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DID POST-EOCENE PYCNODONTS ACTUALLY EXIST?

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Riassunto – L'autore affronta la questione della possibile sopravvivenza dei Picnodonti, pesci fossili attualmente completamente estinti, in periodi più recenti dell'Eocene. Nonostante che la letteratura corrente ponga al Priaboniano il limite superiore di estensione stratigrafica di questi pesci, esistono alcune segnalazioni di resti di Picnodonti in rocce dell'Oligocene e del Miocene. Alcune di queste segnalazioni si riferiscono a materiali attualmente andati perduti, come ha dimostrato l'attuale ricerca. Tuttavia, alcuni ulteriori materiali inediti sembrano riaprire la questione e lasciano aperta la possibilità che, almeno localmente, piccole colonie di Picnodonti abbiano potuto realmente sopravvivere al termine dell'Eocene.

Parole chiave: Picnodonti, Estinzione, Post-Eocene

Abstract – The author discusses the question of the possible survival of Pycnodonts – fossil fish currently completely extinct – beyond the Eocene. Despite the fact that the current literature places the upper limit of stratigraphic distribution of these fishes at the Priabonian, there are some reports of remains of Pycnodonts in the Oligocene and Miocene rocks. Some of these reports refer to specimens currently lost, as current research has shown; but some further unpublished materials seem to re-open the question and leave open the possibility that local and small colonies of Pycnodonts could actually survive after the end of the Eocene.

Key Words: Pycnodonts, Extintion, Post-Eocene

1. – Introduction

The Pycnodonts represent a group of fossil fish that are today completely extinct, although they flourished over a very long period of the Earth's history. They lasted from at least the Ladinian (end of Middle Triassic) to at least the Priabonian (end of the Eocene), which represents a period of about 200 Ma. During this time, the Pycnodonts occupied an important position in the aquatic vertebrate fauna, with their presence extended all over the world; indeed, these fish thrived in marine, brackish and freshwater habits. Many lived in shallow, reef, environments with many of the swimming adaptations common to reef fish (Nursall, 2010), some probably lived in the open water, with a pelagic life (*Gyrodus spp*.; Kriwet & Schmitz, 2005), some were benthonic (*Coccodus*), some were probably cryptic (*Ichthyoceros*), and some occupied, at last temporarily, the freshwater environments (Cavin *et al*., 2020). Their large orbital size suggests that some were nocturnal (*Gyrodus hexagonus*) (Nursall, 2010). Some served as prey (Everhart, 2007), and some others were predators of other fish (Kölbl-Ebert *et al*., 2018; Capasso, 2019), and finally, most were probably armed with an anatomically complex poisonous apparatus (Capasso, 2018).

To give an idea of the impressive biodiversity to which Pycnodonts rose during their very long history, we can simply note that 552 species pertaining to 97 different genera have been described to date. So, in summary, the Pycnodonts were a successful and significant component of the fauna and ecosystems in which they lived throughout the Mesozoic and lower Cenozoic eras (Nursall, 2010).

During this time, the Pycnodonts underwent some remarkable changes to their body shape, even if only single and almost always isolated species have been

described. However, through this they also maintained a remarkable constancy in their general body *bauplan*. In particular, their teeth have maintained an almost constant morphology, from the Middle Triassic to the Upper Eocene, even though they served to procure and process a diet made up of very different foods (from molluscs to fish), in varied environments. This thus demonstrates their great functional adaptability, while they remained within an almost anatomical monotony.

Moreover, the adaptive capacity of the Pycnodonts is definitively demonstrated by their survival through at least two global mortality crises: at the end of the Triassic, and at the end of the Cretaceous (the so-called K-Pg boundary). Following these two events, the Pycnodonts only showed significant demographic decreases in their populations. Their success, however, is demonstrated by the expansions of population size through a series of adaptive radiations. This allowed the Pycnodonts to occupy all of the marine waters of the Earth, with the exception of the seas around Australia, and also to adapt to life in some continental waters, and in brackish and freshwater habitats.

