

SPINOSAURS AS PHYTOSAUR MIMICS: A CASE OF CONVERGENT EVOLUTION BETWEEN TWO EXTINCT ARCHOSAURIFORM CLADES

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Abstract Spinosaurids are a highly morphologically specialized clade of large tetanuran theropod dinosaurs, characterized by their proportionally long, narrow snouts and conical teeth with fluted surfaces. The unusual morphology of spinosaurids has been usually compared with modern crocodylians, but distinct differences between them have been reported as well. Here, numerous craniodental characters that are shared by spinosaurids and large, robust phytosaurs often termed as “brachyrostral” forms are reviewed. Phytosaurs are a clade of carnivorous archosauriforms that resemble crocodylians in overall morphology, and as such a similar lifestyle has been inferred for them as well. Although based on preliminary observations, the shared craniodental characters of spinosaurids and “brachyrostral” phytosaurs, including those not shared with crocodylians, raise the possibility that at least some aspects of the lifestyle of these extinct archosauriform clades were more similar to each other rather than to that of crocodylians.

Keywords: Dinosauria; Theropoda; Spinosauridae; Archosauriformes; Phytosauria; Convergent evolution

INTRODUCTION

Spinosauridae Stromer, 1915 is a clade of large-bodied theropod dinosaurs characterized by their proportionally long, narrow skull with fluted conical teeth, remarkably robust forelimbs with enlarged manual unguals, and tall neural spines on their dorsal vertebrae (Serenó et al., 1998; Holtz, 1998; Ibrahim et al., 2014; Hone & Holtz, 2017). Typically, this group is considered as a sister taxon of Megalosauridae Fitzinger, 1843, together forming a clade Megalosauroidea Fitzinger, 1843 within Tetanurae Gauthier, 1986 (Benson, 2010; Carrano et al., 2012; Hone & Holtz, 2017); meanwhile, at least one study suggested an alternative phylogenetic relationship, which recovered Spinosauridae as a first major clade to diverge from the lineage towards Allosauroidea Marsh, 1878, with Megalosauridae found to be the next major clade to branch off within this lineage (Rauhut & Pol, 2019).

Nevertheless, the distinctive, unusual morphology of spinosaurids strongly implies a very different mode of lifestyle compared to other similarly-sized theropods, and their basic biology and ecology have been of great interest to palaeontologists since their initial discovery and description (Ibrahim et al., 2014; Hendrickx et al., 2016; Hone & Holtz, 2017, 2021). While the palaeoecology of spinosaurids is still debatable – partly due to their rare and often fragmentary fossil record (Hone et al., 2010; Hone & Holtz, 2017 – the general consensus is that these theropods primarily preyed on fish (Charig & Milner, 1986; Sereno et al., 1998; Milner, 2003; Amiot et al. 2010; Ibrahim et al., 2014; Hendrick et al., 2016; Hone & Holtz, 2017). This assertion is supported not only by direct evidence from a *Baryonyx walkeri* Charig & Milner, 1986 specimen with partly digested fish scales in its gut contents (Charig & Milner, 1997) but also by a superficial resemblance of spinosaurid craniodental morphology

to that of modern crocodylians (e.g., Sereno et al., 1998; Holtz, 1998; Rayfield et al., 2007). Indeed, crocodylians and spinosaurids share a number of key features such as conical teeth with fluted surfaces, sinusoidal tooth rows, and an expanded “rosette” bearing enlarged teeth at the anterior tips of their premaxilla and dentary (e.g., Charig & Milner, 1986; Vullo et al., 2016; Hone & Holtz, 2017), so it is certainly reasonable to assume these traits are convergently acquired in both clades due to similar ecological pressure.

However, although it is true that spinosaurids are so similar to crocodiles that they have been often called “crocodile mimics” (Serenó et al., 1998; Holtz, 1998), there are some significant differences as well. The skulls of spinosaurids were not dorsoventrally flattened like those of crocodylians, but rather flattened laterally like those of other theropod dinosaurs (Vullo et al., 2016; Hone & Holtz, 2021). Furthermore, crocodylians do not show down-turning of their snout or a “rosette” at the tip even in the largest ones such as *Sarcosuchus imperator* de Broin & Taquet, 1966 (Datta et al., 2021), a condition that is dissimilar to the downturned “rosette” of spinosaurids (e.g., Dal Sasso et al., 2005). The relative positions of the orbits and nares also show differences (Hone & Holtz 2017, 2019, 2021). These differences suggest that although spinosaurids and crocodiles may have had largely similar ecologies, there were also some notable distinctions, or at least functional differences, in some of their craniodental traits. Vullo et al. (2016) have already pointed out that various parts of the spinosaurid jaws actually bear more resemblances to those of pike conger eels than to those of crocodylians.

Phytosaurs were members of another early archosauriform group that is very similar in general morphology to crocodylians (e.g., overall body shape, elongated snout, conical teeth), and because of their striking similarities to

crocodiles, the ecology of these animals has also been of great interest (e.g., Hunt, 1989, 1994; Stocker & Butler, 2013; Datta et al., 2021). However, not all phytosaurs have a similar appearance, and it has been confirmed that there are notable differences between taxa in the shape of the skull and the shape of the teeth. Hunt (1989) noted three distinct skull morphotypes present among phytosaurs, namely: a morphotype with a slender, elongated snout filled with relatively small, homodont teeth, resembling modern gharials (“dolichorostral” *sensu* Hunt, 1994); a massive, robust-snouted morphotype with heterodont dentition (“brachyrostral” *sensu* Hunt, 1994); and an intermediate form between “brachyrostral” and “dolichorostral” morphotypes (“altirostral” *sensu* Hunt, 1994). Later, Hungerbühler (2000, 2002) pointed out that the distinction between the “altirostral” and “brachyrostral” skull morphotypes is ambiguous, and these are largely identical to each other. Although there remains a possibility that the “brachyrostral” and “dolichorostral” morphotypes may represent sexual dimorphs within one or another phytosaur species (e.g., Zeigler et al., 2003; Hunt et al., 2006), the general consensus is that these two different morphotypes at least differed in their ecological mode, that is, phytosaurs with “dolichorostral” skulls (e.g., *Parasuchushis lopi* Lydekker, 1885) were ecologically analogous to modern gharials, and primarily preyed on small fish, while “brachyrostral” forms (e.g., *Machaeroprotopus mccauleyi* (Ballew, 1989), *Nicrosaurus kapffi* (Meyer, 1860), *Redondasaurus gregorii* Hunt & Lucas 1993) were also capable of predation on relatively larger animals such as terrestrial tetrapods (e.g., Hunt, 1989, 1994; Hungerbühler, 2000; Kimmig & Arp, 2010; Kimmig, 2013; Bestwick et al., 2021; Datta et al., 2021). Indeed, the landmark-based analysis of Datta et al. (2021) found that later-diverging phytosaurs tend to have a more “brachyrostral” skull compared to early-diverging forms, which would further contradict the ‘sexual dimorphism’ hypothesis.

Various hypotheses have been proposed regarding the function of the unique craniodental features of “brachyrostral” phytosaurs (e.g., Hungerbühler, 2000; Datta et al. 2021). Importantly, the results of the geometric morphometric analysis of Datta et al. (2021) show that while there are some similarities between “brachyrostral” phytosaur skulls and large crocodilian skulls in dorsal view, remarkable differences exist in their lateral views, that is, later-diverging phytosaur skulls tend to have a dorsoventrally tall and downturned “rosette” at the tip of their snout. Such differences indicate that although considering their general resemblance there would have been a rather great similarity between the ecologies of phytosaurs and modern crocodilians (e.g., Stocker & Butler, 2013), at least in some aspects of their lifestyle and/or functions of their unique craniodental features, “brachyrostral” phytosaurs were not analogous to modern crocodilians.

This work documents that numerous aspects of the skulls

and teeth of two archosauriform clades often compared to modern crocodilians, i.e., Spinosauridae and Phytosauria Meyer, 1861 (and, from the latter group, mainly the later-diverging forms with “brachyrostral” skull morphotype), are in fact more similar to each other than to those seen in crocodilians. This preliminary comparison also offers certain insights into the widely debated and still enigmatic palaeoecology of both spinosaurids and phytosaurs, and presents another interesting case of convergent evolution between fossil clades.

Institutional abbreviations: FSAC, Faculté des Sciences Ain Chock, Casablanca, Morocco; MSNM, Museo Civico di Storia Naturale, Milan, Italy.

