

CONTROLLED EXCAVATIONS IN THE ROMUALDO FORMATION LAGERSTÄTTE (ARARIPE BASIN, BRAZIL) AND PTEROSAUR DIVERSITY: REMARKS BASED ON NEW FINDINGS

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ABSTRACT

Because of its fossil abundance and exceptional preservation, the Romualdo Formation of the Santana Group has become a famous lithostratigraphic unit of the Araripe Basin. In the past decades, much research has been conducted on the vertebrates of this unit, especially fish and pterosaurs, based mainly on museum collections. Despite the importance of these fossil finds, no stratigraphic information is known about them, because until recently, locals have collected most of the fossils. Here we present the results of the third controlled excavation of these layers. The data from all fossils collected confirm a faunal succession of fish biota. In the upper and most fossiliferous layer, the faunal composition shows a pattern of fish distribution never observed before, indicating that previous categories (abundance versus diversity) do not include the total diversity of fish populations. Pterosaur remains were recorded for the first time in the field, contradicting the general idea that these volant reptiles are common in the Romualdo strata. The specimen was attributed to the clade Anhangueridae because the proportional length of the first wing phalanx is less than twice the length of the wing metacarpal. The controlled excavation showed that the pterosaur assemblages from this formation probably occur in clusters. The known abundance of pterosaurs in the Romualdo Formation has been biased by just a few sites of fossil extraction, and these reptiles do not appear to have been as widespread or abundant as previously thought.

INTRODUCTION

The fossils found in a Fossil-Lagerstätte are always a good source of information about the past biota and environments (Fara et al., 2005; Wang et al., 2005), but to obtain the maximum information from these sites it is critical to understand their stratigraphy. Controlled excavations are a useful way of obtaining this kind of information, providing precise time frames for the fossils as well as apparent variation in faunal composition and abundance (Fara et al., 2005).

The Araripe Basin is a world-famous fossiliferous unit because of its great quantity of important fossil finds. The Romualdo Formation (*sensu* Neumann and Cabrera, 1999) of the Santana Group is the most famous lithostratigraphic unit of the Araripe Basin, because of the abundance and the exceptional preservation of the fossils found in those layers. The fossil biota suggests a diverse paleoenvironment, with numerous species of plants, invertebrates (especially arthropods), and vertebrates known (Maisey, 1991). Among the vertebrate fossils, the pterosaur fauna brought attention to this unit in the past decades due to its great preservation, abundance, and diversity (e.g., Maisey, 1991; Kellner and Tomida, 2000; Rodrigues and Kellner, 2008). Since the

discovery of the first pterosaur record (Price, 1971), ~200 specimens have been collected belonging to 25 different species (Barrett et al., 2008; Witton, 2008). Despite the importance of the pterosaurs finds in the Romualdo Formation, no stratigraphic information is known about them. This creates a scenario of poorly resolved relationships among the fossils from the Romualdo, especially the pterosaurs.

Controlled excavations allow researchers to precisely identify the origin of fossils and associate them with a correct stratigraphy. The work described here is part of an expanded research program that has two main objectives: (1) to provide precise, controlled field data for Araripe fossils; (2) to test and explain the strato-temporal heterogeneity of the fossil assemblages across the basin in relation to paleoenvironmental proxies (see Fara et al., 2005, for a review). During the last eight years, controlled excavations have been done in sites close to the cities of Santana do Cariri, Crato, Missão Velha, Porteiras, and Jardim, all in Ceará state.

GEOLOGICAL SETTING

The Araripe Basin is a Cretaceous sedimentary unit deposited during the opening of the South Atlantic Ocean, and is associated with lacustrine and transitional marine sediments (Valença et al., 2003; Fara et al., 2005). Since the first fossil discoveries, there were different interpretations of the stratigraphy of the region (Small, 1913; Ponte and Appi, 1990; Martill and Wilby, 1993; Neumann and Cabrera, 1999; Martill, 2007). The temporal range of the basin is also controversial. Some estimate the shales to be Aptian (Brito, 1984; Wellnhofer 1985, 1991), while others consider them to be Aptian–Albian (Arai et al., 2000), Albian (Campos and Wenz, 1982; Berthou, 1990), possibly Cenomanian (Martill and Wilby, 1993), or Turonian (Beurlen, 1962). These different estimates of the temporal range of the basin vary on the order of 30 myr (Martill, 2007). This situation makes for very controversial dating and a time chart must be followed in order to precisely identify each fossil found. In this study we followed the stratigraphy of Valença et al. (2003), regarding the time and nomenclatural questions of the basin.

