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PYCNODONTS WERE POLYPHYODONT ANIMALS

SUMMARY

Here, I demonstrate that pycnodonts were polyphyodont animals, through radiographic highlights of dental gems in various states of maturation that are present in both the prearticular and the vomer of at least some Cretaceous genera *Neoproscinetes* and *Phacodus,* and for the Eocene genus *Pycnodus*. I propose the hypothesis that polyphyodonts in pycnodonts involved a differentiated ontogenetic mechanism in young subjects compared to adult ones. In young fish, the growth of the dentition occurred through introdution of new teeth from behind. In adults, only worn teeth were replaced, regardless of their position. The cessation of the ameloblastic activity certainly marked the senescence of the pycnodonts, in which the exhaustion of the ameloblasts prevented dental replacement, making senile subjects edentulous, with bone atrophy and the consequent inability to feed, ultimately leading to the death of the fish.

RIASSUNTO

L'autore dimostra che i picnodonti erano animali polifiodonti, in quanto ha evidenziato, anche radiograficamente, la presenza di gemme dentarie in vari stati di maturazione presenti sia nei pre-articolari che nel vomere almeno nei generi cretacei *Neoproscinetes* e *Phacodus* e nel genere eocenico *Pycnodus*. L'autore propone, inoltre, l'ipotesi che la polifiodontia nei picnodonti implicasse un'ontogenesi differenziata nei soggetti giovani (in accrescimento) rispetto agli adulti. Nei giovani, la crescita della dentatura avveniva attraverso l'apposizione di nuovi denti da dietro. Negli adulti, invece, l'attività ameloblastica consentiva la sostituzione dei soli denti usurati. Verosimilmente, la cessazione dell'attività ameloblastica segnava l'inizio della senescenza nei picnodonti, nei quali l'esaurimento degli ameloblasti impediva la sostituzione dentale, portando i soggetti senili all'edentulia, con atrofia ossea e con conseguente incapacità di nutrirsi e, infine, morte.

INTRODUCTION

The dentition of the pycnodonts has been considered unique by many authors, in the sense that the set of teeth of a given specimen were the result of the generation of a single eruption. However, this view does not explain the following two problems: (i) how the first dentition of a young and a subadult fish, which is evidently made up of fewer and smaller teeth than the adult, reaches the anatomical maturity and functionality of the adult; and (ii) whether, and in what way, the teeth that become worn due to their regular use in chewing are replaced (alternatively, how can an individual survive when their teeth are so worn that they ultimately become useless for chewing)?

These two problems refer to two separate and quite distinct phenomena: (i) the growth and maturation of the first dentition, which reaches the adult configuration through an ontogenetic process that is characteristic for each species; and (ii) the possibility that some (or even all) of the individual teeth might be replaced after the final configuration has been reached, when ontogenesis has ended; i.e., when the typical configuration and dimensions of the adult is attained. This second phenomenon can be realized only if the ameloblasts (i.e., the cells responsible for synthesis of dental crowns) persist also in the adults.

Thus, the first phenomenon relates to the ontogenesis of the dentition, while the second one relates to dental replacement in adults.

Dental ontogenesis in juvenile pycnodonts

Woodward (1895) suggested that in pycnodonts, new teeth are added to the dentition from behind, and that this mechanism would also be the basis for growth of the dentition, which would allow the size of the dental sets to increase along with ontogenesis and growth. Nursall (1999) also assumed that there was a single generation of teeth, and new teeth were added to the dentition from behind, during the growth of each individual.

In support of this hypothesis and of this growth model, data have now been collected concerning the wear patterns of adult dentition, above all through an extensive analysis by Kriwet (2005) on a large number of pycnodont dental apparatuses, as both prearticular and vomer. As he stated: "*wear patterns first occur on anterior teeth and then move posteriorly to the larger posterior teeth with age. Consequently, anterior teeth are mostly smooth, whereas posterior teeth exhibit their original ornamentation. The tooth ornamentation is generally well preserved in juvenile specimens; the ornamentation of teeth is completely lost in senile specimens*." (Kriwet, 2005).

This pattern of dental abrasion can be easily explained by noting that the anterior teeth, both prearticular and vomerine, erupt first, and therefore are used in chewing for a longer time compared to the posterior teeth, which erupt later in the life of the same individual, and therefore are less worn. So, the model proposed by Woodward (1895) to explain the growth of the first dentition of the pycnodonts during ontogeny agrees with the hypothesis of single dental generation, with progressive addition of new dental elements from behind. This model was supported also by both Thurmond (1974) and Nursall (1996).

In describing the new species *Akromystax tilmachiton* of the Cretaceous of Lebanon, Poyato-Ariza and Wenz (2005) identified a specimen in which some dental gems were present inside the bones (which were visible through accidental breaks of the corresponding bone). These were two teeth: one was located in the prearticular, posteriorly, which was interpreted as a tooth in the process of formation that was about to be added to the series of prearticular teeth from behind; the other one was located below a tooth that had already erupted within the dental bone, and was interpreted as a case of a replacement (see above).

