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ANOMOEODUS AEGYPTICUS N. SP. (PISCES, †PYCNODONTIFORMES) FROM THE LATE CRETACEOUS OF THE DAKHLA FORMATION, WESTERN DESERT, EGYPT

SUMMARY

Based on a single right prearticular bone section with partial dentition collected from the lower part of the Beris member, Dakhla Formation (Egypt), dated to the Maastrichtian, the authors describe a new Pycnodont, *Anomoeodus aegypticus*. The planktonic foraminiferal assemblages indicate deposition in a marginal marine environment with open marine influx. The dental apparatus demonstrates the characteristic disposition of the teeth, which are typically semi-spherical, kidney-shaped and elliptical, as seen for the genus *Anomoeodus*. The new species is primarily characterised by the largest teeth not being those of the medial row (located near the symphysis; as seen for all *Anomoeodus*), but those of the primary lateral row.

RIASSUNTO

Basandosi su un osso pre-articolare destro frammentario, con dentatura parziale, raccolto dalla parte inferiore dei cosiddetti "strati di Beris" della Formazione di Dakhla (Egitto), datata al Maastrichtiano, gli autori descrivono il picnodonte *Anomoeodus aegypticus* n. sp. Il fossile è stato trovato in associazione con un'ampia varietà di vertebrati marini (mosasauri, plesiosauri, tartarughe marine, coccodrilli, denti di squalo, ossa e denti di pesci) e occasionali resti vegetali. Le associazioni di foraminiferi planctonici indicano la deposizione in un ambiente marino marginale, con afflusso sporadico dal mare aperto. L'apparato dentario descritto mostra la caratteristica disposizio-

ne dei denti, che sono peraltro tipicamente semisferici, allungati, reniformi, come si vede tipicamente nel genere *Anomoeodus*. La nuova specie è caratterizzata dal fatto che i denti di dimensioni maggiori non appartengono alla fila mediale (localizzati in prossimità della sinfisi), come avviene in tutti gli *Anomoeodus*, ma appartengono alla fila laterale primaria. Ulteriori caratteri sono: (i) I denti di maggiori dimensioni appartengono alla serie primaria laterale; (ii) assenza di diastema; (iii) bassissimo numero di serie dentarie preartcolari (tre); (iv) basso numero di elementi dentari per ciascuna serie prearticolare; (v) le due serie laterali (la primaria e la secondaria) formano fra loro un angolo diedro aperto buccalmente; (vi) la superfice occlusale è concava nei denti di entrambe le serie laterali (primaria e secondaria), convessa in quella dei denti della serie mediale. *Anomoeodus aegypticus* n. sp. ha le sue maggiori affinità anatomiche con *Anomoeodus "specie B"* descritto da Cooper and Mantill (2020) nel Cretaceo superiore del Marocco, che – pertanto – cade nella sinonimia della nuova specie *Anomoeodus aegypticus*.

INTRODUCTION

The Pycnodonts originated in the Tethys at the end of the Middle Triassic. Their oldest fossils are dental remains from northern Italy (Dalla Vecchia and Carnevale, 2011) and southern Germany (Agassiz, 1833-43), but the oldest articulated skeletons are from the Lower Norian of north-eastern Italy (Brunetti *et al*., 2001). Throughout the Jurassic and Cretaceous, the Pycnodonts rapidly spread from these restricted areas, to colonise almost all of the waters of the planet (except Australia), both marine and continental (at least in tropical areas). They reached wide diversification, with at least 57 genera identified for the Late Cretaceous, and probably represented up to 20% of the whole marine ichthyofauna in some places (e.g., in Cerin, France, in the Late Jurassic) (Capasso, 2021).

After this enormous development, both geographic and temporal, and after the great explosion in their biodiversity and their evolutionary success, the Pycnodonts returned to the restricted distribution range of the Tethys alone following the great mass extinction at the end of the Mesozoic. Here, they showed small demographic populations until their total extinction at the end of the Eocene, about 200 million years from their origin.

