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NEW MATERIAL OF PYCNODONTS (ACTINOPTERYGII, † PYCNODONTIFORMES) FROM THE MAASTRICHTIAN DEPOSITS OF DAKHLA BASIN, WESTERN DESERT, EGYPT

SUMMARY

The right prearticular element of the extinct pycnodont fish, *Anomoeodus*, was collected from the Dakhla Formation, north of Teneida village in the Dakhla Oasis, Western Desert, Egypt, dated to the Maastrichtian, Late Cretaceous age. The element is described as a new species, *Anomoeodus teneidaensis*. The hosting layers indicate a marginal marine depositional environment. The teeth exhibit an elliptical to kidney shape and the main characteristic disposition typical of the genus *Anomoeodus*. The new species is characterized by mediolateral spaces between the teeth of the primary and secondary lateral rows. The alveoli of the medial row teeth are more inclined than in other species of the same genus. The identification of *Anomoeodus teneidaensis* significantly increases our understanding of the variety and distribution of pycnodonts in Egypt throughout the Late Cretaceous, and further enhances the known pycnodont biodiversity in North Africa during the Late Cretaceous, suggesting the Dakhla Formation as a significant area for exploring the evolutionary history of these unique fish.

INTRODUCTION

Pycnodonts are an extinct bony fish order, Pycnodontiformes Berg, 1937, that lived in shallow marine, freshwater, and brackish water environments (Capasso, 2021). The pycnodonts were small to medium-sized fish, deep-bodied. They are characterized by robust, flattened domed teeth that crush hard-shelled invertebrates like molluscs, crustaceans, and echinoderms

(Nursall, 1996; Kriwet, 2001). The pycnodonts first appeared in the Tethys ocean at the end of the Middle Triassic, as the oldest articulated skeletons have been discovered in the Lower Norian of the Italian Pre-Alps (Brunetti *et al*., 2001). Pycnodont fossils have existed for 175 million years, from the Triassic to the Eocene. They attained a high level of biological diversity, with at least 62 genera identified for the Late Cretaceous, and they likely accounted for up to 20% of the total marine ichthyofauna in some locations, e.g., Late Jurassic, Cerin, France (Capasso, 2021). To assess the relevance of the new species, it must be considered that pycnodonts began to colonize palaeo-Africa since the Middle Jurassic: Taverne (2019) demonstrated the presence of pycnodont remains of the genus *Congopycnodus* in the Stanleyville Formation (Aalemian-Bathonian) of the Hamamba River region (Democratic Republic of Congo). However, these early African forms, closely related to the Coccodontoidea, were freshwater fishes. In the Upper Jurassic, when pycnodonts thrived widely in the Tethys seas, we recorded only the presence of single dental remains attributed to the genus *Pycnodus* sp. ind. from the Mugher Mudstone Formation, of terrestrial origins and Tithonian in age, in Shewa, Ethiopia. Also in this case, it is a form that lived in continental waters (Goodwin *et al*., 1999).

In the Lower Cretaceous, pycnodont remains absolutely sporadic. We have only two reports of dental remains, both attributed to indeterminate Pycnodontiformes: (i) from the Ksar Metlili Formation, which outcrops at Ksar Met-Lili, Anoual, Figuig, Morocco, dated to the Berriasian (Sigogneau-Russell *et al*.,1988); and from the Chenini Member (Aïn el Guettar Formation), Bir Miteur, Médenine, Tunisia, and dated to the Early/Lower Albian (Bouaziz *et al*.,1988).

In the Upper Cretaceous we suddenly have evidence of an important diffusion of pycnodonts in Africa, both in the North (Morocco, Libya, Tunisia, Egypt) and in the Center (Niger, Mali, Gabon, Congo), to which are added two reports in Madagascar (Capasso, 2021). Among these forms, those referred to Egypt have been very rare; we have only a few bibliographic reports of pycnodonts as follows: (i) isolated teeth of pycnodonts, referred to the species *Stephanodus splendens*, are collected from Sibaiya and Gebel Duwi, Eastern Desert, by Gemmellaro (1920); (ii) Priem (1914) reported the species *Anomoeodus angustus* from the Santonian and Turonian deposits from Abu Roash and Berket El Gazal near Giza. (iii) Weiler (1935) reported *Coelodus* sp. ind., based on dental remains of the Cenomanian deposits from the Western Desert; (iv) Slaughter and Thurmond (1974) reported *Coelodus* sp. ind., based on dental remains from the Bahariya Formation from Gebel El Dist, Bahariya Oasis; (v) Voss *et al*. (2019) recorded the youngest pycnodont remains, represented by *Pycnodus mokattamensis*, that was collected from Late Eocene *Basilosaurus isis* stomach remains at Wadi El-Hitan, Fayoum.