In the end, the extinction of the Pycnodonts occurred equally, probably because they lost out in the biological and ecological competition with the new forms of fish - the Teleosts - the adaptive abilities of which outweighed those of the Pycnodonts.

The question of whether the Pycnodonts survived beyond the end of the Eocene is evidently linked to the possible evidence of fossil remains dated to the Late Cenozoic. In relation to this, it must be underlined that the species that should be a candidate to represent the Upper Cenozoic Pycnodonts must correspond to at least the following two characteristics: (i) it must come from geological contexts that can be dated with certainty; and (ii) we must be certain that it is the remains of a true Pycnodont.

It must be recognized that in terms of these two requirements, at the present state of our knowledge, the number of finds described in the literature that can satisfy these are actually very few, although they do exist, as indicated in the following lines.

2. – Possible Oligocene Pycnodonts

In the literature, there are only the following two reports of possible remains of the Pycnodonts from rock that has been judged to be dated to the Oligocene.

1 *Pycnodontiformes indeterminate*: reported by Koch (1904) from the laminated platting slate and the greyish white pebble slate unearthed on Mount Gellérthegy, on the outskirts of Budapest, Hungary, on the occasion of excavations for a new water tank. Koch (1904) described this fish in some detail, which was the trunk without the tail, with a total maximum height of 15 centimeters. However, he was not able to determine its classification, as he said: "*Von den übrigen Genera der Pycnodonti weicht der Fisch vom Gellérthegy noch mehr ab, und läßt sich somit in keine derselben einreihen.*" ("*The fish from the Gellérthegy it is not comparable with any other genera of the Pycnodonts, and therefore it cannot be classified as any one of them.*").

2 *Pycnodus gosseleti*: described by Winkler (1880) (quoted by Woodward, 1885) on the basis of a partial dentition from the Oligocene clay of Limbourg, Belgium. Woodward (1985) commented on this specimen with the following words: "*Probably not Pycnodont*", but without any direct examination of the fossil.

On the occasion of the preparation of this paper, I tried to trace the enigmatic Hungarian find. Colleagues Dr. Klàra Paloàs and Dr. László Makádi, from the Mining and Geological Survey of Hungary, in Budapest, have searched extensively for this find and have ruled out that it is still kept in their Institute. Also, Dr. István Szente, from the Institute of Geology and Palaeontology of the Eötvös University in Budapest, also searched patiently and long for the find described by Prof. Anton Koch, but he was not able to find it. Dr. István Szente himself told me that, "*The specimen studied by Koch seems to be lost, unfortunately. Koch left a well-arranged collection when he retired in 1913. His successor (Imre Lőrenthey), however, passed away very untimely in 1917, and the Department of Palaeontology at Budapest did not acquire any of this until 1953. In this period, the collection suffered severe damage.*" On the other hand, in two separate papers of Wilhelm Weiler (1933, 1938) described and published the Oligocene fish fauna of the same Buda Hills locality, and there were no remains of Pycnodonts, not even a single tooth. These bibliographical references, therefore, tend to exclude that there were actually Pycnodonts in the Oligocene of the surroundings of Budapest.

Regarding the dental remains described by Winkler (1880) as *Pycnodus gosseleti*, it must be said that they were in a private collection, that of Dr. Jules-Auguste Gosselet, of which after almost 150 years I have not been able to find any trace.

3. – Possible Miocene Pycnodonts

In the literature, there are two more reports of dental remains attributed to the Pycnodonts, here collected from rocks that were certainly of the Miocene age. While assuming that there is no possibility of excluding that the Pycnodonts did live up to such recent times, the mention of these two finds really only has the value of scientific completeness here.

1 *Pycnodus carolinensis*: described by Emmons (1858) on the basis of fragments of dentition from the Miocene of North Carolina, U.S.A..

2 *Pycnodus dutempley*: described by Rouault (1858) (quoted by Woodward, 1885) on the basis of fragments of dentition from the Miocene of Saint Juvat, near Dinan, Côtes-du-Nord, France.

Finally, we remember here that Slaughter (1966) reported the presence of fossil remains named as "*Mesodon" tyroidea* that were collected in the Pleistocene sands of Moore Pit, Texas. Some recent authors have interpreted these as remains pertaining to the Pycnodonts.

