Terrestrial tetrapods in Cretaceous Antarctica

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Abstract: The fossil record of continental vertebrates from Antarctica is practically nonexistent, hence the composition of the supposed Mesozoic terrestrial vertebrate fauna must be inferred indirectly. This may be done using the reconstructed positions of the continents during the Mesozoic. These positions suggest the presence in Antarctica of primitive sauropods, large theropods, hypsilophodontian and iguanodontid ornithopods, ankylosaurs, pterosaurs, crocodilians, lungfish and possibly birds. In the absence of evidence to the contrary, monotremes are considered endemic Australian forms during the Cretaceous. The discovery of hypsilophodontian material in New Zealand corroborates the inference of Antarctic hypsilophodontians from their occurrence in Australia. The existence in the Australian Early Cretaceous of relict taxa and taxa that seem unusual compared to their overseas relatives suggests that the south polar tetrapod fauna was characterized by singular forms.

The Mesozoic terrestrial tetrapods of Antarctica are poorly known. There are specimens from Lower Triassic rocks (Colbert 1974, 1987; Colbert & Cosgriff 1974, Colbert & Kitching 1975, 1977, 1981; Cosgriff 1983; DeFauw 1989) and a single specimen of an ankylosaurian dinosaur from the Upper Cretaceous (Gasparini *et al.* 1987; Olivero *et al.* in press). The Early Triassic (Scythian) fauna includes one or more thecodonts, *Prolacerta*, at least seven therapsids, *Procolophon* and at least two labyrinthodonts. This appears to be an unexceptional Scythian tetrapod fauna (from data given by Thulborn 1986).

It is, however, possible to deduce what forms may have inhabited Antarctica at certain times during the Mesozoic. Such deductions are possible because the geographical pattern of the continents during this time is well understood. Antarctica lay between, on the one hand, Australia and New Zealand, and on the other, Africa and South America (Smith *et al.* 1981). Thus Antarctica was a 'bridge' providing the only land link between Australasia and the other continents (Fig. 1).

Continental taxa that dispersed into Australasia from the other Gondwanan continents or Laurasia must have either dispersed overland across Antarctica or across the sea. Thus comparison of Australasian Mesozoic terrestrial tetrapod taxa with those of Africa and South America provides insight into which taxa inhabited Antarctica. Future discoveries of Antarctic fossils can (in principle) provide a test of this.

Australasian continental tetrapods either originated in Australasia or immigrated from elsewhere. The Permo-Carboniferous glaciations may have overrun most, or all, of Australia (Johnson 1980). If so, most or all post-Carboniferous Australian terrestrial tetrapod lineages must have been immigrants.

This endeavour to deduce the Mesozoic terrestrial tetrapods of Antarctica is limited by the poor record of terrestrial tetrapod fossils for pre-Cenozoic Australasia. Triassic continental tetrapods are unknown in New Zealand, and occur only in the Scythian of Australia. Although these Australian continental tetrapod faunas are of unusual aspect (Thulborn 1986), their constituent taxa are similar to contemporaneous taxa known elsewhere. Because Jurassic continental tetrapods are poorly known in Australia (Molnar 1980*a*), and unknown in New Zealand, only Cretaceous terrestrial tetrapods will be considered.

Many Cretaceous tetrapods from Gondwanaland (especially Australasia) are represented by few and incomplete specimens. Although the specimens often represent distinct species, their higher level affiliations are sometimes unclear. For this reason I have opted in some instances for a category such as 'large theropod' rather than use a potentially misleading or incorrect category such as carnosaur. Recently discovered specimens from Argentina will clarify many of these poorly understood forms, but until that work is completed taxonomic vagueness at higher levels will persist. The approach adopted here is to compare the faunas at sequentially lower taxonomic levels.

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Early Cretaceous tetrapods expected for Antarctica

To begin at the level of Order, large and small theropods, sauropods, large and small ornithopods, pterosaurs, crocodilians, and chelonians are found in Lower Cretaceous rocks on both sides of Antarctica (Fig. 1). Thus we would expect that these inhabited Antarctica during the Early Cretaceous. It is conceivable that pterosaurs, chelonians and crocodilians dispersed, by air and sea respectively, without crossing Antarctica. The other forms would have had some Antarctic populations.