There are only a few bibliographic reports of Pycnodonts for the Cretaceous of Egypt: (i) Gemmellaro (1920) reported three isolated teeth of an indetermined Pycnodontidae from the Maastrichtian of Sciarauna-el-Ghibli (Sibaiya), of Kossie -el -Khadim (Kossier), and of Gebel Duwi. (ii) The same Gemmellaro (1920) reported also some teeth attributed to the specie *Stephanodus splendens*, that Zittel (1888) referred to the family Sparidae, but that Vullo *et al.* (2019) inter-

preted as pycnodont; this specimens were collected from the Maastrichtian of Sciarauna -el -Ghibli (Sibaiya), of Kosseir-el-Khadim, and of Gebel Duwi. (iii) Priem (1908) reported dental remains from the Santonian limestone that outcrops at Abou Roach and at Berak el Gazal, both near Al Jizah, and attributed to the species *Anomoeodus angustus* Agassiz (1833-43). (iv) Priem (1914) reported this same species on the basis of dental remains from the Turonian limestone outcrops at El Gaa, near Abou Roach, Al Jizah. (v) Weiler (1935) described teeth attributed to *Anomoeodus* sp. ind collected in the Cenomanian of the Egyptian part of the Libyan Desert. (vi) Weiler (1935) described also dental remains of *Coelodus* sp. ind. collected in the Egyptian part of the Libyan Desert, and dated to the Cenomanian. (vii) Slaughter and Thurmond (1974) reported the *?Coelodus* sp. ind. on the basis of dental material from the Baharîje Formation, at Gebel el Dist, and dated to the Early/Lower Cenomanian. Finally, (viii) Voss *et al.* (2019) described a left prearticular pertaining to a large-sized specimen of *Pycnodus mokattamensis* that was collected from the stomach of a *Basilosaurus isis*, recently collected at Wadi Al Hitan, dated to the final Eocene.

Despite this relative poverty of finds, the Egyptian finds are of great relevance for the reconstruction of the last phases of the evolutionary history of the Pycnodonts. Indeed, as *Pycnodus mokattamensis* was dated to the end of the Eocene (the Priabonian), this specimen represents the most recent remains of a Pycnodont known today throughout the world. As a consequence, this recent discovery by Voss *et al.* (2019) moved the extinction of the Pycnodonts forward by at least 7 million years with respect to previous knowledge.

The scarcity of Pycnodont remains in the last part of the Late Cretaceous in Egypt, together with the great importance of this northern African species in general, contribute to our understanding of the extinction of the Pycnodonts. This means that the fossils of Egyptian Pycnodonts dating back to the Late Cretaceous and to the Eocene are of crucial importance for the palaeontology of these now completely extinct fish. On this premise, and within the context outlined above, the new species described here is very important not only from the stratigraphic and palaeogeographic points of view, but also from the anatomical, functional and palaeoecological points of view.

GEOLOGICAL SETTING

The exposed sedimentary successions in the W of Dakhla at Gebel Gifata (Fig. 1) ranges in age from Campanian to lower Palaeocene, and contains diverse lithological compositions, different palaeo-environments, and an abundance and variety of fossils. The succession is based by the uppermost part of the Duwi Formation, which is represented by highly fossiliferous phosphatic layers that are capped by fossiliferous limestone, which forms

