

# Preliminary Study on the Reconstruction and Function of the Hyperelongate Neural Spines in the Dorsal Vertebrae of *Deinocheirus mirificus* (Theropoda: Ornithomimosauria)

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**Abstract.** *Deinocheirus* is a bizarre and unique theropod dinosaur. The holotype of *Deinocheirus* was discovered in 1976, but its characteristics and phylogenetic position remained largely enigmatic due to the scarcity of fossil material. This changed in 2014 when Lee et al. described two additional specimens, providing a deeper insight into this mysterious creature. Notably, the smaller specimen MPC-D 100/128 preserved a relatively complete dorsal vertebra with hyperelongated neural spines, reaching up to 8.5 times the height of the corresponding centra. This suggests that *Deinocheirus* possessed a raised dorsal sail or hump-like structure. Elongated neural spines have evolved multiple times in dinosaurs, including in ornithomimosaurs as well as theropods and sauropods of saurischians, with various hypothesized functions such as thermoregulation, fat storage, or sexual display. However, previous research on the neural spines of *Deinocheirus* has been limited to brief description, lacking detailed analysis and leaving the morphology and function of these dorsal structures poorly understood. To better understand the possible dorsal structure of *Deinocheirus* and its ecological role, this study examines the dorsal neural spines of *Deinocheirus* and 26 other dinosaurs. Through measurement and comparative analyses, we categorize the height and width of neural spines into different categories. Our comparison reveal that the neural spines of *Deinocheirus* are most similar to those of *Spinosaurus* and *Ouranosaurus*, with a height ratios exceeding 7 and overall morphology closer to the latter. Additionally, the anteroposterior width of neural spines of *Deinocheirus* is slightly narrower than that of *Spinosaurus* and *Ouranosaurus*. Based on these data and previous studies, we infer that the hyperelongated neural spines of *Deinocheirus* may serve dual functions: supporting a sail related to aquatic habits and a hump associated with an intricate interspinous ligament system, potentially for fat storage to aid in surviving dry seasons. Finally, we discuss avenues for future research, such as bone histology and finite element analysis, which could provide further insights into the morphology and function of the neural spines of *Deinocheirus*.

**Keywords:** Mesozoic; Dinosauria; Functional morphology; Osteology; Sail-Backed.

## 1. Introduction

*Deinocheirus* is a bizarre and unique theropod dinosaur, characterized by its enlarged body, elongated snout, deep mandible, relatively short hindlimbs unsuitable for running, and massive forelimbs [Lee et al., 2014]. The holotype of *Deinocheirus* was discovered in 1976 and consists primarily of enlarged forelimbs, measuring 2.4 meters in length, along with scapulocoracoids [Roniewicz et al., 1970]. Due to the scarcity of fossil materials and its distinctive characteristics, research on *Deinocheirus* remained largely enigmatic for decades, and it was even once misclassified as a carnosaurian dinosaur [Roniewicz et al., 1970]. It was not until 2014 that Lee et al. described two additional specimens, providing further insights into this mysterious creature. The more complete specimen, MPC-D 100/127, is exceptionally well-preserved, lacking only some middle dorsal vertebrae, caudal vertebrae and right forelimb. The other specimen, MPC-D 100/128, represents a younger, sub-adult individual and is about the 74% the size of the former [Lee et al., 2014]. This smaller specimen MPC-D 100/128 preserves a relatively complete dorsal vertebra with hyperelongated neural spines that reach up 8.5 times the height of the corresponding centra, suggesting the presence of a raised dorsal sail or hump-like structure [Bailey, 1997, Lee et al., 2014].



Elongated neural spines have independently evolved multiple times in dinosaurs, including in both ornithischian ornithopods and saurischian theropods and sauropods [Madsen et al., 1976, Bailey, 1997, Harris, 1998, Ibrahim, 2014, Gasulla et al., 2015]. Among sauropods, several diplodocids are particularly noted for their extremely elongated, paired neural spines on cervical vertebrae, such as *Amargasaurus*, *Bajadasaurus*, *Pilmatueia*, and *Rebbachisaurus* [Salgado and Bonaparte, 1991, Ortega et al., 2009, Wilson, J. A., & Allain, R. 2015, Xu et al., 2018, Gallina et al., 2019]. However, these elongated neural spines are primarily prominent in the cervical vertebrae. In addition, given that sauropods are large quadrupeds, their dorsal vertebrae structures offer limited comparative value for understanding *Deinocheirus*. As *Deinocheirus* was bipedal and possessed elongated neural spines mainly on the dorsal vertebrae, theropods and ornithopods with similar features provide more relevant comparisons. Ornithopods such as *Morelladon*, *Hypacrosaurus*, and *Ouranosaurus* exhibit these traits, especially neural spines of *Ouranosaurus* reaching approximately seven times the height of the centrum [Bailey, 1997]. Among theropods, in addition to *Deinocheirus*, groups with prominent dorsal neural spines are mainly distributed in spinosaurs and carcharodontosaurians [Bailey, 1997, Ortega et al., 2010, Ibrahim, 2014]. Spinosaurids, such as *Spinosaurus* and *Ichthyovenator*, developed high neural spines, likely aiding their adaptation to aquatic environments [Bailey, 1997, Ibrahim, 2014]. Meanwhile, carcharodontosaurians such as *Acrocanthosaurus*, *Mapusaurus*, and *Concavenator*, also feature relatively high neural spines [Bailey, 1997, Ortega et al., 2010, Coria et al., 2006], with *Concavenator* being particularly unique due to the elongated neural spines being restricted to the last two dorsal vertebrae [Ortega et al., 2010].

