

Cenozoic dinosaurs in South America – revisited

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Abstract

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Of course there were Cenozoic dinosaurs (theropods) in South America, phorusrhacid (‘terror’) birds among others, but that is not the subject here. Why did anyone think there were Cenozoic (non-avian) theropods in South America? Because of a misinterpretation of Ameghino’s belief that derived mammals lived along with dinosaurs in Late Cretaceous Argentina. But also because isolated theropod teeth were found associated with derived (Eocene) mammal fossils. These turned out to be the teeth of *Sebecus icaeorhinus*. This is a small crocodylomorph, skull length c. 450 mm. More recently discovered sebecosuchians were substantially larger: *Barinasuchus arveloi* had an (estimated) skull length of c. 1000 mm, similar to that of *Daspletosaurus* (1000 mm). These crocodylomorphs are generally believed to have been terrestrial animals, presumably preying on large mammals. Thus, although there were no large non-avian theropods in Cenozoic South America, there were crocodylomorphs that seem to have been ecological vicars of large theropods. The reconstruction of terrestrial trophic networks for large terrestrial tetrapods after the Cretaceous-Paleogene extinctions seems to have been slower than often supposed. At (or near) the Cretaceous-Paleogene boundary, large herbivores turned over from archosaurs to mammals, but turnover of large carnivores was slower. In South America, dinosaur-size crocodylomorphs lived as late as the Miocene. Thus modern terrestrial ecosystems do not, trophically, reflect those of even the Early Neogene in some southern continents. Sebecosuchians, at least in South America, seem to have been unaffected by the Cretaceous-Paleogene extinctions.

Keywords

South America, sebecosuchian, crocodylomorph, Cenozoic, trophic system.

Introduction

Of course there were Cenozoic dinosaurs in South America: birds. But here we examine the notion that non-avian theropod dinosaurs survived into the Cenozoic in South America, in both literal and metaphoric senses. A popular perception is that the terminal Cretaceous extinctions immediately affected all the terrestrial trophic networks of the time, influencing marine, freshwater and land biota. Non-avian dinosaurs, both saurischians and ornithischians, were the large herbivores on land and saurischians the large carnivores. With their extinction both trophic roles were seized by mammals. This happened on all of the landmasses at about the same time, soon - taken to be very soon geologically speaking - after the extinction.

There are few continuous non-marine stratigraphic sections across the Cretaceous-Paleogene boundary, and fewer still are well-studied. Only that of the Alberta-Montana region of the North American Cordillera has been studied in detail (Hartman et al., 2002; Wilson et al., 2014). What is known about the Cretaceous-Paleogene biotic turnover on land is

either extrapolated from what happened in the Alberta-Montana region or interpolated across stratigraphic, and hence temporal, gaps of varying magnitude. By the end of the Cretaceous Australia, New Zealand, Antarctica, Africa, India and Madagascar were isolated (Smith et al., 1994; Ron Blakey website, <http://cpgeosystems.com/paleomaps.html>). South America had been isolated for some time and had established a contact with North America presumably during or just before the Campanian, when hadrosaurs appear in Patagonia. In all these southern lands continuous non-marine sections across the Cretaceous-Paleogene boundary are rare, nonexistent or unstudied. We do not know just when (non-avian) dinosaurs became extinct there. Nor do we know what creatures, if any, immediately replaced them in the trophic network.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; CMN, Canadian Museum of Nature, Ottawa, Canada; DGM, Museu de Ciencias da Terra, Departamento Nacional

de Produção Mineral, Rio de Janeiro, Brazil; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MAAT, Museo Alberto Arvelo Torrealba, Barinas, Venezuela; MLP, Museo de La Plata, La Plata, Argentina.

Eocene dinosaurs in Patagonia

The issue of which lineages made up post-Cretaceous land-dwelling carnivores is related to a largely forgotten episode in the history of vertebrate palaeontology - the supposed occurrence of Cenozoic (non-avian) dinosaurs (Langston, 1956). Reports of Cenozoic dinosaurs started in the late nineteenth century, maybe before, and have continued sporadically since. They are almost always based on incorrect dating, taphonomic or stratigraphic misinterpretation, or incorrect identification (e.g., Eocene hadrosaur material from Niger reported by Nopcsa, 1925, shown to be crocodylomorph by Swinton et al., 1930). The dating errors were almost always due to reworked fossils, material that had recently experienced time-averaging across the Cretaceous-Paleogene boundary. Such instances are known from France (Buffetaut et al., 1980), China (Buck et al., 2002), and the western interior of North America (Argast et al., 1987; Lofgren, 1995; Renne and Goodwin, 2014). Basal Danian, that is post-Cretaceous, non-avian theropod bones have been reported from the Chatham Islands, New Zealand (Stilwell et al., 2006; Stilwell and Håkansson, 2012). Although, given the history of such reports, this report has not met with unanimous acceptance, the transitory survival of some non-avian dinosaurs, especially theropods, beyond the 66 million year 'deadline' seems by no means impossible.

One episode, however, did not involve reworked material - the Eocene dinosaurs of Patagonia reported by Florentino Ameghino (1906). Ironically he did not think the specimens were evidence of Cenozoic (non-avian) dinosaurs, but of derived mammals living in the late Cretaceous (Ameghino, 1906; Simpson, 1932b). This was the critical evidence for his contention that modern mammalian lineages originated in Argentina and later spread across the globe. We don't know how this notion was received in Argentina, but elsewhere enthusiasm was notably lacking (e.g., Loomis, 1913). Indeed, so much so, that the existence of early Cenozoic dinosaurs was considered a more plausible alternative. The notion of Cenozoic dinosaurs may have gained support from the report of (non-avian) theropod teeth in Paleogene beds in Spain by Royo Gómez (1928), discussed by Pereda-Suberbiola et al. (2012). Pereda-Suberbiola et al. were not able to locate the teeth Royo Gómez had photographed but did locate a single theropod-like tooth that proved to be mesoeucrocodylian, perhaps from *Iberosuchus* sp., and so they suggested that Royo Gómez's teeth were also crocodyliform.

But it was not just Ameghino's notion that generated interest in the Cenozoic mammalian faunas of South America. As Simpson (1978 ch. 8) explained, these faunas - apparently initially consisting of marsupials, edentates and ungulates - seemed to have originated from an unduly limited suite of mammals compared to those from the northern hemisphere and Africa. It is now known that other lineages (e.g.

monotremes) were initially present. Expeditions from the U.S.A. were mounted, from Princeton (Hatcher, 1899), Amherst (Loomis, 1913) and the American Museum of Natural History (the Scarritt Expeditions). The goal of these expeditions was to elucidate the origins of the mammalian faunas of Cenozoic Patagonia and hence South America in general (Loomis, 1913, 1914, and especially Simpson, 1978). But the supposed occurrence of derived mammals in the Mesozoic was also of interest (Loomis, 1913) and Simpson's first two papers (1932a, b) on returning from Patagonia concerned this subject.

Ameghino based his identification on isolated teeth. These were attributed to the only known South American (non-avian) theropod at the time, the Argentinian *Genyodectes serus* (Woodward, 1901). One of the teeth, MACN (then MNHN) 10871, figured by Ameghino (1906), and later by Simpson (1932b), is similar to those of *Genyodectes*. In the absence of absolute dating techniques and detailed regional stratigraphic studies, Ameghino's attribution of the rocks and their fossil fauna, the *Notostylops* fauna, to the latest Cretaceous was reasonable. But there was also speculation that the field data were incorrect (Simpson, 1932b). The Scarritt Patagonian Expedition of 1930-1 was undertaken to examine the exposures, determine their date and thus verify or falsify the occurrence of non-avian dinosaurian fossils with those of mammals of Eocene aspect. One could, and presumably some did, wonder why mammalian remains were relatively plentiful, but dinosaurian remains were restricted to an apparently few isolated teeth if the beds were indeed Cretaceous (cf. Simpson, 1978).