NOTES ON THE TAXONOMY

Of note, the taxonomy of some specimens or taxa discussed in this work is controversial. Specimen MSNM V4047 is a large spinosaurine snout from the Cenomanian “Kem Kem Beds” of Morocco, and was initially reported as *Spinosaurus* cf. *S. aegyptiacus* (Dal Sasso et al., 2005). A view that this specimen is indeed referable to *Spinosaurus aegyptiacus* Stromer, 1915 has been widely accepted, and MSNM V4047 was used as the basis for reconstructing the upper jaw morphology of this taxon in numerous studies (e.g., Dal Sasso et al., 2005; Bertin, 2010; Kellner et al., 2011; Ibrahim et al., 2014, 2020; Hone & Holtz, 2017, 2021). Some recent studies, however, have questioned this assumption, and suggested that MSNM V4047 might belong to another contemporaneous spinosaurine taxon, *Sigilmassasaurus brevicollis* Russell, 1996 (Arden et al., 2019; Lakin & Longrich, 2019). *Sigilmassasaurus brevicollis* itself is a controversial taxon, viewed by some as a junior synonym of *Spinosaurus aegyptiacus* (Ibrahim et al., 2014, 2020; Smyth et al., 2020) but considered by others as a distinct taxon (Evers et al., 2015; Arden et al., 2019; Lakin & Longrich, 2019; Hone & Holtz, 2021; McFeeters, 2021). In light of these controversies, the taxon represented by MSNM V4047 is referred to as cf. *Spinosaurus aegyptiacus* in this work. *Oxalaia quilombensis* Kellner, Azeveno, Machado, Carvalho and Henriques, 2011 was regarded as a junior synonym of *Spinosaurus aegyptiacus* by Smyth et al. (2020), yet subsequent studies have supported its validity (Lacerda et al., 2022; Isasmendi et al., 2022). Here, *Oxalaia quilombensis* is provisionally regarded as a valid taxon.

Redondasaurus Hunt & Lucas, 1993 is a phytosaur genus from the Triassic of New Mexico, regarded as a junior synonym of *Machaeroprotopus* Mehl, 1916 by some authors (e.g., Hungerbühler et al., 2013), but considered as a valid genus by others (e.g., Hoffman et al. 2021). Reassessment of the taxonomy of phytosaurs is beyond the scope of this work, and this study chooses to use the name *Redondasaurus* simply for the sake of convenience.

RESULTS

To identify and evaluate potentially convergently acquired traits, the craniodental anatomy of spinosaurids was compared with that of phytosaurs through an extensive review of the literature on their osteology. Then, based on the results of a comprehensive literature on the biomechanics or ecomorphology of various amniotes, including phytosaurs and spinosaurids, possible functional similarities of these convergently shared characteristics between the two groups are inferred.

The shared morphological similarities between spinosaurid theropods and brachyrostral phytosaurs include: 1 - anterior ends of premaxilla and dentary rounded, laterally and ventrally expanded, and bearing enlarged

teeth (this morphology represents the so-called “rosettes”); 2 - a concavity posterior to the premaxillary “rosette” that bears smaller teeth and which the lower jaw “rosette” when the mouth is closed, concavity accompanied by a medial constriction of this part of the snout; 3 - a ventrally convex margin of the upper jaw behind the aforementioned concavity, bearing enlarged teeth; 4 - a down-turned shape of the upper jaw towards its tip so that the anteroventral part of the non-dentigerous region of premaxillary “rosette” is at a similar level with the tooth-row in the more posterior jaw region; 5 - a laterally flattened snout that is moderately deepened dorsoventrally, unlike the dorsoventrally compressed condition seen in crocodylians; 6 - relatively small size of the antorbital fenestra; 7 - a bony palate that is formed by medial exten-

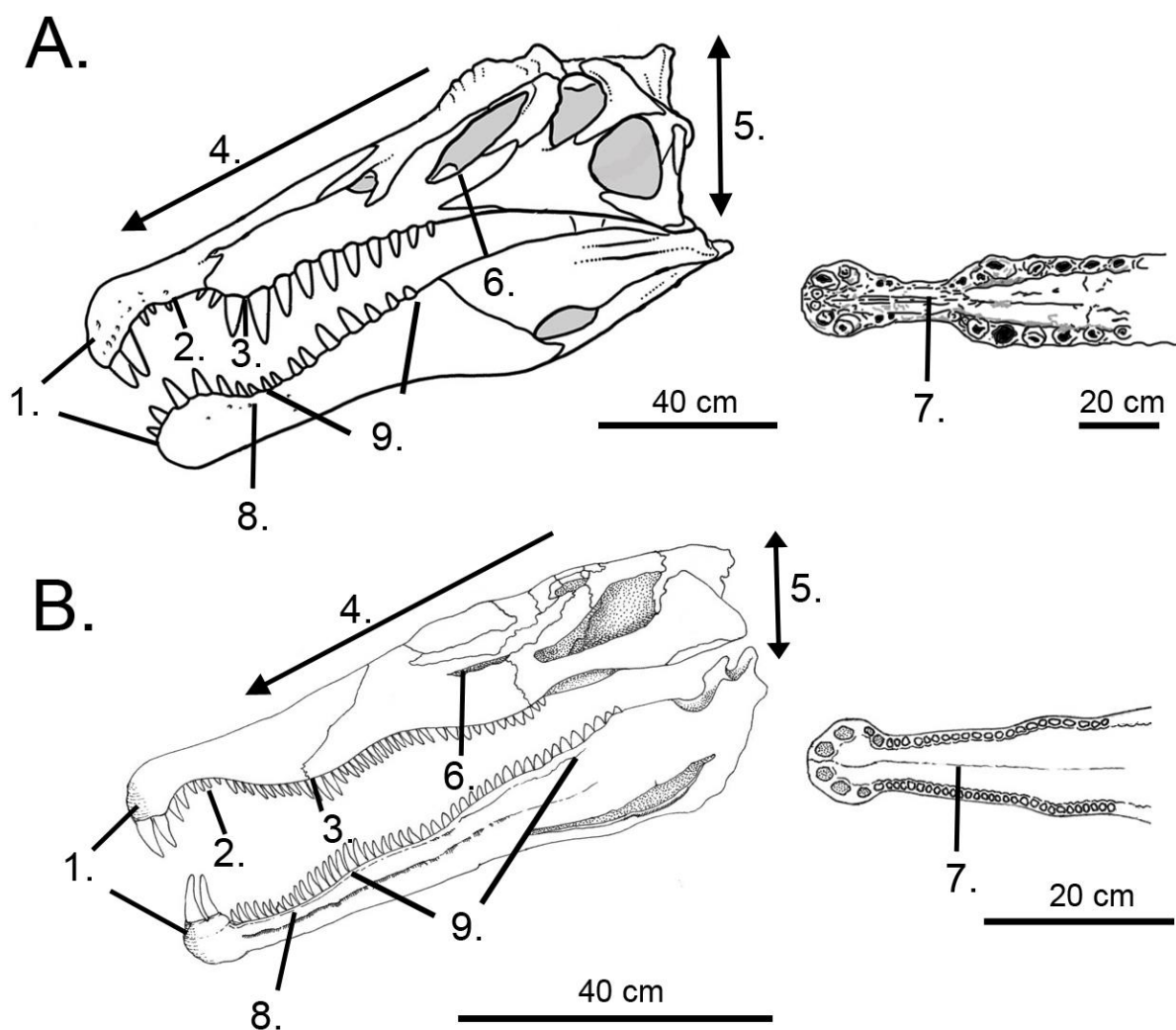


Fig. 1. Convergently shared craniodental characters between Spinosauridae (A) and Phytosauria with “brachyrostral” skull (B). Characters: 1. anterior ends of premaxilla and dentary are rounded, laterally and ventrally expanded and bear enlarged teeth (“rosettes”); 2. a concavity posterior to the premaxillary “rosette” that bears smaller teeth that accommodates the lower jaw “rosette” when the mouth is closed, accompanied by a medial constriction of this part of a snout; 3. a ventrally convex margin of the upper jaw behind concavity bearing enlarged teeth; 4. down-turn of the upper jaw towards its tip so that the anteroventral part of the non-dentigerous region of the premaxillary “rosette” is at the same level with the tooth row in more posterior region; 5. laterally flattened snout that is moderately deepened dorsoventrally, unlike the dorsoventrally compressed condition in crocodylians; 6. relatively small size of an antorbital fenestra; 7. a bony palate that is formed by medial extensions of adjacent bones (e.g., premaxilla, maxilla); 8. a concavity in the anterior part of the dentary that receives a ventral expansion of the upper jaw; 9. lower teeth behind the dentary “rosette” significantly smaller than those of the “rosette”. Images used in A are modified from Bertin (2010) and Ibrahim et al. (2020), and those of B are modified from Spielmann & Lucas (2012).

sions of the adjacent bones (e.g., premaxilla, maxilla); 8 - a concavity at the anterior part of the dentary that receives a ventral expansion of the upper jaw; 9 - the lower teeth behind the dentary “rosette” being significantly smaller than those of the “rosette” (Charig & Milner, 1986; Sereno et al., 1998; Witmer, 1997; Hungerbühler, 2000; Dal Sasso et al., 2005; Hunt et al., 2006; Stocker, 2010; Stocker & Butler, 2013; Butler et al., 2014; Lautenschlager & Butler, 2016; Hone & Holtz, 2017, 2020; Datta et al., 2021; Fig. 1).