In the past, the function of elongated neural spines has been widely debated, with hypotheses including thermoregulation, fat storage, and sexual display [Bramwell et al., 1973, Bailey, 1997]. For instance, the synapsid *Dimetrodon* is well-known for its elongated neural spines, which are believed to have played a role in thermoregulation. Simulation analysis by Bramwell et al. (1973) of *Dimetrodon* suggested that it would take 205 minutes to raise its body temperature from 26°C to 32°C without a sail, but only 80 minutes with one. However, *Dimetrodon* is not only distantly related to dinosaurs phylogenetically, but its neural spines are also morphologically distinct from those in dinosaurs. The neural spines of *Dimetrodon* are slender and cylindrical, suitable for supporting the dorsal sail, while those of dinosaurs like *Ouranosaurus*, *Acrocanthosaurus*, and *Spinosaurus* are significantly wider. The broader structure is more analogous to that of the American bison, serving as attachments for large muscles and ligaments, suggesting a hump-like structure rather than a sail [Bailey, 1997]. Additionally, the expansive area for inter- and supraspinous ligament attachment on the neural spines of *Acrocanthosaurus* indicates that this taxon did not possess a sail like *Dimetrodon*, but instead developed musculature on its back, resembling the structure of bison [Harris, 1998]. In contrast, while Bailey (1997) speculated that *Spinosaurus* may have had a bison-like hump, Ibrahim et al. (2014) argued that its neural spines lacked the well-developed ligament attachment sites seen in *Acrocanthosaurus*, suggesting that the elongated neural spines of *Spinosaurus* were less likely to support a muscle-covered hump, despite their broader shape.

Research on the neural spines of *Deinocheirus* has been limited, with only briefly described in the previous study, leaving the potential reconstruction and function of the structure largely unexplored. To gain better understanding of the dorsal neural spines of *Deinocheirus* and their role within the ecosystem, this study examines the neural spines of *Deinocheirus* in comparison with 26 other dinosaurs. Through measurement, comparative analysis, and reviewing previous studies, different forms of neural spines are categorized to explore their possible functions and ecological applications. Based on the results, this study proposes potential reconstruction and ecological roles for the hyperelongated neural spines of *Deinocheirus*, and discusses directions for further research.

## 2. Research Methods

### 2.1. Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; BMNH, British Natural History Museum, London, UK; BYU, Earth Sciences Museum, Brigham Young University, Provo, USA; CMP-MS, Mas de la Parreta Quarry-Mas de Sabater, Morelia, Mexico; FMNH, Field Museum of Natural History, Chicago, USA; GDF, National Museum of Niger, Niamey, Niger; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCCM, Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain; MOR, Museum of the Rockies, Bozeman, USA; MPC, Paleontological Center of Mongolian Academy of Science, Ulaanbaatar, Mongolia; NCSM, North Carolina State Museum of Natural Sciences, Raleigh, USA; OMNH, Oklahoma Museum of Natural History, Norman, USA; ROM, Royal Ontario Museum, Toronto, Canada; UA, Université d'Antananarivo, Antananarivo; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. ZIN PH, Paleoherpological Collection, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

### 2.2. Terms and definitions

This study categorizes the morphology of dorsal vertebrae into four types based on the dorsoventral height ratio of the neural spine to the centrum (N/C height ratio): Hyperelongate (H), Elongate (E), Normal (N), and Reduced (R). These categories correspond to N/C height ratio values greater than 7, between 4 and 7, between 1.5 and 4, and less than 1.5, respectively. Additionally, the study classifies the width of the vertebrae using the anteroposterior width ratio of the neural spine to the centrum (N/C width ratio). The width categories are defined as Broad (B), Moderate (M), and Narrow (Na), corresponding to N/C width ratio values greater than 1, between 0.5 and 1, and less than 0.5, respectively.

This study collects data on 27 dinosaurs (twelve theropods, five sauropods, seven ornithopods, and three other ornithischians). Among the measurements, seven dinosaurs are known for their elongated neural spines (four theropods, one sauropod, and three ornithopods) are based on the maximum value of the N/C height ratio in the preserved dorsal vertebrae sequence, while the width ratio is measured based on the dorsal vertebrae. The results are shown in Table 1. The measurements are based on the ratios and values given in the previous studies. If there is no measurement data, the measurement is taken from the figures or photos.

## 3. Results

**Table 1.** Comparative measurement data of dorsal neural spines and vertebral bodies of dinosaurs

Species name	specimen		N/C Height Ratio	Location	definition	N/C Width Ratio	definition	references
<i>Deinocoelurus mirificus</i>	MPC-D 100/128	Dinosaurs, Theropods, Ornithomimids	8.5	12th dorsal	H	0.82	M	Lee et al., 2014
<i>Ornithomimidae</i> gen. et sp.	ZIN PH 535/16	Dinosaurs, Theropods, Ornithomimids	1.1	Posterior dorsal	R	0.14	Na	Sues et al., 2014
<i>Nothronychus mckinleyi</i>	MSM P2117	Dinosaurs, Theropods, Therizinosaurs	2.89	Anterior dorsal	N	1.12	B	Hedrick et al., 2015
<i>Buitreraptor gonzalezorum</i>	MPCA 245	Dinosaurs, Theropods, Dromaeosaurs	1.1	Mid dorsal	R	0.75	M	Gianechini et al., 2018

