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Coprinisphaera akatanka isp. nov.: The first fossil brood ball attributable to necrophagous dung beetles associated with an Early Pleistocene environmental stress in the Pampean region (Argentina)

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ABSTRACT

The known ichnospecies of *Coprinisphaera* have been usually linked to dung beetles of coprophagous habits living in grass-dominated environments inhabited by large herbivorous, which provide the dung for constructing brood balls. A new ichnospecies consisting of bispherical and thin-walled structures, *Coprinisphaera akatanka*, is separated from the pear-shaped and thick-walled structures that remains in *C. tonni*. *C. akatanka* consists of an egg chamber separated from the provision chamber by a deep neck. This morphology is comparable with brood balls constructed by extant species of *Canthon* showing necrophagous habits. This similarity suggests that the producers of *C. akatanka* might also display necrophagous feeding habits. The new bispherical structures were found in Sanandresian Aridisols (Early Pleistocene) developed in loess deposits of the Pampean region. Such paleosols record stable floodplains, covered with herbaceous and shrubby vegetation, under a seasonal, semiarid temperate-cold climate during a phase of glacier expansion in Patagonia. Sanandresian Land Mammal Substage shows a sparse record of large herbivorous, potential producers of suitable pads for dung beetles; only *Neuryurus* sp. and *Glossotherium* sp. are recorded in the area. The extinction of autochtonous taxa associated to palaeoenvironmental stress conditions during the Sanandresian Substage and the absence of the allochtonous taxa involved in Great American Biotic Interchange produced a bottleneck for dung availability. Such scenario of reduced dung resources would have favored dung beetle necrophagy in the Pampean region reflected herein with *C. akatanka* record.

1. Introduction

Coprinisphaera ichnospecies, attributed to fossil brood balls of dung beetles (Scarabaeinae), is one of the most common trace fossils of South American Cenozoic paleosols (Genise et al., 2000; Genise, 2004; Laza, 2006a). The ichnogenus included different ichnospecies, mainly differentiated by the location of the egg chamber in relation to the provision chamber (Laza, 2006a). This author included in *Coprinisphaera tonni* both pear-shaped and bispherical brood balls, the latter previously illustrated by Mikuláš and Genise (2003). As the rest of the ichnospecies, *C. tonni* has been attributed to coprophagous beetles and then, related to grass-dominated areas supporting large herbivores that provide dung for their nests (Sánchez et al., 2010a). However, there is no evidence about extant coprophagous beetles producing bispherical brood balls (Halffter and Matthews, 1966; Halffter and Edmonds, 1982).

The Pliocene–Pleistocene outcrops of the Pampean region (Buenos Aires province) of central Argentina (Fig. 1), where *C. akatanka* occurs, are one of the most diverse and historically studied deposits bearing late Cenozoic mammals from Southern South America. Several "South American Land Mammal Ages" (SALMAs) and evolutive events are recognized there (Cione and Tonni, 2005). In addition, paleosols are a significant component of these Late Cenozoic loessic sequences. Particularly, Vorohuean–Sanandresian Substages from Miramar area were studied by Beilinson and Raigemborn (2012), who recognized Calcisols, bioturbated Vertisols and calcic Protosols (Entisols). The ichnological studies mainly focused on vertebrate trace fossils such as mammal palaeocaves (Ameghino, 1908; Frenguelli, 1928; Genise, 1989; Genise and Farina, 2012 and references therein), but the record of invertebrate trace fossils is scarce. The Irene Formation of the Montehermosan Stage at the banks of the Quequén Salado river bears *Coprinisphaera* isp. (Aramayo et al., 2004), whereas in the Sanandresian Substage of the coastal cliffs of Buenos Aires province occur *Coprinisphaera* isp. and *Barberichnus bonaerensis* (Laza, 2006a, b).

In contrast to the Middle Eocene–Lower Miocene Patagonian deposits where dung beetle brood balls parallels the diversification of large autochthonous herbivores (Sánchez et al., 2010a), the Sanandresian Substage reflects the prelude of the Great American Biotic Interchange (GABI), when biomass and diversity of holartic immigrants was still insignificant and the autochthonous families have disappeared in the region (Tonni et al., 1992). This bottleneck, associated with a substantial change

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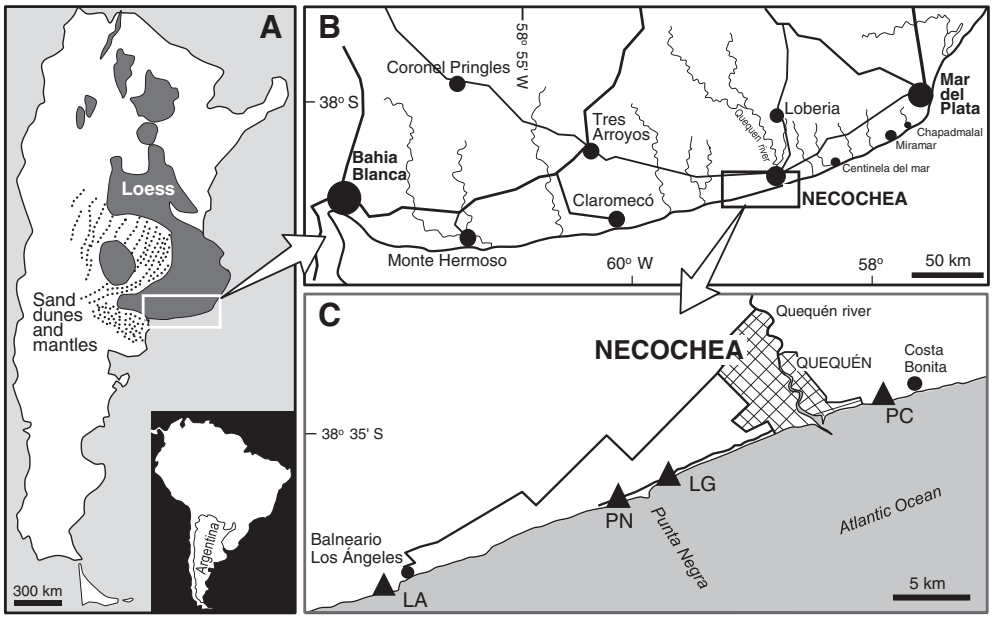