The Romualdo Formation is composed of interbedded shales, marls, and limestones with abundant concretions containing fossils (Valença et al., 2003), especially fish and reptile bones, such as crocodylomorphs (Price, 1959; Maisey, 1991; Riff et al., 2010), as well as turtles (Hirayama, 1998; Oliveira and Romano, 2007), pterosaurs (e.g., Kellner and Tomida, 2000; Kellner and Campos, 2002), and a few dinosaurs (e.g., Kellner and Campos, 2000). Many invertebrates, microfossils (Coimbra et al., 2002), gymnosperms, and a few angiosperms have been identified (Carvalho and Santos, 2005), as well as occurrences of amber (Valença et al., 2003). The lower section of these limestones provides evidence for a short marine transgression. Later in the Albian, the area experienced a more important and somewhat longer-lasting marine invasion, recorded by additional

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marine deposits. This sequence is interpreted as a gulf cycle lake, a part of a system caused by the separation of South America from Africa (Valença et al., 2003).

MATERIAL AND METHODS

Early diagenetic carbonate concretions were collected from the Romualdo Formation during 2005 (17 August–15 September) by systematically quarrying a surface of 5 m² at the Sítio Romualdo (Fig. 1) between the towns of Barbalha and Crato (Ceará State, Brazil; UTM latitude 0420675, longitude 9206178). The surface was divided into 1 m² quadrats and quarried from the top to the base of the layer. We recorded the length, width, depth, and orientation of the concretions, as well as their coordinates in the sampling space. With the objective of analyzing the horizontal distribution of fossils and concretions within the excavation, each fossil was associated with a quadrat, in order to determine the spatial distribution of fossils through each layer. For this work, the methodology of Saraiva et al. (2007) was used for determination of the concretion characteristics, and Fara et al. (2005) for the nomenclature of the sedimentary layers (the names were based on the local informal nomenclature). The pterosaur specimen is housed in the paleovertebrate collection of the Museu Nacional-UFRJ (Universidade Federal de Rio de Janeiro), under the registry number MN 7060-V.

RESULTS

In this excavation we removed 12.32 m³ of sediment and found 202 concretions, 173 of them bearing fossils. Most specimens were fish, but some also comprised a few coprolites and one concretion with pterosaur remains. This is the first evidence of such reptiles since the controlled excavation program began and was found in the laminated shale of the informally named Post-Lajeta layer (layers were established by Fara et al., 2005).

The controlled excavation was divided into several layers, reaching 248 cm deep on the bottom (Fig. 2). Among these layers, there were seven mortality levels, with an increase in the number of fossils toward the top, as previously noted (Fara et al., 2005). Despite being found in a fossiliferous layer, the concretion with the pterosaur remains was not found in one of these mortality levels (Fig. 3).

In order to understand the fossil diversity of this locality we here describe the fossiliferous horizons from the bottom to the top. These layers showed the same characteristics and divisions as proposed by Fara et al. (2005) and give more support to their utilization in controlled excavations. One compaction bias was observed. The upper levels showed a majority of tridimensional fossils, while the lower layers were dominated by concretions bearing compacted individuals.

The basalmost layer consists of a finely laminated, beige shale (248–232 cm; Fig. 2). It corresponds to the base of a previously excavated site called Parque dos Pterossauros close to Santana do Cariri city (see Fara et al., 2005 for a review). This layer includes only three *Cladocyclus* sp. fish, representing 2% of the nodules with macrofossils (Fig. 4).

The Pre-Lajeta layer is composed of a dark-gray shale (208–199 cm) and exhibits three *Tharrias* sp., two *Calamopleurus cylindricus* Agassiz 1841, two indeterminate fish, and two coprolites. This layer represents 5% of the excavated concretions. Above these, the Lajeta level is a clayey limestone (199–191 cm), which does not show calcareous concretions; however, it does contain two-dimensional fish fossils preserved in laminae as noted by previous authors (e.g., Maisey, 1991; Wenz et al., 1993; Maisey et al., 1999; Kellner and Tomida, 2000; Fara et al., 2005).

