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.

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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 holarctic 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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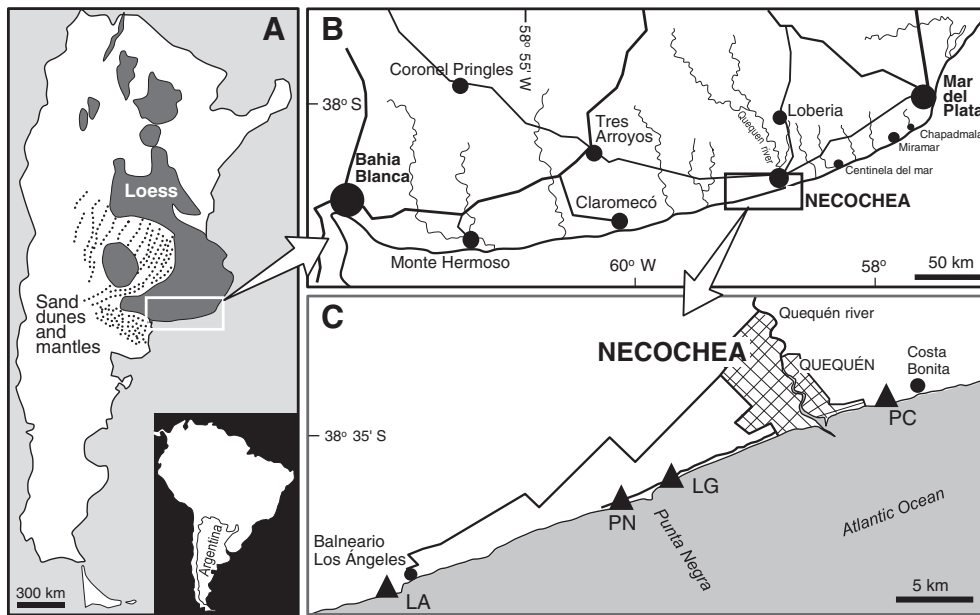*E-mail address:* cantil@macn.gov.ar (L.F. Cantil).

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

Age		Pampean stage		Lithostratigraphic unit	
PLEISTOCENE	Upper	Bonaerian		Punta San Andrés	exposed in Necochea area
	Middle	Ensenadan			
	Lower	**Sanandresian**	Marplatan		
PLIOCENE	Upper	Vorohuean			
		Barrancalobian		Punta Martínez de Hoz	

Fig. 2. Stratigraphy and age of Quaternary deposits in the southern Pampean region.
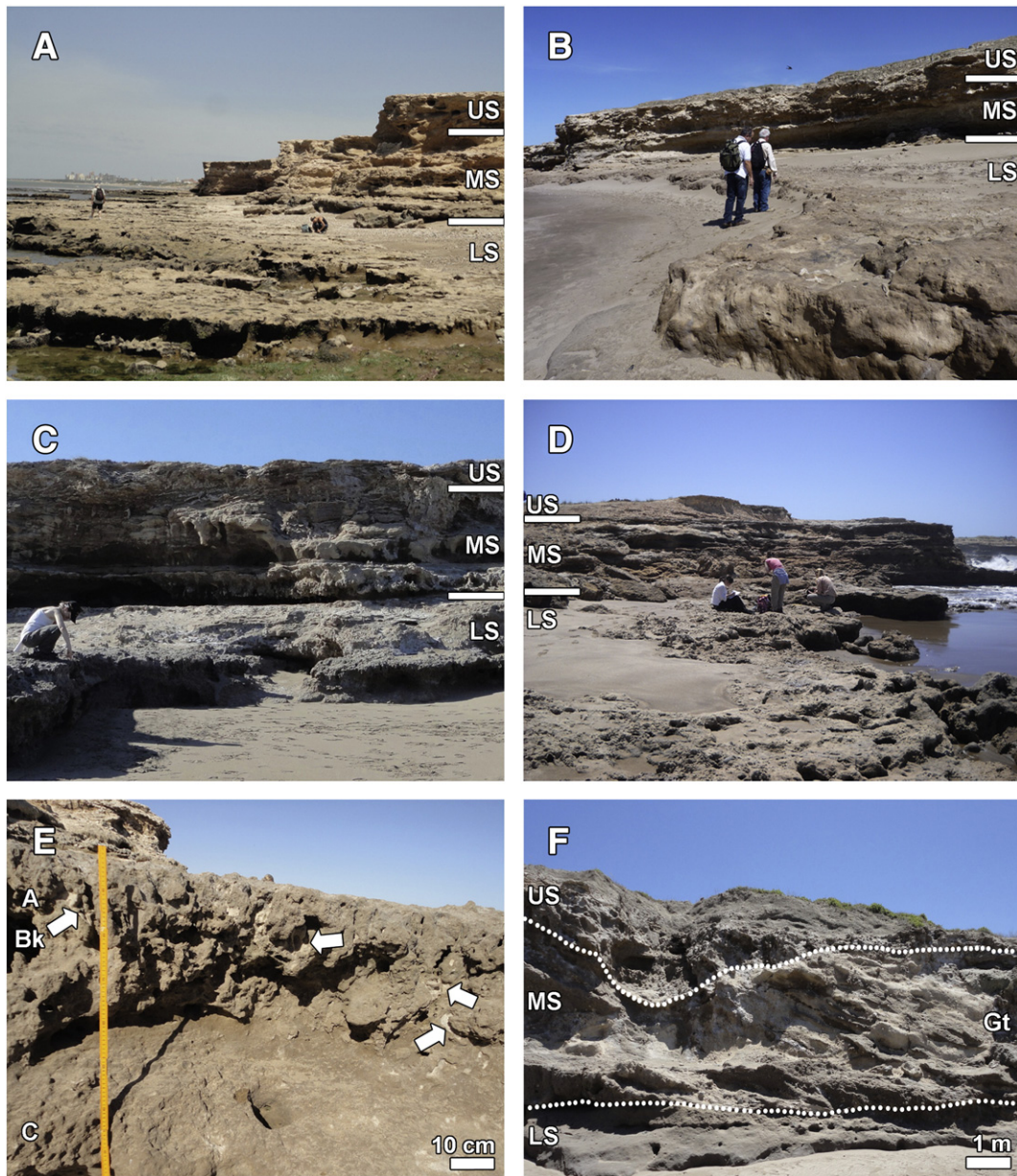
Fig. 3. Studied outcrops. A, Punta Carballido. B, Las Grutas. C, Punta Negra west. D, Los Ángeles (US: upper section, MS: middle section, LS: lower section). E, Pedotype 1 showing a rooted A horizon and carbonate nodules (arrows) in the Bk horizon. Downward changes in weathering are due to decrease in carbonate cementation in the profile. Locality LG. Total thickness 0.9 m. F, Matrix-supported conglomerates with large-scale inclined stratification (Gt), overlying pedogenized siltstones. Locality LG.

identified in exposures along Mar del Plata, Chapadmalal, Miramar, and Centinela del Mar coastal cliffs were grouped in the Punta San Andrés Alloformation (Zárate, 1989; Beilinson, 2009; Cenizo, 2011). At the type locality, the latter is composed by siltstones and silty claystones of aeolian (loessic) and subordinately fluvial origin, intensely modified by pedogenesis (Kraglievich, 1952; Zárate and Fasano, 1984). At Las Grutas and Punta Negra, the lower section contains *Eucelophorus chapalmalensis* and *Ctenomys* aff. *chapalmalensis* (Tonni et al., 1995; Bidegain et al., 2005; Soibelzon et al., 2009), which characterizes the Sanandresian Substage; assigned to the C2 Chron, between 2.59 and 1.81 Ma (Cione and Tonni, 2005) or to the interval 2.4–2.0 Ma (Woodburne et al., 2006). Verzi and Quintana (2005) attributed this stage to the Lower Matuyama Palaeomagnetic Chron (2.58?–2.14 Ma), while Bidegain and Rico (2012) referred the upper part of San Andrés Formation to the Olduvai Subchron (2.02–1.78 Ma) of Gelasian age (International Commission on Stratigraphy, 2012). In summary, the maximum chronologic interval of the Sanandresian beds is 2.59–1.81 Ma (Early Pleistocene). Middle

and upper sections from Necochea area were assigned to the Ensenadan (Middle Pleistocene) and Bonaerian (Late Pleistocene).

