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Short communication

Araripemys barretoi: Paleoecological analysis of a pelomedusoid Chelonia from the Lower Cretaceous of Araripe and Parnaíba basins, Brazil

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ABSTRACT

It is investigated the paleoecology of *Araripemys barretoi* Price, 1973 a pelomedusoid turtle from the Lower Cretaceous (Aptian) of Araripe and Parnaíba basins, Brazil. The analysis of forelimbs proportions allowed to interpret *Araripemys barretoi* as a turtle with a specialized morphology to live in large water bodies, as an agile swimmer. Several postcranial anatomical features suggest that *Araripemys barretoi* was able to live in aquatic environments of distinct magnitudes. This species was abundant throughout the Aptian in the Araripe and Parnaíba basins, where an epicontinental sea once existed, during the first marine ingressions related to the Equatorial Atlantic opening.

1. Introduction

In the Cretaceous sedimentary basins of Brazil, 16 taxa of chelonian fossils are found (Gaffney et al., 2006, 2011; Oliveira and Romano, 2007; Romano et al., 2014; Ferreira et al., 2018a; Hermanson et al., 2020; Batista et al., 2021), mostly from the Bauru and Araripe basins. In the Bauru Basin all fossil turtles are freshwater species. On the other hand, the Aptian chelonian species described from the Araripe Basin present morphological characteristics that suggest adaptations to very distinct living environments. Among the various species from the Araripe Basin, the most common is *Araripemys barretoi* Price, 1973, whose great number of specimens overpass the other chelonian species. *Araripemys barretoi* is also reported from the Parnaíba Basin (Batista and Carvalho, 2007), also located in the northeastern region of Brazil.

In the description of *Araripemys barretoi* by Price (1973), the osteology and the geometric shape of the carapace give it an origin among more primitive chelonians with tendencies towards a marine habitat. Aspects such as rounded, depressed carapace without keels, a short, wide plastron, with bridges attached only to the peripheral plates, with costoperipheral fontanelles and perhaps also plastoperipheral and plastron, indicate an adaptive tendency towards shallow, coastal or even marshy waters (Price, 1973). In the osteological review performed by Maisey (1991), *Araripemys barretoi* was compared with the freshwater turtles Trionychidae due their similarity in the carapace morphology. It was considered an extremely hydrodynamic species, but without any anatomical attribute to a specific environment. According to Oliveira and Romano (2007), *Araripemys barretoi* is the best-known species of the Santana Group (Araripe Basin). However, there are still doubts about its ecology and one of the great uncertainties concerns the environment that this species inhabited, as it is found in sediments of lagoon and marine origin (Araripe et al., 2021; Vallejo et al., 2023). In more recent studies with freshwater chelonians, for

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example *Emydura macquarii* and *Chelodina expansa*, can tolerate periods in hypersaline environments by physiological mechanisms, such as an increase in plasma osmotic pressure in relation to the external environment, in order to reduce the loss of water, without the need for a salt excretion gland, as in marine chelonians (Bower et al., 2016; Agha et al., 2018). This may be an indication that this species may be a chelonian tolerant to a wide range of salinities. Limaverde et al. (2020) carried out an extensive study analyzing factors such as ontogenetic and intraspecific variations, sexual dimorphism and phylogeny, but without any inference concerning the living environment.

The analyses of new specimens of *Araripemys barretoi* allowed evaluating the environmental context where this species lived. The morphological data from tomographic images, direct observations and comparisons with living species from distinct environments permitted a new approach to interpret the paleoecology of this Early Cretaceous pleurodiran turtle. Thus, it is analyzed the causes of the large number of a single species spread in a wide territorial area.