It appears, therefore, that in the pycnodonts there is a growth pattern of the dentition that provided for the anterior teeth (which were mobile and prehensile) to grow locally at the expense of the dental gems in the dental and premaxillar bones, while the posterior teeth grew to reinforce the new teeth from behind. A very similar model is seen for living manatees: these have no incisor or canine teeth anteriorly, and just a set of cheek teeth (so called "labial teeth", without any bone association), which are not clearly differentiated from the morphological point of view. The posterior molar teeth, however, are continuously replaced throughout their life with new teeth that grow at the rear, as the older, worn teeth fall out from farther forwards in the mouth (Figure 1). This process is called "hind molar progression" or "*marching molars*" (Whitloch *et al*., 2013).

Fig. 1 - Extant manatee mandible in which the molar teeth series is seen. The anterior teeth have very worn chewing surfaces, with the enamel layers completely worn (the brown surfaces are due to uncovering of the dentine). Posteriorly, new dental crowns are about to emerge from the alveolar process, which push the front teeth forward. This results in continuous anterior migration of the molars, as the so-called "*marching molars*". From the website: https://app.emaze.com/@AOCRRILL#1.

Dental replacement in the adult pycnodonts

This model, however, does not exclude the hypothesis that worn teeth had the possibility of being replaced, which must be expected above all for the front teeth. As the first report, Hennig (1907) described a single case of a tooth replacement beneath a broken tooth in the vomerine dentition of a *"Palaeobalistum ventralis"* from the Cretaceous of Lebanon, although he assumed that this case was an exceptional circumstance (Figure 2).

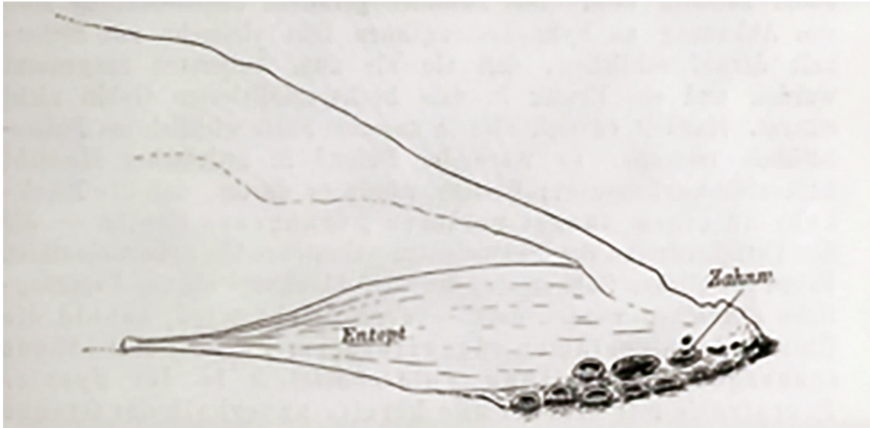

Fig. 2 - For the first time, Hennig (1907) described and represented in this drawing, the case of dental replacement in a pycnodont, "*Palaeobalistum ventralis*", from the Cenomanian of Lebanon. A dental gem (which had eroded the cortical bone) can be seen below a nonposterior tooth of the right lateral row of the vomer. Reproduced from Hennig (1907).

In recent years, evidences have been collected to support the existence of dental replacement in adult pycnodonts, and this phenomenon can no longer be denied. Kriwet (2005) reported many observations: "*Several specimens examined for this study occasionally exhibit an open depression with a newly formed tooth at its bottom, posterior to the last teeth, similar to the condition mentioned by Hennig (1907)*." This kind of "*depression*" in the maxillary bones is well known, and it has been very well documented in many animal species, both living and fossil. This depression represents the impression left in the maxillary or mandibular bones by the growing "*dental gem*", where its mineralized tissues (i.e., dental crown, and possibly the first traces of the root) are also surrounded by ameloblastic tissue, which is highly vascularized when living. This so-called *dental gem* is nothing more than the dental crown being formed, and this derives from activation of ameloblastic tissue that is present even after the formation of the first dental series. Evidently, the dental gem being formed occupies the central part of this cavity (crypt), but it is not imbricated or adhered to the surrounding bone, due to the interposition of a soft tissue cuff. After the death of the animal, these dental gems, which are not strongly connected to the surrounding bone, are lost, even before fossilization begins. This is because the taphonomic phenomena generally lead to decomposition of all of the soft tissues, including the cuff of soft tissue that surrounds the dental gems still under formation. What can be seen in the fossil, therefore, will be nothing more than a niche, or better, it could be called a "fovea" (or crypt), at the centre of which the dental gem was being formed in the living fish. These crypts have been well documented, e.g., by Longbottom (1984) in the extensive material collected in the Eocene of Mali, and consist of many dozens of prearticular and vomerine bones pertaining to large sized adult pycnodonts. It is interesting to note that in these fossils, the crypts that correspond to the assumed lost dental gems that were being formed are located in correspondence with already lost teeth, or below teeth affected by very serious wear (Figure 3A).

Also, although Nursall (1999) firmly believed that the pycnodonts had a single generation dentition, he himself recognized that the finds from Mali represented an evident exception: "*In some Malian Pycnodus spp. studied by Longbottom (1984), irregular clusters of small teeth are found anterior to regular rows of both vomerine and prearticular teeth, leading to the suggestion of replacement of worn out teeth by small irregular disposed teeth. However, this is the only clear example of regeneration and replacement of teeth among pycnodonts*".