On the contrary, I can verify that the "*Mesodon tyroidea*" cited by Slaughter (1966) consists of a shell of a terrestrial mollusc, also named as *Polygyra tyroidea*, and thus it has not relationship with the Pycnodonts.

4. – Possible new materials

To these citations in the literature, we must also add some further specimens, that has not been described to date.

1 - The first one was found on the occasion of the research that was carried out to put together this paper. This unpublished specimen was recognized at the Museo di Palaeontologia dell'Università di Firenze, thanks to activity of the Dr. Elisabetta Cioppi, as described in the following lines. It is a posterior tooth of the prearticular dentition of a large specimen (the isolated tooth is about 18 mm long) of a *Pycnodontiformes undetermined*. It was collected from the so-called "*Lecce stone*", a white limestone that surfaces widely in Salento, in the province of Lecce, southern Italy, and that has been used for centuries for building; this certainly dates to the Miocene. Traces of the characteristic matrix are still clearly visible around the root of the tooth (Figure 1). This finding was acquired by the collections of the Museo di Palaeontologia dell'Università di Firenze in 1868, and it originally belonged to the collection of Dr. Major (no. 4888).

Fig. 1: This isolated tooth pertains certainly to the posterior region of a prearticular of a Pycnodont. The original label written by the first collector, Dr. Major, said: "*Miocene, near Lecce, Otranto*". And in fact, the matrix still contained within the root of the tooth is evidently of yellowish calcarenite, locally called "Lecce stone" of the Miocene, which is well known to palaeontologists for its marine fossils. This specimen (maximum lenght of the tooth = 18 mm ca.) was recently found on the occasion of this research thanks to the collaboration of Dr. Elisabetta Cioppi (Museum of Palaeontology, University of Florence; n. 4888).

Fig. 1: Questo dente isolato appartiene certamente alla regione posteriore di un prearticolare di un picnodonte indeterminato. L'etichetta originale scritta dal primo collezionista, il dottor Major, riportava la seguente dicitura: "Miocene, vicino Lecce, Otranto". Ed infatti la matrice ancora contenuta all'interno della radice del dente è evidentemente di calcarenite giallastra, chiamata localmente "pietra leccese" del Miocene, ben nota ai paleontologi per i suoi fossili marini. Questo esemplare (lunghezza massima del dente = 18 mm circa) è stato recentemente rinvenuto in occasione di questa ricerca grazie alla collaborazione della Dott.ssa Elisabetta Cioppi (Museo di Paleontologia, Università di Firenze; n. 4888).

2 - A second specimen pertained to the old "Capasso Public Collection" (CPC #1912), there is a find that points in the same direction. This is an isolated tooth of a Pycnodont, where the ancient label indicates that it comes from the volcanic "tuff" of Nikolskoe village, Bering Island, Commander Archipelago, Russia. This tooth (Figure 2) was acquired by the Collection between 1915 and 1916, but its collection might also have been from much earlier, and there is no chronological reference that provides any indication of the presumed geological context of the find. However, it has recently been established that the first phase of formation of Bering Island volcanic rock would refer to the end of the Eocene. The only sedimentary and volcano-sedimentary rock on the Island of Bering are the polyfacial deposits of Nikolskaya suite (which consist of the conglomerato-breccias, tuff-breccias, and tuff-conglomerates), and the Komandorskaya series (which consists of the Preobrazhenskaya suite, Gavanskaya suite, Gavrilovskaya suite, and Poludennaya suite) (Borsuk *et al.,* 1984). These sediments were recently dated to the Oligocene, and also contain abundant fossil remains of terrestrial animals and plants (i.e., fossil wood, leaves), as recently reported on by Geologist Alexey Perelygin on the official website of the Commander Islands (http://komandorsky.ru/en /geology-mysteries-2019.html). Dr Perelygin confirmed that the dating of these volcanic tuffs that outcrop on the Island of Bering would indeed be the Oligocene.

