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Review

Functional Morphology of *Spinosaurus Aegyptiacus*' Sail: Thermoregulation, Display, or Hydrodynamic?

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Abstract: This literature review aims to gain a deeper understanding of *Spinosaurus aegyptiacus*'s dorsal sail regarding its function as thermoregulation, display, or hydrodynamic. The function of *S. aegyptiacus*'s dorsal sail has been widely debated for many years. The three most popular hypotheses are that it was used as a biological mechanism of thermoregulation, display, or hydrodynamic. The display hypothesis includes attracting mates, intimidating rivals, and social communication with other members. This literature review delves into each of the three hypotheses using past studies and excavation sites to analyze their validity. For the hydrodynamic aspect, the lifestyle of *S. aegyptiacus* must first be established. Based on existing research, we cannot conclude that there is a definitive primary function of *Spinosaurus aegyptiacus*'s dorsal sail. However, it is likely that its sail served the crucial function of display, since it would have a large surface area and could thus be a distinguishable characteristic of *S. aegyptiacus* that could determine mating success. Additionally, it is probable that the sail had supplementary roles in thermoregulation and hydrodynamics.

Keywords: *Spinosaurus aegyptiacus*; dorsal sail; thermoregulation; display hypothesis; hydrodynamics; dinosaur morphology; functional analysis; paleobiology; thermoregulatory mechanisms; sexual display; social communication; aquatic adaptation; paleontological evidence; hypothesis evaluation; evolutionary biology

Functional Morphology of *Spinosaurus aegyptiacus*' Sail: Thermoregulation, Display, or Hydrodynamic?

The function of *Spinosaurus aegyptiacus*'s dorsal sail has been widely debated for many years. The three most popular hypotheses are that it was used as a biological mechanism of thermoregulation, display, or hydrodynamic. The display hypothesis includes attracting mates, intimidating rivals, and social communication with other members. The hydrodynamic aspect is a topic of debate as well. To analyze this hypothesis, we must determine the validity of claims stating that *Spinosaurus aegyptiacus* lived a semi-aquatic lifestyle.

Spinosaurus aegyptiacus has dimensions of 15-18 m in length, 4-7 m in height during quadrupedal position, and 7-20 metric tons, making it arguably the largest theropod to have ever existed. *S. aegyptiacus* lived during the mid-Cretaceous period, approximately 112 to 93 million years ago. Some notable features were its dorsal sail, elongated skull, robust forelimbs, fin-like tail, and nostrils positioned near the top of its skull. *S. aegyptiacus* inhabited what is now North Africa, with fossil evidence primarily found in regions such as Egypt and Morocco (Heckeberg et al., 2020). During the Cretaceous, this area was a lush, riverine environment, with large river systems and abundant aquatic life.

The purpose of this literature review is to gain a deeper understanding of the functional morphology of *Spinosaurus aegyptiacus*'s dorsal sail. I will delve into each of the three hypotheses, using past studies and excavation sites to analyze their validity. For the hydrodynamic aspect, I will first establish whether *S. aegyptiacus* engaged in a semi-aquatic lifestyle to determine if the hydrodynamic hypothesis should be explored. Finally, I will determine which of the three hypotheses is most accurate for *Spinosaurus aegyptiacus*'s dorsal sail.

Thermoregulation of *Spinosaurus aegyptiacus*'s Dorsal Sail

The thermoregulation hypothesis suggests that the dorsal sail of *Spinosaurus aegyptiacus* played a crucial role in regulating its body temperature, allowing it to efficiently manage heat exchange in its predominantly warm, aquatic habitat. We can analyze this hypothesis by examining thermoregulation in similar creatures, such as modern-day reptiles and sail lizards.

