

NEW OCCURRENCE OF LEPISOSTEID REMAINS (LEPISOSTEIFORMES: LEPISOSTEOIDEA) FROM THE CENOMANIAN OF THE ALCANTARA FORMATION (UPPER CRETACEOUS), MARANHÃO STATE, BRAZIL

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ABSTRACT

Lepisosteioidea is a superfamily of Lepisosteiformes. Its representatives, popularly known as gars, are divided in two families: Lepisosteidae and Obaichthyidae. The Alcântara Formation (Cenomanian) outcroppings discovered along the Maranhão state coast in Northeastern Brazil revealed a diverse ichthyofauna, at which the Lepisosteiformes occurrence was attributed to *Lepidotes* sp. based on morphological descriptions of isolated ganoid scales. Herein we describe new specimens of lepisosteoids, consisting of 5 vertebrae and 24 teeth obtained by sifting. The teeth have acrodin cap and apicobasal ridges, whereas the vertebrae have opisthocelous centra; one of the vertebrae do not exhibit the pattern of centra compression of the lepisosteid vertebral series. Vertebrae and teeth are diagnostic of Lepisosteioidea and Lepisosteidae, respectively. The materials represent the first occurrence of the referred groups in the Cenomanian of Maranhão and expand the previously known lepisosteid record of South America.

Keywords: Teeth, Vertebrae, Morphological description, Cajual Island.

RESUMO

Nova ocorrência de restos de lepisosteídeos (LEPISOSTEIFORMES: LEPISOSTEOIDEA) do Cenomaniano da Formação Alcântara (Cretáceo Superior), estado do Maranhão, Brasil

Lepisosteioidea é uma superfamília de Lepisosteiformes. Seus representantes, popularmente conhecidos como *gars*, são divididos em duas famílias: Lepisosteidae e Obaichthyidae. Afloramentos da Formação Alcântara (Cenomaniano) descobertos ao longo da costa do estado do Maranhão, Nordeste do Brasil revelaram uma diversa ichthyofauna, na qual a ocorrência de Lepisosteiformes foi atribuída a *Lepidotes* sp. baseada na descrição morfológica de escamas ganóides isoladas. Descrevemos aqui novos espécimes de lepisosteóides, consistindo de 5 vértebras e 24 dentes obtidos através de peneiramento. Os dentes apresentam ápice de acrodina e cristas apicobasais e as vértebras apresentam centros opistocélicos; uma das vértebras não exibe o padrão de compressão da série vertebral dos lepisosteídeos. Vértebras e dentes são diagnósticos de Lepisosteioidea e Lepisosteidae, respectivamente. O material representa a primeira ocorrência dos referidos grupos no Cenomaniano do Maranhão e expandem o registro de lepisosteídeos na América do Sul.

Palavras-chave: Dentes, Vértebras, Descrição morfológica, Ilha do Cajual.

INTRODUCTION

Lepisosteiformes (Ginglymodi) is a group of neopterygian fishes found in North and Central Americas and Caribbean Islands, though the group was more widespread and diverse during the Mesozoic and Paleogene times (Grande, 2010; López-Arbarello, 2012; Nelson *et al.*, 2016). Within the Lepisosteiformes clade is included the superfamily Lepisosteioidea. Its representatives,

popularly known as gars, are divided in two families: Lepisosteidae, that includes the extant forms of gars and its earliest record dated back to Late Jurassic, and Obaichthyidae, restricted to Early Cretaceous (López-Arbarello, 2012; Brito *et al.*, 2017). The earliest known Lepisosteioidea is considered a marine taxon, in contrast with all other fossil lepisosteoids.

