



NEW OCCURRENCES OF AMIIDAE (HALECOMORPHI: AMIIFORMES: VIDALAMIINAE) FROM THE BAURU GROUP (LATE CRETACEOUS, BRAZIL) AND COMMENTS ABOUT THEIR INCURSION IN FRESHWATER ENVIRONMENTS IN THE CRETACEOUS OF THE AMERICAS

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ABSTRACT – The Late Cretaceous continental deposits of the Bauru Group of Brazil have a rich vertebrate fossil fauna, but studies on the fossil fishes from the unit are scarce. This paper describes new occurrences of the Vidalamiinae subfamily of the bony fish group Amiidae (Halecomorphi: Amiiiformes). The new occurrences are comprised by three isolated vertebral centra and three isolated teeth from the Marília and Adamantina formations, which were collected in Uberaba and Prata municipalities. The fossils described here not only expand the record of Vidalamiinae for the Bauru Group, but also clarify that the assignment of isolated teeth to this group may now be done with more certainty, which was not the case in many previous studies. Additionally, we also refer the described specimens tentatively to the Vidalamiini, which is the first assignment to this group and to the tribe level for any fish material from the Bauru Group. This study also offers an overview on the paleobiogeography of the Amiidae during the Late Cretaceous and an updated compilation of vidalamiine records during the Cretaceous, with a special focus on the freshwater records of this originally saltwater group. Finally, we also discuss the distribution of the tribes Vidalamiini and Calamopleurini during the Late Cretaceous, and the possibility that the North American and South American vidalamiines may have dispersed between the continents through a land connection.

Keywords: Amiiiformes, Amiidae, Vidalamiinae, Bauru Group, Late Cretaceous, biogeography.

RESUMO – Os depósitos continentais do Cretáceo Superior do Grupo Bauru do Brasil possuem uma rica fauna fóssil de vertebrados, mas os estudos sobre os peixes fósseis da unidade são escassos. Este artigo descreve novas ocorrências da subfamília Vidalamiinae do grupo de peixes ósseos Amiidae (Halecomorphi: Amiiiformes). As novas ocorrências são compostas por três centros vertebrais e três dentes isolados das formações Marília e Adamantina, que foram coletados nos municípios de Uberaba e Prata. Os fósseis aqui descritos não apenas ampliam o registro de Vidalamiinae para o Grupo Bauru, mas também esclarecem que a atribuição de dentes isolados a este grupo pode agora ser feita com mais certeza, o que não era o caso em muitos estudos anteriores. Adicionalmente, também remetemos os espécimes descritos provisoriamente aos Vidalamiini, que é a primeira atribuição a este grupo e ao nível de tribo para qualquer registro de peixes do Grupo Bauru. Este estudo também oferece uma visão geral da paleobiogeografia dos Amiidae durante o Cretáceo Superior e uma compilação atualizada dos registros de vidalamiine durante o Cretáceo, com foco especial nos registros de água doce desse grupo originalmente de água salgada. Por fim, também discutimos a distribuição das tribos Vidalamiini e Calamopleurini durante o Cretáceo Superior e a possibilidade de que os vidalamiines norte-americanos e sul-americanos tenham se dispersado entre os continentes por meio de uma conexão terrestre.

Palavras-chave: Amiiiformes, Amiidae, Vidalamiinae, Grupo Bauru, Cretáceo Superior, biogeografia.

INTRODUCTION

The Bauru Group, which crops out in southeast and central portions of Brazil, is the largest continental unit of South American Cretaceous and yields one of the richest and most diverse fossil assemblages of the Late Cretaceous epoch. This includes a rich vertebrate fauna, including fishes, lissamphibians, turtles, squamates, theropod dinosaurs (including birds), mammals and especially sauropod dinosaurs and crocodylomorphs (see Bertini *et al.*, 1993; Brito *et al.*, 2006; Candeiro *et al.*, 2006; Riff *et al.*, 2012; Martinelli & Teixeira, 2015; França *et al.*, 2016; Brusatte *et al.*, 2017; Castro *et al.*, 2018; Fachini *et al.*, 2020; Iori *et al.*, 2021).

The fish fauna of the Bauru Group includes groups such as Amiiformes (Martinelli *et al.*, 2013; Brito *et al.*, 2017), Siluriformes (Alves *et al.*, 2019; Brito *et al.*, 2020), Osteoglossiformes, Characiformes, Lepisosteiformes (Gayet & Brito, 1989; Brito *et al.*, 2006, 2020; Alves *et al.*, 2013a, 2016, 2021) and Ceratodontiformes (Alves *et al.*, 2013b). The single fossil species ever named for the Bauru Group was a lepisosteiform, *Lepisosteus cominatoï* Silva-Santos, 1984, but it was considered a *nomen dubium* by Grande (2010), with its remains being considered as indeterminate Lepisosteiformes instead because of their fragmentary nature. Other fish records from the Bauru Group consist of relatively scarce descriptions of isolated remains, mainly ganoid scales (*e.g.*, Price, 1955; Arid & Vizzotto, 1963; Mezzalira, 1966; see Brito *et al.*, 2006, Alves *et al.*, 2013a and Martinelli & Teixeira, 2015 for reviews), with the notable exception of the aforementioned *Lepisosteus cominatoï*.

The fish material from the Bauru Group is still comprised largely by fossils that cannot be identified to less inclusive taxonomic levels due to the incompleteness of the remains (Brito *et al.*, 2006; Alves *et al.*, 2013a). However, after the implementation of techniques such as screen-washing by Gayet & Brito (1989) and Bertini *et al.* (1993), which allowed the recovery of smaller fossils (microvertebrates), the paleoichthyofauna of the Bauru Group started to be better understood (see Alves *et al.*, 2013a), and the number of fish fossil descriptions from the unit has slightly increased over the years (*e.g.*, Brito *et al.*, 2006; Alves *et al.*, 2013a, b, 2016, 2019, 2021; Martinelli *et al.*, 2013; Brito *et al.*, 2017, 2020).

This paper offers a new contribution to our knowledge of the Late Cretaceous paleoichthyofauna of the Bauru Group by describing new fish remains from fossil sites in the Uberaba and Prata municipalities of the Brazilian state of Minas Gerais. These are three vertebrae and five teeth of Amiiformes, which complement earlier records of the group from the Bauru Group published by Martinelli *et al.* (2013) and Brito *et al.* (2017).

