

## Dung beetle brood balls from Pleistocene highland palaeosols of Andean Ecuador: A reassessment of Sauer's *Coprinisphaera* and their palaeoenvironments

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### ABSTRACT

Independently, Roselli (1939) and Sauer (1955) described and named similar fossil brood balls from the Paleogene of Uruguay (*Devincenzia murguiai*) and from the Quaternary of Ecuador (*Coprinisphaera ecuadoriensis*), respectively. In their contributions, they illustrated and described fossil brood balls characterized by the presence of a medium-sized hole piercing the wall of spherical to sub-spherical chambers. Newly collected brood balls from palaeosols of the Cangahua Formation (Ecuador), and other previously deposited in ichnological collections from Ecuador, Uruguay, and Argentina, including type material, were revised to update *Coprinisphaera* ichnotaxonomy. *Coprinisphaera ecuadoriensis* Sauer (1955) is a subjective junior synonym of *Coprinisphaera murguiai* (Roselli, 1939). *Coprinisphaera murguiai sensu Laza, 2006* (non Roselli, 1939) is in turn a new ichnospecies named herein *Coprinisphaera lazae* isp. n. Additionally, a new ichnospecies, named herein as *Coprinisphaera kitu* isp. n., was found in the Cangahua Formation. It is represented by a spherical to sub-spherical chamber having a discrete wall, with a crown composed of a hemispherical structure on one pole. The statistical analysis of the size of the two ichnospecies found in the Cangahua Formation suggests that *C. kitu* and *C. murguiai* may represent two stages (closed and emerged balls, respectively) of a unique original morphology (*C. kitu*) and producer. There are no extant dung beetle species that construct brood balls with a morphology similar to that of *C. kitu*. The producer of *C. kitu* would be the recently described fossil Phanaeini, *Phanaeus violeetae*. Phytoliths extracted from infillings of closed *C. kitu* revealed that Poaceae were mostly included in the diet of the herbivores that produced the dung. Considering the vertebrate fossil record for the Pleistocene Cangahua Formation, ground sloths, mastodons, and horses could have been the dung providers. The record of *Tombownichnus plenus*, *Lazaichnus fistulosus*, and *Castrichnus incolumis* suggests the presence of cleptoparasites and detritivores in the dung community. Cangahua sediments accumulated in a volcanoclastic, intermontane setting located at 2500–2900 m.a.s.l. and under fluctuating syneruptive conditions. Changes in facies associations and palaeosol types enable to distinguish three stages in evolution of sedimentation and landscapes. Calcic Andisols, andic Aridisols, and andic Mollisols, in the upper section, are the pedotypes that more commonly include *Coprinisphaera*. The intravolcanic environments where dung beetles, and probably large herbivores, better developed were temperate, seasonal, semiarid to subhumid, grasslands and wooded grasslands. They were covered by ashfalls reworked by wind and minor volcanoclastic flows.

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### 1. Introduction

Dung beetle fossil brood balls, included in the ichnogenus *Coprinisphaera*, are among the first and more common insect trace fossils described from palaeosols, having an ichnofacies dedicated to them (Genise et al., 2000), and a lot of more recent research (Genise, 2004; Laza, 2006; Sánchez and Genise, 2009; Sánchez et al., 2010a,b; and references therein). They were firstly recognized in Argentina and

Uruguay and attributed to dung beetles (Frenguelli, 1938a,b; Roselli, 1939), and secondly in Ecuador (Estrada, 1941; Bruet, 1950; Sauer, 1955, 1956). Frenguelli (1938a,b), who first described fossil brood balls from Argentina, was against naming trace fossils. In 1939, Roselli described *Devincenzia murguiai* from Uruguay. However, this ichnogenetic name was preoccupied (Genise and Bown, 1994). Sauer (1955), having overlooked Roselli's work, named similar fossil brood balls from the Pleistocene Cangahua Formation of Ecuador as *Coprinisphaera ecuadoriensis*. The possible synonymy between *C. murguiai* (Roselli, 1939) and *C. ecuadoriensis* Sauer, 1955 has been a pending ichnotaxonomical issue (Sánchez et al., 2010b). In addition, Laza (2006), who considered the former as a different ichnospecies, included under that

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name Patagonian specimens, which we here describe as a new ichnospecies, *Coprinisphaera lazai* isp. n.

This confusing state of the art called for an ichnotaxonomical arrangement, which is presented herein along with a revision of Sauer's *Coprinisphaera*. In addition, new field work and revision of Ecuadorian ichnological collections revealed the presence of a new brood ball morphology that is described herein as the new ichnospecies *Coprinisphaera kitu* isp. n. Ecuadorian *Coprinisphaera* was statistically analyzed in order to compare the size of both ichnospecies, and to estimate the possible number of dung beetle species involved using the same methodology applied for Patagonian material (Sánchez et al., 2010b). Accordingly, the phytolith content to infer dung provider's diet and vegetation, and traces in the specimens to infer components of the dung community were analyzed following the methodology of Sánchez et al. (2010a) and Sánchez and Genise (2009), respectively.

The Cangahua Formation is a distinctive and typical volcanoclastic succession from the Andean region of Ecuador (Clapperton and Vera, 1986), which apart from *Coprinisphaera*, bears abundant Quaternary mammals (Lujanian chronofauna) (Hoffstetter, 1952; Ficarelli et al., 1992). Although the first mention of the fossil brood balls was more than 70 years ago (Estrada, 1941), the distribution of *Coprinisphaera* and changes in palaeosol types and sedimentary palaeoenvironments along this unit had been neglected until now.

Particular objectives of this contribution are: 1) to redescribe and update the ichnotaxonomy of the Ecuadorian *Coprinisphaera*, 2) to recognize the affinities of the possible producers, 3) to infer the herbivores

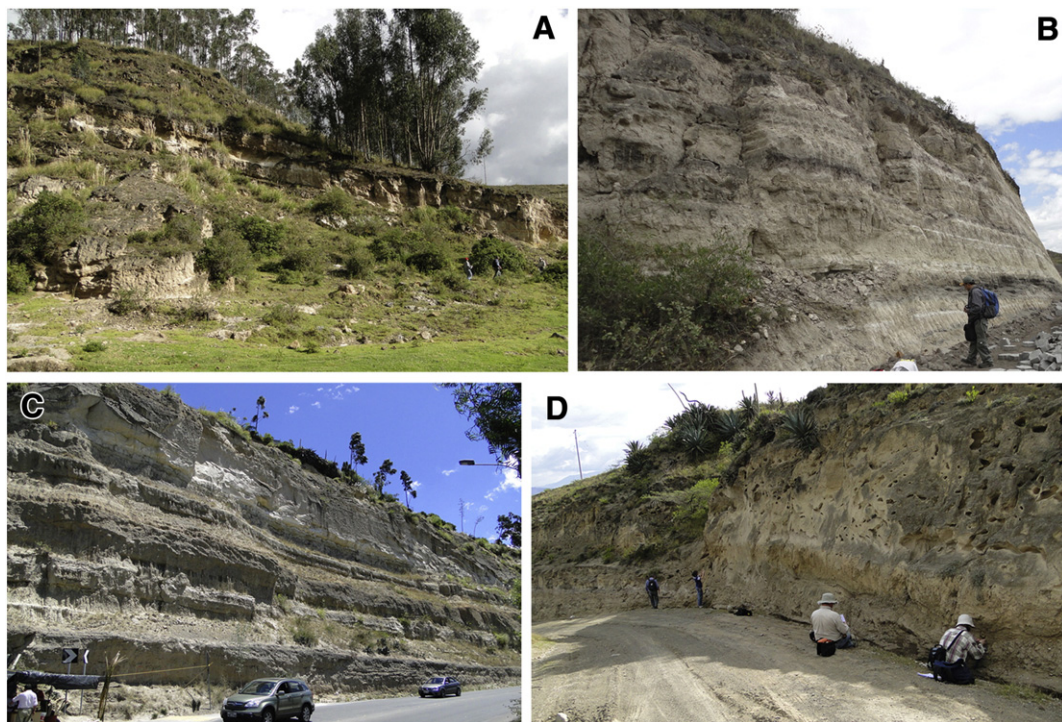
that provided the dung and their diet, 4) to recognize cleptoparasites and detritivores associated with brood balls, 5) to stratigraphically locate Ecuadorian *Coprinisphaera* and to reconstruct its depositional volcanoclastic setting, 6) to characterize palaeosols bearing *Coprinisphaera*, 7) to infer environmental conditions and evolution of the Pleistocene ecosystems inhabited by herbivores and dung beetles.

## 2. Material and methods

During the field work in August 2011, 41 specimens of *Coprinisphaera* were collected at seven localities where the Cangahua Formation crops out in north-central Ecuador. Six of these localities are either in Quito (Universidad Central) or near this city, in the Pichincha province: Tumbaco, Tanda Arriba, Tanda Abajo, La Merced, and Río Chiche bridge (Figs. 1, 2). Only one, Quebrada Chalán, near Punín, is in the Chimborazo province (Figs. 1, 2). Detailed sedimentologic profiles and lithologic sampling were accomplished at these localities. Palaeosols were characterized macro and microscopically, following criteria of Bullock et al. (1985) and Retallack (2001). Collected trace fossils were brought to the laboratory at the Museo de Historia Natural "Gustavo Orcés V.", Escuela Politécnica Nacional (Quito), to be examined along with other material previously deposited there in the Colección de Icnología. This additional material ( $n = 123$ ), collected by one of us (JLRC) comes from two localities of Quito: La Ronda and Escuela Politécnica Nacional, and from another one, Tababela (new airport), near this city (Fig. 1). Further material from Quito ( $n = 17$ ), and others without clear provenance



Fig. 1. Location map. (A) Distribution of the Cangahua Formation (dark grey areas) in the Interandean Depression of northern Ecuador. (B) Detailed map of the area near Quito. Main volcanoes (triangles), studied localities (circles). QCh: Quebrada Chalán, EPN: Escuela Politécnica Nacional.



**Fig. 2.** Main studied localities of the Cangahua Formation. (A) Quebrada Chalán, middle and upper sections. (B) Tanda abajo (Guayllabamba), middle section. (C) Río Chiche bridge, lower and middle sections. (D) Tanda arriba, middle section.

( $n = 4$ ), come from old collections of the Escuela Politécnica Nacional possibly deposited there by W. Sauer or R. Hoffstetter. Table 1 contains all the records of collected *Coprinisphaera*, along with other localities where uncollected specimens were cited in the literature or observed by one of us (JLRC). This table also shows the associated fossil mammals recorded by different authors. In 1955, Sauer had already observed that palaeosols bearing *Coprinisphaera* were richer in mammal remains than beds without them.

Each specimen deposited at the Colección de Icnología was prepared, measured, and labeled. Complete specimens, showing no cracks in the walls, were cut into longitudinal sections involving the medium-sized hole or the crown to measure and observe internal characters. Three closed specimens of the new ichnospecies (*C. kitu*) from La Ronda (EPN-Icn 035, 051, 164) and one without provenance (EPN-Icn 182), which showed unaltered wall, were selected for phytolith analysis. It is assumed that in these completely closed balls, which are quite unusual in southern South America, the infilling preserved into the main chamber represents the original provision of the brood ball, namely the mammal dung used by beetles to make the ball (Sánchez et al., 2010a). Each selected specimen was cut longitudinally, in the same way described above, and a sample of approximately 10 g of infilling of each *C. kitu* was removed to be later processed (Sánchez et al., 2010a). Phytolith extraction was carried out following standardized method of Zucol and Osterrieth (2002), and Sánchez et al. (2010a). Only the fine fraction (3.9–63  $\mu$ ), which contained most phytoliths, was used for identification and counting. Middle (63–250  $\mu$ ) and coarse (above 250  $\mu$ ) fractions, which showed few phytoliths, were preserved for possible future analyses. From each microscope slide, counting points of phytoliths were taken at random until no new morphotypes appeared (Erra, 2011). All phytoliths observed in the microscope field at 400 $\times$  were included in countings, and each morphotype was recognized following the morphological classification of Twiss (1992) modified by Zucol (2001). When the attribution to a morphotype was unclear, it was identified by comparison with published photographs of extant and fossil phytoliths (Gallego and Distel, 2004; Fernández Honaine et al., 2006; Piperno, 2006).

### 3. Geologic setting

Estrada (1941), and later Sauer (1950), were the first to notice the presence of dung beetle fossil brood balls in the Cangahua Formation, a Quaternary volcanoclastic succession bearing abundant fossil vertebrates and widely exposed in the Neogene Interandean Depression or Valley. This north–south oriented, intra-arc basin is located in the northern half of central Ecuador and southern part of Colombia, between the Cordillera Occidental and the Cordillera Real (Fig. 1). It is coincident with the North Volcanic Zone, including numerous strato-volcanoes of Pliocene–Quaternary age, and developed since the Late Miocene (Ficcarelli et al., 1992) as a compressional push-down type basin bounded by reverse faults (Lavenu, 2006).

Mammal remains were intensely studied by Hoffstetter (1952). The fossil fauna is composed dominantly of extinct Proboscidea (mastodons) and Pilosa (mylodonts), and a less proportion of equids, cervids, pastoral cricetids, scarce camelids, lagomorphs, and some carnivores (*Smilodon*) (Ficcarelli et al., 1992, 1997). This vertebrate assemblage was assigned to the Lujanian South America Land Mammal Age (Ficcarelli et al., 1992; Coltorti et al., 1998). In accordance with this fossil content, isotope dating indicates an upper Middle to Late Pleistocene age for the Cangahua Formation. Bristow et al. (1980) reported a >48.8 ka radiocarbon date obtained from a wood fragment, east of the Ilalo volcano. Considering archaeological evidence, microliths and thermoluminescent dating, Clapperton and Vera (1986) proposed an age between 100 and 13 ka for Sangolqui (near Quito) region. Finally, a chronologic range between 260 and 20 ka was postulated by Hall and Mothes (1997) according to an ash flow dated at 211 ka from the Cotopaxi area.

The thickness of the Cangahua Formation decreases regionally to the south (Ficcarelli et al., 1997), from about 100 m in Carchi province (Baldoock, 1982) to 22 m in Chimborazo province. More locally, thickness is variable because the unit constitutes the infilling of an irregular topography that drapes a regional erosional unconformity. Near Bolívar it lies on the volcanic Chota Formation (Ficcarelli et al., 1992). In the Sangolqui–Quito–Guayllabamba region it covers volcanoclastic and



**Table 1**  
Localities of the Cangahua Formation with collected and uncollected *Coprinisphaera* and fossil mammals recorded herein, in the literature, and by one of us (JLRC).