<i>Concavenator corcovatus</i>	MCCM-LH 6666	Dinosaurs, theropods, carcharodontosaurians	5	11th dorsal	E	0.9	M	Ortega et al., 2010
<i>Acrocanthosaurus atokensis</i>	NCSM 14345	Dinosaurs, theropods, carcharodontosaurians	4	last dorsal	E	1.13	B	Bailey.,1997
<i>Ichthyovenator laosensis</i>	BK 10-01	Dinosaurs, Theropods, Spinosaurus	4.1	12th dorsal	E	1.39	B	Allain et al.,2011
<i>Spinosaurus aegyptiacus</i>	BSP 1912 VIII 19	Dinosaurs, Theropods, Spinosaurus	11	Mid dorsal	H	0.9	M	Stromer, 1915
<i>Becklespinax altispinax</i>	BMNH R1828	Dinosaurs, Theropods, Orionosaurs	4.1	Posterior dorsal	E	0.9	M	O'Connor, 2007
<i>Tyrannosaurus rex</i>	FMNH PR2081	Dinosaurs, Theropods, Tyrannosaurus	1	13th dorsal	R	0.51	M	brochu,2003
<i>Majungasaurus crenatissimus</i>	UA 8678	Dinosaurs, Theropods, Abelisaurids	1.2	11th dorsal	R	0.15	Na	O'Connor, 2007
<i>Allosaurus jimmdseni</i>	MOR693	Dinosaurs, Theropods, Allosaurs	1.2	11th dorsal	R	0.82	M	Wilson et al., 2015
<i>Spinophorosaurus nigerensis</i>	GCP-CV-4229	Dinosaurs, Sauropods, Gravisauria	1.3	last dorsal	R	0.64	M	Ortega et al., 2009
<i>Amargasaurus cazai</i>	MACN-N 15	Dinosaurs, Sauropods, Diplodocus	3.5	Mid dorsal	N	—		Salgado and Bonaparte, 1991
<i>Rebbachisaurus garasbae</i>	MNHN-MRS 1958	Dinosaurs, Sauropods, Reptilia	4	Mid dorsal	E	0.88	M	Wilson, J. A., & Allain, R. (2015)
<i>Apatosaurus ajax</i>	OMNH 1382	Dinosaurs, sauropods, apatosaurus	2	Mid dorsal	R	1.1	B	Wedel.,2006
<i>Phuwiangosaurus sirindhornae</i>	BYU 10976	Dinosaurs, Sauropods, Euhelopodidae	2.5	Posterior dorsal	R	0.82	M	Mantilla.,2012
<i>Corythosaurus casuarius</i>	ROM 845	Dinosaurs Ornithopods Hadrosaurs	2	Posterior dorsal	N	—		Dodson, 1975
<i>Parasaurolophus walkeri</i>	ROM 768	Dinosaurs Ornithopods Hadrosaurs	2	Posterior dorsal	N	—		Bailey.,1997
<i>Barsboldia sicinskii</i>	ZPAL MgD-I/11	Dinosaurs Ornithopods Hadrosaurs	2.5	Posterior dorsal	N	0.34	Na	Maryariska and Osmolska, 1981
<i>Lambeosaurus lambei</i>	ROM1218	Dinosaurs Ornithopods Hadrosaurs	2	Posterior dorsal	N	—	—	Bailey.,1997

<i>Morelladon beltrani</i>	CMP-MS-03-02	Dinosaurs, Ornithopods, Iguanodon	4.3	Posterior dorsal	E	0.52	M	Gasulla et al., 2015
<i>Ouranosaurus nigeriensis</i>	GDF300	Dinosaurs Ornithopods Hadrosaurs	7	9th dorsal	H	1	M	Bertozzo et al. 2017
<i>Hypacrosaurus altispinus</i>	AMNH 5206	Dinosaurs Ornithopods Hadrosaurs	4.5	Mid dorsal	E	—	—	Weishampel and Homer, 1990
<i>Montanoceratops cerorhynchus</i>	AMNH 5464	Dinosaurs, Ornithischia, Leptoceratops	1.5	last dorsal	R	—	—	Brown and Schlaikjer, 1942
<i>Wuerhosaurus homheni</i>	IVPP V4006	Dinosaurs, Ornithischia, Stegosaurus	2.8	Posterior dorsal	R	—	—	Maidment et al., 2008
<i>Polacanthus foxii</i>	BEXHM 2002.50.87	Dinosaurs, Ornithischia, Ankylosaurs	1.5	Posterior dorsal	R	0.52	M	Blows et al., 2014

The neural spine to centrum (N/C) height ratio of *Deinocheirus* MPC-D 100/128 is 8.5 [Lee et al., 2014], indicating a hyperelongated spine. Among the dinosaurs examined in this study, only *Spinosaurus* shares a similarly elongated spine type [Ibrahim, 2014], making such a high N/C ratio exceptionally rare. Dinosaurs previously thought to have relatively high neural spines, such as *Acrocanthosaurus*, *Concavenator*, *Ichthyovenator*, *Hypacrosaurus*, and *Morelladon* [Bailey, 1997, Ortega et al., 2010, Allain et al., 2011, Gasulla et al., 2015], typically exhibit N/C ratios between 4 and 5. Although these species have relatively tall neural spines, they still show a significant disparity when compared to *Deinocheirus* and *Spinosaurus*.

Most dinosaurs have a lower N/C ratio, ranging between 1.5 and 4. For example, *Buitreraptor*, *Corythosaurus*, and *Barsboldia* fall within this range. Among these, *Nothronychus* has a ratio of 2.89, which is notably high among general dinosaurs and may represent a shared derived trait of early maniraptorans. However, the absence of this trait in Ornithomimids (e.g., ZIN PH 535/16) suggests that independent evolution cannot be ruled out [Sues et al., 2016].

