve as much heat as possible. One method is to warm blood returning from the extremities. Arteries carrying warm blood to the limbs intermesh with veins returning blood to the core, allowing for heat to transfer from outgoing vessels to incoming vessels – counter current heat transfer (Thomas & Fordyce 2007, Noren et al. 2008). This is a reflection of a larger scale pattern in Antarctic endotherms – retain heat in the core of the body. A prime example of convergent evolution. Cetaceans, pinnipeds and spheniscids all limit blood flow to the skin, which would allow heat to radiate out, by limiting the number of blood vessels which supply blood to the outer layers, constantly maintaining a body surface temperature several degrees lower than the core temperature (Czub & McLachlan 2007). Blood supply may even be diverted towards the core from the extremities at will (Meir et al. 2008).

Insulation has also arisen several times in Antarctic vertebrates. Larger modern vertebrates employ blubber - fat deposits beneath the skin to insulate the core of the animal (Yunoki et al. 2008, McDonald et al. 2008), whereas flying birds rely on integumentary coverings, I.E. feathers, as well as fat deposits (Cardoso 2008). Large fat deposits can have dual functions. Larger animals have less surface area for their volume, or a high surface area to volume ratio. High volume allows the animal to produce more body heat while less surface area limits the amount of heat which can escape the body (Pincheira-Donoso, Hodgsen & Tregenza 2008). This is an ideal state for any animal trying to survive in an excessively cold environment. Yet this is as odds with the fossil record. Polar Allosaurs are renowned for their small size compared to Allosaurs from warmer areas (Molnar 1985), and large vertebrates are generally absent from the Dinosaur Cove fossil beds (though this may be a result of preservation bias) (Rich 1996).

Polar winters are accompanied by prolonged periods of darkness. Modern Antarctic vertebrates are adapted to low light conditions, but this is because of their feeding environment rather than an adaptation to the polar winter. Fossil forms, however, do show adaptations to prolonged darkness. *Laellynasaura amicagraphica* possessed huge eyes and a well developed optic lobe, presumably to maintain activity in darkness (Rich, Vickers-Rich & Gangloff 2002). However, it appears that extinct Antarctic vertebrates lacked specialised thermoregulation adaptations. This would agree with a milder climate in the distant past.

5.3 Behavioural

When faced with a harsh winter or prolonged light or dark conditions, an animal has two options; stay where it is or leave. The latter, migration, requires great potential for mobility and is often employed by long distance swimmers, like whales, or flying birds. Historically this may also have been an option for large extinct fauna such as dinosaurs, dicynodonts, marsupials, marine reptiles and pterosaurs. Migration is nigh on impossible to detect through the use of fossil material, but as Antarctica was connected to warmer landmasses the opportunity was certainly there for seasonal movements (Bell & Snively 2008). Extant species such as rockhopper penguins and some cetaceans engage in seasonal migration (Putz et al. 2006, Gambell 1987).

Alternatively, the animal can conserve the energy required to move such distances and adapt to tolerate the polar winter, and some of these adaptations actually are detectable in fossil material. *Fulgurotherium australe* was a small ornithopod dinosaur from Dinosaur Cove, which was within the Antarctic Circle during the Mesozoic Era (Molnar & Galton 1986). Cross sections of this dinosaurs bones display lines of arrested growth (LAG's), a feature commonly associated with extreme seasonality and hibernation (Chinsamy, Rich & Vickers-Rich 1998). It is at least possible that a few species of dinosaur hibernated during the polar winter. Even before the dinosaurs reptiles were showing evidence of burrowing, an activity often associated with hibernation (Sidor, Miller & Isbell 2008). Presently hibernation is undertaken by only one species, *Notothenia coriiceps*, within the Antarctic Circle (Campbell et al. 2008).

Those animals which remain awake are subject to the extreme Antarctic winter. Emperor penguins huddle to preserve heat (Gilbert et al. 2006), a trait shared by Arctic mammals, while other birds and mammals rely on fat deposits for warmth and food (Cockell, Stokes & Korsmeyer 2000). The onset of polar night sees a step-down in the food web as photosynthesis ceases, thus vertebrates must fast for many weeks on end (Barre 1975). Many notothenioids possess a level of plasticity in their diet, allowing them to overcome, to an extent, the limitations on food stock imposed by spreading sea ice and lack of sunlight (La Mesa, Vacchi & Zunini Sertorio 2000).

