Palaeogeography, Palaeoclimatology, Palaeoecology 361–362 (2012) 21–37

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Exceptional Late Pliocene microvertebrate diversity in northwestern Argentina reveals a marked small mammal turnover

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ARTICLE INFO

Article history:
Received 30 November 2011
Received in revised form 13 July 2012
Accepted 15 July 2012
Available online 24 July 2012

Keywords:
Taphonomy
Uquía Formation
Sigmodontinae
Great American Biotic Interchange
Paleoenvironments
Faunal turnover

ABSTRACT

Despite a century of paleontological work in Neogene sequences of northwestern Argentina there is still much to learn about the biotic diversity in this area during Pliocene times. We report a rich microvertebrate assemblage recovered from Late Pliocene deposits of Uquía Formation, Jujuy Province, northernmost Argentina. Taxa represented in the studied sample include members of Bufonidae (Amphibia: Anura), Iguanoidea (Reptilia: Squamata), Passeriformes (Aves), Argyrolagidae, Didelphidae, Caviidae, Ctenomyidae, Octodontidae, and Cricetidae (Mammalia). Taphonomic attributes indicate that the bone concentration was produced by owls. The remains were disposed highly concentrated suggesting that the assemblage would have been generated in a short lapse, indicating a low time-averaging, retaining the main ecological signals of the past living community. The studied assemblage is noteworthy because it encompasses at least five new genera of cricetid rodents, illustrating the oldest record in northwestern Argentina for this diverse family of mammals. In spite of clear taxonomic differences at specific and generic levels, the structure of the assemblage is ecologically comparable to modern small mammal communities in terms of body mass distribution, trophic structure and abundance, with a dominance of cricetids over marsupials and caviomorph rodents. Striking differences in taxonomic composition between the Uquian assemblage and the coeval record from central Argentina indicate biogeographical distinctions since the Late Pliocene. The new Uquian cricetids show that the early divergence times for phyllotine genera proposed by several authors cannot be supported. The dominance of phyllotines in the assemblage as well as the record of *Microcavia* and an octodontid allow inferring arid or semiarid paleoenvironment conditions, in a more or less open habitat. The studied assemblage reflects a noteworthy faunal turnover, which implies the establishment of cricetid rodents as the dominant group in the small mammal communities. This faunal change can be associated to increasing aridity during Late Pliocene worldwide.

1. Introduction

The main phase of the dispersive event Great American Biotic Interchange (GABI) took place during the Late Pliocene–early Pleistocene (Woodburne, 2010, and references therein). One of the continental beds that documents this span in South America is represented by the outcrops exposed at Quebrada de Humahuaca, northwestern Argentina, referred as Uquía Formation (see Reguero et al., 2007 for a synthesis). A century of paleontological work retrieved a moderate number of vertebrates from this unit, mainly medium and large mammals (De Carles, 1912; Castellanos, 1950; Prado et al., 2000; Reguero et al., 2007). However, the age of this fauna and its temporal relation with potentially contemporary fossil bearing units of Bolivia and central Argentina have not been satisfactorily resolved (MacFadden et al., 1993, 1994; Cione and Tonni, 1995; Flynn and Swisher, 1995; Prado et al., 2000; Tonni and Cione, 2000). An additional obstacle for a comprehensive knowledge of the paleofauna of Uquía

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doi:10.1016/j.palaeo.2012.07.012

Formation arises from the scarcity of small vertebrates. The most recent compilation indicates solely two mammals <250 g recorded, *Ctenomys* and *Microcavia* (Reguero et al., 2007: Table 2). This situation partially reflects the history of the South American paleomammalogy during most of the 20th century, strongly biased toward traditional prospection methods. The recent use of screen-washing techniques (McKenna et al., 1994) has increased the finding of microvertebrate remains in a number of Cenozoic paleontological sites in South America, improving drastically our knowledge on the diversity and evolution of Tertiary and Quaternary South American mammals (e.g., Pardiñas and Lezcano, 1995; Ortiz and Pardiñas, 2001; Goin and Candela, 2004; Voglino and Pardiñas, 2005; Ortiz et al., 2011b). Within this context, microvertebrate assemblages—as those produced by owls—are particularly valuable as a source of data of past communities and environments (e.g., Avery, 1982; Andrews, 1990; López Antoñanzas and Cuenca Bescós, 2002; Avery, 2007).

The contributions on small mammal assemblages of Northwestern Argentina are few and focused on Late Pleistocene and Holocene evidences (Ortiz and Pardiñas, 2001; Teta and Ortiz, 2002; Ortiz and Jayat, 2007; Ortiz et al., 2011a, 2011b, 2012). However, these studies allowed the recognition of major faunal changes, including biological extinctions (Ortiz et al., 2000), altitudinal shifts in the distributional range of some species (Ortiz and Pardiñas, 2001; Ortiz and Jayat, 2007; Ortiz et al., 2011b), and remarkable fluctuations in species abundance (Teta and Ortiz, 2002; Ortiz et al., 2012).