2. Geological context

The Araripe Basin (Appendix A) is known worldwide for its exceptionally well-preserved fossils (Heimhofer et al., 2010; Varejão et al., 2019a), being one of the main Konservat-Lagerstätten from the Cretaceous of Gondwana supercontinent (Maisey, 1991; Martill et al., 2007; Maldanis et al., 2016; Varejão et al., 2019a, 2021a; Dias and Carvalho, 2020, 2022). It is the largest among the interior basins of Northeast Brazil, rectangular shape, longitudinal axis in the EW direction and an area of approximately 12,200 km^2. It is located in the south of Ceará State, extending from the northwest of the state of Pernambuco to the east of the state of Piauí, northeast Brazil (Matos, 1992; Assine, 1992, 2007; Fambrini et al., 2009; Carvalho et al., 2012; Assine et al., 2014; Marques et al., 2014). The lithostratigraphic units are, from lower to upper successions, the Cariri, Brejo Santo, Missão Velha, Rio da Batateira, Santana and Exu formations (Beurlen, 1963, 1971; Ponte and Appi, 1990; Ponte, 1992; Paula-Freitas and Borghi, 2011; Rios-Netto et al., 2012). Assine et al. (2014) and Neumann and Assine (2015) changed the status of the Santana Formation to the Santana Group with the Barbalha, Crato, Ipubi and Romualdo formations. The first record of the fossil chelonian *Araripemys barretoi* was from the Romualdo Formation and later other specimens were found in the Crato Formation (Kischlat and Campos, 1990; Schleich, 1990; Meylan, 1996; Oliveira and Kellner, 2005, 2017; Gaffney et al., 2006; Romano et al., 2013; Limaverde et al., 2020).

The Romualdo Formation is constituted of conglomerates, sandstones, marls, shales, cochinoid and nodular limestones, which indicate hypersaline lagoons and marine environments, and an increasingly continental conditions (Assine et al., 2014). It records an abundant and diverse biota with a high degree of preservation. Foraminifera, palynomorphs, corals, mollusks, arthropods, echinoids, fishes, chelonians, crocodyliforms, pterosaurs, dinosaurs and plants occur in this succession (Martill, 1988; Neumann and Cabrera, 1999; Assine, 2007; Assine et al., 2014; Carvalho and Barreto, 2015; Barros et al., 2019; Carvalho et al., 2019a; Abreu et al., 2020; Araripe et al., 2021; Lopes and Barreto, 2021; Matos et al., 2021).

The Crato Formation is a succession up to 70 m thick containing limestones, shales and sandstones. This unit is interpreted as a wide variety of continental and transitional environments at the end of the Aptian in the Araripe Basin, with the record of the first marine incursions (Varejão et al., 2021a,b). The most abundant, diversified and exceptionally preserved terrestrial biota at a global level is found in the laminated limestones of lacustrine origin of the Crato Formation, a *Lagerstätte* of conservation and concentration. There are fossils of arthropods, fishes, amphibians, chelonians, lizards, crocodyliforms, pterosaurs, dinosaurs, birds, fungi, plant, fragments of algae, pteridophytes, conifers, gnetophytes, angiosperms, coprolites, amber (Menon and Martill, 2007; Assine et al., 2014; Martill et al., 2015; Carvalho et al., 2015, 2019b, 2021a; Scaramuzza dos Santos et al., 2020, 2021), and also dinosaur footprints (Carvalho et al., 2021b).

Other records of *Araripemys barretoi* are found in the Parnaíba Basin (Appendix B) (Batista and Carvalho, 2007). It is located in the central-western portion of Brazil (Vaz et al., 2007), in Maranhão and Piauí, and small areas of Ceará, Bahia, Tocantins and Pará States. Its limits are the Alto Ferrer-Urbano Santos (North), the Borborema Province (East), the Alto São Francisco (South), the Province of Tocantins (West) and to the northwest by the Alto Tocantins (Corrêa-Martins, 2019). The basin has a circular outline, and its Cretaceous succession of up to 1000 m is represented by the Corda, Codó and Itapecuru formations (Góes and Feijó, 1994). The studied fossils come from the Itapecuru Formation.

The Itapecuru Formation consists of conglomerates, sandstones, siltstones, claystones, shales and carbonate levels (Campbell et al., 1949; Azevedo, 1991; Pedrão et al., 2002; Miranda and Rossetti, 2006). Palynological analyzes on samples collected along the Itapecuru River assigned these deposits to the upper Aptian–upper Albian, based on the biostratigraphic range defined by the *Complicatisaccus cearensis*/*Elaterosporites protensus* zones (Pedrão et al., 1996, 2002). However, Ferreira et al. (2020, 2021) restricted these deposits to the upper Aptian. In this lithostratigraphic unit there are fossils of chelonians, sauropod dinosaurs (Carvalho et al., 2003) and theropods Carcharodontosauridae and Spinosauridae (Vilas Bôas et al., 1999; Medeiros and Schultz, 2002; Medeiros, 2006; Medeiros et al., 2007; Batista et al., 2021).