A B

Fig. 2: This isolated tooth pertains certainly to a Pycnodont as was collected in 1915-16 in the "tuff" near the village of Nikolskoe, Island of Bering, Commander Archipelago, that recentely was dated to the Oligocene (maximum lenght of the tooth = 7 mm ca.). CPC #1912.

Fig. 2: Questo dente isolato appartiene sicuramente ad un picnodonte, sebbene indeterminato; esso è stato raccolto nel 1915-16 nel "tufo" affiorante nei pressi del villaggio di Nikolskoe, nell'Isola di Bering, Arcipelago Commander; questa formazione recentemente è stata datata all'Oligocene (lunghezza massima del dente = 7 mm ca.). CPC #1912.

5. – General remarks on the hypothetical post-Eocene Pycnodonts

With regard to the possible presence of Pycnodonts during the Oligocene and Miocene, I must first of all consider that for 123 years, we believed that the Pycnodonts had become extinct in the Bartonian, so around 40 million years ago. This belief was based on the work of Priem (1897), who had described dental remains of the species *Pycnodus mokattamensis* at Gebel Mokattam, in Egypt. Only in 2019 did Voss *et al*. discover a prearticular of a Pycnodont that belonged to the same species as that described by Priem (1897). This was in a nearby field in Wadi Al Hiton, in Egypt, which was certainly dated to the Priabonian, so to about 34 million years ago. This recent discovery prolongs the survival of the Pycnodonts in the Tethys over time, to show that they certainly lived in these seas until the end of the Eocene.

Therefore, today, in light of these new data, it does not seem so unlikely that the Pycnodonts were still sporadically present in the Oligocene in Hungary. However, unfortunately the only specimen described – as we have seen – has been definitively lost, making it impossible today to verify the brief and superficial description made by Prof. Antoni Koch in 1904.

Even the ancient discovery coming from the Commander Arcipelago, therefore, reinforces the doubt that some of the Pycnodonts might have survived during the Oligocene in small isolated populations. However, this does always depend on whether the location of the collection of the sample in question was correctly reported and whether these provisional dates are correct, and assumes that the tooth did not come from secondary sedimentation. What is certain is that this find that refers to a certainly continental sedimentary palaeo-environment is also the northernmost discovery of the Pycnodonts known today.

There is still, however, the specimen found by Dr. Elisabetta Cioppi in the Museum of Florence. It is undoubtedly a Pycnodont tooth, and the matrix of which there are traces is almost certainly the soft calcarenite that surfaces in Salento, near the city of Lecce. This has been dated certainly to the Miocene, as the Burdigalian–Langhian–Tortonian stages. It is equally true that this stone has been excavated for centuries in the quarries around the city of Lecce, with it used for all of the relevant monuments that were built, which now represent the architectural heritage known as "*Lecce Baroque*". No remains of the Pycnodonts have ever been described here, although thousands of fossils of fish, reptiles and marine mammals characteristic of this rock have been found and described by many serious specialists.

These same identical doubts, moreover, have been in place since 1868; i.e., since this find that belonged to the collection of Dr. Major was acquired in the collections of the Museo di Paleontologia dell'Università di Firenze. In fact, on the original cardboard support, Dr. Major had written "*Miocene, near Lecce, Otranto*". However, when the finding was acquired in Florence, the word "*Miocene*" was cancelled, and a new label was superimposed on the old one. This new label bears the following emblematic wording: "*Molto difficile che questo dente di Picnodonte sia stato rinvenuto nel Miocene; presumibilmente esso deve provenire dal calcare cretaceo, che affiora a breve distanza da Lecce*" (which means: "*Very difficult that this Pycnodont tooth was found in the Miocene; presumably it must have come from the Cretaceous limestone, which crops out a short distance from Lecce*") (Figure 3). I am not so sure that we can permanently erase the word "*Miocene*" from the history of the Pycnodonts.