GEOLOGICAL SETTINGS

The Bauru Group is the Upper Cretaceous Sequence of the Bauru Basin, the largest sedimentary basin of that age in South America and one of the best studied continental basins in Brazil, well documented throughout 500 outcrops and thousands of well logs (Batezelli *et al.*, 2019). Extending

over 330,000 km² in an elongated NNE area in south-eastern and central Brazil, the Bauru Basin is best documented in the northwestern Paraná, western São Paulo and Minas Gerais states, with vast areas still to be systematically explored in southwestern Goiás, southeastern Mato Grosso and eastern Mato Grosso do Sul states (Barcelos & Suguio, 1987; Batezelli *et al.*, 2007; Basilici & Dal’Bó, 2010; Menegazzo *et al.*, 2016, Candeiro *et al.*, 2020).

The depositional history of the Bauru Basin was triggered by Early Cretaceous (Aptian–Albian) thermal subsidence, which responded to the previous Paraná–Etendeka basic tholeiitic volcanism, and by a posterior flexural subsidence derived from Santonian uplifts (as the Goiás Alkaline Province and Alto Paranaíba Uplift) which, in turn, were related to the passage of the central-eastern portion of South America over the Trindade Mantle Plume (Ricomini, 1997; Batezelli, 2015). Conditioned by these tectonic events and also by the climate, a sedimentary successions of aeolian facies in a desert environment characterized the first phase of basin fill (the Caiuá Group), followed by a Late Cretaceous (Turonian–Maastrichtian) associations of lacustrine, fluvial and alluvial facies in a semi-arid climate, these composing the different formations of the Bauru Group: Araçatuba, Presidente Prudente, Adamantina, Uberaba and Marília formations, as well other units not yet consensually adopted by geoscientists (Soares *et al.*, 1980; Fernandes & Coimbra, 1996; Batezelli, 2010, 2015; Fernandes & Ribeiro, 2015; Pinheiro *et al.*, 2018). The last generalized deposition event of the Bauru Basin is manifested in the essentially sandstone and heavily cemented packages of the alluvial deposits of the Marília Formation, the thickest of all the sequences of the Bauru Group (Batezelli & Ladeira, 2016).

The Prata site is bedded by strata of the Adamantina Formation, which is comprised mainly of fine sandstones (Dias-Brito *et al.*, 2001; Menegazzo *et al.*, 2016) with ripple-cross lamination or planar- to trough-cross stratification (Menegazzo *et al.*, 2016). Mudstones and conglomerates are also occasionally found in the formation (Menegazzo *et al.*, 2016). The depositional environment of the Adamantina Formation has been described as fluvial, with meandering water bodies as the main agent of sediment transport (Soares *et al.*, 1980; Dias-Brito *et al.*, 2001; Menegazzo *et al.*, 2016). The Adamantina Formation has a very rich fossil record, including crocodyliforms, sauropod and theropod dinosaurs and mammals, amongst other groups (Méndez *et al.*, 2014; Castro *et al.*, 2018; Pinheiro *et al.*, 2018; Silva Junior *et al.*, 2022).

The Uberaba site is bedded by strata of the Marília Formation, which has been described as a sequence of coarse to conglomeratic sandstones, fine-grained sandstones, argillaceous siltstones and carbonate levels (Soares *et al.*, 1980; Salgado & Carvalho, 2008). Its sediments were deposited in alluvial fans, alluvial plains, ephemeral lakes, and braided fluvial systems under a dry, hot climate (Salgado & Carvalho, 2008). The vertebrate fossil record of the Marília Formation is comprised by the groups typically found in the Bauru Group, including fishes, lissamphibians, squamates,

turtles, crocodylomorphs and dinosaurs (e.g., Bertini *et al.*, 1993; Santucci & Bertini, 2001; Candeiro *et al.*, 2006; Martinelli & Teixeira, 2015).

In the region of the Uberaba Municipality, the Marília Formation is divided into two members: Ponte Alta and Serra da Galga (Salgado & Carvalho, 2008). The former is comprised of coarse sandstones, conglomerates and breccias associated with impure carbonates (Salgado & Carvalho, 2008). The latter is formed by fine to coarse-grained sandstones, associated with conglomerates in fining-upwards cycles (Salgado & Carvalho, 2008).

The most significant fossil elements found in Serra da Galga Member are disarticulated bones and fragments (microvertebrate material) whose deposition has been interpreted to have resulted from seasonality in the sedimentary cycles (Garcia *et al.*, 1999; Salgado & Carvalho, 2008). Congruent with this, the fossils described here are isolated and fragmented. According to reviews of Menegazzo *et al.* (2016), the age of the Marília Formation is Maastrichtian, considering the chronostratigraphic occurrence of *Physa mezzalirai*, *P. caiera*, *Ficus globosa*, *F. costata*, *Nitellopsis*, *Amanita australis* and *N. minus*.

The locality in which most of the specimens here described, three isolated vertebral centra (MBC-059-PV, MBC-060-PV and MBC-061-PV) and two teeth (MBC-062-PV and MBC-063-PV), were found is an outcrop of the Serra da Galga Member of the Marília Formation, which overlies the Ponte Alta Member. This outcrop is in the Uberaba Municipality of the Minas Gerais State, beside roadway BR-050 (see Figures 1C and 2B). The other specimens, three teeth (MBC-064-PV, MBC-065-PV and MBC-066-PV) are from an outcrop of the Adamantina Formation, in the Prata Municipality of the Minas Gerais State, beside roadway BR-497 (see Figures 1C and 2A).