Continuing up the sequence, the pterosaur concretion was found in the Post-Lajeta layer, which is a typical concretion-bearing gray shale (191–152 cm; Fig. 2); concretion classification is discussed by Saraiva et



FIGURE 1—Geographic position of the sampling site (Sítio Romualdo) in the Araripe Basin, northeast Brazil. * = site of controlled excavations over the last eight years.

al. (2007). This level also included two specimens of *Vinctifer* sp., four of *Rhacolepis bucalis* Agassiz 1841, one *Tharrias* sp., two *Calamopleurus cylindricus*, and two coprolites, comprising 9% of the fossil finds in the excavation. At the top of the sequence, the Ovos de Peixe layer (between 115–40 cm) comprises 83% of all the concretions found (total for this layer = 144). Here we found 65 specimens of *Vinctifer comptoni*, 34 *R. bucalis*, 11 *Tharrias* sp., one *Calamopleurus cylindricus*, and 15 indeterminate fish fragments. *Rhacolepis* and *Vinctifer* were the most common vertebrate fossils in this layer, as found in previous excavations (Fara et al., 2005). It is important to note, however, that within a distance of 100 m from this excavation, another shows the same proportion of fossils as presented here, except for the absence of flying reptiles.

The pterosaur specimen includes the left wing metacarpal (mcIV = 137 mm) and the first phalanx of the wing digit (ph1d4 = 251 mm). The preserved bones show the proportional length of the first wing phalanx less than twice the length of the wing metacarpal (ph1d4/mcIV = 1.83), a common feature of the Pterodactyloidea (*sensu* Wang et al., 2008). The wing metacarpal is nearly complete, with the dorsal part of the distal articulation broken during the collecting process (Fig. 5). The cranial face of the proximal articulation is very smooth, ending with a tuberculum in its medial portion; laterally it presents two different-sized, weakly convex, articular crested surfaces. The larger one is located in the ventral part, and the smaller, in the dorsal portion. In caudal view the proximal articulation is very rugged. The distal portion of the mcIV is composed only of the ventral articular condyle which is of nearly constant radius and extends onto the anterior surface of mcIV in the form of a tubercle. It is rounded at the end in anterior view, but anteriorly it is restricted to the dorsal surface of the tubercle. Close to it (in caudal view), where a foramen is seen in many pterodactyloids (e.g., *Pteranodon longiceps*, *Anhanguera piscator*, and *A. arariensis*; see Bennett, 2001 for a review), there is a depression never observed before in the Araripe pterosaurs. There is a small groove in cranio-caudal view, near the distal articulation, similar to what is seen in *A. piscator*. Neither muscular insertion nor ligament attachment was observed in any views of this bone; however, the absence of such structures could be due to the preparation process, which could have damaged the most external bone surface in the specific places where those structures usually are found.

The first phalanx of the fourth digit is complete in length (Fig. 6), although the bone surface was broken away in several parts during the preparation. The cortical bone is very thin and is generally thinner along the dorsal margin and thicker on the cranial, caudal, and ventral edges, with the most external surface smooth. Part of the ventral portion of the proximal extremity, which articulates with the wing metacarpal, was broken during the collection process. Despite the absence of the extensor tendon process, there are no structures or marks which indicate the fusion of this process with the phalanx. No visible foramen or depression can be seen in any view, as is usual for other pterosaurs (Bennett, 2001). The distal end of the bone is curved