The lower Maastrichtian deposits of the Dakhla Formation in Dakhla Oasis, Western Desert, Egypt (Fig. 1), contain exceptionally well-preserved marine vertebrate fossils such as marine reptiles (mosasaurs, plesiosaurs, and marine turtles) and fish bones, which are most abundant in the lower layers of the formation (Abu El-Kheir *et al*. 2021b; Abdel Gawad *et al*., 2021).

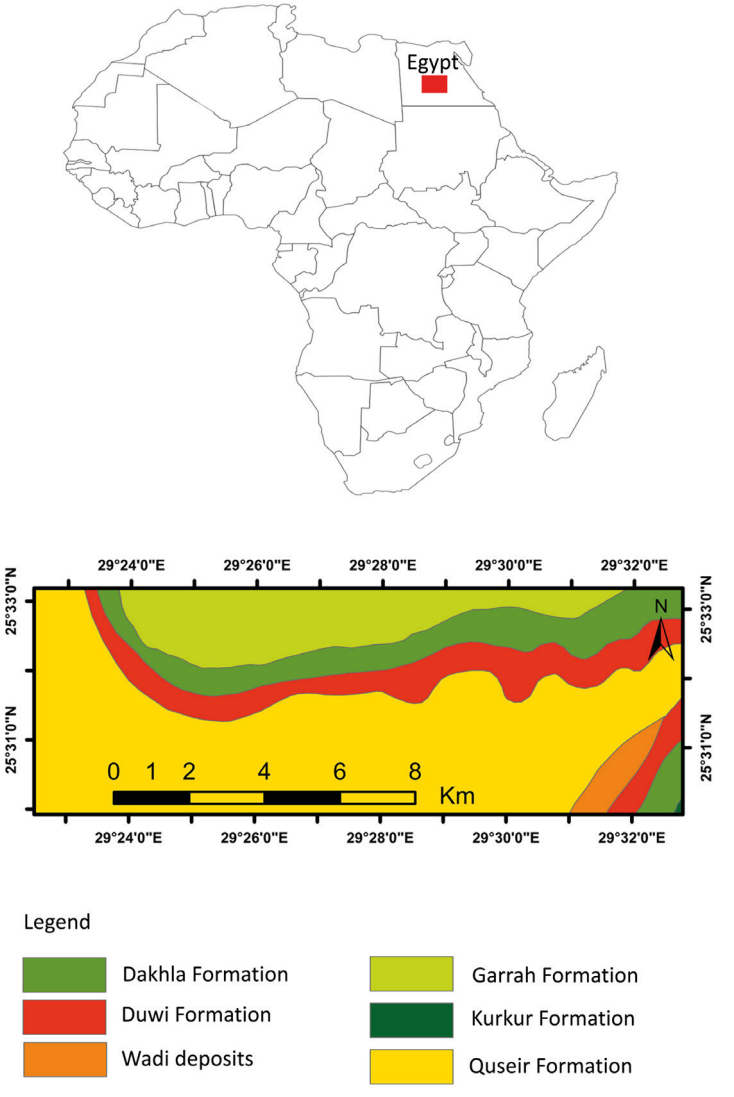

Fig. 1 - Geological map of Dakhla Oasis, the black spot shows the location of the present specimen, northeast of Teneida.

The New Valley Vertebrate Palaeontology Center (New Valley University, Egypt) discovered many localities of sarcopterygians and actinopterygians fish bone remains in the Upper Cretaceous-Palaeocene deposits from Dakhla Oasis during field trips between 2021-2024.

The pycnodont fish were recorded in the Dakhla Formation during the 2021 field trip of the New Valley Vertebrate Paleontology Center (NVP). Abu El-Kheir *et al*. (2021) described a new genus and species of pycnodont, *Diastemapycnodus tavernensis*, based on a well preserved vomerine bone. Finally, Capasso *et al*. (2021) recorded the new species *Anomoeodus egyptiacus*, based on a well preserved prearticular bone.