Some results of the expedition were published by Simpson in 1932(b), and he concluded that teeth superficially like those of theropods were actually canines attributed to an unusual mammal he named *Florentinoameghinia mystica*. The reason for the trivial name, 'mystica', was not given but it proved prescient. Nothing more of the creature has been found, or at least recognised, and despite the proposals of McKenna (1981) and Sereno (1982) that *F. mystica* was a sirenian, since refuted (Wells and Gingerich, 1983), its relationships remain unknown 80-odd years later. It should be noted that the single (incomplete) tooth (AMNH FM 28401, now AMNH FARB 3162, Simpson, 1932b, fig. 6) that Simpson compared to Ameghino's 'dinosaurian' teeth, was only 'probably associated' (Simpson, 1932b pp. 16 and 19; Colbert, 1946) with the holotype of *F. mystica*. Colbert (1946) pointed out that this tooth was unlike that of Ameghino's alleged dinosaur and those of *Sebecus*, but it is now attributed to *Sebecus* (Mehling, pers. comm., 2014).

The holotype specimen of *Sebecus icaeorhinus* was found near the coast of Chubut, at Cañadón (now Arroyo) Hondo. Not only teeth, but much of the skull and mandible and a few pieces of the postcranial skeleton were collected. In his initial description Simpson (1937) was somewhat reticent about just what had been found. He repeatedly refers to it as an 'archaeosaur' rather than using a more specific identification, describes it as "remotely crocodile-like" (p. 1), and even compares it with phytosaurs. He goes on to write

“This animal is so decidedly distinct that detailed comparison with other forms is hardly possible, but it is probably more nearly related to the Crocodilia than to other previously known reptiles. Even this relationship must be remote and any common ancestry could hardly be later than the Triassic and would be doubtfully crocodilian. At the least, *Sebecus* must represent a new suborder of Crocodilia, differing more from the other suborders than they do among themselves, and it may be necessary to place it in a new order of Archaeosauria.” (Simpson, 1937 pp. 1–2).

One wonders if he thought – if even momentarily when it was first seen – that he had indeed found an Eocene (non-avian) theropod dinosaur. However, in *Attending Marvels* (Simpson, 1934) the discovery of *Sebecus* is barely mentioned (“... we find abundant turtles, crocodiles, and birds.”, p. 238), although the arguably less interesting discoveries of *Eocaiman* (p. 87) and *Madtsoia* (p. 210) are mentioned in more detail. Simpson did state (p. 210) that there were no dinosaurs in the beds in which he worked, so whatever he might have thought when the specimen was first seen, he seems to have been aware that it was not dinosaurian by the time he wrote *Attending Marvels*. Further, the remains of *Sebecus* were mixed with those of the turtle *Crossochelys* (now *Niolamia*), so first impressions may well have been confusing.

Perhaps this accounts for another puzzling episode. Simpson collected the material of *Florentinoameghinia* at Cañadón Vaca on 4 February 1931 (Gishlik, pers. comm., 2014) and the holotype material of *Sebecus* on 7 March 1931 (Mehling, pers. comm., 2014). Simpson left Patagonia in June of that year (Simpson, 1934) and the description of *Florentinoameghinia* appeared in September 1932 (Simpson, 1932b). By the time *Florentinoameghinia* was published, Simpson knew of *Sebecus*, and that it had theropod-like teeth, yet he proposed it was the tooth attributed to *F. mystica* that explained Ameghino’s putative (non-avian) theropod teeth, not those of *Sebecus*. He mentions nothing of *Sebecus* in *Attending Marvels* (1934), nor in his later autobiography (1978). We have no idea why Simpson attributed Ameghino’s tooth to *Florentinoameghinia* rather than to *Sebecus*, nor what (or even if) he thought about *Sebecus* during this period. However, Simpson (1937) did later recognise the dinosaur-like character of *Sebecus* teeth and proposed that one of the teeth (presumably MACN 10871) seen by Ameghino was actually from *Sebecus*. The other tooth, MACN 10872, looks to be typically crocodilian as noted by Colbert (1946).

Whatever the understanding of *Sebecus* may have initially been, the postorbital region of its skull clearly indicates that it was crocodylomorph. By the time of Colbert’s 1946 monograph, two other unexpected crocodilians, *Baurusuchus* and *Uruguaysuchus*, represented by skulls and mandibles, had been discovered in South America, and our understanding of the Crocodilia had started its evolution to the modern concept of Crocodylomorpha. Even before, Woodward (1896) briefly described two strange, fragmentary ‘crocodilians’, *Cynodontosuchus* and *Notosuchus*, the first bearing theropod-like teeth. It was clear that *Sebecus* was not a dinosaur, if it

had ever been thought so. In a literal, cladistic sense non-avian theropods did not occur in the Cenozoic of South America, but in a metaphoric, ecological sense it is a different matter.

Miocene ersatz dinosaurs in Venezuela and Peru

The discovery of *Sebecus* was not the first time that theropod-like teeth were seen in crocodylomorphs. But apparently no one associated with *Sebecus* had remembered, or read, these earlier papers (Cuvier, 1824; Marsh, 1871; Woodward, 1896) and these “dinosaur-toothed” forms remained generally ignored until discussed by Langston (1956, 1975). Trenchant, serrate teeth like those of theropods are known as ziphodont teeth (Langston, 1975), although there is some lack of clarity over exactly what the term ‘ziphodont’ means. Langston (1975) proposed it to designate crocodylomorph teeth that were 1, trenchant (laterally compressed and so blade-like in form), 2, curved and 3, serrate on both margins. It is not immediately obvious what Langston meant by “curved”. The other two conditions were thought to have occurred together as they do in most ziphodont teeth whether from crocodylomorphs or other reptiles. But the largest teeth of the flat-headed Australian *Pallimnarchus* are serrate without being trenchant and, as pointed out by Prasad and de Broin (2002), teeth can be trenchant without being serrate, as in *Zulmasuchus* (Buffetaut and Marshall, 1991). Thus lateral compression and serration seem to be two independent traits that, when occurring together, are termed ‘ziphodont’. Langston (1975) also linked ziphodont teeth with elevated, steep-sided (oreinirostral) snouts although it is now known that in Australian mekosuchians, specifically *Mekosuchus whitehunterensis* (Willis, 1997) and *Baru* (Willis et al., 1990; Willis, 1997), oreinirostral snouts can occur with teeth that are not ziphodont. Crocodylomorphs with ziphodont teeth and oreinirostral snouts have been referred to as ‘ziphodont crocodylomorphs’, although the term ‘ziphodont’ refers to the teeth not the form of the snout.

Even the origin of the term ‘ziphodont’ has become unclear. Hecht and Archer (1977) used the form ‘xiphodont’ assuming that it derived from the Greek ‘xiphos’, a kind of short sword. The term apparently does, but not directly. Langston (1975, p. 291 footnote) derived it from Marsh’s (1871) name *Crocodylus ziphodon*.

The most speciose lineage of land-dwelling ziphodont crocodylomorphs is that of *Sebecus*, *Baurusuchus*, and their kin, the sebecosuchians. These forms were predominantly South American, although they also occurred in north Africa (Buffetaut, 1989), western and central Europe (e.g., Berg, 1966; Antunes, 1975; Buffetaut, 1982, 1986), and Pakistan (Wilson et al., 2001). The South American sebecosuchian lineage lasted more than 60 million years from at least the Coniacian in the late Cretaceous (Pol and Gasparini, 2007) to the Miocene (Paolillo and Linares, 2007).