MATERIAL AND METHODS

The material here described consists of eight specimens of amiid fishes: three isolated vertebral centra (MBC-059-PV, MBC-060-PV, MBC-061-PV) and five partially preserved teeth (MBC-062-PV, MBC-063-PV, MBC-064-PV, MBC-065-PV and MBC-066-PV) from the Bauru Group of the Minas Gerais State, Brazil (see “Locality and Horizon”

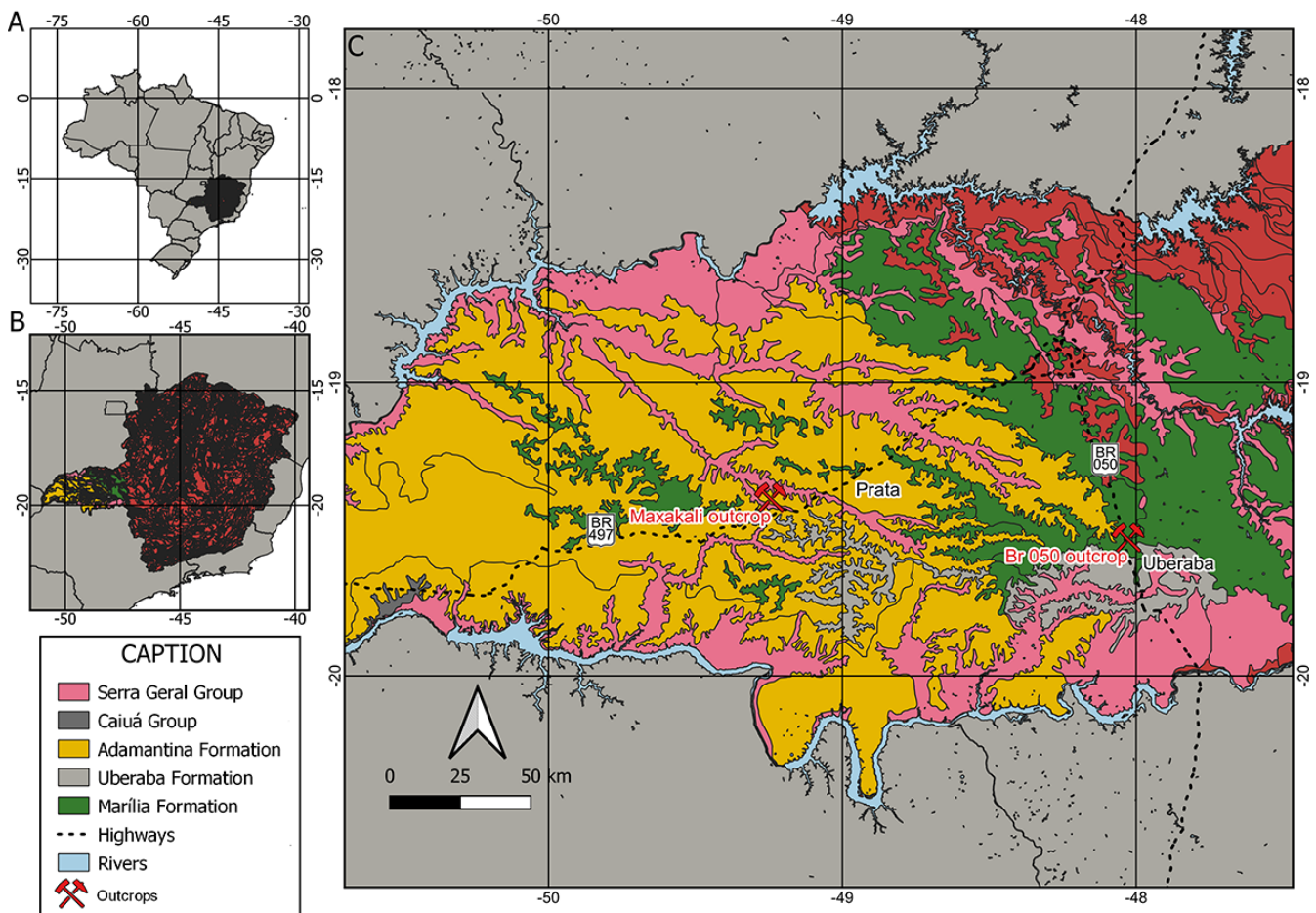


Figure 1. Location map and stratigraphic profile of the Prata and Uberaba localities with Late Cretaceous amiid remains. **A**, map of Brazil, with the Minas Gerais State in black; **B**, geological map of the Minas Gerais State; **C**, geological map of the Minas Gerais State showing the specific locations of the Prata and Uberaba fossil localities. The geological map of the Minas Gerais State is from the geosciences system of the *Serviço Geológico do Brasil* (GeoSGB-CPRM, 2022).