A study conducted by Bramwell & Fellgett (1973) investigated the purpose of *Dimetrodon grandis*' sail. *Dimetrodon* was a prehistoric reptile from the Cisuralian Period of the Early Permian, around 295-272 million years ago. Armed with serrated teeth for slicing through flesh and strong jaws, it was one of the most prevalent predators of its time, being 1.8-4.5 m in length. Its most distinguishable feature is its elongated neural spines that form a dorsal sail structure. *Dimetrodon grandis* is a useful reference creature since the anatomical morphologies of the sail structures regarding *Dimetrodon grandis* and *Spinosaurus aegyptiacus* are similar. The experiment determined the sail as a means of thermoregulation, enabling *Dimetrodon grandis* to be active for a longer duration within the 24-hour period and thus increasing its ability to capture prey. In the morning period, *Dimetrodon grandis* would be able to attain optimal activity temperatures at a faster rate compared to its prey, mostly consisting of poikilothermic animals. Another biological advantage would be towards the end of the day, when it was concluded that the elongated neural structures would be able to retain heat to a certain extent. This enabled *Dimetrodon grandis* to additionally hunt at times when their prey likely had expended most of their energy.

However, it is important to note that the sizes of these creatures are vastly different, playing a role in the extent of thermoregulation, as stated by Bailey (1997). According to Bailey, the sail structure would have proven to be efficient for *S. aegyptiacus* regarding thermal amplification and retention of heat, but due to its larger size compared to *Dimetrodon grandis*, would not be of much use in terms of dissipating heat from its body. Furthermore, a study by Rega et al. (2012) examined the dorsal neural structures of a specimen of *Dimetrodon giganhomogenes*, another species of *Dimetrodon*. The scientists discovered an absence of vascular communicating canals in the sail. This contradicts the belief that there may have been an extensive supply of blood vessels within the elongated neural structures, features that are necessary for the use of thermoregulation.

Modern reptiles have numerous biological structures that parallel those of *Spinosaurus aegyptiacus*, allowing us to gain more insight into the potential functions of *S. aegyptiacus*'s sail. One study by Turner & Tracy (1985) investigated how body size influences the ability of *Alligator mississippiensis* to regulate its body temperature. It examined the relationship between the surface area-to-volume ratio and heat exchange efficiency in alligators of different sizes. The scientists discovered that larger alligators have an increased ability to retain heat due to their lower surface area-to-volume ratio. This allows them to maintain their body temperature more effectively in cooler environments, as they lose heat more slowly compared to smaller individuals. However, the study also addressed that larger reptilians may encounter more difficulty dissipating heat, a conclusion determined by Seebacher et al. (2003) as well. Extrapolating this to *S. aegyptiacus*, it is likely that *S. aegyptiacus*, with a much larger size compared to *Alligator mississippiensis*, would experience an increased ability to retain heat but a decreased ability to dissipate heat through its sail.

Through various comparisons to modern-day reptiles and sail lizards such as *Dimetrodon* and *Alligator mississippiensis*, we can reasonably conclude that *Spinosaurus aegyptiacus*'s sail would have likely proved efficient for retaining thermal energy within the body, but ineffective in dissipating heat. Therefore, it is most probable that the thermoregulation hypothesis of *S. aegyptiacus*'s sail is accurate to a certain extent, and only applies for retention of heat. Hence, this application of *S. aegyptiacus*'s sail is unlikely to be the primary function but rather takes on a supplementary role.

Display of *Spinosaurus aegyptiacus*'s Dorsal Sail

The second plausible hypothesis of *S. aegyptiacus*'s sail function is that it was used as a means of display to surrounding individuals, including attracting mates, intimidating rivals, and

communicating with other members. Though there have been relatively few studies regarding this hypothesis, we can make comparisons to other similar creatures and postulate the accuracy of this hypothesis.