Some useful conjectures may be made regarding lower taxonomic levels, although only a single genus seems to be known from both Australia and other continents (Molnar *et al.* 1981, 1985). The Australian continental crocodilian ('*Crocodylus*' *selaslophensis*) is not allocated at the familial level (Molnar 1980*b*) while the continental chelonian material is either not allocated at the familial level or (in the case of *Chelycarapookus arcuatus*) is assigned to a unique monotypic family of uncertain higher taxonomic affinities. The taxonomy of sauropods and therapods is in a state of flux, so consideration at any level below Order is not useful.

The Australasian ornithischian material seems to represent three families, the Hypsilophodontidae, Iguanodontidae and Nodosauridae. The identification of hypsilophodontids in Australia is sound (Molnar & Galton 1986). The family Iguanodontidae is under revision (Norman & Weishampel pers. comm.) and while the allocation of the Australian genus is secure under the currently accepted definition of this family (Bartholomai & Molnar 1981), the future allocation will depend on the results of this revision. The Australian nodosaurid is based on incomplete material and hence this is a tentative identification (Molnar & Frey 1987). Both iguanodontids and hypsilophodontids are known from Africa (Taquet 1976; Cooper 1985). Nodosaurids occur in Europe, North America and Asia, but are not recognized in either South America or Africa (Molnar & Frey 1987). Nonetheless, they presumably dispersed through Antarctica via Africa or South America. We may thus presume that hypsilophodontids, iguanodontids and nodosaurids occurred in Antarctica (and probably in South America as well, where Early Cretaceous ornithischians are represented only by footprints, Leonardi 1984).

The only Cretaceous terrestrial tetrapod occurring both in Australasia and elsewhere (North America) is the carnosaur *Allosaurus* (Molnar *et al.* 1981, 1985). This genus has been reported in the Jurassic of Africa (Janensch 1925), and a member of the same family in the Jurassic of Argentina (Bonaparte 1986*a*). This suggests that allosaurids occurred in Antarctica.

What appears to be part of the jaw of a temnospondyl amphibian has been found in Lower Cretaceous rocks of the southern coast of Victoria (Jupp & Warren 1986). Before rifting north, this region was adjacent to what is now Antarctica. Thus such creatures would be expected to have lived in Antarctica as well.

The report of a sphenodontian from the Lower Cretaceous of South Africa (Rich *et al.* 1983), together with their widespread distribution earlier in the Mesozoic, suggests that they dispersed across Antarctica to reach what is now New Zealand. If so, why did they not reach Australia? This apparent absence has yet to be explained.

The occurrence of enantiornithine birds in the Early Cretaceous of Australia (Molnar 1986) and Late Cretaceous of Argentina suggests that these may also have inhabited the Antarctic, especially as there is doubt about their flying ability (Walker 1981), and hence their potential for dispersal by air. Their early appearance in Australia suggests that they *may* have originated in Australia.

Early Cretaceous mammals are known from both South America and Australia, but these pertain to different orders. A eupantothere has been found in South America (Bonaparte 1986*b*) and a monotreme in Australia. In the absence of evidence to the contrary, monotremes are here considered to be endemic Australian forms.

The foregoing considerations suggest that the Early Cretaceous fauna of Antarctica would include: sauropods, *Allosaurus* (or at least allosaurids), hypsilophodontians, iguanodontids, nodosaurids, a probable temnospondyl, and (less confidently) chelonians, crocodilians and pterosaurs. Enantiornithine birds were probably present in Early or Late Cretaceous.