Sebecus, like many of the southern South American taxa, was a sebecosuchian of moderate size. The holotype skull was almost half a metre long (46.2 cm, a new estimate after the reconstruction of Molnar, 2010), and the whole creature 2.65 (+/-0.45) metres in length (Pol et al., 2012), although it is not

clear that the holotype skull and the postcranial remains studied by Pol et al. came from individuals of similar size. Other taxa were larger, *Barinasuchus* having been the largest (Paolillo and Linares, 2007).

Although *Barinasuchus arveloi* has been recognised as a large predator (e.g., Riff et al., 2010) it has not been realised that the preserved part of the largest specimen of *Barinasuchus* (MAAT-0260) is nearly the same size as the corresponding part of the holotype skull (CMN 8506) of a mature *Daspletosaurus torosus* (fig. 1). Metric comparison is uncertain because of the incompleteness of the skull of *Barinasuchus*, however the preserved part, the snout back almost to the orbits, of MAAT-0260 is at least 600 mm in length (Paolillo and Linares, 2007, fig. 6). The length of the upper dentition of CMN 8506 is 530 mm (Russell, 1970), and that of the preserved upper dentition of MAAT-0260 is 500 mm (Paolillo and Linares, 2007, fig. 6). Estimating the total length of the skull of MAAT-0260 by superimposing the images in 'Photoshop 12.0 x64', by matching the notches for the dentary caniniform tooth and assuming that the posterior break of the snout was immediately in front of the orbit, to the skulls of *Baurusuchus pachecoi* (Price, 1945) and *Baurusuchus salgadoensis* (Carvalho et al., 2005), gives an estimated total skull length of 950–1100 mm. The total length of the holotype skull of *Daspletosaurus* is 1040 mm and that of the skull of AMNH 5458 (*Gorgosaurus libratus*) is 990 mm (Russell, 1970). Presumably it would be the size of the skull, specifically the length of the tooth rows, that governed the trophic impact. So there was in the Miocene of northern South America a carnivorous crocodylomorph with a skull, or at least a snout, the size of that of a moderately large tyrannosaur, and thus larger than the skulls of land-dwelling carnivorous mammals (fig. 2).

A skull a metre long is not unusual among Cenozoic crocodylomorphs (Gurich, 1912). The Miocene longirostrine *Gryposuchus croizati* attained a skull length of 1.4 metres, with an estimated total length of about 10 metres (Langston and Gasparini, 1997; Riff and Aguilera, 2008) and the broad-snouted *Purussaurus brasiliensis*, also from the Miocene of northern South America, attained a skull length of 1.4 metres (Price, 1964; Riff et al., 2010), with an isolated mandible 1.75 metres long (Price, 1967), and an astounding estimated total length of about 14 metres. Modern crocodilians are creatures that usually dwell, and usually hunt, in the water and along the shore. There is no reason to think that *Purussaurus* (a giant caiman), *Gryposuchus* (a giant gharial-like eusuchian) and such were different in this respect from most living crocodilians (Riff et al., 2010). *Barinasuchus*, however, presumably was different in this regard.

Langston (1965, pers. comm., 1968), unlike Colbert (1946) but like Gasparini (1981, 1984) and Buffetaut (1982), suspected that ziphodont crocodylomorphs were land-dwellers, based on the observations of Kuhn (1938) on an almost complete skeleton from the Geisel Valley of eastern Germany. Kuhn had noted that this skeleton of *Boverisuchus geiselthalensis* had two features anomalous for modern crocodilians. These were a tail round in cross section, rather than laterally flattened as in living crocodilians, and blunt terminal phalanges on the feet, unlike the claws found in most other crocodylomorphs.

Kuhn interpreted these features to indicate that the tail was not used in swimming, and that the feet were adapted to walking on a hard ground surface, not the mud often found along watercourses. Hastings et al. (2014) confirmed that the terminal phalanges were suited for locomotion on land, and found that they showed some similarity to those of the basal horse, *Propalaeotherium*. *Boverisuchus* is now recognised to be a planocraniid ziphodont eusuchian (Brochu, 2013), believed to be convergent with sebecosuchians.

Study of the holotype skull of *Sebecus* (Molnar, 2013) indicated features consistent with terrestrial habits, but not definitively contradicting an amphibious life style. The junior author, in his PhD work in Rio, studied the skeleton of *Baurusuchus salgadoensis* (Carvalho et al., 2005) and found similarities to the limb architecture of (non-avian) theropod dinosaurs (Vasconcellos et al., 2005; Vasconcellos, 2009). These indicate that *Baurusuchus* carried its limbs under the body, parasagittally, unlike living crocodilians. Douglas Riff, also in his PhD work, studied the skeleton of the (ziphodont) baurusuchian *Stratiosuchus maxhechti* (Campos et al., 2001) and found similar features (Riff and Kellner, 2011), confirming that such a posture was likely widespread among sebecosuchian, and even other notosuchian (cf. Pol, 2005; Pol et al., 2012; Nobre, 2004), crocodylomorphs (although Nobre and Carvalho, 2013 describe an exception). Postcranial remains of *Sebecus*, studied by Pol et al. (2012), further indicate terrestrial, if not cursorial, habits. Like tyrannosaurs these crocodylomorphs were probably land-dwelling, not amphibious, creatures.

Daspletosaurus reached a total length of 8–9 metres (Russell, 1970), but it seems likely that *Barinasuchus* would have been shorter than that. *Stratiosuchus* is the only sebecosuchian for which a complete skeletal reconstruction has been published (Riff et al., 2012). The proportion of head length to total length of the reconstructed skeleton appears sufficiently similar to that of the incomplete skeleton of *Baurusuchus salgadoensis* (Carvalho et al., 2005) to suggest that these proportions may have been typical of baurusuchians. Thus these postcrania – the only complete enough – are used to estimate the snout-tail tip length of *Barinasuchus*. In *Stratiosuchus* the skull is approximately one-sixth the total length, and basing one estimate on another, the total length of *Barinasuchus* may have been about 6 metres (fig. 3). These proportions of living crocodilians differ somewhat (Wermuth, 1964) and perhaps they differed between baurusuchians and *Barinasuchus*. The ratio of total length to head length has also been worked out for *Crocodylus porosus* (Bellairs, 1969, p. 471, and references therein) at 7.5:1. The difference from that of *Stratiosuchus* seems due to the relatively longer tail in *C. porosus*. Platt et al. (2011) found that a ratio of 7:1 gives a good estimate of total length for *Crocodylus acutus* in Belize, at least for total lengths to c. 3 metres, and Fukuda et al. (2013) found that ratios from c. 7.0–7.6 were appropriate for individuals of *C. porosus* longer than 3 metres. So if the proportions of *Barinasuchus* were like those of *C. porosus* and *C. acutus*, its total length might have been about 7.5 metres. Wermuth (1964) gives a graph (Abb. 5) of head length against total length for 22 living crocodilian species, expressed