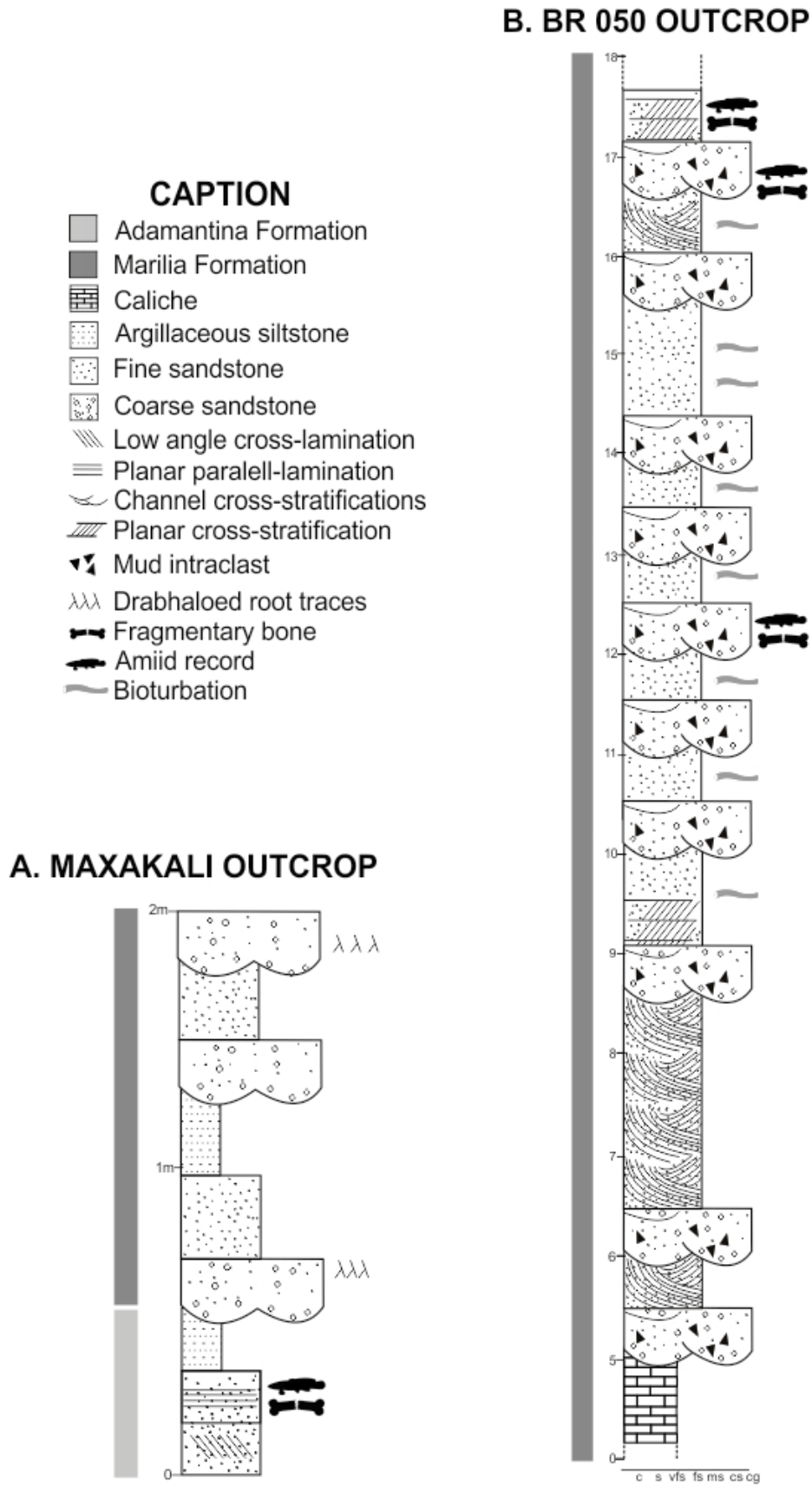


Figure 2. A, stratigraphic profile of the Adamantina Formation “Maxakali” locality (modified from Galhardo, 2012, fig. 10); B, stratigraphic profile from the Marília Formation “BR 050” locality (modified from Salgado & Carvalho, 2008, fig. 2) indicating the levels at which the amiid remains were found.

below for details). They are housed at the collection of the Laboratório de Paleontologia, Universidade Federal de Uberlândia (UFU).

Comparative data were gathered from the literature, mainly following Grande & Bemis (1998), and other relevant literature concerning articulated or disarticulated materials, such as Maisey (1991), Brito *et al.* (2008, 2017), Brinkman *et al.* (2013), and Martineli *et al.* (2013). For osteological nomenclature and abbreviations, we followed the anatomical studies of Grande & Bemis (1998).

Abbreviations. **Haap**, haemal arch articular pit; **naap**, neural arch articular pit; **nf**, notochordal foramen; **pap**, parapophyseal pit; **MBC**, Museu de Biodiversidade do Cerrado, Uberlândia, Brazil.

SYSTEMATIC PALEONTOLOGY

Superclass OSTEICHTHYES Huxley, 1880

Class ACTINOPTERYGII Cope, 1887

Subclass NEOPTERYGII Regan, 1923

Infraclass HOLOSTEI Müller, 1846

Clade HALECOMORPHI Cope, 1872

Order AMIIFORMES Hay, 1929

Family AMIIDAE Bonaparte, 1838

Subfamily VIDALAMIINAE Grande & Bemis, 1998

Tribe cf. Vidalamiini Grande & Bemis, 1998

(Figures 3–4)