The present work describes a new pycnodont taxon, based on a section of a prearticular bone that was collected from the lower layers of the Dakhla Formation (Mawhoob Member), north of Teneida village (northeast of Mut city, Dakhla Oasis). The specimen has diagnostic features which may be considered a new species compared with the other discovered pycnodonts, both Egyptian and other parts of the world. The discovery of new specimens of pycnodont fish in the Western Desert of Egypt may increase our knowledge of the distribution of pycnodonts in the Late Cretaceous of Egypt.

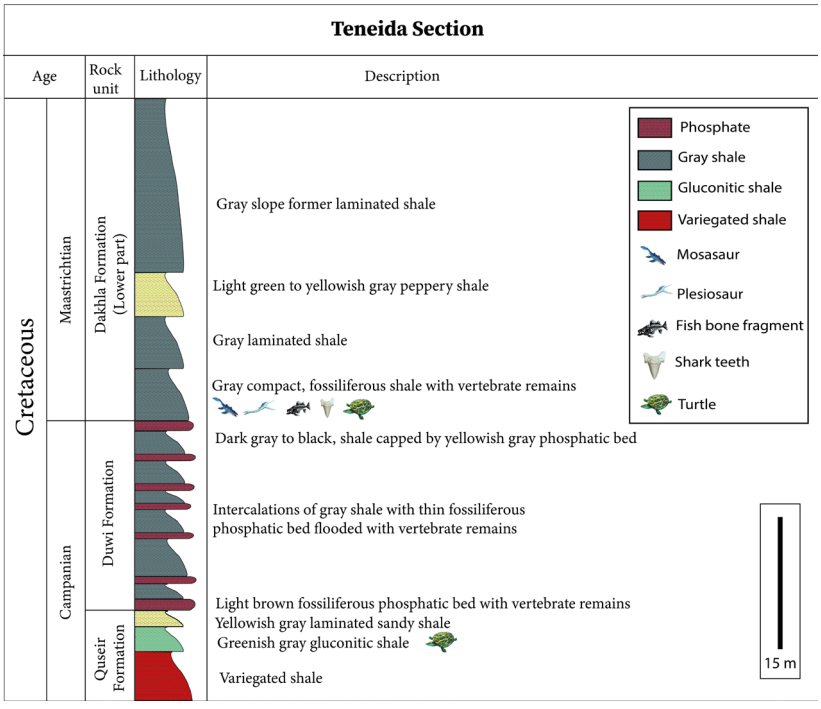

Fig. 2 - Stratigraphic section of the study area, showing the Quseir, Duwi, and Dakhla Formations.

Geological setting

The Dakhla Shale Formation conformably overlies the uppermost part of the Duwi Formation (Campanian, in age), which is composed of phosphatic fossiliferous layers and fossiliferous limestone layers at the top (El Azabi and El Arabi, 2000), and conformably underlies the Tarawan Chalky limestone For-