Isolated materials such as scales and teeth represent the most common fossil remains of gars,

and in addition to the few lepisosteoid vertebrae, they provide an important record favoring the understanding of the historic distribution of the group (Moody & Sutcliffe, 1991; Gottfried & Krause, 1998; Kear *et al.*, 2009; Divay & Murray, 2015; Martinelli & Teixeira, 2015; Pérez-García *et al.*, 2016; Szabó *et al.*, 2016; Alves *et al.*, 2020; Kovalchuk & Anfimova, 2020). The vertebrae with opisthocelous centra and teeth with plicidentine are useful for identifying fragmentary fossil specimens, once they are diagnostic for Lepisosteidae and Lepisosteidae, respectively (Grande, 2010; López-Arbarello, 2012). Few studies described a significative sample of lepisosteoid vertebrae, revealing the patterns of parapophyses orientation and centra compression along the vertebral series of the group (see Grande, 2010; Szabó *et al.*, 2016).

The Alcântara formation is a lithostratigraphic unit that comprises a 35-m succession of sandstones and pelitic deposits related to an incised valley filling, dated as Cenomanian (Pedrão *et al.*, 1993; Klein & Ferreira, 1997; Rossetti & Truckenbrodt, 1997). The Alcântara formation outcroppings were discovered along the Maranhão state coast in Northeastern Brazil, and they revealed a diverse ichthyofauna, at which the Lepisosteiformes occurrence was attributed to *Lepidotes* sp. based on morphological descriptions of isolated ganoid scales. (Carvalho &

Santos, 1992; Medeiros & Schultz, 2001; Medeiros *et al.*, 2014). Scales have been used to identify *Lepidotes* sp. worldwide; however, because isolated ganoid scales are shared by different clades such as the Semionotiformes and Lepisosteiformes, their taxonomic attribution can be erroneous (López-Arbarello, 2012; Meunier *et al.*, 2016; Bittencourt *et al.*, 2017).

Based on teeth and vertebrae morphologies, we register herein a new occurrence of Lepisosteidae in the Cenomanian (Upper Cretaceous) of the Alcântara Formation, Maranhão, expanding the previously known South America Cenomanian record for the group.

MATERIALS AND METHODS

The specimens described herein comprise 24 teeth and five vertebrae of fishes from the Falésia do Sismo (2° 28' 56,31''S; 44° 28' 09,57''O), an outcrop of the Alcântara formation at Cajual Island in Maranhão state, Northeastern Brazil (Figure 1).

The specimens were obtained through sediment sifting of samples collected in 2003 and stored at the fossil collection of the Centro de Pesquisa de História Natural e Arqueologia do Maranhão (CPHNAMA), where they were registered as VT-1541 (teeth) and VT-1540 (vertebrae). Their descriptions were based

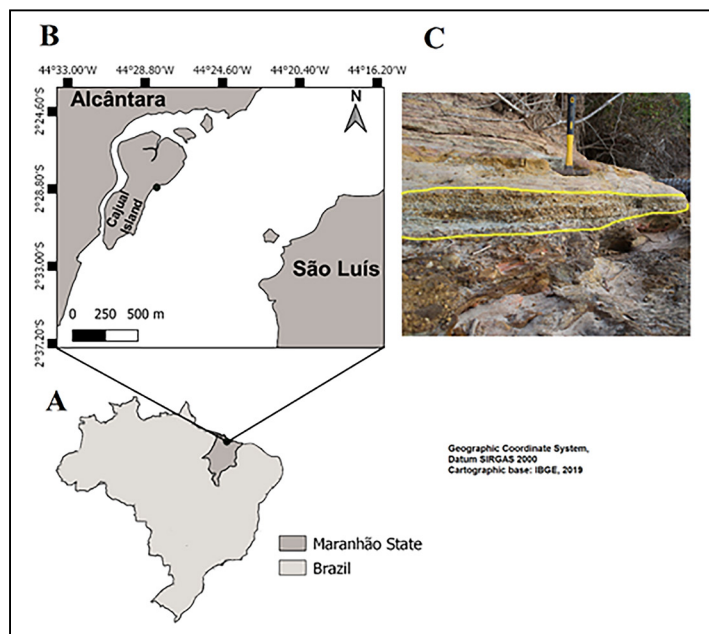


Figure 1. The fossiliferous site. A, Maranhão state, Northeast Brazil. B, Falésia do Sismo (black dot), Cajual Island, Alcântara. C, Detail of the Falésia do Sismo outcrop and the level from which the materials described herein were collected (between yellow lines).

on Grande (2010) monography; and Divay & Murray (2015), which pertain to details of the vertebrae neural and haemal arches, with some nomenclatural differences.