Fig. 1. A, Distribution of Late Cenozoic eolian loess and resedimented loessoid (dark gray) and sand (dots) deposits in Argentina (from Zárate, 2007). B, Location of Necochea area at south of Buenos Aires province. C, Map of the studied localities (triangles) in the coastal cliffs: PC (Punta Carballido), LG (Las Grutas), PN (Punta Negra west) and LA (Los Ángeles).

in palaeoenvironmental conditions, entails a dramatic decrease of dung availability, which might be reflected by dung beetle brood balls. The Late Pleistocene–Holocene extinction of the South American megafauna was envisaged by Halffter (1959, 1991) as a probable cause for the adoption of necrophagous feeding habits in dung beetles.

The objectives of this contribution are: 1) to describe a new ichnospecies of fossil brood ball, *Coprinisphaera akatanka*, 2) to analyze the location of the egg chamber as a useful character to recognize *Coprinisphaera* produced by necrophagous dung beetles, 3) to interpret the record of *Coprinisphaera akatanka* in relation with the large herbivorous scarcity occurred in the Sanandresian Substage of Buenos Aires province (Argentina), and 4) to reconstruct landscape and soils, along with climatic conditions where the Early Pleistocene Pampean dung beetles nested.

2. Geologic setting

2.1. Stratigraphy and age

Definition and treatment of lithostratigraphic divisions in the Late Cenozoic succession of the Pampean region are problematic because some units have local validity or were only differentiated by their content of fossil mammals. Notwithstanding, biozonation allows reasonable correlations among remote exposures of reduced thickness (Cione and Tonni, 2005). The Late Pliocene–Late Pleistocene interval, commonly composed by pedogenized fluvial, eolian (loess), and lacustrine deposits, constitutes the infill of reactivated valleys and floodplains (Zárate, 2005). This pedosedimentary succession includes the Pampeano Formation (Ameghino, 1908; González Bonorino, 1965) and the biostratigraphic Marplatan Stage (divided into Barrancalobian, Vorohuean, and Sanandresian), Ensenadan, and Bonaerian Stages (Fig. 2).

Outcrops in the Necochea area (Fig. 1) have been studied with palaeontological, biostratigraphic, and magnetostratigraphic purposes. According to the mammal record, Tonni et al. (1995) and Vucetich et al. (1997) assigned the lower beds of Punta Negra and Las Grutas to the Late Sanandresian Substage, the middle bed to the Ensenadan Stage, and the upper beds to the Bonaerian Stage. This scheme is also supported by Bidegain et al. (2005, Fig. 2, bed PN2), who recognized a classical Late Ensenadan mammal (*Mesotherium cristatum*) in the upper section of Punta Negra. A partial correlation among Las Grutas, Punta Negra, and Costa Bonita cliffs was proposed by Verzi et al. (2004, Fig. 5) based on the recognition of the *Ctenomys kraglievichi* zone (Lower Bonaerian). However, according to magnetostratigraphic and palaeontological data, Bidegain et al. (2005) considered that Punta Negra and Las Grutas beds are not entirely equivalent due to the intercalation of an erosive surface in the middle part of the last locality. Lower beds from both localities were tentatively correlated because they present normal polarity and include *Eucelophorus chapalmalensis*.

Facies distribution and the mentioned palaeontological and palaeomagnetic antecedents enable the division of the Necochea outcrops into three stratigraphic sections (Fig. 3A–D). Sedimentologic logs from Punta Carballido (PC), Las Grutas (LG), Punta Negra west (PN), and Los Ángeles (LA), where *C. akatanka* occurs, are shown in Fig. 4. The lower section (2.4 m thick) includes massive siltstones and calcic paleosols bearing *Coprinisphaera akatanka*. The middle section (up to 4.2 m thick) is characterized by cross-bedded conglomerates, siltstones, and calcic paleosols. The upper section (3.8 m thick) is formed by siltstones and thick calcretes. The lower section was correlated to the Ensenada Formation by Bidegain et al. (2005), and could be also attributed to the San Andrés Formation (Kraglievich, 1952). Comparable deposits

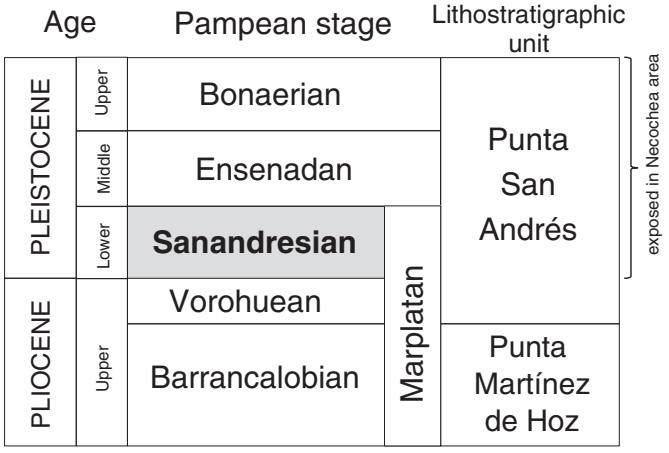

Fig. 2. Stratigraphy and age of Quaternary deposits in the southern Pampean region.

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