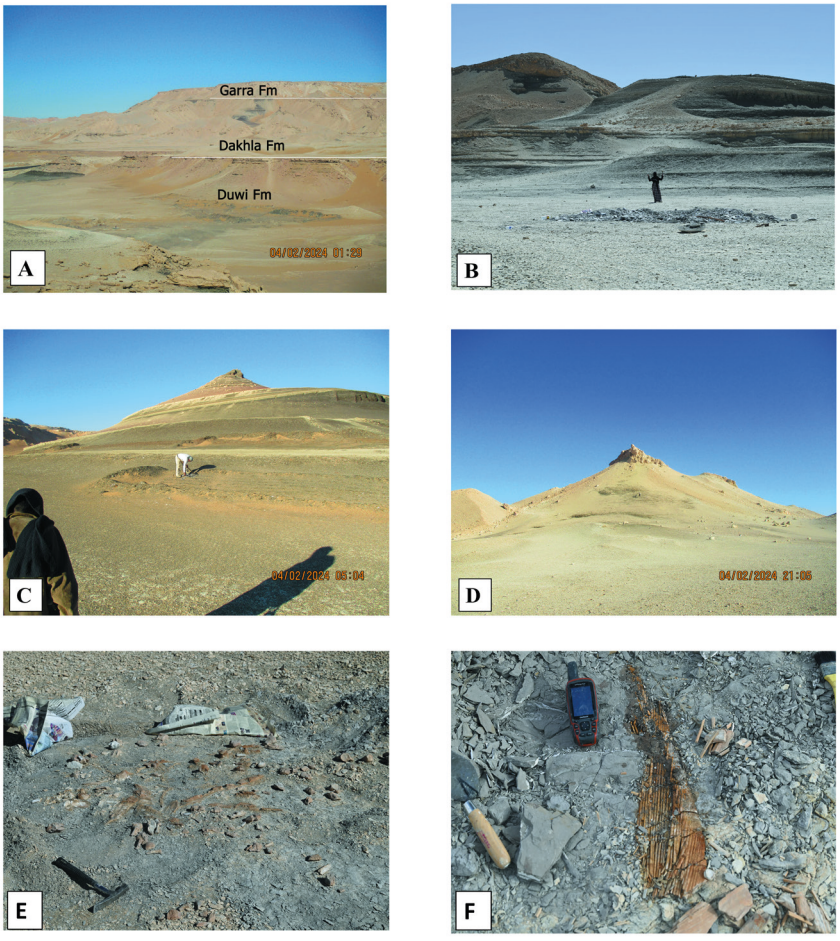

Fig. 3 - A) General view of the upper Cretaceous-Paleocene succession, north of Teneida village, showing the Duwi, Dakhla, and Garra formations. B) Mudstone, shale, and some siltstone intercalations of the Mawhoob Member, the lower part of the Dakhla Formation. C) Shale and fossiliferous sandstone of the Beris Member, the middle part of the Dakhla Formation. D) Gray laminated shale, the upper part of the Dakhla Formation topped by the Garra Formation. E) Partial skeletons of a mosasaur marine reptile embedded in the Mawhoob Member, north of Teneida village. F) Large fin of bony fish of Mawhoob Member.

mation (Abbass and Habib, 1971; Barthel and Herramann-Degen, 1981; Tantawy *et al*., 2001) (Fig. 2). It is composed of about 200 m in thickness of laminated shale, which is intercalated with thin calcareous fossiliferous siltstone, sandstone, and limestone layers (Fig. 3A). The Dakhla Shale Formation was deposited in continental shelf to lagoonal environments. This type section (from which the fossil described in this paper was collected) is divided into four members: Mawhoob, Beris, Lower Kharga, and Upper Kharga (Awad and Ghobrial 1965; Luger 1988; Hewaidy 1997; El-Azabi and El-Araby 2000; Tantawy *et al*. 2001). The Mawhoob Member is composed of about 35 m in thickness of yellow fossiliferous siltstone with laminated shale intercalation (Tantawy *et al*., 2001) (Fig. 3B). The siltstone layer contains fossil remains, such as fragmented fish bone elements (vertebrae, spines, and teeth) and some shark teeth that are affected by weathering and scattered with some mosasaur vertebrae (Abu El-Kheir *et al*., 2021) (Figs. 3C, D).

The Beris Member is composed of about 80 m in thickness of dark laminated shale with intercalations of fossiliferous siltstone, and indicates the middle part of the Dakhla shale Formation (Fig. 3E). The Beris Member is distinguished by the abundance of *Exogyra overwegi* (Bivalvia, Griphaeidae) contained in the calcareous sandstone layers. The Beris Member also contains many marine vertebrate fossils, such as mosasaurs, teeth and vertebrae of plesiosaurs, turtles, crocodile remains, shark teeth, fish bones, wood and plant remains. The Lower and Upper Kharga members are composed of 100 m in thickness of dark laminated shale, which is intercalated with calcareous sandstone and limestone (Fig. 3F). They are separated by the K/Pg boundary, which is represented by an erosional surface of the fossiliferous limestone (Abbass and Habib, 1971; Barthel and Herramann-Degen, 1981; Tantawy *et al*., 2001). These two members are deposited in a middle to outer continental shelf environment. The recent material was collected by the authors during a field trip of the New Valley University Vertebrate Paleontology Centre in February 2024 north of Teneida village.

