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Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians

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ABSTRACT

The upper Aptian-lower Albian lacustrine limestones of the Crato Formation of northeastern Brazil have yielded one of Gondwana's most important Cretaceous fossil assemblages. This assemblage includes a few articulated anuran remains that have been previously referred to a single neobatrachian taxon, *Arariphrynus placidoi* [Leal, M.E.C., Brito, P.M., 2006. Anura do Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. In: Gallo, V., Brito, P.M., Silva, H.M.A., Figueiredo, F.J. (Eds.), Paleontología de Vertebrados. Grandes Temas e Contribuçoes Científicas. Interciencia, Rio de Janeiro, pp. 145–152]. Herein we redescribe these specimens, which document two additional genera and species, *Eurycephalella alcinae* and *Cratia gracilis*, as well as a possible pipoid. Although the monophyly of neobatrachians can be considered a well-corroborated hypothesis, neobatrachian interrelationships are still far from being satisfactorily resolved. In order to address the high-level relationships of the taxa to which these specimens belong, we conducted a phylogenetic analysis of a matrix of 42 taxa, including extant representatives of most of the higher groups of neobatrachians as well as non-neobatrachians, and 75 mostly osteological characters in TNT 1.1 under implied weights with different values of the concavity constant (k). As in other analyses based on morphological data, within Neobatrachia we recovered a monophyletic Ranoides but hyloid taxa appear as stem-ranoids. Our analysis consistently place *A. placidoi* and *E. alcinae* in nested positions among hyloid taxa, although the topology of the tree varies slightly, whereas *C. gracilis* appears to be a stem neobatrachian or have a basal position within crown Neobatrachia. Recent studies based on molecular data have estimated divergence times for several anuran clades and proposed the main radiation of hyloid neobatrachians, excluding the australobatrachians, as a Late Cretaceous-Paleogene event. The taxonomically diverse anurans from the Crato Formation show that some hyloid lineages might have diverged already by the mid Cretaceous and that the early history of neobatrachians is as yet not documented in the fossil record.

1. Introduction

Anurans constitute one of the most morphologically distinct groups of vertebrates. Most living anurans belong to Neobatrachia (Reig, 1958), a group that has been recognized by traditional systematists but also recovered by recent phylogenetic analyses based on morphological (Haas, 2003), as well as DNA-sequence data (Frost et al., 2006; Roelants et al., 2007; Wiens, 2007a). The broad picture of neobatrachian evolution, however, is far from being resolved; the branching pattern is still a subject of intense disagreement (Wiens, 2007b; Frost et al., 2008). Notwithstanding, according to these studies many long-accepted neobatrachian groups of diverse systematic position, such as "Leptodactylidae", "Hylidae", "Telmatobinae", and "*Bufo*", are not monophyletic in their traditional concepts.

Until recently, the earliest unquestionable neobatrachian was from the Turonian–Santonian Araçatuba/Adamantina Formation of central-eastern Brazil. This record consists of a small collection of well-preserved specimens, which still remains undescribed, interpreted by Carvalho et al. (2003) as belonging to a neobatrachian taxon that shares features with some South American hyloids (sensu Frost et al., 2006). More recently, however, the presence of neobatrachians in the older Crato Formation of northeastern Brazil, a unit famous for containing one of Gondwana's most important Cretaceous Konservat Lagerstatten (Maisey, 1991), was reported by Leal and Brito

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(2006). These authors briefly described the fossil material and assigned it to a new genus and species, *Arariphrynus placidoi*, of the nonmonophyletic "Leptodactylidae". Our examination of the same specimens revealed that several features have been misinterpreted by these authors and that the fossils belong to more than one anuran taxon. Moreover, the specimens attributed to *Arariphrynus placidoi* include a mixture of non-neobatrachian and neobatrachian material. Herein we redescribe these specimens and, in order to address the high-level relationships of the taxa to which they belong, we performed a parsimony analysis using 75 morphological characters scored in 39 extant anuran species. These species represent 2 costatan, 4 anomocoelan, and 22 neobatrachian families (Appendix 1) following the taxonomy of Frost (2008).

2. Geological setting and preservational aspects

The Crato Formation is part of the infill of the Araripe Basin, a small intracratonic basin of north-eastern Brazil (Assine, 1992) that lies on the borders of the states of Ceará, Pernambuco, and Piauí (Fig. 1). The tectonic evolution of the Araripe Basin, as well as that of other basins in this region, was closely linked to the opening of the South Atlantic Ocean. Sequences composed of genetically related depositional systems in these basins have been correlated with major episodes in the tectonic history of the rifting involved in the final separation of Africa and South America (Medeiros et al., 2001). In this context, the mainly continental Santana Group, which comprises the Rio da Batateira, Crato, Ipubi, Romualdo, and Arajara formations, represents the postrift stage in the Araripe Basin (Martill, 1993; Neumann and Cabrera, 1999). However, there is still little consensus on the stratigraphic scheme and nomenclature of the Araripe Basin infill (See Martill, 2007a for a review).

