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Controlled excavations in the Romualdo Member of the Santana Formation (Early Cretaceous, Araripe Basin, northeastern Brazil): stratigraphic, palaeoenvironmental and palaeoecological implications

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Abstract

The Romualdo Member of the Santana Formation (Araripe Basin, northeastern Brazil) is famous for the abundance and the exceptional preservation of the fossils found in its early diagenetic carbonate concretions. However, a vast majority of these Early Cretaceous fossils lack precise geographical and stratigraphic data. The absence of such contextual proxies hinders our understanding of the apparent variations in faunal composition and abundance patterns across the Araripe Basin.

We conducted controlled excavations in the Romualdo Member in order to provide a detailed account of its main stratigraphic, sedimentological and palaeontological features near Santana do Cariri, Ceará State.

We provide the first fine-scale stratigraphic sequence ever established for the Romualdo Member and we distinguish at least seven concretion-bearing horizons. Notably, a 60-cm-thick group of layers ("Matracão"), located in the middle part of the member, is virtually barren of fossiliferous concretions.

Moreover, a sample of 233 concretions shows that (i) the stratigraphic distribution of the concretions is very heterogeneous and their density varies from 0.8 to 15 concretions/m^3; (ii) concretions have a preferential, bimodal orientation pattern (major NW–SE axis and secondary ≈N–S axis) throughout the section, suggestive of permanent palaeocurrents of low energy; (iii) few concretions yield the well-preserved vertebrates that have made the Romualdo Member so famous, and those are mainly restricted to four stratigraphic horizons; (iv) only six fish taxa were recovered, the most common being *Vinctifer* and *Tharrhias*, followed by *Cladocyclus*, whereas *Brannerion*, *Calamopleurus* (=*Enneles*) and *Notelops* are rare. No tetrapod was found in the sample; (v) there is a strong stratigraphic control in the distribution of these taxa and one can distinguish at least three major

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assemblages at the same locus. These are, from older to younger, a *Tharrhias*-dominated assemblage, an assemblage dominated by *Tharrhias* and by *Cladocyclus*, and a *Vinctifer*-dominated assemblage. The stratigraphic sequence of these assemblages also corresponds to their ranking in terms of diversity (richness and evenness); (vi) previous accounts on the taxonomic composition and relative abundance of fossils from the Romualdo Member were severely biased toward well-preserved and exotic fossils. They are therefore inappropriate for drawing palaeoecological inferences.

The factors responsible for the variations in faunal composition and abundance patterns across the Araripe Basin remain largely unknown, and we hypothesize that climate and/or palaeogeography might be the major forcing agents. Only fine-scale stratigraphic and palaeontological investigations have the potential to solve this issue. In turn, this work marks the first step of an expanded research program that aims at explaining the spatio-temporal relationships between palaeocommunities and their palaeoenvironment in the Araripe Basin during Aptian/Albian times.

1. Introduction

Fossil–Lagerstätten are extraordinary fossil sites that provide a wealth of information about past biotas. The Romualdo Member of the Santana Formation, in northeastern Brazil, is one of these 'geological miracles' (Davis, 1992). This Aptian/Albian unit, located in the Araripe Basin, is famous because the fossils found in its early diagenetic carbonate concretions have three remarkable characteristics. First, they are highly abundant. They occur continuously along the flanks of a large sedimentary structure, the Chapada do Araripe (Araripe Plateau). Second, they represent an exceptionally diverse fossil biota, with at least seventy species of plants, vertebrates and invertebrates (e.g., Maisey, 1991, 2000; Martill, 1993). The ichthyofauna alone is composed of over nineteen genera belonging to various families (Wenz et al., 1993, Maisey, 2000). Third, the fossils from the Romualdo Member are exceptionally well preserved. Many specimens are fully articulated, and 3-D preservation is common. The most spectacular feature is certainly the high-fidelity preservation of phosphatized soft tissues in both invertebrates and vertebrates (Martill, 1988, 1989, 1990, 2001; Kellner, 1996; Kellner and Campos, 1998; Smith, 1999).

The first scientific studies on the Romualdo Fossil–Lagerstätten were initiated in the 19th century (Gardner, 1841; Agassiz, 1841, 1844; Woodward, 1887), and research has remained intense since then. In particular, and beside innumerable taxonomic descriptions, some authors have noticed significant lithological and palaeontological variations among Araripe's concretions (e.g., Jordan and Branner, 1908; Maisey, 1991, 2000). In fact, each type of concretion lithology seems to yield fossils representing a particular assemblage in terms of taxonomic composition, abundance and size distribution. This apparent correlation might be due to a marked palaeoenvironmental heterogeneity across the basin in Early Cretaceous times. Two key factors seem to be involved: geography and stratigraphy. Geographically, Maisey (1991) distinguished three qualitative lithological types and fossil assemblages with reference to the three principal collecting areas in the Araripe region: Santana do Cariri, Jardim and Missão Velha (Old Mission). The stratigraphic factor is poorly known, but there is apparently more than one layer containing the fossil-bearing concretions (Maisey, 1991, 2000; Martill, 1993).

The fossiliferous concretions from the Romualdo Member undoubtedly offer a unique opportunity to investigate the spatio-temporal structure of past communities at the local and regional scales. However, this enterprise is hindered by a perennial problem affecting a vast majority of Araripe fossils: the absence of precise geographical and stratigraphic data (e.g., Agassiz, 1844; Mabesoone and Tinoco, 1973; Wenz and Brito, 1990; Maisey, 1991; Viana, 2001). Current knowledge on Araripe fossil biotas is largely based on museum specimens with no locality data and on sporadic, limited field observations. Although this unsatisfactory situation does not hamper most systematic and palaeobiological studies (see Leal and Brito, 2004; Buffetaut et al., 2004, for recent

examples), it is a major issue for palaeoecological inferences.

This work is the first 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 spatio-temporal heterogeneity of the fossil assemblages across the basin in relation to palaeoenvironmental proxies.

What are the relative abundances of the various taxa at each site and across the Araripe Basin? Are the lithology and the fossil content of the concretions actually related to geography and/or stratigraphy? What is the nature and the scale of this relation? Does this pattern reflect actual differences in palaeocommunity structure? And how many concretions should be sampled in order to obtain a palaeontologically representative sample?

Here we address some of these issues by presenting the results of controlled excavations in the concretion-bearing shales of the Romualdo Member. We provide a detailed account of the main stratigraphic, sedimentological and palaeontological features observed in one of the three major collecting areas in the Araripe Basin: Santana do Cariri.

2. Geographical and geological setting

The Araripe Basin is a sedimentary structure located in northeastern Brazil. This intracratonic basin contains sediments ranging in age from the Late Jurassic to the earliest Late Cretaceous and its history is closely linked to the opening of the South Atlantic Ocean (Brito-Neves, 1990; Berthou, 1990; Mabesoone, 1994). The Aptian–Albian fluvial, lacustrine and transitional marine sediments (Crato, Ipubi and Santana Formations) were deposited during a post-rift period characterized by a slow subsidence (Ponte and Ponte Filho, 1996; Ponte et al., 2001; Neumann et al., 2003). The stratigraphy of the Araripe Basin and its associated nomenclature have been debated since the pioneering work of Small (1913). Good reviews and recent proposals can be found in Brito (1990), Maisey (1991), Assine (1992), Martill and Wilby (1993), Ponte et al. (2001), Medeiros et al. (2001) and Coimbra et al. (2002). By focusing on the concretion-bearing shales only, the present study is little affected by nomenclatural disputes because this level has commonly be referred to as the Romualdo Member of the Santana Formation (e.g., Beurlen, 1971; Martill and Wilby, 1993).

We conducted excavations on the northern side of the Chapada do Araripe, near the town of Santana do Cariri, southern Ceará State (Fig. 1). The locality (07°11′ 32″S; 39°42′ 52″W) is property of the Universidade Regional do Cariri—URCA, and it is locally known as "Monte Axelrod" or "Parque dos Pterossauros." We adopt hereafter this latter local toponym.

3. Methods

Concretions from the Romualdo Member were collected by systematically quarrying a surface of

Fig. 1. Geographic position of the sampling site (Parque dos Pterossauros) in the Araripe Basin, northeastern Brazil.