MATERIALS AND METHODS

The pycnodont specimen described in this paper is housed in the New Valley Vertebrate Paleontology Center (NVP), New Valley University, Kharga Oasis (Egypt), under No.: NVP024. The specimen is represented by a prearticular bone with the arrangement of two tooth rows and remnants of a third one, including nine teeth.

Photographs were taken using a digital camera (AF-S Nikon 24–120 mm 1:4 G ED VR, Nikon) and lens (AF-S Nikon 70–200 mm 1:2.8E FL ED VR) in normal light. The X-ray analysis (GE X-Ray device, model XS-1A) used a

manual collimator, with max. Kv 150 kV; eq. filtration 1.5 mm aluminum equivalent; and input rating, 24 V, 150 W.

SYSTEMATIC PALAEONTOLOGY

Class: Actinopterygii Klein, 1885
Subclass: Neopterygii Regan, 1923
Superorder: Pycnodontomorpha Nursall, 2010
Order: Pycnodontiformes Berg, 1937
Family: Pycnodontidae Agassiz, 1833
Genus*: Anomoeodus* Forir, 1887
Species: *Anomoeodus teneidaensis* sp. nov.

Diagnosis

The described Egyptian specimen has a complex of anatomical below mentioned characters that are both particular and typical; defining what is here named *Anomoeodus teneidaensis*, n. sp. These include: (i) a very low number of prearticular rows (three); (ii) the presence of spaces between the lateral teeth (diastema); (iii) a small number of teeth in each prearticular row; (iv) the teeth of the primary lateral row are of the largest dimensions; (v) the two lateral rows (primary and secondary) form an obtuse angle with each other, facing the buccal cavity; (vi) the occlusal surface of the primary lateral teeth is convex, while the occlusal surface of the secondary lateral teeth is concave; (vii) the larger posterior teeth of the primary lateral row have a profile with very fine crenulations that give the outer edge of the crown a crenulated appearance.

Occurrence

The present specimen was collected from the base of the Mawhoob Member, Biozone CF7 (Hewaidy *et al*., 2017), within the Dakhla Formation.

The type locality is north of Teneida village, northeast of Mut city, Dakhla Oasis (Egypt).

Etymology

The name *teneidaensis* refers to Teneida village, where the studied specimen was collected, located north of this village.

Description

The described prearticular dental plate section consists of two lateral tooth rows and one row of medial teeth arranged in alveola (Fig. 4A). The speci-