3. Materials and methods

For the morphological analyses, we evaluated the specimens of *Araripemys barretoi* housed in the Macrofossils Collection of the Federal University of Rio de Janeiro, Brazil under the coding numbers UFRJ DG-37R and UFRJ DG-74R (Appendix C), UFRJ DG-675R and UFRJ DG-693R (Appendix D). The specimens tomography were performed at the Museum of Zoology of the University of São Paulo. The tomograph is the Phoenix v|tome|x m microfocus microtomograph from General Electric (industrial model), covering a wide range of resolutions reaching up to 0.5 micrometers (μm) with voltage varying between 180 and 300 kV. Subsequently, the Avizo 7 and Zbrush 2019 softwares were used to clean digitally the fossils from the matrix rock.

A descriptive statistical analysis was performed; we measured the forelimbs of *Araripemys barretoi* and compared them with other living chelonians. For this, it was used the program Past 4.03 (Hammer et al., 2001) and data from Joyce and Gauthier (2004) and Jannello et al. (2018), resulting in two charts. The first one is related to the proportion between the humerus and ulna and its position within a standard deviation already determined by Joyce and Gauthier (2004). The second one is a ternary chart used to insert the *Araripemys barretoi* species in the environmental context in relation to other living chelonians.

4. Results and discussion

4.1. Taphonomic aspects

Araripemys barretoi presents distinct taphonomic signatures for each of the analyzed lithostratigraphic unit. In the Crato Formation, specimens of *Araripemys barretoi* were found in the laminated micritic limestone, whose origin is attributed to transgressive-