Recently Cooper and Martill (2020) erected the new species *Neoproscinetes africanus* from the Middle Cretaceous Hessin-el-Begaa (Morocco), and described a vomerine dentition that shows an unusual cluster of small rounded anterior teeth which are interpreted as "*second generation replacement teeth* ", which would have replaced those lost during chewing, because they were worn and lost. Unfortunately the aforementioned authors expressed their questionable opinion on the frequency with which the described condition appears in pycnonts, when they asserted that "*this mode of tooth replacement looks to be unique in pycnodonts*".

In addition to the already mentioned case, there is a case of replacement of an anterior tooth in the dental bone in a specimen of *Akromystax* of the Cretaceous of Lebanon, as reported by Poyato-Ariza and Wenz (2005).

In this paper, I how new fossil traits that have been analyzed using laboratory techniques (i.e., radiography and tomography), as well as through direct observation, and which clearly demonstrate that cases of dental replacement in adult pycnodonts represent the rule, rather than the exception.

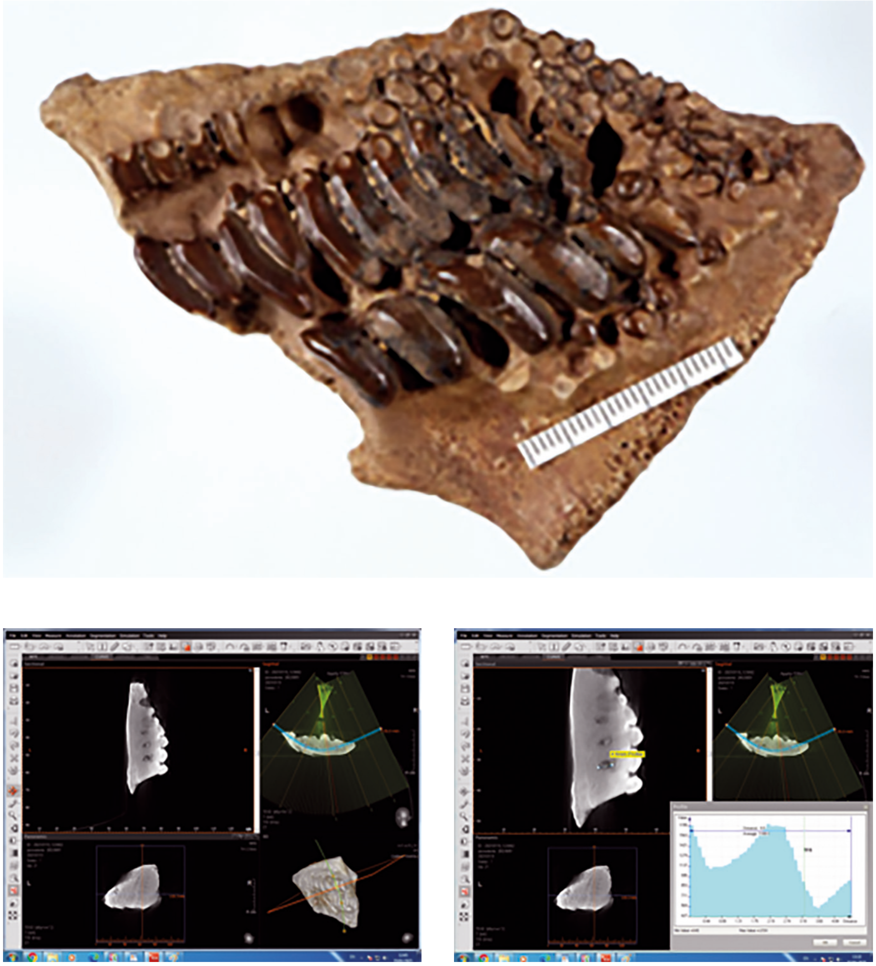

Fig. 3 - A: Inner face of the left prearticular of *Pycnodus maliensis* of the Eocene of Tamaguélelt, Mali. This prearticular dentition is characterised by teeth that are not arranged neatly in rows in the front part. There are also numerous crypts (fovee) left by the growing dental gems (lost during the taphonomic processes). B: Tomography of the same specimen that demonstrates the presence of crypts in the context of the bone; the crypts each contain a dental gem (except the highest located crypt, which has opened to the internal surface of the bone, and has freed its dental gem; this appears as a crypt on external macroscopic examination of the bone surface). Note how the individual crypts are located exactly below, in correspondence with erupted teeth. C: The densitometric analysis in correspondence with the niches shows that the density of the gem (located in the center of the niche) is even greater than that of the surrounding bone: this shows that the gem is made up of a more radio-dense tissue, i.e., dental enamel. CPC # S-487.

MATERIAL AND METHODS

In this paper, I examine seven cases: two from the Cretaceous period of Morocco, three from the Cretaceous period of Brazil, one from the Cretaceous of Texas (USA), and one from the Eocene of Mali. In particular, the cases examined are the following.

(i) Dentitions of two specimens of *Phacodus* sp. ind., collected in the first part of the last century from the Late Cretaceous of the Morocco phosphorites, which belongs to the "Public Collection of Fossil Fish Luigi Capasso" (CPC): teething vomerine no. CPC # S-1905, and a prearticular pair no. CPC # S-1005.