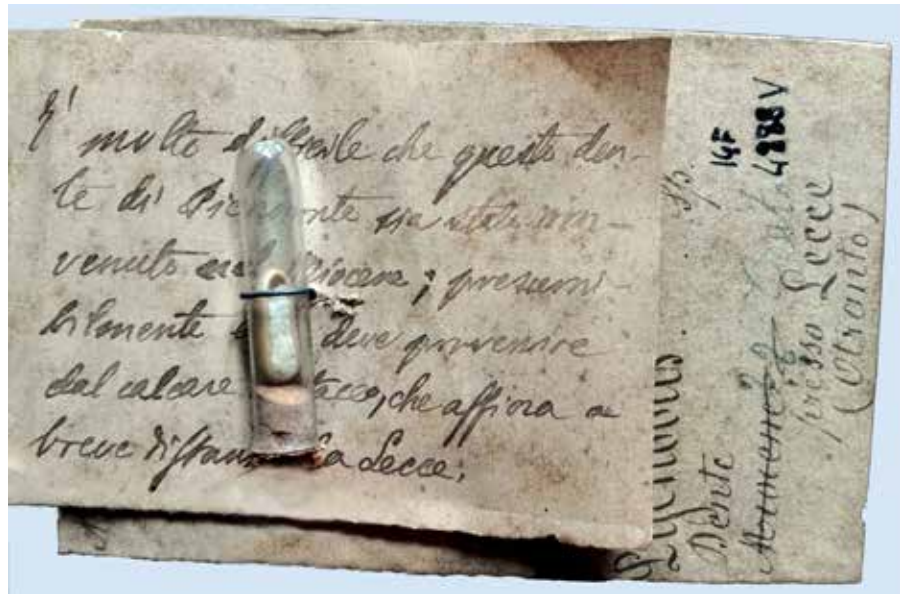

Fig. 3: When the specimen presented in the Figure 1 was taken charge by the collection of the Museo di Paleontologia dell'University of Florence in 1868, the word "*Miocene*" was cancelled, and a new label was superimposed over the old one. This new label bears the following wording: "*Molto difficile che questo dente di Picnodonte sia stato rinvenuto nel Miocene; presumibilmente esso deve provenire dal calcare cretaceo, che affiora a breve distanza da Lecce*" (which literally means: "*It is very difficult that this Pycnodont tooth was found from the Miocene; presumably it must have come from the Cretaceous limestone, which crops out a short distance from Lecce*"). This specimen was recently found on the occasion of this research thanks to the collaboration of Dr. Elisabetta Cioppi (Museum of Palaeontology, University of Florence; n. 4888).
Fig. 3: Quando l'esemplare presentato nella Figura 1 fu preso in carico dalla collezione del Museo di Paleontologia dell'Università di Firenze, nel 1868, la parola "Miocene" fu cancellata dall'antico cartellino e una nuova etichetta fu sovrapposta a quella vecchia. Questa nuova etichetta riporta la seguente dicitura: "Molto difficile che questo dente di Picnodonte sia stato rinvenuto nel Miocene; esso deve provenire dal calcare cretaceo, che affiora a breve distanza da Lecce". Questo esemplare è stato recentemente rinvenuto in occasione di questa ricerca, grazie alla collaborazione della Dott.ssa Elisabetta Cioppi (Museo di Paleontologia, Università di Firenze; n. 4888).

Perhaps we should all remember that we had categorically admitted that the Coelacanths were completely extinct at the end of the Cretaceous, to be sensationally corrected in 1938 by a fisherman who found a living specimen in his net when it was pulled to the surface while fishing in the waters near the mouth of the Chalumna River.

6. – Conclusion

In conclusion, there is – at the present state of our knowledge – no evidence that these reports can be confirmed or denied in terms of their validity in support of the sporadic presence of the Pycnodonts in the Oligocene, and even in the Miocene. The paleontological evidence shows that the Pycnodonts developed their biological continuity from the end of the Middle Triassic (Ladinian) to the end of the Eocene (Priabonian). This does not exclude the possibility that they might have survived sporadically in some strictly localised enclaves. After all, we paleontologists must not miss the historical example of the Coelacanths, which are fish that were considered to be extinct for a long time, but which were discovered unexpectedly to be still alive today in a restricted ocean area off the coast of Madagascar. Thus one lucky, and absolutely unexpected, fishing trip suddenly revised our long-held secular beliefs.

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