Locality	GPS	Associated mammals	References
Altiplano of Ecuador	–	–	Bruet, 1950
Vera street, Quito, Pichincha province	–	Fragments of vertebrate fossils	Sauer, 1955, 1956
Ladrón de Guevara street, Barrio La Floresta, Quito, Pichincha province	S 00°12'46.08" W 78°29'12.88"	–	JLRC
Morales street, Barrio La Ronda (former Quebrada Jerusalem), Quito, Pichincha province	S 0°13'27.7" W 78°30'51.5"	<i>Glossotherium wegneri</i> , <i>Pantera onca andina</i> , <i>Equus andium</i>	Román-Carrión, 2008; 2012b
Rither street, Quito, Pichincha province	–	–	Zunino, 2013
Mariana de Jesús Av., Quito, Pichincha province	S 00°08'08.95" W 78°29'43.39"	–	JLRC
Barrio Llano Chico, Quito, Pichincha province	S 00°08'01.2" W 78°26'26.8"	<i>Stegomastodon</i> sp., <i>Megatherium</i> sp., <i>Glossotherium</i> sp., <i>Equus</i> sp., <i>Palaolama</i> sp., <i>Odocoileus</i> sp.	Hoffstetter, 1952; Spillmann, 1938
Barrio La Magdalena, Quito, Pichincha province	S 00°14'36.85" W 78°31'30.01"	<i>Equus andium</i> .	Spillmann, 1931; JLRC
Parque Metropolitano, Quito, Pichincha province	S 00°11'04.36" W 78°28'24.20"	–	JLRC
Parque La Carolina, Quito, Pichincha province	S 00°10'37.42" W 78°28'58.62"	<i>Equus</i> sp.	JLRC
Universidad Central (campus), Quito, Pichincha province	S 00°12'00" W 78°30'18.2"	–	This contribution
Río Chiche bridge, Quito, Pichincha province	S 00°12'21.5" W 78°22'16.2"	–	Sauer, 1965; this contribution
Escuela Politécnica Nacional (campus), Quito, Pichincha province	S 00°12'40.1" W 78°29'19.4"	–	JLRC
Tababela, Yaruquí (new airport), near Quito, Pichincha province	S 00°08'25.2" W 78°21'07.3"	<i>Equus andium</i> , lagomorphs, rodents	JLRC
Caraburo, NE Quito, Pichincha province	–	<i>Equus andium</i> , <i>Palaolama reissi</i> , <i>Odocoileus virginianus</i> , lagomorphs, rodents	Román-Carrión, 2012a
Quito region, Pichincha province	–	Mastodons, horses, deers	Estrada, 1941
Tumbaco, Puente La Morita near Quito, Pichincha province	S 00°13'40.1" W 78°24'28.7"	<i>Equus andium</i>	This contribution
Tumbaco, Pichincha province	–	–	Custode et al., 1992
Tanda Arriba, Guayllabamba, Pichincha province	N 00°00'25.5" W 78°20'20.8"	<i>Stegomastodon</i> sp., <i>Equus andium</i>	This contribution
Tanda Abajo, Guayllabamba, Pichincha province	S 00°00'28.0" W 78°19'21.6"	Rodents	This contribution
La Merced, Quebrada Santa Ana, Pichincha province	S 00°17'47.7" W 78°24'46.9"	–	Vera, 1977; Clapperton and Vera, 1986; this contribution
Río Inga, Pichincha province	S 00°18'12.41" W 78°21'41.27"	<i>Stegomastodon</i> sp., <i>Glossotherium</i> sp., <i>Equus andium</i>	JLRC
Quebrada Chalán, near Punín, Chimborazo province	S 01°46'36.6" W 78°38'00.8"	<i>Equus andium</i> , <i>Glossotherium</i> sp., <i>Odocoileus</i> sp., lagomorphs	Román-Carrión, 2010; Román-Carrión and Lara, 2011; this contribution
Alor, settlement close to Ficarelli localities in Bolívar, Carchi province	S 00°27'67.56" W 77°54'29.72"	<i>Stegomastodon</i> sp.	JLRC, Ficarelli et al., 1995
Cusubamba, Cotopaxi province	S 01°03'36.41" W 78°41'19.80"	<i>Equus</i> sp., <i>Stegomastodon</i> sp.	JLRC

conglomerate deposits of the Pleistocene Chiche Formation (Clapperton and Vera, 1986). However, Ficarelli et al. (1992) considered this boundary as transitional. In Ambato-Lacatunga provinces (100 km south of Quito) it lies upon tuffs dated in 1.21 Ma (Barberi et al., 1988), corresponding to the Lower Pleistocene Chalupas Formation (Lavenue, 2006). Finally, at Alausi-Riobamba region it covers conglomerates and pyroclastics of the Pleistocene Palmira Formation. The top of the Cangahua Formation is generally eroded and covered by recent deposits or soils. Late Quaternary strata are commonly faulted. The last tectonic phase begun at the end of Pleistocene and is still active in the northern Ecuadorian Andes (Tibaldi and Ferrari, 1992). These authors recognized N–S and NNE–SSW transtensional faults with an *en-echelon* arrangement, as the dominant structural system in the Interandean Depression.

Lithologic composition of the Cangahua Formation is uniform at regional scale. From the Bolívar area, 150 km NE of Quito, Ficarelli et al. (1992) described uncommon lava flow intercalations and facies similar to those mentioned herein. In the Punín area, 180 km S of Quito, the deposits do not differ from those of Pichincha province. Both sections were correlated by the presence of *Haplomastodon* (Ficarelli et al., 1995).

At the localities studied herein (Fig. 2) and considering the most complete profile (i.e. Río Chiche bridge), the Cangahua Formation is divided into three sections (Fig. 3). Each one is characterized by a particular association of depositional (volcaniclastic or siliciclastic) facies and palaeosol types. Fig. 4 shows the correlation of the studied localities on the basis of these properties. Two main types of volcaniclastic facies are recognized (Bellosi et al., 2012). The finer one is the most common in all sections and corresponds to massive or crudely bedded, pyroclastic mudstones and very fine tuffaceous sandstones. Mantle bedding is commonly observed. Color varies from yellowish brown to light greyish brown. Very commonly are modified by pedogenesis (Fig. 5A, B). They are ungraded but some dispersed fine gravel clasts can be included. The lower contact is generally sharp. The second facies predominates in the middle section and corresponds to grey or white, massive or normally graded matrix-supported breccias (Fig. 5C) and pumiceous lapilli, both showing erosive lower contact. Cross-bedding is also observed in some beds. Siliciclastic deposits are very scarce and occur in the lower section. They are fining-upward clast-supported conglomerates with rounded lithic clasts. At La Merced, trough cross-bedded, pyroclastic sandstones were also observed (Fig. 5A). Siliciclastic facies constitute fluvial channel bodies with erosional base. Some of them

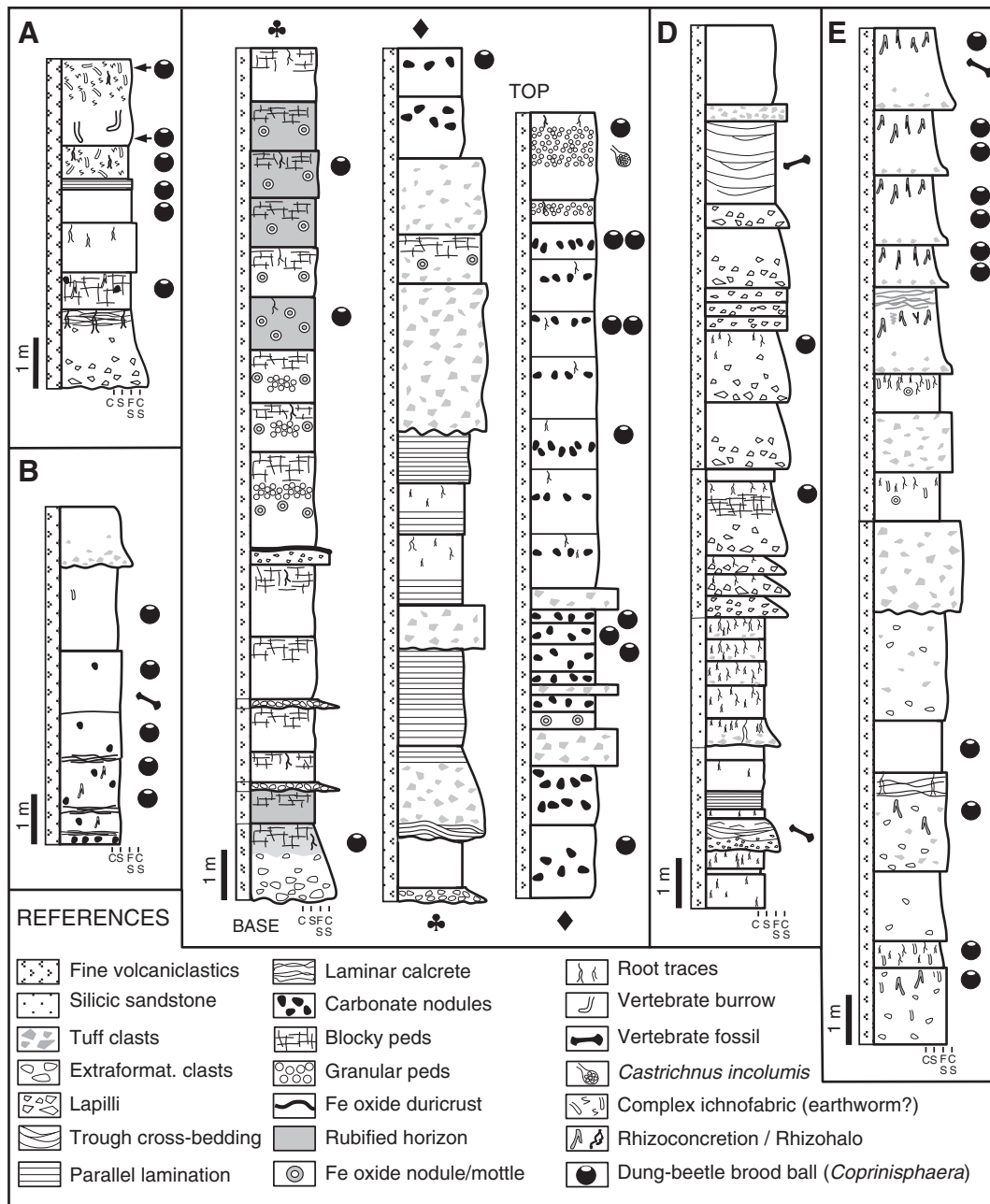


Fig. 3. Sedimentologic profiles at different localities. (A) Tanda Arriba. (B) Tumbaco, north of Ilalo volcano. (C) Río Chiche bridge. (D) Tanda Abajo. (E) Quebrada Chalán in Punín province.

include broken or polished *Coprinisphaera* mixed with soil fragments (Clapperton and Vera, 1986).

### 3.1. Palaeosols

At Río Chiche bridge, 75% of the beds exhibit evidence of modification by soil forming processes, particularly in the lower and upper sections (Fig. 3). At other localities, this proportion ranges from 40% to 70%. Smectite is the dominant clay mineral in these palaeosols (Vera and Lopez, 1986), which commonly preserve 1–10% of total organic matter (Clapperton and Vera, 1986; Vera and Lopez, 1986).

According to field and micromorphologic properties three types of palaeosols were distinguished (Bellosi et al., 2012) (Fig. 6). The first pedotype predominates in the lower and middle sections at Río Chiche bridge and La Merced (Quebrada Santa Ana), and is scarce at

Tanda abajo. It corresponds to moderately developed, structured and slightly reddened Fe-rich palaeosols (Fig. 6A, B). They present three horizons, greyish orange pink to light brownish grey in colour. The surface horizon is intensely rooted. The subsurface horizons (0.3–0.6 m thick) are oxidized and clayey, showing subangular blocky (Fig. 6A, B) or granular ped structure (Bt horizon). Dispersed or grouped ferruginous nodules (Fig. 5I), mottles and undulated to folded, thin (2–6 mm) crusts (Fig. 5E) are also common. Trace fossils are represented by clayey rhizoliths, drab rhizohaloes, and uncommon *Coprinisphaera*. Thin sections exhibit a mixed channel and crack microstructure with scarce and incomplete aggregates, in a continuous non carbonate soil phase (Fig. 7A). Pores are elongate or irregular and generally unconnected. They show thin clay cutans stained by iron oxides (Fig. 7C). Alternatively, spongy and prismatic microstructures are also observed, with higher porosity (20%) formed by interconnected elongate pores. Massive

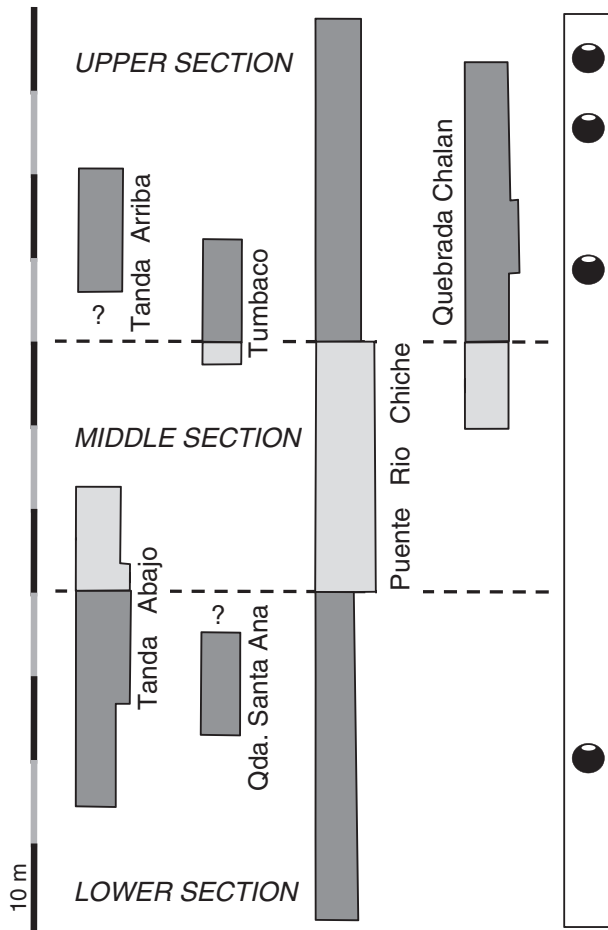


Fig. 4. Correlation of measured profiles in the Cangahua Formation according to facies associations and palaeosol types in the most complete locality (Río Chiche bridge).

or impregnative Fe–Mn nodules and mottles are common (Fig. 7C). The groundmass consists of opaque clay because of the presence of abundant iron-manganese oxides. Recrystallized clay is generally scarce. Grain framework (25–30%) is poorly sorted, constituted by coarse silt and very fine sandstone grains. They correspond to intensely altered rock fragments (mafic volcanic rocks), corroded plagioclase, stained glass shards, hornblende, pyroxene, biotite, quartz, and magnetite. The association of macro and micro pedofeatures of pedotype 1 is indicative of moderately to poorly drained andic Alfisols (Fig. 6A, B).

The second pedotype is yellowish grey or light brown in colour, and occurs at several localities, in the middle and upper sections (Fig. 6C). It is characterized by a calcic horizon composed of carbonate nodules and

rhizoconcretions indicative of a better drainage. Thin laminar (Fig. 5H) or nodular calcretes (Bk horizon), and massive crusts were also observed. Rhizoliths are not commonly preserved, whereas *Coprinisphaera* specimens are abundant in several horizons. A variant observed at Río Chiche bridge (uppermost section) and Tanda Arriba presents a darker surface horizon with rhizoliths, and a subsurface argillic horizon with crumb or fine granular ped structure (Fig. 5B, G), scarce calcareous