The diagnosis was conducted according to Grande (2010) study, using taxonomic arrangements proposed by López-Arbarello (2012), such as the adoption of the superfamily *Lepisosteioidea* (*Obaichthyidae* + *Lepisosteidae*), previously referred to as *Lepisosteiformes*.

RESULTS

VT-1541 consists of 24 conical teeth, apicobasally tall, and slightly curved, reaching its maximal thickness at the base (Figure 2). They show apicobasal-oriented ridges at their bases and acrodin cap with a distinctive “translucent red” color on the apex. The acrodin cap translucent aspect contrasts with the rest of the teeth, which vary in color among the specimens or even within a same specimen with shades of red, brown, and white. The apicobasal-oriented ridges vary in length between

the specimens, from being restricted to the tooth base in some specimens (Figure 2A) to reaching one third of the tooth in others. The conspicuity of the ridges also varies; in some specimens they are well-pronounced (Figure 2B) and in others they are almost imperceptible (Figure 2A). Based on these characteristics and literature comparative analysis it is possible to determinate that these structures belong to *Lepisosteidae*.

VT-1540 consists of five abdominal vertebrae with hourglass shaped opisthocoele centra (Figure 3). Most specimens presented only the bases of the lateral parapophyses and ventral haemal arches preserved.

The vertebrae VT-1440-1, VT-1540-2, VT-1540-3 and VT-1540-4 have 9 mm, 10 mm, 10 mm and 9 mm in length, respectively; they are long and tall. Their elongated aspects suggest that they belong to the end of the abdominal series. VT-1540-5 has 3 mm in length and the others dimensions with similar extent. The centra dorsal surfaces, when preserved, bears a pair of longitudinal parasagittal processes, that enclose the neural canal and separate

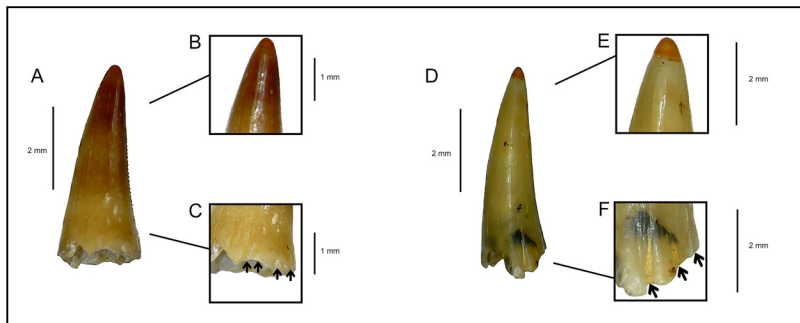


Figure 2. AD, *Lepisosteid* teeth from the Upper Cretaceous (Cenomanian) of the Alcântara Formation (Maranhão, Brazil). BE, acrodin cap detail. CF, apicobasal ridges detail.

