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**+PYCNODONTS (NEOPTERYGII, +PYCNODONTIFORMES)
FROM THE DEL RIO FORMATION (EARLY CENOMANIAN,
CRETACEOUS) OF WACO LAKE, TEXAS (U.S.A.)**

SUMMARY

The author provides the first report of the presence of pycnodonts in the clays of the Del Rio Formation, outcropping on the East bank of the Waco Lake, in central Texas, U.S.A. These fossils were found in association with a rich malacofauna, echinoderms, bryozoans and foraminifera, that were characteristic of coastal marine environments. The findings on which this indication is based are both isolated teeth as well as three dental apparati (one vomer and two prearticulars). Most of these fossils shown the characteristic random disposition of the anterior teeth, which are, moreover, exclusively for pycnodonts pertaining to the genus *Anomoeodus*. The detailed anatomical study of the sample allows the identification of a new genus and species, namely *Globanomoeodus dentesspissim* gen. and sp. nov., as well a new species, namely *Anomoeodus wolfi* sp. nov. The new genus (*Globanomoeodus*) seem to be closely related to *Anomoeodus*, with which it differs for three substantial characters: (i) the circular profile and the semi-spherical shape of the teeth, (ii) their totally unorganized spatial arrangement, and (iii) the presence of teeth also on the oral border (upper edge) of the prearticular. The new species (*A. wolfi*) is characterized by the presence of vomerine teeth that exhibit a very unique sculpture of the occlusal surface, and are arranged in seven parallel rows. Finally, the presence of pycnodont remains in the Waco pit clays, demonstrate the deposition environment of the Del Rio Formation was connected with another, different environment, that of the cliff and the back-cliff of the Cenomanian sea, in which the pycnodonts lived together with other organisms, such as the molluscs of the genera *Gryphaea*, *Inoceramus*, *Ostrea*, etc.

RIASSUNTO

L'autore fornisce la prima segnalazione della presenza di picnodonti nelle argille della Formazione Del Rio, affiorante sulla riva orientale del Lago Waco, nel Texas centrale, Stati Uniti d'America. Questi fossili sono stati trovati in associazione con una ricca malacofauna, echinodermi, briozoi e foraminiferi, caratteristici di ambienti marini costieri. I resti di picnodonti in questione sono sia denti isolati che tre apparati dentali (un vomere e due prearticolari). La maggior parte di questi fossili mostra una disposizione casuale dei denti anteriori, caratteristica del genere *Anomoeodus*. Lo studio anatomico dettagliato di questi fossili consente l'individuazione di un nuovo genere e specie, *Globanomoeodus dentespasim* gen. et sp. nov., nonché di una nuova specie, *Anomoeodus wolfi* sp. nov. Il nuovo genere (*Globanomoeodus*) sembra essere strettamente correlato al genere *Anomoeodus*, rispetto al quale mostra tre differenze sostanziali: (i) il profilo circolare e la forma emisferica dei denti, (ii) la loro disposizione assolutamente casuale e non organizzata in "file", ed infine (iii) la presenza di denti sul bordo orale (bordo superiore) dell'osso prearticolare. La nuova specie (*Anomoeodus wolfi*) è caratterizzata dalla presenza di denti vomerini che presentano una scultura molto singolare della superficie occlusale e sono disposti in sette file parallele. Infine, i resti di picnodonti presenti nelle argille di Waco Pit, potrebbero avere raggiunto l'ambiente di deposizione della Formazione Del Rio provenendo da un ambiente diverso, quello della scogliera e della retro-scogliera del mare cenomaniano, nel quale i picnodonti vivevano insieme ad altri organismi, come i molluschi dei generi *Gryphaea*, *Inoceramus*, *Ostrea*, ed altri simili.

INTRODUCTION

The Del Rio Clay represents an important source of Cretaceous fossils in Central Texas. The fossil assemblage includes numerous species of ammonoids and other molluscs of little dimension and usually well pyritized. In 1887 R. T. Hill named "*Indurated Blue Marl*" these Cretaceous clays, and reported the abundance of very well preserved fossil shells; so, in 1889, the same R. T. Hill named these fossiliferous strata "*Exogyra arietina* Clays", referring to the most common fossil shell present in these Cretaceous clays, and consisting in an extinct species of marine oysters, referred to the family Gryphaeidae.