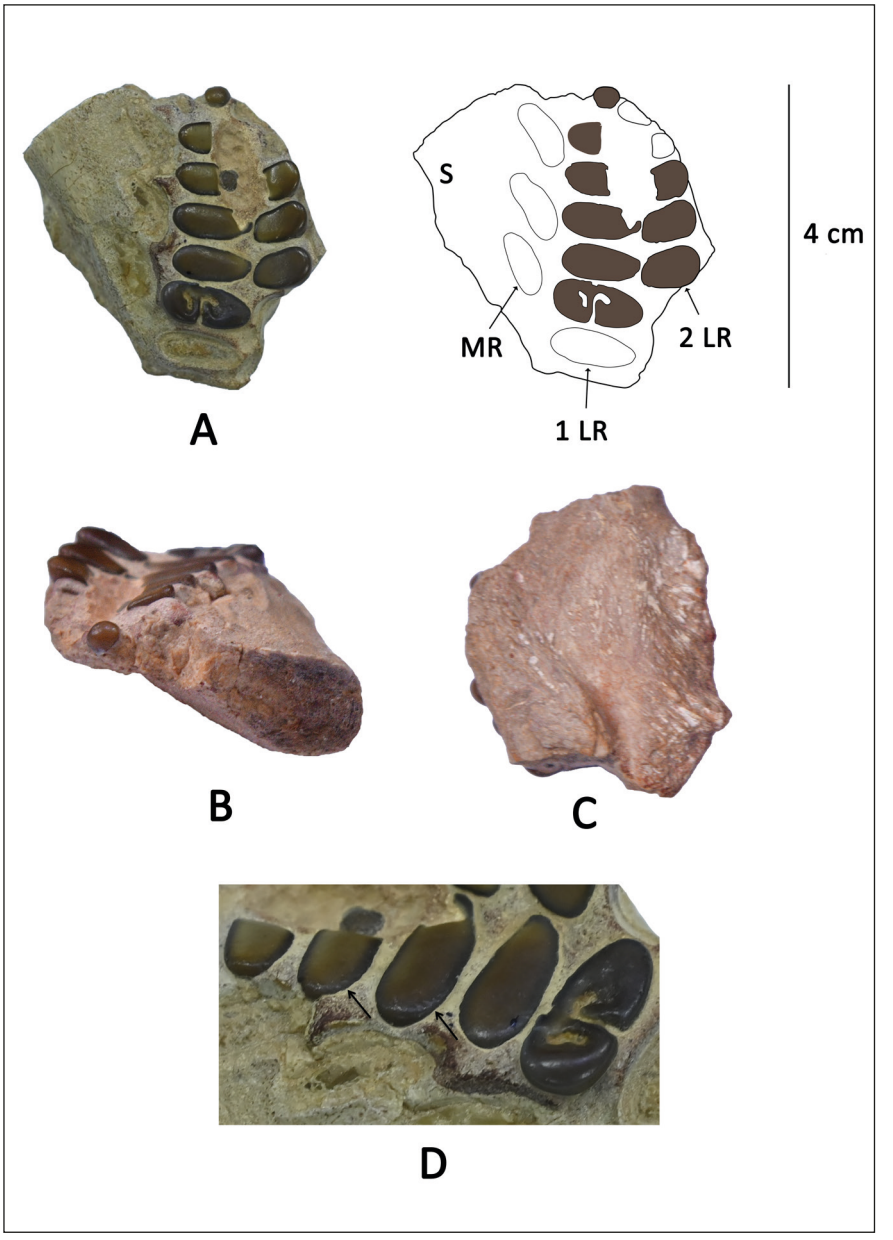

Fig. 4 - NVP024. *Anomoeodus teneidaensis* n. sp., A) occlusal view, B) anterior view, C) Lateral view, D) detail of a posterior tooth of the primary lateral row, showing linear grooves on its occlusal surface and a profile with very fine crenulations.

men is fairly well-preserved with minor damage to the anterior and posterior margins and to the coronoid process.

The prearticular section is convexly elliptical in cross-section and measures 43.27 mm in anteroposterior length, 33.57 mm in width, and a maximum thickness of 13.50 mm at the anterior side. The outer margin of the prearticular bone is thick, dense, and smooth (Fig 4 B, C). The two lateral rows (primary and secondary) form a wide, concave obtuse angle with each other, facing the buccal cavity. The teeth are separated by narrow spaces mediolaterally (diastema). The teeth are not prominent and are deeply embedded in the prearticular bone.

The primary lateral row has the largest teeth dimensions and consists of five elliptical to kidney-shaped teeth, along with one large elliptical-shaped tooth alveolus, missing its crown due to damage. The largest lateral tooth measures 13.16 mm in width and 5.6 mm in length (length*100/width ratio = 42.6). The primary lateral teeth are wider than the secondary lateral teeth. The occlusal surface of the primary lateral teeth is slightly convex (Fig 4 A). The larger posterior teeth of the primary lateral row have a profile with very fine radially arranged denticulations that give the outer edge of the crown a crenulated appearance (Fig. 4 D).

The secondary lateral row consists of three posterior elliptical-shaped teeth, one small spherical-shaped tooth most anteriorly, and two small oval-shaped tooth alveoli, missing their crowns due to damage. The largest lateral tooth measures 8.16 mm in width and 5.12 mm in length (length*100/width ratio = 62.7). The occlusal surface of the secondary lateral teeth is slightly concave.

The medial row consists of three elliptical-shaped tooth alveoli, missing their crowns due to damage. The dimensions of the tooth alveoli in the medial row decrease slightly towards the anterior. The largest alveoli measures 11.8 mm in width and 5.21 mm in length (length*100/width ratio = 44.2).

Unfortunately, the radiographic analysis performed on the described fossil did not yield any useful images to interpret the internal structure of the bone or the possible presence of dental buds underlying the erupted teeth. The high degree of mineral impregnation of the fossil has densely replaced the original organic substances, preventing X-rays, even of high intensity, from passing through.