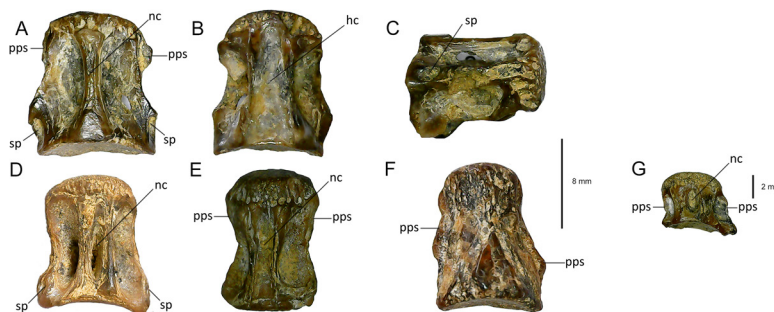


Figure 3. *Lepisosteoid* vertebrae from the Upper Cretaceous (Cenomanian) of the Alcântara Formation (Maranhão, Brazil). ABC, VT-1540-1 in dorsal, ventral and lateral right views. DEFG, VT-1540-2, VT-1540-3, VT-1540-4, and VT-1540-5 in dorsal view. Parapophysis, pps; neural canal, nc; haemal canal, hc; small pit, sp.

two lateral shallow fossae. The neural canals vary in width among the specimens, and in some cases, it is so small that the specimen appears to bear only one longitudinal parasagittal process. Similarly, the centra ventral surfaces bears two longitudinal parasagittal processes that enclose the haemal canal and separate two lateral shallow fossae. The haemal canals also vary in width in the examined specimens. The haemal canals of the specimens are wider than their neural arch.

A lateral bar separates the dorsal and ventral surfaces. In VT-1440-1 and VT-1540-2 it bears a small pit on its posterior region. In posterior view (Figure 5), it is possible to observe the lateral bar and parapophyses vestiges, that vary in orientation. In most specimens they are laterally oriented (Figure 5ABCD), except one in which the orientation is lateroventral (Figure 5E). Based on these characteristics and literature comparative analysis it is possible to determinate that these structures belong to Lepisosteidae.

DISCUSSION

Although the specimens are incomplete, they exhibit a combination of features that are enough to allow their identification. The vertebrae have opisthocoelous centra, a distinctive character of Lepisosteioidea (López-Arbarelo, 2012). Though they could belong to different taxa within the clade, their differences are probably due to their topography,

ontogenetic variation and phylogenetical position. The teeth have the typical lepisosteid aspect with acrodin cap and apicobasal oriented ridges (Gottfried & Krause, 1998; Pérez-García *et al.*, 2016; Szabó *et al.*, 2016; Alves *et al.*, 2020). The ridges represent external expressions of the internal dentine folds, called plicidentine, and within lepisosteoids they are exclusive to Lepisosteidae (Grande, 2010).

Grande (2010) studied the vertebral elements of the extant *Lepisosteus osseus*, Linnaeus, 1758, and *Atractosteus spatula*, Lacepède, 1803, and showed that the parapophyses on the anterior abdominal centra are projected laterally whereas the parapophyses on the posterior abdominal centra are ventrally projected. In addition, the centra become laterally compressed in the posterior elements of the vertebral series (Figure 4). The same pattern was observed in *Atractosteus* sp. from the Upper Cretaceous of Hungary (Szabó *et al.*, 2016). Isolated and incomplete vertebrae are assembled in VT-1540 and any precise ordering of the vertebrae relative position would be hypothetical. The specimens have only the parapophyses bases preserved (Figure 5ACDE), except one in which the whole structures were absent (Figure 5B). Nevertheless, in the specimen where the parapophyses were not preserved, the position of the lateral bar could indicate their possible orientation. The vertebrae exhibit the centrum compression pattern of the lepisosteid vertebral series. However, the vertebrae with lateroventrally oriented parapophyses do not