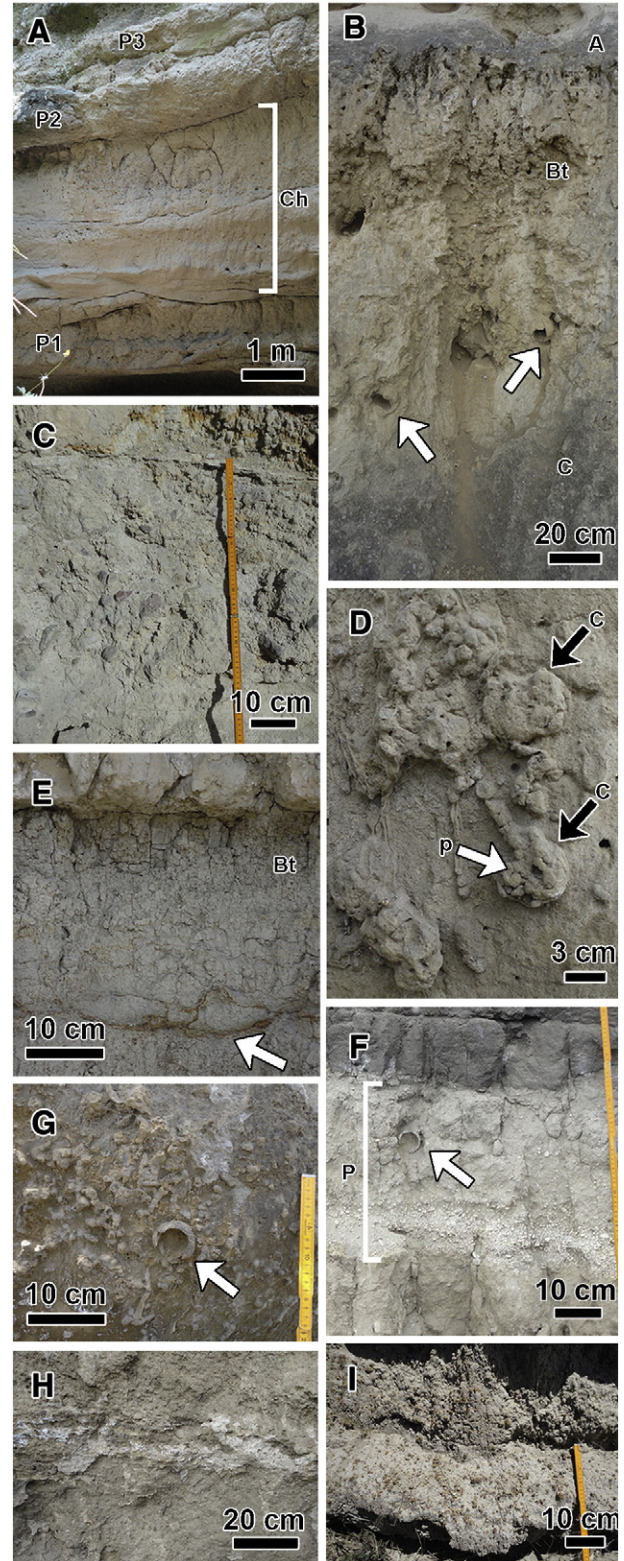


Fig. 5. Depositional facies and palaeosols of the Cangahua Formation. (A) Fluvial channel body (Ch) showing erosive base and pedogenized upper part. Other palaeosols are also shown (P 1, P 2, P 3), lower section, Quebrada Santa Ana (La Merced). (B) Andic Mollisol from the upper section, showing mollic dark A horizon with rhizoliths, argillic horizon (Bt) with crumb ped structure, burrows and *Coprinisphaera* (arrows), Tanda arriba. (C) Matrix-supported, disorganized volcanic breccia. Middle section, Quebrada Chalan. (D) Group of *Castrichnus incolumis*, earthworm aestivation chambers with pellets (p) preserved inside, upper section, Río Chiche bridge. (E) Alfisol (eroded surface horizon) showing blocky peds (Bt horizon) and ferruginous crusts (arrow), lower section, Río Chiche bridge. (F) Andic Entisol (P) with few rhizoliths, developed in a graded volcanoclastic deposit. *In situ Coprinisphaera* (arrow), middle section, Tanda abajo (Guayllabamba). (G) Bt horizon with small granular peds, abundant burrows and *Coprinisphaera* (Mollisol), upper section, Río Chiche bridge. (H) Laminar calcrete, Aridisol, upper section, Tumbaco. (I) Fe nodules in two subsurface (B) horizons. Andic Alfisol, Río Chiche bridge.



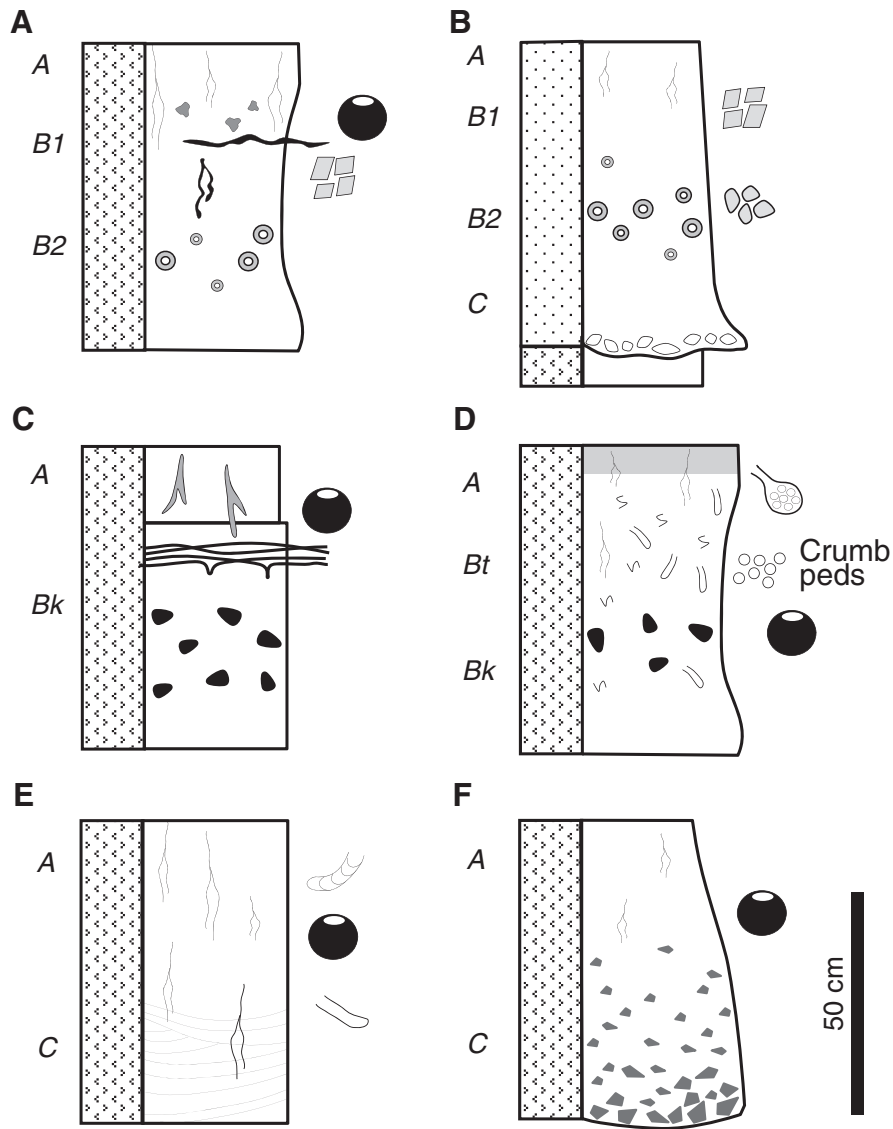


Fig. 6. Representative profiles of palaeosols recognized in the Cangahua Formation. A, B. Alfisols; C. andic Aridisol; D. andic Mollisol; E, F. andic Entisols. See legend in Fig. 3.

nodules, and a network of sinuous and thin burrows (Fig. 6D). Discrete trace fossils include *Coprinisphaera* spp. (Fig. 5B, G) and *Castrichnus incolumis* (Fig. 5D). In thin sections, microstructure mostly looks massive or channel-type locally. Porosity is low (10%), formed by unconnected elongated and circular pores, coated by carbonate (Fig. 7B, D). Clay cutans are very scarce. The groundmass (75%) is formed by slightly recrystallized micrite. A few and small Fe–Mn nodules also occur. The framework includes coarse silt grains of mineral composition similar to the previous pedotype 1. Homogeneous and strongly calcic palaeosols reach a weak to moderate development degree and are classified as calcic Andisols and Aridisols (Fig. 6C), in accordance with carbonate concentration. Palaeosols with a dark surface horizon and an argillic subsurface horizon correspond to andic Mollisols (Fig. 6D).

Palaeosols of the third type show a very weak development and moderate to intense bioturbation composed of rhizoliths, *Coprinisphaera*, meniscate and non meniscate burrows (Fig. 6E, F). Colour ranges from very pale orange to greyish light brown. They are common in the middle and less common in the lower and upper sections. At Río Chiche bridge and Tanda Abajo, they developed on massive pyroclastic mudstones, laminated fine tuffs, pumice ash flows, and volcanic breccias (Fig. 5F). This pedotype presents an upper homogeneous horizon with abundant root traces, meniscate and non meniscate burrows, and scarce

*Coprinisphaera* (Fig. 5F). Rhizoliths are composed of carbonized or clayey material, and rarely of Mn oxides. The lower horizon preserves original bedding and in some cases includes rhizoliths. These very weakly developed palaeosols are considered andic Entisols (Fig. 6E, F).

#### 4. Systematic ichnology

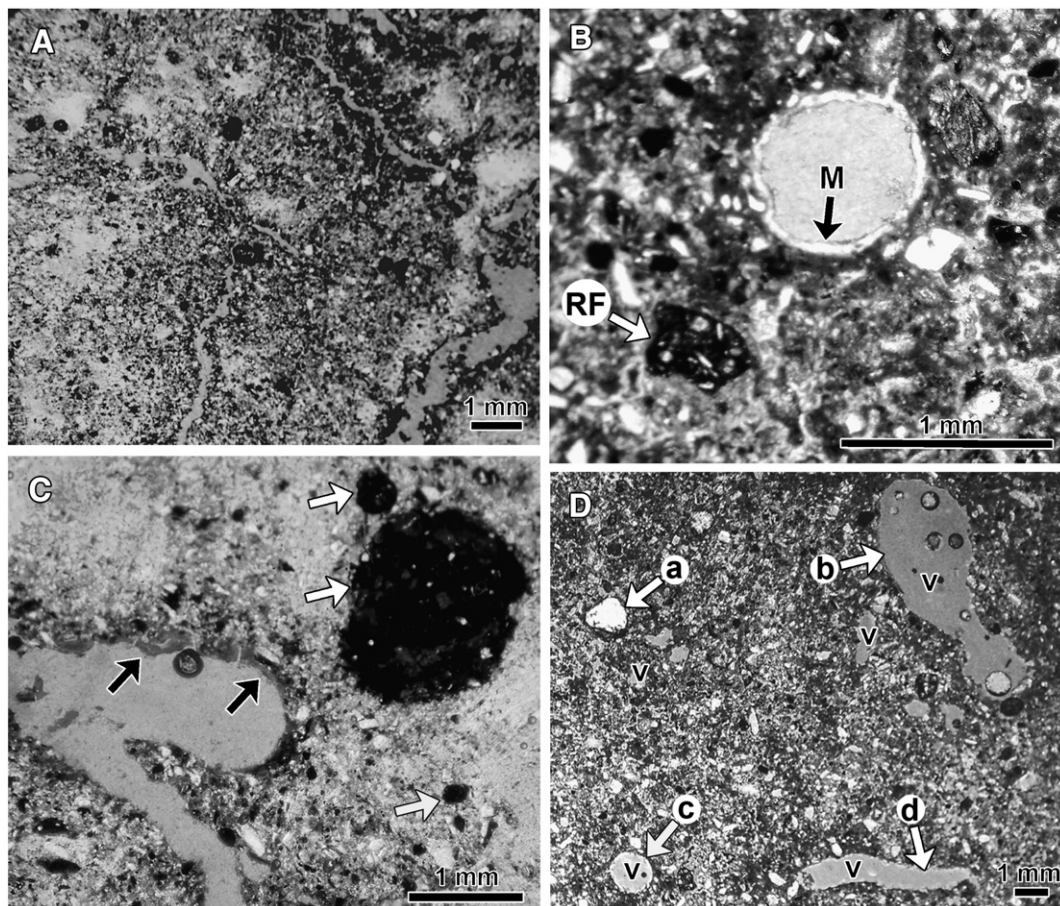
##### 4.1. *Coprinisphaera* Sauer, 1955

###### 4.1.1. Type ichnospecies

*Coprinisphaera murguiai* (Roselli, 1939) (non Laza, 2006) (= *ecuadoriensis* Sauer, 1955).

###### 4.1.2. Emended diagnosis

Spherical, sub-spherical, pear-shaped and bi-spherical chambers having a discrete wall, which may be completely pierced by a medium-sized hole (about  $\frac{1}{4}$  of its diameter) or may show a secondary, smaller chamber connected with the main one by a narrow passage. The internal cavities mostly contain passive fillings or in some cases are empty. Chambers are found isolated in contact with the rock matrix or surrounded by a cavity (modified from Laza, 2006).



**Fig. 7.** Microscopic features of Cangahua palaeosols. (A) Andic Andisol showing channel and crack microstructure, with few and incomplete aggregates, in a continuous soil phase, Quebrada Chalan. (B) Large circular pore coated by micrite (M) and a mafic volcanic rock fragment (RF). (C) Detail of a channel with clay cutans (black arrows) and Fe–Mn nodules (white arrows). (D) Intergrain vesicular pore structure. Large to small voids (v), irregular and elongate, not interconnected. Grain cutan (micrite) surrounding an altered pyroxene (a), micritic pore cutans (b, c and d), calcic Andisol.

#### 4.1.3. Comments

Roselli (1939) described *Devincenzia murguiai* from Uruguay. However, as this ichnogenic name was preoccupied, he replaced it by *Devincenzichnus Roselli* (1976). Meanwhile, Sauer (1955) having overlooked Roselli's work, described similar fossil brood balls as *Coprinisphaera ecuadoriensis* from Ecuador. Roselli (1939) also created the ichnogenus *Fontanai*, which later was interpreted as dung beetle brood balls (Genise and Bown, 1994) and considered as a senior subjective synonym of *Coprinisphaera* Sauer, 1955 (Laza, 2006). Despite this, the proposal to conserve the more used and accepted *Coprinisphaera* by giving it precedence over the rarely used *Fontanai* was accepted by the ICZN (Genise et al., 2006; ICZN, 2008; Krell, 2008). Accordingly, *Coprinisphaera* Sauer, 1955 remained as the valid name for the ichnogenus (Genise and Bown, 1994; Genise, 2004; Laza, 2006).

#### 4.1.4. *Coprinisphaera murguiai* (Roselli, 1939) (Fig. 8A–C)

A complete synonymic list up to 2007 was given by Krell (2007). Herein are included new references and older important ones with nomenclatorial changes.

- 1939 *Devincenzia murguiai* Roselli, p. 81
- 1941 *Bolas de cangagua* Estrada, p. 415
- 1950 *Bolas de cangagua* Bruet, p. 280, pl. I, figs. 2, 3
- 1955 *Coprinisphaera ecuadoriensis* Sauer, p. 123, figs. 2–4 (NEW SYNONYM)
- 1955 *Cangabola ecuadoriensis*: Lengerken, p. 937, figs. 7–9
- 1956 *Coprinisphaera ecuadoriensis*: Sauer, figs. 2–4
- 1959 *Coprinisphaera ecuadoriensis*: Sauer, p. 119

- 1965 *Coprinisphaera ecuadoriensis*: Sauer, p. 271
- 1976 *Devincenzichnus murguiai*: Roselli, p. 167
- 1982 *Coprinisphaera ecuadoriensis*: Martínez, p. 48
- 1994 *Coprinisphaera frenguelli* Genise and Bown, p. 109
- 2000 *Coprinisphaera ecuadoriensis*: Krell, p. 890
- 2004 *Coprinisphaera ecuadoriensis*: Genise, p. 429
- 2006 *Coprinisphaera ecuadoriensis*: Laza, p. 220 (= *C. frenguelli* Genise and Bown, 1994)
- 2007 *Coprinisphaera ecuadoriensis*: Krell, p. 40
- 2007 *Coprinisphaera ecuadoriensis*: Sánchez et al., p. 41
- 2008 *Coprinisphaera ecuadoriensis*: Sánchez et al., p. 162
- 2008 *Coprinisphaera ecuadoriensis*: Román-Carrión, p. 222
- 2009 *Coprinisphaera ecuadoriensis*: Sánchez and Genise, p. 838
- 2010 *Coprinisphaera ecuadoriensis*: Bellosi et al., p. 307
- 2010 *Coprinisphaera ecuadoriensis*: Sánchez et al., p. 227
- 2010 *Coprinisphaera ecuadoriensis*: Román-Carrión, p. 126
- 2012 *Coprinisphaera ecuadoriensis*: Bellosi et al., p. 34

**4.1.4.1. Emended diagnosis.** Isolated spherical to sub-spherical chambers having a discrete wall. In one of its poles, the wall is completely pierced by a medium-sized hole (about  $\frac{1}{4}$  of its diameter), showing cylindrical outline in longitudinal section. There are no remains of a secondary chamber or additional structures surrounding the hole. Passive fill is the norm (modified from Laza, 2006).