Late Cretaceous tetrapods expected for Antarctica

Late Cretaceous terrestrial tetrapods, with the exception of the sauropods and trackways of the Winton Fm. (Coombs & Molnar 1981; Thulborn & Wade 1984) and an unstudied chelonian shell, are unknown in Australia (Fig. 1). Because sauropods and turtles are also known from the Australian Lower Cretaceous, and because the Winton Fm. is of Cenomanian

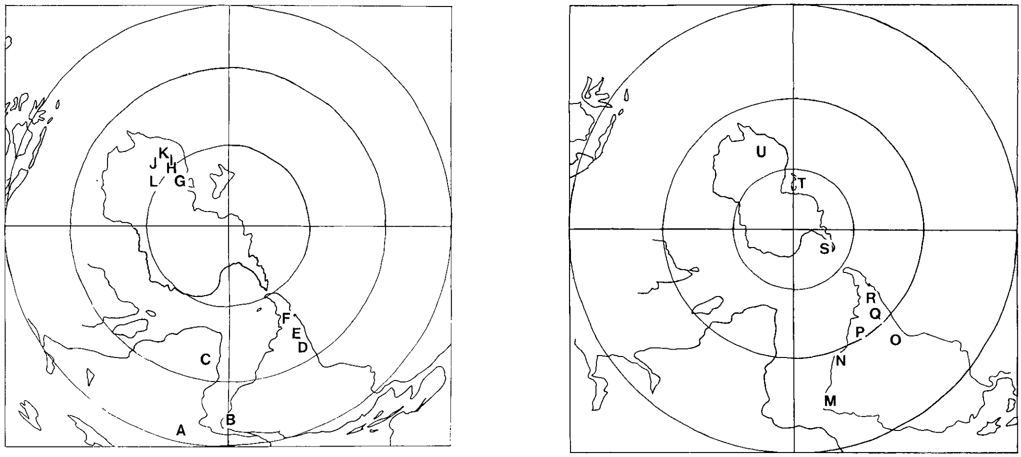

Fig. 1. Positions of the southern continents during the Cenomanian (left) and Campanian (right), in south polar projection. The continents are represented by modern shorelines; terrestrial tetrapod localities by letters. Those for the Early Cretaceous are indicated on the Cenomanian map, and for the Late Cretaceous on the Campanian map. A, Gadoufaoua, Niger (small theropods, sauropods, iguanodonts, hypsilophodonts, crocodiles, chelonians); B, Ceara & Bahia, Brazil (pterosaurs, crocodiles, chelonians); C, Namaqaland, South Africa (hypsilophodont); D, San Luis, Argentina (pterosaurs); E, Neuquen, Argentina (sauropods); F, Chubut, Argentina (large theropods, sauropods); G, Victoria, Australia (small & large theropods, hypsilophodonts, pterosaur, chelonians); H, New South Wales, Australia (large theropod, sauropod, iguanodont, hypsilophodont, crocodile, chelonians); I, southeast Queensland, Australia (ankylosaur); J, west Queensland, Australia (pterosaur); K, central Queensland, Australia (sauropod, iguanodont); L, South Australia, Australia (small theropod); M, Paraiba, Brazil (pterosaurs); N, Parana & Sao Paulo, Brazil (sauropods, crocodiles, chelonians); O, Salta, Brazil (small & large theropods, sauropod, crocodile); P, Uruguay & Entre Rios, Argentina (sauropods, crocodiles); Q, Neuquen & Rio Negro, Argentina (large theropod, sauropods, crocodiles, chelonians); R, Chubut & Santa Cruz, Argentina (sauropods, crocodiles, chelonians); S, James Ross Island (ankylosaur); T, North Island, New Zealand (hypsilophodont, pterosaur); U, central Queensland, Australia (sauropod, chelonian). (Cenomanian map from Smith *et al.* 1981, Campanian from Wiffen & Molnar, in press).

(earliest Late Cretaceous) age, this does not add significantly to what has already been deduced for the Early Cretaceous.

Before separation from Antarctica, New Zealand was a peninsula and tetrapods dispersing into Australia need not have traversed New Zealand. If the terrestrial tetrapods of Campanian–Maastrichtian New Zealand did not arrive by dispersal across the sea, but instead were 'carried along' on New Zealand as it drifted north, then they should provide a sample of the Late Cretaceous continental fauna of Antarctica independent of the deductions based on comparison with Australian forms.