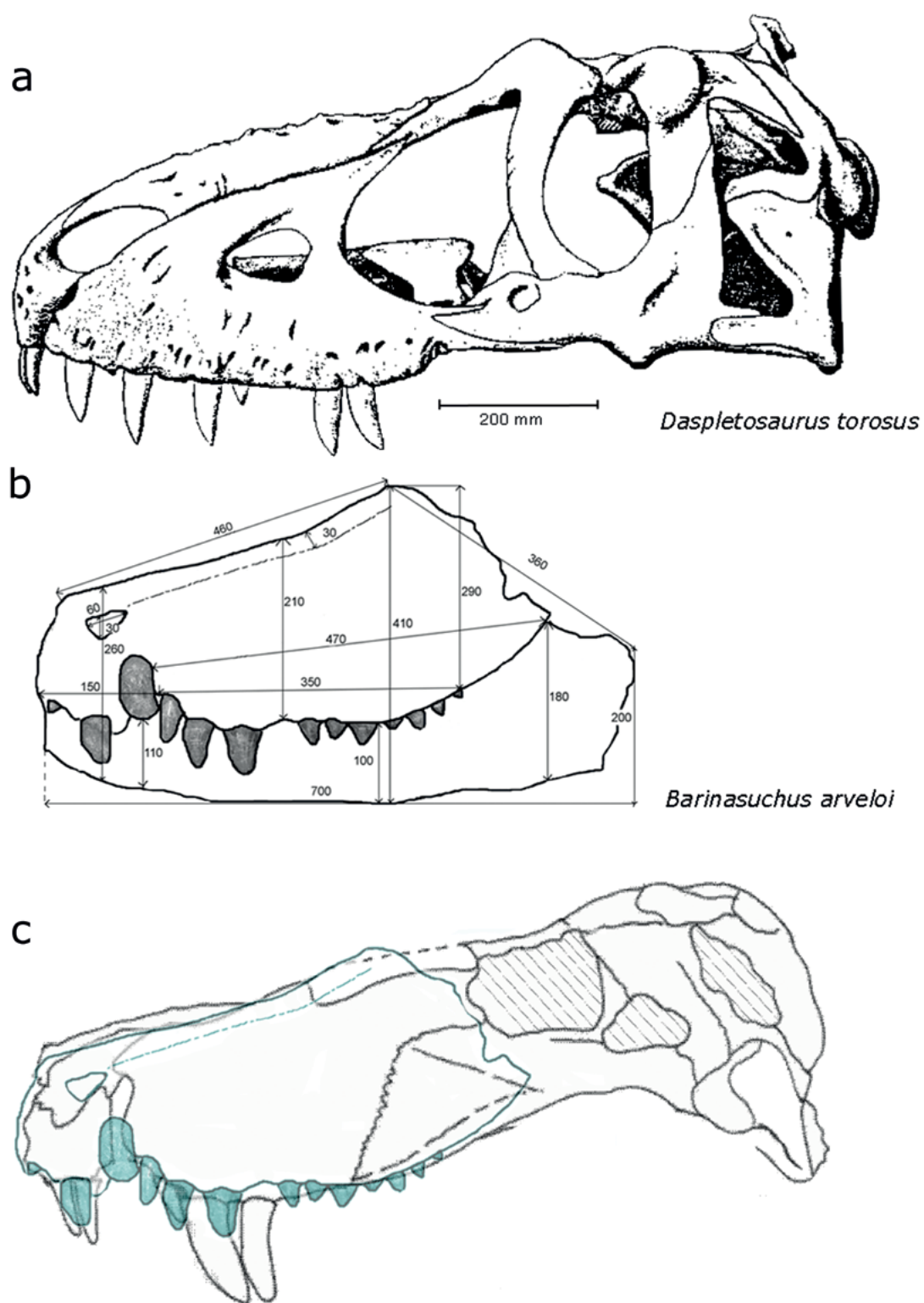


Figure 1. Size comparison of the snout of *Barinasuchus* with the skull of *Daspletosaurus*: a, skull of *Daspletosaurus torosus* (CMN 8506); b, snout and left dentary of the largest known specimen of *Barinasuchus arveloi* (MAAT-0260) with measurements; c, snout of *B. arveloi* superimposed over the outline of the skull of *B. pachecoi* (DGM 299-R), to estimate the length of the *Barinasuchus* skull. (a, modified from Russell, 1970; b, from Paolillo and Linares, 2007; *B. pachecoi* from Carvalho et al., 2005.)

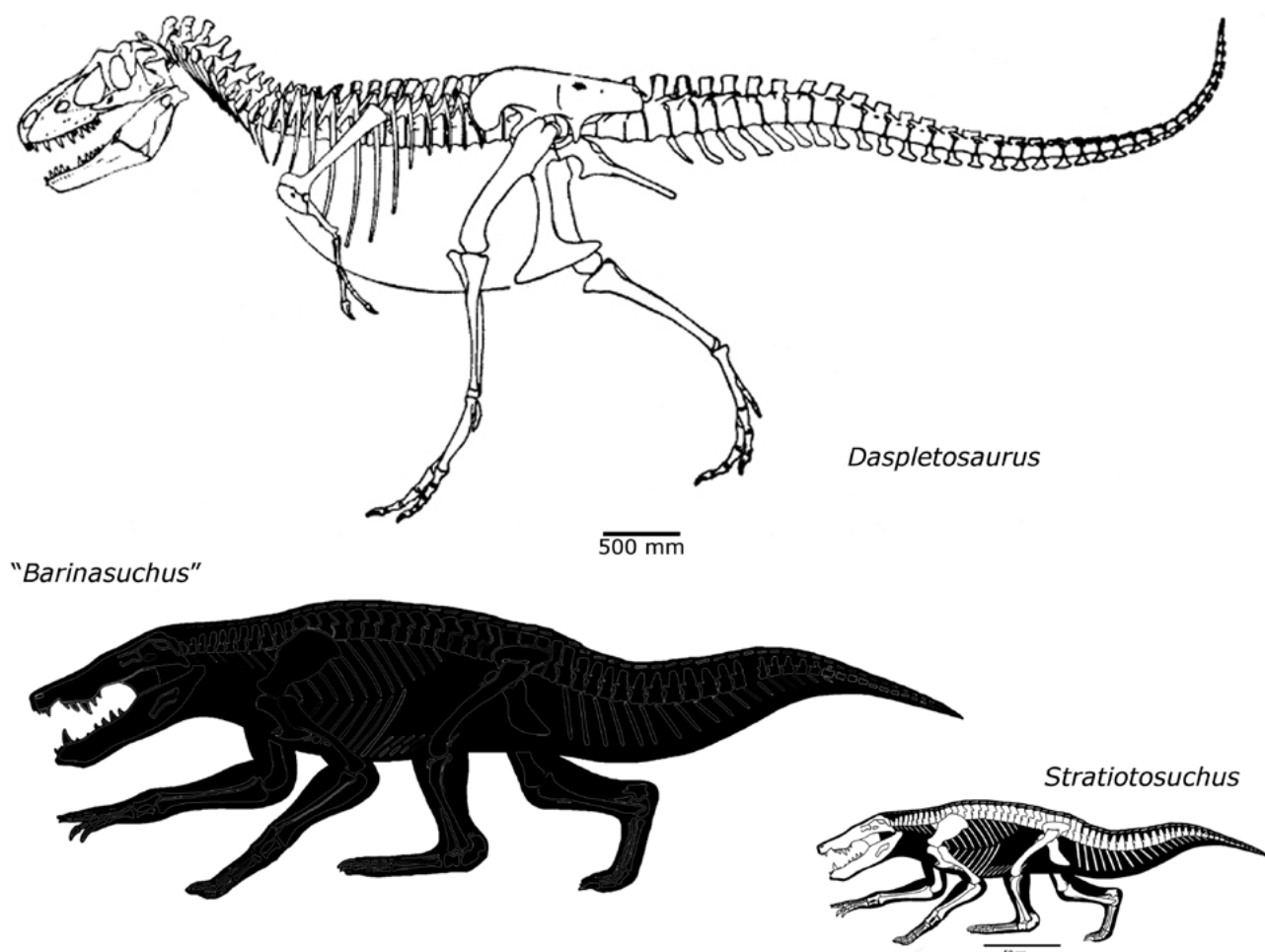


Figure 2. Size comparison of *Barinasuchus* and *Daspletosaurus* (CMN 8506). The silhouette representing *Barinasuchus* is that of *Stratiotosuchus* appropriately enlarged, the actual size of *Stratiotosuchus* is indicated at lower right. (*Daspletosaurus* skeleton from Russell, 1970; *Stratiotosuchus* skeleton modified from Riff et al., 2012.)

in six curves. Depending on which species is used, the total length of *Barinasuchus* would be between about 6.3 to just over 10 metres. So depending on the proportions of head to trunk and to total length, *Barinasuchus* may have been anywhere from about two-thirds to a little over the length of *Daspletosaurus*. But in the absence of contrary evidence the estimate based on the skeleton of *Stratiotosuchus* may be presumed the most likely.