Intriguingly, it appears that overall evolutionary trends of cranial morphology documented in phytosaurs and spinosaurids are broadly similar as well. A landmark-based analysis of Datta et al. (2021) found that later-diverging phytosaurs tend to have a broader premaxillary “rosette” that is also more dorsoventrally thickened and downturned compared to early-diverging ones (Fig. 2A). Within spinosaurids, in later-diverging taxa such as cf. *Spinosaurus aegyptiacus* and *Oxalaia quilombensis*, the premaxillary “rosette” is very expanded, nearly rounded in dorsal or ventral views, whereas in early-diverging spinosaurids like *Baryonyx walkeri* or *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson, Wilson, 1998, it is narrower and more oval in outline

(Dal Sasso et al., 2005; Bertin, 2010; Kellner et al., 2011; Fig. 2B). Additionally, the anteriormost part of the premaxillary “rosette” is even more downturned in cf. *Spinosaurus aegyptiacus* compared to early-diverging spinosaurids (e.g., *Baryonyx walkeri*, *Irritator challengeri* Martill, Cruickshank, Frey, Small, Clarke, 1996) so that this region is about the same level with the maxillary tooth row (Dal Sasso et al., 2005; Fig. 2B). Meanwhile, in early-diverging spinosaurid taxa, the same premaxillary region sits above the level of the maxillary tooth row (Charig & Milner, 1986; Dal Sasso et al., 2005).

The main conclusion of Datta et al. (2021) is that a major trend of cranial evolution in phytosaurs is represented by a tendency of developing a massive, robust snout that corresponds to the “brachyrostral” morphotype. Later-diverging spinosaurids such as *Oxalaia quilombensis* and *Spinosaurus aegyptiacus* represent exceptionally huge animals that were absolutely larger than early-diverging taxa, and thus are more heavily built (Dal Sasso et al., 2005; Kellner et al., 2011; Hone & Holtz, 2017, 2021).

Additionally, later-diverging phytosaurs with brachyrostral skulls tended to have extremely reduced antorbital fenestrae compared to early-diverging taxa with dolichorostral skulls (Datta et al., 2021: fig. 14b; Fig. 2A). In cf. *Spinosaurus aegyptiacus*, a later-diverging

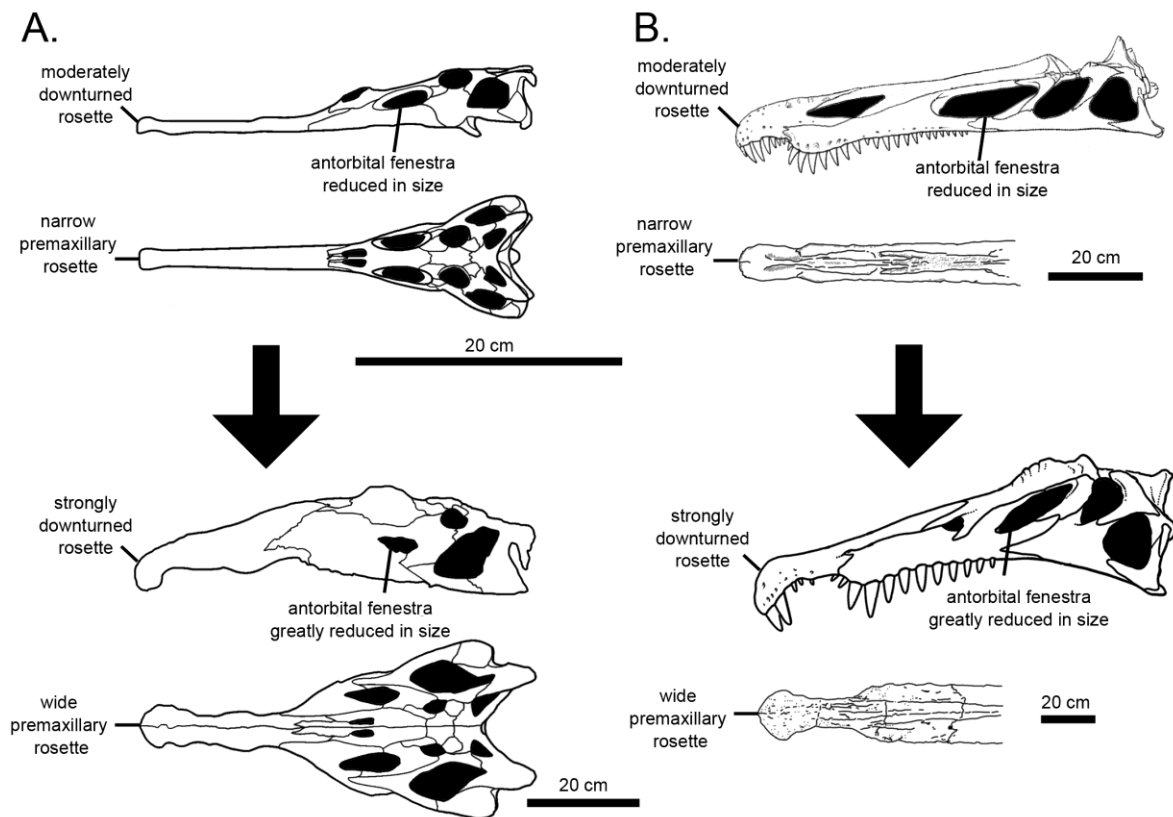


Fig. 2. Cranial evolution of Phytosauria (A) and Spinosauridae (B), with lateral and dorsal views of the skull/snout, shared morphological changes highlighted. Phytosauria is represented by the early-diverging, dolichorostral *Parasuchus hislopi* and the later-diverging, brachyrostral *Machaeroprotopus mccauleyi*. Spinosauridae is represented by the early-diverging *Suchomimus tenerensis* and the later-diverging *Spinosaurus aegyptiacus*. Images used in A are modified from Datta et al. (2021), and those of B, from Sereno et al. (1998) and Ibrahim et al. (2020), respectively.

spinosaurid with an exceptionally large size, the antorbital fenestra is notably reduced compared to early-diverging taxa like *Baryonyx walkeri* (Dal Sasso et al., 2005; Rayfield et al., 2007; Fig. 2B).

In brachyrostral phytosaurs, enlarged teeth sitting at the front of the upper jaw (“tip-of-snout set” *sensu* Hungerbühler, 2000) are separated from the following, smaller premaxillary teeth by a diastema (Hungerbühler, 2000; Stocker, 2010). Such a gap between enlarged teeth and smaller, more posterior teeth at the end of the snout is also present in spinosaurids, but this diastema is short in early-diverging forms like *Suchomimus tenerensis* (Kellner et al., 2011; Fig. 3A). In contrast, in large later-diverging taxa (e.g., *Oxalaia quilombensis*, cf. *Spinosaurus aegyptiacus*), the same diastema is relatively more elongated (Dal Sasso et al., 2005; Kellner et al., 2011; Fig. 3A).

Spinosaurines like *Irritator challengeri* and cf. *Spinosaurus aegyptiacus* can be distinguished from early-diverging baryonychines by their laterocumbent upper jaw teeth, such that the alveoli are partly visible in lateral view (Hendrickx et al., 2019; Isasmendi et al., 2022; Fig. 3B). Teeth with such a splayed morphology can also be seen in some phytosaurs of the brachyrostral morphotype (Hungerbühler, 2000; Hunt et al., 2006: fig. 2; Stocker, 2010: fig. 4; Heckert et al., 2013).