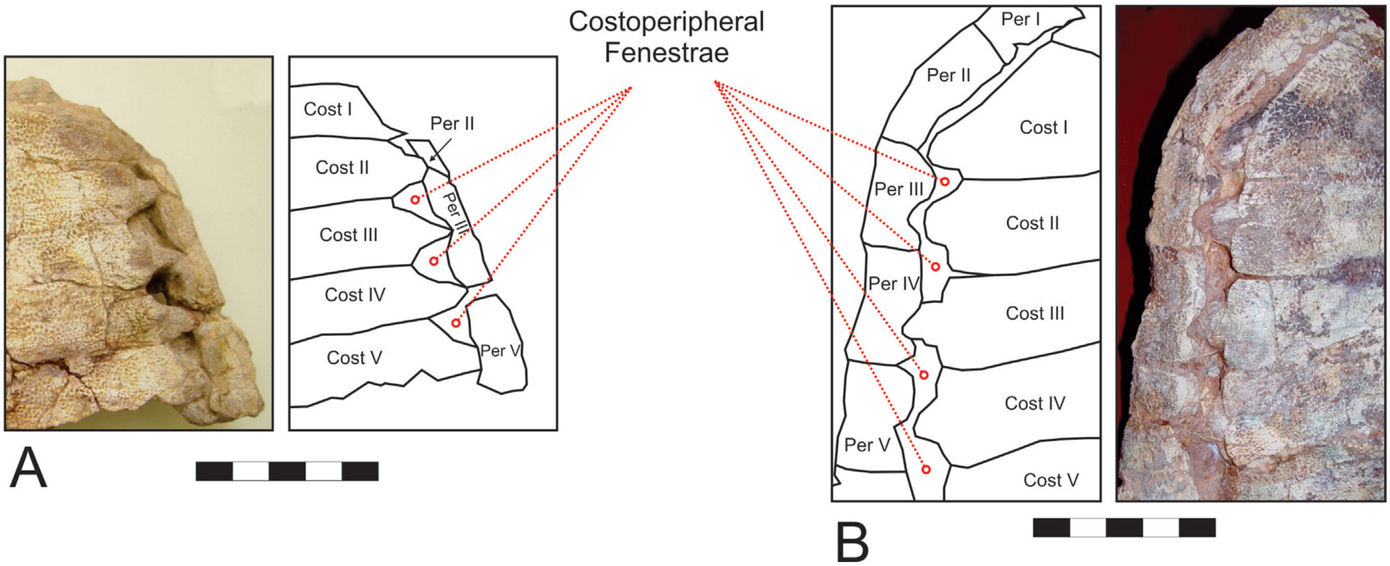

Fig. 1. Specimens of *Araripemys barretoi* from Parnaíba Basin. A – UFRJ DG 37-R and B – UFRJ DG 74-R, ventral view. Cost = Costal Plate, Per = Peripheral Plate. Scale bar with 5 cm.

regressive events associated with a lacustrine system (Neumann, 1999; Neumann et al., 2003). The fossils of this unit are well preserved due to the relationship with microbial mats, that induced the mineralization of the specimens (Dias and Carvalho, 2020). In the Romualdo Formation, *Araripemys barretoi* specimens are found in calcareous nodules. Sedimentary structures of chemical origin, consisting of spheroidal, ovoid, discoid or irregularly shaped aggregates, with a different composition from the rock in which they are contained, indicate precipitation of an aqueous solution during sedimentation (syngenetic concretions). This occurred immediately after or in the early stages of compactation (Scoffin, 1987).

It should be noted that the fossils from these stratigraphic units of the Araripe Basin did not undergo significant transport as postulated by Varejão et al. (2019b), which suggest post-mortem displacement for turtles and other vertebrates. The assertion that these animals lived in riparian forests, nearby rivers and/or shallow lakes and that these animals are rarely preserved is not correct. The number of articulated chelonians of the *Araripemys barretoi* species, housed in several collections, is not consistent with the interpretation of allochthonous species accumulated in a post-mortem environment.

In the Itapecuru Formation, the *Araripemys barretoi* remains are mostly fragmented and deformed. The specimens indicate transport and redeposition in a probable fluvial-estuarine context.

4.2. Morphological characters

Araripemys barretoi presents several anatomical and morphological evidences that allow us to attribute this species to a specific environment. These anatomical unique morphological features can be observed in the shape of the carapace and plastron, and in the overall anatomy of the forelimbs, regarding both its more proximal (e.g. humerus) and distal (claws) elements.

Araripemys barretoi belongs to the monophyletic group Pleurodira, Pelomedusoides (Gaffney et al., 2006), which is currently exclusive of freshwater environments and inhabits the southern hemisphere. Despite the current low diversity (Rhodin et al., 2021), pelomedusoids were a very diverse group during the Cretaceous and Paleogene, dispersed on almost all continents (except Central Asia and Antarctica) (Gaffney et al., 2006, 2011; Ferreira et al., 2018b). Some species such as *Bairdemys thalassica* (Capadore Formation, Miocene of Venezuela) and *Bairdemys venezuelensis* (Urumacu Formation, Miocene of Venezuela) are reported from marine environments close to the coast (Winkler and Sánchez-Villagra, 2006; Ferreira et al., 2015). Microforaminifers were identified in the sedimentary successions in which *Araripemys barretoi* occurs in the Araripe Basin (Goldberg et al., 2019), as well as the paleoenvironmental interpretations (Arai and Assine, 2020; Araripe et al., 2022) for the upper Aptian in Northeast Brazil,