Late Cretaceous terrestrial tetrapods from North Island, New Zealand comprise three specimens, two of which are too incomplete for use here (Molnar 1981*a*; Scarlett & Molnar 1984). The third is an incomplete ilium that pertains to a dryosaur-like ornithopod (Wiffen & Molnar, in press). This occurrence corroborates the inference of Antarctic hypsilophodontians (dryosaurids or hypsilophodontids) derived previously.

Pterosaurs have also been discovered in New Zealand (Wiffen & Molnar 1988 and undescribed material). These indicate that, although pterosaurs need not have dispersed across Antarctica to reach Australia, they did occupy at least the periphery of Antarctica. Given the flight capabilities of pterosaurs this is not surprising.

Other forms may be expected to have inhabited Antarctica from consideration of the modern terrestrial tetrapod fauna of New Zealand. These include ratites, sphenodontians and leiopelmatid frogs (Fleming 1975; Molnar 1981*a*). Evidence of a large terrestrial bird, a phorusrhacoid not a ratite, has been found in Lower Cenozoic rocks of the Antarctic (Case *et al.* 1987). This shows that large ground-dwelling birds could survive in Antarctica at that time.

Although this paper is concerned with terrestrial tetrapods, the logic should apply as well to continental (freshwater) fishes that cannot disperse through the sea. The occurrence of ceratodont lungfish in Australia in both Lower Cretaceous and Miocene (and later) beds, and in the Upper Cretaceous of Argentina (Pascual & Bondesio 1976), leads us to expect Antarctic ceratodontid lungfish. In fact, a fragment of ceratodont lungfish has been discovered in Triassic rocks in Antarctica (Dziewa 1980).

So the Late Cretaceous fauna of Antarctica may be expected to include: hypsilophodontian ornithopods, pterosaurs, ratites, sphenodontians, leiopelmatid frogs, and ceratodont lungfish.

Discussion

At least some elements of the Cretaceous Antarctic terrestrial tetrapod fauna may be predicted from comparison of the Australasian and other Gondwanan terrestrial tetrapod faunas. However, the Australasian tetrapod record shows unusual features that deserve further comment. For example, the prominent role of marsupials in Australia and (until recently) ratites in New Zealand is unmatched elsewhere. These features stem from the isolation of these lands through most of the Cenozoic.

The Australian Mesozoic fauna is distinctive in two respects: it includes taxa that appear to be relicts, and others that seem to have diverged to a significantly greater extent than related forms elsewhere. The unusual character of the Australian terrestrial tetrapod fauna seemingly was already established in the Triassic (Thulborn 1986), although at this time it was the composition of the fauna that was odd and not the relationship of any of its constituent taxa to those of other continents.

Relict taxa are represented in the fossil record (cf. Halstead 1987), although to my knowledge no systematic reviews of their occurrences in the record have been made. An example among Mesozoic terrestrial tetrapods is the Chinese Jurassic temnospondyl (Dong 1985). Relicts are not prominent in the well known Northern Hemisphere Cretaceous tetrapod faunas (western North America, eastern Asia), although they occur among mammals (Fox 1969, 1976, 1984; Lillegraven & McKenna 1986) and dinosaurs (a Late Cretaceous fabrosaurid reported by Weishampel & Weishampel 1983, and probably the segnosaurs, discussed by Paul 1984).

In the Australian Mesozoic, relicts make up a considerable proportion of the known terrestrial vertebrate fauna. Fifteen genera are known from the Jurassic–Cretaceous of Australia of which three, *Allosaurus*, *Austrosaurus*, and *Siderops*, seem to be relicts. In addition there is the apparent temnospondyl from the Victorian Lower Cretaceous (Jupp & Warren 1986).

Siderops kehli (Warren & Hutchinson 1983) and the Victorian temnospondyl persisted well after the majority of temnospondyls became extinct at the end of the Triassic. The Australian *Allosaurus* is Valanginian to Aptian in age (Dettmann 1986). The well known *Allosaurus fragilis* is from the Morrison Formation, usually cited as of Kimmeridgian or Tithonian age. Assuming the latter, the Victorian specimen would be at least 5 Ma younger.