Timing is very important for survival. Antarctic vertebrates have adapted their reproductive cycles and life histories to suit the extreme seasonality. Many species, including the emperor penguin, *Aptenodytes fosteri*, time their breeding season so that chicks are capable of surviving by themselves by the onset of the next winter (Kooyman et al. 2004). Meanwhile, many fish adjust their habitat, staying below 20 m beneath sea level, where the pressure is too great for ice crystals to form (La Mesa, Vacchi & Zunini Sertorio 2000) . Most behaviour exhibited by Antarctic vertebrates is intended to keep warm and retain heat.

6. Discussion

Evolution in Antarctica has produced many novel traits, but has also followed large scale patterns. At present the Antarctic is relatively depauperate in vertebrate diversity, yet supports large populations. Compare this with the tropics which support small populations but are rich in vertebrate species. This is a reflection on the harsh Antarctic environment. Animals are required to become so specialised, and environmental stresses are so high that any creature not perfectly suited to Antarctic conditions is eliminated. The result is a low species turn over rate and minimal inter-specific competition. Antarctic vertebrates find good adaptations and stick with them, while in the tropics animals are engaged in a rapid and continuous arms race as they try to out-compete rival species. Antarctic species will tend to evolve slowly while maintaining high levels of specialisation, tropical species will evolve rapidly in an environment which favours adaptability and generalisation. Compare two bird families: the tropical family psittacidae (parrots) and the polar family spheniscidae (penguins). Spheniscids have managed to radiate into between 17 and 20 extant species. Psittacidae incorporates closer to 330 species (Fain & Houde 2004). The evolutionary consequences of extreme Antarctic conditions are bradytelic, R-selected vertebrate taxa.

Antarctica's current vertebrate fauna assemblage is far from typical. For the majority of natural history conditions were much milder and fostered a much more diverse vertebrate ecosystem. Extinct fauna lacked adaptations to extremely low temperatures and were not as isolated from the other continents which constituted Gondwana (Warner, Rich & Vickers-Rich 1997). However, extreme seasonality did occur, and some adaptations may be seen in the fossil record. Reptiles appear to have dominated the mega fauna during the Mesozoic and displayed adaptive traits convergent with traits exhibited by extant species living in temperate climates, such as hibernation in the grizzly bear, *Ursus arctos horribilis*. However, the bones of *Dinornis sp*. also posses cortical rings, or LAG's, and are not believed to have hibernated (Turvey, Green & Holdaway 2005), highlighting the patchy nature of the fossil record.

Birds and mammals only make fleeting appearances in Antarctica's fossil record, yet it can be assumed that truly terrestrial forms were present on the continent at least until the Late Eocene. These earlier forms are not ancestral to the modern mammal and bird taxa, and so it can be readily assumed that they lacked any cold climate adaptations, resulting in their subsequent local extinction. All extant Antarctic pinnipeds, cetaceans and spheniscids are migrant species, originating from warmer regions. This exposes another trend in Antarctic vertebrate assemblages, all extant forms are the result of a recent migration, no group has an extensive local history except for the notothenioids (Bargelloni et all. 2000). Cetaceans radiated down from the Tethys and New Zealand, the pinnipeds originated in Eurasia and the spheniscids came from lower latitudes of the Southern Hemisphere, all within the last 40 million years (Jadwiszczak 2001). What's more, the modern seals, whales and penguins have not diverged from their ancestral stock by and great degree. Contrast with the notothenioids, which are quite removed from all other modern teleost clades.

Just possibly, extreme Antarctic conditions favour convergent evolution over divergent evolution and also slow down the pace of speciation, instead refining a species. Indeed, an organism must already be rather well adapted to penetrate the Antarctic environment, and as such does not need to change and adapt to any great length before it is adapted enough to thrive (Watermann 1999). Convergent evolution can be seen everywhere in the extant Antarctic fauna. Seals and penguins share a unique circulatory system, and both also utilize blubber, as do whales.

Divergent evolution separates modern Antarctic vertebrates from the rest of the world, but convergent evolution endows them with the most effective adaptations for Antarctic survival.

7. Conclusion

Antarctica is an ever changing land of extremes. However such extreme conditions did not always plague the continent. Through history it has seen the rise and fall of many vertebrate faunal assemblages and helped shape the Earth's modern fauna. In the past, when conditions were milder, it acted as a halfway house, with species passing through between continents. Eventually it developed a unique vertebrate fauna which resembles modern day temperature vertebrates, fauna which are believed to have migrated and hibernated like modern mega fauna. Some smaller vertebrates may also have adapted to extended darkness and remained active during the polar winter. Cenozoic cooling and mass extinction denuded Antarctica of all its terrestrials vertebrates, leaving only marine fishes. These fish diverged greatly from their ancestral stock and developed unique adaptations at a molecular level.