21 m^2 at Parque dos Pterossauros. This surface was divided into 1 m^2 quadrats and was quarried until the base of the member. The length, width and orientation of the concretions were recorded, as well as their coordinates in the sampling space. The position of the concretions in the stratigraphic column was measured at their uppermost point. In a second time, the content of the concretions was examined after they were carefully split into two or more parts. When possible, fossils occurring directly within the surrounding laminated shales were also collected.

Statistical tests on orientation data were performed using Oriana version 2.0 ©. Circular–linear correlation coefficients and their associated probabilities were computed as described by Fisher (1993) and Mardia and Jupp (2000).

We also checked for sampling quality. Basically, as more individuals are sampled, more taxa will be recorded. This is expressed graphically by an individual-based taxon accumulation curve (sensu Gotelli and Colwell, 2001) that rises quickly at first, and then much more slowly as increasingly rare taxa are found. Eventually, the curve reaches an asymptote when the sampling space has been fully explored. To eliminate the influence of the order in which individuals are added to the total, the input order can be randomized many times. The result is a 'smoothed' taxon accumulation curve that is equivalent to a rarefaction curve (Gotelli and Colwell, 2001). We used the program PAST 1.29 (Hammer et al., 2001; Hammer and Harper, 2004) to generate such taxon accumulation curves. This software was also used to calculate and compare diversity indices. Among the latter (reviewed in Magurran, 1988; Krebs, 1989; Hayek and Buzas, 1997), we selected the Shannon index, the Simpson index (referred to as 'dominance' in PAST), the Berger–Parker index and the Fisher's α for two reasons: (i) their sensitivity to sample size is low to moderate; (ii) they illustrate different aspects of diversity, such as richness and evenness (Magurran, 1988). Moreover, we used the randomization procedures implemented in PAST (bootstrapping and permutation of abundance data) for assessing the probability that two assemblages have similar diversity indices.

4. Results

4.1. Stratigraphic section

The Romualdo Member is made of laminated, green to grey (occasionally orange or beige) laminated shales containing numerous carbonate concretions. Although Martill and Wilby (1993) acknowledged that the boundaries of this stratigraphic unit are difficult to define, they proposed a new definition of the Romualdo Member based on a type locality located near the town of Abaiara, at the northeastern tip of the Chapada do Araripe. In contrast to the wider definition of Beurlen (1971), these authors consider the first rounded concretions (above relatively barren clays and shales) to mark the base of the member and the large septarian concretions to indicate its upper boundary. Both these stratigraphic limits are present at Parque dos Pterossauros, and the Romualdo Member (sensu Martill and Wilby, 1993) is about 2.5 m thick at this location. Although this is a low value in the known range of thickness for this unit (see Discussion), all the informal levels recognised in the region by experienced collectors are represented.

Fig. 2 summarises the stratigraphy of the section. The first level, hereafter referred to as the "Base," contains rare concretions in its lower part. The shales are finely laminated, beige in colour and rich in coproliths.

The Base is overlaid by a more or less continuous, 5 to 10 cm thick, clay-rich limestone layer locally named "Lageiro do Peixe." Fossiliferous concretions are embedded (but well individualized) on the lower and upper surfaces of this layer. About 15 cm above the Lageiro stands another, more or less continuous, clayey–limestone level called "Lageta." This layer is only 1.5 to 3 cm thick and it is rich in ostracods. It is framed by two levels of typical concretion-bearing, green/grey shales that we refer to as the Pre-Lageta and Post-Lageta units (the latter being nearly four times thicker than the former).

The Post-Lageta unit is overlaid by a very peculiar, tripartite level called "Matracão." This unit is formed by a 18-cm-thick, concretion-free level surrounded by two layers (locally referred to as Matracão 1 and Matracão 2) that contain few concretions. These concretions are very hard, compact, often grey to dark grey in their centre and rarely fossiliferous.
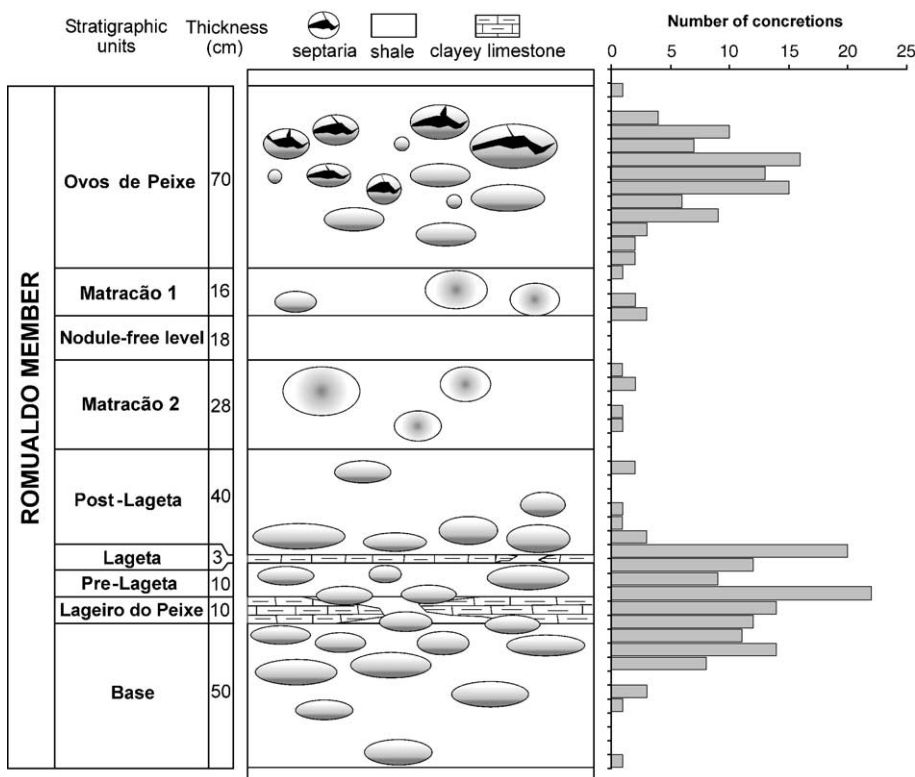
Fig. 2. Stratigraphy and concretion distribution in the Romualdo Member at Parque dos Pterossauros. The histogram gives the number of concretions for each 5-cm interval along the section. The levels 'Matracão 1,' 'Nodule-free level' and 'Matracão 2' altogether form what is referred to as 'Matracão' in the text.

The top level of the Romualdo Member contains numerous septarian concretions, especially in its upper part. These septaria occasionally contain fossil remains (the aspidorhynchid fish *Vinctifer* sp., coproliths). Nut-sized, weathered concretions are also common and seem to have developed around coproliths. Local workers designate this 70-to-100-cm-thick unit as "Ovos de Peixe" (literally "fish eggs"), and we regard the highest concretions to mark its upper limit. It is followed by about 1 m of concretion-free, weathered shales and clays that form the soil at Parque dos Pterossauros.

Most concretions in our sample contain ostracods and their lithology corresponds to what Maisey (1991) defined as the "Santana concretion" type (i.e., poorly laminated limestone matrix, granular in appearance, pale cream or beige in colour and with a very low clay content). The only exceptions are the hard and dark concretions from the Matracão horizons.

As noted by previous authors (e.g., Maisey, 1991; Wenz et al., 1993; Maisey et al., 1999; Kellner and Tomida, 2000), fossils are not found only in carbonate concretions but also in the surrounding shales. We found few, complete or partial, articulated skeletons of small and medium-sized indeterminate fish, as well as some rare plant fragments (cf. *Brachyphyllum* sp.) and numerous coproliths in the shales from the Base and from the lower part of the Ovos de Peixe horizon. Note that these fish remains represent distinct individuals that are not the mere continuation of specimens preserved in nearby carbonate concretions (a situation sometimes observed for fossils of *Vinctifer*; Wenz et al., 1993).