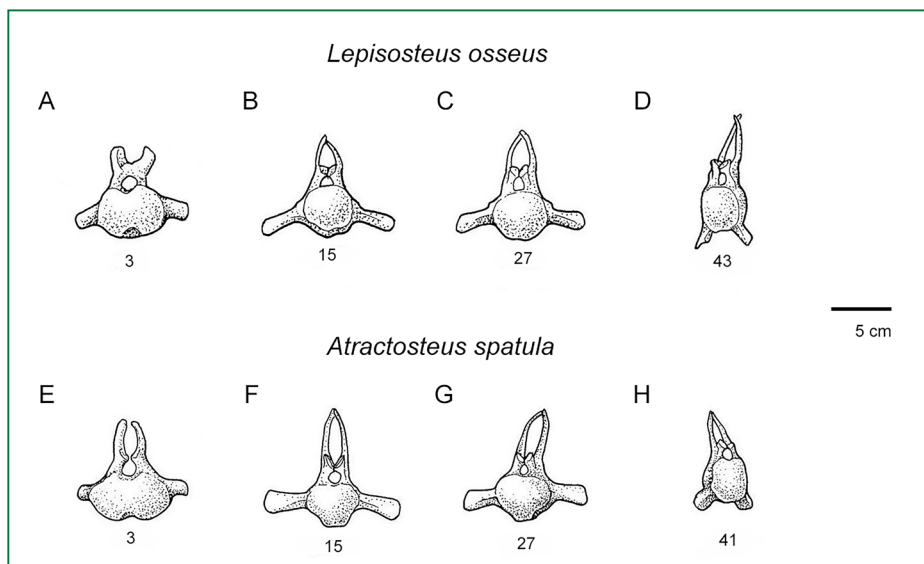


Figure 4. Lepisosteid vertebrae showing the pattern of parapophyses orientation and centra compression along the vertebral abdominal series. The numbers indicate the position of the vertebra on the vertebral series. Modified from Grande (2010).

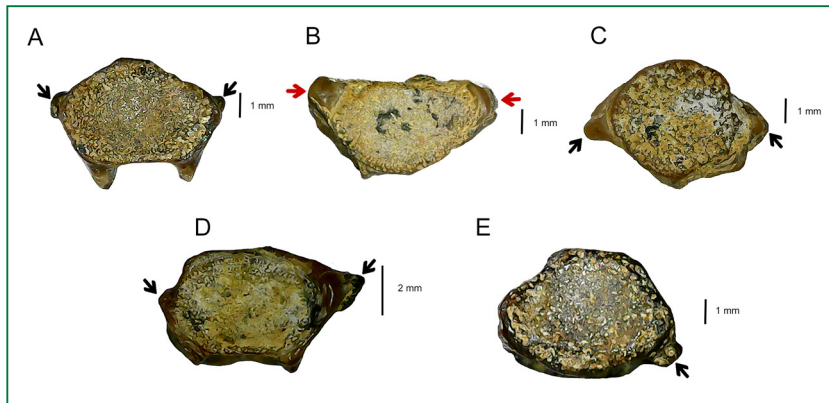


Figure 5. Lepisosteoid vertebrae from the Upper Cretaceous (Cenomanian) of the Alcântara Formation (Maranhão, Brazil) in posterior view. A, VT-1540-1. B, VT-1540-2. C, VT-1540-3. D, VT-1540-5. E, VT-1540-4. Parapophysis (black arrow); lateral bar (red arrow).

have laterally compressed centrum (Figure 5E); this contrasts with the previously mentioned pattern. Again, because of the fragmentary nature of the examined sample, these details are difficult to access and further studies based on best-preserved materials are required to clarify the differences in the centrum compressions described herein.

The external morphologic aspects of isolated scales were used to identify *Lepidotes* sp. from the Cenomanian of Maranhão (Carvalho & Santos, 1992; Medeiros & Schultz, 2001; Medeiros *et al.*, 2014). However, morphological features, such as microtubercles on the ganoine surface and histological details, which can help with taxonomic identification, were not analyzed in the referred studies. Additionally, ganoid scales characters could be homoplastic, which can make taxonomic attribution based solely on isolated specimens erroneous (López-Arbarello, 2012; Meunier *et al.*, 2016; Bittencourt *et al.*, 2017). Therefore, the occurrence of *Lepidotes* sp. in the Cenomanian of Maranhão cannot be determined with certainty and some scales may belong to other taxa. Taking into account the lepisosteid material described herein some of the scales previously referred to *Lepidotes* sp. could actually belong to Lepisosteidae.

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