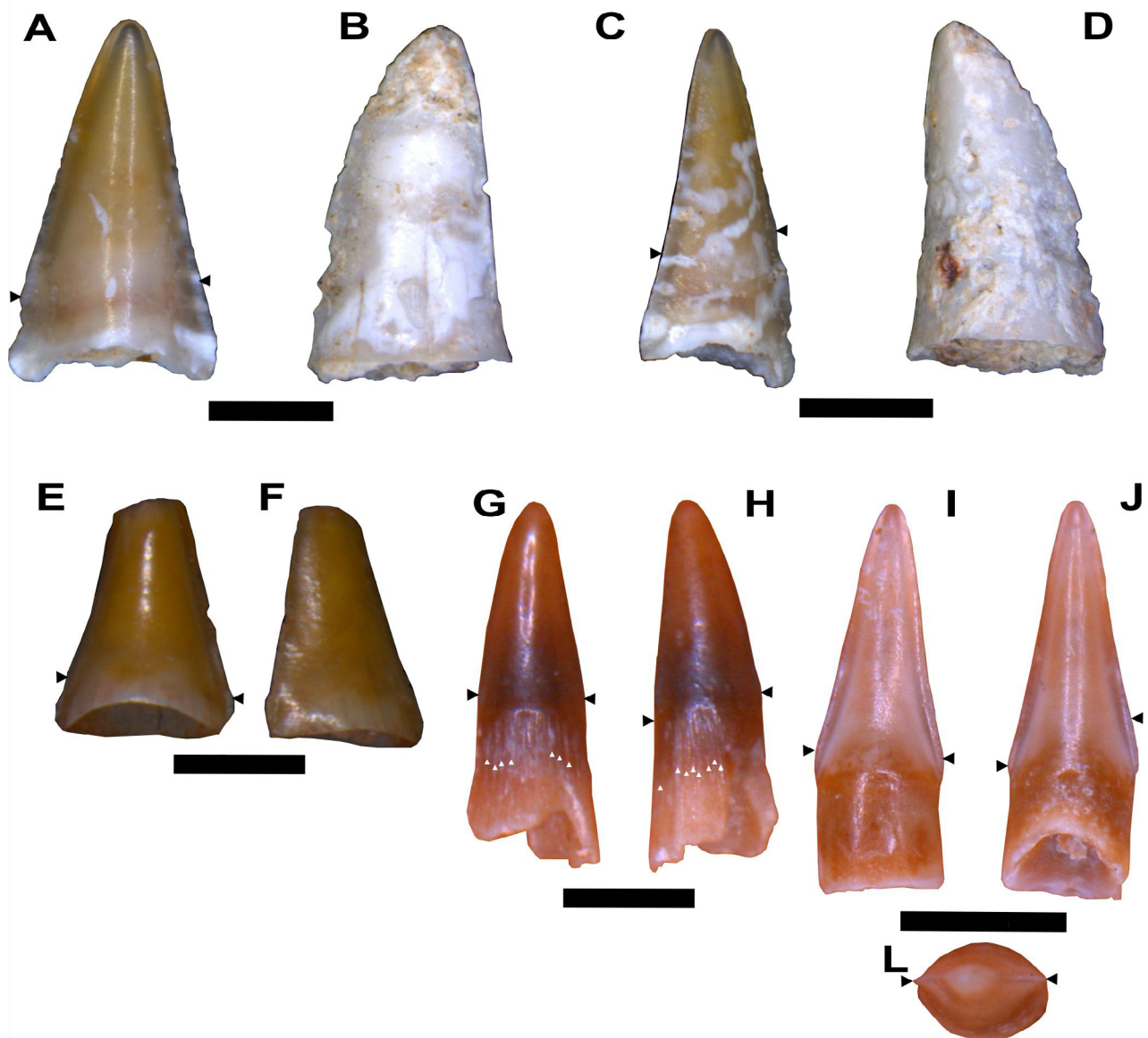


Figure 3. Amiid teeth from the Bauru Group. **A–B**, tooth MBC-062-PV in labial (**A**) and lingual (**B**) views. **C–D**, tooth MBC-063-PV in labial (**C**) and lingual (**D**) views. **E–F**, tooth MBC-064-PV in labial (**E**) and lingual (**F**) views. **G–H**, tooth MBC-065-PV in labial (**G**) and lingual (**H**) views. **I–L**, tooth MBC-066-PV in labial (**I**), lingual (**J**) and occlusal (**L**) views. The black and white arrowhead point, respectively, keel or carinae on margins of tooth and plicidentine arrangement on base of tooth. Scale bars: A–B = 2 mm; C–D = 1,5 mm; E–L = 1 mm.

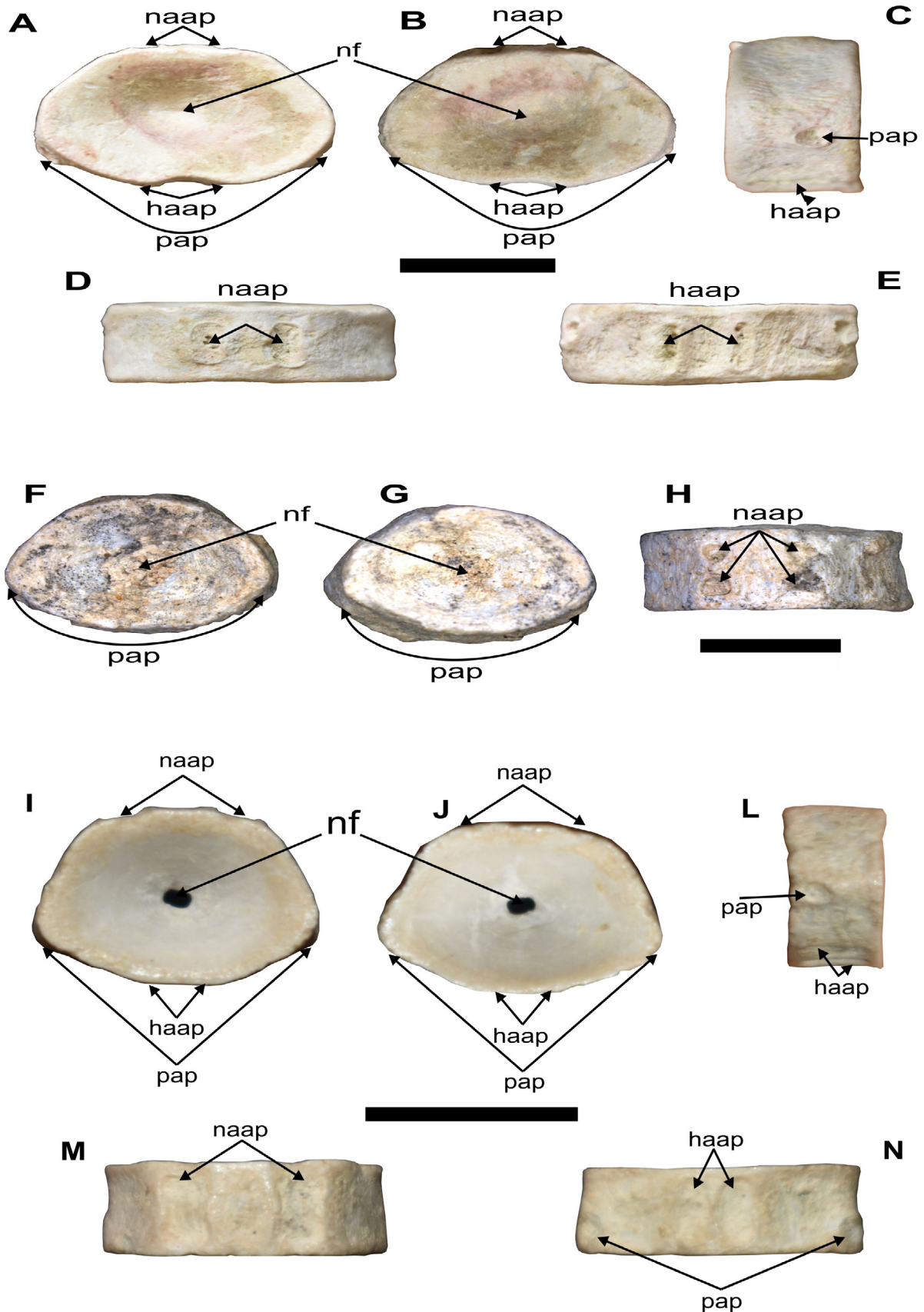


Figure 4. Amiid vertebral centra from the Bauru Group. A–E, vertebral centrum MBC-059-PV in anterior (A) and posterior (B) axial articular, left lateral (C), dorsal (D) and ventral (E) views. F–H, vertebral centrum MBC-061-PV in anterior (F) and posterior (G) axial articular, and dorsal (H) views. I–N, vertebral centrum MBC-060-PV in anterior (I) and posterior (J) axial articular, right lateral (L), dorsal (M) and ventral (N) views. Scale bars: A–H = 10 mm; I–N = 5 mm.

Referred material. Three isolated vertebral centra (MBC-059-PV, MBC-060-PV and MBC-061-PV) and five teeth (MBC-062-PV, MBC-063-PV, MBC-064-PV, MBC-065-PV and MBC-066-PV).

Locality and Horizon. Outcrop in the BR-050 roadway, Uberaba Municipality, Minas Gerais State of Brazil; Serra da Galga Member, Marília Formation, Bauru Group (MBC-059-PV, MBC-060-PV and MBC-061-PV, MBC-062-PV, MBC-063-PV) (Figs. 1C and 2B); outcrop in the BR-497 roadway, Prata Municipality, Minas Gerais State of Brazil; Adamantina Formation, Bauru Group (MBC-064-PV, MBC-065-PV and MBC-066-PV) (Figures 1C and 2A).