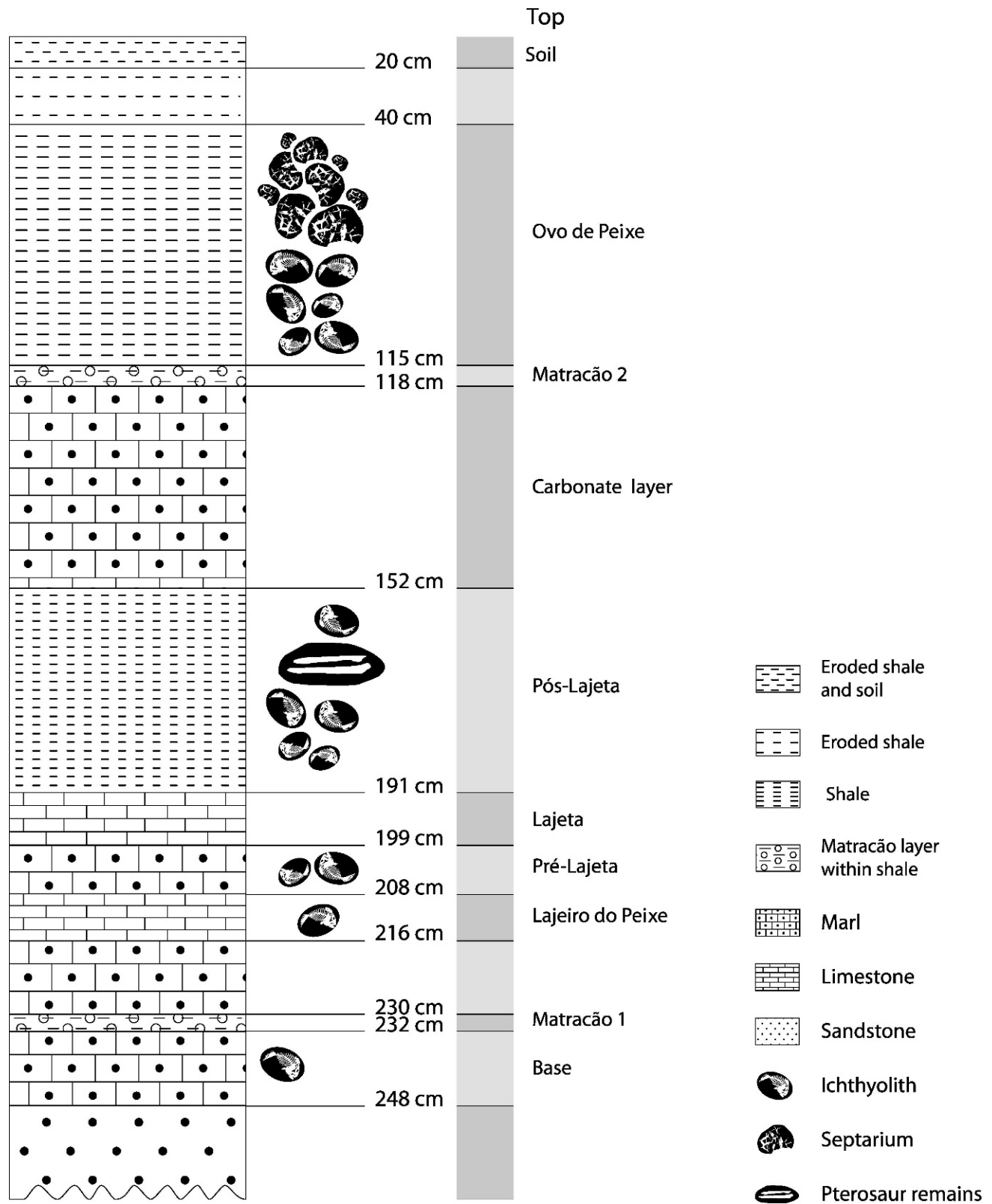


FIGURE 2—Stratigraphic scheme of the controlled excavation at Sitio Romualdo.

backwards. This region has a rugose surface showing the same pattern observed in the proximal region of the wing metacarpal. This type of pattern indicates the insertion of tendons or muscles that connected this bone to the subsequent wing phalanx (see Kellner and Tomida, 2000 for

a review). Also, the absence of the extensor tendon process indicates that this specimen was not ontogenetically mature, as was proposed previously (Wellnhofer et al., 1983; Bennett, 1993; Sayão and Kellner, 1998; Kellner and Tomida, 2000; Sayão, 2003).