**4.1.4.2. Type material of *Coprinisphaera murguiai*.** In 1939, Roselli created *Devincenzia murguiai* to include four different forms of fossil



brood balls, which he considered as an evidence of different steps of the construction of a unique final type. Three of the four forms were described and illustrated: figures 26 and 31(5) show specimen A, figures 27 and 31(6) show specimen B, and figure 28 shows specimen C (Roselli, 1939). However, none of these specimens was designated formally as holotype or paratypes in that original contribution. That illustrated in figure 26 and 31(5) was called genotype by Roselli, but the ichnospecies description was based on the four specimens mentioned. No provenance for this material was provided. In 1976, Roselli replaced *Devincenzia murguiai* by *Devicenzichnus murguiai*. In 1987, Roselli redescribed this ichnospecies and designated a new specimen with the collection number MLR 479 as the “holotype”. Its provenance was a quarry near Arroyo de Las Flores, Departamento de Colonia, Uruguay. He also designated five “paratypes”, without collection number from Cantera Maldonado, Chileno, Cantera Sire, Falda de Cerro, Carmelo, Departamento Colonia, Uruguay. However, in accordance with the International Code of Zoological Nomenclature (ICZN) these posterior designations of types are invalid.

Several years later, in 2006, Laza published a complete review of the ichnogenus *Coprinisphaera*. Therein he considered the six above mentioned specimens as type material of *Coprinisphaera murguiai* (Roselli, 1939). He found that in the collection of the Museo Municipal “Lucas Roselli” the six types were labelled with the same number, 479, by Roselli. Laza (2006) gave letters to this series, naming the “holotype” as MLR 479a, and the “paratypes” as MLR 479b to f. Nevertheless, Laza’s contribution lacks details or illustrations of this series precluding recognition of the specimen for each letter, with the exception of the invalid “holotype” (MLR 479a).

In 2009, during our revision of trace fossils deposited in the Museum, we found five of the six *Coprinisphaera* labelled by Roselli as MLR 479. We found also that some specimens he described in 1987 were the same as he illustrated in 1939, although there was no formal indication of this anywhere. In addition, specimens labels lack the lettering published by Laza in 2006. We used the same procedure of Laza lettering each *Coprinisphaera* labelled as 479 by Roselli. Among the material housed in the museum as MLR 479, we identified the specimen A of figures 26 and 31(5) of the first work of Roselli (1939), which he called the “genotype” and we labelled as MLR 479b. Applying Articles 73 and 74 of the ICZN, and considering first Roselli’s description, we designated this syntype as the lectotype of *murguiai* Roselli, 1939. Among the remaining four specimens labelled as 479, one of them shows several cracks coincident with the brief description of the specimen B of Roselli, 1939. Furthermore, one piece obtained of it as a result from the cracks coincides with the drawing of figure 27 and 31(6). This paralectotype was labelled MLR-479c by us. Specimen C illustrated by Roselli (1939) in figure 28 was also recognized among those labelled as 479. However, this paralectotype, which was labelled MLR 479d by us, is considered herein as a specimen of *Coprinisphaera kraglievichi* (Roselli, 1939). The third paralectotype corresponding to the fourth form mentioned but not described or illustrated by Roselli (1939), could not be identified in the collection. One of the remaining two specimens labelled as 479 was identified as the “holotype” of *murguiai* invalidly designated by Roselli in his subsequent contribution (Roselli, 1987, Lám. 1, fig. 1). Laza (2006) considered this specimen as the valid holotype of *Coprinisphaera murguiai* naming it as 479a in his contribution. This is the only specimen for which the lettering of Laza (2006) could be recognized because he included a brief description and measures in his contribution. We re-labelled this specimen as 479a at the Museum to rescue some of Laza’s original lettering. The remaining one, which was considered by Laza as a valid paratype, was also re-labelled as he indicated (MLR 479e). Despite these two specimens were identified among specimens labelled as 479 by Roselli (1987), and even when both are *murguiai*, none of them are considered herein as paralectotypes because they were not included in syntypes described in 1939.

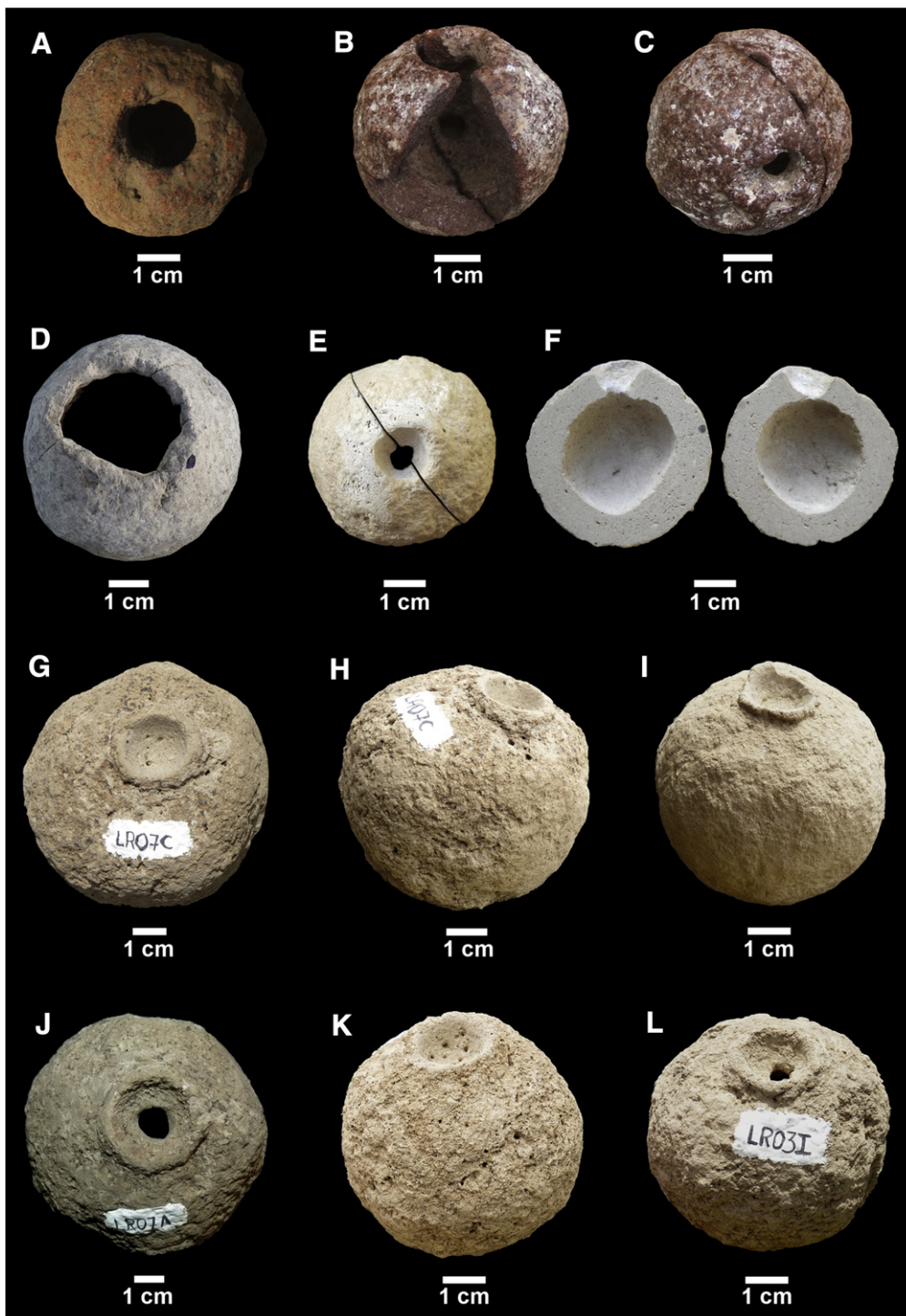
4.1.4.3. *Lectotype*. Specimen originally described as the genotype of *Devincenzia murguiai* by Roselli (1939) and illustrated in figures 26 and 31(5). Later named as MLR 479 by Roselli (1987) and herein labelled MLR 479b, from the Asencio Formation (lower Eocene), Nueva Palmira, Uruguay (Fig. 8A).

4.1.4.4. *Paralectotypes*. Specimens originally described as *Devincenzia murguiai* by Roselli (1939) and illustrated in figures 27 and 31(6), and 28 respectively. Later named as MLR 479 by Roselli (1987) and herein labelled MLR 479c (Fig. 8B, C) and MLR 479d, from the Asencio Formation (lower Eocene), Nueva Palmira, Uruguay.

4.1.4.5. *Type material of Coprinisphaera ecuadoriensis*. In 1955, Sauer created *Coprinisphaera ecuadoriensis* to include an undetermined number of specimens of dung beetle fossil brood balls from the Ecuadorian Cangahua Formation. He mentioned that most of the specimens showed a 2 cm hole in the wall. The only three specimens illustrated show in two cases the medium-sized hole at a pole (Sauer, 1955, figs 2–4), in one case the hole is obliterated by the infilling (Sauer, 1955, fig. 2 left and 3), and the remaining one lacks the typical hole, and preserved remains of worm activity (Sauer, 1955, fig. 5). Specimens studied by Sauer were seemingly housed in the former Escuela Politécnica Nacional of Quito. However in 2010, during our revision of specimens at the ichnological collection of the Museo de Historia Natural “Gustavo Orcés V.” of the Escuela Politécnica Nacional, the three illustrated specimens could not be unequivocally identified. Sixteen specimens without available data of provenance, collector, or year, were previously housed in the collection when one of us (JLRC) became the Curator. These specimens show a small black-ink dot near one of its poles, which is also present in the specimen illustrated by Sauer (1955, fig. 2, right), suggesting that this may be a lot of syntypes originally studied by him. Sauer (1955) designated no holotype and no specimen was labelled as such in the collection. Considering that the illustrated specimens in his contribution could not be identified unequivocally, we designated lectotype of *Coprinisphaera ecuadoriensis* Sauer, 1955 one specimen of this antique lot showing diagnostic characters, which looks like the specimen illustrated by Sauer (1955, fig. 2) (EPN-Icn 002) (Fig. 8D). The paralectotypes, some of them lacking diagnostic characters of this ichnospecies, are fifteen (EPN-Icn 007–021, 182).

4.1.4.6. *Nomenclatorial comments*. *Coprinisphaera murguiai* (Roselli, 1939) and *Coprinisphaera ecuadoriensis* Sauer (1955) share all diagnostic characters. Accordingly, *Coprinisphaera ecuadoriensis* Sauer, 1955 is considered herein a new subjective junior synonym of *Coprinisphaera murguiai* (Roselli, 1939), which remains as the type ichnospecies of the ichnogenus. Probably when revising the Uruguayan collection, Laza (2006) considered a second smaller hole present in specimens labelled 479 ichnotaxonomically more important than the medium-sized one. Herein, those holes are interpreted as *Tombownichnus plenus*, which are common in all *Coprinisphaera* ichnospecies, and represent the entry or exit holes of invading organisms (Mikuláš and Genise, 2003). In some specimens, the diagnostic medium-sized hole is partially broken, hindering even more its ichnospecific identification. In any case, Laza (2006) failed to recognize that *C. murguiai* (Roselli, 1939) was the senior synonym of *C. ecuadoriensis* Sauer (1955). In addition, he included a series of specimens from Patagonia (Argentina), which show a distinct secondary small hemispherical chamber pierced at one pole, in *C. murguiai*. These specimens, considered herein as *C. murguiai sensu* Laza, 2006 (non Roselli, 1939), were also examined for us and formally attributed to a new ichnospecies: *Coprinisphaera lazae* isp. nov.

4.1.4.7. *Description*. The lectotype of *C. murguiai* (Roselli, 1939) (MLR 479 b) (Fig. 8A) is sub-spherical, 42 mm in equatorial diameter, 38 mm high, and with the diagnostic hole of 13 mm in diameter. The paralectotype (MLR 479 c) (Fig. 8B, C) is a fragmented specimen, 40 mm in equatorial diameter, 38 mm high, with the diagnostic hole



**Fig. 8.** (A) Lectotype (MLR 479b), (B, C) one paralectotype (MLR 479c) of *Coprinisphaera murguiai* (Roselli, 1939) from the Asencio Formation (lower Eocene), Nueva Palmira, Uruguay. (D) Lectotype (EPN-Icn 002) of *Coprinisphaera ecuadoriensis* Sauer, 1955. (E, F) upper and sectioned views of the Holotype of *Coprinisphaera lazai* isp. n., respectively, from the Puesto Almendra Member (Middle Eocene–Lower Miocene) of the Sarmiento Formation, Sierra de Talquino (Chubut, Argentina). (G, H) Holotype and (I–L) paratypes of *Coprinisphaera kitu* isp. n. from the Cangahua Formation (Pleistocene), Quito, Ecuador: (G, H) EPN-Icn 003, (I) EPN-Icn 001, (J) EPN-Icn 004, (K) EPN-Icn 005, (L) EPN-Icn 006.

12 mm in diameter, and a wall of 6 mm thick. Both show a specimen of *Tombownichmus plenus* excavated in the wall. The lectotype of *C. ecuadoriensis* Sauer, 1955 (EPN-Icn 002) (Fig. 8D) is sub-spherical, 55 mm in equatorial diameter, 51 mm high, and with the diagnostic hole 23 mm in diameter. This specimen, along with other eleven of the fourteen with no provenance, shows a small, hand-made, black-ink dot (approximately 3 mm) near the hole. The wall shows a lumpy

external surface. Considering data taken from the *C. murguiai* collected, and from others digitally measured from field photographs, specimens show an equatorial diameter ranging from 43.2 mm to 80 mm (mean: 60.5 mm;  $n = 93$ ), a height ranging from 38.8 mm to 75.2 mm (mean: 56.9 mm;  $n = 84$ ), the diagnostic hole ranging from 8.6 mm to 37.4 mm (mean: 17.9 mm;  $n = 94$ ), and a wall thickness that ranges from 3.5 mm to 15 mm (mean: 6.9 mm;  $n = 14$ ). The

wall shows the external surface similar to the *ecuadoriensis* lectotype, and some specimens show small, irregular tunnels excavated on it that are attributable to *Lazaichnus fistulosus* (Mikuláš and Genise, 2003). Most specimens, with the exception of a few cases, also show several *Tombownichnus plenus* (Mikuláš and Genise, 2003), 1–17 mm in diameter, and scarce passive infill inside. Only one specimen (EPN-Icn 041) preserves inside a fragment of the wall of a spherical, smaller chamber similar to that described below for *C. kitu*.

#### 4.1.5. *Coprinisphaera lazai* isp. nov. (Fig. 8E, F)

2006 *Coprinisphaera murguiai* sensu Laza (non Roselli, 1939), p. 217, figs. 3B, 5E, Table 2

2007 *Coprinisphaera murguiai*: Krell, p. 41

2007 *Coprinisphaera murguiai*: Sánchez et al., p. 41

2008 *Coprinisphaera murguiai*: Sánchez et al., p. 162

2009 *Coprinisphaera murguiai*: Sánchez and Genise, p. 838

2010a *Coprinisphaera murguiai*: Sánchez et al., p. 227

2010b *C. isp. A*: Sánchez et al., p. 635

**4.1.5.1. Etymology.** Dedicated to José “Pepe” Laza, a pioneer of modern insect palaeoichnology, who studied, observed and prepared during 30 years specimens of *Coprinisphaera*, and who discovered this ichnospecies and many other ichnologic jewels. He published the first complete revision of the ichnogenus *Coprinisphaera* (2006).

**4.1.5.2. Emended diagnosis.** Isolated spherical to sub-spherical chambers having a discrete wall. At one of its poles, an hemispheric, concave small structure occupies the whole wall thickness. This secondary chamber shows a narrow passage in the centre of its concavity that connects to the main chamber. Passive fill is the norm (modified from Laza, 2006).

**4.1.5.3. Holotype.** One specimen (MACN-Icn 2058, Fig. 8E, F) examined and illustrated by Laza (2006, fig. 3B) under *Coprinisphaera murguiai* sensu Laza, 2006 (non Roselli, 1939) from the Puesto Almendra Member (Middle Eocene–Lower Miocene) of the Sarmiento Formation, Sierra de Talquino (Chubut, Argentina), deposited in the División Icnología of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina).