More relevant to its trophic influence would be its mass. Farlow et al. (2005) estimated total length for a suite of extinct mesoeucrocodylians, but included no sebecosuchians, probably for the good reason that their estimates were based on femoral dimensions, and femora at the time were known only for *Stratiotosuchus maxhecti* and had neither been figured nor described. There are no postcranial remains known of *Barinasuchus*, so we use instead the method of Sereno et al. (2001) to estimate mass. Given all the uncertainties involved this must be considered a very approximate value. Using length estimates derived from *S. maxhecti* and *C. porosus*, we find

1,610 and 1,720 kg respectively. This is not *Daspletosaurus*, with an estimated mass of 2,300 kg (Paul, 1988), but is greater than the largest existing non-aquatic mammalian carnivore, *Ursus maritimus*, (maybe to 800 kg, Nowak, 1991), and about the mass of a Black Rhinoceros (Nowak, 1991). Even if the estimated mass is wrong by 50%, *Barinasuchus* was still more massive than any living mammalian carnivore, and than any known from Cenozoic South America. If, on the other hand, the estimates are believable, *Barinasuchus* was as massive as *Allosaurus fragilis* (as estimated by Paul, 1988). Thus we regard *Barinasuchus* as likely having been a significant predator of the time, and as a likely ecological vicar of non-avian theropod dinosaurs.

We assume that large sebecosuchians had similar dietary requirements to (non-avian) theropods of comparable mass. Would such a sebecosuchian have had a physiology comparable to those of tyrannosaurs? After more than forty years of research and discussion, there is still no consensus regarding the physiology of large non-avian theropods (see e.g., Paul, 2012;

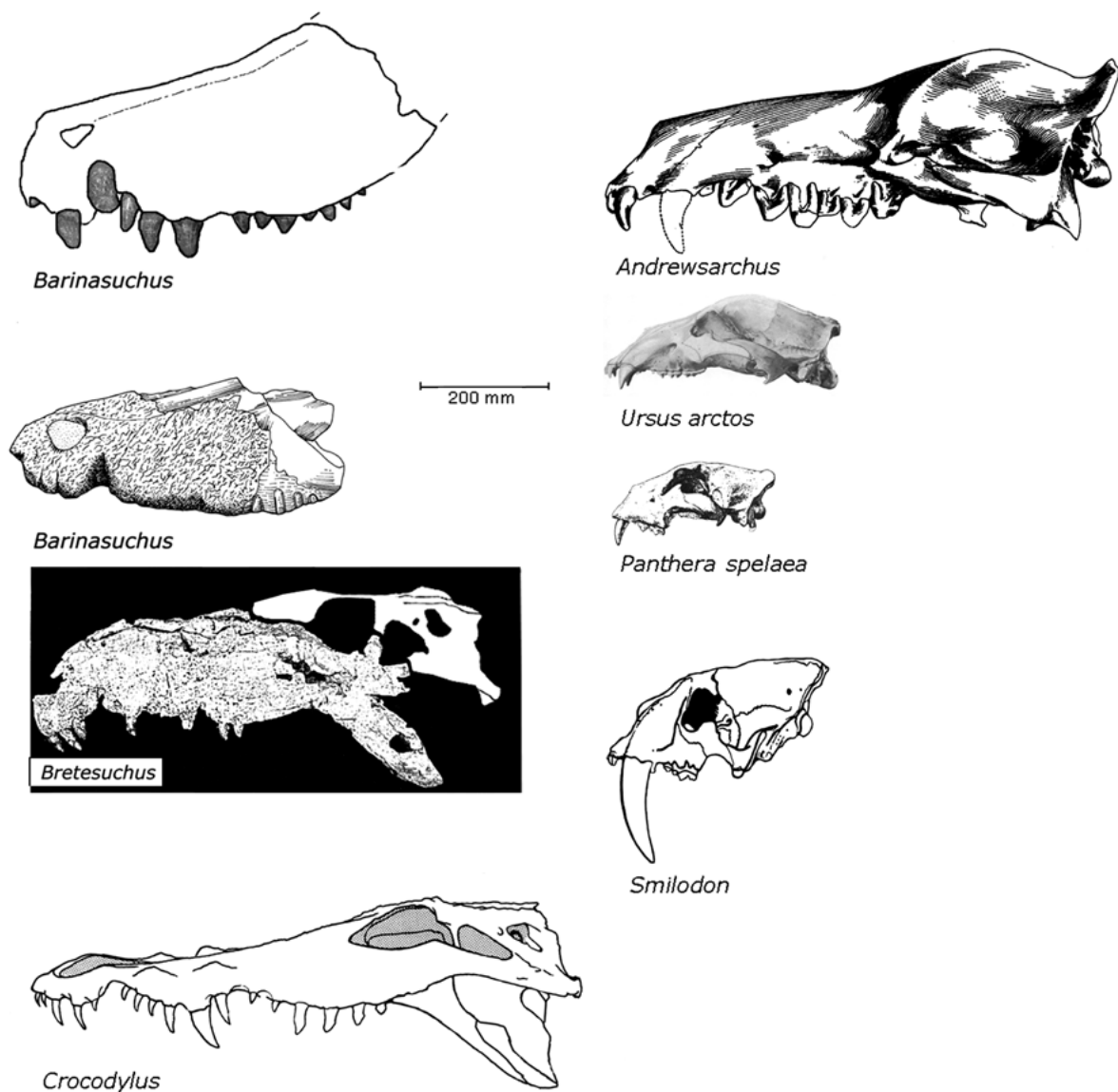


Figure 3. Size comparison of the two known snouts of *Barinasuchus arveloi* with skulls of another large sebecosuchian (*Bretesuchus bonapartei*), *Crocodylus*, and selected carnivorous mammals. The white portion of the image of *Bretesuchus* is intended to indicate the amount of the skull known, not the actual form of the missing portion of the skull. The skull of *Crocodylus* is scaled to the size of the largest known skull of *Crocodylus porosus* according to Greer (1974). (*Barinasuchus* from Paolillo and Linares, 2007, and Buffetaut and Hoffstetter, 1977; *Bretesuchus* modified from Gasparini et al., 1993; *Crocodylus* modified from Schumacher, 1973; *Andrewsarchus* from Osborn, 1924; *U. arctos* from Allen, 1902; *P. spelaea* from Gromova et al., 1964; *Smilodon* from Scheele, 1955.)

Reid, 2012; Ruben et al., 2012). There have been suggestions that the metabolic rates of sebecosuchians were elevated above the rates characteristic of living crocodilians (Seymour et al., 2004), as well as that crocodylomorphs had endothermic ancestors (Seymour et al., 2004), and these rates may have persisted (or re-appeared) in sebecosuchians. It is possible that the physiologies of derived non-avian theropods and sebecosuchians were sufficiently similar that the notion of *Barinasuchus* as an ersatz (non-avian) theropod is reasonable. In the warm to hot climate of

Neogene northern South America (Vanhof and Kaandorp, 2010) large sebecosuchians may have had relatively high metabolic rates, comparable to those of large theropods under similar climatic conditions. Metabolic rates can be estimated from bone histology (but see the caveats of Myhrvold, 2013 regarding published research in this area), but postcranial elements of large Cenozoic sebecosuchians are unknown. Other evidence (from cardiac structure and mitochondrial genome) that elevated metabolic rates may have been plesiomorphic for

crocodylomorphs is summarised by Summers (2005). Even if sebecosuchians did not exhibit physiologies comparable to those of (non-avian) theropods but more like those of modern lepidosaurs, varanid lizards are still important carnivores in modern environments lacking eutherian predators. *Varanus sivalensis* (Falconer, 1868), about the size of mature *Varanus komodoensis*, apparently existed in the presence of significant eutherian carnivores in Siwalik times in southern Asia. More relevant, given that the Paleogene carnivorous mammals of South America were marsupials, is that large varanids, *Varanus komodoensis* (Hocknull et al. 2009) and *V. priscus*, existed along with moderately large carnivorous marsupials in Neogene Australia. This suggests that sebecosuchians would have been important predators regardless of their metabolic rates.