(ii) Three specimens of *Neoproscinetes penalvai*, also collected in the first part of the last century, here from the Cretaceous of Ceara, Brazil, and prepared with acid: two belonging to the CPC (no. CPC # S-1935 and CPC # S-1936), and the one other belonging to the paleontological Collections of the University Museum of Chieti (Inventory no. 20089). The CPC is legally registered by a Decree of the *Ministero per I Beni e le Attività Culturali* under the date of October 11, 1999, following the disposition of Italian Law 1089/39. The specimens of this collection were also subject to prescription for conservation and availability for studies on the basis of Article 30 of Italian Law N° 42/2004.

(iii) One left prearticular bone with many teeth, of *Pycnodus maliensis* of the Eocene of Tamaguélelt, Mali, belonging to the CPC (# S-487).

(iv) One left prearticular bone with few teeth of *Globoanomoeodus dentespassim* of the Cretaceous of Waco Lake, central Texas, USA.

All of the specimens were examined with a stereomicroscope (Wild M 8; Leica). The two specimens from Brazil that were prepared with acid, and the specimen from the Cretaceous of Texas, were subjected to radiographic examination, and the Pycnodont prearticular from Mali was subjected to tomographic examination (Vatech PsX Zenith 3D tomography; using 110.0 kV and 7.0 mA), with the densitometric analysis performed with the Ez3D software.

RESULTS

Direct evidences of dental replacement

A number of indirect clues have provided evidence that dental replacement was common at least in some genera of the adult pycnodonts. Many examples can be found in the extensive material that documents the genus *Phacodus* of the Upper Cretaceous of Morocco. Thousands of dentitions, both prearticular and vomerine, have been collected in many deposits of

Fig. 4 - Vomerine dentition of *Phacodus* sp. ind. from the Late Cretaceous of the Morocco phosphorites. The third tooth of the median row of teeth, as the one composed of the largest elements, has a series of peculiarities: the tooth surface lies on a lower plane to that of all of the neighboring dental elements, which demonstrates that the dental surface of this crown had not yet reached the masticatory plane. Moreover, the ornamentation of the surface of this tooth is very evident (made up of small tubercles), much more so than for the neighboring teeth, showing that the surface of this tooth has not yet been consumed by chewing. Finally, the crown of this tooth appears, divided into two halves. CPC # S-1905.

the famous “*Phosphorites of Morocco*”, and this wide-ranging material offers the possibility to consider dentitions in various stages of evolution and growth, and is also pertinent to adult individuals. For example, Fig 4 shows a vomerine dentition in which the third tooth of the median row of teeth (the one composed of the largest elements) has a series of peculiarities: (i) the tooth surface lies on a lower plane than that of all of the other neighboring dental elements, which demonstrates that the dental surface of this crown had not yet reached the masticatory plane. In other words, this tooth had not yet completed the so-called “functional eruption”, while it had already completed the so-called “anatomical eruption”; and moreover, (ii) the ornamentation of the surface of this tooth (which is made up of small tubercles) is very evident, much more so than that for the neighboring teeth, which shows that the surface of this tooth has not yet been consumed by chewing; and finally, (iii) the crown of this tooth appears to be split, or divided into two halves. These peculiarities indicate that the tooth in question was in the

Fig. 5 - Right prearticular of *Phacodus sp. ind*. from the Late Cretaceous of the Morocco phosphorites, fossilised disarticulated. Below the symphyseal bone surface, there are two crypts left by two erupting dental gems. The more anterior one is still occupied by the dental gem that was being formed, where the crown of the tooth was already completely formed, while its root was still being formed. In the rear crypt, the gem that was in the process of formation was lost, perhaps during the the fossil preparation. CPC # S-1005.

eruption phase, and its positioning almost in the centre of the vomerin dentition allows us to exclude that it is a case of ontogeny due to the addition of a posterior tooth in a young subject. This is obviously a case of replacing a tooth that has fallen out in an adult individual.

A second example is shown in Fig 5, which reproduces the two prearticulars, right and left, of an adult individual of the same species, *Phacodus punctatus*, which also comes from the Upper Cretaceous of the Phosphorites of Morocco. In this case, the two prearticulars have fossilized and shifted together, so that the one on the right shows the large symphyseal surface. This position bared the bone immediately below the symphysis, where there is an almost completely formed dental gem that is already well rooted in the surrounding bone, and is located immediately below the second tooth of the innermost row. There is no doubt that a new tooth was being formed below the crown of a very worn anterior tooth. Other crypts are also visible, and these represent the spaces in which other less advanced tooth formation was taking place, the corresponding crowns of which were in the process of initial ossification, but were lost during diagenesis or during the extraction of the fossil.