**4.1.5.4. Paratypes.** Two specimens (MPEF-IC 2064 and 2185) from the Lower Puesto Almendra Member (Middle Eocene–Upper Eocene) of the Sarmiento Formation, Gran Barranca (Chubut, Argentina), deposited in the Museo Paleontológico Egidio Feruglio (Trelew, Argentina).

#### 4.1.6. *Coprinisphaera kitu* isp. nov. (Figs. 8G–L; 9A–F)

**4.1.6.1. Etymology.** Dedicated to the Quito, which were the natives that lived in the Pichincha province (Ecuador), where is located Quito city, from 500 B.C. until they were assimilated by the Incas, before and during the Spanish conquest.

**4.1.6.2. Holotype.** One specimen (EPN-Icn 003, Fig. 8G, H) from the Pleistocene Cangahua Formation, La Ronda, Quito (Pichincha province, Ecuador) housed in the Colección de Icnología of the Museo de Historia Natural “Gustavo Orcés V.” (Escuela Politécnica Nacional), Quito, Ecuador.

**4.1.6.3. Paratypes.** Four specimens (EPN-Icn 001, 004–006, Fig. 8I–L) from the Pleistocene Cangahua Formation, Campus of the Escuela Politécnica Nacional (EPN-Icn 001) and La Ronda (EPN-Icn 004–006), Quito (Pichincha province, Ecuador) housed in the Colección de Icnología of the Museo de Historia Natural “Gustavo Orcés V.” (Escuela Politécnica Nacional), Quito, Ecuador.

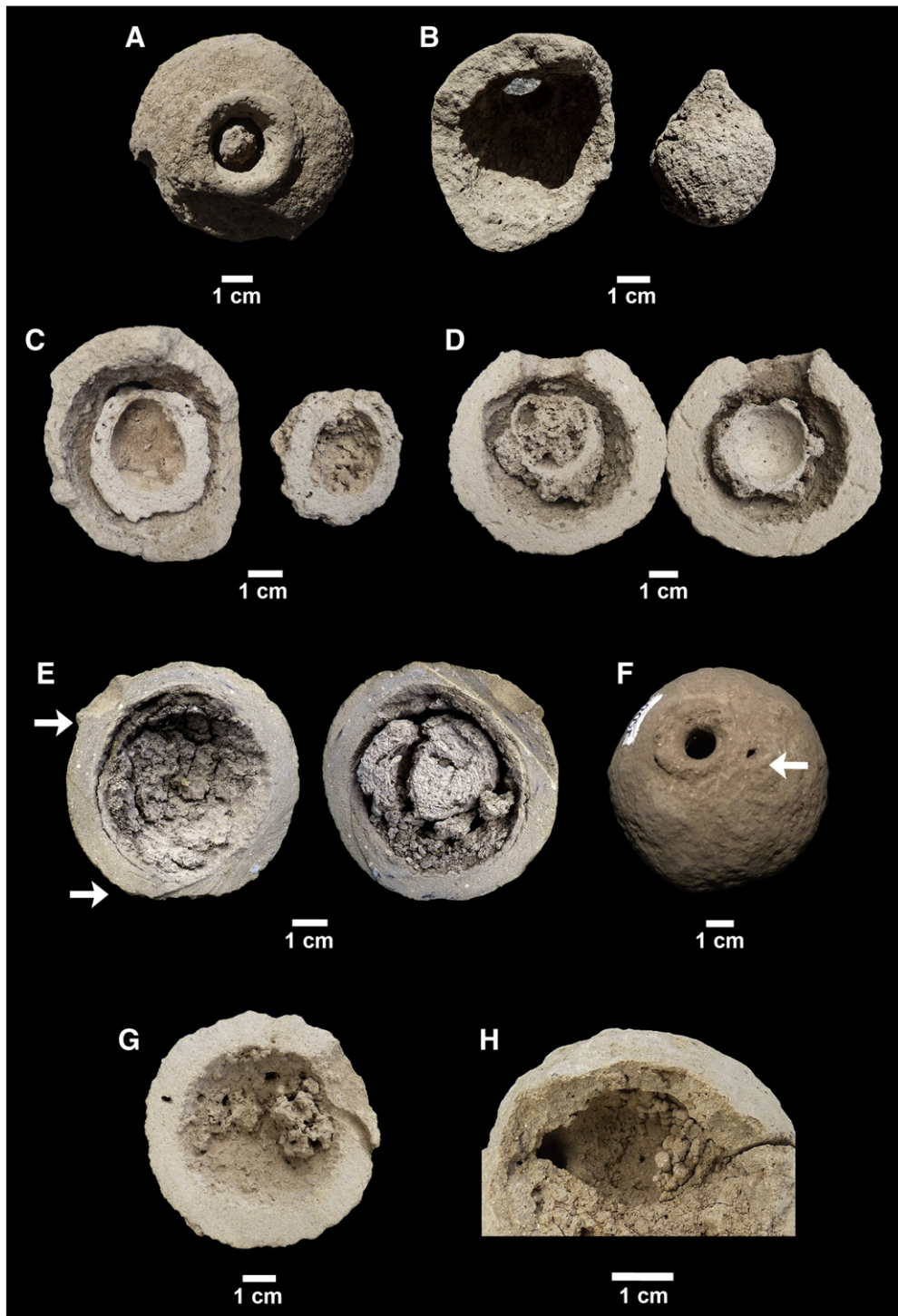
**4.1.6.4. Diagnosis.** Isolated spherical to sub-spherical chambers having a discrete wall, and commonly, a flat surface at one pole. The opposite one bears an hemispherical, concave structure partially included in

the wall, externally surrounded by a rim. The centre of the concavity may show an open, relatively small passage connecting this structure with the main chamber. Specimens with flat surface at one pole, show the hemispherical structure slightly displaced from the opposite pole. Passive fill is the norm.

**4.1.6.5. Comments.** No morphology comparable to *C. kitu* was mentioned by Sauer (1955, 1956). In the old lot of 15 specimens, only one of them (EPN-Icn 182) shows the hemispherical, concave structure that characterizes *C. kitu*, which will be named crown from now on. It was more common in recent collections by one of us (JLRC), and also among those collected in the 2011 field work for this contribution. The crown is unique among described ichnospecies of *Coprinisphaera*. It differs from the hemispheric concavity of *C. lazai* because in the last one it is completely located in the wall thickness, whereas in the former it is located in the superior part of the wall thickness and protrudes from it, showing an external rim. The crown supports the creation of a new ichnospecies, named herein *Coprinisphaera kitu*.

**4.1.6.6. Description.** The holotype (EPN-Icn 003) (Fig. 8G, H) is 67 mm in equatorial diameter, 65 mm high, and the concave crown is 23 mm in diameter and 8 mm deep, showing no holes excavated in its base. The crown shows a rim, 4 mm thick and 4 mm high. This specimen shows a flat base and the crown displaced from the opposite pole (Fig. 8H). Paratypes EPN-Icn 001 and 005 (Fig. 8I and K) are 62 mm and 56 mm in equatorial diameter and 63 mm and 56 mm high, respectively. Their crowns are 20 mm and 25 mm in diameter and 5 mm and 8 mm deep, respectively, showing no holes excavated in their bases. Their rims are 3 mm and 4 mm thick and 2 mm and 3 mm high, respectively. The crown and the wall of EPN-Icn 005 (Fig. 8K) are pierced by tiny holes (about 1 mm of diameter), probable *Tombownichnus plenus* specimens (Mikuláš and Genise, 2003). Paratypes EPN-Icn 004 and 006 (Fig. 8J and L) are 70 mm and 62 mm in equatorial diameter and 64 mm and 59 mm high, respectively. Crowns are 26 mm and 21 mm in equatorial diameter and 9 mm and 5 mm deep, respectively. These structures show a hole excavated in their bases of 8 mm and 5 mm in diameter, respectively. Their rims are 3 mm and 6 mm thick and 5 mm and 3 mm high, respectively. EPN-Icn 004 is the only paratype that shows a flat base and the crown displaced from the opposite pole. In the remaining specimens, the equatorial diameter ranges from 46.7 mm to 75.9 mm (mean: 61.9 mm; n = 46), height ranges from 44.3 mm to 73.3 mm (mean: 61.1 mm; n = 45). The wall, whose thickness ranges from 4.3 mm to 15.5 mm (mean: 8.5 mm; n = 10), usually shows a lumpy external surface (Fig. 8G, H, K, L). Crown diameter ranges from 12.3 mm to 30.6 mm (mean: 22.1 mm, n = 42), and its depth ranges from 1.8 mm to 11.2 mm (mean: 7.0 mm; n = 40). Several specimens show a hole excavated in the base of the crown, whose diameter ranges from 4.7 mm to 17.3 mm (mean: 9.6 mm; n = 32). The rim thickness ranges from 1.6 mm to 6.9 mm (mean: 4.5 mm; n = 36), and its height ranges from 1.8 mm to 5.3 mm (mean: 3.4 mm, n = 43). Two specimens (EPN-Icn 029, 187) preserve inside another chamber (Fig. 9A–D), whose wall thickness ranges from 5.3 mm to 6.4 mm (mean: 5.9 mm). The best preserved inner chamber is pear-shaped, 39 mm in equatorial diameter (Fig. 9B). Other three specimens (EPN-Icn 159, 161, 173) with a complete inner chamber preserve only part of the crown, which is cut by a medium-sized hole. These holes range from 16.5 mm to 17.3 mm (mean: 16.9 mm). Two specimens (EPN-Icn 182, 183) show a flat surface in the base, and the crown displaced from the opposite pole. Four specimens (EPN-Icn 182, 035, 051, 164), showing no holes, preserve the original active infilling inside the ball (Fig. 9E). The remaining ones, broken or with holes, show passive infilling. Most specimens show several tiny, simple holes (about 1 mm in diameter) excavated in the wall (Fig. 8G, H, K), and other show larger holes ranging from 4 mm to 17 mm (Fig. 9F). Both groups of sizes are compatible with typical *Tombownichnus plenus* (Mikuláš and Genise, 2003).





**Fig. 9.** (A, B) Specimen of *Coprinisphaera kitu* (EPN-Icn 029) showing a pear-shaped pupation chamber preserved inside. (C, D) Two specimens of *C. kitu* (EPN-Icn 029, 187) showing a sectioned pupation chamber preserved inside. (E) Longitudinal section of a *C. kitu* paratype (EPN-Icn 004) showing no holes, and with the original provision preserved inside. Note the porous texture of the infilling, the flat surface at the base (arrow), and the hemispherical structure displaced in the opposite pole (arrow). (F) *C. kitu* (EPN-Icn 168) showing a *Tombownichnus plenus* near the crown (arrow) and a hole in the centre of the crown probably made by the larva from inside or by invaders. (G) *C. ispp.* (EPN-Icn 122) showing *Lazaichnus fistulosus*. (H) Detail of *Castrichnus incolumis*, an aestivation chamber of earthworms preserved inside the infilling (EPN-Icn 058).

#### 4.1.7. *Coprinisphaera ispp.* (Fig. 9G, H)

Herein are considered as *Coprinisphaera ispp.* the specimens that lack diagnostic characters to be included in a definite ichnospecies. Considering collected specimens and other measured in the field, most of them are only fragments ( $n = 81$ ), but a few are more complete specimens ( $n = 14$ ) lacking diagnostic characters. In this latter set, the equatorial diameter ranges from 31.5 mm to 73.6 mm (mean:

54.9 mm,  $n = 95$ ), the height ranges from 46.7 mm to 73.7 mm (mean: 58.7 mm,  $n = 21$ ), and the wall thickness ranges from 2.2 mm to 12.7 mm (mean: 6.1 mm,  $n = 88$ ). One complete specimen (EPN-Icn 122, Fig. 9G) shows a hole excavated in the wall that is connected to an internal gallery in the infilling compatible with *Lazaichnus fistulosus*, attributable to earthworms (Mikuláš and Genise, 2003; Sánchez and Genise, 2009). A partially broken *Coprinisphaera*

(EPN-Icn 058, Fig. 9H) preserves inside another trace fossil attributed to earthworms, *Castrichnus incolumis*, which represents an aestivation chamber (Verde et al., 2007). Most of the *Coprinisphaera* spp., both complete or fragmentary, show the wall pierced by small holes from 3 mm to 14 mm compatible with *Tombownichnus plenus* (Mikuláš and Genise, 2003), which could have been made by invading organisms. A few broken *Coprinisphaera* specimens (n = 7) preserves inside, wall fragments of a spherical, smaller chamber, which is similar to that described before for *C. kitu*.

## 5. Statistical analysis

There is a strong correlation ( $r = 0.93$ ) between the equatorial diameter and the height of *C. kitu* (excluding the rim height) and *C. murguiai*. Thus, a Principal Component Analysis (PCA; using a variance–covariance matrix) was carried out.

The first principal component, which explained 96% of total variation and represents the brood ball size, was considered as the dependent variable in a two-tailed t-Student test. The performed t-Student test based on scores from the PCA revealed nonsignificant differences between the mean sizes of *Coprinisphaera kitu* and *C. murguiai* specimens ( $p = 0.39$ ).

## 6. Phytolithic analysis

Phytoliths extracted from the *Coprinisphaera* infilling were represented by seven morphotypes: elongate smooth, elongate sinuous, elongate spiny, conical shaped, rectangular, triangular, and point shaped (Fig. 10). The phytolith samples were characterized by a high percentage of the elongate smooth type (63%). The remaining morphotypes were less common: conical (11%), rectangular (8%), point shaped (7%), elongate sinuous (5%), triangular shaped (4%), and elongate spiny (2%). The elongate class (smooth, sinuous and spiny) and point shaped class (point shaped and triangular) are phytoliths from long-cells and micro-hair or prickles of grass epidermis, respectively, which can be assigned to no particular subfamily (Twiss et al., 1969; Twiss, 1992). In contrast, conical and rectangular types are mainly produced by short cells in the epidermis of Poaceae (Twiss et al., 1969; Twiss, 1992; Bremond et al., 2004).

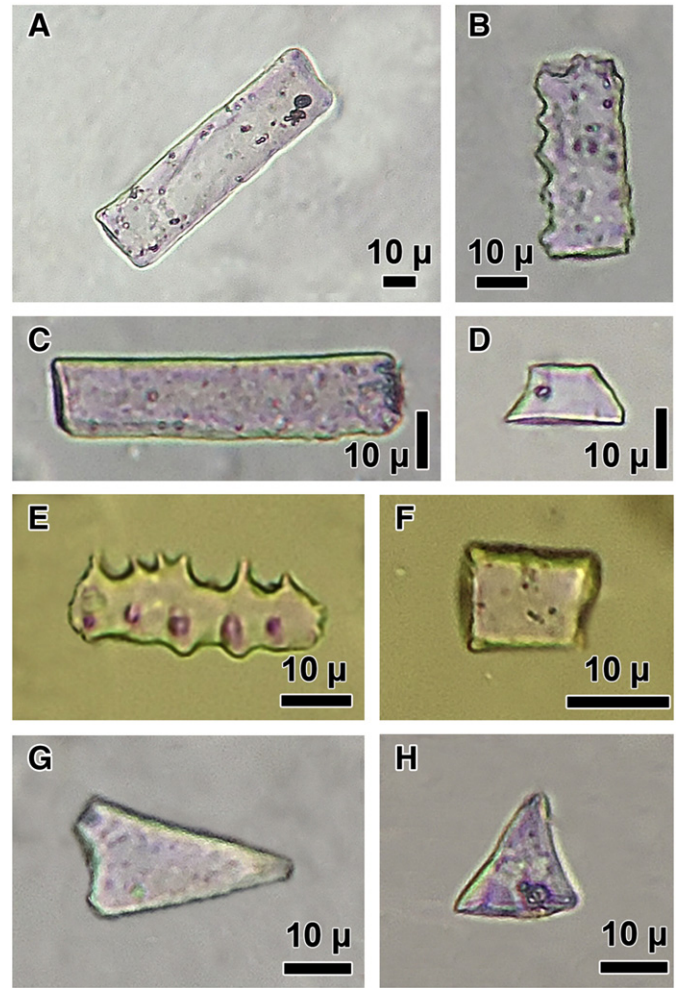
The phytolith assemblage present in the infilling of the *Coprinisphaera* studied herein are characteristic of the Poaceae, more particularly of the Poaceae considering the presence of conical and rectangular phytoliths (19%) and the absence of saddle, dumb-bell and cross shaped morphotypes that are typical of Panicoideae and Chloridoideae.