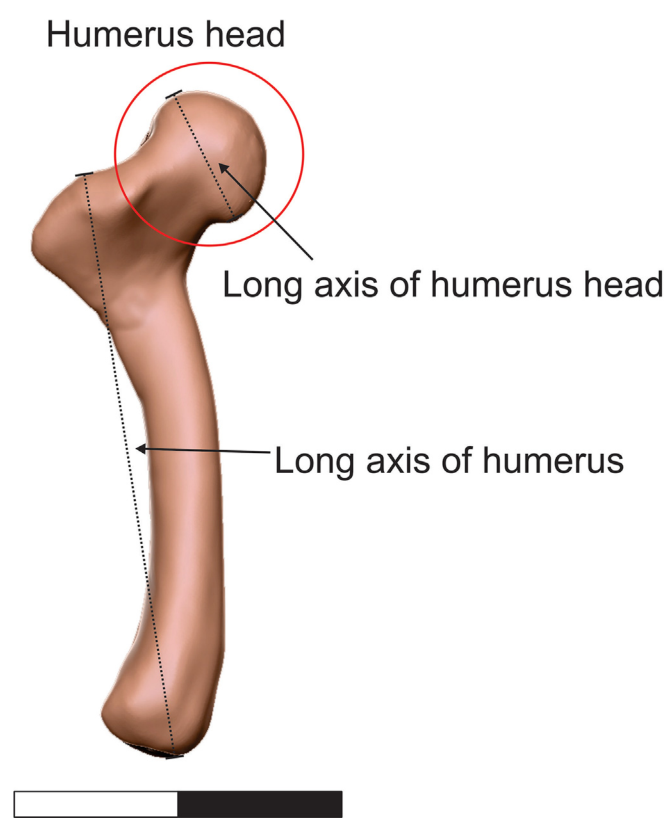

Fig. 2. Digitally prepared humerus of *Araripemys barretoi*, specimen UFRJ DG 74-R. Scale bar 1 cm.

indicate the presence of epicontinental seas. Base on Jannello et al. (2020), Sena et al. (2021) identified a histological pattern in *Araripemys barretoi* that resembles terrestrial animals. However, this shell histology disagrees with the general lake and marine environment suggested by the sediments from which *Araripemys* comes (Oliveira et al., 2011; Carvalho & Barreto 2015; Oliveira & Kellner 2017). Additionally, the combination of taphonomic aspects of *Araripemys barretoi* and the presence of microforaminifers, argue in favor of a nearshore or a fluvial-estuarine context. Further morphological features of *Araripemys barretoi* supporting this hypothesis are discussed below.

A common feature in marine turtles is the salt-secreting gland. Living sea turtles are adapted to withstand high salinities, with glands that eliminate salt excess (Brian and Cowan, 1971), but in fossils, these organs are generally not found (Nicholls, 1997). In modern Chelonia, it is located in the orbital cavity, above the eyes, and can be identified in most skulls by the enlargement of this cavity (Schumacher, 1973). In the studied specimens of *Araripemys barretoi*, the orbital cavity is similar to that of other Pleurodira. Then an interpretation of a strictly marine environment only based on this structure is not supported. However, other anatomical aspects allow elucidating and corroborating *Araripemys barretoi* as living in large water bodies with great depths. Although there isn't clear data concerning the paleobatimetry on Crato, Romualdo and Codó deposits, the frequent presence of microbial intermediation in the carbonate deposition and fossil preservation indicate the photic zone. This is the best depth to the accumulation of the laminated carbonates (Fürsich et al., 2019; Bom et al., 2021; Martill et al., 2021; Storari et al., 2021).

In the carapace of *Araripemys barretoi* specimens (UFRJ DG 37R and UFRJ DG 74R), there are costoperipheral fenestrae. They are hollow spaces between the costal plates and peripheral plates (Fig. 1). The formation of these fenestrae are due to the lack of ossification in the last ontogenetic stages, as observed in living chelonian embryos (Vieira, 2008). This type of structure is present in marine turtles (living and fossil) and in some freshwater species (example *Chelydra serpentina*) (Wyneken, 2001). Gasparini et al. (2007) clarify that the costoperipheral fenestrae have the function of improve mobility in the water. Pough et al. (1989) and Carroll (1988) indicated that this structure is an adaptative features

Fig. 3. Location map of the Araripe and Parnaíba basins during the Aptian. The north of Brazil was still connected to the future African continent. An ingression from the Central Atlantic reached the South Atlantic through an epicontinental seaway that connected several inland basins (Adapted from Arai, 2014).