Very similar situations have been highlighted recently also for specimens

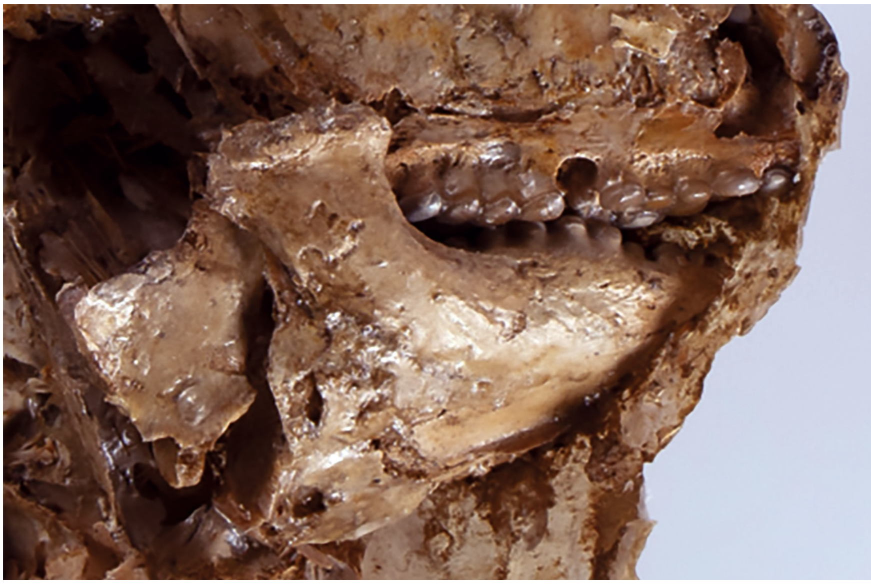

Fig. 6 - Mouth region of an acid-prepared specimen of *Proscinetes penalvai* from the Cretaceous of Ceara, Brazil. The vomer shows a large crypt that had eroded the cortical bone and that contained a dental gem that was being formed, to be ready to replace a worn tooth of the outermost row on the right. The gem that was in the process of formation was lost, perhaps during fossil preparation. MUC # 20089.

of the species *Neoproscinetes penalvai* of the upper Cretaceous of the Crato Formation, Ceara, Brazil. Also in this case the large quantity of available specimens and the extraction techniques of the fossils by controlled acidification for the dissolution of the matrix, have allowed perfectly preserved specimens to be obtained. One of these is shown in Fig. 6, and it shows a gap in the vomer that evidently contained a dental gem that was ready to replace a central tooth of the outermost right row of the vomerine dentition. This represents a very similar case to that described by Hennig (1907) (Fig. 2).

Thin sections provide evidence of dental replacement

A great definitive contribution to the question of the existence of dental replacement in the adult pycnodonts was provided by the study of Kriwet (2005). Here, it was definitively shown that at least in the two pycnodont genera of *Macromesodon* and *Proscinetes*, there was the possibility of dental replacement in adult subjects. Indeed, Kriwet (2005) performed longitudinal sections of prearticular bones pertaining to these two genera, and demonstrated that underneath the erupted teeth, there were dental gems being formed (Fig. 7). These sections definitively demonstrated that in the pycnodonts, ameloblastic tissue persisted even in adults after the end of on-

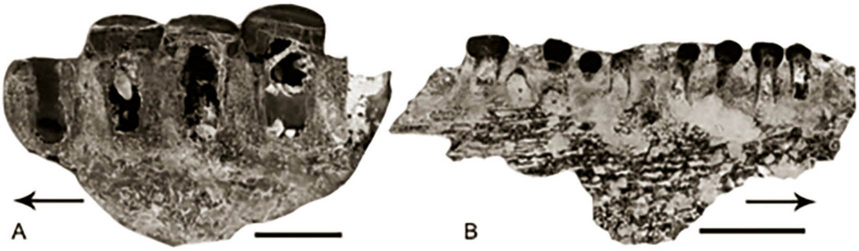

Fig. 7 - Vertical sections of pycnodont vomers from the Kimmeridgian (Late Jurassic) of north-western Germany. The arrows point anteriorly. Scale bars: 10 mm. A, *Macromesodon sp.*. B, *Proscinetes sp.*. There are two teeth well below the occlusal level with relatively thin crown cusps. Although not directly below the functional teeth, these teeth are interpreted here as replacement teeth. From Kriwet (2005). Courtesy of Prof. Jürgen Kriwet, Vienna.

togenesis of the first generation teeth, which allowed the replacement of worn teeth by new erupting teeth, at least in some genera.

Kriwet (2005) also hypothesized that the phenomenon of replacement would occur more frequently in the posterior teeth than the anterior ones. However, this interpretation appears not to be correct, because it is in contrast with the data that demonstrate how the anterior teeth are those that are most exposed to wear, for the reasons that have already been explained above. Moreover, perhaps the presence of teeth growing in the posterior areas of the dentition would not be related to dental replacement, but rather to ontogenetic growth of the dentition, which is limited to young subjects.

X-ray and tomographic evidence of dental replacement

To ascertain the possible presence of dental gems inside the bones of the chewing apparatus of adult pycnodonts, some radiographs and tomographs were obtained. With the X-ray examination, for both specimens examined in this study, I was able to effectively demonstrate the presence of dental gems both in the prearticular bones, and in greater numbers, in the vomer. Radiographically, the dental gems appear as still incomplete dental crowns of varying sizes (which indicates different stages of maturation), and are arranged in an apparently disordered way, as they are not arranged in uniform rows. In both X-rayed specimens, the dental gems are present both inside the prearticular bones and inside the vomer. In the vomer, in particular, the gems are more numerous, and are also widespread very far from the masticatory plane, up to occupying the upper median process of the vomer, which is embedded by the bone laminae of the inferior margin of the mesethmoid (Fig. 8, 9).