Conversely, many dinosaurs have N/C ratios below 1.5. For instance, *Tyrannosaurus* typically has a ratio of around 1, with some specimens (e.g., BHI3033) showing slightly higher values up to 1.2, indicating relatively unremarkable neural spine height (Brochu, 2003). Similarly, *Allosaurus* has an N/C ratio of approximately 1.2. In sauropods, known for their large size and specialized structures, some species like *Rebbachisaurus* and *Amargasaurus* exhibit notably elongated cervical neural spines [Salgado and Bonaparte, 1991, Wilson & Allain, 2015], while their dorsal neural spines are also relatively high. In contrast, other sauropods, such as *Apatosaurus*, *Spinophorosaurus*, and *Phuwiangosaurus*, generally have shorter neural spines.

Herbivorous dinosaurs, including *Parasaurolophus* and *Lambeosaurus*, display N/C ratios between 2 and 4. On average, ornithopods exhibit relatively high N/C ratios, with no values below 1.5. In contrast, non-ornithopod ornithischians generally have lower N/C ratios, around 1.5, as seen in *Polacanthus* and *Montanoceratops*. Even among those with taller neural spines, such as *Wuerhosaurus*, the ratio reaches only about 2.8, still comparatively lower than other ornithopods.

The anteroposterior width ratio of neural spines serves as a key anatomical indicator among dinosaurs. For most dinosaurs, this ratio ranges between 0.5 and 1, encompassing well-known species such as *Tyrannosaurus*, *Concavenator*, and *Becklespinax* [Brochu, 2003, Ortega et al., 2010]. In contrast, species like *Acrocanthosaurus* and *Ouranosaurus* have broader neural spines with ratios exceeding 1, which typically suggests more muscle attachment points along the back [Bailey, 1997]. Some theropods, such as *Majungasaurus*, have notably narrower neural spines, with ratios as low as 0.15

[O'Connor, 2007]. The anterior-posterior width ratio of *Deinocheirus* is around 0.82, placing it in a moderate range similar to many other theropods [Lee et al., 2014]. Only a few theropods, like *Ichthyovenator* and *Acrocanthosaurus*, exceed a ratio of 1 [Allain et al., 2011].

Among ornithopods, there is significant variation in neural spine width. For example, *Barsboldia* has a relatively narrow anteroposterior width ratio of 0.34 [Maryanska and Osmólska, 1981], while *Morelladon* has a more moderate ratio of about 0.52 [Gasulla et al., 2015]. The neural spines of *Ouranosaurus*, known for its tall neural spines, are relatively wide, with a ratio around 1 [Bertozzo et al., 2017]. In sauropods, the anteroposterior width of neural spines is generally moderate, as seen in *Spinophorosaurus* and *Rebbachisaurus*. An exception is *Apatosaurus*, with a ratio exceeding 1, at approximately 1.1 [Salgado and Bonaparte, 1991, Wedel, 2006, Ortega et al., 2009, Mantilla, 2012, Wilson & Allain, 2015]. Data on ornithischians are relatively scarce, but *Polacanthus* presents a moderate neural spine width ratio of 0.52 (Brown and Schlaikjer, 1942, Maidment et al., 2008, Blows et al., 2014).

Combining the width and height measurements, the neural spines of *Deinocheirus* closely resemble those of *Spinosaurus*, both having a height more than eight times the length of the centrum, which classifies them as extremely elongated. While the height of the neural spines of *Ouranosaurus* is comparable to that of *Deinocheirus*, the anteroposterior width of its neural spines is slightly broader. Many theropods, such as *Tyrannosaurus*, *Becklespinax*, and *Ichthyovenator*, have neural spines of moderate anterior-posterior width, but their heights do not reach the elongated ratio seen in *Deinocheirus*. Similarly, the anteroposterior width ratio of *Morelladon* (an ornithopod) is comparable to *Deinocheirus*, but its neural spines are relatively shorter. *Spinosaurus* and *Deinocheirus* stand out as some of the few dinosaur species known to have such a high N/C height ratio, making this extremely elongated spine structure very rare among dinosaurs.

## 4. Discussion

### 4.1. Restoration and Ecological Inference

The collected data indicates that the neural spine elongation in *Deinocheirus* (N/C height ratio of 8.5) is most comparable to that of *Ouranosaurus* (N/C height ratio of 7.5). Both species exhibit an extremely heightened spine morphology, similar to *Spinosaurus*. However, the spine elongation of *Spinosaurus* (N/C height ratio of 11) is still considerably greater than that of both *Deinocheirus* and *Ouranosaurus*. Due to the limited number of specimens, the elongated neural spines are only preserved in the smaller individual, MPC-D 100/127 (Lee et al., 2014). This makes it difficult to determine whether the feature would change in proportion or morphology as the animal matured.

Regarding the N/C width ratio, *Deinocheirus* (0.82) is closer to *Spinosaurus* (0.9) among the extremely elongated dinosaurs, but slightly narrower than *Ouranosaurus* (1.0). However, the ratio for *Deinocheirus* is still within a moderate range and does not show significant variation. Since these three dinosaurs are distantly related, and no other species with similar values have been observed among the ornithischians, ornithomimosaur like *Deinocheirus*, or ornithopods like *Ouranosaurus* (Table 1), it is likely that their extremely elongated neural spines evolved independently rather than from a shared common ancestor.

Based on the morphology of the neural spines, the back structure of *Deinocheirus* appears to be more similar to that of *Ouranosaurus*. However, since this feature is only observed in a smaller individual, it is possible that the structure could resemble that of *Spinosaurus* in adulthood. According to Ibrahim et al. (2014), the neural spines of *Spinosaurus* are likely to have supported a dorsal sail, while *Ouranosaurus* is thought to have had a hump-like structure [Bailey, 1997]. Given the existing data, it is more plausible that *Deinocheirus* had a hump-like structure similar to *Ouranosaurus*. Additionally, periodic droughts in the Nemegt Formation may have resulted in scarce plant resources at certain times [Jerzykiewicz et al., 1991]. The intricate system of interspinous ligaments in the neural spines of *Deinocheirus* [Lee et al., 2014] may have provided attachment points for muscles

that could support a hump and store fat. This suggests that the neural spines of *Deinocheirus* may have functioned in a way similar to a hump structure.