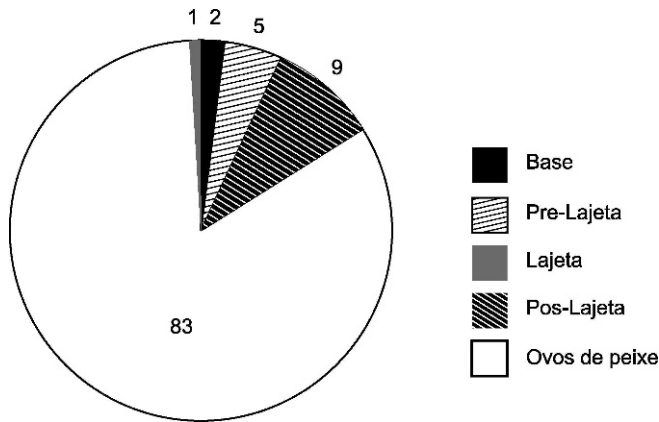


FIGURE 3—Percentages of concretions bearing fossils from the excavated layers.

DISCUSSION

As found in previous excavations (Fara et al., 2005) the most common vertebrate fossils in these layers are the fish *Rhacolepis* and *Vinctifer*. Our results do not agree with the relative abundance categories proposed by Maisey (1991), suggesting that previous sampling of fossils from the Araripe may have been biased. Nevertheless, the current excavation presents some notable differences from earlier ones. While the previous excavation carried out in the Parque dos Pterossauros site showed many fossils in the Lajeiro do Peixe, Pre-Lajeta, Lajeta, and Post-Lajeta layers, during our collections in 2005 only a few fossils were found. We did not find any concretion bearing identifiable fossils in the Lajeiro do Peixe layer, which has previously been the source of many fossils (Fara et al., 2005; Saraiva et al., 2007). This may be an indication that even with controlled excavations, the fossil assemblage of the Araripe is not homogeneous and within a relatively small area, excavations can have very different results. Different authors have addressed the basin environment during its deposition (e.g., Martill, 1988; Valença et al., 2003; Assine, 2007) and despite many opinions, all agree that the basin had different environmental conditions along its borders.

The different distributions of numbers of fossils in the layers of the Romualdo Formation presented here and by Fara et al. (2005) are another indication that, while a part of the basin suffered an event of mass mortality (therefore resulting in a large assemblage of fossils in that area), other parts of the basin did not experience this event. Our results agree with previous descriptions of the succession of fish assemblages in that *Tharrhias* is dominant in the basal level, followed by a mix of *Tharrhias* and *Cladocyclus* in the Post-Lajeta, while *Vinctifer* is dominant in the uppermost Ovos de Peixe layer (Fara et al., 2005). This last horizon in the present excavation, however, differs in content from

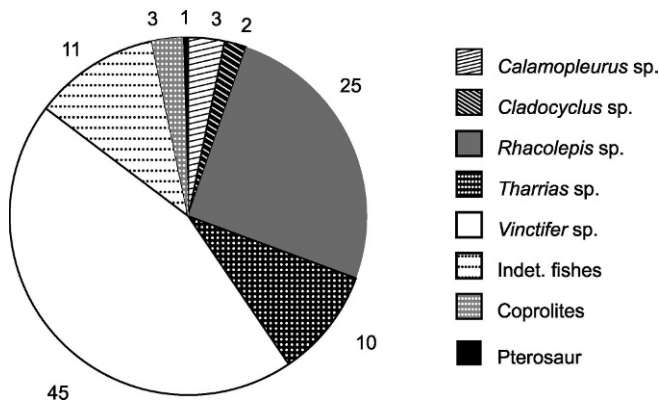


FIGURE 4—Distribution of different species of fossils found.



FIGURE 5—Wing metacarpal of pterosaur MN 7060-V. A) Cranial view. B) Caudal view.

previous collections. According to Fara et al. (2005) this layer is dominated by *Vinctifer* and does not include *Rhacolepis*; while Maisey (1991) noted the latter genus as dominant in the same layer. We observed a combination of both genera, with most *Vinctifer* specimens occurring together with *Rhacolepis* (the second most abundant taxa). Our data support the hypothesis of a faunal succession in the paleolagoon of the Araripe. The fact that these assemblage changes are present at different sites within the basin confirms that faunal replacement happened at different times throughout the basin. These replacement events originated the mass mortality effects cited in the literature (Martill, 1988; Maisey, 1991; Fara et al., 2005).