The sauropod *Austrosaurus* shows several characters that seem to be plesiomorphic for sauropods (Coombs & Molnar 1981): small dorsal pleurocoels, absence of both caudal pleurocoels and supporting buttresses of caudal transverse processes, anteriorly placed caudal neural arches, and elevated femoral head. All but the first of these are also found among the contemporaneous titanosaurids; in fact *Austrosaurus* seems to share almost all features with the titanosaurids, except for their diagnostic procoelous caudals. However, Jurassic sauropods are markedly less plesiomorphic than the Cretaceous titanosaurids (von Huene 1929). Thus it is in order to speak of *Austrosaurus* as a relict of Middle Jurassic sauropods of cetiosaurian aspect. So, to almost as great an extent, are the titanosaurids. Why sauropods of primitive aspect substantially outlasted more derived taxa is not known.

No relict forms are obvious among the 22 South American, or 23 African Early Cretaceous terrestrial tetrapods. This may well reflect some barrier between Australia, on the one hand, and South America and Africa on the other, (such as mountains, epeiric seas or glaciated highlands, cf. Molnar 1981*b*). However Vermeij (1987) has suggested that certain taxa may survive preferentially in polar regions after becoming extinct in more equatorial areas. Thus it is interesting that the Australian Lower Cretaceous sites are generally less distant from the South Pole than are the South American sites (Smith *et al.* 1981). Only the central Queensland sites in Australia did not lie south of the southernmost South American sites (in Chubut, Argentina). The New Zealand ornithopod ilium shows more resemblance to ilia of Upper Jurassic and Early Cretaceous dryosaurid ornithopods, than to ilia of contemporaneous Late Cretaceous taxa (Wiffen & Molnar in press). Thus some Australasian terrestrial tetrapods are consistent with Vermeij's proposal.

The extent of unusual adaptations is difficult to estimate. Australian Cretaceous terrestrial tetrapods seem to have diverged more substantially from the common ancestors shared with non-Australian forms than have most of the non-Australian forms. Many of these features have already been pointed out by Bonaparte (1986*b*) in his survey of the endemic Gondwanan continental vertebrates. The nodosaurid *Minmi paravertebra* shows peculiar ossified aponeuroses and tendons (Molnar & Frey 1987) not found among any other known ankylosaurians. The slenderness of the tibia of the theropod *Kakuru kujani* is matched only by those of *Avimimus portentosus* and *Borogovia gracilicrus*. The raised hollow rostral bulla, the maxillary tooth form and the tooth rows lacking any indication of replacement teeth of *Muttaburrasaurus langdoni* are unmatched in the other iguanodontids. This has led to the suggestion that *Muttaburrasaurus* is not an iguanodontid, which only emphasizes the degree of difference of this form from contemporaneous non-Australian ornithopods. *Chelycarapookus arcuatus* is unusual in certain structures, especially the increased length of the posterior two pairs of ribs and the correspondingly increased size of the posterior neurals (Warren 1969). These features are not matched in other chelonians. However, the internal morphology of the carapace of chelonians is poorly known (Gaffney 1981), so it is not clear that this constitutes as great a divergence from the condition of the common ancestor (as seems to be the case for the dinosaurs discussed above).

Four of the 13 known Early Cretaceous Australian continental tetrapods appear to show substantially greater morphological differences than contemporaneous overseas taxa. Early Cretaceous African tetrapods seem to show nothing out of the ordinary in this regard. However, the remarkable theropod *Spinosaurus aegyptiacus* from Egypt deserves mention. *Spinosaurus* is early Cenomanian in age and hence may well have persisted from the Early Cretaceous; indeed there is a report of an Early Cretaceous *Spinosaurus* (Bouaziz *et al*. 1988). One of the 23 Early Cretaceous African tetrapods appears to have morphological structures (elongate dorsal neural spines) comparable, in their degree of divergence from the presumed ancestral condition, to some of the Australian forms. The South American Early Cretaceous theropod *Carnotaurus sastrei* is comparably outlandish in its development of a deep, short snout and supraorbital horn cores (Bonaparte 1985). This gives ratios of four out of 13 Australian, one out of 23 African and one out of eight South American terrestrial tetrapod species (excluding flying forms) with unusually divergent morphological structures. Again there seems to be an unusual fauna in the Mesozoic south polar regions.