Description. Teeth: five isolated teeth are here described (MBC-062-PV, MBC-063-PV, MBC-064-PV, MBC-065-PV, MBC-066-PV). Two of them are complete, while the other three are broken, with only the crown and part of the base being preserved. They are apicobasally high, being 2.8 mm (Figures 3A–B), 5.5 mm (Figures 3C–D), 5.8 mm (Figures 4E–F), 2.8 mm (Figures 3G–H) and 2.4 mm (Figures 3I–J) in height, reaching their maximal thickness at their base and getting narrower and pointed toward the tip of the crown. They possess a triangular shape in labial and lingual views and are semi-circular in cross section. The surface of the teeth is apparently smooth (unornamented) and bears sufficiently translucent enamel to expose the inner dentine layer and acrodin cap on tip. The teeth show very well-developed keels or carinae on their mesial and distal margins (well-evidenced in Figure 3L), reaching the acrodin cap. One of them (Figures 3G–H) present parallel vertical ridges on the base of the tooth. The arrangement of the vertical ridges represents outer expressions of the dentine fold, which are identified as plicidentine, also observed in the teeth of the lower jaws of *Amia calva* (e.g., Germain & Meunier, 2017).

Vertebral centra: the three specimens here described (MBC-059-PV, MBC-060-PV and MBC-061-PV) are isolated vertebral centra. All of them seem to represent posterior abdominal vertebral positions based on the presence of aortal facets representing haemal arch articular pits on their ventral surface and the ventro-lateral orientation of the parapophyseal articular pits (see Grande & Bemis, 1998). However, these centra represent individuals of vastly different body sizes: 20 mm in length, 10 mm in depth, and 15 mm in height for MBC-059-PV (Figures 4A–E); 7 mm in length, 4 mm in depth, and 6 mm in height for MBC-060-PV (Figures 4I–H); 6.4 mm in length, 5.3 mm in depth and 4.6 mm in height for MBC-061-PV (Figures 4F–H). The three centra are dorsoventrally compressed, wide laterally and amphicoelous (i.e., both their anterior and posterior articular surfaces are concave). The neural arch articular pits of MBC-059-PV and MBC-060-PV are formed by a single pair of foramina, which are hourglass in shape, whereas those of MBC-061-PV are apparently formed by two separate pairs of foramina. However, the right neural arch area is eroded in MBC-061-PV, so that it is possible that this centrum had a single foramen on its right side as well. The lateral surfaces of the centra are formed mostly by longitudinal fibers of bone. The ventral surfaces of the specimens exhibit two longitudinal haemal arch articular pits.

The parapophyses are unfused to the centrum. MBC-059-PV and MBC-060-PV, however, exhibit an evident articular pit for the left parapophysis, which is circular and located near the posterior end of the centrum. The notochordal foramen is closed in MBC-059-PV and MBC-061-PV, but it is open in MBC-060-PV.

DISCUSSION

Taxonomy and comparisons

Despite the difficulties of basing taxonomic identifications only on isolated fish teeth, the teeth we describe here present a singular combination of synapomorphies characteristic of vidalamiine amiids: an elongate acrodin tip and a strongly carinated cross-section on both mesial and distal margins (see Grande & Bemis 1998). These vidalamiine-type teeth have been documented in Cretaceous fossil assemblages, sometimes without being associated to any other material (e.g., Friedman *et al.*, 2003; Buscalioni *et al.*, 2008; Brinkman *et al.*, 2013; Oreska *et al.*, 2013 and other herein). Vidalamiine-like teeth are very common in the Bauru Group (see Martinelli *et al.*, 2013 and Brito *et al.*, 2017 for review). These teeth were historically referred to the Erythrinidae (Characiformes) until Martinelli *et al.*'s (2013) publication (see Gayet & Brito, 1989; Brito *et al.*, 2006; Alves *et al.*, 2016).

Regarding the vertebral centra, MBC-059-PV and MBC-060-PV can be also assigned to Amiidae based on the presence of neural arch articular pits that are hourglass in shape. This feature is observed in extant *Amia calva* Linnaeus, 1866 and it also was confirmed in both fossil amiid subfamilies Amiinae and Vidalamiinae from the Late Cretaceous of Utah (Brinkman *et al.*, 2013). In the case of MBC-061-PV, the presence of four depressions on the dorsal margin for the articulation with the autogenous neural arch is a condition observed by Grande & Bemis (1998: fig. 278) in the most anterior abdominal centra of *Pachyamia mexicana* Grande & Bemis, 1998, and therefore this vertebral centrum can be assigned to the Amiidae as well.

Additionally, these vertebrae can be assigned to the Vidalamiinae for exhibiting parapophyses that are not fused to the centrum, a character that differentiates it from the Amiinae (see Grande & Bemis, 1998).

Finally, considering only diagnostic characters between the two Vidalamiinae tribes, the abdominal vertebrae from the Bauru Group are sub-oval, dorsoventrally compressed and laterally wide. This is a general shape that more closely resembles centra of the Vidalamiini than centra of the Calamopleurini. The same shape was observed by Grande & Bemis (1998) in abdominal vertebrae of *Pachyamia* and *Melvius*, and by us in *Cratoamia gondwanica* Brito, Yabumoto & Grande, 2008 (see Brito *et al.*, 2008: fig. 2). For the three species of *Calamopleurus* (see Maisey, 1991; Grande & Bemis, 1998), abdominal vertebrae are dorsoventrally taller and more laterally compressed. Unfortunately, there is no postcranial skeleton of *Maliamia* for comparisons. Nevertheless, we tentatively assign the specimens here described to the Vidalamiini, based on the general shape of

these abdominal centra, which constitutes the first tribe-level assignment of amiid remains from the Bauru Group. This also constitutes the second assignment of freshwater specimens from the Americas to the Vidalamiini, after the tentative assignment of one vertebral centrum and teeth crowns to the vidalamiin genus *Melvius* by Brinkman *et al.* (2013).

Palaeobiogeography

Amiiformes is a cosmopolitan order of halecomorph fishes with a Pangaean marine origin, which was very diverse during the Mesozoic era (see Grande & Bemis, 1998). Therefore, early freshwater and brackish incursions are an important point about their natural history (for more details, see Grande & Bemis, 1998; Cavin, 2017), which already drove their diversification in early Mesozoic times. Furthermore, the only extant amiid, *Amia calva*, is exclusively found in North American freshwaters (Nelson *et al.*, 2016). Notwithstanding this the understanding about the marine to freshwater ecological switchover of this group is poorly understood, mainly due to gaps in the fossil record.