The fossil fauna includes – other than *Exogyra* – also two very common bivalves: *Gryphaea* and *Pecten*, as well as cephalopoda – such as *Turrilites*, *Scaphites*, *Submantelliceras*. Are also present corals, brittle stars, and several species of echinoids. Finally, the microfossils are particularly abundant. The species *Globigerina infracretacea* represents at last the 30% of the fossil foraminifera (Brown, 1971).

In this context the fossil fish represent rare findings, as demonstrated by the extensive analysis of the fossil communities of the Del Rio Formation in a large series of fossil localities all over the Central Texas performed by Russel Elliot Hinote in 1978. Only isolated shark teeth and isolated bones of actinopterygians were described in the literature (Brown, 1971; Hinote, 1978).

During the years '70 of the past century, the fossils enthusiast George Wolf collected an impressive quantity of fossils in various localities of central U.S.A., but he spent most of his time collecting Cretaceous fossils in the so called Waco Pit, along the East bank of the Waco Lake, in Central Texas; George Wolf had gathered an impressive collection of fossils as well as shells and prehistoric artifacts in his house in Pasadena (Figure 1), and when he passed, in 1982, his son sold his entire collection. Between these fossils collected at Waco Pit, Wolf listed just three specimens of fossil fish bones, and additional 13 isolated teeth, pertaining to †pycnodonts: these 16 specimens were bought by me and belong today to the “*Public Collection of fossil fish Luigi Capasso*”, in Chieti, Italy (PCFFLC).

Considering both the extreme rarity, as well as the high paleontological and palaeoecological value of †pycnodonts in the quoted fossil fish assemblage, this study is devoted to the first reporting of the presence of †pycnodonts in the Del Rio Clays of Central Texas.



Figure 1. George Wolf and his fossil collection in Pasadena, circa 1980.

MATERIAL

The fossils described in this study consists in three fragments of bones and teeth, and in additional 13 isolated teeth of †pycnodonts collected in the years '70 by Georg Wolf in the so called Waco Lake Research Area, commonly known as the Waco Pit; this area is controlled by the U.S. Army Corps of Engineers, and the access should be always permitted by the Military Authorities, just as Wolf has always asked for and obtained; so that all the fossils in question have been regularly collected. The pit is located near the Waco Lake Dam, and was a source of material to build the earthen dam.

The remains of the †pycnodonts that are the object of the present study consist of the following findings, all of which belong to the Public Collection of Fossil Fishes of Luigi Capasso in Chieti (Abruzzo, Italy): (i) a near complete left prearticular, 33 mm long, with all the teeth (PCFFLC no. S-1839); (ii) a partial left prearticular, 17 mm long, with many teeth (PCFFLC no. S-1841); (iii) a near complete vomer, 14 mm long, with near complete dentition (PCFFLC no. S-1840); (iv) 13 isolated teeth (PCFFLC no. S-1885, from A to N). The relevant national interest of this collection – pursuant to Law 1089/39, and its following modifications – was acknowledged by the Ministry for Cultural and Environmental Heritage through the Ministerial Decree of 11 October, 1999. Moreover, this PCFFLC public collection also corresponds to the requisites of the Law on the accessibility of finds, as defined in Article 30 of Law N° 42/2004.

GEOLOGICAL SETTING

The Waco Pit exposed the Del Rio Clays, which is part of the Washita Group. The Washita Group in the Central Texas is the upper most group of the so called "*Comanche Series*", and consists of three formations, in descending order: the Buda Formation, the Del Rio Formation, and the Georgetown Formation (Saribudak, 2016). The Del Rio Formation in Central Texas is almost entirely dark gray, blocky clay, intercalated with a few thin beds of ocherous hematite, limestone, and thinbedded, calcareous siltstones (Brown, 1971).