So it seems as late as the middle Miocene (c. 16–11.6 my) in Venezuela (Paolillo and Linares, 2007) and Peru (Espurt et al., 2011), there was a terrestrial predatory archosaur, a kind of ersatz (small) tyrannosaur, likely larger than most contemporaneous mammals (fig. 4). The notion of Cenozoic non-avian dinosaurs in South America is wrong, but apparently there were ecological vicars of large non-avian theropods.

Trophic role of Cenozoic sebecosuchians

This realisation has interesting implications. Contrary to popular perceptions, it has been known that after the Cretaceous–Paleogene extinctions, all terrestrial trophic systems did not all immediately develop their modern cladistic structure (Rautian and Kalandadze, 1989; Rautian and Sennikov, 2001). Contemporary land-dwelling carnivores and herbivores of moderate to large size – larger than 200 kg, about the size of the American black bear (*Ursus americanus*) – are mammals, and archosaurs are generally restricted to being aerial or amphibious carnivores. Lepidosaurs, other than snakes, today reach large size (mass) only in isolated regions, such as the eastern islands of the Indonesian archipelago. The present distribution of the ora *Varanus komodoensis* however, is likely misleading since Hocknull et al. (2009) demonstrated that the ora was found in Queensland early in the Pliocene, and may have originated there.

Sebecosuchians were present in some diversity during the Paleogene and into the Miocene in southern and northern South America. *Zulmasuchus* and *Bretesuchus* lived during the Palaeocene, *Sebecus*, *Sahitisuchus*, *Ayllusuchus* and *Barinasuchus* in the Eocene, and *Langstonia* and *Barinasuchus* in the Miocene. *Bretesuchus bonapartei* (Gasparini et al., 1993) was second only to *Barinasuchus arveloi* among sebecosuchians in size, with a skull almost 600 mm long as preserved (estimated from Gasparini et al., 1993, fig. 2A). *Barinasuchus* occurred in the Eocene of Argentina (MLP 73-III-15-1, Paolillo and Linares, 2007) as well as the Miocene of Venezuela and Peru (Buffetaut and Hoffstetter, 1977). The Eocene material, a premaxilla and symphyseal region of the mandible (Gasparini, 1984), does not derive from an individual as large as the Peruvian or Venezuelan specimens. Nonetheless it, together with *Bretesuchus*, indicates that large land-dwelling crocodylomorphs persisted in South America throughout the Paleogene and into the Miocene.

Until at least Middle Miocene, South America seems to have had an unusual abundance of large reptilian carnivores of all major lineages, with *Titanoboa cerrejonensis* in the Palaeocene (Head et al., 2009), and *Purussaurus*, *Brachygnathosuchus* (presumably) and *Gryposuchus* in the Miocene (Aguilera et al., 2006; Price, 1967; Mook, 1921; Riff et al., 2008), along with *Stupendemys* (Wood, 1976; Bocquentin and Melo, 2006). These are all generally regarded as amphibious, but there were relatively large (non-mammalian) carnivores on the land in addition to sebecosuchians. Large flightless birds, the phorusrhachoid ‘terror birds’, thrived until the Pleistocene (Tambussi and Degrangé, 2013). Some were apparently more than two metres tall (*Kelenken guillermoi* Bertelli et al., 2007), and one form (*Titanis walleri*) migrated into North America as far as Florida (MacFadden et al., 2007), against the ‘tide’ of south-moving placental carnivores.

Archosaurs (including avian theropod dinosaurs) maintained a prominent role as land-dwelling carnivores in the South American Cenozoic. This role was shared with carnivorous marsupials, even if Marshall (1977) reports that the large and earlier-prominent sparassodont borhyaenids became less diverse in the Late Oligocene and Early Miocene with the diversification of phorusrhachoids and the appearance of the more derived thylacomyid marsupials. The trophic roles of carnivorous theropods were not always and everywhere rapidly (or immediately) occupied by mammals after the Cretaceous–Paleogene extinction. This is already known of course, what is new is the recognition that the role of tyrannosaur-size crocodylomorph archosaurs was also maintained and persisted through the Paleogene and into the Neogene. We predict that other large Cenozoic sebecosuchians will be found.

Clearly, the trophic roles available to sebecosuchians persisted through the Paleogene and into the Neogene in northern South America because the sebecosuchians themselves persisted well into the Miocene. Presumably the trophic roles of smaller (non-avian) theropods also persisted after the Cretaceous–Paleogene extinctions in South America, and were occupied by the smaller sebecosuchians. The smaller *Zulmasuchus querejazus* appears soon after the Cretaceous–Paleogene extinction, in the Tiupampan (Danian)(Buffetaut and Marshall, 1991) about 65–64 million years ago (Woodburne et al., 2014), so within at most 2 million years of the extinction.

This being so, we might ask if sebecosuchians survived, why not (non-avian) theropods (fig. 5)? Perhaps if *Daspletosaurus* were somehow brought into Middle Miocene northern South America they would have survived. Presumably the extinction of (non-avian) theropods was not due to trophic factors in South America. Presumably, also, there was after all some difference between the sebecosuchian lineage and that of (non-avian) theropods that accounts for why all of the latter forms became extinct, although some, at least, of the sebecosuchian lineages survived.

Dying dinosaurs and surviving crocodylomorphs

It is possible that the carnivorous trophic roles of some (non-avian) theropods were already held, at least in part, by sebecosuchians in the Bauru Basin of Brazil before the