To be able to correctly interpret this radiographic information, it is necessary to specify that both individuals of *Neoprosinetes penalvai* subjected

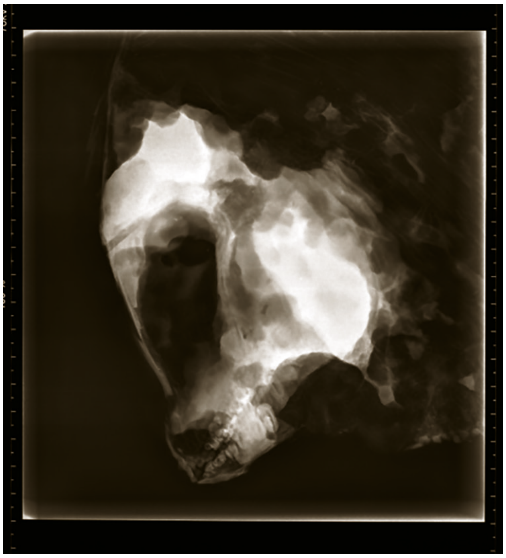

Fig. 8 - X-ray taken in lateral-lateral projection of the head region of an adult specimen of *Neoproscinetes penalvai* (Cretaceous, Brazil), TL = about 370 cm; note the presence of dental gems both at the premaxillary level and at the level of the vomer. Note also how the dental gems in the vomer are particularly abundant, and also occupy the upper part of the bony lamina that connects with the parasphenoid; it should also be noted how the dimensions of these dental gems in the context of the vomer present very variable dimensions, demonstrating different degrees of development and maturation. CPC # S-1935.

to radiography are undoubtedly adults, both from the state of complete ossification of the axial skeleton and tail, and from the considerable general dimensions: CPC S-1935 = TL: 370 mm and MUC no. 20089 = TL: 360 mm. The radiographically demonstrated dental gems, therefore, indicate that dental replacement involved the replacement of the most worn teeth and persisted even in adult individuals of this Pycnodont.

Tomography was performed for the prearicular bone from the Eocene of Mali, which confirmed that the fovee on the internal surface of the prearticular bones are the consequence of bone resorption processes that occurred during the life of the adult fish. This interpretation is based on their regular and clear margins (i.e., not blurred), and their considerable depth (which greatly thinned the underlying bone), especially in the central part of each crypt (Fig. 3B). In addition, in the context of the bone, these tomographs show osteoclastic niches, in the center of each of which there is a dental gem in the process of formation and surrounded by a radiotransparent ring. Below each tooth that has already erupted, there is a crypt with a dental gem in the process of formation, which demonstrates the preparation of a new tooth that would replace the one above it, as soon as that was worn down (Fig. 3B). There is no doubt that these represence dental gems inside the crypts, as demonstrated by the densitometric analysis that showed that the density of the dental gems inside the individual crypts is even greater than that of the surrounding bone (Fig. 3C). Almost all of the the tomographic sections performed confirmed the presence of the crypts with forming dental gems under almost all of the teeth on the chewing surface. All of these tomographic characters show that this examined prearticular of *Pycnododus maliensis* belonged to an adult individual, where the ameloblastic activity was fully effective.

On the contrary, the radiographic analysis of the premaxillary of *Globoanomoeodus* of the Cretaceous of Texas shows the total absence of dental gems; furthermore the bone is thinned. Here, the cortical of the two surfaces (i.e., endo, exo-oral) are close to each other, and almost collapsed, and the bone as a whole appears porotic and atrophic (even if the state of diagenetic mineralization is very advanced) (Fig. 10B, C). All of these tomographic characters are typical of old bone, where the ameloblastic activity has ceased.

Fig. 9 - X-ray taken in lateral-lateral projection of the head region of an adult specimen of *Neoproscinetes penalvai* (Cretaceous, Brazil), TL = about 360 cm; note the presence of dental gems both at the premaxillary level and at the level of the vomer. MUC # 20089.

DISCUSSION

All of these new data provide paleontological evidence that demonstrates how the replacement of worn deciduous teeth by newly formed ones was common to many species and genera of adult pycnodont individuals. This also does not appear to be an occasional observation either, as whenever numerous samples are available, concrete evidence can be found in support of dental replacement. All of these new observations clearly mean that pycnodonts were polyphyodonts.

Polyphyodonts are animals where the teeth are continually replaced, and these also include most toothed fish. The main one of these, and also the best known and studied, is certainly the extant fish *Tilapia mariae*. In this cichlid, the teeth were continuously replaced throughout the life of the fish in cycles of about 100 days (Tuisku and Hildebrand, 1995), and this occurred under close nervous control. Indeed, surgical interruption of the *ramus alveolaris trigemini* nerve unilaterally results in "*no new (replacement) tooth gems formed in the denerved lower jaw*" (Hildebrandt *et al.,* 1995).