One important study was conducted by Tomkins et al. (2010), in which positive allometric relationships were investigated in *Pteranodon*, *Dimetrodon*, and *Edaphosaurus*. The focus of the study was the crest of *Pteranodon* and the sails of *S. aegyptiacus*. The results showed that *Dimetrodon*'s sail might have been used for display if it displayed positive allometry, supporting sexual selection. Similarly, for *Edaphosaurus*, the sail could have been a product of sexual selection if positive allometry is present, indicating its use in visual displays. For *Pteranodon*, the crest likely served as a sexually selected trait, especially if it grew disproportionately larger in larger individuals. As a result, *S. aegyptiacus*'s sail may have served the same purpose as those of *Dimetrodon* and *Edaphosaurus*, playing a role in sexual selection.

Another study by Hone & Naish (2013) highlighted that sail-like structures could serve as ornaments used in sexual selection, similar to how modern animals such as *Pavo cristatus* use visual displays. These structures might have been used to showcase individual fitness, health, or genetic quality to potential mates. Hone & Naish suggest that, in a similar way, dinosaurs with sail-like structures could have used them in sexual selection.

Although there has not been extensive research into the display function of *S. aegyptiacus*'s sail, it is reasonable to conclude that the sail of *Spinosaurus aegyptiacus* served as a display mechanism for attracting mates. The display function was most likely a crucial feature of the sail, since it would have a large surface area and could thus be a distinguishable characteristic of *S. aegyptiacus* that could determine mating success.

Hydrodynamics of *Spinosaurus aegyptiacus*'s Dorsal Sail

To evaluate the hydrodynamic hypothesis of *Spinosaurus aegyptiacus*'s sail, we must first determine whether *S. aegyptiacus* lived a semi-aquatic or primarily terrestrial lifestyle. One well-known study by Ibrahim et al. (2014) examined this through analysis of *S. aegyptiacus* body characteristics. It was found that *S. aegyptiacus* had many components that made it suitable for a semi-aquatic lifestyle. Some of these parts included a streamlined body, dense bones, shortened hind limbs, paddle-like feet, an elongated snout, and nostrils positioned farther back on the skull. All of these features are characteristics that would be of use for a semi-aquatic, piscivore lifestyle, aiding in catching fish, submerging underwater, and swimming. These results have also been confirmed by Arden et al. (2019) and Gimsa & Gimsa (2021).

Additionally, recall how Turner & Tracy stated that for larger *Alligator mississippiensis* individuals, a possible method of dissipating heat from the body would be behavior and usage of the environment. This could be applied to *Spinosaurus aegyptiacus*, as it could have released much of its thermal energy by submerging itself underwater. Furthermore, a study by Vullo et al. (2016) proved that there existed convergent evolution between spinosaurids and predatory pike conger eels regarding jaw structure, tooth placement and appearance, and elongated rostrum. This suggests that *S. aegyptiacus* likely engaged in similar feeding habits as those of the predatory pike conger eel, a significant predator of the ocean. Additional evidence is present in the form of fossils from many African Cretaceous excavation sites. Through these fossils, it is likely that *S. aegyptiacus* coexisted and engaged in competition for food against both terrestrial theropods and aquatic crocodylians.

Another helpful insight into *S. aegyptiacus*'s lifestyle is provided through an experiment conducted by Cuff & Rayfield (2013), in which the scientists analyzed the skull morphology and mechanical performance of *Spinosaurus aegyptiacus* using finite element analysis (FEA). It was found that *S. aegyptiacus* had a long, narrow, and lightweight skull with conical teeth, which is similar to that of modern fish-eating crocodylians such as gharials. Additionally, the skull morphology of *Spinosaurus aegyptiacus* suggests it was adapted for resisting bending and torsional forces, which are key characteristics of piscivory. Through comparative analysis between the skull mechanics of *S. aegyptiacus* with extant crocodylians, it is likely that *S. aegyptiacus* employed a similar feeding strategy,

involving rapid strikes to catch fish and other small aquatic prey. Furthermore, it was determined that, unlike most theropods such *Tyrannosaurus rex*, which had skulls optimized for biting and tearing flesh, *Spinosaurus aegyptiacus* had a skull optimized for seizing and holding onto slippery prey. The mechanical structure of the *S. aegyptiacus* skull supports the idea of lateral sweeping movements to catch prey, similar to the feeding behavior observed in modern crocodylians. Characteristics like these were also observed by Hone & Holtz Jr. (2021).