The number of tetrapods in this excavation was very low, with only the pterosaur MN 7060-V found. Our results add to the growing body of evidence from previous controlled excavations (e.g., Fara et al., 2005; Saraiva et al., 2007) showing that fossils of tetrapods were not common in the basin when compared with the abundance of fish.

Among the pterosaurs of the Araripe Basin, the material presented here shows the three-dimensional preservation for which the Santana fossils are famous (Wellnhofer, 1991; 2008). Due to this great preservation—showing a degree of articulation—a taphonomic bias for the present excavation site is rejected. It is likely that previous collections suffered from collection bias, because most fossils were collected by local non-professionals who focused on larger bones. Current knowledge of Araripe fossil biotas is largely based on museum specimens with no locality data, and on sporadic, limited field observations (Fara et al., 2005). Sites with more tetrapod fossils were extensively dug, instead of others with fewer fossils. The idea that only a limited number of concretions yield the well-preserved vertebrate remains that have made the Santana Group famous (Fara et al., 2005) can also now be applied to pterosaur diversity, as our results contradict previous suggestions of a great abundance of pterosaurs (Martill, 2007).



FIGURE 6—First phalanx of the wing digit of pterosaur MN 7060-V. A) Ventral view. B) Dorsal view. C) Cranial view showing the bone curvature. See text for further explanation.

This collection bias could be one of the explanations for the great number of flying reptiles deposited in institutions all over the world. Our results, along with other controlled excavations, suggest a limited pterosaur fauna within the Lower Cretaceous Araripe Basin (at least in the Romualdo Formation) and enforce the idea that there is not one Romualdo assemblage but rather several of them (Fara et al., 2005). Since there are no other pterosaur remains from other controlled excavations, however, it is impossible to make more inferences regarding the Romualdo assemblages. To confirm this idea more fieldwork is needed, which will bring precise control of not only geographic sampling, but also stratigraphic information. After that occurs, it may be possible to confirm if the fossils of these animals are spread throughout the basin, or clustered in a few specific locations.

Unlike fish, which are restrained in their environment, pterosaurs have a greater capacity to occupy different habitats, and therefore cannot be used to develop environmental interpretations, so a more ecological approach is necessary in order to understand their distribution at the basin.

Regarding pterosaur material, the metacarpal of MN 7060-V is very similar to *Anhanguera piscator* Kellner and Tomida, 2000. The latter species, however, shows a foramen on the cranial face (Kellner and Tomida, 2000) like some of the Romualdo Formation pterosaurs, such as *Santanadactylus pricei* Wellnhofer, 1985 and *Anhanguera araripensis* Wellnhofer, 1985. We did not find any visible foramen in MN 7060-V. The use of such a feature in systematics is not conventional and it is unclear if it has phylogenetic significance, despite such variation.

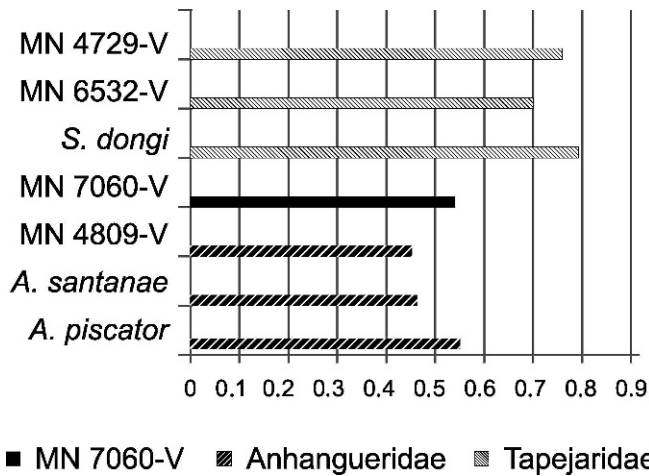


FIGURE 7—Comparison of the metacarpal IV to first wing phalanx bone ratio in MN 7060-V and other pterosaur taxa. See text for further explanation.