2.2. Facies and paleosols of the lower section

The lower section includes massive siltstones and two types of paleosols. Massive siltstones occur in uniform tabular beds, showing poorly defined stratification. Siltstones are well sorted and composed of feldspars, quartz, rock fragments, and volcanic glass shards (in order of importance). Color is pale to dark yellowish brown. This facies is exclusive of the lower section of LG, LA, and PN associated to beds modified by pedogenesis, showing ped structure, rhizoliths, nodules or mottles. Similar massive siltstones with calcareous nodules or crusts, and vertebrate and invertebrate trace fossils were observed at Punta Negra cliff (Vucetich et al., 1997). The mentioned characteristics and the close association with paleosols are typical of eolian loess deposits (Pésci, 1990; Muhs and Bettis, 2003), accumulated on floodplains.
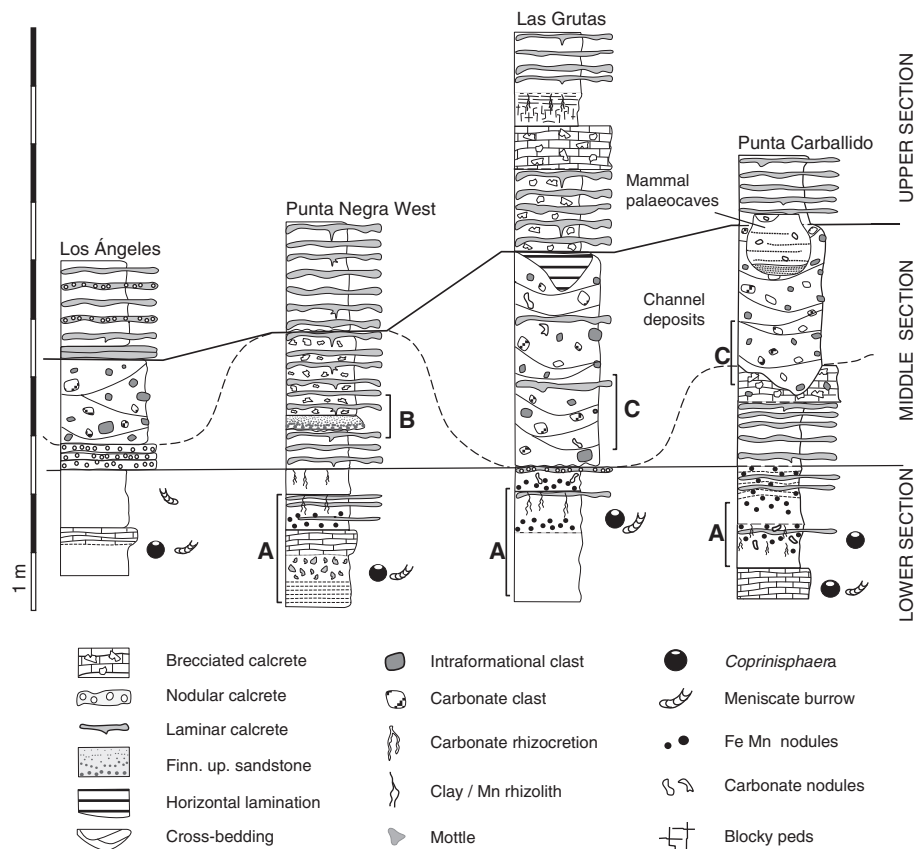
Fig. 4. Sedimentologic logs from coastal cliffs of Necochea area, including the location of *Coprinisphaera* in the lower section. A, *Ctenomys chapalmalensis* Biozone, Sanandresian Substage (Tonni et al., 1995; Bidegain et al., 2005; Soibelzon et al., 2009). B, *Mesotherium cristatum* Biozone, Ensenadean Stage (Bidegain et al., 2005; Soibelzon et al., 2009). C, *Ctenomys kraglievichi* Biozone, Bonaerian Stage (Verzi et al., 2004; Bidegain et al., 2005; Soibelzon et al., 2009).

Paleosols from the lower section are developed on massive siltstones and characterized by carbonate accumulations or calcretes, showing micrite, irregular or tuberose nodules, rhizoconcretions, and indurated continuous layers or crusts. Redoximorphic features produced by gleization or hydromorphism, such as Fe and Mn nodules, mottles, and manganese rhizoliths are also abundant. In some cases, surface (A) layers are not preserved due to horizon welding and erosion (Teruggi and Imbelloni, 1988). Trace fossils are also common features. Recognized trace fossils are *C. akatanka*, *C. murguiai*, *C.* isp., and *Taenidium barretti* (Bradshaw, 1981) (Fig. 5). The latter are sinuous, about 13 mm in diameter, mostly oriented parallel or slightly inclined to bedding. In some cases, these burrows intersect specimens of *Coprinisphaera* (Fig. 5D) or crosscut themselves (Fig. 5E, F). When bioturbation is high (>60%) the horizon shows widespread sediment reworking with few discrete trace fossils. According to these characteristics two pedotypes can be recognized (Fig. 6).

2.2.1. Pedotype 1

2.2.1.1. A horizon. Thickness 0.35–0.40 m. Coarse siltstone, pale yellowish brown (10YR6/2) to grayish orange pink (5YR6/2). Thin (2–4 cm thick) calcic ledges or laminar calcretes. Includes small Fe–Mn nodules. Clayey rhizoliths are abundant, thin (up to 2 mm) and short (up to 10 cm). Scarce black manganese rhizoliths also occur. The groundmass is moderately calcareous. The bioturbation is low to high. Thin sections show very low vesicular and (parallel) channel porosity (5%), formed by unconnected, irregular, and elongated voids. Coarse/fine distribution is chitonic to porphyric (Bullock et al., 1985). The coarse fraction is well sorted and composed of feldspars, quartz, volcanic and sedimentary

rock fragments, mafic minerals and glass shards (in order of importance) (Fig. 7A). The alteration of minerals is moderate. Micritic groundmass is dusky brown, very stained by Fe–Mn oxides. Birrefringence fabric is crystallitic. Small Fe–Mn nodules are very abundant. The voids are coated by calcite (Fig. 7A) or mixed laminated skins composed by Fe–Mn oxides, recrystallized micrite and clay. Ferruginous hypocatings also occur (Fig. 7A).

2.2.1.2. Bkg horizon. Thickness 0.40–0.50 m. Medium siltstone, dark to pale yellowish brown (10YR4/4, 10YR6/2). Abundant and medium to large carbonate nodules (3–12 cm across), laminar calcretes (3–6 cm thick), and large yellowish white rhizoconcretions (5Y9/1) (Fig. 3E). Fe–Mn nodules and small ferruginous, noncalcareous mottles, moderate yellowish brown (10YR5/4) in color. Scarce and thin rhizoliths (Fig. 7B). The bioturbation is low to absent. Thin sections show low (10%) chamber and channel porosity (Fig. 7B), with packing voids. The coarse/fine distribution is porphyric. The coarse fraction is well sorted and composed of feldspars, quartz, rock fragments, and volcanic shards (in order of importance). Alteration of feldspars and rock fragments is moderate to high. The argillic, noncalcareous groundmass is brown, showing irregular impregnation of Fe–Mn oxides defining mottles. The b-fabric is grain-porestriated and speckled. The simple speckled-crystallitic microfabric is formed by clay, lacking highly birefringent streaks. There are abundant Fe–Mn nodules, and scarce but thick compound (clay + Fe–Mn) skins in pores (Fig. 7C, D). Transported soil aggregates are coated by clay skins (Fig. 7D).