Conversely, the discovery of fish vertebrae and scales within the gastroliths of *Deinocheirus* suggests that this dinosaur may have had some aquatic habits, possibly even fishing for food. This raises the question, from the perspective of convergent evolution, of whether *Deinocheirus* might have possessed similar functional adaptations to those of the aquatic *Spinosaurus* [Ibrahim, 2014, Ibrahim, 2020]. In a study by Bramwell et al. (1973), the dorsal sail of *Dimetrodon* was shown to have advantages in regulating body temperature, which is a crucial physiological function for organisms moving between water and land. A considerable body of evidence supports the aquatic lifestyle of *Spinosaurus* [Ibrahim, 2014], while the stomach contents of *Deinocheirus* indirectly suggest similar aquatic traits. It is possible that both species used their dorsal structures for thermoregulation [Lee et al., 2014]. This hypothesis could also explain why *Deinocheirus*, which has well-developed muscles and ligaments suggesting a hump structure, possesses neural spines that are more than twice as tall as those of other dinosaurs known to have humps, such as *Acrocanthosaurus*. It is therefore plausible that the dorsal sail of *Deinocheirus* served functions beyond merely storing fat [Bailey, 1997; Lee et al., 2014].

Additionally, some modern birds, such as the black heron (*Egretta ardesiaca*), spread their wings to create an umbrella-like shadow over the water's surface, a behavior known as "canopy feeding," which attracts fish into the shaded area [Karikehalli, 2019]. However, unlike *Spinosaurus*, *Deinocheirus* does not exhibit many morphological traits indicative of a highly aquatic lifestyle. This suggests that *Deinocheirus* may not have been as specialized for aquatic hunting as *Spinosaurus*, whose back muscles and elongated neural spines appear to be adapted for maneuvering and predating on large aquatic prey [Lee et al., 2014]. Instead, *Deinocheirus* might have been more similar to wading birds, primarily feeding on floating plants along riverbanks while using its semi-sail structure to absorb sunlight for thermoregulation and to catch fish attracted to the shadow.

In summary, our data support that the high neural spines of *Deinocheirus* should have more diverse uses. The main function is to store fat, with a partial hump structure attached by the intricate system of interspinous ligaments. The distal end has a bulge that becomes a dorsal sail, which assists in the aquatic ecology.

## **4.2. Future Research Directions**

Due to the limited access to physical specimens, this study was unable to conduct field visits or directly sample fossil materials. Instead, it relied on measurement data and images from existing literature. Future research could benefit from direct examination of *Deinocheirus* and related species, including field studies and sampling of fossil specimens to validate current findings. Additionally, further research might explore advanced imaging techniques, biomechanical modeling, or comparative studies with both extant and extinct species to better understand the evolutionary significance and functional adaptations of neural spine structures in dinosaurs.

### **4.2.1. Application and analysis of bone histology**

Bone histology is an important step in studying the growth and development patterns of organisms by observing the internal structure of bones under a microscope. By observing the Lines of Arrested Growth (LAG) in bones, scientists can infer the growth rate and age of dinosaurs, and can reflect the annual growth cycle of organisms.

First, we could perform histological studies on the neural spines of *Deinocheirus*, similar to previous research on *Dimetrodon*. By examining its bone tissue, we could observe growth patterns and assess potential impacts on limb function and mobility. Studies on juvenile *Dimetrodon* have shown the presence of woven-fibered bone (WFB) with a high degree of vascularity [Agliaio et al., 2020, Brink et al., 2019]. Additionally, bone histology of the dorsal neural spines of *Lupeosaurus* and *Edaphosaurus* has revealed extensive cancellous bone in the "medullary" area, consisting of a

lamellar bone matrix with distinct growth zones, rings, and dense Sharpey's fibers, especially near the anterior and posterior ridges. This allowed researchers to determine the attachment direction of the Musculi interspinales and interarch muscles [Huttenlocker et al., 2010].

Unlike synapsids such as *Dimetrodon*, histological studies on *Amargasaurus*, a large sauropod, have examined various sections of its dorsal vertebrae. The distribution and orientation of Sharpey's fibers suggest the presence of an extensive interspinous ligament system connecting its continuous semispinous processes [Cerdeña et al., 2021]. As a bipedal theropod, *Deinocheirus* may exhibit different bone histological patterns compared to these synapsids and sauropods. Future studies could focus on identifying muscle or ligament attachment points through Sharpey's fibers, providing a more comprehensive understanding of its anatomy and function.

Other bone histological studies have been conducted on *Amargasaurus*. For example, the dorsal ribs of *Amargasaurus* exhibit a higher number of Lines of Arrested Growth (LAGs) compared to its long bones, which may be related to its growth and developmental patterns [Windholz et al., 2021]. *Deinocheirus* also has some preserved ribs that could be analyzed histologically to better understand its growth patterns, including the possibility of allometric growth.

Similarly, *Acrocanthosaurus*, which also possesses high neural spines, has undergone bone histological analysis. By examining its LAGs, researchers have gathered important insights into its growth pattern. For example, studies on the fibula of *Acrocanthosaurus* (UM 20796), the fibula rib (NCSM 14345), and the tibia (OMNH 10146) have revealed closely spaced LAGs before a period of rapid growth, followed by more widely spaced LAGs. This pattern indicates that *Acrocanthosaurus* experienced a phase of accelerated growth [D'Emic et al., 2012].