4.2. Concretion distribution

We collected a total of 233 concretions from the 53 m³ of shales quarried at Parque dos Pterossauros, that

is, the estimated mean density is 4.4 concretions/m^3 in the Romualdo Member (sensu Martill and Wilby, 1993). However, the stratigraphic distribution of the concretions is in fact very heterogeneous. Concretion density varies from 0.8 concretion/m^3 in the Matracão to 15 concretions/m^3 in the Pre-Lageta unit. Globally, concretion distribution is bimodal through the section (Fig. 2). Most concretions occur in the middle part of the Ovos de Peixe unit and in the layers comprised between the top of the Base and the lower part of the Post-Lageta horizon. Concretion density is particularly high at the Lageiro do Peixe/Pre-Lageta interface, whereas it is very low from the upper part of the Post-Lageta to the base of the Ovos de Peixe.

Also, we tested the spatial distribution of the concretions for homogeneity by applying a χ^2 test. For the entire section, the number of concretions were summed over 3 consecutive quadrats in order to obtain samples of at least 5. The test cannot distinguish the spatial distribution of the concretions from a homogeneous pattern throughout the section (χ^2=9.476, df=6, p=0.148).

4.3. Concretion size and shape

We investigated the morphological characteristics of the concretions in relation to their stratigraphic position. Beside lithology, the overall morphology of the concretions places them also into Maisey's (1991) "Santana" category: circular to ovoid in outline, elongated parallel to the long axis of the fossil and mostly 25–30 cm in length. There is no apparent relationship between the length of the concretions (L) and their position in the section (Fig. 3A). The only feature suggested by our sample is that the 29 concretions occurring from the upper part of the Post-Lageta unit to the base of the 'Ovos de Peixe' unit do not reach 30 cm in length. This is in agreement with the empirical recognition by local workers of a "small-concretion level" in the upper part of the Post-Lageta Unit. It must be noted, however, that our sample is certainly biased against concretions smaller than 5 cm. Indeed, these small-sized, usually weathered and barren nodules are difficult to recover in the field for practical reasons.
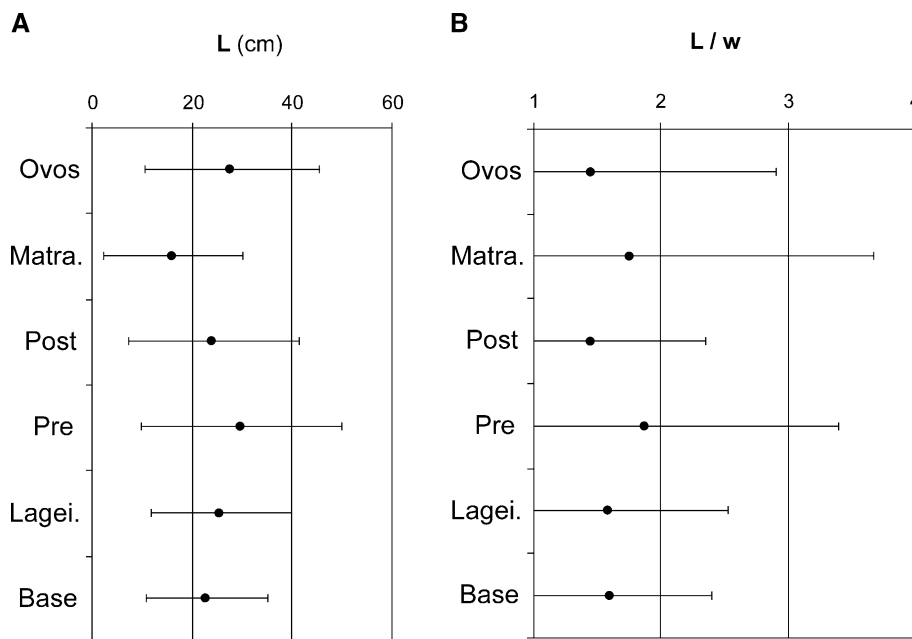

Fig. 3. (A) No relation between the length of the concretions (L) and their stratigraphic position. (B) The overall shape of the concretions, estimated by the length to width ratio (L/w), does not vary significantly across the levels of the Romualdo Member at Parque dos Pterossauros. Error bars represent 95% confidence intervals. Abbreviations are Ovos—Ovos de Peixe; Matra.—Matracão; Post—Post-Lageta; Pre—Pre-Lageta; Lagei.—Lageiro.
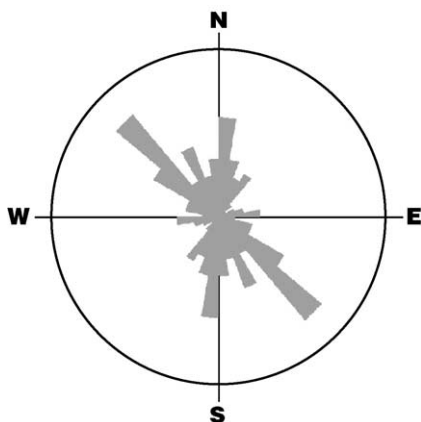
Fig. 4. Bimodal orientation pattern of the concretions sampled at Parque dos Pterossauros. The rose diagram shows the major NW–SE direction and the secondary N–S direction of the concretions ($n=104$).

The shape of the concretions, as assessed by the length to width ratio (L/w), is also homogeneous throughout the section (Fig. 3B), with an mean value of 1.55 for the entire sample. Spherical to sub-spherical concretions ($L/w \approx 1$) are abundant and they occur for all sizes and at all stratigraphic levels.

Maisey (1991, pp. 66–67) recognised twelve shape categories of concretions from the Santana Formation but their relation to stratigraphy could not be established. Some of these categories are well represented in certain levels at Parque dos Pteros-sauros. Maisey's (1991) type "a" (barren concretions, often spherical) is found preferentially in the Matra-cão, whereas type "b" (as "a," but enclosing isolated scraps or coproliths, not necessarily in centre of concretion) is more common in the Ovos de Peixe unit. Category "f" (ovoid concretions not following the shape of fossil specimen but completely enclosing it) is dominant in the Lageiro do Peixe and in the Pre-Lageta units.

Fossils generally occur centrally in the concre-tions, but coprolites or isolated fish scales are not rare in the outer layers. In our sample, four concretions contain each two individuals of the gonorhynchiform *Tharrhias*. These specimens are preserved on different bedding planes within the same composite concretion, and they illustrate Maisey's (1991) concretion category "j" (coalescent

concretions formed around fish remains deposited at different-but-close times). Maisey (1991) noted that such concretions are uncommon and are of the "Jardim" type. Our sample shows that such a pattern occurs also in typical "Santana" concretions from the Lageiro and Pre-Lageta horizons.

4.4. Concretion orientation

The orientation pattern of the concretions is bimodal for the entire sample, the dominating directions being a major NW–SE axis and a secondary $\approx$ N–S axis (Fig. 4). This is the first time such a pattern is reported for the Santana Formation. Statisti-cally, the null hypothesis that the orientation data are uniformly distributed is rejected by both the Rao's spacing test and the Ralleigh's uniformity test (see Batschelet, 1981; Mardia and Jupp, 2000) at $p<0.01$ and $p<0.001$, respectively.

We also performed a Mardia–Watson–Wheeler test (e.g., Mardia and Jupp, 2000) to determine whether the orientation pattern is related to stratig-raphy. This non-parametric test was applied in both pairwise and multisample comparisons (although the Matracão level could not be considered because its sample size for oriented concretions is smaller than 10). In all cases, the null hypothesis of identical distributions cannot be rejected (Table 1). This result is comforted at a finer scale by the absence of any significant correlation between the actual position of the concretions in the section and their orientation (circular–linear correlation coefficient $r=0.15$; $p=0.104$; $n=104$).