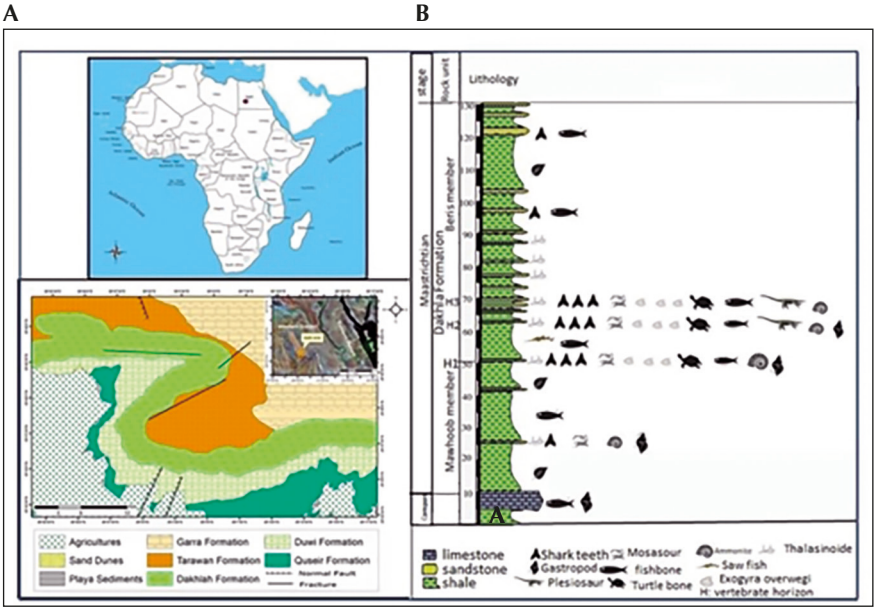

Fig. 1 - Details of the study area. (**A**) Location and geological maps of Gebel Gifata, North Mute, Dakhla Oasis, Western Desert, Egypt. (**B**) Stratigraphic section of the study area, showing the Mawhoob and Beris members of the Dakhla Formation.

the peneplain of the surface of the study area (El Azabi and El Arabi, 2000).

The Dakhla shale Formation conformably overlies the Duwi Formation, and is overlain by the Tarawn chalky limestone Formation (Abbass and Habib, 1971; Barthel and Herramann-Degen, 1981; Tantawy *et al.*, 2001). It is formed of about 200-m-thick fissile shale intercalated with thin siltstone, sandstone and limestone layers. The Dakhla shale facies are deposited in inner neritic to lagoonal environments. It is Mastrichtian to Palaeocene in age, and is divided into four members according to previous studies: the Mawhoob, Baris, lower Kharga and upper Kharga. El Azabi and El Arabi (2000) reported that the members of Dakhla shale were deposited by 10 repeated cycles provided by sea level fluctuations during deposition of the Dakhla Formation.

The Mawhoob member is formed of yellow fossiliferous siltstone with laminated shale intercalation (Tantawy *et al.*, 2001), and it was deposited in the upper lower, middle and upper tidal cycles. The siltstone layer of the Mawhoob member contains separate elements of vertebrate fossils, such as Mosasaur vertebrae, shark teeth, fishbones and elements of giant marine turtles (Abu El-Kheir *et al.*, 2021).

The Beris member represents the middle part of the Dakhla Formation. It is composed of dark laminated shale with fossiliferous siltstone intercalation. It was deposited in shallow subtidal to lower and middle intertidal repeated

cycles (El Azabi and El Arabi, 2000). The Beris member is characterised by its abundance of *Exogyra overwegi* imbedded in the siltstone layers. Expeditions of the New Valley Vertebrate Palaeontology Centre have recorded three main successive vertebrate-bearing horizons in the Beris member, as H-I, H-II and H-III. These vertebrate-bearing horizons are represented in the fossiliferous intercalated siltstone layers, which contain a variety of marine vertebrates, such as partial skeletons of Mosasaurs, Plesiosaurs, turtle bones, fishbones and shark teeth.

The lower and upper Kharga members are composed of dark laminated shale with some intercalation of calcareous sandstone and limestone. They are separated by the K/T boundary, which is represented by the erosive surface of the fossiliferous limestone (Abbass and Habib, 1971; Barthel and Herramann-Degen, 1981; Tantawy *et al*., 2001). The lower and upper Kharga members were deposited in the lower and middle intertidal repeated cycles (El Azabi and El Arabi, 2000).

The present material was collected by the authors during a field trip of the New Valley University Vertebrate Palaeontology Centre in March 2021. It was collected from the third horizon (H-III) of the lower part of the Beris member, of the Dakhla Formation.

MATERIAL AND METHODS

The pycnodont material is housed in the New Valley Vertebrate Palaeontology Centre of New Valley University, Kharga Oasis, New Valley governorate (Egypt), under N° NVP023. The specimen is represented by a right prearticular bone with an arrangement of three teeth arrows, which include 13 complete teeth and 6 tooth roots.

Photographs were taken using a digital camera (Af-S Nikkor 24-120mm 1:4 G ED VR; Nikon) and lens (Af-S Nikkor 70-00 mm 1:28E FL ED VR; Nikon) in normal light. The X-ray analysis (model XS-1A; GE X-Ray Systems) used a manual collimator, with: maximum Kv, 150 vp; eq. filtration, 1.5 mm Al@look vp; and input rating, 24 V, 150 W. The CT scan for the specimen was performed by device Canon CT scanner Aquillion Lightning. model TSX-035A, serial number 7CC2012597.