In the case of vidalamiine amiids, their fossil record is most plentiful during the Cretaceous period (more than 21 records, with five genera and eight species), between the

Valanginian and the Maastrichtian ages, in brackish, coastal margin, marine, and freshwater facies of Europe, the Middle East, North Africa, and North and South America (see Table 1 and Figure 5). According to Grande & Bemis (1998), this subfamily can be divided into two tribes: one with a coastal distribution along North and South America, Europe, and the Middle East, Vidalamiini (*Vidalamia*, *Pachyamia*, *Cratoamia* and *Melvius*; Figure 5B); and another endemic to Gondwana, Calamopleurini (*Calamopleurus* and *Maliamia*; Figure 5C). The allopatric distribution of the Vidalamiini is associated to the Tethys seaway, which extended southward from the shallow waters of the Caribbean Tethys onto the South American continent (as advocated by Brito *et al.*, 2008; see Figure 5B). The distribution of the Calamopleurini is the result of vicariance between two palaeocontinents (Laurasia and Gondwana), which were fully separated by the Late Jurassic, isolating two large areas by expansive, deep-water oceanic regions (Figure 4A). Thereby, this single biogeographical event was responsible for both the dispersion (Vidalamiini) and the isolation (Calamopleurini) of these two taxa. Cavin (2017) advocated that certain vidalamiins (*Cratoamia* in South America, *Vidalamia* in Europe, and *Melvius* in North America) were then “captured” in freshwater environments on the different continents. However, the

Table 1. Temporal and geographical distribution of the Vidalamiinae from the Cretaceous Period.

	Taxon	Unit	Facies	Age	Country	References
1	<i>Vidalamia catalunica</i>	Montsec	Brackish water	Valanginian	Brazil	Wenz (1995)
2	<i>Calamopleurus mawsoni</i>	Marfim Fm.	Brackish water	Hauterivian	Brazil	Maisey (1991)
3	<i>Cratoamia gondwanica</i>	Crato Fm.	Brackish water	Aptian	Brazil	Brito <i>et al.</i> (2008)
4	<i>Ca. cylindricus</i>	Santana Fm.	Brackish water	Aptian	Brazil	Maisey (1991)
5	<i>Ca. cylindricus</i>	Codó Fm.	Brackish water	Aptian	Brazil	Lindoso <i>et al.</i> (2016)
6	Vidalamiinae indet.	Cloverly Fm.	Coastal margin	Aptian	USA	Oreska <i>et al.</i> (2013)
7	Vidalamiinae indet.	Potomac Fm.	Coastal margin	Albian	USA	Frederickson <i>et al.</i> (2018)
8	<i>Pachyamia mexicana</i>	Tlayúa Fm.	Marine beds	Albian	Mexico	Grande & Bemis (1998)
9	Vidalamiinae indet.	Açu Fm.	Freshwater beds	Cenomanian	Brazil	Veiga <i>et al.</i> (2019)
10	<i>Ca. africanus</i>	Kem Kem beds	Freshwater beds	Cenomanian	Morocco	Forey & Grande (1998)
11	<i>P. latimaxillaris</i>	Bet-Meir Fm.	Marine beds	Cenomanian	Israel	Chalifa & Tchernov (1982)
12	Amiidae indet.	Cerro Lisandro Fm.	Freshwater beds	Turonian	Argentina	Salgado <i>et al.</i> (2009)
13	Vidalamiinae indet.	Axel Heiberg Island	Freshwater beds	Turonian	Canadian Artic	Friedman <i>et al.</i> (2003)
14	Vidalamiinae indet.	Cedar Mountain Fm.	Coastal margin	Turonian	USA	Avrahami <i>et al.</i> (2018)
15	Vidalamiini indet.	Cotinguiba Fm.	Marine beds	Turonian	Brazil	Gallo <i>et al.</i> (2007)
16	Vidalamiinae indet.	Araçatuba Fm.	Lacustrine prodeltaic	Turonian	Brazil	Nava <i>et al.</i> (2021)
17	Vidalamiinae indet.	Adamantina Fm.	Freshwater beds	Santonian	Brazil	Martinelli <i>et al.</i> (2013)
18	Vidalamiinae indet.	Iharkut vertebrate site	Freshwater beds	Santonian	Hungary	Szabó & Ősi (2017)
19	Amiidae indet.	Allen Fm.	Freshwater beds	Campanian	Argentina	Bogan <i>et al.</i> (2010)
20	Vidalamiinae indet.	Presidente Prudente Fm.	Freshwater beds	Campanian	Brazil	Alves <i>et al.</i> (2016)
21	? <i>Melvius</i>	Straight Cliffs Fm.	Freshwater beds	Campanian	USA	Brinkman <i>et al.</i> (2013)
22	Vidalamiinae indet.	Judith River Fm.	Freshwater	Campanian	Canada	Brinkman & Neuman (2002)
23	<i>Melvius chaultiodous</i>	Fruitland Fm.	Marine beds	Campanian	USA	Hall & Wolberg (1989)
24	Vidalamiinae indet.	Marília Fm.	Freshwater beds	Maastrichtian	Brazil	Brito <i>et al.</i> (2017)
25	<i>M. thomasi</i>	Hell Creek Fm.	Marine beds	Maastrichtian	USA	Bryant (1987)