Because all but two fossil fishes were aligned along the long axis of the concretions containing

Table 1
Results of the Mardia–Watson–Wheeler test applied to the orientation data of the concretions

	Base	Lageiro	Pre	Post	Ovos
Base	–	**0.492**	**0.703**	**0.47**	**0.431**
Lageiro	1.419	–	**0.53**	**0.234**	**0.011**
Pre	0.705	1.27	–	**0.704**	**0.147**
Post	1.509	2.902	0.702	–	**0.357**
Ovos	1.684	9.011	3.834	2.062	–
Multisample comparison: $W=9.625$; $p=0.292$					

W test statistics given in the lower left corner of the table and p values in bold. Pre—Pre-Lageta unit; Post—Post-Lageta unit.

them, our results suggest a preferential orientation of the fish carcasses by dominating palaeocurrents before burial. The possibility that the concretions were reworked and then oriented is very unlikely because the required energy for the reworking agent is incompatible with sedimentological evidence. Indeed, the surrounding fine-grained laminated shales suggest a low-energy depositional setting, the lamination of the nodules is parallel to that of the shales, and other indices of concretion reworking (e.g., see Fürsich et al., 1992) are absent.

4.5. Concretion content

We found no correlation between the content of the concretions and their length or shape. Concretions are generally circular to ovoid in shape and they do not reflect the fossil outline. Moreover, only 10 to 15% of the specimens are complete or sub-complete skeletons, and they mostly belong to *Tharrhias araripis*. The other vertebrate fossils could not be identified at the species level, and we were thus constrained to conduct our analysis at the generic level. This is due to the incompleteness of the fossil remains and/or their poor preservation in some levels. For example, in the concretions of the Ovos de Peixe

unit, the dominant taxon *Vinctifer* is only represented by isolated scales and by non-cranial body parts covered with scales. Unfortunately, scale anatomy and microstructure cannot be used to distinguish between *V. cromptoni* and *V. longirostris* (Brito, 1997).

The overall taxonomic content of the concretions sampled at Parque dos Pterossauros is summarised Fig. 5A. Vertebrates remains identifiable at least at the generic level are found in 62% of the concretions and they represent actinopterygians only. The other concretions yield undetermined fish parts (31%), twig fragments of the gymnosperm *Brachyphyllum* sp. (0.5%) or nothing but ostracods (6%).

Among the identifiable osteichthyans, *Vinctifer* is the dominant form, followed by *Tharrhias* and *Cladocyclus* (Fig. 5B). These three genera account for 96% of the ichthyofauna at the sampling site, whereas *Notelops*, *Brannerion* and *Calamopleurus* (=*Enneles*) are rare. The absence of the elopomorph *Rhacolepis* is remarkable since this taxon is very abundant in concretions from the Jardim area, where it apparently was a crucial component of the trophic network (Maisey, 1991, 1994).

We have also explored how the taxonomic content of the concretions varies with stratigraphy. Fig. 6 shows that the content is heterogeneously
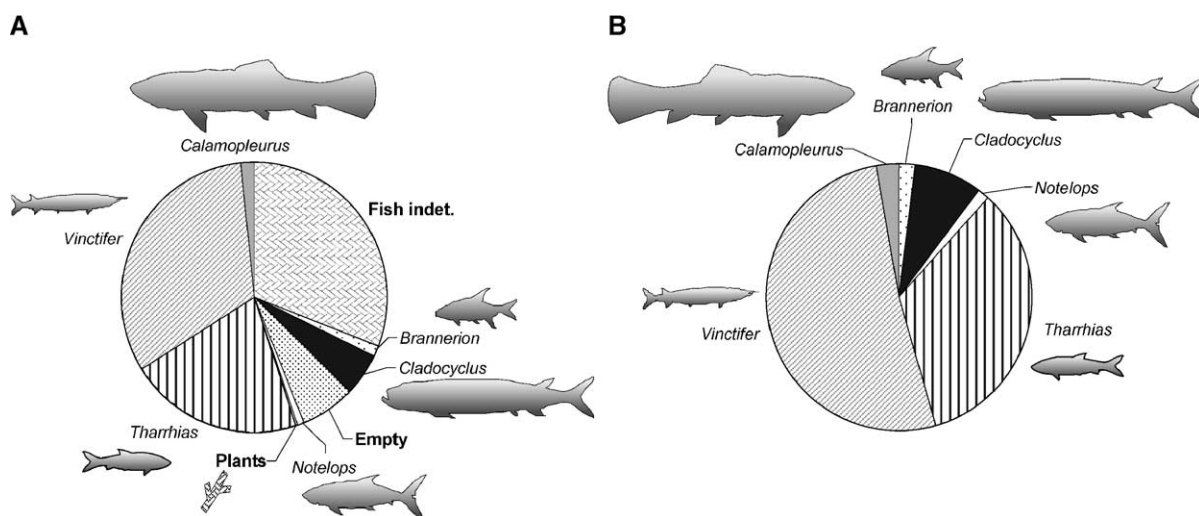

Fig. 5. Content of the concretions sampled from the Romualdo Member at Parque dos Pterossauros. (A) All concretions (*n*=233). The "empty" category refers to barren concretions containing only ostracods. (B) Concretions with generically identifiable fish remains (*n*=145).
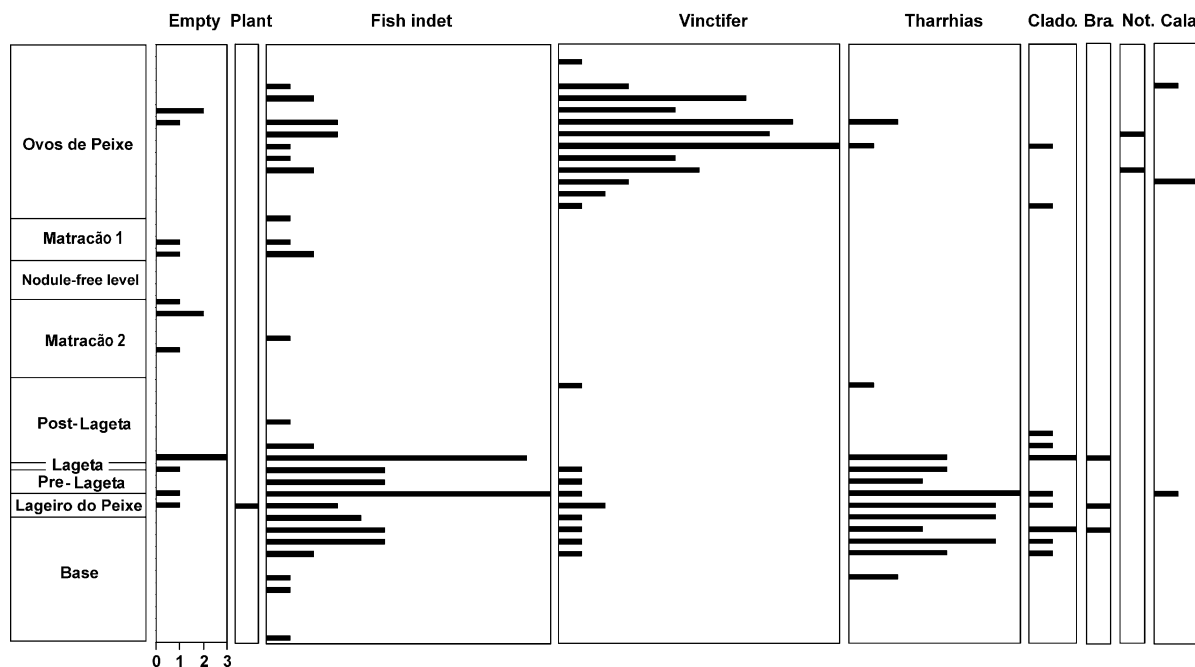
Fig. 6. Concretion content and stratigraphy. The absolute frequencies of the contents are given for each 5-cm-high interval along the section of the Romualdo Member. Abbreviations: indet.—indeterminate; Clado—*Cladocyclus*; Bra.—*Brannerion*; Not.—*Notelops*; Cala.—*Calamopleurus*.

distributed along the section. The most striking feature is the high dominance of *Vinctifer* in the Ovos de Peixe unit (74% of the concretions), whereas *Tharrhias* is the most abundant taxon from the top of the Base to the lowest part of the Post-Lageta unit (23% to 45% of the concretions). This dominance pattern is not exclusive and both taxa co-occur at various levels. Our sample further suggests that *Brannerion* is found only in *Tharrhias*-dominated levels, whereas *Notelops* seems restricted to *Vinctifer*-dominated layers (Fig. 6). The ichthyodectiform *Cladocyclus* is most abundant in the Base and in the Post-Lageta unit, where it represents about 10% of the identifiable specimens. Poorly preserved fish remains and "empty" concretions occur throughout the Romualdo Member and they represent up to half the concretions in some levels (e.g., Pre- and Post-Lageta horizons).