RESULTS

The indicated prearticular section of a Pycnodont (NVP023) can be identified as teeth and fragments of bone pertaining to the genus *Anomoeodeus*.

Class: Osteichthyes
Subclass: Actinopterigi
Superorder: Neopterigi
Order: Pycnodontiformes Berg, 1937
Family: Pycnodontidae Agassiz, 1833
Genus: *Anomoeodus* Forir, 1887
Anomoeodus aegypticus n. sp.

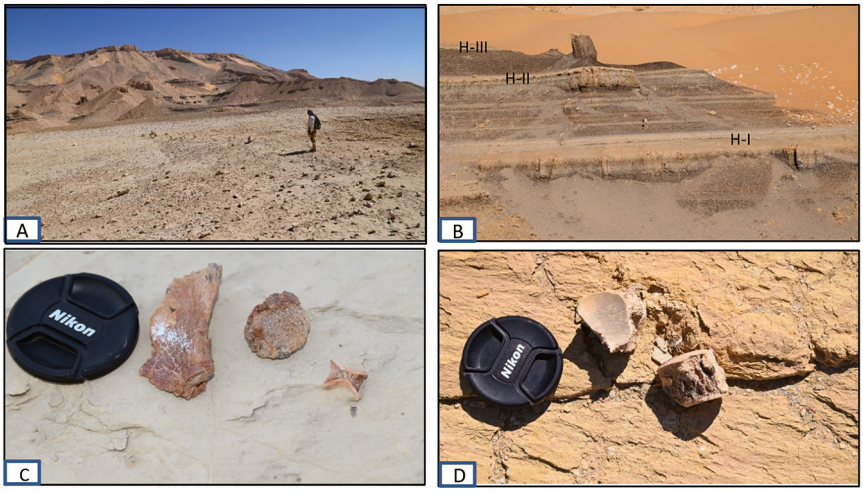

Fig. 2 - (**A**) General view of Gebel Gifata, the type section of the Dakhla Formation and the type locality of *Aegyptopycnodus* gen. nov. (**B**) Lower part of the Beris member, showing the vertebrate-bearing horizons H-I, H-II and H-III. (**C**) Fishbone remnants embedded in the silty sandstone of the second vertebrate-bearing horizon of Gebel Gifata. (**D**) weathered vertebrae of a mosasour embedded in the silty sandstone of the first vertebrate-bearing horizon of Gebel Gifata.

2020 *Anomoeodus* sp. B Cooper et Martill: Cooper and Martill (2020b) pp. 7-10.

Holotype – The single specimen NVP023 (Fig 3); anterior part of an isolated section of a right prearticular bone with partially preserved dental series that include 13 complete teeth and 6 tooth roots.

Repository – The type specimen examined in this study is deposited in the New Valley University, Vertebrate (NVU) Palaeontology Centre, Kharga Oasis, New Valley governorate, Egypt, under N° NVP023.

Definition – The described Egyptian specimen has a complex of anatomical characteristics that are at the same time particular and typical, and that

shape what is called here *Anomoeodus aegypticus*, n. sp. These include: (i) the teeth with the largest dimensions are those of the primary lateral row. (ii) the absence of diastemas in the prearticular series. (iii) a very low number of prearticular batteries (three). (iv) a small number of elements in each prearticular battery. (v) the two lateral rows (primary, secondary) form a concavity angle between them, which faces the buccal cavity. (vi) the occlusal surface is concave in the teeth of both of the lateral rows (primary, secondary), and convex for those of the medial row.

This set of characteristics constitutes a *unicum* that justifies the establishment of a new species for this specimen, although it is a dental specimen, which is unique. This described complex of characteristics are practically superimposable on those that Cooper and Martill (2020b) described for the species *Anomoeodus* sp. B of the Mammites ammonite biozone, chalky-marl facies, Asfla Member, Akrabou Formation, Morocco, and dated to the Upper Cretaceous (Turonian); this, therefore, falls into the synonymy of the new species *Anomoeodus aegypticus*.

Fig. 3 - *Anomoeodus aegypticus* n. sp., holotype. (**A**) Occlusal view. (**B**) Posterior view. (**C**) Lateral view.