The small sample sizes of the Early Cretaceous faunas of these continents implies that this may be nothing more than sampling error. However, an unusual high-latitude mammalian fauna has been reported in North America (Hickey *et al*. 1983). The Australian evidence suggests that the Cretaceous terrestrial tetrapod fauna of the Antarctic regions may have been unique. The role of future discoveries in Antarctica will be critical in corroborating the Australian evidence, and revealing the extent to which these faunal features extended through the south polar regions.

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Appendix: list of continental tetrapods of Cretaceous Gondwanaland (exclusive of India) used in text comparisons

LOWER CRETACEOUS

Brazil:

Pterosauria
- Anhangueridae
  - *Anhanguera blittersdorffi*
- Criorhynchidae
  - *Tropeognathus mesembrinus*
  - *Tropeognathus robustus*
- Ornithocheiridae
  - *Araripedactylus dehmi*
  - *Araripesaurus castilhoi*
  - *Araripesaurus santanae*
  - *Brasileodactylus araripensis*
  - *Cearadactylus atrox*
  - *Santanadactylus araripensis*
  - *Santanadactylus brasiliensis*
  - *Santanadactylus pricei*
  - *Santanadactylus spixi*

Crocodylia
- Pholidosauridae
  - *Sarcosuchus hartii*
- Uruguaysuchidae
  - *Araripesuchus gomesi*

Chelonia
- Araripemyidae
  - *Araripemys barretoi*

Uruguay:

Crocodylia
- Pholidosauridae
  - *Meridiosaurus vallisparadisi*

Argentina:
Theropoda
  Abelisauridae
    Carnotaurus sastrei
Sauropoda
  Brachiosauridae
    Chubutisaurus insignis
  family *incertae sedis*
    Amargasaurus groeberi
Pterosauria
  Pterodaustriidae
    Pterodaustro guinazui
  family *incertae sedis*
    Puntanipterus globosus
Mammalia
  Vincelestidae
    Vincelestes neuquenianus
Algeria:
Theropoda
  family *incertae sedis*
    Carcharodontosaurus saharicus
  Ornithomimidae
    Elaphrosaurus iguidiensis
Sauropoda
  Brachiosauridae
    Rebbachisaurus tamesnensis
Crocodylia
  Dyrosauridae
    Dyrosaurus sp.
  Pholidosauridae
    Sarcosuchus imperator
Squamata
  Simoliophidae
    Lapparentophis defrennei
Tunisia:
Theropoda
  family *incertae sedis*
    Carcharodontosaurus saharicus
    Spinosaurus sp.
Morocca:
Theropoda
  family *incertae sedis*
    Carcharodontosaurus saharicus
Sauropoda
  Brachiosauridae
    Rebbachisaurus garasbae
Crocodylia
  Libycosuchidae
    Libycosuchus sp.
  Thoracosauridae
    Thoracosaurus cherifiensis
Mali:
Sauropoda
  Brachiosauridae
    Rebbachisaurus tamesnensis
Crocodylia
  Dyrosauridae
    Dyrosaurus sp.
Niger:
Theropoda
  family *incertae sedis*
    Bahariasaurus ingens
    Carcharodontosaurus saharicus
    Inosaurus tedreftensis
  Ornithomimidae
    Elaphrosaurus gautieri
    Elaphrosaurus iguidiensis
Sauropoda
  Brachiosauridae
    Rebbachisaurus tamesnensis
  Titanosauridae
    Aegyptosaurus baharijensis
Ornithopoda
  Iguanodontidae
    Ouranosaurus nigeriensis
  Dryosauridae
    Valdosaurus nigeriensis
Crocodylia
  Pholidosauridae
    Sarcosuchus imperator
  Uruguaysuchidae
    Araripesuchus wegeneri
Chelonia
  Araripemyidae
    Taquetochelys decorata
  Pelomedusidae
    Platycheloides cf. *P. nyasae*
    Teneremys lapparenti
Zaire:
Pterosauria
  Ornithocheiridae
    un-named species
South Africa:
Sauropoda
  Camarasauridae?
    Algoasaurus bauri
Ornithopoda
  Hypsilophodontidae?
    Kangnasaurus coetzeei
Stegosauria
  Stegosauridae
    Paranthodon africanus
Sphenodontia
    un-named species
Australia:
Theropoda
  Allosauridae
    Allosaurus sp.
  family *incertae sedis*
    Kakuru kujani
    Rapator ornitholestoides
Sauropoda
  family *incertae sedis*
    Austrosaurus mckillopi
Ornithopoda
  Iguanodontidae
    Muttaburrasaurus langdoni
  Hypsilophodontidae
    Fulgurotherium australe
    2 new spp. in press by Rich & Rich
Ankylosauria
  Nodosauridae
    Minmi paravertebra
Pterosauria
  Ornithocheiridae
    un-named species
Crocodylia
  family *incertae sedis*
    'Crocodylus' selaslophensis