As a whole, one can oppose the Ovos de Peixe unit (where *Vinctifer* is commonly found) to the other levels (except the Matracão) in which concretions yield preferentially *Tharrhias*. Fig. 7 shows typical concretions illustrating this broad dichotomy. Perhaps
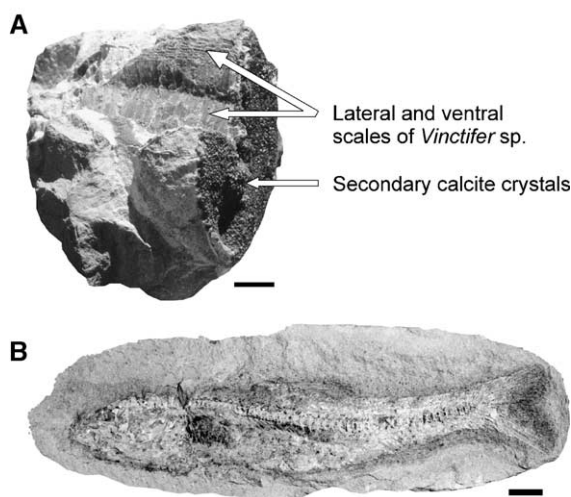

Fig. 7. Representative concretion contents found at Parque dos Pterossauros. (A) Part of a septarian, *Vinctifer*-bearing concretion typical of the Ovos de Peixe horizon. (B) Complete specimen of *Tharrhias araripis* in a concretion from the Lageiro do Peixe horizon. Scale bars represent 20 mm.

the 'sparry concretion assemblage' recognised by Maisey (2000) may coarsely correspond to the fishes from the lower levels (*Tharrhias* common and *Rhacolepis* absent or rare).

4.6. Sampling and assemblage structure

Our excavations at Parque dos Pterossauros yielded only 6 generically identifiable fish taxa while we know that the Romualdo Member has yielded at least 11 genera in concretions of the Santana type (Maisey, 1991; Wenz et al., 1993). Although these estimates of taxonomic richness are established at different scales, they suggest that our sample might not capture the full diversity of the Romualdo Member. We therefore expect each stratigraphic level of this member to have yielded only the most common taxa and that taxonomic richness will increase with further sampling. In order to test this hypothesis, we plotted randomised, individual-based taxon accumulation curves (see Methods) for each fossiliferous level. All curves are far from reaching an asymptote (Fig. 8A), meaning that sampling may indeed be insufficient. Also, the shape of such curves depends, among others, on the pattern of relative abundance among taxa sampled (Tipper, 1979; Colwell and Coddington, 1994; Gotelli and Colwell, 2001; Thompson and Withers, 2003). The

high dominance of a few taxa in an assemblage leads the curve to rise slowly, whereas a more even distribution produces a steep early slope. The former situation is observed for the Ovos de Peixe unit (where *Vinctifer* is highly abundant), whereas the latter situation characterizes the Base, the Lageiro and the Pre-Lageta units (hereafter referred to as BLP-L) where *Tharrhias* dominates with a medium relative abundance.

Diversity indices are also illustrative of this pattern (Fig. 8B). The high dominance of *Vinctifer* in the Ovos de Peixe assemblage leads to the highest values for the Simpson and Berger–Parker indices, and to the lowest values for the Shannon index and Fisher's α. The opposite situation characterizes the *Tharrhias*-dominated BLP-L assemblages, while the Post-Lageta fish fauna is always intermediate between these two extremes from which it cannot be distinguished statistically. In contrast, diversity indices for the BLP-L assemblage are significantly different ($p < 0.05$) from those of the Ovos de Peixe assemblage, except for the Fisher's α. Although the Base, the Lageiro do Peixe and the Ovos de Peixe assemblages have the same taxonomic richness (5 genera), the two former can be regarded as more diverse because the abundance of their taxa is more evenly distributed (higher evenness).
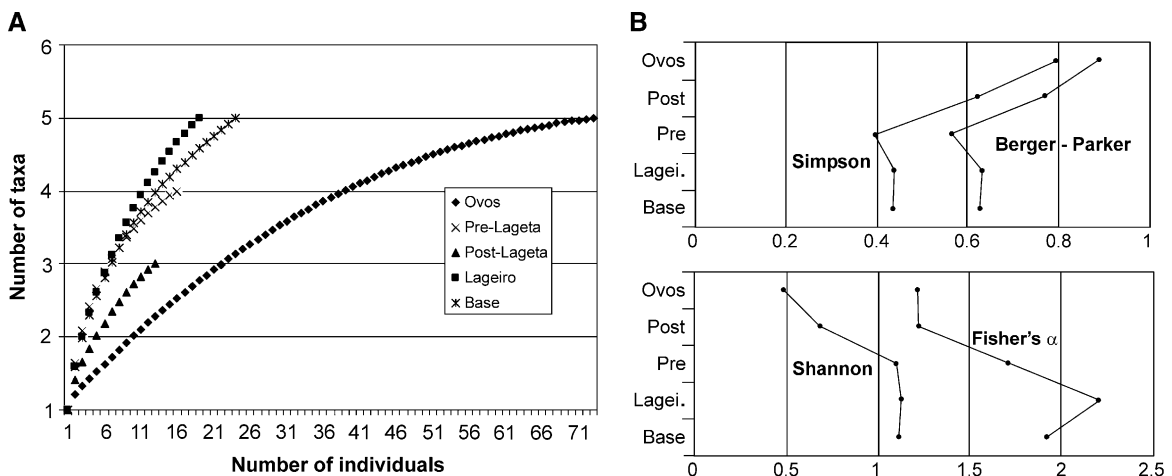

Fig. 8. (A) Randomised generic accumulation curves (rarefaction curves) for the assemblages in the Romualdo Member at Parque dos Pterossauros. The sampling effort (*x*-axis) is represented by the number of collected individuals. (B) Diversity indices of the assemblages found along the section. In both diagrams, the Matracão level is not represented because it did not yield identifiable fish remains. Abbreviation: Lagei.—Lageiro.

5. Discussion

5.1. Stratigraphy and concretions

The thickness of the Romualdo Member varies significantly across the Chapada do Araripe (from 2 to 10 m), but the cause of this variation is unknown (Martill and Wilby, 1993). The section at Parque dos Pterossauros is only 2.5 m thick, but the possibility of a local post-depositional erosion can be excluded because all the levels informally recognised throughout the basin are present at this site. The limited vertical extent of the unit is certainly due to the condensation of some of these levels. In turn, this may affect our estimates of relative thickness and concretion density. However, we believe it does not significantly distort our observations on taxonomic composition and assemblage structure. By identifying the various horizons of the Romualdo Member, we offer a stratigraphic framework for putting our results to the test against future excavations conducted in thicker sections.

This is the first time different concretion horizons are formally identified in the Romualdo Member. Our results show that the nature and the number of concretions vary substantially along the section, and that there are some changes in the lithology of the surrounding shales. We do not, however, question the integrity of the Romualdo Member, but the latter certainly represents slightly different episodes of Araripe's palaeoenvironmental and palaeobiotic states.

Septarian concretions have been reported in the Santana Formation as early as Gardner (1849), although their exact distribution has remained unknown since then. Septaria may represent up to 10% of the concretions in the Jardim area, but they largely are ignored by local collectors because of the bad preservation of their eventual fossil content (Maisey, 1991). Our observations show that septaria actually occur only in the upper part of the Ovos de Peixe unit, horizon into which the sediment forming the concretion suffered dehydration.

Lithological heterogeneity in the Romualdo Member is also well illustrated by the Matracão horizon. This peculiar level contains large and compact concretions whose lithology does not correspond to Maisey's (1991) "Santana" type, in contrast with what

is observed elsewhere in the section. Similar concretions are found near Jardim, but their exact stratigraphic provenance as yet to be identified (work in progress).