2.2.1.3. C horizon. Thickness 0.40–1.10 m. Coarse siltstone, slightly cemented by carbonate, moderate brown (5YR3/6) to pale grayish
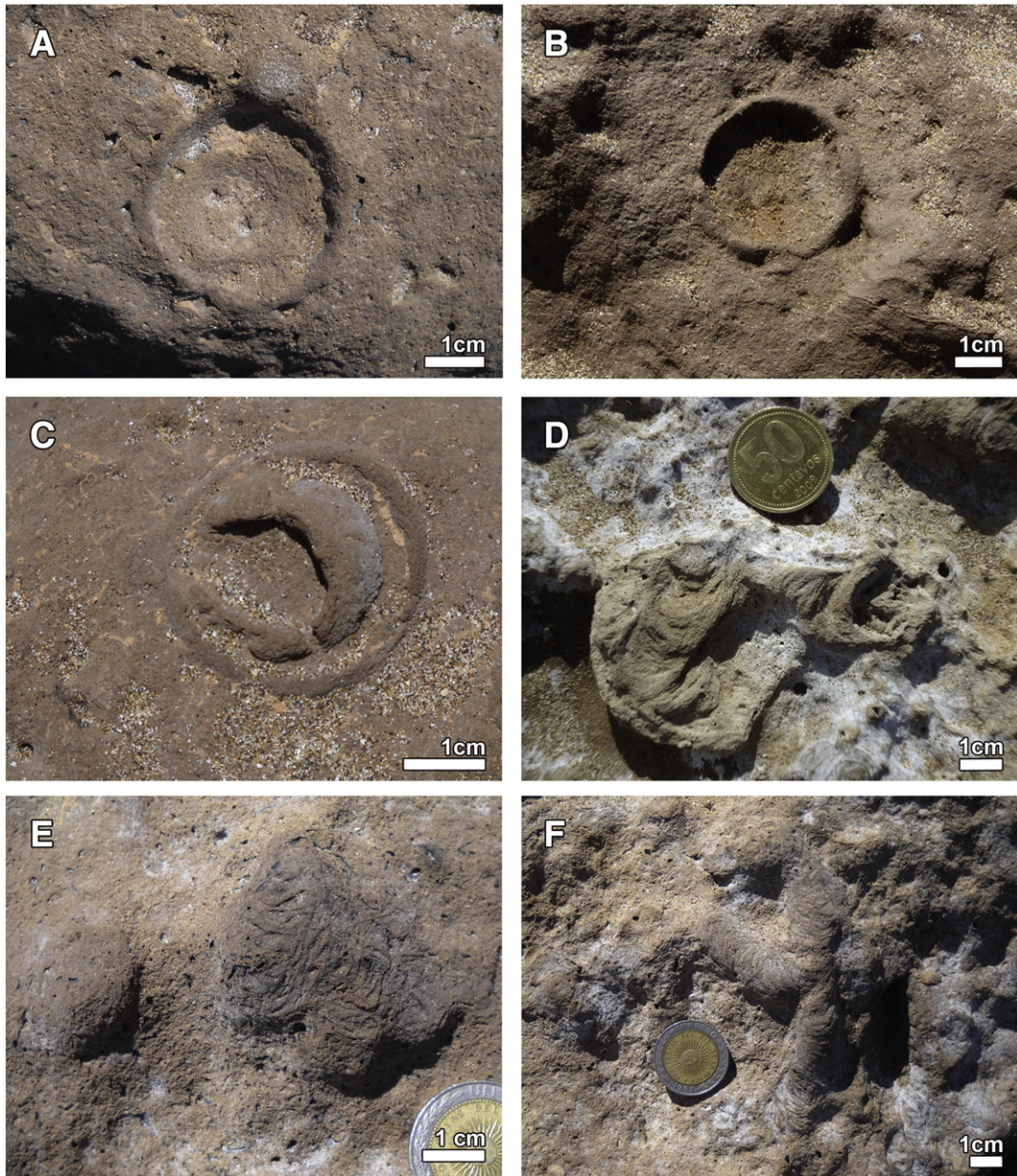
Fig. 5. Fossil brood balls on longitudinal section and meniscate burrows preserved in the same paleosol. A, *Coprinisphaera akatanka*. B, C, *Coprinisphaera* isp. D, *Taenidium barretti* crosscutting an specimen of *Coprinisphaera*. E, F, *Taenidium barretti*.
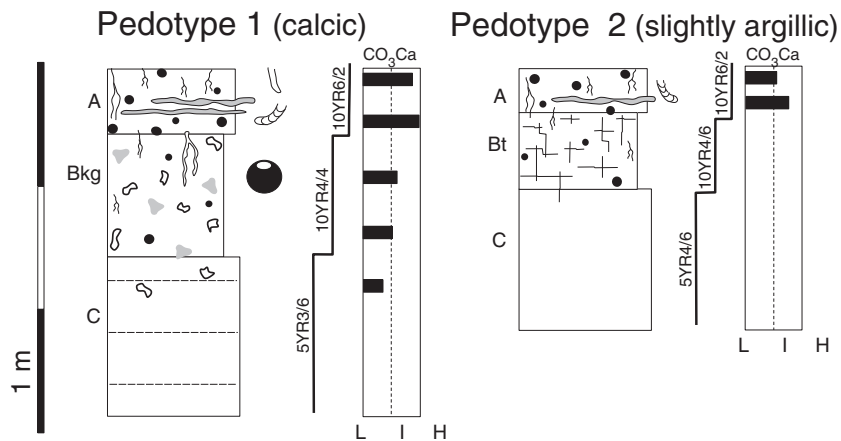

Fig. 6. Schematic profiles of pedotypes observed in the lower section (Sanandresian beds), showing vertical changes in color and carbonate concentration (L: low, I: intermediate, H: high). References in Fig. 3.
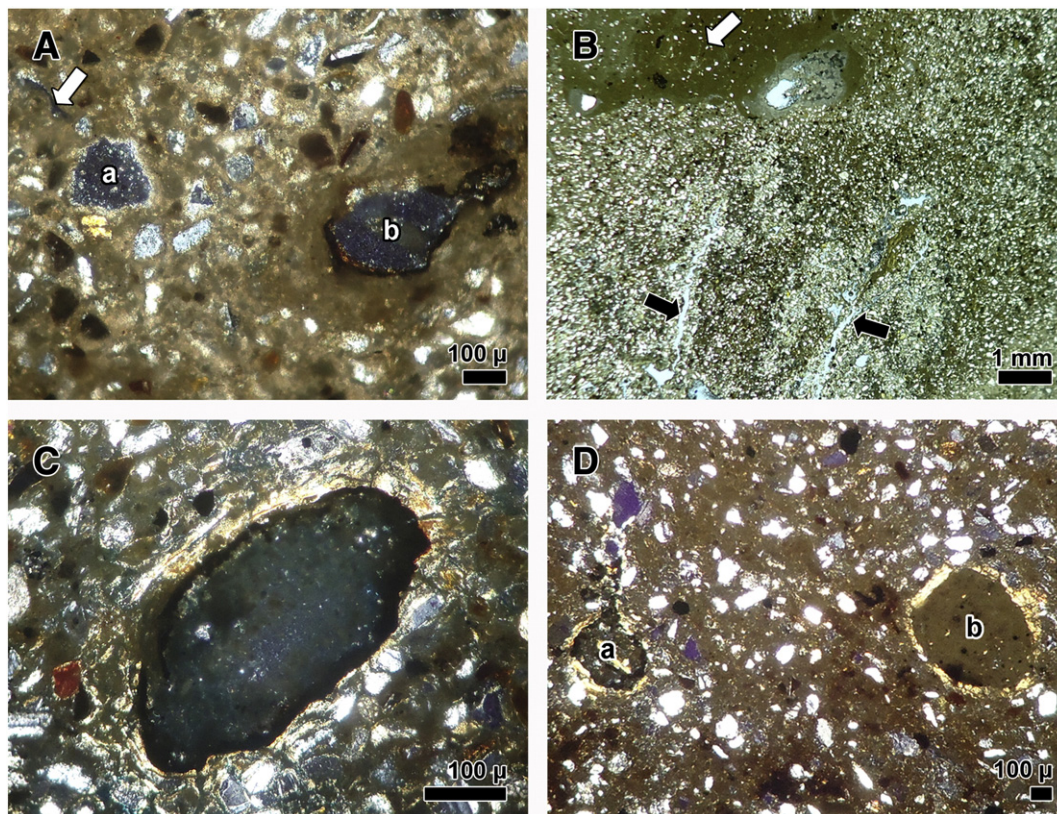
Fig. 7. Microscopic features of paleosols. A, (a) Pore with calcitic coating; (b) ferruginous hypo and quasicoating superimposed on a clay coating. A glass shard is also shown (white arrow). Crossed nichols. B, Dense complete infill of a rhizolith tubule (white arrow) and parallel channel porosity (black arrows). C, Large pore with a compound coating of clay and juxtaposed Fe–Mn oxides. Crossed nichols. D, (a) Pore showing clay and scarce Fe–Mn coatings; (b) soil clast coated by limpid clay. Crossed nichols.

orange (10YR7/2). Massive or relict lamination. Very scarce carbonate nodules in the upper part. No bioturbation.