Aves
- Enantiornithidae
  - *Nanantius eos*

Chelonia
- Chelycarapookidae
  - *Chelycarapookus arcuatus*

Mammalia
- Steropodontidae
  - *Steropodon galmani*

UPPER CRETACEOUS

Brazil:

Sauropoda
- Titanosauridae
  - *Antarctosaurus brasiliensis*
  - *Titanosaurus* sp.

Pterosauria
- Nyctosauridae?
  - *Nyctosaurus? lamegoi*

Crocodylia
- Baurusuchidae
  - *Baurusuchus pachecoi*
- Dyrosauridae
  - *Hyposaurus derbianus*
- Trematochampsidae
  - *Itasuchus jesuinoi*
- Peirosauridae
  - *Peirosaurus torminni*
- family *incertae sedis*
  - *Sphagesaurus huenei*

Squamata
- Iguanidae
  - *Pristiguana brasiliensis*

Chelonia
- Pelomedusidae
  - *Apodichelys lucianoi*
  - *Podocnemis barrisi*
  - *Podocnemis brasiliensis*
  - *Podocnemis elegans*
  - *Roxochelys wanderleyi*

Uruguay:

Sauropoda
- Titanosauridae
  - *Antarctosaurus wichmannianus*
  - *Argyrosaurus superbus*
  - *Laplatasaurus araukanicus*
  - *Titanosaurus australis*

Crocodylia
- Uruguaysuchidae
  - *Uruguaysuchus aznaresi*
  - *Uruguaysuchus terrai*

Bolivia:

Crocodylia
- Baurusuchidae
  - *Cynodontosuchus rothi*

Chelonia
- Pelomedusidae
  - *Roxochelys*? *vilavilensis*

Mammalia
- Didelphidae
  - *Roberthoffstetteria nationalgeographica*
- Hyopsodontidae
  - *Molinodus suarezi*
  - *Tiuclaenus minutus*
- Pantolambdidae
  - *Alcidedorbignya inopinata*
- Eutheria? *incertae sedis*
  - *Andinodus boliviensis*

Peru:

Chelonia
- Pelomedusidae
  - *Roxochelys? vilavilensis*

Mammalia
- Didelphidae
  - *Alphadon austrinum*
  - *Peradectes austrinum*
- Eutheria? *incertae sedis*
  - *Perutherium altiplanense*

Argentina:

Theropoda
- Abelisauridae
  - *Abelisaurus comahuensis*
  - *Xenotarsosaurus bonapartei*
- Noasauridae
  - *Noasaurus leali*
- family *incertae sedis*
  - *Loncosaurus argentinus*
  - *Unquillosaurus ceibalensis*

Sauropoda
- Titanosauridae
  - *Antarctosaurus giganteus*
  - *Antarctosaurus wichmannianus*
  - *Argyrosaurus superbus*
  - *Clasmodosaurus spatula*
  - *Laplatasaurus araukanicus*
  - *Saltasaurus loricatus*
  - *Titanosaurus australis*
  - *Titanosaurus nanus*

Ornithopoda
- Hadrosauridae
  - *Kritosaurus australis*
  - *Secernosaurus koeneri*