Etymology – The specific name is clearly derived from the Latin version of the name of the nation in which the new species was found: Egypt.

Horizon – The second vertebrate-bearing horizon H-III, *Exogyra overwegi* biozone, calcareous sandstone facies, the Beris member, of the Dakhla Formation. Upper Cretaceous (Maastrichtian). The type-locality is Gebel Gifata, 12 km N of Mute, Dakhla Oasis, W Desert, Egypt.

Remarks – The holotype shows all of the typical characteristics of the genus *Anomoeodus* (Pyato-Ariza and Wenz, 2002): the prearticular teeth have an elongated lozenge shape and a sigmoidal profile. They are sinuous, and sometimes have the form of a 'drop', with the apex pointing towards the symphysis region; and they are assembled in batteries (i.e., series or rows), in each of which the individual elements are positioned obliquely. Also, the general morphology of the prearticular teeth varies a lot according to the topographic position within the single batteries: only the rear teeth, which are the largest, have the characteristic elongated lozenge morphology and sigmoidal profile. Instead, the front teeth, which are randomly arranged, are semi-spherical, with an almost perfectly circular profile, and they are small (Fig. 3A).

There appear to be three dental prearticular batteries. The occlusal surface is concave in the teeth of both of the lateral rows (primary, secondary), and convex for those of the medial row. The outer margin of the pre-articular bone is smooth and thin, and sometimes has sharp edges (Fig. 3A, B). The teeth that have the largest dimensions are those of the primary lateral row; it is possible that posteriorly, where the bone is broken and the dentition is not known, the teeth in the medial row might have been larger. Nevertheless, the larger size (even if this might not be the maximum size in the pre-articular dentition) of the teeth of the primary lateral row is strongly characteristic of this specimen.

All these characteristics are typical of the genus *Anomoeodus* (characters #43, #44, #45, #46, #51 of the systematic scheme proposed by Pyato-Ariza and Wenz (2002). However, the number of prearticular dental series is very low, on the basis that Pyato-Ariza and Wenz (2002) considered a variability of a minimum of five to a maximum of six prearticular dental batteries for each side as characteristic of the genus *Anomoeodus*. This might be a typical characteristic of this new species of the Egyptian Upper Cretaceous, and it might indicate the need to establish a new species.

X-ray and CT-scan description: A standard X-ray in a lateral–lateral projection was performed on the right prearticular fragment described above (Fig. 4A), and a series of CT-scan was performed in various projections (Fig 4 B

and C). Unfortunately, the individual teeth are extremely radio-opaque, evidently due to mineralisation with metal salts, and this prevents the fine anatomical details of the relationships between the teeth and bone from being seen; it also prevents any effective survey on the possible presence of gems that might be below the erupted teeth. Nonetheless, both the radiograph and the CT-scan demonstrate the good state of mineralization and trabecular organization of the prearticular bone, with no signs of resorption, which is favourable with an adult, but not elderly, age of the specimen.

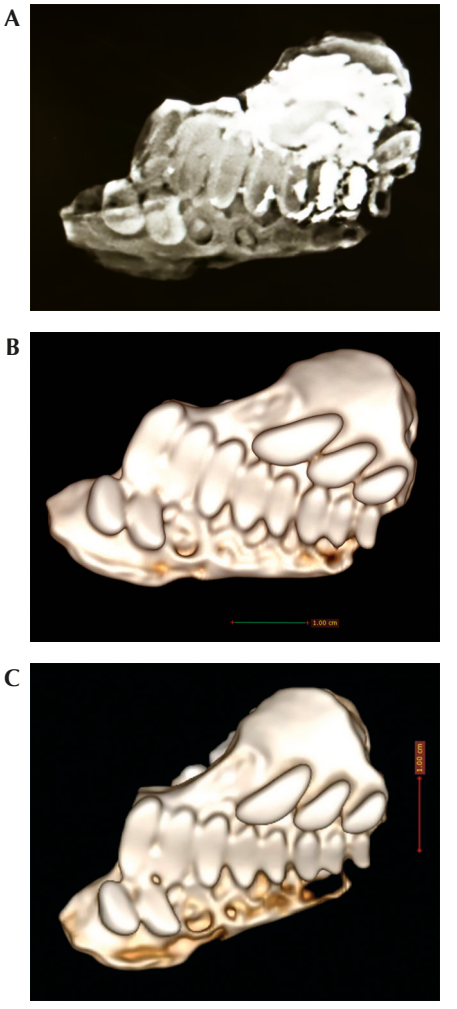

Fig. 4 - X-ray of the holotype of *Anomoeodus aegypticus* n. sp. in a later–lateral projection (**A**). CT-scan of the specimen in two projections (**B**, and **C**).