A later-diverging spinosaurid, *Spinosaurus aegyptiacus*, can be distinguished from other members of this clade by a presence of small teeth that are positioned between

enlarged anteriormost teeth and relatively large, posterior teeth in the dentary (Evers et al., 2015; Hone & Holtz, 2017). While the lower jaw teeth of phytosaurs are generally only divided into an enlarged, tip-of-mandible set and a smaller, dentary set (Hungerbühler, 2000), at least some of the brachyrostral phytosaurs (e.g., *Machaeroprotopus mccauleyi*, *Redondasaurus gregorii*) appear to display a transition from enlarged anterior teeth to smaller teeth in the mid-section, and again to large teeth in the posterior dentary (Hunt et al., 2006: fig. 2; Spielmann & Lucas, 2012: fig. 52).

Despite these numerous similarities that can be observed between the skulls of spinosaurid theropods and certain phytosaurs, there are also clear differences between them, albeit many of these are almost certainly due to the fact that they were completely different groups of organisms. The main differences include the following: 1 - the snout of the phytosaur upper jaw is mainly composed of the premaxilla, whereas that of spinosaurids is formed by the elongated premaxilla, maxilla and nasal; 2 - the bony palate in phytosaurs is only composed of the premaxilla, while that of spinosaurids is formed by medial extensions of the premaxilla and maxilla; 3 - orbits and external nares are positioned dorsally in phytosaurs, whereas nares are laterally positioned and orbits are not dorsally elevated in spinosaurids; and 4 - phytosaur teeth are much more numerous than those of spinosaurids, and are often ziphodont with distinct denticles, a condition unlike the fluted and conical teeth of spinosaurids with very minute

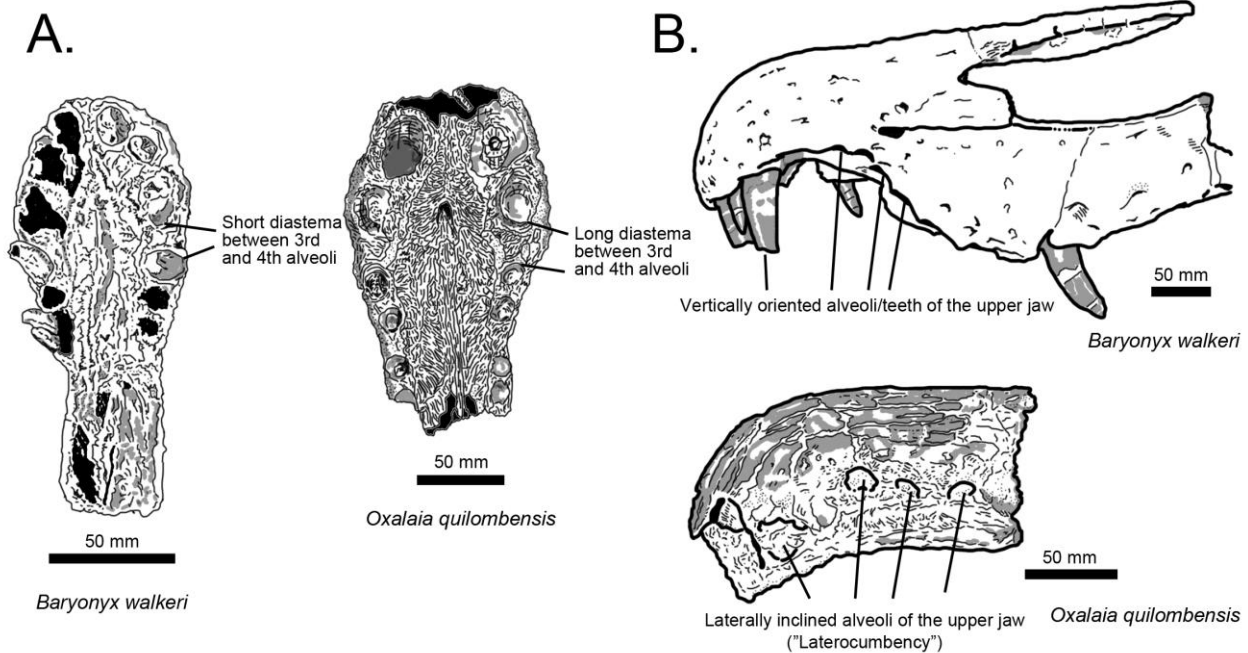


Fig. 3. Differences between the snouts of early-diverging (*Baryonyx walkeri*, after Bertin, 2010) and later-diverging (*Oxalaia quilombensis*, after Kellner et al., 2011) spinosaurid taxa in ventral (A) and lateral (B) views, with morphological differences highlighted.

or no denticles, whereas a conical morphology is often present in phytosaur teeth depending on their dental position (Charig & Milner, 1986; Witmer, 1997; Sereno et al., 1998; Hungerbühler, 2000; Stocker & Butler, 2013; Butler et al., 2014; Lautenschlager & Butler, 2016; Hone & Holtz, 2017, 2021).

DISCUSSION

Functional implications of shared craniodental features between spinosaurids and phytosaurs

Based on shared morphological characters such as fluted, conical teeth and an elongated snout with sinuous oral margin, the ecology and lifestyle of spinosaurids are often compared to those of modern crocodylians, and it is certainly reasonable to consider that many similarities did exist (Sereno et al., 1998; Holtz, 1998; Rayfield et al., 2007; Ibrahim et al., 2014; Hone & Holtz, 2017; Arden et al., 2019). However, there is also a remarkable convergence between phytosaurs with a brachyrostral snout and spinosaurids, including features that are not shared with crocodylians (e.g., down-turning of the premaxillary “rosette”; Datta et al., 2021), raising the possibility that at least some aspects of the lifestyle of spinosaurid theropods were more like those of brachyrostral phytosaurs rather than of crocodylians. Of note, differences in mechanical performance between spinosaurid and brachyrostral phytosaur skulls might have been small, as the largest examples of each clade are broadly similar in size (e.g., Colbert, 1947; Dal Sasso et al., 2005). Many hypotheses have been put forward as to what function the peculiar skull and tooth morphology of phytosaurs might have served in their ecology. Based on these hypotheses proposed previously for brachyrostral phytosaurs, preliminary suggestions can also put forth concerning the function(s) of the peculiar features of the skull and teeth of spinosaurids – that are quite similar in appearance to those of these phytosaurs – might have performed in the ecology of these carnivorous dinosaurs.

Spinosaurids can be readily distinguished from other theropod dinosaurs by the presence of a downturned, expanded “rosette” on their snouts that bears enlarged teeth, with such modifications taken to the extreme in cf. *Spinosaurus aegyptiacus* (Dal Sasso et al., 2005; Hone & Holtz, 2017). In their study of the cranial evolution of phytosaurs, Datta et al. (2021) noted that the widened “rosette” accompanied by large fang-like teeth is advantageous in reducing stresses that are induced by the process of catching and subduing a struggling prey, especially when the skull of the predator is rather slender. Moreover, it was also suggested that the down-turning of the “rosette” would be beneficial for grasping the prey more tightly, as such a modification results in a cage-like skull structure (Datta et al., 2021). Since spinosaurid skulls are very similar to those of brachyrostral phytosaurs regarding this feature, it is reasonable to assume that the “rosettes” at the anterior tip of the spinosaurid premaxilla

and dentary also served a similar function. Of note, Hungerbühler (2000) remarked that the presence of enlarged, conical teeth at the tips of the upper and lower jaws in the brachyrostral phytosaur *Nicrosaurus kapffi* would provide the best leverage for high velocity and maximum momentum during jaw closure, allowing the animal to have a quick, powerful bite. Whenever jaws constructed in this pattern would pierce the flesh through the large conical teeth at the tip, they can instantly kill small prey or inflict serious injury on larger one (Hungerbühler, 2000). Although relatively weak compared to its size, a study of Sakamoto (2022) showed that the bite force of *Spinosaurus aegyptiacus* was not low in absolute terms, and possibly even in the same range with that of some tyrannosaurids. Additionally, this taxon has adaptations that are suitable for generating relatively fast-snapping jaws, such as anteriorly displaced tooth rows and posteriorly oriented cranial muscles (Sakamoto, 2010). These assessments open up the possibility that spinosaurids, including *Spinosaurus aegyptiacus*, also used the enlarged, conical teeth of their “rosettes” as a powerful weapon for hunting small animals, and potentially large ones as well.

Posterior to the concavity that accommodates the dentary “rosette” when the mouth is closed, the upper jaw of both spinosaurids and brachyrostral phytosaurs has a ventral projection that bears a few large teeth. As the relatively posterior position of these teeth within the upper jaw would allow sustaining a strong bite force for a longer period of time, Hungerbühler (2000) assumed that the primary function of these teeth in phytosaurs was to hold the prey firmly and for a long time. Considering their similarity in shape and relative position within the upper jaw, the enlarged teeth in the anterior maxilla of spinosaurids, together with the ventrally convex margin of the jaw segment where these teeth are located, may had also been adapted to perform a similar function. In *Spinosaurus aegyptiacus*, teeth at the posterior part of the dentary are secondarily enlarged (e.g., Evers et al., 2015; Hone & Holtz, 2017), and this may have further enhanced the functional ability of the jaws to hold the prey more firmly.