2.2.2. Pedotype 2

2.2.2.1. A horizon.
Thickness 0.30–0.35 m. Coarse siltstone, pale yellowish brown (10YR6/2) to grayish orange pink (5YR6/2). Thin (2–4 cm thick) calcic ledges, and small Fe-Mn nodules. Noncalcareous groundmass. Scattered, short rhizoliths and low bioturbation. Thin sections exhibit very low vesicular porosity (5%) with isolated pores. Coarse/fine distribution is chitonic to porphyric (Bullock et al., 1985). The coarse fraction is well-sorted and dominated by feldspars, quartz, volcanic rock fragments, and mafic minerals (in order of importance). Grains are moderately altered, primarily in plagioclases and potasic feldspars. Micritic groundmass is dusky brown and intensely stained by Fe-Mn oxides. B-fabric is crystallitic. Abundant Fe-Mn nodules and pores with mixed (Fe-Mn oxides, clays and calcite) laminated skins were observed.

2.2.2.2. Btg horizon.
Thickness 0.25–0.35 m. Clayey siltstone, dark yellowish orange (10YR4/6). Ped structure changes laterally from coarse blocky to granular, defined by discontinuous clay skins. Small iron-manganese nodules. Noncalcareous groundmass. Bioturbation reduced to sparce rhizoliths. Thin sections show very low vesicular, chamber and channel porosity (3%). Scarce, connected and long channel voids, which define large blocky peds. Coarse/fine distribution is porphyric. The coarse fraction is moderately to well sorted, composed of feldspars, quartz, rock fragments, mafic minerals, and glass shards (in order of importance). Mineral alteration is moderate, but higher than in pedotype 1. Clayey groundmass, dark brown with high impregnation of Fe-Mn oxides. Punctuated to grainstriated b-fabric. Plasmic microfabric is simple speckled and undifferentiated, displaying dark, isotropic and nonbright clay. Abundant Fe-Mn nodules, some of them geodic and coated by clay. Laminated and thick mixed (clay + Fe-Mn) cutans are also abundant.

2.2.2.3. C horizon.
Thickness 0.40–1.10 m. Coarse to medium siltstone, moderate brown (5YR4/6). Massive or relict lamination. No bioturbation.

2.3. Middle and upper sections

These sections, which include no *Coprinisphaera*, are described together to aid in the characterization of the whole sequence. They comprise conglomerates or diamictites, sandstones, massive siltstones, abundant and strongly-developed calcretes, and paleosols. Cross-bedded conglomerates are matrix-supported and formed by large carbonate and muddy intraformational clasts, embedded in a silty fine sandstone matrix. This facies occurs in the middle section of the LG, LA, and PC profiles. Alike channel diamictites were described at Las Grutas (upper section) by Bidegain et al. (2005). The basal contact is erosive, ondulated or irregular, and in some cases displays a significant relief (up to 2 m). Top is flat and sharp. Total bed thickness ranges from 1.6 to 3.6 m. Lateral extension exceeds several hundred of meters. In continuous cliffs, conglomerates pinch-out pass laterally to massive siltstones with nodular calcretes. Large-scale through cross-bedding dominates along bed, but some sectors look massive or crudely stratified. Individual sets vary from 0.8 to 2.1 m in thickness, and up to 60 m in lateral extension. Graded sets and large-scale inclined surfaces cross the bed from top to bottom. Intraformational clasts include angular to subrounded carbonate and muddy fragments, and some Fe-Mn nodules. Distribution and placement of clasts is disorganized (vertical or horizontal) and poorly sorted, from 0.4 to 40 cm in size. Carbonate clasts are dominant and correspond to parts of calcrete or transported nodules. Locally, smaller extraformational clasts of probable volcanic origin, are concentrated. The silty matrix is pale yellowish brown

(10YR6/2) and also includes scattered coarse sand grains. In the upper part of the conglomerates, thin secondary calcrete horizons can be intercalated, which follows cross-laminae. At the top of them, lenticular silty sandstones showing fine or convolute lamination and ripple-marks also occur.

Cross-bedded conglomerates constitute the infill of fluvial channels established in silty floodplains. High-sinuosity rivers mobilizing a mixed load are suggested by the large-scale inclined surfaces and tridimensional dunes that are produced through cross-bedding. High-energy streams that resulted in the erosion of river banks are indicated by size (up to 0.4 m) and composition of intraformational clasts. Calcrete reworking is more common in weakly-developed calcretes because disconnected nodules are more easily eroded and transported (Gómez-Gras and Alonso-Zarza, 2003). Sandstone lens at top of channel bodies represent waning current stage and shallowing of channel previous to avulsion. Channel, matrix-supported conglomerates of these sections (Fig. 3F) are very similar to those described by Zárate and Fasano (1989) from the lower section of the Miramar Formation at Chapadmalal-Mar del Plata area. This correlation is confirmed by the identification of Ensenadan fossils in Necochea exposures (Bidegain et al., 2005; Soibelzon et al., 2009). Graded sandstones only appear as a single finning-upward (coarse to medium) bed in the middle section in of PN profile. The basal contact is erosive and covered by small intraformational clasts. Top is sharp. Laterally, this bed is replaced by the cross-bedded conglomerates or calcretes. Graded sandstones probably originate as overbank flows on floodplain.

These sections include pedogenic and scarce groundwater calcretes, along with argillic paleosols. Calcretes developed in siltstones and in diamictites, and are more abundant and thicker in the upper section. They display a wide range of structures and thickness, from isolated and coalescent nodules to thin continuous platty layers, and thick brecciated or recemented levels. Pedogenic carbonate accumulations correspond to stages II to VI in the classification scheme of Machette (1985). They are classified as moderate to strongly developed Aridisols. Thick laminar and brecciated calcretes of the upper section are interpreted as cumulative paleosols, formed under steady sedimentation, high rate of pedogenesis and low erosion.

Argillic paleosols, much less common, are thinner (0.65 m thick) and orange, and occur in the upper section of LG locality. They preserve a surface (A) horizon, moderate yellowish brown (10YR 5/4) that shows platty peds. It is constituted by moderately sorted, coarse siltstone grains of quartz, potassium feldspar, rock fragments, volcanic glass shards and mafic minerals. Top is slightly eroded. The subsurface horizon is a similar medium-coarse siltstone divided in an upper subhorizon (Bt), moderate yellowish orange (10YR 6/4) displaying well-developed blocky peds; and a lower subhorizon (Bw), grayish orange (10YR 7/4), with abundant manganese rhizoliths. At microscope presents chitonic–porphyric coarse/fine distribution and low porosity integrated by large, elongated and unconnected vesicles, packing and channel pores. The groundmass is stained and dark, displaying punctuated b-fabric, abundant Fe–Mn nodules, and mixed (clay and Fe–Mn oxide) skins in pores. These argillic and structured paleosols correspond to Alfisols.

3. Systematic ichnology

Specimens are deposited in the palaeontological collection of the Museo Municipal de Mar del Plata "Lorenzo Scaglia" (MMP/MMPI), in the ichnological collection of the Museo Paleontológico Egidio Feruglio (MPEF-IC) and in the ichnological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Icn). Since *Coprinisphaera akatanka*, the new ichnospecies described below, is separated from *Coprinisphaera tonnii*, the diagnosis of the latter is also included in this section. In descriptions, the main and secondary chambers height is defined as an axis that runs through the two chambers. Orthogonal to the former, the equatorial diameter is defined as the

larger width of the main and secondary chambers, respectively. The Wall Thickness Index (WTI) that represents the percentage of the equatorial diameter of the main chamber occupied by the wall, is defined as the relationship between the wall thickness and the equatorial diameter of the main chamber, multiplied by 200 (see Sánchez, 2009; Sánchez et al., 2010a).