DISCUSSION AND CONCLUSIONS

The genus *Anomoeodus* was established by Forir (1887) on the basis of an isolated prearticular dentition, to which the name of *Pycnodus subclavatus* was attributed. To date, more than 30 species of *Anomoeodus* have been described, well characterised and easily recognizable through the typical way in which the teeth are arranged in the prearticular bone: elongated and large teeth arranged in regular rows posteriorly, and small circular teeth arranged in a disorderly fashion for the anterior region of the single prearticular bone.

From the stratigraphic point of view, and according to Kriwet (2002), *Anomoeodus* appeared in the Kimmeridgian (Upper Jurassic) and survived until the Eocene, although recently Kriwet (2005) himself questioned some of the post-Mesozoic dating of the *Anomoeodus* findings in the literature. The genus *Anomoeodus* is ubiquitous, although it is predominantly limited to the Upper Mesozoic. The most complete specimens come from the Lower Cretaceous in Spain (Kriwet, 1999), from the Upper Cretaceous in England (Woodward, 1917; Kriwet, 2002), from various locations in France (Cornuel, 1877), and from Bohemia (Fritsch, 1878). This last, however, represents the first and oldest configuration of a prearticular attributable to the genus *Anomoeodus*. The genus *Anomoeodus* has also been well demonstrated for the Maastrichtian of Belgium and Holland (Leriche, 1929), for the Upper Cretaceous of Kansas (Shimada and Everhart, 2009), Texas (McKinzie, 2002) and Arkansas (Hussakof, 1947) in the USA, and for Sweden (Bazzi *et al*., 2015).

For the distribution of the genus *Anomoeodus* in Africa, there have been the following six reports. (i) Capasso (2019) described *Anomoeodus* sp. A in the limestone of the 'Azilé series' that outcrops in the port area of Owendo (Gabon). (ii) Cooper and Martill (2020b) attributed to the same *Anomoeodus* sp. A a complete large-sized vomer and two prearticular bones with teeth, collected from the Akrabou formation, near Asfla, Morocco, and dated to the Lower Turonian. (iii) Cooper and Martill (2020b) attributed to the provisional species *Anomoeodus* sp. B a complete large-sized vomer and prearticular bones with teeth, collected from the Akrabou formation, near Asfla, Morocco, and dated to the Lower Turonian; the same Cooper and Martill (2020b) proposed that this species B is very similar to *Anomoeodus* sp. A of the Turonian of Gabon, as described by Capasso (2019). (iv) Weiler (1935) reported teeth attributed to *Anomoeodus* sp. ind. from the Cenomanian of the Egyptian part of the Libyan Desert. (v) Priem (1908) reported dental remains from the Santonian limestone that outcrops at Abou Roach and at Berak el Gazal, both near Al Jizah (Egypt), attributable to *Anomoeodus angustus* Agassiz (1833-43). Finally, (vi) Priem (1914) also reported the same species on the basis of dental remains from the Turonian limestone outcrops at El Gaa, near Abou Roach, Al Jizah (Egypt).

Morphological comparisons between the species described in this study and the other *Anomeodus* species are now carried out in a stringent way specifically for the species already described in Egypt; in particular with *Anomoeodus angustus* and *Anomoedus* sp. B.

We have already addressed the discussion of the total identity between the new species *Anomoeodus aegypticus* and the species *Anomoeodus* sp. B recently described by Cooper and Martill (2020b). The identities here can be well assessed for each of the distinctive characteristics considered particular to both species, and can be suitably assessed by comparing Fig. 5A and B.