For these quoted lithological characteristic, the Del Rio Formation is also known as Del Rio Clays. The Formation is nearly uniform thickness of about 25-26 meters. On a fresh surface these beds are gray in colour; however, on a weathered surface they appear carmine red or brown (Brown, 1971). There is a difference in the paleo-environment characteristics of each formation in the Washita Group. A regression of the warm Cretaceous seas, which had deposited the limestones and calcareous shales of the Georgetown Formation, allowed deposition of the muds and clays of the Del Rio Formation (Brown, 1971).

The sedimentation of the Del Rio Clays occurred during the Late Cretaceous, earliest Cenomanian stage.

SYSTEMATIC PALAEOLOGY

Although not all of the listed materials are univocally classifiable, two of them, i.e. the specimen PCFFLC no. S-1839 and the specimen PCFFLC no. S-1840, can be determined as teeth and fragments of cranial bones from the genera *Globanomoeodus* gen. nov. and *Anomoeodeus*; the specimens PCFFLC no. S-1885, pertaining doubtfully to the genus *Anomoeodus*; and the specimen PCFFLC no. S-1841, pertained to an undetermined †pycnodonts.

Sperclass: Osteichthyes Huxley, 1880
Class: Actinopterygii Cope, 1887
Order: †Pycnodontiformes Berg, 1937
Family: †Pycnodontidae Agassiz, 1833
Genus: *Globanomoeodus* gen. nov.

Type-species

Globanomoeodus dentespassim gen. and sp. nov. (by monotype).

Diagnosis

As for the species (monospecific genus).

Derivatio nominis

The name of the new genus alludes to the spherical shape of all teeth present on the prearticular, as the Latin word “globus” indicate the spherical shape, and the word “anomoeodus” is referred to the close morphological affinity to the genus *Anomoeodus*.

Globanomoeodus dentespassim, n. sp.
(Figure 2)

Holotype and only specimen

Sample PCFFLC no. S-1839, a near complete left prearticular, 33 mm long, with 29 (both complete and incomplete) teeth.

Stratigraphic occurrence

Del Rio Formation, lower Cenomanian stage.

Type locality

Waco Pit, east bank of the Waco lake, Central Texas, U.S.A.

Derivatio nominis

The name of the new species alludes to casual and messy arrangement of the teeth on the prearticular bone; in fact, the name of the specie is composed

by the two Latin words “dentes”, which means teeth, and “passim”, which means untidily arranged.

Diagnosis

†Pycnodont with the following combination of characters: (i) prearticular short and pointed (ii) prearticular teeth semi-spherical, (iii) prearticular teeth not arranged in rows, but distributed in a disorderly, (iv) the maximum dimension teeth situated near a the central area of the inner face of the prearticular (in consequence, the size of teeth increases from the back to the front in the posterior part of the prearticular, while decreasing in the front); (v) presence of great space (diastemata) between the teeth only in the anterior part of the prearticular; (vi) oral border of prearticular wide, but surmounted by some little spherical teeth.

Description

The holotype and single specimen of *Globanomoeodus dentespassim* n. sp. is an isolated prearticular with the near complete dentition, notwithstanding some teeth are broken (but in these cases the corresponding roots are well preserved and visible). On the oral border as well as on the inner face of the bone I can count the presence of 29 teeth. Only in the posterior part these teeth are more or less arranged in parallel rows, but both in the central part and in the anterior part of the internal face of the prearticular the teeth are arranged in a completely casual way, without any regularity. Much space exists between the individual teeth, and this space increases from the back to the front. The size of the teeth is variable: the larger teeth are located in the center of the prearticular and both posteriorly and anteriorly the size of the teeth decreases. All teeth have a perfectly semi-spherical morphology; a single exception is represented by a tooth located at the lower edge of the central part of the internal face of the bone, very close to the symphysis; this tooth (moreover with the broken crown and reduced to little more than its root) has an oval profile, elongated in a mesial-distal direction. The surface of the teeth is always perfectly smooth, without any ornamentation or sculpture. A series of little teeth, prevalently preserved as its roots, are inserted on the oral border of the prearticular, that assume a notched appearance.