3.1. Coprinisphaera akatanka isp. nov.

(Fig. 5A; Fig. 8.)
2003 *Coprinisphaera* isp. Mikuláš and Genise, p. 341, fig. 3I.
2006a *Coprinisphaera tonnii* Laza, p. 230 [*partim*].
2009 *Coprinisphaera* isp. B Sánchez, p. 103.
Holotype: One specimen (MMP 4046) from the Sanandresian Substage beds (Early Pleistocene) of the coastal cliffs of Las Grutas, Necochea, Buenos Aires province, Argentina. The specimen is preserved as a longitudinal half of the entire ball separated from the rock matrix in laboratory.
Paratypes: Four specimens (MMPI 111, 114, MACN-Icn 2404, 2413), from the same locality and Substage of the holotype. Specimens are preserved as a longitudinal half of the entire ball with the rock matrix.
Etymology: akatanka means dung roller beetle in Quechua, native language from some aboriginal communities.
Diagnosis: Isolated, bispherical, and thin-walled structures (WTI ≈ 16). They consist of a main, larger chamber and a secondary, smaller one, externally separated by a deep neck or constriction. Internally, they may be connected by a rounded and open passage. Passive infill is the norm.
Comments: The main ichnotaxobase that distinguishes this ichnospecies from the remaining ones of *Coprinisphaera* is its clear bispherical external shape (Sánchez, 2009). Laza (2006a) grouped bispherical *Coprinisphaera*, particularly the specimen selected herein as holotype of *C. akatanka*, with pear-shaped specimens of his new ichnospecies *C. tonnii*. Specimens of both ichnospecies are internally composed of a main spherical chamber separated from a secondary, smaller one. However, in *C. akatanka*, both spherical chambers are clearly distinguishable by an external deep neck, whereas in *C. tonnii*, this constriction is absent showing a pear-shaped external aspect. In addition, *C. akatanka* has a thin wall in contrast to the thicker one of *C. tonnii*. As recommended by Bertling et al. (2006), this separation is also supported by biological evidence that is discussed below.
Examined material: Seven specimens from Las Grutas (MMPI 102, 115; MMP 108; MACN-Icn 2402, 2403, 2407, 2424), one specimen from Los Ángeles (MACN-Icn 2416) and one from Punta Negra West (MACN-Icn 2437). Specimens are from the same Substage beds of the type material.
Description: In the holotype (MMP 4046; Fig. 8A, B), the main chamber is 44.1 mm in equatorial diameter and 42.2 mm high. It shows a wall, 3.4 mm thick, bearing 3 specimens of *Tombownichnus plenus* Mikuláš and Genise (2003). The secondary chamber is 18.6 mm in equatorial diameter and 14.3 mm high. Its wall is 3.1 mm thick. Both chambers are connected by a passage 9.5 mm in diameter. This specimen was illustrated by Mikuláš and Genise (2003, fig. 3I), and Sánchez (2009, fig. 6F, L). The main chamber of the paratype MMPI 111 (Fig. 8C) is 41.7 mm in equatorial diameter and 40.1 mm high. The wall, 3.1 mm thick, bears 5 specimens of *T. plenus*. The secondary chamber is 16.6 mm in equatorial diameter, 13.5 mm high and its wall is 3.5 mm thick. The connection between both chambers is absent. The main chamber of the paratype MMPI 114 (Fig. 8D) is 40.7 mm in equatorial diameter and 37.2 mm high. Its wall is 3.5 mm thick. The secondary chamber is 20.8 mm in equatorial diameter and 15.1 mm high. Its wall is 3.7 mm thick. Both chambers are connected by a passage 9 mm in diameter. The main chamber of the paratype MACN-Icn 2404 (Fig. 8E) is 47.1 mm in equatorial diameter and 46.7 mm high. Its wall is 3.7 mm thick and bears one specimen of *T. plenus*. The secondary chamber is 20.7 mm in equatorial diameter, the height is 13.9 mm and the wall thickness is 5.1 mm. The passage that connects both
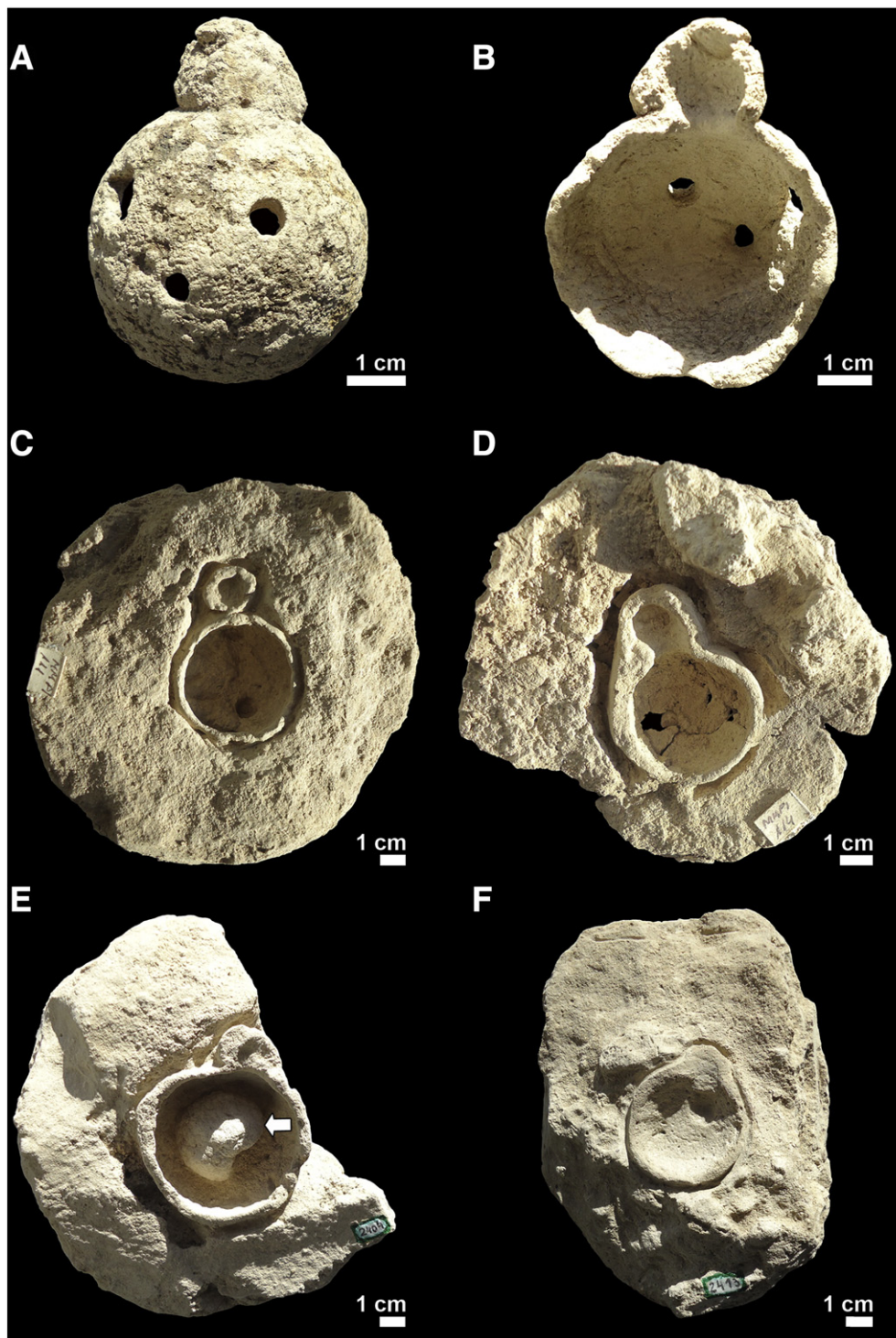
Fig. 8. Types of *Coprinisphaera akatanka* preserved as a longitudinal half of the entire ball. A, B, Internal and external view of the holotype (MMP 4046) bearing 3 specimens of *T. plenus*. C, D, E, F Paratypes included in the rock matrix: MMPI 111, MMPI 114, MACN-Icn 2404 and MACN-Icn 2413 respectively. Specimen MMPI 111 showing no connection between chambers and bearing *T. plenus*. Specimen MACN-Icn 2404 showing another spherical chamber inside the main one (arrow) and *T. plenus*.

chambers is 10.4 mm in diameter. This specimen preserves another spherical chamber inside the main one (Fig. 8E), which is 29.7 mm in equatorial diameter and 31.2 mm high. To avoid sectioning the specimen, the wall thickness of the internal chamber was not measured. The paratype MACN-Icn 2413 (Fig. 8F) is weathered to correctly measure the equatorial diameter and height of the main chamber. Its wall thickness is 3.2 mm. The secondary chamber is 13.7 mm in equatorial diameter and 13.9 mm high. Its wall is 3.7 mm thick. Both chambers are connected by a passage 8.4 mm in diameter.