## 7. Discussion

### 7.1. The fellowship of the dung: providers, beetles, and associates

Field and laboratory work at Ecuador and Uruguay revealed that there are two valid ichnospecies in the Cangahua Formation of the former country: *Coprinisphaera murguiai* (Roselli, 1939), which is a senior synonym of *Coprinisphaera ecuadoriensis* Sauer (1955), and a new ichnospecies, *Coprinisphaera kitu*. As a collateral consequence of this nomenclatorial arrangement, it was necessary to give a new name to *Coprinisphaera murguiai* sensu Laza, 2006 (non Roselli, 1939) from Argentina, which is named *Coprinisphaera lazai* sp. nov. after his discoverer (Appendix 1).

*Coprinisphaera kitu*, the new ichnospecies is rather spherical and particularly characterized by the presence of a hemispherical, concave structure partially included in the wall near one pole, called herein the crown. This structure was neither observed before in other ichnospecies, nor in extant brood balls. It may be interpreted as the base of a spherical and external egg chamber, similar to that of *Coprinisphaera tonnii* (Laza, 2006), or the morphology that take some extant brood balls when the egg chamber is still in construction



**Fig. 10.** Phytolith morphotypes extracted from *Coprinisphaera kitu* infillings. (A) and (C) elongate smooth. (B) Elongate sinuous. (D) Conical shaped. (E) Elongate spiny. (F) Rectangular. (G) Point shaped. (H) Triangular shaped.

(Claude Joseph, 1929). However, this hypothesis is little probable because in more than 40 examined specimens, none shows a complete secondary spherical chamber, and in all of them the crown has the same regular shape. More probably, the crown is a structure with unknown function similar to the cylindrical protuberance finished in a flattened surface constructed by species of the genus *Ontherus* (Halffter and Edmonds, 1982; Sánchez and Genise, 2008). Most specimens of *C. kitu* are closed, meaning that they lack an emergence hole and accordingly that the adult never left the ball. In contrast, and by definition, the other only ichnospecies recorded from the Cangahua Formation, *C. murguiai*, represents specimens bearing an emergence hole.

Is it possible then that *C. murguiai* represents *C. kitu* from which the adults emerged? The presence of the crown pierced by a hole in some *C. kitu* may represent an evidence of emergence, but the size of these holes is comparatively small and probably more related to the activity of the larva from inside, or of external invaders. A few specimens of *C. murguiai*, showing the diagnostic medium-sized hole, preserve also fragments of the crown. The statistical analysis comparing the equatorial diameter and height from both ichnospecies shows that the mean size of the specimens are nonsignificantly different ( $p = 0.39$ ). This evidence along with the presence of only these two ichnospecies in the same outcrops, suggest that *C. kitu* and *C. murguiai* could represent two stages (closed and emerged balls, respectively) of only one original morphology (*C. kitu*) made by a unique producer.



This inference allows estimating an emergence success as the number of emerged balls (*C. murguiai*) in relation to the no emerged ones (*C. kitu*). Considering all specimens of both ichnospecies (*C. murguiai*,  $n = 93$ ; *C. kitu*,  $n = 46$ ), the estimated emergence success is 67%. This percentage is valid for the combination of all generations of dung beetles and years involved, not for a particular generation, in other words, it does not imply that all *Coprinisphaera* were coetaneous. The emergence success is obtained herein for the first time, since in outcrops from Uruguay and Argentina the diversity of ichnospecies and producers involved is very high (Roselli, 1987; Sánchez et al., 2010b).

Sauer (1956) compared the brood balls made by *Oxystemon conspicillatum* (as *Phanaeus conspicillatus* F.) (Phanaeini) from Ecuador with *Coprinisphaera murguiai*. However, as he believed that the spherical shape of the fossil brood balls was the result from the rolling behaviour of beetles, which is absent in this species, he discarded it as a possible producer. *Oxystemon conspicillatum* constructs pear-shaped brood balls that lack the crown of *Coprinisphaera kitu* (Sauer, 1956). Other potential producers, large-sized *Oxystemon* and *Phanaeus* (Phanaeini) from Ecuador, lack brood ball descriptions (Edmonds, 1994; Edmonds and Zidek, 2004; Price and May, 2009). Recently, Zunino (2013) found a head of an adult, which he named *Phanaeus violetae* (Phanaeini), inside a specimen of *Coprinisphaera murguiai* from the Cangahua Formation. If *C. murguiai* represents emerged specimens of *C. kitu*, then the producer of the latter ichnospecies would be *Phanaeus violetae*.

The size of *C. kitu* and *C. murguiai* leads to another question: which were the mammal providers of the dung? The size of brood balls is related to the size of dung pads (Janssens, 1939; Kingston and Coe, 1977; Heinrich and Bartholomew, 1979a,b; Hanski and Cambefort, 1991; Scholtz et al., 2009). Construction of large balls as those described herein, supporting the larval development of large dung beetles is only possible from large dung pads, which in turn can be produced only by large herbivores. From Table 1, which reflects the mammal record of the different localities where *Coprinisphaera* was found, it can be assumed that the most probable candidates are ground sloths, mastodons, and horses because of their size and relative abundance (Table 1).

Phytolith content of *Coprinisphaera* is useful to identify the diet of dung providers (Sánchez et al., 2010a). Some of the Ecuadorian specimens show no emergence hole and an infilling composed of a porous material different from that of the wall and surrounding palaeosol (Fig. 9E). This infilling represents the original dung provision when the larva fails to develop. It is a very remarkable condition of Ecuadorian *Coprinisphaera*, unusual in material from Argentina and Uruguay (Laza, 2006; Sánchez et al., 2010a,b). Phytolith analysis of *C. kitu* infillings showed that the most common morphotypes, which are included in elongate and point shaped classes, are typical graminoid phytoliths, among which the most informative types, conical and rectangular, are characteristic of pooid grasses. The presence of grasses is also supported by 1) palynological evidence from localities of similar age and altitude in the Ecuadorian Andes (Cardenas et al., 2011; Rodríguez and Behling, 2012), 2) inferred diet from coprolites of ground sloths (Hofreiter et al., 2000; Hofreiter et al., 2003; Borrero and Martin, 2012), and 3) inferred diet of mastodons and horses based on dentition (Ficcarelli et al., 1997; Prado et al., 2005).

In addition to dung providers and vegetation, other components of those palaeoecosystems are also evinced by the fossil brood balls. Some *Coprinisphaera* show small burrows in the walls and infillings, which are comparable to *Lizaichnus fistulosus*, attributable to earthworms (Mikuláš and Genise, 2003; Sánchez and Genise, 2009). *Castrichnus incolumis*, the aestivation chamber of an earthworm (Verde et al., 2007) was also found inside a specimen and in palaeosols, suggesting a seasonal climate, or at least periods of dryness or cold weather. *Tombownichnus plenus* preserved in some *Coprinisphaera* could have been made by detritivores or cleptoparasites (Sánchez and Genise, 2009). The presence of these trace fossils reflects better the

diversity of organisms composing the dung community during the Pleistocene.

## 7.2. Andean volcanoclastic landscapes

Sauer (1950) proposed a glacial–interglacial sedimentation model for the Cangahua Formation, where fine grained intervals with palaeosols bearing *Coprinisphaera* formed in semiarid warm savannahs or steppe-like grasslands during interglacial stages. At present, most authors agree in that primary accumulation was driven by volcanoclastic processes (Baldock, 1982; Clapperton and Vera, 1986; Iriondo, 1997) with a mixed provenance of volcanic ashes and subordinated rock powder produced by glacial erosion (Hall and Mothes, 1997). Although aeolian reworking and deposition are evident by facies described herein, volcanic ash transport by wind had to be a subordinated process considering the proximity of volcanoes and the extensive vegetation cover during active accumulation. Bellosi et al. (2012) interpreted the Cangahua Formation as the record of primary and reworked deposition in an inter-montane basin surrounded by numerous active volcanoes and glaciers.

Pleistocene topography of the Interandean Valley can be inferred from geodynamic studies of South American Andes, which reconstruct the evolution of surface relief and present a quantitative estimation of paleoelevation. Geodynamic analyses performed by Gregory-Wodzicki (2000) and Garzzone et al. (2008) in the Eastern Cordillera of Colombia (2° N) and the Altiplano Plateau of Bolivia (16° S), utilized palaeobotanical data (leaf physiognomy) and stable isotope compositions of palaeosol carbonates and authigenic clays. The results suggest that surface uplift of Andean cordillera shows no changes in the last 4 m.y. (Gregory-Wodzicki, 2000; Garzzone et al., 2008). Consequently, it is inferred herein that mean palaeoelevation of the Cangahua scenario was around 2500–2900 m.a.s.l., the current altitude of the studied outcrops.

High mountains of the northern Andes supported glacial advances during the Middle and Late Pleistocene, under the 100 ka astronomical cycles arising from changes in Earth's orbit. Diverse evidences from Perú (Farber et al., 2005), Titicaca lake of Bolivia (Fritz et al., 2007), Venezuela (Mahaney et al., 2008; Stansell et al., 2010) and Argentina (Coronato and Rabassa, 2013a,b), indicate that regional glaciations could have expanded with some interruptions during the lapses 440–140 ka and 24–18 ka BP (Coronato and Rabassa, 2013a,b). Extreme cold or glacial features should be expected considering that the studied sediments accumulated at least at 2500 m.a.s.l. However depositional facies and palaeosols of the Cangahua Formation described herein preserve no evidence of such processes, which were also dismissed by Clapperton and Vera (1986). Accordingly, Cangahua deposition could have occurred in non-glacial conditions, more probably during the 140–24 ka interglacial stage.

Pyroclastic mudstones are attributed herein to subaerial, primary or slightly reworked fine ash fallouts of suspended volcanic dust and fine ash. Following Lajoie and Stix (1992), this interpretation is based on the absence of physical structures, well sorting, non-erosive lower boundary, mantle bedding, and common intercalation of palaeosols. Diagenetic features such as the fine grain-size (silt-very fine sand), mantle bedding, lithologic homogeneity, vertical slopes, gully-type erosion, and interbedded palaeosols were used to interpret the Cangahua Formation as a loess or loessoid deposit (Sauer, 1965; Baldock, 1982; Vera and Lopez, 1986; Clapperton, 1990; Ficcarelli et al., 1992). The absence of carbonate mentioned by Sauer (1950), was deemed by Iriondo (1997) as anomalous for typical loess. However, most of the outcrops of the upper section studied herein comprise pedogenic calcite nodules, carbonate rhizoconcretions or micrite cement, particularly in palaeosols (pedotype 2). Aeolian accumulation is considered the prevailing depositional process, considering the prevalence of tephric loessites in the logged sections. Coarse volcanoclastic breccias and pumice lapilli facies of the middle section, showing normal grading, erosive basal contact and pedogenized top, are interpreted as subaerial high-concentrated



flows. Cross-bedding as that observed in the lower part of some of these beds (e.g. middle section of Río Chiche bridge profile) has been attributed to base-surge deposits (Lajoie, 1984). In accordance with Vera and Lopez (1986) lacustrine deposits have not been identified. Recent pyroclastic flows and falls from the Tungurahua volcano, including scoria and pumice falls and flows, ash falls and surges (Stinton and Sheridan, 2008) are comparable to the facies preserved in the middle section of the Cangahua Formation. Large eruptions, alternating with stasis periods, during the first and last stages are suggested by a higher occurrence of massive fallout deposits. Intercalations of andesitic lava flows, as those from Carchi province, were more common in the Real Cordillera, whereas ash and scoria lapilli falls were transported to the Interandean Depression. It is probable that scoriaceous pyroclastic flows were generated as large debris flows, especially when they melted extensive icecaps located at or near active volcanoes (Hall et al., 2008). Ficarelli et al. (1997) postulated that the Cangahua landscape was comparable to grassland savannah or open woodland according to cranial and dentition characteristics of Gomphotheriidae and the associated Lujanian fauna from Ecuador. More open and warmer landscapes were probably occupied by *Stegomastodon*, whereas colder and higher ones were inhabited by *Cuvieronius* (MacFadden and Shockey, 1997; Prado et al., 2005).

### 7.3. Evolution of the Cangahua palaeoenvironments

Distribution and abundance of depositional facies and palaeosols enable to divide the Cangahua sedimentation and pedogenesis into three stages, which parallel the three identified sections (Bellosi et al., 2012). Pyroclastic ash falls predominated during the initial stage (Middle to Late Pleistocene). Gravel accumulation in fluvial channels, mudflows, and volcanoclastic flows were subordinated. The association of these deposits with argillic, Fe-rich Alfisols of the lower section suggests a stable environment with discontinuous fine pyroclastic sedimentation and minor rivers. Climate was seasonal, subhumid to humid, with frequent water-table fluctuations allowing redox (gleying) conditions in soils. A similar palaeoenvironment was interpreted for the lower section in the Bolivar area according to strongly-developed argillic palaeosols (Ficarelli et al., 1992, 1997). Alfisols with thin (<1.0 m thick) clayey subsurface horizons are commonly associated to woodland or grassy woodland vegetation (Retallack, 2001). This mixed vegetation could be compared to that recognized in slightly older palynological

samples from Cosanga (80 km SW of Quito) which recorded an assemblage of upper montane *Podocarpus* and grasses (Cardenas et al., 2011). Intense bioturbation composed of rhizoliths and burrows suggests relatively high organic productivity. Instead, scarcity of *Coprinisphaera* may be related to reduced population of large mammals.

The second stage (Late Pleistocene) was dominated by volcanoclastic flows and ash falls according to studied facies in the middle section of Río Chiche bridge and Tanda Abajo, respectively (Fig. 3). The lower proportion and very weak development of palaeosols (pedotype 3: andic Entisols) suggest frequently perturbed landscapes with high accumulation rates. Volcanic eruptions during this stage were more continuous. This provoked restrained pedogenesis and maintained the biota in a state of succession, preventing the appearance of the climax vegetation, as often occurs in syneruptive conditions (Harris and Van Couvering, 1995). The almost complete absence of *Coprinisphaera* is probably related to such environmental conditions.

During the last stage (Latest Pleistocene) the environment became more stable, with still frequent fine ash fallouts and very few flows but followed by longer stable periods. The proportion and development degree of palaeosols in the upper section increased notably, suggesting enough time for ecosystem recovery between depositional volcanoclastic events. Palaeosol properties (granular or crumb ped structure) associated to *Castrichnus incolumis* (Verde et al., 2007) confirm that climate during the last stage become seasonal, semiarid to subhumid. Palaeosols with well developed calcic horizons (calcic Andisols, Aridisols) and granular peds (andic Mollisols) imply a reduction in precipitation in comparison to previous stages and more open grass-dominated habitats.