Of note, Bertin (2010) pointed out that the upper jaw in modern *Crocodylus niloticus* Laurenti, 1768 also had enlarged teeth in a position similar to those of cf. *Spinosaurus aegyptiacus*. In *Crocodylus niloticus*, the enlarged teeth in this region are used to crunch bone and compress the prey before swallowing (Njau & Blumenschine, 2006), but Bertin (2010) suggested that – based on the likelihood that osteophagy was not a common practice among theropod dinosaurs (Hone & Rauhut, 2010) – the enlarged anterior maxillary teeth in cf. *Spinosaurus aegyptiacus* were not used primarily for breaking bones, and were more likely to be used to immobilize struggling prey. While this argument is overall plausible, the teeth of *Spinosaurus aegyptiacus* are more closely reminiscent of those of predators that feed on harder prey items like crustaceans, shelly mollusks or

fishes with hard scales (Hone & Holtz, 2021). Spinosaurids had unusually fast tooth replacement rates for theropod dinosaurs, possibly because holding struggling prey in their jaws resulted in frequent tooth loss due to high impact to the teeth (Heckeberg & Rauhut, 2020), or else because their teeth were often worn out rapidly from catching many hard prey items and thus required frequent replacement (Hone & Holtz, 2021). Lastly, anterior maxillary teeth in cf. *Spinosaurus aegyptiacus* are more enlarged and robust compared to those of baryonychines (Dal Sasso et al., 2005; Hendrickx et al., 2019). Based on these points, although the large anterior maxillary teeth of spinosaurids may have been used primarily for grasping struggling prey, it is suggested here that at least in cf. *Spinosaurus aegyptiacus*, these may have been also useful for crushing hard prey items like turtle shells or juvenile dinosaur bones. This is potentially also supported by the aforementioned bite force estimate for *Spinosaurus aegyptiacus* by Sakamoto (2022), which is fairly high in absolute terms.

Besides inferring function(s) of the spinosaurid skull based on inferences made previously about phytosaurs, a reverse reasoning may be also rewarding. In spinosaurids, a secondarily closed roof of the mouth is present (e.g., Sereno et al., 1998; Hone & Holtz, 2017), although it is unlikely that this structure allowed the animal to breathe when submerged as does the secondary palate of crocodylians, as the choana of the spinosaurids is anteriorly positioned as in other theropod dinosaurs (Sues et al., 2002). Instead, this structure in spinosaurids is more likely related to its functional ability to resist biting-induced stresses, bending and torsion, and the biomechanical analysis of Rayfield et al. (2007) demonstrated an increase of such ability compared to other theropods. Phytosaurs also have a partially closed mouth roof that is formed by the medial extensions of the premaxillae, but their choana is, again, not as posteriorly positioned as that of crocodylians (Witmer, 1997; Butler et al., 2014; Lautenschlager & Butler, 2016). This suggests that the premaxillary palate of phytosaurs, like the bony palate of spinosaurids, was not related to respiration while submerged, but instead to enhanced resistance to bite-induced stresses during hunting or feeding, as is supported by the results of a relevant preliminary biomechanical analysis (Lemanis et al., 2019). In addition, a decrease in the size of the antorbital fenestra reduces torsion (Rayfield et al., 2007), and later-branching species in both phytosaurs and spinosaurids have relatively smaller fenestrae compared to early forms (Dal Sasso et al., 2005; Rayfield et al., 2007; Datta et al., 2021: fig. 14b). Here, it is suggested that the convergent decrease of the antorbital fenestra in both clades may be related to their increased ability to resist function-related torsion.

It is noteworthy that many of the craniodental similarities noted here between spinosaurids and brachyrostral phytosaurs are in fact also present in conger eels (Vullo et al., 2016). Vullo et al. (2016) suggested that such unique jaw morphology represents an adaptation for biting and

catching elusive aquatic prey items in low-light condition, and noted that the likely presence of sensory integumentary system in spinosaurid snouts (e.g., Dal Sasso et al., 2005; Ibrahim et al., 2014) supports the idea that spinosaurids used integumentary mechanoreceptors to detect prey items just as modern conger eels do. As noted before, the skulls of phytosaurs with a “brachyrostral” snout morphotype are broadly similar to those of spinosaurids, and numerous foramina – that likely functioned in the same way as sensory organs in crocodylians and spinosaurids – are also present at their snout tips (Datta et al., 2021). While some authors have suggested that the diet of phytosaurs with a brachyrostral skull was likely composed of large, terrestrial animals (e.g., Hunt, 1989, 1994; Hungerbühler, 2000; Datta et al., 2021), the remarkable morphological convergence observed between the jaws of brachyrostral phytosaurs and those of conger eels, and spinosaurids may indicate that aquatic prey items such as fish occupied a significant portion in their diet as well. In brachyrostral phytosaurs, a change from very large, fang-like “rosette” teeth to relatively smaller middle teeth and then back again to large posterior teeth is present in the upper jaw (Hungerbühler, 2000; Stocker, 2010), and such a size variation in the upper dentition has been interpreted as an adaptation for piscivorous ecology (Vullo et al., 2016; Cau, 2020). The conclusions of a microwear textural analysis of phytosaur teeth by Bestwick et al. (2021) are consistent with this hypothesis, as microwear textures found in brachyrostral phytosaurs (e.g., *Nicrosaurus kaffi*, *Smilosuchus lithodendrorum* (Camp, 1930)) largely overlap with those of both carnivorous and piscivorous reptiles, suggesting a broad range of diet for these phytosaurs rather than obligate feeding on a single type of prey.

Comments on the lifestyle of later-diverging spinosaurids and “brachyrostral” phytosaurs

While the main purpose of this review is to identify convergences in craniodental anatomy between “brachyrostral” phytosaurs and spinosaurid theropods, and discuss their functional implications, noting such convergences also allow commenting on previously proposed contentious hypotheses about the lifestyles of spinosaurids (particularly the later-diverging taxon *Spinosaurus aegyptiacus*) and phytosaurs, in order to provide another, novel perspective on these controversial issues. The discovery of the ‘neotype’ (FSAC-KK 11888; see Evers et al., 2015, and Ibrahim et al., 2020a, respectively, for differing opinions on this designation) individual of *Spinosaurus aegyptiacus* revealed that this taxon had remarkably downsized pelvis for its body size, shortened hindlimbs with little open medullary cavity, tetradactyl pes with flat unguals, and elongated tail with extremely elongated neural spines and chevrons (Ibrahim et al. 2014, 2020b). Initially, it has been argued that these features represent adaptations for semiaquatic, or even highly-specialized aquatic lifestyle, interpreting dense

long bones as ballast for submergence, expanded tail as an aquatic propulsor, and pes with spread (possibly webbed) digits supplementing an aquatic locomotion (Ibrahim et al., 2014, 2020b). In their description of two frontals and an isolated frontoparietal of spinosaurid theropods from the Kem Kem Group of Morocco, Arden et al. (2019) furthered such a hypothesis, and even proposed that spinosaurids became progressively more adapted to an aquatic lifestyle, suggesting that (1) the relatively shortened pubis and ischium compared to the ilium in the early-diverging spinosaurine *Ichthyovenator laosensis* might be correlated with increased specialization for an aquatic habit, and (2) that elevated orbits in later-diverging spinosaurines (*Irritator challengeri*, *Sigilmassasaurus brevicollis*, *Spinosaurus aegyptiacus*) may have enabled these to keep their eyes above water-level while the rest of the head was submerged.