Despite this, there has been evidence contradicting the semi-aquatic hypothesis of *S. aegyptiacus*. For instance, a study by Henderson (2018) used digital models and simulations to examine the buoyancy, balance, and stability of *Spinosaurus aegyptiacus* in water. It was determined that *Spinosaurus* would have been highly buoyant, with a center of mass located high above the waterline. This buoyancy would have made it difficult for *Spinosaurus* to submerge and maintain stability while swimming. The study pointed out that the skeletal structure of *Spinosaurus* does not support the idea of it being well-adapted for an aquatic lifestyle. For example, its long, narrow limbs and sail structure could have impeded efficient swimming.

Another study conducted by Sereno et al. (2022) specifically addressed the function of the tail and limbs. They suggested that the tail, which has been interpreted as adapted for aquatic propulsion, could instead be more suited to a terrestrial or semi-aquatic environment. The limb proportions and structure were also reevaluated to argue against a fully aquatic lifestyle. A comparative analysis with modern aquatic and semi-aquatic animals determined that *Spinosaurus aegyptiacus* lacks several key adaptations seen in true marine animals, which challenges the idea that it was a specialized aquatic predator.

Thus, it is most reasonable that *S. aegyptiacus* lived a shoreline lifestyle, wading in the water to catch fish and other prey but not as a specialized aquatic predator. Morphological features such as an elongated skull, conical teeth, streamlined body, increased lateral movement, and nostril position would most likely be used by *S. aegyptiacus* to catch fish and other aquatic creatures from the shoreline area. In addition, *S. aegyptiacus* would have engaged in terrestrial hunting similar to other carnivorous theropods.

As we have concluded that *Spinosaurus aegyptiacus* engaged in a shoreline lifestyle, we can now examine the hydrodynamic hypothesis of *S. aegyptiacus*'s sail. As *S. aegyptiacus* likely did not roam and swim into deeper waters, it is improbable that its sail structure served a significant hydrodynamic purpose. Though it would potentially aid to a certain extent in the water, the sail would mostly cause *S. aegyptiacus* to experience greater water resistance and drag. Therefore, hydrodynamics was likely not the primary function of *S. aegyptiacus*'s dorsal sail, but rather a supplemental feature similar to the thermoregulation aspect.

Conclusion

Limitations on Existing Research

More research needs to be conducted to fully understand the functions of *Spinosaurus aegyptiacus*'s sail, especially the thermoregulation, display, and hydrodynamics aspect of it. For instance, this literature review could not cover the possibility of the sail serving the function of intimidation displays or social communication, since there have been few studies regarding those hypotheses. Most of our understanding is based on comparative analysis with modern creatures, simulations and models, and existing knowledge regarding anatomy and biological processes. There will always be a degree of uncertainty with models, and though *S. aegyptiacus* may be anatomically similar to certain creatures, there are several differences that will be unaccounted for. Therefore, there are numerous limitations to fully determining the lifestyle of *Spinosaurus aegyptiacus* unless further research is conducted.

Takeaway

Based on existing research, we cannot conclude that there is a definitive primary function of *Spinosaurus aegyptiacus*'s dorsal sail. However, it is likely that its sail served the crucial function of display, since it would have a large surface area and could thus be a distinguishable characteristic of *S. aegyptiacus* that could determine mating success, following a well-observed pattern of positive sexual allometry. Additionally, it is probable that the sail had supplementary roles, acting both as a mechanism of thermoregulation and hydrodynamics. It would have proved efficient for retaining thermal energy within *S. aegyptiacus*'s body, but ineffective in dissipating heat. The sail would also function in moderately aiding *S. aegyptiacus* in roaming through the waters near the shoreline. Overall, *Spinosaurus aegyptiacus*'s sail would serve numerous purposes, all supporting it in its shoreline-terrestrial life.

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