In this paper we describe a noteworthy fossil assemblage of microvertebrates recovered from Late Pliocene deposits of Uquía Formation, Jujuy Province, Argentina. Here we document the first amphibians, lizards and birds for this unit as well as novel and enigmatic marsupials and small rodents. Among the latter is documented the oldest indisputable record for cricetids in the region (see Nasif et al., 2009), with representatives of at least three tribes. The dominance of cricetids in the new Uquian studied assemblage prompted the discussion about the important turnover suffered by small mammal communities during the Late Pliocene. Finally, the biogeographical meaning of these new faunistic elements is analyzed at the light of the GABI and paleoenvironments for Late Pliocene times in Northwestern Argentina.

2. Materials and methods

The studied specimens were collected by three of the authors (PEO, MJB, and DAGL) and collaborators and are housed in the fossil vertebrate collection of the Instituto Miguel Lillo, San Miguel de Tucumán, Argentina (PVL). The material was obtained through wet and dry sieving with a 0.1 mm mesh, following the method described in McKenna et al. (1994). The taphonomic history of the sample was assessed through the analysis of bones and teeth surfaces (Andrews, 1990, and references therein). Reported measurements (in millimeters) were obtained using digital calipers and a micrometer eyepiece included in a binocular microscope. Microphotographs were processed in the LAMENOA (Laboratorio de Microscopía Electrónica del Noroeste Argentino, San Miguel de Tucumán, Argentina).

A stratigraphic section was measured in the levels where the fossil assemblage was found. This stratigraphic profile was compared with known sections of the Uquía Formation using main lithological and stratigraphic features, particularly those described in Castellanos (1950) and Reguero et al. (2007). On this basis we suggest possible correlations between these outcrops.

3. Geographic and geologic setting

3.1. Study area

The studied fossil remains were found at San Roque, 4 km SSW Humahuaca, Humahuaca Department, Jujuy Province, Argentina (Fig. 1). This area is today under semiarid conditions, at 2900–3000 m elevation, and belongs to the Prepuna phytogeographical province (sensu Cabrera, 1976). The general landscape is characterized by steppe vegetation with scattered columnar cacti or "cardones" (*Trichocereus* spp.), low bushes, and small trees of "churqui" (*Prosopis ferox*) that can reach up to 3 m in height. The annual mean rainfall in Humahuaca town is 173 mm and the annual mean temperature is 12 °C (minimum mean 2.9 °C, maximum mean 22.5 °C; Buitrago and Larrán, 1994).

3.2. Geology

The Uquía Formation crops out in the Quebrada de Humahuaca, Jujuy Province, northwestern Argentina. A detailed description of the geology, stratigraphy, and fauna of this unit can be seen in Reguero et al. (2007). This unit is found in the context of Eastern Cordillera, usually lying unconformably over Cambrian–Ordovician sedimentary rocks and covered by Quaternary conglomerates and alluvium (Castellanos, 1950; Reguero et al., 2007). The formation is slightly faulted and folded and is mainly composed by siltstones, siltyclaystones, claystones, and sandstones interbeded with tuff and conglomerate beds related to fluvial deposits. Following the stratigraphic scheme of Castellanos (1950), Reguero et al. (2007) distinguished three units: the Lower Unit, characterized by sandy banks, thick conglomerates and a dacitic tuff; the Middle Unit, with more clayey-silt and sandy levels and a higher content of fossils; and the Upper Unit, mainly composed by levels of conglomerates. The Uquía Formation contains tuff horizons that have been dated using radimetric analyses (Marshall et al., 1982). The "Dacitic Tuff" of Castellanos (1950), which is a distinctive element of the Lower Unit, has been dated at Esquina Blanca in 3.54 Ma (Marshall et al., 1982). In the same locality Walther et al. (1998) determined for a second tuff (U1 tuff), about 180 m above the local base (Reguero et al., 2007), an age of 2.5 Ma. According to Reguero et al. (2007), this tuff coincides, in the Esquina Blanca section, with the limit between the Middle and the Upper units. The sum of evidences indicates that the age of the Uquía Formation can be referred for a span from middle Pliocene to early Pleistocene (Marshall et al., 1982; Cione and Tonni, 1995, 1996; Walther et al., 1996; Tonni and Cione, 2000; Reguero et al., 2007).

3.3. Description of the stratigraphic section

The stratigraphic section where the fossils here discussed were found begins with 10 m of well stratified reddish brown beds mainly composed of medium to coarse sandstones and pebbly conglomerates (Fig. 2). Sandstones often show planar lamination and some small lenses of conglomerates. Following this interval the sequence continues with about 70 m of light brown, reddish brown, and less pinkish very well stratified beds that show a reduction of the grain size. The lithology consists of fine to very fine sandstones interbeded with siltstones, claystones, and siltyclaystones, which constitute a fining upward pattern in some cases. Occasionally, some tuff beds are interbeded in the section and some silty sandstones show tuffaceous composition. Additionally, pebbly conglomerate lenses and conglomeratic sandstones are present but restricted to the upper levels of this interval. Sandstone and siltysandstone beds present parallel and cross lamination. Claystones locally present planar lamination and, in some cases, a massive aspect. Rootcasts are very common, more related to the finest sediments and, occasionally, to very fine to fine sandstone levels. Slickenslides are also present but occur locally in a claystone bed. The last 10 m are mainly composed of medium to fine sandstone beds with pebbles showing planar lamination, cross bedding, and cross lamination. Siltstone beds are less common and some of them present vegetal prints. The fossil assemblage was found in the upper levels of the measured section (Figs. 2 and 3), toward the top of a tabular-like bed of poorly consolidated medium to fine sandstone.