Remarks

The described specimen presents strict analogies with the morphology of the genus *Anomoeodus*, in which the prearticular teeth are anteriorly patchy, and only posteriorly arranged in short and more or less distinguishable rows (character 44 of Pyato-Ariza & Wenz, 2002). Notwithstanding, the arrangement of the teeth in the posterior part of the prearticular is not exactly ordered “rows”. On the other hand, a series of characters are quite different between *Anomoeodus* and *Globanomoeodus*. First of all, we can consider that in *Anomoeodus* the prearticular teeth have an elongated lozenge shape and a sigmoidal profile, and are sinuous, and sometimes have the form of

a 'drop', with the apex pointing towards the symphysis region (character 43 of Pyato-Ariza & Wenz, 2002). On this topic we can underline that the semi-spherical prearticular teeth represent an absolute rare morphology inside the †Pycnodontiformes; in fact, only in the three following genera of †Pycnodonts we can observe the presence of teeth with "circular contour": *Iemanja* (Pyato-Ariza & Wenz, 2002), *Mesturus* (Pyato-Ariza & Wenz, 2002), and *Trewavasía* (Nursall & Capasso, 2008).

Already the combination of the two characters – such as (i) teeth with "circular contour", and (ii) arranged anteriorly patchy and posteriorly in rows – justifies the establishment of the new genus widely.

The presence of teeth on the oral edge of the prearticular bone as well as the way of varying the size of the teeth from the center both towards the front and towards the back, are two additional characters that make absolutely unique the morphological combination of the prearticular dentition in the new genus *Globanomoeodus*.



Figure 2. *Globanomoeodus dentepassim* gen. and sp. nov., holotype (CPFFLC, no. S-1839) from Cenomanian clays of Waco lake, Central Texas: inner face of the left prearticular; total length 33 mm.

Genus: *Anomoeodus* Forir, 1887

Anomoeodus wolfi, n. sp.

(Figure 3)

Holotype and only specimen

Sample PCFFLC no. S-1840, a near complete vomer, 14 mm long, with near complete dentition (38 teeth present).

Stratigraphic occurrence

Del Rio Formation, lower Cenomanian stage.

Type locality

Waco Pit, east bank of the Waco lake, Central Texas, U.S.A.

Derivatio nominis

The name of the new species alludes to George Wolf, one of the most active fossils collecting in Waco Pit, that recovered, during the years '70 of the past century, all the specimens described in this paper and furnished it to the author.

Diagnosis

†Pycnodont with the following combination of characters: (i) vomerine teeth arranged in seven rows; (ii) vomerine teeth arranged in regular rows posteriorly, in irregular rows anteriorly; (iii) characteristic dental surface: each vomerine tooth presents a median fossa, with small tubercle in the center, and surrounded by a denticulate ring; (iv) absence of relevant space between the single vomerine teeth, also anteriorly.

Remarks

The vomerine dentition consists of seven longitudinal rows; the dimension of the teeth is maximum in the central row, and decrease in lateral rows; the median row with teeth with a circular profile; the lateral series with teeth with an elliptical profile. As probably the specimen is uncomplete, it is unuseful to determine the maximum number of teeth for each rows. Both in central and in lateral rows are present supernumerary teeth, and some teeth seem divided in two units, demonstrating casual arrangement of the teeth in the each row. All these characteristics are typical of the genus *Anomoeodus* (as proposed by Pyato-Ariza & Wenz, 2002). However, the surface of each known tooth is ornamented by a characteristic sculpture: a little and rounded tubercle occupies the center of the masticatory surface such as the center of a regular depression; around of this depression is present a crown of little denticles that give the tooth profile a notched appearance.

The described combination of characters of the vomerine dentition is typical and indicate the need to establish a new species.



A

B



Figure 3. *Anomoeodus wolfi* sp. nov., holotype (CPFFLC, no. S-1840) from Cenomanian clays of Waco lake, Central Texas: inferior face of the vomer; total length 14 mm (A); detail of the occlusal surface of the biggest tooth showing the characteristic ornamentation and sculpture (B).

cf. Anomoeodus ? ind.
(Figure 4)

Most of †Picnodonts remains collected by George Wolf at Waco Pit are isolated teeth; these are 13 teeth, with very variable dimensions: the largest tooth is 14 mm long, the smallest one is 2 mm long (PCFFLC no. S-1885). Ten of these teeth have a clearly elongated morphology (Figure 4), with a reniform appearance, and represent probably those that come from the back of the prearticular dental series. Additional three teeth have a less elongated, sub-circular profile (Figure 4), and could either be teeth of the front part of the prearticular or, in alternative, vomerine teeth. The elongated and reniform shape of the presumably prearticular teeth is close to that typical of the genus *Anomoeodus*, even if the isolated teeth are very difficult to attribute and this classification remains doubtful.