Specimens of *Coprinisphaera akatanka* (including types) range from 39.3 mm to 47.6 mm in equatorial diameter (n = 13) and from 36.7 mm to 46.7 mm in height (n = 12). The mean value (±SD) of the wall thickness is 3.5 ± 0.2 mm (n = 14). The secondary chambers range from 13.7 mm to 20.8 mm in equatorial diameter and the mean height (±SD) is 13.6 ± 1.1 mm (n = 10). The wall of the secondary chambers range from 3.1 mm to 5.1 mm (n = 12). Two specimens (MACN-Icn 2404, 2424) preserve another spherical chamber inside the main one, 27.4 ± 3.3 mm in equatorial mean diameter (±SD)

and 29.3 ± 2.6 mm in mean height (±SD). The chamber inside the main one in specimen MACN-Icn 2424 shows a wall, 3.6 mm thick, and bears *T. plenus*. Eight specimens including types (MMPI 111, 115, MMP 108, 4046; MACN-Icn 2402, 2404, 2407, 2437) show *T. plenus* and two specimens (MACN-Icn 2403, 2424) show *Tombownichnus pepei* Sánchez and Genise (2009). The material examined contain passive infillings or are empty.

3.2. Coprinisphaera murguiai (Roselli, 1939)

One specimen of this ichnospecies (MACN-Icn 2432) was collected in Las Grutas. It is 42.7 mm in equatorial diameter and the wall, 3.8 mm thick, shows a hole 17.3 mm in diameter. A fragment of wall, probably part of the secondary chamber, is preserved around this hole. The specimen contains passive infillings.

3.3. Coprinisphaera isp.

Twenty nine specimens from Las Grutas (MACN-Icn 2400, 2401, 2405, 2406, 2409, 2410, 2412, 2414, 2417–2423, 2425, 2427, 2431, 2433; MMPI 101, 103, 105–107, 109, 112, 113, 120, 121), four specimens from Punta Negra (MACN-Icn 2408, 2434–2436), and one specimen from Punta Carballido (MACN-Icn 2426) are weathered or broken in such ways that cannot be attributed to a particular ichnospecies (Fig. 5B, C). Those specimens range from 35.2 mm to 50.2 mm in equatorial diameter (n = 33) and from 2 mm to 5.2 mm in wall thickness (n = 34). Eleven specimens (MMPI 109, 113; MACN-Icn 2409, 2415, 2418, 2420, 2422, 2423, 2426, 2435, 2436) preserve another spherical chamber inside the main one (Fig. 5C), which is 28.1 ± 3.2 mm in equatorial mean diameter (±SD) and shows a wall 4.1 ± 1 mm mean thick (±SD). Twenty one specimens (MMPI 101, 103, 105–107, 109, 112, 120; MACN-Icn 2401, 2408, 2410, 2412, 2414, 2419, 2421, 2423, 2425, 2427, 2434–2436) bear *T. plenus*. Two specimens (MACN-Icn 2431, 2434) bear *Lazaichnus fistulosus* Mikuláš and Genise, 2003. The material examined contain passive infillings or are empty.

3.4. Coprinisphaera tonnii Laza 2006

2006 *Coprinisphaera tonnii* Laza, p. 223, fig. 4A, B, E2, E4; p. 230 [*partim*].
2007 *Coprinisphaera tonnii*: Krell, p. 41.
2007 *Coprinisphaera tonnii*: Sánchez et al., p. 41.
2008 *Coprinisphaera tonnii*: Sánchez et al., p. 162.
2009 *Coprinisphaera tonnii*: Sánchez, p. 103.
2010 *Coprinisphaera tonnii*: Bellosi et al., p. 306.
2010 *Coprinisphaera tonnii*: Sánchez et al., p. 633.
2011 *Coprinisphaera tonnii*: Krell and Schawaller, p. 546.
Holotype: One complete specimen (MACN-Icn 1769) from the Colhue-Huapi Member (Lower Miocene) of the Sarmiento Formation at Gran Barranca, Chubut province, Argentina (Fig. 4E2 from Laza, 2006a).
Paratype: One specimen (MACN-Icn 1682) from Puesto Almendra Member (Middle Eocene–Lower Miocene) of the Sarmiento Formation at Gran Barranca, Chubut province, Argentina.
Emended diagnosis: Isolated, pear-shaped and thick-walled structures (WTI ≈ 36), internally composed of a main chamber and a secondary, smaller one, located in the upper protuberance. Both chambers are not separated externally by a deep neck or constriction but internally are clearly apart and may be connected by a small passage. Passive infill is the norm (modified from Laza, 2006a).
Examined material: Twenty two specimens from the Sarmiento Formation in the Chubut province (Argentina). Twenty from Gran Barranca locality: eighteen specimens from the Puesto Almendra Member (MACN-Icn 1611, 2258–2260, 2446–2448, 2450–2458; MPEF-IC 2305, 2307) and two from the Colhue-Huapi Member (MACN-Icn 2449;

MPEF-IC 2306). One specimen from Valle Hermoso (MACN-Icn 2444) and one from Aguada La Escondida (MACN-Icn 2445).

4. Discussion

4.1. Palaeonvironmental reconstruction and paleosols

Pedotype 1 dominates in the lower section along Necochea exposures, where *C. akatanka* occurs. These paleosols are yellowish brown, calcareous and rooted, with Fe–Mn nodules. The high concentration of calcium carbonate is noticed both micro- and macroscopically by the rhizoconcretions and the shallow (<0.2 m deep) calcic and petrocalcic (cemented) horizons. Such features characterize Aridisols (Soil Survey Staff, 1998; Alonso-Zarza and Wright, 2010) or Calcisols (Mack et al., 1993). An aquic hydrologic regime is suggested by the presence of Fe–Mn nodules and manganese rhizoliths in surface and subsurface horizons. Thus, pedotype 1 represents aquic Aridisols. Calcic horizons can be also present in Vertisols and argillic soils such as Mollisols and Alfisols. These orders are ruled out because the absence of slickensides and well-defined ped structure, respectively. The surface horizon is not clearly different from the lower ones. It is slightly lighter, more rooted, bioturbated, and posses more Fe–Mn nodules. The subsurface horizon is less calcic and bioturbated. Zárate and Fasano (1989) considered that Late Cenozoic Pampean calcretes, including those of San Andrés Formation, formed in the vadose zone by pedogenic and nonpedogenic processes. Evidence for a pedogenic origin associated to calcretized lithologies in pedotype 1 includes asymmetric vertical distribution of carbonate, nonmassive laminar calcretes, carbonate nodules with sharp margins (Pimentel et al., 1996), micrite surrounding clastic grains (Retallack, 2001), abundant rooting and rhizoconcretions, and clay illuviation microfabric (Williams and Krause, 1998). The absence of soil aggregates is interpreted as primary due to minimal clay enrichment (chitonic grain-size distribution) and the meager development of the pore system (few vesicular, unconnected pores). Simple speckled, crystallitic and undifferentiated microfabric indicate apedal structure. After-burial modification or destruction of the original ped structure can occur by compaction or other less common secondary processes. However, the studied sequence supported limited burial considering the reduced thickness of overlaying deposits. Capping, continuous and solid or laminar calcic horizons (stages IV–V after Machette, 1985), and the distinction of horizons indicate strong soil development (Machette, 1985; Retallack, 2001). However, the intermediate alteration of feldspars, lithic grains and shards, along with the spreading of the micrite replacing groundmass suggests moderate soil development, conditioned by not humid conditions. Thus, soil development degree of pedotype 1 is strong to moderate.

Pedotype 2 exhibits weaker development, different composition of the subsurface horizon and lesser bioturbation intensity than pedotype 1. Surface horizon is moderately calcareous, with evidences of impeded drainage such as the extended Fe–Mn impregnation and nodules, along with short rhizoliths. The underlying horizon is thin and noncalcic, and includes little illuviated and recrystallized clay. It displays coarse and moderately-defined ped structure formed by a scarce vesicular and channels voids. These features define a weak subsurface clayey horizon (Btg). Chemical weathering of feldspar, volcanic rock fragments and shards is little more advanced than in pedotype 1. This led to an enrichment of clay, recognized by the porphyric coarse/fine distribution. Moderate to low illuviation is evident by the scarce clay coatings, and the simple speckled microfabric denotes apedal structure (Retallack, 2001). These properties point out to a calcic Inceptisol. Argillic soils (e.g. Alfisol, Mollisol) are discharged because insufficient secondary clay increase, likewise Aridisol due to not enough carbonate concentration.