On the other hand, a condition of well documented dental replacement has recently been demonstrated also in the fossil fish *Scheenstia* spp. (Actinopterygii, Ginglymodi, Lepisosteiformes), from the Jurassic of Switzerland (Leuzinger *et al*., 2020). Here, a new model of dental replacement was demonstrated, which also implied a sort of "rotation" of the new gems, according to a complex mechanism whereby they emerged from the gum by inserting themselves into the narrow spaces between two worn deciduous teeth. It also appears relevant to note that the arrangement of the teeth in *Scheenstia* was actually quite peculiar, as these were adapted for a crushing diet (phyllodonty); this is a condition for some extinct ray-finned fish, as well as for the pycnodonts.

At the moment we have no data that can define the extent of this phenomenon. For example, we do not know if the persistence in adults of ameloblastic cells and tissue was common to many or all of the Pycnodonts, or if the phenomenon was restricted maybe to a certain period of time. Above all, we do not know how long the amelogenetic potential persisted in the adults over their lifespan. For some fossil reptiles of the Cretaceous (e.g., *Tyrannosaurus*), it has been shown that when the amelogenetic potential ceases, the individual dies because it can no longer feed. This is due to the loss of the possibility to replace worn and fallen teeth, meaning that the dentition becomes ineffective for the capture and eating of its prey (D'Anastasio *et al.*, 2002).

In light of this, some fossils characterized by an "anomalous" dentition might be interpreted as real examples of dentitions belonging to very old individuals. For example, I myself recently described the species *Globoanomoeodus dentespassim* on the basis of a left prearticular from the Cenomanian of the Del Rio Formation (Texas, USA), which shows a large number of absolutely peculiar characteristics, so much so that it led me to propose a new genus and a new species (Capasso, 2020). In reality, this specimen (Fig 10 A) is characterized, among other things, (i) by a small number of teeth, of (ii) shape and (iii) dimensions very different from each other, which (iv) have almost completely lost their characteristic arrangement of ordered rows. To these characters – which are considered distinctive of the new species – there are others that can be added, which on the contrary, appear to coincide with characteristics of senescence: in particular, the prearticular bone is very thin, with a porous cortex, which could be said to have an "osteoporotic" appearance, as also confirmed by radiographic examination of this holotype (Fig. 10B). The set of these characteristics, both dental and bone, define an "atrophic" prearticular, which is fully compatible with the dentition of an old individual. In this, the ameloblastic activity might have been exhausted and only a few residual teeth have survived, arranged in a rarefied and disordered way, while at the same time the bone that supports them becomes hypotrophic.

From now on, having ascertained that the ameloblastic activity that leads to the formation of the first dentition in the juvenile subjects continues for a long time even in the adult, we will have to consider the possibility that at least part of the dental characteristics of the pycnodonts might be linked to the consequent variability of aging, rather than genetics, with the consequent taxonomic reflexes. Only an extensive examination of a large quantity of finds will make it possible to at least set up further studies to provide answers to these new questions in the future, from this new viewpoint.

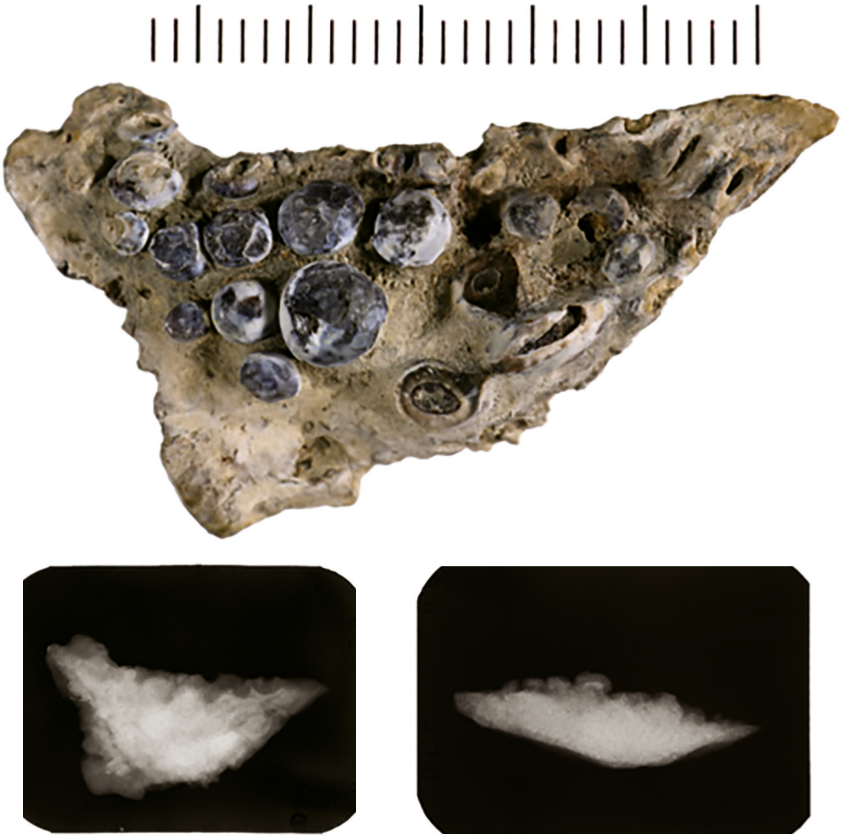

Fig. 10 - A: *Globanomoeodus dentespassim* Capasso (2020), holotype, from the Cenomanian clays of Waco Lake, central Texas: inner face of the left prearticular. B, C: Radiographs of the same specimen showing the total absence of dental buds, the extreme thinness of the bone, and the atrophy of the spongy tissue, with collapse of the cortical bone of the external and internal surfaces. These are all radiological signs of the exhaustion of ameloblastic activity and the atrophy of the old bone. CPC # S-1839.