*Coprinisphaera* is considered an ichnogenus indicative of terrestrial herbaceous communities (Genise et al., 2000; Genise et al., 2010; Melchor et al., 2012), and particularly of open grass-dominated habitats since the Paleogene (Sánchez et al., 2010b). Large *Coprinisphaera kitu* can be only constructed from large dung pads, which in turn can be produced only by large herbivores inhabiting mostly open environments. The morphology and behaviour of dung beetles reflect a strong adaptation to exploit mammal excrement in open grass-dominated habitats (Halfpter and Matthews, 1966; Halfpter and Edmonds, 1982; Hanski and Cambefort, 1991). In turn, this decomposition of dung maintains the nutrient cycles and allows new grasses to grow reflecting the clear relationship between grasses, large herbivores, and dung beetles (Bornemissza, 1969, 1976; Heinrich and Bartholomew, 1979a,b). Accordingly, the highest number of *Coprinisphaera*, and calcic and granular

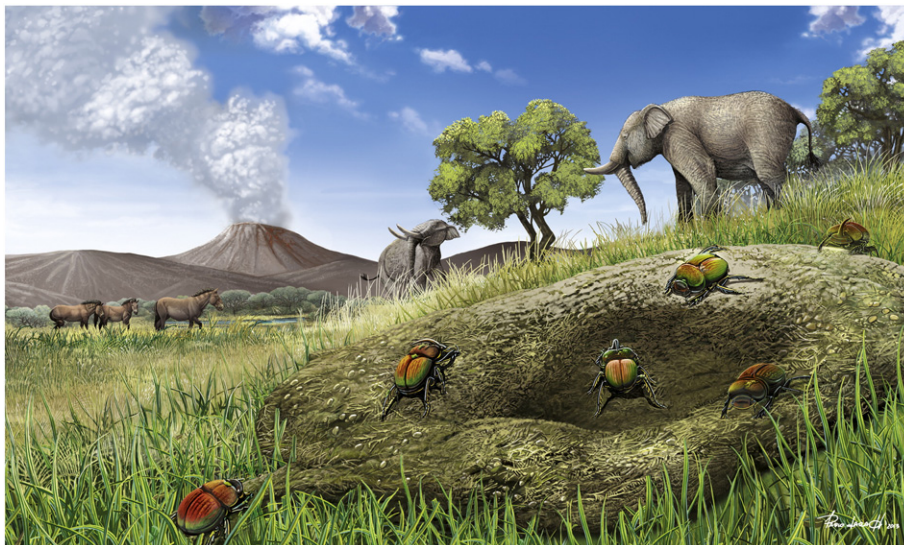


Fig. 11. Reconstruction of the landscape by the Pleistocene (by Pablo Lara Herrera).

palaeosol, in this stage suggests that landscape changed towards more open habitats, where dung beetles, grasses, and large herbivores became increasingly abundant (Fig. 11).

## 8. Conclusions

1. There are two valid ichnospecies in the Cangahua Formation of Ecuador: *Coprinisphaera murguiai* (Roselli, 1939), which is considered herein as a subjective senior synonym of *Coprinisphaera ecuadoriensis* Sauer (1955), and a new ichnospecies, *Coprinisphaera kitu*.
2. *Coprinisphaera murguiai sensu Laza, 2006* (non Roselli, 1939) is a distinct ichnospecies that is named herein *Coprinisphaera lazai* isp. n.
3. The new *Coprinisphaera kitu* is distinguished from the other ichnospecies by an hemispherical, concave structure partially included in the wall at on pole, and externally surrounded by a rim.
4. Statistical analysis of *Coprinisphaera* size revealed that *C. kitu* and *C. murguiai* could represent two stages (closed and emerged balls, respectively) of only one original morphology (*C. kitu*) made by a unique producer.
5. The particular morphology of the *C. kitu* has no extant counterpart. Its producer would be the fossil species *Phanaeus violetae*.
6. Phytolith extracted from *C. kitu* revealed that among phytolith-bearing plants, the Poaceae was dominant in the diet of the herbivores that provided the dung used for provision, which could have been ground sloths, mastodons, and horses.
7. The record of *Tombownichnus plenus*, *Lazaichnus fistulosus*, and *Castrichnus incolumis* suggests the presence of cleptoparasites and detritivores, such as flies, other dung beetles, and earthworms composing the dung community of those palaeoecosystems.
8. Cangahua sediments accumulated in a volcanoclastic, intermontane setting located in central Andes of Ecuador, at a mean palaeoelevation of 2500–2900 m.a.s.l. and under fluctuating syneruptive conditions.
9. The Cangahua Formation can be divided into three sections corresponding to three stages of sedimentation and pedogenesis. The older one include few specimens of *Coprinisphaera* occurring in argillic Alfisols and andic Entisols developed in woodlands and wooded grasslands. The second one, almost without *Coprinisphaera*, reflects an unstable environment produced by intense vulcanism.
10. The association of calcic Andisols, andic Aridisols, andic Mollisols, and abundant *Coprinisphaera* in the upper section suggests a change towards drier grasslands, where dung beetles, grasses, and large herbivores became increasingly abundant.

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## Appendix 1. Examined material of *Coprinisphaera*

### *Coprinisphaera murguiai* (Roselli, 1939)

#### Examined material from Argentina and distribution

One specimen (MACN-Icn 2300) from the Sarmiento Formation (Middle Eocene–Lower Miocene), Sierra de Talquino locality (Chubut, Argentina); 308 specimens from the Sarmiento Formation, Gran Barranca locality (Chubut, Argentina), distinguished by member as follows: 7 specimens (MACN-Icn 1061, 1062, 1068, 1112, 1115, MPEF-IC 720, 721) from the Gran Barranca Member (Middle Eocene), 76 specimens (MACN-Icn 1346–1348, 1352, 1353, 1356, 1358–1365, 1368–1370, 1378, 1381, 1383, 1386–1390; MPEF-IC 667, 689, 693, 722, 2085, 2086, 2088, 2089, 2091, 2092, 2094–2098, 2099, 2101–2103, 2105–2107, 2109, 2111, 2115–2118, 2121–2125, 2129, 2132–2138, 2169–2171, 2173, 2174, 2178, 2179, 2181–2183) from the Lower Puesto Almendra Member (Middle Eocene–Upper Eocene), 103 specimens (MACN-Icn 1397, 1398, MPEF-IC 724–727, 2000–2002, 2004–2014, 2016–2022, 2024, 2025, 2028–2030, 2032–2055, 2057, 2058, 2061–2063, 2065, 2067, 2068, 2070, 2071, 2074–2079, 2081–2084, 2141, 2142, 2145, 2146, 2157, 2168, 2244, 2245, 2247–2249, 2250–2257, 2259, 2297–2299, 2301–2304) from the Upper Puesto Almendra Member (Middle Oligocene–Upper Oligocene), 122 specimens (MACN-Icn 1342–1345, 1407, 1409, 1413–1415, 1440, 1442, 1444, 1489, 1490, 1492, MPEF-IC 634, 729, 731, 732, 2147, 2148, 2151, 2152, 2154–2156, 2158–2167, 2186–2191, 2193–2200, 2201, 2202, 2204–2215, 2217, 2219–2232, 2234, 2236–2243, 2260–2265, 2268–2289, 2291–2296) from the Colhue-Huapi Member (Lower Miocene).

#### Examined material from Ecuador and distribution

All specimens (81) from the Cangahua Formation (Pleistocene). 75 specimens from different localities of the Quito region, Pichincha province: 2 specimens (EPN-Icn 105, 106) with no data of provenance, 11 specimens (EPN-Icn 037, 038, 040–043, 056, 160, 174, 176, 177) from La Ronda, 31 specimens (EPN-Icn 059–061, 063, 064, 067–076, 078–083, 085–087, 089–095) from the campus of the Escuela Politécnica Nacional, 4 specimens (EPN-Icn 099, 101–103) from the campus of the Universidad Central, 13 specimens (EPN-Icn 108, 111–116, 118, 119, 121, 123, 126, 185) from Tababela, 5 specimens (EPN-Icn 145–148, 152) from Tanda Arriba, 5 specimens (EPN-Icn 153–157) from Tumbaco, 4 specimens (EPN-Icn 186, 188, 191–192) from Río Chiche bridge. Six specimens (EPN-Icn 128, 130–132, 139, 140) from Quebrada Chalán, Chimborazo province.

### *Coprinisphaera lazai* isp. nov.

#### Examined material and distribution

One specimen (MACN-Icn 2392) from the Sarmiento Formation (Middle Eocene–Lower Miocene), Sierra de Talquino (Chubut, Argentina). 66 specimens from the Sarmiento Formation, Gran Barranca (Chubut, Argentina), distinguished by member as follows: 30 specimens (MACN-Icn 1349, 1357, 1367, 1384, MPEF-IC 636, 2087, 2088, 2090, 2093, 2100, 2104, 2108, 2110, 2112–2114, 2119, 2126–2128, 2129, 2130, 2131, 2139, 2172, 2175–2177, 2180, 2184) from the Lower Puesto Almendra Member (Middle Eocene–Upper Eocene), 24 specimens (MACN-Icn 1620, MPEF-IC 600, 638, 649, 728, 2003, 2015, 2023, 2026, 2027, 2031, 2056, 2059, 2060, 2066, 2069, 2072, 2073, 2140, 2143, 2144, 2246, 2258, 2300) from the Upper Puesto Almendra Member (Middle Oligocene–Upper Oligocene), 11 specimens (MPEF-IC 2150, 2153, 2192, 2203, 2216, 2218, 2233, 2235, 2266, 2267, 2290) from the Colhue-Huapi Member (Lower Miocene).



*Coprinisphaera kitu* isp. nov.**Examined material and distribution**

All specimens (42) from the Cangahua Formation (Pleistocene), from different localities of the Quito region, Pichincha province: 1 specimen (EPN-Icn 183) with no data of provenance, 32 specimens (EPN-Icn 029, 031–033, 035–036, 039, 045–052, 159, 161–173, 175, 178, 181) from La Ronda, 3 specimens (EPN-Icn 065, 066, 077) from the campus of the Escuela Politécnica Nacional, 3 specimens (EPN-Icn 117, 125, 184) from Tababela, 1 specimen (EPN-Icn 141) from Tanda Abajo, 1 specimen (EPN-Icn 144) from Tanda Arriba, and 1 specimen (EPN-Icn 187) from Río Chiche bridge.

*Coprinisphaera ispp.***Examined material and distribution**

43 specimens collected in the following localities of the Cangahua Formation (Pleistocene) from the Pichincha province: 7 specimens (EPN-Icn 022–028) from La Ronda, 3 specimens (EPN-Icn 062, 084, 088) from campus of the Escuela Politécnica Nacional, 1 specimen (EPN-Icn 096) from Río Inga, 2 specimens (EPN-Icn 100, 104) from campus of the Universidad Central, 5 specimens (EPN-Icn 109, 110, 120, 122, 124) from Tababela, 3 specimens (EPN-Icn 149–151) from Tanda Arriba, 2 specimens (EPN-Icn 143, 144) from Tanda Abajo, 1 specimen (EPN-Icn 158) from La Merced. Seven specimens (EPN-Icn 129, 133–138) from Quebrada Chalán in the Chimborazo province, and only one (EPN-Icn 127) from Alor in the Carchi province.

**References**

- Baldock, J.W., 1982. Geología del Ecuador. Boletín de la explicación del mapa geológico nacional de la República del Ecuador: Dirección de Investigación Geológico-Minera (66 pp.).
- Barberi, F., Coltelli, M., Ferrara, G., Innocenti, F., Navarro, J.M., Santacroce, R., 1988. Plio-Quaternary volcanism in Ecuador. *Geological Magazine* 125, 1–14.
- Belloso, E.S., Laza, J.H., Sánchez, M.V., Genise, J.F., 2010. Ichnofacial analysis of the Sarmiento Formation (Middle Eocene–Lower Miocene) at Gran Barranca, Central Patagonia. In: Madden, R., Carlini, A., Vucetich, M.G., Kay, R. (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change through the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, pp. 306–316.
- Belloso, E., Genise, J., Sánchez, M.V., Román-Carrión, J.L., Cantil, L., 2012. Paleosuelos y trazas fósiles de la Formación Cangahua (Pleistoceno): reconstrucción de un sistema volcánico-intermontano en los Andes centrales de Ecuador. 13ª Reunión Argentina de Sedimentología, Salta, pp. 34–35.
- Bornemissza, G.F., 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). *Pedobiologia* 9, 223–225.
- Bornemissza, G.F., 1976. The Australian dung beetle project 1965–1975. *Australian Meat Research Committee Review* 30, 1–32.
- Borrero, L.A., Martin, F.M., 2012. Aphonic observations on ground sloth bone and dung from Cueva del Milodón, Última Esperanza, Chile: 100 years of research history. *Quaternary International* 278, 3–11.
- Bremond, L., Alexandre, A., Vela, E., Guinot, J., 2004. Advantages and disadvantages of phytolith analysis for the reconstruction of Mediterranean vegetation: an assessment based on modern phytolith, pollen and botanical data (Luberon, France). *Review of Palaeobotany and Palynology* 129, 213–228.
- Bristow, R., Cevallos, L., Longo, R., Masin, M., 1980. Mapa geológico del Ecuador. Hoja 84-SW Sangolquí. Quito.
- Bruet, E., 1950. Le loess de la République de l'Equateur et ses nids fossiles des insectes. *Revue Française d'Entomologie* 17, 280–283.
- Bullock, P., Fedoroff, N., Jongerius, A., Stoops, G., Tursina, T., 1985. Handbook for soil thin section description. *Wine Research Publications, Wolverhampton, UK*.
- Cardenas, M.L., Gosling, W.D., Sherlock, S.C., Poole, I., Toby Pennington, R., Mothes, P., 2011. The response of vegetation on the Andean Flank in western Amazonia to Pleistocene climate change. *Science* 331, 1055–1058.
- Clapperton, C., 1990. Quaternary Glaciations in the Southern Hemisphere. *Quaternary Science Reviews* 9, 121–299.
- Clapperton, C., Vera, R., 1986. The Quaternary glacial sequence in Ecuador, a reinterpretation of the work of W. Sauer. *Journal of Quaternary Science* 1, 45–56.
- Claude Joseph, H., 1929. El *Pinotus torulosus* Eschsch. *Revista Chilena de Historia Natural* 33, 31–46.
- Coltorti, M., Ficarelli, G., Jähren, H., Moreno, M., Rook, L., Torre, D., 1998. The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. *Journal of South American Earth Sciences* 11, 581–586.
- Coronato, A., Rabassa, J., 2013a. Middle Pleistocene Glaciations in the Southern Hemisphere. *Encyclopedia of Quaternary Science* 2, 187–190.
- Coronato, A., Rabassa, J., 2013b. Late Pleistocene Glaciations in South America. *Encyclopedia of Quaternary Science* 2, 250–256.
- Custode, E., De Noni, G., Trujillo, G., Viennot, M., 1992. La Cangahua en el Ecuador: caracterización morfo-edaforológica y comportamiento frente a la erosión. In: Zebrowski, C., Prat, C., Etchevers Barra, J.D., Arias, R.H.M., Miranda, M.M.E. (Eds.), *Suelos volcánicos endurecidos: Terra*, 10, pp. 332–346 (No spécial).
- Edmonds, W.D., 1994. Revision of *Phanaeus* MacLeay. A New World Genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science, Natural History Museum of Los Angeles County* 443, 1–105.
- Edmonds, W.D., Zidek, J., 2004. Revision of the Neotropical Dung Beetle Genus *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana* 11, 1–58.
- Erra, G., 2011. Criterios metodológicos para el estudio y clasificación de fitolitos cuaternarios. *Revista Historia Natural, Tercera serie* 1, 47–64.
- Estrada, A., 1941. Contribución geológica para el conocimiento de la Cangahua de la región interandina y del Cuaternario en general en el Ecuador. *Anales de la Universidad Central Quito* 66, 405–488.
- Farber, D., Hancock, G., Finkel, R., Rodbell, T., 2005. The age and extent of tropical alpine glaciation in the Cordillera Blanca, Peru. *Journal of Quaternary Science* 20, 759–776.
- Fernández Honaine, M., Zucol, A.F., Osterrieth, M.L., 2006. Phytolith assemblages and systematic associations in grassland species of the South-Eastern Pampean Plains, Argentina. *Annals of Botany* 98, 1155–1165.
- Ficarelli, G., Borselli, V., Borselli, V., Coltorti, M., Dramis, E., Fejfar, O., Hirtz, A., Torre, D., 1992. Stratigraphy and paleontology of upper Pleistocene deposits in the Interandean Depression, Northern Ecuador. *Journal of South American Earth Sciences* 6, 145–150.
- Ficarelli, G., Borselli, V., Herrera, G., Moreno Espinosa, M., Torre, D., 1995. Taxonomic remarks on the South American Mastodons referred to *Haplomastodon* and *Cuvieronius*. *Geobios* 28, 745–756.
- Ficarelli, G., Azzaroli, A., Bertini, A., Coltorti, M., Mazza, P., Mezzabotta, C., Moreno Espinosa, M., Rook, L., Torre, D., 1997. Hypothesis on the cause of extinction of the South American Mastodons. *Journal of South American Earth Sciences* 10, 29–38.
- Frenguelli, J., 1938a. Nidi fossili di Scarabeidi e Vespidi. *Bolletino della Società Geologica Italiana* 57, 77–96.
- Frenguelli, J., 1938b. Bolas de escarabeidos y nidos de véspidos fósiles. *Physis* 12, 348–35.
- Fritz, S.C., Baker, P.A., Seltzer, G.O., Ballantyne, A., Tapia, P., Cheng, H., Edwards, R.L., 2007. Quaternary glaciation and hydrologic variation in South American tropics as reconstructed from the Lake Titicaca drilling project. *Quaternary Research* 68, 410–420.
- Gallego, L., Distel, R.A., 2004. Phytolith assemblages in grasses native to central Argentina. *Annals of Botany* 94, 1–10.
- Garzzone, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P., Mulch, A., 2008. Rise of the Andes. *Science* 320, 1304–1307.
- Genise, J.F., 2004. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in paleosols attributed to coleopterans, ants and termites. In: McLroy, D. (Ed.), *The application of ichnology to palaeoenvironmental and stratigraphic analysis: Geological Society of London, Special Publications*, 228, pp. 419–453.
- Genise, J.F., Bown, T.M., 1994. New Miocene scarabid and hymenopterous nests, and Early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos* 3, 107–117.
- Genise, J.F., Mángano, M.G., Buatois, L.A., Laza, J.H., Verde, M., 2000. Insect trace fossil associations in paleosols: the *Coprinisphaera* ichnofacies. *Palaio* 15, 49–64.
- Genise, J.F., Laza, J.H., Rindsberg, A., 2006. The ichnogenus *Coprinisphaera* Sauer 1955: proposed conservation. *The Bulletin of Zoological Nomenclature* 63, 243–246.
- Genise, J.F., Melchor, R.N., Belloso, E.S., Verde, M., Genise, J.F., Melchor, R.N., Belloso, E.S., Verde, M., 2010. Invertebrate and vertebrate trace fossils in carbonates. In: Alonso-Zarza, A.M., Tanner, L. (Eds.), *Carbonates in Continental Settings. Developments in Sedimentology*, 61. Elsevier, Amsterdam, pp. 319–369.
- Gregory-Wodzicki, K.M., 2000. Uplift history of the Central and Northern Andes: a review. *Zoological Society of America Bulletin* 112, 1091–1105.
- Halfiter, G., Edmonds, W.D., 1982. The Nesting Behavior of Dung Beetles (Scarabaeinae). *An Ecological and Evolutionary Approach*. Editorial Galache, Distrito Federal, México.
- Halfiter, G., Matthews, E.G., 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana* 12–14, 1–312.
- Hall, M., Mothes, P., 1997. El origen y edad de la Cangahua superior, valle de Tumbaco, Ecuador. In: Zebrowski, C., Quantin, P., Trujillo, G. (Eds.), *Suelos volcánicos endurecidos, Memoire III Symposium International ORSTOM, Quito*, pp. 19–28.
- Hall, M., Samaniego, P., Le Pennec, J., Johnson, J., 2008. Ecuadorian Andes volcanism: a review of Late Pliocene to present activity. *Journal of Volcanology and Geothermal Research* 176, 1–6.
- Hanski, I., Cambefort, Y., 1991. *Dung beetle ecology*. Princeton University Press, Princeton, New Jersey.
- Harris, J., Van Couvering, J., 1995. Mock aridity and the paleoecology of volcanically influenced ecosystems. *Geology* 23, 593–596.
- Heinrich, B., Bartholomew, G.A., 1979a. Roles of endothermy and size in interand intra-specific competition for elephant dung in an African dung beetles, *Scarabaeus laevistriatus*. *Physiological Zoology* 52, 484–496.
- Heinrich, B., Bartholomew, G.A., 1979b. The ecology of the African dung beetle. *Scientific American* 241, 118–126.
- Hoffstetter, R., 1952. Les mammifères Pleistocènes de la République de l'Equateur. *Memoires de la Societe geologique de France* 31, 1–391.
- Hofreiter, M., Poinar, H.N., Spaulding, W.G., Bauer, K., Martin, P.S., Possnert, G., Pääbo, S., 2000. A molecular analysis of ground sloth diet through the last glaciation. *Molecular Ecology* 9, 1975–1984.
- Hofreiter, M., Betancourt, J.L., Sbriller, A.P., Markgraf, V., McDonalde, H.G., 2003. Phylogeny, diet, and habitat of an extinct ground sloth from Cuchillo Curá, Neuquén Province, Southwest Argentina. *Quaternary Research* 59, 364–378.