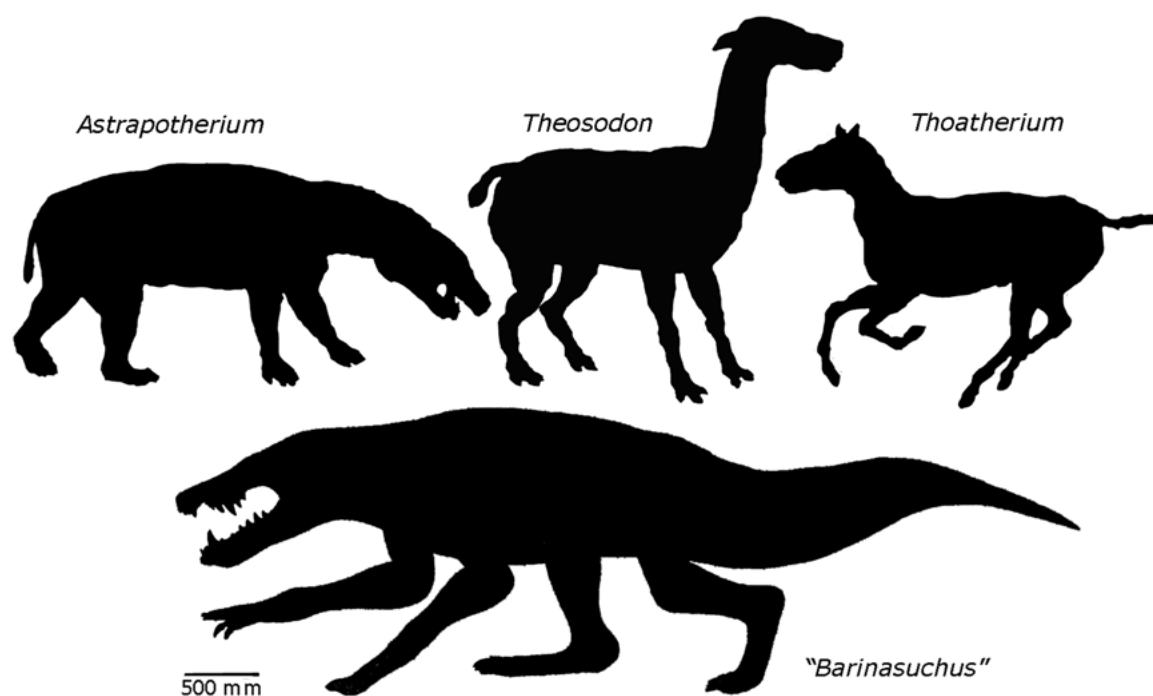


Figure 4. Size comparison of *Barinasuchus* (here represented by the silhouette of *Stratiotosuchus*) with contemporaneous large South American mammals. These particular mammalian taxa are Patagonian, and may not have lived in the same region as the northern South American *Barinasuchus*.

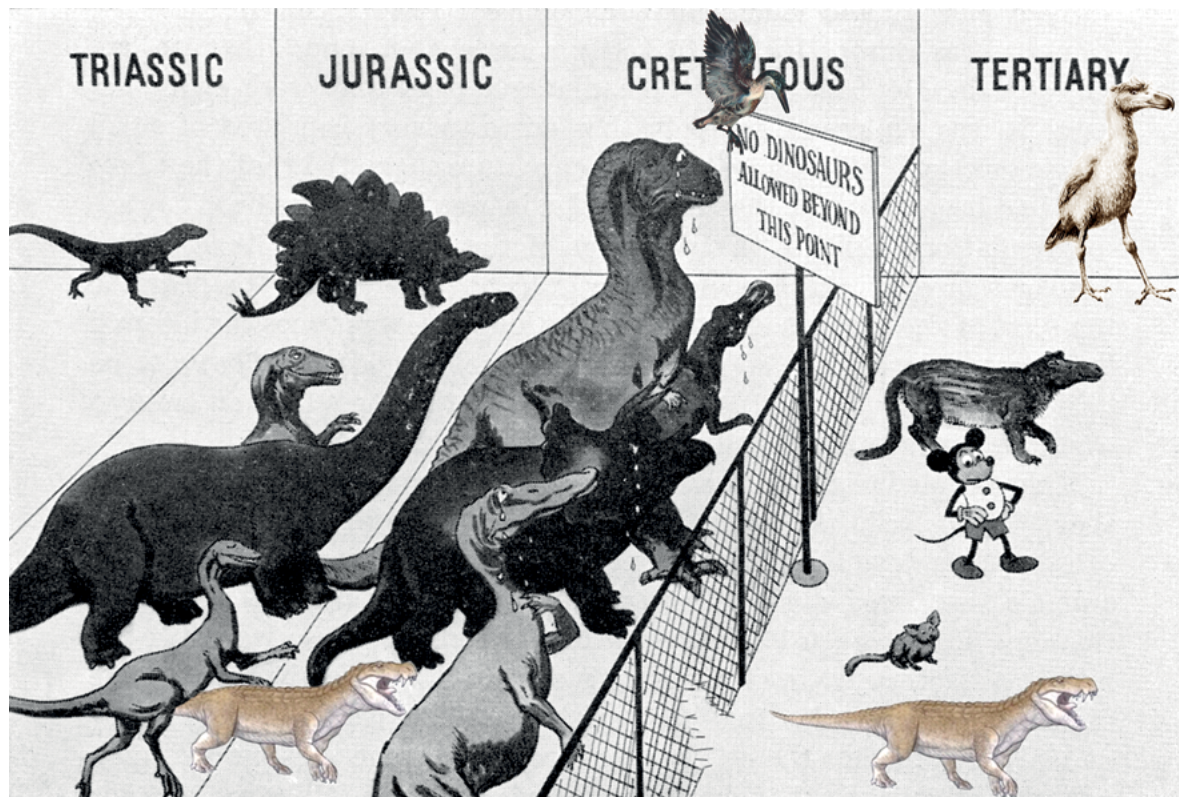


Figure 5. Sebecosuchians (or maybe sebecids) did not seem to notice the Cretaceous-Paleogene extinctions. Modified from cartoon by Michael Ramus in Jepsen, 1964: reprinted by permission of American Scientist, magazine of Sigma Xi, The Scientific Research Society.

Cretaceous-Paleogene extinctions. Non-avian theropods were not entirely absent (Azevedo et al., 2013; Méndez et al., 2012; Bittencourt and Langer, 2011), but their remains are uncommon (Carvalho et al., 2010), often only teeth (Bittencourt and Langer, 2011), whilst a diversity of sebecosuchian (and other) crocodylomorphs are represented by cranial and postcranial material (Carvalho et al., 2010, 2011; Campos et al., 2011; Iori et al., 2013; Martinelli and Teixeira, 2015; Riff et al., 2012). There are (yet) no theropod skulls, but there at least 11 skulls, of varying degrees of completeness, of sebecosuchians - one each of *Aplestosuchus*, *Gondwanasuchus* and *Pissarachampsia*, two of *Campinasuchus* and *Stratiosuchus* and four of *Baurusuchus*, one of which is undescribed (Carvalho et al., 2011). Additionally, these (non-avian) theropods seem to have been usually substantially smaller than contemporaneous Patagonian forms (Bittencourt and Langer, 2011). Carvalho et al. (2010) argue that during the late Cretaceous the Bauru Basin, like much of South America (Chumakov et al., 1995; Hay and Floegel, 2012), was subject to a hot, arid climate with marked seasonality. This climatic regime, apparently suitable for notosuchian crocodylomorphs, was apparently not well-suited to (non-avian) dinosaurs. Thus we suggest that (non-avian) theropods in this part of the world were already relatively rare. Whatever caused their extinction here at the end of the Cretaceous, perhaps some intensification of the aridity, affected already-stressed and presumably reduced (non-avian) theropod populations. Sebecosuchians not only survived but were able to successfully colonize regions not subject to the arid, seasonal climate characteristic of the Late Cretaceous Bauru Basin.

Similar arid zones occurred in much of what is now sub-Saharan African, as well as India and Madagascar (Chumakov et al., 1995; Hay and Floegel, 2012). This, together with the faunal situation in the Bauru Basin, suggests that perhaps crocodylomorphs in these lands occupied other trophic roles elsewhere held by dinosaurs. Chris Brochu suggested (pers. comm., 2013) that perhaps the trophic roles of ornithischians here came to be occupied by crocodylomorphs during the Cretaceous. The apparently herbivorous diet (Buckley et al., 2000; Sereno and Larsson, 2009; Andrade and Bertini, 2008) of some notosuchians and their upright stance (Nobre, 2004; Pol, 2005) suggest that they may have been competitors (or replacers) of small ornithischians. Notosuchians (e.g., *Araripesuchus*, *Uruguaysuchus*, *Mariliasuchus*, *Sphagesaurus*, and possibly *Labidrosuchus*) occurred in South America along with small (herbivorous) ornithomorphs that are only sparsely represented in the fossil record (Coria and Cambiaso, 2007). Beyond South America, there were possibly herbivorous crocodylomorphs in Africa (e.g., *Araripesuchus*, *Libycosuchus*, possibly *Pakasuchus*) during the Late Cretaceous when ornithomorphs are absent from the fossil record (Lamanna et al., 2004) and hence possibly already extinct there. In Madagascar, "*Stegosaurus*" *madagascariensis*, represented by two isolated teeth (Piveteau, 1926), now attributed to an ankylosaur (Maidment et al., 2008), is the only recorded ornithischian. Madagascar is also the home of the presumably herbivorous crocodylomorph *Simosuchus clarki* (Buckley et al., 2000). This situation may also obtain for India, with two or three specimens of ornithischians - also thyreophores (Chakravarti, 1934; Yadagiri and Ayyasami,