Wenz et al. (1993) noticed that small fossil fish are rarely found isolated in concretions but that they more often occur in the surrounding shales. These authors suggested that the size of such fish was insufficient to create the microenvironment necessary for the formation of carbonate concretions. Body size, however, cannot be a paramount factor for triggering concretion genesis. Indeed, many concretions form around small organic nucleus or in the absence of any of them (Maisey, 1991; this study), whereas many specimens (some of them reaching 110 mm in length) can be found in the surrounding shales. Interestingly, those specimens seem to be more frequent in levels where the number of concretions is low (e.g., Base and lower part of the Ovos de Peixe horizon), suggesting that small fish (perhaps juveniles, see Leal and Brito, 2004) invaded the area when palaeoenvironmental factors were not suitable for concretion genesis. It seems that a large biomass of fish carcasses (probably due to mass mortality episodes) may have triggered the rapid formation of micro- or meso-environments favourable to concretion formation through the development of cyanobacterial scums, as suggested by Martill (1988, 2001) and Maisey (1991). If episodes of mass mortality are regarded as the cause of concretion formation, then the *ultimate* cause corresponds to palaeoenvironmental changes, most probably in salinity, temperature or oxygen (see also Weeks, 1953, 1957; Martill, 1988, 2001; Baudin et al., 1990; Maisey, 1991). The nature of these changes will be investigated in the future with stratigraphically calibrated biogeochemical analyses, and we offer here a stratigraphic framework allowing such studies to be carried out.

Even if concretion distribution, shape and lithology are heterogeneous, there is some homogeneity in their size and orientation through the Romualdo Member at Parque dos Pterossauros. Mabesoone and Tinoco (1973) and Maisey (1991) noted that no preferential orientation pattern is determinable in the Santana Formation, and the latter author suggested that strong currents are unlikely because of the fine size of the sediments and of the quality of fossil preservation.

Rather surprisingly, our results show a preferential orientation of the fish carcasses by dominating palaeocurrents before burial. We found a marked bimodal orientation pattern of the concretions at all levels throughout the section, suggesting that dominating currents switched between two preferential directions during sedimentation. These currents were certainly of low energy but strong enough to orientate fish carcasses. This is the first time current patterns are demonstrated in the Santana Formation and they suggest a constant palaeogeographical setting at the local scale during the deposition of the Romualdo Member. Further controlled excavations in other parts of the Araripe Basin will be necessary to check whether this pattern is simply local or regional in scale, thus determining more precisely the corresponding palaeogeographical setting in relation with studies carried out in other stratigraphic units (e.g., Assine, 1994).

5.2. Preservation and sampling

A major result of this study is that only a limited number of concretions yield the well-preserved vertebrate remains that have made the Santana Formation so famous. Maisey (1991) and Wenz et al. (1993), for example, mentioned that fossil fish usually are complete, notably in the "Santana" matrix. Our sample suggests that at best 15% of the concretions yield complete or sub-complete fossil fish remains, and those are mainly found in the BLP-L horizons. In addition, more than one-third of the concretions have a content that is inappropriate for taxonomic analysis at or below the generic level. In turn, this may cause fine-scale biostratigraphic patterns to be overlooked in our sample. Previous accounts on the completeness of fossil specimens actually measured the strong sampling selectivity that have prevailed for Santana fossils over the last century, and this bias is best illustrated by current museum collections.

Also, our data show that sampling of the Romualdo Member must be intense if one wishes to capture uncommon taxa and some rare ones. Given the abundance pattern of the commonest taxa, perhaps as many as 100 or more concretions should be collected from each horizon. This is because less than two-thirds of the concretions yield identifiable fossil remains, and also because the various stratigraphic levels contain different type of assemblages.

However, the taphonomical characteristics of the Romualdo Member suggest that the fish assemblages found within a same unit accurately reflect patterns of abundance in the actual palaeocommunities, at least for the commonest taxa. Indeed, both assumptions of similar preservation potential and of similar mean individual life span (Kidwell, 2001; Vermeij and Herbert, 2004) are reasonably satisfied by these fish assemblages.

5.3. Fossil fish assemblages and palaeoenvironment

The taxonomic distributions observed in the various stratigraphic horizons show that there is not one 'Romualdo Member assemblage,' but several of them. Our sample allows the distinction of at least three major assemblages in terms of diversity: a *Tharrhias*-dominated assemblage (BLP-L levels), an assemblage dominated by *Tharrhias* and by *Cladocyclus* (Post-Lageta) and a *Vinctifer*-dominated assemblage (Ovos de Peixe). Interestingly, the stratigraphic sequence of these assemblages corresponds to their ranking in terms of diversity (Fig. 8B). This suggests a directional change in community structure at the time the Romualdo Member was being deposited. Moreover, the condensation of some of the levels certainly accentuates these observed changes in diversity, and similar investigations in more complete sections will be necessary to assess the actual rate of variation from one assemblage to the next.

Magurran and Henderson (2003) showed that, for modern estuarine fish communities, the commonness and rarity of species are related to their permanence in the assemblage. One can distinguish core species (persistent, abundant and biologically associated with the local habitat) from occasional species (low in abundance, infrequent and with different habitat requirements). Core and occasional species certainly can change their status over time if environmental conditions alter sufficiently (Magurran and Henderson, 2003). Perhaps the main shift from the *Tharrhias* assemblage to the *Vinctifer* assemblage in the Romualdo Member can be interpreted in a similar perspective.

What kind of palaeoenvironmental factor(s) may have ultimately driven such a change? At least two hypotheses can be formulated for future testing. The first one involves climate. In a macro-scale study on modern estuarine and inshore marine fish communities, Genner et al. (2004) showed that regional climatic fluctuations have a dramatic effect on the abundance pattern of dominant species. If such climate-induced changes occurred in Araripe palaeocommunities at the regional scale, we expect (1) to observe a similar assemblage-level response across the entire Araripe Basin; and (2) to find independent evidence of temperature/salinity changes, notably by conducting biogeochemical analyses on stable oxygen isotopes (see also Baudin et al., 1990 for a preliminary investigation of salinity based on organic matter analysis).

The second hypothesis concerns palaeogeographical changes. The configuration of the Araripe Basin certainly was not homogeneous, both spatially and temporally, during the deposition of the Romualdo Member. Localized marine incursions or large freshwater inputs should have led to different community structures across the basin and through time. Such a scenario predicts the occurrence of distinct, contemporaneous assemblages and palaeoenvironmental signals (the study of which will also involve biogeochemical analyses). This is perhaps the reason why there is currently no consensus on the probable palaeoenvironment of the Romualdo Member. Santos and Valença (1968) suggested that the ichthyofauna was primarily made of marine taxa living in estuaries. Martill (1988) postulated a marine environment, whereas Maisey (1991) stated that many evidence point toward an essentially non-marine environment. Mabesoone and Tinoco (1973) adopted a rather intermediate position by suggesting a large embayment environment, connected on one side with the open sea and at the other with a great influx of freshwater. Martill (2001) presents the Romualdo Member as being deposited in 'a shallow lagoon, which was probably connected with the open sea to the north-west, although evidence for this is largely circumstantial. Salinities probably fluctuated between brackish and hypersaline.' The presence of echinoids in the thin limestones just above the Romualdo Member is the clearest evidence of a marine incursion (Maisey, 1991; Martill, 1993, 2001), but this has no direct implication in the interpretation the underlying concretion-bearing shales. The palaeoecology of dominant taxa is not more informative. The genus Vinctifer was a marine form (Moody and Maisey, 1994; Schultze and Stöhr, 1996; Brito, 1997), whereas modern gonorhynchiformes, like Chanos, suggest that Tharrhias may have been living into a marine, brackish or freshwater environment (Schuster, 1960).