to the environment in which chelonians live. The low weight and the greater mobility allow them to live in deeper waters, emerge and submerge quickly, typical of turtles that inhabit large water bodies. However, in *Chelydra serpentina*, the presence of costoperipheral fenestrae indicates that it has a greater control of submersion, as its anatomical shape is not that of an active swimming chelonian. In the plastron of *Araripemys barretoi*, we also observe anatomical features similar to those present in marine chelonians (living and fossil). The reduction of plastron size, presence of fenestrae, accentuated axial and femoral entry are a set of characteristics that gives them greater mobility in the water, relieving weight and improving their hydrodynamics. The living *Chelydra serpentina* species has a similar structure; however, the forelimbs are not adapted for swimming movements, but specialized for walking on riverbeds (Tulli et al., 2022). On the other hand, *Carettochelys insculpta* Ramsay, 1886, has acute axial and femoral recesses, and forelimbs like oars and hindlimbs like rudders, which allow great mobility when submerged, as we suppose in *Araripemys barretoi*. We can also observe similarity between *Araripemys barretoi* and the Trionychidae, with a reduced plastron, making this family excellent swimmers.

The *Araripemys barretoi* humerus allows some ecological inferences. The head of the humerus (Fig. 2) was elongated into an extreme ellipse with its long axis nearly parallel to the shaft humerus shaft, restricting the movements of the forelimb to the vertical plane (Weems and Knight, 2013). In this way, *Araripemys barretoi* was probably unable to walk on the bottom surface, spending most of the time in the water. It is possible to observe this same characteristic in the species *Bairdemys healeyorum* (Weems and Knight, 2013) and sea turtles (Ferreira et al., 2015). Turtles with this type of humeral head usually have strong aquatic adaptations, with limbs functioning like oars and they are active swimmers who live in wide lakes and/or seas (Weems and Knight, 2013). This humero is available for 3D visualization at Mendeley Data (https://doi.org/10.17632/4zryss9zf7.1).

Similarly to the anatomy of the humerus, the claws help to interpret their living environment. Larger claws facilitate walking through the substrate while their absence indicates a specialization for environments with high stand water (Tulli et al., 2022). In many cases, the keratinized structure is lost in the fossilization process, but the digital endings can reveal its structure. In the *Araripemys barretoi* specimens UFRJ DG 74R and UFRJ DG 693R, the arrow-shaped digital ending is not suitable in the vast majority of living freshwater Chelonia, such as *Macrochelys temminckii*, *Chelus fimbriatus* and *Hydromedusa tectifera*, which in turn have long, curved and pointed nails. Therefore, these animals are specialized in walking on substrates and river beds. *Araripemys barretoi* does not present this specialization (Appendix E), an additional difficulty to walk on the bottom of water bodies.

4.3. Paleoecology

Araripemys barretoi forelimb anatomy exhibits probable adaptations to living in different sorts of aquatic environments, which in turn may have facilitated its wide distribution during the Early Cretaceous in the Araripe and Parnaíba basins (Fig. 3). Joyce and Gauthier (2004) carried out an extensive study and managed to define a pattern of relationship between the bones of the forelimbs and the habitat, resulting in two charts, one for proportional analysis and the other ternary, to identify a pattern of distribution by environments. The first one is based on the measurements of the humerus and ulna; the second one is based on the measurements of the humerus, ulna and paw until keratinization. Thus, the humerus of the UFRJ DG 675R and UFRJ DG 693R specimens are 1.52 and 1.6 times larger than the ulna, while the total variation of all species presented in Joyce and Gauthier (2004) ranges from 1.29 to 1.8. As a result, it is possible to consider that both specimens are within the variation pattern of Joyce and Gauthier (2004) (Fig. 4), thus suitable for using the data in the ternary chart. The UFRJ DG 675R specimen is positioned in