If *Deinocheirus* can be studied through bone histology, examining the femur would be particularly beneficial, as this bone typically contains distinct growth lines that can help infer the organism's growth rate and age. By analyzing the annual rings and growth lines of the femur's bone tissue, we could estimate the growth rate of *Deinocheirus*. Given that the specimen MPC-D 100/128 represents a subadult individual [Lee et al., 2014], comparing its Lines of Arrested Growth (LAGs) with those of the adult specimen MPC-D 100/127 could provide insights into the growth transition from subadult to adult stages.

Understanding the growth process of *Deinocheirus*, including whether it exhibits a seasonal growth pattern, is crucial. This could validate the hypothesis that *Deinocheirus* stored fat during the dry season of the Nemegt Formation. If *Deinocheirus* reduced growth during the dry season to conserve fat and accelerated growth during the wet season, it would support the idea that it adapted to seasonal changes in its environment. Verifying this hypothesis would be significant for understanding the ecological strategies of *Deinocheirus*.

#### **4.2.2. Biomechanics and structural analysis**

Finite Element Analysis can help us understand the lifestyle and ecology of dinosaurs by simulating and calculating the load and stress distribution of dinosaur bones and muscles.

Similar studies have been conducted on various dinosaurs, such as *Tyrannosaurus*, *Carnotaurus*, and *Allosaurus* [Mazzetta et al., 2009, Gignac et al., 2017]. These studies utilized computed tomography (CT) scans and finite element analysis (FEA) to simulate the bite force of these carnivorous dinosaurs. The results, showing strong bite forces and stress distribution, underscore their roles as apex predators within their ecological niches [Rayfield et al., 2005]. Finite element analysis has also been applied to the claws of *Therizinosaurus*. This analysis revealed that its claws were adapted for use as grappling hooks during foraging, enhancing its feeding capabilities. These findings highlight a trend of increased functional diversity among maniraptoran-like dinosaurs compared to their theropod ancestors. This divergence in claw morphology parallels the cranial adaptations observed in derived theropods, driven by dietary specialization. This suggests that dietary diversification was a significant factor in shaping the morphological and functional diversity observed in theropod evolution [Lautenschlager et al., 2014, Qin et al., 2023].



Neural spine modeling and mechanical analysis through Finite Element Analysis (FEA) could reveal new insights into the functional morphology of *Deinocheirus*. By employing FEA to simulate stress distribution and mechanical loads on the neural spines, researchers can identify potential attachment points for muscles and ligaments, as well as assess the structural suitability for storing fat or other tissues. For instance, FEA simulations can help determine which areas of the neural spines are optimal for fat storage. This could shed light on the physiological adaptations of *Deinocheirus* in response to seasonal changes. By analyzing how stress is distributed along the neural spines under different mechanical conditions, we can infer the potential functions of these structures. If the neural spines are found to support substantial muscle attachment, this might indicate a role in defense against predators such as *Tarbosaurus*, where robust muscles could help mitigate attacks.

Alternatively, if the simulations show that the neural spines are relatively slender, it might suggest adaptations for aquatic activities similar to those seen in *Spinosaurus*. The neural spines could then play a role in aiding swimming or catching fish, potentially in combination with specialized claw structures. Additionally, FEA could provide insights into the functionality of the claws of *Deinocheirus*. By simulating various mechanical scenarios, we can explore whether these claws served as tools for wading and catching fish, similar to the feeding behaviors observed in some modern wading birds, or if they functioned as defensive weapons against predators. Understanding these aspects will offer a more comprehensive view of how *Deinocheirus* interacted with its environment and adapted to its ecological niche.

#### **4.2.3. Analysis of the possibility of display and behavior**

Since only the specimen MPC-D 100/128 of *Deinocheirus* has been found with dorsal neural spines, it remains uncertain whether this feature is sexually dimorphic or varies with age. The extreme elongation of the neural spines in *Deinocheirus*, combined with their moderate width, makes them a conspicuous feature. This prominence might be more pronounced in males and could potentially change with age, serving as a visual signal for attracting mates or for interspecies recognition. Additionally, these neural spines could function as a display mechanism to enhance the dinosaur's perceived size, serving both a deterrent and defensive role.

The Nemegt Formation, where *Deinocheirus* was found, also housed formidable predators like *Tarbosaurus*. The powerful bite force and predatory capabilities of *Tarbosaurus* would have posed significant survival threats to *Deinocheirus* [Bell et al., 2012]. Evidence from the holotype specimen MPC-D 100/18, which shows bite marks on the gastralia, suggests encounters with *Tarbosaurus* or other large carnivorous dinosaurs, indicating a dangerous environment.

## **5. Conclusion**

In this study, we analyzed the neural spine morphology of *Deinocheirus* MPC-D 100/128 in detail and compared it with the corresponding structures of other dinosaurs. The results show that the degree of neural spine elevation of *Deinocheirus* (N/C height ratio of 8.5) is closest to that of *Ouranosaurus* (7.5), while *Spinosaurus* (11) is significantly higher than the former two. The anterior-posterior width ratio of the neural spine of *Deinocheirus* (0.82) is also between *Spinosaurus* (0.9) and *Ouranosaurus* (1.0), indicating that its structure is very unique among extremely elevated dinosaurs.

Further ecological inferences show that it may have similarities with both *Spinosaurus* and *Ouranosaurus*. The periodic drought in the Nemegt Formation made plants scarce, and the intricate system of interspinous ligaments in the neural spines of *Deinocheirus* may have helped muscle attachment and formed a hump to store fat to cope with seasons of resource shortages. In addition, the fish vertebrae and scales found in the stomach of *Deinocheirus* indicate that it may have had a certain aquatic life, which further supports that its neural spines may have the function of regulating body temperature to adapt to the needs of aquatic ecology.