Such hypotheses of an aquatic spinosaurid lifestyle have been critically reviewed in a number of subsequent publications. In a study using a 3D model to check the buoyancy of animals in water, Henderson (2018) found that even though *Spinosaurus aegyptiacus* could have floated, it was easy to tilt its body sidewise, which was considered to be a body shape unsuitable for aquatic animals. It was thus concluded that it would have stayed mainly on land, strolling along the water's edge, and hunting fish in a bear-like fashion (Henderson, 2018). Hone & Holtz (2019) noted that the elevated orbital rims of spinosaurines did not enhance the ability of these animals to keep their eyes above the surface mainly because their external nares were laterally oriented, and that the shortened nature of the pubis and ischium cannot in itself serve as reliable evidence for aquatic specialization as this condition is also observed in a variety of fully terrestrial theropods. Later, Hone & Holtz (2021) noted that the results of their principal components analysis suggested that the overall skull shape of *Spinosaurus aegyptiacus* is broadly similar to that of other spinosaurids and, for that matter, of other theropods, and does not plot close to those of aquatic or semiaquatic reptiles. Additionally, they suggested that several other terrestrial theropods also have flattened pedal unguals, reminiscent of those of *Spinosaurus aegyptiacus*, and thus their flattened nature in itself cannot be a reliable indicator of semiaquatic or aquatic habit; they also noted that, while the model of Ibrahim et al. (2020b) does suggest that the tail of *Spinosaurus aegyptiacus* was clearly more efficient for swimming than that of other theropods, it was still far behind that of aquatic or semiaquatic animals (Hone & Holtz, 2021). Thus, Hone & Holtz (2021) suggested the unusual tail of *Spinosaurus aegyptiacus* might have been used for socio-sexual display instead, based on the fact that many reptiles with similar structures used them for this same purpose. In a subsequent biomechanical study that used a 3D-life restoration model created through CT-scans of known specimens, Sereno et al. (2022) found that the body of *Spinosaurus aegyptiacus* was too buoyant to submerge into deep water, and its tail could only

provide very slow (~1 m/s) propulsion in water. Based on these observations, Sereno et al. (2022) rejected the hypothesis that *Spinosaurus aegyptiacus* had a “highly-specialized” aquatic lifestyle, and suggested that the infilled nature of the leg bones in this taxon likely represents an adaptation for weight support (graviportality) suitable for a large, bipedal animal with reduced hindlimbs, rather than ballast for submergence (a largely similar opinion is also presented by Myhrvold et al., 2022, in a preprint form). As for phytosaurs, while it is generally assumed that their lifestyle was largely similar to those of modern crocodylians based on their extremely similar bauplan (e.g., Stocker & Butler, 2013), a predominantly or fully terrestrial lifestyle has been suggested for at least some derived phytosaurs (with brachyrostral skull) such as *Nicrosaurus* or *Redondasaurus*, based on their skeletal features that are suggestive of more erect gait capabilities (Kimmig, 2013).

Although the evidence presented in the above-mentioned rebuttals to the claim that *Spinosaurus aegyptiacus* was a semiaquatic or aquatic animal is mostly reasonable, at least some of it deserves further commentary. Even if the relatively short nature of the pubis and/or ischium may not be a strong indicator for an adaptation for aquatic lifestyle, there would have been little strong selective pressure to lead to the extremely shortened whole pelvic girdle and associated hindlimbs, as seen in *Spinosaurus aegyptiacus*, compared to its more basal relatives (i.e., baryonychines), in case spinosaurines hunted exclusively like herons or bears (considered as modern analogues of spinosaurids, including *Spinosaurus aegyptiacus*, by Henderson, 2018, and Hone & Holtz, 2019, 2021, respectively). Additionally, it should be considered that the solid internal bone structure in *Spinosaurus aegyptiacus* is not limited to its hindlimb elements, but can also be seen in a variety of other skeletal parts that are unrelated to weight support such as neural spines or ribs (Ibrahim et al., 2014; Fabbri et al. 2022a), which makes the claim that bone compactness in *Spinosaurus aegyptiacus* is solely related to graviportality, questionable. Meanwhile, the idea that the degree of infilling of the bones is related to the size of the animal is contradicted by the fact that other theropod dinosaurs (e.g., *Tyrannosaurus rex*) with similar, or perhaps even larger, body weight than *Spinosaurus aegyptiacus* actually exhibit less dense long bones (Fabbri et al., 2022a, b). Furthermore, it has been demonstrated that a smaller individual referred to *Baryonyx walkeri* had a higher density of its bones compared to larger individuals of *Suchomimus tenerensis* (Fabbri et al., 2022a), which raises the possibility that even spinosaurids themselves did not exhibit a positive allometry in bone compactness.

In their survey of microanatomical diversity of amniote ribs using 155 extant taxa, Canoville et al. (2016) found that ribs with thick cortices and limited medullary cavities occur almost exclusively in some “amphibious” mammals as well as in those living in water-linked environments (e.g., divers, coastal swimmers), excepting a

few cases that are either fossorial (e.g., *Vombatus ursinus*) or represent some other very unusual instances (e.g., *Macropus rufus*, *Rattus norvegicus*) among mammals. Of note, *Rhinoceros sondaicus*, which was regarded as a terrestrial taxon by Canoville et al. (2016), is also found in the same study to exhibit remarkably thick rib cortices; however, this species in fact spends considerable time in or around watery environments and is sometimes regarded as semiaquatic (Benoit et al., 2020). Obviously, ribs play little role in locomotion, and their microstructure would only modify under limited circumstances such as changes in body weight or its distribution, for reasons such as controlling buoyancy in water (Houssaye et al., 2016). It is also noteworthy that increase of rib compactness is not evident among graviportal amniotes, both extinct and extant (Canoville et al., 2016; Fabbri et al., 2022a).

Collectively, this suite of features suggests that *Spinosaurus aegyptiacus* was at least slightly more adapted to an aquatic lifestyle than its relatives. In the case of derived phytosaurs, although some taxa may have had more efficient terrestrial locomotion compared to modern crocodylians and other phytosaurs (e.g., *Nicrosaurus*; Kimmig, 2013), the dental microwear analysis of Bestwick et al. (2020) revealed that the texture of such taxa still shows great resemblance to those of both carnivorous and piscivorous reptiles, suggesting that they frequently inhabited watery environments for foraging, just like their early-diverging phytosaur relatives.

These assessments, combined with the fact that it would have been difficult for *Spinosaurus aegyptiacus* to both swim fast and sink into deep water (Hone & Holtz, 2021; Sereno et al., 2022), suggest that perhaps the lifestyle of this animal was “intermediate” between the heron-like wading and the crocodile-like specialized aquatic predator models, rather than strictly falling into one of these two. That is, the animal may have lived in waters of moderate depth, and may have spent much of its time as a slow swimmer or living as a bottom walker, occasionally emerging on land as needed. According to the study of Sereno et al. (2022), *Spinosaurus aegyptiacus* was able to stand without losing balance in water depths of about 2.6 m, which was deep enough to submerge the animal up his hip height. In this regard, its lifestyle may have been similar to those of early-diverging stem whales (e.g., pakicetids), as these mammals had highly osteosclerotic ribs and limbs yet lacked any clear adaptations for increased swimming capability (e.g., Thewissen et al., 2001; Gray et al., 2007; Madar, 2007). Such an ecological model is partially supported by the fact that the phenomenon of increased bone density occurs mainly in slow-moving animals that live in relatively shallow water, whereas animals that swim quickly in deep water tend to have lighter bones (Gray et al., 2007; Thewissen et al., 2009).

The similarities of later-diverging phytosaurs to *Spinosaurus aegyptiacus*, such as their relatively straight gait and numerous shared craniodental traits highlighted

in this study, suggest that they may have lived or hunted in largely similar environments as well. However, this, too, is a very tentative suggestion since little study had been devoted to the swimming abilities of phytosaurs, and the fossil record of spinosaurids is still very incomplete and sparse (e.g., Hone & Holtz, 2017). Hopefully, further detailed descriptions of additional spinosaurid fossils together with a thorough biomechanical analysis of phytosaurs will contribute to resolving these issues.

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REFERENCES

- Amiot, R., Buffetaut, E., Lécuyer, C., Wang, X., Boudad, L., Ding, Z., Fourel, F., Hutt, S., Martineau, F. & Medeiros, M.A., 2010. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology*, 38:139–142.
- Arden, T.M.S., Klein, C.G., Zouhri, S. & Longrich, N.R., 2019. Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurs. *Cretaceous Research*, 93:275–284.
- Ballew, K.L., 1989. A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States. In: Lucas, S.G. & Hunt, A.P. (eds.), *Dawn of the Age of Dinosaurs in the American Southwest* (pp. 309–339). New Mexico Museum of Natural History; Albuquerque.
- Benoit, J., Legendre, L.J., Farke, A.A., Neenan, J.M., Mennecart, B., Costeur, L., Merigeaud, S. & Manger, P.R., 2020. A test of the lateral semicircular canal correlation to head posture, diet and other biological traits in “ungulate” mammals. *Scientific Reports*, 10:19602.
- Benson, R.B.J., 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society*, 158:882–935.
- Bertin, T., 2010. A catalogue of material and review of the Spinosauridae. *PalArch's Journal of Vertebrate Palaeontology*, 7:1–39.