The study of community structure and evolution is clearly scale-dependent (e.g., Levin, 1992; Samuels and Drake, 1997), and patterns observed within a local community might be very different from those found over broader areas. Here we have provided the first controlled estimate of alpha diversity (i.e., local diversity, sensu Whittaker, 1960, 1972) for an assemblage of the Santana Formation. However, the absence of any other detailed locality data prevents hierarchically scaled diversity analyses to be made for the Araripe biota. It is indeed too early to assess how within- and among-sample diversity contributed to total diversity (or gamma diversity). The latter, many would hope, could be estimated by the thousands of fossils amassed after a century of effort in the Araripe region. Unfortunately, this is not possible. First because all these fossils are not tied to precise stratigraphic data and they are therefore artificially time-averaged. Second because the sampling of Araripe fossils has been strongly selective (Maisey, 1991; Martill, 1993). Table 2 compares the relative abundances of taxa found in "Santana concretions" as given by Maisey (1991) with those from our own

Table 2
Relative abundance of identifiable taxa found in "Santana concretions"

Taxon	Maisey (1991)	This study
Tharrhias	Abundant	Abundant
Brannerion	Common	Uncommon/Rare
Ararilepidotes	Common	–
Calamopleurus	Common	Uncommon/Rare
Cladocyclus	Uncommon	Common
Axelrodichthys	Uncommon	–
Vinctifer	Rare	Abundant
Rhinobatos	Rare	–
Notelops	Rare	Rare
Tetrapods	Exotic	–
Plants	Exotic	Exotic
Ostracods	Abundant	Abundant

Abundance categories are from Maisey (1991).

grouped sample. The most striking difference concerns the abundance of *Vinctifer*. This taxon is the most common fish in our sample (Fig. 5), whereas Maisey's (1991) survey of museum collections classes it as a "rare" taxon. We interpret this as another evidence illustrating the strong sampling bias in favour of well-preserved specimens, most of which are found in stratigraphic levels underlying the Matracão. Recrystallized, eroded and weathered specimens from the Ovos de Peixe unit (e.g., Fig. 7A), where *Vinctifer* dominates, are usually discarded by collectors although there are one of the missing piece of information for a comprehensive understanding of the Araripe biota.

There are other discrepancies in abundance pattern. For example, *Brannerion* is regarded by Maisey (1991, pp. 62) as the second most abundant taxon after *Tharrhias*, while our sample places it into the 'rare' category. However, such a difference cannot be fully attributed to a bias in museum collections, because our own abundance estimates are based on a relatively limited sample from a single site. Replicate samples would be necessary not only to increase the probability of recovering rare taxa, but also to assess statistically the confidence on our relative abundance patterns (Magurran, 1988; Hayek and Buzas, 1997; Bennington and Rutherford, 1999; Bennington, 2003).

6. Conclusions

The century-old celebrity of the Santana fossils has proved insufficient for a minimal understanding of their spatio-temporal distribution. This study has shown that the Romualdo Member contains at least three successive assemblages at the same locus. Together with the recognition of at least three geographically distinct 'assemblages' by Maisey (1991), this suggests an important spatio-temporal differentiation of Araripe's vertebrate faunas during the Aptian/Albian. Concretions of the "Santana type" are particularly interesting because they seem to be lithologically and palaeontologically very different from the other types of Araripe concretions (Maisey, 1991). By sampling such an extreme in the ecological and lithological spectrum, we propose a geographically and stratigraphically calibrated reference for later comparisons. We urge future studies to adopt a fine-scale stratigraphic resolution because the concretions of the Romualdo Member are heterogeneous in distribution and content. Current knowledge is severely biased toward well-preserved and exotic fossils and it is therefore inappropriate for drawing palaeoecological inferences. Replicate sampling will be developed in the future in order to rigorously assess regional-scale variations in assemblage structure. Similarly, palaeoenvironmental changes will be inferred by conducting systematic biogeochemical investigations. These efforts, together with the present work, are the first steps of an expanded research program that aims at defining the spatio-temporal relationships between biological communities and their palaeoenvironment at the regional scale. The Araripe Basin offers an ideal field of investigation in this perspective.

References

Agassiz, L., 1841. On the fossil found by Mr. Gardner in the Province of Ceará, in the North of Brazil. Edinb. New Philo. J. 30, 82–84.

Agassiz, L., 1844. Sur quelques poissons fossiles du Brésil. C. R. Acad. Sci. Paris 18, 1007–1015.

Assine, M.L., 1992. Análise estratigráfica da Bacia do Araripe, Nordeste do Brasil. Rev. Bras. Geociênc. 22, 289–300.

Assine, M.L., 1994. Paleocorrentes e paleogeographia na Bacia do Araripe, Nordeste do Brasil. Rev. Bras. Geociênc. 24, 223–232.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London.

Baudin, F., Berthou, P.-Y., Herbin, J.P., Campos, D.A., 1990. Matière organique et sédimentation argileuse dans le Crétacé du Bassin d'Araripe. Comparaison avec les données du Crétacé d'autres bassins brésiliens. In: Campos, D.A., Viana, M.S.S., Brito, P.M., Beurlen, G. (Eds.), Atas do I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste. URCA, Crato, pp. 83–93.

Bennington, J.B., 2003. Transcending patchiness in the comparative analysis of paleocommunities: a test case from the Upper Cretaceous of New Jersey. Palaios 18, 22–33.

Bennington, J.B., Rutherford, S.D., 1999. Precision and reliability in paleocommunity comparisons based on cluster-confidence intervals: how to get more statistical bang for your sampling buck. Palaios 14, 506–515.

Berthou, P.Y., 1990. Le bassin de l'Araripe et les petits bassins intracontinentaux voisins (N.E. du Brésil): formation et évolution dans le cadre de l'ouverture de l'Atlantique équatoriale. Comparaison avec les bassins ouest-Africains situés dans le même contexte. In: Campos, D.A., Viana, M.S.S., Brito, P.M., Beurlen, G. (Eds.), Atas do I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste. URCA, Crato, pp. 113–134.

Beurlen, K., 1971. As condições ecológicas e faciológicas da Formação Santana na Chapada do Araripe (Nordeste do Brasil). An. Acad. Bras. Ciênc. 43, 411–415.

Brito, I.M., 1990. Breve historico sobre a estratigrafia da Bacia do Araripe, nordeste do Brasil. In: Campos, D.A., Viana, M.S.S., Brito, P.M., Beurlen, G. (Eds.), Atas do I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste. URCA, Crato, pp. 1–18.

Brito, P.M., 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnementales et biogéographiques. Geodiversitas 19, 681–772.

Brito-Neves, B.B., 1990. A bacia do Araripe no contexto geotectónico regional. In: Campos, D.A., Viana, M.S.S., Brito, P.M., Beurlen, G. (Eds.), Atas do I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste. URCA, Crato, pp. 21–33.

Buffetaut, E., Martill, D.M., Escuillié, F., 2004. Pterosaurs as part of a spinosaur diet. Nature 430, 33.

Coimbra, J.C., Arai, M., Carreño, A.L., 2002. Biostratigraphy of Lower Cretaceous microfossils from the Araripe Basin, north-eastern Brazil. Geobios 35, 687–698.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. Lond., B 345, 101–118.

Davis, P.G., 1992. Geological miracles. Nature 355, 218.

Fisher, N.I., 1993. Statistical Analysis of Circular Data. Cambridge University Press, Cambridge.

Fürsich, F.T., Oschmann, W., Singh, I.B., Jaitly, A.K., 1992. Hardgrounds, reworked concretion levels and condensed horizons in the Jurassic of western India: their significance for basin analysis. J. Geol. Soc. (Lond.) 149, 313–331.

Gardner, G., 1841. Geological notes made during a journey from the coast into the interior of the Province of Ceará, in the north of Brazil, embracing an account of a deposit of fossil fishes. Edinb. New Philo. J. 30, 75–82.

Gardner, G., 1849. Travels in the Interior of Brazil, Principally Through the Northern Provinces. Reeve, Benham and Reeve, London.

Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A., Hawkins, S.J., 2004. Regional climatic warming drives long-term community changes of British marine fish. Proc. R. Soc. Lond., B 271, 655–661.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Hammer, Ø., Harper, D.A.T., 2004. PAST version 1.29, Palaeontological Statistics. User's Guide and application published at: http://folk.uio.no/ohammer/past/index.html.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.

Hayek, L.C., Buzas, M.A., 1997. Surveying Natural Populations. Columbia University Press, New York.