At the same time, we also hope that in the future, specimens of *Deinocheirus* can be studied more thoroughly and in more detail, especially through more fossil evidence and advanced technical means, such as computed tomography (CT scan) and finite element analysis (FEA), to conduct a more in-depth analysis of the structure of *Deinocheirus*'s neural spines, so as to have a more comprehensive understanding of its ecological adaptation and evolutionary background. Through continued research, we can not only better understand the ecology and behavior of *Deinocheirus* and its closely related species, but also provide new perspectives and methods for paleoecology.

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## References

- [1] Allain, R., Xaisanavong, T., Richir, P., & Khentavong, B. (2012). The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the Early Cretaceous of Laos. *Die Naturwissenschaften*, 99(5), 369–377.
- [2] Agliano, A., Sander, P. M., & Wintrich, T. (2021). Bone histology and microanatomy of Edaphosaurus and Dimetrodon (Amniota, Synapsida) vertebrae from the Lower Permian of Texas. *The Anatomical Record*, 304(3), 570–583.
- [3] Brink, K. S., MacDougall, M. J., & Reisz, R. R. (2019). Dimetrodon (Synapsida: Sphenacodontidae) from the cave system at Richards Spur, OK, USA, and a comparison of Early Permian-aged vertebrate paleoassemblages. *Die Naturwissenschaften*, 106(1-2), 2.
- [4] Bailey, J.B. (1997). Neural spine elongation in dinosaurs: sailbacks or buffalo-backs? *Journal of Paleontology*, 71, 1124 - 1146.
- [5] Bell, P. R., Currie, P. J., & Lee, Y. N. (2012). Tyrannosaur feeding traces on *Deinocheirus* (Theropoda: Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia. *Cretaceous Research*, 37, 186–190.
- [6] Bertozzo, F., Dalla Vecchia, F. M., & Fabbri, M. (2017). The Venice specimen of *Ouranosaurus nigeriensis* (Dinosauria, Ornithopoda). *PeerJ*, 5, e3403.
- [7] Blows, W. T., & Honeysett, K. (2014). First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. *Proceedings of the Geologists' Association*, 125(2), 233–251.
- [8] Bramwell, C. D., Fellgett, P.P. (1973) Thermal regulation in sail lizards. *Nature*. 242: 203–205
- [9] Brochu, C. A. (2003). Osteology of *Tyrannosaurus Rex*: Insights from a nearly complete Skeleton and High-Resolution Computed Tomographic Analysis of the Skull. *Journal of Vertebrate Paleontology*, 22(sup4), 1–138
- [10] Cerda, I. A., Novas, F. E., Carballido, J. L., & Salgado, L. (2022). Osteohistology of the hyperelongate hemispinous processes of *Amargasaurus cazau* (Dinosauria: Sauropoda): Implications for soft tissue reconstruction and functional significance. *Journal of Anatomy*, 240(6), 1005–1019.
- [11] D'Emic, M. D., Melstrom, K. M., & Eddy, D. R. (2012). Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 333–334, 13–23.
- [12] Dodson, P. (1975). Taxonomic Implications of Relative growth in Lambeosaurine Hadrosaurs. *Systematic Biology*, 24, 37–54.
- [13] Gignac, P.M., & Erickson, G.M. (2017). The Biomechanics Behind Extreme Osteophagy in *Tyrannosaurus rex*. *Scientific Reports*, 7.
- [14] Gallina, P. A., Apesteguía, S., Canale, J. I., & Haluza, A. (2019). A new long-spined dinosaur from Patagonia sheds light on sauropod defense system. *Scientific Reports*, 9(1), 1392.
- [15] Gasulla, J.M., Escaso, F., Narváez, I., Ortega, F., & Sanz, J.L. (2015). A New Sail-Backed Styracosternan (Dinosauria: Ornithopoda) from the Early Cretaceous of Morella, Spain. *PLoS ONE*, 10.
- [16] Gianechini, F. A., Makovicky, P. J., Apesteguía, S., & Cerda, I. (2018). Postcranial skeletal anatomy of the holotype and referred specimens of *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín 2005 (Theropoda, Dromaeosauridae), from the Late Cretaceous of Patagonia. *PeerJ*, 6, e4558.