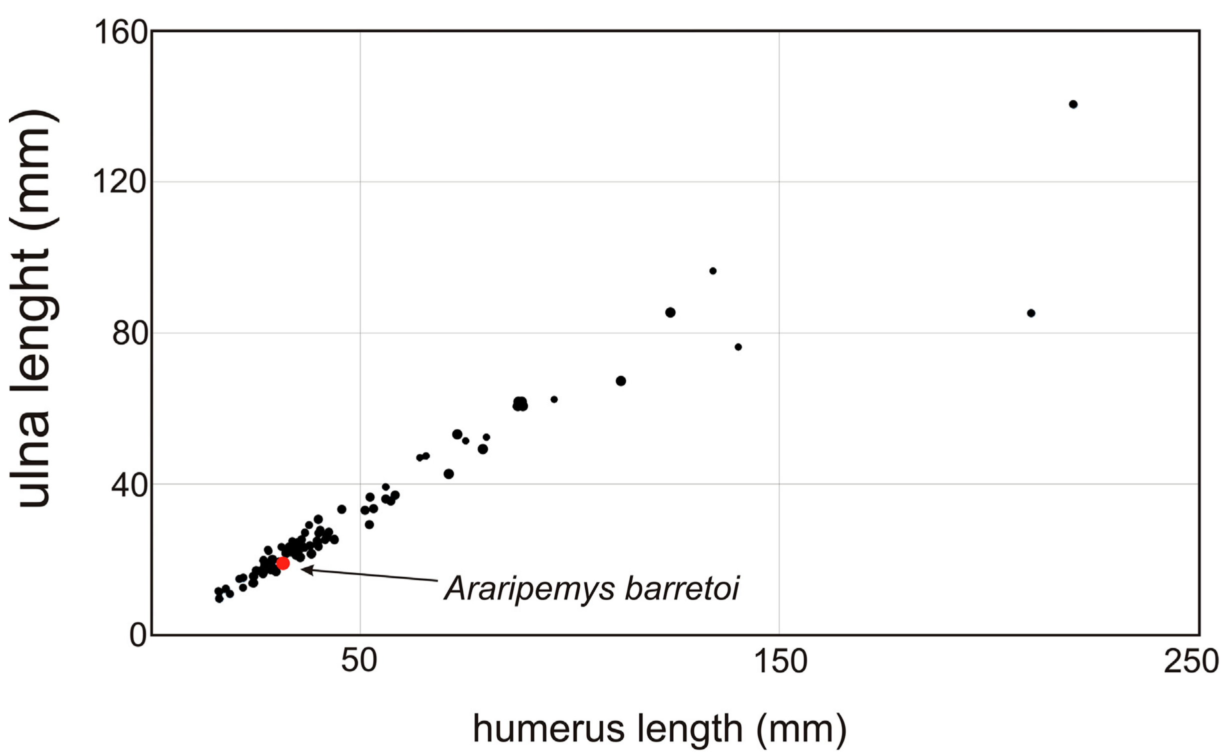

Fig. 4. Correlation between the length of the humerus and the ulna in living turtles, based on Joyce and Gauthier (2004).