Jordan, D.S., Branner, J.C., 1908. The Cretaceous fishes of Ceará, Brazil. Smithson. Misc. Collect. 25, 1–29.

Kellner, A.W.A., 1996. Fossilized theropod soft tissue. Nature 379, 32.

Kellner, A.W.A., Campos, D.A., 1998. Archosaur soft tissue from the Cretaceous of the Araripe Basin, northeastern Brazil. Bol. Mus. Nac. 42, 1–22.

Kellner, A.W.A., Tomida, Y., 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian–Albian), northeastern Brazil. Natl. Sci. Mus. Monogr. 17, 1–135.

Kidwell, S.M., 2001. Preservation of species abundance in marine death assemblages. Science 294, 1091–1094.

Krebs, C.J., 1989. Ecological Methodology. Harper and Row, New York.

Leal, M.E.C., Brito, P.M., 2004. The Ichthyodectiform Cladocyclus Gardneri (Actinopterygii: Teleostei) from the Crato and Santana Formations, Lower Cretaceous of Araripe Basin, north-eastern Brazil. Ann. Paléontol. 90, 103–113.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.

Mabesoone, J.M., 1994. Sedimentology of northeast Brazil. Geol. Dept. Spec. Publ., vol. 2. Univ. Federal Pernambuco, Recife.

Mabesoone, J.M., Tinoco, I.M., 1973. Palaeoecology of the Aptian Santana Formation (northeastern Brazil). Palaeogeogr. Palaeoclim. Palaeoecol. 14, 97–118.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, NJ.

Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422, 714–716.

Maisey, J.G., 1991. Santana Fossils, an Illustrated Atlas. T.F.H. Publications, Neptune City, NJ.

Maisey, J.G., 1994. Predator–prey relationships and trophic level reconstruction in a fossil fish community. Environ. Biol. Fisches 40, 1–22.

Maisey, J.G., 2000. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretac. Res. 21, 281–314.

Maisey, J.G., Campos, D.A., Kellner, A.W.A., 1999. A new specimen of *Obaichthys* (Lepisosteidae) from the Romualdo Member (Albian), Santana Formation, Northeast Brazil. XVI Congr. Bras. Paleont., Boletim de Resumos. URCA, Crato, pp. 62–63.

Mardia, K.V., Jupp, P.E., 2000. Statistics of Directional Data, 2nd Edition. John Wiley and Sons, Chicester.

Martill, D.M., 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Palaeontology 31, 1–18.

Martill, D.M., 1989. The Medusa effect: instantaneous fossilization. Geol. Today 5, 201–205.

Martill, D.M., 1990. Macromolecular resolution of fossilized muscle tissue from an elopomorph fish. Nature 346, 171–172.

Martill, D.M., 1993. Fossils of the Santana and Crato Formations, Brazil. Palaeontol. Assoc. Field Guides Foss. 5, 1–159.

Martill, D.M., 2001. The Santana Formation. In: Briggs, D.E.K, Crowthers, P.R. (Eds.), Palaeobiology, vol. II. Blackwell, Oxford, pp. 351–356.

Martill, D.M., Wilby, P.J., 1993. Stratigraphy. In: Martill, D.M. (Ed.), Fossils of the Santana and Crato Formations, Brazil, Palaeontol. Assoc. Field Guides Foss., vol. 5, pp. 20–50.

Medeiros, R.A., Ponte, F.C., Ponte Filho, F.C., 2001. Análise estratigráphica da Bacia do Araripe: Parte 2. Análises de fácies. In: Barros, L.M., Nuvens, P.C., Filgueira, J.B.M. (Eds.), I e II Simpósios sobre a Bacia do Araripe e Bacias Interiors do Nordeste, 1990–1997. Coleção Chapada do Araripe 1, Crato, pp. 93–99.

Moody, M.J., Maisey, J.G., 1994. New Cretaceous marine vertebrates assemblages from north-western Venezuela and their significance. J. Vertebr. Paleontol. 14, 1–8.

Neumann, V.H., Borrego, A.G., Cabrera, L., Dino, R., 2003. Organic matter composition and distribution through the Aptian–Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. Int. J. Coal Geol. 54, 21–40.

Oriana ©, 2003. Kovach Computing Services, version 2.0.

Ponte, F.C., Ponte Filho, F.C., 1996. Evolução tectônica e classificação da Bacia do Araripe. IV Simp. Cret. Brasil, Boletim de Resumos. Univ. Estadual Paulista, Rio Claro, pp. 123–133.

Ponte, F.C., Medeiros, R.A., Ponte Filho, F.C., 2001. Análise estratigráphica da Bacia do Araripe: Parte 1. Análises de seqüências. In: Barros, L.M., Nuvens, P.C., Filgueira, J.B.M. (Eds.), I e II Simpósios sobre a Bacia do Araripe e Bacias Interiors do Nordeste, 1990–1997. Coleção Chapada do Araripe no. 1, Crato, pp. 83–92.

Samuels, C.L., Drake, J.A., 1997. Divergent perspectives on community convergence. Trends Ecol. Evol. 12, 427–432.

Santos, R.da.S., Valença, J.G., 1968. A Formação Santana e sua paleoictiofauna. An. Acad. Bras. Ciênc. 40, 339–360.

Schultze, H.P., Stöhr, D., 1996. *Vinctifer* (Pisces, Aspidorhynchidae) aus der Unterkreide (oberes Aptium) von Kolumbien. Neues Jahrb. Geol. Paläontol. Abh. 199, 395–415.

Schuster, W.H., 1960. Synopsis of biological data on milkfish *Chanos chanos* (Forskal), 1775. FAO Fish. Biol. Synop. 4, 1–58.

Small, H., 1913. Geologia e suprimento de água subterrânea no Ceará e parte do Píaui. Insp. Obras Contra Secas., Series Geol. 25, 1–180.

Smith, R.J., 1999. Possible fossil ostracod (Crustacea) eggs from the Cretaceous of Brazil. J. Micropalaeontol. 18, 81–87.

Tipper, J.C., 1979. Rarefaction and rare fiction—the use and abuse of a method in paleoecology. Paleobiology 5, 423–434.

Thompson, G.G., Withers, P.C., 2003. Effect of species richness and relative abundance on the shape of the species accumulation curve. Austral Ecol. 38, 355–360.

Vermeij, G.J., Herbert, G.S., 2004. Measuring relative abundance in fossil and living assemblages. Paleobiology 30, 1–4.

Viana, M.S.S., 2001. 164 anos de pesquisas paleontológicas na Chapada do Araripe: Formação Santana (Cretáceo Inferior). In: Barros, L.M., Nuvens, P.C., Filgueira, J.B.M. (Eds.), I e II Simpósios sobre a bacia do Araripe e bacias interiors do Nordeste, 1990–1997. Coleção Chapada do Araripe no. 1, Crato, pp. 195–211.

Weeks, L.G., 1953. Environment and mode of origin and facies relationships of carbonate concretions in shales. J. Sediment. Petrol. 23, 162–173.

Weeks, L.G., 1957. Origin of carbonate concretions in shales, Magdalena Valley, Colombia. Geol. Soc. Amer. bull. 66, 95–102.

Wenz, S., Brito, P.M., 1990. L'ichthyofaune des nodules fossilifères de la Chapada do Araripe (N-E du Bresil). In: Campos, D.A., Viana, M.S.S., Brito, P.M., Beurlen, G. (Eds.), Atas do I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste. URCA, Crato, pp. 337–349.

Wenz, S., Brito, P.M., Martill, D.M., 1993. The fish fauna of the Santana Formation concretions. In: Martill, D.M. (Ed.), Fossils of the Santana and Crato Formations, Brazil. Palaeont. Ass. Field Guide to Fossils, vol. 5, pp. 76–107.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Orgeon and California. Ecol. Monogr. 30, 279–338.

Whittaker, R.H., 1972. Evolution and measurements of species diversity. Taxon 21, 213–251.

Woodward, A.S., 1887. On the fossil teleostean genus *Rhacolepis* Agassiz. Proc. Zool. Soc. Lond. 1887, 535–542.