- Bestwick, J., Jones, A.S., Purnell, M.A. & Butler, R.J., 2021. Dietary constraints of phytosaurian reptiles revealed by dental microwear textural analysis. *Palaeontology*, 64:1–18.
- Butler, R.J., Rauhut, O.W.M., Stocker, M.R. & Bronowicz, R., 2014. Redescription of the phytosaurs *Paleorhinus* (“*Francosuchus*”) *angustifrons* and *Ebrachosuchus neukami* from Germany, with implications for Late Triassic biochronology. *Zoological Journal of the Linnean Society*, 170:155–208.
- Camp, C.L., 1930. A study of the phytosaurs with description of new material from western North America. *Memoirs of the University of California*, 10:1–161.
- Canoville, A., de Buffrénil, V. & Laurin, M., 2016. Microanatomical diversity of amniote ribs: an exploratory quantitative study. *Biological Journal of the Linnean Society*, 118:706–733.
- Carrano, M.T., Benson, R.B.J. & Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 10:211–300.
- Cau, A., 2020. The body plan of *Halszkaraptor escuilliei* (Dinosauria, Theropoda) is not a transitional form along the evolution of dromaeosaurid hypercarnivory. *PeerJ*, 8:e8672.
- Charig, A.J. & Milner, A.C., 1986. *Baryonyx*, a remarkable new theropod dinosaur. *Nature*, 324:359–361.
- Charig, A.J. & Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum Geology*, 53:11–70.
- Colbert, E.H., 1947. Studies of the phytosaurs *Machaeropsopus* and *Rutiodon*. *Bulletin of the American Museum of Natural History*, 88:53–96.
- Dal Sasso, C., Maganuco, S., Buffetaut, E. & Mendez, M., 2005. New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology*, 25:888–896.
- Datta, D., Sharma, K. & Ray, S., 2021. Cranial evolution of the Late Triassic phytosaurs (Diapsida, Archosauria): preliminary observations from landmark-based morphometric analysis. *Historical Biology*, 33:2683–2705.
- de Broin, F. & Taquet, P., 1966. Découverte d'un Crocodylien nouveau dans le Crétacé inférieur du Sahara. *Comptes rendus de l'Académie des sciences de Paris D*, 262:2326–2329.
- Evers, S.W., Rauhut, O.W.M., Milner, A.C., McFeeters, B. & Allain, R., 2015. A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the “middle” Cretaceous of Morocco. *PeerJ*, 3:e1323.
- Fabbri, M., Navalón, G., Benson, R.B.J., Pol, D., O'Connor, J.K., Bhullar, B.-A.S., Erickson, G.M., Norell, M.A., Orkney, A., Lamanna, M.C., Zouhri, S., Becker, J., Emke, A., Dal Sasso, C., Bindellini, G., Maganuco, S., Auditore, M. & Ibrahim, N., 2022a. Subaqueous foraging among carnivorous dinosaurs. *Nature*, 603:852–857.
- Fabbri, M., Navalón, G., Benson, R.B.J., Pol, D., O'Connor, J., Bhullar, B.-A.S., Erickson, G., Norell, M.A., Orkney, A., Lamanna, M.C., Zouhri, S., Becker, J., Dal Sasso, C., Bindellini, G., Maganuco, S., Auditore, M. & Ibrahim, N., 2022b. Sinking a giant: quantitative macroevolutionary comparative methods debunk qualitative assumptions. *bioRxiv*. <https://doi.org/10.1101/2022.05.05.490811>
- Fitzinger, L., 1843. *Systema Reptilium. Fasciculus Primus. Amblyglossae*. Apud Braumüller and Seidel Bibliopolas, Vienna:1–106.
- Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8:1–55.
- Gray, N.-M., Kainec, K., Madar, S., Tomko, L. & Wolfe, S., 2007. Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans. *The Anatomical Record*, 290:638–653.
- Heckeberg, N.S. & Rauhut, O.W.M., 2020. Histology of spinosaurid dinosaur teeth from the Albian-Cenomanian of Morocco: implications for tooth replacement and ecology. *Palaeontologia Electronica*, 23:a48.
- Heckert, A.B., Jenkins, H.S., Lucas, S.G. & Hunt, A.P., 2013. Mandibles of juvenile phytosaurs (Archosauria: Crurotarsi) from the Upper Triassic Chinle Group of Texas and New Mexico, USA. *New Mexico Museum of Natural History and Science Bulletin*, 61:228–236.
- Henderson, D.M., 2018. A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic *Spinosaurus* Stromer, 1915 (Dinosauria: Theropoda). *PeerJ*, 6:e5409
- Hendrickx, C., Mateus, O. & Buffetaut, E., 2016. Morphofunctional Analysis of the Quadrate of Spinosauridae (Dinosauria: Theropoda), and the Presence of *Spinosaurus* and a Second Spinosaurine Taxon in the Cenomanian of North Africa. *PLoS ONE*, 11:e0144695.
- Hendrickx, C., Mateus, O., Araújo, R. & Choiniere, J., 2019. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontologia Electronica*, 22.3.74:1–110.
- Hoffman, D.K., Miller-Camp, J.A. & Heckert, A.B., 2021. Tooth enamel microstructure in North American Phytosauria (Diapsida: Archosauriformes): Implications for biogeography and ecology of a Late Triassic clade of crocodylian-like predators. *Palaeontologia Electronica*, 24.3.a32:1–26.
- Holtz, T.R., Jr., 1998. Spinosaurids as crocodile mimics. *Science*, 282:1276–1277.
- Hone, D.W.E. & Holtz, T.R., Jr., 2017. A century of spinosaurs - a review and revision of the Spinosauridae with comments on their ecology. *Acta Geologica Sinica*, 91:1120–1132.