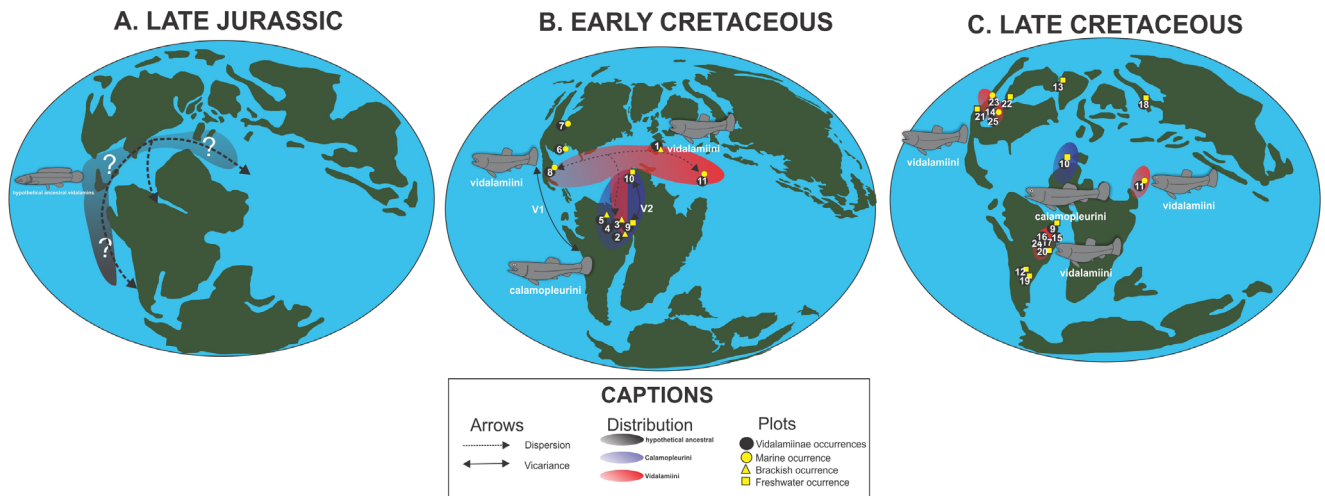


Figure 5. Distribution of Late Mesozoic palaeobiogeographic vidalamiini. 1, Montsec platenkalk, Spain; 2, Marfim Formation, Brazil; 3, Crato Formation, Brazil; 4, Santana Formation, Brazil; 5, Codó Formation, Brazil; 6, Cloverly Formation, USA; 7, Potomac Formation, USA; 8, Tlayua Formation, Mexico; 9, Açú Formation, Brazil; 10, Kem Kem beds, Morocco; 11, Bet-Meir Formation, Israel; 12, Cerro Lisandro Formation, Argentina; 13, Axel Heilberg Island, Canadian Arctic; 14, Cedar Mountain Formation, USA; 15, Cotinguiba Formation, Brazil; 16, Araçatuba Formation, Brazil; 17, Adamantina Formation, Brazil; 18, Iharkut vertebrate site, Hungary; 19, Allen Formation, Argentina; 20, Presidente Prudente Formation, Brazil; 21, Straight Cliffs Formation, USA; 22, Judith River Formation, Canada; 23, Fruitland Formation, USA; 24, Marília Formation, Brazil; 25, Hell Creek Formation, USA. Red circles indicate occurrences of Vidalamiini, and the blue circles the occurrences of Calamopleurini. The dotted arrow indicates dispersion, and the continuous arrow indicates vicariance. The yellow circle, triangle and square represent, respectively, marine, brackish and freshwater facies of amiid occurrences. Palaeobiogeographic maps based on Ron Blakey Paleomaps (www.cpegeosystems.com/paleomaps.html).

current geologic literature suggests that these groups lived in palaeoenvironmental conditions with some degree of marine influence or at least in fluctuating salinities (Maisey, 2000; Brito & Yabumoto, 2011).

Nonmarine records of vidalamiines are scarce and poor, limited to disarticulated remains such as teeth and vertebral centra (e.g., Friedman *et al.*, 2003; Buscalioni *et al.*, 2008; Oreska *et al.*, 2013; Brinkman *et al.*, 2013 and others herein), restricted to Late Cretaceous of North and South America. These records, however, may suggest that the vidalamiine amiids (maybe vidalamiini) could have dispersed once or several times between North and South America during the Late Cretaceous through the fresh waters of a land connection that existed between the two continents in that epoch (see Rage, 1978, 1986; Brochu, 1999; Newbrey *et al.*, 2009; Cidade *et al.*, 2019). This takes in consideration that from the Jurassic until the formation of the Panama isthmus in the Pliocene, North and South America were separated by the sea (Iturralde-Vinent, 2006; O’Dea *et al.*, 2016) and the Late Cretaceous land connection offered an ephemeral opportunity for terrestrial and freshwater vertebrates to disperse between these continents. The number and direction of such dispersal events of the Vidalamiinae depend on an exact determination of the aforementioned records to one of the tribes, as tribe-level assignments of North or South American specimens from the Cretaceous to Vidalamiini are only tentative, and there are no records of Calamopleurini (Table 1). These issues shall be addressed by future studies or, hopefully, by the finding of more complete specimens. Our up-to-date compilation presented in Table 1 and in Figure 4 demonstrates that for the freshwater records, there is already a broad

latitudinal spectrum of distribution during the Cenomanian-Maastrichtian interval, between the temperate higher latitudes (Canadian Arctic) and the lower tropical latitudes (Bauru and Neuquén groups) in the Americas. Additionally, Friedman *et al.* (2003) suggested that vidalamiine fishes could potentially prefer extreme climatic warmth. However, there are no modern representatives of the Vidalamiinae inhabiting these areas to verify these claims. This hypothesis is potentially biased by the incomplete preservation of freshwater sediments in the Early Cretaceous.

CONCLUSIONS

We have here described new occurrences of vidalamiine (cf. Vidalamiini) amiid fish from the Marília Formation of the Bauru Group, represented by three isolated vertebral centra and five isolated teeth, contributing to the knowledge of the palaeoichthyofauna of this unit, which is still little studied. The teeth that here we attribute to Vidalamiinae help to confirm the tentative identifications of previously described Bauru Group teeth tentatively ascribed to these groups. They also allow the assignment to Amiidae of teeth assigned by previous authors to other groups. Additionally, the specimens here described are tentatively assigned to Vidalamiini, representing the first tribe-level assignment of fish material from the Bauru Group.

Our overview on the palaeobiogeography of amiid fishes in the Late Cretaceous of the American continents reinforces that Amiidae is originally a saltwater group that underwent several independent incursions into freshwater habitats. One or more such incursions occurred in the Late Cretaceous of

either North or South America, as suggested by freshwater occurrences of these fishes on both continents, including the ones described in this paper for the Bauru Group. Within this perspective, we suggest that there could have been dispersions of amiid taxa between North and South America in the Late Cretaceous through a land connection that existed between the two continents during the epoch, a hypothesis that must be addressed by future studies.

Additionally, our up-to-date compilation of fossil vidalamiine fishes from the Cretaceous shows that the group already had a broad latitudinal spectrum of distribution during the Turonian-Maastrichtian interval, from temperate higher latitudes to tropical lower latitudes of the Americas. The hypothesis that the Vidalamiinae preferred extreme climatic warmth, however, is not supported by their Cretaceous distribution as it is currently known, although this perspective may be biased by very incomplete preservation of freshwater sediments in the Early Cretaceous.

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