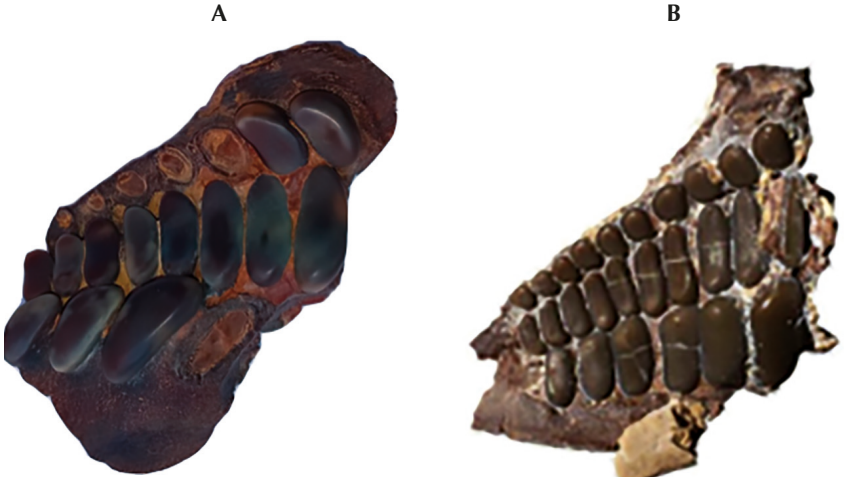

Fig. 5 - Comparison between the inner (endobuccal) face of the right prearticular of *Anomoeodus aegypticus* (**A**) and *Anomoeodus sp. B.* (from Cooper and Martin, 2020b) (**B**).

In the Upper Cretaceous of Egypt, Priam (1908; 1914) described the presence of *Anomoeodus angustus* Agassiz 1833-34 in two different locations; namely, in the Turonian and the Santonian limestone of the surroundings of Al Jizah. Agassiz (1833-43) described this species as *Gyrodus angustus* on the basis of two fragments of dentition from the Cretaceous of England and belonging to the collection of M. Weeker. Based on the description and drawings provided by Agassiz (Fig. 6A, B), it can be seen that the dental characteristics attributed to this species are the elongated shape of the teeth and their oblique position in the dental series.

Woodward (1895) moved this species to the genus *Anomoeodus* on the basis of a series of teeth from the Lower Senonian of Meudon, France. Additional dental materials were attributed to this species from the Senonian of Lewes, S-E England, from the Cenomanian of Saxonia, Germany, from Newtimber, Sussex, England, and from Plänerkalk, near Schlan, Bohemia, Czech Republic

(Woodward, 1893). Finally, Licht and Kogan (2011) described the presence of this same species in the Cretaceous of Saxony by repeating a more precise description of the dental anatomy and premaxillaries, so much so that *Anomoeodus angustus* was finally defined on an acceptable morphological basis.

By an examination and comparison of the materials described and illustrated by Licht and Kogan (2011), we can underline how the differences between *Anomoeodus angustus* and *Anomoeodus aegyptycus* are substantial. Indeed, although in both the species mentioned the dental series that has the largest teeth is undoubtedly the primary lateral, in *Anomoeodus an-*