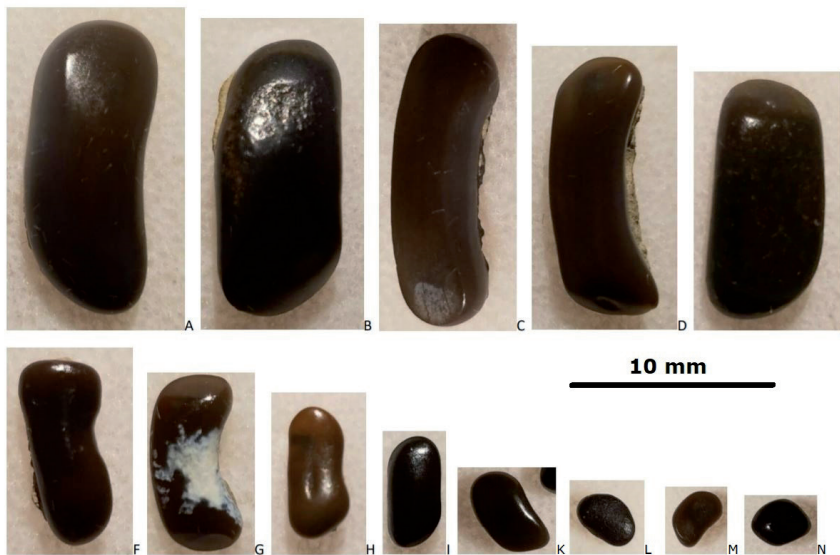


Figure 4. *Cf. Anomoeodus* sp. ind. (PCFFLC, no. S-1885, from A to N) from Cenomanian clays of Waco lake, Central Texas.

Gen. and sp. undetermined
(Figures 5)

One left prearticular (PCFFLC no. S-1841), 17 mm long, represents just a section of the original bone, as the posterior margin was damaged, and also

the coronoid process is present only partially; moreover, the anterior part of this pre-articular is also broken and the apex of the bone is missing, including the more anterior teeth. On the whole, the bone appears relatively short and high, with an overall squat appearance. The inner face of the prearticular shown 17 teeth, arranged in rows; the most internal row show the most maximum size teeth, and the external row is composed by the minimum size teeth. The dimension of the teeth in each row decrease from the back to the front. The occlusal surface of each tooth is perfectly smooth; the teeth of the outermost row have an almost circular profile, those of the middle row are somewhat elongated in the transverse direction, while those of the middle (lower) row are oblong, elliptical, even if, moving anteriorly, also the teeth of this series they tend to take on a less oblong profile.

The complex of characters described in this specimen do not allow to reach the determination of the genus of belonging, even if there is no doubt that it is a pre-articular belonging to a †Pycnodont of the family of †Pycnodontidae Agassiz 1833.



Figure 5. Pycnodontidae undetermined (CPFFLC, no. S-1841) from Cenomanian clays of Waco lake, Central Texas: inner face of the left prearticular; total length 17 mm.

DISCUSSION

The present study has shown above all that the presence of pycnodonts in the context of the fossil fauna characteristic of the Del Rio Formation, but demonstrated, at the same time, that this presence is absolutely sporadic; in fact, the finds found in many years of research are very few. Furthermore, complete bone findings are missing: both the only vomer and the two prearticulars, in fact, show signs of breakage. These facts tend to indicate that the remains of Pycnodonts reached the clays deposition environment of the Del Rio Formation coming from another, different environment, that of the cliff and the back-cliff of the Cenomanian sea, in which the Pycnodonts lived, together with other organisms, especially hard and thick shell molluscs, such as ammonites and oysters, whose fossils are abundant in this same geological context.