Depositional facies and paleosols preserved in the lower section suggest that soils bearing *C. akatanka* originated in distal sectors of a fluvial floodplain, far from the influence of active rivers. Both pedotypes show

no evidence of erosion or truncation of surface horizons (e.g. erosion boundaries, rip-up clasts in C horizons), as it was observed in similar Pampean paleosols (Zárate et al., 2002, 2009). The absence of clear surficial layers in well-drained soils of loess successions can be the response to very slow influx of windblow sediment added to the soil fabric (cumulic horizon) by the action of roots and invertebrates (Mason and Jacobs, 1998). Pedogenic calcification is considered the more prominent process in pedotype 1 (gleyey Aridisols). Wright et al. (1988) demonstrated that laminar calcretes are formed as surface horizons by calcification of horizontal fine root tubules or mats and fungi (rhizogenic calcretes or rootcretes), or by the action of cyanobacteria (Verrecchia et al., 1995), bacteria (Verrecchia and Verrecchia, 1994), and lichens (Klappa, 1979). Rhizoconcretions develop as calcareous encrustations in roots by repeated wetting and drying cycles (Retallack, 2001), or by biogenic mediated calcifications of root cells (Alonso-Zarza et al., 1998). Moderate to good drainage for a part of the year is suggested by the presence of carbonate nodules and depth of rhizoliths. On the other side, widespread redoximorphic features (Fe–Mn groundmass impregnation, nodules, mottles, and pore skins) originated by local waterlogging in the stagnant groundwater zone. Gleying suggests a seasonal high water-table and lowland setting for these paleosols. The concurrence of these features along with calcareous nodules suggests temporal changes in drainage conditions. The Bkg horizons record these characteristics, reflecting aquic conditions. Waterlogging is not a favorable condition for nesting insects, including dung beetles (Genise et al., 2004). Accordingly, brood balls (*Coprinisphaera akatanka*) would have been constructed during dry seasons.

Advanced calcification is a common process in semiarid and arid environments (Buol, 1964; Gile et al., 1965; Rabenhorst and Wilding, 1986). Moisture in pedocals is not sufficient to leach carbonate, reflecting dry seasonal climate (Retallack, 2009), generally with mean annual precipitation less than 650 mm. The coexistence of strong-moderately developed calcretes with gleying features point out to semi-arid mildly-seasonal conditions for pedotype 1. Estimated mean annual precipitation (MAP) is 500–350 mm. A mean annual temperature of 7 °C was proposed by Beilinson and Raigemborn (2012) for Sanandresian paleosols based on geochemical analysis.

Paleosols having loess deposits as parent material are highly fertile because they are rich in unweathered minerals and have high capacity to retain water (Retallack, 2001). Open, low or sparse (xerophytic) vegetation generally prevails on calcrete-bearing soils (Alonso-Zarza and Wright, 2010). It is also supported by size and morphology of rhizoliths, which suggest dominant herbaceous or shrubby plants (Retallack, 2000). According to Birkeland (1999) and Retallack (2001), strong to moderate development degree observed in calcic paleosols represents a lapse of about 10^4–10^5 years of geomorphic stability, little or no erosion and null or very reduced accumulation rate.

Calcic Inceptisols (pedotype 2) probably formed under a precipitation regime slightly lower than the pedalfer-pedocal (or ustic/udic) boundary. This dividing line depends on mean annual temperarture: 500 mm/y in colder climates and 600 mm/year in warmer climates (Birkeland, 1999). However, it is inferred that differences with pedotype 1 are not due to climate differences (MAP) according to the nearby stratigraphic position. The lower carbonate content and the higher clayness of pedotype 2 would record a variation in soil humidity related to drainage conditions and topography. The slightly clayey subsurface horizon with ped structure and clay skins (illuviation argillans) formed above the zone of water table fluctuation.

The Late Pliocene–Early Pleistocene was subject to a global cooling (Tripati et al., 2010; Etourneau et al., 2012). Patagonian and Pampean landscapes and ecosystems were strongly affected by several glacial–interglacial (cold-warm) cycles in the last 5 m.y. (Rabassa et al., 2005). The Early Pleistocene was characterized by intermediate $\delta^{18}O$ values in benthic forams, and cycles of small frequency (41 kyr) and high intensity, governed by the obliquity of the Earth's rotational

axis. Two phases (2.45–2.25 and 2.10–1.65 Ma) of inferred glaciations have been recognized during the Sanandresian Substage according to dated till deposits from Patagonia (Rabassa et al., 2005). These cold events favored aeolian loess transport and accumulation in the Pampean region (Spalletti, 1992; Iriondo, 1999; Muhs and Zárate, 2001). However, a single relationship between climate phase and loess deposition is not proved (Rabassa et al., 2005). Sanandresian semi-arid temperate-cold environments interpreted herein from Necochea paleosols are supported by caviomorph rodents (Verzi and Quintana, 2005). Tonni (2009) inferred important biotic and climatic changes during Late Sanandresian lapse based on the extinction of autochtonous taxa and the advent of mammals adapted to cold-dry conditions related to Patagonian glaciers expansion. This cooling and drying lapse is evidenced by vegetation changes and faunal turnovers. The last include the first appearance of taxa adapted to cooler and more open habitats, along with the extinction of subtropical mammals (Verzi and Quintana, 2005).

Facies, paleosols and calcretes recognized in the Ensenadean and Bonaerian beds of Necochea area record a change in sedimentary environment. In the middle section, a subhumid–semiarid fluvial landscape can be inferred through the conglomerates accumulated in high-sinuosity channels along with the Alfisols and calcic paleosols formed in floodplains and abandoned channel bars. Massive mudstones and well-developed calcretes of the upper section indicate renewed loessic sedimentation and semiarid conditions.

4.2. Dung pad scarcity and the record of necrophagous feeding habits

Coprinisphaera ichnospecies include trace fossils consisting of spherical, subspherical, pear-shaped, and bispherical chambers surrounded by a discrete wall (Genise, 2004). Laza (2006a) grouped pear-shaped with bispherical structures in *C. tonnii* considering that, internally, both show a complete and small secondary chamber separated from the main larger one. The pear-shaped brood balls, which remain as *C. tonnii* according to the present proposal, show a thick wall that contains the entire secondary chamber in a protuberance in the upper part of the structure. In contrast, the new ichnospecies *Coprinisphaera akatanka* (Fig. 8), includes specimens showing thin walls and the secondary chamber separated from the main chamber by a deep neck, determining their bispherical shape. This morphological distinction qualify as different ichnospecies also based on the interpretation of the structures and affinities.

The main chambers mentioned above are interpreted undisputedly as provision chambers, the spherical chambers inside the main ones are interpreted as pupation chambers and the secondary, smaller ones, as egg chambers of dung beetle brood balls (e.g. Genise, 2004; Laza, 2006a; Sánchez et al., 2010b). The unique location of the egg chamber in *C. akatanka*, resulting in a bispherical structure, is the major ichnotaxonomic feature to attribute this ichnospecies to modern representatives. The brood balls of the necrophagous *Canthon cyanellus cyanellus*, *Canthon bispinus*, and *Canthon quinquemaculatus*, are bispherical structures composed of an egg chamber separated from the provisions, which is externally marked by a deep constriction (Judulien, 1899; Halffter et al., 1983; Morelli and González Vainer, 1990; Favila, 2001; Sánchez, 2009; Rueda et al., 2012) (Fig. 9). The similarity between the brood balls of the species of *Canthon* mentioned above and *C. akatanka* suggests that the putative producers of this ichnospecies were related to this extant genus. Moreover, there is no evidence about coprophagous beetles producing bispherical brood balls (Halffter and Matthews, 1966; Halffter and Edmonds, 1982). The size of dung beetle brood balls is related to the size of their producers: large dung beetles produce larger brood balls than small beetles (Halffter and Matthews, 1966; Klemperer and Boulton, 1976; Sato and Imamori, 1987; Scholtz et al., 2009; Sánchez et al., 2010a). The larger size of *C. akatanka* in comparison with the brood ball sizes of the extant necrophagous *Canthon*, whose diameter range from 10 to 20 mm

Fig. 9. External (left) and internal (right) views of a brood ball of *Canthon quinquemaculatus*.

(Judulien, 1899; Morelli and González Vainer, 1990; Favila, 2001), poses the question on how phylogenetically related were *C. akatanka* producers with extant necrophagous *Canthon*.