- [17] Harris, J. D. (1998). A Reanalysis of *Acrocanthosaurus atokensis*, its Phylogenetic Status, and Paleobiogeographic Implications, Based on a New Specimen from Texas: *Bulletin 13* (Vol. 13). New Mexico Museum of Natural History and Science.
- [18] Hedrick, B. P., Zanno, L. E., Wolfe, D. G., & Dodson, P. (2015). The Slothful Claw: Osteology and Taphonomy of *Nothronychus mckinleyi* and *N. graffami* (Dinosauria: Theropoda) and Anatomical Considerations for Derived Therizinosaurids. *PloS one*, 10(6), e0129449.
- [19] Huttenlocker, A. K., Rega, E., & Sumida, S. S. (2010). Comparative anatomy and osteohistology of hyperelongate neural spines in the sphenacodontids *Sphenacodon* and *Dimetrodon* (Amniota: Synapsida). *Journal of morphology*, 271(12), 1407–1421.
- [20] Ibrahim, N., Sereno, P.C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold, N.P., & Iurino, D.A. (2014). Semiaquatic adaptations in a giant predatory dinosaur. *Science*, 345, 1613 - 1616.
- [21] Jerzykiewicz, T., & Russell, D.A. (1991). Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, 12, 345-377.
- [22] Karikehalli, S. (2019, January 17). Watch a black heron fool fish by turning into an umbrella. Retrieved from <https://www.audubon.org/news/watch-black-heron-fool-fish-turning-umbrella>
- [23] Ibrahim N, Sereno PC, Varricchio DJ, Martill DM, Duthiel DB, Unwin DM, Baidder L, Larsson HCE, Zouhri S, Kaoukaya A. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *Zookeys*. 2020 Apr 21;928:1-216. doi: 10.3897/zookeys.928.47517. PMID: 32362741; PMCID: PMC7188693.
- [24] Ibrahim, N., Maganuco, S., Dal Sasso, C. et al. Tail-propelled aquatic locomotion in a theropod dinosaur. *Nature* 581, 67–70 (2020). <https://doi.org/10.1038/s41586-020-2190-3>
- [25] Mazzetta, G. V., Cisilino, A. P., Blanco, R. E., & Calvo, N. (2009). Cranial mechanics and functional interpretation of the horned carnivorous dinosaur *Carnotaurus sastrei*. *Journal of Vertebrate Paleontology*, 29(3), 822-830.
- [26] Lautenschlager, S. (2014). Morphological and functional diversity in therizinosaur claws and the implications for theropod claw evolution. *Proceedings of the Royal Society B: Biological Sciences*, 281(1785), 20140497.
- [27] Lee, Y., Barsbold, R., Currie, P.J., Kobayashi, Y., Lee, H., Godefroit, P., Escuillié, F., & Chinzorig, T. (2014). Resolving the long-standing enigmas of a giant ornithomimosaur *Deinocheirus mirificus*. *Nature*, 515, 257-260.
- [28] Leonardo & José F. Bonaparte. 1991. Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov. de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* 28(3-4): 333-346.
- [29] Maidment, S. C. R., Norman, D. B., Barrett, P. M., & Upchurch, P. (2008). Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). *Journal of Systematic Palaeontology*, 6(4), 367–407.
- [30] Naish D (2011) Theropod dinosaurs. In: Batten DJ (ed) English wealden fossils. The Palaeontological Association, London, pp 526–559
- [31] Osmońska, H. & Roniewicz, E. Deinocheiridae, a new family of theropod dinosaurs. *Palaeontol. Polonica* 21, 5–19 (1970).
- [32] O'Connor, P. M. (2007). THE POSTCRANIAL AXIAL SKELETON OF MAJUNGASAURUS CRENATISSIMUS (THEROPODA: ABELISAUURIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR. *Journal of Vertebrate Paleontology*, 27(sup2), 127–163
- [33] Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature*, 467(7312), 203-206
- [34] Qin, Z., Liao, C. C., Benton, M. J., & Rayfield, E. J. (2023). Functional space analyses reveal the function and evolution of the most bizarre theropod manual unguals. *Communications biology*, 6(1), 181.
- [35] Remes, K., Ortega, F., Fierro, I., Joger, U., Kosma, R., Ferrer, J. M., Project PALDES, Niger Project SNHM, Ide, O. A., & Maga, A. (2009). A new basal sauropod dinosaur from the middle Jurassic of Niger and the early evolution of sauropoda. *PloS one*, 4(9), e6924.
- [36] Rayfield E. J. (2005). Using finite-element analysis to investigate suture morphology: a case study using large carnivorous dinosaurs. *The anatomical record. Part A, Discoveries in molecular, cellular, and evolutionary biology*, 283(2), 349–365. <https://doi.org/10.1002/ar.a.20168> Vidal, D., Mocho, P., Aberasturi, A., Sanz, J. L., & Ortega, F. (2020). High browsing skeletal adaptations in *Spinophorosaurus* reveal an evolutionary innovation in sauropod dinosaurs. *Scientific reports*, 10(1), 6638.
- [37] Watanabe, A., Eugenia Leone Gold, M., Brusatte, S. L., Benson, R. B., Choiniere, J., Davidson, A., & Norell, M. A. (2015). Vertebral Pneumaticity in the Ornithomimosaur *Archaeornithomimus* (Dinosauria: Theropoda) Revealed by Computed Tomography Imaging and Reappraisal of Axial Pneumaticity in Ornithomimosauria. *PloS one*, 10(12), e0145168.
- [38] Wedel, M.J. (2008). Lightening the giants: pneumatic bones in sauropod dinosaurs and their implications for mass estimates.
- [39] Wilson, J. P., Woodruff, D. C., Gardner, J. D., Flora, H. M., Horner, J. R., & Organ, C. L. (2016). Vertebral Adaptations to Large Body Size in Theropod Dinosaurs. *PloS one*, 11(7), e0158962.

- [40] Wilson, J. A. (2012). New vertebral laminae and patterns of serial variation in vertebral laminae of sauropod dinosaurs. *Paleontological Society Papers*, 32(7). Museum of Paleontology, The University of Michigan.
- [41] Wilson, J. A., & Allain, R. (2015). Osteology of *Rebbachisaurus garasbae* Lavocat, 1954, a diplodocoid (Dinosauria, Sauropoda) from the early Late Cretaceous-aged Kem Kem beds of southeastern Morocco. *Journal of Vertebrate Paleontology*, 35(4).
- [42] Windholz, G. J., & Cerda, I. A. (n.d.). Paleohistology of two dicraeosaurid dinosaurs (Sauropoda; Diplodocoidea) from La Amarga Formation (Barremian-Aptian, Lower Cretaceous), Neuquén Basin, Argentina: Paleobiological implications. Universidad Nacional de Río Negro, Instituto de Investigación en Paleobiología y Geología, Río Negro, Argentina.
- [43] Xu, X., Upchurch, P., Mannion, P. D., Barrett, P. M., Regalado-Fernandez, O. R., Mo, J., Ma, J., & Liu, H. (2018). A new Middle Jurassic diplodocoid suggests an earlier dispersal and diversification of sauropod dinosaurs. *Nature communications*, 9(1), 2700.