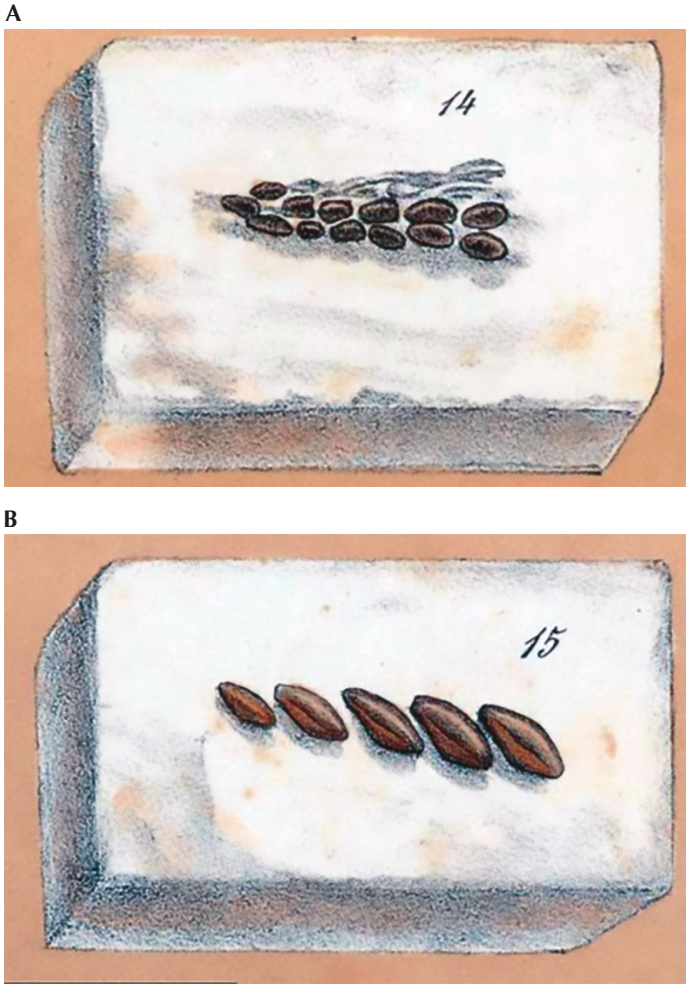

Fig. 6 - *Gyrodus angustus* Agassiz, from Figures 14 (**A**) and 15 (**B**) of Plate 66a of the Atlas of the Volume 2 of Agassiz (1833-43).

gustus the medial series and the secondary lateral series are composed of minute, spherical, almost circular teeth. These are arranged in a way that can be defined as poorly organized, so as not to be able to distinguish the true lateral-most series of teeth, and not even the medial-most series of teeth. Specific comparison of Fig. 7A and B shows that these differences are very evident. Moreover, precisely this same pre-articular dental pattern appears to be characteristic of the species *Agassizilia erfoudina*, as recently described by Cooper and Martill (2020a), of the Middle Cretaceous of the Ifezouane Formation, Kem Kem Group, Morocco (see Fig. 7C).

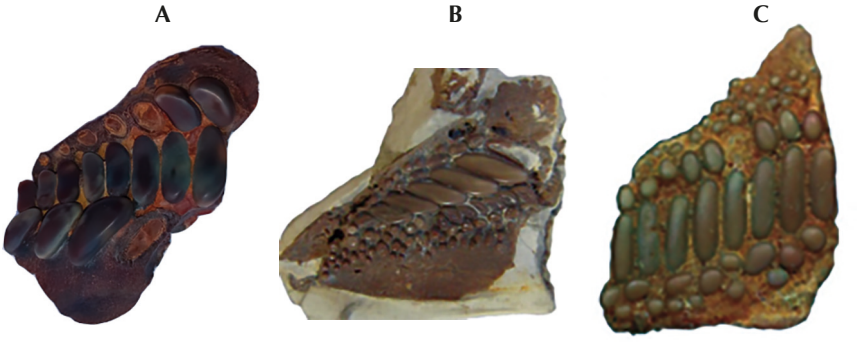

Fig. 7 - Comparison between the inner (endobuccal) face of the right prearticular of *Anomoeodus aegypticus* (**A**), *Anomoeodus angustus* (from Licht and Kogan, 2011) (**B**) and *Agassizilia erfoudina* (from Cooper and Martin, 2020a) (**C**).

The reports by Priem (1908; 1914) of the presence of *Anomoeodus aegyptycus* in the Upper Cretaceous of Egypt must, in our opinion, be considered with a high level of doubt. Both the descriptions and, above all, the illustrations of the dental materials for this determination were based on isolated teeth (Priem, 1908, Plate X, Figs. 1-7). On the basis of these teeth, we can certainly state that attribution to the genus *Anomoeodus* is highly probable, but any further specific determination is not possible. They might be teeth from prearticulars of the lateral primary row of either *Anomoeodus angustus* or *Anomoeodus aegypticus*.

The presence of the remains of *Anomoeodus* in the Maastrichtian (Late Cretaceous) of the Dakhla Formation, Dakhla Oasis, W Desert (Egypt), confirms the reports at the beginning of the last century on the presence of this genus of Pycnodontiformes in the Middle and Upper Cretaceous of Egypt; i.e., of the southern part of the Tethys.

At the palaeoecological level, the presence of Pycnodont remains in association with bivalves and gastropods, as well as marine mammals and reptiles, reinforces the reconstructions according to which the Dakhla Formation was sedimented in the marginal marine palaeoenvironment, in shallow waters, and with occasional connections with the open sea.

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