CONCLUSIONS

The ameloblastic activity in all of the pycnodonts considered from this point of view is not limited to the phases of somatic growth, but continues also in the adult. Ameloblastic activity in pycnodonts might have occurred in slightly different ways, depending on the age of the subject, as summarized schematically in Table 1. During the ontgenetic phase in young subjects in the process of growth, which leads to the formation and eruption of the first dentition, the number of teeth increases due to the introduction of new elements from behind. This model is known as "marching molars", and leads to lengthening of the dental rows, in both the vomer and the prearticular. This phenomenon is demonstrated both by the presence of dental gems in the most posterior region of the prearticular in some juvenile pycnodonts, and - above all - by the dental wear that always affects the anterior teeth to a greater extent, which have chewed longer than the posterior ones.

Table 1 - Description of the different types of tooth generation in pycnodonts.

Age	**Mechanism of tooth generation**	
	Process	**Description**
Juvenile	Ontogeny (so called "marching molar")	Addition of dental elements from behind, and pushing forward of smaller (old and worn) teeth
Adult	Dental replacement	Replacement of worn out teeth, regardless of their position
Senile	Cessation of ameloblastic activity	Progressive tooth loss (which tends towards total edentulousness) associated with bone atrophy of the prearticulars and vomer

Once the adult configuration had been reached, i.e., ontogenesis of the first dentition is complete, the replacement of worn teeth was certainly possible in pycnodonts. This phenomenon had already been intuited by some previous authors (Hennig, 1907; Kriwet, 2005; Nursall, 1996; Poyato-Ariza and Wenz, 2005), but it was always interpreted as a sporadic phenomenon. However, in this paper, I have shown that the sporadicity might be linked to the fact that the dental gems are only exceptionally visible from the outside. On the contrary, radiographs unequivocally demonstrates the presence of dental gems in various degrees of maturation both in the prearticular bones and in the vomer of the adult individuals examined in the present study.

Finally, in adult pycnodonts, the ameloblastic activity was probably exhausted, as still happens today in all of the polyphyodont animals. The disappearance of the ameloblastic tissue stops the ability to replace worn teeth, and slowly leads the elderly animal being unable to feed, which consequently results in its death.

So, having also radiographically (i.e., X-ray and tomography) documented the presence of numerous and widespread dental gems inside prearticular bones and the vomer in certainly adult individuals, this demonstrates unequivocally that pycnodonts were polyphyodont animals (Figure 11A, B).

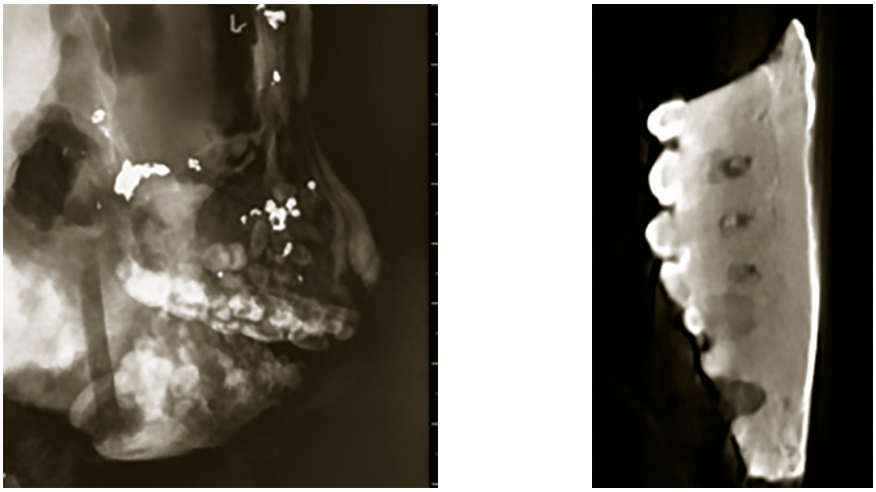

Fig. 11 - A: Detail of the X-ray of the Fig. 8, focusing on the mouth region to show the high number of dental gems inside both the prearticulars as well as – especially – the vomer. B: Dentail of the tomography of Figure 10, focusing on the presence of dental crypts, in the center of which strongly radio-opaque dental gems are seen, located exactly in correspondence with (i.e., below) the already erupted teeth, ready to be replaced by the new dental generation.

This statement is certainly true for the genera *Neoproscinetes* and *Pycnodus*, but concordant data - even if not radiographic - show that polyphyodont condition was also present in other genera *Akromystax*, *Pycnodus*, *Palaeobalistum*, and *Phaccodus*. Everything suggests, therefore, that new extensive studies that include a greater variety of forms will be able to demonstrate how widespread polyphyodont condition actually was in pycnodonts, provided that it was not a condition common to all pycnodonts. The demonstration of polyphyodont condition also opens the possibility to interpret the cessation of ameloblastic activity as the limit to the life span of these extinct animals.

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