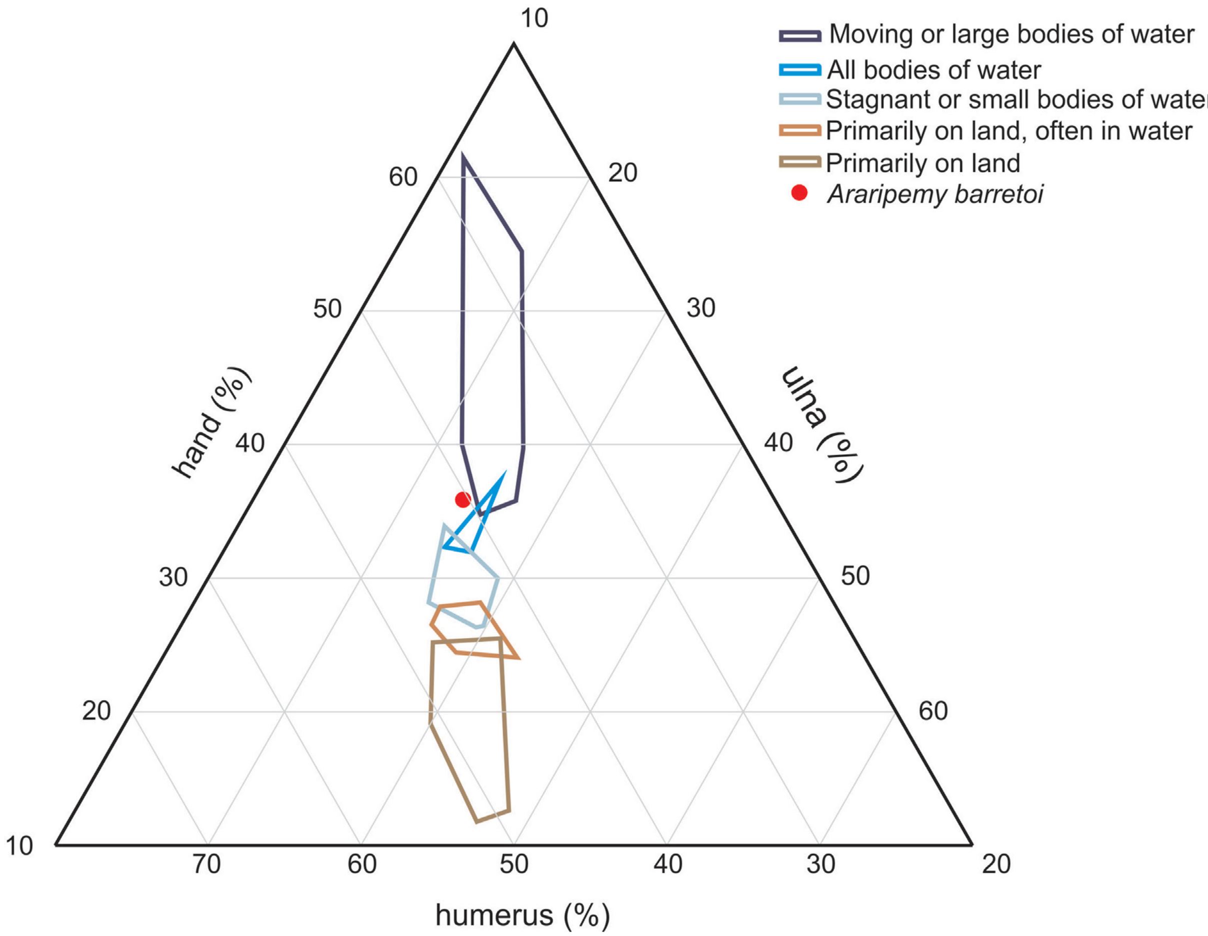

Fig. 5. Distribution by areas in the ternary chart of chelonians studied by Joyce and Gauthier (2004), with the inclusion of *Araripemys barretoi*. This show an adaptation of this species to large bodies of water.

the ternary chart slightly below the members of the Trionychidae family (Fig. 5), corroborating the interpretation of Maisey (1991) about the similarity between the members of the living family Trionychidae and the *Araripemys barretoi* species. The ternary chart allow recognizing a relationship between morphological characteristics and the living environment, identifying diverse types of environments in which these chelonians inhabited. Thus, *Araripemys barretoi* is interpreted in the context of high specialization for aquatic environments with abilities to inhabit bodies of water of different magnitudes, including large ones such as the epicontinental sea proposed for the palaeoenvironment of the region. It is positioned in the same final portion of the chart where the recent marine species *Dermochelys* and *Carettochelys* (freshwater turtles with morphology specialized to move in large bodies of water) are found, and the initial plot area of members of the Cheloniidae and Trionychidae families. Thus, it is plausible to say that *Araripemys barretoi* had an ecological advantage in environments with a wide extension of water without the necessity to be regularly on land, in contrast to the other species of fossil chelonians recorded for the Araripe and Parnaíba Basins.

5. Conclusions

Anatomical aspects of *Araripemys barretoi* and data from the geological context allow us to interpret a plausible living environment to this species. *Araripemys barretoi* was able to live in diverse types of aquatic environments. Therefore, the interpretation of the strictly fluvial life environment is refuted. This species was able to live in environments with variations in salinity, with better mobility in the water than land. Its presence is abundant in the Aptian of the Araripe and Parnaíba basins, where an epicontinental sea once existed, as a result of the first marine ingressions in the equatorial region during the opening of the Atlantic Ocean. In this context, there were favorable conditions for the spreading of this species and its preservation in the Aptian successions of a vast area in the northern region of Brazilian Gondwana.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105503.