The pycnodonts whose remains have come to settle together with the clays of the Del Rio Formation are mainly referable to the genus *Anomoeodus*, or to very similar genera, as seems to be the genus *Globanomoeodus*.

The genus *Anomoeodus* was established by Forir (1887) on the basis of the isolated prearticular dentition, to which the name of *Pycnodus subclavatus* was attributed. To date, more than 30 species of pycnodonts have been described in terms of this genus, which appears 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 way in the anterior region of the single prearticular bone.

In the Cretaceous rocks of Texas McKinzie (2002) reports the presence of the species *Anomoeodus barberi* Hussakof, 1947 from the Ozan Formation of north Texas.

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 localities in France (Cornuel, 1877), and from Bohemia (Fritsch, 1878). The genus *Anomoeodus* has also been well demonstrated for the Maastrichtian of Belgium and Holland (Leriche, 1929), for the Upper Cretaceous of Kansas (Shimada & Everhart, 2009), Texas (McKinzie, 2002), and Arkansas (Hussakof, 1947) in the USA, and for Sweden (Bazzi et al., 2015). Finally, Capasso (2019) reported the presence of the *Anomoeodus sp. A* in the Turonian limestone of the region of the port of Owendo, Gabon, that represent – at today – the most southern locality for this genus all over the world.

From the stratigraphic point of view, and according to Kriwet (2002), *Anomoeodus* appeared in Kimmeridgian (Upper Jurassic) and survived until the Late Cretaceous.

From the point of view of systematic palaeontology, it should be noted that it is very difficult to identify the exact taxonomic position of the new genus *Globanomoeodus*, also because, as Pyato-Ariza & Wenz (2002) have shown, the same genus *Anomoeodus* assumes a somewhat uncertain taxonomic position, and this is certainly due to the scarcity of anatomical characters that distinguish this genus, known almost exclusively through dental remains. Certainly the three major characteristics present in the new genus *Globanomoeodus* are (i) the presence of circular profile of semi-spherical teeth, that are (ii) arranged in an absolutely random manner (almost without configuring real rows), and (iii) that are present also on the oral ridge of the pre-articular bone. We cannot forget that this same combination of characters has so far been described only in the “Val Garza species” of the Norian of the Bergamo, as showed, for example, in the specimen VGA-04, showed by Nursall (2010). Obviously, to the state of our extant knowledge, we are absolutely unable to infer what implications this stringent morphological analogy can have in two species lived in geographical contexts distant some 12,000 kilometers and in geological horizons distant some 110 millions of years.

CONCLUSIONS

The present paper definitively asserts the presence of Pycnodonts in the Early Cenomanian clays of the Del Rio Formation at the Waco Pit, Texas; for the great part, these fossils pertaining to the genus *Anomoeodus* and the genus *Globanomoeodus*, and this paleontological data is – first of all – a confirmation of the ubiquity of this Pycnodonts, that was particularly characteristic of the Middle and Upper Cretaceous.

The great part of the fossils pertaining to the Pycnodonts in the Waco Pit locality are isolated teeth, which morphology is easily matching with the genus *Anomoeodus* or to very similar forms. In addition, I demonstrate the presence of a specimens that have anatomical peculiarities that serves to establish the new species *Anomoeodus wolfi*, and which can be summarised in the presence of seven vomerine rows of high sculptured teeth. Finally, I determined the presence of a new Pycnodont genus and species, such as *Globanomoeodus dentespassim* gen. and sp. nov., that seem to be closely related to *Anomoeodus*, with respect to which it shows two new characters of substantial differences: (i) the circular profile and the semi-spherical shape of the teeth and (ii) the presence of teeth also on the oral edge (upper edge) of the prearticular bone.

At the palaeoecological level, the presence of pycnodont remains in association with bivalves and cliff gasteropods reinforces the reconstructions according to which the Del Rio Formation was deposited in close connection with a coastal environment of high energy (i.e., coastal cliffs).

ACKNOWLEDGEMENTS

The author thanks his colleague Louis Paul Taverne, of the Royal Institute and Museum of Natural Sciences of Belgium in Brussels, for having revised the present study, Dr Christopher Barry for the English revision, and Luciano Lullo and Donatella Del Pizzo for the pictures.

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