- Hone, D.W.E. & Holtz, T.R., Jr., 2019. Comment on: Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. *Cretaceous Research*, 134:104152.
- Hone, D.W.E. & Holtz, T.R., Jr., 2021. Evaluating the ecology of *Spinosaurus*: shoreline generalist of aquatic pursuit specialist? *Palaeontologia Electronica*, 24:a03.
- Hone, D.W.E. & Rauhut, O.W.M., 2010. Feeding behavior and bone utilization by theropod dinosaurs. *Lethaia*, 43:232–244.
- Hone, D.W.E., Xu, X. & Wang, D.-Y., 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. *Vertebrata Palasiatica*, 48:19–26.
- Houssaye, A., Sander, P.M. & Klein, N., 2016. Adaptive patterns in aquatic amniote bone microanatomy—more complex than previously thought. *Integrative and Comparative Biology*, 56:1349–1369.
- Hungerbühler, A., 2000. Heterodonty in the European phytosaur *Nicrosaurus kapffi* and its implications for the taxonomic utility and functional morphology of phytosaur dentitions. *Journal of Vertebrate Paleontology*, 20:31–48.
- Hungerbühler, A., 2002. The Late Triassic phytosaur *Myriosuchus westphali*, with a revision of the genus. *Palaeontology*, 45:377–418.
- Hungerbühler, A., Mueller, B., Chatterjee, S. & Cunningham, D.P., 2013. Cranial anatomy of the Late Triassic phytosaur *Machaeropsopus*, with the description of a new species from West Texas. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103:269–312.
- Hunt, A.P., 1989. Cranial morphology and ecology among phytosaurs. In: Lucas, S.G. & Hunt, A.P. (eds.), *Dawn of the Age of Dinosaurs in the American Southwest* (pp. 349–354). New Mexico Museum of Natural History; Albuquerque.
- Hunt, A.P., 1994. *Vertebrate paleontology and biostratigraphy of the Bull Canyon Formation (Chinle Group, Upper Triassic), east-central New Mexico with revisions of the families Metoposauridae (Amphibia: Temnospondyli) and Parasuchidae (Reptilia: Archosauria)*. Unpublished PhD Thesis, University of New Mexico, Albuquerque, 403 pp.
- Hunt, A.P. & Lucas, S.G., 1993. A new phytosaur (Reptilia: Archosauria) genus from the uppermost Triassic of the western United States and its biochronological significance. *New Mexico Museum of Natural History and Science Bulletin*, 3:193–196.
- Hunt, A.P., Lucas, S.G. & Spielmann, J.A., 2006. Sexual dimorphism in a large brachyrostral phytosaur (Archosauria: Crurotarsi) from the Late Triassic of western North America. *New Mexico Museum of Natural History and Science Bulletin*, 37:563–567.
- Ibrahim, N., Sereno, P.C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold, N. & Iurino, D.A., 2014. Semiaquatic adaptations in a giant predatory dinosaur. *Science*, 345:1613–1616.
- Ibrahim, N., Sereno, P.C., Varricchio, D.J., Martill, D.M., Duthiel, D.B., Unwin, D.M., Baidder, L., Larsson, H.C., Zouhri, S. & Kaoukaya, A., 2020a. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys*, 928:1–216.
- Ibrahim, N., Maganuco, S., Dal Sasso, C., Fabbri, M., Auditore, M., Bindellini, G., Martill, D.M., Zouhri, S., Mattarelli, D., Unwin, D.M., Wiemann, J., Bonadonna, D., Amare, A., Jakubczak, J., Joger, U., Lauder, G.V. & Pierce, S.E., 2020. Tail-propelled aquatic locomotion in a theropod dinosaur. *Nature*, 581:67–70.
- Isasmendi, E., Navarro-Lorbés, P., Sáez-Benito, P., Viera, L.I., Torices, A. & Pereda-Suberbiola, X., 2022. New contributions to the skull anatomy of spinosaurid theropods: Baryonychinae maxilla from the Early Cretaceous of Igea (La Rioja, Spain). *Historical Biology*, 35:909–923.
- Kellner, A.W.A., Azevedo, S.A.K., Machado, E.B., de Carvalho, L.B. & Henriques, D.D.R., 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *Anais da Academia Brasileira de Ciências*, 83:99–108.
- Kimmig, J., 2013. Possible secondarily terrestrial lifestyle in the European phytosaur *Nicrosaurus kapffi* (Late Triassic, Norian): a preliminary study. *New Mexico Museum of Natural History and Science Bulletin*, 61:306–312.
- Kimmig, J. & Arp, G., 2010. Phytosaur remains from the Norian Arnstadt Formation (Leine Valley, Germany), with reference to European phytosaur habitats. *Palaeodiversity*, 3:99–108.
- Lacerda, M.B.S., Grillo, O.N. & Romano, P.S.R., 2022. Rostral morphology of Spinosauridae (Theropoda, Megalosauroidea): premaxilla shape variation and a new phylogenetic inference. *Historical Biology*, 34:2089–2109.
- Lakin, R.J. & Longrich, N.R., 2019. Juvenile spinosaurs (Theropoda: Spinosauridae) from the middle Cretaceous of Morocco and implications for spinosaur ecology. *Cretaceous Research*, 93:129–142.
- Laurenti, J.N., 1768. *Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod auctoritate et consensus*. Thomae, Vienna, Joan, 217 pp.
- Lautenschlager, S. & Butler, R.J., 2016. Neural and endocranial anatomy of Triassic phytosaurian reptiles and convergence with fossil and modern crocodylians. *PeerJ*, 4:e2251.
- Lemanis, R., Jones, A.S., Butler, R.J., Anderson, P.S.L. & Rayfield, E.J., 2019. Comparative biomechanical analysis demonstrates functional convergence between slender-snouted crocodylians and phytosaurs. *PeerJ Preprints*, 7:e27476v1.

- Lydekker, R., 1885. Maleri and Denwa Reptilia and Amphibia. *Palaeontology Indica*, 1:1–38.
- Marsh, O.C., 1878. Notice of new dinosaurian reptiles. *American Journal of Science and Arts*, 15:241–244.
- Madar, S. 2007. The postcranial skeleton of Early Eocene pakicetid cetaceans. *Journal of Paleontology*, 81:176–200.
- Martill, D.M., Cruickshank, A.R.I., Frey, E., Small, P.G. & Clarke, M., 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. *Journal of the Geological Society*, 153:5–8.
- McFeeters, B.D., 2021. New mid-cervical vertebral morphotype of Spinosauridae from the Kem Kem Group of Morocco. *Vertebrate Anatomy Morphology Palaeontology*, 8:182–193.
- Mehl, M.G., 1916. New or little known phytosaurs from Arizona. *Quarterly Bulletin, University of Oklahoma, New Series*, 108:5–28.
- Meyer, H. von., 1860. Briefliche Mittheilung an Prof. Bronn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten Kunde*, 1860:556–560.
- Meyer, H. von., 1861. Reptilien aus dem Stubensandstein des oberen Keupers. *Palaeontographica*, 7:253–346.
- Milner, A.C., 2003. Fish-eating theropods: a short review of the systematics, biology and palaeobiology of spinosaurs. *Journadas Internacionales sobre paleontología de Dinosaurios y su Entoro*, 2:129–138.
- Myhrvold, N., Sereno, P.C., Baumgart, S.L., Formoso, K.K., Vidal, D., Fish, F.E. & Henderson, D.M., 2022. Spinosaurids as ‘subaqueous foragers’ undermined by selective sampling and problematic statistical inference. *bioRxiv*.
<https://doi.org/10.1101/2022.04.13.487781>
- Njau, J.K. & Blumenschine, R.J., 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. *Journal of Human Evolution*, 50:142–162.
- Rauhut, O.W.M. & Pol, D., 2019. Probable basal allosauroid from the early Middle Jurassic Cañadón Asfalto Formation of Argentina highlights phylogenetic uncertainty in tetanuran theropod dinosaurs. *Scientific Reports*, 9:18826.
- Rayfield, E., Milner, A.C., Xuan, V.B. & Young, P.G., 2007. Functional morphology of spinosaur ‘crocodile mimic’ dinosaurs. *Journal of Vertebrate Paleontology*, 27:892–901.
- Russell, D.A., 1996. Isolated Dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Muséum National d’histoire Naturelle. Section C, Sciences de la terre, Paléontologie, Géologie, Minéralogie*, 18:349–402.
- Sakamoto, M., 2010. Jaw biomechanics and the evolution of biting performance in theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, 277:3327–3333.
- Sakamoto, M., 2022. Estimating bite force in extinct dinosaurs using phylogenetically predicted physiological cross-sectional areas of jaw adductor muscles. *PeerJ*, 10:e13731.
- Sereno, P.C., Beck, A.L., Dutheil, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.D., Wilson, G.P. & Wilson, J.A., 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, 282:1298–1302.
- Sereno, P.C., Myhrvold, N., Henderson, D.M., Fish, F.E., Vidal, D., Baumgart, S.L., Keillor, T.M., Formoso, K.K. & Conroy, L.L., 2022. *Spinosaurus* is not an aquatic dinosaur. *eLife*, 11:e80092.
- Smyth, R.S.H., Ibrahim, N. & Martill, D.M., 2020. *Sigilmassasaurus* is *Spinosaurus*: a reappraisal of African spinosaurines. *Cretaceous Research*, 114:104520.
- Spielmann, J.A. & Lucas, S.G., 2012. Tetrapod fauna of the Upper Triassic Redonda Formation east-central New Mexico: the characteristic assemblage of the Apachean land-vertebrate faunachron. *New Mexico Museum of Natural History and Science Bulletin*, 55:1–119.
- Stocker, M.R., 2010. A new taxon of phytosaur (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus* Case, 1922. *Palaeontology*, 53:997–1022.
- Stocker, M.R. & Butler, R.J., 2013. Phytosauria. In: Nesbitt, S.J., Desojo, J.B. & Irmis, R.B. (eds.), *Anatomy, phylogeny and palaeobiology of early archosaurs and their kin* (pp:91–117). *Geological Society Special Publications*, London.
- Stromer, E., 1915. Ergebnisse der Forschungsreisen Prof. E. Stromer in den Wüsten Agyptens. II. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen Königlich-Bayerische Akademie Der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse*, 28:1–32.
- Sues, H.-D., Frey, E., Martill, D.M. & Scott, D.M., 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 22:535–547.
- Thewissen, J.G.M., Williams, E.M., Roe, L.J. & Hussain, S.T., 2001. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature*, 413:277–281.
- Thewissen, J.G.M., Cooper, L.N., George, J.C. & Bajpai, S., 2009. From land to water: the origin of whales, dolphins, and porpoises. *Evolution: Education and Outreach*, 2:272–288.
- Vullo, R., Allain, R. & Cavin, L., 2016. Convergent evolution of jaws between spinosaurid dinosaurs and pike conger eels. *Acta Palaeontologica Polonica*, 61:825–828.

- Witmer, L.M., 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Journal of Vertebrate Paleontology*, 17:1–76.
- Zeigler, K.E., Lucas, S.G. & Heckert, A.B., 2003. Variation in the Late Triassic Canjilon quarry (Upper Chinle Group, New Mexico) phytosaur skulls: evidence of sexual dimorphism. *Paläontologische Zeitschrift*, 77:341–351.