DISCUSSION

The prearticular teeth of *Anomoeodus teneidaensis* have an elliptical shape and are arranged in batteries (i.e., series or rows), with the medial row positioned obliquely. The general morphology of the prearticular teeth varies

within individual rows. This dental form reflects the typical characteristics of the genus *Anomoeodus*, where the teeth are elliptical to kidney-shaped (Capasso *et al*., 2021).

The largest teeth in the dental series are found in the primary lateral row, as observed in most *Anomoeodus* species, such as *A. aegyptiacus, A. angustus*, *A.* sp. B, and *Agassizilia erfoudinai* (Cooper and Martin, 2020a) (Fig. 5).

The prearticular bone of *Anomoeodus aegyptiacus* is thicker compared to *A. teneidaensis*. The lateral posterior tooth (1LR in Figure 4) of the primary row has linear grooves on its occlusal surface and a profile with very fine radially arranged denticulations that give the outer edge of the crown a serrated appearance, differing from the massive surface observed in *A. aegyptiacus*.

The medial series (MR in Figure 4) consists of arranged elliptical-shaped tooth alveoli, similar to *A. aegyptiacus* (Figure 5 B) and to *A.* sp. B (Figure 5 C), but differs from those in *A. angustus* (Figure 5 D), and *Agassizilia erfoudinai* (Figure 5 E), which have minute emi-spherical-shaped teeth. The secondary lateral teeth series is also elliptical-shaped, as in *A. aegyptiacus*, and differs from the more circular spherical-shaped teeth observed in *A. angustus,* and *Agassizilia erfoudinai,* and it also differs from the small, spherical teeth of *A.* sp. B.

The teeth of *Anomoeodus teneidaensis* are deeply embedded in the prearticular bone, in contrast to the more prominent teeth of *A. aegyptiacus*. Additionally, the teeth of *A. aegyptiacus* are larger and denser than those of *A. teneidaensis*. The arrangement of the two primary and secondary lateral tooth rows forms a wider obtuse angle in *A. teneidaensis* compared to *A. aegyptiacus*.

The lateral teeth of *Anomoeodus teneidaensis* have spaces between them, unlike those of *A. aegyptiacus*, where the teeth are very close together. The secondary lateral row comprises posterior elliptical-shaped teeth and anterior minute spherical-shaped teeth, similar to *A. aegyptiacus*. The inclination angle of the medial row in *A. teneidaensis* is greater than in *A. aegyptiacus* and *A. angustus*.

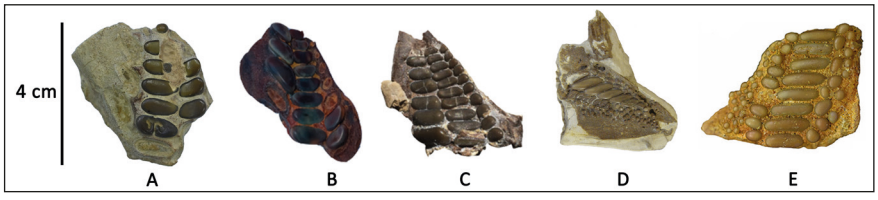

Fig. 5 - Comparison between the inner (endobuccal) face of the right prearticular of A) *Anomoeodus teneidaensis* gn. et sp. n.; B) *Anomoeodus aegypticus* Capasso *et al*. (2021); C) *Anomoeodus* sp. B. (Cooper and Martill, 2020b); D) *Anomoeodus angustus* (Licht and Kogan, 2011); E) *Agassizilia erfoudinai* (Cooper and Martin, 2020a).

In conclusion, the NVP024 *Anomoeodus* specimen differs from other species in the *A.* genus by its elliptical secondary lateral and medial teeth series, while showing similarities to *A. aegypticus*. It is distinguished from *A. aegypticus* by its smaller size, deeply embedded teeth in the prearticular bone, and the presence of spaces between the lateral teeth. For these reasons, the authors propose the designation of the NVP024 specimen as the new species *A. teneidaensis* n. sp.

Paleobiogeography

Pycnodont fossils were widely distributed during the Late Cretaceous. They were occurred in Europe, Asia, North and South America (Poyato-Ariza and Wenz, 2002). Their African occurrence during the Maastrichtian was recorded from several localities, indicating a huge presence within the marine and non-marine aquatic systems, this includes:

The genus *Anomoeodus* belonging to Pycnodontiformes, was recorded in the Maastrichtian Dakhla Formation deposits in Western Desert, Egypt (Capasso *et al*., 2021).