Based on the location of the egg chamber in relation to the provision chamber, Laza (2006a) recognized different morphologies in fossil brood balls on which he based the ichnospecies. Laza (2006a) proposed a morphological evolution for these ichnospecies, from those having egg chambers excavated inside provisions to those in which the egg chambers are completely separated from them. The steps recognized were: a) The egg chamber is located inside provisions in *Coprinisphaera murguiai* (Roselli, 1939); b) upper half included in the wall and the lower half included in the provisions in *Coprinisphaera kheprii* Laza, 2006; c) upper half probably of unpreservable material (dung fibers) and lower half included in the outer side of the wall in *Coprinisphaera lazai* (Sánchez et al., 2013) and d) completely included in a thick wall, in a protuberance in the upper part of the ball in *Coprinisphaera tonnii* Laza 2006. Laza (2006a) grouped those balls showing egg chambers separated by an external deep neck from the main ones, as *C. akatanka*, together with *C. tonnii*. The ichnotaxonomical distinction of *C. akatanka* may be reflected in a new step in this morphological evolution. *Coprinisphaera kraglievichi* (Roselli, 1939), *C. kheprii*, *C. tonnii* and *C. akatanka* are used herein to represent the series (Fig. 10). The higher isolation of the egg chamber from provisions was proposed as a mechanism to avoid contact between the egg and possible cleptoparasites, parasitoids and fungi brought with the provisions (Laza, 2006a; Sánchez, 2009). The provisions used by necrophagous dung beetles are cadaveric remains, particularly meat, tendons, hair, skin, feathers, animal fat (Barattini and Sáenz, 1953; Halffter and Matthews, 1966; Favila, 2001; Cantil et al., 2012) and often carnivore dung (Krell et al., 2003). Necrophagous dung beetles, such as some *Canthon* species (and *C. akatanka* producers), would provide their bispherical brood

balls with the most complete isolation of the egg from provisions, suggesting that carrion would be more readily or harmfully infested than dung (Laza, 2006a; Sánchez, 2009).

It is believed that necrophagy is a derived behavior from coprophagy in Sacarabaeinae (Halffter and Matthews, 1966; Halffter and Edmonds, 1982; Halffter, 1991; Hanski and Cambefort, 1991; Zunino, 2002). It has been also suggested that the adoption of necrophagous habits in South American Scarabaeinae may be linked to reduced dung resources due to the mass extinction of herbivorous megamammals by the Holocene (Halffter, 1959; Halffter and Matthews, 1966; Halffter, 1991). The absence of dung beetle body fossils in South America, including necrophagous taxa, have precluded any test of this hypothesis. Most specimens of *Coprinisphaera* recorded until now in the Asencio Formation (Uruguay; Lower Eocene), Sarmiento Formation (Chubut, Middle Eocene–Lower Miocene), Pinturas Formation (Santa Cruz, Lower Miocene), and Collon-Curá Formation (Neuquén, Río Negro, northern Chubut; Middle Miocene) were attributed to coprophagous beetles (Genise and Bown, 1994; Laza, 2006a; Sánchez et al., 2007; Sánchez, 2009). Only one specimen from the Sarmiento Formation was suggested to be the product of a necrophagous dung beetle due to its scarce phytolith content (Sánchez et al., 2010a). The occurrence of *C. akatanka*, attributable to necrophagous producers, in a sequence with an available mammal record is an opportunity to test Halffter (1959) idea that necrophagy may be triggered by scarcity of herbivore dung, irrespectively of the age considered.

Necrophagous dung beetles that produce large brood balls comparable in size to *C. akatanka*, may exploit small and medium sized carcasses in early stages of decomposition (Martinez, 1959). For coprophagous dung beetles, the potentially exploitable dung for producing large brood balls is that deposited in large dung pads, which is an exclusive character of some groups of large mammals (Halffter and Matthews,
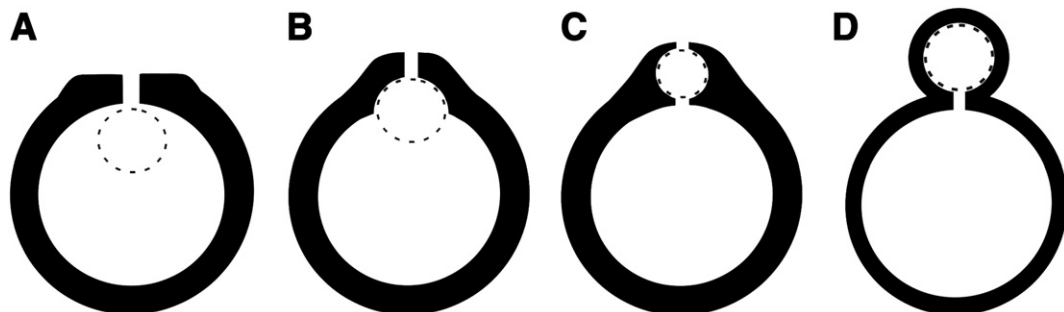

Fig. 10. Different location of the egg chamber in relation to the provisions in *Coprinisphaera*. A, *C. kraglievichi*. B, *C. kheprii*. C, *C. tonnii*. D, *C. akatanka*.

1966; Sánchez et al., 2010a). The fossil mammal record shows that the Sanandresian Substage of the coastal cliffs of Buenos Aires province is dominated by caviomorph and cricetid rodents (Pardiñas, 1995; Vucetich and Verzi, 1995) and, to a lesser extent, marsupials (*Lestodelphys*) and mustelids (*Stipanicicia*) (Cione and Tonni, 2005). All of them are relatively small mammals producing small dung pellets and/or carnivore or insectivore feces. It has been suggested that Equids, particularly *Hippidion*, arrived during the first pulse of the GABI during Vorohuean Substage, based on a single record by Reig (1957) (Alberdi and Prado, 1995b; Cione and Tonni, 2005). Hence, its presence in Sanandresian time cannot be discarded. Beside this record, only *Neuryurus* sp. (Glyptodontidae) and *Glossotherium* sp. (Mylodontinae) were recorded for the Sanandresian Substage of the coastal cliffs of Buenos Aires province (Scillato-Yané et al., 1995; Zurita et al., 2009). The architecture of *Neuryurus* and *Glossotherium* masticatory apparatus suggest herbivorous bulk-feeding habit (Bargo and Vizcaíno, 2008; Vizcaíno et al., 2011). The sparse records of herbivorous megamammals, potential producers of suitable pads for coprophagous dung beetles in Sanandresian beds, is a result of the disappearance in the area of the older xenarthans such as *Trachycalyptus*, *Urotherium*, *Plohophorini*, *Paraglyptodon*, *Glossotheridium*, *Proscelidodon*, and *Scelidotheridium*; and the absence of mastodons and other large herbivores such as *Glyptodon*, *Mylodon*, *Doedicurus*, *Panochtus*, and *Pampatherium*, which arrived later at this region with the GABI during the Ensenadan Stage (Alberdi and Prado, 1995a; Scillato-Yané et al., 1995; Cione and Tonni, 2005). The absence of Litopterna and the taxonomic diversity decrease of Notoungulata during the Marplatan Stage have been also pointed out by Bond et al. (1995). That stage represents a period of reduced faunal diversity following the Chapadmalalan Stage. Only 47% of all species survived in the Barrancalobian Substage (Lower Marplatan), with a significant absence of medium to large mammals (Vizcaíno et al., 2004).

The Pliocene–Pleistocene outcrops of the coastal cliffs from the Buenos Aires province lack other records of *Coprinisphaera*, precluding to trace a detailed relationship with the presence and abundance of large herbivores. However, the Sanandresian bottleneck for dung availability might be a significant feeding stress for triggering the necrophagous feeding behavior in dung beetles that produced *C. akatanka*.

5. Conclusions

1. The new ichnospecies, *Coprinisphaera akatanka*, is separated from *C. tonni* because of its thin walls and bispherical structure consisting of the egg and the provision chambers externally separated by a deep neck or constriction.
2. The bispherical morphology resembles brood balls constructed by necrophagous species of *Canthon*, suggesting that *C. akatanka* is the first *Coprinisphaera* ichnospecies produced by necrophagous dung beetles.
3. The necrophagy of *C. akatanka* producers would be related with the scarcity of dung produced during the Sanandresian Substage due to the extinction of most of the older herbivores and the absence of those that arrived later at the Pampean region during the Ensenadan Stage.
4. *C. akatanka* is recorded in lowland paleosols developed in Pampean loess deposits, from a stable floodplain with slow accumulation rate, covered with herbaceous and shrubby vegetation under a seasonal, semiarid temperate-cold climate during a phase of glacier expansion in Patagonia.

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