- ICZN, 2008. OPINION 2211 (Case 3360) The ichnogenus *Coprinisphaera* Sauer, 1955 (Ichnotaxa, Coprinisphaeridae): generic name given precedence over *Fontanai* Roselli, 1939. The Bulletin of Zoological Nomenclature 65, 318–319.
- Iriondo, M., 1997. Models of aeolian silt deposition in the Upper Quaternary of South America. Journal of South American Earth Sciences 10, 71–79.
- Janssens, A., 1939. Coprini (Coleoptera, Lamellicornia). Exploration du Parc National Albert: Misión G. F. de Witte, 29, pp. 1–104.
- Kingston, T.J., Coe, M., 1977. The biology of a giant dung-beetles (*Heliocopris dilloni*) (Coleoptera: Scarabaeidae). Journal of Zoology 181, 243–263.
- Krell, F.T., 2000. The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera: Polyphaga). Invertebrate Taxonomy 14, 871–905.
- Krell, F.T., 2007. Catalogue of fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mesozoic and Tertiary. Denver Museum of Nature and Science Technical Report 2007–8. 1–61.
- Krell, F.T., 2008. Comments on the proposed conservation of the ichnogenus *Coprinisphaera* Sauer, 1955 (Ichnotaxa, Insecta, Coleoptera, Coprinisphaeridae) (Case 3360; see BZN 63: 243–246). The Bulletin of Zoological Nomenclature 65, 50–59.
- Lajoie, J., 1984. Volcaniclastic Rocks. In: Walker, R.G. (Ed.), Facies Models, second edition. Geological Association of Canada, Ontario, pp. 39–52.
- Lajoie, J., Stix, J., 1992. Volcaniclastic Rocks. In: Walker, R.G., James, N.P. (Eds.), Facies Models: Response to Sea Level Change. Geological Association of Canada, pp. 101–118.
- Lavenu, A., 2006. Neotectónica de los Andes entre 1°N y 47°S (Ecuador, Bolivia y Chile): una revisión. Revista de la Asociación Geológica Argentina 61, 504–524.
- Laza, J.H., 2006. Dung-beetle fossil brood balls: the Ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* (Coprinisphaeridae). Ichnos 13, 217–235.
- Lengerken, H.V., 1955. Die Brutbirnen von *Deltochilum* (Coleopt. Lamellicornia). Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenberg, Mathematisch-naturwissenschaftliche Klasse 4, 933–940.
- MacFadden, B., Shockey, B., 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. Paleobiology 23, 77–100.
- Mahaney, W., Milner, M., Kalm, V., Dirszowsky, R., Hancock, R., Beukens, R., 2008. Evidence for a Younger Dryas glacial advance in the Andes of northwestern Venezuela. Geomorphology 96, 199–211.
- Martínez, S., 1982. Catálogo sistemático de los insectos fósiles de América del Sur. Revista Facultad de Humanidades y Ciencias, Serie Ciencias de la Tierra 1, 29–83.
- Melchor, R.N., Genise, J.F., Buatois, L.A., Umazano, A.M., 2012. Fluvial Environments. In: Knaust, D., Bromley, R. (Eds.), Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology, 64. Elsevier, Amsterdam, pp. 329–378.
- Mikuláš, R., Genise, J.F., 2003. Traces within traces. Holes, pits and galleries in walls and fillings of insect trace fossils in paleosols. Geologica Acta 1, 339–348.
- Piperno, D.R., 2006. Phytoliths: A comprehensive guide for archaeologists and paleoecologists. AltaMira, Lanham, MD.
- Prado, J.L., Alberdi, M., Azanza, B., Sánchez, B., Frassinetti, D., 2005. The Pleistocene Gomphotheriidae (Proboscidea) from South America. Quaternary International 126–128, 21–30.
- Price, D.L., May, M.L., 2009. Behavioral ecology of *Phanaeus* dung beetles (Coleoptera: Scarabaeidae): Review and new observations. Acta Zoológica Mexicana 25, 211–238.
- Retallack, G., 2001. Soils of the Past, 2nd edition. Blackwell Science, London.
- Rodríguez, F., Behling, H., 2012. Late Quaternary vegetation, climate and fire dynamics, and evidence of early to mid-Holocene *Polylepis* forests in the Jimbura region of the southernmost Ecuadorian Andes. Palaeogeography, Palaeoclimatology, Palaeoecology 350–352, 247–257.
- Román-Carrión, J.L., 2008. Rescate de fauna pleistocénica en el centro histórico de Quito – Ecuador. III Congreso Latinoamericano de Paleontología de Vertebrados, Neuquén, Argentina, p. 222.
- Román-Carrión, J.L., 2010. Reanudación de investigaciones paleontológicas en el yacimiento pleistocénico de Punín, Quebrada de Chalán, provincia de Chimborazo, Ecuador. X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología, La Plata, Argentina, p. 126.
- Román-Carrión, J., 2012a. Registro de fauna pleistocénica en Caraburo, nor-oriente de Quito. Revista Politécnica 30, 205–210.
- Román-Carrión, J., 2012b. Hallazgo de megafauna pleistocénica en el centro histórico de Quito. Revista Politécnica 30, 136–146.
- Román-Carrión, J., Lara, P., 2011. La Fauna Fósil de Quebrada Chalán. Ecuador Fósil, fascículo N.-1. Escuela Politécnica Nacional 38.
- Roselli, F.L., 1939. Apuntes de geología y paleontología uruguaya. Sobre insectos del Cretácico del Uruguay o descubrimiento de admirables instintos constructivos de esa época. Boletín de la Sociedad Amigos de las Ciencias Naturales “Kraglievich-Fontana”, Nueva Palmira, Uruguay, 1, pp. 72–102.
- Roselli, F.L., 1976. Contribución al estudio de la geo-paleontología. Departamento de Colonia y Soriano (República Oriental del Uruguay). Edición especial de la Biblioteca de la Sociedad Amigos de las Ciencias Naturales “Kraglievich-Fontana”, Nueva Palmira, Uruguay, p. 173.
- Roselli, F.L., 1987. Paleocnología. Nidos de insectos fósiles de la cobertura Mesozoica del Uruguay: Publicación del Museo Municipal Nueva Palmira, 1, pp. 1–56.
- Sánchez, M.V., Genise, J.F., 2008. Nest and brood chamber structure of two South American dung beetles: *Gromphas lacordairei* Brullé and *Onterhus sulcator* (Fabricius) (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 62, 49–61.
- Sánchez, M.V., 2009. Cleptoparasitism and detritivory in dung beetle fossil brood balls from Patagonia (Argentina). Palaeontology 52, 837–848.
- Sánchez, M.V., Belloso, E.S., Laza, J.H., Genise, J.F., 2007. Evolución de la Icnofauna Terrestre de la Patagonia Central V. Formación Sarmiento, la explosión del Eoceno Medio: V Reunión Argentina de Icnología y Tercera Reunión de Icnología del Mercosur, Ushuaia, p. 41.
- Sánchez, M.V., Laza, J.H., Belloso, E.S., Genise, J.F., 2008. Icnostratigrafía y características de trazas fósiles de escarabajos coprófagos (*Coprinisphaera* spp.) de la Formación Sarmiento (Cenozoico medio): aparición y evolución de ecosistemas de pastizales abiertos. XII Reunión Argentina de Sedimentología, Buenos Aires, p. 162.
- Sánchez, M.V., González, M.G., Genise, J.F., 2010a. Phytolith analysis of *Coprinisphaera*. Unlocking dung beetle behaviour, herbivore diets and palaeoenvironments along the Middle Eocene–Early Miocene of Patagonia. Palaeogeography, Palaeoclimatology, Palaeoecology 285, 224–236.
- Sánchez, M.V., Laza, J.H., Belloso, E.S., Genise, J.F., 2010b. Ichnostratigraphy of Middle Cenozoic dung beetle brood balls (*Coprinisphaera*) from Central Patagonia: insights into the appearance and evolution of the South American grass dominated habitats. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 633–648.
- Sauer, W., 1950. Contribuciones para el conocimiento del Cuaternario en el Ecuador. Anales de la Universidad Central, Quito, 77, pp. 327–364.
- Sauer, W., 1955. *Coprinisphaera ecuadoriensis*, un fósil singular del Pleistoceno. Boletín del Instituto de Ciencias Naturales del Ecuador 1, 123–132.
- Sauer, W., 1956. *Coprinisphaera ecuadoriensis* (Bola de Cangahua) y las esferas elaboradas actualmente por escarabajos de la familia Scarabaeidae. Boletín de Informaciones Científicas Nacionales 75, 550–555.
- Sauer, W., 1959. Merkwürdige Kugeln in Tuffen Ecuadors und ihre Deutung. Natur und Volk 89, 118–124.
- Sauer, W., 1965. Geología del Ecuador. Editorial del Ministerio de Educación, Quito.
- Scholtz, C.H., Davis, A.L.V., Kryger, U., 2009. Evolutionary Biology and Conservation of Dung Beetles. Pensoft Publishers, Bulgaria.
- Spillmann, F., 1931. Die Säugetiere Ecuadors im Wandel der Zeit. Universidad Central. Spillmann, F., 1938. Die fossilen Pferde Ecuadors der Gattung *Neohippus*. Palaeobiológica 6, 372–393.
- Stansell, N., Abbott, M., Rull, V., Rodbell, D., Bezada, M., Montoya, E., 2010. Abrupt Younger Dryas cooling in the northern tropics recorded in lake sediments from the Venezuelan Andes. Earth and Planetary Science Letters 293, 154–163.
- Stinton, A.J., Sheridan, M.F., 2008. Implications of long-term changes in valley geomorphology on the behavior of small-volume pyroclastic flows. Journal of Volcanology and Geothermal Research 176, 134–140.
- Tibaldi, A., Ferrari, L., 1992. Latest Pleistocene–Holocene tectonics of the Ecuadorian Andes. Tectonophysics 205, 109–125.
- Twiss, P.C., 1992. Predicted world distribution of C3 and C4 grass phytoliths. In: Rapp, Mulholland (Ed.), Phytolith Systematics. Plenum Press, New York.
- Twiss, P.C., Suess, E., Smith, R.M., 1969. Morphological classification of grass phytoliths. Soil Science of America, Proceedings 33, 109–115.
- Vera, R., 1977. Esferas de cangahua alóctonas. Escuela Politécnica Nacional. 85–88.
- Vera, R., Lopez, R., 1986. El origen de la Cangahua. Centro Panamericano de Estudios e Investigaciones Geográficas (CEPEIGE), 16, pp. 21–28.
- Verde, M., Jiménez, J.J., Ubilla, M., Genise, J.F., 2007. A new earthworm trace fossil from paleosols: aestivation chambers from the late Pleistocene Sopas Formation of Uruguay. Palaeogeography, Palaeoclimatology, Palaeoecology 243, 339–347.
- Zucol, A.F., 2001. Fitólitos III. Una nueva metodología descriptiva. Asociaciones fitolíticas de *Piptochaetium montevidense* (Stipeae, Poaceae). Boletín de la Sociedad Argentina de Botánica 36, 69–85.
- Zucol, A.F., Osterrieth, M., 2002. Técnicas de preparación de muestras sedimentarias para la extracción de fitólitos. Ameghiniana 39, 379–382.
- Zunino, M., 2013. The first dung beetle retrieved from Coprinisphaeridae ichnofossils: *Phanaeus violeetae* n. sp. (Coleoptera: Scarabaeinae) from Ecuadorian Cangahua balls. Acta Zoológica Mexicana 29, 219–226 (n. s.).