MN 7060-V shows a short wing metacarpal compared to the first wing phalanx. Among the two major groups of pterosaurs from the Araripe Basin, there is a trend toward identification using wing-bone ratios. This feature has been used commonly in previous pterosaur phylogenies (Kellner, 2003; Andres and Ji, 2008; Wang et al., 2008, 2009; Lü et al., 2010). MN 7060-V has an mcIV/ph1d4 ratio of 0.54. Compared with all known anhanguerid specimens that have the wing metacarpal and first wing phalanx preserved (*A. piscator*, *A. santanae* Wellnhofer, 1985, and an undescribed anhanguerid, MN 4809-V), they all exhibit a ratio of <0.6 (Fig. 7). In three tapejarid specimens analyzed (*Sinopterus dongi* Wang and Zhou, 2003; MN 6532-V; and MN 4729-V), the wing metacarpal is long and the ratio is >0.6. Even though the systematic value of this feature has not been supported using a phylogenetic approach, it has a diagnostic potential. Therefore, MN 7060-V can be associated with the Anhangueridae.

The depression seen in the caudal view close to the distal articulation of the wing metacarpal may be of ontogenetic origin, since it was not observed previously in pterosaurs of the Araripe region. The known wing phalanges of the Romualdo Formation pterosaurs show little variation among specimens (Veldmeijer et al., 2009), except relative size, making it difficult to individualize the one from MN 7060-V. The preserved rugose exterior of the wing phalanx may be evidence of cartilage, which, along with the absence of the extensor tendon process, indicates a juvenile to subadult individual (Kellner and Tomida, 2000).

The high number of specimens collected in our excavation contrasts with the potential expected diversity. Currently 25 pterosaur taxa are known for the Santana Group, of which six belong to the Crato Formation and 19 to the Romualdo (Barrett et al., 2008; Witton, 2008). With the exception of *Brasileodactylus*, which appears in both stratigraphic units (Sayão and Kellner, 2000), the pterosaur fauna differs between the two formations. In the lower Crato Formation, taxa are divided equally in two clades: the Anhangueridae and Tapejaridae (see Barrett et al., 2008 for a review). Higher in the Romualdo Formation there are 15 taxa belonging to Anhangueridae versus four from the Tapejaridae (see Rodrigues and Kellner, 2008 for a systematic discussion of the validity of *Anhanguera* clade). This scenario shows that anhanguerids are the best-represented pterosaur clade in the basin. Therefore, we expected that most of the new specimens would belong to this clade. Better stratigraphic control is necessary in order to clarify how this change in local pterosaur diversity might have occurred.

CONCLUSIONS

Our results show that the stratigraphic distribution of fossil populations (Fara et al., 2005) and the known geographic variations

(Maisey, 1991) are insufficient to illustrate the complex biota of the Romualdo Formation. The fish faunal succession proposed by Fara et al. (2005) was confirmed here, with the addition of a new local variation for the Ovos de Peixe layer.

We present the first discovery of a pterosaur in a controlled excavation in the Araripe Basin. Since such excavations began eight years ago, with fieldwork already completed at five different sites, our results seem to indicate that these fossils are not as common as was previously assumed (Martill, 2007) and that previous accounts of the taxonomic composition and relative abundance of pterosaur fossils from the Romualdo Formation were biased. While the Crato and Romualdo Formations have a similar pterosaur fauna (Kellner and Tomida, 2000; Sayão and Kellner, 2000; Unwin and Martill, 2007), some differences can be observed. Tapejarids make up >33% of all identifiable pterosaur remains in the Crato Formation (Unwin and Martill, 2007), but are rarer in the younger Romualdo Formation. Anhanguerids represent the majority of the Romualdo pterosaurs (Kellner and Tomida, 2000; Barrett et al., 2008), with only a few being published from the laminate limestone of the basal Crato Formation.

These controlled excavations showed a pattern that, if observed in subsequent excavations, will confirm that the pterosaur assemblages from the Romualdo Formation form clusters. The supposed abundance of pterosaurs has been probably biased by a few places of fossil localities, and pterosaur distribution might not have been as widespread in the basin as previously thought. More excavations could confirm this scenario and shed much-needed light on this important Fossil Lagerstätte.

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