Ceratopsia
- Protoceratopsidae?
  - *Notoceratops bonarelli*

Crocodylia
- Baurusuchidae
  - *Cynodontosuchus rothi*
- Dolichochampsidae
  - *Dolichochampsa minima*
- Notosuchidae
  - *Notosuchus terrestris*
- family *incertae sedis*
  - *Microsuchus schilleri*

Aves
- Enantiornithidae
  - *Avisaurus sp.*
  - *Enantiornis leali*

Squamata
- Dinilysidae
  - *Dinilysia patagonica*
- Madtsoidae
  - *Alamitophis argentinus*
  - *Patagoniophis parvus*
  - *Rionegrophis madtsoiodes*
- family *incertae sedis*
  - *Dicarlesia incognita*

Chelonia
  Meiolaniidae
    Niolamia argentina
  Pelomedusidae
    Naiadochelys maior
    Naiadochelys patagonica
Mammalia
  Dryolestidae
    Groebertherium novasi
    Groebertherium stipanicici
    Mesungulatum houssayi
  Ferugliotheriidae
    Ferugliotherium windhauseni
  Gondwanatheriidae
    Gondwanatherium patagonicus
  Triconodontidae
    Austrotriconodon ferox
Anura
  Pipidae
    Saltenia ibanezi

Chile:
Sauropoda
  Titanosauridae
    Antarctosaurus sp.
Aves
  Baptornithidae
    Neogaeornis wetzeli

Egypt:
Theropoda
  Spinosauridae
    Spinosaurus aegyptiacus
  family *incertae sedis*
    Bahariasaurus ingens
    Carcharodontosaurus saharicus
    un-named small theropods
Sauropoda
  Titanosauridae
    Aegyptosaurus baharijensis
Crocodylia
  Aegyptosuchidae
    Aegyptosuchus peyeri
    Stromerosuchus aegyptiacus
  Dyrosauridae
    Dyrosaurus sp.
  Libycosuchidae
    Libycosuchus brevirostris
  Stomatosuchidae
    Stomatosuchus inermis
  Trematochampsidae
    Trematochampsa sp.
Squamata
  Simoliophidae
    Simoliophis sp.
Chelonia
  family *incertae sedis*
    Apertotemporalis baharijensis

Sudan:
Crocodylia
  Dyrosauridae
    Dyrosaurus sp.

Morocco:
Squamata
  family *incertae sedis*
    Pachyvaranus crassispondylus

Senegal:
Pterosauria
  Azhdarchidae?
    un-named species

Niger:
Theropoda
  family *incertae sedis*
    Bahariasaurus? sp.
Crocodylia
  Libycosuchidae
    Libycosuchus sp.
  Trematochampsidae
    Trematochampsa taqueti
Squamata
  Madtsoidae
    Madtsoia sp.

Nigeria:
Crocodylia
  Dyrosauridae
    Dyrosaurus sp.
    Sokotosuchus ianwilsoni
Chelonia
  Chelydridae
    Nigeremys gigantea
  Pelomedusidae
    Sokotochelys lawanbungudui
    Sokotochelys umarumohammedi

Madagascar:
Theropoda
  Abelisauridae?
    Majungasaurus crenatissimus
Sauropoda
  Titanosauridae
    Laplatasaurus madagascariensis
Pachycephalosauria
  Pachycephalosauridae
    Majungatholus atopus
Crocodylia
  Trematochampsidae
    Trematochampsa oblita
Squamata
  Madtsoiidae
    Madtsoia madagascariensis

South Africa:
Anura
  Pipidae
    Eoxenopoides reuningi

Australia:
Sauropoda
  family *incertae sedis*
    Austrosaurus sp.
Chelonia
    un-named species

New Zealand:
Theropoda
    un-named large theropod?
Ornithopoda
  Dryosauridae?
    un-named small ornithopod
Pterosauria
    un-named species

To avoid an excessively long list of references the sources for this table have not been cited. They have been deposited in the Geological Society Library and with the British Library at Boston Spa, W. Yorkshire, UK as Supplementary Publication No. SUP 18057 (also available from author on request).

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