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

Chan-gyu Yun

Received: 8 February 2023 / Accepted: 24 August 2023 / Published online: 9 September 2023

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 crocodilians, 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 crocodilians 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 crocodilians, 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 crocodilians.

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 (Sereno 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 Megalosauroidea 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; Hendrickx 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 crocodilians (e.g., Sereno et al., 1998; Holtz, 1998; Rayfield et al., 2007). Indeed, crocodilians 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” (Sereno et al., 1998; Holtz, 1998), there are some significant differences as well. The skulls of spinosaurids were not dorsoventrally flattened like those of crocodilians, but rather flattened laterally like those of other theropod dinosaurs (Vullo et al., 2016; Hone & Holtz, 2021). Furthermore, crocodilians 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 crocodilians.

Phytosaurs were members of another early archosauriform group that is very similar in general morphology to crocodilians (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 dimorphisms 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., Parasuchus lopi Lydekker, 1885) were ecologically analogous to modern gharials, and primarily preyed on small fish, while “brachyrostral” forms (e.g., Machaeroprosopus mccauleyi (Ballew, 1989), Nicrosaurus kapfi (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 Machaeroprosopus 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 crocodilians; 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 crocodilians; 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).]
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 trend 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 walkerii* or *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadileir, Sidor, Varrichio, 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 walkerii*, 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 dolichostral skulls (Datta et al., 2021: fig. 14b; Fig. 2A). In cf. *Spinosaurus aegyptiacus*, a later-diverging

---

Fig. 2. Cranial evolution of Phytosauria (A) and Spinosauroidea (B), with lateral and dorsal views of the skull/snout, shared morphological changes highlighted. Phytosauria is represented by the early-diverging, dolichostral *Parasuchus hislopi* and the later-diverging, brachyrostral *Machaeroprosopus mcauleyi*. Spinosauroidea 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., 2018; 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., *Machaeroprosopus 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](image-url). 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 sinusous oral margin, the ecology and lifestyle of spinosaurids are often compared to those of modern crocodilians, 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 crocodilians (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 crocodilians. 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 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.

Spinosaurs 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 kappfi* 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 tyranosauroids. 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 anterior 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 (Heckelberg & 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. *Spinosaursaurus 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. *Spinosaursaurus aegyptiacus*, these may have been also useful for catching hard prey items like turtle shells or juvenile dinosaur bones. This is potentially also supported by the aforementioned bite force estimate for *Spinosaursaurus 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 crocodilians (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 conditions, 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 crocodilians 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 *Spinosaursaurus 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 *Spinosaursaurus 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 spinosaurs 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 spinosauirine Ichthyovenator laoensis 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 sideways, 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 inflated nature of the leg bones in this taxon likely represents an adaptation for weight support (grapivortality) 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 crocodilians 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 led 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 spinosaurs, 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 graviporality, 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 Suchominimus 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 crocodilians 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 to its 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.

ACKNOWLEDGEMENTS

This comparison was greatly inspired by a work of Romain Vullo and his colleagues, who convincingly presented a case of convergent evolution of jaws between pike conger eels and spinosaurid theropods. This manuscript was improved by insightful comments from reviewers Spencer Lucas (New Mexico Museum of Natural History, Albuquerque), Denver Fowler (Badlands Dinosaur Museum, Dickinson), Nicholas Longrich (University of Bath, Claverton Down), as well as an anonymous reviewer, and by the editor Zoltan Csiki-Sava (University of Bucharest, Bucharest).

REFERENCES


C. angustifrons and 


Carrano, M.T., Benson, R.B.J. & Sampson, S.D., 2012. The phylogeny of 


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.


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 


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 


Spinosaurus Stormer, 1915 (Dinosauria: Theropoda). PeerJ, 6:e5409

Hendrickx, C., Mateus, O. & Buffetaut, E., 2016. Morphofunctional Analysis of the Quadrade of Spinosauroidea (Dinosauria: Theropoda), and the Presence of 