The frog-bearing sequence, the Crato Formation, is up to 100 m thick and comprises several carbonate units separated by sandstones and shales; each carbonate unit is mainly made up of laminated limestones interbedded between fine-to-medium–grained siliciclastics (Viana and Neumann, 2002).The Crato Formation laterally interdigitates with the sandstones and siltstones of the upper part of the Rio da Batateira Formation according to Neumann (1999).

The interpretation of the environmental setting of the laminated limestones is contentious. The Crato succession has been interpreted as deposits of an extensive paleolake (Neumann et al., 2002) situated at 10–15° S of the paleoequator (Martill, 2007b). Cyclical fluctuations in the productivity cycle, perhaps related to vast algal blooms, may have induced the formation of individual carbonate laminae (Heimhofer et al., 2006). It has also been proposed that deposition of the laminated carbonates occurred in a thermally stratified lagoon; rivers from the north and east flowed into waters of the lagoon, where freshwater conditions prevailed (Brito et al., 1998; Martill, 2007b; Martill et al., 2007a; Dietze, 2007). The climate during the deposition of the Crato Formation has been interpreted as semiarid with a marked dry season, based on palynological data (Lima, 1978). Recently, the study of some spore and pollen assemblages has suggested that plant communities supporting seasonally dry as well as generally moist conditions were developed during Crato time, but their chronological and geographical patterns of distribution can not be inferred on the basis of the few available samples (Batten, 2007).

The age of the Crato Formation has been considered as late Aptian according to ostracods (Berthou et al., 1994) and palynomorphs (Pons et al., 1990; Arai et al., 1997; Coimbra et al., 2002; Batten, 2007), although some palynological data suggest that it might be early Albian (Lima, 1978, 1980; Hashimoto et al., 1987).

Outcrops of the Crato Formation along the northeastern margin of the basin have been mined extensively, especially between the towns of Santana do Cariri and Nova Olinda, and around Barbalha, where the frog remains were discovered (Fig. 1). Most of the fossils described from the limestones were collected by local workers; consequently, many lack detailed stratigraphic provenance data, as is the case with the material described herein. Exceptionally well preserved remains of algae, fungi, plants (ferns, gymnosperms, angiosperms), invertebrates (insects, diplurans, arachnids, myriapods, decapods), and vertebrates (fishes, turtles, crocodylomorphs, pterosaurs, dinosaurs, birds) have been recovered from the Crato succession (Moura et al., 2006; Martill et al., 2007b), an assemblage that shows what life was like in an Early Cretaceous low-latitude lacustrine system. However, the anuran remains are comparatively rare. They occur mostly as incomplete skeletons that retain some degree of three-dimensionality. Some of these specimens (e.g. MPSC-An 890, 891, and 893) are fully articulated and preserve the hind limbs, which, remarkably, keep even the delicate terminal phalanges. This completeness indicates that the remains were deposited under low-energy conditions and that they were neither

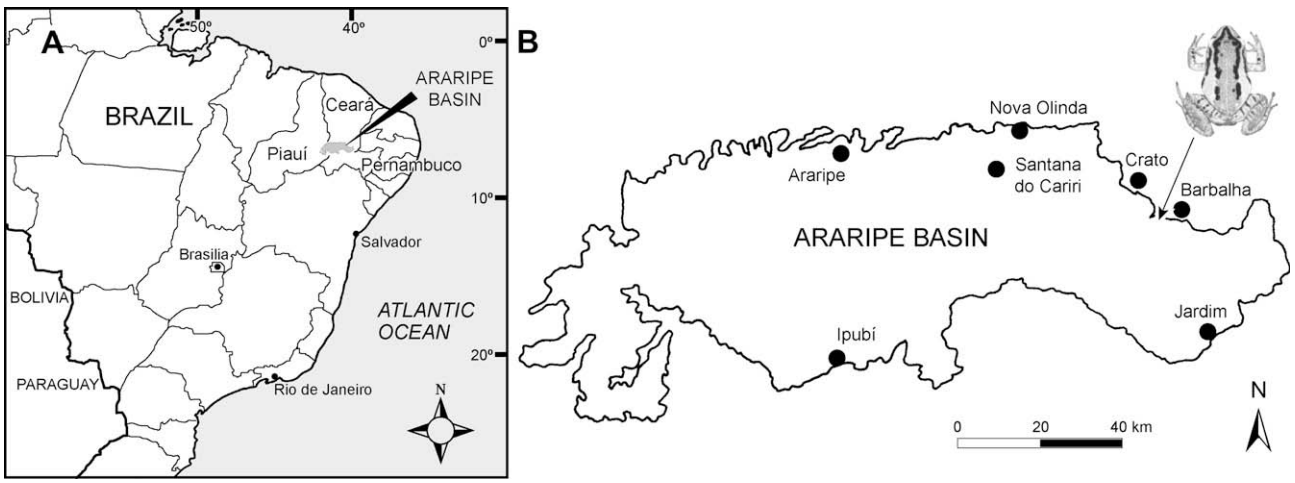

Fig. 1. A, location of the Araripe Basin in northeastern Brazil. B, map of the Araripe Basin showing the location of the quarries of the Crato Formation from which the anurans were discovered.