On land, after the continent had been scraped clean of life by glaciers, new marine mammals and birds colonised, evolving similar adaptations at a larger scale, morphological and behavioural. The end result is the development of a bradytelic vertebrate fauna with many convergent traits.

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9. Appendices

<u>Appendix A. </u>Paleogeography – Antarctica's position

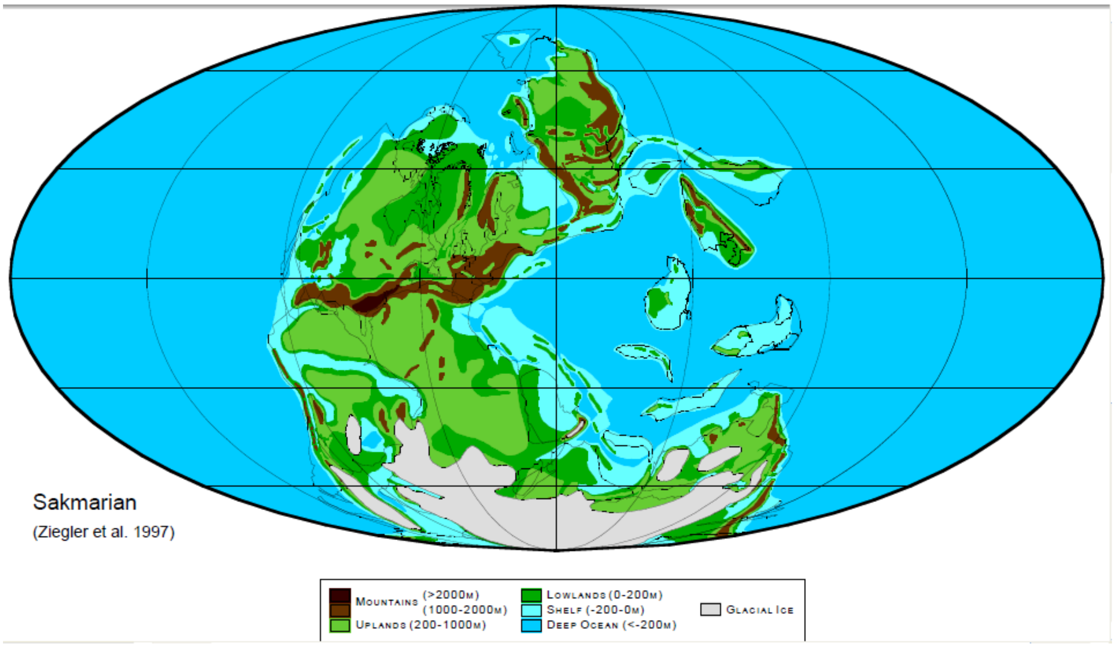

Figure 1. EarlyPermian

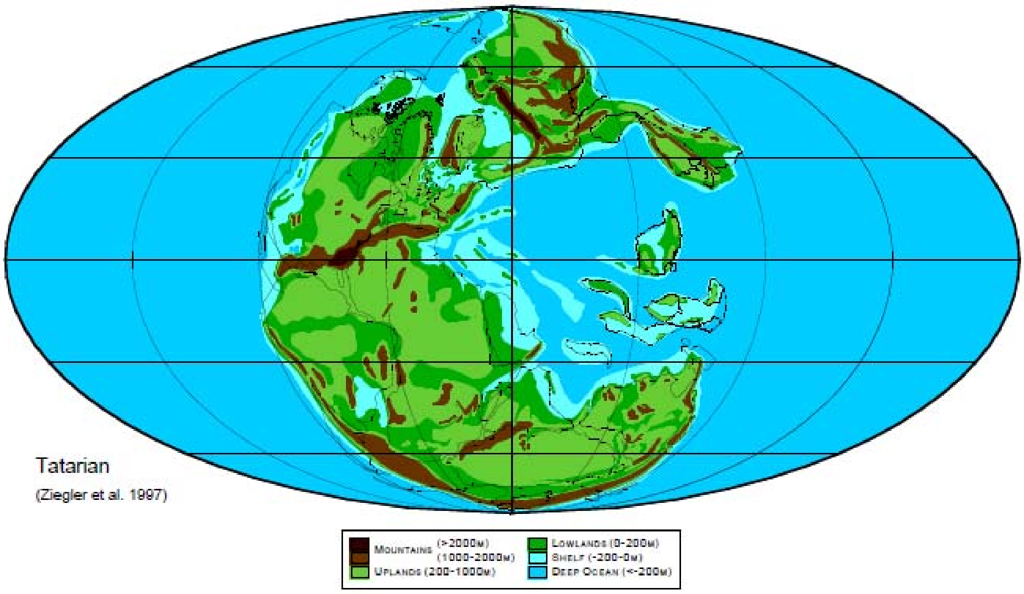

Figure 2. Late Permian

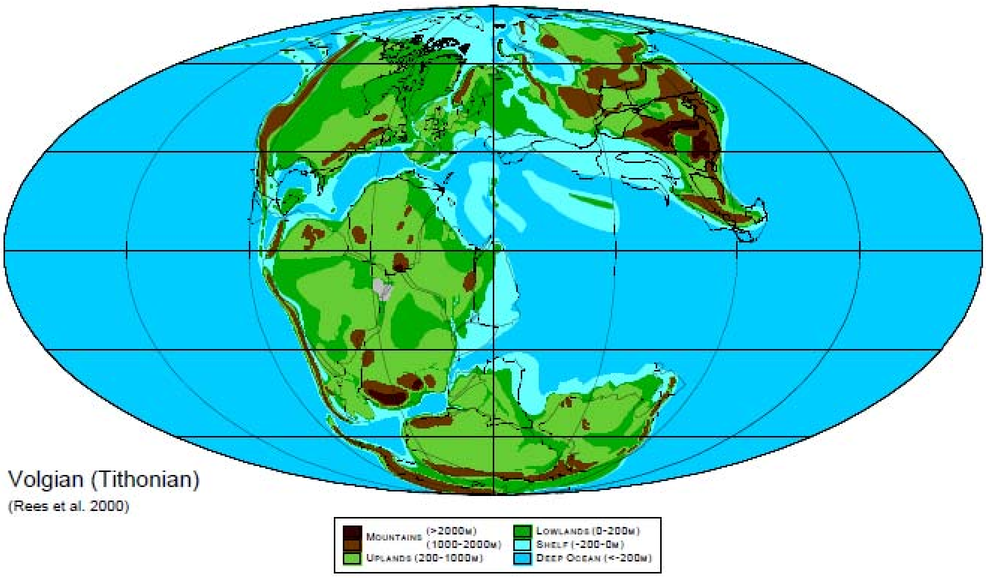

Figure 3. Late Jurassic

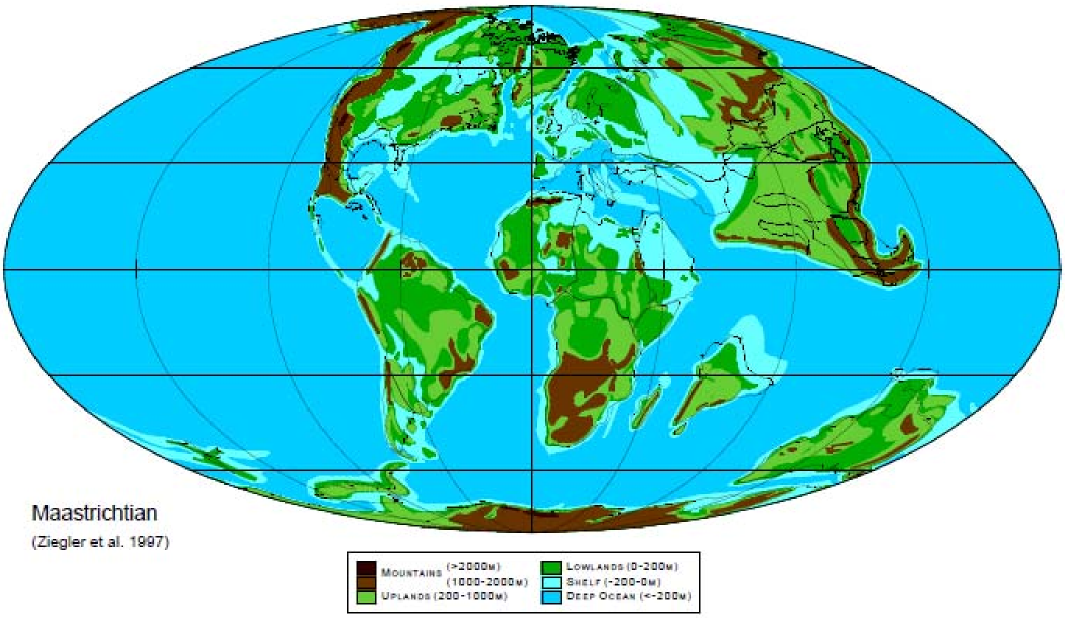

Figure 4. Late Cretaceous