1979) - known only from the Jabalpur region and Tamil Nadu, and apparently absent elsewhere (cf. Prasad, 2012; Prasad and Sahni, 2009). Notosuchians are also reported (Goswami et al., 2013; Mohabey, 1996), although the fossil record in India, as in Madagascar, is quite incomplete. Ornithischians seem to have been uncommon in some parts of South America (unknown in the Bauru Basin), rare in Madagascar and perhaps even extinct in Africa during the Late Cretaceous, well before the Cretaceous-Paleogene event - except for intrusion of hadrosaurs into South America in Campanian-Maastrichtian time. The herbivorous crocodylomorphs that were prominent in those lands may have occupied, at least in part, the trophic role of small ornithischians.

Caveats

We have extended our observations on the large size of Cenozoic sebecosuchians to speculations on the extinctions - and survivals - at the end of the Cretaceous, possibly to the degree commented on by Mark Twain ("... wholesale returns of conjecture out of such a trifling investment of fact." Clemens, 1883). Thus there are several caveats to the speculations presented here.

Not all workers agree on the existence of the Sebecosuchia, although it seems the current consensus (Iori and Carvalho, 2011; Pol and Powell, 2011; Pol et al., 2012, 2014; Bronzati et al., 2012). If the ziphodont taxa here discussed do pertain to two separate lineages, sebecids and baurusuchians as some suggest (Holliday and Gardner, 2012; Riff and Kellner, 2011), then the survival of sebecid crocodylomorphs through the Cretaceous-Paleogene extinctions becomes problematic, depending on the date of origin of the sebecid lineage. As mentioned previously, the oldest sebecid, *Zulmasuchus querejazus*, occurs within about 2 million years of the end of the Maastrichtian. This suggests that the lineage may have originated in the Cretaceous and survived. If so, the conclusions regarding the survival of ziphodont crocodylomorphs in South America across the Cretaceous-Paleogene boundary still stand.

Barinasuchus is represented by only three specimens, all cranial, all incomplete, only two of which represent more than about 10% of the skull and those lack the orbital and postorbital regions. Thus the length and mass estimates are necessarily inexact, because an incomplete skull is used to estimate the skull length, from which the total length is then estimated, and from that the mass. Obviously there is the possibility of error accumulating from estimates based on other estimates that may not be entirely accurate. But our argument does not require complete accuracy, only an approximate figure. We seriously doubt that a creature with a snout over 600 mm long was a small animal, less than three metres in length. As mentioned previously, even if the mass estimate is too large by 50%, *Barinasuchus* was still larger than any contemporaneous land-dwelling mammalian carnivore, and as large as the greatest recorded mass of contemporary land-dwelling carnivores.

Although our argument is based on the Bauru Basin of Brazil, it should be noted that Coria and Cambiaso (2007) attribute the scarcity of small ornithischian remains in the Cretaceous of Patagonia to taphonomic bias. The Late

Cretaceous non-marine record for Africa, India and Madagascar is still very incomplete, so interpretation of their trophic systems is quite speculative. Nonetheless, ornithischians are prominent in the comparably incomplete non-marine tetrapod fossil records of the early Cretaceous of Australia (Kear and Hamilton-Bruce, 2011), and the Late Cretaceous of New Zealand (Molnar and Wiffen, 1994) and Antarctica (Coria et al., 2013, and references cited there). This lends some support to our speculations, and also suggests that although notosuchians may have occurred in Australasia and Antarctica at these times, they were not as prominent and diverse members of the faunas as in South America.

Conclusions

The holotype snout of *Barinasuchus arveloi* was equivalent in size to that of *Daspletosaurus torosus*, and we estimate that the skull was likely nearly the same size. Sebecosuchians were likely land-dwelling predators, implying that such dinosaur-like forms persisted in South America from the Cretaceous well into the Miocene. So in a trophic, ecological (metaphoric) sense the notion of Cenozoic (non-avian theropod) dinosaurs in South America was correct. And there were large avian theropods, phorusrhacids, as well.

In South America, at least, the carnivorous role of the food webs of moderate to large terrestrial tetrapods did not immediately turn over from archosaurs to mammals with the extinction of dinosaurs. The modern structure was likely not achieved until, at the earliest, sometime during the Miocene with the diminution of sparassodont marsupials and phorusrhacids and the entrance of carnivorans from North America. The herbivorous role, however, did turn over (presumably) rapidly with the extinction of the sauropod and ornithischian dinosaurs and the probably herbivorous notosuchian crocodylomorphs, and their replacement by xenarthrans, meridiungulates and other mammals.

Sebecosuchians, (or maybe predatory ziphodont notosuchians, the sebecids) survived the Cretaceous–Paleogene extinctions, although as apparent trophic vicars of non-avian theropods this is contrary to expectation.

The absence of small theropods and ornithischians from the Bauru Basin in the Late Cretaceous suggests that the final extinction of some (non-avian) dinosaurian lineages may have been earlier here than elsewhere. This may well have been due to the hot, arid, seasonal climate prevalent in that Basin to which crocodylomorphs were more suited as proposed by Carvalho et al. (2010). Here the trophic role of moderately large to large land-dwelling carnivore may have turned over some time before the end of the Maastrichtian.

Ornithischian dinosaurs apparently became extinct near the end of the Early Cretaceous in Africa (Lamanna et al., 2004), and very rare in India and Madagascar. They may have been replaced trophically by herbivorous notosuchian crocodylomorphs. Thus some ornithischian lineages, usually thought to have become extinct at the end of the Maastrichtian, became very rare in some parts of the southern hemisphere, and may have actually died out in others, more than 30 million years earlier.

Trophic turnover at higher taxonomic levels (e.g., Archosauria, Lepidosauria, Mammalia) was not always coincident with faunal turnover at lower taxonomic levels (e.g., Ornithischia, Sauropodomorpha, Abelisauria). Archosaurs retained a prominent role as carnivores in South America in spite of the extinction of (non-avian) theropods. And also in spite of the taxonomic turnover of land-dwelling herbivores with the extinction of herbivorous (non-avian) dinosaurs and crocodylomorphs.

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NOTE ADDED IN PROOF

Our assertion, following Lamanna et al. 2004, that ornithischian remains are unknown from the Upper Cretaceous of Africa is incorrect. Discussion with Matt Lamanna and Octávio Mateus revealed that an isolated pedal phalanx of a hadrosauroid was found in middle Maastrichtian rocks in Angola (Mateus et al., 2012). Hadrosauroid remains have also recently been found in latest Campanian to Maastrichtian rocks of the Sultanate of Oman (Buffetaut et al., 2015), part of the Afro-Arabian plate. This brings the Afro-Arabian record into agreement with those of Madagascar and India, where ornithischian remains are present but rare. However, it may be that in Africa, as in South America, hadrosauroids migrated into the region late in the Late Cretaceous, and ornithischians were absent in the pre-Campanian Late Cretaceous. If so, this remains to be demonstrated.

Buffetaut, E., Hartman, A.-F., Al-Kindi, M. and Schulp, A.S. 2015. Hadrosauroid dinosaurs from the Late Cretaceous of the Sultanate of Oman. *Plos One* 10(11): e0142692. doi:10.1371/journal.pone.0142692.

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