Pycnodont fossils are among the many and diverse vertebrate fossil remains found in the Maastrichtian phosphate deposits of the Ouled Abdoun Basin in Morocco (Cooper *et al*., 2022; Longrich *et al*., 2018).

The Maastrichtian deposits in Mali, which are connected to the Trans-Saharan Seaway, have yielded unidentified pycnodont fossils (Parris *et al*., 2007).

Paleoenvironmental Conditions

The Maastrichtian deposits of Africa, where the majority of pycnodont fossils were recorded, indicate shallow marine environments. For instance, the phosphate deposits of the Ouled Abdoun Basin in Morocco indicate a shallow marine environment (El Bamiki, 2020), and the Maastrichtian deposits of the Dakhla Formation also indicate a marginal marine environment (Capasso *et al*., 2021). The presence of pycnodont fossils with other marine vertebrate fossil remains such as mosasaurs, shark teeth, and fish bones, also indicates that.

However, the increased occurrence of pycnodonts in brackish and freshwater environments during the Late Cretaceous is an important part of their paleoenvironmental history. This illustrates that some pycnodont species have the ability to tolerate a wide range of salinities. This allowed them to live in various aquatic habitats, from coastal lagoons and near reefs to estuaries and possibly even river systems, particularly during high sea levels (Cawley and Kriwet, 2024).

Evolutionary implication

The discovery of *Anomoeodus teneidaensis* from the Late Cretaceous deposits of Dakhla Formation in Egypt increases our knowledge of diversity and

distribution of pycnodonts in the Late Cretaceous of Egypt. The observed unique diagnostic dental features of *A. teneidaensis* such as the presence of diastema between the teeth of the primary and secondary lateral rows, and serrated appearance of the larger posterior teeth of the primary lateral row, which indicates an adaptation in the crushing mechanism, and allowing for better breakdown of hard-shelled prey (e.g., molluscs, crustaceans, echinoderms) that may have been abundant in its marginal marine habitat. These features not previously seen in other recorded species.

The recording of *Anomoeodus teneidaensis* adds a new taxon to the widespread distribution of pycnodonts throughout the Late Cretaceous, and the recent recordings of other discoveries from the Dakhla Formation, indicate that the Western Desert of Egypt is a significant area for understanding the evolutionary history of Late Cretaceous pycnodonts.

CONCLUSION

The Late Cretaceous deposits of the Dakhla Formation, Western Desert, Egypt, are notable for their abundance of marine vertebrate fossils, including marine reptiles and fish bones. Pycnodont fish remains have been previously recorded in the Dakhla Formation, including the new genus *Diastemapycnodus tavernensis* Abu El-Kheir *et al*., 2021 and the new species *Anomoeodus aegypticus*.

The newly described *A. teneidaensis* is characterized by three prearticular rows, with the primary lateral row having the largest dimensions. The two lateral rows form an obtuse angle with each other, facing the buccal cavity. The occlusal surface of the primary lateral teeth is convex, and the arrangement of the primary and secondary lateral rows forms an obtuse angle.

These diagnostic features support the classification of the specimen as a new species, *A. teneidaensis*, within the family Pycnodontidae (Agassiz, 1833-1843). This new species contributes to the understanding of the distribution and taxonomy of rare pycnodont fish remains in Egypt and across the African continent.

In this regard, we can conclude that the new species does not change our knowledge of the first forms of pycnodonts in Africa: it remains unchanged, in fact, that these fish began to colonize the waters south of the Tethys only in the Middle Jurassic and all forms of African pycnodonts of the Jurassic and Lower Cretaceous were typical fish of continental waters. The new species, on the other hand, significantly enriches the biodiversity of the pycnodonts of the Upper Cretaceous of North Africa. In more detail, the new species *Anomoeodus teneidaensis* n. sp. joins the already described species *A. aegyptiacus* and *Diastemapycnodus tavernensis*; it is a relatively rich combination of pycnodonts in the African context and demonstrates that these fish

were still very diversified and particularly widespread in the shallow marine waters of the end of the Late Cretaceous in the Dakhla Formation.

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